

Section *Mimadenia*: its phylogenetic relationships within the genus *Mimosa* (Leguminosae, Mimosoideae) using plastid *trnL*–*F* sequence data

C. Bessega^{A,B,D} and R. H. Fortunato^{B,C}

^ALaboratorio de Genética, Departamento de Ecología Genética y Evolución, Facultad de Ciencias Exactas y Naturales, 1428, Buenos Aires, Argentina.

^BConsejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina.

^CInstituto de Recursos Biológicos, INTA, Castelar, 1712, Provincia de Buenos Aires, Argentina and Universidad de Morón, Provincia de Buenos Aires, Argentina.

^DCorresponding author. Email: cecib@ege.fcen.uba.ar

Abstract. *Mimosa* L. includes more than 530 species and is subdivided into five sections, including *Mimadenia* Barneby, *Batocaulon* DC., *Habbasia* DC., *Calothamnos* Barneby and *Mimosa*. It has previously been proposed that *Mimosa* is derived from piptadenioid ancestors and that section *Mimadenia* is a morphological group intermediate between the piptadenioid ancestor and the remaining species from *Mimosa*. The main goals of the present study were to assess the monophyly of the genus *Mimosa* as it is currently described, including representatives of all five sections, test the previous evolutionary hypothesis that section *Mimadenia* is primitive within *Mimosa* and discuss the infrageneric classification from a phylogenetic view. We report a phylogenetic analysis of chloroplast nucleotide sequences of the *trnL* intron and the *trnL*–*trnF* intergenic spacer from 36 species of *Mimosa*, and six related genera. Our analysis indicated that genus *Mimosa* is monophyletic, and the species of section *Mimadenia* constitute a clade sister to the rest of the genus. Although section *Mimadenia*, as described by Barneby (1991), seems to be monophyletic, the remaining sections Barneby (1991) proposed are not resolved as monophyletic. An effort needs to be made towards a new infrageneric classification of *Mimosa* that considers the phylogenetic evidence.

Additional keywords: cpDNA, *Mimadenia*, *Mimosa*, Leguminosae, phylogeny.

Introduction

Mimosa L. is a large pantropical genus of ~530 species (~704 taxa), with most of its diversity occurring at low and middle elevations in tropical regions of America (Barneby 1991; Du Puy *et al.* 2002). However, an important number of species are distributed in warm climates in the USA, north of Argentina and south of Uruguay (Barneby 1991; Frodin 2004). The origin of the genus was proposed to be in South America (Polhill *et al.* 1981) and the main centres of diversity are in Brazil (south of Amazonia) and adjacent areas of Paraguay and Mexico (central and southern Mexico).

Generic classification in *Mimosa* has been conflicting. The first comprehensive taxonomic revision of *Mimosa* was proposed by Bentham (1875, 1876); a classification by Britton and Rose (1928) was largely ignored. Bentham recognised two sections in the genus, including (1) *Mimosa*, with haplostemonous flowers, and (2) *Habbasia* DC., with diplostemonous flowers, each organised in infrasectional ranks. Barneby (1991) presented a new taxonomic treatment of *Mimosa* and recognised the following five sections: *Mimadenia* Barneby, *Batocaulon* DC., *Habbasia* DC., *Calothamnos* Barneby and *Mimosa*.

In Barneby's taxonomic treatment, a hypothetical phylogeny based on morphological characters was presented. According to this hypothesis *Mimosa* was derived from piptadenioid ancestors (Barneby 1991). The presence of petiolar nectaries, ovate anthers, and plants that are trees to woody vines, features that are plesiomorphic in an evolutionary context, led him to suggest that sect. *Mimadenia* should be considered the most primitive within the group (see Fig. 1).

According to Barneby (1991), the other groups of *Mimosa* were derived from sect. *Mimadenia* (Fig. 1). Of these groups, he suggested that section *Batocaulon* was the first to differentiate, mainly on the basis of the setae type, rather than the type of androecium (haplostemonous/diplostemonous). It was also proposed that sections *Habbasia* and *Calothamnos* were derived from section *Batocaulon* (Fig. 1). The haplostemonous representatives of section *Calothamnos* present a derived trait in comparison with *Batocaulon* species; the rudimentary inner set of filaments led Barneby to suggest that the section *Calothamnos* was derived from the diplostemonous section *Batocaulon*.

Barneby stated that in section *Habbasia*, capitate inflorescences, tetramerous flowers, broad plurinerved stipules

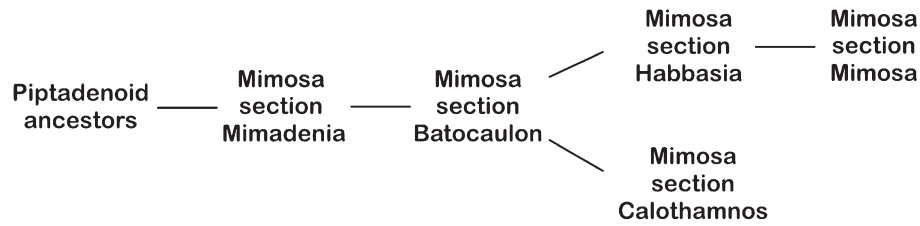


Fig. 1. Evolutionary hypothesis proposed by Barneby (1991).

and setose indumentums must have been stabilised before speciation. Following his evolutionary hypothesis (Fig. 1), section *Habbasia* can be interpreted as a derived group from section *Batocaulon*. Finally, section *Mimosa*, in Barneby's (1991) scheme, shows the most derived features; the representatives of this section are subshrubs to herbs, and show reduction of the leaf, craspedodromous leaflet venation and reduction of petal and androecial numbers (Barneby 1991).

A previous study on the phylogeny of *Mimosa*, based on sequences of the *trnL* intron and *trnL*-*F* intergenic spacer (Bessega *et al.* 2008), indicated that the genus is monophyletic; however, the study of Bessega *et al.* (2008) lacked representatives of section *Mimadenia*. Moreover, that study did not suggest that the four other sections included were natural groups. The species assigned to the sections *Habbasia* and *Batocaulon* were shown as basal and did not constitute differentiated clades. The species analysed from section *Mimosa* and those from section *Calothamnos* were intermingled in the same clade, suggesting that the limits of the sections *Mimosa* and *Calothamnos* required further examination.

The main goal of the present study was to use sequence data from *trnL* intron and *trnL*-*F* intergenic spacer to

- (1) assess the monophyly of the genus *Mimosa* as it is currently described, and including representatives of all five sections;
- (2) test the previous evolutionary hypothesis that section *Mimadenia* is basal within *Mimosa*; and
- (3) identify whether the sections described are natural groups.

For this purpose, representatives from section *Mimadenia*, which were not considered in previous studies, are included and analysed simultaneously with representatives from sections *Batocaulon*, *Habbasia*, *Mimosa* and *Calothamnos*. We present molecular phylogenetic reconstructions for *Mimosa* and some allied genera, by using maximum parsimony and Bayesian inference methods to analyse previously published DNA sequences from plastid *trnL*-*F* regions (Jobson and Luckow (2007) and Bessega *et al.* (2008)).

Materials and methods

Sequence data

The *trnL* intron and the *trnL*-*trnF* intergenic spacer regions previously sequenced by present authors or those that were publicly available in GenBank were analysed for a total of 43 taxa belonging to *Mimosa* and allied genera. The matrix here analysed included 36 species from *Mimosa*, representing the five sections described by Barneby (1991), namely *Mimosa*, *Habbasia*, *Calothamnos*, *Batocaulon* and *Mimadenia*, and

seven taxa that were considered outgroups (Table 1). The outgroups included here represent different genera of tribe Mimoseae and the related tribe Mimosygantheae (Fortunato 2005; Luckow 2005). The choice of outgroups was based on previously published phylogenetic reconstructions (Luckow *et al.* 2003; Jobson and Luckow 2007; Bessega *et al.* 2008) and morphological criteria.

Sequence alignment and phylogenetic analysis

Multiple alignment of DNA sequences was accomplished with the CLUSTALX ver. 1.8 (Thompson *et al.* 1997), followed by minor manual corrections. Both DNA regions were merged in WinClada (Nixon 1999). Uncertain positions located near primer annealing sites and regions in which the alignment was ambiguous were excluded from the dataset. Gaps were treated as missing data in analyses and indels were not coded as additional characters.

Parsimony analysis was conducted with NONA (Goloboff 1998), included in the WinClada software (Nixon 1999), by using 1000 random addition sequences, tree bisections and reconnections (TBR), holding 100 trees per replicate and attempting to swap to completion. Characters were considered unordered and equally weighed. The bootstrap analysis used 1000 replications, each with 10 random additions, holding 10 in each replicate, with a maximum of 100 trees saved per replication and mapped to the majority consensus tree.

Bayesian phylogenetic inference was performed with the program Mr Bayes ver. 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). The most appropriate model of sequence evolution was determined with the program Modeltest 3.7 (Posada and Crandall 1998) on the basis of the Akaike information criterion (AIC) (Posada and Buckley 2004), and the general time-reversible model (GTR+G) was chosen for the analysis. The chains were run for 2 000 000 generations, sampling every 100 generations. Adequate mixing (sampling of tree and parameter space) was judged by movement among chains and by convergence among independent runs with different starting points (Huelsenbeck *et al.* 2002). Inadequate mixing in some initial runs was corrected by adjusting the temperature and rerunning the analysis. We considered that the runs had converged when the convergence diagnostics provided in sump output approached 1 and when clade credibilities (post burn-in), branch lengths and topologies were similar across the two independent runs. Four Markov chain Monte Carlo (MCMC) chains (one cold and three heated), with heating parameter of 0.1, were used, together with the default prior probability density (flat Dirichlet distribution) for the base-frequency parameters. The stationary phases of two independent replicate runs were

Table 1. Voucher specimen information and GenBank accession numbers

Species	GenBank #	Voucher (herbarium)
Tribe Mimosoideae Burkart ^A		
<i>Mimozyanthus carinatus</i> (Griseb.) Burkart	DQ344570, DQ344604	RHF 7567 (BAB)
Tribe Mimosaceae ^A		
<i>Anadenanthera colubrina</i> var. <i>cebil</i> (Griseb.) Altschul.	DQ344571, DQ344605	RHF 7583 (BAB)
<i>Cyclodiscus gabunensis</i> Harms	AY125845	M.S.M. Sosef 645a (BH)
<i>Neptunia pubescens</i> Benth.	DQ344551, DQ344603	RHF 7923 (BAB)
<i>Parapiptadenia excelsa</i> (Griseb.) Burkart	DQ344569, DQ344602	RHF 7669 (BAB)
<i>Piptadenia minutiflora</i> Ducke	DQ784667	C.D.Leme 6 (NY)
<i>Piptadenia viridiflora</i> (Kunth) Benth.	AF522963	C.E. Hughes 1681 (FHO)
<i>Mimosa aculeaticarpa</i> var. <i>biuncifera</i> (Benth.) Barneby	AF278513	Major Howell Seeds (BH)
<i>Mimosa adenotricha</i> Benth.	DQ344579, DQ344613	RHF 8450 (BAB)
<i>Mimosa albida</i> var. <i>wildenowii</i> (Poir.) Rudd.	AF278512	B.B. Kliyggaard 648 (K)
<i>Mimosa balansae</i> Micheli	DQ344552, DQ344585	RHF 7534 (BAB)
<i>Mimosa bifurca</i> Benth. var. <i>bifurca</i>	DQ344553, DQ344586	RHF 7556 (BAB)
<i>Mimosa bonplandii</i> (Hook. & Arn.) Benth.	DQ344581, DQ344615	JAG 92 (BAB)
<i>Mimosa brevipetiolata</i> Burkart	DQ344582, DQ344616	JAG 127 (BAB)
<i>Mimosa candollei</i> R.Grether	DQ344555, DQ344588	RHF 7555 (BAB)
<i>Mimosa colombiana</i> Britton & Killip	DQ784646	Davidse & O. Huber 15198 (NY)
<i>Mimosa debilis</i> Humb. & Bonpl. ex Willd.	DQ344561, DQ344594	RHF 8085 (BAB)
<i>Mimosa detinens</i> Benth.	DQ344558, DQ344591	MAL 4491 (BAB)
<i>Mimosa flagellaris</i> Benth.	DQ344557, DQ344590	RHF 7887 (BAB)
<i>Mimosa guilandinae</i> (DC.) Barneby	DQ784647	M. Nee 42700 (NY)
<i>Mimosa hexandra</i> Micheli	DQ344556, DQ344589	MAL 4584 (BAB)
<i>Mimosa hirsutissima</i> Mart.	DQ344562, DQ344595	RHF 7962 (BAB)
<i>Mimosa leimonias</i> Barneby & Fortunato	DQ344575, DQ344609	EMZ 41158 (BAB)
<i>Mimosa maguirei</i> Barneby	DQ344576, DQ344610	RHF 8418 (BAB)
<i>Mimosa myriadenia</i> var. <i>dispersa</i> Barneby	DQ784648	H. Balslev & E. Madsen
<i>Mimosa nothacacia</i> Barneby	DQ784649	G.P.Lewis et al. 2353 (NY)
<i>Mimosa obstrigosa</i> Burkart	DQ344568, DQ344601	RHF 8077 (BAB)
<i>Mimosa oligophylla</i> Micheli	DQ344574, DQ344608	RHF 8074 (BAB)
<i>Mimosa paupera</i> Benth.	DQ344565, DQ344598	RHF 8018 (BAB)
<i>Mimosa pigra</i> L.	DQ344560, DQ344593	JAG 38 (BAB)
<i>Mimosa pilulifera</i> Benth.	DQ344573, DQ344607	JAG 39 (BAB)
<i>Mimosa polycarpa</i> Kunth	DQ344566, DQ344599	RHF 8019 (BAB)
<i>Mimosa quitensis</i> Benth.	AF278514	B.B. Kliyggaard 647 (K)
<i>Mimosa radula</i> Benth.	DQ344577, DQ344611	RHF 8413 (BAB)
<i>Mimosa revoluta</i> Benth.	DQ784650	G. Beck 14424 (NY)
<i>Mimosa sensibilis</i> Griseb.	DQ344580, DQ344614	RHF 8385 (BAB)
<i>Mimosa setosa</i> Benth. var. <i>setosa</i>	DQ344578, DQ344612	RHF 8445 (BAB)
<i>Mimosa somnians</i> Humb. & Bonpl. ex Willd.	DQ344563, DQ344596	RHF 7953 (BAB)
<i>Mimosa strigillosa</i> Torr. & A.Gray	DQ344567, DQ344600	RHF 8949 (BAB)
<i>Mimosa tenuiflora</i> (Willd.) Poir.	AF522943	CANB 615541
<i>Mimosa tweedieana</i> Barneby ex Glazier & Mackinder	DQ344572, DQ344606	RHF 7949 (BAB)
<i>Mimosa uliginosa</i> Chodat & Hassl.	DQ344564, DQ344597	RHF 8059 (BAB)
<i>Mimosa xanthocentra</i> Mart. var. <i>xanthocentra</i>	DQ344559, DQ344592	RHF 7650 (BAB)

^AFollowing Luckow (2005) and Fortunato (2005).

pooled after discarding trees for each replicate for the burn-in period that included 2500 generations (trees). Consensus-tree topologies and posterior probabilities (PP) based on the different analyses were found to be essentially identical between the different Bayesian runs.

The following herbarium abbreviations are used all throughout

- BAB Instituto de Recursos Biológicos, (Instituto Nacional de Tecnología Agropecuaria)
 BH Cornell University Bailey Hortorium

- FHO University of Oxford Daubeny
 K Royal Botanic Gardens
 NY New York Botanical Garden

Results

The combined *trnL* and *trnL-trnF* matrix (available on request from the corresponding author) included 36 ingroup and seven outgroup taxa. The aligned matrix contained 1272 characters, of which 137 (11%) were phylogenetically informative. In total, 41 indels were found and gaps varied from 1 to 47 bp in length.

Results from the maximum parsimony (MP) and Bayesian analyses exhibited a general correspondence and did not show incongruence of supported nodes; bootstrap-supported (BS) nodes mostly also had high Bayesian PP. MP analysis resulted in 19 MP trees of 482 steps, with CI=0.74 and RI=0.80. The majority-rule consensus tree is presented in Fig. 2 and a tree based on Bayesian inference is shown in Fig. 3.

In the MP and Bayesian analyses, the genus *Mimosa* was recovered as a monophyletic group with moderate support (BS=81%, PP=0.93), in agreement with a previous study where representatives of section *Mimadenia* were lacking (Bessega *et al.* 2008).

In our analysis, the representatives of section *Mimadenia* clustered together with high support in both the MP tree (BS=99%) and in the Bayesian analysis (PP=1). Within section *Mimadenia*, *M. nothacacia* and *M. revoluta* formed a group (BS = 86%, PP = 0.98) sister to a group including the other

species here analysed. Among these, *M. colombiana* and *M. myriadenia* formed a group (BS=100%) on the MP tree that is shown as sister to *M. guilandinae*. Although the last association was not observed in the Bayesian analysis, the topology is consistent.

Excluding section *Mimadenia*, the remaining sections considered by Barneby (1991) do not constitute monophyletic groups. The representatives from section *Habbassia* fall within section *Batocaulon*; however, the relationships of the members cannot be resolved with the sequences here analysed. The representatives of sections *Mimosa* and *Calothamnos* constitute a cluster sister to the clade of *Batocaulon* and *Habbassia* representatives. The *Calothamnos* species included are nested within section *Mimosa* (BS=61%, PP=1). *M. aculeaticarpa* and *M. quitensis* were placed in a clade including *M. detinens* and *M. hexandra* (BS = 79%, PP = 0.98). The position of *M. albida* is not well supported in either of the

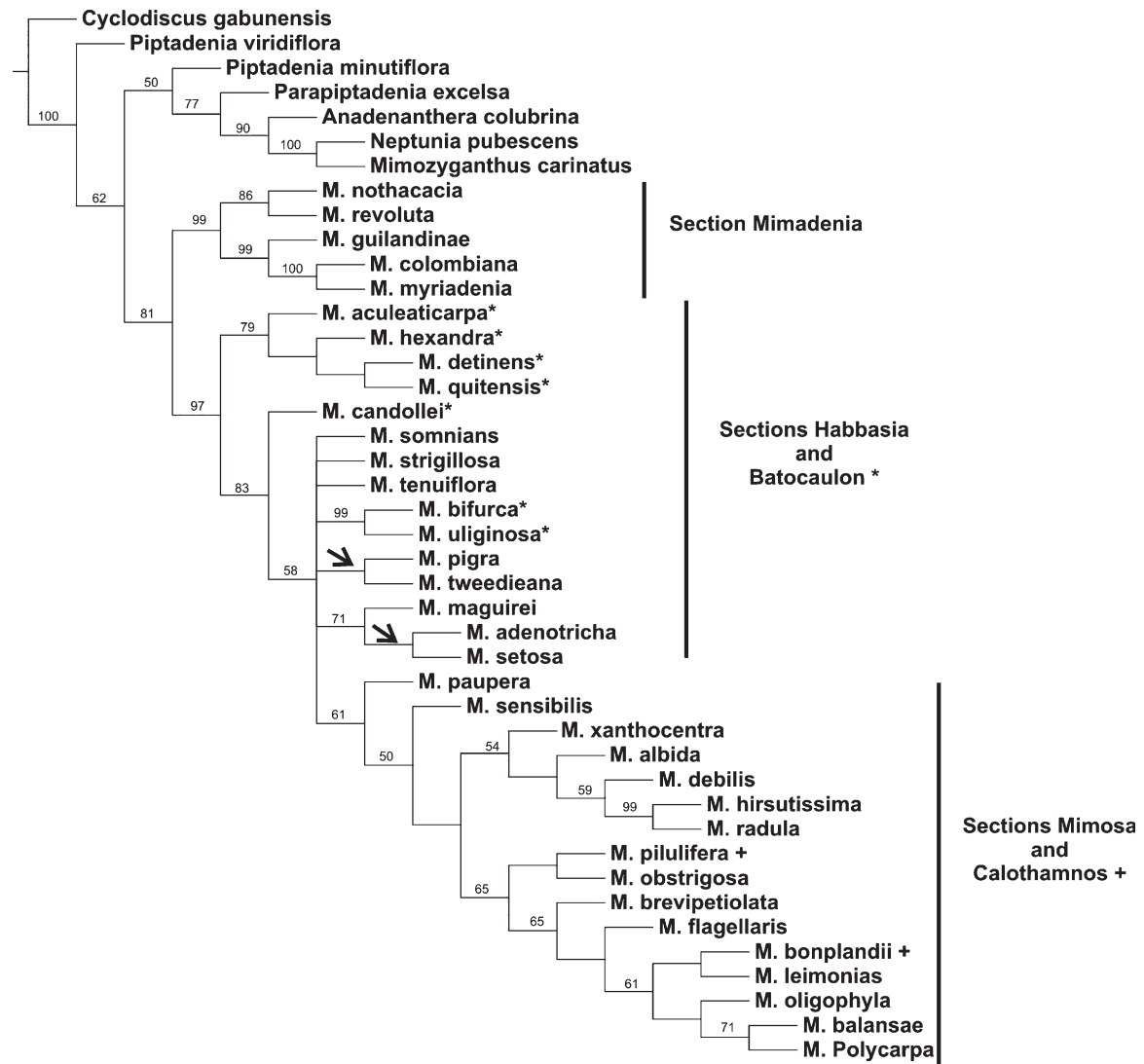


Fig. 2. Majority-rule consensus tree obtained from 19 most parsimonious trees (length = 482 steps, CI = 0.74, RI = 0.80) based on *trnL* intron and *trnL-trnF* intergenic spacer sequence data. Numbers above branches are bootstrap values and branches that collapse in the strict consensus tree are indicated with arrows. The sections of the genus are shown, using the classification of Barneby (1991).

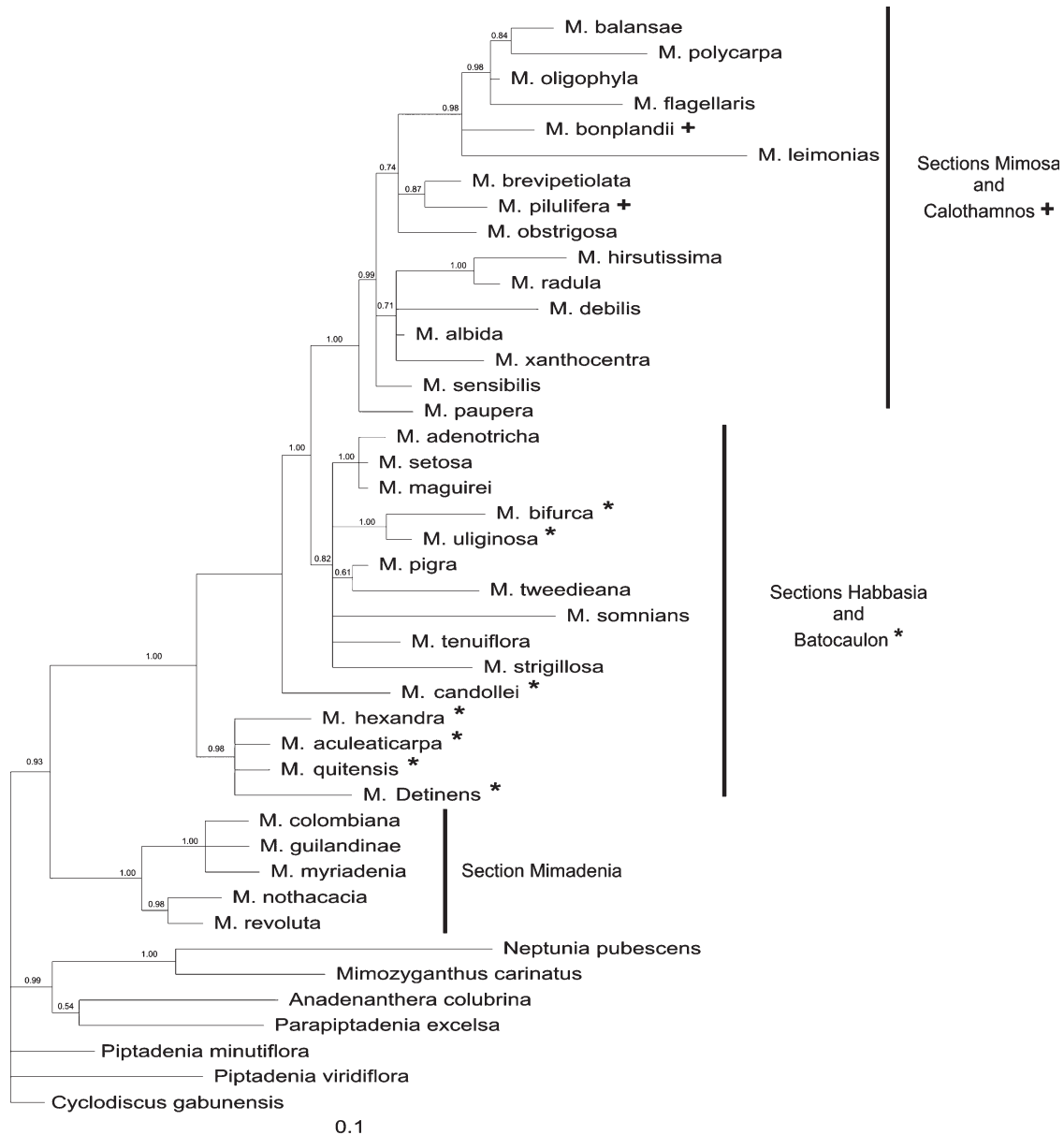


Fig. 3. Majority-rule consensus tree obtained from the Bayesian analysis, based on sequences of the *trnL* intron and *trnL-trnF* intergenic spacer applying the GTR+G model of substitution. Values above branches indicate posterior probabilities. The classification corresponding to Barneby (1991) is indicated at the right-hand side. The scale bar represents 0.1 substitutions per site.

analyses; however, MP and Bayesian analyses both place *M. albida* with *M. xanthocentra*, *M. debilis*, *M. hirsutissima* and *M. radula*.

Discussion

Section Mimadenia

As described in the introduction, the section *Mimadenia* was proposed by Barneby (1991), on the basis of external morphological traits, to be basal within the *Mimosa* and the progenitor of other sections. *Mimadenia* species are trees or

scandent shrubs that have haplostemonous and diplostemonous white to white-green or yellow-green flowers with free filaments and functional petiolar nectaries. These characters led Barneby (1991) to consider this section the more primitive in an evolutionary sequence. Within section *Mimadenia*, two groups were found here. *Mimosa colombiana* and *M. guilandinae*, from series *Glanduriferae*, were clustered with *M. myriadenia*, the only species described in series *Myriadeniae*. The association between these two series was reported by Barneby (1991) who suggested that *M. myriadenia* arose from the same stock as series *Glanduriferae* which lost one

cycle of stamens. This transition might have occurred several times in the evolutionary history of the genus, as described in section *Calothamnus* (see Introduction).

Within section *Mimadenia*, the association observed with *M. revoluta* (series *Revolutae*) and *M. nothoacacia* (series *Nothoacaciae*) was supported by similarity in the cupular petiolar nectaries. *Mimosa myriadenia*, which is shown in another cluster, also has petiolar nectaries; however, it has the typical indumentum of series *Glanduliferae*, as well as the same type of inflorescence and haplostemonous flowers.

Sections *Batocaulon*, *Habbasia*, *Calothamnus* and *Mimosa*

Besega *et al.* (2008) stated that sections *Batocaulon*, *Habbasia*, *Mimosa* and *Calothamnus* might have been derived from a common ancestor, which was also supported by the present analysis. The divisions proposed by Barneby (1991) were not supported by the present work, because the four sections were not resolved as monophyletic. Members of sections *Batocaulon* and *Habbasia* are in multiple positions in the cladogram. Section *Batocaulon* might be at least paraphyletic and is possibly polyphyletic, and the members of section *Habbasia* are unresolved. Phylogenies suggest that the representatives from sections *Batocaulon* and *Habbasia* are early diverged lineages and the representatives from sections *Mimosa* and *Calothamnus* can be considered a more derived natural group. Although few representatives from section *Calothamnus* were included in the present study, namely only *M. bonplandii* and *M. pilulifera*, both the Bayesian and parsimony analyses suggested that it is not a natural group.

According to Bentham (1841), the section *Mimosa* also included all the representatives of Barneby's section *Calothamnus*. In the light of the results obtained here, Bentham's position can be supported by the molecular data. The section *Calothamnus* proposed by Barneby (1991) is equivalent to the section *Mimosa* series *Lepidotae* described by Bentham (1841), which was based on possession of plumose or stelliform setae and haplostemonous flowers.

Within section *Batocaulon*, *M. aculeaticarpa* (series *Acanthocarpae*) and *M. quitensis* (series *Andinae*) are two species that were also not analysed by Besega *et al.* (2008). The relationships among these species cannot be fully resolved with the grouping here, using either the Bayesian or the MP analysis. However, they are grouped within a clade constituted by species from section *Batocaulon* series *Farinosae* (*M. detinens*) and series *Bimucronata* (*M. hexandra*). This grouping of the species can be supported by their potentially synapomorphic traits, including a xerophilous habit and possession of white staminal filaments.

Within section *Mimosa* series *Mimosa*, *M. albida* (subseries *Mimosa*) is grouped with the following species from different subseries: *M. xanthocentra* (subseries *Pudicae*), *M. debilis* (subseries *Mimosa*), *M. hirsutissima* (subseries *Hirsutae*) and *M. radula* (subseries *Polycephalae*). This grouping, although weak, does not give support to Barneby's (1991) proposal for subseries subdivision; however, all of these species are herbs or shrubs, with cauline aculei and spicules.

Final remarks

Our analysis indicated that genus *Mimosa* is monophyletic, the species of section *Mimadenia* constitute a clade sister to the remaining *Mimosa* species. In the present study, 5 of 16 species of section *Mimadenia* are included, and although the number of species is low, it can be considered representative of the section (32%). Moreover, representatives of each series in *Mimadenia* are included. The section *Mimadenia*, as described by Barneby (1991), seems to be a phylogenetically supported group. He proposed a basal and non-evolved place for this section; however, in our analysis the section *Mimadenia* is not a basal group. The position given by Barneby for section *Mimadenia* can be explained by the fact that the members have a tree habit, petiolar nectaries, flowers that are either four- or five-merous and have compound tetrads, features that can be considered to be plesiomorphic from a phylogenetic standpoint.

Following the phylogenetic hypothesis retrieved by analysis of *trnL-trnF* sequences, the remaining sections from genus *Mimosa*, *Batocaulon*, *Habbasia*, *Calothamnus* and *Mimosa* might have derived from a common ancestor and do not constitute natural groups. Further study that incorporates a more intense taxon sampling, especially in section *Calothamnus*, together with a morphological matrix and additional molecular information, is needed for better understanding of the evolution of this complex group of species, where hybridisation and polyploidisation may be important in the speciation process (Morales *et al.* 2010). Finally, if different markers are consistent with the results shown here, an effort needs to be made towards a new infrageneric classification of *Mimosa* that considers the phylogenetic evidence.

Acknowledgements

This work was supported by grants from Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Universidad de Buenos Aires (UBA), PIP 112-200801-00323 and UBACYT X604, given to RHF and CB, respectively.

References

- Barneby RC (1991) *Sensitivae censitae* – A description of the genus *Mimosa* Linnaeus (Mimosaceae) in the New World. *Memoirs of the New York Botanical Garden* **65**, 1–835.
- Bentham G (1841–1842) Notes on Mimoseae with short synopsis of species. *Journal of Botany* **4**, 243–428.
- Bentham G (1875) Revision of the suborder Mimoseae. *Transactions of the Linnean Society of London* **30**, 335–664.
- Bentham G (1876) *Mimosa & Schrankia*. *Flora Brasiliensis* **15**, 296–391.
- Besega C, Hopp HE, Fortunato RH (2008) Toward a phylogeny of *Mimosa* (Leguminosae: Mimosoidae): a preliminary analysis of southern South American species based on chloroplast DNA sequence. *Annals of the Missouri Botanical Garden* **95**, 567–579. doi:10.3417/2006012
- Britton NL, Rose JN (1928) Mimosaceae. *Flora of North America* **23**, 1–194.
- Du Puy DJ, Labat J-N, Rabevohitra R, Villiers J-F, Bossier J, Moat J (2002) 'The Leguminosae of Madagascar.' (Royal Botanic Gardens, Kew: London)
- Fortunato RH (2005) Tribe Mimosoideae. In 'Legumes of the world'. (Eds G Lewis, B Schrire, B Mackinder, M Lock) pp. 184–185. (Royal Botanic Gardens, Kew: London)
- Frodin DG (2004) History and concepts of big plant genera. *Taxon* **53**, 753–776. doi:10.2307/4135449

- Goloboff PA (1998) 'NONA v. 1.9. Program and documentation.' Available at <http://www.cladistics.com/aboutNona.htm> [verified June 2011].
- Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* **17**, 754–755. doi:10.1093/bioinformatics/17.8.754
- Huelsenbeck JP, Larget B, Miller RE, Ronquist F (2002) Potential applications and pitfalls of Bayesian inference of phylogeny. *Systematic Biology* **51**, 673–688. doi:10.1080/10635150290102366
- Jobson RW, Luckow M (2007) A phylogenetic study of genus *Piptadenia* (Benth.) using plastid *trnL*-F and *trnK/matK* sequence data. *Systematic Botany* **32**, 569–575. doi:10.1600/036364407782250544
- Luckow M (2005) Tribe Mimosaeae. In 'Legumes of the world'. (Eds G Lewis, B Schrire, B Mackinder, M Lock) pp.163–183. (Royal Botanic Gardens, Kew: London)
- Luckow M, Miller JT, Murphy DJ, Livshultz T (2003) A phylogenetic analysis of the Mimosoideae (Leguminosae) based on chloroplast DNA sequence data. In 'Advances in legume systematics, 10, higher level systematics'. (Eds BB Klitgaard, A Bruneau) pp. 197–220. (Royal Botanic Gardens, Kew: London)
- Morales M, Wulff AF, Fortunato RH, Poggio L (2010) Chromosome and morphological studies in the *Mimosa debilis* complex (Mimosoideae, Leguminosae) from southern South America. *Australian Journal of Botany* **58**, 12–22. doi:10.1071/BT09132
- Nixon KC (1999) 'Winclada (BETA) ver. 0.9.9.' (Published by the author: Ithaca, NY)
- Polhill RM, Raven PH, Stirton CH (1981) Evolution and systematics of the Leguminosae. In 'Advances in legume systematics, vol. 1'. (Eds RM Polhill, PH Raven) pp. 1–26. (Royal Botanic Gardens, Kew: London)
- Posada D, Buckley T (2004) Model selection and model averaging in phylogenies: advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. *Systematic Biology* **53**, 793–808. doi:10.1080/10635150490522304
- Posada D, Crandall KA (1998) Modeltest: testing the model of DNA substitution. *Bioinformatics* **14**, 817–818. doi:10.1093/bioinformatics/14.9.817
- Ronquist F, Huelsenbeck JV (2003) 'Mr Bayes: Bayesian inference of phylogeny.' Available at <http://mrbayes.csit.fsu.edu> [verified June 2011].
- Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG (1997) The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* **25**, 4876–4882. doi:10.1093/nar/25.24.4876

Manuscript received 7 June 2010, accepted 23 May 2011