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ORIGINAL ARTICLE

Chromosome numbers in the genus *Mimosa* L.: cytotaxonomic and evolutionary implications

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Abstract Chromosome numbers were determined for 125 accessions of 92 taxa of *Mimosa* from all five of Barneby's (Mem New York Bot Gard 65:1–835, 1991) taxonomic sections. For 69 species, 1 subspecies and 8 varieties, chromosome numbers are presented for the first time, for 6 species and 1 variety previously published data have been confirmed and for 3 species and 2 varieties different numbers were found. Results show that 74% of the accessions were diploid ($2n = 2x = 26$) and 26% polyploid, these mostly tetraploid ($2n = 4x = 52$) but with two triploid ($2n = 3x = 39$). These results double the number of *Mimosa* species for which the chromosome count is known from less than 10% previously reported to more than 20%, representing an important advance in the cytotaxonomy of this legume genus. These results together with literature data show that ca. 78% of *Mimosa* species are diploid. Polyploids are present in most of the taxonomic sections and in different lineages across the genus. No particular chromosome number is restricted to a given section or lineage. A possible relation between geography, species distribution, polyploidy and invasiveness was detected, however, further studies based on more accessions, especially from higher latitudes, are required before firm conclusions can be drawn.

Keywords Mimosa · Chromosome numbers · Cytotaxonomy · Evolution · Intraspecific variability · Leguminosae

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Introduction

The genus *Mimosa* L. (Fabaceae-Mimosoideae) comprises around 530 species (ca. 704 taxa), ca. 461 native to the Americas, 31 to Madagascar (mostly endemics), 4 native to east Africa and 4 to southwest Asia (Barneby 1991; Du Puy et al. 2002; Simon 2009). Most of the species occur in the tropics, at low and medium altitudes, but some reach subtropical or warm temperate regions of the U.S.A. in the north and Argentina and Uruguay in the south. Their habitats range from equatorial macrothermic forests to fire-prone tropical savannas, subtropical grasslands, seasonally dry tropical and subtropical forests and thorny scrub vegetation, deserts and many ruderal sites including tropical pastures, with notable adaptations in growth habit across these diverse environments (Barneby 1991; Lewis et al. 2005). Brazil harbours the greatest concentration of species in the genus, especially in the Cerrado region, a zone of high biodiversity, where a quarter of all *Mimosa* species are found, with 74% of these restricted to the Cerrado biome and around 50% endemic (Simon and Proença 2000).

The origin of the genus was probably in the humid regions of South America (Polhill et al. 1981). The main species diversity centres are central Brazil and central and southern Mexico. Smaller centres are located in the Caribbean, espcially Cuba-Hispaniola (Dominican Republic and Haiti), the Orinoco basin and Madagascar (Barneby 1991; Du Puy et al. 2002).

Many species of *Mimosa* are economically important, such as *M. scabrella* Benth., a pioneer tree species in the araucária forests of southern Brazil that may reach 15–20 m in height. It is cultivated for shade in coffee plantations, and the wood is used in building and carpentry, and for cellulose and fuel (Barneby 1991; Caramori et al.1996). Other species are used as living fences (*M. caesalpiniifolia* Benth), in the cosmetic industry and in traditional folk medicine [*M. tenuiflora* (Wild.) Poir.] (Camargo-Ricalde et al. 2001; Lorenzi 2000a; Rivera-Arce et al. 2007). Many *Mimosa* species, due to their nitrogen fixation ability, are also used for soil enrichment and recuperation of degraded land (Dhillion and Camargo-Ricalde 2005). Some other species such as *M. pigra* L. (Lowe et al. 2000) and *M. pudica* L. (Lorenzi 2000b) are among the world's most aggressive invaders outside their native range and are nowadays widespread around the world.

The first critical classification of Mimosaceae and *Mimosa* was by Bentham in 1841 and 1875 and, despite new classification proposals such as that by Britton and Rose in 1928, Bentham's main definitions were maintained by Barneby (1991) in his comprehensive and widely used infrageneric classification and taxonomic revision of *Mimosa*. Barneby (1991) recognised five sections [*Mimadenia* (ca. 15 species), *Batocaulon* (190 species), *Habbasia* (ca. 78 species), *Calothamnos* (ca. 26 species) and *Mimosa* (with ca. 177 species and several subspecies and varieties)], subdivided in 41 series. According to Barneby (1991) and two recent phylogenetic studies (Bessega et al. 2008; Simon et al. 2009) *Mimadenia* is sister to the other species of the genus, and section *Mimosa* is the most derived group and also the section with the most complicated taxonomy. In the densely sampled phylogenetic analysis (Simon 2009; Simon et al. 2009) including 259 species representing all five sections and 37 out of the 41 series proposed by Barneby (1991), it is also clear that while the rest of Barneby's (1991) sections do not form natural monophyletic groups, there is broad overall congruence with Barneby's vision of the genus with many of the other infrageneric groups (series and subseries) recovered as monophyletic.

Although progress is being made towards a new phylogenetic classification of *Mimosa*, as a new infrageneric classification for *Mimosa* has not yet been formally proposed, in this paper we will follow Barneby's (1991) monograph.

Chromosome numbers have been reported for around 67 *Mimosa* taxa, representing less than 10% of all taxa (Federov 1969; Alves and Custódio 1989; Seijo 1993, 1999, 2000; Seijo and Fernández 2001; IPCN 2009). Most of them are diploid with $2n = 2x = 26$ chromosomes. A few are tetraploid ($2n = 4x = 52$) and even fewer are octaploid ($2n = 8x = 104$). Goldblatt (1981) suggested $x = 14$ as the basic number in Mimosoideae, and therefore $x = 13$, found in *Mimosa* and other genera, would probably have been derived by disploidy. In a few cases, there are reports of intraspecific variability in ploidy levels (mostly diploid and tetraploid individuals) as in *M. pudica* (IPCN), *M. somnians* Humb. & Bonpl. ex Willd, *M. debilis* H.B. ex Willd.(Seijo 1993, 1999, 2000) and *M. balansae* Micheli (Seijo and Fernández 2001). For the majority of the species with chromosome counts, only one or a few populations have been analysed. Therefore, the absence of intraspecific variation in ploidy levels could be due to undersampling within the geographic range of a given species.

This work aimed at analysing chromosome numbers in a range of *Mimosa* species in order to broaden the cytogenetic information of this large genus and to investigate the importance of chromosome numbers as a cytotaxonomic character and the role of polyploidy in *Mimosa* evolution.

Materials and methods

Seeds of 125 accessions of 92 *Mimosa* taxa were collected mainly from the Brazilian Cerrado region but also from some other regions of Brazil, Uruguay, Equador, Bolivia, Peru, Honduras, Panama, Mexico, the United States of America, Taiwan, India, Nepal, Burkina Faso and Madagascar (Table 1). Most of the accessions were collected by the authors while a few were obtained from the Millenium Seed Bank (UK), seed companies and other collaborators. Taxonomic vouchers of the accessions are deposited at the following herbaria: FHO (Oxford University, UK), K (Kew, Royal Botanic Gardens, UK), CEN (Embrapa Recursos Genéticos e Biotecnologia, Brazil), UB (Universidade de Brasília, Brazil), RB (Jardim Botânico do Rio de Janeiro, Brazil), UAMIZ (Universidad Autónoma Metropolitana, Mexico), MEXU (Herbario Nacional, Mexico), HUEFS (Universidade Estadual de Feira de Santana, Brazil) and ICN (Departamento de Botânica Universidade Federal do Rio Grande do Sul, Brazil).

Somatic chromosome numbers were determined in root tip cells. Seeds were scarified by a small cut in the testa and germinated in petri dishes with moist filter paper. When the roots were around 1 cm in length, they were pretreated with a saturated solution of paradichlorobenzene for 24 h

Table 1 Accessions and taxa of *Mimosa* analysed, taxonomic section according to Barneby (1991), place and coordinates of collection and chromosome number

Species	Section	Accession	Place of collection	Coordinates	Chromosome no.
M. acantholoba (Willd.) Poir. var. *acantholoba*[a]	*Batocaulon*	Sarkinen, T.E. 2150	Peru, Piura, Morropon	5°13′S, 80°00′W	26
M. acutistipula Benth. var. *acutistipula*[a]	*Mimosa*	Way, M.J. 2438	Brazil, Pernambuco, Petrolina	8°52′S, 40°45′W	52
M. adenocarpa Benth.[a]	*Batocaulon*	Coradin, L. 8532	Brazil, Bahia, Lençóis	12°33′S, 41°22′W	26
M. adenocarpa	*Batocaulon*	Simon, M.F. 728	Brazil, Distrito Federal, Brasília	15°45′S, 47°51′W	26
M. aff. *bathyrrhena* Barneby[a]	*Calothamnos*	Simon, M.F. 874	Brazil		52
M. affinis B.L.Rob.[a]	*Mimosa*	Martinez-Romero, E. s/n	Mexico		26
M. albida Humb. & Bonpl. ex Willd. var. *albida*	*Mimosa*	Way, M.J. 158	Mexico, Yucatan, Opichen	20°33′N, 89°53′W	26
M. albolanata Taub.[a]	*Habbasia*	Simon, M.F. 677	Brazil, Goiás, Pirenopolis	15°47′S, 48°53′W	26
M. antrorsa Benth.[a]	*Habbasia*	Fagg, C.W. 1747	Brazil, Distrito Federal, Brasília	15°51′S, 47°51′W	26
M. apodocarpa Benth.[a]	*Batocaulon*	Simon, M.F.635	Brazil, Tocantins, Filadélfia	7°29′S, 47°55′W	26
M. artemisiana Heringer & Paula[a]	*Batocaulon*	Faria, S.M. 138	Brazil, Minas Gerais, Marliéria	19°42′S, 42°33′W	26
M. bahamensis Benth.[a]	*Batocaulon*	Way, M.J. 100	Mexico, Yucatan, Celestún	20°51′N, 90°07′W	26
M. benthamii Macbride[a]	*Batocaulon*	James, E.K. 335	Mexico, Morelos, Sierra de Huautla	18°29′N, 99°00′W	26
M. bimucronata Kuntze var. *bimucronata*	*Batocaulon*	Simon, M.F. 301	Brazil, Distrito Federal, Brasília	15°43′S, 47°57′W	26
M. bimucronata	*Batocaulon*	Dahmer, N. 46	Brazil, São Paulo, Mogi das Cruzes	23°30′S, 46°10′W	26
M. bimucronata	*Batocaulon*	Dahmer, N. 48	Brazil, São Paulo, Mogi das Cruzes	23°33′S, 46°08′W	26
M. biuncifera Benth.[a]	*Batocaulon*	Newman, M. 284	USA, Arizona	31°43′N, 111°09′W	52
M. blanchetii Benth.[a]	*Batocaulon*	Coradin, L. 6204	Brazil, Bahia	11°27′S, 41°07′W	26
M. borealis A.Gray[a]	*Batocaulon*	Simon, M.F. 873	USA, cultivated in Oxford		26
M. caesalpiniifolia Benth.	*Batocaulon*	Dahmer, N. 50	Brazil, São Paulo, Arujá	23°29′S, 46°15′W	26
M. caesalpiniifolia	*Batocaulon*	Dahmer, N. 35	Brazil, Goiás, Goiânia	16°40′S, 49°18′W	26
M. caesalpiniifolia	*Batocaulon*	Dahmer, N. 29	Brazil, São Paulo, Mogi das Cruzes	23°31′S, 46°13′W	26
M. caesalpiniifolia	*Batocaulon*	Kamiski, P. s/n	Brazil, Roraima		26
M. campicola Harms var. *planipes* Barneby[a]	*Batocaulon*	Simon, M.F. 692	Brazil, Bahia, Morro do Chapéu	11°29′S, 41°19′W	26
M. camporum Benth.[a]	*Habbasia*	Sanou, L. BUR-315	Burkina Faso, Houet, Kokozowe	11°08′N, 4°21′W	26
M. camporum	*Habbasia*	Bako, B.BUR-282	Burkina Faso, Comoe, Yendéré/Niangoloko	10°12′N, 4°59′W	26
M. camporum	*Habbasia*	Faria, S.M. 729	Brazil, Pará, Porto Trombetas	1°40′S, 56°27′W	26
M. candollei R.Grether[a]	*Batocaulon*	Simon MF 644	Brazil, Tocantins, Filadélfia		52
M. cisparanensis Barneby[a]	*Habbasia*	Simon, M.F. 568	Brazil, Mato Grosso, Nobres	14°19′S, 55°24′W	52
M. claussenii Benth.[a]	*Habbasia*	Simon, M.F. 303	Brazil, Distrito Federal	15°43′S, 47°57′W	26
M. claussenii	*Habbasia*	Simon, M.F. 308	Brazil, Goiás	15°58′S, 48°50′W	26

Table 1 continued

Species	Section	Accession	Place of collection	Coordinates	Chromosome no.
M. cordistipula Benth.[a]	*Batocaulon*	Simon, M.F. 693	Brazil, Bahia, Morro do Chapéu	11°29′S, 41°19′W	26
M. cryptothamnos Barneby[a]	*Habbasia*	Simon, M.F. 738	Brazil, Goiás, São João da Aliança	14°52′S, 47°34′W	26
M. debilis Humb. & Bonpl. ex Willd. var. *debilis*	*Mimosa*	Simon, M.F. 778	Brazil, Mato Grosso	15°50′S, 56°06′W	26
M. debilis	*Mimosa*	Simon, M.F. 790	Brazil, Mato Grosso, Chapada dos Guimarães	15°20′S, 55°54′W	26
M. debilis var. *vestita* (Benth.) Barneby	*Mimosa*	Simon, M.F. 783	Brazil, Mato Grosso	15°50′S, 56°05′W	26
M. delicatula Baill.[a]	*Batocaulon*	Sutherland, J.M. 262	Madagascar, Amborosary	25°01′S, 46°38′E	26
M. depauperata Benth.[a]	*Batocaulon*	Simon, M.F. 801	Mexico, Queretaro, Tequisquiapan	20°33′N, 99°54′W	26
M. diplotricha C.Wright ex Sauvalle var. *diplotricha*	*Batocaulon*	Simon, M.F. 304	Brazil, Distrito Federal, Lago Sul	15°52′S, 47°50′W	26
M. diplotricha C. Wright ex Sauvalle	*Batocaulon*	Simon, M.F. 877	Taiwan, Ping-Tung	22°45′N, 120°34′E	26
M. dominarum Barneby[a]	*Habbasia*	Simon, M.F. 776	Brazil, Goiás, Alto Paraíso	14°11′S, 47°29′W	26
M. dysocarpa Benth.[a]	*Batocaulon*	Newman, M. 296	USA, Arizona	31°47′N, 110°49′W	26
M. echinocaula Benth.[a]	*Batocaulon*	Simon, M.F. 312	Brazil, Goiás, Formosa-Itiquira	15°32′S, 47°25′W	26
M. flocculosa Burk.[a]	*Calothamnos*	CNPF s/n	Brazil, Paraná		26
M. foliolosa Benth.[a]	*Habbasia*	Simon, M.F. 321	Brazil, Distrito Federal, Brasília	15°43′S, 47°57′W	26
M. foliolosa	*Habbasia*	Simon, M.F. 663	Brazil, Distrito Federal, Planaltina	15°36′S, 47°44′W	26
M. foliolosa	*Habbasia*	Simon, M.F.672	Brazil, Goiás, Pirenopolis	15°46′S, 48°56′W	26
M. goldmanii B. L. Rob.[a]	*Mimosa*	James, EK 326	México, Morelos, Sierra de Huautla	18°28′N, 99°01′W	52
M. gracilis Benth.[a]	*Batocaulon*	Simon, M.F. 323	Brazil, Minas Gerais, PN Sertão Veredas	15°23′S, 45°54′W	26
M. hamata Willd.	*Batocaulon*	Simon, M.F. 876	Índia		26
M. heringeri Barneby[a]	*Habbasia*	Proença, C.2138	Brazil, Distrito Federal, Gama	16°03′S, 48°03′W	26
M. hexandra Micheli[a]	*Batocaulon*	Way, M.J. 2440	Brazil, Bahia	9°20′S, 40°18′W	26
M. hypoglauca Mart. var. *hypoglauca*[a]	*Mimosa*	Simon, M.F. 723	Brazil, Bahia, Palmeiras	12°45′S, 41°30′W	26
M. incana (Spreng.) Benth.[a]	*Calothamnos*	Dahmer, N. 1	Brazil, Rio Grande do Sul, Porto Alegre	29°53′S, 50°18′W	52
M. incana	*Calothamnos*	Dahmer, N. 2	Brazil, Rio Grande do Sul, Tainhas	29°25′S, 50°30′W	52
M. incana	*Calothamnos*	Dahmer, N. 17	Brazil, Rio Grande do Sul, Caxias do Sul	29°04′S, 51°00′W	52
M. incana	*Calothamnos*	Dahmer, N. 22	Brazil, Rio Grande do Sul, Caxias do Sul	29°15′S, 50°20′W	52
M. incana	*Calothamnos*	Dahmer, N. 26	Brazil, Rio Grande do Sul, São Francisco de Paula	29°25′S, 50°30′W	52
M. invisa Mart. ex Colla var. *invisa*[a]	*Batocaulon*	Feltwell, J. 19	Indonesia, Sulawesi	0°33′N, 123°54′E	26
M. lacerata Rose[a]	*Batocaulon*	Simon, M.F. 806	Mexico, Queretaro, Toliman	20°51′N, 99°52′W	26

Table 1 continued

Species	Section	Accession	Place of collection	Coordinates	Chromosome no.
M. latispinosa Lam.[a]	*Batocaulon*	Sutherland, J.M. 206	Madagascar, Tana	18°54′S, 47°30′E	26
M. luisana Brandegee[a]	*Batocaulon*	Way, M.J. 09	Mexico, Puebla, San Jose Axuxco	18°11′N, 97°11′W	26
M. melanocarpa Benth.[a]	*Habbasia*	Simon, M.F. 675	Brazil, Goiás, Pirenópolis	15°46′S, 49°00′W	26
M. misera Benth.[a]	*Batocaulon*	Simon, M.F. 703	Brazil, Bahia, Xique-Xique	10°57′S, 42°43′W	26
M. monancistra Benth.[a]	*Batocaulon*	Simon, M.F. 809	Mexico, Guanajuato, San Miguel Allende	21°01′N, 100°47′W	26
M. neptuniodes Harms[a]	*Habbasia*	Wood, J.R.I. 22123	Bolivia, Santa Cruz	17°33′S, 63°21′W	26
M. niederleinii Burk.[a]	*Mimosa*	Dahmer, N. 23	Brazil, Rio Grande do Sul, Tainhas	29°16′S, 50°19′W	52
M. nuda Benth. var. *nuda*[a]	*Mimosa*	Simon, M.F. 793	Brazil, Mato Grosso, Chapada dos Guimarães	15°20′S, 56°46′W	52
M. nuttallii (DC.) B.L.Turner[a]	*Batocaulon*	Simon, M.F. 875	USA, cultivated in Oxford		26
M. nuttallii	*Batocaulon*	Allen, B. CBG-05-100	USA, Kansas	39°06′N, 96°36′W	26
M. ophthalmocentra Mart. Ex Benth.[a]	*Batocaulon*	Way, M.J. 2434	Brazil, Pernambuco, Petrolina	9°02′S, 40°38′W	26
M. orthocarpa Spruce Ex Benth.[a]	*Batocaulon*	Grether, R. 2907	Mexico, Veracruz, Las Choapas	18°01′N, 95°08′W	26
M. orthocarpa	*Batocaulon*	Simon, M.F. 855	Mexico, Veracruz, Acayucan	17°58′N, 95°11′W	26
M. papposa Benth. var. *papposa*[a]	*Mimosa*	Proença, C 3431	Brazil, Distrito Federal	15°35′S, 48°04′W	26
M. pigra L. var. *dehiscens* (Barneby) D.Glazier & Mackinder	*Habbasia*	Dahmer, N. 28	Brazil, São Paulo, Mogi das Cruzes	23°31′S, 6°13′W	52
M. pigra var. *dehiscens*	*Habbasia*	Dahmer, N. 32	Brazil, Goiás, Caldas Novas	17°44′S, 48°38′W	52
M. pigra var. *dehiscens*	*Habbasia*	Sarkinen, T.E. 2059	Bolivia, La Paz, Sud Yungas	16°23′S, 67°31′W	26
M. pigra var. *dehiscens*	*Habbasia*	Simon, M.F. s.n.	Brazil, Goiás, Cristalina	16°46′S, 47°36′W	26
M. pigra var. *dehiscens*	*Habbasia*	Simon, M.F. 799	Brazil, Mato Grosso, Pocone	16°30′S, 56°42′W	52
M. polyantha Benth.[a]	*Batocaulon*	Simon, M.F. 827	Mexico, Sinaloa, Rosario	22°53′N,105°48′W	26
M. polyantha	*Batocaulon*	Way, M.J. WSO21	Mexico, Oaxaca, San Juan de los Cues	18°02′N, 97°03′W	26
M. polycarpa Kunth var. *subandina* Barneby[a]	*Mimosa*	Sarkinen, T.E. 2061	Bolivia, La Paz, Sud Yungas	16°23′S, 67°31′W	26
M. polydactyla Humb. & Bonpl. ex Willd.[a]	*Mimosa*	Thomas, S.M. 30/3	Ecuador, Napo, Coca		26
M. polydactyla	*Mimosa*	Coradin, L. 8682	Brazil, Bahia, Ilhéus	14°44′S, 39°09′W	26
M. polydidyma Barneby[a]	*Batocaulon*	Simon, M.F. 719	Brazil, Bahia, Palmeiras	12°38′S, 41°33′W	26
M. pteridifolia Benth.[a]	*Batocaulon*	Simon, M.F. 311	Brazil, Goiás, Formosa	15°32′S, 47°25′W	26
M. pudica L.	*Mimosa*	MSB 19956			52
M. pudica L. var. *hispida* Brenan[a]	*Mimosa*	Simon, M.F. 893	Brazil, Distrito Federal	15°44′S, 47°52′W	52
M. pudica	*Mimosa*	Beer, L. 394	Nepal		52
M. pycnocoma Benth.[a]	*Habbasia*	Simon, M.F. 868	Brazil, Goiás, Cavalcante	13°32′S, 47°29′W	52
M. radula Benth.[a]	*Mimosa*	Simon, M.F. 296	Brazil, Goiás, Pirenopolis	15°48′S, 48°50′W	26
M. revoluta Benth.[a]	*Mimadenia*	Sarkinen, T.E. 2074	Bolivia, La Paz, Inquiisivi	16°41′S, 67°14′W	26

Table 1 continued

Species	Section	Accession	Place of collection	Coordinates	Chromosome no.
M. robusta R. Grether[a]	*Batocaulon*	Simon, M.F. 863	Mexico, Jalisco, Puerto Vallarta	20°29′N, 105°18′W	52
M. rubicaulis Lam. ssp. *himalayana* (Gamble) H. Ohashi[a]	*Batocaulon*	Thomas, S.M. 24/1	Nepal		26
M. scabrella Benth.[a]	*Calothamnos*	Dahmer, N. 14	Brazil, Rio Grande do Sul, Caxias do Sul	29°08′S, 51°05′W	52
M. scabrella	*Calothamnos*	Lima, H.C. 4055	Brazil, Minas Gerais, Ouro Preto	20°17′N, 45°30′W	52
M. schomburgkii Benth.[a]	*Batocaulon*	Hellin, J.J. 15	Honduras, Colon	15°45′N, 85°44′W	26
M. sensitiva L. var. *sensitiva*[a]	*Mimosa*	Conceição, S.F. 284	Brazil, Bahia		26
M. sericantha Benth.[a]	*Batocaulon*	Simon, M.F. 410	Brazil, Tocantins	10°26′S, 46°27′W	26
M. setosa Benth. var. *paludosa* (Benth.) Barneby[a]	*Habbasia*	Simon, M.F. 306	Brazil, Distrito Federal	15°45′S, 47°51′W	26
M. setosa var. *paludosa*	*Habbasia*	Simon, M.F. 666	Brazil, Distrito Federal, Brasília	15°45′S, 47°51′W	52
M. setosa var. *paludosa*	*Habbasia*	Dahmer, N. 27	Brazil, São Paulo, Mogi das Cruzes	23°32′S, 46°12′W	52
M. setosa var. *paludosa*	*Habbasia*	Dahmer, N. 49	Brazil, São Paulo, Mogi das Cruzes	23°28′S, 46°14′W	52
M. setosa Benth. var. *urbica* Barneby[a]	*Habbasia*	Simon, M.F. 730	Brazil, Distrito Federal, Brasília	15°45′S, 47°51′W	26
M. setosissima Taub.[a]	*Habbasia*	Simon, M.F. 290	Brazil, Goiás, Cocalzinho	15°48′S, 48°47′W	26
M. similis Britton & Rose[a]	*Batocaulon*	James, E.K. 229	Mexico, Queretaro, Cadereyta	20°55′N, 99°45′W	26
M. similis	*Batocaulon*	Simon, M.F. 807	Mexico, Queretaro, Cadereyta	20°56′N, 99°44′W	26
M. skinneri Benth. var. *skinneri*[a]	*Mimosa*	James, E.K. 244	Mexico, Jalisco, Tepic	21°14′N, 104°38′W	52
M. somnians Humb. & Bonpl. ex Willd.	*Habbasia*	Grether, R. 2901	Mexico, Jalisco	21°18′N, 104°39′W	52
M. somnians	*Habbasia*	Simon, M.F. 797	Brazil, Mato Grosso, Poconé	16°20′S, 56°38′W	26
M. somnians	*Habbasia*	Way, M.J. 2476	Brazil, Rio Grande do Norte	4°53′S, 37°17′W	52
M. somnians var. *viscida* (Willd.) Barneby	*Habbasia*	Simon, M.F. 863	Brazil, Goiás, Alto Paraíso	14°05′S, 47°30′W	26
M. sparsiformis Barneby[a]	*Mimosa*	Dahmer, N. 15	Brazil, Rio Grande do Sul, Caxias do Sul	29°08′S, 51°03′W	39
M. sparsiformis	*Mimosa*	Dahmer, N. 52	Brazil, Rio Grande do Sul, Caxias do Sul	29°12′S, 51°17′W	39
M. splendida Barneby[a]	*Habbasia*	Simon, M.F. 316	Brazil, Goiás, C. Veadeiros	14°10′S, 47°35′W	26
M. tenuiflora (Willd.) Poir.[a]	*Batocaulon*	Camargo-Ricalde, S.L. 98	Mexico, Oaxaca, Zanatepec	16°26′N, 95°01′W	26
M. tenuiflora	*Batocaulon*	Way, M.J. 2441	Brazil, Bahia	9°20′S, 40°13′W	26
M. ulei Taub. var. *ulei*[a]	*Habbasia*	Simon, M.F. 758	Brazil, Goiás, Alto Paraíso	14°09′S, 47°37′W	26
M. uraguensis Hook. & Arn.	*Batocaulon*	Simon, M.F.862	Uruguay, cultivated in Oxford		26
M. ursina Mart.[a]	*Mimosa*	Simon, M.F. 704	Brazil, Bahia, Xique-Xique	10°57′S, 42°43′W	26

Table 1 continued

Species	Section	Accession	Place of collection	Coordinates	Chromosome no.
M. velloziana Mart. var. *velloziana*[a]	*Mimosa*	Dahmer, N. 45	Brazil, São Paulo, Mogi das Cruzes	23°30′S, 46°10′W	52
M. velloziana var. *velloziana*	*Mimosa*	Simon, M.F. 302	Brazil, Distrito Federal	15°43′S, 47°57′W	52
M. velloziana var. *velloziana*	*Mimosa*	Simon, M.F. 665	Brazil, Distrito Federal, Planaltina	15°35′S, 47°42′W	52
M. verrucosa Benth.[a]	*Batocaulon*	Conceição, A.A. 1522	Brazil, Bahia	10°00′S, 42°47′W	26
M. virgula Barneby[a]	*Mimosa*	Simon, M.F. 294	Brazil, Goiás, Pirenópolis	15°50′S, 48°54′W	26

[a] First determination of chromosome number

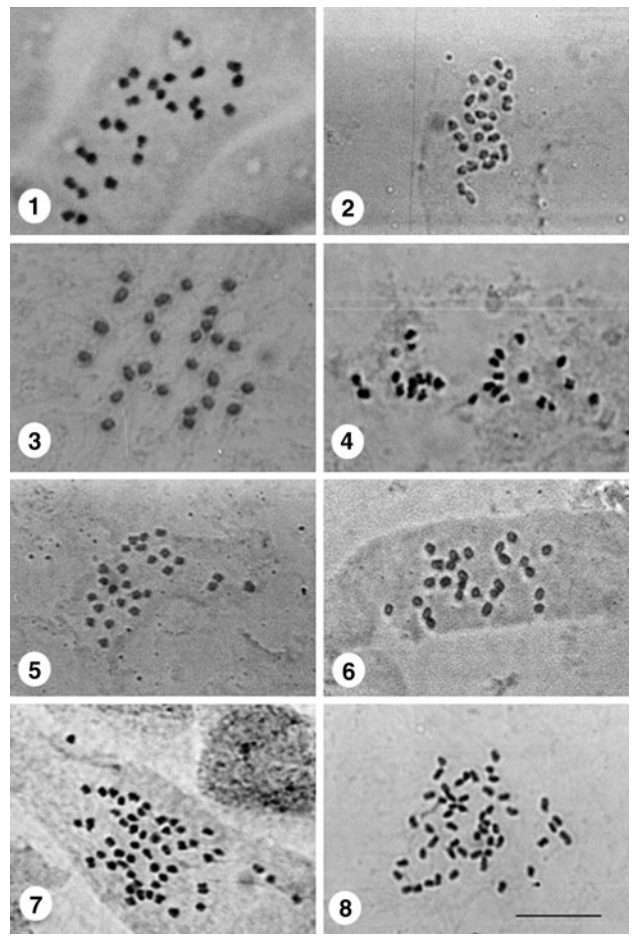
at 4°C, fixed in 6:3:1 (ethanol:chloroform:acetic acid) for 12–24 h and stored in 70% alcohol below 0°C until required. Slides were prepared by hydrolyzing the roots with 1 N HCl at 60°C for 8–10 min and staining with the Feulgen technique for 2–3 h (sometimes followed by a 2% pectinase treatment for 2 min) and squashed in propionic carmine. At least ten cells with good chromosome spreading and at equivalent contraction were analysed per plant. The best cells were photographed and/or registered by a digital image capturing system.

Results

Chromosome numbers were determined for the 125 accessions of 92 taxa (from 83 species and one subspecies) of *Mimosa* (Table 1). For 69 species, 8 varieties and 1 subspecies, chromosome numbers are presented here for the first time, for 6 species and 1 variety previously published counts data have been confirmed, and for 3 species and 2 varieties different numbers were found (Table 1). Results show that 92 (74%) of the accessions analysed are diploid ($2n = 2x = 26$) (Figs. 1–6) and 33 (26%) are polyploid, 31 of which are tetraploid ($2n = 4x = 52$) (Figs. 7, 8) and the 2 accessions of *M. sparsiformis* Barneby are triploid ($2n = 3x = 39$). This is the first report of a triploid species in the genus. Polysomaty, the occurrence in the root tips of a varying, generally low, percentage of cells with double the normal chromosome number, was reported in some (26.5%) of the accessions (data not shown).

Mimosa chromosomes are small, ca. 1–2 μm (Fig. 1). Chromosome measures were not made for all species, but as seen in Fig. 1, there are probably differences in chromosome size among some species and a tendency for tetraploid species to have smaller chromosomes than diploid ones.

Following Barneby's (1991) infrageneric classification, in section *Mimadenia*, the only species analysed (*M. revoluta* Benth.) is diploid. This is the first chromosome number determination in this section.



Figs. 1–8 **Fig. 1** *Mimosa delicatula* Sutherland, J.M. 262 ($2n = 26$). **Fig. 2** *M. rubicaulis* ssp. *himalayana* Thomas, S.M. 24/1 ($2n = 26$). **Fig. 3** *M. orthocarpa* Grether, R. 2907 ($2n = 26$). **Fig. 4** *M. antrorsa* Fagg, C.W. 1747 ($2n = 26$). **Fig. 5** *M. claussenii* Simon, M.F. 308 ($2n = 26$.). **Fig. 6** *M. monancistra* Simon, M.F. 809 ($2n = 26$). **Fig. 7** *M. scabrella* Dahmer, N. 14 ($2n = 52$). **Fig. 8** *M. robusta* Simon, M.F. 863 ($2n = 52$)

The samples analysed for section *Batocaulon* (Table 1) are the most representative in terms of geographic range. The 50 accessions and 43 taxa (41 species) analysed were collected in several regions of the world, including Brazil (21 taxa), Mexico (10 taxa), U.S.A. (4 taxa), Madagascar (2 taxa), Peru, Taiwan, India, Indonesia, Honduras and Uruguay. Thirty-eight species and one subspecies are diploid [*M. acantholoba* (Willd.) Poir. var. *acantholoba, M. adenocarpa* Benth., *M. apodocarpa* Benth., *M. artemisiana* Heringer & Paula, *M. bahamensis* Benth., *M. benthamii* Macbride, *M. bimucronata* Kuntze, *M. bimucronata* Kuntze var. *bimucronata, M. blanchetii* Benth., *M. borealis* A.Gray, *M. caesalpiniifolia*, *M. campicola* Harms var. *planipes* Barneby, *M. cordistipula* Benth., *M. delicatula* Baill., *M. depauperata* Benth., *M. diplotricha* C.Wright ex Sauvalle var. *diplotricha, M. dysocarpa* Benth., *M. echinocaula* Benth., *M. gracilis* Benth., *M. hamata* Willd., *M. hexandra* Micheli, *M. invisa* Mart. ex Colla var. *invisa, M. lacerata* Rose, *M. latispinosa* Lam., *M. luisana* Brandegee, *M. misera* Benth., *M. monancistra* Benth., *M. nuttallii* (DC.) B.L.Turner, *M. ophthalmocentra* Mart. ex Benth., *M. orthocarpa* Spruce ex Benth., *M. polyantha* Benth., *M. polydidyma* Barneby, *M. pteridifolia* Benth., *M. rubicaulis* Lam. ssp. *himalayana* (Gamble) H. Ohashi, *M. schomburgkii* Benth., *M. sericantha* Benth., *M. similis* Britton & Rose, *M. tenuiflora*, *M. uraguensis* Hook. & Arn. and *M. verrucosa* Benth.] and three are tetraploid [*M. biuncifera* Benth., *M. candollei* R. Grether (=*M. quadrivalvis* L. var. *leptocarpa* (DC.) Barneby) and *M. robusta* R.Grether].

Nine accessions of four species of section *Calothamnos* were analysed: one, *M. flocculosa* Burk., is diploid, and three, *M.* aff. *bathyrrhena* Barneby, *M. incana* (Spreng.) Benth. and *M. scabrella*, are tetraploid. In section *Habbasia* 34 accessions of 18 species and 2 varieties were examined: 15 are diploid [*M. albolanata* Taub., *M. antrorsa* Benth., *M. camporum* Benth., *M. claussenii* Benth., *M. cryptothamnos* Barneby, *M. dominarum* Barneby, *M. foliolosa* Benth., *M. heringeri* Barneby, *M. melanocarpa* Benth., *M. neptuniodes* Harms, *M. setosa* Benth. var. *urbica* Barneby, *M. setosissima* Taub., *M. somnians* Humb. & Bonpl. var. *viscida* (Willd.) Barneby, *M. splendida* Barneby, *M. ulei* Taub. var. *ulei*], 2 (*M. pycnocoma* Benth. and *M. cisparanensis* Barneby) are tetraploid and in 3 species intraspecific variability for chromosome number (diploid and tetraploid accessions) was verified: *M. pigra* L. var. *dehiscens* (Barneby) D.Glazier & Mackinder, *M. setosa* Benth. var. *paludosa* (Benth.) Barneby, and *M. somnians* Humb. & Bonpl. ex Willd., all with $2n = 26$ and $2n = 52$ chromosomes.

Of the 19 species (24 accessions) studied from section *Mimosa*, 11 are diploid [*M. affinis* B.L.Rob., *M. albida* Humb. & Bonpl. ex Willd. var. *albida, M. debilis* Humb. & Bonpl. ex Willd., *M. debilis* var. *debilis*, *M. debilis* var. *vestita* (Benth.) Barneby, *M. hypoglauca* Mart. var. *hypoglauca*, *M. papposa* Benth. var. *papposa*, *M. polycarpa* Kunth var. *subandina* Barneby, *M. polydactyla* Humb. & Bonpl. ex Willd., *M. radula* Benth., *M. sensitvia* L. var. *sensitiva, M. ursina* Mart., *M. virgula* Barneby), 7 are tetraploid (*M. acutistipula* Benth. var. *acutistipula, M. goldmanii* B.L.Rob., *M. niederleinii* Burk., *M. nuda* Benth. var. *nuda, M. pudica* L., *M. pudica* L. var. *hispida* Brenan, *M. skinneri* Benth. var. *skinneri, M. velloziana* Mart.) and 1 is triploid (*M. sparsiformis* Barneby). No ploidy level above the tetraploid was found in the material analysed here (Table 1).

Discussion

This study doubles the number of *Mimosa* species with chromosome number determinations, from less than 10% to more than 20% of all taxa including accessions from all five sections and covering a broad taxonomic and geographical range when compared with previous studies (Table 1), therefore representing a significant contribution to the cytotaxonomy of this important legume genus.

With ca. 145 taxa analysed so far (Table 1; Federov 1969; Alves and Custódio 1989; Seijo 1993, 1999, 2000; Seijo and Fernández 2001; IPCN 2009), ca. 78% of the *Mimosa* species are diploid, ca. 17% are tetraploid, rather similar to what we have found, ca. 3% octaploid and ca. 2% other chromosome numbers. According to these data, chromosome number cannot be considered a clear cut cytotaxonomic diagnostic character in the genus, as no particular chromosome number is restricted to any of Barneby's (Barneby 1991) sections, and polyploids are present in all sections, except *Mimadenia*, where only one species was examined.

The number of species we analysed in each section, 1 out of 15 in *Mimadenia* (6%), 41 out of 190 in *Batocaulon* (21%), 18 out of 78 in *Habbasia* (23%), 4 out of 26 in *Calothamnos* (15%) and 19 out of 177 in *Mimosa* (11%), can be considered representative for each section, except for *Mimadenia* and *Mimosa* which were undersampled. When these data are joined to information from the literature, the percentage of studied species remains the same for *Mimadenia* (6%, only one species) and increases to 27% in *Batocaulon*, 28% in *Habbasia*, 23% in *Calothamnos* and 20% in *Mimosa.* In all sections diploid species predominate, and tetraploid taxa are found in all but *Mimadenia*, but are apparently more frequent in sections *Calothamnos* and *Mimosa.* Octaploids have been found in sections *Calothamnos* and *Mimosa* and the only triploid (*M. sparsiformis*) so far reported along with a hexaploid accession of *M. pudica* is from section *Mimosa.*

The chromosome numbers reported here plus those of literature (Federov 1969; Alves and Custódio 1989; Seijo 1993, 1999, 2000; Seijo and Fernández 2001; IPCN 2009) lead to the conclusion that the majority of *Mimosa* species and taxa are diploid, but polyploidy has played a role in the genus evolution and speciation. Comparing our results with recent molecular phylogenetic studies (Simon 2009; Simon et al. 2009), we found that polyploid species occur in different parts across the *Mimosa* phylogeny. This suggests that duplication of chromosome numbers evolved several times in the genus and that polyploidy is not restricted to any particular clade within *Mimosa*. On the contrary, it seems that polyploids arose independently from ancestors with lower ploidy levels and are present in divergent lineages in the genus.

Regarding intraspecific variability in chromosome numbers, published data indicate variability (sometimes related to varieties) for *M. pudica*, *M. balansae*, *M. debilis, M. somnians, M. pigra* and *M. setosa*. These initial reports are amplified here, where more accessions were analysed for some species. For example, for *M. pigra* var. *dehiscens,* we analysed five accessions from different localities, four from Brazil (São Paulo, Mato Grosso, and Goiás at Caldas Novas and Cristalina) and one from Bolivia (Table 1). Three Brazilian accessions were tetraploid and the Bolivian plus the Cristalina accessions were diploid. No obvious relation between geographical origin and ploidy level has been found. Seijo (1999) found intraspecific variability for two Argentinian accessions of *M. pigra*, a diploid one of *M. pigra* var. *dehiscens* and a tetraploid one for *M. pigra* var. *pigra.* For *M. setosa* var. *paludosa* studied in this paper, three tetraploid accessions were found (one from São Paulo and the others from Distrito Federal) (Table 1) and one diploid was also collected in Distrito Federal. For *M. somnians*, the accessions collected in Mato Grosso were diploid and the one from Rio Grande do Norte was tetraploid (Table 1). Seijo (1993, 2000) also reported diploid and tetraploid accessions in *M. somnians.* Seijo (2000) reported $2n = 26$ for *M. debilis* var. *vestita* collected in Paraguay and $2n = 52$ for *M. debilis* var. *debilis* from Argentina (Seijo 1993, 1999). Finally, for *M. pudica* most of the authors found tetraploidy, in accordance with our results (Table 1), but there are reports of $2n = 44$ and $2n = 78$ chromosomes, besides the most common $2n = 52$ (IPCN 2009; Seijo 1999). It is notable that polyploidy and infraspecific variability in chromosome number are often associated with widespread polymorphic species or species complexes, such as *M. setosa* or the *M. debilis*/*M. nuda* alliance.

The extent of intraspecific variability in chromosome numbers in the genus *Mimosa* still remains to be determined, due to rather limited sample sizes and rather restricted collection sites. In order to resolve that, intensive collections of several populations throughout the area of distribution of the species should be made.

According to Stebbins (1971), polyploids generally have a wider geographic distribution, being very good colonisers of new habitats and maybe more aggressive than their diploid relatives. It is striking that at least seven of the known *Mimosa* polyploids, *M. debilis*, *M. nuda*, *M. pigra*, *M. pudica*, *M. candollei, M. somnians* and *M. velloziana*, are weedy opportunistic species that are geographically widespread across the neotropics, often locally abundant, forming dense thickets on disturbed ruderal sites. Two of these, *M. pigra* and *M. pudica*, are amongst the world's most aggressive invasive weeds and are now naturalised and forming damaging invasive thickets across extensive parts of Africa, India and South-east Asia.

Another possible relation is that of polyploidy and higher latitudes. Seijo and Fernández (2001), studying species from southern South America, suggested that higher ploidy levels were found in higher latitudes. Among the species collected in northern Argentina between latitudes 27°S and 29°S, *M. vellosiella* Burk., *M. oligophylla* Micheli and *M. flagelaris* Benth. were diploid, *M. velloziana* was tetraploid, one accession of *M. balansae* Micheli was diploid and the other tetraploid. Between 32°S and 35°S, of the three species studied, *M. sprengelli* DC. and *M. ramulosa* Benth. were octaploid and *M. adpressa* Hooker & Arnott was tetraploid. *M. rocae* Lorentz & Niederlein collected at 38.5°S was also octaploid. Examining Table 1, it can be seen that of the four species collected in Rio Grande do Sul, southern Brazil (ca. 29°S), three, *M. incana*, *M. niederleinii* and *M. scabrella*, are tetraploid and *M. sparsiformis* is triploid. The tetraploid *M. biuncifera* was collected in Arizona, U.S.A. at 31°N. A few polyploid species have also been found at lower latitudes (Table 1), including *M. cisparanensis*, *M. velloziana*, *M. pycnocoma*, *M. pudica* and tetraploid accessions of *M. pigra*.

All these data suggest a possible relation among geography, species distribution, polyploidy and invasiveness in *Mimosa*, however, many more chromosome counts of a wider range of species and accessions, from other localities and especially higher latitudes, are needed before firm conclusions about the relationships can be drawn.

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