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ORIGINAL ARTICLE

Chromosome studies in southern species of *Mimosa* (Fabaceae, Mimosoideae) and their taxonomic and evolutionary inferences

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Abstract In this work, chromosome numbers and karyotype parameters of 36 taxa of the genus *Mimosa* were studied, especially from the southern South America center of diversification. Results support that $x = 13$ is the basic chromosome number in the genus. Polyploidy is very frequent, ca. 56 % of the total of the studied species here are polyploid, confirming that polyploids are more frequent at higher latitudes. The most common ploidy levels found are $2x$ and $4x$, but some species studied exhibit $6x$ and $8x$. In different groups, several ploidy levels were found. Parameters of chromosome size show statistically significant differences between close species, and asymmetry index A_2 exhibited low variation between them. It is possible to infer variations of chromosome size between diploids and tetraploids and between basal and derived taxa. The present studies confirm or reveal polyploidy in several groups of South America which are highly diversified in the southernmost area of distribution of the genus, such as sect. *Batocaulon* ser. *Stipellares* and sect. *Calothamnos*. Our data are discussed in a taxonomic context, making inferences about the origin of some polyploid taxa. Polyploidy could be an important phenomenon that increases the morphologic diversity and specific richness in southern South America. On basis of our data, it is possible to hypothesize hybridization between same-ploidy level or different ploidy level taxa. As already shown in the literature, our results confirm the importance of the polyploidy in the speciation of the genus.

Keywords Chromosome · Cytogenetics · Hybridization · *Mimosa* · Mimosoideae · Polyploidy

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Introduction

Mimosa L. (Fabaceae, Mimosoideae) is the third most diverse genus among Mimosoids, with ca. 540 species (Simon et al. 2011; Bessega and Fortunato 2011). This genus has two diversification centers: (a) Madagascar, Mesoamerica, southern Mexico, the Antilles, Hispaniola and the Orinoco Basin; and (b) southern South America, which comprises the Amazon Basin, the Brazilian Planoaltine and adjacent areas from Argentina, Uruguay and Paraguay (Barneby 1991).

Bentham (1876) carried out the first monograph of this genus and proposed two sections, *Habbasia* and *Mimosa;* both were distinguished by number of stamens. Barneby (1991) proposed five sections, based on the indumentum, petiolar nectaries and number of stamens: (1) *Mimadenia* Barneby (=vines and shrubs with petiolar nectaries from the tropical Andes and the Amazonian region); (2) Sect. *Batocaulon* DC. (=diplostemonous fertile flowers and indumentum with no calcarate hairs); (3) *Habbasia* DC.,

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(=diplostemonous fertile flowers and indumentum of calcarate setae); (4) *Calothamnos* Barneby (=haplostemonous fertile flowers and indumentum of branched hairs: plumose setae and stellate, even in the corolla lobes); (5) *Mimosa* (=indumentum variable, at least in the corolla, without plumose setae or stellate hairs; haplostemonous fertile flowers).

However, new phylogenetic analyses using cpDNA and morphological characters suggest that the sections that Barneby (1991) proposed are not monophyletic (Bessega et al. 2008; Bessega and Fortunato 2011; Simon et al. 2011). In these studies, some representatives of Sect. *Batocaulon* appear clustered with representatives of Sect. *Habbasia*; on the other hand, the representatives of Sect. *Calothamnos* appear clustered with others from Sect. *Mimosa.* The group *Batocaulon–Habbasia* appears to be more basal and the group *Calothamnos–Mimosa* appears to be more derived, coinciding partially with Barneby (1991), but completely with the proposal of Bentham (1876).

Despite the advances in the phylogeny of the genus, the proposal of infrageneric division of Barneby (1991) is currently valid, since the phylogeny does not resolve certain clades and it is still analyzing. Thus, the proposal of Barneby (1991) is used to discuss new information about taxonomy, evolution and cytogenetics of *Mimosa* (Dahmer et al. 2011; Simon et al. 2011; Morales et al. 2011, 2012, 2013).

According to previous studies, the basic chromosome number of this genus is $x = 13$ (Isely 1971; Goldblatt 1981); infrequently, other chromosome numbers were observed in the literature (Coleman and DeMenezes 1980; Santos et al. 2012). Fabaceae has the basic chromosome number $x = 7$, and phenomena of polyploidy and dysploidy could have an important role in the evolution of the family (Goldblatt 1981; Poggio et al. 2008). In *Mimosa,* the most frequent cited ploidy levels are $2x$ and $4x$, but $3x$, $6x$ and $8x$ have also been mentioned in the literature (Isely 1971; Goldblatt 1981; Seijo 1993, 1999, 2000 Seijo and Fernández 2001; Goldblatt and Johnson 2002; Morales et al. 2010, 2011, 2012; Olkolski and Schifino Wittmann 2011; Dahmer et al. 2011).

The karyotype of *Mimosa* has been poorly studied: Morales et al. (2011) found that the karyotype is relatively symmetric in seven diploid species from Southern South America; the chromosomes are metacentric and submetacentric. Endemic species from Sect. *Batocaulon* Ser. *Farinosae* Barneby had larger chromosomes than other species, and these differences could be associated with variations in the environment and geographic distribution of the studied taxa. Marçal de Sousa et al. (2013) arrived to similar conclusions regarding for the karyotype parameters by studying *M. caesalpiniifoli* Benth., which exhibits B chromosomes.

In this work, we present cytogenetic studies for 36 taxa of the genus *Mimosa,* especially the southernmost groups of South America diversification center. Chromosome number, ploidy level, and chromosome size were evaluated. These data are discussed in relation to the taxonomy, morphologic variability and geographic distribution of the studied entities.

Materials and methods

Plant material

The voucher specimens and samples used to perform the cytogenetic studies (seeds and fixed buds) were collected during field trips in northeastern Argentina, southern Brazil and Paraguay. They were deposited at the herbaria of Instituto de Recursos Biológicos, CIRN, INTA (BAB), Instituto de Botánica del Nordeste, CONICET–UNNE (CTES), Instituto de Botánica Darwinion, CONICET–Academia Nacional de Ciencias Exactas y Naturales (SI), Argentina; Departamento de Botánica, FCQ, UNA (FCQ), Paraguay; and Museu Botânico Municipal (MBM) in Brazil (Tables 1, 2, 3, 4).

To discuss the taxonomy of the studied entities, additional specimens from following herbaria were studied: BAB, CTES, G, LPB, MBM, MO, SI, SP, SPF, USZ. All specimens were identified according to Barneby (1991), but also with consideration of the list of taxa and identification keys in Izaguirre and Beyhaut (2003).

Chromosome numbers

For the mitosis studies, root meristems obtained from seeds germinated on Petri dishes were used. The 1–2 cm root tips were pretreated with 0.002-M 8-hydroxyquinoline at room temperature for 4–7 h and then fixed in absolute ethanol–glacial acetic acid (3:1) or absolute ethanol–lactic acid (5:1). For the meiosis studies, floral buds in different stages were collected in the field, and fixed in ethanol:glacial acetic acid: chloroform (6:3:1) or ethanol–glacial acetic acid (3:1).

The material fixed and conserved in 70 % ethanol was washed in buffer solution of 0.01-M citric acid–sodium citrate at pH 4.6 and then transferred to an enzymatic solution containing 2 mL cellulase 2 % (Ozonuka R-10, Merck KGaA, Damstadt, Germany) and 20 % liquid pectinase for 7,200–9,000 s at 37 °C. The material was washed again with buffer solution.

Slides were stained with haematoxylin and DAPI. In the first case, root tips were macerated in a drop of dye (acetic haematoxylin), and the 'squash' technique was applied. In each sample, 10–20 metaphases were counted. In the

Table 1 Chromosome numbers in *Mimosa* from Southern South America

Section	Series	Taxon	Chromosome number	Voucher specimens	Locality	Coordinates
Batocaulon DC.	*Stipellares* Benth.	*M. bifurca* Benth. var. *bifurca*	$2x = 26$*	MM 626	Argentina. Corrientes: La Cruz	29°10S 56°37′W
		M. urugüensis Hook. & Arn.	$2x = 26$ (Seijo 1993; Dahmer et al. 2011; Morales et al. 2011)	Pn.n.	Argentina. Entre Ríos: San José	30°23′S 58°45′W
		M. uliginosa Chodat & Hassl.	$2x = 26$ (Seijo 1993; Morales et al. 2011)	RHF9010	Argentina. Misiones: Bonpland	
		M. burkartii Marchiori & Sobral	$4x = 52$*	Pn.n.	Uruguay: Piriápolis Cerro San Antonio	34°54′S 55°17′W
		M. amphigena Benth. var. *trachycarpoides* Burkart	$4x = 52$*	GG704	Uruguay: Lavalleja	34°22′S 55°13′W
		M. cruenta Benth. var. *cruenta*	$4x = 52$*	GG695	Uruguay: Rivera	30°54′S 55°31′W
	Bimucronatae Benth.	*M. bimucronata* (DC.) Kuntze var. *bimucronata*	$2x = 26$, $x = 13$II (Seijo 1999; Dahmer et al. 2011)	RHF9028	Argentina. Misiones: San Javier	27°53′S 55°07′W
	Leiocarpae Benth.	*M. fiebrigii* Hassl.	$2x = 26$*	MM857	Brasil. Mato Grosso do Sul: Porto Murtinho	21°42′S 57°53′W
		M. insignis (Hassl.) Barneby	$x = 13$II*	RHF9336	Paraguay: Sierra del Amambay	22°40′S 56°09′W
		M. glutinosa Malme	$2x = 26$*	MM855	Brasil. Mato Grosso do Sul: Porto Murtinho	21°42′S 57°53′W
Batocaulon	*Caesalpiniifoliae* Barneby	*M. caesalpiniifolia* Benth.	$2x = 26$ (Alves and de Carvalho Custódio 1983; Dahmer et al. 2011; Marçal de Sousa et al. 2013)	ANM6024	Brazil. Paraná: Caiobá	25°51′S 48°33′W
	Paucifoliatae Benth.	*M. gracilis* Benth. subsp. *filiformis* (Benth.) Barneby var. *leiocarpa* (Benth.) Barneby	$x = 13$II*	RHF9092	Argentina. Corrientes: San Miguel	28°0′S 57°36′W

Section	Series	Subseries	Taxon	Chromosome numbers	Voucher specimens	Locality	Coordinates
Habbasia DC.	*Habbasia*	–	*M. pigra* L. var. *dehiscens* Barneby ex Glazier & Mackinder	$2x = 26$ (Seijo 1999; Dahmer et al. 2011)	RHF8881	Argentina. Corrientes: Paso de la Patria	27°19′S 58°35′W
					RHF8554	Paraguay. Caaguazú: Coronel Oviedo	25°25′S 56°27′W
					MM572	Argentina. Corrientes: Riachuelo	27°35′S 58°45′W
			M. pigra var. *pigra*	$4x = 52$ (Seijo 1999; Dahmer et al. 2011)	MM285	Argentina: Isla Martín García	34°11′S 58°15′W
					RHF8910	Argentina. Misiones: Candelaria	27°28′S 55°44′W

Table 1 continued

Section	Series	Subseries	Taxon	Chromosome numbers	Voucher specimens	Locality	Coordinates
	Somniantes		*M. somnians* Humb. & Bonpl. ex Willd. subsp. *somnians* var. *somnians*	$x = 13$II (Seijo 1993)	MM639	Argentina. Corrientes: Ituzaingó	27°36′S 56°41′W
		–		$4x = 52$ (Seijo 2000)	RHF8529	Paraguay. Paraguarí: desvío a Lago Ypoá	25°55′S 57°26′W
					RHF8835	Paraguay. San Pedro: San Estanislao	24°39′S 56°26′W
Mimosa	*Myriophyllae* Barneby	–	*M. myriophylla* Bong. ex Benth.	$4x = 52$*	RHF9094	Argentina. Corrientes: Santo Tomé	28°33′S 56°03′WG
	Mimosa	*Polycarpae*	*M. polycarpa* Kunth var. *spegazinii* (Pirotta ex Hook.) Burkart	$2x = 26$ (Seijo 1993)	IF20060920	Argentina. Misiones: Santa Ana	27°22′S 55°34′W
			M. balansae M. Micheli	$4x = 52$ (Seijo and Fernández 2001)	MM606	Argentina. Corrientes: Itá Corá	29°12′S 58°04′W
		Pedunculosae	*M. pauperoides* (Burkart) Fortunato	$6x = 78$*	MM612, 613	Argentina. Corrientes: Mercedes	29°12′S 58°05′W
			M. brevipetiolata Burkart var. *hirtula* (Burkart) Barneby	$4x = 52$ (Seijo 1999)	RHF8912	Argentina. Misiones: Loreto	27°19′S 55°32′W
		Obstrigosae	*M. adpressa* Hook. & Arn.	$4x = 52$ (Seijo and Fernández 2001)	RHF 9068	Argentina. Corrientes: La Cruz	29°10′S 56°38′W
		Mimosa	*M. velloziana* Mart. var. *velloziana*	$4x = 52$ (Dahmer et al. 2011)	RG2026	Argentina. Salta: Orán	23°08′S 64°20′W
					MM125	Argentina. Salta: Orán, Finca San Ignacio	23°08′S 64°20′W
Mimosa	*Mimosa*	*Mimosa*	*M. sensibilis* Griseb. var. *sensibilis*	$2x = 26$*	MM947	Brazil. Mato Grosso do Sul: Corumbá	19°01′S 57°39′W
		Pudicae	*M. xanthocentra* Mart. var. *mansii* (Benth.) Barneby	$2x = 26$ (Morales et al. 2011)	RHF8814	Paraguay. Cordillera: Arroyos y Estos	25°04′S 57°06′W
					RHF9180	Paraguay. Central: Emboscada	25°09′S 57°21′W
					RHF9199	Paraguay. San Pedro: San Estanislao	24°39′S 56°26′W
					RHF9238	Paraguay. Amambay: Camino a Pedro J. Caballero	22°39′S 55°59′W
			M. xanthocentra var. *subsericea* (Benth.) Barneby	$2x = 26$ (Seijo 2000)	MM 267	Argentina. Corrientes: Ituzaingó	27°36′S 56°41′W
					RHF9295	Paraguay. Amambay: Parque Nacional Cerro Corá	22°37′S 55°59′W

Table 1 continued

Section	Series	Subseries	Taxon	Chromosome numbers	Voucher specimens	Locality	Coordinates
			M. xanthocentra aff. var. *mansii*	$2x = 26$*	RHF9168	Paraguay. Paraguarí: Tobatí	25°16′S 57°05′W
		Hirsutae	*M. monadelpha* Chodat & Hassl. var. *glabrata* (Hassl.) Barneby	$2x = 26$*	RHF9207	San Pedro: San Estanislao	24°39′S 56°26′W
Calothamnos			*M. bonplandii* (Gillies ex Hook. & Arn.) Benth.	$4x = 52$*	JHnn	Argentina: Ciudad de Buenos Aires	34°36′S 58°23′W
			M. pilulifera Benth. var. *pilulifera*	$4x = 26$II*	MM284	Argentina: Isla Martín García	34°11′S 58°15′W
			M. pilulifera var. *pseudoincana* (Burkart) Barneby	$4x = 52$*	RHF9549	Brazil. Paraná. Rio das Pedras	25°21′S, 51°21′W
			M. lepidorepens Burkart	$8x = 104$*	RHF9463	Brazil. Santa Catarina: Serra do Quiririí	26°08′S 49°01′W
			M. berroi Burkart	$8x = 104$*	MM690	Uruguay. Lavalleja	34°22′S 55°14′W
			M. rocae Lorentz et Niederl.	$8x = 104$ (Seijo and Fernández 2001)	MM314	Argentina. Buenos Aires: Tandil	37°19′S 59°09′W
			M. scabrella Benth.	$4x = 52$ (Dahmer et al. 2011, 2013; Olkolski and Schifino Wittmann 2011)	RHF9560	Brazil. Santa Catarina: Serra do Quiririí	26°08′S 49°01′W
			M. daleoides Benth.	$8x = 104$ (Coleman and DeMenezes 1980; Seijo 1999)	RHF8536	Paraguay. Caaguazú: Caaguazú	25°27°S 56°01 W
			M. urticaria Barneby	$4x = 52$*	RHF9536	Brazil. Paraná: Ortigueira	24°12′S 50°55′W

References of voucher specimens: *ANM* Ana M. Molina, *GG* Gustavo Giberti, *MM* Matías Morales, *RHF* Renée H. Fortunato, *P* Patricia Prüner, *RG* Rosa Guaglianone. *n.n.* not number of collection registered

* New chromosome number. Literature references indicate previous reports (references are fully described in the text)

Table 2 Chromosome size and ploidy levels in species of *Mimosa*

Taxon	Ploidy level	TCL (μm)	CLHG (μm)	TCA (μm^2)	CAHG (μm^2)	A_2*
Sect. *Batocaulon*						
Ser. *Leiocarpae*						
M. glutinosa	2*x*	41.60 ± 8.13	20.80 ± 4.06	26.07 ± 6.12	13.04 ± 3.06	0.27 ± 0.03[a]
M. fiebrigii	2*x*	29.57 ± 3.33	14.78 ± 1.66	15.47 ± 1.73	7.73 ± 0.87	0.26 ± 0.09[a]
Ser. *Bimucronatae*						
M. bimucronata var. *bimucronata*	2*x*	42.14 ± 10.17	20.97 ± 5.08	25.31 ± 6.13	10.49 ± 5.24	0.23 ± 0.01[a]
Ser. *Caesalpiniifoliae*						
M. caesalpiniifolia	2*x*	36.12 ± 4.62	18.06 ± 2.31	20.76 ± 1.66	10.97 ± 0.83	0.17 ± 0.03[a]
Ser. *Stipellares*						
M. burkartii	4*x*	62.83 ± 1.14	15.71 ± 0.57	54.41 ± 8.57	13.60 ± 4.28	0.17 ± 0.01[a]
M. urugüensis	2*x*	40.56 ± 1.00	20.28 ± 0.05	37.20 ± 0.50	18.60 ± 0.25	0.17 ± 0.03[a]
M. bifurca var. *bifurca*	2*x*	31.82 ± 2.12	15.91 ± 1.06	20.94 ± 1.21	10.47 ± 0.60	0.21 ± 0.02[a]
M. uliginosa	2*x*	40.00 ± 2.03	20.00 ± 1.01	35.01 ± 2.37	17.50 ± 1.18	0.14 ± 0.03[a]
M. amphighen var. *trachycarpoides*	4*x*	59.52 ± 15.53	14.88 ± 7.76	37.87 ± 14.51	9.47 ± 3.63	0.26 ± 0.03[a]
M. cruent var. *cruenta*	4*x*	58.00 ± 6.61	14.50 ± 3.30	39.63 ± 6.61	9.91 ± 1.65	0.20 ± 0.08[a]
Sect. *Habbasia*						
M. pigra var. *pigra*	4*x*	56.49 ± 13.87	14,12 ± 6,93	37.38 ± 16.99	9.35 ± 8.49	0.25 ± 0.02[a]
M. pigra var. *dehiscens*	2*x*	29.11 ± 4.64	14.56 ± 2.32	20.24 ± 7.19	10.12 ± 3.59	0.19 ± 0.03[a]
M. somnians var. *somnians*	4*x*	50.58 ± 0.81	16.36 ± 0.40	21.14 ± 7.30	11.67 ± 5.83	0.21 ± 0.03[a]
Sect. *Mimosa*						
Ser. *Mimosa*						
Subser. *Polycarpae*						
M. polycarpa var. *spegazinii*	2*x*	24.06 ± 4.11	12.03 ± 2.06	12.84 ± 3.08	6.41 ± 1.54	0.22 ± 0.04[a]
M. balansae	2*x*	39.04 ± 0.69	19.52 ± 0.34	34.12 ± 5.75	17,06 ± 2.87	0.19 ± 0.05[a]
Subser. *Pedunculosae*						
M. pauperoides	6*x*	130.81 ± 23.15	21.80 ± 11.57	107.53 ± 21.67	17.92 ± 10.83	0.22 ± 0.01[a]
M. brevipetiolata var. *hirtula*	4*x*	46.56 ± 5.22	11.64 ± 1.31	28.48 ± 7.01	7.12 ± 1.75	0.19 ± 0.05[a]
Subser. *Pudicae*						
M. xanthocentra var. *subsericea*	2*x*	21.85 ± 3.85	10.93 ± 1.92	12.62 ± 4.8	6.31 ± 2.4	0.17 ± 0.05[a]
M. xanthocentra var. *mansii*	2*x*	33.06 ± 4.75	18.07 ± 2.37	21.85 ± 3.63	10.94 ± 1.81	0.18 ± 0.02[a]
M. xanthocentra aff. var. *mansii*	2*x*	21.80 ± 1.07	10.90 ± 0.53	16.35 ± 2.24	8.17 ± 1.12	0.18 ± 0.08[a]
M. velloziana var. *velloziana*	4*x*	58.14 ± 4.99	15.24 ± 2.94	33.54 ± 3.06	8.38 ± 1.53	0.17 ± 0.01[a]
M. sensibilis var. *sensibilis*	2*x*	30.98 ± 0.32	15.49 ± 0.16	18.16 ± 1.35	9.08 ± 0.67	0.17 ± 0.06[a]
Sect. *Calothamnos*						
M. urticaria	4*x*	53.82 ± 0.10	13.45 ± 0.02	28.88 ± 5.72	7.22 ± 1.43	0.23 ± 0.04[a]
M. scabrella	4*x*	59.36 ± 5.42	14.84 ± 1.35	29.51 ± 7.95	7.93 ± 1.20	0.29 ± 0.05[a]
M. pilulifera var. *pseudincana*	4*x*	43.27 ± 5.83	10.82 ± 1.46	21.28 ± 2.65	5.32 ± 0.66	0.22 ± 0.02[a]
M. bonplandii	4*x*	51.91 ± 6.78	12.98 ± 1.69	29.41 ± 5.86	7.35 ± 1.46	0.23 ± 0.03[a]
M. berroi	8*x*	112.29 ± 7.72	14.36 ± 0.97	59.12 ± 9.29	7.39 ± 1.16	0.24 ± 0.01[a]

* Different letters indicate statistically significant differences. Tukey's test ($\alpha = 0.05$)

second case, root tips were macerated in a drop of acetic acid solution (45 %). After, the slides were counterstained with 4′,6-diamidino-2-phenylindole (DAPI) (1 μg McIlvaine's citrate buffer/mL, pH 7) for 10 min at room temperature, and subsequently mounted in antifade solution. The slides were photographed with Leyca DMLB Photomicroscope and DFC350 FX digital camera.

Chromosome size and chromosome morphology

To analyze the chromosome morphology, at least five individuals in each taxon and more than ten mitotic cells by individual were studied. The selected cells were analyzed by means of the Micromeasure Program (Reeves 2001). Chromosome size was determined by measuring the total

Table 3 Chromosome size parameters in diploids and tetraploids; statistical differences by means of Kruskal–Wallis–multiple comparison hoc tests

Ploidy level	CLHG (μm)	CAHG (μm^2)
2*x*	18.78 ± 6.39[a]	11.96 ± 5.25[a]
4*x*	13.74 ± 2.16[b]	8.80 ± 3.34[b]

Table 4 Chromosome size parameters in different taxonomic groups of *Mimosa;* statistical differences by means of Kruskal–Wallis–multiple comparison hoc tests

Taxon	Ploidy level	CLHG (μm)	CAHG (μm^2)
Sect. *Batocaulon* Ser. *Stipellares*		$H = 6.61$, $p = 0.2498$	$H = 9.21$, $p = 0.0999$
M. bifurca var. *bifurca*	2*x*	15.91[a]	10.46[a]
M. uliginosa	2*x*	20.00[a]	17.50[b]
M. urugüensis	2*x*	20.28[a]	18.60[b]
M. amphigena var. *trachycarpoides*	4*x*	14.88[a]	9.47[a]
M. cruenta Benth. var. *cruenta*	4*x*	14.50[a]	9.91[a]
M. burkartii Marchesi	4*x*	15.71[a]	13.60[a,b]
Sect. *Habbasia* Ser. *Habbasia*		$H = 0.05$; $p > 0.99$	
M. pigra var. *dehiscens*	2*x*	14.56[a]	
M. pigra var. *pigra*	4*x*	14.12[a]	
Sect. *Mimosa* Ser. *Mimosa* Subser. *Pudicae* and *Pedunculosae*		$H = 6.41$; $p = 0.0365$	$H = 6.20$; $p = 0.0413$
M. brevipetiolata var. *hirtula*	4*x*	11.80 ± 1.80[a]	6.98 ± 2.46[b]
M. pauperoides	6*x*	21.80 ± 3.86[a]	17.92 ± 3.61[a]
M. pauperoides	4*x*	12.68 ± 0.01[a]	10.71 ± 0.01[b]
M. balansae	2*x*	19.28 ± 0.36[a]	16.51 ± 2.76[b]

chromosome length (TCL), chromosome length per haploid genome (CLHG), total chromosome area (TCA) and chromosome area per haploid genome (CAHG). The Interchromosomal Asymmetry Index (A_2) was calculated based on Romero-Zarco (1986), by means of the following formula:

$$A_2 = SX^{-1},$$

where S represents standard deviation and X the mean of chromosome length.

Statistical analyses

To know the variation of chromosome size between the ploidy levels and taxa, mean values of CLHG and CAHG were compared. The variables were evaluated by means of Shapiro-Wilks with modifications (Mahibbur and Govindarajulu 1997), in order to analyze if the variables were normally or no normally distributed. The variation between ploidy levels was studied including all taxa involved, while the variation between taxa was studied in some infraspecific or interespecific groups.

Since the variables of chromosome size were not normally distributed, the non-parametric Kruskal–Wallis test (Kruskal and Wallis 1952) was used to detect differences between groups. To know which groups differed significantly, the means were compared by means of the multiple comparison post-hoc test (Zar 2010).

In the case of A_2, the mean values were evaluated by means of the analysis of variance, in order to detect statistically significant differences between taxa. A Tukey's test was applied to analyze between which taxa the differences were significant. All the analyses of this work were performed by means of the Infostat program (Di Rienzo et al. 2009).

Results

Chromosome numbers

Chromosome numbers of 36 taxa were studied. The following 19 chromosome numbers are new reports (Tables 1, 2, 3, 4; Figs. 1, 2, 3): $2x = 26$ for *M. gracilis* subsp. *filiformis* var. *leiocarpa*, *M. bifurca* Benth. var. *bifurca, M. insignis* (Hassl.) Barneby, *M. glutinosa* Malme, *M. fiebrigii* Hassl., *M. monadelpha* Chodat & Hassl. var. *glabrata* (Hassl.) Barneby, *M. sensibilis* Griseb. var. *sensibilis, M. xanthocentra* Mart. aff. var. *mansii* (Benth.) Barneby; $4x = 52$ for *M. urticaria* Barneby, *M. bonplandii* Benth., *M. pilulifera* Benth. var. *pilulifera, M. pilulifera* var. *pseudoincana* (Burkart) Barneby, *M. cruenta* Benth. var. *cruenta, M. amphigena* Burkart var. *trachycarpoides* Burkart, *M. burkartii* Marchesi, *M. myriophylla* Bong. ex Benth.; *M. pauperoides* (Burkart) Fortunato; $6x = 78$, for *M. pauperoides;* and $8x = 104$, for *M. berroi* Burkart and *M. lepidorepens* Barneby.

Meiotic studies were performed on *M. somnians* var. *somnians, M. bimucronata* var. *bimucronata, M. insignis* and *M. gracilis* var. *leiocarpa.* In all cases, the meiosis was regular, with formation of bivalents (Fig. 1f–g; Table 1), and we did not observe bitetrads in this material. Polysomaty was observed in almost all studied species, with exception of *M. urugüensis.* This is a very common phenomenon in the majority of the species of this genus (Seijo 1993; Olkolski and Schifino Wittmann 2011).

The following chromosome numbers confirm previous reports (Table 1; Figs. 1, 2, 3): $2x = 26$ for *M. urugüensis*

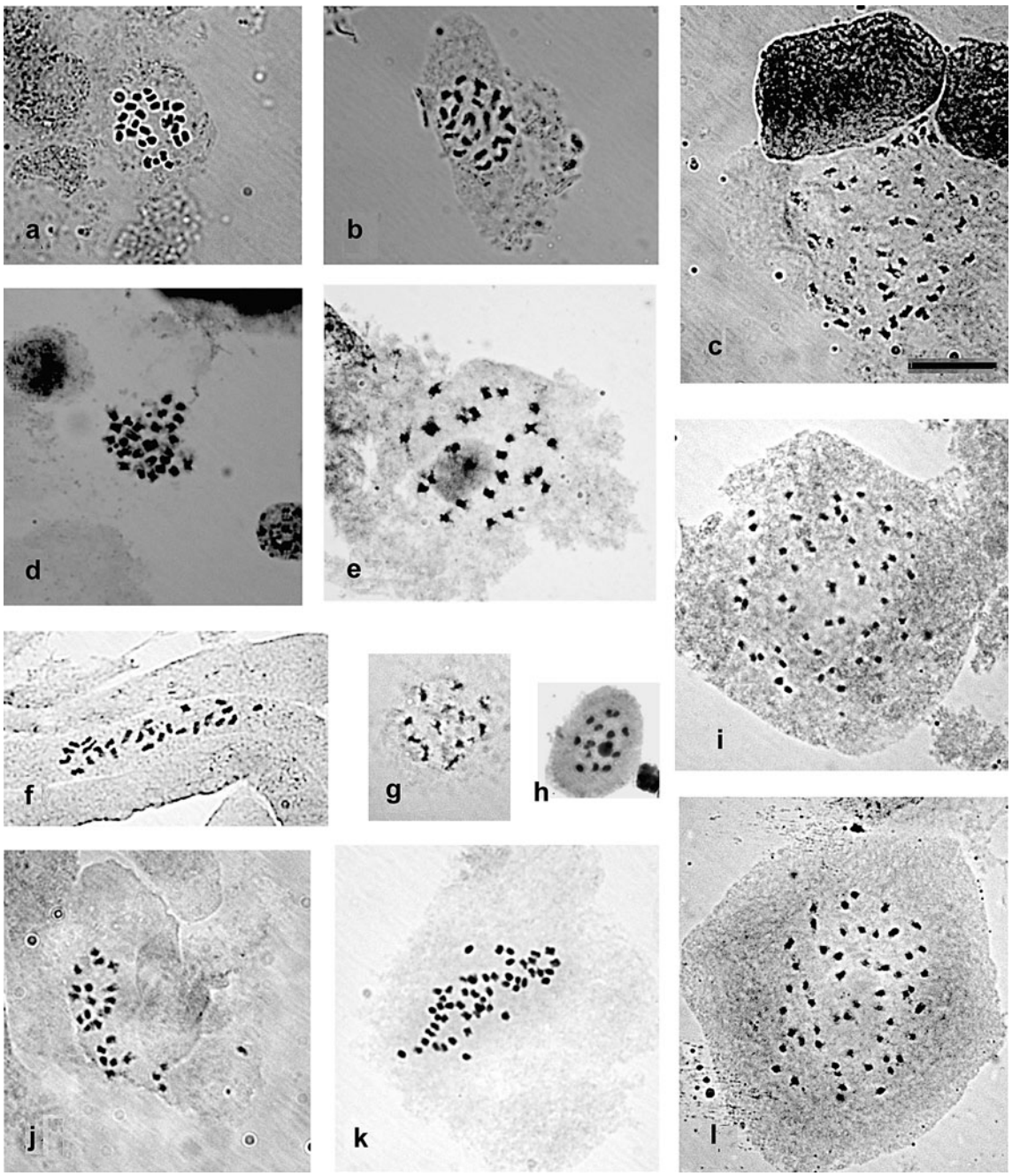

Fig. 1 Chromosome numbers of *Mimosa*: **a** *M. glutinosa,* $2x = 26$; **b** *M. fiebrigii,* $2x = 26$; **c** *M. burkartii,* $4x = 52$; **d** *M. bimucronata* var. *bimucronata,* $2x = 26$; **e** *M. uliginosa,* $2x = 26$. **f** *M. caesalpiniaefolia,* $2x = 26$; **g**, **h** *M. gracilis* subsp. *filiformis* var. *leiocarpa,* $x = 13$II; **g** Diplotene; **h** Diacinesis; **i** *M. cruenta* var. *cruenta,* $4x = 52$; **j** *M. pigra* var. *dehiscens,* $2x = 26$; **k** *M. somnians* var. *somnians,* $4x = 52$; **l** *M. amphigena* var. *trachycarpoides,* $4x = 52$. *Scale bar* 10 μm

Hook. & Arn., *M. uliginosa* Chodat & Hassl., *M. caesalpiniifolia* Benth., *M. somnians* Humb. & Bonpl. ex Willd. var. *somnians, M. pigra* L. var. *dehiscens, M. bimucronata* (DC.) Kuntze var. *bimucronata, M. polycarpa* Kunth var. *spegazzinii* (Pirotta ex Hook.) Burkart, *M. xanthocentra* var. *mansii, M. xanthocentra* var. *subsericea* (Benth.) Barneby, *M. balansae* M. Micheli; $4x = 52$ for *M. scabrella* Benth., *M. furfuracea* Benth., *M. somnians* var. *somnians, M. adpressa, and M. brevipetiolata* Burkart var. *hirtula* (Burkart) Barneby; $8x = 104$, for *M. daleoides* Benth. and *M. rocae* Lorentz & Nied.

In the section *Batocaulon,* members of the series *Bimucronatae* Barneby, *Paucifoliatae* Benth., *Caesalpiniifoliae* Benth. and *Stipellares* Benth, were studied. These taxa are generally diploid; only some species of Ser. *Stipellares,* such as *M. cruenta, M. amphigena* and *M. burkartii,* were

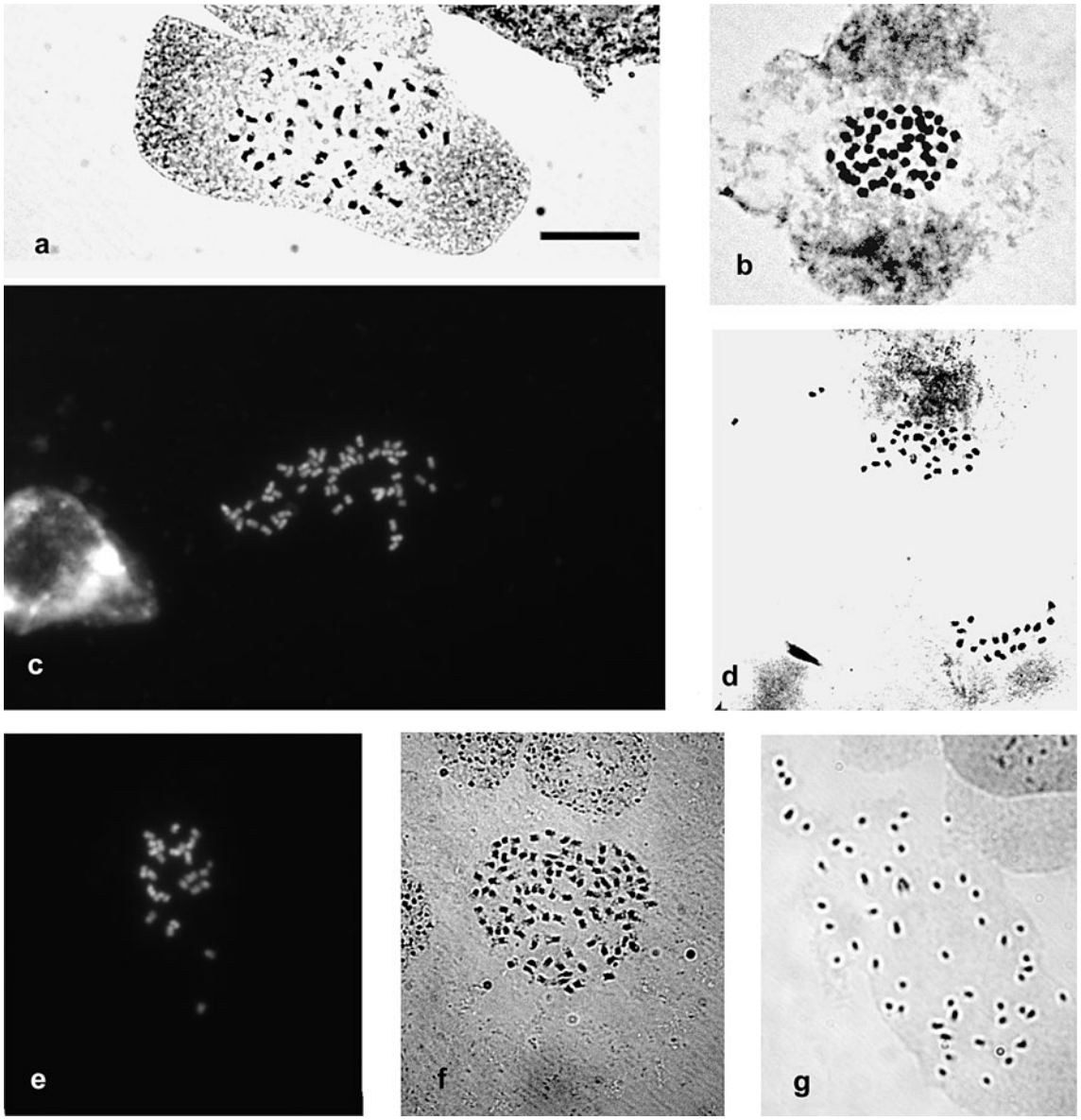

Fig. 2 Chromosome numbers of *Mimosa*. **a** *M. pigra* var. *pigra,* $4x = 52$; **b** *M. myriophylla,* $4x = 52$; **c** *M. velloziana* var. *velloziana,* $4x = 52$; **d** *M. pauperoides,* $4x = 52$; **e** *M. sensibilis* var. *sensibilis,* $2x = 26$; **f** *M. berroi,* $8x = 104$; **g** *M. bonplandii,* $4x = 52$. *Scale bar* 10 μm

tetraploids (Fig. 1a–i, l). In Sect. *Habbasia,* two taxa were studied, *M. pigra* var. *pigra* (from Ser. *Habbasia*) and *M. somnians* var. *somnians* (from Ser. *Bipinnatae* DC.). Both exhibited two ploidy levels, $2x$ and $4x$. (Figs. 1j–k, 2a).

In the section *Mimosa*, different ploidy levels were found: taxa with $2x = 26$, $4x = 52$ and $6x = 78$. In the present work, several taxa were studied from Ser. *Myriophyllae*: *M. myriophylla,* $4x = 52$, and Ser. *Mimosa* Subseries *Polycarpae* Barneby, *Pudicae* (Benth.) Barneby, *Pedunculosae* (Benth.) Barneby, *Hirsutae* (Benth.) Barneby, and *Mimosa.* The members studied of subseries *Polycarpae, Pudicae* and *Hirsutae* were diploids, while members of *Pedunculosae* exhibited two ploidy levels, $4x$ and $6x$. In Subser. *Mimosa,* two ploidy levels were found, $2x$ and $4x$. Finally, in Sect. *Calothamnos,* all the species were polyploids, tetraploid and octaploid (Figs. 2, 3; Table 1).

Chromosome size

The TCL showed values between 21.80 μm in individuals from *M. xanthocentra* complex, to 130.81 μm, in *M. pauperoides,* while CLHG varied from 10.90 μm in individuals from the "*M. xanthocentra"* complex to 20.97 μm in *M. bimucronata* var. *bimucronata* and 21.80 in *M. pauperoides*. The TCA ranged from 12.62 μ in *M.*

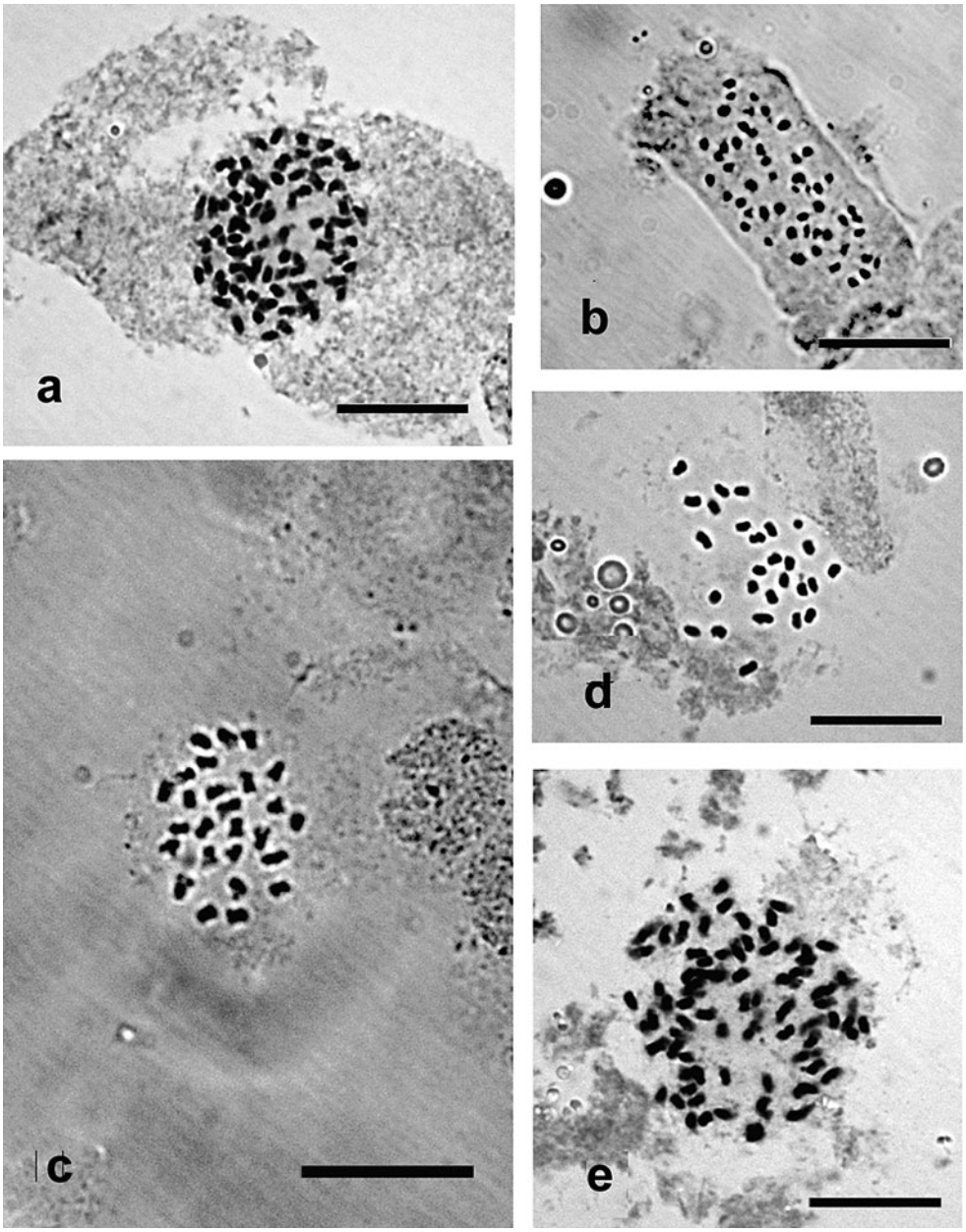

Fig. 3 Chromosome numbers of *Mimosa.* **a** *M. pauperoides,* $6x = 78$; **b** *M. brevipetiolata* var. *hirtula,* $4x = 52$;**c** *M. monadelpha,* $2x = 26$; **d** *M. balansae,* $2x = 26$; **e** *M. pauperoides,* $6x = 78$. *Scale bar* 10 μm

xanthocentra var. *subsericea* to 107.53 μm in *M. pauperoides.* In the case of CAHG, the values ranged from 5.32 μm in *M. pilulifera* var. *pseudoincana* to 18.60 μm in *M. urugüensis* (Table 2; Fig. 4).

Chromosome parameters

The Shapiro–Wilks test showed that the variables of chromosome size, CLHG and CAHG did not show a normal distribution ($W = 0.94$; $p = 0.0130$), although Levene's test showed that variances were relatively homogeneous. For this reason, these variables were analyzed by means of the Kruskal–Wallis non-parametric test (Tables 3, 4).

The study of variation of chromosome size according to the ploidy levels included all species which was possible to obtain an adequate number of good metaphases. The results of univariate analyses showed that tetraploids have significant differences with the diploids; the octaploids and hexaploids have been not included because they comprised very few samples (Table 3).

Statistical analyses to evaluate the mean values of CLHG and CAHG between taxa were performed in three groups: *M. pigra,* Sect. *Batocaulon* Ser. *Stipellares,* and

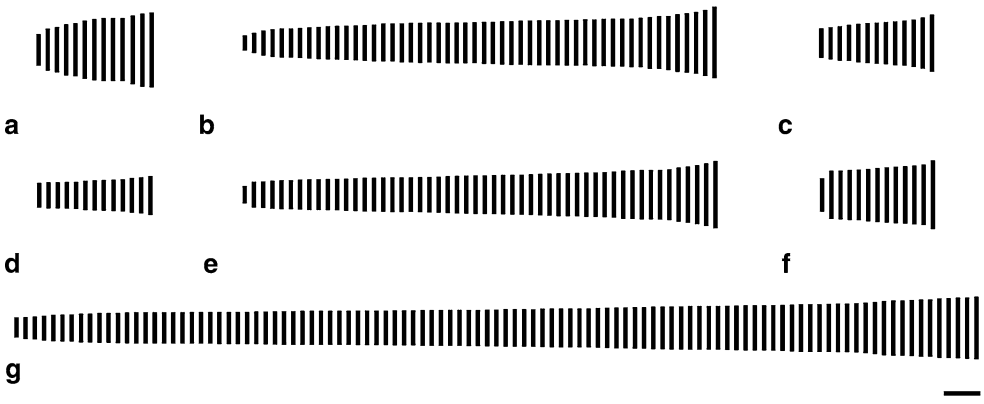

Fig. 4 Karyograms of *Mimosa* species. **a** *M. glutinosa,* $2x = 26$; **b** *M. amphigena* var. *trachycarpoides,* $4x = 52$; **c** *M. xanthocentra* var. *mansii,* $2x = 26$; **d** *M. pigra* var. *dehiscens,* $2x = 26$; **e** *M. pigra* var. *pigra,* $4x = 52$; **f** *M. balansae,* $2x = 26$; **g** *M. berroi,* $8x = 104$. Haploid complement of diploids and entire set of polyploids. *Scale bar* 1 μm

Sect. *Mimosa* Ser. *Mimosa* Subser. *Pudicae-Pedunculosae* complex. The Kruskal–Wallis test and multiple comparison post-hoc test showed not significant differences between taxa in *M. pigra*. However, Ser. *Stipellares* and the Subseries *Pudicae-Pedunculosae* complex showed significant differences between taxa (Table 4).

The index A_2 exhibited a normal distribution (Shapiro Wilks test: $W = 0.97$; $p = 0.4475$) and for this reason ANOVA, and Tukey's test, were applied. The results did not show significant differences between taxa, and values ranged from 0.14 in *M. uliginosa* to 0.29 in *M. scabrella* (Table 2). In consequence, the karyotype of the species studied is relatively symmetric, as well it is possible to observe in representative karyograms of diploid, tetraploid and octaploid taxa (Fig. 4).

Discussion

The results support $x = 13$ as the basic chromosome number of the genus *Mimosa,* as was postulated by Isely (1971) and confirmed by several authors (Elias 1974; Coleman and DeMenezes 1980; Goldblatt 1981; Alves and de Carvalho Custódio 1983; Seijo 1993, 1999, 2000; Seijo and Fernández 2001; Morales 2011; Morales et al. 2010, 2011, 2012; Dahmer et al. 2011; Olkolski and Schifino Wittmann 2011). In this paper, it was found a high percentage of polyploid taxa (ca. 56 % of the studied species). This amount differs notably from previous works: for example, Dahmer et al. (2011) reported 26 % of polyploid taxa in its studies, and it was estimated that ca. 22 % of all studied species of the genus exhibit polyploidy (Elias 1974; Coleman and DeMenezes 1980; Goldblatt 1981; Seijo 1993, 1999, 2000; Seijo and Fernández 2001; Morales 2011; Morales et al. 2010, 2011, 2012; Dahmer et al. 2011; Dahmer et al. 2013).

M. pudica L. (Nazeer and Madhusoodanan 1982), *M. campicola* Harms (Santos et al. 2012), and *M. pauperoides* have $6x$ (Table 1), and this ploidy level was not found in other mimosas. It is interesting that *M. pauperoides* and *M. campicola* exhibit also the tetraploid cytotype. Hexaploid mimosas are not frequent, and we think that it is because effective reproductive isolation between diploid and related tetraploid diploid taxa exists.

With regard to chromosome size, the species studied have generally chromosomes smaller than 2 μm in length, similarly to other groups of Mimosoids, such as *Pithecellobium* Mart., *Acacia* Mill. and *Prosopis* L. (Gómez-Acevedo and Tapia-Pastrana 2003; Tapia-Pastrana and Gómez–Acevedo 2005). In general terms, the species studied of section *Batocaulon* appear to have the largest chromosomes, while those of Sect. *Mimosa* and *Calothamnos* have the smallest chromosomes.

The asymmetry index A_2 and karyograms show an apparent uniformity in the chromosome size into the same set of chromosomes (Fig. 4). There are not statistically significant differences between taxa, and the results coincide with other studies from our group (Morales 2011; Morales et al. 2011). It is very common in *Mimosa* that, when the karyotype is visualized, there is a tenuously gradual decrease in the chromosome length, from the largest to the smallest chromosome pair (Morales 2011; Morales et al. 2011). The presence of few differences in the length of chromosomes within the haploid complement could be characteristic of the genus.

It is interesting that Sect. *Batocaulon* Ser. *Stipellares* was the one that showed taxa with two ploidy levels. Diploid *M. urugüensis* comprises large shrubs or treelets restricted to the Uruguay River Basin, while the tetraploid *M. cruenta* var. *cruenta, M. burkartii* and *M. amphigena* var. *trachycarpoides* are generally small subshrubs from temperate, rocky savannas of Argentina and Uruguay (Fig. 5a). *M. urugüensis* is morphologically close to the tetraploid entities (Barneby 1991) and it could be involved in the origin of these taxa. The differences in chromosome size between diploid and tetraploid taxa show significant differences, and it could be interesting to the cytotaxonomy and evolution of the group.

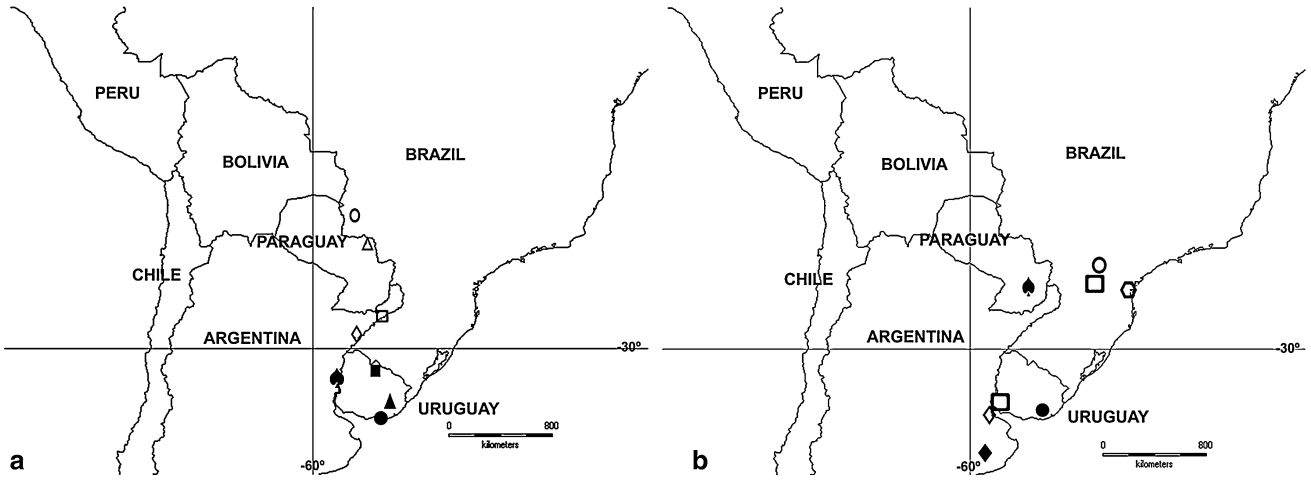

Fig. 5 **a** Voucher's localities of species of the Sect. *Batocaulon* Ser. *Stipellares. Open circle*: *M. glutinosa. Open triangle*: *M. insignis. Open diamond*: *M. bifurca* var. *bifurca. Open square*: *M. uliginosa. Filled triangle*: *M. cruenta* var. *cruenta. Filled square*: *M. amphigena* var. *trachycarpoides. Filled circle*: *M. burkartii. Filled heartin*: *M. urugüensis;* **b** Voucher's localities of species of the Sect. *Calothamnos. Open circle: M. lepidorepens* and *M. scabrella. Open square: M. pilulifera. Open diamond: M. bonplandii. Filled circle: M. berroi. Filled diamond M. rocae. Filled heartin: M. daleoides*

In Sect. *Habbasia* Ser. *Bipinnatae,* the accessions studied of *M. somnians* var. *somnians* confirm that the Argentinean populations of this taxon are diploid and the Paraguayan populations are tetraploid. Study of several specimens did not find obvious morphological differences between the diploid and tetraploid individuals, and it would support the hypothesis of the presence of cryptic species in this complex, as previously observed in *M. debilis* Humb. & Bonpl. ex Willd. (Morales et al. 2010).

In *M. pigra* (Sect. *Habbasia* ser. *Habbasia*), our reports here as well as previous works (Seijo 1999; Dahmer et al. 2011), suggest that the var. *dehiscens* is diploid while the var. *pigra* is tetraploid. It is interesting that polyploid *M. pigra* var. *pigra* has adaptations for floating and hydrochore dispersal, and is found along river banks of the Paraná–Río de la Plata Basin, while *M. pigra* var. *dehiscens* does not have this adaptation and occurs generally in inner lowlands (Barneby 1991; Ulibarri et al. 2002; Morales 2011). Although previous authors did not find a clear distribution pattern of the cytotypes studying tropical accessions of this species (Dahmer et al. 2011), we can visualize a distinct ecological and geographical pattern between diploid and polyploid accessions in southernmost area of distribution of *M. pigra.* On the other hand, according to our field observations, no intermediate individuals between the varieties were found in the areas where both grow in sympatry; in addition, no triploid individuals were found. These data are evidences of a possible reproductive isolation between both taxa, but more intensive studies in the areas of sympatry will be needed to confirm these observations.

In Sect. *Mimosa* Ser. *Mimosa* Subser. *Pudicae*, *M. balansae* is morphologically close to members of Subser. *Pedunculosae,* especially *M. brevipetiolata* var. *hirtula* and *M. pauperoides.* There was controversy in the past about the identity of these (Fortunato 1989; Barneby 1991). *M. pauperoides* exhibits intermediate characters between *M. brevipetiolata* var. *hirtula* and *M. balansae;* in our study, we observed that the three taxa grow in sympatry in northeastern Argentina. According to our field and herbarium observations, the morphology supports the hypothesis that tetraploid and hexaploid individuals of *M. pauperoides* are allopolyploids, originating by hybridization between diploid *M. balansae* and tetraploid *M. brevipetiolata* and later polyploidization.

M. xanthocentra is a species with high morphological variation and extensively disseminated in Southern South America (especially in Southern Brazil, Paraguay, Bolivia and Northeastern Argentina) which forms a taxonomic complex. Barneby (1991) proposed several infraspecific taxa: three subspecies *subsericea, mansii,* and *xanthocentra,* and several varieties. Here, we described the chromosome number and size of individuals of subspecies *mansii* and *subsericea,* as well as one accession with intermediate morphology between them. All the studied individuals were diploid, and it is in concordance with previous reports in the subsp. *subsericea* (Seijo 2000). The presence of intermediate forms between the subspecies could suggest the presence of hybridization between diploid taxa.

All species of Sect. *Calothamnos* studied here are polyploids—tetraploids and octaploids—and these results are in concordance with previous studies (Seijo 1999; Seijo and Fernández 2001; Dahmer et al. 2011). It is interesting that the taxa of this section are generally well circumscribed in their morphology and geographic distribution.

The majority of these are endemic or highly restricted, especially in warm temperate or subtropical areas of southern South America (Fig. 5b), and their origin remains unclear: the main distinctive characters of some species of this section, such as yellow corollas and staminodia, are not frequently found in *Mimosa* (Burkart 1948; Barneby 1991). All these taxa coincided that they have not obvious ancestors, when molecular or morphology is analyzed. This fact and the high morphological and ecological specialization of the group (all are adapted to subtropical, warm temperate or tropical highland grasslands) could suggest that they are a group of paleopolyploid taxa, whose diploid ancestors are extinct.

Bessega and Fortunato (2011) and Simon et al. (2011) found that Sect. *Batocaulon* Ser. *Farinosae* and *Bimucronatae* constitute the most basal clade in southern South America. Their members are diploid, according to Seijo (1999), Dahmer et al. (2011), Morales et al. (2011), and the present study (Table 1). In taxa from other more derived clades, such as Sect. *Batocaulon* Ser. *Stipellares* (Table 1) and *M. pigra* (Seijo 1999; Dahmer et al. 2011) (Sect. *Habbasia* Ser. *Habbasia*), it is possible to observe different ploidy levels and polyploid taxa. Finally, the members of some most derived clades, which group together members of sections *Mimosa* and *Calothamnos,* are polyploids or have different ploidy levels. The presence of several ploidy levels in different clades suggests that several independent events of polyploidization are involved, as well was postulated previously (Morales 2011; Dahmer et al. 2011).

It is mentioned that the frequency of polyploids and the ploidy levels increase with the latitude (Stebbins 1971). Seijo and Fernández (2001) hypothesized that it could be the case of *Mimosa.* In their study that comprised species from Argentina and Uruguay, they found that the species or individuals located in the southernmost area of distribution were polyploids, while the proportion of diploids was increased at lower latitudes. In the present work, we observed that the groups growing in the southernmost area of distribution of the genus are mainly polyploids. For example: *M. pigra, M. bonplandii, M. pilulifera* (tetraploid species, in the Río de la Plata Basin, 34°S); *M. burkartii* (octaploid, Uruguay grasslands, 34°S) and *M. rocae* (octaploid, Buenos Aires rocky grasslands, 38°S) (Fig. 5). It explains the comparatively high percentage of polyploids that we found, which differs from 22 % of polyploids in all species studied previously (Dahmer et al. 2011). In spite of the clear distribution pattern in many groups of *Mimosa,* where polyploids generally occur at high latitudes (Seijo and Fernández 2001; Morales et al. 2010; Dahmer et al. 2011), a detailed geographic and cytologic study is still needed to give more solid evidence to this hypothesis.

Another interesting topic is the variation in chromosome size, which appears to be generally correlated with the genome size (Ouzu et al. 1997). In *Mimosa,* chromosome size is variable between related taxa, and, in some groups, there are significant differences between polyploids and their related diploids, such as in Sect. *Batocaulon* Ser. *Stipellares*. The general trend in the studied species of the genus appears to be that tetraploids have uniformly small chromosomes, although the decrease in the chromosome size with the ploidy level is not consistent in all the infraspecific groups: in *M. pigra* there were no differences found between cytotypes, and polyploid *M. pauperoides,* with $2n = 6x = 78$ (Fig. 5a, e) and tetraploid *M. quadrivalvis* var. *leptocarpa,* with $2n = 4x = 52$ (Santos et al. 2012) appeared with large chromosomes. The variation in chromosome size is more visible in the analysis of mean values, since statistically significant differences appear between the diploids and tetraploids (Table 3). It is not possible to infer a trend in the octaploid and hexaploid taxa, since few of these polyploids were found in *Mimosa.*

Among the diploid taxa studied here, the variation in chromosome size, especially in CLHG, is higher than in polyploid taxa, and it is more visible when previous results are also compared (Morales et al. 2011). The variation in the diploid entities could be associated with environmental conditions, as was observed previously in other South American mimosas (Morales et al. 2011), and in other Mimosoids, as *Acacia* and *Prosopis* (Gómez-Acevedo and Tapia-Pastrana 2003).

On the other hand, it has been frequently documented that the major trend in the vascular plants is a decrease in the genome size (per haploid genome), when a polyploidization event occurs (Leitch et al. 2008), and it appears to be the case in the genus *Mimosa.* Except for the hexaploid *M. pauperoides,* the remainder of the polyploid taxa studied in this work shows a relatively small chromosome size.

It is possible to find many cases in the literature, where polyploidy is associated with a decreasing genome size, in terms of DNA content per haploid genome (Soltis et al. 2003; Kellogg and Bennetzen 2004). Several authors postulated that these changes could be involved in the genetic and cytogenetic diploidization of polyploids. It is interesting to observe that, in other taxonomical groups, the polyploidy appears to generate non-random deleting of coding and non-coding sequences, activation of genes and retroelements, and chromosome reorganization, gain or loss of chromosomes or entire genomes (Ma and Gustafson 2006; Feldman and Levy 2005).

Notably, *Mimosa* is a Neotropical genus with high diversification, and polyploidy is an important evolutionary mechanism; it was confirmed by us and all previous studies in cytogenetics of *Mimosa* (Seijo 1993, 1999; Seijo and Fernández 2001; Dahmer et al. 2011). In general terms, it is possible to visualize a reduction of the chromosome size, and possibly of the genome size, when polyploidy occurs,

but it is not observed in all groups studied. On the other hand, hybridization between diploid and polyploid individuals may occur in some groups. In this work, we found some evidences of allopolyploidy; polyploids of different origin are highly possible in *Mimosa*, since our recent reports suggest autopolyploidy in *M. debilis* (Morales et al. 2010) or *M. diversipila* M. Micheli (Morales et al. 2013). The elucidation of the origin of polyploids seems to be very important to resolve the taxonomy (Soltis et al. 2007). All these evolutionary mechanisms could be associated with different environmental adaptations and could contribute to produce the high morphological variability that can be observed in the majority of Neotropical mimosas.

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