Karyotype studies in *Mimosa* (Mimosoideae, Leguminosae) from Southern South America and ecological and taxonomic relationships

**MORALES MATÍAS**\(^1,2\)*, **ARTURO F. WULFF**\(^2,4\), **RENÉE H. FORTUNATO**\(^1,2,3\) and **LIDIA POGGIO**\(^2,4\)

\(^1\)Facultad de Agronomía y Ciencias Agroalimentarias, Universidad de Morón: Cabildo 134, (B1708JPD), Morón, Argentina.
\(^2\)CONICET (Argentina).
\(^3\)Instituto de Recursos Biológicos, CIRN-INTA (Hurlingham, Argentina), Las Cabañas y Los Reseros s/n (1686), Hurlingham, Argentina.
\(^4\)Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Intendente Güiraldes y Costanera Norte (CI42EHA), Buenos Aires, Argentina.

**Abstract** — In this work we studied the chromosome number and karyotype formula of seven species of *Mimosa* L. (Mimosoidea, Leguminosae). The chromosome number \(2n = 2x = 26\) for *M. detinens* Benth., *M. hexandra* M. Micheli, *M. ostenii* Speg. ex Burkart and *M. xanthocentra* Mart. var. *mansii* (Benth.) Barneby are new records, while the chromosome number \(2n = 2x = 26\) for *M. debilis* var. *debilis*, *M. urugüensis* Hook. and Arn. and *M. uliginosa* Chodat and Hasl. confirm previous records. Karyotype formulae revealed the existence of metacentric and submetacentric chromosomes, and the chromosomal asymmetry indexes did not show significant differences between taxa. The chromosome length of xerophilous and endemic *M. detinens* and *M. ostenii* differed from the rest of species, indicating that this parameter could have taxonomic value. In addition, the relationship between total chromosome length and climatic parameters showed that diploid species of marginal areas of distribution have a larger chromosome size, and that this could be related with mechanisms of ecological adaptation.

**Key words**: Chromosome, Cytogenetics, Karyotype, Leguminosae, Mimosa, Mimosoideae.

**INTRODUCTION**

*Taxonomy, distribution and phylogeny of the genus* - The genus *Mimosa* L. comprises ca. 540 species of pantropical and pantropical distribution (SIMON et al. 2011). This genus has two centers of diversification: 1) central and southern Mexico, Cuba, Hispaniola and Orinoco basin and Madagascar, and 2) southern South America, which includes Amazonas basin, Brazilian Planalto, Paraguay, Northern Argentina and Uruguay (BARNEBY 1991).

In southern South America, *Mimosa* is highly diversified in *campos* and *cerrados* from the Brazilian Planalto. In Argentina, this genus is particularly abundant in northeastern and northwestern extremes, where 85-90% of the species grow. Some taxa extend or are restricted to the southernmost regions of distribution of the genus, where the temperature is lower and frosts are more frequent (BURKART 1948; FORTUNATO et al. 2008). A similar situation is observed in North America, where only a few species are found in the temperate areas of the United States (BARNEBY 1991).

BENTHAM (1876) realized the first monograph on this genus and recognized two sections: *Habbbasia* DC. and *Eumimosa*. Later, BARNEBY (1991) revised the neotropical species and proposed five sections: *Mimadenia* (with diplostemonous flowers and extrafloral nectaries), *Batocaulon* DC. (=diplostemonous flowers, within extrafloral nectaries), *Habbbasia* DC. (=diplostemonous flowers, extrafloral nectaries absent, indumen-
Cytological studies - The cytology of this genus is poorly studied. The chromosome number and ploidy levels are known in only 20% of its species. Most studies have been carried out in Southern South America. The most cited chromosome numbers are $2n=2x=26$ and $2n=4x=52$, but also $2n=3x=39$, $2n=6x=78$ and $2n=8x=104$ have been found (Coleman and DeMenezes 1980; Goldblatt 1981a; Alves and Carvalho-Custódio 1983; Goldblatt 1984, 1988; Goldblatt and Johnson 1998; Seijo 1993, 1999; Seijo and Fernández 2001; Dahmer et al. 2011).

Isely (1971) postulated that the basic chromosome number is $x=13$, which was confirmed by other authors (Goldblatt 1981a; Seijo 1993, 1999, 2000; Seijo and Fernández 2001). However, it is important to point out that, in Mimosoids, $x=13$ is considered a chromosome number derived by disyndonty from $x=14$ (Poggio et al. 2008).

In Mimosa, polyploidy is a frequent phenomenon, because ca. 22% of the species studied have high levels of ploidy, i.e. $4x$, $6x$ or $8x$ (Goldblatt 1981, 1984, 1985, 1988; Goldblatt and Johnson 1990, 1998; Seijo 1993, 1999; Goldblatt and Johnson 2000; Seijo 2000; Seijo and Fernández 2001; Goldblatt and Johnson 2003, 2006; Morales et al. 2007; Dahmer et al. 2011). In some groups of this genus, polyploidy would be an important mode of speciation, as discussed in M. debilis Humb. and Bonpl. ex Willd. complex (Morales et al. 2010). In the southernmost species, polyploidy appears to be a mechanism to colonize new habitats (Seijo and Fernández 2001). However, entire role of polyploidy in the evolution and geographic distribution of Mimosa requires a study of more chromosome counts from a wide range of species and accessions, especially from higher latitudes (Dahmer et al. 2011).

Like in other Mimosoids, chromosomes of Mimosa are very small, and it is difficult to obtain cells adequate for karyological studies (Stebbins 1971; Seijo 1993; Shukor et al. 1994). This is one of the reasons that explain the absence of karyotype studies in this genus. Thus, the aim of this work was to study karyotypical parameters in different species of Mimosa from Southern South America that were included in the sections Batoaulon and Mimosa. We discussed the data obtained based on the systematic position and geographic distribution of the taxa.

MATERIAL AND METHODS

Plant material - We collected vouchers in Argentina and Paraguay during field trips carried out from 2005 until 2008. We deposited the specimens at the Instituto de Recursos Biológicos, CIRN-INTA, Buenos Aires, Argentina (BAB) and Facultad de Ciencias Químicas, Universidad de Asunción, Paraguay (FCQ), with duplicates in Instituto de Botánica Darwinion (SI) and Instituto de Botánica del Nordeste (CTES) (Table 1).

We determined the specimens according to the proposals of Barneby (1991), and recent contributions of Fortunato et al. (2008) and Morales and Fortunato (2010). The geographic distribution of the taxa was inferred from taxonomic bibliography (Barneby 1991), observations during field trips, and records of herbarium specimens from the following institutions: BA, BAA, BAF, BAB, CGMS, CORD, CPAP, CTES, FCQ, G, ICN, LIL, LPB, MBM, MO, NY, RB, SI, SP, SPF (see Appendix). We mentioned Ecoregions following Olson et al. (2001). Instituto de Clima y Agua, CIRN-INTA (Hurlingham, Argentina), provided us with climatic data from the localities or closest locality where the specimens were collected.

Chromosome studies - Seeds were simultaneously collected with plant material during the field trips. For the mitotic studies, were used root meristems obtained from seeds germinated on Petri dishes at room temperature. Root tips (1-2 cm) were pretreated with 8-hydroxyquinoline 0.002 M at room temperature for 4-5 h and then fixed in absolute 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 pH 4.6 and then transferred to an enzymatic solution containing 2 ml cellulase 2% (Ozonuka R-10) and 20% liquid pectinase for 120-150' at 37°C, and washed again with buffer solution.

The root tips obtained were macerated in
a drop of dye (acetic hematoxylin), and the “squash” technique was applied. In each sample, we counted 10-20 metaphases and conserved the slides with Euparal as a mounting medium.

Karyotypical studies - To analyze karyotype formulae, karyotypical parameters (total chromosome length (TCL) and asymmetry indexes), and the corresponding idiograms, we selected the best mitotic metaphases that showed similar chromosome condensation (5-10 cells per individual, and 2-4 individuals in each taxon). We used the chromosome nomenclature according to LEVAN et al. (1964): “m” for metacentric and “sm” for submetacentric chromosomes. TCL was measured with Micromeasure Program (REEVES 2004). Intra- and interchromosomal asymmetry indexes, A1 and A2, were calculated, according to ROMERO ZARCO (1986). To calculate these indexes, we used the following formulae:

\[
A1 = 1 - \frac{\sum qi}{pi} \frac{n}{n}
\]

where qi represents the mean length of the short arm, pi the mean length of the long arm in each pair of homologous chromosomes, and n the number of pairs or groups of homeologous chromosomes, and

\[
A2 = SX^{-1}
\]

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

We tested the differences in karyotypical parameters with KRUSKAL-WALLIS’S method (1952) and carried out comparisons of pairs among mean values of ranges. Mean values and standard deviation were calculated for each parameter. The statistical analysis was carried out with Infostat program (DI RIENZO et al. 2009).

RESULTS

Chromosome numbers - All the taxa studied were diploid, with 2n=2x=26 (Table 1; Fig. 1 A-G). Chromosome numbers of M. detinens Benth., M. ostenii Speg. ex Burkart and M. xanthocentra var. mansii were first records, while those of M. hexandra M. Micheli, M. debilis var. debilis, M. uliginosa Chodat and Hassl. and M. urugüensis Hook. and Arn. confirmed previous reports.

Karyotype formula - The study of chromosome morphology showed that M. detinens, M. ostenii, M. uliginosa had ca. 7-8 metacentric and the rest submetacentric or metacentric-submetacentric. Instead, M. hexandra, M. urugüensis, M. debilis var. debilis and M. xanthocentra var. mansii presented 10-11 metacentric and 1-2 submetacentric or metacentric-submetacentric chromosomes (Table 2; Fig. 2 A-G).

Karyotype parameters - Regarding the A1 index, variations detected in the karyotype formula showed differences between species of Ser. Farinosae, which had a higher number of submetacentric chromosomes, and M. hexandra, M. xanthocentra, M. urugüensis and M. debilis var. debilis, which had a higher proportion of metacentric chromosomes. The A2 asymmetry index revealed that the chromosome size did not vary notably within each taxon but varied significantly between the studied taxa.

TCL showed significant differences only at p=0.05, and we observed that the species of M.

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Table 1 — Vouchers, localities and chromosome numbers of Mimosa species from Southern South America.

| Taxon                    | Voucher                      | Locality    | Previous records |
|--------------------------|------------------------------|-------------|------------------|
| M. detinens Benth.       | R. H. Fortunato et al. 9453 (BAB) | ARG. Córdoba. | *                |
| M. ostenii Burkart       | M. Morales et al. 617 (BAB)   | ARG. Entre Ríos. | *                |
| M. uliginosa Chod. & Hassl. | R. H. Fortunato et al. 9010 (BAB) | ARG. Corrientes. | Seijo, 1993    |
| M. urugüensis Hook. & Arn. | Prüner s.n. (BAB 92350) | ARG. Entre Ríos. | Seijo, 1993    |
| M. hexandra M. Micheli   | F. Mereles & R. Degen 6023 (MO 5303427) | PAR. Presidente Hayes. | *                |
|                          | R. H. Fortunato et al. 9176 (BAB) | PAR. Central. | *                |
| M. debilis Humb. & Bonpl. ex Willd. var. debilis | R. H. Fortunato et al. 7298 (BAB) | ARG. Salta. | Seijo, 2000 |
| M. xanthocentra Mart. var. mansii (Benth.) Barneby | R. H. Fortunato et al. 9180 (BAB) | PAR. Central. | *                |
|                          | R. H. Fortunato et al. 9200 (BAB) | PAR. San. Pedro. | *                |

* indicates first chromosome countings. All species showed the chromosome number 2x=26.
Sect. *Batocaulon* Ser. *Farinosae* analyzed (*M. detinens* and *M. ostenii*) had larger chromosomes and differed significantly from *M. xanthocentra*, *M. hexandra*, and *M. debilis* var. *debilis*. *M. urugüensis*, *F. M. xanthocentra var. mansii*. *G. M. uliginosa*.

**DISCUSSION**

Chromosome numbers of *M. detinens*, *M. ostenii* and *M. xanthocentra var. mansii* are first records, while those of *M. hexandra*, *M. debilis* var. *debilis*, *M. urugüensis* and *M. uliginosa* confirm previous records (Seijo 1993; Seijo 1999; Morales et al. 2010; Dahmer et al. 2011). The studies confirm $x = 13$ as the basic chromosome number of the genus (Isely 1971; Goldblatt 1981b). It is remarkable that various morphological groups with different cytotypes (2x and 4x) have been previously recorded in *M. debilis* var. *debilis* (Morales et al. 2010). The individuals studied in this work belong in morphology and geographic distribution to *M. debilis* var. *debilis sensu stricto*, and, in concordance with previous studies, had $2n = 2x = 26$.

The visualization of chromosome constrictions constitutes a problem to carry out karyo-
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...type studies in Mimosoids (José G. Seijo, pers. comm.; Shukor et al. 1994; Morales et al. 2010), but the technique used in the present work allowed us to observe the chromosome morphology in most of the species. Our results indicate that the karyotype of the species of Mimosa studied is relatively symmetric, with metacentric and submetacentric chromosomes. This is reflected in the low asymmetric index \(A_1\) of all the species. Thus, the studied species of Mimosa have a karyotype similar to that of other Mimosoids, such as Pithecellobium Mart., Acacia Mill., and Prosopis L., where other authors also found a high proportion of metacentric and submetacentric chromosome pairs (Gómez Acevedo and Tapia Pastrana 2003; 2005).

The \(A_2\) asymmetry index was relatively low and did not show differences among taxa. Our studies about chromosome size showed that the chromosomes of Mimosa are small, generally smaller than 2 µm, in agreement with that found in other genera of Mimosoids (Seijo 1993; Sukor et al. 1994; Seijo 1999, 2000; Seijo and Fernández 2001). We found significant differences among the taxa studied. The species of Ser. Farinosae (M. detinens and M. ostentii) had larger chromosome size. Although the number of species studied is low, it is interesting to observe

Different letters indicate significant differences, applying Kruskal Wallis test: *p = 0.01; **p = 0.05. TCL = Total Chromosome Length.
that the species with larger chromosome length also showed a karyotype with lowest metacentric: submetacentric chromosomes relation, which is observed in the high intrachromosomal asymmetry. Only *M. urugüensis* combined high length chromosome with relatively symmetric karyotype (Table 2, Fig. 2). This trend was found in other groups of Legumes, such as *Phaseolus*.

Fig. 3 — Geographic distribution of *Mimosa* species studied. A) Sect. *Batocaulon*. B) Sect. *Mimosa*. 
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(MERCADO-RUARO and DELGADO-SALINAS 2009), in which species with high TCL had more symmetric karyotype.

It is interesting to point out that a high correlation between parameters of chromosome size, such as TCL and total chromosome area, and nuclear DNA content has been found in previous works (OUZU et al. 1997; MOHANTY et al. 2004). For this reason, it is possible to suppose that significant differences in chromosome size could reflect variations in genome size.

The data presented here suggest that TCL could be useful to distinguish taxa, for example *Mimosa* Sect. *Batocaulon* Ser. *Farinosae*. It is important to point out that this Series comprises only four species that are xerophilous trees endemic of Chaco and adjacent areas, whose morphological characters seem to be generally stable in the populations. Contrarily, the rest of the Series and Subseries studied are subshrubs or shrubs with a wide subtropical distribution, which exhibit high morphological diversification. In this way, it is important to observe that Ser. *Farinosae* could be distinguished from other groups of this genus by some chromosome parameters. Furthermore, decisive conclusions about the relation between karyotypic parameters and taxonomy in *Mimosa* must be supported by studying a larger number of populations in each taxon.

Regarding the geographic distribution, according to our observations and those of others (BURKART 1948; BARNEBY 1991; SIMON and PROENÇA 2000; SEIJO and FERNÁNDEZ 2001). So, the marginal areas of distribution in southern South America could be the highest latitudes of its distribution area, with colder climate (Table 4), such as the Dry Chaco, Pampas and Espinal ecoregions. Relatively few species of *Mimosa* grow in these regions (BURKART 1948; FORTUNATO et al. 2008), possibly because most of the species of this genus cannot adapt to extreme climatic conditions.

We related the variation in TCL to some climatic data of voucher localities, such as annual mean temperature, annual total rainfall and annual frost frequency, and found that the species collected in areas with highest number of annual days with frosts had highest TCL values (Fig.

| Taxon                  | Ploidy levels | Geographic distribution and latitudinal range | Ecoregion                  |
|------------------------|---------------|---------------------------------------------|-----------------------------|
| *M. detinens* Griseb.  | 2x            | Bolivia, Paraguay and Argentina (21-31ºS)    | Dry Chaco                  |
| *M. ostenii* Burkart    | 2x            | Argentina and Uruguay (30-33ºS)              | Espinal                    |
| *M. hexandra* M. Micheli| 2x           | Brazil, Paraguay and Argentina (19-28ºS, en el S de Sudamérica) | Dry and Humid Chaco       |
| *M. uliginosa* Chodat & Hassl. | 2x       | Brazil, Paraguay and Argentina (22-29ºS)    | Alto Paraná Atlantic Forests, Mesopotamic Savannas, Uruguayan Savanna |
| *M. urugiensis* Hook. & Arn. | 2x     | Argentina and Uruguay (27-33ºS).            | Alto Paraná Atlantic Forests, Mesopotamic Savannas, Uruguayan Savanna, Espinal. |
| *M. debilis* Humb. & Bonpl. ex Wildl. var. debilis | 2x     | Brazilian Planalto to Northern Argentina (8-27ºS). | Madeira-Tapajós moist Forests, Pantanal, Cerrado, Dry and Humid Chaco. |
| *M. xanthocentra* Mart. var. mansii (Benth.) Barneby | 2x | Brazil, Bolivia, Paraguay and Northern Argentina (14-27ºS). | Southern Yungas, Dry Chaco, Humid Chaco, Cerrado, Chiquitano Dry Forests. |

Table 3 — Geographic distribution of *Mimosa* species from Southern South America.
5A). In addition, TCL decreased with annual mean temperature (Fig. 5B). In this way, our data appear to be in agreement with that obtained by other authors, who found that species comparatively more tolerant to frosts and low temperatures had an increased genome size (Wakamiya et al. 1993; MacGillivray and Grime 1995; Suda et al. 2003; Knight et al. 2005).

This relation between environment and karyotype parameters could indicates that varia-

**Table 4** — Climatic data from collection localities of plant material studied.

| Locality                          | Annual rainfall (mm) | Annual frost frequency (days) | Annual average temperature (ºC) | Potential evapotranspiration (mm) |
|-----------------------------------|----------------------|-------------------------------|---------------------------------|----------------------------------|
| Gualeguaychú                      | 1105,2               | 10                            | 18                              | 1087,2                           |
| Concordia, Entre Ríos, Argentina   | 1330,4               | 8,6                           | 18,8                            | 1073,8                           |
| Mercedes, Corrientes, Argentina   | 1463,3               | 6,2                           | 19,9                            | 1188,1                           |
| Tandil, Buenos Aires, Argentina    | 901,3                | 13,9                          | 13,9                            | 988,9                            |
| Posadas, Misiones, Argentina      | 1787,1               | 0,5                           | 22,1                            | 1261,1                           |
| Corrientes Aero, Corrientes, Argentina | 1424,2            | 1                             | 21,6                            | ND                               |
| Formosa, Formosa, Argentina       | 1417,8               | 0,7                           | 22,7                            | 1438,8                           |
| Villa María, Córdoba, Argentina   | 827,7                | 24,1                          | 18,3                            | ND                               |
| Orán, Salta, Argentina            | 995,8                | 1,5                           | 22,1                            | 1102,8                           |
| Paso de los Libres, Corrientes, Argentina | 1560              | 2                             | 20,1                            | 1207,7                           |

1Data provided by Instituto de Recursos Biológicos, CIRN–INTA (Hurligham, Argentina). ND: No data.
tion in chromosome size, and eventually in genome size, could have an adaptive value, allowing certain species of *Mimosa* to grow or even colonize adverse environments, in our case, the marginal, coldest and driest areas from Southern South America. GÓMEZ ACEVEDO and TAPIA PASTRANA (2003) found certain relation between chromosome length and environmental adaptation in *Acacia* and *Prosopis*, and it is possible that this pattern also appears in other Mimosoids genera, such as *Mimosa*.

It is important to point out that other mechanisms, such as polyploidy, could be operating to colonize adverse environments or adapt to specific ecological niches, especially in higher latitudes (STEBBINS 1971; SOLTIS et al. 2003). SEIJO and FERNÁNDEZ (2001) found cytological evidence supporting this hypothesis in the genus *Mimosa*; they observed that polyploid frequency and ploidy levels increase with latitude, but it was only analyzed in a few species from Southernmost South America and it cannot still be extrapolate to all taxa of megadiverse genus *Mimosa*. In the present work we only studied some diploid taxa of *Mimosa*, whose mechanism of adaptation or dispersion could be a variation in genome size.

Conclusions - We report the karyotype of *M. detinens*, *M. ostenii*, *M. hexandra*, *M. debilis*, *M. xanthocentra*, *M. uliginosa* and *M. uragüensis* for the first time; these species have a relatively symmetric karyotype and small size of chromosomes, like that observed in other Mimosoids. These results indicate that there are inter-specif-
ic differences in the formula and asymmetry of the karyotype and chromosome size, although a larger number of specimens and populations from Southern South America are necessary to deduce the evolutionary changes in the karyotype. In addition, we found significant differences among species in chromosome length, which could be related to their ability to adapt or colonize adverse environments, especially at highest latitudes, with colder climatic conditions. We may also conclude that variations in chromosome size are related with geographic dispersion or ecological adaptation in some diploid species of the genus *Mimosa*. However, to infer this hypothesis to other groups of the genus, it is necessary more karyological data, especially for the species that grow in other geographic regions.

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APPENDIX

Additional selected specimens examined:

M. hexandra M. Micheli — P. Arenas 1390, R.H. Fortunato et al. 873, 9176 (BAB); Ginzburg et al. 514 (BAB); W. Hahn 2371 (BAB); A. Krapovickas 986 (SI); M. Luckow et al. 4504 (BAB); F. Merle & R. Degen 6023 (MO 5303427); A. Ragone & D. Cozzo 1976 (SI); Rojas 7839, 10277a (SI); T.M. Pedersen 6034 (SI); E.M. Zardini & P. Aquino 31814 (BAB); E.M. Zardini & N. Duarte 49880 (BAB); E. M. Zardini & Godoy 50019 (BAB); E.M. Zardini & L. Guerrero 31882, 31913 (BAB); E.M. Zardini & T. Tilliera 39032, 34882, 34904 (BAB).

M. uliginosa Chod. & Hassl. — R.H. Fortunato et al. 8039, 9067 (BAB); M. DeMatteis et al. 288 (BAB); U. Eskeache 4895 (BAB); M. Morales et al. 660 (BAB); T. Ibarrola 1069 (BAB); A. Krapovickas et al. 15085 (SI); V. Maruñak 58 (BAB, SI); R. Martínez Crovetto 8672 (BAB); R. Martínez Crovetto & Chiarini 6189 (BAB); A. Schinini & A. Fernández 6152 (BAB); J.G. Seijo 266, 330, 360 (BAB); Spazzagnini s.n. (BAB 17369); Zambini s.n. (BAB 28384).

M. uruguayensis Hook. & Arn. — N. Bacigalupo & R. Guaglianone 1566 (BAB); R.H. Fortunato et al. 9099 (BAB); A. Krapovickas et al. 21072 (SI); A. Lourtiet et al. 2745 (SI); M. Málaga de Romero et al. 3134 (BAB); P. Priñer (BAB 92350), same collector (BAB 92353); R. Martínez Crovetto & Grondona 4388 (BAB).

M. detinens Benth. — Bartlett 19811, 20105, 20447 (SI); S. Beck & Liberhan 9463 (SI); A. Burkart 20205 (SI); Cordina 35 (SI); Dimitri & Piccinini 53 (BAB 68154); R.H. Fortunato et al. 1525 (BAB, SI); R.H. Fortunato & M. Luckow 7532 (BAB); Gautier 51 (BAB 65019); W. Hahn 1856 (BAB, SI); A. Krapovickas 839 (SI); A. Krapovickas & Cristóbal 46282 (BAB); Laras & Vogt 5224 (SI); Larzo 1712, 2188 (SI); M. Luckow et al. 4491 (BAB); Maldonado Brezzone 1546 (SI); V. Maruñak et al. 450 (SI); T. Meyer 2245 (SI); E. Nicolosi 2759 (SI); Ragone & Cozzo 2678 (SI); T. Rojas 2134, 4839 (SI); Sayago 213, 376, 2049, 2246 (SI); G.J. Seijo & A. Krapovickas 1948 (BAB, SI); Soriano 572 (BAB, SI); G. Schulz 10595 (SI); R. Vanni et al. 1946 (SI); E.M. Zardini & N. Duarte 49916 (BAB).

M. ostenni Burkart — N.M. Bacigalupo & R. Guaglianone 1582 (BAB); R. Guaglianone et al. 174 (BAB); Molfinio & Clos s.n. (BAB 44.264); M. Morales et al. 617 (BAB).

M. xanthocentra var. mansiti — R.H. Fortunato et al. 846, 1057, 9180, 9200 (BAB); K.R. Laitart 39 (BAB); A. de Oliveira s.n. (BAB); E.M. Zardini & R. Velázquez 25377 (BAB).

M. debilis Humb. & Bonpl. ex Willd. var. debilis — M.M. Arbo 1733 (CTES 91908), 4877 (BAB); S. Beck 3338 (NY); S. Beck & R. Seidel 12378 (BAB); Berti & Escalante 512 (SI); G. Black 5720090 (SI); G. Black & D. Magalhães 51-13387 (SI); B. Bruderer 318 (LPB); A.L. Cabrera & al. 34715 (SI); Cárdenas 4747 (LIL 361516); E.C. Clos 6036 (BAB 51823); D. C. Daly & al. 2133 (LPB); R. de Michel 211 (NY); R. H. Fortunato & al. 817, 818, 824, 1055, 1150, 1156, 1158, 3402, 4099, 7000, 7955, 8534, 8620, 8603, 8741, 8790, 8808, 8826, 8851, 8886, 8899, 9254, 9264, 9307, 9354 (BAB); Fuentes & G. Navarro 2642 (CTES); G. Gehrt 3792 (SI); O. Handro 44675 (SI); G. Hatschbach 2157, 6910, 18863 (SI), 29498 (MO), 58793 (MBM 156870); G. Hatschbach & Guimarães 21977 (SI); R. Kieslinger & al. 9621 (SI); T. Killeen 884, 2412 (LPB); A. Krapovickas & C.L. Cristóbal 34337, 43172 (CTES), 45514 (BAB); A. Krapovickas & A. Schinini 31419 (CTES 118087), 32290 (CTES 110754), 36285 (LIL 103298); A. Krapovickas et al. 14293 (BA), 32872, 33278 (CTES); R.M. Harley & R. Souza 11031 (MO); Herninger 5475 (SI); M.J.G. Hopkins & al. 64 (BAB); J.H. Hunziker 2960 (SI); H.F. Leitão Filho 907 (SI); M. Luckow & al. 4480 (BAB); H. Luederwaldt 13112 ex Hero® Museu Paulista 2140 (SI); A. Macedo & Alvaro Luz 1571 (SI); F. Mereles 2859 (BAB), 4120 (MO); T. Meyer 21666 (LIL); M. Molina & al. 1781 (BAB); M. Moraes 341 (NY); M. Morales & J. G. Seijo 233, 238, 246, 261 (BAB); O. Moreno & M. Belgrano 5013 (SI); O. Mora- rone & al. 2972 (SI); T.M. Pedersen 3271 (BAB); G. Pérez & al. 2982 (BAB); J.M. Pires 9078 (SI); S. Pierotti 2713 (LIL 233552); V.J. Pott & A. Pott 4777 (MBM); V.J. Pott et al. 1223 (CTES 201178); A. Prossen s.n. (LIL 32189); R. Rossov & al. 608 (BAB); G.H. Rua 424 (BAA); C. Saraiva Toledo 1325 (SI); A. Schinini & M. DeMatteis 33863 (FCQ); S. Sede & al. 63 (BAB); R. Seidel & S.G. Beck 192, 391 (BAB); J.G. Seijo 268, 452, 920 (BAB), 1220 (CTES); J.G. Seijo & V. Solís Nefsa 3169, 3283 (CTES); J.G. Seijo et al. 2944, 2991, 3838 (CTES); J.M. Silva & al. 1864 (CTES 282760); L.B. Smith & al. 14533 (CTES); J.C. Solomon 7603 (MO 2992215, NY); G. Spazzagnini s.n. (BAB 15718); Villa Carenzo 140 (LIL); Wolf & al. 209 (SI) L.O. Williams 5631 (SI); E.M. Zardini & R. Britex 52814 (BAB); E.M. Zardini & J. Fernández 45995 (BAB); E.M. Zardini & R. Gamarras 56602 (BAB); E.M. Zardini & L. Guerrero 55322, 55980 (BAB); E.M. Zardini & Velázquez 25650, 26006 (BAB); E.M. Zardini & M. Vera 53537 (BAB).

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