

Chromosome and morphological studies in the *Mimosa debilis* complex (Mimosoideae, Leguminosae) from southern South America

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Abstract. *Mimosa debilis* Humb. & Bonpl. ex Willd. and *M. nuda* Benth. were grouped in specific and infraspecific complexes. Both taxa showed exomorphological similarities, with conflicts in their taxonomic circumscription and present different ploidy levels. The objective of the present contribution was to analyse chromosome numbers of different populations and to evaluate morphological characters of specimens from Paraguay, Argentina and boundary regions. Chromosome numbers of *M. debilis* var. *debilis* ($2n = 2x = 26$ and $2n = 4x = 52$) confirmed previous reports, whereas those of *M. nuda* var. *glaberrima* ($2x = 26$, $4x = 52$), *M. nuda* var. *gracilipes* ($2x = 26$, $4x = 52$) and *M. nuda* var. *nuda* ($4x = 52$) are presented for the first time. Variation was observed in habit, foliar and floral morphology and was correlated with the chromosome number and the geographical distribution of the taxa. Groups with stable morphological characters and restricted geographic distribution were identified. Also, the results showed a pattern of hybrid swarms and polyploids of different origin that may explain the existence of taxonomic conflicts in the *M. debilis*–*M. nuda* species complex. On the basis of these results, *M. nuda* should be included in the synonymy of *M. debilis*.

Introduction

Southern South America was reported a centre of diversification of the pantropical and subpantropical genus *Mimosa* L. (Barneby 1991: 6–7; Bessega *et al.* 2008). In that region, Bentham (1876) included *M. debilis* and related taxa, *M. nuda* Benth., *M. rixosa* Mart., *M. platyphylla* Benth., *M. obtusifolia* Willd., and *M. angusta* Benth., in the section *Mimosa*. This group is represented by species with haplostemonous flowers and pinnate leaflets. Burkart (1945) described *M. parapiensis* Burkart from eastern Bolivia and *M. argentinensis* Burkart from northern Argentina. The same author, in the monograph of the Argentinean species, followed Bentham's proposal but recognising *M. argentinensis* (Burkart 1948: 204–219). Later Barneby (1991: 533–559), in his taxonomic evaluation for the American continent, proposed that this group be placed in the section *Mimosa*, subseries *Mimosa*, and in southern South America, considered *M. rixosa*, *M. obtusifolia* and *M. argentinensis* in synonymy with *M. debilis* and *M. nuda*, proposing infraspecific levels (varieties) for both taxa. He also recognised *M. platyphylla* with specific rank, and *M. angusta* at varietal level as *M. nuda* var. *angusta* (Benth.) Barneby.

Barneby (1991: 536–537) distinguished *M. nuda* and *M. debilis* by the pubescence, secondary venation and margins

of leaflets, pubescence of corolla lobes and fruit type. *M. nuda* comprised specimens with leaflets generally glabrous, with craspedodrome secondary venation and corneous, continuous margin, glabrous corolla lobes, and fruit from a typical craspedium to legume, sometimes with articles partially dehiscent. *M. debilis* was characterised by leaflets hispid or strigose, sometimes glabrous, with brochidodrome or eucamptodrome secondary venation and discontinuous margins, puberulent corolla lobes and typical craspedium. *M. platyphylla* had intermediate characters between *M. nuda* and *M. debilis*, and was described by leaflets hirsute, craspedodrome secondary venation and corneous, continuous and setose margins.

During the taxonomic studies of southern South American species, Morales and Fortunato (2001) reported difficulties in Barneby's (1991: 546–559) taxonomic circumscription, showing that *M. debilis* and *M. nuda* were grouped in respective infraspecific complexes. Recently, Morales and Fortunato (in press) did not find morphological discontinuity in these taxa and proposed inclusion of *M. nuda* and *M. platyphylla* in the synonymy of *M. debilis*. They found many intermediate specimens between the taxa, and proposed recognition of one species with a high morphological variability.

In *M. nuda*, Barneby (1991: 553–558) distinguished the typical variety with glabrous leaflet margins, located only in Brazil and Bolivia, and the varieties *gracilipes*, *glaberrima* and *angusta*, with setose leaflet margins, dispersed throughout southern South America. The var. *angusta* was characterised by narrowly elliptic leaflets. The varieties *glaberrima* and *gracilipes* have oblanceolate to obovate leaflets, and were differentiated by the size of leaflets and growth habit.

Barneby (1991: 546–552) recognised the following two varieties in *M. debilis*: *M. debilis* var. *parapitiensis* (Burkart) Barneby, with glabrous stems and craspedia, from eastern Bolivia, and *M. debilis* var. *vestita* (Benth.) Barneby, which comprised erect subshrubs with unarmed stems, growing from Bolivia to adjacent regions of Brazil.

Morales and Fortunato (in press) proposed to recognise *M. debilis* var. *angusta* (Benth.) Morales & Fortunato (= *M. nuda* var. *angusta*). According to these authors, *M. debilis* var. *debilis* and *angusta* show a stable relation between length and width in the major leaflets of specimens.

The karyology of the genus *Mimosa* has not been sufficiently studied and the chromosome number of only 9–10% of the species is known. The basic chromosome number is $x = 13$ (Isely 1971; Elias 1974; Goldblatt 1981), and on that basis, 30–35% of species were reported as polyploids, especially taxa from southern South America (Seijo 2000; Seijo and Fernández 2001; Goldblatt and Johnson 2002; Morales *et al.* 2007). In the complex *M. debilis*–*M. nuda*–*M. platyphylla* (Barneby 1991: 546–559), chromosome numbers of $2n = 2x = 26$ and $2n = 4x = 52$ were

reported for *M. debilis*. In this taxon, the diploid cytotype was cited from Paraguay (Seijo 2000) and Brazil (Coleman and DeMenezes 1980), and the tetraploid cytotype from Argentina (Seijo 1993, 1999). The existence of different ploidy levels in *M. debilis* was mentioned as a potential source of problems for taxonomic circumscription (Morales and Fortunato in press).

On the basis of the different taxonomic circumscriptions (Barneby 1991: 533–559; Morales and Fortunato in press), we herein correlate the morphology, ploidy level and the geographical distribution of specimens of *M. debilis* from southern South America, with the aim of clarifying the taxonomy of the complex.

Material and methods

Plant material

Voucher specimens collected during field trips in north-eastern Argentina and Paraguay were deposited at the herbarium 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, and the Departamento de Botánica, FCQ, UNA (FCQ), Paraguay (Table 1).

The geographic distribution of taxa was studied, comparing the coordinates with ecoregions and soil types. The ecoregions mentioned follow Olson *et al.* (2001), and the soil types are cited on the basis of specimen herbaria reports and field observations

Table 1. Chromosome numbers, localities and voucher specimens of the complex *Mimosa nuda*–*M. debilis* in southern South America

Taxon	$2n$	Figure	Locality and voucher specimen
^A <i>M. debilis</i> Humb. & Bonpl. ex Willd. var. <i>debilis</i> s.l.	26	2d	Paraguay, Department San Pedro. R. H. Fortunato <i>et al.</i> 9214 (BAB)
	52		Argentina, Corrientes, Department Ituzaingó. M. Morales and J. G. Seijo 246 (BAB)
	52	Argentina, Misiones, Department Candelaria. R. H. Fortunato <i>et al.</i> 8904 (BAB)	
	52	Argentina, Corrientes, Department Ituzaingó. R. H. Fortunato <i>et al.</i> 8899 (BAB)	
^A <i>M. debilis</i> Humb. & Bonpl. ex Willd. var. <i>debilis</i> s.s.	26	2e	Argentina, Salta, Department Gral. San Martín. R. H. Fortunato <i>et al.</i> 7000 (BAB)
	26		Argentina, Salta, Department Orán. R. H. Fortunato <i>et al.</i> 7298 (BAB)
	26		Paraguay, Department Boquerón. R. H. Fortunato <i>et al.</i> 8741 (BAB)
	26		Paraguay, Department Pte. Hayes. R. H. Fortunato <i>et al.</i> 8790 (BAB)
	26		Paraguay, Department Pte. Hayes. R. H. Fortunato <i>et al.</i> 8794 (BAB)
	26		Paraguay, Department Boquerón. M. Luckow <i>et al.</i> 4480 (BAB)
^B <i>M. nuda</i> var. <i>nuda</i> s.l. (intermediate between <i>M. nuda</i> var. <i>nuda</i> and <i>M. nuda</i> var. <i>glaberrima</i>)	52	2a	Paraguay, Department San Pedro. R. H. Fortunato <i>et al.</i> 9354 (BAB)
^B <i>M. nuda</i> Benth. var. <i>gracilipes</i> (Harms) Barneby	26	2c	Paraguay, Department Cordillera. R. H. Fortunato <i>et al.</i> 8808 (BAB)
	52		Paraguay, Department Cordillera. R. H. Fortunato <i>et al.</i> 8808 (BAB)
	52		Paraguay, Department Cordillera. R. H. Fortunato <i>et al.</i> 8805 (BAB)
^B <i>M. nuda</i> var. <i>glaberrima</i> (Chod. & Hassl.) Barneby	26	2f	Paraguay, Department Amambay. R. H. Fortunato <i>et al.</i> 9228 (BAB)
	26		Paraguay, Department Amambay. R. H. Fortunato <i>et al.</i> 9254 (BAB)
	26		Paraguay, Department Amambay. R. H. Fortunato <i>et al.</i> 9307 (BAB)
	52		Argentina, Corrientes, Department Berón de Astrada. M. Morales and J. G. Seijo 233 (BAB)
	52		Argentina, Corrientes, Department Ituzaingó. M. Morales and J. G. Seijo 261 (BAB)
<i>M. debilis</i> s.l. (intermediate between <i>M. nuda</i> and <i>M. debilis</i>)	52		Paraguay, Department Central. R. H. Fortunato <i>et al.</i> 9189 (BAB)
	52		Paraguay, Department San Pedro. R. H. Fortunato <i>et al.</i> 9356 (BAB)

^AChromosome counting of *M. debilis* confirmed previous records: $2n = 26$ (Coleman and DeMenezes 1980; Seijo 2000) and $2n = 52$ (Seijo 1993, 1999).

^BChromosome numbers of *M. nuda* and their varieties are novel.

during the collecting trips. Nomenclature and geographic distribution of soil orders are according to Global Soil Regions map (USDA–NRCS 2005).

Chromosome studies

Seeds were collected during field trips carried out between 2005 and 2008 in Argentina and Paraguay. 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).

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, Darmstadt, Germany) and 20% liquid pectinase for 7200–9000 s at 37°C. The material was washed again with buffer solution.

Root tips were macerated in a drop of dye (acetic hematoxylin), and the ‘squash’ technique was applied (Egozcue 1971). In each sample, ~10–20 metaphases were counted. The samples were conserved with Euparal as a mounting medium. The slides are lodged in one collection, which was deposited in Laboratorio de Ecología, Citogenética y Evolución, Facultad De Ciencias Exactas y Naturales, Universidad de Buenos Aires.

Morphological studies

In the present analysis, ~350 specimens were studied from the following herbaria: BA, BAA, BAB, BM, CTES, FCQ, G, LIL, MBM, MCNS, MO, SI and SP (Appendix 1). The collections were determined according to Barneby (1991: 536–558) and compared with the nomenclatural types of the taxa.

The morphological characterisation was carried out by classical techniques. Plant parts were boiled in water to ease the stereomicroscopic observation with WILD M5-26530 (Wild, Heerbrugg, Sankt Gallen, Ostschweiz, Switzerland). The following qualitative characters were selected and analysed: habit growth; pubescence and presence of aculei in the stems; pubescence, secondary venation and margin of leaflets; pubescence of corolla lobes; and pubescence and dehiscence of fruits. The following quantitative characters were measured: length of petioles, leaf stalks and peduncles; length and width of leaflets and fruits and capitula diameter. Terms of pubescence and form of leaflets were mentioned according to Lawrence (1951).

With regard to foliar morphology, studies of secondary venation were conducted according to de Strittmater (1973) and the terminology proposed by Hickey (1974); the types of leaflets margin were cited according to Barneby (1991: 536–537), as follows:

(1) types of secondary venation: (i) *craspedodrome venation* – secondary nerves anastomosing with the margin; (ii) *brochidodrome venation* – secondary nerves fused in a single series of prominent arches; (iii) *euamptodrome venation* – secondary nerves gradually diminishing to the apex into the margin; they are connected to supra-adjacent secondary nerves by a single series of transversal nerves and do not show prominent marginal arches.

(2) types of leaflet margin: (i) *corneous, continuous* – the marginal nerve is observed as a pallid and continuous, either setose or glabrous band; (ii) *discontinuous* – the margin of leaflets shows setae, but does not show a uniform band.

Results and discussion

In the morphological analysis, specimens were determined to be *M. nuda* var. *glaberrima* (Chod. & Hassl.) Barneby, *M. nuda* var. *gracilipes* (Harms) Barneby, *M. debilis* var. *debilis* s.s., *M. debilis* var. *debilis* s.l., *M. nuda* var. *nuda* s.l. and *M. nuda* var. *nuda* s.s., and material with intermediate characters between those taxa (Table 2). Chromosome studies were carried out in 20 accessions, and following Barneby’s proposal (1991: 532–559), these belonged to four taxa of the complex from Argentina and Paraguay (Fig. 1). The present study confirmed $x = 13$ as basic chromosome number of the genus.

The chromosome number and ploidy level of *M. nuda* var. *glaberrima*: $2n = 2x = 26$, $2n = 4x = 52$, *M. nuda* var. *gracilipes*: $2n = 2x = 26$, $2n = 4x = 52$ and *M. nuda* var. *nuda*: $2n = 4x = 52$ are reported for the first time, whereas those of *M. debilis* var. *debilis*, $2n = 2x = 26$, and $2n = 4x = 52$, confirm previous reports (Coleman and DeMenezes 1980; Seijo 1993, 1999, 2000) (Table 1, Fig. 2a–g). The chromosomes are very small, with the length within the range of 0.5–2.3 μm . In all the specimens evaluated, the centromere was difficult to visualise in most of the chromosomes, which prevented recognition of their morphology and other parameters of the karyotype.

The present results showed the existence of intermediate specimens between *M. debilis* and *M. nuda*, with variability in the secondary venation and the margins of leaflets and pubescence of corolla lobes, confirming the observations of Morales and Fortunato (in press). Nevertheless, secondary venation and the margins of leaflets, in combination with other characters (growth habit and pubescence of leaflets), geographical distribution and chromosome number, allowed the identification of some groups, as follows:

Mimosa debilis var. *debilis* s.s.

M. debilis var. *debilis sensu* Barneby (1991: 548–549)–*M. debilis* var. *parapitiensis* (Burkart) Barneby *sensu* Barneby (1991: 549–550)–*M. argentinensis* Burkart *sensu* Burkart (1945, 1948: 217–218)–*M. argentinensis* var. *saltensis* Burkart *sensu* Burkart (1948: 219)–*M. debilis sensu* Benth (1876).

The populations of this group represent the typical specimens of *M. debilis* var. *debilis*, according to proposal of Barneby (1991: 547–548). These individuals are characterised by leaflets oblanceolate to obovate, with brochidodrome or more rarely euamptodrome secondary venation and discontinuous margins. Other qualitative characters, such as aculei of stems, growth habit and pubescence of leaflets, stems and pods are variable (see full description below¹).

One population of northern Argentine (in Salta province) had glabrous stems and strigose leaflets, whereas other specimens of Argentine Yungas showed stems variable in pubescence, and leaflets strigose only in the abaxial face of lower pair in each pinna. Furthermore, the populations studied in Argentine Chaco, Brazil, Paraguay and Bolivia showed specimens intermediate between these combinations of pubescence.

Table 2. Classification of studied specimens of *Mimosa nuda* Benth.–*M. debilis* Humb. & Bonpl. ex Willd. complex according to morphological studies

RHF, Renée H. Fortunato; MM, Matías Morales; JGS, José G. Seijo; AK, Antonio Krapovickas; ML, Melissa Luckow; CandDM, Coleman and DeMenezes; Voucher specimens of previous records: AK 45514 (BAB), Seijo 2000; CandDM 16, 31 (SP), Coleman and DeMenezes 1980; GJS 143 (BAB), Seijo 1993; GJS 920 (BAB), Seijo 1999

Classification	<i>Mimosa debilis</i> var. <i>debilis</i> s.s.	Intermediate between <i>M. debilis</i> var. <i>debilis</i> s.s. and <i>M. nuda</i> var. <i>glaberrima</i>	<i>M. nuda</i> var. <i>gracilipes</i> – <i>M. nuda</i> var. <i>glaberrima</i>	Intermediate between <i>M. nuda</i> var. <i>gracilipes</i> – <i>M. nuda</i> var. <i>glaberrima</i> and <i>M. debilis</i> var. <i>debilis</i> s.l. = <i>M. rixosa</i>	<i>M. nuda</i> var. <i>nuda</i> s.l.	<i>M. nuda</i> var. <i>nuda</i> s.s.	
Growth habit	Erect to procumbent subshrubs or frutescent herbs	Procumbent to decumbent subshrubs or frutescent herbs	Procumbent to decumbent subshrubs or frutescent herbs	Procumbent to decumbent subshrubs or frutescent herbs	Erect or suberect subshrubs (2x) to procumbent to decumbent subshrubs or frutescent herbs (4x)	Procumbent subshrubs	Erect subshrubs
Leaflets – secondary venation	Brochodrome, rarely eucamptodrome	Narrowly anastomosing to anastomosing with marginal nerve, eucamptodrome or brochodrome	Anastomosing with the marginal nerve	Generally anastomosing with the marginal nerve	Eucamptodrome or anastomosing with the marginal nerve	Anastomosing with the marginal nerve	Anastomosing with the marginal nerve
Leaflets – margin	Discontinuous	Discontinuous or comeous, continuous, setose	Comeous, continuous and setose	Comeous, continuous and setose	Generally comeous, continuous, and setose	Comeous, continuous and glabrous	Comeous, continuous and glabrous
Leaflets – pubescence	Glabrous, strigose in both faces or only strigose in the abaxial face of first leaflets	Glabrous or setose in the abaxial face of the first leaflets	Glabrous or setose in the abaxial face of the lower pair of leaflets in each pinna	Scarcely hirsute or puberulent in both faces	Hirsute in both faces	Glabrous	Glabrous
Geographical distribution	E Bolivia, W Paraguay, boundary areas of Brazil and NW Argentina	Brazil, Bolivia, E Paraguay, NE Argentina	Brazil, Bolivia, E Paraguay, NE Argentina	Brazil, E Paraguay, NE Argentina	Brazil, Bolivia, E Paraguay, NE Argentina	E Paraguay	Brazil
Voucher specimens analysed (present and previous records)	RHF 7000 ^A , 7298 ^A , 8741 ^A , 8790 ^A , 8794 ^A (BAB), AK 45514 ^A (BAB), ML 4480 ^A (BAB)	RHF 9356 ^B (BAB)	RHF 8805 ^B , 8808 ^C , 9189 ^B , 9228 ^A , 9254 ^A , 9307 ^A (BAB), MM and GJS 233 ^B (BAB)	MM and GJS 261 ^B (BAB); GJS 920 ^B (BAB)	CandDM 16 ^A , 31 ^A (SP); RHF 8899 ^B , 8904 ^B , 9214 ^A (BAB); MM 644 ^B , MM and GJS 246 ^B (BAB), GJS 143 ^B (BAB)	RHF 9354 ^B (BAB)	No chromosome counting reported

^A2n = 26. ^B2n = 52. ^C2n = 26 and 2n = 52.



Fig. 1. Map of chromosome numbers in *Mimosa debilis* Humb. & Bonpl. ex Willd.–*M. nuda* Benth. complex. *M. debilis* var. *debilis* s.s., $2x=26$ (black circles). *M. debilis* var. *debilis* s.l. = *M. rixosa* Mart., $2x=26$ (black triangles). *M. debilis* var. *debilis* s.l. = *M. rixosa* Mart., $4x=52$ (grey triangles). *M. nuda* var. *glaberrima* (Chod. & Hassl.) Barneby, $2x=26$ (black squares). *M. nuda* var. *glaberrima*, $4x=52$ (grey squares). *M. nuda* var. *gracilipes* (Harms) Barneby, $2x=26$ and $4x=52$ (black hexagon). *M. nuda* var. *nuda* s.l., $4x=52$ (grey pentagon). Intermediate between *M. nuda* and *M. debilis* var. *debilis* s.s., $4x=52$ (black and white square). Intermediate between *M. nuda* var. *gracilipes*–*M. nuda* var. *glaberrima* and *M. debilis* var. *debilis* s.l., $4x=52$ (stars).

For this reason, in the present work, all populations are considered as a unique group, with glabrous to strigose leaflets and a typical secondary venation and margins. They are restricted to sandy soils (entisols and aridisols) from eastern Bolivia, western Paraguay, contiguous areas of Brazil and north-western Argentina (Fig. 3), in the ecoregions of Dry Chaco, Humid Chaco, Southern Andean Yungas and boundary area, or Chaco and Yungas, according to Cabrera (1976). In this group, previous chromosome reports $2n=2x=26$ were confirmed (Seijo 2000).

Description

Erect to procumbent subshrubs or frutescent herbs 0.30–1 m tall. Stems unarmed or armed with infrastipular, sometimes infrapetiole aculei, subglabrous to hispid. Leaf stalks 0.5–7.8 cm; rachis of pinnae including pulvinus 0.3–2.2 cm long; leaflets $0.5\text{--}4.6 \times 0.2\text{--}2.3$ cm, oblanceolate to obovate, glabrous, strigose on both faces, sometimes only strigose in the abaxial face of first pair, with secondary venation brochidodrome or more rarely eucamptodrome and the margin discontinuous and setose. Peduncles 0.2–4.8 cm long; capitula 3–6(–8) mm in diameter; corolla lobes generally puberulent. Craspedia $0.6\text{--}3.2 \times (0.2)\text{--}0.25\text{--}0.55$ cm, replum and valves subglabrous to hispid.

Mimosa debilis var. *debilis* s.l. complex

M. rixosa Mart. *sensu* Benth (1876) and Burkart (1948: 211–214).

This complex is grouped following Benth (1876) and Burkart (1948: 211–214) and it includes only specimens with oblanceolate to obovate, hirsute and puberulent leaflets with corneous, continuous and setose margins. In this group, secondary venation is craspedodrome and/or eucamptodrome

(Table 2). Other characters are highly variable in the analysed populations (see full description below²).

The individuals analysed grew in ferralitic soils (oxisols and ultisols) from Brazil, Bolivia, Paraguay and north-eastern of Argentina (Fig. 3), in ecoregions of Cerrado, Dry Chiquitano Forest and Alto Paraná Atlantic Forest.

In agreement with reports of Coleman and DeMenezes (1980) and Seijo (1993, 1999), two cytotypes with differences in habit and latitudinal distribution were found and these are as follows: (1) diploid, $2n=26$: erect and suberect subshrubs from Southern Brazil and eastern Paraguay and (2) tetraploid, $2n=52$: procumbent to decumbent subshrubs and frutescent herbs, from north-eastern Argentina (Fig. 1).

Description

Erect to procumbent subshrubs or frutescent herbs 0.50–2.50 m tall. Stems armed with infranodal, sometimes, infrastipular aculei, hispid to strigose. Leaf stalks 0.7–9.5 cm long; rachis of pinnae including pulvinus 0.3–3.3 cm long; leaflets $0.7\text{--}6.6 \times 0.2\text{--}3.5$ cm, oblanceolate to obovate, hirsute and puberulent, with secondary venation eucamptodrome or craspedodrome and margins corneous, continuous and setose. Peduncles 0.1–5.6 cm long; capitula 3.5–6(–7) mm in diameter; corolla lobes puberulent. Craspedia $0.6\text{--}1.8 \times 0.3\text{--}0.5$ cm, replum and valves hispid.

Mimosa nuda var. *gracilipes*–*M. nuda* var. *glaberrima* complex

M. nuda Benth. var. *glaberrima* (Chod. & Hassl.) Barneby *sensu* Barneby (1991: 554–555)–*M. nuda* var. *gracilipes* (Harms) Barneby *sensu* Barneby (1991: 555–556)–*M. glaucescens* Benth. *sensu* Benth (1876).

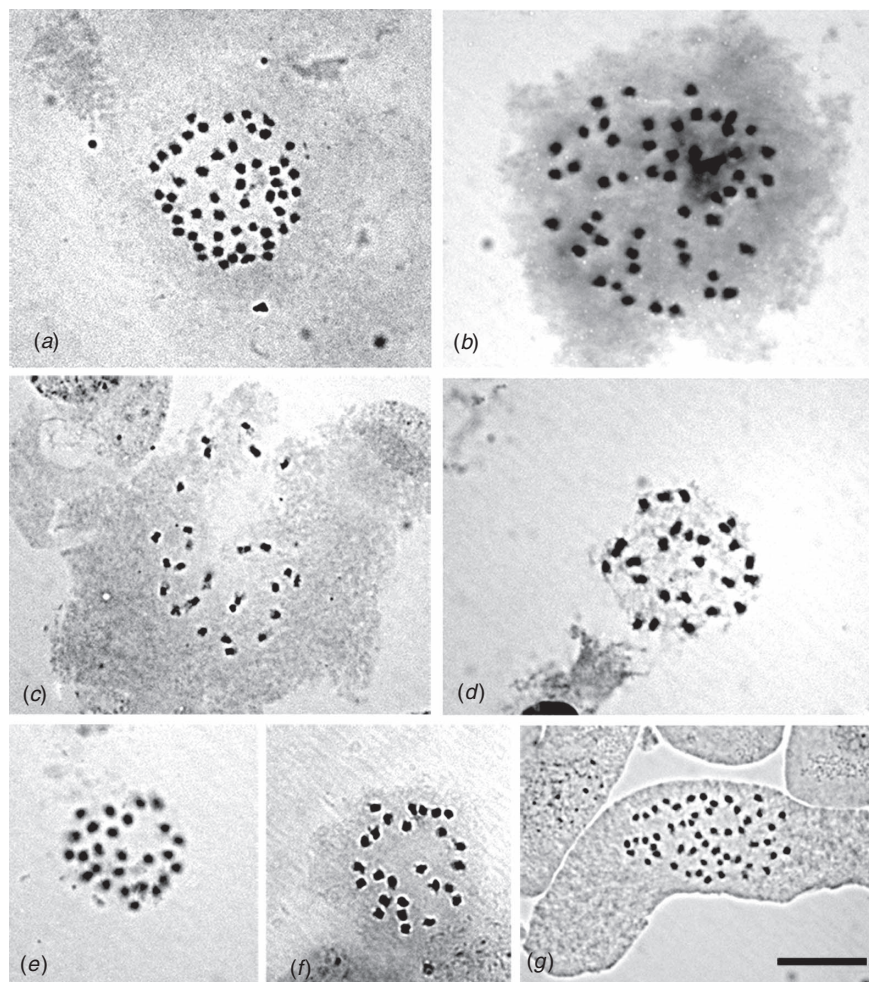


Fig. 2. Mitotic metaphases of *Mimosa debilis* Humb. & Bonpl. ex Willd. and *M. nuda* Benth. (a) *M. nuda* var. *nuda*, $2n=4x=52$; (b) *M. nuda* var. *glaberrima* (Chodat & Hassl.) Barneby, $2n=4x=52$; (c) *M. nuda* var. *gracilipes* (Harms) Barneby, $2n=2x=26$; (d) *M. debilis* var. *debilis* s.l., $2n=2x=26$; (e) *M. debilis* var. *debilis* s.s., $2n=2x=26$; (f) *M. nuda* var. *glaberrima*, $2n=2x=26$; (g) *M. nuda* var. *gracilipes*, $2n=4x=52$. Scale bar = 10 μm .

This complex is represented by specimens with oblanceolate to obovate and glabrous leaflets (or leaflets only setose on the abaxial face of the lower pair in each pinna), with secondary venation craspedodrome and corneous, continuous and setose margins (Table 2). Both varieties were separated by habit and size of leaflets (Barneby 1991: 554–555), although recently, Morales and Fortunato (in press) found a continuous range in the leaflets size and an important number of intermediate specimens between both taxa. In the present work, many specimens with intermediate characters were found (see also Appendix 1), confirming the proposal of Morales and Fortunato (in press). For this reason, both varieties are considered as a unique taxonomic entity in the present work.

The results of the present study showed diploid and tetraploid populations, and also one population with diploid and tetraploid individuals was observed in Cordillera, Paraguay (see Table 1, voucher *R. H. Fortunato et al. 8808*). All specimens of *M. nuda* var. *gracilipes*–*M. nuda* var. *glaberrima* analysed grew in sympatry in eastern Paraguay, north-eastern Argentina and some parts of southern Brazil (Fig. 3), on sandy soils

(generally entisols, ultisols and alfisols) in ecoregions of Cerrado, Alto Paraná Atlantic Forest and Humid Chaco.

Nevertheless, the morphological analysis did not show differences between the diploid and tetraploid cytotypes, which grew in sympatry, suggesting that are autopolyploids or allopolyploids among species or varieties with high affinity. Although taxa with different ploidy levels may constitute a taxonomic species, at a biological level, they could be considered as cryptic and reproductively isolated species (Grant 1981).

Description

Erect to procumbent subshrubs or frutescent herbs 0.30–1.50 m tall. Stems unarmed or armed with infrastipular, sometimes infrapetiolar aculei, glabrous or rarely hispid. Leaf stalks 1.2–8 cm long; rachis of pinnae including pulvinus 0.5–3.4 cm long; leaflets 0.5–6.2 \times 0.2–3.1 cm, oblanceolate to obovate, glabrous, sometimes setose on the abaxial face of the lower pair in each pinna, with secondary venation craspedodrome

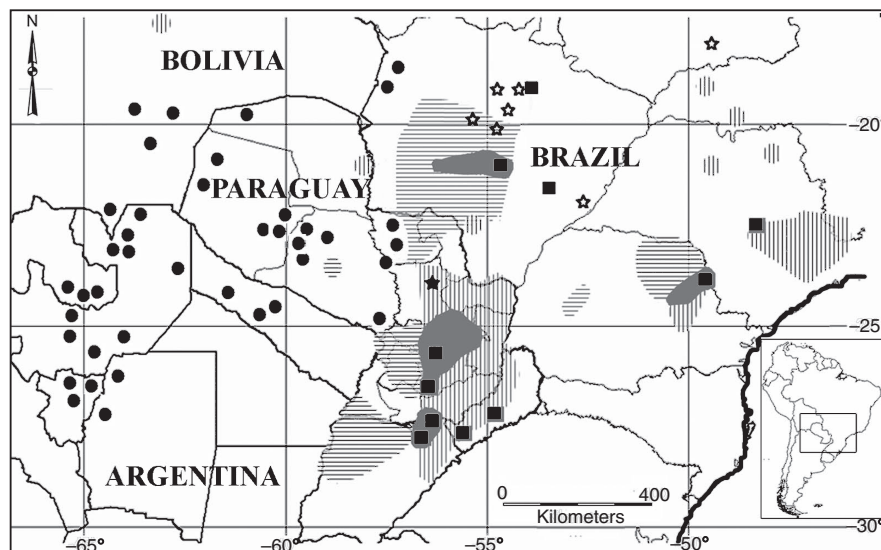


Fig. 3. Geographic distribution of taxonomic groups and intermediate specimens of *Mimosa debilis*–*M. nuda* complex. *M. debilis* Humb. & Bonpl. ex Willd. var. *debilis* s.s., $2x = 26$ (black circles). *M. nuda* Benth. var. *glaberrima* (Chod. & Hassl.) Barneby–*M. nuda* var. *gracilipes* (Harms) Barneby and intermediate exemplars with *M. debilis* var. *debilis* s.s. (horizontal bars). *M. debilis* var. *debilis* s.l. = *M. rixosa* Mart., $2x = 26$ and $4x = 52$ (vertical bars). Areas of sympatry between *M. debilis* var. *debilis* s.l. and *M. nuda* var. *gracilipes*–*M. nuda* var. *glaberrima* (grey zones). Specimens with intermediate characters between *M. debilis* var. *debilis* s.l. and *M. nuda* var. *gracilipes*–*M. nuda* var. *glaberrima*, $4x = 52$ (black squares). *M. nuda* var. *nuda* s.s., within data of chromosome number (stars).

and margins corneous, continuous and setose. Peduncles 0.2–5.2 cm long; capitula 3–6(–8) mm in diameter; corolla lobes glabrous or puberulent. Craspedia or legumes $0.8\text{--}2.4 \times 0.3\text{--}0.5$ cm, replum and valves glabrous to hispid.

Mimosa nuda var. *nuda* s.s.

M. nuda Benth. var. *nuda sensu* Barneby (1991: 558–559)–*M. nuda* and *M. gymmoloma sensu* Benth (1876).

These specimens were included strictly in *M. nuda* var. *nuda*, according to Barneby (1991: 558–559), and are represented by erect and glabrous subshrubs, with narrowly elliptic to oblanceolate leaflets whose secondary venation is craspedodrome and the marginal nerve is corneous, continuous and glabrous. These individuals are restricted to areas of Cerrado in central Brazil (Fig. 3) and some parts of Bolivia. The chromosome number of this group is unknown.

Description

Erect and uniformly glabrous or subglabrous subshrubs 0.50–2.50 m tall. Stems unarmed. Leaf stalks 1.7–10.3 cm long; rachis of pinnae including pulvinus 0.7–2.3 cm long; leaflets $1.1\text{--}7.8 \times 0.4\text{--}4.6$ cm, narrowly elliptic to oblanceolate, with secondary venation craspedodrome and margins corneous, continuous and glabrous. Peduncles 0.3–4.7 cm long; capitula 3–7 mm diameter; corolla lobes glabrous. Craspedia or legumes $0.6\text{--}2.3 \times 0.3\text{--}0.5$ cm.

It was possible to identify the four groups cited above, although there were other tetraploid individuals that showed intermediate morphological characters, suggesting the existence of polyploids of hybrid origin. These specimens were grouped on the basis of morphological, geographical and cytological characters, as follows:

- M. debilis* var. *debilis* s.l. and *M. nuda* var. *gracilipes*–*M. nuda* var. *glaberrima*. These specimens are variable in habit and foliar morphology between Groups 2 and 3. They are procumbent to decumbent subshrubs or frutescent herbs, and have leaflets that are scarcely hirsute or puberulent on both sides, with craspedodrome secondary venation and corneous, continuous and setose margins. These specimens were found in southern Paraguay and north-eastern Argentina (Fig. 3), in the ecotone regions between sandy (*M. nuda* var. *gracilipes*–*M. nuda* var. *glaberrima*) and ferrallitic soils (*M. debilis* var. *debilis* s.l.), growing in sympatry with all these taxa. The chromosome number analysed confirmed previous reports $2n = 4x = 52$, cited for specimens growing in this ecotone regions (Seijo 1993, 1999). Furthermore, in northern Paraguay and some regions of southern Brazil, there are also ecotones (Fig. 3) where these critical individuals grow, suggesting that hybrid swarms could exist in intermediate habitat.
- M. debilis* var. *debilis* s.s. and *M. nuda* var. *gracilipes*–*M. nuda* var. *glaberrima*. These intermediate specimens present leaflets with different shape and size, discontinuously corneous margins, or narrowly anastomosing to anastomosing with it, forming a continuous marginal nerve, corolla lobes glabrous to puberulent, and also variability in the habit from decumbent, procumbent, ascending to erect subshrubs, with aculeate to unarmed stems. These possible hybrids grow together in sympatry with the varieties of *M. nuda* in eastern Paraguay and north-eastern Argentina in similar ecological environments (Fig. 3).
- M. nuda* var. *gracilipes*–*M. nuda* var. *glaberrima* and *M. nuda* var. *nuda* s.s. The analysed population is

represented by glabrous plants and corresponds to *M. nuda* var. *nuda*; however, on the basis of its procumbent habit and oblanceolate leaflets, it is close to *M. nuda* var. *glaberrima*. These individuals could have been derived by hybridisation between different populations of this group (Table 1, Figs 1, 3).

Conclusions

The data obtained in the present study did not agree with the Barneby's (1991: 533–559) proposal that recognises from southern South America three species, namely *M. nuda*, *M. debilis* and *M. platyphylla*. The results of the present work suggested that it is not possible to distinguish more than one taxonomic species, supporting the proposal of Morales and Fortunato (in press), in regard to the inclusion of *M. nuda* in the synonymy of *M. debilis*.

It is possible to identify the diploid populations of Chaco and Yungas phytogeographic regions, with brochidodrome or eucamptodrome secondary venation and discontinuous margins of leaflets, and in the adjacent areas, intermediate specimens with *M. nuda* can be detected. *M. debilis* var. *debilis* s.l. and *M. nuda* var. *gracilipes*–*M. nuda* var. *glaberrima* showed morphological and geographical differences; however, tetraploid specimens with intermediate characters were found between both groups (Fig. 3).

In the present study, it was also possible to postulate the existence of one or more polyploid complexes and a pattern of hybrid zones, which would explain the problems of taxonomic circumscription (Burkart 1948: 211–219; Bentham 1876; Barneby 1991: 533–558; Morales and Fortunato 2001, in press). The phenomena of hybridisation and polyploidy could lead a mode of speciation in *M. debilis*, via the formation of hybrid complexes.

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Appendix 1

List of selected analysed specimens of *Mimosa nuda* Benth. and *M. debilis* Humb. & Bonpl. ex Willd. from southern South America.

M. nuda var. *gracilipes* (Harms) Barneby

BRAZIL. Mato Grosso do Sul. Etchichury s.n. (SI). **PARAGUAY.** Dpto Amambay: E. M. Zardini 4082 (BAB). Dpto Central: E. M. Zardini and P. Aquino 30882 (BAB), E. M. Zardini and T. Tilleria 33695 (BAB). Dpto Cordillera: R. H. Fortunato *et al.* 8805, 8808 (BAB), E. Hassler 7041, 8838 (G), E. M. Zardini, 7619 (BAB). Dpto Guairá: E. Ginzburg 605 (BAB). Dpto Misiones: Rossengurt 5950 (LIL), E. M. Zardini and L. Guerrero 55322 (BAB). Dpto Paraguari: E. M. Zardini 31336, 34945 (BAB). Dpto Presidente Hayes: E. M. Zardini and M. Vera 57224 (BAB). **ARGENTINA.** Corrientes. E. Cano and Cámara Hernández 779 (BAA), R. Carnevali 477, 1055 (CTES). R. Vanni *et al.* 1477 (CTES).

M. nuda var. *glaberrima* (Humb. & Bonpl. ex Willd.) Barneby

BRAZIL. Goiás: M. M. Arbo *et al.* 3284 (BAB), G. Hatschbach 60270 (MBM 164621), G. Hatschbach and J. Cordeiro 51804 (MBM 118859), Oliveira *et al.* 324 (BAB). Mato Grosso do Sul: G. Hatschbach 33960 (MBM 29241), 58793 (MBM 156870), G. Hatschbach *et al.* 59005 (SI), 73149 (MBM 279856), A. Krapovickas 29893 (CTES 117409), A. Krapovickas and C. Cristóbal 34337 (CTES), A. Pott *et al.* 10582 (MBM 302029), 10799 (MBM 302048), O. S. Ribas and L. B. S. Pereira 2376 (MBM 220698). Minas Gerais: G. Hatschbach *et al.* 54931 (MBM 140987), A. Krapovickas *et al.* 33324 (MBM 125681), J. Paula Souza 3838 (CTES). Paraná: M. G. Caxambú 761 (MBM 304500), G. Hatschbach 6910 (SI), 45987 (MBM 78523), O. S. Ribas *et al.* 1687 (MBM 209049), O. S. Ribas and J. Cordeiro 1081 (MBM 149674), J. M. Silva *et al.* 1864 (CTES 28760, MBM 204728), L. B. Smith *et al.* 14533 (SI). **BOLIVIA.** Dpto Santa Cruz, Pcia. Chiquitos: M. Cárdenas 4534 (LIL 53322). **PARAGUAY.** Dpto Amambay: J. Fernández Casas 4046 (MO 3614102), R. H. Fortunato *et al.* 923, 1150, 1158, 9228, 9243, 9252, 9254, 9307; E. Hassler 5921 (G); T. Rojas 6578 (SI), Schwarz 12196 (CTES); J. C. Solomon 7070 (MO); N. Soria 7371 (BAB). Dpto Caaguazú: J. Fernández Casas 3809 (MO 3614101). Dpto Canindeyú: A. Schinini and M. DeMatteis 33330 (BAB). Dpto Central: R. H. Fortunato 8851 (BAB), Schwarz 11492 (LIL 374888), E. M. Zardini 24165 (BAB). Dpto Cordillera: E. Hassler 6786 (G), E. M. Zardini and U. Velázquez 27032 (BAB). Dpto Cordillera: E. Hassler 1143 (G); E. Lurvey 236 (MO), A. Schinini 3616 (CTES 91886). Dpto Paraguari: R. H. Fortunato 8521 (BAB), B. Sparre and F. Vervoorst 659 (CTES 91922, LIL). Dpto San Pedro: R. H. Fortunato *et al.* 9203 (BAB), E. M. Zardini and R. Vera 48265 (BAB). **ARGENTINA.** Corrientes: T. Ibarrola 3732 (LIL 136536), R. Martínez Crovetto and Leguizamón 5445 (BAB), M. Morales and J. G. Seijo 233 (BAB), S. Tressens 5218 (CTES 241564). Formosa: R. H. Fortunato 4099 (BAB). Misiones: A. Burkart 15315 (SI), R. Martínez Crovetto 9853 (CTES 102714).

M. debilis Humb. & Bonpl. ex Willd. var. *debilis* s.s.

PANAMÁ. R. H. Fortunato *et al.* 8474 (BAB), C. Hicken s.n. (SI 27766). **BRAZIL.** Mato Grosso: G. Hatschbach 34063 (CTES 145763). Mato Grosso do Sul: G. Hatschbach 29519 (MBM 21119), 60838 (MBM 167186), G. Hatschbach and Guimarães 21977 (SI), V. J. Pott and A. Pott 4779 (MBM), V. J. Pott *et al.* 1223 (CTES 201178). Rondônia: A. Ducke 23243 (SI), L. O. A. Texeira 575 (CTES 117417). **BOLIVIA.** Dpto Beni: E. De La Sota 765, 4253 (SI), A. Krapovickas and A. Schinini 34795 (CTES 102961), J. C. Solomon 7603 (MO 2992215). Dpto Chuquisaca: Saravia Toledo and N. Joaquín 10311 (CTES 182987), 10546 (CTES). Dpto Santa Cruz: A. L. Cabrera and M. Gutiérrez 33601 (SI), M. Cárdenas 4747 (LIL 361516), A. Krapovickas and A. Schinini 36285 (CTES 103298), J. G. Seijo *et al.* 2944, 3732 (CTES), J. G. Seijo and V. Solís Neffa 3169 (CTES), no data of collector nor collection number (LIL 130142). Dpto Tarija: T. Meyer 21666 (LIL 517055), S. Pierotti 7253 (LIL 233552), J. C. Solomon 10079 (CTES). **PARAGUAY.** Adamoli 27 (BAA). Dpto Alto Paraguay: L. Pérez and G. Navarro 8306 (BAB). Dpto Boquerón: P. Arenas 1113 (BAB), L. August 347 (CTES 301854), R. H. Fortunato *et al.* 8603, 8605, 8622, 8741, 8790, 8794 (BAB), A. Krapovickas and C. Cristóbal 44220 (SI), M. Luckow *et al.* 4480 (BAB), F. Mereles 4120 (BAB), L. Pérez *et al.* 2620 (BAB), A. Schinini 25639 (CTES), E. M. Zardini and N. Duarte 49844 (BAB). Dpto Central: B. Pérez 539 (BAB), A. Schinini 2148 (BAB). Dpto. Concepción: R. Degen 2389 (CTES 225980), R. H. Fortunato *et al.* 824 (BAB), E. M. Zardini and L. Guerrero 53794 (BAB). Dpto Presidente Hayes: P. Arenas 1570 (BA), R. H. Fortunato *et al.* 8784, 8790, 8794 (BAB), A. Krapovickas and C. Cristóbal 45514 (BAB), E. Nicora 9755 (SI), L. Pérez *et al.* 2982 (BAB), E. M. Zardini 45995 (BAB). Dpto San Pedro: Wolf *et al.* 209 (SI). **ARGENTINA.** Jujuy: no data (LIL 70182), D. Abbiatti and M. R. Figueroa 3010 (CTES 117824), O. Ahumada 6631 (CTES 220566), A. L. Cabrera 30192, 34336, 34715 (SI), N. Deginani 43 (SI), Holmberg s.n. (BAB 12651), Hunziker and Caso 6137 (SI), J. H. Hunziker 2960, 10260 (SI), O. Morrone *et al.* 2972 (SI), F. Rial Alberti 466 (BAB), A. Roitman *et al.* 643 (SI), A. Schinini and R. Vanni 22431 (CTES 102930), J. G. Seijo *et al.* 2781 (SI), J. G. Seijo and A. Krapovickas 1943 (CTES 310568), C. Taylor 11339 (SI). Formosa: Bordón 98 (CTES 110835), R. H. Fortunato *et al.* 3402, 4393 (BAB), J. G. Seijo 1220 (CTES). Salta: C. Calcagnani 900 (BAB 7742), R. H. Fortunato *et al.* 7000, 7117, 7298, 7856 (BAB), P. Hoc and A. Lamarque 58 (BAB 91916), P. Jörgensen 383 (SI), A. Krapovickas 7991 (SI), A. Krapovickas *et al.* 28317 (CTES 110828), A. Krapovickas and A. Schinini 30573 (CTES 110829), Legname 5934 (LIL), E. R. Luna 796 (CTES 102928), F. E. Luna 1452 (CTES 113582), R. Martínez Crovetto 3689 (BAB), T. Meyer 18312 (CTES 117637), J. Morello and A. R. Cuezco 264 (CTES), L. Novara 6535 (MCNS), L. Novara and J. Ibáñez 10933 (CTES), C. Saravia Toledo 1325 (SI), 14565 (CTES), C. A. Spegazzini (BAB 13979), J. A. Tolaba 1499 (SI), 3258 (CTES 394932), Vallesjos 13 (BAB), Varela and Bianchi 1412 (MCNS), Villa Careno 140 (LIL 448977). Santiago del Estero: A. M. Molina 1781 (BAB), Vaca and Villa Careno 2798 (BAB), Venturi 6037 (BAB). Tucumán: E. Dinelli 794 (BAB 25707), Gautier 46 (BAB 35578), Lorentz s.n. (SI), R. Rocha 3780 (CTES 117973), R. Rossow 608 (BAB), C. A. Spegazzini (BAB 15200, 15223), Venturi 288 (BAB).

M. debilis var. *debilis* s.l. = *M. rixosa* Mart

SURINAM. Hostmann 1233 (BM). **BRAZIL.** Amazonia: G. Black et D. Magalhães s.n. (SI 138387), A. Ducke s.n. (SI). Distrito Federal: F. H. F. Oldenburger and Mecenas 2066 (CTES 174528). Goiás: M. M. Arbo 3501 (BAB). Mato Grosso: Herninger 5475 (SI). Mato Grosso do Sul: G. Hatschbach 23697 (SI), G. Hatschbach *et al.* 74006 (MBM 276722), G. Hatschbach and O. Guimaraes 21977 (MBM 11217). Minas Gerais: A. Ferreira 494 (CTES 118009), A. Macedo and Alvaro Luiz 1571 (SI), Martius s.n. (SI), L. O. Williams 5631 (SI). Pará: G. Black 5720090 (SI). Paraná: J. M. Cruz *et al.* 74 (MBM 238221), L. T. Dombrowski and P. Scherer Neto 1585 (MBM 284115), G. Hatschbach 2157, 3074 (SI), 38073 (MBM 54239), O. S. Ribas and L. B. Pereira 1687 (MBM 209049), 1767 (MBM 209048). São Paulo: Coleman and DeMenezes 16 (SP 152411), 31 (SP 152412), Gottsberger 14 (SI), O. Handro 44675 (SI), A. B. Joly 415 (SI), M. Kühlmann 3509 (SI), H. Luederwalcht 13112 (SI), O. S. Ribas *et al.* 5034 (MBM 284144), 5042 (MBM 279304). **BOLIVIA.** Santa Cruz: J. H. Hunziker and M. D. Hunziker 13228 (SI), J. H. Hunziker and A. Wulff 12926 (SI 51980), A. Krapovickas *et al.* 31687 (CTES 118087), A. Krapovickas and A. Schinini 31419 (CTES), M. Menacho and R. Rea 397 (CTES 293658), O. Morrone and M. Belgrano 5013 (SI), J. G. Seijo and V. Solís Neffa 3172, 3214 (CTES). **PARAGUAY.** Alto Paraguay: Woolston 468 (SI). Alto Paraná: M. G. López 266 (SI). Caaguazú: R. H. Fortunato *et al.* 8534 (BAB), J. E. Montes 11058 (CTES 102969), T. Rojas 14449 (CTES 91927), A. Schinini *et al.* 28145 (CTES 225958), 36161 (CTES 337425), E. M. Zardini and L. Guerrero 55980 (BAB), E. M. Zardini and H. Velázquez 25498, 25650, 25951, 26006 (BAB). Caazapá: N. Soria 3311 (SI), B. Sparre and F. Vervoorst 2247 (LIL). Canindeyú: S. Sede *et al.* 63 (BAB), E. M. Zardini and I. Chaparro 50646 (BAB), E. M. Zardini and M. Vera 47892 (BAB). Cordillera: A. Schinini 2543 (CTES). Guairá: B. Balansa 1453 (G), E. Bordas 3818 (CTES 103946), P. Jörgensen 4555 (MO 971849), T. Rojas 12501 (SI). San Pedro: R. H. Fortunato *et al.* 8826, 9193, 9214 (BAB), A. Krapovickas *et al.* 14293 (BAA), T. M. Pedersen 11147 (SI). **ARGENTINA.** Corrientes: M. M. Arbo 6415 (CTES), M. M. Arbo and A. Schinini 8745 (CTES 329965), De Marco *et al.* 10687 (CTES), R. Carnevali 1570 (CTES), Clos 6036 (BAB 51823), R. H. Fortunato *et al.* 3478, 7955, 8899 (BAB), G. Giberti and O. Ahumada 12 (CTES), A. Krapovickas *et al.* 16560 (MO 2038568), M. Morales *et al.* 644, 670 (BAB), M. Morales and J. G. Seijo 240, 246 (BAB), R. A. Spegazzini s.n. (BAB 10037, 10052, 10073), R. Vanni *et al.* 591 (CTES 117738). Misiones: Berti and Escalante 512 (SI), A. Burkart 15195, 15393 (SI), J. L. Fontana 239 (BAB), Grunner 665 (BAB 55777), R. H. Fortunato *et al.* 3926, 7964, 8904 (BAB), Giambagio no data (SI 15477), C. Hicken 171, 199 (SI), Isouribehere s.n. (BAB 24081), Jeckeln 31 (SI), A. de Llamas s.n. (BAB 13166), 12 (BAB 1069), 653 (BAB), R. Martínez Crovetto 8251, 9532 (BAB), J. E. Montes 1869 (SI), O. Morrone *et al.* 1015 (SI), Martinelli 6 (SI), L. Parodi 4155, 4305 (SI), M. Rodríguez 871 (BAB), A. Schinini and J. Daviña 24728 (CTES 103886), Schwarz 588 (CTES), Schwindt 1104 (CTES), 2941 (CTES 91918), 3988 (BAA), J. G. Seijo 143, 268, 378, 532 (BAB), 277 (CTES 305355), C. Spegazzini no data (BAB 18272, 19693, 19694), F. Zuloaga *et al.* 5332 (SI).

M. nuda var. *nuda* s.s.

BRAZIL. Goiás: A. Krapovickas *et al.* 33278 (CTES). Mato Grosso: W. R. Anderson 11240 (CTES 111199), G. Hatschbach 34122 (MBM 29291). Mato Grosso do Sul: A. Krapovickas 32872 (CTES 117722), A. Krapovickas and C. Cristóbal 34406 (CTES 135206), A. Pott 6173 (COR 9633), A. Pott and S. G. Nunes 7736 (COR 15352). Minas Gerais: A. Macedo 4195 (SI). **BOLIVIA.** Dpto Santa Cruz: B. Bruderreck 115 (BAB), A. Krapovickas 36443 (BAB), J. G. Seijo and V. Solís Neffa 3290 (CTES).

M. nuda var. *nuda* s.l.

PARAGUAY. San Pedro: R. H. Fortunato *et al.* 9354 (BAB), E. M. Zardini and L. Guerrero 46658 (BAB).

Intermediate between M. debilis var. *debilis* s.l. = *M. rixosa* and *M. nuda* var. *gracilipes*–*M. nuda* var. *glaberrima*

BRAZIL. Distrito Federal: J. H. Kirkbride 1040 (CTES 170349), 3083 (CTES 102992), 5513 (CTES), Pires 9078 (SI). Goiás: W. R. Anderson 7100 (MBM 100397), G. Hatschbach *et al.* 70450 (MBM 246945). Mato Grosso: R. M. Harley et R. Souza 11031 (MO), Herninger 7435 (SI). Mato Grosso do Sul: G. Hatschbach 23967 (MBM 13716), 29424 (MBM 21123), A. Krapovickas and C. Cristóbal 43172 (CTES 147056), A. Pott 8251 (COR), O. S. Ribas and L. B. S. Pereira 2595 (MBM). Minas Gerais: M. M. Arbo 4877 (BAB). Paraná: G. Hatschbach 3605 (MBM 42291), 6910 (MBM 44229), 18863 (SI). **PARAGUAY.** Alto Paraná: K. Fiebrig 5932 (SI). Guairá: P. Jörgensen 3635 (MO 971464). Itapúa: J. de Egea *et al.* 289 (CTES 409014), T. M. Pedersen 3271 (G), E. M. Zardini 51977, 55538 (BAB), E. M. Zardini and R. Gamarra 51964, 59389, 59447, 59480 (BAB), E. M. Zardini and J. Rodríguez 51687 (BAB). **ARGENTINA.** Corrientes: R. Carnevali 4622 (CTES), A. Honfi and J. J. Daviña 971 (CTES 324908), M. Morales and J. G. Seijo 237, 256, 261 (BAB). Misiones: J. Daviña *et al.* 145 (CTES 209952), J. G. Seijo 452, 920 (BAB).

Intermediate between M. debilis var. *debilis* s.s. and *M. nuda* var. *gracilipes*–*M. nuda* var. *glaberrima*

BRAZIL. Paraná: J. Carneiro 1050 (MBM 256944), M. G. Caxambú 388 (MBM 294721). Mato Grosso do Sul: A. Krapovickas et C. L. Cristóbal 42968 (CTES 146742), O. S. Ribas and L. B. S. Pereira 2521 (MBM 220678). **BOLIVIA.** Dpto. Santa Cruz: A. Fuentes and G. Navarro 2613 (CTES 298661), A. Krapovickas and A. Schinini 31419 (CTES). **PARAGUAY.** E. Hassler 8511 (G). Amambay: J. Fernández Casas 6220 (G). Central: R. H. Fortunato *et al.* 8850 (BAB), E. M. Zardini 35274 (BAB), E. M. Zardini and Malme 25440 (BAB). Canindeyú: E. M. Zardini 50682 (BAB). Concepción: R. H. Fortunato *et al.* 817 (BAB). Cordillera: W. Hahn no data, 2036 (BAB), E. Hassler 3350 (G), A. Schinini 2318 (CTES 140449), E. M. Zardini 25808 (BAB), E. M. Zardini and P. Aquino 28765 (BAB), E. M. Zardini and R. Velázquez 26266, 26705 (BAB). Guairá: T. Rojas 3708 (SI). Misiones: A. Schinini and R. Vanni 26042, 26118 (BAB). Ñeembucú: G. Schulz 7767 (SI). Paraguari: W. Hahn 2374 (BAB). Presidente Hayes: E. Simonis and W. Hahn 1 (G). San Pedro:

R. H. Fortunato *et al.* 9356 (BAB), W. Hahn 1172 (BAB), T. M. Pedersen 9377 (MBM), E. M. Zardini 56508 (BAB). **ARGENTINA.** Corrientes: R. Carnevali 6107 (CTES 150161), R. H. Fortunato *et al.* 8886 (BAB), C. Hicken 338 (SI), A. Krapovickas and C. Cuarín 20913 (BAA), M. Morales and J. G. Seijo 235, 238 (BAB), E. Nicora (BAA 429), A. Schinini *et al.* 21779 (CTES).

Intermediate between M. nuda var. glaberrima and M. nuda var. gracilipes

BRAZIL. Mato Grosso do Sul: Etchichury s.n. (SI). **PARAGUAY.** Amambay: Schwarz 12146 (CTES), E. M. Zardini and P. Báez 52270 (BAB). Caaguazú: F. Casas 3809 (G). Central: E. Hassler 8002 (G), H. J. Kaplan 566 (BAB). Canindeyú: E. M. Zardini 50682 (BAB). Cordillera: E. Hassler 3350 (BAB), E. M. Zardini and R. Degen 3678 (BAB). Itapúa: E. M. Zardini and R. Gamarra 55602 (BAB). Misiones: E. M. Zardini and L. Guerrero 55322 (BAB). Paraguairí: B. Sparre and F. Vervoorst 216 (BAB). **ARGENTINA.** Corrientes: C. Hicken 342 (SI), U. Eskuche 2088 (BAB), T. M. Pedersen 14826 (CTES), J. G. Seijo 329 (SI).