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Revisiting the inflorescence structure, the floral traits and pollen aggregations of four species of *Mimosa* (Leguminosae, Caesalpinioideae) occurring in Mexico

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Abstract

Background: With 615 species worldwide, *Mimosa* is among the largest genera of the Leguminosae family, and Mexico is the second center of distribution of the genus after Brazil, with 105 species. In recent years, interest has arisen in morphological and anatomical characters of the flower in relation to floral visitors in *Mimosa*.

Questions: What is the relationship between inflorescence type, number and arrangement of flowers on the floral axis? What are the morphological and anatomical characters of the floral whorls that distinguish the *Mimosa* species? Which is the pollen-stigma relationship, how does it influence the reproductive strategies?

Study species: *Mimosa affinis* B.L.Rob., *M. albida* Humb. & Bonpl. ex Willd., *M. lactiflua* Delile ex Benth., and *M. polyantha* Benth.

Study area: Southeastern Morelos and southwestern Puebla, Mexico.

Methods: A comparative study of inflorescence morphometry in capitula and spikes was carried out, to evaluate the merism variability of flowers in anthesis, the comparative morphoanatomy of flowers and pollen aggregations.

Results: Statistical analysis showed differences in morphometric characters of inflorescence, flower and pollen aggregation. There are anatomical differences in the flowers such as: various types of trichomes on the bracteole, perianth and ovary; fusion of the stamens at the base; poriform and crateriform stigma; paracytic stomata; striate cuticle in epidermal cells.

Conclusions: The species showed morphological and anatomical differences in inflorescence, flower and pollen aggregation, generating relevant information to understand *Mimosa*'s reproductive strategies although further studies of floral characters are needed regarding the interactions with floral visitors.

Keywords: floral morphometry, floral micromorphology, inflorescence structure, palynology.

Resumen

Antecedentes: Con 615 especies a nivel mundial, *Mimosa* es uno de los géneros más diversos de la familia Leguminosae y México es el segundo centro de distribución después de Brasil, con 105 especies. En años recientes ha surgido interés por los caracteres morfológicos y anatómicos de la flor relacionados con visitantes florales en *Mimosa*.

Preguntas: ¿Cuál es la relación del tipo de inflorescencia con el número y arreglo de las flores en el eje floral? ¿Qué caracteres morfológicos y anatómicos de los verticilos florales distinguen a las especies de *Mimosa*? ¿Cuál es la relación polen-estigma y cómo influye en sus estrategias reproductivas?

Especies en estudio: *Mimosa affinis*, *M. albida*, *M. lactiflua* y *M. polyantha*.

Área de estudio: Sureste de Morelos y suroeste de Puebla, México.

Métodos: Se realizó un estudio comparativo de morfometría de las inflorescencias en capítulos y espigas, para evaluar la variabilidad del merismo de flores en antesis, de morfoanatomía de las flores y de las asociaciones polínicas.

Resultados: El análisis estadístico mostró diferencias en los caracteres morfométricos de inflorescencia, flor y polen agregado. Existen diferencias anatómicas en las flores como: diferentes tipos de tricomas en bractéola, perianto y ovario; fusión basal de estambres; estigma poriforme y crateriforme; estomas paracíticos; epidermis con cutícula estriada.

Conclusiones: Las especies presentaron diferencias morfológicas y anatómicas en la inflorescencia, flor y asociación polínica, generando información relevante para comprender las estrategias reproductivas de *Mimosa*, aunque son necesarios más estudios de caracteres florales en relación con los visitantes florales.

Palabras clave: estructura de la inflorescencia, morfometría floral, micromorfología floral, palinología.

The family Leguminosae is one of the largest in the world, with ca. 770 genera (LPWG 2013, 2017) and it is one of the most highly represented families in Mexico (Rzedowski 1991, Sousa *et al*. 2004). Notable among its genera, *Mimosa* is placed in the subfamily Caesalpinioideae, tribe Mimoseae (LPWG 2017, Queiroz *et al*. 2024), in the Mimosa clade. The genus comprises 615 species (Borges *et al*. 2024) divided into five sections (*M*. sect. *Mimadenia* Barneby, *M*. sect. *Batocaulon* DC., *M*. sect. *Calothamnos* Barneby, *M*. sect. *Habbasia* DC., and *M*. sect. *Mimosa*), with 42 series and 37 subseries (Barneby 1991, Grether 2000).

Mimosa is characterised by a persistent fruit margin, in addition, some characters as the flower grouping in inflorescences such as capitula, spikes or racemes, the presence of sessile or rarely pedicellate flowers, tetramerous or pentamerous, or rarely trimerous, the presence of diplostemonous or haplostemonous flowers or of staminodes, the number of stamens (4, 5, (6), 8, 10), filaments free or basally fused, exserted, gynoecium sessile or stipitate, linear to oblong or elliptical, glabrous to pubescent or setose (Grether *et al*. 2007, Martínez-Bernal *et al*. 2008, Borges & Pirani 2017), stigma poriform, cupuliform, tubular, obliquely infundibuliform (Grether 1997) or crateriform (Martínez-Olivares 2014) have made it possible to distinguish groups of species of *Mimosa* at the infrageneric level.

In particular, *M*. sect. *Mimosa* is an infrageneric group with neotropical distribution, with great diversification in South America, occurring in Central America, and reaching up to the tropic of Cancer, at 23° 26' 17" north latitude, in the state of Sinaloa, represented in Mexico only by 21 species (Grether 1997, Grether *et al*. 2015). On the other hand, *M*. sect. *Batocaulon* includes 77 species in Mexico, most of them endemic to the country.

Another character that has proven relevant for species recognition is the type of pollen association, in the tribe Mimoseae the pollen arrangement is extremely variable across and sometimes within genera (Queiroz *et al*. 2024), conferring an advantage in pollen dispersal, protection against desiccation in arid environments (Santos-Silva *et al*. 2013) and the opportunity to germinate and fertilized all ovules within the ovary (Capucho & Teixeira 2020); in *Mimosa* it is possible to recognise polyads (12 to 16 monads), ellipsoidal or spheroidal octads and tetrahedral or tetragonal tetrads which are discoid, spheroidal, oviform to pyriform or rhomboidal in shape and vary in terms of size. In *M*. sect. *Batocaulon* both octads and tetrads are present, while in *M*. sect. *Mimosa* only tetrahedral and tetragonal tetrads are known up to date. Differentiation has also been observed in exine ornamentation and aperture diameter (Guinet 1981, Caccavari 1985, 1986, 1987, 1988, 2002, Chehaibar 1988, Grether & Martínez-Bernal 1996, Grether 1997, Martínez-Bernal 2003, Flores-Cruz *et al*. 2006, Lima *et al*. 2008, Santos-Silva *et al*. 2013, Martínez-Olivares 2014, Medina-Acosta 2016, Medina-Acosta *et al*. 2019).

Studies that analyse the relationship between pollen aggregation type and stigma in *Mimosa* are limited, particularly in *M*. sect. *Mimosa* and *M*. sect. *Batocaulon*, specially in species distributed in Mexico, so more studies are needed. Martínez-Olivares (2014) analysed the morphometric characteristics of the inflorescences and flowers of five *Mimosa* species, members of *M*. sect. *Batocaulon* and *M*. sect. *Habbasia*, occurring in Mexico, demonstrating the relationship between the shape and depth of the stigma, the shape and dimensions of the pollen grains, as well as the viability, production of pollen grains, and germination of the pollen tubes. This author recorded different shapes of the stigma and associated them with the size and number of tetrads or polyads that it can capture. Seijo & Solís-Neffa (2004) and Guglielmi & Teixeira (2024) reported the relationship between the internal diameter of the poriform stigma and the dimensions of the ellipsoidal octad in *M. bimucronata* (DC.) Kuntze and *M. caesalpiniifolia* Benth. (*M*. sect. *Batocaulon*), indicating that these features only permit the capture of one octad positioned longitudinally in the stigma.

Considering the importance of the inflorescence as the pollination unit in Mimoseae (Arroyo 1981), the studies of inflorescence and floral structure in more species of the genus are needed. In this regard, Grether & Camargo-Ricalde (1993) have reported variations in the number of lobes per corolla (4 or 5) and in the number of stamens per flower (8 or 10) for *M. bahamensis* Benth., both variations being found in the flowers of the same inflorescence (capitulum) and in different capitula of the same individual. In addition, recent studies on comparative floral development in four species of *Mimosa*: *M. pudica* L. (*M*. sect. *Mimosa*) and *M. bimucronata* with tetramerous flowers, *M. caesalpiniifolia* Benth. with trimerous flowers and *M. candollei* R.Grether with pentamerous flowers (*M*. sect. *Batocaulon*) provide new data about merism variability in mimosoids, where the merism (or merosity) is the number of floral parts per whorl in the flower, usually based on the parts of the perianth (Ronse De Craene 2016, 2022). Something that is constantly an undergoing change is the merism in the genus *Mimosa* with the flowers having whorls composed of 3, 4, 5 or 6 units; main results of Gonçalves *et al*. (2024) show that predominant merism is varying in some cases, and that the variability is associated to actinomorphic flowers and their arrangement in the inflorescence. The diplostemonous androecium and the pentamerous perianth are considered plesiomorphic; the haplostemonous androecium and the tetramerous, trimerous and hexamerous flowers are derived from the pentamerous ones. They show that this wide variation in the floral merism is a result of the absence of organs from the beginning of development, although Ronse De Craene (2016) mentions that it is also influenced by the reduction of available space in the floral meristem due to larger primordia preventing the development of other organs, leading to the hypothesis that the reduction in the number of initial primordia in the floral meristem results in variability of shapes and sizes and the number of organs.

Inflorescence structure as the pollination unit, floral morphological characters and pollen aggregation types are relevant in species reproductive strategies; the following studies are outstanding: the floral morphology of six species of *M*. sect. *Habbasia* ser. *Setosae* (Borges & Pirani 2017), the micromorphology of the flower in 28 species of *M*. sect. *Calothamnos* (Grohar *et al*. 2021) and the pollen association types of 219 of a total of 615 *Mimosa* species (Medina-Acosta *et al*. 2019, Borges *et al*. 2024).

Thus, the objectives of the present work were to perform a comparative study of the inflorescence structure, including the flower arrangement in heads and spikes, as well as the morphometry of the flowers, to evaluate the whorls of the flowers at anthesis, the comparative anatomy of the flower whorls and the morphoanatomy of the pollen aggregations for contributing to the distinction at the specific level and their implications in the reproductive strategies of four species of *Mimosa* occurring in Mexico.

Materials and methods

Selection of species and collection sites. Four species of the genus *Mimosa* belonging to different sections and series were selected (Barneby 1991) in consideration of their geographic distribution: *endemic to Mexico, **endemic to Mexico and Central America, and ***wide distribution in the Americas; their habit associated to the habitat, inflorescence type, pollen aggregation type and including the individuals with flowers in anthesis. The species studied were as follows: ***M. affinis* B.L.Rob. (*M*. sect. *Mimosa* ser. *Mimosa*), ****M. albida* Humb. & Bonpl. ex Willd. (*M*. sect. *Mimosa* ser. *Mimosa*), **M. lactiflua* Delile ex Benth. (*M*. sect. *Mimosa* ser. *Lactifluae*) and **M. polyantha* Benth. (*M*. sect. *Batocaulon* ser. *Distachyae*). Collection of material was carried out in the municipalities of Jolalpan (*M. affinis*, *M. lactiflua* and *M. albida*) and Teotlalco (*M. albida* and *M. polyantha*) in southwestern Puebla, and in the municipality of Axochiapan (*M. polyantha*) in southeastern Morelos (Figure 1A-D, Table S1).

For each species, five individuals in the flowering period were chosen. From each individual, 15 inflorescences were selected (75 per species, 300 in total), which were transported in the following manner: 5 inflorescences at anthesis per individual were placed in bottles and fixed in FAA (formalin: glacial acetic acid: ethanol: distilled water, 2: 1: 10: 7 v/v) and then preserved at 70 % ethanol until analysis (Márquez-Guzmán *et al*. 2016), for a total of 25 inflorescences per species. Additionally, 5 inflorescences with flower buds and 5 inflorescences with flowers in anthesis per individual were stored separately in paper bags (50 per species in total), they were dehydrated for counting flowers per inflorescence and pollen processing.

The voucher specimens were incorporated into the collection of the Herbario Metropolitano (UAMIZ) at Universidad Autónoma Metropolitana, Campus-Iztapalapa (Table S1).

Inflorescence and flower characterisation. The inflorescences of each species were characterised according to the length of the floral axis, the width of the spike or capitulum inflorescence and the length of the peduncle; and the number of flowers per inflorescence was counted. To characterise the flowers, the length of the calyx and the corolla, the pedicel of the flower, the antisepalous and antipetalous stamens, the length and width of the anthers, the length of the gynoecium and stipe of the ovary and the length and width of the bracteole were measured. The number of corolla lobes, ovules per ovary and the number of stamens per flower were also recorded. For each variable, 25 measurements were made per individual (125 in total per species), with a Quasar model QM15 stereo microscope, and a Zaigen ocular micrometer (1 mm).

Descriptions of the morphological characters of the inflorescences and flowers are based on the terminology employed in Barneby (1991), Grether *et al*. (2007), Martínez-Bernal & Grether (2006), and Martínez-Bernal *et al*. (2008).

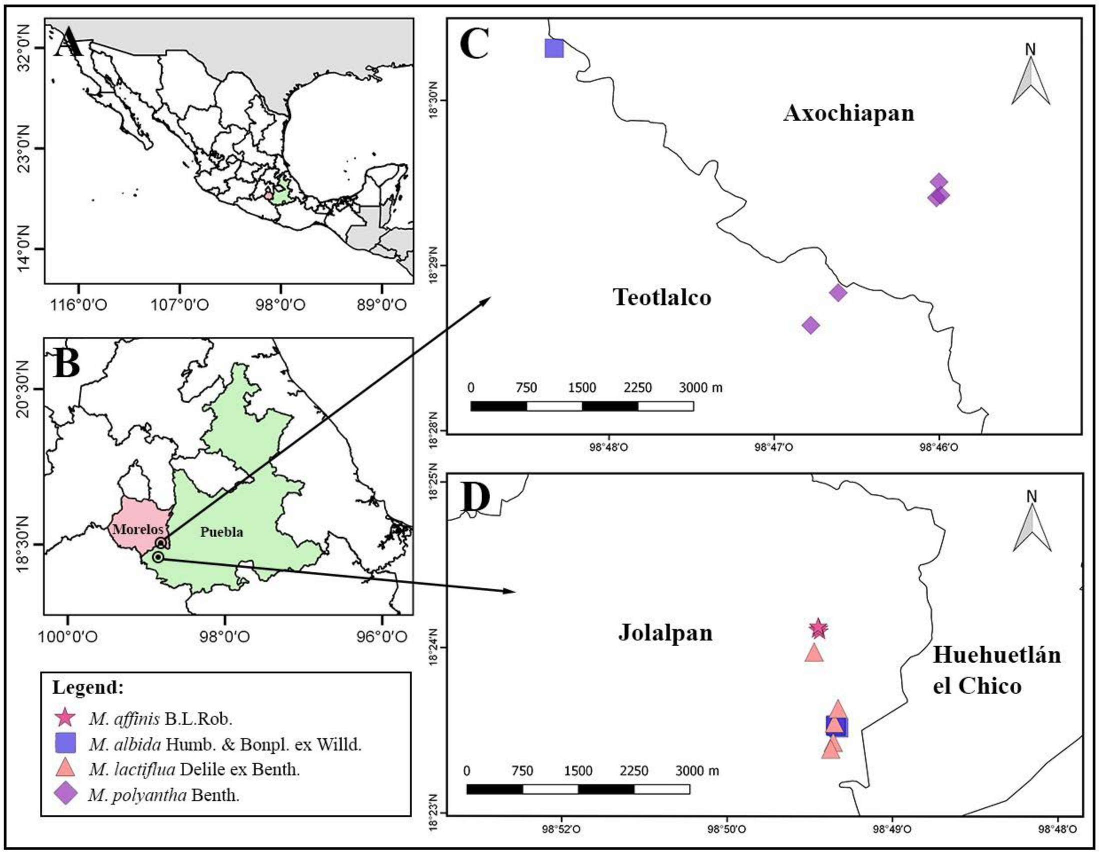

Figure 1. Study areas and the collection of individuals of the four species of *Mimosa*. A. Mexico. B. Location of the states of Morelos and Puebla in Mexico. C, D. Collection sites in the municipalities of Axochiapan (C), Morelos, Teotlalco (C) and Jolalpan (D), Puebla, Mexico.

Floral micromorphology under scanning electron microscopy. Nine flowers in ethanol at 70 % were selected and dissected from the basal, middle and apical portions of the inflorescences of each species (36 in total) and placed in sample holders, dehydrated for 30 minutes using 96 % ethanol solution, transferred to pure ethanol (100 %) for 15 minutes, then in a methanol solution for 24 h. The samples were critical-point dried, mounted on pins and coated with gold. The photomicrographs were taken with electron microscopes: a Carl Zeiss EVO 50, a JEOL JSEM 6390 and a JEOL JSM 5900LV.

The terminology used in the descriptions of the floral characters observed under SEM is based on Luckow & Grimes (1997), Crang *et al*. (2019) and Grohar *et al*. (2021).

Pollen morphology under light and scanning electron microscopy. For the pollen analysis under light microscopy (ML), 50 flower buds per individual (250 in total), previously dehydrated, were selected and processed according to Erdtman's acetolysis method (1960) modified by Martínez-Hernández (1970). Measurements were taken in 25 pollen aggregates per individual (125 per species, 500 in total) of the major and minor diameters and of the diameter in polar view. Additionally, in 25 monads the polar and equatorial axes, exine thickness and pore diameter were measured, and the number of pores per monad was counted. The photomicrographs were taken through a Carl Zeiss Axiophot microscope.

The methodology proposed by Medina-Acosta (2016) was followed in the processing of the pollen viewed under scanning electron microscopy (SEM); to this end, three flower buds per species were selected and the anthers were extracted. The samples were observed and photographed with scanning electron microscopes Carl Zeiss EVO 50 and JEOL JSM 5900LV. Palynological descriptions are based on the terminology employed in Punt *et al*. (2007) and Medina-Acosta *et al*. (2019).

Statistical analyses. The continuous and discrete quantitative variables obtained from the morphological characters of the inflorescence, the flower and the palynological characters did not meet the assumptions of normality and homoscedasticity of variances, so they were analysed using the Kruskal-Wallis test ($P < 0.05$), followed by a Mann-Whitney U test. To determine the relationship between the inflorescence and flower variables, a Spearman correlation analysis was carried out (Gotelli & Ellison 2012, Sokal & Rohlf 1980). All analyses were performed using NCSS 2020 software.

Results

Comparative inflorescence structure and flower morphometry. *Mimosa affinis* is a decumbent, annual herbaceous plant (Figure 2A, C), *M. albida* (Figure 2D, E, H) and *M. lactiflua* (Figure 2I, J) are shrubby species, in contrast to *M. polyantha* which is arboreal (Figure 2L, M, O) (Table 1).

The flowers were grouped in inflorescences that may be capitula with ascending flowers (*M. affinis*, Figures 2B, 4A), globose capitula (*M. albida*, Figures 2F, G, 3A, 4B, and *M. lactiflua*, Figures 2K, 3B-E, 4C) or spikes (*M. polyantha*, Figures 2N, 3F, 4D) (Table 1). *Mimosa polyantha* exhibited the greatest floral axis length, while *M. affinis* displayed the shortest; no statistically significant differences were found between *M. albida* and *M. lactiflua* (Figure 5A, Table 2). *Mimosa affinis* showed the narrowest floral axis, followed by *M. polyantha*, while *M. albida* and *M. lactiflua* had the widest floral axis with no significant differences (Figure 5B, Table 2). As to the inflorescence peduncle, *M. lactiflua* exhibited the greatest length and *M. polyantha* the shortest (Figure 5C, Table 2).

In three species (*M. affinis*, *M. albida* y *M. lactiflua*) the sexual system is andromonoecious, while in *M. polyantha* it is hermaphroditic. The bisexual flowers numbering from 8 (*M. affinis*) to 131 (*M. lactiflua*) per inflorescence and staminate flowers from 1 (*M. affinis, M. albida* and *M. lactiflua*) to 91 (*M. albida*) per inflorescence, while in *M. polyantha*, spikes have 59 to 91 bisexual flowers only (Tables 1, 2). *Mimosa affinis* had the smallest number of flowers per inflorescence, and *M. albida* and *M. lactiflua* the largest number of flowers (Figure 5D, Table 2). It should be noted that the flowers were sessile in three of the species and that *M. polyantha* was the only species with pedicellate flowers (Table 2). Each flower is subtended by a bracteole along the floral axis of a capitulum or spike (Figure 4E-H).

All species showed significant differences in perianth length, with *M. lactiflua* showing the greatest length and *M. affinis* the shortest length (Figure 5E, Table 2). Likewise, all species exhibited a campanulate calyx, with margin glabrous or with different types of trichomes (Table 1), however, the number of lobes in *M. affinis*, *M. albida* and *M. lactiflua* is 4 (Figure 4E-G), in contrast to *M. polyantha* with calyx 4-5 lobed (Figure 4H); the shortest length was observed in *M. affinis*, followed by *M. albida* and *M. lactiflua*, and the greatest in *M. polyantha* (Figure 5F, Table 2).

The corolla may have 4 lobes (in *M. affinis*, *M. albida* and *M. lactiflua*, Figure 4E-G, I-K, respectively) or 4-5 lobes (in *M. polyantha*, Figure 4H, L), the free portion (lobes) 1/4 (*M. affinis*), 1/3 (*M. albida* and *M. lactiflua*) or 1/2 the length of the corolla (*M. polyantha*), strigose in *M. albida* or glabrous in the rest of the species, with a deep pink, pink or white colour (Table 1); *M. affinis* also displayed the shortest corolla length, followed by *M. albida* and *M. polyantha*, while *M. lactiflua* showed the greatest (Figure 5G, Table 2).

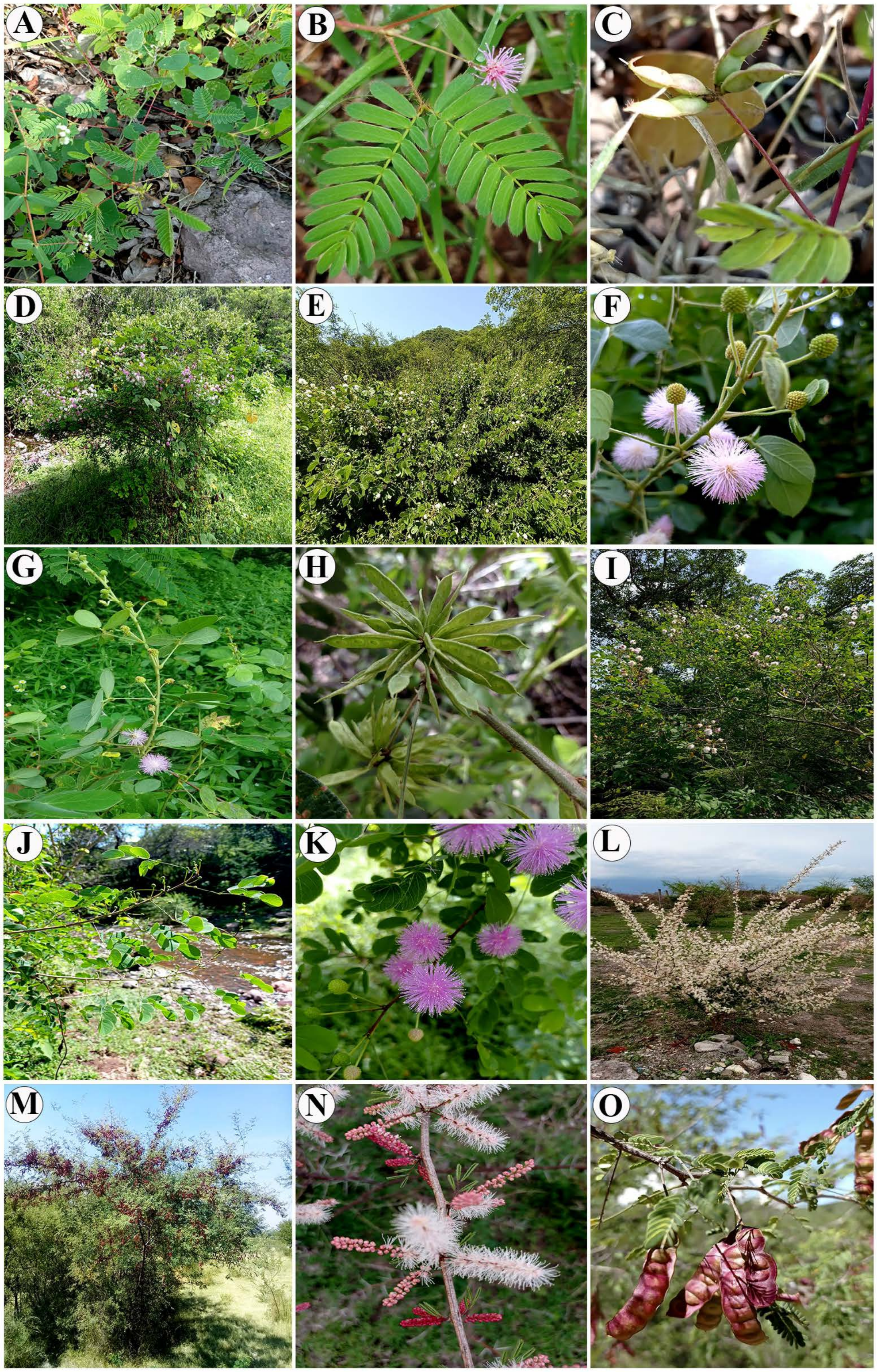

Figure 2. Growth forms in four species of *Mimosa*. A-C. *M. affinis*: Decumbent annual herb (A), inflorescence in capitulum with ascending flowers (B), and fruits (C). D-H. *M. albida*: Shrubby habit (D, E), flowers in globose capitula and flower buds (F, G), and immature fruits (H). I-K. *M. lactiflua*: Shrubs (I, J), inflorescences in globose capitula and branches with immature capitula (K). L-O. *M. polyantha*: Shrubby (L) and arboreal habit (M), inflorescences in spikes (N), and fruits (O).

Table 1. Inflorescence and floral morphology and palynological characters of four species of *Mimosa*.

Characters / Species	***M. affinis***	***M. albida***	***M. lactiflua***	***M. polyantha***
Floral morphological characters				
- Growth form	Decumbent herb	Shrub	Shrub or tree	Tree or shrub
***Inflorescence*:**				
- Type	Capitulum with ascending flowers	Globose capitulum	Globose capitulum	Spike
- Peduncle indumentum	Hispid to glabrous	Strigose	Glabrous	Tomentulose
- Total number of flowers	8 to 16	81 to 138	66 to 131	59 to 91
- Bisexual flowers	8 to 16	39 to 110	51 to 131	59 to 91
- Staminate flowers	1 to 2	1 to 91	1 to 74	Absent
***Bracteole*:**				
- Shape	Linear to lanceolate	Linear	Spatulate	Oblanceolate
- Indumentum	Glabrous	Setose	Glabrous	Tomentose
***Calyx*:**				
- Shape	Campanulate	Campanulate	Campanulate	Campanulate
- Number of lobes	4-lobate	4-lobate	4-lobate	4-5 lobate
- Indumentum	Glabrous	Glabrous	Glabrous	Glabrous
- Border	Ciliate	Setose	Glabrous	Ciliate
***Corolla*:**				
- Number of lobes	4–lobate	4–lobate	4–lobate	4–5 lobate
- Lobes	Free in 1/4 of corolla length	Free in 1/3 of corolla length	Free in 1/3 of corolla length	Free in 1/2 of corolla length
- Indumentum	Glabrous	Strigose	Glabrous	Glabrous
- Colour	Intense pink	Intense pink or pink	Pink	Pink or white
***Androecium*:**				
- Number of stamens	4	4	4	8 to 10 (11)
- Stamen colour	Lilac	Lilac	Lilac	Pink
- Anther insertion	Dorsifixed	Dorsifixed	Dorsifixed	Dorsifixed
- Anther shape	Oblong	Oblong	Oblong	Oblong
- Anther colour	Purple, yellow	Yellow	Yellow	Yellow
***Gynoecium*:**				
- Number of ovules per ovary	1 to 3	5 to 7	3 to 6	7 to 10
- Stigma form	Crateriform	Poriform	Poriform	Poriform
Palynological characters				
- Association of pollen grains	Tetrad	Tetrad	Tetrad	Octad
- Type	Tetrahedral	Tetrahedral	Tetrahedral	Rotated
- Shape	Ovoid to spheroidal	Spheroidal	Spheroidal	Ellipsoidal
- Ornamentation	Verrucate	Microverrucate, microverrucate-rugulate	Microverrucate, microverrucate-rugulate	Microverrucate-rugulate
- Monads shape	Pyramidal	Pyramidal	Pyramidal	Pyramidal or trapezoidal
- Number of apertures	3	3	3	3–4

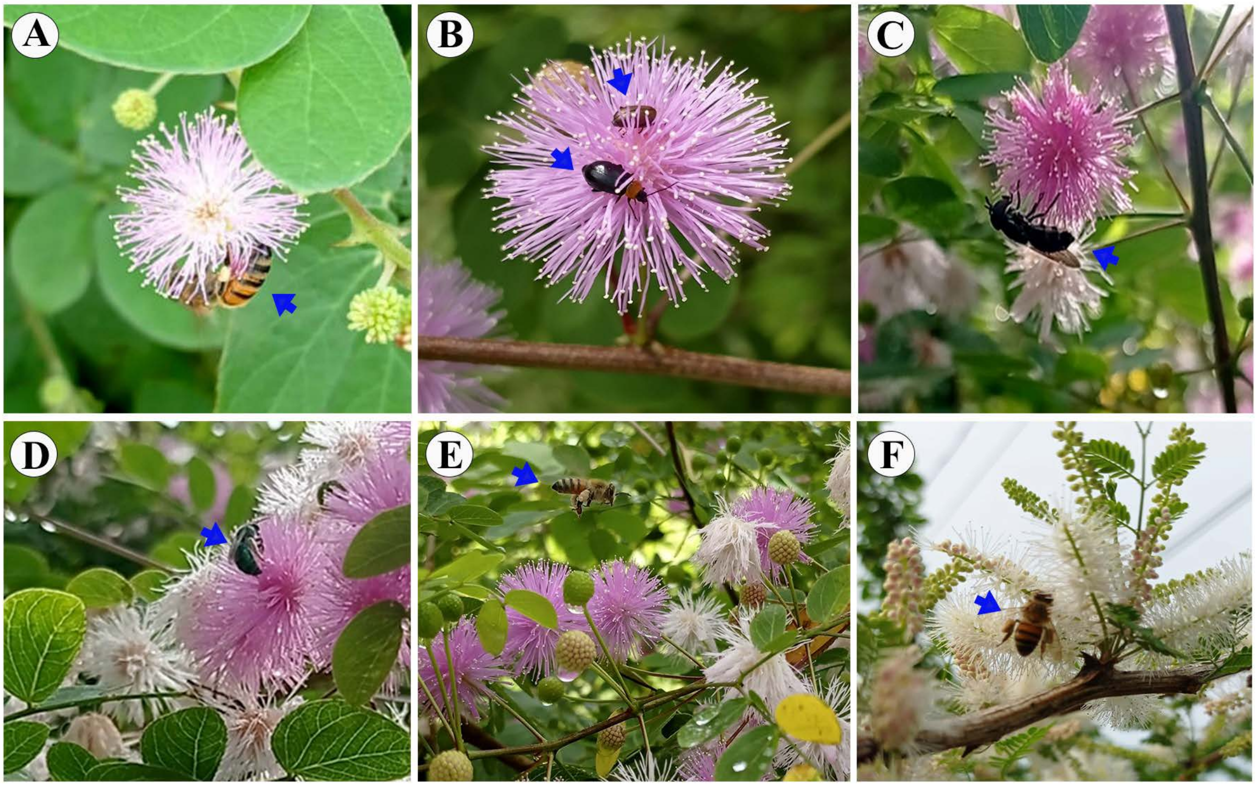

Figure 3. Flower visitors in three species of *Mimosa*. A. *M. albida* with a member family of Apidae foraging in the globose capitulum. B-E. *M. lactiflua*, flower visitors of Order Coleoptera and family Chrysomelidae (B), floral visitor of family Apidae (C, D, E). F. *M. polyantha* with a member family of Apidae foraging in the spikes. Blue arrows: pointing to the floral visitors.

Table 2. Statistical analysis of the inflorescence and the flower morphology. Analysis of variance, Kruskal-Wallis followed by Mann-Whitney U based on mean ± standard error (SE). Means with different letters are significantly different ($P < 0.05$).

Variables	Species	Mean ± SE	Smallest value	Largest value
***Inflorescence morphology* (*n* = 25)**				
Floral axis length (cm)	*M. affinis*	0.37 ± 0.01 ^{c}	0.28	0.48
	M. albida	1.52 ± 0.07 ^{b}	1.03	2.30
	M. lactiflua	1.57 ± 0.04 ^{b}	0.99	1.90
	M. polyantha	3.86 ± 0.19 ^{a}	2.15	2.32
Floral axis width (cm)	*M. affinis*	0.57 ± 0.01 ^{c}	0.48	0.72
	M. albida	1.58 ± 0.07 ^{a}	1.07	2.30
	M. lactiflua	1.62 ± 0.03 ^{a}	1.03	1.98
	M. polyantha	1.14 ± 0.04 ^{b}	0.72	1.59
Peduncle length (cm)	*M. affinis*	1.74 ± 0.08 ^{b}	1.02	3.02
	M. albida	1.54 ± 0.17 ^{b}	0.63	3.13
	M. lactiflua	2.33 ± 0.08 ^{a}	1.58	3.10
	M. polyantha	0.82 ± 0.07 ^{c}	0.24	1.83
Number of flowers per inflorescence	*M. affinis*	11.44 ± 0.42 ^{c}	8	16
	M. albida	110.48 ± 2.81 ^{a}	81	138
	M. lactiflua	107.84 ± 3.70 ^{a}	66	131
	M. polyantha	78.36 ± 2.03 ^{b}	59	92

Variables	**Species**	**Mean ± SE**	**Smallest value**	**Largest value**
Perianth length (mm)	*M. affinis*	1.27 ± 0.01 ^{d}	0.63	1.70
	M. albida	1.71 ± 0.02 ^{c}	0.90	2.26
	M. lactiflua	2.06 ± 0.01 ^{a}	1.47	2.45
	M. polyantha	1.84 ± 0.01 ^{b}	1.29	2.26
Calyx length (mm)	*M. affinis*	0.16 ± 0.007 ^{d}	0.08	1.00
	M. albida	0.22 ± 0.005 ^{c}	0.12	0.34
	M. lactiflua	0.40 ± 0.01 ^{b}	0.03	0.62
	M. polyantha	0.54 ± 0.006 ^{a}	0.42	0.70
Corolla length (mm)	*M. affinis*	1.17 ± 0.01 ^{d}	0.62	1.89
	M. albida	1.56 ± 0.02 ^{c}	0.82	2.09
	M. lactiflua	1.96 ± 0.07 ^{a}	1.10	7.98
	M. polyantha	1.69 ± 0.07 ^{b}	1.21	2.21
Pedicel length (mm)	*M. polyantha*	0.11 ± 0.03	0.02	0.25
Number of stamens per flower	*M. affinis*	4.00 ± 0.00 ^{b}	4	4
	M. albida	4.00 ± 0.00 ^{b}	4	4
	M. lactiflua	4.00 ± 0.00 ^{b}	4	4
	M. polyantha	8.22 ± 0.10 ^{a}	5	11
Antisepalous stamen length (mm)	*M. affinis*	2.74 ± 0.02 ^{d}	2.06	3.26
	M. albida	5.03 ± 0.11 ^{b}	2.26	7.25
	M. lactiflua	6.37 ± 0.06 ^{a}	4.15	8.44
	M. polyantha	3.26 ± 0.03 ^{c}	2.12	3.99
Antipetalous stamen length (mm)	*M. polyantha*	4.04 ± 0.03	2.83	4.76
Anther length (mm)	*M. affinis*	0.24 ± 0.003 ^{c}	0.17	0.35
	M. albida	0.33 ± 0.007 $^{a b}$	0.16	0.52
	M. lactiflua	0.32 ± 0.003 ^{b}	0.22	0.39
	M. polyantha	0.34 ± 0.005 ^{a}	0.22	0.51
Anther width (mm)	*M. affinis*	0.27 ± 0.003 ^{c}	0.19	0.36
	M. albida	0.36 ± 0.003 ^{a}	0.22	0.45
	M. lactiflua	0.36 ± 0.003 ^{a}	0.28	0.45
	M. polyantha	0.30 ± 0.003 ^{b}	0.22	0.39
Ovary and style length (mm)	*M. affinis*	2.61 ± 0.02 ^{d}	1.64	3.14
	M. albida	5.16 ± 0.08 ^{b}	1.70	8.50
	M. lactiflua	7.06 ± 0.09 ^{a}	2.49	9.14
	M. polyantha	3.79 ± 0.04 ^{c}	2.09	4.59
Stipe of ovary length (mm)	*M. affinis*	0.04 ± 0.002 ^{c}	0.02	0.08
	M. albida	0.11 ± 0.003 ^{a}	0.02	0.17
	M. lactiflua	0.07 ± 0.001 ^{b}	0.05	0.08
	M. polyantha	0.11 ± 0.002 ^{a}	0.02	0.17

Variables	**Species**	**Mean ± SE**	**Smallest value**	**Largest value**
Ovary length (mm)	*M. affinis*	0.41 ± 0.007 ^{c}	0.28	0.65
	M. albida	0.58 ± 0.008 ^{a}	0.42	0.87
	M. lactiflua	0.49 ± 0.01 ^{b}	0.28	0.79
	M. polyantha	0.56 ± 0.01 ^{a}	0.36	0.79
Ovary width (mm)	*M. affinis*	0.25 ± 0.003 ^{b}	0.17	0.34
	M. albida	0.28 ± 0.009 ^{a}	0.17	0.68
	M. lactiflua	0.25 ± 0.004 ^{b}	0.17	0.36
	M. polyantha	0.22 ± 0.002 ^{c}	0.14	0.31
Ovary thickness (mm)	*M. affinis*	0.16 ± 0.001 ^{c}	0.14	0.22
	M. albida	0.20 ± 0.008 ^{a}	0.11	0.45
	M. lactiflua	0.18 ± 0.002 ^{b}	0.14	0.27
	M. polyantha	0.20 ± 0.002 ^{a}	0.11	0.28
Number of ovules per ovary	*M. affinis*	1.88 ± 0.03 ^{d}	1	3
	M. albida	6.16 ± 0.04 ^{b}	5	7
	M. lactiflua	4.09 ± 0.05 ^{c}	3	6
	M. polyantha	8.68 ± 0.07 ^{a}	7	10
Bracteole length (mm)	*M. affinis*	1.13 ± 0.01 ^{b}	0.62	1.67
	M. albida	1.23 ± 0.02 ^{a}	0.51	2.22
	M. lactiflua	0.70 ± 0.01 ^{c}	0.39	1.08
	M. polyantha	0.55 ± 0.01 ^{d}	0.34	0.92
Bracteole width (mm)	*M. affinis*	0.22 ± 0.004 ^{c}	0.02	0.31
	M. albida	0.23 ± 0.01 ^{c}	0.08	0.68
	M. lactiflua	0.26 ± 0.004 ^{b}	0.17	0.52
	M. polyantha	0.29 ± 0.006 ^{a}	0.14	0.84

The stamens varied in number. The species of *M.* sect. *Mimosa* with the lowest number of stamens per flower were *M. affinis, M. albida* and *M. lactiflua* (Figure 4I-K), while *M. polyantha* (*M.* sect. *Batocaulon*) had the highest number (Figures 4H, L, 5H, Tables 1, 2), showing slight fusion only at the base of the filaments. They may be antisepalous or antipetalous; in species of *M.* sect. *Mimosa* only 4 antisepalous stamens are present, but the shortest filaments were observed in *M. affinis* and the longest were those of *M. lactiflua* (Figure 5I, Table 2), while *M. polyantha*, as a member of *M.* sect. *Batocaulon*, was the only species that also exhibited antipetalous stamens (Table 2). All species present dorsifixed anthers (Figure 4E-L, Table 1), the shortest and narrowest anthers were observed in *M. affinis*, in contrast to *M. polyantha* which showed the longest anthers, but they were less narrow than those of *M. albida* and *M. lactiflua* (Figure 5J, K, Table 2).

The greatest length of the ovary and the style occurred in *M. lactiflua,* and the shortest in *M. affinis* (Figure 5L, Table 2). The length of the ovary stipe was shorter in *M. affinis* and longer in *M. albida* and *M. polyantha* (Figure 5M, Table 2). *Mimosa affinis* had the smallest thickness and smallest length of the ovary, having *M. albida* and *M. polyantha* the longest and thickest, however, the ovary of *M. polyantha* is narrower than that of *M. albida* (Figure 5N-P, Table 2). The mean number of ovules per ovary varied, the lowest value (1.88 ± 0.03) recorded by *M. affinis* and the highest (8.68 ± 0.07) by *M. polyantha* (Figure 5Q, Table 2). A vestigial gynoecium was observed in the three species with staminate flowers. The stigma, observed in surface view, was poriform, except in *M. affinis,* which had a crateriform stigma (Table 1).

The bracteoles were linear to lanceolate or spatulate, and they may nearly or completely cover the entire flower (*M. affinis*, Figure 4E) or the fused part of the corolla (*M. albida*, Figure 4F), measuring twice the length of the calyx

(*M. lactiflua*, Figure 4G), with setose or glabrous indumentum, while in *M. polyantha* the bracteoles were oblanceolate, equal in length to the calyx, with tomentose indumentum (Figure 4H). *Mimosa polyantha* displayed the shortest and widest bracteoles, and *M. albida* the longest, but the width of the latter did not differ from that of *M. affinis* (Figure 5R, S, Tables 1, 2).

Correlation analyses indicated that there is a positive correlation between the length of the floral axis and the number of flowers per inflorescence (*rho* = 0.35, df = 23, *P* = 0.0003), while, there is a negative correlation between perianth length and bracteole length, as the perianth increases in size when the bracteole length decreases (*rho* = -0.41, df = 123, *P* = 0.0001), except in *M. affinis*. Likewise, as the length of the ovary increases so does the number of ovules (*rho* = 0.42, df = 123, *P* = 0.0001), while as the width of the ovary increases the number of ovules decreases (*rho* = -0.26, df =123, *P* = 0.0001), in contrast, as the thickness of the ovary increases, the number of ovules also increases (*rho* = 0.23, df = 123, *P* = 0.0001). On the other hand, there is a positive correlation between the length of the antisepalous stamens and the length of the gynoecium (ovary, style, and stipe) (*rho* = 0.86, df = 123, *P* = 0.0001).

Pollen morphometry and its interspecific variation. The species studied showed two types of pollen aggregation: tetrahedral tetrads and octads (Table 1). Tetrahedral tetrads were observed in *M. affinis* (Figure 6A-F), *M. albida* (Figure 6G, H, M) and *M. lactiflua* (Figure 6J-L, N). Rarely, the three species also exhibited tetragonal tetrads (Figure 6I); both types of tetrads were spheroidal to ellipsoidal in shape, acalymmate, and their dimensions in the diameter in polar view showed significant differences in three species, *M. albida* had the tetrads of smallest diameter and *M. affinis* exhibited the largest diameter (Table 3). Rotated octads were observed in *M. polyantha*, ellipsoidal to spheroidal in shape, heteromorphic, acalymmate (Figure 6O-U), it was the only species with a major and minor diameter (Figure 5T, Table 3). All four species displayed significant differences in the polar and equatorial axes of the monads. *Mimosa affinis* showed the highest values, *M. albida* the lowest polar axis value, while *M. polyantha* and *M. albida* showed the lowest equatorial axis value (Figure 5U, V, Table 3). The porate apertures, with three (Figures 6B, C, K) or four pores per monad (Figure 6O-Q), were distributed in a subequatorial position; pore diameter was smallest in *M. polyantha* and largest in *M. affinis* (Figure 5W, Table 3); operculum was observed in three species (Figure 6B, M, T, U) with 0.82-2.68 µm long and 1.06-3.24 µm wide. The exine showing verrucate ornamentation (Figure 6C, E, F), with verrucae 1.07 µm long and 0.79 µm wide, and microverrucate and microverrucate-rugulate ornamentation (Figure 6M, N, T, U), with microverrucate ranging 0.41-0.60 µm long and 0.34-0.47 µm wide. It ought to be mentioned that *M. affinis* had the thickest exine, while between *M. albida* and *M. lactiflua* there were no differences, and the lowest thickness value was recorded by *M. polyantha* (Figure 5X, Table 3). A distal margo was observed at the boundary of the proximal face of the monads (Figure 6N, T, U) measuring 0.51-0.72 µm thick.

Micromorphological characters of the flower. The floral anatomical characteristics observed under SEM showed variability in the surface of the epidermal cells and their derivatives in all four *Mimosa* species (Figures 7A-WA, 8A-Y).

In all species, the bracteole, calyx, petals, anther connective, ovary and style, in surface view, exhibited polyhedral epidermal cells with different contours: rectangular (Figures 7I, N, Q, 8H, MA), triangular (Figure 7R, S), pentagonal or hexagonal (Figures 7WA, 8I, U). The bracteole showed cilia, micropapillate elongated unicellular trichomes and pedicellate glandular trichomes (Figure 7J, K, HB); it may exhibit paracytic stomata (Figure 7I), and its apex was spherical in some cases (Figure 7HC). The size of the epidermal cells of the calyx varied: 22.10-28.93 µm long and 17.07-23.54µm wide; the margin of the lobes showed epidermal derivatives such as cilia, micropapillate elongated unicellular trichomes (Figure 7H, HD, M, N) or pedicellate glandular trichomes (Figure 7HD), or no trichomes at all (Figure 7L). The petal epidermal cells were 26.45-41.18 µm long and 19.60-27.22 µm wide; at the apex of the lobes, clavate trichomes (Figure 7O, R) or micropapillate elongated unicellular trichomes were observed (Figure 7P, PA), as well as some paracytic stomata (Figure 7O, PA, R, S).

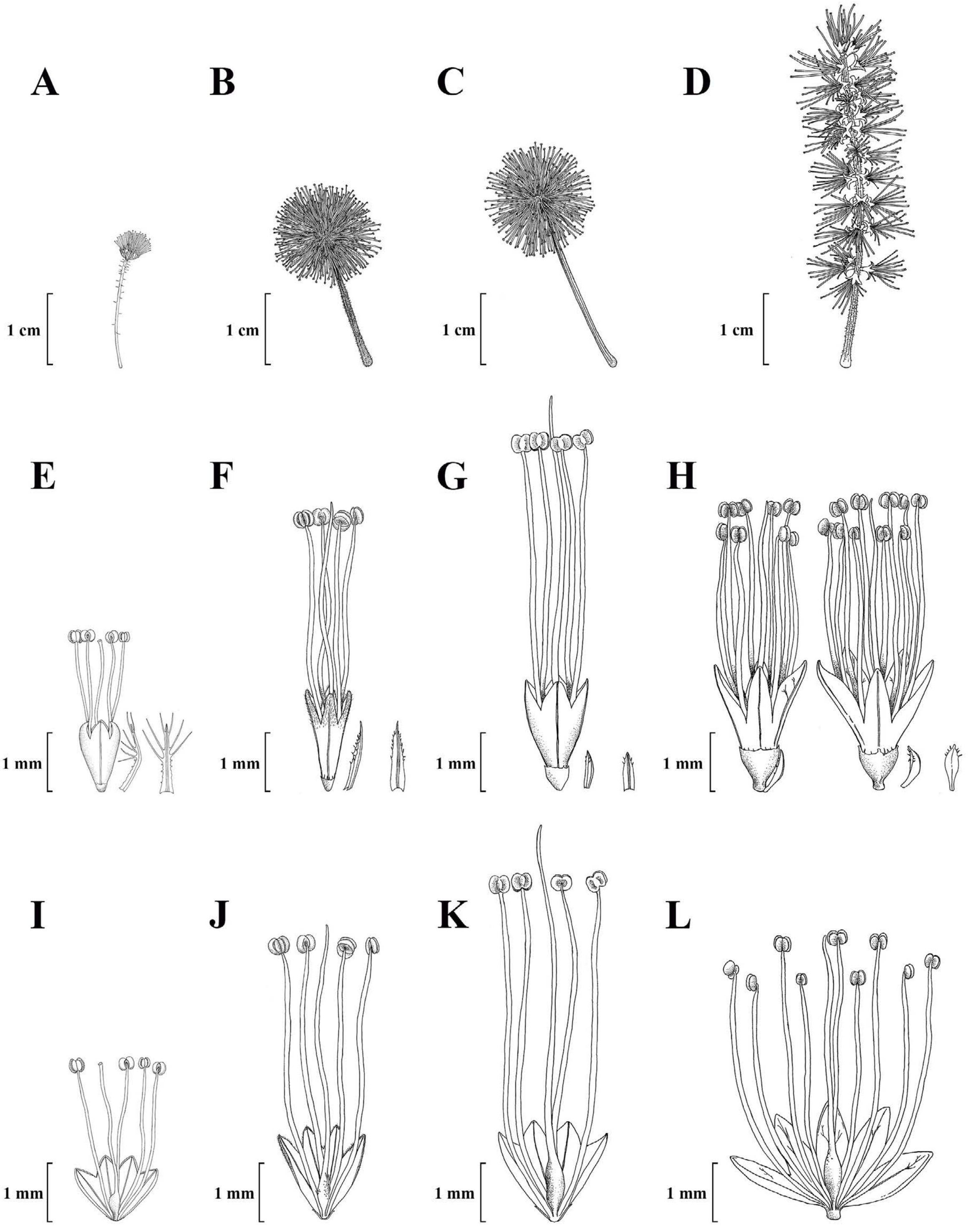

Figure 4. Inflorescence and flower morphology in *M. affinis* (A, E, I), *M. albida* (B, F, J), *M. lactiflua* (C, G, K) and *M. polyantha* (D, H, L). A-D. Inflorescence in capitulum with flowers ascending (A), globose capitula (B, C) and spike (D). E-H. Flowers with bracteoles in lateral and abaxial views, calyx campanulate, corolla lobes free in 1/4 (E), 1/3 (F, G) and 1/2 (H) of corolla length. I-L. Flowers with extended corolla, can be observed the detail of the stamens, anthers, ovary, style, and stigma can be observed.

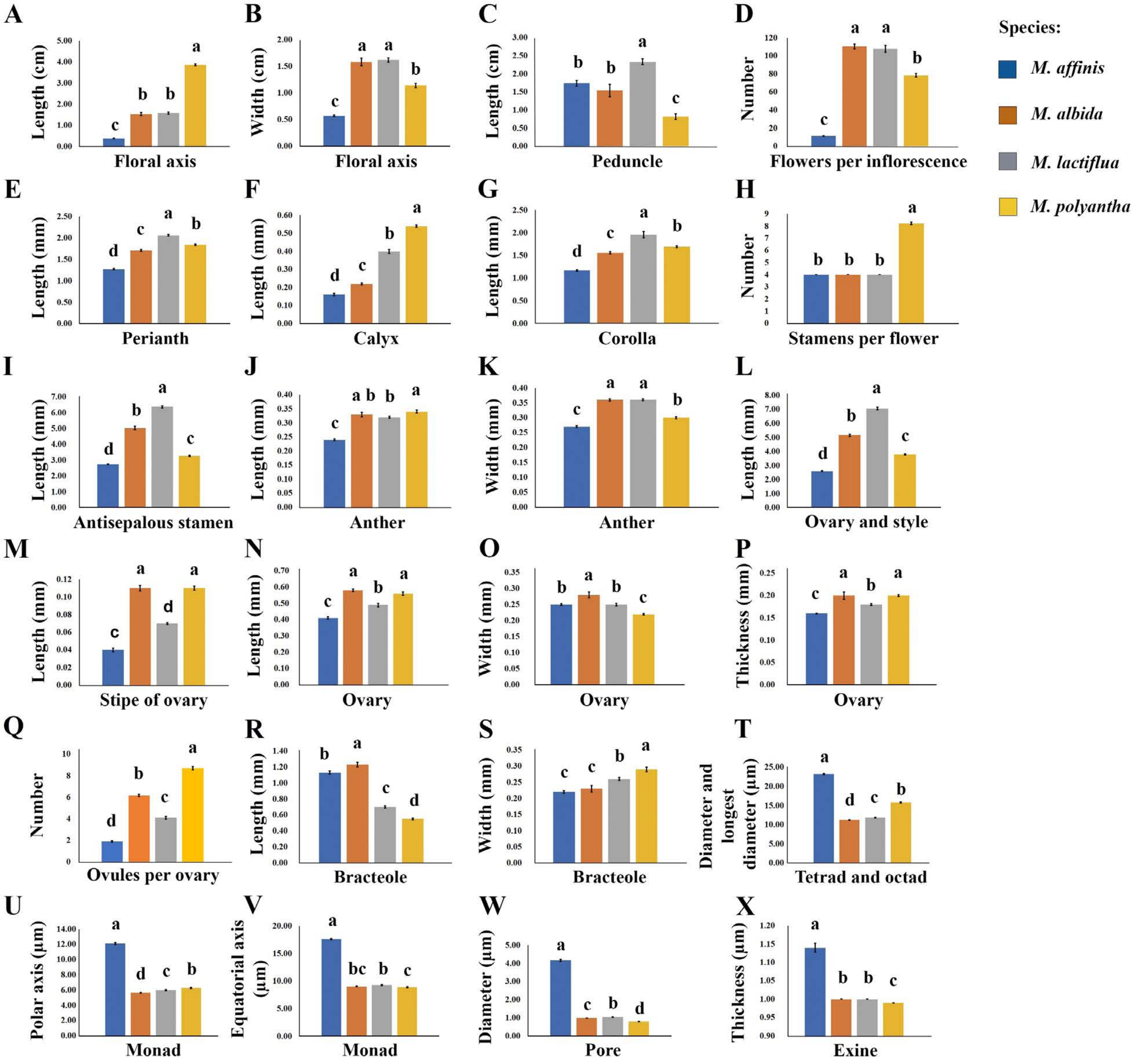

Figure 5. Morphometric analysis in four species of the genus *Mimosa*. A-D. Inflorescence. E-Q. Flower. R-S. Bracteole. T-X. Pollen aggregations. In all cases $n = 125$. Analysis of variance, Kruskal-Wallis followed by Mann-Whitney U based on ± standard error (SE). Means with different letters are significantly different ($P < 0.05$).

In the androecium, the filaments (Figure 7T-V, W) showed papillate epidermal cells (Figure 7VA), with a pentagonal or hexagonal contour (Figure 7WA), and the cuticle ornamentation was rugulate to rugulate-striate. The filament epidermal cells measured 31.60-66.58 µm long and 15.39-31.78 µm wide (Figure 7T, U), and the stamens were slightly fused basally (Figure 8A-D); anthers showed two thecae, each with two pollen sacs (Figure 8E, F); the contour of the cells was irregular and the cuticle ornamentation rugulate-striate (Figure 8G); at the level of the connective, all species exhibited a cuticle with striate ornamentation (Figure 8H-J).

The species studied had a superior, unilocular, unicarpellate ovary (Figure 8K-N), with 1 to 3, 3 to 7, or 7 to 10 ovules per ovary (Figure 8Q-T), and epidermal cells ranging 12.18-13.50 µm long and 9.03-10.24 µm wide (Figure 8LA, MA, O, P). The ovary walls exhibited multiseriate trichomes (Figure 8LA), short cilia (Figure 8K, P) or spherical trichomes (Figure 8N, O, P); the style was long and narrow (Figure 8U), the apex attenuate, the epidermal cells

35.28-49.99 µm long and 6.39-15.45 µm wide, cuticle ornamentation rugulate (Figure 8UA); stigma terminal (Figure 8V-Y), crateriform (Figure 8V), poriform (Figure 8W, X) or obliquely poriform (Figure 8Y).

Discussion

This is the second study carried out on *Mimosa* species distributed in Mexico after Martínez-Olivares (2014), where the anatomical characters of the flowers are studied and the first one to provide detailed information on the epidermal derivatives existing in Mexican species and to use the different types of trichomes and their combinations as distinctive characters of the species.

Inflorescence structure and floral characters. The inflorescence is considered as the pollination unit in Mimoseae (Arroyo 1981, Kenrick & Knox 1989). The inflorescence of *Mimosa* structured in globose capitulum, capitulum with ascendent flowers or in spikes offers different shapes as a whole, and attractive colours due mainly to the filaments (intense pink, pink, lilac) contrasting with the yellow anthers. Insects are visitors and pollinators of species of this genus (Dutra *et al*. 2009, Silva *et al*. 2011). We discuss here, the relation of inflorescence and flower structures to floral visitors.

In the studied *Mimosa* species, anthesis occurs acropetally, from the basal to the apical portions of the inflorescence and they open in the morning, although it has been reported that anthesis is nocturnal in *M. lewisii* Barneby (Vogel *et al*. 2005).

The elongated spikes of *M. polyantha* exhibited between 59 to 91 flowers, in contrast to the globose capitulum inflorescences of *M. albida* and *M. lactiflua*, which showed between 66 to 138 flowers, and the quite different capitulum with ascending flowers of *M. affinis*, the species with the lowest number of flowers in Mexico, in which the flowers varied 8 to 16 per inflorescence. It is interesting to note that the number of flowers in the spikes of *M. polyantha* lies in the range of the globose capitula of *M. albida* and *M. lactiflua*, therefore the type of inflorescence is not relevant in these three studied species, although the structure of the capitulum with a few ascending flowers of *M. affinis* suggest a different strategy of pollination.

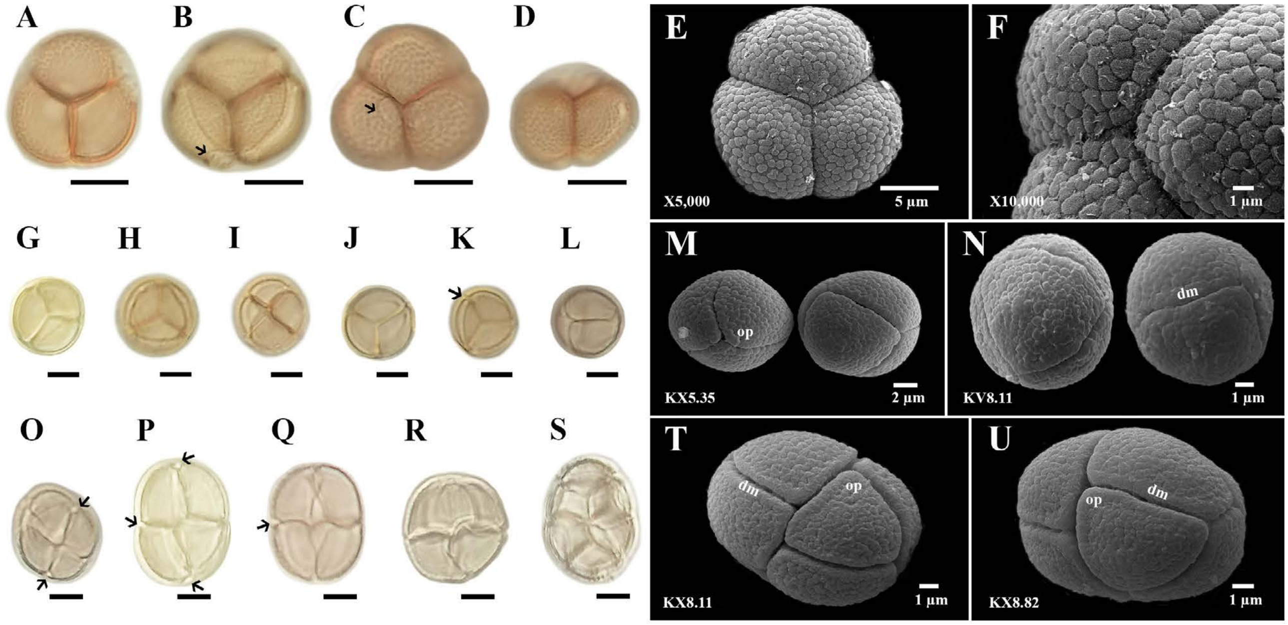

Figure 6. Photomicrographs of pollen aggregations of *Mimosa*. A-F. *M. affinis*: tetrahedral tetrads, ovoid shape (A-C, E) and lateral view (D), with ornamentation verrucate (C, E, F). G-I, M. *M. albida*: tetrahedral tetrads (G, H, M), and tetragonal tetrad (I), both spheroidal shapes, with ornamentation regulate-microverrucate (M). J-L, N. *M. lactiflua*: tetrahedral tetrad, spheroidal shape, lateral view (L), with ornamentation rugulate-microverrucate (N). O-U. *M. polyantha*: octads, rotate, ellipsoidal (P, Q, T, U) and spheroidal (R) shape, with ornamentation microverrucate to rugulate-microverrucate (T, U). Abbreviations: dm: distal margo; op: operculum. Black arrows: pores. Bar scale in ML: 5 (G-L, O-S) and 10 µm (A-D).

Table 3. Statistical analysis of pollen morphology. Analysis of variance, Kruskal-Wallis followed by Mann-Whitney U based on ± standard error (SE). Means with different letters are significantly different ($P < 0.05$).

Variables	Species	Mean ± SE	Smallest value	Largest value
Diameter in polar view * and longest diameter ** (µm)	*M. affinis* *	23.23 ± 0.14 ^{a}	18.67	26.97
	M. albida *	11.29 ± 0.03 ^{d}	10.50	12.33
	M. lactiflua *	11.85 ± 0.12 ^{c}	9.83	14.90
	M. polyantha **	15.81 ± 0.15 ^{b}	13.00	20.00
Smallest diameter (µm)	*M. polyantha*	11.95 ± 0.12	10.00	16.00
Monad polar axis (µm)	*M. affinis*	12.11 ± 0.10 ^{a}	10.00	16.00
	M. albida	5.64 ± 0.04 ^{d}	5.00	7.00
	M. lactiflua	5.98 ± 0.06 ^{c}	4.00	7.20
	M. polyantha	6.28 ± 0.06 ^{b}	5.00	9.00
Monad equatorial axis (µm)	*M. affinis*	17.64 ± 0.13 ^{a}	14.00	22.00
	M. albida	9.06 ± 0.05 ^{bc}	7.00	10.00
	M. lactiflua	9.30 ± 0.11 ^{b}	7.00	12.60
	M. polyantha	8.89 ± 0.10 ^{c}	6.80	12.00
Exine thickness (µm)	*M. affinis*	1.14 ± 0.01 ^{a}	1.00	1.50
	M. albida	1.00 ± 0.00 ^{b}	1.00	1.00
	M. lactiflua	1.00 ± 0.01 ^{b}	1.00	1.00
	M. polyantha	0.99 ± 0.0008 ^{c}	0.95	1.00
Pore diameter (µm)	*M. affinis*	4.17 ± 0.06 ^{a}	3.00	6.00
	M. albida	0.99 ± 0.002 ^{c}	0.90	1.10
	M. lactiflua	1.03 ± 0.006 ^{b}	0.95	1.20
	M. polyantha	0.79 ± 0.007 ^{d}	0.60	0.95

Furthermore, it has been reported that other species with inflorescence arranged in spikes, such as *M. luisana* Brandegee and *M. benthamii* J.F.Macbr. may have 30 to 70, or 230 to 300 flowers, respectively (Martínez-Bernal & Grether 2006, Martínez-Olivares 2014). In the side of capitula with a few flowers like those of *M. affinis*, other species, such as *M. camporum* Benth. (Martínez-Olivares 2014) and *M. guilandinae* (DC.) Barneby (Martínez-Bernal *et al*. 2008) have a minimum of 10 flowers, and *M. turneri* Barneby, has capitula with 5 to 25 flowers (Grether 2023). The highest number of flowers per capitulum (180) has been recorded in *M. roemeriana* Scheele and *M. hystricina* (Small ex Britton & Rose) B.L.Turner (Grether 2023). This reduction in the number of flowers per inflorescence (*M. affinis*) is related to the evolutionary trend in the genus *Mimosa* towards the reduction of floral parts, such as the number of stamens, corolla lobes, as well as the acquisition of staminodes in species diverging in the Pliocene and Pleistocene (Velázquez-Castañeda *et al*. 2024).

In the present study, the proportion of bisexual and staminate flowers in the inflorescences of each of the species was calculated with a broad sample for the first time. Bisexual flowers predominated by 48 to 100 %, in both capitula and spikes, the proportion of staminate flowers varied from 1 to 65 % in capitula; this latter range occurred in *M. albida*, while in *M. lactiflua* bisexual flowers varied from 77 to 100 % and in *M. affinis* it is 96 % per capitulum. In these three species, the presence of bisexual flowers in the middle and apical part and staminate flowers in the middle and basal, or only basal part (*M. affinis*) of the inflorescence suggest a mechanism that maximizes the resources allocated to reproductive functions (Diggle 1993, Hokche & Ramírez 2006), common in species andromonoecious with large and costly fruits, whose production is physiologically limited (Cardoso *et al*. 2018). Only in *M. polyantha* were 100 % of the bisexual flowers. This latter species could disperse pollen and pollinate flowers from other individuals (xenogamy, Cardoso *et al*. 2018) and would form seeds with a high level of genetic variation, contributing to success in the face of drastic environmental changes (Orozco Arroyo & Vázquez Santana 2013).

Mimosa affinis, M. albida and *M. lactiflua* showed merism stability, not associated to the number of flowers per capitulum nor the congestion of flowers in the inflorescences, contrasting to merism variability observed by Gonçalves *et al*. (2024) in the flowers of *M. pudica* L., also belonging to *M.* sect. *Mimosa*. In contrast, *M. polyantha* had tetramerous and pentamerous, diplostemonous flowers, occasionally, two or three filaments, fuse up to half their length, and this was not observed in the rest of the species studied; this species showed merism variability, coinciding with findings in *M. caesalpiniifolia* Benth., *M. hexandra* Micheli and *M. candollei* R.Grether, also members of *M.* sect. *Batocaulon* (Gonçalves *et al*. 2024), however, these latter three species have inflorescences arranged in capitula, while *M. polyantha* has spikes, although the number of flowers per inflorescence is not related to the merism variability, as *M. polyantha* has an intermediate number in contrast to the studied species with capitula (Table 1).

In the androecium, all four species exhibited a slight fusion of the filaments at the base, as reported in *M. strigillosa* Torr. & A.Gray (Ramírez-Domenech & Tucker 1989) and *M. setosa* Benth. (Borges & Pirani 2017) forming a small staminal tube. However, basal fusion of stamens is rare in the genus *Mimosa*, which shows a predominance of stamens free down to the base.

In *M. affinis*, *M. albida* and *M. lactiflua*, flowers with a vestigial gynoecium were found, reported as staminate flowers (Grether 1997) or as a rudimentary carpel in the center of the flower, derived from organ abortion in the development of the floral whorls (Gonçalves *et al*. 2024). It should be noted that in *M. polyantha* some flowers with a double pistil were found in the apical portion of the spike, which has not been reported in any other species of the genus and it remains to be determined whether both are functional.

In the four studied species, the calyx is campanulate while various shapes have been described in other mimosas, *e.g.*, discoid, cupuliform and patelliform (Grohar *et al*. 2021). The calyx margin exhibited trichomes of different types in agreement with the descriptions of Grohar *et al*. (2021), who also describe the calyx margin as undulate, toothed, lobed, irregular and straight, the latter characteristic coinciding with our observations in *M. affinis* (Figure 7L). In the studied species, the calyx covers the base of the other floral whorls but it is very short and has not a relevant role for protection of the floral bud but it does for attraction of pollinators, as in the case of *M. polyantha* by glandular trichomes at the calyx margin, that could be functioning as secretors of aromatic substances (Rudall 2007, Tölke *et al*. 2020).

As for the bracteole, different shapes and sizes were observed, which provides protection to the floral bud; this coincides with reports regarding other families of angiosperms (Cruz Durán & Rosas López 2013), and we consider that it also provides support to the flower. Variation was also observed in the indumentum of the bracteoles, which is consistent with Martínez-Bernal & Grether (2006); these epidermal derivatives may participate in the protection of the floral buds, reducing the possible action of insects and herbivores (Liakoura *et al*. 1997, Mauricio & Rausher 1997, Werker 2000, Santos-Silva *et al*. 2013), or they may be modified for nectar secretion (Davis *et al*. 1988, Pacini *et al*. 2003). In *M. affinis*, the bracteoles are long setose on the margins, completely covering the buds and ca. 2/3 of the perianth length in mature flowers (Figure 7E); furthermore, they provide support and protection by being persistent even though the flowers have been fertilized. Their role is relevant in this herbaceous species, considering the low number of flowers per capitulum, and the risk of loss of flowers by animal passing through the grass areas in the disturbed tropical deciduous forest where the species grows.

The type of inflorescence and the floral morphology of the studied species agrees with the observations made by various authors in the genus *Mimosa* (Borges & Pirani 2013, 2017, Morales *et al*. 2020); although previous floral anatomical works are scarce, such as the studies conducted by Martínez-Olivares (2014) and Wyatt & Lipow (2021).

Floral micromorphology. The morphology and density of trichomes vary considerably among mimosoids and, in *Mimosa*, the type of trichome is an infrageneric diagnostic character, which has allowed the description of new taxa and the revision of taxonomic complexes (Santos-Silva *et al*. 2013, Grohar *et al*. 2021, Silveira *et al*. 2019). In several species of the genus, a variety of trichomes are present on the surface of different organs and different types can even be observed on the same organ, forming two layers of the indumentum (Santos-Silva *et al*. 2013). According to Werker (2000), the variation in the anatomical characteristics, location and development of trichomes is due to their functions, which include reducing thermal load, reflecting ultraviolet light, increasing tolerance to freezing, maintaining water balance and providing protection against insects and herbivores (Liakoura *et al*. 1997, Mauricio & Rausher 1997). In *Mimosa*, it has been demonstrated that trichomes evolved independently in different lineages (homoplasy) and, probably, simple trichomes or cilia are the ancestral states in the genus, while pedicellate trichomes

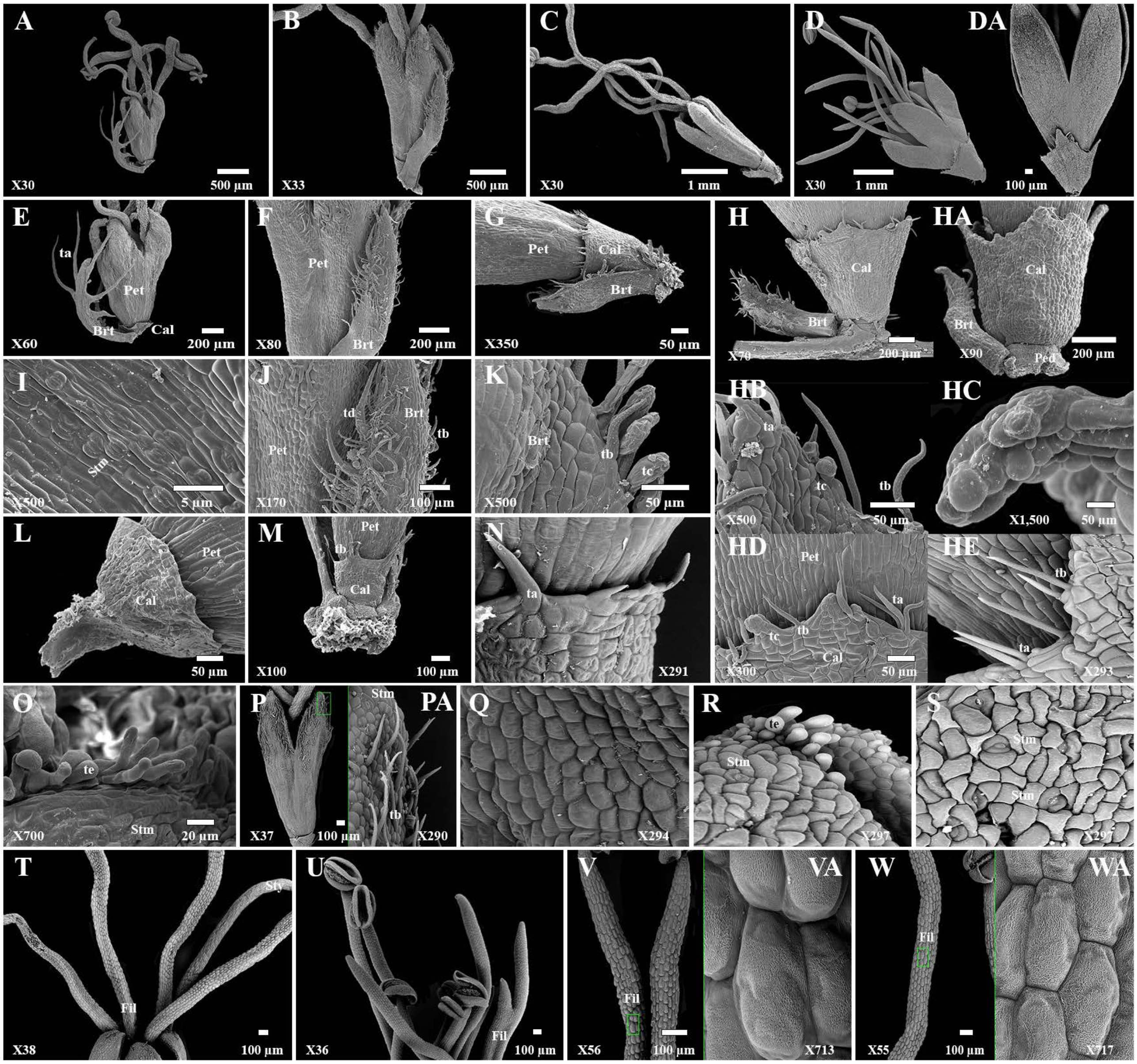

Figure 7. Micromorphology of bracteoles, calyxes, corollas and stamens in *Mimosa*. *M. affinis* (A, E, I, L, O). *M. albida* (B, F, J, M, P, PA, V, VA). *M. lactiflua* (C, G, K, N, Q, T, W, WA). *M. polyantha* (D, DA, H-HE, R, S, U). A-E. Panoramic view of flowers: tetramerous (A-C, DA, E) and pentamerous (D) flowers. F-HA. Bracteole and calyx. I-K, HB. Cell surface of bracteole, with paracytic stomata (I). HC. Apex of bracteole with possible glandular trichome. L-N, HD, HE. Close-up of the cell surface of calyx. O-S. Petals. Margin of petals with clavate (O, R) and elongated micropapillate unicellular trichomes (P, PA), cell surface, with cells polyhedral in outline (Q, R, S), and paracytic stomata (O, PA, R, S). T, U, V, W. Filaments. Cell wall of filament epidermal cells papillate (VA) in outline, pentagonal or hexagonal (WA), and cuticle with rugulate or rugulate-striate ornamentation (VA, WA). Abbreviations: Brt: bracteole; Cal; calyx; Fil: filament; Pet: petal; Stm: stomata; ta: cilia; tb: elongated micropapillate unicellular trichome; tc: glandular trichome with pedicel; td: multiseriate trichome; te: clavate trichome.

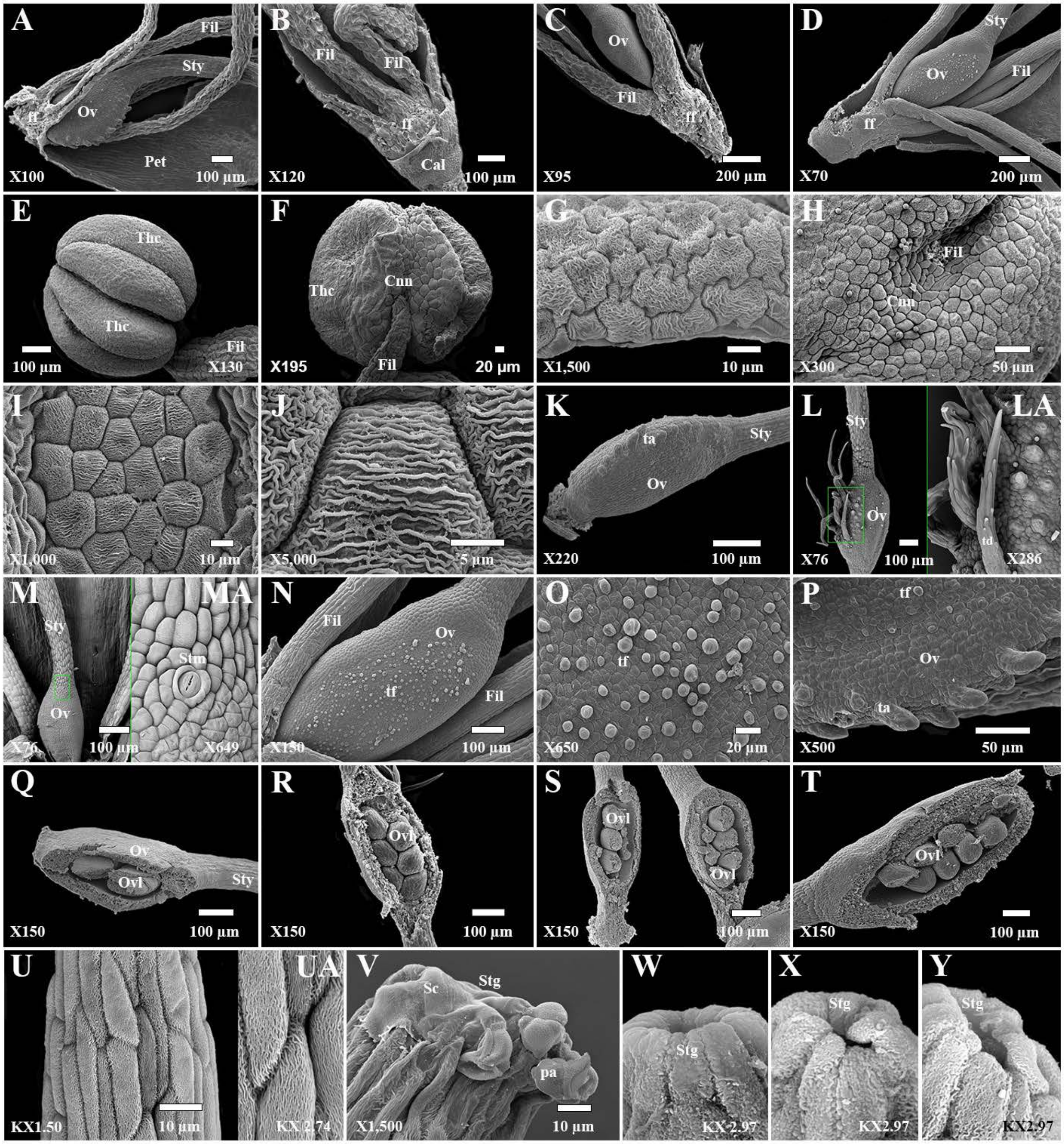

Figure 8. Micromorphology of stamens, anthers, ovaries, styles, and stigmata in *Mimosa*. *M. affinis* (A, G, I-K, P, Q, V). *M. albida* (B, E, H, L, LA, R, W). *M. lactiflua* (C, F, M, MA, S, X). *M. polyantha* (D, N, O, T, U, UA, Y). A-D. Slight fusion of stamens at the base (ff). E-J. Anther, ventral view (E) and dorsal view (F), cell surface with rugulate-striate ornamentation (G), cell surface of connective (H) with cells polyhedral in outline (I) and cuticle with striate ornamentation (J). K-P. Ovary, with cilia (K, P), multiseriate (L, LA) and unicellular spheroidal (N, O) trichomes, cell surface with polyhedral cells (LA, MA, O, P), and paracytic stomata (MA). Q-T. Ovaries with ovules. U-UA. Cell surface of style, cuticle with rugulate ornamentation (UA). V-Y. Stigmata, crateriform (V) and poriform (W-Y). Abbreviations: Cnn: connective; Fil: filament; ff: filament fusion; Ov: ovary; Ovl; ovule; pa: pollen aggregations; Sc: stigma secretion; Stm: stomata; Stg: stigma; Sty: style; ta: cilia; td: multiseriate trichomes; tf: unicellular spheroidal trichomes.

have evolved on many occasions, in several lineages of the genus. Likewise, sessile glandular trichomes are not an ancestral state and are found as a derived state in more recent clades, as are branched multicellular trichomes (Santos-Silva *et al*. 2013).

The apex and margin of the petals displayed elongated, micropapillate and clavate unicellular trichomes, in mature flowers in three of the studied species, and this trait is shared with other species of the mimosoid clade (Gonçalves *et al*. 2024). In *M. bimucronata*, osmophores secreting a fruity fragrance were detected at the petal margins (Silva *et al*. 2011), which are associated with attraction of floral visitors (Aguilar Sierra & Smith Pardo 2009). Furthermore, Ramírez-Domenech & Tucker (1990) and Gonçalves *et al*. (2024) found that the papillate trichomes on the adaxial surface and apex of the petals have an important role to the efficient closure of the floral bud, to epidermal fusion of the free margins of the petals in final stages of development, as the petals exceed the calyx and they function as the main organ of bud protection; our results coincide in the trichomes found on the adaxial surface and margin of the corolla lobes of *M. albida*, that could give additional protection to the bud and the mature flower, and their abundance could be relevant for landing of visitors and pollinators, as they are pollen foraging. Additionally, this can occur in the ovary (except in *M. lactiflua*), since the size of the trichomes increases significantly when fertilization has taken place. The completely glabrous calyx, corolla, and bracteoles of *M. lactiflua* combined to the very long and ornamented filaments and the densely flowered capitulum sustained by a strong and long peduncle conform another strategy for attraction of visitors and pollinators that do not need to land on the flower perianth, but they do on the striate ornamentation of the filament epidermal cells. It should be noted that, in *M. polyantha*, some paracytic stomata were observed at the apex of the petals and this has only been previously reported in *Acacia celastrifolia* Benth. (Prenner 2011) and recently in *M. caesalpiniifolia*, *M. bimucronata* and *M. candollei* (Gonçalves *et al*. 2024).

Pollen morphology. The intraspecific differences found in association shape and size of diverse pollen samples, collected in different locations and states, are due to the response of their harmomegathic system to environmental changes. Polymorphism in the pollen aggregations of the genus *Mimosa* has been studied by El Ghazali (1997), who found that *M. pigra* L. may exhibit four variations of tetrads, namely tetrahedral, oval, tetragonal and rhomboidal tetragonal, ranging in shape from spheroidal to ellipsoidal. The octads observed in *M. polyantha* showed heteromorphism in the monads, and the number of apertures depended on their shape: if it was trapezoidal, it had four pores and if pyramidal (also present in tetrads) it had three; the position of the apertures was subdistal. Grether (1997) and Martínez-Bernal (2003), using light microscopy, reported that *M. polyantha* shows rotated, ellipsoidal octads with a major diameter of 14-16 µm, a minor diameter of 10-12 µm, and microverrucate ornamentation. These characters coincide with the results obtained in the present work. However, observations under SEM showed that the exine ornamentation also exhibits a fusion of microverrucae forming rugulae, resulting in rugulate-microverrucate ornamentation.

As for *M. affinis*, Grether (1997) reported that the tetrad has a diameter of (9) 10 (11) µm, with pores 0.6 µm in diameter, exine 0.6 µm thick and microverrucate ornamentation, which differs from the results presently obtained. This difference is most likely due to environmental conditions and the rainy season, as indicated by Guinet (1986) in species of the genus *Acacia* Mill. subgenus *Phyllodineae* (DC.) Ser., since in this study the samples of *M. affinis* were collected in the field and came from a disturbed tropical deciduous forest and Grether (1997) conducted the pollen study using herbarium specimens from the Mesoamerican region, where *M. affinis* grows in humid tropical areas.

The size of the tetrahedral tetrads we observed in *M. albida* does not concur with the descriptions given by Guinet (1969), Sorsa (1969), Grether (1997) and Martínez-Bernal (2003), who reported tetrads with a diameter of 8-9.1 µm, exine 0.6 µm thick, pores 0.6 µm in diameter and psilate ornamentation using light microscopy. However, the results obtained in our study do coincide with the microverrucate ornamentation observed by Grether (1997) and with the type of association in tetrahedral, spheroidal tetrads reported by Guinet (1969), Grether (1997) and Martínez-Bernal (2003); this difference in size may be due to the temperature and availability of water in the environment from which the pollen samples of the species came, as occurs in species of the formerly genus *Acacia*, subgenera *Aculeiferum*, *Acacia* and *Phyllodineae* on the Australian continent (Guinet 1986), influencing the morphological differences of the pollen and their harmomegathic systems. The same phenomenon was observed in *M. lactiflua*, with reports of tetrads measuring 9.3-11.0 µm in diameter, exine 0.5-0.6 µm thick and pores of 0.6 µm in diameter (Chehaibar 1988, Martínez-Bernal 2003), in contrast to our results, which show a greater exine thickness and a larger pore diameter.

Inflorescence, floral morphology and pollen associations. Among the species with capitate inflorescences, it was observed that *M. lactiflua* exhibits the widest capitula, with the longest peduncle, as well as the largest flowers, the greatest number of bisexual flowers, and tetrahedral, spheroidal tetrads, which may be related to the attraction of floral visitors. In contrast, *M. affinis* was the species with the smallest capitula and flowers, in addition to their ascending position and the length of the bracteole that completely covered the corolla in mature flowers, suggesting that this species needs to protect its flowers (Cruz Durán & Rosas López 2013) since it is an annual decumbent herbaceous plant that needs to ensure its reproduction and fruit development. Respect to the pollen association, it shows tetrahedral, oval tetrads with a larger diameter compared to those of *M. albida* and *M. lactiflua*, and even larger than the octads of *M. polyantha.* This suggests that *M. affinis* has a very different dispersal strategy for its pollen grains compared to the other three species studied; its herbaceous habit would require floral visitors to transport the pollen, and the diameter of its tetrads as well as its verrucate ornamentation would allow greater adherence to the body of the insect when the pollen would be transported. *Mimosa affinis* displayed the shortest stamens and the largest tetrahedral tetrads, while *M. lactiflua* had the longest stamens and, together with *M. albida*, the smallest tetrahedral tetrads, even smaller than the octads of *M. polyantha*. It should be noted that Harder & Johnson (2008) report that the formation of aggregated pollen occurs primarily in animal-pollinated taxa.

Another character associated with the success of plant species is the number of pollen grains that the stigma can receive, since a strong correlation has been reported between the depth of the stigma and the size of the pollen grain (Cruden & Lyon 1985). In *M. camporum*, an obliquely crateriform stigma has been observed with a wide and concave surface, and with no stigmatic chamber. The stigma can receive between 2 and 15 tetrahedral tetrads on its surface (Martínez-Olivares 2014); this coincides with our findings in *M. affinis*, which showed a crateriform stigma, with secretion on its surface and many tetrahedral tetrads (Figure 8V). Both *M. albida* and *M. lactiflua* exhibited poriform stigma associated with tetrahedral, spheroidal tetrads and, according to Martínez-Olivares (2014), this type of stigma can hold one to three tetrads in its stigmatic chamber, which may ensure the total pollination of the ovules in a flower. There are differences in the dimensions of the stigmatic chamber of some species, *e.g.,* in *M. benthamii* var. *benthamii*, it is small or pit-shaped, 22 µm deep and the stigmatic orifice 13 µm in diameter, as occurs in *M. luisana* (Martínez-Olivares 2014), furthermore, in *M. microphylla* the diameter of the stigmatic cup ranged 37.5-62.5 µm (Wyatt & Lipow 2021). Our results show a different strategy in *M. polyantha*, because the poriform stigma is slightly inclined, in a terminal position, unlike the other two species with poriform stigmata (*M. albida* and *M. lactiflua*) and it is associated to rotated, ellipsoidal octads, suggesting that one octad, positioned longitudinally in the stigma, would be sufficient to pollinate at least eight of the ten ovules that the flower of this species has. This case is similar to the reported findings in *M. bimucronata*, in which the analysis of pollination efficiency revealed that 33 % of the flowers had an octad correctly located in the stigmatic pit (Seijo & Solís-Neffa 2004). Other stigma forms have been reported, such as the tubular form in *M. pigra* L. var. *pigra*, with a stigmatic chamber 139 µm deep and a stigmatic orifice 42 µm in diameter, in addition to a cupuliform stigma in *M. quadrivalvis* L. var. *quadrivalvis*, its stigmatic chamber 157 µm long and its stigmatic orifice 38 µm in diameter; both stigmas are associated with tetragonal, rhomboidal, spheroidal and ellipsoidal tetrads; the tubular and cupuliform stigmata can receive from 1 to 3 pollen associations (Martínez-Olivares 2014). Angiosperms that shed pollen grains in tetrads and polyads increase the probability of dispersal, and of access to many stigmata in inflorescence and a greater pollination of ovules, giving them a high probability of contributing to the next generation of sporophytes (Harder & Johnson 2008).

The zoophilic pollination syndrome is related to the whole of floral traits, implicating the attraction of a particular pollinator (Proctor *et al.* 1996), although in the case of flowers with a generalized pollination syndrome, various associated floral visitors can exist. This latter case occurs with the flowers of the genus *Mimosa*, in which, the scarce studies on this issue show that the floral visitors obtain a pollen resource reward (Dutra *et al.* 2009, Silva *et al.* 2011), and, in doing so, they transport large amounts of pollen while visiting dozens of capitula in the same individual, facilitating self-fertilization (Silva *et al*. 2011); one of the main floral visitors reported is *Apis mellifera* L. (with 92.8 % of diurnal visits), among other species of the orders Diptera and Coleoptera and of the families Apidae, Halictidae, and Megachilidae (Aguilar Sierra & Smith Pardo 2009, Dutra *et al*. 2009, Silva *et al*. 2011), whose attraction is due to the lilac, pink or intense pink colour of the filaments and the yellow colour of the anthers (Milet-Pinheiro *et al*. 2012), as well as the slight fruity odour given off by the osmophores present on the edges of the petals, as occurs in *M. bimucronata* (Silva *et al*. 2011), since the flowers of the genus *Mimosa* do not present floral nectaries (Barneby 1991, Lewis & Elias 1981) that allow the production of nectar and serve as a reward to the pollinator. Members of the families Apidae, Chrysomelidae and Order Coleoptera have been observed visiting the individuals of *M. albida*, *M. lactiflua* and *M. polyantha* studied in this work (Figure 3A-F). Orozco Arroyo & Vázquez Santana (2013) mention that bisexual flowers have the opportunity to self-pollination when pollen falls on the stigma of the same flower (autogamy), this may be occurring in *M. polyantha* with bee visits, as the gynoecium is slightly shorter than the antipetalous stamens, but longer than the antisepalous stamens (heteranthery, Cardoso *et al*. 2018). In the case of bisexual flowers of *M. albida* and *M. lactiflua* individuals, pollen foraging by bees could lead to xenogamy or geitonogamy (fertilization between gametes from different flowers of the same individual, Cardoso *et al*. 2018).

In the studied *Mimosa* species, the characters with taxonomic relevance were habit, inflorescence type, number of bisexual and staminate flowers per inflorescence, number of stamens and ovules per ovary; in terms of floral anatomical characters, they were type of trichomes on the sepal margin, on the petals and in the ovary, as well as the type of stigma and the type of pollen association. The studied species of *M.* sect. *Mimosa* showed merism stability, while the species belonging to *M.* sect. *Batocaulon* showed merism variability in mature flowers. The pollen-stigma relationship offered insight into the reproductive strategies of species of the genus *Mimosa,* and this is the first work that has generated detailed knowledge of floral morphoanatomy, relating the different characters with floral visitors, although it is necessary to broaden the study of the floral traits in conjunction with the ecological interactions of the species.

Anatomical and histochemical studies of bracteoles, sepals, petals, stamens, and gynoecium are needed to determine which are the secretory structures related to rewards and attraction of floral visitors and pollinators, as well as those acting as protection against herbivory and pathogens in species of the genus *Mimosa*.

Supplementary material

Table S1 mentioned in this article can be accessed here: https://doi.org/10.17129/botsci.3633

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