



## Pollen morphology of Brazilian species of *Verbesina* L. (Heliantheae - Asteraceae)<sup>1</sup>

Giselle Lopes Moreira<sup>2\*</sup> , Taciana Barbosa Cavalcanti<sup>3</sup> , Cláudia Barbieri Ferreira Mendonça<sup>4</sup>   
and Vânia Gonçalves-Esteves<sup>4</sup> 

Received: November 10, 2018

Accepted: December 18, 2018

### ABSTRACT

There are nine species of the plant genus *Verbesina* in Brazil, which are distributed in the Northeast, Center-West, Southeast and South regions of the country. The objective of the present study was to describe the pollinic morphology of eight of these species to better characterize them and evaluate potential species-level taxonomic characters. Acetolysed pollen material was measured within seven days under light microscopy, while non-acetolysed pollen grains were used for scanning electronic microscopy. The pollen grains were found to be oblate-spheroidal, medium-sized, isopolar, monads that are 3-colporate with a subtriangular amb, a small polar area, a long colpus, a longitudinal endoaperture, a cavate exine and an echinate sexine. Although the shape of the pollen grains of these Brazilian species of *Verbesina* is homogeneous, some attributes were observed to be useful for characterizing the species, such as exine thickness, distance between spines and side of the apocolpus.

**Keywords:** Brazil, Compositae, Heliantheae, morphology, pollen, *Verbesina*

## Introduction

The family Asteraceae, order Asterales (APG IV 2016) has a holistic distribution but is common in the dry and open tropical montane climate zone (Anderberg *et al.* 2007). The family includes 13 subfamilies, 44 tribes, about 1,700 genera and proximately 27,000 species, and represents about 10 % of all Angiosperms (Funk *et al.* 2009; Panero *et al.* 2014; Panero & Crozier 2016). There are about 2,097 species of Asteraceae grouped among 289 genera in Brazil (Flora do Brasil 2020).

The genera *Verbesina* belongs to the tribe Heliantheae (subtribe Verbesininae) and possesses around 300 species distributed throughout the Americas, with the most occurring in Mexico and the Andes (Panero 2007). Nine

species have been recorded in Brazil, which are distributed in the Northeast, Southeast, Center-West and South regions of the country, especially in forest environments.

Pollen morphology has contributed to characterizing and differentiating taxa of Asteraceae at the subfamily, tribe and subtribe levels (Skvarla & Turner 1966; Bolick 1991; Cancelli *et al.* 2007; Coutinho & Dinis 2007; Wortley *et al.* 2007; Stanski *et al.* 2016; among others), however, few studies have focused on pollen morphology for distinguishing species of Asteraceae because pollen grains have been found to be morphologically homogeneous within the same genus (Gonçalves 1976). Nonetheless, pollen morphology has been used to distinguish species of some genera of the tribe Heliantheae, such as *Ambrosia*, *Clibadium*, *Eclipta*, *Parthenium*, *Viguiera*, *Xanthium* and *Wedelia* (Gonçalves-Esteves & Esteves 1986; 1989a; b).

<sup>1</sup> Part of the doctoral thesis of the first author.

<sup>2</sup> Universidade de Brasília, 70910-900, Brasília, DF, Brazil

<sup>3</sup> Embrapa Recursos Genéticos e Biotecnologia, 70770-917, Brasília, DF, Brazil

<sup>4</sup> Museu Nacional, Universidade Federal do Rio de Janeiro, 20940-040, Rio de Janeiro, RJ, Brazil

\* Corresponding author: giselle.bio25@gmail.com



Most studies involving pollen morphology of *Verbesina* have been descriptive, such as Gonçalves (1976), who analyzed 17 species, including three Brazilian species (*Verbesina diversifolia* [= *V. macrophylla*], *V. glabrata* and *V. sordescens*); Roubik & Moreno (1991) who studied *V. gigantea* of Panama; Sanchez & Lupo (2009) who investigated *V. lilloi* from Argentina; and Jesus & Lima (2013) who reported on *V. macrophylla* from Bahia, Brazil. Other references to *Verbesina* are pollen catalogs such as Cancelli *et al.* (2010) for Rio Grande do Sul, Brazil, with *V. glabrata* and *V. sordescens*; and Radaeski *et al.* (2014; 2016) with *V. sordescens*.

Some studies that have addressed the pollen morphology of *Verbesina* have indicated the existence of characters with potential use for characterizing and differentiating species of the genus. Harker & Jiménez-Reyes (2002) found that some pollen grain characters, such as shape, size, number of spicules, transverse size colpus and polar area index, were useful for separating *Verbesina barrancae* and *V. crocata*, two morphologically close Mexican species.

The objective of the present study was to describe the pollen morphology of eight Brazilian species of *Verbesina* to better characterize the species of the genus and to evaluate potential species-level taxonomic characters.

## Materials and methods

Pollen material was obtained from floral buds of specimens of eight species of *Verbesina* (*V. baccharifolia* Mattf., *V. bipinnatifida* Baker, *V. floribunda* Gardner, *V. glabrata* Hook. & Arn., *V. luetzelburgii* Mattf., *V. macrophylla* (Cass.) S.F. Blake, *V. nicotianifolia* Baker, *V. sordescens* DC.) deposited in the following herbaria: BHCB, CEN, HUUS, HUEFS, MBML, RB, UB (Thiers 2017) (Tab. 1).

Pollen material was prepared for light microscopy using acetolysis following the method of Erdtman (1952), with the modifications proposed by Melhem *et al.* (2003). Acetolysed pollen grains were measured within seven days of their preparation, in accordance with Salgado-Labouriau (1973). Twenty-five measurements of polar diameter (PD) and equatorial diameter (ED) in equatorial view, and 10 measurements of the equatorial diameter in polar view (EDPV) and apocolpium side (AS), were made on standard material distributed among at least three slides. For other dimensions, such as those of apertures, exine layers and diameters of comparison material, 10 pollen grains were measured on at least in three slides and the arithmetic mean calculated. Description of polar area and aperture size followed the classification established by Faegri & Iversen (1966) for the polar area index. Pollen grain size classes follow Erdtman (1952).

Permanent slides of pollen material generated for this study are deposited in the Laboratory of Palynology of the National Museum of the Federal University of Rio de Janeiro.

For scanning electron photomicrography, two to three anthers were removed from flowers or flower buds extracted from herbarium specimens. The anthers were macerated using properly flamed forceps and stylus to release non-acetolysed pollen grains over a metallic stub previously covered with double-sided carbon tape. The material was sputter-coated with gold for approximately three minutes and then analyzed and photomicrographed using a JSM-5310 scanning electron microscope at the Optical and Scanning Microscopy Laboratory, Federal University of Rio de Janeiro.

To assess whether pollen characteristics discriminated the studied species of *Verbesina*, a principal component analysis (PCA) was performed using eleven metric variables. The results were biplotted on a graph with axes 1 and 2 of the PCA.

## Results

The pollen grains of the studied species of *Verbesina* were found medium-sized (25–50  $\mu\text{m}$ ) oblate-spheroidal, isopolar, monads with a subtriangular amb, (PD/ED 0.95–0.99) (Tab. 2).

The confidence interval 95 % for polar diameter (PD) in equatorial view ranged 25.3–42.3  $\mu\text{m}$ , with the lowest values being for *Verbesina macrophylla* (25.3–26.3  $\mu\text{m}$ ) and the greatest for *V. baccharifolia* (39.5–42.3  $\mu\text{m}$ ) (Tab. 2).

All species had a low polar area index (0.35–0.48  $\mu\text{m}$ ) (Tab. 2), were 3-colporate, and had: long colpus (9.3–14.5 x 2.9–5.0  $\mu\text{m}$ ), acute apices, alongate endoaperture (2.2–4.6 x 8.8–14.2  $\mu\text{m}$ ) with constriction, caveate exine (2.2–3.4  $\mu\text{m}$ ) echinate sexine, spines (4.0–5.9 x 3.0–4.1  $\mu\text{m}$ ) with perforations at the base, and distance between spines of 6.1–8.6  $\mu\text{m}$ . The colpus with medium constrictions is more perceptible in *V. floribunda*. The longest colpus was found in *Verbesina luetzelburgii* (14.5  $\mu\text{m}$ ) and the shortest in *V. nicotianifolia* (9.3  $\mu\text{m}$ ); *V. luetzelburgii* (4.6  $\mu\text{m}$ ) had the longest endoaperture while *V. bipinnatifida* (2.2  $\mu\text{m}$ ) had the shortest; and *V. floribunda* (14.2  $\mu\text{m}$ ) had the largest endoaperture while *V. bipinnatifida* and *V. macrophylla* (8.8  $\mu\text{m}$ ) had the smallest (Tab. 3).

In all species the exine was found to be caveate and echinate (Figs. 1, 2). The sexine and nexine were almost always of the same thickness, but when they did differ the sexine was thicker than the nexine. Mean width exine ranged 2.2–3.4  $\mu\text{m}$  (Tab. 3). The sexine and nexine are very close to the cavea, making it difficult to see.

Four to six pairs of spines were observed around the aperture in equatorial view (Figs. 1D, H, L, P, 2D, H, L, P), which were longer than wide and with perforations at the base. The shortest spines were found in *Verbesina macrophylla* (4.0  $\mu\text{m}$ ) while the longest were for *V. baccharifolia* (5.9  $\mu\text{m}$ ). The distance between spines varied (6.1–8.6  $\mu\text{m}$ ), with it being the greatest in *V. floribunda* (8.6  $\mu\text{m}$ ) and least in *V. sordescens* (6.1  $\mu\text{m}$ ) (Tab. 3).





**Table 1.** Species used in the morphological analysis of pollen grains in *Verbesina* L. (Asteraceae-Heliantheae).

Species	Voucher	Herbarium
<i>Verbesina baccharifolia</i> Mattf.	Ganev 363, Ganev 1824, Ganev 1928	HUEFS, HUEFS, HUEFS
<i>Verbesina bipinnatifida</i> Baker	Moreira <i>et al.</i> 116, Vervloet & Bausen 164, Lombardi & Salino 1671	CEN, MBML, BHCB
<i>Verbesina floribunda</i> Gardner	Moreira <i>et al.</i> 102, Moreira <i>et al.</i> 101, Forzza <i>et al.</i> 3066	CEN, CEN, RB
<i>Verbesina glabrata</i> Hook. & Arn.	Moreira <i>et al.</i> 115, Fontana & Toniato 619, Moreira <i>et al.</i> 103	CEN, BML, CEN
<i>Verbesina luetzelburgii</i> Mattf.	Moreira <i>et al.</i> 117, Moreira <i>et al.</i> 118, Moreira <i>et al.</i> 119	CEN, CEN, CEN
<i>Verbesina nicotianifolia</i> Baker	Proença 865	UB
<i>Verbesina macrophylla</i> (Cass.) S.F. Blake	Moreira <i>et al.</i> 112, Moreira <i>et al.</i> 110, Moreira <i>et al.</i> 111	CEN, CEN, CEN
<i>Verbesina sordescens</i> DC.	Wasum s.n., Wasum 3706, Scur 1136	HUCS 12414, HUCS, HUCS

**Table 2.** Measurements of pollen grains in Brazilian *Verbesina* L. (Heliantheae-Asteraceae) species in equatorial view: (n=25) and polar view: (n=10); PAI = polar area index.

Species	Equatorial View			Polar View		
	Polar diameter (µm)	Equatorial diameter (µm)	PD/ED	Equatorial Diameter (µm)	Apocolpous Side (µm)	PAI
<i>V. baccharifolia</i> Mattf.	35.0(40.9)50.0	37.5(41.9)50.0	0.98	37.5(41.5)45.0	15.0(17.8)22.5	0.43
<i>V. bipinnatifida</i> Baker	27.5(31.0)40.0	27.5(31.9)40.0	0.97	25.0(31.2)35.0	10.0(13.5)15.0	0.43
<i>V. floribunda</i> Gardner	30.0(34.2)45.0	30.0(35.6)42.5	0.96	32.5(36.0)40.0	10.0(12.5)15.0	0.35
<i>V. glabrata</i> Hook. & Arn.	30.0(33.3)37.5	32.5(34.2)37.5	0.97	30.0(32.7)35.0	12.5(14.7)15.0	0.45
<i>V. luetzelburgii</i> Mattf.	32.5(37.0)40.0	35.0(37.3)40.0	0.99	37.5(39.2)42.5	15.0(16.7)17.5	0.43
<i>V. macrophylla</i> (Cass.) S.F. Blake	25.0(25.8)27.5	25.0(27.2)30.0	0.95	25.0(26.7)27.5	10.0(12.7)15.0	0.48
<i>V. nicotianifolia</i> Baker	27.5(30.9)35.0	27.5(31.4)37.5	0.98	30.0(32.7)35.0	12.5(14.2)15.0	0.43
<i>V. sordescens</i> DC.	30.0(33.1)37.5	32.5(34.8)37.5	0.95	32.5(35.0)37.5	15.0(16.2)17.5	0.46

**Table 3.** Measurements of the aperture and layers of exine pollen grains in Brazilian *Verbesina* L. species (Heliantheae-Asteraceae); n=10; DBS = distance between spines; \* measured without the spines.

Specie	Colpus		Endoaperture		Exine layers*			Spine		
	length (µm)	width (µm)	length (mm)	width (µm)	exine	sexine	nexine	length (µm)	width (µm)	DBS
<i>V. baccharifolia</i> Mattf.	14.4	5.0	4.4	12.6	3.3	1.7	1.6	5.9	4.1	7.9
<i>V. bipinnatifida</i> Baker	11.5	3.2	2.2	8.8	3.4	1.7	1.7	4.5	3.5	7.0
<i>V. floribunda</i> Gardner	10.6	2.9	4.3	14.2	3.4	1.9	1.5	5.3	3.3	8.6
<i>V. glabrata</i> Hook. & Arn.	14.1	4.5	4.2	12.3	2.8	1.4	1.4	5.0	3.1	7.5
<i>V. luetzelburgii</i> Mattf.	14.5	4.6	4.6	12.7	3.3	1.7	1.6	5.8	3.7	6.9
<i>V. macrophylla</i> (Cass.) S.F. Blake	9.7	3.3	3.7	8.8	2.6	1.6	1.0	4.0	3.0	6.7
<i>V. nicotianifolia</i> Baker	9.3	3.9	3.0	9.5	2.2	1.2	1.0	4.8	3.0	6.5
<i>V. sordescens</i> DC.	10.4	4.9	3.9	10.4	2.9	1.9	1.0	5.2	3.4	6.1

*Verbesina glabrata* was the only species to exhibit variation in pollen grain shape, ranging from oblate-spheroidal to prolate-spheroidal (Tabs. 2, 4). The mean PD and ED of the comparison material of *V. macrophylla* were 31.9 µm and 32.6 µm, respectively, which differed from that of the standard material (25.8 µm and 27.2 µm, respectively), however, pollen grain shape did not differ. The comparison material for the other species had means that fell within the range found for the standard material.

*Principal component analysis (PCA)*

The first two axes of the PCA explained 83.6 % of the variability of the analyzed data. The first axes explained 64.8 % of the data, with *Verbesina bipinnatifida*, *V. macrophylla* and *V. nicotianifolia* having, in general, the lowest values for PD, ED, EDPV, colpus length, endoaperture length and spine length, while *Verbesina baccharifolia* and *V. luetzelburgii* had

**Table 4.** Measurements of pollen grains of comparison materials in Brazilian *Verbesina* L. (Heliantheae - Asteraceae) species in equatorial view: n=10;  $\bar{x}$  = arithmetic mean.

Species	Polar diameter (PD)	Equatorial diameter (ED)	PD/ED
	$\bar{x}$	$\bar{x}$	
<i>V. baccharifolia</i> Mattf.	38.0	39.5	0.96
	37.5	38.3	0.98
<i>V. bipinnatifida</i> Baker	30.3	30.5	0.99
	30.5	31.5	0.97
<i>V. floribunda</i> Gardner	32.0	33.2	0.96
	34.2	35.2	0.97
<i>V. glabrata</i> Hook. & Arn.	35.0	36.5	0.96
	38.5	37.7	1.02
<i>V. luetzelburgii</i> Mattf.	36.7	38.5	0.95
	37.0	37.5	0.99
<i>V. macrophylla</i> (Cass.) S.F. Blake	32.3	32.5	0.99
	31.5	32.7	0.96
<i>V. sordescens</i> DC.	36.8	37.5	0.98
	37.5	38.3	0.98



the highest values for these attributes. These attributes were closely correlated, as shown in Figure 3.

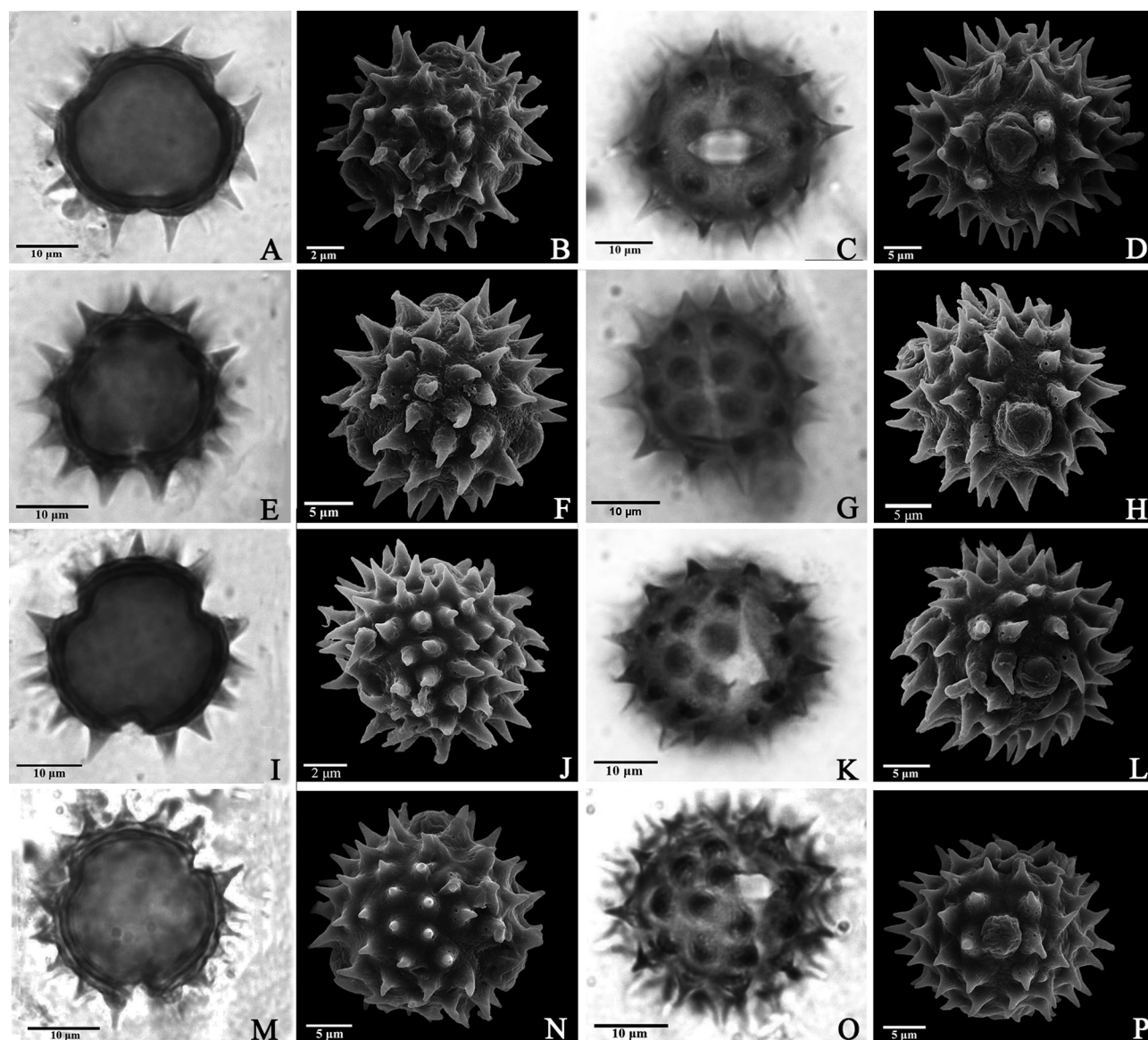
The second axis explained 18.8% of the data, with *Verbesina floribunda* having the highest values for distance between spines (DBS), exine thickness and endoaperture width, and the lowest values for the apocolpus side (AS) index and colpus width.

## Discussion

Pollen grains of *Verbesina* can be classified as the "Aspilia" type described by Salgado-Labouriau (1973),

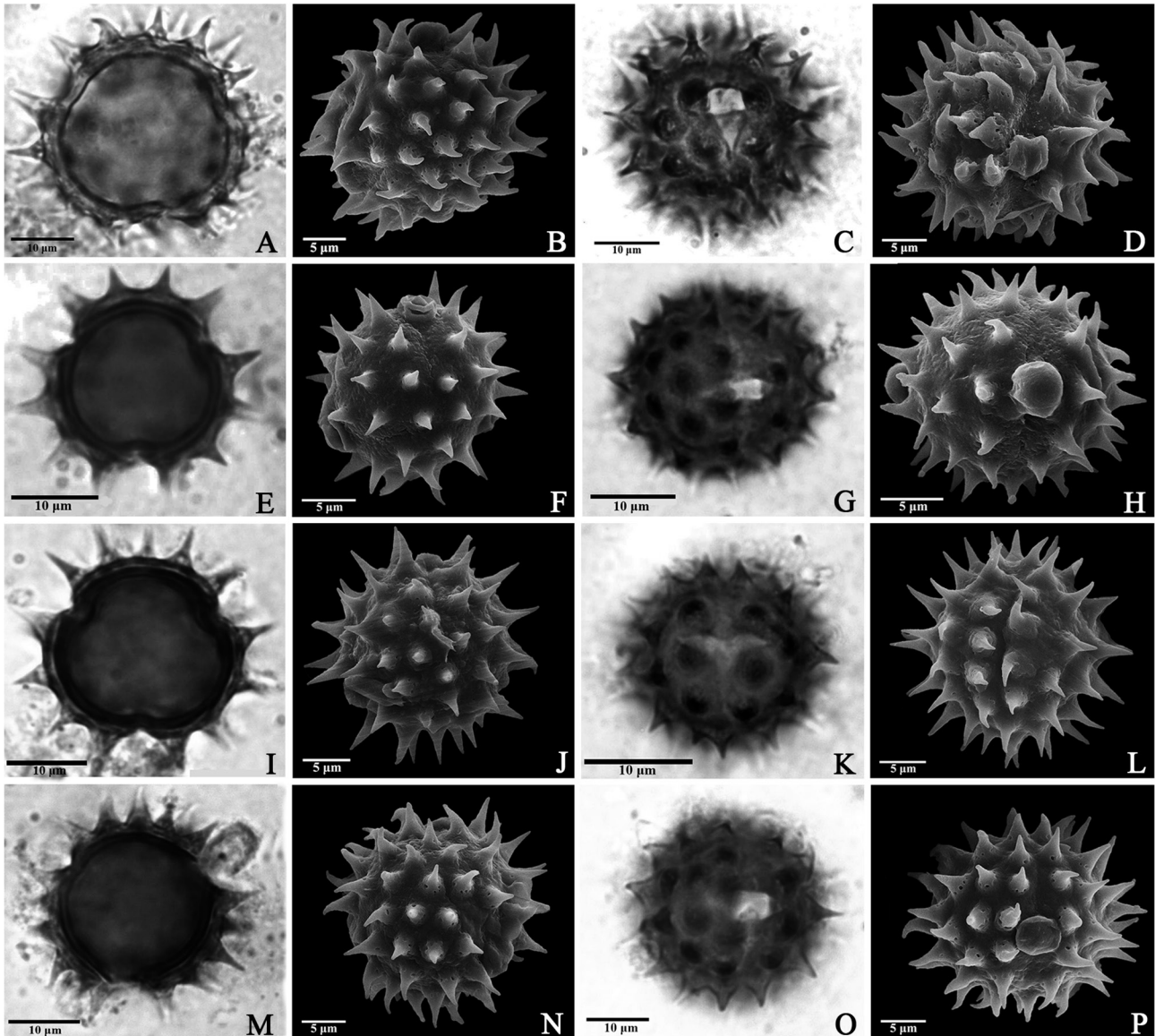
because they are medium to large in size, 3-colporate, and lalongate, with an endoaperture with a medium constriction, an echinate exine and conical spines with perforations at the base.

Previous studies of *Verbesina* have shown that pollen grain shape can vary from suboblate to prolate-spheroidal (PD / ED 0.75-1.14), with oblate-spheroidal to prolate-spheroidal being most common, as was reported by Gonçalves (1976) who analyzed 17 species of *Verbesina*, including three Brazilian species (*V. diversifolia* DC = *V. macrophylla*, *V. glabrata* and *V. sordescens*). These differences in pollen grain shape (Gonçalves 1976; Jesus & Lima 2013; Radaeski *et al.* 2016) (Tab. 5) are



**Figure 1.** Photomicrographs and electromicrographs of pollen grains of Brazilian *Verbesina* L. (Heliantheae-Asteraceae) species. 1st and 3rd columns - Photomicrographs under light microscopy; 2nd and 4th columns - electromicrographs in SEM. *Verbesina baccharifolia* - polar view: **A.** optical section, **B.** general aspect; equatorial view: **C.** optical section, **D.** aperture. *Verbesina bipinnatifida* - polar view: **E.** optical section, **F.** general aspect, equatorial view: **G.** optical section, **H.** aperture. *Verbesina floribunda* - polar view: **I.** optical section, **J.** general aspect, equatorial view: **K.** general aspect, **L.** aperture. *Verbesina glabrata* - polar view: **M.** optical section, **N.** general aspect, equatorial view: **O.** general aspect, **P.** aperture.





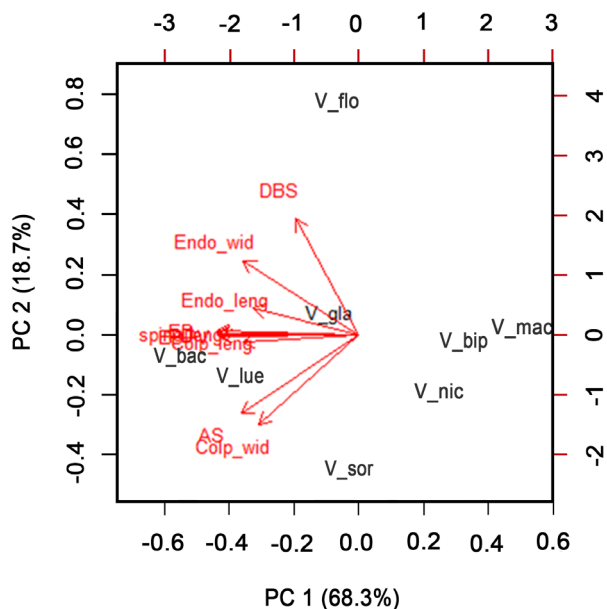
**Figure 2.** Photomicrographs and electromicrographs of pollen grains of Brazilian *Verbesina* L. (Heliantheae-Asteraceae) species. 1<sup>st</sup> and 3<sup>rd</sup> columns - Photomicrographs under light microscopy; 2<sup>nd</sup> and 4<sup>th</sup> columns - electromicrographs in SEM. *Verbesina luetzelburgii* - polar view: **A.** optical section, **B.** general aspect; equatorial view: **C.** optical section, **D.** aperture. *Verbesina macrophylla* - polar view: **E.** optical section, **F.** general aspect, equatorial view: **G.** optical section, **H.** aperture. *Verbesina nicotianifolia* - polar view: **I.** optical section, **J.** general aspect, equatorial view: **K.** general aspect, **L.** aperture. *Verbesina sordescens* - polar view: **M.** optical section, **N.** general aspect, equatorial view: **O.** general aspect, **P.** aperture.

**Table 5.** Shape of pollen grains and presence of cavea reported in previous studies that dealt with Brazilian taxa of the genus *Verbesina* (Heliantheae-Asteraceae).

Specie	Shape	Exine / thickness	Reference	Present study
<i>Verbesina glabrata</i> Hook. & Arn.	prolate-spheroidal	-	Gonçalves 1976	oblate-spheroidal to prolate-spheroidal
	spheroidal	not caveate	Cancelli <i>et al.</i> 2010	
<i>Verbesina macrophylla</i> (Cass.) S.F. Blake	prolate-spheroidal	-	Gonçalves 1976	oblate-spheroidal
	prolate-spheroidal	caveate	Jesus & Lima 2013	
<i>Verbesina sordescens</i> DC.	prolate-spheroidal	-	Gonçalves 1976	oblate-spheroidal
	oblate-spheroidal	caveate	Cancelli <i>et al.</i> 2010	
	oblate-spheroidal	caveate	Radaeski <i>et al.</i> 2014	
	prolate-spheroidal	cavea / 1µm	Radaeski <i>et al.</i> 2016	







**Figure 3.** Analysis of principal components composed of metric variables of pollen from *Verbesina* L. (Heliantheae-Asteraceae). Variables in red mean: PD - polar diameter in equatorial view, ED - equatorial diameter, EDPV - equatorial diameter in polar view, AS - apocolpus side, colp-leng: colpus length, colp-wid: colpus width, endo-leng: length of endoaperture, endo-wid: width of endoaperture, spine-leng: length of spine, DBS - distance between spines. The species names are abbreviated.

consistent with the high coefficient of variation found, which in the present study ranged 4.6-10.4 % for PD and 4.7-11.6 % for ED, showing that the shape of the pollen grain is variable.

The presence of a cavea has been reported to be very common in the tribe Heliantheae (Cancelli *et al.* 2007; Stanski *et al.* 2013; Radaeski *et al.* 2016). In some genera the cavea is evident and its thickness easily measured, as observed by Magenta *et al.* (2010) with *Viguiera*, for which it ranged 0.8-1.5µm.

Due to the proximity of the sexine and nexine, the cavea in *Verbesina* is difficult to visualize, which can lead to the false impression of its non-existence, as pointed out by Cancelli *et al.* (2010) for *Verbesina glabrata*. Some studies of species of *Verbesina* did not indicate the presence of a cavea, while others indicated that only the exine is of the cavea; only Radaeski *et al.* (2016) reported measurements of the cavea, which was 1µm for *V. sordescens* (Tab. 5).

Although the pollen grains of the studied Brazilian species of *Verbesina* exhibited homogeneity of shape, aperture type, and ornamentation of the sexine, some attributes show potential usefulness for characterizing species, such as the distance between spines, and dimensions of the apocolpus side and aperture. Thus, these characters of pollen grains have potential taxonomic value for distinguishing species.

## Acknowledgements

Thanks go to the Coordination of Improvement of Higher Education Personnel for the granting the doctoral scholarship to the first author; to the Federal District Research Support Foundation (FAPDF – 01/2016) for financial support; and to CNPq for a productivity grant (Vania Gonçalves-Esteves and Cláudia B.F. Mendonça).

## References

- Anderberg AA, Baldwin BG, Bayer RG, *et al.* 2007. Compositae. In: Kubitzki K. (ed.) The families and genera of vascular plants. New York, Springer. p. 61-87.
- APG IV – The Angiosperm Phylogeny Group. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* 181: 1-20.
- Bolick MR. 1991. Pollen diameter, exine thickness, and ultrastructure type in the tribes of the Compositae. *Compositae Newsletter* 19: 17-21.
- Cancelli RR, Cardoso A, Evaldt P, Bauermann SG. 2007. Catálogo palinológico de táxons da família Asteraceae Martinov. no Rio Grande do Sul - Parte I. *Pesquisas, Botânica* 58: 347-374.
- Cancelli RR, Cardoso A, Evaldt P, Bauermann SG. 2010. Catálogo palinológico de táxons da família Asteraceae Martinov, no Rio Grande do Sul, Brasil. *Iheringia, Série Botânica* 65: 201-280.
- Coutinho AP, Dinis AM. 2007. A contribution to the ultrastructural knowledge of the pollen exine in subtribe Inulinae (Inuleae, Asteraceae). *Plant Systematics and Evolution* 269: 159-170.
- Erdtman G. 1952. Pollen morphology and plant taxonomy – Angiosperms. Stockholm, Almqvist and Wiksell.
- Faegri G, Iversen J. 1966. *Textbook of modern pollen analysis*. Copenhagen, Scandinavian University Books.
- Flora do Brasil 2020 em construção. 2018. Asteraceae. Jardim Botânico do Rio de Janeiro. <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB55>. 26 Jan. 2018.
- Funk VA, Susanna A, Stuessy TF, Robinson H. 2009. Classification of Compositae. In: Funk VA, Susanna A, Stuessy TF, Bayer RJ. (eds.) *Systematics, evolution, and biogeography of Compositae*. Vienna, Austria, IAPT. p. 171-176.
- Gonçalves VB. 1976. Contribuição ao estudo palinológico da Tribo Heliantheae (Compositae). *Revista Brasileira de Biologia* 36: 157-166.
- Gonçalves-Esteves V, Esteves R. 1986. Contribuição ao estudo polínico da tribo Heliantheae (Compositae) IV. *Boletim do Museu Nacional, Botânica* 74: 1-14.
- Gonçalves-Esteves V, Esteves R. 1989a. Contribuição ao estudo polínico da tribo Heliantheae (Compositae) VI. *Boletim do Museu Nacional, Botânica* 80: 1-11.
- Gonçalves-Esteves V, Esteves R. 1989b. Contribuição ao estudo polínico da tribo Heliantheae (Compositae) VII. *Boletim do Museu Nacional, Botânica* 82: 1-11.
- Harker M, Jiménez-Reyes N. 2002. *Verbesina barrancae* (Compositae, Heliantheae), a new species from Jalisco, Mexico. *Brittonia* 54: 181-189.
- Jesus EA, Lima LCL. 2013. Morfologia polínica de espécies de Asteraceae ocorrentes em uma área de Mata Ombrófila Densa, Alagoinhas, Bahia, Brasil. In: XVII Jornada de Iniciação Científica, Universidade do Estado da Bahia. p. 1-2.
- Magenta MAG, Nunes AD, Mendonça CBF, Gonçalves-Esteves V. 2010. Palynotaxonomy of Brazilian *Viguiera* (Asteraceae) Species. *Boletín de la Sociedad Argentina de Botánica* 45: 285-299.
- Melhem TS, Cruz-Barros MAV, Corrêa AMS, Makino-Watanabe H, Silvestre-Capelato MSF, Gonçalves-Esteves V. 2003. Variabilidade polínica em plantas de Campos de Jordão (São Paulo, Brasil). *Boletim do Instituto de Botânica* 16: 9-104.



- Panero JL. 2007. Tribe Heliantheae - *Verbesina*. In: Kubitzki K. (ed.) The families and genera of vascular plants. [s.l.]. New York, Springer. p 440-477.
- Panero JL, Crozier BS. 2016. Macroevolutionary dynamics in the early diversification of Asteraceae. *Molecular Phylogenetics and Evolution* 99: 116-132.
- Panero JL, Freire SE, Espinar LA, Crozier BS, Barboza GE, Cantero JJ. 2014. Resolution of deep nodes yields an improved backbone phylogeny and a new basal lineage to study early evolution of Asteraceae. *Molecular Phylogenetics and Evolution* 80: 43-53.
- Radaeski JN, Evaldt ACP, Bauermann SG, Lima GL. 2014. Diversidade de grãos de pólen e esporos dos campos do Sul do Brasil: descrições morfológicas e implicações paleoecológicas. *Iheringia, Série Botânica* 69: 107-132.
- Radaeski JN, Evaldt ACP, Bauermann SG. 2016. Morfologia polínica de espécies da família Asteraceae Martinov nos Cerros da Campanha do Rio Grande do Sul, Brasil. *Iheringia, Série Botânica* 71: 357-366.
- Roubik DW, Moreno JE. 1991. Pollen and spores of Barro Colorado Island. Vol. 36. St. Louis, Missouri Botanical Garden.
- Salgado-Labouriau ML. 1973. Contribuição à palinologia dos cerrados. Rio de Janeiro, Academia Brasileira de Ciências.
- Sanchez AC, Lupo LC. 2009. Asteraceae de Interés en la Melisopalinoología. Bosque Montano de las Yungas (Jujuy - Argentina). *Boletín de la Sociedad Argentina de Botánica* 44: 57-64.
- Skvarla J, Turner BL. 1966. Systematic implications from electron microscopic studies of Compositae pollen- A review. *Annals of the Missouri Botanical Garden* 53: 220-256.
- Stanski C, Luz CFP, Nogueira A, Nogueira MKFS. 2013. Palynology of species in the Astereae and Heliantheae tribes occurring in the region of Campos Gerais, Paraná State, Brazil. *Iheringia, Série Botânica* 68: 203-214.
- Stanski C, Nogueira NKFS, Luz CFP. 2016. Palinologia de espécies de Asteraceae de utilidade medicinal para a região dos Campos Gerais, Ponta Grossa, PR, Brasil. *Hoehnea* 43: 349-360.
- Thiers B. 2017. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih>. 10 nov. 2017.
- Wortley AH, Funk VA, Robinson H, Skvarla JJ, Blackmore S. 2007. A search for pollen morphological synapomorphies to classify rogue genera in Compositae (Asteraceae). *Review of Palaeobotany and Palynology* 146: 169-181.

