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Original Paper

Pollen morphology of selected species of Anacardiaceae and its taxonomic significance

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Abstract

In the present work, the pollen morphology of 22 species of Anacardiaceae was analysed, occurring in the state of Bahia, Brazil. The palynological material was obtained from specimens deposited in herbaria. The pollen grains were acetolysed, measured, illustrated and described under light and scanning electron microscopies. The quantitative data were statistically analysed according to sample size. The analysed species presented pollen grains in monads, small to medium sized, isopolar, amb circular to subtriangular, with shapes varying from oblate-spheroidal to prolate, 3-colporate, with fastigium in some species. The exine ornamentation was characterized as psilate, striate, microreticulate-striate, striato-perforate, suprastriato-infra(micro)reticulate. The pollen morphology variation confirms the eurypalynous character of the family. The attributes of the apertures and exine may collaborate in the taxonomic circumscription and provide a clarification of the phylogenetic relationships of the group.

Key words: Anacardieae, Palynology, pollen grains, Rhoeae, Spondiadeae.

Resumo

No presente trabalho, foi analisada a morfologia polínica de 22 espécies de Anacardiaceae, ocorrentes no estado da Bahia, Brasil. O material polinífero foi obtido a partir de espécimes depositados em herbários. Os grãos de pólen foram acetolisados, mensurados, ilustrados e descritos sob microscopias de luz e eletrônica de varredura. Os dados quantitativos foram analisados estatisticamente de acordo com o tamanho da amostra. As espécies analisadas apresentaram grãos de pólen em mônades, pequenos a médios, isopolares, amb circular a subtriangular, com formas variando de oblata-esferoidal a prolata, 3-colporados, com fastígio e/ou ponte em algumas espécies. A ornamentação da exina caracterizou-se como psilada, estriada, microrreticulada-estriada, estriada-perfurada, supraestriada-infra(micror)reticulada. A variação morfopolínica confirma o caráter euripolínico da família. As características aperturais e da exina são atributos que podem colaborar com a circunscrição taxonômica e entendimento das relações filogenéticas do grupo.

Palavras-chave: Anacardieae, Palinologia, grãos de pólen, Rhoeae, Spondiadeae.

Introduction

Anacardiaceae is comprised of resiniferous plants, with stipulate leaves, superous ovary with apotropic ovule (Barroso 1991; Souza & Lorenzi 2005; Santos *et al.* 2008). It has a widespread distribution and is currently represented by 81 genera and circa 800 species (Pell *et al.* 2011), with 15 genera and 64 species recorded in Brazil (Silva-Luz *et al.* 2020). The family is commonly known for its high economic value, with the commercialization of its fruits and pseudo-fruits, and its application in the ornamental, pharmaceutical and wood industry (Souza & Lorenzi 2005; Pereira PS *et al.* 2014). Presently, Anacardiaceae is classified in the order

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Sapindales (Chase *et al.* 1993; APG IV 2016). Studies based on the morphology, anatomy, floral biology and geographic distribution, conducted by Engler (1883, 1892, 1897), and confirmed by Scholz (1964), divide the taxa of the family in five tribes: Mangiferae (= Anacardieae), Dobineeae (= Dobinaeae), Rhoideae (= Rhoeae), Semecarpeae and Spondieae (= Spondiadeae).

Wannan & Quinn (1990, 1991) have recognized two groups within the family, based on the fruit anatomy (endocarp *Anacardium*-type and *Spondias*-type), floral morphology and flavonoids. Such groups were later supported and confirmed by molecular studies developed by Pell (2004), circumscribing the subfamilies Anacardioideae, which includes the tribes Anacardieae, Dobineae, Rhoeae, and Semecarpeae; and Spondioideae, which comprises species of the tribe Spondiadeae. According to Wannan (2006), subfamily Anacardioideae has a clearly identified synapomorphy, the antisepalous fertile carpel, while Spondioideae does not possess a clearly identified synapomorphy; to Pell (2011), further efforts will be required to establish the monophyly of this subfamily.

Palynologically, the family is considered eurypalynous, for the variation in morphological characters of the aperture details and exine ornamentation. However, studies in pollen morphology of Anacardiaceae are deficient and scarce. A small number of taxa in the family has been palynologically analysed, mainly works on palynological flora (Erdtman 1943, 1952; Salgado-Labouriau 1973; Miranda & Andrade 1990; Roubik & Moreno 1991; Anzótegui 1992, 2001; Martinez-Hernandez *et al*. 1993; Gonçalves-Esteves & Ferreira 1994; Barros *et al.* 1999; Takeda *et al.* 2000; Melhem *et al.* 2003; Willard *et al*. 2004; Leal & Lorscheitter 2006; Macedo *et al.* 2009; Sánchez-Dzib *et al*. 2009; Garcia *et al.* 2011; Evaldt *et al.* 2013; Pereira ASS *et al.* 2014; Silva *et al.* 2014, 2016; Ybert *et al*. 2016; Luz *et al*. 2018).

Few studies focused exclusively on Anacardiaceae palynology have been found: Perveen & Qaiser (2010), which analysed species of the genus *Rhus* L. in Pakistan; Suárez *et al.* (2019), who analyzed the pollen morphology of the six species of *Schinopsis* restricted to the South American subtropical forests of Chaco. In Brazil, Pereira ASS *et al.* (2014) conducted a palynological study of *Anacardium* L. in the state of Pará, under light microscopy and scanning electron microscopy. In Bahia, only Silva *et al.* (2016) have addressed the pollen morphology of some species of Anacardiaceae in the "Flora polínica das caatingas (Estação Biológica de Canudos)" (Palynologycal Flora of the caatingas). In these circumstances, it is clear that the palynological descriptions of species of Anacardiaceae in the world, in Brazil and in Bahia, are deficient and scarce, considering their representativity in the region, level of endemism, and degree of economic importance to the regions where they are native. Many taxa of the family never had their pollen morphology analysed and described, and the need for palynological studies in the group is mentioned by Mitchell & Daly (2015).

In the face of the lack of data on pollen morphology of Anacardiaceae, especially in Brazil, and considering the importance and representativity of the family, we here present a palynological characterization of the species of Anacardiaceae present in the state of Bahia, with the goal of widening the palynological knowledge and contributing to taxonomic studies of the group.

Materials and Methods

The pollen material (flowers and/or flower buds) of species of Anacardiaceae was collected from specimens deposited at the HUEFS (Herbário da Universidade Estadual de Feira de Santana) and HUNEB (Herbário da Universidade do Estado da Bahia) herbaria. The specimens documented in the state of Bahia, Brazil were selected based on a survey on the platform SpeciesLink (<http://www.splink.org.br>) and the material for study was selected based on the availability of polyniferous material in the specimens deposited in the visited herbaria.

For each species, a specimen was defined as "standard", marked with (*) in the Tables 1 and S1 (available on supplementary material <https://doi.org/10.6084/m9.figshare.16864627.v1>), which was used as basis for the descriptions and the illustrations. As "comparison material", more than two specimens of each species were examined, whenever possible, which are also listed in the Table 1. The pollen grains were treated with acetolysis (Erdtman 1960), following the modifications proposed by Melhem *et al.* (2003). Whenever possible, a random selection of 25 pollen grains was sampled for measuring, under light microscopy, of the following main morphometric parameters: equatorial diameter in equatorial view (EDe), polar diameter in equatorial view (PDe) and equatorial diameter in polar view (EDp). For the remaining parameters - Polar Area Index (PAI) (follows

Table 1 – Examined material in the morphological analysis of pollen grains of Anacardiaceae.

Species	Code	Locality (Brazil, Bahia)	Voucher	Herbarium
Anacardium humile Engl.	AnH	Cocos	*L.P. Queiroz 11003**	HUEFS
		Rui Barbosa	*L.P. Queiroz 9395*	HUEFS
		Morro do Chapéu	*L.P. Queiroz 13285*	HUEFS
Anacardium occidentale L.	AnO	Pilão Arcado	*L.P. Queiroz 10886**	HUEFS
		Rui Barbosa	*L.P. Queiroz 9392*	HUEFS
		Salvador	*L. Araújo et al. 16*	HUEFS
Apterokarpos gardneri (Engl.) Rizzini	ApG	Casa Nova	*C. Correia 460**	HUEFS
		Casa Nova	*C. Correia 434*	HUEFS
Astronium concinnum Schott.	AsC	Amargosa	*J.L. Paixão 1304**	HUEFS
		Morro do Chapéu	*J.G. Carvalho-Sobrinho 129*	HUEFS
		Feira de Santana	*A.A. Santos 2456*	HUEFS
Astronium fraxinifolium Schott.	AsF	São Desidério	*S. Reis 37**	HUEFS
		Itaguari	*M.L.S. Guedes 13689*	HUEFS
		São Desidério	*S. Reis 158*	HUEFS
Astronium graveolens Jacq.	AsG	Barra	*A.M. Miranda 6356**	HUEFS
		Rio de Contas	*R.M. Harley 54671*	HUEFS
		Riachão das Neves	*E. Melo 2761*	HUEFS
Cyrtocarpa caatingae J.D.Mitch. & Daly	CyC	Iaçu	*G.C.P. Pinto 20280**	HUEFS
		Rio de Contas	*R.M. Harley 55196*	HUEFS
		Maracás	*E. Melo 10595*	HUEFS
Lithraea molleoides (Vell.) Engl.	LiM	Rio de Contas	*F.H. Nascimento 212**	HUEFS
		Caetité	*C. Correia 506*	HUEFS
Mangifera indica L.	MaI	Jeremoabo	*L. Araújo et al. 81**	HUEFS
		Maragojipe	*B.F. Santana 209*	HUEFS
		Senhor do Bonfim	*A.C.R. Assis 100*	HUNEB
Myracrodruon urundeuva Allem.	MyU	Paramirim	*E. Melo 1952**	HUEFS
		Paramirim	*A.A. Conceição 1952*	HUEFS
		Itaquari	*F. França 3632*	HUEFS
Schinopsis brasiliensis Engl.	ScB	Paramirim	*A.A. Conceição 1957**	HUEFS
		Juazeiro	*K.R.S. Mariano 14*	HUEFS
		Brotas de Macaúbas	*A.A. Conceição 2234*	HUEFS
Schinus terebinthifolius Raddi.	ScT	Santa Terezinha	*E. Melo 9564**	HUEFS
		Mundo Novo	*L. Araújo 03*	HUEFS
		Feira de Santana	*C. Correia 27*	HUEFS
Spondias caatingae P.C.L. Carvalho & Van den Berg.	SpC	Iaçu	*C. Van den Berg 1974**	HUEFS

Species	Code	Locality (Brazil, Bahia)	Voucher	Herbarium
		Iaçu	*C. Van den Berg 1977*	HUEFS
		Cruz das Almas	*C. Van den Berg 1978*	HUEFS
Spondias mombin Jacq.	SpM	Ilhéus	*L.A. Mattos-Silva 4288**	HUEFS
		Ilhéus	*J.L. Haje 1429*	HUEFS
Spondias purpurea L.	SpP	Serra Preta	*C. Van den Berg 1965**	HUEFS
Spondias tuberosa Arruda	SpT	Abaré	*E. Melo 7046**	HUEFS
		Queimadas	*M.D. Fadigas 03*	HUEFS
		Canudos	*F.H.M. Silva 443*	HUNEB
Spondias venulosa Mart. *ex* Engl.	SpV	Rui Barbosa	*L.P. Queiroz 9805**	HUEFS
		Feira de Santana	*E. Melo 5459*	HUEFS
Tapirira guianensis Aubl.	TaG	Feira da Mata	*A. Rapini 1449**	HUEFS
		Jeremoabo	*E. Melo 4272*	HUEFS
		Pindobaçu	*L.A. Sousa 205*	HUNEB
Tapirira marchandii Engl.	TaM	Mucugê	*L.P. Queiroz 1877**	HUEFS
Tapirira obtusa (Benth.) J.D.Mitch.	TaO	Abaíra	*W. Ganev 1206**	HUEFS
		Lençóis	*L.S. Funch 171*	HUEFS
		Rio de Contas	*F.H.F. Nascimento 242*	HUEFS
Thyrsodium schomburgkianum Benth.	Tsch	Una	*J.G. Jardim 100**	HUEFS
Thyrsodium spruceanum Benth.	Tspr	Entre Rios	*M. Sobral 8432**	HUEFS
		Mata de São João	*M.C. Ferreira 1325*	HUEFS
		Entre Rios	*M.N.S. Stapf 227*	HUEFS

Iversen & Troels-Smith 1950, Faegri & Iversen 1966). Colpus and endoaperture dimensions (length and width) and exine thickness - the measurements of 10 pollen grains, per specimen, were used.

Statistical analyses included the calculation of the arithmetic average ($\bar{x}$), sample standard deviation (s), averaged standard deviation ($s\bar{x}$), coefficient of variability (CV), confidence interval of 95% (IC) and range (R) for the measurements with a sampling size of 25. For the remaining measurements, with sampling size of 10, only the arithmetic average was calculated. A multivariate analyses was conducted (Principal Component Analysis - PCA) with the quantitative data of the pollen grains from the "standard specimens", to assess if the morphometric data as a whole would all the grouping of species by similarity of the measurements; for such analysis, 11 metric variables were used [EDe, PDe, EDp, ratio between Ede and Pde (classification of shape follows Erdtman 1952), PAI, colpus length, colpus width, endoaperture width, endoaperture height, thickness of the sexine and nexine]. Both the ordination of the data in the multivariate analysis, as the Tukey test, were conducted in PC-ORD 5.0 software (McCune & Mefford 2011).

For analysis of the ornamentation under scanning electron microscope (SEM), the acetolysed pollen grains were washed and dehydrated in a graded alcohol series (50, 70, 90 and 100%). The absolute alcohol containing the pollen grains was dripped onto the SEM stubs and, after completely drying, they were sputter-coated in high-vaccum with gold, electromicrographed and described.

The pollen morphological characters were analysed and described according to the terminology by Punt *et al.* (2007), for LM, and Hesse *et al.* (2009), for SEM. Photomicrographs were obtained on a Zeiss Axioskop Plus with a coupled Sony Cyber-shot DSC-W7 camera, at

the Laboratory of Palynological Studies (LAEP) at the Campus VII of the Universidade do Estado da Bahia, and the SEM electromicrographs were obtained with a Quanta 250 (FEI Company) Microscope, at the Electronic Microscopy Center (CME) of the Universidade Estadual de Santa Cruz (UESC). Permanent slides were deposited at the pollen reference collection of the Laboratory of Palynological Studies (LAEP) of the Universidade do Estado da Bahia, Campus VII, Senhor do Bonfim, Bahia, Brazil.

Results

The species of Anacardiaceae analysed in this study (Figs. 1-5) presented monad pollen grains, small to medium sized, isopolar, oblate-spheroidal to prolate, amb circular to subtriangular, polar area very small or small (Tabs. S1; S2, available on supplementary material <https://doi.org/10.6084/m9.figshare.16864627.v1>). The apertural type is characterized as 3-colporate; with long to very long colpus; lolongate or lalongate endoapertures (elliptical, fusiform or in H). In some species, there is presence of fastigium and constriction of the endoaperture. The LM and SEM analyses revealed a range of variation in the exine ornamentation: psilate, striate, microreticulate-striate, striato-perforate and suprastriato-infra(micro)reticulate. The presence of elongated muri (striae), parallel or subparallel, on the surface of the pollen grains is the basic sculpturing type to the group.

Tribe Anacardieae

Species analysed: *Anacardium humile* Engl.; *Anacardium occidentale* L.; *Mangifera indica* L. (Figs. 1; 4; Tabs. S1; S2, available on supplementary material <https://doi.org/10.6084/m9.figshare.16864627.v1>).

Medium sized pollen grains, subprolate to prolate, subtriangular to subcircular amb.

Aperture: 3-colporate, angulaperturate, when presenting subtriangular amb. Long to very long colpus, tapered or sharp ends. Lalongate [elliptical, rectangular and in H (*M. indica* - Fig. 1f)] or lolongate endoapertures.

Exine: striato-microreticulate under LM (Fig. 1d) and suprastriato-inframicroreticulate or striate-perforate, under SEM (Fig. 4a-c). Sexine thicker than the nexine (Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.16864627.v1>).

Morphologically, the pollen grains of the analysed species of Anacardieae are similar in size and aperture type. It is noted, however, that *A. occidentale* presents larger axis and apertures, when compared to *Mangifera indica*, which presents the lowest values of axis, among all the species of the tribe. We have also observed that the "comparison specimens" shows values of axis within the variation range of their respective "standard specimens" (Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.16864627.v1>).

Under SEM, the margines of the pollen grains colpi of the Anacardieae species have no undulation (Fig. 4a-b), with a psilate colpus margo in *Anacardium humile* (Fig. 4a) and *A. occidentale* (Fig. 4b). A granulate apertural membrane was observed in *A. occidentale* and *M. indica*.

The endoapertures are lalongate in *A. humile* and *M. indica*, lolongate in *A. occidentale* (Fig. 1c); generally with tapering ends (*A. humile*), rectangular and constricted, in H, in the pollen grains of *M. indica* (Fig. 1f). In general, under LM, the majority of the pollen grains present a striato-microreticulate exine (Fig. 1d). In the species *A. humile* and *A. occidentale*, under SEM, it was possible to distinguish an inframicroreticulum. In these species, the exine of the pollen grains is characterized as suprastriato-inframicroreticulate, with sinuous striae, of high muri, branched in some areas, predominantly continuous and long, spaced in the direction of the polar axis, in some areas are juxtaposed with some transverse striae mainly in the apocolpium, with irregular lumens of infrareticulum, with a variety of shapes and sizes in *A. humile* (Fig. 4a) and with juxtaposed striae, of high muri, continuous and long in the polar direction, branched in some areas in *A. occidentale* (Fig. 4b). Under SEM, the surface in *M. indica* presented striate-perforate, with low muri striae, comparatively less sinuous striae, disposed very close together, with some transverse striae in the apocolpium, striae short and very branched (Fig. 4c). These differences in shape and organization of the muri were considered a diagnostic character for the separation of the genera of Anacardiaceae here analysed.

Tribe Rhoeae

Species analysed: *Apterokarpos gardneri* (Engl.) Rizzini; *Astronium conccinum* Schott; *Astronium fraxinifolium* Schott; *Astronium graveolens* Jacq.; *Lithraea molleoides* (Vell.) Engl.; *Myracrodruon urudeuva* Allem.; *Schinopsis brasiliensis* Engl.; *Schinus terebinthifolia* Raddi;

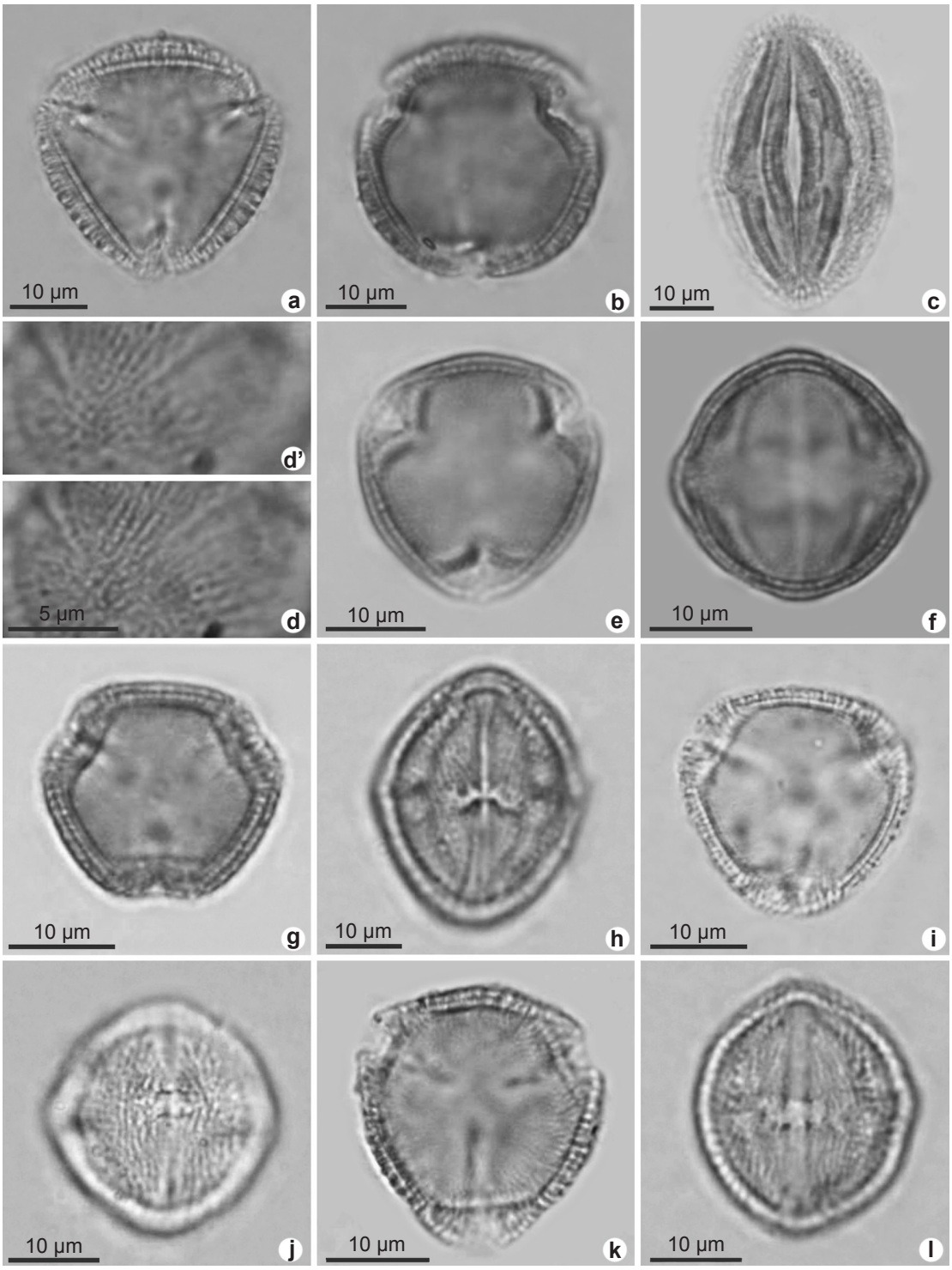

Figure 1 – a-l. Photomicrographs (LM) of pollen grains of the Anacardiaceae species – a-f. Anacardieae – a. *Anacardium humile* – optical section in polar view; b-d. *A. occidentale* – b. optical section in polar view; c. detail of the aperture; d-d'. LO-analysis; e-f. *Mangifera indica* – e. optical section in polar view; f. detail of the aperture; g-l. Rhoeae – g-h. *Apterokarpos gardneri* – g. optical section in polar view; h. surface and detail of the aperture; i-j. *Astronium concinnum* – i. optical section in polar view; j. surface and detail of the aperture; k-l. *A. fraxinifolium* – k. optical section in polar view; l. surface and detail of the aperture.

Thyrsodium schomburgkianum Benth.; *Thyrsodium spruceannum* Benth. (Figs. 1; 2; 4; 5; Tabs. S1; S2, available on supplementary material <https://doi.org/10.6084/m9.figshare.16864627.v1>).

Medium-sized pollen grains (except for *A. fraxinifolium*, where they are small, oblate-spheroidal, spheroidal, prolate-spheroidal, subprolate, subcircular, circular or subtriangular amb, with presence of fastigium (*L. molleoides* - Fig. 2c-d).

Aperture: 3-colporate; angulaperturate, when presenting subtriangular amb. Long to very long colpus, with tapering ends. Lalongate endoapertures; tapering, rounded or straight ends; superior or inferior limits are parallel or concave, with contour without undulation (except for *A. gardneri*, where it is undulate - Fig. 2h).

Exine: Psilate (*T. spruceannum*, Fig. 5b), suprastriato-infra(micro)reticulate, microreticulate-striate (*A. gardneri*, Fig. 4d), striato-perforate (*S. terebinthifolia*). Sexine thicker than the nexine.

The smallest pollen grains were observed in *A. conccinum* and *S. brasiliensis* (19.1 µm), and the largest were observed in *L. molleoides* with 37 µm (Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.16864627.v1>). The data have demonstrated, however, that despite the observed variability in the diameter of the pollen grains, the category of medium size is maintained among the specimens of each species, except for *A. fraxinifolium*, for which diameters lower than 25 µm were recorded (S. Reis 37 - "standard specimen", Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.16864627.v1>), therefore belonging to the category of small size. However, the "comparison specimens" presented values higher than 25, which had an impact on the variation of the pollen grains, varying from small to medium size.

Apterokarpos gardneri and *Schinopsis brasiliensis* possess colpus with a differentiated margo (Fig. 4d,l). In *A. gardneri*, the muri are distributed up to the proximities of the margo, which is fine and subtle, sometimes discontinuous, while in *S. brasiliensis* the margo is comparatively thicker (SEM - Fig. 4l). Under larger amplifications in SEM, the pollen grains of *Apterokarpos gardneri*, *Astronium conccinum*, *A. fraxinifolium*, *Lithraea molleoides*, *Myracrodruon urudeuva*, *Schinus terebinthifolia* and *Thyrsodium spruceannum* presented a granulate apertural membrane, with heterogeneous granules in what concerns distribution and size (Figs. 4d,f-h,j; 5a-b).

The most significant difference found among the pollen grains of the taxa of tribe Rhoeae is the exine ornamentation. This can be distinguished by the organization of the muri. Under LM, the pollen grains are described as striato-microreticulate or striato-reticulate (*Schinopsis brasiliensis* - Fig. 2h). However, under the greatest amplification provided by SEM, it was not possible to observe the (micro)reticulum in most species. In *Apterokarpos gardneri*, however, the ornamentation of the exine can be described as microreticulate-striate, which separates it from all the other species of Rhoeae here analysed. At the apocolpium it is more microreticulate-striate. The shallow, parallel or subparallel muri are more cross-linked to form a reticulum in the grooves, with irregular lumens with a variety of shapes and sizes. Near to the colpus the reticulum mesh diminished, and the psilate colpus margo is very thin, while the lumens at the mesocolpus are smaller as perforations (Fig. 4d).

Species *Astronium conccinum*, *Lithraea molleoides* and *Schinopsis brasiliensis* (Fig. 4e-f,h,k,l) share many similarities in the organization of the sinuous striae with high muri, branched in some areas, subparallel in the direction of the apocolpium and heterobrochate infrareticulum. *A. conccinum* and *S. brasiliensis* are distinguished from *L. molleoides* for presenting a thicker apertural margo (Fig. 4f,l), with striae that become fused when approaching it. In addition, *S. brasiliensis* presents some transverse striae near the apertures (Fig. 4l), a character which separates it from the other two species.

In *Astronium fraxinifolium*, *Myracrodruon urudeuva* and *Schinus terebinthifolia* (Figs. 4g,i;5a), the striae are shallow, parallel in the direction of the poles and juxtapposed, especially in *A. fraxinifolium* (Fig. 4g), which is distinguished from the remaining species for being more closely juxtapposed, in comparison. *M. urudeuva* and *S. terebinthifolia* present striae with branched muri, more spaced between them on the apocolpium, when compared to the mesocolpium, sometimes recurved (Fig. 5a) as it approaches the apocolpium. In *S. terebinthifolia* it was also possible to observe perforations associated with striae. Despite the striate pattern being characteristic of most species of Rhoeae, the ornamentation of the exine in *Thyrsodium* spp. was scabrate under LM and, under SEM, psilate (Fig. 5b), which sets it apart from the remaining species.

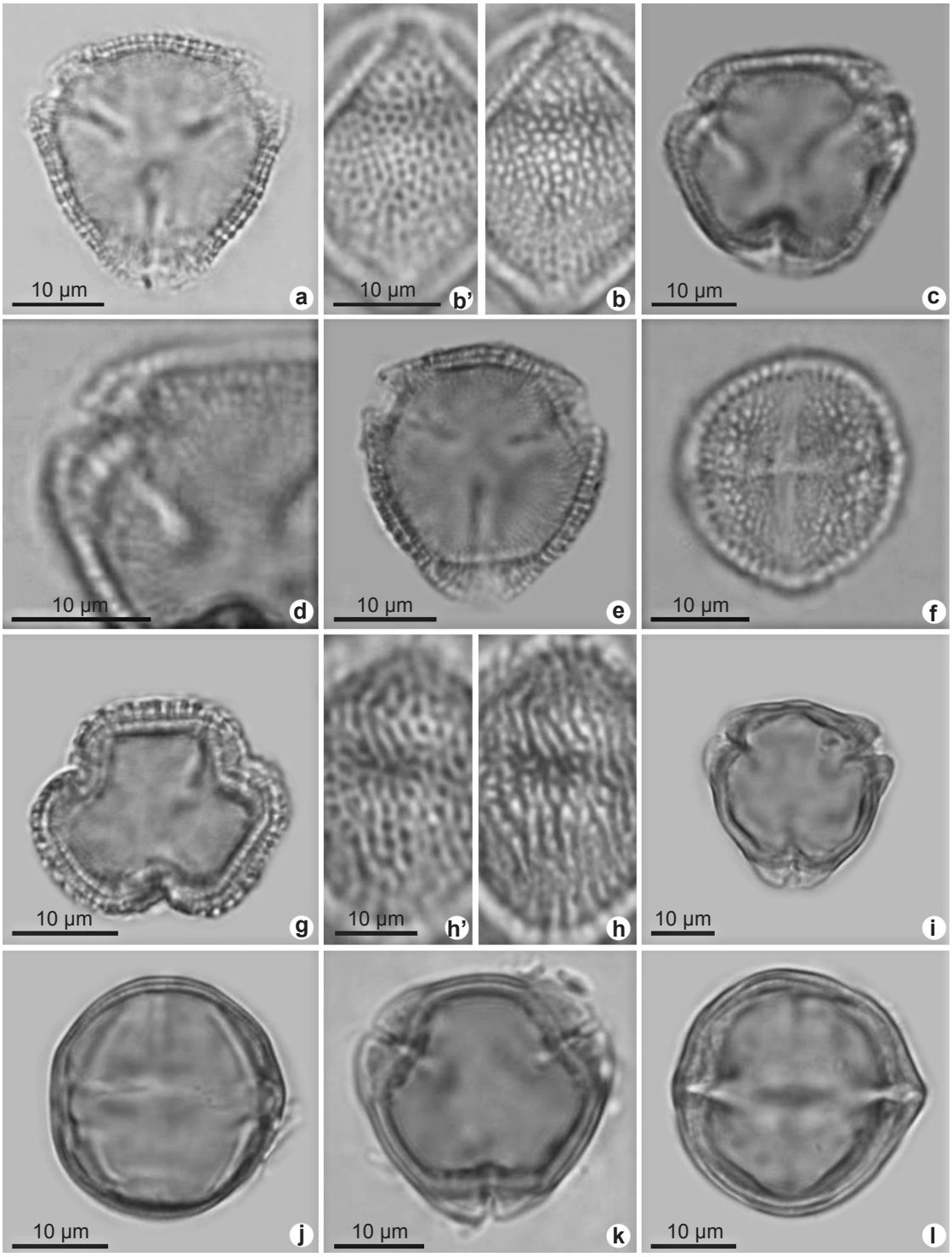

Figure 2 – a-l. Photomicrographs (LM) of pollen grains of the Anacardiaceae species (Rhoeae) – a-b. *Astronium graveolens* – a. optical section in polar view; b-b'. LO-analysis; c-d. *Lithraea molleoides* – c. detail of the aperture; d. LO-analysis; e-f. *Myracrodruon urudeuva* – e. optical section in polar view; f. surface and detail of the aperture; g-h. *Schinopsis brasiliensis* – g. optical section in polar view; h-h'. LO-analysis; i-j. *Thyrsodium schomburgkianum* – i. optical section in polar view; j. optical section in equatorial view; k-l. *T. spruceannum* – k. optical section in polar view; l. optical section in equatorial view.

Tribe Spondiadeae

Species analysed: *Cyrtocarpa caatingae* J.D.Mitch. & Daly; *Spondias caatingae* P.C.L. Carvalho & Van den Berg; *Spondias purpurea* L.; *Spondias mombin* Jacq.; *Spondias tuberosa* Arruda; *Spondias venulosa* Mart. *ex* Engl.; *Tapirira guianensis* Aubl.; *Tapirira marchandii* Engl.; *Tapirira obtusa* (Benth.) J.D.Mitch. (Figs. 3; 5; Tabs. S1; S2, available on supplementary material <https://doi.org/10.6084/m9.figshare.16864627.v1>).

Medium-sized pollen grains, prolate, subprolate to prolate-spheroidal (*T. obtusa*), circular to subcircular amb, with presence of a fastigium (*S. caatingae*, *S. mombin*, *S. purpurea* - Fig. 3b,e).

Aperture: 3-colporate. Long to very long colpus, tapering or rounded ends (*Cyrtocarpa caatingae*). Lalongate endoapertures, rounded, tapering or straight ends, superior and inferior limits are parallel or concave.

Exine: Striate, suprastriato-inframicroreticulate, striato-perforate. Ornamental elements free in the lumina (*Cyrtocarpa caatingae* - Fig. 5c). Sexine thicker than the nexine.

In most species of the tribe Spondiadeae here analysed, it was possible to visualize colpus with a granulate apertural membrane (Fig. 5g,h,j,k), granules distributed in a homogeneous or heterogeneous pattern in the species.

The endoapertures of the of the analysed species' pollen grains presented a diversity of shapes: the superior and inferior limits ranged between parallel (*Spondias purpurea*, *Tapirira* spp. Fig. 3f,l) and concave (remaining species), with elliptical shape (rounded ends) or fusiform (tapering ends). In *S. tuberosa* and *T. obtusa*, we have observed the presence of both elliptical and fusiform endoapertures. The endoapertures of *Cyrtocarpa* are difficult to visualize under LM and, often, it is not possible to document their ends.

The species *Spondias caatingae*, *S. purpurea* and *S. mombin* presented pollen grains with a fastigium (Fig. 3b,e). A characteristic present in the species of *Spondias* (except *S. purpurea*) was the presence of a protrusion over the endoapertures formed by the margins of the colpus, observed under LM (Fig. 3c,h,j) and under SEM, in the species *S. mombin*, *S. tuberosa* and *S. venulosa* (Fig. 5f-i).

The ornamentation of the exine in the pollen grains, of all species of Spondiadeae here analysed, presented a striate pattern. *Cyrtocarpa caatingae*, presented suprastriato-inframicroreticulate exine, with granules inside the lumina (Fig. 5c) and perforations near the colpus; with short and sinuous striae, of high muri, very branched, comparatively more spaced and parallel in the direction of the poles, with a more irregular disposition close to the apertures. A great part of these characteristics significantly separates the species *C. caatingae* from the remaining species of tribe Spondiadeae.

Spondias caatingae, *S. tuberosa* and *S. venulosa* presented pollen grains striato-perforate, with perforations of different diameters (Fig. 5e,g-i), while in the other species of the genus *Spondias* and *Tapirira*, only striae were observed under SEM. The species *Tapirira* presented, under SEM (Fig. 5j-l), juxtapposed striae, predominantly continuous and long, distributed in parallel in the direction of the poles, branched and sinuous in some areas; sometimes with some transverse striae in the mesocolpium in *T. obtusa* (Fig. 5l), or with intertwined branches on the mesocolpium in *T. marchandii* (Fig. 5k), what differentiates them from each other.

Quantitative analysis

From the graphic representation of the standard deviation (Fig. 6), it is possible to infer that the taxa of *Anacardium*, *Spondias* and *Thyrsodium* genera are distinguished from the remaining species by the larger values of equatorial diameter in equatorial view (EDe) and *Astronium graveolens* and *Lithraea molleoides* present intermediate diameters values of their pollen grains. *Anacardium* species, *Lithraea molleoides* and *Spondias* species produced the largest values of polar diameter in equatorial view (PDe) and the analyzed species form a large continuous group by data from equatorial diameter in polar view (EDp) with the highest diameter values are for the pollen grains of *Anacardium* species, *Lithraea molleoides*, *Spondias* and *Thyrsodium* species (Fig. 6).

The Tukey test fleshed out a significant difference between *Cyrtocarpa caatingae* and all the species of *Spondias*, as they presented clearly higher values of the diameters of the pollen grains. *Anacardium humile*, although presenting higher values of equatorial diameter in equatorial view (EDe) and in polar view (EDp), it was not separated from the remaining taxa through the results of the Tukey test. The species *Apterokarpos gardneri*, *Astronium* species, *C. caatingae*, *Mangifera indica*, *Myracrodruon urudeuva*, *Schinopsis brasiliensis*, *Schinus terebinthifolia* and *Tapirira* species form a

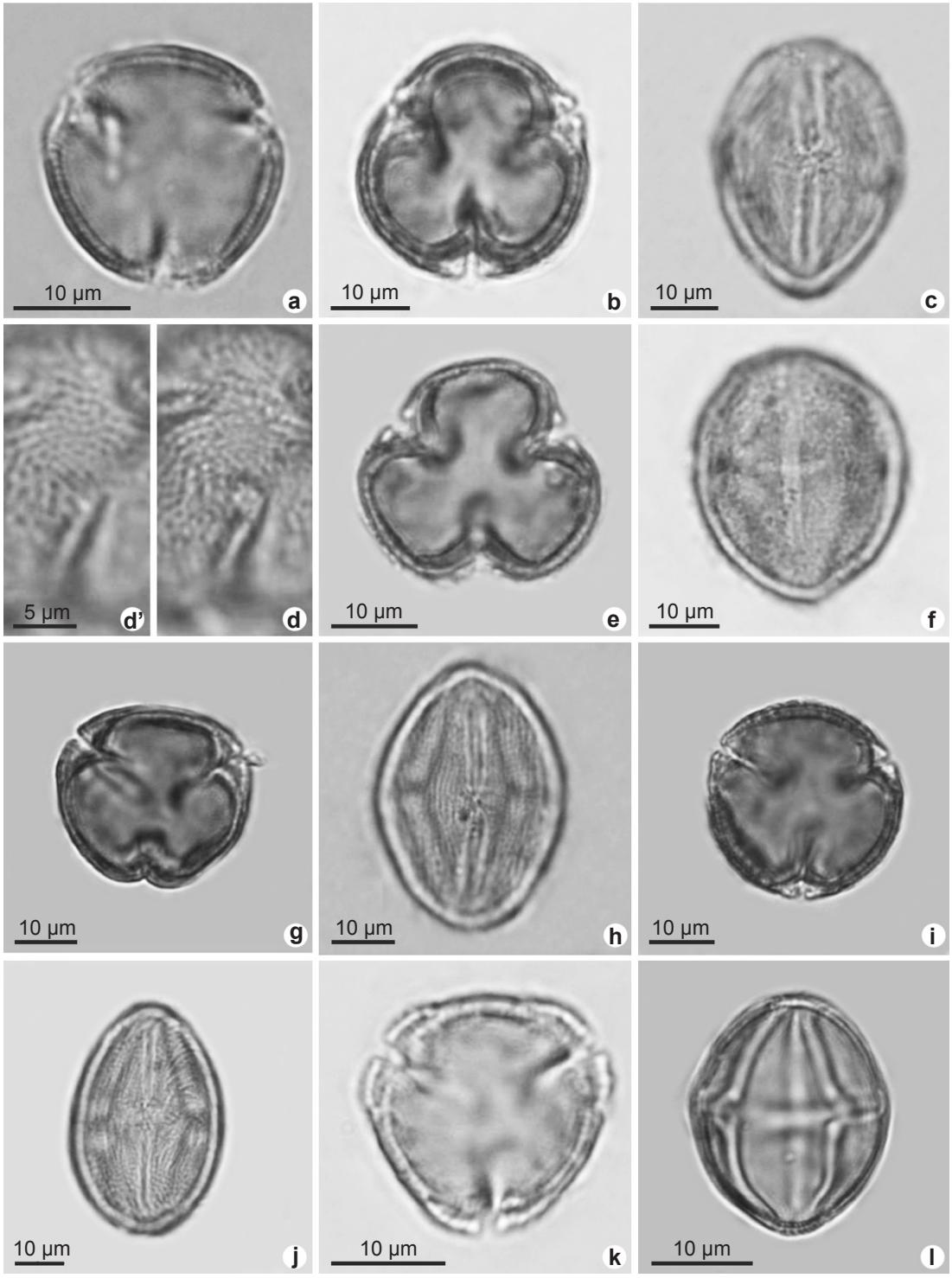

Figure 3 – a-l. Photomicrographs (LM) of the pollen grains of the Anacardiaceae species (Spondiadeae) – a. *Cyrtocarpa caatingae* – optical section in polar view; b-d. *Spondias caatingae* – b. optical section in polar view; c. surface and detail of the aperture; d-d'. LO-analysis; e-f. *S. purpurea* – e. optical section in polar view; f. surface and detail of the aperture; g-h. *S. tuberosa* – g. optical section in polar view; h. surface and detail of the aperture; i-j. *S. venulosa* – i. optical section in polar view; j. surface and detail of the aperture; k. *Tapirira marchandii* – optical section in polar view; l. *T. obtusa* – optical section in equatorial view.

group with the smallest polar diameter in equatorial view (PDe).

Anacardium humile pollen grains diameters are presented in the Tukey test with a significant difference in comparison to *Cyrtocarpa caatingae* and *Schinopsis brasiliensis*, which presented lower values for the diameters.

The multivariate analysis, the principal component analysis (PCA) summarized 79.01% of the variability of the analyzed quantitative data in its first two axes (Fig. 7).

The first axis explained 54.56% of the analyzed pollen data, and the metric variables that most contributed to the ordering of the species were EnL (Endoaperture Length), Sex (Sexine Thickness) and EcL (Colpus Length) (Tab. 2). We can, then, observe that the *Anacardium occidentale* and *Anacardium humile* form a distinct group from the others because they have the highest values for the main variables of this axis.

The second axis of the analysis contributed to explaining 24.52% of the pollen data analyzed. For the ordering of the species according to this axis, the most significant variables were EnL (Endoaperture Length), EcL (Colpus Length) and PDe (Polar Diameter in equatorial view). Along this axis, we highlight the proximity of *Spondias* species with the highest values for the variables related to that axis (positioned on the negative side), as well as *Lithraea molleoides*.

In addition, *Spondias* species also have the largest diameter measurements, the highest P/E ratio, and the longest colpus length, which contributed to their ordering on the negative side of axis 2. Among the species of this genus, *Spondias caatingae* is separated from the others for its greater values of Colpus Length, Endoaperture Length and Sexine.

Astronium fraxinifolium has the smallest diameters, shortest colpus length and endoaperture width, which contributed to distancing it from other species of the genus.

Discussion

Morphological characterization of pollen grains of Anacardiaceae

Based on fruit morphological and anatomical characters, *Anacardium* possesses the basic characteristics of the subfamily Anacardioideae (Wannan 2006). Palynologically, this genus stands out for presenting pollen grains with a striato-microreticulate exine, confirming the taxonomical affinities existing between their species. The palynological descriptions here presented for the species of *Anacardium* agree with the literature in terms of size, except for Silva *et al.* (2014), which documented large pollen grains for the species *A. occidentale*.

The shape of the pollen grains of the species of *Anacardium* here analysed agrees with the results by Silva *et al.* (2014) and Pereira ASS *et al.* (2014), for the species *A. occidentale*. However, it disagrees with those presented by Miranda & Andrade (1990), who described the pollen grains as suboblate; and Silva *et al.* (2016) as oblate spheroidal, for the same species. Pereira ASS *et al.* (2014), when studying *A. humile*, considered the pollen grains as prolate-spheroidal, differing from the subprolate shape documented in this work for that species.

Previous works, focusing on pollen of *Anacardium,* have reported lolongate endoapertures in *A. occidentale* (Silva *et al.* 2014). Often, the pollen grains' apertures of these species are difficult to visualize under LM, which makes it difficult to obtain a better description and delimitation of the endoapertures (Miranda & Andrade 1990).

The striate pattern of the ornamentation of the pollen grains' exine of *Anacardium* is in agreement with the information available in the consulted specialized literature, except for Roubik & Moreno (1991) and Pereira ASS *et al.* (2014), who describe a reticulate exine for *A. humile* and *A. occidentale*, respectively. In studies under LM, some details of the exine's surface can be overlooked. Salgado-Labouriau (1973), Miranda & Andrade (1990), and Silva *et al.* (2014) observed striae only in the analysed species of *Anacardium*, while Silva *et al.* (2016), with the surface detail provided by SEM, have identified, additionally to the striae, a reticulum in the pollen grains of *A. occidentale*. In this study, the same species was described as having a striato-microreticulate exine.

Mora *et al.* (2013) have documented 3-porate pollen grains in *Mangifera indica*, differing from the evidence found in the literature and from the results in the present study for the family Anacardiaceae, where colporate grains are standard. The striato-microreticulate ornamentation, observed in this study, both under LM as well as SEM, differs from the standard striate pattern described by Aftab & Perveen (2006), and rugulate-striate as observed by Martinez-Hernandez *et al.* (1993), under LM analysis.

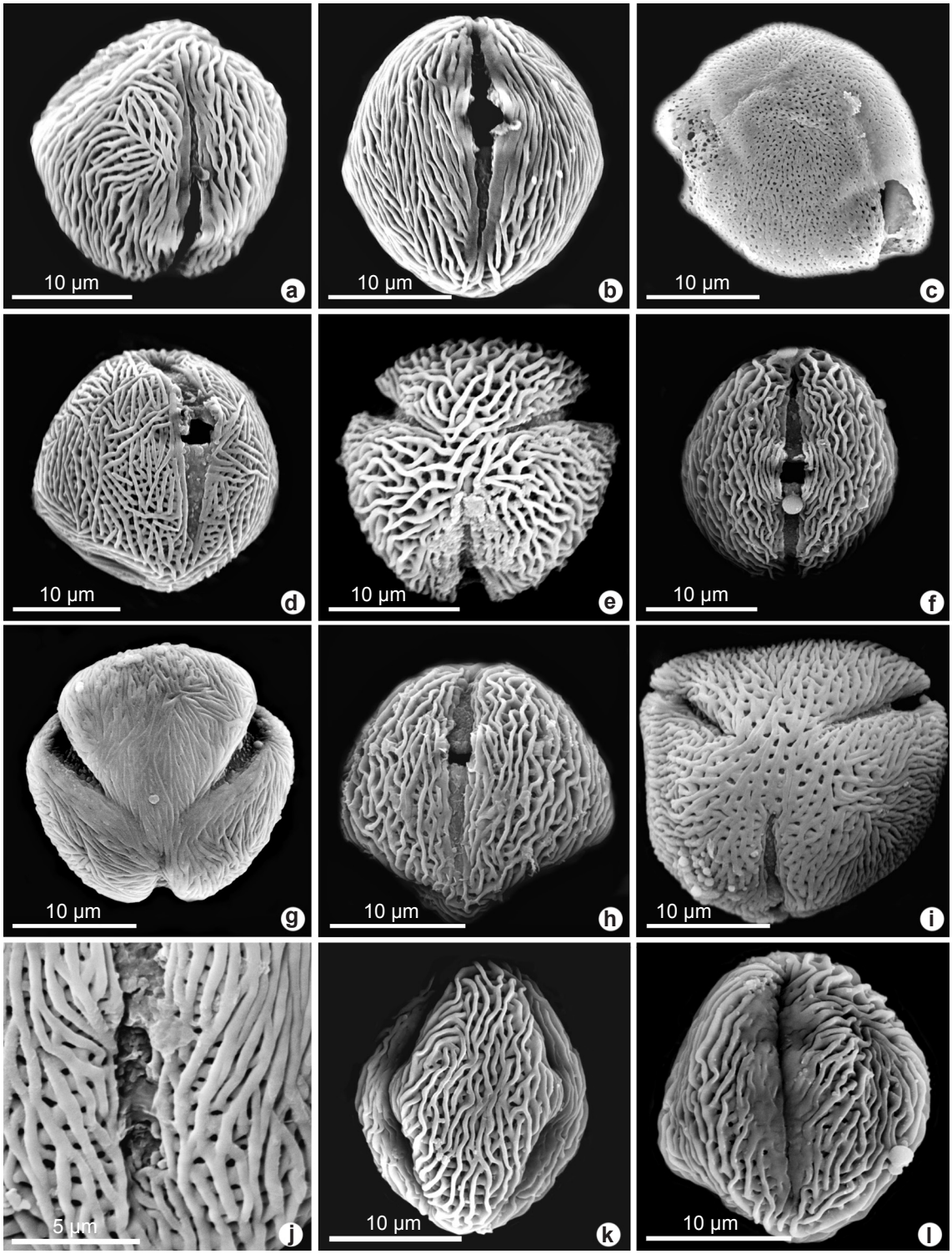

Figure 4 – a-l. Electromicrographs (SEM) of pollen grains of the Anacardiaceae species – a-c. Anacardieae – a. *Anacardium humile*; b. *A. occidentale*; c. *Mangifera indica*; d-l. Rhoeae – d. *Apterokarpos gardneri*; e-f. *Astronium conccinum*; g. *A. fraxinifolium*; h. *Lithraea molleoides*; i-j. *Myracrodruon urudeuva*; k-l. *Schinopsis brasiliensis*.

The species of Rhoeae presented heterogeneous characteristics of pollen morphology, in what concerns size, shape, organization of the apertures, ornamentation and exine sculpture, which have expressed differences between the analysed taxa. There are no records in the literature of the pollen morphology of the *Apterokarpos* and *Thyrsodium* species, therefore the descriptions here provided are original for these genera. *Apterokarpos gardneri* is a monotypic species, endemic of Northeastern Brazil, and is, for the first time, here, palynologically characterized. The occurrence of microreticulate-striate exine, under SEM, is unique among the studied taxa, making a diagnostic character for the species. The informations contained in this work for *A. gardneri* corroborated, in the largest part, the characteristics of the species of the subfamily Anacardioideae. However, the *Thyrsodium* spp. are different from the other species of Anacardiaceae, studied here, as they are the only ones to present pollen grains with psilate exine.

The apertural type, amb and ornamentation pattern of the exine of the *Astronium* species described in this work corroborate the data in the literature for *A. fraxinifolium* and *A. balansae* (Anzótegui 2001). Sanchez-Dzib *et al.* (2009), using LM, have documented the pollen grains of *A. graveolens* as having reticulate exine, differing from our results here presented for this character, also under LM. We have not encountered, in the literature, palynological descriptions of the pollen morphology of the species *A. conccinum*.

Anzótegui (2001) and Macedo *et al.* (2009) have characterized the pollen grains of the *Lithraea* species, reporting the majority of the pollen characteristics as similar to the ones presented in the current work for *L. molleoides*. However, the authors cited above do not document the presence of a fastigium in the genus, which was documented in the species here analysed.

The pollen grains of *Myracrodruon urudeuva* were described by Silva *et al.* (2014), which results were similar to the ones here presented. The size, shape, apertures and exine ornamentation of the pollen grains of *Schinus terebinthifolia* were also analysed by Anzótegui (2001) and Silva *et al.* (2014), under LM, according to the data presented here. The shape and exine ornamentation disagree with the data presented by Willard *et al.* (2004), described as finely reticulate.

In the literature, there is evidence of pollen data for the species of *Spondias* only in the works of Martinez-Hernandez *et al.* (1993), Garcia *et al.* (2011) and Silva *et al.* (2016). The results for type, number and organization of the apertures, are in agreement with what has already been described for some taxa of the genus. Martinez-Hernandez *et al.* (1993) have described for *S. mombin*, pollen grains with rugulate-striato-perforate exine. The data here presented disagrees with those by these authors, in what concerns the exine ornamentation, both under LM as well as under SEM.

Spondias tuberosa is a species that is native of the caatinga, which had only been previously palynologically analysed by Silva *et al.* (2016). Most characteristics of the pollen morphology here reported to this species agree with the previous authors. For the species *Cyrtocarpa caatingae*, *S. caatingae*, *S. purpurea* and *S. venulosa*, and *Tapirira* spp., no records of palynological analyses were found in the specialized literature. Thus, the information here presented is the first-time documentation of pollen morphology for these taxa.

Although, in the literature, there were no palynological descriptions available for the species of *Tapirira*, the classification of Mitchell & Mori (1987), which included *Tapirira* and *Spondias* in the tribe Spondiadeae, suggest that the shape (prolate to subprolate) and the amb (circular to subcircular), are characteristics shared by both genera. The characters observed in the species of *Tapirira* are rather homogeneous in relation to the characteristics of the family, and several diagnostic elements can be found, especially in the organization of the striae.

Taxonomic implications of the pollen morphology

Pell (2004) and Pell *et al.* (2011) have proposed the organization of the taxa of Anacardiaceae into two subfamilies, sustained mostly by the structure and anatomy of the fruit, which is classified into basic types. The subfamily Anacardioideae comprises the species of the tribes Anacardieae, Dobineae, Rhoeae and Semecarpeae, which are phylogenetically well supported. Palynologically, the characteristics described in this work support this taxonomic organization, based on the medium size of the pollen grains; 3-colporate apertural type; colpus with tapering ends; exine with striate pattern; sexine thicker than the nexine. The species of genus *Thyrsodium*, however, do not share the striate pattern of the exine ornamentation with the remainder of the group. The subfamily Spondioideae is composed

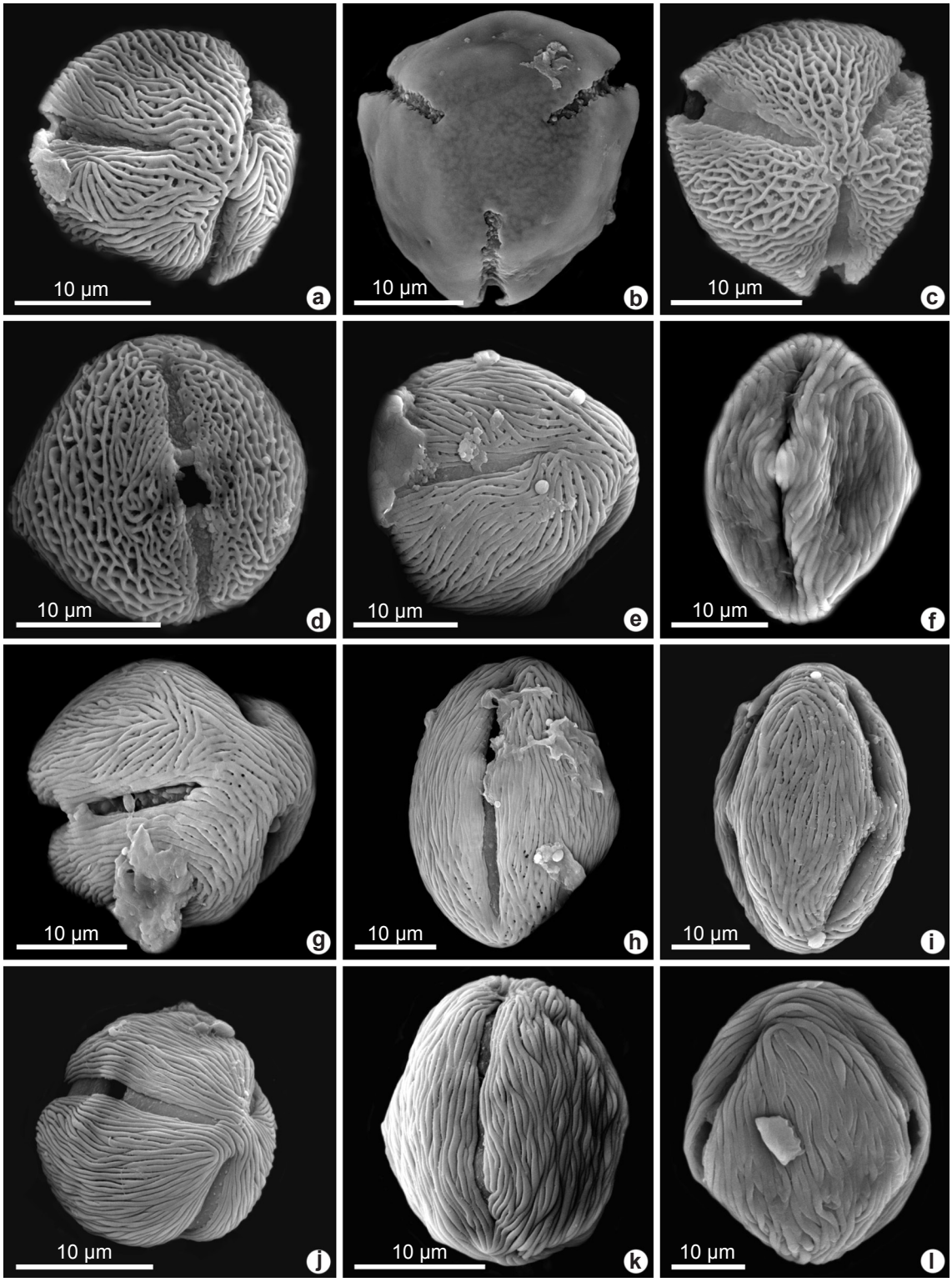

Figure 5 – a-l. Eletromicrographs (SEM) of pollen grains of the Anacardiaceae species – a-b. Rhoeae – a. *Schinus terebinthifolia*; b. *Thyrsodium spruceannum*; c-l. Spondiadeae – c-d. *Cyrtocarpa caatingae*; e. *Spondias caatingae*; f. *S. mombin*; g-h. *S. tuberosa*; i. *S. venulosa*; j. *Tapirira guaianensis*; k. *T. marchandii*; l. *T. obtusa.*

essentially by the taxa belonging to the tribe Spondiadeae. Palynologically, given the data here documented, they share the size, prolate shape (except for *T. obtusa*), apertural type and striate pattern of the exine ornamentation.

Tribe Anacardieae is represented in this work by the genera *Anacardium* and *Mangifera*, which based on the anatomy of the endocarp, are phylogenetically close (Pell 2004; Wannan 2006). The palynological analysis of the species of *Anacardium* and *Mangifera indica* conducted in this work, suggests that both taxa present pollen grains with subprolate shape, circular to subcircular amb, endoapertures with rounded ends, and suprastriato-inframicroreticulate (*Anacardium* spp.) or striato-perforate (*M. indica*) exine. These shared palynological characteristics support the existing taxonomic affinities between these genera, and their placement within this tribe.

The species of tribe Rhoeae here analysed present pollen characteristics that are shared by all taxa. However, they reveal significant variation in terms of size, shape, amb, apertures and exine ornamentation. Macromorphologically, tribe Rhoeae is sustained by the presence of three carpels and fruit epidermis lignified (Pell & Urbatsch 2001). Palynologically, the pattern of ornamentation of the exine constitutes an important characteristic to support a taxonomic approximation within the group. In the morphopalynological context of tribe Rhoeae, in what concerns the exine ornamentation, most species present striate pollen grains. Species of *Astronium*, *Lithraea*, *Myracrodruon*, *Schinopsis* and *Schinus* shared homogeneous characteristics in what concerns the organization of the striae: branched and subparallel in the direction of the apocolpium. Wannan (2006), in its analysis, has revealed that the genera *Astronium* and *Schinopsis* possess an approximation strongly supported by the presence of resin producting structures. On the other hand, the species of genus *Thyrsodium* here analysed have demonstrated to be more distant, considering the striate character of the tribe, since they have exhibited psilate pollen grains.

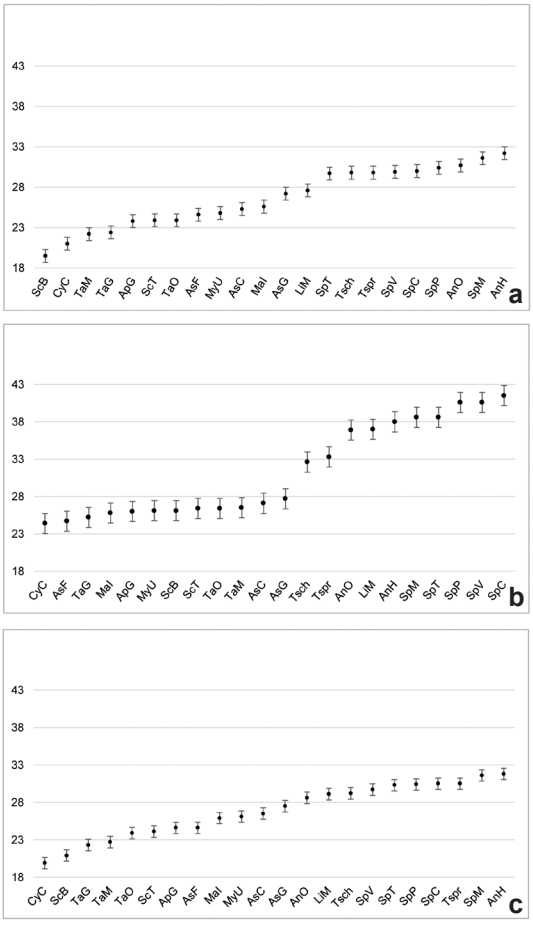

Figure 6 – a-c. Graphic representation of the distribuition of the variable diameter of pollen grains of Anacardiaceae species – a. equatorial diameter in polar view; b. polar diameter in equatorial view; c. equatorial diameter in equatorial view. The superior and inferior limits represent the standard deviation, the median circles represent the arithmetic average. Values are provided in µm. Species codes follow Table 1.

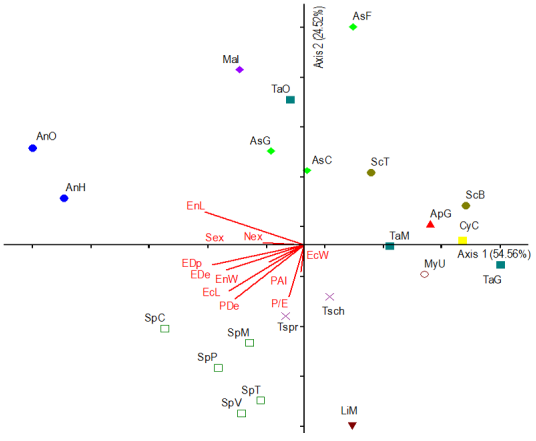

Figure 7 – Ordination, by Principal component analysis (PCA), of the analysed species of Anacardiaceae, in function of the metric variables of the pollen grains. Species codes follow Table 1.

Table 2 – Pearson and Kendall correlation coefficients for pollen grain metric variables of the first and the second axis of the PCA ordination, in species of Anacardiaceae.

Variables	Acronym	Principal components	
		Axis 1	Axis 2
Equatorial diameter in polar view	EDp	-0.2643	-0.1975
Polar diameter in equatorial view	PDe	-0.3174	-0.4521
Equatorial diameter in equatorial view	EDe	-0.2337	-0.2153
Ratio between PDe and EDe	P/E	-0.0451	-0.1316
Polar area index	PAI	-0.0121	-0.0544
Colpus length	EcL	-0.3558	-0.4510
Colpus width	EcW	-0.0009	-0.0655
Endoaperture width	EnW	-0.2240	-0.2543
Endoaperture height	EnL	-0.6956	0.6423
Sexine	Sex	-0.3257	0.0643
Nexine	Nex	-0.0775	0.0302

Spondiadeae is a tribe with weak phylogenetic support, composed by the genera *Cyrtocarpa*, *Spondias* and *Tapirira*, represented in this study. Biochemical studies that discuss the presence of fisetin in the heartwood and absence of amentoflavone in leaves are the basis for the phylogenetic support of these genera in the tribe (Wannan 2006). Palynologically, the characteristics shared by all the studied taxa of tribe Spondiadeae are subcircular to circular amb, and shape within the prolate class (subprolate to prolate) (except for *T. obtusa*). Wannan (2006) suggests that the approximation of *Cyrtocarpa* and *Tapirira* is better phylogenetically supported (90% bootstrap), here confirmed by the morphopalynological analyses of the species of these genera, mainly in terms of the sculpture of the striate exine, differing in the disposition of the striae: juxtapposed in *Tapirira* spp., while spaced between them, with an inframicroreticulum, in *C. caatingae.*

Pereira *et al*. (2015), when doing a phytochemical analysis of five species of *Spondias*, proposed a phylogenetic reconstruction of the studied taxa. The authors sustain a greater affinity between *S. venulosa* e *S. mombin*, and a weaker between these species and *S. purpurea*. The study of the pollen morphology of these taxa, here conducted, reveals many shared similarities between them, especially the presence of a protusions over the endoaperture, except in *S. purpurea*, agreeing with the authors in what concerns the separation of this species in relation to the others.

The Tukey test significantly separates *Cyrtocarpa caatingae* from the remaining species of *Spondias*, differing from the classification of Pell (2004), which places the genera in the same subfamily (Spondiadeae), and also reveals a phylogenetic proximity with strong support (76% bootstrap).

The PCA ordination, in comparison with the tribal classification of the species of Anacardiaceae, corroborates the placement of *Anacardium* species and *Mangifera indica* in tribe Anacardieae, while the remaining species are not ordinated according to Engler's classification (1897), reinforced by Pell & Urbatsch (2001).

The morphopalynological characteristics here presented support the eurypalynous character of family Anacardiaceae. The most diverging attributes within the group which can assist in taxonomy are the variation in the apertures and exine ornamentation, as well as presence of fastigium and constriction of the endoaperture in some taxa.

Medium-sized, 3-colporate pollen grains are present in all of studied species, which may represent a synapomorphy for the species studied in the family. Although the exine presents striate ornamentation in most species (except for

Thyrsodium spp.), we have observed variation in terms in size, shape and endoapertures; and disposition and organization of the striea, in addition to the presence of other sculptural elements of the exine. Such variation helps in the palynotaxonomic discussion at generic and infrageneric level.

Anacardiaceae is still palynologically little known since many of the taxa are here characterized for the first time. The study of the pollen morphology of the taxa of Anacardiaceae contributes to a wider knowledge of the Brazilian and worldwide Pollen Flora, potentially collaborating with the taxonomic circumscription and improved understanding of the phylogenetic relationships in the group.

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References

Aftab R & Perveen A (2006) A palynological study of some cultivated trees from Karachi. Pakistan Journal of Botany 38: 15-28.

APG IV - 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.

Anzótegui LM (1992) Anacardiaceae. *In*: Pire SM, Anzotegui LM & Cuadrado GA (eds.) Atlas palinológico del Nordeste Argentino. I: Amaranthaceae, Anacardiaceae, Apocynaceae, Araliaceae y Sapindaceae. D'Orbignyana 7: 1-75.

Anzótegui LM (2001) Anacardiaceae. *In*: Pire SM, Anzótegui LM & Cuadrado GA (eds.) Flora Polinica del Nordeste Argentino. Editorial Universitaria de la Universidad Nacional del Nordeste, Corrientes. Pp. 19-26.

Barros MA, Barth O & Costa KMR (1999) Catálogo sistemático de plantas arbóreas no Brasil Meridional. XXXII: Anacardiaceae. Leandra 14: 17-24.

Barroso GM (1991) Sistemática de angiospermas do Brasil. Vol. 2. UFV, Viçosa. 377p.

Chase MW, Soltis DE, Olmstead RG, Morgan D, Les DH, Mishler BD, Duvall MR, Price RA, Hills HG, Qui YL, Kron KA, Rettig JH, Conti E, Palmer JD, Manhart JR, Sytsma KJ, Michaels HJ, Kress WJ, Karol KG, Clark WD, Hedren M, Gaut BS, Jansen RK, Kim, KJ, Wimpee CF, Smith JF, Furnier GR, Strauss SH, Xiang QY, Eguiarte LEE, Golenberg E, Learn GH, Graham SW, Barret SCH, Dayanandan S & Albert VA (1993) Phylogenetic of seend plants: an analysis of nuncleotide sequences from the plastid gene rbcL. Annals of the Missouri Botanical Garden 80: 528-580.

Engler A (1883) Anacardiaceae. *In*: De Candolle AP & De Candolle AC (eds.) Monographie Phanerogamarum, Masson, Paris. Pp. 171-546.

Engler A (1892) Anacardiaceae. *In*: Engler A & Pratl N (eds.) Die natürlichen Pflanzen-familienp, Engelmann, Leipzig. Pp. 138-178.

Engler A (1897) Nachträge zum II-IV. *In*: Engler A & Prantl K (eds.) Die natürlichen Pflanzen-familien, Engelmann, Leipzig. 214p.

Erdtman G (1943) An introduction to Pollen Analysis. Chronica Botanica Company, Waltham. Pp. 1-239.

Erdtman G (1952) Pollen Morphology and Plant Taxonomy- Angiosperms. Almqvisit & Wiksell, Stockholm. 539p.

Erdtman G (1960) The acetolysis method. A revised description. Svensk Botanisk Tidskrift 39: 561-564.

Evaldt ACP, Bauermann SG & Souza PA (2013) Descrições morfológicas de palinomorfos holocênicos de um fragmento da Savana Estépica Parque em Barra do Quaraí, Rio Grande do Sul, Brasil. Pesquisas em Geociências 40: 209-232.

Faegri K & Iversen J (1966) Terminology in palynology. Pollen Spores 8: 407-408.

Gonçalves-Esteves V & Ferreira CB (1994) Estudo polínico em plantas de restiga do estado do Rio de Janeiro: Anacardiaceae Lindl. e Capparaceae Juss. Boletim do Museu Nacional, Nota Suplementar de Botânica 90: 1-13.

Hesse M, Halbritter H, Weber M, Buchner R, Frosch-Radivo A, Ulrich S & Zetterm R (2009) Pollen terminology: an illustrated handbook. Springer-Verlag, Viena. 266p.

Iversen J & Troels-Smith J (1950) Pollenmorphologischen definitionen und typen. DanmarksGeologiske undersøgelse. Række IV 3: 1-54.

Leal MG & Lorscheitter ML (2006) Pólen, esporos e demais palinomorfos de sedimentos holocênicos de uma floresta paludosa, Encosta Inferior do Nordeste, Rio Grande do Sul, Brasil. Iheringia Série Botânica 61: 13-47.

Luz CFP, Barros MA & Barth OM (2018) Pollen morphology of arboreal eudicotyledons of Serra da Capoeira Grande, Pedra Branca Geological Massif, Rio de Janeiro, Brazil. Iheringia Série Botânica 73: 308-328.

Macedo RB, Souza PA & Bauermann SG (2009) Catálogo de polens, esporos e demais palinomorfos em sedimentos holocênicos de Santo Antônio da Patrulha, Rio Grande do Sul, Brasil. Iheringia Série Botânica 64: 43-78.

McCune B & Mefford MJ (2011) PC-ORD. Multivariate analysis of ecological data (Version 5). MjM

Software, Gleneden Beach. Available at <https://www.wildblueberrymedia.net/pcord-6-fixes>. Access on 11 March 2020.

Melhem TS, Cruz-Barros MAV, Corrêa AS, Makino-Watanabe H, Silvestre-Capelato MSF & Esteves VLG (2003) Variabilidade polínica em plantas de Campos de Jordão (São Paulo, Brasil). Boletim do Instituto de Botânica 16: 9-104.

Miranda MM & Andrade TA (1990) Fundamentos de palinologia: principais tipos de pólen do litoral cearense. Editora da Universidade Federal do Ceará, Fortaleza. 99p.

Mitchell JD & Mori SA (1987) The cashew and its relatives (*Anacardium*: Anacardiaceae). Memoirs of The New York Botanical Garden 42: 1-76.

Mitchell JD & Daly DC (2015) A revision of *Spondias* L. (Anacardiaceae) in the Neotropics. Phytokeys 55: 1-92.

Mora YAF, Medina WF & Rincón YMB (2013) Morfologia polínica de espécies arbóreas predominantes de San Jose de Cúcuta. Revista Mundo FESC 6: 58-74.

Pell SK & Urbatsch LE (2001) Tribal relationships and character evolution in the cashew family (Anacardiaceae): inferences from three regions of the chloroplast genome. American Journal of Botany 88: 1-32.

Pell SK (2004) Molecular systematics of the cashew Family (Anacardiaceae) [dissertation]. Lousiana State University, Baton Rouge. 193p.

Pell SK, Mitchell JD, Miller AJ & Lobova TA (2011) Anacardiaceae. *In*: Kubitzki K (ed.) The families and genera of vascular plants. Springer-Verlag 10: 7-50.

Pereira ASS, Felix-da-Silva MM, Barbosa CVO & Smith CB (2014) Estudo polínico de *Anacardium* L. (Anacardiaceae) no estado do Pará (Amazônia Oriental), Brasil. Biota Amazônia 4: 57-61.

Pereira C, Oliveira LL, Gonçalves R, Amaral AC, Kuster RM & Sakuragui CR (2015) Phytochemical and Phylogenetic Análisis of *Spondias* (Anacardiaceae). Química Nova 38: 813-816.

Pereira PS, Barros LM, Brito AM, Duarte AE & Maia AJ (2014) Uso da *Myracrodruon urundeuva* Allemão (aroeira-do-sertão) pelos agricultores no tratamento de doenças. Revista Cubana de Plantas Medicinales 19: 51-60.

Perveen A & Qaiser M (2010) Pollen Flora if Pakistan - LXVI: Anacardiaceae. Pakistan Journal of Botany 42: 1401-1406.

Punt W, Hoen PP, Blackmore S, Nilsson S & Le Thomas A (2007) Glossary of pollen and spore terminology. Review of Paleobotany and Palynology 143: 1-81.

Roubik DW & Moreno JE (1991) Pollen and spores of Barro Colorado Island. Saint Louis. Missouri Botanical Garden 36: 1-268.

Salgado-Labouriau ML (1973) Contribuição à Palinologia dos Cerrados. Academia de Ciências, Rio de Janeiro. 291p.

Sanchez-Dzib YLA, Sosa-Najera S & Lozano-Garcia MS (2009) Morfologia polínica de espécies de lá Selva Mediana Subperonnifolia em la Cuenca del Rio Candelaria, Campeche. Boletín de la Sociedad Botánica de México 84: 83-104.

Silva CI, Fonseca VLI, Groppo M, Bauermann SG, Saraiva AM, Queiroz EP, Evaldt ACP, Aleixo KP, Castro JP, Castro MMN, Faria LB, Caliman MJF, Wolff JL, Paulino Neto HF & Garofalo CA (2014) Catálogo polínico das plantas usadas por abelhas no campus da USP de Ribeirão Preto. Holos, Ribeirão Preto. 153p.

Silva FHM, Santos FAR & Lima LCL (2016) Flora polínica das caatingas: Estação Biológica de Canudos (Canudos, Bahia, Brasil). Micron Bahia, Feira de Santana. 120p.

Silva-Luz CL, Pirani JR, Pell SK & Mitchell JD (2020) Anacardiaceae. *In*: Flora do Brasil 2020. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro. Available at <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB44>. Access on 14 September 2020.

Souza VC & Lorenzi H (2005) Botanica Sistemática. Ilustrado para identificação das famílias de Angiospermas da flora brasileira, baseado em APGII. Instituto Plantarum de Estudos da Flora LTDA, Nova Odessa. 640p.

Takeda IJM, Farago PV, Souza MKF & Gelinski VV (2000) Catálogo Polínico do Parque Estadual de Vila Velha, Paraná - 1ª Parte. Publicatio UEPG - Biological and Health Sciences 6: 61-73.

Wannan BS & Quinn CJ (1990) Pericarp structure and generic affinities in the Anacardiaceae. Botanical Journal of the Linnean Society 102: 225-252.

Wannan BS & Quinn CJ (1991) Floral structure and evolution in the Anacardiaceae. Botanical Journal of the Linnean Society 107: 349-385.

Wannan BS (2006). Analysis of generic relationships in Anacardiaceae. Blumea 51: 165-195.

Willard DA, Bemhard CE, Weimer L, Cooper SR, Gomez D & Jensen J (2004) Atlas of pollen and spores of the Florida Everglades. Palynology 28: 175-227.

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