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Pollen morphology of succulent and fruiting plants

Morfologia polínica de plantas suculentas e frutíferas

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ABSTRACT
Pollen grains represent crucial structures for the reproductive success of angiosperms, characterized by the presence of the intine (inner wall) and exine (outer wall), which are highly resistant for protection and maturation until pollen tube germination. These two walls contain the main morphological components used in pollen characterization. To contribute to palynological studies on succulent and ornamental species, the pollen morphology of the species *Haworthia attenuata* (Haw.) Haw. (Asphodelaceae), *Echeveria agavoides* Lem. (Crassulaceae), *Eugenia brasiliensis* Lam. (Myrtaceae), and *Psidium guajava* L. (white and red cultivars) (Myrtaceae) was analyzed. The plants were collected during field trips. Closed flower buds were removed, preserved, and acetolyzed. Slides were prepared and examined under light microscopy and SEM.All species present pollen grains in monads. *Haworthia attenuata* has large, monocolpate, bilaterally symmetrical, heteropolar grains, elliptical shape, and foveolate exine. *Echeveria agavoides* has medium-sized, 3-colporate, radially symmetrical, isopolar grains, subprolate shape, subtriangular amb, and microverrucate/perforate exine.*Eugenia brasiliensis* has small, 3-colporate, radially symmetrical, isopolar grains, oblate shape, triangular ambit, and verrucate exine. *Psidium guajava* has small, 3-colporate, radially symmetrical, isopolar, angularly aperturate grains, oblate shape, subcircular ambit (white cultivar)/lobed (red cultivar), and microgranulated/ verrucate (white cultivar)/ granulated (red cultivar) exine.
Keywords: Asphodelaceae, characterization, Crassulaceae, Myrtaceae, palynology.

RESUMO
Os grãos de pólen representam estruturas cruciais para o sucesso reprodutivo das angiospermas, caracterizadas pela presença da intina (parede interna) e exina (parede externa), muito resistentes para a proteção e a maturação até a germinação do tubo polínico. Essas duas paredes apresentam os principais componentes morfológicos utilizados na caracterização polínica. Visando contribuir com estudo palinológico sobre espécies de suculentas e ornamentais, analisou-se a morfologia polínica das espécies *Haworthia attenuata* (Haw.) Haw. (Asphodelaceae), *Echeveria agavoides* Lem. (Crassulaceae), *Eugenia brasiliensis* Lam. (Myrtaceae) e *Psidium guajava* L. (variedades branca e vermelha) (Myrtaceae). As plantas foram coletadas durante saídas a campo. Os botões florais fechados foram retirados, conservados, acetolisados e foram preparadas lâminas, examinadas em microscopia de luz e MEV. Todas as espécies apresentam grãos de pólen em mônades. *Haworthia attenuata* tem grãos grandes, monocolpados, bilateralmente simétricos, heteropolares, forma elíptica, exina foveolada. *Echeveria agavoides* tem grãos médios, 3-colporados, radialmente simétricos, isopolares, forma subprolata, âmbito subtriangular, exina microverrucada/perfurada. *Eugenia brasiliensis* tem grãos pequenos, 3-colporados, radialmente simétricos, isopolares, forma oblata, âmbito triangular, exina verrucada. *Psidium guajava* possui grãos pequenos, 3-colporados, radialmente simétricos, isopolares, anguloaperturados, forma oblata, âmbito subcircular (variedade branca) / lobado (var. vermelha), exina microgranulada / verrucada (var. branca) / granulada (var. vermelha).
Palavras-chave: Asphodelaceae, caracterização, Crassulaceae, Myrtaceae, palinologia.

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INTRODUCTION

Pollen grains represent the male structures in angiosperm reproduction, characterized by the presence of intine (inner wall) and exine (outer wall), important for their resistance, essential for the maturation and germination of the pollen tube. The outer layer is provided by microfibers and embedded amorphous materials, which play a vital role in retaining pollen moisture on the stigma, providing strength to the pollen tube for its development and the inner layer is similar to that of a common plant cell (SUÁREZ-CERVERA *et al.*, 2002). These two walls and their arrangement constitute the main morphological components used in palynological characterization, which classifies pollen grains in terms of unit, size, apertures, amb, polarity, symmetry, shape and ornamentation, the latter of which can vary from a smooth coating to ornate, presenting small details that facilitate the exit of the pollen tube. Taxonomic identification generally occurs at the genus or family level, and may even reach the species level.

Succulents are plants that retain liquids in their vegetative organs, such as leaves and stems, and belong to different botanical families. These plants can be used in landscaping projects, either in combination with other plants or alone. The cultivation of ornamental plants is a practice that dates to antiquity and is associated with the aesthetic value attributed to plants with unique characteristics. The use of ornamental plants directly impacts environmental and socioeconomic issues, as non-native (exotic) species are frequently used in gardening design. Investigating the pollen morphology of succulent species is important, given their frequent growth and decorating popularity. Furthermore, several families and genera of succulents still have unclear taxonomic status, including the cytological perspective, and palynological data contribute to solving species delimitations, hybridizations, systematic determinations for floricultural purposes, among other issues.

Fruit trees are plants capable of producing fruit that, in angiosperms, is formed in mature ovary and can be dry or fleshy. In the flower, the ovary serves to protect the ovules until they are fertilized and become seeds. Fruits can be consumed by animals or humans, and in horticultural terms, the term fruit tree is limited to those that provide fruit for human consumption. The scientific study and cultivation of fruits is called pomology. Current fruit trees have been extensively studied since the Modern Age, aiming for better productivity, quality, and health, through agricultural improvement, including genetics, exhibiting distinct features in relation to the original species. In this sense, the pollination of fruit trees has been largely studied, especially for temperate climate fruits. However, studies on fruits from tropical climates are still scarce. For fruit plants, palynological knowledge is important for selection and breeding applications, and the morphological description of pollen grains is relevant for research on reproduction, taxonomic definitions, species protection, and other aspects.

In this context, this study was developed to contribute to palynological knowledge on species of fruit trees and succulent ornamental plants.

MATERIAL AND METHODS

The species of succulents *Haworthia attenuata* (Haw.) Haw. (Asphodelaceae) and *Echeveria agavoides* Lem. (Crassulaceae) were studied as well as the fruit trees *Eugenia brasiliensis* Lam. (Myrtaceae) (Brazilian cherry or grumichama) e *Psidium guajava* L. (common guava, cultivars white and red) (Myrtaceae) (figure 1). The specimens came from the Botanical Garden of the University of the Joinville Region, in Joinville, Santa Catarina.

The closed buds were removed and preserved in acetic acid until acetolysis and, shortly before acetolysis, the buds were opened, the anthers removed, and macerated in a Petri dish, followed by acetolysis (placed in acidic solutions, specific substances, and centrifuged) (ERDTMANN, 1960). The acetolyzed pollen grains were mounted in glycerol gelatin on light microscope slides (five slides for each species).

Fresh pollen slides were also prepared with glycerin to highlight details with stain, as per Barth & Barbosa (1971). To this end, the anthers were macerated, and then a drop of fructose solution (50 ml of water to 10 g of fructose) was added, followed by a drop of fuchsin solution (13 drops of dye to 20 ml of water). The fructose solution gives the appearance of fresh pollen, with a relatively turgid appearance, similar to the natural appearance of the grains. In this process, the internal contents of the grain are still present, unlike the acetolysis process, where this content is removed, causing the acetolyzed grain to eventually have a slightly wilted exine. Fuchsin dye was added to obtain better visualization of the characterization aspects of pollen grains (ALEXANDER, 1980).

All slides were preserved in the pollen library of the Univille Bee Laboratory (Label). The slides were observed under a light microscope (400x) using “Dino-Eye Capture 2.0” software.

The pollen grains on the slides were photographed, with 25 replicates for each view (equatorial and polar). The following parameters were measured in micrometers (μm): equatorial diameter and polar axis (for dicotyledonous grains) and major equatorial diameter and polar diameter (for monocotyledonous grains), as well as exine thickness for both types of grains (monocotyledonous and dicotyledonous) (SALGADO-LABOURIAU, 2006).

The grains were classified based on characteristics such as pollen unit, size, amb, symmetry, polarity, shape, apertures, and ornamentation (PUNT *et al.*, 2007) and the data were tabulated (Microsoft Excel).

Additionally, samples were analyzed using Scanning Electron Microscopy (SEM) at the State University of Santa Catarina (Udesc). To achieve this, the anthers of buds preserved in acetic acid were removed and macerated on coverslips to mechanically release the grains using tweezers and a drop of acetic acid. The grains were then metallized with gold-palladium, analyzed, and photographed.

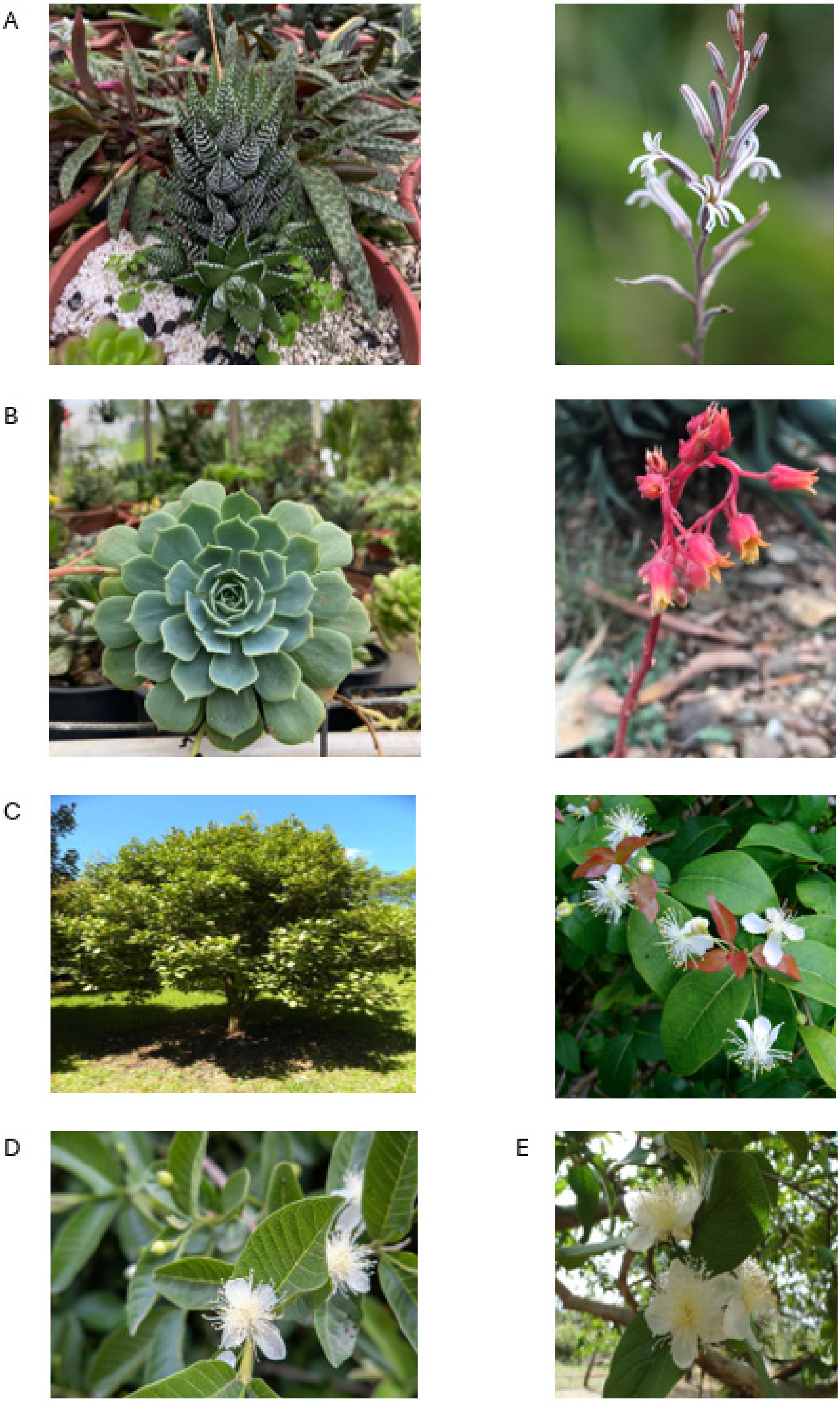

Figure 1 – Images of the studied species. A) *Haworthia attenuata* plant and flowering; B) *Echeveria agavoides* plant and flowering; C) *Eugenia brasiliensis* plant and flowering; D) *Psidium guajava* (white cultivar) flowering; E) *Psidium guajava* (red cultivar) flowering. Source: primary.

RESULTS

The results are presented in tables 1 and 2 and in figures 2, 3, 4, 5, 6, and 7. All species present pollen grains in monads. Regarding symmetry, *Haworthia attenuata* has bilaterally symmetrical grains, while the other species have radially symmetrical grains. Regarding polarity, *Haworthia attenuata* has heteropolar grains, while the other species have isopolar grains.

Table 1 – Morphometric data of pollen grains of the analyzed species. Legend: P = polar axis; E = equatorial diameter. Numerical data in average and micrometers (µm).

Species	P/E	Shape	Exine	Apertures
Haworthia attenuata	----	------	1,98	Monocolpate
Echeveria agavoides	1,20	Subprolate	1,58	Tricolporate
Eugenia brasiliensis	1,40	Oblate	1,54	Tricolporate
Psidium guajava (white cultivar)	0,68	Oblate	2,10	Tricolporate
Psidium guajava (red cultivar)	0,71	Oblate	1,56	Tricolporate

Table 2 – Morphometric data of pollen grains of the analyzed species. Numerical data in average and micrometers (µm).

Species	Ornamentation	Amb	Polar diameter	Lateral/ longitudinal equatorial diameter	Size
Haworthia attenuata	foveolate	elliptic	33,18	52,42	large
Species	**Ornamentation**	**Amb**	**Polar axis**	**Equatorial diameter**	
Echeveria agavoides	microverrucate perfurated	subtriangular	34,91	28,94	medium
Eugenia brasiliensis	verrucate	triangular	15,37	21,63	small
Psidium guajava (white cultivar)	microgranulate verrucated	subcircular	15,16	22,20	small
Psidium guajava (red cultivar)	granulate	lobate	15,52	21,68	small

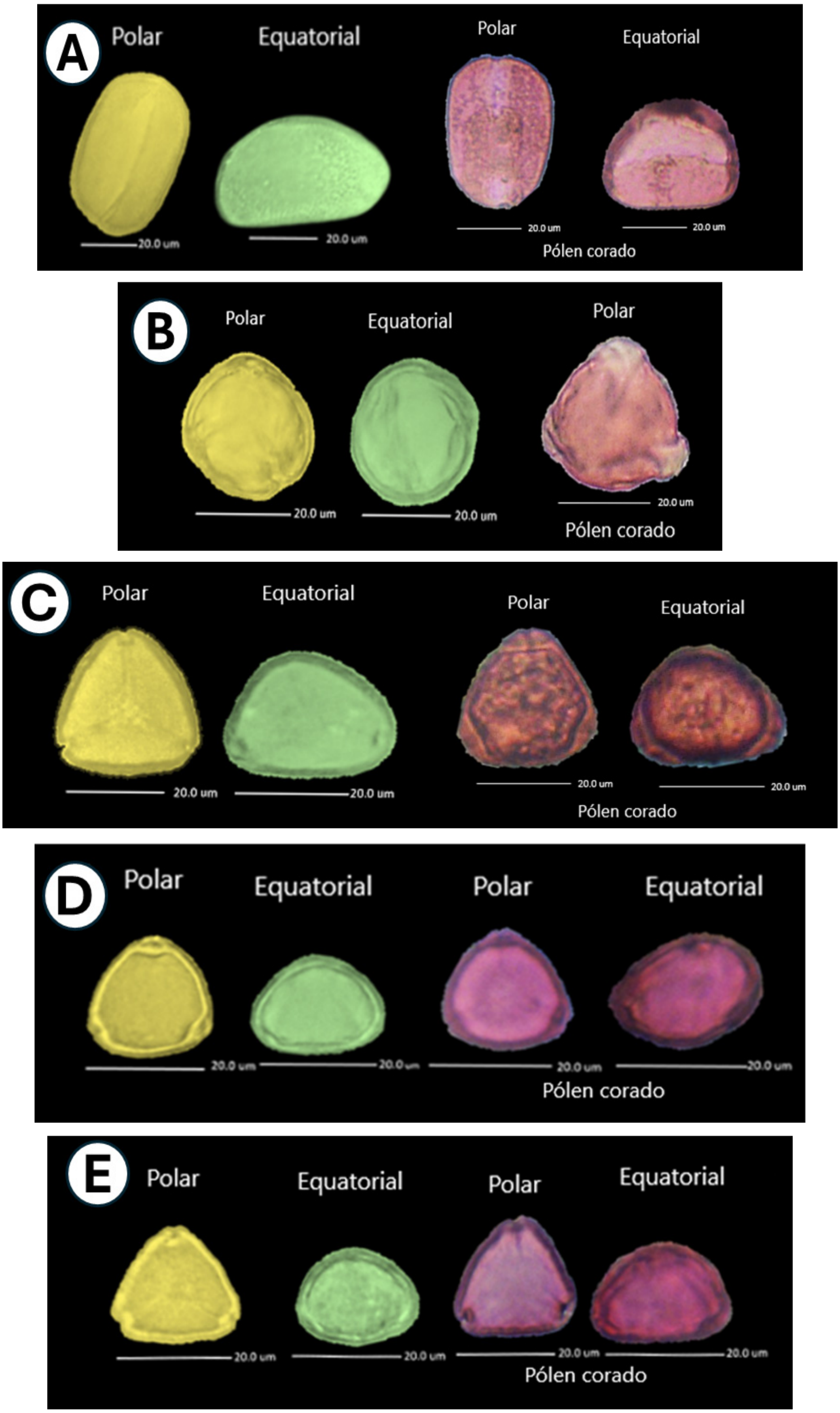

Figure 2 – Images of the pollen grains of the studied species. A) *Haworthia attenuata*; B) *Echeveria agavoides*; C) *Eugenia brasiliensis*; D) *Psidium guajava* (white cultivar); E) *Psidium guajava* (red cultivar). Legend: "polen corado" = stained pollen. Source: primary.

The images of pollen grains of the analyzed species, subjected to scanning electron microscopy at the State University of Santa Catarina (Udesc), are shown in figures 3 to 7.

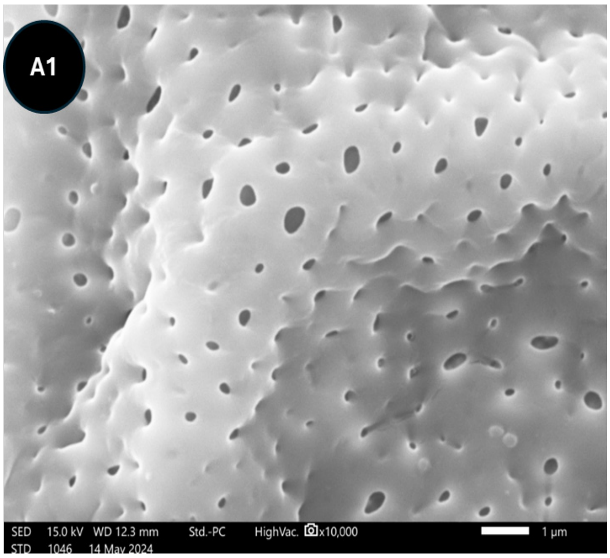

Figure 3 – Pollen grain of the species *Haworthia attenuata* seen under SEM. A1) Polar axis (exine). Source: primary.

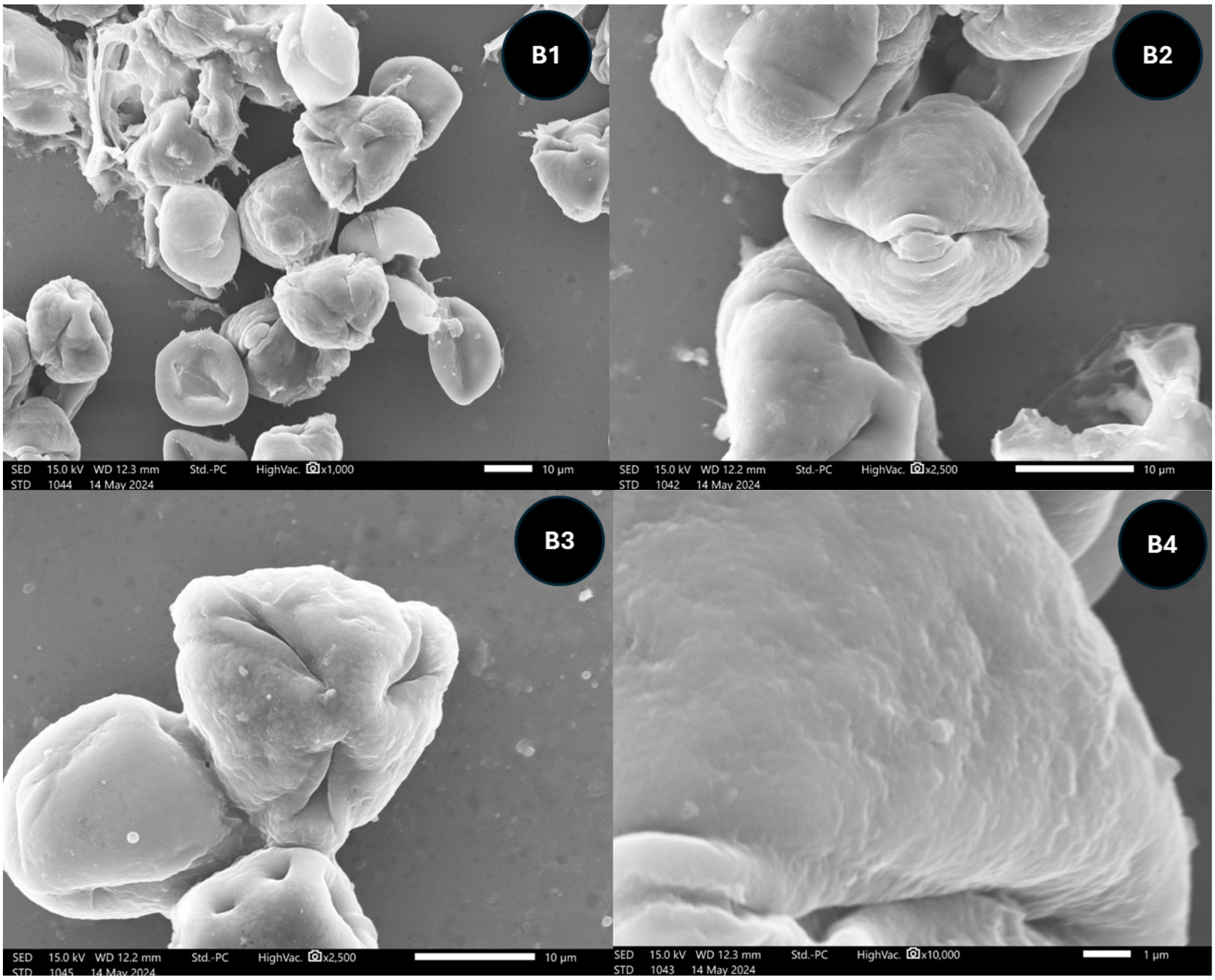

Figure 4 – Pollen grains of the species *Echeveria agavoides* seen under SEM. B1) Grains in polar axis and equatorial diameter; B2) equatorial diameter; B3) polar axis; B4) polar axis (exine). Source: primary.

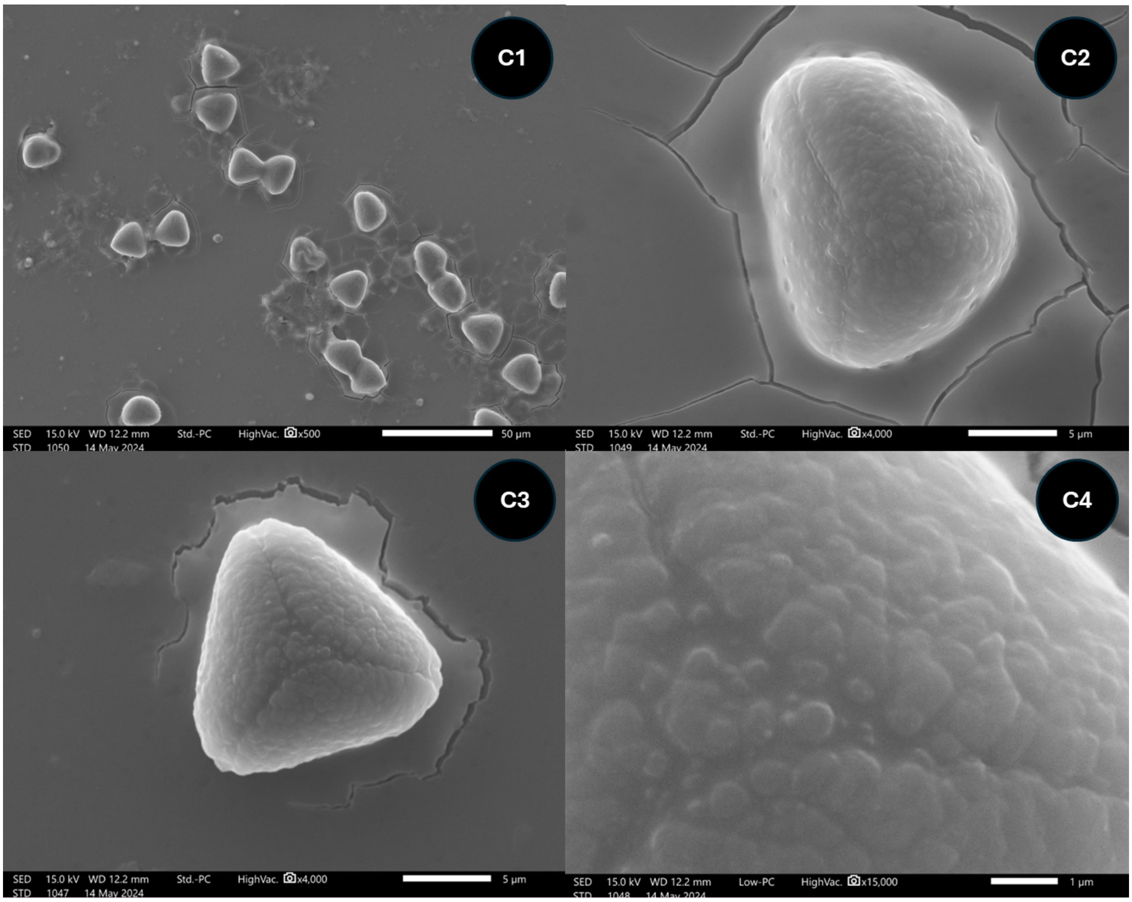

Figure 5 – Pollen grains of the species *Eugenia brasiliensis* seen under SEM. C1) Grains in polar axis and equatorial diameter; C2) polar axis; C3) polar axis; C4) polar axis (exine). Source: primary.

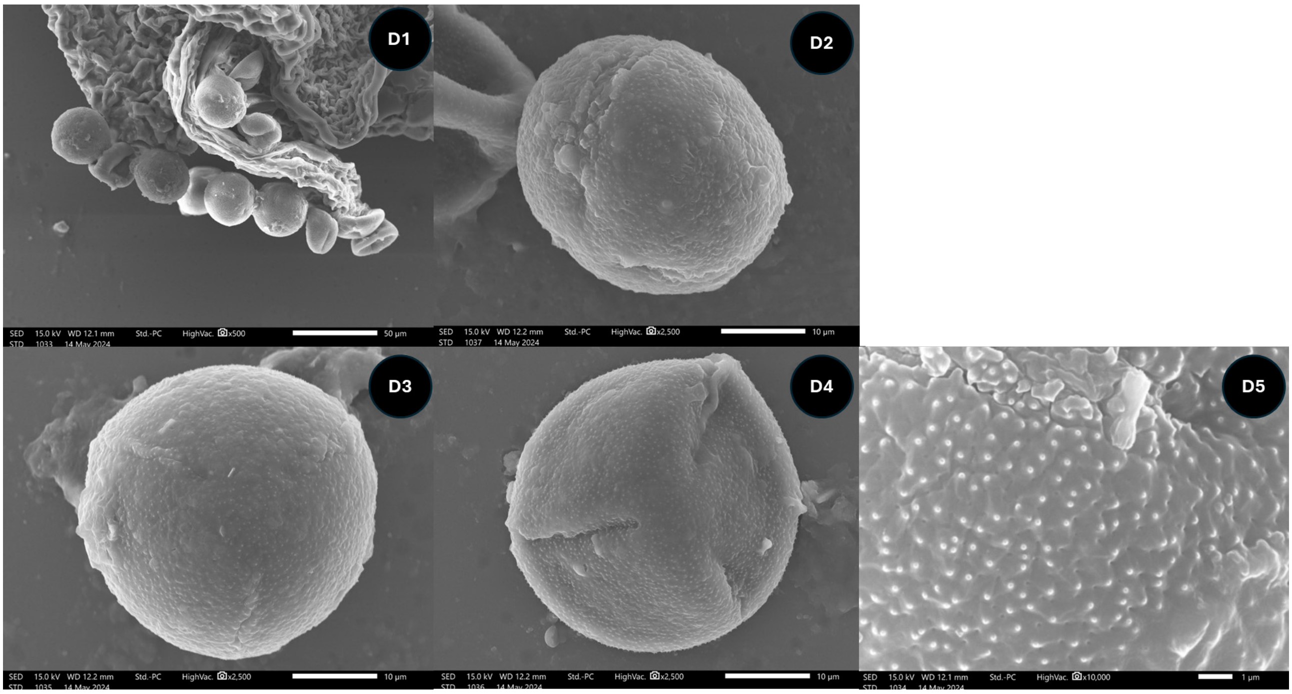

Figure 6 – Pollen grains of the species *Psidium guajava* (white cultivar) seen under SEM. D1) Grains in polar axis and equatorial diameter; D2) equatorial diameter; D3 and D4) polar axis; D5) polar axis (exine). Source: primary.

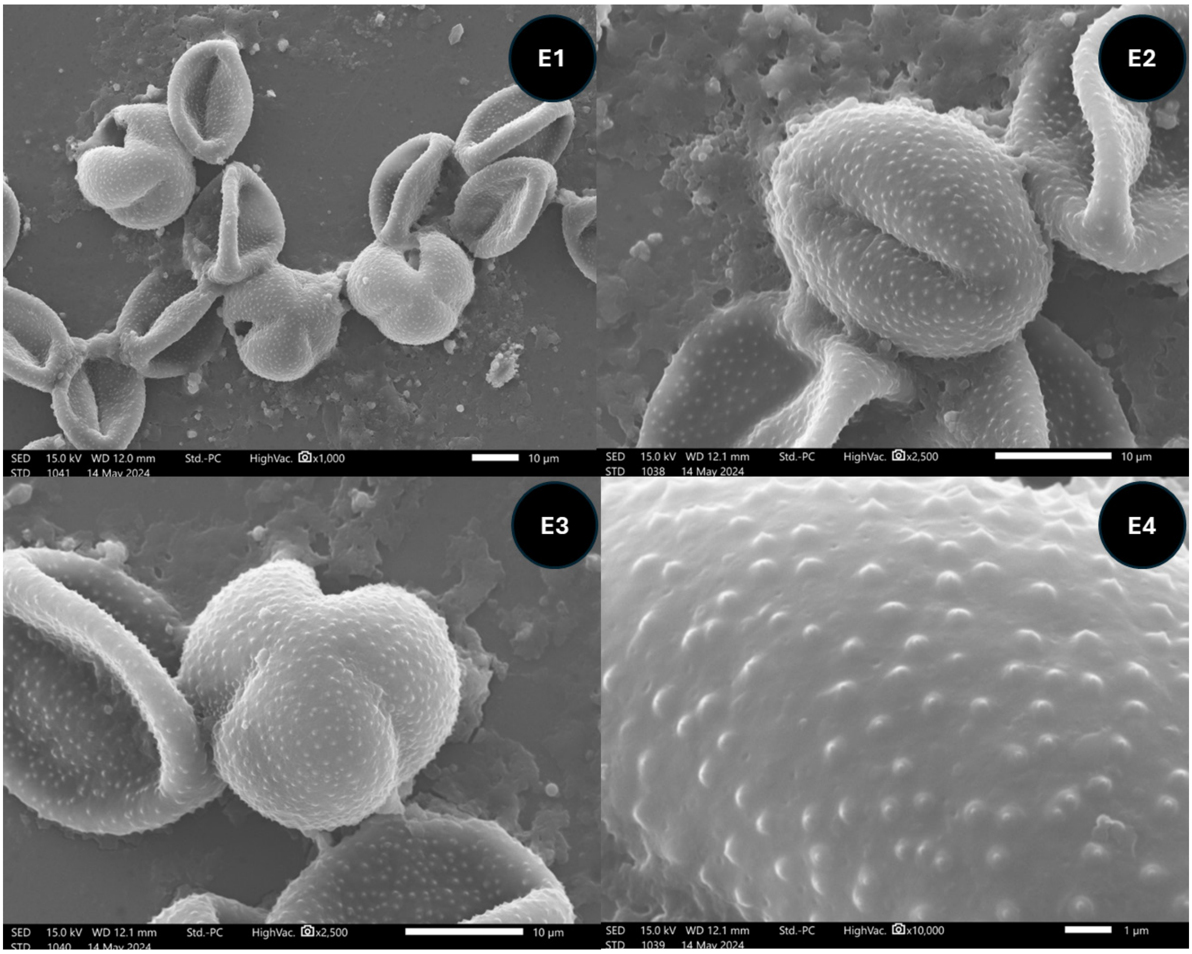

Figure 7 – Pollen grains of the species *Psidium guajava* (red cultivar) seen under SEM. E1) Grains in polar axis and equatorial diameter; E2) equatorial diameter; E3) polar axis; E4) polar axis (exine). Source: primary.

DISCUSSION

ASPHODELACEAE

The *Haworthia attenuata* grains studied here were large and had foveolate exine. This species was previously included in the subgenus *Hexangulares* of *Haworthia* and the species included in the subgenus *Hexangulares* have been elevated to the genus *Haworthiopsis* in 2013, *Haworthiopsis* meaing "like the genus *Haworthia*" due to the similarities of both taxa (GILDENHUYS & KLOPPER, 2016).

Hallbritter & Buchner (2016) report that *H. herbacea* and *H. truncata* have a perforated, verrucate exine and medium size, with these species being *Haworthia* (*Haworthia).* Furthermore, Stebler (2024a, 2024b, 2024c) reports medium-sized grains for *Haworthia (H.) arachnoidea*, *H. (H.) emelyae*, and *H. (H.) mucronata*, with exines ranging from reticulate to scabrate/ verrucate and from reticulate to rugulate (under light microscopy).

The foveolate exine is described for another *Haworthia* species by Pereira & Mouga (2024), namely *H. cymbiformis*, which showed medium size and is included in *Haworthia (Haworthia).* Foveolate ornamentation is defined as ornamentation with pits, holes, or tectal depressions greater than 1 µm in diameter, present in semi-tectate or tectate pollen grains, where the distance between the tectal holes, or depressions in the tectal, is greater than the diameter of the depressions (PRAGLOWSKI & PUNT, 1973).

Pollen grain variability is one of the characteristics used in interspecific determination. The study of diversity of palynological patterns observed in *Haworthia* species can contribute to clarifying the subgeneric and, therefore, taxonomic determination.

H. attenuata, distributed in the Eastern Cape of South Africa, from the Gamtoos River in the west to the Mbashe River in the east, is a small plant that grows among rocks, grass, and under shrubs, with fleshy leaves that store water, giving the plant the ability to survive periods of drought and drought (GOLDBLATT & MANNING, 2000).

CRASSULACEAE

González-Mancera *et al.* (2018) describe the pollen grains of 20 species of the genus *Echeveria* as isopolar, tricolporate, medium to small in size, with a nearly circular amb, radial symmetry, and a spheroidal shape, with a rugulate exine up to 1 micrometer thick.

Pereira & Mouga (2024), in turn, reported palynologically the species *Echeveria chroma* (hybrid created by Renee O'Connell), *Echeveria pallida* E. Walther, and *Echeveria pulidonis* E. Walther, as tricolporate, radially symmetrical, isopolar, with a circular amb, medium in size, with a prolate-spheroidal and oblate-spheroidal shape, and an exine thickness of 1.58/ 2.29/ 2.16 micrometers, respectively, and psilate.

The pattern of *E. agavoides* studied here shows tricolporate grains, of medium size, subtriangular in scope, isopolar, subprolate, with a perforated microverrucate exine with thickness of 1.58 micrometers. A reinforcement of the margins of the openings was observed here, which Pereira & Mouga (2024) also mention, and which constitutes a *margo* (*sensu* HESSE *et al*., 2009). González-Mancera *et al*. (2018) cite this structure (the *margo*) as the *operculum* (thickened margin of the aperture (*sensu* IVERSEN & TROELS-SMITH, 1950).

On the other hand, Stebler (2024d, e, f, g, h) cites, for the species *Echeveria coccinea, E. derenbergii, E. diffractens*, *E. laui,* and *E. leucotricha,* tricolporate and rarely tetracolporate grains, of medium size, with a scabrous psilate exine (under light microscopy), unornamented aperture membrane, *colpi* with *margo*, small to medium polar field, isopolar, radially symmetrical, flattened to slightly spheroidal.

Thus, it can be seen that *Echeveria* grains maintain a relatively uniform pattern, with grains with a nearly circular amb, tricolporate aperture, variations occurring in the thickness and ornamentation of the exine and the presence or absence of *margo*. In the present study, no tetracolporated grains were observed.

Echeveria is a large genus of Crassulaceae (150 species), with a wide geographic distribution, extending from Texas to Argentina, distributed primarily in Mexico (127 species) where it is one of the most important in that country, as 97.2% of its species are endemic there (VILLASEÑOR, 2016).

Echeveria is a polyploid genus, with a great diversity of species and morphologies. It is of particular interest in cytogenetic research due to its variety of chromosome numbers and ploidy levels (endopolyploidy) (PALOMINO *et al*., 2021). The formation of cells with very large nuclei is a consequence of endopolyploidization. Endopolyploidization can be triggered by stress caused by environmental changes, such as low and high brightness, temperature changes, water stress, etc., as part of a response that allows these plants to adapt to these conditions and overcome the physical or genomic damage resulting from stress (UHL, 2006). However, since morphological differences within species are not all consistently correlated with differences in ploidy, and since different chromosomal variants cannot always be reliably identified by their morphology, a study of a possible correlation between variations in pollen morphology and ploidy levels could contribute to knowledge about the taxonomy of the genus and the evolution of the species, in addition to the fact that this information could provide useful knowledge for biotechnology, conservation, and floriculture programs.

MYRTACEAE

Eugenia

According to several authors, summarized in Patel *et al.* (1984), the pollen grains of Myrtaceae and, specifically, *Eugenia*, present a recurrent pattern, namely, small to medium size, tricolporate, isopolar, triangular amb, oblate, and angularly aperturate. Mouga *et al.* (2015) report, for *E. involucrata* and *E. uniflora*, medium and small pollen grains, isopolar, triaperturate, angularly aperturate with short *colpi,* oblate, with triangular and subtriangular amb, granular and microgranulated exine with a thickness of 1.71 to 0.68 micrometers, respectively, parasyncolpate, with an apocopial area in *E. uniflora*. Heigl (2021), in turn, reports that *E. buxifolia* pollen grains are in monads, small, synaperturate, isopolar, oblate, with a triangular amb, tricolporate, angular-aperturate, and psilate. The species analyzed here, *Eugenia brasiliensis*, amply confirms these characteristics, except by the fact that, in the present work, the grains showed a verrucate exine. The description of RCPol (2025) for *Eugenia brasiliensis* corroborates the description of the present study, except for the *fastigium* that is mentioned but that was not visualized here.

Psidium

In terms of general pattern, the grains of the two cultivars (white and red) of *Psidium guajava* analyzed here follow the palynological profile of Myrtaceae, namely, in terms of shape (peroblate to suboblate), polarity (isopolar), symmetry (radial) (SILVA, 2014).

The grains of both varieties here studied are small, isopolar, syncolpate, tricolporate, and have long *colpi.* The amb of the white cultivar is subcircular, while that of the red cultivar is lobed. The exine ornamentation is microgranular and verrucate in the white cultivar and granulate in the red cultivar. The exine is thinner in the red cultivar and thicker in the white cultivar. In other words, there are several differences between the two cultivars. Thuaytong & Anprung (2011), who studied white and red cultivars of guava trees, found differences in bioactive and prebiotic properties between the two. Although cultivars are not, in terms of genetics, different species yet, data suggest that the white and red cultivars could be approaching the condition of differing taxa. Tuler *et al*. (2016), analyzing several *Psidium* species, state that three characteristics best explained the taxonomic groups formed in their analysis: type of exine ornamentation, P-EV size (polar diameter in equatorial view), and pollen shape. *Psidium* is considered one of the most difficult genera for species delimitation within the Myrtaceae of the Americas because the pollen characters of the various species are not exclusive to *Psidium* and the species are circumscribed by a set of shared characters, making the limits of some species difficult to discern (KUBO, 2023). Therefore, confirmations at the molecular biology level are necessary to complement the data found here.

CONCLUSION

The pollen grains of the analyzed species show remarkable similarities with data from the literature, while exhibiting subtle differences in some respects. These small nuances, although subtle, highlight the individuality of pollen characteristics, enhancing the understanding of the diversity among the studied species.

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