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Palynological characterization of succulents of the families Asphodelaceae and Asteraceae

Caracterização palinológica de suculentas das famílias Asphodelaceae e Asteraceae

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ABSTRACT
This study aimed to analyze palynologically succulent species: Asphodelaceae: *Haworthia chloracantha* Haw., *Haworthia cymbiformis* (Haw.) Duval, *Haworthia limifolia* (=*Haworthiopsis limifolia*) Marloth and Asteraceae: *Othonna capensis* LH Bailey and *Senecio peregrinus* Griseb. Closed buds were preserved in acetic acid, the acetolyzed grains were arranged on microscope slides, and 50 pollen grains of each species were photographed. Using light optical microscopy, measurements were made of each grain in the polar and equatorial views, in micrometers (μm). For scanning electron microscopy (SEM), the anthers were macerated on microscope slides to release the grains, which were metallized with gold-palladium and photographed. In Asphodelaceae, the grains are monads, monosulcate, medium to large in size, elliptical in scope, bilaterally symmetric, heteropolar, with foveolate, ornamentation microreticulate, perforated, mean exine thickness 1.98-1.42-2.21 micrometers. In Asteraceae, the grains are monads, tricolporate, medium in size, circular to subcircular in scope, radially symmetric, isopolar, oblate-spheroidal and prolate-spheroidal in shape, with perforated echinate ornamentation, average exine thickness 4.08-4.41 micrometers. The pattern of the grains of *Haworthia* are in line with literature of Asphodelaceae, although the verrucate exine was not observed in this study. For *Othonna* and *Senecio,* the echinate ornamentation and thicker exine are in line with the pattern of the Asteraceae.
Keywords: *Haworthia*; morphology; *Othonna*; pollen; *Senecio*.

RESUMO
Este trabalho visou analisar espécies de suculentas: Asphodelaceae: *Haworthia chloracantha* Haw., *Haworthia cymbiformis* (Haw.) Duval, *Haworthia limifolia* (=*Haworthiopsis limifolia*) Marloth e Asteraceae: *Othonna capensis* LH Bailey e *Senecio peregrinus* Griseb. Botões fechados foram preservados em ácido acético, os grãos acetolisados, dispostos em lâminas de microscopia, e 50 grãos de pólen de cada espécie foram fotografados. Em microscopia óptica de luz, realizaram-se medidas de cada grão nas vistas polar e equatorial, em micrômetros (μm). Para a microscopia eletrônica de varredura (MEV), as anteras foram maceradas em lamínulas para liberar os grãos, que foram metalizados com ouro-paládio e fotografados. Em *Haworthia* (Asphodelaceae), os grãos são mônades, monossulcados, tamanho médio a grande, âmbito elíptico, simetria bilateral, heteropolares, ornamentação foveolada, microrreticulada, perfurada, espessura média da exina 1,98-1,42-2,21 micrômetros. Em Asteraceae, os grãos são mônades, tricolporados, tamanho médio, âmbito circular a subcircular, simetria radial, isopolares, forma oblato-esferoidal e prolato-esferoidal, ornamentação equinada perfurada, espessura média da exina 4,08-4,41 micrômetros. Os grãos de pólen de *Haworthia* concordam com a literatura de Asphodelaceae, embora haja algumas variações, tais como a exina verrugosa, não observada neste estudo. Para *Othonna* e *Senecio*, a ornamentação equinada e a exina mais espessa estão em consonância com o padrão da família Asteraceae.
Palavras-chave: *Haworthia*; morfologia; *Othonna*; pólen; *Senecio*.

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INTRODUCTION

Succulent plants are characterized by their ability to accumulate water in their tissues, maintaining reserves during periods of scarce rainfall, reflecting an adaptation to drought conditions. This water can be stored in the leaves, trunks and roots, giving these plants a turgid appearance (SOUZA, 2021). Succulents do not belong to a single plant family, but to more than 40 distinct families, with emphasis on Cactaceae, Crassulaceae, among others, according to Griffiths & Males (2017), reporting that the diversity of biochemical and anatomical arrangements that allow succulents to maintain high water potential, even in periods of drought, include mucilage, large vacuoles, trichomes, diffuse and shallow roots, three-dimensional venation, thick and waxy cuticles, few stomata, high fiber content and high thermal capacity, among other ecophysiological strategies employed by these plants and that, although they represent only about 3% to 5% of flowering plants, succulents have a small but significant and prominent proportion in the plant kingdom.

Plants of the Asphodelaceae family belong to the order Asparagales and present a great diversity of habits, ranging from geophytes to highly specialized succulent plants, stemless herbs, shrubs, climbers and large trees with leaves arranged in terminal rosettes (SMITH & VAN WYK, 1998). The inflorescences are organized in racemes or panicles, with a peduncle that is generally well developed and distinct from the vegetative part of the plant, without leaves or bracts; therefore, easy access is possible for any floral visitor and potential pollinators; normally, only a limited number of flowers open simultaneously in the inflorescence, and promotes cross-pollination, as visitors are encouraged to search for pollen on several plants (VAN JAARSVELD & FORSTER, 2001). In their natural habitat, these species are found in the Old World in arid regions of the temperate, subtropical and tropical zones, with a main distribution center in southern Africa; however, due to their aesthetic appeal, they are cultivated and found throughout the world (KLOPPER *et al*., 2010).

Asteraceae is one of the largest plant families, comprising approximately 10% of all angiosperm flora, and the family is included in the order Asterales, comprising a diversity of species of economic relevance, as well as some plants that exhibit succulence (WILSON, 1986). Most Asteraceae are represented by small herbs or shrubs, with rare occurrences of trees, and approximately 98% of the genera that make up the family consist of small plants, with a greater concentration in the mountainous tropical regions of South America, but found in various types of habitats (JOLY, 1967). The most striking peculiarity of this family is the inflorescence in chapters, formed by smaller units of sessile flowers, making its species pollinated by various types of insects (ELOMAA *et al*., 2018). Pollen characteristics have been widely used in determining phylogenetic relationships within the Asteraceae family (PANERO & FUNK, 2002).

Possessing great nutritional, ecological and reproductive value, pollen differs taxonomically in shape and structure (MOUGA & DEC, 2012). As highlighted by Marcotte (2019), the outer wall of the pollen grain (exine) is reinforced to prevent damage during transport, and is composed of sporopollenin, while the inner layer (intine) is similar to that of a common plant cell. Not limited to taxonomy, palynology has also been useful in genetic and evolutionary studies, forensic science, allergy research, tracking the generational history of individual species and taxa, paleoclimatic studies and analyses of human impact on vegetation (ERDTMAN, 1943).

Investigating the pollen morphology of succulent species is important, given their ornamental popularity associated with the frequent cultivation of these plants. They constitute a relevant functional group in the context of floricultural botany and systematics, and several families and genera of succulents are still in an unclear taxonomic situation, including from a cytological point of view. Thus, Ramdhani *et al.* (2011) emphasize the need for research on pollination and reproductive biology of *Haworthia* and the delimitation of the genus *Senecio*, as well as the genus *Othonna,* which are uncertain and poorly understood (OLIVEIRA, 2014; MAGOSWANA *et al.*, 2019). In this context, the present study aims to contribute to the palynological and taxonomic knowledge of the mentioned succulent taxa, through the morphological characterization of pollen grains.

MATERIAL AND METHODS

Six botanical species originating from South Africa were selected, with samples coming from cultivation sites located in the region of Joinville, Santa Catarina, Brazil: *Haworthia chloracantha* Haw., *Haworthia cymbiformis* (Haw.) Duval, *Haworthia limifolia* Marloth, *Othonna capensis* LH Bailey, *Senecio peregrinus* Griseb (figure 1).

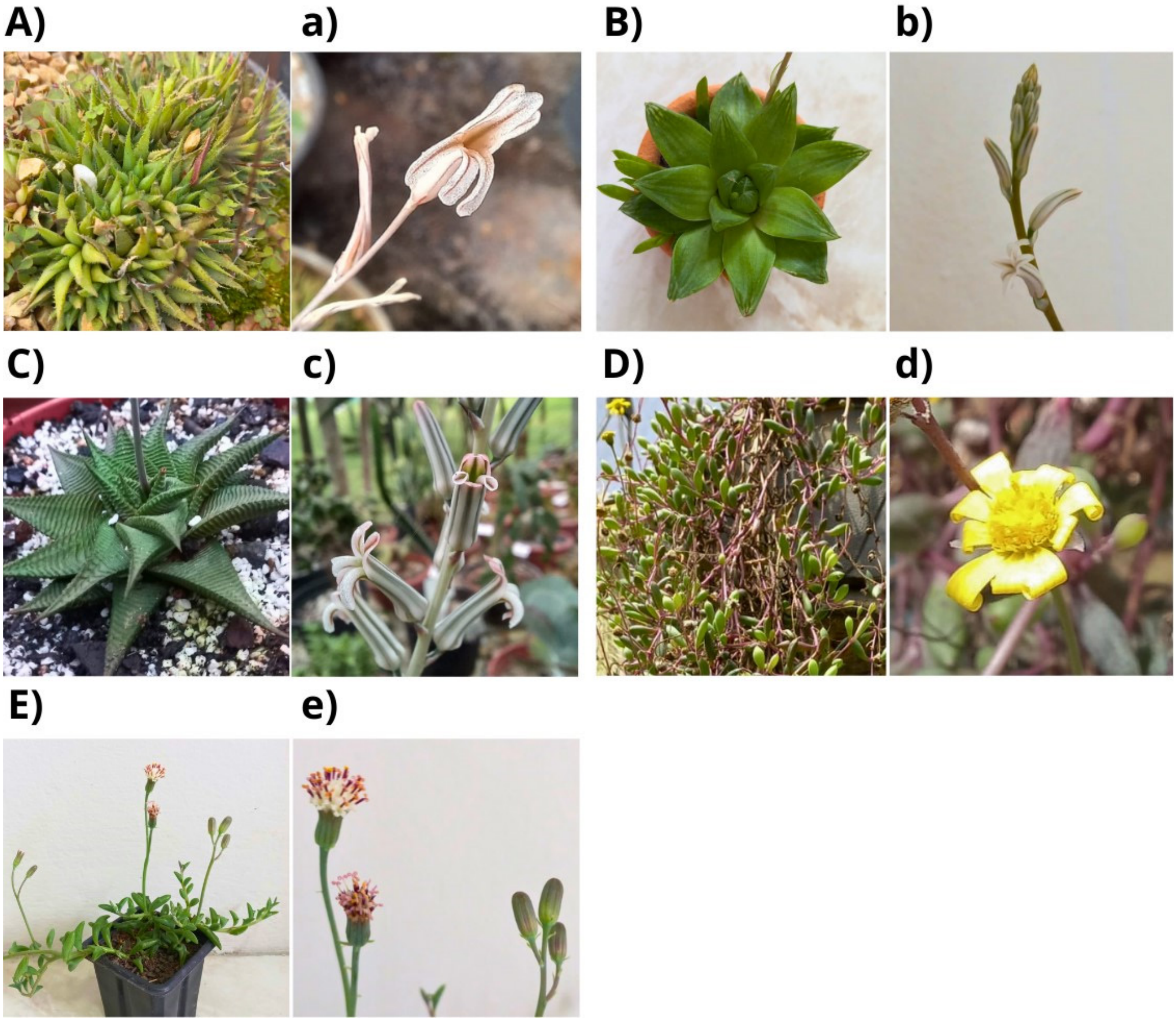

Figure 1 – Photographs of the studied species; on the left (A-F) (uppercase letters), followed by the photos of their respective flowers on the right (a-f) (lowercase letters). A – (Asphodelaceae) *Haworthia chloracantha*; B – (Asphodelaceae) *Haworthia cymbiformis*; C – (Asphodelaceae) *Haworthia limifolia* (=*Haworthiopsis limifolia*); D – (Asteraceae) *Othonna capensis*; E – (Asteraceae) *Senecio peregrinus*. Source: primary.

Initially, closed buds of the identified species were collected and preserved in acetic acid (ERDTMAN, 1960). For acetolysis, the buds were opened, the anthers were removed, macerated, and subjected to acetolysis (ERDTMAN, 1952). Microscopy slides with acetolyzed pollen grains were mounted and observed under a light microscope (five slides per species). The analysis of the pollen grains on the slides was performed, and the photos were taken at 400x magnification and with the aid of the “Dino-Eye Capture 2.0” software. For each species, 25 replicates were performed for each type of view (equatorial and polar), measuring the following parameters in micrometers (μm): equatorial diameter and polar axis (for dicotyledonous grains) or major and minor equatorial diameter and polar diameter (for monocotyledonous grains), in addition to exine thickness for both types of grains (mono and dicotyledonous) (SALGADO-LABOURIAU, 2007). The slides were preserved in the Bee Laboratory (Label) at Univille. In addition, samples were analyzed using scanning electron microscopy (SEM) at the State University of Santa Catarina (Udesc). For this, the anthers of the buds preserved in acetic acid were removed and macerated on microscopy slides to mechanically release the grains, with the aid of tweezers and a drop of acetic acid. The grains were subsequently metallized with gold-palladium, analyzed and photographed.

The measurements were tabulated (Microsoft Excel) in order to obtain the size range (Xmin-Xmax), the arithmetic mean and the standard deviation. The data were assembled in tables, with the respective measurements of the pollen grains in the polar and equatorial views, measurement of the exine thickness and other characteristics (pollen unit, size, scope, symmetry, polarity, shape, openings, ornamentation) (PUNT *et al.*, 2007).

RESULTS

The descriptions of the monocotyledonous species studied are below (table 1 and figure 2):

Haworthia chloracantha

Description: monad, average size, elliptic amb, bilateral symmetry, heteropolar, biconvex shape.
Apertures: monossulcate.
Exine: average thickness 1,98 (minimum 1,38; maximum2,42; standard deviation 0,26), ornamentation microreticulate perforate.
Measurements: average polar diameter 26,05 (minimum 22,76; maximum 30,34; standard deviation 1,87); average smaller equatorial diameter 37,96 (minimum 33,18; maximum 42,53; standard deviation 2,71); average greater equatorial diameter 27,35 (minimum 24,94; maximum 30,18; standard deviation 1,46).

Haworthia cymbiformis

Description: monad, average size, elliptic amb, bilateral symmetry, heteropolar, flat convex shape.
Apertures: monossulcate.
Exine: average thickness 1,42 (minimum 1,09; maximum 1,64; standard deviation 0,14), ornamentation foveolate.
Measurements: average polar diameter 28,26 (minimum 25,35; maximum 30,81; standard deviation 1,51); average smaller equatorial diameter 42,26 (minimum 38,30; maximum 48,76; standard deviation 2,59); average greater equatorial diameter 28,34 (minimum 24,00; maximum 31,53; standard deviation 2,08).

Haworthia limifolia (=Haworthiopsis limifolia)

Description: monad, great size, elliptic amb, bilateral symmetry, heteropolar, flat convex shape.
Apertures: monossulcate.
Exine: average thickness 2,21 (minimum 1,28; maximum 2,84; standard deviation 0,37), ornamentation perforate.
Measurements: average polar diameter 35,96 (minimum 29,28; maximum 40,51; standard deviation 3,21); average smaller equatorial diameter 50,66 (minimum 36,16; maximum 63,34; standard deviation 5,77); average greater equatorial diameter 39,38 (minimum 24,53; maximum 44,92; standard deviation 5,27).

Table 1 – Morphological data of pollen grains of the monocotyledonous species analyzed. Data presentation: maximum, (mean), minimum and standard deviation respectively. All measurements were performed in micrometers (μm).

N	Species	Polar axis (P)	Smaller equatorial diameter (E1)	Greater equatorial diameter (E2)	Exine thickness	Shape
1	*Haworthia chloracantha*	30,34 (26,05) 22,76 1,87	42,53 (37,96) 33,18 2,71	30,18 (27,35) 24,94 1,46	2,42 (1,98) 1,38 0,26	Biconvex
2	*Haworthia cymbiformis*	30,81 (28,26) 25,35 1,51	48,76 (42,26) 38,30 2,59	31,53 (28,34) 24,00 2,08	1,64 (1,42) 1,09 0,14	Flat convex
3	*Haworthia limifolia*	40,51 (35,96) 29,28 3,21	63,34 (50,66) 36,16 5,77	44,92 (39,38) 24,53 5,27	2,84 (2,21) 1,28 0,37	Flat convex

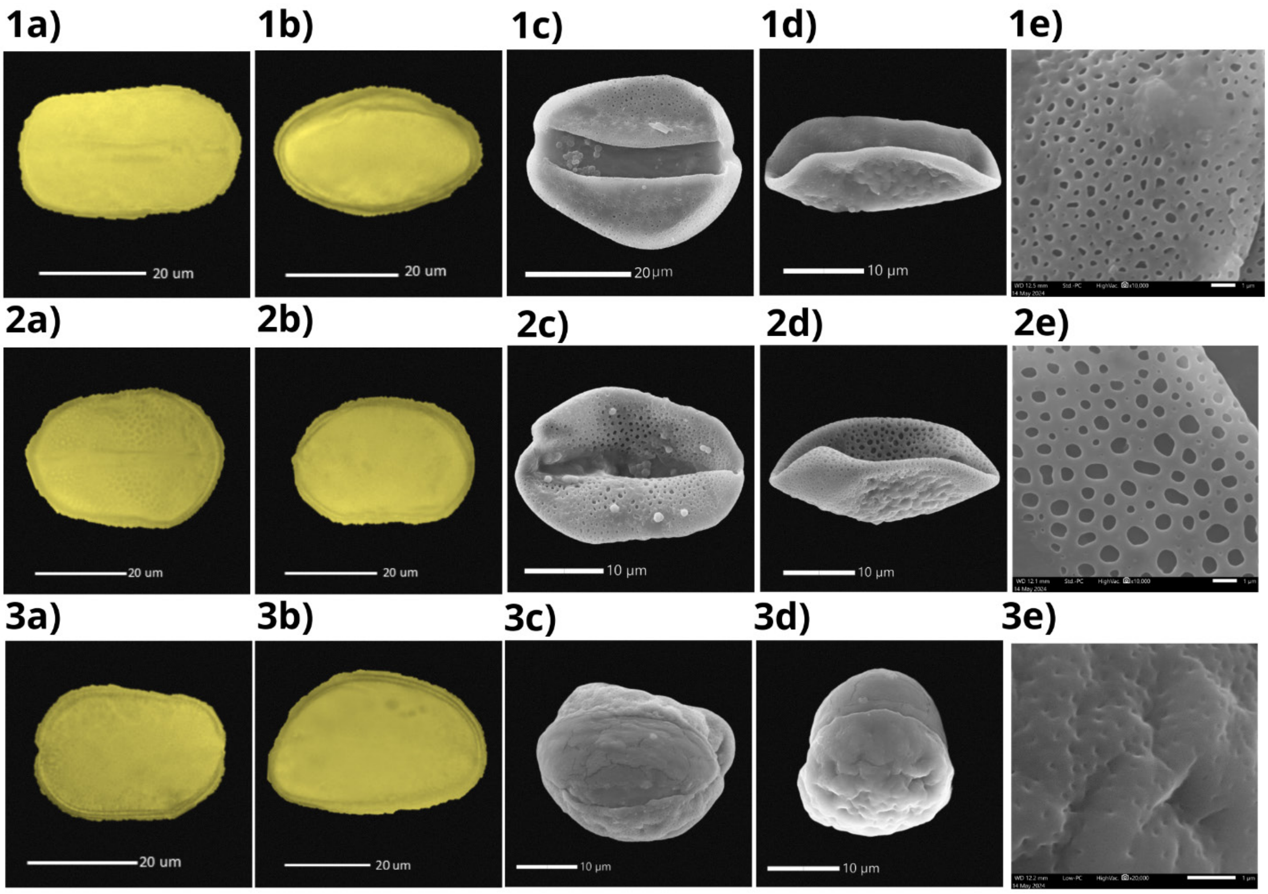

Figure 2 – Images of pollen grains of succulent monocotyledonous species in LM (a – polar view; b – equatorial view) and SEM (c – polar view; d – equatorial view; e – exine). 1a-1e) *Haworthia chloracantha*; 2a-2e) *Haworthia cymbiformis*; 3a-3e) *Haworthia limifolia* (=*Haworthiopsis limifolia*). Source: primary.

The descriptions of the eudicotyledonous species studied are in table 2 and figure 3.

Othonna capensis

Description: monad, average size, circular amb, radial symmetry, isopolar, oblate-spheroidal shape.
Apertures: tricolporate.
Exine: average thickness 4,08 (minimum 2,90; maximum 5,53; standard deviation 0,62), ornamentation echinate perforate (heigh 3,70; base 4,41; distance between spines 5,00).
Measurements: average polar axis 24,64 (minimum 21,34; maximum 29,68; standard deviation 2,29); average equatorial diameter 26,14 (minimum 20,14; maximum 29,21; standard deviation 1,99).

Senecio peregrinus

Description: monad, average size, subcircular amb, radial symmetry, isopolar, prolate-spheroidal shape.
Apertures: tricolporate.
Exine: average thickness 4,41 (minimum 3,49; maximum 5,20; standard deviation 0,56), ornamentation echinate perforate (heigh 2,92; base 3,52; distance between spines 5,43).
Measurements: average polar axis 29,92 (minimum 27,27; maximum 32,24; standard deviation 1,55); average equatorial diameter 29,62 (minimum 26,30; maximum 33,42; standard deviation 1,78).

Table 2 – Morphological data of pollen grains of eudicotyledonous species analyzed. Data presentation: maximum, (mean), minimum and standard deviation respectively. All measurements were performed in micrometers (µm).

N	Species	Polar axis (P)	Equatorial diameter (E)	Exine thickness	Shape	Spines height (base) distance between spines
4	*Othonna capensis*	29,68 (24,64) 21,34 2,29	29,21 (26,14) 20,14 1,99	5,53 (4,08) 2,90 0,62	Oblate-spheroidal	3,70 (4,41) 5,00
5	*Senecio peregrinus*	32,24 (29,92) 27,27 1,55	33,42 (29,62) 26,30 1,78	5,20 (4,41) 3,49 0,56	Prolate-spheroidal	2,92 (3,52) 5,43

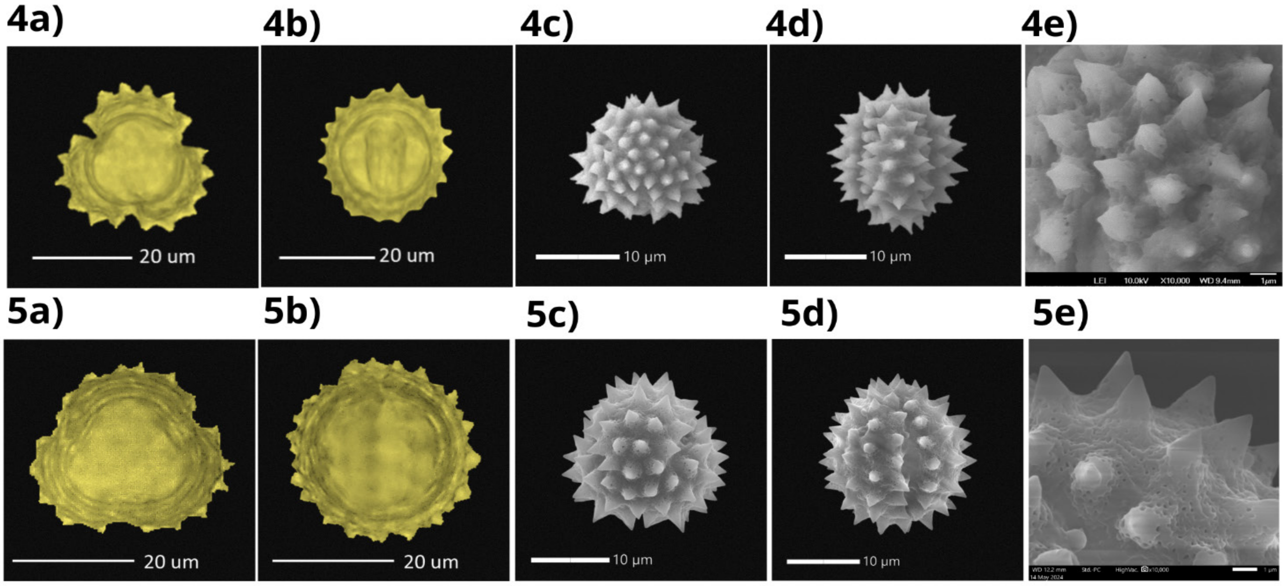

Figure 3 – Images of pollen grains of succulent eudicotyledonous species in LM (a – polar view; b – equatorial view) and SEM (c – polar view; d – equatorial view; e – exine). 4a-4e) *Othonna capensis*; 5a-5e*) Senecio peregrinus*. Source: primary.

Figure 4 shows general images of pollen grains in SEM of succulent species. It is worth noting that the vacuum under which the grains were subjected in SEM caused them to appear dry.

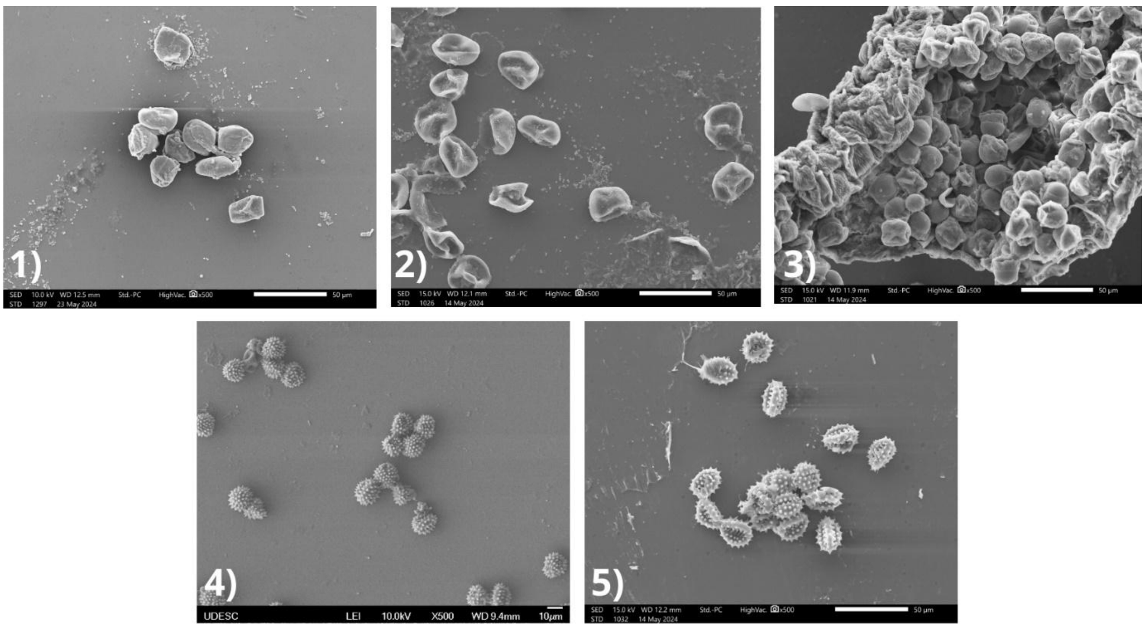

Figure 4 – General images of pollen grains in SEM of succulent species. 1) *Haworthia chloracantha*; 2) *Haworthia cymbiformis*; 3) *Haworthia limifolia* (=*Haworthiopsis limifolia*); 4) *Othonna capensis*; 5) *Senecio peregrinus*. Source: primary.

DISCUSSION

ASPHODELACEAE

In general, in the present study, the pollen grain of the genus *Haworthia* presented the following pattern of morphological characteristics: solitary free grains, monosulcate, medium to large size range, elliptical amb, bilateral symmetry, heteropolar, biconvex to flat convex shape (=elliptical), perforated, foveolate and perforated microreticulate ornamentation.

According to Penet *et al.* (2005), monosulcate pollen is frequently identified in many families of lower asparagoids, ranging from Hypoxidaceae to the best documented species in Asphodelaceae and, in addition, this type of pollen is also observed in the family Iridaceae, which also shares similar palynological patterns with Asphodelaceae.

The succulents of the Asphodelaceae family in the present study are representatives of the clade of the higher asparagales. According to Furness & Rudall (2006), operculate pollen is relatively rare in the clade of the higher asparagales, but occurs in representatives of several families of the lower asparagales. In this study, no operculum was observed.

Regarding the types of ornamentation of the exine of the grains studied here, the perforated microreticulate ornamentation was observed in *Haworthia chloracantha*. Praglowski & Punt (1973) define microreticulate ornamentation as a delicate network consisting of tiny walls enclosing lumens less than 1 μm wide, with the width of the walls equal to or less than the width of the lumen, and perforated ornamentation as a roof with perforations (dots) with a diameter of less than 1 μm and with the distance between the perforations greater than 1 μm. Foveolate ornamentation was noted in the species *Haworthia cymbiformis*, which is defined as an ornamentation that has foveolae, holes or tectal depressions with more than 1 μm in diameter, present in semitectate or tectate pollen grains, and the distance between the tectal holes, or depressions in the tectum, is greater than the diameter of the depressions (PRAGLOWSKI & PUNT, 1973). In *Haworthia limifolia* the ornamentation was only perforated.

Halbritter & Buchner (2016a, 2016b) mention grains similar to those studied here for *Haworthia herbacea* and *H. truncata*, except for the ornamentation of the exine, which the authors report as being perforated/verrucate, which was not verified in the present study. These authors also noted the presence of Ubisch bodies in *H. truncata*, which corroborates the observations made in SEM for the species studied here. Ubisch bodies are polymorphic elements of sporopollenin produced by the tapetum in the anthers (HALBRITTER *et al*., 2018a). These elements can be observed in figure 2: (2c). In addition, Stebler (2024a, 2024b, 2024c) reports medium-sized grains for *Haworthia arachnoidea, H. emelyae* and *H. mucronata*, with exine ranging from reticulate to scabrate/ verrucate and from reticulate to rugulate.

From a systematic point of view, *Haworthia* is a group that requires taxonomic studies because, according to Bayer (2009), in the initial classification carried out by Linnaeus, four plants were grouped as a single species in *Aloe*, generating nomenclature inconsistencies; furthermore, the small flowers led these plants to be treated as a single genus and the broad classification of the subfamily Alooideae caused the differences that distinguish the three groups of *Haworthia* (*Haworthia* subg. *Haworthia*; *Haworthia* subg. *Hexangulares*; *Haworthia* subg. *Robustipedunculares*) to be lost and resulted in disagreements at the generic level. Another factor of imprecision is the collectible appeal with associated horticulture, which leads to the profusion of names for the species. Ramdhani *et al.* (2011) conducted a study in Molecular Biology that confirmed that the genus is paraphyletic in phylogenetic terms, which contributes to the confusing scenario of *Haworthia*. According to Bayer (2009), hybridization occurs between subgenera of *Haworthia* and other genera of Alooideae because reproductive barriers tend to be weak or absent due to the similarity of floral structure between these taxa, with no differentiation occurring through ecological barriers, such as vegetation, geology and soil type. It is considered that *Haworthia (*subg. *Haworthia*) is in active speciation, triggering the radiation of many lineages from southern Africa, however, it is still unclear which biological characteristics drive the rapid speciation in *Haworthia* (RAMDHANI *et al*., 2011). Pollinator specialization has been documented as an event that reinforces early speciation in many plant taxa, a phenomenon already documented in the flora of southern Africa (VAN DER NIET *et al*., 2006). Still according to Ramdhani *et al.* (2011), contemporary speciation in *Haworthia*, together with ongoing hybridization, explains the lack of monophyly, the complex taxonomy and the presence of specialized species restricted to specific habitats.

The sulcate pollen grain is universal in Asphodelaceae and in species of *Haworthia* and *Bulbinella*, being found co-occurring with trichotomosulcate grains (SCHULZE, 1975). The tectum varies from sparsely perforated in most genera to densely perforated and, in *Eremurus,* the pollen is distinctly reticulate (SMITH & VAN WYK, 1998). In some genera, there is an abrupt transition from a perforated sexine to a smooth surface without perforations in the apertural region (SMITH & TIEDT, 1991; SMITH & VAN WYK, 1992). Zavada (1983) observed that the structure of the pollen wall of *Haworthia* is tectate-columellate, with no evident endexine.

The genus *Haworthia* (Asphodelaceae) is widely distributed in South Africa and can be found as far as Swaziland and southern Namibia (BREUER & METZING, 1997). Regarding the subgenera that make up *Haworthia* (*Haworthia* subg. *Haworthia*; *Haworthia* subg. *Hexangulares*; *Haworthia* subg. *Robustipedunculares*), these are distinguished in floral, geographic and behavioral terms (BAYER, 2009).

Smith *et al.* (2001) found significant differences in nectar concentrations between *Haworthia* subgenera; thus, *Haworthia* subg. *Hexangulares* and *Haworthia* subg. *Robustipedunculares* exhibit hexose-rich nectar and *Haworthia* subg. *Haworthia* has a lower concentration. Furthermore, white tubercles on the leaves are a characteristic of *Haworthia* subg. *Hexangulares* and subg. *Robustipedunculares* (DARU *et al*., 2013).

*Haworthia chloracantha (*subg. *Haworthia*) has been assessed as a vulnerable species in the South African Red List of Plants (HELME *et al*., 2014). For *Haworthia cymbiformis* (subg. *Haworthia*), as it is a variable species and difficult to distinguish from other *Haworthia*, until it is taxonomically resolved, the risk of extinction could not be assessed (VON STADEN *et al*., 2014). As for *Haworthia limifolia* (=*Haworthiopsis limifolia*) (subg*. Hexangulares*), it is worth noting that the genus *Haworthiopsis* was created in 2013 to accommodate the species classified in the subgenus *Hexangulares* of the genus *Haworthia* (GILDENHUYS & KLOPPER, 2016) and the species was assessed as vulnerable in the South African Red List of Plants (WILLIAMS *et al.*, 2014).

ASTERACEAE

The notable characteristic of the inflorescence of this family is that pollen is produced in portions and supplied more uniformly throughout the flowering period due to the subdivision of the inflorescence into flowers of the peripheral rays and flowers of the central yellow disk (ERBAR & LEINS, 1995). The family presents great morphological diversity in its floral attributes, which is essential for identifying tribes and genera, and this wide variation makes taxonomic understanding difficult (ROQUE & BAUTISTA, 2008).

However, the pollen morphology of the taxon is characteristic and consistent with most palynological studies on Asteraceae. Thus, the pollen grains of this family are distinct due to their echinate ornamentation with an irregular pattern of spines and relatively small size, which differentiates them from similar ones from other families. It is important to remember that pollen grains similar to those of Asteraceae are found in the families Malvaceae and Convolvulaceae (ADEKANMBI, 2009). In general, Asteraceae pollen grains have thicker exine and their echinate ornamentation increases the chances of successful fertilization, due to the presence of spines that help in adherence to the body of the pollinating agent, allowing the grains to be deposited in the gynoecium (female part of the flower), more precisely in the stigma (KENNEDY, 2017).

In Asteraceae, succulent species are limited to only a small number of genera, including *Notonia, Kleinia, Senecio* and *Othonna* and not all species in these genera are succulent (TIMONIN *et al.*, 2015).

Othonna

According to Magoswana *et al.* (2017), *Othonna* L. is a polymorphic genus of about 120 species of perennial, succulent or subsucculent herbs or shrubs, concentrated in the Greater Cape Floristic Region (GCFR) of South Africa, but extending as far south as Namibia, Angola and Zimbabwe.

The South African species of *Othonna* were last revised by Harvey in 1865 and, consequently, many species, especially in the winter rains region, remain poorly understood. Thus, *Othonna* (Asteraceae), from a taxonomic point of view, presents an uncertain delimitation and several attempts have been made to better define it, with many species remaining poorly understood (MAGOSWANA *et al.*, 2019).

The species *Othonna capensis* is highly appreciated by collectors, having the popular name “ruby necklace” due to the reddish-purple hue of its stem, which stands out even more in high light conditions, and its leaves are arranged alternately along the stem, resembling, both them and the flowers, the shapes found in several species of *Senecio* (OYAMA JUNIOR, 2019b).

The palynological characterization made by Buchner & Halbritter (2010) for the species *Othonna herrei* reports a monad pollen unit, small size (10-25 *µm*), isopolar, spheroidal shape, circular amb, tricolporate, and perforated echinate ornamentation. On the other hand, Stebler (2024d) mentions the pollen grain of *Othonna herrei* as being medium-sized, isopolar, spheroidal to slightly oblate in shape, triangular in amb, tricolporate, echinate, with unornamented opening membranes and medium-sized polar field. It can thus be seen that the descriptions differ slightly for the same species. In the species studied here (*O. capensis*), the pollen is medium-sized, oblate-spheroidal in shape and circular in scope. Thus, the pattern is similar.

Senecio

Senecio is one of the largest genera of flowering plants, distributed practically worldwide, including annual, perennial, aquatic, mountain, shrub and small tree plants (PELSER *et al.*, 2007). Popularly known as “dolphin string”, *Senecio peregrinus* is a hanging succulent presented by cultivation sites as a hybrid between *Senecio rowleyanus*, known as “pearl string” and *Senecio articulatus* (OYAMA JUNIOR, 2019a). It was reported by Kite & Smith (1997) that, in relation to the species *Senecio articulatus*, the inflorescences of this plant were composed of small discoid capitula of small cream-colored flowers that produced a very foul odor, more noticeable in the morning, and the researchers believed that, because the inflorescences were relatively inconspicuous, the odor would play a role in attracting pollinators. *Senecio peregrinus*, the result of the hybridization of the two species mentioned, has the same type of inflorescence and may have inherited this characteristic odor from *Senecio articulatus*, ensuring better reproductive chances. Osman (2011) categorized the pollen type of *Senecio* in the tribe Senecioneae as tricolporate. In the study conducted by Blanca López *et al.* (1991), the pollen type of *Senecio* is characterized as isopolar, equinate, with radial symmetry and, in an equatorial perspective, has a circular to elliptical shape, while in a polar view, its lobes are circular, with an oblate-spheroidal to prolate-spheroidal shape, medium size, the spines exhibiting perforations in the basal area, which are larger than those located in the rest of the hood and with a sharp but not perforated tip. The results of the present research are in agreement with the general observations made by the aforementioned authors. Hallbritter (2016), Hallbritter & Buchner (2016c), Hallbritter & Kohler (2016), Hallbritter & Weis (2018), Hallbritter & Berger (2019), Hallbritter & Auer (2020, 2022), Halbritter *et al*. (2021) and Hallbritter & Heigl (2021) present 26 species of *Senecio*, very uniform, in an echinate, tricolporate pollen type, of small/medium size, with echinate/perforate or microreticulate exine. In turn, Stebler (2024e, 2024f, 2024g) describes three species of *Senecio* (*S. cineraria*, *S. herreanus*, *S. jacobaea*), which show a medium-sized, equinate, tricolporate grain pattern, with a ring in the pore, but this last characteristic was not observed in the present study.

When comparing the results of the present study of the genus *Senecio* with other pollen analyses of some species of the same genus (*Senecio jacobaea, Senecio abrotanifolius* and *Senecio disjunctus*) that, however, did not exhibit succulent characteristics, no significant difference was identified in the morphology of the pollen grains (HALBRITTER, 2016a, 2016b; HALBRITTER & BERGER, 2019; HALBRITTER & HEIGL, 2021). Thus, the pollen grains of *Senecio* from the present study are very similar to the grains of other species of the same genus, even though these do not present the morphological characteristic of succulence. This may reflect the fact that taxonomy is still a more significant factor in grain morphology than environmental influence and that the succulence of the species does not appear to be an expressive factor in the morphology of these pollen grains.

González-Mancera *et al.* (2018), however, emphasize that the morphology of the pollen grain of succulents is in tune with the arid environments to which these plants had to adapt and argue that, to face dehydration, the pollen grain undergoes a structural process in which it modifies its shape to accommodate variations in the volume of the cytoplasm, a process called harmomegaty. The aforementioned authors also point out the opercula of the pollen grains they studied, which are configured as thickenings in the exine, covering most of the openings, for protection against pathogens and grain dehydration. Observed in the present study, the echinate ornamentation and the greater thickness of the exine of the grains of Asteraceae species confirm the literature, considering the pattern of the family. However, in the present study, the operculum covering the openings was not found. Asteraceae species that are succulent probably adopted succulence as an adaptation to arid climates and the influence of this characteristic on the reproduction of these species is not completely studied and is possibly independent.

CONCLUSION

The pattern of characteristics found in *Haworthia* pollen grains, namely, n monads, monosulcate, medium to large in size, with elliptical amb, bilateral symmetry, heteropolar, biconvex to flat convex shape (=elliptical), microreticulate/reticulate ornamentation, was expected and also matches the specific literature of the genus and the family in which it is allocated (Asphodelaceae). Habitat destruction due to urban and industrial expansion, competition with invasive plants and the collection of wild plants for the succulent trade are the main threats to *Haworthia* species, an important genus due to the interactions they maintain with fauna in inhospitable regions and the peculiar adaptations they display for arid regions. Palynological knowledge about the species contributes to the taxonomy of the genus and to the definitions of extinction threats. For the Asteraceae *Othonna* and *Senecio*, the conformation observed in the pollen grains, such as the echinate ornamentation and the greater thickness in the exine of the grains, confirms the literature, considering the family standard.

The palynological structural similarities between species belonging to the same families, whether Asphodelaceae or Asteraceae, support their probable taxonomic position, point to interspecific relationships, and the variations support their identities, reinforcing them as distinct species. The pollen morphology of succulents reflects harmomegaty, and the characteristics and configurations of the pollen grain are correlated with the adaptation to variations in the degree of hydration and the xerophytic environment in which they developed, as well as reflecting the taxonomy itself, which is shown in the grains and follows the patterns of the families and genera. Pollen architecture plays a crucial role in the taxonomy of angiosperms, providing information about their interrelationships. The present study contributes to future comparative palynological research or to systematic analyses related to the taxonomy of species.

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