An Acad Bras Cienc (2024) 96(3): e20231007 DOI 10.1590/0001-3765202420231007
Anais da Academia Brasileira de Ciências | *Annals of the Brazilian Academy of Sciences*
Printed ISSN 0001-3765 I Online ISSN 1678-2690
www.scielo.br/aabc | www.fb.com/aabcjournal

CELLULAR AND MOLECULAR BIOLOGY

Comparative Leaf Anatomy under Sun and Shade Conditions and Pollen Morphology of *Chrysophyllum rufum* Mart. (Sapotaceae)

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Abstract: *Chrysophyllum rufum* leaves collected under different light conditions provide information on how this fact can influence the morphology of the species. The anatomy techniques applied to the samples showed that there were discreet differences in the characters considered diagnostic. This indicates that the plant is capable of adapting, despite its prevalence in both dry and humid environments. The pollen grains were acetolyzed, measured, described qualitatively, analyzed quantitatively, and illustrated using light microscopy (LM).

Key words: Anatomy, Chrysophylloideae, micromorphology, palynology.

INTRODUCTION

Chrysophyllum L. is the second largest genus of Sapotaceae in number of species, covering about 45 species in the Neotropics. Classified within the subfamily Chrysophylloideae, the genus presents trees or shrubs, absent stipules, axillary inflorescence, unisexual or bisexual flowers, rarely solitary, fruits with one or more seeds, laterally compressed, with a smooth and shiny seed coat, and a vertical embryo. The leaves are widely spaced, usually alternate, with brochidodromous or eucamptodromous venation, tertiary veins parallel to the secondary veins and descending from the margin (Pennington 1990, Faria et al. 2017, Swenson et al. 2020).

Chrysophyllum rufum Mart. is a shrub or small tree up to 12m in height. It is distinguished by its indumentum with ferruginous hairs on the abaxial surface of leaves, glabrescent in adaxial surface, and with coriaceous texture. Its venation pattern is eucamptodromous-brochidodromous, and midrib slightly sunken on upper surface (Pennington 1990). Research on this species is limited, with the most recent studies being conducted by Lima et al. (2017), focusing on the morphological characteristics of the fruit, seed, and seedling, and by R.C.S.L. Santos (unpublished data), who investigated the anatomy, histochemistry, and leaf architecture of the species in the state of Bahia.

The functional and structural characteristics of plants changes in response to environmental factors to which they are exposed refer to phenotypic plasticity, and this plasticity is important for the organism to survive in heterogeneous environments or under variable environmental conditions (Valladares et al. 1997, Sultan 2003, Corrêa 2003).

The level of light is one of the most influential factors that affect the structure of a mature leaf during its development. Anatomical variation in the leaf can induce consequences of significant impacts on photosynthesis due to the environment. Light regulations and CO_2 profiles in leaves, as well as the maximization of photosynthetic efficiencies, may be a result of these structural variations (Dickison 2000).

Leaf response to light conditions varies greatly between species (Rijkers et al. 2000). Light is a fundamental component for plant growth because, in addition to providing energy for photosynthesis, it also offers signals that reflect on its development through light receptors sensitive to different intensities. In this way, changes in light levels to which a given species is adapted can adapt the plant to different types of physiological responses in its biochemical, anatomical and growth characteristics (Atroch et al. 2001). Therefore, variations in light intensity to which leaves are exposed can result in morphoanatomical modifications that serve as a basis for distinguishing sun leaves from shade leaves (Smith et al. 1997).

The pollen morphology of different species of Sapotaceae has been described by Harley (1991). Regarding *Chrysophyllum* L., the most recent work is that of Souza et al. (2021), which focused on species occurring in the state of Bahia. While these studies aim to encompass as many species as possible, they are not complete, necessitating a greater effort to provide a more thorough description of the species within the genus. This is especially pertinent when dealing with the *Chrysophyllum* L. genus, which faces some challenges in species delineation, making palynology a useful tool allied to the correct description of the taxa.

In this way, in order to contribute to the knowledge about the species, providing new and relevant information about leaf anatomy under different light conditions and regarding the description of pollen grains for the species, this study presents results that can encourage further research on this species.

MATERIALS AND METHODS

The leaves samples were obtained from specimens of *Chrysophyllum rufum* Mart. occurring on the *Campus* of the State University of Feira de Santana, Bahia, Brazil, and the pollen materials were obtained from dried herbarium specimens (Table I). Mature leaves were collected between the 2nd and 4th node of the plant, on branches exposed to different light intensities (only sun and only shade) and preserved in 70% alcohol until processing (Kraus & Arduin 1997).

For leaf anatomy, freehand cross-sections of the petiole and the leaf blades at the apex, base, middle region, and margin, were stained with astra blue and safranin or alcian blue and safranin (9:1) (Kraus & Arduin 1997), and were analyzed.

The dissociation of the leaf epidermis was performed using the Jeffrey technique on portions of the leaf blade, following the methodology described in Kraus & Arduin (1997). The stomatal density per square millimeter was determined according to Laboriau et al. (1961), through counting on cleared leaves under a Zeiss Axiophot optical microscope equipped with a bright-field camera.

For pollen morphology, the pollen grains were acetolysed according to the methods of Erdtman technique (1960), measured and examined by light microscope (LM). Pollen diameters (n=25) and the other characteristics (of aperture and exine thickness, n=10) were

Table I. Specimens used in analysis of leaf anatomy and pollen morphology of *Chrysophyllum rufum* Mart., Bahia, Brazil.

Species	State	Voucher
Chrysophyllum rufum Mart.	BA	HUEFS 244201 HUEFS 123131* CEPEC 114091* CEPEC 97733*

***Material used in pollen morphology.**

measured in the pollen samples under LM. Statistical analysis was conducted to obtain the means (x), standard deviation (sx), standard error (s), 95% confidence intervals (CI), coefficient of variability (V), and range (R). The mean was calculated for exine thickness, length and width of apertures. Photomicrographs were performed with a light microscope Leica ICC50W for LM fotos.

The leaf anatomy descriptions followed the nomenclature proposed by Howard (1979), Theobald et al. (1979), and Metcalfe & Chalk (1983), while the pollen descriptions and terminology follows the guidelines proposed by Punt et al. (2007) and Erdtman (1952).

RESULTS

The cross-sections of *Chrysophyllum rufum* leaves exhibit a straight shape on the adaxial surface of the petiole of shade leaves, and a concavo-convex shape in the petiole of sun leaves (Fig. 1a). In leaves of both light conditions, the petiole consists of an epidermal cell layer followed by layers of angular collenchyma – three layers in sun leaves and between four and five layers in shade leaves (Fig. 2a). The vascular bundle displays internal xylem and external phloem, characterizing a closed collateral vascular bundle (Fig. 1c; Fig. 2d). The presence of sclerenchyma cells around the vascular bundle

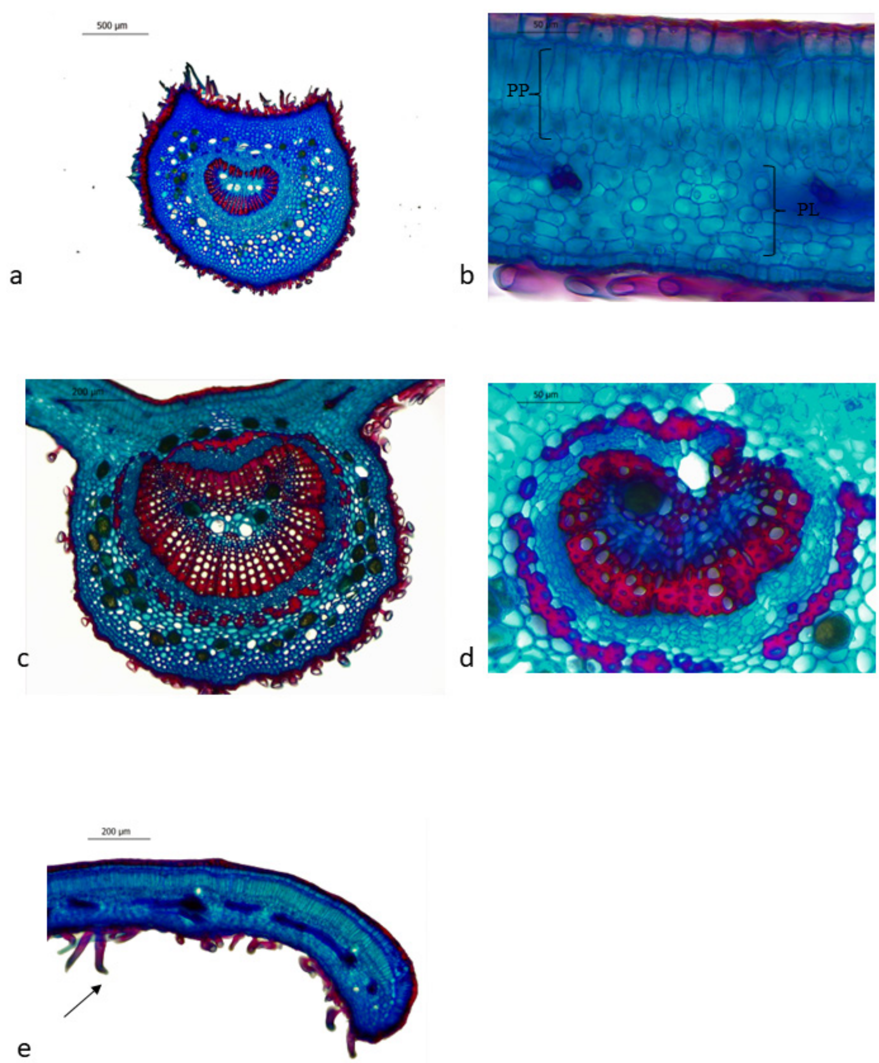

Figure 1. Cross section of the sun leaf of *C. rufum* Mart. a- Petiole; b- Mesophyll of *C. rufum* showing palisade (PP) and lacunous (PL) parenchymas; c- Cross section of the main vein of the *C. rufum* Mart leaf; d- Central vascular bundle; e- Cross section of the maple with emphasis on trichomes (arrow).

is discontinuous, and the medulla is filled with parenchymal cells in both types of leaves (Fig. 1d; Fig. 2c). Calcium oxalate crystals are present in the cortex, as well as latex canals.

In a frontal view, the leaf blade of *C. rufum* presents intercostal epidermal cells with polygonal shapes and sinuous to very sinuous anticlinal walls – in sun and shade leaves, respectively. Costal cells have straight shapes with straight anticlinal walls in leaves of both light conditions (Fig. 3a; Fig. 4a). In sun leaves, the cells have a larger diameter on the abaxial surface, measuring between 3.02 - 1.54 µm, but occupy a larger area on the adaxial surface, with an average of 1430±72.4 cells per mm^2 (Fig. 3c). In shade leaves, epidermal cells measure 3.60 - 1.77 µm, with larger cells on the adaxial surface and covering an area of 1355±56.6 cells per mm^2 on the abaxial surface (Fig. 4d). In lateral view, the epidermis is homogenous and uniseriate, consisting of only one cell layer.

Trichomes of the malpighiaceous type were present on the abaxial surfaces of sun and shade leaves, with a higher density on shade leaves,

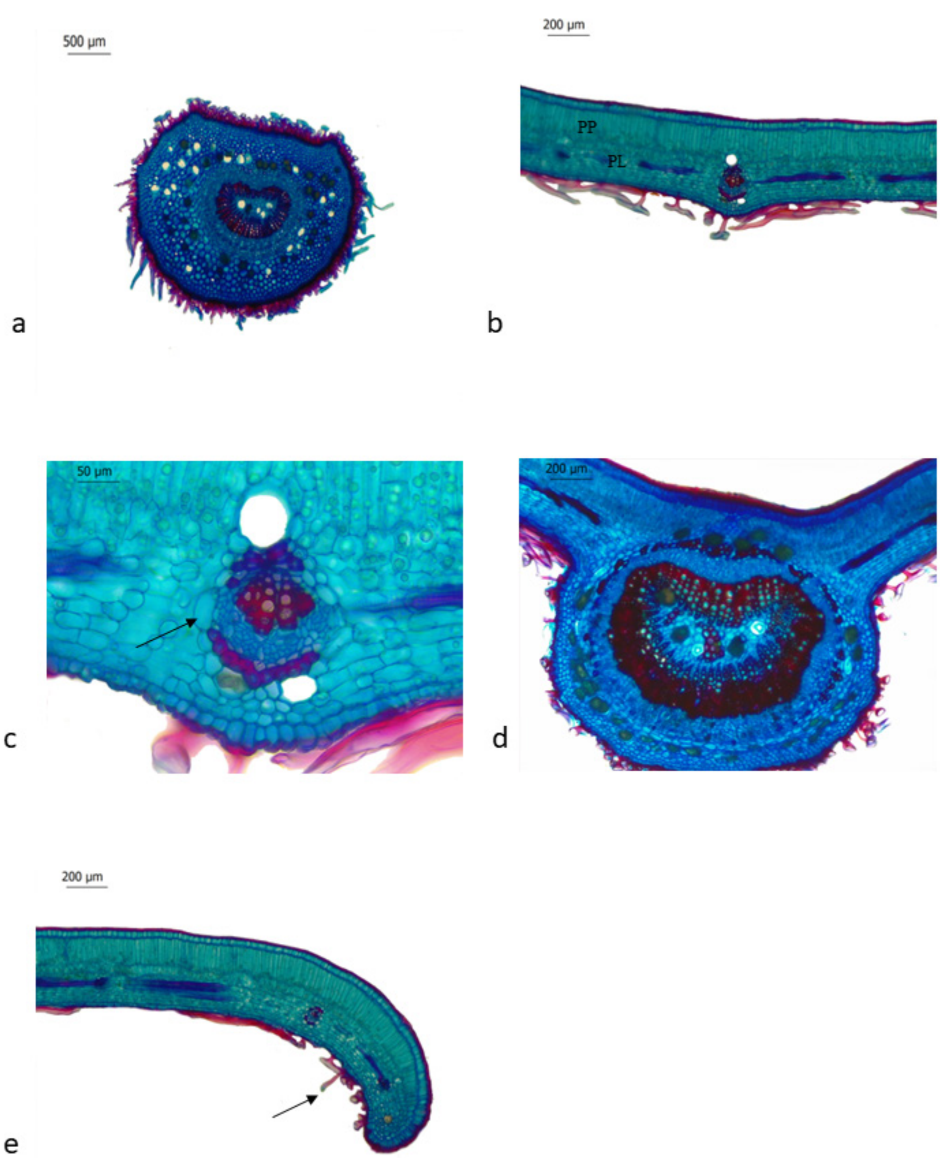

Figure 2. **Cross-section of the shade leaf of *C. rufum* Mart. Individual 1: a- Petiole; b- Cross-section of the mesophyll showing palisade (PP) and spongy (PL) parenchyma; c- *C. rufum* mesophyll with emphasis on the accessory bundle (arrow); d- Central vascular bundle; e- Cross-section of the margin, with emphasis on the trichome (arrow).**

exhibiting 152±7.24 trichomes per mm^2 (Fig. 3d; Fig. 4c). Trichome scars were detected on the adaxial surface of leaves, indicating that there were trichomes in that region at some point during leaf development, classifying the leaf as glabrescent. According to cuticle measurements, it is considered very thin, ranging from 0.23-0.33 µm in shade leaves, and 0.83 µm in sun leaves.

Anisocytic stomata are present on the abaxial surface of the leaves, classifying them as hypostomatic. Stomatal density was higher in sun leaves, with 128±5.64 stomata per mm^2, and they are in both costal and intercostal cells. The number of cells surrounding the stomata, were between four and six cells, exhibit striated ornamentation (Fig. 3b; Fig. 4b).

The mesophyll consists of palisade parenchyma with closely packed cells and spongy parenchyma containing globular cells in lateral view, and brachiform cells in longitudinal view. Sclerenchyma cells of the fiber type are present in the mesophyll and around continuous the central vascular bundle. On the adaxial side of the leaves, there are layers of angular collenchyma, with three to four layers in sun leaves, and four to five layers in shade leaves (Fig. 1b; Fig. 2b).

The leaf margin is flexed with an epidermal cell layer with cuticle overlap and continuous palisade parenchyma in the distal portion of the margin. Collenchyma cells are visible in the distal portion of the margin. The cuticle exhibits flange ornamentation. All these characteristics are present in both sun and shade leaves (Fig. 1e; Fig. 2e).

The pollen grains of *Chrysophyllum rufum* are monads, isopolar, small to medium-sized, prolate (Fig. 5a), 3-colporate, ectoapertures elongated to the poles with tapered ends, lalongate endoaperture (Fig. 5d), presence of a costa (Fig. 5c), sinuaperturate, and subtriangular to subcircular in shape (Fig. 5b). The exine is psilate, and regarding sexine and nexine, the pollen grains of *C. rufum* have equal thickness measurements (Table II).

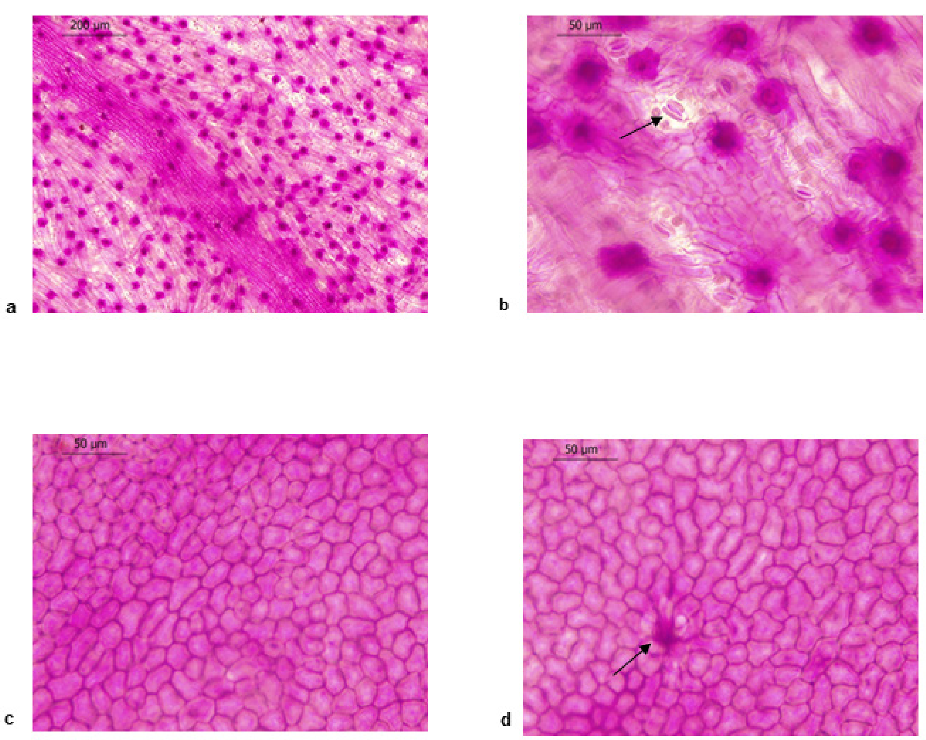

Figure 3. **Frontal view of the epidermis of the sun leaf of *Chrysophyllum rufum* L. a-b: Abaxial surface of *Chrysophyllum rufum* Mart. showing trichome scars and stomata (arrow indicating anisocytic-type stomate) c-d: Adaxial surface of *C. rufum* Mart. showing leaf surface cells and malpighiaceous trichome scar (arrow indicating malpighiaceous trichome scar).**

DISCUSSION

The characteristics of the sun and the shade leaves of *C. rufum* are in accordance with the description provided by Pennington (1990), which include the dorsiventral mesophyll organization, the presence of malpighiaceous trichomes, the presence of laticifers and white latex, as well as the brochidodromous-eucamptodromous venation.

Some studies suggest that in environments with higher light irradiation – generally - plants tend to have smaller leaves to minimize potential negative effects of overheating and high transpiration (Marques et al. 1999, Klich 2000, Mendes et al. 2001, Castro & Alvarenga 2002). Plants with larger leaves (foliar expansion) in shaded environments employ a compensatory strategy due to the limited amount of light they receive, optimizing it to enhance physiological processes related to development and growth (Campos & Uchida 2002), thus increasing the plant's competitive advantage for light acquisition, as it is in lower supply (Espindola Junior 2006). The variations in leaf size observed in sun and shade leaves of *C. rufum* may be incorporated into the range of variation described taxonomically by Pennington (1990) and Monteiro et al. (2007).

The change in the internal leaf structure is related to light capture, as the columnar arrangement of palisade parenchyma cells (and a possible increase in their number) allows for more efficient light transmission, thus avoiding photo-inhibition (Taiz & Zeiger 2004). Leaf thickness and leaf area may also be inversely proportional due to the different amounts of light they receive. Leaves in higher light conditions may have greater thickness and reduced exposed area due to the addition of photosynthetic tissues and intercellular spaces, resulting in a larger leaf volume (Boeger & Poulson 2006). Dickison (2000) suggests that the development of palisade parenchyma, especially in sun leaves, is likely related to photosynthetic capacity.

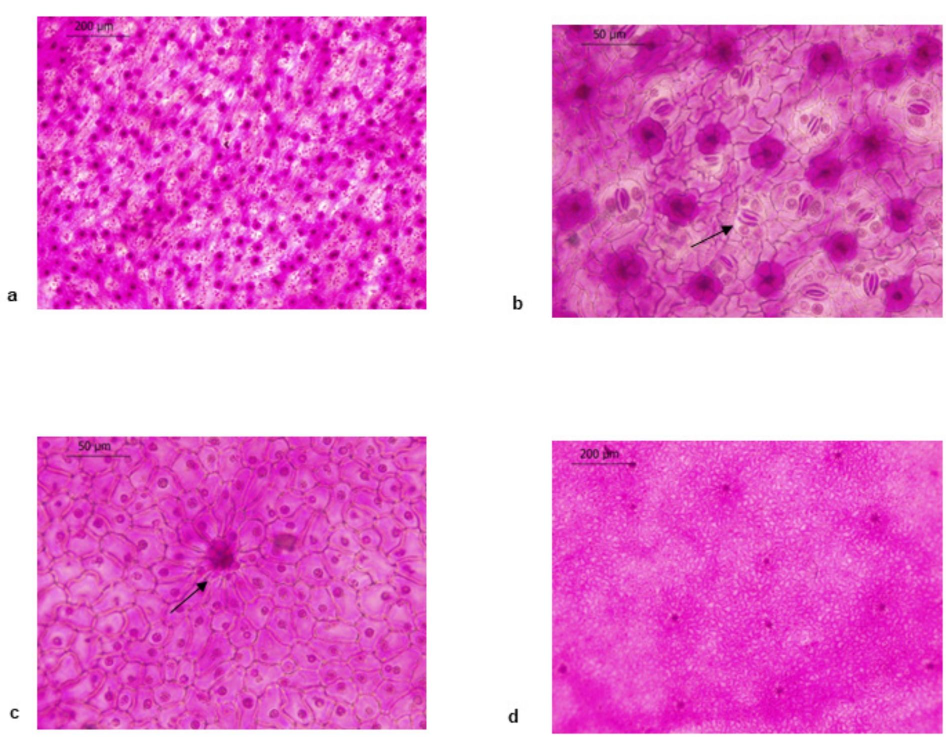

Figure 4. Frontal view of the epidermis of the shade leaf of *Chrysophyllum rufum* L. a-b: Abaxial surface of *Chrysophyllum rufum* Mart. showing trichome scars and stomata (arrow indicating anisocytic-type stomate) c-d: Adaxial surface of *C. rufum* Mart. showing leaf surface cells and malpighiaceous trichome scar (arrow indicating malpighiaceous trichome scar).

According to Esau (1977), the presence of collenchyma is common in plants and can be interpreted as an aid in minimizing wilting effects. Similarly, the formation of crystals, as a control process, may require a mechanism for regulating calcium levels in the plant. These crystals are believed to promote the removal of oxalate in plants that cannot metabolize them, protecting against herbivores (Esau 1977). Laticifers, as mentioned by Metcalfe & Chalk (1972), can be found either clustered along the veins, dispersed within the mesophyll, or in both forms simultaneously.

Stomata are directly related to the leaf's photosynthetic capacity, and any alteration in their quantity affects stomatal conductance. Thus, a higher stomatal density is required for greater CO_2 absorption (Abrans et al. 1992, Evans 1999). The cuticle is effective in reducing water loss, reflecting light, and regulating temperature, especially in leaves that are more exposed to solar radiation (Fermino Jr et al. 2004). Metcalfe & Chalk (1972) had already mentioned that in this genus, the abaxial surface of the cuticle may exhibit striated, granulated, or ridged ornamentation. This style was also observed on the adaxial surface of shade leaves. The leaf characteristics, such as a very thick cuticle, biseriate palisade parenchyma, dense lacunose parenchyma, the presence of crystals, among other features, are related to a possible xeromorphic character of the plant (Esau 1977, Dickinson 2000).

Studies on the pollen morphology of *Chrysophyllum* L. are scarce, and therefore, the genus remains relatively understudied. The work of Harley (1991) for the neotropical species is the most comprehensive to date. The pollen description data presented in this work align with results from other studies on pollen grains for this genus, including size, shape, and exine measurements (sexine and nexine), which

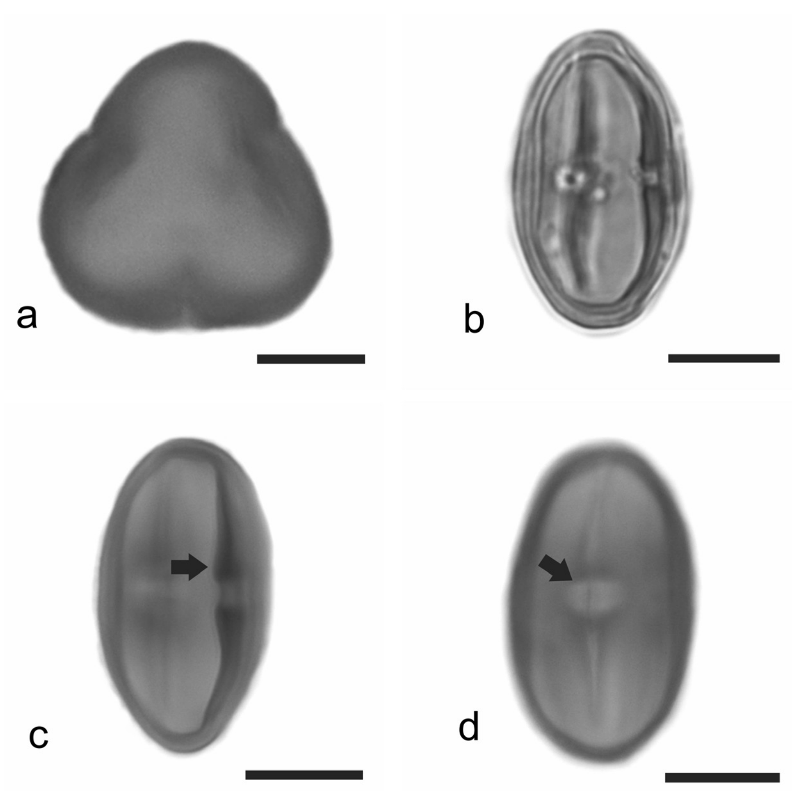

Figure 5. **Pollen grains of *Chrysophyllum rufum* Mart. a: Polar view (with optical section); b Equatorial view (with optical section); c: Equatorial view, with emphasis on aperture with costa (arrow); d: Equatorial view, with emphasis on pore aperture (arrow). Scale bar = 10µm; Caption: Optical section = c/op.**

Table II. Morphometric characters of pollen grains from *Chrysophyllum rufum* Mart. occurring in Bahia.

Species/Specimen	DP		DE		DEp		P/E	Ecto	Endo	Sex	Nex
	x±Sx	Fv	x±Sx	Fv	x±Sx	Fv					
Chrysophyllum rufum Mart.											
Amorim 6190	24,3±0,30	22,5-27,5	16,2±0,25	15-17,5	17,5±0,17	15-22,5	1,50	20,0x2,5	2,3x2,9	0,87	0,82
Funch 616	26,4±0,29	25-30	14,3±0,27	12,5-17,5	-	-	1,84	-	-	0,8	0,95
Guedes 10486	26,4±0,32	22,5-30	14,9±0,22	12,5-17,5	15,2±0,15	12,5-17,5	1,77	23,6x2,3	2,2x3,6	0,9	0,9

DP= polar diameter; DE= equatorial diameter; DEp= equatorial diameter in polar view; x= arithmetic mean; Sx= standard deviation of the mean; Fv= range of variation; Ecto= length x width of the ectoaperture; Endo= length x height of the endoaperture; Sex= sexine; Nex=nexine; measurements in µm.

support the circumscription provided by Souza et al. (2021) for *C. rufum* from the state of Bahia. These findings also corroborate the description of *Chrysophyllum* L. species cited by Harley (1991), such as *C. argenteum, C. flexuosum*, *C. gonocarpum*, and others, which also exhibit parameters equivalent to those described in this study.

The quantitative parameters used for the classification of apertures, and diameters, are like data presented in Souza et al. (2021), demonstrating that even though the specimens come from different locations, the pollen grains retain the inherent characteristics of the species. Thus, it is possible to conclude that the pollen grains of the analyzed species exhibit characteristics that allow for the correct classification of the sample in relation to the pollen grains of the genus *Chrysophyllum* L.

Acknowledgments

The present work was carried out with the support of the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brazil (CAPES) - Finance Code 001. The authors also thank the Postgraduate Program in Plant Genetic Resources (PPGRGV), the Laboratory of Plant Micromorphology (LAMIV) of Department of Biological Sciences, State University of Feira de Santana (UEFS), Bahia, Brazil.

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How to cite
SANTOS RCSL & CARNEIRO CE. 2024. Comparative Leaf Anatomy under Sun and Shade Conditions and Pollen Morphology of *Chrysophyllum rufum* Mart. (Sapotaceae). An Acad Bras Cienc 96: e20231007. DOI 10.1590/0001-3765202420231007.

Manuscript received on September 12, 2023;
accepted for publication on October 20, 2023

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Author contributions

The authors played a fundamental role in the study, with both agreeing on the execution of the work, writing, review, and translation. Rísia Cean S. de L. Santos conducted the experiments from which the presented results were obtained, which is part of her ongoing thesis. She also wrote and reviewed the article. Cláudia Elena Carneiro actively participated in the review and translation of the article and supervised the work's execution.

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