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Anatomy of the aerial vegetative organs of *Phoradendron strongylocladoss* Eichler (Viscaceae)

Anatomia dos órgãos vegetativos aéreos de Phoradendron strongyloclados Eichler (Viscaceae)

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Resumo

Phoradendron strongyloclados Eichler é uma hemiparasita vulgarmente conhecida como erva-de-passarinho. Representantes do gênero *Phoradendron* são utilizados na medicina popular, porém pouco se sabe sobre *P. strongyloclados*, inclusive sobre a sua estrutura anatômica. O presente trabalho objetivou descrever a anatomia dos órgãos vegetativos aéreos de *P. strongyloclados*. Para tal fim foi utilizada metodologia usual em anatomia vegetal. As folhas possuem cutícula espessa, epiderme uniestratificada, estômatos paracíticos e mesofilo isobilateral. O catafilo é bilobado, com mesofilo homogêneo e vascularização. O caule possui secção transversal elíptica em estrutura primária. Em estrutura secundária, mantém os tecidos fotossintetizantes e a epiderme. A medula é esclerificada. O lenho é desenvolvido, rígido, fibroso, com elementos de vaso curtos e placa de perfuração simples. Os raios são heterocelulares e suas células podem conter cristais prismáticos. O arranjo compacto das células parenquimáticas, cutícula espessa, alta lignificação e a baixa relação superfície/volume; folhas pequenas, carnudas e espaçadas caracterizam xeromorfia.

Abstract

Phoradendron strongyloclados Eichler is a hemiparasite commonly known as mistletoe. Representatives of the genus Phoradendron are used in folk medicine, but little is known about P. strongyloclados, including its anatomical structure. The present work aimed to describe the anatomy of the aerial vegetative organs of P. strongyloclados. For this purpose, the usual methodology in plant anatomy was used. The leaves have thick cuticle, unistratified epidermis, paracytic stomata and isobilateral mesophyll. The cataphyll is bilobed, with homogeneous mesophyll and vascularization. The stem has an elliptical cross section in primary structure. In a secondary structure, it maintains the photosynthetic tissues and the epidermis. The pith is sclerified. The wood is developed, rigid, fibrous, with short vessel elements and simple perforation plate. Rays are heterocellular and their cells may contain prismatic crystals. The compact arrangement of parenchyma cells, thick cuticle, high lignification and low surface/volume ratio; small, fleshy, closely spaced leaves characterize xeromorphy.

Introduction

The Viscaceae family, together with three other families from the order Santalales, is part of a group called mistletoes, so named mainly because of the dispersal carried out by birds (Cazetta; Galetti, 2003). It is constituted of seven genera: *Arceuthobium* M.Bieb., *Dendrophthora* Eichler, *Ginalloa* Korth., *Korthalsella* Tiegh., *Notothixos* Oliver, *Phoradendron* Nutt., and *Viscum* L., harboring ca. of 450 species distributed worldwide (Kuijt; Hansen, 2015). The family genera are hemiparasites of stems, that is, they are part of a group of woody plants, aerial obligate parasites with a range of adaptations associated with their habit, including the haustorium, which anchors and vascularly connects the mistletoe herb to the host (Watson, 2004).

In general, mistletoes are considered undesirable plants. However, despite causing damage to their hosts, some species can be considered important elements in the ecological regulation of forests (Arruda et al., 2013). Corroborating this statement, Watson (2001) considers mistletoes as a key resource of forests and woods, since these plants serve as food to a great diversity of birds, as well as a nesting site and even habitat.

Besides their ecological importance, the medicinal potential of mistletoes has been demonstrated, mainly in the area of ethnopharmacology. Indian sandalwood (*Santalum album* L.) is widely used in folk medicine. Also, it is economically important in the perfumery industry and in the manufacturing of oils (Metcalfe; Chalk, 1957). Representatives of *Phoradendron* are also used in domestic medicine whose effectiveness is proven, highlighting the antimicrobial, immunomodulatory, and anti-inflammatory action, being a potential for the manufacture of phytotherapeutics (Gonzales et al., 2000; Varela et al., 2004).

Phoradendron is the largest genus of Viscaceae, housing 234 species (Kuijt, 2003). In Brazil, it is represented by 41 species, of which 11 are endemic (Dettke; Caires, 2021). It is one of the most aggressive genera in parasitism, and can cause changes in host plant growth, reproduction, anatomy, photosynthetic performance and transpiration (Rigon; Cervi, 2013; Teixeira-Costa; Ceccantini, 2015). It is widely found parasitizing urban trees (Leal et al., 2006), compromising its vigor and, consequently, its landscape benefits. In addition, when it comes to trees used in the various productive sectors, there is the economic aggravating factor, since it leads to a reduction in wood production, flowering, and fruiting of the affected trees (Wood; Reilly, 2004; Szmidla et al., 2019).

Phoradendron strongyloclados Eichler is a species of wide geographic distribution, occurring in almost the entire Brazilian territory (Reif; Andreata, 2006; Dettke; Caires, 2021). Even so, in the carried out bibliographic survey, no anatomical study on *P. strongyloclados* was found. Therefore, this species is not yet structurally understood.

The knowledge of the anatomical structure of this species is important for understanding the Brazilian flora and the diversity of the genus itself, offering subsidies to differentiate phenotypes within the species and obtain parameters for interspecific comparisons, thus being a valuable taxonomic tool. It also helps in ecological and physiological studies, widely carried out on plants of economic importance and pest control. Finally, it can support works focused on the medicinal use of mistletoes, providing information on possible tissues that produce active principles and better conditions for harvesting and storage (Dôres, 2007). Thus, the present work aimed at carrying out a pioneer study on the anatomical structure of the aerial vegetative organs of *P. strongyloclados*, making use of histochemical inferences for a better understanding of the chemical properties of the analyzed tissues.

Material and Methods

Three individuals of *Phoradendron strongyloclados* Eichler (Viscaceae) that parasitize a tree of the species *Peltophorum dubium* (Spreng.) Taub. (Fabaceae), popularly known as “canafístula”, were studied. The mentioned plants grow on the Vitória da Conquista *Campus* of the Universidade Estadual do Sudoeste da Bahia - UESB. Vitória da Conquista is located at the geographic coordinates 15º 95’ S, 40º 88’ W, 839 meters of altitude, being one of the municipalities in the semi-arid region of Bahia under the influence of a high-altitude tropical climate. The vouch material was deposited in the Universidade Estadual de Santa Cruz - UESC Herbarium, under the registration number 24,111. From the collected individuals, leaf, cataphyll, and stem samples were obtained in primary and secondary structure. For each procedure, three repetitions were performed per organ of each individual studied.

For analysis under the light microscope, free-hand sections were performed with the aid of razor blades, thus obtaining fresh paradermal, transversal and longitudinal cuts of the leaf blade, cataphylls and stem, in primary and secondary structure. In the latter case, radial and tangential longitudinal cuts were also made. For contrast and metachromasia, the sections were stained with Toluidine blue O 0.025% in McIlvaine buffer at pH 4.0 (Vidal, 1977; Ribeiro; Leitão, 2020) for 15 minutes. For observing lipid structures, such as the cuticle, Sudan IV dye was employed (Johansen, 1940). After staining, the sections were washed in distilled water. Part of the sections was also observed without staining to obtain information on the natural colors of the tissues. The slides were mounted with a coverslip and distilled water.

A Leica light microscope, model DM750, equipped with an ICC50HD digital image acquiring system (Leica Microsystems, Wetzlar, Germany) and polarization feature was used for the analysis of the slide set. The images were obtained and processed using the Leica LAS EZ software.

For Scanning Electron Microscopy (SEM) analysis, part of the leaf, cataphyll and stem samples in primary structure was fixed in a solution containing glutaraldehyde and paraformaldehyde (Karnovsky, 1965) for 48 h at 6ºC, washed in distilled water and partially dehydrated up to ethanol 70%. Subsequently, the samples were rehydrated in an ethyl/ketone series, adhered to aluminum stubs and observed in a Quanta 250 scanning electron microscope (FEI Company, Oregon, USA) equipped with a digital image acquiring system, at 12Kv in environmental mode (Bozzola; Russell, 1992).

Results

Leaf

The *Phoradendron strongyloclados* individuals grow in clusters in the canopy of the host tree (Figure 1a). The leaf is persistent, subsessile, elliptical, crass, of dark green color, and with acrodromous venation. Anatomically, it is characterized by having a unistratified epidermis consisting of cells tending to a rectangular shape (Figure 1b, c, e). The cuticle is remarkably thick, displaying a light green

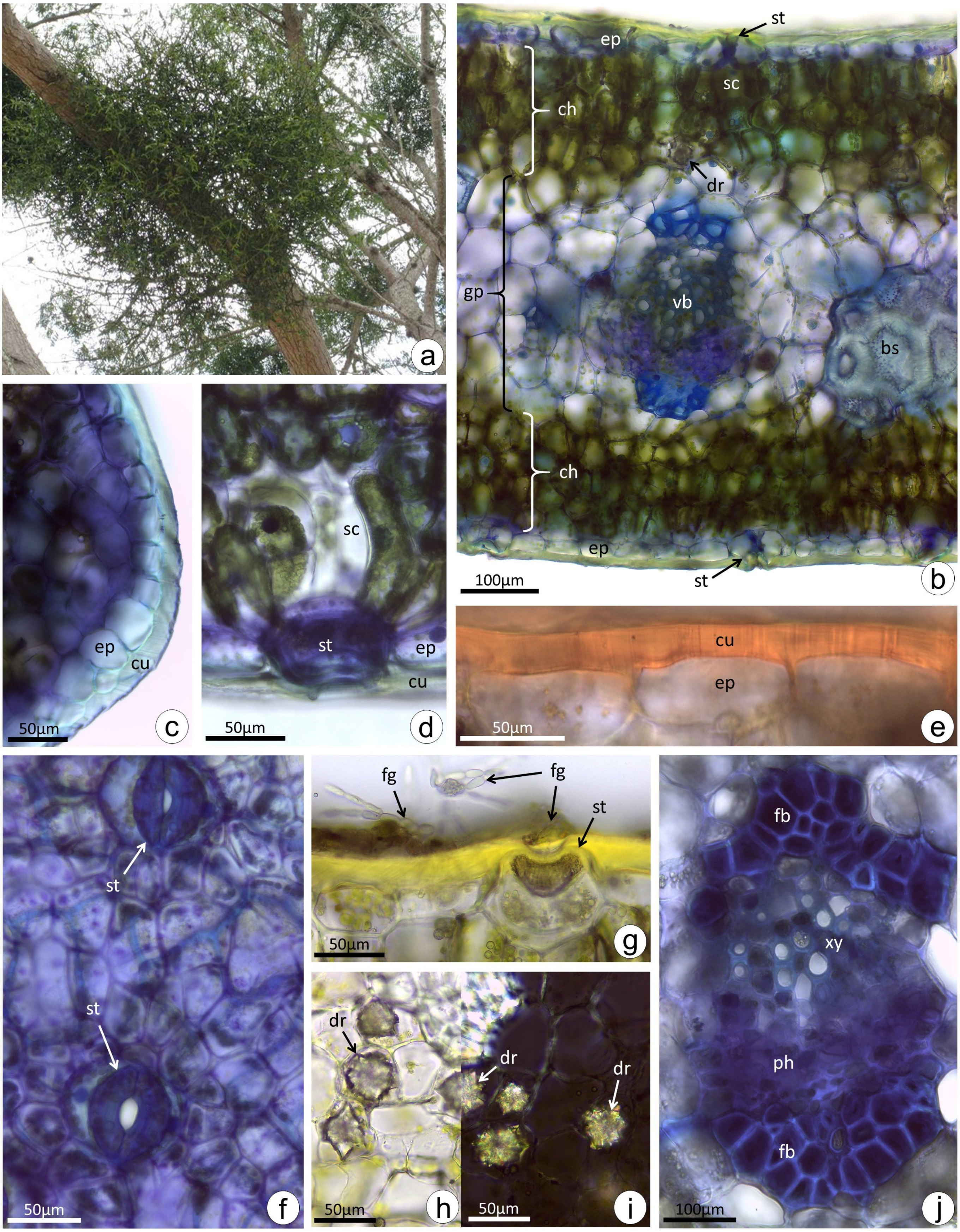

Figure 1. *Phoradendron strongylocIados* in loco (a), and it leaf in cross-sections (a-e, g-j) and in paradermal section (f). a. General aspect of the plant in its habitat. b. Panorama of the mesophyll. c. Leaf edge. d. Detail of the chlorenchyma, showing stomata and substomatic chamber. e. Epidermis stained with Sudan IV. f. Paracytic stomata. g. Fungi presence on the epidermis. h. Mesophyll with druses. i. Mesophyll with druses under polarized light. j. Vascular bundle. Abbreviations: bs - brachysclereids, ch- chlorenchyma, cu- cuticle, dr- druse, ep- epidermis, fb- fibers, fg- fungi, gp- ground parenchyma, ph- phloem, sc- substomatic chamber, st- stoma, vb- vascular bundle, xy- xylem.

coloration with Toluidine blue O at pH 4.0 (TBO) (Figure 1c, d), with an extreme affinity for Sudan IV (Figure 1e).

The stomata are paracytic (Figure 1f) and occur on both sides of the leaf (Figure 1b). They are randomly distributed, without any orientation tendency of the guard cells, being at the same level as the other epidermal cells (Figure 1b, d, g). The content of the guard cells had a higher affinity for TBO than that of the ordinary cells (Figure 1f). Fungal hyphae may grow on the epidermis, even reaching the stomatal ostiole (Figure 1g).

The mesophyll is isobilateral heterogeneous, consisting of four to seven strata of isodiametric cells of ground parenchyma, involved on both sides by two to five strata of chlorenchyma (Figure 1b) whose cells are slightly palisaded in some portions (Figure 1d). Mesophyll cells are compactly arranged, delimiting minimal intercellular spaces, yet the substomatic chambers are relatively large and conspicuous (Figure 1d).

There occur isolated brachysclereids or in small groups, with thick walls that stain bluish-green with TBO (Figure 1b). There also occur idioblasts containing calcium oxalate crystals of the druse type dispersed in the mesophyll (Figure 1b, h, i).

The leaf vascularization consists of approximately nine vascular bundles, similar in size, without highlighting the main vein and without projecting a salience on any of the leaf faces. The bundles are collateral and present fiber hubcaps adjacent to the two conductive tissues. The fibers walls had dark blue to almost black when stained with TBO (Figure 1j).

Cataphyll

Also associated with the nodes, there occur cataphylls, which consist of a small foliate appendage that involves the internode base and has two opposite apices (Figure 2a). Both epidermises are stomata devoid. Their cells are flattened on the adaxial surface. The cuticle of the abaxial epidermis is notably thicker and displays a greenish color with TBO (Figure 2b). The edge of the cataphyll is ornamented by long papillae (Figure 2c, d).

The mesophyll of the cataphyll consists of four to seven layers of chlorenchyma, whose cells are slightly flattened (Figure 2b). The vascular bundles, consisting of xylem and phloem, are diminutive, with fibers only associated with the phloem (Figure 2e). As in the other organs studied here, the presence of brachysclereids (Figure 2f) and druse-containing idioblasts are noticed, although at a lower frequency.

Stem

The *P. strongyloclados* stem follows a pattern where opposing branches are observed coming from the central axis, with up to six branches per node (Figure 3a). It has an herbaceous-stem aspect, although it performs secondary growth and acquires considerable rigidity. The young stem has a rhombi-ellipsoid shape (Figure 3b) and the secondary stem is cylindrical when viewed in cross-section (Figure 3a). The epidermis consists of rectangular cells, whose outer periclinal wall is lined with an extremely thick cuticle that stains light blue with TBO (Figure 3d). The stomata are paracytic, transversely oriented in relation to the organ axis (Figure 3c), and are subtended by evident substomatic chambers (Figure 3d).

In the first expanded internode, the cortex is homogeneous with approximately five to seven strata of chlorenchyma and three innermost strata of ground parenchyma (Figure 3d). In this region also occur a large number of druses (Figure 3d, e). As from the second internode, nearly fully or fully developed brachysclereids also occur (Figure 3d).

In primary structure, the vascular system is formed by open collateral vascular bundles arranged in the eustelic pattern (Figure 3b, e). The pith is constituted by ground parenchyma with isodiametric round outlined cells. Similar to the cortex, there are druses and groups of brachysclereids (Figure 3f).

When the stem is in secondary structure (Figure 4a), the epidermis is persistent and the cuticle progressively increases in thickness as the stem ages. There is no periderm formation, only lenticels (Figure 4b). The cortical cells are more expanded. The chlorenchyma remains in its dark green color (Figure 4b).

The wood is the most developed tissue of the stem, being extremely rigid due to the strong presence of lignified fibers (Figure 4c), especially in the portions closest to the point of insertion into the host (Figure 4a). In this region, there occurs the sclerification of the pith, whose cells can accumulate prismatic crystals and whose cell walls assume the typical bluish-green coloration with TBO (Figure 4d). The axial parenchyma is diffuse to diffuse-in-aggregates (Figure 4a, c) and the rays are heterocellular, with procumbent, square and up right cells (Figure 4e), and multiseriate in width (Figure 4f), with occurrence of calcium oxalate crystals of the prismatic-type (Figure 4e, g). The vessel elements are short and possess simple perforation plate (Figure 4f), and the vessels can occur isolated or in long radial rows (Figure 4a, c).

Discussion

In *Phoradendron strongyloclados*, the walls of the epidermal cells of the leaf and stem assumed moderate metachromasia with Toluidine blue O pH 4.0 (TBO), expressed by the purple coloration. As TBO is a cationic dye with a planar structure, metachromasia reveals a high availability of anionic radicals (Vidal, 1977; Figueiredo et al., 2007), which indicates a hydrophilic nature (Ribeiro; Leitão, 2020).

The leaf cuticle, like the other studied organs, is characterized by being thick, and by its strong affinity for Sudan IV, revealing its lipidic nature (Holloway, 1982). The low affinity for TBO, assuming a light greenish-blue color throughout its extension, is typical for cuticles of fresh sections submitted to this dye (Ribeiro; Leitão, 2020), demonstrating low availability of anionic radicals, which corroborates its hydrophobicity. In addition to its high resistance to losing water to the environment, the cuticle can protect against excessive light or solar radiation (Alquini et al., 2003), which is expected to be advantageous for a tree canopy parasite exposed to direct sunlight radiation.

The mechanical rigidity provided by the robust cuticle can be a defense against the attack of pathogens. A large hyphae number was observed in the epidermal region, however, no pathological damage was observed in the inner tissues. Despite the stomata being an access route, it is known that host-pathogen specificity is still required for the attack to take place (Stangarlin et al., 2011). The cuticle characteristics of *P. strongyloclados* corroborate with other

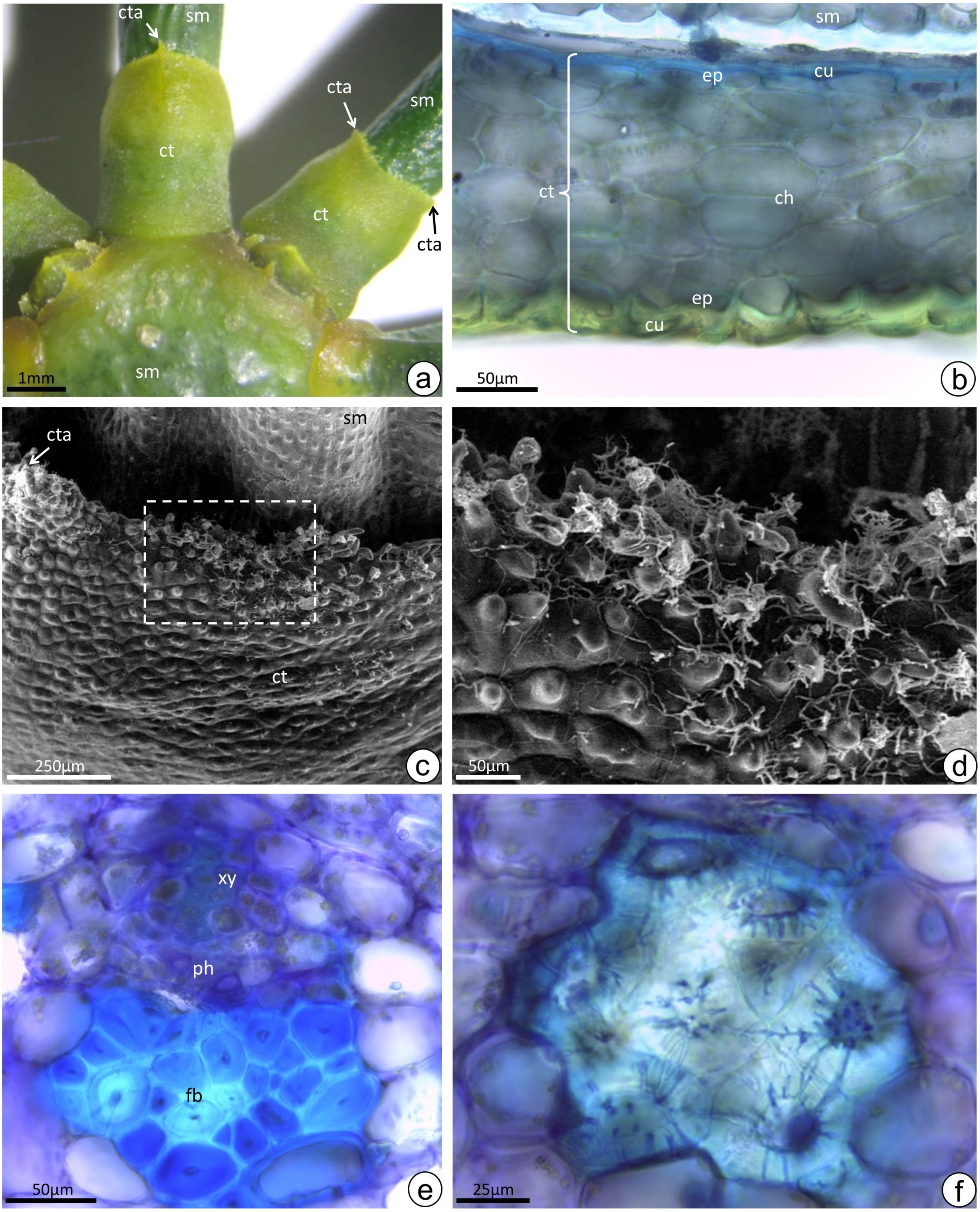

Figure 2. Cataphyll of *Phoradendron strongyloclados* in macro view (a), in cross-sections (b, e, f) and under scanning electron microscopy (c, d). a. Cataphylls. b. Cross-section of the cataphyll involving the stem. c. Panorama of the cataphyll involving the stem. d. Detail of the cataphyll edge, indicated by the rectangle in c. e. Cross-section of the cataphyll in its proximal region, evidencing a vascular bundle. f. Brachysclereids. Abbreviations: ch- chlorenchyma, ct- cataphyll, cta- cataphyll apex, cu- cuticle, ep- epidermis, fb- fibers, ph- phloem, sm- stem, xy- xylem.

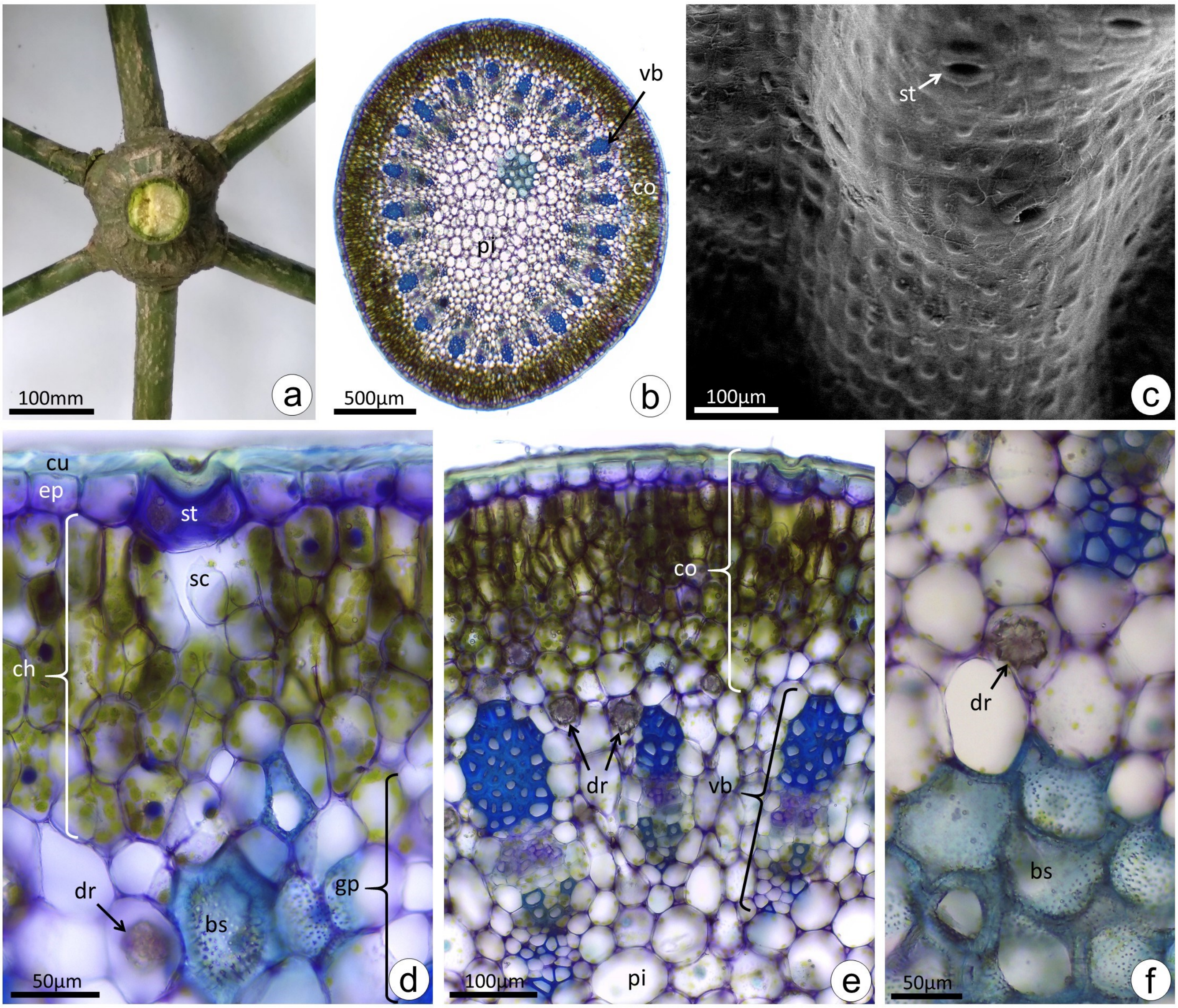

Figure 3. *Phoradendron strongyloclados* stem in primary (b-f) and secondary structure (a) in macro view (a), cross-sections (b, d-f), and under scanning electron microscopy (c). a. Macro view of a node with six branches. b. Overview. c. Stomata transversal orientation in the stem. d. Detail of the cortex. e. General aspect of the cortex, three vascular bundles, and the part of the periphery of the pith. f. Detail of part of the pith. Abbreviations: bs- brachysclereids, ch- chlorenchyma, co - cortex, cu- cuticle, dr- druse, ep- epidermis, gp- ground parenchyma, pi- pith, sc- substomatic chamber, st- stoma, vb- vascular bundle.

reports on the genus, such as those of Gómez-Sánchez et al. (2011) for *P. brachystachyum* (DC.) Eichler, *P. carneum* Urb. and *P. forestierae* B.L.Rob. & Greenm., which could be a pattern for the group.

The paracytic stomata are typical of the mistletoes, as in the order Santalales (Metcalfe; Chalk, 1957). This terminology was first described for this type of stoma by these authors and was later used in several subsequent works on this group (Venturelli, 1984; Varela; Gurni, 1995; Varela et al., 2001; Varela; Gurni, 2003; Wilson; Calvin, 2003; Varela et al., 2004; Ferreira et al., 2007; Dettke; Milaneze-Gutierre, 2009a, b; Gómez-Sánchez et al., 2011; Caires; Leitão, 2015; Gallego et al., 2018).

The *P. strongyloclados* stem stomata orientation, transversely to the organ axis, is reported in several species of the genus (Cannon, 1901; Dettke; Milaneze-Gutierre, 2009b), being characteristic of Viscaceae/Loranthaceae (Metcalfe; Chalk, 1957). However, in *P. perrottetii* (DC.) Eichler, the stem stomata can be randomly oriented in some regions (Dettke; Milaneze-Gutierre, 2009b).

The *P. strongyloclados* mesophyll consists of rounded to slightly palisade cells, in a compact arrangement, delimiting few intercellular spaces. This type of adaptation may be associated with a greater ability to tolerate water stress (Evert, 2006).

The vascular bundles are open collateral and their cellular types showed different affinities for TBO. The sieve tube elements and the companion cells had their walls stained in an intense purple, resulting from metachromasia, indicating an expressive pectic fraction (Canteri et al., 2012). In the analyzed leaves, the xylem and the phloem fibers had their walls stained in more bluish tones, suggesting less lignification (Ribeiro; Leitão, 2020).

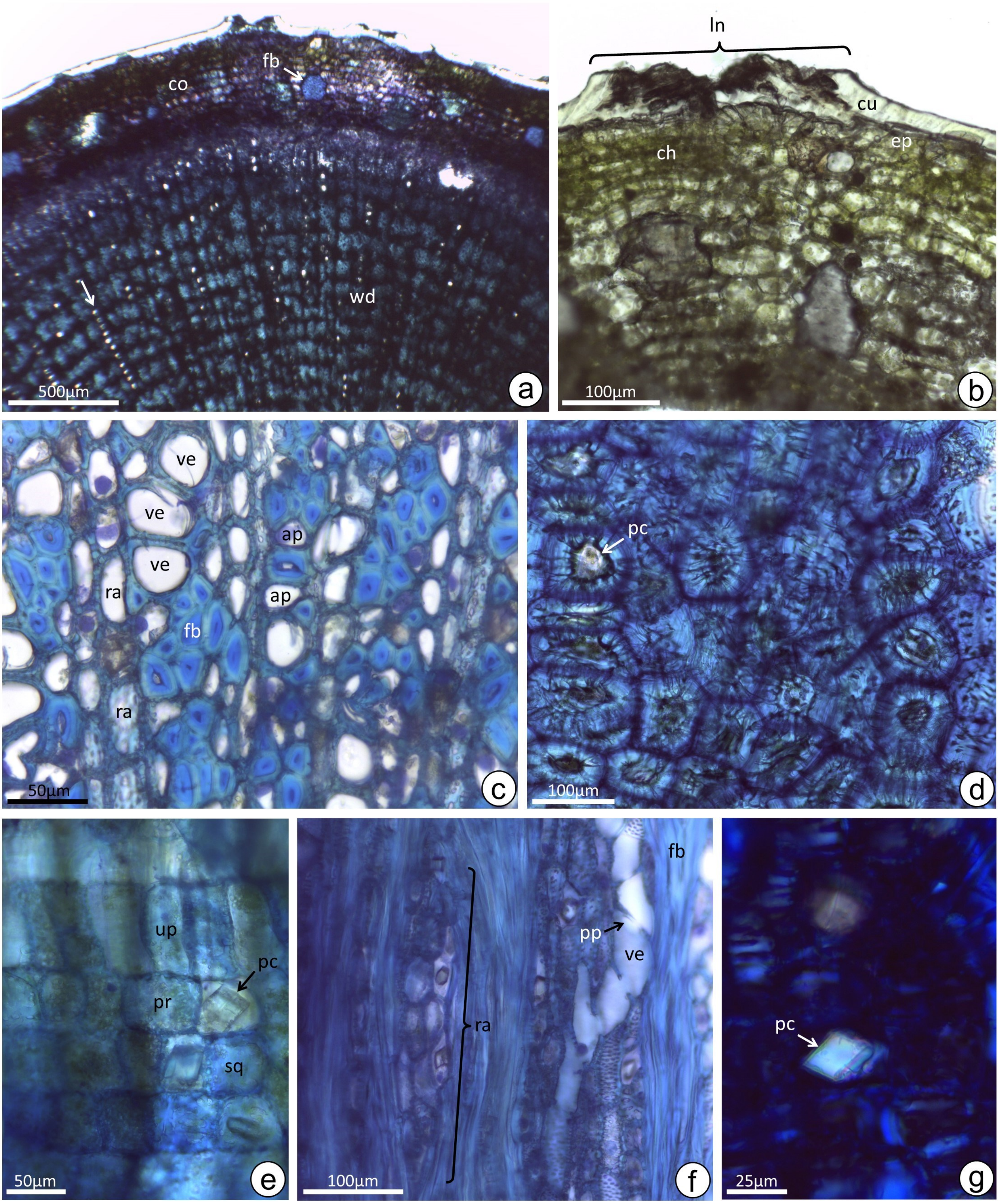

Figure 4. *Phoradendron strongyloclados* stem in secondary structure in cross-sections (a-d), radial longitudinal-sections (e, g), and tangential-section (f). a. General aspect of the stem in secondary structure, showing vessels in a radial row (arrow). b. Cortex with chlorenchyma and lenticel. c. Wood detail. d. Sclerified pith. e. Xylematic ray evidencing the cellular types. f. Xylematic ray evidencing the number of series. g. Detail of a prismatic crystal in the ray, under polarized light. Abbreviations: ap - axial parenchyma, ch- chlorenchyma, co- cortex, cu- cuticle, ep- epidermis, fb- fibers, ln- lenticel, pc- prismatic crystal, pp- perforation plate, pr- procumbent cell, ra- ray, sq- square cell, up- upright cell, ve- vessel element, wd- wood.

The cataphyll is a typical structure in Viscaceae (Kuijt, 2013), but is little known anatomically in the group (Kuijt, 2003). In the present work, it was verified that this structure has a homogeneous internal organization, constituted by chlorenchyma, indicating photosynthetic capacity. The *P. strongyloclados* cataphyll gathers characteristics that are slightly different from those observed in the other studied organs, such as, for example, the epidermis, which has flat cells and a highly papillose cuticle, especially in the border region. This type of projection has been described for other hemiparasites (Varela et al., 2001; Varela; Gurni, 2003) and even for other species of the genus, but normally in the epidermal cells of the stem (Dettke; Milaneze-Gutierre, 2009b) and in the leaf (Varela et al., 2004; Ferreira et al., 2007), with no description for the cataphyll to the moment.

Although relatively inconspicuous, vascular bundles occur in the cataphylls of *P. strongyloclados*. This type of foliaceous appendage, in general, presents simple anatomical characteristics, as reported in vascularized cataphylls of *Mapania sylvatica* Aubl. (Cyperaceae), with plain epidermal cells, thick cuticle, and absence of stomata (Silva et al., 2014). While the cataphyll of *Smilax polyantha* Griseb. (Smilacaceae) is devoid of vascularization (Martins; Appezzato-da-Glória, 2006). According to Kuijt (1959), there is no consensus regarding the definition of cataphyll for Viscaceae. Some authors describe them as reduced leaves or sterile branches. As the *P. strongyloclados* cataphyll has certain similarities with cataphylls described for species that are not even part of the Viscaceae family, it is coherent to use this name for this structure. Due to the fact they have two apices, it can be concluded that the cataphyll of *P. strongyloclados* is bilobate, possibly being the fusion of two foliaceous structures. Finally, studies of the anatomical structure of the cataphylls for the different species of *Phoradendron* and in Viscaceae should be stimulated, in order to analyze their function and evolutionary origin.

The thickened walls of the vessel elements, of the stem fibers in secondary structure, of the brachysclereids found in the different organs, as well as of the pith parenchyma of the stem in secondary structure, assumed a greenish color with TBO. Such coloration is typical of lignified walls when submitted to this dye (O'Brien et al.,1964; Ribeiro; Leitão, 2020), being, therefore, a valuable histochemical inference for the presence of lignin impregnating the walls of the aforementioned cell types.

Brachysclereids and fibers, as they are cells with highly lignified walls, are rigid and, therefore, they are structures often related to sustentation. Furthermore, the fibers associated with the phloem may also be an indicative of a protective function against pathogen attacks on this tissue (Medeiros et al., 2003), since it is a highly caloric source due to the presence of sucrose. While the *P. strongyloclados* brachysclereids, due to their late maturation and occurrence in internal tissues, isolated or in small groups, may not act much in the sustentation, with their function being, therefore, difficult to interpret using the data obtained in the present work.

It was observed that a periderm does not develop in the *P. strongyloclados* stem in secondary structure, there is, however, only the lenticels formation. The lack of periderm is typical for the genus (Kuijt, 2003). Dettke and Milaneze-Gutierre (2009b) point out that this characteristic is a possible synapomorphy of the group, highlighting the need for further studies in this regard. For now, it can be speculated that the development suppression of an opaque coating system may be directly related to the maintenance of full photosynthetic activity of the subjacent cortical chlorenchyma, allowing similar levels of light rays penetration in this tissue during the stem secondary growth. Also, the continuity of cuticle secretion even during secondary growth may be a strategy to maintain its efficiency in waterproofing, while it is stretched by the stem circumference increase. This species is morphologically characterized by having leaves that are relatively small and spaced by long internodes. Therefore, the sum of the stem surface corresponds to an important fraction of the entire *P. strongyloclados* shoot, and, in fact, the maintenance of photosynthetic tissues in the older stems can be interpreted as a valuable strategy for the photosynthetic efficiency of a plant with a small leaf surface.

The stem wood of *P. strongylocaldos*, as well as the one reported for *P. linearifolium* Eichler, *P. obtusissimum* (Miq.) Eichler, *P. perrottetii*, *P. piperoides* (Kunth) Trel., and *P. quadrangulare* (Kunth) Griseb. (Dettke; Milaneze-Gutierre, 2009b) form a continuous ring. While in *P. flavescens* var *macrophyllum* Engelm. (= *P. serotinum* subsp. *macrophyllum* (Engelm.) Kuijt) is reported a non-usual secondary growth very distinct due to the production of only parenchymatic cells by the interfascicular cambium, conferring the aspect of elongated and individualized vascular bundles to the secondary structure (Calvin, 1967). In *P. villosum* (Nutt.) Engelm. (= *P. serotinum* subsp. *tomentosum* (DC.) Kuijt) is reported a little fibrous wood and, consequently, a condition of stem fragility of this species (Cannon, 1901), in contrast to what was observed in *P. strongyloclados*. The simple perforation plate observed in the vessel elements in the present work is reported for other representatives of the genus (Ashworth; Santos, 1997), being typical for Viscaceae/ Loranthaceae (Rizzini, 1952; Metcalfe; Chalk, 1957).

In the *P. strongyloclados* tissues were found crystalliferous cells containing druse or single crystals. Such crystals consist of calcium oxalate. It is known that their formation is related to calcium regulation, plant protection against herbivory, and metal detoxification (Franceschi; Nakata, 2005). In addition, it has even been reported that crystal formation in mistletoes occurs as a result of increased calcium levels within the plant (Stahl, 1919). The occurrence of prismatic crystals in the rays can be of taxonomic importance, and this feature is also found in *P. pauciflorum* Torr. (= *P. bolleanum* (Seem.) Eichler) and *P. serotinum* subsp. *tomentosum*, but absent in *P. californicum* Nutt., and *P. serotinum* subsp. *macrophyllum* (Ashworth; Santos, 1997). These authors even used this feature to elaborate a dichotomous key of wood anatomical features to distinguish these four native taxa from California.

Conclusion

In the light of all the observations of the anatomical characteristics and histochemical inferences, such as the compact arrangement of parenchyma cells, thick cuticle, high tissue lignification, and the noticeable low surface/volume ratio due to the small, fleshy, and spaced leaves, it is noticed that *P. strongyloclados* is a xerophyte. The maintenance of its green parts in secondary structure appears to be a strategy to compensate for the low leaf surface area. Its cataphylls, although simple, are vascularized and their function and taxonomic potential are still poorly understood. The anatomical features brought to light here may provide taxonomic support.

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Authorship Contributions

Conceptualization: CAEL, CSC. Data curation: MGO, CAEL. Formal Analysis: MGO, CAEL. Investigation: MGO. Methodology: CAEL, MGO. Project administration: CSC. Resources: CAEL. Supervision: CAEL, CSC. Validation: CAEL, CSC. Visualization: MGO. Writing – original draft: MGO. Writing – review & editing: CAEL, CSC, MGO.

Conflict of Interest

The authors declare that there are no conflicts of interest to report.

Data Availability

The complete set of data analyzed during the current study are presented in the body of the manuscript.

Ethical Compliance

Not applicable.

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