

**Comparative anatomy of the roots in development of nine epiphytes monocots from Brazilian Atlantic Forest**

**Anatomia comparada das raízes em desenvolvimento de nove monocotiledôneas epífitas da Mata Atlântica Brasileira**

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**ABSTRACT**

This study describes and compares root anatomical adaptations in nine monocots: Orchidaceae (*Brasiliorchis chrysantha*, *Gomesa flexuosa*, *Isochilus linearis*, *Leptotes bicolor* and *Trichocentrum pumilum*), Bromeliaceae (*Aechmea distichantha*, *Billbergia nutans* and *Vriesea flava*) and Araceae (*Philodendron propinquum*) epiphytes in Parana state, Brazil. Orchidaceae and Bromeliaceae have velamen radicum. Evident exodermis and endodermis in all species, cortex in the Bromeliaceae divided in three parenchyma. The immature and mature regions of the roots are different between species. Anatomical characteristics of roots related to epiphytism, such as velamen, tilosome, thick exodermis and endodermis, tracheoid idioblasts, idioblasts with raphides and aerenchyma are presents. In species that grow in the sunniest strata, it was observed that the deposition of lignin in the cell wall of the exoderm and endoderm in "O" already occurs just above the differentiated region from the primary meristems. The number of strata of the velamen was higher in these species, reaffirming that the environmental pressure throughout the evolutionary process selected genotypes that are more resistant to conditions with less water availability.

**Keywords:** Araceae, Bromeliaceae, Monocots, Orchidaceae, Velamen.

## RESUMO

Este estudo descreve e compara adaptações anatômicas radiculares em nove monocotiledôneas: Orchidaceae (*Brasiliorchis chrysantha*, *Gomesa flexuosa*, *Isochilus linearis*, *Leptotes bicolor* e *Trichocentrum pumilum*), Bromeliaceae (*Aechmea distichantha*, *Billbergia nutans* e *Vriesea flava*) e Araceae (*Philodendron propinquum*) epífitas do estado do Paraná, Brasil. Orchidaceae e Bromeliaceae apresentam velame. Exoderme e endoderme evidentes em todas as espécies, córtex nas Bromeliaceae divididos em três parênquimas. As regiões imaturas e maduras das raízes são diferentes entre as espécies. As características anatômicas das raízes relacionadas ao epifitismo presentes são: velame, tilossomo, exoderme e endoderme espessas, idiosblastos traqueoidais, idiosblastos com ráfides e aerênquima. Nas espécies que crescem nos estratos mais ensolarados, observou-se que a deposição de lignina na parede celular da exoderme e endoderme em "O" já ocorre pouco acima da região diferenciada a partir dos meristemas primários. O número de estratos do velame foi maior nessas espécies, reafirmando que a pressão ambiental ao longo do processo evolutivo selecionou genótipos mais resistentes a condições com menor disponibilidade hídrica.

**Palavras-chave:** Araceae, Bromeliaceae, Monocotiledônes, Orchidaceae, Velame.

## 1 INTRODUCTION

Epiphytes are commonly found in tropical rain forests (Kress 1986). Of the families represented by at least one habitually epiphytic species in the Neotropics, the Orchidaceae are by far the most important with ten times as many epiphytic neo-tropical species as runners-up Araceae and Bromeliaceae (Gentry & Dodson 1987).

Orchidaceae comprise approximately 850 genera and 20,000 species (Dressler 1993). In Brazil, the family is represented by 250 genera and 2,760 species and is widespread throughout the country (Flora do Brasil 2020a, in construction). The species of this group have very specialized features that have allowed them to adapt to different environments; many grow in temperate regions, but they are most abundant and diverse in the tropics (Dressler 1981, 1993, Englert 2000).

Bromeliaceae comprise 3,172 species and 58 genera, which are almost exclusively distributed in the Neotropics (Luther 2008). In Brazil there are 50 genera and 1,394 species (Flora do Brasil 2020b, in construction). The group is particularly suitable for epiphytic plant life, many species are endemic to certain habitats or regions, and species richness is greatest in the Atlantic Forest ecosystem (Smith & Downs 1974, Fontoura 1995, Luther 2008).

Araceae comprise about 105 genera and over 3,500 species, which are distributed mainly in tropical regions and are mostly epiphytes (about 86%) (Croat 1998). In Brazil, the family is represented

by 47 genera and 519 species distributed throughout the country (Flora do Brasil 2020c, in construction).

As in other monocots, the primary root or radicle of Araceae (Coelho 2000) and Bromeliaceae (Silva & Scatena 2011) has a short life, and in the adult plant the roots are adventitious and develop from stem tissues. In orchids, undifferentiated embryos form a polarized structure called a protocorm; the posterior extremity of the protocorm forms trichomes similar to the absorbent trichomes of roots, while adventitious roots are formed endogenously in the protocorm tissue (Silva & Milaneze-Gutierrez 2004b). Thus, the anatomical descriptions of the adult roots of the species in these families are based on their adventitious roots, which may have a uniseriate epidermis, with a developed absorbent hair region (Tomlinson 1969), or a pluristratified epidermis that is the velamen (Pita & Menezes 2002, Segecin & Scatena 2004, Lobo *et al.* 2008).

The thickness of the walls of the velamen and exodermis cells varies depending on the relative air humidity (Dycus & Knudson 1957). Benzing *et al.* (1982) reported that the walls of most velamen cells are thin and often have perforations that allow water passage, but that the walls of cells in the inner layer of the velamen are thick. Further, over each passage cell there is the fibrous body that condenses atmospheric moisture prior to its passage to the underlying absorbing cells (Benzing *et al.* 1982). Pridgeon *et al.* (1983) called the fibrous body a tilosome.

The velamen and exodermis of Orchidaceae roots have been studied extensively. Most species of Orchidaceae have velamen with or without tilosomes, an exodermis with passage cells, and endodermis cells with U-shaped wall thickenings (Pridgeon *et al.* 1983, Stern *et al.* 2004). In addition, in the majority of species the root is a polyarch and the medulla is well developed (Oliveira & Sajo 1999).

According to Oliveira (2011) the cortex of aerial roots of Araceae consists of parenchyma cells and may have intercellular spaces and a sheath (sclerenchymatous ring); the endodermis, which is formed by a layer of flat or cylindrical parenchyma cells, may exhibit secondary thickening; and in the central cylinder, the xylem and phloem are alternate and surrounded by fibers or can be lobed-shaped with the xylem and phloem in an alternate and radial arrangement.

The cortex of the adventitious roots of Bromeliaceae is delimited by an exodermis and endodermis, with several layers of parenchyma cells, intermediated by a sclerotic cylinder (Krauss 1949, Tomlinson 1969). Lobo *et al.* (2008) have described that the cortex of the adventitious root of *Dyckia brevifolia* and *D. distachya* is composed of exodermis, parenchyma, interspersed with a sclerenchymal ring, and endodermis.

Zotz & Winkler (2013) highlighted the adaptive characters of epiphytic taxa in these families that are related to the environment in which these species grow, such as absorptive trichomes in bromeliads and the velamentous roots of aerial roots of orchids, aroids and other monocotyledons and the presence of impermeable layers that prevent loss of water after being absorbed by these structures. Given that many monocot families have epiphytic species, studies are needed to compare the anatomical adaptations of epiphytes belonging to different families native to the same location. In order to describe the anatomy of the roots of epiphytic species of the Orchidaceae, Bromeliaceae and Araceae families that occur in the same vegetation formation and whose adaptive anatomical structures have long been described in the literature, we would like to answer with this study the following questions: 1) The number of layers of the velamen and exodermis can be related to the stratum in which the species is growing most often? Species common to strata that receive a higher incidence of light differentiate impermeable layers more quickly, such as, for example, the “O” thickening in the exodermis and endodermis?

## 2 MATERIAL AND METHODS

In this study we analyzed the roots of nine monocots: *Brasiliorchis chrysantha* (Barb.Rodr.) R.B.Singer et al., *Gomesa flexuosa* (Lodd.) M.W.Chase & N.H.Williams, *Isochilus linearis* (Jacq.) R. Br., *Leptotes bicolor* Lindl. and *Trichocentrum pumilum* (Lindl.) M.W.Chase & N.H.Williams (Orchidaceae), *Aechmea distichantha* Lem., *Billbergia nutans* H. Wendl. and *Vriesea flava* And. Costa, H. Luther & Wand (Bromeliaceae) and *Philodendron propinquum* Schott (Araceae). The classification of the epiphytic habit follows Benzing (1990) (Table 1).

The samples were collected in 2011 in an area of suppressed vegetation near the Mauá Hydroelectric Plant, ecotone region between the Semideciduous Seasonal Forest and Araucaria forest located between the municipalities of Telêmaco Borba and Ortigueira, in Parana State, Brazil (24°03'32,8"S, 50°42'30,1"W, 1020 m elevation). The habitat (stratum / luminosity) from which the samples were collected are shown in table 1. Live specimens were brought to Maringá, in northwestern Paraná (23°25'S, 51°57"W, 542 m elevation), and cultivated at Maringá State University (UEM). The specimens were grown under a screen that produced 50% shade, in pots with a porous substrate (charcoal and pine bark), and watered daily with a rain jet irrigation system to maintain a high relative air humidity that is similar to the natural habitat (Araucaria forest) of the species. For each species, root samples of about six months, in contact with the substrate, kept in the above environment were fixed in FAA 70 (50ml Formaldehyde 37%, 50ml Ethanol 70% and 900ml Glacial Acetic Acid) and then

stored in 70% ethanol (Johansen 1940) and the vouchers (whole specimens with flowers) deposited in the Herbarium of the Maringá State University (HUEM) (Table 1).

For the anatomical study, samples were collected from at least three individuals of each species. The cross and longitudinal sections of the immature (distal root) and mature (proximal root) regions of the roots were made freehand using a sodium hypochlorite (30%) clean shaving blade stained with a mixture of Safranin and Astrablue and mounted on semi-permanent histological slides with glycerin gelatin (Kaiser 1880, Burger & Richter 1991).

Photomicrographs were taken with a Leica ICC 50 microscope. The scales in the illustrations were obtained using the same optical conditions for each sample.

Transverse and longitudinal sections of mature and immature regions and the surface of the roots were analyzed using scanning electron microscopy (SEM). The samples were fixed in glutaraldehyde and dehydrated in a graded series of ethanol for 15 minutes in each solution. The material was then dried with a critical point dryer (Baltec PCD 030) using CO<sub>2</sub> (Horridge & Tamm 1969). Subsequently, they were placed on metal stubs and sputter coated using a Shimadzu IC-50. The SEM analysis was made using a Shimadzu SS 550 microscope. The scales of electron micrographs were directly printed on the photos.

### 3 RESULTS

In the species of Orchidaceae (Fig. 1-2, 4a-j), and Bromeliaceae (Fig. 3a-I, 4k-p) the roots have velamen, but in the Araceae species (Fig. 3J-L, 4q-r) the epidermis is unistratified. There is an evident exodermis and endodermis in all species and the cortex in the Bromeliaceae species is divided into external, middle and inner parenchyma (Fig. 1a-l, 2a-u, 3a-i, 4a-p).

Among the species, there is variation in the root structure (number of cell layers and the structure of the cell walls). Based on the development stage of the root, immature (distal region) and mature (proximal region), the number of cell layers in the velamen varies in some species and in others it loses the same [see Table 1 and illustrations: *Brasiliorchis chrysantha* (Fig. 1a-b, 2a-c), *Gomesa flexuosa* (Fig. 1c-e, 2d-g) *Isochilus linearis* (Fig. 1f-h, 2h-m), *Leptotes bicolor* (Fig. 1i-j, 2n-q) *Trichocentrum pumilum* (Fig. 1k-l, 2r-u) *Aechmea distichantha* (Fig. 3a-c) *Billbergia nutans* (Fig. 3d-f) *Vriesea flava* (Fig. 3g-i)].

In most of the studied Orchidaceae species the velamen has radially elongated cells represented only by the cell walls with a variable secondary thickening of suberin and lignin. The striations of the cell wall are thin (*Brasiliorchis chrysantha*) (Fig. 2a-c) to thick (*Isochilus linearis* and *Gomesa flexuosa*) (Fig. 2h-j, 2d-g), more or less anastomosed, helicoidal lines. In older areas of the root the secondary

thickening increases, accentuating this aspect that can vary from reticulated (*B. chrysantha*, *I. linearis* and *Leptotes bicolor*) (Fig. 2c, 2i, 2q) to slightly fluted (*G. flexuosa*) (Fig. 2g) or striated (*Trichocentrum pumilum*) (Fig. 2s).

In *Brasiliorchis chrysantha* and *Gomesa flexuosa* the cells last layer of the velamen are smaller and do not elongate in a radial direction (Fig. 2b-c, 2e-g); however, the underlying cells are radially expanded. In *Isochilus linearis* the first layer of the velamen, the cells last layer of the velamen, has periclinally elongated cells with a continuous thickening of suberin in the inner periclinal walls; the suberin thickening is discontinuous in the anticlinal walls (Fig. 2i-m).

In *Leptotes bicolor*, in both immature and mature roots, the velamen cells are isodiametric in transverse and longitudinal section (Fig. 1i-j, 2n-o) and have anastomosed helical secondary thickenings that give the walls a striated appearance (Fig. 2n-o). In the cells last layer of the velamen, incomplete anastomoses give the cells a perforated appearance (Fig. 2p-q).

In *Trichocentrum pumilum* the cells underlying the velamen are larger than the velamen cells and are stretched radially (Fig. 1k-l, 2r-u). In younger areas the cell walls of the cells last layer of the velamen have discontinuous secondary thickening (Fig. 2r, t) but in older areas they are continuously thick and have a striated appearance (Fig. 2s, u). Irregular fungal hyphae were observed in *Brasiliorchis chrysantha*, *Gomesa flexuosa*, *Isochilus linearis* and *Leptotes bicolor* in the regions where the roots were in contact with the substrate (Fig. 1k).

In the bromeliads *Aechmea distichantha* (Fig. 3a-c), *Billbergia nutans* (Fig. 3d-f) and *Vriesea flava* (Fig. 3g-i), the velamen cells are isodiametric in cross section, elongated in longitudinal section, and have no secondary thickening. The cells last layer of the velamen in *A. distichantha* (Fig. 3a-c) and *B. nutans* (Fig. 3d-f) has absorbent hairs in the regions where the roots were in contact with the substrate.

Table 1. Anatomical characteristics of the roots, classification, and stratum of occurrence/presence of light of nine epiphytic species native of Paraná state, Brazil.

Anatomical characteristics Region of root	Number of velamen layers		Number of cortex layers		Exodermis thickening		Endodermis thickening		N° xylem and phloem poles		Habitat			Voucher HUEM
	Imm.	Mat.	Imm.	Mat.	Imm.	Mat.	Imm.	Mat.	Imm.	Mat.	Type	Strat	Lumi	
Orchidaceae														
<i>Brasiliorchis chrysantha</i>	5-7	8-10	8-9	8-9	U	U	O	O	16-20	21-25	Hol	H	Su	28079
<i>Gomesa flexuosa</i>	2-4	5-7	5-6	5-6	U	O	O	O	11-15	16-20	Hol	M	Su	27895
<i>Isochilus linearis</i>	2-4	2-4	13-15	15-17	U	U	O	O	11-15	11-15	Hol	M	Sh	20482
<i>Leptotes bicolor</i>	2-4	2-4	7-8	7-8	U	U	O	O	6-10	6-10	Hol	M	Sh	28080
<i>Trichocentrum pumilum</i>	2-4	2-4	7-8	7-8	U	O	O	O	6-10	11-15	Hol	M	Sh	28081)
Bromeliaceae														
<i>Aechmea distichantha</i>	5-7	11-12	12	12	O	O	O	O	16-20	16-20	Hol/ Ter	L/M	Su/Sh	28578
<i>Billbergia nutans</i>	5-7	8-10	4-8	4-8	O	O	U	O	6-10	11-15	Hol	M	Sh	27894
<i>Vriesea flava</i>	2-4	5-7	3	9	O	O	O	O	11-15	26-30	Hol	L	Sh	27892
Araceae														
<i>Philodendron propinquum</i>	Absent		9	9	O	O	O	O	11-15	11-15	Hem	L	Sh	28577

Imm.: immature region; Mat.: mature region. Type: Hem: Hemiepiphyte; Hol: Holoepiphyte; Ter: terrestrial, according Benzing (1990). Strat: Stratum: (H: high, M; medium, L: low). Lumi: Luminosity (Su: sun; Sh: shade).

In *Philodendron propinquum* the epidermis cells are isodiametric and elongated in cross and longitudinal section, respectively; absorbent hairs occur in these cells in the regions where the roots were in contact with the substrate (Fig. 3j-l), which are absent in older regions (Fig. 3k).

The root cortex of the Orchidaceae and Araceae species is differentiated into an exodermis, cortical parenchyma and endodermis. In *Brasiliorchis chrysantha* (Fig. 1a-b, 2d-e), *Gomesa flexuosa* (Fig. 1c-e, 2d-e), *Isochilus linearis* (Fig. 1f-h, 2h-j), *Leptotes bicolor* (Fig. 1i-j), and *Trichocentrum pumilum* (Fig. 1k-l, 2r-s) the exodermis is uni-stratified and in *Philodendron propinquum* it has two or three layers (Fig. 3j-k).

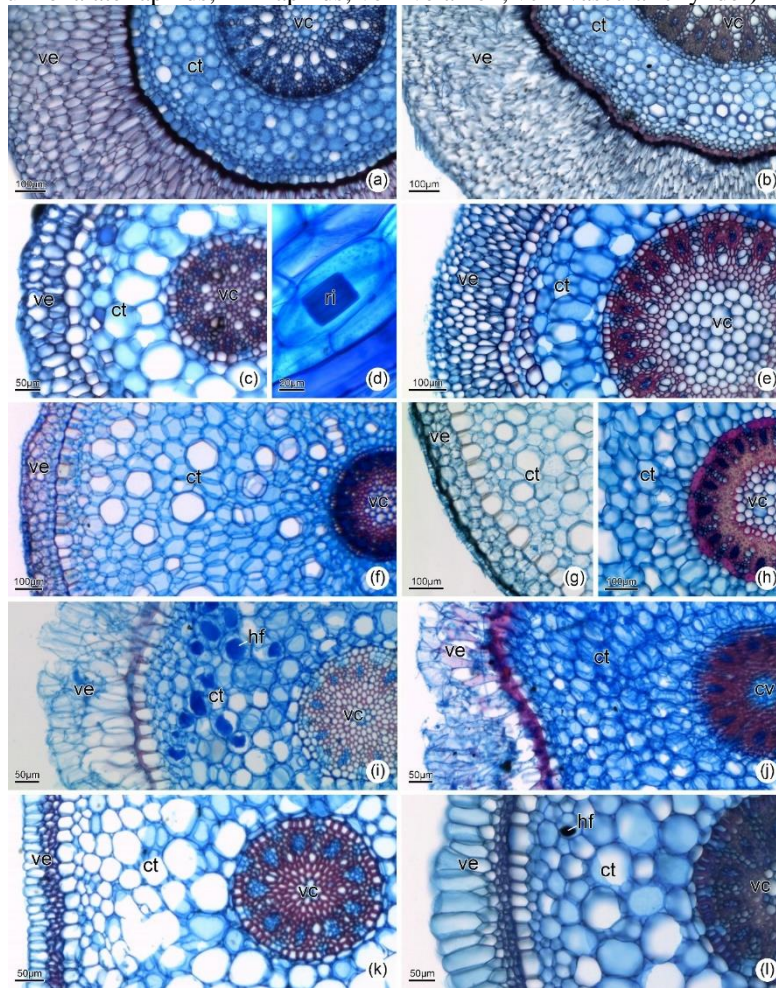
In the three species of Bromeliaceae the cortex is differentiated into an exodermis, cortex and endodermis (Fig. 3g-h, a-b, d-e). The exodermis is pluristratified and comprises lignified cells. The number of exodermis layers increases as the root becomes older; in *V. flava* the cell layers increase from four to seven, in *A. distichantha* from two to five, and in *B. nutans* from two to nine. The initial parenchymatous median cortex becomes sclerenchymatous in older regions of *V. flava* (Fig. 3g-h) and *B. nutans* roots (Fig. 3d-e). The inner cortex consists of aerenchyma and the endodermis. The endodermis, in older regions, has cells with lignified O-shaped wall thickenings. In the external and median cortex, in both immature and mature roots, intercellular spaces are less evident.

In all of the studied species the exodermis has cells that are isodiametric in cross section and elongated in longitudinal section; for both sections, the passage cells are isodiametric in shape. In all of the Orchidaceae, in the younger regions of the root the wall thickening of the exodermis cells is U-shaped in the external periclinal and in the anticlinal walls, except for the passage cells (Fig. 2h, j, a, d, r, n). In older regions the U-shaped thickening remains in *Isochilus linearis* (Fig. 2i) and accentuates in *Brasiliorchis chrysantha* (Fig. 2b) and *Leptotes bicolor* (Fig. 1j). In *Gomesa flexuosa* and *Trichocentrum pumilum* this thickening becomes O-shaped in older regions (Table 1).

In Bromeliaceae and Araceae species the thickening of the exodermis cells is O-shaped (Fig. 3g-h, a-b, d-e, j-k, Table 1). In the mature regions of the roots of all species, except *Gomesa flexuosa* and *Trichocentrum pumilum*, a marked increase in the thickening of the exodermis cell walls and a reduction of the cell lumen was observed. However, the passage cell walls did not thicken. In all Orchidaceae species studied, spongy tilosomes occur in the walls of the velamen cells that are in contact with the passage cells (Fig. 1e-f).



Figuras 1a-l: General aspects of immature (left) and older (right) regions of roots of Orchidaceae in transversal section. a-b: *Brasiliorchis chrysantha*; c-e: *Gomesa flexuosa* (image in “d” showing crystalliferous idioblasts bearing calcium oxalate raphids in cortical parenchyma); f-h: *Isochilus linearis*; i-j: *Leptotes bicolor*; k-l: *Trichocentrum pumilum*. (ct – cortex; hf – idioblasts bearing calcium oxalate raphids; ri – raphids; ve – velamen; vc – vascular cylinder)



The cortical parenchyma cells in the Orchidaceae species have thin walls and are isodiametric in cross section and elongated in longitudinal section (Fig. 1a-l). The number of layers in the cortical parenchyma of the immature and mature regions are in the table 1, *Brasiliorchis chrysantha* (Fig. 1a-b), *Gomesa flexuosa* (Fig. 1c-e), *Isochilus linearis* (Fig. 1f-h), *Leptotes bicolor* (Fig. 1i-j) and *Trichocentrum pumilum* (Fig. 1k-l). The cells of the cortical layer near the exodermis and endodermis are smaller than the cells of the central zone, except in *T. pumilum* where only the cells of the cortical layer near to the exodermis are smaller (Fig. 1a-l).

Crystalliferous idioblasts containing raphides are present in the cortex in *Gomesa flexuosa* (Fig. 1d), *Isochilus linearis*, *Leptotes bicolor* and *Trichocentrum pumilum*. In addition, tracheoidal idioblasts are present in cortical and medullary parenchyma in *Brasiliorchis chrysantha* (Fig. 1a-b). The fungal

hyphae were present in the parenchyma of all of the regions where the roots were in contact with the substrate in all Orchidaceae species studied.

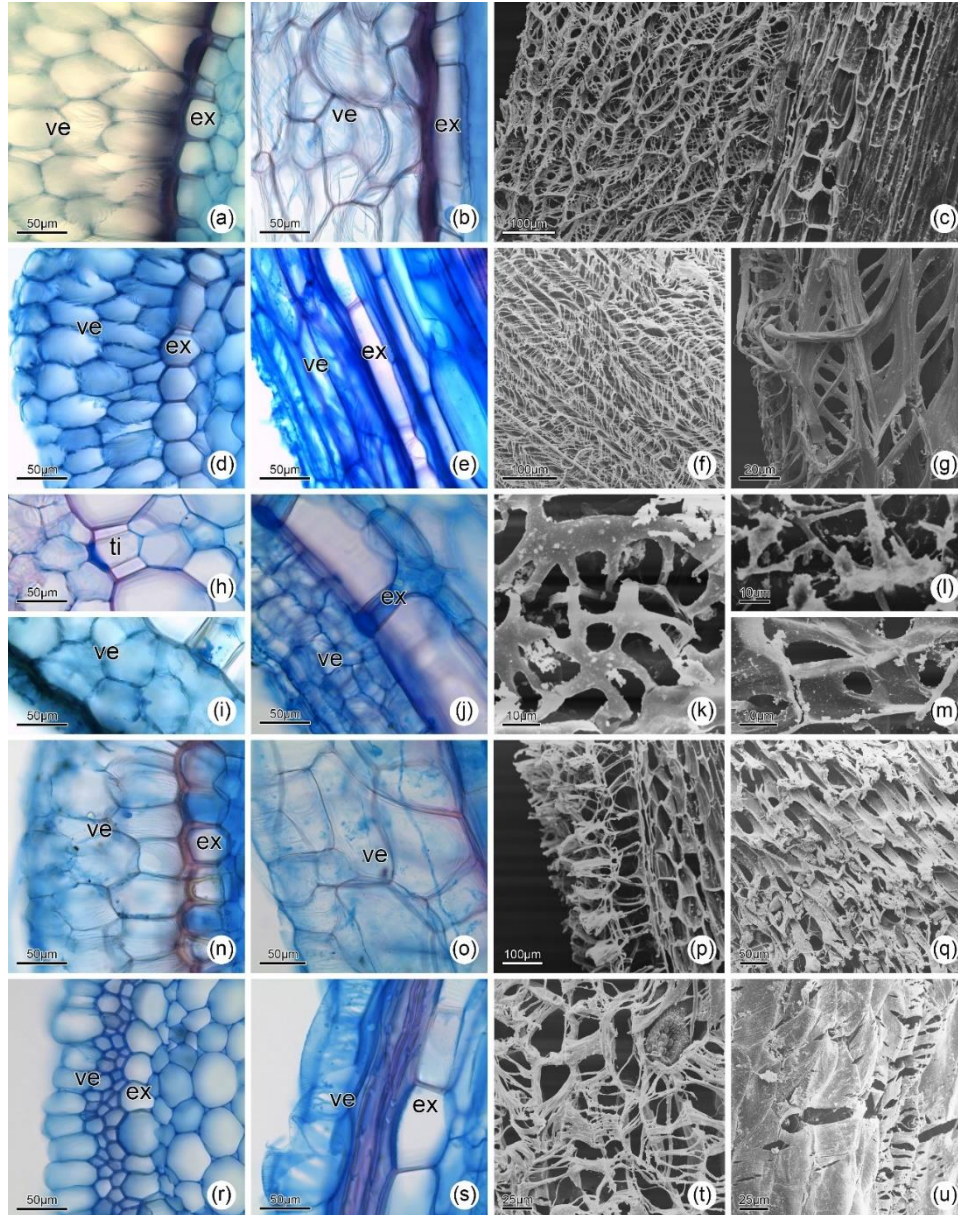
In the Bromeliaceae species, in the region of the immature root, the median cortical parenchyma cells have thin walls and are isodiametric in transverse section and elongated in longitudinal section. When immature, this region ranged from 3 to 12, depending on the specie (table 1), *Aechmea distichantha* (Fig. 3a), *Billbergia nutans* (Fig. 3d) and *Vriesea flava* (Fig. 3g). For the mature region of the root, in *A. distichantha* there are no changes (Fig. 3b), in *B. nutans* the cell walls become very thick and lignified and the median cortex no longer differs from the external cortex, and in *V. flava* the number of layers increases to nine and the cells form secondary lignified walls (Fig. 3h). In this species, in the older root regions, the cortex is divided into two regions, external cortex, formed by the exoderms of cells with lignified walls and the median cells with lignified walls, and internal cortex (Fig. 3e). The internal cortex is arechymatous and differentiates in younger regions of the root in *V. flava* and *B. nutans* (Fig. 3g-h, d-e) and only older regions of the root in *A. distichantha* (Fig. 3a-b). In *A. distichantha*, the aerenchyma of the internal cortex differs by the lysis of cells in the older regions of the root (Fig. 3b). The intercellular spaces are present in *A. distichantha*, *B. nutans* and *V. flava* (Fig. 3b, d-e, g-h).

In Araceae, the cortical parenchyma cells are abundant (as in the Orchidaceae species). There are about nine layers of cells, which have thin walls that are transversally isodiametric and longitudinally elongate. In this region there are two distinct areas, an external area of around five cell layers with randomly arranged cells and an internal area with larger cells that are radially aligned with the endodermis; this characterizes the internal layer as a meristematic endodermis (Fig. 3j-k). The exodermis comprises three layer of cells that become sclerified in older regions of the roots. Large secretory ducts, apparently of schizogenous origin, are arranged in a circle outside the cortex. In older regions about two or three layers of cells around the ducts become sclerified (Fig. 3k).

In all of the species studied the endodermis is unistratified (Fig. 4a-r). The cells are isodiametric in transverse section and elongate in longitudinal section, with O-shaped or U-shaped thickenings. The passage cells in the endodermis have thin walls and are opposite the xylem poles (Fig. 4a-r). In the immature and mature regions of the roots of *Brasiliorchis chrysantha* (Fig. 4a-b), *Gomesa flexuosa* (Fig. 4c-d), *Isochilus linearis* (Fig. 4e-f), *Leptotes bicolor* (Fig. 4g-h), *Trichocentrum pumilum* (Fig. 4i-j), *Vriesea flava* (Fig. 4o-p) and *Philodendron propinquum* (Fig. 4q-r) there is an endodermis with cells that have thickening in the internal and external periclinal and anticlinal walls, which results in O-shaped cell wall thickening. In immature regions of the roots of *Aechmea distichantha* (Fig. 4k-l) and

*Billbergia nutans* (Fig. 4m) the thickening in the anticlinal and internal periclinal walls is U-shaped. However, in older regions of the roots of *B. nutans* this thickening extends to the external periclinal wall, which creates an O-shaped cell wall thickening (Fig. 4n) (Table 1).

Figuras 2a-u: Photomicrographs and electromicrographs (SEM) showing velamen in transversal section (a, c, d, h-i, n, r), longitudinal section (b, e, g, j, m, o-p, s) and on the surface view (f, k-l, p-q, t-u) of immature (a-b, d-e, h, j-k, m-n, p, r, t) and mature (c, g, i, l, q, s, u) roots. a-c: *Brasiliorchis chrysantha*; d-g: *Gomesa flexuosa*; H-M: *Isochilus linearis* (image in h showing tilosome in the exodermis); n-q: *Leptotes bicolor*; r-u: *Trichocentrum pumilum*. (ex – exodermis; ti – tilosome; ve – velamen)

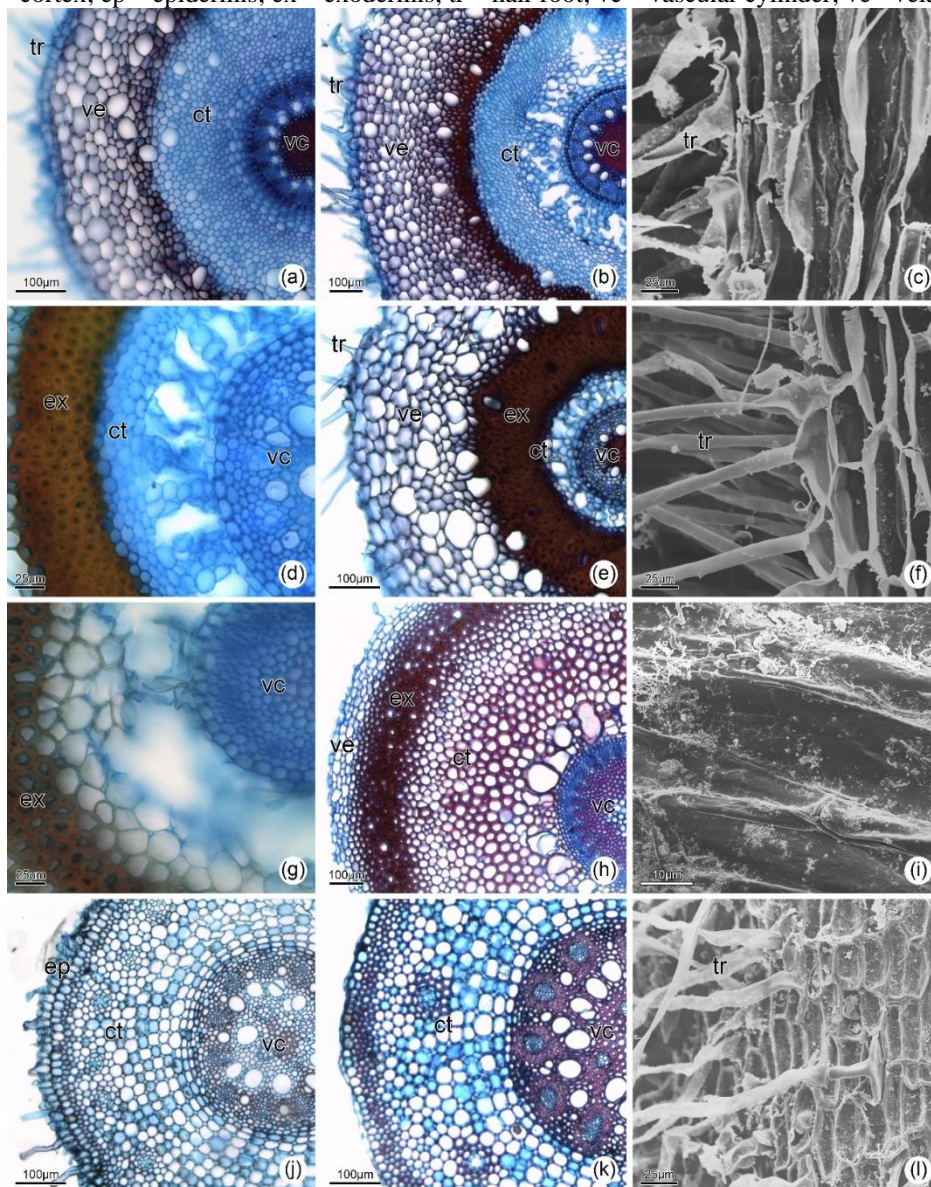


In all of the species studied, the vascular cylinder is delimited by the pericycle, which is uniseriate with thin-walled cells in the immature regions of the root (Fig. 4e, a, c, i, g, o, k, m, q). In older regions there is thickening in the cell walls of *Gomesa flexuosa* (Fig. 4d), *Isochilus linearis* (Fig.

4f), *Leptotes bicolor* (Fig. 4h), *Trichocentrum pumilum* (Fig. 4j), *Billbergia nutans* (Fig. 4n), *Vriesea flava* (Fig. 4p) and *Philodendron propinquum* (Fig. 4r).

In the roots of all of the studied species the vascular cylinder is a polyarch, which is formed by alternately arranged xylem and phloem bundles (Table 1). Large, isolated vessel elements, which delimit the medulla, were observed in the latter three species (Fig. 4k-l, m-n, q-r) and *G. flexuosa* (Fig. 4c-d).

Figuras 3a-l: Photomicrographs (a-b, d-e, g-h, j-k) and eletromicrographs (SEM) (c, f, i, l) of Bromeliaceae (a-i) and Araceae (j-l) in transversal section (a-b, d-e, g-h, j-k), longitudinal section (c, f) and on the surface view (i, l) of immature (a, d, f, g, i-j) and mature (b-c, e, h, k-l) roots. a-c: *Aechmea distichantha*; d-f: *Billbergia nutans*; g-i: *Vriesea flava*; j-l: *Philodendron propinquum*. (ct – cortex; ep – epidermis; ex – exodermis; tr – hair root; vc – vascular cylinder; ve - velamen)



In almost all of the species studied the medulla comprises parenchyma that are isodiametric in transversal section and elongated in longitudinal section. In immature and mature regions of the roots, these cells have thick lignified walls in *Gomesa flexuosa* (Fig. 4c-d), *Leptotes bicolor* (Fig. 4g-h), *Trichocentrum pumilum* (Fig. 4i-j), and *Aechmea distichantha* (Fig. 4k-l); the thickening is greatest in older regions. In *Brasiliorchis chrysantha* (Fig. 4a-b) and *Isochilus linearis* (Fig. 4e-f) thickening occurs in older regions in the central part of the medulla, as well as in the perimedullary layers where it is more accentuated in older regions. In *Billbergia nutans* (Fig. 4m-n), *Vriesea flava* (Fig. 4o-p), and *Philodendron propinquum* (Fig. 4q-r) the sclerification occurs in older regions of the root. It should be noted that the sclerification process in the Orchidaceae species, *V. flava* and the Araceae species occurs from the immature region to the mature region, which starts in the parenchyma cells between the vascular bundles and continues to the perimedullary sheath until the central region. The central region is very sclerified in *A. distichantha* (Fig. 4l), *B. nutans* (Fig. 4n) and *P. propinquum* (Fig. 4r).

#### 4 DISCUSSION

The presence of velamen in the roots of Orchidaceae and Bromeliaceae species has been recorded in various studies about Orchidaceae (Holtzmeier *et al.* 1998, Stern & Whittenw 1999, Oliveira & Sajo 1999, Stern *et al.* 2004, Silva & Milaneze-Gutierrez 2004a, Costa *et al.* 2012, Saoncella *et al.* 2017), Bromeliaceae (Krauss 1949, Tomlinson 1969, Pita & Menezes 2002, Segecin & Scatena 2004, Proença & Sajo 2008, Silva 2010) and Araceae (Ferreira *et al.* 2006, Oliveira 2011).

The epivelamen has been described for Orchidaceae by Oliveira & Sajo (1999) and Moraes (2011) and for Bromeliaceae by Segecin & Scatena (2004) and Silva & Scatena (2011).

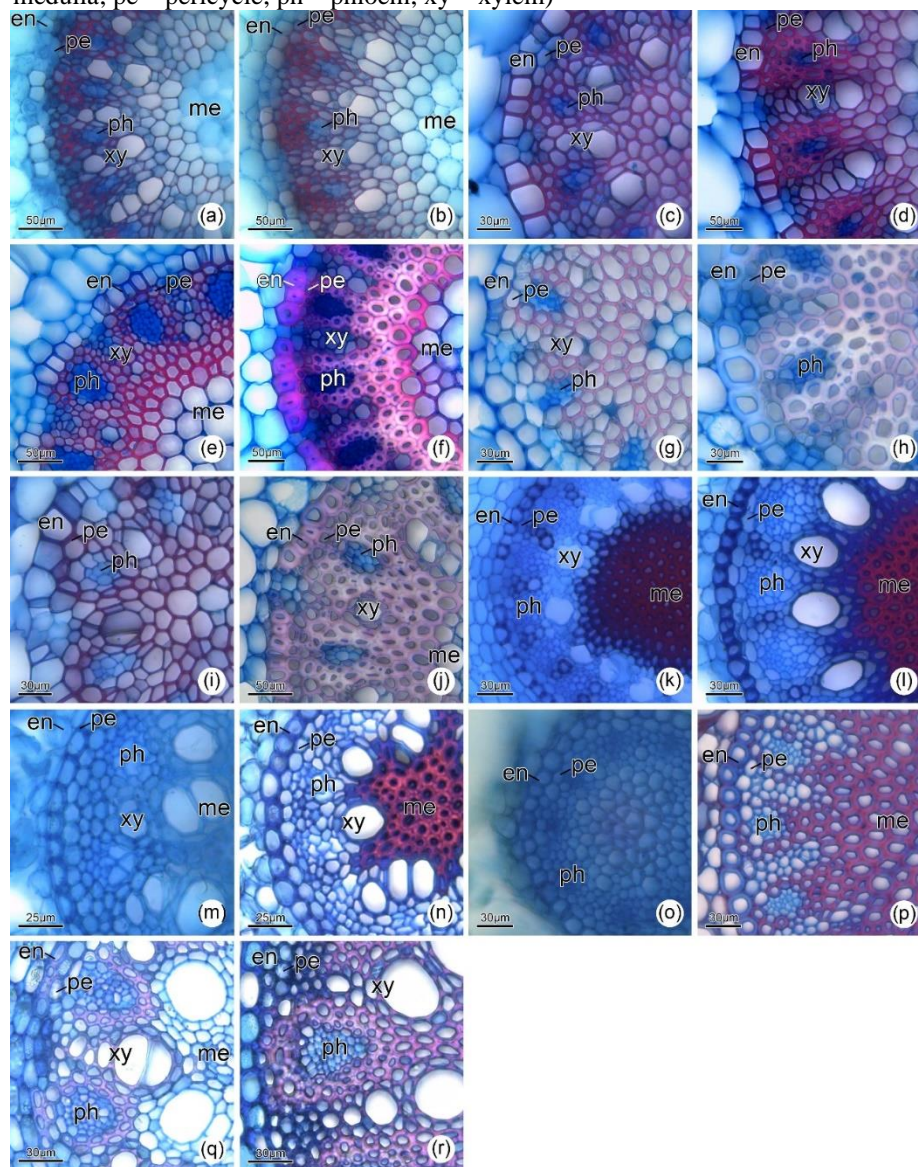
In the Orchidaceae, the number of velamen layers varied between species and root development stage. Authors as Benzing *et al.* (1982), Silva & Milaneze-Gutierrez (2004a), Silva *et al.* (2010) and Piazza *et al.* (2015) observed uniestratified to multiestratified velamen in Orchidaceae species. This variation has been described for several monocots families by Fahn (1978) and Mauseth (1988). Sandford & Adanlawo (1973) analyzed 76 species of epiphytic Orchidaceae in West Africa in the number of velamen layers and found that environmental conditions and concluded that in dry environments, velamen has numerous layers of cells, while in humid environments the velamen has fewer layers of cells.

A pluristratified velamen has been described for many Bromeliaceae species by Pita & Menezes (2002), Segecin & Scatena (2004), Proença & Sajo (2008), Silva (2010) and Silva & Scatena (2011). In this study, the mature root region of *Aechmea distichantha*, which can be found in both sunny and

shaded habitats, dry or humid environment, presented velamen with a greater number of layers in relation to *Billbergia nutans* and *Vriesea flava*, species of shaded habitat and humid environment.

Chomicki *et al.* (2015) found that velamen radicum of epiphytic orchids plays a pivotal role in UV-B protection, an essential adaptation to the water-limited epiphytic habit, and based on orchid phylogeny calibrated over time, the functionality of the orchid velamen probably contributed to the family's expansion into rainforest canopies during the Cenozoic.

Figuras 4a-r: Details of transversal sections of the endodermis and central cylinder of immature (left) and mature (right) roots. a-b: *Brasiliorchis chrysantha*; c-d: *Gomesa flexuosa*; e-f: *Isochilus linearis*; g-h: *Leptotes bicolor*; i-j: *Trichocentrum pumilum*; k-l: *Aechmea distichantha*; m-n: *Billbergia nutans*; o-p: *Vriesea flava*; q-r: *Philodendron propinquum*. (en – endodermis; me – medulla; pe – pericycle; ph – phloem; xy – xylem)



Zotz *et al.* (2017) reported the presence of a velamen in approximately 240 genera of terrestrial monocots (162 genera of orchids and 74 non-orchids) and in one genus of dicots. Although many works report the presence of velamen, Kowalski *et al.* (2019) analyzed the root apical meristem in longitudinal sections of Bromeliaceae species and observed only anticlinal divisions of the protodermis and concluded that there is a uniseriate epidermis.

Joca *et al.* (2017) compared anatomical features with nutrient uptake rates (specifically of phosphorus and rubidium) of roots of 18 taxa of epiphytic orchids and noted that the relative proportion of the velamen of the cross-sectional area varied from 11 to 97%, where the species with the largest relative velamen area facilitate the flow of water and nutrients, and species with larger relative proportion of vascular cylinder and cortex have a greater number of protoxylem strands and passage cells of the endo-dermis. Joca *et al.* (2020) searched the chemical composition of cell walls in velamentous roots in 18 epiphytic orchid species and observed species invest in pectin deposition with high methyl-esterification being able to increase their capacity to absorb water through gel formation in the velamen, and suggested that pectins are also essential for the stability and mechanical support of velamen cells. Of the species of Orchidaceae studied, *Brasiliorchis chrysantha* and *Gomesa flexuosa* in sunny habitats, dry environment, presented a greater number of velamen layers and a greater number of xylem and phloem poles when compared with species of shaded habitat, humid environment.

The species of Araceae studied has a root with a unistratified epidermis. Despite the long time since velamen was first described for roots of Araceae species by Engler (1912), Mathews *et al.* (1997) reported the occurrence of a fake that resembled a false multiple epidermis in *Philodendron lacerum* and Vianna *et al.* (2001), stated that the organization of root coverage in cross-sectional view could give a false impression of a multistratified epidermis in *P. bipinnatifidum*.

Silva *et al.* (2010) observed a unistratified epidermis in all terrestrial Orchidaceae species. Oliveira (2011) observed in the roots of Araceae species uniseriate epidermis with epidermal appendages, periderm with lenticels and thick periderm with an outer layer of suberin. Finally, Kowalski & Tardivo (2015) observed an unistratified epidermis in *Vriesea platynema*, a epiphytic species that can also grow in soil or on rocks.

The presence of tilosomes is a feature also described by Chatin (1856), Oudemans (1861), Benzing *et al.* (1982), Pridgeon *et al.* (1983) and Silva *et al.* (2010). Kedrovski & Sajo (2019) believe that probably the tilosomes have two functional phases: in young tissues, they increase the symplast connection, facilitating transport over the outer root regions, like the wall-membrane apparatus of

transfer cells; in mature tissues, they protect, direct solutes to the passage cells, imposing a physicochemical barrier for pathogens and recognizing symbionts.

An exodermis is a common characteristic in Orchidaceae (Benzing *et al.* 1982, Stern *et al.* 2004) and could have resulted as a response water loss and to increase mechanical protection (Silva & Scatena 2011). In turn, the *Philodendron* and bromeliad species studied have a pluristratified exodermis, which is common in Bromeliaceae (Pita & Menezes 2002, Segecin & Scatena 2004, Proença & Sajo 2008).

Cortical parenchyma is sclerenchymatous in older regions of the roots of *Vriesea flava* and *Billbergia nutans* (Bromeliaceae). According to Olatunji & Nengim (1980), the presence of secondary cell wall thickening is associated with mechanical support.

The secretory ducts in cortical parenchyma of the *Philodendron propinquum* were also observed by Vianna *et al.* (2001) in *P. bipinnatifidum*. Secretions are characterized as mucilage, resin and latex and the mucilage can be related to water and carbohydrate reserve, in addition to water balance and resistance against drought and the resin works to protect against herbivory (Fahn 1978, Mayo *et al.* 1997). The radical cortex subdivided and with intercellular spaces in the analyzed bromeliads was also observed by Segecin & Scatena (2004) in *Tillandsia*. According to Meyer (1940), the intercellular spaces in the internal cortex of the roots of Bromeliaceae transport water by capillary action.

The unistratified endodermis and pericycle have also been reported for Orchidaceae (Oliveira & Sajo 1999; Silva *et al.* 2010), Bromeliaceae (Pita & Menezes 2002, Segecin & Scatena 2004, Silva 2010, Silva & Scatena 2011,) and Araceae (Oliveira 2011). However, Vianna *et al.* (2001) observed that the pericycle of *Philodendron bipinnatifidum* comprises one to two cell layers.

For the endodermis, thickening of the cell walls is an adaptive characteristic to the epiphytic environment (Segecin & Scatena 2004, Proença & Sajo 2008, Lobo *et al.* 2008, Silva & Scatena 2011). Passage cells are characteristic was also described for Orchidaceae by Silva & Milaneze-Gutierrez (2004a) and Silva *et al.* (2010), and Bromeliaceae by Pita & Menezes (2002) and Silva & Scatena (2011). Schreiber *et al.* 1994 obtained direct chemical evidence, in roots of *Clivia miniata*, that the Casparian strips contain lignin as a major cell wall polymer.

A single-walled pericycle were also reported for Orchidaceae by Oliveira & Sajo (1999), Silva & Milaneze-Gutierrez (2004a) and Silva *et al.* (2010) and Bromeliaceae by Proença and Sajo (2008), Lobo *et al.* (2008), Silva (2010) and Silva & Scatena (2011). The polyarc vascular cylinder has also been reported for Orchidaceae by Kedrovski *et al.* (2013) and for Bromeliaceae by Ferreira *et al.* (2006).



The results described in the present work reaffirm that the variations observed in the number of layers of the velamen and in the thickening of the cells of the exodermis/endodermis are related to the strata in which the species are most frequently found. Velamen is absent only in *Philodendrom propinquum*, considered a primary epiphyte of low and shaded stratum, with roots in contact with the soil. In Orchidaceae, *Isochilus linearis*, *Leptotes bicolor*, and *Trichocentrum pumilum* the differentiated velamen has 2-4 layers and are species of medium and shaded stratum, *Gomesa flexuosa* has 5-7 layers and is of medium and sunny stratum, already *Brasiliorchis chrysantha* presents in the mature area of the velamen 8-10 layers and is of high and sunny location. In the Bromeliaceae, *Vriesea flava* presents in the mature region of the velamen 5-7 layers and has a low, shaded location, *Billbergia nutans* presents in the mature region of the velamen 8-10 layers and is of medium and shaded location, and finally, *Aechmea distichantha* presents in the mature area of the velamen 11-12 layers and can be of low/medium and sunny/shaded location. With regard to thickening in the exodermis/endodermis, in more frequent species in places with a higher luminous incidence, the roots differentiate thickening in "O" more quickly than in those more frequently found in raised environments.

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