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Radicular anatomy of twelve representatives of the Catasetinae subtribe (Orchidaceae: Cymbidieae)

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ABSTRACT

Considering that the root structure of the Brazilian genera belonging to the Catasetinae subtribe is poorly known, we describe the roots of twelve representatives from this subtribe. For anatomical analysis, the roots were fixed in FAA 50, preserved in ethanol 70% and sectioned at its medium region using razor blades. The sections were stained with 0.05% astra blue and safranin and mounted in glycerin. For the identification of starch we used Lugol's solution; for lignin, floroglucin chloridric; for lipids, Sudan III, and for flavanoids, potassium hydroxide. The relevant aspects were registered using a digital camera joined with an Olympus microspope (BX51 model). The structural similarities of all roots support the placement of the subtribe Catasetinae into the monophyletic tribe Cymbidieae. Some root features are restricted to one or two taxa and can be useful in the systematics of the subtribe. For example, the occurrence of flavonoidic crystals characterizes the genera *Catasetum* and *Cychnodes*, and the number of the velamen layers and the shape of the epivelamen cells are useful to confirm the taxonomic position of *Clowesia amazonica*. The presence of velamen and flavonoidic crystals was interpreted as an adaptation to the epiphytic habit.

Key words: Epiphytism, morphoanatomy, orchid, systematic.

INTRODUCTION

Orchidaceae, one of the greatest families of angiosperms, includes about 780 genera and 25,000 species (Pridgeon et al. 2009) particularly well represented in tropical and subtropical environments (Pabst and Dungs 1975, 1977). It is divided into five subfamilies: Apostasioideae, Vanilloideae, Cypripedioideae,

Correspondence to: Cristiano Pedroso de Moraes E-mail: pedroso@uniararas.br Orchidoideae and Epidendroideae, according to recent molecular analyses (Chase et al. 2003).

The subtribe Catasetinae belongs to Epidendroideae and includes seven genera that grow in tropical areas of America from the sea level to more than 1,000 meters high (Hoehne 1940, Romero 1990, Pridgeon et al. 2009). Some genera present the particularity of emitting forked, erect and acuminate root branching with negative geotropism that performs a function analogous to pneumatophores. This fact is observed when the roots overlap in thicker layers. These ramifications can be observed, for instance, in *Catasetum fimbriatum* Lindl., which is used by cultivator to immediate identification only by observing these ramifications that stand out among the other species studied herein (Hoehne 1949).

The Catasetinae subtribe presents a sympodial growth, with well-developed pseudobulbs that promote the storage of water during dry periods, and decidual leaves after matured (Dodson 1975, Moraes and Almeida 2004). They appear mainly in the top of trees, from where their roots, usually pulpous, absorb nutrients (Hoehne 1938). These are always side roots and often adventitious (Hoehne 1949), which emerge from nodules of the rhyzoma rings. The roots of the orchids are revested by a velamen, which is responsible for the photosynthesis functions, gaseous exchanges, fixation and nutrient absorption that comes from organic and liquid substances (Hoehne 1949, Sanford and Adanlawo 1973, Haas and Carothers 1975, Benzing and Friedman 1981, Pridgeon et al. 1983, Singh 1986, Oliveira and Sajo 1999).

Stern and Judd (2001) described the anatomy of the vegetative organs of several Catasetinae, mainly of the Amazon region. However, there is little information about the root organization in the native genera that also inhabit the remaining Brazilian regions, as the *Catasetum*, *Clowesia*, *Cycnoches* and *Mormodes*, which totalize about 250 species of terrestrial and epiphytic orchids (Dodson 1975, Pridgeon et al. 2009). The present study aims to describe the root structure of the twelve most representative Brazilian species included in these genera and point out features that could represent adaptations to the epiphytic habit and/or are useful for taxonomic purposes.

MATERIALS AND METHODS

The material comes from the collection of Greenhouse of the Centro Universitário Hermínio Ometto - Uniararas, Araras, SP (VHO), where they are registered as follow: *Catasetum barbatum* Lindl. (VHO: 16; 20; 23), *Catasetum cernuum* Rchb. f. (VHO: 65; 78; 79), *Catasetum discolor* Lindl. (VHO: 90; 91; 94), *Catasetum fimbriatum* Lindl. (VHO: 08; 10; 11), *Catasetum pileatum* Rchb. f. (VHO: 86; 88; 92), *Catasetum saccatum* Lindl. (VHO: 52; 59; 68), *Clowesia amazonica* K.G. Lacerda & V.P. Castro (VHO: 45; 46; 48), *Clowesia rosea* Lindl. (VHO: 51; 54; 55), *Cycnoches haagii* Barb. Rodr. (VHO: 93; 96; 98), *Cycnoches loddigesii* Lindl. (VHO: 92; 99; 102); *Mormodes elegans* F. E. L. Miranda (VHO: 100; 101; 108) and *Mormodes tapoaynensis* F.E. L. Miranda & K.G. Lacerda (VHO: 112; 116; 118).

The root diameter of each species was measured in 20 samples at 2 centimeters from the apex using a digital Digimess[®] pachymeter. The radius was calculated using d=2r (Moreira and Isaias 2008), and data were submitted to the ANOVA variance analysis and to the Tukey text at 5% of probability.

For the anatomical analysis, the roots were fixed in FAA 50 and preserved in ethanol 70% (Johansen 1940). They were freehand sectioned at the median region, using blade razors. The sections were stained with 0.05% astra blue and safranin (Bukatsh 1972) and mounted in glycerin. The starch was identified by the Lugol solution (Bürcherl 1962); the lignin by the Floroglucin plus Chloridric Acid (Jansen 1962); the lipids by the Sudan III (Jansen 1962) and the flavonoids by the potassium hydroxide (Costa 1982). The anatomical aspects were recorded with a digital camera connected to an Olympus microscope (model BX51).

RESULTS

The roots of all species studied (Figures 1-4) are similar in possessing three distinct regions: velamen, parenchymatous cortex and vascular cylinder. In some species, like *Catasetum discolor* (Figure 1A), the root diameter is bigger than in others that shows reduced diameter, such as Catasetum pileatum (Figure 1C) and Mormodes tapoavensis (Table I). The velamen, present in all roots (Table I), is three-layered in *Clowesia amazonica* (Figure 2G), five-layered in Clowesia rosea, Cycnoches haagii (Figure 2H-I) and Mormodes elegans (Figure 2K), seven-layered in Catasetum barbatum (Figure 2A), eight-layered in Catasetum discolor (Figure 2C), Cycnoches loddigesii (Figure 2J) and Mormodes tapoayensis (Figure 2L), nine-layered in Catasetum *cernuum*, *Catasetum fimbriatum* (Figure 2B and D) and Catasetum piletaum (Figure 2E), and elevenlavered in Catasetum saccatum (Figure 2F). The velamen is formed by cells of variable shapes (Figure 2) and with different secondary thickened walls depending on the species. The cells of the epivelamen (outer laver) are slightly smaller than those of the inner layers, excepted for Clowesia amazonica (Figure 2G) with cells of the same size (Figure 1-2). The endovelamen cells are isodiametric and possess thickened walls forming stripes or lines with a variable arrangement according to the species (Figure 2A-F; H-K). The velamen cells possess suberin and lignin in their walls as identified by the Sudan III and by the Floroglucin plus Chloridrid Acid, respectively (Table I).

In all species analyzed, the cortex shows an identifiable exodermis close to the velamen, a median cortex and an endodermis in contact to the central cylinder (Figure 1). In the exodermis, the cells are bigger than those of other cortical layers and thin-walled, except for the outer periclinal walls (Figure 2). The cells are long, short and alternate among themselves. The long cells do not have protoplasts and the short ones, the passage cells, present dense content and thin walls (Figure 2).

Internally to the exodermis, the cortical parenchyma is 8-9 layered in *Catasetum fimbriatum* (Figure 1B), *Catasetum saccatum*, Catasetum pileatum and Clowesia rosea (Figure 1C-D), 10-11 layered in Catasetum cernuum, 11-12 layered layered in Clowesia amazonica and Cycnoches loddigesii, 12-13 layered in Catasetum discolor (Figure 1B) and Mormodes tapoavensis, 13-14 layered in Catasetum barbatum and Mormodes elegans (Figure 1F), and 14-15 layered in Cycnoches haagii (Figure 1E) (Table I). The cells of these layers are isodiametric and vary in size. They delimit small intercellular spaces and possess walls with anastomosed thickening (Figures 1, 5A). Idioblasts with flavonoidic crystals are common in this region (Figure 5D), except for Clowesia amazonica, Clowesia rosea, Mormodes elegans and Mormodes tapoayensis (Table I), with do not present crystals. In all roots, the layers close to the exodermis and to the endodermis are formed by small cells (Figure 1). Idioblasts with raphides and hyphae of fungi were observed around the exodermis (Figure 1A-B, D).

The endodermis is one-layered and its cells present O-thickened walls, except for the passage ones, opposite to the xylem poles, with thin walls (Figures 3 and 4). The roots are polyarc, with eight protoxylem poles in *Catasetum pileatum* (Figure 3E), nine in Mormodes tapoayensis (Figure 3L), ten in Clowesia amazonica and Clowesia rosea (Figure 3G-H), twelve in Catasetum barbatum (Figure 3A), thirteen in Catasetum saccatum (Figure 3F), Cycnoches haagii, Cycnoches loddigesii and Mormodes elegans (Figure 3I-K), fourteen in Catasetum cernuum (Figure 3B) and Catasetum fimbriatum (Figure 3D), and fifteen in Catasetum discolor (Figure 3C). The pith is formed by parenchymatous cells with anastomosed thickening in their walls (Figure 5B), except for Catasetum pileatum and Mormodes tapoayensis (Table I). Starch grains are frequent in this region, in Cycnoches loddigesii, Mormodes elegans (Figure 5E) and Mormodes tapoayensis as observed by tests with Lugol.



Figure 1 – Cross sections of the roots showing the general structure. A, *Catasetum discolor* Lindl. B, *Catasetum fimbriatum* Lindl. C, *Catasetum pileatum* Rchb. f. D, *Clowesia rosea* Lindl. E, *Cycnoches haagii* Lindl. F, *Mormodes elegans* F. E. L. Miranda. ve = velamen, co = cortex; cv = vascular cylinder; hf = hyphae micorrhyzic fungi. Bars = 100 µm.



Figure 2 – Radicular cross sections showing the velamen. A, *Catasetum barbatum* Lindl. B, *Catasetum cernuum* Rchb. f. C, *Catasetum discolor* Lindl. D, *Catasetum fimbriatum* Lindl. E, *Catasetum pileatum* Rchb. f. F, *Catasetum saccatum* Lindl. G, *Clowesia amazônica* K.G. Lacerda and V.P. Castro. H, *Clowesia rosea* Lindl. I, *Cycnoches haagi* Barb. Rodr. J, *Cycnoches loddigesii* Lindl. K, *Mormodes elegans*. F. E. L. Miranda. L, *Mormodes tapoayensis* F.E. L. Miranda and K.G. Lacerda. ep = epivelamen; rp = raphydes. Bars = 50 µm.



Figure 3 – Cross sections of the roots showing variation in the number of protoxylem poles. A, *Catasetum barbatum* Lindl. B, *Catasetum cernuum* Rchb. f. C, *Catasetum discolor* Lindl. D, *Catasetum fimbriatum* Lindl. E, *Catasetum pileatum* Rchb. f. F, *Catasetum saccatum* Lindl. G, *Clowesia amazônica* K.G. Lacerda and V.P. Castro. H, *Clowesia rosea* Lindl. I, *Cycnoches haagi* Barb. Rodr. J, *Cycnoches loddigesii* Lindl. K, *Mormodes elegans*. F. E. L. Miranda. L, *Mormodes tapoayensis* F.E. L. Miranda and K.G. Lacerda. Bars = 100 µm.



Figure 4 – Radicular cross sections in the outer region of the vascular cylinder. A, *Catasetum barbzatum* Lindl. B, *Catasetum cernuum* Rchb. f. C, *Catasetum discolor* Lindl. D, *Catasetum fimbriatum* Lindl. E, *Catasetum pileatum* Rchb. f. F, *Catasetum saccatum* Lindl. G, *Clowesia amazônica* K.G. Lacerda and V.P. Castro. H, *Clowesia rosea* Lindl. I, *Cycnoches haagi* Barb. Rodr. J, *Cycnoches loddigesii* Lindl. K, *Mormodes elegans*. F. E. L. Miranda and K.G. Lacerda. en = endodermis; p = pericycle. Bars = 50 µm.



Figure 5 – Cross sections showing cortical and pith parenchyma. A, parietal anastomosed thickening in cortical parenchyma cells of *Catasetum discolor* Lindl. B, parietal anastomosed thickening in cells of the pith parenchyma of *Catasetum barbatum* Lindl. C, raphydes of Calcium oxalate present in the cortical parenchyma of *Catasetum cernuum* Rchb. f. D, flavonoidic crystal present in the cortical parenchyma of *Catasetum saccattum* Lindl. E, starch grains present in the pith parenchyma of *Mormodes elegans* F. E. L. Miranda. Bars: = 50 µm.

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TABLE I

ngencial wall; O = Thickening in O; Sg = Starch grains; Fc = Flavonoidic Crystal; Rp = Raphydes of Calcium oxalate; + = presence; - = absence

			Medium	Velamen	Exodermis	Central	Endodermis	Protoxylem	Cortical Parenchyma	Pith Parenchyma	
Species	Ambient	Habit of growing	diameter of the roots (cm)	Number of cell layers	Kind of parietal wthickening	Number of cell layers	Kind of parietal thickening	Number of poles	Ocurrence of parietal anastomosed thickening	Ocurrence of parietal anastomosed thickening	Idioblasts
Catasetum barbatum	RF	Epi	0,3D1	7	TE	13-14	0	12	+	+	Fc, Rp
Catasetum cernuum	RF, SF	Epi	0,4C	6	TE	10-11	0	14	+	+	Fc, Rp
Catasetum discolor	GW, RE	Epi ,Ter, Rup	0,6A	8	TE	12-13	0	15	+	+	Fc, Rp
Catasetum fimbriatum	CE, SF	Epi	0,5B	6	TE	8-9	0	14	+	+	Fc, Rp
Catasetum pileatum	RF	Epi	0,2E	6	TE	8-9	0	8	+		Fc, Rp
Catasetum saccatum	RF	Epi	0,4C	11	TE	8-9	0	13	+	+	Fc, Rp
Clowesia amazonica	RF	Epi	0,3B	3	TE	11-12	0	10	+	+	Rp
Clowesia rósea	\mathbf{SF}	Epi	0,3D	5	TE	8-9	0	10	+	+	Rp
Cycnoches haagii	RF	Epi	0,4C	5	TE	14-15	0	13	+	+	Fc, Rp
Cycnoches loddigesii	RF	Epi	0,4C	8	TE	11-12	0	13	+	+	Fc, Rp, Sg
Mormodes elegans	RF	Epi	0,4C	5	TE	13-14	0	13	+	+	Rp, Sg
Mormodes tapoayensis	RF	Epi	0,2E	8	TE	12-13	0	6	+	ı	Rp, Sg

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 1 Numbers followed by same letters in column do not differ by Tukey test at 5%

DISCUSSION

The roots of all plants studied possess a velamen that is a specialized epidermis of several layers of thin-walled cells (Pridgeon 1987). Besides Orchidaceae, the velamen also occurs in other monocotyledons such as Araceae. Liliaceae. Dioscoreaceae, Taccaceae, Amaryllidaceae and Commelinaceae (Dahlgren and Clifford 1982). Although the velamen is associated to the epiphytic habit (Engard 1944, Dycus and Knudson 1957), it is present in some terrestrial orchids (Porembski and Barthlott 1988, Stern et al. 1993a, b, Kurzweil et al. 1995) and absent in some representatives of this family (Singh 1986). In most species studied here, the velamen is 5-11 layered, as described by Stern and Judd (2001) for the Catasetinae they analyzed. Only Clowesia amazonica possesses a thin three-layered velamen (Table I) that is probably related to the strictly humid epiphytic environment where the specie lives. Once the velamen works protecting the root against the heating and the consequent water loss (Pridgeon 1987, Gonzaga and Gonzaga 1996), a thickened tissue is more frequent in species that grow in dry and hot conditions (Gonzaga and Gonzaga 1996, Moreira and Isaias 2008) than in Cl. amazonica.

According to Sanford and Adanlawo (1973), the velamen comprises the epivelamen (the outer layer) and the endovelamen (the inner layer). In most of the studied roots, the cells of the epivelamen are smaller than those of the endovelamen, as in other Catasetinae (Stern and Judd 2001). Only in *Clowesia amazonica* (Figure 2G) the cells of the epivelamen are the same size of the inner ones, as reported for some Cymbidieae (Pridgeon et al. 2009), wich is a tribe that includes the Catasetinae subtribe.

Within Catasetinae, thin velamen and epivelamen cells with the same size of the cortical ones seems to be exclusive to *Clowesia amazonica*, which indicates that these features are diagnostic for the species. According to Moreira and Isaias (2008) and Porembski and Barthlott (1998), the number of velamen layers and the shape of the epivelamen cells are constant in mature tissues within the species even under different environmental conditions.

Suberin and lignin on the velamen cell walls, as observed here for most species, are frequent in Orchidaceae roots although their deposit degree varies among species (Noel 1974, Benzing et al. 1983). According to Noel (1974), they provide mechanical support avoid cellular collapse during dehydration.

Tilossomes or covering cells, frequently observed in the inner velamen layer of orchids roots, seem to be absent in Catasetinae, since they do not appear neither in the studied species nor in those described by Stern and Judd (2001). These cells are also absent in the subtribe Zygopetalinae (Stern et al. 2004), confirming its close relationship to Catasetinae.

Some exodermis features, such as isodiametric cells with thickened outer periclinal walls, occur in all studied species and were also described for other Catasetinae (Oliveira and Sajo 1999, Stern and Judd 2001). According to Haberlandt (1914), the velamen-exodermis set works as a system where the suberized/lignified elongated cells of the exodermis protect the cortical parenchyma from dehydration, and the thin-walled cells lead nutritive substances from the velamen to the cortex.

In *Catasetum* species, the root cortex is 8-14 layered, as observed by Stern and Judd (2001) for other representatives of the same genus. On the other hand, the root cortex of the *Clowesia*, *Cycnoches* and *Mormodes* species studied here are 8-12, 11-15 and 12-14 layered (Table I) while those described by Stern and Judd (2001) are 6-9, 7-13 and 10-13 layered. However, according to Alconero (1968), the environmental conditions can determine variations in the number of cortex layers. These conditions could thus explain the differences observed, within the three genera, comparing our results to those of Stern and Judd (2001).

the environment influences the development of An Acad Bras Cienc (2012) 84 (2)

Idioblasts with raphides, as observed in the root cortex, are frequent in Orchidaceae and in other monocotyledons, such as Liliaceae, Arecaceae and Commelinaceae (Metcalfe 1963). They come from cells produced by unequal divisions in the fundamental meristem (Shushan 1959, Chiang 1970).

Idioblasts with flavonoid crystals characterize the roots of Catasetum and Cychnoches, and are absent in Clowesia and Mormodes. This suggests that this feature is useful on the generic delimitation within Catasetiane as proposed by Oliveira-Pires et al. (2003) for Laelinae (Orchidaceae). Flavonoid crystals occur in all plant organs (Zuanazzi 2001) and constitute the most common polyphenol compound of the plants (Pietta et al. 1989). Their presence is related to many factors, such as infection, temperature, nourishment, injury, sugar and nitrogen metabolism and quantity of radiation (Blank 1947). Some studies show an increase of flavonoids compounds, both in crystalized and non-crystalized forms in organs exposed to light (Hillis and Swain 1959, Bohm 1987, Holst 1977). Considering that both Catasetum and Cycnoches grow in higher strata than the ones of Clowesia and Mormodes, the occurrence of flavonoid crystals in both former genera may be related to UV absorption as pointed out by Harborne (1977) for the Angiosperms.

The presence of an O thickening in the endodermis cells of all studied species corroborates the data of Stern and Judd (2001) for other Catasetinae. This feature was also described for representatives of other subtribes included in Cymbidieae, such as Cymbidiinae, Cyrtopodiinae, Eulophiinae and Oncidiinae (Stern and Judd 2002, Pridgeon et al. 2009).

Endomycorrhizic associations, as those observed here, are common in orchids. They establish during plant germination and favor its development and establishment helping in the nutrients uptake (Arditti 1967). Many orchids keep this association during the whole life, while others become independent when adult (Arditti 1967, Sanford 1974). According to Sanford (1974), the orchids that depend on this association are partially saprophytic once the organic compounds are also provided by fungi by active transport and not only by diffusion.

Porembski and Barthlott (1988) classified orchid roots into 12 types according to the occurrence and combination of the following features: epivelamen, number of velamen layers, type of wall thickening in the velamen and exodermis cells, and number of cortex layers. All the roots studied here correspond to the Porembski and Barthlott's (1988) Cymbidium type in having epivelamen, exodermis cells with thickened outer periclinal walls and cortex with more than eight layers. This root uniformity support the Chase et al. (2003) analyses that recognize just one monophiletic tribe, Cymbidieae, formed by Catasetinae, Coeliopsidinae, Cyrtopodiinae, Cymbidiinae, Eriopsidinae, Eulophiinae, Maxillariinae, Oncidiinae, Stanhopeinae, Vargasieliinae and Zygopetalinae.

Like in other Catasetinae (Stern and Judd 2001), the root pith is parenchymatous and its cell walls possess anastomosed thickenings. In Cycnoches loddigesi, Mormodes elegans and Mormodes tapoayensis the pith cells contain starch, which indicates a possible storage function, as suggested by Haberlandt (1914). The physicalchemical properties, granular molecular structure, morphological pattern of deposition, size and form of the native starch grains of different species and its presence or absence in tissues compounds of vegetative organs are characters used to help taxonomic characterizations in plants when there is doubt on its outter morphology (Esau 1972, Galliard 1987, Wang and White 1994). The presence of starch in both Mormodes species can be useful in the genus characterization.

The number of the velamen and cortex layers,

root structure and, consequently, its diameter. For example, in dry environments a reduced number of cortical layers are formed, suggesting that a small distance between the substract and the stele would help the water absorption in these conditions (Fahn 1982). Moreover, when growing in dump soil, the rice roots form a thick cortex (Duarte et al. 1993), and Venkatraman and Thomas (1922) noticed that, for sugar cane cultivars, the relation between the cortex and vascular cylinder thickening was bigger when the plants grow in soaked soils.

There is a direct relation between the root diameter and the number of protoxylem poles in the studied species. For example, in *Catasetum discolor* with 15 poles, the roots possess the biggest diameter, and in *Catasetum pileatum* with eight poles, the roots are the thinnest ones. The occurrence of this relation is reinforced by the fact that although *Cycnoches haagii* and *Catasetum saccatum* present, respectively, the higher number of cortical and velamen layers, they no dot have thick roots due to their small number of protoxylem poles (Table I).

RESUMO

Considerando que a estrutura das raízes de gêneros brasileiros pertencentes à subtribo Catasetinae é pouco conhecida, descrevemos as raízes de doze representantes desta subtribo. Para análise anatômica, as raízes foram fixadas em FAA 50, preservadas em álcool 70% e seccionadas na sua região média usando lâminas de barbear. Os cortes foram corados com astra blue e Safrablau 0,05% e montados em glicerina. Para a identificação do amido, utilizou-se a solução de Lugol; da lignina, floroglucina clorídrica, dos lipídios, Sudan III e dos flavonóides, hidróxido de potássio. Os aspectos relevantes foram registrados usando câmera digital acoplada a um microscópio Olympus (modelo BX51). As semelhancas estruturais observadas entre todas as raízes estudadas confirmam a inclusão da subtribo Catasetinae na tribo monofilética Cymbidieae. Algumas características radiculares são restritas a um ou dois táxons e podem ser úteis na taxonomia da subtribo.

Por exemplo, a ocorrência de cristais flavonoídicos caracteriza os gêneros *Catasetum* e *Cychnodes* e o número de camadas do velame associado à forma das células do epivelame são úteis para confirmar a posição taxonômica de *Clowesia amazônica*. A presença de velame e de cristais flavonoídicos foi interpretada como adaptações ao hábito epifítico.

Palavras-chave: Epifitismo, morfoanatomia, orquídea, sistemática.

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