Rodriguésia 68(4): 1207-1215. 2017
http://rodriguesia.jbrj.gov.br
DOI: 10.1590/2175-78602017684055

The odd roots of *Campylocentrum* (Angraeciinae-Orchidaceae): an anatomical study of its morphologically variable roots

Edlley Pessoa[1,2], *Emília Arruda*[2], *Fillype Fernando da Silva Domingos Pereira*[2] & *Marccus Alves*[1]

Abstract

Although some anatomical studies have been performed in Angraecinae, knowledge about the anatomy of the genus *Campylocentrum* is as yet incipient. The aim of this study is to anatomically characterize the structure of the different kinds of roots in the genus. Roots from 12 species were analyzed, including all the morphological variation in the genus (smooth and granulose surface). The leafless species are characterized by endovelamen, exodermal and endodermal cell walls thicker than in the leafy species. The species with terete leaves can be split in two groups: one constituting *C. poeppigii*, whose roots have a granulose surface produced by numerous unicellular, absorbent hairs; the second formed by six species from the Atlantic Forest. In this second group, the same granulose root appearance is produced by tufts of epivelamen in addition to the unicellular, absorbent root hairs. The other species in the genus, with conduplicate leaves, do not present a pattern for grouping. Some of them, such as *C. serranum* and *C. micranthum*, share a similar structure with the leafless species, but with thinner exodermal and endodermal cell walls. Other species, such as *C. crassirhizum* and *C. jamaicense*, are the only ones in the genus with O-thickened cells in the exodermis.
Key words: anatomy, Neotropics, Vandeae, velamen.

Resumo

Embora alguns estudos anatômicos tenham sido produzidos para Angraecinae, o conhecimento sobre a anatomia do gênero *Campylocentrum* ainda é incipiente. O objetivo desse estudo é caracterizar anatomicamente a estrutura dos diferentes tipos de raízes do gênero. Raízes de 12 espécies foram analisadas, incluindo toda a variação morfológica do gênero (superfície granulosa e lisa). As raízes das espécies áfilas são caracterizadas pelas paredes das células do endovelame, exoderme e endoderme mais espessadas que aquelas das espécies foliosas. As espécies com folhas cilíndricas podem ser separadas em dois grupos: um constituído somente por *C. poeppigii*, que possui raízes com superfície granulosa produzida por numerosos pelos radiculares unicelulares; e um segundo grupo formado por seis espécies da floresta Atlântica, onde a mesma aparência granulosa das raízes é produzida por tufos de epivelame, além da presença de pelos radiculares unicelulares. As outras espécies do gênero, com folhas conduplicadas, não apresentam um padrão para agrupamento. Algumas delas, como *C. serranum* e *C. micranthum*, compartilham uma estrutura similar a das espécies áfilas, mas com paredes das células da exoderme e endoderme mais finas. Outras espécies, como *C. crassirhizum* e *C. jamaicense*, são as únicas no gênero com células da exoderme espessadas em O.
Palavras-chave: anatomia, Neotrópicos, Vandeae, velame.

Introduction

Being a group of epiphytic orchids, *Campylocentrum* has several adaptations for the life form. Some of them permit the existence of leafless plants with chlorophyll-containing roots and with aeration units regulating gas exchange which are analogous to the stomatal complexes of leaves, making the roots the major photosynthetic organ in this group (Schimper 1888; Benzing & Ott 1981; Benzing *et al.* 1983; Pridgeon 1987).

Although some anatomical studies have been performed in subtribe Angraecinae (tribe Vandeae),

[1] Universidade Federal de Pernambuco, Lab. Morfo-Taxonomia Vegetal, Depto. Botânica, CCB, Av. Prof. Moraes Rêgo s/n, 50670-901, Recife, PE, Brasil.
[2] Universidade Federal de Pernambuco, Lab. Anatomia Vegetal, Depto. Botânica, Av. Prof. Moraes Rêgo s/n, 50670-901, Recife, PE, Brasil.
[3] Author for correspondence: edlley_max@hotmail.com

knowledge about the anatomy of the Neotropical genera is still rudimentary. Within the vegetative portion, especially the roots, morphological descriptions are available for nine species of *Campylocentrum* (Carlsward *et al.* 2006; Bogarin & Pupulin 2010).

The first species to be anatomically described was *C. grisebachii* Cogn., a leafless species studied by Goebel (1922). Four other leafless ones were analyzed by Bogarin & Pupulin (2010), Carlsward *et al.* (2006), Stern (2014) and Winter *et al.* (1985). Roots of four leafy species have also been described (Bogarin & Pupulin 2010; Carlsward *et al.* 2006).

A general description of the root anatomy in the genus was provided by Carlsward (2006, 2014). *Campylocentrum* is characterized by a velamen with one to three layers; exodermal cells ∩- to ○-thickened; endodermal cells ○-thickened, and a vascular cylinder with six to nine xylems poles and vascular tissue embedded in sclerenchyma.

Campylocentrum is a Neotropical genus comprising about 70 species which belongs to the subtribe Angraeciinae (Carlsward 2014). According to Cogniaux (1906), the genus can be organized into three sections: *C.* sect. *Campylocentrum* (originally *C.* sect. *Eucampylocentrum*), species with well developed stems and leaves, *C.* sect. *Dendrophylopsis,* leafless species, and the monospecific *C.* sect. *Pseudocampylocentrum,* species with developed stems but reduced leaves.

Campylocentrum sect. *Campylocentrum sensu* Cogniaux (1906) includes two groups with different leaf and root morphology, one with conduplicate leaves and a smooth external root surface (the typical velamen in orchids), and another group with terete leaves and a granulose to tuberculate external root surface (an unusual velamen) (Pessoa & Alves 2016) (Fig. 1a-d).

The group of species with terete leaves, included by Cogniaux (1906) in *C.* sect. *Campylocentrum*, has never been analyzed anatomically before. However, roots with a granulose surface are present in at least one genus of Vandeae (*Microcoelia* Lindl., *vide* Cribb 2015), but is not clear if this feature is analogous in these genera.

The aim of this study is to anatomically describe the roots in species of *Campylocentrum* and their variation. This information will provide a better understanding of the genus and possibly support the taxonomic groups proposed by Cogniaux (1906) based on anatomical variation.

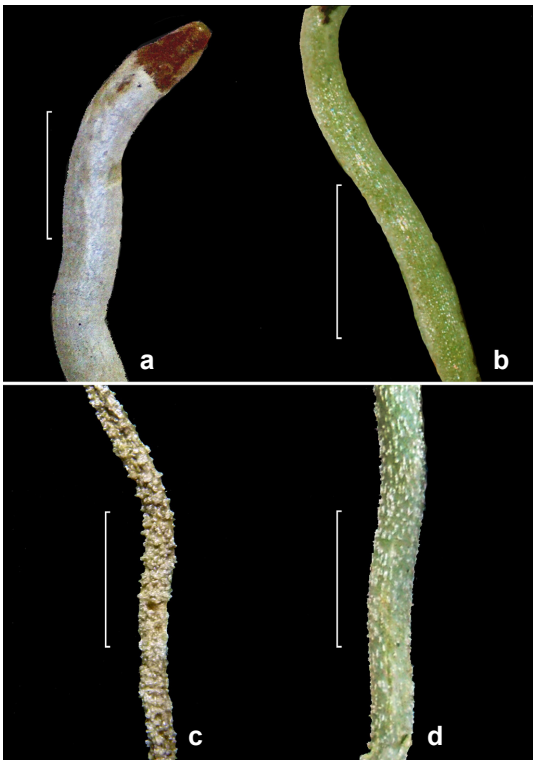

Figure 1 – a-d. fresh roots – a. *C. crassirhizum*; b. *C. paludosum*; c. *C. ornithorrhynchum*; d. *C. poeppigii*. Scale bar = 1 cm.

Material and Methods

Roots from 12 species were studied, eight of which were collected in the field and four from herbarium specimens (Tab. 1). Sampling included the three sections of the genus, organized here in three morphological groups: leafless plants (2 spp.); leafy with smooth velamen (3); leafy with granulose velamen (7). For ten species, only one specimen of was analyzed due to their rareness (Tab. 1).

Samples of the median area of young roots of species collected in the field were fixed in 50% formaldehyde-Acetic acid- Alcohol (50% FAA) or in 1% glutaraldehyde + 4% formaldehyde in 0.1M sodium phosphate buffer, at pH 7.2 for 48h (McDowell & Trump 1976), then washed and stored in 70% ethanol (Johansen 1940). Materials obtained from herbarium specimens were rehydrated in boiled water with 50% glycerin, then washed thoroughly in tap water, and stored in 70% ethanol (Smith & Smith 1942, modified).

All samples were dehydrated in an increasing ethanol/tertiary butyl alcohol series and embedded

Table 1 – Species studied (LL = Leafless; SM = leafy with smooth roots; GR = leafy with granulose roots; CA = *C.* sect. *Campylocentrum*; DE = *C.* sect. *Dendrophylopsis*; PS = *C.* sect. *Pseudocampylocentrum*).

Species	Voucher	LL	SM	GR	CA	DE	PS
C. crassirhizum	*E. Pessoa et al.1092* (UFP) *E. Pessoa et al. 1187* (UFP)		×		×		
*C. grisebachii***	*E. Pessoa & B.M. Carvalho 1188* (UFP)	×				×	
*C. labiaki**	*D.A. Folli 2150* (RB)			×	×		
C. micranthum	*E. Pessoa et al. 1217* (UFP)		×		×		
C. ornithorrhynchum	*E. Pessoa et al. 1239* (UFP) *R.Romanini 18135* (SP)			×	×		
C. paludosum	*M. Mirana 87* (UFP)	×				×	
*C. parahybunense**	*A. Korte & A. Kniess 2230* (FURB)			×	×		
C. pernambucense	*E. Pessoa et al. 1085* (UFP)			×	×		
*C. poeppigii**	*E. Pessoa et al. 693* (UFP)			×			×
C. sellowii	*E. Pessoa & B.M. Carvalho 1189* (UFP)			×	×		
C. serranum	*E. Pessoa et al.945* (UFP)		×		×		
*C. wawrae**	*R.C. Mota 3153* (BHCB)			×	×		

*Herbarium specimens; **three specimens under the same voucher.

in paraffin (Ruzin 1999). Transverse (TS) and longitudinal (LS) sections of the roots were cut on a rotary microtome (10–12 μm) and stained with Astra blue and safranin (9:1), a modification of the methodology described by Bukatsch (1972). The slides were mounted in Canada balsam. The sections were submitted to histochemical analyses with Ferric chloride (Johansen 1940), Lugol (Johansen 1940), Sudan IV (Pearse 1985), for the detection of phenolic substances, starch and lipids respectively. The sections submitted to histochemical treatment were not mounted. The material was analyzed and all images captured by an Olympus CX31 and Leica DM500 microscope with the aid of Leica software.

Results

Velamen

In *Campylocentrum* the velamen comprises two layers in the majority of the species studied (Figs. 2a,b,d-e; 3a-c), except to *C. crassirhizum* and *C. ornithorrhynchum* with two to three layers of cells (Tab. 2).

The epivelamen is composed of only one layer in all species analyzed, the cells were isodiametric (Fig. 3a-c) to radially elongated (Fig. 3d), and U-thickened in almost all species analyzed (Fig. 3a-d), except in *C. ornithorrhynchum* (thin walled) (Figs. 2a-e; 3a-d). Although epivelamen tufts were not cited by Carlsward (2006, 2014) for the genus, they occur in *C. labiakii* Pessoa & Alves*, C. ornithorrhynchum, C. parahybunense* (Barb. Rodr.) Rolfe, *C. pernambucense* Hoehne, *C. sellowii* (Rchb.f. & Warm.) Rolfe, and *C. wawrae* (Rchb.f. & Warm.) Rolfe (Tab. 2; Fig. 2b-d). The tufts are formed by randomly distributed cells which extend externally from the epivelamen; the subtending cells in the tufts are sometimes elongated as well (Fig. 2b-d).

On the other hand, absorbent root-hairs were observed in *C. labiaki, C. parahybunense, C. poeppigii* (Rchb.f.) Rolfe, and *C. wawrae* (Tab. 2; Fig. 2e). Linear thickenings, forming stretch marks or channels in the cell walls of the epivelamen, were observed in almost all species analyzed (Fig. 3a).

The endovelamen comprised one or two layers of cells in *C. crassirhizum, C. ornithorrhynchum*, and only one layer of cells in all other species examined (Tab. 2; Figs. 2; 3). Endovelamen cells were radially elongated, the external layer was ○-thickened, and the internal layer, when present, was ∩-thickened (Figs. 2c; 3a-d).

Cortex

The number of cell layers in the cortex varies from six to 14 - *C. grisebachii*, *C. micranthum*, *C. pernambucense*, *C. sellowii*, and *C. serranum* have up to seven layers, while only *C. poeppigii* and *C. wawrae* have 11 to 14 (Tab. 2; Fig. 2a,b).

Exodermal cells were radially elongated in all species, being ○-thickened in *C. crassirhizum* and ∩-thickened in all other species analyzed (Tab. 2; Figs. 2; 3). Aeration complexes were observed only in *C. grisebachii* and *C. pernambucense* (Fig. 3b). The endodermis consisted of one layer of hexagonal cells in all species, being ○-thickened with the presence of passage cells in almost all of them, except in *C. parahybunense, C. sellowii*, and *C. serranum*, whose cells were thin walled and passage cells were absent (Tab. 2; Fig. 4a-e).

Fungal hyphae were observed only in *C. crassirhizum* (cortex and velamen), *C. grisebachii* and *C. serranum* (cortex) (Fig. 5a). Water-storage idioblasts were present in the cortical parenchyma of *C. grisebachii* and *C. ornithorrhynchum* (Fig. 5b).

Raphides and starch grains were observed in the cortex of all species analyzed (Fig. 5c,d).

Stele

The pericycle had one cell layer in *C. grisebachii*, *C. labiaki, C. ornithorrhynchum*, *C parahybunense,C. poeppigii*, *C. sellowii* and *C. wawrae* (Fig. 4a-e), and one to two layers of cells in *C. crassirhizum, C. paludosum*, *C. pernambusence*, *C. micranthum*, and *C. serranum* (Fig. 4a-e). Pericyclic cells were thin-walled opposite xylem and thick-walled opposite phloem tissue (Fig. 4a-e). Pith cell walls were thickened in *C. crassirhizum*, *C. grisebachii*, *C. ornithorrhynchum,* and *C. pernambucense* (Fig. 4a-e).

Steles were composed of alternating clusters of xylem and phloem cells with six protoxylem poles in *C. crassirhizum*, *C. labiaki*, *C. pernambucense*, *C. serranum* and *C. wawrae;* seven poles in *C.*

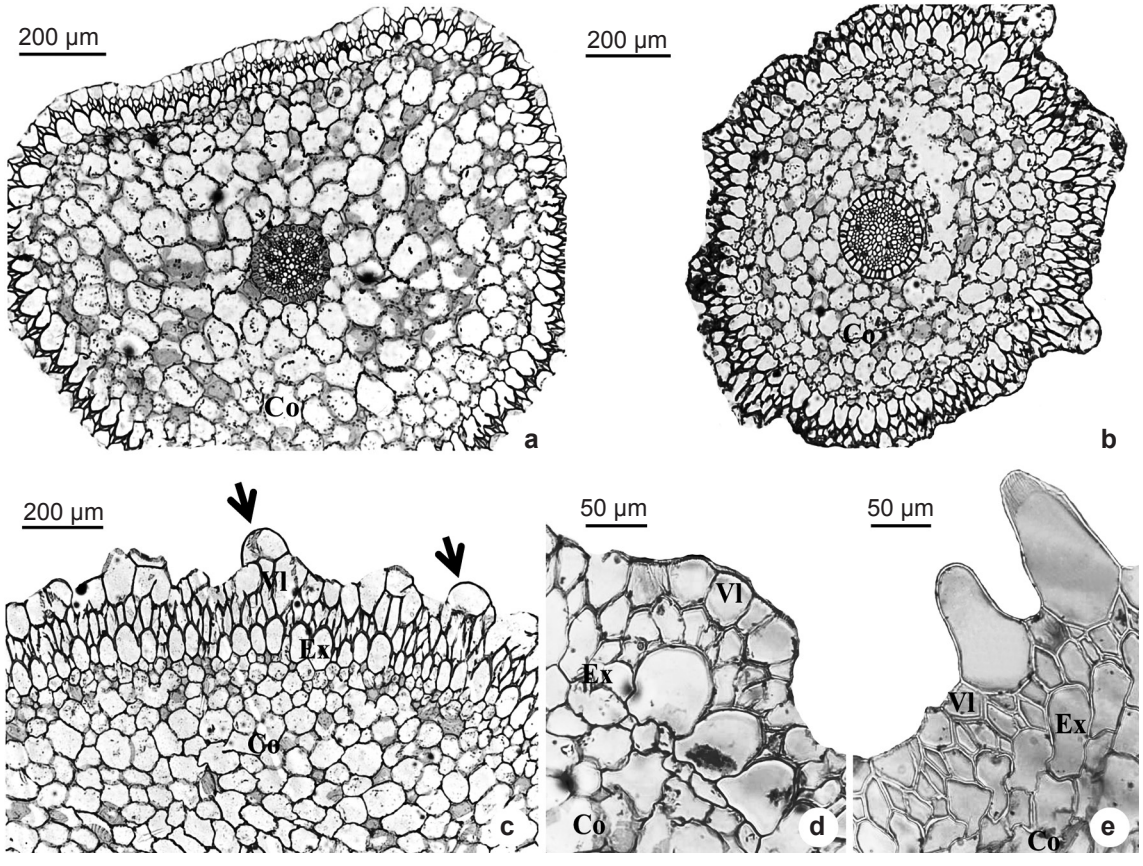

Figure 2 – a-e. roots, TS – a. general aspect of *Campylocentrum grisebachii*; b. general aspect of *Campylocentrum pernambucense*; c. undulating epivelamen with tufts in *Campylocentrum ornithorryncum*; d. undulating epivelamen with tufts in *Campylocentrum pernambucense*; e. epivelamen showing absorbent root-hairs in *Campylocentrum poeppigii*. (Co = Cortex; Ex = Exodermis; Vl = Velamen; Arrows = tufts).

Table 2 – Principal anatomical root characters used to distinguish species of *Campylocentrum*.

	Velamen	Absorbent root hairs	Tufts	Exodermis	Cortex	Endodermis	Number of poles
C. crassirhizum	2–3-layered	Absent	Absent	○-tichened	7–10-layered	○-tichened	6
C. grisebachii	2-layered	Absent	Absent	∩-thickened	6–7-layered	○-thickened	7
C. labiaki	2-layered	Present	Present	∩-thickened	7-layered	○-thickened	6
C. micranthum	2-layered	Absent	Absent	∩-thickened	6–7-layered	○-thickened	9
C. ornithorrhynchum	2–3-layered	Absent	Present	∩-thickened	8–10-layered	○-thickened	11
C. paludosum	2-layered	Absent	Absent	∩-thickened	9–10-layered	○-thickened	7
C. parahybunense	2-layered	Present	Present	∩-thickened	8–10-layered	Thin walled	9
C. pernambucense	2-layered	Present	Present	∩-thickened	7-layered	○-thickened	6
C. poeppigii	2-layered	Present	Absent	∩-thickened	11-layered	Thin walled	9
C. sellowii	2-layered	Absent	Present	∩-thickened	6–7-layered	Thin walled	8
C. serranum	2-layered	Absent	Absent	∩-thickened	6–7-layered	Thin walled	6
C. wawrae	2-layered	Present	Present	∩-thickened	11–14-layered	○-thickened	6

grisebachii and *C. paludosum*; eight poles *C. sellowii*; nine poles in *C. micranthum*, *C. parahybunense* and *C. poeppigii*; and eleven poles in *C. ornithorrhynchum* (Tab. 2; Fig. 4a-e).

Discussion

According to Porembski & Barthlott (1988) the velamen of orchids is classified into 12 types. *Campylocentrum* fits within the "*Vanda* Type", which is characterized by a less than five-layered velamen, differentiated into large-celled epivelamen and comparatively small-celled endovelamen, the latter with cell walls thicker than those of the epivelamen; exodermis cells often much larger than the velamen cells; and tracheoidal idioblasts in the cortex occasionally present. The structure of the roots of *Campylocentrum* and its sister genus *Dendrophylax* (Carlsward *et al.* 2003) is very similar, making it impossible to distinguish them solely by these overlapping characters (Carlsward *et al.* 2006).

Although absorbent root hairs were observed here in five species and also in *C. generalense* by Bogarin & Pupulin (2010) and C. *pachyrrhizum* by Carlsward *et al.* (2006), they were more numerous in *C. peoppigii* and gave the velamen surface a slightly granulose texture (Fig. 1d). On the other hand, the same surface texture is found in other species, where it is produced by tufts of epivelamen, and according to Carlsward *et al.* (2006), it can also be found in *Tridactyle* Schltr., an African genus of Angraeciinae.

According to the general anatomical description of the root structure in the genus provided by Carlsward *et al.* (2006), ○-thickened cells in the exodermis had only been observed in *C. jamaicense* [published as *C. micranthum*, voucher checked and corrected (*Ackerman 3341*)] by Carlsward *et al.* (2006). Such cells were found here also in *C. crassirhizum*, which is morphologically related to *C. jamaicense*. Both species share oblong, conduplicate leaves with a strongly 2-lobed apex (Pessoa *et al.* 2015). The majority of species have the exodermis with ∩-thickened cell walls, however they were apparently thicker in the leafless species (although we did measure it), a state which was also observed by Bogarin & Pupulin (2010) in *C. generalense*. The function of the thicker endovelamen, exodermal and endodermal cell walls in this group is unclear, but may be indicative of a means to prevent water loss via transpiration and also to provide support and protect the cortex and the vascular tissue from mechanical damage and cell collapse during periods of drought dryness (Noel 1974; Benzing & Ott 1981; Benzing *et al.* 1982; Benzing *et al.* 1983; Carlsward *et al.* 2006).

Although Carlsward *et al.* (2006) describe the endodermal cells as ○-thickened for all species in the genus, in *C. parahybunense, C. poeppigii, C. sellowii* and *C. serranum* the endodermial cells were thin walled (Fig. 4d). The walls of the endodermal cells in the leafless species were thicker, as also observed by Bogarin & Pupulin (2010).

Carlsward *et al.* (2006) analyzed roots with six to nine poles in the vascular cylinder but *C. ornithorrhynchum*, with 11 poles, holds the record for the highest number found in the genus. According to Pridgeon (1987), the number of poles is consistent and is useful for delimiting species of Orchidaceae. However, according to Rütter & Stern (1992) it can vary among different specimens of the same species and also in the same root at different height levels. Meanwhile, Rütter & Stern (1992) and Rosso (1966) indicated that root diameter and the number of poles of protoxylem are related. Ontogenetic studies must confirm the variation of number of poles and its use as diagnostic character in the family. This is the main reason why no claim for species delimitation in *Campylocentrum* can be stated yet on this matter. Additionally, no correlation between the number of poles root diameter has been found too which is exemplified in *C. crassirhizum* and *C. sellowii*. For these two species which have thicker roots, six and eight poles respectively were found. For other species of *Campylocentrum* with thinner roots, nine and eleven poles were found.

In summary, the leafless species analyzed show the same basic structure, with a two-layered velamen, endovelamen, exodermal and endodermal cell walls thicker than those in the leafy species, and vascular cylinder with six or seven xylem poles (Fig. 6c,g).

The group of species with terete leaves and granulose roots can be split in two. One group comprises a single species, *C. poeppigii*, known

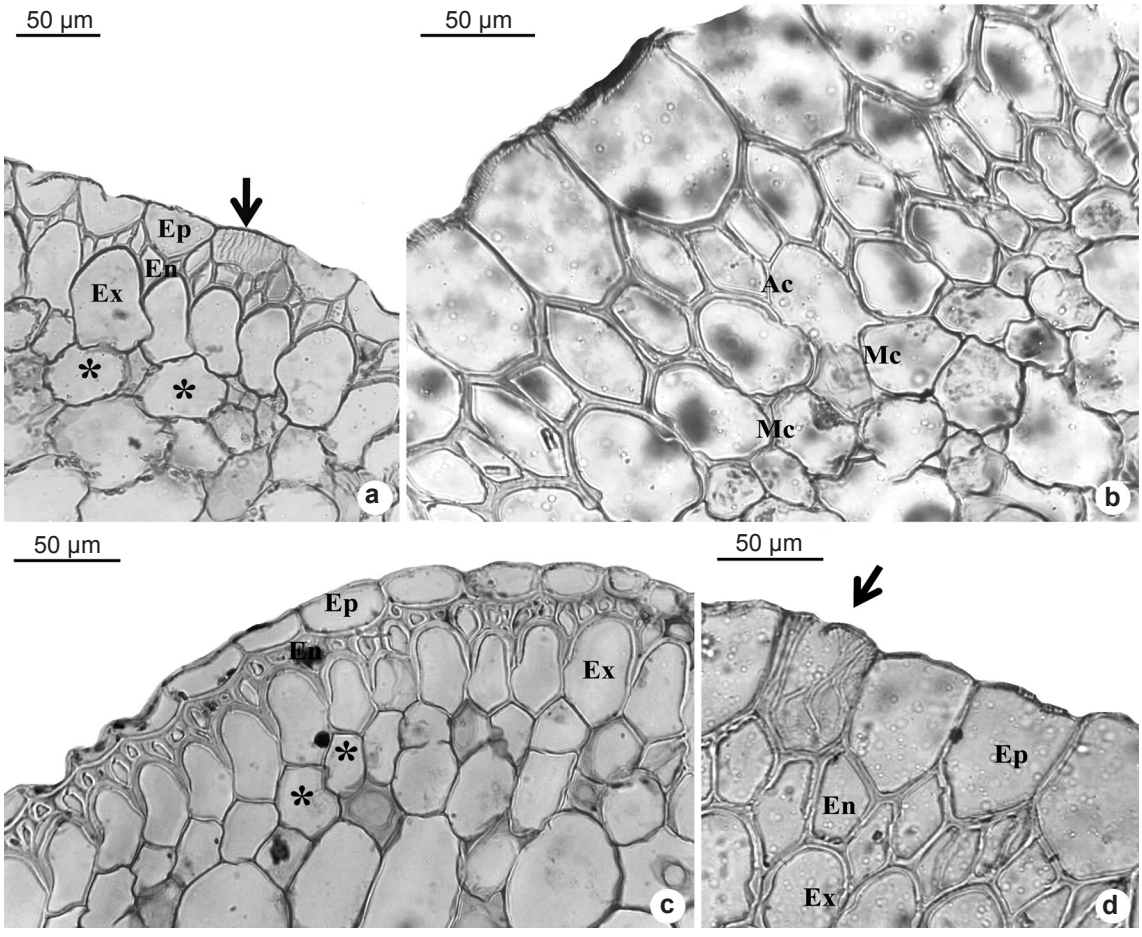

Figure 3 – a-e. roots, TS – a. *Campylocentrum parahybunense*, endovelamen (En) cells radially elongate and exodermis (Ex) showing ∩-thichened cell walls, cells with linear thickening forming pores in the cell walls (arrow); b. aeration complex (Ac) in *Campylocentrum grisebachii*, endovelamen (En) showing one layer of ○-thickened cells; c. *Campylocentrum paludosum* showing endovelamen with thicker cell walls; d. cells with linear thickening forming stretch marks or channels in the cell walls (arrow) in *Campylocentrum crassirhizum*. (En = Endovelamen; Ep = Epivelamen; Ex = Exodermis; Mc = Modified cortical cell.

from Mexico to northern Brazil and included in *C.* sect. *Pseudocampylocentrum*, in which the granulose surface is produced by numerous unicellular, absorbent hairs (Fig. 6d,h). The second sub-group is formed of six species distributed along the Atlantic coast of Brazil and included in *C.* sect. *Campylocentrum*, their roots have a similar external morphology, but in this case all species have tufts of epivelamen in addition to unicellular, absorbent root hairs (Fig. 6b,f). This second sub-group had not been anatomically analyzed before, making this study the first to describe its roots.

The other species in the genus (with conduplicate leaves and smooth roots) do not present any patterns for grouping. Some of them, such as *C. serranum* and *C. micranthum*, have a structure similar to the leafless species, but with thinner exodermal and endodermal cell walls. Other species,

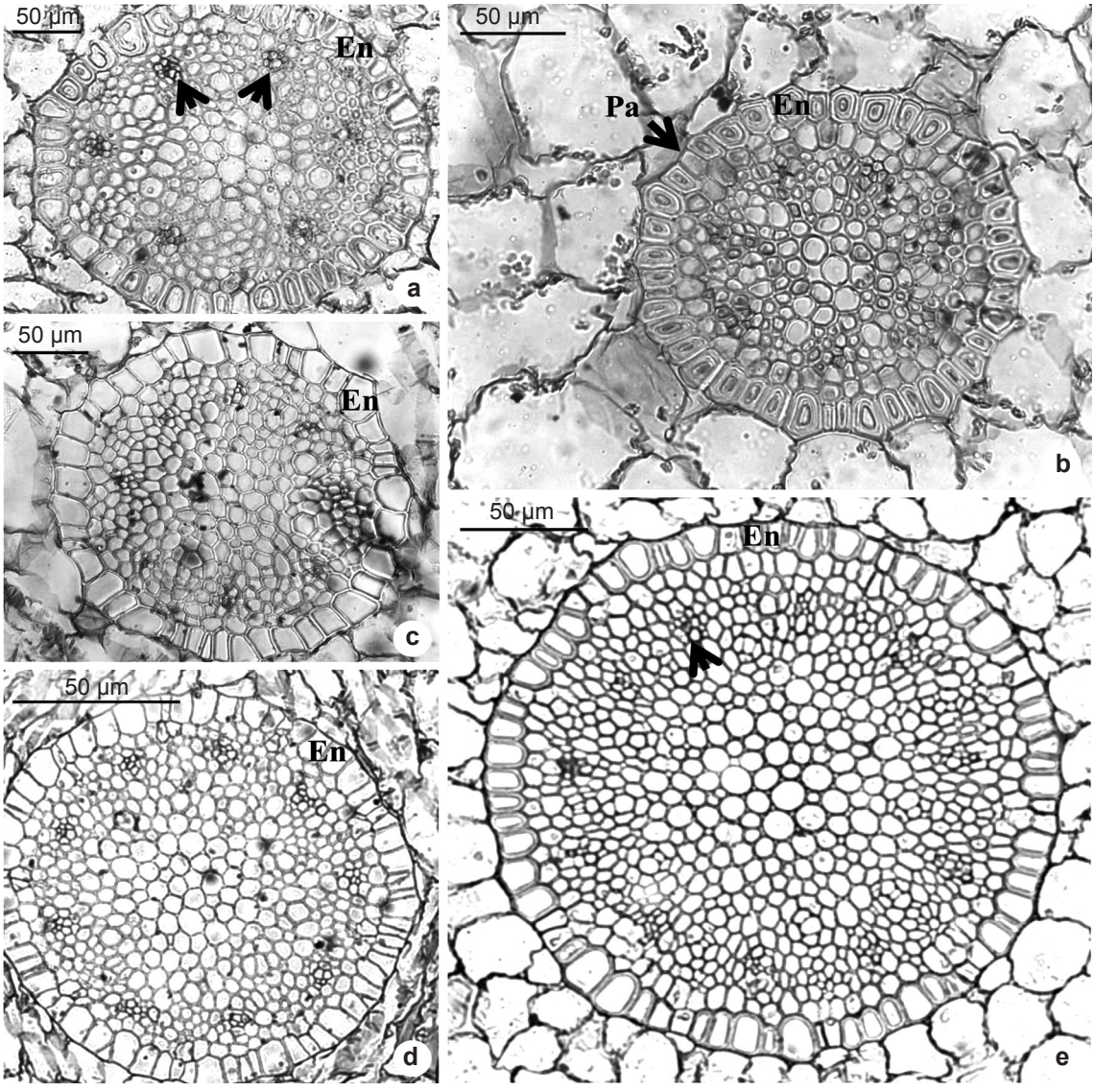

Figure 4 – a-e. roots, TS showing stele – a. six protoxylem poles in *Campylocentrum crassirhizum*. Note endodermis (En) cells ○-thickened; b. seven protoxylem poles and endodermis (En) cells ○-thickened in *Campylocentrum grisebachii*. Note passage cells (Pa) in the endodermis; c. eight protoxylem poles in *Campylocentrum sellowii*. Note endodermis (En) cells are thin walled; d. nine protoxylem poles and endodermis (En) cells thin walled in *Campylocentrum poeppigii*; e. eleven protoxylem poles and endodermis (En) cells ○-thickened in *Campylocentrum ornithorrynchum*. (Arrow = Phloem; En = Endodermis).

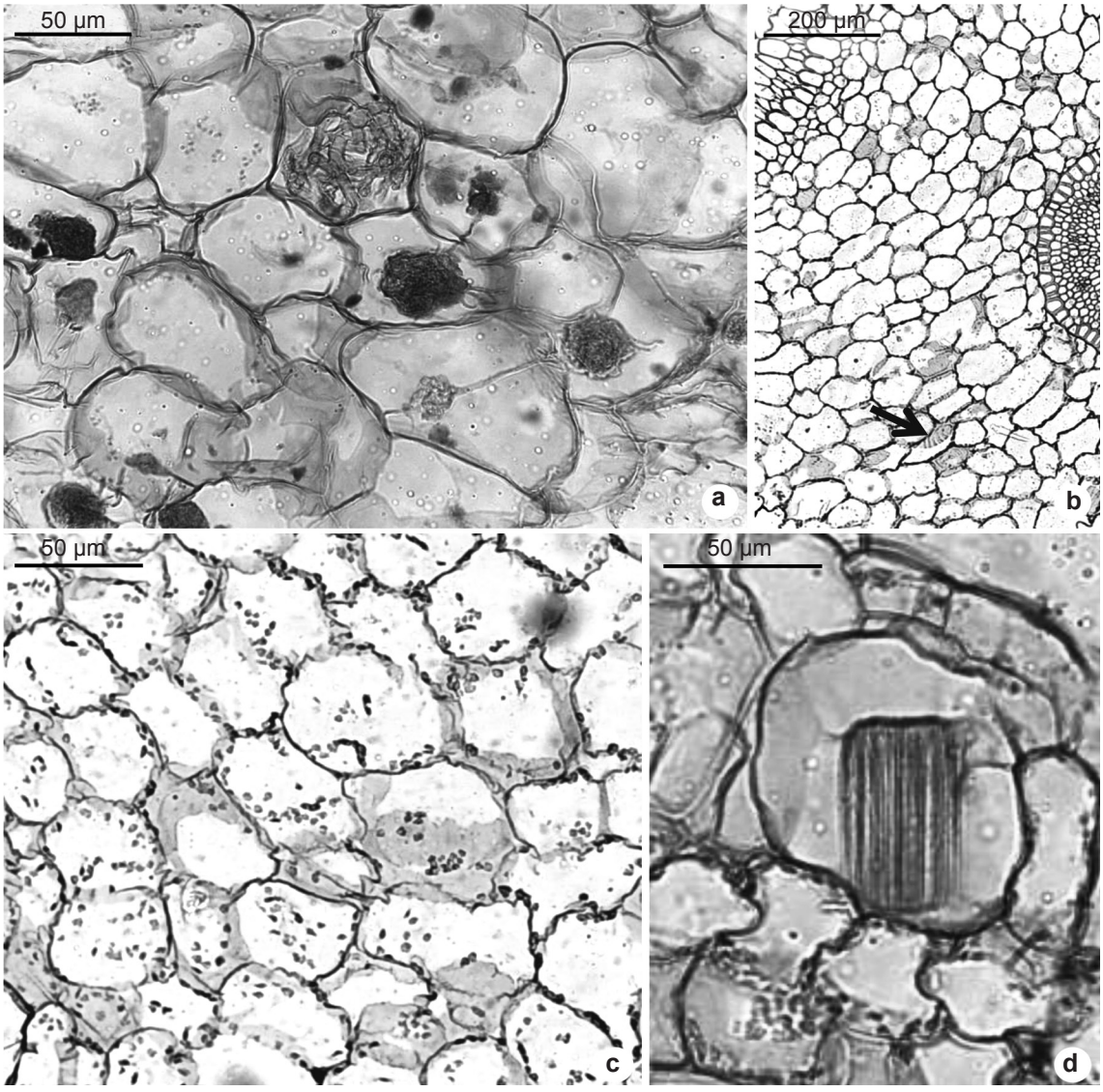

Figure 5 – a-d. roots, TS – a. fungal hyphae in cortex of *Campylocentrum serranum*; b. water-storage idioblasts (arrow) in cortex of *Campylocentrum ornithorrhyncum*; c. starch grains in cortex of *Campylocentrum wawrae*; d. root LS showing one raphide crystal in cortex of *Campylocentrum grisebachii*.

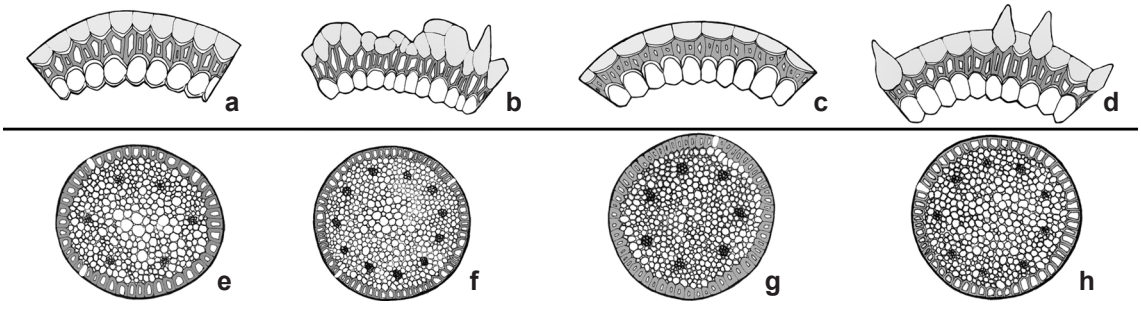

Figure 6 – a-h. schemes of the main types of roots in TS – a-d. velamen + exodermis – a. *C. crassirhizum*; b. *C. ornithorrhynchum*; c. *C. paludosum*; d. *C. poeppiggii* (epivelamen = light gray; endovelamen = dark gray; exoderm = White); e-h. endodermis + stele – e. *C. crassirhizum*; f. *C. paludosum*; g. *C. ornithorrhynchum*; h. *C. poeppiggii* (endodermis = dark gray; xylem poles = black).

such as *C. crassirhizum* and *C. jamaicense*, are the only ones in the genus known to have ○-thickened cells in the exodermis (Fig. 6a-e).

Acknowledgments

We are indebted to those who funded our field research, including CAPES, CNPq, INCT-Herbário Virtual, the U.S. National Science Foundation (DEB-0946618), Velux Stiftung, and the Beneficia Foundation. The authors thank Regina Carvalho for the line drawing, Scott Heald for his review of the English of the manuscript, and two reviewers for their valuable suggestions.

References

Benzing DH & Ott DW (1981) Vegetative reduction in epiphytic Bromeliaceae and Orchidaceae: its origin and significance. Biotropica 13: 131-140.

Benzing DH, Ott DW & Friedman WE (1982) Roots of *Sobralia macrantha* (Orchidaceae): structure and function of the velamen-exodermis complex. American Journal of Botany 69: 608-614.

Benzing DH, Friedman WE, Peterson G & Renfrow A (1983) Shootlessness, velamentous roots, and the pre-eminence of Orchidaceae in the epiphytic biotope. American Journal of Botany 70: 121-133.

Bogarín D & Pupulin F (2010) The genus Campylocentrum (Orchidaceae: Angraecinae) in Costa Rica: a revision. Harvard Papers in Botany 15: 353-414.

Bukatsch F (1972) Bemerkungen zur Doppelfärbung Astrablau-Safranin. Microkosmos 61: 255.

Carlsward BS, Whitten WM & Williams NH (2003) Molecular phylogenetics of neotropical leafless Angraecinae (Orchidaceae): reevaluation of generic concepts. International Journal of Plant Sciences 164: 43-51.

Carlsward BS, Stern WL & Bytebier B (2006) Comparative vegetative anatomy and systematics of the angraecoids (Vandae, Orchidaceae) with an emphasis on the leafless habit. Botanical Journal of Linnean Society, 151: 165-218.

Carlsward BS (2014) *Campylocentrum*. *In*: Pridgeon AM, Cribb PJ, Chase MW & Rasmussen FN (eds.) Genera Orchidacearum. Vol. 6. Oxford University Press, Oxford. Pp. 370-372.

Cogniaux CA (1906) *Campylocentrum*. *In*: Martius CFP Von, Eichler AW & Urban I (eds.) *Flora brasiliensis*. Typographia Regia C. Wolf *et* fil., Monachii *et* Lipsie. Vol. 3, pars 6, pp. 503-524.

Cribb P (2015) *Microcoelia*. *In*: Pridgeon AM, Cribb PJ.; Chase MW & Rasmussen FN (eds.) Genera Orchidacearum. Vol. 6. Oxford University Press, Oxford. Pp. 407-411.

Johansen D (1940) Plant Microtechnique. McGraw-Hill Book Company, Inc, New York. 523p.

Goebel K von (1922) Erdwurzel mit Velamen. Flora (Jena) 115: 1-25.

McDowell EM & Trump B (1976) Histological fixatives for diagnostic light and electron microscopy. Archives of Pathololgy & Laboratory Medicine 100: 405-414.

Noel ARA (1974) Aspects of cell wall structure and development of the velamen in *Ansellia gigantea* Reichb. f. Annals of Botany 38: 495-504.

Pearse AGE (1985) Histochemistry - theoretical and applied: preparative and optical technology. Churchill Livingston, Edinburgh. 624p.

Pessoa E, Maciel JR & Alves M (2015) *Campylocentrum brevifolium* (Lindl.) Pessoa E & Alves M. A neglected orchid species from Atlantic Forest of Brazil. Kew Bulletin 70: 43.

Pessoa E & Alves M (2016) Taxonomic revision of *Campylocentrum* (Orchidaceae-Vandeae-Angraecinae): species with terete leaves. Systematic Botany 41: 700-713.

Porembski S & Barthlott W (1988) Velamen radical micromorphology and classification of Orchidaceae. Nordic Journal of Botany 8: 117-137.

Pridgeon AM (1987) The velamen and exodermis of orchid roots. *In*: Arditti J (ed.). Orchid biology: reviews and perspectives. Cornell University Press, Ithaca. Pp. 30-56.

Rosso SW (1966) The vegetative anatomy of the Cypripedioideae (Orchidaceae). Journal of Linnean Society, Botany 59: 309-341.

Rütter BE & Stern WL (1992) An assessment of quantitative features of velamen stratification and protoxylem strands in roots of Orchidaceae. Lindleyana 9: 219-225.

Ruzin SE (1999) Plant Microtechnique and Microscopy. Oxford University Press, New York. 322p.

Schimper AFW (1888) Die epiphytische vegetation Amerikas. Botanische Mitteilungen aus den Tropen, II. Gustave Fischer Verlag, Jena. 173p.

Smith FH & Smith EC (1942) Anatomy of the inferior ovary of Darbya. American Journal of Botany 29: 464-471.

Stern LW (2014) Anatomy of the Monocotyledons. Volume X: Orchidaceae. Oxford University Press, Oxford. 262p.

Winter K, Medina E, Garcia V, Mayoral ML & Muniz R (1985) Crassulacean acid metabolism in roots of a leafless orchid, Campylocentrum tyrridion Garay & Dunsterv. Journal of Plant Physiology 118: 73-78.

Editor de área: Dr. Diego Demarco
Artigo recebido em 05/09/2016. Aceito para publicação em 14/02/2017.