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Anatomy of the adventitious roots of *Philodendron* (Araceae) and its importance for the systematics of the genus

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Abstract. The genus *Philodendron* Schott comprises the following three currently accepted subgenenera: *P.* subg. *Philodendron, P.* subg. *Pteromischum* and *P.* subg. *Meconostigma*; however, these lack a well-defined classification. In the present study, we examined anatomically samples of adventitious roots in species of the group, so as to establish aspects relevant for taxonomic purposes. The anatomical analyses emphasised the characteristics of the steles in cross-sections of the root samples from regions near the apex to the most mature zones. A species of a closely related genus *Adelonema*, namely *A. crinipes*, was included in the study to clarify the results. Our results indicated notable differences in the species of the subgenus *Meconostigma*, mainly in terms of the presence (and variations) of a lobed stele, whereas the cylindrical stele stood out among the common characteristics in *P.* subg. *Philodendron*, *P.* subg. *Pteromischum* and the related species *A. crinipes*. Moreover, the characteristics shared by *P.* subg. *Philodendron* and *P.* subg. *Pteromischum* corroborated the phylogenetic hypothesis that these two taxa were more closely related to one another than to *P.* subg. *Meconostigma.*

Additional keywords: lobed stele, *Meconostigma*, root anatomy, taxonomy.

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Introduction

Philodendron Schott is the second-largest genus in the Araceae family in numbers of species and its representatives are found in many different habitats (Mayo *et al*. 1997; Govaerts and Frodin 2002). Studies conducted by Mayo (1988, 1989, 1991) contributed greatly to the taxonomy of the genus, especially the designations of the subgenera *Philodendron*, *Pteromischum* and *Meconostigma* as currently accepted. The most recent review was performed by Krause (1913); however, there is still no definitive classification for this genus (Gauthier *et al*. 2008), emphasising the importance of analyses in species of the group, so as to complement molecular studies that have indicated the need for phylogenetic alterations.

Phylogenetic work by Mayo (1989) considered *P.* subg. *Meconostigma* as a sister group to the subgenera *Philodendron* and *Pteromischum*, whereas the studies conducted by Loss-Oliveira *et al*. (2016) found subgenus *Meconostigma* to be monophyletic, whereas subgenus *Philodendron* was polyphyletic, grouping with *Pteromischum* species. However, Loss-Oliveira *et al*. (2016) consider the genus *Philodendron* as monophyletic. Gauthier *et al*. (2008) established possible phylogenetic hypothesis involving the genera *Philodendron* and *Homalomena*. These authors positioned *P.* subg. *Pteromischum* as the sister group to *Homalomena americana*, forming the sister group with other subgenera *Philodendron* and *Meconostigma*. This hypothesis would result in the inclusion of *H. americana* in the genus *Philodendron*. The genus *Homalomena* is a polyphyletic group, with neotropical and Asian species of *Homalomena* forming different clades (Gauthier *et al*. 2008). The neotropical *Homalomena* species were subdivided into section *Adelonema* and section *Curmeria*; the following new species were proposed: *Adelonema orientalis*, *A. palidinervia*, *A. panamensis* and *A. yanamonoensis* (Yeng *et al*. 2016).

Thus, the genus *Philodendron*, *Adelonema* and *Curmeria* form a monophyletic group.

The roots of *Philodendron* species show significant differences in terms of morphological and anatomical characteristics (French 1987*a*, 1987*b*; Mayo *et al*. 1997). These distinctions are important for facilitating the identification of root types and can potentially be taxonomically informative characteristics for the group. Previous studies on the adventitious roots of *Philodendron* have identified anatomical differences among the different subgenera, such as the presence of a lobed stele (or variations in this form), which was observed only in species *P.* subg. *Meconostigma* (Mayo 1991; Tenorio *et al*. 2014). Thus, so as to examine the possible existence of interspecific and intraspecific morphological variation, it is necessary to investigate the types of roots found in the species of the genus to determine its taxonomic and phylogenetic importance.

Dimorphism is frequently observed in the roots of *Philodendron*, with the presence of feeding roots and anchor roots on the same plant. This could be due to the function of the root, because the feeding roots reach the soil and absorb nutrients, whereas the anchor roots provide support for the plant (Mayo *et al*. 1997). According to Mayo *et al*. (1997), in *Araceae* with root dimorphism, the anchor roots are more abundant than are the feeders in some stem nodes. Tenorio *et al*. (2014) suggested that these types need to be reviewed, given the variety of habits that occur among distinct species, or even among individuals of the same species.

Because of the morphological diversity and different habits, the roots of the species in the group tend to present morpho-functional variation, even among populations of the same species, such as the form of the stele in individuals of *P. corcovadense* (Tenorio *et al*. 2014); however, some anatomical characteristics may occur in response to environmental conditions. The presence of a sclerified exodermis, for example, was conceptualised by French (1987*a*) as a diagnostic character for *Philodendron*. This characteristic is perceived to occur in response to the environment when desiccation of other tissues may occur (Tenorio *et al*. 2014), showing that these roots have the ability to adapt when exposed to adverse environmental conditions.

Some anatomical similarities between the species of the genus *Philodendron* Schott and genus *Homalomena* Schott have been observed, such as the presence of a sclerified exodermis and resin ducts with a sclerified sheath (French 1987*a*, 1987*b*), and a closer phylogenetic relationship between the groups has been suggested, as previously mentioned.

The present study was designed to investigate the anatomy of the adventitious roots of *Philodendron* species, including the related species *Adelonema crinipes* (Engl.) Sy.Y.Wong & Croat (=*Homalomena crinipes* Engl.), so as to identify useful taxonomic characteristics to elucidate the systematic relationships and, subsequently, discuss these observations in terms of phylogenetic hypotheses that were presented for the subgenera.

Materials and methods

Botanical material

Adventitious roots of 20 species of the genus *Philodendron* (Table 1) were collected in their natural habitat, representing a variety of habits, namely terrestrial, epiphyte, rupestral and nomadic vines (ex hemiepiphytes, see Zotz 2013). We consulted experts on this family of plants for selection and collection of species, so as to ensure the viability of the collection and correct identification of the material. The material was fixed in FPA (50 mL of 95% ethanol, 5 mL of propionic acid, 10 mL of formaldehyde and 35 mL of distilled water; Ruzin 1999) and stored in 70% ethanol (Johansen 1940). Three individuals of each species were examined and the control specimens were deposited in the Herbarium of the National Museum (R) and Jardim Botanical Garden, Rio de Janeiro (JB). Eleven species of the subgenus *Philodendoron* were studied, representing their sections and including seven of *Meconostigma* and two of the subgenus *Pteromischum*. So as to complement the analysis, a species of the genus *Adelonema* (*A. crinipes*) was included (Table 1).

Optical microscopy

Free-hand cross-sections were cut with the aid of the Ranvier microtome from the regions close to the root apex up to the most mature zones. Thinner sections of the most mature regions were obtained by fixing samples in pure polyethylene–glycol (PEG) and sectioning to a thickness ranging from 18 to 20 μm with a Spencer rotary microtome (Burger and Richter 1991). For *A. crinipes*, longitudinal sections were also cut. The sections were clarified in 70% sodium hypochlorite, neutralised in acetic acid 30% and washed in distilled water. Mixture of Astra blue and safranin (Bukatsch 1972) was used for staining. Subsequently, the sections were dehydrated in an increasing alcohol series, transferred to xylene and assembled with permount to obtain permanent sildes (Johansen 1940).

In the present work, roots with a differentiated metaxylem, and also those with a cork layer when fully formed, were considered mature.

Documentation

Images of optical microscopy were obtained by using a video camera Olympus Q Colour 5 coupled with a microscope Olympus BX, at the Department of Botany, National Museum, Universidade Federal do Rio de Janeiro, Brazil.

Results

External morphology

The species of the subgenera *Philodendron* and *Pteromischum* have thin roots (Fig. 1A–D). The subgenus *Meconostigma* has thicker and more rigid roots, especially in terrestrial individuals and in regions farther away from the root apex (Fig. 1E, F). All examined roots presented younger, thinner regions with lateral roots, and frequently presented hairs. The feeding roots and those of terrestrial plants were often quite long (>1 m). *Adelonema crinipes* is a rhizomatous herb in which root dimorphism is not established. In this species, short and slender roots, with projections of small lateral roots along the entire length of the organ, were observed (Fig. 2A–C).

Anatomy

The root epidermis did not demonstrate any characteristics that were satisfactorily informative in terms of the taxonomy of the studied groups, consisting of one or two cell layers in most of the

Table 1. Species studied

Subgenus	Section	Species	Habit	Location of collection	Voucher
Philodendron	Calostigma	*Philodendron billietiae* Croat	Nomadic vines	Reserva Ducke, Manaus, Amazonas, Brasil	RB00875526
Philodendron	Calostigma	*Philodendron cordatum* Kunth ex Schott	Nomadic vines	Jardim Botânico, RJ, Brasil	RFA 37309
Philodendron	Baursia	*Philodendron crassinervium* Lindl.	Epiphyte	Floresta da Tijuca, RJ, Brasil	RB00752148
Philodendron	Baursia	*Philodendron glaziovii* Hook.f.	Epiphyte Terrestrial	Floresta da Tijuca, RJ, Brasil Floresta da Tijuca, RJ, Brasil	RB00473387
Philodendron	Calostigma	*Philodendron hastatum* K.Koch & Sello	Nomadic vines	Floresta da Tijuca, RJ, Brasil	RB97077
Philodendron		*Philodendron linnaei* Kunth	Epiphyte	Reserva Ducke, Manaus, Amazonas, Brasil	RB00686927
Philodendron		*Philodendron melinonii* Brongn. ex Regel	Terrestrial	Jardim Botânico, RJ (Amazonas), Brasil	RB00840402
Philodendron	Calostigma	*Philodendron pachyphyllum* K.Krause	Rupicolous	Reserva Ducke, Manaus, Amazonas, Brasil	HUEFS00168178
Philodendron	Schizophyllum	*Philodendron pedatum* (Hook.) Kunth	Nomadic vines	Estrada da Vista Chinesa, RJ, Brasil	RB473918
Philodendron	Schizophyllum	*Philodendron ruthianum* Nadruz	Epiphyte	Floresta Tijuca, RJ, Brasil	RB00825679
Philodendron	Polyspermium	*Philodendron scandens* K.Koch & Sello	Nomadic vines	Jardim Botânico, RJ, Brasil	RB474176
Meconostigma	–	*Philodendron bipinnatifidum* Schott	Terrestrial Nomadic vines	Jardim Botânico, RJ, Brasil Jardim Botânico, RJ, Brasil	RB600428
Meconostigma	–	*Philodendron brasiliensis* Engl.	Pudgy terrestrial	Jardim Botânico, RJ, Brasil	RB00718275
Meconostigma	–	*Philodendron corcovadense* Kunth	Nomadic vines	Jardim Botânico, RJ, Brasil	RFA37490
Meconostigma	–	*Philodendron solimoesense* A.C.Sm.	Nomadic vines	Amazonas, Brasil	INPA00188989
Meconostigma	–	*Philodendron speciosum* Schott ex Engl.	Terrestrial	Jardim Botânico, RJ	RB1025660
Meconostigma	–	*Philodendron undulatum* Engl.	Nomadic vines Terrestrial	Teresópolis, RJ, Brsasil Jardim Botânico, RJ, Brasil	RB00706767
Meconostigma	–	*Philodendron williamsii* Hook.f.	Terrestrial/Rupicolous	Bahia, Brasil	HUEFS00168178
Pteromischum	–	*Philodendron oblongum* (Vell.) Kunth	Nomadic vines	Floresta da Tijuca, RJ, Brasil	RB682559
Pteromischum	–	*Philodendron propinquum* Schott	Nomadic vines	Floresta da Tijuca, RJ, Brasil	RB473988
Adelonema Schott		*Adelonema crinipes* (Engl.) S.Y.Wong & Croat	Terrestrial: rhizomatous herb	Jardim Botânico, RJ, Brasil	RB93529

examined roots (Fig. 3A) and with hairs most frequently being present in the regions near the apex (Fig. 3B). In the exodermis, one or more layers of cells with a thickening and sclerified walls were observed, especially in mature regions (Fig. 3C–F); among the various cells observed in the different subgenera studied, these were the most relevant for the taxonomy of the group.

Philodendron subg. *Philodendron*

In the species of this subgenus, we observed exodermis with cylindrical cells, presenting a quadrangular shape in some roots (Fig. 3C). In the cortical region, which is divided into external, medial and internal sections because of the different characteristics and organisation of the cells (Fig. 4A), the external cortex is composed of small cells, more juxtaposed, whereas in the middle cortex, larger cells were observed, with scattered organisation, showing conspicuous intercellular spaces in all types of root. In the internal cortical region, the roots have a radially arranged parenchyma with intercellular spaces (Fig. 4D), and, in the endodermis, there was an asynchronous maturation, reaching Stage III (Fig. 4E, F), where it is possible to observe the schizogen origin of the resin ducts. In addition, resin ducts with a sclerified sheath were observed (Fig. 5A, B) along the entire cortex, and the ducts of the external cortex are wrapped by a parenchymatic or partially sclerified sheath.

In the stele, the characteristics of the pericycle were similar to those of the endodermis, thus presenting cells with thickened walls in most species. In the vascular system, we observed a frequency of long strands of phloem, arranged alternately with the short cords (Fig. 4E, F). In regard to the shape, the roots present a cylindrical stele (Fig. 6A) of a type varying between protostele and medulated protostele (Fig. 5A, B); in species with root dimorphism, the medulated protostele was common among the anchor roots, whereas, in the feeding roots, there was variation between medulated protostele and protostele possessing metaphloem inclusion (Fig. 6A).

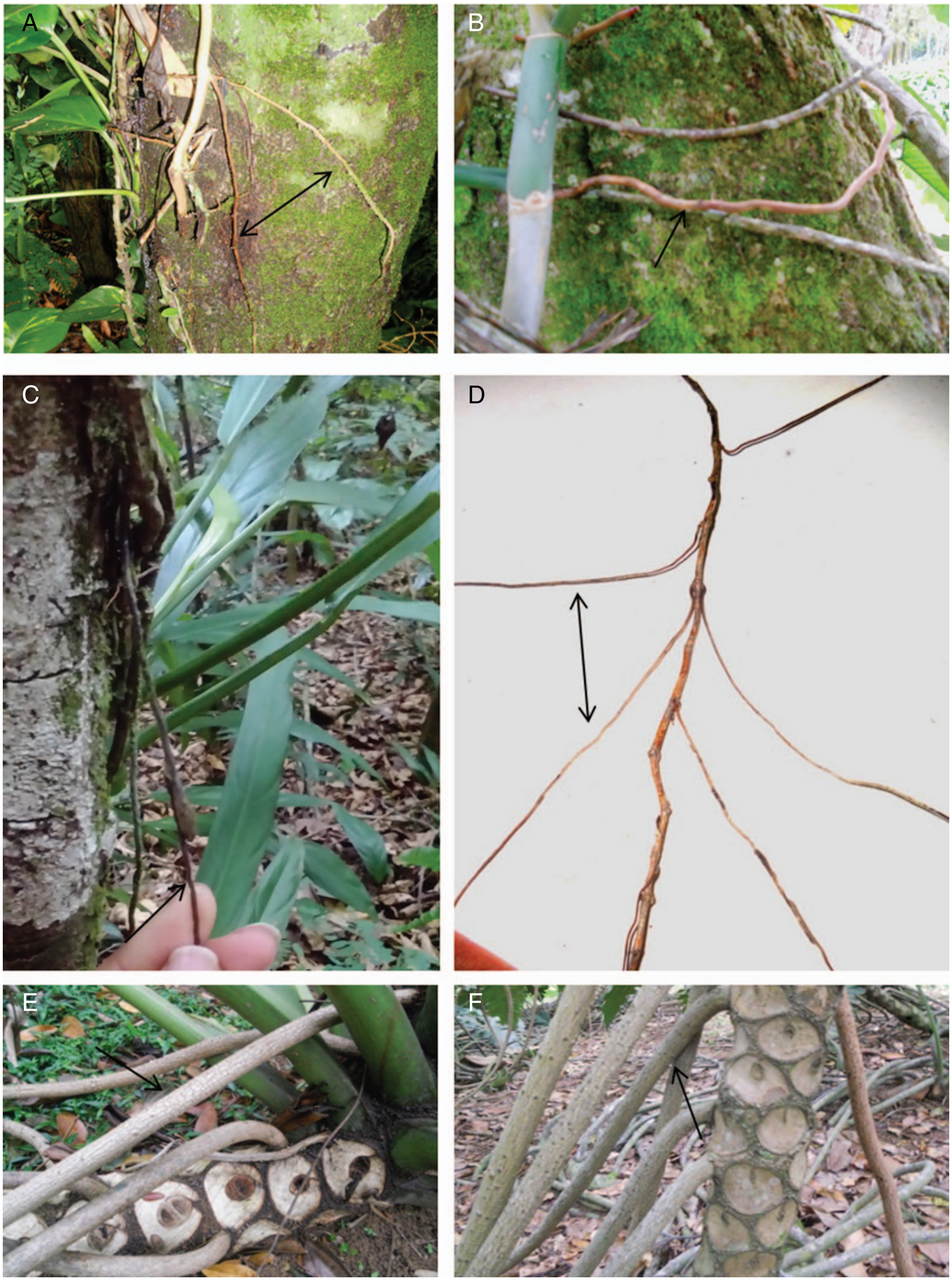

Fig. 1. A–F. External morphology of adventitious roots. A, B. Species of *Philodendron* subg. *Philodendron*: *P. pedatum* (A) and *P. ruthianum* (B). C, D. Species of *P*. subg. *Pteromischum*: *P. oblongum* (C) and *P. propinquum* (D). In both subgenera, it is possible to observe thinner roots (arrows). E, F. Terrestrial species of *P*. subg. *Meconostigma*: *P. bipinnatifidum* (E) and *P. undulatum* (F). This subgenus shows a greater thickening of the roots (arrows).

Philodendron subg. *Pteromischum*

First, it is important to clarify that we will now focus on the particular characteristics observed only in this subgenus, because most of the characteristics that have been described for this subgenus are equivalent to those previously mentioned in *P*. subg. *Philodendron*. Thus, quadrangular cells (Fig. 3D) were observed in the exodermis, with this form of cells more evident in younger regions of the root. Regarding the cortical region, the general characteristics, such as the cell division, size

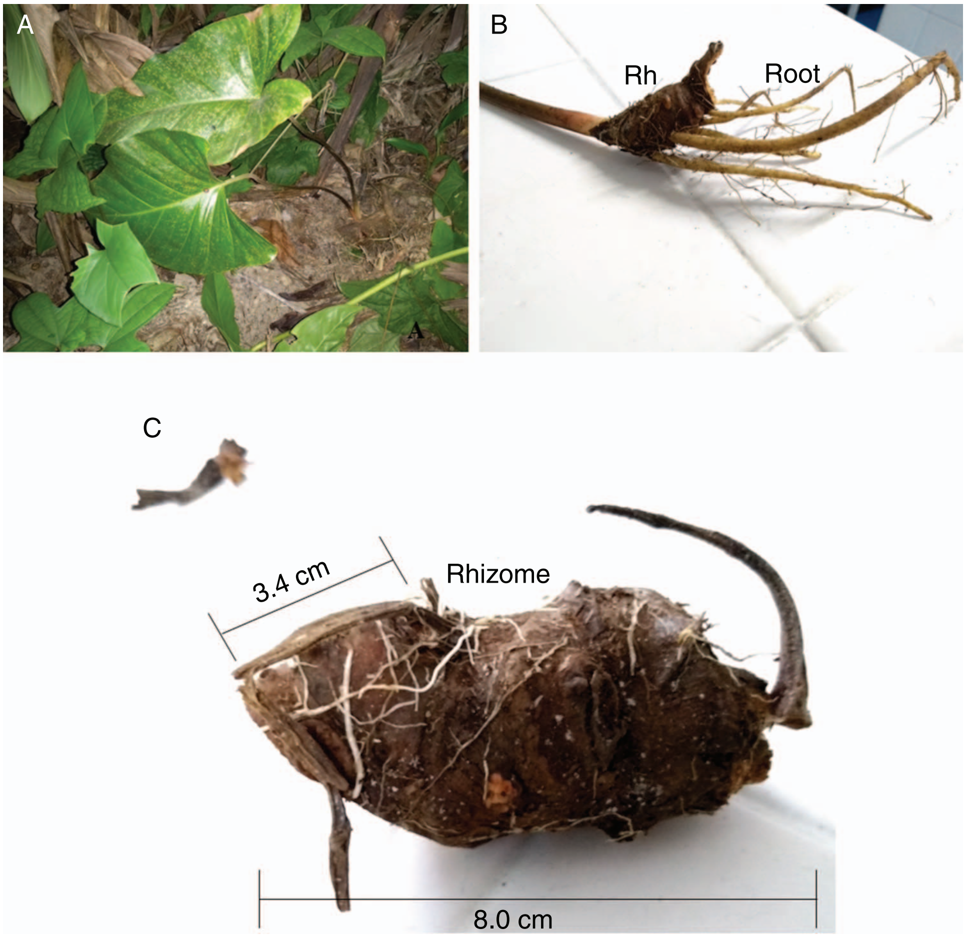

Fig. 2. A–C. External morphology of *Adelonema crinipes*. A. Rhizomatous herbaceous plant. B. Detail of tuberous rhizome (Rh) and roots. C. Rhizome in greater detail, measuring ~8.0 cm in length and 3.4 cm in thickness.

and organisation of the external, middle and internal areas, including the endodermis and the resin ducts, follow what has been previously described, with the following being particularly prominent in this subgenus: sheath sclerified in all the resiniferous ducts and external cortex with sclerified cells, forming multiple layers in the mature roots (Fig. 4C).

The stele has a cylindrical shape (Fig. 6A) and its first observed tissue, the pericycle, also follows the characteristics described above. In the vascularisation, the long strands of phloem are present only in the feeding roots, with approximately two or three strands present, depending on the species. As for the type of stele, it depends on the type of root, being protostele in the feeding roots and medulated protostele in the anchor roots.

Philodendron subg. *Meconostigma*

Among the subgenera analysed, subgenus *Mecanostigma* presented the most distinguishing characteristics in the attributes of the endodermis, in which cells with oblong shape were observed (Fig. 3E, F). Regarding the cells of the external cortex, there were periclinal divisions, giving rise to the cork layer, which gradually replaces the epidermis and exodermis until these tissues are no longer perceived in the mature root (Fig. 4B). The aspects of the medial and internal cortical regions were the same as previously described, with the last mature endoderm in Stage I, with Caspary strip being present even in mature portions (Fig. 4D), in all species studied. It is also noteworthy that, in this subgenus, the ducts were surrounded by a parenchymal sheath (Fig. 5C, D).

In regard to the stele, cells with thin walls in the pericycle were observed; these were lobed, varying from three to eight lobes depending on the species, habit or the type of the root (Fig. 6B–F). Moreover, in these species, the stele often presented a larger diameter, and, therefore, may present a greater number of lobes in more mature regions. It is important to mention that in terrestrial *P. williamsii*, as well as in the root of *P. bipinnatifidum*, the stele presented gradual modifications during the development of the root, being cylindrical or partially lobed in the early stages of the development and lobed in the more mature regions (Fig. 6C–F, 7A–F). The stele type varied between protostele and medullated protostele (Fig. 5A, B); in the anchoring roots of species with root dimorphism, the presence of a medullated protostele was common, whereas, in feeder roots, there was variation between a medullated protostele and protostele, or even metaphloem (Fig. 6A).

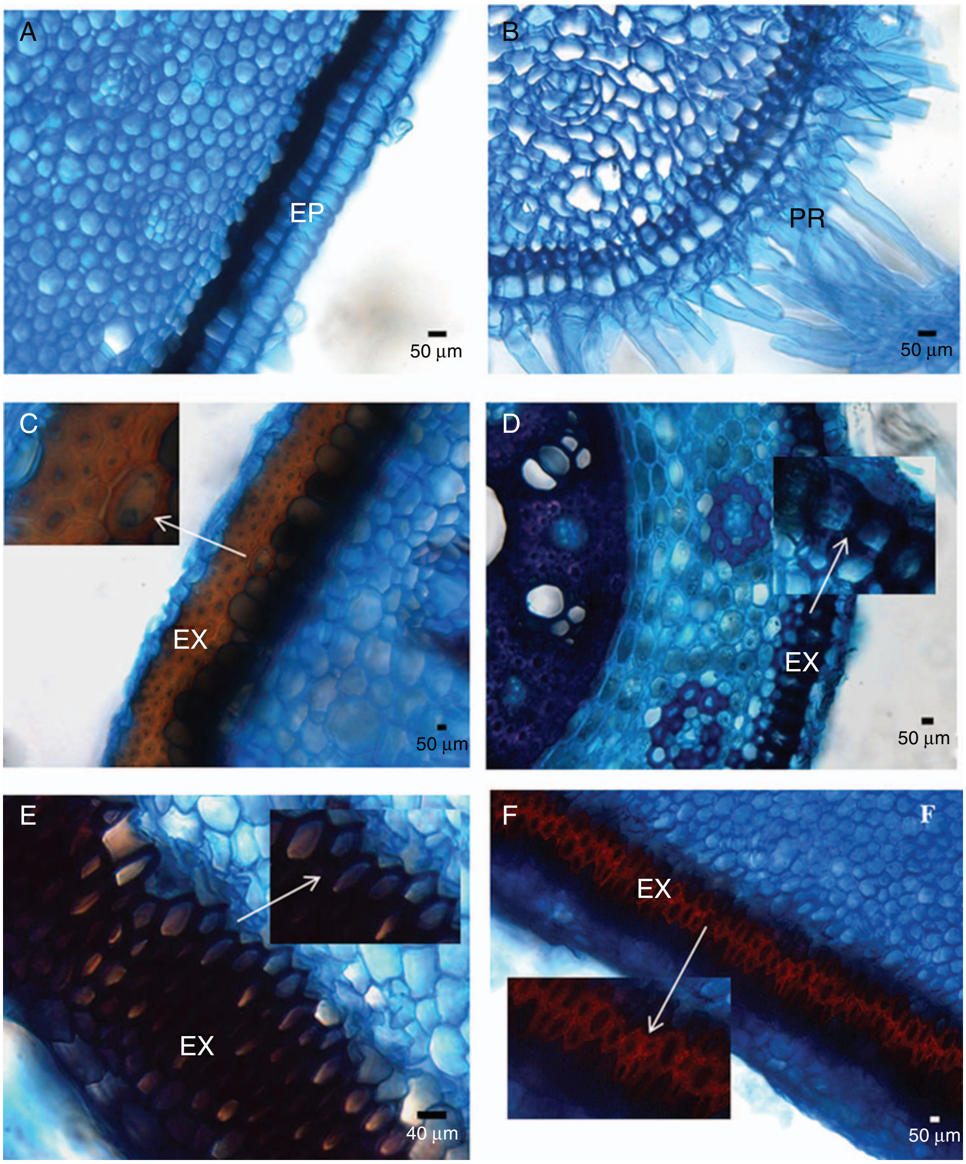

Fig. 3. A–F. Transverse sections of the adventitious roots: epidermis and exodermis. A, B. *Philodendron scandens* with biserial epidermis in the feeder root (A); anchor root with evident hairs (B). C. *Philodendron billietiae*, subgenus *Philodendron*; exodermis with cylindrical cells, in detail (arrow). D. *Philodendron propinquum* subg. *Pteromischum*; in detail (arrow), exodermis with quadrangular cells. E, F. Species of *P.* subg. *Meconostigma*: *P. solimoesense* (E) and *P. williamsii* (F). In these species, the angular shape of the cells can be observed, in detail (arrow). In all cases, the exodermis has cells with thickened and sclerified walls. EP, epidermis; PR, root hairs; EX, exodermis.

So as to better define the results for each subgenus, we also present the particularities of the results pertinent to the systematic grouping in Table 2, highlighting the anatomical characteristics of each species analysed. Table 3 summarises these results for each subgenus.

Adelonema crinipes

The epidermal tissue presents a pyloric area (Fig. 8A) and is composed of cylindrical cells with thin walls. In what corresponds to the exodermis, we observed multiple layers of unsclerified cells that were smaller and arranged in juxtaposition (Fig. 8B). However, the parenchyma of the cortical region has starch reserves (Fig. 8C), following the same organizational patterns (external, medium and internal) as previously described (Fig. 8D). It is important to emphasise that the resinous ducts are surrounded by sheath parenchyma (Fig. 8E), as discussed for *P.* subg. *Meconostigma*, but being more common in the external and internal cortex, whereas, in the middle cortex, idioblasts were observed containing calcium

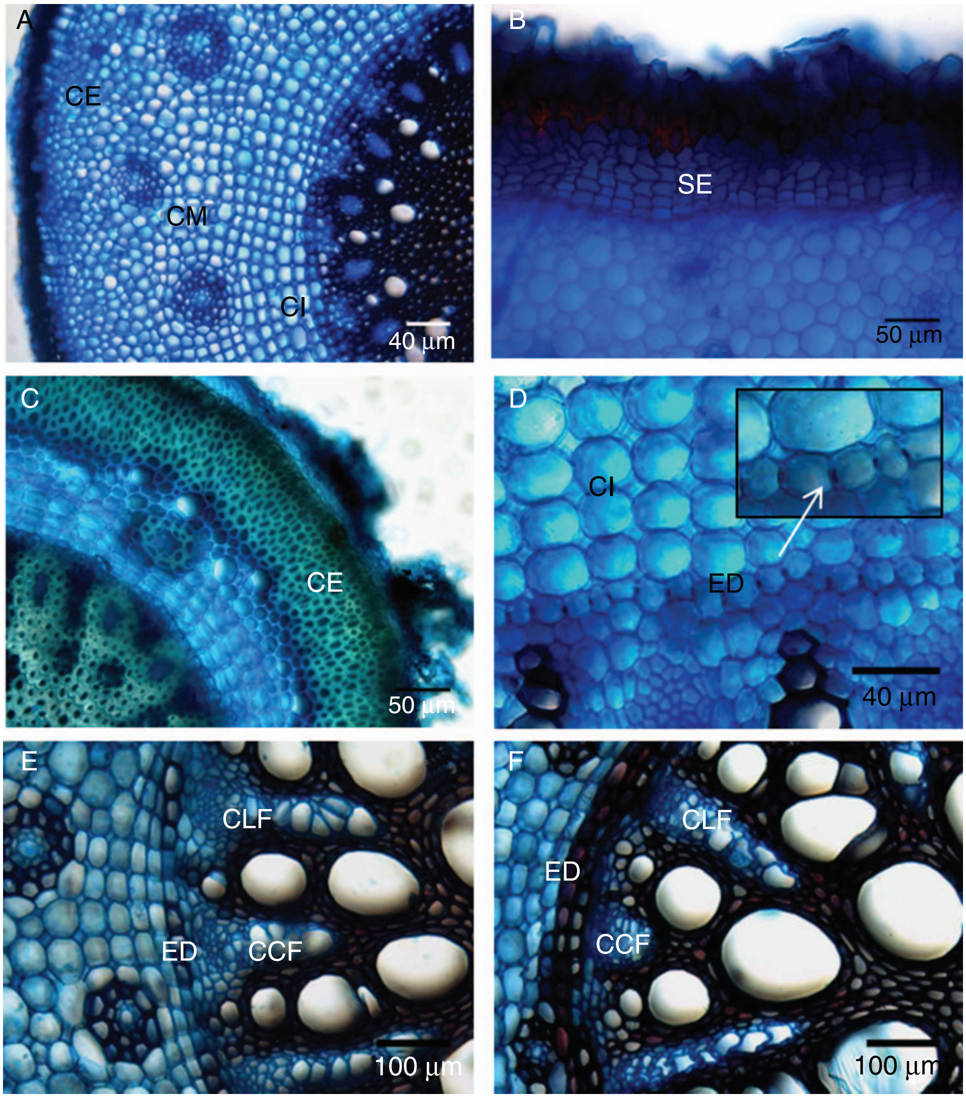

Fig. 4. A–F. Transverse sections of the adventitious roots: cortex. A. *Philodendron glaziovii*, division of the cortical region. B. *P. bipinnatifidum*, formation of the stratified super. C. *P. propynchum*, external cortex, standardised; multiple layers in the mature root. D. *P. corcovadense* subg. *Meconostigma*, internal cortex with radial arrangement of cells; in mature Stage I endoderm, the prominent Casparian strips can be observed, in detail (arrow). *E*, *F. P. hastatum* subg. *Philodendron*, mature endoderm Stage III, asynchronous maturation; in E, observe the thickening present only in the walls of the cells situated opposite the phloem strands, whereas, in B, all cells have thickened and sclerified walls. CE, external cortex; CM, mean cortex; CI, internal cortex; SE, stratified cortex; ED, endoderm; CCF, phloem short cord; CLF, long phloem strand.

oxalate crystals of the type drusos. The mature endodermis remains in Stage I, in which the striations of the Casparian strip are prominent.

As to the stele, the pericycle cells follow the endodermal features, with regard to thin walls. In regard to the shape, a cylindrical stele, of the medullated protostele type (Fig. 8F), and the vascularisation follow the usual pattern for the radicular organ, with protoxylem and metaxylem alternating with short phloem strings.

Discussion

Our results showed that *P.* subg. *Philodendron* and *P.* subg. *Pteromischum* are more closely related among themselves in terms of important shared anatomical features. The anatomy of the root of *P.* subg. *Meconostigma* showed distinct differences that distinguished it from the other two subgenera, including the presence of a lobed stele (and variations of this organ). As such, our data corroborated the phylogenetic hypothesis of Mayo

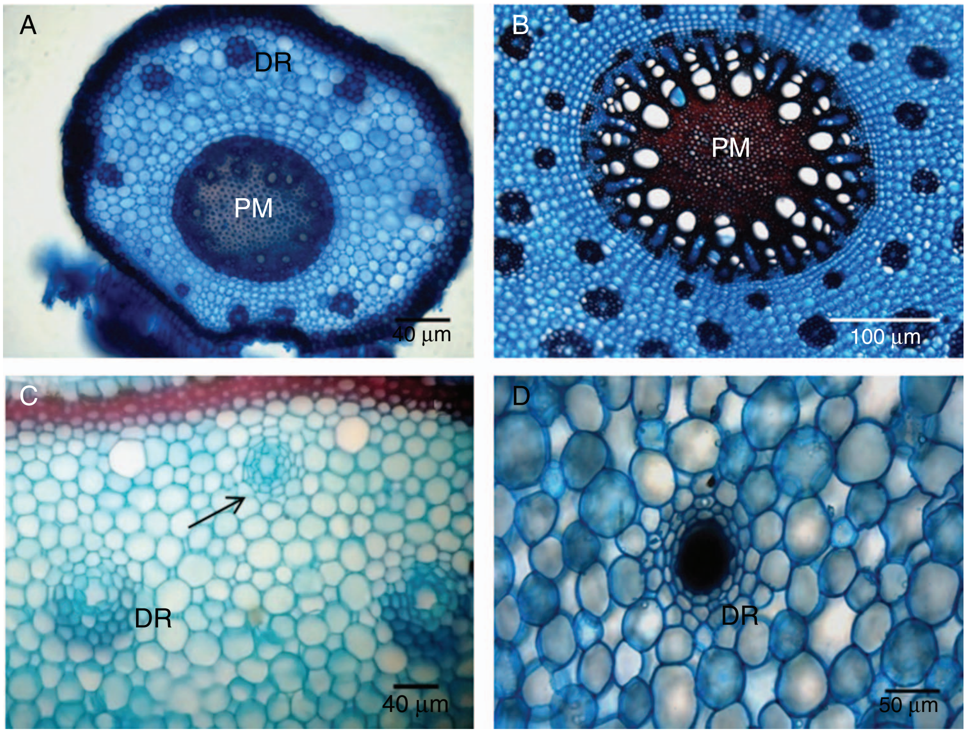

Fig. 5. A–D. Transverse sections of adventitious roots: resinous ducts. A. *Philodendron oblongum* subg. *Pteromischum*. B. *Philodendron ruthianum* subg. *Philodendron*. In A and B, ducts with a sclerified sheath can be observed. C. *Philodendron billietiae* subg. *Philodendron*; the partially sclerified sheath and also the parenchymal sheath (arrow) in the outermost ducts can be observed. D. *Philodendron williamsii* subg. *Meconostigma*. In A and B, the stele type can be still observed, being protostele in both cases. DR, resinous duct; PM, medullated protostele.

(1989), which considered the subgenus *Meconostigma* as the sister clade to the subgenera *Philodendron* and *Pteromischum.* The analyses of Loss-Oliveira *et al*. (2016) also indicated close relationships between species of the last two subgenera.

According to Canal *et al*. (2018), the genera *Philodendron* and *Adelonema* correspond to a monophyletic group, inferring that the subgenera *Philodendron, Pteromischum* and *Meconostigma* were recovered in two distinct lineages, one containing the subgenera *Meconostigma* and *Pteromischum* and the other containing the subgenus *Philodendron*.

The molecular study of Loss-Oliveira *et al*. (2016) contributed to a better understanding of phylogeny and taxonomy of the genus *Philodendron* and focused on the evolutionary relationships among the three subgenera of *Philodendron*. These authors reported the monophyletic nature of the subgenus *Meconostigma* and the polyphyletic nature of the subgenus *Philodendron*, grouping the species of the latter with those of the subgenus *Pteromischum*.

Here, we have presented diagnostic features for the subgenera examined in terms of essentially all of their root tissues. The cortical region, for example, deserves attention because of the formation of a stratified cork layer in the species of the subgenus *Meconostigma*, with several layers of cells with sclerified walls composing the external cortex in mature roots of *P.* subg. *Pteromischum*. According to Tenorio *et al* (2014), the sclerified cells represent adaptations to desiccation in the species of this subgenus. The presence of parenchyma or partially sclerified sheaths terminating only the outermost resin ducts in the subgenus *Philodendron* was very relevant and naturally characterises the species of this group.

Within this context, the root exodermis also provides relevant taxonomic characteristics for the species of the genus *Philodendron* because of the different forms of the cells that compose the tissues, being cylindrical or quadrangular in the subgenus *Philodendron*, quadrangular in *P.* subg. *Pteromischum* (indicating close proximity between these two subgenera), and in the form of a lozenge in *P.* subg. *Meconostigma*. As such, the distinctive forms of the exodermis root-cell walls provide an additional diagnostic character for the species of the subgenus *P.* subg. *Meconostigma*. In terms of root exodermis development, Enstone *et al.* (2002) reported its relationship with water-stress situations and its function in avoiding root dehydration; stress situations could accelerate the development of this tissue, as well as the development of endodermis. According to French (1987*a*, 1987*b*), a sclerified exodermis is characteristic of the roots of the genus *Philodendron*, although it may also occur in the genus *Homalomena*, and this characteristic, when considered in conjunction with the parenchymal sheaths of the resin ducts

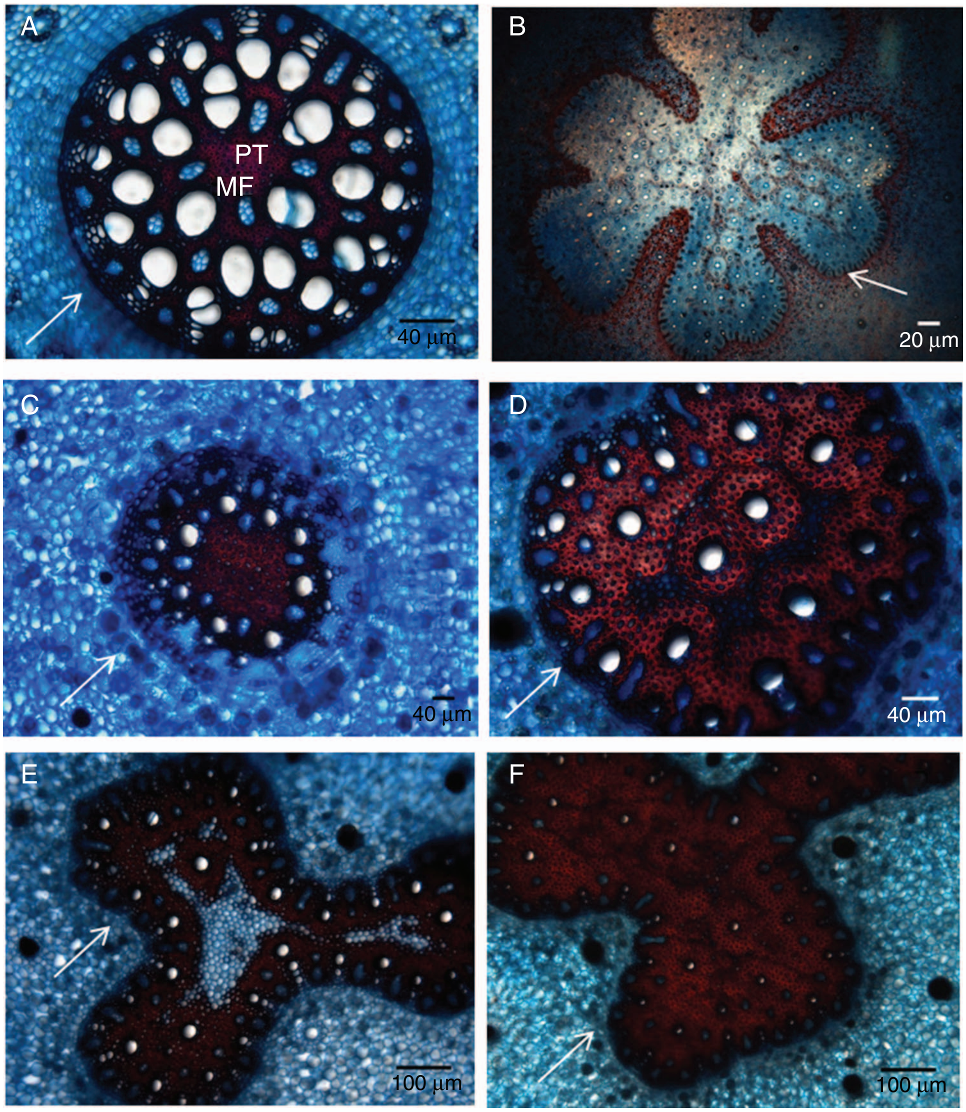

Fig. 6. A–F. Transverse sections of the adventitious roots: stele. A. *Philodendron propinquum* subg. *Pteromischum*, the cylindrical stele (arrow) is highlighted. B. *Philodednron bipinnatifidum* subg. *Meconostigma*, with lobed stele (arrow), composed of six lobes in the root of the anchor type. C–F. *Philodendron williamsii* subg. *Meconostigma*; stele can be observed at the following distances from the root apex: 1 cm (C), 30 cm (D), 60 cm (E), 90 cm (F). C. The cylindrical shape in the early stages of the development (arrow). E, F. Lobed shape, composed of three lobes in the mature root (arrow), is verified. PT, protostele; MF, metaphloem.

(as observed in species *P*. subg. *Meconostigma* in the present study), suggests a relationship between *Homalomena* and *Philodendron*.

The mature endodermis also demonstrates anatomical features that are taxonomically useful, because it contains thick, sclerified cells in the subgenera *Philodendron* and *Pteromischum*, representing Stage III of maturation, whereas the presence of Casparian strips in *Meconostigma* defines Stage I of maturation. Peterson and Enstone (1996) described the stages of maturation of the endodermis, with Stage I cells demonstrating only Casparian strips organised radially in the protoxylem, whereas Stage II demonstrates a suberin layer; Stage III shows the formation of a thick and frequently lignified layer of internal cellulose to the suberin layer. According to those authors, the last degree of maturation is asynchronous, with the first thicknesses occurring in the cells that face the phloem, and this later establishes in the other tissue constituents. According to Esau (1974), the Casparian canals are present in the absorption regions of the young roots, although we have observed here that the roots of the species of the subgenus *Meconostigma* maintain these canals even in mature regions (which usually show less activity in terms of absorption). Both the presence of evident

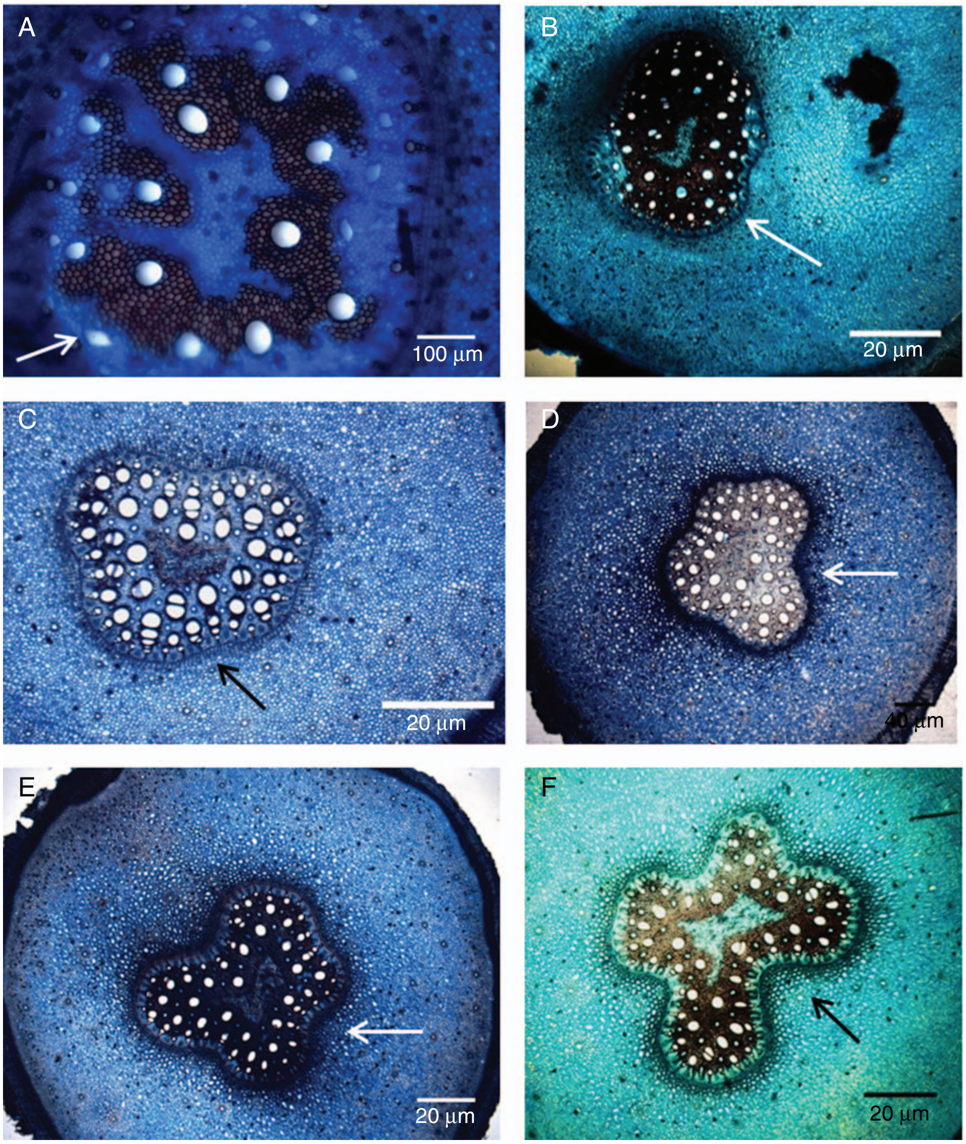

Fig. 7. A–F. Transverse sections of the feeder root of *Philodendron bipinnatifidum*: lobed stele. Modifications in the shape of the stele (arrow) at the following distances from the root apex: 1 cm (A), 10 cm (B), 20 cm (C), 30 cm (D) and 50–90 cm (F).

Casparian canals and the absence of sclerified endodermal cells were considered by Mayo (1991) to be possible diagnostic features for the subgenus *Meconostigma.*

Lobed steles were observed only in the species of the subgenus *Meconostigma*. Mayo (1991) also reported the presence of lobed steles in the species of this same subgenus, and it was observed in the present study that the vascular cylinder is normally circular in the genus *Philodendron*. Variation in the stele type was reported by Tenorio *et al* (2014) in an anatomical study of *P. corcovadense* roots, with a cylindrical stele occurring in a terrestrial individual and a lobed stele in a rupestral plant.

It is noteworthy that some anatomical characters did not demonstrate variation among the different subgenera analysed, including the presence of sclerified cell walls in the exodermis, internal cortical cells arranged radially, and the presence of metaphloem (which had previously been described by Tenorio *et al*. (2012) for species of the subgenus *Meconostigma*). The present study has confirmed that metaphloem can be observed in specimens of the subgenera *Philodendron* and *Pteromischum*. According to Alonso *et al*. (2004) and Tenorio *et al*. (2014), the radial organisation of internal cortical cells results from the meristematic activity of the endodermis.

Table 2. Potentially useful characteristics for group systematics
Mature endoderm, according to Peterson and Enstone (1996)

Species	Habit	Root type	Epidermis	Exodermis	External sclerified cortex	Stratified cork	Resinous duct sheath	Endodermis maturity	Type of stele	Shape of stele
Philodendron hastatum	Nomadic vine	Anchor-feeder	Uniseriate	Multisseriate; cylindrical cells	Absent	Absent	Partially sclerified or sclerified	Stage III	Protosteles	Cylindrical
Philodendron glaziovii	Epiphyte	Anchor-feeder	Biseriate	Uniseriete; quadrangular cells	Absent	Absent	Partially sclerified or sclerified	Stage I	Medullated protostele	Cylindrical
Philodendron glaziovii	Terrestrial	Anchor-feeder	Uniseriete	Multisseries; cylindrical cells	Absent	Absent	Partially sclerified or sclerified	Stage III	Medullated protostele	Cylindrical
Philodendron crassinervium	Epiphyte	Anchor-feeder	Uniseriete	Uniseriate; cylindrical cells	Absent	Absent	Partially sclerified or sclerified	Stage III	Medullated protostele	Cylindrical
Philodendron ruthianum	Epiphyte	Anchor-feeder	Uniseriate	Uniseriate; cylindrical cells	Absent	Absent	Partially sclerified or sclerified	Stage III	Medullated protostele	Cylindrical
Philodendron billietiae	Nomadic vine	Anchor	Uniseriate	Multiseriate; cylindrical cells	Absent	Absent	Partially sclerified or sclerified	Stage III	Medullated protostele	Cylindrical
Philodendron billietiae	Nomadic vine	Feeder	Uniseriate	Multiseriate; cylindrical cells	Absent	Absent	Partially sclerified or sclerified	Stage III	Medullated protostele	Cylindrical
Philodendron linnaei	Epiphyte	Anchor-feeder	Uniseriate	Multisseries; cylindrical cells	Absent	Absent	Partially sclerified or sclerified	Stage I	Medullated protostele	Cylindrical
Philodendron pachyphyllum	Rupicolous	Anchor-feeder	Biseriate	Uniseriate; quadrangular cells	Present	Absent	Partially sclerified or sclerified	Stage I	Medullated protostele	Cylindrical
Philodendron melinonii	Terrestrial	Anchor-feeder	Uniseriate	Uniseriate; cylindrical cells	Absent	Absent	Partially sclerified or sclerified	Stage I	Medullated protostele	Cylindrical
Philodendron scandens	Nomadic vine	Anchor	Biseriate	Uniseriate; cylindrical cells	Absent	Absent	Partially sclerified or sclerified	Stage I	Medullated protostele	Cylindrical
Philodendron scandens	Nomadic vine	Feeder	Biseriate	Uniseriate; cylindrical cells	Absent	Absent	Partially sclerified or sclerified	Stage I	Protostele	Cylindrical
Philodendron cordatum	Nomadic vine	Anchor	Uniseriate	Multisseries; cylindrical cells.	Absent	Absent	Partially sclerified or clerified	Stage III	Medullated protostele	Cylindrical
Philodendron cordatum	Nomadic vine	Feeder	Uniseriate	Biseriate; cylindrical cells.	Absent	Absent	Partially sclerified or sclerified	Stage III	Medullated protostele	Cylindrical
Philodendron pedatum	Nomadic vine	Anchor	Uniseriete	Uniseriete; cylindrical cells.	Absent	Absent	Partially sclerified or sclerified	Stage III	Medullated protostele	Cylindrical
Philodendron pedatum	Nomadic vine	Feeder	Uniseriete	Uniseriete; cylindrical cells.	Absent	Absent	Partially sclerified or sclerified	Stage III	Medullated protostele	Cylindrical
Philodendron bipinnatifidum	Terrestrial	Anchor-Feeder	Uniseriete	Multisseries; lozenge-shaped cells	Absent	Present	Parenchymatous	Stage I	Protosteles	Lobed: 6 lobes
Philodendron bipinnatifidum	Nomadic vine	Anchor	Uniseriate	Multisseries; lozenge-shaped cells	Absent	Present	Parenchymatous	Stage III	Protosteles	Lobed: 6–8 lobes in the mature root.
Philodendron bipinnatifidum	Nomadic vine	Feeder	Uniseriate	Multisseries; lozenge-shaped cells	Absent	Present	Parenchymatous	Stage I	Medullated protostele	Lobed: 4 lobes
Philodendron undulatum	Nomadic vine	Anchor-feeder	Uniseriate	Uniseriate; lozenge-shaped cells	Absent	Present	Parenchymatous	Stage I	Protosteles	Lobed: 4 lobes
Philodendron undulatum	Terrestrial	Anchor-feeder	Uniseriate	Uniseriate; lozenge-shaped cells	Absent	Present	Parenchymatous	Stage I	Protosteles	Lobed: 5 lobes
Philodendron williamsii	Terrestrial	Anchor-feeder	Uniseriate	Uniseriate; lozenge-shaped cells	Absent	Present	Parenchymatous	Stage I	Medullated protostele	Initially cylindrical; lobed on mature root: 3 lobes.
Philodendron williamsii	Rupicolous	Anchor-feeder	Biseriate	Multisseries; lozenge-shaped cells	Absent	Present	Parenchymatous	Stage I	Protosteles	Lobed: 4 lobes
Philodendron solimoesense	Nomadic vine	Anchor-feeder	Uniseriate	Multisseries; lozenge-shaped cells	Absent	Absent	Parenchymatous	Stage I	Protosteles	Lobed: 5 lobes
Philodendron corcovadense	Nomadic vine	Anchor-feeder	Uniseriate	Uniseriate; lozenge-shaped cells	Absent	Present	Parenchymatous	Stage I	Protosteles	Lobed
Philodendron speciosum	Terrestrial	Anchor-feeder	Uniseriate	Uniseriate; lozenge-shaped cells	Absent	Present	Parenchymatous	Stage I	Medullated protostele	Lobed: 6 lobes
Philodendron brasiliensis	Terrestrial (paludoso)	Anchor-feeder	Uniseriate	Uniseriate; lozenge-shaped cells	Absent	Present	Parenchymatous	Stage I	Protosteles	Lobed: 4 lobes
Philodendron oblongum	Nomadic vine	Anchor	Uniseriate	Uniseriate; quadrangular cells	Present	Absent	Sclerified	Stage III	Medullated protostele	Cylindrical
Philodendron oblongum	Nomadic vine	Feeder	Uniseriate	Uniseriate; quadrangular cells	Present	Absent	Sclerified	Stage III	Protosteles	Cylindrical
Philodendron propinquum	Nomadic vine	Anchor	Uniseriate	Uniseriate; quadrangular cells	Present	Absent	Sclerified	Stage III	Medullated protostele	Cylindrical
Philodendron propinquum	Nomadic vine	Feeder	Uniseriate	Uniseriate; quadrangular cells	Present	Absent	Sclerified	Stage III	Protosteles	Cylindrical
Adelonema crinipes	Terrestrial (rhizomatous herb)	Anchor-feeder	Uniseriate	Multiseriate;	Absent	Absent	Parenchymatous	Stage I	Medullated protostele	Cylindrical

Table 3. Anatomical characteristics possibly useful for the taxonomy in *Philodendron* Schott.

Parameter	*Philodendron*	*Pteromischum*	*Meconostigma*
Epidermis	Uni or biseriate	Uniseriate	Uniseriate
Exodermal cell shape	Cylindrical or quadrangular	Quadrangular	Lozenge-shaped
Sclerified external cortex	Absent	Present	Absent
Storied cork formation	Absent	Absent	Present or absent
Sheath of the resinous duct	Sclerified	Sclerified	Parenchymatous
Maturity of endoderm	Stage III	Stage III	Stage I
Shape of stele	Cylindrical	Cylindrical	Lobed
Cell thickening in the pericycle	Present or absent	Present	Absent
Long strands of phloem	Present	Present	Absent

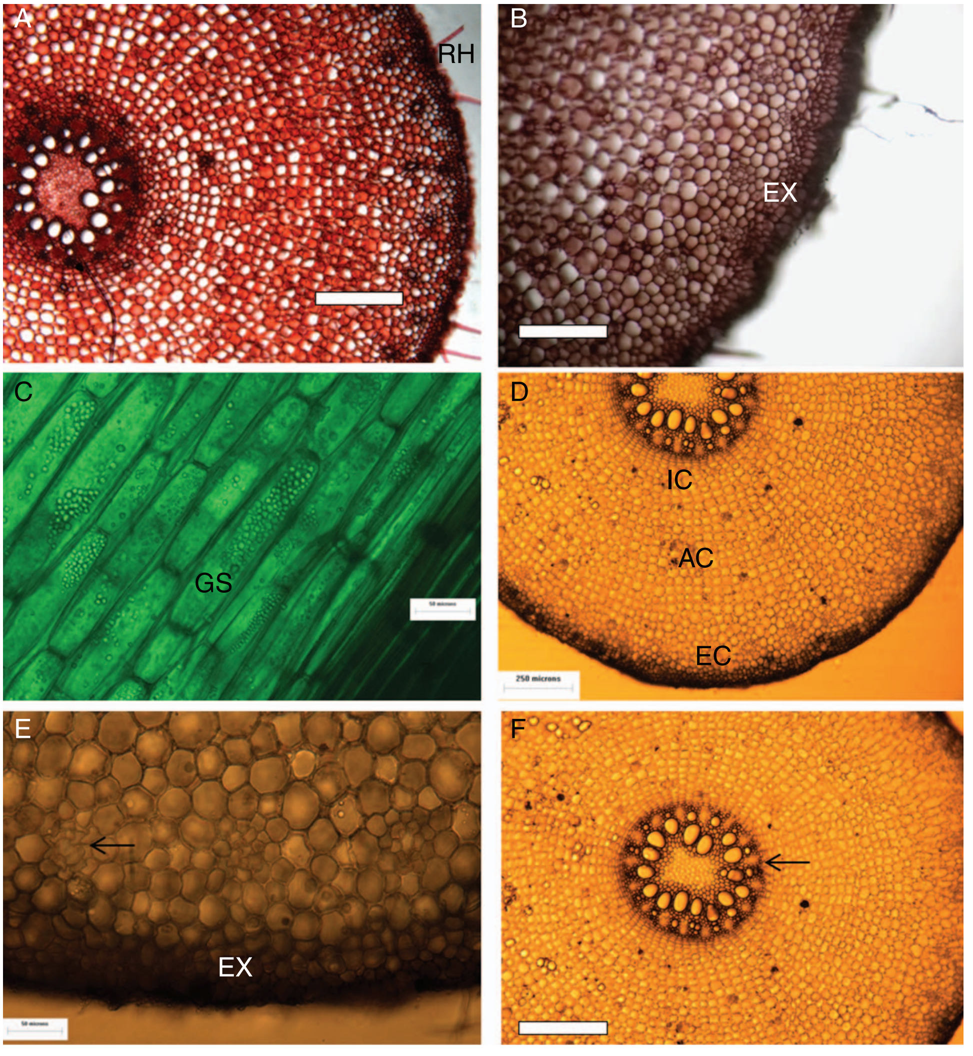

Fig. 8. A–F. Transverse and longitudinal sections of the root of *Adelonema crinipes*. A. Epidermis in cross-section, showing the root (RH). B. Exodermis not sclerified with smaller cells than in other tissues. C. Longitudinal section of the cortical parenchyma, showing the starch grains. D. Cross-section of the cortical region, the organisation of the cells in external (EC), medium (AC) and internal (IC) cortex can be observed. E. Resiniferous ducts in the external cortex (arrow), the parenchymatic sheath is prominent; the tissue cells of the exodermis (EX) can be observed in greater detail. F. Stele in cross-section (arrow); it is possible to observe the cylindrical shape of the medulated protostele type, that is, with cells of parenchyma filling the centre of the structure. Vertical bars: 200 µm (A), 200 µm (B) and 250 µm (F).

Conclusions

The data presented here indicated that the species of the subgenera *Philodendron* and *Pteromischum* share a large number of anatomical characteristics, such as sclerified sheaths terminating the resin ducts, the presence of long strands of phloem and a cylindrical stele, corroborating previously published reports that have suggested these two subgenera to be closely related. Moreover, these subgenera also share anatomical similarities with the species *A. crinipes*, such as, for example, the shape of the stele. However, individuals of *P.* subg. *Meconostigma* demonstrated different characteristics, especially the presence of a lobed stele, lozenge-shaped cells in the exodermis, the formation of a stratified cork layer, and parenchymal sheaths that involve resin ducts, the latter being the only state of a character shared with *A. crinipes*. These characteristics contribute greatly to the systematics of the genus *Philodendron* and add to the available information about this group.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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