



On the structure of leaf and trichomes, and its bearing on the taxonomy of *Leandra* and *Miconia* (Miconieae, Melastomataceae)

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ABSTRACT

The literature reveals difficulties in taxonomic and phylogenetic delimitations of *Miconia* Ruiz & Pav. and *Leandra* Raddi (Melastomataceae), it's suggested that leaf anatomical characters, particularly the trichomes, can be useful within the genera. Characters related to the trichomes and leaf blade structure of 15 species of Miconieae (five species of *Leandra* and ten species of *Miconia*) were evaluated as a taxonomic criterion to separate the selected species. In addition, some considerations were made about the structure of the leaves, which can be affected by environmental factors. Leaf samples were obtained from herbaria and anatomically investigated using optical microscopy and scanning electron microscopy. Leaves are hypostomatous, dorsiventral or isobilateral, and exhibit epidermis in general with non-glandular and glandular trichomes. A hypodermis has been found only in *Miconia theaezans*. Conical trichomes and mixed trichomes (non-glandular and glandular) are present only in the five species of *Leandra*. Dendritic trichomes have been found in species of both genera. Leaf features of potential taxonomic significance are the trichome types, presence of hypodermis, number of layer palisade parenchyma, occurrence of gelatinous fibers, midrib structure, and margin structure. Xeromorphic and sclerophyllous features are present in *Leandra* and *Miconia* species, and *Leandra microphylla* may be considered a xerophyte.

Keywords: Conical trichome, dendritic trichome, hypodermis, leaf margin, mesophyll structure, midrib structure.

Introduction

Miconieae Mart. is considered the tribe with the greatest diversity of species within Melastomataceae (Michelangeli *et al.* 2008; Penneys *et al.* 2022; Ulloa Ulloa *et al.* 2022). Among its genera, *Miconia* Ruiz & Pav. and *Leandra* Raddi deserve to be highlighted because they are genera considered the most representative in number of species of the tribe

(Michelangeli *et al.* 2004; Oliveira 2007; Camargo 2008; Penneys *et al.* 2022).

In Brazil, *Miconia* and *Leandra* are widely distributed in areas of Atlantic Rainforest and “Cerrados”, and are considered typical elements of these vegetation formations (Flora e Funga do Brasil 2023). Currently, 176 species of *Leandra* and 271 species of *Miconia* s.s. have been recorded in Brazil, with the genera comprising ca. 200 and 2000

Received August 22, 2023; Accepted March 19, 2024

Editor-in-Chief: Thaís Elias Almeida; Associate Editor: Bruno Garcia Ferreira

How to cite:

Martarelli TMM, Rodrigues KF, Souza LA. 2024. On the structure of leaf and trichomes, and its bearing on the taxonomy of *Leandra* and *Miconia* (Miconieae, Melastomataceae). *Acta Botanica Brasilica* 38: e20230206.

doi: [10.1590/1677-941X-ABB-2023-0206](https://doi.org/10.1590/1677-941X-ABB-2023-0206)



species, respectively (Michelangeli *et al.* 2019; Goldenberg *et al.* 2023).

Phylogenetic analyses of Miconieae at the genus and tribe levels have shown a lack of monophyly among traditional taxa, and that the morphological characters used in the tribe's taxonomy are tenuous and not very consistent (*sensu* Penneys *et al.* 2022). *Leandra* and *Miconia* were treated here as distinct genera in Miconieae, but recently Michelangeli *et al.* (2022) proposed that the tribe be recognized with the single genus *Miconia*. With this monogeneric proposal, these authors consider it urgent to have a consistent revised infrageneric taxonomy, within a framework that encompasses the entire genus.

Leaf structure and trichome morphology of leaves or flowers have been used as significant characters in the taxonomy of Melastomataceae (Metcalf & Chalk 1957; Wurdack 1986; Guimarães *et al.* 1999; Reis *et al.* 2005; Oliveira 2007; Donato *et al.* 2018; Carmo *et al.* 2019; Gonçalves-Silva *et al.* 2019; Gonçalves *et al.* 2023). Leaf structural characters investigated as a contribution to the taxonomy of *Leandra* or *Miconia* were reported by Gonçalves-Silva *et al.* (2019) and Müller *et al.* (2020). In *Leandra* and *Miconia* the trichome morphology provide many important features which are of taxonomic value at the specific level (Gonçalves-Silva *et al.* 2019; Gonçalves *et al.* 2023).

The species of *Leandra* and *Miconia* selected for study include plants that live in forests and rupestrian fields, five species of *Leandra* (or 2.27% of 176 spp.) and 10 of *Miconia* (4% of 270 spp.). The main purpose of this investigation was to ascertain the usefulness of leaf structure and trichome morphology as criterion for characterization of species of both genera. In addition to ensuring data for use in Miconieae taxonomy, we consider it important to make some leaf structural ecological considerations, especially because these species occur in different environments.

Material and Methods

Plant material and sample preparation

Three samples of leaves were used for each of the 15 species studied of Miconieae belonging to the genera *Leandra* and *Miconia* (Tab. 1) were analyzed anatomically. Completely expanded leaves from the third to fifth stem nodes were obtained from vouchers from the herbarium of the Municipal Botanical Museum of Curitiba (MBM) and from the State University of Maringá (HUEM), Brazil. The leaves were previously rehydrated in boiling water, immersed in 5% potassium hydroxide (KOH) for two hours and submitted to the 10%, 30%, 50% and 70% ethyl series, according to Smith & Smith (1942). Successively, the leaves were fixed in a solution of Glutaraldehyde in phosphate buffer (Karnovsky 1965) and in FAA 50 (Formaldehyde,

Acetic acid and 50% Ethyl alcohol; 1:1:18) and stored in 70% ethanol (Johansen 1940). Analysis under a light microscope

Median and margin fragments of the leaf lamina with 1×1 size were submitted to 80%, 90% and 100% ethyl alcohol series and embedded in Leica® HistoResin, according to the manufacturer's instructions. The embedded material was sectioned transversely to the rotation microtome (Easy Path and HistoCore BLOCUT), in sections from 5 to 7µm in thickness, and stained in 0.05% Toluidine Blue in acetate buffer (pH 4.7) (O'Brien *et al.* 1964). The sections were illustrated using a Leica ICC50 light microscope with an attached digital camera, using the Leica Application Suite 1.8 software, through digital image capture.

Analysis under a scanning electron microscope (SEM)

The scanning electron microscope (SEM) analysis was performed with glutaraldehyde 5% fixed material. After washing in 0.1 M sodium cacodylate buffer, leaf fragments were dehydrated in graded ethanol series, critical point drying with CO₂, mounted on aluminum stubs, coated with gold (Horridge & Tamm 1969). The samples were examined in a Scanning Electron Microscope Quanta 250 (Fei-Oxford Instruments, Oxfordshire, United Kingdom) operating between 15–25kV, and the images were captured digitally. Lamina trichomes were described according to Wurdack (1986)'s atlas of hairs (trichomes). The convex walls of the glabrous leaf epidermis of *Miconia dodecandra* were described according to the terminology of Barthlott & Hunt (2000).

Results and Discussion

Leaf features and their taxonomic importance in *Miconia* and *Leandra*

The surface of the leaf lamina is flat, but this surface is wavy (undulations) in *Leandra microphylla* (Fig. 1A) and *Leandra nianga* (Fig. 1B) (Tab. 2). All studied species of *Leandra* and *Miconia* have hypostomatous lamina (Fig. 1 C, G, I), and consists of uniseriate and cuticularized epidermis on both surfaces (Fig. 1A-I). In general, the cuticular layer is thick on the adaxial surface and comparatively thinner on the abaxial surface (Fig. 1A-I). Seen in cross-section the epidermal cells of both surfaces are rounded, rectangular, square or slightly prismatic; it is common for cells on the abaxial surface to be slightly smaller in size than those on the adaxial surface (Fig. 1A-I). Phenolic derivatives were seen in the epidermal cells of the adaxial surface of *M. dodecandra* (Fig. 2G), *Miconia prasina* (Fig. 1D) and *Miconia valtherii* (Fig. 1C) and on the abaxial surface of *M. prasina* (Fig. 1D). Trichomes are always present, but never in *Miconia pusiliiflora*.

Table 1. Species of *Leandra* and *Miconia* that were selected for study, including information on Brazilian collection sites and herbarium registration (vouchers) and the type of vegetation where the species were found (HUEM=Herbário da Universidade Estadual de Maringá, Brasil; MBM=Museu Botânico Municipal de Curitiba, Brasil).

Species	Collection locations	Vouchers	Type of Vegetation
<i>Leandra melastomoides</i> var. <i>major</i> Cogn.	Mata da Balsa do Rio Iapó, Tibagi, Paraná state	HUEM 32556	Campos Gerais (Rupestrian Fields)
<i>Leandra microphylla</i> Cogn.	Parque Estadual Guartelá, Tibagi, Paraná state	MBM 399775	Campos Gerais (Rupestrian Fields)
<i>Leandra nianga</i> (DC.) Cogn.	Ouro Branco, Minas Gerais state	HUEM 6954	Rupestrian Fields
<i>Leandra purpurascens</i> (DC.) Cogn.	Parque Estadual Guartelá, Tibagi, Paraná state	HUEM 33143	Campos Gerais (Rupestrian Fields)
<i>Leandra xanthocoma</i> (Naudin) Cogn.	Telêmaco Borba, Paraná state	HUEM 10413	Atlantic Forest
<i>Miconia budlejoides</i> Triana	Paranaguá, Paraná state	MBM 275914	Atlantic Forest
<i>Miconia cinerascens</i> Miq.	Morretes, Paraná state	MBM 225484	Atlantic Forest
<i>Miconia dodecandra</i> Cogn.	Morro do Quitambém, Paraná state	MBM 222733	Campos Gerais (Rupestrian Fields)
<i>Miconia fallax</i> DC.	Kilômetro 32, São Paulo, São Paulo state	HUEM 7310	Atlantic Forest
<i>Miconia prasina</i> (Sw.) DC.	Tanquarussu, Mato Grosso do Sul state	HUEM 28535	Cerrado
<i>Miconia pusilliflora</i> (DC.) Naudin	Pontal do Paraná, Paraná state	MBM 271515	Atlantic Forest
<i>Miconia sellowiana</i> Naudin.	Parque Estadual Guartelá, Tibagi, Paraná state	HUEM 24957	Campos Gerais (Rupestrian Fields)
<i>Miconia splendens</i> (Sw.) Griseb.	Tanquarussu, Mato Grosso do Sul state	HUEM 28508	Cerrado
<i>Miconia theaezans</i> (Bonpl.) Cogn.	Parque Estadual Vila Velha, Ponta Grossa, Paraná state	HUEM 34632	Campos Gerais (Rupestrian Fields)
<i>Miconia valtherii</i> Naudin	São Miguel Arcanjo, São Paulo state	HUEM 6767	Atlantic Forest

A subepidermal layer was found on the adaxial surface of the leaf of *Miconia theaezans* (Fig. 1E), which was interpreted by Costa (1977) as hypodermis based on the observation that it originates from the subepidermal layer of the young mesophyll that undergoes periclinal divisions. This layer is made up of achlorophyllous, thin-walled parenchymatous cells, some of which are larger and have druses. In the study of leaves of some species of *Leandra* and *Miconia*, carried out by Gonçalves-Silva *et al.* (2019), a hypodermis was also recorded, but on the abaxial face of *Miconia ligustroides* (DC.) Naudin. Oliveira (2007) also refers to the presence of hypodermis in a leaf of *Miconia latecrenata* (DC.) Naudin. Hypodermis is referred to in the anatomical characterization of Melastomataceae for the genus *Miconia* by Metcalfe & Chalk (1957).

The Miconieae leaves investigated here are dorsiventral or bifacial (Fig. 1A-I), but *Miconia sellowiana* exhibits isobilateral mesophyll (Fig. 1G) (Tab. 2). The number of cell-layers of the palisade parenchyma varies between species (Tab. 2) and the spongy parenchyma is multiseriate (Fig. 1A). In the mesophyll, cells with druses and cells with phenolic derivatives frequently occur. Some species, such as *M. pusilliflora* (Fig. 1H), *M. sellowiana* (Fig. 1G) and *M. splendens* (Fig. 1I), show subepidermal idioblasts with druse within the palisade parenchyma. It is noteworthy that the palisade layer may exhibit phenolic content in the subepidermal palisade layer of *M. valtherii* (Fig. 1C) and *M. prasina* (Fig. 1D).

Dorsiventral or centric leaf is recorded as an anatomical character for Melastomataceae (Metcalfe & Chalk 1957), and for some other studied species of *Leandra* and *Miconia* (Oliveira 2007; Gonçalves-Silva *et al.* 2019). Isobilateral

leaf, like that found here in *M. sellowiana*, seems to be infrequent in the family. Attention has been drawn to the fact that this species typically occurs in the rupestrian fields of Guartelá State Park (Tibagi, state of Paraná, Brazil), which are characterized by small-sized vegetation, which develops in shallow soil or rocky outcrops, and has structural adaptations aimed at water stress. It should be noted that Reis *et al.* (2005) also investigated the leaf of *M. sellowiana* occurring in the Cerrado of the state of São Paulo (Brazil), but interpreted the palisade parenchyma of the abaxial surface of the mesophyll, with shorter cells, as belonging to the spongy parenchyma.

The smaller veins consist of collateral vascular bundle and are surrounded by parenchymatic bundle sheath (endoderm) (Fig. 1G-I). Parenchymatous or collenchymatous bundle sheath extensions were recorded on the laminae of *Miconia cinerascens* and *M. theaezans* (Fig. 1E), on both sides of the vascular bundle. All species have a midrib (Fig. 2A-D) and medium-sized veins with a protrusion on the abaxial surface. The midrib consists of uniseriate epidermis on the abaxial surface, with a generally thick cuticular layer, and trichomes may occur (Fig. 2A-D). Under this epidermis there are collenchyma and parenchyma (Fig. 2A-D), which may have cells with druses or phenolic derivatives. There is a U or V vascular cylinder, with phloem on both sides of the xylem, cambium and reduced secondary vascular growth (Fig. 2A-D); in addition to this larger cylinder, one (Fig. 2C) or two smaller additional bundles may occur on the adaxial region of the rib (Tab. 2). The adaxial region of the vein may contain mesophyll, with palisade or spongy parenchyma or be devoid of it, showing collenchyma or parenchyma (Fig. 2A-D) (Tab. 2). The midrib of *Leandra*



Table 2. Structural characters of the leaf lamina of the 15 species of *Leandra* and *Miconia*.

Species/ Features	Lamina surface/ epidermis	Indumentum	Hypodermis	Mesophyll	Palisade parenchyma layers	Midrib (meso- phyll/ additional bun- dles)	Lamina margin
<i>Leandra melastomoides</i>	Flat	Both surfaces (not dense)	Absent Crystal in subepidermal layer	Dorsiventral	1 cell layer	Present/absent	Not observed
<i>Leandra microphylla</i>	Wavy surfaces (both)	Both surfaces (dense)	Absent	Dorsiventral	3-4 cell layers	Present/ 1 small bundle	Parenchyma
<i>Leandra nianga</i>	Wavy adaxial surface	Both surfaces (not dense)	Absent	Dorsiventral	3 cell layers	Absent/absent	Parenchyma (with gelatinous fibers)
<i>Leandra purpurascens</i>	Flat	Both surfaces (dense)	Absent	Dorsiventral	1 or 2 cell layers	Present/absent	Collenchyma, palisade, spongy parenchyma
<i>Leandra xanthocoma</i>	Flat	Both surfaces (not dense)	Absent	Dorsiventral	2 cell layers	Present/absent	Not observed
<i>Miconia budlejoides</i>	Flat (with epidermal crystals)	Glabrous/adaxial Hairy/abaxial (dense)	Absent	Dorsiventral	1 cell layer	Absent/absent	Parenchyma
<i>Miconia cinerascens</i>	Flat	Both surfaces (dense)	Absent	Dorsiventral	2 cell layers	Absent/absent	Parenchyma
<i>Miconia dodecandra</i>	Flat	Glabrous/adaxial Hairy/abaxial (dense)	Absent Crystal in subepidermal layer	Dorsiventral	1 cell layer	Present/1 small bundle	Palisade parenchyma
<i>Miconia fallax</i>	Flat	Glabrous/adaxial Hairy/abaxial (dense)	Absent	Dorsiventral	2 cell layers	Absent/absent	Parenchyma
<i>Miconia prasina</i>	Flat	Glabrous/adaxial Hairy/abaxial (not dense)	Absent	Dorsiventral	3 cell layers	Absent/ 1 small bundle	Collenchyma
<i>Miconia pusilliflora</i>	Flat	Glabrous (both surfaces)	Absent	Dorsiventral	2 or 3 cell layers	Absent/ 2 small bundles	Collenchyma, parenchyma
<i>Miconia sellowiana</i>	Flat	Both surfaces (not dense)	Absent Crystal in subepidermal layer	Isobilateral	2 cell layers (adaxial) 1 or 2 cell layers (abaxial)	Absent/ 1 small bundle	Collenchyma
<i>Miconia splendens</i>	Flat	Glabrous/adaxial Hairy/abaxial (not dense)	Absent	Dorsiventral	1 or 2 cell layers	Absent/ 2 small bundles	Collenchyma
<i>Miconia theezans</i>	Flat	Glabrous/adaxial Hairy/abaxial (not dense)	Absent Druse in subepidermal layer	Dorsiventral	2 cell layers	Absent/ 1 small bundle	Collenchyma
<i>Miconia valtherii</i>	Flat	Both surfaces (dense)	Absent	Dorsiventral	2 cell layers	Absent/absent	Parenchyma

purpurascens has collenchyma and mesophyll on the adaxial region (Fig. 2D). The epidermis of the adaxial surface of the midrib shows much resemblance to the epidermis of the lamina (Fig. 2A-D).

The vascular system of the midrib of almost all 15 species of *Leandra* and *Miconia* is characterized by the form of an open arch, but in the case of *L. microphylla* (Fig. 2A) this arch is almost closed. As pointed by Reis *et al.* (2005) most species of *Miconia* and two species of *Leandra* [*Leandra aurea* (Cham.) Cogn. and *Leandra lacunosa* Cogn.] have a closed arch. Therefore, this feature may be taxonomically useful for separating species within the genus, but it is unreliable for separating both genera.

The margin of the leaf lamina has epidermis, eventually with trichomes, and the nature of the subepidermal tissue

may vary (Tab. 2). The margin of *L. purpurascens* has collenchyma and chlorophyll tissue (palisade and spongy parenchyma) (Fig. 2F), while *M. dodecandra* has only palisade parenchyma (Fig. 2G). *Leandra nianga's* margin deserves some attention because it exhibits gelatinous fibers (Fig. 2E).

The leaves of *Leandra* and *Miconia* possess many anatomical features of potential taxonomic significance (Tab. 2), particularly associated with the types of trichomes (Tab. 3). For *Leandra*, features such as number of palisade parenchyma cell-layers, presence of gelatinous fibers, arrangement of the vascular system of the midrib (open or nearly closed arch), mesophyll in the midrib, presence of a smaller vascular bundle (additional bundles) on the adaxial region of the midrib and margin lamina structure can be employed. In the case of *Miconia* species, the significant

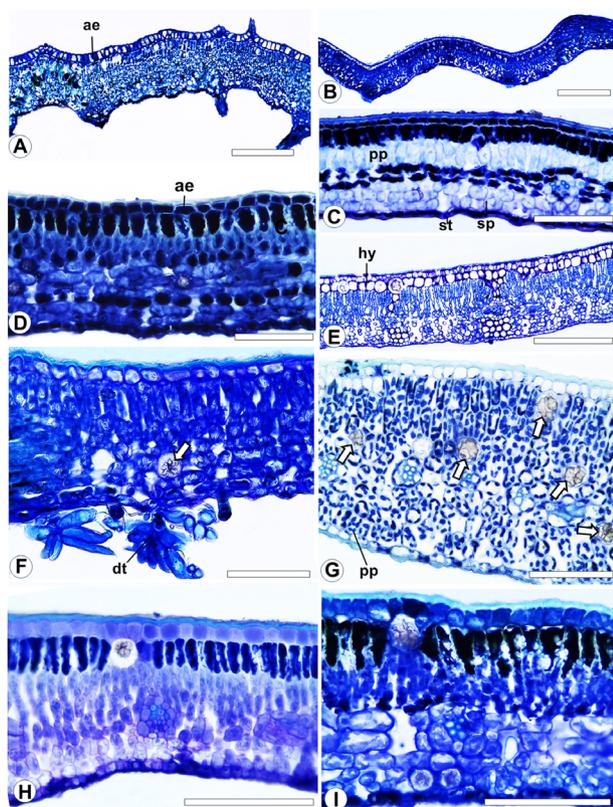


Figure 1. Lamina structure of *L. microphylla* (A), *L. nianga* (B), *M. valtherii* (C), *M. prasina* (D), *M. theaezans* (E), *M. budlejoides* (F), *M. sellowiana* (G), *M. pusilliflora* (H) and *M. splendens* (I), in cross-sections. A,B. Laminae with re-entrances. C,D. Dorsiventral laminae with 2 cell-layers of palisade parenchyma, and phenolic derivatives in the epidermis and mesophyll. E. Dorsiventral lamina with hypodermis and bundle sheath extension (white arrow). F. Dorsiventral lamina (1 cell-layer of palisade parenchyma) exhibiting dendritic and glandular trichomes. G. Isobilateral lamina with druses in the mesophyll. H,I. Dorsiventral laminae (2-3 cell-layers of palisade parenchyma) exhibiting subepidermal druses and phenolic derivatives. (ae=adaxial surface epidermis; dt=dendritic trichome; hy=hypodermis; pp=palisade parenchyma; sp=spongy parenchyma; st=stomata; white arrow=druse). Scale bars: 150µm (A,B), 50µm (C-I).

characters are the presence of hypodermis, presence of crystal in subepidermal cells, type of mesophyll (dorsiventral or isobilateral), number of palisade parenchyma layers, additional vascular bundles on the adaxial region of the midrib, mesophyll on the adaxial region of the midrib and leaf margin structure.

Trichome types as a diagnostic character in the genera

Trichomes are present in 14 of the 15 species studied, on both surfaces or on a single epidermal surface; only *M. pusilliflora* does not have trichomes on the epidermis (Fig. 3A). The five species of *Leandra* have conical trichomes with

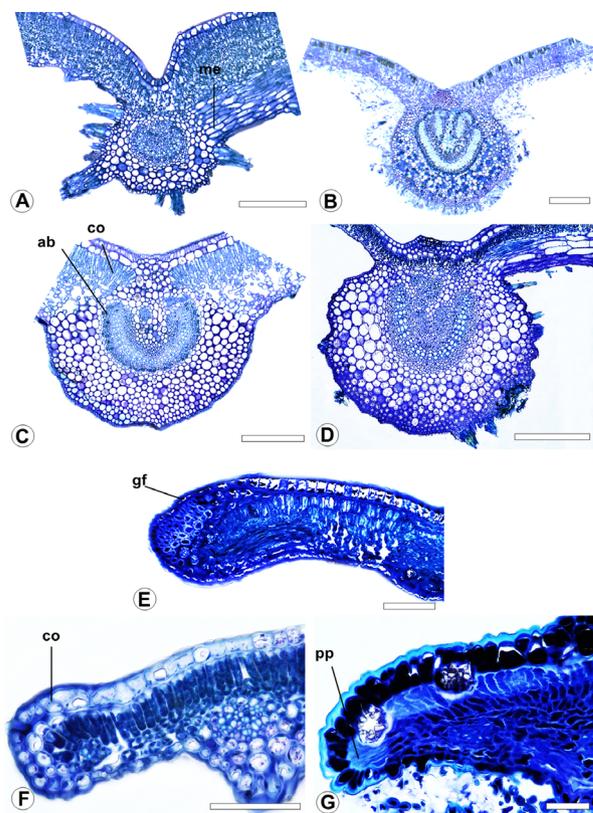


Figure 2. Midrib and margin structure of *Leandra microphylla* (A), *L. cinerascens* (B), *Miconia theaezans* (C), *L. purpurascens* (D), *L. nianga* (E), *L. purpurascens* (F) and *M. dodecandra* (G), in cross-sections. A-D. Midribs with almost closed (A) and U-shaped vascular cylinders; presence of mesophyll in A, collenchyma in B and C, and collenchyma and mesophyll in D (adaxial surface). E-G. Margins with gelatinous fibers, collenchyma and palisade parenchyma, respectively. (ab=additional vascular bundle; co=collenchyma; gf=gelatinous fibers; me=mesophyll; pp=palisade parenchyma). Scale bars: 300µm (A,B), 200µm (C-E), 100µm (G), 50µm (F).

rough surface and enations well developed or of reduced size (Tab. 3); in *Leandra*, glandular, dendritic and mixed trichomes were also registered (Tab. 3) (Fig. 3B, 3C, 3D and 3E). *Miconia* leaves are devoid of conical trichomes, but commonly have dendritic trichomes (Fig. 3F and 3G); glandular trichomes and vermiform trichomes were found only in *Miconia fallax* (Fig. 3H). It must be pointed out here that some authors (Baumgratz & Ferreira 1980; Oliveira 2007) have described the dendritic trichomes in *M. dodecandra* (Tab. 3) as stellate. The classification of dendritic trichomes compared to stellate trichomes is not very clear in the terminology of Wurdack (1986). For this author, many of these stellate trichomes have an erect central arm, but show similarity to the dendritic type.

The taxonomic value of the trichome characters has been used in Melastomataceae by classic authors as Metcalfe & Chalk (1957), Baumgratz & Ferreira (1980) and Wurdack (1986). Since then, several studies have been carried out as a taxonomic contribution to the family, such as Carmo



Table 3. Morphology of the indumentum of the 15 species of *Leandra* and *Miconia*.

Species/Features	Trichomes/adaxial surface	Trichomes/abaxial surface	Pubescence (adaxial)	Pubescence (abaxial)
<i>Leandra melastomoides</i>	Conical ^{1a} Glandular ^{2a} Mixed ^{3a}	Conical ^{1a} Dendritic ^{4a}	Sparse trichomes	Low density
<i>Leandra microphylla</i>	Conical ^{1b}	Conical ^{1c}	Low density	Dense
<i>Leandra nianga</i>	Conical ^{1d}	Conical ^{1e} Glandular ^{2b} Mixed ^{3b}	Sparse trichomes	Sparse trichomes
<i>Leandra purpurascens</i>	Conical ^{1f}	Conical ^{1g} Dendritic ^{4a}	Sparse trichomes	Dense
<i>Leandra xanthocoma</i>	Conical ^{1h}	Conical ^{1h}	Low density	Low density
<i>Miconia budlejoides</i>	Glabrous	Dendritic ^{4b}	Glabrous	Dense
<i>Miconia cinerascens</i>	Dendritic ^{4c} Glandular ^{2c}	Dendritic ^{4c}	Few dense	Dense
<i>Miconia dodecandra</i>	Glabrous ⁵ (high-domed convex structure)	Dendritic ^{4d}	Glabrous	Dense
<i>Miconia fallax</i>	Glabrous	Vermiform	Glabrous	Dense
<i>Miconia prasina</i>	Glabrous	Dendritic ^{4b}	Glabrous	Sparse trichomes
<i>Miconia pusilliflora</i>	Glabrous	Glabrous	Glabrous	Glabrous
<i>Miconia sellowiana</i>	Dendritic ^{4b} Glandular ^{2c}	Dendritic ^{4b} Glandular ^{2c}	Sparse trichomes	Sparse trichomes
<i>Miconia splendens</i>	Glabrous	Dendritic ^{4b}	Glabrous	Low density
<i>Miconia theaezans</i>	Glabrous	Glandular ^{2d}	Glabrous	Sparse trichomes
<i>Miconia valtherii</i>	Dendritic ^{4b}	Dendritic ^{4b}	Dense	Dense

et al. (2019), Gonçalves-Silva et al. (2019) and Gonçalves et al. (2023). Our results confirm the diagnostic importance of the trichomes in *Leandra* and *Miconia* (Tab. 3), but that it must be associated with the structural characters of the leaf lamina. Conical trichomes and mixed trichomes (non-glandular and glandular) are present only in the five species of *Leandra*. *Miconia* trichomes are similar, in general they are dendritic with small variations in size and arms (terete or thin-walled arms). Leaves of *M. valtherii* and *M. dodecandra* are distinguished from the other investigated species, the former for exhibiting vermiform trichomes and the latter for presenting convex structures in high-domed (according to the terminology of Barthlott & Hunt 2000). It is emphasized that these domes resemble Wurdack's (1986) bulla-based trichomes without enations, except for the shape of the apex which is rounded rather than tapered.

The conical trichomes on the leaves of *Leandra* species have raised doubts as to their essentially protodermal origin. Figure 2A shows the base of some conical trichomes that can be interpreted as being of protodermal and subprotodermal origin. Gonçalves-Silva et al. (2019) investigated conical trichomes from *Leandra* leaves and also questioned whether they are actually trichomes (protodermal origin)

or emergences (protodermal and subprotodermal origin), based on Uphof (1962) and Evert (2013). Our conception of a conical trichome for *Leandra* does not invalidate the thesis that this appendage may be an emergency, but as suggested by Gonçalves-Silva et al. (2019) only its ontogeny can indicate its nature.

Some considerations about the structure of the leaf lamina that may be related to environmental factors

The leaves of the 15 species of *Leandra* and *Miconia* species investigated belong to plants collected in forests, but which can also occur in rupestrian fields (described on the labels of the material collected from the species). The leaf analysis has revealed structural characters that may have some relevant relationship with environmental factors, such as luminosity, water stress and wind. All species have stomata on the lower leaf surface and away from direct sunlight which can reduce water loss by transpiration, as suggested by Dickison (2000). Leaf structural variation affected by environmental factors has been reported in *Leandra* and *Miconia* species, such as *M. ibaguensis* (Bonpl.) Triana and *M. stenostachya* Schrank & Mart. ex DC. (Marques

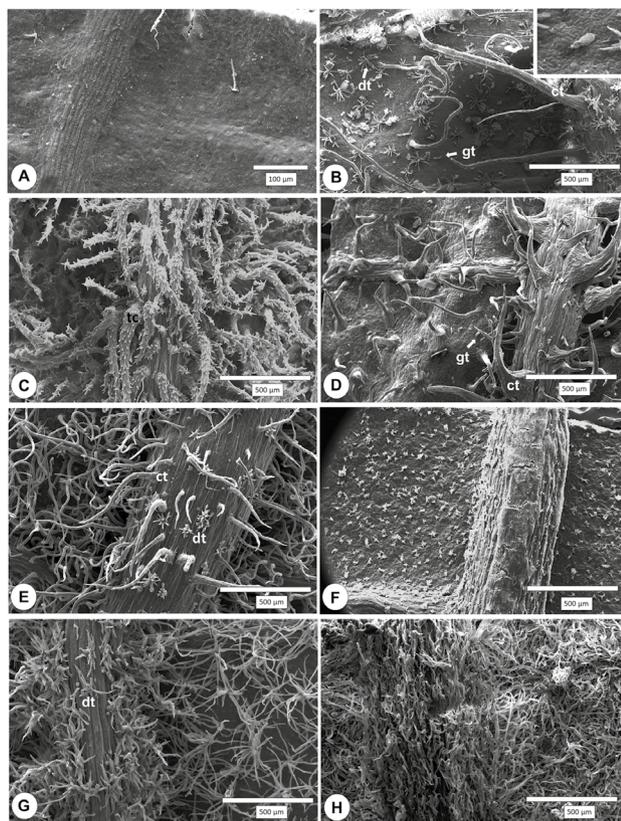


Figure 3. Morphology of trichomes in Scanning Electron Microscopy (SEM). A. Glabrous abaxial epidermal surface in *Miconia pusilliflora*. B. Long conical and filamentous trichomes, dendritic trichomes with short axis in *Leandra melastomoides*; detail of glandular trichome. C. Long conical trichomes with projections in *Leandra microphylla*. D. Conical and glandular trichomes in *Leandra xanthocoma*. E. Dendritic-type trichomes in *Leandra purpurascens*. F. Dendritic trichomes with short axis and laminar branches in *Miconia splendens*. G. Moderately long dendritic trichomes in the epidermis of *Miconia valtherii*. H. Vermiform trichomes in *Miconia fallax*. (ct=conical trichome; dt=dendritic trichome; gt=glandular trichome).

et al. 2000), *M. tristis* Spring and *M. doriana* Cogn. (Souza & Marquete 2000), *M. sellowiana* (Boeger *et al.* 2008), *L. aurea* (Cham.) Cogn., *L. polystachya* (Naudin) Cogn., *L. sericea* DC., *M. albicans* (Sw.) Triana, *M. hyemalis* A. St.-Hill. & Naudin and *M. ligustroides* (DC.) Naudin. (Gonçalves-Silva *et al.* 2019), and *M. nervosa* (Müller *et al.* 2020). Other structural characters that can restrict water loss (*sensu* Dickison 2000) were observed in these species, such as reduced leaf size, small undulations on the abaxial surface, thick cuticle on the adaxial surface, increase in trichome density, subepidermal layer (hypodermis), increase in the number of palisade parenchyma layers in the mesophyll, and presence of gelatinous fibers (Tab. 2 and 3).

Leandra microphylla (Tab. 2 and 3) may be considered a xeromorphic species, from the rupestrian fields of Paraná (Brazil); it exhibits leaf characters considered xeromorphic

or sclerophyllous by Dickison (2000), such as reduced leaf size, undulations on the abaxial surface, trichome density, extensive development of palisade parenchyma in the mesophyll. The xeromorphic condition seems to also occur in *L. nianga* (Tab. 2 and 3) from Minas Gerais (Brazil), which shows some characters possibly related to water stress, such as undulations on the abaxial surface, three layers of palisade parenchyma, and gelatinous fibers.

Xeromorphic or sclerophyllous features have been recorded in other species (Tab. 2 and 3), such as thick cuticular layer, subepidermal crystals, hypodermis, isobilateral mesophyll and trichome density, but which may have a protective function under high light conditions (Dickison 2000), serving according to this author to increase the reflective power of the leaf and protect the photosynthetic cells of the mesophyll against excessive radiation. Xeromorphy was also found in some species of *Leandra* and *Miconia* by Gonçalves-Silva *et al.* (2019), but the authors reported that *Leandra* species have a smaller number of specialized structures for reduction or compensation of water loss than *Miconia* species.

Conclusion

The leaves of the 15 species of *Leandra* and *Miconia* provide many important structural features which have taxonomic value at the specific level. The analysis showed that some characters typically occur in some taxa: conical trichomes only in the genus *Leandra* and vermiform trichomes only in *Miconia*. Hypodermis in *Miconia theaezans*, quasi-concentric midrib in *Leandra microphylla*, and isobilateral mesophyll in *Miconia sellowiana*. Leaf features of potential taxonomic significance are the trichome types, presence of hypodermis, layer number of palisade parenchyma, occurrence of gelatinous fibers, midrib structure, and margin lamina structure. Xeromorphic and sclerophyllous features are present in *Leandra* and *Miconia* species, and *Leandra microphylla* may be considered a xerophyte.

Acknowledgements

The authors thank CAPES (Coordination of Higher Education Personnel Improvement, Brazil) and CNPq (National Council for Scientific and Technological Improvement, Brazil) for financing part of the work carried out (Master's and Research Productivity Scholarships), and to the Herbarium of the State University of Maringá (HUEM) and the Botanical Museum of Curitiba (MBM) for authorizing the collection of botanical material.

Authors' Contributions

TMMM did the collection of material, separation, fixation and blocking of material, sectioned and staining of slides,



figures of slides. TMMM and LAS did the analysis of slides, analysis using a scanning electron microscope (SEM) and tables. KFR did the correction and confirmation of the chosen species. All the authors participated in the bibliographic survey, article writing and corrections.

Conflict of interest

The authors declare they have no conflict of interests.

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