



Original article

Leaf epidermal micromorphology of the abaxial surface of *Myrcia* DC. species (Myrtaceae)

Lucas Herberts-Sousa¹ , Anelise Gabriela Grotto¹ , Duane F. Lima¹ , Eve J. Lucas² , Fernanda Maria C. de Oliveira³

¹Postgraduate Program in Biology of Fungi, Algae and Plants, Universidade Federal de Santa Catarina, Florianópolis, 88040-900, Brazil

²Herbarium, Royal Botanic Gardens, Kew, Richmond, TW9 3AE, United Kingdom

³Department of Botany, Universidade Federal de Santa Catarina, Florianópolis, 88040-535, Brazil

*Corresponding author: lucasherberts@live.com

Received 24 January 2025 | Accepted 25 June 2025 | Published 22 October 2025

How to cite: Herberts-Sousa, L., Grotto, A.G., Lima, D.F., Lucas, E.J. & Oliveira, F.M.C. (2025) "Leaf epidermal micromorphology of the abaxial surface of *Myrcia* DC. species (Myrtaceae)" *Heringeriana Special Issue Myrtaceae* (2025): e918065. doi.org/10.70782/heringeriana.v19i1.918065

Abstract: Myrtaceae is widely distributed in tropical regions, playing significant ecological and economic roles. Within this family, *Myrcia* stands out for its taxonomic complexity due to high morphological homogeneity, which complicates the identification of species and sections. This study aims to analyze and describe micromorphological characteristics of *Myrcia* leaves to contribute to the characterization of the genus and its infrageneric groups, as well as to generate data to support future taxonomic studies. The abaxial surface of leaves from 73 *Myrcia* species was analyzed using scanning electron microscopy (SEM). Characteristics of stomata, cuticle, epicuticular waxes, and trichomes were observed. Stomata, classified as anomocytic and paracytic, showed variations in height relative to epidermal cells. The cuticle exhibited smooth and striated patterns, while epicuticular waxes ranged from smooth to plate-like, fimbriate, and granular. Glandular and non-glandular trichomes, the latter with uniseriate, dibrachiate, stellate, and branched forms, were documented, revealing wide variation in density, distribution and length. None of the analyzed characters distinctly defined the ten infrageneric groups of *Myrcia* due to high plasticity. However, some patterns were observed, such as the predominance of dibrachiate trichomes in *M. sects. Calyptanthus* and *Sympodiomyrcia*. This study provides valuable new data for the taxonomy of *Myrcia* and future micromorphological research.

Keywords: Anatomy, Myrteae, stomata, trichomes, cuticle.

Resumo: (Micromorfologia epidérmica foliar da superfície abaxial das espécies *Myrcia* DC. (Myrtaceae)) Myrtaceae é amplamente distribuída nas regiões tropicais, desempenhando papéis ecológicos e econômicos importantes. Dentro dessa família, o gênero *Myrcia* se destaca pela complexidade taxonômica devido à alta homogeneidade morfológica, o que dificulta a identificação de espécies e seções. Este estudo tem como objetivo analisar e descrever características micromorfológicas de folhas de *Myrcia* a fim de contribuir para a caracterização do gênero e de seus grupos infragenéricos, bem como gerar dados que subsidiem futuros estudos taxonômicos. A face abaxial de folhas de 73 espécies de *Myrcia* foram analisadas por meio de microscopia eletrônica de varredura. Características de estômatos, cutícula, ceras epicuticulares e tricomas foram observadas. Os estômatos foram classificados como anomócíticos e paracíticos, apresentando variações na altura em relação às células epidérmicas. A cutícula mostrou padrões lisos e estriados, enquanto as ceras epicuticulares variaram de lisas a plaquetadas, fimbriadas e granulares. Foram documentados tricomas glandulares e tectores, estes últimos com formas unisseriadas, dibraquiadas, estreladas e ramificadas, revelando ampla variação em densidade, distribuição e comprimento. Nenhum dos caracteres analisados claramente caracterizou os dez grupos infragenéricos de *Myrcia*, devido à elevada plasticidade. Porém, alguns padrões puderam ser observados, como a predominância de tricomas dibraquiados em *M. sects. Calyptanthus* e *Sympodiomyrcia*. Os dados levantados neste trabalho podem fornecer subsídios para a taxonomia de *Myrcia* e futuros estudos micromorfológicos.

Palavras-chave: Anatomia, Myrteae, estômatos, tricomas, cutícula.

Introduction

Myrtaceae belongs to the order Myrtales, clade Rosids, subclade Malvids (APG-IV, 2016) comprising 130 genus and around 6,200 species (Plants of the World Online, 2023). It has an extensive global distribution with predominance in tropical regions (Wilson, 2011). The plants in this family are trees or shrubs, with simple, opposite or alternate leaves, particularly with secretory cavities for essential oils, polystemonous flowers and an inferior ovary (APG IV, 2016; Wilson, 2011). *Myrcia* DC., tribe Myrteae, is one of the ten largest genera in the family with 744 species and a distribution restricted to the Neotropics (Santos et al., 2024). Of these, 409 species occur in Brazil, with species richness especially high in the Atlantic Forest (Santos et al., 2025). The genus is defined by its foliaceous cotyledons, with bi- or trilobular ovaries containing two ovules, seeds with soft testa and inflorescences that are generally panicle-like (Lucas et al., 2011). Currently, *Myrcia* includes in its circumscription the traditional genera *Calyptanthus* Sw., *Gomidesia* O.Berg and *Marlierea* Cambess.; its current classification is based on ten monophyletic groups that correspond to nine sections (*M. sect. Aguava* (Raf.) D.F. Lima & E. Lucas, *M. sect. Aulomyrcia* (O. Berg) Griseb., *M. sect. Calyptanthus* (Sw.) A.R. Lourenço & E. Lucas, *M. sect. Eugeniopsis* (O. Berg) M.F. Santos & E. Lucas, *M. sect. Gomidesia* (O. Berg) B.S. Amorim & E. Lucas, *M. sect. Myrcia*, *M. sect. Reticulosae* D.F. Lima & E. Lucas, *M. sect. Sympodiomyrcia* M.F. Santos & E. Lucas and *M. sect. Tomentosae* E. Lucas & D.F. Lima) and a clade informally named “clade 10” (Lucas et al., 2011; Amorim et al., 2019).

The definition of each of these groups is given through a few floral characters, such as the morphology of the anthers and calyces, but vegetative characteristics, such as the growth pattern of the branches, are also useful (Lucas et al., 2011). However, there is a high degree of homoplasy in the morphological characters of *Myrcia* (Lucas et al., 2011; Vasconcelos et al., 2017). This, combined with the high number of species in the genus and the morphological homogeneity within it, can make it difficult to clarify the infrageneric groups and species.

Micromorphological and anatomical characteristics of vegetative organs can help to characterize taxa and solve delimitation problems, especially in taxa that have similar external morphologies, as is the case within Myrtaceae (e.g. Cardoso and Sajo, 2004; Cardoso et al., 2009; S. M. Gomes et al., 2009; Retamales and Scharaschkin, 2015; Oliveira et al., 2018; Wagner et al., 2023). However, compared to the great richness of species in the family Myrtaceae, there are still few studies that report novel trait datasets. In particular, the diversity of trichomes and other characteristics of the leaf epidermis (such as waxes and stomatal complexes) of *Myrcia* have been little investigated, with some analyses based on anatomical sections for taxonomic purposes, sampling sparse species from all sections of *Myrcia*, except *M. sect. Eugeniopsis* (e.g. D. M. S. Gomes and Neves, 1993; S. M. Gomes et al., 2009; Bezerra, 2013; Wagner et al., 2023), or generalized descriptions of indumentum in taxonomic works (e.g.

Lima, 2017 [*M. sect. Aguava*]; Santos et al., 2018 [*M. sect. Sympodiomyrcia*]). The latter generally limits itself to characterize the color, density and type of trichomes as observed under light microscopy. Characteristics of the leaf epidermis can be taxonomically relevant, as has already been demonstrated in Melastomataceae (Wurdack, 1962) and Lamiaceae (Gul et al., 2019) and should be explored in greater detail. It is worth noting that few of the studies cited used SEM to describe leaf epidermal structures in *Myrcia* (S. M. Gomes et al., 2009; Donato & Morretes, 2011; Bezerra, 2013).

Thus, this study aimed to analyze and describe micromorphological characters of the abaxial epidermal surface of *Myrcia* leaves, using scanning electron microscopy (SEM), in order to verify those that may assist in the characterization of infrageneric groups. In addition, this study contributes to the provision of data that can be used as subsidies in future taxonomic works.

Material and Methods

Leaf blades of 73 species of *Myrcia* were analyzed from exsiccatae deposited in the K and FLOR herbaria (acronyms according to Thiers, 2024). The list of species and respective vouchers are presented in Table 1. Species from all sections of *Myrcia* and “clade 10” were sampled. The taxonomic nomenclature and infrageneric positioning of the species follow Santos *et al.* (2024). Species were selected to ensure sampling was representative as well as to cover different types of trichomes. Identifications of specimen sampled were verified by taxonomic experts in the group as Dr. Duane F. Lima and Dr. Eve Lucas. The abaxial surface of fully expanded leaves was analyzed using scanning electron microscopy (SEM). Leaves were removed from herborized specimens, and their median portion, adjacent to the main vein, was cut out and fixed to metal stubs with double-sided carbon tape and subjected to gold metallization (Sputtering EMSCD500/Leica), according to the methodology of Silveira (1989). The analysis was performed using a Hitachi SEM S-4700-II microscope at the Jodrell Laboratory (Royal Botanic Gardens, Kew, United Kingdom) and a JEOL JSM-6390LV microscope at the Central Laboratory of Electron Microscopy (LCME; Universidade Federal de Santa Catarina, Brazil). The equipment used in each analysis is indicated in Table 1.

To describe the observed structures, specific bibliography was used. The classification of stomata, cuticle and trichome types was based on Evert (2013) and Werker (2000), while the classification of epicuticular waxes was based on Barthlott *et al.* (1998), except for fimbriated epicuticular wax, which was defined by Bezerra (2013). Due to the difficulty in distinguishing between cuticle layers and epicuticular waxes, we combined both characteristics in the descriptions. Thus, at the Appendix, when more than one character is cited, the first refers to the cuticle and the second to the waxes.

Through SEM images, the following characteristics of the abaxial surface leaf blade of 73 *Myrcia* species

were observed: types of stomata (anomocytic and/or paracytic), stomata level in relation to the epidermis (below, level or above), cuticles and epicuticular waxes (smooth, striated, thin, plate-like, fimbriated or granular), tector and glandular trichomes, morphology of tector trichomes (simple unicellular, dibrachiate, hook-shaped, stellate, branched), leaf blade indumentum (whether dense, moderate or sparse). In the latter case, indumentum was considered dense when the epidermis was not visible due to

complete cover by trichomes; moderate when the epidermis was barely visible; and sparse when the epidermis was clearly visible. It was not possible to describe some of the characteristics of the common cells of the epidermis, such as the contour of the epidermal cells, shape and quantity of the roof cells of the secretory cavities, due to large depositions of wax and/or trichomes that can cover them. Other structures such as stomata, trichomes and epicuticular waxes were described when distinction was possible.

Table 1: *Myrcia* species analyzed, organized by section, with their respective vouchers indicating where the scanning electron microscopy (SEM) was conducted.

Section	Species	Voucher	SEM
<i>Aguava</i>	<i>Myrcia cuprea</i> (O.Berg) Kiaersk.	G.L.Sobel et al. 4584	Kew
	<i>Myrcia guianensis</i> (Aubl.) DC.	S.Gonzales & E.Fonty 1831	Kew
	<i>Myrcia laricina</i> (O.Berg) Burret ex Luetzelb.	Gardner 2874	Kew
	<i>Myrcia nivea</i> Cambess.	D.F.Lima & R.Morokawa 471	Kew
	<i>Myrcia rufipes</i> DC.	M.L.Kawasaki et al. 7722	Kew
	<i>Myrcia siriacoana</i> Glaz. ex P.O.Rosa & Proença	D.F.Lima et al. 505	Kew
	<i>Myrcia subalpestris</i> DC.	D.F.Lima & R.Trad 514	Kew
	<i>Myrcia subalpestris</i> (= <i>M. subverticillaris</i> (O.Berg) Kiaersk.)	D.F.Lima & R.Morokawa 464	Kew
	<i>Myrcia tortuosa</i> (O.Berg) N.Silveira	E.Onishi & S.G.Fonseca 184	Kew
	<i>Myrcia tortuosa</i> (= <i>M. linguiformis</i> (O.Berg) N.Silveira)	D.F.Lima & R.Morokawa 457	Kew
	<i>Myrcia vestita</i> DC.	D.F.Lima & R.Morokawa 455	Kew
<i>Aulomyrcia</i>	<i>Myrcia abbotiana</i> (Urb.) Alain	E.Lucas et al. 1108	Kew
	<i>Myrcia amazonica</i> DC.	D.F.Lima et al. 417	Kew
	<i>Myrcia cana</i> (McVaugh) E.Lucas & C.E.Wilson	S.S.Tillett et al. 751-27	Kew
	<i>Myrcia decorticans</i> DC.	M.Landim 1476	Kew
	<i>Myrcia florifera</i> (McVaugh) Gaem. & E.Lucas	A.C.Araújo et al. 1885	Kew
	<i>Myrcia multiflora</i> (Lam.) DC.	E.Lucas et al. 824	Kew
	<i>Myrcia neomontana</i> E.Lucas & C.E.Wilson	R.C.Ek et al. 1768	Kew
	<i>Myrcia neuwiedeanana</i> (O.Berg) E.Lucas & C.E.Wilson	V.G.Staggemeier & J.E.Q.Faria 771	Kew
	<i>Myrcia obversa</i> (D.Legrand) E.Lucas & C.E.Wilson	A.Amorim et al. 449	Kew
	<i>Myrcia racemosa</i> (O.Berg) Kiaersk.	S.A.Mori et al. 10844	Kew
	<i>Myrcia saxatilis</i> (Amshoff) McVaugh	J.J. de Granville & F.Crozier 13565	Kew

Continued on next page

Table 1: *Myrcia* species analyzed, organized by section, with their respective vouchers indicating where the scanning electron microscopy (SEM) was conducted. (Continued)

Section	Species	Voucher	SEM
<i>Calyptanthes</i>	<i>Myrcia calderonii</i> (Standl.) A.R.Lourenço & Sánchez-Cháv.	B.Vazquez 557	Kew
	<i>Myrcia chytraculia</i> (L.) A.R.Lourenço & E.Lucas	J.Marin 180	Kew
	<i>Myrcia glomerata</i> (Cambess.) G.P.Burton & E.Lucas	E.Lucas et al. 183	Kew
	<i>Myrcia fasciculata</i> (O.Berg) K.Campbell & K.Samra	J.J.Wurdack & L.S.Adderley 43528	Kew
	<i>Myrcia loranthifolia</i> (DC.) G.P.Burton & E.Lucas (= <i>Calyptanthes brasiliensis</i> Spreng.)	J.E.Q.Faria et al. 2497	Kew
	<i>Myrcia loranthifolia</i> (= <i>Calyptanthes grandifolia</i> O.Berg)	L.P. de Queiroz et al. 1293	Kew
	<i>Myrcia neoclusiifolia</i> A.R.Lourenço & E.Lucas	R.C.Forzza et al. 4398	Kew
	<i>Myrcia strigosa</i> A.R.Lourenço & E.Lucas	G.Hatschbach & C.Koczizki 20886	Kew
<i>Eugeniopsis</i>	<i>Myrcia clauseniana</i> (O.Berg) A.Maruy. & Gaem.	M.L.Kawasaki & M.C.Henrique 7627	Kew
	<i>Myrcia eugeniopsoides</i> (D.Legrand & Kausel) Mazine	E.Barbosa & L.B.Pereira 38	Kew
	<i>Myrcia ferruginosa</i> Mazine	M.F.Santos et al. 689	Kew
	<i>Myrcia hatschbachii</i> D.Legrand	G.Hatschbach 30964	Kew
	<i>Myrcia oblongata</i> DC.	M.F.Santos et al. 667	Kew
	<i>Myrcia subacuminata</i> (Kiaersk.) M.F.Santos	J.E.Q.Faria & V.G.Staggemeier 2525	Kew
	<i>Myrcia suberosa</i> M.F.Santos & T.Fern.	Farney 3134	UFSC
	<i>Myrcia teuscheriana</i> (O.Berg) M.F.Santos	E.Lucas et al. 673	Kew
	<i>Myrcia vellozoi</i> Mazine	V.G.Staggemeier & M.G.G.Camargo 828	Kew
<i>Gomidesia</i>	<i>Myrcia brasiliensis</i> Kiaersk.	S.J.Gomes da Silva et al. 161	Kew
	<i>Myrcia carvalhoi</i> NicLugh.	M.F.Santos et al. 217	Kew
	<i>Myrcia cerqueiria</i> (Nied.) E.Lucas & Sobral	E.M.Nic Lughadha et al. 182	Kew
	<i>Myrcia eriocalyx</i> DC.	E.M.Nic Lughadha et al. 211	Kew
	<i>Myrcia florida</i> Lem.	E.M.Nic Lughadha et al. 173	Kew
	<i>Myrcia hartwegiana</i> (O.Berg) Kiaersk.	K.Matsumoto et al. 837	Kew
	<i>Myrcia hebepetala</i> DC.	M.M.Saavedra et al. 914	Kew
	<i>Myrcia mischophylla</i> Kiaersk.	D.F.Lima et al. 416	Kew
	<i>Myrcia pubescens</i> DC.	D.F.Lima & R.Trad 539	Kew
	<i>Myrcia reticulata</i> Cambess.	M.F.Santos et al. 803	Kew
	<i>Myrcia spectabilis</i> DC.	E.Lucas et al. 217	Kew

Continued on next page

Table 1: *Myrcia* species analyzed, organized by section, with their respective vouchers indicating where the scanning electron microscopy (SEM) was conducted. (Continued)

Section	Species	Voucher	SEM
<i>Myrcia</i>	<i>Myrcia aliena</i> McVaugh	D.C.Daly et al. 1893	Kew
	<i>Myrcia albotomentosa</i> DC.	D.F.Lima et al. 499	Kew
	<i>Myrcia bella</i> Cambess.	D.F.Lima & R.Trad 520	Kew
	<i>Myrcia bracteata</i> (Rich.) DC.	G.T.Prance et al. 10615	UFSC
	<i>Myrcia isaiana</i> G.M.Barroso & Peixoto	G.Hatschbach & A.R.Campos 57921	UFSC
	<i>Myrcia retorta</i> Cambess.	D.B.Falkenberg s.n. (FLOR 39200)	UFSC
	<i>Myrcia rupicola</i> D.Legrand	R.Reitz & R.M.Klein 10321	UFSC
	<i>Myrcia splendens</i> (Sw.) DC.	R.Reitz & R.M.Klein 17420	UFSC
	<i>Myrcia tafelbergica</i> Amshoff	B.Hoffman et al. 1765	Kew
	<i>Myrcia tocaninensis</i> Glaz. ex P.O.Rosa & Proença	H.S.Irwin et al. 32901	UFSC
<i>Reticulosae</i>	<i>Myrcia aethusa</i> (O.Berg) N.Silveira	J.A.Jarenkow 2033	UFSC
	<i>Myrcia pubipetala</i> Miq.	R.Santos & A.J.Aguiar s.n. (FLOR 29350)	UFSC
	<i>Myrcia venulosa</i> DC.	L.B.Smith et al. 16054	UFSC
<i>Sympodiomyrcia</i>	<i>Myrcia ferruginea</i> (Poir.) DC.	Fundación Biológica Puerto Rastrojo CHI-22	Kew
	<i>Myrcia subcordata</i> DC.	L.B.Smith & R.M.Klein 14416	UFSC
<i>Tomentosae</i>	<i>Myrcia anomala</i> Cambess.	A.Krapovickas et al. 45966	Kew
	<i>Myrcia selloi</i> (Spreng.) N.Silveira	D.B.Falkenberg 1814	UFSC
	<i>Myrcia selloi</i> (= <i>M. larutoteana</i> Cambess.)	R.Kummrow 542	UFSC
	<i>Myrcia tomentosa</i> (Aubl.) DC.	A.R.Silva & E.L.Siqueira 464	UFSC
	<i>Myrcia verticillaris</i> O.Berg	M.Sobral & J.N.Marchiori 4539	UFSC
Clado 10	<i>Myrcia maximiliana</i> O.Berg	M.F.Santos et al. 750	Kew e UFSC
	<i>Myrcia pulvinata</i> B.S.Amorim	Souza 389	UFSC
	<i>Myrcia robusta</i> Sobral	E.J.Lucas et al. 727	UFSC

Results

The shape variety of these structures is presented in Figures 1-4 and compiled at the Appendix. A summary of the most relevant characteristics of the infrageneric groups of *Myrcia* is shown in Table 2. Two types of stomata were found in the analyzed species: anomocytic (Fig. 1A) and paracytic (Fig. 1B), with the latter being predominant. While most sections presented both types, *Myrcia* sect. *Gomidesia* presented only paracytic ones, while *M.* sect. *Sympodiomyrcia* and *M.* sect. *Reticulosae* presented only anomocytic ones (Appendix and Table 2). Stomata can be located above (Fig. 1E), level (Fig. 1D) or, more rarely, below (Fig. 1C) the other epidermal cells (Appendix and Table 2).

The cuticle of the analyzed species may be smooth (Fig. 2A-B) or striated (Fig. 2C) in different regions of the leaf sample. Epicuticular waxes have different shapes, such as smooth and thin (Fig. 2B) without any type of ornamentation; deposited in platelets (Fig. 2D) in which the deposition occurs in the form of flat crystalloids attached to the surface by its narrowest side and may form different angles; fimbriated (Fig. 2E) with the deposition of wax formed by microtubules with regular distribution and without fragmentation; or in granules (Fig. 2F) in which there is the deposition of rounded or isodiametric granules. All infrageneric groups of *Myrcia* presented mostly smooth cuticle with the striated condition being rarer (Appendix and Table 2). Wax forming granules were observed in all sections, except *M.* sect. *Eugeniopsis*. The presence

of fimbriated wax was rarely seen, only in *Myrcia* sect. *Eugeniopsis* and *M.* sect. *Calyptanthus* (Appendix and Table 2).

Species analyzed have glandular and tector structures (Fig. 3A); glandular trichomes do not occur in isolation but are usually observed mixed with tector trichomes (Appendix). Only 20 species of the 73 analyzed had glandular trichomes. Glandular trichomes have a prominent head, larger than the base, but with a crumpled appearance, probably due to the herborizing process used to prepare exsiccatae (Fig. 3A). Tector trichomes were found on all the species sampled, except for *M. selloi* (= glabrous *M. laruotteana*). These can be simple unicellular (Fig. 3A), dibrachiate (Fig. 3B), hook-shaped (Fig. 3C), stellate (Fig. 3D) or branched (Fig. 3E). Simple unicellular trichomes can be short (Figs. 2A-B; 3F) or elongated (Figs. 2A-B; 3A). Branched trichomes have a common base (Fig. 3E), branching with both ends facing in the same direction. Dibrachiate trichomes have a common base but two tips facing in opposite directions, forming a characteristic “T” (Fig. 3B). Hook-shaped trichomes can be short or elongated and have a tapered, curved tip, forming the hook (Fig. 3C). Stellate trichomes have multiple tips (Fig. 3D) and were only noted on *M. subacuminata*. Some trichomes may have dilated bases (Fig. 3F).

The sampled species of *Myrcia* sect. *Calyptanthus* and *M.* sect. *Sympodiomyrcia* have a predominance of dibrachiate trichomes, although some have simple unicellular trichomes, but always in conjunction with dibrachiate trichomes. *Myrcia* sect. *Aulomyrcia* and *M.* sect. *Eugeniopsis* have a wide variation between dibrachiate and simple unicellular trichomes, occurring alone or together.

The other sections (including “clade 10”) have a predominance of simple unicellular trichomes, with some variations to dibrachiate or hook-shaped (Appendix and Table 2).

Another characteristic analyzed in the trichomes was its length, which could be short ($\leq 150\mu\text{m}$) (Figs. 2A-B; 3F) or long ($> 150\mu\text{m}$) (Figs. 2A-B; 3A). There was high variability between the species analyzed, and only for the *Aguava* section this was a relevant character, with all species analyzed presenting long tector trichomes. *Myrcia rufipes* has a combination of long and short trichomes. We also analyzed the position of the trichomes, which can be erect (Fig. 2C; 3F) or adpressed (lying on the epidermis; Fig. 2A; 2B; 3C), and whether the trichomes have straight axes (Fig. 2A) or tortuous, sometimes with a spiral aspect (Fig. 1E, 4A, 4B). Finally, about the indumentum, the samples had leaves with dense (Fig. 4A), sparse (Fig. 4B) and moderate indumentum (Fig. 4C). The indumentum classification criteria was the visibility of other epidermal cells, with dense indumentum not allowing the ordinary epidermal cells to be seen (Fig. 4A); sparse indumentum has trichomes that are distant from each other (Fig. 1D; 2B; 3C) or groups of isolated trichomes (Fig. 4B) and the ordinary epidermal cells are not covered by such trichomes; the moderate with close trichomes, the ordinary epidermal cells are not completely covered (Fig. 1E; 2A; 3A; 3D-F; 4C). However, in some cases, species have a greater number of trichomes distributed on the leaf blade (Fig. 4A), a greater concentration of trichomes on the leaf veins (Fig. 4B), or on the midvein (Fig. 4C). Only *Myrcia selloi* (= *M. laruotteana*) has a glabrous leaf (Fig. 4D). The density of trichomes is highly variable among the species analyzed (Appendix).

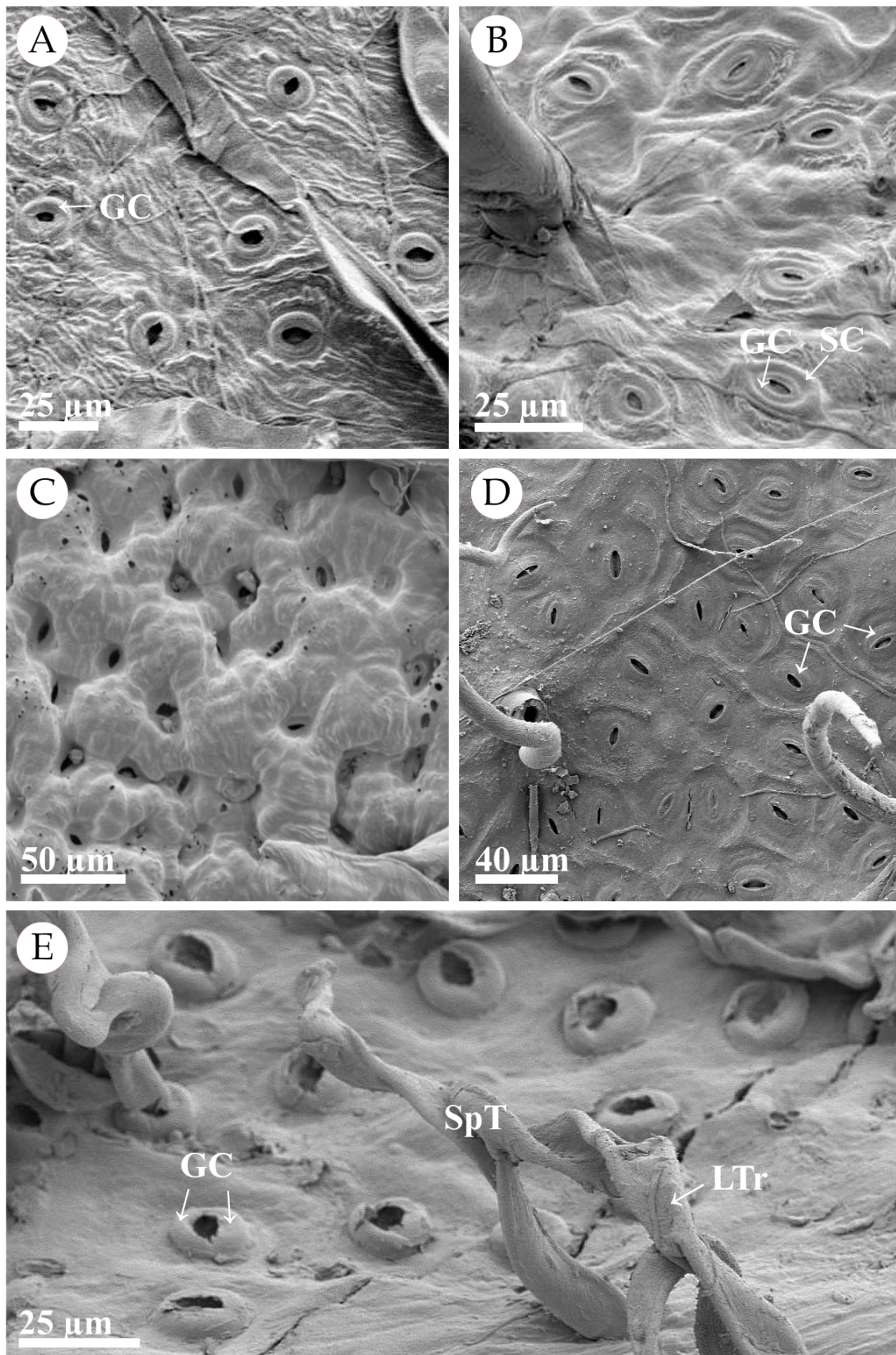


Figure 1: Aspect of the abaxial surface of the leaf limb of *Myrcia* species showing the stomata complexes. A. *M. chytraculia*, anomocytic stomata with prominent guard cells (GC). B. *M. ferruginosa*, paracytic stomata showing the guard cells (GC) and the subsidiary cells (SC); C. *M. loranthifolia*, stomata below the ordinary epidermal cells; D. *M. anomala*, stomata level with the other epidermal cells with barely perceptible guard cells (GC); E. *M. ferruginea*, stomata above the other epidermal cells, showing the guard cells and long trichomes (LTr) and spiral trichomes (SpT).

Table 2. Summary of the micromorphological characteristics of the abaxial epidermis of the *Myrcia* infrageneric groups. See Appendix for more details.

Infrageneric group/ attribute	Stomatal level	Stomatal type	Type of tec- tor trichome	Base of tector tri- chome	Cuticle and wax
<i>M. sect. Aguava</i>	Above, rare levelled	Paracytic or anomocytic	Simple uni- cellular, rare dibrachiate	Simple or bulging	Smooth, rare with granules
<i>M. sect. Aulomyrcia</i>	Levelled, rare above	Paracytic or anomocytic	Simple uni- cellular or dibrachiate, rare hook- shaped or branched	Simple or bulging	Smooth, rare with granules
<i>M. sect. Calyptranthes</i>	Levelled or above, rare below	Anomocytic	Dibrachiate or simple unicel- lular (but al- ways with di- brachiates)	Simple	Smooth or striated, rare with granules or fimbriate
<i>M. sect. Eugeniopsis</i>	Levelled, rare above	Paracytic, rare anomocytic	Simple uni- cellular or dibrachiate, rare stellate	Simple	Smooth or striated, rare fimbriate
<i>M. sect. Gomidesia</i>	Above, rare levelled	Paracytic	Simple uni- cellular or hook-shaped, rare di- brachiate or branched	Simple, rare bulging	Smooth, rare striated or with granules
<i>M. sect. Myrcia</i>	Above or lev- elled, rare be- low	Paracytic, rare anomocytic	Simple uni- cellular, rare dibrachiate	Simple or bulging	Smooth, rare with granules
<i>M. sect. Reticulosae</i>	Levelled or above	Anomocytic	Simple uni- cellular, rare dibrachiate	Simple or bulging	Smooth, with gran- ules or plates
<i>M. sect. Sympodiomyrcia</i>	Above or be- low	Anomocytic	Dibrachiate or simple unicel- lular (but al- ways with di- brachiates)	Simple	Smooth or with granules
<i>M. sect. Tomentosae</i>	Levelled, rare above	Paracytic, rare anomocytic	Simple uni- cellular	Simple, rare bulging	Smooth or with granules
Clade 10	Above or lev- elled	Anomocytic or paracytic	Simple uni- cellular, rare hook-shaped	Simple or bulging	Smooth, rare with granules

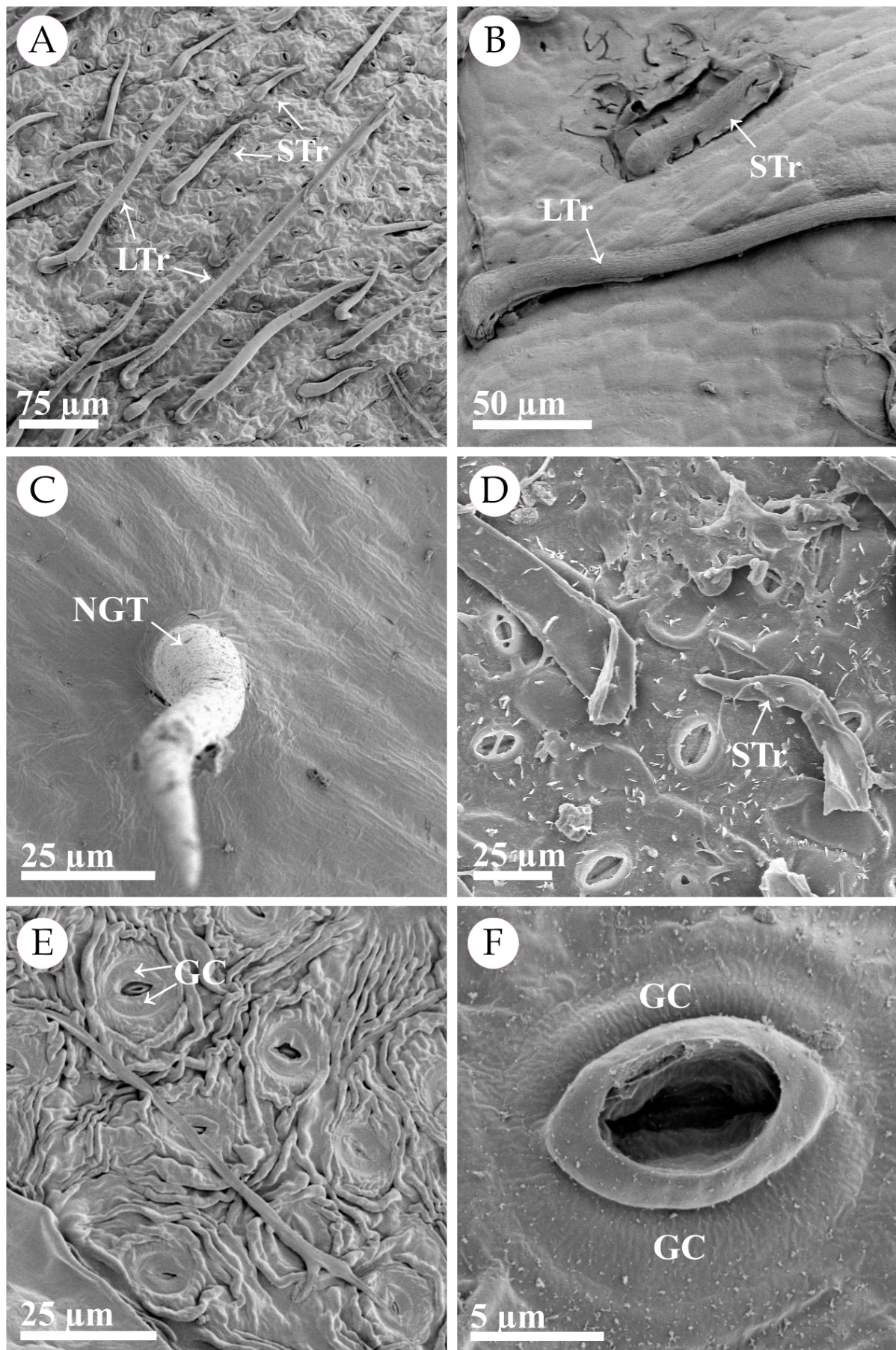


Figure 2. Aspect of the abaxial surface of the leaf limb of *Myrcia* species showing cuticle, wax and trichomes. A. *M. brasiliensis*, smooth cuticle, long (LTr) and short (STr) unicellular simple tector trichomes; B. *M. cana*, smooth cuticle, long (LTr) and short (STr) unicellular simple tector trichomes; C. *M. pubescens*, striated cuticle and unicellular tector trichome (NGT); D. *M. pubipetala*, plate-like wax and tector trichomes; E. *M. hatschbachii*, fimbriated wax and anomocytic stomata showing the guard cells (GC); F. *M. aulomyrcioides*, granular wax and paracytic stomata showing the guard cells (GC).

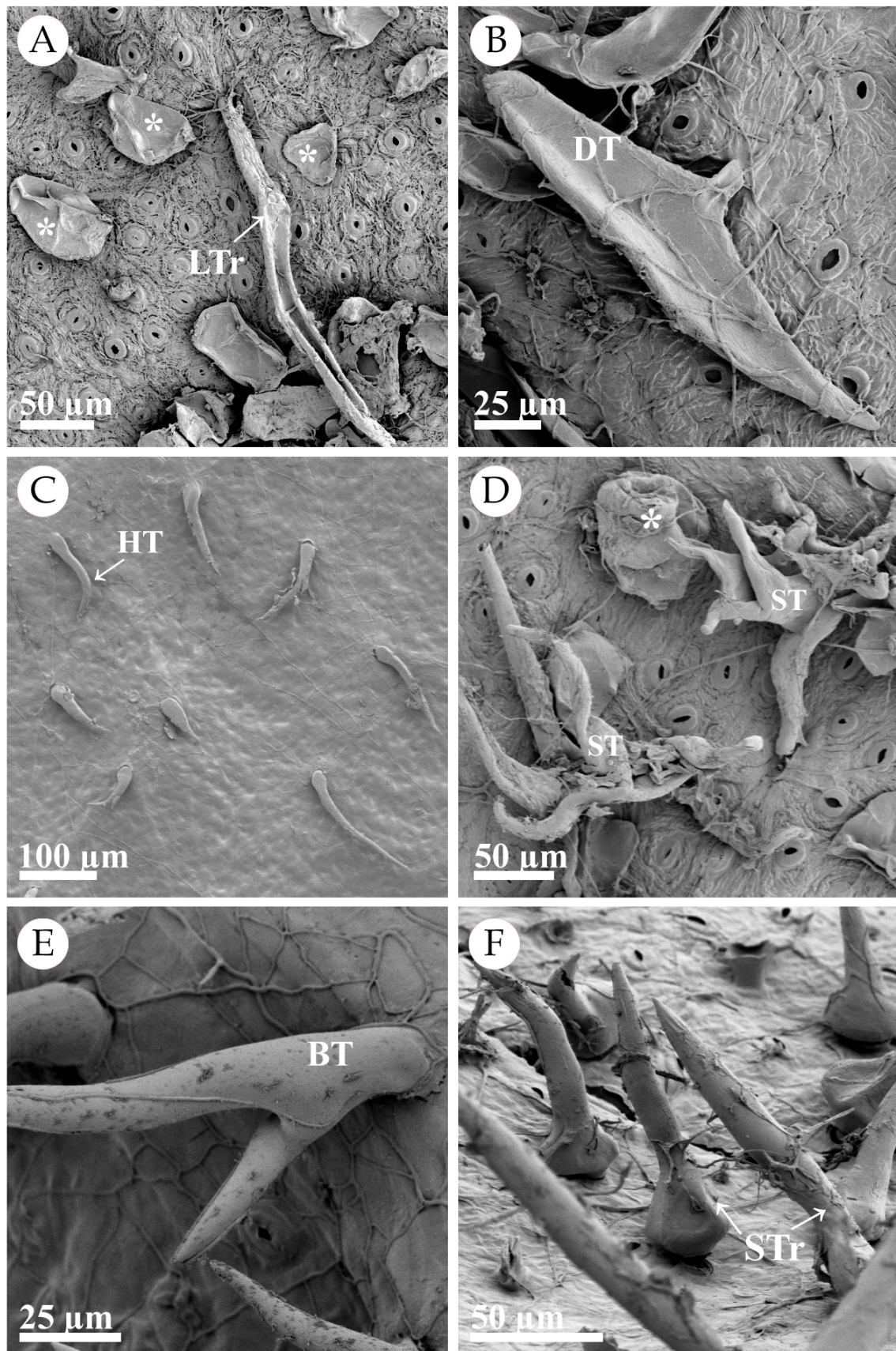


Figure 3. Aspect of the abaxial surface of the leaf limb of *Myrcia* species showing different types of trichomes. A. *M. teuscheriana*, tector (arrowhead) and glandular trichomes (*); B. *M. chytraculia*, dibrachiate trichome (DT); C. *M. hartwegiana*, short trichomes (STr) on a hook (HG); D. *M. subacuminata*, stellate (ST) and glandular (*) trichome; E. *M. hebeptala*, branched trichome (BT) with a simple base; F. *M. maximiliana*, short trichomes (STr) and erect with a bulging base.

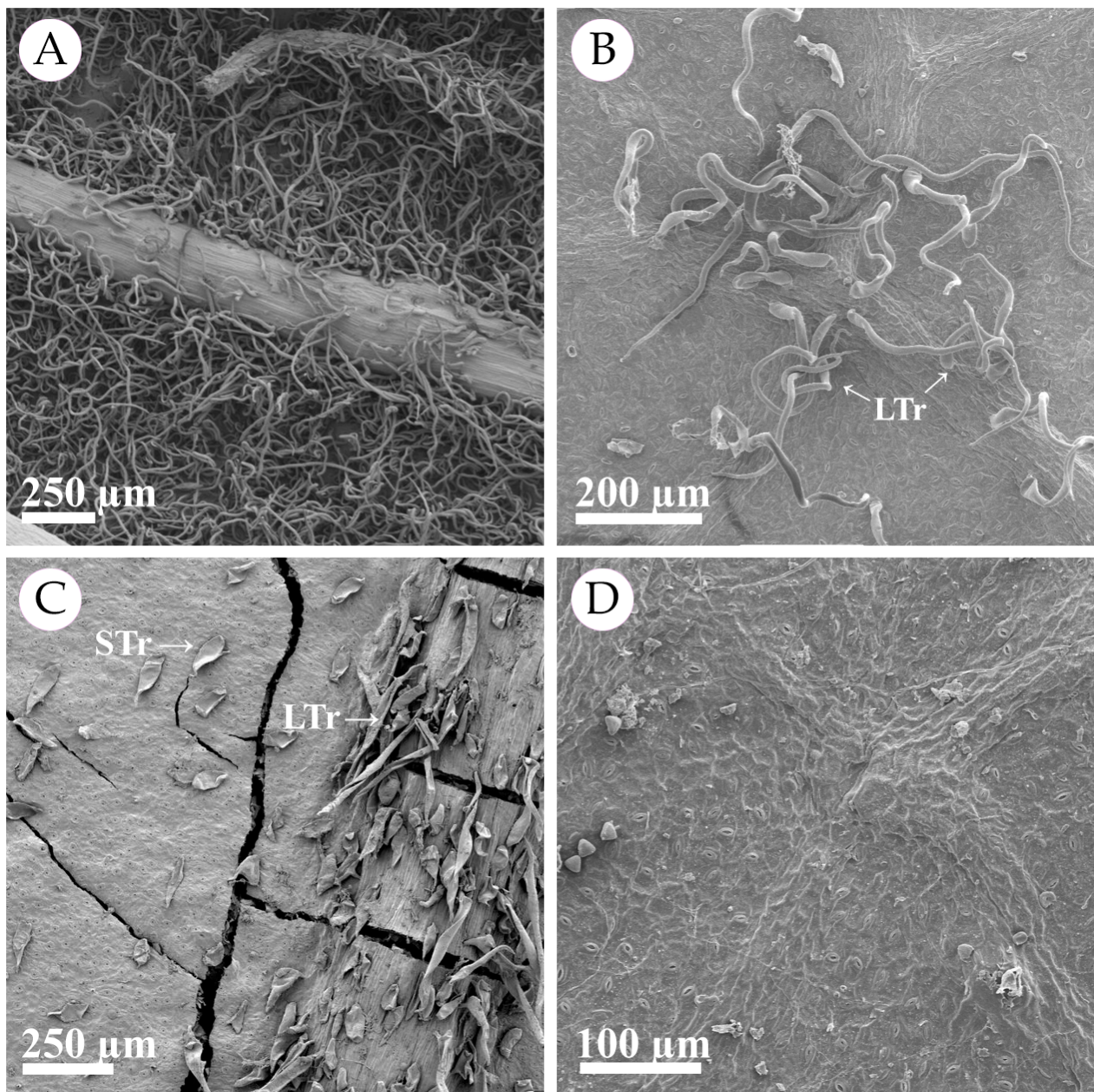


Figure 4. Aspect of the abaxial surface of the leaf limb of *Myrcia* species showing the general indumentum. A. *M. laricina*, leaf pilosity, sparse trichomes on the midvein; B. *M. tomentosa*, leaf with short indumentum, long trichomes (LTr) concentrated on the veins; C. *M. eugeniopoides*, moderately pilose leaf, higher concentration of long trichomes (LTr) on the midvein and short trichomes (STr) outside the midvein; D. *M. selloi* (= *M. laruotteana*), glabrous leaf.

Discussion

Analysis of the abaxial surface of the leaf limb epidermis of the *Myrcia* species sampled revealed a high variety of micromorphological characteristics between the different sections of the genus. Using SEM images, it was possible to describe the form of deposition of epicuticular waxes and cuticles, the type of stomata complexes and the level of the guard cells in relation to the other epidermal cells, and the type and distribution of trichomes. This is the first study to analyze the leaves of many species of the genus (73) using SEM, and the characters described here significantly increase our knowledge of the micromorphology of Myrtaceae overall.

The stomata found in the species sampled are of the paracytic and anomocytic type, corroborating the characteristics frequently described for the family (Bandulska, 1931; Metcalfe & Chalk, 1950; Jorge et al., 2000; S. M. Gomes et al., 2009; Bezerra, 2013; Larocca et al., 2015; Lemos et al., 2020). However, cyclocytic stomata have already been reported in species of *Leptospermum* J.R. Forst. & G. Forst., and anisocytic stomata in species of *Myrcia* (as in *M. spectabilis* and *M. neosuaveolens*), *Myrtus* L., *Syzygium* P. Browne ex Gaertn. and *Eugenia* L. (Johnson, 1980; Callado, 1993; D. M. S. Gomes & Neves, 1993; S. M. Gomes et al., 2009; Al-Edany & Al-Saadi, 2012; Souza, 2015). The type of stomata does not seem to be relevant for distinguishing *Myrcia* groups, varying

greatly between the species studied, although *M. sects. Gomidesia*, *Sympodiomyrcia* and *Reticulosae* had a single type in our sample (paracytic in the former and anomocytic in the two latter).

The height of the guard cells in relation to the other epidermal cells is a very variable characteristic, with species commonly found with stomata above or at the same level as the other epidermal cells. Stomata below the other cells are rare and were only seen in *M. loranthifolia*, *M. retorta*, and *M. subcordata* (each one from a different section). These characteristics were also found by Cardoso et al. (2009), Fontenelle et al. (1993), Boeger & Wisniewski (2003), and Gomes et al. (2009) in species of *Myrcia* and other genera of Myrtaceae. It is also possible to verify that this character can vary between individuals of the same species, as is the case of *Myrcia multiflora*, which has stomata at the same level as the other epidermal cells (verified here and by Donato and Morretes, 2011) or above the level (Jorge et al., 2000). On the other hand, *Myrcia loranthifolia*, *M. subalpestris*, *M. tortuosa* and *M. selloi*, the only species that had more than one specimen analyzed in this study, showed no intraspecific variation. It is important to note that the height of the guard cells in relation to the other epidermal cells is a very plastic characteristic, varying in relation to the environment in which the plants occur (Esau, 1960). Therefore, this characteristic needs to be analyzed in a larger number of specimens, preferably occurring in different environments, to account for possible phenotypic plasticity.

The pattern of epicuticular wax deposition may have some taxonomic value in Myrtaceae, as observed in *Eucalyptus* (Carr et al., 1985), but it was not informative for diagnosing *Myrcia* groups. In species studied, the most common wax deposition pattern is smooth, with small granules and/or striations are often present, as already recorded for the family (Jorge et al., 2000; D. M. S. Gomes & Neves, 1993; Bezerra, 2013; Souza, 2015). In addition, smooth, ornamented and striated cuticles have also been reported for Myrtaceae (Machado et al., 1987; Jorge et al., 2000; Donato & Morretes, 2007).

Also, on deposition patterns of the cuticle and epicuticular waxes, Hallam (1970) and Hallam & Chambers (1970) reported that the environment can interfere with the thickness and pattern of this deposition in Myrtaceae. This is evident when we compare the observations of Jorge et al. (2000) and Bezerra (2013), who highlight the presence of wax with granule deposition in *Myrcia guianensis*, with what was found in the sample analyzed in our study, whose wax and cuticle are smooth. Similarly, the sample of *Myrcia neoclusiifolia* analyzed here has a smooth to fimbriated cuticle and wax deposition, which is a slight variation on the uniquely fimbriated form described by Bezerra (2013). This variation in cuticle and wax deposition may also be related to the environment in which individuals occur. For example, the specimen of *Myrcia guianensis* analyzed in this study was collected in a humid forest area in French Guiana, while the one sampled by Bezerra (2013) was sampled in Cerrado areas, which are characterized by higher rates of luminosity and transpiration (Salatino et al., 1987).

Trichomes are epidermal appendages of recognized taxonomic importance due to its morphological variety and density on vegetative and reproductive organs, especially leaves (Appezato-da-Glória & Carmello-Guerreiro, 2006; Esposito-Polesi et al., 2011). In Myrtaceae, the trichomes that prevail are unicellular, tector and unbranched, although dibrachiate trichomes (T-shaped) have also been described for some species associated with *Myrceugenia* O. Berg, *Myrcia* and *Eugenia* (Bandulska, 1931; Metcalfe & Chalk, 1950; Landrum & Kawasaki, 1997; S. M. Gomes et al., 2009). In the present study, we found predominantly unicellular and dibrachiate trichomes. All species analyzed from *Myrcia* sects. *Calyptanthus* and *Sympodiomyrcia* and several species of *M. sects. Aulomyrcia* and *Eugeniopsis* have dibrachiate trichomes (solely or mixed with simple unicellular ones). These four sections house the vast majority of species originally described in the previously recognized but non-monophyletic genera *Calyptanthus* and *Marlierea* (Lucas et al., 2018; Santos et al., 2024), which had previously been differentiated from *Myrcia*, in addition to calyx characteristics, by the type of indumentum, with dibrachiate trichomes observed to be frequent in the first two genera and absent in the latter (McVaugh, 1958). However, as observed here and in other studies (e.g., Lima, 2017), some species originally circumscribed in *Myrcia* also have the dibrachiate type (e.g., *M. aethusa* and *M. guianensis*). In fact, this type is sometimes quite difficult to identify under an optical microscope, as it is easily confused with simple unicellular adpressed trichomes and, therefore, its frequency in *Myrcia* may be underestimated. McVaugh (1969) also argued that the dibrachiate trichome may be a specialization in *Myrcia*, and that developmental studies should be carried out. In any case, it seems that this condition has appeared several times in the evolutionary history of *Myrcia*, since it appears in sections that are not necessarily related (Lucas et al., 2011; Amorim et al., 2019). The only groups that did not show dibrachiate trichomes were *M. sect. Tomentosae* and “clade 10”.

Finally, branched, hooked and stellate trichomes (the latter only seen in *M. subacuminata*) were also observed in the material analyzed, as well as the presence of glandular trichomes. These characteristics also occur in species from other Myrtaceae genera, such as *Psidium* L. and *Callistemon* R.Br., and prove useful in distinguishing the species of these genera (Al-Edany & Al-Saadi, 2012).

As expected, the density and distribution of trichomes varied greatly between the species analyzed. Among the patterns observed, there is the possibility of trichomes with different morphologies occurring in the same sample, for instance, dibrachiate together with simple trichomes, or even tector together with glandular trichomes. It was also observed that the distribution of trichomes can be uneven, for example, leaves which have simple short trichomes all over the abaxial surface, but in the midvein have a greater or lesser concentration of elongated trichomes. This differentiation in density and types of trichomes is commonly reported in morphological descriptions of *Myrcia* species based on observation under an optical microscope and often has taxonomic value in

differentiating species (Lima, 2017; Santos et al., 2018; Salgueirinho, 2020). In the *Aulomyrcia* section, scarce tector trichomes were observed on the lamina and in greater quantity on the midvein in *M. amazonica*, *M. obversa* and *M. racemosa*. Furthermore, and considering that the species analyzed come from different environments, the density of the trichomes varied greatly between the species studied, with some having such a high density of trichomes that it was not possible to observe the stomata or the other epidermal cells (e.g., *M. albotomentosa*). At the other extreme, only one of the species analyzed, *M. selloi* (= *M. laruotteana*) had no trichomes on the abaxial surface, but it is worth noting that this species shows variation in the presence and density of leaf trichomes (Lannoy et al., 2019).

Conclusion

The micromorphological studies conducted in this study are promising for *Myrcia*, providing informative descriptions of the species studied through SEM analysis. No characters were found that clearly diagnose the infrageneric groups, but some patterns could be observed, such as the shape of the predominantly dibrachiate trichomes in *M. sects. Calyptranthes* and *Sympodiomyrcia*. It is worth noting that relatively few species of *M. sect. Reticulosae* and *M. sect. Sympodiomyrcia* were sampled in this work, which reinforces the need for further studies on these sections. The data analyzed here can help future studies, with wider samples, focused on species delimitation and intraspecific phenotypic plasticity. We also emphasize that increasing the size of the available dataset of type, size and density of trichomes on the abaxial surface is valuable and this information should, whenever possible, be reported in detail in species descriptions to amplify information available.

Acknowledgements

We thank staff at the Jodrell Lab (RBG, Kew) and the LCME (UFSC, Brazil) for providing the necessary equipment for the analyses, the K and FLOR herbaria for authorizing using material from exsiccatae. We are grateful to C. Prychyd and M. Conejero (RBG, Kew) for their assistance in the laboratory. We would also like to thank the following funding agencies: Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Brazil) for the scientific initiation scholarship awarded to LHB, Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, Brazil) for the master's scholarship awarded to AGG, and Fundação de Amparo à Pesquisa e Inovação do Estado de Santa Catarina (FAPESC, Brazil) for the post-doctoral scholarship awarded to DFL.

References

- Al-Edany, T. Y., & Al-Saadi, S. A. M. (2012). Taxonomic significance of anatomical characters in some species of the family Myrtaceae. *American Journal of Plant Sciences*, 3(5), 572–581. <https://doi.org/10.4236/ajps.2012.35069>
- Amorim, B. S., Vasconcelos, T. N., Souza, G., Alves, M., Antonelli, A., & Lucas, E. (2019). Advanced understanding of Phylogenetic Relationships, Morphological Evolution and Biogeographic History of the mega-diverse plant genus *Myrcia* and its relatives (Myrtaceae: Myrteae). *Molecular Phylogenetics and Evolution*, 138, 65–88. <https://doi.org/10.1016/j.ympev.2019.05.014>
- APG-IV. (2016). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society*, 181, 1–20.
- Appenzato-da-Glória, B., & Carmello-Guerreiro, S. M. (2006). *Anatomia Vegetal* (Vol. 2). Viçosa: Editora UFV.
- Bandulska, H. (1931). On the cuticles of some Recent and Fossil Myrtaceae. *Botanical Journal of the Linnean Society*, 48(325), 657–671.
- Barthlott, W., Neinhuis, C., Cutler, D., Ditsch, F., Meusel, I., Theisen, I., & Wilhelmi, H. (1998). Classification and Terminology of Plant Epicuticular Waxes. *Botanical Journal of the Linnean Society*, 126(3), 237–260. <https://doi.org/10.1111/j.1095-8339.1998.tb02529.x>
- Bezerra, K. M. G. (2013). *Estudos taxonômicos e anatômicos dos gêneros Calyptranthes Sw., Marlierea Cambess., Myrceugenia O.Berg e Myrcia sect. Aulomyrcia (O.Berg) Griseb. (Myrtaceae) no Distrito Federal* [Doctoral dissertation, PhD Thesis. Botânica, Universidade de Brasília, Brasília - DF].
- Boeger, M. R. T., & Wisniewski, C. (2003). Comparação da Morfologia Foliar de espécies arbóreas de três estádios sucessionais distintos de Floresta Ombrófila Densa (Floresta Atlântica) no Sul do Brasil. *Brazilian Journal of Botany*, 26, 61–72. <https://doi.org/10.1590/S0100-84042003000100007>
- Callado, C. H. (1993). Anatomia foliar de *Eugenia cuprea* (Berg) NDZ. e *Marlierea suaveolens* Gard.(Myrtaceae). *Rodriguésia*, 45(71-75), 25–37. <https://doi.org/10.1590/12175-7860199319974549717503>
- Cardoso, C., Proença, S., & Sajo, M. (2009). Foliar Anatomy of the subfamily Myrtoideae (Myrtaceae). *Australian Journal of Botany*, 57(2), 148–161. <https://doi.org/10.1071/BT07176>
- Cardoso, C., & Sajo, M. d. G. (2004). Vascularização foliar e a identificação de espécies de *Eugenia* L.(Myrtaceae) da Bacia Hidrográfica do Rio Tibagi, PR. *Brazilian Journal of Botany*, 27, 47–54. <https://doi.org/10.1590/S0100-84042004000100006>

- Carr, D., Carr, S., & Lenz, J. R. (1985). Oriented arrays of epicuticular wax plates in *Eucalyptus* species. *Protoplasma*, 124(3), 205–212. <https://doi.org/10.1007/BF01290771>
- Donato, A. M., & Morretes, B. L. (2007). Anatomia foliar de *Eugenia brasiliensis* Lam. (Myrtaceae) proveniente de áreas de restinga e de floresta. *Revista Brasileira de Farmacognosia*, 17(3), 426–443. <https://doi.org/10.1590/S0102-695X2007000300018>
- Donato, A. M., & Morretes, B. L. (2011). Morfo-anatomia foliar de *Myrcia multiflora* (Lam.) DC. – Myrtaceae. *Rev. bras. plantas med.*, 13, 43–51. <https://doi.org/10.1590/S1516-05722011000100007>
- Esau, K. (1960). *Anatomy of Seed Plants*, 376.
- Esposito-Polesi, N. P., Rodrigues, R. R., & Almeida, M. (2011). Anatomia Ecológica da folha de *Eugenia glazioviana* Kiaersk (Myrtaceae). *Revista Árvore*, 35(2), 255–263. <https://doi.org/10.1590/S0100-67622011000200010>
- Evert, R. F., & Esau, K. (2013). *Anatomia das Plantas de Esau: Meristemas, Células e Tecidos do corpo da planta: sua Estrutura, Função e Desenvolvimento*. Editora Blucher.
- Fontenelle, G., Gomes, D., & Machado, R. (1993). Anatomia foliar de *Gomidesia martiana* Berg e *Gomidesia feniziana* Berg (Myrtaceae). *Revista Brasileira de Botânica*, 16(1), 17–30.
- Gomes, D. M. S., & Neves, L. J. (1993). Anatomia foliar de *Gomidesia spectabilis* (DC) Berg e *Gomidesia nitida* (Vell.) Legr. (Myrtaceae). *Rodriguésia*, 45(71-75), 51–70. <https://doi.org/10.1590/2175-7860199319974549717505>
- Gomes, S. M., Somavilla, N. S. D. N., Gomes-Bezerra, K. M., Miranda, S. C., Carvalho, P. S., & Graciano-Ribeiro, D. (2009). Anatomia Foliar de espécies de Myrtaceae: Contribuições à Taxonomia e Filogenia. *Acta Botanica Brasilica*, 23, 224–238. <https://doi.org/10.1590/S0102-33062009000100024>
- Gul, S., Ahmad, M., Zafar, M., Bahadur, S., Sultana, S., Ashfaq, S., Ullah, F., Kilic, O., Hassan, F. u., & Siddiq, Z. (2019). Foliar epidermal anatomy of Lamiaceae with special emphasis on their trichomes diversity using scanning electron microscopy. *Microscopy Research and Technique*, 82(3), 206–223. <https://doi.org/10.1002/jemt.23157>
- Hallam, N. (1970). Growth and regeneration of waxes on the leaves of *Eucalyptus*. *Planta*, 93(3), 257–268. <https://doi.org/10.1007/BF00387646>
- Hallam, N., & Chambers, T. (1970). The leaf waxes of the genus *Eucalyptus* L'Heritier. *Australian Journal of Botany*, 18(3), 335–386. <https://doi.org/10.1071/BT9700335>
- Johnson, C. T. (1980). The leaf anatomy of *Leptospermum* forst. (myrtaceae). *Australian Journal of Botany*, 28(1), 77–104. <https://doi.org/10.1071/BT9800077>
- Jorge, U. I., Aguiar, J. P., & Silva, M. L. P. (2000). Anatomia Foliar de pedra-hume-caá *Myrcia sphaerocarpa*, *Myrcia guianensis*, *Eugenia puniceifolia* – Myrtaceae. *Acta Amazonica*, 30(1), 49–57. <https://doi.org/10.1590/1809-43922000301057>
- Landrum, L. R., & Kawasaki, M. L. (1997). The genera of Myrtaceae in Brazil: an illustrated synoptic treatment and identification keys. *Brittonia*, 49(4), 508–536. <https://doi.org/10.2307/2807742>
- Lannoy, L. C., Goldenberg, R., & Lima, D. F. (2019). Taxonomic Rearrangements and Typifications in *Myrcia* sect. Tomentosae (Myrteae, Myrtaceae). *Phytotaxa*, 404(3), 111–120. <https://doi.org/10.11646/phytotaxa.404.3.3>
- Larocca, D., Tiago, A., Veiga, J., Tiago, P., & Silva, I. (2015). Morfoanatomia de *Myrcia splendens* (Sw.) DC. (Myrtaceae) ocorrente em um enclave de Savana Amazônica. *Enciclopédia Biosfera*, 11(21), 2308–2318.
- Lemos, V. O. T., Lucena, E. M. P., Bonilla, O. H., Edson-Chaves, B., & Freitas, M. A. (2020). Anatomia ecológica foliar de *Myrcia guianensis* (Aubl.) DC. na restinga cearense. *Ciência Florestal*, 30(2), 307–322. <https://doi.org/10.5902/1980509830997>
- Lima, D. (2017). *Estudos filogenéticos e taxonômicos em Myrcia DC. sensu lato (Myrtaceae), com ênfase no clado Guianensis* [Doctoral dissertation, PhD. Thesis. Biologia Vegetal, Universidade Estadual de Campinas, Campinas - SP]. <https://doi.org/10.47749/T/UNICAMP2017.994247>
- Lucas, E. J., Amorim, B. S., Lima, D. F., Lima-Lourenço, A. R., Nic Lughadha, E. M., Proença, C. E. B., Rosa, P. O., Rosário, A. S., Santos, L. L., & Santos, M. F. (2018). A new infra-generic classification of the species-rich Neotropical genus *Myrcia* sl. *Kew Bulletin*, 73(9). <https://doi.org/10.1007/s12225-017-9730-5>
- Lucas, E. J., Matsumoto, K., Harris, S. A., Nic Lughadha, E. M., Benardini, B., & Chase, M. W. (2011). Phylogenetics, Morphology, and Evolution of the large genus *Myrcia* sl (Myrtaceae). *International Journal of Plant Sciences*, 172(7), 915–934. <https://doi.org/10.1086/660913>
- Machado, R. D., Costa, C. G., & Fontenelle, G. B. (1987). Anatomia foliar de *Eugenia sulcata* Spring ex Mart. (Myrtaceae). *Acta Botanica Brasilica*, 1, 275–285. <https://doi.org/10.1590/S0102-33061987000300026>
- McVaugh, R. (1958). Myrtaceae. In B. Maguire & J. Wurdack (Eds.), *The Botany of the Guayana Highland. III* (pp. 62–91, Vol. 10).
- McVaugh, R. (1969). Myrtaceae. In B. Maguire & J. Wurdack (Eds.), *The Botany of the Guayana Highland. VIII* (pp. 55–286, Vol. 18).
- Metcalf, C. R., & Chalk, L. (1950). *Anatomy of the Dicotyledons: Leaves, Stem, and Wood in relation to taxonomy with notes on economic uses* (Vol. 1). Londres: Oxford Clarendon Pres.
- Oliveira, M. I. U., Rebouças, D. A., Leite, K. R. B., Oliveira, R. P., & Funch, L. S. (2018). Can leaf morphology and anatomy contribute to species delimitation? A case in the *Campomanesia xan-*

- thocarpa* complex (Myrtaceae). *Flora*, 249, 111–123. <https://doi.org/10.1016/j.flora.2018.10.004>
- Plants of the World Online. (2023). Facilitated by the Royal Botanic Gardens, Kew. <https://powo.science.kew.org>
- Retamales, H. A., & Scharaschkin, T. (2015). Comparative leaf anatomy and micromorphology of the Chilean Myrtaceae: Taxonomic and ecological implications. *Flora - Morphology, Distribution, Functional Ecology of Plants*, 217, 138–154. <https://doi.org/10.1016/j.flora.2015.10.005>
- Salatino, A., Montenegro, G., & Salatino, M. L. F. (1987). Microscopia eletrônica de varredura de superfícies foliares de espécies lenhosas do Cerrado. *Revista Brasileira de Botânica*, 9, 117–24.
- Salgueirinho, T. (2020). *Revisão taxonômica de Myrcia sect. Reticulosae (Myrtaceae)* [Doctoral dissertation, MS Thesis. Instituto de Pesquisas do Jardim Botânico do Rio de Janeiro, RJ].
- Santos, M. F., Amorim, B. S., Burton, G. P., Fernandes, T., Gaem, P. H., Lourenço, A. R. L., Lima, D. F., Rosa, P. O., Santos, L. L., Staggemeier, V. G., Vasconcelos, T. N. C., & Lucas, E. J. (2025). *Myrcia*. In *Flora e funga do brasil*. Jardim Botânico do Rio de Janeiro, Retrieved in 10 March 2025. <https://floradobrasil.jbrj.gov.br/FB10660>
- Santos, M. F., Amorim, B. S., Burton, G. P., Faria, J. E., Fernandes, T., Flickinger, J. A., Gaem, P. H., Landrum, L. R., Lima, D. F., Proença, C. E., et al. (2024). A taxonomic account of Myrciinae (Myrteae, Myrtaceae): generic and sectional placement of forgotten species and a list of all accepted species. *Phytotaxa*, 674(2), 129–170. <https://doi.org/10.11646/phytotaxa.674.2.1>
- Santos, M. F., Lucas, E., & Sano, P. T. (2018). A taxonomic monograph of *Myrcia* sect. *Sympodiomyrcia* (Myrteae, Myrtaceae). *Phytotaxa*, 380(1), 1–114. <https://doi.org/10.11646/phytotaxa.380.1.1>
- Silveira, M. (1989). O preparo de amostras biológicas para microscopia eletrônica de varredura. In W. Souza (Ed.), *Manual sobre técnicas básicas em microscopia eletrônica de varredura* (pp. 71–82, Vol. 1). Sociedade Brasileira de Microscopia Eletrônica.
- Souza, M. (2015). *Estudos em Eugenia L. (Myrtaceae) na Amazônia Central: Taxonomia com o uso de ferramentas morfoanatômicas* [Doctoral dissertation, PhD. Thesis. Universidade Federal do Amazonas, Manaus - AM].
- Thiers, B. (2024). *Index herbariorum*: a global directory of public herbaria and associated staff. <https://sweetgum.nybg.org/science/ih/>
- Vasconcelos, T. N. C., Proença, C. E. B., Ahmad, B., Aguilar, D. S., Aguilar, R., Amorim, B. S., Campbell, K., Costa, I. R., De-Carvalho, P. S., Faria, J. E. Q., Giarretta, A., Kooij, P. W., Lima, D. F., Mazine, F. F., Peguero, B., Prenner, G., Santos, M. F., Soewarto, J., Wingler, A., & Lucas, E. J. (2017). Myrteae Phylogeny, Calibration, Biogeography and Diversification Patterns: Increased understanding in the most species rich tribe of Myrtaceae. *Molecular Phylogenetics and Evolution*, 109, 113–137. <https://doi.org/10.1016/j.ympev.2017.01.002>
- Wagner, M. A., Lucas, E. J., Soffiatti, P., Cabral, W. S., Portella, P. R., & Fiaschi, P. (2023). Leaf Morphology and Anatomy in *Myrcia* sect. *Aulomyrcia* (Myrtaceae): Species Circumscription and Characterization of Clades. *Botany*, 101(11), 513–531. <https://doi.org/10.1139/cjb-2023-0038>
- Werker, E. (2000). *Trichome Diversity and Development*. Academic Press. [https://doi.org/10.1016/S0065-2296\(00\)31005-9](https://doi.org/10.1016/S0065-2296(00)31005-9)
- Wilson, P. G. (2011). Myrtaceae. In K. Kubitzki (Ed.), *The families and genera of vascular plants. 10: Flowering plants: Eudicots. Sapindales, Cucurbitales, Myrtaceae* (pp. 212–271). Springer Heidelberg Dordrecht, London, New York.
- Wurdack, J. J. (1962). Melastomataceae of Santa Catarina. *Sellowia*, 14, 109–217.



Appendix. Micromorphological characteristics of the abaxial surface of *Myrcia* spp. obtained from scanning electron microscopy (SEM) images. Species are organized by section.

Section	Species	Stomatal level	Stomas	Trichomes	Tector trichomes morfology	Tector trichomes lenght	Tector trichomes axis	Tector trichomes orientation	Tector trichomes base	Trichomes distribution	Cuticle and wax
<i>Aguava</i>	<i>M. cuprea</i>	Above the epidermis	Paracytic	Tector	Simple unicellular	Elongated	Straight	Adpressed	Bulging	Dense	Smooth
	<i>M. guianensis</i>	Leveled	Paracytic	Tector	Simple unicellular and dibrachiate	Elongated	Straight	Adpressed	Bulging	Sparse, dense on the midvein	Smooth
	<i>M. laricina</i>	Above the epidermis	Anomocytic	Tector	Simple unicellular	Elongated	Tortuous	Erect and adpressed	Bulging	Dense, sparse on the midvein	Smooth
	<i>M. nivea</i>	Above the epidermis	Anomocytic	Tector	Simple unicellular	Elongated	Tortuous	Erect and adpressed	Bulging	Moderate, dense on the midvein	Smooth
	<i>M. rufipes</i>	Above the epidermis	Paracytic	Tector	Simple unicellular	Short and elongated	Straight and tortuous	Erect	Simple	Moderate	Smooth
	<i>M. siriacoana</i>	Above the epidermis	Paracytic	Tector	Simple unicellular	Elongated	Straight and tortuous	Erect and adpressed	Simple	Moderate	Smooth with granules
	<i>M. subalpestris</i>	Above the epidermis	Anomocytic	Tector	Simple unicellular	Elongated	Tortuous	Erect	Simple	Dense	Smooth

Section	Species	Stomatal level	Stomas	Trichomes	Tector trichomes morfology	Tector trichomes lenght	Tector trichomes axis	Tector trichomes orientation	Tector trichomes base	Trichomes distribution	Cuticle and wax
<i>Aguava</i>	<i>M. subalpestris</i> (= <i>M. subverticillaris</i>)	Above the epidermis	Paracytic	Glandular and tector	Simple unicellular	Elongated	Tortuous	Erect	Simple	Dense	Smooth
	<i>M. tortuosa</i>	Above the epidermis	Anomocytic	Tector	Simple unicellular	Elongated	Tortuous	Erect and adpressed	Bulging	Dense	Smooth
	<i>M. tortuosa</i> (= <i>M. linguiformis</i>)	Above the epidermis	Paracytic	Tector	Simple unicellular	Elongated	Tortuous	Erect	Simple	Dense, moderate on the midvein	Smooth
	<i>M. vestita</i>	Unable to identify	Unable to identify	Tector	Simple unicellular	Elongated	Straight and tortuous	Erect	Unable to identify	Dense	Unable to identify
<i>Aulomyrcia</i>	<i>M. abbotiana</i>	Leveled	Paracytic	Tector	Dibrachiate	Short	Straight	Adpressed	Simple	Sparse	Smooth
	<i>M. amazonica</i>	Leveled	Paracytic	Glandular and tector	Simple unicellular, branched and dibrachiate	Elongated	Straight and tortuous	Erect and adpressed	Simple	Sparse, moderate on the midvein	Smooth
	<i>M. cana</i>	Leveled	Anomocytic	Tector	Simple unicellular and hook-shaped	Short and elongated	Straight	Adpressed	Bulging	Sparse	Smooth
	<i>M. decorticans</i>	Leveled	Anomocytic	Tector	Dibrachiate	Short and elongated	Straight	Adpressed	Simple	Sparse	Smooth with granules
	<i>M. florifera</i>	Above the epidermis	Paracytic	Tector	Simple unicellular and dibrachiate	Short and elongated	Straight	Adpressed	Bulging	Sparse	Smooth
	<i>M. multiflora</i>	Leveled	Anomocytic	Glandular and tector	Dibrachiate	Elongated	Straight	Adpressed	Simple	Sparse	Smooth

Cont.

Section	Species	Stomatal level	Stomas	Trichomes	Tector trichomes morfology	Tector trichomes lenght	Tector trichomes axis	Tector trichomes orientation	Tector trichomes base	Trichomes distribution	Cuticle and wax
<i>Aulomyrcia</i>	<i>M. neomontana</i>	Leveled	Paracytic	Tector	Simple unicellulares	Elongated	Straight	Adpressed	Bulging	Sparse	Smooth to slightly striated
	<i>M. neuwiedeanana</i>	Leveled	Anomocytic	Tector	Dibrachiate and hook-shaped	Short and elongated	Straight	Adpressed	Simple	Sparse	Smooth
	<i>M. obversa</i>	Above the epidermis	Paracytic	Tector	Simple unicellular and hook-shaped	Short and elongated	Straight	Adpressed	Bulging	Sparse, moderate on the midvein	Smooth
	<i>M. racemosa</i>	Leveled	Paracytic	Glandular and tector	Simple unicellular and hook-shaped	Short and elongated	Straight	Adpressed	Simple	Sparse, moderate on the midvein	Smooth
	<i>M. saxatilis</i>	Leveled	Anomocytic	Glandular and tector	Simple unicellular	Elongated	Straight	Adpressed	Simple	Sparse	Smooth
<i>Calyptanthus</i>	<i>M. calderonii</i>	Above the epidermis	Anomocytic	Glandular and tector	Simple unicellular and dibrachiate	Elongated	Straight	Adpressed	Simple	Sparse	Striated
	<i>M. chytraculia</i>	Slightly above the epidermis	Anomocytic	Tector	Dibrachiate	Short and elongated	Straight	Adpressed	Simple	Sparse	Smooth
	<i>M. fasciculata</i>	Leveled	Paracytic	Glandular and tector	Dibrachiate	Elongated	Tortuous	Erect and adpressed	Simple	Dense	Smooth
	<i>M. glomerata</i>	Leveled	Paracytic	Glandular and tector	Simple unicellular and dibrachiate	Elongated	Straight	Adpressed	Simple	Moderate	Smooth

Cont.

Section	Species	Stomatal level	Stomas	Trichomes	Tector trichomes morfology	Tector trichomes lenght	Tector trichomes axis	Tector trichomes orientation	Tector trichomes base	Trichomes distribution	Cuticle and wax
<i>Calyptanthus</i>	<i>M. loranthifolia</i> (= <i>C. brasiliensis</i>)	Below	Anomocytic	Tector	Simple unicellular and dibrachiate	Short and elongated	Straight and tortuous	Adpressed	Simple	Dense	Striated with granules
	<i>M. loranthifolia</i> (= <i>C. grandifolia</i>)	Below	Anomocytic	Tector	Simple unicellular and dibrachiate	Short and elongated	Straight and tortuous	Adpressed	Simple	Moderate, sparse on the midvein	Striated
	<i>M. neoclusiifolia</i>	Leveled	Paracytic	Tector	Simple unicellular and dibrachiate	Short and elongated	Tortuous	Erect	Simple	Dense	Smooth and fimbriated
	<i>M. strigosa</i>	Above the epidermis	Anomocytic	Glandular and tector	Simple unicellular, branched and dibrachiate	Short and elongated	Straight and tortuous	Erect and adpressed	Simple	Moderate, dense on the midvein	Smooth with slight striations
<i>Eugeniopsis</i>	<i>M. clausseniana</i>	Leveled	Anomocytic	Tector	Simple unicellular	Elongated	Tortuous	Erect	Simple	Sparse	Smooth
	<i>M. eugeniopsoides</i>	Leveled	Paracytic	Tector	Simple unicellular and dibrachiate	Short and elongated	Straight and tortuous	Adpressed	Simple	Sparse, moderate on the midvein	Smooth and fimbriated
	<i>M. ferruginosa</i>	Leveled	Paracytic	Tector	Simple unicellular	Elongated	Straight	Erect	Simple	Sparse	Smooth
	<i>M. hatschbachii</i>	Leveled	Anomocytic	Tector	Dibrachiate	Short and elongated	Straight	Adpressed	Simple	Moderate	Striated
	<i>M. oblongata</i>	Leveled	Unable to identify	Tector	Dibrachiate	Unable to identify	Straight	Adpressed	Simple	Dense	Smooth
	<i>M. subacuminata</i>	Slightly above the epidermis	Paracytic	Glandular and tector	Simple unicellular and stellate	Elongated	Straight	Erect and adpressed	Simple	Moderate	Smooth to slightly striated

Cont.

Section	Species	Stomatal level	Stomas	Trichomes	Tector trichomes morfology	Tector trichomes lenght	Tector trichomes axis	Tector trichomes orientation	Tector trichomes base	Trichomes distribution	Cuticle and wax
<i>Eugeniopsis</i>	<i>M. suberosa</i>	Above the epidermis	Paracytic	Tector	Simple unicellular	Short	Straight	Erect	Simple	Sparse	Striated
	<i>M. teuscheriana</i>	Above the epidermis	Paracytic	Glandular and tector	Simple unicellular and dibrachiate	Short and elongated	Straight	Erect	Simple	Sparse, moderate on the midvein	Striated
	<i>M. vellozoi</i>	Leveled	Paracytic	Tector	Dibrachiate	Short and elongated	Straight	Adpressed	Simple	Sparse	Smooth to slightly striated
<i>Gomidesia</i>	<i>M. brasiliensis</i>	Leveled to slightly above the epidermis	Paracytic	Tector	Simple unicellular and hook-shaped	Short and elongated	Straight	Adpressed	Simple	Moderate	Smooth with granules
	<i>M. carvalhoi</i>	Leveled	Paracytic	Glandular and tector	Simple unicellular and dibrachiate	Elongated	Straight	Erect	Simple	Sparse, moderate on the midvein	Smooth with granules
	<i>M. cerqueiria</i>	Above the epidermis	Paracytic	Tector	Simple unicellular and hook-shaped	Short and elongated	Straight	Adpressed	Bulging	Moderate	Smooth
	<i>M. eriocalyx</i>	Unable to identify	Unable to identify	Tector	Simple unicellular	Elongated	Straight and tortuous	Erect	Simple	Dense	Smooth
	<i>M. florida</i>	Above the epidermis	Paracytic	Tector	Simple unicellular and hook-shaped	Short and elongated	Straight and tortuous	Erect and adpressed	Simple	Moderate	Smooth

Cont.

Section	Species	Stomatal level	Stomas	Trichomes	Tector trichomes morfology	Tector trichomes lenght	Tector trichomes axis	Tector trichomes orientation	Tector trichomes base	Trichomes distribution	Cuticle and wax
<i>Gomidesia</i>	<i>M. hartwegiana</i>	Unable to identify	Unable to identify	Glandular and tector	Hook-shaped	Short and elongated	Straight	Adpressed	Simple	Sparse	Smooth and granular
	<i>M. hebepetala</i>	Above the epidermis	Paracytic	Glandular and tector	Simple unicellular, branched and hook-shaped	Short and elongated	Straight	Erect and adpressed	Simple	Moderate	Smooth
	<i>M. mischophylla</i>	Leveled	Paracytic	Tector	Simple unicellular	Elongated	Tortuous	Erect	Simple	Dense	Smooth
	<i>M. pubescens</i>	Slightly above the epidermis	Paracytic	Tector	Simple unicellular	Short and elongated	Straight	Erect	Simple	Moderate	Smooth with slight striations
	<i>M. reticulata</i>	Above the epidermis	Paracytic	Tector	Simple unicellular	Short and elongated	Straight	Erect	Simple	Moderate	Smooth
	<i>M. spectabilis</i>	Slightly above the epidermis	Unable to identify	Glandular and tector	Simple unicellular and hook-shaped	Short and elongated	Straight	Erect and adpressed	Bulging	Moderate, dense on the midvein	Smooth
<i>Myrcia</i>	<i>M. aliena</i>	Leveled	Paracytic	Tector	Simple unicellular	Short and elongated	Straight and tortuous	Adpressed	Bulging	Sparse, moderate on the midvein	Smooth
	<i>M. albotomentosa</i>	Unable to identify	Unable to identify	Tector	Simple unicellular	Elongated	Tortuous	Erect	Unable to identify	Dense	Unable to identify
	<i>M. bella</i>	Above the epidermis	Paracytic	Glandular and tector	Simple unicellular and hook-shaped	Short and elongated	Straight and tortuous	Adpressed	Bulging	Moderate	Smooth
	<i>M. bracteata</i>	Leveled	Paracytic	Tector	Simple unicellular	Elongated	Straight	Adpressed	Simple	Sparse	Smooth

Cont.

Section	Species	Stomatal level	Stomas	Trichomes	Tector trichomes morfology	Tector trichomes lenght	Tector trichomes axis	Tector trichomes orientation	Tector trichomes base	Trichomes distribution	Cuticle and wax
<i>Myrcia</i>	<i>M. isaiana</i>	Above the epidermis	Anomocytic	Tector	Simple unicellular	Elongated	Straight and tortuous	Adpressed	Simple	Sparse	Smooth
	<i>M. retorta</i>	Below	Unable to identify	Glandular and tector	Simple unicellular	Short and elongated	Tortuous	Adpressed	Bulging	Moderate	Smooth
	<i>M. rupicola</i>	Leveled	Anomocytic	Tector	Simple unicellular and dibrachiate	Short and elongated	Straight	Adpressed	Bulging	Moderate	Smooth
	<i>M. splendens</i>	Above the epidermis	Paracytic	Tector	Simple unicellular and hook-shaped	Short and elongated	Straight and tortuous	Adpressed	Simple	Moderate	Smooth
	<i>M. tafelbergica</i>	Above the epidermis	Paracytic	Tector	Simple unicellular and hook-shaped	Short and elongated	Straight	Adpressed	Bulging	Sparse	Smooth
	<i>M. tocaninensis</i>	Above the epidermis	Paracytic	Tector	Simple unicellular	Short and elongated	Straight	Adpressed	Bulging	Dense	Smooth with granules
<i>Reticulosae</i>	<i>Myrcia aethusa</i>	Leveled	Anomocytic	Glandular and tector	Simple unicellular and dibrachiate	Short and elongated	Straight	Adpressed	Simple	Sparse	Smooth with granules
	<i>M. pubipetala</i>	Leveled	Anomocytic	Tector	Simple unicellular and dibrachiate	Short and elongated	Straight	Adpressed	Bulging	Moderate	Smooth at some points on the plate
	<i>M. venulosa</i>	Above the epidermis	Anomocytic	Tector	Simple unicellular	Elongated	Tortuous	Erect	Simple	Moderate	Smooth

Cont.

Section	Species	Stomatal level	Stomas	Trichomes	Tector trichomes morfology	Tector trichomes lenght	Tector trichomes axis	Tector trichomes orientation	Tector trichomes base	Trichomes distribution	Cuticle and wax
<i>Tomentosae</i>	<i>M. anomala</i>	Leveled	Paracytic	Tector	Simple unicellular	Elongated	Tortuous	Erect	Bulging	Sparse	Smooth
	<i>M. selloi</i>	Leveled	Paracytic	Glandular and tector	Simple unicellular	Unable to identify	Straight	Erect	Simple	Sparse	Smooth with granules
	<i>M. selloi</i> (= <i>M. laruotteana</i>)	Leveled	Paracytic	Glabrous	Glabrous	-	Glabrous	Glabrous	Glabrous	Glabrous	Smooth
	<i>M. tomentosa</i>	Above the epidermis	Paracytic	Tector	Simple unicellular	Elongated	Tortuous	Erect	Simple	Sparse	Smooth
	<i>M. verticillaris</i>	Leveled	Anomocytic	Tector	Simple unicellular	Short	Straight	Erect	Simple	Sparse	Smooth with granules
<i>Sympodiomyrcia</i>	<i>M. ferruginea</i>	Above the epidermis	Anomocytic	Tector	Dibrachiate	Short and elongated	Tortuous	Erect and adpressed	Simple	Moderate	Smooth
	<i>M. subcordata</i>	Below	Anomocytic	Tector	Simple unicellular and dibrachiate	Short and elongated	Tortuous	Adpressed	Simple	Moderate	Smooth with granules
Clado 10	<i>M. maximiliana</i>	Above the epidermis	Anomocytic	Glandular and tector	Simple unicellular and hook-shaped	Short and elongated	Straight	Erect	Bulging	Moderate, sparse on the midvein	Smooth
	<i>M. pulvinata</i>	Slightly above the epidermis	Anomocytic	Tector	Simple unicellular	Short	Straight	Adpressed	Simple	Sparse	Smooth
	<i>M. robusta</i>	Leveled	Paracytic	Tector	Simple unicellular	Elongated	Tortuous	Adpressed	Simple	Dense	Smooth with granules