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

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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. *Calyptranthes* 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 anomocíticos 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. *Calyptranthes* 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 trilocular 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 *Calyptranthes* 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. *Calyptranthes* (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 exsicatae 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 Apendix, 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**
Aguava	*Myrcia cuprea* (O.Berg) Kiaersk.	G.L.Sobel et al. 4584	Kew
	Myrcia guianensis (Aubl.) DC.	S.Gonzales & E.Fonty 1831	Kew
	Myrcia laricina (O.Berg) Burret ex Luetzelb.	Gardner 2874	Kew
	Myrcia nivea Cambess.	D.F.Lima & R.Morokawa 471	Kew
	Myrcia rufipes DC.	M.L.Kawasaki et al. 7722	Kew
	Myrcia siriacoana Glaz. ex P.O.Rosa & Proença	D.F.Lima et al. 505	Kew
	Myrcia subalpestris DC.	D.F.Lima & R.Trad 514	Kew
	Myrcia subalpestris (= *M. subverticillaris* (O.Berg) Kiaersk.)	D.F.Lima & R.Morokawa 464	Kew
	Myrcia tortuosa (O.Berg) N.Silveira	E.Onishi & S.G.Fonseca 184	Kew
	Myrcia tortuosa (= *M. linguiformis* (O.Berg) N.Silveira)	D.F.Lima & R.Morokawa 457	Kew
	Myrcia vestita DC.	D.F.Lima & R.Morokawa 455	Kew
Aulomyrcia	*Myrcia abbotiana* (Urb.) Alain	E.Lucas et al. 1108	Kew
	Myrcia amazonica DC.	D.F.Lima et al. 417	Kew
	Myrcia cana (McVaugh) E.Lucas & C.E.Wilson	S.S.Tillett et al. 751-27	Kew
	Myrcia decorticans DC.	M.Landim 1476	Kew
	Myrcia florifera (McVaugh) Gaem. & E.Lucas	A.C.Araújo et al. 1885	Kew
	Myrcia multiflora (Lam.) DC.	E.Lucas et al. 824	Kew
	Myrcia neomontana E.Lucas & C.E.Wilson	R.C.Ek et al. 1768	Kew
	Myrcia neuwiedeana (O.Berg) E.Lucas & C.E.Wilson	V.G.Staggemeier & J.E.Q.Faria 771	Kew
	Myrcia obversa (D.Legrand) E.Lucas & C.E.Wilson	A.Amorim et al. 449	Kew
	Myrcia racemosa (O.Berg) Kiaersk.	S.A.Mori et al. 10844	Kew
	Myrcia saxatilis (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
Calyptranthes	*Myrcia calderonii* (Standl.) A.R.Lourenço & Sánchez-Cháv.	B.Vazquez 557	Kew
	Myrcia chytraculia (L.) A.R.Lourenço & E.Lucas	J.Marin 180	Kew
	Myrcia glomerata (Cambess.) G.P.Burton & E.Lucas	E.Lucas et al. 183	Kew
	Myrcia fasciculata (O.Berg) K.Campbell & K.Samra	J.J.Wurdack & L.S.Adderley 43528	Kew
	Myrcia loranthifolia (DC.) G.P.Burton & E.Lucas (= *Calyptranthes brasiliensis* Spreng.)	J.E.Q.Faria et al. 2497	Kew
	Myrcia loranthifolia (= *Calyptranthes grandifolia* O.Berg)	L.P. de Queiroz et al. 1293	Kew
	Myrcia neoclusiifolia A.R.Lourenço & E.Lucas	R.C.Forzza et al. 4398	Kew
	Myrcia strigosa A.R.Lourenço & E.Lucas	G.Hatschbach & C.Koczizki 20886	Kew
Eugeniopsis	*Myrcia clausseniana* (O.Berg) A.Maruy. & Gaem.	M.L.Kawasaki & M.C.Henrique 7627	Kew
	Myrcia eugeniopsoides (D.Legrand & Kausel) Mazine	E.Barbosa & L.B.Pereira 38	Kew
	Myrcia ferruginosa Mazine	M.F.Santos et al. 689	Kew
	Myrcia hatschbachii D.Legrand	G.Hatschbach 30964	Kew
	Myrcia oblongata DC.	M.F.Santos et al. 667	Kew
	Myrcia subacuminata (Kiaersk.) M.F.Santos	J.E.Q.Faria & V.G.Staggemeier 2525	Kew
	Myrcia suberosa M.F.Santos & T.Fern.	Farney 3134	UFSC
	Myrcia teuscheriana (O.Berg) M.F.Santos	E.Lucas et al. 673	Kew
	Myrcia vellozoi Mazine	V.G.Staggemeier & M.G.G.Camargo 828	Kew
Gomidesia	*Myrcia brasiliensis* Kiaersk.	S.J.Gomes da Silva et al. 161	Kew
	Myrcia carvalhoi NicLugh.	M.F.Santos et al. 217	Kew
	Myrcia cerqueiria (Nied.) E.Lucas & Sobral	E.M.Nic Lughadha et al. 182	Kew
	Myrcia eriocalyx DC.	E.M.Nic Lughadha et al. 211	Kew
	Myrcia florida Lem.	E.M.Nic Lughadha et al. 173	Kew
	Myrcia hartwegiana (O.Berg) Kiaersk.	K.Matsumoto et al. 837	Kew
	Myrcia hebepetala DC.	M.M.Saavedra et al. 914	Kew
	Myrcia mischophylla Kiaersk.	D.F.Lima et al. 416	Kew
	Myrcia pubescens DC.	D.F.Lima & R.Trad 539	Kew
	Myrcia reticulata Cambess.	M.F.Santos et al. 803	Kew
	Myrcia spectabilis 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
Myrcia	*Myrcia aliena* McVaugh	D.C.Daly et al. 1893	Kew
	Myrcia albotomentosa DC.	D.F.Lima et al. 499	Kew
	Myrcia bella Cambess.	D.F.Lima & R.Trad 520	Kew
	Myrcia bracteata (Rich.) DC.	G.T.Prance et al. 10615	UFSC
	Myrcia isaiana G.M.Barroso & Peixoto	G.Hatschbach & A.R.Campos 57921	UFSC
	Myrcia retorta Cambess.	D.B.Falkenberg s.n. (FLOR 39200)	UFSC
	Myrcia rupicola D.Legrand	R.Reitz & R.M.Klein 10321	UFSC
	Myrcia splendens (Sw.) DC.	R.Reitz & R.M.Klein 17420	UFSC
	Myrcia tafelbergica Amshoff	B.Hoffman et al. 1765	Kew
	Myrcia tocantinensis Glaz. ex P.O.Rosa & Proença	H.S.Irwin et al. 32901	UFSC
Reticulosae	*Myrcia aethusa* (O.Berg) N.Silveira	J.A.Jarenkow 2033	UFSC
	Myrcia pubipetala Miq.	R.Santos & A.J.Aguiar s.n. (FLOR 29350)	UFSC
	Myrcia venulosa DC.	L.B.Smith et al. 16054	UFSC
Sympodiomyrcia	*Myrcia ferruginea* (Poir.) DC.	Fundación Biológica Puerto Rastrojo CHI-22	Kew
	Myrcia subcordata DC.	L.B.Smith & R.M.Klein 14416	UFSC
Tomentosae	*Myrcia anomala* Cambess.	A.Krapovickas et al. 45966	Kew
	Myrcia selloi (Spreng.) N.Silveira	D.B.Falkenberg 1814	UFSC
	Myrcia selloi (= *M. laruotteana* Cambess.)	R.Kummrow 542	UFSC
	Myrcia tomentosa (Aubl.) DC.	A.R.Silva & E.L.Siqueira 464	UFSC
	Myrcia verticillaris O.Berg	M.Sobral & J.N.Marchiori 4539	UFSC
Clado 10	*Myrcia maximiliana* O.Berg	M.F.Santos et al. 750	Kew e UFSC
	Myrcia pulvinata B.S.Amorim	Souza 389	UFSC
	Myrcia robusta 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. *Calyptranthes* (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. *Calyptranthes* 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$150um) (Figs. 2A-B; 3F) or long (>150µm) (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).

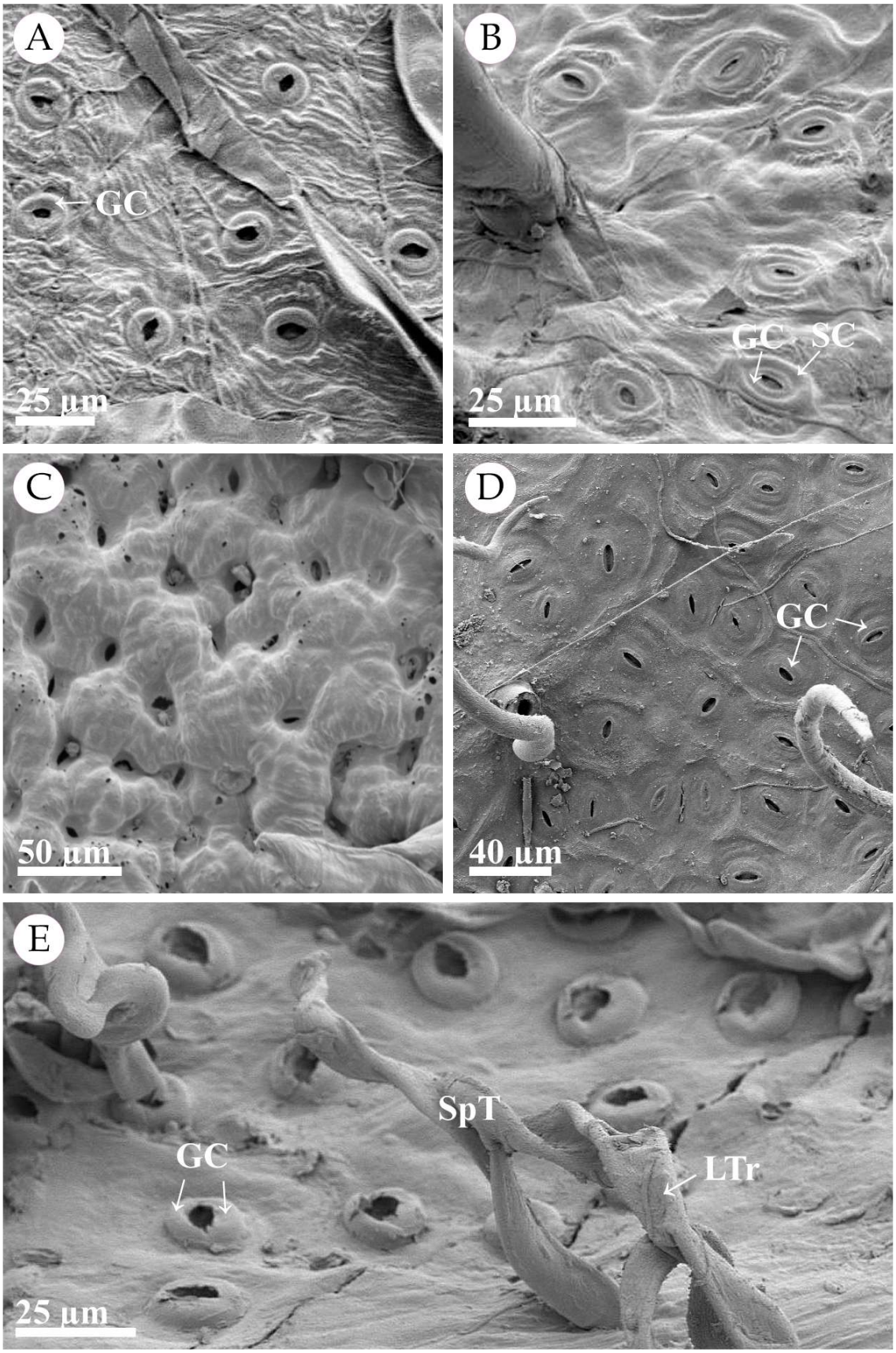


Figure 1: Aspect of the abaxial surface of the leaf limb of *Myrcia* species showing the stomata complexes. A. *M. chytraculia*, anomocytic stomata with prominent guard cells (GC). B. *M. ferruginosa*, paracytic stomata showing the guard cells (GC) and the subsidiary cells (SC); C. *M. loranthifolia*, 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 tector 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 tector trichome**	**Base of tector trichome**	**Cuticle and wax**
M. sect. *Aguava*	Above, rare levelled	Paracytic or anomocytic	Simple unicellular, rare dibrachiate	Simple or bulging	Smooth, rare with granules
M. sect. *Aulomyrcia*	Levelled, rare above	Paracytic or anomocytic	Simple unicellular or dibrachiate, rare hook-shaped or branched	Simple or bulging	Smooth, rare with granules
M. sect. *Calyptranthes*	Levelled or above, rare below	Anomocytic	Dibrachiate or simple unicellular (but always with dibrachiates)	Simple	Smooth or striated, rare with granules or fimbriate
M. sect. *Eugeniopsis*	Levelled, rare above	Paracytic, rare anomocytic	Simple unicellular or dibrachiate, rare stellate	Simple	Smooth or striated, rare fimbriate
M. sect. *Gomidesia*	Above, rare levelled	Paracytic	Simple unicellular or hook-shaped, rare dibrachiate or branched	Simple, rare bulging	Smooth, rare striated or with granules
M. sect. *Myrcia*	Above or levelled, rare below	Paracytic, rare anomocytic	Simple unicellular, rare dibrachiate	Simple or bulging	Smooth, rare with granules
M. sect. *Reticulosae*	Levelled or above	Anomocytic	Simple unicellular, rare dibrachiate	Simple or bulging	Smooth, with granules or plates
M. sect. *Sympodiomyrcia*	Above or below	Anomocytic	Dibrachiate or simple unicellular (but always with dibrachiates)	Simple	Smooth or with granules
M. sect. *Tomentosae*	Levelled, rare above	Paracytic, rare anomocytic	Simple unicellular	Simple, rare bulging	Smooth or with granules
Clade 10	Above or levelled	Anomocytic or paracytic	Simple unicellular, rare hook-shaped	Simple or bulging	Smooth, rare with granules

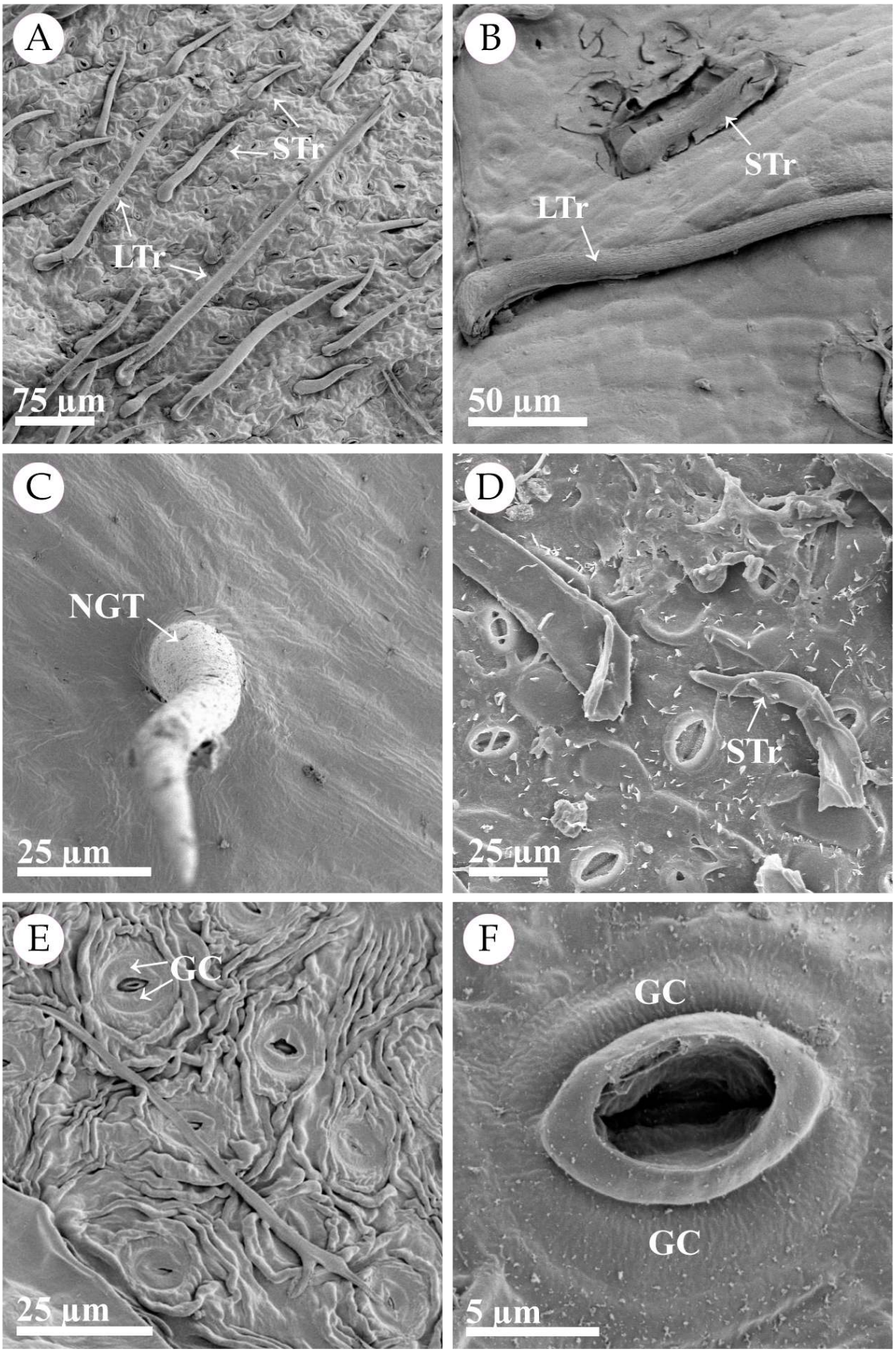


Figure 2. Aspect of the abaxial surface of the leaf limb of *Myrcia* species showing cuticle, wax and trichomes. A. *M. brasiliensis*, smooth cuticle, long (LTr) and short (STr) unicellular simple tector trichomes; B. *M. cana*, smooth cuticle, long (LTr) and short (STr) unicellular simple tector trichomes; 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).

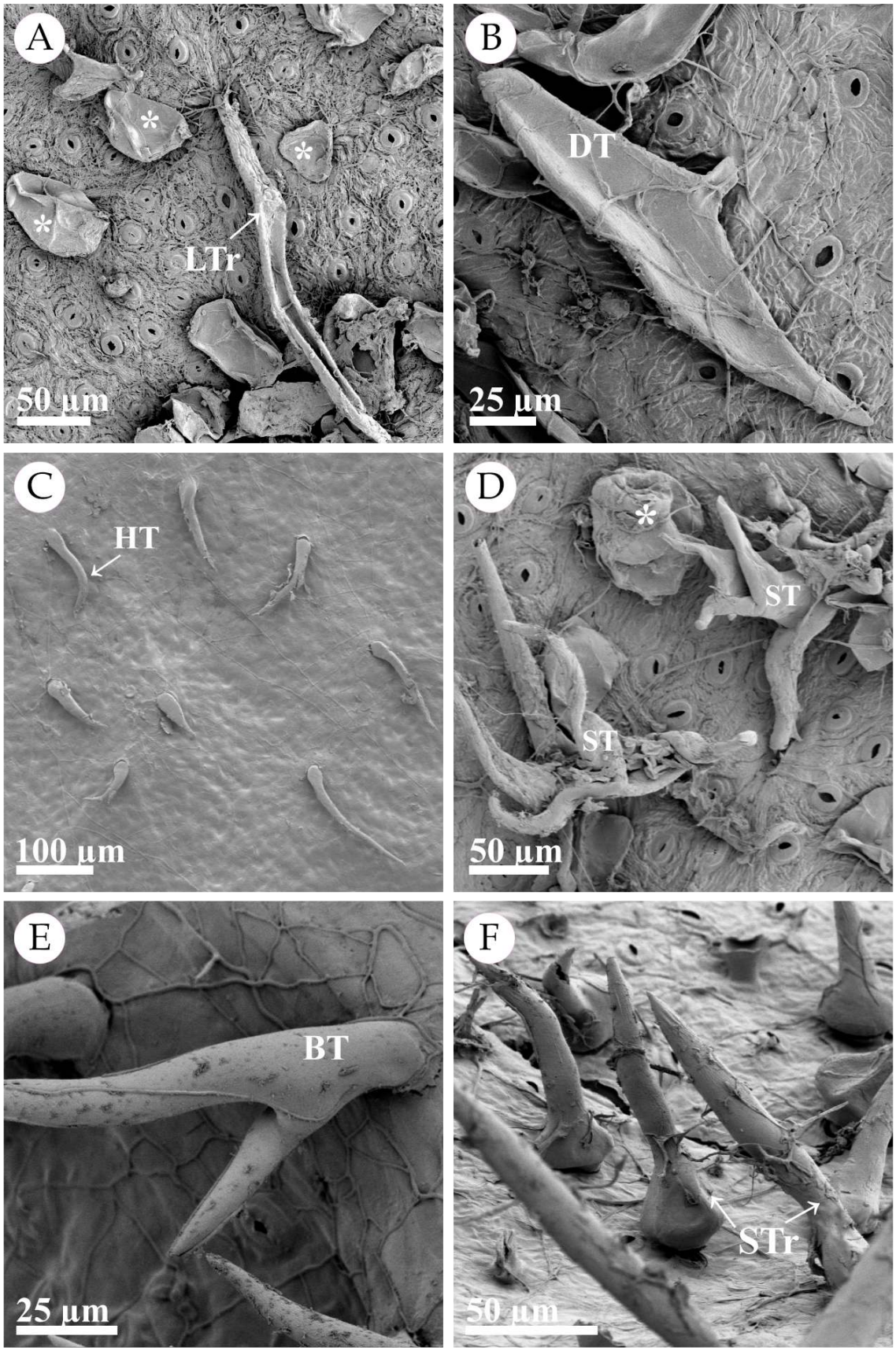


Figure 3. Aspect of the abaxial surface of the leaf limb of *Myrcia* species showing different types of trichomes. A. *M. teuscheriana*, tector (arrowhead) and glandular trichomes (*); B, *M. chytraculia*, dibrachiate trichome (DT); C. *M. hartwegiana*, short trichomes (STr) on a hook (HG); D. *M. subacuminata*,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

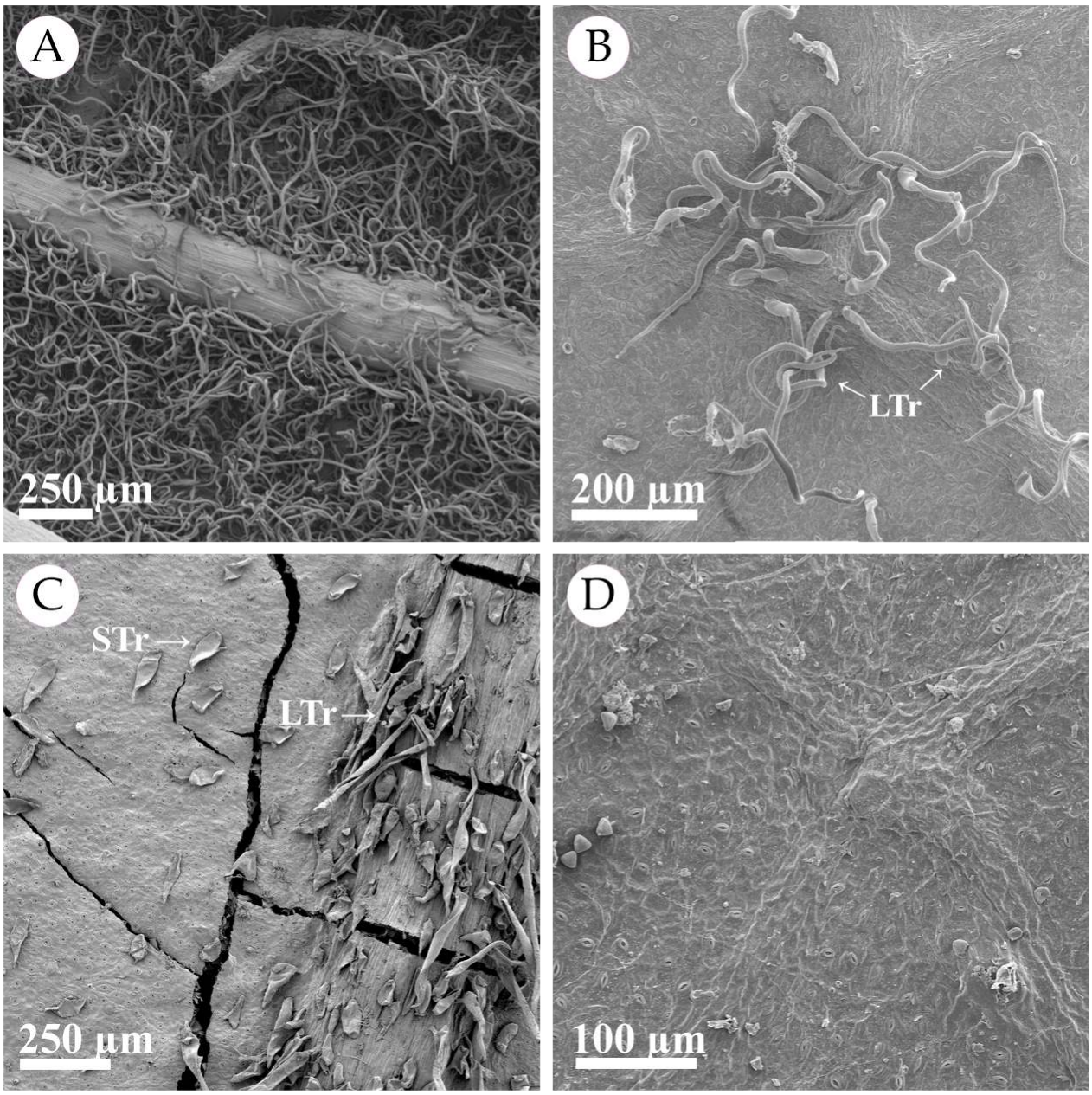


Figure 4. Aspect of the abaxial surface of the leaf limb of *Myrcia* species showing the general indumentum. A. *M. laricina*, leaf pilosity, sparse trichomes on the midvein; B. *M. tomentosa*, leaf with short indumentum, long trichomes (LTr) concentrated on the veins; C. *M. eugeniopsoides*, moderately 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.

Discusssion

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 (Appezzato-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. *Calyptranthes* 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 *Calyptranthes* 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.

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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
Aguava	*M. cuprea*	Above the epidermis	Paracytic	Tector	Simple unicellular	Elongated	Straight	Adpressed	Bulging	Dense	Smooth
	M. guianensis	Leveled	Paracytic	Tector	Simple unicellular and dibrachiate	Elongated	Straight	Adpressed	Bulging	Sparse, dense on the midvein	Smooth
	M. laricina	Above the epidermis	Anomocytic	Tector	Simple unicellular	Elongated	Tortuous	Erect and adpressed	Bulging	Dense, sparse on the midvein	Smooth
	M. nivea	Above the epidermis	Anomocytic	Tector	Simple unicellular	Elongated	Tortuous	Erect and adpressed	Bulging	Moderate, dense on the midvein	Smooth
	M. rufipes	Above the epidermis	Paracytic	Tector	Simple unicellular	Short and elongated	Straight and tortuous	Erect	Simple	Moderate	Smooth
	M. siriacoana	Above the epidermis	Paracytic	Tector	Simple unicellular	Elongated	Straight and tortuous	Erect and adpressed	Simple	Moderate	Smooth with granules
	M. subalpestris	Above the epidermis	Anomocytic	Tector	Simple unicellular	Elongated	Tortuous	Erect	Simple	Dense	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
Aguava	*M. subalpestris* (=*M. subverticillaris*)	Above the epidermis	Paracytic	Glandular and tector	Simple unicellular	Elongated	Tortuous	Erect	Simple	Dense	Smooth
	M. tortuosa	Above the epidermis	Anomocytic	Tector	Simple unicellular	Elongated	Tortuous	Erect and adpressed	Bulging	Dense	Smooth
	M. tortuosa (=*M. linguiformis*)	Above the epidermis	Paracytic	Tector	Simple unicellular	Elongated	Tortuous	Erect	Simple	Dense, moderate on the midvein	Smooth
	M. vestita	Unable to identify	Unable to identify	Tector	Simple unicellular	Elongated	Straight and tortuous	Erect	Unable to identify	Dense	Unable to identify
Aulomyrcia	*M. abbotiana*	Leveled	Paracytic	Tector	Dibrachiate	Short	Straight	Adpressed	Simple	Sparse	Smooth
	M. amazonica	Leveled	Paracytic	Glandular and tector	Simple unicellular, branched and dibrachiate	Elongated	Straight and tortuous	Erect and adpressed	Simple	Sparse, moderate on the midvein	Smooth
	M. cana	Leveled	Anomocytic	Tector	Simple unicellular and hook-shaped	Short and elongated	Straight	Adpressed	Bulging	Sparse	Smooth
	M. decorticans	Leveled	Anomocytic	Tector	Dibrachiate	Short and elongated	Straight	Adpressed	Simple	Sparse	Smooth with granules
	M. florifera	Above the epidermis	Paracytic	Tector	Simple unicellular and dibrachiate	Short and elongated	Straight	Adpressed	Bulging	Sparse	Smooth
	M. multiflora	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
Aulomyrcia	*M. neomontana*	Leveled	Paracytic	Tector	Simple unicellulares	Elongated	Straight	Adpressed	Bulging	Sparse	Smooth to slightly striated
	M. neuwiedeana	Leveled	Anomocytic	Tector	Dibrachiate and hook-shaped	Short and elongated	Straight	Adpressed	Simple	Sparse	Smooth
	M. obversa	Above the epidermis	Paracytic	Tector	Simple unicellular and hook-shaped	Short and elongated	Straight	Adpressed	Bulging	Sparse, moderate on the midvein	Smooth
	M. racemosa	Leveled	Paracytic	Glandular and tector	Simple unicellular and hook-shaped	Short and elongated	Straight	Adpressed	Simple	Sparse, moderate on the midvein	Smooth
	M. saxatilis	Leveled	Anomocytic	Glandular and tector	Simple unicellular	Elongated	Straight	Adpressed	Simple	Sparse	Smooth
Calyptranthes	*M. calderonii*	Above the epidermis	Anomocytic	Glandular and tector	Simple unicellular and dibrachiate	Elongated	Straight	Adpressed	Simple	Sparse	Striated
	M. chytraculia	Slightly above the epidermis	Anomocytic	Tector	Dibrachiate	Short and elongated	Straight	Adpressed	Simple	Sparse	Smooth
	M. fasciculata	Leveled	Paracytic	Glandular and tector	Dibrachiate	Elongated	Tortuous	Erect and adpressed	Simple	Dense	Smooth
	M. glomerata	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
Calyptranthes	*M. loranthifolia* (=*C. brasiliensis*)	Below	Anomocytic	Tector	Simple unicellular and dibrachiate	Short and elongated	Straight and tortuous	Adpressed	Simple	Dense	Striated with granules
	M. loranthifolia (=*C. grandifolia*)	Below	Anomocytic	Tector	Simple unicellular and dibrachiate	Short and elongated	Straight and tortuous	Adpressed	Simple	Moderate, sparse on the midvein	Striated
	M. neoclusiifolia	Leveled	Paracytic	Tector	Simple unicellular and dibrachiate	Short and elongated	Tortuous	Erect	Simple	Dense	Smooth and fimbriated
	M. strigosa	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
Eugeniopsis	*M. clausseniana*	Leveled	Anomocytic	Tector	Simple unicellular	Elongated	Tortuous	Erect	Simple	Sparse	Smooth
	M. eugeniopsoides	Leveled	Paracytic	Tector	Simple unicellular and dibrachiate	Short and elongated	Straight and tortuous	Adpressed	Simple	Sparse, moderate on the midvein	Smooth and fimbriated
	M. ferruginosa	Leveled	Paracytic	Tector	Simple unicellular	Elongated	Straight	Erect	Simple	Sparse	Smooth
	M. hatschbachii	Leveled	Anomocytic	Tector	Dibrachiate	Short and elongated	Straight	Adpressed	Simple	Moderate	Striated
	M. oblongata	Leveled	Unable to identify	Tector	Dibrachiate	Unable to identify	Straight	Adpressed	Simple	Dense	Smooth
	M. subacuminata	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
Eugeniopsis	*M. suberosa*	Above the epidermis	Paracytic	Tector	Simple unicellular	Short	Straight	Erect	Simple	Sparse	Striated
	M. teuscheriana	Above the epidermis	Paracytic	Glandular and tector	Simple unicellular and dibrachiate	Short and elongated	Straight	Erect	Simple	Sparse, moderate on the midvein	Striated
	M. vellozoi	Leveled	Paracytic	Tector	Dibrachiate	Short and elongated	Straight	Adpressed	Simple	Sparse	Smooth to slightly striated
Gomidesia	*M. brasiliensis*	Leveled to slightly above the epidermis	Paracytic	Tector	Simple unicellular and hook-shaped	Short and elongated	Straight	Adpressed	Simple	Moderate	Smooth with granules
	M. carvalhoi	Leveled	Paracytic	Glandular and tector	Simple unicellular and dibrachiate	Elongated	Straight	Erect	Simple	Sparse, moderate on the midvein	Smooth with granules
	M. cerqueiria	Above the epidermis	Paracytic	Tector	Simple unicellular and hook-shaped	Short and elongated	Straight	Adpressed	Bulging	Moderate	Smooth
	M. eriocalyx	Unable to identify	Unable to identify	Tector	Simple unicellular	Elongated	Straight and tortuous	Erect	Simple	Dense	Smooth
	M. florida	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
Gomidesia	*M. hartwegiana*	Unable to identify	Unable to identify	Glandular and tector	Hook-shaped	Short and elongated	Straight	Adpressed	Simple	Sparse	Smooth and granular
	M. hebepetala	Above the epidermis	Paracytic	Glandular and tector	Simple unicellular, branched and hook-shaped	Short and elongated	Straight	Erect and adpressed	Simple	Moderate	Smooth
	M. mischophylla	Leveled	Paracytic	Tector	Simple unicellular	Elongated	Tortuous	Erect	Simple	Dense	Smooth
	M. pubescens	Slightly above the epidermis	Paracytic	Tector	Simple unicellular	Short and elongated	Straight	Erect	Simple	Moderate	Smooth with slight striations
	M. reticulata	Above the epidermis	Paracytic	Tector	Simple unicellular	Short and elongated	Straight	Erect	Simple	Moderate	Smooth
	M. spectabilis	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
Myrcia	*M. aliena*	Leveled	Paracytic	Tector	Simple unicellular	Short and elongated	Straight and tortuous	Adpressed	Bulging	Sparse, moderate on the midvein	Smooth
	M. albotomentosa	Unable to identify	Unable to identify	Tector	Simple unicellular	Elongated	Tortuous	Erect	Unable to identify	Dense	Unable to identify
	M. bella	Above the epidermis	Paracytic	Glandular and tector	Simple unicellular and hook-shaped	Short and elongated	Straight and tortuous	Adpressed	Bulging	Moderate	Smooth
	M. bracteata	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
Myrcia	*M. isaiana*	Above the epidermis	Anomocytic	Tector	Simple unicellular	Elongated	Straight and tortuous	Adpressed	Simple	Sparse	Smooth
	M. retorta	Below	Unable to identify	Glandular and tector	Simple unicellular	Short and elongated	Tortuous	Adpressed	Bulging	Moderate	Smooth
	M. rupicola	Leveled	Anomocytic	Tector	Simple unicellular and dibrachiate	Short and elongated	Straight	Adpressed	Bulging	Moderate	Smooth
	M. splendens	Above the epidermis	Paracytic	Tector	Simple unicellular and hook-shaped	Short and elongated	Straight and tortuous	Adpressed	Simple	Moderate	Smooth
	M. tafelbergica	Above the epidermis	Paracytic	Tector	Simple unicellular and hook-shaped	Short and elongated	Straight	Adpressed	Bulging	Sparse	Smooth
	M. tocantinensis	Above the epidermis	Paracytic	Tector	Simple unicellular	Short and elongated	Straight	Adpressed	Bulging	Dense	Smooth with granules
Reticulosae	*Myrcia aethusa*	Leveled	Anomocytic	Glandular and tector	Simple unicellular and dibrachiate	Short and elongated	Straight	Adpressed	Simple	Sparse	Smooth with granules
	M. pubipetala	Leveled	Anomocytic	Tector	Simple unicellular and dibrachiate	Short and elongated	Straight	Adpressed	Bulging	Moderate	Smooth at some points on the plate
	M. venulosa	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
Tomentosae	*M. anomala*	Leveled	Paracytic	Tector	Simple unicellular	Elongated	Tortuous	Erect	Bulging	Sparse	Smooth
	M. selloi	Leveled	Paracytic	Glandular and tector	Simple unicellular	Unable to identify	Straight	Erect	Simple	Sparse	Smooth with granules
	M. selloi (=*M. laruotteana*)	Leveled	Paracytic	Glabrous	Glabrous	-	Glabrous	Glabrous	Glabrous	Glabrous	Smooth
	M. tomentosa	Above the epidermis	Paracytic	Tector	Simple unicellular	Elongated	Tortuous	Erect	Simple	Sparse	Smooth
	M. verticillaris	Leveled	Anomocytic	Tector	Simple unicellular	Short	Straight	Erect	Simple	Sparse	Smooth with granules
Sympodiomyrcia	*M. ferruginea*	Above the epidermis	Anomocytic	Tector	Dibrachiate	Short and elongated	Tortuous	Erect and adpressed	Simple	Moderate	Smooth
	M. subcordata	Below	Anomocytic	Tector	Simple unicellular and dibrachiate	Short and elongated	Tortuous	Adpressed	Simple	Moderate	Smooth with granules
Clado 10	*M. maximiliana*	Above the epidermis	Anomocytic	Glandular and tector	Simple unicellular and hook-shaped	Short and elongated	Straight	Erect	Bulging	Moderate, sparse on the midvein	Smooth
	M. pulvinata	Slightly above the epidermis	Anomocytic	Tector	Simple unicellular	Short	Straight	Adpressed	Simple	Sparse	Smooth
	M. robusta	Leveled	Paracytic	Tector	Simple unicellular	Elongated	Tortuous	Adpressed	Simple	Dense	Smooth with granules