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Comparative floral anatomy of 10 species of Myrteae (Myrtaceae) and phylogenetic implications

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ABSTRACT. This study evaluated and described the comparative floral anatomy of Myrteae species to facilitate species characterization. Buds and flowers collected from the herbarium were subjected to herborization reversion, and the fresh material was prepared using standart techniques, for further analysis with a light optical microscope. There was little variation in the tissues that comprise the floral whorls of the studied species. Bracteoles were observed in six taxa, and the mesophyll may consist of fundamental or spongy parenchyma. The vascular bundles of the pedicel, with a siphonostelic arrangement, are individualized in a monocycle of eight to ten vascular bundles from the base of the ovary. The ovary wall has three regions in the mesophyll composed of fundamental or spongy parenchyma: the outer region, which contains secretory cavities; the median region, which contains large vascular bundles of the monocycle; and the inner region, which contains carpellary vascular bundles. In the perianth, the number of vascular bundles varies, and they are surrounded by fundamental or spongy parenchyma. The ovules are campylotropous. The anthers are tetrasporangiate, but in *Eugenia uniflora*, there is no secretory cavity in the connective. The number of vascular bundles in the style varies from four to seven. Characteristics that may indicate evolutionary trends and that should be explored further include: (1) the ratio of placental height to ovule number (2) the ratio of the number of vascular bundles of the monocyclic to the number of carpels, and (3) the presence of secretory cavities in the inner part of the hypanthium. These findings contribute to the phylogenetic resolution and systematic understanding of Myrteae.

Keywords: Subtribes of Myrteae; floral vasculature; gynoecium; hypanthium.

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Introduction

Myrtaceae includes about 6,000 species in 144 genera (Plants of the World Online, 2025), distributed across Australia, Southeast Asia, tropical America, and South America, with few representatives in Africa (Wilson et al., 2001). Of the 20 recognized tribes in the family (Wilson et al., 2005; Wilson et al., 2022), Myrteae stands out, as half of its species diversity occurs in Brazil, where 29 genera and 1,200 species are recognized (Myrtaceae in Flora e Funga do Brasil, 2025).

The study performed by Lucas et al. (2007), considering embryo characteristics, average number of ovules per ovary, placentation, and vessel elements, combined with biogeography and molecular data, organized the tribe Myrteae into seven informal subtribal groups: *Plinia, Eugenia, Myrcia, Myrceugenia, Myteola, Pimenta,* and Australasian. Vasconcelos et al. (2017) reformulated the cladistic organization of Lucas et al. (2007). Based on this hypothesis, Lucas et al. (2019) proposed a new classification for the tribe Myrteae, in which the three subtribes proposed by Berg (1885–1886; 1857–1859), Myrciinae, Eugeniinae, and Myrtinae, were added to the subtribes Pimentinae, Ugninae, Luminae, Pliniinae, Blepharocalycinae, and Descasperminae.

The understanding of evolutionary relationships in Myrteae is based on analyses combining molecular data and morphological descriptions of reproductive organs, mainly floral ones, with emphasis on those developed by Lucas et al. (2007; 2011; 2018), Snow et al. (2011), Mazine et al. (2014), Mazine et al. (2016), Mazine et al. (2018), Giaretta et al. (2019), Vasconcelos et al. (2015; 2017), Vasconcelos et al. (2018), Vasconcelos et al. (2019). Despite these advances, the contribution of anatomical studies to the phylogeny of the family and tribe remains largely unexplored.

Some floral characters were examined for this purpose or for descriptive purposes, with an emphasis on studies addressing the vascularization of the gynoecium and/or describing other floral anatomical characters (Schmid 1972a,b,c; Volgin & Stepanova, 200Martos et al.04; Khalifa et al., 2009; Costa et al., 2010; Pires & Souza 2011; Pimentel et al., 2014; Martos et al., 2017; Harthman et al., 2018; Carneiro et al., 2024).

Considering that more anatomical studies of reproductive organs can provide data for better and safer interpretations regarding the evolution of some characters, this work comparatively describes the floral anatomy of 10 Myrteae species to assist in characterizing the species and subsidizing future phylogenetic questions about the family.

Materials and methods

Flower buds at the pre-anthesis stage and flowers at anthesis of 10 species belonging to eight subtribes of Myrteae *sensu* Lucas et al. (2019) were used (Table 1). Almost all the botanical material originated from vouchers deposited in the collections of the Municipal Botanical Museum of Curitiba (MBM) and the Herbarium of the State University of Maringá (HUEM), duly identified by specialists in the family.

Table 1. Studied species of tribe Myrtae used in the floral anatomy analyses, and their respective vouchers and collector numbers.

Subtribe	Taxon	Voucher	Collector
Eugeniinae	*Eugenia uniflora* L.	HUEM 21658	Romagnolo, MB 3252
		HUEM 28729	L.G. Polizelli s.n.
Pimentinae	*Acca macrostema* (Ruiz & Pav. ex G.Don) McVaugh	MBM 87478	Landrum, LR 4572
		MBM 87479	Landrum, LR 4568
		MBM 87480	Landrum, LR 4574
	Psidium oligospermum Mart. ex DC.	MBM 333830	Guedes, ML; et al.
		MBM 345839	Ribeiro, T; et al. 485
Ugninae	*Myrteola nummularia* (Lam.) O.Berg	MBM 148897	Pedersen, TM 14275
Luminae	*Myrceugenia oxysepala* (Burret) D.Legrand & Kausel	MBM 80127	Kummrow, R 2150
		HUFSJ 2254	Hatschbach, G; Barbosa, E & Costa, EF 79111
	Myrceugenia ovalifolia (O.Berg) Landrum	MBM 388010	Uhlmann, A 484
		MBM 390609	Brotto, ML 1618
Myrciinae	*Myrcia legrandii* A.R.Lourenço & E.Lucas	MBM 39865	Hatschbach, G 13127
		MBM 39866	Hatschbach, G 7744
Pliniinae	*Plinia rivularis* (Cambess.) Rotman	MBM 66539	José, 182
		MBM 297133	Barbosa, E; Costa, EF 964
Blepharocalycinae	*Blepharocalyx salicifolius* (Kunth) O.Berg	MBM 346074	Chagas; Silva, F; et al. 2024
		MBM 347724	Staggemeier, VG 65
		MBM 387731	Lozano, ED; Saridakis, DP 2032
Myrtinae	*Myrtus communis* L.	MBM 98991	Lewalle, J 10337

Nine genera were analyzed according to availability: *Acca* O.Berg, *Blepharocalyx* O.Berg, *Myrcia* DC. ex Guill., *Eugenia* P.Micheli ex L., *Myrceugenia* O.Berg, *Myrteola* O.Berg, *Myrtus* Tourn. ex L., *Plinia* Blanco, and *Psidium* L. *Eugenia* specimens were collected and fixed in a formaldehyde, acetic acid, and 50% ethanol solution (FAA 50) for one day, after which they were stored in 70% ethanol (Johansen, 1940). Branches were herborized and deposited at HUEM. Depending on material availability, samples of one to three individuals per species were analyzed. The description included a comparison of the cut materials, which was repeated to increase the reliability of the presented results.

The dried herbarium buds and flowers underwent the herborization reversal process (Smith & Smith, 1942) and were stored in 70% ethanol (Johansen, 1940). For the accomplishment of the anatomical studies, all the material was embedded in historesin following the manufacturer's instructions. Serial cross-sections and longitudinal sections were cut to a thickness of 7 µm using a manual rotary microtome. The sections were stained with Toluidine blue in an acetate buffer solution at pH 4.7 (O'Brien et al., 1964).

The prepared slides were examined using a Leica DM 500 microscope, coupled with a Leica ICC50 digital microscope camera and Leica Application Suite software, version 1.8.

The term hypanthium is defined according to Dahlgren and Thorne (1984), who characterized the true hypanthium in Myrtales as a cup-shaped extension that originates from the floral tube or receptacle, regardless of the position of the ovary. The terms gynoecial hypanthium (the portion fused to the ovarian wall) and perigynous hypanthium (the free portion) are in accordance with Leins et al. (1972). In our descriptions of the inferior ovary (formed by the gynoecial hypanthium and carpel tissue), we recognize the same layers as in a gynoecium with a superior ovary, as described by Carneiro et al. (2024): the outer epidermis, the ovarian mesophyll, and the inner epidermis that delimit the locule.

Results

Table 2 summarizes the comparative data of the floral parts examined and described for the Myrteae species.

Table 2. Comparative floral anatomy of species representing the subtribes of the Tribe Myrteae *sensu* Lucas et al. (2019). (Subtribes: 1. Myrtinae, 2. Blepharocalycinae, 3. Pliniinae, 4. Myrciinae, 5. Luminae, 6. Ugninae, 7. Pimentinae, 8. Eugeniinae).

Taxon	Trichomes						Vascular bundles					Druses					Gynoecium		
	Pd	Br	Ov	Hy	Sp	Pt	Br	Rp	Sp	Pt	St	Pd	Ov	Hy	Sp	Pt	Lc	Ol	Plac
^{1}*Myrtus communis*	-	-	-	-	#	#	3	9	#	#	6	+	-	#	#	#	3	> 2	#
^{2}*Blepharocalyx salicifolius*	-	*	-	-	-	-	*	8	5	3	4	+	+	+	-	-	2	> 2	lower
^{3}*Plinia rivularis*	-	*	-	-	±	±	*	10	5	5	4	-	-	+	-	-	2	2	lower
^{4}*Myrcia legrandii*	+	*	+	-	-	#	*	10	*	*	6	±	+	-	*	*	2	2	lower
^{5}*Myrceugenia ovalifolia*	+	±	+	+	±	-	1	9	3	3	6	+	+	+	+	+	3	> 2	lower
^{5}*Myrceugenia oxysepala*	+	±	+	+	+	-	3	9	7	3	5-7	+	+	+	-	#	3	> 2	lower
^{6}*Myrteola nummularia*	-	-	-	±	#	#	1	10	#	#	6-7	+	+	-	#	#	3	> 2	#
^{7}*Acca macrostema*	+	±	±	±	+	-	1	8	5	5	6-7	-	-	-	-	-	2	> 2	upper
^{7}*Psidium oligospermum*	-	*	-	-	#	#	*	10	#	#	6	+	+	#	#	#	3	> 2	upper
^{8}*Eugenia uniflora*	-	±	-	-	-	+	1	8	9	9	2	+	+	+	-	-	2-3	> 2	upper

+ = present; - = absent; ± = few; # = character not described by the authors or not observable in the analyzed material; * = missing structure; Br = bracteole; Fl = stamen filament; Hy = hypanthium; Lc = number of carpels and locules; Ov = ovary; Ol = number of ovules per locule; Pd = pedicel; Plac = placenta position (lower or upper half of the central axis of the ovary); Pt = petal; Pr = perianth; Rp = receptacle; Sp = sepal; St = style.

General aspect of the flower

Dichlamydeous flowers have four sepals and four petals that are individualized during anthesis, except in *Myrcia legrandii* and *Myrceugenia ovalifolia*, which open as a calyptra. The ovary is inferior and fused to the gynoecial hypanthium wall (Figure 1A-G).

Placentation is axial, and the ovules are arranged in longitudinal rows. The placenta is prominent in *Acca macrostema* (Figure 1A) and *Psidium oligospermum* (Figure 1B). In these two species and in *Eugenia uniflora* (Figure 1C), the placenta is positioned in the upper half of the central axis of the ovary. In *Myrceugenia ovalifolia, M. oxysepala* (Figure 1D), *Myrcia legrandii* (Figure 1E), *Blepharocalyx salicifolius* (Figure 1F), and *Plinia rivularis* (Figure 1G), the placenta is placed in the lower half of the central axis of the ovary.

The style length is variable and associated with the length of the perigynous hypanthium; its apex is curved in the floral bud (Figure 1G). The androecium consists of numerous stamens arranged over the perigynous hypanthium with straight or curved filaments facing downwards in the floral bud (Figure 1F-G).

Floral anatomy

Pedicel

The floral pedicel presents a circular outline that becomes elliptical at the node where the bracteoles originate (Figure 2A-B). It is covered by uniseriate epidermis and tector trichomes in four species (Figure 1A, D-E; 2B-D). The trichomes are simple in *Acca macrostema* (Figure 2C) and dibrachiate (T-shaped) in *Myrceugenia ovalifolia*, *M. oxysepala* (Figure 1D), and in *Myrcia legrandii* (Figure 1E and 2D).

The cortex and medulla are parenchymatous in *Psidium oligospermum* (Figure 2A), *Acca macrostema* (Figure 2B), *Myrcia legrandii* (Figure 2D), *Eugenia uniflora*, *Myrceugenia ovalifolia,* and *Plinia rivularis.* In *Psidium oligospermum* (Figure 2A) and *A. macrostema* (Figure 2B), sclereids occur in the medulla. Spongy parenchyma is present in the cortex and medulla of *M. oxysepala, Miyrteola nummularia* (Figure 2E), and *Myrtus communis*, but only in the medulla of *Blepharocalyx salicifolius* (Figure 2F-G).

Subepidermal secretory cavities (Figure 2A-B, D-E) are observed in all taxa, and may occur more internally, whereas druses (Figure 2D, G) occur in seven species (*Blepharocalyx salicifolius*, *Myrcia legrandii*, *Eugenia uniflora*, *Myrceugenia ovalifolia*, *M. oxysepala*, *Myrteola nummularia,* and *Psidium oligospermum*).

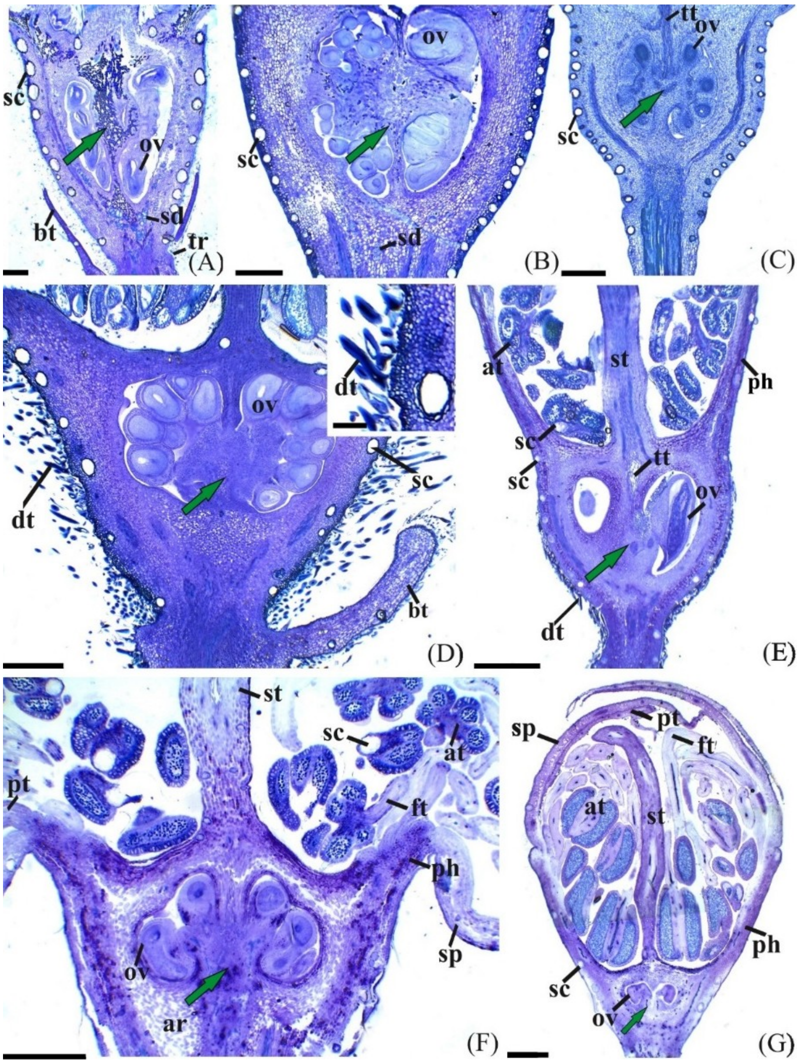

Figure 1. General aspects of floral buds in longitudinal sections of Myrteae representatives. A. *Acca macrostema*. B. *Psidium oligospermum*. C. *Eugenia uniflora*, D. *Myrceugenia oxysepala*. E. *Myrcia legrandii*. F. *Blepharocalyx salicifolius*. G. *Plinia rivularis*. Note that the placenta occupies a medial position in A, B, and C, and a basal position in D, E, F, and G. Note the dibrachiate tector trichome detail in the upper right corner of D. In G, note that both the style and the stamen filaments are curved in the flower bud (ar: aerenchyma; at: anther; bt: bracteole; dt: dibrachiate tector trichome; ft: stamen filament; ov: ovule; ph: perigynous hypanthium; pt: petal; sc: secretory cavity; sd: sclereids; sp: sepal; st: style; tr: simple tector trichome; tt: transmitting tissue; green arrow: placenta height. Scale bars: 500 μm).

Bracteole

At the base of the flower, the siphonostele of the pedicel divides, generating two gaps, from which a vascular bundle moves to each of the two opposite bracteoles (Figure 3A). In *Myrtus communis* and *Myrteola nummularia,* the bracteoles are alternate.

The bracteoles have a concave-convex contour in cross-section, covered by uniseriate epidermis (Figure 3B-G), with convex-papillary outer periclinal wall on the abaxial surface in *Myrceugenia oxysepala* (Figure 3C), and *Myrteola nummularia*. No bracteoles were observed on the peduncle of *Myrcia legrandii*, *Blepharocalyx salicifolius*, *Plinia rivularis,* and *Psidium oligospermum*.

Dibrachiate tector trichomes occur on both faces, with a higher density on the abaxial surface in *Myrceugenia ovalifolia* and *M. oxysepala* (Figure 3B). Simple tector trichomes occur on the margins in *Eugenia uniflora* (Figs. 3D-E). These simple trichomes are rare and only occur on the abaxial surface in *Acca macrostema* (Figure 3G). The bracteole is glabrous in *Myrteola nummularia* and *Myrtus communis* (Figure 3F).

The mesophyll is homogeneous parenchymatous in *Eugenia uniflora* (Figure 3D-E), *Myrteola nummularia, Acca macrostema* (Figure 3G), and *Myrceugenia ovalifolia*. In *M. oxysepala*, it is dorsiventral (Figure 3B-C), and in *Myrtus communis* (Figure 3F), it is filled with homogeneous spongy parenchyma. Subepidermal secretory cavities (3B-C, G) are present in all species, whereas druses (Figure 3D-E) were observed in seven species (Table 2).

In general, bracteoles are vascularized by a single collateral vascular bundle of larger caliber, though smaller ones may occur (Figure 3B, F).

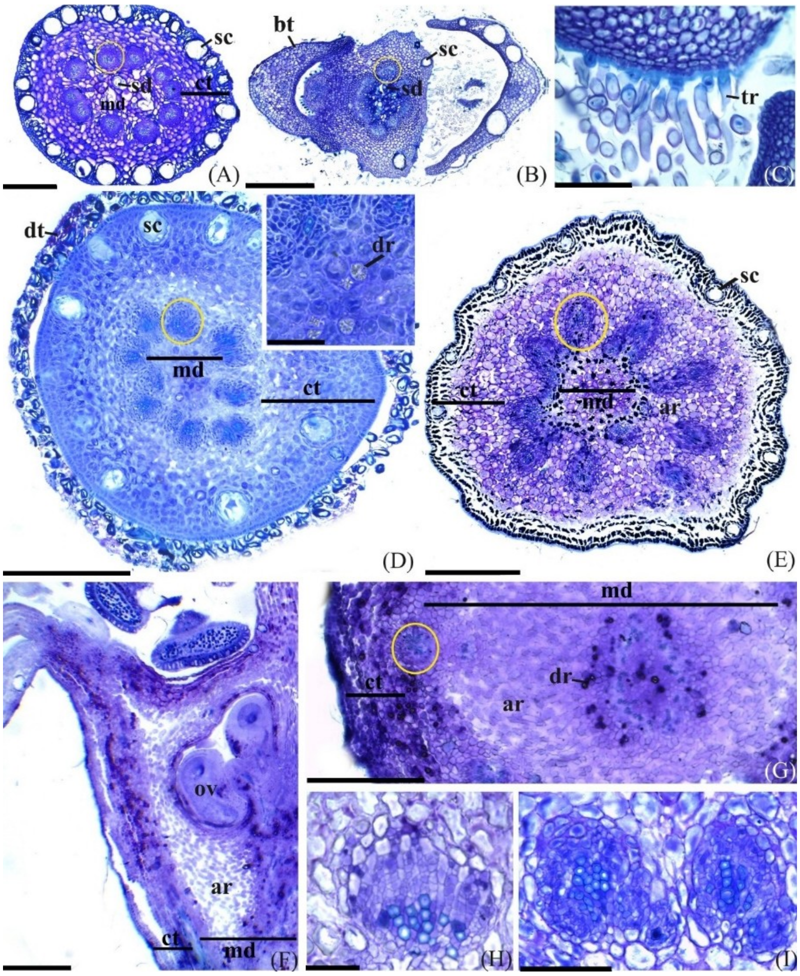

Figure 2. General aspects (A-B, D-G) and details (C, H-I) in cross sections of the pedicel (A-E, G-I) and longitudinal section of the ovary (F) in Myrteae. A. *Psidium oligospermum.* B-C. *Acca macrostema.* D, I. *Myrcia legrandii.* E. *Myrteola nummularia.* F-G. *Blepharocalyx salicifolius.* H. *Myrceugenia ovalifolia.* Note the parenchymatic cortex and medulla and medullary sclereids in A-B. In C-D, note the simple (C) and dibrachiate (D) trichomes. In A-B and D-E, the vascular bundles present an eustelic organization. In D, the cortex and medulla are parenchymatous, and crystal idioblasts containing druses occur in these regions (detail of the medulla in the upper right). In E, note the aerenchyma in the cortex and medulla, and in F-G, only in the medulla. In H, the vascular bundle is collateral, and in I, it has a U-shaped outline (ar: aerenchyma; bt: bracteole; ct: cortex; dt: dibrachiate tector trichome; ep: epidermis; dr: druse; md: medulla; sc: secretory cavity; sd: sclereid; tr: simple tector trichome; yellow circle: large vascular bundle of the eustele. Scale bars: H = 20 µm, I = 40 µm, C = 100 µm, E = 200 µm, A, D, G = 300 µm, B = 400 µm, F = 500 µm).

Gynoecium

In cross-section, the ovary has a circular outline, except in *Myrceugenia oxysepala* (Figure 4A), where it is octagonal with edges, and in *Eugenia uniflora* and *Myrteola nummularia* (Figure 4B), where it is slightly angular. The outer epidermis is uniseriate, with simple tector trichomes in *Acca macrostema* (Figure 1A, 4C). These tector trichomes are dibrachiate in *Myrcia legrandii* (Figure 1E, 4D), *Myrceugenia ovalifolia* (Figure 1D, 4E), and *M. oxysepala* (Figure 4A). The inner epidermis is also uniseriate and glabrous.

The ovarian mesophyll consists of three regions: an outer region, a median region, and an inner region. These regions are parenchymatous in *Myrceugenia oxysepala* (Figure 4A), *Acca macrostema* (Figure 4C), *Myrcia legrandii* (Figure 4D), *Eugenia uniflora*, *Plinia rivularis* (Figure 4F), and *Psidium oligospermum*. In *Myrteola nummularia* (Figure 4B) and *Myrtus communis*, the median and inner regions of the ovarian mesophyll are spongy parenchyma. In *Blepharocalyx salicifolius* and *Myrceugenia ovalifolia* (Figure 4E), the outer and median ovarian mesophyll is parenchymatous, while the inner region is spongy parenchymatous. Secretory cavities (Figure 4A-F) are present in the outer mesophyll of all taxa. Druses are scattered throughout the mesophyll of *A. macrostema*, *B. salicifolius*, *M. legrandii*, *E. uniflora*, *M. oxysepala,* and *P. oligospermum* (Table 2).

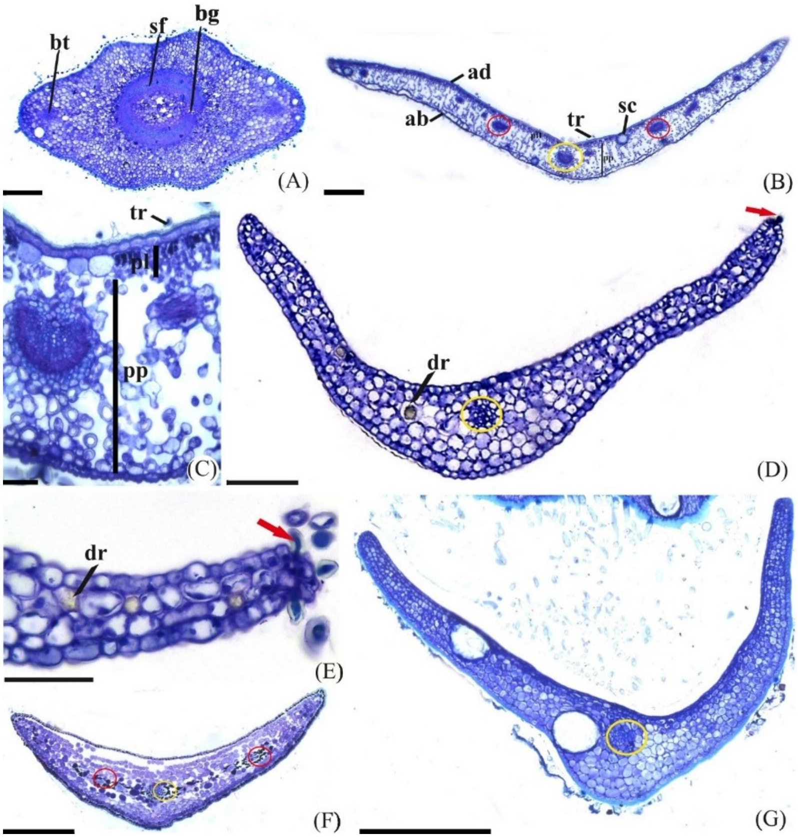

Figure 3. Pedicel node (A) and bracteoles (B-G) in cross sections. General views (A, B, D, F-G) and details (C, E). A. *Myrceugenia ovalifolia*. Note the siphonostele and the vascular trace toward each of the two bracteoles. B-C. *Myrceugenia oxysepala*. The spongy parenchyma is abundant, and there are three larger-caliber vascular bundles. D-E. *Eugenia uniflora*. Note the homogeneous parenchymatous mesophyll, only one vascular bundle of larger caliber, and trichomes on the margin. F. *Myrtus communis*. Note the mesophyll, which is constituted by spongy parenchyma and three vascular bundles of larger caliber. G. *Acca macrostema*. The parenchymatous mesophyll is homogeneous and compact, with only the vascular bundle of the central vein standing out. (ab: abaxial surface; ad: adaxial surface; bg: bracteole gap; bt: bracteole trace; dr: druse; pl: palisade parenchyma; pp: spongy parenchyma; sc: secretory cavity; sf: siphonostele; tr: tector trichome; red circles: lateral veins; yellow circles: vascular bundle of the central vein; red arrow: margin trichome. Scale bars: E = 12 µm, D = 25 µm, C = 50 µm, B, F-G = 300 µm, A = 400 µm).

Vascularization of the gynoecium originates in the conducting vascular bundles of the pedicel siphonostele (Figure 3A), which separate in the vicinity of the ovary base into larger peripheral vascular bundles (Figure 2A-E; Table 2). In the central axis of the ovary, the locules communicate via a compitum that is characterized by septum division that connects one locule to another. In the compitum region, the larger vascular bundles are eight in *Blepharocalyx salicifolius, Acca macrostema* (Figure 4C), and *Eugenia uniflora*; nine in *Myrtus communis*, *Myrceugenia ovalifolia* (Figure 4A), and *M. oxysepala* (Figure 4E), and ten in *Myrteola nummularia* (Figure 4B), *Myrcia legrandii* (Figure 4D), *Psidium oligospermum,* and *Plinia rivularis* (Figure 4F).

The ovary has two carpels, two locules, and two ovules per locule in *Myrcia legrandii* (Figure 4D) and *Plinia rivularis* (Figure 4F). In *Acca macrostema* (Figure 1A, 4C) and *Blepharocalyx salicifolius*, the ovary has two carpels and two locules, as in the previous two species, but each locule contains more than two ovules. The ovary of *Eugenia uniflora* may be bilocular or trilocular, with several ovules per locule (Figure 1B). In *Myrceugenia oxysepala* (Figure 4A), the ovary is trilocular throughout its length, as are the ovaries of *M. ovalifolia* (Figure 4E), *Myrtus communis*, *Psidium oligospermum,* and *Myrteola nummularia* (Figure 4B), with several ovules per locule.

The ovule is anatropous, tending to campylotropous, in *Psidium oligospermum* (Figure 5A), *Acca macrostema,* and *Myrteola nummularia*; it is campylotropous in other species (Figure 5B). The ovule is bitegmic, except in *Eugenia uniflora*, and the funicle is short. In the median region of the ovule, the outer integument has two to three layers of cells, and the inner integument has two layers (Figure 5A-C). These layers increase near the zig-zag micropyle (Figure 5D).

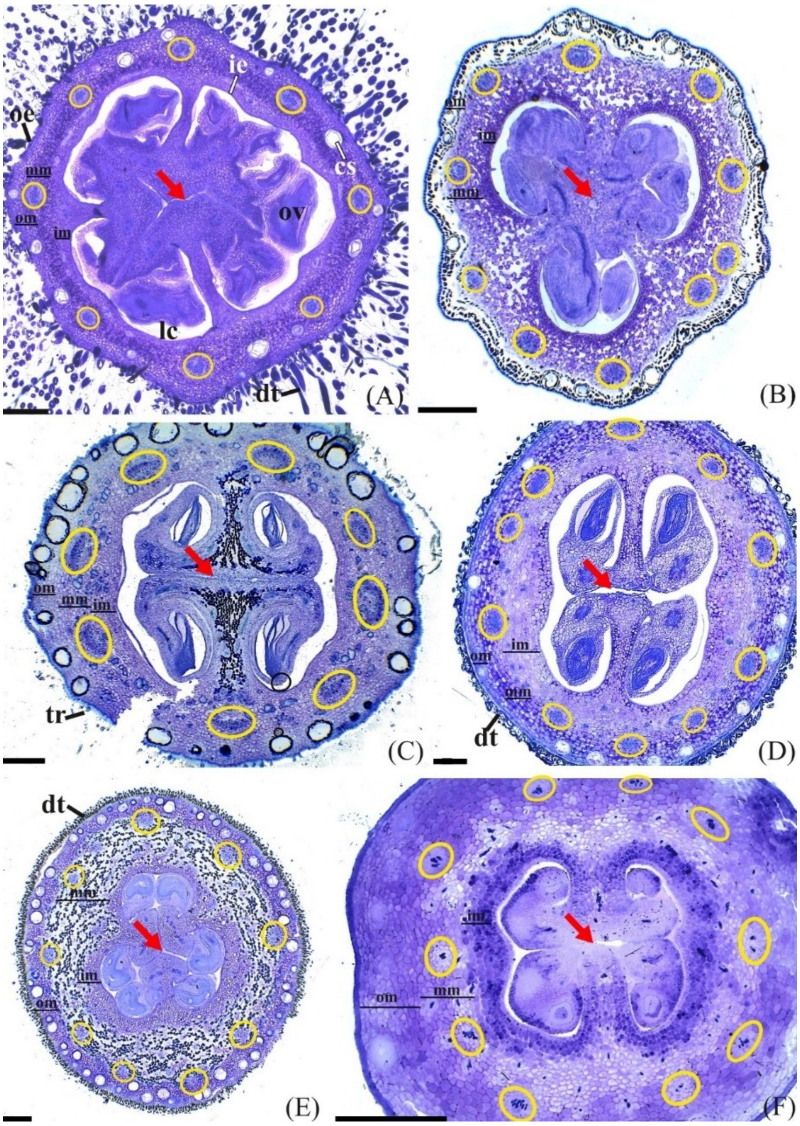

Figure 4. General aspect of the ovaries in cross sections in the compitum region. A. *Myrceugenia oxysepala*. Note the octagonal aspect, the outer epidermis with long, thick-walled dibrachiate trichomes, and the homogeneous parenchymatous ovarian mesophyll. B. *Myrteola nummularia*. Note the slightly angular aspect, the glabrous epidermis, and the median ovarian mesophyll composed of spongy parenchyma. C. *Acca macrostema*. Note the sclereids in the median ovarian mesophyll and the simple tector trichomes. D. *Myrcia legrandii*. Note the dibrachiate tector trichomes on the outer epidermis. E. *Myrceugenia ovalifolia*. Note the dibrachiate tector trichomes on the outer epidermis, the homogeneous parenchymatous outer and median ovarian mesophyll, and the spongy inner parenchymatous mesophyll. F. *Plinia rivularis*. Note the homogeneous parenchymatous mesophyll (dr: druse; dt: dibrachiate tector trichome; ie: inner epidermis; im: inner ovarian mesophyll; lc: locule; mm: median ovarian mesophyll; oe: outer epidermis; om: outer ovarian mesophyll; ov: ovule; sc: secretory cavity; tr: simple tector trichome; yellow circle: larger vascular bundles; red arrow: compitum. Scale bars: A = 200 µm, B-F = 300 µm).

The compitum is covered by transmitting tissue (Figure 4A-F). Toward the apex of the ovary, the compitum decreases, leaving a small slit with loose transmitting tissue, composed of elongated cells (Figure 5E-H).

The style shows an uniseriate epidermis and parenchymatous tissue (Figure 5I), except in *Myrtus communis* (Figure 5J) and *Blepharocalyx salicifolious* (Figure 5K), where collenchymatous tissue is present. The central transmitting tissue is loose within the central axis of the ovary (Figure 5I-K). The number and type of vascular bundles that vascularize the style vary within and between species (Figure 5I-K, Table 2), and may be collateral or U-shaped collateral.

Perigynous hypanthium

The perigynous hypanthium has an outer and inner uniseriate epidermis (Figure 6A-D). Tector trichomes were observed in large numbers in the outer and inner epidermis of *Myrceugenia ovalifolia* (Figure 6A), *M. oxysepala,* and *Acca macrostema.* In *Myrteola nummularia*, trichomes in the inner epidermis occur at a lower density. The other taxa are glabrous (Figure 6C-D).

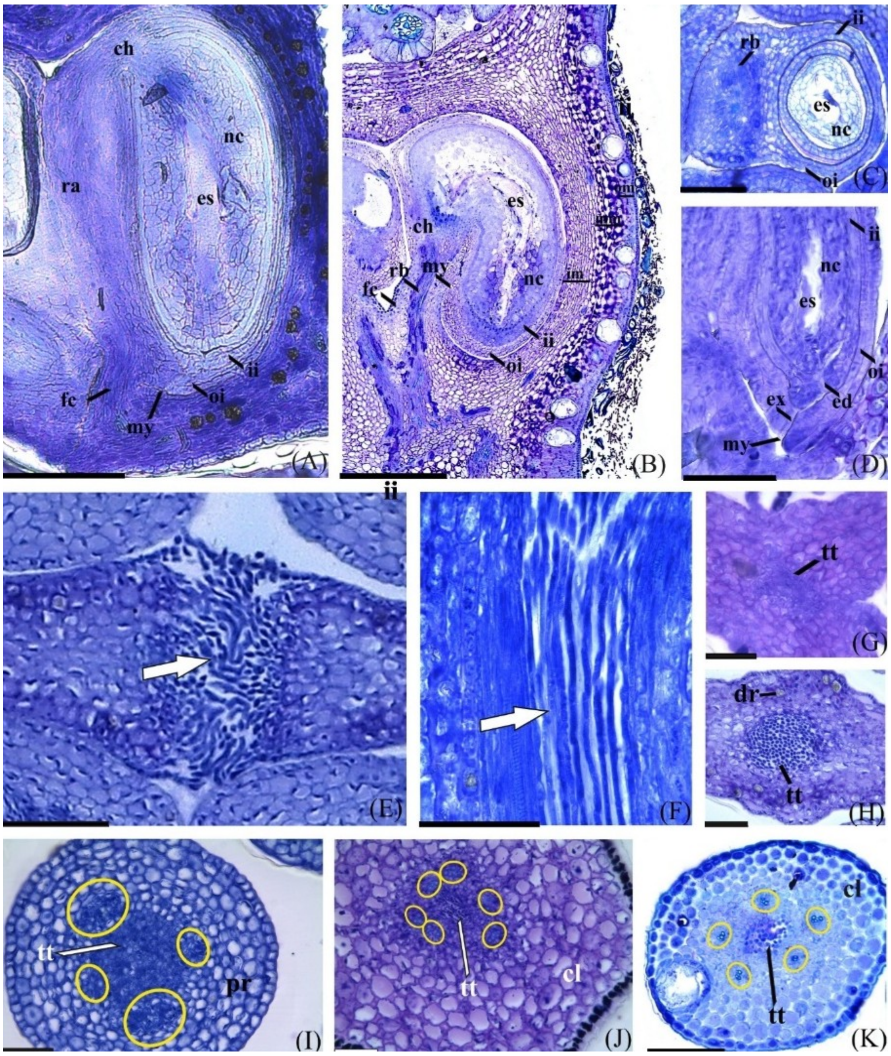

Figure 5. Longitudinal (A-B, D, F) and cross (C, E, G-K) sections of the ovule (A-D), central axis toward the apex of the ovary (E-H) and style (I-K). A. *Psidium oligospermum.* B, E, H. *Myrcia legrandii.* C. *Myrceugenia oxisepala.* D. *Myrteola nummularia.* F. *Myrceugenia ovalifolia.* G, J. *Myrtus communis*. I. *Eugenia uniflora.* K. *Blepharocalyx salicifolius*. A-B. General aspects, highlighting in A the anatropous ovule tending to campylotropous, and in B, the campylotropous ovule. C. Note the outer integument with 2-3 layers of cells and the inner integument with 2 layers in the median region of the ovule. D. A detail showing the 'zig-zag' micropyle. E-H. Central axis above the compitum with loose transmitting tissue consisting of elongated cells. I-K. Note the variation in the number of vascular bundles (ch: chalaza; cl: collenchyma; dr: druse; ed: endostome; es: embryo sac; ex: exostome; fc: funicle; ii: inner integument; im: inner ovarian mesophyll; mm: median ovarian mesophyll; my: micropyle; nc: nucellus; oi: outer integument; om: outer ovarian mesophyll; ra: raphe; rb: rapheal vascular bundle; tt: transmitting tissue; yellow circle: vascular bundle; white arrow: elongated cells of transmitting tissue. Scale bars: G, I-K = 50 µm; C-F, H = 100 µm; A = 150 µm; B = 300 µm).

The mesophyll is parenchymatic in *Acca macrostema*, *Blepharocalyx salicifolius*, *Myrcia legrandii*, *Eugenia uniflora* (Figure 6C), *Myrceugenia ovalifolia*, *Myrtus communis*, *Plinia rivularis* (Figure 6D), and *Psidium oligospermum*. Aerenchyma occurs in the entire mesophyll of *Myrceugenia ovalifolia* (Figure 6A), in an outer position in *M. oxysepala*, and in a central position in *Myrteola nummularia* (Figure 6B). Secretory cavities with varied distributions and sizes were observed in this region (Figure 6A-D). Druses were only observed in *M. oxysepala, B. salicifolius*, *E. uniflora* (Figure 6C), and *P. oligospermum*. Secretory cavities also occur beneath the inner epidermis in *M. legrandii* and *M. communis*.

Immersed in the parenchyma occur vascular bundles of larger caliber (Figure 6A-D), originating from the gynoecial hypanthium, which branch out into the perigynous hypanthium (Figure 6D). They constitute the main bundles of the sepals and petals (Figure 6E).

Androecium

The androecium is formed by several stamens (Figure 1D-G, 6D-E) with filaments that have an uniseriate epidermis, vascularized by a collateral or collateral C-shaped vascular bundle that is immersed in the parenchyma tissue (Figure 6F). Druses were observed in the filaments of *Myrceugenia ovalifolia* (Figure 6F) and

Psidium oligospermum. Between the two anther thecae, the stamen filament tissue continues into the connective tissue (Figure 6G-H). At the anther apex, a secretory cavity is observed (Figure 6H), except in *Eugenia uniflora* and *Plinia rivularis* (Figure 1G).

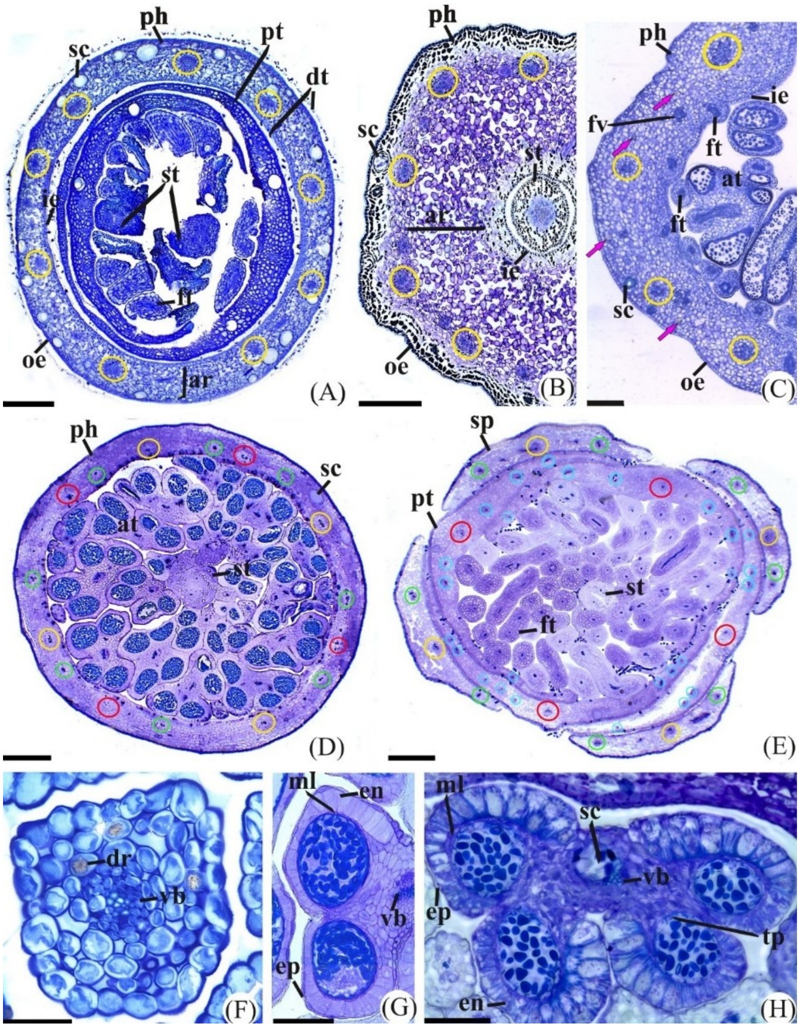

Figure 6. Cross sections of the perigynous hypanthium (A-D), perianth (E), stamen filament (F) and anther (G-H). A, F. *Myrceugenia ovalifolia.* B. *Myrteola nummularia.* C. *Eugenia uniflora.* D-E, G. *Plinia rivularis.* H. *Myrcia legrandii.* A. Note the tector trichomes in the outer and inner epidermis and the mesophyll composed of aerenchymatous tissue. B. Note the central position of the aerenchyma. C-D. Note the glabrous outer and inner epidermis and the mesophyll constituted by homogeneous parenchyma. D-E. Note the individualization of the vascular bundles that will extend to the sepals and petals, as well as their ramifications. F. Note the collateral vascular bundle. G-H. Note the anther layers; the middle layers are crumpling, the tapetum is degenerating, and the endothecium cells thicken and lignify (ar: aerenchyma; at: anther; blue circles: vascular bundles of the minor veins of the petals; dr: druse; dt: dibrachiate tector trichome; en: endothecium; ep: epidermis; ie: inner epidermis; oe: outer epidermis; ft: stamen filament; fv: filament vascular bundle; green circles: vascular bundles of the minor veins of the sepals; ml: middle layers; ph: perigynous hypanthium; pt: petal; red circles: large vascular bundles that run toward the petals; sc: secretory cavity; sp: sepal; tp: tapetum; st: style; vb: vascular bundle; yellow circle: large vascular bundle that run toward the sepals. Scale bars: F = 50 μm; G-H = 100 μm; A-E = 300 μm).

In the floral bud, the anthers are tetrasporangiate with an uniseriate epidermis and an endothecium with an elongated anticlinal wall and lignified thickenings (Figure 6G-H). One or two medium layers collapse, and the secretory tapetum gradually degrades (Figure 6G-H). Druses may be present on the anthers of *Eugenia uniflora*, *Myrceugenia oxysepala,* and *Psidium oligospermum*.

The analysis of the androecium of *Myrteola nummularia*, as well as the average number of layers of the anthers of *Acca macrostema*, *Eugenia uniflora*, *Myrceugenia oxysepala*, *Myrtus communis,* and *Psidium oligospermum*, was not possible.

Perianth

The sepals are fused to form a calyptra in *Myrceugenia ovalifolia* (Figure 7A-B) and *Myrcia legrandii* (Figure 7C). In cross sections, they are convex-concave in shape (Figure 7B, D-E). The epidermis on both faces is uniseriate and may be convex-papillose on the adaxial surface in *Myrceugenia oxysepala* (Figure 7D-E) and on the abaxial surface in *Plinia rivularis* (Figure 7F). Tector trichomes were observed on both surfaces of *M. ovalifolia* (Figure 7A-B), on the abaxial surface and margin of *M. oxysepala* (Figure 7D-E), and on the adaxial surface and margin of *P. rivularis* (Figure 7F). In *Acca macrostema,* the trichomes occur only on the adaxial surface (Figure 7G). In *Blepharocalyx salicifolius*, *M. legrandii,* and *Eugenia uniflora* (Figure 7H), the trichomes are absent.

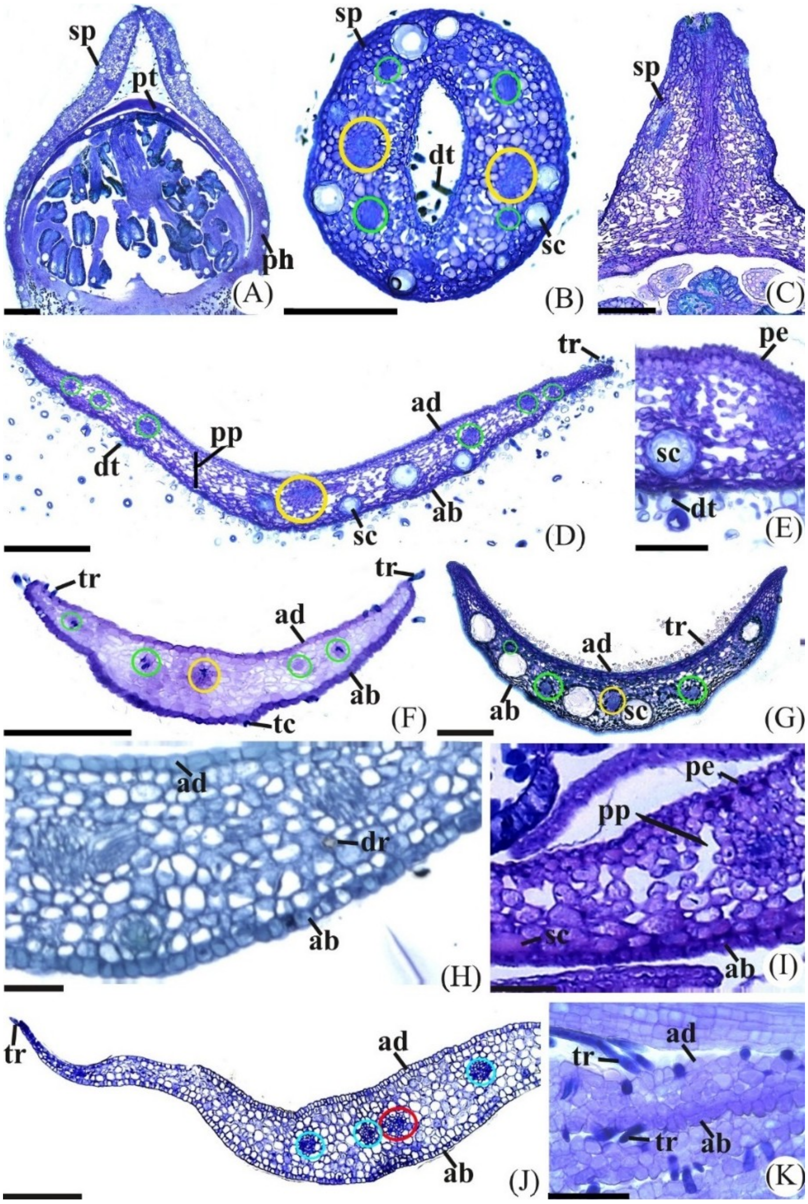

Figure 7. General aspects (A-D, F-G, J) and details (E, H-I, K) of the perianth in longitudinal (A, C) and cross (B, D-K) sections. A-H. Sepals. I-K. Petals. A-B. *Myrceugenia ovalifolia*. C. *Myrcia legrandii.* D-E, I. *Myrceugenia oxysepala*. F, K. *Plinia rivularis.* G. *Acca macrostema*. H, J. *Eugenia uniflora*. A-C. Apex of the floral bud, evidencing the non-individualized sepals that form the calyptra. Note in ‘C’ the central tissue that joins the sepals; D-E. Note the dibrachiate tector trichomes on both faces, and the spongy parenchymatous mesophyll with secretory cavities on the abaxial surface. F. Note the rare simple tector trichomes only on the adaxial surface and margin, and the homogeneous parenchymatous mesophyll. G. Note the higher density of simple tector trichomes on the adaxial surface only. H. Note the glabrous epidermis and the homogeneous parenchymatous mesophyll. I. Note the epidermal cells with convex-papillose contour on the adaxial surface and the spongy parenchymatous mesophyll. J. Note the trichomes on the margins and the homogeneous parenchymatous mesophyll. K. Note the sparse trichomes on both surfaces (ab: abaxial surface; ad: adaxial surface; blue circles: vascular bundles of the minor veins of the petals; dr: druse; dt: dibrachiate tector trichome; green circles: vascular bundles of the minor veins of the sepals; pt: petal; sc: secretory cavity; sp: sepal; tr: simple tector trichome; yellow circle: central vascular bundle. Scale bars: I = 12 μm; H, J = 50 μm; E, G, K = 100 μm; C = 200 μm; D, F = 300 μm; A-B = 500 μm).

The mesophyll of the sepals is homogeneous (Figure 7A-G), and spongy parenchyma occurs in *Blepharocalyx salicifolius*, *Myrceugenia ovalifolia* (Figure 7A-B), *Myrcia legrandii* (Figure 7C), and *M. oxysepala* (Figure 7D-E). Druses can be found in *B. salicifolius* and *Eugenia uniflora* (Figure 7H). Secretory cavities occur in a subepidermal abaxial position (Figure 7A-B, D-E, G).

The vascularization of the sepals is formed by collateral vascular bundles. The central bundle is of a larger caliber, while the others are smaller (Figure 7B, D, F-G).

The petals are also concave-convex in shape (Figure 6E). In *Myrcia legrandii*, the petals are absent. The epidermis is uniseriate on both surfaces (Figure 7I-K), being convex-papillose on the adaxial surface in *Myrceugenia oxysepala* (Figure 7I) and on both faces in *Plinia rivularis* (Figure 6E, 7K). Tector trichomes are only present on the margins in *Eugenia uniflora* (Figure 7J), and are sparse on both surfaces in *P. rivularis* (Figure 7I). The other species are glabrous. The mesophyll is homogeneous (Figure 7I-K), in five of the analyzed species, it is parenchymatic, and spongy in *Myrceugenia oxysepala* (Figure 7I). Secretory cavities are present in most of the studied species (Figure 7I), except in *Eugenia uniflora* (Figure 7J).

A vascular bundle of larger caliber is present in the midrib of the petals (Figure 6E, 7J). Smaller vascular bundles occur on each side of the central one (Figure 6E, 7J). The perianth of *Myrtus communis*, *Myrteola nummularia,* and *Psidium oligospermum* could not be analyzed due to a lack of material.

Discussion

General aspects of the flower

The superior ovary is present in older lineages of the family, such as the tribe Xanthosthemonae, as well as in more recent subfamilies of Myrtaceae, such as the subfamily Heteropyxidoideae (*Psiloxylon* Thouars ex Tul), according to the geological dating pointed out by the study by Thornhill et al. (2015). However, the presence of an inferior ovary in most Myrtaceae has long been recognized (Wilson et al., 2005, 2022), as has been recorded for the studied species. Nevertheless, records of a semi-inferior ovary exist for *Luma apiculata* (DC.) Burret. (Belsham & Orlovich, 2003) and *Myrcia rosangelae* NicLugh. (Lughadha, Lucas, Sobral, & Woodgyer, 2012), species belonging to distinct subtribes of Myrteae. These records suggest that the semi-inferior ovary condition in Myrteae and the superior ovary in Heteropyxidoideae may be a reversion to the ancestral character.

The varying heights at which ovules are inserted in the analyzed species align with the descriptions of Lucas et al. (2007), who observed that, in the Myrteae ancestor, the ovules were attached to a protruding placenta or along a non-peltate placenta in one or more rows, and that they would have originated independently in the Australasian group (Subtribe Decasperminae), *Myrteola* group (Subtribe Ugninae), and *Pimenta* group (Subtribe Pimentinae), and in the genus *Myrcianthes* (Subtribe Eugeniinae). The transition to the arrangement in which the ovules arise from a single point in the septum in the *Eugenia* group (Subtribe Eugeniinae) and in the *Plinia* group + *Algrizea* (Subtribe Pliniinae) + *Myrcia* group (Subtribe Myrciinae) would also have occurred independently (Lucas et al., 2007).

Considering the mid-to-low position of the placenta in the genera of the Subtribes Myrciinnae and Pliniinae, a possible synapomorphy noted by Lucas et al. (2007) can be reinforced. This position was also observed in the two *Myrceugenia* species analyzed (Subtribe Luminae) and in *Blepharocalyx salicifolius* (Subtribe Blepharocalycinae), sister groups to Myrciinnae and Pliniinae (Vasconcelos et al., 2019; Staggemeier et al., 2024). In the phylogeny of Vasconcelos et al. (2017), a specific group was created for *Blepharocalyx* as a sister group to the *Psidium* group (Subtribe Pimentinae). However, in our study, *Psidium oligospermum* had ovules inserted in the upper portion of the septum. Although the nature of placentation has been identified as a character with limited use for defining groups within Myrteae, according to Lucas et al. (2007), placental height appears to be a promising character for evolutionary interpretations, although broader sampling and ontogenetic studies are required to validate its systematic value.

Bracteoles

There are a few anatomical descriptions of bracteoles for the studied groups. In this tribe, the morphology of this structure is important in the delimitation of lower taxonomic categories. For example, in *Eugenia*, bracteole morphology has systematic relevance and can be used for distinguishing recognized sections and species (Bünger et al., 2016; Mazine et al., 2016). In the present study, the existence of bracteoles was not verified in *Plinia rivularis*. This structure merits more attention in future anatomical analyses of all subtribes of Myrteae.

Gynoecium

All analyzed taxa exhibited the monocyclic distribution pattern of larger-caliber vascular bundles in the floral tube, *sensu* Schmid (1972a). This same pattern was described by Pimentel et al. (2014), Martos et al. (2017), and Carneiro et al. (2024). Harthman et al. (2018) described a polycyclic pattern in *Myrcia splendens*

(Sw.) DC, *Luma apiculata* (DC.) Burret, and *Ugni candollei* (Barnéoud) O.Berg. The difference in patterns is due to the region of the flower in which the bundles were analyzed. Importantly, Schmid (1972a) stated that the terms monocyclic, zonocyclic, and polycyclic are better applied to regions of the flower in the vicinity of the locule, since even the zonocyclic flowers, in the most basal region, are monocyclic. Thus, there is a need to standardize the region analyzed for classifying the types of arrangements of the larger-caliber bundles in the floral tube (Carneiro et al., 2024), as was done in the present work.

Among the species examined, four have a bicarpellary gynoecium (*Acca macrostema, Myrcia legrandii, Plinia rivularis,* and *Blepharocalyx salicifolius*), whereas five have three carpels (*Myrteola nummularia, Myrceugenia ovalifolia, Myrceugenia oxysepala, Psidium oligospermum,* and *Myrtus communis*), which is consistent with previous descriptions for the respective genera (Bünger et al., 2012; Pimentel et al., 2014; Martos et al., 2017; Harthman et al., 2018; Vasconcelos et al., 2019; Carneiro et al., 2024). The variation in the number of carpels in *Eugenia uniflora* was also observed by Sbais et al. (2022) in *Eugenia subterminalis* DC., a species that can have two to three carpels. However, in *E. ramboi* D.Legrand, only three carpels were found (Sbais et al., 2022). These results demonstrate that, although this character delimits genera/subtribes, small variations can occur.

The number of ovules found in the studied species aligns with the literature data (Landrum & Kawasaki, 1997; Pimentel et al., 2014; Martos et al., 2017; Vasconcelos et al., 2019; Carneiro et al., 2024). According to Vasconcelos et al. (2019), the presence of two ovules per locule in Myrciinae and Blepharocalycinae is a reduction of multiseriate placentae with a higher number of ovules/locule as observed in many Pliniinae (a sister group to Myrciinae) and in some individuals of *Blepharocalyx salicifolius*, including the specimen analyzed in the present study.

The campylotropous ovule, which occurs in most of the species described in this study, is the most common type found in other species of the tribe (Martos et al. 2017; Sbais et al., 2022; Carneiro et al., 2024).

Perigynous hypanthium

The histology and vascularization of the perigynous hypanthium follow the patterns observed in the literature (Martos et al., 2017; Carneiro et al., 2024), except *Myrceugenia oxysepala* and *Myrteola nummularia,* which present spongy parenchymatous mesophyll. Similar to *Myrcia legrandii* and *Myrtus communis*, Carneiro et al. (2024) describe secretory cavities in the inner portion of the hypanthium in *Myrcia subcordata.* This may be an interesting character to evaluate in future studies.

The position of the stamens, folded within the flower buds, commonly found in Myrtaceae, is explained by ontogenesis (Vasconcelos et al., 2018). During this process, the stamen primordia develop in a restricted manner on the edge of the hypanthium (Vasconcelos et al., 2018). This leaves a gap below the youngest staminal ring during hypanthium expansion, which acquires a cup-like appearance (Vasconcelos et al., 2018). Thus, the positioning of the stamens is a physical phenomenon in which the positive gravitropism doubles the stamens when space is available (Vasconcelos et al., 2018).

Androecium

In all described species, the structure of the stamens reinforced the descriptions found in other studies with Myrteae species (Landrum & Bonilla, 1996; Costa et al., 2010; Pires & Souza, 2011; Martos et al., 2017; Carneiro et al., 2024). There is variation in the presence or absence of secretory cavities in the connective tissue in Myrteae (Carneiro et al., 2024), and this secretory structure is absent only in *Eugenia uniflora* according to the results of the present study and those of Costa et al. (2010), and in *E. pitanga* (O. Berg) Nied. (Martos et al., 2017). Secretory cavities occur in other tribes of Myrtaceae (Ladd, 2024) and are considered a synapomorphy for the family (Stevens, 2001).

Perianth

Costa et al. (2010) and Martos et al. (2017) discussed the anatomy of the sepal in Myrteae and described the mesophyll of the studied species as homogeneous parenchymatous. However, the sepals in *Acca macrostema, Myrcia legrandii, Myrceugenia ovalifolia,* and *Myrceugenia oxysepala* presented spongy parenchymatous mesophyll.

Martos et al. (2017) stated that comparing the vascularization of sepals to that of other species described in the literature reveals a reduction to a single vascular bundle in the most derived clades, according to the topology of Lucas et al. (2007). However, our findings and those of Carneiro et al. (2024) do not support this assertion because the number of vascular bundles in sepals appears highly variable and lacks a clear evolutionary signal.

Indumentum

The distribution of trichomes in different parts of the flower varies within and between species (Table 2) and is useful in infrageneric categories. For example, in *Myrcia*, the presence of trichomes on the inner surface of the hypanthium is taxonomically useful at the section level (Lucas et al., 2018). The results found for *M. legrandii* agree with Lucas et al. (2018) for the *Myrcia* sect. *Calyptranthes*, to which this species is circumscribed, where the inner region of the hypanthium is glabrous.

Conclusion

A comparative analysis of the flowers of the investigated taxa revealed that anatomical traits, particularly placental height, vascular patterning, and the presence of secretory cavities in the inner part of the hypanthium, warrant inclusion in future phylogenetic matrices of Myrteae and may clarify evolutionary transitions within the tribe.

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