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Abstract—With ca. 2500 species, Myrteae is the largest tribe of Myrtaceae and one of the most diverse groups of flowering plants in the tropical Americas. In light of recent systematics adjustments, the present study is a review and provides new insights into floral diversity and evolution in Myrteae. General aspects of floral ontogeny and morphology for the fifty currently accepted genera plus all accepted sections within the large genera *Eugenia* and *Myrcia* are summarized based on current morphological data. The discussion provides a broader understanding of the floral diversity across the tribe, highlighting developmental modes, ecological traits, and specializations in reproductive strategies. Hypotheses to be tested in future studies are also presented and discussed.

Keywords—Androecium, evolution, gynoecium, perianth, morphology, ontogeny.

Myrtaceae are a large angiosperm family, half of the biodiversity (ca. 2500 species; WCSP 2018) occuring within the monophyletic tribe Myrteae (sensu Wilson et al. 2005). Myrteae species are distributed in both the Paleotropics and the Neotropics, with a more expansive diversity (ca. 2000 species) in the latter. This tribe comprises some of the highest diversity of tree species in South American forests and savannas (Oliveira-Filho and Fontes 2000; Françoso et al. 2016; Beech et al. 2017; Cardoso et al. 2017), where it has a critical ecological role as important supplier of flowers and fruit that sustain associated fauna throughout the year (Staggemeier et al. 2010, 2017). Consequently, recent studies have advocated Myrteae as a useful model group for testing hypotheses of biodiversity, ecology, evolution, and conservation in Neotropical environments (Murray-Smith et al. 2009; Giaretta et al. 2015; Lucas and Bünger 2015; Staggemeier et al. 2015).

Despite its important ecological role in some Neotropical habitats, the systematic and evolutionary relationships of Myrteae have been elusive due to high levels of homoplasy, such that characters of taxonomic relevance at the generic level are usually difficult to identify (McVaugh 1968; Landrum and Kawasaki 1997). Initial molecular phylogenetic studies (Lucas et al. 2005, 2007) showed that characters traditionally used, such as the embryo type (Berg 1855–1856), had little power to accurately explain relationships in Myrteae and that morphologically characterized natural groups were few and poorly understood. Given recent systematic rearrangements in the tribe (Lucas et al. 2007, 2018, 2019; Mazine et al. 2016; Vasconcelos et al. 2017b), a search for characters that diagnose monophyletic groups is highly desirable. Recent studies (e.g. Vasconcelos et al. 2015) demonstrate that despite its apparent homogeneous morphology, some floral traits can help diagnose lineages within Myrteae. The periodic reassessment of morphology in light of recent phylogenies provides reciprocal illumination of patterns and process, and is important for future studies of systematics, ecology, and evolution.

This study aims to summarize data on floral morphological diversity across Myrteae. By assembling information from the literature, herbarium material, floral ontogeny, and field observations, the purpose is to recommend more reliable diagnostic characters to help diagnose genera and subtribes, stimulate debate on form and function, and generate new hypotheses concerning the systematics, ecology, and evolution to be tested by future studies.

Materials and Methods

Buds and flowers of Myrteae were collected in the field and from the living collections and herbarium material at the Royal Botanic Gardens Kew (herbarium K, Thiers 2018). Fruits were analyzed in some cases, but only to emphasize patterns of structures that remain from flowers. Fruits, seeds, and embryo traits, although important in Myrteae systematics (Landrum and Kawasaki 1997), are not the focus here. Floral morphology for forty-three of the forty-nine currently recognized Myrteae genera was surveyed from spirit collections and herbarium material (see Appendix 1). No suitable material bearing flowers could be analyzed for *Acca* (two species), *Amomyrtella* (two species), *Curitiba* (one species), *Lithomyrtus* (11 species), *Myrtella* (two species), or *Pseudanamomis* (one species), so floral morphology in these genera is described from the literature only. All other floral descriptions are based on herbarium specimens, spirit collections (Appendix 1), and literature. For the largest genera (*Myrcia* ca. 800 species, Lucas et al. 2018; *Eugenia*, ca. 1000 species, Mazine et al. 2016), specimens representing all accepted sections also were analyzed. Herbarium specimens surveyed were those identified by specialists. Buds and flowers were boiled to re-hydrate tissues for dissection. Descriptions of anthesis are based on comparison of buds and open flowers from herbarium specimens and field observations during field expeditions between 2013 and 2016.

Discussions of floral ontogeny are based exclusively on specimens preserved in ethanol 70% or FAA in the field. For SEM preparation, buds were dissected and passed through an ethanol series through full dehydratation, critical point dried using an Autosamdri-815B critical-point dryer, mounted on stubs, platinum coated using a Quorum Q-150-T sputter coater, and analyzed under a Hitachi cold field emission SEM S-4700-II.

The topology presented in the section "Taxonomic Treatment" is a schematic drawing that summarizes current understanding of relationships within Myrteae. No phylogenetic analysis was performed here; the tree results merely from visual inspection of topologies presented by different studies. It combines information found in phylogenetic inferences from Lucas et al. (2005, 2007, 2011), Costa (2009), De-Carvalho (2013), Mazine et al. (2014), Bünger et al. (2016), Santos et al. (2017), and Vasconcelos et al. (2017b). Where the support for a relationship was low or where results from different studies disagreed, nodes were collapsed into polytomies.

Results

Bracteoles—Nearly all flowers of Myrtaceae are subtended by two bracteoles. Faria (2014) comments that *Eugenia splendens* may be exceptional for the apparent lack of bracteoles, as they are not visible in most collections of this species even at very early stages of flowering. Bracteoles appear to develop simultaneously in tetramerous species or with a small developmental gap between each bracteole in pentamerous species (Vasconcelos et al. 2017a). At early stages of ontogeny the bracteoles cover the bud completely, but remain relatively small compared to the fully formed bud at late stages of

development. Bracteole morphology has systematic relevance in some groups. In *Eugenia*, for instance, sections can be recognized by the presence of filiform bracteoles (i.e. *Eugenia* sect. *Pilothecium*), whereas others have distinct caducous bracteoles at the fruiting stage (i.e. *Eugenia* sect. *Speciosae*) (Bünger et al. 2016; Mazine et al. 2016).

Perianth (Calyx and Corolla)—The calyx and corolla usually are treated together (e.g. Endress 1994) even though they may have distinct evolutionary histories (Ronse De Craene 2008). Historical taxonomic interest in perianth characters of Myrteae dates to Linnaeus (1753), who divided *Myrtus* from *Eugenia* based on merosity; more recent interest, especially in the calyx (e.g. Landrum 1984, Lucas et al. 2011), reflects some common modifications (e.g. "closed calyces," see below) and its frequent persistence at fruiting. Most floral diversity in Myrteae reflects two types of calyx organization: pentamerous, with classic imbricate quincuncial aestivation (i.e. two sepals outside, two sepals inside, and one intermediate; Figs. 1Ai–iv, 2A); or tetramerous, with two pairs of sepals developing decussately (Figs. 1Bi–iv, 2C). Dimerous flowers are rare, but occur in at least one species of *Blepharocalyx* (*B. eggersii*), which lacks ontogenetic evidence for development of a second pair of sepals and/or petals (Figs. 1Ci–iv, 2D). Perianth development follows a mirror-image proccess in flowers of opposite sides in an inflorescence. In pentamerous species, perianth parts are formed in an imperfectly sequential, spiral process, either clockwise or counterclockwise (Fig. 1D).

Sepals are usually the same size in mature buds, but both pentamerous and tetramerous flowers may have sepals slightly to strongly unequal in size even at late stages. Such size distinctions usually do not significantly change overall floral symmetry (e.g. Fig. 2E), but are taxonomically relevant at the species level in some groups (e.g. Sobral 2005, for *Eugenia inversa*). Complete calyx fusion is homoplastic and appears in a few to several species in different lineages (Fig. 2H, I; e.g. Landrum 1984, in *Myrceugenia*; Parra-O and Bohorquez-Osorio 2016, in *Myrcianthes*). This is achieved by late-congenital fusion, a mode of development where the sepals are initially free but tissues fuse from the base during development. In this way, at late stages of floral development, individual sepals are no longer recognizable and the fully formed calyx appears to cover the bud completely. This character state is named "closed calyx in the bud" in the Myrtaceae literature and is common also in other tribes (e.g. Eucalypteae, Wilson 2011; for evolutionary interpretation of this character see Vasconcelos et al. 2017a, and Giaretta et al. 2019). The anthetic behavior of this structure varies from being a deciduous calyptra to irregular tearing (i.e. tissues tear at random points during anthesis; Fig. 2H) or regular tearing (i.e. tissues tear at points where sepals are adjacent, during anthesis; Fig. 2I), patterns with historical taxonomic relevance (McVaugh 1968; Wilson et al. 2016; Lucas et al. 2018).

The corolla develops after the calyx (i.e. centripetal organ formation). Petals are always alternisepalous and are usually present in the same number as sepals. Flowers with five sepals develop five petals in alternate positions, following the same imbricate quincuncial aestivation pattern (Figs. 1Aiv, 2B). Flowers with four sepals tend to have four petals that are almost simultaneously initiated, in contrast to the decussate pattern of the sepals (Fig. 1Bii, iv). Petals are either rounded or elliptic and are attached to the hypanthium by a short, thickened, and somewhat consticted base, making them fall off easily after anthesis. There are few exceptions in corolla

arrangement among all 50 genera. The most remarkable ones are in the tetramerous genus *Octamyrtus*, where a second corolla whorl and sometimes two to four extra petals develop (up to 12 petals in total; Scott 1978b; Craven 2006; Snow et al. 2011); and in *Myrtus*, where narrow petals develop into a variable number of whorls (Mulas and Fadda 2004).

Shifts back and forth between tetramerous and pentamerous flowers are likely to have occurred multiple times in Myrteae. Variation between four and five perianth parts is commonly observed at infrageneric and even at infraspecific levels (e.g. Fig. 2F, G). The norm, however, is that the lower the taxonomic level the more stable the merosity. Therefore, it is difficult to estimate with precision which pattern is the plesiomophic state for the tribe, but merosity is still an important component of generic identification in Myrteae (e.g. keys in Landrum and Kawasaki 1997, Sobral 2003, and Mazine et al. 2014).

Androecium and Hypanthium Extension—The androecium has historically been neglected in Myrteae systematics. The almost invariable polystemonous flowers produce low noticeable variation in this organ. Therefore, references to the taxonomic relevance of the androecium are virtually absent in classical Myrteae taxonomic literature (even in extensive reviews such as McVaugh 1968 and Landrum and Kawasaki 1997). However, Vasconcelos et al. (2015) show that the androecium harbors valuable taxonomic characters, especially when considered in concert with hypanthium development (e.g. Belsham and Orlovich 2002, 2003; Vasconcelos et al. 2017a, 2018).

The definition of "hypanthium" is inconsistent in the literature. General floral morphologists define the hypanthium as a cup-shaped structure that involves the ovary in perigineous and epigineous flowers (Weberling 1989; Endress 1994). Weberling's hypanthium overlaps with his definition of the floral receptacle, for which he states that the "[perianth and androecium] appear inserted on the edge of the hypanthium, or so called receptacle" (Weberling 1989, p. 20). While some authors prefer to use the term "receptacle" (e.g. Ronse De Craene and Smets 1992, 1993), most Myrtaceae literature adopts the term "hypanthium" to refer to the tissue between perianth and gynoecium (e.g. Proença et al. 2006; Snow and Wilson 2010; Amorim and Alves 2012; Martos et al. 2017). To our knowledge, no study has yet explicitly tested the evolutionary origin of this structure in Myrteae and we also do not aim to solve this issue here. We will here use the same definition as in other Myrtaceae literature, referring to the hypanthium as a tissue between the base of the ovary and the perianth on which the staminal rings are formed.

It is on the inner apical surface of this tissue that stamen primordia appear and stamens of the polyandrous androecium develop (Ronse De Craene and Smets 1991; Belsham and Orlovich 2002, 2003). In this sense, it is impossible to fully separate androecium from hypanthium when discussing floral morphology and ontogeny of Myrteae. In Myrteae, mature flowers present two main hypanthium types: these can be either extend above the ovary line, forming a hypanthium cup or tube (e.g. as in *Myrcia* and *Siphoneugena*), or terminate at the same position as the summit of the ovary (e.g. as in *Eugenia*). Development of these two patterns is similar during floral ontogeny; the difference is mainly the extent to which stamen primordia cover the tissue during early stages of development.

Androecium development in Myrteae starts with the appearance of two (or more) stamen primordia at the flanks of each petal (Belsham and Orlovich 2002, 2003; Vasconcelos et al. 2017a, 2018). Sequentially, more primordia develop
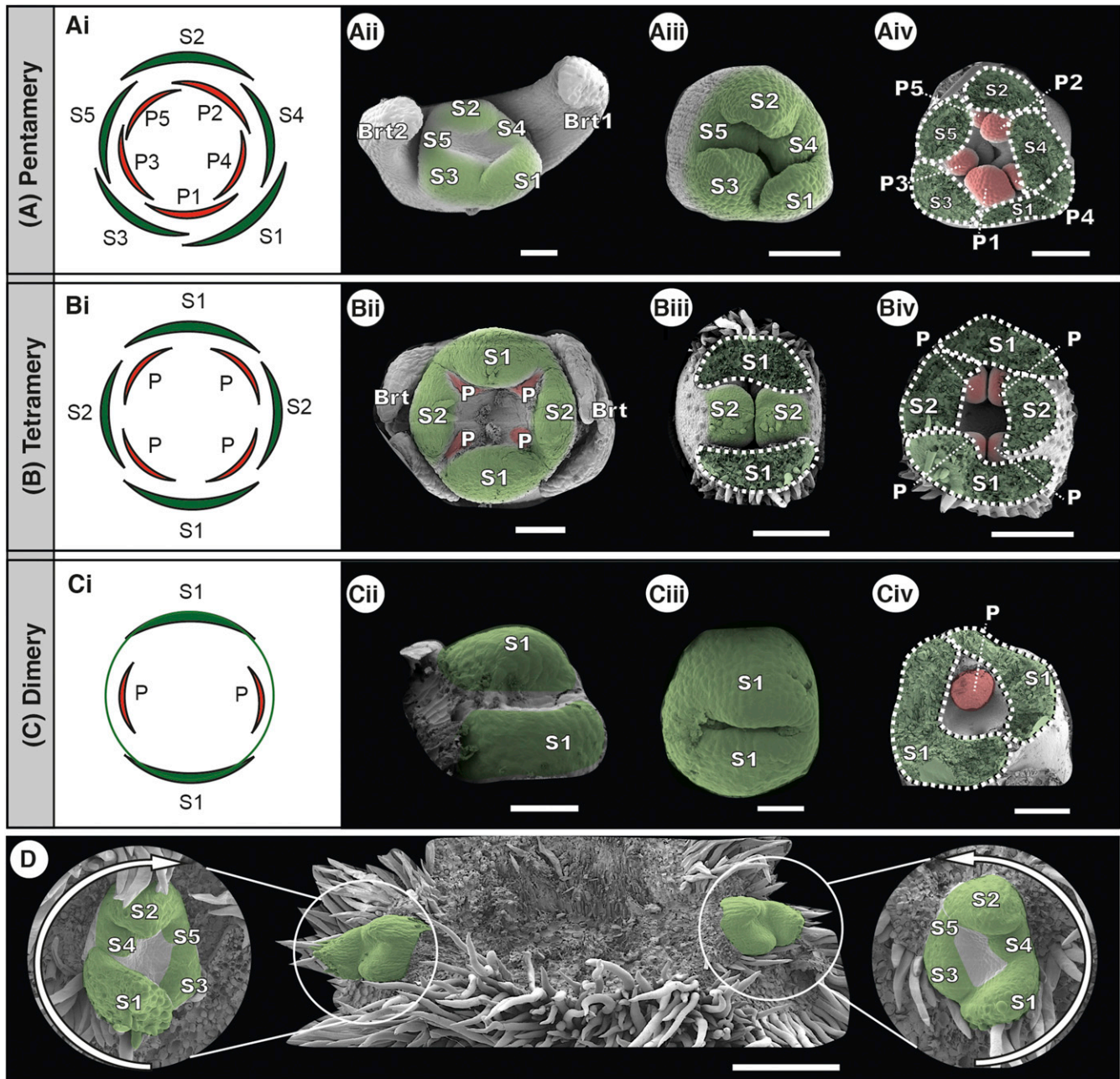
Fɪɢ. 1.   Patterns of perianth arrangement in Myrteae. A. Pentamerous flowers with imbricate quincuncial sepals and petals. Diagram(Ai) and ontogenetic sequence (Aii–Aiv) in *Myrcia guianensis* (*Myrcia* sect. *Aguava*). B. Tetramerous flowers with decussate sepals and four petals that initiate simultaneously. Floral diagram (Bi) and ontogenetic sequence (Bii–Biv) in *Eugenia ligustrina* (*Eugenia* sect. *Eugenia*) (Bii) and *Eugenia stipitata* (*Eugenia* sect. *Pilothecium*) (Biii, Biv). C. Dimerous flowers of *Blepharocalyx eggersii*. Floral diagram (Ci) and ontogenetic sequence (Cii–Civ; two petals initiate in the axils of each sepal, but just one is seen in Biv). D. Clockwise and anticlockwise direction of perianth development in opposite flowers of *Myrcia spectabilis* (*Myrcia* sect. *Gomidesia*), highlighting the mirror-image pattern and imperfectly sequential spiraal development of perianth parts in pentamerous flowers. Dashed outlines represent dissected structures. Brt = bracteole; S = sepals; P = petals. Scale: 50 μm (Aii, Bii, Cii, Ciii); 100μm (Aiii, Aiv, Biii, Civ); 150 μm (Biv, D).

forming the first staminal ring. This is contrary to other Myrtaceae where secondary polyandry occurs and obhaplostemonous primary stamen primordia give rise to secondary stamen primordia (e.g. *Melaleuca*; Carrucan and Drinnan 2000); in Myrteae there is no clear distinction between primary and secondary stamen primordia. After the first staminal ring is formed, more stamen primordia initiate centripetally. The degree to which these primordia cover the inner hypanthial surface determines the final position of the stamens within the flower (Vasconcelos et al. 2015, 2018). When stamen primordia cover the entirety of the hypanthium

tissue up to the stylar base (Fig. 3Ai), stamens in the bud appear straight and no hypanthial tube is visible (Fig. 3Aii–iv). When the stamen primordia cover just a restricted area at the hypanthium rim during development (Fig. 3Ci), stamens fold into the area provided by the "bare" hypanthium tissue, resulting in curved stamens at anthesis and a hypanthium tube of variable length (Fig. 3Cii–iv) (see also Vasconcelos et al. 2018). Straight vs. incurved stamens is a trait with high systematic relevance, explaining some suprageneric relationships recovered by the molecular phylogeny of Myrteae (Lucas et al. 2007; Vasconcelos et al. 2015, 2017b). A third variation is the
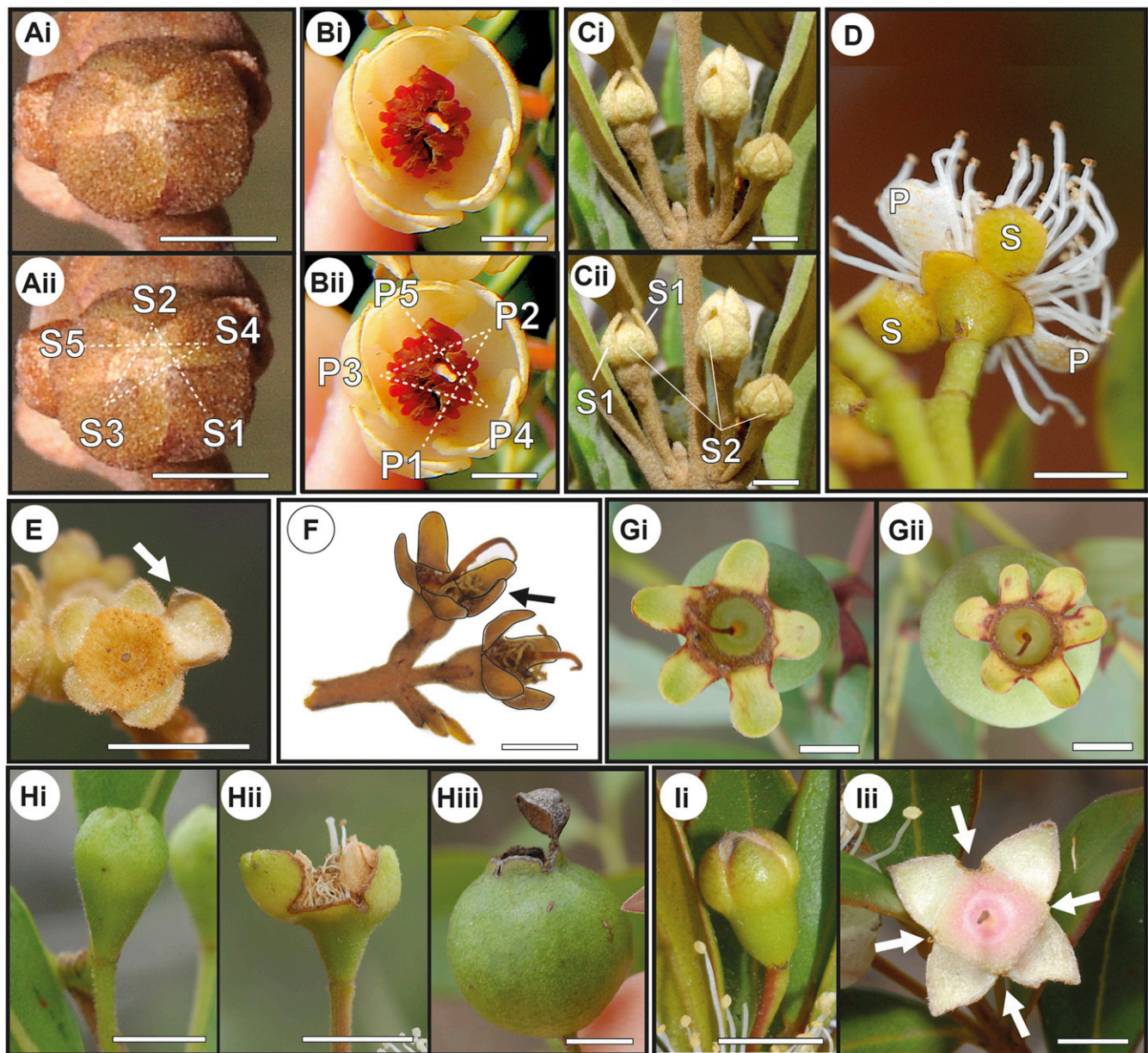
Fig. 2. Field pictures showing diversity of perianth arrangements in Myrteae. A. Buds of *Myrcia* sp. (*M.* sect. *Gomidesia*) showing pentamerous flowers with imbricate quincuncial sepals. B. Flowers of *Ugni candolei*, showing a similar pattern in its petals. C. Young buds of *Myrceugenia alpigena*, showing the first pair of decussate sepals larger than the second pair. D. Dimerous flowers of *Blepharocalyx eggersii*, showing a pair of petals and a pair of sepals. E. Unequal sepals in old flowers of *Myrcia splendens* (*Myrcia* sect. *Myrcia*). F. Variation of merosity in two flowers of the same inflorescence in *Algrizea minor* and (G) in the same individual of *Campomanesia adamantium*. H. Calyx fusion in *Psidum* sp., showing (Hii) torn calyx after anthesis and (Hiii) a calyptra remaining at fruiting stage. I. Partial sepal fusion in *Accara elegans*, showing (Iii) scars from where the sepals tore at anthesis. S = sepals; P = petals. Scale: 2.5 mm (Ai–ii, D, Iii); 5 mm (Bi–ii, Ci–ii, E, F, Gi–ii, Hi–iii, Ii). All pictures by T. N. C. Vasconcelos or E. J. Lucas.

discontinuous androecium observed in *Lenwebbia*, *Luma*, *Myrceugenia, Temu*, and some *Pimenta* species (Belsham and Orlovich 2003), here interpreted as an intermediary arrangement between the straight and incurved stamen types. In these flowers, the first stamens develop from primordia below each petal while only subsequent stamens form a continuous ring (Fig. 3Bi; Belsham and Orlovich 2003). This discontinuous development gives the stamens a posture that has been described as "semi-folded" in the bud (Fig. 3Bii–iv; Vasconcelos et al. 2015).

Anthers are always tetrasporangiate, consisting of four pollen sacs that differentiate at later stages of floral development at the distal portion of each filament. Abaxial pollen sacs are usually smaller than adaxial ones, and latrorse dehiscence occurs by a simple longitudinal slit, with tearing of the thin tissue between each pair of pollen sacs (as in most eudicots; Endress 1994). Anthers are dorsifixed, except in *Ugni* and *Uromyrtus* where they are somewhat basifixed (Snow and Guymer 2001; Wilson 2011). During anthesis, or even slightly before, tissue that connects each pair of pollen sac tears. At this point, the walls of all four locules retract completely, giving an opening of ca. 180 degrees for each lateral pair of pollen sacs. Specialized connectives and dehiscence behavior can occur, e.g. apiculate connectives in some species of *Campomanesia* (Landrum 1986) and disproportionally long anthers with slightly dislocated pollen sacs in *Myrcia* sect. *Gomidesia* (Lucas
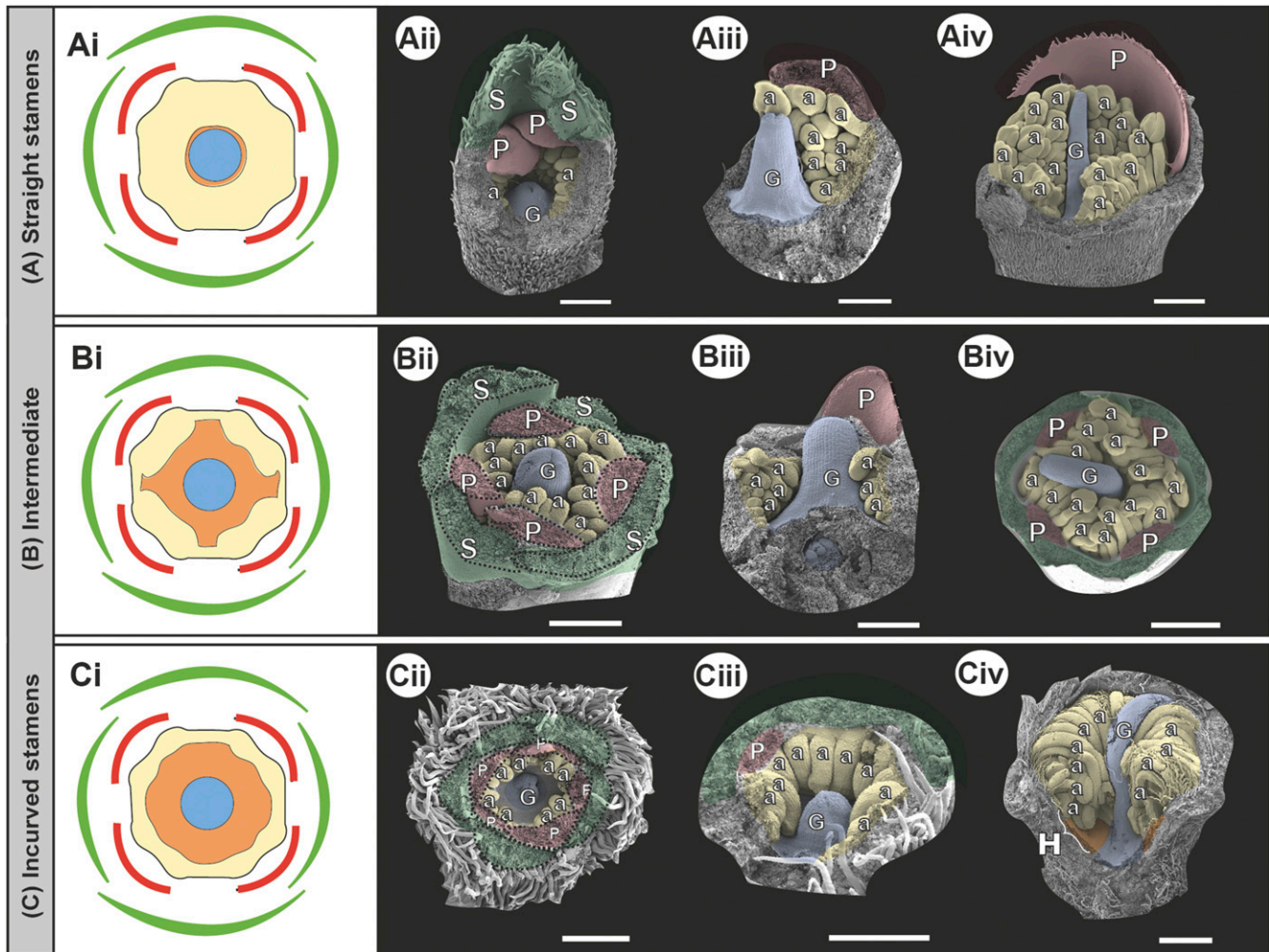
FIG. 3. Three main patterns of stamen formation on the hypanthium in Myrteae. A. Straight stamen developmental pathway, where stamen primordia cover the whole hypanthial tissue. Floral diagram (Ai) and ontogenetic sequence (Aii–iv) in *Eugenia bunchosiifolia* (*E.* sect. *Speciosae*). B. Semi-folded stamen pathway, where stamen primordia arise in discontinuous rings on the hypanthial tissue. Floral diagram (Bi) and ontogenetic sequence (Bii–iv) in *Luma apiculata*. C. Folded stamen developmental pathway, where stamen primordia are restricted to the rims of the hypanthial tissue. Floral diagram (Ci) and ontotogenetic sequence (Cii–iv) in *Myrcia subcordata* (*M.* sect. *Sympodiomyrcia*). A = androecium; G = gynoecium; P = petal; S = sepal. Scale: 10 μm (F); 250 μm (Aii, Aiii, Bii, Biii, Cii, Ciii, E); 500 μm (Aiv, Biv, Civ).

et al. 2011). In the latter, possibly due to uneven growth of the connective (Vasconcelos et al. 2017a), locule wall retraction is not always complete, giving a poricidal aspect associated with adaptation to buzz pollination (Proença 1992; Nic Lughadha 1998). Pollen grains are small to medium sized, usually ranging from 14 μm to 22 μm (except *Octamyrtus*, where pollen grains are up to 44 μm; Thornhill et al. 2012), triangular shaped and brevicolpate, with little variation among most Myrteae lineages (see review by Thornhill et al. 2012).

Gynoecium—The gynoecium is the most variable floral organ in Myrteae. Characters related to the gynoecium are present in buds, flowers, and fruits (when well dissected, locules and aborted ovules can be seen against the ovary wall). Traits of the gynoecium are usually infragenerically consistent and supragenerically variable, highlighting the convenience of this character for taxonomic diagnosis (as discussed by Bentham 1869, and Kausel 1956). During the last decades, several genera were described supported by characters of the gynoecium (e.g. *Accara*, Landrum 1990; *Chamguava*, Landrum 1991; *Gossia,* Snow et al. 2003). Overall gynoecium morphology also has a strong evolutionary component, as it constrains

the width of the stigma (e.g. Fig. 4), the length of the style, and possibly the number of ovules that can be fertilized (see sections *Ovule Oversupply* and *Herkogamy and Strategies to Avoid Selfing* below). Variation in the morphology of this structure is, however, difficult to record. The position of the inferior ovary and distinct patterns of ovule arrangement, placentation, and carpel fusion are only evident when information from transverse, longitudinal, and tangential sections are combined (see Figs. 5, 6).

Early stages of gynoecium development in Myrteae are visible by a depression that appears in the center of the developing flower, simultaneous to androecium initiation. Carpels appear to initiate free, but fuse just after initiation (i.e. late-congenital fusion), so that it is usually possible to recognize how many locules will be formed by the shape of the initial depression (Figs. 4A, B, 5A, B; see also Vasconcelos et al. 2017a, 2018). Tissues around the depression swell sequentially to form a proto-stigma. In species with multiple locules, the depression is larger and consequently the proto-stigma is broader, forming a stigma that is capitate or peltate, contrasting with a usually simple one in species with fewer locules
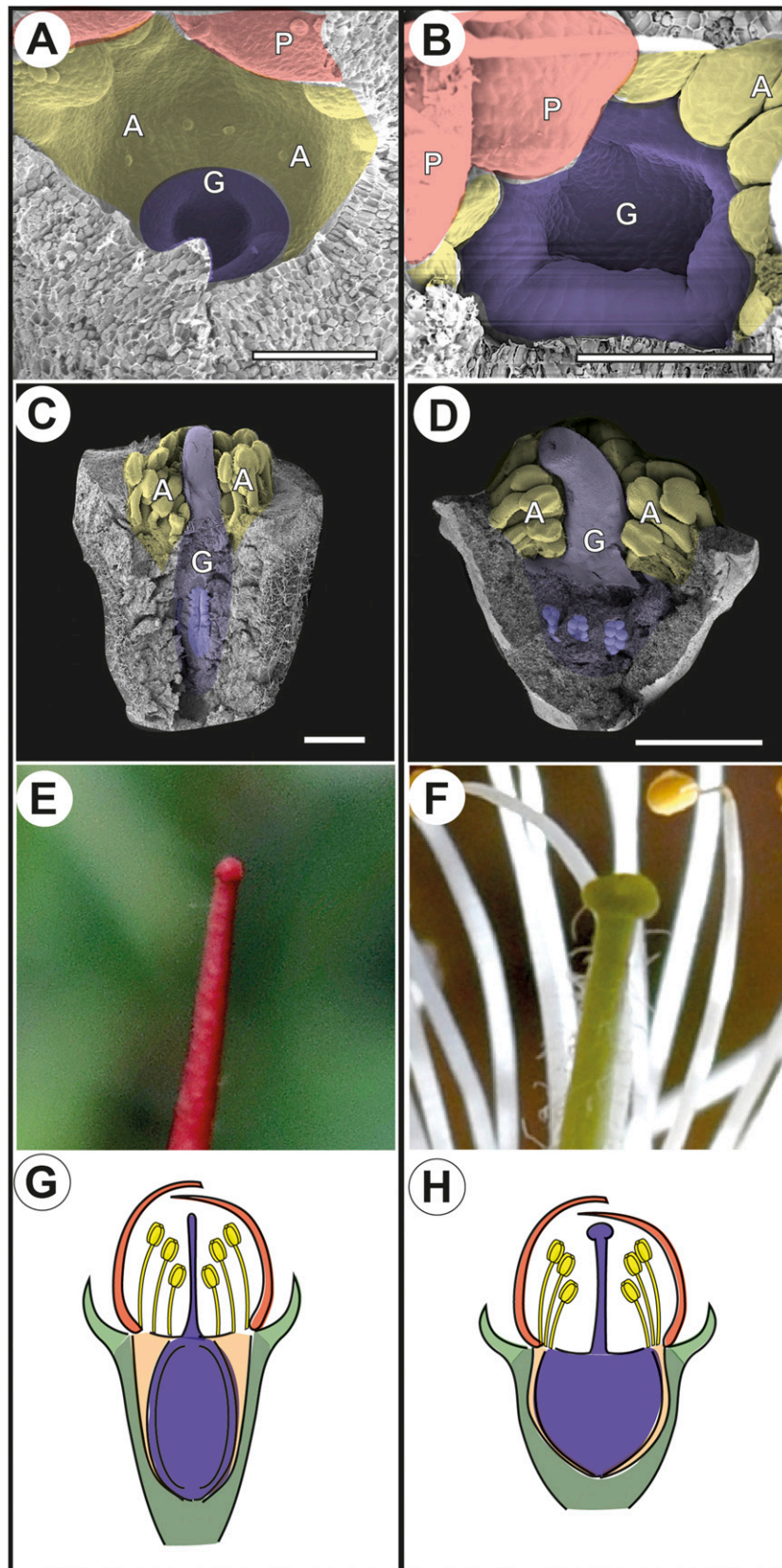
FIG. 4. Distortions in flower architecture caused by differences in the gynoecium development between two closely related genera. A, C, E, G. *Feijoa sellowiana*; B, D, F, H. *Campomanesia adamantium*. A, B. Early flower development, showing a small ovary depression in (A) *F. sellowiana* and a (B) larger one in *C. adamantium*. C, D. Longitudinal section of mature buds; note stamens slightly dislocated upwards in (D) due to the robust gynoecium. E, F. Comparison between (E) simple stigma of *F. sellowiana* and (F) capitate stigma of *C. adamantium*. G, H. Diagram of longitudinal section in mature bud showing changes in architecture resulting from variation in gynoecium development. A = androecium; G = gynoecium; P = petal. Scale: 50 μm (A, B); 250 μm (C); 500 μm (D). Color code: green = sepals, red = petals, yellow = androecium, orange = hypanthium, blue = gynoecium.

FIG. 5. Diagrams of transverse sections of ovaries in Myrteae flowers, showing variation in the number of locules, number of ovule series on placenta, and carpel fusion. A. Number of carpels usually relates to the number of locules, unless fusion is not complete (few exceptions). B. Format of depression left on the base of the bud at early developmental stages, suggesting late-congenital fusion of carpels. C. Arrangement of ovules on placenta varies from uniseriate to multiseriate. D. Examples of incomplete carpel closure. *Psidium* ovule arrangement and placenta format is variable and may range from uni- to multiseriate.

Fig. 6.   Diagrams of tangential and longitudinal sections of ovaries of Myrteae; showing variation in the number of ovule series and of placenta length. Note that variation in number of ovule series on the placenta can only be verified in tangential sections. Examples of tangential sections (i–v) showing (i) uniseriate ovule arrangement on short placenta (*Pimenta pseudocaryophyllus*); (ii) biseriate ovule arrangement on medium sized placenta (*Ugni candolei*); (iii) biseriate ovule arrangement on elongated placenta and incompletely fused carpels (*Feijoa sellowiana*); (iv) multiseriate ovule arrangement on medium sized placenta (*Chamguava shippii*); (v) two ovules over a short placenta (*Blepharocalyx eggersii*).

(Fig. 4A–F). Meanwhile, during early ovary development, each locule forms an individual chamber around the center of the ovary. At this point, a central axis protrudes from the base while an apical septum elongates from the apex, forming a central septum and the locule walls (Pimentel et al. 2014). The point where the central basal axis and apical septum meet can be very tightly closed, or slightly to completely open, providing connection between locules in some genera (e.g. *Feijoa*, *Myrtus*, *Rhodamnia*, Fig. 3D; see also Pimentel et al. 2014, and Harthman et al. 2018).

In most genera, placentation is axial and the placenta develops from the central axis or along the edges of the points where locule walls meet at the center of the ovary. Ovules develop attached to the placenta, and can be uniseriate (Fig. 6i; e.g. most Decasperminae), biseriate (Fig. 6ii; e.g. some Ugninae) or multiseriate (Fig. 6iv, e.g. most Eugeniinae and Myrtinae; see also Fig. 5C). In Myrciinae and some Blepharocalycinae (notably *Blepharocalyx eggersii*), the reduced number of ovules per locule make this character difficult to interpret. Here we hypothesize that the two ovules per locule found in these groups are reductions from multiseriate arrangements with higher number of ovules per locule, as observed in most Pliniinae (sister group to Myrciinae) and some individuals of *Blepharocalyx salicifolius*.

The placenta is itself variable in development and format. In subtribe Pimentinae (e.g. *Feijoa*, *Psidium*) the placenta is frequently well developed, and the diminutive ovules appear organised in crowns around the protruded tissue in tangential dissections (Fig. 6iii). On the other hand, most species of the Myrciinae and Eugeniinae subtribes, for instance, show poorly developed placentas, having ovules that appear to cover the whole placenta tissue in tangential dissections. The shape of the placenta, a character cited as important in some studies (Landrum 1991, 1992; Snow 2000), may be misleading because it distorts when the number of locules changes. In other words, species in the same genus have different placenta shapes depending on the number of locules (as it happens in some *Campomanesia*). The number of ovules per locule and number of locules are commonly variable at lower taxonomic levels, but some evolutionary trends can be useful to diagnose species and genera (e.g. the common two ovules per locule in *Myrcia*, Landrum and Kawasaki, 1997; and the three locules in *Myrcia* sect. *Aguava* and *M.* sect. *Reticulosae*, Lucas et al. 2018).

In conclusion, the systematic importance of the gynoecium includes the following characters: 1) Arrangement of ovules on the placenta (uniseriate, biseriate, multiseriate); 2) Number of locules; 3) Number of ovules per locule; and 4) Stigma type (useful to separate some genera and species, but not always consistent). These characters usually allow identification to a genus or group of genera with reasonable confidence (see Table 1).

Trichomes—Pubescence, a characteristic of most Myrteae flowers, is typically from single-celled trichomes (Fig. 7A) that give a silky appearance to the tissue where they grow. The presence or absence of hairs and where they occur on the floral surface is often taxonomically consistent and thus useful for systematics. Examples include silky appearance of *Myrcia* sect. *Myrcia* buds, in contrast to other *Myrcia* sections (Berg 1855–1856; Lucas et al. 2011, 2018); pubescent flowers of the Decasperminae that distinguish them from other sympatric Myrtaceae in the Australasian region (Ashton 2011); dibrachiate hairs that occur in *Myrceugenia* and *Myrcia* (Landrum 1981a, 1981b) and in some *Eugenia*, *Ugni*, and *Calycolpus*

species (L. Landrum pers. comm.); and hairs on the locular walls in *Eugenia* sect. *Pillothecium* and some *Pimenta* (Fig. 7B; Faria 2014). The evolutionary significance of the presence of these trichomes is not clear, but similar indumenta are associated with protection against predators (e.g. Breedlove and Ehrlich 1972; Fig. 7C) and reflective properties against solar radiation (Miller 1986).

Oil Glands and Elaiophores—Myrtaceae are renowned for their oil glands (Evert 2006; Wilson 2011), and Myrteae flowers are no exception. Oil glands are present in all floral tissues, but can be particularly prominent on the anther, connective, and style wall (Fig. 7F, G; e.g. Landrum and Kawasaki 1997; Snow 2009). These glands lack stomata or clear secretory specialization, but may present some systematic or ecological relevance (suggested by Landrum and Bonilla 1996). Correlation of this character with environmental variables is, however, weakly supported (Vasconcelos et al. 2019). A few species present small cavities on the surface of the floral receptacle around the stylar base (Fig. 7D). These are at a similar position to nectary tissue in other Myrtaceae (O'Brien et al. 1996; Ronse De Craene 2010), but lack clear secretory structures (Fig. 7E; see also Vasconcelos et al. 2018). There is no strong support for nectar production in Myrteae (Gressler et al. 2006); such cavities were shown to be elaiophores in *Myrtus* and suggested as nectary relics that are now only phenolic producers (Ciccarelli et al. 2008). These serve to attract pollinators, and although no evidence for scent acting as reward has ever been documented, some Neotropical bees that visit Myrteae species (e.g. *Euglossini*, Nic Lughadha and Proença 1996) are known to be phenolic foragers (Cameron 2004).

Androdioecy: More Common Than Acknowledged—Most Myrteae flowers are hermaphroditic, with an androecium and a gynoecium developing as previously described. In a few species, however, individual plants within a population bear apparently hermaphrodite flowers while others bear only male flowers. This trend, known as androdioecy, is fairly common in Myrtaceae (see also Ashton 2011, for *Syzygium*). Androdioecious species are present in at least seven Myrteae genera (*Pimenta*, *Psidium*, *Myrcia*, *Eugenia*, *Decaspermum*, *Kanakomyrtus*, and *Myrtastrum*; Van Wyk and Lowrey 1988; Nic Lughadha and Proença 1996; Snow et al. 2003; Wilson 2011; Byng et al. 2016; T. Vasconcelos pers. obs.) and their broad phylogenetic distribution indicates that this trend may be more common than previously appreciated. Plants bearing male flowers produce buds that have either an atrophied gynoecium (Fig. 8) or an additional whorl of stamens at the equivalent position to the gynoecium (T. Vasconcelos pers. obs.). In three genera (*Eugenia*, *Pimenta*, *Decaspermum*), there is evidence that the breeding system is functionally dioecious, where the apparently hermaphrodite flowers do not produce viable pollen (Chapman 1964; Kevan and Lack 1985; Byng et al. 2016).

Ovule Oversupply—Even though the number of ovules varies within a genus, most genera present a standard range of seed number. For most *Eugenia* and *Myrcia* species for example, seed number is usually one or two regardless of the number of ovules produced (Fig. 9A; Berg 1855–1856; Lucas et al. 2007; Staggemeier et al. 2017; a similar pattern was observed in cultivated *Luma apiculata*, Fig. 9B). On the other hand, *Plinia*, *Myrceugenia*, and *Myrtus* produce few seeds (less than ten, Fig. 9C) and *Feijoa*, *Psidium*, and *Rhodomyrtus* produce multiple seeds (frequently over 25; Landrum and Kawasaki 1997; Wilson 2011). According to Landrum (1982),

TABLE 1. Floral formulae and diagnostic characters in Myrteae subtribes (floral formulae after Prenner et al. 2010). * Floral formulae and stigma types in *Myrtella* and *Lithomyrtus* are based on Wilson (2011). ** *Calyptrogenia, Hottea,* and *Pseudanamomis* are not represented due to their nested phylogenetic placement and future synonymization in *Eugenia.*

Clade	Genus	Floral formulae	Ovule arrangement on placenta	Stigma	Position of stamens in the bud
Decasperminae	*Archirhodomyrtus*	♂ K5* C5* A∞* Ĝ(2–3)┼ Vx∞	Uniseriate	Capitate	Straight
	Austromyrtus	♂ K5* C5* A∞* Ĝ(2)┼ Vx10–20	Apparently biseriate	Simple	Straight
	Decaspermum	♂♀ K4–5* C4–5*A∞* Ĝ(5)┼ Vx10	Uniseriate	Capitate	Straight
	Gossia	♂ K4–5*C4–5*A∞*Ĝ(2)┼Vx5–20	Multiseriate	Simple	Straight
	Kanakomyrtus	♂♀ K4–5* C4–5* A∞* Ĝ(2–4)┼ Vx∞	Uniseriate	Capitate (lobed)	Straight to semi-curved
	*Lithomyrtus**	♂ K5* C4–5* A∞* Ĝ(2)┼ Vx2	(not seen)	Simple or capitate	(not seen)
	*Myrtella**	♂ K5* C5* A∞* Ĝ(2–3)┼ Vx4–12	(not seen)	Simple or capitate	(not seen)
	Octamyrtus	♂ K4* C4*+4*+2↓ A15–20*Ĝ(3)┼ Vx∞	Uniseriate	Capitate	Straight
	Pilidiostigma	♂ K4–5*C4–5*A∞* Ĝ(1–3)┼ Vp-Vx∞	Uniseriate	Capitate	Straight
	Rhodamnia	♂K4–5* C4–5* A∞* Ĝ(2–3)┼ Vp10–20	Uni- or biseriate	Simple or capitate	Straight
	Rhodomyrtus	♂K5* C5* A∞* Ĝ(3)┼Vx∞	Uniseriate	Capitate	Straight
	Uromyrtus	♂K5* C5* A∞* Ĝ(3)┼ Vx10–20	Uniseriate	Simple	Straight
General ground plan		**♂K4–5*C4–5*A∞*Ĝ(2–3)┼Vx5-∞**	**Uniseriate**	**Simple or capitate**	**Straight**
Blepharocalyinae	*Blepharocalyx eggersii*	♂K(2)*C2*A∞*Ĝ(2)┼Vx4–8	Multiseriate	Simple	Strongly incurved
	Blepharocalyx salicifolius	♂K4*C4*A∞* Ĝ(2)┼Vx4–16	Multiseriate	Simple	Strongly incurved
General ground plan		**♂K(2)-4*C2–4*A∞*Ĝ(2) ┼Vx4–16**	**Multiseriate**	**Simple**	**Strongly incurved**
*Eugeniinae**	*Eugenia*	♂♀K4(4)*C4*A∞*Ĝ(2)┼Vx4-∞	Multiseriate	Simple	Straight
	Myrcianthes	♂K5(5)*C5*A∞*Ĝ(2)┼Vx∞	Multiseriate	Simple	Straight
General ground plan		**♂K4*C4*A∞*Ĝ(2)┼Vx4-∞**	**Multiseriate**	**Simple**	**Straight**
Luminae	*Luma*	**♂K4*C4*A∞*Ĝ(2)┼Vx∞**	Uniseriate	Simple	Semi-curved
	Myrceugenia	**♂K4(4)*C4*A∞*Ĝ(2)┼Vx∞**	Uniseriate	Simple	semi-curved
	Nothomyrcia	**♂K4*C4*A∞*Ĝ(2)┼Vx∞**	Uniseriate	Simple	semi-curved
	Temu	**♂K4*C4*A∞*Ĝ(2) ┼Vx∞**	Uniseriate	Simple	semi-curved
General ground plan		**♂K4*C4*A∞* Ĝ(2) ┼Vx∞**	Uniseriate	Simple	semi-curved
Myrciinae	*Myrcia*	♂K5(5)*C5*A∞* Ĝ(2–3) ┼Vx4–6	Multiseriate	Simple	Strongly incurved
General ground plan		**♂K5(5)*C5*A∞* Ĝ(2–3) ┼Vx4–6**	**Multiseriate**	**Simple**	**Strongly incurved**
Ugninae	*Lenwebbia*	♂K4*C4*A∞* Ĝ(3) ┼Vx∞	Uniseriate	Simple	Semi-curved
	Lophomyrtus	♂K4*C4*A∞* Ĝ(2–3) ┼Vx∞	Uniseriate	Simple	Semi-curved
	Myrteola	♂K4–5*C4–5*A10–30* Ĝ(2–3) ┼Vx∞	Uniseriate	Simple	Straight
	Neomyrtus	♂K5*C5*A∞* Ĝ(2) ┼Vp∞	Biseriate	Simple	Straight
	Ugni	♂K5*C5*A20–30* Ĝ(3) ┼Vx∞	Biseriate	Simple	Straight
General ground plan		**♂K4–5*C4–5*A20-∞* Ĝ(2–3) ┼Vx∞**	**Uni- or Biseriate**	**Simple**	**Straight or Semi-curved**
Myrtinae	*Accara*	♂K(4)*C4*A∞* Ĝ(4) ┼Vx∞	Bi- or Multiseriate	Simple	Straight
	Calycolpus	♂K5(5)* C5* A∞* Ĝ(4–6) ┼Vx∞	Multiseriate	Simple to slightly capitate	Straight
	Chamguava	♂K(4)* C4* A∞* Ĝ(2) ┼Vx∞	Multiseriate	Simple	Straight
	Myrtus	♂K5* C5* A∞* Ĝ(3) ┼Vx∞	Multiseriate	Simple	Straight
General ground plan		**♂K4–5* C4–5* A∞* Ĝ(2–4) ┼Vx∞**	**Multiseriate**	**Simple**	**Straight**
Pimentinae	*Acca**	♂K4* C4* A∞* Ĝ(2) ┼Vx∞	(not seen)	Simple	(not seen)
	Campomanesia	♂K5(5)* C5* A∞* Ĝ(2–18)┼Vx ∞	Uniseriate	Capitate	Straight
	Curitiba	♂K4* C4* A∞* Ĝ(2)┼Vx∞	Uniseriate	Simple	Straight
	Feijoa	♂K5* C4–5* A15–30* Ĝ(4)┼Vx∞	Biseriate	Simple	Straight
	Legrandia	♂♀K4* C4* A∞* Ĝ(2–3) ┼Vx∞	Uniseriate	Simple	Straight
	Mosiera	♂K4* C4* A∞* Ĝ(2–3)┼Vx∞	Multiseriate	Capitate	Straight
	Myrrhinium	♂♀K4*C4*A4–8:∞⁰∂ Ĝ(2)┼Vx7–15	Uniseriate	Simple	Straight
	Pimenta	♂♀ K4–5* C4–5* A∞* Ĝ(2)┼Vx 1–8	Uniseriate	Simple	Semi-curved
	Psidium	♂♀K4–5(4–5)*C4–5*A∞*Ĝ(2–5)┼Vx∞	Multiseriate	Capitate	Straight
General ground plan		**♂K4–5* C4–5* A∞* Ĝ(2–∞)┼Vx∞**	**Uni- or Multiseriate**	**Simple or Capitate**	**Straight**
Pliniinae	*Algrizea*	♂K5* C5* A∞* Ĝ(2)┼Vx3–6	Multiseriate	Simple	Strongly incurved
	Myrciaria	♂K4* C4* A∞* Ĝ(2)┼Vx4–6	Multiseriate	Simple	Strongly incurved
	Neomitranthes	♂K(4)* C4ʳ * A∞* Ĝ(2)┼ Vx4–8	Multiseriate	Simple	Strongly incurved
	Plinia	♂K4(4)* C4* A∞* Ĝ(2)┼Vx6–10	Multiseriate	Simple	Strongly incurved
	Siphoneugena	♂K4(4)* C4 * A∞* Ĝ(2)┼ Vx4–8	Multiseriate	Simple	Strongly incurved
General ground plan		**♂K4(4)* C4* A∞* Ĝ(2)┼Vx4–8**	**Multiseriate**	**Simple**	**Strongly incurved**

Campomanesia is also peculiar in producing several ovules but just one seed per locule, resulting in few seeds per fruit given the common multiloculate state in the genus. In this way, ovule oversupply, i.e. the production of more ovules than will be fertilized (Rosenheim et al. 2016), occurs at different levels throughout Myrteae. Taxa that are single or few-seeded are concentrated in the largest lineages (i.e. Eugeniinae, Myrciinae, Pliniinae), regardless of the number of ovules produced. Constraining the number of ovules that can be fertilized may have given an advantage to certain lineages, allowing the
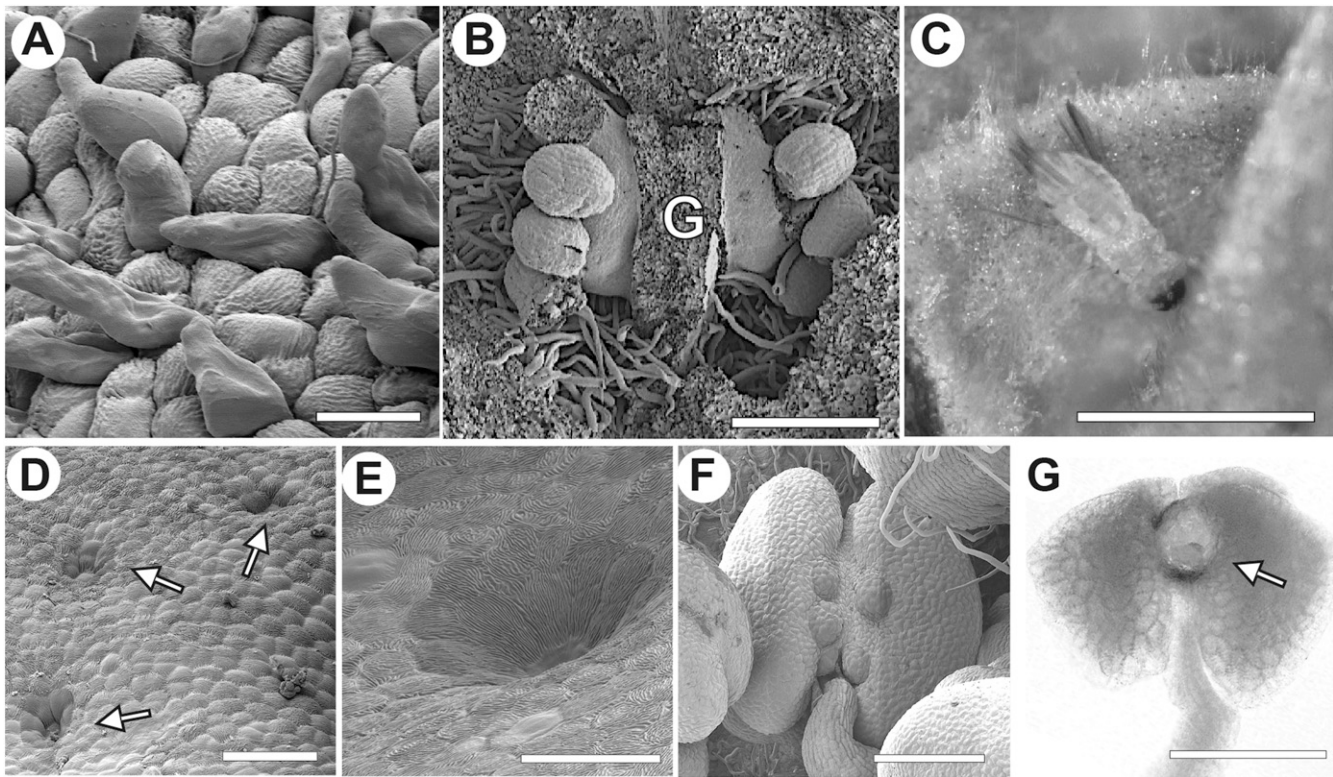
Fig. 7.   Trichomes, elaiophores, and anther glands in Myrteae flowers. A. Single celled trichomes (hairs) developing on external calyx and hypanthium surface of a *Myrcia splendens* (*M.* sect. *Myrcia*) bud. B. Similar trichomes growing on the inner surface of the locule wall in *Eugenia itajurensis* (*E.* sect. *Pilothecium*). C. Termite inside a pubescent bud of *Myrcia* sect. *Gomidesia*. D, E. Elaiophores in (D) *Pimenta dioica* (indicated by arrows) and in (E) *Rhodamnia cinerea*. F, G. Anther oil gland in (F) *Rhodomyrtus tomentosa* and (G) *Myrcia rubella* (*M.* sect. *Aulomyrcia*) (arrow). G = gynoecium. Scale: 25 µm (A); 50 µm (D, E); 250 µm (B, F, G); 3 mm (C).

development of larger seeds that are better adapted to certain environments (e.g. rainforests; Foster 1986), conferring a strategy of shift from quantity to quality (Schupp 1993).

Herkogamy and Strategies to Avoid Selfing—Genera and groups of genera present different strategies to avoid selfing. In species with folded stamens, the style elongates earlier than the stamens, thus presenting discrete protogyny that may help avoid self-pollination (Fig. 10A; most Myrteae are self-incompatible, Nic Lughadha and Proença 1996). Species with straight stamens usually have both stamens and style at approximately the same height after anthesis, with pollen ready for collection as soon as the flower opens, increasing the chances of self-pollination (see discussion in Vasconcelos et al. 2015). Some species of *Eugenia* and *Psidium* avoid self pollination by presenting style gigantism, where the style stands twice as high as the anthers during anthesis (see Vasconcelos et al. 2018, for *Eugenia*). This strategy may be linked with higher diversity in these groups (Vasconcelos et al. 2017b), with further evidence from similar trends in other plant groups (de Vos et al. 2014). Heterostyly is not evident in any species, but cannot be ruled out until more extensive surveys are carried out.

Common Pollination Strategies—Most Myrteae share a similar pollination strategy. Anthesis commonly occurs just before sunrise and is concentrated in the months between September and December (i.e. spring in the southern hemisphere, Staggemeier et al. 2010), although it may extend considerably beyond that depending on local conditions. Flowers of Myrteae offer pollen as the main or sole reward (Gressler et al. 2006) and are visited by a range of insects, with bees considered the most general and effective pollinators (Nic Lughadha and Proença 1996; Gressler et al. 2006). Most flowers can be loosely classified into two subcategories based on display. The first is a stamen-dependent display (also called brush blossom, Johnson and Briggs 1984), where stamens are the main component of floral visual attraction (Fig. 10C). In this case, the perianth reflexes backwards when the flower opens and is thought to play a less important role than the stamens in pollinator attraction. The second trend is a petaloid display, wherein the larger non-reflexed petals represent the most conspicuous visual attraction (Fig. 10D), and in which filaments are commonly shorter than in more stamen-dependent displays. Many intermediates are observed, but even closely related taxa may represent extremes in this continuum (e.g. the petaloid *Calycolpus* vs. the more stamen-dependent *Myrtus*, both in subtribe Myrtinae). A similar variation between stamen-dependent and petaloid display also is observed in other Neotropical pollen-flowers, such as Solanaceae and Melastomataceae (Buchmann and Cane 1989; Kriebel and Zumbado 2014), and may be related to sub-syndromes of pollen-gathering bee pollination.

Uncommon Pollination Strategies—Pollination by vertebrates is rare in Myrteae, but exists in at least two genera. The bird pollinated *Myrrhinium* and *Feijoa* show similar floral strategies: decreased numbers of stamens, increased filament length, red colored display, and thick-sweet petals (Fig. 10B), the latter being the main reward for pollinators (Roitman et al. 1997). Reduced number of stamens is especially extreme in *Myrrhinium*, where just four to six stamens develop (Landrum 1986). The fact that *Feijoa* and *Myrrhinium*
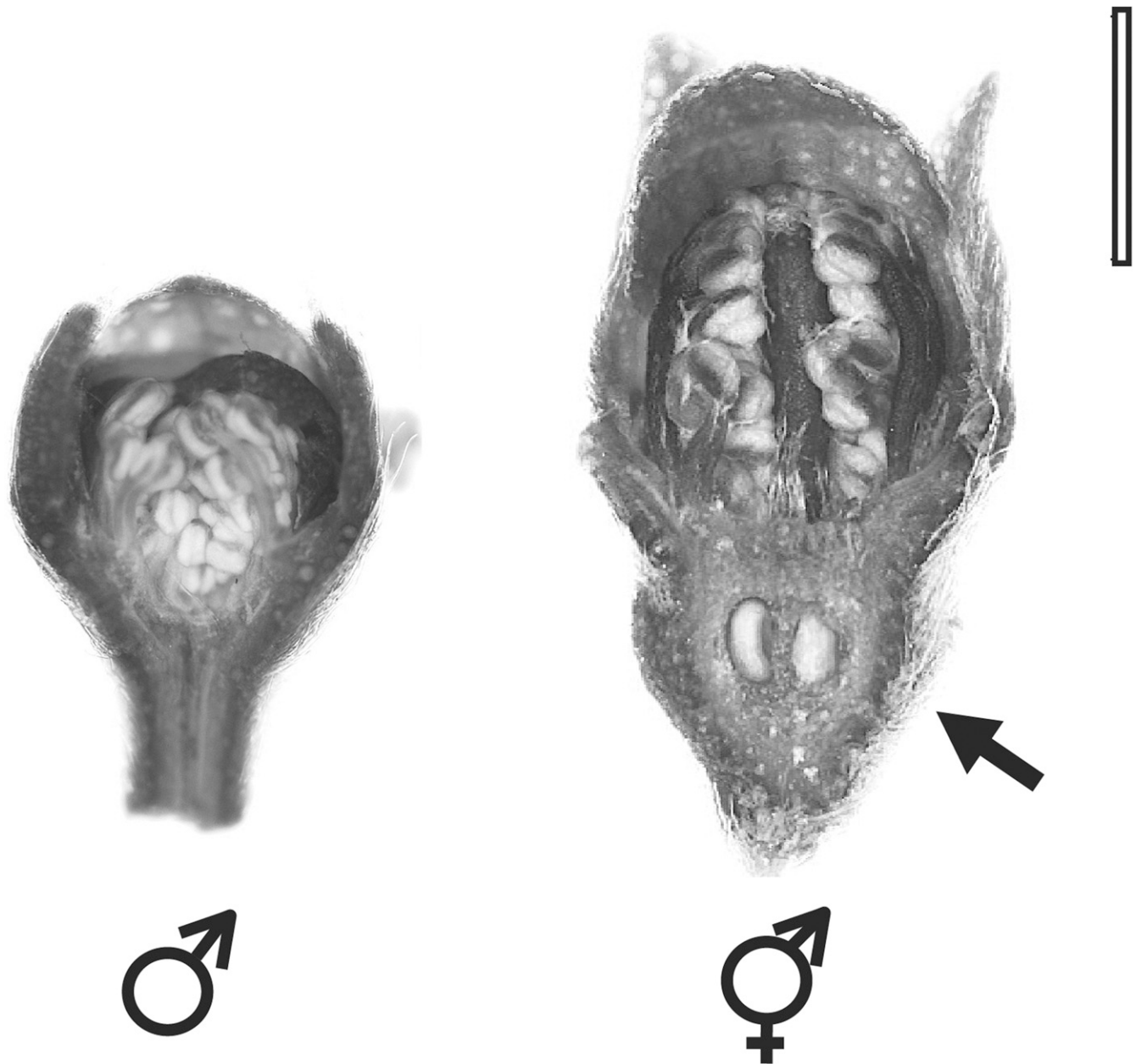
Fig. 8.   Androdioecy in *Decaspermum*. Flower on the left has aborted gynoecium (staminate flower), while in the flower on the right gynoecium and androecium are formed (hermaphrodite). Scale bar = 10 mm.

represent species-poor clades (one species each) suggests that specialization towards bird pollination has not been advantageous for Myrteae diversification. It is important to reiterate that Myrteae flowers usually do not produce nectar, and thus cannot benefit from the most successful bird pollinators in the Neotropics, the hummingbirds, as have other diverse and sympatric bird pollinated groups such as Bignonieae (Alcantara and Lohmann 2010) and *Costus* (Kay et al. 2005; see also Rocca and Sazima 2010). Other unusual floral displays that resemble pollination syndromes associated to birds, bats, or flightless vertebrates are observed in the Decasperminae (e.g. long stamens and petals forming a tube in *Octamyrtus*; White 1951; Craven 2006) and *Eugenia* from the Pacific and Madagascar regions (*Eugenia* sect. *Jossinia*; e.g. long stamens and petals forming a tube in *E. bullata* and thick bracteoles subtending flowers in *E. ambanizanensis*).

Observations in the field that can confirm such specializations are, however, not available for these taxa yet.

Taxonomic Treatment

Recent phylogenetic studies, coupled with monographs and revisions, indicate high levels of homoplasy in many floral traits (e.g. merosity, fused calyx, trichomes, locule, and ovule number). Observation of a single organ is usually systematically irrelevant; combinations of traits, however, can identify a genus or a group of genera with fair confidence (Table 1). The overall floral pattern found in each subtribe is described below.

Blepharocalycinae, Myrciinae, and Pliniinae—The subtribe Blepharocalycinae, consisting of *Blepharocalyx* as the sole genus, historically has been considered closely related to the

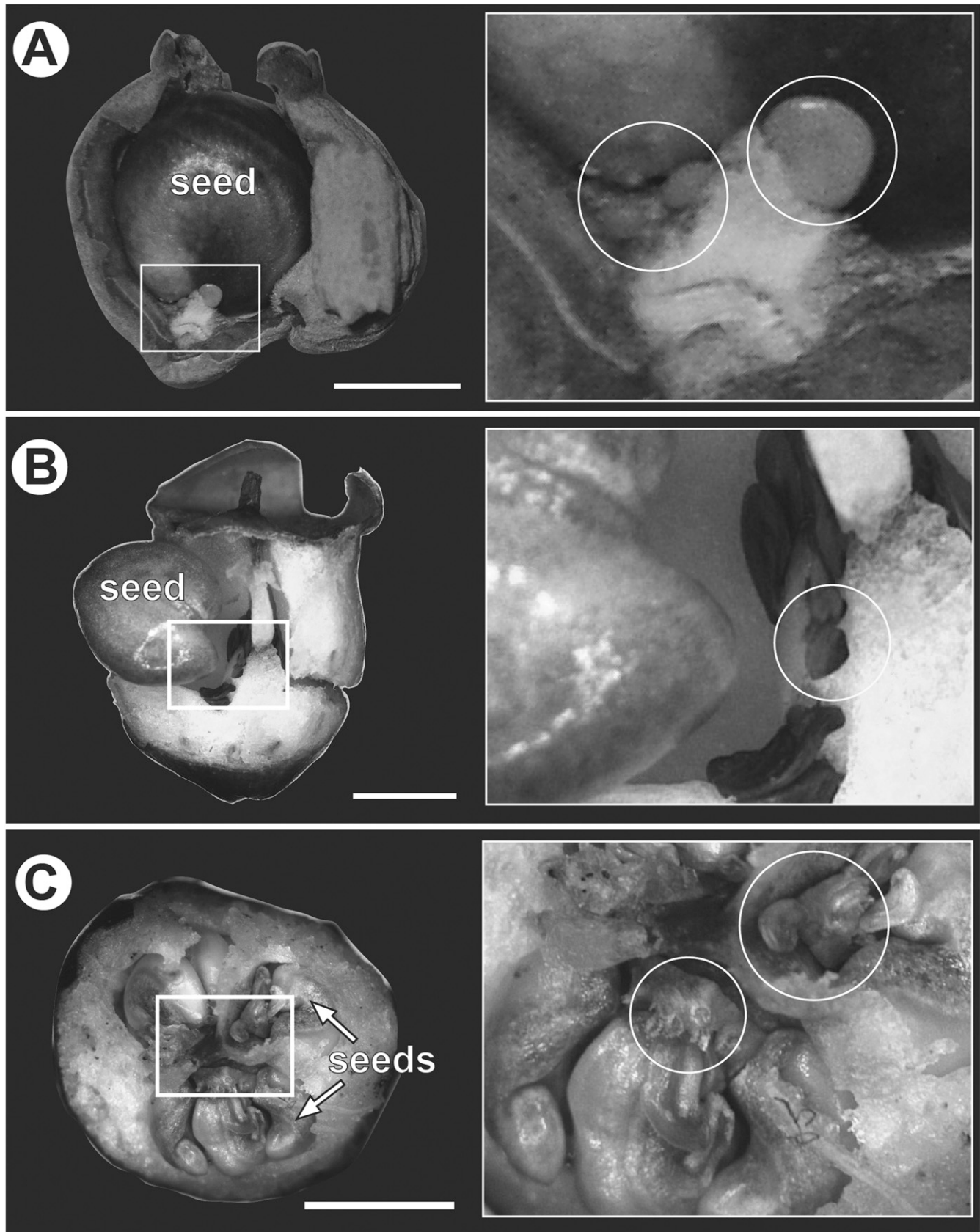FIG. 9. Distinct degrees of ovule oversupply in fruits of similar size. Distinct lineages present from a few to several aborted ovules in the mature fruit. A. *Myrcia spectabilis* (*M.* sect. *Gomidesia*), showing three aborted ovules and one seed. B. *Luma apiculata*, showing several aborted ovules and one seed. C. *Myrtus communis*, showing several aborted ovules and several seeds. Scale bar = ca. 5 mm.
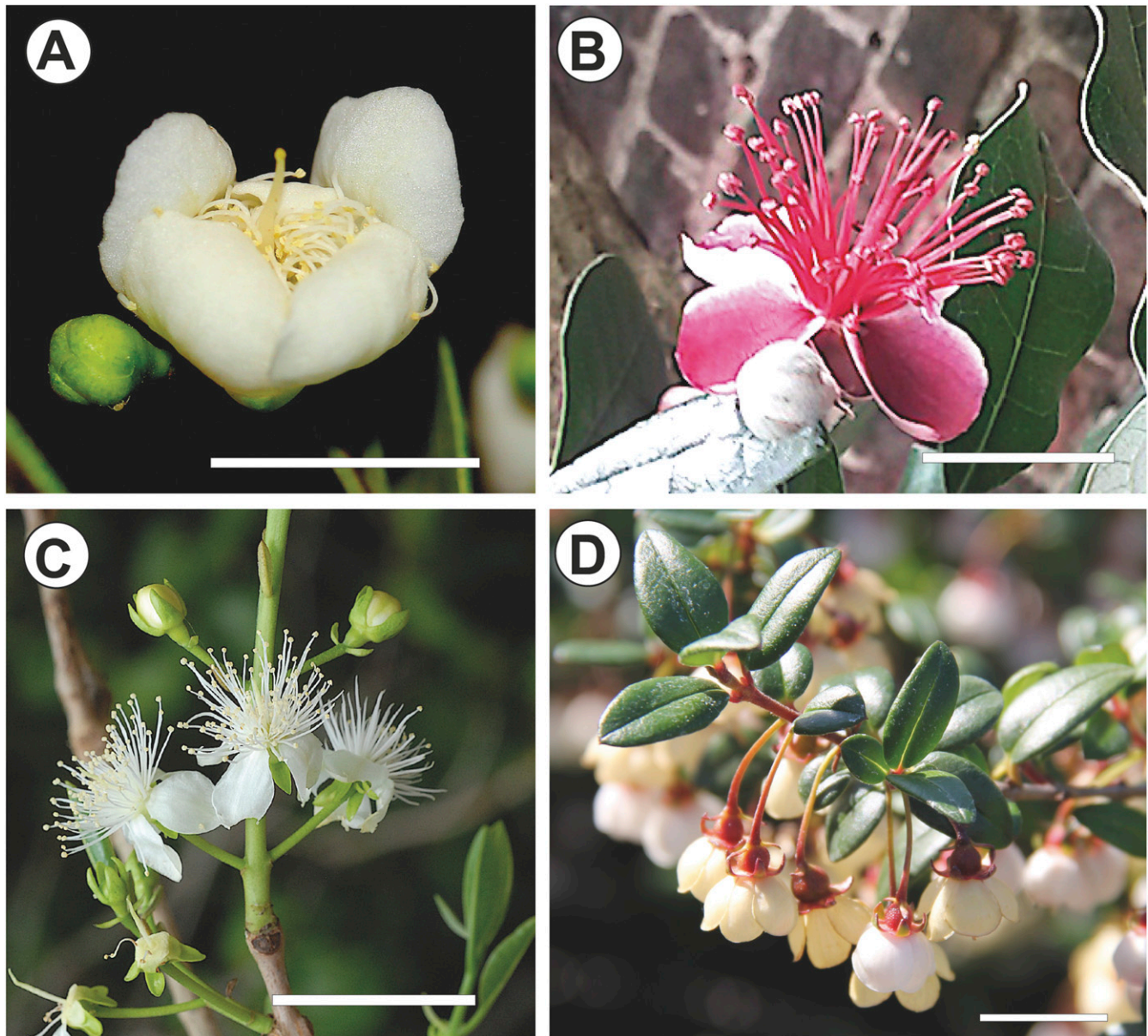
Fig. 10. Diversity of floral display strategies in Myrteae. A. Protogyny in *Luma apiculata*. B. Red showy flowers of the bird-pollinated *Feijoa sellowiana*. C. Brush-blossom display in *Eugenia bunchosiifolia (E.* sect. *Speciosae)*. D. Petaloid display in *Ugni candolei*. Scale bar = ca. 10 mm.

Pimentinae and Myrtinae genera, based mainly on embryo morphology (Landrum 1986). In terms of floral architecture, however, Blepharocalycinae flowers are similar to those of the Myrciinae and Pliniinae genera (Fig. 11B–D). Floral characters shared by all three subtribes include strongly incurved stamens (Vasconcelos et al. 2015), the multiseriate ovule arrangement on the placenta (visible when ovule number is above two per locule), and a low number of ovules per ovary (Lucas et al. 2007). The locules are usually two, or less commonly, three. Within the Pliniinae and Myrciinae genera, the flowers are highly homogeneous, such that variation that diagnoses infrageneric groups in the large genus *Myrcia* comes from traits such as hairs, calyx fusion, relative hypanthium projection above the ovary, and thickness of the staminal ring (Lucas et al. 2018). Pliniinae and Myrciinae always appear as sister groups in phylogenetic analyses, with high statistical support from bootstrap and posterior probability. Different

studies indicate Blepharocalycinae in different positions within Myrteae (see also Murillo-A et al. 2013), and its phylogenetic position within the tribe remains unresolved (Lucas et al. 2007, 2019; Vasconcelos et al. 2017b).

Decasperminae—Decasperminae is the only subtribe in Myrteae restricted to the Australasian and Pacific geographic regions (Lucas et al. 2007; Vasconcelos et al. 2017b). Its flowers commonly present a pinkish display (Fig. 11G–I), distinct from the usually white corollas of Neotropical subtribes. Possibly due to its older age and broad geographical distribution (Vasconcelos et al. 2017b), few morphological characters are exclusive and constant enough to be defined as diagnostic in the group. In general, pentamery is the most common perianth arrangement, although tetramerous flowers are found in *Octamyrtus*, *Rhodamnia*, some species of *Decaspermum* and *Pilidiostigma* (Snow 2004), and in the New Caledonian species *Rhodomyrtus andromedoides* Pancher ex Guillaumin (Scott
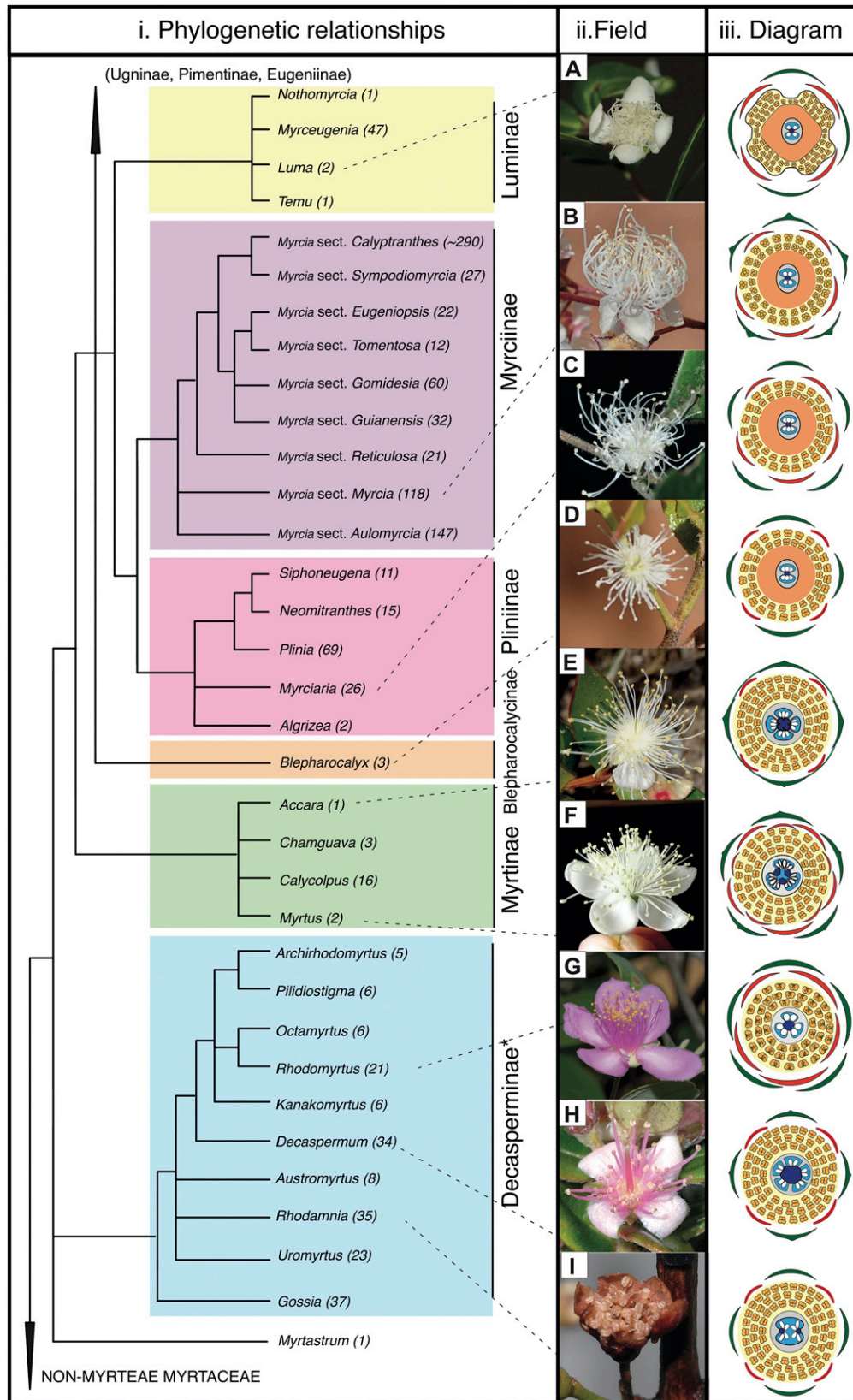
Fɪɢ. 11.   Simplified phylogeny of Myrteae (i), field pictures (ii), and floral diagrams (iii) of selected species. Topology is a summary of total molecular evidence (nuclear and plastidial) found by Lucas et al. (2005, 2007, 2011); Costa (2009); De-Carvalho (2013); Mazine et al. (2014); Bünger et al. (2016), Santos et al. (2017) and Vasconcelos et al. (2017b). Represented clades are those with strong PP (> 0.95) and bootstrap (> 70) support by the majority of studies. Poorly supported relationships are collapsed into polytomies. Numbers between brackets represent estimated species diversity per tip. (A) *Luma apiculata*; (B) *Myrcia linearifolia (M.* sect. *Myrcia)*; (C) *Myrciaria floribunda*; (D) *Blepharocalyx salicifolius*; (E) *Accara elegans*; (F) *Myrtus communis*; (G) *Rhodomyrtus tomentosa*; (H) *Decaspermum vitis-idea*; (I) *Rhodamnia cinerea*. *Lithomyrtus* and *Myrtella* are still to be phylogenetically placed within Decasperminae. Color code in floral diagrams: green = sepals, red = petals, yellow = androecium, orange = hypanthium, blue = gynoecium.

1978b, 1979; Snow 2000). The fused calyx, a common feature found in flowers of Neotropical Myrteae, appears to be absent in subtribe Decasperminae. Staminal primordia are spread over the entire hypanthium, resulting in straight stamens in the bud (Vasconcelos et al. 2015). Locule number is variable, but the most common pattern is trilocular. The unilocular ovary of *Rhodamnia* (Scott 1979) appears derived from incomplete fusion of the bi- or tricarpelar ovary (Figs. 5D, 11I), resulting in a parietal arrangement. Ovule organization on the placenta is mostly uniseriate, giving a lamelliform aspect to the placenta in bilocular species (terminology used by Snow et al. 2003). *Gossia* is unusual in the sense that it presents a multiseriate arrangement of ovules over the placenta (Snow et al. 2003).

The clade formed by *Rhodomyrtus* (a polyphyletic genus; see Snow et al. 2011), *Octamyrtus*, *Kanakomyrtus*, *Pilidiostigma*, and *Archirhodomyrtus* ("KARPO" clade, supported by PP > 0.95 and bootstrap > 90, Snow et al. 2011; Vasconcelos et al. 2017b) has several shared floral modifications. These include a thin, partial to nearly complete membranous partition between most or all ovules (named a "pseudo-septum"; Scott 1978b, 1978c) and peltate stigmas. Flowers of *Octamyrtus* are similar to those of *Rhodomyrtus* in general morphology, the main difference being an additional whorl of longer petals that gives its display a characteristic tubular appearance (Craven et al. 2016), and the stamens and style often projecting well above the tips of the corolla. Although still to be sampled in phylogenetic studies, *Myrtella* and *Lithomyrtus* have clear traits of Decasperminae and thus are treated as such here and in Lucas et al. (2019). These two genera present a non-elongated hypanthium, bi- to tetralocular ovaries, and uniseriate ovule arrangement on the placenta (Scott 1978a, 1979; Snow and Guymer 1999). The lack of a capitate/peltate stigma and pseudo-septum between ovules suggest that their position will be other than within the KARPO clade.

Eugeniinae—Eugeniinae includes *Myrcianthes*, *Eugenia*, and several small genera that are nested in the latter according to molecular evidence (Mazine et al. 2014; Byng et al. 2016; Vasconcelos et al. 2017b). Some of these have recently undergone synonymization (e.g. *Calycorectes*, *Monimiastrum*, *Hexachlamys, Meteoromyrtus*) or are in the process of it (*Calyptrogenia*, *Pseudanamomis*, *Hottea*). Whereas *Myrcianthes* is a relatively small genus mostly from the Andean region (Grifo 1992), *Eugenia*, in its broader circumscription, is the largest and most widespread genus of Myrteae, with ca. 1000 species distributed throughout the Neotropics, New Caledonia, Madagascar, Continental Africa, and India (Van der Merwe et al. 2005; Mazine et al. 2014, 2016; Byng et al. 2016; Wilson and Heslewood 2016). *Myrcianthes* generally is pentamerous, whereas most *Eugenia* are tetramerous (with the notable exception of *E.* sect. *Hexachlamys*, Mazine et al. 2016). In both genera staminal primordia cover the whole hypanthium during flower development, resulting in straight stamens in the bud in most cases (Vasconcelos et al. 2015, 2018). Species formely treated in *Monimiastrum* have stamens covering the whole inner layer of their highly elongated hypanthia, resulting in somewhat curved stamens that are exceptional in *Eugenia* (see Scott 1980; Snow 2008; Giaretta et al. 2019). Ovaries are mostly bilocular, with a small central placenta attached to a single point in the septum (Landrum and Kawasaki 1997). Ovule arrangement over the placenta for the great majority is multiseriate.

Floral morphology is homogeneous throughout the vast majority of the ca. 1000 species of *Eugenia* (Figs. 12A, B) and,

traditionally, morphological characters that separate sections within the genus are related to non-floral aspects (e.g. seeds and inflorescences; Mazine et al. 2014, 2016). However, some floral variation may have systematic relevance. These include presence of trichomes and their location (Faria 2014), the length of the style (Vasconcelos et al. 2018), and calyx modifications (aspect and fusion; Bünger et al. 2016; Giaretta et al. 2019). Section *Pilothecium*, for example, can be identified by the presence of hairs in the ovary (a character shared with some genera of Pimentinae; Faria 2014), whereas most members of *Eugenia* sect. *Umbellatae* have styles that are twice as long as the stamens, compared to styles of similar size to stamens in other clades (Vasconcelos et al. 2018). Furthermore, sect. *Phyllocalyx* is recognizable by the leafy aspects of sepals, which are morphologically similar to their bracteoles (Berg 1855–1856; Bünger et al. 2016). Some fundamental differences in the gynoecium were observed in two lineages arising from the deepest nodes of *Eugenia*. *Eugenia* sects. *Pseudeugenia* and *Pilothecium* are exceptional in having apparent uniseriate arrangement of ovules over the placenta in some species (e.g. *Eugenia stipitata*, T. Vasconcelos pers. obs.) and frequently more than two locules (Faria 2014; Mazine et al. 2016), resembling some genera in the sister group Pimentinae (e.g. *Campomanesia*).

Luminae—Luminae includes four genera of distinct morphology and taxonomic history. *Myrceugenia*, the largest of them with ca. 50 recognized species (WCSP 2018), has historically been associated with Myrciinae based on embryo characters (McVaugh 1968), but it grouped with *Luma, Temu,* and *Nothomyrcia* in recent phylogenetic studies (Lucas et al. 2007; Murillo-A and Ruiz 2011; Murillo-A et al. 2012; Vasconcelos et al. 2017a). The genera share common floral traits, including tetramery, discontinuous staminal rings giving stamens a semifolded posture prior to anthesis, and two–four locular ovaries with uniseriate ovule organization (Fig. 11A). The style is usually long and folds on top of the anthers in the bud.

Myrtinae—The close relationship between the only Mediterranean Myrtaceae, the genus *Myrtus*, and a group of Neotropical genera has been recently clarified (see Vasconcelos et al. 2017b). These four genera (*Myrtus*, *Calycolpus*, *Accara*, and *Chamguava*) form the recircumscribed subtribe Myrtinae and share multiseriate ovule organization over subpeltate but elongated placentas, in contrast to other sympatric Myrteae genera with multiseriate ovules attached to a minute placenta (e.g. *Eugenia*; Landrum 1990, 1991; Landrum and Kawasaki 1997). The perianth is pentamerous in *Myrtus* (Fig. 11F) and *Calycolpus*, but tetramerous in *Accara* (Fig. 11E) and *Chamguava*. *Myrtus* frequently has an additional but reduced whorl of petals (Mulas and Fadda 2004; T. Vasconcelos pers. obs.).

Pimentinae—The genera of Pimentinae present, along with Decasperminae, the broadest flower diversity in Myrteae. Flowers are either tetramerous or pentamerous, but variation is common even at the species level (e.g. in *Psidium guajava*, *Campomanesia adamantium*; see Fig. 2G). Locularity ranges from bilocular to multilocular, sometimes reaching 18 locules in some *Campomanesia* (Landrum 1986), but locularity also is commonly variable at lower taxonomic levels. Stamens are mostly straight in the bud, with the exception of *Pimenta*, where the stamen primordia developing in a discontinuous ring result in a semi-folded posture in the bud (Vasconcelos et al. 2015; Fig. 3B). Stigmas can be capitate, which sometimes is a good character to separate Pimentinae from other sympatric Myrteae (Bentham 1869). *Psidium*, *Myrrhinium*, and
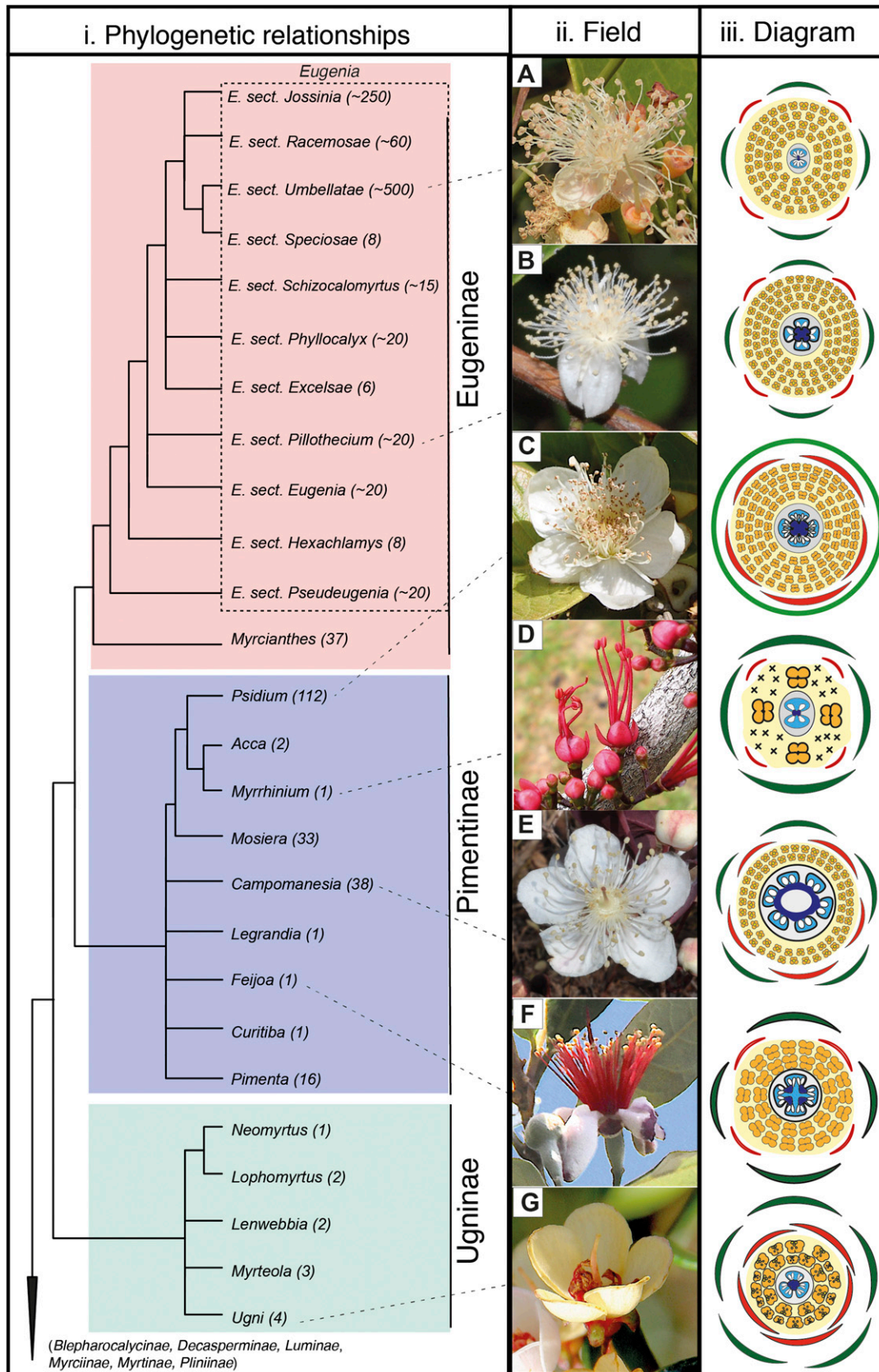
FIG. 12.   Simplified phylogeny of Myrteae (i), field pictures (ii) and floral diagrams (iii) of selected species. Topology is a summary of total molecular evidence (nuclear and plastidial) found by Lucas et al. (2005, 2007, 2011); Costa (2009); De-Carvalho (2013); Mazine et al. (2014); Bünger et al. (2016), Santos et al. (2017) and Vasconcelos et al. (2017b). Represented clades are those with strong PP (> 0.95) and bootstrap (> 70) support by the majority of studies. Poorly supported relationships are collapsed into polytomies. Numbers between brackets represent estimated species diversity. (A) *Eugenia bimarginata* (*E.* sect. *Umbellatae*); (B) *Eugenia stipitata* (*E.* sect. *Pilothecium*); (C) *Psidium guajava*; (D) *Myrrhinium atropurpureum*; (E) *Campomaneia adamantium*; (F) *Feijoa sellowiana*; (G) *Ugni candolei*. Color code in floral diagrams: green = sepals, red = petals, yellow = androecium, orange = hypanthium, blue = gynoecium. Photo in (D) by I. R. Costa.

Mosiera form a strongly supported clade (Vasconcelos et al. 2017b) but differ in some fundamental aspects of flower organization. *Mosiera* and most *Psidium* (e.g. *Psidium guajava*, *P. guineense*; Fig. 12C) have a multiseriate ovule arrangement on the placenta, and locules that can be only partially fused (Landrum 1992). *Myrrhinium* presents an apparent uniseriate ovule arrangement, a strong reduction in number of stamens (Landrum and Kawasaki 1997), and structures resembling staminodes on the base of the hypanthium that may represent aborted filaments (crosses in floral diagram, Fig. 12D). Flowers of *Feijoa* are distinct from the other Pimentinae and Myrteae by their hairy anthers (unique amongst the genera) and distinct multilocular ovaries wherein the central axis is not fused, giving the impression of a unilocular chamber (Fig. 12F; Dettori and Di Gaetano 1991).

Ugninae—Ugninae is the smallest subtribe treated here. It represents ca. 15 species distributed in five small genera (Lucas et al. 2007; Wilson 2011; Vasconcelos et al. 2017b). Merosity is useful for generic delimitation: *Ugni* and *Neomyrtus* are pentamerous while *Myrteola*, *Lophomyrtus*, and *Lenwebbia* are mostly tetramerous (Landrum 1988a, 1988b; Snow et al. 2003). Stamens are mostly straight in the bud (Vasconcelos et al. 2015). Ovaries are either bi-or tri-locular and ovule arrangement is uni- or bi-seriate, never multiseriate. *Ugni* has an overall distinct floral morphology from other Ugninae genera, with a campanulate corolla formed by relatively large petals, which occur on strongly reflexed pedicels, resembling some Ericaceae and members of *Uromyrtus* (Fig. 12G; Wilson 2011); the red anthers are sagitate and longitudinally covered in oil glands. *Lenwebbia* has an unusual androecium morphology. The staminal base is slightly fused and the discontinuous rings are similar to those of the Luminae, giving the stamens a semi-folded aspect in the bud (Vasconcelos et al. 2015). *Myrteola*, a genus with distribution in Patagonia and the Falkland Islands, presents small flowers with few, small stamens but a relatively high number of ovules, increasing the ovule/pollen ratio that may characterize a selection-induced evolutionary change in breeding system (Cruden 1977). *Neomyrtus* and *Lophomyrtus*, the only Myrteae genera native to New Zealand, form a clade in the phylogeny (Lucas et al. 2007). In overall flower aspect, however, *Neomyrtus* has some similarities to *Ugni* (larger glandulous anthers, biseriate ovules on the placenta), while *Lophomyrtus* (Belsham and Orlovich 2002) resembles *Lenwebbia* (stamens with a somewhat semi-folded posture in the bud, uniseriate ovules on the placenta).

Incertae Sedis—According the new subtribe circumscription of Lucas et al. (2019), three genera are considered incertae sedis (unplaced) in Myrteae: *Amormytus*, *Myrtastrum*, and *Amormyrtella*. The first two have been included in previous phylogenetic studies, but uncertain placement challenges their inclusion in a particular subtribe (Lucas et al. 2005, 2007; Vasconcelos et al. 2017b; Murillo-A et al. 2012). The last one is yet to be included in molecular analysis so its phylogenetic position is unknown. *Myrtastrum*, a mono-specific genus endemic to New Caledonia, has an unusual floral structure relative to other extant Myrteae. The stigma is capitate, but the style is shorter than the anthers (protoandry), a pattern not observed elsewhere in the tribe. Petals are shorter than sepals, restricting the degree to which the corolla reflexes (T. Vasconcelos pers. obs.). The gynoecium is three locular with incomplete fusion and ovule arrangement and has been described as biseriate (Scott 1979), but seems to be in fact uniseriate. *Amomyrtella*, a genus from the Andes, is described

as a taxon of morphologically distinct flowers (Landrum and Morocho 2011), with anthers up to 2 mm and trilocular ovaries with biseriate ovule arrangement on placenta. Even though such descriptions are similar to those of some Ugninae (e.g. *Ugni*), preliminary results from ITS sequencing provide evidence that *Amomyrtella* will be placed within Pimentinae (T. Vasconcelos, unpublished data).

DISCUSSION

The general floral ground plan of subtribes in Myrteae does not differ significantly and is similar to that of other tribes of Myrtaceae (Wilson 2011), but combinations of floral traits are somewhat diagnostic of subtribes. In terms of systematic relevance, the general sequence in order of floral character stability from higher to lower taxonomic levels is: androecium structure (stamen primordia distribution over the hypanthium and their posture in the pre-anthetic bud), gynoecium structure (origin of placenta and ovule arrangement), and lastly perianth structure (number of parts and degree of fusion).

In groups with uniform traits such as Myrteae, careful morphological studies that reveal discrete changes responsible for flexibility of reproductive strategies are the most relevant for evolutionary understanding. In Myrteae, these include subtle herkogamic effects, changes from brush-blossom to a petaloid display (and vice versa) and poorly understood changes in the evolution of floral features that affect both phases of reproduction (i.e. pollination and seed dispersal), such as androdioecy and ovule oversupply (i.e. changes in the gynoecium seem to constrain the number of ovules that can form seeds). Variation in flower size and number per inflorescence, total number of ovules per flower, and number and size of anthers (a proxy for pollen investment) also are likely to affect diversification rates in different ways and should be studied in conjunction with phylogenies in future research. The gynoecium, a hidden and difficult structure to analyze, appears to be especially meaningful in the evolution and systematics of Myrteae. Ovary development appears to influence the number of seeds, the development of the embryos, and to balance self vs. cross-pollination (by strong style elongation in some groups) and pollen competition (Mulcahy and Mulcahy 1987). More studies of ovary structure and evaluation of its role in these processes will be profitable. Furthermore, fine changes in one floral whorl lead to spatial changes that affect the development of the next whorl (e.g. Fig. 4), showing the importance of considering the whole flower system in conjunction as a single unit under natural selection.

AUTHOR CONTRIBUTIONS

All authors contributed with designing the research, collecting the data, and writing of the manuscript.

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Appendix 1. List of analyzed specimens. All vouchers deposited in herbarium K. Species name and authorship according to the WCSP (2018). Brazilian states are abbreviated as: AM = Amazonas, BA = Bahia, DF = Distrito Federal, ES = Espirito Santo, GO = Goiás, MG = Minas Gerais, PE = Pernambuco, PR = Paraná, RJ = Rio de Janeiro, RR = Roraima, SP = São Paulo, TO = Tocantins.

Blepharocalycinae: *Blepharocalyx eggersii* (Kiaersk.) Landrum, B W. Nelson 923, Brazil (AM); *Blepharocalyx eggersii* (Kiaersk.) Landrum, T.Vasconcelos 458, Brazil (BA); *Blepharocalyx salicifolius* (Kunth) O.Berg, J.A. Ratter 5984, Brazil (MS); *Blepharocalyx salicifolius* (Kunth) O.Berg, J.E.Q Faria 4050, Brazil (DF); *Blepharocalyx salicifolius* (Kunth) O.Berg, T.R.S. Silva 13494, Brazil (MG). **Decasperminae:** *Archirhodomyrtus beckleri* (F.Muell.) A.J.Scott, B. Gray 1548, Australia (Queensland); *Archirhodomyrtus turbinata* (Schltr.) Burret, J. Soewarto HB 11, New Caledonia; *Archirhodomyrtus turbinata* (Schltr.) Burret, PS Green 1258, New Caledonia; *Austromyrtus dulcis* (C.T.White) L.S.Sm., S. Belsham M77, Australia (Queensland); *Decaspermum parviflorum* (Lam.) A.J.Scott, T. Vasconcelos 728, Malayisia (Sabah); *Decaspermum parviflorum* (Lam.) A.J.Scott, T. Vasconcelos 730, Malayisia (Sabah); *Decaspermum vitis-idaea* Stapf, T. Vasconcelos 729, Malayisia (Sabah); *Gossia bidwillii* (Benth.) N.Snow & Guymer, L.S. Smith 4516a, Australia (Queensland); *Kanakomyrtus longipetiolata* N.Snow, H.S. Mackee 32732, New Caledonia; *Octamyrtus arfancensis* Kaneh. & Hatus. ex C.T.White, P. Van Royen 7925, New Guinea; *Octamyrtus pleiopetala* Diels, D.R. Pleyte 209, New Guinea, ; *Octamyrtus* sp., Johns 9885, New Guinea; *Pilidiostigma tropicum* L.S.Sm., PiF 27636, Australia (Queensland); *Pilidiostigma tropicum* L.S.Sm., S.F. Kajewski 1265, Australia (Queensland); *Rhodamnia cinerea* Jack, T.Vasconcelos 672, Singapore; *Rhodamnia dumetorum* (DC.) Merr. & L.M.Perry, Schanzer I. et al. 148c, Australia; *Rhodomyrtus tomentosa* (Aiton) Hassk., Amin and Francis SAN116159, NA (from the US spirit collection); *Rhodomyrtus tomentosa* (Aiton) Hassk., Eyde 4/79, NA (from the MO spirit collection); *Rhodomyrtus tomentosa* (Aiton) Hassk., T. Vasconcelos 678, Singapore; *Rhodomyrtus tomentosa* (Aiton) Hassk., T. Vasconcelos 726, Malayisia (Sabah); *Uromyrtus archboldiana* (Merr. & L.M.Perry) A.J.Scott, P. Puradyatmika 7425, New Guinea; *Uromyrtus emarginata* (Pancher ex Baker f.) Burret, T. Vasconcelos 605, New Caledonia; *Uromyrtus emarginata* (Pancher ex Baker f.) Burret, T. Vasconcelos 628, New Caledonia. **Eugeniinae:** *Myrcianthes fragrans* (Sw.) McVaugh, T.Vasconcelos 535, Costa Rica; *Myrcianthes fragrans* (Sw.) McVaugh, R. Chaco'n 350, NA; *Myrcianthes pungens* (O.Berg) D.Legrand, J.E.Q. Faria 4277, Brazil (DF); *Calycorectes acutatus* (Miq.) Toledo, T. Vasconcelos 506, Brazil (DF); *Calycorectes bergii* Sandwith, J.G. Myers 5955, French Guiana; *Eugenia ligustrina* (Sw.) Willd., Hamilton M.A. 570, British Virgin Islands; *Eugenia ligustrina* (Sw.) Willd., T.Vasconcelos 570, Dominican Republic; *Eugenia uniflora* L., T. Vasconcelos s.n., RBG Kew living collection (native to Brazil); *Eugenia splendens* O.Berg, J.E.Q.Faria 4196, Brazil (BA); *Hexachlamys edulis* (O.Berg) Kausel & D.Legrand, T.M. Pedersen 2756, Brazil (SP); *Eugenia bullata* Pancher ex Guillaumin, T.Vasconcelos 608, New Caledonia; *Eugenia malangensis* (O.Hoffm.) Nied., Brenan 7962, South Africa; *Eugenia malangensis* (O.Hoffm.) Nied., Brenan 8024, South Africa; *Eugenia malangensis* (O.Hoffm.) Nied., Greenway 8129, South Africa; *Eugenia malangensis* (O.Hoffm.) Nied., Robson 342, South Africa; *Eugenia paludosa* Pancher ex Brongn. & Gris, T.Vasconcelos 646, New Caledonia,; *Eugenia roseopetiolata* N.Snow & Cable, T. Vasconcelos s.n., RBG Kew living collection (native to Madagascar); *Eugenia involucrata* DC., J.E.Q. Faria 4047, Brazil (DF); *Eugenia involucrata* DC., T.Vasconcelos 256, Brazil (DF); *Eugenia involucrata* DC., T.Vasconcelos 734, Brazil (DF); *Eugenia itajurensis* Cambess., J.E.Q. Faria 4250, Brazil (BA); *Eugenia klotzschiana* O.Berg, Heringer et al. 1975, Brazil (GO); *Eugenia pohliana* DC., J.E.Q. Faria 4184, Brazil (BA); *Eugenia stipitata* McVaugh, T.Vasconcelos 677, Singapore (cultivated, native to Brazilian Amazon); *Eugenia victoriana* Cuatrec., T.Vasconcelos 717, Singapore (cultivated, native to Colombia); *Eugenia azurensis* O.Berg, J.E.Q. Faria 4186, Brazil (BA); Eugenia azurensis O.Berg, T.Vasconcelos 433, Brazil (BA); *Eugenia pyriformis* Cambess., L.M. Borges 1090, Brazil (RJ); *Eugenia pyriformis* Cambess., Reitz & Klein 11341, Brazil (RJ); *Eugenia angustissima* O.Berg, D.F. Lima 489, Brazil (GO); *Eugenia biflora* (L.) DC., T.Vasconcelos 589, Dominican Republic; *Eugenia longiracemosa* Kiaersk., T.Vasconcelos 310, Brazil (AM); *Eugenia paracatuana* O.Berg, P.O. Rosa 1399, Brazil (GO); *Eugenia bunchosiifolia* Nied., T. Vasconcelos 466, Brazil (ES); *Calyptrogenia cuspidata* Alain, E. Lucas 1125, Dominican Republic; Eugenia aff. schunkei McVaugh, A. Giaretta 1419, Brazil (AM); *Eugenia bahiensis* DC., J.E.Q. Faria 4229, Brazil (BA); *Eugenia coffeifolia* DC. Vel. *Eugenia adenocalyx* DC., A. Giaretta 1441, Brazil (RR); *Eugenia pluriflora* DC., Hatschbach 19022, Brazil (PR); *Eugenia protenta* McVaugh, T. Vasconcelos 350, Brazil (AM); *Eugenia punicifolia* (Kunth) DC., J.E.Q. Faria 4051, Brazil (DF); *Eugenia punicifolia* (Kunth) DC., J.E.Q. Faria 4237, Brazil (ES); *Eugenia punicifolia* (Kunth) DC., T. Vasconcelos 284, Brazil (GO); *Eugenia punicifolia* (Kunth) DC., T. Vasconcelos 475, Brazil (MG); *Eugenia stictosepala* Kiaersk., J.E.Q. Faria 4269, Brazil (ES); *Hottea ekmanii* (Urb.) Borhidi, E. L. Ekman 2502c, Dominican Republic; Incertae sedis: *Amomyrtus luma* (Molina) D. Legrand & Kausel, RBGE 1996- 1065, RBG Edimburg living collection (native to Chile); *Myrtastrum rufopunctatum* (Pancher ex Brongn. & Gris) Burret, M.W. Callmander 796, New Caledonia. **Luminae:** *Blepharocalyx*

cruckshanksii (Hook. & Arn.) Nied, M.F. Gardner 4193, Chile; *Luma apiculata* (DC.) Burret, T. Vasconcelos s.n., RBG Kew living collection (native to Chile); *Myrceugenia alpigena* (DC.) Landrum, J.E.Q. Faria 4264, Brazil (MG); *Myrceugenia alpigena* (DC.) Landrum, T. Vasconcelos 489, Brazil (MG); *Myrceugenia bananalensis* Gomes-Bezerra & Landrum, J.E.Q. Faria 4048, Brazil (DF); *Myrceugenia bananalensis* Gomes-Bezerra & Landrum, J.E.Q. Faria 4049, Brazil (DF); *Myrceugenia planipes* (Hook. & Arn.) O.Berg, E. J. Lucas s.n., RBG Kew living collection (native to Chile). **Myrciinae:** *Myrcia guianensis* (Aubl.) DC., D.F. Lima 463, Brazil (MG); *Myrcia laxiflora* Cambess., E. Lucas 1221, Brazil (BA); Myrcia nivea Cambess., D.F. Lima 492, Brazil (GO); Myrcia sp., D.F. Lima 483, Brazil (MG); *Calyptranthes multiflora* Poepp. ex O.Berg, A. Giaretta 1429, Brazil (AM); *Calyptranthes multiflora* Poepp. ex O.Berg, A. Giaretta 1431, Brazil (AM); *Calyptranthes multiflora* Poepp. ex O.Berg, T. Vasconcelos 379, Brazil (AM); *Marlierea excoriata* Mart., T. Vasconcelos 493, Brazil (MG); Marlierea glabra Cambess., J.E.Q. Faria 4246, Brazil (ES); *Marlierea neuwiedeana* (O.Berg) Nied., T. Vasconcelos 467, Brazil (ES); *Marlierea umbraticola* (Kunth) O.Berg, T. Vasconcelos 311, Brazil (AM); *Myrcia amazonica* DC., T. Vasconcelos 591, Brazil (SP); *Myrcia hirtiflora* DC., T. Vasconcelos 440, Brazil (BA); *Myrcia rubella* Cambess., D.F. Lima 495, Brazil (GO); *Myrcia strigipes* Mart., J.E.Q. Faria 6303, Brazil (RJ); *Calyptranthes aff. blanchetiana* O.Berg, E. Lucas 1208, Brazil (BA); *Calyptranthes brasiliensis* Spreng., J.E.Q. Faria 4244, Brazil (BA); *Calyptranthes grammica* (Spreng.) D.Legrand, T.Vasconcelos 483, Brazil (MG); *Calyptranthes lucida* Mart. ex DC., T.Vasconcelos 259, Brazil (DF); *Calyptranthes pallens* Griseb., T.Vasconcelos 534, Costa Rica; *Calyptranthes thomasiana* O.Berg, T.Vasconcelos s.n., RBG Kew living collection (native to British Virgin Islands); *Mitranthes clarendonensis* (Proctor) Proctor, T.Vasconcelos 510, Jamaica; *Mitranthes ottonis* O.Berg, E. Otto 272, Jamaica; *Myrcia multipunctata* Mazine, J.E.Q. Faria 4236, Brazil (ES); *Myrcia multipunctata* Mazine, T.Vasconcelos 801, Brazil (MG); *Myrcia fenzliana* O.Berg, E. Nic-Lughada H50637, Brazil (BA); *Myrcia* sp.1, T. Vasconcelos 500, Brazil (MG); *Myrcia spectabilis* DC., E. Lucas 1210, Brazil (BA); *Myrcia spectabilis* DC., E. Lucas 1214, Brazil (BA); *Myrcia aff. eriopus* DC., E. Lucas 1205, Brazil (BA); *Myrcia cardiaca* O.Berg, T.Vasconcelos 274, Brazil (GO); *Myrcia linearifolia* Cambess., P.O. Rosa 1402, Brazil (GO); *Myrcia paivae* O.Berg, T.Vasconcelos 298, Brazil (AM); *Myrcia paivae* O.Berg, T.Vasconcelos 516, Costa Rica; *Myrcia splendens* (Sw.) DC., G.C. Herrera 9932, NA; *Myrcia splendens* (Sw.) DC., T.Vasconcelos 250, Brazil (DF); *Myrcia splendens* (Sw.) DC., T.Vasconcelos 587, Dominican Republic; *Myrcia splendens* (Sw.) DC., T.Vasconcelos 753, Brazil (ES); *Myrcia sylvatica* (G.Mey.) DC., E. Lucas 1222, Brazil (BA); *Myrcia pubipetala* Miq., E. Lucas 477, Brazil (SP); *Myrcia amplexicaulis* (Vell.) Hook.f., E. Lucas 1207, Brazil (BA); *Myrcia mucugensis* Sobral, JEQ Faria 4197, Brazil (BA); *Myrcia mucugensis* Sobral, T. Vasconcelos 441, Brazil (BA); *Myrcia subcordata* DC., JEQ Faria 4257, Brazil (ES); *Myrcia trimera* Sobral, E. Lucas 1219, Brazil (BA); *Myrcia truncada* Sobral, E. Lucas 1216, Brazil (BA); *Myrcia laruotteana* Cambess., J.E.Q. Faria 4046, Brazil (DF); *Myrcia tomentosa* (Aubl.) DC., P.O. Rosa 1379, Brazil (DF); *Myrcia tomentosa* (Aubl.) DC., T.Vasconcelos 262, Brazil (DF). **Myrtinae:** *Accara elegans* (DC.) Landrum, T.Vasconcelos 485, Brazil (MG); *Accara elegans* (DC.) Landrum, T.Vasconcelos 490, Brazil (MG); *Calycolpus goetheanus* (Mart. ex DC.) O.Berg, T.Vasconcelos 332, Brazil (AM); *Chamguava schippii* (Standl.) Landrum, D.Aguilar 9833, Costa Rica; *Chamguava schippii* (Standl.) Landrum, P.H. Gentle 8354, Costa Rica; *Myrtus communis* L., E. Lucas 211, RBG Kew living collection (native to Mediterranean region); *Myrtus communis* L., T. Vasconcelos s.n., RBG Kew living collection (native to Mediterranean region). **Pliniinae:** *Algrizea macrochlamys* (DC.) Proença & NicLugh, E. Melo 4496, Brazil (BA); *Algrizea minor* Sobral, Faria & Proença,

J.E.Q. Faria 4157, Brazil (BA)*; Myrciaria aff. glazioviana* (Kiaersk.) G.M.Barroso ex Sobral, T.Vasconcelos 413, Brazil (BA); *Myrciaria floribunda* (H.West ex Willd.) O.Berg, R.M. Harley 54895, Brazil (BA); *Myrciaria floribunda* (H.West ex Willd.) O.Berg,, T.Vasconcelos 380, Brazil (AM); *Myrciaria glanduliflora* (Kiaersk.) Mattos & D.Legrand, T.Vasconcelos 479, Brazil (BA); *Neomitranthes cordifolia* (D.Legrand) D.Legrand, M.C. Souza 550, Brazil (RJ); *Neomitranthes obscura* (DC.) N.Silveira, A.M. Carvalho 816, Brazil (SP); *Plinia cauliflora* (Mart.) Kausel, T.Vasconcelos 388, Brazil (DF) (cultivated); *Plinia nana* Sobral, A. Stadnik 348, Brazil (MG); *Siphoneugena delicata* Sobral & Proença, T.Vasconcelos 760, Brazil (ES); *Siphoneugena densiflora* O.Berg, G. Martinelli 11939, NA. **Pimentinae:** *Feijoa sellowiana* (O.Berg) O.Berg, Spirit collection 14462, RBG Kew living collection (native to southern Brazil); *Feijoa sellowiana* (O.Berg) O.Berg, T.Vasconcelos s.n., RBG Kew living collection (native to southern Brazil); *Capomanesia adamantium* (Cambess.) O.Berg, T. Vasconcelos 273, Brazil (DF); *Campomanesia adamantium* (Cambess.) O.Berg, T.Vasconcelos 293, Brazil (GO); *Campomanesia adamantium* (Cambess.) O.Berg, T.Vasconcelos 474, Brazil (GO); *Campomanesia guazumifolia* (Cambess.) O.Berg, A Lobao 1372, Brazil (SP); *Campomanesia simulans* M.L.Kawas., T.Vasconcelos 472, Brazil (MG); *Campomanesia velutina*, T.Vasconcelos 507, Brazil (DF); *Legrandia concinna* (Phil.) Kausel, Germain s.n., Chile; *Mosiera longipes* (O.Berg) Small, M.A. Hamilton 630, Sadle 186 Turks and Caicos Islands; *Myrrhinium atropurpureum* Schott, C. Farney 2265, Brazil (RJ); *Myrrhinium atropurpureum* Schott, G. Hatchbachi 61056, Brazil (RJ); *Myrrhinium atropurpureum* Schott, M. Souza s.n., Brazil (RJ); *Pimenta berciliae* T. Vasc. & B. Peguero, T.Vasconcelos 578, Dominican Republic; *Pimenta dioica* (L.) Merr., T.Vasconcelos 534, Costa Rica; *Pimenta pseudocaryophyllus* (Gomes) Landrum, A.P. Duarte 8722, Brazil (SP); *Pimenta pseudocaryophyllus* (Gomes) Landrum, E. Lucas 193, Brazil (SP); *Pimenta pseudocaryophyllus* (Gomes) Landrum, H.C. de Lima 3453, Brazil (SP); *Pimenta pseudocaryophyllus* (Gomes) Landrum, H.S. Irwin 19844, Brazil (GO); *Pimenta pseudocaryophyllus* (Gomes) Landrum, T. Vasconcelos 403, Brazil (MG); *Pimenta racemosa* (Mill.) J.W.Moore, F. Axelrod 7796, Dominican Republic; *Psidium acranthum* Urb., T.Vasconcelos 579, Dominican Republic; *Psidium brownianum* Mart. ex DC., T.Vasconcelos 465, Brazil (BA); *Psidium firmum* O.Berg, T.Vasconcelos 290, Brazil (GO); *Psidium friedrichsthalianum* (O.Berg) Nied., T.Vasconcelos 522, Costa Rica; *Psidium guajava* L., T.Vasconcelos 389, Brazil (DF) (cultivated); *Psidium guajava* L., T.Vasconcelos 585, Dominican Republic (cultivated); *Psidium guineense* Sw., B.S.Amorim 1913, Brazil (PE); *Psidium guineense* Sw., T.Vasconcelos 279, Brazil (GO); *Psidium laruotteanum* Cambess, J.E.Q. Faria 4276, Brazil (GO); *Psidium myrsinites* DC., T.Vasconcelos 503, Brazil (GO); *Psidium myrtoides* O.Berg, T.Vasconcelos 402, Brazil (SP); *Psidium oligospermum* Mart. ex DC., F. Franca 5431, Brazil (BA); *Psidium oligospermum* Mart. ex DC., F.F.Mazine 1346, Brazil (ES); *Psidium riparium* Mart. ex DC., J.E.Q. Faria 4107, Brazil (TO); *Psidium rufum* Mart. ex DC., J.E.Q. Faria 4271, Brazil (MG); Ugniinae: *Lenwebbia prominens* N.Snow & Guymer, G.P. Guymer AQ424641, Australia (Queensland); *Lenwebbia prominens* N.Snow & Guymer, L. Bird AQ424632, Australia (Queensland); *Lophomyrtus obcordata* (Raoul) Burret, Cult Lord Headfort (Kew id:16201), New Zealand; *Lophomyrtus obcordata* (Raoul) Burret, Melville 5751, New Zealand; *Lophomyrtus obcordata* (Raoul) Burret, Spirit collection 10291, New Zealand; *Myrteola nummularia* (Lam.) O.Berg, G.T.Prance 28535, Falklands; *Myrteola nummularia* (Lam.) O.Berg, M.F. Gardner 3579, Falklands; *Neomyrtus pedunculata* (Hook.f.) Allan, B.H.Macmillan 76/102, New Zealand; *Neomyrtus pedunculata* (Hook.f.) Allan, Colens 1714, New Zealand; *Ugni candolei* (Barnéoud) O.Berg, T.Vasconcelos s.n., RBG Kew living collection (native to Chile); *Ugni myricoides* (Kunth) O.Berg, T.Vasconcelos 533, Costa Rica.