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A New Subtribal Classification of Tribe Myrteae (Myrtaceae)

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Abstract—A new classification of the predominantly Neotropical tribe Myrteae is proposed to replace Berg’s three traditional subtribes, the Myrciinae, Eugeniinae, and Myrtinae. Nine subtribes are here proposed that are supported by molecular and morphological data. In addition to the three traditionally recognized but modified here, subtribe Pimentinae (originally described as Pimentoideae) is reinstated and five new subtribes are proposed: **Blepharocalycinae**, **Decasperminae**, **Luminae**, **Pliniinae**, and **Ugninae**. A key to the nine subtribes is followed by descriptions of each, listing genera included, approximate species numbers, general distribution patterns, and notes. The genera *Feijoa* O. Berg and *Temu* O. Berg are reinstated. Morphological structures of importance for classification of Myrteae subtribes are illustrated.

Keywords—Large genera, taxonomy, tropical.

Myrtaceae is a pantropical family with an eastern Gondwanan origin (Thornhill et al. 2015) and ca. 6000 species distributed through Australasia and the Pacific, tropical and subtropical America, and with a modest African representation (WCSP 2018). Members of Myrtaceae are trees or shrubs with high ecological significance in tropical biomes where species are predominantly fleshy fruited. The ecological importance of tropical Myrtaceae is particularly well documented in the Neotropics, where flowers and fleshy fruits provide an important food source for insects, mammals, and birds year-round (Staggemeier et al. 2017) and where fruit and seed morphology and seed germination relative to embryo structure vary significantly (Landrum and Stevenson 1986; Nic Lughadha and Proença 1996; Pizo 2002; Gressler et al. 2006). In contrast, karyology (Costa et al. 2008) and floral morphology vary much less (Lucas et al. 2007; Vasconcelos et al. 2018, 2019a) making consistent species level taxonomy a challenge.

Wilson et al. (2005) provided a molecular-based subfamilial classification of Myrtaceae, dividing the family into subfamilies Psiloxylloideae and Myrtoideae including two and fifteen tribes respectively. All South American Myrtaceae except for a single species, *Metrosideros stipularis* (Hook. & Arn.) Hook.f., fall in tribe Myrteae DC. Circumscription of tribe Myrteae (De Candolle et al. 1827) has remained essentially the same through nearly two centuries. Exceptions are the exclusion of *Xanthomyrtus* into tribe Tristanieae (Landrum and Stevenson 1986; Wilson et al. 2005; Biffin et al. 2010), and the removal of *Syzygium* P. Browne ex Gaertn. and synonyms into tribe Syzygieae (Schmid 1972; Wilson et al. 2005; Thornhill et al. 2015). The embryo-based subtribal arrangements of the 19th and 20th centuries (see Berg 1855–1856, 1859; Niedenzu 1893; Kiaerskou 1893; Kausel 1956; McVaugh 1968) are summarized and reviewed using molecular systematics by Lucas et al. (2007), Murillo-A et al. (2013), and Vasconcelos

et al. (2017b). Those studies have provided a clearer understanding of natural relationships within tribe Myrteae and produced informal groups and arrangements of clades with informal names that have fallen into common usage and now warrant formalizing. As currently circumscribed, Myrteae comprises ca. 50 genera (Wilson 2010) and ca. 2500 species (WCSP 2018) and has been recognized as a viable predictor of total tree species diversity in ecological studies of some neotropical biomes (Murray-Smith et al. 2009; Lucas and Bünger 2015). Phenological analyses of Myrteae demonstrate its potential for use in studies of response to climate change (Staggemeier et al. 2010, 2015).

MATERIALS AND METHODS

Taxonomy and species numbers per subtribe follow the WCSP (2018) except when otherwise specified. The classification is based on the latest phylogenetic hypothesis of Myrteae (Vasconcelos et al. 2017b). Geographical ranges are taken from WCSP (2018). As evidenced by centuries of taxonomy leading to this point, provision of an accurate, natural, subtribal classification of tribe Myrteae is not easy. Myrteae presents strong morphological conservatism and has relatively homogeneous flowers for a group that is estimated to be at least 40 million years old (Vasconcelos et al. 2017b). Homoplasy, likely due to parallelism (Vasconcelos et al. 2017a), is common and similar structures are distributed throughout the tribe with low correspondence to phylogenetic signal. Single diagnostic traits for individual clades are rarely present, but evolutionary trends can characterize flowers of natural groups, especially at lower taxonomic levels (genera, species). Thus, the systematic value of observations of a single organ is often low, but combinations of traits allow genera or groups of genera to be identified with confidence (see Vasconcelos et al. 2019b). For this reason, the key provided is complex and exceptions to the couplets are common; these exceptions are flagged clearly in the key.

Characters used here for subtribal descriptions are those highlighted in other works as diagnostic and are as consistent as possible with the phylogenetic hypothesis on which the classification is based. The systematic importance of stamen numbers is highlighted by Nic Lughadha (1997) and Vasconcelos et al. (2015), with the significance of their posture in

bud highlighted in the latter study. Myrteae inflorescences are discussed in depth by Briggs and Johnson (1979) and Giarretta et al. (in prep.). Considering these studies, we here take the view that although racemes, panicles, botryoids, or any 'conflorescence' (sensu Briggs and Johnson 1979) produced in a single season's growth can terminate in flowers, these do not represent truly terminal or determinate inflorescences. For these reasons, inflorescences reported here as solitary are prefixed with "apparently" to emphasize our understanding that there are no truly terminal or determinate inflorescences in Myrteae, but that all such structures form part of a 'frondo-bracteose' structure where leaves are mixed with arrangements of axillary flowers while the whole structure can continue to grow at the apex (McVaugh 1956). This counters other available systems based on different criteria (e.g. ontogenetic development in Claßen-Bockhoff and Bull-Hereñu 2013) that provide alternative interpretations of inflorescence architecture.

RESULTS

The resulting classification scheme is as stable as possible at this time, with few radical further changes anticipated, even though four genera remain unplaced. Topological modification from the phylogeny of Vasconcelos et al. (2017b) to accommodate a shift in understanding of the relationship of the *Pimenta* and *Psidium* groups (noted below) reflects the constant quest for more data and greater statistical support, common after multiple iterations of successively more stable molecular-based classifications.

Lucas et al. (2007) provided a rudimentary discussion of the subtribes that are here formalized and compared to those of previous researchers, with a focus on the enduring 'three subtribes' classification of Berg (1855–1856) and the informal groups of McVaugh (1968). In summary, in our circumscription Myrceinae remains the same, Eugeniinae loses *Plinia* and related genera to the Pliniinae, and Myrtinae is divided into five subtribes (Blepharocalycinae, Decasperminae, Myrtinae, Pimentinae and Ugninae). The remaining subtribe, Luminae, comprises genera that McVaugh (1968) did not associate with any of the major evolutionary lineages, as well as *Temu* O. Berg. The monogeneric *Blepharocalycinae* is created for *Blepharocalyx* O. Berg, a genus that has changed position in previous phylogenetic studies, but that frequently appears alone, sister to other, major clades. In a minority of molecular phylogenies (e.g. Murillo-A et al. 2012, 2013), *Blepharocalyx* and *Temu* (a monospecific genus consisting of *Temu cruckshanksii* (Hook. & Arn.) O. Berg, at times recognized as *Blepharocalyx cruckshanksii* (Hook. & Arn.) Nied., emerge together. This has raised doubt as to whether they may be related, but we believe

that *Blepharocalyx* is sufficiently genetically distinct from other Myrteae, and that long branch attraction (Felsenstein 1978) in molecular analyses likely is responsible for it grouping with unrelated species.

Article 10.6 of the International Code of Nomenclature for Algae, Fungi, and Plants (Turland et al. 2018) states that the type of a subdivision of a family must be the same as that of the generic name on which it is based. The subtribes presented here are named after the oldest available accepted genus in each group that thereby become the type of its subtribe.

TAXONOMIC TREATMENT

MYRTEAE DC. in Schltld., *Linnaea* 2: 504. Jul 1827. TYPE GENUS: *Myrtus* L.

Trees, shrubs, or subshrubs; trichomes simple or dibrachiate. **Leaves** simple, mostly opposite, decussate; occasionally sub-opposite or verticillate. Blade margins entire, rarely crenate; pellucid gland dots frequently visible. **Inflorescences** axillary or functionally terminal or determinate, or indeterminate, occasionally ramiflorous or cauliflorous; architecture reflecting wide variation of a bracteate shoot; flowers from solitary to forming complex dichasial, racemose, or paniculate arrangements. **Flower** perianth in two whorls; calyx lobes free, or if fused then opening by tearing or as a calyptra; petals free, white, pink, or rarely red or purplish; stamens free, numerous (rarely reduced to less than 10), straight or folded in bud; anthers versatile, dehiscing by longitudinal slits; stigma mostly simple, sometimes capitate, or peltate; ovary inferior, 2- or 3-locular, exceptionally to 18 locules, locules with two to many ovules per locule in one, two, or multiple series; placentation axile or exceptionally functionally parietal (appearing parietal as a result of incomplete fusion of an otherwise axile arrangement), ovules radiating, sometimes pendulous. **Fruit** indehiscent, fleshy. **Seeds** 1 to numerous; embryo variable; cotyledons free to completely fused, rudimentary to well-developed, varying in shape from linear, laminar, plano-convex, or foliaceous; hypocotyl rudimentary to well-developed, varying in shape from deltoid, elliptical, or linear, if linear straight, curved, C-shaped, cochlear, or coiled, usually external or lateral to the cotyledons, rarely internal (for further discussion of the Myrteae embryo, see Landrum and Sharp 1989; Wilson et al. 2005; Proença et al. 2006).

KEY TO SUBTRIBES

Morphological structures generally reliable for classification of Myrteae subtribes and referred to in the following key are illustrated in Figs. 1, 2.

1. Stamens folded in the bud, testa membranous, cotyledons free, either leafy and folded or reduced or swollen and starchy, hypocotyl encircling the cotyledons or reduced or so rudimentary as to appear absent 2
2. Inflorescence a panicle, exceptionally reduced to three or fewer flowers per axil; calyx (4)5-merous or fused Myrceinae
2. Inflorescence variable but not paniculate except in *Blepharocalyx eggersii* (Kiaersk.) Landrum; calyx 4(5)-merous or fused 3
3. Inflorescence cymose; cotyledons reduced, indistinct from hypocotyl, embryo C-shaped or spiraled Blepharocalycinae
3. Inflorescence variable; cotyledons leafy and folded or slightly swollen and starchy, embryo reniform 4
4. Hypanthium extended into a tube beyond ovary apex; cotyledons swollen and starchy, hypocotyl absent or strongly reduced, cotyledons and hypocotyl rarely only somewhat developed, or (for *Algrizea* in eastern Brazil) not swollen and starchy Pliniinae
4. Hypanthium not extended beyond ovary apex; cotyledons leafy and folded or somewhat reduced and reniform, hypocotyl fully or partly encircling the cotyledons, if cotyledons non-folded then from Chile or Argentina Luminae
1. Stamens straight in the bud, testa bony or membranous, cotyledons fused or free, never leafy and folded, hypocotyl never encircling the cotyledons 5
5. Flowers 4-merous, exceptionally 5–6-merous; seed testa membranaceous (exceptionally hard in *Eugenia* subg. *Hexachlamys*), cotyledons swollen and starchy, hypocotyl reduced; ovules emerging from the septum from a central placenta; seeds few, usually one, or rarely (reported from Madagascar) many per fruit Eugeniinae
5. Flowers 5(4)-merous; seed testa membranous or bony; usually many seeds per fruit 6

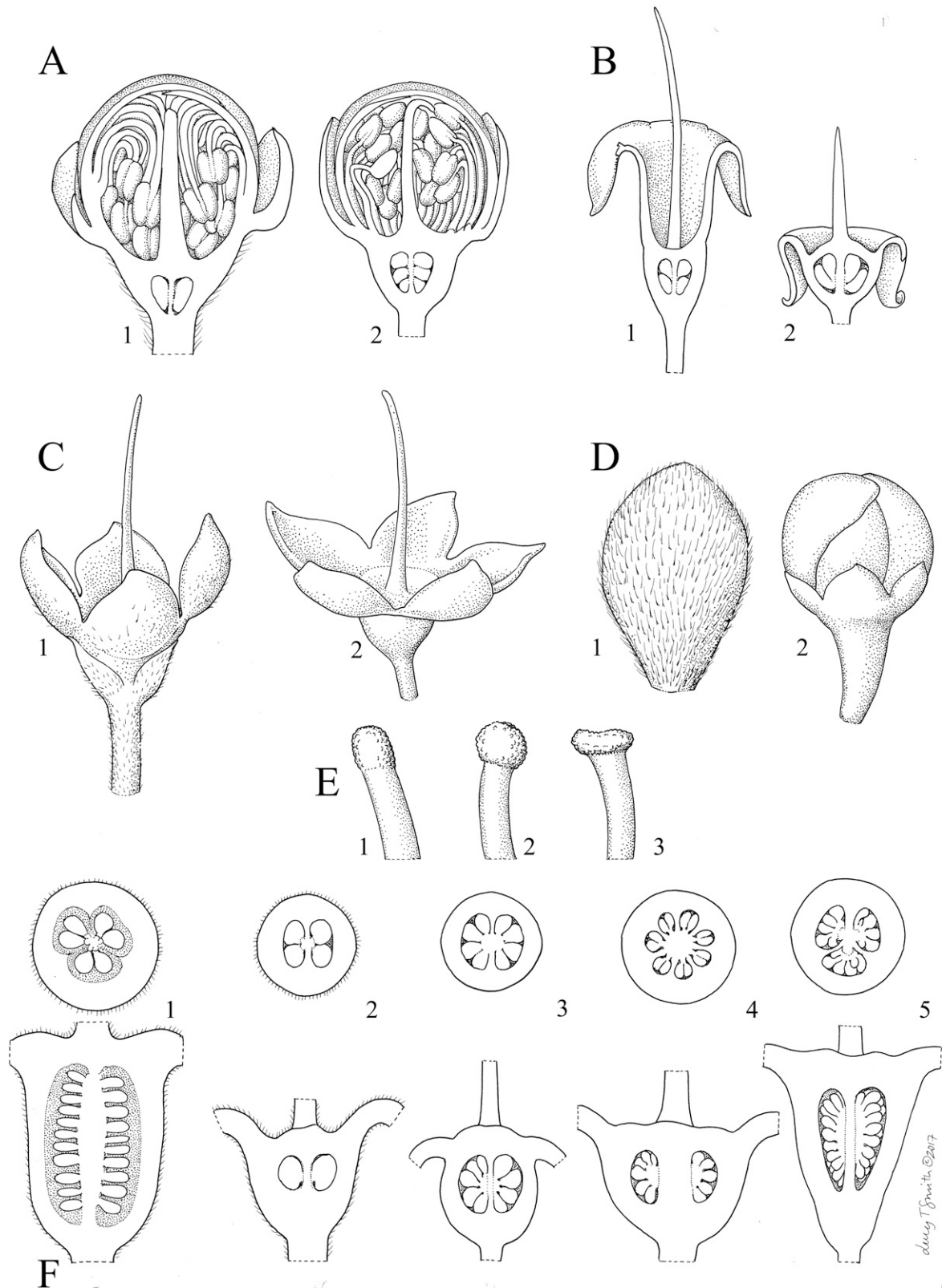


FIG. 1. Morphological structures of importance for classification of Myrteae subtribes. A. Posture of stamens in bud. A1. Folded (*Myrcia splendens*). A2. Straight (*Eugenia punicifolia*). B. Nature of the hypanthium. B1. Extended (*Siphoneugenia dussii*). B2. Not extended (*Myrcia laruotteana*). C. Merosity. C1. 4-merous (*Myrceugenia* sp.). C2. 5-merous (*Campomanesia xanthocarpa*). D. Calyx lobes in bud. D1. Fused (*Calyptranthes grandis*). D2. Free (*Myrtus communis*). E. Form of stigma. E1. Simple (*Myrcia splendens*). E2. Capitate (*Rhodamnia cinerea*). E3. Peltate (*Rhodomyrtus novoguineensis*). F. Placentation. F1. 3-locular ovary with many ovules per locule; ovules biseriate, placentation along length of septum; seeds ultimately separated by false-septa (*Rhodomyrtus tomentosa*). F2. 2-locular ovary with two ovules per locule; placentation central (*Myrcia splendens*). F3. 2-locular ovary with multiple ovules per locule; placentation central (*Eugenia uniflora*). F4. 7-locular ovary with multiple ovules per locule; ovules biseriate, placentation central (*Campomanesia adamantium*). F5. 3-locular ovary with many ovules per locule; ovules multiseriate, placentation along length of septum (*Myrtus communis*). Scale bars are omitted as the images depict characters only.

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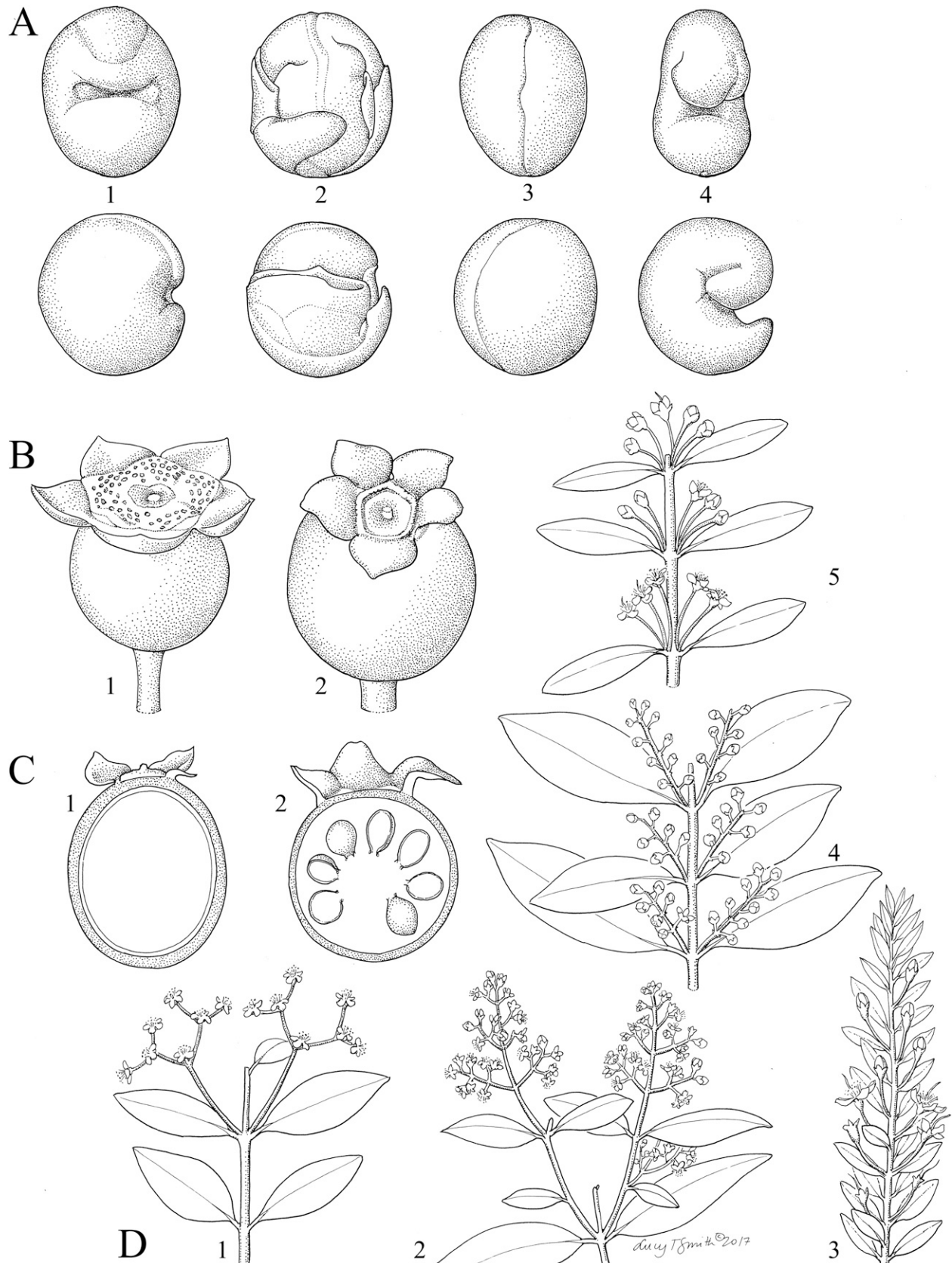


FIG. 2. Morphological structures of importance for classification of Myrteae subtribes. A. Embryo. A1. Cotyledons and hypocotyl homogenous and fused (*Eugenia*). A2. Cotyledons leafy and conduplicate, hypocotyl encircling cotyledons (*Myrcia*). A3. Cotyledons and hypocotyl homogenous but free of each other (*Plinia*). A4. Cotyledons free and reduced, hypocotyl poorly developed, embryo C shaped or lightly spiraled (*Pimenta*). B. Staminal disc. B1. Thick staminal scars covering summit of ovary (*Psidium*). B2. Thin staminal scars indistinct (*Myrcia*). C. Fruits containing seeds. C1. Single, large seed (*Eugenia*). C2. Many small seeds (*Ugni*). D. Inflorescence. D1. Dichasium (*Blepharocalyx*). D2. Panicle (*Myrcia*). D3. Leafy raceme or 'frondo-bracteose shoot' (*Myrtus*). D4. Raceme (*Eugenia*). D5. Fascicle (*Myrceugenia*). Scale bars are omitted as the images depict characters only.

6. Calyx lobes free, petals and/or stamens often pinkish in vivo; fruits usually with many seeds; inflorescence of solitary flowers or more commonly cymose; exclusive to Australasia and the Pacific (excluding New Zealand) Decaspermiae
6. Calyx lobes free, partially or completely fused, petals and stamens white, exceptionally red in *Acca*, *Feijoa*, and *Myrrhinium*; inflorescence variable; Neotropics, Mediterranean, New Zealand (one genus, *Lenwebbia*, in Australia, *Psidium* widely cultivated and naturalized through the tropics) 7
7. Shrubs exclusive to high altitudes over 2500 m or temperate latitudes, never from the Caribbean; calyx lobes often acutely pointed; leaves less than 3 cm long; flowers solitary, often pendulous; cotyledons and hypocotyl of about equal length Ugninae
7. Shrubs or trees rarely above 2500 m or from temperate latitudes; calyx lobes usually rounded; leaves usually longer than 3 cm; inflorescence cymose, sometimes compound, paniculate, racemose, or flowers solitary 8
8. Style often capitate (simple in *Pimenta*, in which case plant strongly aromatic), locules 1–5(–18), placentation usually in one or more series along an often-well-developed placenta; seeds often numerous (> 10 except in single-seeded *Pimenta*) Pimentinae
8. Style simple (plant not strongly aromatic), locules 2–4, placentation usually around a protruding, peltate placenta, seeds usually fewer than 10 Myrtinae

1. **Blepharocalycinae** E. Lucas & T. Vasc. subtrib. nov. TYPE
GENUS: *Blepharocalyx* O. Berg, *Linnaea* 27: 412. 1856.

Shrubs or trees to 30 m; trichomes simple; vessel element scalariform perforation plates absent in the xylem. **Inflorescences** in complex, branching dichasia of up to 35 flowers or in panicles; bracteoles falling after anthesis. **Flower** perianth (2–)4-merous, calyx lobes free or fused, opening with or without longitudinal tearing or as a calyptra; petals white; hypanthium not or slightly (to 1 mm) extended beyond the ovary; staminal ring rounded or square; stamens 80–170, folded in the bud; stigma simple; ovary bilocular with (2–) 5–15(–20) ovules per locule; ovules inserted at a single point on the septum. **Fruits** not exceeding 1 cm diam. **Seeds** 1 to few; embryo C-shaped or spiraled; cotyledons reduced or hypocotyl somewhat extended when embryo spiraled, testa soft.

Range—Blepharocalycinae is widespread in the Neotropics from the lesser Antilles south to Uruguay; in wet and dry habitats.

Sole Genus—*Blepharocalyx* O. Berg.

Note—Landrum (1986) monographed the genus *Blepharocalyx* and recognized three species. However, *Blepharocalyx cruckshanksii* (Hooker & Arn.) Nied. was found by Lucas et al. (2007) to emerge in a separate clade, associated with *Myrceugenia* (see below under Luminae).

2. **Decaspermiae** E. Lucas & T. Vasc. subtrib. nov. TYPE
GENUS: *Decaspermum* J.R. Forst. & G. Forst., *Char. Gen. Pl.*: 73. 1776.

Trees to 20 m, shrubs or subshrubs; trichomes simple; vessel element scalariform perforation plates absent in the xylem. **Inflorescence** mostly cymose, also solitary or in racemose or paniculate bracteate shoots; bracteoles with variable persistence after anthesis. **Flower** perianth (4)5-merous, symmetry somewhat bilateral in *Octamyrtus*, calyx lobes free; petals white or less often pink or red; hypanthium not or slightly (to 1 mm) extended beyond the ovary; staminal ring rounded; stamens 35–220, straight in the bud, exceptionally curved in *Kanakomyrtus*; stigma simple, capitate, peltate or lobed; ovaries 1- to multi-locular (13 locules counted in *Decaspermum*) with 2–many ovules per ovary; placentation apical and protruding or along length of septum, functionally parietal resulting from incomplete locule fusion in *Rhodammia*. **Fruits** not exceeding 2 cm. **Seeds** usually numerous; cotyledons usually reduced and hypocotyl C-shaped, sometimes spiraled; testa usually bony.

Range—Decaspermiae is endemic to the Austro-Pacific and Southeast Asia.

Included Genera—*Archirhodomyrtus* (Nied.) Burret, *Austromyrtus* (Nied.) Burret, *Decaspermum* G.R. & G. Forst., *Gossia* N.Snow & Guymer, *Kanakomyrtus* N.Snow, *Lithomyrtus*

F.Muell., *Myrtella* F.Muell., *Octamyrtus* Diels, *Pilidiostigma* Burret, *Rhodammia* Jack, *Rhodomyrtus* (DC.) Rchb., *Uromyrtus* Burret.

Note—Decaspermiae arises from one of the oldest nodes of Myrteae and is sister to the clade comprising the remaining subtribes. Horizontally arranged seeds separated by thinly membranous false-septa (Scott 1978c) are common in this subtribe. Decaspermiae includes a strongly supported clade (Vasconcelos et al. 2017b) comprising *Archirhodomyrtus*, *Kanakomyrtus*, *Octamyrtus*, *Pilidiostigma*, and *Rhodomyrtus*, further united morphologically by having a peltate stigma, which in the case of *Kanakomyrtus* is prominently lobed. Embryo morphology in this subtribe is less variable than in Myrtinae but the cartilaginous testa of *Pilidiostigma* shows that, as in Myrtinae, morphological variation of the seed exists in this early diverging lineage also. *Myrtella* and *Lithomyrtus* are placed in Decaspermiae on the basis of shared bi- to tetralocular ovaries, uniseriate placentation, and Australasian distribution. Further descriptive data regarding the genera of this group can be found in Scott (1978a, 1978b, 1978c, 1979a, 1979b), Snow (1999, 2004, 2009), Snow and Guymer (1999, 2001), and Snow et al. (2003, 2011).

3. **EUGENIINAE** O. Berg, *Linnaea* 27: 4. 1855 (as 'Eugenioidae').
TYPE GENUS: *Eugenia* P.Micheli ex L., *Sp. Pl.*: 470. 1753.

Subshrubs, shrubs, or trees to 30m; trichomes simple; vessel element scalariform perforation plates absent in the xylem. **Inflorescences** axillary, occasionally ramiflorous or cauliflorous, usually indeterminate but architecture variable, flowers apparently solitary, in fascicles, glomerules, racemose bracteate shoots or sometimes dichasia and exceptionally racemose panicles; bracteoles usually persistent after anthesis. **Flower** perianth (2–)4(–6)-merous, calyx lobes free or fused and opening by longitudinal tearing or as a calyptra; petals white or less frequently pink; hypanthium never extending beyond the ovary (except in species from the Mauritian archipelago, previously placed in *Monimiastrum* J.Guého & A.J.Scott, where the hypanthium is extended in the bud and tears at anthesis); staminal ring rounded, stamens 30–600, straight in the bud (except in species from the Mauritian archipelago, previously placed in *Monimiastrum*, where stamens are folded in the bud); stigma simple; ovary usually 2-locular occasionally with 3 or 4 locules; 2–many ovules per locule; ovules attached at a single point on septum. **Fruits** not exceeding 10 cm diam. **Seeds** usually one (rarely to 15, see Snow et al. 2015); cotyledons occasionally free, plano-convex, but most commonly partially or completely fused; hypocotyl reduced; testa soft or rarely cartilaginous.

Range—Eugeniinae is the only subtribe of Myrteae with a pantropical range. The center of species diversity is tropical

America, where it is widespread from southern Florida to northern Argentina.

Included Genera—*Calyptrogenia* Burret, *Eugenia*, *Hottea* Urb., *Myrcianthes* O. Berg, *Pseudanmomis* Kausel.

Note—Several small, narrowly endemic genera in this clade are not monophyletic as currently circumscribed (Mazine et al. 2014; Wilson and Heslewood 2016; Vasconcelos et al. 2017b) and nomenclatural adjustments are ongoing (Mazine et al. 2018; Giaretta et al. 2018; Flickinger et al. in prep.). Giaretta et al. (in prep.) report an unusual species of *Eugenia* from the Neotropics with an extended hypanthium and stamens folded in the bud.

4. **Luminae** E. Lucas & T. Vasc. subtrib. nov. TYPE GENUS: *Luma* A. Gray, U.S. Expl. Exped., Phan. 1: 535. 1854. Proc. Amer. Acad. Arts 3: 52 (1853).

Trees or shrubs; trichomes dibrachiate (*Temu*, most *Myrceugenia*), or simple (some *Myrceugenia*, *Nothomyrcia*, *Luma*); vessel element scalariform perforation plates often present in the xylem. **Inflorescences** axillary, usually solitary or dichasial but also compound dichasia or bracteate shoots in which flowers can appear solitary or racemose; fascicles in which peduncles superimposed in a row in the axils of leaves or bracts are also frequent; bracteoles usually persistent in fruit. **Flower** perianth 4-merous, calyx lobes free or occasionally fused and opening as a calyptra; petals white; hypanthium never or rarely minutely extending beyond the ovary; staminal ring rounded or slightly quadrangular; stamens 40–500, semi-curved in bud; stigma simple; ovary bi- to tetra-locular with many ovules per locule; ovules inserted along the length of the septum. **Fruits** not exceeding 2 cm diam. **Seeds** one to a few; cotyledons foliaceous and folded and surrounded by long hypocotyl, reduced with C-shaped hypocotyl or plano-convex surrounded by a short hypocotyl; testa mostly soft.

Range—Luminae occurs in (usually higher altitude) tropical to sub-temperate parts of South America; it has a disjunct distribution, occurring in Chile and south-central and eastern Brazil up to Bahia (Murillo-A et al. 2016). Species of Luminae do not occur in the Chaco or Pampas drylands of southern South America.

Included Genera—*Luma*, *Myrceugenia* O. Berg, *Nothomyrcia* Kausel, *Temu* O. Berg.

Note—*Amomyrtus* groups with *Myrceugenia* (with low statistical support, i.e. bootstrap < 50% and posterior probability < 0.95; Vasconcelos et al. 2017b) and occurs within the range of the subtribe. However, Lucas et al. (2007) presented evidence for placement of *Amomyrtus* in Pimentinae. Landrum and Salywon (2004) noted that pentamerous flowers, hard seeds 4–6 mm long, and moderately to strongly aromatic leaves distinguish *Amomyrtus* from other genera of southern South American Myrteae. They also suggested that *Amomyrtus* may be related to *Lophomyrtus*, *Pimenta*, and *Amomyrtella*, based on morphology and secondary chemicals. Some molecular studies indicated a close relationship with *Legrandia* (Murillo-A et al. 2013). Further systematic evidence is therefore awaited before definitive placement of *Amomyrtus*. Berg (1855–1856) associated *Myrceugenia* with subtribe *Myrciinae* O. Berg on the basis of having green, folded cotyledons; however, no molecular evidence supports this arrangement. All molecular studies place *Blepharocalyx cruckshanksii* in Luminae, independent of other species of *Blepharocalyx*. *Blepharocalyx cruckshanksii* was originally described in *Eugenia*

(Hooker and Arnott 1833). Its affinity to *Luma* was recognized by Gray (1853) but it was considered close to *Blepharocalyx* O. Berg by others (Berg 1861; Burret 1941; Landrum 1986). Berg erected the genus *Temu* (that he compared to his *Blepharocalyx*) to accommodate it, but Niedenzu (1893) later synonymized *Temu* under *Blepharocalyx*. McVaugh (1956, p. 146) stated “the name *Temu* is untenable because it is an orthographic variant of the earlier *Temus* Molina.” *Temu* O. Berg has not been formally rejected nor is there evidence of taxonomic confusion of this nature. For these reasons, the names *Temu* O. Berg and *Temu cruckshanksii* (Hook. & Arn.) O. Berg are here reinstated. Morphological characters supporting the inclusion of *Temu cruckshanksii* in Luminae are the shared dichasial inflorescences, an open calyx with four persistent lobes, and a shared southwestern South American distribution.

5. **MYRCIINAE** O. Berg, *Linnaea* 27: 4. 1855 (as ‘Myrcioideae’).

TYPE GENUS: *Myrcia* DC. ex Guill. in J.B.G. Bory de Saint-Vincent, Dict. Class. Hist. Nat. 11: 401. 1827, *nom. cons.*

Trees to 20 m, exceptionally higher, to shrubs or sub-shrubs; trichomes simple, sometimes dibrachiate; vessel element scalariform perforation plates absent in the xylem. **Inflorescence** a well-developed panicle, sometimes with reduced internodes giving the appearance of a thyrses, rarely reduced to three or a single flower(s), terminal flowers often in groups of three; bracteoles variously caducous or persistent after anthesis. **Flower** perianth (4)5-merous, calyx lobes free or fused, opening by longitudinal or transverse tearing, or calyptrate; petals white, sometimes atrophied; hypanthium often extending into a tube beyond the ovary; staminal ring rounded; stamens (30–)50–300, curved in the bud; stigma simple, very exceptionally somewhat capitate; ovary 2- or 3(4)-locular, with 2 or 3(–9) ovules per locule; ovules arising at a single point on septum, usually below the mid-point. **Fruits** not exceeding 3 cm diameter. **Seeds** usually one; cotyledons foliaceous and folded, surrounded by a long hypocotyl; testa membranaceous.

Range—Myrciinae is endemic to and widespread in tropical America, from the United States (Florida) and Mexico to Argentina; it is absent west of the Andes except in the far north of the range in ombrophilous forest.

Included Genera—*Myrcia*.

Note—Following multiple molecular based phylogenetic studies (e.g. Santos et al. 2017; Wilson et al. 2016), Lucas et al. (2018) synonymized *Calyptanthus* Sw., *Marlierea* Cambess., and *Mitranthes* O. Berg in *Myrcia* and provided a subgeneric classification for the genus; nomenclatural transfers of all Myrciinae species to *Myrcia* is ongoing (Lourenço et al. 2018; Campbell et al. in prep.).

6. **MYRTINAE** Nied. In H.G.A. Engler & K.A.E. Prantl, Nat. Pflanzenfam. III, 7: 62, 64. 1893. TYPE GENUS: *Myrtus* Tourn. ex L., Sp. Pl.: 471. 1753.

Trees or shrubs to 10 m; trichomes simple, dibrachiate in some *Calycolpus*; vessel element scalariform perforation plates absent in the xylem. **Inflorescences** apparently solitary or fasciculate; bracteoles usually caducous after anthesis. **Flower** perianth 4–5-merous, calyx lobes free, partially fused or fused in which case opening by lateral tearing; petals white; hypanthium never extending beyond the ovary; staminal ring rounded; stamens 150–300, straight in the bud; stigma simple; ovary bi- to tetra-locular with many ovules per ovary; ovules inserted along the septum or placentation peltate. **Fruits** not

exceeding 2 cm. **Seeds** few to ca. 200 (in *Calycolpus*); cotyledons usually reduced and hypocotyl C-shaped; testa bony or membranaceous in *Chamguava*.

Range—*Myrtus* is endemic to the perimeter of the Mediterranean. The remaining genera are found in the wet forests of Central America (*Chamguava*), Amazonia (*Calycolpus*), and to southeast Brazil, though not in the Andes south of Ecuador. *Accara* is endemic to the rock outcrops (campo rupestre) of Minas Gerais, Brazil.

Included Genera—*Accara* Landrum, *Calycolpus* O. Berg, *Chamguava* Landrum, *Myrtus*.

Note—Myrtinae as circumscribed here does not match the circumscription of previous authors (e.g. Berg 1855–1856; McVaugh 1968; Landrum 1981, 1986). Those latter authors included more species with reduced cotyledons and C-shaped or spiraled cotyledons, an arrangement shown by Vasconcelos et al. (2017b) to have multiple independent origins. That latter analysis suggests that ancestral Myrtinae were a widespread group that encompassed a wide variation of embryo and other characters. Diversification events within the group are all found to be older than 20 million years (Vasconcelos et al. 2017b), suggesting that these are diverse remnants of that morphological spectrum, and that from this ancestral group extant lineages emerged with extant embryo type variation arising multiple times each, and with unique cases of reversals or parallelisms.

7. **Pliniinae** E. Lucas & T. Vasc. subtrib. nov. TYPE GENUS: *Plinia* Plum. ex L., Sp. Pl.: 516. 1753.

Trees to 30 m, shrubs or subshrubs; trichomes simple; vessel element scalariform perforation plates absent in the xylem. **Inflorescences** usually glomerulous or a short bracteate shoot or dichasial in *Algrizea*; bracteoles caducous after anthesis. **Flower** perianth 4(5)-merous, parts free or calyx calyptrate and opening by longitudinal tearing, perianth sometimes circumscissile and falling with the calyx at anthesis, petals white; hypanthium extending beyond the summit of ovary, sometimes forming a conspicuous tube; staminal ring rounded; stamens 45–250, curved in the bud; stigma simple; ovary bilocular with 2–many ovules per ovary; ovules inserted at a single point on septum, usually below the midpoint or inserted along its lower part. **Fruits** not exceeding 5 cm. **Seeds** usually one or few; cotyledons starchy, swollen, plano-convex, free, hypocotyls reduced (except in *Algrizea*, see below); testa membranous.

Range—Pliniinae is widespread in the Neotropics with high diversity in humid forests.

Included Genera—*Myrciaria* O. Berg, *Neomitranthes* D. Legrand, *Plinia*, *Siphoneugena* O. Berg, *Algrizea* Proença & Nic Lugh.

Note—Pliniinae represents genera previously classified with *Eugenia* (O. Berg 1855–1856; McVaugh 1968), but which now are associated with strong support in all modern phylogenies as sister to subtribe Myrciinae. These subtribes share curved stamens in the bud and reduced numbers of locules and ovules. *Algrizea* is the only genus in the subtribe with dichasial inflorescences, a developed hypocotyl and free, saddle-shaped cotyledons (Proença et al. 2006), and usually five calyx lobes, although examples are reported with four (Vasconcelos et al. 2019b).

8. **PIMENTINAE** O. Berg, Linnaea 27: 4. 1855 (as 'Pimentoideae'). TYPE GENUS: *Pimenta* Lindl., Coll. Bot.: t. 19. 1821.

Myrrhiniinae O. Berg, Linnaea 27: 4. 1855 (as 'Myrrhiniinae'). syn. nov. TYPE GENUS: *Myrrhinium* Schott, Syst. Veg. 4: 404. 1827.

Trees to 30 m, shrubs or subshrubs; trichomes simple; vessel element scalariform perforation plates absent in the xylem. **Inflorescences** of apparently solitary flowers or in fascicles or racemose bracteate shoots with internodes of varying length, or simple to compound dichasia; bracteoles usually caducous after anthesis. **Flower** perianth (4–)5-merous, calyx lobes free or fused, opening by longitudinal tearing, or rarely calyptrate then falling as a calyptra; petals white (red in *Acca*, *Feijoa*, and *Myrrhinium*); hypanthium not or slightly (to 1 mm) extended beyond the ovary; staminal ring rounded or pentagonal; stamens 60–700 (4–6 in *Myrrhinium*), straight in the bud; stigma simple or capitate; ovary bi- to multi-locular with many ovules per ovary; ovules inserted along the length of the septum or pendulous or rarely partially parietal. **Fruits** not exceeding 12 cm. **Seeds** usually numerous; cotyledons usually reduced, hypocotyls somewhat enlarged, C-shaped to subglobose to spiraled; testa cartilaginous to bony.

Range—Pimentinae is widespread from the Greater Antilles and Central America, to Uruguay and southern Chile in South America. Some species of *Psidium* are aggressive invaders of other tropical habitats (Lowe et al. 2000), e.g. *Psidium cattleianum* Sabine (Hawaii, other Pacific Islands, and Mauritius). *Pimenta* and *Psidium* are widely cultivated and introduced throughout the tropics.

Included Genera—*Acca* O. Berg, *Campomanesia* Ruiz. & Pav., *Curitiba* Salywon & Landrum, *Feijoa* O. Berg, *Legrandia* Kausel, *Mosiera* Small, *Myrrhinium* Schott, *Pimenta* Lindl., *Psidium*.

Note—Berg's (1855–1856) 'Pimentoideae' and 'Myrrhiniinae,' with incorrect subtribe terminations, were included in Myrtinae by Niedenzu (1893). However, with the correct termination, they remain the earliest available legitimate names for the subtribe comprising *Pimenta* and/or *Myrrhinium* (Art. 19.4 ex 5; Turland et al. 2018). Pimentinae was selected over Myrrhiniinae as the genus *Pimenta* is more widely known than *Myrrhinium*.

Landrum (1986) comprehensively monographed many genera in this subtribe, and Landrum and Stevenson (1986) thoroughly reviewed embryo types in subtribe Myrtinae sensu Berg (1855–1856). The cartilaginous testa of the seeds of some species of Pimentinae and other subtribes was a character used by previous authors (e.g. Kausel 1956; Briggs and Johnson 1979) to unite them into a taxonomic group named differently by the differing authors. This 'Campomanesia complex' (Landrum and Sharp 1989) subsequently was shown to be polyphyletic (Lucas et al. 2007).

Acca (*A. sellowiana*, see below), *Campomanesia*, *Curitiba*, and *Legrandia* consistently group, as do *Mosiera*, *Myrrhinium*, and *Psidium* (Lucas et al. 2007; Vasconcelos et al. 2017b; V. Staggemeier unpubl. data). However, the relationship between these groups and *Pimenta* receives low statistical support and changes between analyses. Morphological similarity between these genera is strong however, and as a result of this and the statistical uncertainty, the conservative approach is taken here to include all genera in a single subtribe. Costa et al. (2015) demonstrated *Myrrhinium* (from the Brazilian Atlantic Forest) to be related to the Andean species of *Acca* (*A. lanuginosa* and *A. macrostema*), but not to *A. sellowiana*. The type species of *Acca* is *A. lanuginosa*, in which case *Acca* sensu Landrum (1986) is polyphyletic and the names *Feijoa* O. Berg,

and *Feijoa sellowiana* (O. Berg) O. Berg are here reinstated for the charismatic and widely cultivated *Acca sellowiana* (vern. Feijoa, Pineapple guava) that falls within Pimentinae. The stamens of *Myrrhinium* are apparently folded in the bud, however, the fold is plicate or 'zig-zag' rather than incurved to the hypanthium, and thus not homologous with the 'folded stamen' character state presented by Vasconcelos et al. (2019b).

9. **Ugninae** E. Lucas & T. Vasc. subtrib. nov. TYPE GENUS: *Ugni* Turcz., Bull. Soc. Imp. Naturalistes Moscou 21(1): 579. 1848.

Small trees to 5 m, shrubs or subshrubs; trichomes simple; vessel element scalariform perforation plates present in the xylem. **Inflorescences** usually solitary and uniflorous or occasionally triflorous; bracteoles persistent or caducous after anthesis. **Flower** perianth 4- or 5-merous, calyx lobes free; petals white; hypanthium never extending beyond the ovary; staminal ring rounded; stamens (8-)40-180, straight in the bud; stigma simple; ovary rarely apparently unilocular, usually bi- to tri-locular with many ovules per locule; placentation along length of septum or pendulous or apparently parietal. **Fruits** not exceeding 1 cm diam. **Seeds** usually numerous; cotyledons reduced; hypocotyl C-shaped; testa bony.

Included Genera—*Lenwebbia* N. Snow & Guymer, *Lophomyrtus* Burret, *Myrteola* O. Berg, *Neomyrtus* Burret, *Ugni*.

Range—Ugninae are found mostly in subtemperate and alpine biomes of South and Central Americas and New Zealand, at altitudes up to the tree line. *Lenwebbia* is found at lower altitudes in eastern Australia.

Note—All analysed species of Ugninae have scalariform vascular plates associated with frost resistance (Jansen et al. 2004, Lucas et al. 2007, Telford unpubl. data). Ugninae have an unusual disjunct distribution through high southern latitudes and often at high altitude. The presence of scalariform plates may be associated with survival in these habitats.

GENERA INCERTAE SEDIS

Amomyrtella is a genus of two species from Argentina not sampled in any published molecular phylogeny. Unpublished ITS molecular data (Vasconcelos pers. comm.) suggest that *Amomyrtella* may be included in subtribe Pimentinae.

Amomyrtus is a Chilean genus of two species. Previous molecular studies (Salywon 2003; Lucas et al. 2007) suggested that *Amomyrtus* is related to *Legrandia*, whereas Vasconcelos et al. (2017b) found *Amomyrtus* as sister to the *Myrceugenia* group but without statistical support. The latter showed that the chloroplast regions support the *Amomyrtus* - *Myrceugenia* relationship, while nuclear data support the *Amomyrtus* - *Legrandia* relationship.

Myrtastrum is a monotypic genus endemic to New Caledonia. The phylogenetic position of *Myrtastrum* appears to be sister to the rest of Myrteae (Vasconcelos et al. 2017b) but statistical support is not significant, and its phylogenetic position can vary. For this reason, a subtribe is not here suggested for *Myrtastrum*, although this may prove to be necessary in the future.

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AUTHOR CONTRIBUTIONS

EL and TV prepared the manuscript. All authors generated extensive data on which this study is based and contributed essential discussion, commentary, and observation to the contents of the work. All authors participated in the assembly and refinement of the final version of the paper.

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