



A new infra-generic classification of the species-rich Neotropical genus *Myrcia* s.l.

E. J. Lucas¹, B. S. Amorim², D. F. Lima³, A. R. Lima-Lourenço¹, E. M. Nic Lughadha¹, C. E. B. Proença⁴, P. O. Rosa⁵, A. S. Rosário⁶, L. L. Santos⁷, M. F. Santos⁸, M. C. Souza⁹, V. G. Staggemeier¹⁰, T. N. C. Vasconcelos¹ & M. Sobral¹¹

Summary. A new classification of the large Neotropical genus *Myrcia* s.l. is proposed. Nine sections are presented that correspond to recently published clades. Of these nine sections, sects. *Myrcia*, *Aulomyrcia* and *Sympodiomyrcia* are already published, sects. *Reticulosae* and *Tomentosae* are new sections, sect. *Eugeniopsis* is a new combination whilst sects. *Aguava*, *Calyptanthes* and *Gomidesia* are new combinations at a new rank (comb. & stat. nov.). Six lectotypifications are made for sections or genera. Estimates of species per section are listed.

Key Words. classification, large-genera, Myrtaceae, systematics, taxonomy.

Introduction

Currently comprising c. 850 accepted species (World Checklist of Selected Plant Families (WCSP) 2017) but reduced according to the most recent morphological and phylogenetic studies (Staggemeier *et al.* 2015; Santos *et al.* 2016; Wilson *et al.* 2016; Vasconcelos *et al.* 2017; Lima *et al.* in prep.; Amorim *et al.* in prep.) to c. 800 species, *Myrcia* s.l. (*sensu* Lucas *et al.* 2007, 2011) is the fourth largest genus of Myrtaceae after *Eucalyptus*, *Eugenia* and *Syzygium*, and one of the largest exclusively Neotropical genera. Taken in this sense, it is a monophyletic group (Santos *et al.* 2016) including the previously accepted genera *Calyptanthes*, *Marlierea* and *Gomidesia* and their synonyms. The rationale and justification for this circumscription is detailed elsewhere (Lucas *et al.* 2007, 2011). The nomenclatural conservation of *Myrcia* over *Calyptanthes* (Lucas & Sobral 2011) was approved by the General Committee for Botanical Nomenclature (Wilson 2017). *Myrcia* s.l. is a widespread Neotropical genus defined by the combined morphological characters of foliaceous cotyledons, a soft seed coat, bi- or trilobular ovaries (occasionally with 4 – 8 locules) containing two ovules per locule and determinate inflorescences in panicles or dichasia, very rarely reduced to few or single flowers

(e.g. Kollman & Sobral 2006). Further taxonomic discussion and the history of previous sub-generic division within *Myrcia* s.l. is given by Lucas *et al.* (2011) and Santos *et al.* (2016).

Myrcia s.l. has high species diversity in the Amazon and the Caribbean, however, diversity is highest in the Brazilian Cerrado and Atlantic forest biomes (WCSP 2016) where it is of particular ecological importance (Mori *et al.* 1983), an indicator of total angiosperm diversity (Murray-Smith *et al.* 2009) and can be used to set conservation priorities (Lucas & Bunger 2015). *Myrcia* species have a critical ecological role, sustaining a complex ecological network of interactions with insects (mainly bees) via their flowers and with a wide range of vertebrate frugivores from small birds to larger mammals that disperse their fleshy fruits (Nic Lughadha & Proença 1996; Pizo 2002; Gressler *et al.* 2006; Staggemeier *et al.* 2017). Due to the size of the genus and morphological homogeneity within it, species of *Myrcia* s.l. are perceived as difficult to identify and/or study. Species are often omitted or mis-named in ecological inventories or surveys of Neotropical forests (e.g. Martini *et al.* 2007; Rigueira *et al.* 2013; Moro *et al.* 2014), a serious problem for biodiversity management and an impediment to research (Goodwin *et al.* 2015). The Web of Science (2016) lists 275

Accepted for publication 28 November 2017. Published online 26 March 2018

¹ Royal Botanic Gardens, Kew, Richmond, Surrey, UK. e-mail: e.lucas@kew.org

² Universidade do Estado do Amazonas, 69058-807, Manaus, Amazonas, Brazil.

³ Universidade Estadual de Campinas, Campinas, São Paulo, Brazil.

⁴ Universidade de Brasília, Brasília, Brazil.

⁵ Jardim Botânico de Brasília, Brasília, Brazil.

⁶ Universidade do Estado do Pará, Belém, Pará, Brazil.

⁷ Universidade Federal Rural de Pernambuco, Recife, Brazil.

⁸ Universidade Federal de São Carlos, Sorocaba, São Paulo, Brazil.

⁹ Universidade Federal Rural do Rio de Janeiro, Rio de Janeiro, Brazil.

¹⁰ Universidade Estadual Paulista "Júlio de Mesquita Filho", Rio Claro, Brazil.

¹¹ Universidade Federal de São João Del-Rei, São João del-Rei, Minas Gerais, Brazil.

publications based on the above-mentioned traditional genera of *Myrcia* s.l. This is in contrast to the nearly eight times more publications listed for the comparably sized genus, *Rhododendron* L. (Ericaceae). To stimulate, and now facilitate research, in particular monographic revision, of *Myrcia* s.l. it is desirable to provide a framework from which discrete groups of species can be selected for study.

The phylogenetic review based on a molecular phylogeny of *Myrcia* s.l. of Lucas *et al.* (2011) described nine morphologically coherent clades within the group. These clades now serve as manageable units, taken up in current discussion and used to delimit much-needed, subsequent systematic studies in the group (e.g. Staggemeier *et al.* 2015; Santos *et al.* 2016; Wilson *et al.* 2016; Lima *et al.* in prep.; Amorim *et al.* in prep.). The nine clades have a mixture of published or informal sectional names (Lucas *et al.* 2007) that have now passed into casual and in one case, premature use (Nic Lughadha *et al.* 2010). Sect. *Myrcia* results from de Candolle's division of *Myrcia* into two sections whilst sect. *Aulomyrcia* (O. Berg) Griseb. results from Grisebach's (1860) reduction of *Aulomyrcia* O. Berg to sectional status. Sect. *Sympodiomyrcia* M. F. Santos & E. Lucas (Santos *et al.* 2016) is a product of recent taxonomic focus on that group. Provision of formal names for the remainder of these taxa is now a logical and necessary step to allow formal, systematic use in current and future studies.

Materials and Methods

The following classification follows the generic concept discussed in Lucas & Sobral (2011) and the phylogenetic hypothesis based on combined evidence from sequences of the ITS and ETS regions of nuclear DNA and the *psbA-trnH*, *trnL-F* and *matK* regions of the chloroplast genome presented by Lucas *et al.* (2011) supplemented by information from the expanded phylogenetic studies of *Myrcia* s.l. of Santos *et al.* (2016), Staggemeier *et al.* (2015), Wilson *et al.* (2016) and Lima *et al.* (in prep.; incorporating phylogenomic techniques) and also by morphological traits discussed in all of those studies. The species sampling of Lucas *et al.* (2011) was designed to maximise included morphological and geographical variation. The result includes species from almost all previously described supra-generic groups (see Lucas *et al.* 2011) but is biased geographically towards eastern Brazil due to the availability of collections from there.

Results and analysis

The analysis includes representative species from the Amazon and the Caribbean, however it is acknowledged

that *Myrcia* is least well known from the Guayana shield and the western Amazon and it is from these areas that species remain most difficult to classify. Extensive herbarium study nevertheless reveals little morphology that cannot be readily accommodated in this scheme with the exception of species of the uniquely uni-ocular Caribbean genus *Mozartia* Urb., currently in synonymy of *Myrcia* (WCSP 2016). Santos *et al.* (2016) however, demonstrate the affinities of *Mozartia* species to be with those of *Myrcia* sect. *Aulomyrcia*. Two remaining sources of phylogenetic and thus taxonomic uncertainty are firstly, the relationship of species such as *Myrcia robusta* Sobral (2007: 75) that consistently (Santos 2014; Santos *et al.* 2016; Lima *et al.* in prep.) emerge in their own clade with poorly supported relationships to other clades. Morphologically these species are very similar to sect. *Reticulosae* resulting in their inclusion in that section. This clade may well warrant description as a new section when it is better understood. Secondly, in *Myrcia elevata* M. F. Santos (in Santos *et al.* 2015: 103) the hypanthium extends above the summit of the ovary and tears at anthesis; the number of calyx lobes varies from five to four and they are reflexed after anthesis. These characters suggest a relationship with *Myrcia* sect. *Aulomyrcia* however, Santos *et al.* (2016) show that *M. elevata* emerges in the clade corresponding to *Myrcia* sect. *Myrcia*. *Myrcia elevata* has a pubescent floral disc that may reflect a relationship with *Myrcia* sect. *Myrcia* and other species, and specimens previously of unknown affinity, are now under consideration as a group that may also warrant future description at sectional level.

The clades defined in this hypothesis are diagnosable by unique morphological characters or combinations of these characters, although one or more may often be absent or poorly pronounced. In addition, clades are well supported by Bayesian posterior probabilities and bootstrap analysis (Lucas *et al.* 2011; Santos *et al.* 2016), although relationships between clades are less robust. Future analysis is likely to increase resolution between groups and it is predicted that newly included species will be recognised within these sections or as independent, species-poor clades meriting recognition at the same rank.

Assigning sectional names in a large, nomenclaturally fraught genus can be complicated. Priority for the autonym, the name of the section that includes the generitype (in this case *Myrcia* sect. *Myrcia*), dates from the first publication of any sectional name (ICN; McNeill *et al.* 2007). In *Myrcia* this is 1828, when de Candolle recognised two sections, both of which are now considered synonyms of sect. *Myrcia* (note, Lucas *et al.* (2011) erroneously suggest that the first sectional division of *Myrcia* was by Grisebach in 1864). As names have priority only at the rank at which they are published, genus names although published earlier, could not take priority over the names of published sections. With these rules and the objective

Table 1. Current species numbers for species allocated to each section of *Myrcia* s.l. Numbers in brackets are additional species uncertainly placed in the section.

Section	Number of species
<i>Aulomyrcia</i>	140 (11)
<i>Calyptranthes</i>	277 (2)
<i>Gomidesia</i>	57 (6)
<i>Aguava</i>	32
<i>Myrcia</i>	120 (19)
<i>Eugeniopsis</i>	22 (2)
<i>Sympodiomyrcia</i>	26
<i>Reticulosae</i>	23 (2)
<i>Tomentosae</i>	9 (2)
Section unknown or not <i>Myrcia</i> s.l.	24
Total	774

of nomenclatural stability in mind, we propose the following classification, dividing *Myrcia* into nine sections. For names for which have not already been assigned types, types are designated. Some of the proposed sections may be split after future analysis but their names will be retained by the residual group that includes the type.

A key to the sections of *Myrcia* s.l. is provided followed by a diagnosis of each section and short discussion; finally, an estimate of current numbers of species per section is provided (Table 1). Species were assigned to sections using the clades returned from molecular analysis as a guide to natural species groupings (thus clades correspond to sections; see Fig. 1) and assigning species to each section after study of types, specimens and protologues. Species placement per section fluctuates as researchers adjust analyses and concepts but it is unlikely that these proportions will change radically in the future. A list of species per section will be published after nomenclatural transfers from *Marlierea* and *Calyptranthes* are complete.

Taxonomic Treatment

***Myrcia* DC.** (de Candolle 1827: 401) **nom. cons.**

Lectotype: *M. bracteolaris* (Poir.) DC. designated by McVaugh (1956: 143).

Aguava Raf. (Rafinesque 1838: 107). Type: *Aguava guianensis* (Aubl.) Raf. *Eugenia guianensis* Aubl., *Hist. Pl. Guiane* 1: 506 (Aublet 1775).

Aulomyrcia O. Berg (1855: 35). Type: *Aulomyrcia multiflora* (Lam.) O. Berg. *Eugenia multiflora* Lam., *Encycl.* 3: 202 (Lamarck 1789).

Calyptranthes Sw. (Swartz 1788: 79.). Type: *Calyptranthes chytraculia* (L.) Sw. *Myrtus chytraculia* L., *Syst. Nat. ed.* 10: 1056 (Linnaeus 1759).

Cumetea Raf. (Rafinesque 1838: 106). Type: *Cumetea alba* Raf.

Gomidesia O. Berg (1855: 5). Type: *Gomidesia spectabilis* (DC.)

O. Berg. (1857: 12) designated by McVaugh (1956:

141). *Myrcia spectabilis* DC., *Prodr.* 3: 248 (de Candolle 1828).

Marlierea Cambess. in A. St. Hil. (Saint-Hilaire 1829: 373, t. 156). Type: *Marlierea suaveolens* Cambess.

Krugia Urb. (Urban 1893: 375). Type: *Krugia elliptica* (Griseb.) Urb. *Marlierea elliptica* Griseb., *Fl. Brit. W. I.*: 233 (Grisebach 1860).

Mozartia Urb. (Urban 1923: 87). Type: *Mozartia gundlachii* (Krug & Urb.) Urb. *Myrcia gundlachii* Krug & Urb., *Bot. Jahrb. Syst.* 19: 581 (Urban 1895).

Rubachia O. Berg (1856: 11), *p.p.*, (see explanation in Lucas *et al.* (2016)). Type: *Rubachia spiciflora* O. Berg.

Trees, shrubs or sub-shrubs; hairs simple, sometimes dibrachiate; *inflorescence* usually a regularly branching panicle but sometimes very reduced, terminal *flowers* usually in groups of three or in a sub-opposite arrangement upon the rachis to form a spike; bracts and bracteoles rounded or acute, caducous or sometimes persistent after fruit fall; cataphylls present or not at leaf nodes; perianth (0 –) 4 – 5 (– 7)-merous, hypanthium extending into a tube beyond the ovary, calyx lobes free or partially or totally fused, opening by longitudinal or transverse tearing or circumscissile and falling as a calyptra at anthesis; disc flat and hairy or glabrous with hypanthium extending into a tube beyond the ovary; stamens many, usually less than 200; ovary usually bi- to tri-locular (rarely 4 – 8 locules) with 2 (rarely 1 or 3 – 8) ovules per locule; ovules arising at a single point on the septum, usually slightly below the mid-point; anthers tetrasporangiate and bilocular at anthesis with thecae of equal height or vertically displaced, often with an apical oil gland; *fruit* a fleshy berry, globose or cylindrical usually with persistent calyx lobes, cotyledons foliaceous and folded, encircled by a long hypocotyl; testa soft; scalariform plates absent.

1. *Myrcia* sect. *Calyptranthes* (Sw.) A. R. Lourenço & E. Lucas stat. nov.

<http://www.ipni.org/urn:lsid:ipni.org:names:77173693-1>

Calyptranthes Sw., *Prodr.* 5: 79 (Swartz 1788). Type: *Calyptranthes chytraculia* (L.) Sw. (Swartz 1788: 79). Basionym: *Myrtus chytraculia* L., *Syst. Nat., ed.* 10: 1056 (Linnaeus 1759).

Mitranthes O. Berg. **synon. nov.** (1856: 136). Type: *Mitranthes ottonis* O. Berg.

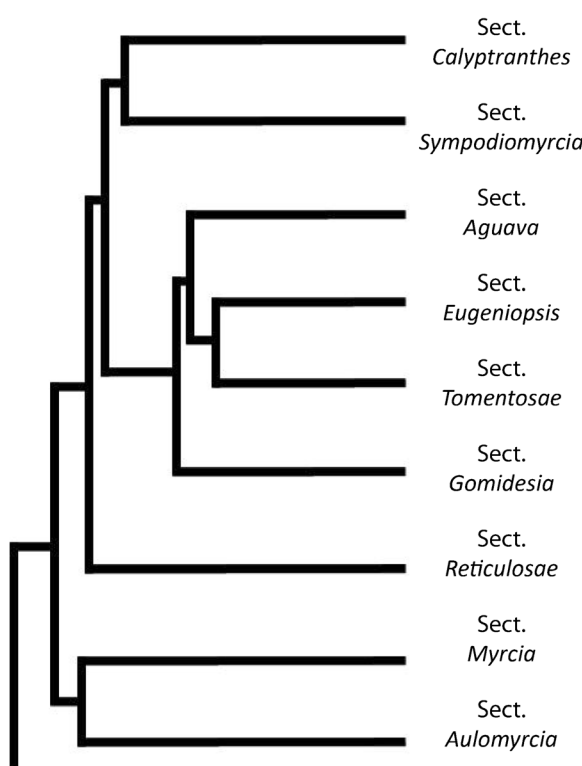
Trees or shrubs bearing pale yellow to red or brown, simple or often t-shaped, bristling trichomes; branch-

Key to the sections of *Myrcia* s.l.

1. Floral disc pilose, hypanthium apparently not, or very shortly extended above summit of the ovary 2
 Floral disc glabrous (exceptionally with hairs at base of style), hypanthium extended above summit of the ovary .3
2. Floral disc flat and covered in stiff trichomes, also visible in fruit; staminal ring thickened, usually comprising more than 60% of disc; anthers with equal sized thecae that recurve and open fully at dehiscence; fruits mostly markedly longer than wide, occasionally globose sect. **5. Myrcia**
 Floral disc flat to concave with appressed hairs, also visible in fruit; staminal ring comprising no more than 30% of disc; anthers often with vertically displaced thecae and retaining curvature at dehiscence; fruits globose sect. **3. Gomidesia**
3. Calyx lobes partially or completely fused in the bud, tearing on opening or falling as a calyptra; or if free, central point of attachment to flower narrower than width of sepal with lateral, horizontal fissures between lobe and hypanthium rim. Fruiting calyx with or without calyx lobe remains 4
 Calyx lobes free in the bud, opening regularly without tearing, not falling as a calyptra; fruits with distinct, persistent calyx lobes 7
4. Inflorescence with exclusively opposite flowers; vegetative branching usually sympodial, cataphylls usually present at leafy nodes 5
 Inflorescence with alternate or sub-opposite flowers; vegetative branching not sympodial, cataphylls occasional and indistinct 6
5. Calyx fused into a calyptra, falling completely at anthesis or remaining attached at a single point on rim; fruiting calyx without or occasionally with calyptra remains sect. **1. Calyptranthes**
 Calyx lobes free, not fused into a calyptra, attachment at central point of lobe narrower than total width with horizontal fissures between lobe and hypanthium rim or rarely (*Myrcia insigniflora*) tearing vertically through it sect. **7. Sympodiomyrcia**
6. Trichomes usually reddish; leaf surfaces often markedly discoloured in dried material, pellucid dots densely aggregated, young branchlets often mottled by darkened lenticels; inflorescence usually a regular, triangular panicle, never markedly asymmetrical or with flattened branchlets sect. **2. Eugeniopsis**
 Trichomes not reddish; leaf surfaces not markedly discoloured, pellucid dots not densely aggregated, young branchlets without darkened lenticels; inflorescence a regular, triangular panicle or long, markedly asymmetrically branched terminal paniculate whorls or with flattened branchlets emerging from leafy nodes in bundles sect. **9. Aulomyrcia**
7. Ovary 2-locular, staminal ring glabrous, comprising less than 30% of total disc width 8
 Ovary 3-locular, staminal ring pubescent or rarely glabrous, comprising more than 30% of total disc width 9
8. Hypanthium often constricted below the disc in bud; calyx lobes acute and strongly reflexed at anthesis appearing distinctly star-shaped particularly in fruit; leaves often concentrated and whorled at ends of branchlets, giving a congested appearance, as in *Prunus*, whorls subtended by brachyblasts sect. **8. Tomentosae**
 Hypanthium not constricted below the disc; calyx lobes various; leaves evenly distributed over branchlets, not congested, brachyblasts absent sect. **9. Aulomyrcia**
9. Leaves distinctly reticulate, veins raised both abaxially and adaxially, often with large and very distinct gland dots; entire plant often covered in a grey or reddish-brown felted hairs; staminal ring and often base of style lightly to densely pubescent sect. **6. Reticulosae**
 Venation not markedly reticulate, gland dots not notably distinct; plant usually not densely pubescent; staminal ring and style base glabrous sect. **4. Aguava**

lets compressed or flattened to terete, sometimes two to four-winged with distal ends of wings between the leaf-bases at opposite sides of a node, often bearing lenticels; branching sympodial, frequent in vegetative and fertile branches; bracteoles linear, rounded or triangular and acute, usually caducous; *inflorescence* paniculate, often with an abortive, congested terminal primary axis or occasionally reduced with a single terminal flower, *flowers* opposite, terminal flowers in groups of three; buds apiculate; petals 0–2 (–5), small,

calyx fused and calyptrate, circumscissile and falling as a calyptra at anthesis, or remaining attached by a small piece of tissue at one side of the hypanthium; anther thecae symmetrical, reversing curvature on dehiscence, exposing interior of sacs as a convex surface; floral disc glabrous; staminal ring narrow, usually comprising less than 30% of total disc width; hypanthium glabrous internally, extending into a turbinate tube beyond the ovary; ovary bi-locular (rarely 3–4, in species described as *Mitranthes*), with 2 ovules per



Locularity	Calyx fusion	Sympodial branching	Ovary summit	Staminal ring	Hypanthium extension
2	fused	Y (N)	glabrous	narrow, glabrous	Y
2 (-6)	rarely partially fused	Y (N)	glabrous	narrow, glabrous	Y
3	free	N	glabrous	thickened, glabrous	Y
2	free or fused	N (Y)	glabrous	narrow, glabrous	Y
2	free	N	glabrous	narrow, glabrous	short
2-3 (-5)	free	N	pubescent	narrow, sericeous	short
3	free	N	trichomes often at style base	thickened, with trichomes	short
2	free	N	pubescent	usually thickened, sericeous	short (Y)
2	free or partially fused	N (Y)	glabrous	narrow, glabrous	Y (short)

Fig. 1. Summarised phylogenetic tree of *Myrcia* s.l. modified from Santos *et al.* (2017) and Lima *et al.* (2017) with generalised key diagnostic characters for each *Myrcia* section. N = No; Y = Yes.

locule; *fruits* globose with persistent apical hypanthium tube, calyptra generally falling or occasionally still attached at one side of the rim.

DISTRIBUTION. Moist forests (Amazon and Atlantic) and cerrado (including gallery forest) of Central and South America and throughout the Caribbean; relatively few species extending to associated drier habitats.

NOTES. Section *Calyptranthes* comprises plants with wide variation in leaf and inflorescence structure but all with a perfect calyptra. Wilson *et al.* (2016) use DNA sequence data of a representative species sample to show that the majority of species described as *Calyptranthes* emerge in this clade. To date, a single species with inflorescences that do not match the above description (Wilson *et al.* 2016) emerges in *Myrcia* sect. *Aulomyrcia*. The same study shows a pattern of evolutionary distinction between a clade of Caribbean and Amazonian species and those of the Atlantic forest and Cerrado. Some *Myrcia* s.l. species, particularly from the Amazon and Guayana shield, (e.g. *Martiera uniflora*, *Martiera salticola*) have completely closed buds that tear open irregularly at anthesis leaving several portions of calyx 'lobe', one often markedly larger and interpreted as a calyptra by previous authors. These species require further study, including with molecular approaches.

Berg (1855 – 1856) described the multilocular, calyptrate genus *Mitranthes* without fruit. McVaugh (1968) then treated some *Mitranthes*, subsequently collected in fruit, as *Psidium* based on embryo characters but noted multilocular, calyptrate species with foliaceous, folded embryos that resembled *Myrcia*. On the basis of this confusion, McVaugh (1968) finally placed *Mitranthes* among his 'imperfectly known genera'. Examination of these 'myrcioid' *Mitranthes* in the herbarium and in the field revealed them to strongly resemble species of section *Calyptranthes* in their extremely pronounced and regular sympodial branching and perfect calyptra as well as pale brown to red bristling trichomes. Species described as *Mitranthes* have larger flowers and fruits than those of section *Calyptranthes* (for images, see <http://myrcia.myspecies.info/>). Detailed taxonomic and nomenclatural summaries of *Calyptranthes* can be found in McVaugh (1958) and in Rosário *et al.* (2014); the latter work provides additional characterisation to the original authorship.

2. *Myrcia* sect. *Eugeniopsis* (O. Berg) M. F. Santos & E. Lucas comb. nov.

<http://www.ipni.org/urn:lsid:ipni.org:names:77173695-1>

Eugeniopsis O. Berg, *Linnaea* 27: 80 (1855). Type: *Myrcia multipunctata* Mazine (in Mazine *et al.* 2014: 99).

Basionym: *Eugenia laevigata* DC. (de Candolle 1828: 283).

Marlierea subg. *Eugeniopsis* (O. Berg) Kiaersk. (Kiaerskou 1893: 50)

Marlierea sect. *Eugeniopsis* (O. Berg) Nied. (Nieden zu 1893: 76).

Marlierea sect. *Pseudocalyptra* D. Legrand (1975: 7).

Type: *Marlierea eugeniopsoides* (D. Legrand & Kausel) D. Legrand (1975: 7).

Trees or *shrubs*, hairs usually reddish and t-shaped; pellucid dots dense on leaves and reproductive structures; branchlets terete, often bearing lenticles; branching usually monopodial (rarely sympodial) bracteoles rounded or acute, usually caducous; *inflorescence* usually a regularly branching panicle with an abortive, congested terminal primary axis, terminal *flowers* in groups of three; buds clavate (rarely turbinate or globose); petals (4 –) 5, calyx partially fused (calyx lobes rarely free or completely fused), tearing open parallel to hypanthial tissue, tearing usually regularly; anther thecae of equal height, reversing curvature on dehiscence, exposing interior of sacs as a convex surface; floral disc glabrous; staminal ring narrow, usually comprising less than 30% of total disc width; hypanthium extending into an abruptly flared tube beyond the ovary; ovary bi-locular with 2 ovules per locule; *fruits* globose or obovoid with persistent, apical hypanthium tube, calyx remains generally falling.

DISTRIBUTION. Atlantic Forest with occasional occurrences in campos rupestres.

NOTES. *Myrcia* sect. *Eugeniopsis* species are united by the following suite of characters that are not always all present: leaves with open venation, distinct, regular, medium sized gland dots, leaf mid-vein and young branchlets distinctively covered in lenticles, inflorescence usually regularly branching, floral buds clavate (rarely globose or turbinate), calyx lobes partially fused (rarely totally fused or free) and deciduous parallel to the hypanthium ring. *Myrcia* sect. *Eugeniopsis* includes most species previously described as *Eugeniopsis* O. Berg (1855 – 56, 1857 – 58; see Lucas *et al.* 2011) but also *Myrcia eugeniopsoides* (D. Legrand & Kausel) Mazine and *Myrcia oblongata* DC. Berg (1855 – 56, 1857 – 58) treated three myrcioid genera with tearing calyces, describing *Rubachia* as well as *Eugeniopsis*. Berg distinguished *Marlierea* by its completely or nearly completely closed bud whereas *Rubachia* and *Eugeniopsis* were distinguished by their short sepals in bud, 3 – 5 sepals in the case of *Rubachia* that eventually tear to the summit of the ovary, and 4 sepals in *Eugeniopsis* that tear more or less regularly into the hypanthium without reaching the ovary. Bentham & Hooker (1865) included the latter two genera in a more inclusive *Marlierea* before Kiaerskou (1893) and Niedenzu (1893) circumscribed three (homonym) generic subdivisions (subgenera or sections, respectively) within *Marlierea*:

Eumarlierea, *Rubachia* and *Eugeniopsis*. Legrand (1962) recognised only *Marlierea* section *Marlierea* (with two subsections; subsect. *Clausae*, bud closed, tearing into 4 – 5 lobes, and subsect. *Apertae*, bud open, tearing into (3) 4 – 5 lobes, with *Rubachia* in the synonymy of the latter subsection) and section *Eugeniopsis*, eventually describing a third section, *Pseudocalyptra* (Legrand 1975) to house *Marlierea eugeniopsoides* after its transfer from *Calyptanthes*.

3. *Myrcia* sect. *Gomidesia* (O. Berg) B. S. Amorim & E. Lucas comb. & stat. nov.

<http://www.ipni.org/urn:lsid:ipni.org:names:77173711-1>

Gomidesia O. Berg, *Linnaea* 27: 5 (1855). Type: *Gomidesia spectabilis* (DC.) O. Berg. (1857: 12) designated by McVaugh (1956: 141). Basionym: *Myrcia spectabilis* DC., *Prodr.* 3: 248 (1828).

Cerqueiria O. Berg (1856: 5). Type: *Cerqueiria sellowiana* O. Berg.

Trees or *shrubs*, often covered in a brownish pubescence, hairs simple or unevenly dibrachiate; branchlets terete; branching usually monopodial; bracteoles usually caducous; *inflorescence* formed from confluences of 2 – 6 (– 8) generally symmetrical uniflorescences; buds globose; perianth usually 5-merous, petals and equally sized sepals distinct and imbricate, abaxially pubescent, calyx lobes generally truncate or rounded, rarely acute; anthers with the internal sac of each pair of locules clearly or slightly overtopping the external sac, open thecae retaining or losing curvature on dehiscence but never reversing and exposing interior of sacs as a convex surface; floral disc pubescent, usually with a light covering of appressed hairs; staminal ring narrow, usually comprising less than 30% of total disc width; hypanthium internally glabrous or pubescent, extending into a short tube beyond the ovary; ovary 2 – 3 (–5)-locular with 2 ovules per locule; *fruits* globose, often pubescent, with persistent calyx lobes erect at apex.

DISTRIBUTION. Atlantic coastal and associated lowland, montane and gallery forests and cerrado, extending to the Amazon and Caribbean.

NOTES. Species of section *Gomidesia* are defined by the frequent, but not exclusive, combination of silky white, yellow, brown or red pubescence, specialised vertically displaced anthers, a prolonged, internally pubescent hypanthium and usually truncate, erect calyx lobes, particularly in fruit. Abaxial venation in this group is often prominent. The genus *Gomidesia* was described based almost entirely on the presence of anthers with displaced thecae (Nic Lughadha 1997) but in some species this character is not pronounced. Nic Lughadha *et al.* (2010) discuss *Myrcia* 'section *Gomidesia*' even though it was not then published at this rank. The name is here validated. Amorim *et al.* (in prep.) will provide a more detailed phylogenetic review of this section.

4. Myrcia sect. **Aguava** (Raf.) D. F. Lima & E. Lucas
comb. & stat. nov.

<http://www.ipni.org/urn:lsid:ipni.org:names:77173712-1>

Aguava Raf., *Sylva Tellur.*: 107 (Rafinesque 1838).

Lectotype, designated here: *Aguava guianensis* (Aubl.) Raf. (Rafinesque 1838: 107). Basionym: *Eugenia guianensis* Aubl., *Hist. Pl. Guiane* 1: 506 (Aublet 1775).

Atomostigma Kuntze (1898: 76). Type: *Atomostigma mattogrossense* Kuntze.

Calyptromyrcia O. Berg (1856: 34). Type: *Calyptromyrcia cymosa* O. Berg

Trees, shrubs or *woody sub-shrubs*; hairs simple; branchlets usually terete or sometimes tetragonal; branching not sympodial; bracteoles rounded or acute, usually caducous; *inflorescences* usually a symmetrical, regularly branching triangular panicle; buds globose; perianth 5-merous, petals and sepals distinct and imbricate, sepals internally pubescent; anther thecae of equal heights, reversing curvature on dehiscence, exposing interior of sacs as a convex surface; floral disc glabrous; staminal ring glabrous and somewhat thickened, usually comprising 30 – 40% of total disc width; hypanthium internally glabrous extending into a flared tube beyond the ovary; ovary consistently tri-locular with 2 ovules per locule; fruits globose, with persistent calyx lobes and flared hypanthium tube at apex.

DISTRIBUTION. Common throughout the distribution of *Myrcia* s.l., found in all tropical biomes including very wet and dry habitats.

NOTES. *Myrcia* sect. *Aguava* is well defined by the characters of a regularly branching multi- or pauciflorous panicle, the hypanthium extended beyond the ovary and internally glabrous, five non-tearing, regular calyx lobes, a moderately thickened, glabrous staminal ring and a tri-locular ovary. Individuals are usually glabrous or glabrescent. The most common and widespread species of this group is *Myrcia guianensis* which has a steadily increasing synonymy (Lima 2017, Lima *et al.* in prep.). *Myrcia* sect. *Aguava* differs from the other trilocular sect. *Reticulosae* in leaf characters (thicker leaves with more prominent venation and large gland-dots in the latter group) and in pubescence on the staminal ring and style base (trichomes are present on these structures in the latter group). *Myrcia* sect. *Aguava* differs from sect. *Aulomyrcia* in its venation (mid-vein impressed in the latter group while flat or adaxially prominent in sect. *Aguava*) and its locularity (bilocular in the latter group).

5. Myrcia sect. **Myrcia**. Type: *Myrcia bracteolaris* (Poir.) DC.

Myrtus bracteolaris Poir. in Lam., *Encycl.* 4: 411 (Lamarck 1798).

Myrcia sect. *Oocarpae* DC. (de Candolle 1828: 255).
Lectotype designated here: *Myrcia formosiana* DC. (de Candolle 1828: 255).

Myrcia sect. *Sphaerocarphae* DC. Type: *M. bracteolaris* (Poir.) DC. (de Candolle 1828: 245).

Myrcia sect. *Debracteatae* Nied. (Nieden zu 1893: 75).
Lectotype designated here: *Myrcia splendens* DC. (de Candolle 1828: 244).

Myrcia sect. *Bracteatae* O. Berg ex Nied. Lectotype designated here: *Myrcia bracteata* (Rich.) DC. (de Candolle 1828: 245).

Eugenia bracteata Rich., *Actes Soc. Hist. Nat. Paris* 1: 110 (Richard 1792).

Cumetea Raf. (Rafinesque 1838: 106). Lectotype designated here: *Cumetea alba* Raf.

Calycampe O. Berg (1856: 129). Type designated by McVaugh (1956: 138): *Calycampe latifolia* O. Berg

Myrcia sect. *Eumyrcia* Griseb. **nom. inval.** (Art. 21.3 ICBN (McNeill *et al.* 2012)).

Trees, shrubs or *woody sub-shrubs*; hairs simple; branchlets terete or sometimes tetragonal; branching not sympodial; venation often closed with little distinction between primary and secondary veins; bracteoles rounded or acute, usually caducous; *inflorescences* usually a symmetrical, regularly branching triangular panicle; buds globose; perianth 5-merous, petals and sepals distinct and always free, imbricate and acute, abaxially and/or adaxially pubescent, adaxial hairs frequently silver, silky and appressed; anther thecae of equal heights, reversing curvature on dehiscence, exposing interior of sacs as a convex surface; floral disc flat and pubescent, typically hard to distinguish from broad, densely sericeous staminal ring comprising 60% or more of disc width, occasionally less thick but always sericeous with stiff hairs; hypanthium short, scarcely extending into a tube beyond the ovary, outer surface with appressed, silky hairs to copiously lanate; ovary bi-locular with 2 ovules per locule; *fruits* cylindrical, with persistent calyx lobes held separated and erect at apex.

DISTRIBUTION. Common throughout the distribution of *Myrcia* s.l.

NOTES. Section *Myrcia* is a clearly defined group with five free calyx lobes and almost always, a distinctive broad, flat, pubescent disc and commonly cylindrical, rarely globose fruits. The most common and widespread species is *Myrcia splendens*, however there are many other very distinct species within the group. *M. splendens* is a species within which it is extremely difficult to draw morphological species boundaries and has become something of a 'dustbin' species to which widely differing specimens have been assigned without exhaustive study. This section is under focused study by Lima dos Santos (in prep.).

6. *Myrcia* sect. *Reticulosae* D. F. Lima & E. Lucas sect. nov. Type: *Myrcia reticulosa* Miq. (Miquel 1850: 794).

<http://www.ipni.org/urn:lsid:ipni.org:names:77173713-1>

Trees or *shrubs*; often covered in a grey or reddish-brown felt, particularly on young branches, hairs simple; branchlets terete; branching not sympodial; venation distinctly rugose, often with one or few large and distinct glands per vein reticulation, veins raised abaxially and adaxially; bracteoles rounded or acute, usually caducous; *inflorescences* usually a symmetrical, regularly branching triangular panicle; buds globose; perianth 5-merous, petals and sepals distinct and imbricate, sepals internally pubescent, often acute and ciliate; anther thecae of equal heights, reversing curvature on dehiscence, exposing interior of sacs as a convex surface; floral disc pubescent at the base of style or glabrous; staminal ring with trichomes, thickened, usually comprising 30 – 40%, occasionally a little more, of total disc width; hypanthium internally glabrous, extending into a somewhat flared tube beyond the ovary; ovary tri-locular with 2 ovules per locule; fruits globose, often with persistent calyx lobes and the hypanthium tube flared at the apex.

DISTRIBUTION. Atlantic coastal forests, cerrado and campos rupestres.

NOTES. Species of sect. *Reticulosae* share several characteristics with sect. *Aguava* such as regularly branching inflorescences, regular calyx lobes and consistent tri-locularity. However, DNA-based evidence repeatedly supports independent origins for these clades (Lucas *et al.* 2011; Lima *et al.* in prep.), a pattern supported by morphological differences such as the former section having highly reticulate, textured leaves with large, widely spaced pellucid gland dots, an often waxy cover on the adaxial surface of the leaf and a consistently hairy staminal ring. Section *Reticulosae* currently includes species from a clade of uncertain placement, namely *Myrcia maximiliana* O. Berg, *M. pulvinata* B. S. Amorim, *M. robusta* Sobral, *M. thomasii* B. S. Amorim & A. R. Lourenço and *M. unana* Sobral, Faria & Villaroel; these species are placed here for now due to their congruent morphology.

7. *Myrcia* sect. *Sympodiomyrcia* M. F. Santos & E. Lucas (2016: 759). Type: *Myrcia subcordata* DC. (de Candolle 1828: 253).

Trees or *shrubs*; hairs dibrachiata; branching sympodial or monopodial; branchlets often terete or winged with distal ends of wings terminating at leaf petioles; cataphylls usually present at the base of internodes; bracteoles generally lanceolate or ovate, usually caducous; *inflorescence* a panicle, usually branching from a

single point at the base, with two to more than ten branches of similar dimensions; terminal *flowers* in groups of three or often only one flower; buds turbinate or clavate (rarely globose); perianth (3 –) 4 – 5 (– 7)-merous, calyx lobes internally glabrous or pubescent, usually distinct from the hypanthium, free, tearing regularly, parallel to rim of hypanthium upon opening, except in *Myrcia insigniflora* M. F. Santos (2014: 99); anther thecae of equal heights, reversing curvature on dehiscence, exposing interior of sacs as a convex surface; floral disc glabrous; staminal ring narrow, comprising less than 30% of total disc width; hypanthium internally glabrous, extending into a turbinate or clavate tube beyond the ovary; ovary bi-locular with usually 2 ovules per locule, although occasional collections of *M. subavenia* are reported with ten seeds (Faria pers. comm.); *fruits* globose with persistent apical hypanthium tube, calyx lobes usually falling or remnants occasionally still attached.

DISTRIBUTION. Atlantic Forest, cerrado (campo rupestre and riparian forest, not savanna), and a disjunct distribution in the Guiana Shield.

NOTES. Section *Sympodiomyrcia* is clearly defined by the combined characters of: presence of cataphylls at the base of the internodes; inflorescence with sympodial basal branching in which two or more branches of similar dimensions are developed; inflorescence with apical branching always opposite; turbinate or clavate floral buds (rarely globose); the hypanthium elongated above the ovary and not tearing during anthesis and free calyx lobes that are deciduous parallel to the hypanthium rim. The free calyx lobes detach from the rim of the hypanthium in mature flowers and fruit, usually via horizontal fissures along the rim, suggesting a close relationship with section *Calyptranthes*. Sympodial branching (mostly found in the inflorescence basal branching) is also reminiscent of section *Calyptranthes*; bud shape and mature fruits are also similar particularly after removal of the calyx lobes. *Myrcia insigniflora* is an exception to these floral features with the hypanthium tearing vertically during anthesis and persistent calyx lobes. However, most characters of *M. insigniflora* are congruent with section *Sympodiomyrcia* including the presence of cataphylls and the architecture of the inflorescence.

8. *Myrcia* sect. *Tomentosae* E. Lucas & D. F. Lima sect. nov. Type: *Myrcia tomentosa* (Aubl.) DC. (de Candolle 1828: 245).

<http://www.ipni.org/urn:lsid:ipni.org:names:77173714-1>

Eugenia tomentosa Aubl., *Hist. Pl. Guiane* 1: 504 (Aublet 1775).

Trees, shrubs or woody sub-shrubs; hairs simple; branchlets terete; branching usually monopodial with leaves concentrated and whorled at ends of branchlets giving a congested appearance such as in *Prunus*, whorls commonly subtended by clusters of acute to elliptic brachyblasts; bracteoles usually triangular and sharply acute, usually persistent after fruit fall; *inflorescence* usually an asymmetrical, irregularly branching panicle giving a zig-zagged appearance and occasionally appearing spike-like; buds ovate, often with a constriction or slight constriction beneath ovary; perianth 5-merous, sepals distinct, triangular, acute, imbricate and adaxially pubescent; anther thecae of equal heights, reversing curvature on dehiscence, exposing interior of sacs as a convex surface; floral disc glabrous; staminal ring narrow, comprising less than 30% of total disc width; hypanthium usually internally glabrous extending into a short tube beyond the ovary; ovary bi-locular with 2 ovules per locule; *fruits* globose, rarely exceeding 8 mm diam., with triangular calyx lobes strongly reflexed and appressed to fruit in a characteristic star shape.

DISTRIBUTION. Common throughout the distribution of *Myrcia* s.l.

NOTES. Section *Tomentosae* is a well-defined, widespread section but includes relatively few species. It is easily defined by buds with a distinct constriction below the ovary, small flowers and fruits relative to the other sections and the characteristic reflexing of the regular, free calyx lobes, in particular in fruit. Other distinctive characters are a pruinous indument at the base of branches and often congested branchlets interspersed with persistent bracts. The section is easy to define and distinct morpho-types can be recognised as separate species (e.g. *Myrcia tomentosa* (Aubl.) DC., *M. laruotteana* Cambess). Population level studies (Lima *et al.* 2015) show that a morphological continuum exists that agrees to some extent with geographical distribution and genetic variation within populations is greater than among populations. This implies that the populations are genetically similar and genetic flow takes place between them. Santos *et al.* (2016) indicate this to be one of the youngest clades in *Myrcia* s.l.; this may explain the lack of genetic distinction. The study concludes that clear morphological and genetic definition of species within this group is not straightforward task.

9. *Myrcia* sect. *Aulomyrcia* (O. Berg) Griseb. (Grisebach 1860: 234).

Aulomyrcia O. Berg, *Linnaea* 27: 35 (1855). Lectotype (designated by McVaugh 1956: 137): *Myrcia multiflora* (Lam.) DC. (de Candolle 1828: 244).

Eugenia multiflora Lam. (Lamarck 1789: 302).

Krugia Urb. (Urban 1893: 375). Type: *Krugia elliptica* (Griseb.) Urb.

Marlierea elliptica Griseb. (Grisebach 1860: 234).

Myrcia sect. *Aulomyrcia* Nied. as "Sect. 1. *Eu-Aulomyrcia*".

Lectotype designated by Lucas *et al.* (2016): *Myrcia pyrifolia* (Desv.) Nied. (Niedenzu 1893: 76).

Eugenia pyrifolia Desv. ex Ham. (Hamilton 1825: 44).

Marlierea Cambess. in A. St. Hil. (Saint-Hilaire 1829: 373). Type: *Marlierea suaveolens* Cambess.

Mozartia Urb. (Urban 1923: 87). Type: *Mozartia gundlachii* (Krug. & Urb.) Urb.

Myrcia gundlachii Krug & Urb. (Urban 1895: 581).

Marlierea sect. *Myrciopsis* McVaugh (1958: 79) [Unintentionally published as sect. *Myrcioides* (McVaugh 1963)]. Type: *Marlierea bipennis* (O. Berg) McVaugh (1956: 189).

Myrciaria bipennis O. Berg (1862: 259).

Myrcia sect. *Armeriela* McVaugh (1968: 378). Type:

Myrcia inaequiloba (DC.) Lemée (1954: 150).

Eugenia inaequiloba DC. (de Candolle 1828: 282).

Rubachia O. Berg (1856: 11), *p.p.*, (see explanation in Lucas *et al.* 2016). Type: *Rubachia spiciflora* O. Berg.

Trees or shrubs; hairs mostly simple, dibrachiate in some species; branchlets terete; branching usually monopodial; bracteoles usually triangular and acute, usually persistent after fruit fall; *inflorescence* variable from a triangular, asymmetrical panicle to a single terminal whorl representing a compression of all primary inflorescence nodes, with long, irregularly branched primary axes that appear asymmetrical, often with a zig-zagged appearance and occasionally appearing spike-like, occasional clusters of shorter panicles with flattened rachises emerging from leaf nodes, apparently in clumps; buds clavate or ovate; perianth 4 – 5-merous, calyx lobes free to partially or completely fused, often irregularly sized, opening regularly or irregularly tearing vertically through the calyx and hypanthial tissue, leaving calyx lobes of markedly different sizes or of regular triangles in a 'star' shape, where tears are deep, staminal scars appear at the tips of calyx lobes; anther thecae of equal heights, reversing curvature on dehiscence, exposing interior of sacs as a convex surface; floral disc glabrous; staminal ring narrow usually glabrous, occasionally pubescent, comprising less than 40% of total disc width; hypanthium extending somewhat beyond the ovary but inconspicuous after deep tearing; ovary bi-locular with 2 ovules per locule; *fruits* globose.

DISTRIBUTION. Amazon forest, the Guayana shield, Caribbean and the Atlantic coastal forests (particularly Bahia and Espírito Santo), extending to associated drier habitats.

NOTES. Detailed discussion of the taxonomic and nomenclatural history of *Myrcia* section *Aulomyrcia* can be found in Lucas *et al.* (2016).

Acknowledgements

We recognise with gratitude, the input of an anonymous reviewer with scrupulous attention to nomenclatural

detail. This work is the culmination of nearly ten years of taxonomic consideration. People without whose input this paper would not have been possible from the laboratory, herbarium and field, are very many. We gratefully acknowledge particular assistance from Daniela Zappi, Christine Wilson, Jomar Jardim, Lidyane Aona, Jair Faria, Fiorella Mazine, Diego Bogarin, Keron Campbell, Jim Clarkson, Teodoro Clase, Tracey Commock, Lazlo Cziba, Dion Devey, Edith Kapinos, Judeen Meikle, William Milliken and Felix Forest. Matheus F. Santos received a Post-doctoral Fellowship (PDJ) from CNPq Brazil (150217/2016-1). Duane F. Lima received sandwich and PhD fellowships from CNPq (205237/2014-2; 165669/2013-6). These grants contributed directly to this research.

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