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Systematic Studies in Myrtaceae of the Greater and Lesser Antilles

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

SYSTEMATIC STUDIES IN MYRTACEAE OF THE GREATER AND LESSER ANTILLES

A dissertation submitted in partial fulfillment of

the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

BIOLOGY

by

Jonathan A. Flickinger

2020

To: Dean Michael R. Heithaus
College of Arts, Sciences and Education

This dissertation, written by Jonathan A. Flickinger, and entitled Systematic Studies in Myrtaceae of the Greater and Lesser Antilles, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

Heather Bracken-Grissom

Grenville Draper

Brett Jestrow

Jennifer Richards

Javier Francisco-Ortega, Major Professor

Date of Defense: October 21, 2020

The dissertation of Jonathan A. Flickinger is approved.

Dean Michael R. Heithaus
College of Arts, Sciences and Education

Andrés G. Gil
Vice President for Research and Economic Development
and Dean of the University Graduate School

Florida International University, 2020

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CHAPTER I

Material for Chapter I first appeared in an article titled “A new species of *Eugenia* (Myrtaceae) from the island of Anguilla”, in Harvard Papers in Botany vol. 23, 2018, pp. 213–216 and is reprinted here with permission of the editors of Harvard Papers in Botany.

CHAPTER II

This is the accepted version of the following article: Flickinger, J. A., B. Jestrow, R. Oviedo Prieto, E. Santiago-Valentín, J. Sustache-Sustache, F., Jiménez-Rodríguez, K. C. St. E. Campbell, and J. Francisco-Ortega. 2020. A phylogenetic survey of Myrtaceae in the Greater Antilles with nomenclatural changes for some endemic species. Taxon 69: 448–480, which has been published in final form at [https://doi.org/10.1002/tax.12263]. This article may be used for non-commercial purposes in accordance with the Wiley Self-Archiving Policy [http://www.wileyauthors.com/self-archiving].

ALL OTHER WORK

DEDICATION

To my uncle, Terry A. Adams (1950–2018).

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ABSTRACT OF THE DISSERTATION

SYSTEMATIC STUDIES IN MYRTACEAE OF THE GREATER AND LESSER ANTILLES

by

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Florida International University, 2020

Miami, Florida

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The Myrtaceae, or myrtle family, are a group of flowering trees and shrubs represented in the Americas by over 2000 species of the predominantly Neotropical tribe Myrteae. Recent progress on the challenging systematics of the group has been achieved through molecular phylogenetics, but few of the almost 500 species endemic to the islands of the Greater and Lesser Antilles in the Caribbean have been included in either phylogenetic or revisionary studies. The purpose of my dissertation is therefore to contribute to the description and phylogenetic classification of Antillean Myrtaceae. The first study describes *Eugenia walkerae*, a new species of conservation concern endemic to the island of Anguilla in the Lesser Antilles. The second study surveys the diversity of Myrtaceae present in the Greater Antilles. Members of all genera native to the region were sampled through field work across the region and included in a phylogeny inferred from one nuclear and three chloroplast genetic regions with known representatives of major clades. On the basis of the results, three Greater Antillean endemic genera (*Calyptrogenia*, *Hottea*, and *Mitranthes*) are reduced to synonyms, *Pseudanamomis* and *Calycolpus* sensu Bisse are found to be polyphyletic, and the Greater Antillean species of

Plinia are included within *Myrciaria*. The presence of two new lineages in the region within subtribe Myrtinae and *Eugenia* is also identified. The third study revises the taxonomy of the Lathberry Clade, a novel group of seven species of *Eugenia* distributed from Puerto Rico through the Lesser Antilles. The morphology and seed coat structure of each species of this clade were examined from herbarium material, and a phylogeny was inferred from three non-coding nuclear genetic regions. The results of these investigations are summarized in a taxonomic treatment including extinction risk assessments. My dissertation shows that the outstanding diversity of Myrtaceae in the Greater and Lesser Antilles consists mostly of species of major lineages also found on adjacent continents. It also lays a foundation for further descriptive and phylogenetic work needed to advance the systematics of Myrtaceae in the region.

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PREFACE

Chapters I and II were submitted for publication and formatted according to journal specifications. Acronyms used for herbaria throughout the work follow Index Herbariorum:

Thiers, B. 2020. [continuously updated] *Index Herbariorum: A global directory of public herbaria and associated staff.* New York Botanical Garden's Virtual Herbarium. Available from: http://sweetgum.nybg.org/science/ih/ (last accessed July 2020).

INTRODUCTION

Systematics, encompassing the documentation, classification, and explanation of biodiversity (Daly et al. 2010), is an essential area of research for the conservation and sustainable use of the world’s plant life (Prance 1995). Of the approximately 330000 known species of land plants (Christenhusz and Byng 2016), an estimated 1/5 are threatened with extinction (Brummit et al. 2015). These threatened species are concentrated in hotspots of biodiversity, including almost all tropical islands (Myers et al. 2000). Such areas are thus logical priorities for both conservation and biodiversity studies. My dissertation contributes to the systematics of a species-rich and taxonomically challenging group of plants to inform conservation efforts in the Caribbean Island Biodiversity Hotspot, encompassing the islands of the Greater and Lesser Antilles (Smith et al. 2004).

Systematic Background**—**The Myrtaceae, or myrtle family, are a group of approximately 6000 species of flowering plants found in tropical and warm temperate regions around the world (Govaerts et al. 2020). Its members are trees and shrubs, rarely lianas (e.g., in *Metrosideros* Gaertn., Wilson 2011), that are frequently encountered in tropical forests (Gentry 1988). Myrtaceae are characterized by possession of terpenoid-producing oil glands (secretory cavities) on the vegetative parts and anther connectives as well as by syncolporate pollen grains (Johnson and Briggs 1984). The flowers are usually bisexual and radially symmetrical with an inferior, compound ovary and a 4–5-merous perianth (Dahlgren and Thorne 1984). Well known members of the family include fruit trees such as guava (*Psidium guajava* L.); sources of essential oils such as allspice (*Pimenta diocia* (L.) Merr.), clove (*Syzygium aromaticum* (L.) Merr. & L.M.Perry), and tea tree (*Melaleuca alternifolia* (Maiden & Betche) Cheel); and species grown for timber and wood pulp such as various species of *Eucalyptus* L'Her. (Wilson 2011). In addition, some members, e.g., bottlebrush (*Melaleuca* L. spp.), are cultivated as ornamentals or find use in floristry, including the juvenile foliage of *Eucalyptus* spp. and flowers of *Leptospermum* J.R. Forst & G.Forst.

All species of Myrtaceae native to the Caribbean region belong to the tribe Myrteae DC., one of 15 currently recognized tribes within subfamily Myrtoideae Sweet (Wilson et al. 2005). In contrast to subfamily Psiloxyloideae Schmid, Myrtoideae includes plants characterized by polystemonous flowers (Schmid 1980). Fleshy fruits occur within several groups of Myrtoideae, but the two principal fleshy-fruited clades are the tribes Myrteae, which is predominantly Neotropical, and Syzygieae P.G. Wilson, which is limited to the Paleotropics (Wilson 2011). Myrteae differ morphologically from Syzygieae in typically possessing simple or dibrachiate trichomes, axillary inflorescences, and bitegmic ovules (Schmid 1972, Wilson 2011). In total, there are ca. 46 genera (Vasconcelos et al. 2017b) and ca. 2500 species of Myrteae (Govaerts et al. 2020). Over 2000 of these species, representing 30 genera, occur in the New World (Govaerts et al. 2020), and all species native to this region except for *Metrosideros stipularis* (Hook. & Arn.) Hook.f. belong to Myrteae (McVaugh 1968).

The numerous species of Myrtaceae in the New World are considered a taxonomically challenging group. McVaugh (1968) succinctly stated the problem they pose: "The species of American Myrtaceae are distressingly alike in aspect and in most individual characters, making identification and classification of both genera and species a correspondingly difficult and tedious matter." McVaugh's remark, however, may give the false impression that all species of Myrteae look the same. In contrast, Bisse (1979) summarized the situation as follows: “The great uniformity in the *Bauplan* of the Myrtaceae-Myrtoideae makes it difficult to divide them up into genera in the sense of natural phylogenetic groups, while at the species level, there exist highly individual taxa that are generally easily distinguished” (author’s translation). The issue, therefore, is not that all species of Myrteae look the same and diversity is cryptic—indeed, the differences among species may be quite striking—but that it is difficult to identify taxonomically useful characters and that variation within genera is perceived to be as great as variation among genera, which, as is clear from the review of McVaugh (1968), have traditionally been a focus of controversy. In combination with the large number of species involved, taxonomic uncertainties, particularly at the generic level, impede identification, as well as the completion of comparative studies, by greatly increasing the number of species that must be considered.

***Research Needs*—**Phylogenetic studies of Myrteae are accordingly needed to provide an objective basis for classification that reflects evolutionary relationships. Molecular phylogenetic studies in particular can help overcome problems with homoplasy in classifications solely determined by phenotypic characters. For example, fusion of the calyx, which has been used to segregate taxa at the generic level, has occurred independently in several genera (Landrum 1984) and even multiple times through different mechanisms within genera (Vasconcelos et al. 2017a, Giaretta et al. 2019). Similarly, the three basic embryo types of de Candolle (1827), which were long used for the definition of subtribes, were each shown to have evolved multiple times within the tribe (Lucas et al. 2005, 2007). These examples highlight how characters and classifications can be re-evaluated in a phylogenetic context, but phylogenetic studies also importantly facilitate comparative studies of taxa by defining manageable, monophyletic units to serve as appropriate units of study. The need for descriptive taxonomic studies of New World Myrtaceae to complement phylogenetic work remains strong as new species continue to be discovered and further information accumulates on known species, demanding a synthesis of new findings. Thus, both phylogenetic and descriptive taxonomic studies are critical for advancing the field of Myrteae systematics.

The species of Myrtaceae that occur in the Greater and Lesser Antilles merit attention for their contributions to the diversity of this globally significant region as well as to the tribe Myrteae. These islands account for almost all of the species of Myrtaceae in the Caribbean Island Biodiversity Hotspot, which also includes the Bahamas Archipelago and minor islands off the northern coast of South America (Smith et al. 2004). The native flora of the Greater and Lesser Antilles plus the Bahamas Archipelago, the West Indies sensu Acevedo-Rodríguez and Strong (2008, 2012), consists of over 10000 taxa (species and infraspecies) of seed plants, of which approximately 70% are endemic to the region (Acevedo-Rodríguez and Strong 2012). Myrtaceae are the fifth most diverse family in the West Indian flora with close to 500 endemic taxa, most of which are restricted to the Greater Antilles (Acevedo-Rodríguez and Strong 2012). At the generic level, there are approximately 180 endemic genera of seed plants in the Caribbean Island Biodiversity Hotspot (Francisco-Ortega et al. 2007), including three genera of Myrtaceae that are recognized as endemic to the Greater Antilles (Acevedo-Rodríguez and Strong 2012). Altogether, approximately one-fifth of the species of Myrteae are restricted to the Antilles. Inclusion of these species in studies of the group is therefore necessary to obtain a comprehensive understanding of its diversity and evolution. Unfortunately, relatively few Caribbean species have been the subject of recent phylogenetic or descriptive taxonomic studies.

Previous Studies**—**Since the last attempt to treat all known New World species of Myrtaceae by Otto Berg (1855–1856, 1858, 1861, 1863), taxonomic treatments of Myrtaceae have necessarily been restricted in scope to smaller regions. Only two works published over a century ago specifically dealt with Myrtaceae of the Caribbean Islands on a regional scale. The earlier work by Hjalmar Kiaerskou (1889–1890), treated about 60 species that were mostly collected by Baron von Eggers, Leopold Krug, Paul Sintenis, and Augustin Stahl. The work by Ignatz Urban (1894–1895) was considerably more comprehensive, treating 177 species and numerous synonyms in a systematic arrangement. Urban’s study quickly became outdated by continued taxonomic research, largely by Urban himself. Especially noteworthy are several of the papers he authored describing the collections of Erik Ekman from Cuba (Urban 1923, 1928) and Hispaniola (Urban 1926, 1927, 1929, 1931), which contain detailed descriptions of many new species together with critical observations on those already known.

The most recent taxonomic syntheses are provided by the floristic treatments listed by Acevedo-Rodríguez and Strong (2008, Table 1). Coverage within the Greater Antilles by these treatments is limited to single islands or nations, which severely restricts their utility for understanding taxa and their relationships. A few supplementary works on Myrtaceae are noted here. For Cuba, these include revisions of *Pimenta* Lindl. and *Myrtus* L., along with numerous novelties, published by Attilla Borhidi and Onaney Muñiz (1977, 1978); treatments of *Calycolpus* O.Berg (Bisse 1983), *Mosiera* Small

(Bisse 1986), and *Pseudanamomis* Kausel (Bisse 1985) by Johannes Bisse; a synopsis of subtribe Myrtinae Nied. by Armando Urquiola Cruz and collaborators (Urquiola Cruz et al. 2014); and a revision of the genus *Plinia* L. by Zenia Acosta Ramos (2014). For Jamaica, George Proctor (1982) published what amounted to a revision of the Greater Antillean endemic genus *Mitranthes* O.Berg along with descriptions of endemic species in several genera. Although there have not been major taxonomic updates for Hispaniola, Brigido Peguero published summaries of the diversity (2007) and uses of this family (2011) on the island and two further works dealing with recent collections of the Hispaniolan endemic genus *Calyptrogenia* Burret (Peguero et al. 2005a, 2005b). A few taxonomic changes for the Myrtaceae of Puerto Rico were included in the summary of the flora by Frank Axelrod (2011).

Taxonomic studies that are not limited by geography have also dealt with some Antillean species. A monograph of the mostly Caribbean genus *Pimenta* (Landrum 1986) treated 13 insular species (11 endemic), excluding five recently recognized taxa (Urquiola et al. 2008, Vasconcelos et al. 2018, Flickinger et al. 2020). Landrum's (1986) monograph of *Pimenta* also included a phylogeny inferred from morphological features for the 15 recognized species of the genus. The same work (Landrum 1986) included an account of *Blepharocalyx* O.Berg, which has one species, *Blepharocalyx eggersii* (Kiaersk.) Landrum, that is native to the Lesser Antilles. *Siphoneugena dussii* (Krug & Urb.) Proença, which is native to Puerto Rico and the Lesser Antilles, was treated in a revision of *Siphoneugena* O.Berg (Proença 1990), while *Myrcianthes fragrans* (Sw.) McVaugh and *Eugenia* (=*Pseudanamomis*) *umbellulifera* (Kunth) Krug & Urb., both widespread species with dichasial inflorescences, were considered in a revision of

Myrcianthes O.Berg (Grifo 1992). The latter study also featured a generic-level phylogenetic analysis of subtribe Eugeniinae O.Berg using morphology, which included the Greater Antillean endemic genus *Hottea* Urb. A synopsis of *Myrciaria* O.Berg (Sobral 1993), a genus also traditionally assigned to subtribe Eugeniinae, recognized four Antillean species (two endemic). Fifteen insular species (14 endemic), excluding four recently recognized taxa from Cuba (Urquiola Cruz and Acosta Ramos 2008), were treated in a monograph of the Caribbean genus *Mosiera* Small (Salywon 2003). Finally, four species (none endemic) of the closely related genus *Psidium* L. occurring in the Greater and Lesser Antilles have been included in partial taxonomic treatments of the genus (Landrum 2003, 2017). The total number of Antillean species treated by these studies as accepted by their authors is thus 40 or less than 10% of the species in the region.

Approximately the same number of native Antillean species have been included in published molecular phylogenetic studies, at least 12 of which have contributed novel DNA sequence data for these species (Lucas et al. 2005, van der Merwe et al. 2005, Lucas et al. 2007, Lucas et al. 2011, Mazine et al. 2014, Staggemeier et al. 2015, Santos et al. 2016, Wilson et al. 2016, Wilson and Heslewood 2016, Vasconcelos et al. 2017b, Mazine et al. 2018, Amorim et al. 2019). Sampled taxa include 18 species of *Eugenia* L. (including *Calyptrogenia* p.p., *Hottea*, and *Pseudanamomis* Kausel), 16 of *Myrcia* Guill. (including *Calyptranthes* Sw. and *Mitranthes*), four of *Pimenta,* two of *Psidium,* and one each of *Mosiera*, *Myrciaria*, and *Myrcianthes*. The total number of native species treated by these studies is thus 43, but only 21 of them are endemic to the Antilles. Most of the remaining are widespread taxa that were not necessarily sampled from the Caribbean.

Among the endemics, only four genera (*Eugenia*, *Myrcia*, *Pimenta*, and *Psidium*) are represented, and *Myrcia* sect. *Calyptranthes* (Sw.) A.R.Lourenço & E.Lucas accounts for ten of these. These considerations clearly indicate a need for greater representation of species endemic to the Greater and Lesser Antilles in future phylogenetic studies of Myrteae.

***Goal and Overview*—**To summarize the preceding, the New World species of Myrtaceae (tribe Myrteae) are a diverse, widespread, and taxonomically difficult group. Both descriptive and phylogenetic studies are essential for further progress with the systematics of the group. The need for additional research is particularly acute for the approximately 500 species of Myrtaceae in the Antilles. Treatments of the group on a regional scale are over 100 years old, and relatively few species have been included in either phylogenetic or monographic studies. The goal of my dissertation, accomplished through a series of related studies, is thus to further describe and classify the diversity of Myrtaceae across the Greater and Lesser Antilles according to its evolutionary history.

Chapter I contributes to these objectives through description of a rare new species of *Eugenia* endemic to the Lesser Antilles. The paper describes the first new species of *Eugenia* from the Caribbean Islands in 10 years and the second of the 21st century (Borhidi 2008, Govaerts et al. 2020).

Chapter II provides the evolutionary context for this dissertation. Its subject is a molecular phylogenetic study of Myrtaceae in the Greater Antilles. The primary objectives were to identify the main lineages of Myrtaceae present in the region and to recognize potential clades of endemic species for further systematic study. Species were sampled from each genus native to the Greater Antilles from across the region and analyzed together with representatives of known clades from outside of the Caribbean Islands. Several groups of endemic species were specifically targeted for evaluation: the three recognized genera endemic to the Greater Antilles, the taxonomic concepts of *Calycolpus* and *Pseudanamomis* proposed by Bisse (1983, 1985), and the species of the ill-defined genus *Plinia* endemic to Hispaniola and Cuba. Chapter II also proposes taxonomic changes in accordance with the results.

Finally, Chapter III builds upon the phylogenetic results by examining a group of species identified within *Eugenia* in greater depth. The third study consists of a revision of the Lathberry Clade, a group of seven species distributed from Puerto Rico to the Lesser Antilles. It includes critical comparison of the morphology of each species, a phylogenetic analysis using nuclear genetic regions, a descriptive taxonomic and nomenclatural treatment, and extinction risk assessments. The features that distinguish the Lathberry Clade from all other species of *Eugenia* in the Greater and Lesser Antilles are also discussed. To the best of our knowledge, ours is the first attempt to revise a monophyletic group within *Eugenia* sect. *Umbellatae* O.Berg.

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CHAPTER I

A NEW SPECIES OF EUGENIA (MYRTACEAE) FROM THE ISLAND OF ANGUILLA

Abstract

Eugenia walkerae, a new species from the island of Anguilla, is described and illustrated. This species is only known from five herbarium collections, and additional field work is needed to determine its current conservation status. It resembles the Puerto Rican endemic *Eugenia woodburyana*, and its seeds are comparable to those described for certain species of Eugenia from southern Africa. This is the second species of seed plant currently recognized as endemic to Anguilla.

Keywords: endemic, Lesser Antilles, systematics, taxonomy

Introduction

In the Flora of the Lesser Antilles, McVaugh (1989) included a brief description of a Myrtaceous plant unknown as to genus and species from the island of Anguilla. The description was based upon two sterile collections made by the French botanist Père Casimir Le Gallo in 1955. As reported by Howard and Kellogg (1987), efforts to relocate this distinctive species at the same locality in 1985 were unsuccessful; however, ten years later, two additional collections of the same species in flower and fruit were made by Mary Morris Walker. An undivided, globular embryo and a single axillary flower that lacks a prolonged hypanthium but has a 4-lobed, open calyx persistent on the mature fruit indicate that the plant in question is a species of *Eugenia* L. Since it is distinct from all others known to me from the Antilles, it is here described as a new species.

Taxonomic Treatment

Eugenia walkerae J. A. Flickinger, *sp. nov.* TYPE: ANGUILLA. Katouche Valley, 12 February 1995, (fl, fr), *M. Walker 95-016* (Holotype: A). Fig. 1.1.

Eugenia ramulis minute hispidis, caeterum glabra; foliis obovatis v. ellipticis, 8.5–18 mm longis × 5–12 mm latis, apice rotundato v. retuso, basi late cuneata v. convexa, margine incrassato, recurvato, nervis lateralibus inconspicuis, crasse coriaceis, dicoloribus, subtus conspicue glandulosis; floribus solitariis ex axillis foliorum, pedicellis 2.5 mm longis, alabastris 3.5 mm longis × 2.5 mm latis, lobis calycis inaequalibus, majoribus rotundatis, minoribus triangularibus; baccis ellipsoidalibus, 6–7 mm diametro, glandulosis; embryone glanduloso, maculam fuscatam praebenti.

Shrub, glabrous except for the young twigs; hairs simple, pale; new growth arising from axillary buds, with a few pairs of decussate, rounded to triangular, dark bud scales at base, slightly flattened, hispidulous, brown; older twigs terete, glabrescent, glandular-verrucose, becoming smooth and developing a lightly fissured, gray bark. *Leaves* opposite, petiolate, glabrous even when young; petioles semiterete, 1–2 mm long × 1 mm wide, leaving a U-shaped bundle scar upon abscission; blades obovate to elliptical, 8.5–18 mm long × 5–12 mm wide, ca. 1.5 times as long as wide, apex rounded to retuse, base broadly cuneate or convex, margin incrassate, recurved, pale and decurrent into petiole, coriaceous, discolorous, drying light brown below, darker above; venation brochidodromous, midvein plane above, slightly prominent proximally below, lateral veins obscure, 4–6 pairs, departing from the midvein at an angle of 45–60°, forming an arching marginal vein ca. 1 mm from the margin; adaxial surface slightly impressed-punctate to plane; abaxial surface prominently and conspicuously glandular. *Inflorescences* axillary on new growth, solitary, one-flowered. *Flowers* pedicellate; pedicels terete, 2.5 mm long × 0.3 mm wide, sparsely glandular; bracteoles free, ovate, 0.7 mm long in bud, glandular, ciliate, persistent, 1 mm long × 1 mm wide in fruit; buds obovoid, 3.5 mm long × 2.5 mm wide; calyx 4-lobed, open in bud, glandular, ciliate, larger lobes rounded, concave, 1.4 mm long × 1.9 mm wide in fruit, smaller lobes triangular, 0.8 mm long × 1.2 mm wide in fruit, rounded at apex; petals glandular. *Fruits* prolate ellipsoidal to spheroidal, 6–7 mm diam. when dry, crowned by the persistent, erect calyx lobes, glandular, ripening black; pericarp thin and fleshy with longitudinally-oriented fibers and a membranous endocarp; 1-seeded. *Seeds* rounded; seed coat yellow-brown, more or less smooth on exterior surface, mottled brown on interior surface, with a hard outer palisade layer, a fibrous middle layer, and a series of inner periclinal layers appearing whitish in cross-section; embryo ellipsoidal, 6 mm long × 5 mm diam., undivided, surface yellow-gray, wrinkled, glandular, with a dark spot near one end and a slightly raised stripe 0.5–1 mm wide running lengthwise from the end opposite the spot along the side opposite the same for somewhat greater than 1/2 the length of the embryo.

Eponymy: *Eugenia walkerae* is named for the collector of the type specimen, Mary Morris Walker (1923–2012), in recognition of her contributions to the botany of Anguilla through the Anguilla Flora Project (Walker et al., 2005).

Additional specimens examined: ANGUILLA. S rim of Katouche Valley near Governor's House, 4 February 1995, (fr), *M. Walker 95-04* (A). The Valley, plateau calcaire, près de la chapelle catholique, alt. 15 m, 5 September 1955, (st), *C. Le Gallo 2480* (NY [image]). The Valley, plateau calcaire, à' l'ouest de la chapelle catholique, alt. 15–20 m, 5 September 1955, (st), *C. Le Gallo 2482* (WAG [two sheets, images]). The Valley, plateau calcaire, alt. 20 m, 5 September 1955, (st), *C. Le Gallo 2493* (NY [image]).

Phenology: collected with flowers and fruits in February.

Habitat and distribution: *Eugenia walkerae* is endemic to Anguilla, where it has been found in two separate areas (Fig. 1.2). The Le Gallo collections were made at low elevation on limestone in The Valley, the island’s capital, whereas the Walker collections are from the nearby Katouche Valley. On a note included in the fragments folder of *Walker 95-04* (A), two question marks appear to indicate uncertainty as to the exact locality. The Katouche Valley supports dry evergreen forest vegetation restricted to a few sheltered sites on the island (Walker et al., 2005).

Conservation status: The current status of this species in the wild is unknown. As a single-island endemic with few collections, it is likely of conservation concern; however, the Katouche Valley is being preserved for eco-tourism (O. Hodge, pers. comm.).

Discussion

The dimensions of the petioles and leaf blades given above are based on physical examination of Walker's two collections. These differ only slightly from the dimensions of the Le Gallo collections reported by McVaugh (1989), which were subsequently confirmed from images of the specimens.

Among its congeners in the region, *Eugenia walkerae* resembles *E. woodburyana* Alain of western Puerto Rico in its coriaceous leaves drying darker above and hispidulous twigs. The leaves of *Eugenia woodburyana* are generally larger and more elliptical, and the venation is prominulous. Hairs are also found at least on the petiole and along the margins of the leaves, as well as on the flowers and fruits. In flower, *Eugenia woodburyana* differs in its short axillary racemes of 2–4 flowers with calyx lobes more or less equal in size and a ridged hypanthium. Its fruits are much larger (2 cm diam.) and 8-winged.

Comparison of the seeds of *Eugenia walkerae* with the detailed descriptions available for seeds of species of *Eugenia* native to southern Africa allows for interpretation of some of the features described above. Seed coats of southern African species develop from the outer integument, and possess a mesophyll-derived layer consisting of “haphazardly arranged fibre-like sclereids” (van Wyk and Botha, 1984), which corresponds well with the fibrous middle layer observed in *Eugenia walkerae* seeds. The outer palisade layer of the seed coat described above is characteristic of species of group X in southern Africa. In contrast, most group Y species possess an epidermal layer that is poorly differentiated from the mesotesta (van Wyk and Botha, 1984). The embryo of *Eugenia walkerae*, though undivided, also more closely resembles that of group X species in having a glandular surface and possessing a dark spot that probably marks the location of the radicle (van Wyk, 1980). The significance of the raised stripe is unclear. More detailed descriptions of seed and embryo characters, especially for Neotropical species, may prove useful in the classification of this large genus.

Howard and Kellogg (1987) accept only a single endemic species of spermatophyte for the flora of Anguilla, their newly described *Rondeletia anguillensis* R. A. Howard & E. A. Kellogg. The description of *Eugenia walkerae* thus brings the total number of endemics to two. Previously, one other species of Myrtaceae was recognized as endemic to Anguilla, *Myrtus anguillensis* Urb. This taxon is now generally referred to

Mosiera longipes (O. Berg) Small (Govaerts et al., 2018), a Caribbean species at the edge of its range in the Leeward Islands.

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Figures

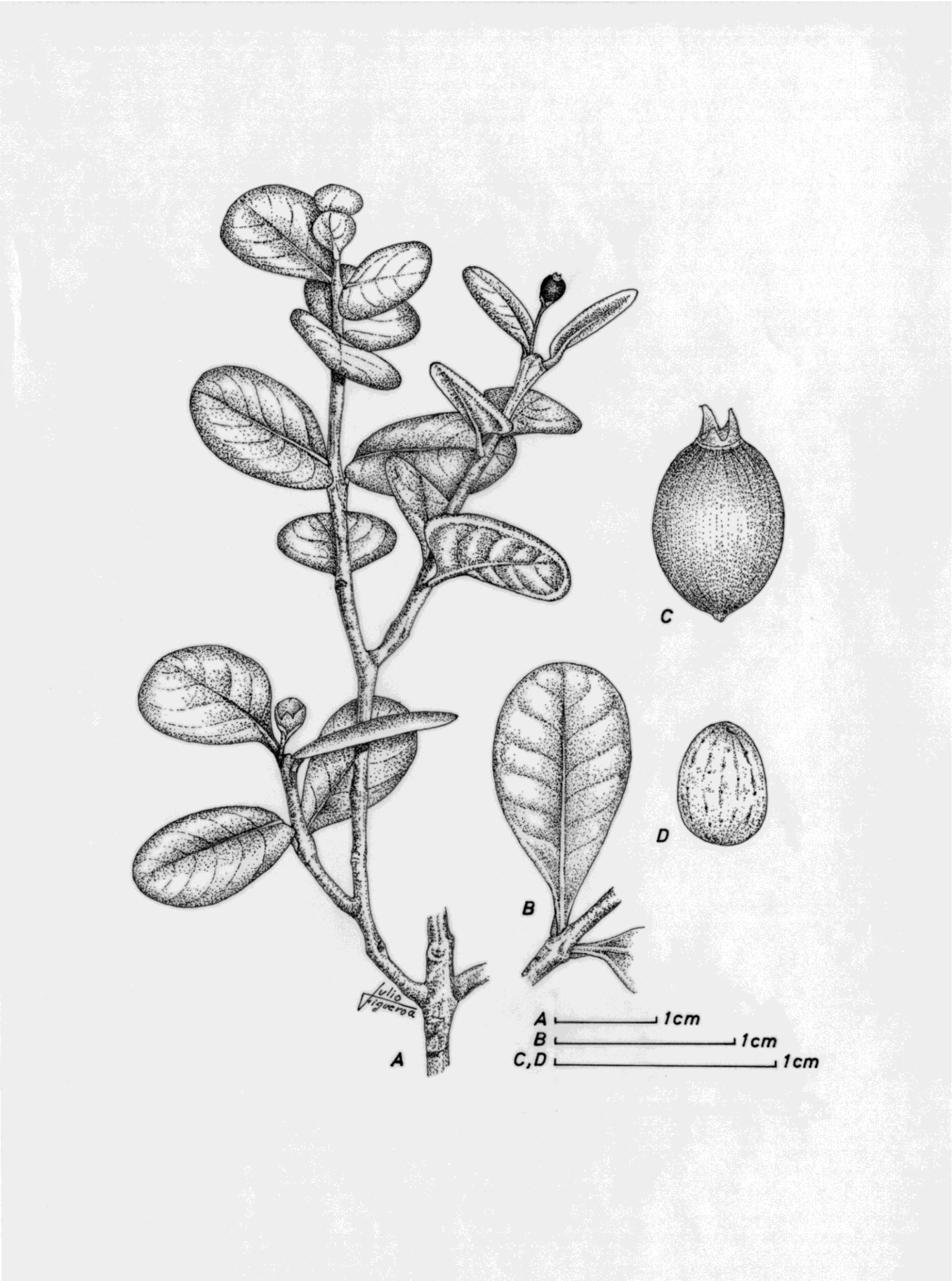

Figure 1.1. *Eugenia walkerae* J. A. Flickinger. **A,** habit; **B,** leaf; **C,** mature fruit; **D,** embryo. From *M. Walker 95-016* (A).

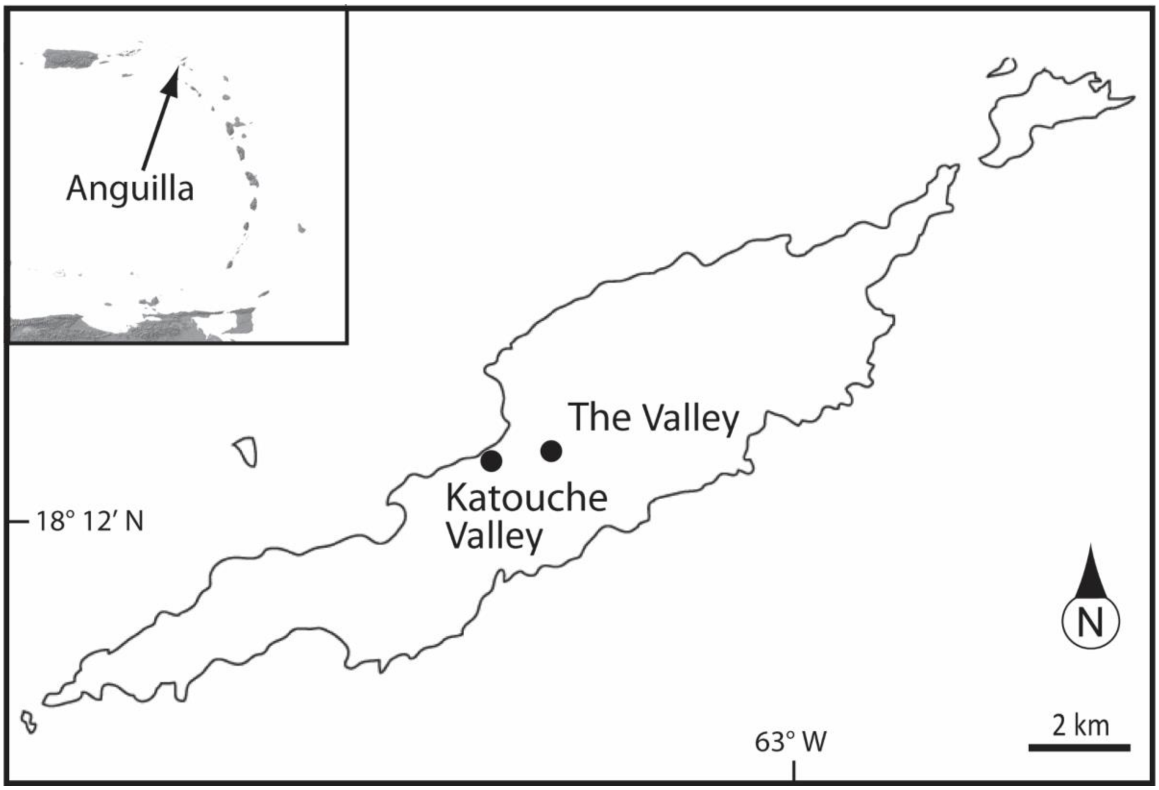

Figure 1.2. Map of collection sites for *Eugenia walkerae* on Anguilla.

CHAPTER II

A PHYLOGENETIC SURVEY OF MYRTACEAE IN THE GREATER ANTILLES WITH NOMENCLATURAL CHANGES FOR SOME ENDEMIC SPECIES

Abstract

Myrtaceae are a large family of trees and shrubs, including ca. 2500 species within the predominantly Neotropical and taxonomically problematic tribe Myrteae. Nearly 500 species of Myrteae are endemic to the Caribbean Islands Biodiversity Hotspot, but few have been represented in phylogenetic systematic studies to date. The major goals of this survey are to identify the main lineages of Myrteae present in the Greater Antilles and potential clades for further investigation. Specific objectives are to evaluate the monophyly and placement of the following: (1) the three genera of Myrtaceae considered endemic to the Caribbean Islands (*Calyptrogenia*, *Hottea* and *Mitranthes*); (2) *Calycolpus* and *Pseudanamomis* sensu Bisse; and (3) Greater Antillean species of *Plinia*. To accomplish these aims, species of Myrtaceae representing all genera native to the Greater Antilles were sampled from across the region for placement within previously established phylogenetic frameworks for Myrteae and the large genus *Eugenia*. In total, 160 terminal taxa of Myrtaceae (89 Caribbean Islands endemics) were analyzed for this study. Phylogenetic inference was conducted by maximum parsimony and Bayesian methods on alignments of DNA sequence data from one nuclear (ITS) and three chloroplast (*psbA-trnH, ndhF-rpl32*, *trnL-trnF*) regions. Results of both types of analysis were congruent with each other and with the major clades recovered in previous studies, but some conflict was observed between nuclear and chloroplast regions involving congeneric species. *Calycorectes (=Hottea) ekmanii* from eastern Cuba was found to be closely related to *Calycolpus* within subtribe Myrtinae. Subtribes Myrciinae, Pliniinae, Pimentinae (*Pimenta* and *Psidium* groups) and Eugeniinae contained other Greater Antillean species. Sampled species of *Plinia* from Cuba emerged within

Myrciaria, and *Mitranthes* was found to be non-monophyletic. All sampled species of *Eugenia* endemic to the Caribbean fell within *E.* sect. *Excelsae* (including *Calycolpus* sensu Bisse), *E.* sect. *Racemosae* and *E.* sect. *Umbellatae* except for *E. cycloidea*, which was associated with the Old World species of *E.* sect. *Jossinia*. Within *Eugenia* sect. *Umbellatae*, Caribbean species formed two major clades, designated CI and CII, containing species of *Calyptrogenia* and *Hottea* from southern Hispaniola, a polyphyletic *Pseudanamomis* sensu Bisse and the Lathberry Clade, a novel group of *Eugenia* species centered in Puerto Rico and the Virgin Islands. *Calyptrogenia* and *Hottea* species from southern Hispaniola are transferred to *Eugenia* along with *Pseudanamomis nipensis*, while *Mitranthes* species are transferred to *Myrcia*. Two additional combinations are made within *Eugenia* and *Pimenta* in accordance with the results, and lectotypes are designated as appropriate.

Keywords: Biodiversity hotspot, Caribbean, islands, Myrteae, Neotropics

Introduction

Myrtaceae are a family of flowering plants consisting of over 6000 species (WCSP, 2020) of trees and shrubs found throughout tropical and warm temperate regions of the world (Lucas, 2007). A recent phylogenetic classification of the family (P. Wilson & al., 2005) recognizes 17 tribes. The largest of these is the predominantly Neotropical tribe Myrteae DC., which contains ca. 2500 species (WCSP, 2020) in an estimated 46 genera (Vasconcelos & al., 2017b). This tribe includes such well-known economic plants as guava and allspice, as well as others noted for their fruits, essential oils, use as ornamentals or invasive tendencies (P. Wilson, 2011). Species of Myrteae are common in all but the driest terrestrial habitats of the Neotropics (Kawasaki & Holst, 2004), where members of this tribe are readily recognized by the presence of simple, opposite, entire, exstipulate leaves with glandular punctations and a marginal vein; 4- to 5-merous flowers with a whitish corolla, many stamens, an inferior ovary and hypanthium; and fleshy, indehiscent fruits (Landrum & Kawasaki, 1997).

Though easily recognized as a group, Myrteae are challenging to classify because of the large number of species and difficulty circumscribing morphologically coherent, monophyletic subgroups. The same uniformity in most floral and vegetative features (McVaugh, 1956; Bisse, 1979) that facilitates recognition of the tribe also constrains the supply of taxonomically useful characters, while those features that vary may do so even among apparently closely related species (Urban, 1894–1895). Generally, some combination of floral and seed characters, such as inflorescence structure, calyx merosity, ovary structure and form of the mature embryo, are needed to place a species within a genus, but ripe fruits and flowers are seldom available simultaneously (Landrum & Kawasaki, 1997).

Neotropical Myrteae have traditionally been divided into three groups (de Candolle, 1827), each characterized by a different type of embryo. In the last comprehensive treatment of the species, these groups formed the basis of a subtribal classification by Berg (1855–1856), who described the embryo types as follows: (1) the Myrtoid (or Pimentoid) embryo with short cotyledons, a long hypocotyl and an overall curved form; (2) the Myrcioid embryo with contortuplicate, foliaceous cotyledons and an elongate hypocotyl; and (3) the Eugenioid embryo with fleshy cotyledons having varying degrees of fusion and a short hypocotyl. For the recognition of genera, Berg (1855–1856) emphasized features of the calyx. A more synthetic approach to classification was taken by McVaugh (1968), and his somewhat broader generic concepts have greatly influenced subsequent treatments of the group. Unfortunately, many taxa of Neotropical Myrtaceae above the rank of species remain difficult to diagnose.

Because they exploit an additional rich source of character data, molecular systematic studies of the Myrteae are useful for studying confusing patterns of morphological variation and for constructing new classifications that better reflect evolutionary relationships within the group. Such studies hold potential for resolving problematic generic boundaries, identifying unique lineages for conservation, subdividing large taxa into manageable units for further study and understanding a wide variety of evolutionary phenomena. Previous molecular phylogenetic studies of Myrtaceae (Gadek & al., 1996; P.G. Wilson & al., 2001; Sytsma & al., 2004; P. Wilson & al., 2005; Biffin & al., 2010; Thornhill & al., 2015) established the monophyly of the Myrteae, excluding fleshy-fruited *Syzygium* Gaertn. and its segregates. Those focused on the tribe itself (Lucas & al., 2005, 2007; Murillo-A. & al., 2013; Vasconcelos & al., 2017b) found that the three subtribes based on embryo type of Myrtinae Nied., Eugeniinae O.Berg and Myrciinae O.Berg, the latter traditionally including *Myrceugenia* O.Berg (Landrum, 1981), are non-monophyletic. Subsequently, 10 informally named suprageneric groups were identified (Vasconcelos & al., 2017b) and published as a new system of nine subtribes (Lucas & al., 2019), in which the informal *Psidium* L. and *Pimenta* Lindl. groups were combined. Molecular phylogenetic studies have also been conducted to identify major clades within the large genera *Myrcia* Guill. (e.g., Lucas & al., 2011; Amorim & al., 2019) and *Eugenia* L. (e.g., Mazine & al., 2014, 2018), serving as a basis for new phylogenetic classifications of both genera (Mazine & al. 2016, 2018; Lucas &

al., 2018). Other phylogenetic studies have focused on smaller generic (Murillo-A & al., 2012) or infrageneric (Staggemeier & al., 2015; Bünger & al., 2016; Santos & al., 2016) taxa in conjunction with molecular dating or biogeographic analyses. Still others have aimed at clarifying generic limits (Snow & al., 2011; da Cruz & al., 2013; C. Wilson & al., 2016) or placement of individual anomalous taxa (Wilson & Heslewood, 2016; Giaretta & al., 2019a). Together, these phylogenetic studies have greatly improved our knowledge of Myrteae systematics, but with few exceptions (van der Merwe & al., 2005; Snow & al., 2011; C. Wilson & al., 2016; Wilson & Heslewood, 2016), they have primarily focused on South American taxa.

Myrtaceae in the Caribbean Islands**—**Myrtaceae of the Caribbean Islands merit attention because of their considerable diversity and prominence within the rich and imperiled flora of the region. As used here, the term “Caribbean Islands” refers to the Greater and Lesser Antilles plus the Bahamas Archipelago (Fig. 2.1) and is equivalent to the “West Indies” of Acevedo-Rodríguez and Strong (2008). These islands are considered a global hotspot of biodiversity, where exceptional concentrations of endemic species are threatened by high rates of habitat loss (Myers & al., 2000; Mittermeier & al., 2005). The region has had a complex geological and environmental past and a continuous biota since the mid-Eocene (Iturralde-Vinent & MacPhee, 1999; Graham, 2003). These historical factors are reflected in the flora’s diverse affinities, which are primarily to adjacent continental landmasses (Santiago-Valentín & Olmstead, 2004; Francisco-Ortega & al., 2007; Acevedo-Rodríguez & Strong, 2008; Nieto-Blázquez & al., 2017), as well as in the outstanding level of plant endemism, which is comparable to that of other large, tropical oceanic island systems (Francisco-Ortega & al., 2007).

With nearly 500 endemic species and infraspecific taxa of Myrteae (Acevedo-Rodríguez & Strong, 2008), the Caribbean Islands are also a major center of diversity for the group. Myrtaceae are a common element in the Caribbean flora, and Caribbean native species are used for a wide variety of purposes, including as sources of food, flavoring, medicine and wood (Peguero, 2011). In terms of the total number of native and endemic taxa, the family ranks fifth in the region (Acevedo-Rodríguez & Strong, 2012), but it is the most species-rich family of woody plants in the seasonally dry tropical forests prevalent throughout the Caribbean Islands (Gentry, 1995). It also includes two of the top ten most diverse genera in the region: *Eugenia*, which with over 200 native and endemic taxa (species and infraspecies) ranks second after an expanded *Miconia* Ruiz. & Pav. (Michelangeli & al., 2019), and *Myrcia* (=*Calyptranthes* Sw.), with over 100 taxa (Acevedo-Rodríguez & Strong, 2012). Of the approximately 50 native species of Myrtaceae in the Lesser Antilles, McVaugh (1989) listed 10 taxa that are restricted to these islands and an additional five that are shared exclusively with the Greater Antilles, while the only endemic member of the family reported for the Bahamas is *Mosiera androsiana* (Urb.) Salywon (Correll & Correll, 1982; WCSP, 2020). Thus, the great majority of Caribbean Islands endemic Myrtaceae are restricted to the Greater Antilles, and these islands form the focus of the present study.

***Focal Groups*—Endemic Genera.** The Greater Antilles also contain several taxonomically problematic species groups that warrant investigation. These include the three genera recognized as endemic to the West Indies by Acevedo-Rodríguez & Strong (2012): *Calyptrogenia* Burret, *Hottea* Urb. and *Mitranthes* O.Berg. Vasconcelos & al. (2017b) demonstrated that *Hottea* (represented by *H. neibensis* Alain) and *Calyptrogenia* (represented by *C. cuspidata* Alain and *C. grandiflora* Burret) emerge within *Eugenia*, while *Mitranthes* (represented by *M. clarendonensis* (Proctor) Proctor and *M. glabra* Proctor) emerges in *Myrcia* sect. *Calyptranthes* (Sw.) A.R.Lourenço & E.Lucas. *Calyptrogenia biflora* Alain was also sampled and found to emerge within *Psidium* (Vasconcelos & al., 2017b). These findings clearly indicate that these three groups cannot be maintained as independent genera; however, more precise phylogenetic placements of these taxa, particularly with respect to other Caribbean endemic species, are desirable for understanding the evolution of the unique features that led to their recognition.

Mitranthes was described by Berg (1855–1856) within subtribe Eugeniinae to accommodate five species sharing a hypanthium prolonged beyond the summit of the ovary and calyptrate calyx, but the embryos of these species were unknown to him. Niedenzu (1893) recognized the genus in an altered sense within subtribe Myrtinae, excluding elements which he referred to *Psidium* and including *Marlieriopsis* Kiaersk., a monotypic genus with a Myrtoid embryo (Kiaerskou, 1889–1890). Burret (1941), who considered the genus artificial, appended several South American species along with *Mitranthes urbaniana* Burret from Jamaica. These species were all known to share a calyptrate calyx and basal placentae bearing multiple, ascending ovules. At the same time, Burret designated *Mitranthes ottonis* O.Berg (Fig. 2.2C) from western Cuba the type of the genus. Legrand (1958) restricted *Mitranthes* to 11 Eugenioid species from Brazil distinguished by their prolonged hypanthium, calyptrate calyx and multiovulate locules. A few South American species were subsequently added; all have since been removed, principally to the Brazilian genus *Neomitranthes* D.Legrand (WCSP, 2020). In contrast, McVaugh (1968) considered the genus to be Myrcioid based on examination of

Jamaican material later described by Proctor (1982), who recognized a total of five species of *Mitranthes* from Jamaica. Both McVaugh (1968) and Landrum (1984) supposed that the genus, interpreted as a Myrcioid group restricted to Cuba and Jamaica, is closely related to *Myrcia* sect. *Calyptranthes*, from which it differs only in its multi-ovulate locules ranging in number from 1–5.

Calyptrogenia was described by Burret (1941) for calyptrate species with the placentation and embryonic structure of *Eugenia*, including *Mitranthes riedeliana* O.Berg from Brazil and four Haitian species: *Calyptrogenia bracteosa* (Urb.) Burret, *C. ekmanii* (Urb.) Burret, *C. grandiflora* and *C. jeremiensis* (Urb. & Ekman) Burret. Burret also considered this genus artificial. The Haitian species were transferred from various genera, and *Calyptrogenia ekmanii* was designated the type. Another Brazilian species, *Calyptrogenia hatschbachii* D.Legrand, was described by Legrand (1958), who distinguished *Calyptrogenia* from his concept of *Mitranthes* by its lack of a prolonged hypanthium. Landrum (1984) accommodated *Calyptrogenia hatschbachii* within *Myrceugenia*, while Mattos (1990) treated both Brazilian species in *Neomitranthes*. More recently, *Mitranthes riedeliana* has been placed in *Eugenia* (Giaretta & al., 2018). Only two other species, both from the Dominican Republic, have been assigned to *Calyptrogenia*: *Calyptrogenia biflora* and *C. cuspidata*. Except for *Calyptrogenia jeremiensis*, all of the rather infrequent Hispaniolan species have reportedly been recollected on that island (Peguero & al., 2005b; Majure & al., 2013). A tentative record of *Calyptrogenia jeremiensis* from western Jamaica (Proctor, 1958, 1972) was considered erroneous by Liogier (1989). *Calyptrogenia ekmanii* has also been reported from eastern Jamaica based on a sterile specimen (Proctor, 1958).

Hottea, typified by *H. miragoanae* Urb., was initially described by Urban (1929) for three species from the Massif de la Hotte (Fig. 2.1), a physiographic region characterized by a discontinuous complex of mountains that stretches across most of the southern peninsula of Haiti (Ekman, 1928; Lewis & Draper, 1990). The distinctive features of *Hottea* are a fused calyx that splits in two (or rarely three) lobes down to the staminal disk at anthesis and a corolla of 1–4 unequal petals. The cotyledons were initially described as connate along the margins only based upon the apparently immature embryo of *Hottea torbeciana* Urb. & Ekman. Later, the embryo of *Hottea goavensis* Urb. was described as conferruminate (Urban, 1931). With the description of *Hottea neibensis* from the mountains of western Dominican Republic, the range of the genus was extended outside of Haiti (Liogier, 1973). Borhidi (1993) then transferred to *Hottea* two species from eastern Cuba described in *Calycorectes* O.Berg, *H. ekmanii* (Urb.) Borhidi and *H. moana* (Borhidi & O.Muñiz) Borhidi (Fig. 2.2A, B), based on unspecified epidermal, ovarian and embryological studies. A relationship between the Haitian species of *Hottea* and *Calycorectes ekmanii* Urb. from Cuba was earlier supposed by Urban (1929), as the species share a fused calyx. The two Cuban species have since been treated as a single species of *Mosiera* Small (Greuter & Rankin-Rodríguez, 2016b, 2017). Of the original Haitian species, only *Hottea torbeciana* is known to have been recollected (Majure & al., 2013).

Generic Concepts of Johannes Bisse. A second class of taxonomically problematic species groups pertinent to the Greater Antilles are the concepts of *Calycolpus* O.Berg and *Pseudanamomis* Kausel advocated by Johannes Bisse in his studies on the Myrtaceae of Cuba (Fig. 2.3B–D). Although recent treatments of

Calycolpus (Landrum, 2010) and *Pseudanamomis* (Grifo, 1992, 2003) excluded the species Bisse transferred to these genera, his expanded circumscriptions gained acceptance in recent works on the flora of Cuba (Urquiola Cruz & al., 2014; González-Torres & al., 2016; Greuter & Rankin Rodríguez, 2016b, 2017). Study of the species assigned by Bisse to both genera is also justified to evaluate their potential formation of monophyletic groups. Bisse (1979) explained his motivation for recognizing *Calycolpus* and *Pseudanamomis* in the flora of Cuba in a short paper in which he outlined characters deemed useful for delimiting genera within the fleshy-fruited Myrtaceae: inflorescence structure and position, ovary structure correlated with the number of seeds in the mature fruit, calyx structure, leaf venation and hair type. The diversity of Cuban species of *Eugenia*, especially with respect to inflorescence and leaf architecture, led Bisse (1979) to believe that the genus was not monophyletic. Based on this conclusion, he proceeded to re-assign species of *Eugenia* in Cuba to other genera.

To *Calycolpus,* Bisse (1983) assigned five species from eastern Cuba, four species described in *Eugenia* and one in *Psidium*, that share axillary, umbelliform inflorescences, 4–6-seeded fruits and a type of venation observed in *Calycolpus goetheanus* (DC.) O.Berg in which the basal lateral nerves are recurved. Multi-seeded fruits served to distinguish these species from the typically single-seeded fruits of *Eugenia*; however, the soft seed coats of these species were compared with those of *Eugenia*. Subsequently, *Eugenia beyeri* Urb. and *E. vitis-idaea* C.Wright non Raoul were transferred to *Calycolpus* as *C. beyeri* (Urb.) Urquiola (Urquiola Cruz & al., 2008) and *C. vitis-idaea* Greuter & R.Rankin (Greuter & Rankin Rodríguez, 2016a), respectively.

To the monotypic genus *Pseudanamomis*, Bisse (1985) added 12 additional species of *Eugenia*. These species were distinguished by their relatively large leaves, drying dark brown to black or olive-green above, with conspicuous intercostal veins, as well as by their unusually large flowers with a fleshy, flat hypanthium and transversely dehiscent calyx lobes borne in contracted dichasia on old wood. Bisse also reported that the embryos of three Cuban species possess partially fused cotyledons and, in at least one of these, the placentation described by Kausel (1956), i.e., a warty placenta arising from the center of the dissepiment. Two Cuban species of *Pseudanamomis* sensu Bisse, *Eugenia catingiflora* Griseb. and *E. jambosoides* Griseb., were previously placed in *E.* sect. *Catingopsis* Griseb. together with another Cuban endemic, *E. megalopetala* Griseb. The large flowers and stamens of the three species of *Eugenia* sect. *Catingopsis* were compared with those of *Catinga* Aubl. (Grisebach, 1866), a South American genus of two species now referred to *Eugenia* (Mazine & al., 2016). Urban (1894–1895) had already associated *Eugenia catingiflora* and *E. jambosoides* to the exclusion of *E. megalopetala* within a group that also included *E. sessiliflora* Vahl and *E. cordata* (Sw.) DC. from Puerto Rico and islands to the east. Though Urban considered this group artificial, Bisse (1985) treated *Eugenia sessiliflora* as a synonym of *E. cordata* and transferred all four of these species to *Pseudanamomis* along with two Mexican species, *E. trunciflora* (Schltdl. & Cham.) G.Don and *E. macrocarpa* Schltdl. & Cham, and seven other Cuban endemic species. These other Cuban species were previously placed near one another by Urban (1928), except for the undescribed *Eugenia victorinii* Alain (Fig. 2.3D) and *Pseudanamomis nipensis* Bisse.

In addition, Bisse (1986) circumscribed the genus *Mosiera*, typified by *M. longipes* (O.Berg) Small from southern Florida and the Caribbean Islands, to include 20 species from Cuba described variously in *Myrtus* L., *Eugenia* and *Psidium* based on differences in vegetative, floral and fruit morphology and anatomy (Bisse, 1977, 1986; Bisse & Rankin Rodríguez, 1984). *Mosiera* has since been adopted as a valid genus that includes additional species in Mesoamerica, Cuba, Hispaniola, Puerto Rico and the Bahamas (Landrum, 1992; Borhidi, 1993; Salywon, 2003, 2007; Salywon & Landrum, 2007; Urquiola Cruz & Acosta Ramos, 2008); however, Landrum (1992) considered *Psidium guineense* Sw. misplaced within it.

***Plinia*.** A final focal group in this study are the species of *Plinia* L. endemic to the Greater Antilles (Fig. 2.2D). In particular, the Cuban species were mentioned by McVaugh (1968) as being vegetatively distinct from the continental species and possibly misplaced. The limits of *Plinia* are unclear, as briefly reviewed by Barrie (2004), and there are indications that the genus is not monophyletic as currently circumscribed (Vasconcelos & al., 2017b; Amorim & al., 2019). In the Greater Antilles, the genus consists of 13 recognized species from Cuba (Acosta Ramos, 2014) and eight species from Hispaniola (Liogier, 1989). Several of these rare species were described from sterile material, but some have become better known through more recent collections (Peguero, 2007; Urquiola Cruz & Acosta Ramos, 2009; Acosta Ramos 2014).

Plinia was described as a monotypic genus (Linnaeus, 1753) from the illustrations of Plumier (1703). Urban (1919) interpreted *Plinia pinnata* L., the type of the genus, as a Lesser Antillean species he identified with *Marlierea glomerata* O.Berg. Urban’s understanding of these names was discussed by McVaugh (1968, 1969), who accepted his identification of *Plinia pinnata*. The characters of the genus as originally understood by Urban (1919) are as follows: inflorescences glomerate and borne on old wood, calyx tube (i.e., hypanthium) prolonged beyond the ovary, calyx initially fused and splitting into 4–5 lobes at anthesis, ovary bilocular with two ovules per locule, fruits 1-seeded, cotyledons free and plano-convex. Two additional Antillean species were accordingly recognized by him, *Plinia cubensis* (Griseb.) Urb. from Cuba and *P. dussii* (Krug & Urb.) Urb. from the Lesser Antilles (Urban, 1919). The latter species is now placed within *Siphoneugena* O.Berg, a related genus distinguished by its circumscissile hypanthium and typically 3- to 5-ovulate locules (McVaugh 1963; Proença, 1990). Additional species of *Plinia* have since been described from Cuba (Urban, 1923, 1928; Borhidi & Muñiz, 1977; Urquiola Cruz & Acosta Ramos, 2009; Acosta Ramos, 2014) and Hispaniola (Urban 1929, 1931). *Marlierea sintenisii* Kiaersk. from Puerto Rico has also been treated within *Plinia* (Britton & Wilson, 1925); however, its paniculate inflorescence is out of place in *Plinia*, and this transfer has not been accepted in subsequent studies of the flora of Puerto Rico (Little & al., 1974; Liogier, 1994; Axelrod, 2011).

Urban (1929) considered Greater Antillean *Plinia* species to be closely related to *Myrciaria floribunda* (Willd.) O.Berg, which belongs to a genus characterized by its circumscissile hypanthium, typically biovulate locules, free calyx lobes and fused or free and plano-convex cotyledons (Berg 1855–1856; McVaugh, 1963; Landrum & Kawasaki, 1997). The calyx tube of Greater Antillean *Plinia* species was described by Urban (1923, 1929) as constricted above the ovary, beyond which point it is deciduous, leaving a circular scar on the fruit. Furthermore, Urban included species within *Plinia* having cotyledons that he described as partially fused, e.g. *P. asa-grayi* (Krug & Urb.) Urb.

(Urban, 1894–1895, 1923), or conferruminate, e.g. *P. acutissima* Urb. (Urban, 1929), although the latter were excluded from among the Cuban species by Acosta Ramos (2014). Species of *Plinia* in the Greater Antilles thus seemingly combine features of both *Myrciaria* O.Berg and *Plinia*.

Objectives**—**The overall goals of this survey are to identify the main lineages of Myrteae present in the Greater Antilles and potential clades for further investigation. The monophyly and placement of the following three classes of taxonomically problematic groups reviewed above are specifically investigated: (1) species assigned to the Caribbean Islands endemic genera *Calyptrogenia*, *Hottea* and *Mitranthes*, including those from Cuba; (2) *Calycolpus* and *Pseudanamomis* sensu Bisse (1983, 1985); and (3) species of *Plinia* from the Greater Antilles.

Material and Methods

Taxonomic Sampling and Marker Selection**—**Species of Myrtaceae, including representatives of all genera native to the Greater Antilles, were sampled from across the region through field collections in Cuba (including the Isle of Pines), Hispaniola (Dominican Republic and Haiti), Jamaica, Puerto Rico and the Virgin Islands (St. John). Figure 2.1 shows the locations of field collections within the Greater Antilles included in this study. Additional material was included from cultivated plants, herbarium specimens and the Hawaiian Plant DNA Library (Morden & al., 1996; Randell & Morden, 1999). Field collections emphasized focal groups. All species of *Eugenia* endemic to Puerto Rico recognized by Axelrod (2011) were sampled, and types of genera were included when possible. In addition, sequences for 38 species were retrieved from GenBank to provide representation of each major suprageneric group of Vasconcelos & al. (2017b) and each section of *Eugenia* recognized by Mazine & al. (2018), including ungrouped species. Previously sequenced species were selected to minimize missing data. Based on the results of preliminary analyses that placed *Calycorectes ekmanii* and *Eugenia cycloidea* Urb. apart from other Caribbean species with members of subtribe Myrtinae and *E.* sect. *Jossinia* (DC.) Nied., respectively, both clades were sampled more intensively to identify the closest relatives of these two Greater Antillean endemics. Five species from three different tribes (Metrosidereae Peter G.Wilson, Syzygieae Peter G.Wilson and Tristanieae Peter G.Wilson) of the "BKMMST clade," a strongly supported group of six tribes including the Myrteae (Biffin & al., 2010), were used as outgroups. In total, 160 species and infraspecific taxa were analyzed. These include 89 Caribbean Island endemics, of which 77 have never been sequenced before. Appendix 2.1 lists the voucher specimens for all species included in this study.

One nuclear (ITS) and three chloroplast regions (*psbA-trnH*, *ndhF-rpl32*, *trnL-trnF*) were selected for PCR amplification and sequencing. Both ITS and *psbA-trnH* display high levels of variation at low taxonomic levels and have been used in many of the previous phylogenetic studies of Myrteae cited above. The *ndhF-rpl32* intergenic spacer was selected to provide additional chloroplast data because of its utility across angiosperms as well as variation within *Eucalyptus* L'Hér. (Shaw & al., 2014). To increase overlap in sequence data between newly sequenced and previously sequenced species, the slower evolving *trnL-trnF* region, including the *trnL* intron and *trnL-trnF* intergenic spacer, was also sequenced for a representative subsample of approximately half of the terminal taxa sequenced for this study. GenBank accession numbers for all analyzed sequences are provided in Appendix 2.1.

DNA Extraction, Amplification and Sequencing**—**Total genomic DNA was extracted from approximately 0.05 g of dried leaf material using a DNeasy Plant Mini Kit (Qiagen, Hilden, Germany). In the few cases in which this method did not yield useable DNA, protocol D of Souza & al. (2012), which employs sorbitol buffer washes and extraction with a high-salt CTAB buffer to remove polysaccharides, was followed with the addition of *N*-lauroylsarcosine (Russell & al., 2010). Table 2.1 gives the primers and PCR protocols used in this study. Because of the length of the *ndhF-rpl32* spacer, forward and reverse internal primers were designed for use in conjunction with the universal primers of Shaw & al. (2007) to aid in amplification. The primers and protocols for ITS and *psbA-trnH* follow those of Lucas & al. (2007). PCR was carried out in 25 μL reaction volumes using a SimpliAmp Thermal Cycler (Thermo Fisher Scientific, Waltham, Massachusetts, U.S.A.). The reaction mixture was prepared using a RED Master Mix Kit (Genesee Scientific, San Diego, California, U.S.A.) containing 0.2 mM each dNTP, 0.1 units/μL Taq DNA polymerase and 1.5 mM $MgCl_2$, to which 1× TBT-Par reagent (Samarakoon & al., 2013), 0.6 μM forward and reverse primers and 1 μL DNA extract were added. PCR products were purified using ExoSap-IT (Affymetrix, Cleveland, Ohio, U.S.A.) before cycle sequencing with a Big Dye Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, California, U.S.A.). Sequences were analyzed on an Applied Biosystems 3100 Genetic Analyzer at the Florida International University DNA Core Facility. Cleaning and assembly of sequence reads were performed using Geneious software (Biomatters, Auckland, New Zealand) with ambiguous bases indicated with IUPAC ambiguity codes (Cornish-Bowden, 1985).

***Sequence Data Alignment and Coding*—**Alignments of each amplified region were constructed with MAFFT v. 7 (Katoh & Standley, 2013) run on the MAFFT web server (Katoh & al., 2017) using the E-INS-i algorithm and default parameters. Alignments were then inspected to recognize microstructural motifs in chloroplast regions and adjusted accordingly (Kelchner, 2000). Manual adjustments to the alignment were also made to ensure consistent alignment of the same site patterns. Indels of differing length were only aligned if identical over their region of overlap. Three classes of problematic site patterns were recognized: homonucleotide repeats containing substitutions, repeat indels with substitutions not present in both copies and ambiguous gap placements affecting non-conserved sites. The first of these was dealt with by removing all gaps from within the homonucleotide region and justifying the alignment in a direction that maximized the number of shared substitutions. In this way, the alignment of substitutions is dictated by length mutational differences. The other two site pattern classes were aligned to minimize mutations at more conserved sites while maintaining a consistent alignment pattern. The number of gaps was minimized except at the coding ends of sequences, where they were freely introduced to avoid spurious mismatches. To evaluate the effect of including these problematic regions, an alignment was prepared in which gaps of ambiguous alignment were treated as regions of uncertain homology (Borsch et al., 2003) and removed along with the other two classes of problematic site patterns for separate analysis. One inversion flanked by inverted repeats was recognized within the *psbA-trnH* region and observed to be variable within at least one species of *Eugenia*. The less frequent inversion configuration was therefore reverse complemented in all sequences in which it occurred to match the others (Whitlock & al., 2010). Coding portions of chloroplast regions were trimmed from all alignments before phylogenetic analysis because of lack of variation and low coverage at sequence ends.

Informative gaps were coded as separate binary characters for parsimony analyses according to the simple gap coding method of Simmons & Ochoterena (2000) provided that gaps were more than one base in length, ends of overlapping gaps were separated by more than one base and both gap ends fell neither within nor immediately adjacent to masked regions. These restrictions were designed to prevent coding of gaps based on errors in the sequence data or alignment, and gaps not meeting these restrictions were ignored. Three non-informative gaps found within informative ones in the chloroplast regions were also coded to differentiate between species sharing the same state for the more inclusive gap, whether absent or inapplicable, without sharing the same site pattern.

Phylogenetic Analyses**—**Both parsimony and Bayesian methods of phylogenetic inference were performed on sequence alignments of ITS (nrDNA), chloroplast (cpDNA) and the combined data including all sites, as well as the combined data with regions of uncertain alignment masked as explained above. In preliminary analyses, *Eugenia umbellulifera* (Kunth) Krug & Urb. grouped with two different sections of *Eugenia* depending on whether the phylogeny was inferred from nrDNA or cpDNA data partitions and the method of analysis used to analyze the combined data. Furthermore, this species appeared on an unusually long branch in separate analyses of nrDNA sequence data and parsimony analyses of the combined sequence data. The full, combined data matrix was therefore also re-analyzed by both methods with *Eugenia umbellulifera* excluded to explore the effect of this species on the rest of the phylogeny. Following the method of Wiens (1998), congruence between nrDNA and cpDNA alignments was first assessed by inspection of separately analyzed data sets before combining, with areas of disagreement considered doubtful. Instances of incongruence were recognized as statistically well-supported conflicting clades, defined as bootstrap support (BS) ≥70% or posterior probability (PP) ≥0.95.

Parsimony analyses were conducted on gap-coded alignments using PAUP* v. 4.0a (Swofford, 2003) with equal weighting of characters, unordered, equally weighted state changes and gaps treated as missing data. Heuristic searches for most parsimonious (MP) trees were conducted using the parsimony ratchet (Nixon, 1999) as implemented in PAUPRat (Sikes & Lewis, 2001). The percentage of characters to perturb was empirically determined to be 10% for the nrDNA alignment and 20% for all others. Ratchet searches were performed in batches of 10 runs consisting of 200 iterations beginning from different random starting points. Searches were terminated once two successive batches failed to alter the strict consensus of MP trees. 10000 bootstrap replicates were run on the CIPRES Science Gateway (Miller & al., 2010) to evaluate the statistical support of branches (Felsenstein, 1985). Each bootstrap replicate consisted of 5 random taxon addition replicates followed by TBR branch swapping, holding 10 trees at each step and saving no more than 1 tree per replicate.

For Bayesian analyses, data partitioning and model selection were first jointly conducted in PartitionFinder2 (Guindon & al., 2010; Lanfear & al., 2016) using the Bayesian information criterion (Schwarz, 1978). Separate data blocks were defined for each chloroplast intergenic spacer, the *trnL* intron, each rRNA gene, ITS1 and ITS2. Models were selected from the GTR model space using the greedy algorithm (Lanfear & al., 2014) with branch lengths linked across partitions. Bayesian phylogenetic inference was conducted using MrBayes v. 3.2.6 (Altekar & al., 2004; Ronquist & al., 2012) run on the CIPRES Science Gateway (Miller & al., 2010) with the BEAGLE library (Ayres & al., 2012). The simplest models of nucleotide substitution and among-sites rate variation fully implemented in MrBayes were set for each partition according to the selections made by PartitionFinder2. MCMC analyses were run for 10000000 generations, sampling every 1000 trees. Each analysis consisted of 2 runs of 4 chains (1 cold, 3 heated). Analyses were performed in triplicate for each alignment to verify convergence onto the same posterior distribution of trees. The standard deviation of the split frequencies was used to assess convergence. All generations before this value remained below 0.01 were discarded as burn-in. In addition, likelihood trace plots and effective sample sizes of parameters were examined using Tracer v. 1.7.1 (Rambaut & al., 2018) to assess mixing and convergence of analyses.

Results

A total of 417 DNA sequences were produced for this study, with an additional 100 retrieved from the GenBank database. The complete, concatenated alignment of DNA sequences with data blocks and excluded regions marked is available as a nexus-formatted supplementary data file (Supplementary File 2.1). Coded gaps are available in a separate nexus file (Supplemenary File 2.2). Details on alignment characteristics, gap coding, model selection and partitioning schemes are presented in Table 2.2.

Bayesian and parsimony analyses of the complete, combined sequence data are presented in Figs. 2.4 and 2.5, respectively. Designations for major suprageneric clades follow the taxonomy of Lucas & al. (2019) with the exception that the *Psidium* and *Pimenta* groups (subtribe Pimentinae O.Berg) of Vasconcelos & al. (2017b) are treated separately. It should be noted that subtribes Eugeniinae, Myrciinae and Myrtinae/ Pimentinae have historically been used in broader senses to correspond with the three embryo types explained above. Designations for infrageneric clades in *Eugenia* follow Mazine & al. (2018). No cases of conflicting clades that were statistically well-supported in equivalent Bayesian and MP analyses were observed, but several instances of well-supported incongruence between separately analyzed nrDNA (Fig. 2.6) and cpDNA (Fig. 2.7) data sets were identified. Conflicts are restricted to relationships among congeneric species, which are usually closely related. These conflicts do not affect the conclusions of this study, and all are mentioned in the appropriate section of the discussion. Analysis of the combined data with masked sites (Fig. 2.8) likewise supports the conclusions of this study, but the resultant topology is generally less resolved. The number, length and consistency index of MP trees found for each alignment are given in Table 2.2.

Monophyly of tribe Myrteae received strong support (PP 1.0, BS 100%), and seven major, statistically well-supported ingroup clades were recovered (Figs. 2.4, 2.5). The deepest relationships within Myrteae between the monotypic genus *Myrtastrum* Burret, subtribes Decasperminae E.Lucas & T.N.C.Vasconc. and Myrtinae and the rest of the tribe, the “Main Neotropical Lineage” of Vasconcelos & al. (2017b), differed between Bayesian (Fig. 2.4A) and parsimony analyses (Fig. 2.5A), but none of these relationships were well-supported by either method. In the Bayesian analysis, *Myrtastrum rufopunctatum* (Brongn. & Gris) Burret was placed sister to the remaining members of the tribe, and Decasperminae and Myrtinae formed a clade sister to the Main Neotropical Lineage. In contrast, the parsimony analysis placed Decasperminae sister to the rest of the tribe and *Myrtastrum* and Myrtinae successively sister to the Main Neotropical

Lineage. The Main Neotropical Lineage received poor support in the parsimony analysis (BS 56%) but maximum support (PP 1.0) in the Bayesian analysis. Within it, the following five major clades were recovered: (1) the *Psidium* group of subtribe Pimentinae (PP 1.0, BS 100%), represented by *Psidium*, including *Calyptrogenia biflora*, and *Mosiera*; (2) the *Pimenta* group of subtribe Pimentinae (PP 1.0, BS 87%), represented by *Pimenta*, including *Myrcia paganii* Krug & Urb.; (3) subtribe Luminae E.Lucas & T.N.C.Vasconc. (PP 1.0, BS 65%), represented by *Luma* A.Gray and *Myrceugenia*; (4) subtribes Myrciinae plus Pliniinae E.Lucas & T.N.C.Vasconc. (PP 1.0, BS 70%), represented by *Myrcia*, *Mitranthes*, *Algrizea* Proença & NicLugh., *Plinia*, *Siphoneugena* and *Myrciaria*; and (5) subtribe Eugeniinae (PP 1.0, BS 73%), represented by *Myrcianthes* O.Berg and *Eugenia*, including *Pseudanamomis nipensis*, *Calyptranthes pachyadenia* Urb. & Ekman, the remaining species of *Calyptrogenia* and *Hottea*.

Within *Eugenia*, six major clades of sectional rank were recovered in addition to five sections represented by a single species and four ungrouped species (Figs. 2.4B, 2.5B). The Bayesian analysis (Fig. 2.4B) resolved the successive divergence of *Eugenia* sect. *Pseudeugenia* Mazine & Faria, *E.* sect. *Hexachlamys* (O.Berg) Mazine, *E.* sect. *Pilothecium* (Kiaersk.) D.Legrand and *E.* sect. *Eugenia*. In contrast, relationships between these early-diverging lineages were unresolved in the parsimony analysis (Fig. 2.5B) except for the sister relationship between *Eugenia* sect. *Pseudeugenia* and the rest of the genus. *Eugenia umbellulifera* appeared either within *E.* sect. *Excelsae* Mazine & E.Lucas on a relatively long branch in the parsimony analysis or sister to *E.* sect. *Jossinia* plus *E. cycloidea* (Fig. 2.3A) in the Bayesian analysis. When *Eugenia umbellulifera* was excluded from the analysis, *E.* sect. *Schizocalomyrtus* (Kausel) Mattos formed a well-supported clade with *E.* sect. *Excelsae* (PP 1.0, BS 83%), and these two sections formed a clade together with *E.* sect. *Phyllocalyx* Nied. in the Bayesian analysis (PP 1.0). Both *Eugenia* sect. *Umbellatae* O.Berg and its sister relationship to *E.* sect. *Speciosae* Bünger & Mazine lacked support. Within *Eugenia* sect. *Umbellatae*, however, a clade excluding *E. pseudopsidium* Jacq. and *E. punicifolia* (Kunth) DC. was recovered in the Bayesian analysis (PP 0.96) that included a strongly supported Clade C (PP 1.0, BS 98%) sensu Mazine & al. (2018) along with three species of *Eugenia* from outside of the Caribbean, including *E. coronata* Schumach. & Thonn. from West Africa. Two major subclades were resolved within Clade C, CI and CII, plus *Eugenia walkerae* Flickinger. Clades CI and CII were both resolved with maximum PP, but only Clade CI received good support from the parsimony analysis (BS 83%). Clade CII was, however, present in the strict consensus of MP trees inferred from the complete data.

Species endemic to the Greater Antilles fell within subtribes Myrtinae, Pimentinae (including the *Psidium* and *Pimenta* groups), Myrciinae, Pliniinae (Figs. 2.4A, 2.5A) and Eugeniinae (Figs. 2.4B, 2.5B). Within *Eugenia*, they were found in *E.* sect. *Umbellatae*, *E.* sect. *Excelsae* and *E.* sect. *Racemosae* O.Berg, with *Eugenia cycloidea* forming a clade with *E.* sect. *Jossinia* (PP 1.0, BS 98%). Species of *Plinia* endemic to Cuba emerged within *Myrciaria* (PP 1.0, BS 97%), while the two species described under *Calycorectes* from eastern Cuba formed a clade with *Calycolpus* (PP 1.0, BS 91%). *Hottea*, excluding the Cuban species, and *Calyptrogenia*, excluding *C. biflora*, both emerged within Clade CI of *Eugenia* sect. *Umbellatae*. *Hottea* was placed as sister to a weakly supported clade of Cuban endemics (PP 85, BS 76%), while the placement of *Calyptrogenia* within Clade CI was uncertain. *Mitranthes*, the third regionally endemic genus, was found to be non-monophyletic within *Myrcia* sect. *Calyptranthes* (PP 1.0, BS 97%). Within *Eugenia*, neither of the two generic concepts of Bisse evaluated here formed a monophyletic group. The two sampled species of *Calycolpus* sensu Bisse emerged within *Eugenia* sect. *Excelsae*, while Caribbean Islands endemic species of *Pseudanamomis* were placed apart from the type species, *E. umbellulifera*, within Clades CI and CII of *E.* sect. *Umbellatae*. Other findings pertinent to Greater Antillean species are discussed by group below.

Discussion

The results of this study are concordant with those of other phylogenetic analyses of Myrteae (Lucas & al., 2005, 2007; Murillo-A. & al., 2013; Vasconcelos & al., 2017b) in the major suprageneric groups recovered and in the general lack of support for relationships between them within the Main Neotropical Lineage. An exception is that subtribes Myrciinae and Pliniinae were not resolved as separate monophyletic entities. Myrciinae consists of a broadly circumscribed *Myrcia* inclusive of *Calyptranthes, Gomidesia* O.Berg and *Marlierea* Cambess. (Lucas & al., 2018), while Pliniinae consists of *Algrizea*, *Myrciaria*, *Neomitranthes*, *Plinia* and *Siphoneugena* (Lucas & al., 2007; Vasconcelos & al., 2017b). Both groups have received high support in other phylogenetic studies based on more extensive taxon sampling and sequencing of additional cpDNA markers (Lucas & al., 2011; Staggemeier & al., 2015; Santos & al, 2016, 2017; Amorim & al., 2019) and are characterized by different embryo types; they are therefore discussed separately below. Within *Eugenia*, major clades agree with those found by Mazine & al. (2014, 2018). In contrast to previous phylogenetic studies of Myrteae reporting few, if any, well-supported instances of incongruence between nrDNA and cpDNA data partitions (Lucas & al., 2005, 2007; van der Merwe & al., 2005; Mazine & al., 2014, 2018; Bünger & al., 2016; Santos & al., 2016; C. Wilson & al., 2016; Wilson & Heslewood, 2016; Vasconcelos & al., 2017b), several such instances, which affected relationships between congeneric species, were observed in this study. Cytonuclear discord involving congeneric species has also been reported in phylogenetic studies of *Eugenia* sect. *Hexachlamys* (da Cruz & al., 2013) and *Myrceugenia* (Murillo-A. & al., 2012). It is likely that the concentrated sampling of species from the Greater Antilles undertaken here resulted in selection of species that are closely related and hence more likely to exhibit incomplete lineage sorting or reticulate relationships (Degnan & Rosenberg, 2009). In support of this explanation, most cases of conflict that were detected in this study involve morphologically similar species. A general pattern evident in the results is that clades endemic to the Caribbean Islands nest within mainly continental lineages. Exceptions at the generic level include *Pimenta* and *Mosiera*, which are primarily Caribbean genera.

This study exhibits a bias towards sampling of Caribbean taxa and, within the region, towards certain taxonomically problematic groups. Somewhat less than one-fifth of the total of native and endemic species occurring in the Caribbean Islands were included, and relatively few species from neighboring regions were sampled. For this reason, emphasis is placed on identification of lineages for further study and placement of already defined groups such as the endemic genera. Where recovered groups of species are considered closely related, they are briefly characterized.

***Clades in the Greater Antilles*—Myrtinae.** The placement of *Calycorectes ekmanii* and *C. moana* Borhidi & O.Muñiz within subtribe Myrtinae, which is not otherwise known to occur in the Caribbean Islands, is an unexpected finding of this study. According to Borhidi & Muñiz (1976), *Calycorectes moana* is distinguished from *C. ekmanii* by its glabrous new growth, glands on the abaxial leaf surfaces, longer pedicels, primarily 4-merous calyx (see below) and cylindrical versus turbinate hypanthia. Although these characters do not appear to consistently distinguish between two entities, the names as used here are applied to material collected from localities mentioned in the protologues of the respective species. In what follows, they are held to be synonymous in agreement with Greuter & Rankin Rodríguez (2016b, 2017) and treated under the earliest applicable name, *Calycorectes ekmanii*. A distinctive feature of this species is its apparently completely fused calyx that opens at anthesis by regular tears along visible sutures into four concave-triangular lobes. The same type of calyx is found in *Mosiera nipensis* Salywon & Landrum, another species from the Sierra de Nipe of eastern Cuba (Fig. 2.1). Its calyx was originally described as valvate, with the lobes possibly connate along their edges, and compared with that of *Accara elegans* (O.Berg) Landrum (Salywon & Landrum, 2014). In contrast, the calyx of other species of *Mosiera* is imbricate and tears only slightly or not at all at anthesis (Landrum, 1992; Salywon, 2003). Seeds of *Mosiera nipensis* have a hard, lustrous seed coat and a Myrtoid embryo with relatively short cotyledons (Salywon & Landrum, 2014). Based on comparison of the holotype specimen of *Mosiera nipensis* (*C.V. Morton & J. Acuña 3262* [US No. 1782979!]) with recent collections of *Calycorectes ekmanii*, *M. nipensis* is an additional heterotypic synonym. The type of *Eugenia stenoptera* Urb., or “negracuba,” (*J.A. Shafer 7810* [NY barcodes 00099318, 00099319 (images!)]) represents a similar species from the province of Guantánamo with a 4-merous calyx that, according to Hilaire (2000), is fused in the bud. Its taxonomic status requires further investigation.

Comparing *Calycorectes ekmanii* to the four other genera of subtribe Myrtinae, the monotypic South American genus *Accara* Landrum has a similar calyx, but it differs in its tetralocular rather than bilocular ovary and an embryo with cotyledons about as long as the hypocotyl (Landrum, 1990). Central American *Chamguava* Landrum also has a 4-merous calyx, and in *C. schippii* (Standl.) Landrum, the calyx is fused and tears irregularly or in four lobes; however, the seed coat in this genus is membranous, and the embryo is starchy with a swollen hypocotyl (Landrum, 1991). *Myrtus* and *Calycolpus*, on the other hand, are both characterized by a 5-merous calyx with the exception of the fused, irregularly tearing calyx of *C. aequatorialis* Landrum (Landrum, 2010). In all of the genera of Myrtinae, flowers are either solitary or few and borne from a contracted, bracteate shoot, and tetragonal to 4-winged twigs are common.

The results of this study indicate that the closest known relatives of *Calycorectes ekmanii* (including *C. moana*) are species of *Calycolpus* sensu Landrum (2010), but it is unclear whether these continental species form a paraphyletic group with respect to *Calycorectes ekmanii*. The placement of this Greater Antillean species within *Calycolpus* in both separate (Figs. 2.6A, 2.7A) and combined analyses (Figs. 2.4A, 2.5A, 2.8A) is doubtful considering the low support values, the low sequence divergence for the involved species, the possible impact of missing cpDNA data (*ndhF-rpl32* for all species of *Calycolpus*, *trnL-trnF* for *C. legrandii* Mattos and *C. moritzianus* (O.Berg) Burret) and the conflicting placements of *C. goetheanus* as either sister to *C. moritzianus* (nrDNA, Fig. 2.6A) or *C. cochleatus* McVaugh (cpDNA, Fig. 2.7A). The principal morphological distinction between *Calycorectes ekmanii* and *Calycolpus* as circumscribed by Landrum (2010) is the 4-merous, completely fused calyx. It should be noted that the calyx of *Calycorectes ekmanii* was originally described as predominantly 5-merous and only rarely 4-merous. In contrast, the calyx of both *Calycorectes moana* and *Mosiera nipensis* was described as 4-merous, and more recent collections of *C. ekmanii* reviewed for this study, including material from the type locality, all have 4-merous flowers. Furthermore, the flowers of extant type material (*E.L. Ekman 9879* [S No. S03-2100 (image!)]; J. Lundberg, pers. comm.) are also 4-merous. It may be that the material described by Urban (1923) was anomalous. Occasional 4-merous flowers have also been reported for some species of *Calycolpus*, although the calyx of these species is never completely fused (Landrum, 2010). Aside from the calyx, *Calycolpus* has similar seeds and embryos, and other gross morphological features of *Calycorectes ekmanii* fall within the range of variation present in the genus.

Based on the results presented here, *Calycorectes ekmanii* could reasonably either be treated as a disjunct species of *Calycolpus* or as an independent genus. Description of a new genus would be undesirable if it led to a paraphyletic *Calycolpus*, but the first option would be acceptable from a phylogenetic point of view regardless of whether *Calycorectes ekmanii* is sister to *Calycolpus* or emerges within it. Placing *Calycorectes ekmanii* in *Calycolpus*, however, would require further reducing the set of characters useful for diagnosing *Calycolpus* (Landrum, 1989) by including a species with a 4-merous calyx. Except for two species with a fused, irregularly tearing calyx (*Chamguava schippii* and *Calycolpus aequatorialis*), calyx merosity would otherwise be consistent within the genera of Myrtinae, and it is a generally useful feature for distinguishing between the Neotropical genera with Myrtoid embryos (see keys in Landrum & Kawasaki, 1997; Landrum, 2010). For these reasons, taxonomic transfer of *Calycorectes ekmanii* is delayed until more decisive evidence from morphological or molecular sources can be brought to bear upon the issue.

***Psidium* Group.** In the Greater Antilles, the *Psidium* group of subtribe Pimentinae contains *Psidium* and *Mosiera*. Here sampling was extended to include types of both genera, as well as species from the center of diversity of *Mosiera* on Cuba. Within *Mosiera*, there was little sequence divergence in the selected markers, and all the resolved nodes in the cpDNA topology (Fig. 2.7A) conflicted with the single well-supported internal node in the nrDNA topology (Fig. 2.6A). Sampled species of *Psidium* from the Greater Antilles formed a clade (PP 1.0, BS 93%) that included the widespread *P. salutare* (Kunth) O.Berg in the combined Bayesian (Fig. 2.4A) and cpDNA analyses but that excluded this species in the combined parsimony (Fig. 2.5A) and nrDNA analyses. *Psidium salutare* is quite distinct from the rest of the clade in its low, rhizomatous growth habit, defined marginal vein and open calyx (Landrum, 2003). Its close relationship to *Psidium rotundatum* Griseb. may be a signature of reticulation, as both species occur in western Cuba. Three of the species (*Calyptrogenia biflora* and *Psidium sessilifolium* Alain from Hispaniola and *P. harrisianum* Urb. from Jamaica) in this Greater Antillean clade have been treated as synonyms of *P. amplexicaule* Pers., a species reported from Brazil as well as the Caribbean Islands. All are similar in their orbicular, coriaceous and sessile to nearly sessile leaves with a few pairs of spreading veins and fused, irregularly tearing calyx (Landrum, 2017). *Psidium rotundatum* and *P. acranthum* Urb. from Hispaniola and *P. parvifolium* Griseb. from Cuba, which differs from the rest in having petiolate leaves with ovate blades tapered towards the base, were also placed in this clade. These and related species in the Greater Antilles are in need of critical study. As the genus also contains such diverse, unsampled species as *Psidium sintenisii* (Kiaersk.) Alain from Puerto Rico, it is unlikely that all of the Caribbean members of *Psidium* will form a subclade.

***Pimenta* Group.** The *Pimenta* group of subtribe Pimentinae was represented solely by *Pimenta* in this study, but it contains a few other South American genera (Vasconcelos & al., 2017b). *Pimenta pseudocaryophyllus* (Gomes) Landrum from Brazil is the only species of *Pimenta* that occurs outside of the Caribbean region. This species appeared either as sister to the rest of the species sampled here (nrDNA, Fig. 2.6A) or weakly associated with two Cuban endemics (cpDNA, Fig. 2.2A). Its placement as sister to the rest of the genus in all combined analyses (Figs. 4A, 5A, S3A) seems more likely, given its distinctive hard seed coat and geographic isolation from the other species (Landrum, 1986). More comprehensive sampling, especially including species endemic to Jamaica, will be necessary to arrive at a phylogenetic framework for the genus. Nevertheless, three maximally supported lineages of Caribbean species can be recognized: *Pimenta dioica* (L.) Merr., a Caribbean native and type of the genus; *P. filipes* (Urb.) Burret plus *P. podocarpoides* (Areces) Landrum, both Cuban endemics; and a group of five taxa native to the Caribbean Islands that share a 5-merous calyx, bilocular ovary and protruding placenta bearing multiple ovules.

The two sampled Cuban species were originally described in *Myrtekmania* Urb., a formerly recognized genus endemic to Cuba. Both *Myrtekmania* and *Krokia* Urb., another formerly recognized genus endemic to the Greater Antilles, were distinguished by their unilocular ovary. Burret (1941) treated the two genera within separate sections of *Pimenta*, while Borhidi & Muñiz (1978) united all unilocular species under *Krokia*, defining three sections based on the number of ovules per locule: *Krokia* sect. *Moamyrta* Borhidi, including *P. podocarpoides*; *K.* sect. *Myrtekmania* (Urb.) Borhidi & O.Muñiz, including *P. filipes*; and *K.* sect. *Krokia*, which was not sampled here. Landrum (1986) did not regard the number of ovules per locule as a consistent character and refrained from formally subdividing the genus.

The other clade of Caribbean species contains *Pimenta racemosa* (Mill.) J.W.Moore, *Myrcia paganii* and *P. haitiensis* (Urb.) Landrum. This last species was formerly recognized within the monotypic, Hispaniolan endemic genus *Cryptorhiza* Urb. *Myrcia paganii* was described from a sterile collection from northern Puerto Rico and doubtfully placed in *Myrcia* (Urban 1894–1895). *Myrcia* and *Pimenta* may easily be confused, as both genera contain species with paniculate inflorescences, a 5-merous open calyx and dibrachiate hairs. Recently collected fertile material of *Myrcia paganii* demonstrates that this taxon possesses a 5-merous calyx, bilocular ovary and protruding placenta bearing multiple ovules, supporting its placement within this clade of *Pimenta* species. *Pimenta berciliae* T.N.C.Vasconc. & Peguero and *P. yumana* (Alain) T.N.C.Vasconc., both from Hispaniola, have also been found to be closely related to *P. racemosa*. The first species possesses a unilocular ovary, while the other has 4-merous flowers along with the similar Hispaniolan species, *Pimenta samanensis* (Alain) Peguero; all possess protruded placentae bearing multiple ovules (Vasconcelos & al., 2018b). These results suggest that recognition of *Pimenta* sect. *Amomis* (O.Berg) Nied. for a clade of Caribbean species sharing this type of placentation may be justified. Within the clade of species sampled here, the three varieties of *Pimenta racemosa* failed to cluster together, and another instance of conflict between topologies inferred from cpDNA and nrDNA was found in the alternative placements of *P. haitiensis* as either sister to *P. racemosa* var. *ozua* (Urb. & Ekman) Landrum or to the rest of the species of the clade, respectively.

Myrciinae. The great majority of species of Myrciinae in the Greater Antilles were historically assigned to *Calyptranthes*. Following conservation of the name *Myrcia* against *Calyptranthes* (K. Wilson, 2017), *Calyptranthes* is now treated as a section of *Myrcia* (Lucas & al., 2018), and new names and combinations in *Myrcia* have recently been made for the species (Lourenço & al., 2018; Campbell & al., 2019). *Myrcia* sect. *Calyptranthes* was poorly sampled in this study relative to its considerable diversity in the Caribbean Islands, but previous work has found that Caribbean endemic species of the section do not form a clade (Staggemeier & al., 2015; Santos & al, 2016, 2017; C. Wilson & al., 2016). Further discussion of relationships is therefore restricted to *Mitranthes* and a clade of endemic species of *Myrcia* outside of this section.

Mitranthes can be concluded to be biphyletic, as the Cuban endemic species *M. ottonis* is more closely related to *Myrcia pinetorum* (Britton & P.Wilson) Z.Acosta & K.Samra from the Isle of Pines than to the Jamaican species of *Mitranthes* (Figs. 2.4A, 2.5A). The latter form a morphologically coherent group sharing sessile leaves, few-flowered inflorescences with rather large flower buds and multi-ovulate locules. Examination of the fertile material of *Mitranthes ottonis* included in this study revealed flowers with an ovary divided into three locules, each with multiple ovules born on a U-shaped placenta, which agrees with the description of this species by Berg (1855–1856).

Thus, the multi-ovulate locule appears to have evolved at least twice within *Myrcia* sect. *Calyptranthes*. One of the Jamaican species of *Mitranthes*, *M. urbaniana*, was not listed in the treatment of the group by Proctor (1982). Based on the description of this species by Burret (1941), it is doubtlessly closely related to the other Jamaican species, but its precise identification is uncertain. *Mitranthes urbaniana* is only known from the type collection near Troy in Jamaica (see below), where *M. macrophylla* Proctor and *M. maxonii* Britton & Urb. have also been recorded.

All the Caribbean endemic species of *Myrcia* outside of *M.* sect. *Calyptranthes* that were sampled here formed a clade (PP 1.0, BS 85%), including *M. abbottiana* (Urb.) Alain from Hispaniola and *M. apodocarpa* Urb., *M. retivenia* (C.Wright) Urb. and *M.* sp. 1 from Cuba. *Myrcia abbottiana* was formerly placed in *Mozartia* Urb., a Greater Antillean endemic genus distinguished by its unilocular or incompletely bilocular ovary with 1–2 basal ovules (Urban 1923, 1928). As previously suggested by McVaugh (1968), Lucas & al. (2018) placed *Mozartia* within *Myrcia* sect. *Aulomyrcia* (O.Berg) Griseb. *Myrcia* sp. 1 shares the peculiar gynoecium of *Mozartia*, but the ovary of *Myrcia retivenia* was described as typically bilocular (Urban, 1923). Another Cuban species formerly assigned to *Mozartia*, *Myrcia manacalensis* Urb., was reported to have flowers completely lacking a style and ovary and supposed to be dioecious (Urban, 1923). Observations on *Myrcia* (=*Mozartia*) *albescens* (Alain) Alain, also from Cuba, suggest that it is androdioecious, as there are hermaphrodite and staminate flowers on separate collections (*J. Pipoly & C. Panfet 24924* & *24918*, respectively [FTG]). Androdioecy has been found in seven genera of Myrteae, representing four of the subtribes plus *Myrtastrum* (Vasconcelos & al., 2019). In *Myrcia*, androdioecy has previously been reported for a few South American members of the genus (Nic Lughadha & Proença, 1996). Cryptic dioecy, in which the hermaphrodite flowers produce inviable pollen, has been demonstrated in species of *Pimenta* (Chapman, 1964), *Decaspermum* J.R.Forst. & G.Forst (Kevan & Lack, 1985) and *Eugenia* from southern Africa (van Wyk & Lowrey, 1988) and the Comoros archipelago (Byng & al., 2016). On islands, high rates of dioecy may have evolved to avoid self-fertilization following colonization (Baker, 1967). Greater Antillean species of *Myrcia* (and other genera) should therefore be more closely investigated for these conditions.

Pliniinae. The major finding within this group is the placement of the three sampled species of *Plinia* from Cuba within a *Myrciaria* clade that excludes the single continental species of *Plinia* sampled in this study (Figs. 2.4A, 2.5A). Within this clade, separate analysis of cpDNA (Fig. 2.7A) supported a sister relationship between *Myrciaria vexator* McVaugh and *M. glazioviana* (Kiaersk.) Sobral from South America, while nrDNA (Fig. 2.6A) supported the combined topology. In either case, the Cuban species were placed within a clade containing the widespread *Myrciaria floribunda* and *M. borinquena* Alain from Puerto Rico (PP 1.0, BS 78%). Greater Antillean species of *Plinia*, along with *Myrciaria*, can be distinguished from other *Plinia* species by the circular scar left on the fruit by the deciduous calyx, notwithstanding the fused calyx and divided embryos exhibited by species such as *P. stenophylla* Urb. from Cuba. The feature of the fused calyx cannot by itself be used to delimit genera of Myrtaceae, as it seems to have evolved repeatedly in many genera (Landrum, 1984) and even multiple times within genera (Vasconcelos & al., 2017a; Giaretta & al., 2019b). In the case of embryos, the degree of fusion of the cotyledons in genera with Eugenioid embryos has been variously emphasized (Kausel, 1956) or discounted (Legrand, 1975) as taxonomically useful. In *Myrciaria glazioviana*, this character was found to be variable for individual plants (Sobral, 2006). Its utility for distinguishing between *Myrciaria* and *Plinia* is not supported by the results presented here.

Further studies of *Plinia* are needed to clarify generic boundaries within subtribe Pliniinae; however, the limited sampling of the clade in this and other phylogenetic studies of the Myrteae (Lucas & al., 2007; Vasconcelos & al., 2017b; Amorim & al., 2019) suggests that *Myrciaria* should be recognized as a distinct monophyletic genus including the Greater Antillean species of *Plinia*. Though these species appear to be closely related, greater sampling is needed to determine whether they form a clade endemic to the Caribbean Islands. Species delimitation within the group is also controversial. Five Greater Antillean species have been treated as synonyms of *Myrciaria floribunda*, while *Plinia haitiensis* Urb. & Ekman was placed in the synonymy of the otherwise South American *M. tenella* (DC.) O.Berg (Sobral, 1993). Studies of *Plinia* from Cuba are ongoing in connection with the *Flora de la República de Cuba* project, and the species of *Plinia* from Hispaniola should be reassessed before new combinations are made.

Eugeniinae. A difference in this study from the results of Mazine & al. (2018) is that *Eugenia* sect. *Pilothecium*, represented by *E. stipitata* McVaugh from South America, did not appear as sister to *E.* sect. *Eugenia* in the combined analyses of the full data (Figs. 2.4B, 2.5B). A sister relationship between the two sections received strong support (PP 1.0) in separate analysis of cpDNA (Fig. 2.7B), as well as the combined analysis of the masked alignment (Fig. 2.8B). This conflicts with the nrDNA topology

(Fig. 2.6B), in which a strongly supported clade (PP 1.0) was found that included *Eugenia* sect. *Eugenia* but excluded *E. stipitata*. In addition, the “Persistent Bracteoles Clade,” a group composed of *Eugenia* sect. *Jossinia, E.* sect. *Racemosae, E.* sect. *Speciosae* and *E.* sect. *Umbellatae*, (Mazine & al., 2018) was not recovered.

The position of *Eugenia* (=*Pseudanamomis*) *umbellulifera* within the genus is equivocal. This species, which is found in northern South America and the Caribbean Islands, appeared sister to a clade of Old World species in the analysis of Vasconcelos & al. (2017b). In the present study, separate analysis of cpDNA placed *Eugenia umbellulifera* in a clade with *E.* sect. *Jossinia* and *E. cycloidea* (PP 1.0; see below), while analysis of nrDNA placed this species on a relatively long branch sister to the Caribbean endemic members of *E.* sect. *Excelsae,* albeit with low support (PP 0.85). The appearance of *Eugenia umbellulifera* on an unusually long branch in the parsimony analysis of the combined data and the separate analysis of nrDNA sequence data in conjunction with the increased support for *E.* sect. *Excelsae* (PP 0.98 to 1.0, BS 54% to 91%) and two clades of related sections described above when *E. umbellulifera* was excluded, suggest that its placement within *E.* sect. *Excelsae* may be spurious. Alternatively, the observed conflict may be real signal from a past hybridization event. Chloroplast capture is a likely explanation for widespread observations of cytonuclear discord in plants involving both closely and distantly related species (Rieseberg & Soltis, 1991). Whatever its origins, *Eugenia umbellulifera* is anomalous within *Eugenia* because of its peculiar dichasial inflorescence, often 5-merous flowers with deciduous calyx lobes and only partially fused cotyledons (Kausel, 1956; Grifo, 1992, 2003). The first two of these characters also clearly distinguish it from *Pseudanamomis* sensu Bisse. It is perhaps best regarded as a distinct lineage.

Eugenia sect. *Racemosae* contains *E. eggersii* Kiaersk. from Puerto Rico and a clade of closely related species from Cuba and Hispaniola (PP 1.0, BS 99%) that are characterized by sericeous hairs on the flowers and vegetative buds, triangular sepals and often mucronate leaves. Relationships within this clade were poorly resolved except that *Eugenia tuberculata* (Kunth) DC. from Cuba was placed as sister to the rest. Its species are diverse in leaf size and shape, which varies from ovate to acicular, degree of pubescence, habit and habitat. Inflorescence form is also variable, ranging from subsessile clusters to the elongate racemes typical of the section, and variation is frequently observed within species, e.g. *Eugenia lineata* (Sw.) DC. (Fig. 2.3E), or even individuals. Urban (1928) considered the numerous, often difficult-to-identify species of this “*rigidifolia-heterophylla*” group to be distinct forms of restricted distribution.

Eugenia cycloidea represents another newly reported lineage for the Caribbean Islands. This species is endemic to eastern Cuba, where it is a characteristic element of charrascales, a type of scrub vegetation occurring on serpentine-derived soils (Borhidi, 1996). The closest relatives of *Eugenia cycloidea* in the present study are species assigned to *E.* sect. *Jossinia*. Mazine & al. (2018) recognized this section for a clade of Old World species, which they distinguished from *Eugenia* sect. *Umbellatae* principally by its styles of approximately the same length as the stamens and the occurrence of cryptically dioecious species (see above under Myrciinae). Style gigantism, in which the style is folded in bud and approximately twice as long as the stamens at anthesis, was proposed as a distinctive feature of *Eugenia* sect. *Umbellatae* (Vasconcelos & al., 2018a).

It appears that this feature is not entirely consistent, at least within Clade C (Fig. 2.3C–D, F); however, the extent and nature of the variation is unknown. The Old World species formerly recognized in *Jossinia* DC. are otherwise poorly differentiated from Neotropical species of *Eugenia* (Schmid, 1972). *Eugenia cycloidea* is not known to be dioecious, and parsimony analysis of the combined data provided weak support (BS 65%) for a monophyletic *E.* sect. *Jossinia* sister to *E. cycloidea*. Therefore, until the relationship between the two taxa can be resolved, *Eugenia cycloidea* is left unassigned to a section of *Eugenia*.

Eugenia sect. *Excelsae* contains a maximally supported clade of endemic species from Hispaniola and Cuba, including the two sampled species of *Calycolpus* sensu Bisse (1983). These species are distinguished from *Calycolpus* as circumscribed by Landrum (2010) by their 4-merous calyx, soft seed coat and presumably Eugenioid embryo. *Eugenia lineolata* Urb. & Ekman, the sole representative of *E.* sect. *Excelsae* from Hispaniola included in this study, *E. excisa* Urb. (Fig. 2.3B) and *Calyptranthes pachyadenia* have leaves with prominulous, fine, ascending lateral veins. This venation is shared with *Eugenia lindahlii* Urb. & Ekman, another member of the section from Hispaniola (Mazine & al., 2018). *Calyptranthes pachyadenia* was described from sterile material and is misplaced within *Myrcia* sect. *Calyptranthes*, members of which frequently have closely spaced lateral veins. This species also has an acuminate leaf apex like *Eugenia lineolata*, in contrast to the emarginate leaf apices typical of the other species. The clade formed by *Eugenia ligustroides* Urb., *E. lucens* Alain and *E*. sp. 2 was supported by nrDNA, but separate analysis of cpDNA placed *Eugenia ligustroides* sister to *Calyptranthes pachyadenia* plus *E. excisa*. Except for *Calyptranthes pachyadenia* from the Sierra de Escambray of central Cuba (Fig. 2.1), these five species are restricted to eastern Cuba. *Psidium reversum* Urb. is notable among the unsampled species of *Calycolpus* sensu Bisse as the only one not placed in *Eugenia*. It was described from sterile material, but Bisse (1983) depicted flowers and fruits that suggested its placement in *Eugenia.* In contrast, Urquiola Cruz & al. (2014) illustrated a Myrtoid embryo for the species. Its generic placement therefore requires clarification.

Eugenia sect. *Umbellatae* is by far the largest section of the genus. Members of this section from the Caribbean Islands and surrounding continental landmasses have been found to form a monophyletic group designated Clade C by Mazine & al. (2018). In that study, Clade C comprised *Eugenia dictyophylla* Urb. and its sister group, which included four species sampled here: *Eugenia axillaris* Sw. (Willd.), *E. laevis* O.Berg, *E. monticola* (Sw.) DC. and *E. rhombea* (O.Berg) Krug & Urb. Clade C is divided into two strongly supported subclades: Clade CI, the larger of the two, and Clade CII, which contains *Eugenia dictyophylla* and related species. As circumscribed here, Clade C also includes *Eugenia walkerae*, a recently described species whose placement relative to Clades CI and CII lacks strong statistical support. This species, the only Lesser Antillean endemic included in the analysis, is restricted to Anguilla (Fig. 2.1), and it appears to be more closely related to Greater Antillean than to other Lesser Antillean species (Flickinger, 2018). Outside of Clade C, two widespread species native to opposite ends of the Greater Antilles, *Eugenia punicifolia* and *E. pseudopsidium*, were also placed within this section. Although these two species formed a clade here, McVaugh (1989) considered *Eugenia pseudopsidium* difficult to distinguish from *E. lambertiana* DC., a species that was not found to be closely related to *E. punicifolia* by Mazine & al. (2018).

The placement of *Eugenia coronata*, a shrub from the savannahs and coastal forests of West Africa (Hutchinson & Dalziel, 1954), within *E.* sect. *Umbellatae* indicates that species of *Eugenia* in the Old World are not restricted to *E.* sect. *Jossinia*, but its position within the section is uncertain from the limited sampling of members from outside of the Caribbean region. Approximately 21 species of *Eugenia* are reported from West Africa (WCSP, 2020), but no others have been included in phylogenetic studies of *Eugenia* to date.

Clade CI contains endemic species from Cuba, Hispaniola and Jamaica as well as several species that occur outside of the Caribbean Islands. The following five highly supported lineages were recovered, but the relationships between them were unresolved: (1) *Eugenia victorinii* plus *E. retinadenia* C.Wright (PP 1.0, BS 83%). These species are from the Isle of Pines and the nearby province of Pinar del Río in western Cuba, respectively. *Eugenia victorinii*, which inhabits white sand savannahs, possesses a low, rhizomatous growth habit that distinguishes it from other species of *Pseudanamomis* sensu Bisse and is unusual in the Greater Antilles. (2) *Calyptrogenia* (PP 1.0, BS 100%). The two species sampled here include the type of the genus. See below for further discussion. (3) *Eugenia rhombea*, a widespread Caribbean species, plus two Jamaican endemics, *E. websteri* Proctor and *E.* sp. 1 (PP 1.0, BS 96%). The two Jamaican species differ in habit, but *Eugenia websteri* and *E. rhombea* are alike in exhibiting a tendency toward ramiflory and possessing relatively large, strongly concave sepals that are persistent on the fruits, a feature that is also evident in some other Jamaican endemic species. (4) A group comprising *Eugenia crenulata* (Sw.) Willd. from Cuba and Hispaniola and four non-Caribbean Islands endemics (PP 1.0, BS 100%). *Eugenia* *crenulata* has flowers in short axillary racemes similar to *E. axillaris* and *E. monticola*, a species that appears to intergrade with *E. foetida* Pers. (McVaugh, 1989). *Eugenia hypargyrea* Standl., the only species restricted to continental North America that was included in this study, and *E. laevis* formed a separate sublineage sister to the rest of this fourth group. Both species share dibrachiate hairs with *Eugenia hiraeifolia* Standl., a Central American endemic that occupied a similar position in relation to *E. laevis* in the phylogeny of Mazine & al. (2018). (5) *Hottea* plus a group of nine Cuban endemics (PP 1.0, BS 92%). See below for further discussion of *Hottea* (PP 1.0, BS 99%). The Cuban species of this lineage fell into two well-supported clades. One of these contains the core group of Cuban endemics that best exemplifies the concept of *Pseudanamomis* advocated by Bisse (1985). In this clade (PP 1.0, BS 99%), flowers are usually sessile and borne on old wood, but *Eugenia maestrensis* Urb. (Fig. 2.3C) has axillary flowers with pedicels that are sometimes elongated. The affinity of *Eugenia laeteviridis* Urb. to these species was previously suggested by Hilaire (2000) based on its similar leaves, shortly pedicellate flowers and deciduous calyx lobes. The material of *Eugenia cati* Britton & P.Wilson and *E. catingiflora* analyzed in this study was collected from type localities, as these species have been treated as synonymous (Alain, 1953). Differences in leaf form between the two taxa along with their failure to group together in the phylogenetic analysis support their recognition as distinct species. Separate analysis of cpDNA resolved *Eugenia maestrensis* as sister to the rest, while analysis of nrDNA placed *E. cati* in this position, with *E. maestrensis* sister to *Pseudanamomis nipensis*. The other clade of Cuban endemics (PP 1.0, BS 90%) is more xerophytic, containing species that exhibit smaller leaves and less conspicuous venation. The flowers of these species are sessile or nearly so and may commonly be found on younger growth. Conflicting relationships were also found within this sublineage, with *Eugenia piedraensis* Urb. appearing either sister to *E. mensurensis* Urb. (cpDNA) or *E. naguana* Urb. (nrDNA).

Hottea and *Calyptrogenia* were supposed to be closely related by McVaugh (1968). Though these two small genera overlap in range and share a fused calyx that differentiates them from *Eugenia*, the results of the present study indicate that the two groups are distinctive, non-sister taxa. Species of *Hottea* from southern Hispaniola are quite similar to each other in habit and almost certainly form a monophyletic group. Flower buds of *Hottea neibensis* have been classified as having a “Petaloid” pattern of development (Giaretta & al., 2019b). In this type, the outer pair of sepals are fused, while the inner remain free, appearing petaloid. The reduced number of petals described for some species of *Hottea* perhaps includes petaloid sepals. Unfortunately, most species are known only from historic type collections. The same developmental pathway for the fused calyx characterizes *Calyptrogenia cuspidata*, but in this species, anthesis occurs by transverse rather than longitudinal tearing of the calyx (Giaretta & al., 2019b). Though originally assigned to diverse genera, the similar habits of southern Hispaniolan species of *Calyptrogenia* likewise suggest that the group is monophyletic. As far as is known, all of the species possess a calyptrate calyx and relatively large, elongate fruits (Peguero & al., 2005a), but *Calyptrogenia jeremiensis* has only been collected once in sterile condition, disregarding its report from Jamaica (*G.R. Proctor 10416* [IJ]). The placement of this species in *Eugenia* is therefore uncertain. As it was originally described in *Eugenia* and resembles the better-known species of *Calyptrogenia* from southern Hispaniola, it is retained in this genus below. Recent collections of *Calyptrogenia* *grandiflora* from the Dominican Republic (Peguero & al., 2005b) differ from the type collection from Haiti in their shorter fruiting pedicels. Furthermore, the ovary of this species was described as having the structure of that of *Psidium*, with ovules borne over the surface of a protruded, bifurcate placenta (Urban, 1931). Flower buds of *Calyptrogenia cuspidata* collected for this study possess a slightly protruded placenta that is apically bilobed, appearing heart-shaped. If produced further into the locule, such a placenta would resemble that depicted for *Calyptrogenia grandiflora*. Thus, in view of the overall similarity of *Calyptrogenia grandiflora* to other species of the group, the differences with *Psidium* noted by Urban (1931), and the observations on the placentation of *C. cuspidata*, *C. grandiflora* may also be safely referred to *Eugenia*.

Clade CII contains species endemic to the Caribbean Islands from Hispaniola eastward, including all but one of the species endemic to Puerto Rico and the Virgin Islands. The clade is divisible into four main lineages, between which relationships are uncertain: (1) *Eugenia dictyophylla* and *E. pubicalyx* Alain from Hispaniola (PP 1.0, BS 98%). Both these species share lanceolate leaves with clearly visible reticulate venation. (2) *Eugenia fajardensis* (Krug & Urb.) Urb. plus *E. woodburyana* Alain (PP 0.99, BS 62%). These rare, vegetatively similar species are restricted to eastern (including Vieques and Culebra) and western Puerto Rico, respectively (Trejo-Torres & al., 2014). *Eugenia woodburyana* has distinctive winged fruits, but both species possess ridged hypanthia. (3) *Eugenia borinquensis* Britton (Fig. 2.3F) plus *E. stahlii* (Kiaersk.) Krug & Urb (PP 1.0, BS 100%). This pair of species inhabits high elevation forests in Puerto Rico and may have the largest flowers of any native species of Myrtaceae in the Antilles. They were described in *Myrtus* subgen. *Eugeniomyrtus* Kiaersk. because of their arcuate embryos

(Kiaerskou, 1889–1890). (4) A group of Caribbean Islands endemics designated the “Lathberry Clade” (PP 1.0, BS 98%) after the common name for *Eugenia cordata* (Britton & Wilson, 1925). This group contains all species of *Eugenia* in Puerto Rico and the Virgin Islands flowering predominantly on old wood. In addition, all species exhibit a large deletion in the *psbA-trnH* intergenic spacer region. Parsimony analysis of the combined data provided support for a close relationship between *Eugenia borinquensis* plus *E. stahlii* and the Lathberry Clade (BS 77%), while analysis of the masked and cpDNA alignments supported a relationship to *E. fajardensis* plus E. *woodburyana* (PP 1.0). A revisionary study of the Lathberry Clade that will provide further details on the circumscription and characterization of the group is underway (Flickinger, in prep.).

Biogeographic Implications**—**The biogeography of the Caribbean Islands is of considerable interest because of the antiquity of the islands and their balance between relative isolation and proximity to two continents (Ricklefs & Bermingham, 2008). Neither molecular dating nor biogeographic analyses were attempted here in accordance with the limitations of this study mentioned above. Nevertheless, some preliminary remarks can be made on the biogeographic implications of some newly identified lineages and patterns in the phylogenetic results.

Previous biogeographic analyses have inferred a South American origin for Neotropical Myrteae (Lucas & al., 2007; Thornhill & al., 2015; Vasconcelos & al., 2017b), and the tendency of insular Caribbean lineages to be nested within widespread genera is consistent with these results. Vasconcelos & al. (2017b) used a dated phylogeny calibrated with pollen fossils to find that South America was also the most likely ancestral range of Myrtinae, the earliest divergent subtribe of Myrteae present in the

Caribbean. Although these authors favored using pollen fossils over macrofossils to date their phylogeny because they considered the pollen record for Myrteae more reliable and it reduced the number of inferred long-distance dispersal events, it is interesting to note that the earlier divergence times they estimated using macrofossils led to a shift in the ancestral range at the crown node of Myrtinae to North/Central America, where *Chamguava* is found today. During the early to mid-Tertiary, when Myrtinae was diversifying (Thornhill & al., 2015; Vasconcelos & al., 2017b), warmer temperatures and close connections between North America, Europe and Asia facilitated plant dispersal across the Northern Hemisphere (Tiffney & Manchester, 2001). An early Tertiary presence of *Myrtus* ancestors in Laurasia (Thornhill & al., 2015) or their dispersal through North America and into Europe somewhat later during this period (Vasconcelos & al., 2017b) have been suggested as explanations for the disjunct presence of *Myrtus* in the Mediterranean region. Indeed, fossil fruits and seeds possibly related to extant Myrteae were reported from the Paleocene of North Dakota and Eocene of British Columbia (Pigg & al., 1993). Future analyses will need to account for the presence of *Calycorectes ekmanii* in the Greater Antilles. Recognition of this third lineage of Myrtinae confined to the Northern Hemisphere, especially if *Calycorectes ekmanii* proves to be sister to *Calycolpus*, could perhaps favor early diversification of Myrtinae outside of South America.

The biogeographic implications of newly identified links between Old World and New World species in *Eugenia* are unclear because of uncertainty in the placement of *E. cycloidea* and *E. coronata* with respect to their closest relatives in this study and the need for additional sampling of species outside of the Neotropics. An eastward round-the-world migration from out of tropical regions of the New World was previously proposed for *Eugenia* sect. *Jossinia* (Mazine & al., 2018). A sister relationship between *Eugenia cycloidea* and *E.* sect. *Jossinia* would suggest that this species is a relictual element, as serpentine areas of Cuba are noted for harboring old lineages (Borhidi, 1996). In the case of *Eugenia coronata*, it will be necessary to refine its placement within *E.* sect. *Umbellatae*. The West African distribution of this species is likely explicable in terms of long-distance dispersal between Africa and the Americas (Renner, 2004; Christenhusz & Chase, 2013).

Considering relationships between the Caribbean Islands, *Eugenia* provides the best opportunity to observe biogeographic trends on account of its diversity in the region and more extensive sampling in this study, including all species endemic to Puerto Rico. The most striking result is the broad east-west geographic divide reflected in the two subclades of Clade C. Clade CI links Caribbean Islands endemics from Hispaniola to the west to species found in Mexico and Central America. These include widespread Caribbean native species such as *Eugenia axillaris*, *E. foetida* and *E. monticola* that find apparently close relatives in continental species such as *E. acapulcensis* Steud., *E. capuli* (Schltdl. & Cham.) Hook. & Arn. and *E. liebmannii* Standl. (McVaugh, 1963). Clade CII contains species from Hispaniola to the east, possibly including *Eugenia walkerae* from the Lesser Antilles. The phylogenetic placement of other Lesser Antillean endemics would be of considerable interest for further understanding the nature of this geographical trend. Links between Hispaniola and Cuba were observed within *Eugenia* sect. *Excelsae* and *E.* sect. *Racemosae,* as well as in Clade CI of *E.* sect. *Umbellatae*. There is a tendency for species within these islands not to form monophyletic groups (Santiago-

Valentin & Olmstead, 2004), but it is unclear from the present study whether this is also the case in *Eugenia* because of missing taxa and uncertainties in relationships.

Taxonomic Treatment

The following treatment completes the necessary nomenclatural changes (new combinations and new names) for *Calyptrogenia*, *Hottea*, *Mitranthes* and *Pseudanamomis*. New combinations are also made for *Calyptranthes pachyadenia* and *Myrcia paganii* in accordance with the results of the phylogenetic study. In all cases, a single collection had already been selected in the protologue as the type. Lectotypes are designated as appropriate to narrow these choices to a single specimen. Most of the concerned species were described by Urban from the collections of Ekman. These can be found in many herbaria (Lanjouw & Stafleu, 1957), but in the absence of extant type material at B (R. Vogt, pers. comm.), duplicates at S were selected. When more than one specimen with the same collection number was present there, preference was given to the highest quality fertile specimen. Only those isolectotypes are listed that were either especially relevant for selection of the lectotype or that were physically examined by the author.

Eugenia P.Micheli ex L., Sp. Pl. 1: 470. 1753 – Type (designated by M.L.Green in Sprague & al., Nom. Prop. Brit. Bot.: 158. 1929): *E. uniflora* L.

= *Hottea* Urb. in Ark. Bot. 22A(10): 40. 1929 – Type: *H. miragoanae* Urb.

= *Calyptrogenia* Burret in Notizbl. Bot. Gart. Berlin-Dahlem 15: 541, 545. 1941 ≡ *Neomitranthes* subgen. *Calyptrogenia* (Burret) Mattos in Loefgrenia 99: 5. 1990 – Type: *C. ekmanii* (Urb.) Burret

= *Pseudanamomis* Kausel in Ark. Bot., n.s., 3: 511. 1956 – Type: *P. umbellulifera* (Kunth) Kausel (≡ Myrtus umbellulifera Kunth)

Note. – See Mazine & al. (2016, 2018) for additional synonyms. In treating *Calyptrogenia* as a subgenus of *Neomitranthes,* Mattos (1990) cited *N. ekmanii* (Urb.) Mattos as the type; however, this combination was based on *Calyptropsidium ekmanii* Urb. rather than *Calyptranthes ekmanii* Urb., which was not mentioned in this publication. The latter is the type of *Calyptrogenia* and therefore also that of *Neomitranthes* subgen. *Calyptrogenia* according to Article 7.3 of the *International Code of Nomenclature* (ICN; Turland & al., 2018). Because *Calyptrogenia* has priority over *Neomitranthes,* the name is incorrect.

1. ***Eugenia ayitiensis*** Flickinger, **nom. nov.** ≡ *Eugenia malangensis* Urb. & Ekman in Ark. Bot. 21A(5): 30. 1927, nom. illeg., non *Eugenia malangensis* (O.Hoffm.) Nied. 1893 ≡ *Hottea malangensis* Urb. in Ark. Bot. 24A(4): 31. 1931 – **Lectotype (designated here):** Haiti. Massif de la Selle, Port-au-Prince, Morne Malanga, top of the mountain, 1475 m alt., 28 Jan 1926, *E.L. Ekman H 5468* (S No. S05-3129 [image!]; isolectotypes: S No. S07-10360 [image!], US barcodes 00118041!, 00774222!).

Note. – Ayiti is the Haitian Creole name for Haiti.

2. ***Eugenia bissei*** Flickinger, **nom. nov.** ≡ *Pseudanamomis nipensis* Bisse in Feddes Repert. 96: 512. 1985, non *Eugenia nipensis* Urb. 1928 – **Lectotype (designated here):** Cuba. Oriente [Holguín], Sierra de Nipe, Mayarí Abajo, Loma de Winch, charrascales, 400–600 m alt., Apr 1968, *J. Bisse & E. Köhler 7002* (HAJB

barcode HAJBG000801 [image!]; isolectotypes: HAJB barcode HAJBG000802 [image!], JE barcode JE00004994 [image!]).

Note. – The specific epithet honors German botanist Johannes Bisse (1935–1984), founder of the Jardín Botánico Nacional de Cuba and one of the foremost students of the Cuban flora in the second half of the 20th century. Bisse (1985) cited a specimen at HAJB as the holotype; however, two specimens of the type collection are found there. Gutiérrez Amaro & al. (1998) listed a "holotype" and an "isotype" specimen at HAJB without directly citing a barcode or other identifier for the type element. The specimen they annotated as the "holotype" is here designated the lectotype.

3. ***Eugenia burretii*** Flickinger, **nom. nov.** ≡ *Calyptropsidium ekmanii* Urb. in Ark. Bot. 24A(4): 17, t. 1. 1931, non *Eugenia ekmanii* (Urb.) Flickinger ≡ *Calyptrogenia grandiflora* Burret in Notizbl. Bot. Gart. Berlin-Dahlem 15: 545. 1941, non *Calyptrogenia ekmanii* (Urb.) Burret 1941, nec *Eugenia grandiflora* O.Berg 1858 ≡ *Neomitranthes ekmanii* (Urb.) Mattos in Loefgrenia 99: 6. 1990 – **Lectotype (designated here):** Haiti. Massif de la Hotte, western group, Les Anglais, southern slope of Morne l'Etang, ca. 1400 m alt., very rare, 21 July 1928, *E.L. Ekman H 10360* (S No. S10-6265 [image!]; isolectotypes: IJ No. 18858!, S No. S-R-9440 [image!], US barcode 00117683!).

Note. – The specific epithet honors German botanist and noted palm specialist Maximilian Burret (1883–1964) for his contributions to Myrteae taxonomy. According to Art. 41.6 of the ICN (Turland & al., 2018), *Neomitranthes ekmanii* was validly published despite the incorrect citation of the place and date of publication of the basionym.

4. ***Eugenia crispula*** (Urb.) Flickinger, **comb. nov.** ≡ *Psidium crispulum* Urb. in Ark. Bot. 17(7): 44. 1921[1922] ≡ *Hottea crispula* (Urb.) Urb. in Ark. Bot. 22A(10): 42. 1929 **– Lectotype (designated here):** Haiti. Dép. Sud, "Morne de la Hotte in declivibus australibus montium occidentalium ad Ma Blanche," ca. 800 m alt. and above, 8 Aug 1917, *E.L. Ekman H 598* (S No. S05-3128 [image!]).

5. ***Eugenia cryptocardia*** Flickinger, **nom. nov.** ≡ *Calyptrogenia cuspidata* Alain in Phytologia 61(1): 356. 1986, non *Eugenia cuspidata* O.Berg 1857 – Holotype: Dominican Republic. Barahona, Monteada Nueva, Caña Brava, in rain forest, 1300 m alt., 15 June 1968, *A.H. Liogier 11636* (US barcode 00054813!; isotype: GH No. 00936794!).

Note. – The specific epithet refers to the heart-shaped appearance of the placenta.

6. ***Eugenia ekmanii*** (Urb.) Flickinger, **comb. nov.** ≡ *Calyptranthes ekmanii* Urb. in Ark. Bot. 22A(10): 32. 1929 ≡ *Calyptrogenia ekmanii* (Urb.) Burret in Notizbl. Bot. Gart. Berlin-Dahlem 15: 545. 1941 – **Lectotype (designated here):** Haiti. Massif de la Hotte, eastern group, Petit-Goâve, Fort-Gary, at the fortress, 1175 m alt., 3 Aug 1926, *E.L. Ekman H 6583* (S No. S05-2621 [image!]; isolectotypes: IJ No. 17033!, S No. S05-2623 [image!], US barcodes 00117816!, 00773842!).

Note .– *Eugenia ekmanii* (Urb.) Mattos was not validly published according to Arts. 41.5 and 41.6 of the ICN (Turland & al., 2018) because the date was omitted in the citation of the basionym (Mattos, 2005).

7. ***Eugenia goavensis*** (Urb.) Flickinger, **comb. nov.** ≡ *Hottea goavensis* Urb. in Ark. Bot. 24A(4): 29. 1931 – **Lectotype (designated here):** Haiti. Massif de la Hotte, eastern group, Grand-Goâve, Morne Descassiers, Eocene limestone, ca. 1200 m

alt., rare, 28 Jan 1928, *E.L. Ekman H 9528* (S No. S12-12693 [image!]; isolectotypes: IJ No. 18746!, S No. S-R-10350 [image!], US barcode 00623510!).

8. ***Eugenia jeremiensis*** Urb. & Ekman in Ark. Bot. 24A(4): 29. 1931 ≡ *Calyptrogenia jeremiensis* (Urb. & Ekman) Burret in Notizbl. Bot. Gart. Berlin-Dahlem 15: 545. 1941 – **Lectotype (designated here)**: Haiti. Massif de la Hotte, western group, Jérémie, at Source-Cahouane, mountainside, ca. 200 m alt., 4 July 1928, *E.L. Ekman H 10235* (S No. S05-2911 [image!]; isolectotypes: IJ No. 18845!, S No. S07-9232 [image!], US barcode 00118013!).

9. ***Eugenia miragoanae*** (Urb.) Flickinger, **comb. nov.** ≡ *Hottea miragoanae* Urb. in Ark. Bot. 22A(10): 40. 1929 – **Lectotype (designated here):** Haiti. Massif de la Hotte, group Morne Rochelois, Miragoane, limestone crag near Quatre-Chemins, 1000 m alt., 31 Oct 1927, *E.L. Ekman H 9199* (S No. S05-3131 [image!]; isolectotypes: IJ No. 18658!, S No. S07-4056 [image!], US barcodes 00512676!, 00604496!).

10. ***Eugenia neibensis*** (Alain) Mattos in Loefgrenia 122: 2. 2006 ≡ *Hottea neibensis* Alain in Phytologia 25(5): 269. 1973 ≡ *Calycorectes minutifolius* Mattos in Loefgrenia 113: 1. 1999, nom. superfl. ≡ *Eugenia minutifolia* Mattos in Loefgrenia 120: 7. 2005, nom. superfl. et illeg., non *Eugenia minutifolia* (Mattos & D.Legrand) Mattos 1984 – Holotype: Dominican Republic. Sierra de Neiba, near La Doscientos, rain forest, 1750–1850 m alt., common in dense forest, 5–7 Sept 1968, *A.H. Liogier 12523* (NY barcode 00099336 [image!]; isotype: US barcode 00118241!).

Note. – *Calycorectes minutifolius* was published as a new species based on the holotype of *Hottea neibensis* (Mattos, 1999). The name is therefore superfluous under

Art. 52 of the ICN (Turland & al., 2018). *Eugenia minutifolia* Mattos was intended as a new combination based on *Calycorectes minutifolius* (Mattos, 2005). It is validly published as a replacement name for *Calycorectes minutifolius* (Arts. 6.12, 6.14) despite being illegitimate as both a superfluous name and a later homonym of *Eugenia minutifolia* (Mattos & D.Legrand) Mattos. Although *Eugenia neibensis* was published without citation of *Hottea neibensis* (Mattos, 2006), it is treated as a new combination based on *H. neibensis* in accordance with Art. 41.8(c), as it would otherwise be validly published as a replacement name for *E. minutifolia* Mattos.

11. ***Eugenia pachyadenia*** (Urb. & Ekman) Flickinger, **comb. nov.** ≡ *Calyptranthes pachyadenia* Urb. & Ekman in Symb. Antill. 9: 481. 1928 ≡ *Myrcia pachyadenia* (Urb. & Ekman) Z.Acosta & K.Samra in Phytotaxa 406(3): 152. 2019 – **Lectotype (designated here):** Cuba. Santa Clara [Sancti Spiritus], mountains of the Siguanéa-Trinidad group, Pico Potrerillo, on the top of this mountain, 30 Mar 1924, *E.L. Ekman 18963* (S No. S05-2733 [image!]).

12. ***Eugenia roseauxensis*** Flickinger, **nom. nov.** ≡ *Hottea micrantha* Urb. & Ekman in Ark. Bot. 24A(4): 30. 1931, non *Eugenia micrantha* DC. 1828 ≡ *Hottea goavensis* var. *micrantha* (Urb. & Ekman) Borhidi in Acta Bot. Hung. 29: 186. 1983 – **Lectotype (designated here):** Haiti. Massif de la Hotte, western group, Les Roseaux, Nan-Patates, in forest, 1000 m alt., common, 17 Sept 1928, *E.L. Ekman H 10704* (S No. S05-3130 [image!]; isolectotypes: IJ No. 18910!, S No. S07-10359 [image!], US barcode 00623509!).

    Note. – The specific epithet refers to the type locality in Dép. Grand'Anse, Haiti.

13. ***Eugenia torbeciana*** (Urb. & Ekman) Flickinger, **comb. nov.** ≡ *Hottea torbeciana* Urb. & Ekman in Ark. Bot. 22A(10): 41. 1929 – **Lectotype (designated here):** Haiti. Massif de la Hotte, western group, Torbec, Formon, forest on limestone, ca. 1000 m, not rare, 4 Jan 1927, *E.L. Ekman H 7582* (S No. S05-3132 [image!]; isolectotype: IJ No. 18272!).

14. ***Eugenia urbanii*** Flickinger, **nom. nov.** ≡ *Calyptropsidium bracteosum* Urb. in Ark. Bot. 21A(5): 20. 1927, non *Eugenia bracteosa* DC. 1828 ≡ *Calyptrogenia bracteosa* (Urb.) Burret in Notizbl. Bot. Gart. Berlin-Dahlem 15: 546. 1941 – **Lectotype (designated here):** Haiti. Massif de la Hotte, western group, Torbec, near La Hatte-Esmangard, rocky place, limestone, 400 m alt., 9 Dec 1925, *E.L. Ekman H 5355* (S No. S-R-9436 [image!]; isolectotypes: IJ No. 16552!, S No. S10-6264 [image!]).

Note. – The specific epithet honors eminent German botanist Ignatz Urban (1848–1931) for his extensive and painstaking work on the Antillean flora, including Myrtaceae.

Myrcia DC. ex Guill. in Bory, Dict. Class. Hist. Nat. 11: 401. 1827, nom. cons. – Type (designated by McVaugh in Taxon 5(1): 143. 1956): *M. bracteolaris* (Poir.) DC.

= *Mitranthes* O.Berg in Linnaea 27: 316. 1856 – Type (designated by Burret in Notizbl. Bot. Gart. Berlin-Dahlem 15: 536. 1941): *M. ottonis* O.Berg.

Note. – See Lucas & al. (2018) for additional synonyms. McVaugh (1968) accepted Burret's (1941) statement that *Mitranthes ottonis* "ist die Leitart der Gattung" as typifying the genus. Although elsewhere in the same publication Burret used the term "Typus," it seems reasonable to interpret "Leitart" as an equivalent term under Art. 7.11 of the ICN (Turland & al., 2018). It cannot, in this case, be understood as a reference to the first listed, or "lead," species of the genus. McVaugh's interpretation is therefore followed.

15. ***Myrcia asperorum*** Flickinger, **nom. nov.** ≡ *Mitranthes macrophylla* Proctor in J. Arnold Arbor. 63(3): 280. 1982, non *Myrcia macrophylla* DC. 1828 – Holotype: Jamaica. Trelawny, near Crown Lands road extension, 4.5–5 miles northwest of Troy, wooded rocky limestone hilltop, ca. 2000 feet alt., 4 Jan 1975, *G.R. Proctor 34573* (IJ No. 60070!; isotypes: FTG barcode 00048143!, US barcode 00117703!).

Note. – The leaves of this species are not especially large compared to those of other species of *Myrcia*, and there are already multiple epithets with this meaning in the genus. The new epithet refers to the "rough places" inhabited by this and related species of Jamaican *Mitranthes*, which occur on jagged limestone in a region of karst in central Jamaica known as the Cockpit Country (Fig. 2.1).

16. ***Myrcia chionantha*** Flickinger, **nom. nov.** ≡ *Mitranthes nivea* Proctor in J. Arnold Arbor. 63(3): 278. 1982, non *Myrcia nivea* Cambess. 1832 – **Lectotype (designated here):** Jamaica. St. Ann, Mason River district, ca. 3 miles due northwest of Kellits P.O., wooded limestone hilltop, ca. 2300 feet alt., 30 June 1965, *G.R. Proctor 26480* (LL barcode 00372172 [image!]).

Note. – The specific epithet refers to the snowy appearance of this species when in full bloom (Proctor, 1982). A holotype was cited without specifying the herbarium. No duplicates were found at the following herbaria: A, FTG, GH, IJ, MICH, SJ, UCWI and US. Since there was no statement that the material was collected in unicate, it is possible that a duplicate might exist elsewhere. A lectotype is therefore designated.

17. ***Myrcia clarendonensis*** (Proctor) Flickinger, **comb. nov.** ≡ *Calyptranthes clarendonensis* Proctor in Rhodora 60: 323. 1959 ≡ *Mitranthes clarendonensis* (Proctor) Proctor in J. Arnold Arbor. 63(3): 280. 1982 – Holotype: Jamaica. Clarendon, Peckham Woods, on rocky limestone hilltop, ca. 2500 feet alt., 23 Dec 1955, *G.R. Proctor 11399* (IJ No. 19862!; isotypes: US barcodes 00117811!, 00997538!).

18. ***Myrcia maxonii*** (Britton & Urb.) Flickinger, **comb. nov.** ≡ *Calyptranthes maxonii* Britton & Urb. in Symb. Antill. 7: 296. 1912 ≡ *Mitranthes maxonii* (Britton & Urb.) Proctor in J. Arnold Arbor. 63(3): 278. 1982 – **Lectotype (designated here):** Jamaica. Crown lands, 4 miles west of Troy, forest opening, ca. 750 m alt., 29 June 1904, *W.R. Maxon 2896* (NY barcode 00084478 [image!]; isolectotype: US barcode 00117837!).

Note. – On a note attached to the US duplicate, Maxon requested that Britton be shown the more complete material of this specimen. In the absence of an indication that either Britton or Urban saw the US specimen, the NY specimen was selected.

19. ***Myrcia ottonis*** (O.Berg) Flickinger, **comb. nov.** ≡ *Mitranthes ottonis* O.Berg in Linnaea 27: 316. 1856 ≡ *Calyptranthes ottonis* (O.Berg) C.Wright in Anales Acad. Ci. Méd. Habana 5: 429. 1869 ≡ *Chytraculia ottonis* (O.Berg) Kuntze in Revis. Gen. Pl. 1: 238. 1891 – **Lectotype (designated here):** Cuba. “Habitat ad ripam amnis St. Juan,” *E. Otto 272* (K barcode K000331506 [image!]).

= *Myrcia coriacea* var. *acutifolia* Griseb., Cat. Pl. Cub.: 86. 1866 – Holotype: Cuba. *C. Wright 2419* (GOET barcode GOET008248 [image!]).

Note. – Howard (1988) conducted a thorough study of Charles Wright's collections from Cuba, in which the specimen at GOET is considered the holotype of *Myrcia coriacea* var. *acutifolia*. Because Wright's collections from 1863 were evidently received by Grisebach without labels and the numbers assigned to Wright's collections do not necessarily correspond to individual gatherings, the type locality of this taxon in western Cuba is uncertain. Howard (1988: App. #1) cites sheets marked *2419* on the labels used for distributing the specimens at GH (barcode 00071065 [image!]) and NY (barcode 00099342 [image!]). The GH sheet bears collector's labels dated 30 May and 21 June from Retiro, while the NY sheet bears a collector's label that states, "edge of river Sagua . . . June 25." According to Howard (1988: App. #3) Retiro is a finca near Taco Taco in Pinar del Río, and Sagua is a locality near Bahía Honda in present-day Artemisa.

20. ***Myrcia psilophylla*** Flickinger, **nom. nov.** ≡ *Mitranthes glabra* Proctor in J. Arnold Arbor. 63(3): 280. 1982, non *Myrcia glabra* (O.Berg) D.Legrand 1961 – Holotype: Jamaica. St. Ann, Douglas Castle district, wooded limestone hillside, 2100–2300 feet alt., 22 January 1966, *G.R. Proctor 26833* (IJ No. 39998!).

Note. – The specific epithet refers to the glabrous leaves of this species.

21. ***Myrcia urbaniana*** (Burret) Flickinger, **comb. nov.** ≡ *Mitranthes urbaniana* Burret in Notizbl. Bot. Gart. Berlin-Dahlem 15: 537. 1941 – Type: Jamaica. Near Troy, ca. 700 m alt., Apr 1916, *J.R. Perkins 977* (n.v.).

Note. – See above for discussion of the affinities of this species. No type material could be located at B or at the following herbaria known to have Perkins's Jamaica collections: A, F, G, GH and K (Vegter, 1983).

Pimenta Lindl. in Coll. Bot. 4: sub t. 19. 1821 – Type: *P. officinalis* Lindl. (≡ Myrtus pimenta L.)

22. ***Pimenta paganii*** (Krug & Urb.) Flickinger, **comb. nov.** ≡ *Myrcia paganii* Krug & Urb. in Bot. Jahrb. Syst. 19: 587. 1895 – **Lectotype (designated here):** Puerto Rico. Sierra de Lares, "in sylva primaeva," 16 Feb 1887, *P. Sintenis 6220* (K barcode K000035926 [image!]).

Note. – No duplicates of this collection have been located. In addition, the label is embossed with "Herb. Krug et Urban.," with "(non distribuda)" written on it. These unusual circumstances suggest that this specimen might have been the one specimen used by Urban to describe the plant, but this cannot be concluded with certainty. A lectotype is therefore designated. The type of *Myrcia margarettae* (Alain) Alain (*A.H. Liogier 9400* [NY barcode 00084565 (image!)]) is a strikingly similar plant from Puerto Rico that may prove to be synonymous.

Conclusion

This survey provides, for the first time, an overview of the diversity of Myrtaceae present in the Caribbean Islands based on inferred evolutionary relationships. As a result of this phylogenetic approach, two lineages are newly reported for the Greater Antilles. The first of these is subtribe Myrtinae, which is represented by *Calycorectes ekmanii*. This species is closely related to *Calycolpus*, but further study is needed to provide a basis for an appropriate taxonomic change. The second new lineage is represented by *Eugenia cycloidea*, which finds close relatives among the Old World species of *E.* sect. *Jossinia*. Additional study of this species is also warranted to clarify its placement within the genus. Though not pertinent to the Caribbean Islands, *Eugenia coronata* is identified as representing a second distinct lineage of *Eugenia* present in Africa. The results of this study also suggest potential clades formed by Caribbean Islands endemics within several genera, including the Lathberry Clade. The identification of these groups will facilitate further systematic studies both within and outside of the Caribbean Islands.

With respect to the specific objectives of this study, both *Calyptrogenia* and *Hottea* belong within Clade CI of *Eugenia* sect. *Umbellatae*. *Hottea* is closely related to a group of Cuban endemics, while the affinities of *Calyptrogenia* remain unclear. Species of both genera from southern Hispaniola are considered monophyletic. In contrast, *Mitranthes* is concluded to be biphyletic. *Pseudanamomis* sensu Bisse is a polyphyletic group of species only distantly related to the type of the genus. Nevertheless, there is a core group of Cuban endemics within this concept that includes at least one additional species. The sampled species of *Calycolpus* sensu Bisse belong in *Eugenia* sect. *Excelsae* along with other species of *Eugenia* endemic to Cuba and Hispaniola. Based on the placement of three Cuban taxa, species of *Plinia* from the Greater Antilles belong in *Myrciaria*. This result is supported by the circular scar left on the fruit by the deciduous calyx. The Greater Antillean members of this genus are left in *Plinia* pending additional revision, but new combinations, new names and lectotypifications are made as appropriate for the other focal groups in addition to two misplaced species described from sterile collections.

Future phylogenetic studies of Myrtaceae in the Caribbean Islands should prioritize more extensive sampling of species in adjacent regions, particularly Central America and the Lesser Antilles, to identify additional links to species from outside the Greater Antilles. Further sampling of groups within the islands will also be necessary both to explore the potential clades identified here and to identify new ones. The close associations observed between species on different islands demonstrate the necessity of sampling across islands, but Cuba, with its outstanding diversity, and Jamaica, which was represented by relatively few species in this study, merit particular attention. Sequencing of additional markers will likely be needed to improve resolution within the groups identified here; however, observations of conflicting relationships between apparently closely related species implied by nrDNA and cpDNA indicate the need to consider the possibilities of reticulation and incomplete lineage sorting. The use of multiple unlinked markers is therefore recommended for more narrowly focused studies (Naciri & Linder, 2015). As noted above, this phylogenetic survey provides an incomplete picture of Myrtaceae in the Caribbean Islands. It is hoped that it will stimulate further systematic research on species of Myrteae from throughout the Caribbean region.

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Tables

Table 2.1. PCR primers and amplification protocols used to generate sequence data for this study.

Region	**Primer**	**Reference**	**PCR Protocol**
ITS	17SE 26SE	Sun & al., 1994	94° C, 2 min.; (94° C, 1 min.; 52° C, 1 min.; 72° C, 1 min.) × 30
psbA-trnH	trn H (GUG) psb A	Hamilton, 1999	94° C, 4 min.; (94° C, 1 min.; 48° C, 1 min.; 72° C, 2 min. 30 s) × 30
ndhF-rpl32	ndhF (*Eucalyptus*) rpl32-R (*Eucalyptus*)	Shaw & al., 2014	80° C, 5 min.; (94° C, 1 min.; 50° C, 1 min.; 72° C, 2 min.) × 35; 72° C, 5 min.
ndhF-rpl32	ndhF (universal) Rev. Int.: 5′-TCTTTTCTTTTAAGTCTATTTCTTCT-3′	Shaw & al., 2007; This Study	80° C, 5 min.; (94° C, 1 min.; 50° C, 1 min.; 72° C, 2 min.) × 35; 72° C, 5 min.
ndhF-rpl32	Fwd. Int.: 5′-TCATTAACTAATTCATGGTAGAAC-3′ rpl32-R (universal)	This Study; Shaw & al., 2007	80° C, 5 min.; (94° C, 1 min.; 55° C, 1 min.; 72° C, 2 min.) × 35; 72° C, 5 min.
trnL-trnF	c f	Taberlet & al., 1991	80° C, 5 min.; (94° C, 1 min.; 50° C, 1 min.; 72° C, 2 min.) × 35; 72° C, 5 min.

Table 2.2. Summary of analyzed alignments, including the length of DNA sequence alignments in number of base pairs, percent variability and number of parsimony informative characters (PIC's) in the sequence data, number of coded gaps, partitioning scheme and models of sequence evolution selected by PartitionFinder2 for Bayesian inference and the number of unique most parsimonious (MP) trees found along with their length and consistency index (CI).

Alignment	**Aligned Length**	**Percent Variable (PIC's)**	**Coded Gaps**	**Data Partitions**					**MP Trees (Length/CI)**
				18S, 5.8S & 26S rRNA's	**ITS1 & ITS2**	***psbA-trnH***	***ndhF-rpl32* & *trnL-trnF***	***trnL* intron**	
ITS	943	36.4% (255)	3	TRNEF+I+G	TRNEF+I+G	n/a	n/a	n/a	3134 (1471/0.364)
Chloroplast	2979	22.6% (351)	30[1]	n/a	n/a	TVM+G		K81UF+G	4914 (1256/0.685)
Combined (Complete)[2]	3922	25.91% (606)	30[1]	TRNEF+I+G	TRNEF+I+G	TVM+G	TVM+G	K81UF+G	3767 (2790/0.500)
Combined (Masked)	3397	24.5% (483)	30[1]	TRNEF+I+G	TRNEF+I+G	TVM+G		K81UF+G	3151 (2040/0.542)

[1] Includes three gaps that are not parsimony informative.

[2] The same models of sequence evolution and partitioning scheme were selected for this alignment when *Eugenia umbellulifera* was excluded.

Figures

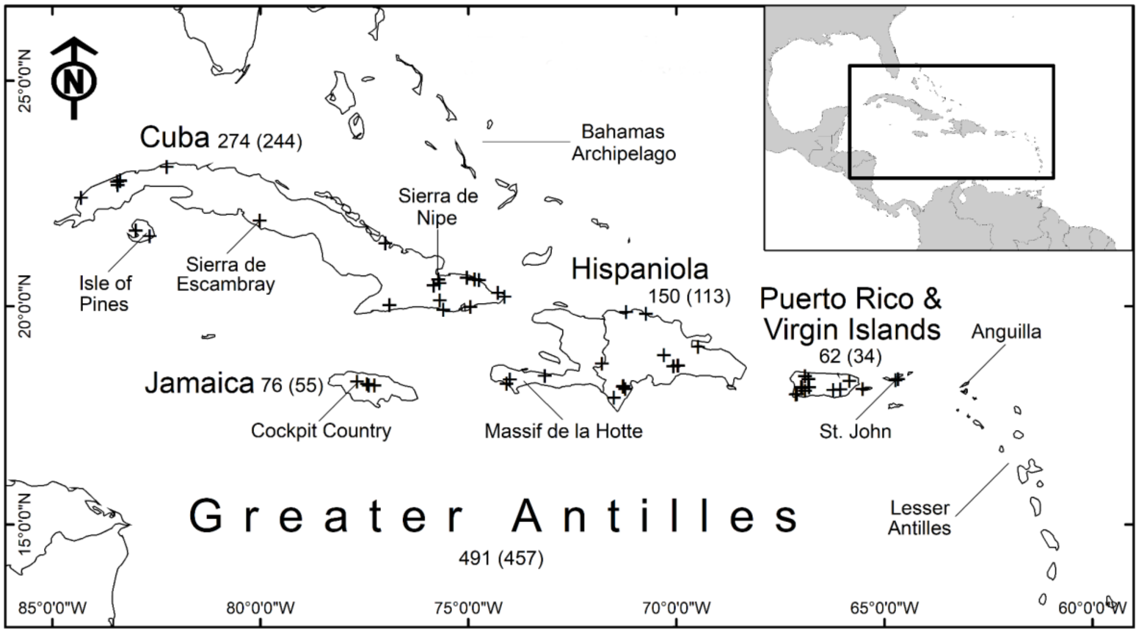

Fig. 2.1. Map of the Caribbean Islands, including the Greater and Lesser Antilles plus the Bahamas Archipelago. Locations of specific islands and regions mentioned in the text are indicated. For the Greater Antilles, numbers beside the names of islands or island groups give the number of native followed by the number of endemic species of Myrtaceae for that area (WCSP, 2020). Sites of all field collections in the Greater Antilles for material sequenced in this study are marked with plus symbols (+).

Figure 2.2. Representatives of focal groups of Myrtaceae from the Greater Antilles. **A–B,** *Calycorectes ekmanii* Urb. (= *Hottea moana* (Borhidi & O.Muñiz) Borhidi), flowers (A) and habit (B); **C,** *Mitranthes ottonis* O.Berg, flowers; **D,** *Plinia orthoclada* Urb., fruit — Photo credit: A–B, J. Flickinger; C, M. Calonje; D, N. Tiernan.

Figure 2.3. Representatives of selected lineages of *Eugenia* from the Greater Antilles. **A,** *Eugenia cycloidea* Urb. (*E.* aff. sect. *Jossinia*), fruit; **B,** *Eugenia excisa* Urb. (*E.* sect. *Excelsae*; *Calycolpus* sensu Bisse), leaves; **C,** *Eugenia maestrensis* Urb. (*E.* sect. *Umbellatae,* Clade CI; *Pseudanamomis* sensu Bisse), flower; **D,** *Eugenia victorinii* Alain (*E.* sect. *Umbellatae,* Clade CI; *Pseudanamomis* sensu Bisse), flower and fruit; **E,** *Eugenia lineata* (Sw.) DC. (*E.* sect. *Racemosae*), fruit; **F,** *Eugenia borinquensis* Britton (*E.* sect. *Umbellatae,* Clade CII), flower. — Photo credit: A–C, E & F, J. Flickinger; D, R. Oviedo Prieto.

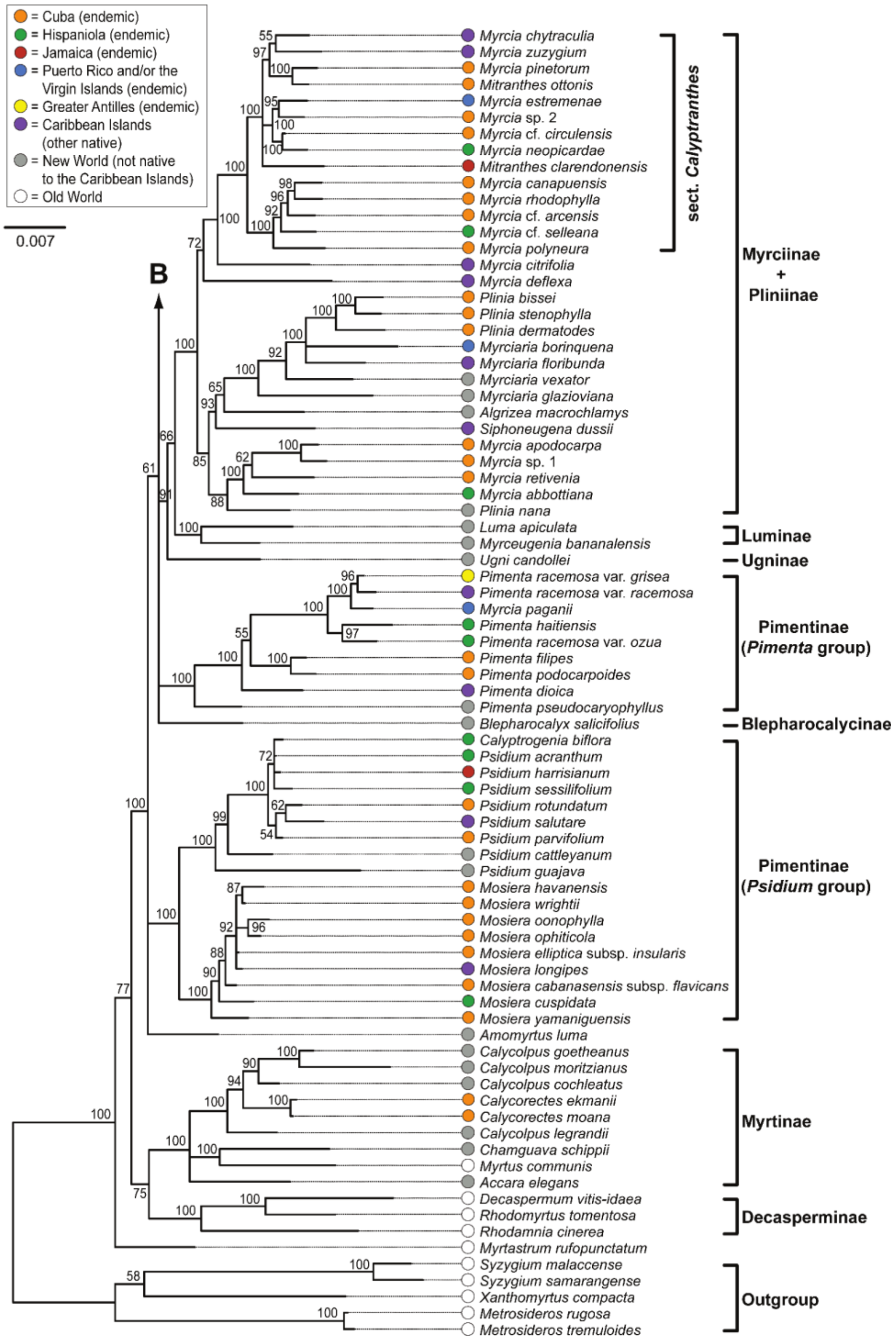

Figure 2.4A. Majority-rule consensus tree resulting from Bayesian analysis of the full, combined ITS, *psbA-trnH*, *ndhF-rpl32* and *trnL-trnF* sequence data. Part A shows the root portion of the tree; part B, subtribe Eugeniinae. Posterior probabilities are indicated as percentages above branches. Values found after removal of *Eugenia umbellulifera* from the alignment are shown within parentheses for selected branches. (continued on next page)

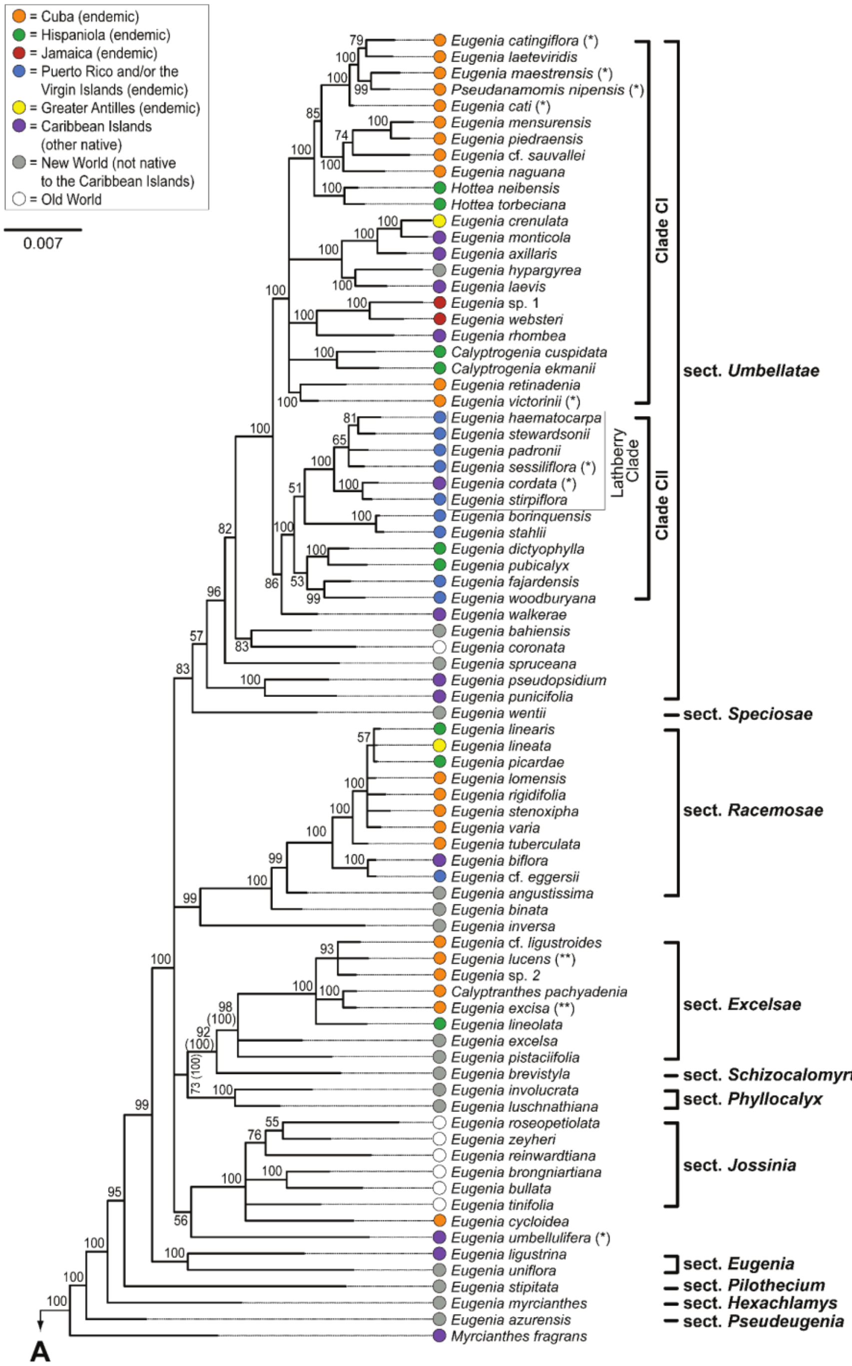

Figure 2.4B. (continued from previous page) Subtribes are labeled according to Lucas & al. (2019) with the *Psidium* and *Pimenta* groups of Vasconcelos & al. (2017b) treated separately. *Myrcia* sect. *Calyptranthes* is labeled in the Myrciinae + Pliniinae clade, and sections of *Eugenia* are labeled according to Mazine & al. (2018) in Eugeniinae. Species of *Eugenia* corresponding to *Pseudanamomis* sensu Bisse (1985) are indicated by a single asterisk, while those of *Calycolpus* sensu Bisse (1983) are indicated by a double asterisk. Scale units are expected number of substitutions per site.

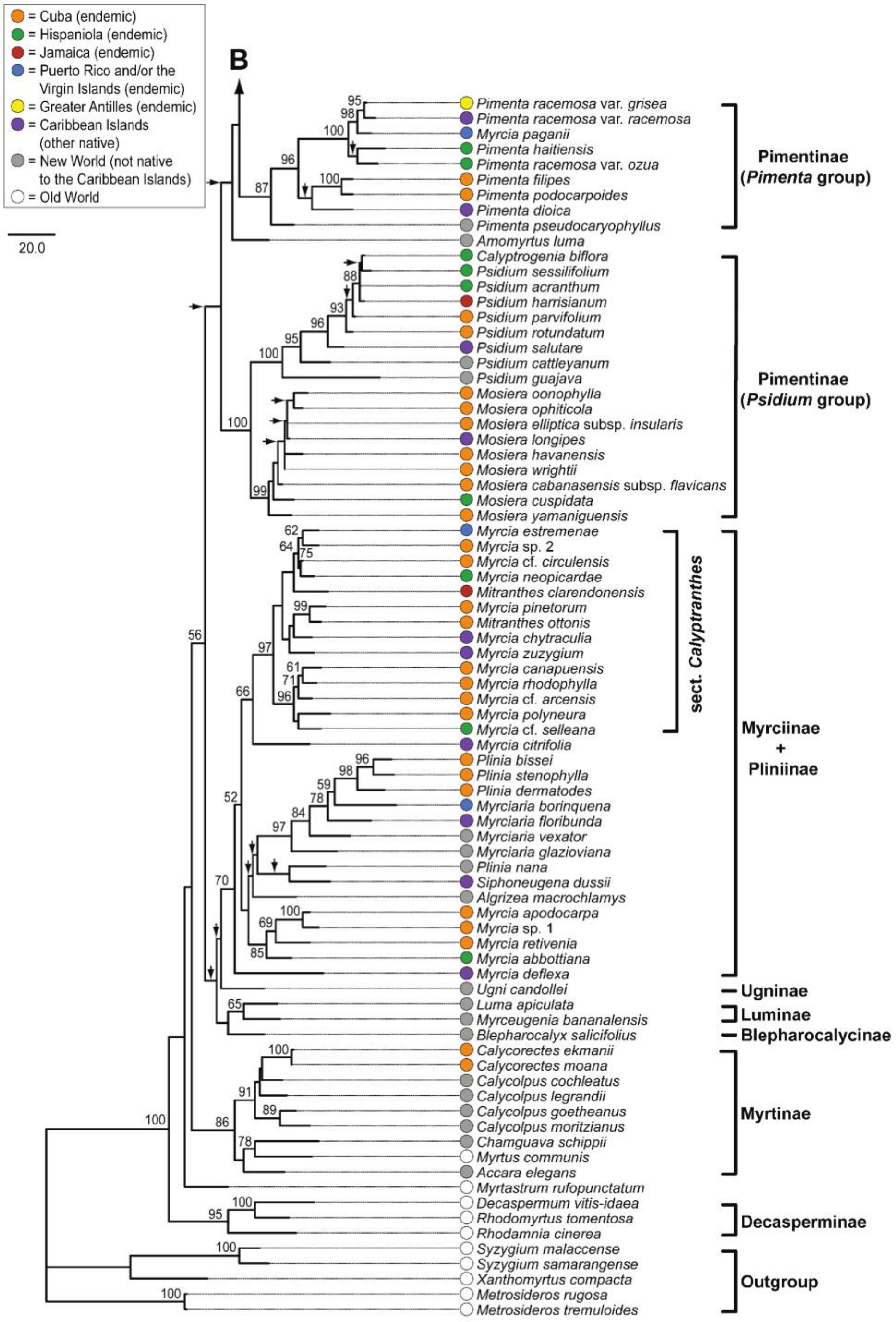

Figure 2.5A. One of the 3767 unique most parsimonious (MP) trees (length = 2790, consistency index = 0.500) found from analysis of the full, combined ITS, *psbA-trnH*, *ndhF-rpl32* and *trnL-trnF* sequence data. Part A shows the root portion of the tree; part B, subtribe Eugeniinae. Bootstrap support percentages are shown above branches. Values found after removal of *Eugenia umbellulifera* from the alignment are shown within parentheses for selected branches. (continued on next page)

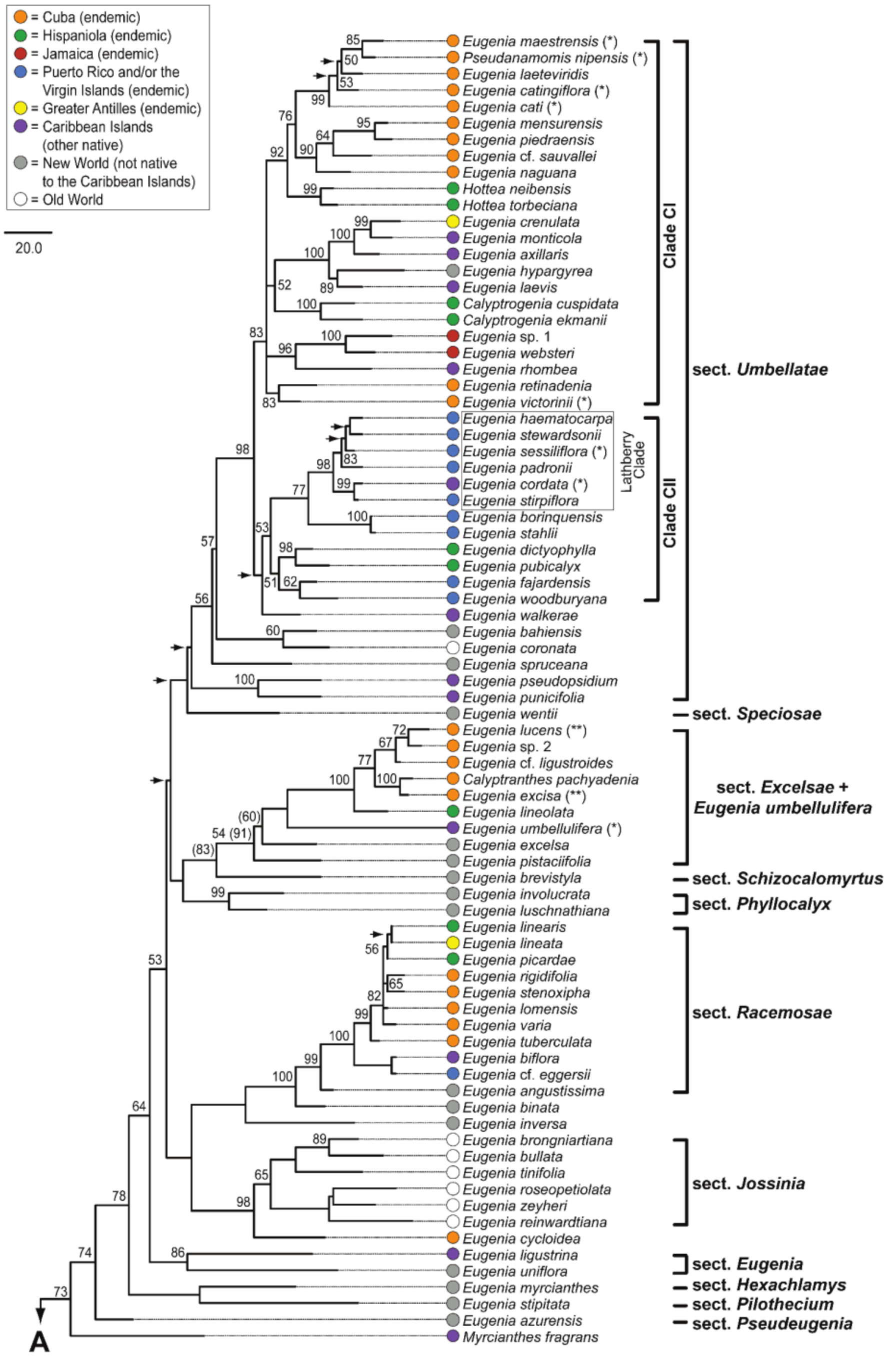

Figure 2.5B. (continued from previous page) Arrows indicate branches not present in the strict consensus of MP trees. Subtribes are labeled according to Lucas & al. (2019) with the *Psidium* and *Pimenta* groups of Vasconcelos & al. (2017b) treated separately. *Myrcia* sect. *Calyptranthes* is labeled in the Myrciinae + Pliniinae clade, and sections of *Eugenia* are labeled according to Mazine & al. (2018) in Eugeniinae. Species of *Eugenia* corresponding to *Pseudanamomis* sensu Bisse (1985) are indicated by a single asterisk, while those of *Calycolpus* sensu Bisse (1983) are indicated by a double asterisk.

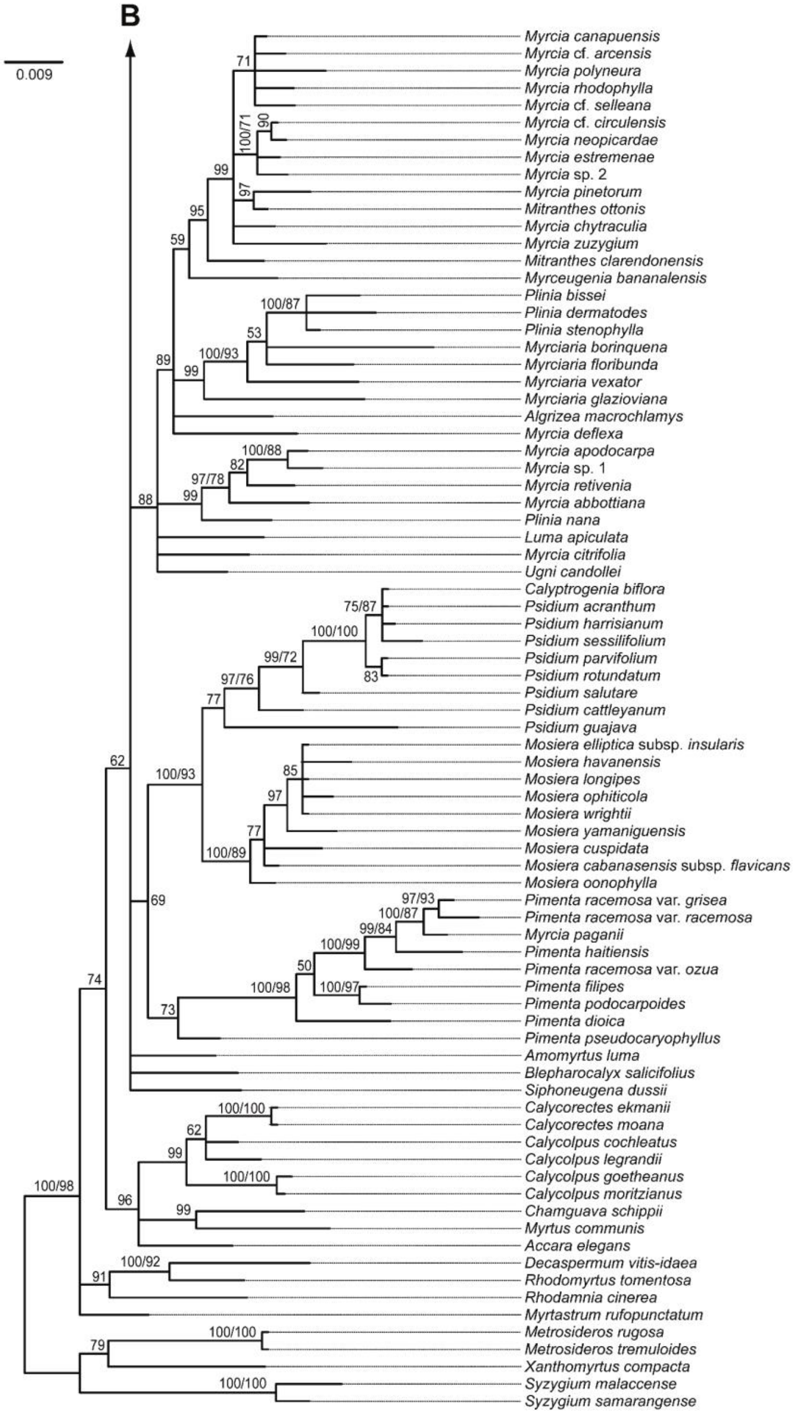

Figure 2.6A. Majority-rule consensus tree resulting from separate analysis of the full, nuclear (ITS) sequence data by Bayesian inference. Part A shows the root portion of the tree; part B, subtribe Eugeniinae. Posterior probabilities are indicated as percentages above branches. Bootstrap support percentages ≥70 from the equivalent parsimony analysis are indicated following a slash. (continued on next page)

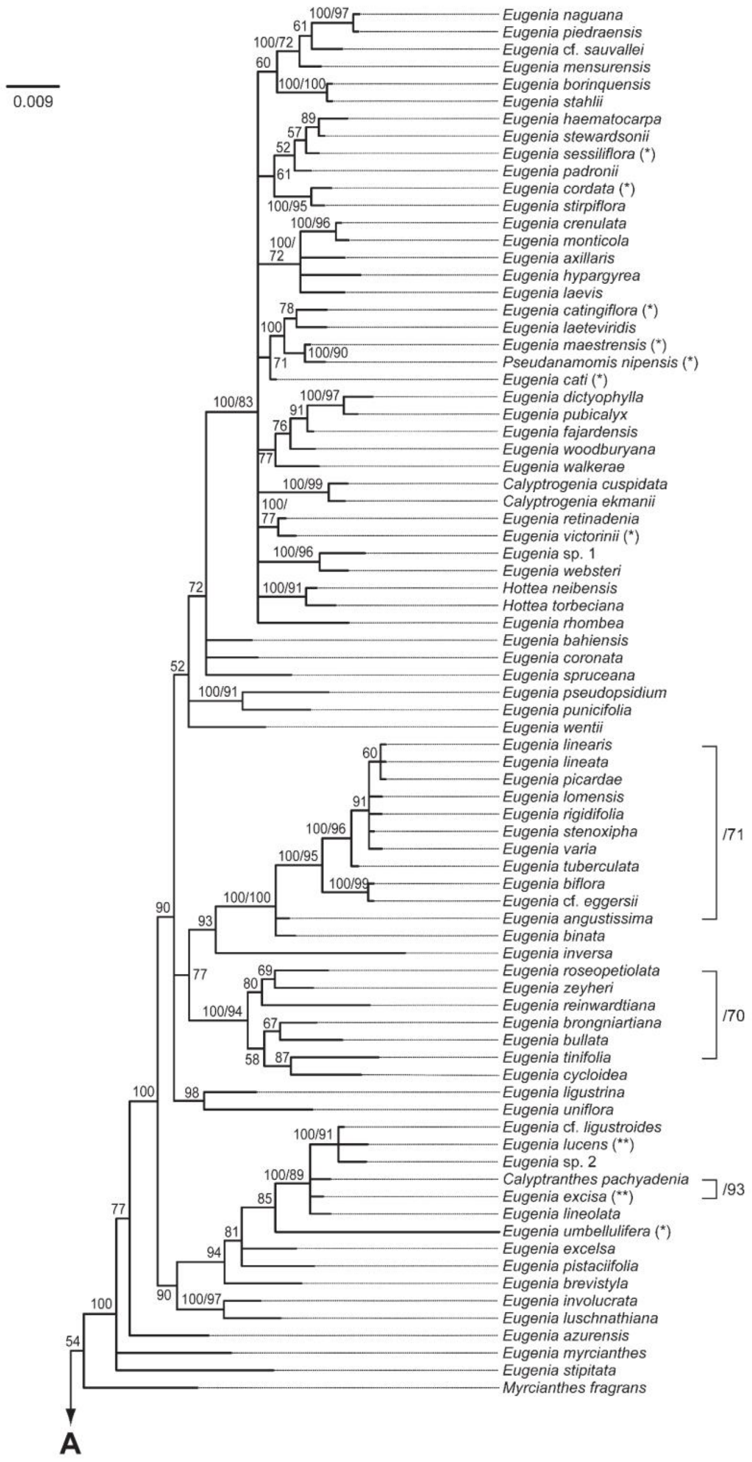

Figure 2.6B. (continued from previous page) Values for three clades that did not appear in the Bayesian analysis are shown at right. Species of *Eugenia* corresponding to *Pseudanamomis* sensu Bisse (1985) are indicated by a single asterisk, while those of *Calycolpus* sensu Bisse (1983) are indicated by a double asterisk. Scale units are expected number of substitutions per site.

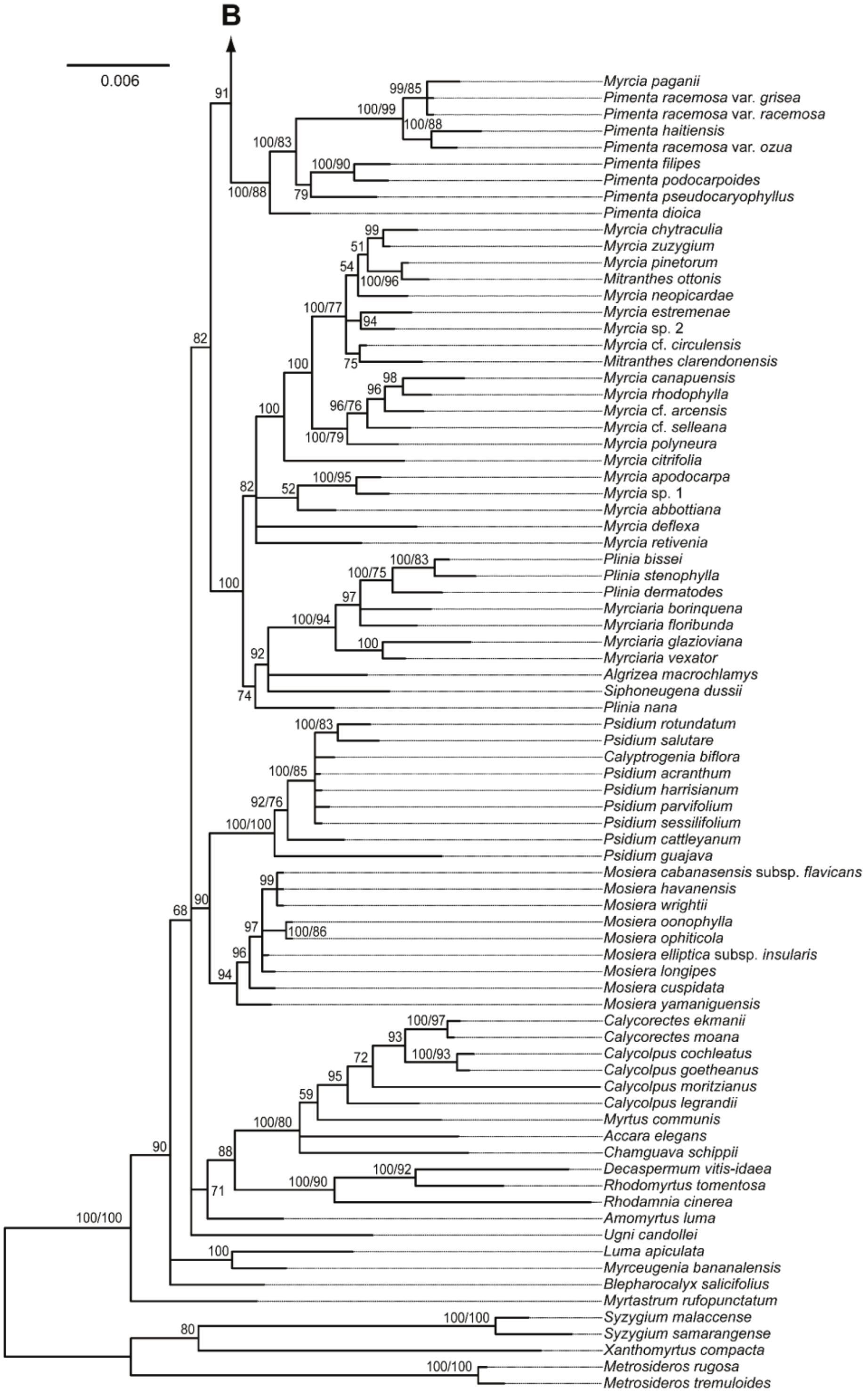

Figure 2.7A. Majority-rule consensus tree resulting from separate analysis of the full, chloroplast (*psbA-trnH*, *ndhF-rpl32* and *trnL-trnF*) sequence data by Bayesian inference. Part A shows the root portion of the tree; part B, subtribe Eugeniinae. Posterior probabilities are indicated as percentages above branches. (continued on next page)

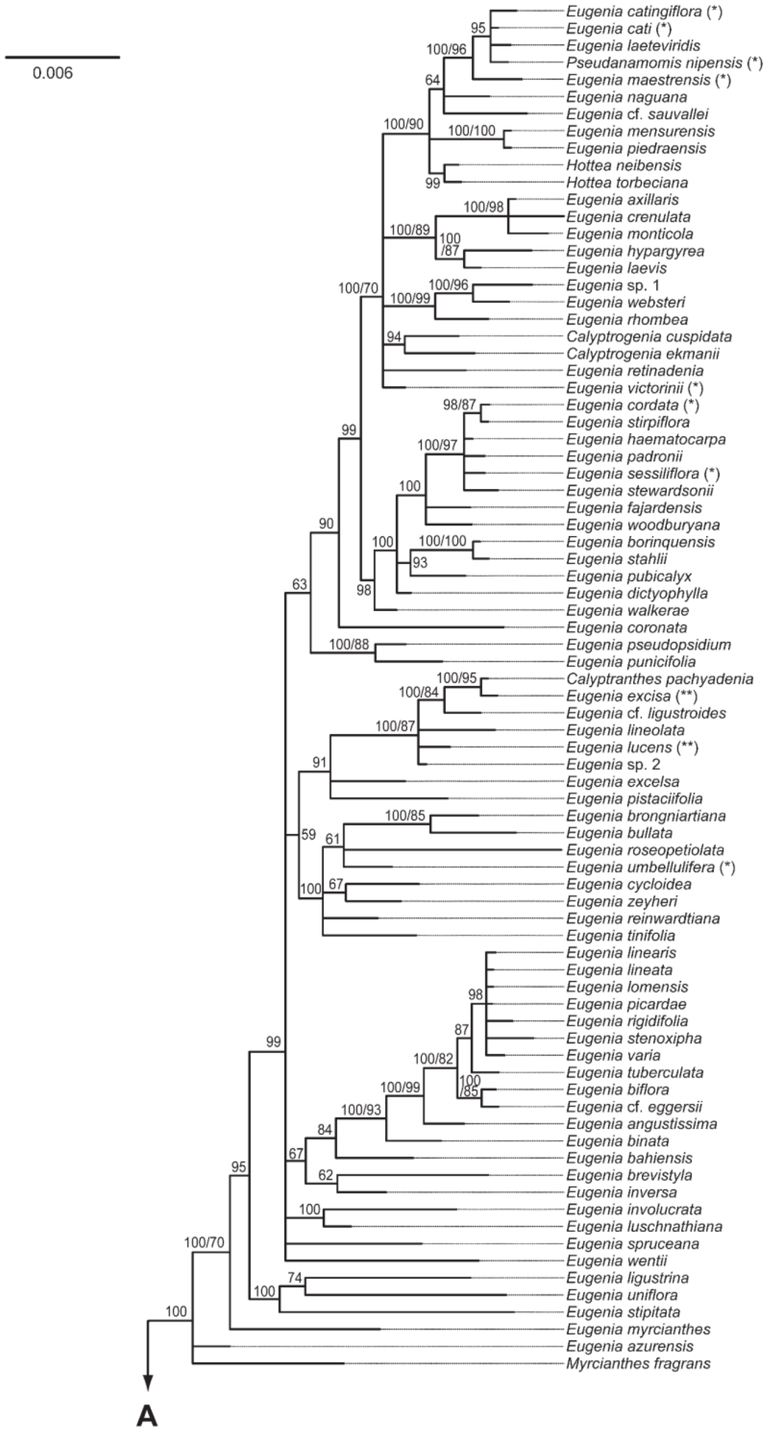

Figure 2.7B. (continued from previous page) Bootstrap support percentages ≥70 from the equivalent parsimony analysis are indicated following a slash. Species of *Eugenia* corresponding to *Pseudanamomis* sensu Bisse (1985) are indicated by a single asterisk, while those of *Calycolpus* sensu Bisse (1983) are indicated by a double asterisk. Scale units are expected number of substitutions per site.

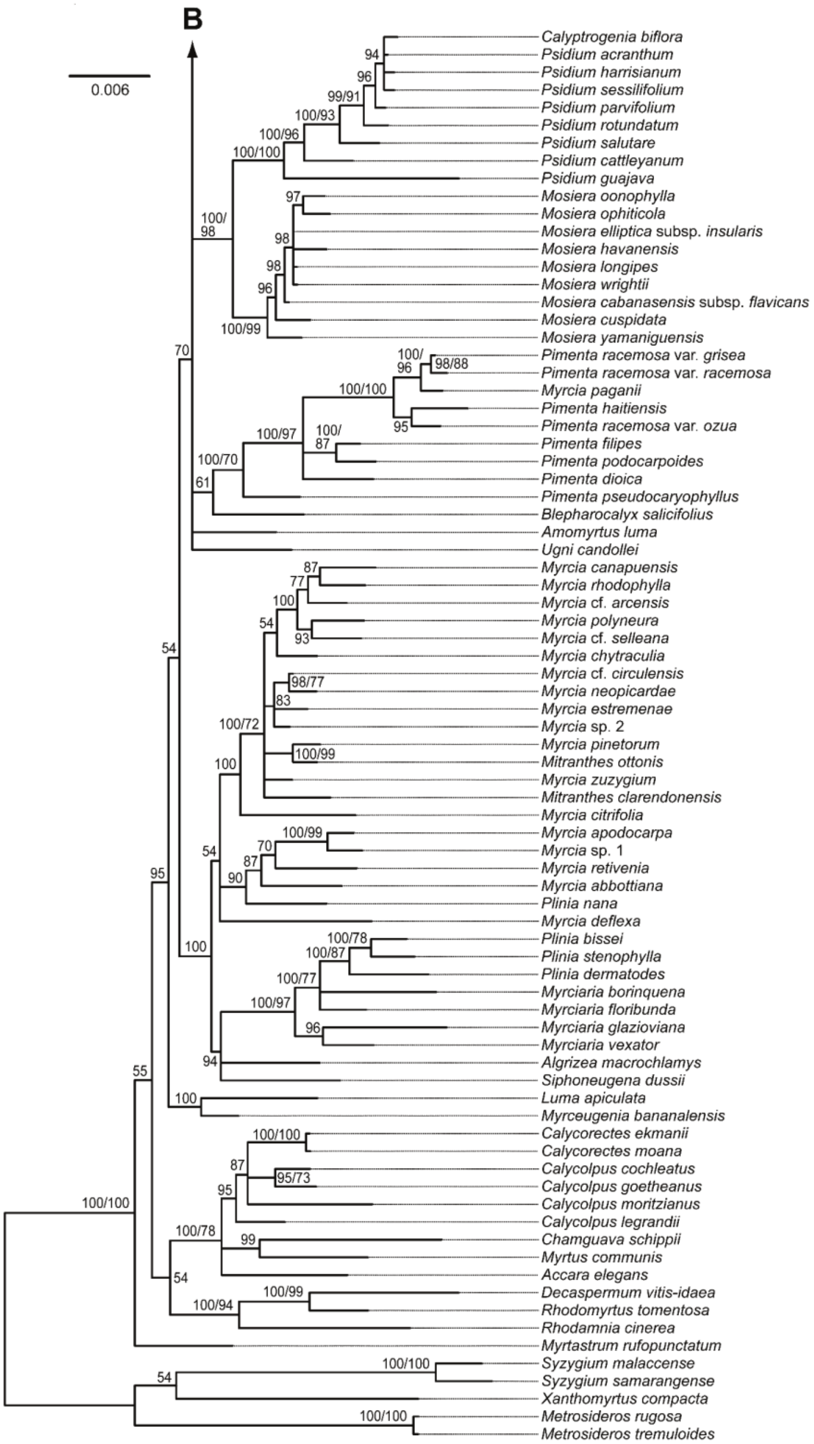

Figure 2.8A. Majority-rule consensus tree resulting from Bayesian analysis of the combined ITS, *psbA-trnH*, *ndhF-rpl32* and *trnL-trnF* sequence data with masking of ambiguously aligned sites. Part A shows the root portion of the tree; part B, subtribe Eugeniinae. Posterior probabilities are indicated as percentages above branches. (continued on next page)

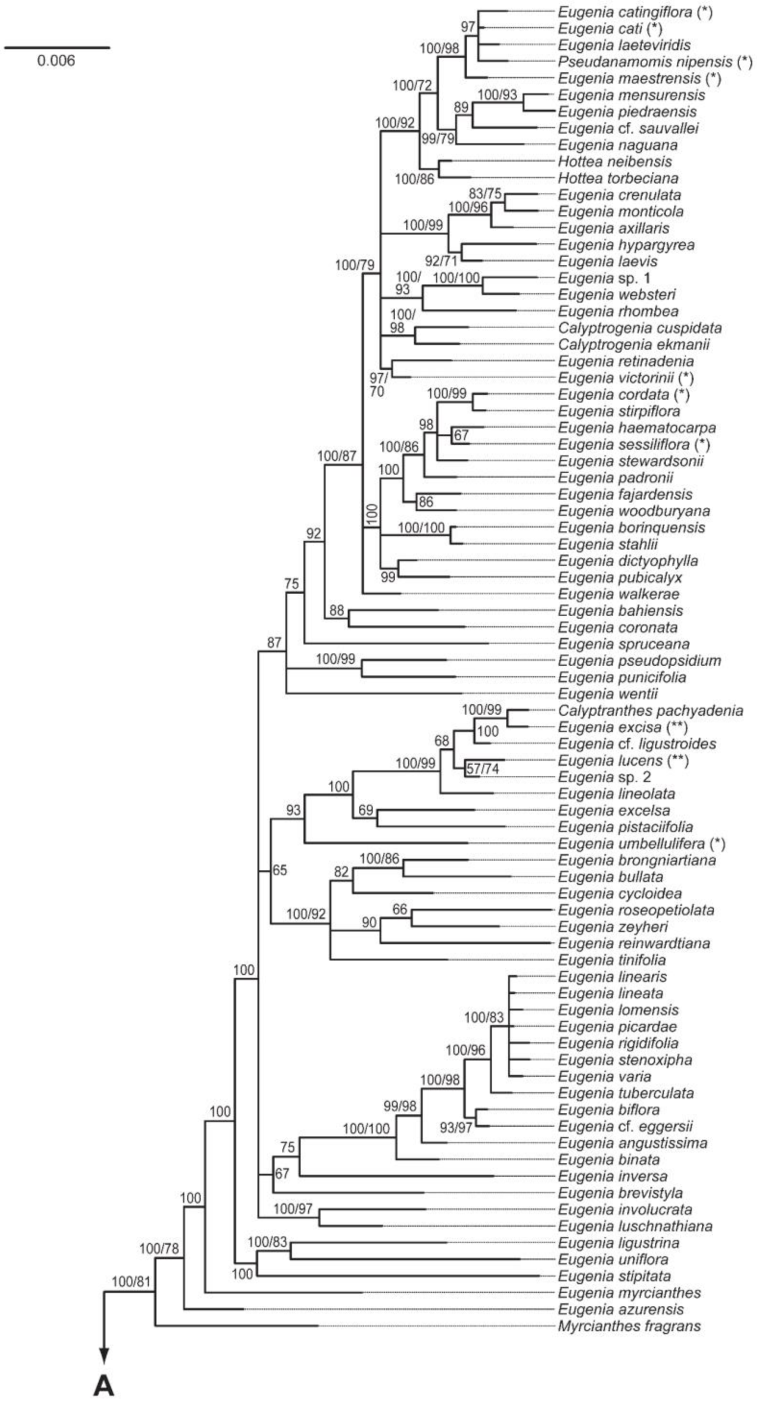

Figure 2.8B. (continued from previous page) Bootstrap support percentages ≥70 from the equivalent parsimony analysis are indicated following a slash. Species of *Eugenia* corresponding to *Pseudanamomis* sensu Bisse (1985) are indicated by a single asterisk, while those of *Calycolpus* sensu Bisse (1983) are indicated by a double asterisk. Scale units are expected number of substitutions per site.

Appendix

Appendix 2.1. Voucher specimens and GenBank accession numbers for DNA sequences. Duplicates of Flickinger collections may be found at the following herbaria: HAC, HAJB, IJ, JBSD, SJ, UCWI and UPR. Newly generated sequences are indicated with an asterisk (*). A dash (–) indicates missing sequences. Botanic gardens: FTBG = Fairchild Tropical Botanic Garden; JBN = Jardín Botánico Nacional "Dr. Rafael Ma. Moscoso;" RBGK = Royal Botanic Gardens, Kew.

Taxon name; country/cultivated, major political subdivision (when known)/botanic garden and accession number (if applicable), collection date (if applicable), collector(s) and number (herbarium code); ITS, *psbA-trnH, ndhF-rpl32, trnL-trnF*.

Accara elegans (DC.) Landrum; Brazil, Minas Gerais, *Vasconcelos 485* (K); MF954013.1, MF954271.1, –, –. ***Algrizea macrochlamys*** (DC.) Proença & NicLugh.; Brazil, Bahia, *Giulietti & Harley 1648* (K); AM234126.1, AM489809.1, –, JN091320.1. ***Amomyrtus luma*** (Molina) D.Legrand & Kausel; cultivated, Royal Botanic Garden Edinburgh, *IIECH & RBGE 100* (E); AM234073.1, AM489811.1, –, MF954135.1. ***Blepharocalyx salicifolius*** (Kunth) O.Berg; Brazil, Minas Gerais, *Vasconcelos 482* (K); MF954018.1, MF954275.1, –, MF954139.1. ***Calycolpus cochleatus*** McVaugh; Guyana, Cuyuni-Mazaruni, *K.J. Wurdack & al. 5903* (ASU); MN295266*, MN295083*, –, MN443057*. ***Calycolpus goetheanus*** (DC.) O.Berg; Brazil, Amazonas, *Vasconcelos 332* (K); MF954019.1, MF954276.1, –, MF954140.1. ***Calycolpus legrandii*** Mattos; Brazil, Bahia, *M. Ibrahin & al. 28* (ASU); MN295267*, MN295084*, –, –. ***Calycolpus moritzianus*** (O.Berg) Burret; Colombia, Santander, *Parra-O. 480* (COL); KU945986.1, KU945999.1, –, –. ***Calycorectes ekmanii*** Urb.; Cuba, Holguín, *J. Flickinger & al. 46* (FTG); MN295264*, MN295081*, MN475988*, MN443056*. ***Calycorectes moana*** Borhidi & O.Muñiz; Cuba, Holguín, *J. Flickinger & al. 61* (FTG); MN295265*, MN295082*, MN475989*, –. ***Calyptranthes pachyadenia*** Urb. & Ekman; Cuba, Sancti

Spíritus, 26.08.2018, *R. Verdecia s.n. 2018-001* (FTG); MN295257*, MN295074*, MN475981*, –. ***Calyptrogenia biflora*** Alain; Dominican Republic, Santo Domingo, *J. Flickinger & al. 2015-DR-9* (FTG); MN295249*, MN295066*, MN475973*, MN443052*. ***Calyptrogenia cuspidata*** Alain; Dominican Republic, Barahona, *J. Flickinger & al. 2015-DR-7* (FTG); MN295250*, MN295067*, MN475974*, MN443053*. ***Calyptrogenia ekmanii*** (Urb.) Burret; Haiti, Sud, *J.D. Skean Jr. & al. 5061* (FLAS); MN295251*, MN295068*, MN475975*, MN443054*. ***Chamguava schippii*** (Standl.) Landrum; Costa Rica, , *Santamaria-Aguilar 9833* (K); MF954027.1, MF954285.1, –, MF954149.1. ***Decaspermum vitis-idaea*** Stapf; Malaysia, Sabah, *Vasconcelos 729* (K); MF954030.1, MF954288.1, –, MF954152.1. ***Eugenia angustissima*** O.Berg; Brazil, Goiás, *Vasconcelos 405* (K); MF954032.1, MF954290.1, –, MF954154.1. ***Eugenia axillaris*** (Sw.) Willd.; cultivated, FTBG acc. #2001-0233B, *J. Flickinger 2015-FTG-9* (FTG); MN295268*, MN295085*, MN475990*, –. ***Eugenia azurensis*** O.Berg; Brazil, Bahia, *Faria 4186* (K); MF954033.1, MF954291.1, –, MF954155.1. ***Eugenia bahiensis*** DC.; Brazil, Espírito Santo, *Faria 4229* (K, UB); MH446018.1, MH446076.1, –, –. ***Eugenia biflora*** (L.) DC.; Puerto Rico, Vieques, *J. Flickinger & al. 114* (FTG); MN295269*, MN295086*, MN475991*, MN443058*. ***Eugenia binata*** Mazine & Sobral; Brazil, São Paulo, *Colleta 1208* (ESA); MH446016.1, MH446074.1, –, –. ***Eugenia borinquensis*** Britton; Puerto Rico, Cayey, *J. Flickinger & E. Santiago 124* (FTG); MN295270*, MN295087*, MN475992*, –. ***Eugenia brevistyla*** D.Legrand; Brazil, Paraná, *Mazine 993* (ESA, K, SORO); KJ187614.1, KJ469663.1, –, MF954157.1. ***Eugenia brongniartiana*** Guillaumin; New Caledonia, , *Pillon 176* (K, NOU); KJ187615.1, KJ469664.1, –, –. ***Eugenia bullata*** Guillaumin; New Caledonia, , *Vasconcelos 608* (K); MF954034.1, MF954292.1, –, MF954158.1. ***Eugenia cati*** Britton & P.Wilson; Cuba, Santiago de Cuba, 17.10.2015, *J.L. Gómez & al. s.n. 001* (FTG); MN295272*, MN295089*, MN475994*, –. ***Eugenia catingiflora*** Griseb.; Cuba, Pinar del Río, 10.06.2016, *R. Oviedo & R. Chaves s.n. 2016-004* (FTG); MN295271*, MN295088*, MN475993*, MN443059*. ***Eugenia cordata*** var. ***cordata***; U.S. Virgin Islands, St. John, 26.05.2017, *E. Gibney s.n. 01* (FTG); MN295273*, MN295090*, MN475995*, –. ***Eugenia coronata*** Schumach. & Thonn.; cultivated, FTBG acc. #X.1-369B, *J. Flickinger 109* (FTG); MN295274*, MN295091*, MN475996*, MN443060*. ***Eugenia crenulata*** (Sw.) Willd.; Dominican Republic, Barahona, *J. Flickinger & al. 2015-DR-6* (FTG); MN295275*, MN295092*, MN475997*, MN443061*. ***Eugenia cycloidea*** Urb.; Cuba, Holguín, *J. Flickinger & al. 57* (FTG); MN295276*, MN295093*, MN475998*, MN443062*. ***Eugenia dictyophylla*** Urb.; cultivated, JBN, *J. Flickinger & al. 2015-DR-28* (FTG); MN295277*, MN295094*, MN475999*, MN443063*. ***Eugenia* cf. *eggersii*** Kiaersk.; Puerto Rico, Adjuntas, *J. Flickinger & al. 77* (FTG); MN295278*, MN295095*, MN476000*, –. ***Eugenia excelsa*** O.Berg; Brazil, Paraná, *Lucas 125* (ESA, K); KJ187621.1, KJ469670.1, –, –. ***Eugenia excisa*** Urb.; Cuba, Holguín, *J. Flickinger & al. 52* (FTG); MN295279*, MN295096*, MN476001*, –. ***Eugenia fajardensis*** (Krug & Urb.) Urb.; cultivated, Arboreto Parque Doña Inés, *J. Flickinger & al. 110* (FTG); MN295280*, MN295097*, MN476002*, –. ***Eugenia haematocarpa*** Alain; Puerto Rico, Cayey, *E. Santiago 2018-1* (FTG); MN295281*, MN295098*, MN476003*, –. ***Eugenia hypargyrea*** Standl.; Mexico, Veracruz, *P. Carilla-Reyes & D. Cabrera-Toledo 5231* (XAL); MN295282*, MN295099*, MN476004*, –. ***Eugenia inversa*** Sobral; Brazil, Espírito Santo, *Faria 4230* (K, UB); MH446021.1, MH446079.1, –, –. ***Eugenia***

involucrata DC.; Brazil, Distrito Federal, *Vasconcelos 256* (K); MF954035.1, MF954293.1, –, MF954159.1. ***Eugenia laeteviridis*** Urb.; Cuba, Santiago de Cuba, 22.02.2018, *R. Oviedo & al. s.n. 2018-03* (FTG); MN295283*, MN295100*, MN476005*, –. ***Eugenia laevis*** O.Berg; Haiti, Sud, *J. Flickinger & al. 100* (FTG); MN295284*, MN295101*, MN476006*, –. ***Eugenia ligustrina*** (Sw.) Willd.; cultivated, JBN, *J. Flickinger & al. 2015-DR-29* (FTG); MN295286*, MN295103*, MN476008*, MN443064*. ***Eugenia* cf. *ligustroides*** Urb.; Cuba, Holguín, 21.03.2018, *J.L. Gómez & al. s.n. 2018-003* (FTG); MN295285*, MN295102*, MN476008*, –. ***Eugenia linearis*** O.Berg; Dominican Republic, Pedernales, *J. Flickinger & al. 2015-DR-8* (FTG); MN295288*, MN295105*, MN476010*, MN443066*. ***Eugenia lineata*** (Sw.) DC.; Haiti, Nippes, *J. Flickinger & al. 102* (FTG); MN295289*, MN295106*, MN476011*, –. ***Eugenia lineolata*** Urb. & Ekman; Dominican Republic, Santo Domingo, *J. Flickinger & al. 2015-DR-18* (FTG); MN295287*, MN295104*, MN476009*, MN443065*. ***Eugenia lomensis*** Britton & P.Wilson; Cuba, Granma, *J. Flickinger & al. 21* (FTG); MN295290*, MN295107*, MN476012*, –. ***Eugenia lucens*** Alain; Cuba, Holguín, *J. Flickinger & al. 55* (FTG); MN295291*, MN295108*, MN476013*, –. ***Eugenia luschnathiana*** (O.Berg) B.D.Jacks.; cultivated, FTBG acc. #X.3-48B, *J.R. Abbot 24204* (FTG); MN295292*, MN295109*, MN476014*, MN443067*. ***Eugenia maestrensis*** Urb.; Cuba, Granma, *J. Flickinger & al. 20* (FTG); MN295293*, MN295110*, MN476015*, –. ***Eugenia mensurensis*** Urb.; Cuba, Holguín, *J. Flickinger & al. 30* (FTG); MN295294*, MN295111*, MN476016*, MN443068*. ***Eugenia monticola*** (Sw.) DC.; cultivated, JBN, *J. Flickinger & al. 2015-DR-27* (FTG); MN295295*, MN295112*, MN476017*, MN443069*. ***Eugenia myrcianthes*** Nied.; Brazil, *Mazine 1091* (ESA, K); KJ187652.1, KJ469702.1, –, –. ***Eugenia naguana*** Urb.; Cuba, Granma, *J. Flickinger & al. 26* (FTG); MN295296*, MN295113*, MN476018*, –. ***Eugenia padronii*** Alain; Puerto Rico, Sabana Grande, *J. Flickinger & E. Santiago 70* (FTG); MN295297*, MN295114*, MN476019*, –. ***Eugenia picardae*** Krug & Urb.; Dominican Republic, Barahona, *J. Flickinger & al. 2015-DR-2* (FTG); MN295298*, MN295115*, MN476020*, MN443070*. ***Eugenia piedraensis*** Urb.; Cuba, Holguín, *J. Flickinger & al. 48* (FTG); MN295299*, MN295116*, MN476021*, –. ***Eugenia pistaciifolia*** DC.; Brazil, Bahia, *Faria 1782* (UB); MH446001.1, MH446058.1, –, –. ***Eugenia pseudopsidium*** Jacq.; Puerto Rico, Salinas, *E. Santiago 2017-7* (FTG); MN295300*, MN295117*, MN476022*, MN443071*. ***Eugenia pubicalyx*** Alain; Dominican Republic, Santo Domingo, *J. Flickinger & al. 2015-DR-11* (FTG); MN295301*, MN295118*, MN476023*, MN443072*. ***Eugenia punicifolia*** (Kunth) DC.; Brazil, Mato Grosso, *Mazine 1065* (ESA, K, SORO); KJ187638.1, KJ469686.1, –, MF954162.1. ***Eugenia reinwardtiana*** (Blume) DC.; cultivated, Marie Selby Botanical Gardens, *Holst 8870* (K, SEL); MH446015.1, MH446073.1, –, –. ***Eugenia retinadenia*** C.Wright; Cuba, Pinar del Río, 10.06.2016, R. Oviedo & R. Chaves s.n. 2016-003 (FTG); MN295302*, MN295119*, MN476024*, –. ***Eugenia rhombea*** (O.Berg) Krug & Urb.; Cuba, Guantánamo, 16.09.2016, *R. Oviedo & al. s.n.* (HAC); MN295303*, MN295120*, MN476025*, MN443073*. ***Eugenia rigidifolia*** A.Rich.; Cuba, Pinar del Río, 23.06.2017, *R. Oviedo s.n. 2017-004* (FTG); MN295304*, MN295121*, MN476026*, –. ***Eugenia roseopetiolata*** N.Snow & Cable; cultivated, RBGK, *Vasconcelos s.n.* (K); MF954040.1, MF954298.1, –, MF954164.1. ***Eugenia* cf. *sauvallei*** Krug. & Urb.; Cuba, Cuidad de la Habana, 26.08.2017, *R. Oviedo & A. Hernandez s.n. 2017-007* (FTG);

MN295305*, MN295122*, MN476027*, –. ***Eugenia sessiliflora*** Vahl; Puerto Rico, Lajas, *J. Flickinger & al. 120* (FTG); MN295306*, MN295123*, MN476028*, –. ***Eugenia* sp. 1**; Jamaica, Trelawny, *J. Flickinger & al. 2016-J-16* (FTG); MN295307*, MN295124*, MN476029*, –. ***Eugenia* sp. 2**; Cuba, Guantánamo, 08.06.2018, *Z. Acosta & J.L. Gómez s.n. 2018-001* (FTG); MN295308*, MN295125*, MN476030*, –. ***Eugenia spruceana*** O.Berg; French Guiana, *Holst 9465* (SEL); MH445994.1, MH446051.1, –, –. ***Eugenia stahlii*** (Kiaersk.) Krug & Urb.; Puerto Rico, Maricao/San German, *J. Flickinger & E. Santiago 67* (FTG); MN295309*, MN295126*, MN476031*, MN443074*. ***Eugenia stenoxipha*** Urb.; Cuba, Guantánamo, 18.05.2017, *R. Oviedo & al. s.n. 2017-001* (FTG); MN295310*, MN295127*, MN476032*, –. ***Eugenia stewardsonii*** Britton; Puerto Rico, Adjuntas, *J. Flickinger & al. 76* (FTG); MN295311*, MN295128*, MN476033*, –. ***Eugenia stipitata*** McVaugh; cultivated, FTBG acc. #991790A, *J. Flickinger 90* (FTG); MN295312*, MN295129*, MN476034*, MN443075*. ***Eugenia stirpiflora*** (O.Berg) Krug & Urb.; U.S. Virgin Islands, St. John, 10.05.2017, *E. Gibney s.n.* (U.S. National Park Service VIIS-1658); MN295313*, MN295130*, MN476035*, MN443076*. ***Eugenia tinifolia*** Lam.; Mauritius, *Page 25* (MAU); MH445984.1, MH446041.1, –, –. ***Eugenia tuberculata*** (Kunth) DC.; Cuba, Cuidad de la Habana, 26.08.2017, *R. Oviedo & A. Hernandez s.n. 2017-006* (FTG); MN295314*, MN295131*, MN476036*, –. ***Eugenia umbellulifera*** (Kunth) Krug & Urb.; cultivated, FTBG acc. #68390A, *J. Flickinger 2015-FTG-4* (FTG); MN295315*, MN295132*, MN476037*, MN443077*. ***Eugenia uniflora*** L.; U.S.A., Florida, *J. Flickinger 2015-FL-1* (FTG); MN295316*, MN295133*, MN476038*, MN443078*. ***Eugenia varia*** Britton & P.Wilson; Cuba, Pinar del Río, 10.06.2016, *R. Oviedo & R. Chaves* s.n. 2016-006

(FTG); MN295317*, MN295134*, MN476039*, –. ***Eugenia victorinii*** Alain; Cuba, Isla de Juventud, 21.06.2016, *R. Oviedo & al. s.n. 2016-009* (FTG); MN295318*, MN295135*, MN476040*, MN443079*. ***Eugenia walkerae*** Flickinger; Anguilla, *M. Walker 95-016* (A); MN295319*, MN295136*, MN476041*, MN443080*. ***Eugenia websteri*** Proctor; Jamaica, Trelawny, *J. Flickinger & al. 2016-J-8* (FTG); MN295320*, MN295137*, MN476042*, –. ***Eugenia wentii*** Amshoff; French Guiana, , *Holst 9421* (CAY, SEL); KJ187651.1, KJ469701.1, –, –. ***Eugenia woodburyana*** Alain; Puerto Rico, Cabo Rojo, *J. Flickinger & al. 126* (FTG); MN295321*, MN295138*, MN476043*, MN443081*. ***Eugenia zeyheri*** (Harv.) Harv.; South Africa, *Maurin 1800* (JRAU); MH445980.1, MH446037.1, –, –. ***Hottea neibensis*** Alain; Dominican Republic, Elias Piña, *J. Flickinger & al. 2015-DR-1* (FTG); MN295322*, MN295139*, MN476044*, MN443082*. ***Hottea torbeciana*** Urb. & Ekman; Haiti, Sud, *G.M. Ionta & al. 2047* (FLAS); MN295323*, MN295140*, MN476045*, –. ***Luma apiculata*** (DC.) Burret; cultivated, RBGK, *Lucas 208* (K); AM234101.1, AM489843.1, –, KP722331.1. ***Metrosideros rugosa*** A.Gray; U.S.A., Hawaii, *S. Grose 24* (HAW); MN295324*, MN295141*, MN476046*, MN443083*. ***Metrosideros tremuloides*** (A.Heller) Rock; U.S.A., Hawaii, *L.S. Reynolds 175* (HAW); MN295325*, MN295142*, MN476047*, –. ***Mitranthes clarendonensis*** (Proctor) Proctor; Jamaica, Trelawny, *J. Flickinger & al. 2016-J-7* (FTG); MN295326*, MN295143*, MN476048*, MN443084*. ***Mitranthes ottonis*** O.Berg; Cuba, Pinar del Río, 23.06.2017, *R. Oviedo & al. s.n. 2017-003* (FTG); MN295327*, MN295144*, MN476049*, MN443085*. ***Mosiera cabanasensis* subsp. *flavicans*** (Urb. & Ekman) Borhidi; Cuba, Holguín, *J. Flickinger & al. 33* (FTG); MN295330*, MN295147*, MN476052*, –. ***Mosiera cuspidata*** Salywon; Dominican

Republic, Hato Mayor, *R. Rodríguez & al. 1464* (FTG); MN295328*, MN295145*, MN476050*, –. ***Mosiera elliptica* subsp. *insularis*** Urquiola; Cuba, Isla de Juventud, 23.06.2016, *R. Oviedo & R. Chaves s.n. 2016-013* (FTG); MN295329*, MN295146*, MN476051*, –. ***Mosiera havanensis*** (Urb.) Bisse; Cuba, Ciudad de la Habana, 16.06.2018, *R. Oviedo & J.C. Alvares s.n. 2018-02* (FTG); MN295331*, MN295148*, MN476053*, –. ***Mosiera longipes*** (O.Berg) Small; Dominican Republic, Puerto Plata, *J. Flickinger & al. 2015-DR-23* (FTG); MN295332*, MN295149*, MN476054*, MN443086*. ***Mosiera oonophylla*** (Urb.) Bisse; Cuba, Guantánamo, 17.09.2016, *R. Oviedo & al. s.n.* (HAC); MN295333*, MN295150*, MN476055*, –. ***Mosiera ophiticola*** (Britton & P.Wilson) Bisse; Cuba, Holguín, *J. Flickinger & al. 56* (FTG); MN295334*, MN295151*, MN476056*, –. ***Mosiera wrightii*** Borhidi; Cuba, Holguín, *J. Flickinger & al. 42* (FTG); MN295335*, MN295152*, MN476057*, –. ***Mosiera yamaniguensis*** Urquiola & Z.Acosta; Cuba, Holguín, *J. Flickinger & al. 63* (FTG); MN295336*, MN295153*, MN476058*, MN443087*. ***Myrceugenia bananalensis*** Bezerra & Landrum; Brazil, Distrito Federal, *Faria 4049* (K); MF954052.1, MF954389.1, –, MF954173.1. ***Myrcia abbottiana*** (Urb.) Alain; Dominican Republic, *Lucas 1108* (K); KU898328.1, KU898436.1, –, KU898491.1. ***Myrcia apodocarpa*** Urb.; Cuba, Guantánamo, 08.06.2018, *Z. Acosta & J.L. Gómez s.n. 2018-002* (FTG); MN295338*, MN295155*, MN476060*, –. ***Myrcia* cf. *arcensis*** Z.Acosta & K.Samra; Cuba, Granma, *J. Flickinger & al. 24* (FTG); MN295254*, MN295071*, MN475978*, –. ***Myrcia canapuensis*** (Urb.) Z.Acosta & K.Samra; Cuba, Holguín, 21.03.2018, *J.L. Gómez & al. s.n. 2018-002* (FTG); MN295252*, MN295069*, MN475976*, –. ***Myrcia chytraculia*** (L.) A.R.Lourenço & E.Lucas; Jamaica, Saint Ann, *J. Flickinger & al. 2016-J-5* (FTG);

MN295253*, MN295070*, MN475977*, –. ***Myrcia* cf. *circulensis*** Z.Acosta & K.Samra; Cuba, Granma, *J. Flickinger & al. 22* (FTG); MN295256*, MN295073*, MN475980*, –. ***Myrcia citrifolia*** (Aubl.) Urb.; Dominican Republic, Monseñor Nouel, *J. Flickinger & al. 2015-DR-26* (FTG); MN295339*, MN295156*, MN476061*, MN443089*. ***Myrcia deflexa*** (Poir.) DC.; Puerto Rico, Maricao, *J. Flickinger & E. Santiago 71* (FTG); MN295340*, MN295157*, MN476062*, MN443090*. ***Myrcia estremenae*** (Alain) E.Lucas & Acev.-Rodr.; Puerto Rico, Hatillo, *J. Flickinger & al. 88* (FTG); MN295255*, MN295072*, MN475979*, –. ***Myrcia neopicardae*** K.Campbell & Peguero; Dominican Republic, Santo Domingo, *J. Flickinger & al. 2015-DR-10* (FTG); MN295258*, MN295075*, MN475982*, –. ***Myrcia paganii*** Krug & Urb.; Puerto Rico, Quebradillas, *J. Flickinger & al. 85* (FTG); MN295341*, MN295158*, MN476063*, MN443091*. ***Myrcia pinetorum*** (Britton & P.Wilson) Z.Acosta & K.Samra; Cuba, Isla de Juventud, 22.06.2016, *R. Oviedo & al. s.n. 2016-011* (FTG); MN295259*, MN295076*, MN475983*, –. ***Myrcia polyneura*** (Urb.) Borhidi; Cuba, Holguín, 21.03.2018, *J.L. Gómez & al. s.n. 2018-004* (FTG); MN295342*, MN295159*, MN476064*, –. ***Myrcia retivenia*** (C.Wright) Urb.; Cuba, Holguín, 13.06.2018, *Z. Acosta & J.L. Gómez s.n. 2018-004* (FTG); MN295343*, MN295160*, MN476065*, MN443092*. ***Myrcia rhodophylla*** (Ekman & Urb.) Z.Acosta & K.Samra; Cuba, Granma, *J. Flickinger & al. 28* (FTG); MN295260*, MN295077*, MN475984*, –. ***Myrcia* cf. *selleana*** (Urb. & Ekman) K.Campbell & Peguero; Dominican Republic, Barahona, *J. Flickinger & al. 2015-DR-5* (FTG); MN295261*, MN295078*, MN475985*, MN443055*. ***Myrcia* sp. 1**; Cuba, Holguín, 13.06.2018, *Z. Acosta & J.L. Gómez s.n. 2018-005* (FTG); MN295344*, MN295161*, MN476066*, –. ***Myrcia* sp. 2**; Cuba, Holguín, 21.03.2018, *J.L. Gómez &*

al. s.n. 2018-001 (FTG); MN295262*, MN295079*, MN475986*, –. ***Myrcia zuzygium*** (L.) A.R.Lourenço & E.Lucas; Dominican Republic, Santo Domingo, *J. Flickinger & al. 2015-DR-15* (FTG); MN295263*, MN295080*, MN475987*, –. ***Myrcianthes fragrans*** (Sw.) McVaugh; cultivated, FTBG acc. #97607A, *J. Flickinger 2015-FTG-2* (FTG); MN295337*, MN295154*, MN476059*, MN443088*. ***Myrciaria borinquena*** Alain; Puerto Rico, Yauco, *J. Flickinger & E. Santiago 79* (FTG); MN295345*, MN295162*, MN476067*, MN443093*. ***Myrciaria floribunda*** (Willd.) O.Berg; Puerto Rico, Quebradillas, *J. Flickinger & al. 87* (FTG); MN295346*, MN295163*, MN476068*, MN443094*. ***Myrciaria glazioviana*** (Kiaersk.) G.M.Barroso ex Sobral; Brazil, Bahia, *Vasconcelos 413* (K); MF954061.1, MF954397.1, –, MF954177.1. ***Myrciaria vexator*** McVaugh; cultivated, FTBG acc. #X.5-36B, *J. Flickinger 2015-FTG-5* (FTG); MN295347*, MN295164*, MN476069*, MN443095*. ***Myrtastrum rufopunctatum*** (Pancher ex Brongn. & Gris) Burret; New Caledonia, *Soewarto HB 10* (K); MF954065.1, MF954401.1, –, MF954181.1. ***Myrtus communis*** L.; cultivated, RBGK, *Lucas 211* (K); AM234149.1, AM489872.1, –, KP722327.1. ***Pimenta dioica*** (L.) Merr.; cultivated, FTBG acc. #2006-0855A, *J. Flickinger 2016-FTG-3* (FTG); MN295348*, MN295165*, MN476070*, MN443096*. ***Pimenta filipes*** (Urb.) Burret; Cuba, Las Tunas, *J. Flickinger & al. 15* (FTG); MN295349*, MN295166*, MN476071*, –. ***Pimenta haitiensis*** (Urb.) Landrum; cultivated, FTBG acc. #2013-968, *J. Flickinger 107* (FTG); MN295351*, MN295168*, MN476073*, –. ***Pimenta podocarpoides*** (Areces) Landrum; Cuba, Holguín, 15.06.2018, *Z. Acosta & J.L. Gómez s.n. 2018-007* (FTG); MN295353*, MN295170*, MN476075*, MN443097*. ***Pimenta pseudocaryophyllus*** (Gomes) Landrum; Brazil, , *Lucas 161* (K); AM234083.1, AM489876.1, –, MF954185.1. ***Pimenta***

racemosa* var. *grisea (Kiaersk.) Fosberg; Puerto Rico, Maricao, *J. Flickinger & E. Santiago 72* (FTG); MN295350*, MN295167*, MN476072*, –. ***Pimenta racemosa* var. *ozua*** (Urb. & Ekman) Landrum; cultivated, JBN, *J. Flickinger & al. 2015-DR-30* (FTG); MN295352*, MN295169*, MN476074*, –. ***Pimenta racemosa* var. *racemosa***; cultivated, FTBG acc. #2002-0450A, *J. Flickinger 89* (FTG); MN295354*, MN295171*, MN476076*, –. ***Plinia bissei*** Z.Acosta & Urquiola; Cuba, Holguín, 09.06.2018, *Z. Acosta & J.L. Gómez s.n. 2018-003* (FTG); MN295355*, MN295172*, MN476077*, –. ***Plinia dermatodes*** Urb.; Cuba, Pinar del Río, 08.08.2018, *Z. Acosta & A. Gallardo-Cruz s.n. 2018-008* (FTG); MN295356*, MN295173*, MN476078*, –. ***Plinia nana*** Sobral; Brazil, Minas Gerais, *Mazine 662* (ESA); KU898288.1, MF954404.1, –, MF954187.1. ***Plinia stenophylla*** Urb.; Cuba, Holguín, 14.06.2018, *Z. Acosta & J.L. Gómez s.n. 2018-006* (FTG); MN295357*, MN295174*, MN476079*, –. ***Pseudanamomis nipensis*** Bisse; Cuba, Holguín/Santiago de Cuba, 21.03.2018, *J.L. Gómez & al. s.n. 2018-005* (FTG); MN295366*, MN295183*, MN476088*, –. ***Psidium acranthum*** Urb.; cultivated, JBN, *J. Flickinger & al. 2015-DR-31* (FTG); MN295358*, MN295175*, MN476080*, MN443098*. ***Psidium cattleyanum*** Afzel. ex Sabine; cultivated, The Kampong, National Tropical Botanical Garden acc. #2005-2-158-001, *J. Flickinger 2015-FL-02* (FTG); MN295359*, MN295176*, MN476081*, MN443099*. ***Psidium guajava*** L.; cultivated, FTBG acc. #982201A, *J. Flickinger 2015-FTG-8* (FTG); MN295360*, MN295177*, MN476082*, MN443100*. ***Psidium harrisianum*** Urb.; Jamaica, Trelawny, *J. Flickinger & al. 2016-J-9* (FTG); MN295361*, MN295178*, MN476083*, –. ***Psidium parvifolium*** Griseb.; Cuba, Holguín, *J. Flickinger & al. 47* (FTG); MN295362*, MN295179*, MN476084*, –. ***Psidium rotundatum*** Griseb.; Cuba, Pinar del Río, 10.06.2016, *R.*

Oviedo & R. Chaves s.n. 2016-001 (FTG); MN295363*, MN295180*, MN476085*, –. ***Psidium salutare*** (Kunth) O.Berg; Cuba, Pinar del Río, 24.06.2017, *R. Oviedo & al. s.n. 2017-005* (FTG); MN295364*, MN295181*, MN476086*, –. ***Psidium sessilifolium*** Alain; Dominican Republic, Puerto Plata, *J. Flickinger & al. 2015-DR-21* (FTG); MN295365*, MN295182*, MN476087*, –. ***Rhodamnia cinerea*** Jack; Singapore, *Vasconcelos 672* (K); MF954074.1, MF954410.1, –, MF954192.1. ***Rhodomyrtus tomentosa*** (Aiton) Hassk.; U.S.A., Florida, *J. Flickinger 2016-FL-2* (FTG); MN295367*, MN295184*, MN476089*, MN443101*. ***Siphoneugena dussii*** (Krug & Urb.) Proença; Puerto Rico, Maricao/San German, *J. Flickinger & E. Santiago 68* (FTG); MN295368*, MN295185*, MN476090*, MN443102*. ***Syzygium malaccense*** (L.) Merr. & L.M.Perry; cultivated, FTBG acc. #2013-0459 A, *J. Flickinger 2015-FTG-1* (FTG); MN295369*, MN295186*, MN476091*, MN443103*. ***Syzygium samarangense*** (Blume) Merr. & L.M.Perry; cultivated, FTBG acc. #63139, *J. Flickinger 108* (FTG); MN295370*, MN295187*, MN476092*, MN443104*. ***Ugni candollei*** (Barnéoud) O.Berg; cultivated, RBGK, *Vasconcelos s.n.* (K); MF954076.1, MF954412.1, –, MF954195.1. ***Xanthomyrtus compacta*** (Ridl.) Diels; Indonesia, Irian Jaya, *Edwards 4213A* (K); AM234148.1, AM489887.1, –, MF954196.1.

CHAPTER III

A TAXONOMIC REVISION OF THE LATHBERRY CLADE OF *EUGENIA* (MYRTACEAE)

Abstract

The Lathberry Clade includes seven species of *Eugenia* sect. *Umbellatae* (Myrtaceae) distributed from Puerto Rico through the Lesser Antilles. Members of the Lathberry Clade are trees and shrubs distinguished from other Antillean species by a combination of dull twigs, glabrous leaves with the midvein typically raised, glomerate or fasciculate inflorescences predominantly borne below the leaves on old wood, the inflorescence bracts closely spaced and ascending, and spheroidal fruits turning red or purple at maturity, the calyx lobes erect or torn away. A large deletion in the *psbA-trnH* intergenic spacer region is unique to members of the clade. Morphology, leaf venation, and seed coat anatomy of the Lathberry Clade are examined, and a phylogeny constructed using non-coding nuclear genetic regions is presented. The taxonomic treatment includes a key to the species, distribution maps, and extinction risk assessments. *Eugenia sintenisii* from Puerto Rico and *E. cordata* var. *caribaea* (nom. et stat. nov.) from the Lesser Antilles are recognized in place of *E. cordata* var. *sintenisii*, while *Eugenia earhartii* is synonymized with *E. stirpiflora*. Six lectotypes are designated.

Keywords: Antilles, endemic species, single copy nuclear gene, seed coat

Introduction

Eugenia L. (Myrtaceae) is a genus of trees and shrubs of the fleshy-fruited tribe Myrteae DC. found in tropical and subtropical regions around the world (Wilson 2011). It ranks as one of the largest genera of seed plants with over 1100 species (Frodin 2004), approximately 900 of which are restricted to the Neotropics (Govaerts et al. 2020). Within Myrteae, *Eugenia* is generally distinguished by its 4-merous perianth, racemose or uniflorous inflorescence, bilocular ovary with multiple ovules attached near the center of the septum on a pad-like placenta, and embryo producing massive, fused cotyledons (Landrum and Kawasaki 1997); however, exceptions to all of these features occur within the genus as presently circumscribed according to the results of phylogenetic studies (van der Merwe et al. 2005, Mazine et al. 2014, Wilson and Heslewood 2016, Vasconcelos et al. 2017, Mazine et al. 2018, Giaretta et al. 2019, Flickinger et al. 2020).

The most recent, phylogenetic classification of *Eugenia* recognizes 11 sections in three subgenera (Mazine et al. 2018). Most of the Neotropical species of *Eugenia* belong to *E*. sect. *Umbellatae* O.Berg (Mazine et al. 2016) within *E.* subg. *Eugenia*. The section is characterized by uniflorous or racemose inflorescences with a contracted rachis and flowers lacking the foliaceous calyx lobes of *Eugenia* sect. *Phyllocalyx* Nied. or *E.* sect. *Speciosae* (Mazine et al. 2016). A phylogenetic study of *Eugenia* emphasizing *E.* sect. *Umbellatae* identified seven geographically correlated clades, including a clade of species from the Caribbean region designated Clade C (Mazine et al. 2018). Clade C was further divided into two subclades, CI and CII, following a phylogenetic study of Myrtaceae species from across the Greater Antilles (Flickinger et al. 2020). The concept of the Lathberry Clade, named after *Eugenia cordata* var. *cordata*, or lathberry (Britton and Wilson 1925), was proposed for the lineage within Clade CII containing all of the species of *Eugenia* sect. *Umbellatae* from Puerto Rico and the Virgin Islands that primarily flower below the leaves on old wood (Flickinger et al. 2020). Members of the lineage were also noted to uniquely possess a large deletion in the *psbA-trnH* intergenic spacer region (Flickinger et al. 2020, Supplementary File 3.1). As recognized here, the Lathberry Clade includes seven species and eight distinct taxa.

Further study of the Lathberry Clade is needed to understand patterns of character variation and relationships within the group. In general, the distribution of morphological and anatomical features within *Eugenia* is poorly understood. The Lathberry Clade presents an opportunity to study morphological diversity within a well-defined monophyletic group, but additional precise observations are needed to evaluate the taxonomic relevance of various attributes. Identification of characters that unite the members of the group and distinguish it from other similar species of *Eugenia* sect. *Umbellatae* is especially desirable from a taxonomic viewpoint. Resolution of relationships within the Lathberry Clade, which are mostly uncertain at present (Flickinger et al. 2020), is also desirable to help refine existing taxonomic concepts and to provide a phylogenetic context for understanding all aspects of the evolution of the group. Moreover, members of the Lathberry Clade would benefit from current assessments of their conservation statuses using information on their distribution and other biological properties provided by a taxonomic revision, as all species are endemic to the Caribbean Island Biodiversity Hotspot (Smith et al. 2004). The objectives of the present study are therefore to (1) provide detailed morphological descriptions for each taxon within a comparative framework; (2) determine which features distinguish the Lathberry Clade from other Antillean species; (3) present a phylogenetic hypothesis for the group using nuclear genetic data; (4) update the taxonomy and nomenclature, including designation of lectotypes; and (5) compile information on the occurrence of each species to assess extinction risks.

Materials and Methods

***Specimens*—**Herbarium specimens from the following institutions were examined for this study: A, FTG, GH, MAPR, NY, SJ, UPR, UPRRP, and US. Digital images of specimens were also requested from the following European herbaria: AMD, C, G-DC, K, L, P, U, and WAG. Additional images of type material were accessed through the Global Plants (Global Plants Initiative 2020) and Virtual Herbarium Berolinense (Curators Herbarium B 2020) online databases. Fourteen collections were made by us through field expeditions on Puerto Rico and Vieques between 2017 and 2019, with an additional four collections made for this study on Saint John in 2017.

***Species Concept*—**Species recognition follows the phylogenetic species concept of Nixon and Wheeler (1990), according to which species are the smallest groups of one or more populations that are distinguished from other such groups by some combination of fixed, diagnostic character states. The existence of such fixed differences provides evidence of cessation of gene exchange between phylogenetic species. Variation within and between localized populations was assessed from herbarium specimens, which allowed for the greatest sampling of individuals. Given the constraints of herbarium taxonomy, the attributes considered as potential diagnostic characters were restricted to those morphological features readily observed from preserved specimens (Snow 1997). The emphasis on fixed phenotypic differences links species to the unique roles they play within an ecosystem (Freudenstein et al. 2017). Though it is difficult in practice to infer character state fixation with a high degree of certainty (Wiens and Servedio 2000), character states were treated as fixed or variable within a hypothesized species on the basis of the available evidence from direct observations and reports. Recognition of infraspecific taxa was reserved for cases in which distinctive phenotypes could not be assumed to be fixed within the constituent populations (Nixon and Wheeler 1990).

Morphology and Anatomy—Flowers and mature fruits with seeds were sampled from representative specimens and rehydrated for dissection. Flower parts, including bracteoles, were measured under a stereoscope fitted with a reticle. All other measurements are of dried material unless otherwise noted. The same flower parts expanded to varying degrees when rehydrated but were never larger than a few tenths of a millimeter compared to dry material. A range of values for the dimension of a flower part preceded by “ca.” indicates that the maximum value was measured on dried material. Thin slices of rehydrated embryos were placed in a few drops of iodine-potassium iodide (IKI) solution to test for the presence of starch. Anther glands were counted under a compound light microscope after bleaching five stamens per dissected flower for approximately 5 min (Landrum and Bonilla 1996). Dried leaves of two species were cleared, bleached, and stained with acid fuchsin following the procedure of Vasco et al. (2014). Leaves were then transferred through an alcohol dehydration series to xylene and mounted between glass slides in Permount (Thermo Fisher Scientific, Waltham, Massachusetts) before imaging with a flatbed scanner. Air-dried seed coats sectioned through the hilum were prepared for scanning electron microscopy (SEM) by mounting on aluminum stubs and sputter-coating with gold. Samples were examined with a JSM 5900LV microscope (JEOL, Tokyo, Japan) at the Florida Center for Analytical Electron Microscopy at Florida International University.

***Survey of Antillean* Eugenia**—A survey of *Eugenia* species from across the Greater and Lesser Antilles was conducted to identify additional distinguishing features for the Lathberry Clade. Note that every species of *Eugenia* native to the Bahamas also occurs in the Antilles (Govaerts et al. 2020). Although one would ideally consider all relatives of a group, critical examination, let alone DNA sequencing, of every possible member of *Eugenia* sect. *Umbellatae* would be impracticable. The strategy adopted here for further characterization of the Lathberry Clade was to narrow the pool of potential close relatives by geographic origin and then by inflorescence position and type. Inflorescence characters were chosen first of all because of their significance for recognizing the Lathberry Clade, but they are also frequently described and easily observed, thus providing a convenient means of identifying similar species. Considering the geographic structure evident in the phylogeny of *Eugenia* sect. *Umbellatae* (Mazine et al. 2018) and Clade C (Flickinger et al. 2020), as well as the recovery of clades of Antillean species in phylogenetic studies of other groups (e.g., Michelangeli et al. 2008, Irimia et al. 2015), the Lathberry Clade was characterized with respect to all other ramiflorous or cauliflorous species from the Greater and Lesser Antilles that possess glomerate or fasciculate inflorescences.

The World Checklist of Myrtaceae (Govaerts et al. 2020) was used to build checklists of native species of *Eugenia* for each island or island group in the Greater and Lesser Antilles, and the list of species was screened using standard floras for the region (Alain 1953, Proctor 1972, Liogier 1989, McVaugh 1989). For Cuba, the list of species was first narrowed using the tabulation of species of *Eugenia* by inflorescence type and position of Hilaire (2000). Protologues were consulted for species not included in the floras, and additional observations were made on specimens from FTG, GH, HAC, HAJB, IJ, UCWI, and US as well as images of types available through the Global Plants Initiative (2020).

The following criteria were followed to evaluate inflorescence type and position. Glomerate and fasciculate inflorescence types were distinguished from extended racemes by possessing an inflorescence axis of no more than 5 mm in length. The lengths of short shoots observed in the Lathberry Clade were always less than this cut-off value, which McVaugh (1989) used as an upper limit for the length of short but evident racemes in Lesser Antillean species of *Eugenia*. A species was considered to be ramiflorous or cauliflorous only if it does not regularly bear inflorescences in the axils of foliage or scale leaves on young, leafy portions of stems. Thus, some exceptions were allowed to account for both the inflorescences frequently produced at old, leafless nodes in many species of Antillean *Eugenia* that otherwise bear inflorescences on young, leafy portions of the stem and the occasional inflorescence borne in the axils of foliage leaves or at the base of young twigs in the Lathberry Clade.

***Phylogeny*—**Field collections of each species of the Lathberry Clade were made to obtain genetic material for phylogenetic analysis (see above). The DNA sequence data were also obtained from an herbarium specimen of *Eugenia cordata* from Saint Kitts in the Lesser Antilles (Appendix 3.1). The ingroup was represented by a total of 12 samples. Each of the seven ingroup species, with the exceptions of *Eugenia sintenisii* Kiaersk. and *E. stewardsonii* Britton, was sampled from two different sites. One sample each of four species drawn from the other three lineages of Clade CII were used for the outgroup: *Eugenia pubicalyx* Alain from Hispaniola and *Eugenia borinquensis* Britton, *Eugenia stahlii* (Kiaersk.) Krug & Urb., and *Eugenia woodburyana* Alain from Puerto Rico. Thus, the outgroup included three of the four Puerto Rican endemics of *Eugenia* sect. *Umbellatae* outside of the Lathberry Clade. Two nrDNA regions, ITS and ETS (5′ external transcribed spacer between the transcription initiation site and the18S rRNA gene), were selected for sequencing; these regions were chosen on the basis of their widespread use in plant phylogenetics at low taxonomic levels as a result of their rapid evolution (Calonje et al. 2009, Poczai and Hyvönen 2010). Ten low-copy nuclear regions were also screened using the primers developed for Myrtaceae by Pillon et al. (2014) in an effort to identify conserved single-copy regions with sufficient variation for phylogenetic analysis, as such markers provide independent estimates of the phylogeny while reducing problems associated with paralogy (Duarte et al. 2010). Selection criteria were successful amplification of a single band, sequence variability for ingroup taxa, avoidance of simple sequence repeats (SSR's), and no evidence of more than two alleles per sample. A single intron of the *MeNu79* locus was selected according to these criteria. In addition, the two chloroplast intergenic spacer regions utilized by Flickinger et al. (2020), *psbA-trnH* and *ndhF-rpl32*, were sequenced for each species. Herbarium vouchers and GenBank accession numbers for DNA sequences are listed in Appendix 3.1.

Genomic DNA was extracted from approximately 0.05 g of dried leaf material using a DNeasy Plant Mini Kit (Qiagen, Hilden, Germany). For *Eugenia borinquensis* and *E. stahlii*, DNA was extracted using a high-salt CTAB buffer (protocol D of Souza et al. 2012) with *N*-lauroylsarcosine (Russell et al. 2010). PCR amplification was performed using a SimpliAmp Thermal Cycler (Thermo Fisher Scientific) in 25 μL reaction volumes with the following components: RED Master Mix Kit (Genesee Scientific, San

Diego, California) containing 0.2 mM each dNTP, 0.1 units/μL Taq DNA polymerase, and 1.5 mM $MgCl_2$; 1× TBT-Par reagent (Samarakoon et al. 2013); 0.6 μM forward and reverse primers; and 1 μL DNA extract. PCR primers and conditions (Table 3.1) followed those of Lucas et al. (2007) for ITS, ETS, and *psbA-trnH* and Pillon et al. (2014) for *MeNu79*. After amplification, PCR products were purified with ExoSap-IT (Affymetrix, Cleveland, Ohio) and cycle sequenced using a Big Dye Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, California). All sequences were analyzed at the Florida International University DNA Core Facility on an Applied Biosystems 3100 Genetic Analyzer. Geneious v. 11.1.5 (Biomatters, Auckland, New Zealand) was used to assemble and clean the resulting chromatograms. Double peaks or other ambiguities in the chromatograms were indicated using IUPAC ambiguity codes (Cornish-Bowden 1985). If more than one ambiguity was found, sequences of selected low-copy nuclear regions were cloned to confirm their single copy nature, explore relationships between alleles, and obtain allelic-level data for coalescent-based species tree analysis. The PCR products were purified from a low-melt agarose gel and cloned with a TOPO TA Cloning kit (Thermo Fisher Scientific). At least 10 bacterial colonies per cloned product were selected for PCR amplification using the original primers and Protocol 6.3 of McPherson and Møller (2000): 5 min at 94° C, 30 cycles of 30 s at 94° C, 30 s at 55° C, 1 min at 72° C, and a final extension of 1 min at 72° C. Amplification products were then sequenced as described above. Haplotypes were determined from alignments of cloned sequences, which were assumed to correspond to alleles if only two were present. Alleles were arbitrarily designated either “A” or “B” in heterozygous individuals.

Sequence alignments for all regions were constructed using MUSCLE (Edgar 2004) with a maximum of eight iterations. Gaps were manually inserted to avoid spurious mismatches towards the ends of alignment, and a short section of nine nucleotides in the *ndhF-rpl32* region for which the alignment was ambiguous was excluded from subsequent analyses. A short inversion located between two inverted repeats in the *psbA-trnH* region was also reverse-complemented such that the configuration of the sequence was the same for all samples (Whitlock et al. 2010). The NEXUS formatted DNA sequence alignments are provided in Supplementary File 3.1. Two informative gaps in the chloroplast regions were coded as binary characters for parsimony analysis according to the simple gap coding method of Simmons and Ochoterena (2000). The inversion was not coded because its orientation varied within species. Alignments of ITS, ETS, *MeNu79*, and the combined chloroplast regions were analyzed separately by parsimony and maximum likelihood methods. The nuclear regions were then combined by concatenation and analyzed by parsimony and maximum likelihood using consensus sequences for *MeNu79* in heterozygous individuals. The combined nuclear data were also analyzed by a coalescent-based method of species tree inference using allelic sequences for *MeNu79*. The cpDNA regions were not analyzed together with the nuclear regions because of insufficient sequence variation within the ingroup.

Parsimony analyses were conducted in PAUP* v. 4.0a (Swofford 2003). Characters were equally weighted; gaps were treated as missing data; and character state changes were unordered and equally weighted. Most parsimonious trees were found by branch-and-bound searches saving all most parsimonious trees. Statistical support for branches was assessed using 1000 bootstrap replicates (Felsenstein 1985). Each bootstrap replicate consisted of either a branch-and-bound search without saving all most parsimonious trees or, in the case of the cpDNA and *MeNu79* alignments, five random taxon addition replicates followed by TBR branch swapping holding 10 trees at each step and saving no more than 10 trees from each replicate. All trees were rooted on the branch leading to the ingroup when possible because of uncertainty over the closest outgroup.

For maximum likelihood analyses, PartitionFinder2 (Guindon et al. 2010, Lanfear et al. 2017) was used to select an appropriate model of DNA sequence evolution from the general time reversible model space. Models were selected using the corrected Akaike information criterion (Hurvich and Tsai 1989). Because coding portions of sequenced regions contained little if any variation, each amplified region was treated as a single data block. All possible partitioning schemes for the concatenated analysis were evaluated with branch lengths linked across partitions. Maximum likelihood phylogenetic inference was conducted in IQ-TREE v. 1.6.12 (Nguyen et al. 2015, Chernomor et al. 2016). Each analysis consisted of 1000 standard bootstrap replicates (Felsenstein 1985) followed by 10 maximum likelihood estimation runs with the option to collapse near-zero length branches invoked. As for the parsimony analyses, all trees were rooted on the branch leading to the ingroup when possible.

Bayesian species tree analysis was conducted by *BEAST in BEAST v. 2.6.2 (Bouckaert et al. 2019). The *BEAST method co-estimates gene trees and species trees from multi-locus data (Heled and Drummond 2010). Each nuclear region was treated as a separate unlinked partition with modeling of ambiguities. Models of sequence evolution were set using those selected by the Bayesian information criterion (Schwarz 1978) in PartitionFinder2 to approximate Bayesian model comparison procedures. A separate uncorrelated relaxed clock model with a lognormal distribution of rates (Drummond et al. 2006) was employed for each partition. The substitution rates for all partitions and the mean clock rate for *MeNu79* were fixed to 1, with the clock rates for the other partitions estimated relative to that of *MeNu79*. A Yule model (Yule 1925, Harding 1971) was used for the species tree prior, and a constant population size was assumed, given the limited amount of data for estimation of this parameter. Each *BEAST analysis was run for 50000000 generations, sampling trees and other parameters every 5000 generations. Full details on other options are included in the BEAST XML file (Supplementary File 3.2). After removal of the first 10% of samples as burn-in, convergence and mixing behavior of the Markov Chain Monte Carlo runs were assessed from the trace plots of parameters in Tracer (Rambaut et al. 2018). An effective sample size of at least 200 was required for each estimated parameter. Species tree analyses were run three times to ensure convergence onto the same posterior distribution. The log files from each run were then combined with the LogCombiner program of BEAST for a single estimate of the species tree, using the same 10% burn-in for each file and down-sampling to every 15000 generations.

Extinction Risk**—**Conservation statuses were assessed as far as possible according to IUCN Red List categories and criteria (IUCN 2012) from herbarium specimen data. Extent of occupancy (EOO) and area of occupancy (AOO) were calculated for each taxon with GeoCAT (Bachman et al. 2011) using 2 × 2 km^2 grid squares. Herbarium specimens were first georeferenced, ignoring vague localities when a more precise one in the specified area was available. All non-duplicate points were used for calculations. The IUCN Red List category for which these values qualify a taxon are given in parentheses. Note that additional conditions must be met for a species to be listed in a threatened category under criterion B. The number of points within protected areas was determined using spatial data from the Puerto Rico Protected Areas Database (PACAT 2018) for occurrences in Puerto Rico and the World Database on Protected Areas (UNEP-WCMC and IUCN 2020) for occurrences elsewhere.

Results

***Taxonomic History*—**The first species of the Lathberry Clade to be described was *Eugenia cordata* (Sw.) DC. by Olof Swartz, a Swedish botanist who collected in the Caribbean (Jamaica, Hispaniola, and Cuba) during 1784–1786 and wrote its first flora (Stearn 1980). Swartz described this species under *Myrtus* L. (Swartz 1788). Later, he cited material collected by Julius Philipp Benjamin von Rohr (Swartz 1797–1806), a Danish resident of Saint Croix from 1757–1791 who travelled widely in the Caribbean beginning in 1786 (Urban 1902). Around this same time period, Hans West, a Danish rector of a school in Christianssted, Saint Croix, from 1788–1800, collected the type of *Eugenia sessiliflora* Vahl. West primarily collected on Saint Croix but also on Saint Thomas, Vieques, Puerto Rico, and Martinique (Urban 1902). He sent his collections to Copenhagen, where many new taxa were described by Martin Vahl, a Norwegian-born botanist and pupil of Linnaeus (West 1793, Stafleu and Cowan 1986). Another contemporary, the French botanist Louis Claude Marie Richard, collected the type of *Eugenia stirpiflora* (O.Berg) Krug & Urb. while visiting various islands in the Antilles during 1786–1787, but financial difficulties prevented him from publishing his discovery (Urban 1902). Instead, this species was described decades later under *Myrciaria* O.Berg

(Berg 1861) by Otto Carl Berg, a German professor of pharmaceutical botany who completed a revision of Neotropical Myrtaceae (Stafleu and Cowan 1976).

In the 19th century, the type of the Lesser Antillean taxon described as *Eugenia sessiliflora* DC. was collected by Italian botanist Carlo Giuseppe Bertero, who traveled in the Caribbean during 1816–1821. Bertero’s collections from the Caribbean were distributed from Turin, Italy by his teacher Giovanni Batista Balbis to, among others, the Swiss botanist Augustin Pyramus de Candolle at Geneva, following determination by Curt Sprengel at Halle in Germany (Delprete et al. 2002). Two additional taxa were first collected by German apothecary and plant collector Paul Ernst Emil Sintenis, who visited Puerto Rico during 1884–1887 at the direction of Ignatius Urban (Urban 1902). Urban was a German botanist whose influential work on the Caribbean Islands included a flora of Puerto Rico (Stafleu and Cowan 1986, Liogier 1996). Sintenis collected specimens of *Eugenia sintenisii* and *E. stewardsonii*, which were described by Hjalmar Kiaerskou, a Danish botanist and educator who studied Neotropical Myrtaceae (Urban 1902). Because Kiaerskou (1889–1890) considered *Eugenia stewardsonii* to be a variety of *E. cordata*, the type of *E. stewardsonii* was collected and described by American botanist Nathaniel Lord Britton. Britton collected throughout the Caribbean Islands in the early 20th century and co-authored a flora of Puerto Rico and the Virgin Islands (Gleason 1960). He participated in 16 expeditions to Puerto Rico with his wife and other collaborators from 1906–1933 (Sastre-D.J. and Santiago-Valentín 1996).

The final two Puerto Rican species were first described in the 20th century by the French-born botanist Henri Eugene Liogier y Allut, also known as Hermano Alain. Liogier began his botanical studies after moving to Cuba as a member of the La Salle

Brothers, a Roman Catholic congregation dedicated to education. He is the author of recent floras of Cuba (with Herman León), Hispaniola, and Puerto Rico (González García 2018). *Eugenia haematocarpa* Alain, was collected by Leslie R. Holdridge, an American forester and ecologist who collected in Puerto Rico, Saint John, and Haiti in the 1930's and 1940's (Lanjou and Stafleu 1957, Liogier 1996). *Eugenia padronii* Alain, although originally collected by Liogier as early as 1963, was first found in flower and fruit by Rubén Padrón, the keeper of Maricao Commonwealth Forest (Puerto Rico) after whom the species is named (Liogier 1986).

Eugenia cordata and *E. sessiliflora* Vahl, as Caribbean species sharing laterally borne, glomerate inflorescences, were first treated together in *Myrtus* by Sprengel (1824–1828) and then in *Eugenia* by de Candolle (1828). The species were also placed together in the revision of Neotropical species by Berg (1855–1856) and the floristic treatments of Eggers (1876, 1879). Urban (1894–1895), in his treatment of Caribbean taxa, placed the two species in successive groups. The first group consisted of *Eugenia cordata*, in which he included *E. stewardsonii*, *E. sintenisii*, and *E. sessiliflora* DC. He combined the latter two taxa into *Eugenia cordata* var. *sintenisii* (Kiaersk.) Krug & Urb. The second group, considered artificial by Urban, included *Eugenia sessiliflora* Vahl and two species of *E.* sect. *Catingopsis* Griseb., a taxon for three Cuban species with large flowers in glomerate inflorescences described by Grisebach (1866). Urban (1894–1895) also recognized the affinity of *Myrciaria stirpiflora* O.Berg to both *Eugenia cordata* and *E. sessiliflora* Vahl and transferred the species to *Eugenia*. Britton and Wilson (1925) provided a key to the species of *Eugenia* in Puerto Rico and the Virgin Islands in which members of the Lathberry Clade were grouped together by their tendency to flower on old wood. These authors placed *Eugenia stirpiflora* in the synonymy of *E. cordata* while recognizing *E. sintenisii*, inclusive of *E. sessiliflora* DC., and *E. stewardsonii* as separate species. A similar course was followed by Little et al. (1974) and Liogier (1994), the latter recognizing *Eugenia sintenisii* as a variety of *E. cordata*. Liogier (1994) also added *Eugenia padronii*, which he considered to be closely related to *E. sessiliflora* Vahl (Liogier 1986), to the group of Puerto Rican species flowering on old wood.

Eugenia cordata has also been placed in Buxaceae (Willdenow 1805, Sprengel 1824–1828, Baillon 1859) and *Pseudanamomis* Kausel (Bisse 1985), an originally monotypic genus of Myrtaceae (Kausel 1956) nested within *Eugenia* (Vasconcelos et al. 2017, Flickinger et al. 2020). *Pseudanamomis* sensu Bisse consists of 13, mostly Cuban species held together by, among other features, contracted inflorescences often borne at leafless nodes. Bisse's expanded concept of *Pseudanamomis* was rejected by Grifo (1992) and shown to be polyphyletic by Flickinger et al. (2020).

Morphology and Anatomy—All members of the Lathberry Clade are small trees or shrubs 5–10 (–15) m in height. In *Eugenia cordata*, *E. haematocarpa*, and *E. sessiliflora*, plants are frequently multi-stemmed. Extension growth occurs in distinct flushes, and branch outgrowth is proleptic. A few pairs of opposite, decussate scale leaves separated by elongated internodes are found at the proximal end of each growth unit. Both monopodial and sympodial growth occur. Frequently, the terminal bud aborts after a few nodes and is replaced by a pair of axillary branches. Trichomes are simple and translucent, appearing either white or pale yellow- to red-brown. On the floral disks, the hairs are usually darker brown. A grayish, flaky bark develops with age.

Twigs. A useful distinction may be made between three developmental stages: (1) new growth, (2) the young, most recently matured twigs, and (3) older twigs. On herbarium specimens, new growth typically dries a darker color, and glands are visible on the twigs and both leaf surfaces. The glands are no longer apparent on the fully expanded young twigs, which dry yellow-brown in most species. Older twigs of *Eugenia haematocarpa* are reddish-brown, while those of *E. sintenisii* and *E. stewardsonii* have patches of various shades of brown. In other species, all but the most recent growth units are gray, but young twigs of *Eugenia padronii* first pass through a characteristic stage in which they are smooth and pallid before turning gray.

The axillary buds are inconspicuous and generally not apparent until they begin to grow. They are protected by a few pairs of scale leaves that vary from short and rounded through triangular to ovate forms. The outermost pair of scales are flap-like and frequently take on the appearance of the surrounding surface of the twig. In some species, up to three superposed buds are evident, flattened against the twig in profile. They are covered by a single pair of scales that bulges distally. Flower buds are similar in appearance to vegetative buds in early stages of growth. In *Eugenia cordata*, inflorescences were found both above and below axillary branches.

Leaves. Leaves are evergreen and coriaceous, varying in thickness. At least a few leaves usually persist at the distal nodes of the penultimate growth increment. Leaves of a species may vary from clearly petiolate to subsessile or be sessile when there is no separation between the blade tissue and the point of attachment of the leaf to the stem at the swollen leaf base. The petiole, when present, is not sharply delineated from the blade, as the margin of the blade is decurrent into the petiole; however, the petiole typically dries a darker color. In the Lathberry Clade, the petiole is at most shallowly concave and never deeply channeled. The shape of the blade within species is variable with respect to the relative position of the widest portion near (elliptical), below (ovate), or above (obovate) the middle, and, in *Eugenia sessiliflora*, the blade may be approximately as long as wide and orbicular. A distinction is made between the apex, or distal quarter of the blade (Ellis et al. 2009) and the tip at the very end of the blade (Snow et al. 2003). The apex varies from rounded to pointed at an acute or obtuse angle to, in *Eugenia haematcoarpa*, acuminate. The tip is always blunt, i.e., rounded, in the Lathberry Clade. The leaf base, like the apex, is also variable. In particular, species whose leaves are usually cordate at the base may be almost or completely rounded. The leaf margin is always at least a little recurved, strongly so in *Eugenia sessiliflora* and *E. stirpiflora*. It is paler and somewhat thickened in most species. An adaxially raised midvein is typical of the Lathberry Clade. This feature refers to the relief of the vein above the surrounding surface of the blade; it is separate from modifications to the vein itself (McVaugh 1956), such as the basal groove that is observed in some members. The abaxial surface of the mature leaf is finely punctate and lighter in color than the adaxial surface, on which the glands are scarcely visible. The leaves dry darker on the adaxial surface, eventually blackening in most species.

Figure 3.1 shows the venation in cleared leaves of *Eugenia sintenisii* (Fig. 3.1A) and *E. stewardsonii* (Fig. 3.1B). These species were highlighted because of the significance of venation characters for distinguishing between them, but the pattern of venation they exhibit is representative of the Lathberry Clade as a whole. The framework of the secondary, or costal, veins is brochidodromous, with a continuous intramarginal vein that arches between the secondaries. The intercostal tertiary veins are reticulate. They form an admedially ramified composite vein that may itself be branched, usually toward the subjacent secondary vein. A series of loops around the intramarginal vein are formed by exterior tertiary veins. The quarternary veins are also reticulate, and at least one additional order of venation is clearly discernable. The degree to which the venation is visible on the adaxial leaf surface varies. The venation of *Eugenia haematocarpa*, *E. sessiliflora* and *E. stewardsonii* is conspicuously reticulate, while only the midvein may be apparent in *E. padronii*.

Inflorescences. Precise descriptions of the inflorescences are made difficult by their contracted nature. The axis of the inflorescence and its bracts are often completely hidden by the flowers or are embedded in woody tissue. Depending on whether the pedicels are elongated or not, the inflorescences are described as glomerate or fasciculate. Within the Lathberry Clade, fascicles with elongated pedicels are mainly associated with the two cauliflorous species, *Eugenia haematocarpa* and *E. stirpiflora*. The inflorescences of other species are predominantly ramiflorous. Most taxa also occasionally flower in the axils of foliage or scale leaves. Such axillary inflorescences are usually found on the penultimate growth unit, but they may also be found at the base of the young twigs. Axillary inflorescences are particularly common in *Eugenia cordata* var. *cordata*, in which they are sometimes observed on more distal positions of the young twigs as well. In *Eugenia cordata*, the two cauliflorous species, and rarely in *E. sessiliflora*, the axis of the inflorescence is evident as a short shoot bearing multiple pairs of bracts, each subtending a solitary flower. The bracts of these shoots cover the axis.

They are typically similar in form to the bracteoles (see below), which are more conspicuous, or else reduced like the bud scales.

Pedicels were observed in all species but *Eugenia sintenisii*, for which there were few fertile collections available for study. In species characterized by sessile to subsessile flowers, these took the form of a dilated, puberulous internode less than 1 mm long that developed between the bract and the bracteoles. These pedicels were more readily observed in fruiting material. Exceptionally, a single specimen of *Eugenia cordata* var. *cordata* (*Britton & Shafer 636* (US)) exhibited a slender pedicel 1.5 mm long.

A pair of well-developed bracteoles occurs immediately below the flower and persists into the fruiting stage. In *Eugenia cordata*, the bracteoles become indurated and remain on the bare, persistent inflorescences. The margins of the bracteoles extend around the base of the flower but are almost always free from one another. In *Eugenia sintenisii* and *E. stewardsonii*, the margins overlap at the widest point in the flowering stage. The bracteoles of these two species also tend to be emarginate. The bracteoles of all species are held close to the sides of the hypanthium. Their length in proportion to that of the hypanthium is variable, but generally they cover up to 1/3 of the side of the hypanthium in the relatively large flowers of *Eugenia sessiliflora* and *E. stirpiflora*, up to 1/2 of the side of the hypanthium in flowers of *E. padronii* and *E. haematocarpa*, and up to the whole side of the hypanthium in the relatively small flowers of *E. cordata*, *E. sintenisii*, and *E. stewardsonii*. The adaxial side of the bracteoles in *Eugenia cordata* and *E. sessiliflora* is thickened toward the base and partially fused with the distal end of the rudimentary pedicel. In *Eugenia sessiliflora*, the central portion of the bracteole may become dark and hardened on the abaxial surface. Colleters were observed in the axils of the bracteoles in *Eugenia cordata*, *E. haematocarpa*, and *E. sessiliflora*. These are broad, flattened structures ca. 0.1 mm long, arranged in a single row, either rounded or pointed at the end, opaque, and white to dark brown in color. No obvious evidence of secretion by the colleters was visible on the dried material examined.

Flowers. The biseriate perianth consists of four calyx lobes and four petals. The lobes of the calyx occur in two unequal pairs, the outer always shorter than the inner. Their abaxial surface resembles that of the hypanthium except that it is never densely hairy. The adaxial surface of both the calyx lobes and the petals is smooth. The calyx lobes of *Eugenia haematocarpa* are unusual in that both surfaces are white like the petals. At anthesis, the lobes of all species are reflexed, creating a crease that sets them off from the hypanthium. During fruit development, the lobes frequently tear away from the rim of the hypanthium, leaving a scar. The exception to this is *Eugenia padronii*, in which the calyx lobes are erect and persistent on the fruits. The petals differ from the calyx lobes in being thinner, fugacious, and narrowed toward the base. Although not completely equal in size, they are not obviously paired like the calyx lobes. The corolla is pure white or tinged pink.

Stamens are borne on a thickened disk immediately inside of the perianth. The outer border of the floral disk may be circular or squarish, while the inner border is circular. The disk itself is minutely and often densely puberulous. The indumentum then obscures the round, pitted scars left when the stamens detach. The stamens are arranged in multiple series and are more numerous in larger flowers. In bud, the filaments are folded into a compact mass with the anthers on the surface. The anthers are dorsixified and bear two lateral thecae that dehisce by longitudinal slits. The connective bears a single, large, obovoidal gland at its apex. Below this is a variable number of smaller, spherical glands. A range of 0–14 glands was encountered, with particularly large variation observed within *Eugenia cordata*. Bleaching the anthers for gland observation also revealed epidermal cells with undulate anticlinal walls and pollen grains with a triangular amb.

The gynoecium consists of an inferior ovary included in hypanthial tissue and a slender, elongate style tapered to a small stigmatic surface. The surface bounded by the floral disk with the style at its center is referred to as the apex of the ovary. The style folds over the mass of stamens in bud, resulting in a bend that is visible after anthesis. The ovary is bilocular with axile placentation. In most species, the locule walls and septum are smooth, but their surface exhibits yellow pustular glands in *Eugenia padronii*. The ovules are ventral hypotropous and attached to a small area near the center of the septum. They form a compact mass that fills the locule. The number of ovules per locule varied from 8–49 across all species.

Fruits. Fruits are spheroidal, ranging from globose to somewhat prolate or oblate. Multi-seeded fruits were observed in *Eugenia stewardsonii*. These fruits are easily recognized by the constriction between the two locules when seeds develop in both, but the number of seeds within each locule is not obvious externally. In *Eugenia stewardsonii*, one locule of a constricted fruit was found to have two seeds that were flattened on one side such that they fit together to fill the available space. The fruits of *Eugenia padronii* were described as two-seeded (Liogier 1986), and loose seeds flattened on one side were observed on the holotype. Other examined fruits of this species were single-seeded. When ripe, fruits are red or sometimes purple. The pericarp is fleshy but rather thin. It consists of three layers: an outer skin (exocarp), an inner layer surrounding the seed (endocarp), and a layer of succulent tissue in between (mesocarp). The endocarp varies from a translucent membrane to an opaque, brown, papery layer. In all species, conspicuous strands of whitish vascular tissue run longitudinally through the pericarp. The dark brown, undeveloped ovules are easily seen in mature fruits, flattened against the wall of the locule around the placenta.

Seeds. Seeds are ellipsoidal to reniform but may be almost globose or, in multi-seeded fruits, flattened on one side. The main external feature is the hilum. For most species, this is a small, elliptical area with the long axis oriented perpendicular to that of the seed. In *Eugenia haematocarpa* and *E. sessiliflora*, the hilum is more irregular in outline and expanded around 1/4 to 1/2 the circumference of the seed. In the similarly sized seeds of *Eugenia stirpiflora*, the hilum is elliptical and up to 1/4 the circumference of the seed. The external surface of the seed coat is either smoothish in *Eugenia sintenisii* and *E. stewardsonii* or dull and irregular but not rough. In *Eugenia sessiliflora*, the outer surface is more or less rugose. The color of the seed coat when dry is yellow-brown in most species but darker gray-brown in *Eugenia stewardsonii*. The interior surface is smooth and darker than the exterior with pale flecks or streaks. A narrow stripe beginning near the hilum runs longitudinally around the dorsal side, sometimes at an oblique angle. The stripe is impressed and rounded at the end near the hilum but may be emarginate in *Eugenia sessiliflora*. In *Eugenia padronii*, *E. sintenisii*, and *E. stewardsonii*, the stripe is indistinct, visible mainly as a translucent area in the seed coat when held to the light. In the other species, various patterns of pale markings render the stripe clearly visible. In all species, it is a relatively thin place in the seed coat that loses definition as it runs around the dorsal side.

In cross-section, the seed coat appears to have four layers. The outermost layer is an even, compact shell that is tough yet flexible, providing the seed coat with mechanical strength. Beneath this is a loosely organized layer of periclinally oriented, brown fibers. This layer contains a third, thin, white layer best seen near the hilum. The fourth layer is a thin and dark, translucent membrane that lines the inner surface of the seed coat. The seed coat is thickest at the hilum, where the brown fibrous layer is most developed and a pad of tissue clings to the outside surface. The outermost layer is absent in this area. The whitish layer extends into the seed through the hilum and around the sides. It is gradually lost as the fibrous layer and, with it, the seed coat become thinner. The thinnest portion of the seed coat is opposite the hilum, where the stripe is found. In this region, only the outermost and innermost layers may be evident in cross-section.

Seed coat structure was also investigated by SEM. Figure 3.2A–E shows sections through the seed coats of four species. Seed coat structure was found to be similar for the four investigated species, varying principally in the thickness of the layers. The outermost, or palisade, layer is one cell thick, consisting of radially elongated cells with thick and pitted anticlinal walls (Fig. 3.2A). This layer is absent over the hilum, where a mound of tissue derived from the funiculus or placenta may be present (Fig. 3.2B). Beneath the palisade layer are many periclinally oriented cells with relatively thick, pitted walls. Cells of this layer were sectioned in various planes. Toward the inside of the seed coat, cells with helically thickened walls occur in periclinal strands (Fig. 3.2C–E), which extend through the seed coat at the hilum (Fig. 3.2C). The innermost layer is a thin membrane lacking a clear cellular structure (Fig. 3.2A–E). Figure 3.2F shows the smooth outer surface of the seed coat.

The embryo is reniform to varying extents, although the perhaps immature embryo in material examined of *Eugenia sintenisii* was ellipsoidal or ovoidal. On the surface, the embryo has a slightly raised stripe that matches the slightly depressed stripe of the seed coat. Glands are sometimes visible along its length. The other main surficial feature is a dark spot located near one end, displaced towards the ventral side and within the stripe. This spot is commonly elevated, and at least a few glands are evident in its vicinity. Below the dark, glandular spot, a small, triangular or rounded flap pointing towards the hilum was observed in some embryos of *Eugenia padronii*, *E. sessiliflora, E. sintenisii*, and *E. stewardsonii*. Almost all of the embryos dissected for this study exhibited incomplete fusion of the cotyledons. Incomplete fusion was recognized by observation of smooth, appressed, water-repellent surfaces within the cotyledonary mass. The extent to which the cotyledons were free from one another varied considerably. In some embryos, there was a short internal fissure in the center that could easily be missed. In others, the fissure extended much of the length of the embryo, even reaching the surface and leaving a short slit on the exterior. Still others exhibited an extended, unfused surface. In one embryo of *Eugenia stewardsonii*, the unfused region was semi-flabellate, extending the length of the embryo and curved towards the dorsal side. A similar pattern was observed in an embryo of *Eugenia cordata*, but in this case, the unfused surface did not lie along a single plane. A final variation was observed in a large embryo of *Eugenia sessiliflora*, in which the embryo was hollow with an unfused strip leading from the central cavity towards the surface. Thin slices of all dissected embryos blackened when exposed to IKI, indicating the presence of starch.

***Survey of Antillean* Eugenia**—Table 3.2 lists Antillean species of *Eugenia* outside of the Lathberry Clade known to have contracted inflorescences predominantly borne below the leaves on old wood. A total of 15 species were identified from Cuba, Jamaica, and the Lesser Antilles. The features that distinguish the Lathberry Clade from these similar species are discussed below.

***Phylogeny*—**All 10 of the screened low-copy nuclear loci successfully amplified, but primers for *MeNu18* and *MeNu47* yielded more than one band for some samples. Six loci (*MeNu5*, *MeNu13*, *MeNu18*, *MeNu39*, *MeNu61*, and *MeNu62*) contained potentially useful SSR's. A large repeat indel, which created alignment difficulties, was present in *MeNu47* as reported for *Psidium guajava* L. (Pillon et al. 2014). Although variable, *MeNu21* was rejected after cloning, as more than two haplotypes were found in at least one species. The evolution of this locus was not further investigated. *MeNu79*, which corresponds to an indel of a protein-coding gene putatively homologous to *SGR6* in *Arabidopsis thaliana* (L.) Heynh., was selected for further analysis for its ease of amplification and sequencing, variability, and conserved single-copy status among the species under consideration. Table 3.3 presents selected alignment characteristics as well as the models of DNA sequence evolution chosen for the performed analyses.

The results of the phylogenetic analyses of the combined nuclear regions are presented in Figures 3.3 and 3.4. The maximum likelihood tree from the concatenated analysis (Fig. 3.3) closely corresponds to one of the six most parsimonious trees. Monophyly of the Lathberry Clade received 100% bootstrap support from both maximum likelihood and parsimony methods of analysis, and all ingroup species exclusively possessed the same large deletion in the *psbA-trnH* cpDNA region (Supplementary File 3.1). Different samples of each species grouped together with high support with the exception of the low support found for *Eugenia sessiliflora*. Regarding relationships between species, *Eugenia stirpiflora* and *E. cordata* were resolved as successive sister groups to the rest of the Lathberry Clade; however, bootstrap values for these relationships were modest. Only two species were consistently placed sister to one another: *Eugenia sintenisii* and *E. stewardsonii*. The concept of *Eugenia cordata* var. *sintenisii* applied to plants from both the Lesser Antilles and Puerto Rico was not supported, as the sampled plant from Puerto Rico corresponding to the type of the variety, *Eugenia sintenisii*, did not form a clade with the representative of *E. cordata* from Saint Kitts (SK in Figs. 3.3, 3.5–3.9, Appendix 3.1).

The results from separately analyzed regions (Figs. 3.5–3.9) are consistent with the results of the concatenated nuclear regions with two major exceptions. The trees inferred from ITS sequence data (Fig. 3.5) grouped *Eugenia stirpiflora* and *E. cordata* together as sister species with high bootstrap support in contrast to the ETS (Fig. 3.6) and *MeNu79* (Figs. 3.7–3.8) topologies, in which *E. stirpiflora* was sister to the rest of the Lathberry Clade. The other exception was that a clade composed exclusively of *Eugenia stirpiflora* and the sample of *E. cordata* from Saint John in the Virgin Islands (SJ in Figs. 3.3, 3.5–3.9, Appendix 3.1) was recovered from the cpDNA sequence data (Fig. 3.9). This result is supported by a short indel in the *ndhF-rpl32* region (Supplementary File 3.1).

The species tree inferred from nuclear data by *BEAST is presented in Fig. 3.4. Aside from the strong support for the monophyly of the Lathberry Clade and the placement of *Eugenia sintenisii* and *E. stewardsonii* as sister taxa, the posterior probabilities of branches on the maximum clade credibility tree were low, reflecting uncertainty over ingroup relationships. The successive divergence of *Eugenia stirpiflora* and *E. cordata* was nevertheless recovered as in the concatenated analysis.

Discussion

Comparisons of the morphological and anatomical characters of the Lathberry Clade show that this group may be distinguished from all other species of *Eugenia* in the Antilles by a combination of dull twigs, glabrous leaves with a raised midvein (almost plane in *Eugenia padronii* and towards the base of some specimens of *E. haematocarpa*), glomerate or fasciculate inflorescences predominantly borne below the leaves on old wood (i.e., ramiflorous or cauliflorous), with closely spaced, ascending bracts, and spheroidal fruits turning red or purple at maturity, with the calyx lobes erect or torn away. A large deletion in the *psbA-trnH* intergenic spacer region is unique to members of the clade. Phylogenetic analyses provide support for the monophyly of the Lathberry Clade and the species concepts adopted here, but the phylogeny of the group remains uncertain. From a conservation standpoint, most taxa of the Lathberry Clade are not in immediate danger of extinction, but their relatively restricted ranges are cause for concern. Continued monitoring and preservation of suitable habitat are therefore important to ensure that they continue to thrive.

Below, some aspects of the morphology and anatomy of the Lathberry Clade are discussed. This is followed by comparisons to Antillean species of *Eugenia* with similar inflorescences and interpretation of the phylogenetic results. Finally, the findings of this study are synthesized in a taxonomic treatment of the Lathberry Clade that provides further details on extinction risk assessments.

Morphology and Anatomy—Growth habit and environment are strongly correlated in the Lathberry Clade: there is a clear tendency for species of mesic environments to be arborescent and species of drier environments to be shrubby. This is reflected in the growth form listed first in the descriptions below. In other respects, vegetative growth is similar to that described for *Eugenia foetida*, and, as in this species, there is probably more than one flush of growth per year (Tomlinson 2001).

Twigs. Twigs offer a number of useful characters for distinguishing among species of Myrteae. For example, the form, color, and manner by which the epidermis is lost of twigs were considered important characters in *Psidium* (Landrum 2017). Variation in the depth at which the first periderm originates correlated with the structure of the phellem has also been observed among species of *Eugenia* from southern Africa (van Wyk et al. 1980). In the Lathberry Clade, differences in twig color and morphology may be explained by how the epidermis and subsequently produced periderms mature. The pale gray color of older twigs appears to result from the accumulation of aged dermal layers. Variations in how these aged layers are lost to reveal underlying brownish layers of the bark provide a possible explanation for the observed diversity. Thus, the smooth, pallid layer on the twigs of *Eugenia padronii* could be interpreted as an aged, persistent epidermis, while the brownish older twigs of *E. haematocarpa* could be a consequence of the aged dermal layers quickly peeling away. The patchy appearance of the older twigs of *Eugenia sintenisii* and *E. stewardsonii* would then result from the gray dermal layers being lost over time in flakes. If, however, these layers were to accumulate faster than they were lost, the older twigs would appear uniformly grayish as in other species of the Lathberry Clade.

Superposed accessory buds, which may or may not be evident externally, are a common feature in Myrtaceae (Burrows et al. 2008). These were also described in *Eugenia foetida* (Tomlinson 2001). The distal bulging of a group of superposed buds suggests that the uppermost bud is dominant. Thus, the other buds would be phylloscopic accessory buds (Briggs and Johnson 1979, Weberling 1988). Since inflorescences may be borne immediately above or below a branch that presumably originated from the same group of axillary buds, the fate of an individual bud, whether flowering or vegetative, does not seem to be determined by its position within the group.

Leaves. A few foliar features are characteristic of the Lathberry Clade. Leaves of all species are quite glabrous, even when young, and blunt at the tip. The latter feature prevails among the Antillean members of *Eugenia* sect. *Umbellatae*. There is also a tendency in the Lathberry Clade for the leaves to dry black on the adaxial surface, although the color of the dried leaf surfaces exhibits some variation from one specimen to another. The major exceptions to this tendency are the thicker leaves of *Eugenia sessiliflora* and *E. stirpiflora*, which nevertheless dry noticeably darker adaxially. Another characteristic feature of leaves in the Lathberry Clade is the adaxially raised midvein. A raised midvein that is grooved towards the base may also be described as biconvex (Holst 2003). In cases where the edges of a grooved midvein are almost plane, the midvein may appear to be impressed into the lamina, making it difficult to always clearly distinguish raised and impressed types. This is the case with some specimens of

Eugenia haematocarpa, but the groove is relatively narrow and does not continue into the petiole, which in the Lathberry Clade is plane to shallowly concave above.

Members of the Lathberry Clade also share a basic pattern of leaf venation (Fig. 3.1). Two features of this pattern, the intramarginal and composite veins, are subject to differing interpretations according to their development. Carr et al. (1986) distinguished between paramarginal and intramarginal veins in Myrtaceae on the basis of whether the perimarginal vein sensu Ellis et al. (2009) is formed by the coalesced lateral (secondary) veins or originates independently of these, respectively. In the latter case, the venation would be considered acrodromous, in agreement with Klucking (1988), rather than brochidodromous. These authors speculated that both types of perimarginal vein occur among the Neotropical species. To the extent that it is possible to judge from the mature leaf, the Lathberry Clade appears to possess paramarginal veins. Ontogeny also bears upon the interpretation of the composite vein, which is here viewed as a product of the coalesced tertiary veins. Similar veins in species of *Eugenia* from Argentina have been interpreted as intersecondary veins (González 2011, González 2016). Intersecondary veins follow similar courses to the major secondaries but often do not reach the margin and are intermediate in gauge between the major secondaries and tertiaries (Ellis et al. 2009). The intermediate veins observed in the Lathberry Clade, however, are always strongly developed at the margin and sometimes do not reach the midvein. When the composite vein is especially well developed, it can be distinguished from the secondary veins by observing its effect on the intramarginal vein, which arches between the secondaries but is barely deflected by the composite veins (McVaugh 1956).

Inflorescences. Given the significance of inflorescence characters for recognition of the Lathberry Clade, and the confusion over terminology used to describe reproductive shoots of flowering plants (Endress 2010), it seems appropriate to clarify some aspects of inflorescence morphology pertinent to the group. The basic structure of inflorescences in the Lathberry Clade is racemose, bearing individual flowers laterally along an indeterminate axis. Racemes have also been referred to as “bracteate shoots” in Myrteae (Landrum and Kawasaki 1997), for racemes with reduced leaves (bracts) can sometimes be found alongside shoots bearing solitary flowers in the axils of typical foliage leaves (McVaugh 1956); however, the inflorescences of the Lathberry Clade are always well-differentiated and clearly recognizable as such. According to the more precise system of classification of inflorescences by Briggs and Johnson (1979), the anthotelic uniflorescences of *Eugenia* are monads that are arranged in blastotelic, racemiform conflorescences. The inflorescence axes referred to here would be the main axes of conflorescences (R_Z); the pedicels, peduncles (or hypopodia); and the bracteoles, as the only phyllomes of the uniflorescence, prophylls. The terms “pedicel” and “bracteole” are here used in their traditional senses for the sake of continuity with other treatments (e.g., Berg 1855–1856, McVaugh 1989). Briggs and Johnson (1979) also described a case in which the conflorescence of *Eugenia* is reduced to a short shoot, or brachyblast, as in members of the Lathberry Clade. They reported that these brachyblasts are formed from the growth of multiple seasons and are sometimes capable of branching and continued flower production. Although branching of short shoots was not observed in the Lathberry Clade, further observations on living plants would be helpful to establish whether the short shoots are capable of perennial growth and flower production.

The almost complete limitation of inflorescences to older portions of the stem is a particularly significant character for the Lathberry Clade. This is termed ramiflory or cauliflory according to whether the inflorescences are borne on branches or trunks, respectively. Ramiflory can be explained by the prolonged dormancy of normally produced axillary buds. This may be deduced from the occasional occurrence of inflorescences in the leaf axils or in association with the leaf scars on older twigs. The cauliflorous condition is probably just an extreme form of ramiflory, but large and loosely organized clusters of flowers in *Eugenia haematocarpa* suggest that adventitious buds may also be involved. Evidence for flowering from both exogenous, preventitious buds and endogenous, adventitious buds has been found in tree species from both temperate and tropical areas (Fink, 1983). Another possible explanation for large, cauliflorous flower clusters is branching of the inflorescence axes toward the base, where it would be difficult to observe externally.

One of the few morphological features whose distribution in *Eugenia* is well understood is relatively broad bracteoles persistent at anthesis. These are characteristic of the Persistent Bracteole Clade, which consists of *Eugenia* sect. *Jossinia* (DC.) Nied., *E.* sect. *Racemosae* O.Berg, *E.* sect. *Speciosae,* and *E.* sect. *Umbellatae* (Mazine et al. 2018). The systematic relevance of floral colleters, on the other hand, is less clear. Colleters were previously reported in the axils of the bracteoles of other species of *Eugenia* and genera of Myrteae by Pimentel et al. (2014). Foliar colleters in Myrtaceae, which were interpreted as rudimentary stipules by Weberling (1956), were investigated by Silva et al. (2012). The floral colleters observed in the Lathberry Clade are similar to the euryform type of foliar colleter described by the latter authors. They are probably present in all members of the Lathberry Clade, but these structures are difficult to observe from dried material and were not further investigated in this study.

Flowers. Studies of the floral morphology of Myrteae, especially those with a developmental component, have illuminated the systematic significance of a variety of floral attributes in the otherwise rather similar flowers of members of the tribe (Vasconcelos et al. 2019). A few specializations found in the flowers of the Lathberry Clade are considered further below. First, a constant feature of Myrteae worth commenting upon is epigynous perianth insertion and the accompanying inferior ovary (Wilson 2011). The nature of the adnate hypanthium in Myrtaceae, whether appendicular or receptacular in origin, has been subject to various interpretations (Schmid 1972a). Recently, Harthman et al. (2018) used evidence from floral vasculature to argue that both types are present in Myrteae. The description of the calyx as lobed in the present study rather than consisting of individual sepals is not meant to imply an appendicular origin of the hypanthium. Instead, it describes how the lobes appear to be basally confluent around the rim of the hypanthium.

One floral feature investigated in this study was the number of glands in the anther connective. Anther glandularity was found to be useful for distinguishing between Myrtoid genera (Landrum and Bonilla 1996), but this character is largely unexplored in *Eugenia*. Though few conclusions can be drawn on the basis of the limited sampling here, further observations on anther glandularity in *Eugenia* could perhaps reveal patterns of variation across the genus or within species. Of the two features incidentally observed by bleaching the anthers, triangular pollen grains are typical for the family (Patel et al. 1984), while the general distribution of the undulate anticlinal walls of the epidermal cells on anthers and other organs across Myrteae is unknown. Such cell walls were, however, observed on the adaxial surface of the leaves of the Caribbean species *Eugenia axillaris* (Sw.) Willd. (Haron and Moore 1996).

The bilocular ovary of the Lathberry Clade with axile placentae, bearing multiple ovules from the center of the septum is typical for *Eugenia*. Two notable features of the gynoecium observed here are bent styles and the glandular locule walls of *Eugenia padronii*. A bent style is characteristic of members of *Eugenia* sect. *Umbellatae* and may be a synapomorphy for this taxon (Vasconcelos et al. 2018). In contrast, the occurrence of glands (i.e., secretory cavities) within the wall of the ovary adjacent to the locules is unusual. This condition was previously reported for *Eugenia mandevillensis* Urb. from Jamaica (Schmid 1972b). The position of glands in the pericarp varies within Myrteae (Galan et al. 2016). Elsewhere in the tribe, glandular locule walls characterize *Campomanesia* Ruiz & Pav. (Landrum 1982).

Fruits. The precise form of the fruit is determined by the number, shape, and orientation of the seed or seeds that develop within it. In species with large fruits and a single, almost spherical seed (*Eugenia haematocarpa*, *E. sessiliflora*, and *E. stirpiflora*), the fruits are globose. In other species, the fruits are somewhat prolate or oblate depending on the orientation of the seed(s). Multi-seeded fruits probably occur occasionally in species other than *Eugenia padronii* and *E. stewardsonii*, but they seem to be particularly common in *E. stewardsonii*. Fruit color, usually red when ripe in the Lathberry Clade, has also been reported to be purple or black. Descriptions of black fruits probably refer to a dark purple color.

Seeds. Seeds of Myrteae are rarely described in detail. No doubt this is partly attributable to the scarcity of mature seeds in herbarium collections. The morphology of the embryo has received the most attention since it was first employed by de Candolle (1827) to subdivide the group in a scheme adopted and elaborated upon by Berg (1855–1856) as a system of subtribes. Embryonic form was later employed by Kausel (1956) as a character to recognize additional groups at the level of subfamily and genus. His particular emphasis on the degree of fusion of the cotyledons of Eugenioid embryos—i.e., embryos with fleshy cotyledons and a short hypocotyl (Berg 1855–1856)—was criticized by McVaugh (1968) and Legrand (1975), among others. Characters of the seed coat and embryo were used by Landrum (1986) to group the five genera of the *Campomanesia* complex, and anatomical features of the seed coat were found to be taxonomically useful for discriminating among the Myrtoid genera (Landrum and Sharp 1989)—i.e., those genera possessing embryos with short cotyledons, a long hypocotyl and an overall curved form (Berg 1855–1856). Subsequent treatments of a few Myrtoid genera have thus included investigation of seed coats by SEM (Landrum 1990, Salywon 2003, Salywon and Landrum 2007, Landrum 2010). Grifo (1992) also reported differences among genera after using SEM to investigate the surface of the seed coats of *Eugenia pyriformis* Cambess., *Myrciaria floribunda* (Willd.) O.Berg, and various species of *Myrcianthes* O.Berg. In *Eugenia*, van Wyk and Botha (1984) conducted a developmental study of the seeds of southern African species. These authors found differences in the structure of the testa, the development of the hilar region, and the presence of glands in the embryo between two kinds of seeds, corresponding to species of the informally identified Groups X and Y. Although these two groups were not recovered in a recent phylogenetic analysis of the genus, in which they emerged in *Eugenia* sect. *Jossinia* (Mazine et al. 2018), their descriptions provide a convenient point of comparison for the seeds of the Lathberry Clade, which are most similar to those of Group X. Observations on seed coats and embryos made in this study will therefore be interpreted in light of their results.

The more or less reniform seeds of the Lathberry Clade probably result from the ovule becoming amphitropous as the seed develops (van Wyk and Botha 1984). A micropyle is not visible at maturity. In southern African species, it is located near the hilum on the ventral surface of the seed and is obscure at maturity (van Wyk and Botha 1984). The elliptical hilum found in the Lathberry Clade corresponds with that observed in Group X species. In contrast, the seeds of Group Y were characterized by an expanded hilar region covering one whole hemisphere of the seed (van Wyk and Botha 1984). As noted above, the hilum may be disproportionately expanded around the circumference of the seed in *Eugenia haematocarpa*, *E. sessiliflora*, and, to a lesser extent, *E. stirpiflora*. More observations would be useful to assess the variation in hilum size in these species and to determine whether there are size differences between them. As these are the largest seeds of the group, it may be that expansion of the hilum is related to seed size in the Lathberry Clade.

The dorsal stripe that is the other obvious feature of the seed coat is related to both the areolae of Group X species and the depression present in the seed coat of Group Y species (van Wyk and Botha 1984). The areolae are two horseshoe-shaped areas in the inner surface of the seed coat. They are connected by their open ends on the ventral side and thus form a single continuous region (van Wyk 1980). This areolar region is thicker and darker than the rest of the seed coat and is abundantly vascularized (van Wyk 1984). In every respect the areolae are the inverse of the dorsal stripe, and these features appear to be two different ways of describing the same pattern. The dorsal stripe is the salient feature in the Lathberry Clade, as the areolar region would cover most of the seed coat. Van Wyk and Botha (1984) also describe a shallow depression extending dorsally from the micropyle on the inside of the seed coat in Group Y. The seed coat in this area is lighter and thinner than its surroundings, often mottled, and with little, if any, vasculature. Although the micropyle was not observed in the Lathberry Clade, the same could be said for the dorsal stripe, which is obviously extended around the dorsal side in four of the species of this group. Thus, the depression seems to be a foreshortened stripe, and the described differences between Groups X, Y, and the Lathberry Clade are simply a matter of emphasis. The darker area of the seed coat may develop through the extension of vascular tissue into the integument or else correspond to the chalaza (van Wyk and Botha 1984). Additional ontogenetic studies could help to clarify this point and establish the likely homology of these regions in different species of *Eugenia*. The pale or marbled appearance of the dorsal stripe probably results from variation in tannin content within groups of cells in this area, as was found in the subepidermal layer of the seed coat in Group Y (van Wyk and Botha 1984).

Considering the anatomy of the seed coat, the smooth external surface of the seed coat of *Eugenia cordata* var. *cordata* viewed with SEM (Fig. 3.2F) contrasts with both the pulpy outer layer found in *Psidium* and the tessellated hexagonal pattern found in other Myrtoid genera. The bony seed coats of many Myrtoid genera also possess a denser cellular structure (Landrum and Sharp 1989). The layers of the seed coat observed by light microscopy and SEM, however, are readily identified with the components of the seed coat of Group X species described by van Wyk and Botha (1984). The outer palisade layer (exotesta; Fig. 3.2A, B, D, E) corresponds to the single layer of radially elongated macrosclereids with abundantly pitted walls. A similar layer is absent in Group Y over the hilar hemisphere, where the tissue derived from the placenta, septum, and pericarp adheres to the seed. Likewise, in the Lathberry Clade, the palisade layer is clearly absent over the hilum (Fig. 3.2B, C), where the innermost layer of the pericarp tends to adhere to the placental tissue, and this is accentuated in those species with an expanded hilum. The brown fibrous layer of the seed coat (mesotesta; Fig. 3.2A–E) corresponds to the layer of pitted, elongated cells, which could be described as fiber-sclereids, whose loose organization results from a period of intrusive growth (van Wyk and Botha 1984). The whitish layer extending laterally from the hilum is identified with the helically thickened cells observed by SEM (Fig. 3.2C–E). They correspond to tracheary elements, whose presence in the seed coat may be the result of lateral extension of the vascular bundles of the funiculus or, alternatively, expansion of the chalaza (van Wyk and Botha 1984). Finally, the thin and darkly colored innermost layer of the seed coat observed in the Lathberry Clade (Fig. 3.2A–E) probably corresponds to crushed remnants of the inner integument, as the rest of the seed coat develops from the outer integument (van Wyk and Botha 1984).

There is a need for more detailed descriptions of the seed coat in *Eugenia* to understand how its structure varies across the genus. The seed coat of *Eugenia walkerae* Flickinger, a related species of Clade C of *Eugenia* sect. *Umbellatae* (Flickinger et al. 2020), was reappraised in light of the present findings. Though initially described as three-layered (Flickinger 2018), all four of the layers described here are evident along with the hilum and dorsal stripe. Within the Lathberry Clade, a combination of seed size, color and appearance of the dorsal stripe of the seed coat are sufficient to distinguish among the species, with the possible exception of *Eugenia sintenisii* and *E. stewardsonii*. The seeds of *Eugenia sintenisii* appear to be smaller and lighter in color than those of *E. stewardsonii*; however, the seeds of only a single collection of *E. sintenisii* species were examined, and, the shape of the embryo and smaller fruit size, suggest that these seeds may not have been fully ripe. Indeed, Van Wyk and Botha (1984) cautioned against studying seed characters from herbarium material, for which it is difficult to assess seed maturity.

The morphology of embryos in *Eugenia* poses a few problems of interpretation. The raised dorsal stripe, which may simply be a consequence of the development of the seed coat, is evidently widespread in *Eugenia*. Alternative explanations for this feature include the zone of fusion of the cotyledons in *Eugenia stipitata* subsp. *sororia* McVaugh (dos Anjos and Ferraz 1999) and the mark left by the raphe in *E. pyriformis* (Justo et al. 2007). Both of these species belong outside of the Persistent Bracteoles Clade in *Eugenia* sect. *Pilothecium* (Kiaersk.) D.Legrand. There seems to be little evidence for the first alternative, while the raphe would be expected to extend from the hilum to the chalazal region. In *Eugenia*, the dark, glandular spot that is usually displaced toward the ventral side of the embryo has been identified as a radicular protuberance (van Wyk 1980, van Wyk and Botha 1984, Justo et al. 2007) or meristematic zone (dos Anjos and Ferraz 1999). Similarly, Landrum and Stevenson (1986) identified a meristem at the tip of the hypocotyl as the origin of the radical in their survey of Myrtoid embryos. Justo et al.

(2007) used SEM to show that there is a short embryonic axis in the seeds of *Eugenia pyriformis* hidden within the cotyledonary mass, with only the root apical meristem visible on the surface of the embryo as a dark spot. Therefore, the dark, glandular spot probably corresponds to the root apical meristem in the Lathberry Clade as well. The interpretation of the rounded or triangular flap found nearby in some embryos is uncertain, but observations on germinating seeds might help to clarify its significance.

Variations observed in embryos of the Lathberry Clade seems to have little taxonomic significance. Although consistent differences in embryo glandularity were reported for the southern African species of *Eugenia* (van Wyk 1980, van Wyk and Botha 1984), gland visibility on the surface of the embryo may be related to factors such as the state of maturity of the embryo, the color that it dries, and even lighting (Snow et al. 2003). The degree of fusion of the cotyledons was found to vary considerably within species such that it is difficult to identify any differences among species. In the few cases in which an extended, unfused surface was observed, it was similar in outline to those illustrated for southern African species of *Eugenia* (van Wyk 1980) and *E.* (=*Pseudanamomis*) *umbellulifera* (Kunth) Krug & Urb. (Kausel 1956). The cotyledons of species of *Eugenia* from throughout Africa appear to be consistently partially fused (van Wyk and Botha 1984). Considering the possibility that the partial fusion may easily be overlooked, the same may be true in the Lathberry Clade. Embryos are therefore described as apparently completely fused when no indication of partial fusion was observed.

The descriptions of embryos below are comparable to the description by Urban (1894–1895) for a member of the Lathberry Clade as impunctate, with the cotyledons conferruminate or free along a very narrow line in the middle and an impressed radicle 1/2–3/5 the length of the embryo, the very tip of which is punctiform-prominulous. Because this author included *Eugenia stewardsonii* in his concept of *E. cordata* var. *cordata* and cited fruiting collections of both, exactly which species he described is uncertain. The description nevertheless highlights the same features. The major difference is that he interpreted the raised dorsal stripe as an adnate radicle.

***Survey of Antillean* Eugenia**—The combination of diagnostic features listed above was derived from comparisons between members of the Lathberry Clade and other ramiflorous or cauliflorous species of *Eugenia* with glomerate or fasciculate inflorescences throughout the Antilles. The criteria followed for recognition of these inflorescence characters attempted to make meaningful distinctions between inflorescence types and positions, but such distinctions must be admitted to be arbitrary to some extent. In the case of inflorescence types, contracted inflorescences such as glomerules and fascicles differ from racemes only in the length of the inflorescence axis. Nevertheless, a distinction made on this basis is often useful. Mazine et al. (2014), for example, distinguished between extended racemes that have pedicels no more than twice as long as the internodes between pairs of flowers along the rachis, which characterize *Eugenia* sect. *Racemosae*, and short racemes and other contracted inflorescence types that have pedicels at least four times as long, which characterize *E.* sect. *Umbellatae*. Some Antillean endemic species, however, may bear extended racemes in combination with inflorescences that lack a well-developed axis, as observed by Urban (1928) and Hilaire (2000). This observation necessitates consideration of the full range of variation present in a species for accurate categorization. Further distinction between species with short racemes and even more reduced types, which was not attempted here, seems tenuous, although it may sometimes be convenient (Proctor 1957). In the case of inflorescence position, the need to evaluate whether the inflorescences are predominantly borne on old wood or new introduced some ambiguity into how species were categorized. Actually, the timing of flowering in relation to shoot growth and leaf lifespan were both employed as criteria for recognition of ramiflorous and cauliflorous species. Since, however, it is uncommon for leaves to persist on portions of the shoot older than the two most recent growth increments, the age of the shoot and whether it bears leaves are closely correlated. Allowing for some variation in inflorescence position within species still greatly narrowed the pool of species, demonstrating that ramiflory and cauliflory are relatively uncommon among Antillean species of *Eugenia*. Features of the species identified by employing these criteria are discussed in what follows.

The identified species from Cuba (Table 3.2) were all formerly included in *Pseudanamomis* sensu Bisse (1985) with the sole exception of *Eugenia laeteviridis* Urb. A few similar *Pseudanamomis* species, as far as known, regularly bear flowers in leaf axils: *Eugenia cati* Britton & P.Wilson, *E. maestrensis* Urb., and *E. bissei* Flickinger. Flickinger et al. (2020) showed that these three species form a clade with *Eugenia laeteviridis* and *E. catingiflora* Griseb. For two other *Pseudanamomis* species, *Eugenia gibberosa* Urb. and *E. samuelssonii* Ekman & Urb., the predominant position of the inflorescences is difficult to assess, but at least some are ramiflorous. Bisse (1985) also included *Eugenia cupuligera* Urb. within *Pseudanamomis* with *E. brunescens* Urb. as a synonym. In describing *Eugenia cupuligera*, Urban (1923) drew attention to several peculiar features. In fact, the jointed twigs with swollen nodes, 5-merous, cup-like calyx with 10 radiating lines within, and asymmetrically developed fruits strongly suggest a species of *Mouriri* Aubl., a genus of Melastomataceae that is frequently confused with Myrtaceae (Morley 1976, Landrum and Kawasaki 1997). Type material of *Eugenia brunescens* (*Ekman 15876* (S [No. S03-297, image!])), however, appears to be a species of *Eugenia*. Further study is needed to identify a non-molecular character that can distinguish between these Cuban species and the Lathberry Clade, but the olive-green color that sometimes develops on the adaxial leaf surface (Bisse 1985) is not found in the Lathberry Clade.

No species from Hispaniola meeting the criteria for inflorescence type and position were identified. A few species may nevertheless be mentioned. *Eugenia gonavensis* Urb. is a poorly known species that bears many inflorescences at older leafless nodes as well as in the leaf axils. This species occasionally produces a basal peduncle a few millimeters in length, suggestive of a more extended raceme. In addition, it is distinguished by the adpressed trichomes on the flowers, which are never found in the Lathberry Clade. Also notable is a group of four similar species with fasciculate inflorescences, including *Eugenia chrootricha* Urb., *E. dictyophylla* Urb., *E. pubicalyx*, and *E. reticularis* O.Berg. *Eugenia dictyophylla* and *E. pubicalyx* were placed in Clade CII (Flickinger et al. 2020) and are thus closely related to the Lathberry Clade. The four species share lanceolate leaves with conspicuously reticulate venation, often mucronate leaf apices, and deeply impressed midveins. The inflorescences are borne in leaf axils or at leafless nodes, but in the latter case, the inflorescences are found towards the ends of the twigs, perhaps where the leaves were prematurely lost. Other differences from the

Lathberry Clade are hairs on the young leaves and abaxial surface of the calyx lobes except for in the almost glabrous *Eugenia dictyophylla* (Urban 1924).

Species with contracted inflorescences predominantly borne below the leaves on old wood from Jamaica (Table 3.2) include *Eugenia websteri* Proctor, which superficially resembles *E. sessiliflora* Vahl. It differs from the Lathberry Clade at least in its impressed glands on the upper leaf surface and lustrous young twigs. This species was placed within Clade CI with an unidentified species from Jamaica with relatively large leaves and a midvein deeply impressed into the petiole (Flickinger et al. 2020), thus resembling *Eugenia amplifolia* Urb., *E. lamprophylla* Urb., and *E. marchiana* Griseb, which share ramiflorous fascicles. *Eugenia crassicaulis* Proctor, which has subsessile flowers borne singly or in pairs at leafless nodes, was compared to these species by Proctor (1982). Aside from the impressed midvein, the relatively large, often connate bracteoles of these species differ from those typically observed in the Lathberry Clade. Other Jamaican endemic species with relatively large flowers borne in the leaf axils are possibly related. *Eugenia eperforata* Urb. bears flowers in both the leaf axils and at leafless nodes, but the predominant position of the inflorescences is difficult to assess from the limited collections seen. It is distinct from members of the Lathberry Clade in its chartaceous leaves that are granular-punctate on both surfaces and apiculate bracteoles (Urban 1909).

Among the identified Lesser Antillean endemics (Table 3.2), Liogier (1963) compared *Eugenia haematocarpa* to *E. duchassaingiana* O.Berg, presumably because of its similar leaf form and ramiflorous fascicles. This species from the larger islands of the Lesser Antilles is quite distinct from the Lathberry Clade in its appressed pubescent leaves and elongated, yellow to orange fruits. The sympatric *Eugenia greggii* (Sw.) Poir.

shares elongated fruits and a pale indumentum on the lower leaf surface, but in this species, inflorescences may be up to 1 cm long and are usually borne in the leaf axils (McVaugh 1989). *Eugenia hodgei* McVaugh is perhaps the most similar species to the Lathberry Clade in the Lesser Antilles. This species has only been recorded from Dominica and Martinique (Rollet 1993). It has short fascicles borne predominantly at leafless nodes, but the midvein is usually broadly depressed, tending towards grooved with raised edges. In contrast to the ascending bracts that mostly cover the axis of the short shoots in the Lathberry Clade, the bracts of *Eugenia hodgei* are held almost perpendicular to the axis in flowering specimens. McVaugh (1975) also drew attention to the thickened floral disk with conspicuous, pale staminal scars. Furthermore, from the few specimens examined, there seem to be tendencies for the calyx lobes to crumple after anthesis and for the fruits to be irregular, possibly as a result of multiple seeds developing. *Eugenia dussii* Krug & Urb. is an apparently similar species from the Lesser Antilles that has also been recorded from both Trinidad and Tobago (Baksh-Comeau et al. 2016). McVaugh (1973) discussed the lectotypification of *Eugenia dussii* with a specimen collected by Alexander Anderson that he identified with *Caryophyllus cotinifolius* Mill., a species of uncertain geographic origin. Whether or not one accepts this interpretation, the image of the lectotype of *Eugenia dussii* (*Anderson s.n.* (K [barcode K000276343])) compares favorably with physically examined isotypes of *E. hodgei* (*Hodge et al. 2230* (US [barcodes 00324469, 00997515])), with which it appears to agree entirely in vegetative characteristics and to share inflorescences borne mostly below the leaves. From the descriptions of these species by McVaugh (1973, 1989), the main difference would appear to be the shorter pedicels of *Eugenia hodgei*.

Other ramiflorous species with contracted inflorescences in the Lesser Antilles have distributions that extend into South America. *Eugenia lambertiana*, with fasciculate inflorescences, differs clearly from the Lathberry Clade in its yellow or orange fruits with the calyx lobes flattened over the disk (McVaugh 1989). *Eugenia tapacumensis* was cited by Urban (1894–1895) from Martinique and Saint Vincent; however, neither McVaugh (1989) nor Acevedo-Rodríguez and Strong (2012) accepted the presence of this species in the Lesser Antilles. McVaugh (1989) noted that fertile collections referred to *Eugenia tapacumensis* from the Lesser Antilles seem to differ from *Eugenia lambertiana* only in their obtuse and connate bracteoles. South American collections were distinguished by McVaugh (1969) also by their arcuate-conduplicate leaves and relatively short calyx lobes that are not reflexed at anthesis. Acevedo-Rodríguez and Strong (2012) considered *Eugenia tapacumensis* to be a synonym of *E. stictopetala* DC. A clade of *Eugenia lambertiana* plus *E. stictopetala* was found to be sister to the rest of Clade E within *E.* sect. *Umbellatae* (Mazine et al. 2018). Finally, *Eugenia coffeifolia* DC., a species with glomerate inflorescences and a distribution that also extends into South America, may be mentioned. This species flowers abundantly both in the leaf axils and at leafless nodes on older twigs. It differs in its chartaceous leaves with an impressed midvein, bracteoles almost covering the hypanthium, and peculiar biovulate locules. Unlike the preceding, it is a member of *Eugenia* sect. *Excelsae* (Mazine et al. 2018).

Phylogeny**—**This study is believed to be the first to employ low-copy nuclear genes for phylogenetic inference in Neotropical Myrtaceae. The *MeNu79* gene intron exists in a single copy in the investigated species and exhibits levels of variation comparable to those of commonly used nrDNA regions (Table 3.3). Although *MeNu79* may be more difficult to amplify from degraded material than multi-copy nrDNA and cpDNA markers, it should be considered as an additional source of evidence for future phylogenetic studies of Myrteae.

The results of the phylogenetic analyses (Figs. 3.3, 3.4) provide further support for the monophyly of the Lathberry Clade as well as for recognition of *Eugenia sintenisii* on morphological grounds as a distinct species from *E. cordata*, including populations from the Lesser Antilles. Aside from strong support for *Eugenia sintenisii* and *E. stewardsonii* as sister taxa, which was also expected from their numerous similarities, strong support for relationships between the members of the Lathberry Clade is lacking. *Eugenia stirpiflora* may tentatively be regarded as the sister group of the rest of the species, but additional data would be useful to corroborate this hypothesis.

Two statistically well-supported instances of topological conflict between separately analyzed regions were observed. The conflict between ITS and ETS (Figs. 3.5, 3.6) with respect to the placement of *Eugenia cordata* as sister to *E. stirpiflora* or else to *E. sessilflora* plus the four Puerto Rican endemic species, respectively, is interesting in that these regions are physically separated from one another only by the 18S rRNA gene. As a result, the phylogenetic signals of ITS and ETS are usually congruent, and they are often combined for analysis. Recombination between the two loci could nevertheless explain the observed conflict (Calonje et al. 2009). Incongruence between the two regions could also have arisen through phylogenetic error related to the mutational dynamics of DNA sequences or a failure to account for these through analytical means (Som 2014). A lack of conserved mutations from the time interval between the divergence of *Eugenia cordata* and *E. stirpiflora*, given the lower variability of ITS sequences (Table 3.3), could have prevented recovery of the branch that separates these species in the ETS and *MeNu79* topologies (Figs. 3.6–3.8). In the second instance, the sample of *Eugenia cordata* from Saint John in the Virgin Islands (SJ) shared the same cpDNA haplotype with *E. stirpiflora* (Supplementary File 3.1) rather than with the sample of *E. cordata* from Saint Kitts in the Lesser Antilles (SK). This situation could potentially have arisen through lineage sorting (Doyle 1992), which can be accounted for through species tree methods of phylogenetic analysis. Another possibility is that some amount of introgression has occurred between the two species. In fact, all three samples sharing the same haplotype were collected on Saint John, and cytoplasmic gene flow is a frequently observed phenomenon in plants that could explain this incongruence (Rieseberg and Soltis 1991). Further investigation is required to evaluate the alternative explanations offered for these topological differences.

The results of Flickinger et al. (2020), based on ITS and three cpDNA regions (*psbA-trnH*, *ndhF-rpl32*, and *trnL-trnF*), supported a sister relationship between *Eugenia cordata* (SJ) and *Eugenia stirpiflora* from Europa Bay on Saint John (EB in Figs. 3.3, 3.5–3.9, Appendix 3.1), but other relationships within the clade were unresolved. The different resolution presented here, if not preferred, should at least caution against drawing conclusions from limited evidence. In the same study (Flickinger et al. 2020), *Eugenia borinquensis* plus *E. stahlii* appeared as sister to the Lathberry Clade, and the two other lineages of Clade CII, represented here by *E. pubicalyx* and *E. woodburyana*, formed another clade. These relationships, which lacked strong support, are nevertheless consistent with the present results, as monophyly of the outgroup in the maximum likelihood trees (Figs. 3.3, 3.6–3.9) is arbitrary and poorly supported by the *BEAST species tree (Fig. 3.4). Ultimately, additional genetic evidence, ideally from multiple unlinked markers, is needed resolve relationships within Clade CII, which would provide valuable insights into the evolution of *Eugenia* on the Puerto Rican Bank.

Taxonomic Treatment

KEY TO THE SPECIES OF THE LATHBERRY CLADE

1. Leaf blade 11–22 cm long, subcoriaceous, the apex typically acute to acuminate. 2. *Eugenia haematocarpa*

1′. Leaf blade less than 8.5 cm long or thickly coriaceous if longer (up to 13 cm long), the apex typically rounded or obtuse, never acuminate. 2

2. Leaves thickly and rigidly coriaceous, the midvein raised above; leaf margin strongly recurved; floral disks greater than 4.5 mm across; dried fruits at least 1.5 cm diam. 3

2′. Leaves thinly coriaceous, or if thickly coriaceous, then pliable and the midvein more or less plane above; leaf margin recurved but not strongly so, merely downturned; floral disks less than 3.5 mm across; dried fruits less than 1.0 cm diam. 4

3. Leaves petiolate, the base of the blade tapering; tertiary veins conspicuously reticulate; inflorescences ramiflorous; flowers sessile or subsessile; hypanthium tomentose. 4. *Eugenia sessiliflora*

3′. Leaves sessile, the base of the blade cordate to rounded; tertiary veins inconspicuous; inflorescences cauliflorous; flowers pedicellate, the pedicels at least 5 mm long; hypanthium glabrous. 7. *Eugenia stirpiflora*

4. Young twigs becoming smooth and pallid with age; older twigs gray; axillary buds glabrous; leaf blades at least ca. 2 times as long as wide, often much more so, thickly coriaceous; midvein more or less plane above; secondary veins only faintly visible above; flowers often with pedicels greater than 1 mm long, beset with conspicuous yellow glands. 3. *Eugenia padronii*

4′. Young twigs only rarely becoming smooth and pallid; older twigs gray or various shades of brown; axillary buds puberulent; leaf blades up to ca. 2 times as long as wide; thinly coriaceous; midvein raised above; secondary veins evident above; flowers sessile or subsessile, rarely pedicellate, the glands inconspicuous, typically drying dark. 5

5. Bark of older twigs gray, lacking clearly visible reddish brown patches; flowers borne on short shoots with persistent, indurate bracts; coastal scrub or dry forests from eastern Puerto Rico through the Lesser Antilles. 6

5′. Bark of older twigs gray, flaking off to reveal a layer with reddish brown patches; flowers in tight clusters obscuring the bracts; mesic forests of Puerto Rico. 7

6. Base of leaf blade cordate to rounded; young twigs puberulent, the hairs persistent. 1a. *Eugenia cordata* var. *cordata*

6′. Base of leaf blade attenuate; young twigs essentially glabrous to puberulent, the hairs often lost at maturity. 1b. *Eugenia cordata* var. *caribaea*

7. Tertiary and composite veins of dried leaves weakly visible; leaf blade dull when dry, the base attenuate; leaves shortly petiolate, the petiole at least 2 mm long. 5. *Eugenia sintenisii*

7′. Tertiary and composite veins of dried leaves conspicuous, forming a coarse reticulum; leaf blade typically lustrous when dry, the base cordate to rounded (except in some plants from Carite Commonwealth Forest); leaves subsessile or shortly petiolate. 6. *Eugenia stewardsonii*

1. EUGENIA CORDATA (Sw.) DC., Prodr. 3: 272. 1828, non *E. cordata* (Hochst.) M.A.Lawson, Fl. Trop. Afr. 2: 438. 1871, nom. illeg. *Myrtus cordata* Sw., Prodr.: 78. 1788. *Pseudanamomis cordata* (Sw.) Bisse, Feddes Repert. 96: 511. 1985. TYPE: India occidentalis, (fl), *J.P.B. von Rohr s.n.* (lectotype designated by McVaugh [as holotype], Fl. Lesser Antilles 5: 485. 1989: BM [barcode BM000953768, image!]).

1a. EUGENIA CORDATA VAR. CORDATA

Myrtus ramiflora Vahl in H. West, Bidr. Beskr. Ste Croix: 290. 1793. TYPE: U.S. VIRGIN ISLANDS. Saint Croix, (fl), *H. West s.n.* (lectotype, here designated: C "Herb. M. Vahl, ramiflorus, dedit Dr West, ex Insula St. Crucis" [image!]).

Tricera cordifolia Willd., Sp. Pl., ed. 4, 4(1): 339. 1805. *Buxus cordifolia* (Willd.) Spreng., Syst. Veg., ed. 16, 3: 847. 1826. TYPE: Ind. occid., (fl), *s.coll.*, *s.n.* (lectotype designated by McVaugh [as holotype], Fl. Lesser Antilles 5: 485. 1989: B-W [barcode B -W 17385 -01 0, image!]).

Shrub or small tree up to 7 m, often multi-stemmed, the young twigs and inflorescences puberulous; bark pale gray, becoming rough and fissured, shed in flakes. **Twigs** yellow-brown, a reddish brown layer occasionally visible between the fissures, puberulous when young, the trichomes persistent; older twigs gray; axillary buds flattened against the twig, 2 or 3 superposed, forming a distally bulging group up to ca. 1

mm long, puberulous. **Leaves** subsessile; petiole up to 1 mm long × 1–1.5 mm wide; blade ovate, elliptical or obovate, 1.1–5.4 (–8.4) cm long × 0.6–3.3. (–4.2) cm wide, ca. 1–2 (–2.8) times as long as wide, the apex obtuse to rounded or emarginate, the base cordate to rounded, the margin pale, incrassate, recurved; venation brochidodromous, forming an arching intramarginal vein ca. 1–2 mm from the margin, the midvein raised adaxially, often with a medial wrinkle along its length when dry, the secondary veins prominulous on both surfaces, 5–6 pairs, at an angle of 50–70° to the midvein, the tertiary veins somewhat less visible; abaxial surface drying chocolate-brown, finely punctate; adaxial surface blackening, the glands obscure except toward the base of the midvein; coriaceous, lustrous when fresh, dull when dry. **Inflorescences** glomerules of few (typically 2–4) flowers or uniflorous, borne on short shoots up to 3.3 mm long, mostly ramiflorous, occasionally in leaf axils, rarely terminal, solitary or up to 3 superposed, persistent; bracts rounded to obtuse, acute, or emarginate, subequal to the bracteoles, mostly glabrous, persistent and becoming indurated; pedicels absent or up to 1 mm long in fruit, stout, puberulous (rarely slender, terete, 1.5 mm long); bracteoles free, persistent and becoming indurated, ovate-triangular or elliptical, 0.3–0.6 mm long × 0.5–0.6 mm wide, the apex rounded to obtuse or acute, the margin ciliate, the abaxial surface glandular. **Flowers** perfect; bud pyriform, the globe of the bud 2.2–2.3 mm diam; hypanthium campanulate, 1.2–1.3 mm long, densely glandular; calyx lobes concave, rounded, the outer pair 0.8–1.1 mm long × 1.2–1.6 mm wide, the inner pair 1.4–1.9 mm long × 1.4–2.1 mm wide, the margin scarious, ciliate, the abaxial surface glandular; petals elliptical, 1.8–3.0 mm long × 1.4–2.0 mm wide, white, the apex rounded to obtuse, the margin ciliate, the abaxial surface glandular; disk circular to squarish, 0.3–0.6 mm wide ×

1.4–2.0 mm diam, puberulous; stamens ca. 30–48 in few series, the filament 1.7–5.0 mm long, the anther 0.4–0.6 mm long, the connective with 1 large terminal gland and 0–5 smaller glands below; style 3.7–5.0 mm long, bent, tapered to a punctiform apex; ovary glabrous at the apex, bilocular, the placentae arising from near the center of the septum; ovules 9–19 per locule, forming a compact mass. **Fruits** globose, 6-10 mm long × 5–8 mm diam when dry, crowned by the rim of the hypanthium, from which the calyx lobes have commonly torn away, red or black when ripe, single-seeded, the pericarp thin. **Seeds** ellipsoidal, 4–8 mm long × 4–6 mm diam, the hilum a transversely oriented ellipse ca. 2.5 mm across; seed coat ca. 0.1–0.4 mm thick, yellow-brown and uneven on the exterior, darker with pale streaks and a slightly depressed, marbled dorsal stripe ca. 1 mm wide on the interior; embryo subreniform, with a dark glandular spot near one end, the cotyledons partially fused, appressed.

Habitat and Distribution—Coastal scrub and dry forests up to ca. 400 m, often on rocks. *Eugenia cordata* var. *cordata* is distributed from the east coast of Puerto Rico through the Virgin Islands, with an apparently disjunct population on Saint Barthélemy (Fig. 3.10).

***Phenology*—**Collected with flowers all months; with fruits, all but April, August, and October through November.

***Common Names*—**Lathberry: Virgin Islands (Britton and Wilson 1925). Mérizyé: Saint Barthélemy (Fournet 2002).

***Extinction Risk*—**Estimated EOO = 14368.82 km^2 (VU) and AOO = 132 km^2 (EN) from 41 points, 11 of which are located in protected areas. This taxon appears to be relatively common in the Virgin Islands, and the AOO is probably significantly underestimated; however, it occurs in similar habitats as *Eugenia sessiliflora* and may therefore be susceptible to the same threats (see below). On the island of Puerto Rico, *Eugenia cordata* is rare and not recently collected. Suggested status: LC.

***Notes*—**The leaves of this taxon are quite variable in size and shape. The typical leaf form is ovate with a cordate base and very short petiole. Three unnumbered collections by H. F. A. Eggers from Saint Croix with unusually large leaves (Wills Bay, 20 Sep 1873; Nordkysten, 25 Oct 1873 (st); vej til Elizas Retreat, 14 Apr 1875), whose dimensions are given in parentheses in the above description, were annotated by Kiaerskou as a form of *Eugenia cordata*. In the 1873 collections, the leaves are long and narrow, approaching lanceolate. Similar, though smaller, leaves are present on collections from other islands. The leaf base of *Eugenia cordata* var. *cordata* also varies from cordate, with well-developed basal lobes, to rounded. Because of the decurrent leaf margins, it is difficult to separate plants of this and the next variety with an almost rounded leaf base. Eggers (1879) reported “cuneate” leaves for this species, which he referred to as *Eugenia lateriflora* Willd. Urban (1894–1895) interpreted this statement as an indication of the presence of his concept of *Eugenia cordata* var. *sintenisii* in the U.S. Virgin Islands (then the Danish West Indies). Since, however, Eggers tentatively included *Eugenia sessiliflora* DC. in *Eugenia lateriflora*, it is uncertain whether this was meant to apply to plants from the Virgin Islands. Urban also reported *Eugenia cordata* var. *sintenisii* from Tortola, citing a collection by L. C. Richard. Unfortunately, this specimen could not be located. A modern collection of *Eugenia cordata* from Mt. Eagle on Saint Croix (*Liogier 35050*), included here under *E. cordata* var. *cordata*, exhibits some leaves that are rounded at the base and some leaves that are cuneately narrowed toward the base.

Other collections from this site possess either a typical, cordate leaf base (*Proctor 20446*) or rounded leaf base (*Britton et al. 141*). Although the nature of this variation is unclear, it is doubtful whether the shape of the leaf base can be considered a fixed character state within populations of *Eugenia cordata* in the Virgin Islands.

Myrtus ramiflora was described with a brief diagnosis ("Foliis ovalibus, sessilibus, glabris, floribus infra foliaceis") attributed to Vahl (West 1793). Five specimens of *Eugenia cordata* housed at C bear labels with the epithet "ramiflor-a/us". These include the lectotype of *Myrtus ramiflora* and a specimen collected by J. Ryan (*Ryan s.n.*). The remaining three specimens are listed in Table 3.4 (nos. 3, 6, and 9) along with other historic collections reviewed for this study for which the collector, island of occurrence, or determination was uncertain. All were probably collected on Saint Croix, and aside from the two specimens ex herbarium Liebmann (Table 3.4, nos. 6 and 9), they share somewhat larger leaves that are elliptical to obovate and almost rounded at the base. Most of the leaves are also young and therefore with less conspicuous venation and a slightly different color on the abaxial surface compared to mature leaves. In other respects, these specimens agree with *Eugenia cordata*, and one bears a typical ovate leaf with a clearly cordate base (*Ryan s.n.*). Specimens with a similar leaf form have been collected on Saint Croix and other islands. These include a collection by J. P. B. von Rohr from Saint Croix (*von Rohr s.n.*), which is therefore probably not from the same gathering as the lectotype of *Eugenia cordata*, and a specimen ex herbarium Puerari at G-DC (Table 3.4, no. 16). The lectotype of *Myrtus ramiflora* is the only one at C that is clearly marked as originating from Vahl's herbarium.

Pseudanamomis cordata was recently reported from Cuba without citation of a collection (Greuter and Rankin-Rodríguez 2017). This report is considered erroneous.

Additional Specimens Examined—**British Virgin Islands.**—GUANA: Palm Ghut, 50–100 ft., 18 Nov 1986, (fl), *Proctor 42561* (NY, SJ); E ridge of Pyramid Hill, 250–400 ft., 17 Nov 1986, (fl), *Proctor 42527* (SJ); N slope of Pyramid Hill, 100–125 ft., 29 May 1993, (fr), *Proctor 48820* (SJ).—JOST VAN DYKE: top of ridge N of Great Bay, 11 Apr 1967, (st), *Little 21960* (UPR, US); mountain slope NE of Great Bay, 500 ft., 12 Apr 1967, (fl), *Little 21978* (A, UPR, US); mountain slope NE of Great Bay, 500 ft., 12 Apr 1967, (st), *Little 21978A* (UPR, US); South Side, N side of road, 750 m E of Foxy's Restaurant, 18.4407°N, 64.7397°W, 70 m, 3 Jul 2005, (fr), *Hamilton 144* (K [image], UPRRP).—TORTOLA: 3 May 1919, (fl), *Fishlock 406* (K [image]); Fish Bay to Road Town, 13–17 Febr 1913, (st), *Britton & Shafer 904* (K [image], NY, US); Hog Valley Point, 4 May 1919, (fl), *Fishlock 405* (K [image], NY); roadside between Joe's Hill and Meyers, 300 m, 24 Aug 1965, (fl), *D'Arcy 214C* (A); Paraquita Bay, [18.424611°, –64.580661°], 30–40 m, 10 Jun 2011, (fr), *Fonseca MF059* (UPRRP).—VIRGIN GORDA: 200 ft., 21 Jun 1969, (fr), *Little 23814* (NY, US); 200 ft., 21 Jun 1969, (fl), *Little 23817* (NY, US); 1969, (st, fl), *Woodbury s.n.* (NY, UPR × 2); 21 Jun 1969, (fl), *Woodbury s.n.* (UPR); Deep Bay, drainage 1/2 mile E, 20 ft., 18 Mar 1972, (st), *Little 26156* (NY, US); Gorda Peak National Park, upper slopes and summit of Gorda Peak, 1200–1359 ft., 19 Jul 1986, (fl), *Proctor & Barwick* 41962 (SJ); North Sound, 29 Oct 1918, (fl), *Fishlock 25* (GH, NY). **Puerto Rico.**—CEIBA: Ceiba Playa, 18 Feb 1926, (st), *Gleason & Cook K-37* (NY); Isla Piñeros, 30 Jul 1966, (st), *Woodbury s.n.* (US); Isla Piñeros, Roosevelt Roads Naval Res., 10 ft., 30 Jul 1966, (st), *Little 21682* (GH, NY, UPR, US).—CULEBRA: 3–12

Mar 1906, (st), *Britton & Wheeler 39* (NY, US); top of the hill, NW side of the cemetery, 16 Feb 2000, (st), *Sustache 283* (SJ).—VIEQUES: 2 Jun 1972, (st), *Woodbury s.n.* (NY, UPR); Laguna Jamuel [Yanuel], in slope of N side of Laguna Jamuel, 16 Jun 1999, (fl), *Sustache & Quevedo 22* (SJ); National Wildlife Refuge, E tract, W side of the peninsula between Ensenada Honda and Bahía Jalova, [18.11692°, –65.34225°], 5–10 ±7.6 m, 28 Feb 2009, (st), *Breckon et al. 9257* (MAPR, UPRRP); Bo. Puerto Diablo, E tract of Vieques NWR, SW side of Peninsula Carrenero between Ensenada Honda and Fanduca beach, 18.114975°N, 65.343281°W, 9 m, 20 Jun 2018, (st), *Flickinger et al. 113* (FTG). **Saint Barthélemy.**—Morne Larigot, 100 m, 12 Nov 1952, (fl), *Le Gallo 1091* (NY); Petite Saline, ca. 100 m, 19 Feb 1953, (st), *Le Gallo 2023* (A); Petite Saline, 100 m, 19 Feb 1953, (st), *Le Gallo 2027* (WAG × 2 [images]); Morne de Petite Saline, 70 m, 28 Dec 1953, (fl), *Le Gallo 2201* (A); morne entre Saline et St. Jean, 7 Sep 1951, (fl), *Le Gallo 63* (WAG × 2 [images]); morne entre Saline et St. Jean, 7 Sep 1951, (st), *Le Gallo 587* (U [image]); Morne Larigot, 19 Jun 1952, (st), *Le Gallo 819* (U [image]); St. Jean, 12 Feb 1952, (st), *Le Gallo 471* (WAG [image]). **U.S. Virgin Islands.**—SAINT CROIX: (fl, fr), *Pflug s.n.* (C [image]); (fl), *Rohr s.n.* (S [image]); (fl), *Richard s.n.* (P [image]); (fl), *Ryan s.n.* (C [image]); (fl), *West s.n.* (L [image]); (fl), *Benzon s.n.* (C [image]); (fl, fr), *Oersted s.n.* (C [image]); 1870, (fl), *Eggers s.n.* (C [image]); East Ridge, Davis Bay, 16–18 Apr 1984, (st), *Liogier 35046* (UPR); . . . til Elizas Retreat, 12 Nov 1871, (fl), *Eggers s.n.* (C [image]); vej til Elizas Retreat, 14 Apr 1875, (st), *Eggers s.n.* (C [image]); Fair Plains, 29 Sep 1874, (fl, fr), *Eggers s.n.* (C [image]); Maroon Ridge area NE of Springgarden, on wooded crest of hill, ca. 800 ft., 4 Sep 1988, (fl), *Proctor 44988* (SJ); in monte Caerulae et adjacentibum, (fl), *Richard s.n.* (P [image]); Mt. Eagle, 17–25 Mar

1923, (st), *Britton et al. 141* (NY); Mt. Eagle, 17 Apr 1984, (st), *Liogier 35050* (UPR); E slope of Mt. Eagle, ca. 750 ft., 21–23 Dec 1959, (fl, fr), *Proctor 20446* (A); Nordkysten, 25 Oct 1873, (st), *Eggers s.n.* (C [image]); Nordkysten, 25 Oct 1873, (fl), *Eggers s.n.* (C [image]); Parasol Hill, 14 Oct. 1923, (fl), *Thompson 421* (NY, UPR, US); Rohrs Minde, 3 Sep 1871, (fr), *Eggers s.n.* (C [image]); Wills Bay, 20 Sep 1873, (st), *Eggers s.n.* (C [image]).—SAINT JOHN: (fl), *Ravn s.n.* (S [image]); 31 Jan 1892, (st), *Warming 942* (C [image]); Bordeaux, 4 Jun 1984, (fr), *Woodbury 217* (UPR); Coral Bay, 20 Feb 1906, (st), *Raunkiaer s.n.* (US); Cruz Bay, Mary Holter Road, 40 m, 17 Jan 1988, (fl), *Acevedo-Rodríguez et al. 2344* (NY, UPR, UPRRP, US); East End Quarter, W of Newfound Bay, 7 Feb 1991, (fr), *Acevedo-Rodríguez 4148* (NY, UPR, US); near Lamosure [Lameshur], 10–12 Feb 1913, (fl), *Britton & Shafer 636* (NY, US); eastern side of Minna Hill, 13 Jan 1990, (fr), *Acevedo-Rodríguez & Aleman 3205* (NY, UPR, US); Mollendal, 600 ft., 31 Dec 1887, (st), *Eggers 3298* (C × 2 [images]); Privateer Bay, 18.336658°N, 64.668822°W, 40 m, 26 May 2017, (st), *Gibney s.n.* (FTG); Vestende, 13 Feb 1906, (st), *Raunkiaer s.n.* (P [image]).—SAINT THOMAS: (fl), *Oersted s.n.* (C [image]); Nov 1880, (fl), *Eggers 141* (GH); May 1881, (fl), *Eggers 345* [ed. Toepffer] (K [image], P × 3 [images]); May 1881, (fl), *Eggers 345* [com. Rensch] (AMD [image]); 1881, (fl), *Eggers s.n.* (US); 3 Jan 1896, (st), *Paulsen 144B* (C [image]); 11 Dec 1905, (st), *Raunkiaer 2313* (C [image]); Belgian Road, 31 Jan–4 Feb 1913, (fl), *Britton et al. 37* (NY, US); Cowells Hill, 100 m, Dec 1887, (fl), *Eggers 295* (P [image]); Cowells Hill, 6 Nov 1880, (fl), *Eggers s.n.* (NY); Frenchmans bay, Jun 1883, (fl), *Eggers s.n.* (NY); Frenchmansbay Estate, 22 Jan 1914, (st), *Ostenfeld 190* (US); Greater St. James (between St. Thomas and St. John), N slope, southernmost hill, ca. 20 m, 14 Apr 1968, (st), *Byer 68-1125*

(UPRRP); Lovenlund, 1 Feb 1905, (st), *Raunkiaer s.n.* (C [image]); Paradise Bay, 1–9 Mar 1925, (fr), *Britton & Britton 209* (GH, NY, UPR, US); Water Island, 24 Jul 1967, (st), *Mercado et al. 67-1532* (UPRRP); Water Island, 11 Feb 1971, (fr), *Woodbury et al. W.I. 221* (UPR × 2); Water Island, 17 Jun 1970, (fl, fr), *Woodbury s.n.* (UPR, US, NY); Water Island, NE, 22 m, 24 Jul 1967, (st), *Mercado et al. 67-1516* (UPRRP).

1b. ***Eugenia cordata* var. *caribaea*** Flickinger, nom. et stat. nov. *Eugenia sessiliflora* DC., Prodr. 3: 273. 1828, nom. illeg., non *E. sessiliflora* Vahl, Symb. 3: 64. 1794. TYPE: S.-Domingo, (fl), *C.G. Bertero s.n.* (lectotype, here designated: G-DC [barcode G00658525, image!]).

Shrub or small tree up to 8 m, the inflorescences and usually the young twigs puberulous; bark gray, shed in flakes or vertical strips. **Twigs** yellow-brown, puberulous or glabrous when young, the trichomes soon lost; older twigs gray, sometimes becoming smooth and pallid first; axillary buds flattened against the twig, 2 or 3 superposed, forming a distally bulging group up to ca. 1 mm long, puberulous. **Leaves** shortly petiolate or subsessile; petiole up to 3 mm long × 1–1.5 mm wide, concave above; blade elliptical, varying from almost oblong to suborbicular, occasionally ovate or obovate, 1.9–6.9 cm long × 1.1–4.7 cm wide, ca. (1.0–) 1.5–2.0 (–2.6) times as long as wide, the apex rounded, obtuse, or rarely acute with a blunt tip, the base cuneate to rounded, attenuated into the petiole, the margin pale, incrassate, recurved; venation brochidodromous, forming an arching intramarginal vein ca. 1–3 mm from the margin, the midvein raised adaxially, often with a medial wrinkle along its length when dry, the secondary veins prominulous on both surfaces, 5–7 pairs, at an angle of 55–70° to the midvein, the tertiary veins somewhat less visible; abaxial surface drying chocolate-brown, finely punctate; adaxial surface blackening, the glands obscure except toward the base of the midvein; coriaceous, dull when dry. **Inflorescences** glomerules of few (typically 2–4) flowers or uniflorous, borne on short shoots up to 2.8 mm long, ramiflorous, solitary or 2 superposed, rarely clustered, persistent; bracts rounded to obtuse, subequal to the bracteoles, mostly glabrous, persistent and becoming indurated; pedicels absent or up to 0.6 mm long, stout, puberulous; bracteoles free, persistent and becoming indurated, ovate-triangular or elliptical, 0.4–0.8 mm long × 0.6–1.1 mm wide, the apex rounded to obtuse or acute, the margin ciliate, the abaxial surface glandular. **Flowers** perfect; bud pyriform, the globe of the bud ca. 2.6 mm diam; hypanthium campanulate, 1.0–1.1 mm long, densely glandular; calyx lobes concave, rounded, the outer pair 1.0–2.0 mm long × 1.8–2.8 mm wide, the inner pair 1.4–2.3 mm long × 1.9–2.7 mm wide, the margin scarious, ciliate, the abaxial surface glandular; petals elliptical, 2.1–3.0 mm long × 1.7–2.9 mm wide, white, the apex rounded, the margin ciliate, the abaxial surface glandular; disk circular to squarish, 0.4–0.7 mm wide × 1.6–2.5 mm diam, densely puberulous; stamens ca. 32 in few series, the filament 1.8–4.6 mm long, the anther 0.4–0.8 mm long, the connective with 1 terminal gland and 2–14 smaller glands below; style 3.3–4.9 mm long, bent, tapered to a punctiform apex; ovary glabrous at the apex, bilocular, the placentae arising from near the center of the septum; ovules 8–17 per locule, forming a compact mass. **Fruits** globose, 4–9 mm long × 6–10 mm diam when dry, crowned by the rim of the hypanthium, from which the calyx lobes have commonly torn away, red or purple when ripe, single-seeded, the pericarp thin. **Seeds** ellipsoidal, 6–6.5 mm long × 5–6 mm diam, the hilum a transversely oriented ellipse ca. 1 mm across; seed coat 0.1–0.4 mm thick, yellow-brown and uneven on the exterior, darker with pale streaks and a slightly depressed, marbled dorsal stripe ca. 1 mm wide on the interior; embryo subreniform, with a dark, glandular spot near one end, the cotyledons partially fused, appressed.

Etymology—The varietal epithet refers to the distribution of this plant throughout the "Caribees" (Fig. 3.10).

Habitat and Distribution—Coastal scrub, dry forests, and woodlands up to ca. 250 m, often on rocks. *Eugenia cordata* var. *caribaea* has been recorded from most islands of the Lesser Antilles from Saint-Martin to the Grenadines (Fig. 3.10). A collection by F. Masson (Table 3.4, no. 26) may be a record of this taxon from Nevis.

Phenology—Collected with flowers all months but February and September; with fruits, all but September and December through January.

Common Names—White wattle: Barbuda. Tapwood: Montserrat. Mérizyé, zikak: Guadeloupe and Martinique (Fournet 2002). Mérisier bord de mer: La Désirade and Martinique. Bois créole, bois ti feuilles: Martinique. The common name "zicaque" listed by McVaugh (1989), was found on a specimen from Dominica (*Hodge s.n.*) misidentified as *Chrysobalanus icaco* L.

Extinction Risk—Estimated EOO = 59631.75 km^2 (LC) and AOO = 104 km^2 (EN) from 29 points, 12 of which are located in protected areas. This taxon appears to be relatively common in the Lesser Antilles, and the AOO is probably significantly underestimated. For example, Pratt et al. (2009) listed several localities for *Eugenia cordata* var. *caribaea* on Antigua, and Howard (1952) stated that it is relatively common in woodlands in the Grenadines. Suggested status: LC.

Notes—This variety differs from the preceding in its attenuated leaf base and glabrescent young twigs. The indumentum of the young twigs varies in density and is sometimes barely evident except near the nodes. The trichomes themselves are often ephemeral, the young twigs thus appearing glabrous when mature. In contrast, the young twigs of *Eugenia cordata* var. *cordata* are always puberulous. Leaves vary significantly in the ratio of length to width and the extent to which the leaf base is attenuated into the petiole. Collections with leaves widest at or slightly above the middle that gradually taper toward a relatively elongated petiole closely resemble *Eugenia sintenisii*. At the other extreme are collections in which the leaf base is abruptly attenuated or almost rounded at the base. Since the rounded leaf base is intermediate between cordate and attenuated types, it is difficult to make a clear distinction between the two extremes, but no population with a cordate leaf base in the Lesser Antilles is known apart from on Saint Barthélemy. Relatively few collections from any one island in the region are available to assess variation in leaf form within populations. Nevertheless, the evidently high frequency of plants with a prolonged, attenuated leaf base obviously contrasts with the high frequency of plants with a cordate leaf base in populations from the Virgin Islands. This pattern of variation is consistent with recognition of an infraspecific taxon according to the phylogenetic species concept followed here (Nixon and Wheeler 1990). McVaugh (1989) also mentioned more highly contracted inflorescences as a distinguishing trait, but inflorescence measurements for *Eugenia cordata* var. *caribaea* were almost as long as for those of *E. cordata* var. *cordata*. There is perhaps a greater tendency toward ramiflory in *Eugenia cordata* var. *caribaea*, as inflorescences were not observed in the leaf axils.

In the protologue of *Eugenia sessiliflora* DC., de Candolle (1828) cited a collection by C. G. Bertero from Hispaniola along with three doubtful synonyms: *Myrtus sessiliflora* Sprengel, *Eugenia sessiliflora* Vahl, and “Eugenia laterifolia Pers.” (see Notes under *Eugenia sessiliflora* Vahl). Two branches collected by Bertero, likely distributed together, and mounted onto the same sheet labeled “Myrtus ramiflora DC.” were located at G-DC among undetermined material of *Eugenia* (L. Gautier, pers. comm.). The branch selected as the lectotype, labeled “*Eugenia lateriflora* W” in Bertero’s hand, bears a few flowers on a single inflorescence. The other branch (barcode G00658526, image!) is referable to *Eugenia foetida* Pers. and bears two pedicels. It is labeled as follows: “Eugenia lateriflora Poir., S. Doming., Bertero, M. Balbis 1821.” Thus, de Candolle likely assumed that all of the material on the sheet originated from Hispaniola (Santo Domingo), and although “Eugenia lateriflora Poir.” was not mentioned by Poiret (1813), it is sufficiently similar to “E. laterifolia Pers.” as possibly to have been confused. Since no other specimens at G-DC definitely related to *Eugenia sessiliflora* DC. have been located, it is likely that this sheet constitutes the original material referenced in the protologue. De Candolle’s diagnosis of “floribus subsessilibus” more accurately describes the designated lectotype specimen, and this author described the inflorescences of *Eugenia cordata* and *E. laterifolia* Willd. in similar terms (de Candolle 1828). Otherwise, the description of the leaves and glabrous branches could apply to either specimen. According to his field book, Bertero observed *Eugenia lateriflora* on Guadeloupe (L. Guglielmone, pers. comm.), where both *E. foetida* and *E. cordata* var. *caribaea* occur (Govaerts et al. 2020).

The interpretation of *Eugenia sessiliflora* DC. accepted here was first adopted by Berg (1855–1856), who cited two collections by H. R. Wullschlägel from Antigua (*Wullschlägel 222 & 223*). Grisebach (1859–1864), who considered *Eugenia cordata* to be a form of *Eugenia sessiliflora* DC., also cited Wullschlägel's collections under this name. Similar conclusions were reached by Eggers (1879) and Kiaerskou (1889–1890), the latter author correctly recognizing the priority of *Eugenia cordata* for the species, before Urban (1894–1895) subsumed the name in *Eugenia cordata* var. *sintenisii*. *Eugenia sessiliflora* DC. was applied to a collection of *Eugenia foetida* made by R. de la Sagra (*Sagra s.n.* P [image!]) in Cuba by Richard (1845) and Grisebach (1866). Later, Sauvalle (1869) tentatively placed *Eugenia sessiliflora* sensu Richard under *E. buxifolia* (Sw.) Willd., nom illeg. (=*E. foetida* Pers.).

Additional Specimens Examined—**Antigua and Barbuda.**—ANTIGUA: Five Islands, 10 Jul 1938, (fl), *Box 1503* (A, US × 2); Gracebay, 1849, (fl), *Wullschlägel 223* (M [image]); Gracehill, 1849, (fl), *Wullschlägel 222* (M [image]); The Savannah, 2 Aug 1937, (fl), *Box 939* (US × 2).—BARBUDA: The Highlands, ca. 130 m, 15 May 1937, (fr), *Box 619* (US); Long Grass Savanna, 3 m, 16 Oct 1944, (fl), Beard 378 (A, NY). **Dominica.**—Cabrits, 26 Jun 1982, (fl), *Barrier 3594* (NY); Portsmouth, rocky, wooded slopes of the West Cabrit, 183 m, 27 Jul 1938, (fl), *Hodge 484* (GH); Portsmouth, rocky wooded slopes of the West Cabrit, 183 m, 27 Jul 1938, (fl), *Hodge s.n.* (GH [ex ECON]); West Cabrit, Portsmouth, 183 m, 27 Jul 1938, (fl), *Hodge 582* (NY); along trail on East Cabrit, 25 m, 5 Jun 1977, (fl), *Nicolson 4202* (US). **Guadeloupe.**—BASSE-TERRE: Forêt domaniale de la Basse Terre, Batterie de Deshaies, 28 Jul 1980, (fl), *Barrier 2390* (A, C [image], NY, US); Deshaies, Ancienne batterie en bord de mer, 10 Jun 1982, (fr), *Barrier*

3521 (NY); Forêt domainale de Basse Terre, Batterie de Deshaies, 6 Oct 1982, (fr), *Barrier 3527* (P [image]); Batterie Deshaies, 20 m, 10 Oct 1984, (fl), *Rollet HBR 1689* (A); Vieux Fort, 70–250 m, 29 May 1897, (fl, fr), *Duss 3893* (GH, NY × 2, US); Vieux-Fort, 27 Oct 1935, (st), *Stehlé 374* (P [image]).—LA DÉSIRADE: plage, 20 m, 19 Aug 1945, (fl), *Stehlé & Stehlé 7050* (US × 2). **Martinique.**—Commune des Anses d'Arlet, Cap Salomon, [14.512347°, –61.092817°], 190 m, 30 Jul 2015, (fl, fr), *Delnatte & Rolle 3325* (NY, US); Anses d' Arlet, Grand Anse, pied du Morne Baguidi, 24 Jul 1991, (fl), *Sastre 8940* (A, P [image]); Presqu' île de la Caravelle, commune of Trinite, 5 Aug 1939, (fl), *Egler 39-260* (NY); Presqu' île de la Caravelle, dans la réserve, 23 Jul 1991, (fl), *Sastre 8935* (A); Caravelle, 21 Jan 1968, (fl), *Maurice 29* (P [image]); Caravelle, 21 Oct 1967, (fl), *Maurice 4* (P [image]); Caravelle, 0–50 m, 20 Jul 1945, (fl), *Stehlé & Stehlé 5989* (US × 2); Caravelle, 20 m, 12 Jun 1945, (fl), *Stehlé & Stehlé* 6249 (US); Caravelle, 10 m, 19 Jun 1945, (fl), *Stehlé & Stehlé 6800* (US); Tartane a Caravelle, 15 m, 19 Jun 1945, (fl), *Stehlé & Stehlé 6828* (US); La Demarche, 30 Apr 1968, (fl), *Maurice 71* (P [image]). **Montserrat.**—Center Hills, Pelican Ghaut, along main trail, 21 Nov 2005, (fl), *Greenaway et al. JG20* (K [image]). **Saint Kitts and Nevis.—**SAINT KITTS: along rocky coast between Guana Point and Green Point, 5–25 ft., 27 Dec 1958, (fl), *Proctor 18502* (A, US); Sir Timothy's Hill, near summit, [17.280000°, –62.681667°], 184 m, 12 Aug 2013, (fl, fr), *Carrington 2338* (US); Sir Timothy's Hill, 50–750 ft., 28 Dec 1959, (fl), *Proctor 20498* (A). **Saint Lucia.**—(fl), *Anderson s.n.* (K [image]); Gros Islet, Cas en Bas beach, track at south end, 300 m from beach, [14.083833°, –60.928817°], ca. 5 m, 2 Jul 2006, (fl), *Graveson 2106* (UPRRP); on peninsula west of Vieux Fort, 22 Apr–18 May 1950, (fl, fr), *Howard 11420* (A, NY, UPRRP). **Saint Vincent and the Grenadines.—**

BECQUIA: hills south of Port Elizabeth, 24 Feb–6 Mar 1950, (fr), *Howard 11243* (A); 500–1200 ft., May, (fl), *Joseph B.133* [for Smith] (K [image]); uphill of Port Elizabeth, [13.016633°, –61.237867°], 342 ft., 28 Jul 2007, (st), *Carrington & Sabir SC2194* (US).—CANOUAN: along trail to top of Mt. Royal, 7–25 Mar 1950, (fl), Howard 11080 (A).—MUSTIQUE: Jun, (fl), *Smith G145* (K [image]).—SAINT VINCENT: comm. Sep 1889, (fl), *Smith & Smith 1558* (GH, NY). **Saint-Martin.**—Île Tintamarre, 100 m, 23 Aug 1945, (fl), *Stehlé & Stehlé 7124* (US). **Sint Eustatius.**—Gilboa Hill, 1906, (fl), *Boldingh 1121* (U [image]); near Gilboa Hill, 80 m, 31 Jul 1953, (st), *Stoffers 4029* (U [image]); near Gilboa Hill, 80 m, 31 Jul 1953, (fl), *Stoffers 4030* (A); Northern Mountains, trail to Venus Bay, W slope opposite Mount Gilboa, [17.507833°, –62.985500°], ca. 50 m, 7 May 2012, (fl, fr), *Axelrod et al. 15051* (UPRRP); Northern Mountains, trail to Venus Bay, valley next to Mount Gilboa, [17.496500°, –62.981167°], ca. 50 m, 19 Nov 2013, (fr), *Axelrod et al. 15472* (UPRRP); Northern Mountains, trail to Jenkins Bay, along stream bed, [17.513667°, –62.983000°], ca. 10 m, 19 Nov 2013, (fl, fr), *Axelrod et al. 15489* (UPRRP, US); from Signal Hill to Venus Bay, 1906, (st), *Boldingh 960 B* (U [image]); near White Wall, 1906, (fl, fr), *Boldingh 1266 B* (U [image]).

2. EUGENIA HAEMATOCARPA Alain, Bull. Torrey Bot. Club 90(3): 190. 1963. TYPE:

> PUERTO RICO. Barrio Maizales, Del Valle Tract on the southern side of the Luquillo Mts., 1000 ft. elev., 9 May 1939, (fl, fr), *L.R. Holdridge 37* (lectotype, here designated: NY! [barcode 00084538]; isolectotypes: NY! [barcode 00084537], UPR! [barcode UPR 05731]).

Small tree or shrub up to 6 m, often multi-stemmed, the vegetative growth glabrous except for the axillary buds, the inflorescences and flowers with a short indumentum; bark grayish and lightly fissured, shed in rectangular flakes. **Twigs** yellow- to reddish-brown when young, peeling; older twigs grayish; axillary buds pointed in profile, at or slightly above the leaf axil, pilose or almost glabrous. **Leaves** shortly petiolate; petiole almost plane to concave above, 2–6 mm long × 2–3 mm wide; blade ovate to elliptical, infrequently obovate, 11.2–22.3 cm long × 5–11.1 cm wide, ca. 1.5–2.5 times as long as wide, the apex acute to acuminate with a blunt tip, infrequently rounded, the base cordate to rounded, the margin pale, not thickened, plane; venation conspicuously reticulate, brochidodromous, forming an arching intramarginal vein ca. 3–5 mm from the margin, the midvein raised adaxially, grooved below the middle, becoming plane near the base, the secondary veins prominulous on both surfaces, 8–12 pairs, at an angle of 55–70° to the midvein, the tertiary veins forming a plainly visible composite vein subequaling the secondaries; abaxial surface drying chocolate-brown, finely punctate; adaxial surface blackening, the glands obscure; subcoriaceous, reddish to yellow-green and limp on new growth, becoming dark green and stiffening. **Inflorescences** fascicles of few to many flowers borne on short shoots, cauliflorous, solitary or clustered; peduncle rarely developed, up to 2.5 mm long, puberulous; bracts acute to obtuse or rounded, up to 0.7 mm long, sparsely puberulous, the blackened base persistent; pedicels terete, 1.0–11.8 (–18 in fruit) mm long × 1 mm diam, strigulose-puberulous; bracteoles free, ovate-triangular, 0.6–1.0 mm long × 0.9–1.0 mm wide, the apex acute, the margin ciliate, the abaxial surface glandular, mostly glabrous. **Flowers** perfect; bud pyriform, the globe of the bud 3.7–4.1 mm diam; hypanthium campanulate, 1.4–1.6 mm long, tomentose; calyx lobes concave, rounded, white, the outer pair 1.3–1.6 mm long × 2.7–3.1 mm wide, the inner pair 2.1–4.6 mm long × 3.5–4.4 mm wide, the margin scarious, ciliate, the abaxial surface inconspicuously glandular on the outer lobes, mostly glabrous; petals elliptical to obovate 4.5–7.0 mm long × 3.9–5.7 mm wide, white, the apex rounded, the margin ciliate, the abaxial surface glandular; disk circular, 0.6–1.0 mm wide × 2.6–3.6 mm across, puberulous, especially around the inner margin, the disk itself sparsely so; stamens ca. 100 in multiple series, the filament 6.2–11.7 mm long, the anther 0.6–0.8 mm long, the connective with 1 terminal gland and 1–9 smaller glands below; style 11–13 mm long, bent, tapered to a punctiform apex, glabrous; ovary glabrous at the apex, bilocular, the placentae arising from near the center of the septum; ovules 18–28 per locule, forming a compact mass. **Fruits** globose, 1.8–2.2 cm long × 2.1–2.4 cm diam when dry (2.2–2.6 cm long × 2.3–2.9 cm diam when fresh), crowned by the raised and more or less circular rim of the hypanthium, from which the calyx lobes have commonly torn away, the remnants of these sometimes visible, blood-red when ripe, single-seeded, the pericarp thin, wrinkled when dry, with a brown, papery inner layer adhering to the seed. **Seeds** globose, almost as large as the dried fruits, the hilum expanded around ca. 1/3 the circumference; seed coat 0.5–1.2 mm thick, dull brown around the hilum, otherwise yellow-brown and uneven on the exterior, darker with pale flecks and a depressed, mostly pale dorsal stripe ca. 2 mm wide on the interior; embryo broadly reniform, strongly puckered on the ventral side, with a raised spot visible near one end when dry, the cotyledons apparently completely fused.

Habitat and Distribution—Moist to wet forests from ca. 200–600 m in the Sierra de Luquillo, Sierra de Cayey, and northern karst region of Puerto Rico (Fig. 3.11).

***Phenology*—**Collected with flowers in May and June; with fruits, April through May, August, and December through January.

***Common Name*—**Uvillo: Puerto Rico.

***Extinction Risk*—** Estimated EOO = 1794.89 km^2 (EN) and AOO = 20 km^2 (EN) from 7 points, 5 of which are located in protected areas. This species was assessed as EN D (WCMC 1998) and appears on the U.S. Fish and Wildlife Service's list of endangered species (USFWS 2020). *Eugenia haematocarpa* continues to be threatened by land management activities and stochastic events such as landslides and hurricanes. In total, 1426 individuals are known from 17 localities, eight of which are located in protected areas (USFWS 2019). All these localities are in the three regions shown in Fig. 3.11. Though populations at some sites consist of few individuals, successful recruitment has been observed in two populations (USFWS 2014, USFWS 2019). This species has also been successfully propagated from seed (Santiago-Valentín and Rivera-Martínez 2019). Both AOO and, to a lesser extent, EOO are probably significantly underestimated from specimen data. Further demographic observations could justify transferring this species to a lower risk category in the near future, but a cautious approach is followed here. Suggested status: EN D.

***Notes*—**The whitish sepals are an unusual feature in *Eugenia*. The taste of the fruit was compared to that of *Syzygium jambos* (L.) Alston by Holdridge.

***Additional Specimens Examined*—Puerto Rico.**—15 May 1971, (fl), *Woodbury s.n.* (NY); cult. Arboreto Parque Doña Inés, Fundación Luis Muñoz Marín, Carr. 877, km 0.4, (Mun. San Juan, Bo. Sabana Llana Sur), 18 Jun 2018, (st), *Flickinger et al. 112* (FTG).—CAYEY: Bo. Guavate, Sierra de Cayey, near summit of mogote-like hill (not limestone) 0.4 km due N of Vereda de los Baldíos at W boundary of Carite Forest Reserve, ca. 650 m, 15 May 1992, (fr), *Proctor et al. 47939* (SJ); Bo. Quebrada Arriba, Sierra de Cayey, Área Protegida Natural La Robleda (Para La Naturaleza), N-facing slope along old road, 26 Jun 2018, (fl), *Flickinger et al. 123* (FTG).—ISABELA: Bo. Planas, Pueblito de Ponce, Guajataca Forest Reserve, Trail #2., 269 m, 8 Apr 2009, (fr), *Monsegur 1049* (MAPR); Bo. Planas, Guajataca State Forest, N of trail #2, between trails 1 and 17, 219 m, 22 Jan 2005, (fr), *Trejo & Delgado 2830* (NY).—RÍO GRANDE: El Verde, 2000 ft., Jun 1962, (st), *Woodbury s.n.* (NY); El Verde, 1971, (st), *Woodbury s.n.* (NY); El Verde, 15 May 1976, (st), *Woodbury s.n.* (NY); Sierra de Luquillo, Caribbean National Forest, Road 186, beside a small quebrada midway between Quebrada Grande and junction of Road 956, 11 Dec 1997, (fr), *Proctor et al. 51520* (SJ); along El Verde road west of Río Grande crossing , ca. 1200 ft., 30 Aug 1940, (fr), *Holdridge 221* (NY); Bo. Guzmán Arriba, Sierra de Luquillo, Carr. PR 186, along the bank of a stream, 460 m, 31 Aug 2018, (st), *Santiago-Valentín & Sustache ESV 2018-1* (FTG).

3. EUGENIA PADRONII Alain, Phytologia 61(6): 359. 1986. TYPE: PUERTO RICO. Maricao State Forest, [about 800 m alt.], January 1986, (fl, fr), *A.H. Liogier 35806* [coll. R. Padrón] (holotype: UPR! [barcode UPR 05732]; isotype: NY! [barcode 00084584]).

Tree or shrub up to 15 m, beset with yellow, pustular glands on the new growth, almost glabrous; bark grayish and lightly fissured. **Twigs** yellow-brown when young, becoming smooth and pallid; older twigs gray; axillary buds flattened against the twig in the leaf axil, glabrous except for the cilia of the bud scales. **Leaves** petiolate; petiole concave above, 4–8 mm long × 1–1.5 mm wide; blade ovate, elliptical, or obovate 2.7–11.9 cm long × (0.5–) 1.2–3.8 cm wide, varying from ca. 2–4 times as long as wide on reproductive individuals to as much as ca. 12 times as long as wide on seedlings, the apex rounded, the base acute, the margin pale, incrassate, recurved; venation brochidodromous, forming an arching intramarginal vein ca. 1–3 mm from the margin, the midvein more or less plane, slightly grooved toward the base adaxially, the secondary veins slightly raised or obscure adaxially, prominulous abaxially, 7–10 pairs, at an angle of 35–65° to the midvein, the tertiary veins scarcely visible; abaxial surface drying brown, a few glands sometimes visible, especially toward the base; adaxial surface drying darker with age, the glands obscure; coriaceous, reddish on new growth, dull, slightly fragrant. **Inflorescences** fascicles or glomerules of few (typically 2–6 [–10]) flowers, mostly ramiflorous, occasionally in leaf axils, apparently solitary; bracts rudimentary; pedicels absent or 1–2.5 mm long × 0.4–0.7 mm wide, tetragonal, yellow-brown; bracteoles free, ovate-triangular or elliptical, 0.5–0.8 mm long × 0.8–1.0 mm wide, the apex rounded or obtuse to acute, the base often asymmetrical, the margin ciliate, the abaxial surface glandular. **Flowers** perfect; bud n.v.; hypanthium campanulate, 1.6–2.0 mm long, beset with yellow pustular glands; calyx lobes concave, rounded, the outer pair 1.0–1.4 mm long × 2.0–2.8 mm wide, the inner pair 1.2–2.1 mm long × 2.5–3.4 mm wide, the margin scarious, ciliate, the abaxial surface densely glandular; petals elliptical, 3.2–3.9 mm long × 3.2–3.4 mm wide, white, the apex rounded, the margin ciliate, the abaxial surface glandular; disk circular to squarish, 0.5–0.6 mm wide × 2.5–3.2 mm across, puberulous; stamens ca. 60 in few series, the filament 2.0–4.8 mm long, the anther 0.4–0.6 mm long, the connective with 1 terminal gland and 0–3 smaller glands below; style 4.5–7.5 mm long, bent, tapered to a punctiform apex; ovary, glabrous at the apex, bilocular, the locule walls and septum with yellow, pustular glands, the placentae arising from near the center of the septum; ovules 23–49 per locule, forming a compact mass.

Fruits globose, 7–8 mm long × 6–6.5 mm diam, crowned by the erect, persistent calyx lobes, red or black when ripe, 1–2-seeded, the pericarp fleshy, with yellow, pustular glands within. **Seeds** ellipsoidal to reniform or flattened on one side in 2-seeded fruits, 5.5–6 mm long × 5 mm diam (4 mm diam in flattened seed), the hilum a transversely oriented ellipse ca. 2 mm across; seed coat 0.1–0.4 mm thick, yellow-brown and uneven on the exterior, darker with pale streaks and a thin, translucent dorsal stripe on the interior; embryo subreniform, with a dark glandular spot near one end, the cotyledons apparently completely fused or partially fused and appressed.

Habitat and Distribution—Moist to wet forests from ca. 100–800 m over limestone or serpentine. *Eugenia padronii* is restricted to western Puerto Rico in and around Maricao, Susúa, Guajataca, and Río Abajo Commonwealth Forests (Fig. 3.11).

***Phenology*—**Collected with flowers in January through March, June, and October through November; with fruits, January, March, and November.

***Extinction Risk*—**Estimated EOO = 763.84 km^2 (EN) and AOO = 32 km^2 (EN) from 17 points, 15 of which are located in protected areas. Although this species has been collected from a limited number of areas, the populations present in Maricao and Susúa Commonwealth Forests appear to be healthy and successfully reproducing. Suggested status: LC.

***Notes*—**The leaves of this species are thick yet flexible. Their marked change in dimensions occurs gradually as the plant matures. Another notable feature is the prominent, yellow glands that occur even within the walls of the locules.

Additional Specimens Examined—**Puerto Rico.**—Maricao State Forest, 800 m, 27 Dec 1963, (st), *Liogier 10457* (MAPR, US); Maricao State Forest, 800 m, 30 Mar

1964, (st), *Liogier 10770* (US); Maricao State Forest, 800 m, 15 Mar 1994, (fl), *Liogier 37227* [Padrón] (FTG); Maricao State Forest, 700 m, 26 Jun 1963, (st), *Liogier 9708* (NY, US); Maricao State Forest, Jul 1961, (st), *González Más* 1920 (MAPR); Maricao, on route 120, km. 16.6, 800 m, Oct 1988, (fl), *Liogier 36623* (NY); Monte del Estado, 10 Jun 1970, (fl), *Woodbury s.n.* (NY, UPR, US); Monte del Estado Forest, near top, 20 Jun 1970, (fl), *Woodbury 20401* (NY); Monte del Estado, 18 millas al surest de Mayagüez, ambos lados carretera 120, km 16 hm 9, [18.155556°, –66.993056°], 700 m, 6 May 1990, (st), *Caminero & García 160* (MAPR); Río Abajo Forest, 400 m, 27 Sep 1985, (st), *Liogier 35679* (UPR); Susúa Forest, 8 Dec 1966, (st), *Woodbury s.n.* (FTG, NY, US); Susúa Forest Reserve, 19 Oct 2000, (fl), *Vilmond s.n.* (MAPR, UPRRP).—ARECIBO: Bo. Río Arriba, area to N of temporary S end of new Rt. 10, on top of mogote, [18.335333°, –66.676333°], ca. 375 m, 18 Oct 1995, (st), *Axelrod 9284* (UPRRP); Bo. Río Arriba, area to NW of temporary S end of new Rt. 10 (near Rt. 621), along trail among mogotes, [18.335333°, –66.675833°], ca. 325 m, 18 Jan 1996, (st), *Axelrod & Acevedo 9604* (UPRRP); [Bo. Río Arriba], Río Abajo Forest Reserve, [18.335000°, –66.679722°], 340 m, 18 Jan 1996, (st), *Acevedo-Rodríguez & Axelrod 7787* (US).—ISABELA: Guajataca forest, 23 Jan 1966, (st), *Woodbury s.n.* (NY); Guajataca Forest Reserve, Trail 2, N side, just passing intersections with trail 3, coming from trail 1, 18 Mar 1999, (st), *Trejo-Torres et al. 1311* (UPRRP); Guajataca State Forest, PR 2 due PR 446, 6 Nov 2001, (st), *Sustache & Dávila 692* (SJ); Bo. Planas, Pueblito de Ponce, Guajataca Forest Reserve, at the end of trail #2, to the western boundary of the forest, [18.421667°, –66.978889°], 250 m, 11 Jun 2009, (st), *Monsegur 1033* (MAPR).—MARICAO: Bo. Maricao Afuera, Bosque Estatal de Maricao (Maricao Commonwealth Forest), trail to hightest point of Alto del

Descanso from PR 120, 9 Mar 2019, (fr), *Monsegur 1685* (FTG); Bo. Maricao Afuera, Bosque Estatal de Maricao, on NE-facing slope above the SW side of Hwy. 120 at km 17.0, [18.159722°, –66.998611°], 730 m, 31 May 1991, (st), *Caminero et al. 470* [W-22] (MAPR); Bo. Maricao Afuera, Río Maricao drainage, on slope behind radio antennas N of Hwy. 120 km 15.8, [18.156944°, –66.990278°], 800 m, 3 Feb 1995, (st), *Cedeño & Velez 428* (MAPR); Bo. Maricao Afuera, Río Maricao drainage, N of Hwy. 120, km 14.8, [18.150556°, –66.982778°], 850 m, 23 Sep 1996, (st), *Cedeño et al. 1036* (MAPR).—QUEBRADILLAS: Guajataca, Road 119 at km 16.4, limestone hill (mogote) accessed from private property, 18.40529°N, 66.9044°W, 406 m, 20 Feb 2017, (st), *Flickinger et al. 83* (FTG).—SABANA GRANDE: Maricao State Forest, inside Centro Recreativo Cabanas del Monte del Estado by cabin C-8, 18.1417°N, 66.974783°W, 868 m, 14 Feb 2017, (st), *Flickinger & Santiago-Valentín 70* (FTG).—SAN GERMÁN: Maricao State Forest, vicinity of Campamento Buena Vista, above Casa Piedra, ca. 800 m, 12 Jun 1986, (st), *Proctor & Padrón 41817* (SJ); Bo. Hoconuco Alto, Maricao Forest Reserve, 50 × 25 m seed bank plot adjacent to dirt road that is off of route 120 at km 16.8, [18.156111°, –66.998889°], 675 m, 23 Jun 1999, (st), *Delgado 8* (MAPR).—YAUCO: Susúa State Forest, along Quebrada Peces above road crossing, 190–200 m, 3 Jul 1990, (st), *Proctor & Köhler 46434* (SJ); Bo. Collores, Susúa Commonwealth Forest, Quebrada Grande, on steep W-facing slope just above high-water bench along river, [18.075722°, –66.896028°], 150 m, 7 Feb 1995, (fl), *Breckon et al. 4526* (SJ, UPRRP); Bo. Susúa Alta, Bosque Estatal de Susúa, aproximadamente 1.5 km norte de la oficina del bosque, siguiendo una carretera paralela a Río Loco, entre el primer y el segundo cruce que la carretera da al río, en el lado norte de la carretera, [18.091667°, –66.908333°], 150–200 m, 30 Oct 1990, (fl), *García 3279* (MAPR, UPRRP); Bo. Susúa Alta, Bosque Estatal de Susúa, aproximadamente 2 km norte de la oficina del bosque, entre el segundo y el tercer cruce de la carretera sobre Río Loco, en dirreción noroeste, en las márgenes de una quebrada, 170 m, 17 Nov 1990, (fl, fr), *García & Vázquez 3321* (MAPR, UPRRP); Bo. Susúa Alta, Susúa Forest Reserve, along Río Loco, down from old forest road from W border of Reserve, 175 m, 27 Mar 1997, (fr*)*, *Axelrod et al. 10186* (UPRRP); Bo. Susúa Alta, Bosque Estatal de Susúa, trail along Río Loco, near first river crossing heading N from facilities, 18.070548°N, 66.905921°W, 107 m, 24 Jun 2018, (st), *Flickinger & Santiago-Valentín 118* (FTG).

4. EUGENIA SESSILIFLORA VAHL, Symb. Bot. 3: 64. 1794, non *E. sessiliflora* DC., Prodr. 3: 273. 1828, nom. illeg. *Eugenia lateriflora* Willd., Sp. Pl., ed. 4, 2(2): 961. 1799, nom. superfl. *Myrtus sessiliflora* (Vahl) Spreng., Syst. Veg. 2: 479. 1825. TYPE: U.S. VIRGIN ISLANDS. [Saint Croix], (fr), *H. West s.n.* (lectotype, here designated: C [barcode C10015727, image!]; possible isolectotypes: B-W [barcode B -W 09504 -01 0 image!], C [barcode C10015728, image!], G [barcode G00223976, image!], G-DC [barcode G00658409 image!], HAL [barcode HAL0089625, image!], S [no. S 07-9894, image!]).

Shrub or small tree up to 5 m, often multi-stemmed, the vegetative growth glabrous except for the axillary buds, the inflorescences and flowers with a short indumentum; bark pale gray, lightly fissured. **Twigs** yellow-brown when young; older twigs grayish; axillary buds rounded in the leaf axil, puberulous. **Leaves** petiolate; petiole almost plane to concave above, 2–7 mm long × 1–2.5 mm wide; blade ovate, elliptical, obovate, or orbicular, 2.8–13.2 cm long x 1.7–8.5 cm wide, ca. 1–1.5 (–2) times as long as wide, the apex acute to obtuse with a blunt tip, rounded, or occasionally emarginate, the base acute to rounded, the margin strongly recurved; venation conspicuously reticulate, brochidodromous, forming an arching intramarginal vein ca. 2 mm from the margin, the midvein raised adaxially, grooved toward the base, the secondary veins prominulous on both surfaces, 6–8 pairs, at an angle of 50–70° to the midvein, the tertiary veins forming a plainly visible composite vein subequaling the secondaries; abaxial surface drying coppery brown, finely and densely punctate; adaxial surface drying darker, sometimes grayish, the glands impressed and inconspicuous except toward the base; thickly and rigidly coriaceous, yellow on new growth, lustrous, pungently fragrant. **Inflorescences** glomerules of few (typically 2–4) flowers or uniflorous, with an axis of up to 4 mm long sometimes developed, ramiflorous, rarely in leaf axils, solitary or 2 superposed; bracts acute to obtuse or rounded, subequal to the bracteoles, mostly glabrous or pubescent; pedicels absent or up to 0.8 mm long, stout, yellow-brown, sparingly pubescent; bracteoles free, hardened near the center, ovate-triangular, ca. 0.5–2.0 mm long × 1.6–2.4 mm wide, the apex acute to obtuse or rounded, the margin ciliate, the abaxial surface mostly glabrous. **Flowers** perfect; bud obovoid to pyriform, the globe of the bud ca. 4.9–6.9 mm diam; hypanthium obconical to campanulate, 2.5–3.7 mm long, even or costate when dry, glandular, tomentose; calyx lobes concave, rounded, resembling the hypanthium in color or reddish brown, the outer pair 1.8–3.8 mm long × 3.5–5.3 mm wide, the inner pair 3.8–5.0 mm long × 4.6–7.0 mm wide, the margin scarious, ciliate, the abaxial surface glandular, mostly glabrous; petals elliptical to oblong or obovate, 4.8–8.8 mm long × 3.0–6.0 mm wide, white or reddish, the apex rounded, the margin ciliate, the abaxial surface glandular; disk circular, 1.0–2.0 mm wide × ca. 5.6–6.7

mm across, inclined inward, densely puberulous; stamens ca. 200 in multiple series, the filament 1.9–8.8 mm long, the anther 0.6–1.0 mm long, the connective with 1 large terminal gland and 0–7 smaller glands below; style 7.5–9.4 mm long, bent, tapered to a punctiform apex, sparsely pilose, the hairs ascending, ca. 0.4 mm long; ovary tomentose at the apex, bilocular, the placentae arising from near the center of the septum; ovules 15–44 per locule, forming a compact mass. **Fruits** globose, 1.3–3.4 cm long × 1.5–3.2 cm diam when dry, the calyx lobes persistent or torn away, red when ripe, single-seeded, the pericarp relatively thick (ca. 1–3.5 mm when dry), with a brown, papery inner layer adhering to the seed, fragrant. **Seeds** ellipsoidal, 1.6–2.5 cm long × 1.2–2.2 cm diam, the hilum expanded around ca. 1/4–1/2 the circumference; seed coat hard, 0.3–1.6 mm thick, yellow-brown and rugose on the exterior, darker with pale flecks and a slightly depressed, streaked dorsal stripe ca. 4–5 mm wide on the interior; embryo reniform, sometimes hollow, with a dark glandular spot near one end, the cotyledons partially fused, appressed.

Habitat and Distribution—Coastal scrub, dry forests, and other exposed sites up to ca. 850 m, often on rocky slopes. *Eugenia sessiliflora* is distributed from Puerto Rico through the Virgin Islands. On Puerto Rico, it occurs in the southwest, northeast, and Sierra de Cayey (Fig. 3.11). This species occurs over serpentine at Peñones de Melones.

Phenology**—**Collected with flowers in March through December; with fruits, March through November.

Extinction Risk**—** Estimated EOO = 14327.68 km^2 (VU) and AOO = 108 km^2 (EN) from 38 points, 17 of which are located in protected areas. This species was recently assessed as NT B1ab(iii,v), with threats including development, fires, invasive species, and climate change (Bárrios and Hamilton 2018). The range estimates of Bárrios and Hamilton (2018), including reports of *Eugenia sessiliflora* from Jost van Dyke, Great Camanoe, Great Dog, and Beef Island in the British Virgin Islands, were slightly smaller for EOO and ca. 55% larger for AOO. The assessment of these authors is adopted here: NT B1ab(iii,v).

Notes—Leaves and fruits of this species possess a strong, pleasant aroma. The relatively large, lustrous leaves, and smooth, gray bark are further attractive features. Reddish flowers have been observed on collections from Cerro Mariquita in the Sierra Bermeja. The minimum leaf dimensions were measured on a collection from Tetas de Cayey at the upper elevational limit for the species (*ESV 2019-4*). Despite its widespread occurrence, *Eugenia sessiliflora* seems not to have been collected on Puerto Rico before 1954 (*Little 16426*).

The protologue of *Eugenia sessiliflora* (Vahl 1794) only cites material from Saint Croix collected by H. West. The specimens cited above as possible isolectotypes all have some indication of having originated directly or indirectly from Vahl's herbarium or of having been collected by West. They are probably best regarded as syntypes, since it is uncertain whether they all belong to the same gathering. West also collected on other islands within the range of *Eugenia sessiliflora* (Urban 1902).

"Eugenia sessiflora," as it appeared in *Bidrag til Beskrivelse over Ste Croix* by West (1793), is a nomen nudum and therefore not validly published. *Eugenia lateriflora* is a superfluous name with the same type as *E. sessiliflora* because Willdenow (1805) cited Vahl's (1794) exact diagnosis for *E. sessiliflora* after his own without indicating a different type (Turland et al. 2018). Willdenow's diagnosis was in turn repeated verbatim by Persoon (1806–1807) under the name "Eugenia laterifolia" without any additional description. "Eugenia laterifolia Pers." is therefore here regarded as a correctable typographical error (Turland et al. 2018) rather than a nomenclatural novelty. The designation "Eugenia venosa"—non Lam., Encycl. 3: 200. 1789—was proposed by L. C. Richard on an herbarium specimen label but never validly published. Similarly, Bisse annotated the possible isolectotype specimen of *Eugenia sessiliflora* at HAL as "Pseudanamomis lateriflora" in 1984. This designation did not appear in his posthumous publication on *Pseudanamomis* (Bisse 1985), in which *Eugenia sessiliflora* Vahl was listed as a synonym of *Pseudanamomis cordata*. The intended synonym may have been *Eugenia sessiliflora* DC.

The nomenclature of *Eugenia sessiliflora* has been a source of confusion for various authors. De Candolle (1828) seems to have been uncertain of the correct application of *Eugenia sessiliflora* Vahl, which he listed as a tentative synonym of both *E. lateriflora* and *E. sessiliflora* DC. In the case of *Eugenia lateriflora*, which he used in the correct sense for *E. sessiliflora* Vahl, the uncertainty was stated to be because of Vahl's (1794) description of the leaves as oblong as opposed to de Candolle's own description for *E. lateriflora* of "foliis obovato-subrotundis." De Candolle's usage of "oblong" and related terms for leaf shape were discussed by Ricket (1954). In fact, the leaves of the referenced specimen at G-DC are almost orbicular. Grisebach (1859–1864, 1860–1862, 1866) misapplied *Eugenia lateriflora* to *E. foetida*, citing collections by J. Macfadyen and W. T. March (*March 1683* & *1684*, K [images!]) from Jamaica and F. Rugel (*Rugel 602*, K, L [images!]) and C. Wright (*Wright 1613*, K, P [images!]) from

Cuba. According to Urban (1894–1895) and Britton and Millspaugh (1920), *Eugenia lateriflora* was used in the same sense by Gardiner and Brace (1890) in a provisional list of the flora of the Bahamas. Eggers (1876, 1879), followed by Millspaugh (1902), misapplied *Eugenia lateriflora* to *E. cordata* in their studies of the flora of the Virgin Islands.

Additional Specimens Examined—**British Virgin Islands.**—TORTOLA: 4 May 1919, (fl), *Fishlock 408* (K [image]); Hog Valley Point, 4 May 1919, (fl), *Fishlock 406* (NY × 2); Rogue Bay Point, forested area, 18.4537°N, 64.6034°W, 20–30 m, 11 July 2013, (fl), *Hamilton MAH 1136* (K [image]); Two Ghut, forested area, 18.3941°N, 64.6636°W, 118 m, 16 Jul 2013, (fl), *Hamilton MAH 1170* (K [image]).—VIRGIN GORDA: 1969, (fl), *Woodbury s.n.* (UPR); Biras Hill, 18.4982°N, 64.3518°W, 10–50 m, 10 Jul 2012, (st), *Hamilton MH 891* (K [image]); Deep Bay, drainage 1/2 mile E, 5 ft., 18 Mar 1972, (fl, fr), *Little 26150* (NY, US). **Puerto Rico.—**CABO ROJO: Bo. Boquerón, summit of Peñones de Melones, ca. 100 m, 27 Aug 2002, (fl), *Axelrod et al. 12222* (MAPR, UPRRP); Bo. Boquerón, westernmost hill of Peñones de Melones, [17.994806°, –67.209167°], 10–60 m, 29 Aug 1996, (fl), *Breckon & Cedeño 4865* (MAPR, UPRRP); Bo. Boquerón, N slope of Punta Melones, [17.991667°, –67.207333°], 20–45 m, 4 Jun 1994, (st), *Axelrod & Thomas 7836* (NY, UPRRP); Bo. Llanos Costa, Sierra Bermeja al NE del Cerro Mariquita, [18.002222°, –67.110000°], 290–300 m, 22 Oct 1994, (fl, fr), *Cabezudo 6* (MAPR); Bo. Llanos Costa, Sierra Bermeja, NE side of Cerro Mariquita, [18.002222°, –67.110000°], 290–300 m, 7 May 1994, (st), *Breckon 4447* (MAPR); Bo. Llanos Costa, Sierra Bermeja, NE side of Cerro Mariquita, [18.002222°, –67.110000°], 280–300 m, 5 Oct 1993, (st), *Breckon & Rice 4311* (MAPR); Bo. Llanos Costa, Sierra

Bermeja, upper slopes and summit of Cerro Mariquita, 250–301 m, 20 Sep 1987, (fl), *Proctor et al. 43952* (SJ); Bo. Llanos Costa, Sierra Bermeja, upper slopes and summit of Cerro Mariquita, 250–301 m, 11 Oct 1987, (fl, fr), *Proctor & McKenzie 44017* (FTG, SJ, US); [Bo. Llanos Costa], Sierra Bermeja, upper slopes and summit of Cerro Mariquita, 225–300 m, 5 Jul 1992, (fr), *Axelrod & Chavez 4805* (UPRRP); [Bo. Llanos Costa], Sierra Bermeja, upper slopes and summit of Cerro Mariquita, ca. 225–300 m, 21 Dec 1991, (fl), *Axelrod et al. 3415* (MAPR, NY, UPRRP); [Bo. Llanos Costa], Sierra Bermeja, Cerro Mariquita, on slope, 16 Aug 1992, (st), *Liogier 37016* (UPR); Bo. Llanos Costa, Sierra Bermeja, Cerro Mariquita, [18.002167°, –67.111278°], 301 m, 19 Sep 1996, (fl), *Breckon 4872* (MAPR, UPRRP); [Bo. Llanos Costa], Sierra Bermeja, Cerro Maraquita, 12 Mar 1989, (st), *Liogier 36844* [coll. Vives] (UPR); Bo. Llanos Costa, N slopes of Cerro Mariquita, [18.002833°, –67.112450°], 902 ft. (275 m), 14 Aug 2001, (fr), *Salywon et al. 1268* (UPRRP); Bo. Llanos Costa, ridge on N slope of Cerro Mariquita from farm, [18.003500°, –67.113833°], ca. 250 m, 7 Apr 2003, (fl), *Axelrod et al. 12489* (UPRRP); Bo. Llanos Costa, summit and E ridge of Cerro Mariquita, 225–300 m31 May 1993, (fr), *Axelrod & Sastre 6238* (UPRRP).—COAMO: NE of Coamo, Rd. 150, Apr 1969, (fr), *Woodbury s.n.* (NY × 2, UPR); Bo. Cuyón, along road 14 at km 45, in forest on steep hillside above road, [18.097500°, –66.308611°], 220 m, 17 Feb 2000, (st), *Breckon & Vélez 6017* (MAPR); Bo. Cuyón, Las Piedras Chiquitas, N slope, E end, [18.067833°, –66.268000°], ca. 450 m, 21 Jul 1995, (fl), *Axelrod & Santiago* 9137 (UPRRP); [Bo. Cuyón], Las Piedras Chiquitas, on slopes, 600 m, 16 Dec 1986, (st), *Liogier & Proctor 36192* (UPR).—CULEBRA: Culebra Complex, 14 Jun 1969, (st), *Woodbury et al. s.n.* (UPR, US); Flamenco, Victor Gonzales Property, close to the helipad, boundary with Culebra NWR, [18.331944°, –65.308056°], 99 m, 6 May 2009, (fr), *Monsegur & Pacheco 1070* (MAPR); Playa Flamenco, quebrada pedregosa seca, al extremo E de la playa, [18.329583°, –65.312717°], 15 m, 4 Aug 2005, (st), *Trejo et al. 3029* (UPR); Monte Resaca, 15 Feb 2003, (st), *Puente s.n.* (SJ); colina entre Playa Resaca y Pta. Flamenco, ladera bajando a Playa Resaca, ca. 50 m, 20 Sep 1997, (fl), *Trejo & Aragón 1070* (UPRRP).—FAJARDO: Cabeza Chiquita, ca. 0 m, 28 Nov 1979, (fl), *Liogier et al. 30090* (NY, US); Cabeza de San Juan, NE end of Puerto Rico, 25 ft., 6 Aug 1954, (fl), *Little 16426* (NY, UPR, US); Las Croabas, 8 Aug 1963, (fl, fr), *Woodbury s.n.* (UPR × 2); Las Croabas, May 1962, (fl), *Woodbury s.n.* (UPR); Las Croabas, 7 Apr 1963, (st), *Woodbury 6013* (NY, UPR × 3, US).—LAJAS: Bo. Llanos, S-facing slope near top of hill, Finca Maria Luisa, Sierra Bermeja, 17.997884°N, 67.099367°W, 195 m, 25 Jun 2018, (st), *Flickinger et al. 120* (FTG).—RÍO GRANDE: Bo. Zarzal, 0.9 km NNW of Cerro Bravo, ca. 0 m, 28 Dec 1986, (st), *Proctor 42770* (SJ).—SALINAS: top of Cerro Cariblanco, 18 May 1967, (st), *Woodbury s.n.* (UPR); Bo. Lapa, Las Piedras Chiquitas, along ridge of peaks, 500–550 m, 17 Jan 1993, (st), *Axelrod & Sastre 5610* (UPRRP); Bo. Lapa, Las Tetas de Cayey, upper slope and summit of W peak, on brink of high cliff, 830–840 m, 30 May 1988, (st), *Proctor & Díaz 44767* (SJ); Bo. Lapa, Tetas de Cayey (W peak), S-facing side, growing on the upper border of the cliffs, approximately 25 m below the peak, 18.09299°N, 66.23105°W, 854 m, 26 Jan 2019, (st), *Santiago-Valentín & Sustache ESV 2019-4* (FTG).—VIEQUES: Cerro Pirata, summit ridge, 5 Jun 1978, (st), *Fosberg 57645* (US); Mt. Pirata, 22 Jun 1966, (st), *Woodbury & Martorell V-60* (UPR); Monte Pirata, 200 m, 10 Sep 2005, (fr), *Ackerman 3870* [UPR Plant Taxonomy class] (UPRRP); Monte Pirata, ESE summit ridge, [18.095500°, –65.551500°], ca. 280 m, 8 Jun

2006, (fr), *Axelrod et al. 13570* (MAPR, UPRRP); Monte Pirata, ladera empinada, al sur de la antena, 5 Jun 2005, (fl), *Trejo 2979* (SJ, UPR); Monte Pirata, N slope, in forest bordering telephone lines, 31 Jul 1992, (fl), *Axelrod et al. 5079* (UPRRP); upper slope of Monte Pirata, 200–300 m, 22 Sep 1983, (st), *Proctor et al. 39546* (SJ); National Wildlife Refuge, W tract, ridge ESE of summit of Monte Pirata, [18.095111°, –65.550556°], 280–290 ±14.5 m, 18 Nov 2007, (fr), *Breckon & Franz 8465* (MAPR); USFWS Refuge in western Vieques, steep ENE-facing slope of Monte Pirata below summit, [18.093056°, –65.550278°], 275 m, 23 Oct 2002, (fl, fr), *Breckon et al. 6717* (MAPR, NY); Bo. Puerto Diablo, E tract of Vieques NWR, Puerto Negro, 18.15658°N, 65.364969°W, 19 m, 21 Jun 2018, (fl), *Flickinger et al. 115* (FTG); Bo. Punta Arenas, Monte Pirata, at SE of the heliport, following the trail behind the antenna fence at the ridge of the mountain, [18.092778°, –65.549722°], 253 m, 16 Jan 2003, (st), *Caraballo Ortiz & Vives 367* (MAPR, UPR). **U.S. Virgin Islands.**—SAINT CROIX: (fl), *Liebmann s.n.* (C [image]); Christianssted, 1870, *Eggers s.n.* (C [image]); ved Christianssted, Aug 1874, (fl), *Eggers s.n.* (C [image]); . . . til Elizas Retreat, 12 Nov 1871, (fl), *Eggers s.n.* (C [image]).—SAINT JOHN: Bordeaux Mt., 27 May 1982, (st), *Woodbury 106* (UPR); Concordia, 60 m, 24 Jun 1989, (fl), *Acevedo-Rodríguez & Chinea 2763* (NY, US); East End Quarter, easternmost part of island, east of Southside Pond, 100 m, 19 Aug 1987, (fl), *Acevedo-Rodríguez et al. 1830* (NY, US); Long Bay, 18.335841°N, 64.674883°W, 22.5 m, 26 May 2017, (st), *Gibney s.n.* (FTG).—SAINT THOMAS: 70 m, 7 Jul 1985, (fl), *Grifo & Matuszak 41* (NY); Cowells Batteri, 18 Oct 1874, *Eggers s.n.* (C [image]); H . . . Island, in bay SE of St. Thomas, middle of island, ca. 4 m, 27 Jul 1967, (fr), *Byer & Mercado*

67-2115 (UPRRP); Water Island, 17 Jun 1971, (st), *Woodbury s.n.* (NY, UPR, US); Water Island, NE, 25 m, 24 Jul 1967, (st), *Mercado et al. 67-1523* (UPRRP).

5. EUGENIA SINTENISII Kiaersk., Bot. Tidsskr. 17(4): 263, t. 7c, fig. 3. 1890, non *E. sintenisii* (Kiaersk.) Krug & Urb., Bot. Jahrb. Syst. 19(5): 650. 1895, nom. illeg. *Eugenia cordata* var. *sintenisii* (Kiaersk.) Krug & Urb., Bot. Jahrb. Syst. 19(5): 656. 1895. TYPE: PUERTO RICO. Prope Cayey ad rivulum Morillos, 25 October 1885, (fl), *P.E.E. Sintenis 2101* (lectotype designated by McVaugh, Fl. Lesser Antilles 5: 486. 1989: C [barcode C10022802, image!]; isolectotypes: GH [barcode 00069181, image!], K [barcode 000775623, image!], LD × 2 [nos. 1804834, 1804770, images!], US! [barcode 00594642]).

Small tree or shrub up to 10 m, glabrous except near the axillary buds; bark gray to brown, lightly fissured. **Twigs** yellow-brown when young; older twigs with a gray periderm, flaking off to reveal a layer with reddish brown patches; axillary buds flattened against the twig, 2 or 3 superposed, forming a distally bulging group ca. 1–1.5 mm long, puberulous, with minute hairs scattered across surrounding surfaces of the proximal ends of the internodes, especially within the grooves on either side of the compressed young growth, and the adaxial surface of young petioles. **Leaves** petiolate; petiole almost plane to concave above, 2–5.5 mm long × 1–1.5 mm wide; blade elliptical to obovate, 1.8–6.6 cm long × 1.0–3.9 cm wide, ca. 1.5–2 (–2.8) times as long as wide, the apex rounded to obtuse, the base cuneate to almost rounded and abruptly attenuate, the margin pale, slightly thickened, recurved; venation brochidodromous, forming an arching intramarginal vein ca. 1 mm from the margin, the midvein raised adaxially, often with a medial wrinkle along its length when dry, the secondary veins prominulous on both surfaces, 6–9 pairs, at an angle of 50–70° to the midvein, the tertiary veins forming a composite vein distinctly subordinate to the secondaries, mostly obscure; abaxial surface chocolate-brown when dry, finely punctate, the glands inconspicuous; adaxial surface blackening, the glands obscure; subcoriaceous, dull when dry. **Inflorescences** glomerules of up to 6 flowers, mostly ramiflorous, occasionally in leaf axils; bracts rounded or acute to obtuse, ca. 0.75 mm (ex descr.), sometimes rudimentary; pedicels absent; bracteoles free, ovate 0.3–0.5 mm long × 0.5–0.7 mm wide, the apex rounded or emarginate, the margin ciliate, the abaxial surface glandular. **Flowers** perfect; bud n.v.; hypanthium 0.5–0.8 mm long, glandular; calyx lobes concave, rounded, ca. 0.8 mm long × 1.6 mm wide, the margin scarious, ciliate, the abaxial surface glandular; petals (ex descr. et fig.) broadly elliptical, ca. 2 mm long, the apex rounded, the abaxial surface glandular; disk squarish, 0.4–0.5 mm wide × 0.9–1.4 mm across, puberulous; stamens (ex descr.) numerous, ca. 3 mm long; style (ex descr. et fig.) ca. 5–7 mm long, bent, tapered to a punctiform apex; ovary glabrous at the apex, bilocular, the placentae arising from near the center of the septum; ovules 13–14 per locule, forming a compact mass. **Fruits** globose, 2–4 mm long × 5–7 mm diam when dry, crowned by the persistent calyx lobes, these sometimes tearing away, red when ripe, single-seeded, the pericarp thin. **Seeds** ellipsoidal to ovoid, 5–6 mm long × 4 mm diam, the hilum a transversely oriented ellipse ca. 1.0 mm across; seed coat 0.1–0.2 mm thick, yellow-brown and smoothish on the exterior, darker with pale streaks and a thin translucent dorsal stripe on the interior; embryo ellipsoidal or ovoid, with a dark glandular spot near one end, the cotyledons partially fused, appressed.

Habitat and Distribution—Moist to wet forests from ca. 200–800 m. *Eugenia sintenisii* is found in the Sierra de Cayey, the western end of the Cordillera Central, and the northern karst regions of Puerto Rico (Fig. 3.12). This species occurs over serpentine in Susúa Commonwealth Forest.

Phenology**—**Collected with flowers in February, June, and October; with fruits, April through June.

Common Name— Murta: Puerto Rico (Urban 1894–1895).

Extinction Risk**—**Estimated EOO = 2797.85 km^2 (EN) and AOO = 56 km^2 (EN) from 15 points, nine of which are located in protected areas. This species is infrequently collected and does not seem to be common in the areas in which it occurs. It has not recently been recollected at the western end of its range at Monte Montoso, where it was found at the top within a remnant patch of forest (Britton 1915). Towards the eastern edge of its range in the Sierra de Cayey, it has not recently been recollected at the type locality near Cayey or near Aibonito. Loss of populations at these sites would reduce AOO by ca. 20% and the number of locations to 10. Evidence for a continuing decline would qualify this taxon for the VU rating. Suggested status: NT B1ab(ii,iv)+B2ab(ii,iv).

Notes**—**Leaves of this species are typically obovate with a rounded apex and always noticeably attenuated into the petiole and dull when dry. The tertiary and composite veins are usually only weakly visible on the leaf surfaces. In contrast to *Eugenia stewardsonii*, the tertiary veins do not form a coarse reticulum, and the higher order veinlets are inconspicuous (Fig. 3.1A). Britton and Wilson (1925) described the calyx lobes of *Eugenia sintenisii* as ca. 1 mm long, while the larger pair of calyx lobes of *E. stewardsonii* was described as ca. 2 mm long. It is uncertain whether the calyx lobes are in fact generally shorter in *Eugenia sintenisii* because of the scarcity and poor quality of the available flowering material of this species.

Eugenia sintenisii and *E. cordata* var. *sintenisii* have frequently been circumscribed to include the Lesser Antillean taxon that is here recognized as *E. cordata* var. *caribaea*.

Additional Specimens Examined—**Puerto Rico.**—Sosúa [Susúa], Feb 1995, (st), *Liogier 37386* [Francis] (UPR).—AIBONITO: Bo. Pasto, 25 Nov 1885, (st), *Sintenis 2867* (C [image], L [image]).—ARECIBO: Domingito [Dominguito], 15 May 1912, (fr), *Cowles 294* (NY); Bo. Dominguito, Mata de Plátano Natural Reserve, southeast boundary with El Tallonal Private Reserve, S of [18.410033°, –66.726750°], 184 m, 3 Oct 2003, (st), *Trejo-Torres & Marcano 2420* (UPR); Bo. Miraflores, Sector Biáfara, Finca Dentón, entering Road 637, between Roads 656 and 638, about 1 km S, through a private paved road lower mogote slope, [18.399650°, –66.663450°], 167 m, 28 Nov 2003, (st), *Trejo et al. 2479* (GH, SJ, UPR).—CAMUY: Piedra Gorda, [18.4176063°, –66.8790158°], 24 Sep 2003, (st), *Carlo et al. 66* (UPR).—CAYEY: prope Cayey, 13 Oct 1885, (st), *Sintenis 2221* (C [image]); Bo. Cercadillo, Sector Cielito, Road 7737, 26 Jul 1981, (st), *Salgado s.n.* (SJ); Bo. Matón Arriba, Cuevas de Doña Vina, entrance at Road 1 km 62.3, down the slope, ca. [18.101917°, –66.194467°], 534 m, 7 Oct 2004, (st), *Trejo et al. 2802* (UPR); Bo. Pasto Viejo, Tetas de Doña Juana, 500 m, 21 Oct 1981, (st), *Liogier et al. 32545* (UPR); Bo. Quebrada Arriba, Sierra de Cayey, Área Protegida Natural La Robleda (Para La Naturaleza), along old road, 18.088843°N, 66.150841°W, 26 Jun 2018, (st), *Flickinger et al. 122* (FTG).—MARICAO: Monte Montoso, 13 Feb 1915, (fl), *Britton & Cowell 4121* (NY, UPR, US).—QUEBRADILLAS: Bo. Charcas, W slope and summit of mogote "Cerro Papito", 0.7 km due SSE of Charcas Village, 230–320 m, 23 Jun 1994, (fl, fr), *Proctor et al. 49395* (FTG, SJ).—SALINAS: near Las Tetas [de Cayey], 600 m, 14 Mar 1979, (st), *Liogier et al. 28451* (UPR); [Tetas de Cayey], between E and W Peaks, 700 m, 14 Mar 1979, (st), *Liogier et al. 28443* (UPR); Bo. Lapa, Tetas de Cayey (W peak), forest area along the NW edge of the forest, close (5 m) to open pasture area, 18.09358°N, 66.23143°W, 838 m, 26 Jan 2019, (st), *Santiago-Valentín & Sustache ESV 2019-1* (FTG).—VEGA BAJA: [18.42114242°, –66.3854493°], 29 Aug 2002, (st), *Carlo et al. 154* (UPR).—YAUCO: Bo. Susúa Alta, Bosque Estatal de Susúa, aproximadamente 100 m al sureste del último cruce de la carretera que va dentro del bosque siguiendo las márgenes de Río Loco en dirección noroeste, 180 m, 6 Apr 1991, (fr), *García & Román 3449* (MAPR, UPR, UPRRP).

6. EUGENIA STEWARDSONII Britton, Bull. Torrey Bot. Club 51(1): 11. 1924. TYPE: PUERTO RICO. Monte Torecilla, mountain summit, 900–1100 m alt., 19–20 March 1915, (fr), *N.L. Britton, J.F. Cowell, and S. Brown 5603* (lectotype, here designated: NY! [barcode 00099321]; isolectotypes: UPR! [barcode UPR 05735], US! [barcode 00737068]).

Eugenia cordata var. *ovata* Kiaersk., Bot. Tidsskr. 17(4): 258. 1890. TYPE: PUERTO RICO. Prope Adjuntas in sylvis primaevis montium Cerrote, 27 May 1886, (st), *P.E.E. Sintenis 4416* (lectotype, here designated: C [barcode C10022803, image!]; isolectotypes: K [barcode K000775621, image!], L [no. L.2507695, image!], P [barcode P05239150, image!]).

Small tree or shrub up to 8 m, glabrous except near the axillary buds; bark gray, fissured. **Twigs** yellow-brown when young; older twigs with a gray periderm, flaking off to reveal a layer with reddish brown patches; axillary buds flattened against the twig, 2 or 3 superposed, forming a distally bulging group ca. 1–1.5 mm long, puberulous, with minute hairs scattered across surrounding surfaces of the proximal ends of the internodes, especially within the grooves on either side of the compressed young growth, and the adaxial surface of young petioles. **Leaves** subsessile or shortly petiolate; petiole up to 3 (–5) mm long × 1–1.5 mm wide; blade ovate to elliptical, rarely obovate, 2.0–6.9 (–8.1) cm × 1.3–5.4 cm wide, ca. 1.5–2 (–3.8) times as long as wide, the apex obtuse to acute with a blunt tip or rounded, the base subcordate, varying from rounded with a slight pucker at the junction with the petiole to having well-developed basal lobes (rarely cuneate), the margin pale, slightly thickened, recurved; venation brochidodromous, forming an arching intramarginal vein ca. 2 mm from the margin, the midvein raised adaxially, often with a medial wrinkle along its length when dry, the secondary veins prominulous on both surfaces, ca. 8–9 (–12) pairs, at an angle of 55–70° to the midvein, the tertiary veins forming a plainly visible composite vein subequaling the secondaries, a coarse reticulum evident; abaxial surface drying chocolate-brown, finely punctate, the glands inconspicuous; adaxial surface blackening, often supporting epiphylls, the glands obscure; subcoriaceous, frequently lustrous when dry, pungently fragrant. **Inflorescences** glomerules of few to many flowers, mostly ramiflorous, occasionally in leaf axils, apparently solitary; bracts rounded, up to 0.6 mm long; pedicels absent or up to 0.3 mm long (0.5 mm in fruit), stout, yellow-brown, puberulent; bracteoles free, elliptical, 0.4–0.8 mm long × 0.9–1.3 mm wide, the apex rounded or emarginate, the margin ciliate, the abaxial surface glandular. **Flowers** perfect; bud pyriform, the globe of the bud ca. 2.3 mm diam; hypanthium campanulate, 0.9–1.0 mm long, glandular; calyx lobes concave, rounded or emarginate, the outer pair 0.7–1.1 mm long × 1.2–1.4 mm wide, the inner pair 1.0–1.9 mm long × 1.4–1.8 mm wide, the margin scarious, ciliate, the abaxial surface glandular; petals elliptical, 2.3–2.6 mm long × 2.2–2.6 mm wide, white, the apex rounded, the margin ciliate, the abaxial surface glandular; disk circular to squarish, 0.3–0.5 mm wide × 1.1–1.6 mm across, puberulous; stamens ca. 48–64, in few series, tardily deciduous, the filament 2.6–6.3 mm long, the anther globose, 0.4–0.5 mm long, the connective with 1 terminal gland and 0–4 smaller glands below; style 5.0–6.0 (–8.6) mm long, bent, tapered to a punctiform apex; ovary glabrous at the apex, bilocular, the placentae arising from near the center of the septum; ovules 16–27 per locule, forming a compact mass. **Fruits** globose, rarely constricted about the axis and bilobed, 3–7.5 mm long × 6–9.5 mm diam, crowned by the persistent calyx lobes, these sometimes tearing away, red when ripe, 1–3 (–4?)-seeded, the pericarp thin. **Seeds** reniform or flattened on one or more sides in multi-seeded fruits, 6–9 mm long × 5 mm diameter, the hilum a transversely oriented ellipse ca. 1.0 mm across; seed coat 0.1–0.3 mm thick, gray-brown and smoothish on the exterior, dark brown with pale streaks and a thin, translucent dorsal stripe on the interior; embryo reniform, with a dark glandular spot near one end, the cotyledons apparently completely fused or partially fused and appressed.

Habitat and Distribution—Wet forests, mostly above ca. 900 m. *Eugenia stewardsonii* is distributed across the Cordillera Central of Puerto Rico (Fig. 3.12). It occurs at lower elevations down to ca. 500 m at the western end of its range in Maricao Commonwealth Forest, where it occurs over serpentine, and ca. 600 m at the eastern edge of its range in Carite Commonwealth Forest.

Phenology—Collected with flowers in April and December through February; with fruits, February through June.

Extinction Risk—Estimated EOO = 660.34 km^2 (EN) and AOO = 48 km^2 (EN) from 17 points, 10 of which are located in protected areas. This species appears to be common at the sites where it occurs. *Eugenia stewardsonii* may be especially vulnerable to the effects of climate change, as most populations grow near the tops of the highest mountains on the island. Suggested status: LC.

Notes— Leaves of this species are typically ovate with an obtuse apex, cordate base, and very short petiole. The leaf base may be cordate, rounded, or even obtuse on specimens from Maricao Commonwealth Forest. The leaves are usually quite lustrous when dry; however, some intrapopulation variation was noted in this character at Monte Guilarte (*Axelrod et al. 11370* & *11371*), and the leaf surfaces are frequently obscured by epiphylls. The composite veins are clearly visible and sometimes almost as strong as the secondary veins. Judging from the cleared leaves (Fig. 3.1B), the difference in the visibility of these veins between *Eugenia sintenisii* and *E. stewardsonii* is probably more related to characteristics of the mesophyll than to the veins themselves, but the tertiary and higher order veins form a noticeably coarser reticulum that is evident on the leaf surfaces. This character is the most reliable way to tell *Eugenia sintenisii* and *E. stewardsonii* apart and allows for the diagnosis of two distinct phylogentic species. It probably reflects a small difference in the ecological niche of these two taxa.

A few collections made by R. O. Woodbury from Carite Commonwealth Forest are unusual in having more narrowly elliptical leaves, mostly obtuse or acute at the base, with a well-developed petiole. The dimensions of these leaves are given in parentheses in the above description. Otherwise, these specimens are typical of *Eugenia stewardsonii*, and one of the Carite specimens (*Woodbury s.n.*, Jan 1976) bears a cordate leaf towards the base of the twig. The collection from Guavate (*Woodbury s.n.*, 27 Apr 1962) is the most extreme in its departure from the typical leaf form, for which reason it was initially identified as *Eugenia sintenisii*. One of the duplicates at SJ specifies "east of communication towers." This suggests that the collection was made at a relatively high elevation of ca. 900 m, where *Eugenia stewardsonii* is commonly found. The other duplicate at SJ consists of two twigs that differ in whether the leaf base is predominantly acute or obtuse to rounded. The unusual variation in leaf form observed in these collections from Carite could be explained by phenotypic plasticity (non-heritable variation), character transformation (Davis and Nixon 1992), hybridization with the similar *Eugenia sintensii*, or ancestral polymorphism (Nixon and Wheeler 1990); however, neither hybridization nor phenotypic plasticity alone are likely explanations given that *Eugenia sintenisii* has not been collected in this area and similar variation has not been observed in other populations. Further genetic investigation would be useful for selecting among these possibilities.

Sintenis 4416 was chosen over *Sintenis 4319* as the lectotype because no specimen of the former was located at C. This taxon was assigned to "Eugenia cordata var. genuina" by Urban (1894–1895).

Additional Specimens Examined**—Puerto Rico.**—Carite, Sep, (st), *Woodbury s.n.* (NY); Carite, Jan 1976, (st), *Woodbury s.n.* (NY); Toro Negro, Cerro de Punta, 1300 m, 21 Jul 1962, (st), *Liogier 9524* (NY, MAPR); between Cerro Punta and Cerro Maravilla, 1000 m, 23 May 1984, (st), *Liogier & Martorell* (NY); Guavate, E of communication towers, 27 Apr 1962, (fl, fr), *Woodbury s.n.* (NY, SJ × 2); Guilarte Forest, 950 m, 16 Jan 1980, (fl), *Liogier et al. 30259* (NY, US); Maricao, 1961, (st), *González Más* (MAPR); Maricao forest, Jul 1961, (st), *González Más 1907* (MAPR); Maricao State Forest, 600–800 m, 2 Jul 1962, (st), *Liogier 9335* (MAPR, NY); Toro Negro, carretera 143 al sur del mirador, 31 Dec 1982, (fl), *Acevedo 14* (SJ).—ADJUNTAS: prope Adjuntas in sylva primaeva montis Cienega, 16 May 1886, (fr), *Sintenis 4319* (L [image], NY, US); near Pico Guilarte, 1000 m, 16 Jul 1963, (st), *Liogier 10007* (GH, MAPR, NY, US); Bo. Guilarte, Monte Guilarte Forest Reserve, trail up Monte Guilarte, ca. 1100 m, 11 Jan 2001, (fl), *Axelrod et al. 11370* (UPRRP); Bo. Guilarte, Monte Guilarte Forest Reserve, trail up Monte Guilarte, ca. 1100 m, 11 Jan 2001, (st), *Axelrod et al. 11371* (UPRRP); Bo. Guilarte, Monte Guilarte Forest Reserve, trail to summit of Monte Guilarte, 1050–1200 m, 28 Mar 2001, (fr), *Axelrod & Montalvo 11601* (MAPR, UPRRP, US); [Bo. Guilarte], Monte Guilarte, SW of Adjuntas in the Cordillera Central, ca. 1000 m, 15 Jun 1975, (fr), *Judd 532* (A); Bo. Limaní, Guilarte Commonwealth Forest, Cerro La Silla de Calderon, NW to SW facing slopes along old dirt road near summit, [18.156667°, –66.808056°], 1050–1100 m, 16 Feb 1991, (fl), *Breckon et al. 3810* [J4] (MAPR); Bo. Limaní, near summit of La Silla de Calderón, ca. 1150 m, 8 Feb 2001, (fl), *Axelrod et al. 11449* (MAPR, UPRRP, US); [Bo. Limaní], La Silla de Calderon, Trail 2, 18.152966°N, 66.80685°W, 1093 m, 15 Feb 2017, (fl, fr), *Flickinger et al. 78* (FTG); [Bo. Limaní], La Silla de Calderon, Trail 2, 18.153266°N, 66.808266°W, 1096 m, 15 Feb 2017, (st), *Flickinger et al. 76* (FTG); Bo. Limaní, Flanks and summit of peak due N of La Silla de Calderón, [18.160500°, –66.808389°], 1060 m, 5 Feb 1998, (st), *Breckon et al. 5555* (MAPR).—BARRANQUITAS: La Torrecilla, Oct 1974, (st), *Woodbury s.n.* (NY);

La Torrecilla, (st), *Woodbury s.n.* (NY); Bo. Barrancas, upper NE slope and summit of Monte La Torrecilla, 920–950 m, 28 Jan 1988, (fl), *Proctor & Thomas 44445* (SJ).—JAYUYA: Cordillera Central, vicinity of Monte Jayuya, N side of Road 143, km 18.7, 1230–1240 m, 26 Aug 1983, (st), *Proctor 39442* (SJ).—MARICAO: Bo. Maricao Afuera, Bosque Estatal de Maricao, on the N side of Hwy. 120 at km 14.0, across from the Observation Tower, [18.145833°, –66.980556°], 850 m, 15 May 1991, (st), *Caminero et al. 429* [M-19] (MAPR); Bo. Maricao Afuera, Río Maricao margins, 480 m, 27 Jan 1995, (fl), *Cedeño & Acosta 422* (MAPR); Bo. Maricau Afuera, Río Maricao margins, [18.161111°, –66.988056°], 500 m, 5 Feb 1994, (fl), *Cedeño & Cabezudo 231* (MAPR, NY, SJ, UPRRP).—OROCOVIS: en el km 26.7 de la Carretera 149, [18.158333°, –66.516667°], 900 m, 25 Feb 1989, (fr), *Zanoni et al. 42114* (MAPR).—PATILLAS: Bo. Muñoz Rivera, Carite Forest Reserve, ca. 0.5–1 km up river flowing into Charco Azul, [18.091667°, –66.021667°], ca. 625 m, 1 Dec 2006, (st), *Axelrod et al. 13712* (UPRRP).—PEÑUELAS: Bo. Rucio, Cordillera Central, Cerro Garrote and ridge north, 970–1020 m, 28 Mar 1987, (fr), *Proctor & Haneke* 43237 (SJ, US).

7. EUGENIA STIRPIFLORA (O.Berg) Krug & Urb., Bot. Jahrb. Syst. 19(5): 672. 1895.

Myrciaria stirpiflora O.Berg, Linnaea 30(6): 702. 1861. TYPE: U.S. VIRGIN ISLANDS. In sylvis montanis St. Joannis, (st), *L.C. Richard s.n.* (lectotype [or perhaps holotype] designated by McVaugh, Fl. Lesser Antilles 5: 486. 1989: P [barcode P05257505, image!]).

Eugenia earhartii Acev.-Rodr., Brittonia 45(2): 133, fig. 2. 1993. TYPE: U.S. VIRGIN ISLANDS. St. John, Reef Bay Quarter, White Cliffs area, 55 m elev., 26 August

1987, (fl), *P. Acevedo-Rodríguez, A. Reilly, and J. Earhart 2030* (holotype: US! [barcode 00406265], isotype: NY [barcode 00038820, image!]).

Shrub or small tree up to 8 m, almost glabrous; bark light brown or grayish, shed in irregular flakes. **Twigs** yellow-brown when young (reddish when fresh), becoming darker; older twigs grayish, stubby; axillary buds minute bulges in the leaf axils, glabrous except for the cilia of the bud scales. **Leaves** sessile; blade ovate to elliptical, 2.7–8.3 cm long × 1.7–6.4 cm, ca. 1–3 times as long as wide, the apex rounded or acute to obtuse with a blunt tip, the base subcordate, the margin strongly recurved; venation brochidodromous, forming an arching intramarginal vein ca. 5 mm from the margin, the midvein raised adaxially, convex or grooved towards the base, the secondary veins prominulous above, more so below, 6–8 pairs, at an angle of 50–70° to the midvein, the tertiary veins scarcely visible above, obscure below; abaxial surface drying brownish, wrinkled admedially and along the midvein towards the base, finely punctate, the glands inconspicuous and sometimes very sparse; adaxial surface drying darker, with a few inconspicuous glands towards the base of the midvein; stiffly and thickly coriaceous, lustrous, yellow-green on new growth. **Inflorescences** fascicles of many flowers borne on short shoots, cauliflorous, clustered in tight knots; bracts acute, subequal to the bracteoles; pedicels terete, 5–15 mm long × 0.5–1.0 mm in diameter, persistent; bracteoles free or confluent at the base, ovate, 0.9–1.0 mm long × 0.8–1.0 mm wide when dry, the apex obtuse, the margin ciliate, the abaxial surface glandular. **Flowers** perfect bud pyriform, the globe of the bud ca. 4–5 mm diam (ex fig.); hypanthium campanulate, ca. 3.0 mm long when dry, glandular; calyx lobes concave, rounded, 3–4 mm long (ex descr.), the margin scarious, ciliate, the abaxial surface glandular; petals n.v.; disk circular, 1.4–1.8 mm wide × 5.1–5.5 mm across when dry, densely puberulous; stamens n.v.; style ca. 10 mm long when dry, bent, tapered to a punctiform apex; ovary n.v. **Fruits** globose, 2 cm long × 2–3 cm diam when dry, purple or red when ripe, single-seeded, the pericarp thin. **Seeds** globose, almost as large as the dried fruits, the hilum a transversely oriented ellipse ca. 8.5–14 mm across, ca. 1/8–1/4 the circumference; seed coat hard, 3 mm thick, yellow-brown and uneven on the exterior, somewhat smoother and dark brown with a slightly depressed, marbled dorsal stripe ca. 1–2 mm wide on the interior also visible externally; embryo slightly reniform, strongly wrinkled on the outer surface when dry, the cotyledons apparently completely fused.

Habitat and Distribution—Rocky, coastal scrub from ca. 30–200 m. *Eugenia stirpiflora* is restricted to Saint John, where it occurs on Minna Hill and between Europa Bay and White Cliffs (Fig. 4.12).

Phenology**—**Collected with flowers in August; with fruits, January. Acevedo-Rodríguez (1993) cited an additional flowering specimen (*Woodbury 523*) collected in October, and L. C. Richard reported flowers in April and May and fruits in June (Berg 1861).

Extinction Risk**—**Estimated EOO = 8 km^2 (CR) and AOO = 8 km^2 (CR) from 2 points, two of which are located in protected areas. This species is known from two populations, the one on Minna Hill consisting of only a few individuals (Acevedo-Rodríguez 1993). Both populations are protected within Virgin Islands National Park. Monitoring of these populations is urgently needed to assess their viability. Seed predation, though commonly observed in *Eugenia*, is a potential concern, as half of the examined fruits showed evidence of insect damage. Seed predation by insect larvae, especially Coleoptera, may be one of the main factors affecting reproductive success in *Eugenia* (Silva and Pinheiro 2009). Hurricanes could also have potentially devastating effects on this species. Suggested status: VU D2.

***Notes*—**Both Urban (1894–1895) and Acevedo-Rodríguez (1993) directly compared this species to *Eugenia cordata* and *E. sessiliflora.* The label of the type specimen for *Eugenia stirpiflora* describes the flowers and fruits, but these are not present on the specimen. According to L. C. Richard's description, the fruits are sweet.

The designation "Eugenia trunciflora"—non *E. trunciflora* (Schltdl. & Cham.) G.Don, Gen. Hist. 2: 867. 1832, nec *E. trunciflora* Ridl., Fl. Malay Penins. 1: 724. 1922, nom. illeg.—was proposed by L. C. Richard on the label of the type specimen but not validly published.

***Additional Specimens Examined*—U.S. Virgin Islands.**—SAINT JOHN: eastern side of Minna Hill, 13 January 1990, (fr), *Acevedo-Rodríguez & Aleman 3204* (ASU [image], US); Virgin Islands National Park, Minna Hill, 191.7 m, 28 May 2017, (st), *Gibney s.n.* (U.S. National Park Service, VIIS); Reef Bay Quarter, along trail to White Cliffs, 60 m, 1 Jan 1991, (fr), *Acevedo-Rodríguez 5233* (US); Virgin Islands National Park, Europa Bay/White Cliffs, 28 m, 10 May 2017, (st), *Gibney s.n.* (U.S. National Park Service, VIIS).

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Tables

Table 3.1. PCR primers and amplification conditions used in this study.

Region	**Primers**	**Reference**	**Conditions**
ITS	17SE 26SE	Sun et al. 1994	94° C, 2 min.; (94° C, 1 min.; 52° C, 1 min.; 72° C, 1 min.) × 30
ETS	Myrt (F) ETS-18S	Lucas et al. 2007; Wright et al. 2001	94° C, 4 min.; (94° C, 1 min.; 50° C, 1 min.; 72° C, 1 min.) × 30
MeNu79	MeNu79 F MeNu79 R	Pillon et al. 2014	94° C, 2 min.; (94° C, 1 min.; 63° C, 1 min.; 72° C, 1 min.) × 38; 72° C, 5 min.
psbA-trnH	trn H (GUG) psb A	Hamilton 1999	94° C, 4 min.; (94° C, 1 min.; 48° C, 1 min.; 72° C, 2 min. 30 s) × 30
ndhF-rpl32	ndhF (*Eucalyptus*) rpl32-R (*Eucalyptus*)	Shaw et al. 2014	80° C, 5 min.; (94° C, 1 min.; 50° C, 1 min.; 72° C, 2 min.) × 35; 72° C, 5 min.

Table 3.2. List of species of *Eugenia* from the Greater and Lesser Antilles outside of the Lathberry Clade that have glomerate or fasciculate inflorescences predominantly borne below the leaves on old wood. An asterisk indicates taxonomic doubt. See discussion for further information.

Species	**Distribution**
Eugenia brunescens Urb.	Cuba
Eugenia catingiflora Griseb.	Cuba
Eugenia cupuligera Urb.*	Cuba
Eugenia jambosoides Griseb.	Cuba
Eugenia laeteviridis Urb.	Cuba
Eugenia amplifolia Urb.	Jamaica
Eugenia crassicaulis Proctor	Jamaica
Eugenia lamprophylla Urb.	Jamaica
Eugenia marchiana Griseb.	Jamaica
Eugenia websteri Proctor	Jamaica
Eugenia duchassaingiana O.Berg	Lesser Antilles
Eugenia dussii Krug & Urb.	Lesser Antilles plus Trinidad and Tobago
Eugenia hodgei McVaugh	Lesser Antilles
Eugenia lambertiana DC.	Lesser Antilles to South America
Eugenia stictopetala DC.* (=*E. tapacumensis* O.Berg)	Lesser Antilles to South America

Table 3.3. Summary of DNA alignments, including total length, percentage of variable positions, number of parsimony-informative characters (PIC's), models of sequence evolution chosen by the corrected Akaike information criterion (AICc) for maximum likelihood analysis of separate and combined nuclear regions, and models of sequence evolution chosen by the Bayesian information criterion (BIC) for *BEAST species tree analysis.

Region	**Aligned Length**	**Percent Variable/ Number PIC's**	**AICc Model (Separate)**	**AICc Model (Combined)**[1]	**BIC Model**
ITS	790	5.2% / 31	HKY+I	TRN+I	K80+I
ETS	523	8.6% / 32	TRN+I	TIM+I	K80+I
MeNu79[2]	789	5.4% (8.5%) / 23 (28)	TRN+G	TRN+I	HKY+G
cpDNA[3]	1525	1.8% / 12	TVM	n/a	n/a

[1] Each region was a separate partition.

[2] Figures in parentheses and the model selected by the BIC apply to the alignment of allelic sequences.

[3] Gap coding resulted in the addition of 2 more parsimony informative characters.

Table 3.4. Examined images of herbarium specimens for which the collector, island of occurrence, or determination was uncertain. Each sheet with one or more specimens is a single row entry. Rows are numbered (No.) and sorted by taxon as determined here and then current herbarium (Hb.). Numbering of multiple specimens mounted on a single sheet follows the markings on sheets. The text of original labels is transcribed, with semi-colons separating individual labels. Ellipses indicate symbols, illegible writing, or other content specified in brackets. Notes on collectors are from Urban (1902) unless otherwise indicated.

No.	**Taxon**	**Hb.**	**Historic Hb.**	**Label Text and Phenology**	**Notes**
1	*Eugenia cordata* var. *cordata*	B-W	n/a	on folder: 9555; Polyandria Monogynia, Myrtus cordata . . . [diagnosis] Swartz prod. 78., Habitat in India occidentali . . . ; on sheet: Vahl. W., M. cordata, 1. (fl)	Barcode B -W 09555 -01 0.
2	*Eugenia cordata* var. *cordata*	C	Hornemann	Myrt. cordata Sw. ex Ind. occid.—Sw. (fl)	n/a
3	*Eugenia cordata* var. *cordata*	C	1/3: M. Vahl 3/3: Liebmann	1/3: Myrtus cordata West (fl, fr); 2/3: h: in Ste. Cruce, L, Eugenia, Myrtus ramiflorus (fl, fr); 3/3: Myrtus? ex Ind. occid. (fl)	F. M. Liebmann collected on St. Croix and possibly Puerto Rico 1841; Cuba, 1843.
4	*Eugenia cordata* var. *cordata*	C	N. Hofman Bang	Myrtaceae Eugenia cordata; Myrtus cordata, ex India occidentali, . . . Lund (fl)	n/a
5	*Eugenia cordata* var. *cordata*	C	Schumacher	Eugenia, Ind. occid., D Benzon (fl)	P. E. Benzon collected on St. Croix, St. John, and St. Thomas 1817–1848.
6	*Eugenia cordata* var. *cordata*	C	1/4: M. Vahl 2/4: M. Vahl 3/4: Liebmann 4/4: M. Vahl	1/4: *Pflug s.n.* (St. Croix, see text); 2/4: cordata, Dedit Dr West (fl); 3/4: Eugenia ramiflora (fr); 4/4: Myrtus cordata (fl)	Pflug collected on St. Croix at the end of the 18th century. Liebmann (see #3).

No.	**Taxon**	**Hb.**	**Historic Hb.**	**Label Text and Phenology**	**Notes**
7	*Eugenia cordata* var. *cordata*	C	N. Hofman Bang	Myrtus cordata . . . Doni Vahl (fl)	n/a
8	*Eugenia cordata* var. *cordata*	C	1/2: Schumacher 2/2: Schumacher	1/2: Myrtus cordata . . . h. in S. Cruce (fl); 2/2: *Ryan s.n.* (St. Croix, see text)	J. Ryan collected on St. Croix, St. John, and Montserrat during the second half of the 18th century. Brother collected on Trinidad.
9	*Eugenia cordata* var. *cordata*	C	1/2: Liebmann 2/2: Liebmann	1/2: Myrtus cordata, Eugenia sessiliflora, ex Ind. occid. (fl); 2/2: Myrtus cordata Sw., ramiflora, Ind. occid. (fl)	Liebmann (see #3).
10	*Eugenia cordata* var. *cordata*	C	S. Drejer	Ind. occid. W., Dr Ravn, Myrtus cordata (fl)	P. Ravn collected on St. Croix, St. John, St. Thomas, and Vieques 1819–1839.
11	*Eugenia cordata* var. *cordata*	C	M. Vahl	Dr West (fl)	n/a
12	*Eugenia cordata* var. *cordata*	C	Schumacher	Eugenia sessiliflora, Myrtus cordata . . . (fl)	n/a
13	*Eugenia cordata* var. *cordata*	C	Schumacher	Eugenia sessiliflora, Myrtus cordata, Ryan Lam . . . (fl)	Ryan (see #8).
15	*Eugenia cordata* var. *cordata*	C	n/a	1/2: Myrtus cordata, ex Antillis . . . (fl); 2/2: ded. Ryan, Eugenia sessiliflora (fl)	Ryan (see #8).
16	*Eugenia cordata* var. *cordata*	G-DC	Puerari	Eugenia ramiflora (fl)	Barcode G00658524.
17	*Eugenia cordata* var. *cordata*	L	n/a	No. 18, Eggers Fl. Ind. Occ. Exsicc. Ser. 2, Myrtac.; 18. Eugenia lateriflora W. (fl)	No. L.2508325.

No.	Taxon	Hb.	Historic Hb.	Label Text and Phenology	Notes
18	*Eugenia cordata* var. *cordata*	M	Schreber	Myrtus cordata Swartz; No. 13 Eugenia; Eugenia? cordata Dc., St. Lucia? St. Thomas? Crudy? (fl)	Crudy collected in the Bahamas and on St. Thomas and St. Lucia before 1810. Barcode M-0137708.
19	*Eugenia cordata* var. *cordata*	MA	n/a	Myrtus cordata Swartzii, 2088; Plantae Novae Hispaniae. a Sessé, Mociño, Castillo et Maldonado lectae (1787–1795–1804). Eugenia cordata (Sw.) DC., No. 2088 (st)	Probably collected by H. West as evinced by handwriting. Could also have been collected by Sessé & Mociño on Puerto Rico 1796–1797 (Blanco and Puig-Samper 2003). Barcode MA 603224; Chicago Natural History Museum Negative No. 47166.
20	*Eugenia cordata* var. *cordata*	P	Antoine Laurent de Jussieu	Myrtus cordata Sw., Ste. Croix. antillis, dedit . . . Vahl 1799 (fl)	No. P00678225.
21	*Eugenia cordata* var. *cordata*	P	A. N. Desvaux	Eugenia cordata . . . [citations], Myrtus— . . . [citations], habitat in Antillis. (fl)	Barcode P05238849.
22	*Eugenia cordata* var. *cordata*	P	Poiret, Moquin-Tandon, E. Cosson	Myrt. cordata Sw. (fl)	Barcode P05238855. On sheet with *Myrciaria cordata* O.Berg.
23	*Eugenia cordata* var. *cordata*	S	n/a	No. S08-855: Eugenia cordata, Sw. scripsit; Eugenia cordata DeCand., Myrtus cordata Swartz., Ind. Occid.: Swartz (fl); No. S13-23361: Eugenia sessiliflora DC. var. (fl)	n/a
24	*Eugenia cordata* var. *cordata*	S	n/a	Myrtus cordata Sw.; dedit. Hornemann (fl)	No. S08-856

No.	Taxon	Hb.	Historic Hb.	Label Text and Phenology	Notes
25	*Eugenia cordata* var. *caribaea* ?	C	1/2: M. Vahl 2/2: M. Vahl	1/2: Myrtus lateralis (Plinia), ded. Dr . . . (fl) 2/2: Plinia, ded. Dr . . . [same as 1/2] (fl, fr)	Tentatively annotated as *Eugenia cordata* var. *sintensii* by Urban.
26	*Eugenia cordata* var. *caribaea* ?	LINN	n/a	Myrtus ramiflora, Nevis rupibus, Masson (fl)	F. Masson collected in the Lesser Antilles and Jamaica 1779–1781.
27	*Eugenia sessiliflora*	C	1/2: Hornemann 2/2: Hornemann	1/2: habeo sub nom. Eugen. foetida (fl); 2/2: Eugenia sessiliflora Vahl, St. Croix (fl)	n/a
28	*Eugenia sessiliflora*	C	n/a	In monte . . . ?, 5/47, Leg. Oersted (st)	A. S. Oersted collected on St. Croix, St. Thomas, and Jamaica and in the Lesser Antilles 1845–1846.
29	*Eugenia sessiliflora*	P	L. Cl. Richard, (Guyanensi-Antillanum)	No. 29. Eugenia venosa . . . [description], Euge. lateriflora? Vahl. Symb., non Myrtus cotynifolio . . . frequens in sylvalis montosis Ste. Crucis et St. Joannis (st)	Barcode P05238180.
30	*Eugenia sessiliflora*	P	L. Cl. Richard (Guyanensi-Antillanum)	29. Eugenia venosa (fl)	Barcode P05238182.

Figures

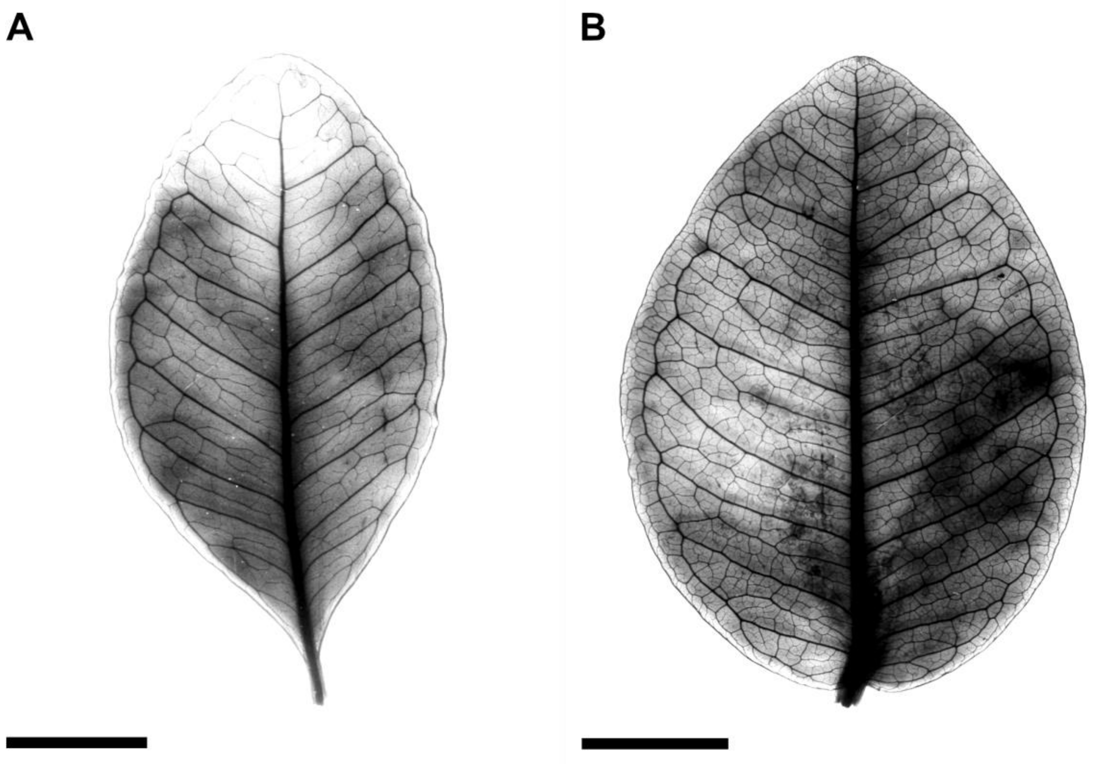

Figure 3.1. Scans of cleared leaves showing pattern of venation in the Lathberry Clade. **A.** *Eugenia sintenisii, Flickinger et al. 122* (FTG). **B.** *E. stewardsonii, Flickinger et al. 76* (FTG). Scale bars = 1 cm.

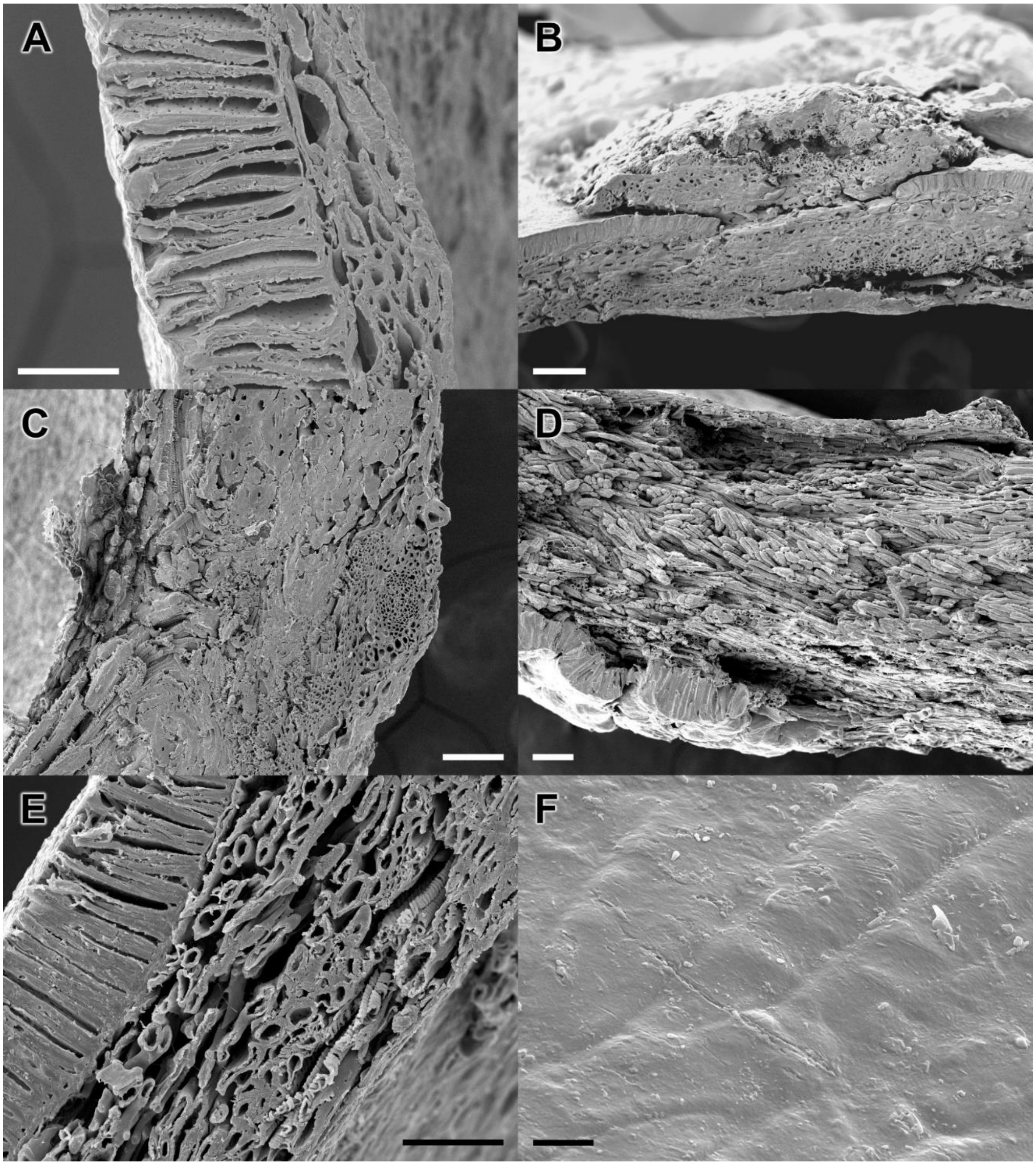

Figure 3.2. Scanning electron micrographs of seed coats in the Lathberry Clade. **A.** *Eugenia padronii*: transverse cross-section, thin portion of seed coat away from hilum; *Monsegur 1685* (FTG). **B.** *E. stewardsonii*: transverse cross-section, hilar region with mound of tissue; *Axelrod & Montalvo 11601* (MAPR). **C.** *E. cordata* var. *cordata*: transverse cross-section, hilar region; *Proctor 48820* (SJ). **D.** *Eugenia sessiliflora*: transverse cross-section, edge of hilum; *Axelrod & Sastre 6238* (UPRRP). **E, F.** *Eugenia cordata* var. *cordata*: E, longitudinal cross-section, thick portion of seed coat near hilum; F, external surface; *Woodbury et al. W.I. 221* (UPR). Scale bars: A, E = 50 µm. B, C, D = 100 µm. F = 5 µm.

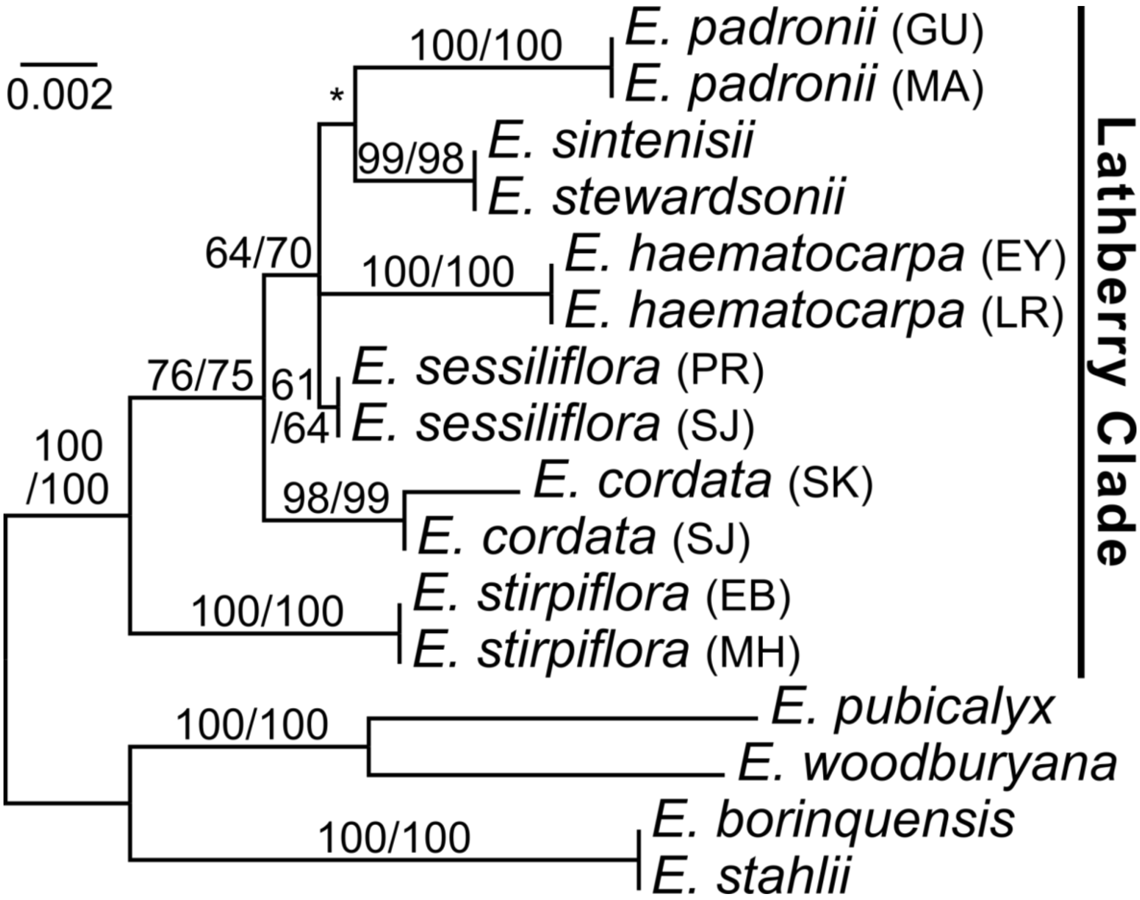

Figure 3.3. Maximum likelihood tree inferred from concatenated ITS, ETS, and *MeNu79* DNA sequence data. Two-letter sample codes distinguish different collections of the same species following Appendix 3.1. Bootstrap support percentages ≥50 are shown above branches with values from the equivalent parsimony analysis following the slash. An asterisk marks a branch not present in the strict consensus of the six most parsimonious trees. Scale units are expected number of substitutions per site.

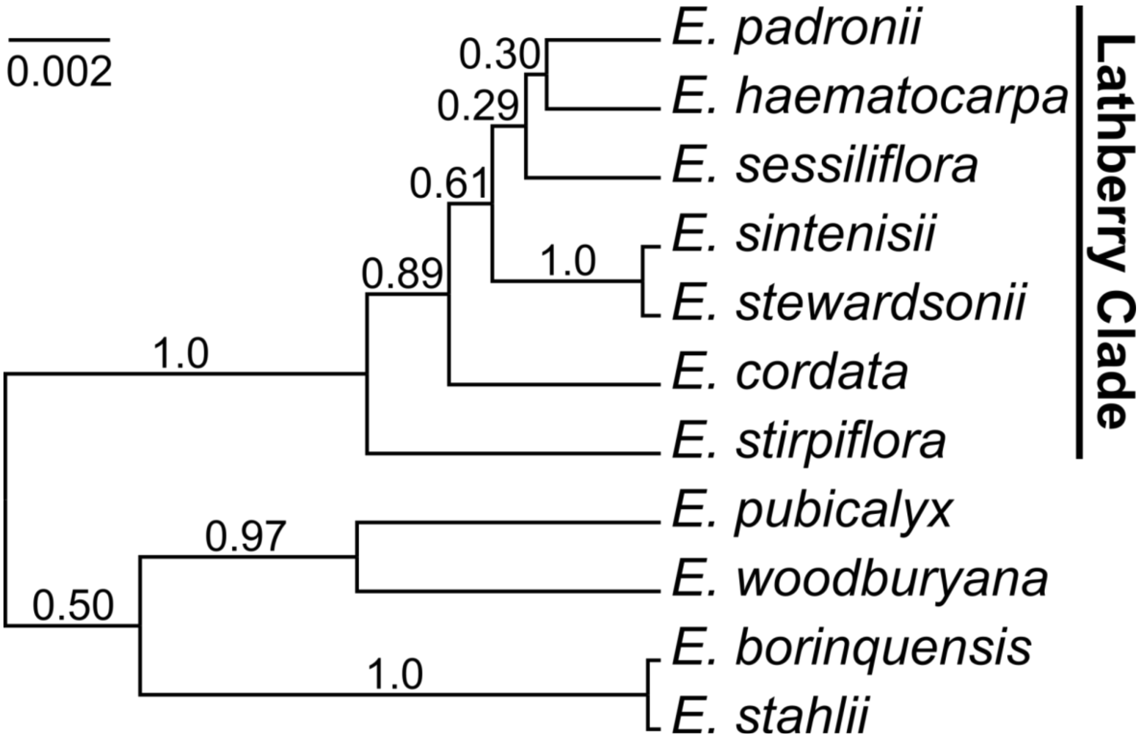

Figure 3.4. Maximum clade credibility species tree with mean node heights inferred from ITS, ETS, and *MeNu79* DNA sequence data using *BEAST. Posterior probabilities are shown above branches. Scale units are expected number of substitutions per site.

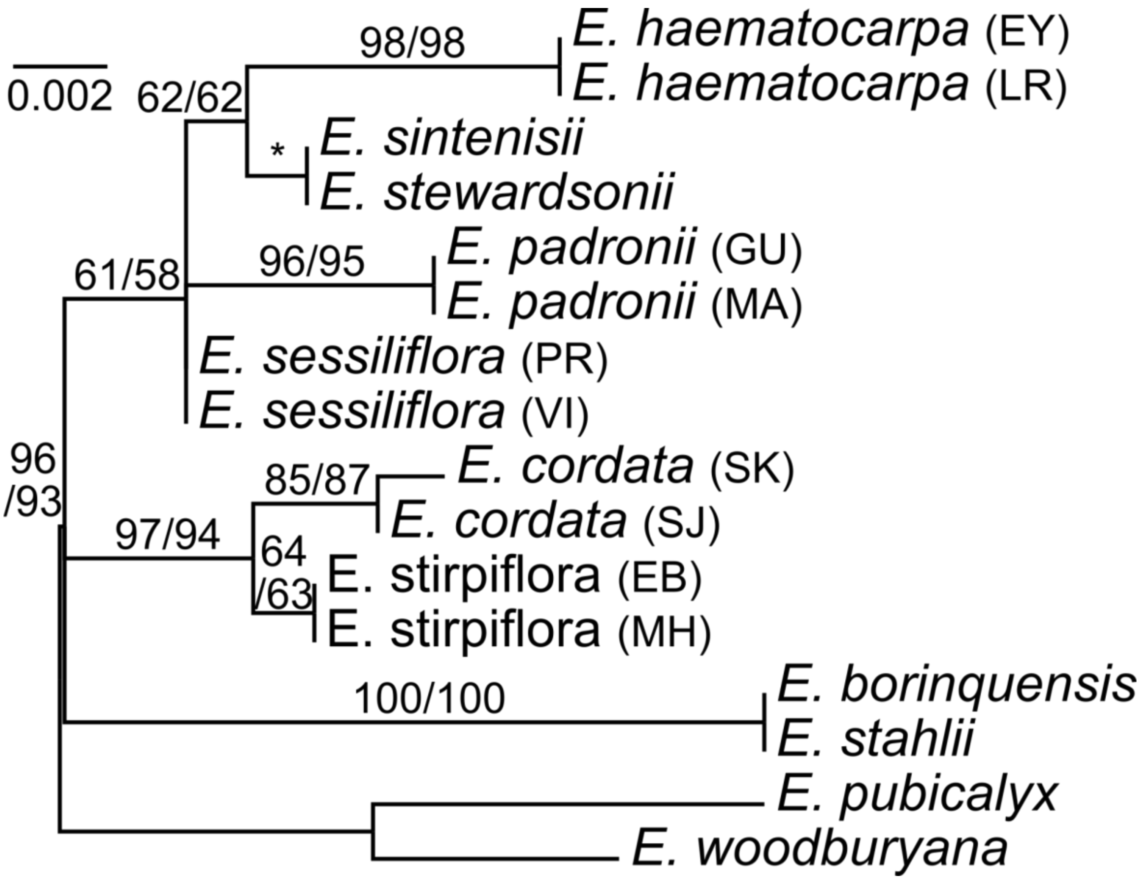

Figure 3.5. Maximum likelihood tree inferred from ITS DNA sequence data. Two-letter sample codes distinguish different collections of the same species following Appendix 3.1. Bootstrap support percentages ≥50 are shown above branches with values from the equivalent parsimony analysis following the slash. An asterisk marks a branch not present in the strict consensus of the eight most parsimonious trees. Scale units are expected number of substitutions per site.

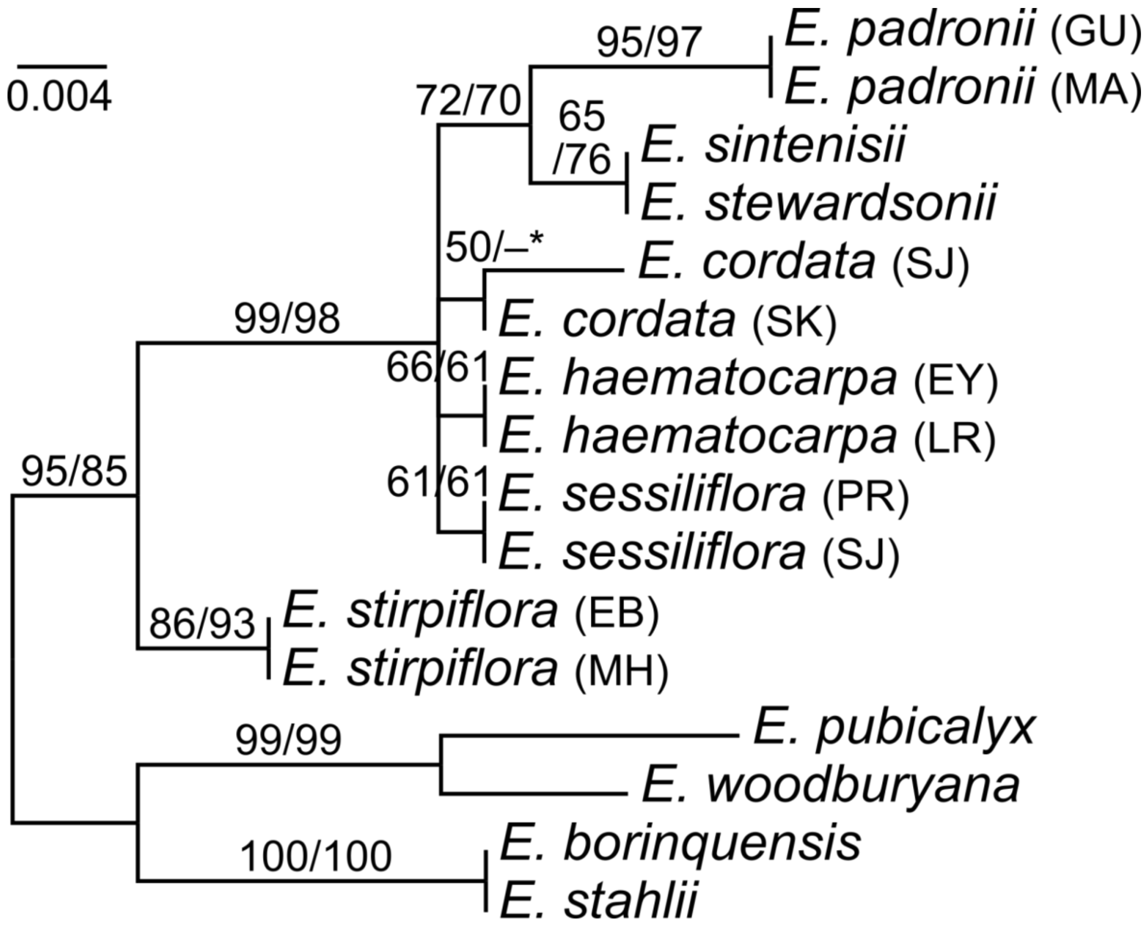

Figure 3.6. Maximum likelihood tree inferred from ETS DNA sequence data. Two-letter sample codes distinguish different collections of the same species following Appendix 3.1. Bootstrap support percentages ≥50 are shown above branches with values from the equivalent parsimony analysis following the slash. An asterisk marks a branch not present in the strict consensus of the four most parsimonious trees. Scale units are expected number of substitutions per site.

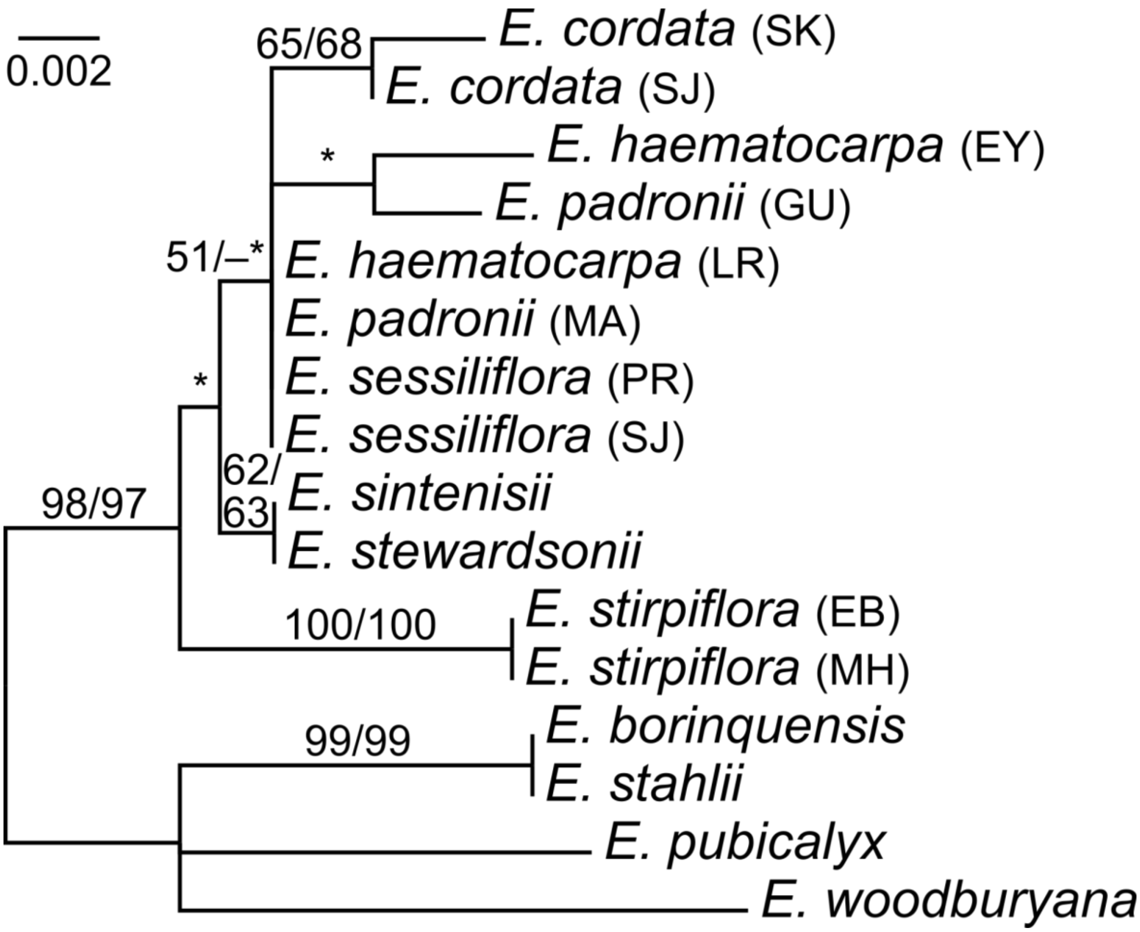

Figure 3.7. Maximum likelihood tree inferred from *MeNu79* consensus DNA sequence data. Two-letter sample codes distinguish different collections of the same species following Appendix 3.1. Bootstrap support percentages ≥50 are shown above branches with values from the equivalent parsimony analysis following the slash. Asterisks mark branches not present in the strict consensus of the 270 most parsimonious trees. Scale units are expected number of substitutions per site.

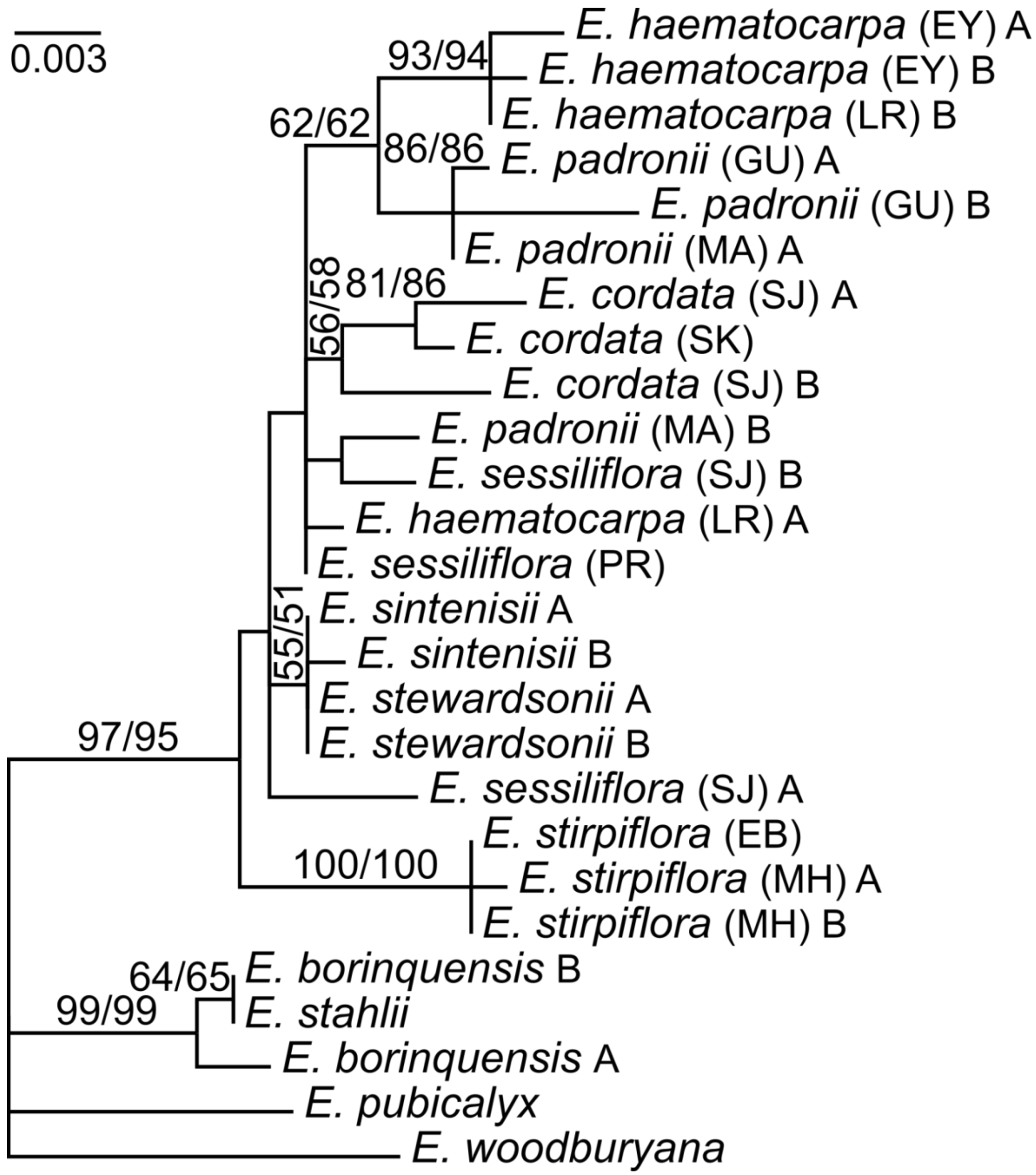

Figure 3.8. Maximum likelihood tree inferred from *MeNu79* allelic DNA sequence data. Two-letter sample codes distinguish different collections of the same species following Appendix 3.1. “A” and “B” distinguish different alleles from heterozygous samples. Bootstrap support percentages ≥50 are shown above branches with values from the equivalent parsimony analysis following the slash. All branches were present in the strict consensus of the three most parsimonious trees. Scale units are expected number of substitutions per site.

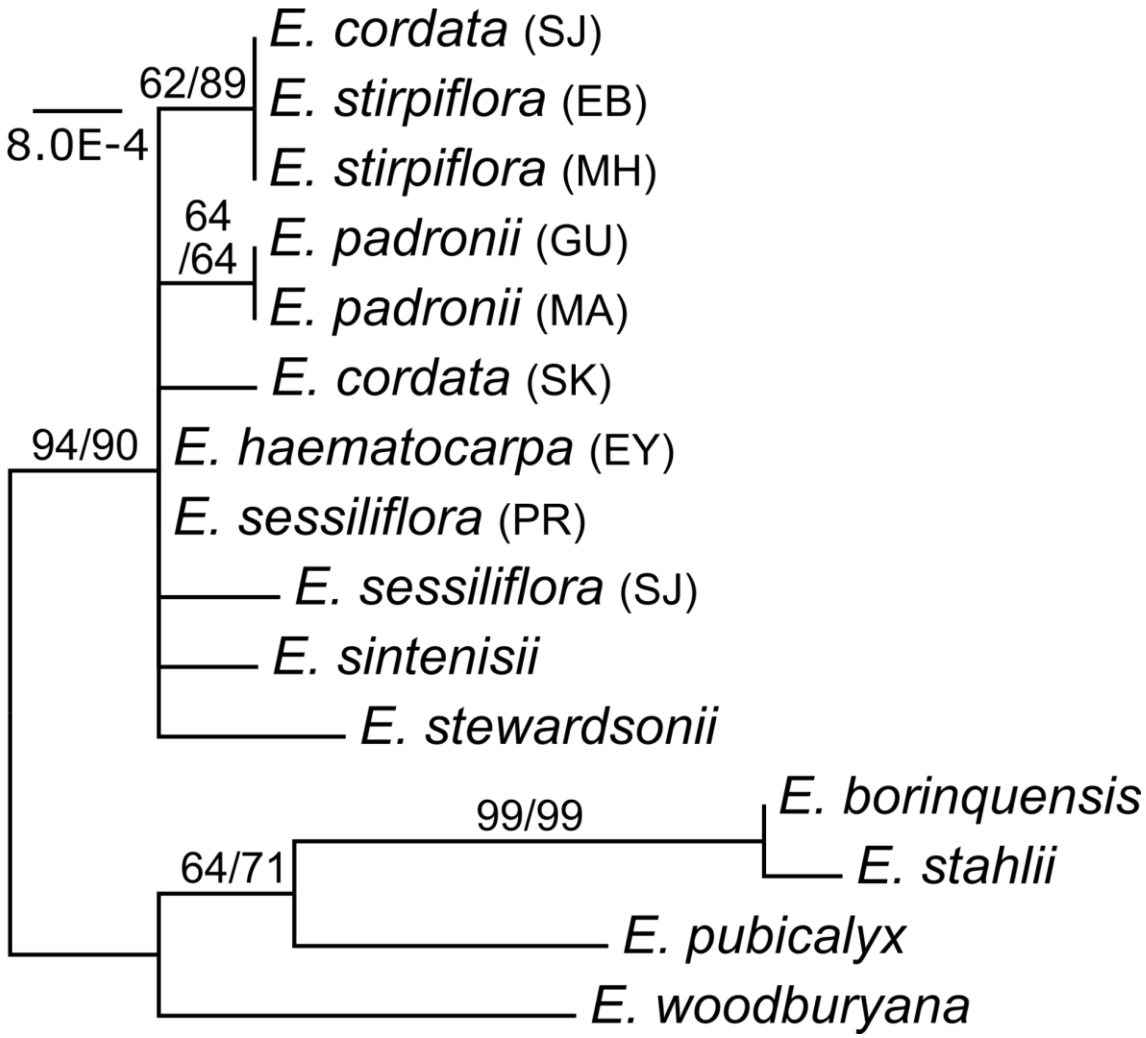

Figure 3.9. Maximum likelihood tree inferred from cpDNA (concatenated *psbA-trnH* and *ndhF-rpl32*) sequence data. Two-letter sample codes distinguish different collections of the same species following Appendix 3.1. Bootstrap support percentages ≥50 are shown above branches with values from the equivalent parsimony analysis following the slash. All branches were present in the strict consensus of the two most parsimonious trees. Scale units are expected number of substitutions per site.

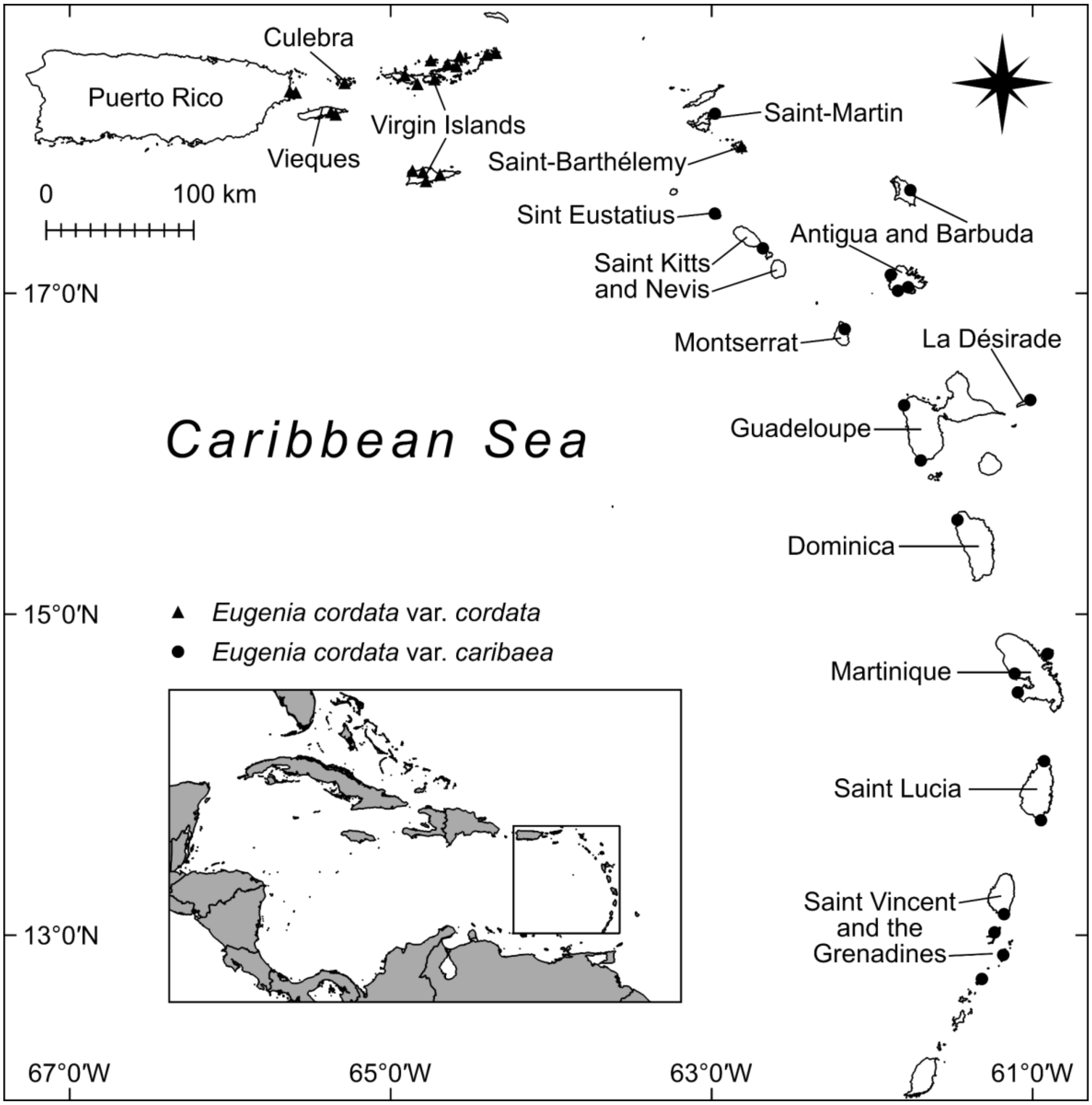

Figure 3.10. Distribution map of *Eugenia cordata* var. *cordata* and *E. cordata* var. *caribaea*.

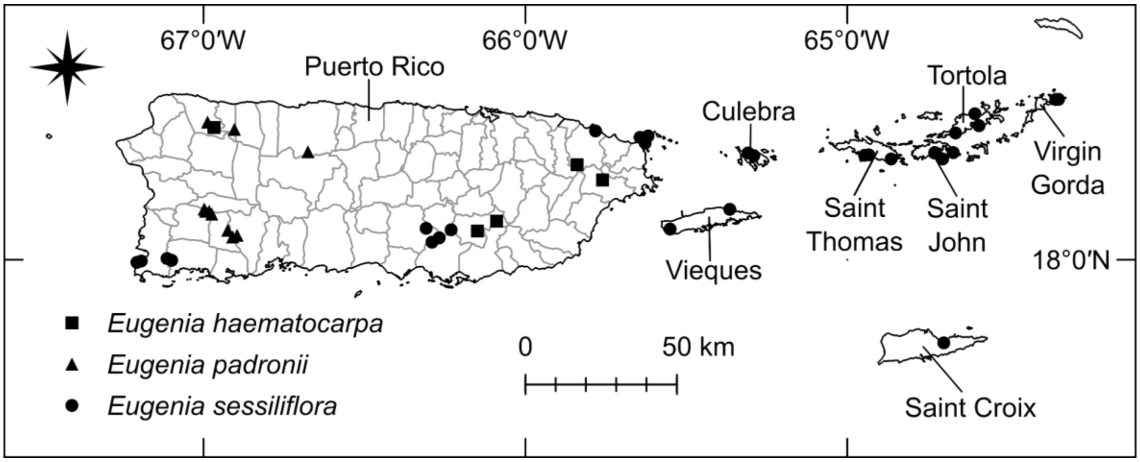

Figure 3.11. Distribution map of *Eugenia haematocarpa*, *E. padronii*, and *E. sessiliflora*.

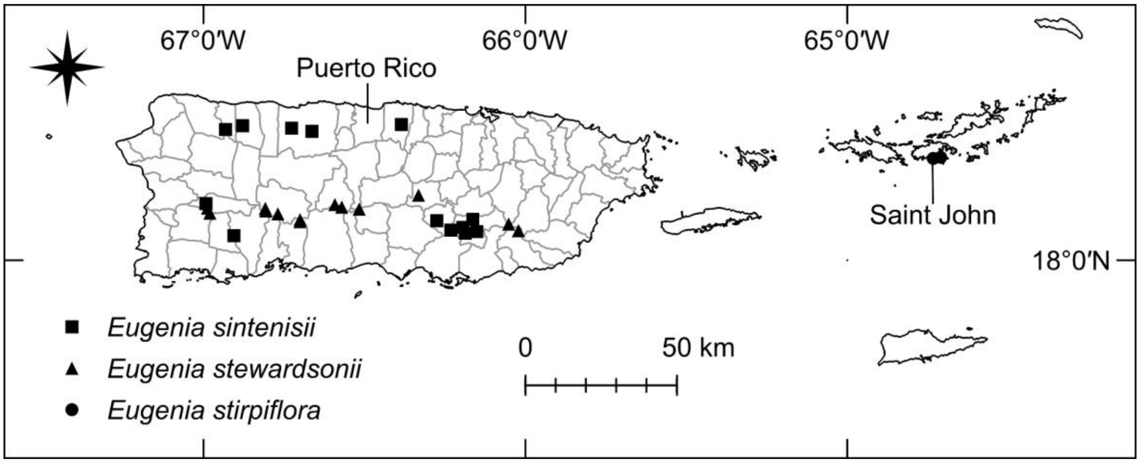

Figure 3.12. Distribution map of *Eugenia sintenisii*, *E. stewardsonii*, and *E. stirpiflora*.

Appendices

Appendix 3.1. Voucher specimens and GenBank accession numbers for DNA sequences. Duplicates of Flickinger collections may also be found at SJ and UPR. An asterisk indicates sequences generated for this study; a dash, missing data. Species name; sample code (if applicable; see Figs. 3.3 and 3.5–3.9), country, major subdivision, voucher, ITS, ETS, *MeNu79* (A & B if heterozygous), *psbA-trnH*, *ndhF-rpl32*.

Ingroup: *Eugenia cordata* (Sw.)DC.; SJ, U.S. Virgin Islands, St. John, *Gibney s.n. 26.05.2017-01* (FTG), MN295273, MT632197*, MT632223* & MT632224*, MN295090, MN475995; SK, Saint Kitts and Nevis, Saint Kitts, *Carrington 2338* (US), MT623508*, MT632196*, MT632222*, MT632217*, MT632211*. *Eugenia haematocarpa* Alain; EY, Puerto Rico, Río Grande, *Santiago-Valentín & Sustache ESV 2018-1* (FTG), MN295281, MT632198*, MT632225* & MT632226*, MN295098, MN476003; LR, Puerto Rico, Cayey, *Flickinger et al. 123* (FTG), MT623509*, MT632199*, MT632227* & MT632228*, —, —. *Eugenia padronii* Alain; GU, Puerto Rico, Quebradillas, *Flickinger et al. 83* (FTG), MT623510*, MT632200*, MT632229* & MT632230*, —, MT632212*; MA, Puerto Rico, Sabana Grande, *Flickinger & Santiago-Valentín 70* (FTG), MN295297, MT632201*, MT632231* & MT632232*, MN295114, MN476019. *Eugenia sessiliflora* Vahl; PR, Puerto Rico, Salinas, *Santiago-Valentín & Sustache ESV 2019-4* (FTG), MT623511*, MT632203*, MT632234*, MT632218*, MT632213*; SJ, U.S. Virgin Islands, Saint John, *Gibney s.n. 26.05.2017-02* (FTG), MT623512*, MT632204*, MT632235* & MT632236*, —, MT632214*. *Eugenia sintenisii* Kiaersk.; Puerto Rico, Cayey, *Flickinger et al. 122* (FTG), MT623513*, MT632205*, MT632237* & MT632238*, MT632219*, MT632215*. *Eugenia stewardsonii* Britton; Puerto Rico, Adjuntas, *Flickinger et al. 76* (FTG), MN295311, MT632207*, MT632240* & MT632241*, MN295128, MN476033. *Eugenia stirpiflora*

(O.Berg) Krug & Urb.; EB, U.S. Virgin Islands, St. John, *Gibney s.n.* (U.S. National Park Service VIIS-1658), MN295313, MT632208*, MT632242*, MN295130, MN476035; MH, U.S. Virgin Islands, Saint John, *Gibney s.n.* (U.S. National Park Service VIIS-1659), MT623514*, MT632209*, MT632243* & MT632244*, —, MT632216*.

Outgroup: *Eugenia borinquensis* Britton; Puerto Rico, Cayey, *Flickinger & Santiago-Valentín 124* (FTG), MN295270, MT632195*, MT632220* & MT632221*, MN295087, MN475992. *Eugenia pubicalyx* Alain; Dominican Republic, Santo Domingo, *Flickinger et al. 2015-DR-11* (FTG), MN295301, MT632202*, MT632233*, MN295118, MN476023. *Eugenia stahlii* (Kiaersk.) Krug & Urb.; Puerto Rico, Maricao/San German, *Flickinger & Santiago-Valentín 67* (FTG), MN295309, MT632206*, MT632239*, MN295126, MN476031. *Eugenia woodburyana* Alain; Puerto Rico, Cabo Rojo, *Flickinger et al. 126* (FTG), MN295321, MT632210*, MT632245*, MN295138, MN476043.

Appendix 3.2. Index to numbered collections cited in the text. The numbers in parentheses correspond to the numbering of taxa in the treatment and in the following list. Type collections are indicated with an asterisk.

Numerical List of Taxa—1a. *Eugenia cordata* var. *cordata*; 1b. *E. cordata* var. *caribaea* Flickinger; 2. *E. haematocarpa* Alain; 3. *E. padronii* Alain; 4. *E. sessiliflora* Vahl; 5. *E. sintenisii* Kiaersk.; 6. *E. stewardsonii* Britton; 7. *E. stirpiflora* (O.Berg) Krug & Urb.

Index to Numbered Collections—*Acevedo 14* (6); *Acevedo-Rodríguez, P. 4148* (1a), *5233* (7); *Acevedo-Rodríguez, P. & Aleman, O. I. 3204* (7), *3205* (1a); *Acevedo-Rodríguez, P. & Axelrod, F. 7787* (3); *Acevedo-Rodríguez, P. & Chinea, D. 2763* (4); *Acevedo-Rodríguez, P. et al. 1830* (4), *2030** (7), *2344* (1a); *Ackerman, J. D. 3870* (4); *Axelrod, F. 5079* (4), *9284* (3); *Axelrod, F. & Acevedo, P. 9604* (3); *Axelrod, F. & Chavez, P. 4805* (4); *Axelrod, F. & Montalvo, R. 11601* (6*); Axelrod, F. & Santiago, E. 9137* (4); *Axelrod, F. & Sastre, I. 5610* (4), *6238* (4); *Axelrod, F. & Thomas, R. 7836* (4); *Axelrod, F. et al. 3415* (4) *10186* (3), *11370* (6), *11371* (6), *11449* (6), *12222* (4), *12489* (4), *13570* (4), *13712* (6), *15051* (1b), *15472* (1b), *15489* (1b); *Barrier, S. 2390* (1b), *3521* (1b), *3527* (1b), *3594* (1b); *Beard, J. S. 378* (1b); *Boldingh, I. 1121* (1b), *1266 B* (1b); *Box, H. E. 619* (1b), *939* (1b), *1503* (1b); *Breckon 4447* (4); *Breckon, G. J. 4872* (4); *Breckon, G. J. & Cedeño, J. A. 4865* (4); *Breckon, G. J. & Franz, N. 8465* (4); *Breckon, G. & Rice, S. 4311* (4); *Breckon, G. J. & Vélez, J. 6017* (4); *Breckon et al. 3810 (J4)* (6), *4526* (3), *5555* (6), *6717* (4), *9257* (1a); *Britton, N. L. & Britton, E. G. 209* (1a); *Britton, N. L. & Cowell, J. F. 4121* (5); *Britton, N. L. & Shafer, J. A. 636* (1a), *904* (1a); *Britton, N. L. & Wheeler, W. M. 39* (1a); *Britton, N. L. et al. 37* (1a), *141* (1a), *5603** (6); *Byer, M. D. 68-1125* (1a); *Byer, M. D. & Mercado, T. 67-2115* (4); *Cabezudo, N. I. 6* (4);

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CONCLUSION

The goal of this dissertation was to further describe and classify Myrtaceae (tribe Myrteae DC.) in the Greater and Lesser Antilles according to their evolutionary history. Each of the included studies addressed an aspect of the central problem of Myrteae systematics using a different mode of research, but all were unified by a concern for classification and a regional approach. Their findings are important for understanding plant biodiversity in the Antilles, as well as for obtaining a more comprehensive picture of the diversity of Myrtaceae in the New World. These studies will also facilitate future descriptive and phylogenetic research on Antillean Myrtaceae and, hopefully, inspire greater appreciation for this group.

Findings and Significance**—**Chapter I described *Eugenia walkerae* Flickinger from Anguilla. Although this species is limited to a single island, its description was a byproduct of research considering *Eugenia* L. throughout the Caribbean Islands. In general, the Caribbean is one of the better collected areas in the tropics (Prance and Campbell 1988), and Anguilla, a relatively small, flat island with a total flora of only a few hundred species (Howard and Kellogg 1987), would seem to be an unlikely place to discover a new species. These circumstances suggest the importance of continued exploration and basic research on the flora of the region. Discovery of *Eugenia walkerae* also contributed to the phylogenetic study of Chapter II, in which it was included as the sole Lesser Antillean endemic. Its equivocal position relative to other species of *Eugenia* sect. *Umbellatae* O.Berg from the Caribbean requires further investigation, but the most urgent research need concerning this species is for its conservation status to be assessed.

The objectives of Chapter II were to identify the main lineages of Myrteae that occur in the Greater Antilles and potential clades for further study. Summarized taxonomically, this research showed that species of Myrtaceae native to the Greater and Lesser Antilles belong to six out of the nine recognized subtribes (Blepharocalycinae E.Lucas & T.Vasc., Eugeniinae O.Berg, Myrciinae O.Berg, Myrtinae Nied., Pliniinae E.Lucas & T.Vasc., and Pimentinae O.Berg); ten out of the ca. 46 genera (*Blepharocalyx* O.Berg, *Eugenia, Mosiera* Small, *Myrcia* Guill., *Myrcianthes* O.Berg, *Myrciaria* O.Berg, *Pimenta* Lindl., *Plinia* L., *Psidium* L., and *Siphoneugena* O.Berg), none of which are endemic; and four out of the eleven sections of *Eugenia* (*E.* sect. *Eugenia*, *E.* sect. *Excelsae* Mazine & E.Lucas, *E.* sect. *Racemosae* O.Berg, and *E.* sect. *Umbellatae*). At least one additional genus, possibly endemic, and one additional section of *Eugenia* are also represented. Within the same genus, recovered insular lineages were typically younger than continental lineages. These results indicate that Antillean Myrtaceae are, for the most part, subsamples of the major lineages of continental areas. The briefly discussed clades of endemic species identified serve as suggestions for future lines of research, but further evaluation of the groups, especially within a phylogenetic context, will be necessary to refine taxonomic concepts. Chapter III was conceived as a model study of this type.

One of the major consequences of the initial phylogenetic study presented in Chapter II is the clarification of the genera of Myrtaceae in the Greater Antilles. An exception is the unresolved issue of where to place the lineage represented by *Calycorectes ekmanii* Urb. Generic concepts within Myrteae have long been a perplexing issue (McVaugh 1968). Molecular phylogenetic studies that have addressed generic-level taxonomy (e.g., Lucas et al. 2011, Snow et al. 2011, Mazine et al. 2014, Wilson and Heslewood 2016) have helped to stabilize concepts. Only four recognized genera of Myrteae remain to be sampled in a phylogenetic study, and three of these are restricted to Australasia (Vasconcelos et al. 2017). The definite trend is for genera to become more inclusive as smaller segregates, e.g., *Hottea* Urb., are absorbed.

Another major consequence of this initial phylogenetic study is the recognition that the outstanding diversity of Antillean Myrtaceae is primarily at the species level. Most major clades of Myrteae appear to have originated in South America (Lucas et al. 2007, Thornhill et al. 2015, Vasconcelos et al. 2017), and almost all of the New World genera occur in Brazil (Landrum and Kawasaki 1997). The Brazilian Atlantic Forest biome has played a particularly important role in the diversification of the large genera *Eugenia* (Mazine et al. 2018) and *Myrcia* (Santos et al. 2007), and the family is especially diverse and common in this area today (Mori et al. 1983). Thus, a focus on South American taxa in initial phylogenetic studies of Myrteae, though limiting, does not seem to have seriously distorted the systematics of the group.

Chapter III examined in detail the systematics of the Lathberry Clade in the Antilles. The five main objectives for the taxonomic revision of the Lathberry Clade were at least partially accomplished. First, a combination of features was identified that allow for this group to be distinguished from all others in the Greater and Lesser Antilles. Morphological features differentiating the Lathberry Clade from certain species, e.g., *Eugenia catingiflora* Griseb. and relatives, nevertheless remain obscure. Second, morphological descriptions were provided for each recognized taxon, helping to clarify the diagnostic differences between species according to a phylogenetic species concept

(Nixon and Wheeler 1990). Seed coats and embryos, which are often passed over in descriptions, were also treated in depth. Both appear to be basically similar in structure across the genus (van Wyk 1980, van Wyk and Botha 1984, dos Anjos and Ferraz 1999, Justo et al. 2007), but variation in the seed characters may be taxonomically useful. Third, a phylogeny of the Lathberry Clade based on three variable nuclear genetic regions was presented. *Eugenia stirpiflora* (O.Berg) Krug & Urb. was recovered as sister to the rest of the species, but an uncertain sister group for the Lathberry Clade and limited resolution within the ingroup hindered further inference on its evolution. Fourth, taxonomic and nomenclatural updates were made in accordance with the results of the morphological and phylogenetic studies. This is the most comprehensive treatment of the included species to date and the first to treat all of the relevant taxa together. Fifth, a conservation status was suggested for each taxon using occurrence data from herbarium collections. These data probably represented the ranges expressed as extent of occupancy well, while area of occupancy appears to have been significantly underestimated in most cases. Although range estimates alone are insufficient to categorize a species as threatened according to criterion B of the IUCN Red List (IUCN 2012), two species, *Eugenia haematocarpa* and *E. stirpiflora*, were assessed as threatened with extinction according to criterion D.

More broadly, the revision of the Lathberry Clade provides a point of reference for future descriptive studies within the exceptionally diverse *Eugenia* sect. *Umbellatae*. The taxonomic significance of most of the described features is presently unknown. Detailed observations on more species, ideally within a phylogenetic context, will be necessary to understand variation in characters within the genus. Future investigations may lead to reinterpretations of characters and identify new sources of comparative data.

Future Studies—This work lays a foundation for future phylogenetic studies of Myrtaceae involving taxa from the Greater and Lesser Antilles. The phylogenetic survey of Chapter II was an efficient means of determining which lineages of this group occur in the region while simultaneously evaluating several taxonomic concepts. This same approach would be profitable for further exploration of species-rich groups in the Antilles such as *Eugenia* sect. *Umbellatae* and *Myrcia* sect. *Calyptranthes* (Sw.) A.R.Lourenço & E.Lucas. The latter clade was poorly represented in this work. Within *Eugenia* sect. *Umbellatae*, there appears to be a high degree of geographic structure, with sampled taxa from the Caribbean falling within Clade C (Mazine et al. 2018). Additional sampling of species from areas neighboring the Greater Antilles (Mexico, Central America, and the Lesser Antilles) should therefore be prioritized for evaluating the limits of Clade C and identifying further subclades. Inclusion of species from these areas could also allow for historical biogeographic inference aimed at better understanding the evolutionary history of the Caribbean flora.

As the outlines of genera and other major clades become clear, a taxon-centered approach is preferable for phylogenetic studies. Any of the briefly characterized groups described in Chapter II are potential subjects for further investigation, although further sampling informed by careful study and observations will be necessary to establish their monophyly. Observations of conflict between nuclear and chloroplast genetic markers in Chapters II and III, as well as limitations in resolution when using relatively few genetic regions, suggest that more data-intensive approaches will be necessary for phylogenetic inference at lower taxonomic levels.

It bears re-emphasis that much more effort should be directed towards the "difficult and tedious" (McVaugh 1968) task of describing and classifying the species of Myrtaceae in the Caribbean Islands in order to make further progress in the systematics of the group. Experience gained while working on this dissertation suggests that relatively little is known about most Antillean endemic species of Myrtaceae. Thus, there is a high potential for descriptive studies to make valuable contributions to our knowledge of the properties, distribution, taxonomy, and current status of these plants. Phylogenetics can aid but not substitute for this work. The production of phylogenetically informed synopses of species-rich groups like *Eugenia* would be helpful to direct attention towards taxa in need of study while summarizing current knowledge, but the completion of more detailed revisionary or monographic accounts is ultimately necessary for scientific and conservation purposes (Stuessy 1975, Prance 1995).

***Final Thoughts*—**This dissertation considered the organismal diversity of Myrtaceae in the Greater and Lesser Antilles in an objective manner. Such treatment, while appropriate, runs the risk of reducing the things considered to abstract units of evolution. As author Wendell Berry (2000) wrote, "We should recognize the insufficiency, to our life here among the creatures, of the abstract categories of reductionist thought. . . For the human necessity is not just to know, but also to cherish and protect the things that are known, and to know the things that can be known only by cherishing." These words speak of a tension between our efforts to comprehend the natural world and our subjective valuation of it through personal experience. Far from leading us to devalue plants, systematic botany should be a tool that helps us to appreciate them in all of the concrete glory in which they—as practitioners of botanical Latin sometimes put it—rejoice (*gaudens*). It has been my privilege to gain some measure of first-hand knowledge of the plants treated herein. This work is offered in the hope that it will both inform and inspire the reader to “cherish and protect” the living things it attempts to comprehend.

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