

Renato Goldenberg
Fabián A. Michelangeli
Frank Almeda *Editors*

Systematics, Evolution, and Ecology of Melastomataceae

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Foreword

I first came across Melastomataceae 42 years ago, in 1980, when Klaus Kubitzki, who had just come back from Brazil, suggested I should work on ant/plant interactions or bee/flower interactions for my doctoral dissertation. I decided on the latter topic, but soon realized that melastomes would afford me an opportunity to also study the former. The systematics of the family began to interest me only during my postdoc with John Wurdack (1921–1998) at the Smithsonian in Washington in the mid-1980s. It was there that Frank Almeda and I first got to know each other, during one of his regular visits to the US National Herbarium. Besides doing monographic and floristic work, Frank moved forward the study of the chromosomes and seed morphology of Melastomataceae with broad taxon sampling and state-of-the-art microscopy, the hope being that these traits would turn out taxonomically useful. In 1997, I met Fabián Michelangeli, who was then doing his doctoral research on *Tococa*, one of the ant-plant clades in the Melastomataceae. This topic immediately brought us together since I had also worked on *Tococa* and done ant-exclusion experiments on one of its species (Renner 1997; Renner and Ricklefs 1998). Fabián and I were both interested in the application of computer-based phylogenetics, but at the time we were still relying on morphological data. Renato Goldenberg and I began corresponding in the early 1990s, initially about apomixis, which he had studied in southern Brazilian species, but later mostly about Renato's efforts with Frank, Fabián, and others on the Nomenclator for *Miconia* (Goldenberg et al. 2013). From our first personal meeting—in Munich, Germany—I mostly recall being struck by Renato's ambition and decisiveness. It is an immense pleasure therefore to have been asked by this team—Renato Goldenberg, Fabián Michelangeli, and Frank Almeda—to provide a foreword for this book, a milestone achievement in our understanding of the systematics, evolution, biogeography, and ecology of the Melastomataceae.

The editors have brought together 72 authors from 17 countries to accomplish this first modern synthesis of research focusing on this family; they provide background on their aims, and the book's content, in their preface. I can therefore use this foreword to reminisce on the progress that we have made in our understanding over the past 30–40 years. Given that the World's population has increased from

5.4 in 1991 to 7.8 billion today, and that there are now more systematists than ever before, it is expected that the number of people working on Melastomataceae has increased. An argument can be made, however, that the scope and quality of work on this family has increased disproportionately. One measure of this is provided by a symposium on the systematics and evolution of the Melastomataceae that I organized at the Smithsonian Institution in Washington in 1991. Among the six or seven speakers were Thomas Morley (1917–2002), James Maxwell (1945–2015), John Wurdack, and Frank Almeda. Henri Jacques-Félix (1907–2008) could not attend for health reasons, meaning that there was no presentation at all on African Melastomataceae. Seen from today, we had almost no understanding of the age of the family, its biogeography, the relationships between Olisbeoideae and Melastomoideae, the role of hybridization, the function of the dimorphic stamens, or the true taxon diversity and endemism. On all these topics, there has been tremendous progress over the past 30 years as documented in this volume.

The year 1991 had been chosen for the Melastomataceae symposium at the Smithsonian to commemorate the publication of Celestin Alfred Cogniaux's (1891) *Monographiae Melastomacearum*, the last book to deal with the systematics of entire family. In a way, it is this work that is being replaced by this volume, which presents a new classification for the subfamilies, tribes, and allocation of genera (Penneys et al., Chapter "A New Melastomataceae Classification Informed by Molecular Phylogenetics and Morphology"; Stone, Chapter "Phylogeny and Circumscription of the Subfamily Olisbeoideae"; and other chapters in Part II). Systematists today work in teams, rather than alone as we did well into the early 1990s. The internet, which officially began on 1 January 1983, with the full impact felt in herbaria from 1985 onwards, has made it easier to find, share, and discuss data and insights. The worldwide data accessibility and teamwork leads to consensus classifications, with more people buying into particular arrangements of higher taxa. The classification in this volume by Penneys and colleagues (Chapter "A New Melastomataceae Classification Informed by Molecular Phylogenetics and Morphology") is based on nuclear and plastid DNA sequences from 2435 species (2973 terminals) representing 158 of 175 currently accepted genera. This means that the deeper relationships in the Melastomataceae are now clear. With solid phylogenies in hand, we can apply molecular-clock approaches to infer the dispersal and radiation of particular clades. Twenty years ago, with my then-students Gudrun Clausing (now Kadereit) and Karsten Meyer, I was involved in the "switch" from morphology-based to DNA-based attempts at discerning relationships and geographic histories (e.g., Renner and Meyer 2001; Clausing and Renner 2001; Renner 2004). However, when it comes to melastomes, my first love remained their pollination and function of their stamens (Luo et al. 2008), and their capacity for asexual reproduction (apomixis). On these and other ecological, physiological, and cytological aspects, too, there has been great progress over the past 30 years as documented by dedicated chapters in this volume.

A third measure of progress is the increase in number of species and our understanding of species ecology. For the "Monographiae," Cogniaux revised 2731 species (and 555 varieties, not always easy to interpret today), 793 of them new to

science. The work involved is unimaginable today, for example, Cogniaux wrote to Asa Gray that it had taken him “much longer than I thought at first” to prepare the alphabetical index to the c. 8000 names treated in the “Monographiae” (Renner 1990). According to data in this volume, the family now comprises 5858 species, over twice as many than in 1891. I suspect that collecting of herbarium specimens between 1991 and 2021 has not matched that during 1971–1990. Nevertheless, we are reaping the fruits of the earlier collecting in novel ways: Firstly, by obtaining DNA sequences from herbarium collections and secondly, but applying computer-based approaches to the analysis of georeferenced museum collections. For example, Michelangeli et al. (Chapter “Historical Biogeography of the Neotropical Miconieae (Melastomataceae) Reveals a Pattern of Progressive Colonization Out of Lowland South America”) have investigated the biogeographic patterns of Miconieae based on 90,000 distribution records for over 1000 species. This type of analysis allows an understanding of niche occupation and radiation into new niches that was not possible 30 years ago, but that depends on, and is limited by, herbarium collections.

A final argument supporting the need for this single-volume compilation dedicated to the Melastomataceae is that a book with numerous authors collaborating in dynamically changing teams will give the new classification of the family the proper outing and weight. The current knowledge and still-open questions are here for all to find, accept, and improve. Of my own classification (Renner 1993) nothing remains except the subfamily Kibessioideae, which I resurrected following Charles Naudin (1849–1853). Naudin was a pioneer of experimental research on hybridization, and his thinking is known to have influenced Darwin (Marza and Cerchez 1967). Thinking about this, the greatest success for this volume will be if it encourages, and facilitates, the interconnectedness of research not only among those interested in Melastomataceae today, but also others who may know little about this tropical group, but who are seeking to address evolutionary or ecological questions for which melastomes would make great study objects. As Renato Goldenberg, Frank Almeda, and Fabián Michelangeli write in their preface, this book should spur a new generation of research topics to be addressed in the family.

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Preface

This volume summarizes much of what is currently known about the systematics, phylogeny, classification, biogeography, and ecology of Melastomataceae, one of the ten largest families of flowering plants. The family is largely a tropical one that is mostly unknown to people who have spent their lives in temperate latitudes. A few northern-hemisphere garden-lovers will recognize the glory bushes (*Pleroma*) or a few species of *Medinilla* that are cultivated in greenhouses, while some North Americans might be familiar with the several species of meadow beauties (*Rhexia*) that are distributed across a good part of the eastern United States. On the other hand, anyone with some experience in tropical and subtropical floras around the world has surely encountered the extraordinary diversity of species presented by this family. Although it is one of the easiest to recognize at the family level, the task of identifying genera and species has typically been an onerous one for the generalist. Despite its size and diversity, we suspect that the primarily tropical distribution of Melastomataceae has contributed to its almost forgotten and largely unknown status in terms of systematics, evolution, and ecology. Redressing this shortcoming by bringing together the many recent research advances focused on Melastomataceae into one volume is a major objective of this book.

Unlike the Asteraceae, Fabaceae, Orchidaceae, and Poaceae—larger widespread flowering plant families that have attracted an army of specialists—relatively few botanists have gravitated to the Melastomataceae. Until the end of the twentieth century, few systematists dedicated all or a portion of their careers to botanical research on the Melastomataceae in a global or regional context. These included A. P. de Candolle (1778–1841) in Geneva, D. Don (1799–1841) in London, C. V. Naudin (1815–1899) in Paris, J. J. Triana (1828–1890), a Colombian and the first Latin American specialist who conducted field work and study visits to European herbaria, C. A. Cogniaux (1841–1916) in Brussels, H. A. Gleason (1882–1975) in New York, R. C. Bakhuizen van den Brink, Jr. (1911–1987) in Leiden, H. Jacques-Félix (1907–2008) in Paris, and J. J. Wurdack (1921–1998) in Washington, D.C.

In the last two and a half decades, the number of researchers working on various aspects of melastome systematics, ecology, and evolution has grown exponentially.

This has involved everything from herbarium-based alpha-level taxonomic studies and phylogenetic reconstructions using DNA sequence data to studies focused on biogeography and reproductive biology. Most importantly, many new students of the family based in melastome-rich countries, especially in the neotropics, have made field-based studies a critical centerpiece of their research efforts.

We find ourselves at a historically unique crossroad with respect to melastome research since we now have a sizeable cadre of researchers asking significant evolutionary questions and generating a wealth of new data that are ripe for a first-ever modern synthesis. It is hoped that this book fills that need.

We have brought together a diverse community of 72 authors from 17 countries to accomplish this synthesis. This volume consists of 34 chapters grouped into four sections. The first section introduces the Melastomataceae with chapters on overall diversity and distribution, classification history prior to the molecular era, morphological variability, and historical biogeography in a global context. The second section provides a new phylogenetically based classification of the family and summarizes what we now know about each of the subfamilies and tribes based on comparative morphological and molecular data sets. We used this opportunity to assemble a third section that addresses advances in a diverse set of subjects ranging from floral ontogeny, seed morphological features, chromosome number evolution, pollination biology, aspects of reproductive biology, and patterns of diversification and biogeography of Miconieae, the largest tribe in the family. The fourth and final section deals with some broad ecological topics including species distributions along soil gradients, seed germination ecology, seed dispersal, and the ecology of naturalized species of Melastomataceae around the world. We conclude the volume with a statement of future prospects emphasizing avenues of research in need of sustained attention.

In putting this volume together, each author was given free rein to gather a team of collaborators and to develop text appropriate to each chapter topic. We avoided establishing strict content guidelines to accommodate available information for each chapter and to encourage individual creativity. Some chapters are literature reviews while others incorporate previously unpublished data. Because of space limitations, authors were encouraged to provide relevant supplemental data pertinent to their chapters that will be available online at Springer Nature. We recognize that some important topics have not been treated here such as gall morphology and biology, the meager fossil record, and ethnomedicinal uses and pharmacological properties. These are topics for a future volume or book-length volumes of their own.

For the sake of brevity and uniformity, we have adopted some conventions that depart from standard practices. Authorities for scientific names are given only in Chapters “Melastomataceae: Global Diversity, Distribution, and Endemism” and “A New Melastomataceae Classification Informed by Molecular Phylogenetics and Morphology” instead of the first time they are used in each chapter, since these are now generally available in a number of online venues. Types for names are also generally not provided except for newly proposed taxa such as tribes in Chapter “A New Melastomataceae Classification Informed by Molecular Phylogenetics and Morphology” or where tribal names with priority have been newly adopted.

Books of this type put a spotlight on a group of organisms by integrating information from a variety of disciplines, whether they are descriptive, experimental, or historical in nature. It is our hope that this volume will bring the Melastomataceae to the attention of a much broader audience. Beyond being a summary of our current knowledge on the systematics, ecology, and evolution of Melastomataceae, we hope this book highlights the gaps in knowledge that need to be filled and spurs a new generation of research topics in the family.

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Acknowledgments

We are grateful to all of our melastome colleagues who agreed to contribute to this project. They took precious time from their busy schedules to write chapters for this book and unflinchingly responded to our requests for changes, both big and small, to their manuscripts. We also thank the many reviewers who have given freely of their time and expertise to evaluate the scientific content and presentation of book chapters. Their constructive comments and suggestions have increased the accuracy and improved the quality of every chapter. All chapters have been reviewed by two or more specialists, all of whom are named and thanked in each chapter if they chose not to remain anonymous. For the chapters that involved all three book editors as co-authors, we invited guest editors to handle the review process; for this, we give special thanks to Lucas Bacci, Agnes Dellinger, Peter Fritsch, Walter Judd, Ricardo Pacifico, and Carmen Ulloa.

We also take this opportunity to pay tribute to the important early work and achievements of our predecessors who are mentioned in the Preface and in Chapter “Classification History of the Melastomataceae: Early Beginnings Through the Pre-molecular Era”. These individuals produced seminal studies of the Melastomataceae, all based on fewer collections and none of the sophisticated technology available to us today. Their collective work provides the critical foundation that has allowed the growing community of melastome researchers to identify knowledge gaps, test relationships, and advance our overall understanding of the family.

We will also want to thank João Pildervasser, scientific editor at Springer Nature, who believed we had an important subject to present from the start. We are also grateful to Sowmya Thodur, production editor of books at Springer Nature for all of her guidance through the publication process, and the staff at Springer Nature for assistance during book format design, production, and all the attendant details required to bring a book of this kind to completion.

Finally, we owe much gratitude to our home institutions—the California Academy of Sciences, the New York Botanical Garden, and the Universidade Federal do Paraná. They have provided us with ongoing financial and logistical support and a stable home base to pursue our research passions focused on the megadiverse Melastomataceae over many years.

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Fabián A. Michelangeli is the Abess Curator of Tropical Botany in the Institute of Systematic Botany of the New York Botanical Garden. He studied Biology in his native Caracas at the Universidad Central de Venezuela and obtained a PhD in Plant Sciences from Cornell University. His research focuses on the systematics, taxonomy, and evolution of tropical plants, especially on the family Melastomataceae. He also teaches in the graduate program in Biology at the City University of New York and Forestry and Environmental Sciences at Yale University. He has been an Associate Editor of *Brittonia* since 2004.

Frank Almeda is Curator Emeritus of Botany in the Institute for Biodiversity Science and Sustainability at the California Academy of Sciences (CAS) where he also served two terms as Director of Research. He did his undergraduate work in Botany and Bacteriology at the University of South Florida (Tampa) and then earned a PhD in Plant Sciences at Duke University. His research focuses on the Systematics and evolution of tropical vascular plants with a special emphasis on Melastomataceae

and Symplocaceae. Before official retirement, he was also Research Professor of Biology at San Francisco State University (SFSU) where he served as major professor to numerous graduate students in the SFSU/CAS joint training program, an activity that he continues. He currently serves on the Editorial Board of Harvard Papers in Botany.

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Part I
An Introduction to Melastomataceae

Melastomataceae: Global Diversity, Distribution, and Endemism



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Introduction

The Melastomataceae are among the 10 largest families of flowering plants with an estimated 173 genera and some 5858 species. The family has a long history of classification (Almeda, chapter “Classification History of the Melastomataceae: Early Beginnings Through the Pre-molecular Era”) and is divided into three major clades, the Kibessioideae (Renner, chapter “The Subfamily Kibessioideae, its Tribe Pternandreae, and its Sole Genus, *Pternandra*”), the Melastomatoideae (see individual tribe chapters) and the Olisbeoideae (Stone, chapter “Phylogeny and Circumscription of the Subfamily Olisbeoideae”). The majority of genera have a tribal placement confirmed by molecular analysis and supported by morphological characters (Michelangeli et al. 2020; Penneys et al., chapter “A New Melastomataceae Classification Informed by Molecular Phylogenetics and Morphology”), including

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six genera placed in three newly described tribes (Penneys et al., chapter “A New Melastomataceae Classification Informed by Molecular Phylogenetics and Morphology”). While the Kibessioideae are paleotropical, the Melastomatoideae and Olisbeoideae are pantropical, as are three tribes (the Astronieae, Melastomateae, and Sonerileae) within the Melastomatoideae. About 64% (3741) of the species of the Melastomataceae occur in the Americas, 25% (1472) in Asia and Oceania, 5.5% (349) in Madagascar, and 5.5% in continental Africa (326). The family is subcosmopolitan, mainly distributed in tropical and subtropical regions, but some species reach temperate latitudes. Melastomes range in elevation from sea level to about 4500 m in the tropical Andes of South America. Although some species occur in seasonally dry habitats in Africa, Madagascar, Sri Lanka, Thailand, and Brazil, there are no Melastomataceae in true desert environments. No genera are native to both the New and Old Worlds, but a few genera are disjunctly distributed between Africa, Madagascar, and Asia, e.g., *Lijndenia*, *Medinilla*, and *Memecylon*.

Studies have heavily focused on the New World Melastomataceae with recent treatments, revisions, or monographs (see Michelangeli et al. 2020). Africa, with fewer species, mostly in the Melastomateae and Olisbeoideae, has also been the subject of recent phylogenetic and monographic publications (Stone 2012, 2014; Veranso-Libalah et al. 2017a, 2021). In contrast, the Asian tropics are poorly studied, with large genera like *Astronia*, *Astronidium*, *Medinilla*, *Melastoma*, *Oxyspora*, *Phyllagathis*, and *Sonerila* in need of modern revisions. Since 2000, 674 new species of Melastomataceae have been published: 446 for the Americas, 166 for Asia, 31 for continental Africa, and 31 for Madagascar and the Mascarenes.

In the following, we present a summary of the number of species and distribution of all genera of the Melastomataceae following the recent tribal classification by Michelangeli et al. (2020) and Penneys et al. (chapter “A New Melastomataceae Classification Informed by Molecular Phylogenetics and Morphology”).

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Results

This section provides separate accounts of melastome diversity and distribution in the Americas, Africa and Madagascar, and Asia and Oceania (Fig. 1), followed by a detailed summary (see Annotated Checklist) of species numbers and distributions of all genera sorted by taxonomic rank (subfamily, tribe) and geography (Fig. 2). For the Americas, the current distributions are found in the Vascular Plants of the Americas' website (Ulloa Ulloa et al. 2018): www.tropicos.org/project/VPA. Information on the nomenclature of the family is available at www.melastomataceae.net.



Fig. 1 Melastomataceae from various continents. Clockwise from top left: *Blakea maurofernan-deziana*, Central America (photograph by F. Almeda, Costa Rica); *Meriania aurata*, South America (photograph by L. Jost, Ecuador); *Tristemma mauritianum*, Africa (photograph by F. Almeda, Madagascar); *Melastoma malabathricum*, South Pacific Islands (photograph by D.S. Penneys); *Osbeckia octandra*, Southeast Asia (photograph by F. Almeda, Sri Lanka); *Melastomastrum capitatum*, continental Africa (Photograph by R. E. Gereau, Democratic Republic of Congo)

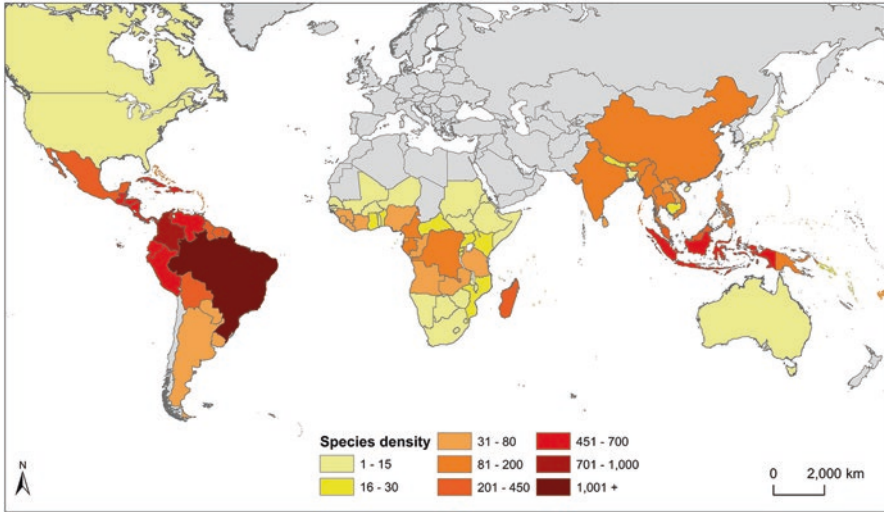


Fig. 2 Melastomataceae species density by country or areas. For the Americas, the geographical areas include North America (Canada and the United States), Central America, West Indies, Guianas, and the Southern Cone, following the arrangement of Ulloa Ulloa et al. (2017)

Currently, there are 3 recognized subfamilies, the largest (the Melastomatoideae) with 21 tribes. All genera are now placed in tribes, but some have not been sampled in a molecular phylogenetic context (see Penneys et al., chapter “A New Melastomataceae Classification Informed by Molecular Phylogenetics and Morphology”).

The Dinophoreae, Dissochaeteae, Feliciadamieae, and Kibessioideae are exclusively distributed in the Old World; the Melastomateae, Ollisbeoideae, and Sonerileae are pantropical; the Astronieae are amphi-Pacific; and the remaining 15 tribes are New World endemics (i.e., the Bertolonieae, Cyphostyleae, Eriocnemeae, Henrietteae, Lavoisierae, Lithobieae, Marcetiae, Merianieae, Miconieae, Pyramieae, Pyxidanthae, Rhexieae, Rupestreeae, Stanmarkieae, and Trioleneae) (Fig. 3).

The total number of Melastomataceae genera is 173 with ca. 5858 species (see Annotated Checklist). There are 84 genera currently recognized in the New World with ca. 3742 accepted species. In the Old World, there are ca. 89 genera comprising ca. 2117 species (see Annotated Checklist). Generic delimitation problems, especially within the Sonerileae, prevent us from having a clear picture of the number of genera and species, and the lack of monographs, large regional floras, and phylogenetic analyses hinders our estimates of species numbers in Asia.

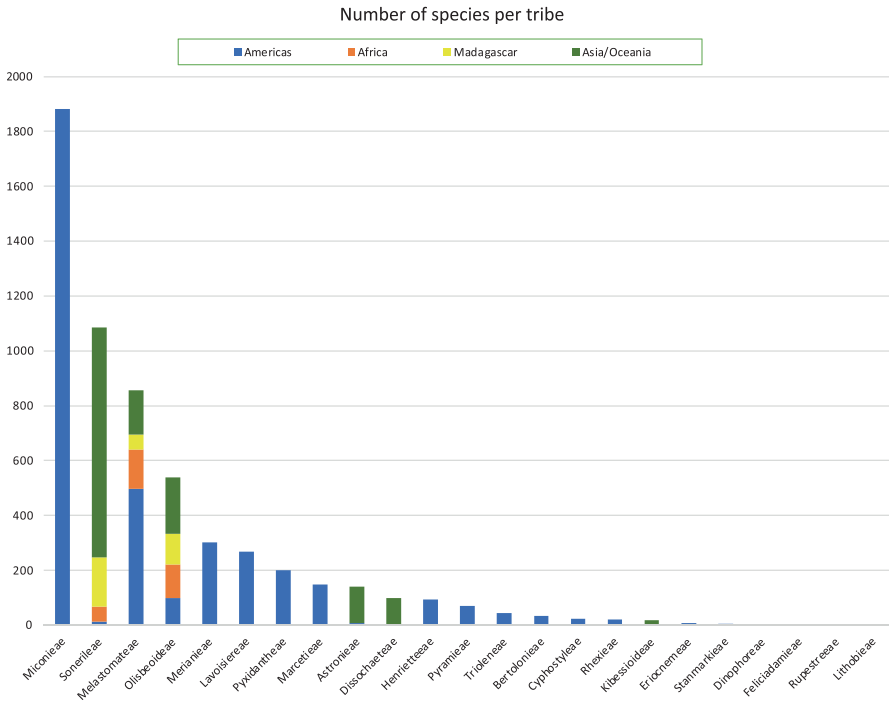


Fig. 3 Number of species of Melastomataceae by tribe/subfamily and geographical area

Americas

The New World harbors 3741 species of Melastomataceae in 84 genera and in two subfamilies: the Olisbeoideae (2 gen./99 spp.) and the Melastomatoideae with 18 tribes: Astronieae (1 gen./7 spp.), Bertolonieae (1/35), Cyphostyleae (4/25), Eriocnemeae (3/7), Henrietteae (3/95), Lavoisieriae (3/~269), Lithobieae (1/1), Marcetieae (20/~149), Melastomateae (17/~496), Merianieae (8/~301), Miconieae (1/1901), Pyramieae (4/70), Pyxidanthaeae (2/204); Rhexieae (3/21), Rupestreae (1/2), Sonerileae (6/12), Stannarkieae (2/4), and Trioleneae (2/43). They occur across North and South America, but most of the species (3689) are found in the tropics from western and southern Mexico throughout Central America to Bolivia and Brazil and the Caribbean. The most diverse genus by far is *Miconia* with 1901 currently known species, followed by five genera with more than 100 species, *Microlicia* (258), *Blakea* (192), *Pleroma* (161), *Meriania* (120), and *Chaetogastra* (117); 48 genera are represented by less than 10 species and, of these, 17 are mono-specific (*Bisglaziovia*, *Brasilianthus*, *Dicrananthera*, *Eriocnema*, *Leiostegia*, *Lithobium*, *Maguireanthus*, *Mallophyton*, *Neblinantha*, *Nepsera*, *Ochtheophilus*, *Opisthocentra*, *Quipuanthus*, *Rostranthera*, *Sandemania*, *Schwackaea*, and *Tateanthus*).

The majority of species (2632) are restricted to a single country or area (following the Vascular Plant of the Americas arrangement), and fewer than 100 species are

widespread. A few species have escaped cultivation to become noxious weeds elsewhere (e.g., *Miconia calvescens* DC., with beautiful purple-colored abaxial leaf surfaces is called the Purple Plague in Hawaii). The most invasive species is Koster's Curse ((*Clidemia hirta* (L.) D. Don, now *Miconia crenata* (Vahl) Michelang.), which is naturalized in tropical Africa, Indian Ocean islands, Asia, Oceania, Australia, and Hawaii (see DeWalt et al., chapter "Ecology and Control of Naturalized Melastomataceae").

With some 1453 species, Brazil is by far the country with the highest melastome diversity in the Americas and globally (Fig. 2). Nearly two-thirds (929) of the species are endemic (Baumgratz et al. 2010; Goldenberg et al. 2020a). These species are centered in the Cerrado and the campo rupestre, the Atlantic Forest (see Bacci et al., chapter "Colonization and Diversification of Melastomataceae in the Atlantic Forest of South America"), and also in and around the Amazon basin, mostly near the wetter areas closer to the Andes to the west, the Guiana Shield to the north, and the transition to the Cerrado to the south. In all, 11 genera are endemic to Brazil: *Bertolonia* (near-endemic), *Bisglaziovia*, *Brasilianthus*, *Cambessedesia*, *Eriocnema*, *Fritzschia*, *Lithobium*, *Merianthera*, *Microlicia* (nearly endemic), *Physeterostemon*, and *Rupestrea*. Another six genera are largely centered in or have their greatest diversity in Brazil: *Huberia*, *Marcetia*, *Pleroma*, *Pterolepis*, *Rhynchanthera*, and *Siphanthera*. The uniquely Brazilian vegetation known as campo rupestre at higher elevations (mostly from about 800 to 2000 m), on the Cadeia do Espinhaço in Minas Gerais and Bahia states, is noted for its high incidence of generic and species-level endemism in a number of angiosperm families. In virtually all campo rupestre areas that have been studied to date, the Melastomataceae are typically one of the 10 or 12 families represented by the greatest number of species (Harley 1995; Giulietti and Pirani 1997; Pacifico and Almeda, chapter "Lavoisierae, a Neotropical Tribe with Remarkable Endemism on Eastern Brazilian Mountaintops").

The tropical Andes with 1964 species is another hotspot on the South American continent with most species in the montane cloud forests. Colombia has 991 spp., Peru 663 spp., Venezuela 636 spp., Ecuador 602 spp., and Bolivia 331 spp. The endemic and near-endemic genera of the tropical Andes are *Allomaieta*, *Alloneuron*, *Andesanthus* (nearly endemic), *Brachyotum*, *Bucquetia*, *Castratella*, *Centradeniastrum*, *Chaetolepis* (nearly endemic), *Chalybea*, *Kirkbridea*, *Quipuanthus*, and *Wurdastom*.

Amazonia (as defined by Cardoso et al. 2017, i.e., land below 1000 m elevation) harbors around 690 species, many of them widely distributed or found in more than one country. The most species-rich areas in western and northern Amazonia are near the foothills of the Andes or the Guiana Highlands. Amazonian-centered genera are *Acanthella*, *Bellucia*, *Henriettea*, *Opisthocentra*, and *Pachyloma*.

Among the tropical Andean countries, Colombia is a notable center of diversity. It has 991 species in 54 genera, 326 (ca. 33%) of which are endemic to the country. The distribution of melastome species among the 10 biogeographic regions of Colombia recognized by Bernal et al. (2016) is heavily concentrated in the Andes with 650 species (ca. 65%); some 261 (40%) species are endemic. *Miconia*, with 543 species, constitutes nearly 55% of melastome species in the country (Almeda

et al. 2016b; Michelangeli et al. 2020). The Sierra Nevada de Santa Marta (SNSM) in northern Colombia, the world's highest coastal mountain, is a displaced fault-bounded block that is isolated from the continuous ranges of the Andes by wide alluvial plains. This massif has long been recognized for its biological diversity and endemism, but much of the area remains insufficiently explored (Rangel and Garzón 1997). To date, some 17 genera and 86 species of Melastomataceae have been reported for the SNSM. In all, one genus, *Kirkbridea*, and 15 species are endemic to the SNSM (Alvear et al. 2015). Because of its large size (12,000 sq. km), elevation (5775 m), habitat diversity, and geographic position in northernmost Colombia, the SNSM could have played a stepping stone role in the migration of the Melastomataceae from the Andes to Central America, which is reflected in species distributions and affinities of these two regions (Alvear et al. 2015). At about 10.5° N, the range is actually farther from the equator than Panama and most of Costa Rica, which are to its southwest and west, respectively.

The Guiana Shield (Guyana, Suriname, French Guiana, Venezuelan Guayana, and neighboring Brazil) has a unique flora with some 450 species (Berry et al. 2002). Endemic genera to this region are *Appendicularia*, *Comoliopsis*, *Leiostegia*, *Maguireanthus*, *Mallophyton*, *Neblinantha*, *Ochthephilus*, *Rostranthera*, *Tateanthus*, and *Tryssophyton*. Two genera disjunct between the Andes and the Guiana Shield are *Boyania*, with one species in Caquetá (Colombia) and one in Guyana, and *Phainantha*, with one species on the sandstone table tops of the Cordillera del Cóndor in southeastern Ecuador and four in southeastern Venezuela and western Guyana. *Macrocentrum* is also mostly centered in the Guiana Shield with 25 species, but one species is endemic to the Coastal Cordillera of Venezuela and 2 to the Andes of Ecuador and Peru.

The Mexican and Central American region represents the northern center of diversity for the family in the western hemisphere. It has 546 species in 29 native genera (plus *Heterotis* and *Pleroma*, introduced adventives) representing 11 tribes of the Melastomatoideae plus the Olisbeoideae (Almeda 2009). Many species in several genera are shared with the tropical Andes and the adjacent areas of South America, but an impressive 317 species (58%) are endemic to the region. A heavy concentration of this diversity is centered in Costa Rica and Panama where 166 species (ca. 30%) are endemic. Species numbers decrease as one moves northward to Mexico where some 204 species occur (Villaseñor 2016; Zabalgoitia et al. 2020). Much of the diversity in Mexico is centered in the southern states of Oaxaca, Chiapas, and Veracruz with the 48 endemic Mexican species scattered throughout the southern and western states of the country. Two genera, *Heterocentron* and *Stanmarkia*, are restricted to the Mexican/Central American region and two others, *Centradenia* and *Pilocosta*, have all but one of their species restricted to the region, which makes them near-endemics.

In the Greater Antilles, some 452 species are found. There are no genera endemic to this region, although several radiations in the Miconieae and Merianieae have occurred. However, 392 species (87%) are endemic to the region, with most of them being single island endemics. In the Lesser Antilles, there are 66 species, and 13 of