PHYLOGENOMICS AND TAXONOMIC IMPLICATIONS OF OLD WORLD MELASTOMATACEAE

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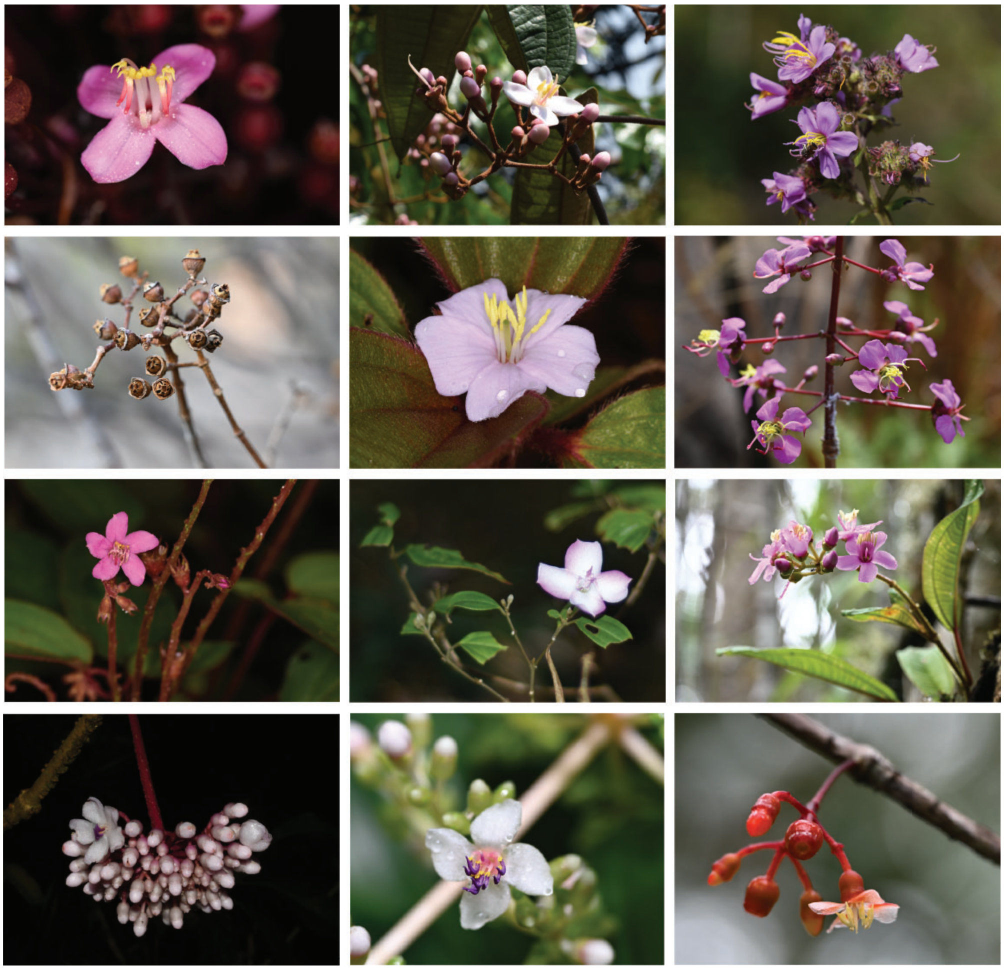

Luo Chen

München, 13 Dezember 2024

PREFACE

Statutory declaration

Herewith I certify under oath that I wrote the accompanying Dissertation myself.

Title: Phylogenomics and taxonomic implications of Old World Melastomataceae

In the thesis no other sources and aids have been used than those indicated. The passages of the thesis that are taken in wording or meaning from other sources have been marked with an indication of the sources (including the World Wide Web and other electronic text and data collections). Furthermore, all parts of the thesis that were de novo generated with the help of artificial intelligence tools were identified by footnotes/annotations at the appropriate places and the artificial intelligence tools used were listed. The prompts used were listed in the appendix. This statement applies to all text, graphics, drawings, sketch maps, and pictorial representations contained in the Work.

Declaration

Hereby I declare

- ☑ that this work, complete or in parts, has not yet been submitted to another examination institution.
- ☑ that I did not undergo another doctoral examination without success.

München, 11 März 2025	Luo Chen
Place, date	Signature

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Veranso-Libalah, M.C., Mertes, H., Stone, R.D., **Chen, L.**, St´evart, T., Almeda, F., van der Burgt, X.M., Kadereit, G. (2023). Phylogeny and systematics of the tribe Sonerileae (Melastomataceae) in Africa: A revised taxonomic classification. *Journal of Systematics and Evolution*, 61(4), 657–681.

Veranso-Libalah, M.C., **Chen, L.**, Bidault, E. (2023). Vivipary, a rare phenomenon in Afrotropical Melastomataceae. *Plant Ecology and Evolution*, 156(3), 333–338.

Declaration of contribution as co-author

This dissertation includes four chapters representing the studies I conducted during my PhD.

Chapter 2: **Chen, L.**, Kadereit, G., Veranso-Libalah, M.C., 2023. Combining Angiosperms353 and Sanger data provides support for the reinstatement of the genus *Myrianthemum* (Melastomataceae). Botanical Journal of the Linnean Society 203, 123-133.

Contributions: I conceptualized and designed the project in collaboration with Marie Claire Veranso-Libalah (MCVL). I performed data collection and analysis, including DNA extraction, Sanger sequencing, wood anatomy and seed morphology examination, and phylogenetic analysis. I prepared all figures, and drafted and revised the manuscript. Throughout the project, I was supervised by MCVL and Gudrun Kadereit (GK).

Chapter 3: Quakenbush, J.P.*, **Chen, L.***, Penneys, D.S., Barkman, T.J., Liu, Y., Yakandawala, D., Veranso-Libalah, M.C., Kadereit, G., 2024. Systematics of the fleshy-fruited Sonerileae (Melastomataceae). Taxon, online version published.

(Shared first authorship with J. Peter Quakenbush)

Contributions: I conceptualized and designed the project with J. Peter Quakenbush (JPQ) and GK. I conducted DNA extractions with JPQ and prepared the plates sent to Rapid Genomics (Gainesville, FL, USA) for sequencing. I performed the phylogenetic analysis and prepared figures 1–5 and all supplementary figures and tables. I wrote most of the Materials and Methods and the Results sections. I contributed to the Introduction and the Discussion sections, which were drafted by JPQ. Throughout the project, I was supervised by MCVL and GK.

Chapter 4: **Chen, L.**, van der Burgt, X., Haba, P., Kadereit, G., Veranso-Libalah, M.C. Phylogenomics of African Melastomateae (Melastomataceae): Revisiting generic relationships, placement of three enigmatic taxa, and description of two new genera. Taxon, under review.

Contributions: I conceptualized and designed the project in collaboration with MCVL. I performed the phylogenetic analysis and prepared tables as well as figures 3 and 4. I wrote most of the Materials and Methods and the Results section. I contributed to the Introduction and the Discussion sections, which were primarily written by MCVL. I was supervised by MCVL throughout the project.

Chapter 5: **Chen, L.**, Veranso-Libalah, M.C., Quakenbush, J.P., Morales-Briones, D.F., Kadereit, G. Comprehensive and sustainable utilization of genomic resources: Integrating target enrichment, genome skimming, RNA-seq, and deep genome skimming for improved phylogenetic resolution in Sonerileae (Melastomataceae). Drafted manuscript.

Contributions: I conceptualized and designed the project. I performed all data analyses, prepared all figures and tables, and drafted the manuscript. I was supervised by Diego F. Morales-Briones and GK throughout the project.

Supervisors' signatures

J. Peter Quakenbush's signature

To my family and 雯洁

CONTENTS

SUMMARY

My PhD dissertation focuses on the phylogenetics of the Old World Melastomataceae, utilizing newly generated and publicly available Sanger and next-generation sequencing (NGS) data. Melastomataceae are one of the largest flowering plant families, comprising approximately 173 genera and 5,858 species, with 2,117 species across 89 genera in the Old World. When I began my PhD, our understanding of the phylogenetic relationships within Melastomataceae was largely based on sequences from a few DNA markers generated through Sanger sequencing, which is prone to random errors in phylogenetic inference and often insufficient for resolving the phylogeny of groups with complex evolutionary histories. To improve our understanding of the phylogenies in Old World Melastomataceae, I studied three tribes: Dissochaeteae, Melastomateae, and Sonerileae. Together, these tribes include 76 genera and 1,500 species in the Old World, accounting for 70.9% of species and 85.4% of genera within this region.

By combining target enrichment and Sanger sequencing data, we found that the African endemic *Medinilla mirabilis* is sister to the tribe Dissochaeteae rather than grouping with other *Medinilla* species. This finding is supported by morphological and wood anatomical evidence. To reflect these results, we reinstated the genus *Myrianthemum* and included it within Dissochaeteae, expanding the previously Southeast Asian tribe to include Africa.

Nearly 40% of the species in the tribe Sonerileae have fleshy fruits and belong to six genera: *Medinilla*, *Pachycentria*, *Plethiandra*, *Heteroblemma*, *Catanthera*, and *Kendrickia*. We reconstructed the phylogeny of the fleshy-fruited Sonerileae for the first time using 385 nuclear and 81 plastid loci, which were recovered from target enrichment and publicly available NGS data. Our results revealed that the fleshy-fruited Sonerileae are not monophyletic and belong to three distinct clades: *Kendrickia* is sister to the Afrotropical endemic clade; *Heteroblemma* and *Catanthera* form a clade closely related to some species of *Phyllagathis* and *Driessenia*; and *Medinilla* forms a clade with *Pachycentria* and *Plethiandra* nested within it. To achieve monophyly for *Medinilla*, we synonymized *Pachycentria* and *Plethiandra* under *Medinilla*, redefined the genus, and provided new names for the species previously belonging to *Pachycentria* and *Plethiandra*. Additionally, we identified and characterized 15 clades within the newly defined *Medinilla*, which can serve as a basis for future infrageneric classification.

With all recognized Old World genera sampled, including three enigmatic taxa (*Dissotis leonensis*, *D. splendens*, and *Dionychastrum schliebenii*) that had never been sequenced before, we revisited the phylogeny of the Old World Melastomateae using 384 nuclear loci recovered from target enrichment data. Our results confirmed previous findings based on Sanger data, showing that the Old World Melastomateae are monophyletic, comprising two primary lineages: the Euheterotis and the

Pseudoheterotis clades. Additionally, we found that the Malagasy clade is sister to the Asian clade, both nested within the African lineages. All Old World genera, except *Osbeckia* and *Melastomastrum*, were recovered as monophyletic. *Dissotis leonensis* and *D. splendens* formed distinct clades and were not closely related to *Dissotis*, which was supported by morphological, seed, and wood anatomical evidence. To reflect these findings, we established two new genera, *Allodissotis* and *Paleodissotis*, treated *D. leonensis* and *D. splendens*, and provided an updated key to the African Melastomateae.

Finally, using a newly developed reference comprising 5,626 loci based on genomic and transcriptomic data, we integrated newly generated and publicly available NGS data from multiple sources to reconstruct a well-supported, near-comprehensive (41/46 genera) phylogeny for Sonerileae. The Neotropical lineages and the African endemic *Benna* are successively sister to the rest of the tribe, which consists of a clade comprising the Sri Lankan endemic *Kendrickia* and Afrotropical Sonerileae, and a primarily Asian clade. Phylogenetic relationships within both the Afrotropical and Asian clades were largely consistent with previous studies based on Sanger sequencing and genome resequencing data, respectively. Our analyses also provided evidence of rapid radiation within the Asian Sonerileae, likely driven by a whole genome duplication event that occurred before the divergence of the two major clades within the Asian lineage.

CHAPTER 1

GENERAL INTRODUCTION

1.1. Evolution of sequencing strategies for phylogenetic studies

In the broadest sense, a phylogeny is defined as a tree containing nodes connected by branches, representing the persistence of genetic lineages through time (Yang and Rannala, 2012). In the field of plant systematics, an accurate phylogeny is essential not only for understanding the relationships among species, populations, or genes but also for tracing the origin and evolution of key traits (Lamichhaney et al., 2015; Satterlee et al., 2024), estimating the timing of evolutionary events (Silvestro et al., 2021; Álvarez-Carretero et al., 2022), reconstructing ancestral geographic distributions (Ramírez-Barahona et al., 2020; Jin et al., 2021), detecting whole genome duplications (WGD) (Dehal and Boore, 2005; Jiao et al., 2011; Yang et al., 2018), and numerous other applications.

In the early days of plant systematics, characters for phylogenetic analysis relied primarily on morphological, as well as anatomical, cytological, and phytochemical traits (Fairbrothers et al., 1975; Raven, 1975; Bremer, 1985; Doyle and Donoghue, 1986). However, these characters are often susceptible to convergent or parallel evolution (Wake et al., 2011), and the number of reliable homologous characters is limited (Delsuc et al., 2005). The introduction of macromolecular markers significantly expanded the range of characters available for phylogenetic analysis. Protein-based markers like isozymes were successfully used to address questions in species-level systematics, reticulate evolution, and polyploidy (Brown, 1990; Crawford, 2000). With the introduction of DNA-based markers, such as RFLP (Restriction Fragment Length Polymorphism), AFLP (Amplified Fragment Length Polymorphism), RAPD (Random Amplified Polymorphic DNA), and SSR (Simple Sequence Repeat) markers, even greater resolution became possible (Wolfe and Liston, 1998). However, it was the development of DNA sequencing that fundamentally changed research approaches in the field.

In the late 1980s and early 1990s, DNA sequences obtained via Sanger sequencing began to be widely used in phylogenetic analysis (Zurawski and Clegg, 1987; Palmer et al., 1988; Baldwin, 1992; Hamby and Zimmer, 1992). A milestone study by Chase et al. (1993) reconstructed the phylogeny of seed plants using the plastid gene *rbcL*, and many of its conclusions remain valid today. Even today, Sanger sequencing data continue to play an important role in reconstructing phylogenetic relationships in different plant lineages (Doğru-Koca, 2024; Ling et al., 2024; Madhani et al., 2024). Despite the wide range of applications, phylogenetic information derived from a few loci using Sanger sequencing is prone to stochastic errors due to the limited sequence length, which makes it insufficient to resolve lineages with complex evolutionary histories, such as those involving rapid radiations (Pease et al., 2016; Stiller et al., 2024), hybridization and introgression (Morales-Briones et al., 2020; Stiller et al., 2024), horizontal gene transfer (HGT) (Gogarten and Townsend, 2005; Dunning et al., 2019), or recent WGD (Yang et al., 2018; Leebens-Mack et al., 2019). The advances in high-throughput sequencing (HTS) technologies offer an opportunity to address these challenges by providing phylogenetic signals from hundreds to thousands of loci.

HTS includes both the short-read next-generation sequencing (NGS) (e.g., 454 and Illumina) and long-read third-generation sequencing (e.g., PacBio and Nanopore) (Guo et al., 2023). Although HTS is becoming increasingly affordable, identifying the most cost-effective markers for phylogenetic analysis remains crucial. This need has driven researchers to develop various sequencing strategies to accommodate different research objectives and budgets.

Whole genome sequencing (WGS) theoretically provides access to the complete genetic information carried by the three genomes (nuclear, plastid, and mitochondrial). In flowering plants, genome sizes vary widely, ranging from ~60 Mb to 148 Gb (Pellicer and Leitch, 2020). WGS captures data from single nucleotide substitutions in both coding and non-coding regions, as well as rare structural changes in the genome (Rokas and Holland, 2000), such as indels (Redelings and Suchard, 2007) and gene rearrangements (Schultz et al., 2023). This approach has been applied to phylogenetic studies of specific plant groups (Guo et al., 2024; Wan et al., 2024) and the whole angiosperms (Zhao et al., 2021).

However, effective WGS, particularly using long-read sequencing technologies, typically requires at least 40-50x coverage and relies on high-quality DNA as input (Li and Harkess, 2018). This requirement presents challenges for many plant systematics studies, which often rely on herbarium specimens with degraded DNA and are limited by budget constraints, particularly for plants with large genomes. Consequently, many alternative sequencing strategies have been widely used. Below, we discuss some of the most commonly used strategies.

Transcriptome sequencing, or RNA-Seq, was originally developed for transcriptome profiling (Wang et al., 2009). When applied to phylogenetic studies, RNA-Seq targets cDNA that is reverse-transcribed from RNA, typically focusing on mRNA, including sequences from nuclear and organellar genomes. This approach is a reliable method with comparable accuracy to WGS for phylogenetic analysis (Cheon et al., 2020) and has been widely adopted in plant phylogenetics (Wickett et al., 2014; Yang and Smith, 2014; Leebens-Mack et al., 2019). Nevertheless, due to the instability of RNA, its isolation generally requires fresh material or material stored at -80 °C. Although some recent studies have shown that silica gel-dried material can be used (Chen et al., 2022; He et al., 2022; Ruiz-Vargas et al., 2024), the material needs to be either stored at -20 °C or used for RNA extraction within one year of collection. However, using silica-dried material might be risky and effectively excludes the possibility of using herbarium specimens, which often contain highly degraded RNA.

Genome skimming is similar to WGS but performed at low coverage. While some nuclear loci (Straub et al., 2012; Besnard et al., 2014; Pezzini et al., 2023; Pouchon and Boluda, 2023) and mitochondrial loci (Straub et al., 2012; Fonseca and Lohmann, 2020) can be recovered using this method, it is most commonly used in plant systematics to sequence plastomes (Zhang et al., 2020; Li et al., 2021) and nuclear ribosomal DNA (nrDNA) (Zeng et al., 2018; Nevill et al., 2020) due to the high-copy numbers of plastid DNA and nrDNA in plant cells. Genome skimming has also been demonstrated to be effective for extracting phylogenetic information from historical herbarium specimens (Besnard et al., 2014; Bakker et al., 2015; Zeng et al., 2018), making it a valuable tool for utilizing older or degraded plant material in systematic studies.

Target enrichment sequencing, or target capture, is similar to genome skimming but involves an additional step before sequencing. The DNA libraries are hybridized with target-specific probes to selectively enrich genomic regions of interest, resulting in higher coverage of these regions in the sample (Mamanova et al., 2010). Similar to genome skimming, historical herbarium specimens can also be used for target enrichment (Gardner et al., 2020; Zuntini et al., 2024). Target enrichment has proven highly successful in advancing plant phylogenetics across various taxonomic levels, from population-level studies (Villaverde et al., 2018; Jiménez-Mena et al., 2022) to reconstructing phylogeny for the entire angiosperm (Zuntini et al., 2024). Off-target sequences and paralogs are two common issues with target enrichment (Baker et al., 2021), although both have also been useful. Off-target sequences often contain abundant organellar and nrDNA loci, which can provide additional phylogenetic information (Weitemier et al., 2014; Allio et al., 2020; Mendoza et al., 2020), while paralogs can be used to improve phylogenetic resolution (Gardner et al., 2020; Ufimov et al., 2022) and to detect polyploidy events (Morales-Briones et al., 2021). Another challenge with target enrichment is the variable gene recovery rate when using universal probe sets like Angiosperms353, which may not perform well in some lineages (Baker et al., 2021). Designing a set of custom probes can improve capture efficiency but is often time-consuming and costly.

Hyb-Seq, as used here to refer to the sequencing strategy involving sequencing both enriched (target enrichment) and unenriched (genome skimming) libraries, is different from its original meaning where Hyb-Seq is synonymous with target enrichment alone (Weitemier et al., 2014). Targeting nuclear and organellar loci in a single probe set is generally not recommended because the coverage of nuclear loci may be affected due to the high copy number of organellar loci (Andermann et al., 2020). Hyb-Seq enables simultaneously targeted sequencing of abundant nuclear loci and genome skimming of organellar genomes and high-copy nuclear loci like rDNA (Dodsworth et al., 2019). This strategy has been successfully applied to cost-effectively obtain phylogenetic information from both nuclear and plastid genomes (Muñoz-Rodríguez et al., 2018; Villaverde et al., 2018).

Deep Genome Skimming (DGS) is a relatively newly coined, somewhat paradoxical term (Liu et al., 2021), but it has been explored for quite some time to recover low-copy nuclear loci from genome skimming data (Blischak et al., 2014; Berger et al., 2017; Vargas et al., 2019; Zhang et al., 2019), dating back to even the first paper proposing the concept of genome skimming (Straub et al., 2012). DGS builds on the concept of genome skimming but with a higher sequencing depth. However, since there is no clear definition of how “low” the coverage should be for genome skimming, there is similarly no precise definition of how "deep" the sequencing should be for DGS. Genome resequencing is commonly used in crop genetics and population-based studies where a reference genome assembly is available. In practice, genome resequencing often falls within the definition of DGS (Du et al., 2018; Zhao et al., 2019). Zhang et al. (2019), using Hexapoda data sets, demonstrated that it is feasible to extract hundreds to thousands of BUSCOs (Benchmarking Universal Single-Copy Orthologs) and UCEs (ultraconserved elements) from low-coverage genome sequencing data with a minimum coverage of 10x needed for BUSCOs and 5x for UCEs. Interestingly, their results indicated that 20x coverage may represent a threshold, as most statistics reached convergence after 20x. Liu et al. (2021) reached similar conclusions using Vitaceae data sets. Their results indicated that 10x is the minimum coverage needed to recover single-copy nuclear genes (SCNs) from genome skimming data, and the phylogenetic topology recovered from 10x data was similar to that from 20x data. DGS can also be applied to herbarium specimens (Liu et al., 2021; Liu et al., 2022a; Chen et al., 2023a). The advantage of DGS over currently popular target enrichment is that it does not require designing probes or additional lab work while simultaneously capturing hundreds to thousands of nuclear loci and organellar genomes in a single sequencing run. Additionally, the data can easily be reutilized and integrated into future studies. However, the main drawback is that DGS is most effective with relatively small genomes, as sequencing larger genomes can become expensive due to the high coverage required.

RAD-Seq (Restriction-site Associated DNA Sequencing) originally referred to a specific method introduced by Baird et al. (2008), but over time, it has been used to describe a wide range of methods that rely on restriction enzymes to select the loci for sequencing (Andrews et al., 2016). These methods include those that sequence fragments adjacent to the restriction enzyme cut sites, such as the original RAD-Seq (Baird et al., 2008) and 2bRAD (Wang et al., 2012), as well as methods that sequence fragments flanked by two cut sites, such as genotyping by sequencing (GBS) (Elshire et al., 2011) and double-digest RAD (ddRAD) (Peterson et al., 2012). Interestingly, the term GBS is sometimes used to encompass all these methods (e.g., Vaux et al. 2023), leading to some confusion in terminology; see Campbell et al. (2018) for further discussion on the naming confusion).

Overall, RAD-Seq methods provide a cost-effective way to obtain hundreds to thousands of loci across the genome with relatively high coverage (Andrews et al., 2016). RAD-Seq methods were originally optimized for high-molecular-weight genomic DNA, which is typically not available for highly degraded DNA from herbarium specimens (Andrews et al., 2016), and it has been found that DNA degradation poses a significant challenge for RAD-Seq (Graham et al., 2015). However, there have been successful reports of applying RAD-Seq to herbarium specimens (Massatti et al., 2016; Jordon-Thaden et al., 2020; Comito et al., 2022). The major drawbacks of RAD-Seq methods include missing data, which can be particularly severe for divergent taxa (McKain et al., 2018), the limited length of each locus, which affects coalescent-based species tree inference (McKain et al., 2018; Hühn et al., 2022), and challenges in identifying orthology, especially in the absence of a reference genome (McKain et al., 2018). Despite these limitations, RAD-Seq methods have been successfully applied to many shallow-scale phylogenetic studies (Fernández-Mazuecos et al., 2017; Spriggs and Fertakos, 2021; Messerschmid et al., 2023).

1.2. Molecular systematics of the Melastomataceae

A recently published book comprehensively reviews the systematics, evolution, and ecology of the plant family Melastomataceae (Goldenberg et al., 2022). The family includes 173 genera and approximately 5,858 species, placing it among the ten largest flowering plant families. The family is predominantly tropical, with 3,742 species in 84 genera found in the New World and 2,117 species in 89 genera in the Old World (Ulloa Ulloa et al., 2022).

The work on the systematics of Melastomataceae began with the establishment of the family in 1789 in Jussieu's *Genera plantarum* (de Jussieu, 1789), where only nine genera were included. Subsequent efforts to delimit and classify the family were made by several botanists, including David Don (Don, 1823), Augustin Pyramus de Candolle (de Candolle, 1828a, b, c), Charles Victor Naudin (Naudin, 1849-1853), José Jerónimo Triana (Triana, 1866; Triana, 1871 [“1872”]), Joseph Dalton Hooker (Hooker, 1867), Célestin Alfred Cogniaux (Cogniaux, 1883–1888, 1891), Fridolin Krasser (Krasser, 1893), Gerardus J. C. M. van Vliet (van Vliet, 1981) and his associates (van Vliet et al., 1981), and Susanne S. Renner (Renner, 1993). These researchers worked on refining the delimitation of the family and proposed various infrafamilial classifications based on morphological and anatomical evidence. All these efforts, in combination with extensive botanical collections from across the tropics, led to the recognition of two subfamilies, nine tribes, and 166 genera within Melastomataceae, as well as six genera in Memecylaceae in the last major classification of the family before the molecular era (Renner, 1993). For more detailed information on the historical development of Melastomataceae systematics, see Almeda (2022) "Classification History of the Melastomataceae: Early Beginnings Through the Pre-molecular Era."

Melastomataceae were first sequenced in two phylogenetic studies of Myrtales using *rbcS* (Martin and Dowd, 1986) and *rbcL* (Conti et al., 1996), respectively. Clausing and Renner (2001) were the first to apply molecular phylogenetics to a family-wide analysis of Melastomataceae using three plastid loci. Their findings revealed that neither the Old World nor the New World Melastomataceae are monophyletic. Additionally, they found that Melastomataceae are sister to Memecylaceae and provided the first insights into the relationships among the various tribes within the family. Following this initial work, numerous studies employing Sanger sequencing have been conducted to investigate specific tribes and genera within Melastomataceae. Examples include studies on tribes such as Melastomateae (Michelangeli et al., 2012; Veranso-Libalah et al., 2017; Veranso-Libalah et al., 2020), Dissochaeteae (Kartonegoro et al., 2021), Sonerileae (Zhou et al., 2019a; Veranso-Libalah et al., 2023), and Pyramieae (Bochorny et al., 2019), as well as on genera like *Merianthera* (Goldenberg et al., 2012), *Miconia* (Goldenberg et al., 2008), and *Memecylon* (Stone, 2014). Recently, a phylogenetic analysis with the most comprehensive sampling to date included 2,973 terminals, 2,435 Melastomataceae species, and 158 of the recognized 177 genera, using two nuclear loci and seven plastid loci. The resulting phylogeny was used to propose a new classification system for Melastomataceae, representing a comprehensive summary of our understanding of the above-species level systematics of the family in the Sanger sequencing era. In this system, the treated 177 genera and 5,858 species were grouped into three subfamilies: Olisbeoideae, Kibessioideae, and Melastomatoideae. The subfamily Melastomatoideae were further divided into 21 tribes (Penneys et al., 2022).

Phylogenomic studies in Melastomataceae began with plastid phylogenomics when the first 16 plastomes were assembled and annotated using genome skimming data (Reginato et al., 2016). Since then, major studies involving plastid phylogenomics, beyond just reporting a single or a few plastome assemblies, have been conducted only in Sonerileae (Zhou et al., 2019b; Zhou et al., 2022) and *Miconia* (Majure et al., 2023). As of October 29, 2024, there are 221 plastomes, representing 169 taxa of Melastomataceae, available on GenBank.

Nuclear phylogenomic studies in Melastomataceae have followed two major approaches: one based on target enrichment and the other on WGS and resequencing.

In the first approach, a set of Melastomataceae-specific probes was developed, containing 384 loci, of which 266 loci are derived from the Angiosperms353 project, while the remainder are Melastomataceae-specific (Jantzen et al., 2020). This probe set has been used in a large international collaborative effort to sequence the entire family, with published studies on *Memecylon* (Amarasinghe et al., 2021a; Amarasinghe et al., 2021b) and *Tibouchina* (Jantzen et al., 2022). The probe set was further cleaned and expanded to include additional sequences from the mega353 target file (McLay et al., 2021) for improved sequence recovery (Dagallier and Michelangeli, 2024). Utilizing the original Angiosperms353 probe set, Maurin et al. (2021) conducted a phylogenomic study of Myrtales, including 194 taxa from Melastomataceae, representing the first phylogenomic study with family-wide sampling for Melastomataceae.

The second approach, based on WGS and resequencing, is currently limited to a study on the tribe Sonerileae. Similar to other studies, this study used ten transcriptomes from Asian Sonerileae to identify single-copy orthologs (SCOs). These SCOs were then mapped to a newly sequenced draft genome of *Tigridiopalma magnifica* to verify copy numbers. A partial genome of *Bredia hirsuta* was subsequently constructed by recovering intron sequences of the SCOs from the resequencing data of *Bredia hirsuta*. Resequencing data from 223 accessions, representing 205 species (primarily from Sonerileae, but also including species from Dissochaeteae, Melastomateae, Blakeeae, and Bertolonieae), were mapped to the partial genome of *Bredia hirsuta*. Additionally, the authors generated a genomic SNP data set by mapping resequencing data to the draft genome of *Tigridiopalma magnifica* and also constructed a plastome data set (Zhou et al., 2022).

Currently, three genomes from Melastomataceae have been sequenced and made publicly available, including two from Melastomateae and one from Sonerileae: *Melastoma dodecandrum* (Hao et al., 2022), *Melastoma candidum* (Zhong et al., 2023), and *Barthea barthei* (Huang et al., 2024). These newly sequenced genomes were included in phylogenetic analyses, though Melastomataceae were represented by only one to three species in each analysis. While these studies provided limited insights into infrafamilial phylogeny, they offered valuable insights beyond generating genomic resources, including the evolution of trichomes (Zhong et al., 2023), the genetic basis of flower color variation (Huang et al., 2024), and the evolution of creeping stems and heteranthery (Hao et al., 2022). Furthermore, all three studies found evidence of whole genome duplications (WGDs) within the family (Hao et al., 2022; Zhong et al., 2023; Huang et al., 2024).

1.3. The Old World Melastomataceae and aims of the dissertation

In the latest infrafamilial classification system (Penneys et al., 2022), the 2,117 species and 89 genera of Old World Melastomataceae are classified into all three subfamilies of the family: Olisbeoideae, Kibessioideae, and Melastomatoideae. Within Melastomatoideae, six tribes include Old World genera: Astronieae, Sonerileae, Dissochaeteae, Dinophoreae, Melastomateae, and Feliciadamieae. Of these groups, Olisbeoideae, Astronieae, Sonerileae, and Melastomateae have a disjunct distribution between the Old World and the New World, while the other groups are endemic to the Old World. Compared to the New World Melastomataceae, the Old World counterparts have generally been less studied (Goldenberg et al., 2022), with many taxa never included in molecular phylogenetic analyses.

When I started my PhD in April 2021, my two supervisors, Gudrun Kadereit and Marie Claire Veranso-Libalah, along with our collaborators, had just initiated a project to sequence the entire Melastomataceae family using the Hyb-Seq strategy combining genome skimming and target enrichment using the Melastomataceae probe set. This project aimed to include as many species as possible, with our particular focus on the Old World, especially the Afrotropical taxa. By that time, phylogenomic analysis of the Old World Melastomataceae had only been conducted on Asian Sonerileae using plastomes (Zhou et al., 2019b) and *Memecylon* (Olisbeoideae) with target enrichment data (Amarasinghe et al., 2021a). The newly generated Hyb-Seq data provided an opportunity to improve our understanding of the systematics of Old World Melastomataceae.

In this study, we used newly generated Hyb-Seq data, in combination with publicly available Sanger sequencing and NGS data, to investigate the phylogenies of the Old World Melastomataceae. We aimed to (1) improve our understanding of the systematics and evolution of the Old World Melastomataceae, and (2) explore optimal approaches for integrating different sequencing data sets. We focused on the tribes Dissochaeteae (Fig. 1), Sonerileae (Fig. 2), and Melastomateae (Fig. 1), which together encompass 76 genera and 1,500 species, accounting for 70.9% of the species and 85.4% of the genera within the Old World Melastomataceae (Ulloa Ulloa et al., 2022). Below are the specific research questions addressed in each chapter:

Chapter 1: Can Sanger sequencing data still be utilized effectively in an era dominated by HTS? Does the morphologically unique African endemic species *Medinilla mirabilis* truly belong to *Medinilla*? Where is it placed in the phylogeny?

Chapter 2: Can target enrichment data be used to resolve the phylogeny of the fleshy-fruited Sonerileae (*Catanthera*, *Heteroblemma*, *Kendrickia*, *Medinilla*, *Pachycentria*, and *Plethiandra*)? Do fleshy-fruited Sonerileae form one clade? With dense sampling, is the mega-diverse widely distributed genus *Medinilla* monophyletic?

Chapter 3: Can target enrichment data resolve the phylogeny of the Old World Melastomateae? With comprehensive sampling covering all Old World genera of Melastomateae, are the inter-generic relationships consistent with previous results obtained from Sanger sequencing data? Where are the three enigmatic, newly sampled species placed in the phylogeny?

Chapter 4: Is it possible to find an optimal approach to integrate different NGS data, including DGS, target enrichment using different probe sets, Hyb-Seq, and RNA-Seq? What are the phylogenetic relationships between and within the Neotropical, Afrotropical, and Asian Sonerileae? Can the new phylogeny help determine the placement of WGD? Is there a link between WGD and the rapid radiation of the tribe in tropical Asia?

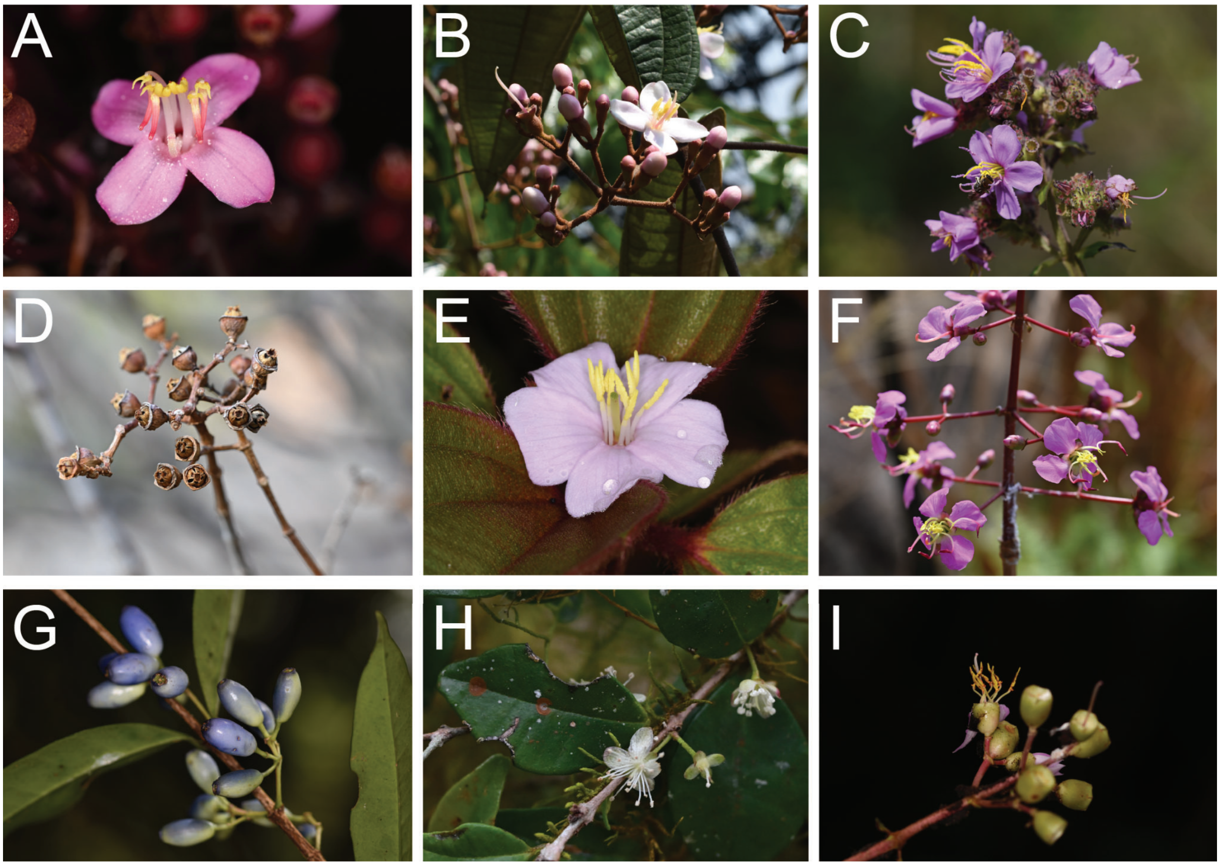

Fig. 1 Representative species of the Old World Melastomataceae:

Dissochaeteae: A. *Myrianthemum mirabile* (Cameroon); B. *Dissochaeta fallax* (Java, Indonesia)

Melastomateae: C. *Dupineta brazzae* (Cameroon); D. *Dionycha bojerii* (Madagascar); E. *Tristemma mauritianum* (Cameroon), F. *Dichaetanthera crassinodis* (Madagascar)

Olisbeoideae: G. *Memecylon nodosum* (Cameroon), *Memecylon* sp. (Madagascar)

Dinophoreae: I. *Ochthocharis dicellandroides* (Cameroon)

Photos by Luo Chen (including all photos in Figure 2).

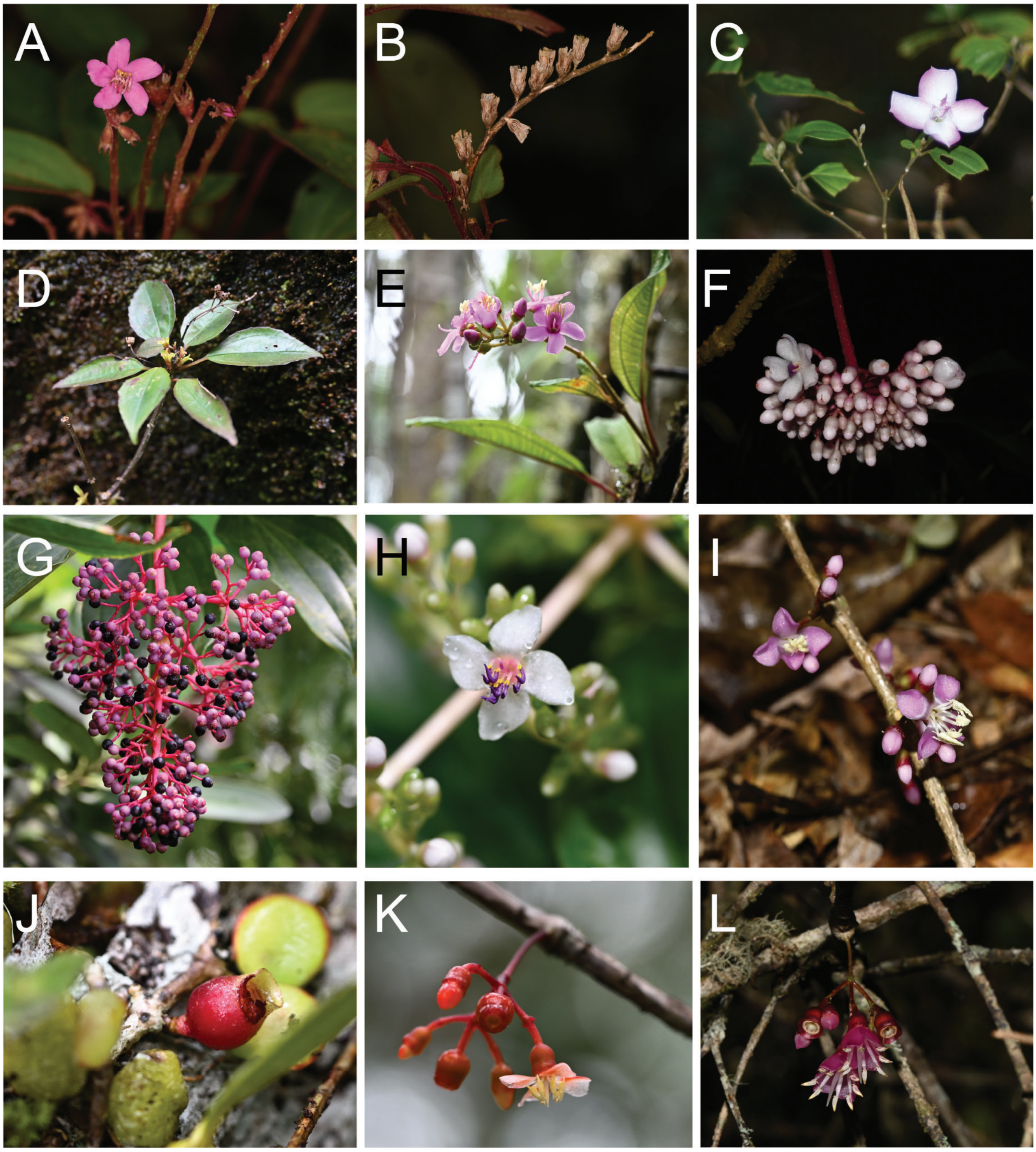

Fig. 2 Representative species of the Old World Melastomataceae, continued:

Sonerileae: A, B. *Mendelia mollis* (Cameroon); C. *Barthea barthei* (China); D. *Tashiroea quadrangularis* (China); E. *Gravesia laxiflora* (Madagascar); F. *Medinilla alpestris* (Sumatra, Indonesia); G. *Medinilla banahaensis* (Munich botanical garden; originally from the Philippines); H. *Medinilla pendula* (Munich botanical garden; originally from the Philippines); I. *Medinilla chermezonii* (Madagascar); J. *Medinilla sedifolia* (Madagascar); K. *Medinilla baroni* (Madagascar); L. *Medinilla papillosa* (Madagascar)

CHAPTER 2

COMBINING ANGIOSPERMS353 AND SANGER DATA PROVIDES SUPPORT FOR THE REINSTATEMENT OF THE GENUS MYRIANTHEMUM (MELASTOMATACEAE)

Chen, L., Kadereit, G., Veranso-Libalah, M.C. (2023)

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Original Article

Combining Angiosperms353 and Sanger data provides support for the reinstatement of the genus *Myrianthemum* (Melastomataceae)

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ABSTRACT

The increasing availability of DNA sequence data, in particular target enrichment data based on the universal Angiosperms353 probe set, but also accumulated Sanger data from previous phylogenetic studies, is facilitating the placement of taxa that are difficult to place with certainty based on morphological evidence alone. Here, we investigate phylogenetic relationships of *Medinilla mirabilis* (Melastomataceae), a species distributed in central Africa and currently classified in the mega-diverse genus *Medinilla* of tribe Sonerileae. *Medinilla mirabilis* is a twining liana with verticillate leaves when young, spherical inflorescences, 4-merous flowers, dimorphic stamens, and baccate fruits. Our results revealed that *M. mirabilis* is sister to tribe Dissochaeteae and only distantly related to *Medinilla.* We also provide new data on wood anatomical and seed morphological characters of *M. mirabilis*. The alternate inter-vessel pits in *M. mirabilis* and Dissochaeteae are consistent with the phylogenetic placement. Seeds of *M. mirabilis* are similar to those of Dissochaeteae and of *Medinilla.* Due to its unique morphology and phylogenetic position, we propose to reinstate the monospecific genus *Myrianthemum* with *Myrianthemum mirabile.* This necessitates expansion of the Southeast Asian tribe Dissochaeteae to include *Myrianthemum* as its only African member. Our study of *M. mirabile* demonstrates that the combined application of Angiosperms353 and Sanger data is a cost-effective approach to phylogenetically place enigmatic taxa.

Keywords: Africa; seed morphology; wood anatomy; phylogenetics

INTRODUCTION

Every year, ~2000 new plant species are described (Christenhusz and Byng 2016), and many are rediscovered and collected. Phylogenetic placement of these species has important implications for our understanding of their evolutionary history. The most intuitive and cost-effective way to phylogenetically place a taxon that remained unsampled is to add new data to existing sequencing data. Until recently, this has been done using Sanger sequencing data. Within Melastomataceae, phylogenetic placement using Sanger sequencing data has resulted in the descriptions of new genera [e.g. *Benna* Burgt & Ver.-Lib. (van der Burgt *et al.* 2022) and *Nothodissotis* Ver.-Lib. & G.Kadereit (Veranso-Libalah *et al.* 2019)] and new tribes [e.g. Marcetieae (Rocha *et al.* 2018), Lithobieae, and Eriocnemeae (Penneys *et al.* 2020)]. Also, *Cailliella* Jacq.-Fél., until recently only known from its type specimen, was confirmed as a member of tribe Melastomateae based on a recent collection (Veranso-Libalah *et al.* 2021). Over the last three decades, millions of Sanger sequences have been generated and used for phylogenetic studies. However, the use of only few Sanger-sequenced genes can result in stochastic errors and often does not provide enough information to achieve phylogenetic resolution (Jeffroy *et al.* 2006, Kapli *et al.* 2020).

Angiosperms353 (Johnson *et al.* 2018) is a set of target enrichment probes designed to capture 353 putatively single-copy protein-coding nuclear genes. As a universal probe set for angiosperms, Angiosperms353 is being used in 'The Plant and Fungal Trees of Life' Project (PAFTOL; www.paftol.org),

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which aims at generating target enrichment data for all genera of flowering plants (Baker *et al.* 2021a). To increase data usability, Angiosperms353 has also been included in the design of group-specific probe sets (Angiosperms353-related) (Jantzen *et al.* 2020, Ogutcen *et al.* 2021, Acha and Majure 2022). The rapid accumulation of Angiosperms353 and Angiosperms353-related data is making it possible for us to place a taxon of interest in the flowering plant tree of life using phylogenomic data, which can greatly reduce the aforementioned stochastic errors and provide more sequence information. For example, phylogenomic data for 412 families, 7514 genera, and 9404 species have been released in the Kew Tree of Life Explorer Release 2.0 (https://treeoflife.kew.org/release-history). However, although a large quantity of data has been generated, many genera (especially from the tropics) remain unsampled. Given the vast diversity of flowering plants (~14 000 genera and ~325 000 species; Antonelli *et al.* 2020), it will take time before a few taxa of interest can be placed phylogenetically at genus or even species level using Angiosperms353 data. One expedient approach to this problem is to additionally use Sanger sequencing data accumulated over the past three decades. The combination strategy of using both Angiosperms353 and Sanger sequencing data so far has only been used to investigate generic limits in Urticaceae (Wells *et al.* 2021).

Melastomataceae, with 173 genera and ~5858 species (Ulloa Ulloa *et al.* 2022), belong to Myrtales (Maurin *et al.* 2021). Using the Angiosperms353 probe set, Maurin *et al.* (2021) provided the most comprehensive phylogeny to date for Myrtales, representing ~76% of the generic diversity of the order. In Melastomataceae, 193 species representing 116 genera and 19 tribes were included in this analysis. Most of the unsampled or under-sampled taxa of Melastomataceae are restricted mainly to the Old World. One such taxon is *Medinilla* Gaudich. ex DC., a morphologically diverse genus with 379 species in the Afrotropics, Asia, and Oceania (Liu *et al.* 2022), of which only three Southeast Asian and one Malagasy species were sampled by Maurin *et al.* (2021). *Medinilla* has been treated in either tribe Dissochaeteae (e.g. Triana, 1871 [‘1872’], Van Vliet *et al.* 1981) or Miconieae (Renner 1993) based on morphological and anatomical evidence, but molecular phylogenetic analyses of a few representatives have revealed that although the monophyly of *Medinilla* and its circumscription remain to be resolved, all the sampled species belong to Sonerileae (Zhou *et al.* 2019, 2022, Kartonegoro *et al.* 2021, Penneys *et al.* 2022, Veranso-Libalah *et al.* 2022).

In tropical Africa and Madagascar, there exist 73 species of *Medinilla*, of which 70 are endemic to Madagascar, the center of diversity. Only three species occur in mainland Africa, i.e. *Medinilla engleri* Gilg, a rare species endemic to Tanzania, *Medinilla mannii* Hook. f., which is widely distributed in West-Central Africa and the Gulf of Guinea islands, and *Medinilla mirabilis* (Gilg) Jacq.-Fél. (Fig. 1) occurring in Central African countries (Fig. 2) (Veranso-Libalah *et al.* 2022). *Medinilla mirabilis* can easily be distinguished from the other two mainland African species by its growth form (twining liana), leaf arrangement (leaves verticillate in young and alternate in old parts of a plant), its spherical inflorescence composed of many cymes, and its dimorphic stamens. The other two African species are epiphytic shrubs with opposite leaves, fewer flowers, and equal to subequal stamens. *Medinilla mirabilis* was first described in 1897 as *Myrianthemum mirabile* Gilg (Engler, 1897) and later transferred to *Medinilla* by Jacques-Félix (1977) who believed that *Myrianthemum mirabile* fits into the very diverse and widespread palaeotropical genus *Medinilla*, despite its marked differences from the other two mainland African *Medinilla* species (Jacques-Félix 1977). *Myrianthemum* Gilg has since been treated as a synonym of *Medinilla*. Although widely collected within its distribution range, *M. mirabilis* has not been included in any phylogenetic study, so its tribal and generic placement remain untested.

Before the molecular era, both wood anatomical (Koek-Noorman *et al.* 1979, Van Vliet 1981, Van Vliet *et al.* 1981, Welle and Koek-Noorman 1981) and seed morphological characters (Whiffin and Tomb 1972, Michelangeli 2000) were used for the tribal and generic classification of Melastomataceae, and many aspects of the classification based on wood anatomical evidence (Van Vliet *et al.* 1981) have been supported by molecular data (Clausing and Renner 2001, Penneys *et al.* 2022). In particular, Dissochaeteae were divided into two subtribes based on wood anatomy: Medinillinae, including *Medinilla* and its alliance, and Dissochaetinae including most genera still belonging to Dissochaeteae. Seed morphological studies in Miconieae (Ocampo and Almeda 2013) and the whole family (Ocampo *et al.* 2022) indicated that seed morphology does not reflect phylogenetic relationships, although it is quite conserved in Melastomateae (Veranso-Libalah *et al.* 2020). However, as many species of Melastomataceae have not been included in wood anatomical and seed morphological studies, it remains unknown whether these characters can provide useful information for generic delimitation.

In this paper, using Angiosperms353 data and the phylogenomic framework generated by Maurin *et al.* (2021), we investigate the tribal and generic placement of *M. mirabilis*. Additional Sanger data are used to overcome the problem of insufficient taxon sampling for phylogenomic data. We use the phylogenetic placement of *M. mirabilis* to demonstrate that combining Angiosperms353 and Sanger data is a cost-effective way to investigate the phylogenetic placement of taxa. Furthermore, we provide new data on the wood anatomy and seed morphology of *M. mirabilis* and compare them with existing data.

MATERIALS AND METHODS

Taxon sampling and DNA extraction

We sampled four individuals of *M. mirabilis* for the phylogenetic study. Sample *Medinilla_mirabilis* 1928 was used for both Sanger and target enrichment sequencing, while the other three samples were only Sanger sequenced. For the target enrichment data, raw data of all 194 Melastomataceae samples generated by Maurin *et al.* (2021) were accessed from the European Nucleotide Archive (ENA) using enaBrowserTools (https://github.com/enasequence/enaBrowserTools). In addition, 10 CAP (Crypteroniaceae–Alzateaceae-–Penaeaceae) clade species were included as outgroups. For the Sanger data, we retrieved sequences of 152 taxa from GenBank covering most major clades of Melastomataceae identified by Penneys *et al.* (2022), including 31 plastomes. Dissochaeteae and Sonerileae were densely sampled. The script ‘get_annotated_regions_from_gb.py’ (https://

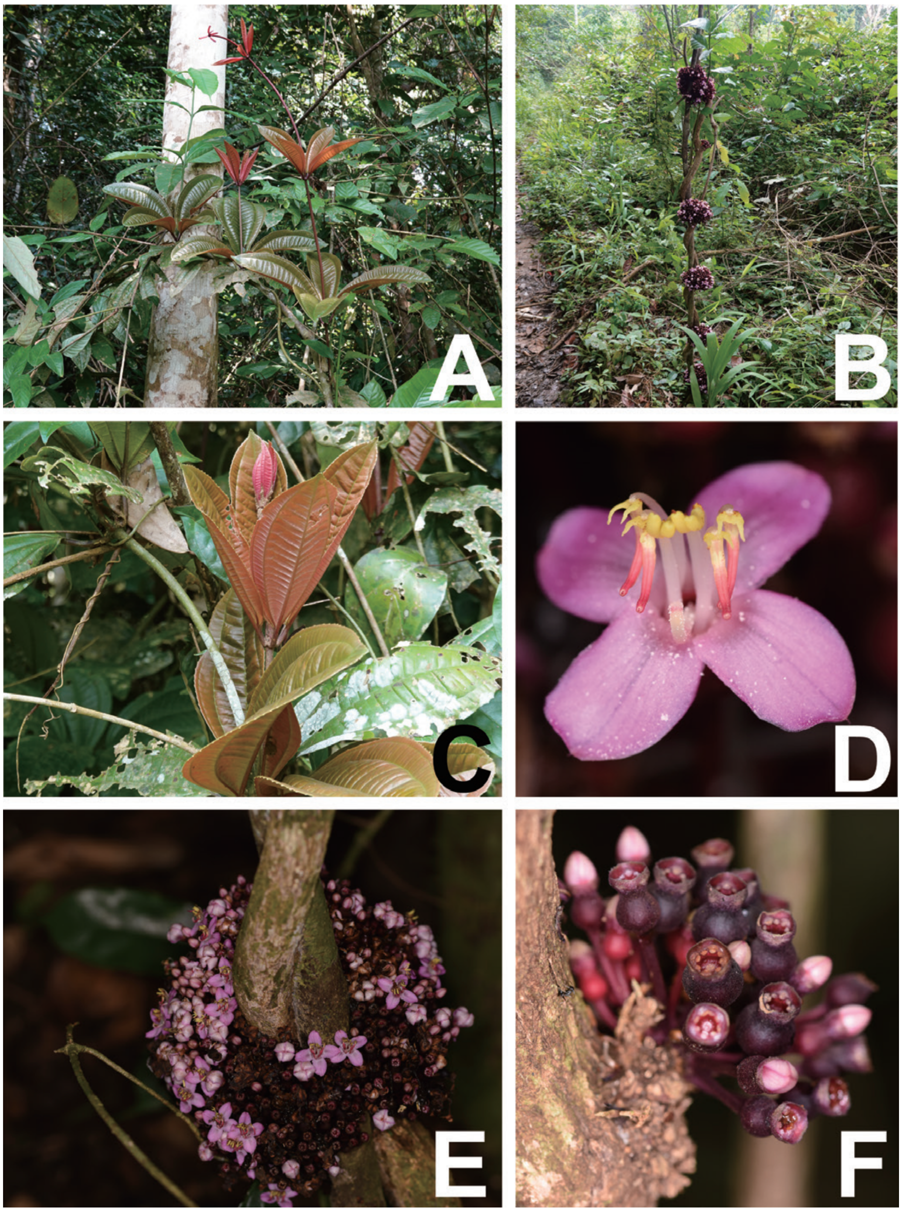

Figure 1. Photographs of *Medinilla mirabilis* in its natural habitat. A, young twigs with verticillate leaves. B, mature stem coiling around the stem of a tree. C, young leaves with clearly dentate leaf margins. D, close-up image of a single flower. E, spherical inflorescence composed of many cymes. F, fruits. All photos by Luo Chen.

github.com/Kinggerm/GetOrganelle/blob/master/Utilities/get_annotated_regions_from_gb.py) was used to extract plastid regions of interest from these 31 plastomes. In total, the target enrichment data included 205 samples, while the Sanger data included 156 samples. Detailed information on the taxa sampled, accession numbers, and vouchers can be found in Supplementary Table S1.

Total genomic DNA was extracted from silica-dried leaves or herbarium specimens using a modified CTAB protocol (Doyle and Doyle 1987, Majure *et al.* 2019). DNA concentration was measured with a Qubit 4 fluorometer.

Sequence assembly of target enrichment data

The extracted DNA of *Medinilla_mirabile* 1928 was sent to Rapid Genomics (Gainesville, FL, USA) for library preparation, target enrichment, and next-generation sequencing. Melastomataceae-specific probes developed by Jantzen *et al.* (2020) were used to capture the targeted 384 loci, of which 266 are from the Angiosperms353 project.

Raw sequences were trimmed with Trimmomatic v.0.39 (Bolger *et al.* 2014). We recovered the target loci from both paired and unpaired trimmed sequences using HybPiper (Johnson *et al.* 2016). As it has been demonstrated that the mega353 target file can improve locus recovery (McLay *et al.* 2021), the target file we used for recovery was a tailored mega353 file containing transcriptome sequences from Myrtales species and the original default353 file. Since using a target file containing protein sequences for mapping yields better results than using a target file containing nucleotide sequences, we used DIAMOND for mapping (see https://

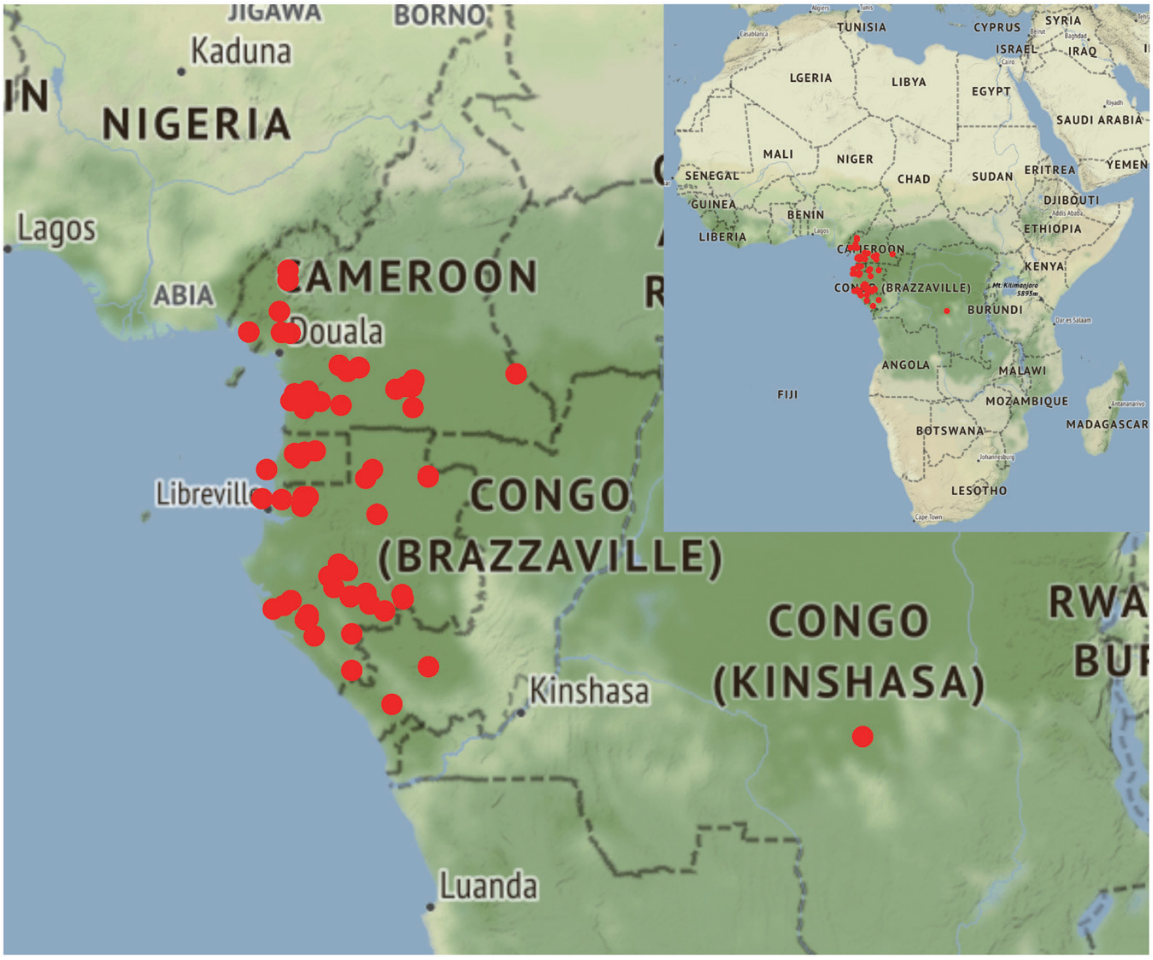

Figure 2. Geographical distribution of *Medinilla mirabilis*.

github.com/mossmatters/HybPiper/wiki/ for detailed explanation). Before mapping, the tailored mega353 file was filtered using a script provided by the authors of HybPiper (https://github.com/mossmatters/HybPiper/files/8933179/get_inframe_targetfile.py.gz) to rewrite the sequences in multiples of three and remove sequences that have stop codons in any forward frame. We ran the HybPiper command 'hybpiper paralog_retriever' to retrieve both the main sequence and putative long paralogues for orthologue inference.

Retrieved loci were first aligned using MAFFT v.7.453 (Katoh and Standley 2013) with the algorithm L-ENS-I and the function 'reversing complete sequences' (--adjustdirectionaccurately). The alignments were trimmed with Phyutility v.2.7.1 (Smith and Dunn 2008) to remove sites missing 90% data. We discarded short sequences (< 50 bp) and gappy sequences (missing 90% sites) before generating single-gene trees, for which IQ-Tree v.2.1.3 (Minh *et al.* 2020) was used with 1000 ultrafast bootstrap replicates. Raw single-gene trees were first trimmed by masking the monophyletic and paraphyletic tips that belong to the same taxon following Yang and Smith (2014) and Morales-Briones *et al.* (2021). TreeShrink v.1.3.7 (Mai and Mirarab 2018) was later used to remove outlier long branches with default settings.

We employed DISCO (Willson *et al.* 2021) to decompose the single-gene trees for species tree inference. DISCO takes the Newick format gene trees as input, roots, and labels the internal nodes as either duplication or speciation events using ASTRAL-Pro's method (Zhang *et al.* 2020), and decomposes the gene trees with its decomposition algorithm. We ran DISCO with default settings except for using the option -m 20 for filtering trees with fewer than 20 taxa.

Sequence assembly of Sanger data

Two nuclear (ITS and ETS) and four plastid loci (*psbK-psbI*, *ndhF*, *rbcL*, and *rpl16*) were amplified with the primers used by Kartonegoro *et al.* (2021). Only ITS-241r, instead of the reverse primer ITS2-MEL R, was used for amplifying ITS2. We followed the PCR protocols used by Veranso-Libalah *et al.* (2017) and Kartonegoro *et al.* (2021) with minor modifications. Details of the PCR amplification are given in Table 1. Sequencing was performed either at the Institute of Systematics, Biodiversity and Evolution of Plants or the sequencing service of the Faculty of Biology, LMU Munich, Germany. Sequencher v.5.1 (Gene Codes Corp., Ann Arbor, MI, USA) was used to manually edit and assemble the raw sequencing data. MAFFT was used for sequence alignment with the '--adjustdirection' option used.

Phylogenetic analyses

For the target enrichment data, after decomposition, both coalescent and concatenation methods were used to estimate the species tree. For the coalescent analysis, ASTRAL v.5.7.7 (Zhang

Table 1. PCR primers used in this study

Locus	Primer	Primer sequence, 5′→3′	Source
ITS	ITS1-MEL F	GGAGAAGTCGTAACAAGGTTTC	Veranso-Libalah *et al.* (2017)
	ITS1-MEL R	CTTGCGTTCAAAGAATTGATGG	
ITS	ITS2-MEL F	CGGCTCTTGCATCGATGAAG	Veranso-Libalah *et al.* (2017)
	ITS-241r	CAGTGCCTCGTGGTGCGACA	Michelangeli *et al.* (2004)
ETS	ETS NY320 F	AGACAAGCATATGACTACTGGCA	Kartonegoro *et al.* (2021)
	ETS 1428 Mel Spec R	ACGTGTCGCGTCTAGCAGGCT	
psbK-psbI	psbK F	TTAGCCTTTGTTTGGCAAG	Reginato *et al.* (2010)
	PsbI R	AGAGTTTGAGAGTAAGCAT	
ndhF	ndhF-972 F	GTCTCAATTGGGTTATATGATG	Olmstead and Sweere (1994)
	ndhF-1603 R	GCATAGTATTGTCCGATTCATRAGG	
ndhF	ndhF-1318 F	GGATTAACYGCATTTTATATGTTTCG	Olmstead and Sweere (1994)
	ndhF-1955 R	CGATTATATGACCAATCATATA	
rbcL	rbcL-1 F	ATGTCACCACAAACRGAGACTAAAGC	de Groot *et al.* (2011)
	rbcL-1361 R	TCAGGACTCCACTTACTAGCTTCACG	
rpl16	rpl16-71 F	GCTATGCTTAGTGTGTGACTCGTTG	Jordan *et al.* (1996)
	rpl16-1516 R	CCCTTCATTCTTCCTCTATGTTG	Kelchner and Clark (1997)

et al. 2018) was used with the decomposed gene trees as input. For the concatenation analysis, we concatenated the gene alignments that correspond to the decomposed gene trees using the script ca_disco.py (https://github.com/JSdoubleL/DISCO/blob/master/ca_disco.py) and then inferred the maximum-likelihood (ML) phylogeny using IQ-Tree as described above.

For the Sanger data, we generated three concatenated alignments using FASconCAT-G v.1.04 (Kück and Longo 2014) for phylogenetic inference: (i) an alignment containing 154 chloroplast sequences, (ii) an alignment comprising 141 nuclear sequences, and (iii) an alignment including 156 both nuclear and chloroplast sequences. The ML analysis was performed as described above.

All phylogenetic trees were visualized using ITOL v.6.6 (Letunic and Bork 2021).

Distribution map

We accessed all available distribution records of *M. mirabilis* from GBIF [GBIF.org (1 January 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.febs8q] and further used herbarium specimens from BRLU, BR, and P. Information regarding all records used are listed in Supplementary Table S2. Visualization was performed using ggmap v.3.0.1 (Kahle and Wickham 2013) in R Statistical Software v.4.2.2 (R Core Team 2022).

Wood anatomy and seed morphology

The wood sample analyzed was collected from specimen *Medinilla mirabilis* 35_21. Following Van Vliet (1981), we studied those three characters that were used to categorize Dissochaeteae, i.e. arrangement of inter-vessel pits, vessel element diameter, and ray width. Following Jansen *et al.* (1998), the dry wood sample was first softened by soaking in a mixture of glycerin/water (1:10 volume ratio) for 2 days. Tangential sections 25–30 μm thick were cut with a sledge microtome (Microm, Heidelberg, Germany), mounted on slides, and subsequently embedded in ROTI Histokitt (Carl Roth, Karlsruhe, Germany). The embedded slides were observed under a light microscope (Leica DM750, Wetzlar, Germany) equipped with Leica LAS X software. Vessel element diameter data were obtained from 12 measurements (Supplementary Table S3).

Seed morphological character examination was performed using a scanning electron microscope (Leo 438VP, Carl Zeiss AG, Oberkochen, Germany). Seeds were collected from the specimen *Medinilla mirabilis* 35_21. Following Ocampo *et al.* (2022), seed morphology was described using 14 characters (Supplementary Table S3).

RESULTS

Phylogenetic placement of *Medinilla mirabilis*

Medinilla mirabilis is recovered in all analyses as sister to Dissochaeteae *s.s.* recently circumscribed by Kartonegoro *et al.* (2021). The species is neither part of Miconieae nor of Sonerileae and does not group with the other species of *Medinilla s.s.* which are part of Sonerileae.

In the Angiosperms353 data, five species of tribe Dissochaeteae belonging to *Dissochaeta* and *Diplectria* were sampled, and *M. mirabilis* is strongly supported as sister to these species. The clade comprising *M. mirabilis* and Dissochaeteae is most closely related to the South American tribe Pyramieae. These results are consistent between the concatenation (Supplementary Fig. S1) and coalescent analyses (Fig. 3).

In the three Sanger data sets (Fig. 3, Supplementary Figs S2, S3), Dissochaeteae are well represented with all six genera and ~50% of its species sampled. Phylogenetic relationships recovered among analyses from different data sets are mostly consistent. In all three analyses, the four accessions of *M. mirabilis* sampled form a clade that is highly supported as sister to a monophyletic group comprising all Dissochaeteae species.

Wood anatomy and seed morphology

Inter-vessel pits in *M. mirabilis* are alternate in spite of the presence of some elongated pits (Fig. 4). Vessel element diameter

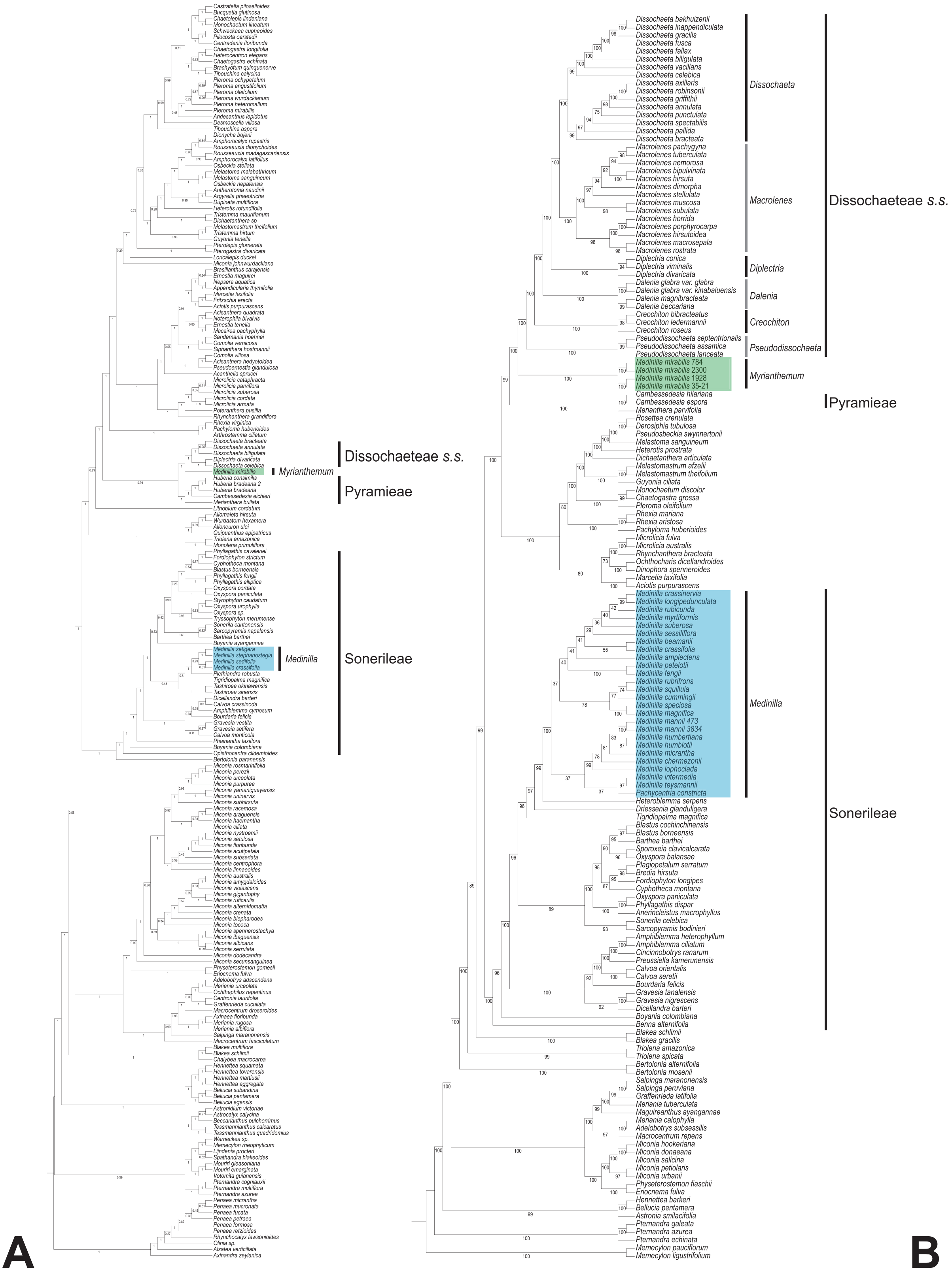

Figure 3. Phylogenetic trees inferred from target enrichment data using the coalescent method (A) and Sanger data using both nuclear and chloroplast sequences (B).

varies from 18.6 to 76.9 µm (Supplementary Table S3). Only uniseriate and biseriate rays were found (Fig. 4).

Seeds are numerous, ovoid, and angled. The lateral symmetrical plane and antiraphal symmetrical plane are both ovate. An appendage is absent. An expansion at the base of the seed is not evident. Multicellular sculpturing is absent, individual cells are elongated, anticlinal boundaries are undulate, and periclinal walls are flat to convex (Supplementary Table S3; Fig. 5).

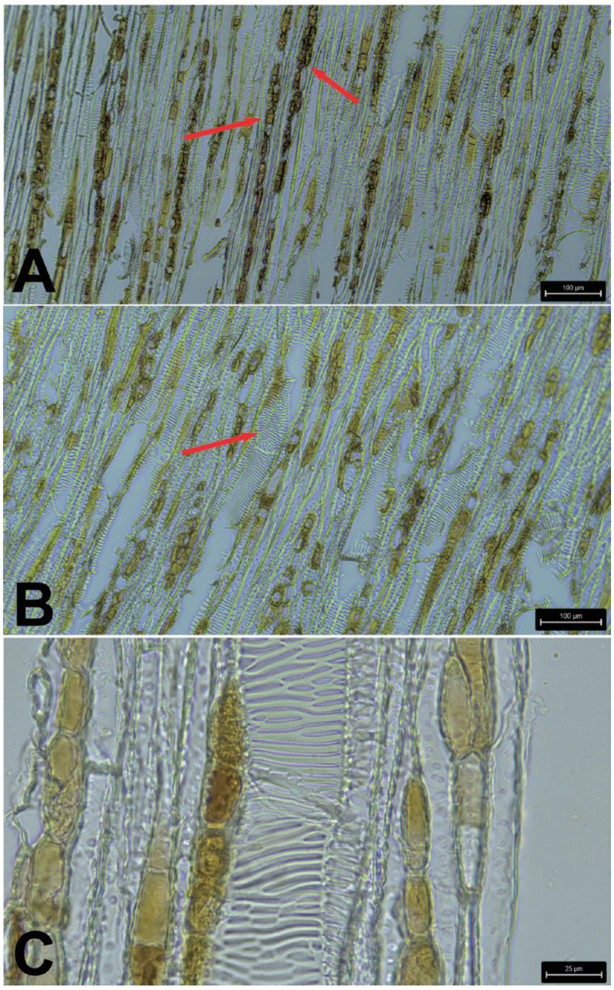

Figure 4. Tangential sections of *Medinilla mirabilis* wood. A (×10), rays (indicated by arrows) are uniseriate or biseriate. B (×10), inter-vessel pits (indicated by arrows) are alternate. Note that infrequently some pits are elongated, forming a scalariform or reticulate arrangement. C (×40), close-up image of a vessel element.

DISCUSSION

Placement of Medinilla mirabilis and its implication

Our phylogenetic analyses using both the Sanger data and Angiosperms353 data showed clearly that *M. mirabilis* is phylogenetically distinct and not closely related to *Medinilla*. Our results do not support Jacques-Félix's (1977) treatment of the species, which he transferred from *Myrianthemum* to *Medinilla*. *Medinilla mirabilis* is most closely related to the Southeast Asian endemic tribe Dissochaeteae (Fig. 3, Supplementary Figs S1–S3).

In terms of wood anatomy, the arrangement of inter-vessel pits in *Medinilla* is distinctly scalariform with narrow rays and narrow vessel elements (see Van Vliet 1981: plate 3) instead of being mostly alternate and infrequently scalariform or reticulate as in *M. mirabilis* (Fig. 4). Overall the inter-vessel pit arrangement in *M. mirabilis* is quite similar to that of Dissochaeteae (= subtribe Dissochaetinae; see Van Vliet 1981: plate 8). The narrow rays and vessel element diameters of *M. mirabilis* are different from those found in Dissochaeteae, where rays can be up to seven cells wide and vessel element diameters are wide (Kartonegoro *et al.* 2022, Kartonegoro *et al.* 2021). However, not all genera of Dissochaeteae have multiseriate rays. Only uniseriate and biseriate rays as seen in *M. mirabilis* have also been found in *Creochiton* and *Pseudodissochaeta* (Van Vliet 1981). In general, lianas tend to have large vessel elements for efficient water and nutrient transport (Carlquist 1985, Ewers and Fisher 1991, Angyalossy *et al.* 2012). The widest vessel element observed in *M. mirabilis* was only 76.9 µm, which is narrower than in some genera of Dissochaeteae [e.g. (58–) 96–215 (–283) µm in *Dissochaeta*]. However, vessel element diameters in *Pseudodissochaeta* were up to 84 µm (Van Vliet 1981), which is similar to those of *M. mirabilis*.

In terms of seed morphology, the seeds of *M. mirabilis* are quite similar to those of Dissochaeteae in almost all characters examined. However, the seeds of *Medinilla* also have similar characters (Supplementary Table S2, Fig. 5; Ocampo *et al.* 2022). As stated above, phylogeny and seed morphology often do not fit well in Melastomataceae (Ocampo *et al.* 2022).

Based on the most recent delimitation of Dissochaeteae, it is a Southeast Asian tribe with six genera (i.e. *Creochiton*, *Dalenia*, *Diplectria*, *Dissochaeta*, *Macrolenes*, and *Pseudodissochaeta*) and ~90 species (Kartonegoro *et al.* 2022). Morphologically, they are mostly woody climbers or creepers, have interpetiolar outgrowths, thyrsoid inflorescences, 4-merous flowers with dimorphic or isomorphic stamens, and baccate fruits. Anatomically, inter-vessel pits are arranged in an alternate pattern, vessel elements are comparatively wide, and multiseriate rays are present (Van Vliet 1981, Maxwell 1983, Kartonegoro *et al.* 2021, 2022). As a liana with interpetiolar outgrowths, eight dimorphic stamens, baccate fruits, and alternate inter-vessel pits, *M. mirabilis* fits well into Dissochaeteae. It can be differentiated from other Dissochaeteae by its verticillate leaf arrangement when young and its spherical inflorescences composed of many cymes (Diels *et al.* 1898).

Based on the morphological and molecular evidence provided, we propose that the genus *Myrianthemum* be reinstated to include *Myrianthemum mirabile* as its sole species (hereafter *M. mirabile* is used to replace *M. mirabilis*). The species is restricted to central African forests and has been found in Cameroon, Gabon, Congo, Equatorial Guinea, and Democratic Republic of Congo (Fig. 2). A variety of the species, *M. mirabile* var. *dentata* nom. nudum (Rendle *et al.* 1913), has been reported from Oban, southern Nigeria, which is the only collection known from Nigeria. It is uncertain whether this specimen was indeed collected in Nigeria because continuous forest covers southwest Cameroon and southeast Nigeria. Specimens of *M. mirabile* with dentate leaf margins seem to be quite frequent and have been collected in different countries (e.g. Fig. 1C). The isotype in Paris also has dentate leaf margins (MNHN-P-P04807525). This shows that *M. mirabile* can have entire or dentate leaves.

Irrespective of its unique morphology and geographical distribution, we advocate inclusion of *M. mirabile* in an expanded Dissochaeteae (Fig. 3). Tribe Dissochaeteae, currently endemic to Southeast Asia, would then include one African taxon, *M. mirabile*. In Melastomataceae, only six of the 23 major clades are distributed disjunctly across major biogeographical realms (Reginato *et al.* 2022). An expanded Dissochaeteae belongs among such clades with a disjunct distribution. Since the Neotropical tribe Pyramieae is sister to Dissochaeteae, the

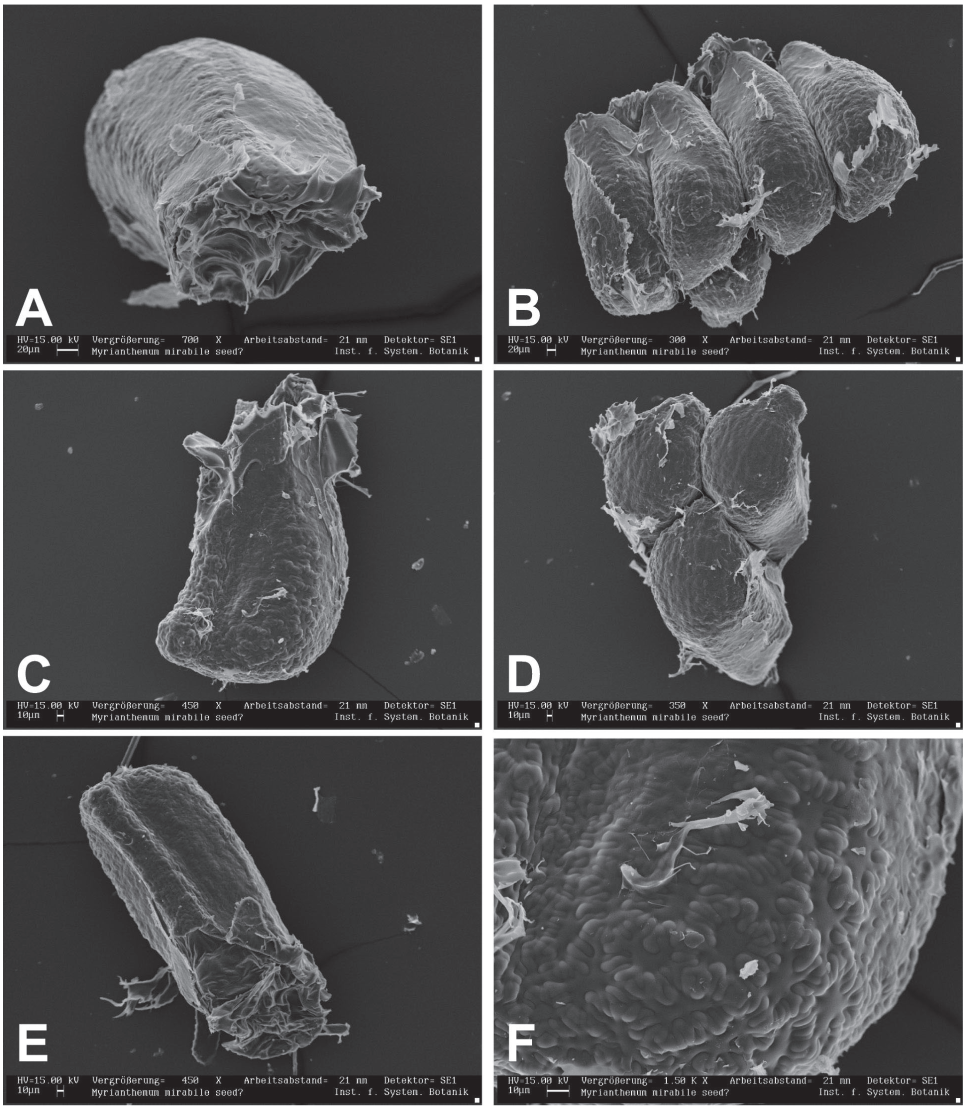

Figure 5. Scanning electron micrographs of *Medinilla mirabilis* seeds.

inclusion of *M. mirabile* may imply that this may be another example of dispersal from the Neotropics to Africa and then to Southeast Asia (Reginato *et al.* 2022).

Combining Sanger and Angiosperms353 data is cost-effective to place a taxon of interest on the flowering plant tree of life

Despite the challenges of missing data and gene duplication, Angiosperms353 has proven to be an effective tool for elucidating phylogenetic relationships among angiosperms at different levels and in different groups (Baker *et al.* 2021b, McDonnell *et al.* 2021). However, until Angiosperms353 instead of Sanger data is used as a general approach for DNA barcoding, many taxa will remain insufficiently sampled. Sanger data provide a potential solution for filling this sampling gap. Our study has shown that using Sanger data, all genera of Dissochaeteae were well represented, which allowed us to confidently conclude that *M. mirabile* is sister to Dissochaeteae. This would not have been possible with only phylogenomic data because several genera were unsampled. Our strategy can be used in any group for which Angiosperms353 or Angiosperms353-related data are available (Antonelli *et al.* 2021, Clarkson *et al.* 2021, Maurin *et al.* 2021, Haigh *et al.* 2023).

TAXONOMIC TREATMENT

Myrianthemum Gilg in Engler & Prantl, Nat. Pflanzenfam. Nachtr.: 266 (1897)

Type : *Myrianthemum mirabile* Gilg.

Notes : *Myrianthemum* is monospecific.

Myrianthemum mirabile Gilg in Engler & Prantl, Nat. Pflanzenfam. Nachtr.: 266 (1897); Mon. Afr. Pfl. 2: 33 (1898); ≡ *Medinilla mirabile* (Gilg) Jacq.-Fél., Adansonia sér. 2, 17(1): 78 (1977).

Type : Soyaux 361, Sibange farm, Munda region, Gabon (Holotype: B delet.; Isotype: P barcode P04807525!).

Specimens examined : CAMEROON. South Region: Ngovayang Massif, Ngovayang Village, *Droissart et al. 1928* (BRLU BRLU0000695). GABON. Ogooué-Maritime:

Moukalaba-Doudou National Park, ~50 km S of Mandji, *Sosef 2300* (BR BR0000019009421); Woleu-Ntem: 0.5 km E of Tchimbélé, *Wieringa 784* (BR BR0000019009445).

Notes : *Myrianthemum mirabile* was mentioned in the description of *Myrianthemum* (*descriptio generico-specifica*) and was therefore validly published in 1897. The species itself was later described in 1898. *Myrianthemum mirabile* occurs in Cameroon, Gabon, Congo, Equatorial Guinea, and Democratic Republic of Congo. Only one specimen (BM 014630982!) was collected in Oban, southern Nigeria. As this is the only collection known from Nigeria, it is somewhat uncertain if it was indeed collected in Nigeria because continuous forest covers southwest Cameroon and southeast Nigeria and all other specimens have been collected on the Cameroon side.

SUPPLEMENTARY DATA

Supplementary data are available at *Botanical Journal of the Linnean Society* online.

Figure S1. ML tree inferred from concatenated target enrichment data.

Figure S2. ML tree inferred from Sanger chloroplast data.

Figure S3. ML tree inferred from Sanger nuclear data.

Table S1. Accession numbers for downloaded and newly generated sequences, along with voucher information.

Table S2. Distribution records of *Medinilla mirabilis*.

Table S3. Vessel element diameter and seed morphological characters of *Medinilla mirabilis*.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY

The raw target enrichment reads and Sanger sequences are archived in the National Center for Biotechnology Information (NCBI) Sequence Read Archive (PRJNA961328) and GenBank (accession numbers available in Supplementary Table S1), respectively.

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CHAPTER 3

SYSTEMATICS OF THE FLESHY-FRUITED SONERILEAE (MELASTOMATACEAE)

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RESEARCH ARTICLE

Systematics of the fleshy-fruited Sonerileae (Melastomataceae)

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Abstract With approximately 1080 species, Sonerileae is the second-largest tribe in the Melastomataceae. Approximately 40% of the Sonerileae species belong to fleshy-fruited genera (*Catanthera*, *Heteroblemma*, *Kendrickia*, *Medinilla*, *Pachycentria*, *Plethiandra*). Relatively few species, especially of the fleshy-fruited taxa, have been sampled for phylogenetic study. Consequently, there is huge uncertainty resulting in many unanswered questions about their evolutionary history, including the monophyly of the largest genus, *Medinilla*. In this study, the phylogeny of the fleshy-fruited Sonerileae was reconstructed using 385 nuclear and 81 plastid protein-coding loci recovered from newly generated target capture and off-target reads data, and previous studies. Our study revealed that the fleshy fruited Sonerileae belong to three lineages. *Kendrickia* is sister to an Afrotropical endemic clade. *Heteroblemma* and *Catanthera* belong to a second clade and are most closely related to some *Phyllagathis* and *Driessenia* species. *Medinilla* forms a third clade that also includes *Pachycentria* and *Plethiandra*. Within *Medinilla*, 15 clades are identified and characterized. To make *Medinilla* monophyletic, the genus is redefined to include *Pachycentria* and *Plethiandra*. Major lineages identified within *Medinilla* lay the groundwork for an infrageneric classification system. Areas of the phylogenetic tree with high conflict or weak sampling are identified to aid further studies in the tribe.

Keywords *Medinilla*; nuclear and plastid phylogeny; Paleotropics; phylogenomics; target enrichment; taxonomic treatment

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

With nearly 6000 species, the Melastomataceae are among the 10 most species-rich plant families (Ulloa Ulloa & al., 2022). They are an important ecological component of primarily tropical habitats worldwide and serve as a major evolutionary study system (Goldenberg & al., 2022). The second-largest tribe in the family is Sonerileae, consisting of well over 1000 species (Liu & al., 2022; Penneys & al., 2022). Generic delimitation has been notoriously problematic in this tribe, hampering understanding of its diversity. Sonerileae currently includes 46 genera (Liu & al., 2022; Lin & al., 2022; Liu & al., 2024), 40 of which have capsular fruits. However, approximately 40% of Sonerileae species have fleshy fruits. Fleshy-fruited genera include *Medinilla* Gaudich. ex DC., *Pachycentria* Blume, *Plethiandra* Hook.f., *Heteroblemma* (Blume) Cámara-Leret & al., *Catanthera* F.Muell., and *Kendrickia* Hook.f.

Medinilla is by far the largest and most widely distributed of these fleshy-fruited genera (Liu & al., 2022). It is the most species-rich genus in Sonerileae and third most species-rich genus in Melastomataceae. At present, 368 accepted species are found in the wet Paleotropics, from Africa to Polynesia (Govaerts, 2024). However, the exact number of species is unclear. The last comprehensive revision of *Medinilla* dates back to Cogniaux (1891), a time when 75% of the species we recognize today were yet to be described. Subsequent revisions are either outdated or absent, leaving significant gaps in our

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understanding of the genus, particularly in regions with high diversity like Madagascar and New Guinea (Cámara-Leret & al., 2020). Most species are covered in regional lists and revisions; see Veranso-Libalah & al. (2023) for Africa; Perrier de la Bâthie (1951) for Madagascar and the Comoro Islands; Sasidharan & Sujanapal (2005) for the Western Ghats; Bremer & Lundin (1988) for Sri Lanka; Chen & Renner (2007) for the *Flora of China*; Renner & al. (2001) for the *Flora of Thailand*; Kartonegoro (2023) for Malesia; Merrill & Perry (1943) for the Solomon Islands; and Smith (1985) for Fiji.

Medinilla is also the most poorly defined of the fleshy-fruited genera (Liu & al., 2022; Penneys & al., 2022). Regalado (1990, 1995) and Bodegom & Veldkamp (2001) provided a detailed overview of its complex taxonomic history. Currently, *Medinilla* is understood as a heterogeneous group of terrestrial shrubs, climbers, and epiphytes, often distinguished by isomorphic stamens, weakly produced connective, and anther appendages (two ventral, one dorsal; Regalado, 1995). However, exceptions abound, and the genus has been notoriously hard to delimit. Regalado (1995: 117) described the situation as a "taxonomic impasse". He envisioned *Medinilla* as a central plexus from which small satellite genera have been separated. Kadereit (2005: 128) considered the genus "probably polyphyletic", as did Veranso-Libalah & al. (2023). The latter study was based on the combined sequences of two nuclear and three plastid markers. Seventeen *Medinilla* species were resolved in two clades, though these were not strongly supported. *Pseudodissochaeta* Nayar (Kartonegoro & al., 2020, 2021) and *Myrianthemum* Gilg (Chen & al., 2023) were considered synonyms of *Medinilla* until recently, but morphological and molecular evidence has helped demonstrate that these two genera belong to the berry-fruited tribe Dissochaeteae. Other recent studies have supported the monophyly of *Medinilla* (Maurin & al., 2021; Zhou & al., 2019, 2022), but all suffer from limited sampling and a serious lack of crucial taxa (e.g., other fleshy-fruited Sonerileae). The inclusion of sequences from *Pachycentria* introduces a challenge to the presumed monophyly of *Medinilla*, as indicated by studies conducted by Kartonegoro & al. (2021) and Chen & al. (2023). The results suggest that *Medinilla* is paraphyletic when *Pachycentria* is accepted. To thoroughly test the monophyly of *Medinilla*, there is a clear necessity for comprehensive sampling, not only within *Medinilla* itself, but also across all other fleshy-fruited genera.

No comprehensive infrageneric classification system for *Medinilla* exists to guide the sampling; however, many distinctive morphological groups within *Medinilla* have been recognized. *Carionia* Naudin, *Cephalomedinilla* Merr., *Dactyliota* Blume, *Diplogenea* Lindl., *Erpetina* Naudin, *Hypenanthe* Blume, and *Triplectrum* D.Don ex Wight & Arn. are generic names considered synonymous with *Medinilla*. Several sections have been proposed as well: *M.* sect. *Medinilla* (= "*M.* sect. *Campsoplacuntia* Blume" [Blume, 1831] = "*M.* sect. *Eu-Medinilla* Bakh.f." [Bakhuizen van den Brink, 1943], both not validly published), *M.* sect. *Sarcoplacuntia* Blume (Blume, 1831), *M.* sect. *Apateon* Blume (Blume, 1849), *M.* sect. *Heteromedinilla* Bakh.f. (Bakhuizen van den Brink, 1943), *M.* sect. *Septatae* H.Perrier (with three subgroups; Perrier de la Bâthie, 1951), and *M.* sect. *Adhaerentes* H.Perrier (with six subgroups; Perrier de la Bâthie, 1951). Informal species alliances have also been recognized. Veldkamp (1978, 1988) revised species in the *M. myrtiformis*-alliance. Regalado (1990, 1995) treated 11 and 12 species alliances in his revisions of Bornean and Philippine *Medinilla*, respectively. In the most comprehensive classification system to date, Clausing (1999) sorted 215 species into Group 1 (with 13 major alliances excluding *Heteroblemma*) and Group 2 (with four major alliances). Soon after, Bodegom & Veldkamp (2001) identified and revised the pseudostipular species of *Medinilla*. Despite these efforts, a significant challenge remains because there is considerable overlap of species between many groups, and numerous species are left unassigned. The complexity of *Medinilla*'s diversity necessitates the identification of major lineages within the genus. This task is critical for gaining a more nuanced understanding of the intricate relationships among species and a prerequisite for any further evolutionary study of the Asian Sonerileae.

Pachycentria (including *Pogonanthera* Blume) consists of eight species in Malesia, with two of them being widespread (Clausing, 2000). It is characterized by a small ovary in a strongly constricted, urceolate hypanthium and seeds with comb-shaped testa cells (Clausing, 2000). Ventral anther appendages are generally lacking. The dorsal appendage can be frayed, bifurcated, or tufted (*Pogonanthera*). Baillon (1879) considered *Pachycentria* conspecific with *Medinilla* and maintained *Pogonanthera* with doubt. Clausing (2000) combined *Pachycentria* and *Pogonanthera* and tentatively maintained their distinction from *Medinilla*. Kartonegoro & al. (2021) found support (posterior probability [PP] = 1, Bayesian inference; bootstrap [BS] = 85, maximum likelihood; BS = 65, parsimony analysis) for two *Pachycentria* species being nested among 13 *Medinilla* species, based on the combination of two nuclear and four chloroplast markers. Using the same markers and a maximum likelihood approach, Chen & al. (2023) found full support for one *Pachycentria* species being nested among 24 *Medinilla* species. For a better understanding of the generic limits of *Medinilla*, and to verify the relationship and make necessary taxonomic changes, additional samples of *Pachycentria* are needed.

Plethiandra consists of eight species in Malesia, mostly confined to Borneo (Kadereit, 2005). It is easily recognized by its 6-merous flowers, polystaminate androecium, and inappendiculate anthers. Initially, *Plethiandra* was placed in the tribe Astronieae (Hooker, 1867), largely because of longitudinal anther dehiscence. Cogniaux (1891) maintained this association but classified several new species that now belong to this group as *Medinillopsis* Cogn. and *Medinilla robusta* Cogn. Stapf (1895) recognized the close affinity of *Plethiandra* to *Medinilla* and concluded the original anther description was misrepresentative. Taxonomists have continued to tentatively maintain the distinction (Kadereit, 2005), but *Plethiandra* is still often accidentally included in *Medinilla*. For example, during the sorting of undetermined specimens of *Medinilla* from Borneo, *Plethiandra* is inevitably intermixed (J.P. Quakenbush, pers. obs.); and the “*Medinilla* sp. nov. Lin681” in Zhou & al. (2022) is *P. robusta* (Cogn.) Nayar. So far, molecular insights have been limited. Clausing & Renner (2001) did not resolve the relationships between 6 *Medinilla*, 2 *Plethiandra*, and 17 other Sonerileae. Maurin & al. (2021) found *P. robusta* sister to four *Medinilla*, with full support, based on target capture data. It remains to be seen whether this relationship to *Medinilla* will hold with greater sampling.

Heteroblemma was revised and established as a genus by Cámara-Leret & al. (2013). Previously, it was treated as a section of *Medinilla* (Blume, 1849). A total of 15 species are recognized in Vietnam and Malesia (Govaerts, 2024). *Heteroblemma* is generally characterized by a stele that is lobed in transverse section (see Cámara-Leret & al., 2013), alternate leaves (via strong anisophylly and abortion) with prominent transverse venation, sessile and fascicled flowers along the stem, isomorphic stamens, hard berries (sclerified pericarp), and papillate seeds. Molecular data show *Heteroblemma* and *Medinilla* in separate clades (Zhou & al., 2019, 2022). In a plastome phylogeny (Zhou & al., 2022: fig. S6), three *Heteroblemma* and four *Phyllagathis* Blume species formed a mixed clade sister to eight *Medinilla* species. In a nuclear genomic phylogeny (Zhou & al., 2022), the same *Heteroblemma* accessions were monophyletic and part of a clade including nine *Phyllagathis* and seven *Driessenia* Korth. species. Notably, they were not sister to *Medinilla*. Despite this discordance, sampled *Heteroblemma* and *Medinilla* were clearly separate in both cases.

Catanthera was revised by Nayar (1982). It also has a long association with *Medinilla*; for example, Mansfeld (1926) transferred some members of *Hederella* Stapf (later synonymized as *Catanthera*) to *Medinilla*, and Bakhuizen van den Brink (1943) thought it should be a section of *Medinilla*. *Catanthera* includes 19 species restricted to Malesia (Govaerts, 2024). It shares the atypical wood anatomy of *Heteroblemma* and is generally distinguished by opposite or alternate leaves with more obscure transverse venation; axillary or cauliflorous, umbellate or paniculate inflorescences; isomorphic or dimorphic stamens; soft, juicy berries (weakly sclerified pericarp); and smooth seeds. Clausing & Renner (2001) found weak support for a close relationship between *Catanthera* and *Heteroblemma* based on evidence from three chloroplast markers. Subsequent studies have not sampled these taxa to verify this relationship, but their close association has been accepted due to morphological similarity and shared geography (e.g., Cámara-Leret & al., 2013; Liu & al., 2022).

Kendrickia is enigmatic, monotypic, and most likely only found in Sri Lanka. Though it has been reported from the Anamala Hills (Clarke, 1879) and South India more generally (Triana, 1871; Bremer & Lundin, 1988), no specimens have been found to verify this. Like *Heteroblemma* and *Catanthera*, it has a lobed stele in transverse section and a climbing habit. It is distinguished by opposite, isophyllous leaves with obscure transverse venation; terminal or axillary inflorescences; isomorphic stamens; fleshy capsules that rupture at maturity; and smooth, prism-shaped seeds. Despite the unique morphological traits (e.g., fruit and seed type), and a geographic distribution outside of Malesia, Clausing & Renner (2001) found support (BS = 94) for a *Catanthera* and *Kendrickia* clade sister (BS = 50) to *Heteroblemma* based on sequences from a single chloroplast marker (*ndhF*). This close relationship has been accepted by subsequent authors (e.g., Cámara-Leret & al., 2013; Liu & al., 2022). However, this limited molecular evidence needs verification.

In light of the evidence, Liu & al. (2022) divided the fleshy-fruited Sonerileae into two alliances. The *Medinilla*-alliance includes *Medinilla*, *Pachycentria*, and *Plethiandra*. It is characterized by typical wood anatomy (i.e., terete stele) and soft, juicy berries. The monophyly of *Medinilla* is in question, and its major lineages are poorly understood. The *Heteroblemma*-alliance includes *Heteroblemma*, *Catanthera*, and *Kendrickia*, characterized by atypical wood anatomy (i.e., lobed stele) and either hard berries, soft, juicy berries, or fleshy capsules. While genera in this alliance are well-defined, their relationship to each other and the *Medinilla*-alliance requires further exploration.

In this study, we aim to investigate the phylogenetic relationships among the fleshy-fruited genera of Sonerileae and answer the following questions: (1) Do fleshy-fruited genera of Sonerileae form two clades? and (2) Is *Medinilla* monophyletic? Additionally, we intend to identify major lineages within *Medinilla* and update the taxonomy to reflect these natural groups more accurately.

■ MATERIALS AND METHODS

Sampling, DNA extraction, library preparation, target capture, and sequencing. — Silica dried plant material and (rarely) herbarium material were targeted from species belonging to the formal and informal groups discussed in the introduction and major clades identified by Zhou & al. (2019, 2022). Species from major biogeographic realms where *Medinilla* species naturally occur were also targeted, namely the Afrotropical, Indomalayan, Australasian, and Oceanian realms of Olson & al. (2001). Apart from *Plethiandra* and *Catanthera*, type species for all other fleshy-fruited Sonerileae genera have been sampled, including *Heteroblemma alternifolium* (Blume) Cámara-Leret & al., *Kendrickia walkeri* (Thwaites) Hook.f. ex Triana, *Medinilla medinilliana* (Gaudich.) Fosberg & Sachet, and *Pachycentria constricta* (Blume) Blume. Total genomic DNA was extracted using a modified CTAB method (Majure & al., 2019). Instead of isolating a pellet of DNA, samples were directly cleaned with a QIAquick PCR purification kit (QIAGEN, Hilden, Germany). Quality and yield of the DNA samples were checked using a Qubit 4 (Thermo Fisher Scientific, Waltham, Massachusetts, U.S.A.).

Library preparation, target sequence capture, and sequencing were performed by Rapid Genomics LLC (Gainesville, Florida, U.S.A.), using their high-throughput sequencing workflow and proprietary chemicals. A set of Melastomataceae-specific probes (Jantzen & al., 2020) targeting 384 loci, including 266 loci from the Angiosperms353 project (Johnson & al., 2019), were used to hybridize with the library inserts. Paired-end reads (2 × 150 base pairs) were generated on the Illumina NovaSeq 6000 system (San Diego, California, U.S.A.).

In addition to the 126 samples sequenced in this study, we utilized data from various sources. Raw data from 66 accessions sequenced using Angiosperms353 probes (Maurin & al., 2021) were obtained from the European Nucleotide Archive (ENA) using enaBrowserTools (https://github.com/enasequence/enaBrowserTools). RNA-seq data for *Medinilla magnifica* Lindl. (Leebens-Mack & al., 2019) were accessed from the NCBI Sequence Read Archive (SRA). Furthermore, whole-genome resequencing data from 83 accessions from Zhou & al. (2019, 2022) were incorporated. For a complete list of samples, including voucher information and corresponding SRA or ENA accession numbers, refer to Appendix 1.

Nuclear data processing and analysis. — Raw reads of target capture and RNA-seq data were processed to remove adaptors, trim low-quality bases, trim polyG and polyX tails, and filter out very short reads with fastp (-g -x -r -l 30 -5 --cut_front_window_size 1 -3 _tail_window_size 1 --detect_adapter_for_pe) (Chen & al., 2018). HybPiper v.2.1.1 (Johnson & al., 2016) was used to recover targeted nuclear loci using the updated Melastomataceae probe set (Dagallier & Michelangeli, 2024) as reference file. Diamond (Buchfink & al., 2015) was employed for read mapping to have better recovery.

To extract reads from the whole-genome resequencing data from Zhou & al. (2019, 2022), reads from 12 *Medinilla* species obtained via target capture in the present study were mapped to a draft genome of *Tigridiopalma magnifica* C.Chen using BWA-MEM (Li & Durbin, 2010). The resulting BAM files were merged into one using SAMtools v.1.2.1 (Li & al., 2009). The overall depth of each position was calculated, and a BED file containing regions with depth >600 (>50 per sample) was output using BEDtools (Quinlan & Hall, 2010). Whole-genome resequencing data were then mapped to the reference genome. Finally, reads aligned to the regions listed in the BED file were extracted, and sequence assembly was carried out using HybPiper as described above.

The HybPiper command “paralog_retriever” was run to retrieve all the gene copies of the recovered loci for orthology inference. The sequences of each locus were aligned using MAFFT v.7.453 (Katoh & Standley, 2013) with the method L-INS-I to provide accuracy. Reverse complement sequences were generated, if necessary, and were aligned with other sequences using the function “--adjustdirectionaccurately”. Phyutility v.2.7.1 (Smith & Dunn, 2008) was subsequently used to trim the alignments. Sites missing 90% or more data were deleted. Sequences with more than 90% gaps or that were too short (<50 base pairs) were also removed. IQ-Tree v.2.1.3 (Minh & al., 2020) was used to infer single gene trees with 1000 ultrafast bootstrap replicates. If a taxon was represented by monophyletic or paraphyletic tips, single gene trees were trimmed to keep only the tips with the most unambiguous characters, following Yang & Smith (2014) and Morales-Briones & al. (2021). TreeShrink v.1.3.7 (Mai & Mirarab, 2018) was used with default settings to remove abnormally long branches from the single gene trees and the corresponding sequences from the alignments.

DISCO v.1.3.1 (Willson & al., 2022) was used to infer orthologs. DISCO takes gene trees as input, roots and labels the internal nodes as either duplication or speciation events using the method implemented in ASTRAL-Pro (C. Zhang & al., 2020), and decomposes the gene trees with its decomposition algorithm. DISCO was run with default settings except the option “-m 20” was used for filtering trees with less than 20 tips. Finally, ASTRAL v.5.7.8 (C. Zhang & al., 2018) was used with the decomposed gene trees as input to infer the species tree (nuclear tree). Branch support was quantified by local posterior probability (LPP; Sayyari & Mirarab, 2016). A concatenation tree was also inferred. We concatenated gene alignments corresponding to the decomposed gene trees into a supermatrix using AMAS (Borowiec, 2016). A maximum likelihood (ML) phylogeny was estimated in IQ-Tree. The IQ-Tree option “-m MFP + MERGE” was used to select the best-fitting partition scheme and models before tree reconstruction.

Plastid loci assembly and phylogenomic analysis. — Plastid loci were recovered from off-target reads of the target capture data using HybPiper. Annotated plastomes of *Medinilla magnifica* (MT043350) and the aforementioned 83 accessions representing all major clades within Sonerileae, coupled with 18 plastomes representing most Melastomataceae tribes treated by Penneys & al. (2022), were used to extract protein-coding genes for target file construction using a script developed by R. Zhang & al. (2020, https://github.com/Kinggerm/GetOrganelle/blob/master/Utilities/get_annotated_regions_from_gb.py). BWA (Li & Durbin, 2009) was used for read mapping. Samples with less than seven genes recovered were excluded from further analysis. The HybPiper command “retrieve_sequences” was used to retrieve the recovered plastid sequences, which were combined with sequences from the annotated Sonerileae and Dissochaeteae plastomes. Sequence alignment for each plastid gene, as well as gene concatenation and ML phylogeny estimation, was performed using the same approach as the nuclear data. Coalescent analysis was not conducted for plastid data, as the whole plastome has been suggested to be treated as a coalescent gene (Doyle, 2022).

■ RESULTS

Phylogenetic analyses. — The phylogeny of the fleshy-fruited Sonerileae was reconstructed in three different ways based on two different sets of data (Figs. 1–5). Due to the tendency of the concatenation approach to ignore evolutionary heterogeneity across different genes and the observed implausible placements of some taxa in the concatenation tree (e.g., *Medinilla stephanostegia* Stapf and *M. setigera* Miq., suppl. Fig. S1), we discuss only the coalescent tree for the nuclear data here. The final DISCO-ASTRAL tree based on nuclear sequence data (NAT; short "nuclear tree") includes 272 samples (79 samples from Zhou & al. [2019, 2022], one sample from Leebens-Mack & al. [2019], 66 samples from Maurin & al. [2021], and 126 samples sequenced in the present study) and is based on 599 single-gene trees generated by DISCO. For a summary of targeted genes recovered for each sample, refer to suppl. Table S1. The partitioned ML concatenation tree based on 81 plastid protein-coding genes (PCT; short "plastid tree") includes 224 samples (84 whole plastomes, 45/66 samples from Maurin & al. [2021]; and 95/126 samples sequenced in the present study). Each sample

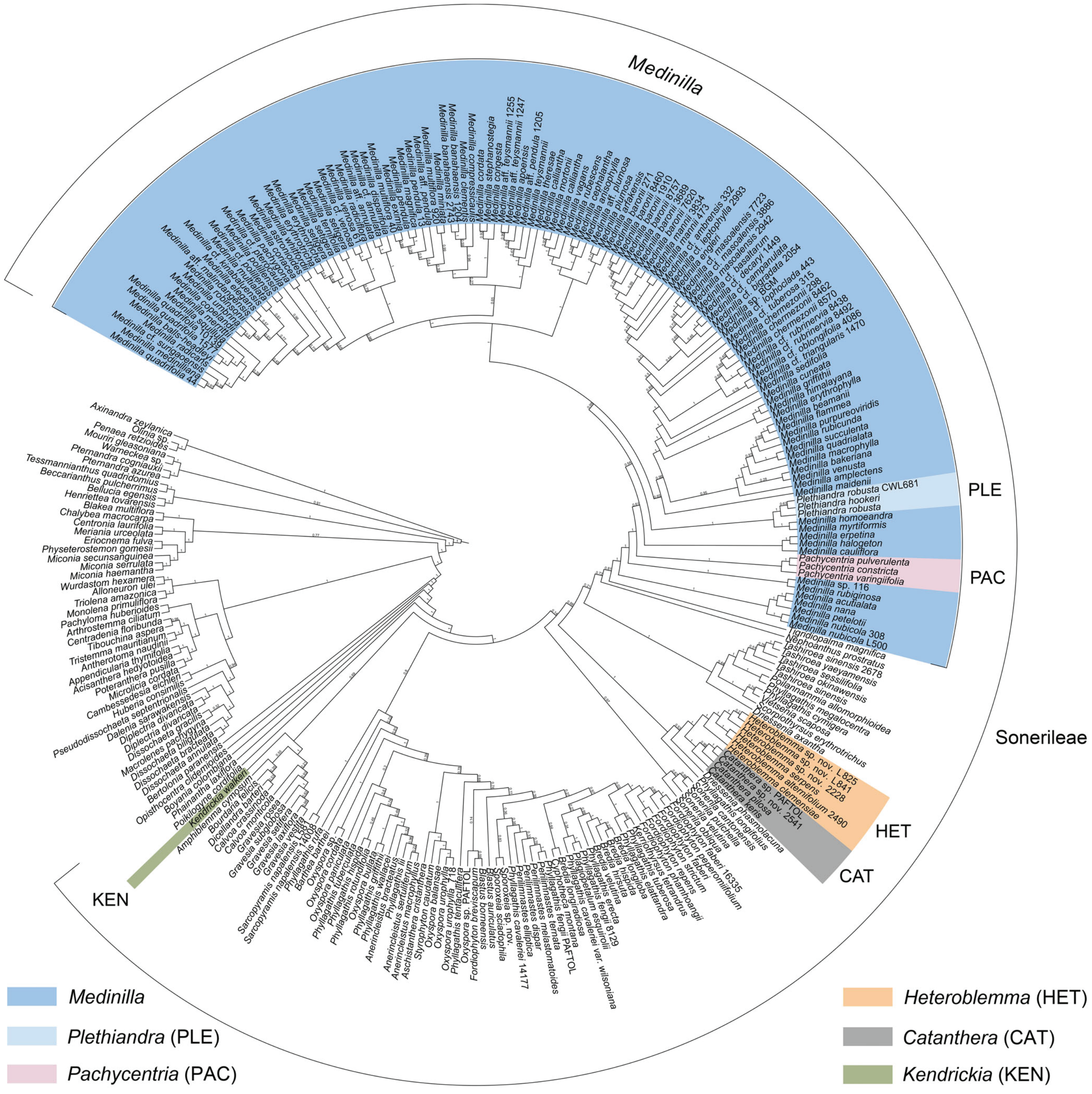

Fig. 1. DISCO-ASTRAL tree based on 272 samples and 385 nuclear genes showing the relationships of the fleshy-fruited Sonerileae genera (colored ranges) in the context of Sonerileae (bracketed range). Local posterior probabilities (LLP) are shown above the branches.

is represented by at least seven loci (see suppl. Table S1). The total combined sequence length of the plastid supermatrix is 69,943 base pairs, 33.96% of which is gaps/missing data.

In the nuclear tree (Fig. 1), fleshy-fruited Sonerileae are resolved in three separate clades. *Kendrickia* is sister to the Afrotropical clade (NAT: LPP = 0.69). Notably, *Kendrickia* does not fall within the Asian Superclade to which the other fleshy-fruited genera belong (NAT: LPP = 1). *Kendrickia* was excluded from the plastid analysis due to low sequence recovery (Fig. 2). In the nuclear tree (Fig. 1), four species of *Catanthera* and six of *Heteroblemma* have full support as monophyletic sister clades. They belong to a clade that includes *Phyllagathis longifolius* (Cogn.) J.F.Maxwell and *Driessenia phasmolacuna* C.W.Lin (NAT: LPP = 1). *Tigridiopalma* C.Chen is sister to *Medinilla* (NAT: LPP = 0.81). In the plastid tree (Fig. 2), *Heteroblemma* is not monophyletic. Four samples are sister to three *Catanthera*, and this clade is sister to two samples of *Heteroblemma*, which are sister to *P. longifolius*. This *Catanthera*-*Heteroblemma*-*Phyllagathis longifolius* clade is sister to the *Medinilla* clade. *Driessenia phasmolacuna* is resolved in the sister group to these two clades, along with other *Driessenia* and *Phyllagathis* species. All these relationships have strong support (PCT: BS = 98–100).

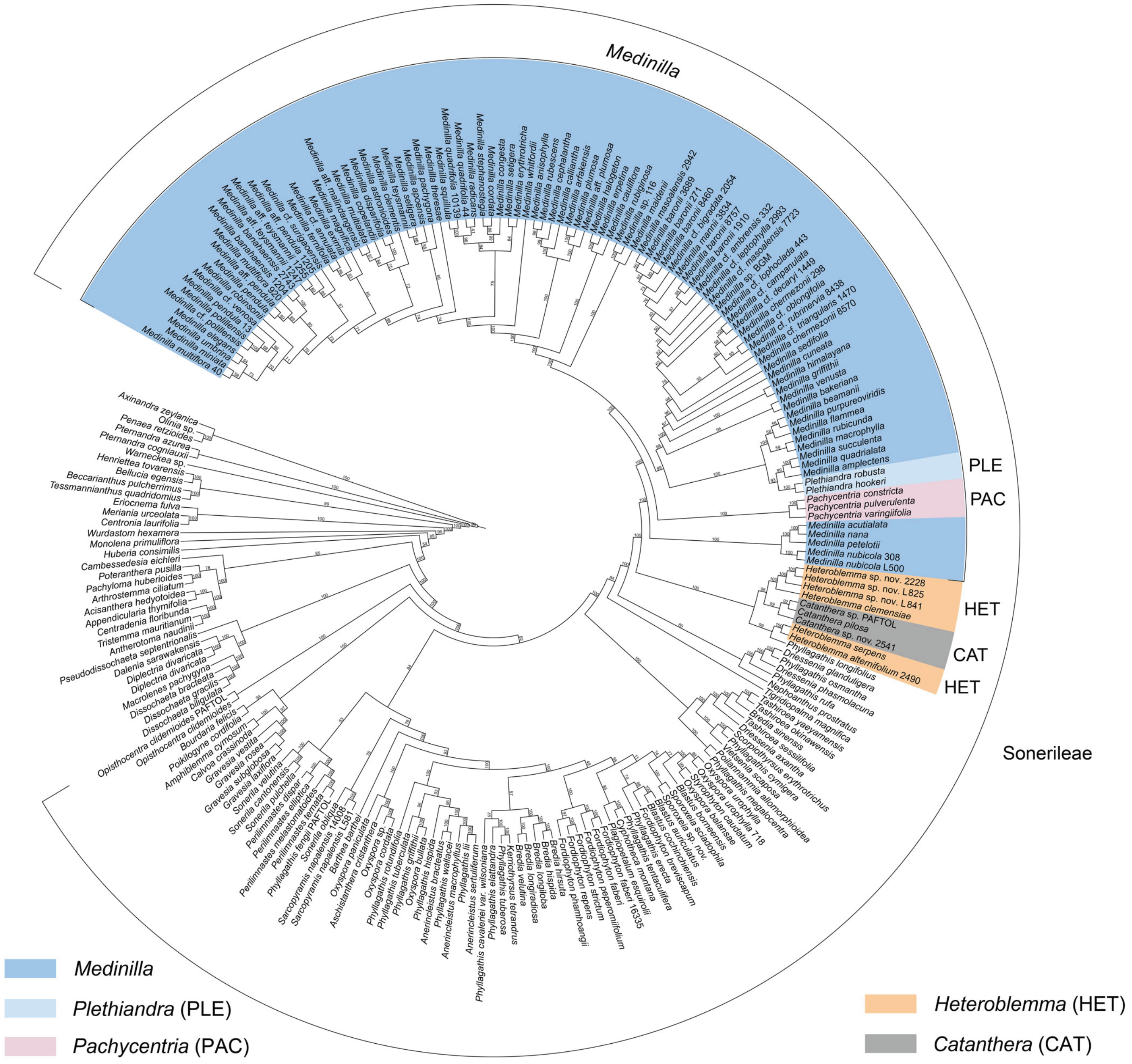

Fig. 2. Maximum likelihood plastid tree based on 224 samples and 81 genes showing the relationships of the fleshy-fruited Sonerileae genera (colored ranges) in the context of Sonerileae (bracketed range). Bootstrap (BS) support values are shown above the branches.

Both phylogenies resolve *Medinilla* as paraphyletic with respect to *Pachycentria* and *Plethiandra* (NAT: LPP = 1, PCT: BS = 100; Figs. 1–3), with the latter two genera being monophyletic. Including *Pachycentria* and *Plethiandra*, there are seven "Early Diverging Clades" (Fig. 3). The *M. nubicola*-alliance (NAT: LPP = 1; PCT: BS = 100; Fig. 3) is sister to all other *Medinilla* species sampled (NAT: LPP = 1; PCT: BS = 100) in both analyses. In the nuclear tree (Fig. 3, left), the *M. rubiginosa*-alliance diverges next (NAT: LPP = 1), followed by *Pachycentria* (NAT: LPP = 1). Then the *M. erpetina*-alliance diverges (NAT: LPP = 1), but the placement has low support (NAT: LPP = 0.61). The *M. myrtiformis*-alliance (NAT: LPP = 1) and *Plethiandra* (NAT: LPP = 1) form the next sister group (NAT: LPP = 1), but with low support (NAT: LPP = 0.54). Similarly, the placement of the *M. maidenii*-alliance has low support (NAT: LPP = 0.65). It is resolved as sister to the Western Superclade (Fig. 3, left; NAT: LPP = 0.98). The Western Superclade (Fig. 4) consists of the *M. rubicunda*-alliance (NAT: LPP = 0.95), *M. erythrophylla*-alliance (NAT: LPP = 1), *M. cuneata*-alliance, *M. sedifolia*-alliance, and *M. viscoides*-alliance (NAT: LPP = 1). The Eastern Superclade (Fig. 5, left; NAT: LPP = 1) consists of three clades: the *M. arfakensis*-alliance (NAT: LPP = 1) and *M. anisophylla*-alliance (NAT: LPP = 1) are sister groups (NAT: LPP = 1) and together are sister to the *M. medinilliana*-alliance (NAT: LPP = 1).

Most of the major *Medinilla* clades recovered in the nuclear tree (Figs. 3–5, left) were also strongly supported in the

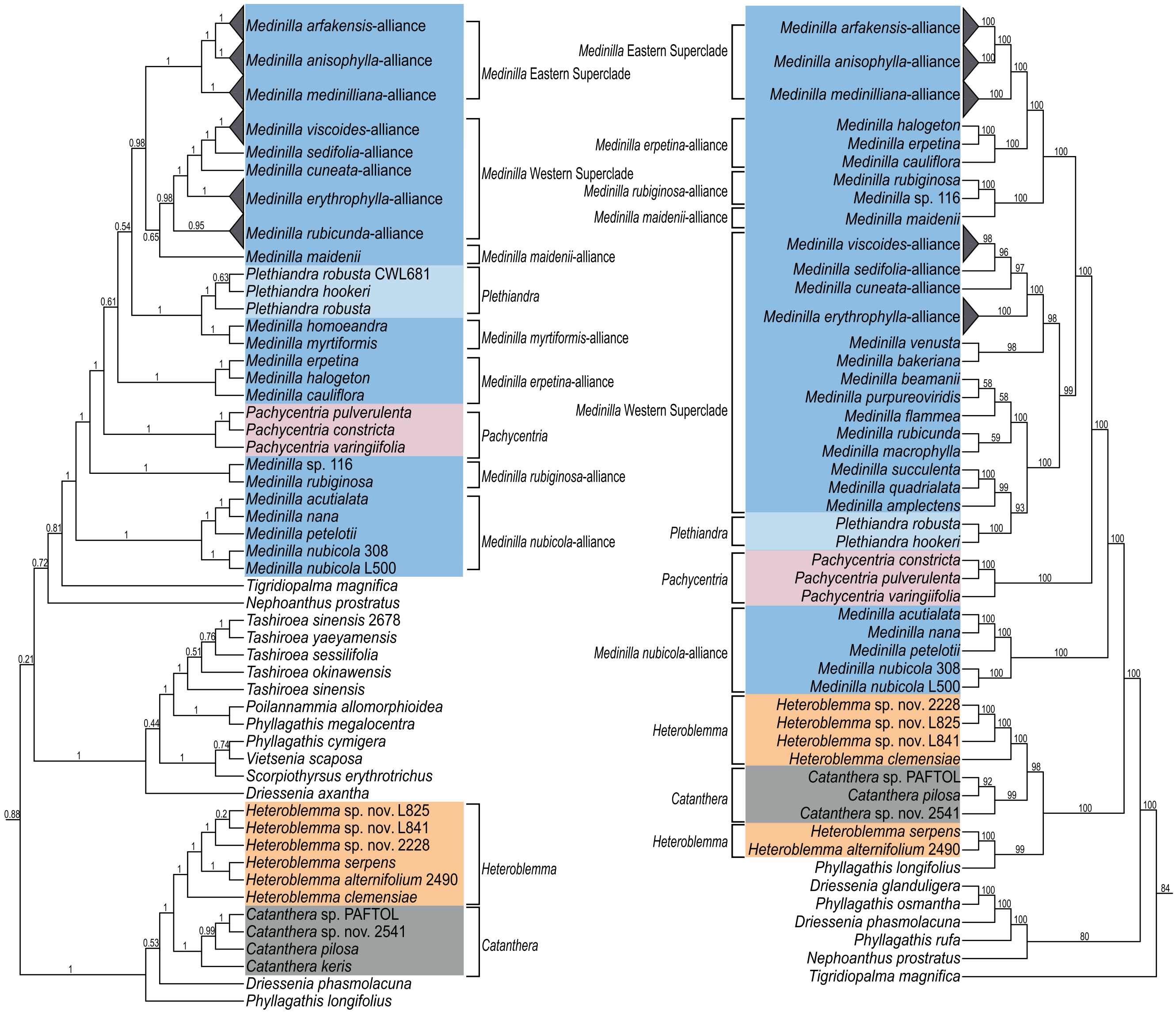

Fig. 3. DISCO-ASTRAL nuclear tree **(left)** based on 272 samples and 385 genes and maximum likelihood plastid tree **(right)** based on 224 samples and 81 genes showing the Early Diverging Clades of *Medinilla* and sister taxa. Local posterior probabilities (nuclear tree) and bootstrap support values (plastid tree) are shown above the branches

plastid tree (Figs. 3–5, right), but their relationships to each other often differ, especially in the case of the Early Diverging Clades (Fig. 3). *Pachycentria* diverges after the *M. nubicola*-alliance (PCT: BS = 100). The *M. maidenii*-alliance is sister (PCT: BS = 100) to the *M. rubiginosa*-alliance (PCT: BS = 100). These are sister (PCT: BS = 100) to the *M. erpetina*-alliance (PCT: BS = 100) and the Eastern Superclade (PCT: BS = 100). *Plethiandra* is resolved among species from the *M. rubicunda*-alliance (PCT: BS = 100, Fig. 4), which is resolved in two separate clades (PCT: BS = 99). There are many inconsistencies between the species relationships of the *M. viscoides*-alliance. Similarly, there are many inconsistencies within the *M. medinilliana*-alliance (Fig. 5).

■ DISCUSSION

Our phylogenetic study representing 227 accessions of Sonerileae, including 141 accessions of *Medinilla* and allies, revealed that the fleshy-fruited Sonerileae belong to at least three different clades within the tribe: (1) *Kendrickia*, (2) *Heteroblemma/Catanthera*-alliance, and (3) *Medinilla* (including *Pachycentria* and *Plethiandra*). *Kendrickia* is resolved in an isolated phylogenetic position and is not part of the *Heteroblemma/Catanthera*-alliance. *Pachycentria* and *Plethiandra* are nested within *Medinilla*. Each clade is discussed below. For *Medinilla*, 15 major lineages were identified and are further discussed below. These lineages are ordered based on their appearance in the nuclear tree (Fig. 3, left), indicating the estimated divergence from the *Medinilla* type species (*M. medinilliana*). The observation of widespread discordance between the nuclear and plastid trees is discussed in the respective sections.

***Kendrickia.* —** *Kendrickia* (Fig. 6A) is not closely related to any of the other fleshy-fruited, climbing Sonerileae with lobed steles. Thus, fleshy fruit and atypical xylem evolved convergently in Sonerileae at least twice, the latter probably in relation to the root climbing habit (Cámara-Leret

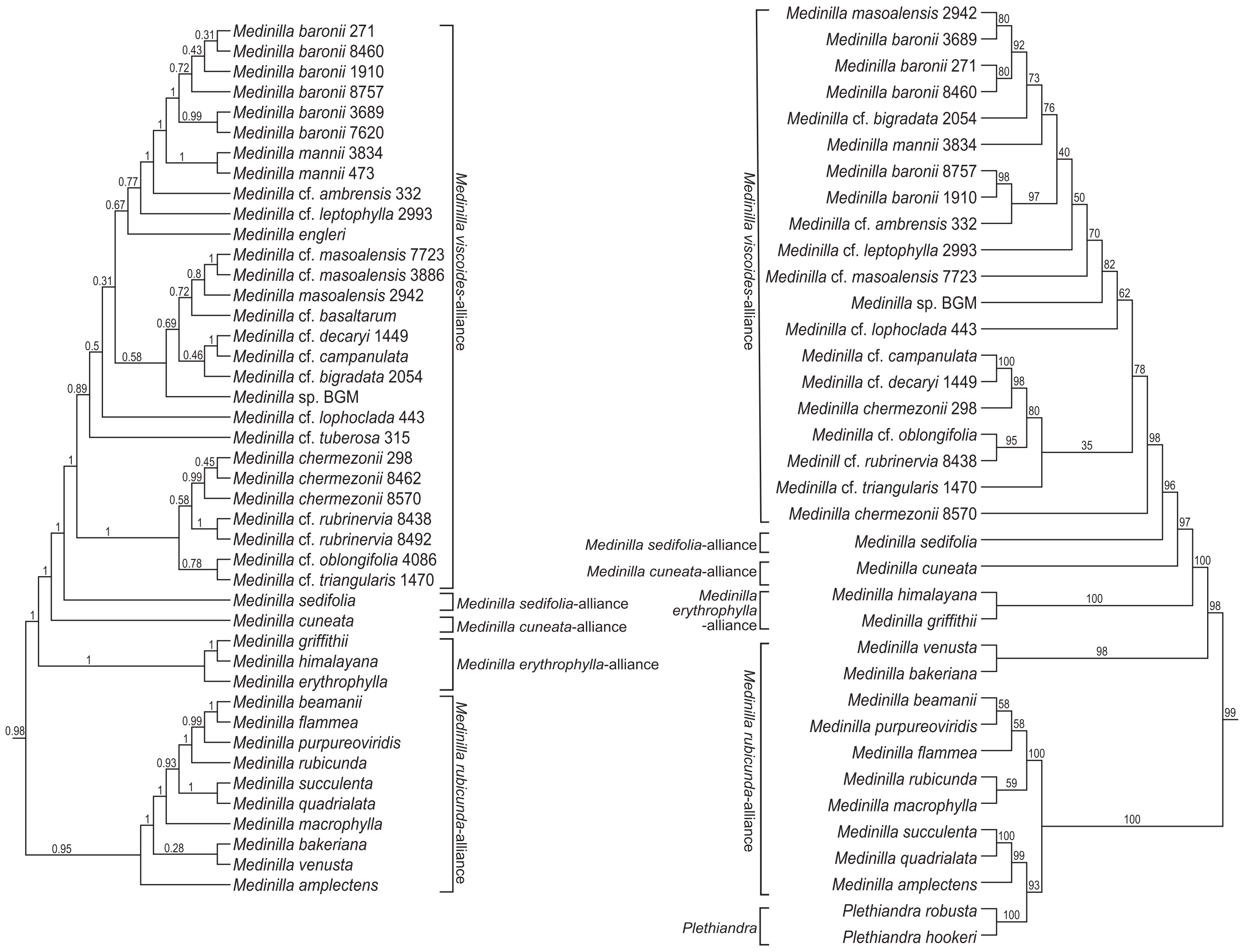

Fig. 4. Alliances within the Western Superclade of *Medinilla* are shown on a DISCO-ASTRAL nuclear tree **(left)** based on 272 samples and 385 genes and a maximum likelihood plastid tree **(right)** based on 224 samples and 81 genes. Local posterior probabilities (nuclear tree) and bootstrap support values (plastid tree) are shown above the branches

& al., 2013). Rather, *Kendrickia* is sister to the Afrotropical clade of Sonerileae in the nuclear tree (Fig. 1) (see Liu & al., 2022; Veranso-Libalah & al., 2023), albeit with low support (NAT: LPP = 0.69). Plastid sequences from *Kendrickia* were not included in the analysis, so this relationship could not be re-tested. However, there are some noteworthy morphological similarities to the Afrotropical Superclade. For instance, some *Gravesia* Naudin, *Dicellandra* Hook.f., and *Calvoa* Hook.f. are root-climbers (Veranso-Libalah & al., 2023). Additionally, the first two have pyramidal and wedge-shaped seeds, respectively, somewhat resembling the prism-shaped seeds of *Kendrickia*. Furthermore, fruit dehiscence in *Dicellandra* is somewhat akin to *Kendrickia*, via the rupturing of the capsule wall. The fleshy capsules of

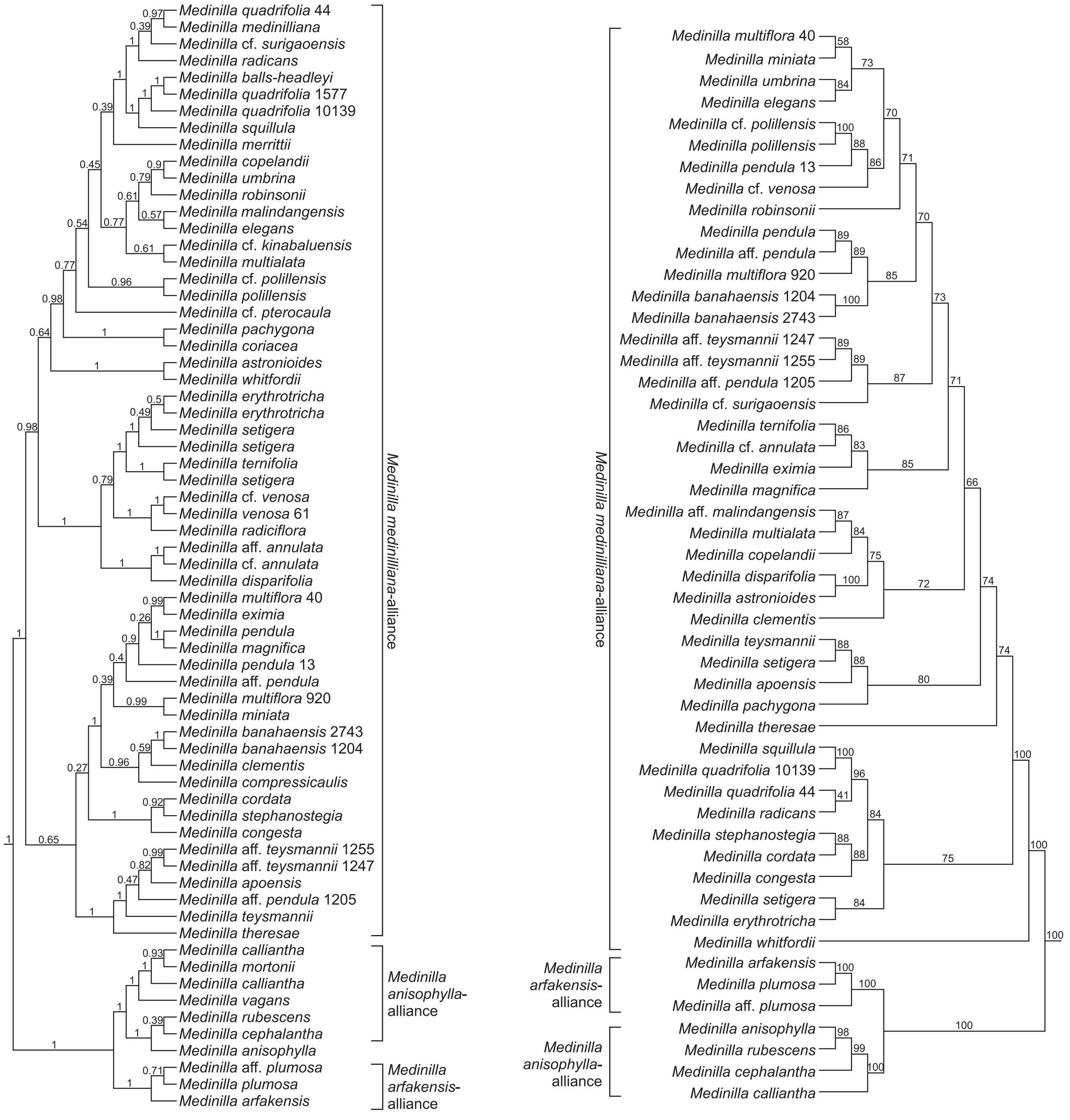

Fig. 5. DISCO-ASTRAL nuclear tree **(left)** based on 272 samples and 385 genes and maximum likelihood plastid tree **(right)** based on 224 samples and 81 genes showing the Eastern Superclade of *Medinilla*. Local posterior probabilities (nuclear tree) and bootstrap support values (plastid tree) are shown above the branches

Kendrickia rupture when ripe and have only a superficial resemblance with the berries of *Medinilla*, *Catanthera*, and *Heteroblemma*. These results raise new questions about *Kendrickia*'s phylogenetic relationships and geographic origins.

***Catanthera* and *Heteroblemma*. —** The close relationship between *Catanthera* (Fig. 6B) and *Heteroblemma* (Fig. 6C) is robustly supported, forming a clade with full support in the nuclear tree (Fig. 3, left). However, the plastid tree (Fig. 3, right) presents a more complex picture. Our study represented the first inclusion of *Catanthera* in a phylogenomic study and included twice as many *Heteroblemma* samples as Zhou & al. (2022), and the same relationship with *Phyllagathis* was resolved with full support. Specifically, *Heteroblemma* from Vietnam are sister to *Catanthera*, while *Heteroblemma* from Malesia are part of a clade that includes a capsular-fruited *Phyllagathis* species. Despite this, given *Heteroblemma*'s morphological cohesion and strong support from the nuclear tree, it is still reasonable to treat it as a distinct genus. The topology of both trees supports the continued recognition of *Catanthera*.

The relationship of *Catanthera* and *Heteroblemma* to *Medinilla* is conflicting, similar to the results of previous studies (Zhou & al., 2019, 2022). In our plastid tree (Figs. 2, 3), *Catanthera* and *Heteroblemma* are part of a clade sister to *Medinilla*, which also includes *Phyllagathis longifolia*. Despite different taxon sampling, Zhou & al. (2022) also identified a similar clade, comprising *Phyllagathis* characterized by thyrsoid inflorescences (which includes *P. longifolia*) and *Heteroblemma*, as being closely related to *Medinilla*. Furthermore, these particular *Phyllagathis* species are distinct from other species in the genus due to their narrowly campanulate to cylindrical hypanthium. In our nuclear tree (Figs. 1, 3), *Tigridiopalma* is sister to *Medinilla*, together forming a clade sister to *Nephoanthus* C.W.Lin & T.C.Hsu. In comparison, Zhou & al. (2022) discovered a clade that combines *Tigridiopalma* and *Nephoanthus* as a sister group to *Medinilla*. To account for the observed widespread phylogenetic discordance in Sonerileae, Zhou & al. (2022) identified several contributing factors, including random noise from uninformative genes, incomplete lineage sorting (ILS), and hybridization or introgression. It is worth noting that branch lengths are very short in this area and support values are low (suppl. Figs. S2, S3). Therefore, the discord may not be real. Whatever the case, these relationships are still not well understood and warrant further exploration. Including the type species of *Catanthera*, *C. lysipetala* F.Muell., in future analyses will be crucial for any subsequent taxonomic revisions. Until the phylogeny is better resolved, it remains unclear if fleshy fruit evolved independently here as well.

***Medinilla* overview. —** The limits of *Medinilla* were rigorously tested, incorporating all major taxonomic groups and alliances either directly or indirectly via similar/associated taxa. Species were sampled from across the geographic range of *Medinilla*, spanning from West Africa to the Solomon Islands, and from China to Australia, encompassing the four greatest centers of species diversity: Madagascar, Borneo, the Philippines, and New Guinea. Notably, both *Pachycentria* and *Plethiandra* are nested among *Medinilla* species (Figs. 1–3). With the inclusion of these two genera, *Medinilla* can be distinguished from all other taxa in Sonerileae by the combination of typical xylem (vs. lobed in cross-section) and berry fruit. While these similar traits are also found in the Dissochaeteae, they can be distinguished by alternate intervessel pits (as opposed to being scalariform in *Medinilla*; see Van Vliet, 1981), interpetiolar ridges, and generally more chartaceous leaves with basal acrodromous venation. Phylogenetically, *Medinilla* can be identified as the most exclusive clade containing *M. medinilliana* and *M. nubicola* Ohwi. Major clades are divided into three groups: the Early Diverging Clades, the Western Superclade, and the Eastern Superclade.

The Early Diverging Clades (Fig. 3) include some members that were previously considered as separate genera, such as *Pachycentria*, *Erpetina*, and *Plethiandra*. Each of these genera is characterized by atypical anthers, usually lacking ventral and sometimes dorsal appendages. They also encompass species from *Medinilla* sect. *Heteromedinilla* and the *M. suberosa*-alliance (Clausing, 1999). The species within these clades range from the lower Himalayas to Vanuatu.

Fig. 6. Fleshy-fruited Sonerileae with atypical xylem configuration. **A**, *Kendrickia* flower and leaves (*Bathiya Gopallawa KED 01*; Sri Lanka); **B**, *Catanthera* sp. fruit and stem cross-section with lobed xylem cross-section (*Darin Penneys 2523*; Borneo); **C**, *Heteroblemma clemensiae* flowers and buds (*Maxim Nuraliev 1345*; Vietnam). — Photos: A, Bathiya Gopallawa; B, Darin Penneys; C, Maxim Nuraliev.

Seven species alliances from the Early Diverging Clades are discussed below.

The Western Superclade primarily consists of species found west of Huxley's modification of the Wallace Line (i.e., the Huxley Line; see Ali & Heaney, 2021). Major clades within this superclade diverge successively as the sampling progresses further west. The *Medinilla rubicunda*-alliance, primarily from Sundaland, includes species placed in *M.* sect. *Sarcoplacuntia*, *M.* sect. *Apateon*, *M.* sect. *Heteromedinilla*, and various informal alliances treated by Regalado (1990, 1995) and Clausing (1999). The *M. erythrophylla*-alliance, from mainland Asia (and Hainan), includes a species placed in the *M. suberosa*-alliance (Clausing, 1999). *Medinilla cuneata* (Thwaites) K.Bremer & Lundin is found in Sri Lanka, and shares similarities with other species in the region. Meanwhile, the *M. sedifolia* Jum. & H.Perrier and *M. viscoides* Triana alliances are from the Afrotropical realm, primarily Madagascar. *Triplectrum* is associated with the *M. sedifolia*-alliance, and *Diplogenea*, *M.* sect. *Septatae*, *M.* sect. *Adhaerentes*, and Clausing's (1999) Group 2 are associated with the *M. viscoides*-alliance. Five species alliances from the Western Superclade are discussed below.

The Eastern Superclade primarily comprises samples collected east of Huxley's Line. This superclade is split into two major clades. One consists of samples from New Guinea, the Bismarck Archipelago, and the Solomon Islands (the *Medinilla arfakensis* Baker f. and *M. anisophylla* Merr. alliances). The other clade (the *M. medinilliana*-alliance) is mainly composed of Philippine species. Nested within these clades are samples from other regions in the Indomalayan, Australasian, and Oceanian realms. Notably, the *Medinilla* type species (*M. medinilliana*) belongs to this clade, along with species once considered *Dactyliota*, *Hypenanthe*, and *Carionia*. *Cephalomedinilla* is also associated with this clade. Additionally, several *M.* sect. *Sarcoplacuntia* and *M.* sect. *Heteromedinilla* species, all species sampled from *M.* sect. *Medinilla*, and many species sampled from the informal alliances treated by Regalado (1990, 1995) and Clausing (1999; Group 1) were resolved within this superclade. Three species alliances from the Eastern Superclade are discussed below, for a total of 15 alliances.

***Medinilla nubicola*-alliance.** — The relationship of *Medinilla nubicola* (= *M. fengii* (S.Y.Hu) C.Y.Wu & C.Chen) and *M. petelotii* Merr. (Fig. 7A) was initially established by Zhou & al. (2019, 2022), along with their sister position to a few other *Medinilla* species. In this study, two additional associates were identified, and their sister relationship to the rest of *Medinilla* is fully supported by both nuclear and plastid trees. Notably, some species in this clade were originally associated with *Pachycentria*. For example, *P. formosana* Hayata and *P. fengii* S.Y.Hu are synonyms of *M. nubicola*. *Medinilla nana* S.Y.Hu was compared to *P. fengii* in the protologue (Hu, 1952), and *M. arunachalica* G.D.Pal (not sampled but very similar to *M. nana*) was compared to *M. maingayi* C.B.Clarke (Pal, 1995), a subspecies of *P. glauca*. Clausing (2000) excluded *M. nubicola* from *Pachycentria* based on seed morphology, a distinction supported here. In this alliance, anthers are falcate, with long or nearly absent (*M. nubicola*), needle-like, ventral appendages and a tapered dorsal spur (Fig. 7A). These species are found in mainland Asia and Taiwan.

***Medinilla rubiginosa*-alliance.** — Two species from New Guinea were resolved in a fully supported clade by both datasets (Fig. 3). However, placement varies between the datasets. According to the nuclear tree (Fig. 3, left), the *Medinilla rubiginosa*-alliance diverged after the *M. nubicola*-alliance. Conversely, in the plastid tree (Fig. 3, right), the *M. rubiginosa*-alliance is associated with *M. maidenii* F.Muell. (Fig. 7G; see *M. maidenii*-alliance) and is sister to the *M. erpetina*-alliance and the Eastern Superclade. All of these clades overlap in distribution and are found east of the Wallace Line.

Shared traits of the *Medinilla rubiginosa*-alliance include hairiness, leaves with nerves arising near the base, terminal inflorescences, conspicuous bracts, and somewhat verrucose berries (Fig. 7B). In the case of *M. rubiginosa* Cogn., anthers have three, relatively equal appendages pointing basally. Anther details of *Medinilla* sp. 116 are unknown.

Clausing (2000) excluded *Medinilla rubiginosa* (Fig. 7B; = *Pogonanthera hexamera* Baker f.) from *Pachycentria*, a decision fully supported in this study. It has not been associated with any other taxonomic groups. However, *M. pulleana* Mansf. is a similar species from New Guinea that was transferred to *Hypenanthe* by Bakhuizen van den Brink (1943) because of its hairiness and conspicuous bracts. Clausing (1999) also placed *M. pulleana* with *Hypenanthe* species, but in its own subgroup, noting its closer resemblance to other New Guinea species than those of *Hypenanthe*. Subsequently, Bodegom & Veldkamp (2001) characterized a group of pseudostipular species from New Guinea and the Bismarck Archipelago. While the presence of pseudostipules in *M. pulleana* is ambiguous, it closely resembles the group in every other respect. Similarly, both species in the *M. rubiginosa*-alliance lack definite pseudostipules, but they share other similarities with the pseudostipular group. Bodegom & Veldkamp (2001) postulated that the pseudostipular species belong to a larger group including non-pseudostipular species, and a close relationship between the *M. rubiginosa*-alliance and the pseudostipular species is expected but requires further verification.

***Pachycentria*-alliance.** — Nuclear and plastid trees (Fig. 3) consistently support the monophyly of *Pachycentria* as circumscribed by Clausing (2000), and its placement within *Medinilla*. However, placement of *Pachycentria* within *Medinilla* varies between datasets. In the nuclear tree (Fig. 3, left), *Pachycentria* diverges after the *M. rubiginosa*-alliance, while in the plastid tree (Fig. 3, right), it diverges after the *M. nubicola*-alliance. Despite limited sampling (three out of eight species), the inclusion of the type species (*P. constricta*) and the two most morphologically divergent taxa (*P. varingiifolia* Blume and *P. pulverulenta* (Jack) Clausing [Fig. 7C]) ensured robust testing. Notably, *P. varingiifolia* with its remarkably large flowers and dimorphic stamens with ventral appendages, was resolved as sister to the other two species. On the other hand, *P. pulverulenta* (≡ *Pogonanthera pulverulenta* Jack) has auriculate leaf bases and a tuft of hairs instead of a dorsal appendage. Despite these morphological differences, they share the diagnostic traits of this clade, i.e., small ovary in a strongly constricted, urceolate hypanthium, and seeds with comb-shaped testa cells.

***Medinilla erpetina*-alliance. —** *Erpetina* (Fig. 7D) was established by Naudin in 1851 and later transferred to *Medinilla* by Triana in 1871. This move receives robust support from molecular data. *Medinilla erpetina* Triana forms part of

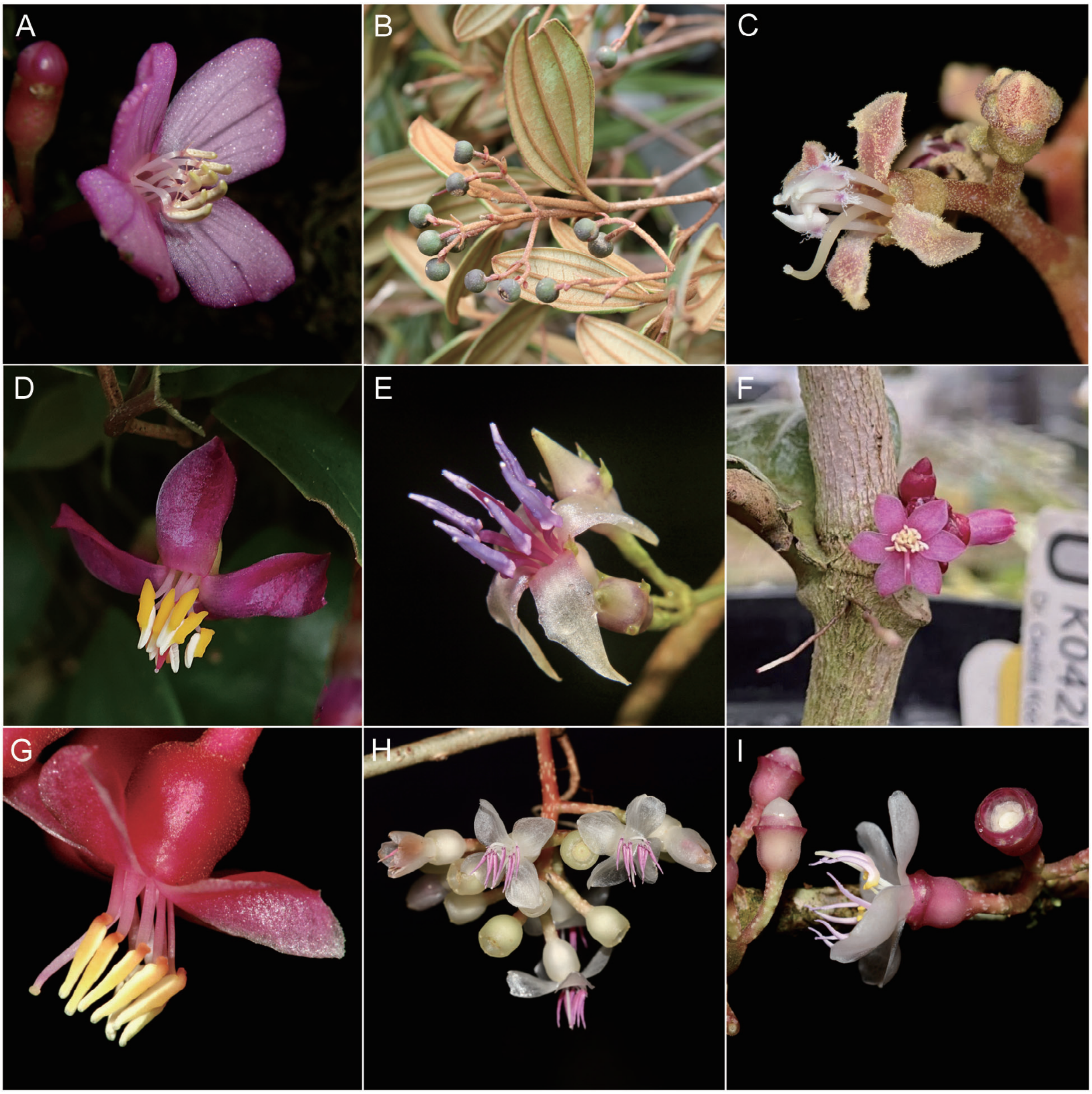

Fig. 7. Representatives from major lineages identified within *Medinilla*: **A**, *M. petelotii* in the *M. nubicola*-alliance (Vietnam); **B**, *M. rubiginosa* in the *M. rubiginosa*-alliance (*Barry Conn 5361*; New Guinea); **C**, *M. pulverulenta* in the *Pachycentria*-alliance (Marie Selby Botanical Gardens, accession number: 2016-0223A; cultivated, originating from a grower in Lao PDR); **D**, *M. erpetina* in the *M. erpetina*-alliance (Solomon Islands); **E**, *M. myrtiformis* in *M. myrtiformis*-alliance (*PLSPH 807*; Philippines); **F**, *M. robusta* in the *Plethiandra*-alliance (*Che-Wei Lin 681*; cultivated at Dr. Cecilia Koo Botanic Conservation Center, originally from Borneo); **G**, *M. maidenii* in the *M. maidenii*-alliance (Marie Selby Botanical Gardens, accession number: MSBG2002-0198B; cultivated, originally from New Guinea); **H**, *M. rubicunda* in the *M. rubicunda*-alliance (*AVAMR 16*; Philippines); **I**, *M. griffithii* in the *M. erythrophylla*-alliance (*Kate Armstrong 2903*; Myanmar). — Photos: A, Maxim Nuraliev; B, Shelley James (https://png-bpbm.smugmug.com/Collections/Melastomataceae/i-zCQmK4z); C, Wade Collier, courtesy of Marie Selby Botanical Gardens; D, Patrick Blanc; E, Mc Andrew Pranada; F, Wei-Yen Chen; G, Phil Nelson, courtesy of Marie Selby Botanical Gardens; H, Maverick Tamayo; I, Kate Armstrong.

a three-species clade, with full support from both molecular datasets (Fig. 3). In the nuclear tree (Fig. 3, left), this clade diverged after *Pachycentria*, while in the plastid tree (Fig. 3, right), it is sister to the Eastern Superclade. Indeed, all three species within this clade are found east of the Wallace Line, in the Bismarck Archipelago, Solomon Islands, and Vanuatu.

Species within this clade are characterized as epiphytic shrubs or climbers with few-flowered, axillary inflorescences. They possess anthers with a prominent dorsal appendage and no ventral appendages. Clausing (1999) placed *Medinilla cauliflora* Hemsl. and *M. halogeton* S.Moore within the *M. suberosa*-alliance, a combination and expansion of Regalado's *M. succulenta* Blume (1990) and *M. palawanensis* Regalado alliances (Group 9; 1995). However, other members of the *M. suberosa*-alliance tested in our study (*M. amplectens* Regalado, *M. erythrophylla* Lindl., *M. quadrialata* Ohwi ex Regalado, *M. succulenta*) were resolved in the *M. rubicunda* (Jack) Blume and *M. erythrophylla* alliances. Anther details for *M. palawanensis* are insufficiently known, but a more recently described species and presumed close relative, *M. ultramaficola* Quakenbush & al., has anthers somewhat consistent with those of the *M. erpetina*-alliance, having a long dorsal appendage and essentially lacking ventral appendages (Quakenbush & al., 2020). More sampling from Palawan is needed to better understand this group.

***Medinilla myrtiformis*-alliance.** — The two species resolved in this clade were initially classified in genera other than *Medinilla*. *Medinilla myrtiformis* Triana (Fig. 7E) was first described as *Aplectrum* Blume (= *Diplectria* (Blume) Rchb., tribe Dissochaeteae) and later transferred to *Medinilla* by Triana (1871). It is also synonymous with *Kibessia celebica* Miq. Similarly, *M. homoeandra* (Stapf) M.P.Nayar was initially classified as *Anplectrum* A.Gray (= *Diplectria*), and later transferred to *Medinilla* by Nayar (1966). These taxonomic reclassifications find full support from molecular evidence in both the nuclear and plastid trees (Fig. 3).

Both species are part of the previously identified *Medinilla myrtiformis*-alliance, a group characterized by shared traits that have been recognized for a long time (e.g., notes on *M. cardiophylla* Merr. in Merrill, 1910). Veldkamp (1978, 1988) undertook a revision of the group, with further contributions from Regalado (1990, 1995) and Clausing (1999). The defining features of this alliance are anthers that lack ventral appendages and have a short, triangular, dorsal plectrum. Additional shared traits include very narrow, divaricate branches; few-flowered, axillary cymes; and ovate-lanceolate petals. While *M. muricata* Blume was initially placed within this group by Regalado (1990), it differs from typical members by a few key traits, such as petal shape (rounded vs. pointed) and anther appendages (ventral lobes present vs. absent). Recognizing these distinctions, Clausing (1999) placed *M. muricata* in a separate alliance. Flowers remain unknown for several other species assigned in this group, including *M. benguetensis* Elmer, *M. gracilis* Veldkamp, and *M. salicina* Ohwi ex Regalado. Therefore, further investigations and testing are necessary to inform our understanding of these species.

Medinilla homoeandra is native to Borneo, while *M. myrtiformis* is found in Wallacea, which includes the Philippines (see Ali & Heaney, 2021). The alliance, including some unsampled species like *M. ericoidea* Steenis in New Guinea, demonstrates a widespread distribution in Malesia, spanning the Wallace Line. This distribution pattern aligns with other alliances, such as *Pachycentria*, the *M. rubicunda*-alliance, and the *M. medinilliana*-alliance. In the nuclear tree (Fig. 3, left), the *M. myrtiformis*-alliance was resolved as sister to *Plethiandra*. Unfortunately, too few sequences were recovered to include this alliance in the plastid tree and confirm this relationship.

***Plethiandra*-alliance.** — *Plethiandra* is distinguished by its 6-petaled flowers, more than double that number of stamens, and anthers without appendages. Molecular data fully supports the inclusion of *Plethiandra* in *Medinilla* (Figs. 1–4). The monophyly of *Plethiandra* is also well-supported. Although the type species, *P. motleyi* Hook.f., was not included in the analyses, the sampled *P. hookeri* Stapf and two accessions of *P. robusta* (Cogn.) Nayar (Fig. 7F), representing two out of eight species, were resolved together. *Plethiandra* stands out as one of the most easily distinguished groups, and its monophyly has never been in question (Kadereit, 2005). However, the position of *Plethiandra* within *Medinilla* varies depending on the dataset. In the nuclear tree (Fig. 3, left) it appears as a sister to the *M. myrtiformis*-alliance, positioned among the Early Diverging Clades of *Medinilla*. The reduced anther appendages observed in the *M. myrtiformis*-alliance, along with the absence of appendages in *Plethiandra*, suggest a potential affinity. Yet no samples of the *M. myrtiformis*-alliance were included in the plastid tree to verify this relationship. According to the plastid tree (Fig. 3, right), *Plethiandra* is nested among other Bornean taxa of the *M. rubicunda*-alliance.

***Medinilla maidenii*-alliance.** — The classification of *Medinilla maidenii* (Fig. 7G) from New Guinea has long been uncertain. Mueller (1886) expressed no objection to placing it in *Pachycentria* due to atypical anthers for *Medinilla*. Anthers lack ventral appendages and possess a blunt dorsal projection. He also drew parallels with *Pternandra*, because the thecae are separated giving the appearance of dehiscence via a slit. Molecular evidence clearly places *M. maidenii* within *Medinilla*, but its internal placement remains ambiguous and in need of further exploration. In the nuclear tree (Fig. 3, left), it was resolved with low support as sister to the Western Superclade (NAT: LPP = 0.65), while in the plastid tree (Fig. 3, right), it was placed with full support as sister to the *M. rubiginosa*-alliance. The plant habit aligns more with the Western Superclade, whereas the geographic distribution aligns more with the *M. rubiginosa*-alliance. Notably, the anther morphology does not resemble either group. Kartonegoro (2023) synonymized three taxa from New Guinea with *M. maidenii*, and several additional taxa from New Guinea share a similar growth form and inflorescences (e.g., *M. nabirensis* Karton. and *M. papulosa* Ohwi). Targeting these would help better understand the group.

***Medinilla rubicunda*-alliance. —** Ten samples were resolved in a well-supported clade in the nuclear phylogeny (NAT: LPP = 0.95; Fig 4, left), originating from Sundaland (nine) and New Guinea (one), representing a sister group to species found further west. In the plastid tree, eight of these samples were resolved together (PCT: BS = 100), but *Plethiandra* is also included. The remaining two species, *Medinilla venusta* King and *M. bakeriana* Mansf., are resolved together in the sister group.

Members of the *Medinilla rubicunda*-alliance are epiphytic shrubs with often warty stems and glabrous nodes. Inflorescences lack persistent or conspicuous bracts and bracteoles, and they exhibit variable architectures. In paniculate inflorescences, branches are not arranged in a regular whorled pattern. The hypanthium is glabrous; anthers are equal, isomorphic, and possess two ventral lobes and generally a small dorsal spur. This alliance shares similarities with the *M. erythrophylla*-alliance, which is part of its sister group. Phylogenetic estimates suggest that previous classifications of these species (Blume, 1831, 1849; Bakhuizen van den Brink, 1943; Regalado, 1990, 1995; Clausing, 1999) are either polyphyletic or insufficient to capture the diversity within the *M. rubicunda*-alliance. Targeted sampling from Sundaland would likely help fill in gaps related to this group.

In the nuclear tree (Fig. 4, left), *Medinilla beamanii* Regalado was resolved within a clade comprising *M. rubicunda* samples. These species share strong morphological similarities with *M. beamanii*, differing primarily in having a longer peduncle and more umbellate inflorescences. *Medinilla rubicunda* (Fig. 7H) is widespread and very polymorphic (Regalado, 1990, 1995), and it currently includes eight heterotypic synonyms (Kartonegoro, 2023), indicating a potential for further expansion of the species complex or, alternatively, the necessity for a more detailed examination that may lead to a re-evaluation of species limits. A study specifically focused on this species complex would be crucial in clarifying the relationships and boundaries within it.

***Medinilla erythrophylla*-alliance. —** Three samples from Myanmar form a clade with full nuclear support (Fig. 4, left). Although only two out of the three samples were included in the plastid tree, they also form a well-supported clade (Fig. 4, right). This clade is part of the Western Superclade, spanning from Malesia (primarily Sundaland) to the Afrotropical realm. Stamens are somewhat unequal to dimorphic in these species. *Medinilla pauciflora* Hook.f. ex Triana (not sampled) is similar to *M. himalayana* Hook.f. ex Triana but has a more condensed inflorescence. Both lack a dorsal anther appendage (Clarke, 1879). *Medinilla griffithii* C.B.Clarke (Fig. 7I) also lacks a dorsal anther appendage. *Medinilla erythrophylla* has dimorphic stamens and lacks a dorsal appendage on the larger anthers. It is also known to have swollen roots. Clausing (1999) placed *M. erythrophylla* in the *M. suberosa*-alliance that included *M. palawanensis*. *Medinilla palawanensis* is very similar in habit to *M. hainanensis* Merr. & Chun (a synonym of *M. erythrophylla*) and *M. ultramaficola* (which has swollen roots). Targeting these taxa is crucial for a better understanding of this clade.

***Medinilla cuneata*-alliance. —** *Medinilla cuneata*, from Sri Lanka, is found in a distinct lineage of its own, sister to the Afrotropical taxa in both nuclear and plastid trees (Fig. 4). Its stems are rather succulent and inflorescences are reduced to single flowers on leafless nodes. Anthers in this species are broadly lanceolate, possessing both ventral lobes and a dorsal spur. *Medinilla anamalaiana* Sasidh. & Sujanapal (Western Ghats) and *M. maculata* Gardner (Sri Lanka) are morphologically similar species from the same region and probably belong to this clade.

***Medinilla sedifolia*-alliance. —** *Medinilla sedifolia* (Fig. 8A), originating from Madagascar, is resolved as sister to the rest of the Afrotropical *Medinilla* in both nuclear and plastid trees (Fig. 4). Perrier de la Bâthie (1951) and Clausing (1999) treated it in its own subgroup of *M.* sect. *Septatae* and Group 2, respectively. The species strongly resembles *M. beddomei* C.B.Clarke of the Western Ghats, initially classified as *Triplectrum*. Shared characteristics between these species include a creeping habit, narrow stems, flaky reddish bark, rusty to powdery pubescence on young parts, equal, succulent orbicular leaves, solitary axillary flowers, dimorphic stamens and long blunt ventral and dorsal anther appendages. Another creeping species in this region is *M. prostrata* Jum. & H.Perrier, with fairly succulent, round leaves, pubescence, solitary flowers in leaf axils, shorter lobed anther appendages and ovary wholly adherent to the hypanthium (vs. separate). Perrier de la Bâthie (1951) did not consider *M. prostrata* very close to *M. sedifolia* because of its distinct anthers and ovary adherence, and he instead placed *M. prostrata* in sect. *Adhaerentes*. Nevertheless, the usefulness of concrescence for phylogenetic inference has not found molecular support (see the *M. viscoides*-alliance discussion below). The connections between these species (plus the pseudotubular-flowered species discussed in the *M. viscoides*-alliance) suggest multiple Madagascar-India connections, warranting further study.

***Medinilla viscoides*-alliance. —** All species sampled from the Afrotropical realm form a fully supported clade (Fig. 4). *Medinilla mannii* Hook.f. and *M. engleri* Gilg, the only two species found on the African continent, are nested among the Malagasy species, indicating their likely origin. *Medinilla sedifolia* discussed above, is sister to all other samples. Excluding *M. sedifolia*, the stamens of the remaining species are easily characterized by long, subulate ventral appendages and a prominent dorsal appendage, exemplified by *M. cordifolia* Baker ex H.Perrier (Fig. 8B). However, some species from Madagascar, such as *M. papillosa* Baker, exhibit considerable differences. In these species, flowers are nectariferous and relatively large, and the corollas never open fully, forming a pseudotube. The stamens have exceptionally long, broad filaments and much shorter anthers, nearly or entirely lacking appendages. Some species from the Comoro Islands (e.g., *M. fasciculata* Baker), the Western Ghats (e.g., *M. malabarica* Bedd. & C.E.C.Fisch.) and Sri Lanka (*M. fuchsioides* Gardner; Fig. 8C) share this distinctive morphology. The similarities among these disjunct pseudotubular species may be the result of convergent evolution or dispersal across the Indian Ocean. More sampling is needed to verify the placement and relationships of these species.

Swollen/tuberous roots are a noteworthy trait common in this alliance (e.g., *Medinilla mannii*, *M. baronii* Baker, and *M. lophoclada* Baker). They would certainly increase drought tolerance but can be formicarial as well (Quakenbush & Chen, pers. obs.). Such roots are also observed in *M. erythrophylla*, *M. maidenii*, *M. ramiflora* Merr., *M. ultramaficola*, and *Pachycentria constricta*. Thus, it appears to be a widespread trait among the Early Diverging Clades and the Western Superclade.

The first species described in the Afrotropical realm, *Medinilla viscoides*, was classified as *Diplogenea*, as was *M. mannii* (with uncertainty). Both Perrier de la Bâthie (1951) and Clausing (1999) grouped *M. viscoides* with *M. chermezonii* H.Perrier. While *M. viscoides* was not sampled in our study, *M. mannii* and multiple samples of *M. chermezonii* were. Both were resolved in this clade, providing strong molecular evidence for including *Diplogenea* in

Fig. 8. Representatives from major lineages identified within *Medinilla*, continued: **A**, *M. sedifolia* from the *M. sedifolia*-alliance (Marie Selby Botanical Gardens, accession number: 2013-2217A; cultivated, originally from Madagascar); **B**, *M. cordifolia* from the *M. viscoides*-alliance (Madagascar); **C**, *M. fuchsioides*, alliance unknown (Sri Lanka); **D**, *M. arfakensis* from the *M. arfakensis*-alliance (*Shelley James 1867*; Solomon Islands); **E**, *M. heteromorphophylla* from the *M. anisophylla*-alliance (*Porter Lowry 6861*; Vanuatu); **F–I**, *M. medinilliana*-alliance: **F**, *M. stephanostegia* (*Darin Penneys 2451*; Borneo); **G**, *M. magnifica* (Philippines); **H**, *M. quadrifolia* (= *M. trianae*; *Peter Quakenbush 44*; Philippines); **I**, *M. venosa* (*Peter Quakenbush 61*; Philippines). — Photos: A, Wade Collier, courtesy of Marie Selby Botanical Gardens; B, Maxim Nuraliev; C, Bathiya Gopallawa; D, Shelley James (https://png-bpbm.smugmug.com/Fieldwork/Guadalcanal2015/Collections/SAJ1867); E, Porter Lowry II (https://www.tropicos.org/image/100153215, CC BY-NC-ND 3.0, https://creativecommons.org/licenses/by-nc-nd/3.0/, image cropped; F, Darin Penneys; G–I, Peter Quakenbush.

Medinilla. Species in this clade also correspond to two sections, *M*. sect. *Septatae* and *M*. sect. *Adhaerentes*. These were based on the degree of adherence of the hypanthium to the ovary (Perrier de la Bâthie, 1951). Both sections are represented by multiple taxa in our study, and they do not receive molecular support. Additionally, species in this clade correspond to Clausing's (1999) Group 2, which includes four alliances: *M. ericarum* Jum. & H.Perrier, *M. humblotii* Cogn., *M. parvifolia* Triana, and *M. sedifolia*. The *M. sedifolia*-alliance is discussed above, the *M. parvifolia*-alliance does not gain molecular support, and sampling was insufficient to test the *M. humblotii* and *M. ericarum* alliances. Weak branch support, particularly in the plastid phylogeny, combined with short branch lengths (suppl. Figs. S2, S3) and discordance among the phylogenies, prevents further division of this group. Therefore, increased sampling, detailed morphological comparisons, and a comprehensive revision of species are critically needed. Additionally, incorporating more plastid loci, such as the entire plastome, is essential for a deeper understanding of the internal relationships within this group.

***Medinilla arfakensis*-alliance. —** Three samples from New Guinea, the Bismarck Archipelago, and the Solomon Islands (Fig. 8D) were resolved in a clade fully supported by both nuclear and plastid trees (Fig. 5). However, species identification is challenging due to the limited knowledge of taxa in this region. A comprehensive revision and more fieldwork are urgently needed. The clade is sister to the *Medinilla anisophylla*-alliance discussed below. Both of these are sister to the *M. medinilliana*-alliance, and collectively form the Eastern Superclade. Regalado (1990) previously considered many of the species in New Guinea as part of his *M. magnifica*-alliance. Clausing (1999) later expanded the *M. magnifica*-alliance, including several species from New Guinea (e.g., *M. arfakensis*). However, this expanded alliance was found to be polyphyletic with sampled species split between the *M. arfakensis* and *M. medinilliana* alliances. The *M. arfakensis*-alliance tends to have a prominent dorsal appendage and small or absent ventral appendages, while similar species in the *M. medinilliana*-alliances tend to have a small dorsal spur and more prominent ventral lobes. Undoubtedly, there are more species from New Guinea and surrounding islands belonging to this clade. To gain a better understanding of this group, more extensive sampling and foundational taxonomic work are essential.

***Medinilla anisophylla*-alliance. —** A clade consisting of seven taxa from the Solomon Islands is fully supported by both phylogenies and is sister to the *Medinilla arfakensis*-alliance (Fig. 5). These species are pubescent climbers with strongly anisophyllous leaves, prominent and persistent floral bracts, pubescent hypanthia, and robust dorsal appendages on the anthers (e.g., Fig. 8E). When present, the ventral appendages are much less prominent than the dorsal appendage. Despite differences in anther morphology, these taxa share strong similarities with some species resolved in or associated with the *M. medinilliana*-alliance (see discussion below). For example, Merrill & Perry (1943) considered *M. cephalantha* Merr. & L.M.Perry and *M. sessilis* Merr. & L.M.Perry as part of the same "section" as *Cephalomedinilla*. Another species from Vanuatu, undoubtedly belonging in this clade, is *M. heterophylla* A.Gray, which was likened to *Dactyliota* (Gray, 1854). These apparent similarities are likely the result of convergent evolution. Additional taxa from the Bismarck Archipelago (e.g., *M. pubiflora* Merr. & L.M.Perry; NGF 31506, BISH & L), Micronesia (i.e., Kosrae), Fiji, Wallis and Futuna, Samoa, and American Samoa are likely part of this clade as well. Notably, *M. calliantha* Merr. & L.M.Perry was not resolved as monophyletic and might need revision.

***Medinilla medinilliana*-alliance. —** A large clade primarily composed of Philippine taxa, including the type species (*Medinilla medinilliana*), was resolved with full support by both datasets (Figs. 5, 8F–I). This clade extends its distribution to include Vietnam, Borneo, Guam, New Guinea, the Solomon Islands, and Australia, making this the most widespread and species-rich clade identified in this study. The alliance is characterized by an exceptionally high degree of polymorphism, rendering it challenging to precisely define. The considerable diversity within this clade is evident from the various genera that were historically associated with it. As earlier noted in the *Medinilla* overview, species once classified as *Hypenanthe* (*M. venosa* Blume), *Dactyliota* (*M. setigera*), and *Carionia* (*M. whitfordii* Merr.) were resolved within this alliance. Regalado (1995) included the first two in his Group 10, where he also placed *Cephalomedinilla* (not tested). Morphological characteristics, including habit, stem, leaf, inflorescence, and floral details are consistent with this group. Therefore, it is reasonable to include *Cephalomedinilla* within this alliance as well. Many species from other described groups were resolved within this clade, especially those from Regalado (1990, 1995) and Clausing (1999; Group 1). Only the small *M. stephanostegia*-alliance (Fig. 8F; 60% of the species sampled) found support without the need for modification.

In general, the anthers of taxa within the *Medinilla medinilliana*-alliance are narrow and curved, consisting of two distinct colors (e.g., yellow and purplish). The ventral lobes tend to be more prominent than the dorsal spur, or both ventral and dorsal appendages are long and conspicuous. Although, anthers in the *M. rubicunda*, *M. erythrophylla*, *M. cuneata*, and *M. sedifolia* alliances of the Western Superclade may share some similarities, species in the *M. medinilliana*-alliance can be distinguished by additional traits. These distinctive features include setose nodes, inflorescences with regularly whorled branches, conspicuous bracts, membranous calyx rim, and/or 6-merous flowers. Whorled leaves, pubescent or thick hypanthium, heteranthery, and/or bicolored anthers serve as reliable indicators of this clade as well, although these traits may occasionally appear in the Western Superclade.

Despite the widespread phylogenetic discordance observed between the two phylogenies, some clades within the nuclear tree exhibit morphological coherence. For instance, the *Medinilla medinilliana*-*M. whitfordii* clade, supported by the nuclear tree (NAT: LPP 0.64; Fig. 5, left), consists of terrestrial shrubs or climbers with a thick hypanthium (e.g., >1 mm). Many also have whorled leaves, 5- or 6-merous flowers, and heteranthery. Another coherent clade, the *M. erythrotricha* Elmer-*M. disparifolia* C.B.Rob. clade (NAT: LPP 1; Fig. 5, left), are all terrestrial shrubs or climbers as well. Bracts tend to be prominent, and the hypanthium tends to be pubescent with a membranous calyx rim. The *M. magnifica*-*M. clementis* Merr. and *M. teysmannii* Miq.-*M. theresae* Fernando clades tend to be epiphytic shrubs with setose nodes and many-flowered inflorescences. However, additional targeted systematic work is needed to further characterize and understand these groups. Several species, including *M. multiflora* Merr., *M. pendula* Merr., *M. quadrifolia* Blume, and *M. setigera* are not monophyletic and in need of taxonomic review.

■ CONCLUSIONS

We provide a substantial advancement towards a well-sampled and resolved phylogeny of fleshy-fruited Sonerileae. The *Medinilla*-alliance, characterized by a typical wood stele and soft, juicy berries, is monophyletic. However, *Medinilla* in its current circumscription is paraphyletic because *Pachycentria* and *Plethiandra* are nested within the clade. To ensure monophyly of *Medinilla*, a number of taxonomic changes are proposed and outlined in the taxonomic treatment section. Including *Pachycentria* and *Plethiandra*, 15 major lineages within *Medinilla* are identified, laying the basic structure for a comprehensive infrageneric classification system and serving as guidance for future systematic work. More sampling, especially from Madagascar, India, Sundaland, and New Guinea is needed to explore the limits and internal relationships of these lineages further.

In contrast to the typical wood stele of the *Medinilla*-alliance, the *Heteroblemma*-alliance, characterized by lobed stele and various fruit types, is polyphyletic. *Kendrickia* is sister to an Afrotropical superclade, while *Heteroblemma* and *Catanthera* belong to a mostly Asian superclade. Plastid sequences of *Kendrickia* are still lacking and will help verify the relationship. Both *Heteroblemma* and *Catanthera* could benefit from an in-depth sampling, especially from east of the Wallace Line, which has no representation yet. *Heteroblemma* in particular requires further attention, because it was only resolved as monophyletic in the nuclear tree. Plastid sequences showed Bornean species with a closer relationship to *Phyllagathis* species. The origin of this discordance needs further exploration.

■ TAXONOMIC TREATMENT

In this section, *Medinilla* is redefined. Given the conflicts observed between the nuclear and plastid phylogenies, and the difficulty in characterizing each clade identified within *Medinilla*, we decided not to recognize 15 separate genera for the 15 clades or recognize the early-branching clades as distinct genera. Instead, we choose to synonymize *Pachycentria* and *Plethiandra*. Synonymous genera are listed, including *Pachycentria*, *Plethiandra*, their synonyms, and types. A new diagnosis, new description, distribution, and notes on the correct authorship of *Medinilla* are given. To provide *Medinilla* names for *Pachycentria* taxa, eight new name combinations are effected and one name is reinstated. To provide *Medinilla* names for *Plethiandra* species, four replacement names are provided, three new name combinations are effected, and one name is reinstated. Accepted species follow Clausing (2000) and Kadereit (2005).

Medinilla Gaudich. ex DC., Prodr. 3: 167. 1828 [*Medinilla* Gaudich., Voy. Uranie: t. 106. 1829 & 484. 1830, isonym] – Type: *Medinilla medinilliana* (Gaudich.) Fosberg & Sachet (≡ *Melastoma medinilliana* Gaudich.; ≡ *Medinilla rosea* Gaudich., nom. illeg.).

= *Diplogenea* Lindl. in Quart. J. Sci. Lit. Arts 1828(2): 122. 1828 – Type: *Diplogenea viscoides* Lindl. (≡ *Medinilla viscoides* (Lindl.) Triana).

= *Pachycentria* Blume in Flora 14: 519. 1831 – Type: *Pachycentria constricta* (Blume) Blume in Flora 14: 520. 1831 (≡ *Medinilla constricta* (Blume) Quakenbush & Luo Chen, this paper), **syn. nov.**

= *Pogonanthera* Blume in Flora 14: 520. 1831 – Type: *Pogonanthera pulverulenta* (Jack) Blume (≡ *Medinilla pulverulenta* (Jack) Quakenbush & Luo Chen, this paper), **syn. nov.**

= *Triplectrum* D.Don ex Wight & Arn., Prodr. Fl. Ind. Orient. 1: 324. 1834 – Type: *Triplectrum radicans* D.Don ex Wight & Arn. (≡ *Medinilla beddomei* C.B.Clarke).

= *Dactyliota* Blume, Mus. Bot. 1(2): 21. 1849 – Type: *Dactyliota bracteata* (Blume) Blume (≡ *Medinilla bracteata* Blume).

= *Hypenanthe* Blume, Mus. Bot. 1(2): 21. 1849 – Type: *Hypenanthe venosum* (Blume) Blume (≡ *Medinilla venosa* Blume).

= *Carionia* Naudin in Ann. Sci. Nat., Bot., sér. 3, 15: 311, t. 15. 1851 – Type: *Carionia elegans* Naudin (≡ *Medinilla coronata* Regalado).

= *Erpetina* Naudin in Ann. Sci. Nat., Bot., sér. 3, 15: 299. 1851 – Type: *Erpetina radicans* Naudin (≡ *Medinilla erpetina* Triana).

= *Plethiandra* Hook.f. in Bentham & Hooker, Gen. Pl. 1(3): 772. 1867 – Type: *Plethiandra motleyi* Hook.f. (≡ *Medinilla polystaminea* Quakenbush & Luo Chen, this paper), **syn. nov.**

= *Medinillopsis* Cogn. in Candolle & Candolle, Monogr. Phan. 7: 603. 1891 – Type (designated by Kadereit in Edinburgh J. Bot. 62(3): 131. 2005): *Medinillopsis beccariana* Cogn. (≡ *Medinilla incognita* Quakenbush & Luo Chen, this paper), **syn. nov.**

= *Cephalomedinilla* Merr. in Philipp. J. Sci., C, 5: 204. 1910 – Type: *Cephalomedinilla anisophylla* Merr. (≡ *Medinilla microcephala* Regalado).

Diagnosis. – *Medinilla* can be distinguished from all other Sonerileae by the combination of typical xylem (vs. lobed in cross-section) and berry fruit. *Medinilla* can be distinguished from the Dissochaeteae by its wood anatomy (e.g., distinctly scalariform intervessel pits; Van Vliet, 1981), the absence of interpetiolar ridges (Veldkamp, 1978), and leaf venation (generally suprabasal acrodromous vs. basal acrodromous). At present, *Medinilla* can be phylogenetically defined as the most exclusive clade containing *M. medinilliana* and *M. nubicola*.

Description. – Terrestrial shrubs/small trees, lianas, primary hemiepiphytes, and epiphytes; roots sometimes swollen; stems terete or tetragonal, sometimes 4–8-winged, glabrous or pubescent; nodes often thickened, with or without setae; leaves opposite or whorled, glabrous or pubescent, sessile or petiolate, sometimes with pseudostipules, strongly anisophyllous to equal, usually coriaceous or fleshy, venation generally suprabasal acrodromous, with 1 to many nerves, base variable (e.g., peltate, auriculate, obtuse, acute), apex variable (e.g., retuse, obtuse, acute), margin entire; inflorescences terminal, axillary, or cauline, cymose, 1- to many-flowered, diffuse to densely congested, solitary to fascicled, lax to erect, with or without showy bracts and bracteoles, glabrous or pubescent; flowers 4–6(–7)-merous; hypanthium variable (e.g., ovoid, campanulate, cylindrical, urceolate), occasionally bumpy or with long outgrowths, glabrous or pubescent; calyx rim (limb) variable (e.g., truncate, dentate, regularly or irregularly lobed, variously flared); petals broadly or narrowly oblique, apex rounded or pointed, white, pink, lavender, orange, or red, recurved, spreading, cupped, or pseudotubular; stamens generally double the petal number, e.g. 8–12, but more than double (polyandrous) in the *Plethiandra* clade; filaments strap-shaped, pale; anthers white, yellow, pink, red, blue, purple, or a combination thereof, isomorphic, subequal, or dimorphic, opening by 1(–2) pores, variously arranged (e.g., evenly distributed, in one or two groups); pedoconnective not or hardly produced at the base, with or without dorsal and ventral appendages; dorsal appendage forming a triangular plectrum, subulate or spatulate spur of various lengths, split into two, frayed, or presenting as a tuft of hairs; ventral appendages long or short, subulate or lobed; ovary partially to wholly adnate to the calyx, usually separated by extra-ovarian chambers (corresponding to stamen number and length of anther/filament), 4–6-locular, placentation axial, apex concave or convex, glabrous; style straight or hooked; stigma punctate to capitate; fruit baccate (an accessory fruit with a fleshy hypanthium), ovoid, globose, urceolate, or ellipsoid, green, white, pink, yellow, orange, red, or some combination thereof when immature, green, blue, dark purplish-black when mature; seeds few to many, minute to ~1.5 mm, semi-ovate to irregularly ovoid or angular, testa smooth to papillate, testa cells interdigitate to comb-shaped, hilum basal, raphe often evident.

Distribution. – Afrotropical, Indomalayan, Australasian, and Oceanian biogeographic realms, i.e., throughout much of the wet Paleotropics.

Notes. – Authorship for *Medinilla* is often erroneously cited. For example, Regalado (1990, 1995) cited "Gaudich. (1826)", Veranso-Libalah & al. (2023) cited "Gaudich. (1830)", and Kartonegoro (2023) cited "Gaudich. (Candolle, 1828)". However, Augustine Pyramus de Candolle was the first to validly publish *Medinilla* in mid-March 1828. Candolle had early access to Gaudichaud-Beaupré's material, which was not published until 1829 and 1830 (see references in list of synonyms above). Candolle cited Gaudichaud-Beaupré's unpublished work, and provided his own, at times conflicting, description. Thus, the correct authorship is Gaudich. ex DC., and "*Medinilla* Gaudich." is an isonym (Art. 6, Note 2). For a detailed explanation of the issue, see Bodegom & Veldkamp (2001), which we verified with Kanchi Gandhi (Harvard University, pers. comm.). *Diplogenea* was published soon after, in October of 1828 and does not have priority.

Medinilla names for accepted *Pachycentria* taxa

Refer to Clausing (2000) for a full list of heterotypic synonyms.

Medinilla constricta (Blume) Quakenbush & Luo Chen, **comb. nov.** ≡ *Melastoma constrictum* Blume, Bijdr. Fl. Ned. Ind.: 1072. 1826 ≡ *Pachycentria constricta* (Blume) Blume in Flora 14: 520. 1831 – Lectotype (designated by Bakhuizen van den Brink, Contr. Melastom.: 126. 1943): Indonesia, Java, *Blume s.n.* (L barcode L 0043192!).

Note. – Blume did not cite specimens in his descriptions of melastomes, nor did he use collection numbers. Clausing (2000) designated this *Blume s.n.* as the lectotype; however, Bakhuizen van den Brink (1943) had already unambiguously specified *Blume s.n.* in L under the name *Melastoma constrictum* Blume as the type, thereby designating the lectotype.

Medinilla glauca (Triana) Quakenbush & Luo Chen subsp. ***glauca***, **comb. nov.** ≡ *Pachycentria glauca* Triana in Trans. Linn. Soc. London 28(1): 89. 1871 – Holotype: Presumably Malaysia, Sarawak, 1853, *Lobb s.n.* (K barcode K000867434!).

Note. – The type is not *Beccari 415* (FI; G-DC barcode G00316263!; K barcode K000867435!) as cited by Clausing (2000). Though *Beccari 415* is on the same sheet as *Lobb s.n.*, only "Lobb, 1853" was mentioned in the protologue.

Medinilla glauca subsp. ***maingayi*** (C.B.Clarke) Quakenbush & Luo Chen, **comb. nov.** ≡ *Medinilla maingayi* C.B. Clarke in Hooker, Fl. Brit. India 2: 549. 1879 ≡ *Pachycentria maingayi* (C.B.Clarke) J.F.Maxwell in Gard. Bull. Singapore 31(2): 203. 1978 ≡ *Pachycentria glauca* subsp. *maingayi* (C.B.Clarke) Clausing in Blumea 45(2): 356. 2000 – **Lectotype (designated here):** Singapore, Sep 1867, *Maingay 806* (K barcode K000867442 [photo!]).

Note. – *Maingay 806* and *Maingay 807* (K barcode K000867441!) were syntypes, from which *Maingay 806* was selected as the lectotype as it is a higher-quality specimen.

Medinilla hanseniana (Clausing) Quakenbush & G.Kadereit, **comb. nov.** ≡ *Pachycentria hanseniana* Clausing in Blumea 45(2): 356. 2000 – Holotype: Indonesia, Kalimantan Tengah, Kualakuayan, camp at logging road c. 9 km W of Pemantang logging camp (2°00′00.0″S; 112°28′00.0″E), c. 50 m a.s.l., 1 Apr 1984, *Hansen 1336* (C barcodes C10014970! & C10014971!, mounted on two sheets, plus material in alcohol [15759!]).

Medinilla microsperma (Becc.) Quakenbush & Luo Chen, **comb. nov.** ≡ *Pachycentria microsperma* Becc. in Malesia 2: 238, t. 58, fig. 1–9. 1886 – Lectotype (designated by Clausing in Blumea 45(2): 359. 2000 [as ‘holotype’]): Malaysia, Sarawak, Kuching, Aug 1865, *Beccari 404* (FI barcode FI1009763 [photo!]; isolectotype: K barcode K000867433!).

Note. – *Beccari 404* was listed along with *Beccari 2054* (FI barcode FI1009764 [photo!]) and *Beccari 2163* (FI barcode FI1009762 [photo!]) in the protologue and was therefore a syntype. Clausing (2000) selected *Beccari 404* as the holotype, while lectotype would have been the correct term.

Medinilla microstyla (Becc.) Quakenbush & Luo Chen, **comb. nov.** ≡ *Pachycentria microstyla* Becc. in Malesia 2: 239. 1886 – **Lectotype (designated here):** Malaysia, Sarawak, Kuching, Sep 1865, *Beccari 604* (FI barcode FI1008769 [photo!]).

Note. – *Beccari 403* (FI barcode FI1008770 [photo!]) and *Beccari 604* were syntypes. *Beccari 604* was selected as the lectotype because it is the higher-quality specimen.

Medinilla pulverulenta (Jack) Quakenbush & Luo Chen, **comb. nov.** ≡ *Melastoma pulverulentum* Jack in Trans. Linn. Soc. London 14(1): 19. 1823 ≡ *Pogonanthera pulverulenta* (Jack) Blume in Flora 14: 521. 1831 ≡ *Pachycentria pulverulenta* (Jack) Clausing in Blumea 45(2): 362. 2000 – **Neotype (designated here):** Malaysia, Malacca, Cape Rochado, 1822, *Wallich Cat. No. 4086* (K barcode K001038107 [photo!]; isoneotypes: K barcodes K001038108 [photo!], K000867081 [photo!]).

Notes. – Jack’s original specimen was likely lost in a shipwreck in 1824, necessitating the need for a neotype (Kartonegoro, 2023). In the protologue, Jack noted the frequent presence of this species in Singapore and Sumatra in the neighborhood of the sea. The neotype is selected from the same general time period, range, and habitat. It shows the auriculate leaves and terminal, paniculate inflorescences characteristics of this species. There is another *Wallich 4086* at K (barcode K000867082 [photo!]) that belongs to a different species, likely *Medinilla erythrophylla* (see discussion of *M. rubicunda* in Kartonegoro, 2023).

Medinilla varingiifolia (Blume) Nayar in Blumea 18: 567. 1970 ≡ *Melastoma varingiifolium* Blume in Bijdr. Fl. Ned. Ind.: 1071. 1825 ≡ *Pachycentria varingiifolia* (Blume) Blume in Flora 14: 520. 1831 – Lectotype (designated by Bakhuizen van den Brink, Contr. Melastom.: 127. 1943): Indonesia, West Java, Preanger Regencies, G. Megamendoeng, c. 1800 m a.s.l., *Kuhl & van Hasselt s.n.* (L barcode L 0537312!; isolectotypes: E barcode E00276216!, L barcodes L 0537310!, L 0537311!).

Notes. – Clausing (2000) indicated *Kuhl & van Hasselt s.n.* (L barcode L 0537312!) was the holotype and there were two isotypes in L (L 0537310!, L 0537311!). There is also an “isotype” in E (E00276216!). Since Blume did not cite specimens in his descriptions, these must be lecto- and isolectotypes, designated by Bakhuizen van den Brink (1943). Only L 0537311 and E00276216 indicate Kuhl & van Hasselt as the collectors. It is unclear when the annotation for L 0537311 was added, but possibly when Bakhuizen van den Brink revisited the specimen in 1970, as there are several annotations in the same blue ink and handwriting. The annotation for E00276216 was added in 2008 by Cámara-Leret. The specimen with Bakhuizen van den Brink’s original type label from 1941 (L 0537312) lists Blume as the collector in the metadata provided by L. Metadata indicates that the remaining specimen (L 0537310) is from an unknown collector. Earlier authors (e.g., Naudin, 1851; Cogniaux, 1891) cited Blume without number as the type. Therefore, it is unclear who the collector(s) of these specimens is/are, but it is clear which sheet Bakhuizen van den Brink designated as the type. Two other specimens in P were donated by Blume and may also constitute original material (P05259271 [photo!], P05259273 [photo!]).

Medinilla vogelkopensis (Clausing) G.Kadereit & Luo Chen, **comb. nov.** ≡ *Pachycentria vogelkopensis* Clausing in Blumea 45(2): 367. 2000 – Holotype: New Guinea, Vogelkop Peninsula, S. slope of Mt. Nettoti, path Andjai-Wekari R., 1650 m a.s.l., 30 Nov 1961, *Van Royen & Sleumer 7902* (L barcode L.2552237!; isotypes: A barcode 00102617!, K barcode K000867428 [photo!]).

Note. – *Reksodihardjo 336* (L barcode L 0357265!) was labeled as an isotype by Clausing in 1999, but it was not designated as such by Clausing (2000). It is part of the original material but is not a type.

Medinilla names for accepted *Plethiandra* species

Refer to Kadereit (2005) for a full list of heterotypic synonyms.

Medinilla hookeri (Stapf) Quakenbush & Luo Chen, **comb. nov.** ≡ *Plethiandra hookeri* Stapf in Trans. Linn. Soc. London, Bot. 4(2): 163. 1894 – Lectotype (designated by Nayar in Reinwardtia 9(1): 147. 1974 [as ‘holotype’]): Malaysia, Sabah, Mt. Kinabalu, 2200 m a.s.l., received Aug 1892, *Haviland 1169* (K barcode K000867423!; isolectotype: SAR!).

Notes. – *Haviland 1169*, without indication of herbarium, was designated as the type by Stapf in the protologue. Nayar (1974) specified the K specimen as the holotype, but because another specimen was located in SAR, the K specimen must be the lectotype and the SAR specimen is the isolectotype.

Medinilla incognita Quakenbush & Luo Chen, **nom. nov.** ≡ *Medinillopsis beccariana* Cogn. in Candolle & Candolle, Monogr. Phan. 7: 603. 1891 ≡ *Plethiandra beccariana* (Cogn.) Merr. in J. Straits Branch Roy. Asiat. Soc. 84(Spec. No.): 448. 1921 – Holotype: Malaysia, Sarawak, Bintulu, Sep 1867, *Beccari 4004* (FI barcode FI008756!; isotype: K barcode K000867427!).

Notes. – *Medinilla incognita* is a replacement name for *Medinillopsis beccariana*, because *Medinilla beccariana* Cogn. already exists for another species. "*Incognita*" is in reference to this species' long-hidden identity as *Medinilla*. Though Kadereit (2005) identified the FI specimen as the lectotype and the K specimen as the isolectotype, Cogniaux (1891) sufficiently designated the FI specimen as the holotype when he listed "*Beccari n. 4004* in hb. propr." Nayar (1974) rightly identified the K specimen as the isotype.

Medinilla migrans Quakenbush & Luo Chen, **nom. nov.** ≡ *Medinillopsis sessiliflora* Cogn. in Candolle & Candolle, Monogr. Phan. 7: 603. 1891 ≡ *Plethiandra sessiliflora* (Cogn.) Merr. in J. Straits Branch Roy. Asiat. Soc. 84(Spec. No.): 449. 1921 – Holotype: Singapore, Mar 1866, *Beccari s.n*. (FI barcode FI008757!; isotype: BR barcode BR0000030784208 [photo!]).

Notes. – *Medinilla migrans* is a replacement name for *Plethiandra sessiliflora*, because *M. sessiliflora* Regalado already exists. "*Migrans*" recognizes that this is the only *Plethiandra* species found outside of Borneo. Since Cogniaux indicated "Beccari in hb. propr.", the FI specimen can be considered the holotype. Both Nayar (1974) and Kadereit (2005) viewed an isotype in K. Record of this could not be found again online, but another isotype was located in BR.

Medinilla polystaminea Quakenbush & Luo Chen, **nom. nov.** ≡ *Plethiandra motleyi* Hook.f. in Bentham & Hooker, Gen. Pl. 1(3): 772. 1867 – Holotype: Malaysia, Sabah, Labuan, *Motley 380* (K barcode K000867421!).

Notes. – *Medinilla polystaminea* is a replacement name for *Plethiandra motleyi*, because *M. motleyi* Hook.f. ex Triana already exists. The epithet from the heterotypic synonym *P. acuminata* Merr. cannot be used either, because *M. acuminata* Merr. already exists. *Medinilla polystaminea* is the type species of *Plethiandra*, and the name acknowledges the most unique feature of this group—its many stamens. Hooker did not cite a specimen in the protologue, only a location: Borneo, at the summit of Mt. "Gurrong-say", here interpreted as Gunong Jay, a hill opposite Brunei, as it reads on the specimen in K, stamped with "Herbarium Hookerianum 1867", accompanied by illustrations "fr[om]. type". The specimen is labeled as the holotype and was treated as such by Nayar (1974), though Kadereit (2005) identified it as a lectotype.

Medinilla rejangensis (Stapf) Quakenbush & Luo Chen, **comb. nov.** ≡ *Plethiandra rejangensis* Stapf in Hooker's Icon. Pl. 25: sub t. 2418. 1895 – Holotype: Malaysia, Sarawak, Rejang, Sibu, Nov 1891, *Haviland d.g.k.a. 545* (K barcode K000867424!).

= *Plethiandra cuneata* Stapf in Hooker's Icon. Pl. 25: sub t. 2418. 1895 – Lectotype (designated by Nayar in Reinwardtia 9(1): 151. 1974 [as 'holotype']): Malaysia, Sarawak, Selabat rock, sea coast, Mar 1891, *Haviland c.m.l.a. 179* (K barcode K000867425!; isolectotypes: BM barcode BM000793046!, K barcode K000867426!, SAR!, SING!).

Notes. – *Medinilla rejangensis* is the new name combination for *Plethiandra cuneata*; because *M. cuneata* (Thwaites) K.Bremer & Lundin already exists, and *P. rejangensis* Stapf is the next-earliest, legitimate name for this taxon. Stapf did not indicate a herbarium for the type specimen of *P. rejangensis*. However, the *Haviland 545* specimen cited here is the only known specimen. Though Kadereit (2005) treated it as a lectotype, Nayar (1974) considered it the holotype and it is labeled as such. Stapf did not indicate a herbarium or collection number for the type of *P. cuneata* either. Nayar (1974) designated a K specimen as the holotype and a BM specimen as an isotype, which indeed should be cited as the lectotype and one isolectotype (Kadereit 2005). Kadereit (2005) listed two additional isolectotypes from SAR and SING. It was found that "*Haviland c.m.l.a. 68*" (K barcode K000867426!) is also labeled as the holotype. On the BM and K (K000867425) specimens of *Haviland 179*, the "68" has been crossed out and replaced with "179". Clearly, these all belong to the same collection.

Medinilla robusta Cogn. ≡ *Plethiandra robusta* (Cogn.) Nayar in Reinwardtia 9(1): 148. 1974 – **Lectotype** (first step designated by Kadereit in Edinburgh J. Bot. 62(3): 137. 2005, **second-step designated here**): Malaysia, Sarawak, Kuching, *Beccari 542* (FI barcode FI1007953!; isolectotypes: FI barcode FI1007954!, K barcode K000 867419!).

Notes. – Kadereit (2005) designated *Beccari 542* in FI as the lectotype. However, two such specimens were found; so one is selected as a lectotype here. With the designation of a lectotype, there are residual syntypes and isosyntypes: Malaysia, Sarawak, *Beccari 573* (FI barcode FI1007955 [photo!]); Malaysia, Sarawak, Kuching, *Beccari 851* (BR barcode 000005214761 [photo!], FI barcodes FI1007949!, FI1007950!); Malaysia, Sarawak, Bintulu, Nov 1867, *Beccari 4049* (FI barcodes FI1007951!, FI1007952!, K barcode K000867420 [photo!]).

Medinilla stapfii Quakenbush & Luo Chen, **nom. nov.** ≡ *Plethiandra sessilis* Stapf in Hooker's Icon. Pl. 25: t. 2418. 1895 – Holotype: Malaysia, Sarawak, Penrissen, Jun 1890, *Haviland 6893* (K barcode K000 867417!).

Notes. – *Medinilla stapfii* is a replacement name for *Plethiandra sessilis*, because *M. sessilis* Merr. & L.M.Perry already exists. It is named in honor of Otto Stapf, the original author of this species, and in recognition of his taxonomic contributions to the clade. In the protologue, Stapf indicated a *Haviland* collection (*s.n.*) of an epiphyte from Borneo, Sarawak River, as the type. Nayar (1974) noted that *Haviland c.c.f.a 93* (K) was the holotype. Kadereit (2005) indicated *Haviland 6893* was the lectotype. The "68" is above the "93" on the herbarium label and was overlooked by Nayar, and the original label contains all the information noted by Stapf. Since no other original material is known, this specimen is considered the holotype.

Medinilla tomentosa (G.Kadereit) G.Kadereit, **comb. nov.** ≡ *Plethiandra tomentosa* G.Kadereit in Edinburgh J. Bot. 62(3): 141. 2005 – Holotype: Malaysia, Sarawak, Lambir National Park, Miri, 4th Division, 4 Jul 1983, *Bernard Lee S.46581* (AAU! [no herbarium code on specimen]; isotype: K barcode K000867416 [photo!], KEP!, L n.v., SAN n.v.).

Note. – Kadereit (2005) only listed the AAU and KEP specimens. Another has been located in K, and from the herbarium labels at AAU and K, it can be seen that duplicates were also sent to L and SAN.

■ DATA AVAILABILITY

All sequencing data generated in this study are deposited in the National Center for Biotechnology Information (NCBI) Sequence Read Archive (BioProject: PRJNA1121116). All sequence alignments, gene trees, and species trees generated in this study are available at Zenodo (https://doi.org/10.5281/zenodo.11521564).

■ AUTHOR CONTRIBUTIONS

JPQ, LC, MCVL, TJB, and GK designed the project. JPQ and LC performed the research. LC and JPQ conducted data collection, analysis, and interpretation, with assistance from MCVL, GK, DSP, TJB, YL, and DY. JPQ and LC drafted the manuscript. All authors contributed to the revision process.

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Appendix 1A. Samples sequenced in this study.

Taxon, lab code, locality, *collector* and *collection number* (herbarium), SRA accession.

Catanthera keris Veldkamp, CATAKERI_223, Halmahera, Indonesia, *T. Fatisa 223* (L), SAMN41736323; ***Catanthera pilosa*** M.P.Nayar, CATPIL_126, Sabah, Malaysia, *Clausing, G. 126* (MJG), SAMN41736324; **Catanthera sp. nov.**, CSP_2541, Sabah, Malaysia, *Penneys, D.S. 2541* (BRIT), SAMN41736325; ***Fordiophyton faberi*** Stapf, FFORD_16335, Zhejiang, China, *Ge, Bin-Jie & al. 16335* (CSH), SAMN41736326; **Heteroblemma sp. nov.**, Halt_2228, Vietnam, *Nuraliev, M. 2228* (MW), SAMN41736327; ***Heteroblemma alternifolium***, Halt_2490, Sabah, Malaysia, *Penneys, D.S. 2490* (BRIT), SAMN41736328; ***Heteroblemma clemensiae*** Cámara-Leret, Hcle_1655, Vietnam, *Nuraliev, M. 1655* (MW), SAMN41736329; ***Kendrickia walkeri*** Hook.f., KEN_WALKERI, Sri Lanka, *Yakandawala, D. & Gopallawa, B. KED01* (PDA), SAMN41736330; ***Medinilla acutialata*** Pócs & Khoi, Macu_2512, Vietnam, *Nuraliev, M. 2512* (MW), SAMN41736331; ***Medinilla*** aff. ***annulata*** C.B.Rob., MSP, cultivated; likely orig. Mindoro, Philippines, *Bouman, R. s.n.*, Living materal, accession nr. HBL 20120209 (Hortus Botanicus Leiden), SAMN41736332; ***Medinilla*** aff. ***malindangensis*** Merr., MMALI_1351, Mindanao, Philippines, *PLSPH 1351* (CMUH, BRIT), SAMN41736333; ***Medinilla*** aff. ***pendula*** Merr., MELME_1205, Mindanao, Philippines, *PLSPH 1205* (CMUH, BRIT), SAMN41736334; ***Medinilla*** aff. ***pendula***, MSP_1258, Mindanao, Philippines, *PLSPH 1258* (CMUH, BRIT), SAMN41736335; ***Medinilla*** aff. ***plumosa*** Mansf., Mtey_61, West New Britian, Papua New Guinea, *James, S.A. 61* (BISH, LAE), SAMN41736336; ***Medinilla*** aff. ***teysmannii*** Miq., MTEYS_1247, Limbawon, Mindanao, Philippines, *PLSPH 1247* (CMUH, BRIT), SAMN41736337; ***Medinilla*** aff. ***teysmannii*** Miq., MTEYS_1255, Mindanao, Philippines, *PLSPH 1255* (CMUH, BRIT), SAMN41736338; ***Medinilla anisophylla*** Merr., MANIS_10815, Vanikolo, Solomon Islands, *SITW 10815* (TNM), SAMN41736339; ***Medinilla apoensis*** C.B.Rob., Mapo_665, Mindanao, Philippines, *PLSPH 665* (CMUH, BRIT), SAMN41736340; ***Medinilla arfakensis*** Baker f., Marf_9755, Guadalcanal, Solomon Islands, *SITW 9755* (TNM), SAMN41736341; ***Medinilla astronioides*** Triana, MASTR_47, Luzon, Philippines, *Quakenbush, J.P. 47* (LBC), SAMN41736342; ***Medinilla bakeriana*** Mansf., Mbak_813, Morobe, Papua New Guinea, *James, S.A. 813* (BISH, CAS, M), SAMN41736343; ***Medinilla balls-headleyi*** F.Muell., MBALL_185, cultivated; orig. Australia, *Quakenbush, J.P. 185*; Living material, accession nr. 1988-0073 (Marie Selby Botanical Gardens), SAMN41736344; ***Medinilla banahaensis*** Elmer, MSP_1204, Mindanao, Philippines, *PLSPH 1204* (CMUH, BRIT), SAMN41736345; ***Medinilla banahaensis***, MBANA_2743, Luzon, Philippines, *Fernando, E.S. 2743* (CAS), SAMN41736346; ***Medinilla baronii*** Baker, MEDIMICR_271, Madagascar, *Ramahenina, J.A. & al. 271* (MO), SAMN41736347; ***Medinilla baronii***, MHUMB_3689, Madagascar, *Ravelonarivo 3689* (MO), SAMN41736348; ***Medinilla baronii***, MMICR_1910, Madagascar, *Bernard 1910* (MO), SAMN41736349; ***Medinilla baronii***, MMICR_7620, Madagascar, *Antilahimena, P. 7620* (MO), SAMN41736350; ***Medinilla baronii***, MMICR_8460, Madagascar, *Antilahimena, P. 8460* (MO), SAMN41736351; ***Medinilla baronii***, MMICR_8757, Madagascar, *Antilahimena, P. 8757* (MO), SAMN41736352; ***Medinilla calliantha*** Merr. & L.M.Perry, Mcal_9612, Guadalcanal, Solomon Islands, *SITW 9612* (TNM), SAMN41736353; ***Medinilla calliantha***, MCALL_5653, Isabel, Solomon Islands, *SITW 5653* (TNM), SAMN41736354; ***Medinilla cauliflora*** Hemsl., Mcau_1709, Kolombangara, Solomon Islands, *SITW 1709* (TNM), SAMN41736355; ***Medinilla cephalantha*** Merr. & L.M.Perry, Mcep_10138, Malaita, Solomon Islands, *SITW 10138* (TNM), SAMN41736356; ***Medinilla*** cf. ***ambrensis*** Jum. & H.Perrier, MHUMB_332, Madagascar, *Rakotonirina 332* (MO), SAMN41736357; ***Medinilla*** cf. ***annulata*** C.B.Rob., Mcer_229, New Britian, Papua New Guinea, *James, S.A. 229* (BISH, M), SAMN41736358; ***Medinilla*** cf. ***basaltarum*** Jum. & H.Perrier, MBASA_316, Madagascar, *Martial 316* (MO), SAMN41736359; ***Medinilla*** cf. ***bigradata*** H.Perrier, MOBLO_2054, Madagascar, *Bernard 2054* (MO), SAMN41736360; ***Medinilla*** cf. ***campanulata*** Jum. & H.Perrier, MINTE, cultivated; orig. Madagascar, *Silber, M. s.n.*, Living materal, accession nr. 1967/0301-1 (Munich Botanical Garden), SAMN41736361; ***Medinilla*** cf. ***decaryi*** H.Perrier, Msp_1449, cultivated; orig. Madagascar, *Newman, M.F. 1449* (E), SAMN41736362; ***Medinilla*** cf. ***kinabaluensis*** Regalado, MKINA_2449, Sabah, Malaysia, *Penneys, D.S. 2449* (BRIT), SAMN41736363; ***Medinilla*** cf. ***leptophylla*** Baker, MALBI_2993, Madagascar, *Ravelonarivo 2993* (MO), SAMN41736364; ***Medinilla*** cf. ***lophoclada*** Baker, MLOPH_443, Madagascar, *Razafindraibe 443* (MO), SAMN41736365; ***Medinilla*** cf. ***masoalensis*** Jum. & H.Perrier, MPARV_7723, Madagascar, *Antilahimena, P. 7723* (MO), SAMN41736366; ***Medinilla*** cf. ***masoalensis***, MRUBE_3886, Madagascar, *Ravelonarivo 3886* (MO), SAMN41736367; ***Medinilla*** cf. ***oblongifolia*** Cogn., MMAND_4086, Madagascar, *Ravelonarivo 4086* (MO), SAMN41736368; ***Medinilla*** cf. ***polillensis*** C.B.Rob., MPOLI_SN, Luzon, Philippines, *Elias, A. s.n.* (M), SAMN41736369; ***Medinilla*** cf. ***pterocaula*** Blume, MPTER_2540, Sabah, Malaysia, *Penneys, D.S. 2540* (BRIT), SAMN41736370; ***Medinilla*** cf. ***rubrinervia*** Jum. & H.Perrier, MOBLO_8438, Madagascar, *Antilahimena, P. 8438*

Appendix 1A. Continued.

(MO), SAMN41736371; ***Medinilla*** cf. ***rubrinervia***, MOBLO_8492, Madagascar, *Antilahimena, P. 8492* (MO), SAMN41736372; ***Medinilla*** cf. ***surigaoensis*** Regalado, MSURI_1407, Camiguin, Philippines, *PLSPH 1407* (CMUH, BRIT), SAMN41736373; ***Medinilla*** cf. ***triangularis*** Jum. & H.Perrier, MTRIA_1470, Madagascar, *Bernard 1470* (MO), SAMN41736374; ***Medinilla*** cf. ***tuberosa*** Jum. & H.Perrier, MBASA_315, Madagascar, *Martial 315* (MO), SAMN41736375; ***Medinilla*** cf. ***venosa*** (Blume) Blume, MPHIL, Luzon, Philippines, *Quakenbush, J.P. 55* (M), SAMN41736376; ***Medinilla chermezonii*** H.Perrier, MCHER_298, Madagascar, *Ramahenina 298* (MO), SAMN41736377; ***Medinilla chermezonii***, MCHER_8462, Madagascar, *Antilahimena, P. 8462* (MO), SAMN41736378; ***Medinilla chermezonii***, MEDICHER_8570, Madagascar, *Antilahimena, P. & al. 8570* (MO), SAMN41736379; ***Medinilla clementis*** Merr., Mcle_1049, Mindanao, Philippines, *PLSPH 1049* (CMUH, BRIT), SAMN41736380; ***Medinilla compressicaulis*** Merr., MCOMP_2303, Mindanao, Philippines, *Penneys, D.S. 2303* (CAS), SAMN41736381; ***Medinilla congesta*** Merr., Mcon_2172, Negros, Philippines, *PLSPH 2172* (CMUH, BRIT), SAMN41736382; ***Medinilla copelandii*** Merr., Mcop_1009, Marilog, Mindanao, Philippines, *PLSPH 1009* (CMUH, BRIT), SAMN41736383; ***Medinilla cordata*** Merr., MCORDA_2750, Luzon, Philippines, *Fernando, E.S. 2750* (CAS), SAMN41736384; ***Medinilla coriacea*** Merr., MCORI_58, Luzon, Philippines, *Quakenbush, J.P. 58* (LBC), SAMN41736385; ***Medinilla cuneata*** (Thwaites) K.Bremer & Lundin, MED_CUNEATA, Sri Lanka, *Yakandawala, D. & Gopallawa, B. MED02* (PDA), SAMN41736386; ***Medinilla disparifolia*** C.B.Rob., MDISP, Luzon, Philippines, *Quakenbush, J.P. 52* (LBC), SAMN41736387; ***Medinilla elegans*** Elmer, MELEG_2306, Mindanao, Philippines, *Penneys, D.S. 2306* (CAS), SAMN41736388; ***Medinilla engleri*** Gilg, Meng_2739, Tanzania, *Lovett, J. 2739* (M), SAMN41736389; ***Medinilla erpetina*** Triana, Merp_9083, Malaita, Solomon Islands, *SITW 9083* (TNM), SAMN41736390; ***Medinilla erythrophylla*** Lindl., MRUBI_3970, Myanmar, *Armstrong, K.A. & al. 3970* (NY), SAMN41736391; ***Medinilla erythrotricha*** Elmer, MERYT_1085, Mindanao, Philippines, *PLSPH 1085* (CMUH, BRIT), SAMN41736392; ***Medinilla erythrotricha***, Matt_2759, Mindanao, Philippines, *PLSPH 2759* (CMUH, BRIT), SAMN41736393; ***Medinilla griffithii*** C.B.Clarke, Mgri_1432, Myanmar, *Little, D. & al. 1432* (NY), SAMN41736394; ***Medinilla halogeton*** S.Moore, Mhal_2633, Choiseul, Solomon Islands, *SITW 2633* (TNM), SAMN41736395; ***Medinilla himalayana*** Hook.f. ex Triana, MHIMA_1908, Myanmar, *Armstrong, K.A. & al. 1908* (NY), SAMN41736396; ***Medinilla homoeandra*** (Stapf) M.P.Nayar, Mhom_2441, Sabah, Malaysia, *Penneys, D.S. 2441* (BRIT), SAMN41736397; ***Medinilla macrophylla*** Blume, MMACR_7591, Sarawak, Malaysia, *SFC 7591* (SFC, SING), SAMN41736398; ***Medinilla maidenii*** F.Muell., Mcoc_198, Western New Guinea, Indonesia, *Quakenbush, J.P. 198*; Living material, accession nr. 2002-0198 (Marie Selby Botanical Gardens), SAMN41736399; ***Medinilla mannii*** Hook.f., MEDIMANN_3834, Equatorial Guinea, *Carvalho 3834* (BR), SAMN41736400; ***Medinilla mannii***, MMANN_473, Uganda?, *Hafashimana 473* (K), SAMN41736401; ***Medinilla masoalensis*** Jum. & H.Perrier, MCORD_2942, Madagascar, *Ravelonarivo 2942* (MO), SAMN41736402; ***Medinilla medinilliana*** (Gaudich.) Fosberg & Sachet, MMEDI, Guam, *Peck, N.M. s.n.* (GUAM), SAMN41736403; ***Medinilla merrittii*** Merr., MMEGA_57, Luzon, Philippines, *Quakenbush, J.P. 57* (LBC), SAMN41736404; ***Medinilla miniata*** Merr., MMINI_SN, Luzon, Philippines, *Luther, H.E. s.n.* (SEL), SAMN41736405; ***Medinilla mortonii*** Hemsl., MMORT_10123, Malaita, Solomon Islands, *SITW 10123* (TNM), SAMN41736406; ***Medinilla multialata*** Quisumb. & Merr., Mmult_926, Camiguin, Philippines, *PLSPH 926* (CMUH, BRIT), SAMN41736407; ***Medinilla multiflora*** Merr., Mmyr_40, Luzon, Philippines, *Quakenbush, J.P. 40* (LBC), SAMN41736408; ***Medinilla multiflora***, MCAMI_920, Camiguin, Philippines, *PLSPH 1441* (CMUH, BRIT), SAMN41736409; ***Medinilla myrtiformis*** (Naudin) Triana, MMYRT_59, Luzon, Philippines, *Quakenbush, J.P. 59* (LBC), SAMN41736410; ***Medinilla nana*** S.Y.Hu, Mnan_2628, Vietnam, *Nuraliev, M. & Vislobokov 2628* (MW), SAMN41736411; ***Medinilla nubicola*** Ohwi, MED_FENGII, Taiwan, *Edinburgh Taiwan Expedition (1993) 308* (E), SAMN41736412; ***Medinilla pachygona*** C.B.Rob., Mpac_2745, Luzon, Philippines, *Fernando, E.S. 2745* (CAS), SAMN41736413; ***Medinilla pendula*** Merr., MGUIT_13, Sibuyan, Philippines, *JTA & ZDM 13* (LBC), SAMN41736414; ***Medinilla pendula***, MPEND_1051, Mindanao, Philippines, *PLSPH 1051* (CMUH, BRIT), SAMN41736415; ***Medinilla plumosa*** Mansf., MRHOD_319, Papua New Guinea, *James, S.A. 319* (BISH, CAS, M), SAMN41736416; ***Medinilla polillensis*** C.B.Rob., Mpol_1500, Negros, Philippines, *PLSPH 1500* (CMUH, BRIT), SAMN41736417; ***Medinilla quadrialata*** Ohwi ex Regalado, MQUADRIA_7579, Sarawak, Malaysia, *SFC 7579* (SFC, SING), SAMN41736418; ***Medinilla quadrifolia*** (Blume) Blume, Mqua_10139, Malaita, Solomon Islands, *SITW 10139* (TNM), SAMN41736419; ***Medinilla quadrifolia***, MQUAD_1577, Papua New Guinea, *Brownless, P. 1577* (E), SAMN41736420; ***Medinilla quadrifolia***, MRADICAN_44, Luzon, Philippines, *Quakenbush, J.P. 44* (LBC), SAMN41736421; ***Medinilla radicans*** (Blume) Blume, MRADI_2192, Vietnam, *Penneys, D.S. 2192* (CAS), SAMN41736422; ***Medinilla radiciflora*** Quisumb. & Merr., MRADI_1360, Mindanao, Philippines, *PLSPH 1360* (CMUH, BRIT), SAMN41736423; ***Medinilla robinsonii*** Elmer, MROBI_1101, Mindanao, Philippines, *PLSPH 1101* (CMUH, BRIT), SAMN41736424; ***Medinilla rubescens*** Merr. & L.M.Perry, MRUBE_432, Guadalcanal, Solomon Islands, *SITW 432* (TNM, TAIF), SAMN41736425; ***Medinilla rubiginosa*** Cogn., Mrub_732, Morobe, Papua New Guinea, *James, S.A. 732* (BISH, LAE, CAS, M), SAMN41736426; ***Medinilla setigera*** (Blume) Miq., MINVO_2650, Luzon, Philippines, *Fernando, E.S. 2650* (CAS), SAMN41736427; ***Medinilla setigera***, MCOGN_1133, Mindanao, Philippines, *PLSPH 1133* (CMUH, BRIT), SAMN41736428; **Medinilla sp.**, MERIC, cultivated; orig. Madagascar, *Silber, M. s.n.*, Living materal, accession nr. 1967/0366-1 (Munich Botanical Garden), SAMN41736429; **Medinilla sp.**, Msp_116, Morobe, Papua New Guinea, *James, S.A. 116* (BISH), SAMN41736430; ***Medinilla squillula*** Veldkamp, MEDISQUI_7287, Indonesia, *P.P. Lowry II & P.B. Phillipson 7287* (MO), SAMN41736431; ***Medinilla succulenta*** (Blume) Blume, Msuc_190, Malaysia, *Quakenbush, J.P. 190*. Living material, accession nr. 2015-0378 (Marie Selby Botanical Gardens), SAMN41736432; ***Medinilla ternifolia*** Triana, MTERN_42, Luzon, Philippines, *Quakenbush, J.P. 42* (LBC), SAMN41736433; ***Medinilla teysmannii*** Miq., Mtey_192, Luzon, Philippines, *Quakenbush, J.P. 192* (M), SAMN41736434; ***Medinilla theresae*** Fernando, MTHER_1331, Mindanao, Philippines, *PLSPH 1331* (CMUH, BRIT), SAMN41736435; ***Medinilla umbrina*** Elmer, Mumb_2275, Mindanao, Philippines, *Penneys, D.S. 2275* (CAS), SAMN41736436; ***Medinilla vagans*** Merr. & L.M.Perry, MVAGA_1662, Kolombangara, Solomon Islands, *SITW 1622* (TNM), SAMN41736437; ***Medinilla venosa*** (Blume) Blume, MVENO_61, Luzon, Philippines, *Quakenbush, J.P. 61* (LBC), SAMN41736438; ***Medinilla venusta*** King, Mven_69568, Pahang, Malaysia, *Davis, P.H. 69568* (E), SAMN41736439; ***Medinilla whitfordii*** Merr., MWHIT_2810, Luzon, Philippines, *Fernando, E.S. 2810* (CAS), SAMN41736440; ***Pachycentria constricta*** (Blume) Blume, Pcon_1576, Sabah, Malaysia, *Brownless, P. 1576* (E), SAMN41736441; ***Pachycentria pulverulenta*** (Jack) Clausing, Ppul_194, cultivated; orig. unknown, *Quakenbush, J.P. 194* (M), SAMN41736442; ***Pachycentria varingiifolia*** Blume, Pvar_79, Sumatra, Indonesia, *Barber, S. 79* (E), SAMN41736443; ***Phyllagathis cavaleriei*** Guillaumin, PCAVA_14177, Fujian, China, *Su, Xiang-Xiu 14177* (CSH), SAMN41736444; ***Phyllagathis fengii*** C.Hansen, PFENG_8129, Yunnan, China, *Wang, Zheng-Wei & al. 8129* (CSH), SAMN41736445; ***Plethiandra hookeri*** Stapf, PHOOK_2463, Sabah, Malaysia, *Penneys, D.S. 2463* (BRIT), SAMN41736446; ***Sarcopyramis napalensis*** Wall., SNEPA_14008, Fujian, China, *Su, Xiang-Xiu 14008* (CSH), SAMN41736447; ***Tashiroea sinensis*** Diels, BSINE_2678, Zhejiang, China, *Ge, Bin-Jie & al. 2678* (CSH), SAMN41736448.

Appendix 1B. Whole-genome resequencing data from Zhou & al. (2022).

Taxon, sample name, locality, *collector* and *collection number* (herbarium), Genbank plastome accession, SRA accession.

Amphiblemma cymosum Naudin, Am, Kew, OL813705, SRR26639412; ***Anerincleistus bracteatus*** C.Hansen, L698, Sarawak, Malaysia, *Zhou & al. 698* (SYS), MK994899, SRR26639365; ***Anerincleistus macrophyllus*** Bakh.f., L699nn, Sarawak, Malaysia, *Zhou & al. 699* (SYS), OL813731, SRR26639361; ***Anerincleistus sertuliferum*** (Cogn.) J.F.Maxwell, L675, Sarawak, Malaysia, *Zhou & al. 675* (SYS), MK994888, SRR26639441; ***Aschistanthera cristanthera*** C.Hansen, 820, Kon Tum, Vietnam, *Liu & al. 826* (SYS), OL813688, SRR26639440; ***Barthea barthei*** (Hance ex Benth.) Krasser, LGH, Shenzhen, China, *Y.C. Cai s.n.* (SYS), MK994907, SRR26639404; ***Blastus auriculatus*** Y.C.Huang, L613, Hekou, Nanxi, China, *Liu 613* (SYS), MK335944, SRR26639403; ***Blastus borneensis*** Cogn. ex Boerl., L805, Nam Đông, Vietnam, *Liu & al. 806* (SYS), OL813683, SRR26639402; ***Blastus cochinchinensis*** Lour., L446, Fengkai, Guandong, China, *Liu 446* (SYS), MK994909, SRR26639401; ***Bredia hirsuta*** Blume, 634, Okinawa, Japan, *Liu 634* (SYS), MK994872, SRR26639400; ***Bredia hispida*** J.H.Dai & Ying Liu, L764, Xuyong, Sichuan, China, *Liu 764* (A, PE, SYS), OL813735, SRR26639399; ***Bredia longiloba*** (Hand.-Mazz.) Diels, L544, Zixi, Jiangxi, China, *Liu 544*

Appendix 1B. Continued.

(SYS), MK994825, SRR26639398; ***Bredia longiradiosa*** C.Chen ex Govaerts, L486, Longzhou, Guangxi, China, *Liu 486* (SYS), MK994807, SRR26639397; ***Bredia velutina*** Diels, L612, Jinping, Yunnan, China, *Liu 612* (SYS), MK994859, SRR26639395; ***Cyphotheca montana*** Diels, L596, Jinping, Yunnan, China, *Liu 596* (SYS), MK994852, SRR26639394; ***Dalenia sarawakensis*** (M.P.Nayar) Karton., L656, Sabah, Malaysia, *Zhou & al. 656* (SYS), OL813723, SRR26639443; ***Diplectria divaricata*** (Willd.) Kuntze, CWL696, Sabah, Malaysia, *C.W. Lin 696* (TAIF), OL813710, SRR26639442; ***Dissochaeta gracilis*** Blume, 601, Java, Indonesia, *Fan 15704* (SYS), MK994855, SRR26639396; ***Driessenia axantha*** Korth., M26, Kuching, Malaysia, *Zhou & al. M26* (SYS), OL813740, SRR26639393; ***Driessenia glanduligera*** Stapf, L657n, Sabah, Malaysia, *Zhou & al. 657* (SYS), MK994879, SRR26639392; ***Driessenia phasmolacuna*** C.W. Lin, t659, Sarawak, Malaysia, *C.W. Lin 659* (TAIF), MK994923, SRR26639391; ***Fordiophyton breviscapum*** (C.Chen) Y.F.Deng & T.L.Wu, L441, Ruyuan, Guangdong, China, *Liu 441* (SYS), MK994788, SRR26639390; ***Fordiophyton faberi*** Stapf, L480, Pingnan, Guangxi, China, *Liu 480* (SYS), MK994805, SRR26639389; ***Fordiophyton peperomiifolium*** (Oliv.) C.Hansen, L432, Qingyuan, Guangdong, China, *Liu 432* (SYS), MK994785, SRR26639388; ***Fordiophyton phamhoangii*** (V.T.Pham, V.T.Chinh & Ranil) T.V.Do & Ying Liu, L826, Đại Lộc,Vietnam, *Liu & al. 820* (SYS), OL813693, SRR26639387; ***Fordiophyton repens*** Y.C.Huang ex C.Chen, L513, Pingbian, Yunnan, China, *Liu 513* (SYS), MK994815, SRR26639386; ***Gravesia laxiflora*** (Naudin) Drake, L3725, Madagascar, *Wang 3725* (IBSC), OL813718, SRR26639384; ***Gravesia rosea*** (Cogn.) H.Perrier, L3748, Madagascar, *Wang 3748* (IBSC), OL813719, SRR26639383; ***Gravesia subglobosa*** H.Perrier, L3761, Madagascar, *Wang 3761* (IBSC), OL813720, SRR26639382; ***Heteroblemma* sp. nov.**, L825, Kon Tum, Vietnam, *Liu & al. 825* (SYS), OL813692, SRR26639381; ***Heteroblemma* sp. nov.**, L841, Bi doup Nui Ba, Vietnam, *Liu & al. 842* (SYS), OL813702, SRR26639379; ***Heteroblemma serpens*** (Stapf) Cámara-Leret, Ridd.-Num. & Veldkamp, L671, Sarawak, Malaysia, *Liu 671* (SYS), MK994886, SRR26639380; ***Kerriothyrsus tetrandrus*** (Nayar) C.Hansen, 794, Vu Quang, Vietnam, *Liu & al. 794* (SYS), OL813681, SRR26639378; ***Macrolenes pachygyna*** (Korth.) M.P.Nayar, 687, Sarawak, Malaysia, *Zhou & al. 687* (SYS), MK994894, SRR26639385; ***Medinilla amplectens*** Regalado, L663n, Sabah, Malaysia, *Zhou & al. 663* (SYS), MK994882, SRR26639377; ***Medinilla beamanii*** Regalado, L658, Sabah, Malaysia, *Zhou & al. 658* (SYS), MK994880, SRR26639375; ***Medinilla eximia*** (Jack) Blume, CWL697, Sabah, Malaysia, *C.W. Lin 697* (TAIF), OL813711, SRR26639372; ***Medinilla flammea*** C.W.Lin, CWL698, Sabah, Malaysia, *C.W. Lin 698* (TAIF), OL813712, SRR26639371; ***Medinilla nubicola*** Ohwi, L500, Malipo, Yunnan, China, *Liu 500* (SYS), MK994809, SRR26639373; ***Medinilla petelotii*** Merr., L589, Malipo, Yunnan, China, *Liu 589* (SYS), MK994847, SRR26639376; ***Medinilla purpureoviridis*** C.W.Lin, CWL682, Sarawak, Malaysia, *C.W. Lin 682* (TAIF), OL813708, SRR26639368; ***Nephoanthus prostratus*** (C.Hansen) C.W.Lin & T.C.Hsu, T640, Gia Lai Province, Vietnam, *C.W. Lin 640* (TAIF), MK994919, SRR26639421; ***Opisthocentra clidemioides*** Hook.f., Opisthocentra_clidemioides, *M.K. Caddah 578* (NY, UPCB), KX826828, SRR26639439; ***Oxyspora balansae*** (Cogn.) J.F.Maxwell, 793, Tam Dao, Vietnam, *Liu & al. 793* (SYS), OL813680, SRR26639434; ***Oxyspora bullata*** (Griff.) J.F.Maxwell (= ***Allomorphia malaccensis*** Ridl.), M44, Kuala Lumpur, Malaysia, *Zhou & al. M44* (SYS), OL813742, SRR26639437; ***Oxyspora paniculata*** DC., L523, Malipo, Yunnan, China, *Liu 523* (SYS), MK994819, SRR26639436; ***Oxyspora* sp.**, L681, Sarawak, Malaysia, *Zhou & al. 681* (SYS), MK994891, SRR26639438; ***Oxyspora urophylla*** (Diels) Y.M.Shui, 718, Jinping, Yunnan, China, *Liu 718* (SYS), MK994903, SRR26639423; ***Perilimnastes ternata*** (C.Chen) Ying Liu, L582, Xinyi, Guangdong, China, *Liu 582* (SYS), MK994844, SRR26639414; ***Perilimnastes dispar*** (Cogn.) Ying Liu, M20, Sabah, Malaysia, *Zhou & al. M20* (SYS), MK994910, SRR26639432; ***Perilimnastes melastomatoides*** (Merr. & Chun) Ying Liu, L447, Lingshui, Hainan, China, *Liu 447* (SYS), MK994914, SRR26639424; ***Phyllagathis cavaleriei*** Guillaumin, L599, Hongya, Sichuan, China, *Liu 599* (SYS), MK994854, SRR26639435; ***Phyllagathis cymigera*** C.Chen, L624, Malipo, Yunnan, China, *Liu 624* (SYS), MK994864, SRR26639433; ***Phyllagathis elattandra*** Diels, L554, Guiping, Guangxi, China, *Liu 554* (SYS), MK994830, SRR26639431; ***Phyllagathis erecta*** (S.Y.Hu) C.Y.Wu ex C.Chen, L507, Malipo, Yunnan, China, *Liu 507* (SYS), MK994811, SRR26639430; ***Phyllagathis griffithii*** King, PS, Malaysia, *W.L. Ng s.n.* (SYS), OL813744, SRR26639429; ***Phyllagathis hispida*** King, LM49, Kuala Lumpur, Malaysia, *Zhou & al. M49* (SYS), MK994783, SRR26639428; ***Phyllagathis lii*** C.W.Lin, Chien F.Chen & T.Y.A.Yang, t667, Sarawak, Malaysia, *C.W. Lin 667* (TAIF), MK994924, SRR26639427; ***Phyllagathis longifolia*** (Cogn.) J.F.Maxwell, L688, Sarawak, Malaysia, *Zhou & al. 688* (SYS), OL813673, SRR26639426; ***Phyllagathis megalocentra*** C.Hansen, L838, Bi doup Nui Ba, Vietnam, *Liu & al. 840* (SYS), OL813699, SRR26639425; ***Phyllagathis osmantha*** (M.P.Nayar) Cellin. (= ***Cyanandrium osmanthus*** M.P.Nayar), T567a, Sarawak, Malaysia, *C.W. Lin 567* (TAIF), MK994915, SRR26639422; ***Phyllagathis rotundifolia*** (Jack) Blume, M50, Kuala Lumpur, Malasysia, *Zhou & al. M50* (SYS), MK994912, SRR26639420; ***Phyllagathis rufa*** (Stapf) Cellin. (= ***Cyanandrium rufum*** Stapf), L679, Sarawak, Malaysia, *Zhou & al. 679* (SYS), MK994890, SRR26639419; ***Phyllagathis tentaculifera*** C.Hansen, 722, Jinping, Yunnan, China, *Liu 722* (SYS), MK994782, SRR26639418; ***Phyllagathis tuberculata*** King, M43, Kuala Lumpur, Malasysia, *Zhou & al. M43* (SYS), OL813741, SRR26639417; ***Phyllagathis tuberosa*** (C.Hansen) Cellin. & S.S.Renner (= ***Tylanthera tuberosa*** C.Hansen), B2567, Ubon Ratcharhani, Thailand, *J. Wai 2567* (PSU), OL813706, SRR26639416; ***Phyllagathis wallacei*** C.W.Lin, Chien F.Chen & T.Y.A.Yang, L686, Sarawak, Malaysia, *Zhou & al. 686* (SYS), MK994781, SRR26639415; ***Plagiopetalum esquirolii*** (H.Lév.) Rehder, 714, Malipo, Yunnan, China, *Liu 714* (SYS), OL813675, SRR26639413; ***Plethiandra robusta*** (Cogn.) Nayar, CWL681, Sarawak, Malaysia, *C.W. Lin 681* (TAIF), OL813707, SRR26639370; ***Poilannammia allomorphioidea*** C.Hansen, L837, Bi doup Nui Ba, Vietnam, *Liu & al. 837* (SYS), OL813698, SRR26639411; ***Pseudodissochaeta septentrionalis*** (Smith) Nayar, L618, Malipo, Yunnan, China, *Liu 618* (SYS), MK994778, SRR26639374; ***Sarcopyramis napalensis*** Wall., L581, Zhangjiajie, Hunan, China, *Liu 581* (SYS), MK994843, SRR26639410; ***Scorpiothyrsus erythrotrichus*** (Merr. & Chun) H.L.Li, L454, Ledong, Hainan, China, *Liu 454* (SYS), MK994794, SRR26639409; ***Sonerila obliqua*** Korth., 682, Sarawak, Malaysia, *Zhou & al. 682* (SYS), OL813672, SRR26639408; ***Sonerila pulchella*** Stapf, L668B, Sabah, Malaysia, *Zhou & al. 668* (SYS), MK994884, SRR26639407; ***Sonerila velutina*** Cogn., L683, Sarawak, Malaysia, *Zhou & al. 683* (SYS), MK994892, SRR26639406; ***Sporoxeia sciadophila*** W.W.Sm., L524, Malipo, Yunnan, China, *Liu 524* (SYS), MK994820, SRR26639405; ***Sporoxeia* sp. nov.**, L732, Jinxiu, Guangxi, China, *Liu 732* (SYS), OL813733, SRR26639369; ***Styrophyton caudatum*** (Diels) S.Y.Hu, L615, Malipo, Yunnan, China, *Liu 615* (SYS), MK994860, SRR26639367; ***Tashiroea sessilifolia*** (H.L.Li) R.Zhou & Ying Liu, L540, Huaiji, Guangdong, China, *Liu 540* (SYS), MK994824, SRR26639366; ***Tashiroea yaeyamensis*** Matsum, 631, Iriomote, Japan, *Liu 631* (SYS), MK994870, SRR26639364; ***Tigridiopalma magnifica*** C.Chen, L429, Gaozhou, Guangdong, China, *Liu 429* (SYS), MF663760, SRR26639363; ***Vietsenia scaposa*** C.Hansen, L812, BàNà nature reserve, Vietnam, *Liu & al. 812* (SYS), OL813686, SRR26639362.

Appendix 1C. Raw data from 66 accessions sequenced using Angiosperms353 probes (Maurin & al., 2021).

Taxon, ENA accession number.

Acisanthera hedyotoidea Triana, ERR5034394; ***Alloneuron ulei*** Pilg., ERR5033900; ***Antherotoma naudinii*** Hook.f., ERR5034364; ***Appendicularia thymifolia*** DC., ERR5033928; ***Arthrostemma ciliatum*** Pav. ex D.Don, ERR5033988; ***Axinandra zeylanica*** Thwaites, ERR4180211; ***Beccarianthus pulcherrimus*** (Merr.) J.F.Maxwell, ERR5034360; ***Bellucia egensis*** (DC.) Penneys & al., ERR5034969; ***Bertolonia paranensis*** (Wurd.) Baumgratz, ERR5034815; ***Blakea multiflora*** D.Don, ERR5033893; ***Bourdaria felicis*** A.Chev., ERR5034861; ***Boyania colombiana*** Humberto Mend., ERR5033996; ***Calvoa crassinoda*** Hook.f. ex Triana, ERR5034961; ***Calvoa monticola*** A.Chev., Hutch. & Dalziel, ERR5034860; ***Cambessedesia eichleri*** Cogn., ERR5033896; ***Catanthera* sp.**, ERR5084316; ***Centradenia floribunda*** Planch., ERR5033989; ***Centronia laurifolia*** D.Don, ERR5033942; ***Chalybea macrocarpa*** (L.Uribe) M.E.Morales & Penneys, ERR5033895; ***Dicellandra barteri*** Hook.f., ERR5034066; ***Diplectria divaricata***, ERR5034955; ***Dissochaeta annulata*** Hook.f. ex Triana, ERR5034109; ***Dissochaeta biligulata*** Korth., ERR5034954; ***Dissochaeta bracteata*** (Jack) Blume, ERR5034361; ***Eriocnema fulva*** Naudin, ERR5033955; ***Fordiophyton strictum*** Diels, ERR5034373; ***Gravesia setifera*** H.Perrier, ERR5033993; ***Gravesia vestita*** (Baker) H.Perrier, ERR5034959; ***Henriettea tovarensis*** (Cogn.) Penneys, Michelang., Judd & Almeda, ERR5101682; ***Huberia consimilis*** Baumgratz, ERR5033897; ***Medinilla rubicunda*** (Jack) Blume, ERR5034962; ***Medinilla sedifolia*** Jum. & H.Perrier, ERR5034679; ***Medinilla setigera*** Mig., ERR5034963; ***Medinilla stephanostegia*** Stapf, ERR5034375; ***Meriania urceolata*** Triana, ERR5033948; ***Miconia haemantha*** (Triana ex Cogn.) Skean, Judd & Majure, ERR5033960; ***Miconia secunsanguinea*** Ocampo

Appendix 1C. Continued.

& Almeda, ERR5033957; ***Miconia serrulata*** (DC.) Naudin, ERR5033969; ***Microlicia cordata*** (Spreng.) Cham., ERR5033980; ***Monolena primuliflora*** Hook.f., ERR5033997; ***Mouriri gleasoniana*** Standl., ERR5033986; ***Olinia* sp.**, ERR5084279; ***Opisthocentra clidemioides*** Hook.f., ERR5033999; ***Oxyspora cordata*** (Stapf) C.Hansen, ERR5034964; Oxyspora **sp.**, ERR5084301; ***Oxyspora urophylla*** (Diels) Y.M.Shui, ERR5034960; ***Pachyloma huberioides*** Triana, ERR5033990; ***Penaea retzioides*** (Sond.) Byng & Christenh., ERR5034677; ***Perilimnastes elliptica*** (Stapf) Ying Liu, ERR5034378; ***Phainantha laxiflora*** (Triana) Gleason, ERR5034000; ***Phyllagathis fengii*** C.Hansen, ERR5034379; ***Physeterostemon gomesii*** Amorim & R.Goldenb., ERR5034829; ***Plethiandra robusta*** (Cogn.) Nayar, ERR5034875; ***Poikilogyne cordifolia*** Mansf., ERR7599824; ***Poteranthera pusilla*** Bong., ERR5033981; ***Pternandra azurea*** (Blume) Burkill, ERR5034362; ***Pternandra cogniauxii*** M.P.Nayar, ERR5034363; ***Sonerila cantonensis*** Stapf, ERR5033995; ***Tashiroea okinawensis*** Matsum., ERR5034371; ***Tashiroea sinensis*** Diels, ERR5034064; ***Tessmannianthus quadridomius*** Wurdack, ERR5034953; ***Tibouchina aspera*** Aubl., ERR5033922; ***Triolena amazonica*** (Pilg.) Wurdack, ERR5033998; ***Tristemma mauritianum*** J.F.Gmel., ERR5034374; ***Warneckea* sp.**, ERR5084257; ***Wurdastom hexamera*** (Wurdack) B.Walln., ERR5033901.

Appendix 1D. RNA-seq data for *Medinilla magnifica* Lindl. (Leebens-Mack & al., 2019).

Medinilla magnifica, SRA accession number ERR2040321.

CHAPTER 4

PHYLOGENOMICS OF AFRICAN MELASTOMATEAE (MELASTOMATACEAE): REVISITING GENERIC RELATIONSHIPS, PLACEMENT OF THREE ENIGMATIC TAXA AND DESCRIPTION OF TWO NEW GENERA

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Taxon, under review

Phylogenomics of African Melastomateae (Melastomataceae): Revisiting generic relationships, placement of three enigmatic taxa and description of two new genera

Running title: Phylogenomics of African Melastomateae

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Abstract

Evolutionary relationships within the Melastomateae, a diverse tribe within the Melastomataceae, are not yet completely resolved, and some putative paleoendemic taxa that might alter relationships are still unsampled. This study employs a phylogenomic approach, utilizing target capture data, to revisit generic relationships and shed light on the placement of three enigmatic taxa (*Dissotis leonensis, D. splendens* and *Dionychastrum schliebenii*) within the African Melastomateae. Using 90 accessions (63 newly sequenced), spanning known genera, unplaced taxa and phylogenetically unsampled taxa, and leveraging high-throughput sequencing and Melastomataceae-specific baits, we capture a set of 384 putatively single-copy protein-coding nuclear loci.

Overall, our phylogenomic results with hundreds of loci are similar to previous results based on 3-5 Sanger-sequenced loci. Our analyses reaffirm the monophyly of the Old World Melastomateae, its two primary lineages, Euheterotis clade and Pseudoheterotis clade, and a sister group relationship of the Malagasy and Asian Melastomateae which are nested within the African Melastomateae. Except for *Melastomastrum*, which is not monophyletic in our analyses, the rest of the African genera previously circumscribed are again recovered. For the Guinea endemic *Dissotis splendens* we create the new genus *Allodissotis* and the new combination *Allodissotis splendens*. We also elevate *Dissotis* subgen. *Paleodissotis* to the rank of genus, with *Dissotis leonensis* from Guinea and Sierra Leone as the lone species, for which we create the new combination *Paleodissotis leonensis*. Morphologically, seed and wood anatomy of *Allodissotis splendens* and *Paleodissotis leonensis* support their placement in the tribe Melastomateae, with the latter being one of the early diverging lineages. Our study presents the first molecular insight into the Uluguru Mountains (Tanzania) endemic species *Dionychastrum schliebenii*, revealing it as sister to the Easter African endemic *Dissotidendron* clade.

Key words

Paleoendemic; Guinea; Morphology; Phylogeny; Rediscovery; Sierra Leone; Systematics; Taxonomic treatment; Tanzania; Target capture

INTRODUCTION

Sometimes rare and isolated taxa that are geographically remote and/or morphologically unique represent cases of paleoendemism, i.e. evolutionary old lineages that survived in a certain area. Such taxa are precious but due to their rarity in collections often difficult to obtain. As they might link distantly related lineages and strongly impact phylogenetic reconstructions it is worth undertaking an extra effort to include them in phylogenetic studies. Cai & al. (2023) identified warm and wet climates, geographic isolation, and long-term climatic stability as drivers of phylogenetic endemism which is often found in tropical mountainous areas. The African Melastomateae belonging to the tribe Melastomataceae revealed quite a number of enigmatic taxa which remained unplaced at first.

Melastomataceae are one of the largest families of flowering plants with ~173 genera, >5800 species, and with greatest diversity in the Neotropics and Southeast Asia (Ulloa Ulloa & al., 2022). Within the subfamily Melastomatoideae, the pantropical Melastomateae are one of 21 tribes currently recognized (Penneys & al., 2022). The previous study by Michelangeli & al (2013) showed that the Melastomateae (excluding Marcetieae) are a monophyletic group, but the New World members are not monophyletic because the Old World subclade is phylogenetically nested within the tribe. The first phylogeny and comprehensive overview of generic relationships within African Melastomateae (Veranso-Libalah & al., 2017) had significant implications, including a revised classification that led to the reinstatement, description and re-delimitation of several genera. However, phylogenetic relationships within the large *Dissotis* Benth. s.l. and allies clade remained unresolved. This clade comprised of *Antherotoma* (Naudin) Hook.f., other African *Osbeckia* L, and species of *Dissotis* s.l. Notably, the study pointed out that the relationships within the tribe would benefit from additional sampling and more data to elucidate the relationships within the tribe, particularly for the monospecific genera *Cailliella* Jacq.-Fél., *Dionychastrum* A.Fern. & R.Fern., and *Nerophila gentianoides* Naudin. The latter, formerly known as *Chaetolepis gentianoides* (Naudin) Jacq.-Fél., represented an African Melastomateae species originally included in the neotropical genus *Chaetolepis* (DC.) Miq.

In a subsequent publication, a new genus, *Nothodissotis* Ver.-Lib. & G.Kadereit endemic to Atlantic Central Africa, was described integrating molecular and morphological data (Veranso-Libalah & al., 2019). In the next publication, Veranso-Libalah & al. (2020) delved into the intricate task of resolving phylogenetic relationships within the previously ambiguous *Dissotis* and allies clade. Utilizing molecular phylogenetic findings and ancestral character reconstruction, *Dissotis* s.l. remained polyphyletic with no morphological synapomorphies. This study provided a revised classification of *Dissotis* s.l. and its allies, and led to the description of five additional new genera and generic reinstatements and re-circumscriptions. Remarkably, the circumscription of *Dissotis* s.str. underwent a substantial reduction to only six species (Veranso-Libalah & al., 2020), a notable refinement from its previous representation of around 108 species (see Renner 1993, Jacques-Félix 1994), prior to Veranso-Libalah & al. (2017). In 2016, the threatened monospecific genus *Cailliella praerupticola* Jacq.-Fél. was rediscovered, a species endemic to the sandstone plateau region of Guinea and previously known only from its type material. Veranso-Libalah & al. (2021) conducted a phylogenetic analysis that intricately positioned this species within the evolutionary context of African Melastomateae. They suggested that *Cailliella praerupticola* might be an "evolutionary relict" or "paleoendemic" within African Melastomateae.

Despite significant advancements in unraveling phylogenetic relationships and establishing generic boundaries within African Melastomateae, certain taxa with intriguing and distinctive morphologies, such as *Dionychastrum schliebenii* A.Fern. & R.Fern., *Dissotis splendens* A.Chev. & Jacq.-Fél., and *Dissotis leonensis* Hutch. & Dalziel, have remained unsampled in a phylogenetic context. Remarkably, the latter two species remain unplaced within any of the currently accepted African Melastomateae genera (Veranso-Libalah & al., 2017, 2019, 2020, 2021, 2022; Ulloa Ulloa & al., 2022).

Out of the 199 known mainland African Melastomataceae species belonging to the subfamily Melastomatoideae, Guinea is home to approximately 63 species, with nine of them being endemic, and six narrowly near-endemic species that also extend to Sierra Leone. Among these near-endemics, *Dissotis leonensis* (Fig. 1) was initially described from the Kessewe Hills (Kasewi Hills) in Sierra Leone by Hutchinson & Dalziel (1927). Subsequently, it was also collected on Mont Gangan in Guinea during Chevalier's collection expedition in 1934. This distinctive species is endemic to the sandstone table mountains at elevations above 500 meters in Guinea and Sierra Leone (Couch & al., 2019).

Jacques-Félix (1981) proposed an infrageneric classification for *Dissotis* introducing four subgenera (subg. *Dissotis*, subg. *Dupineta* (Raf.) A.Fern. & R.Fern., subg. *Dissotidendron* A.Fern. & R.Fern., and subg. *Paleodissotis* Jacq.-Fél.). However, with the exception of subg. *Paleodissotis*, the other three subgenera are now recognized as distinct genera (Veranso-Libalah & al., 2017, 2020). *Dissotis leonensis* is the sole species in subg. *Paleodissotis* (Jacques-Félix, 1981). In recent years, Kew botanists collected *D. leonensis* in 2013 – 2019 during expeditions to Guinea. With silica-dried samples now available, issues related to DNA quality and quantity have been addressed, enabling the phylogenetic placement of this species among other African Melastomataceae.

Dissotis splendens (Fig. 2), the other unplaced Guinea endemic species, was originally described by Jacques-Félix (1932). This species is endemic to the high-altitude sandstone bowal grasslands plateaus of Kounounkan, Kindia, and Mont Gangan, all of which are part of the unique Fouta Djallon habitat in Guinea. Until recently, only five collections of *D. splendens* are known (GBIF, 2024a). However, during expeditions to Guinea between 2016 and 2019, Kew botanists collected five new specimens of the species. Initially, Jacques-Félix (1981) assigned this species in subg. *Dissotis*, sect. *Macrocarpae* A.Fern. & R.Fern. (now recognized as *Feliciotis* Ver.-Lib. & G.Kadereit), despite having quite distinct emergence compared to those found in species of *Feliciotis*. With these recent collections now available, *D. splendens* which had remained unplaced in the updated classifications of African Melastomateae (Veranso-Libalah & al., 2017, 2020; Ulloa Ulloa & al., 2022), can be included in molecular phylogenetic studies. Another phylogenetically enigmatic species of African Melastomateae is *Dionychastrum schliebenii*, an endemic to the Uluguru Mountains of Tanzania. This species was thought to morphologically share affinities with *Dionycha* Naudin, a Melastomateae genus endemic to Madagascar (Fernandes & Fernandes, 1956; Jacques-Félix, 1995). Both taxa are deciduous shrubs with cymose inflorescences, isomorphic stamens, calyx-tube, and capsules that are not contracted above. Unfortunately, there have been no recent collections of *Dionychastrum schliebenii*, with the last collection dating back to 1970. Only thirteen herbarium specimens have been collected since 1933 (GBIF, 2024b).

While field expeditions are generally crucial for re-collecting iconic taxa alongside silica-dried samples, this is not always feasible for all taxa. Despite being an extraordinary resource for researching the world's plant diversity, herbaria collections are largely underutilized in molecular research (Buerki & Baker, 2016). The high-throughput sequencing approach has shown success in dealing with highly fragmented herbarium DNA (Brewer & al., 2019; Kates & al., 2021). The development of Melastomataceae-specific baits by Jantzen & al. (2020), targeting 384 loci, including 266 from the Angiosperms353 project (Johnson & al., 2018), now enables the capture of hundreds of putatively single-copy protein-coding nuclear genes. By utilizing target capture data and ensuring a comprehensive representation of African Melastomateae genera, our study aims to address pivotal questions: (i) Are the previously established phylogenetic relationships, derived from Sanger sequencing data, still valid? (ii) What are the phylogenetic positions of previously unsampled enigmatic taxa? Ultimately, our study concludes with a revised classification of African Melastomateae.

■ MATERIALS AND METHODS

Taxon sampling. — In our study, we incorporated a total of 90 accessions. Of these, 23 were obtained from Maurin & al. (2021) based on Angiosperms353 baits. Additionally, transcriptomes of three Southeast Asian taxa were included: *Osbeckia stellata* Buch.-Ham. ex D.Don (SRR22557471), *Melastoma candidum* D.Don (SRR22574045), and *Melastoma dodecandrum* Lour. (CRR290829). We generated new target capture data for 63 accessions and genome skimming data for one accession, representing 53 African Melastomateae species with all traditionally recognized African genera sampled (Jacques-Félix 1995; Veranso-Libalah & al., 2017, 2020, 2022). Furthermore, we included one, three, and four accessions belonging to *Dionychastrum schliebenii*, *Dissotis splendens*, and *D. leonensis*, respectively. The accession from *Dion. schliebenii* was from a herbarium specimen collected from 1933. As part of the outgroup, we sampled six New World Melastomateae taxa (see Michelangeli & al. 2013).

DNA extraction and Sequencing. — Total genomic DNA was extracted from silica-dried leaves or herbarium specimens using a modified CTAB protocol (Doyle & Doyle, 1987; Majure & al., 2019). DNA concentration was quantified using a Qubit 4 fluorometer (Thermo Fisher Scientific, Waltham, MA, USA). Subsequently, the extracted DNA samples were sent to Rapid Genomics (Gainesville, FL, USA) for library preparation, hybrid enrichment, and next-generation sequencing. The Melastomataceae-specific baits developed by Jantzen & al. (2020) were used to target and capture 384 loci, of which 266 are from the Angiosperms353 project (Johnson & al., 2018).

Assembly of target loci. — FastQC (http://www.bioinformatics.babraham.ac.uk/projects/fastqc/) was used to check quality of the raw data. We used Fastp v0.23.2 (Chen & al., 2018) (-g -x -r -l 30 -5 --cut_front_window_size 1 -3 _tail_window_size 1 --detect_adapter_for_pe) to cut adapters and filter sequences. Target loci recovery was carried out using HybPiper v2.1.2 (Johnson & al., 2016) with DIAMOND (Buchfink & al., 2021) as the mapping tool. As a cleaned Melastomataceae probe set (Dagallier & Michelangeli, 2024) can improve recovery, we used it as the target file when running HybPiper. Recovery statistics were checked in HybPiper, and both the main sequence (selected among contigs based on the coverage depth or, when depth is similar, the percent identity to the reference) and alternative gene copies (possible paralogs) were retrieved using ‘paralog_retriever’ for subsequent phylogenetic analyses.

Phylogenetic analyses. — Following Chen & al. (2023), the retrieved sequences were aligned using MAFFT v7.453 (Katoh & Standley, 2013). Subsequently, the alignments were trimmed using Phyutility v.2.7.1 (Smith & Dunn, 2008), and sequences that were either very short (< 50 bp) or exhibited significant gaps (missing 90% of sites) were removed. Single gene trees were then built using IQ-Tree 2.2.0.3 (Minh & al., 2020). After masking monophyletic and paraphyletic tips of the gene trees following Yang & Smith (2014) and Morales-Briones & al., (2021), we deleted abnormally long branches using TreeShrink v.1.3.7 (Mai & Mirarab, 2018). Three different methods were employed to infer the final species tree.

Firstly, DISCO (Decomposition Into Single-COpy gene trees; Willson & al., 2022) was used to infer orthology by decomposing multi-copy gene trees into single-copy trees based on Astral-Pro's (Zhang & al., 2020) rooting and tagging algorithms. Only trees with at least nine tips were retained, and a coalescent-based species tree was subsequently inferred with ASTRAL v.5.7.8 (Zhang & al., 2018). Secondly, we concatenated gene alignments corresponding to single-copy gene trees identified in the first method into a supermatrix using AMAS (Borowiec, 2016) and performed partitioned phylogenetic analysis based on it in IQ-TREE (v. 2.2.0.3) (Minh & al., 2020) with 1000 ultrafast bootstraps. "MFP+MERGE" option in IQ-TREE was employed to find the best-fitting partitioning scheme and substitution models. Lastly, ASTRAL-Pro v1.5.1.3 (Zhang & Mirarab, 2022) was used to directly infer species tree from multi-copy gene trees. The resulting trees were visualized using ggtree (Yu, 2020) in R (R Core Team, 2023).

Wood anatomy. — A wood sample of *D. leonensis* (*Burgt 2199*) was obtained from K. Initially, the dried wood sample underwent a softening process by soaking it in a glycerin/water mixture (1:10 volume ratio) for a duration of five days. Tangential sections 20–35 µm thick were cut with a sledge microtome (Microm, Heidelberg, Germany). These sections were mounted on slides and embedded in ROTI Histokitt (Carl Roth, Karlsruhe, Germany). The embedded slides were observed under a light microscope (Leica DM750, Wetzlar, Germany) equipped with Leica LAS X software. Terminology follows (Van Vliet, 1981; Van Vliet & al., 1981b, 1981a).

Seed morphology. — Using the seeds of *D. leonensis* (*Burgt 2103*) and *D. splendens* (*Burgt 2254*), both obtained from K, seed morphological characters were examined using a scanning electron microscope (Leo 438VP, Carl Zeiss AG, Oberkochen, Germany). Seed morphology was described following Ocampo & al. (2014).

■ RESULTS

Recovery statistics and data sets. — Recovery statistics for all samples obtained via HybPiper are provided in supporting information Table S1. Transcriptomic and sequencing skimming data yielded significantly better results, generating between 52,696,792 and 141,268,822 reads, and recovering 356 to 377 sequences. In contrast, the target capture approach produced 131,414 to 13,011,506 reads and recovered between 103 and 331 sequences. In the ASTRAL-Pro analysis, 385 gene trees containing paralogs were directly used to infer the species tree. For the DISCO analysis, these gene trees were employed in the identification of 685 putatively single-copy gene trees, which were then utilized for the DISCO-ASTRAL analysis. The alignments of these single-copy gene trees were concatenated into a supermatrix for the DISCO-IQTREE analysis, covering 635,444 columns and including 99,750 parsimony-informative sites.

Phylogenetic relationships. — The nuclear phylogenetic trees generated using two coalescent-based methods (DISCO-ASTRAL and ASTRAL-Pro) and one concatenation-based method (DISCO-IQTREE) have overall similar topologies (Figs. 3, 4). Generally, the backbone of the phylogenetic trees is well-supported except for three nodes having relatively low local posterior probability (LPP: < 0.7) in the DISCO-ASTRAL tree (Fig. 3). The Paleotropical Melastomateae are monophyletic, but the African Melastomateae are not monophyletic since the Malagasy and Asian endemic genera are nested within them (Figs. 3, 4).

All African genera are recovered as monophyletic, except for *Melastomastrum* Naudin. All sampled accessions of *Dissotis leonensis* form a monophyletic group that is placed as the first-branching lineage of the "Pseudoheterotis" clade sensu Veranso-Libalah & al. (2017). In all three trees, *Cailliella praerupticola* is sister to *Tristemma* Juss. and *Melastomastrum*, but the latter forms three distinct lineages. All accessions of *M. theifolium* (G.Don) A.Fern. & R.Fern. and *M. segregatum* (Benth.) A.Fern. & R.Fern. sampled each form well-supported clades. *Melastomastrum porteresii* (Jacq.-Fél.) Ver.-Lib. & G.Kadereit forms another segregate clade with another *Melastomastrum* sp. (Figs. 3, 4).

Within the "Euheterotis" clade sensu Veranso-Libalah & al. (2017), the remaining major lineages branch off successively starting with *Dichaetanthera* Juss. It forms a monophyletic clade subdivided into two lineages. In the DISCO-ASTRAL and ASTRAL-Pro trees, one lineage composed of the African endemic *Dichaetanthera* species, while the other comprises the Malagasy endemic species (Fig. 4). In the DISCO-IQTREE tree, the Tanzanian and Zambian endemic *D. erici-rosenii* (R.E.Fr.) A.Fern. & R.Fern. is sister to the Malagasy endemic species, and the other two African species form a clade. *Heterotis* Benth. diverged next followed by *Dissotidendron* (A.Fern. & R.Fern.) Ver.-Lib. & G.Kadereit (Fig. 4). *Dionychastrum schliebenii* is either sister to *Dissotidendron* as in the DISCO-IQTREE and ASTRAL-Pro trees, or weakly resolved within *Dissotidendron* as in the DISCO-ASTRAL tree (Fig. 4).

In all trees, the Asian and Australian endemic genera form a monophyletic group sister to a clade composed of Malagasy endemic genera. *Osbeckia* does not form a clade; instead, all sampled *Melastoma* L. form a clade that is nested within it (Figs. 3, 4). The three Malagasy endemic genera (i.e., *Rousseauxia* DC., *Amphorocalyx* Baker, and *Dionycha*) do not separate from each other, and the relationships among different accessions are not well supported in the coalescent trees (Fig. 4)

In all phylogenetic trees, *Nothodissotis* branches off next, followed by *Dupineta* Raf. All accessions of *Dissotis splendens* included in the analyses form a clade (Figs. 3, 4). After *D. splendens*, the monospecific *Pseudosbeckia* A.Fern. & R.Fern. and *Rosettea* Ver.-Lib. & G.Kadereit branch off successively. The remaining clades branch off similarly: *Derosiphia* Raf., *Dissotis*, and the FAEP clade (composed of *Feliciotis speciosa* (Taub.) Ver.-Lib. & G.Kadereit, *Almedanthus pachytrichus* (Gilg ex R.E.Fr.) Ver.-Lib. & R.D.Stone, *Eleotis welwitschii* (Cogn.) Ver.-Lib. & R.D.Stone and *Pyrotis gilgiana* (De Wild.) Ver.-Lib. & R.D.Stone), followed by

Nerophila Naudin and *Antherotoma*. Within the FAEP clade, the internal relationships vary across the three different trees, with low LPP in the two coalescent trees (Figs. 3, 4).

■ DISCUSSION

With all currently recognized genera sampled in our phylogenomic analysis of target capture data, we have largely improved evolutionary relationships among African Melastomateae. Despite some differences among the trees, the clades identified in previous phylogenetic studies based on Sanger sequencing data are reaffirmed. As reported in previous studies (Michelangeli & al., 2013; Veranso-Libalah & al., 2017), Old World Melastomateae form a monophyletic lineage. The relationships within African Melastomateae based on our analysis are largely congruent with previous phylogenetic trees generated from concatenated datasets of one or two nuclear loci and two or three plastid loci (Veranso-Libalah & al., 2017, 2019, 2020, 2021). The two primary clades of Paleotropical Melastomateae identified in our results correspond to the Euheterotis clade and the Pseudoheterotis clade proposed by Veranso-Libalah & al. (2017). The main incongruence with former analyses is *Melastomastrum*, which was previously recovered as monophyletic, albeit with weak internal support. In our current analyses, all *Melastomastrum* species sampled diverge successively and *Tristemma* is nested within them (Figs. 3, 4). To gain a better understanding of its phylogenetic relationships with *Cailliella*, *Tristemma*, and within the group, more extensive sampling of *Melastomastrum* is required.

Like previous studies, the Malagasy and Asian endemic Melastomateae lineages are nested within the African Melastomateae (Veranso-Libalah & al., 2017, 2022). In our results, both the Malagasy and Asian Melastomateae are each monophyletic and sister clades (Figs. 3, 4). Within the Malagasy clade, none of the three endemic genera is well delimited. Within the Asian clade, *Melastoma* is nested within *Osbeckia*. Veranso-Libalah & al. (2020) identified two distinct clades for Malagasy endemic and Asian endemic Melastomateae. However, these two clades were not sister groups, and the sampling was inadequate for generic delimitation. Maurin & al. (2021) also recovered a monophyletic group of both Malagasy and Asian genera, but *O. stellata* was positioned as the sister to Malagasy endemic genera which were not well delimitated, while the rest of the Asian species formed a monophyletic group. To elucidate the generic boundaries and the relationship between Asian and Malagasy endemic taxa, more extensive sampling of both groups is needed.

In all trees generated in our study, the FAEP clade — comprising *Feliciotis* Ver.-Lib. & G.Kadereit, *Almedanthus* Ver.-Lib. & R.D.Stone, *Eleotis* Ver.-Lib. & R.D.Stone and *Pyrotis* Ver.-Lib. & R.D.Stone — is consistently well supported (Figs. 3, 4). However, the internal relationships within this clade vary among the different trees. This clade was previously identified by Veranso-Libalah & al. (2020). Both *Almedanthus* and *Pyrotis* are monotypic genera, whereas *Feliciotis* and *Eleotis* contain 12 and four species, respectively. To gain a better understanding of the phylogenetic relationships within this clade, additional sampling of *Feliciotis* and *Eleotis* is necessary.

In this paper, we do not discuss in detail the phylogenetic relationships or morphological apomorphies of all previously sampled African genera (see Veranso-Libalah & al., 2017, 2018, 2020, 2021), since all these clades are still well-supported and recovered in this study. In the next paragraphs, we discuss the phylogenetic placement and morphology of *Dissotis leonensis*, *D. splendens* and *Dionychastrum schliebenii*.

Phylogenetic placement of *Dissotis leonensis*. — Our phylogenetic analyses confirm the placement of *D. leonensis* in the tribe Melastomateae, as suggested by Jacques-Félix (1981, 1995), who considered this species as one of the earliest diverging lineages of the tribe with several primitive characters. Indeed, *D. leonensis* represents an early diverging lineage of African Melastomateae and is undoubtedly a paleoendemic and relictual species. Although all the Pseudoheterotis genera plus *D. leonensis* have tardily caducous to persistent sepals, other morphological characters in the latter are quite unique.

Morphologically, *D. leonensis* is atypical by several unique features. It is a shrub or treelet, typically attaining a height of about 3 to 4 meters, deciduous during dry season with new leaves emerging after flowering (Fig. 1). The twigs and branches are densely covered with fine warty and stellate hairs (Fig. 1). The inflorescence is a cyme, and each flower bears two caducous bracts. The hypanthium is campanulate and covered with tubercules and stellate hairs (Fig. 1). The seed characters of *D. leonensis* are very similar to those of other Melastomateae taxa (Figs. 5E-H; see Whiffin & Tomb, 1972; Grimm & Almeda, 2013; Ocampo & al., 2022). The inflorescence and wedge-shaped seeds of *D. leonensis* resemble those of *Sakersia* Hook.f. (= *Dichaetanthera* Endl.) (Chevalier, 1934; Jacques-Félix, 1995). The presence of staminal dimorphism, along with its capsular fruit, has been the primary basis for placing *D. leonensis* within *Dissotis* (Chevalier, 1934; Jacques-Félix, 1995). Normally, *Dissotis leonensis* has dimorphic stamens (Fig. 1), but one deviating specimen (*Burgt 2276*, collected on 12 February 2019) with isomorphic stamens was noted. This collection is leafless, as are other flowering collections of *D. leonensis*. We think this might be a new, closely related species. More collections are necessary during various phenological stages of the plants before a decision can be made.

Within the Melastomataceae, interxylary (included) phloem is found only in *Pternandra* Jack and members of subfamily Olisbeoideae but not among woody members of the Melastomatoideae (Van Vliet & al., 1981a; Dahlgren & Thorne, 1984; Van Vliet & Baas, 1984). Jacques-Félix (1995: 250) cited unpublished data by D. Normand reporting that *Dissotis leonensis* has intraxylary phloem, and erroneously referring to it as “included phloem”. He made a further error by comparing the character of intraxylary phloem present in *D. leonensis* with the character of interxylary (included) phloem found in the Memecyleae (= Olisbeoideae). In *D. leonensis*, the intraxylary phloem is present, similar to other taxa in Melastomatoideae, as opposed to interxylary phloem in the form of elongated tangential clusters in the Olisbeoideae (Van Vliet, 1981; Van Vliet & al., 1981a, 1981b).

Dissotis leonensis is clearly unrelated to *Dissotis* s.s. and can no longer be treated in subg. *Paleodissotis*. With its unique morphology and phylogenetic placement, the subg. *Paleodissotis* is elevated to the rank of genus (see Taxonomic Treatment section).

Phylogenetic placement of *Dissotis splendens*. — This is the first time *D. splendens* has been included in any molecular phylogenetic analyses. As previously proposed based on morphology (Jacques-Félix, 1955, 1981), its placement in Melastomateae is here confirmed. In all three phylogenetic trees, *D. splendens* is sister to a large clade composed of *Pseudosbeckia*, *Rosettea*, *Dissotis*, *Antherotoma*, *Derosiphia*, *Feliciotis*, *Almedanthus*, *Eleotis*, *Pyrotis*, and *Nerophila*.

Morphologically distinct from other African Melastomateae, *D. splendens* is a shrub up to 2 meters in height with quadrangular stems and an inflorescence forming a terminal panicle (Fig. 2). The bracts are caducous. The hypanthium is covered by scabrid, long stalked stellate hairs, and has discoid or orbicular apex (Fig. 2). The sepals are early caducous and have an apex with stellate hairs (Fig. 2). The stamens are dimorphic, with a connective and two ventral appendages just above the filament. The seeds of *D. splendens* are cochleate with tubercules (Fig. 5A-D) and very similar to those of other taxa of Melastomateae (see Whiffin & Tomb, 1972; Grimm & Almeda, 2013; Ocampo & al., 2022). Initially, Jacques-Félix (1981) assigned this species in subg. *Dissotis*, sect. *Macrocarpae*. *Feliciotis* species exhibit recognizable synapomorphies, including 5-merous flowers usually arranged in terminal cymes or occasionally panicles, bracts that are either scarious or foliaceous, and densely silvery-sericeous pubescence on the hypanthium (Fernandes & Fernandes, 1970; Wickens, 1975; Jacques-Félix, 1981, 1995; Veranso-Libalah & al., 2020). Despite having the apex of these emergences being discoid or orbicular, *D. splendens* was placed under *D.* sect. *Macrocarpae* (Jacques-Félix 1981).

Our molecular analyses neither support this species as part of *Dissotis* sect. *Macrocarpae* (now *Feliciotis*) nor *Dissotis* s.s. It is clearly a unique evolutionary entity based on molecular and morphological data. So far, this taxon is only known from Guinea. Due to the evidence outlined above *D. splendens* is best placed in a genus of its own (see Taxonomic Treatment section).

Phylogenetic placement of *Dionychastrum schliebenii*. — Using leaf samples from a herbarium specimen collected in 1933 (*Schlieben 3601*, K), *Dion. schliebenii* is included in phylogenetic studies for the first time. *Dionychastrum schliebenii* is known only from the Uluguru mountains of Tanzania. In all trees, it is recovered either within or sister to the *Dissotidendron* clade. *Dissotidendron* currently consists of 11 species; all but *Dissotidendron cordatum* (Gilg) Ver.-Lib. & G.Kadereit, are endemic to East Africa. *Dissotidendron cordatum* is endemic to the Katanga region of the Democratic Republic of Congo.

Dionychastrum schliebenii is the only African Melastomateae species lacking a crown of hairs on the ovary apex, a character often used to define the tribe Melastomateae. Nevertheless, it is unquestionably a Melastomateae. Previous publications (Fernandes & Fernandes, 1956; Jacques-Félix, 1995) suggested that this species is closely related to the Malagasy endemic *Dionycha*. However, our molecular results clearly show otherwise. *Dionychastrum* can be differentiated from *Dionycha* by having 5-merous flowers, persistent calyx lobes, curved pedoconnectives, anthers with a single anterior pore, and a glabrous and exserted capsule apex (Veranso-Libalah & al., 2017). Morphologically, *Dionycha* is a shrub or treelet with deciduous leaves, 4-merous flowers, caducous sepal lobes, isomorphic stamens, and connectives lacking a posterior claw but having lateral appendages. Jacques-Felix (1995) suggested that the lengthening process of the connective might have independently occurred in *Dionychastrum* (compare *Dionycha*) and other genera like

Dichaetanthera and *Dissotis*. This is confirmed by our molecular results, as none of these genera are closely related.

Morphologically, *Dionychastrum* is more closely related to *Dissotidendron*. They both share the following characteristics: shrubs or shrublets, rarely trees; mostly deciduous; leaf surfaces rugose to bulbous; flowers 5-merous; calyx-lobes caducous, or persistent, without intersepalar appendages. Except for *Dion. schliebenii* with homomorphic stamens, the rest of the *Dissotidendron* species have markedly unequal or dimorphic stamens. We recommend retaining *Dionychastrum* as a separate genus from *Dissotidendron*, unless further evidence emerges to suggest otherwise.

■ TAXONOMIC TREATMENT

Based on morphology and phylogeny, we instate a new genus for *Dissotis* subgen. *Paleodissotis*, and a new genus for *D. splendens*. To accommodate these changes, two new combinations are instated. We also designate a lectotype. We also provide a updated key to the African Melastomateae.

Revised key to the genera of African Melastomateae including *Allodissotis* and *Paleodissotis*

1 Trees or shrubs; hypanthium margin truncate or with short sepals, leaving the corolla exposed in bud; flowers tetramerous; seeds with dorsal hyaline papillae .... *Dichaetanthera*

1 Herbs, subshrubs or shrubs; hypanthium with well- developed sepals, contorted and concealing the corolla in young bud stage; flowers tetra- or pentamerous (rarely hexa- or heptamerous); seeds without hyaline papillae 2

2 Herbs; sepals persistent; stamens isomorphic (except *T. cornifolium*), with anthers erect; hypanthium with hairs often arranged in complete or incomplete rings (rarely glabrous or hairy all over); fruit fleshy, baccate, irregularly bursting .... *Tristemma*

2 Herbs, subshrubs or shrubs; sepals persistent or caducous; stamens heteromorphic or isomorphic with anthers spreading or curved; hypanthium variously pubescent but not arranged in rings; fruit dry, capsular, bursting regularly via valves 3

3 Leaves sessile or amplexicaul 4

3 Leaves petiolate (except *Feliciotis sessilicordata*) 6

4 Stems, leaves and hypanthium covered with dense stellate and/or glandular hairs appearing dusty; sepals persistent .... *Argyrella*

4 Stems, leaves and hypanthium glabrous or glabrescent; sepals persistent or caducous 5

5 Stems thick and somewhat fleshy, winged; hypanthium glabrous with prominent longitudinal nerves; bracts and sepals persistent; leaf and calyx margins conspicuously ciliate, appearing dentate .... *Anaheterotis*

5 Stems slender and non-fleshy, unwinged; hypanthium glabrous or glabrescent without longitudinal nerves; bracts and sepals caducous; leaf and calyx margins entire .... *Eleotis*

6 Sepals persistent; intersepalar appendages absent or present 7

6 Sepals caducous (sometimes tardily so); intersepalar appendages always present 15

7 Herbs or subshrubs; flowers solitary or arranged in heads or cymes (rarely panicles), separately involucrate by several pairs of leaves or bracts 8

7 Herbs, subshrubs or shrubs; flowers in cymes or panicles but not involucrate 11

8 Herbs; intersepalar appendages present; flowers tetra- (rarely penta-)merous; bracts small (<4 mm long), persistent or caducous...9

8 Herbs, subshrubs or shrubs; intersepalar appendages absent; flowers pentamerous; bracts large (>4 mm long), persistent 10

9 Flowers tetra- or pentamerous, solitary or arranged in cymes or panicles; bracts caducous; pedoconnective and staminal appendages rudimentary or absent .... *Nerophila*

9 Flowers tetramerous, arranged in heads (panicle in *A. gracilis*); bracts persistent; pedoconnective present with bilobed staminal appendages ....*Antherotoma*

10 Shrubs; flowers solitary; stamens isomorphic, with two ventral appendages and one dorsal appendage, pedocon- nective not developed, anthers erect; seeds finely echinulate, curved only towards the top, cuneate at base with an elongated hilum ....*Cailliella*

10 Herbs or subshrubs/shrubs; flowers solitary or in heads; stamens iso- or dimorphic, with two ventral appendages, no dorsal appendage, pedoconnectives well developed, anthers falcate or sigmoid; seeds tuberculate, cochleate and without a hilum .... *Melastomastrum*

11 Herbs, decumbent or rooting at the nodes (sometimes erect); flowers solitary or in cymes (rarely panicles); bracts small (<4 mm long), persistent or caducous 12

11 Subshrubs or shrubs; flowers in cymes or panicles; bracts large (>4 mm long), caducous ... 13

12 Decumbent herbs; hypanthium with stalked stellate emergences (simple eglandular hairs in *H. decumbens*); flowers in cymes; seeds rough with tubercles arranged in parallel rows, with a basal aril (this sometimes very short) .... *Heterotis*

12 Decumbent or erect herbs; hypanthium usually glabrous or with glandular hairs (simple eglandular hairs in G. pyg- maea); flowers solitary (panicle in *G. jacquesii*); seeds smooth or with tubercles not arranged in parallel rows, not arillate .... *Guyonia*

13 Leaves evergreen, small, 1.5–2.5 × 1–1.5 cm; intersepalar appendages present but reduced to a bristle; stamens isomorphic .... *Dionychastrum*

13 Leaves deciduous, much larger; intersepalar appendages absent; stamens usually dimorphic ……………………………………………………... 14

14 Branches finely verrucose and covered with stellated hairs; inflorescence cyme; hypanthium campanulate, and covered with tubercules and stellate hairs……………….. *Dissotidendron*

14 Branches glabrous or with simple hairs; inflorescence cymes or panicles; hypanthium campanulate, and covered with tubercules and stellate hairs …………..……. *Paleodissotis*

15 Shrubs; sepals asymmetrical, notched at apex; leaves deciduous ....*Nothodissotis*

15 Herbs, subshrubs or shrubs; sepals ± symmetrical, entire; leaves evergreen..........................16

16 Low perennial herb with numerous stems arising from a woody rootstock; leaf base attenuate, with an indistinct or contracted petiole .... *Pyrotis*

16 Annual or perennial herbs, subshrubs or shrubs without a woody rootstock; leaf base cuneate to rounded or subcor- date, with a distinct petiole 17

17 Annual or perennial herbs; hypanthium with simple or stellate hairs or both 18

17 Subshrubs or shrubs; hypanthium pubescence various but not stellate 20

18 Stems and petioles reddish-maroon; hypanthium with a distinct subspherical base and cylindrical apex, base covered with stellate emergences, apex with simple pubescence; stamens isomorphic ....*Derosiphia*

18 Stems and petioles not reddish-maroon; hypanthium urce- olate, tubulate or campanulate, glabrous or with simple or stellate hairs; stamens dimorphic 19

19 Hypanthium with persistent stellate-pedicellate hairs, not accrescent in fruit; intersepalar appendages present; sepals glabrous or with sparse simple hairs on the back, apex with stellate appendages; fruits lacking a long neck with longitudinal ribs ....*Dissotis*

19 Hypanthium with caducous, simple or stellate hairs, accrescent in fruit; intersepalar appendages present or absent; sepals with short simple hairs on the back, apex ciliate; fruits developing a long neck with longitudinal ribs .... *Dupineta*

20 Sepals tardily caducous; stamens isomorphic, opening by an extrorse pore; leaves distinctly bicoloured, dark green above and yellowish-green beneath .... *Pseudosbeckia*

20 Sepals early caducous; stamens dimorphic (except *Rosettea thollonii*), opening by an introrse pore; leaves dark green on both surfaces 21

21. Monospecific and narrowly endemic genera 22

21. Not monospecific and widely distributed genera 23

22. Endemic to Guinea; hypanthium with scabrid, long stalked stellate hairs, apex disc-like or orbicular; sepals apex with stellate hairs, flowers ……………....……………...…….. *Allodissotis*

22. Endemic to East Africa (Tanzania, Zambia, Democratic Republic of Congo), hypanthium with large, reflexed scale-like appendages abruptly narrowed to 1 or several setae; flowers 1–3 ....*Almedanthus*

23. Stems with always opposite leaves arising from each node; leaf margins entire, third-order veins absent on both surfaces; true and leafy bracts present, tardily caducous; hypanthium covered with dense silvery-sericeous pubescence ....*Feliciotis*

23. Stems with whorled or opposite leaves arising at each node; leaf margins serrate, dentate or crenate, third-order veins prominent on both surfaces; true bracts present, leafy bracts absent, early caducous; hypanthium pubescence various but not densely silvery-sericeous .... *Rosettea*

Allodissotis Ver.-Lib. & Burgt, **gen. nov.** – Type: *Allodissotis splendens* (A.Chev. & Jacq.-Fél.) Ver.-Lib. & Burgt (≡ *Dissotis splendens* A.Chev. & Jacq.-Fél.).

Morphological description. – In comparison to other African Melastomateae, *Allodissotis* is a shrub up to 2 m tall with quadrangular stems; inflorescence terminal panicle; hypanthium with scabrid, long stalked stellate hairs, apex disc-like or orbicular; sepals are early caducous, apex with stellate hairs; stamens dimorphic, connective and two ventral appendages present just above the filament (Fig. 2).

Allodissotis splendens Ver.-Lib. & Burgt, **comb. nov.** ≡ *Dissotis splendens* A.Chev. & Jacq.-Fél., Bull. Mus. Natl. Hist. Nat., Ser. ii, iv. 686 (1932). **Lectotype** (**designated here**): Guinea, Environs de Kindia, 1929-1932, *Jacques-Félix 207* (P00412558!).

Distribution. – Guinea (Fig. 7a).

Etymology. – The generic name *Allodissotis* simply means looks like *Dissotis*.

Seed morphology. – *Allodissotis splendens:* Seed ovoid; lateral symmetrical plane ovate, antiraphal symmetrical plane ovate to suboblong. Individual cells isodiametric to elongated, anticlinal boundaries undulate; periclinal walls flat to convex or par-convex, microrelief sometimes striate or verrucose (Fig. 5).

Note: In the protologue of *Dissotis splendens*, Chevalier & Jacques-Félix (1932: 686) cited *Jacques-Félix 207* as the type specimen. We located four specimens housed in P, all part of the same field collection as the type in the original description but none of them was designated as the holotype. We selected P00412558 as the lectotype, and P00412556, P00412555 and P00412557 as isolectotypes.

Dionychastrum A.Fern. & R.Fern. in Bol. Soc. Brot., sér. 2, 30: 169. 1956 – Type: *Dionychastrum schliebenii* A.Fern. & R.Fern.

Dionychastrum schliebenii A.Fern. & R.Fern. in Bol. Soc. Brot., sér. 2, 30: 169. 1956 – Holotype: Morogoro, Uluguru Mountains, Mbambaku Peak, 26 Feb 1933, *H-J.E. Schlieben 3601* (PRE0342271-0!; isotypes: BR0000006260293!, EA000002110!, EA000002111!, K000312750!, K000312751!, LISC002432!, MO-313699!)

Distribution. – Tanzania (Fig. 7b).

Paleodissotis (Jacq.-Fél.) Ver.-Lib. & Burgt, **stat. nov.** ≡ *Dissotis* subg. *Paleodissotis* Jacq.-Fél. in Adansonia, sér. 2, 20(4): 421. 1981 – Type: *Paleodissotis leonensis* (Hutch. & Dalziel) Ver.-Lib.

Morphological description. **–** In comparison to other African Melastomateae, *Paleodissotis* is a shrub, treelet up to 3 to 4 m in height, deciduous during dry season with new leaves emerging after flowering; young branches finely verrucose and covered with stellated hairs; inflorescence cyme; each flower bears two caducous bracts; hypanthium campanulate, and covered with tubercules and stellate hairs; calyx-lobes tardily caducous; stamens or dimorphic, with a connective and bilobed appendages (Fig. 1).

Paleodissotis leonensis (Hutch. & Dalziel) Ver.-Lib. & Burgt, **comb. nov.** ≡ *Dissotis leonensis* Hutch. ex Lane-Poole, Trees, Shrubs, Herbs & Climbers of Sierra Leone, 34 (1916), *nomen*; Hutch. & Dalziel, Fl. W. Trop. Afr. [Hutchinson & Dalziel] i. 211 (1927); Hutchinson & Dalziel in Kew Bull. 1928: 222 – Holotype: Sierra Leone, Mangui Trig point 4 Kessewe Hills, 500 m., 22 Feb 1913, *Lane-Poole 126* (K000313149!).

Distribution. – Guinea, Sierra Leone (Fig. 7c).

Seed morphology. – Paleodissotis leonensis: Seed ovoid occasionally angled; lateral symmetrical plane ovate, antiraphal symmetrical plane ovate to suboblong. Individual cells isodiametric to elongated, anticlinal boundaries undulate; periclinal walls flat to convex or par-convex, microrelief verrucose (Fig. 5E-H).

Wood anatomy. – Growth rings faint, Vessels diffuse (7) 9 – 11 (18)/mm^2, solitary and in radial multiples of 2 – 5 (– 9), tangential diameter (28 –) 52 – 86 (– 109) µm, radial diameter up to 127 um, walls 2 – 4 µm thick. Vessel member length (140) 250 – 320 (– 480) µm. Inter-vessel pits alternate, (6 – 16 µm). Vessel—ray and vessel—parenchyma pits large and simple or with narrow borders, alternate/opposite to transitional and scalariform. Fibres dimorphous, (460) 530 – 680 (– 910) µm long, septate. Rays (8 –) 11 – 16 (– 19)/mm, uniseriate, rarely with a small biseriate portion (Fig. 6).

■ CONCLUSION

Target capture appears promising even for very old samples of Melastomataceae with highly fragmented and low DNA concentration. Overall, the phylogenetic results previously obtained using Sanger-sequenced data are congruent with target capture data using hundreds of loci.

While numerous papers have been published in recent years to elucidate phylogenetic relationships among African Melastomateae, Malagasy and Asian Melastomateae have remained poorly sampled. Since these lineages are nested within African Melastomateae, resolving their generic relationships will provide a better understanding of the evolution of the Paleotropical Melastomateae. Additionally, extensive sampling of *Melastomastrum* is required to test the monophyly of the genus and determine if the morphologically unique Guinean species *M. porteresii* and *M. theifolium* var. *controversum* belong to this clade. Also, *Antherotoma densiflora* (Gilg) Jacq.-Fél which were once circumscribed in *Dissotis* is still unplaced and *A. irvingiana* (Hook.) Jacq.-Fél. which from suggested to be excluded from *Antherotoma* are still not sampled in this study, hence it would be nice to include them in future studies.

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Figure 1

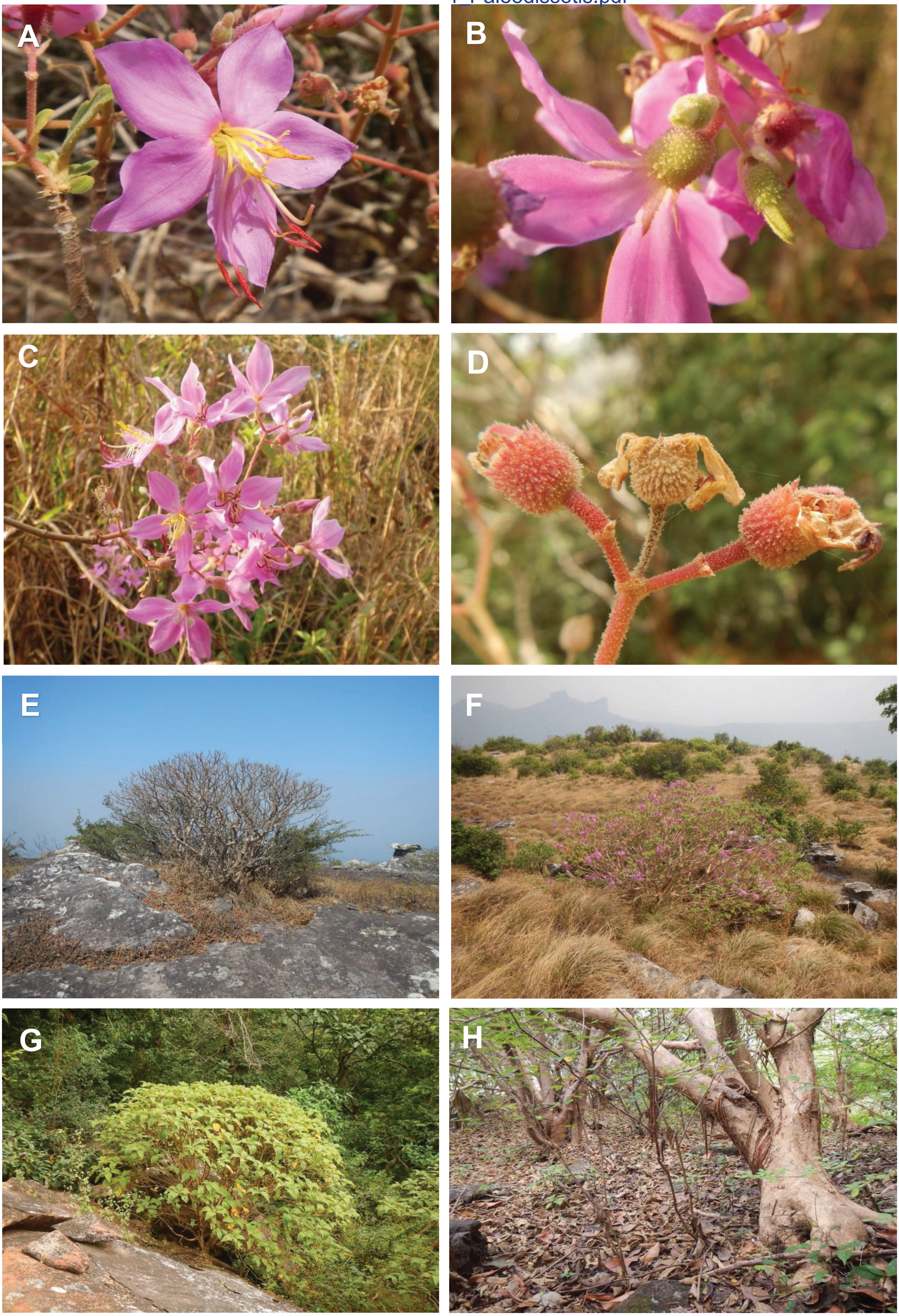


Figure 2

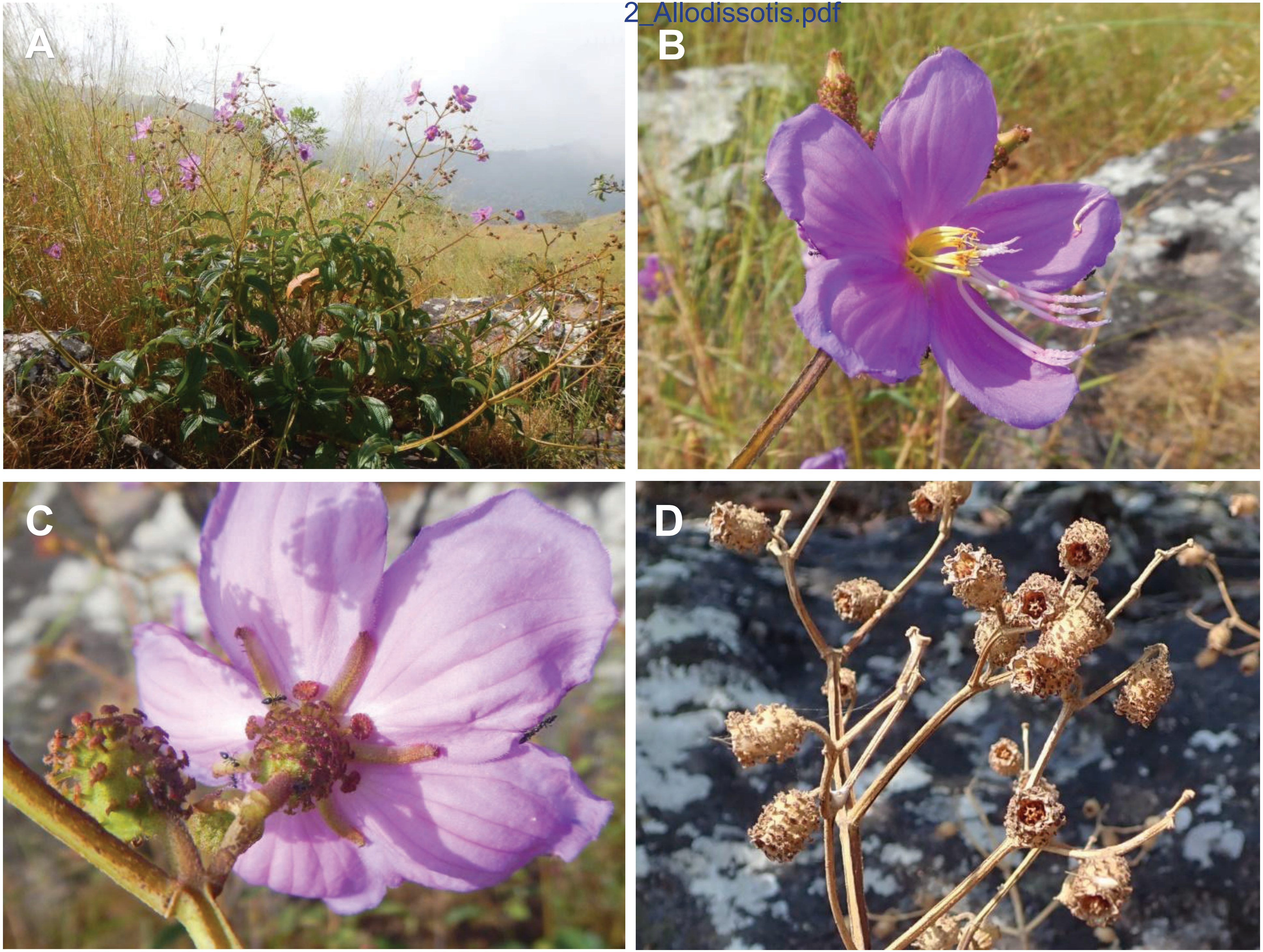
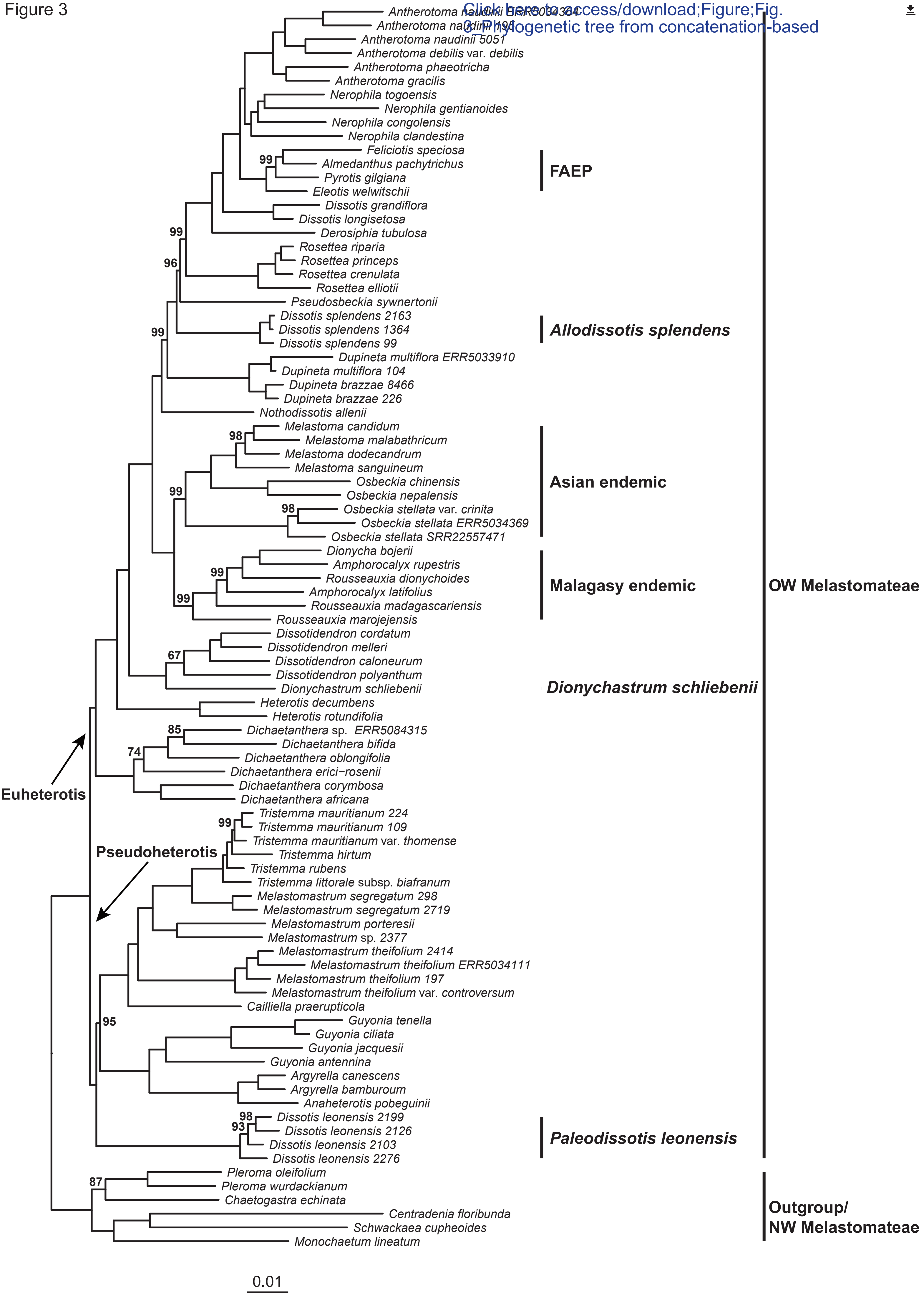


Figure 3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Nerophila togoensis
Nerophila gentianoides
Nerophila congolensis
Nerophila clandestina
Feliciotis speciosa
Almedanthus pachytrichus
Pyrotis gilgiana
Eleotis welwitschii
Dissotis grandiflora
Dissotis longisetosa
Derosiphia tubulosa
Rosettea riparia
Rosettea princeps
Rosettea crenulata
Rosettea elliotii
Pseudosbeckia sywnertonii
Dissotis splendens 2163
Dissotis splendens 1364
Dissotis splendens 99
Dupineta multiflora ERR5033910
Dupineta multiflora 104
Dupineta brazzae 8466
Dupineta brazzae 226
Nothodissotis allenii
Melastoma candidum
Melastoma malabathricum
Melastoma dodecandrum
Melastoma sanguineum
Osbeckia chinensis
Osbeckia nepalensis
Osbeckia stellata var. crinita
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Osbeckia stellata SRR22557471
Dionycha bojerii
Amphorocalyx rupestris
Rousseauxia dionychoides
Amphorocalyx latifolius
Rousseauxia madagascariensis
Rousseauxia marojejensis
Dissotidendron cordatum
Dissotidendron melleri
Dissotidendron caloneurum
Dissotidendron polyanthum
Dionychastrum schliebenii
Heterotis decumbens
Heterotis rotundifolia
Dichaetanthera sp. ERR5084315
Dichaetanthera bifida
Dichaetanthera oblongifolia
Dichaetanthera erici−rosenii
Dichaetanthera corymbosa
Dichaetanthera africana
Tristemma mauritianum 224
Tristemma mauritianum 109
Tristemma mauritianum var. thomense
Tristemma hirtum
Tristemma rubens
Tristemma littorale subsp. biafranum
Melastomastrum segregatum 298
Melastomastrum segregatum 2719
Melastomastrum porteresii
Melastomastrum sp. 2377
Melastomastrum theifolium 2414
Melastomastrum theifolium ERR5034111
Melastomastrum theifolium 197
Melastomastrum theifolium var. controversum
Cailliella praerupticola
Guyonia tenella
Guyonia ciliata
Guyonia jacquesii
Guyonia antennina
Argyrella canescens
Argyrella bamburoum
Anaheterotis pobeguinii
Dissotis leonensis 2199
Dissotis leonensis 2126
Dissotis leonensis 2103
Dissotis leonensis 2276
Pleroma oleifolium
Pleroma wurdackianum
Chaetogastra echinata
Centradenia floribunda
Schwackaea cupheoides
Monochaetum lineatum
99
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67
85
74
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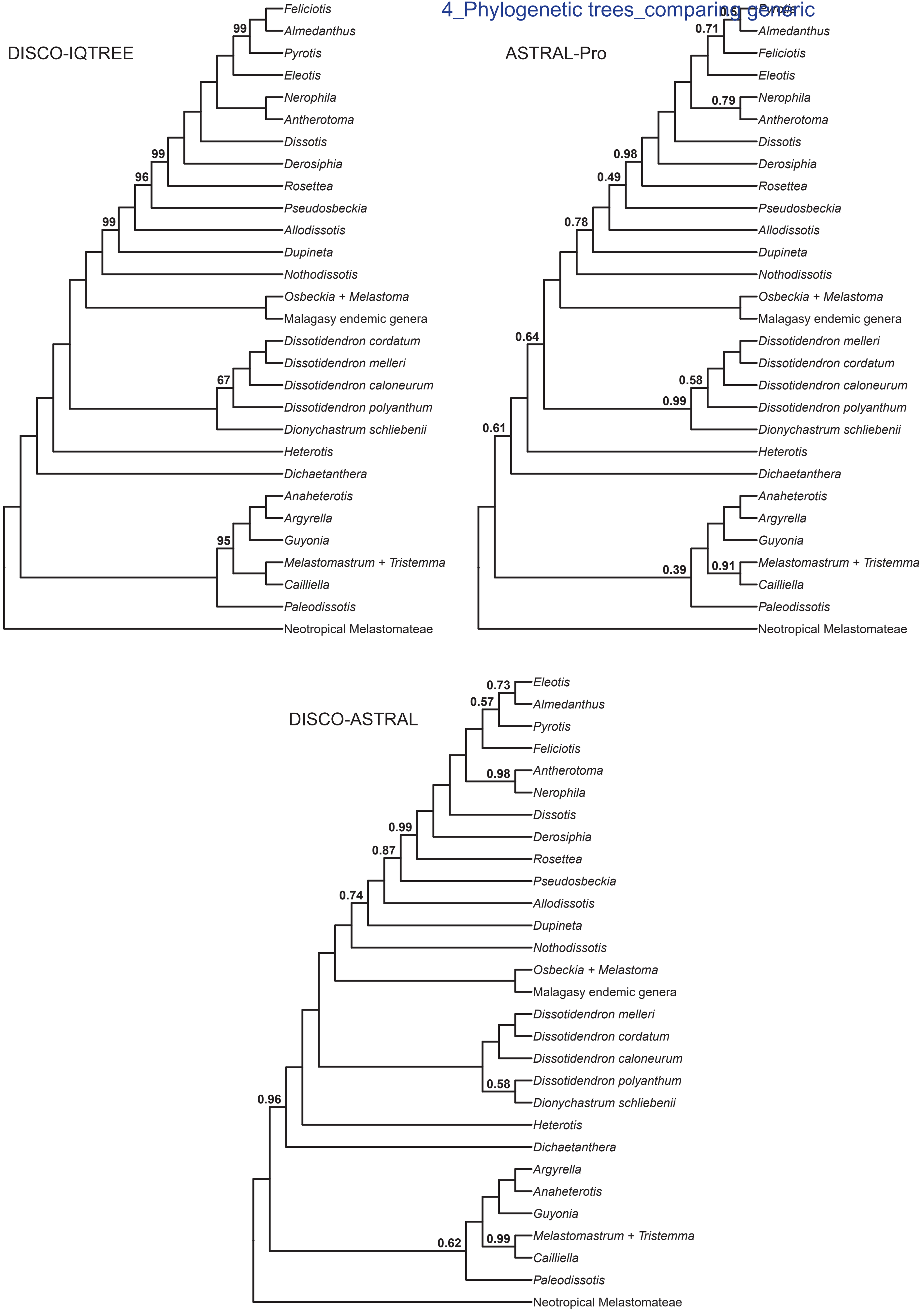
95
98
93
87
FAEP
Allodissotis splendens
Asian endemic
Malagasy endemic
Dionychastrum schliebenii
Paleodissotis leonensis
OW Melastomateae
Outgroup/
NW Melastomateae
Euheterotis
Pseudoheterotis
0.01

Figure 4


DISCO-IQTREE
Feliciotis
Almedanthus
Pyrotis
Eleotis
Nerophila
Antherotoma
Dissotis
Derosiphia
Rosettea
Pseudosbeckia
Allodissotis
Dupineta
Nothodissotis
Osbeckia + Melastoma
Malagasy endemic genera
Dissotidendron cordatum
Dissotidendron melleri
Dissotidendron caloneurum
Dissotidendron polyanthum
Dionychastrum schliebenii
Heterotis
Dichaetanthera
Anaheterotis
Argyrella
Guyonia
Melastomastrum + Tristemma
Cailliella
Paleodissotis
Neotropical Melastomateae
99
99
96
99
67
95
ASTRAL-Pro
Pyrotis
Almedanthus
Feliciotis
Eleotis
Nerophila
Antherotoma
Dissotis
Derosiphia
Rosettea
Pseudosbeckia
Allodissotis
Dupineta
Nothodissotis
Osbeckia + Melastoma
Malagasy endemic genera
Dissotidendron melleri
Dissotidendron cordatum
Dissotidendron caloneurum
Dissotidendron polyanthum
Dionychastrum schliebenii
Heterotis
Dichaetanthera
Anaheterotis
Argyrella
Guyonia
Melastomastrum + Tristemma
Cailliella
Paleodissotis
Neotropical Melastomateae
0.5
0.71
0.79
0.98
0.49
0.78
0.64
0.58
0.99
0.61
0.39
0.91
DISCO-ASTRAL
Eleotis
Almedanthus
Pyrotis
Feliciotis
Antherotoma
Nerophila
Dissotis
Derosiphia
Rosettea
Pseudosbeckia
Allodissotis
Dupineta
Nothodissotis
Osbeckia + Melastoma
Malagasy endemic genera
Dissotidendron melleri
Dissotidendron cordatum
Dissotidendron caloneurum
Dissotidendron polyanthum
Dionychastrum schliebenii
Heterotis
Dichaetanthera
Argyrella
Anaheterotis
Guyonia
Melastomastrum + Tristemma
Cailliella
Paleodissotis
Neotropical Melastomateae
0.73
0.57
0.98
0.99
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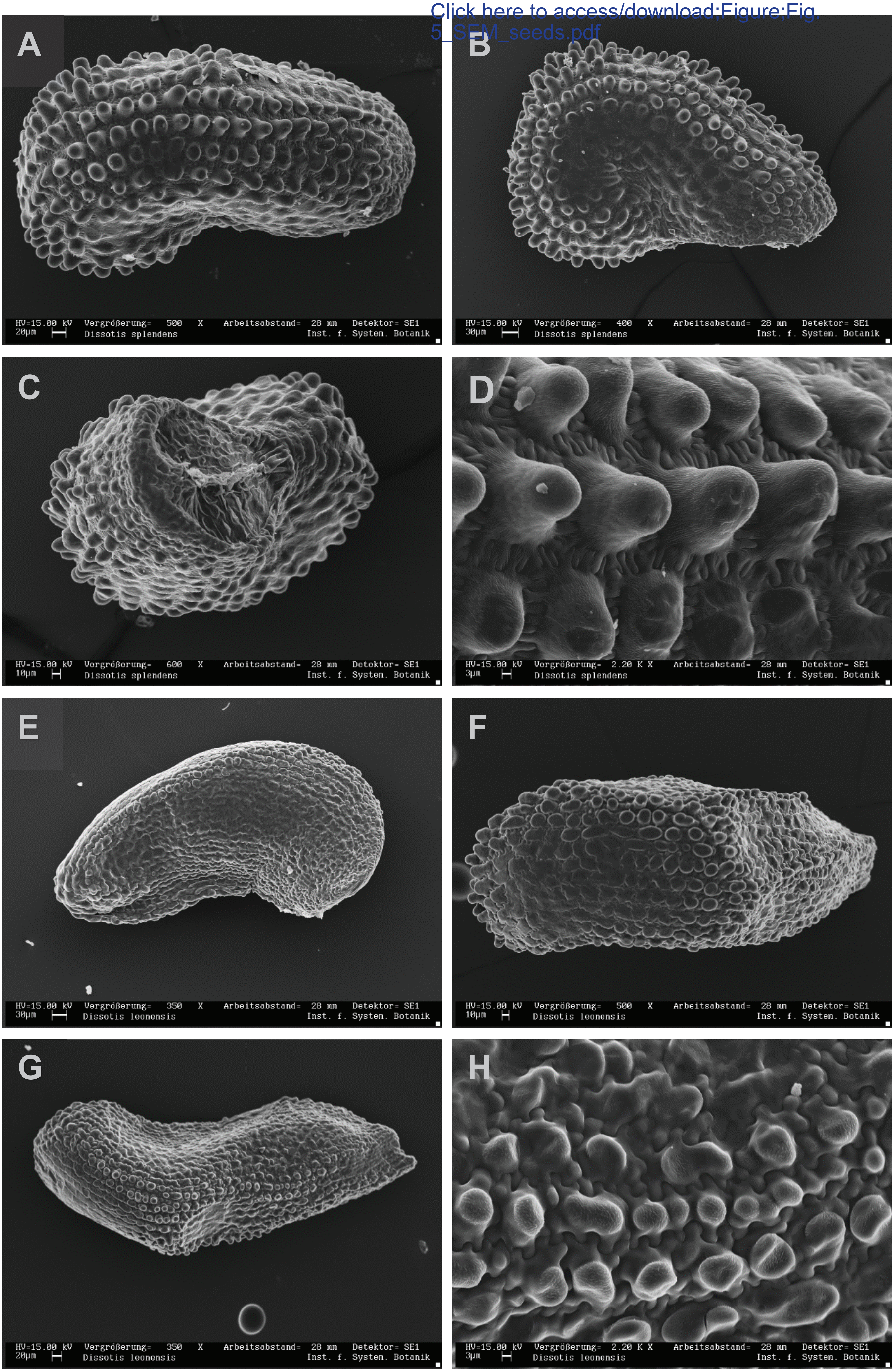
0.74
0.58
0.96
0.62
0.99

Figure 5


A
HV=15.00 kV Vergrößerung= 500 X Arbeitsabstand= 28 mm Detektor= SE1
20µm
Dissotis splendens
Inst. f. System. Botanik
B
HV=15.00 kV Vergrößerung= 400 X Arbeitsabstand= 28 mm Detektor= SE1
30µm
Dissotis splendens
Inst. f. System. Botanik
C
HV=15.00 kV Vergrößerung= 600 X Arbeitsabstand= 28 mm Detektor= SE1
10µm
Dissotis splendens
Inst. f. System. Botanik
D
HV=15.00 kV Vergrößerung= 2.20 K X Arbeitsabstand= 28 mm Detektor= SE1
3µm
Dissotis splendens
Inst. f. System. Botanik
E
HV=15.00 kV Vergrößerung= 350 X Arbeitsabstand= 28 mm Detektor= SE1
30µm
Dissotis leonensis
Inst. f. System. Botanik
F
HV=15.00 kV Vergrößerung= 500 X Arbeitsabstand= 28 mm Detektor= SE1
10µm
Dissotis leonensis
Inst. f. System. Botanik
G
HV=15.00 kV Vergrößerung= 350 X Arbeitsabstand= 28 mm Detektor= SE1
20µm
Dissotis leonensis
Inst. f. System. Botanik
H
HV=15.00 kV Vergrößerung= 2.20 K X Arbeitsabstand= 28 mm Detektor= SE1
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Dissotis leonensis
Inst. f. System. Botanik

Figure 6

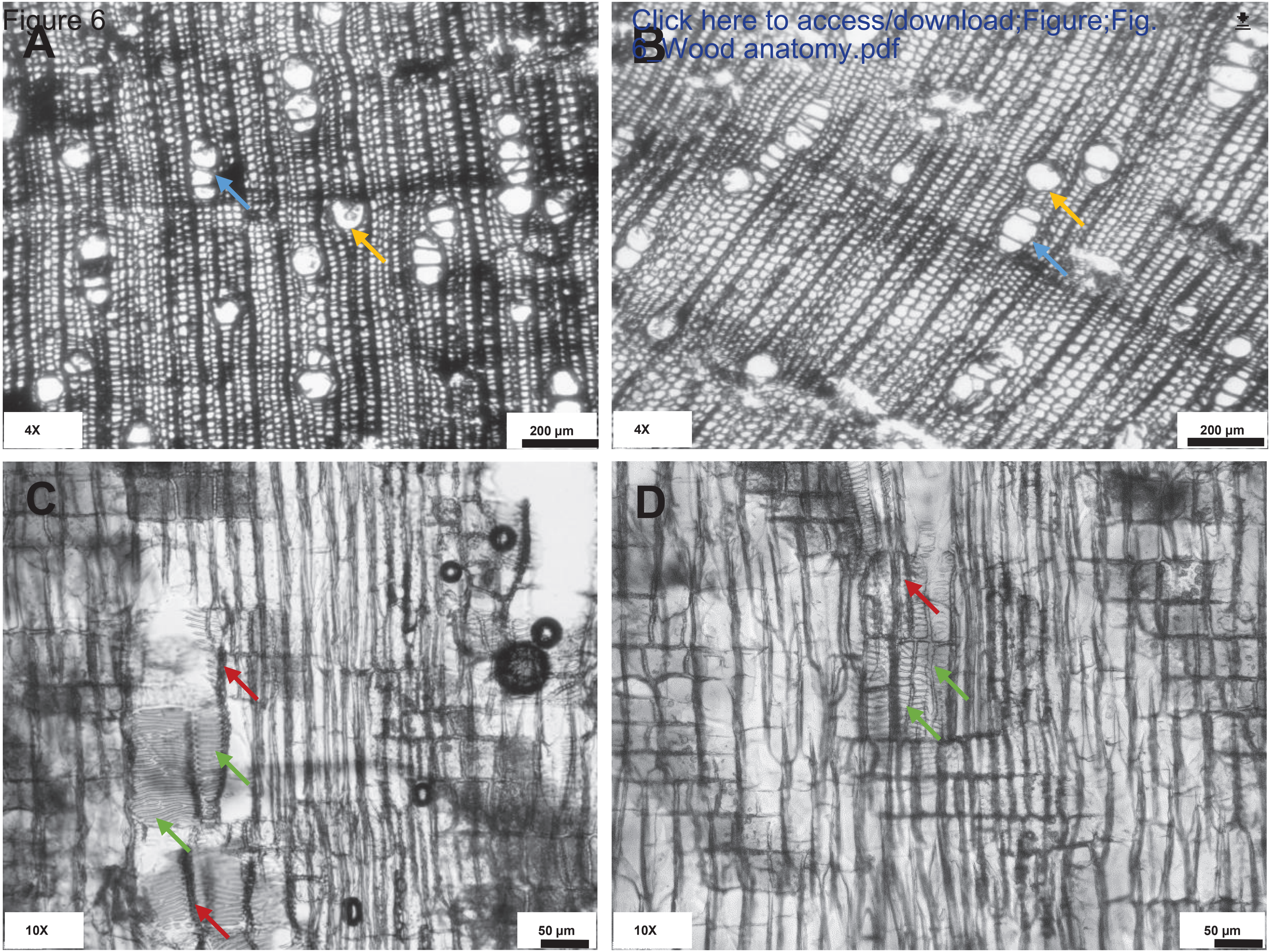
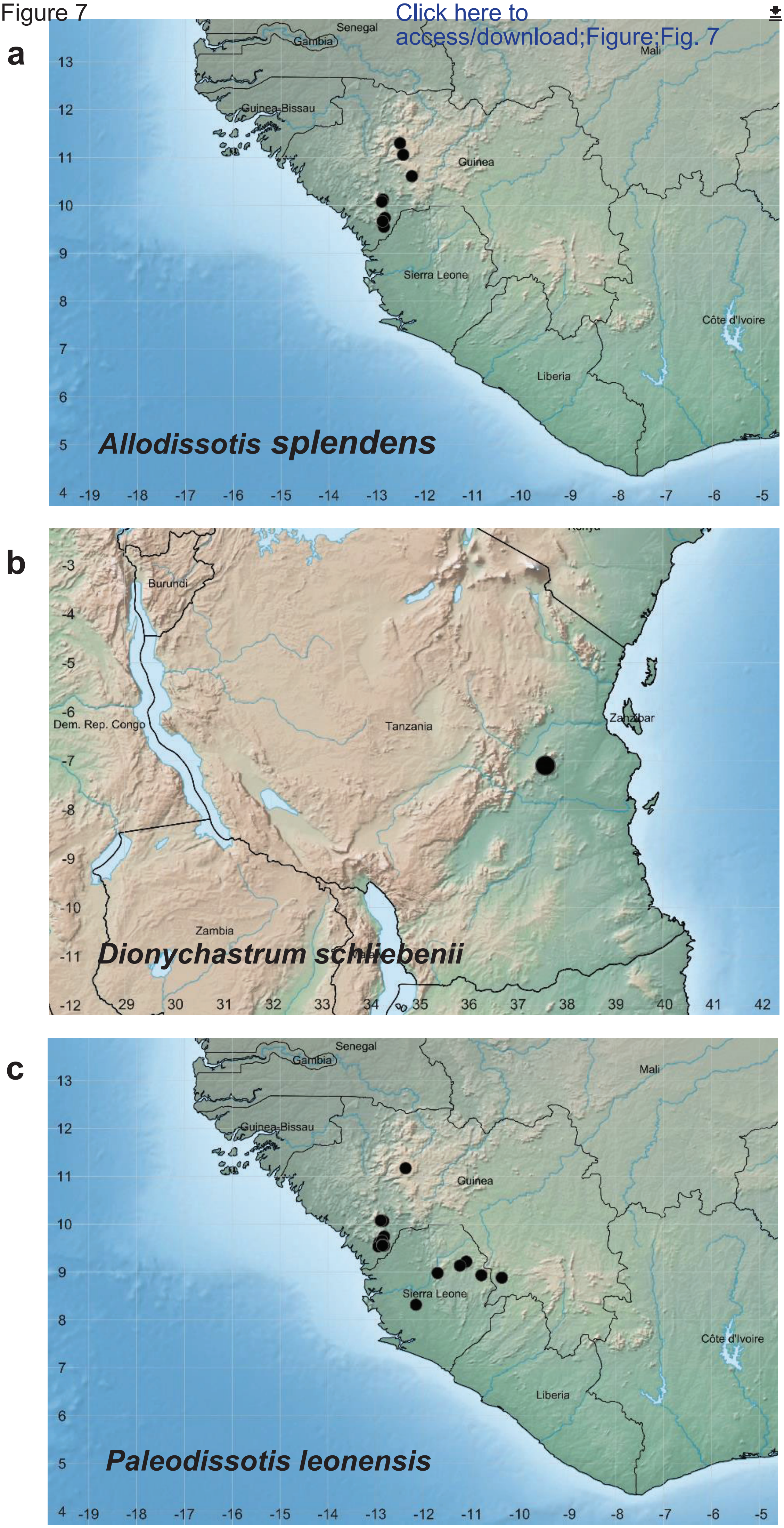


Figure 7


a
Senegal
Gambia
Mali
Guinea-Bissau
Guinea
Sierra Leone
Côte d'Ivoire
Liberia
Allodissotis splendens
13
12
11
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6
5
4
-19
-18
-17
-16
-15
-14
-13
-12
-11
-10
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-8
-7
-6
-5
b
Burundi
Dem. Rep. Congo
Tanzania
Zanzibar
Zambia
Kenya
Dionychastrum schliebenii
-3
-4
-5
-6
-7
-8
-9
-10
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41
42
c
Senegal
Gambia
Mali
Guinea-Bissau
Guinea
Sierra Leone
Côte d'Ivoire
Liberia
Paleodissotis leonensis
13
12
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-17
-16
-15
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-13
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Figure captions

Fig. 1. *Paleodissotis leonensis* (Hutch. & Dalziel) Ver.-Lib. & Burgt. A flower showing dimorphic stamens; B flower showing hypanthium; C inflorescence; D mature fruits. E leafless and sterile plant in high altitude grassland habitat; F flowering plant; G sterile plant with leaves; H stem. A, D from Burgt et al. 2103, 16 April 2017; B – C observation in Sula Mts, Sierra Leone, 14 March 2014; E – H observations on Kounounkan Plateau, Guinea, 1 Dec. 2017; 19 April 2017; 25 Nov. 2017; 26 Nov. 2017. Photos: Xander van der Burgt.

Fig. 2. *Allodissotis splendens* (A.Chev. & Jacq.-Fél.) Ver.-Lib. & Burgt. A plant in high altitude grassland habitat; B flower showing dimorphic stamens; C flower showing hypanthium with capitate appendages; D mature fruits. A – C from Burgt et al. 2163, 28 Nov. 2017; D from Burgt et al. 2254, 3 Feb. 2019. Photos: Xander van der Burgt.

Fig. 3. Phylogenetic tree inferred using the concatenation-based method (DISCO-IQTREE) showing relationships of African Melastomateae and the placement of *Allodissotis*, *Dionychastrum* and *Paleodissotis*. Boostrap support values below 100% are indicated on the branch.

Fig. 4. Phylogenetic trees inferred using the coalescent-based methods (DISCO-ASTRAL and ASTRAL-Pro) and concatenation-based method (DISCO-IQTREE) comparing generic relationships among African Melastomateae. In the DISCO-IQTREE phylogeny, bootstrap support values below 100% are shown on the branch. In the DISCO-ASTRAL and ASTRAL-Pro phylogenies, local posterior probabilities below 1 are indicated on the branch.

Fig. 5. Scanning electron micrographs. A-D, Seeds of *Allodissotis splendens* (Burgt 2254); E-H, seeds of *Paleodissotis leonensis* (Burgt 2103).

Fig. 6. Wood anatomical sections of *Paleodissotis leonensis*. A-B, Radial sections; C-D, Tangential sections. Orange arrows indicate solitary vessels, light blue arrows indicate multiple vessels, green arrows show alternate inter-vessel pits, and red arrows show rays.

Fig. 7. Distribution of a. *Allodissotis splendens* **b.** *Dionychastrum schliebenii* and **c.** *Paleodissotis leonensis*

CHAPTER 5

COMPREHENSIVE AND SUSTAINABLE UTILIZATION OF GENOMIC RESOURCES: INTEGRATING TARGET ENRICHMENT, GENOME SKIMMING, RNA-SEQ, AND DEEP GENOME SKIMMING FOR IMPROVED PHYLOGENETIC RESOLUTION IN SONERILEAE (MELASTOMATACEAE)

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Manuscript

Comprehensive and Sustainable Utilization of Genomic Resources: Integrating Target Enrichment, Genome Skimming, RNA-Seq, and Deep Genome Skimming for Improved Phylogenetic Resolution in Sonerileae (Melastomataceae)

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Abstract

The advent of new next-generation sequencing (NGS) methods has revolutionized phylogenetics, yet challenges remain in effectively utilizing data from a wide range of sources. In this study, we combine target enrichment, genome skimming, RNA-Seq, and deep genome skimming (DGS) data to reconstruct the phylogenetic relationships within Sonerileae, the second-largest tribe in the Melastomataceae. We sampled 178 accessions representing 41 of the 46 genera in Sonerileae, including newly sequenced Hyb-Seq and DGS data along with publicly available NGS data. A newly developed reference comprising 5,626 loci was employed to integrate data from different sources. Our analyses provide a well-supported, near-comprehensive phylogeny for the tribe, outperforming previous and current studies that used only the probe set as reference. We found evidence of rapid diversification within the Asian Sonerileae, which is likely driven by a whole-genome duplication that occurred before the divergence of the two major clades within the Asian lineage. This study provides an effective and sustainable approach to integrating genomic data from multiple sequencing strategies for phylogenetic analysis and contributes a more robust phylogeny and novel insights into the evolutionary history of Sonerileae.

Keywords

Anomaly zone; deep genome skimming; Melastomataceae; phylogenetics; polytomy; rapid diversification; RNA-Seq; Sonerileae; target enrichment; whole genome duplication.

Introduction

The increasing availability of next-generation sequencing (NGS) data has significantly changed the field of phylogenetics in the past 10 years (Guo et al., 2023). Due to varying research objectives, material quality, and cost considerations, a variety of sequencing strategies have been established for phylogenetic studies.

Target enrichment, or target capture, is currently among the most popular approaches. It selects targeted genomic regions before sequencing, providing a cost-effective approach to obtain hundreds to thousands of loci for phylogenomic studies (Mandel et al., 2014). This method has proven effective across various taxonomic levels, from population (Villaverde et al., 2018; Jiménez-Mena et al., 2022) to higher taxonomic ranks, such as Asterales (Benítez-Villaseñor et al., 2023). A universal probe set targeting 353 nuclear loci across angiosperms (Angiosperms353) has been successfully used to resolve numerous flowering plant lineages, including species sampled from herbarium specimens over 200 years old (Zuntini et al., 2024).

Originally, genome skimming was developed as a method of low-coverage sequencing to capture high-copy genomic regions (Straub et al., 2012). It is widely applied in organellar genome sequencing due to the high copy numbers of plastid and mitochondrial genomes (Twyford and Ness, 2017; Trevisan et al., 2019). Additionally, it has been suggested that low-copy nuclear loci can be identified from skimming data (Straub et al., 2012; Blischak et al., 2014; Pezzini et al., 2023; Pouchon and Boluda, 2023).

Hyb-Seq was initially proposed to sequence targeted genomic regions using on-target reads and to recover high-copy genomic regions through off-target reads from the enriched library (Weitemier et al., 2014), which makes it essentially interchangeable with target enrichment. However, the term's meaning has evolved in some cases, where it refers to an approach that involves sequencing both enriched (target enrichment) and unenriched (genome skimming) libraries (Villaverde et al., 2018; Dodsworth et al., 2019) to improve recovery of the high-copy regions of the genome. In this paper, we adopt the latter definition.

RNA-Seq, or transcriptome sequencing, was originally developed for transcriptome profiling (Wang et al., 2009), but it has since demonstrated great utility in phylogenetic studies (Oakley et al., 2012; Wickett et al., 2014; Leebens-Mack et al., 2019). When orthologs are accurately identified, the phylogenetic results are comparable to those obtained from whole genome sequencing (Cheon et al., 2020). The challenge with RNA-Seq is that total RNA extraction requires fresh tissue or flash-frozen tissue stored at -80°C (Chomczynski and Sacchi, 2006). Although a few studies (Chen et al., 2022; He et al., 2022; Ruiz-Vargas et al., 2024) have successfully extracted RNA from silica-dried plant tissues, this approach has not been widely tested across different groups and remains impractical for herbarium specimens.

Deep genome skimming (DGS) builds on standard genome skimming by employing deeper sequencing depth, with a minimum of 10× for optimal high-quality, single-copy nuclear gene assembly (Liu et al., 2021). This allows for the assembly of numerous single nuclear genes, as well as complete plastomes and mitochondrial genomes, without the need for target enrichment. This approach has recently been applied to various lineages of organisms (Liu et al., 2021; Yang et al., 2023; Hu et al., 2024; Quattrini et al., 2024). It has proven to be particularly effective for groups with relatively small genomes (e.g., ~500 Mb in Liu et al. 2021; ~900 Mb in Yang et al. 2023; ~500-750 Mb in Quattrini et al. 2024) but can also be applied to relatively large genomes as long as a sufficient number of reads are generated (e.g., ~3 Gb in Hu et al. 2024).

Despite the potential to significantly improve data utilization and the general importance of sustainable data use, no study has yet explored the optimal approach to integrate these different types of data. A common strategy is to recover loci targeted for enrichment from RNA-Seq and DGS data (Bossert et al., 2019; Wang et al., 2024). However, as more data is generated by different labs using various sequencing strategies, it becomes increasingly necessary to identify an effective approach for integrating all NGS data sets available for a given group of organisms.

The Melastomataceae are one of the ten largest families of flowering plants, comprising approximately 5,858 species across 173 genera in 21 tribes (Ulloa Ulloa et al., 2022). The Sonerileae are the second-largest tribe within Melastomataceae, containing 46 genera and around 1,080 species distributed throughout the tropics (Lin et al., 2022; Liu et al., 2022; Veranso-Libalah et al., 2023; Liu et al., 2024b; Quakenbush et al., 2024). The generic delimitations within Sonerileae have long been unresolved because many of the morphological traits used are homoplasious, and sampling for molecular phylogenetic studies has been limited (Zhou et al., 2019a; Zhou et al., 2019b). A recent phylogenomic study (Zhou et al., 2022) on the Asian Sonerileae, which sampled most recognized Asian genera and reconstructed their phylogeny using DGS data, identified 34 lineages within the Asian Sonerileae. Based on the results of this study, the genus *Perilimnastes* was reinstated (Liu et al., 2024b), and *Nephoanthus* was newly described (Lin et al., 2022). Another phylogenomic study focused on the systematics of fleshy-fruited Sonerileae, using mostly target enrichment data, revealed that the fleshy-fruited Sonerileae are polyphyletic. Consequently, *Pachycentria* and *Plethiandra* were synonymized under *Medinilla* (Quakenbush et al., 2024). However, African and Neotropical lineages remain under-represented in both studies. A separate phylogenomic study (Maurin et al., 2021) using Angiosperms353 on the Myrtales included some African and Neotropical Sonerilean genera, but the sampling was limited because the study focused on familial relationships within the order. While the Kew Tree of Life Explorer (Baker et al., 2021) is gradually incorporating more species, the sampling for Sonerileae remains limited. Consequently, our understanding of the relationships among African, Asian, and Neotropical Sonerileae is still primarily based on a Sanger sequence-based phylogeny (Veranso-Libalah et al., 2023), where Neotropical genera and the African endemic *Benna* are identified as successfully sister to the remainder of the tribe, which is divided into an African-Malagasy endemic clade and a predominantly Asian clade. Based on this study, the genus *Mendelia* was described, and *Bourdaria* was reinstated.

A well-represented and well-supported phylogeny is crucial for understanding the relationships among the African, Asian, and Neotropical Sonerileae. In this study, we developed a new reference comprising 5,626 loci for Melastomataceae based on genomic and transcriptomic data. Using this inclusive reference, we reconstructed a near-comprehensive phylogeny for the tribe by integrating newly generated Hyb-Seq and DGS data, along with all available NGS data, including RNA-Seq, DGS, target enrichment from different bait sets, Hyb-Seq, and annotated genomes. Based on the resulting phylogeny, we also explored gene tree discordances and detected potential whole-genome duplication (WGD) events.

Materials and Methods

Sampling and sequencing

We sampled 178 accessions, including 173 from Sonerileae, representing 41 of the 46 genera. This includes four of the six Neotropical genera, all nine Afrotropical endemic genera, 28 of the 31 Asian endemic genera, and the only Afrotropical-Asian disjunct genus within the tribe, *Medinilla*, for which we sampled all alliances recognized by Quakenbush et al. (2024). Except for *Phyllagathis scortechinii*, all other 33 Asian lineages identified by Zhou et al. (2022) supported by both the single-copy ortholog (SCO) and genomic SNP data sets were included. Additionally, we selected four *Melastoma* and one *Osbeckia* species from the tribe Melastomateae as outgroups. To obtain a near-complete genus-wide phylogeny, we incorporated a variety of data types: among the 178 accessions, 72 were newly sequenced, 15 were RNA-Seq data accessed from the NCBI Sequence Read Archive (SRA) and China National GeneBank (CNGB), two were annotated genomes, 19 were Angiosperms353 target enrichment data accessed from the European Nucleotide Archive (ENA), and 70 were DGS data accessed from the SRA. Details on the vouchers and accession numbers are provided in Supplementary Table S1.

Of the 72 newly sequenced samples, 71 were Hyb-Seq data. DNA extraction, library preparation, target enrichment, and next-generation sequencing were performed by Quakenbush et al. (2024). The Melastomataceae probes (Jantzen et al., 2020) were used to capture 384 loci in the target enrichment, while for genome skimming, 1 Gb of data was generated. One sample (*Mendelia mollis*) was DGS data. Library preparation and sequencing for this sample were performed at Novogene Europe (Cambridge, UK). Paired-end reads were generated on the Illumina NovaSeq X Plus system, with a requested data yield of 6 GB.

Nuclear reference construction

To effectively integrate the various data in this study, a new nuclear reference sequence file was developed using 16 RNA-Seq samples and two annotated genomes: *Melastoma candidum* (Zhong et al., 2023) and *Barthea barthei* (Huang et al., 2024). The 16 RNA-Seq samples include five species from Melastomateae, twelve species from Sonerileae, and one species from Miconieae. The pipeline described here largely followed Morales-Briones et al. (2020). Raw reads of the RNA-Seq data were processed to correct random sequencing errors using Rcorrector v1.0.6 (Song and Florea, 2015), remove adapters and low-quality sequences with Trimmomatic v0.39 (Bolger et al., 2014), and filter organelle reads using Bowtie2 v 2.4.5 (Langmead and Salzberg, 2012). De novo transcriptome assembly was performed using Trinity v2.13.2 (Grabherr et al., 2011), followed by quality assessment and filtering of low-quality transcripts with Transrate v1.0.3 (Smith-Unna et al., 2016) and removal of chimeric transcripts following Yang and Smith (Yang and Smith, 2013) with a blast-based method. Filtered transcripts were clustered into putative genes using Corset v1.09 (Davidson and Oshlack, 2014) with the longest transcript kept. Identification of coding sequences (CDS) was performed using TransDecoder v5.3.0 (Haas et al., 2013). Before homology inference, transcript redundancy was further reduced using CD-HIT v4.8.1 (Fu et al., 2012). Homology was inferred by first performing all-by-all BLASTN v2.10.0+ (Camacho et al., 2009) for the 16 transcriptomes and two annotated genomes, and then using MCL (van Dongen and Abreu-Goodger, 2012) to group transcripts into clusters, with the hit fraction cutoff and inflation values set as 0.4 and 1.4, respectively. The resulting 12,497 clusters were aligned using MAFFT v7.525 with the “localpair” algorithm (Katoh and Standley, 2013). The aligned clusters were trimmed using Phyutility v.2.7.1 (Smith and Dunn, 2008) to discard columns with more than 90% missing data. Single homologous gene trees were inferred using IQ-Tree v2.3.5 (Minh et al., 2020), with ModelFinder (Kalyaanamoorthy et al., 2017) employed to select the best substitution model. The raw single trees were trimmed by masking monophyletic and paraphyletic tips that belong to the same species, followed by pruning spurious long branches with TreeShrink v1.3.9 (Mai and Mirarab, 2018). The MO (monophyletic outgroup) method (Yang and Smith, 2014) was employed for orthology inference. Gene trees without taxon duplication were retained as one-to-one orthologs if they had monophyletic outgroups. For trees with taxon duplication, only those with monophyletic, non-repetitive outgroups were rerooted, and the orthologous subtree with the highest taxon number was retained. The resulting orthologs with less than 12 taxa were discarded. We also filtered gene trees if the Sonerileae or Melastomateae taxa do not form a monophyletic clade. The corresponding fasta files of the final gene trees were written, combined, and checked with Hybpiper (Johnson et al., 2016) "check_targetfile" and trimmed with "fix_targetfile" to filter sequences with low-complexity regions. To assess the overlap among the newly developed reference, the Melastomataceae probe set, and the Angiosperms353 probe set (specifically a tailored mega353 file for Myrtales, see McLay et al., 2021 and Chen et al. 2023), we built a local BLAST database from the new reference using "makeblastdb" (Camacho et al., 2009) and searched the sequences against the other two references using "blastn" with default settings.

Reads processing, assembly, and reference loci recovery

Reads processing, assembly, and reference loci recovery were conducted using Captus v.1.0.1 (Ortiz et al., 2023). Since the sequences from the RNA-Seq samples and annotated genomes used to construct the 5,626-loci reference were already available, these data were excluded from this step. Target enrichment and skimming data from the Hyb-Seq generated in this study were first merged. Raw reads from the DGS, Angiosperms353 target enrichment, and Hyb-Seq data were trimmed with BBDuk from BBTools (Bushnell, 2022), following the default settings in Captus. The cleaned reads were then *de novo* assembled into contigs using MEGAHIT (Li et al., 2015) with default parameters. Reference loci were recovered from the assemblies using Scipio (Hatje et al., 2011) with the minimum percentage of identity ("--nuc_min_identity") and coverage ("--nuc_min_coverage") to the reference set as 80 and 50, respectively. The newly constructed 5,626-loci reference was used for loci recovery.

To compare the performance of our 5,626-loci reference with the Melastomataceae probe set, which contains 396 loci (Jantzen et al., 2020; Dagallier and Michelangeli, 2024), we also recovered these 396 loci from the 178 assemblies, including the RNA-Seq samples.

Orthology inference

The recovered reference loci were retrieved using Captus for further analysis. For the 5,626-loci data set, reference sequences from Sonerileae and Melastomateae were added to each cluster. This step was not necessary for the 396-loci data set. Each cluster was aligned and trimmed using MAFFT and Phyutility, following the same procedures as in the nuclear reference construction. Sequences shorter than 100 bp or with more than 90% missing sites were discarded. Single gene trees were inferred using IQ-Tree, with the GTRGAMMA substitution model and branch support assessed via 1,000 ultrafast bootstrap replicates.

Monophyletic and paraphyletic tips were pruned, spurious long branches were trimmed, and orthology inference using the MO method followed the same approach as in nuclear reference construction. The five sampled Melastomateae species were set as outgroups, and only trees with at least 18 tips were retained. We calculated the occupancy of each taxon in the final orthologs for the 5,626-loci data set.

Phylogenetic analyses

The orthologs were realigned, trimmed, and gene trees were inferred using the same methodology as in the orthology inference. A species tree (ST1) was then reconstructed using ASTRAL-IV v1.19.4.5 (Zhang et al., 2018; Zhang and Mirarab, 2022; Tabatabaee et al., 2023), with *Osbeckia stellata* designated as the outgroup to improve the accuracy of branch length estimation. Additionally, an alternative species tree (ST2) was inferred, excluding *Boyania ayangannae* and *Tryssophyton merumense*, which were sequenced in the Angiosperms353 project and implausibly placed in the initial tree (discussed in further detail in Results). Since ASTRAL-IV computes branch lengths in substitution-per-site units, a third species tree (ST3), also excluding these two taxa, was inferred using ASTRAL v5.7.8 (Zhang et al., 2018), which calculates branch lengths in coalescent units. The orthologs identified from the 396-loci data set were also realigned, trimmed, and used for species tree (ST4) inference with ASTRAL-IV. We also inferred a species tree (ST5) for the 16 RNA-Seq samples and two annotated genomes used for reference construction using the 5,626 orthologs identified using MO. The phylogenetic results were visualized using *ggtree* v3.10.0 (Yu et al., 2017) in R v4.3.2 (R Core Team, 2024).

Assessing gene tree conflicts

The quartet-based method Quartet Sampling (QS) (Pease et al., 2018) was used to assess the level of discordance among gene trees. For a given phylogeny, any internal branch can divide the tree into four sets of taxa. QS repeatedly and randomly selects one taxon from each set and evaluates the likelihoods of all three possible topologies: one that is concordant and two that are discordant with the given phylogeny, based on the given sequence data. The species tree ST2 and an alignment generated by concatenating gene alignments used for gene tree inference with AMAS (Borowiec, 2016) were used as input. For each internal branch, 6,000 replicates were performed, and the "--genetrees" option was used to enable partitioned analysis. Likelihood evaluations were carried out using RaxML (Stamatakis, 2014). Quartet concordance (QC), Quartet Differential (QD), and Quartet Informativeness (QI) scores were quantified. The QS results were visualized using an R script developed by Liu et al. (2024a).

Polytomy test and anomaly zone detection

Due to the presence of many short branches in the species tree, a polytomy test was carried out using ASTRAL v5.7.8 (-t 10) following Sayyari and Mirarab (2018). This test evaluates the null hypothesis that the branch has zero length and, therefore, should be replaced with a polytomy. The polytomy test was conducted using the species tree ST2 and the corresponding gene trees as inputs.

Anomaly zones occur when the most frequently observed gene tree topology is discordant with the species tree, which often arises when branches in the species tree are very short (Degnan and Rosenberg, 2006). Following Linkem et al. (2016), the boundary of the anomaly zone, denoted as $\alpha(x)$, is calculated. If the length of the descendant internal branch is shorter than $\alpha(x)$, the parent-child internode pairs fall within the anomaly zone. The species tree ST3 was used as input.

Mapping gene duplications

To detect and place potential WGD events in Sonerileae, we used the 12,497 homologous gene trees inferred during the development of the nuclear reference, following the same procedures as Yang et al. (2018). First, orthogroups were extracted from these gene trees, using *Miconia bicolor* as the outgroup and requiring the inclusion of at least 8 of the 17 ingroup taxa. Next, we mapped gene duplication events onto the rooted species tree ST5. We employed two alternative filtering approaches. The first filter retained orthogroups based on the average bootstrap support across their branches, keeping only those with an average bootstrap value of at least 75%. The second filtering approach identified the most recent common ancestor (MRCA) of the taxa within a given gene tree node. For gene duplication events to be considered, the sister clade in the gene tree had to be a subset of the corresponding sister clade in the species tree. Additionally, we analyzed 5,626 homologous gene trees inferred from the orthology inference for the 5,626-loci data set. Orthogroups were extracted from these gene trees, using the five Melastomateae species as outgroups and requiring a minimum inclusion of 88 of the 171 Sonerileae species. These orthogroups were then mapped onto the rooted species tree ST2. For this data set, we applied only the bootstrap filtering approach due to the computational burden. The resulting trees with the proportions of gene duplications indicated at each node were visualized using ggtree.

Results

New reference

The newly developed reference includes 5,626 loci represented by 76,834 sequences. The length of each locus ranges from 300 to 11,127 bp, with an average of 1,419 bp and a median of 1,275 bp. According to the BLAST results, 176 of these loci are putatively the same as those in the Angiosperms353 loci, and 221 are putatively the same as those in the Melastomataceae probe set. For details of the matching loci, see Supplementary Table S2.

Orthology inference

Both the newly developed 5,626-loci reference and the Melastomataceae probe set were used for phylogenetic analysis. We obtained 5,606 orthologs from the 5,626-loci data set, while 191 orthologs were retrieved from the 396-loci data set. We calculated the frequency of taxa in the final sets of orthologs. The representation across different sequencing strategies for the 5,626-loci data set was as follows (Supplementary Table S3; Fig. 1): Annotated genome samples had 2,350 to 5,461 loci represented (average 3,906); RNA-Seq samples had 1,543 to 5,118 loci (average 2,633, median 1,917); Hyb-Seq samples had 45 to 3,884 loci (average 2,461, median 2,873); Angiosperms353 samples had 4 to 1,159 loci (average 434, median 306); and DGS samples had 932 to 4,212 loci (average 3,170, median 3,358). The representation across different sequencing strategies for the 396-loci data set is listed in Supplementary Table S4 (see also Supplementary Fig. S1).

Phylogenetic analyses

The species tree ST1 (Supplementary Fig. S2), which includes two samples representing the two Neotropical species, *Boyania kenwurdackii* and *Tryssophyton merumense*, sequenced using the Angiosperms353 probe set, is topologically almost identical to species tree ST2 (Fig. 2), which excludes these two samples, except for their placements. In ST1, they were placed within the Asian clade, which contradicts previous studies (Baker et al., 2021; Veranso-Libalah et al., 2023), whereas other samples of these species were placed as part of a grade with other Neotropical species. Interestingly, even studies using the same data (Baker et al., 2021; Maurin et al., 2021) showed conflicting placements: Maurin et al. (2021) positioned them as sister to the Asian Sonerileae, while Baker et al. (2021) grouped them within the Asian clade. To clarify this, the same accession of *B. kenwurdackii* (*Michelangeli 2486*) was re-sequenced using the Melastomataceae probe set and was found to form a grade with other Neotropical species and the African endemic *Benna*, consistent with earlier phylogenies. This suggests that the publicly available data (accession numbers ERR5101684 for *B. kenwurdackii* and ERR5034396 for *T. merumense*) might have data management issues, affecting previous results. Therefore, we decided to exclude these two samples from other analyses in this paper.

The species tree ST2 inferred from the 5,626-loci data set is well-resolved with most nodes fully supported (LPP = 1) (Fig. 2) The Neotropical taxa (*Opisthocentra*, *Boyania colombiana*, *Boyania kenwurdackii*, *Phainantha*) are successive sisters to the rest of the tribe, followed by the African endemic *Benna*, and then *Kendrickia* plus the Afrotropical endemic clade. After these, the tree reveals a primarily Asian clade. Within the Afrotropical clade, *Gravesia* is sister to all other genera, followed by a grade composed of *Bourdaria*, *Dicellandra*, *Calvoa*, *Mendelia*, and *Preussiella*. *Amphiblemma* is sister to *Cincinnobotrys* (Fig. 2).

Within the primarily Asian clade, *Poikilogyne* is sister to the remaining taxa, where all 33 sampled lineages and nine clades (Clade A-I) identified by Zhou et al. (2022) were recovered. The remaining taxa form two major clades. The first corresponds to Clade C, which includes *Medinilla*, *Tigridiopalma*, and *Nephoanthus* (formerly the *Phyllagathis prostrata* clade). The second major clade contains the remaining genera, starting with a lineage largely corresponding to Clade A, now incorporating *Catanthera*. This clade includes *Heteroblemma*, *Catanthera*, the *Phyllagathis* (thyrsoid) clade, the *Phyllagathis* (pentamerous) clade, and the *Driessenia* (isomorphic) clade. The next branching clade is Clade B, comprising *Tashiroea*, *Poilannammia*, *Scorpiothyrsus*, and *Driessenia axantha*. Following this is *Sonerila*, and then Clade D, which contains *Sarcopyramis* and *Barthea*. Next is a clade that includes Clade E (comprising *Anerincleistus*, *Phyllagathis griffithii*-*Oxyspora bullata*, and *Phyllagathis tuberculata*-*P. hispida*), *Oxyspora paniculata*, *Phyllagathis rotundifolia*, and Clade F (which includes *Aschistanthera*, *Styrophyton*, and the *Oxyspora* (Bornean) clade). This is followed by *Perilimnastes* (formerly the *Phyllagathis* (raphides) clade), then Clade G (consisting of *Sporoxeia*, *Phyllagathis cavaleriei*, *Cyphotheca*, and *Plagiopetalum*), then *Fordiophyton*, and finally Clade I (which includes *Bredia*, *Blastus*, and Clade H, containing *Kerriothyrsus*, *Phyllagathis erecta*, and *Fordiophyton breviscapum*).

The species tree ST4 (Supplementary Fig. S3) inferred from the 396-loci data set receives less support (LPP < 0.7) for many nodes but is topologically similar to ST2, with some conflicting relationships. The first branching clade is also *Opisthocentra*, but it is followed by a clade comprising *Boyania colombiana* and *Phainantha*, then *Benna*, *Boyania kenwurdackii*, and *Poikilogyne*. Within the Afrotropical clade, relationships are mostly identical to ST2, except one species of *Gravesia* is placed elsewhere, as sister to the Asian Clade C. Within the primarily Asian clade, *Sonerila* is sister to the rest instead of *Poikilogyne*, and *Sonerila* is resolved as paraphyletic, with one species as sister to Clade B. Following this, Clade C diverges rather than belonging to the two major clades. The first major clade includes both Clades B and C. The second major clade diverges starting from Clade D, followed sequentially by Clades E, F, then *Perilimnastes*, *Fordiophyton*, Clade G, and finally Clade I. Notably, the Bornean *Oxyspora* species are not resolved as monophyletic. Additionally, some branches of ST4 are notably long, including the Afrotropical *Medinilla* clade, *Catanthera*, *Calvoa*, and *Oxyspora* species sequenced using the Angiosperms353 probe set. These clades generally include taxa with very low sequence recovery.

The only difference between species trees ST3 and ST2 is that the branch length of ST3 is measured in coalescent units. Species tree ST5 (Supplementary Fig. S4), inferred using transcriptomic and genomic data, is topologically consistent with ST2.

Gene tree conflicts

The QS analysis revealed abundant conflicts among gene trees, with branches showing low local posterior probabilities (LPP) often exhibiting high discordance (Fig. 2; Supplementary Fig. S5). In the backbone, notable areas of low support and high discordance include the lineages leading to *Boyania kenwurdackii* (LPP = 0.41, QC/QD/QI = 0.14/0.38/0.25), the node separating *Poikilogyne* from other Asian Sonerileae (LPP = 0.80, QC/QD/QI = 0.03/0.73/0.34), and the node separating Asian Clade A from its sister clade (LPP = 0.48, QC/QD/QI = 0.0081/0.96/0.19). Additionally, the lineage leading to *Phainantha* and the node separating Clade F and Clade E + *Oxyspora paniculata* + *Phyllagathis rotundifolia* exhibited counter-support ($QC < 0$), with LPP = 0.45, QC/QD/QI = −0.28/0.11/0.48 and LPP = 0.08, QC/QD/QI = −0.013/0.8/0.22, respectively. Within the identified major clades, many branches have high LPP but are weakly supported ($QC < 0.2$), particularly within the Asian clade.

Polytomy test and anomaly zone detection

Five short branches failed to reject the null hypothesis that the branch length is zero and should, therefore, be replaced by a polytomy ($p > 0.05$) (Fig. 3; Supplementary Fig. S6). These branches are the branch splitting the Asian Clade A from other clades, the branch splitting *Sarcopyramis* and *Barthea*, the branch splitting *Oxyspora paniculata* and Clade E + *Phyllagathis rotundifolia*, a branch within *Fordiophyton s.s.*, and the branch splitting *Kerriothyrsus* and *Phyllagathis erecta*.

Forty-three pairs of internodes fell within the anomaly zone (Fig. 3; Supplementary Fig. S7), two of which are along the backbone, while the remaining are confined to the Asian clade. All the five branches that failed to reject the null hypothesis of the polytomy test are in the anomaly zone.

Mapping gene duplications

We mapped the 12,497 gene trees used for reference construction to the species tree ST5, applying two different filtering approaches. With tree topology filtering, the proportion of duplications per node ranged from 0.03% to 39.51% (average 8.21%, median 0.98%), with significantly higher values at the node splitting *Medinilla* from other Sonerileae (39.51%) and the MRCA of the outgroup Melastomateae (34.63%). Filtering by average bootstrap values showed a similar range (0.04% to 43.47%, average 9.61%, median 1.85%), with the same nodes having elevated values (43.47% and 33.25%, respectively) **(**Fig. 4a; Supplementary Fig. S8**)**.

Additionally, we mapped the 5,626 gene trees used for orthology inference from the 5,626 data set to the species tree ST2, filtering by average bootstrap values. The proportion of duplications per node ranged from 0.02% to 73.5% (average 3.23%, median 0.26%), with five nodes showing significantly higher values: the node (53.38%) separating *Benna* from other Sonerileae, the node (73.51%) separating the *Kendrickia* + Afrotropical clade from the primarily Asian clade, the node (37.86%) separating the two major clades within the primarily Asian clade (corresponding to the node splitting *Medinilla* from other Sonerileae), a node (28.97%) within *Medinilla* and a node (47.51%) within *Heteroblemma* (Fig. 4b; Supplementary Fig. S9).

Discussion

An Effective Approach to Integrating Sequencing Data Across Multiple Sources

Efforts to combine data from various sources, including target enrichment data, have primarily focused on recovering targeted loci from other data sets (Bossert et al., 2019; Wang et al., 2024). In this study, we used both the newly developed reference and the Melastomataceae probe set for loci recovery. The phylogenetic tree inferred from the Melastomataceae probe set loci was overall less well-supported compared to the phylogenetic tree based on the data set acquired by using the new reference loci (Fig. 2; Supplementary Fig. S3). Several well-established genera were not resolved as monophyletic in the former tree but were monophyletic in the latter.

It has been suggested that increasing the number of gene trees can improve the accuracy of species tree inference (Zhang et al., 2018), particularly under conditions of high ILS (Molloy and Warnow, 2017). It has also been mathematically demonstrated that the number of true gene trees required by ASTRAL to accurately reconstruct the species tree is proportional to the inverse of the shortest branch length (Shekhar et al., 2018). Given the high level of ILS observed in the Asian Sonerileae in this study (Fig. 3; Supplementary Table S5) and previous study (Zhou et al., 2022), it is likely that the phylogenetic informativeness of the Melastomataceae probe set is insufficient for certain parts of the tree. This limitation may be further exacerbated by the low on-target rate of this probe set (Amarasinghe et al., 2021; Jantzen et al., 2022; Quakenbush et al., 2024).

The phylogenetic relationships within the Asian Sonerileae have long been unresolved, even when phylogenomic data was used (Baker et al., 2021; Maurin et al., 2021). In our study, most nodes of the Asian Sonerileae were resolved, consistent with the results of Zhou et al. (2022), where 332 orthologs were obtained by sequencing a genome and several transcriptomes, followed by retrieving orthologs from genome resequencing data (DGS data) through read mapping. Our comparable results, achieved with a more inclusive approach that does not require genome sequencing and can accommodate diverse sequencing data sets, including target enrichment data, demonstrate the potential of this method for obtaining accurate phylogenies.

By including a large number of loci in the reference file, we increased the likelihood of maximizing the use of sequenced reads data. Nearly half of the Angiosperms353 loci (176 out of 353) and more than half of the Melastomataceae probe set loci (221 out of 396) were found to match these orthologs (Supplementary Table S2). Notably, 8 out of 17 taxa sequenced using Angiosperms353 had more than 400 loci represented in the orthologs (Supplementary Table S3), surpassing the number of targeted loci, suggesting that off-target reads can be effectively utilized (Allio et al., 2020; Costa et al., 2021; Reichelt et al., 2021; Lagou et al., 2024). Additionally, we demonstrated that Hyb-Seq and DGS can recover thousands of loci, with DGS performing slightly better (Hyb-Seq: average 2,461, median 2,873; DGS: average 3,170, median 3,358). The sizes of the sequenced Melastomataceae genomes range from 246.4 to 299.8 Mb (Hao et al., 2022; Zhong et al., 2023; Huang et al., 2024), making it easy to achieve high coverage with genome sequencing, which may explain the effectiveness of Hyb-Seq and DGS in this study. Since DGS does not require target enrichment, it also reduces the time and costs associated with designing and developing baits, performing extensive lab work, and using chemicals. The method employed in this study offers a promising approach for integrating data generated from different sequencing strategies.

Phylogenetic Relationships within Sonerileae

By integrating various types of sequencing data, we generated a well-supported, near-comprehensive, genus-wide phylogeny for Sonerileae (Fig. 2). This phylogeny is largely consistent with previous studies (Baker et al., 2021; Zhou et al., 2022; Veranso-Libalah et al., 2023) regarding the relationships among the African, Asian, and Neotropical clades but provides greater resolution and improved sampling within those clades. The Neotropical lineages and the African endemic *Benna* are successively sister to the rest of the tribe, which is further divided into a predominantly Afrotropical clade and a primarily Asian clade.

After excluding the samples of *Tryssophyton merumense* and *Boyania kenwurdackii* which likely have data management issues (see Results), the remaining four sampled Neotropical species from three genera appear as the first diverging lineages in the tribe. This pattern is similar to the results of Baker et al. (2021) and Veranso-Libalah et al. (2023), although the exact branching order of these lineages differs. The lineages leading to *Boyania kenwurdackii* and *Phainantha laxiflora* were not well-supported and exhibited high discordance (LPP = 0.41, QC/QD/QI = 0.14/0.38/0.25; LPP = 0.45, QC/QD/QI = −0.28/0.11/0.48). These two taxa were represented by only 45 and 306 sequences, respectively. Incorporating more well-sequenced Neotropical taxa, including the unsampled monotypic genera *Neblinanthera* and *Tateanthus*, along with new accessions of *Tryssophyton*, may help clarify the relationships of these clades and assess whether gene flow contributed to the weak support.

The placement of the Sri Lankan endemic *Kendrickia* as sister to the Afrotropical clade, first identified by Quakenbush et al. (2024) with *Kendrickia* represented by 255 loci, has been confirmed by our results with 2,873 loci representing it. The internal relationships across different genera within the Afrotropical clade are largely consistent with the Sanger sequence-based phylogeny (Veranso-Libalah et al., 2023), with the exception of the *Amphiblemma-Cincinnobotrys-Preussiella* clade. In our phylogeny, *Amphiblemma* is sister to *Cincinnobotrys*, whereas, in the Sanger phylogeny, *Amphiblemma* is sister to *Preussiella*. Our results support the taxonomic treatments by Veranso-Libalah et al. (2023), which separate *Mendelia* from *Amphiblemma* and *Bourdaria* from *Cincinnobotrys*.

Poikilogyne comprises 28 species (POWO, 2024), with 26 endemic to New Guinea, one (*P. biporosa*) endemic to Borneo, and one (*P. cordifolia*) found in both New Guinea and northern Australia (Field, 2012). The genus has been suggested to be morphologically distinct from other Asian Sonerileae (Zhou et al., 2022). *Poikilogyne* was first included in a phylogenetic analysis in the Angiosperm Tree of Life (Baker et al., 2021), where *P. cordifolia* was weakly supported (LPP = 0.64) as sister to all other sampled Paleotropical species, though this placement was not discussed. In this study, using the same data, we placed it as sister to the rest of the Asian Sonerileae. However, the corresponding node was not strongly supported (LPP = 0.80, QC/QD/QI = 0.03/0.73/0.34). More sequencing efforts in this genus are necessary to clarify its phylogenetic position, which is also crucial for understanding the biogeographic history of the tribe.

Zhou et al. (2022) identified 34 lineages (potentially representing genera after taxonomic revision) and nine major clades within the remaining Asian Sonerileae. In this study, we sampled all but one of these clades (*Phyllagathis scortechinii*) and also included many newly sequenced fleshy-fruited taxa. All 33 sampled clades and the nine major clades were successfully recovered, corroborating the findings of Zhou et al. (2022).

However, there are four discordant placements between our species tree (Fig. 2) and the Astral coalescent tree from Zhou et al. (2022). These discrepancies involve the placements of *Oxyspora paniculata*, *Driessenia axantha*, *Phyllagathis fengii*, and the sister group of Clade B. In our phylogeny, *Oxyspora paniculata* is sister to Clade E, whereas Zhou et al. (2022) placed it as sister to Clade F. The support is weak in both phylogenies, and the branch shows strong discordance (LPP = 0.31, QC/QD/QI = 0.0033/0.94/0.24; LPP = 0.64, QC/QD/QI = −0.26/0.28/0.81). In our phylogeny, this branch was found to be very short and failed the null hypothesis of the polytomy test (Fig. 2; Supplementary Fig. S6), indicating a hard polytomy. In our phylogeny, *Driessenia axantha* is nested within Clade B, while in Zhou et al. (2022) it is placed as sister to Clade B. In our analysis, the placement was well-supported based on LPP but weakly supported based on the QC score (LPP = 1, QC/QD/QI = 0.0043/0.98/0.21), whereas it was fully supported (LPP = 1, QC/QD/QI = 1/−/1) in Zhou et al. (2022). In our results, Clade B is sister to a large clade including Clades D-I (LPP = 0.97, QC/QD/QI = 7e−04/0.99/0.17), whereas in Zhou et al. (2022), it is sister to Clade C (LPP = 0.62, QC/QD/QI = 0.13/0.71/0.86). The branch was weakly supported in both trees and fell within the anomaly zone (Fig. 3), indicating ILS. Our result is consistent with the tree (Supplementary Fig. S4) based on genomic and transcriptomic data. Additionally, *Phyllagathis fengii* was placed within *Plagiopetalum* in our tree, whereas Zhou et al. (2022) placed it within *Cyphotheca*. Notably, this species is represented by different accessions in the two trees, suggesting either a potential identity issue with the species or questioning the validity of the species.

The placements of the fleshy-fruited taxa are consistent with Quakenbush et al. (2024). *Kendrickia* is sister to the Afrotropical clade, and *Heteroblemma* and *Catanthera* form a clade that is sister to the *Phyllagathis* (thyrsoid) clade. The former genera *Pachycentria* and *Plethiandra* are nested within *Medinilla*. Within the highly diverse genus *Medinilla*, all 15 clades identified by Quakenbush et al. (2024) are recovered, with most internal relationships aligning closely. The exception is *Medinilla maidenii*, which in our phylogeny forms a clade with the *Medinilla* Western + Eastern Superclade with full support (LPP = 1), whereas Quakenbush et al. (2024) found it formed a clade with the *Medinilla* Western Superclade, albeit with low support (LPP = 0.65). QS results for the branch (QC/QD/QI = 0.035/0.9/0.34) indicate rapid radiation, rather than gene flow, which is further confirmed by the anomaly zone test. The internode pair between the MRCAs of *M. maidenii* + *Medinilla* Western + Eastern Superclade and *Medinilla* Western + Eastern Superclade falls into the anomaly zone, suggesting ILS. This serves as an example of improving accuracy of the species tree inference by increasing the gene number in the context of ILS.

WGD and the Radiation of Sonerileae

We identified two nodes with significantly elevated proportions of duplications based on transcriptomic and genomic data (Fig. 4a). One of these nodes, which splits *Medinilla* from other Sonerileae, was also detected in our broader analysis, which combined data from various sources and covered most genera of Sonerileae. This node corresponds to the split between the two major clades within the primarily Asian clade. Based on a recent Ks plot analysis (Huang et al., 2024), two WGD events were detected for *Barthea* that occurred after the divergence of Melastomataceae and Myrtaceae: one shared by *Barthea* (Sonerileae) and *Melastoma* (Melastomateae), and another after the divergence of *Barthea* and *Melastoma*. However, the precise placement of these WGD events was unresolved. According to our findings, the WGD event occurring after the divergence of Sonerileae and Melastomateae is likely situated at the node splitting the two major clades within the primarily Asian clade. Notably, over 80% of species within Sonerileae fall into these two clades, where branch lengths are short, and all polytomies and nearly all but two pairs of internodes falling within the anomaly zone are found in these clades (Fig. 3; Supplementary Table S5), suggesting rapid radiations. The WGD might have driven the tribe's rapid diversification in Asia by providing genetic material (Tank et al., 2015; Van de Peer et al., 2017). This is supported by the analysis of the genome of *Barthea barthei*, which found that the recent WGD events led to the expansion of gene families (Huang et al., 2024).

The other node identified by our transcriptomic and genomic data set is the MRCA of *Melastoma* and *Osbeckia*. This node was not detected in the broader analysis because only orthologous sequences were used to represent outgroups when inferring homologous gene trees. Our finding supports previous studies that identified a WGD event occurring after the divergence of *Melastoma* (Melastomateae) and *Barthea* (Sonerileae) and before the split between *Melastoma* and *Osbeckia* (Huang et al., 2024).

The broader analysis detected four additional WGD events within Sonerileae. The two events within *Heteroblemma* and *Medinilla* remain to be tested, while the two detected in the backbone contradict the genomic syntenic and Ks plot analyses (Huang et al., 2024). Whether these two events represent false positives or not remains uncertain. If confirmed, this discrepancy could be due to tandem duplication or transposable element (TE)-mediated duplication (Zhang et al., 2022) or assembly errors leading to misidentification of gene copies (Lagou et al., 2024). Genome or transcriptome sequencing of taxa from *Heteroblemma*, *Medinilla*, the Afrotropical clade, and/or *Benna* would help clarify these findings.

Conclusions

In this study, we demonstrated the potential of integrating various types of NGS data for phylogenetic analysis by constructing an inclusive reference based on publicly available genomic and transcriptomic data. Applying this approach to Sonerileae resulted in a well-represented and well-supported phylogeny, which further provided insights into its evolutionary history, including evidence of its radiation in Asia following a WGD. This approach shows promise for unifying heterogeneous NGS data generated through different sequencing strategies and can be broadly applied to other groups facing similar challenges.

However, constructing such a reference relies on high-quality transcriptomic or genomic data, which is not always available for all groups, potentially necessitating new transcriptome sequencing. Additionally, while the WGD identified using genomic and transcriptomic data was successfully detected with the combined dataset, we also identified several WGDs along the backbone of the tribe that are putatively false-positive, as this is discordant with evidence from Ks plots (Huang et al., 2024). This suggests caution is needed when interpreting gene duplication mapping results using gene trees based on this approach.

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Figure Legends

Figure 1. Distribution of orthologs per taxon by different sequencing strategies in the final 5,606 orthologs from the 5,626-loci data set.

Figure 2. ASTRAL species tree ST2 inferred from 176 taxa and 5,606 orthologs obtained from the 5,626-loci data set, showing the relationships within Sonerileae. Local posterior probabilities (LPP) are shown above the branches where LPP < 1. Quartet Sampling (QS) results are shown under the branches for the backbone nodes where LPP < 0.95 with three QS scores: Quartet Concordance (QC), Quartet Differential (QD), and Quartet Informativeness (QI).

Figure 3. Cladogram of the ASTRAL species tree ST3, with internode pairs within the anomaly zone highlighted in red and their branch lengths labeled above. Circled numbers indicate branches that fail to reject the null hypothesis of the polytomy test.

Figure 4. Proportion of gene duplications mapped onto the Sonerileae phylogeny. Values above the branches indicate the proportion of orthogroups exhibiting duplications, with only values above 20% shown. (a) Genomic and transcriptomic data set, filtered by average bootstrap support (left) or tree topology (right). (b) Combined data set, filtered by average bootstrap support.

Supplementary Fig. S1. Distribution of orthologs per taxon by different sequencing methods in the final 191 orthologs from the 396-loci data set.

Supplementary Fig. S2. ASTRAL species tree ST1 inferred from 178 taxa (including *Tryssophyton merumense* and *Boyania kenwurdackii* A353) and 5,606 orthologs from the 5,626-loci data set, showing the relationships within Sonerileae. Local posterior probabilities (LPP) are shown above branches where LPP < 1.

Supplementary Fig. S3. ASTRAL species tree ST4 inferred from 176 taxa and 191 orthologs from the 396-loci data set, showing the relationships within Sonerileae. Local posterior probabilities (LPP) are shown above branches where LPP < 1.

Supplementary Fig. S4. ASTRAL species tree ST5 inferred from 18 taxa and 5,626 orthologs using only genomic and transcriptomic data, showing the relationships within Sonerileae. Local posterior probabilities (LPP) are shown above branches where LPP < 1.

Supplementary Fig. S5. Gene tree conflicts measured with Quartet Sampling (QS) analysis. Each branch is annotated with three QS scores: Quartet Concordance (QC), Quartet Differential (QD), and Quartet Informativeness (QI).

Supplementary Fig. S6. Results of the polytomy test mapped onto the phylogeny of Sonerileae (ST2), with p-values greater than zero labeled above the branches. The p-values greater than 0.05 are shown in red.

Supplementary Fig. S7. Results of the anomaly zone test mapped onto the phylogeny of Sonerileae (ST3), with branch lengths labeled above each branch. Branches that fall within the anomaly zone are highlighted in red.

Supplementary Fig. S8. Proportion of gene duplications mapped onto the Sonerileae phylogeny (ST5) inferred from genomic and transcriptomic data. Values above the branches indicate the proportion of orthogroups exhibiting duplications, filtered by (a) average bootstrap support or (b) tree topology.

Supplementary Fig. S9. Proportion of gene duplications mapped onto the phylogeny of Sonerileae (ST2). Values above the branches represent the proportion of orthogroups showing duplications, filtered by average bootstrap support.

Supplementary Table S1 Detailed list of taxa sampled in this study, including voucher information for newly generated data and accession numbers for public data.

Supplementary Table S2 Matching loci between the newly developed reference comprising 5,626 loci and the Melastomataceae probe set containing 396 loci, and the Angiosperms353 probe set.

Supplementary Table S3 Frequency of taxa in the final orthologs for the 5,626-loci data set. Taxa sequenced using the same strategy are additionally separately listed.

Supplementary Table S4 Frequency of taxa in the final orthologs for the 396-loci data set. Taxa sequenced using the same strategy are additionally separately listed.

Supplementary Table S5 Results of the anomaly zone test. 'x' represents the length of the parent branch, while 'y' represents the length of the child branch (branch lengths are labeled above the branches in Fig. 4). $\alpha(x)$ represents the limit of the anomaly zone for the internode length. If 'y' is less than $\alpha(x)$, then the pair of internodes falls within the anomaly zone.

Fig. 1

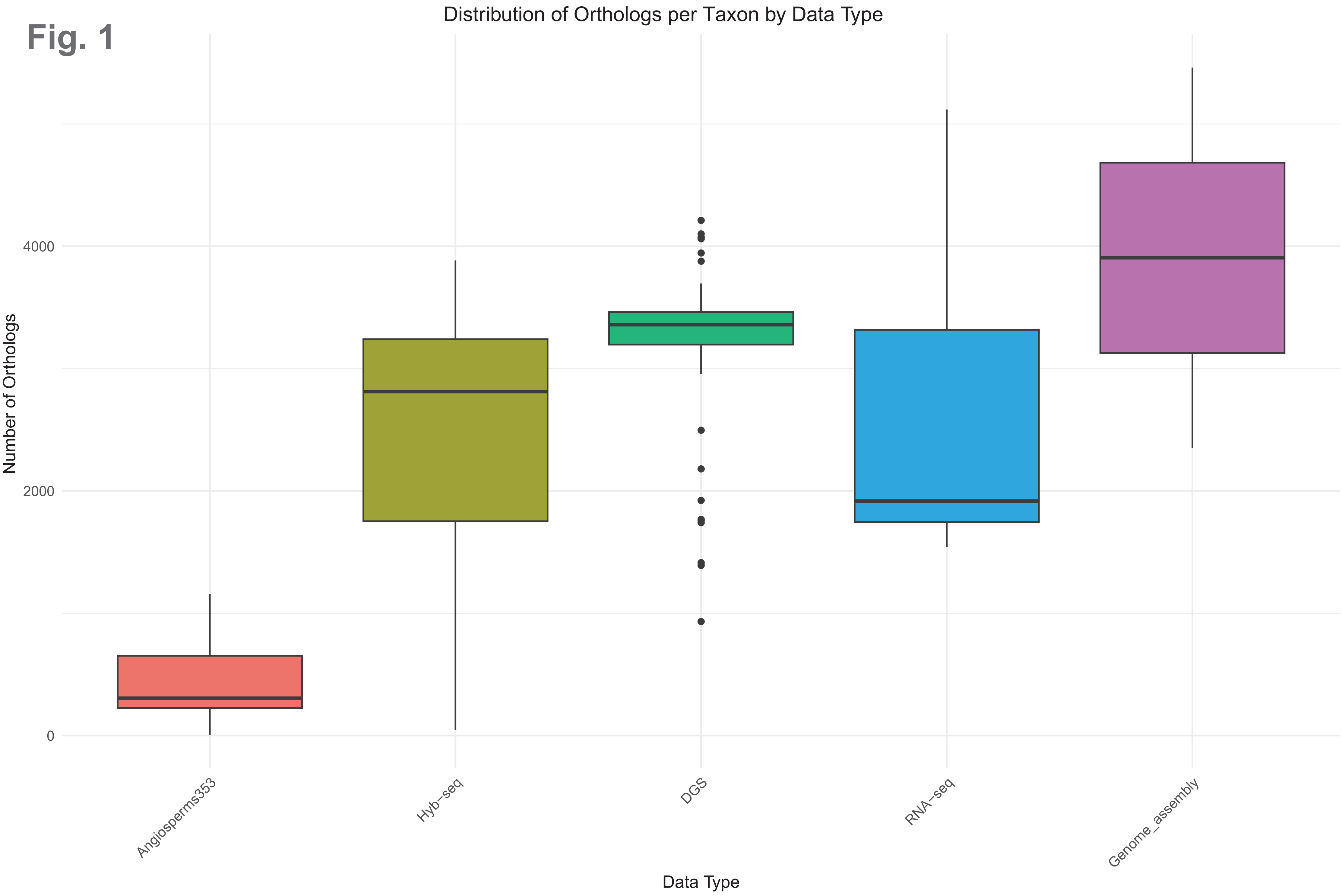

Distribution of Orthologs per Taxon by Data Type
Number of Orthologs
0
2000
4000
Data Type
Angiosperms353
Hyb−seq
DGS
RNA−seq
Genome_assembly

Fig. 2

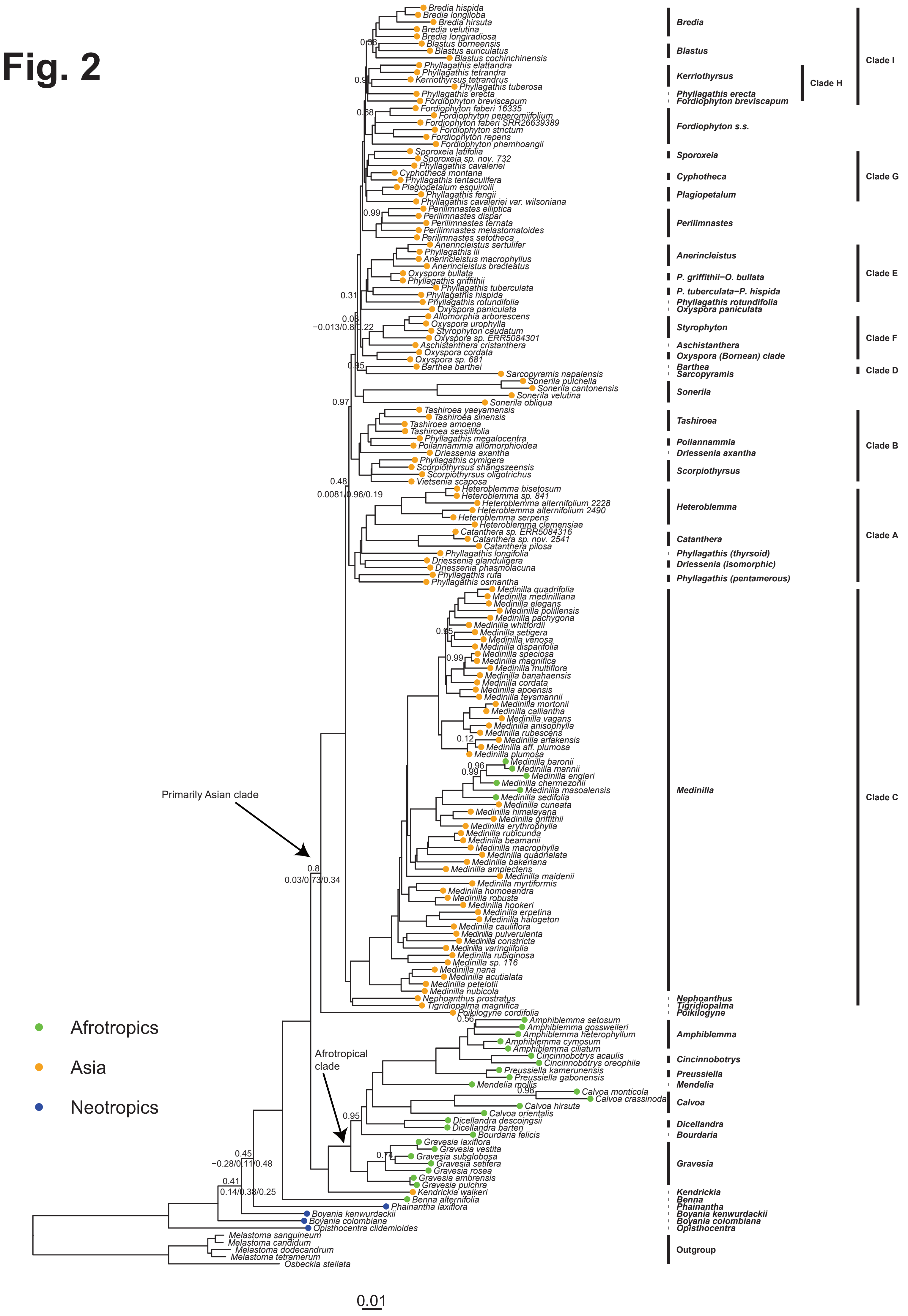

Bredia hispida
Bredia longiloba
Bredia hirsuta
Bredia velutina
Bredia longiradiosa
Blastus borneensis
Blastus auriculatus
Blastus cochinchinensis
Phyllagathis elattandra
Phyllagathis tetrandra
Kerriothyrsus tetrandrus
Phyllagathis tuberosa
Phyllagathis erecta
Fordiophyton breviscapum
Fordiophyton faberi 16335
Fordiophyton peperomiifolium
Fordiophyton faberi SRR26639389
Fordiophyton strictum
Fordiophyton repens
Fordiophyton phamhoangii
Sporoxeia latifolia
Sporoxeia sp. nov. 732
Phyllagathis cavaleriei
Cyphotheca montana
Phyllagathis tentaculifera
Plagiopetalum esquirolii
Phyllagathis fengii
Phyllagathis cavaleriei var. wilsoniana
Perilimnastes elliptica
Perilimnastes dispar
Perilimnastes ternata
Perilimnastes melastomatoides
Perilimnastes setotheca
Anerincleistus sertulifer
Phyllagathis lii
Anerincleistus macrophyllus
Anerincleistus bracteatus
Oxyspora bullata
Phyllagathis griffithii
Phyllagathis tuberculata
Phyllagathis hispida
Phyllagathis rotundifolia
Oxyspora paniculata
Allomorphia arborescens
Oxyspora urophylla
Styrophyton caudatum
Oxyspora sp. ERR5084301
Aschistanthera cristanthera
Oxyspora cordata
Oxyspora sp. 681
Barthea barthei
Sarcopyramis napalensis
Sonerila pulchella
Sonerila cantonensis
Sonerila velutina
Sonerila obliqua
Tashiroea yaeyamensis
Tashiroea sinensis
Tashiroea amoena
Tashiroea sessilifolia
Phyllagathis megalocentra
Poilannammia allomorphioidea
Driessenia axantha
Phyllagathis cymigera
Scorpiothyrsus shangszeensis
Scorpiothyrsus oligotrichus
Vietsenia scaposa
Heteroblemma bisetosum
Heteroblemma sp. 841
Heteroblemma alternifolium 2228
Heteroblemma alternifolium 2490
Heteroblemma serpens
Heteroblemma clemensiae
Catanthera sp. ERR5084316
Catanthera sp. nov. 2541
Catanthera pilosa
Phyllagathis longifolia
Driessenia glanduligera
Driessenia phasmolacuna
Phyllagathis rufa
Phyllagathis osmantha
Medinilla quadrifolia
Medinilla medinilliana
Medinilla elegans
Medinilla polillensis
Medinilla pachygona
Medinilla whitfordii
Medinilla setigera
Medinilla venosa
Medinilla disparifolia
Medinilla speciosa
Medinilla magnifica
Medinilla multiflora
Medinilla banahaensis
Medinilla cordata
Medinilla apoensis
Medinilla teysmannii
Medinilla mortonii
Medinilla calliantha
Medinilla vagans
Medinilla anisophylla
Medinilla rubescens
Medinilla arfakensis
Medinilla aff. plumosa
Medinilla plumosa
Medinilla baronii
Medinilla mannii
Medinilla engleri
Medinilla chermezonii
Medinilla masoalensis
Medinilla sedifolia
Medinilla cuneata
Medinilla himalayana
Medinilla griffithii
Medinilla erythrophylla
Medinilla rubicunda
Medinilla beamanii
Medinilla macrophylla
Medinilla quadrialata
Medinilla bakeriana
Medinilla amplectens
Medinilla maidenii
Medinilla myrtiformis
Medinilla homoeandra
Medinilla robusta
Medinilla hookeri
Medinilla erpetina
Medinilla halogeton
Medinilla cauliflora
Medinilla pulverulenta
Medinilla constricta
Medinilla varingiifolia
Medinilla rubiginosa
Medinilla sp. 116
Medinilla nana
Medinilla acutialata
Medinilla petelotii
Medinilla nubicola
Nephoanthus prostratus
Tigridiopalma magnifica
Poikilogyne cordifolia
Amphiblemma setosum
Amphiblemma gossweileri
Amphiblemma heterophyllum
Amphiblemma cymosum
Amphiblemma ciliatum
Cincinnobotrys acaulis
Cincinnobotrys oreophila
Preussiella kamerunensis
Preussiella gabonensis
Mendelia mollis
Calvoa monticola
Calvoa crassinoda
Calvoa hirsuta
Calvoa orientalis
Dicellandra descoingsii
Dicellandra barteri
Bourdaria felicis
Gravesia laxiflora
Gravesia vestita
Gravesia subglobosa
Gravesia setifera
Gravesia rosea
Gravesia ambrensis
Gravesia pulchra
Kendrickia walkeri
Benna alternifolia
Phainantha laxiflora
Boyania kenwurdackii
Boyania colombiana
Opisthocentra clidemioides
Melastoma sanguineum
Melastoma candidum
Melastoma dodecandrum
Melastoma tetramerum
Osbeckia stellata
0.38
0.9
0.68
0.99
0.31
0.08
−0.013/0.8/0.22
0.95
0.97
0.48
0.0081/0.96/0.19
0.95
0.99
0.12
0.96
0.99
0.8
0.03/0.73/0.34
0.56
0.98
0.95
0.74
0.45
−0.28/0.11/0.48
0.41
0.14/0.38/0.25
Primarily Asian clade
Afrotropical clade
0.01
Bredia
Blastus
Kerriothyrsus
Phyllagathis erecta
Fordiophyton breviscapum
Fordiophyton s.s.
Sporoxeia
Cyphotheca
Plagiopetalum
Perilimnastes
Anerincleistus
P. griffithii−O. bullata
P. tuberculata−P. hispida
Phyllagathis rotundifolia
Oxyspora paniculata
Styrophyton
Aschistanthera
Oxyspora (Bornean) clade
Barthea
Sarcopyramis
Sonerila
Tashiroea
Poilannammia
Driessenia axantha
Scorpiothyrsus
Heteroblemma
Catanthera
Phyllagathis (thyrsoid)
Driessenia (isomorphic)
Phyllagathis (pentamerous)
Medinilla
Nephoanthus
Tigridiopalma
Poikilogyne
Amphiblemma
Cincinnobotrys
Preussiella
Mendelia
Calvoa
Dicellandra
Bourdaria
Gravesia
Kendrickia
Benna
Phainantha
Boyania kenwurdackii
Boyania colombiana
Opisthocentra
Outgroup
Clade H
Clade I
Clade G
Clade E
Clade F
Clade D
Clade B
Clade A
Clade C
● Afrotropics
● Asia
● Neotropics

Fig. 3

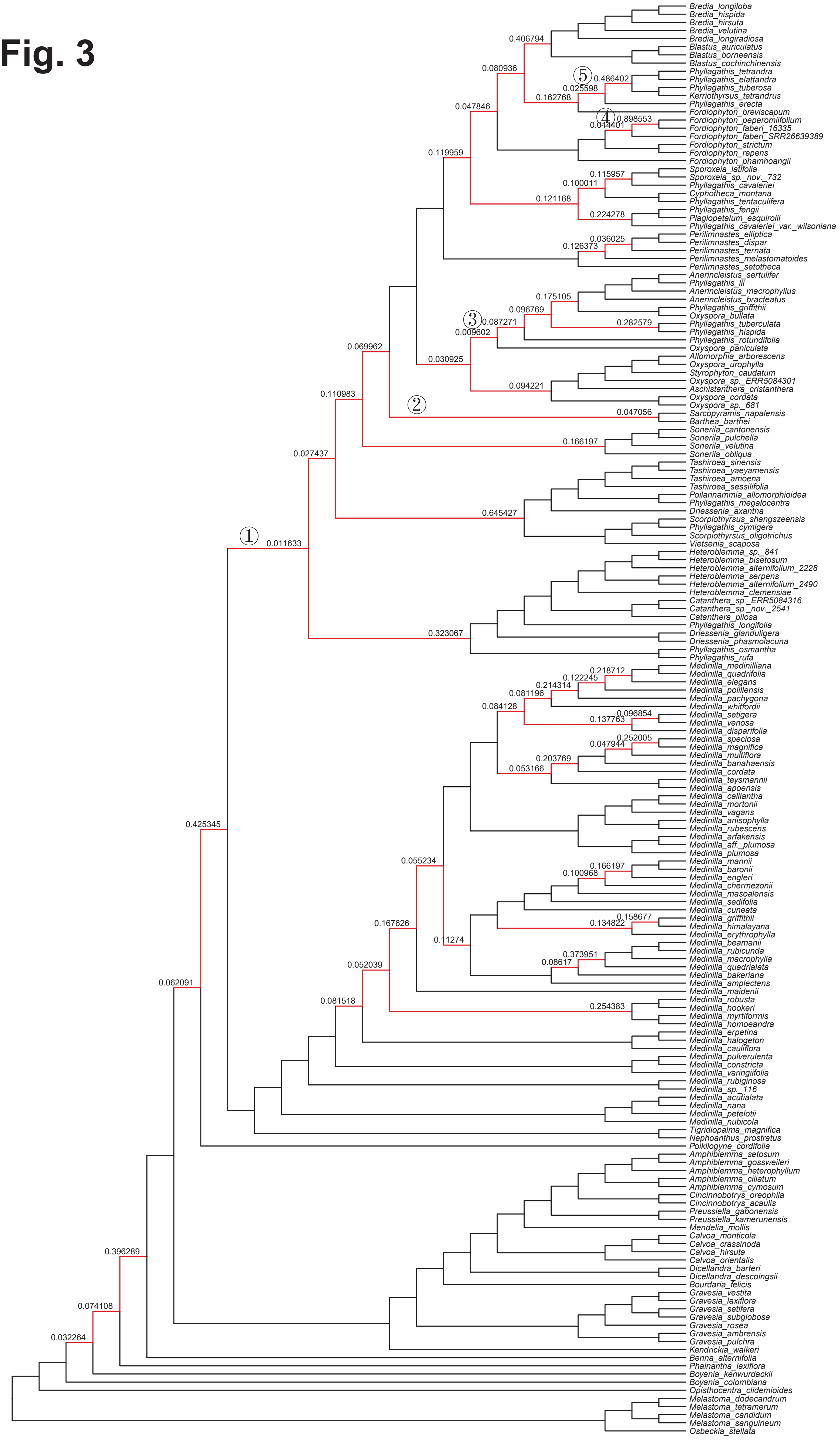
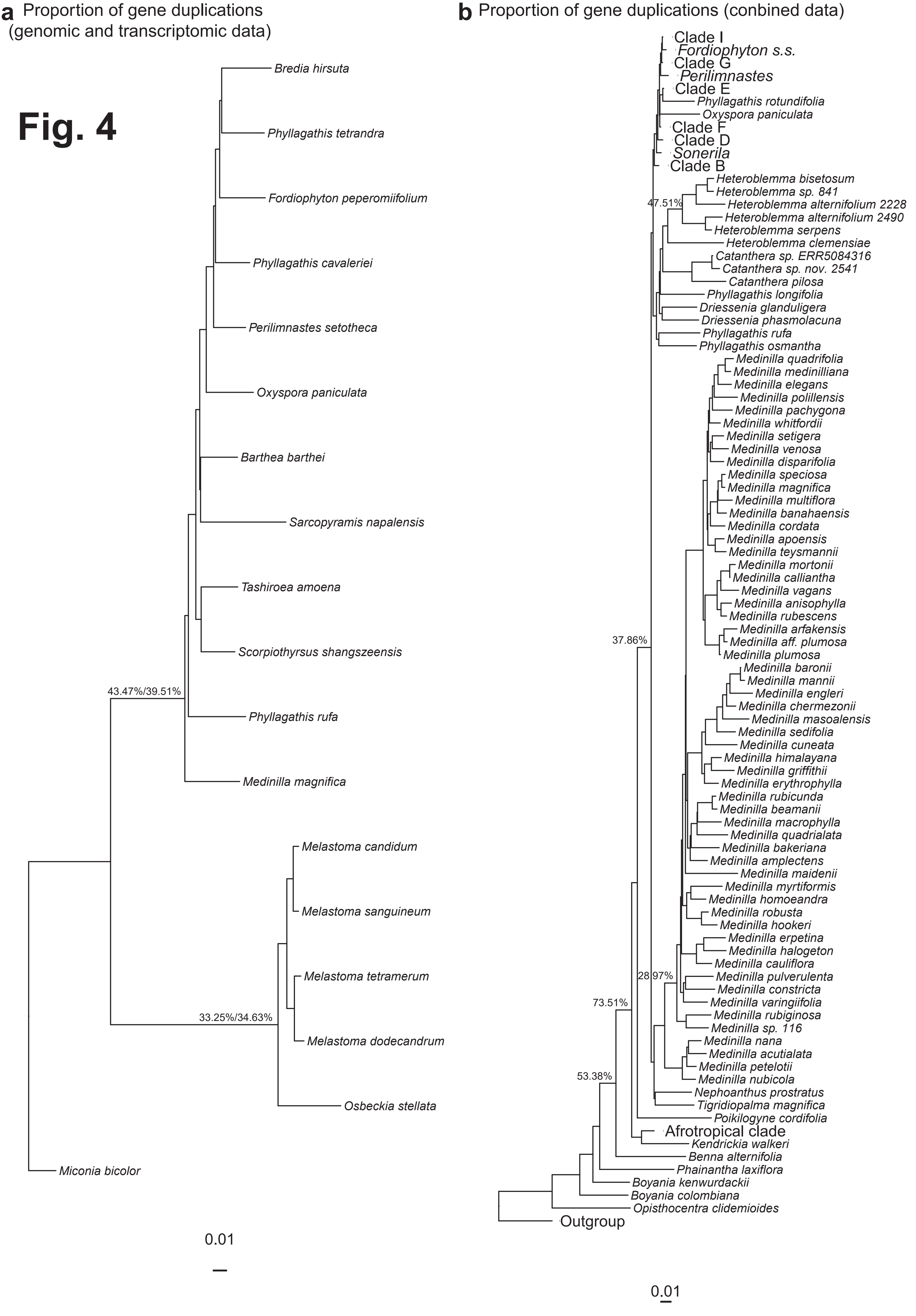

Bredia_longiloba
Bredia_hispida
Bredia_hirsuta
Bredia_velutina
Bredia_longiradiosa
Blastus_auriculatus
Blastus_borneensis
Blastus_cochinchinensis
Phyllagathis_tetrandra
Phyllagathis_elattandra
Phyllagathis_tuberosa
Kerriothyrsus_tetrandrus
Phyllagathis_erecta
Fordiophyton_breviscapum
Fordiophyton_peperomiifolium
Fordiophyton_faberi_16335
Fordiophyton_faberi_SRR26639389
Fordiophyton_strictum
Fordiophyton_repens
Fordiophyton_phamhoangii
Sporoxeia_latifolia
Sporoxeia_sp._nov._732
Phyllagathis_cavaleriei
Cyphotheca_montana
Phyllagathis_tentaculifera
Phyllagathis_fengii
Plagiopetalum_esquirolii
Phyllagathis_cavaleriei_var._wilsoniana
Perilimnastes_elliptica
Perilimnastes_dispar
Perilimnastes_ternata
Perilimnastes_melastomatoides
Perilimnastes_setotheca
Anerincleistus_sertulifer
Phyllagathis_lii
Anerincleistus_macrophyllus
Anerincleistus_bracteatus
Phyllagathis_griffithii
Oxyspora_bullata
Phyllagathis_tuberculata
Phyllagathis_hispida
Phyllagathis_rotundifolia
Oxyspora_paniculata
Allomorphia_arborescens
Oxyspora_urophylla
Styrophyton_caudatum
Oxyspora_sp._ERR5084301
Aschistanthera_cristanthera
Oxyspora_cordata
Oxyspora_sp._681
Sarcopyramis_napalensis
Barthea_barthei
Sonerila_cantonensis
Sonerila_pulchella
Sonerila_velutina
Sonerila_obliqua
Tashiroea_sinensis
Tashiroea_yaeyamensis
Tashiroea_amoena
Tashiroea_sessilifolia
Poilannammia_allomorphioidea
Phyllagathis_megalocentra
Driessenia_axantha
Scorpiothyrsus_shangszeensis
Phyllagathis_cymigera
Scorpiothyrsus_oligotrichus
Vietsenia_scaposa
Heteroblemma_sp._841
Heteroblemma_bisetosum
Heteroblemma_alternifolium_2228
Heteroblemma_serpens
Heteroblemma_alternifolium_2490
Heteroblemma_clemensiae
Catanthera_sp._ERR5084316
Catanthera_sp._nov._2541
Catanthera_pilosa
Phyllagathis_longifolia
Driessenia_glanduligera
Driessenia_phasmolacuna
Phyllagathis_osmantha
Phyllagathis_rufa
Medinilla_medinilliana
Medinilla_quadrifolia
Medinilla_elegans
Medinilla_polillensis
Medinilla_pachygona
Medinilla_whitfordii
Medinilla_setigera
Medinilla_venosa
Medinilla_disparifolia
Medinilla_speciosa
Medinilla_magnifica
Medinilla_multiflora
Medinilla_banahaensis
Medinilla_cordata
Medinilla_teysmannii
Medinilla_apoensis
Medinilla_calliantha
Medinilla_mortonii
Medinilla_vagans
Medinilla_anisophylla
Medinilla_rubescens
Medinilla_arfakensis
Medinilla_aff._plumosa
Medinilla_plumosa
Medinilla_mannii
Medinilla_baronii
Medinilla_engleri
Medinilla_chermezonii
Medinilla_masoalensis
Medinilla_sedifolia
Medinilla_cuneata
Medinilla_griffithii
Medinilla_himalayana
Medinilla_erythrophylla
Medinilla_beamanii
Medinilla_rubicunda
Medinilla_macrophylla
Medinilla_quadrialata
Medinilla_bakeriana
Medinilla_amplectens
Medinilla_maidenii
Medinilla_robusta
Medinilla_hookeri
Medinilla_myrtiformis
Medinilla_homoeandra
Medinilla_erpetina
Medinilla_halogeton
Medinilla_cauliflora
Medinilla_pulverulenta
Medinilla_constricta
Medinilla_varingiifolia
Medinilla_rubiginosa
Medinilla_sp._116
Medinilla_acutialata
Medinilla_nana
Medinilla_petelotii
Medinilla_nubicola
Tigridiopalma_magnifica
Nephoanthus_prostratus
Poikilogyne_cordifolia
Amphiblemma_setosum
Amphiblemma_gossweileri
Amphiblemma_heterophyllum
Amphiblemma_ciliatum
Amphiblemma_cymosum
Cincinnobotrys_oreophila
Cincinnobotrys_acaulis
Preussiella_gabonensis
Preussiella_kamerunensis
Mendelia_mollis
Calvoa_monticola
Calvoa_crassinoda
Calvoa_hirsuta
Calvoa_orientalis
Dicellandra_barteri
Dicellandra_descoingsii
Bourdaria_felicis
Gravesia_vestita
Gravesia_laxiflora
Gravesia_setifera
Gravesia_subglobosa
Gravesia_rosea
Gravesia_ambrensis
Gravesia_pulchra
Kendrickia_walkeri
Benna_alternifolia
Phainantha_laxiflora
Boyania_kenwurdackii
Boyania_colombiana
Opisthocentra_clidemioides
Melastoma_dodecandrum
Melastoma_tetramerum
Melastoma_candidum
Melastoma_sanguineum
Osbeckia_stellata
0.406794
0.080936
⑤
0.486402
0.025598
0.162768
0.047846
④
0.898553
0.014401
0.119959
0.115957
0.100011
0.121168
0.224278
0.036025
0.126373
0.175105
0.096769
③
0.087271
0.009602
0.282579
0.069962
0.030925
0.110983
0.094221
②
0.047056
0.166197
0.027437
0.645427
①
0.011633
0.323067
0.218712
0.122245
0.214314
0.081196
0.084128
0.096854
0.137763
0.252005
0.047944
0.203769
0.053166
0.425345
0.055234
0.166197
0.100968
0.167626
0.158677
0.134822
0.11274
0.373951
0.08617
0.052039
0.062091
0.081518
0.254383
0.396289
0.074108
0.032264

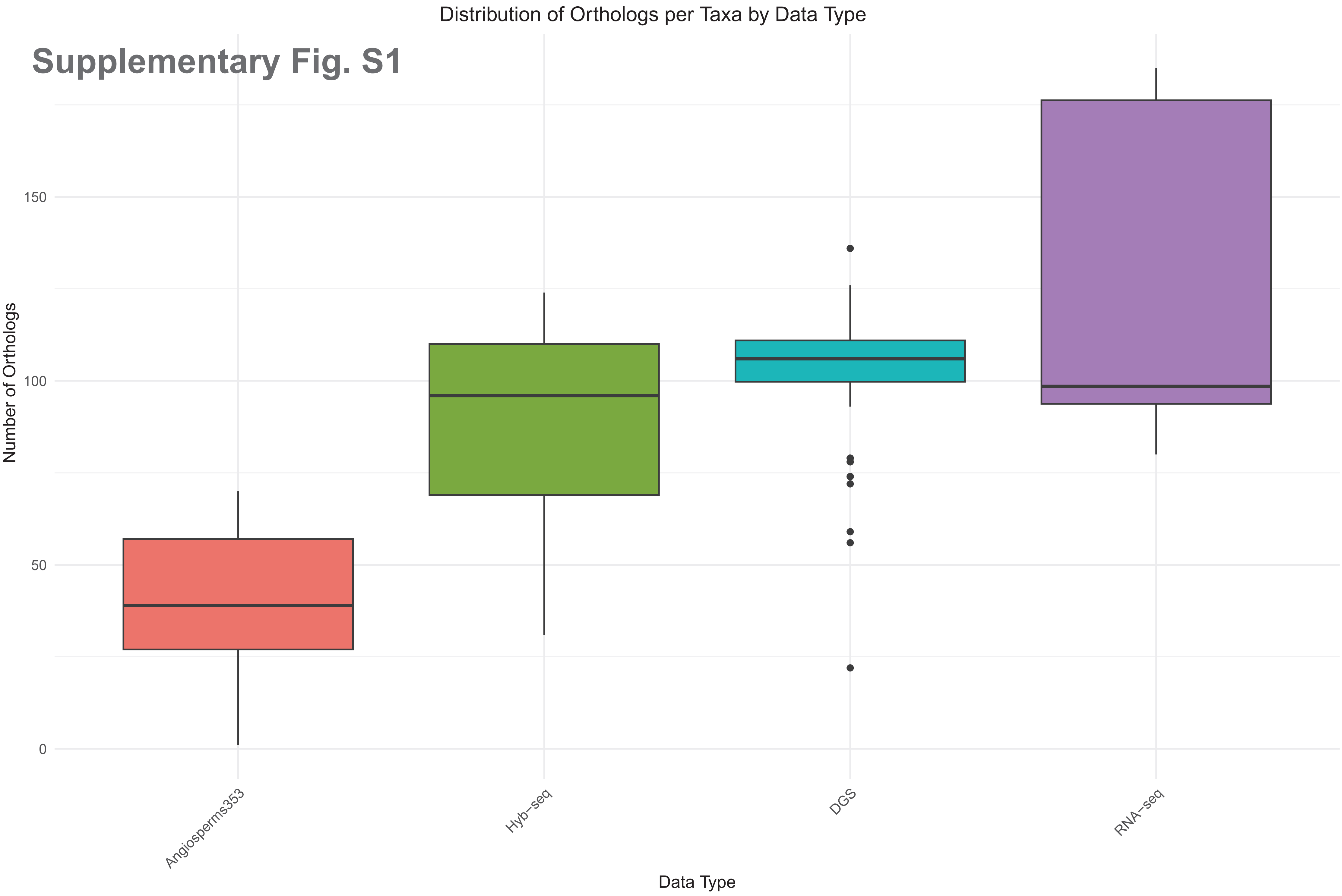
Fig. 4



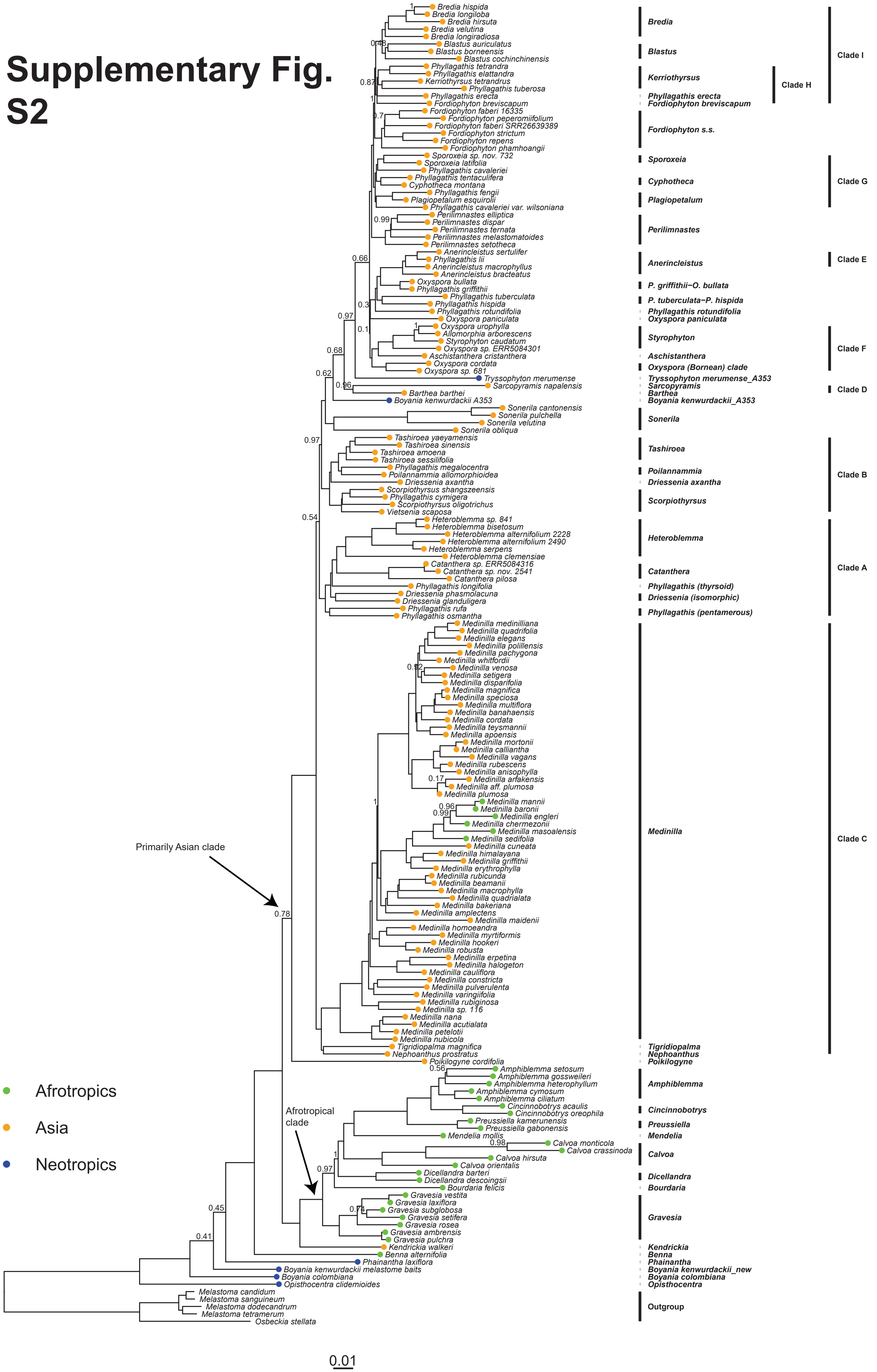
a Proportion of gene duplications (genomic and transcriptomic data)

b Proportion of gene duplications (conbined data)

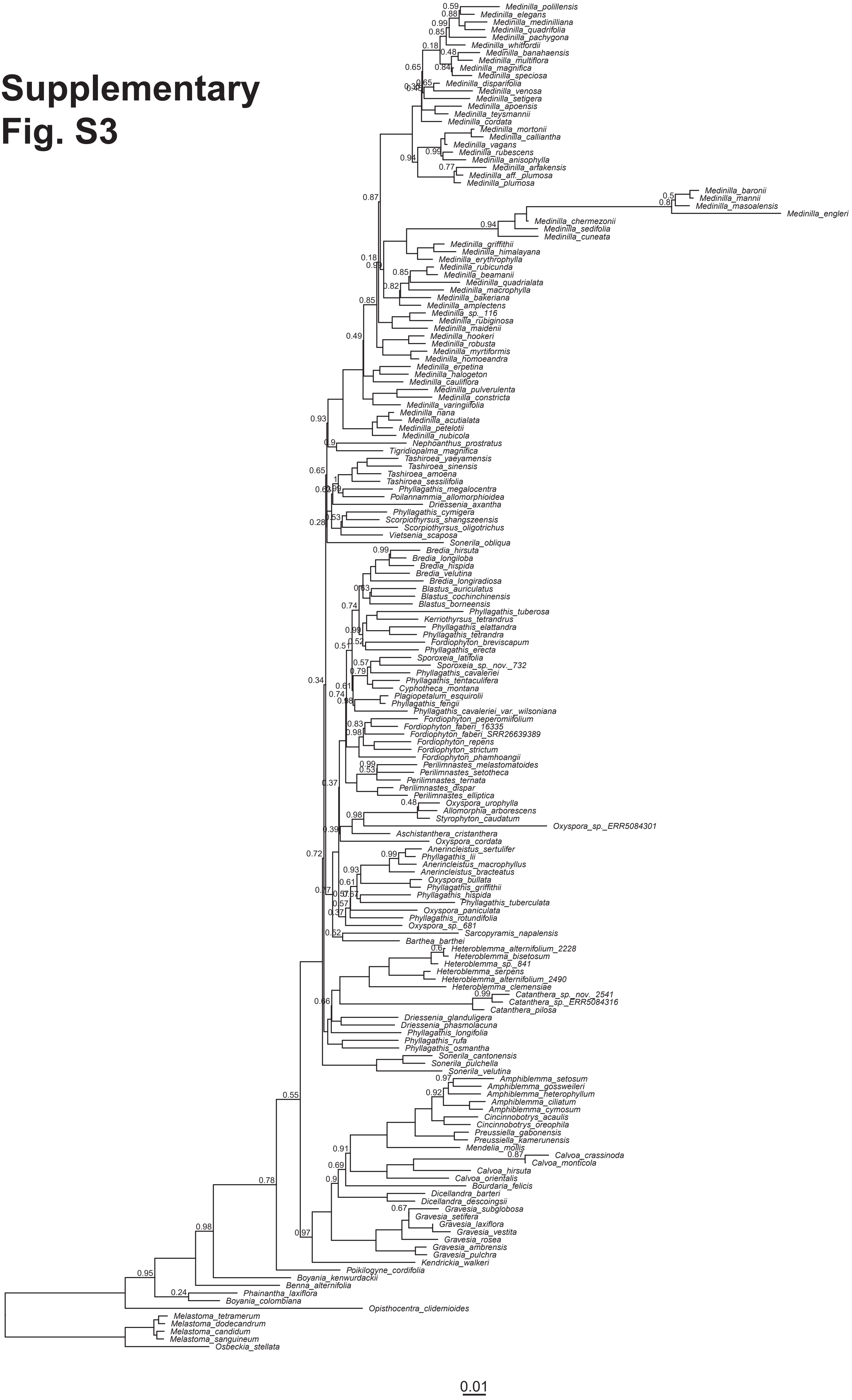
Supplementary Fig. S1



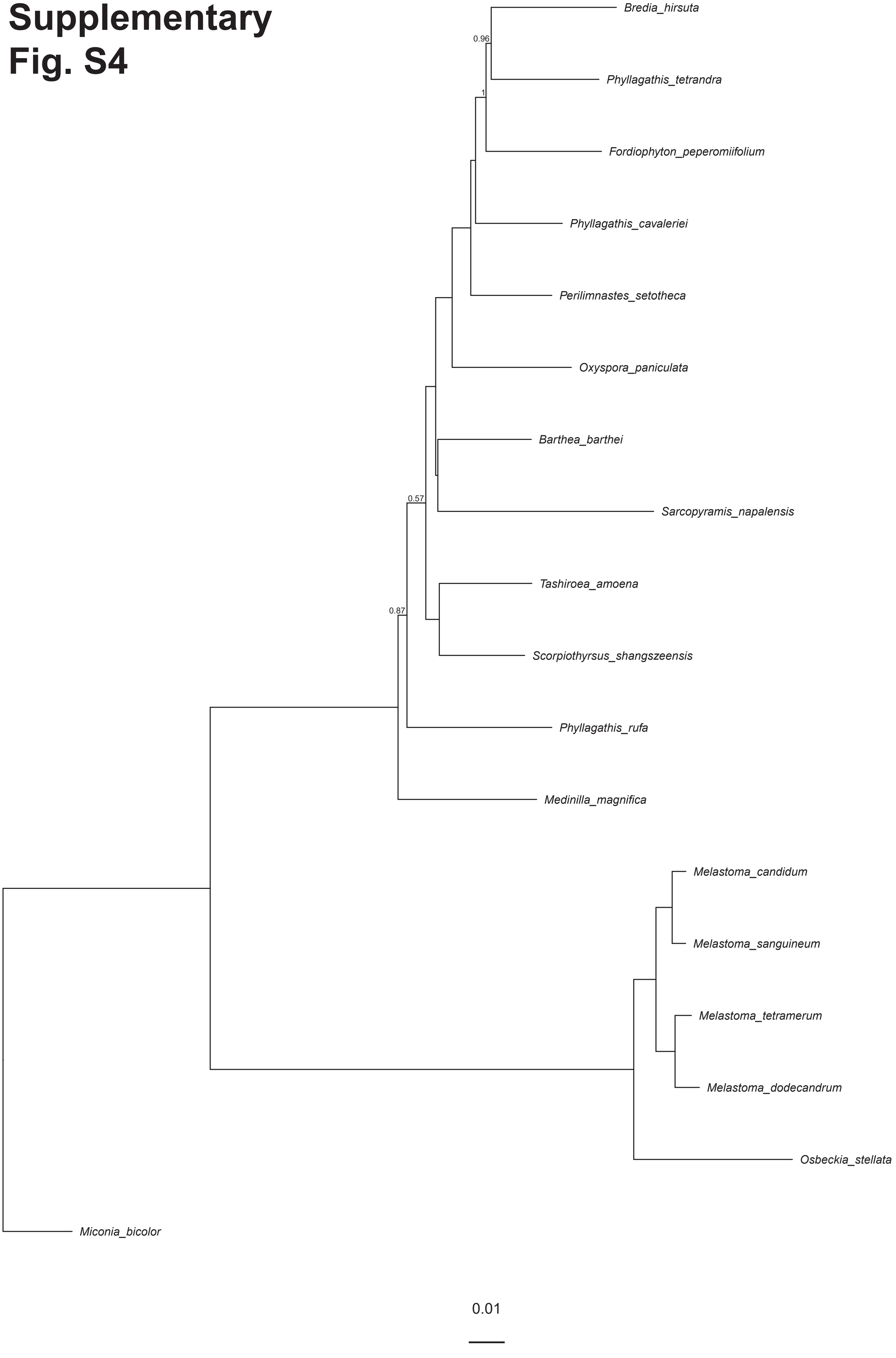
Supplementary Fig. S2



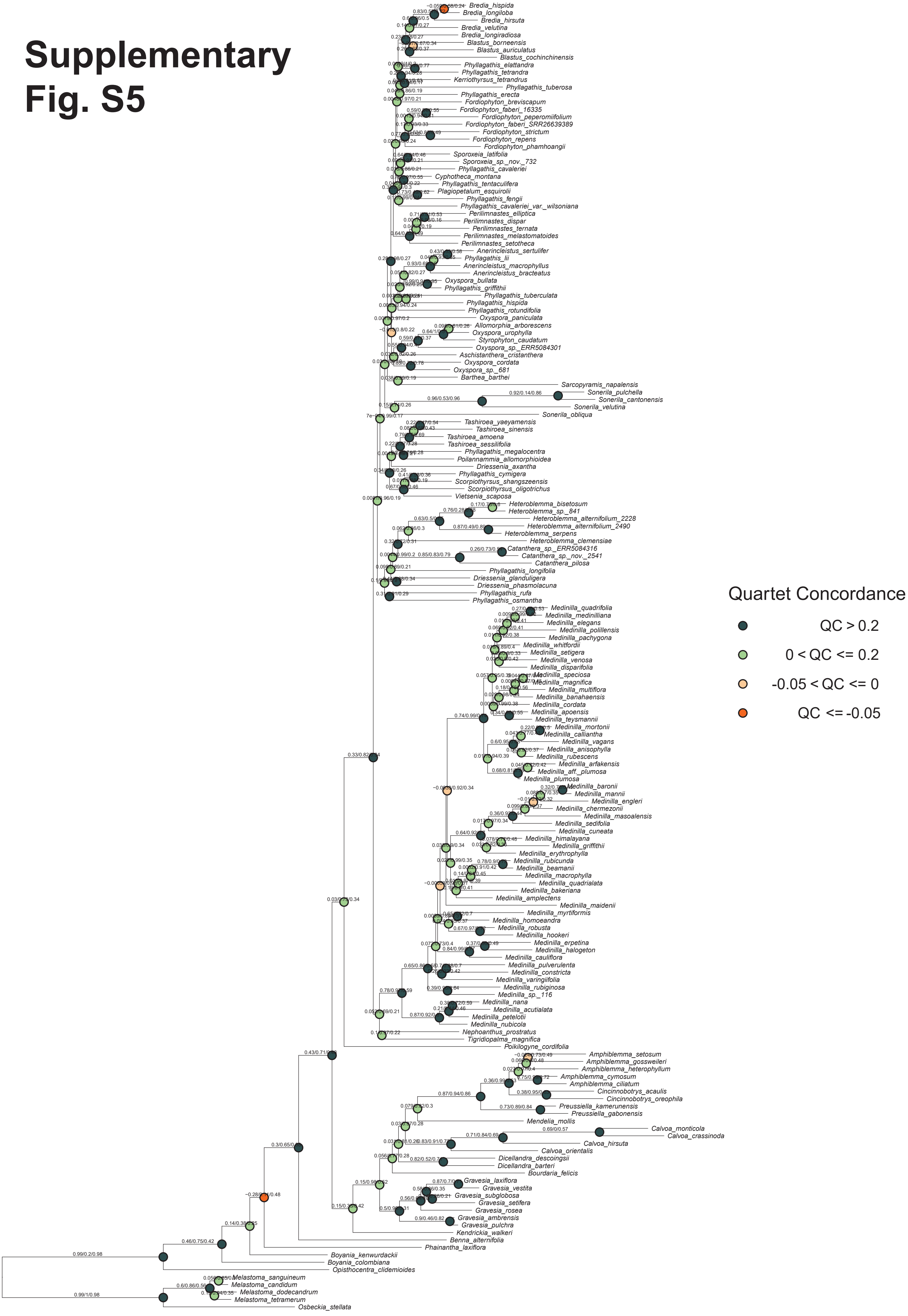
Supplementary Fig. S3



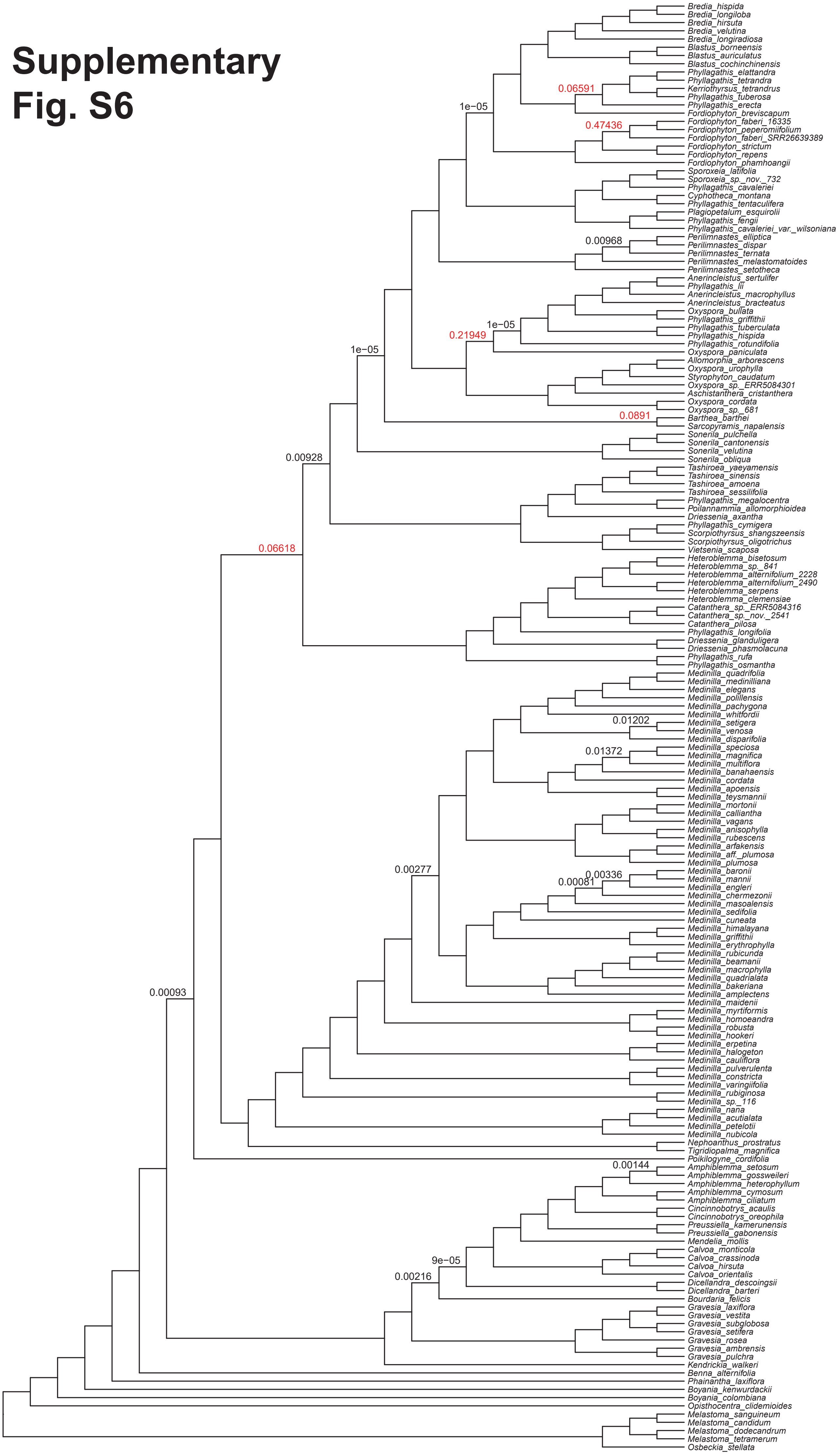
Supplementary Fig. S4



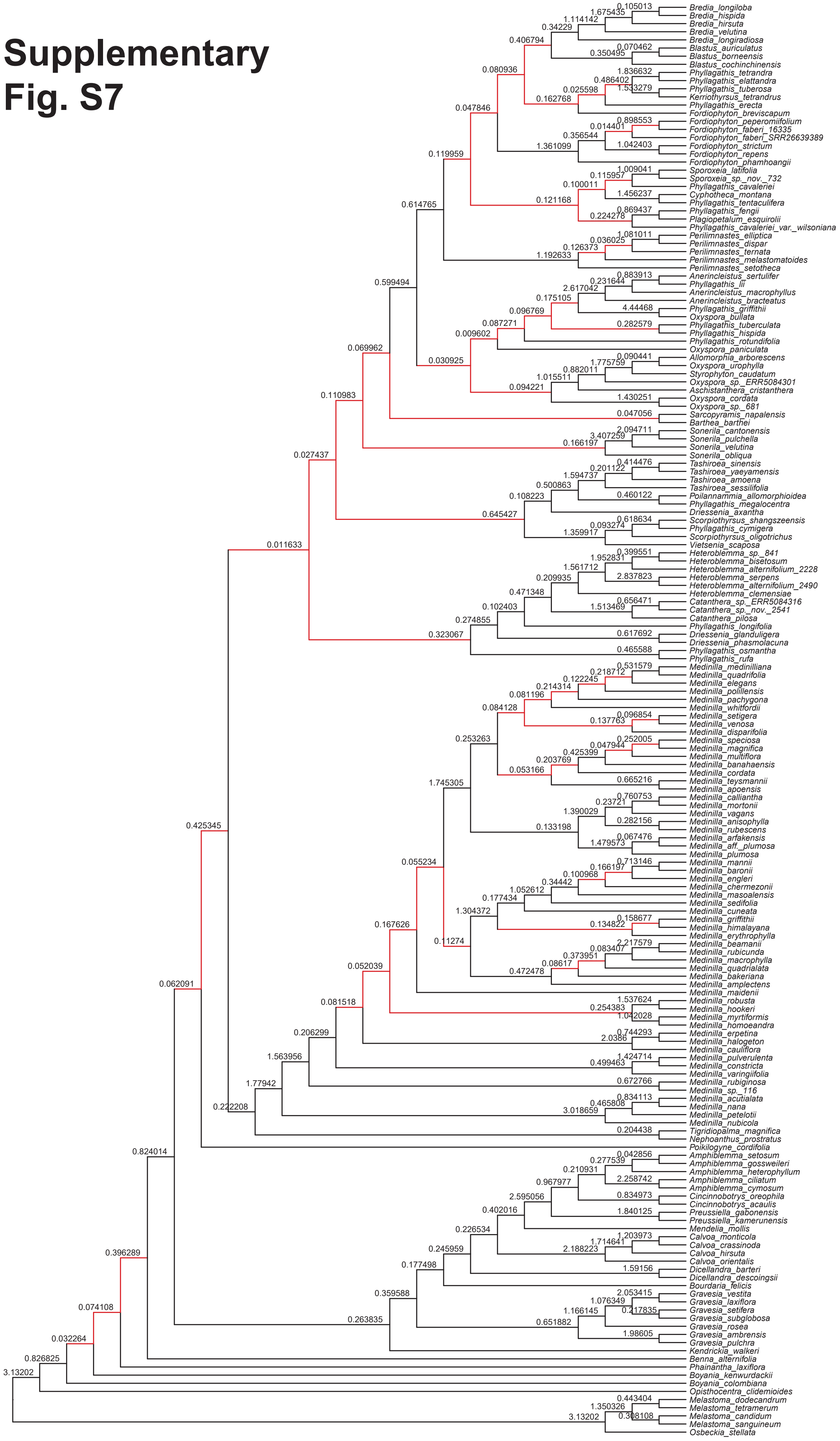
Supplementary Fig. S5



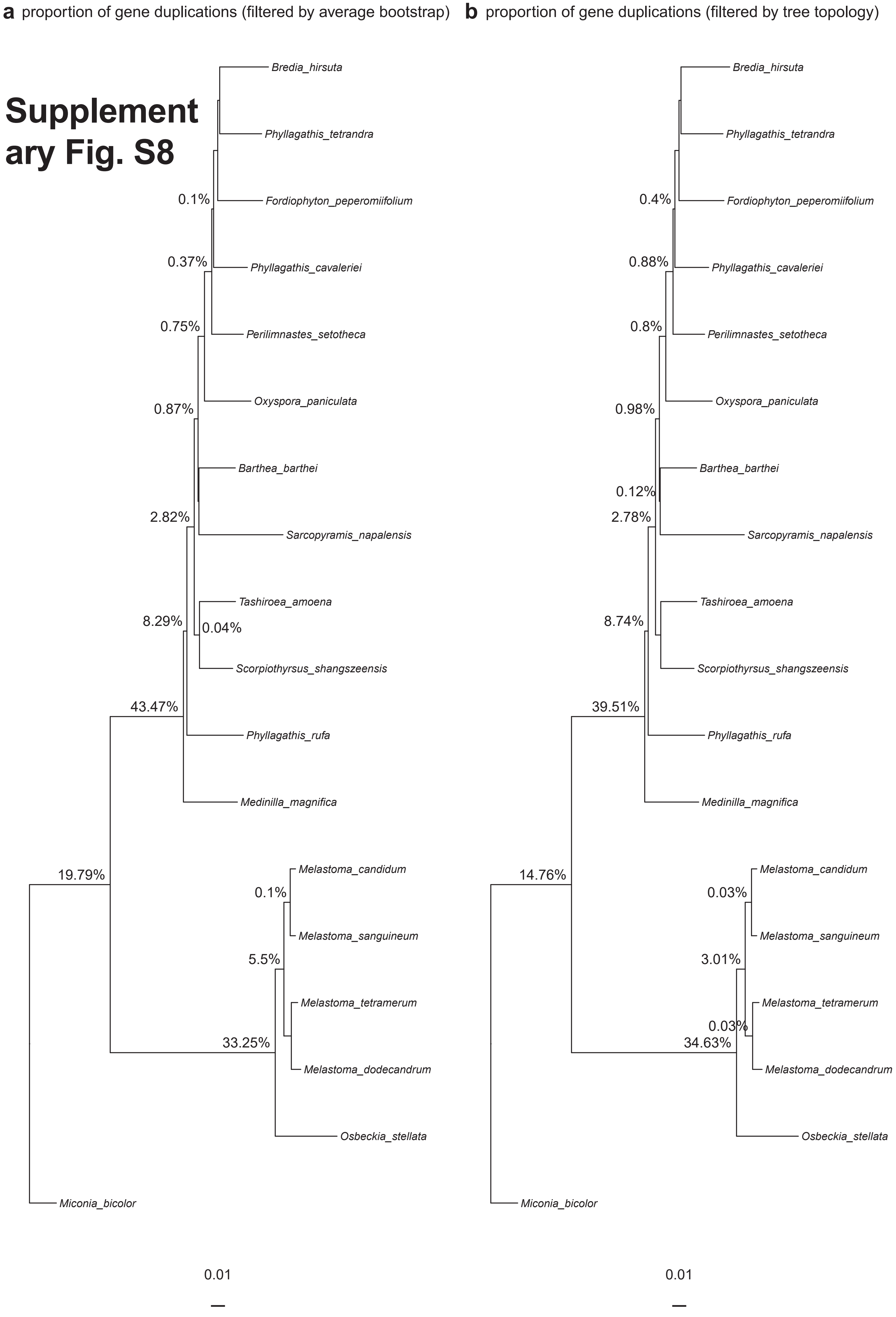
Supplementary Fig. S6



Supplementary
Fig. S7

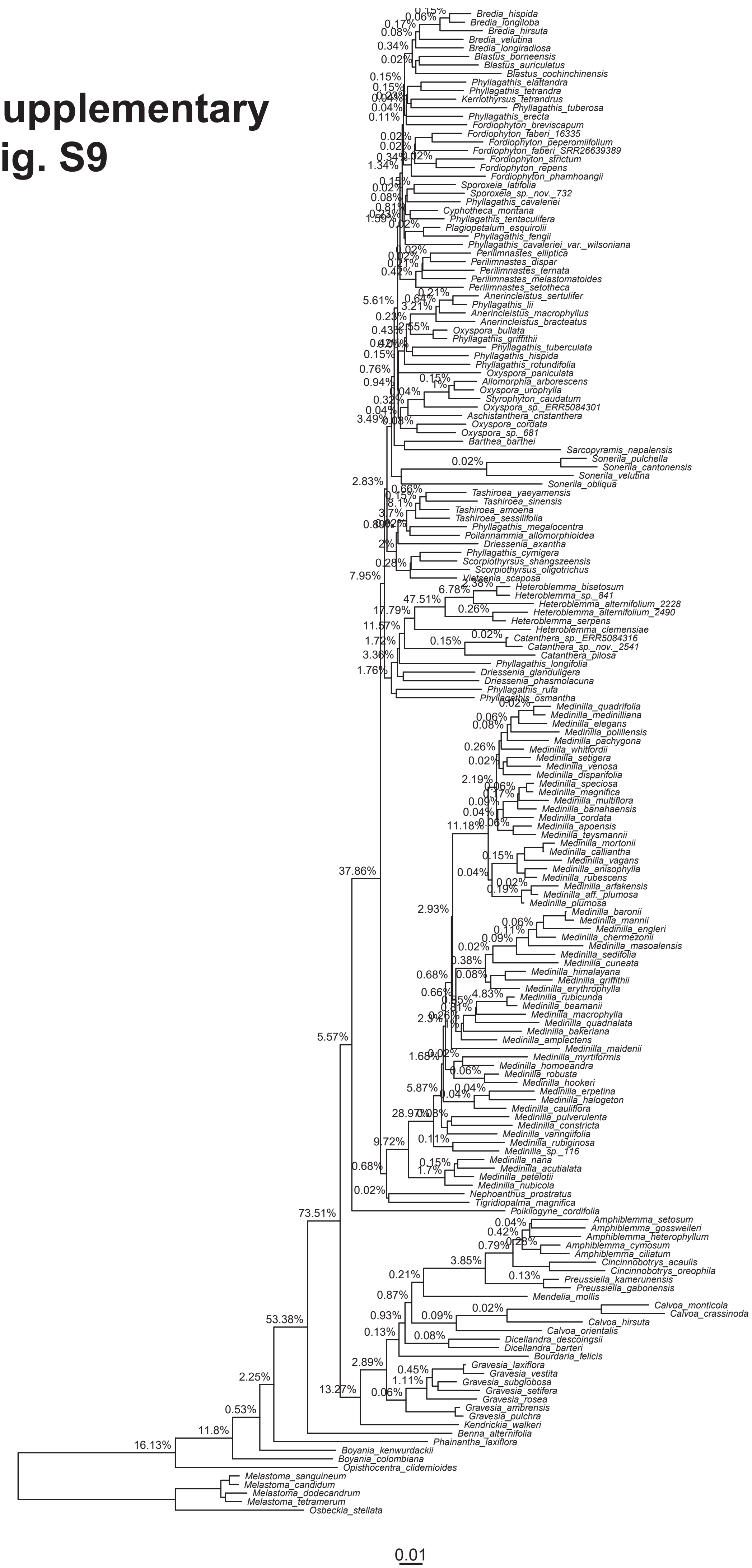


Supplementary Fig. S8



a proportion of gene duplications (filtered by average bootstrap) **b** proportion of gene duplications (filtered by tree topology) proportion of gene duplications (filtered by average bootstrap)

Supplementary Fig. S9



CHAPTER 6

GENERAL DISCUSSION

The four chapters of my PhD (Chapters 2-5) focused primarily on resolving phylogenies of Old World Melastomataceae, which is essential for developing a natural classification system for the family and enriching our understanding of plant diversity. This work also serves as a basis for further studies on the evolution, ecology, and conservation of Melastomataceae. Additionally, we highlighted the value of utilizing Sanger sequencing data in the genomic era and explored an approach for integrating various types of NGS data in phylogenetic analysis.

6.1. New insights into the systematics and evolution of the Old World Melastomataceae

Before my PhD started, phylogenetic analyses of the Old World Melastomataceae primarily relied on a limited number of loci from Sanger sequencing, with only a few exceptions (Zhou et al., 2019b; Amarasinghe et al., 2021a). During my PhD, through a major effort to perform Hyb-Seq on the Old World Melastomataceae and integrate publicly available data, we gained new insights into the phylogenetic relationships of three tribes: Dissochaeteae, Melastomateae, and Sonerileae, which collectively account for 70.9% of Paleotropical species and 85.4% of Paleotropical genera. Informed by these newly acquired phylogenies, we also made some taxonomic treatments to better reflect the evolutionary history of these groups and explored the rapid radiation of Sonerileae in Asia (Table 1).

6.1.1. Dissochaeteae

The tribe Dissochaeteae was established by Triana (1866), with eleven genera included. Over time, many of these genera were either synonymized or moved out of the tribe, while new genera were incorporated; see Kartonegoro et al. (2022a) for a review. Using two nuclear (nrETS and nrITS) and four chloroplast markers (*ndhF*, *psbK-psbI*, *rbcL*, and *rpl16*), Kartonegoro et al. (2021) found that the previously defined Dissochaeteae were not monophyletic and subsequently redefined the tribe to include six genera: *Pseudodissochaeta*, *Creochiton*, *Dalenia*, *Diplectria*, *Macrolenes*, and *Dissochaeta*.

In Chapter 2 of my dissertation, we investigated the phylogenetic relationships of *Medinilla mirabilis*. *Medinilla mirabilis* is a liana endemic to central African countries. Its unique morphology makes it easy to be distinguished from the other two *Medinilla* species occurring in mainland Africa. Initially described as *Myrianthemum mirabile* (Engler, 1897), it was later transferred to *Medinilla* (Jacques-Félix, 1977), though this treatment had never been tested with molecular phylogenetics. Historically, *Medinilla* was often associated with Dissochaeteae (Triana, 1871 [“1872”]; van Vliet et al., 1981), but more recent molecular studies placed it within Sonerileae (Zhou et al., 2019b; Kartonegoro et al., 2021). To clarify the phylogenetic placement of *M. mirabilis*, we employed both target enrichment and Sanger sequencing data. The target enrichment data revealed that *M. mirabilis* is phylogenetically distant from the other sampled *Medinilla* species and is instead sister to a clade formed by two sampled Dissochaeteae genera, *Dissochaeta* and *Diplectria* (Chapter 2, Fig. 3). The Sanger data, which included all currently recognized genera and approximately 50% of the species of Dissochaeteae, further revealed that *M. mirabilis* is sister to a clade formed by all sampled Dissochaeteae (Chapter 2, Fig. 3). This result was further supported by wood anatomical evidence. We found that the arrangement of inter-vessel pits in *M. mirabilis* is alternate (Chapter 2, Fig. 4), similar to that in Dissochaeteae but different from the scalariform arrangement in *Medinilla* (van Vliet, 1981). Morphologically, *M. mirabilis* is a liana with interpetiolar outgrowths, 4-merous flowers, and baccate fruits (Chapter 2, Fig. 1), all of which is consistent with traits observed in Dissochaeteae. Based on the phylogenetic, wood anatomical, and morphological evidence we gathered, we proposed to reinstate the genus *Myrianthemum*, with *Myrianthemum mirabile* as its sole species, and placed this monotypic genus within the tribe Dissochaeteae (Table 1). This change extended the formerly Southeast Asian-endemic tribe to Africa.

6.1.2. Melastomateae

The tribe Melastomateae, as currently defined, comprise 44 genera and 823 species, including 17 genera and 499 species in the New World and 27 genera and 324 species in the Old World (Veranso-Libalah et al., 2022). The tribe was established by Bartling (1830). According to the current Code (Turland et al., 2018, Art. 19.4), Melastomateae is the valid name, although historically, the earlier-established name Osbeckieae (de Candolle, 1828a) was more commonly used. The tribal and generic circumscriptions of Melastomateae have long been highly variable; see Veranso-Libalah et al. (2022) for a review. Molecular systematics was first applied to Melastomateae, focusing primarily on the New World groups, using one nuclear locus (nrITS) and two plastid loci (*accD-psaI* and *psbK-psbI*) (Michelangeli et al., 2012). The tribe was resolved as non-monophyletic and consisted of two distinct clades: the *Marcetia* alliance, which was later formally described as the tribe Marcetieae (Rocha et al., 2016), and the core Melastomateae. Despite limited sampling, Old World Melastomateae were found to form a clade, with the Asian clade and Malagasy clade nested within the African species (Michelangeli et al., 2012). Using the same markers but with a more comprehensive sampling of the African groups, Veranso-Libalah et al. (2017) investigated the phylogenetic relationships of the African Melastomateae, and the results were mostly consistent with those of Michelangeli et al. (2012) regarding the relationships among the African, Asian, Malagasy, and Neotropical groups. In this study, *Dinophora* was sequenced for the first time, placed outside Melastomateae, and later included in the newly described tribe Dinophoreae (Penneys et al., 2022). A subsequent phylogenetic analysis with further in-depth sampling of the *Dissotis* and allies clade made the sampling of the African Melastomateae nearly complete (Veranso-Libalah et al., 2020). These two studies, along with the description of the new genus *Nothodissotis* (Veranso-Libalah et al., 2019) and the placement of *Cailliella* (Veranso-Libalah et al., 2021), have significantly advanced our understanding of the systematics of Paleotropical Melastomateae and led to a revision of the African Melastomateae.

In Chapter 4 of my dissertation, we conducted the first phylogenomic study of the Old World Melastomateae using target enrichment data sequenced with the Melastomataceae probe set. This study included all currently recognized Paleotropical genera, particularly three previously unsampled enigmatic species: *Dissotis leonensis*, *D. splendens*, and *Dionychastrum schliebenii*. Our nuclear phylogenomic results are largely congruent with previous studies based on Sanger sequencing data (Michelangeli et al., 2012; Veranso-Libalah et al., 2017; Veranso-Libalah et al., 2020). Apart from *Melastomastrum*, which was found to be non-monophyletic with *Tristemma* nested within it, all other previously circumscribed African genera were recovered as monophyletic (Chapter 4, Figs. 3&4), providing support for the previous revisions and taxonomic treatments (Veranso-Libalah et al., 2017; Veranso-Libalah et al., 2020). The Old World Melastomateae form a monophyletic lineage comprising two primary clades: the Pseudoheterotis clade and the Euheterotis clade, initially proposed by Veranso-Libalah et al. (2017). The Asian endemic clade is sister to the Malagasy endemic clade, and they are nested within the African taxa, making the African Melastomateae paraphyletic (Chapter 4, Figs. 3&4). The monophyly of the Asian endemic clade and the Malagasy endemic clade, as well as their sister-group relationship, have been identified in previous studies (Michelangeli et al., 2012; Veranso-Libalah et al., 2017). However, our study revealed that the sampled *Osbeckia* species do not form a clade, with *Melastoma* nested among them. The non-monophyly of *Osbeckia* was previously observed in a phylogenomic analysis of Myrtales (Maurin et al., 2021), where, with less comprehensive sampling, *Osbeckia stellata* was found to be sister to the Malagasy endemic clade. The four newly sampled *Dissotis leonensis* accessions form a clade that is sister to the rest of the Pseudoheterotis clade, whereas the three newly sampled *D. splendens* accessions form a distinct clade within the Euheterotis clade. *Dionychastrum schliebenii* is the sole species in the genus *Dionychastrum*, and the only sampled accession of *D. schliebenii* was found to be either sister to *Dissotidendron* or nested within *Dissotidendron* depending on the analysis (Chapter 4, Figs. 3&4). Based on the phylogenetic and morphological evidence, we described two new genera: *Allodissotis* and *Paleodissotis* (Table 1).

In Chapter 5, we mapped homologous gene trees onto a species phylogeny based on transcriptomic and genomic data and found a significantly elevated proportion of gene duplications at the most recent common ancestor (MRCA) of the Asian Melastomateae, which suggests a WGD event. This finding supports earlier genomic analyses that detected a WGD occurring after the divergence of Melastomateae and Sonerileae, which appears to be shared among the sampled Asian Melastomateae species (Hao et al., 2022; Zhong et al., 2023; Huang et al., 2024). However, due to limited sampling, we could only determine that this WGD occurred after the divergence of Melastomateae and Sonerileae, which is shared by the Asian Melastomateae.

6.1.3. Sonerileae

With 46 genera and 1,080 species, the pantropical tribe Sonerileae are among the largest tribes in Melastomataceae (Lin et al., 2022; Liu et al., 2022b; Veranso-Libalah et al., 2023; Liu et al., 2024). The tribe was established by Triana (1866), with six genera included. Traditionally, the delimitation of Sonerileae from other groups, such as Dissochaeteae and Oxysporeae, has been problematic, with numerous changes across different classification systems based on morphology; see Liu et al. (2022b) for a review. Previous phylogenetic studies based on Sanger sequencing data with limited sampling within Sonerileae revealed a close relationship between Sonerileae and Oxysporeae, and they are phylogenetically distant from Dissochaeteae (Zeng et al., 2016; Bacci et al., 2019; Kartonegoro et al., 2021). In the latest classification for the family, Oxysporeae has been incorporated into Sonerileae (Penneys et al., 2022). Several studies with major sequencing efforts focusing on Asian Sonerileae or African Sonerileae have been conducted. A study with in-depth sampling of the Asian Sonerileae based on Sanger sequencing data (Zhou et al., 2019a), followed by a study with increased sampling using plastome data (Zhou et al., 2019b), provided preliminary insights into the phylogenetic relationships within the Asian Sonerileae. These studies showed that many Asian Sonerileae genera, such as *Phyllagathis* and *Bredia*, are not monophyletic (Zhou et al., 2019a; Zhou et al., 2019b). A study with a dense sampling of the African Sonerileae (Veranso-Libalah et al., 2023) tested the monophyly of the African Sonerileae genera and resulted in the description of the genus *Mendelia* and the reinstatement of *Bourdaria* (Table 1).

In Chapters 3 and 5 of my dissertation, we investigated the phylogenetic relationships of the fleshy-fruited Sonerileae using primarily target enrichment data sequenced with the Melastomataceae probe set (Chapter 3) and studied the entire tribe by integrating various NGS data sets (Chapter 5).

Although most genera (41 out of 46) in Sonerileae have capsular fruits, nearly 40% of Sonerileae species have fleshy fruits and belong to six fleshy-fruited genera: *Medinilla*, *Pachycentria*, *Plethiandra*, *Heteroblemma*, *Catanthera*, and *Kendrickia*. Very few species from these genera had been sampled in previous phylogenetic analyses. In Chapter 3, using newly generated target enrichment data and publicly available data, we sampled all fleshy-fruited genera, with a particular emphasis on the megadiverse genus *Medinilla*. Our nuclear and plastid phylogenomic analyses revealed that the fleshy-fruited Sonerileae are non-monophyletic and belong to three distinct lineages: *Kendrickia* is sister to the Afrotropical Sonerileae; *Catanthera* and *Heteroblemma* form a clade that is most closely related to some species of *Phyllagathis* and *Driessenia*; and *Medinilla* is non-monophyletic, with *Pachycentria* and *Plethiandra* nested within it. To achieve the monophyly of *Medinilla*, we synonymized *Pachycentria* and *Plethiandra* under *Medinilla* (Table 1) and made the necessary taxonomic treatments for the new names. Within the redefined *Medinilla*, we identified 15 clades and discussed them.

In Chapter 5, we sampled 178 accessions representing 41 of the 46 genera in Sonerileae, including newly generated Hyb-Seq and DGS data, along with publicly available data. Using a newly developed reference comprising 5,626 loci, we provided a well-supported, near-comprehensive phylogeny for the tribe. The Neotropical genera (*Opisthocentra*, *Boyania colombiana*, *Boyania kenwurdackii*, *Phainantha*) and the African endemic *Benna* are successively sister to the rest of the tribe, which consists of a clade comprising the Sri Lankan endemic *Kendrickia* and Afrotropical Sonerileae, and a primarily Asian clade. The phylogenetic relationships within the Afrotropical clade are largely consistent with the Sanger sequence-based phylogeny (Veranso-Libalah et al., 2023), except for the *Amphiblemma*-*Cincinnobotrys*-*Preussiella* clade. In our phylogeny, *Amphiblemma* is sister to *Cincinnobotrys*, whereas, in the Sanger-based phylogeny, *Amphiblemma* is weakly supported as sister to *Preussiella*. The separation of the genus *Mendelia* from *Amphiblemma* and the reinstatement of *Bourdaria* from *Cincinnobotrys* by Veranso-Libalah et al. (2023) based on Sanger data are supported by our phylogenomic results. With the genome of *Tigridiopalma magnifica* sequenced and in-depth sequencing of Asian Sonerileae, Zhou et al. (2022) identified 34 clades within Asian Sonerileae. In our analysis (Chapter 5, Fig. 2), we identified 35 clades in total. Of the 34 clades previously identified by Zhou et al. (2022), we sampled 33, all of which were confirmed in our study. Additionally, we included *Catanthera* and *Poikilogyne* in our sampling. Our dense sampling of the fleshy-fruited Sonerileae confirmed the results obtained using the Melastomataceae probe set (Chapter 3), including the placement of *Catanthera* as sister to *Heteroblemma*. Despite being represented by only one species, *Poikilogyne*, which comprises 28 species mostly endemic to New Guinea, was placed as sister to the other Asian Sonerileae. Since many of these clades have not yet been treated, additional taxonomic work is required to describe and formally recognize these clades (Table 1).

Rapid radiations were observed within the Asian Soneileae but not in the Afrotropical clade. Of the 43 internode pairs that fall within the anomaly zone, 41 are found within Asian Sonerileae, while two are along the backbone, and none are present in the Afrotropical clade (Chapter 5, Fig. 3). Similarly, all five short branches that failed to reject the null hypothesis in the polytomy test are also within Asian Sonerileae (Chapter 5, Fig. 3). This pattern suggests rapid radiations in Asian Sonerileae, which is not observed in Afrotropical Sonerileae. A node with a significantly elevated proportion of duplications was identified based on transcriptomic and genomic data (Chapter 5, Fig. 4a), suggesting a possible WGD event. The same node was also detected in our broader analysis, which integrated data from multiple sources and included most genera of Sonerileae (Chapter 5, Fig. 4b). In this analysis, it was placed at the node where the primarily Asian clade diverges. A recent Ks plot analysis (Huang et al., 2024) identified two WGD events in *Barthea* which occurred after the divergence of Melastomataceae and Myrtaceae: one event is shared by *Barthea* (Sonerileae) and *Melastoma* (Melastomateae), while the other occurred after the divergence of *Barthea* and *Melastoma*. However, the precise placement of these WGD events was unresolved. Our findings suggested that the WGD event occurring after the divergence of Sonerileae and Melastomateae is likely situated at the node separating the two major clades within the primarily Asian clade., which includes over 80% of the species in the whole tribe. The WGD might have contributed to the tribe's rapid diversification in Asia by providing genetic material (Tank et al., 2015; Van de Peer et al., 2017). This hypothesis is further supported by an analysis of the genome of *Barthea barthei*, which revealed that the recent WGD events led to the expansion of gene families (Huang et al., 2024).

6.2. Optimal approaches for integrating different sequencing data sets

The last three decades have witnessed a significant transformation in the methods used to generate sequencing data for phylogenetic studies. The advent of Sanger sequencing enabled researchers to explore evolutionary relationships within groups of interest by analyzing genetic information encoded in DNA sequences. With advances in sequencing technology and the reduction of sequencing costs, we have entered an era where phylogenetic studies using just a few markers have been largely been replaced by approaches that utilize HTS to analyze hundreds to thousands of genomic loci. Various sequencing strategies have been developed to accommodate different research objectives, material quality, and cost constraints, including WGS, RNA-Seq, genome skimming, target enrichment, Hyb-Seq, DGS, and RAD-Seq. As a plant systematist, gathering as much data as possible from the group under study is crucial. During my PhD, I aimed to integrate newly generated data with publicly available Sanger and NGS data to more effectively investigate the phylogenetic relationships of the Old World Melastomataceae.

In Chapter 2, by combining Angiosperms353 and Sanger sequencing data, we successfully placed *Medinilla mirabilis* as sister to the tribe Dissochaeteae. Using target enrichment data, we could place *M. mirabilis* as a close relative of Dissochaeteae s.s. by sequencing a single sample and leveraging publicly available Angiosperms353 data. However, due to the limited sampling of the Angiosperms353 data set, we were uncertain about the exact relationship between *M. mirabilis* and Dissochaeteae s.s. Thanks to the extensive accumulation of Sanger data, we could further confirm that *M. mirabilis* is indeed sister to Dissochaeteae s.s. rather than nested within it. These results highlight the enduring importance of Sanger data in an era when substantial sequencing efforts are ongoing but are still not comparable to the extensive historical accumulation of Sanger sequencing data.

In Chapter 5, we used a newly developed reference file based on existing genomic and transcriptomic data and demonstrated that including a larger number (5,626) of loci in the reference significantly improved the phylogenetic results. This approach proved effective for integrating NGS data from different sequencing strategies. The phylogeny inferred from the loci targeted by the Melastomataceae probe set was outperformed by the phylogeny inferred from the new reference (Chapter 5, Fig. 2; Supplementary Fig. S3). Generally, it has been suggested that increasing the number of gene trees can improve the accuracy of species tree inference (Zhang et al., 2018). By incorporating a larger number of carefully selected loci in the reference, we increased the likelihood of maximizing the use of sequenced read data, including loci that are randomly sequenced, such as those from genome skimming, RNA-Seq, DGS, as well as off-target reads from target enrichment. For example, *Gravesia setifera*, sequenced using the Angiosperms353 probe set, was represented by only one locus when the Melastomataceae probe set was used for sequence recovery, resulting in its ambiguous placement outside *Gravesia*. With 16 loci represented using the new reference, *G. setifera* was plausibly placed as nested within *Gravesia.*

6.3. Perspectives of future studies on systematics and evolution of the Old World Melastomataceae

During my PhD, particularly from the findings presented in Chapter 5, we found that DGS appears to be an optimal sequencing strategy for Melastomataceae. This is due to the relatively small genome size reported for Melastomataceae (less than 400 Mb) and the ability of DGS to recover thousands of nuclear loci and complete organellar genomes. Consequently, we advocate for the broader application of DGS within Melastomataceae. Additionally, there is a pressing need to sequence more genomes from this family, as it remains one of the least sequenced among the largest 15 flowering plant families (https://www.plabipd.de/, accessed 4 December 2024).

Of the six tribes in the subfamily Melastomatoideae that contain Old World species, this dissertation focused on three: Dissochaeteae, Melastomateae, and Sonerileae. The findings presented here are only the beginning of a deeper understanding of the systematics and evolution of the Old World Melastomataceae. Below, I outline future research directions and some questions that need further exploration for the tribes studied. I will also discuss the Old World tribes (Feliciadamieae, Astronieae, and Dinophoreae) and subfamilies (Kibessioideae and Olisbeoideae) not covered in this dissertation.

Dissochaeteae (Figure 1) are a relatively well-studied tribe within the Old World Melastomataceae, with clearly delimited genera (Kartonegoro et al., 2021) and most genera recently revised (e.g., Veldkamp et al. (1978) for *Diplectria*; Kartonegoro and Veldkamp (2013) for *Creochiton*; Kartonegoro et al. (2018) for *Dissochaeta*; Kartonegoro et al. (2019) for *Macrolenes*; Kartonegoro et al.

(2020) for *Pseudodissochaeta*). Biogeographical reconstruction suggested a Neotropical origin of the tribe, followed by migration to Southeast Asia via North America (Kartonegoro et al., 2022b). However, the recent inclusion of *Myrianthemum* within the tribe (Chapter 2) and the close relationship of Feliciadamieae with Dissochaeteae (discussed below) will likely alter the inferred biogeographical history of Dissochaeteae. Furthermore, the phylogenetic relationships inferred from Sanger sequencing (Kartonegoro et al., 2021) still need to be tested with phylogenomic data for more robust conclusions.

In Chapter 4, all currently recognized Old World Melastomateae genera (Figure 1) were sampled, and the resulting phylogeny was largely consistent with previous Sanger-based phylogenies (Veranso-Libalah et al., 2017; Veranso-Libalah et al., 2020). However, our analysis also revealed that within the Asian clade, *Osbeckia* was paraphyletic with *Melastoma* nested within it. Additionally, the internal relationships within the FAEP clade, which includes *Feliciotis*, *Almedanthus*, *Eleotis*, and *Pyrotis*, were discordant across different phylogenies. Each genus in this clade was represented by only one species in our sampling, but it is important to note that both *Almedanthus* and *Pyrotis* are monotypic, whereas *Feliciotis* and *Eleotis* contain 12 and four species, respectively. The three Malagasy genera, *Rousseauxia*, *Amphorocalyx*, and *Dionycha*, could not be separated from each other. Furthermore, *Melastomastrum* was found to be non-monophyletic, with *Tristemma* nested within it. To resolve all these issues, increased sampling across these genera is necessary to better understand their phylogenetic relationships. Although *Dionychastrum schliebenii* was sometimes placed as nested within *Dissotidendron* (Chapter 4, Fig. 4), we decided not to transfer it to *Dissotidendron*. The discordance among different phylogenies needs to be further explored to provide better guidance for potential future taxonomic treatment of this species. In addition, determining the exact timing and placement of the potential WGD event that occurred before the divergence of *Melastoma* and *Osbeckia* (Chapter 5) could provide valuable insights into its potential role in the emergence of the pedo-connective clade in the family to which Melastomateae belongs.

A major focus of this dissertation (Chapters 3 and 5) was on the largest Old World tribe, Sonerileae (Figure 2). Although the New World has only six genera and 13 species (Ulloa Ulloa et al. 2022; Michelangeli 2023), these Neotropical species are important for studying the Old World groups due to their placements in the phylogeny (Chapter 5). Of the six genera, two monotypic genera, *Neblinanthera* and *Tateanthus*, have never been sequenced. The two sequenced *Boyania* species, *B. colombiana* and *B. kenwurdackii*, did not form a clade (Chapter 5), which is consistent with previous studies based on Sanger sequencing (Bacci et al., 2019) and target enrichment data (Maurin et al., 2021). The placement of *Tryssophyton merumense*, sequenced using Angiosperms353, appeared implausible in the phylogeny (see the Discussion of Chapter 5). Therefore, extensive sequencing of these Neotropical species is crucial to resolve these issues. All African genera were included in our analysis (Chapter 5), but the sampling was insufficient to provide insights into the phylogenetic relationships within many genera, particularly in species-rich genera such as *Amphiblemma*, *Calvoa*, and *Gravesia*. *Gravesia* is morphologically diverse, with five species in mainland Africa and 111 in Madagascar (Liu et al., 2022b). Its evolutionary success in Madagascar is an intriguing subject for further study, and a biogeographical analysis could help reveal whether *Gravesia* originated from mainland Africa or Madagascar. Additionally, the only publicly available genome of the tribe is from *Barthea barthei*, which belongs to the Asian clade. Sequencing genomes from African and Neotropical species and comparing them with the genome of *Barthea* would help to further confirm the observed WGD and understand its influence on the genome. It may also provide insights into why the tribe exhibits notable radiations on islands.

For Asian Sonerileae, formal descriptions of the clades identified by Zhou et al. (2022) remains to be performed for proper recognition. Additionally, it has been suggested to treat the genus *Vietsenia* in *Scorpiothyrsus* based on phylogenetic and morphological evidence, but the treatment has yet to be performed. Three genera (*Boerlagea*, *Neodriessenia*, and *Stussenia*) remain to be sampled for phylogenetic analysis. Every year, many new Asian Sonerileae species are described based on morphological characters, but the lack of comprehensive phylogenetic analyses for many genera makes it challenging to test the placement of these new species in a phylogenetic context. For example, 16 species have been described from *Sonerila* since 2023 (Naive and Quakenbush, 2023; Sae Wai and Hu, 2023; Nguyen et al., 2024a; Nguyen et al., 2024b; Pillai et al., 2024). However, no phylogenetic analysis has been performed to resolve the phylogeny of *Sonerila*. Therefore, efforts on taxonomic revision and phylogenetic analysis are needed. Although both *Heteroblemma* and *Catanthera* were recovered as monophyletic in the nuclear phylogeny (Chapter 3, Fig. 1; Chapter 5, Fig. 2), *Heteroblemma* was found to be non-monophyletic with *Catanthera* nested within it in the plastid tree (Chapter 3, Fig. 2). It remains unclear whether the observed cytonuclear discordance is caused by gene flow, and further studies, preferably with better sampling, are needed to understand the evolutionary history of these two genera. We identified 15 alliances within *Medinilla*, which could serve as a basis for future infrageneric classification (Chapter 3). The disjunct distribution of *Medinilla* across the Afrotropics, Asia, and the Pacific islands warrants further study to understand its biogeographic history. Additionally, it would be interesting to investigate the reasons behind the genus's significant radiation in island regions such as Madagascar, the Philippines, and New Guinea.

Feliciadamieae are a monospecific tribe described by Penneys et al. (2022) based on the Guinea endemic species *Feliciadamia stenocarpa*. *Feliciadamia stenocarpa* was previously known only from its type locality and had never been included in any phylogenetic analysis. Due to its limited sampling and unique morphology, Feliciadamieae was the only tribe that could not be placed in the new classification system for the family based on molecular data, although it was suggested to belong to Melastomatoideae

(Penneys et al., 2022) The species has been rediscovered thanks to recent expeditions by our collaborators from Kew and Guinea. Using target enrichment data and a similar methodology to Chapter 2, we found that *F. stenocarpa* is closely related to the newly defined Dissochaeteae comprising Asian Dissochaeteae and *Myrianthemum*. The exact placement of *F. stenocarpa* remained uncertain, as concatenation and coalescent analyses of the nuclear data yielded conflicting topologies. The concatenated nuclear tree supported *F. stenocarpa* as nested within the newly defined Dissochaeteae, sister to the Asian Dissochaeteae, while the coalescent nuclear tree supported *F. stenocarpa* as sister to the entire newly defined Dissochaeteae. To further explore the observed discordance, we employed genome skimming for a subsampled data set comprising nine species. By analyzing 11,830 nuclear orthologous genes and plastomes, we found evidence suggesting that the discordance might be explained by hybridization. Our gene flow analysis indicates that *Myrianthemum* is a hybrid with genetic contributions from Asian Dissochaeteae, which may explain the closer relationship between *Myrianthemum* and Asian Dissochaeteae observed in the coalescent phylogeny. The manuscript describing our study on Feliciadamieae has already been submitted for peer review.

Astronieae, as traditionally defined, include four genera: *Astrocalyx* (1 sp.), *Astronia* (59 spp.), *Astronidium* (67 spp.), and *Beccarianthus* (9 spp.), which are endemic to Southeast Asia and the Pacific islands (Mancera et al., 2022). The only phylogenetic analysis of the tribe with sufficient sampling for generic delimitation is based on morphological data (Mancera et al., 2022). This study identified six clades within Astronieae: *Astrocalyx*, *Astronia*, and *Astronidium* were recovered as monophyletic, while *Beccarianthus* was found to be biphyletic consisting of two clades, *Beccarianthus* s.s. and the Papuasian *Beccarianthus*. Additionally, some species from the Neotropical genus *Tessmannianthus* formed a clade that was sister to Astronieae, which is consistent with a phylogenomic study on Myrtales, in which one species each of *Astrocalyx*, *Astronidium*, and *Beccarianthus* formed a clade sister to a clade comprising two *Tessmannianthus* species. Penneys et al. (2022) included the entire genus *Tessmannianthus* within Astronieae, thus expanding the tribe to five genera and 143 species, although one *Tessmannianthus* species sampled by Mancera et al. (2022) did not group with the other sampled *Tessmannianthus* species. The tribe is still awaiting its first molecular phylogenetic study with extensive sampling to clarify the generic boundaries and evaluate the inclusion of the Neotropical *Tessmannianthus* within *Astronieae*.

Dinophoreae (Figure 1) are a newly established tribe that includes eight species across three genera: the African endemic genera *Dinophora* (1 sp.) and *Phaeoneuron* (2 spp.), and the Southeast Asian endemic *Ochthocharis* (5 spp.) (Penneys et al., 2022). While the three genera formed a clade in the phylogenetic analysis that led to the establishment of the tribe, only one species from each genus was sampled, leaving the generic boundaries within the tribe unresolved (Penneys et al., 2022). Future sampling, particularly from the largest genus *Ochthocharis*, is needed to better understand the relationships and boundaries among these genera.

The subfamily Kibessioideae consist of a single genus, *Pternandra*, which includes 15 species distributed throughout tropical Asia to tropical Australia (Renner, 2022). While several species of *Pternandra* have been included in phylogenetic analyses, no study has yet focused specifically on resolving the phylogenetic relationships within the genus.

The subfamily Olisbeoideae (Figure 1) are pantropical and consist of six genera and 556 species, with four genera and 457 species found in the Old World: *Lijndenia* (16 spp.), *Memecylon* (391 spp.), *Spathandra* (1 sp.), and *Warneckea* (49 spp.). Traditionally, they were often placed in a separate family, Memecylaceae (Stone, 2022). The phylogenetic relationships among Olisbeoideae, Kibessioideae, and Melastomatoideae have been conflicting and remain unresolved (Zhou et al., 2019b; Maurin et al., 2021; Chen et al., 2023b). Understanding the phylogenetic placements of the three subfamilies is crucial for elucidating the evolutionary history of the family. Previous studies based on Sanger sequencing data (Stone, 2006; Stone and Andreasen, 2010; Stone, 2014) and target enrichment data (Amarasinghe et al., 2021a) have provided preliminary insights into the phylogenetic relationships within Olisbeoideae. However, these analyses were limited by incomplete sampling, and further inclusion of additional species with NGS data is necessary to resolve their evolutionary relationships.

Table 1. Genera treated in the Melastomataceae book chapters for Dissochaeteae (Kartonegoro et al. 2022a), Melastomateae (Veranso-Libalah et al., 2022), and Sonerileae (Liu et al., 2022b) and subsequent taxonomic changes. Genera marked with an asterisk (*) indicate that they are currently non-monophyletic and require re-delimitation.

Tribe Dissochaeteae	Tribe Melastomateae	Tribe Sonerileae
Kartonegoro et al. 2022a	**Veranso-Libalah et al., 2022**	**Liu et al., 2022b**
Creochiton	*Almedanthus*	*Amphiblemma*
Dalenia	*Amphorocalyx*	*Anerincleistus**
Diplectria	*Anaheterotis*	*Aschistanthera*
Dissochaeta	*Antherotoma*	*Barthea*
Macrolenes	*Argyrella*	*Benna*
Pseudodissochaeta	*Cailliella*	*Blastus*
	Derosiphia	*Boerlagea*
Genus newly included	*Dichaetanthera*	*Boyania*
Myrianthemum (Chapter 2)	*Dionycha*	*Bredia*
	Dionychastrum	*Calvoa*
	Dissotidendron	*Catanthera*
	Dissotis	*Cincinnobotrys*
	Dupineta	*Cyphotheca**
	Eleotis	*Dicellandra*
	Feliciotis	*Driessenia*
	Guyonia	*Fordiophyton*
	Heterotis	*Gravesia*
	Melastoma	*Heteroblemma*
	*Melastomastrum**	*Kendrickia*
	Nerophila	*Kerriothyrsus**

	Nothodissotis	*Medinilla*
	*Osbeckia**	*Neblinanthera*
	Pseudosbeckia	*Neodriessenia*
	Pyrotis	*Opisthocentra*
	Rosettea	*Oxyspora*
	Rousseauxia	*Pachycentria* (synonymized in Chapter 3)
	Tristemma	*Phainantha*
		Plethiandra (synonymized in Chapter 3)
	Genera newly included	*Phyllagathis*
	Allodissotis (Chapter 4)	*Plagiopetalum**
	Paleodissotis (Chapter 4)	*Poikilogyne*
		*Poilannammia**
		Preussiella
		Sarcopyramis
		*Scorpiothyrsus**
		Sonerila
		*Sporoxeia**
		Stussenia
		*Styrophyton**
		Tashiroea
		Tateanthus
		Tigridiopalma
		Tryssophyton
		Vietsenia (to be synonymized)
		Genera newly included

		Bourdaria (Veranso-Libalah et al. 2023)
		Mendelia (Veranso-Libalah et al. 2023)
		Nephoanthus (Lin et al. 2022)
		Perilimnastes (Liu et al. 2024)
		Genera to be described
		Driessenia (isomorphic)
		Fordiophyton breviscapum
		Oxyspora (Bornean) clade
		P. griffithii−O. bullata
		P. tuberculata−P. hispida
		Phyllagathis (pentamerous)
		Phyllagathis (thyrsoid)
		Phyllagathis cavaleriei
		Phyllagathis erecta
		Phyllagathis scortechinii

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Education

- **2013 – 2017**
  B.Sc., China Agricultural University
  Advisor: Prof. Dr. Bo Hong
  Thesis: The adaptive relationship between numbers and types of suckers and drought resistance in chrysanthemum
- **2017 – 2021**
  M.Sc., Institute of Botany, Chinese Academy of Sciences (IBCAS)
  Advisor: Prof. Dr. Xiao-Quan Wang
  Thesis: A phylogenomic and biogeographic study of Podocarpaceae
- **2021 - Present**
  PhD student, LMU Munich
  Advisor: Prof. Dr. Gudrun Kadereit
  Thesis: Phylogenomics and taxonomic implications of Old World Melastomataceae

Research Experience

- **2015 – 2016**
  Bachelor Student, China Agricultural University
  The dwarfing effects of two plant growth regulators with different concentrations on chrysanthemum plants
- **2016 – 2017**
  Bachelor Student, China Agricultural University
  The relationship between sucker morphological traits and drought tolerance in 22 chrysanthemum cultivars
- **Spring 2017**
  Flower Recognition App Program Intern, Microsoft Research Asia (MSRA)
  Plant image identification; review and modification of descriptions for hundreds of species; collaboration with developers to improve data quality and identification accuracy for the Flower Recognition app, an AI-driven tool for plant recognition.
- **2017 – 2020**
  Master Student, State Key Laboratory of Systematic and Evolutionary Botany, IBCAS
  Phylogenomic, biogeographic, and trait analysis of Podocarpaceae using RNA-Seq data
- **Dec 2021 – Dec 2023**
  Research Assistant, Botanische Staatssammlung München
  Type specimen digitization
- **Apr 2021 – Present**
  PhD Student, LMU Munich
  Systematics of the Old World Melastomataceae

Field Work (Specimen Collection and Ecological Observation)

- Oct 2016: Aquatic plants in the Huai River Basin, China
- May 2017: Conifers in Zhejiang, China
- Aug 2017: *Rhododendron* and conifers in Jilin, China
- Jun 2018: *Ephedra* in Gansu and Shaanxi, China
- Aug 2018: Gymnosperms and *Rhododendron* in Java and Sumatra, Indonesia
- Jun 2022: Vascular plants in Cameroon
- Sep 2023 - Nov 2023: Melastomataceae in Madagascar

Herbaria Visited

- China: CSH, PE, WH
- Germany: M
- Madagascar: TAN
- US: MO, NY

Conferences and Seminars

Talks and Posters

- Oct 2021: Meeting of the section biodiversity and evolutionary biology, German Botanical Society, online
  Talk: New insights into the phylogeny and character evolution of Podocarpaceae inferred from transcriptomic data (second best student talk)
- Sep 2022: Presentation ”Expedition to Cameroon - start of a new botanical partnership in tropical Africa”, Munich, Germany
  Talk: *Medinilla mirabile* - the story of a melastome species
- May 2023: NYBG Science Seminars, New York, US
  Talk: Combining Angiosperms353 and Sanger data provides support for the reinstatement of the genus *Myrianthemum* (Melastomataceae)
- Aug 2023: Meeting of the Section Biodiversity & Evolutionary Biology, German Botanical Society, Giessen, Germany
  Poster: *Medinilla* (Melastomataceae) redefined
- Jul 2024: International Botanical Congress, Madrid, Spain
  Poster: Phylogenetic relationships and biogeography of fleshy-fruited Sonerileae (Melastomataceae)

Other Attended Conferences

- Dec 2017: The 2nd Systematic Biology Forum, Beijing, China
- Nov 2018: Chinese National Symposium on Systematic and Evolutionary Botany, Wuhan, China
- Sep 2022: Bauhin 2022: 400 Years of Botanical Collections, Basel, Switzerland

Publications

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- **Chen, L.**, Jin, W.-T., Liu, X.-Q., Wang, X.-Q. (2022). New insights into the phylogeny and evolution of Podocarpaceae inferred from transcriptomic data. *Molecular Phylogenetics and Evolution*, 166, 107341. link