

Phylogeny and systematics of African Melastomateae (Melastomataceae)

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Abstract Melastomateae are the most species-rich (185 spp./13 gen.) and morphologically diverse tribe within the African Melastomataceae. In this study we present the first in-depth phylogenetic analysis of African Melastomateae using sequences generated from one nuclear (nrITS) and two plastid spacers (*accD-psaI*, *psbK-psbL*) sampling 183 accessions representing 75 African, 10 Madagascan and 7 Asian species and a broad outgroup sampling. We infer phylogenetic relationships using maximum likelihood, maximum parsimony and Bayesian approaches and propose a revised generic classification of African Melastomateae based on our molecular trees in combination with a careful reassessment of morphological variation. Our phylogenetic analyses support the monophyly of Old World Melastomateae except *Dinophora* which clearly falls outside Melastomateae. Asian and Madagascan endemic genera of Melastomateae are nested among the African genera. Of the African genera only two monophyletic groups, *Dichaetanthera* and *Tristemma*, are recovered in addition to the monospecific *Pseudosbeckia* lineage, while *Antherotoma*, *Dissotis* and *Heterotis* as currently circumscribed are polyphyletic. However, the subgenera and sections of these genera are mostly recovered as morphologically distinct and molecularly well-supported clades. Isomorphism versus dimorphism of the stamens is found to be an unreliable character when delimiting genera in Melastomateae. We propose the reinstatement of *Argyrella* and *Dupineta*, a new status at generic rank for *Dissotis* subg. *Dissotidendron*, a broadened circumscription of *Guyonia* (to include the species previously placed in *Heterotis* sect. *Cyclostemma*), and description of a new, monospecific genus *Anaheterotis* for the *Heterotis pobeguinii* lineage. *Heterotis* is maintained at generic rank but with a narrower circumscription in comparison to earlier treatments. We accommodate the rare *Osbeckia porteresii* lineage from Mt. Nimba (Guinea) within an expanded *Melastomastrum*. To complete our generic realignment, a total of 42 new combinations are effected at the species level and below, and a key is provided for the 12 genera presently recognised in African Melastomateae. Denser taxonomic sampling and sequencing of more loci will be needed to resolve relationships within the large clade of *Dissotis* s.str. and allies (including *Antherotoma* as well as three West African species erroneously placed in the otherwise Asian *Osbeckia*).

Keywords Africa; *Dissotis*; *Heterotis*; Melastomataceae; Melastomateae; molecular phylogenetics; systematics; taxonomy

Supplementary Material Electronic Supplement (Figs. S1 & S2) and DNA sequence alignment files are available in the Supplementary Data section of the online version of this article at <http://ingentaconnect.com/content/iapt/tax>

■ INTRODUCTION

Melastomataceae s.l. (incl. Memecylaceae, cf. APG, 2009) constitute a characteristic element of numerous tropical ecosystems and range among the largest tropical plant families worldwide. According to Renner & al. (2007–), Melastomataceae comprise ca. 170 genera and 5000 species with greatest diversity in the Neotropics (ca. 3000 spp.), followed by Southeast Asia (ca. 1000), with moderate diversities in Madagascar (ca.

330) and Africa (ca. 320). They exhibit a wide variety of life forms from trees, shrubs, woody climbers to herbs and grow in a wide range of habitats, from lowland to montane tropical forests, in savannas as well as in disturbed secondary vegetation (Renner, 1993; Clausen & Renner, 2001). However, their systematics and phylogenetic relationships, particularly in the Paleotropics, remain poorly understood.

The tribe Melastomeae was first proposed by Bartling (1830) to include species having poricidal anthers. This tribe

was later split based on biogeography, anther structure and nature of pubescence (Triana, 1865, 1872; Cogniaux, 1891). Cogniaux (1891) placed the African and Asian genera in Osbeckieae and the American genera in Tibouchineae. This classification scheme was widely accepted and used (Van Tieghem, 1891; Krasser, 1893; Jacques-Félix, 1981, 1995; Van Vliet & al., 1981) until Renner (1993) merged these two segregate tribes resurrecting Melastomeae [from here on referred to as “Melastomateae”. The generic name *Melastoma* L. is of Greek origin and is a neuter noun. The plural of *stoma* is *stomata*, and “Melastomataceae” is thus the correct family name corresponding to the generic name *Melastoma*, not “Melastomaceae” as used by Cogniaux (1981) and other earlier authors. As such, “Melastomateae” is the correct tribal name corresponding to the generic name *Melastoma*, not “Melastomeae” as used by Renner (1993) and other later authors. See the online Indices Nominum Supragenericorum Plantarum Vascularium by Reveal (2011–)].

This pantropical tribe now comprises about 870 species in 47 genera (Michelangeli & al., 2013). In Africa, Melastomateae are the most diverse melastome tribe with about 185 species in 13 genera (Wickens, 1975; Renner, 1993) although only ten genera were recognised by Jacques-Félix (1995). While currently ca. 66% of the African species belong to the diverse genus *Dissotis* Benth., seven genera comprise only 2–15 species and three are monospecific (Jacques-Félix, 1995) (Table 1).

Morphologically, African Melastomateae are diverse, offering a multitude of characters for generic and species delimitation (Figs. 1, 2). Growth forms range from herbs to trees, plants are glabrous to densely pubescent, and the number of longitudinal leaf nerves varies between 3 and 11. Floral morphology has been particularly important in delimiting taxa, e.g., floral merosity (4- or 5- or rarely 6-merous); persistent or caducous calyx-lobes; presence or absence of intersepalal appendages; type and nature of calyx-tube pubescence; stamens isomorphic or dimorphic; pedoconnective and staminal appendages present or absent; arcuate or linear pedoconnectives; and lobed, bilobed or clavate to 3-cuspidate staminal appendages (Figs. 1, 2). Capsule and seed morphology have also offered diagnostic characters for species delimitation. On the basis of this morphological diversity, several generic and infrageneric classification schemes have been proposed (Table 1) for African Melastomateae (Bentham, 1849; Naudin, 1850, 1853; Triana, 1872; Cogniaux, 1891; Fernandes & Fernandes, 1969; Jacques-Félix, 1981, 1995; Van Vliet & al., 1981).

Bentham (1849) recognised only four genera: *Heterotis* Benth., *Dissotis*, *Tristemma* Juss. and *Osbeckia* L., and he proposed the first infrageneric classification of *Heterotis* with four sections, though only two of them (sect. *Heterotis*, sect. *Cyclostemma* Benth.) were later recognised by Jacques-Félix (1981, 1995). Triana (1872) recognised five additional genera (*Dichaetanthera* Endl., *Antherotoma* Hook.f., *Guyonia* Naudin, *Dinophora* Benth., *Nerophila* Naudin), and he also transferred all species treated in *Heterotis* sect. *Leiocalyx* Planch. ex Benth., *H.* sect. *Wedeliopsis* Planch. ex Benth. and *Melastomastrum* Naudin to *Tristemma*. Fernandes & Fernandes (1969) recognised four additional genera (*Pseudosbeckia*

A.Fern. & *R.Fern.*, *Cailliella* Jacq.-Fél., *Dionychastrum* A.Fern. & *R.Fern.*, *Derosiphia* Raf.) and transferred all species of *Heterotis* to *Dissotis*. They also proposed a new infrageneric classification of *Dissotis* which consisted of six subgenera, i.e., subg. *Dissotis*, subg. *Dupineta* (Raf.) A.Fern. & *R.Fern.*, subg. *Dissotidendron* A.Fern. & *R.Fern.*, subg. *Osbeckiella* A.Fern. & *R.Fern.*, subg. *Heterotis* (Benth.) A.Fern. & *R.Fern.* and sect. *Argyrella* (Naudin) A.Fern. & *R.Fern.*, and within subg. *Dissotis* they recognised four sections, i.e., sect. *Dissotis*, sect. *Macrocarpae* A.Fern. & *R.Fern.*, sect. *Squamulosae* A.Fern. & *R.Fern.* and sect. *Sessilifoliae* A.Fern. & *R.Fern.* This classification scheme by Fernandes & Fernandes (1969) was further modified by Jacques-Félix (1981, 1995) who proposed an additional subgenus *Paleodissotis* Jacq.-Fél. within *Dissotis*, and transferred the species of subg. *Osbeckiella* to *Antherotoma* and reinstated *Heterotis* at generic rank. Within *Heterotis* he recognised three sections, i.e., sect. *Heterotis*, sect. *Argyrella* (Naudin) Jacq.-Fél. and sect. *Cyclostemma*. He also transferred *Nerophila* to *Chaetolepis* (DC.) Miq., an otherwise New World genus of Melastomateae (Table 1; see also Grimm & Almeda, 2013).

While most genera of African Osbeckieae (Melastomateae) have always been placed in this tribe, the positions of *Dinophora* and *Guyonia* remain controversial. *Dinophora* has been treated in Rhexieae (Bentham, 1849), Bertolonieae (Van Tieghem, 1891), Melastomateae (Triana, 1872; Baillon, 1877; Cogniaux, 1891; Gilg, 1898; Engler, 1921; Renner, 1993; Stevens, 2001–) and Dissochaeteae (Jacques-Félix, 1983, 1995; Leistner, 2005). Several authors have treated *Guyonia* within the Old World Melastomateae (Triana, 1872; Van Tieghem, 1891; Krasser, 1893; Engler, 1921; Renner, 1993). However, Jacques-Félix (1995) treated it in Tibouchineae (New World Melastomateae) because of its tibouchinoid seeds which are elongate-cochleate, somewhat smooth or asperulate having very shallowly raised surface cells (see description of *Chaetolepis* seeds; Whiffin & Tomb, 1972) and also because of its chromosome number $n = 9$ (Favarger, 1962).

Molecular phylogenetic analyses have been widely used in resolving phylogenetic relationships at tribal (Meyer, 2001; Fritsch & al., 2004; Michelangeli & al., 2004, 2013; Penneys & Judd, 2013) and generic levels in Melastomataceae (Ionta & al., 2007; Reginato & al., 2010; Stone & Andreasen, 2010; Stone, 2014; Kriebel, 2016; Reginato & Michelangeli, 2016). The study by Clausing & Renner (2001) suggested that Melastomateae are monophyletic, but Michelangeli & al. (2013), studying the phylogenetic relationships of New World Melastomateae based on a wide sampling, showed that Melastomateae sensu Renner (1993) are diphyletic. Two non-sister clades, the “Marcetia and allies” and the “core Melastomateae” were recovered and supported by molecular and morphological characters (Michelangeli & al., 2013). Also, the Old World Melastomateae formed a monophyletic lineage, but the Madagascan endemic and Asian Melastomateae genera were found to be nested among the African Melastomateae (Clausing & Renner, 2001; Michelangeli & al., 2013). Nevertheless, the African members of Melastomateae are notoriously understudied and only barely represented with only 7 (<4%) of the ca. 185 species so far

Table 1. Summary of the major inter- and infrageneric classifications proposed for the African Melastomataceae and the revised classification based on the molecular phylogenetic analyses conducted in this study.

Bentham, 1849	Triana, 1872	Fernandes & Fernandes (1954a, 1969)	Jacques-Félix (1981, 1995)	This study
<i>Dissothis</i> Benth.	<i>Dissothis</i> Benth. sect. <i>Eudissothis</i> Triana sect. <i>Heterotis</i> Benth. sect. <i>Argyrella</i> Naudin	<i>Dissothis</i> Benth. subg. <i>Dissothis</i> Benth. sect. <i>Dissothis</i> Benth. sect. <i>Macrocarpae</i> A.Fern. & R.Fern. sect. <i>Squamulosae</i> A.Fern. & R.Fern. sect. <i>Sessilifoliae</i> A.Fern. & R.Fern. subg. <i>Dissothis</i> Benth. subg. <i>Dupineta</i> (Raf.) A.Fern. & R.Fern. subg. <i>Osbeckiella</i> A.Fern. & R.Fern. sect. <i>Osbeckiella</i> A.Fern. & R.Fern. subg. <i>Heterotis</i> Benth. sect. <i>Heterotis</i> Benth. sect. <i>Argyrella</i> (Naudin) A.Fern. & R.Fern.	<i>Dissothis</i> Benth. (±120) subg. <i>Dissothis</i> Benth. sect. <i>Dissothis</i> Benth. sect. <i>Macrocarpae</i> A.Fern. & R.Fern. sect. <i>Squamulosae</i> A.Fern. & R.Fern. sect. <i>Sessilifoliae</i> A.Fern. & R.Fern. subg. <i>Paleodissothis</i> Jacq.-Fél. subg. <i>Dissothis</i> Benth. subg. <i>Dupineta</i> (Raf.) A.Fern. & R.Fern. subg. <i>Osbeckiella</i> A.Fern. & R.Fern. sect. <i>Osbeckiella</i> A.Fern. & R.Fern. sect. <i>Senegambia</i> Jacq.-Fél.	* <i>Dissothis</i> Benth. (±50; <i>D. grandiflora</i> Benth.) subg. <i>Dissothis</i> Benth. sect. <i>Dissothis</i> Benth. (<i>D. grandiflora</i> Benth.) sect. <i>Macrocarpae</i> A.Fern. & R.Fern. (<i>D. speciosa</i> Taub.) sect. <i>Squamulosae</i> A.Fern. & R.Fern. (<i>D. longicaudata</i> Cogn.) sect. <i>Sessilifoliae</i> A.Fern. & R.Fern. (<i>D. welwitschii</i> Cogn.) subg. <i>Paleodissothis</i> Jacq.-Fél. (<i>D. leonensis</i> Hutch. & Dalziel)
Treated in <i>Dissothis</i> sect. <i>Argyrella</i> Naudin	Treated in <i>Dissothis</i> sect. <i>Argyrella</i> (Naudin) A.Fern. & R.Fern.	Treated in <i>Dissothis</i> subg. <i>Dupineta</i> (Raf.) A.Fern. & R.Fern.	Treated in <i>Heterotis</i> sect. <i>Argyrella</i> (Naudin) Jacq.-Fél.	<i>Argyrella</i> Naudin (6; <i>A. canescens</i> (E.Mey. ex Graham) Harv.)
Treated in <i>Tristemma</i> Juss.	Treated in <i>Dissothis</i> subg. <i>Dissothis</i> Benth. & R.Fern.	Treated in <i>Dissothis</i> subg. <i>Dissothis</i> Benth. & R.Fern.	Treated in <i>Dissothis</i> subg. <i>Dissothis</i> Benth. & R.Fern.	<i>Dupineta</i> (Sm.) Raf. (6; <i>D. multiflora</i> (Sm.) Raf.)
<i>Tristemma</i> Juss. (including <i>Melastomastrum</i> , <i>Heterotis</i> sect. <i>Leiocalyx</i> and sect. <i>Wedeliopsis</i>)	Treated in <i>Tristemma</i> Juss.	Treated in <i>Dissothis</i> subg. <i>Dissothis</i> Benth. & R.Fern.	Treated in <i>Dissothis</i> subg. <i>Dissothis</i> Benth. & R.Fern.	<i>Dissothis</i> Naudin (A.Fern. & R.Fern.) Veranso-Libalah & G.Kaderit stat. nov. (11; <i>D. meleri</i> (Hook.f.) Veranso-Libalah & G.Kaderit
<i>Tristemma</i> Juss.	<i>Tristemma</i> Juss.	<i>Melastomastrum</i> Naudin	<i>Melastomastrum</i> Naudin (6)	<i>Melastomastrum</i> Naudin (6; including <i>O. porteresii</i> Jacq.-Fél. (<i>M. capitatum</i> (Vahl) A.Fern. & R.Fern.))
<i>Heterotis</i> Benth. sect. <i>Heterotis</i> Benth. sect. <i>Cyclostemma</i> Benth. sect. <i>Leiocalyx</i> Benth. sect. <i>Wedeliopsis</i> Benth.	Treated in <i>Dissothis</i> sect. <i>Heterotis</i> Benth.	Treated in <i>Dissothis</i> subg. <i>Heterotis</i> (Benth.) A.Fern. & R.Fern.	Treated in <i>Heterotis</i> sect. <i>Cyclostemma</i> Benth.	<i>Tristemma</i> Juss. (16; <i>T. mauritanum</i> J.F.Gmel.)
Treated in <i>Heterotis</i> sect. <i>Cyclostemma</i> Benth.	Treated in <i>Dissothis</i> sect. <i>Heterotis</i>	Treated in <i>Dissothis</i> subg. <i>Heterotis</i>	Treated in <i>Heterotis</i> sect. <i>Cyclostemma</i>	<i>Dichaeatanthera</i> Endl. (8; <i>D. articulata</i> Endl.)
		<i>Pseudosbeckia</i> A.Fern. & R.Fern.	<i>Pseudosbeckia</i> A.Fern. & R.Fern. (1)	<i>Heterotis</i> Benth. (6; <i>H. rotundifolia</i> (Sm.) Jacq.-Fél.)
		Treated in <i>Dissothis</i> sect. <i>Sessilifoliae</i>	Treated in <i>Heterotis</i> sect. <i>Cyclostemma</i>	Treated in <i>Guyonia</i>
				<i>Pseudosbeckia</i> A.Fern. & R.Fern. (1; <i>P. swynnertonii</i> (Baker f.) A.Fern. & R.Fern.)
				<i>Anaheterotis</i> Veranso-Libalah & G.Kaderit gen. nov.

<i>Osbeckia</i> L.	<i>Dionychastrum</i> A. Fern. & R. Fern.	<i>Dionychastrum</i> A. Fern. & R. Fern. (1)	<i>Dionychastrum</i> A. Fern. & R. Fern. (1)
	<i>Antherotoma</i> Hook.f.	<i>Antherotoma</i> Hook.f. (11; included subg. <i>Osbeckiella</i>)	<i>Antherotoma</i> Hook.f. (11; <i>A. naudinii</i> Hook.f.)
	<i>Guyonia</i> Naudin	<i>Guyonia</i> Naudin (1; treated in <i>Tibouchineae</i>)	<i>Guyonia</i> Naudin (14; <i>G. tenella</i> Naudin, including most species treated in <i>H. sect. Cyclostemma</i> Benth.)
	<i>Osbeckia</i> L.	<i>Cailliella</i> Jacq.-Fél.	<i>Cailliella</i> Jacq.-Fél. (1; <i>C. praerupticola</i> Jacq.-Fél.)
	<i>Nerophila</i> Naudin (treated in <i>Osbeckiaceae</i>)	<i>Osbeckia</i> L. (4)	*African <i>Osbeckia</i> (3)
	<i>Derosiphia</i> Raf.	<i>Chaetolepis</i> Miq. (1; treated in <i>Dissochaeteae</i>)	<i>Chaetolepis</i> Miq. (1; treated in <i>Dissochaeteae</i>)
Treated in <i>Osbeckia</i> sect. <i>Podocaelia</i> Benth.		<i>Derosiphia</i> Raf. (included in <i>Dissotis</i> subg. <i>Dupineta</i> (Raf.) A. Fern. & R. Fern as <i>Dissotis tubulosa</i> (Sm.) Triana)	* <i>Dissotis tubulosa</i> (Sm.) Triana (1)
<i>Dinophora</i> Benth. (treated in <i>Rhexiaceae</i>)	<i>Dinophora</i> Benth. (treated in <i>Osbeckiaceae</i>)	<i>Dinophora</i> Benth. (1; treated in <i>Dissochaeteae</i>)	Unplaced (1; not a <i>Melastomateae</i>)

Types are only provided for the classification proposed in this study. The number of species per genus as suggested by Jacques-Félix (1995) and in this study are indicated in brackets and bold. * Indicates all the genera included in the informal *Dissotis* and allies clade.

included in any phylogenetic analyses (Clausing & Renner, 2001; Michelangeli & al., 2013).

It is unknown if African Melastomateae genera, subgenera and sections as currently recognized by Jacques-Félix (1981, 1995) represent natural lineages. Therefore, a well-sampled molecular phylogeny is needed to set the basis for an updated generic and infrageneric classification of African Melastomateae. The present phylogenetic study is based on sequence variation in three DNA regions (ITS, *accD-psaI*, *psbK-psbL*), and includes representatives of almost all currently recognised genera, subgenera and sections of African Melastomateae. The specific goals of this study are (1) to resolve phylogenetic relationships among genera, subgenera and sections within the African Melastomateae, and (2) to propose a revised generic classification.

■ MATERIALS AND METHODS

Sampling and outgroups. — We included a total of 183 accessions of which 116 represent 75 species and 10 of the 13 traditionally recognised African genera (Fernandes & Fernandes, 1969; Wickens, 1975; Renner, 1993; Jacques-Félix, 1995). We were unable to obtain samples of three monospecific genera, namely *Cailliella*, *Dionychastrum* and *Nerophila*. Within *Dissotis* s.l. (Fernandes & Fernandes, 1969), we sampled 58 species to test if the updated inter- and infrageneric groups proposed by Jacques-Félix (1995) represent natural lineages (Table 1). Three of the four recognised *Dissotis* subgenera (i.e., subg. *Dissotis*, subg. *Dissotidendron*, subg. *Dupineta*) are represented in this study. We were unable to sample *Dissotis leonensis* Hutch. & Dalziel, an endemic of Sierra Leone and Guinea-Conakry and the only species of *Dissotis* subg. *Paleodissotis*. However, we sampled all four sections (sect. *Dissotis*, sect. *Macrocarpae*, sect. *Sessilifoliae*, sect. *Squamuloseae*) of *D. subg. Dissotis* and all three sections (sect. *Agryrella*, sect. *Cyclostemma*, sect. *Heterotis*) of *Heterotis* (Fernandes & Fernandes, 1969; Jacques-Félix, 1981) (see Table 1). Seventeen Madagascan and Asian Melastomateae were also sampled as part of the Old World Melastomateae. Ten of ca. 48 Madagascan species were sampled, with 5 species representing all three Madagascan endemic genera (*Amphorocalyx* Baker, *Rousseauxia* DC., *Dionycha* Naudin). Two (*Melastoma*, *Osbeckia*) of the three Asian Melastomateae genera representing 7 of ca. 83 species were also sampled. The Madagascan endemic *Dissotis pauciflora* (Baker) Jacq.-Fél. (formerly *Rhodosepala pauciflora* Baker) was not sampled. As outgroups, we included 3 species of *Miconieae*, 3 of *Merianieae*, 2 of *Rhexiaceae*, 1 of *Physeterostemon*, 3 of *Microlicieae*, 37 (14/30 genera) of New World Melastomateae and 2 species of *Cambessedesia* DC. Voucher information and GenBank accession numbers are available in Appendix 1.

Morphological data were obtained from the literature and supplemented by our own observations. Field observations were conducted in Cameroon (July–October 2014), and study of herbarium material was made through visits to BR and BRLU, loans from BR, BRLU, C, EA, K, MO, WAG and

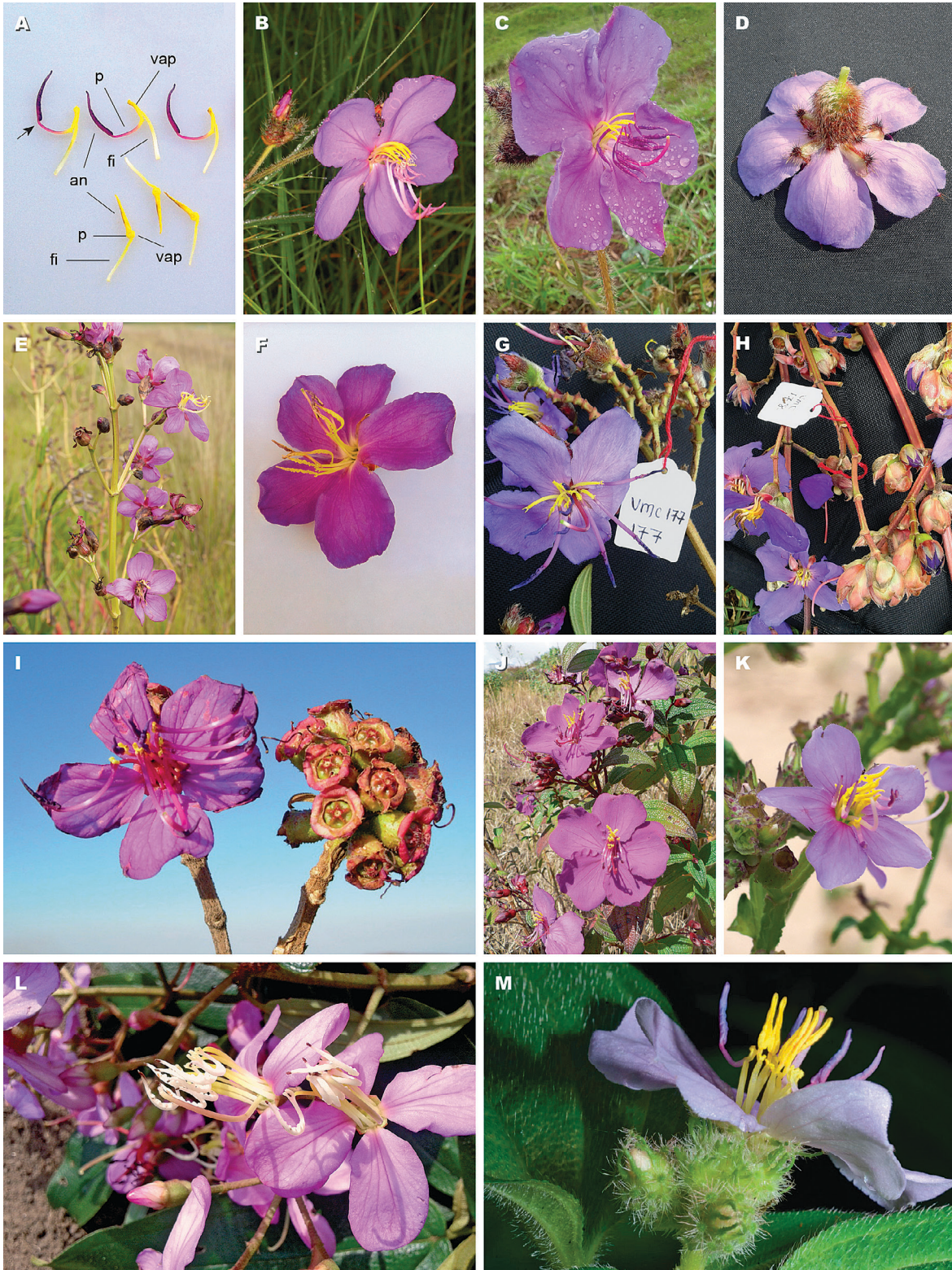


Fig. 1. Flowers of representatives of African Melastomateae with focus on stamen morphology. **A**, Features of typical Melastomateae stamens (an, anther; fi, filament; p, pedoconnective; vap, ventral appendage; arrow indicates position of dorsal appendages if present); **B**, *Dissotis grandiflora* (subg. *Dissotis* sect. *Dissotis*); **C & D**, *Dissotis longisetosa* (subg. *Dissotis* sect. *Dissotis*); **E**, *Dissotis welwitschii* (subg. *Dissotis* sect. *Sessilifoliae*); **F**, *Dissotis perkinsiae* (subg. *Dissotis* sect. *Macrocarpae*); **G**, *Dissotis princeps* (subg. *Dissotis* sect. *Squamulosae*); **H**, *Dissotis thollonii* var. *elliotii* (subg. *Dissotis* sect. *Squamulosae*); **I**, *Dissotidendron melleri*; **J**, *Dissotidendron johnstonianum*; **K**, *Dupineta brazzae*; **L**, *Dichaetanthera corymbosa*; **M**, *Dupineta multiflora*. — Photographs by M.C. Veranso-Libalah (A, C, D, F–H, L), P.B., Phillipson (B), D. Goyder (E, K), R. v. Blittersdorff (I, J), E. Bidault (M).



Fig. 2. Representatives of African Melastomateae. **A**, *Argyrella canescens*; **B**, *Heterotis prostrata*; **C**, *Antherotoma irvingiana*; **D**, *Osbeckia decandra*; **E**, *Antherotoma naudinii*; **F**, *Dissotis tubulosa*; **G** & **H**, *Melastomastrum porteresii*; **I**, *Melastomastrum segregatum*; **J**, *Melastomastrum theifolium*; **K**, *Tristemma mauritanium*; **L**, *Dinophora spenneroides*; **M**, *Pseudosbeckia swynertonii*. — Photographs by B. Wursten (A, E, I, M), V. Droissart (B), M.C. Veranso-Libalah (C, F, J–L), E. Bidault (D, G, H).

UPS, and through online repositories from BM (<http://data.nhm.ac.uk/>), LISC (<http://actd.iict.pt/>), P (<https://science.mnhn.fr/all/search>), WAG (<http://bioportal.naturalis.nl/>), Z (<http://www.herbarien.uzh.ch/en/Datenbanken.html>) and COI (raw catalogue of specimens was provided but not yet publicly available online). Most of the type specimens and protologues of African Melastomateae were seen except for those types that were kept in Berlin and destroyed during World War II. A list of the specimens examined for morphological characters is available from the first author on request.

DNA extraction, amplification and sequencing. — Total genomic DNAs were extracted from silica-gel dried or herbarium material using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany), with modification to the manufacturer's protocol following Goldenberg & al. (2008). During the lysis stage, 30 µl Proteinase-K was added to all samples which were incubated at 42°C for 20–22 hours.

In order to resolve the phylogenetic relationships amongst the African Melastomateae, we sequenced one nuclear locus (the nuclear ribosomal internal transcribed spacer [nrITS] region) and two plastid spacers, *accD-psaI* and *psbK-psbL*. The ITS region has been used widely in resolving phylogenetic relationships within several tribes and genera in Melastomataceae (Michelangeli & al., 2004, 2008, 2013; Ionta & al., 2007; Goldenberg & al., 2008; Stone & Andreasen, 2010; Penneys & Judd, 2013; Stone, 2014; Majure & al., 2015). We designed some new specific ITS primers for amplification and sequencing (Table 2). The *accD-psaI* and *psbK-psbL* intergenic spacers have proven to be variable at tribal and generic levels in Melastomataceae. These regions have already been employed to resolve the phylogeny of the Blakeaceae (Penneys & Judd, 2013), New World Melastomateae (Michelangeli & al., 2013) and several other genera of Melastomataceae (Reginato & al., 2010; Kriebel & al., 2015; Reginato & Michelangeli, 2016). An added advantage of using these markers was to obtain numerous previously published (GenBank) sequences of New World Melastomateae and other tribes for use as outgroups in this study. The *psbK-psbL* plastid region was amplified using the primers published by Reginato & al. (2010), and the *accD-psaI* region was amplified using the primers designed by Small & al. (1998). All primers used in this study are shown in Table 2.

Polymerase chain reactions (PCR) were performed with a total volume of 25 µl containing the following: 16.0 µl water, 1 µl template DNA, 2.5 µl 10× PCR buffer (Sigma-Aldrich, Hamburg, Germany), 2.5 µl MgCl₂ (25 mM), 1.0 µl each of 10 µM primers, 0.5 µl dNTPs (10 mM), 0.25 µl bovine serum albumin (10 µg/µl) and 0.25 µl of *Taq* polymerase. The PCR protocols for amplifying *accD-psaI* and *psbK-psbL* followed those in Penneys & Judd (2013) with minor modification as follows: (*accD-psaI*) 94°C for 3 min, 33 cycles of 94°C for 45 s, 64°C for 45 s and 72°C for 105 s, followed by 72°C for 6 min; (*psbK-psbL*) 94°C for 2 min, 40 cycles of 94°C for 30 s, 55°C for 30 s and 72°C for 30 s, followed by 72°C for 7 min. The ITS region was amplified in two parts (ITS 1, ITS 2), since amplifying the whole ITS fragment was problematic. Both ITS parts were amplified as follows: 94°C for 1 min, 35 cycles of 94°C for 20 s, 63°C for 30 s and 72°C for 1 min, followed by 94°C for 20 s, 55°C for 80 s and 72°C for 8 min.

The amplified products were cleaned using “ExoSAP-IT” (Affymetrix, Santa Clara, California, U.S.A.). Cycle sequencing was carried using Big Dye Terminator v.3.1 reagents (Applied Biosystems, Darmstadt, Germany) with the same forward and reverse primers as used in the amplification of *accD-psaI*, *psbK-psbL* and ITS 1. However, for ITS2 a different reverse primer was used for sequencing (see Table 2). Sequencing was done at StarSEQ (Mainz, Germany) or using a 3130xl Genetic Analyzer (Applied Biosystems) at the Institute of Ecology, Johannes Gutenberg-University, Mainz, Germany.

Phylogenetic inference. — Contigs of forward and reverse sequences were assembled and manually edited using Sequencher v.4.1.4 (Gene Codes Corp., Ann Arbor, Michigan, U.S.A.). Sequence alignment was done manually using Mesquite v.3.04 (Maddison & Maddison, 2015). We conducted phylogenetic analyses using maximum likelihood (ML), maximum parsimony (MP) and Bayesian inference (BI) methods. First, we separately analysed each of the three datasets (ITS, *accD-psaI*, *psbK-psbL*). Then we combined the two plastid datasets (*accD-psaI*, *psbK-psbL*) into a single one. Since trees based on the three single and the combined plastid markers revealed no well-supported conflict (ML or MP bootstrap values ≥ 70% or BI posterior probability ≥ 0.95), we concatenated all three datasets for all subsequent analyses. The best-fitting

Table 2. Primers of the three markers used in this study.

Marker	Primer name	Primer sequence 5'→3'	Source
ITS	ITS-241r	CAG TGC CTC GTG GTG CGA CA	Michelangeli & al. (2004)
ITS	ITS2-MEL2 R	CCA CCT TCC AGT GAA CTT GG	This study (sequencing primer ITS 2 reverse)
ITS	ITS2-MEL F	CGG CTC TTG CAT CGA TGA AG	This study
ITS	ITS1-MEL F	GGA GAA GTC GTA ACA AGG TTT C	This study
ITS	ITS1-MEL R	CTT GCG TTC AAA GAA TTG ATG G	This study
<i>accD</i>	<i>accD</i> F	GGG ATA TCA TTA TTG CCG AAC C	Small & al. (1998)
<i>psaI</i>	<i>psaI</i> R	AGA AGC CAT TGC AAT TGC CGG AAA	Small & al. (1998)
<i>psbK</i>	<i>psbK</i> F	TTA GCC TTT GTT TGG CAA G	Reginato & al. (2010)
<i>psbL</i>	<i>psbL</i> R	AGA GTT TGA GAG TAA GCA T	Reginato & al. (2010)

model for nucleotide substitutions was determined using the Akaike information criterion (AIC) in jModelTest2 v.2.1.6 (Darriba & al., 2012). The best substitution model for the individual and combined data was GTR+I+G, so the combined dataset was analysed using this single model.

The ML trees were generated using RAxML v.8.2.8 and inferred under default settings (Stamatakis, 2014). The MP analyses were carried out in PAUP* v.4.0b10 (Swofford, 2002). A heuristic search was conducted of 1000 replicates with random sequence addition, TBR branch swapping and MulTrees on. Swapping was performed on a maximum of 50 trees (nchuck = 50). All characters were unordered and equally weighted, and gaps were treated as missing data. Bootstrap values (Felsenstein, 1985) were calculated from 10,000 replicates using a heuristic search using TBR branch swapping and one random addition-sequence replicate. BI was performed using BEAST v.1.8.2 (Drummond & Rambaut, 2007). All BI analyses were conducted under the GTR+I+G substitution model with gamma distribution in four categories and Birth-Death process chosen as the tree prior. We ran two independent Markov chain Monte Carlo (MCMC) runs of 20 million generations each, sampling every 2000 generations, starting with a random tree. The individual output log files were examined using Tracer v.1.5 (Rambaut & Drummond, 2009) to assess convergence. Both runs had an ESS value greater than 200. The resultant tree files were combined using LogCombiner v.1.8.0 (Drummond & Rambaut, 2007). The first 2000 trees (20%) were discarded as burn-in, and a maximum clade credibility (MCC) tree was constructed using TreeAnnotator v.1.8.0 (Drummond & al., 2012).

■ RESULTS

Molecular variation. — We generated a total of 286 new DNA sequences for African Melastomateae, i.e., 103 sequences for ITS, 115 for *psbK-psbL* and 78 for *accD-psaI* (see Appendix 1). The combined dataset contained 3061 characters from all three markers (ITS, *accD-psaI*, *psbK-psbL*). Of the total of 183 accessions, 138 were represented by sequence data from all three loci and 45 accessions were represented by two loci. The plastid and nuclear markers are relatively variable (Table 3) and therefore most of the major clades were recognised in the plastid and nuclear gene trees, respectively, even though the backbone was generally not well supported (Electr. Suppl.: Figs. S1, S2).

Major phylogenetic relationships among clades. — Tree topologies from the ML, MP and BI analyses were very similar with a well-resolved backbone (Fig. 3) allowing for comparison between trees. We considered the clades as resolved when the bootstrap values from the ML (BS) and MP (PBS) analyses were $\geq 70\%$ and the posterior probability (PP) was ≥ 0.95 for the BI analysis. Old World Melastomateae formed a well-supported, monophyletic group (BS 100/PBS 100/PP 1) in the ML, MP and BI analyses (Fig. 3), except for the monospecific genus *Dinophora* which was recovered in a polytomy including Rhexieae, one New World Melastomateae clade (*Aciotis* D. Don and allies), Microlicieae and a large clade containing both the New World (*Tibouchina* Aubl. and allies; *Pterolepis* Schrad. + *Pterogastra* Naudin) and Old World Melastomateae (Figs. 3, 4A).

The Old World Melastomateae are part of a trichotomy with two New World Melastomateae clades, i.e., *Pterolepis* plus *Pterogastra* on the one hand and *Tibouchina* and allies on the other. At their root, the Old World Melastomateae are split into two primary clades, Pseudoheterotis and Euheterotis (these clade names are informal and proposed for the first time in this study, Fig. 4B; Electr. Suppl.: Figs. S1, S2). The Pseudoheterotis clade is composed of *Guyonia* s.l. (including *Heterotis* sect. *Cyclostemma*), *Argyrella* Naudin (*Heterotis* sect. *Argyrella*), *Anaheterotis* Veranso-Libalah & G. Kadereit (*Heterotis pobe-guinii* (Hutch. & Dalziel) Jacq.-Fél.; see Taxonomic Treatment), *Melastomastrum* s.l. (including *Osbeckia porteresii* Jacq.-Fél.) and *Tristemma* s.l. (including *M. cornifolium* (Benth.) Jacq.-Fél.). The Euheterotis clade comprises *Dichaetanthera*, *Dissotidendron* Veranso-Libalah & G. Kadereit (*Dissotis* subg. *Dissotidendron*; see Taxonomic Treatment), *Heterotis* (*H.* sect. *Heterotis*), Asian Melastomateae (*Osbeckia* s.str. and *Melastoma*), Madagascan endemic genera (*Amphorocalyx*, *Rousseauxia*, *Dionycha*), *Dupineta* Raf. (*Dissotis* subg. *Dupineta*; see Taxonomic Treatment), *Pseudosbeckia*, *Dissotis* subg. *Dissotis* (all four sections), *Antherotoma*, and the remaining African *Osbeckia* species recognised by Jacques-Félix (1995). According to the most recent generic delimitation within the African Melastomateae (Jacques-Félix, 1981, 1995), in addition to the monospecific *Pseudosbeckia* lineage, only two well-supported monophyletic groups are recovered in our analyses, i.e., *Dichaetanthera* and *Tristemma*. The remaining genera, i.e., *Dissotis*, *Heterotis*, *Antherotoma*, *Osbeckia* and *Melastomastrum* are all polyphyletic (Fig. 4B; Electr. Suppl.: Figs. S1, S2).

Table 3. Summary statistics of genomic regions sequenced for phylogenetic analyses of African Melastomateae.

Marker	Accessions sampled	% Missing data	Aligned base pairs	Variable sites	% Variable sites	Conserved sites	Parsimony-informative sites (PIS)	% PIS	Model
nrITS	173	4	1030	482	47	509	399	39	GTR+I+G
<i>accD-psaI</i>	151	17	1458	448	31	810	288	20	GTR+I+G
<i>psbK-psbL</i>	180	2	573	237	41	265	180	31	GTR+I+G
Combined	183	8	3061	1167	38	1584	879	29	GTR+I+G

Best-fit substitution model estimated under the AIC criterion using jModelTest.

Within the Pseudoheterotis clade, two of the three *Heterotis* sections are recovered as monophyletic (Fig. 4B), i.e., *H.* sect. *Argyrella* and *H.* sect. *Cyclostemma* (now included in *Guyonia*). In turn, these two sections plus *H. pobeguinii* form a well-supported monophyletic group (BS 100/PBS 98/PP 1) that is sister to a well-supported clade (BS 100/PBS 100/PP 1) containing *Melastomastrum* s.l. and *Tristemma* s.l. (Fig. 4B; Electr. Suppl.: Figs. S1, S2).

Within the Euheterotis clade, there is successive branching of clades with *Dichaetanthera* branching off first, followed by the well-supported monophyletic *Dissotidendron* (BS 100/PBS 100/PP 1). Next is *Heterotis* sect. *Heterotis* (*Heterotis*), a strongly supported clade (BS 100/PBS 100/PP 1), followed by the Asian Melastomateae genera and another clade consisting of the Madagascan endemic genera (Fig. 3, 4B; Electr. Suppl.: Figs. S1, S2). Next to the Madagascan endemic genera is *Dupineta*, a well resolved clade (BS 100/PBS 100/PP 1), although its sister-group relationship to *Pseudosbeckia* plus the *Dissotis* and allies clade is not strongly supported (BS 89/PBS 77/PP 0.56). Next to *Dupineta* is the monospecific *Pseudosbeckia* lineage. Lastly, we recovered a large clade of *Dissotis* and allies with partially supported internal subclades, composed of *Dissotis* s.str. (excluding subg. *Dupineta* and *Dissotidendron*), *Antherotoma*, *Dissotis tubulosa* (Sm.) Triana and African *Osbeckia* (BS 94/PBS 91/PP 0.95; Figs. 3, 4B; Electr. Suppl.: Figs. S1, S2). Within *Dissotis* and allies, *D.* subg. *Dissotis* and *Antherotoma* are polyphyletic (Fig. 4; Electr. Suppl.: Figs. S1, S2).

DISCUSSION

Overview of Melastomateae. — The traditional circumscription of the Old World Melastomateae (Osbeckieae) as first suggested by Cogniaux (1891) is recovered and strongly supported as monophyletic in our ML, MP and BI analyses (BS 100/PBS 100/PP 1). The Old World Melastomateae are in a trichotomy with two New World Melastomateae clades (a small *Pterolepis* and *Pterogastra* clade and a large *Tibouchina* and allies clade; Figs. 3, 4; Electr. Suppl.: Figs. S1, S2) and these results are similar to those earlier published by Michelangeli & al. (2013). The core Melastomateae sensu Michelangeli & al. (2013) are characterised by cochleate seeds with tuberculate testa (Whiffin & Tomb, 1972), stamens usually with a pedoconnective with one or more ventral appendages and the ovary with a crown of persistent bristles (absent in *Guyonia ciliata* Hook.f.). The ovary in New World Melastomateae is free (including *Guyonia*) whereas the Old World Melastomateae have ovaries more or less fused to the hypanthium (Jacques-Félix, 1995).

Placement of *Dinophora*. — *Dinophora* was first placed in Rhexieae, and *Spennera* Mart. ex DC. (now *Aciotis*) was suggested as its closest relative (Bentham, 1849). It was later treated in Bertolonieae because its seed anatomy and geographic distribution are similar to those of African *Ochthocharis* G. Don (Van Tieghem, 1891). *Dinophora* has also been treated in Osbeckieae (Triana, 1872; Baillon, 1877; Cogniaux, 1891; Gilg, 1898; Engler, 1921; Renner, 1993; Stevens, 2001–) although its fruits are fleshy compared to the rest of the Old World Melastomateae (except *Tristemma* and *Melastoma* which have berry-like fruits). Lastly, because of its baccate fruit and chromosome number $n = 12$ (Favarger, 1962) it has been treated in Dissochaeteae (Jacques-Félix, 1983, 1995; Leistner, 2005).

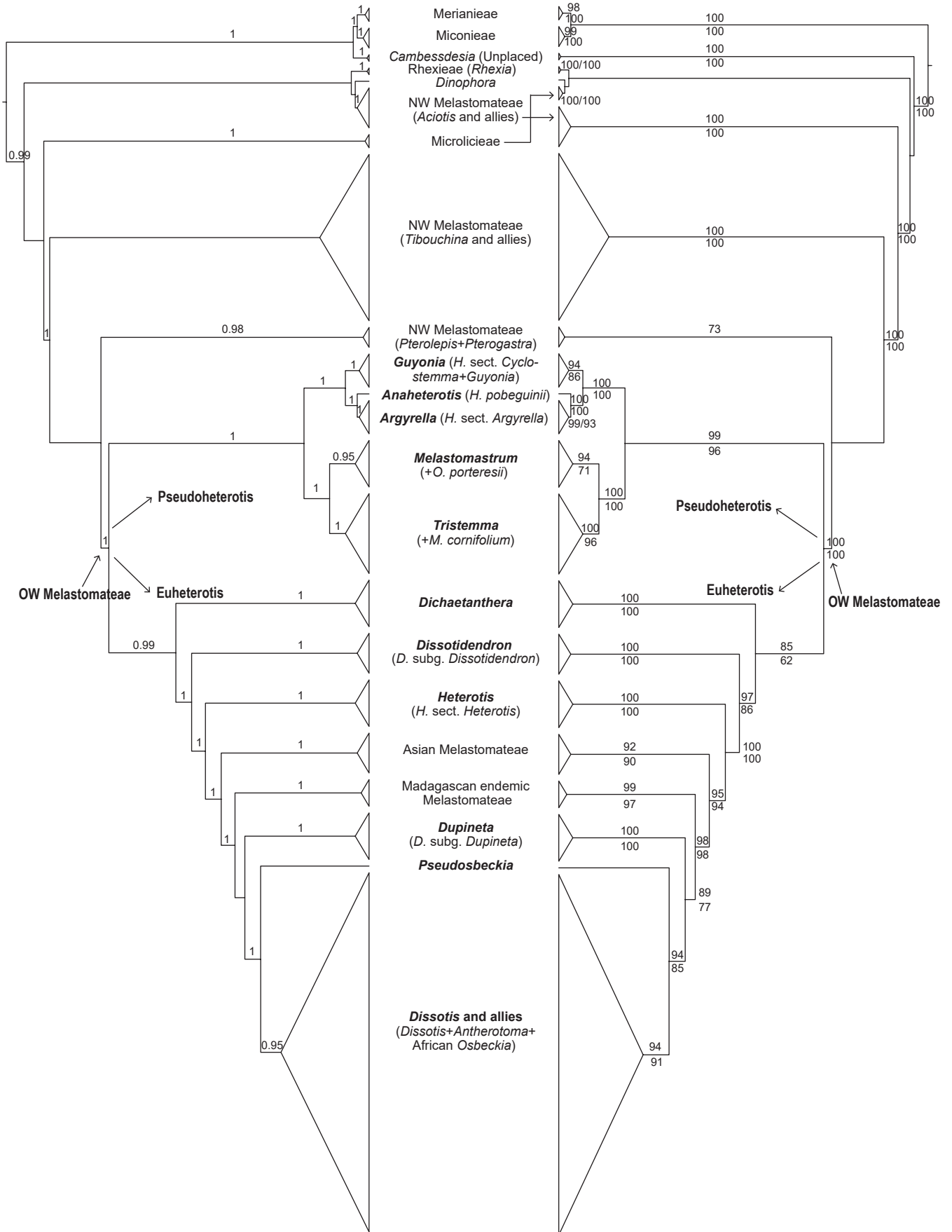
In our molecular phylogenetic analyses, *Dinophora* is part of a polytomy with Rhexieae, one New World Melastomateae clade (*Aciotis* and allies), Microlicieae and the large clade consisting of the further two New World Melastomateae clades plus the Old World clade (Figs. 3, 4A; Electr. Suppl.: Figs. S1, S2). Our analyses therefore suggest that *Dinophora* does not belong in the “core Melastomateae” sensu Michelangeli & al. (2013). In subsequent analyses it will be necessary to increase the sampling of Dissochaeteae before any decision concerning the tribal placement of *Dinophora* can be made.

Revised generic classification of African Melastomateae.

— Our molecular phylogenetic study provides the first in-depth sampling of African Melastomateae including most genera (10/13) and approximately 42% of the species. With this dense sampling, we succeeded to recover as monophyletic several genera, subgenera and sections that have been suggested in earlier systematic treatments based on morphology (Bentham, 1849; Fernandes & Fernandes, 1969; Jacques-Félix, 1981, 1995) (compare Table 1; Figs. 1–4; Electr. Suppl.: Figs. S1, S2). To accommodate phylogenetically isolated members of previously recognised genera and to avoid polyphyletic taxa, we propose several taxonomic adjustments and new combinations in African Melastomateae (see Taxonomic Treatment). All taxonomic groups proposed here ensure that all taxa represent monophyletic lineages (Fig. 4; Electr. Suppl.: Figs. S1, S2; Table 1).

In previous taxonomic treatments, staminal morphology has been very important for the delimitation of genera in Old World Melastomateae. For instance, isomorphic stamens were used to separate *Osbeckia* from *Dissotis* (Bentham & Hooker, 1867; Fernandes & Fernandes, 1954a). Isomorphic stamens have the same colour and are equal to subequal in size while dimorphic stamens differ in colour and are markedly unequal in size (Figs. 1, 2). Mapping of stamen-type (isomorphic versus dimorphic) on the species included in our phylogeny shows that this character is very unstable and changes frequently in many subclades of Melastomateae respectively (Fig. 4B). For

Fig. 3. Major clades recovered in the phylogenetic analyses of African Melastomateae based on combined nuclear (nrITS) and plastid (*accD-psaI*, *psbK-psbL*) data. Tree topology resulting from the Bayesian inference analysis (left) with posterior probabilities above branches. Tree resulting from the maximum likelihood (ML) analysis (right) with ML bootstrap support values above branches and bootstrap support values resulting from the parsimony analysis below branches. In the OW Melastomateae clade, the major clades recognised in this study are given in bold and old taxonomic names in brackets.

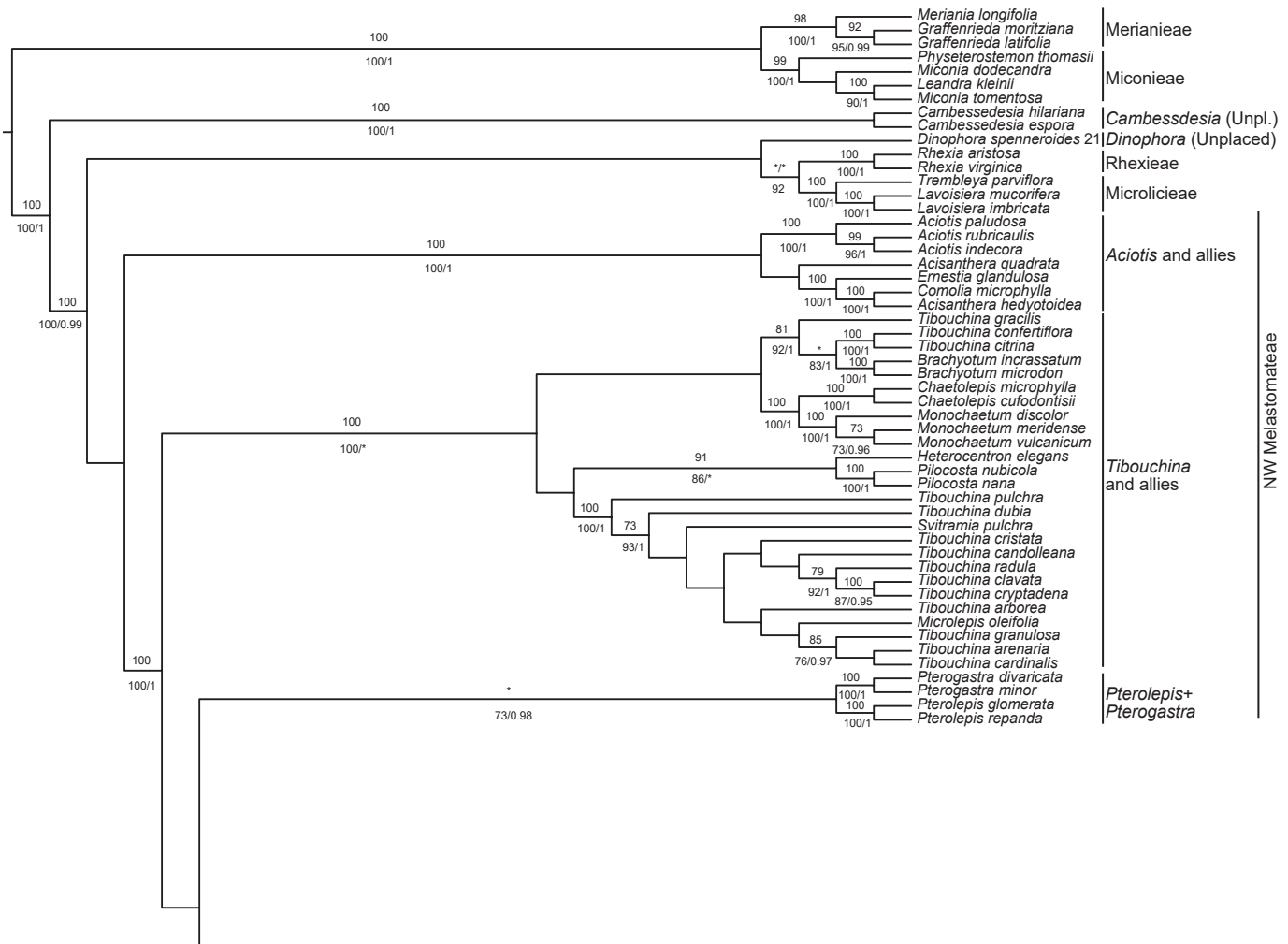


example, within *Heterotis* and *Antherotoma*, *H. buettneriana* (Cogn. ex Büttner) Jacq.-Fél. and *A. naudinii* Hook.f. are the only species with isomorphic stamens. In contrast to some previous taxonomic treatments we consider isomorphism versus dimorphism of stamens as an unreliable character when delimiting genera in Melastomateae.

Generic limits within the Pseudoheterotis clade. — The Pseudoheterotis clade comprises the following subclades: *Guyonia*, *Argyrella*, *Melastomastrum*, *Tristemma* and the monospecific *Anaheterotis* lineage. This clade contains all the species earlier treated in *Heterotis* sect. *Cyclostemma*, sect. *Leiocalyx*, and sect. *Wedeliopsis* by Bentham (1849) and in *H.* sect. *Argyrella* and sect. *Cyclostemma* by Jacques-Félix (1981, 1995) (Table 1).

Guyonia. — *Heterotis* sect. *Cyclostemma* s.str. (Jacques-Félix, 1981, 1995) comprises ca. 12 species in three morphologically and ecologically distinct groups. The first group consists

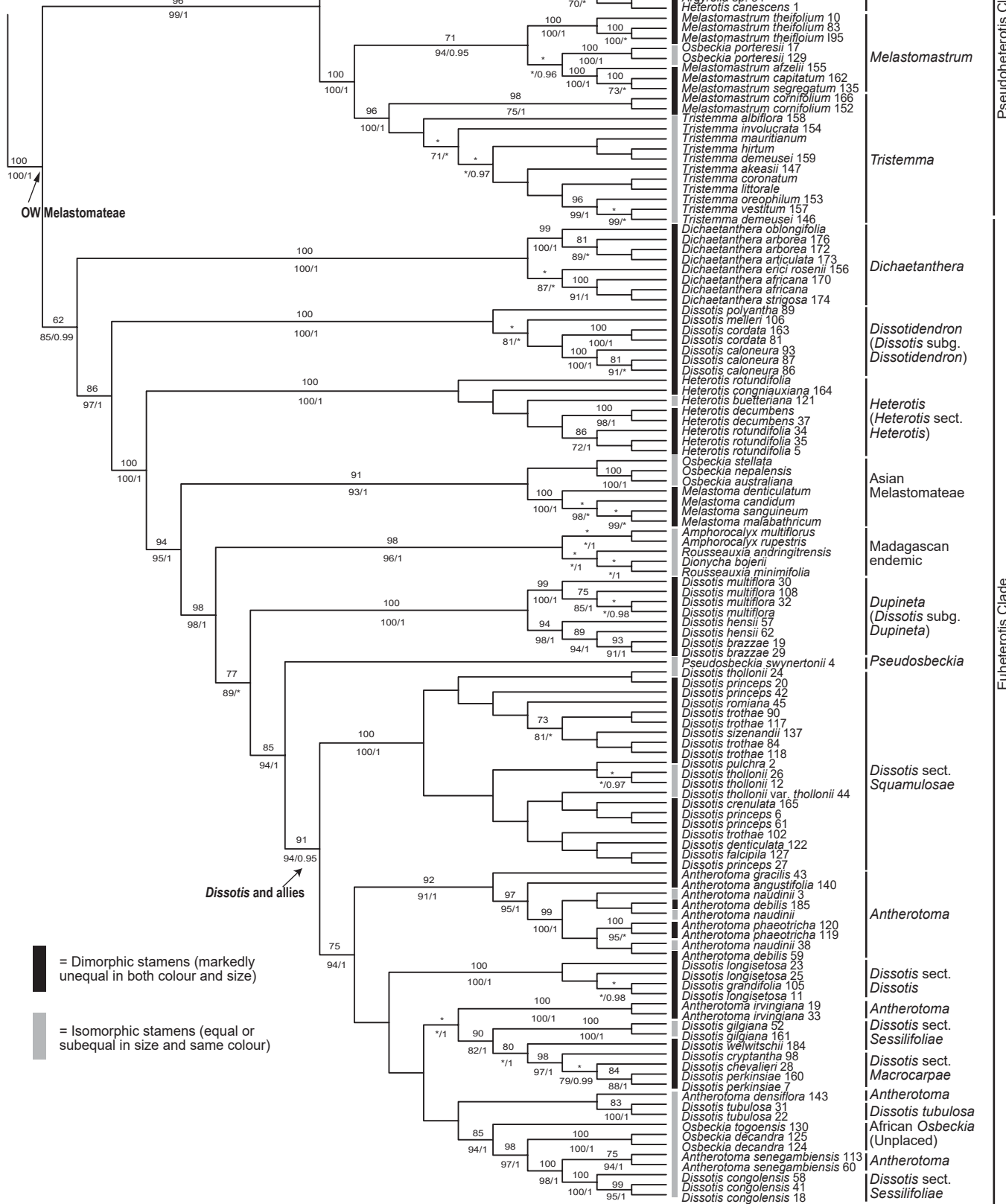
of six species: *H. arenaria* Jacq.-Fél., *H. cinerascens* (Hutch.) Jacq.-Fél., *Dissotis glandulosa* A.Fern. & R.Fern., *H. obamae* Lejoly & Lisowski, *H. rupicola* (Gilg ex Engl.) Jacq.-Fél., and *H. seretii* (De Wild.) Jacq.-Fél. This group is characterised by sessile leaves with flattened petioles, no intersepal appendages and is mainly found in montane grassland habitats. The second group consists of five species including *H. antennina* (Sm.) Benth., *H. entii* (J.B.Hall) Jacq.-Fél., *Dissotis humilis* A.Chev. & Jacq.-Fél., *H. pygmaea* (A.Chev. & Jacq.-Fél.) Jacq.-Fél., and *H. sylvestris* (Jacq.-Fél.) Jacq.-Fél., which are mainly found in wet habitats. They are also characterized by adventitious roots, intersepal appendages, and distinctly petiolate leaves. The third group is monospecific and consists of *H. jacquesii* (A.Chev.) Aké Assi (= *Dissotis jacquesii* A.Chev.), which is morphologically different from all other species of *H.* sect. *Cyclostemma*. Initially *H. jacquesii* had been included in *Dissotis*, but already Feissly (1964) suggested to remove it



to Fig. 4B (ingroup)

Fig. 4A & B. Maximum likelihood (ML) phylogenetic cladogram of African Melastomateae with representatives of Asian and Madagascan Melastomateae, and outgroups (Rhexieae, Microlicieae, Miconieae, Meranieae, *Cambessedesia*, NW Melastomateae) derived from the combined data matrix (nrITS, *accD-psaI*, *psbK-psbL*). Values above branches refer to bootstrap values resulting from the parsimony analysis (only values ≥ 70), values below branches refer to bootstrap values resulting from the ML analysis (only values ≥ 70) and posterior probabilities resulting from Bayesian inference (only values ≥ 0.95). An asterisk (*) denotes a branch supported by either bootstrap or posterior probability only.

to Fig. 4A (outgroup)



from *Dissotis* because it lacks intersepal appendages and the whole plant is entirely covered by glandular hairs. It has a chromosome number of $n = 16$ (Favarger, 1952, 1962).

Our molecular analyses included 4 of these 12 species (*H. antennina*, *H. arenaria*, *H. jacquesii*, *H. seretii*) representing all three groups. These species formed a monophyletic clade together with *Guyonia* (Figs. 3, 4B; Electr. Suppl.: Figs. S1, S2), a genus with two species, i.e., the widespread Guinean-Congolian *G. ciliata* and the poorly known type *G. tenella* Naudin from Guinea. *Guyonia* has been suggested to be closely related to the neotropical *Aciotis* (Jacques-Félix, 1995). However, according to our results *Guyonia* clearly belongs to Old World Melastomateae and is sister to *H. jacquesii* (Fig. 4B; Electr. Suppl.: Figs. S1, S2; Table 1).

The phylogenetic position of *H. sect. Cyclostemma* plus *Guyonia* is well apart from *Heterotis* sect. *Heterotis* which clearly indicates that it should be recognised at the generic level. As defined here, an expanded *Guyonia* comprises 14 species, including the 12 previously treated in *H. sect. Cyclostemma*. Morphologically, *Guyonia* s.l. are decumbent, rarely erect herbs, geophytes (sometimes forming tuber-like underground structures during unfavourable conditions) with one to few flowers and persistent calyx-lobes.

***Heterotis* sect. *Argyrella*.** — The genus *Argyrella* was first described by Naudin (1850) and later treated as *Dissotis* sect. *Argyrella* (Naudin) Triana (Triana, 1872). Fernandes & Fernandes (1969, 1970) transferred *D. canescens* (E.Mey. ex Graham) Hook.f. and another species, *D. angolensis* Cogn. to *Dissotis* subg. *Argyrella*. These two species together with four other *Dissotis* species previously treated in the “séries des *Dissotis* canescents” (Jacques-Félix, 1953) were then transferred to *Heterotis* sect. *Argyrella* (Naudin) Jacq.-Fél. (Jacques-Félix, 1981, 1995). These species are found mainly in moist habitats such as marshes, swamps, wet depressions and mountain valleys.

In our phylogenetic analyses, we sampled three of the six species of this section. These three representative species clearly formed a monophyletic group (BS 99/PBS 93/PP 1) which is sister to *Heterotis pobeguinii* (Figs. 3, 4B; Electr. Suppl.: Figs. S1, S2). *Argyrella* species are also morphologically well defined and are characterised by being erect herbs with an indumentum of stellate and/or glandular hairs, paniculate inflorescences and tri-cuspidate anther appendages (Fig. 2). According to Jacques-Félix (1995), *H. sect. Argyrella* should be upgraded to generic rank if more substantial taxonomic evidence is found. Based on their distinct morphology and the molecular results presented here, we strongly support Jacques-Félix’s (1995) proposition and here raise *H. sect. Argyrella* to generic rank (Table 1; see Taxonomic Treatment).

***Heterotis pobeguinii*.** — This species, endemic to Guinea and Sierra Leone, is a glabrous herb, morphologically unique and easy to recognise by its prominently ciliate leaf margins and long, lax, terminal panicles. It was initially described as *Dissotis pobeguinii* Hutch. & Dalziel, with *D. cinerascens* Hutch. suggested as its closest relative (Hutchinson & Dalziel, 1928) although they are morphologically very distinct. *Dissotis pobeguinii* was later treated in *Dissotis* sect.

Sessilifoliae together with *D. buraeavii* (Cogn.) A.Fern. & R.Fern and *D. welwitschii* Cogn. mainly because of being glabrous (Fernandes & Fernandes, 1954a). Most recently, it was treated in *H. sect. Cyclostemma* by Jacques-Félix (1981, 1995).

We included *D. welwitschii*, type of *D. sect. Sessilifoliae* in our analyses and found it nested within the large *Dissotis* and allies clade. Also, *Heterotis pobeguinii* is strongly supported as sister to *Argyrella* although they are morphologically very different (Fig. 4B; Electr. Suppl.: Figs. S1, S2). Given its distinct morphology together with our molecular results, we neither support the placement of *H. pobeguinii* in *D. sect. Sessilifoliae* nor in *H. sect. Cyclostemma* as suggested earlier. We instead propose that *H. pobeguinii* be recognized as the separate, monospecific genus *Anaheterotis* (see Taxonomic Treatment).

***Melastomastrum*.** — *Melastomastrum* was first described by Naudin (1850) and consisted of one species, *M. erectum* (Guill. & Perr.) Naudin. This species had been earlier described as *Tristemma erectum* Guill. & Perr. (Guillemin & al., 1833) and later treated as *Dissotis erecta* (Guill. & Perr.) Dandy (Andrews, 1950). This species was then reinstated to *Melastomastrum* (Fernandes & Fernandes, 1954b, 1956a; Jacques-Félix, 1975) (compare Table 1) and is now treated as a synonym of *M. capitatum* (Vahl) A.Fern. & R.Fern. *Melastomastrum* sensu Jacques-Félix (1975) comprises six species with eight varieties in three morphologically distinct groups (Fig. 2). The first group consists of *M. capitatum*, *M. afzelii* (Hook.f.) A.Fern. & R.Fern., *M. segregatum* (Benth.) A.Fern. & R.Fern., and *M. autranianum* (Cogn.) A.Fern. & R.Fern. (the latter not sampled in our study), which are mainly herbs with large 5-merous flowers, distinctly dimorphic stamens, pubescent pedicels and calyx-tube, attenuate to rostrate anthers, linear anther appendages and a valvate capsular fruit. The second group is monospecific and consists of *M. theifolium* with its two varieties, i.e., var. *theifolium* and var. *controversum* (A.Chev. & Jacq.-Fél.) Jacq.-Fél. This species is a hemicyptophyte with slender woody stems, oblong sepals, completely glabrous calyx-tube, clavate anther appendages and a dorsal spur on the internal anthers. The third group is also monospecific and consists of *M. cornifolium* which is similar to the species in the first group except for its poorly developed ring of bristles about mid-way on its calyx-tube, similar to the well-developed complete or incomplete ring of bristles found on the calyx-tube of *Tristemma* species.

Our molecular analyses included five of the six species representing all three morphological groups. Groups one and two formed a monophyletic clade together with *Osbeckia porteresii* (BS 94/PBS 71/PP 0.95; see Fig. 4B; Electr. Suppl.: Figs. S1, S2) while *M. cornifolium* was resolved as sister to *Tristemma* (BS 100/PBS 96/PP 1).

Osbeckia porteresii is a small shrub endemic to Mt. Nimba in Guinea. It has a glandular indumentum, persistent calyx-lobes and bracts (leafy), and isomorphic stamens with attenuate anthers lacking both a pedoconnective and an appendage. The original description of *O. porteresii* (Jacques-Félix, 1939) was based on two collections, i.e., *Portères 3175* and *Jacques-Félix 1933*. The latter collector was not able to observe flowers at the time of collection, but based on the former

collection, the flowers were described as yellow (Jacques-Félix, 1939). Observations of mounted herbarium specimens show that the flowers appear yellowish, a colour not found in African Melastomateae species except in *Nerophila* (now treated in the otherwise neotropical genus *Chaetolepis*; see Jacques-Félix, 1995; Grimm & Almeda, 2013). Recent collections in MO (*Bidault 200 & 667, Lerat 36 & 11*) and online photographs (<http://www.tropicos.org/ImageSearch.aspx>) show that the flowers of *O. porteresii* are pink and not yellow as stated in the protologue (M.C. Veranso-Libalah, pers. obs.; Fig. 2). More surprisingly, no previous studies of this species have mentioned the presence of large leafy persistent bracts which enclose the flowers (a character it shares with *Melastomastrum* and *Tristemma*). It greatly differs from the other African *Osbeckia* species, i.e., *O. decandra* (Sm.) DC., *O. praviantha* Jacq.-Fél. and *O. togoensis* Leuenb. in being a small shrub with glandular hairs and persistent calyx-lobes and bracts while the other species are herbs with caducous calyx-lobes and bracts. Our molecular results clearly suggest *O. porteresii* should not be placed within *Osbeckia*, but instead it is nested within the *Melastomastrum* clade (Fig. 4B; Electr. Suppl.: Figs. S1, S2).

The phylogenetic position of *O. porteresii* was quite astonishing at first sight, but based on several synapomorphies shared with *Melastomastrum*, we suggest broadening the circumscription of *Melastomastrum* to include *O. porteresii*. *Melastomastrum* as defined here will include five species (excluding *M. cornifolium*) and *O. porteresii*.

Tristemma. — This genus consists of 15 species and 7 varieties (Jacques-Félix, 1976, 1986, 1995), mainly distributed in Africa (from the Sudanian to Zambezi regions, but prominently present in East and West Africa especially in the Guinean-Congolian region) with only *T. mauritanum* J.F.Gmel. also known from Madagascar and the Mascarene Islands. Morphologically, *Tristemma* is close to *Melastomastrum*, and all species within these two genera were treated in *Tristemma* by Triana (1872). They share calyx-tubes without intersepal appendages, persistent calyx-lobes, and two large persistent bracts concealing the flower. Based on staminal characters and the nature of the calyx-tube pubescence, Jacques-Félix (1975) separated these two genera again. Traditionally, *Tristemma* has been characterised by brachymorphic flowers with isomorphic stamens, calyx-tubes with one or more complete to incomplete rings of bristles and baccate fruits bursting irregularly (Fig. 2).

Our molecular analyses included 10 of the 15 species of *Tristemma* which formed a well-supported monophyletic group (BS 100/PBS 96/PP 1) that also includes *M. cornifolium* (Figs. 3, 4B; Electr. Suppl.: Figs. S1, S2). The latter species is endemic to humid areas and marshes in West Africa (Guinean region) and was originally described as *Heterotis cornifolia* Benth. (Benth., 1849), later treated as *Dissotis cornifolia* (Benth.) Hook.f. (Hooker, 1871; Keay, 1954), as *Tristemma cornifolium* (Benth.) Triana (Triana, 1872) and lastly as *M. cornifolium* (Jacques-Félix, 1975). Morphologically, *M. cornifolium* is very similar to the other *Melastomastrum* species, except that it has a poorly developed ring of bristles about mid-way on its calyx-tube, very similar to that seen in *Tristemma* species. This ring of bristles in *M. cornifolium* was described by Favarger

(1962) as an incomplete form of the bristles found in *Tristemma*, while Feissly (1964) described them as a rudimentary crown of bristles similar to those in *Tristemma*. These bristles also have glandular hairs (Feissly, 1964), which are absent in the rest of the *Tristemma* and *Melastomastrum* species, except in *Osbeckia porteresii* which our phylogenetic results have shown to be a member of *Melastomastrum*.

In view of our molecular results, we feel it is necessary to broaden the circumscription of *Tristemma* to include *M. cornifolium* in order to avoid the need to create several new combinations and monospecific genera. *Tristemma* as defined here will now comprise 16 species with 7 varieties.

Generic limits within the Euheterotis clade. — The Euheterotis clade is very large, with several morphologically well-defined and phylogenetically well-supported subclades (except for the *Dissotis* and allies clade). Within Euheterotis the following successively branching clades are recognised: *Dichaetanthera*, *Dissotis* subg. *Dissotidendron*, *Heterotis* s.str., Asian Melastomateae, Madagascan endemic Melastomateae, *Dupineta*, *Pseudosbeckia* and the large clade of *Dissotis* and allies. We will discuss in detail these individual clades in the order of their successive branching below. However, due to the poor internal resolution of clades within *Dissotis* and allies, we will only briefly discuss *Dissotis*, *Antherotoma*, and African *Osbeckia*.

Dichaetanthera. — *Dichaetanthera* has ca. 30 species with about 8 in Africa and the rest in Madagascar (Jacques-Félix, 1983; Renner, 1993). With only six of these species sampled in this study, *Dichaetanthera* is recovered as a strongly supported monophyletic clade (BS 100/PBS 100/PP 1; Figs. 3, 4B; Electr. Suppl.: Figs. S1, S2). *Dichaetanthera* species are mainly deciduous trees or large shrubs with leathery leaves, 4-merous flowers with very short persistent calyx-lobes, and seeds cuneate to subcochleate with a lateral hilum and hyaline papillae on the back (Wickens, 1975; Fernandes & Fernandes, 1978; Jacques-Félix, 1983) (Fig. 1). Within *Dichaetanthera*, four sections have been proposed: sect. *Pseudodionycha* Cogn., sect. *Hysteranthia* Cogn., sect. *Rutenbergianae* H.Perrier and sect. *Dichaetanthera* (Cogniaux, 1891; Perrier de la Bâthie, 1932; 1951). These sections are yet to be tested in a phylogenetic context.

Dissotis subg. Dissotidendron. — This subgenus was originally thought to be endemic to East Africa (Fernandes & Fernandes, 1969; Wickens, 1975; Jacques-Félix, 1981, 1995). Morphologically, ten species were placed in it, characterised as trees or shrubs with rugose leaf surfaces and 5-merous flowers borne in panicles with the calyx-tube campanulate and calyx-lobes persistent (Fernandes & Fernandes, 1969) (Fig. 1). Our phylogenetic analyses included three of the ten species and strongly support the monophyly of *D.* subg. *Dissotidendron* (BS 100/PBS 100/PP 1). *Dissotis cordata* Gilg, a species endemic to the Katanga region of the Democratic Republic of the Congo also falls in this group (Figs. 3, 4B; Electr. Suppl.: Figs. S1, S2; Table 1).

Together with its unique morphology, our molecular results clearly suggest that *D.* subg. *Dissotidendron* can no longer be treated as a subgenus within *Dissotis*. We therefore

propose to elevate *D.* subg. *Dissotidendron* to generic rank (see Taxonomic Treatment). *Dissotidendron* as defined in this study will now include 11 species, 10 previously treated in *D.* subg. *Dissotidendron* and with *D. cordatum* as a new addition.

Heterotis sect. Heterotis. — *Heterotis* was first described by Benth (1849) comprising four sections: sect. *Heterotis*, sect. *Cyclostemma*, sect. *Leiocalyx* and sect. *Wedeliopsis*. All species treated in the latter two sections were later included in *Melastomastrum* (Naudin, 1850) while the species in sect. *Heterotis* and sect. *Cyclostemma* were later treated in *Dissotis* sect. *Heterotis* (Benth.) Hook.f. (Hooker, 1871). More recently, Fernandes & Fernandes (1969) treated all species originally placed in *H.* sect. *Heterotis* and sect. *Cyclostemma* in *D.* subg. *Heterotis* and *D.* subg. *Dissotis*, respectively. After studying staminal morphology, Jacques-Félix (1981) reinstated the species in *D.* subg. *Heterotis* as *H.* sect. *Heterotis*. This section currently includes seven species characterised by being decumbent herbs rooting at nodes, calyx-tubes with stellate emergences (except in *H. decumbens* (P.Beauv.) Jacq.-Fél. which has simple hairs), intersepalal appendages with stellate hairs on the apex and calyx-lobes persistent (Fig. 2). The group is widely distributed in Africa, from the Guinean-Congolian region through the Sudanian to the Zambezan region. *Dissotis fruticosa* (Brenan) Brenan & Keay, *H. buettneriana*, and *Dissotis cogniauxiana* A.Fern. & R.Fern. are restricted to the Congolian region whereas *H. prostrata* (Thonn.) Benth., *H. decumbens* and *H. rotundifolia* (Sm.) Jacq.-Fél. are widely distributed in Africa. *Heterotis prostrata* (often wrongly identified as *H. rotundifolia*) is also quite weedy and has been documented as invasive in parts of Asia, North America, Oceania, Central America and the Caribbean (CABI, 2014; Judd & al., 2011).

Our molecular analyses included four of the seven species of *H.* sect. *Heterotis*, and for these a well-supported clade is recovered (BS 100/PBS 100/PP 1; Figs. 3, 4B; Electr. Suppl.: Figs. S1, S2). Our molecular results clearly exclude *H.* sect. *Argyrella* and sect. *Cyclostemma* from *Heterotis* sensu Jacques-Félix (1981) (see Table 1). We here suggest maintaining *Heterotis* at generic rank as originally proposed by Benth (1849), but with a considerably narrower circumscription in comparison to the more recent treatments of this genus by Jacques-Félix (1981, 1995) (see Table 1 and Taxonomic Treatment).

Asian Melastomateae. — *Melastoma* (>50 spp.) is the most diverse genus of Asian Melastomateae, followed by *Osbeckia* with ca. 30 species and *Otanthera* Blume with 3 species (Renner, 1993; Meyer, 2001). Our molecular analyses included only seven of these Asian species (four of *Melastoma* and three of *Osbeckia*), which are recovered in a well-supported (BS 93/PBS 91/PP 1) monophyletic group (Figs. 3, 4B; Electr. Suppl.: Figs. S1, S2). This clade is found nested within African Melastomateae. Renner & Meyer (2001) suggested that the Asian *Melastoma* and *Osbeckia* were likely derived from African or Madagacan ancestors. However, little is currently known about the phylogenetic relationships of these Asian species.

Madagascan endemic Melastomateae. — Madagascar currently has about 48 Melastomateae species in eight genera (Perrier de la Bâthie, 1951; Renner, 1993, Jacques-Félix,

1995). These are: *Dichaetanthera* (ca. 23 spp.), *Rousseauxia* (ca. 13 spp.), *Amphorocalyx* (5 spp.), *Dionycha* (3 spp.), *Antherotoma* (1 sp.), *Melastoma* (1 introduced sp.), *Rhodosepala* (now *Dissotis*; 1 sp.) and *Tristemma* (1 sp.). Our analyses included six *Dichaetanthera* species (two from Madagascar and four from Africa), and these together formed a monophyletic group as already discussed above. We also sampled *T. mauritianum* and *Antherotoma naudinii* which are also distributed in Africa, and these species were recovered in the *Tristemma* and *Dissotis* and allies clades, respectively. Also, five species representing all three Madagascan endemic genera (*Amphorocalyx*, *Rousseauxia*, *Dionycha*) were sampled, and these species formed a monophyletic group (BS 96/PBS 98/PP 1; Figs. 3, 4B; Electr. Suppl.: Figs. S1, S2). Nevertheless, we recommend more in-depth studies of this Madagascan Melastomateae lineage, to understand better their morphology, phylogenetic relationships and biogeography.

Dissotis subg. Dupineta. — The genus *Dupineta* was first described as monospecific with only *Dupineta multiflora* (Sm.) Raf. (Rafinesque, 1838). It was later treated with an expanded circumscription as a subgenus of *Dissotis* (Fernandes & Fernandes, 1969; Jacques-Félix, 1981, 1995). *Dissotis* subg. *Dupineta* consists of six species widely distributed in Africa (Jacques-Félix, 1981, 1995). This subgenus is morphologically characterised by 5-merous flowers in panicles of cymes, intersepalal appendages absent, hypanthial emergences caducous, stamens dimorphic, appendages bifid, and calyx-tube accrescent in fruit with distinct longitudinal ribs (Fig. 1). The West African *D. tubulosa* was included in this subgenus by Jacques-Félix (1995) because of its accrescent calyx-tube. However, it is very different from the rest of the species by being an annual herb with stamens isomorphic, hypanthial emergences persistent and fruits lacking longitudinal ribs.

Our molecular analyses included four of the six species treated in this subgenus by Jacques-Félix (1995), namely: *D. brazzae* Cogn., *D. multiflora* (Sm.) Triana, *D. hensii* Cogn. and *D. tubulosa*. Our phylogenetic results strongly support (BS 100/PBS 100/PP 1) the monophyly of *D.* subg. *Dupineta* s.str. (excluding *D. tubulosa*) although its relationship to *Pseudosbeckia* and the Madagascan endemic clade is not well resolved (see Figs. 3, 4B; Electr. Suppl.: Figs. S1, S2). Based on the unique morphology of species in *D.* subg. *Dupineta* together with molecular evidence, we strongly support the exclusion of *D. tubulosa* from *D.* subg. *Dupineta* and suggest reinstating *D.* subg. *Dupineta* to generic rank (see Rafinesque, 1838) (Table 1 and Taxonomic Treatment). *Dissotis tubulosa* is found nested within the large clade of *Dissotis* and allies in our molecular results.

Pseudosbeckia. — *Pseudosbeckia swynnertonii* (Baker f.) A.Fern. & R.Fern. is a monospecific lineage only known from the Chimanimani Mountains of Zimbabwe and adjacent Mozambique. It was originally described as *Osbeckia swynnertonii* Baker f. because of its isomorphic stamens and 5-merous flowers (Rendle & al., 1911). Fernandes & Fernandes (1954a, c) found that this species has a distinct but short pedoconnective with two ventral appendages when compared to *Osbeckia* species, and they placed it first in *Dissotis* as

D. swynnertonii (Baker f.) A.Fern. & R.Fern. before transferring it to *Pseudosbeckia* (Fernandes & Fernandes, 1956a, b). It is a shrub with 5-merous flowers in cymes of 1–3 flowers, sepals tardily caducous, and anthers erostrate and opening by a terminal introrse pore (Fig. 2). In our molecular analyses this monospecific genus is recovered as sister to the large, internally unresolved clade consisting of *Dissotis* s.str. and allies (Figs. 3, 4B; Electr. Suppl.: Figs. S1, S2).

***Dissotis* and allies.** — Our molecular phylogenetic results recovered a large clade of *Dissotis* and allies with partial internal resolution (BS 94/PBS 91/PP 0.95; see Fig. 3). This large clade contains all species of *D.* subg. *Dissotis* and its four sections (sect. *Dissotis*, sect. *Macrocarpae*, sect. *Sessilifoliae*, sect. *Squamulosae*) as well as *Antherotoma*, *D. tubulosa* (previously placed in *D.* subg. *Dupineta*; Fernandes & Fernandes, 1969; Jacques-Félix, 1995) and two African *Osbeckia* species (*O. decandra*, *O. togoensis*; see Fig. 4B; Electr. Suppl.: Figs. S1, S2). Three *Dissotis* sections (sect. *Dissotis*, sect. *Macrocarpae*, sect. *Squamulosae*) each formed well-supported clades, as did the species of *Antherotoma* treated in *D.* sect. *Osbeckiella* sensu Jacques-Félix (1981). Nevertheless, the poor resolution of this part of the phylogenetic tree does not allow us to propose a new generic classification for this very large and morphologically diverse clade. To resolve phylogenetic relationships between all genera, sections and species, it will be necessary to sequence additional loci and also to sample more extensively the species belonging to this large clade. For the time being, we suggest maintaining *Dissotis* s.str. (including subg. *Dissotis* and subg. *Paleodissotis*) and *Antherotoma*. However, one firm conclusion is that the genus *Osbeckia* s.str. (Asian *Osbeckia*) does not occur in Africa.

Morphologically, this is a diverse clade of shrubs, subshrubs, perennial or annual herbs with paniculate, cymose, capitulate inflorescences or solitary flowers, which are 4- or 5-(6)-merous, calyx-tubes glabrous or pubescent, calyx-lobes persistent, tardily or early caducous, stamens isomorphic or dimorphic, pedoconnective and appendages present or absent.

***Dissotis*.** — Our phylogenetic analyses showed that *Dissotis* s.l. (sensu Fernandes & Fernandes, 1969; Wickens, 1975; Jacques-Félix, 1981, 1995) is polyphyletic with two of its subgenera (subg. *Dissotidendron*, subg. *Dupineta*) distantly related to *Dissotis* s.str. as defined by its type *D. grandiflora* Benth. We sampled ten species of *D.* sect. *Squamulosae* and two species of *D.* sect. *Dissotis* (*D. grandiflora*, *D. longisetosa* Gilg & Ledermann ex Engl.). These two sections were each recovered as well-supported clades (BS 100/PBS 100/PP 1; see Fig. 4B; Electr. Suppl.: Figs. S1, S2). We also sampled four species previously treated in *Dissotis* sect. *Macrocarpae*, and this group is recovered as monophyletic in our analyses (BS 82/PBS 90/PP 1; see Fig. 4B; Electr. Suppl.: Figs. S1, S2). Our molecular analyses included three species of *D.* sect. *Sessilifoliae*, i.e., *D. congolensis* (Cogn. ex Büttner) Jacq.-Fél., *D. gilgiana* Hutch. & Dalziel and *D. welwitschii* (the type, Fig. 1). *Dissotis congolensis* is part of a clade with *Antherotoma senegambiensis* (Guill. & Perr.) Jacq.-Fél., *O. togoensis* and *O. decandra*, while *D. gilgiana* is recovered as sister to *D. welwitschii* and *D.* sect. *Macrocarpae* (Fig. 4B; Electr. Suppl.: Figs. S1, S2).

According to Wickens (1975), the four sections (sect. *Dissotis*, sect. *Squamulosae*, sect. *Macrocarpae*, sect. *Sessilifoliae*) of *D.* subg. *Dissotis* as proposed by Fernandes & Fernandes (1969) were ill-defined, and he did not use them in his treatment for the *Flora of tropical East Africa*. Although we are able to recognise all these sections in our molecular and morphological analyses, we do not provide any taxonomic suggestions for these clades because of the only partially resolved backbone and internal branches within the large clade of *Dissotis* s.str. and allies.

***Antherotoma*.** — *Antherotoma* s.l. (sensu Jacques-Félix (1995) comprises 11 species and is distributed in continental Africa, apart from the type *A. naudinii* Hook.f. which is also found in the Comoro Islands and Madagascar. Our molecular analyses included five and three species of *D.* sect. *Osbeckiella* and sect. *Senegambia*, respectively. We recovered a well-supported clade (BS 91/PBS 92/PP 1) containing all species earlier treated in *D.* sect. *Osbeckiella* (Jacques-Félix, 1981). On the other hand, the three species sampled of *D.* sect. *Senegambia*, i.e., *A. senegambiensis*, *A. irvingiana* (Hook.f.) Jacq.-Fél. and *A. densiflora* (Gilg) Jacq.-Fél., do not form a monophyletic clade but fall in different positions in the tree (Fig. 4B; Electr. Suppl.: Figs. S1, S2). *Antherotoma senegambiensis*, for example, groups with *Dissotis congolensis* which is also supported by the morphological similarity between these two species. However, from our current molecular sampling, we cannot definitely conclude whether *Antherotoma* should retain all species formerly treated in *D.* sect. *Senegambia* and *D.* sect. *Osbeckiella* as done by Jacques-Félix (1995).

African *Osbeckia*. — In studying staminal morphology of African Melastomateae, Jacques-Félix (1981) confirmed the occurrence of four *Osbeckia* species (*O. decandra*, *O. porteresii*, *O. praviantha*, *O. togoensis*) in Africa. He further suggested that *Antherotoma* is sister to *O. decandra* which has characteristic osbeckioid stamens, but he could not suggest any relatives for *O. porteresii* or *O. togoensis*. The last species is a small shrub with a dense indumentum of white hairs, stamens subequal but not dimorphic and endemic to Togo. *Osbeckia praviantha* on the other hand is morphologically very similar to *O. decandra*: these are annual herbs having isomorphic stamens with neither a pedoconnective nor an appendage and are endemic to West Africa (Fig. 2). As discussed earlier, our molecular results place *O. porteresii* in the *Melastomastrum* clade and further support *Osbeckia* s.str. as a strictly SE Asian genus with no known representatives in Africa. Nonetheless, the African species previously placed in *Osbeckia* are morphologically very different from *Dissotis* and *Antherotoma* and would require a new generic or subgeneric classification after a more comprehensive phylogenetic and morphological study. Two poorly collected *Osbeckias* (*O. albiflora* Cogn. ex De Wild. & Th.Dur., *O. pusilla* De Wild.) from the Democratic Republic of the Congo are morphologically very close to *D. congolensis* and are likely synonyms of that species. Also *O. calotricha* Gilg which is currently known from a single type specimen (P00412554!) and *O. drepanosepala* Gilg which has no type but a well described species in Gilg (1898), are all probably synonyms of *Antherotoma senegambiensis*.

***Dissotis tubulosa*.** — This species, distributed from Guinea and Sierra Leone to Cameroon, is morphologically unique but taxonomically problematic. It was first described as *Osbeckia tubulosa* Sm. (Smith, 1813), and then transferred to *Dissotis* by Triana (1872). The species has also been placed in two monospecific genera, i.e., *Derosiphia* Raf. (Rafinesque, 1838) and *Podocaelia* A.Fern. & R.Fern. (Fernandes & Fernandes, 1962). *Dissotis tubulosa* was again transferred to *Dissotis* subg. *Dupineta* (Jacques-Félix, 1981, 1983) although morphologically different from the rest of the species in this group. It is an annual herb, calyx-tube with persistent stellate emergences, stamens isomorphic and fruits accrescent but lacking longitudinal ribs (Fig. 2). From our phylogenetic results, this species cannot be included in *D.* subg. *Dupineta*. Nevertheless, whether to treat *D. tubulosa* as a monospecific genus as suggested by previous authors cannot be decided in this study.

Placement of unsampled genera. — Our current molecular sampling of African Melastomateae lacks two monospecific genera; *Cailliella* and *Dionychastrum*. However, based on morphology we suggest that *Cailliella* may be a close relative of *Melastomastrum*. They share persistent calyx-lobes and 5-merous flowers subtended by an involucre of bracts. *Cailliella* is different from the other African Melastomateae species by being a shrub, glabrescent with age, young branches yellow with dense strigose hairs, nodes swollen, flowers subtended by 2–3 pairs of leaves, pedoconnective absent, connectives with sharp dorsal spur and two lateral linear lobes.

Morphologically, *Dionychastrum* is very similar to *Dionycha*, a Madagascan endemic genus. They are both deciduous shrubs with cymose inflorescence, isomorphic stamens, calyx-tube and capsule not contracted above. *Dionychastrum* differs from *Dionycha* by the following characters: 5-merous flowers, calyx-lobes persistent, pedoconnectives curved, anthers with one anterior pore, capsule apex glabrous and exerted.

Also *Chaetolepis*, the only NW genus which is represented in Africa by one species, *C. gentanoides* was unsampled. Based on its morphology, this species would probably be placed within the *Dissotis* and allies clade and not in NW Melastomateae. Nevertheless, we treat this species in *Chaetolepis* until it is phylogenetically sampled.

Recommendations. — Although several representatives of African Melastomateae are included in our phylogenetic analyses, a denser taxonomic sampling and further morphological studies of *Guyonia* (species formerly treated in *H.* sect. *Cyclostemma*), *Melastomastrum*, *Dichaetanthera* (all four sections) and *Dissotis* s.str. and allies (*Antherotoma*, *Dissotis* and African *Osbeckia*) will be necessary to understand better their ecology, systematics and morphological divergence. Also the monospecific genera *Cailliella*, *Dionychastrum*, *Nerophila* (now *Chaetolepis*) and *Rhodosepala* (now *Dissotis*) need to be sampled. Lastly, the Madagascan and Asian Melastomateae genera are poorly represented. Only 7 of ca. 48 Madagascan Melastomateae species and two of the three Asian Melastomateae genera (ca. 7/83 species) are included in our phylogenetic analyses.

■ TAXONOMIC TREATMENT

Based on the phylogenetic and morphological results presented in this paper, we here propose the following changes/revisions to the classification of African Melastomateae: (1) the genera *Argyrella* Naudin and *Dupineta* Raf. are reinstated; (2) a new status at generic rank is proposed for *Dissotis* subg. *Dissotidendron* A.Fern. & R.Fern.; (3) the new monospecific genus *Anaheterotis* Veranso-Libalah & G.Kadereit is described for *Heterotis pobeguinii* (Hutch. & Dalziel) Jacq.-Fél.; and (4) a broader circumscription of *Guyonia* is provided to include all species formerly treated in *H.* sect. *Cyclostemma* Benth. Jacques-Félix (1981, 1995) had previously reinstated *Heterotis* Benth., and our results support the continued recognition of this genus, but with a narrower circumscription that excludes *H.* sect. *Cyclostemma* and sect. *Argyrella* (Naudin) Jacq.-Fél. A total of 42 new combinations are effected at the species level and below, some of which represent taxa that were not included in our phylogenetic analyses. The new combinations for these unsampled taxa are thus based on comparative morphology and not on molecular results. The positions of the specific nucleotide substitutions used for molecular diagnosis are based on the sequence alignments we have provided in the electronic supplementary material.

We also provide a key to the 12 African Melastomateae genera recognised in this study (Table 1). In addition, we treat *Dissotis* Benth. and allies in one informal clade. This clade consists of *Dissotis* s.str. (including *D.* subg. *Paleodissotis* Jacq.-Fél. and the four sections of *D.* subg. *Dissotis*) together with *Antherotoma* Naudin (including *Dissotis* subg. *Osbeckiella* A.Fern. & R.Fern. and *D.* sect. *Senegambia* Jacq.-Fél.), *Dissotis tubulosa* (Sm.) Triana (previously treated in *D.* subg. *Dupineta* (Raf.) A.Fern. & R.Fern.), and three African species of *Osbeckia* L. (i.e., *O. decandra* (Sm.) DC., *O. praviantha* Jacq.-Fél., *O. togoensis* Leuenb.). In a follow-up study, we will aim to resolve further the phylogenetic relationships and classification within the *Dissotis* and allies clade.

Taxonomic note. — The genus *Kadalia* Raf. was published with two types, *Osbeckia antennina* Sm. and *Osbeckia rotundifolia* Sm. (Rafinesque, 1838). In our phylogenetic analyses both types were recovered in two different genera, *O. antennina* Sm. in *Guyonia* Naudin and *O. rotundifolia* Sm. in *Heterotis* Benth. Since the generic name *Kadalia* is older and has priority over both *Heterotis* and *Guyonia*, it will be required that either *Kadalia antennina* (Sm.) Raf. or *Kadalia rotundifolia* (Sm.) Raf. be chosen as the type of *Kadalia* if this name were to be used. Stone & Veranso-Libalah (2017), discuss the nomenclatural issues concerning the name *Kadalia* in detail and suggested it should be outrightly rejected, since it has not been used and wrongly typified. Also, rejecting *Kadalia* will maintain nomenclatural stability and avoid the creation of several new combinations (i.e., six in the case of *Heterotis* and fifteen in *Guyonia*). As a result, we do not use the name *Kadalia* but instead treat *Guyonia* (including *G. antennina* (Naudin) Veranso-Libalah & R.D.Stone) and *Heterotis* (including *H. rotundifolia* (Sm.) Jacq.-Fél.) as two segregate genera.

Key to genera

- 1 Creeping plants rooting at the nodes 2
- 1 Erect plants not rooting at the nodes 3
- 2 Calyx-tube with stalked stellate emergences (except *H. decumbens*); intersepalal appendages acute to oblong, the apex with stellate hairs; seeds cochleate, visibly arillate **Heterotis**
- 2 Calyx-tube glabrescent, glandular or with simple setose emergences; intersepalal appendages subulate or dentritic, the apex without stellate hairs; seeds elongate-cochleate with sparse tubercles **Guyonia**
- 3 Calyx-lobes persistent 4
- 3 Calyx-lobes caducous 11
- 4 Calyx-tube with 1 or more rings of bristles; fruit a berry or indehiscent capsule **Tristemma**
- 4 Calyx-tube glabrous or with bristles but these not in rings; fruits capsular, dehiscent 5
- 5 Deciduous shrubs or trees 6
- 5 Perennial herbs or subshrubs 9
- 6 Shrubs glabrescent with age; leaf surface with dense strigose hairs; flowers solitary with an involucre of 2–3 pairs of leaves **Cailliella**
- 6 Shrubs or trees not glabrescent with age; leaf surface with setae having bulbous bases, becoming rugose or coarse; flowers in heads, cymes or panicles and lacking an involucre 7
- 7 Leaves 1.5–2.5 × 1–1.5 cm; flowers 5-merous, borne in simple cymes of 1–3 flowers; intersepalal appendages present; stamens isomorphic **Dionychastrum**
- 7 Leaves 6.5–12 × 2.5–7 cm; flowers 4- or 5-merous, borne in panicles; intersepalal appendages absent; stamens dimorphic 8
- 8 Flowers 4-merous; calyx-lobes short or absent, exposing the corolla in bud; pedoconnectives with linear appendages; seeds with hyaline papillae on the back .. **Dichaetanthera**
- 8 Flowers 5-merous; calyx-lobes large, concealing the corolla in bud; pedoconnectives with lobed, broad and obtuse appendages; seeds lacking hyaline papillae on the back **Dissotidendron**
- 9 Flowers in heads or solitary surrounded by large persistent bracts **Melastomastrum**
- 9 Flowers in racemes or panicles surrounded by small or large leafy caducous bracts 10
- 10 Plant glabrous; leaves and petioles reddish to purplish, margins densely serrate ending in very prominent ciliate hairs; each flower surrounded by two large leafy bracts, calyx-tube glabrous **Anaheterotis**
- 10 Plant shortly stellate-pubescent; leaves and petioles appearing dusty or tomentose, margins entire to serrulate; each flower subtended by a pair of small bracts; calyx-tube with only stellate or intermixed with simple, often gland-tipped hairs **Argyrella**
- 11 Flowers 5-merous; calyx-tube accrescent in fruit, developing a long neck with longitudinal ribs **Dupineta**
- 11 Flowers 4- or 5-merous; calyx-tube not accrescent in fruit and lacking a long neck with longitudinal ribs 12

- 12 Leaves distinctly bicoloured, dark green above and yellowish-green beneath; flowers 5-merous; anthers erostrate, opening by an extrorse pore; seeds cochleate, covered with rather elongate tubercles arranged in parallel lines **Pseudosbeckia**
- 12 Leaves mostly monocoloured, if bicoloured then not as above; flowers 4- or 5-merous; anthers rostrate or oblong, opening by an introrse pore; seeds cochleate but tubercles not in parallel lines **Dissotis and allies**

Chromosome numbers. — Chromosome numbers of many African Melastomateae species remain unknown, even though it is very important in the delineation of certain genera. Based on the studies of Favarger (1952, 1962) and Farron & Favarger (1952), the following African Melastomateae genera can be identified with their respective chromosome numbers in brackets; *Heterotis* ($n = 15$), *Dupineta* ($n = 10$), *Melastomastrum* ($n = 17$), *Tristemma* ($n = 17$), *Argyrella* ($n = 17$) and *Guyonia* ($n = 9, 12$ [only *G. jacquesii*]). So far, all the species in the *Dissotis* allies clade whose chromosome numbers are known, have $n = 10$. It will be necessary to study the chromosome number of more African Melastomateae species especially in the *Dissotis* and allies clade, since this together with other taxonomic evidence, may help resolve the relationships in this unresolved clade.

1. **Anaheterotis** Veranso-Libalah & G.Kadereit, **gen. nov.**
– Type: *Anaheterotis pobeguini* (Hutch. & Dalziel) Veranso-Libalah & G.Kadereit (\equiv *Dissotis pobeguini* Hutch. & Dalziel).

Morphological diagnosis. – *Anaheterotis* differs from *Argyrella*, its closest relative, by the following combination of characters: erect, entirely glabrous herb except for its prominently ciliate leaf margins, leaf blades with 5 conspicuous adaxial longitudinal nerves, few-flowered paniculate inflorescence, and flowers enclosed by two leafy bracts. *Argyrella* is an erect herb entirely covered with tomentose stellate and/or glandular hairs and leaf margins more-or-less entire.

Molecular diagnosis. – *Anaheterotis* also differs from the other African Melastomateae genera by one nrITS nucleotide substitution: (indel)-to-G at position 913; and one *accD-psaI* nucleotide substitution: C-to-A at position 1070 (summarised in Table 4).

- Anaheterotis pobeguini** (Hutch. & Dalziel) Veranso-Libalah & G.Kadereit, **comb. nov.** \equiv *Dissotis pobeguini* Hutch. & Dalziel, Fl. W. Trop. Afr. 1: 211. 1927 \equiv *Heterotis pobeguini* (Hutch. & Dalziel) Jacq.-Fél. in Adansonia, sér. 2, 20: 419. 1981 – **Lectotype (designated here):** Guinea, Douné (Baffing), *H. Pobéguin 1695* (K barcode K000313170!; isolectotypes: P barcodes P00412581! & P00412582!).

Note. – In the protologue of *Dissotis pobeguini*, Hutchinson & Dalziel (1927: 211) cited *Pobéguin 1695* as the type specimen. We located three specimens, two housed in P and one in K, all part of the same field collection as the type in the original description but none of them was designated as

Table 4. Diagnostic nucleotide substitutions in plastid (*accD-psaI*, *psbK-psbL*) and nuclear ribosomal (ITS) markers among African Melastomateae.

Position in alignment		Specific substitutions	Comment
Anaheterotis			
ITS	913	G	– (rest of the African Melastomateae genera have an indel)
<i>accD-psaI</i>	1070	A	C (rest of the African Melastomateae genera)
Argyrella			
ITS	293–294	AA	AC (<i>Dichaetanthera</i> Endl., <i>Dissotidendron</i> (A.Fern. & R.Fern.) Veranso-Libalah & G.Kadereit, <i>Heterotis</i> Benth.) AT (<i>Anaheterotis</i> Veranso-Libalah & G.Kadereit, <i>Guyonia</i> Naudin, <i>Melastomastrum</i> Naudin, <i>Tristemma</i> Juss.) GC (<i>Dissotis</i> and allies, <i>Dupineta</i>)
	621–623	TGG	CCG (<i>Dichaetanthera</i> , <i>Dissotis</i> Benth. and allies, <i>Dupineta</i> (Sm.) Raf.) TCG (<i>Dissotis tubulosa</i> (Sm.) Triana) GCG (<i>Pseudosbeckia</i>) CGG (<i>Anaheterotis</i> , <i>Guyonia</i> , <i>Heterotis</i> , <i>Melastomastrum</i> , <i>Tristemma</i>) GCA (<i>Dissotidendron</i>)
	716–720	AGC GA	TGT GT (<i>Anaheterotis</i> , <i>Guyonia</i>) TGC GC (<i>Dichaetanthera</i> , <i>Dissotidendron</i> , <i>Dissotis</i> and allies, <i>Dupineta</i> , <i>Heterotis</i>) TGG AC (<i>Dissotis tubulosa</i>)
	775–777	GAA	CAT (<i>Dissotis</i> and allies, <i>Dupineta</i>) GAG (<i>Anaheterotis</i> , <i>Dichaetanthera</i> , <i>Guyonia</i> , <i>Heterotis</i> , <i>Melastomastrum</i> , <i>Tristemma</i>) TAG (<i>Dissotidendron</i>)
<i>psbK-psbL</i>	293–294	CT	TC (<i>Dupineta</i>) CC (rest of the African Melastomateae genera)
<i>accD-psaI</i>	108	G	T (rest of the African genera included in this study)
	503	A	G (rest of the African genera included in this study)
	518	A	G (rest of the African genera included in this study)
	1296	G	T (rest of the African genera included in this study)
Dissotidendron			
ITS	264–269	CCGTCC	Duplication of CCGTCC from position 258–263
	271–277	-----	Deletion of GAGGCC from position 271–277
	606	A	C (rest of the African genera) G (<i>Argyrella</i>)
	623–624	GA	GG (<i>Anaheterotis</i> , <i>Argyrella</i> , <i>Dichaetanthera</i> , <i>Heterotis</i> , <i>Melastomastrum</i> , <i>Pseudosbeckia</i> , <i>Tristemma</i>) CG (<i>Dissotis</i> and allies, <i>Dupineta</i> , <i>Guyonia</i>)
	635–636	TG	CA (<i>Anaheterotis</i> , <i>Argyrella</i> , <i>Guyonia</i> , <i>Pseudosbeckia</i>) TA (<i>Dichaetanthera</i> , <i>Dissotis</i> and allies, <i>Dupineta</i> , <i>Heterotis</i> , <i>Melastomastrum</i> , <i>Tristemma</i>) GA (<i>Dissotis tubulosa</i>)
	861	C	A (<i>Dissotis</i> sect. <i>Dissotis</i>) T (rest of the African Melastomateae genera)
<i>psbK-psbL</i>	93	A	T (<i>Dupineta</i> , <i>Heterotis</i>) G (<i>Dichaetanthera</i> , <i>Guyonia</i>) – (rest have an indel [deletion])
<i>accD-psaI</i>	334	G	T (rest of the African Melastomateae genera) – (<i>Anaheterotis</i> , <i>Argyrella</i> , and some <i>Dissotis</i> sect. <i>Squamulosae</i>)
	427	A	C (rest of the African Melastomateae genera) – (some <i>Dissotis</i> sect. <i>Squamulosae</i>)
Dupineta			
ITS	325–326	AC	GT (<i>A. irvingiana</i> , <i>Dissotis</i> sect. <i>Macrocarpae</i>) AT (rest of the African Melastomateae genera)
	703–704	TT	– (rest of the African Melastomateae genera have indels, deletion)
	705–706	TG	CA (<i>Dissotis tubulosa</i>) CG (rest of the African Melastomateae genera)

Table 4. Continued.

Position in alignment		Specific substitutions	Comment
<i>psbK-psbL</i>	241	T	G (rest of the African Melastomateae genera)
	259	A	T (rest of the African Melastomateae genera)
	292–293	T	C (rest of the African Melastomateae genera)
	342	G	T (rest of the African Melastomateae genera)
	446–447	TT	CG (<i>Guyonia</i>) AT (<i>Melastomastrum theifolium</i>) CT (rest of the African Melastomateae genera)
<i>accD-psaI</i>	128	A	C (rest of the African Melastomateae genera)
	435	C	G (rest of the African Melastomateae genera) – (some <i>Dissotis</i> sect. <i>Squamulosae</i>)
	450	G	T (rest of the African Melastomateae genera)
	984–985	GT	AT (rest of the African Melastomateae genera) AG (some <i>Melastomastrum</i>)
<i>Guyonia</i>			
ITS	127	T	G (rest of the African Melastomateae genera)
	711	T	C (rest of the African Melastomateae genera)
	713	T	C (rest of the African Melastomateae genera)
	739	A	G (rest of the African Melastomateae genera)
<i>accD-psaI</i>	1032–1039	-----	CATTATTT (rest of the African Melastomateae genera)
	1045–1046	--	CA (rest of the African Melastomateae genera)
<i>Heterotis</i>			
ITS	64	T	C (<i>Dichaetanthera</i> , <i>Dissotis</i> and allies, <i>Guyonia</i>) A (<i>Anaheterotis</i> , <i>Argyrella</i> , <i>Dissotidendron</i> , <i>Dupineta</i> , <i>Pseudosbeckia</i> , <i>Melastomastrum</i> , <i>Tristemma</i>)
	203–205	CAA	Duplication of CAA from the position 200–202
	235–236	TT	TG (<i>Anaheterotis</i> , <i>Argyrella</i> , <i>Dichaetanthera</i> , <i>Dissotidendron</i> , <i>Guyonia</i> , <i>Melastomastrum</i> , <i>Tristemma</i>) CG (<i>Dissotis</i> and allies, <i>Dupineta</i>)
<i>psbK-psbL</i>	253	T	A (rest of the African Melastomateae genera)
	323	C	A (rest of the African Melastomateae genera)
<i>accD-psaI</i>	1154	G	T (rest of the African Melastomateae genera)
<i>Melastomastrum</i>			
<i>psbK-psbL</i>	163	T	C (rest of the African Melastomateae genera)
	261	T	C (rest of the African Melastomateae genera)
<i>accD-psaI</i>	1181–1182	CA	CC (<i>Tristemma</i>) TG (rest of the African Melastomateae genera)
<i>Tristemma</i>			
ITS	71	C	– (rest of the African Melastomateae genera have an indel)
<i>psbK-psbL</i>	47	C	T (rest of the African Melastomateae genera)
	67–68	--	AT (rest of the African Melastomateae genera)
	78–79	CG	CC (<i>Anaheterotis</i> , <i>Argyrella</i> , <i>Dichaetanthera</i> , <i>Guyonia</i> , <i>Melastomastrum</i> ,) GC (<i>Dissotidendron</i> , <i>Dissotis</i> and allies, <i>Heterotis</i> , <i>Pseudosbeckia</i>)
	130	C	T (rest of the African Melastomateae genera)
<i>accD-psaI</i>	86	A	T (rest of the African Melastomateae genera)
	1045	T	C (rest of the African Melastomateae genera)
	1174–1175	CC	CA (<i>Melastomastrum</i>) TG (rest of the African Melastomateae genera)

Melastomateae genera: *Anaheterotis*, *Argyrella*, *Dichaetanthera*, *Dissotidendron*, *Dissotis* and allies, *Dupineta*, *Heterotis*, *Guyonia*, *Melastomastrum*, *Pseudosbeckia* and *Tristemma*.

Positions are based on the sequence alignments provided in the electronic supplementary material.

the holotype. We selected K000313170 as the lectotype because it has Pobéguin's original label with his collection number, the specimen probably studied by Hutchinson and Dalziel, is in agreement with the original description, is complete and well preserved.

2. *Argyrella* Naudin in Ann. Sci. Nat., Bot., sér. 3, 13: 300. 1850 ≡ *Dissotis* sect. *Argyrella* (Naudin) Triana in Trans. Linn. Soc. London 28: 58. 1872 ("1871") ≡ *Dissotis* subg. *Argyrella* (Naudin) A.Fern. & R.Fern. in Bol. Soc. Brot., sér. 2, 43: 289. 1969 ≡ *Heterotis* sect. *Argyrella* (Naudin) Jacq.-Fél. in Adansonia, sér. 2, 20: 419. 1981 – Type (designated by Fernandes & Fernandes in Bol. Soc. Brot., sér. 2, 43: 289. 1969): *A. incana* (E.Mey. ex Walpers) Naudin (= *A. canescens* (Graham) Harv.).

Morphological diagnosis. – *Argyrella* differs from *Anaheterotis*, its closest African relative, by the following combination of characters: erect herbs with soft tomentose stellate and/or glandular hairs on the entire plant, inflorescence paniculate, intersepal appendages reduced or absent and large stamens with tricuspidate appendages while smaller stamens have bilobed appendages. *Anaheterotis* is an erect glabrous herb except for its prominently ciliate leaf margins.

Molecular diagnosis. – *Argyrella* also differs from the other African Melastomateae genera at the following nrITS nucleotide positions: AC/AT/GC-to-AA substitution at positions 293–294, CCG/TCG/GCG/CGG/GCA-to-TGG substitution at positions 621–623, TGTGT/TGCCC/TGGAC-to-AGCGA substitution at positions 716–720 and CAT/GAG/TAG-to-GAA substitutions at positions 775–777; two *psbK-psbL* nucleotide substitutions, TC/CC-to-CT at positions 293–294; and four *accD-psaI* nucleotide substitutions, T-to-G at positions 108 and 1296, and G-to-A at positions 503 and 518 and T-to-G at position 1296 (summarised in Table 4).

Argyrella amplexicaulis (Jacq.-Fél.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis gilgiana* Hutch. & Dalziel, Fl. W. Trop. Afr. 1: 212. 1927, nom. illeg. ≡ *Dissotis amplexicaulis* Jacq.-Fél. in Bull. Mus. Natl. Hist. Nat., sér. 2, 8: 108. 1936 ≡ *Heterotis amplexicaulis* (Jacq.-Fél.) Aké Assi in Bull. Mus. Natl. Hist. Nat., sér. 4, 9: 459. 1987 – **Lectotype (designated here)**: Mali, Sicoro, *Chevalier 228* (K barcode K000313145!; isolectotype: P barcode P00412566!).

Note. – In the protologue of *Dissotis gilgiana*, Hutchinson & Dalziel (1927: 212) cited *Chevalier 228* as the type specimen. We located two specimens housed in P and K, both part of the same field collection. However, neither of them was designated as the holotype. Since Hutchinson and Dalziel mainly worked in K, they likely studied the specimen housed in K. As such, we selected K000313145 as the lectotype and P00412566 as the isolectotype.

Argyrella angolensis (Cogn.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis angolensis* Cogn. in Candolle & Candolle, Monogr. Phan. 7: 371. 1891 ≡ *Heterotis angolensis* (Cogn.) Jacq.-Fél. in Adansonia, sér. 2, 20: 420.

1981 – Holotype: Angola, Huíla, Lubango, Ferrão da Sola, *Welwitsch 914* (G-DC barcode G00319500!; isotypes: BM barcode BM000902303!, C barcode C10000969!, K barcode K000313397!, LD barcode 1246147!, LISU barcode LISU209421!, M barcode M-0105939!, P barcode P00412567!, PRE barcode PRE0341342-0!).

Note. – One collection of *Heterotis angolensis* from Poli, north Cameroon (*Raynal 13096*, P barcode P05222487!) was cited in the *Flore du Cameroun* (Jacques-Félix, 1983). However, we identify this collection as *Argyrella canescens* (E.Mey. ex Graham) Harv.

Argyrella bambutorum (Gilg & Ledermann ex Engl.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis bambutorum* Gilg & Ledermann ex Engl., Veg. Erde 9(3,2): 750. 1921 ≡ *Heterotis angolensis* var. *bambutorum* (Gilg & Ledermann ex Engl.) Jacq.-Fél. in Adansonia, sér. 2, 20: 420. 1981 – Neotype (designated by Jacques-Félix in Satabié & Leroy, Fl. Cameroun 24: 47. 1983): Cameroon, Bambuto Mts., *Jacques-Félix 2662* (P barcode P05222490!).

Note. – *Dissotis bambutorum* (≡ *Argyrella bambutorum* in the present treatment) was treated by Jacques-Félix (1983) in *Flore du Cameroun* as an isomorphic variety of the otherwise dimorphic *Heterotis angolensis* (≡ *Argyrella angolensis* in the present treatment). However, the stamens of *A. bambutorum* are isomorphic.

Argyrella linearis (Jacq.-Fél.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis linearis* Jacq.-Fél. in Bull. Inst. Franç. Afrique Noire 15: 980. 1953 – **Lectotype (designated here)**: Guinea, Dinguiraye, *Jacques-Félix 1467* (P barcode P00412580!; isolectotype: K barcode K000313147!).

Note. – In the protologue of *Dissotis linearis*, Jacques-Félix (1953: 80) cited *Jacques-Félix 1467* as the type specimen. We located two specimens housed in P and K, all part of the same field collection as the type. However, neither of them was designated as the holotype. We selected P00412580 as the lectotype because it has Jacques-Félix's original label with his collection number, the specimen is in agreement with the original description, is likely the specimen studied by Jacques-Félix, is complete and well preserved.

Argyrella sessilis (Hutch. ex Brenan & Keay) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis sessilis* Hutch. ex Brenan & Keay in Kew Bull. 7: 545. 1953 ("1952") – Holotype: Sierra Leone, Bitumane Peak, *Glanville 386* (K barcode K000313144!).

Other included species. – *Argyrella canescens* (E.Mey. ex Graham) Harv.

3. *Dissotidendron* (A.Fern. & R.Fern.) Veranso-Libalah & G.Kadereit, **stat. nov.** ≡ *Dissotis* subg. *Dissotidendron* A.Fern. & R.Fern. in Bol. Soc. Brot., sér. 2, 43: 289. 1969 – Type: *Dissotidendron melleri* (Hook.f.) Veranso-Libalah & G.Kadereit.

Morphological diagnosis. – *Dissotidendron* can be distinguished from *Dichaetanthera* Endl. by the following combination of characters: trees or shrubs, mostly deciduous; leaf surfaces rugose; flowers 5-merous; calyx-lobes persistent with no intersepalal appendages. *Dichaetanthera* are trees or shrubs with 4-merous flowers.

Molecular diagnosis. – *Dissotidendron* also differs from the other African Melastomateae genera in the following nrITS nucleotide positions: a tandem duplication of CCGTCC (264–269) from positions 258–263, deletion of GAGGCC at positions 271–277, C/G-to-A substitution at position 606, GG/CG-to-GA substitution at positions 623–624, CA/TA/GA-to-TG at positions 635–636, A/T-to-C at position 861; one *psbK-psbL* nucleotide substitution, T/G/indel-to-A at position 93; and two *accD-psaI* nucleotide substitutions: T/indel-to-G at position 334, C/indel-to-A at position 427 (summarised in Table 4).

Dissotidendron apricum (Gilg ex Engl.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis aprica* Gilg ex Engl., Veg. Erde 9(3,2): 749. 1921 – **Lectotype (designated here):** Tanzania, Lindi District, Rondo (Muera) Plateau, *Busse 2577* (EA barcode EA000003766!).

Note. – In the protologue of *Dissotis aprica*, Engler (1921: 749) cited a specimen collected from Tanzania, Lindi District, Rondo (Muera) Plateau by *Busse 2577* and housed in B as the type. Unfortunately, this specimen was likely destroyed during World War II since there was no trace of it in B. We located and selected EA000003766 as the lectotype because it is probably part of the same field collection and in good condition.

Dissotidendron arborescens (A.Fern. & R.Fern.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis arborescens* A.Fern. & R.Fern. in Bol. Soc. Brot., sér. 2, 29: 51. 1955 – Holotype: Tanzania, Iringa District, Sao Hill, *Greenway 6176* (EA barcode EA000001983!; isotypes: K barcode K000313066!, PRE barcode PRE0341343-0!).

Dissotidendron bussei (Gilg ex Engl.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis bussei* Gilg ex Engl., Veg. Erde 9(3,2): 749. 1921 – **Neotype (designated here):** Tanzania, Dodoma, Mpwapwa District, Kibakwe division, Mbuga yard, Mbuga village, Mafermera subvillage, Rubeho mountains, Langangulu river ca. 200–300 m S and N of foot track to Dibulilo subvillage, *Kayombo & al. 4914* (MO!; isoneotype: EA!).

Note. – In the protologue of *Dissotis bussei*, Engler (1921: 749) cited a specimen collected from Tanzania, Mpwapwa District, Kiboriani Mts. by *Busse* with no collection number and housed in B as the type. Unfortunately, this specimen was likely destroyed during World War II since there was no trace of it in B and we were unable to locate any specimen from the same field collection in other herbaria. We selected *Kayombo & al. 4914* housed in MO as the neotype because it is complete and well preserved.

Dissotidendron caloneurum (Gilg ex De Wild.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis caloneura* Gilg ex De

Wild. in Ann. Mus. Congo Belge, Bot., sér. 4, 2(1): 116. 1913 ≡ *Dissotis caloneura* Gilg ex Engl., Veg. Erde 9(3,2): 749. 1921, isonym – **Neotype (designated here):** Tanzania, T4, Kigoma District, Mt. Livandabe (Lubalisi), *Bidgood & al. 4178* (P barcode P05281276!; isoneotypes: C!, K).

= *Dissotis venulosa* Hutch., Botanist S. Afr.: 512. 1946, in adnot. – Type: Zambia, Mbala District, Lake Chila, *Hutchinson & Gillett 3887* (K barcode K000313393!).

Note. – In the protologue of *Dissotis caloneura*, De Wildeman (1913: 116) cited a specimen collected from Mt. Minta, M'Lolose by *Kässner* with collection number 2960 (13 May 1908) and housed in Berlin as the type. Unfortunately, this specimen was probably destroyed during World War II since there was no trace of it in B but we were able to locate three specimens from the same field collection housed in BM (BM000902299!), P (P05223126!) and K!. The BM specimen is a mounted sheet of *D. trothae* Gilg and a single flower fragment of *D. caloneura* in an envelope while the other specimens in P and K are only mounted sheets of *D. trothae*.

Also, in another protologue of *Dissotis caloneura*, Engler (1921: 749) cited a specimen collected from Katanga, Mt. Nunta by *Kässner* with collection number 2960 (1908 expedition). We were unable to locate this specimen which was also likely stored in B and destroyed during the World War II. However, we think this was the same specimen cited by De Wildeman of which only a flower fragment is available and housed in BM. As a result, we selected P05281276 as the neotype.

Dissotidendron caloneurum var. *confertiflorum* (A.Fern. & R.Fern.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis caloneura* var. *confertiflora* A.Fern. & R.Fern. in Bol. Soc. Brot., sér. 2, 34: 59, fig. 1. 1960 – Holotype: Tanzania, Ufipa District, Kito (Keto) Mt., *Richards 6176* (K barcode K000313068!).

Dissotidendron caloneurum var. *pilosum* (A.Fern. & R.Fern.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis caloneura* var. *pilosa* A.Fern. & R.Fern. in *Kirkia* 1: 73, fig. 7. 1961 – Holotype: Zambia, Luanshya, *Fanshawe 3118* (K barcode K000313391!).

Dissotidendron caloneurum var. *setosius* (A.Fern. & R.Fern.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis caloneura* var. *setosior* A.Fern. & R.Fern. in Bol. Soc. Brot., sér. 2, 30: 171, fig. 5. 1956 – Holotype: Tanzania, Kigoma District, Kafulu, *Eggeling 6172* (EA barcode EA000001984!; isotype: K barcode K000313067!).

Dissotidendron cordatum (Gilg) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis cordata* Gilg in Engler, Monogr. Afrik. Pflanzen-Fam. 2: 17. 1898 – **Neotype (designated here):** Democratic Republic of the Congo, Kakalalwe, *Malaisse & al. 533* (BR barcode BR0000017293129!; isoneotype: BR barcode BR0000017293112!).

= *Dissotis derriksiana* P.A.Duvign. in Bull. Soc. Roy. Bot. Belgique 90: 257. 1958, **syn. nov.** – Holotype:

Democratic Republic of the Congo, Haut-Katanaga, Dikuluwe, *Duvigneaud & Damblon 3088D* (BRLU barcode BRLU0000090023040!; isotype: BRLU barcode BRLU0000090023248!).

Note. – In the protologue of *Dissotis cordata*, Gilg (1898: 17) cited a specimen collected from “Oberes Congogebiet, Baschilange, am Lulufluss” by *Pogge* with collection number 134. Unfortunately, this specimen was likely destroyed during World War II since there was no trace of it in B and we were unable to locate any specimen from the same field collection in other herbaria. We selected 0000017293129 in BR as the neotype because it is complete and well preserved.

Also, the original description of *Dissotis derriksiana* by *Duvigneaud* (1958: 257) clearly matches that of *D. cordata*. Hence, *Dissotis derriksiana* is treated as a synonym of *Dissotidendron cordatum*.

Dissotidendron dicaetantheroides (Wickens) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis dicaetantheroides* Wickens in *Kew Bull.* 29(1): 141. 1974 – Holotype: Tanzania, Morogoro District, Nguru Mts., *Drummond & Hemsley 1960* (K barcode K000313063!; isotypes: EA barcodes EA000001980! & EA000003753!, K barcode K000313062!).

Dissotidendron glandulicalyx (Wickens) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis glandulicalyx* Wickens in *Kew Bull.* 29(1): 142. 1974 – Holotype: Tanzania, Mpanda District, Kungwe Mt., *Harley 9542* (K barcode K00313065!).

Dissotidendron johnstonianum (Baker f.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis johnstoniana* Baker f. in *Trans. Linn. Soc. London, Bot.* 4(1): 14. 1894 – Holotype: Malawi, Mlanje Mt., *Whyte 74* (K barcode K000313388!).

Dissotidendron johnstonianum* var. *strigosum (Brenan) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis johnstoniana* var. *strigosa* Brenan in *Mem. New York Bot. Gard.* 8: 440. 1954 – Holotype: Malawi, Mlanje Mt., Chambe Plateau, *Brass 16757* (K barcode K000313387!; isotypes: BM barcode BM000580060!, BR barcode BR0000006494551!; PRE barcode PRE0601890-0!; SRGH barcode SRGH0106508-0!).

Dissotidendron lanatum (A.Fern. & R.Fern.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis lanata* A.Fern. & R.Fern. in *Bol. Soc. Brot., sér. 2*, 43: 294. 1969 – Holotype: Malawi, Northern Prov., Mafinga Mts., *Robson 533* (K barcode K000049527!; isotypes: BM barcode BM000902405!, LISC barcode LISC 002950!, SRGH barcode SRGH0106556-0!).

Dissotidendron melleri (Hook.f.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis melleri* Hook.f. in *Oliver, Fl. Trop. Afr.* 2: 451. 1871 – Holotype: Malawi, Mt. Chiradzura, Manganja range, *Meller s.n.* (K barcode K000313390!).

= *Dissotis whytei* Baker in *Bull. Misc. Inform. Kew* 1897: 267. 1897 – Holotype: Malawi, Zomba Mt., *Whyte s.n.* (K barcode K000313389!).

Dissotidendron melleri* var. *greenwayi (A.Fern. & R.Fern.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis greenwayi* A.Fern. & R.Fern. in *Bol. Soc. Brot., sér. 2*, 30: 172. 1956 ≡ *Dissotis melleri* var. *greenwayi* (A.Fern. & R.Fern.) A.Fern. & R.Fern. in *Bol. Soc. Brot., sér. 2*, 46: 68. 1972 – Holotype: Tanzania, Rungwe District, R. Kiwira, *Greenway 8410* (EA; isotype: K barcode 00313064!).

= *Dissotis rubroviolacea* Gilg in *Bot. Jahrb. Syst.* 30: 365. 1901 – **Lectotype (designated here):** Tanzania, N. Mt. Rungwe, *Goetze 1136* (BM barcode BM000902402!; isolectotype: P barcode P00412542!).

Note. – In the protologue of *Dissotis rubroviolacea*, Gilg (1901: 365) cited a specimen collected from Tanzania, N. Mt. Rungwe by *Goetze* with collection number 1136 and housed in B as the type. This specimen was likely destroyed during World War II since there was no trace of it in B but we were able to locate two specimens from the same field collection housed in BM and P. As a result we selected BM000902402, as the lectotype and P00412542 as the isolectotype.

Dissotidendron polyanthum (Gilg) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis polyantha* Gilg in *Engler, Monogr. Afrik. Pflanzen-Fam.* 2: 16. 1898 – **Neotype (designated here):** Tanzania, Morogoro, Kilosa district, T6, Ukwiva forest reserve, Kifuluma area, *Festo & al. 1901* (MO barcode MO-2721881!; isoneotype: C!).

Note. – In the protologue of *Dissotis polyantha*, Gilg (1898: 16) cited a specimen collected from Tanzania, Usagara, Kifuru (Central Uluguru) by *Stuhlmann* with collection number 9081 and housed in B as the type. Unfortunately, this specimen was likely destroyed during World War II since there was no trace of it in B and we were unable to locate any specimen from the same field collection in other herbaria. As a result, we selected MO-2721881 as the neotype.

4. ***Dupineta*** Raf., *Sylva Tellur.*: 101. 1838 ≡ *Dissotis* subg. *Dupineta* (Raf.) A.Fern. & R.Fern. in *Bol. Soc. Brot., sér. 2*, 43: 288. 1969 – Type: *Dupineta multiflora* (Sm.) Raf.

Morphological diagnosis. – *Dupineta* differs from *Pseudosbeckia* A.Fern. & R.Fern. by the following combination of characters: perennial shrublets, inflorescence a panicle of cymes, flowers 5-merous with small caducous bracts, calyxlobes early caducous, intersepal appendages absent, stamens dimorphic, appendages bifid, calyx-tube accrescent in fruit and developing distinct longitudinal ribs. *Pseudosbeckia* is a shrub with flowers 5-merous, sepals tardily caducous, stamens isomorphic, fruiting capsule widely campanulate and not accrescent.

Molecular diagnosis. – *Dupineta* also differs from the other African Melastomateae genera in the following nrITS nucleotide positions: GT/AT-to-AC substitution at positions 325–326, TT insertion at positions 703–704, CA/CG-to-TG substitution at positions 705–706; five *psbK-psbL* nucleotide

substitutions: a G-to-T substitution at position 241, T-to-G substitution at position 259, C-to-T substitution at position 293, T-to-G substitution at position 342, CG/AT/CT-to-TT substitution at positions 446–447; and four *accD-psal* nucleotide substitutions: C-to-A substitution at position 128, G/indel-to-C substitution at position 435, a T-to-G substitution at position 450, AT/AG-to-GT substitution at positions 984–985 (summarised in Table 4).

Dupineta brazzae (Cogn.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis brazzae* Cogn. in Candolle & Candolle, Monogr. Phan. 7: 372. 1891 – **Lectotype (designated here):** Gabon, Franceville, *de Brazza 43* (P barcode P00412522!; isolectotypes: BR barcode BR0000006493585!, P barcodes P00412521! & P00412523!).

= *Dissotis tanganyikae* Kraenzl. in Vierteljahrsschr. Naturf. Ges. Zürich 76: 150. 1931 – Holotype: Democratic Republic of the Congo, Katanga, Kibandu, *Kassner 3055a* (Z barcode Z-000015029!).

Note. – In the protologue of *Dissotis brazzae*, Cogniaux (1891: 372) cited *de Brazza 43*, housed in P as the type specimen. We located four specimens, three housed in P and one in BR, all part of the same field collection but none of them was designated as the holotype. We selected P00412522 as the lectotype.

Dupineta hensii (Cogn.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis hensii* Cogn. in Candolle & Candolle, Monogr. Phan. 7: 372. 1891 – Holotype: Democratic Republic of the Congo (Zaire), Bangala, *Hens 129* (BR barcode BR0000006493509!; isotypes: P barcode P00412536!; Z barcodes Z-000015020! & Z-000015021!).

Dupineta loandensis (Exell) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis loandensis* Exell in J. Bot. 67 (Suppl. 1): 179. 1929 – **Lectotype (designated here):** Angola, Luanda, Cazengo District, *Gossweiler 697* (BM barcode BM000902404!; isolectotypes: K barcode K00313356!; P barcode P00412541!).

Note. – In the protologue of *Dissotis loandensis*, Exell & al. (1929: 179) cited *Gossweiler 697* as the type specimen. We located three specimens housed in BM, K and P from the same field collection but none of them was designated as the holotype. Since Exell worked in BM, we think he likely studied BM000902404 and therefore it was selected as the lectotype.

Dupineta pauwelsii (Jacq.-Fél.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis pauwelsii* Jacq.-Fél. in Bull. Jard. Bot. Natl. Belg. 44(1–2): 162. 1974 – Holotype: Democratic Republic of the Congo, District du Bas-Congo, environs de Kimvula, *Pauwels 2719* (BR barcode BR0000006422837!; isotype: P barcode P06602990!).

Other included species. – *Dupineta multiflora* (Sm.) Raf.

5. **Guyonia** Naudin in Ann. Sci. Nat., Bot., sér. 3, 14: 149. 1850 – Type: *Guyonia tenella* Naudin.

= *Afzeliella* Gilg in Engler, Monogr. Afr. Pflanzen-Fam. 2: 4. 1898 – Type: *Afzeliella ciliata* (Hook.f.) Gilg.

= *Heterotis* sect. *Cyclostemma* Benth. in Hooker, Niger Fl.: 349. 1849 – Type: *Heterotis antennina* Benth.

Morphological diagnosis. – *Guyonia* differs from *Argyrella* and *Anaheterotis* by the following characters: mostly herbaceous geophytes rooting at the nodes, except *G. jacquesii* (A.Chev.) Veranso-Libalah & R.D.Stone which is lignified; no hypanthial emergences; calyx-tube glabrous (glandular hairs in *G. jacquesii*); intersepalal appendages present or absent; flowers solitary or in cymes of 1–3 flowers. *Argyrella* and *Anaheterotis* are erect herbs and the inflorescence a panicle.

Molecular diagnosis. – *Guyonia* also differs from the other African Melastomateae genera in the following nrITS nucleotide positions: G-to-T substitution at position 127, C-to-T substitution at positions 711 and 713 and G-to-A substitution at position 739; and two *accD-psal* nucleotide substitutions: deletion of CATTATTT at positions 1032–1039 and deletion of CA at positions 1045–1046 (summarised in Table 4).

Guyonia antennina (Sm.) Veranso-Libalah & R.D.Stone, **comb. nov.** ≡ *Osbeckia antennina* Sm. in Rees, Cycl. 25. 1813 ≡ *Heterotis antennina* (Sm.) Benth. in Hooker, Niger Fl.: 349. 1849 ≡ *Dissotis antennina* (Sm.) Hook.f. in Oliver, Fl. Trop. Afr. 2: 449. 1871 – **Lectotype (designated here):** Sierra-Leone, *Afzelius s.n.* (BM barcode BM000902302!; isolectotype: K barcode K000313180!).

Note. – In the protologue of *Osbeckia antennina*, Smith (1813) cited *Afzelius s.n.* as the type specimen. We located two specimens housed in BM and K likely from the same field collection but neither of them was designated as the holotype. Since Smith worked in BM, he likely studied BM000902302 and therefore it was selected as the lectotype.

Guyonia arenaria (Jacq.-Fél.) Veranso-Libalah & R.D.Stone, **comb. nov.** ≡ *Heterotis arenaria* Jacq.-Fél. in Bull. Mus. Natl. Hist. Nat., B, Adansonia, sér. 4, 9(3): 255. 1988 (“1987”) – Holotype: Gabon, 15 km environ au Sud de Mayoumba, *De Wilde & al. 629* (WAG barcode WAG0002339!; isotype: WAG barcode WAG0002338!).

Guyonia ciliata Hook.f. in Oliver, Fl. Trop. Afr. 2: 443. 1871 ≡ *Afzeliella ciliata* (Hook.f.) Gilg in Engler, Monogr. Afr. Pflanzen-Fam. 2: 5. 1898 – **Neotype (designated here):** Liberia, Lofa, East of Nekebuzu, *Jongkind & al. 11859* (WAG barcode WAG.1488062!; isoneotypes: BR barcode BR00000016915534!, MO barcode MO-2970207!).

= *Guyonia intermedia* Cogn. in De Wildeman & Durand, Pl. Thonn. Congol.: 30. 1900 ≡ *Afzeliella intermedia* (Cogn.) Gilg in Mildbraed, Wiss. Erg. Deut. Zentr.-Afr. Exped., Bot.: 582. 1913 – Holotype: Democratic Republic of the Congo (Zaire), Ngali, *Thonner 21* (BR barcode BR00000008953339!; isotype: BR barcode BR00000008953667!).

Note. – In the protologue of *Afzeliella ciliata*, Gilg (1898: 5) cited a specimen collected from Sierra-Leone by *Afzelius* with no collection number and housed in B as the type.

Unfortunately, this specimen was probably destroyed during World War II since there was no trace of it in B and we were unable to locate any specimen from the same field collection in other herbaria. We selected WAG.1488062 as the neotype.

Guyonia cinerascens (Sm.) Veranso-Libalah & R.D.Stone, **comb. nov.** ≡ *Dissotis cinerascens* Hutch. in Bull. Misc. Inform. Kew 1921: 372. 1921 ≡ *Heterotis cinerascens* (Hutch.) Jacq.-Fél. in Adansonia, sér. 2, 20: 419. 1981 – Holotype: Northern Nigeria, Neill's Valley, 2 miles east of Government Station, Naraguta, *H.V. Lely* 259 (K barcode K000313164!).

Guyonia entii (J.B.Hall) Veranso-Libalah & R.D.Stone, **comb. nov.** ≡ *Dissotis entii* J.B.Hall in Kew Bull. 24: 346. 1970 ≡ *Heterotis entii* (J.B.Hall) Jacq.-Fél. in Adansonia, sér. 2, 20: 419. 1981 – Holotype: Ghana, West Region, Aiyinasi, edge of small stream in forest, *Hall GC35533* (K barcode K000313173!; isotypes: GC barcode GC000007519!, LISC barcode LISC 002431!, P barcode P00412575!, WAG barcode WAG0002331!).

Guyonia glandulosa (A.Fern. & R.Fern.) Veranso-Libalah & R.D.Stone, **comb. nov.** ≡ *Dissotis glandulosa* A.Fern. & R.Fern. in Bol. Soc. Brot., sér. 2, 43: 293. 1969 – Holotype: Zambia, Mwinilunga Distr., sources of R. Zambesi, dry sandy woodland, *Robinson 5990* (SRGH barcode SRGH0106559-0!).

Guyonia humilis (A.Chev. & Jacq.-Fél.) Veranso-Libalah & R.D.Stone, **comb. nov.** ≡ *Dissotis humilis* A.Chev. & Jacq.-Fél. in Bull. Mus. Natl. Hist. Nat., sér. 2, 4: 684. 1932 – Holotype: Guinea, Kindia, *Jacques-Félix 220* (P barcode P00412576!).

Guyonia jacquesii (A.Chev.) Veranso-Libalah & R.D.Stone, **comb. nov.** ≡ *Dissotis jacquesii* A.Chev. in Bull. Mus. Natl. Hist. Nat., sér. 2, 4: 686. 1932 ≡ *Heterotis jacquesii* (A.Chev.) Aké Assi in Bull. Mus. Natl. Hist. Nat., sér. 4, 9: 459. 1987 – **Lectotype (designated here)**: Guinea, Kindia and Mont Gangan, *Jacques-Félix 240* (P barcode P00412577!; isolectotypes: P barcodes P00412578! & P00412579!).

Note. – In the protologue of *Dissotis jacquesii*, Chevalier in Jacques-Félix (1932: 686) cited *Jacques-Félix 240*, housed in P as the type specimen. We located three specimens in P, all part of the same field collection but none of them was designated as the holotype. We selected P00412577 as the lectotype because it has Jacques-Félix's original label with his collection number, the specimen he probably studied, is in agreement with the original description, is complete and well preserved.

Guyonia obamae (Lejoly & Lisowki) Veranso-Libalah & R.D. Stone, **comb. nov.** ≡ *Heterotis obamae* Lejoly & Lisowki in Syst. & Geogr. Pl. 69(2): 185. 1999 – Holotype: Equatorial Guinea, Rio Muni, Ndote Sud, près du village Etembue, *Lejoly & Elad 98/112* (BRLU barcode BRLU0010836!).

Guyonia pygmaea (A.Chev. & Jacq.-Fél.) Veranso-Libalah & R.D.Stone, **comb. nov.** ≡ *Dissotis pygmaea* A.Chev. & Jacq.-Fél. in Bull. Mus. Natl. Hist. Nat., sér. 2, 4: 685. 1932 ≡ *Heterotis pygmaea* (A.Chev. & Jacq.-Fél.) Jacq.-Fél. in Adansonia, sér. 2, 20: 419. 1981 – **Lectotype (designated here)**: Guinea, environs de Kindia, *Jacques-Félix 195* (P barcode P00412585!; isolectotype: P barcode P00412586!).

Note. – In the protologue of *Dissotis pygmaea*, Chevalier & Jacques-Félix (Jacques-Félix, 1932: 685) cited *Jacques-Félix 195* as the type specimen. We located two specimens housed in P, both part of the same field collection but neither of them was designated as the holotype. We selected P00412585 as the lectotype because it has Jacques-Félix's original label with his collection number, is in agreement with the original description, is complete, well preserved and likely the specimen studied by Chevalier and Jacques-Félix.

Guyonia rupicola (Gilg ex Engl.) Veranso-Libalah & R.D. Stone, **comb. nov.** ≡ *Dissotis rupicola* Gilg ex Engl., Veg. Erde 9(3,2): 748. 1921 ≡ *Heterotis rupicola* (Gilg ex Engl.) Jacq.-Fél. in Adansonia, sér. 2, 20: 419. 1981 – **Lectotype (designated here)**: Liberia, *Dinklage 2139* (B barcode B 10 0159359!; isolectotypes: B barcodes B 10 0159360!, B 10 0159361! & B 10 0159362!).

= *Dissotis glauca* Keay in Kew Bull. 7: 545. 1953 (“1952”) ≡ *D. rupicola* Hutch. & Dalziel, Fl. W. Trop. Afr. 1: 211. 1927; in Bull. Misc. Inform. Kew 1928: 221. 1928, nom. illeg., non *D. rupicola* Gilg ex Engl. – Holotype: Sierra Leone, Sugar Loaf Mt., *Scott-Elliott 3977* (K barcode K000313166!; isotype: K barcode K000313168!).

Note. – In the protologue of *Dissotis rupicola*, Hutchinson & Dalziel (1927: 748) cited *Dinklage 2139*, housed in B as the type specimen. We located four specimens in B, all part of the same field collection but none of them was designated as the holotype. We selected B 10 0159359 as the lectotype because it has Dinklage's original label with his collection number, is in agreement with the original description, is complete and well preserved.

Guyonia seretii (De Wild.) Veranso-Libalah & R.D.Stone, **comb. nov.** ≡ *Dissotis seretii* De Wild. in Ann. Mus. Congo Belge, Bot., sér. 5, 2(3): 328. 1908 ≡ *Heterotis seretii* (De Wild.) Jacq.-Fél. in Adansonia, sér. 2, 20: 419. 1981 – Holotype: Democratic Republic of the Congo, Bokoyo, *Seret 587* (BR barcode BR0000006421205!).

Guyonia seretii var. *gracilifolia* (Wickens) Veranso-Libalah & R.D.Stone, **comb. nov.** ≡ *Dissotis seretii* var. *gracilifolia* Wickens in Kew Bull. 29(1): 141. 1974 – Holotype: Tanzania, Kigoma Distr., Kabogo Mts., *Azuma 1014* (EA barcode EA000001979!).

Guyonia sylvestris (Jacq.-Fél.) Veranso-Libalah & R.D.Stone, **comb. nov.** ≡ *Dissotis sylvestris* Jacq.-Fél. in Bull. Mus. Natl. Hist. Nat., sér. 2, 10: 632. 1939 (“1938”) ≡ *Heterotis sylvestris* (Jacq.-Fél.) Jacq.-Fél. in Adansonia, sér. 4, 16

(2–4): 272. 1995 – **Lectotype (designated here):** Guinea, Macenta, forêt du Ziama, *Jacques-Félix 2088* (P barcode P00412591!; isolectotype: K barcode K000313189!).

Note. – In the protologue of *Dissotis sylvestris*, Jacques-Félix (1939: 632) cited *Jacques-Félix 2088* as the type specimen. We located two specimens housed in P and K, both part of the same field collection but neither of them was designated as the holotype. We selected P00412591 as the lectotype because it has Jacques-Félix’s original label with his collection number, is in agreement with the original description, likely the specimen he studied, is complete and well preserved.

Other included species. – *Guyonia tenella* Naudin.

6. *Heterotis* Benth. in Hooker, Niger Fl.: 347. 1849 ≡ *Dissotis* sect. *Heterotis* (Benth.) Hook.f. in Oliver, Fl. Trop. Afr. 2: 447. 1871 ≡ *Dissotis* subg. *Heterotis* (Benth.) A.Fern. & R.Fern. in Bol. Soc. Brot., sér. 2, 43: 286. 1969 – Type: *Heterotis rotundifolia* (Sm.) Jacq.-Fél.

Morphological diagnosis. – *Heterotis* can be distinguished from the other African Melastomateae genera by the following combination of characters: decumbent herbs, leaves orbicular to ovate-lanceolate, hypanthium with stalked emergences, flowers large, 5-merous, calyx-lobes persistent, apex of intersepal appendages with stellate emergences, seeds cochleate and visibly arillate.

Molecular diagnosis. – *Heterotis* also differs from the other African Melastomateae genera in the following nrITS nucleotide positions: C/A-to-T substitution at position 64, tandem duplication of CAA at positions 203–205, TG/CG-to-TT substitution at positions 235–236; two *psbK-psbL* nucleotide substitutions: A-to-T substitution at position 253, A-to-C substitution at position 323; and one *accD-psaI* nucleotide substitution: T-to-G substitution at position 1154 (summarised in Table 4).

Heterotis cogniauxiana (A.Fern & R.Fern.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Osbeckia welwitschii* Cogn. in Candolle & Candolle, Monogr. Phan. 7: 333. 1891 ≡ *Dissotis cogniauxiana* A.Fern. & R.Fern. in Garcia de Orta 2: 175. 1954 (in obs.); in Bol. Soc. Brot., sér. 2, 28: 67. 1954 – Holotype: Angola, Pungo Andongo, rio Cuanza, pr. de Sansamanda, *Welwitsch 907* (G-DC barcode G00319429!; isotypes: BM barcode BM000902297!, COI barcode COI00005417!, K barcode K000313363!, LISU barcode LISU209417!, P barcode P000412573!)

Heterotis fruticosa (Brenan) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Dissotis rotundifolia* var. *fruticosa* Brenan in Kew Bull. 5: 227. 1950 ≡ *Dissotis fruticosa* (Brenan) Brenan & Keay in Kew Bull. 7: 547. 1953 (“1952”) – Holotype: Nigeria, Ondo, *Keay 22569* (K barcode K000313153!).

Other included species. – *Heterotis buettneriana* (Cogn. ex Büttner) Jacq.-Fél., *H. decumbens* (P.Beauv.) Jacq.-Fél., *H. prostrata* (Thonn.) Benth., *H. rotundifolia* (Sm.) Jacq.-Fél.

7. *Melastomastrum* Naudin in Ann. Sci. Nat., Bot., sér. 3, 13: 296, t. 5. 1850 – Type: *Melastomastrum capitatum* (Vahl) A.Fern. & R.Fern.

= *Heterotis* sect. *Leiocalyx* Planch. ex Benth. in Hooker, Niger Fl.: 350. 1849 – Type: *Heterotis segregata* Benth.

= *Heterotis* sect. *Wedeliopsis* Planch. ex Benth. in Hooker, Niger Fl.: 351. 1849 – Type: *Heterotis theifolia* (G.Don) Benth.

Morphological diagnosis. – *Melastomastrum* can be differentiated from *Tristemma* Juss., its closest relative, by the following combination of characters: subshrubs or woody herbs with large 5-merous flowers surrounded by an involucre of persistent bracts, calyx-tube campanulate, stamens dimorphic (except in *M. porteresii* (Jacq.-Fél.) Veranso-Libalah & G.Kadereit) and fruits capsular with cochleate seeds. *Tristemma* has calyx-tubes with a ring of bristles midway, stamens isomorphic (except *T. cornifolium* (Benth.) Triana) and fruits baccate.

Molecular diagnosis. – *Melastomastrum* also differs from the other African Melastomateae genera by two *psbK-psbL* nucleotide substitutions: C-to-T substitution at positions 163 and 261; and one *accD-psaI* nucleotide substitutions: CC/TG-to-CA substitution at positions 1181–1182 (summarised in Table 4).

Melastomastrum porteresii (Jacq.-Fél.) Veranso-Libalah & G.Kadereit, **comb. nov.** ≡ *Osbeckia porteresii* Jacq.-Fél. in Bull. Mus. Natl. Hist. Nat., sér. 2, 10: 630. 1939 (“1938”) – **Lectotype (designated here):** Guinea (Guinée française), Mont Nimba, *Portères 3175* (P barcode P00412494!; isolectotype: P barcode P00412494!).

Note. – In the protologue of *Osbeckia porteresii*, Jacques-Félix (1939: 630) cited *Portères 3175* as the type specimen. We located two specimens housed in P, both part of the same field collection but neither of them was designated as the holotype. We selected P00412494 as the lectotype because it has Portères’ original label with his collection number, the specimen probably studied by Jacques-Félix, is in agreement with the original description, is complete and well preserved.

Other included species. – *Melastomastrum afzelii* (Hook.f.) A.Fern. & R.Fern., *M. afzelii* var. *dialonkeanum* Jacq.-Fél., *M. afzelii* var. *lecomteanum* (Hutch. & Dalziel) Jacq.-Fél., *M. afzelii* var. *paucistellatum* (Stapf) Jacq.-Fél., *M. autranianum* (Cogn.) A.Fern. & R.Fern., *M. autranianum* var. *latibracteatum* (De Wild.) Jacq.-Fél., *M. capitatum* (Vahl) A.Fern. & R.Fern., *M. capitatum* var. *silvaticum* Jacq.-Fél., *M. segregatum* (Benth.) A.Fern. & R.Fern., *M. theifolium* (G.Don) A.Fern. & R.Fern.

8. *Tristemma* Juss., Gen. Pl.: 329. 1789 – Type: *Tristemma mauritianum* J.F.Gmel.

Morphological diagnosis. – *Tristemma* differs from *Melastomastrum*, its closest African Melastomateae relative, by the following combination of characters: fruit indehiscent, calyx with 1 to several discrete rings of bristles, stamens isomorphic except in *T. cornifolium*.

Molecular diagnosis. – *Tristemma* also differs from the other African Melastomateae genera by one nrITS nucleotide substitution: C insertion at position 71; four *psbK-psbL*

nucleotide substitutions: a T-to-C substitution at positions 47 and 130, deletion of AT at positions 67–68, CC/GC -to-CG substitution at positions 78–79; and four *accD-psal* nucleotide substitutions: T-to-A substitution at position 86, C-to-T substitution at position 1045 and CA/TG-to-CC substitution at positions 1174–1175 (summarised in Table 4).

Other included species. – *Tristemma akeassii* Jacq.-Fél., *T. albiflorum* (G.Don) Benth., *T. camerunense* Jacq.-Fél., *T. cornifolium* (Benth.) Triana, *T. coronatum* Benth., *T. demusei* De Wild., *T. hirtum* P.Beauv., *T. involucreatum* Benth., *T. leiocalyx* Cogn., *T. littorale* Benth., *T. mauritanum* J.F.Gmel., *T. oreophilum* Gilg, *T. oreothamnus* Mildbr., *T. rubens* A.Fern. & R.Fern., *T. schliebenii* Markgr., *T. vestitum* Jacq.-Fél.

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LITERATURE CITED

- Andrews, F.W.** 1950. *The flowering plants of the Anglo-Egyptian Sudan*, vol. 1. Scotland: Buncle.
- APG** 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161: 105–121. <https://doi.org/10.1111/j.1095-8339.2009.00996.x>
- Baillon, H.** 1877 (“1880”). *Histoire des plantes*, vol. 7, *Mélastomacées, Cornacées, Ombellifères, Rubiacées, Valérianaçées, Dipsacacées*. Paris: Librairie Hachette. <https://doi.org/10.5962/bhl.title.40796>
- Bartling, F.G.** 1830. *Ordines naturales plantarum*. Gottingae [Göttingen]: sumtibus Dieterichianis. <http://bibdigital.rjb.csic.es/ing/Libro.php?Libro=5595>
- Bentham, G.** 1849. Melastomataceae. Pp. 344–358 in: Hooker, W.J. (ed.), *Niger flora*. London: Hippolyte Baillièrre. <https://doi.org/10.5962/bhl.title.594>
- Bentham, G. & Hooker, J.D.** 1867. *Genera plantarum*, vol. 1(3). Londini [London]: venit apud Reeve & Co. <https://doi.org/10.5962/bhl.title.747>
- CABI** 2014 (last modified 5 Mar 2014). *Heterotis rotundifolia* (pink lady). In: Invasive Species Compendium. <http://www.cabi.org/isc/datasheet/120226> (accessed 20 Jun 2016).
- Clausing, G. & Renner, S.S.** 2001. Molecular phylogenetics of Melastomataceae and Memecylaceae: Implications for character evolution. *Amer. J. Bot.* 88: 486–498. <https://doi.org/10.2307/2657114>
- Cogniaux, C.A.** 1891. Melastomataceae. In: Candolle, A. de & Candolle, C. de (eds.), *Monographiae phanerogamarum*, vol. 7. Parisiis [Paris]: sumptibus G. Masson. <https://doi.org/10.5962/bhl.title.45961>
- Darriba, D., Taboada, G.L., Doallo, R. & Posada, D.** 2012. jModel-Test 2: More models, new heuristics and parallel computing. *Nature, Meth.* 9: 772. <https://doi.org/10.1038/nmeth.2109>
- De Wildeman, E.** 1913. Études sur la Flore du Katanga. *Ann. Mus. Congo Belge. Bot.*, sér. 4, 1: 1–207.
- Drummond, A.J. & Rambaut, A.** 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *B. M. C. Evol. Biol.* 7: 214. <https://doi.org/10.1186/1471-2148-7-214>
- Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A.** 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molec. Biol. Evol.* 29: 1969–1973. <https://doi.org/10.1093/molbev/mss075>
- Duvigneaud, P.** 1958. Etudes sur la végétation Katanga et des ses sols metalliferes. Réalisées sous l’égide du Fonds National de la Recherche Scientifique, avec l’aide de l’Union Minière du Haut-Katanga. Communication No I. La végétation du Katanga et de ses sols métallifères. *Bull. Soc. Roy. Bot. Belgique* 90(2): 127–286.
- Engler, A.** 1921. *Die Pflanzenwelt Afrikas insbesondere seiner tropischen Gebiete: Grundzüge der Pflanzenverbreitung in Afrika und die Charakterpflanzen Afrikas*, vol. 3(2), *Charakterpflanzen Afrikas (insbesondere des tropischen): Die Familien der afrikanischen Pflanzenwelt und ihre Bedeutung in derselben*, 2, *Die dikotyledonen Angiospermen Euphorbiaceae, Sapindales–Umbelliflorae (Schluß)*. Die Vegetation der Erde 9. Leipzig: Engelmann. <https://doi.org/10.5962/bhl.title.50144>
- Exell, A.W., Good, R., Norman, C., Greves, S. & Moore, S.** 1929. Mr. John Gossweiler’s Portuguese West African plants (part 1). *J. Bot.* 67 (Suppl. 1): 177–203.
- Farron, C. & Favarger, C.** 1983–84. Contribution à la cytotaxonomie des Melastomatacées africaines. *Garcia de Orta, Sér. Bot.* 6(1–2): 83–88.
- Favarger, C.** 1952. Recherches sur quelques Mélastomacées d’Afrique occidentale. *Ber. Schweiz. Bot. Ges.* 62: 5–65.
- Favarger, C.** 1962. Nouvelles recherches cytologiques sur les Mélastomatacées. *Ber. Schweiz. Bot. Ges.* 72: 290–305.
- Feissly, C.** 1964. Sur l’ornementation du tube calicinal de quelques Osbeckiées africaines. *Bull. Soc. Neuchâtel. Sci. Nat.* 87: 137–170.
- Felsenstein, J.** 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39: 783–791. <https://doi.org/10.2307/2408678>
- Fernandes, A. & Fernandes, R.** 1954a. Sur la position systématique de la section *Pseudodissotis* Cogn. du genre *Osbeckia* L. (Note préliminaire). *Bol. Soc. Brot.*, sér. 2, 28: 65–76.
- Fernandes, A. & Fernandes, R.** 1954b. Contribuição para o conhecimento das Melastomatáceas da Guiné Portuguesa. *Garcia de Orta* 2: 273–285.
- Fernandes, A. & Fernandes, R.** 1954c. Contribution to the knowledge of the Melastomataceae of Moçambique. *Bol. Soc. Brot.*, sér. 2, 28: 205–214, 6 pl.
- Fernandes, A. & Fernandes, R.** 1956a. Revisão das Melastomatoideae do East African Herbarium e do Southern Rhodesia Government Herbarium. *Mem. Soc. Brot.* 11: 65–96.
- Fernandes, A. & Fernandes, R.** 1956b. Melastomataceae africanae novae vel minus cognitae – III. *Bol. Soc. Brot.*, sér. 2, 30: 167–186, 25 pl.
- Fernandes, A. & Fernandes, R.** 1962. O que é *Osbeckia tubulosa* Sm.? Pp. 1–9 in: *Estudos científicos oferecidos em homenagem ao Prof.*

- Doutor J. Carrington da Costa por ocasião do seu 70º aniversário – Abril de 1961. Lisbon: Junta de Investigações do Ultramar.
- Fernandes, A. & Fernandes, R.** 1969. Melastomataceae africanae novae vel minus cognitae – V. *Bol. Soc. Brot.*, sér. 2, 43: 285–306, 17 pl.
- Fernandes, R. & Fernandes, A.** 1970. Melastomataceae. Pp. 114–165 in: Exell, A.W., Fernandes, A. & Mendes, E.J. (eds.), *Conspectus florum Angolensis*, vol. 4. Lisbon: Junta de Investigações do Ultramar e Instituto de Investigação Científica de Angola.
- Fernandes, R. & Fernandes, A.** 1978. Melastomataceae. Pp. 220–276 in: Launert, E. (ed.), *Flora Zambesiaca*, vol. 4. Richmond: Royal Botanic Gardens, Kew.
- Fritsch, P.W., Almeda, F., Renner, S.S., Martins, A.B. & Cruz, B.C.** 2004. Phylogeny and circumscription of the near-endemic Brazilian tribe Microlicieae (Melastomataceae). *Amer. J. Bot.* 91: 1105–1114. <https://doi.org/10.3732/ajb.91.7.1105>
- Gilg, E.** 1898. *Monographieen afrikanischer Pflanzen-Familien und -Gattungen*, vol. 2, *Melastomataceae*. Leipzig: Engelmann. <https://doi.org/10.5962/bhl.title.53505>
- Gilg, E.** 1901. Melastomataceae. Pp. 365–367 in: Engler, A. Berichte über die botanischen Ergebnisse der Nyassa-See und Kinga-Gebirgs-Expedition der Hermann- und Elise- geb. Heckmann-Wentzel-Stiftung. IV. Die von Goetze am Rukwa-See und Nyassa-See sowie in den zwischen beiden Seen gelegenen Gebirgsländern, insbesondere dem Kinga-Gebirge gesammelten Pflanzen, nebst einigen Nachträgen (durch * bezeichnet) zu Bericht III. *Bot. Jahrb. Syst.* 30: 239–445.
- Goldenberg, R., Penneys, D.S., Almeda, F., Judd, W.S. & Michelangeli, F.A.** 2008. Phylogeny of *Miconia* (Melastomataceae): Patterns of stamen diversification in a megadiverse neotropical genus. *Int. J. Pl. Sci.* 169: 963–979. <https://doi.org/10.1086/589697>
- Grimm, D. & Almeda, F.** 2013. Systematics, phylogeny and biogeography of *Chaetolepis* (Melastomataceae). *J. Bot. Res. Inst. Texas* 7: 217–263.
- Guillemin, J.-A., Perrottet, G.S. & Richard, A.** 1833 (“1830–1833”). *Florae Senegambiae tentamen*. Parisiis [Paris]: apud Treuttel et Würtz. <https://doi.org/10.5962/bhl.title.595>
- Hooker, J.D.** 1871. Melastomaceae. Pp. 439–464 in: Oliver, D. (ed.), *Flora of tropical Africa*, vol. 2. London: L. Reeve. <https://doi.org/10.5962/bhl.title.42>
- Hutchinson, J. & Dalziel, J.M.** 1927. *Flora of west tropical Africa*, vol. 1(1). London: The Crown Agents for the Colonies.
- Hutchinson, J. & Dalziel, J.M.** 1928. Tropical African plants: III. *Bull. Misc. Inform. Kew* 1928: 211–229. <https://doi.org/10.2307/4107692>
- Ionta, G.M., Judd, W.S., Williams, N.H. & Whitten, W.M.** 2007. Phylogenetic relationships in *Rhexia* (Melastomataceae): Evidence from DNA sequence data and morphology. *Int. J. Pl. Sci.* 168: 1055–1066. <https://doi.org/10.1086/518837>
- Jacques-Félix, H.** 1932. Sur quelques Melastomacées nouvelles ou peu connues de l’Afrique occidentale. *Bull. Mus. Natl. Hist. Nat.*, sér. 2, 6: 678–687.
- Jacques-Félix, H.** 1939 (“1838”). Sur quelques Melastomacées africaines. *Bull. Mus. Natl. Hist. Nat.*, sér. 2, 10: 630–642.
- Jacques-Félix, H.** 1953. Sur quelques Melastomaceae d’Afrique. *Bull. Inst. Franç. Afrique Noire* 15: 972–1001.
- Jacques-Félix, H.** 1975 (“1974”). Le genre *Melastomastrum* Naudin (Melastomataceae). *Bull. Mus. Natl. Hist. Nat.*, Sér. 3, Bot. 17: 49–84.
- Jacques-Félix, H.** 1976. Le genre *Tristemma* Jussieu (Melastomataceae). *Bull. Mus. Natl. Hist. Nat.*, Sér. 3, Bot. 28: 137–207.
- Jacques-Félix, H.** 1981. Observations sur les caractères staminaux et la classification des Osbeckieae (Melastomataceae) capsulaires africaines. *Adansonia*, sér. 2, 20: 405–429.
- Jacques-Félix, H.** 1983. Mélastomatacées. In: Satabié, B. & Leroy, J.-F. (eds.), *Flore du Cameroun*, vol. 24. Yaounde: Délégation Générale à la Recherche Scientifique et Technique.
- Jacques-Félix, H.** 1986. Description d’un *Tristemma* (Melastomataceae) nouveau du Gabon. *Bull. Mus. Natl. Hist. Nat.*, B, *Adansonia* 8: 191–193.
- Jacques-Félix, H.** 1995. Histoire des Melastomataceae d’Afrique. *Bull. Mus. Natl. Hist. Nat.*, B, *Adansonia* 16: 235–311.
- Judd, W.S., Ionta, G.M., Skean, J.D., Campbell, K., Jr. & Penneys, D.S.** 2011. Noteworthy collections of *Heterotis rotundifolia* in Jamaica and Dominica. *Castanea* 76: 311–312. <https://doi.org/10.2179/11-011.1>
- Keay, R.W.J.** 1954. *Flora of west tropical Africa*, ed. 2, vol. 1(1). London: Crown Agents for Oversea Governments and Administrations.
- Krasser F.** 1893. Melastomataceae. Pp. 130–199 in: Engler, A. & Prantl, K. (eds.), *Die natürlichen Pflanzenfamilien* III(7). Leipzig: Engelmann.
- Kriebel, R.** 2016. Phylogenetic placement of the monotypic genus *Schwackaea* (Melastomeae: Melastomataceae) and the evolution of its unique fruit. *Int. J. Pl. Sci.* 177: 440–448. <https://doi.org/10.1086/685689>
- Kriebel, R., Michelangeli, F.A. & Kelly, L.M.** 2015. Discovery of unusual anatomical and continuous characters in the evolutionary history of *Conostegia* (Miconieae: Melastomataceae). *Molec. Phylog. Evol.* 82: 289–313. <https://doi.org/10.1016/j.ympev.2014.09.021>
- Leistner, O.A.** 2005. *Seed plants of southern tropical Africa: Families and genera*. Pretoria: South African Botanical Diversity Network.
- Maddison, W.P. & Maddison, D.R.** 2015. Mesquite: A modular system for evolutionary analysis, version 3.04 <http://mesquiteproject.org> (accessed 15 Dec 2015).
- Majure, L.C., Neubig, K.M., Skean, J.D., Bécquer, E.R. & Judd, W.S.** 2015. Evolution of the sandpaper clade (Miconieae, Melastomataceae). *Int. J. Pl. Sci.* 176: 607–626. <https://doi.org/10.1086/682148>
- Meyer, K.** 2001. Revision of the Southeast Asian genus *Melastoma* (Melastomataceae). *Blumea* 46: 351–398.
- Michelangeli, F.A., Penneys, D.S., Giza, J., Soltis, D., Hils, M.H. & Skean, J.D.** 2004. A preliminary phylogeny of the tribe Miconieae (Melastomataceae) based on nrITS sequence data and its implications on inflorescence position. *Taxon* 53: 279–290. <https://doi.org/10.2307/4135608>
- Michelangeli, F.A., Judd, W.S., Penneys, D.S., Skean, J.D., Bécquer-Granados, E.R., Goldenberg, R. & Martin, C.V.** 2008. Multiple events of dispersal and radiation of the tribe Miconieae (Melastomataceae) in the Caribbean. *Bot. Rev. (Lancaster)* 74: 53–77. <https://doi.org/10.1007/s12229-008-9004-x>
- Michelangeli, F.A., Guimaraes, P.J.F., Penneys, D.S., Almeda, F. & Kriebel, R.** 2013. Phylogenetic relationships and distribution of New World Melastomeae (Melastomataceae). *Bot. J. Linn. Soc.* 171: 38–60. <https://doi.org/10.1111/j.1095-8339.2012.01295.x>
- Naudin, C.** 1850. Melastomacearum monographicae descriptionis. *Ann. Sci. Nat., Bot.*, sér. 3, 13: 273–303.
- Naudin, C.** 1853 (“1849–1853”). *Melastomacearum monographicae descriptionis*. Parisiis [Paris]: apud Victor Masson. [Consolidated reprint of a series of papers originally published in *Ann. Sci. Nat., Bot.*, sér. 3]. <https://doi.org/10.5962/bhl.title.12248>
- Penneys, D.S. & Judd, W.S.** 2013. Combined molecular and morphological phylogenetic analyses of the Blakeeae (Melastomataceae). *Int. J. Pl. Sci.* 174: 802–817. <https://doi.org/10.1086/670011>
- Perrier de la Bâthie, H.** 1932. Les Mélastomacées de Madagascar. *Mém. Acad. Malgache* 12: 1–292, 10 pl.
- Perrier de la Bâthie, H.** 1951. *Flore de Madagascar et des Comores (plantes vasculaires)*, vol. 153, *Mélastomatacées*. Paris: Firmin-Didot. <https://doi.org/10.5962/bhl.title.6600>
- Rafinesque, C.S.** 1838. *Sylva telluriana*. Philadelphia: printed for the author and publisher. <https://doi.org/10.5962/bhl.title.248>
- Rambaut, A. & Drummond, A.J.** 2009. Tracer, version 1.5. <http://tree.bio.ed.ac.uk/software/tracer/> (accessed 01 Dec 2009).
- Reginato, M. & Michelangeli, F.A.** 2016. Untangling the phylogeny of *Leandra* s.str. (Melastomataceae, Miconieae). *Molec. Phylog. Evol.* 96: 17–32. <https://doi.org/10.1016/j.ympev.2015.11.015>
- Reginato, M., Michelangeli, F.A. & Goldenberg, R.** 2010. Phylogeny

- of *Pleiochiton* (Melastomataceae, Miconieae): Total evidence. *Bot. J. Linn. Soc.* 162: 423–434.
<https://doi.org/10.1111/j.1095-8339.2009.01022.x>
- Rendle, A.B., Baker, E.G., Moore, S. & Gepp, A.** 1911. A contribution to our knowledge of the flora of Gazaland: Being an account of collections made by C. F. M. Swynnerton, Esq., F.L.S. *J. Linn. Soc. London, Bot.* 40: 1–245.
- Renner, S.S.** 1993. Phylogeny and classification of the Melastomataceae and Memecylaceae. *Nordic J. Bot.* 13: 519–540.
<https://doi.org/10.1111/j.1756-1051.1993.tb00096.x>
- Renner, S.S. & Meyer, K.** 2001. Melastomeae come full circle: Biogeographic reconstruction and molecular clock dating. *Evolution* 55: 1315–1324. <https://doi.org/10.1111/j.0014-3820.2001.tb00654.x>
- Renner, S.S., Triebel, D., Almeda, F., Stone, R.D., Ulloa, C., Michaelangeli, F.A., Goldenberg, R. & Mendoza, H. (eds.)** 2007–. MEL names – A database with names of Melastomataceae. <http://www.melastomataceae.net/MELnames/> (accessed Feb 2014).
- Reveal, J.L.** 2011–. Indices Nominum Supragenericorum Plantarum Vascularium. <http://www.plantsystematics.org/reveal/pbio/fam/allspgnames.html>
- Small, R.L., Ryburn, J.A., Cronn, R.C., Seelanan, T. & Wendel, J.F.** 1998. The tortoise and the hare: Choosing between noncoding plastome and nuclear *Adh* sequences for phylogeny reconstruction in a recently diverged plant group. *Amer. J. Bot.* 85: 1301–1315.
<https://doi.org/10.2307/2446640>
- Smith, J.E.** 1813. *Osbeckia*. In: Rees, A., *The Cyclopaedia*, vol. 25. London: printed for Longman, etc.
<https://doi.org/10.5962/bhl.title.59683>
- Stamatakis, A.** 2014. RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Stevens, P.F.** 2001–. Angiosperm Phylogeny Website, version 12, July 2012 [and more-or-less continuously updated since]. <http://www.mobot.org/MOBOT/research/APweb/> (accessed 27 Dec 2015).
- Stone, R.D.** 2014. The species-rich, paleotropical genus *Memecylon* (Melastomataceae): Molecular phylogenetics and revised infrageneric classification of the African species. *Taxon* 63: 539–561.
<https://doi.org/10.12705/633.10>
- Stone, R.D. & Andreasen, K.** 2010. The Afro-Madagascan genus *Warneckea* (Melastomataceae): Molecular systematics and revised infrageneric classification. *Taxon* 59: 83–92.
- Stone, R.D. & Veranso-Libalah, M.C.** 2017. (2527) Proposal to reject the name *Kadalia* (Melastomataceae: Melastomateae). *Taxon* 66: 758–759. <https://doi.org/10.12705/663.26>
- Swofford, D.L.** 2002. PAUP*: Phylogenetic analysis using parsimony (*and other methods), version 4. Sunderland, Massachusetts: Sinauer. <http://paup.csit.fsu.edu/> (accessed 10 Dec 2014).
- Triana, J.J.** 1865. Dispositio Melastomacearum. *Bull. Congr. Int. Bot. Hort. Amsterdam* 1865: 457–461.
- Triana, J.J.** 1872 (“1871”). Les Mélastomacées. *Trans. Linn. Soc. London* 28(1): 1–188.
<https://doi.org/10.1111/j.1096-3642.1871.tb00222.x>
- Van Tieghem, P.** 1891. Classification anatomique des Mélastomacées. *Bull. Soc. Bot. France* 38: 114–124.
<https://doi.org/10.1080/00378941.1891.10828542>
- Van Vliet, G.J.C.M., Koek-Noorman, J. & Ter Welle, B.J.H.** 1981. Wood anatomy, classification and phylogeny of the Melastomataceae. *Blumea* 27: 463–473.
- Whiffin, T. & Tomb, A.S.** 1972. The systematic significance of seed morphology in the neotropical capsular-fruited Melastomataceae. *Amer. J. Bot.* 59: 411–422. <https://doi.org/10.2307/2441552>
- Wickens, G.E.** 1975. Melastomataceae. In: Polhill, R.M. (ed.), *Flora of tropical East Africa*. London: Crown Agents for Oversea Governments and Administrations.

Appendix 1. Voucher information (Species name, Synonym, Country, Region, Collector number, herbarium code, herbarium barcode or sheet number and Lab code if available). GenBank accessions numbers are given for all nrITS, *psbK-psbL*, *accD-psaI* sequences included in this study. Missing sequence data is indicated by a dash (-). DNA sequences newly generated for this study are marked with an asterisk (*).

OUTGROUP: *Aciotis indecora* (Bonpl.) Triana, French Guiana, *C.V. Martin 411* (NY), JQ730039, JQ730250, JQ730459; *Aciotis paludosa* (Mart. ex DC.) Triana, Brazil, *P. Guimarães 317* (RB), JQ730040, JQ730251, JQ730460; *Aciotis rubricaulis* (Mart. ex DC.) Triana, Brazil, *R. Goldenberg 850* (NY), JQ730042, JQ730253, JQ730462; *Acisanthera hedyotidea* (C.Presl.) Triana, Guyana, *K.J. Wurdack 4145* (NY), JQ730044, JQ730255, JQ730464; *Acisanthera quadrata* Pers., Venezuela, *F.A. Michelangeli 826* (BH), JQ730045, JQ730256, JQ730465; *Brachyotum incrassatum* E.Cotton, Ecuador, *J.L. Clark 8896* (NY), JQ730056, JQ730267, JQ730475; *Brachyotum ledifolium* (Desr.) Triana, Ecuador, *D.S. Penneys 1554* (FLAS), JQ730057, JQ730268, JQ730476; *Cambessedesia espora* (A.St.Hil. ex Bonpl.) DC., Brazil, *P. Guimarães 397* (RB), JQ730062, JQ730273, JQ730481; *Cambessedesia hilariana* (A.St.Hil. ex Bonpl.) DC., Brazil, *P. Guimarães 405* (RB), JQ730063, JQ730274, JQ730482; *Chaetolepis cfodontisii* Standl., Costa Rica, *F.A. Michelangeli 1160* (NY), JQ730067, JQ730278, JQ730485; *Chaetolepis microphylla* (Bonpl.) Miq., Brazil, *F.A. Michelangeli 1268* (NY), JQ730068, JQ730279, JQ730486; *Comolia microphylla* Benth., Guyana, *K.M. Redden 454* (NY), JQ730070, JQ730281, JQ730488; *Dinophora spenneroides* Benth., Cameroon, SW, Mundemba, *M.C. Veranso 107* (MJG), 20950, DINOSPEN21, KX889227*, KY284746*, -; *Ernestia glandulosa* Gleason, French Guiana, *C.V. Martin 471* (NY), JQ730080, JQ730293, *Graffenrieda latifolia* (Naudin) Triana, Venezuela, *F.A. Michelangeli 794* (BH), AY460450, JQ730297, JQ730503; *Graffenrieda moritziana* Triana, Venezuela, *F.A. Michelangeli 832* (BH), AY460451, JQ730298, JQ730504; *Heterocentron elegans* (Schltdl.) Kuntze, U.S.A. (collected in cultivation outside native range), cultivated in NYBG (NY), JQ730085, JQ730299, JQ730506; *Lavoisiera imbricata* (Thunb.) DC., Brazil, *R. Goldenberg 820* (NY), JQ730091, JQ730304, JQ730511; *Lavoisiera mucrifera* Mart. ex Schrank ex DC., Brazil, *P. Guimarães 345* (RB), JQ730092, JQ730305, JQ730512; *Leandra cf. kleinii* Brade, *R. Goldenberg 728* (UPCB), EU055693, GQ139258, GQ139342; *Meriania longifolia* (Naudin) Cogn., Venezuela, *F.A. Michelangeli 610* (BH), AY460454, JQ730316, JQ730526; *Miconia dodecandra* (Desr.) Cogn., Dominican Republic, *W.S. Judd 8093* (FLAS), AY460506, JQ730317, JQ730527; *Miconia tomentosa* (Rich.) D.Don ex DC., Brazil, *F.A. Michelangeli 1344* (NY), EF418905, JQ730318, JQ730528; *Microlepis oleifolia* (DC.) Triana, Brazil, *R. Goldenberg 1036* (NY), JQ730107, JQ730319, JQ730529; *Monochaetum discolor* H.Karst. ex Triana, Venezuela, *I. Capote 811* (NY), JQ730109, JQ730321, JQ730531; *Monochaetum meridense* (Klotzsch ex H.Karst.) Naudin, Venezuela, *I. Capote 862* (NY), JQ730111, JQ730323, JQ730533; *Monochaetum volcanicum* Cogn., Costa Rica, *F.A. Michelangeli 718* (BH), JQ730114, JQ730326, JQ730536; *Physeterostemon tomasii* Amorim, Michelangeli & Goldenb. Brazil, *A. Amorim 5054* (NY), JQ730121, JQ730332, JQ730542; *Pilocosta nana* (Standl.) Almeda & Whiffin, Costa Rica, *R.C. Moran 6928* (NY), JQ730123, JQ730334, JQ730544; *Pilocosta nubicola* Almeda, Costa Rica, *D.S. Penneys 1775* (FLAS), JQ730124, JQ730335, JQ730545; *Pterogastra divaricata* (Bonpl.) Naudin, Venezuela, *F.A. Michelangeli 540* (BH), JQ730126, JQ730337, JQ730547; *Pterogastra minor* Naudin, Brazil, *G.A. Romero 1682* (CAS), JQ730127, JQ730338, JQ730548; *Pterolepis glomerata* (Rottb.) Miq., French Guiana, *C.V. Martin 419* (NY), JQ730129, JQ730340, JQ730550; *Pterolepis repanda* (DC.) Triana, Brazil, *F. Almeda 7731* (CAS), JQ730131, JQ730342, JQ730552; *Rhexia aristosa* Britton, U.S.A., *R.F.C. Naczi 12065* (NY), JQ730134, JQ730345, JQ730555; *Rhexia virginica* L., U.S.A., *F.A. Michelangeli 1448* (NY), JQ730136, JQ730346, JQ730557; *Rousseauxia andringitensis* (H.Perrier) Jacq.-Fél., Madagascar, *F. Almeda 9390* (CAS), JQ730139, JQ730350, JQ730561; *Rousseauxia minimifolia* (Jum. & H.Perrier) Jacq.-Fél., Madagascar, *F. Almeda 8704* (CAS), JQ730140, JQ730351, JQ730562; *Svitramia pulchra* Cham., Brazil, *P. Guimarães 388* (RB), JQ730145, JQ730356, JQ730567; *Tibouchina arborea* (Gardn.) Cogn., Brazil, *P. Guimarães 324* (RB), JQ730152, JQ730363, JQ730575; *Tibouchina arenaria* Cogn., Brazil, *P. Guimarães 352* (RB), JQ730153, JQ730364, JQ730576; *Tibouchina candolleana* (DC.) Cogn., Brazil, *J. Lima 711* (NY), JQ730164, JQ730375, JQ730585; *Tibouchina cardinalis* (Bonpl.) Cogn., Brazil, *P. Guimarães 407* (RB), JQ730165, JQ730376, JQ730586;

Appendix 1. Continued.

Tibouchina citrina (Naudin) Cogn., Bolivia, *M. Nee* 55308 (NY), JQ730171, JQ730380, JQ730592; *Tibouchina clavata* (Pers.) Wurdack, Brazil, A.K.A. Santos 696 (UFB), JQ730172, JQ730381, JQ730593; *Tibouchina confertiflora* (Naudin) Cogn., Bolivia, *M. Nee* 55377 (NY), JQ730175, JQ730384, JQ730595; *Tibouchina cristata* Brade, Brazil, J.F.A. Baumgratz 819 (R), JQ730177, JQ730386, JQ730597; *Tibouchina cryptadana* Gleason, Venezuela, F.A. Michelangeli 708 (NY), JQ730178, JQ730387, JQ730598; *Tibouchina dubia* (Cham.) Cogn., Brazil, I.G. Varassin 101 (UFCB), JQ730179, JQ730388, JQ730599; *Tibouchina gracilis* (Bonpl.) Cogn., Brazil, P. Guimarães 336 (RB), JQ730190, JQ730398, JQ730610; *Tibouchina granulosa* (Desr.) Cogn., Brazil, P. Guimarães 378 (RB), JQ730191, JQ730399, JQ730611; *Tibouchina pulchra* (Cham.) Cogn., Brazil, J.F.A. Baumgratz 1068 (R), JQ730222, JQ730430, JQ730642; *Tibouchina radula* Markgr., Brazil, R. Goldenberg 1281 (NY), JQ730223, JQ730431, JQ730643; *Trembleya parviflora* Cogn., Brazil, R. Goldenberg 824 (NY), JQ730242, JQ730451, JQ730663. — **INGROUP: Amphorocalyx multiflorus** Baker, Madagascar, *F. Almeda* 8669 (CAS), JQ730046, JQ730257, JQ730466; *Amphorocalyx rupestris* H.Perrier, Madagascar, *F. Almeda* 8723 (CAS), JQ730047, JQ730258, JQ730467; *Anaheterotis pobeguini* (Hutch. & Dalziel) Veranso-Libalah & G.Kadereit (*Heterotis pobeguini*), Guinea, A.S. Goman 259 (BR), BR0000017294690, HETEPOBE132, KX889284*, KY284809*, KY284710*; *Antherotoma angustifolia* (A.Fern. & R.Fern.) Jacq.-Fél., Zambia, M.G. Bingham 9607 (WAG), WAG.1091744, ANTHANGU140, KX889210*, KY284727*, KY284649*; *Antherotoma debilis* (Sond.) Jacq.-Fél., Angola, Cuando Cubango, D. Goyder 8094 (K), ANTHDEBI185, -, KY284728*, KY284650*; *Antherotoma debilis* (Sond.) Jacq.-Fél., Mozambique, Bilene, J.E. Burrows 14526 (BNRH), ANTHDEBI59, -, KY284729*, KY284651*; *Antherotoma densiflora* (Gilg) Jacq.-Fél., Tanzania, S. Bidgood & al. 2728 (WAG), WAG.1091979, ANTHDENSE143, KX889211*, KY284730*, -, *Antherotoma gracilis* (Cogn.) Jacq.-Fél., Angola, Bamps & al. 4165 (BR), BR0000018229899, ANTHGRAC43, KX889212*, KY284731*, -, *Antherotoma irvingiana* (Hook.f.) Jacq.-Fél., Cameroon, NW, Sabga, M.C. Veranso 226 (MJG), 20985, ANTHIRV133, KX889213*, KY284732*, KY284652*; *Antherotoma irvingiana* (Hook.f.) Jacq.-Fél., Cameroon, NW, Mbiame, M.C. Veranso 199 (MJG), 20954, ANTHIRV19, KX889214*, KY284733*, KY284653*; *Antherotoma naudinii* Hook.f., Zimbabwe, Chimanimanis, B. Wursten 2271 (BR), BR-SIL-SP-8448, ANTHNAUD3, KX889215*, KY284734*, KY284654*; *Antherotoma naudinii* Hook.f., Cameroon, NW, Mbiame, M.C. Veranso 200 (MJG), 20955, ANTHNAUD38, KX889216*, KY284735*, KY284655*; *Antherotoma naudinii* Hook.f., Madagascar, *F. Almeda* 8624 (CAS), JQ730259, -, *Antherotoma phaeotricha* (Hochst.) Jacq.-Fél. var. *phaeotricha*, Tanzania, Kagera, Bukoba, L. Festo 708 (MO), MO-2721884, ANTHPHAE119, KX889217*, KY284736*, KY284656*; *Antherotoma phaeotricha* (Hochst.) Jacq.-Fél. var. *phaeotricha*, Tanzania, Kagera, Bukoba, D. Sitoni & al. 1032 (MO), MO-2721889, ANTHPHAE120, KX889218*, KY284737*, KY284657*; *Antherotoma senegambiensis* (Guill. & Perr.) Jacq.-Fél., Tanzania, Kagera, Bukoba, Festo 1184 (MO), MO-2721879, ANTHSENE113, KX889219*, KY284738*, KY284658*; *Antherotoma senegambiensis* (Guill. & Perr.) Jacq.-Fél., Zimbabwe, B. Wursten 2269 (BR), BR-SIL-SP-8328, ANTHSENE60, KX889220*, KY284739*, -, *Argyrella amplexicaulis* (Jacq.-Fél.) Veranso-Libalah & G.Kadereit (*Heterotis amplexicaulis*), Guinea, Nzérékoré, G. Traore 29 (BR), BR0000016915527, HETEAMPL54, KX889273*, KY284798*, KY284702*; *Argyrella bambutorum* (Gilg & Ledermann ex Engl.) Veranso-Libalah & G.Kadereit (*Heterotis angolensis* var. *bambutorum*), Cameroon, NW, Mbiame, M.C. Veranso 202 (MJG), 20956, HETEANGO39, KX889274*, KY284799*, KY284703*; *Argyrella bambutorum* (Gilg & Ledermann ex Engl.) Veranso-Libalah & G.Kadereit (*Heterotis angolensis* var. *bambutorum*), Cameroon, NW, Bui, M.C. Veranso 188 (MJG), 20984, HETEANGO8, KX889275*, KY284800*, KY284704*; *Argyrella canescens* (E.Mey. ex Graham) Harv. (*Heterotis canescens*), Zimbabwe, Chimanimanis, B. Wursten 2880 (BR), BR-SIL-SP-8409, HETECANE1, KX889279*, KY284804*, KY284706*; *Argyrella canescens* (E.Mey. ex Graham) Harv. (*Heterotis canescens*), Cameroon, Adamawa, Ngaoundere, M.C. Veranso 154 (MJG), 20962, HETECANE36, KX889280*, KY284805*, KY284707*; *Argyrella sp.*, Tanzania, S. Bidgood, D. Sitoni & al. 3935 (C), HETERICH94, KX889285*, KY284810*, KY284711*; *Dichaetanthera africana* (Hook.f.) Jacq.-Fél., Gabon, Wieringa & al. 3817 (BR), DICHAFRI170, KX889221*, KY284740*, -, *Dichaetanthera africana* Jacq.-Fél., Gabon, S. Smith 1885 (US), JQ730074, JQ730285, JQ730492; *Dichaetanthera arborea* Baker, Madagascar, Toamasina, Atsinanana, A. Razanatsima 823 (MO), MO-2303613, DICHARBO172, KX889222*, KY284741*, KY284659*; *Dichaetanthera arborea* Baker, Madagascar, G. Clausen & al. 281 (MJG), DICHARBO176, KX889223*, KY284742*, -, *Dichaetanthera articulata* Endl., Madagascar, Toamasina, D. Ravelonarivo & F. Edmond 4320 (MO), MO-2698044, DICHARTI173, KX889224*, KY284743*, -, *Dichaetanthera erici-rosenii* (R.E.Fr.) A.Fern. & R.Fern., Tanzania, Rukwa, Sumbawanga, H.H. Schmidt & al. 1190 (MO), 4627710, DICHERIC156, KX889225*, KY284744*, -, *Dichaetanthera oblongifolia* Baker, Madagascar, *F. Almeda* 7926a (CAS), JQ730075, JQ730286, JQ730493; *Dichaetanthera strigosa* (Cogn.) Jacq.-Fél., Gabon, Haut-Ogooue, A.F. Bradley & al. 1016 (MO), MO-275871, DICHSTRI174, KX889226*, KY284745*, -, *Dionycha bojeri* Naudin, Madagascar, *F. Almeda* 8626 (CAS), JQ730076, JQ730287, JQ730494; *Dissotidendron caloneurum* (Gilg ex Engl.) Veranso-Libalah & G.Kadereit (*Dissotis caloneura*), Tanzania, S. Bidgood & al. 4484 (C), DISSCALO86, KX889230*, KY284749*, KY284662*; *Dissotidendron caloneurum* (Gilg ex Engl.) Veranso-Libalah & G.Kadereit var. *caloneurum* (*Dissotis caloneura* var. *caloneura*), Burundi, S. Ntore 119 (BR), BR0000017295017, DISSCALO87, KX889232*, KY284751*, -, *Dissotidendron caloneurum* var. *pilosum* (A.Fern. & R.Fern.) Veranso-Libalah & G.Kadereit (*Dissotis caloneura* var. *pilosa*), N. Rhodesia (Zimbabwe), Luanshya, D.B. Fanshawe 3123 (BR), BR0000013426354, DISSCALO93, KX889231*, KY284750*, KY284663*; *Dissotidendron cordatum* (P.A. Duvign) Veranso-Libalah & G.Kadereit (*Dissotis derriksiana*), D.R. Congo, F. Malaisse, E. Semereab & G. Handjila 533 (BR), BR0000017293129, DISSDERR163, KX889239*, KY284759*, -, *Dissotidendron cordatum* (P.A. Duvign) Veranso-Libalah & G.Kadereit (*Dissotis derriksiana*), D.R. Congo, Fungurume, I. Parmentier, Kisimba & Sahato 4433 (BR), BR000000972923, DISSDERR81, KX889240*, KY284760*, -, *Dissotidendron melleri* (Hook.f.) Veranso-Libalah & G.Kadereit (*Dissotis melleri*), Tanzania, Iringa, Njombe, O.A. Kibure 745 (MO), MO-2721895, DISSMELL106, KX889248*, KY284769*, -, *Dissotidendron polyanthum* Gilg (*Dissotis polyantha*), Tanzania, L. Festo, M.A. Mwangoka & R. Mbalo 1901 (C), DISSPOLY89, KX889254*, KY284775*, -, *Dissotis chevalieri* Gilg, Cameroon, Adamawa, Lac Tison, M.C. Veranso 130 (MJG), 20982, DISSPERK28, KX889252*, KY284773*, KY284679*; *Dissotis congolensis* (Cogn. ex Büttner) Jacq.-Fél., Cameroon, Adamawa, Tibati, M.C. Veranso 151 (MJG), 20973, DISSCONG18, -, KY284753*, KY284664*; *Dissotis congolensis* (Cogn. ex Büttner) Jacq.-Fél., Gabon, Haut-Ogooue, G.M. Walters 1004 (MO), MO-228453, DISSCONG41, KX889234*, KY284754*, KY284665*; *Dissotis congolensis* (Cogn. ex Büttner) Jacq.-Fél., Gabon, L.J.T. White 693 (MO), MO-2721893, DISSCONG58, KX889235*, KY284755*, KY284666*; *Dissotis crenulata* Cogn., Angola, B. Goyder, Baker & Clark 7476 (GRA), DISSCREN165, KX889236*, KY284756*, KY284667*; *Dissotis cryptantha* Baker, Tanzania, Rukwa, Mpanda, W.R.Q. Luke & al. 16225 (MO), MO-2721885, DISSCRYP98, KX889237*, KY284757*, KY284668*; *Dissotis denticulata* A.Fern. & R.Fern., Zambia, D.K. Harder & al. 2249 (WAG), WAG.1091980, DISSDENT122, KX889238*, KY284758*, -, *Dissotis facipila* Gilg, Zambia, Lisombo, J. Loveridge 859 (BR), BR0000013426262, DISSFALC127, KX889241*, KY284761*, KY284669*; *Dissotis gilgiana* De Wild., D.R. Congo, R. Desenfans 5537 (BRLU), DISSCFGILG161, KX889233*, KY284752*, -, *Dissotis gilgiana* De Wild., D.R. Congo, M. Schajjes 2005 (BR), BR0000017295055, DISSGILG52, KX889242*, KY284762*, -, *Dissotis grandiflora* Benth., Guinea, Phillipson 6387 (MO), MO-2721314 & MO-2721315, DISSGRAN105, KX889243*, KY284763*, KY284670*; *Dissotis longisetosa* Gilg & Ledermann ex Engl., Cameroon, NW, Mbiame, M.C. Veranso 203 (MJG), 20977, DISSLONG11, KX889245*, KY284766*, KY284673*; *Dissotis longisetosa* Gilg & Ledermann ex Engl., Cameroon, NW, Mbiame, M.C. Veranso 205 (MJG), 20958, DISSLONG23, KX889246*, KY284767*, KY284674*; *Dissotis longisetosa* Gilg & Ledermann ex Engl., Cameroon, NW, Bui, M.C. Veranso 178 (MJG), 20969, DISSLONG25, KX889247*, KY284768*, KY284675*; *Dissotis perkinsiae*, Cameroon, NW, Bui, M.C. Veranso 179 (MJG), 20968, DISSPERK7, KX889253*, KY284774*, KY284680*; *Dissotis perkinsiae* Gilg, Cameroon, NW, Mbiame, M.C. Veranso 196 (MJG), 20952, DISSSCHW160, KX889261*, KY284783*, KY284688*; *Dissotis princeps* (Bonpl.) Triana, Cameroon, Adamawa, Ngaoundere, M.C. Veranso 156 (MJG), 20961, DISSPRIN20, KX889255*, KY284776*, KY284681*; *Dissotis princeps* (Bonpl.) Triana, Cameroon, NW, Santa, M.C. Veranso 231 (MJG), 20992, DISSPRIN27, KX889256*, KY284777*, KY284682*; *Dissotis princeps* (Bonpl.) Triana, Cameroon, NW, Bui, M.C. Veranso 181 (MJG), 20953, DISSPRIN42, KX889257*, KY284778*, KY284683*; *Dissotis princeps* (Bonpl.) Triana, Zimbabwe, Chimanimanis, B. Wursten 2256 (BR), BR-SIL-SP-8385, DISSPRIN6, KX889258*, KY284779*, KY284684*; *Dissotis princeps* (Bonpl.) Triana, Mozambique, O. Maurin 3393 (UJ), UJ09328, DISSPRIN61, KX889259*, KY284780*, KY284685*; *Dissotis pulchra* A.Fern. & R.Fern., Zimbabwe, Chimanimanis, B. Wursten 2277 (BR), BR-SIL-SP-8445, DISSPULC2, -, KY284781*, KY284686*; *Dissotis romiana* De Wild., D.R. Congo,

Appendix 1. Continued.

Oso de Nzilo, *M. Schaijies* 2348 (BR), BR0000013426477, DISSROMI45, KX889260*, KY284782*, KY284687*; *Dissotis sizenandii* Cogn., D.R. Congo, *S. Ntore* 232 (BR), BR0000016153400, DISSSIZE137, KX889262*, KY284784*, KY284689*; *Dissotis thollonii* Cogn. ex Büttner var. *elliottii*, Cameroon, NW, Mbiame, *M.C. Veranso* 208 (MJG), 20967, DISSTHOL12, KX889263*, KY284785*, KY284690*; *Dissotis thollonii* Cogn. ex Büttner var. *elliottii*, Cameroon, Adamawa, Tibati, *M.C. Veranso* 144 (MJG), 20959, DISSTHOL24, KX889264*, KY284786*, KY284691*; *Dissotis thollonii* Cogn. ex Büttner var. *elliottii*, Cameroon, Adamawa, Tibati, *M.C. Veranso* 145 (MJG), 20960, DISSTHOL26, KX889265*, KY284787*, KY284692*; *Dissotis thollonii* Cogn. ex Büttner var. *thollonii*, Congo, *L. Devred* 509 (BR), BR0000016908123, DISSTHOLT44, KX889266*, KY284788*, KY284693*; *Dissotis trothae* Gilg, Tanzania, Rukwa, Nkasi, *General collector - SHCP* 322 (MO), MO-2454118, DISSTROT102, KX889267*, KY284789*, –; *Dissotis trothae* Gilg, Tanzania, Iringa, Makete, *J. Lovett* 4716 (MO), MO-2721846, DISSTROT117, KX889268*, KY284790*, KY284694*; *Dissotis trothae* Gilg, Tanzania, Rukwa, Mpanda, *Luke* 16260 (MO), MO-2721886, DISSTROT118, KX889269*, KY284791*, KY284695*; *Dissotis trothae* Gilg, Burundi, *S. Ntore* 142 (BR), BR0000016993273, DISSTROT90, –, KY284793*, KY284697*; *Dissotis tubulosa* (Sm.) Triana, Cameroon, NW, Donga-Mantung, Akweto, *M.C. Veranso* 221 (MJG), 20957, DISSTUBU22, KX889270*, KY284794*, KY284698*; *Dissotis tubulosa* (Sm.) Triana, Cameroon, NW, Bambili, *M.C. Veranso* 217 (MJG), 20979, DISSTUBU31, KX889271*, KY284795*, KY284699*; *Dissotis weltwitschii* Cogn., Angola, Moxico Province, *D. Goyder* 8240 (K), DISSWELT184, –, KY284796*, KY284700*; *Dissotis trothae* Gilg, Burundi, *S. Ntore* 224 (BR), BR0000016993280, DISSTROT84, –, KY284792*, KY284696*; *Dupineta brazzae* (Cogn.) Veranso-Libalah & G.Kadereit (*Dissotis brazzae*), Cameroon, NW, Santa, *M.C. Veranso* 234 (MJG), 20975, DISSBRAZ19, KX889228*, KY284747*, KY284660*; *Dupineta brazzae* (Cogn.) Veranso-Libalah & G.Kadereit (*Dissotis brazzae*), Cameroon, NW, Donga-Mantung, Akweto, *M.C. Veranso* 215 (MJG), 20981, DISSBRAZ29, KX889229*, KY284748*, KY284661*; *Dupineta hensii* (Cogn.) Veranso-Libalah & G.Kadereit (*Dissotis hensii*), D.R. Congo, Itindi, *E. Boyekoli* 110 (BR), BR-SIL-SP-3226, DISSHENS57, KX889244*, KY284764*, KY284671*; *Dupineta hensii* (Cogn.) Veranso-Libalah & G.Kadereit (*Dissotis hensii*), D.R. Congo, Bomane, Aruwimi river, *E. Boyekoli* 595 (BR), BR-SIL-SP-3871, DISSHENS62, –, KY284765*, KY284672*; *Dupineta multiflora* (Sm.) Veranso-Libalah & G.Kadereit (*Dissotis multiflora*), Gabon, Ogooué-Ivindo, *L. White* 481 (MO), 6454998, DISSMULT108, KX889249*, KY284770*, KY284676*; *Dupineta multiflora* (Sm.) Veranso-Libalah & G.Kadereit (*Dissotis multiflora*), Cameroon, Littoral, *M.C. Veranso* 174 (MJG), 20951, DISSMULT30, KX889250*, KY284771*, KY284677*; *Dupineta multiflora* (Sm.) Veranso-Libalah & G.Kadereit (*Dissotis multiflora*), Cameroon, SW, Mundemba, *M.C. Veranso* 104 (MJG), 20964, DISSMULT32, KX889251*, KY284772*, KY284678*; *Dupineta multiflora* (Sm.) Raf. (*Dissotis multiflora*), Gabon, *S. Smith* 1886 (US), JQ730077, JQ730288, JQ730495; *Guyonia antennaria* (Benth.) Veranso-Libalah & R.D.Stone (*Heterotis antennaria*), Guinea, *Nimba Botanic Team* JR1031 (WAG), WAG.1092926, HETEANTE148, KX889276*, KY284801*, KY284705*; *Guyonia arenaria* (Jacq.-Fél.) Veranso-Libalah & R.D.Stone (*Heterotis arenaria*), Gabon, Ogooué-Maritime, *J.C.M. Mbembo & al.* 171 (BR), BR000000946821, HETEAREN46, KX889277*, KY284802*, –; *Guyonia ciliata* Hook.f., Liberia, *C.C.H. Jongkind* 11859 (BR), BR0000016915534, GUYOCIL131, KX889272*, KY284797*, KY284701*; *Guyonia ciliata* Hook.f., Cameroon, *P. Mambo* 248 (NY), JQ730084, –, JQ730505; *Guyonia jacquesii* (A.Chev.) Veranso-Libalah & R.D.Stone (*Heterotis jacquesii*), Guinea, *C.C.H. Jongkind* 7437 (WAG), WAG0237101, HETEJACQ144, KX889283*, KY284808*, –; *Guyonia seretii* (De Wild.) Veranso-Libalah & R.D.Stone (*Heterotis seretii*), D.R. Congo, *M. Schaijies* 2080 (BR), BR0000016904798, HETESERE48, KX889289*, KY284814*, –; *Heterotis buettneriana* (Cogn. ex Büttner) Jacq.-Fél., Gabon, Estuaire, *E.L.A.N. Simons & R. Westerduijn* 291 (MO), MO-2454117, HETEBUET121, KX889278*, KY284803*, –; *Heterotis cogniauxiana* (A.Fern. & R.Fern.) Veranso-Libalah & G.Kadereit, Angola, *B. Goyder, Baker & Clark* 7373 (GRA), HETECOGN164, KX889281*, KY284806*, KY284708*; *Heterotis decumbens* (P.Beauv.) Jacq.-Fél., Gabon, *S. Smith* 1705 (US), JQ730088, JQ730302, JQ730509; *Heterotis decumbens* (P.Beauv.) Jacq.-Fél., Cameroon, South, Kribi, *M.C. Veranso* 170 (MJG), 20978, HETEDECUC37, KX889282*, KY284807*, KY284709*; *Heterotis prostrata* (Thonn.) Benth., Cameroon, Littoral, Edea, *PK37, M.C. Veranso* 177 (MJG), 20963, HETEROTU34, KX889286*, KY284811*, KY284712*; *Heterotis prostrata* (Thonn.) Benth., Cameroon, SW, Mundemba, *M.C. Veranso* 119 (MJG), 20991, HETEROTU35, KX889287*, KY284812*, KY284713*; *Heterotis prostrata* (Thonn.) Benth., cult. Botanic Garden Meise (BR), 19851681, HETEROTU5, KX889288*, KY284813*, KY284714*; *Heterotis rotundifolia* (Sm.) Jacq.-Fél., Dominica, *D.S. Penneys* 1304 (FLAS), JQ730089, JQ730290, –; *Melastoma candidum* D.Don, Taiwan, *C.H. Chen* 6443 (TAIE), JQ730103, JQ730312, JQ730522; *Melastoma denticulatum* Labill., New Caledonia, *M.P. Simmons* 1842 (BH), JQ730104, JQ730313, JQ730523; *Melastoma malabathrichum* L., China, *D.S. Penneys* 1998 (CAS), JQ730105, JQ730314, JQ730524; *Melastoma sanguineum* Sims, China, *D.S. Penneys* 2000 (CAS), JQ730106, JQ730315, JQ730525; *Melastomastrum afzeli* (Hook.f.) A.Fern. & R.Fern., Guinea, *C.C.H. Jongkind* 10424 (BR), BR0000013189273, MELAAFZE155, KX889290*, KY284815*, KY284715*; *Melastomastrum capitatum* (Vahl) A.Fern. & R.Fern., Tanzania, Kigoma, *C.J. Kayombo & Frank M. Mbago* 1158 (MO), MO-04127, MELACAPI162, KX889291*, KY284816*, KY284716*; *Melastomastrum porteresii* (Jacq.-Fél.) Veranso-Libalah & G.Kadereit (*Osbeckia porteresii*), Guinea, *G. Traore* 48 (BR), BR0000016974258, OSBEPOR129, KX889299*, KY284825*, KY284721*; *Melastomastrum porteresii* (Jacq.-Fél.) Veranso-Libalah & G.Kadereit (*Osbeckia porteresii*), Guinea, Nimba Mt., *C.C.H. Jongkind* 7439 (MO), 6177076, OSBEPOR117, KX889300*, KY284826*, –; *Melastomastrum segregatum* (Benth.) A.Fern. & R.Fern., Gabon, *F.J. Breteler* 13067 (BR), BR0000007000271, MELASEGR135, KX889294*, KY284819*, KY284717*; *Melastomastrum theifolium* (G.Don) A.Fern. & R.Fern., Cameroon, NW, Mbiame, *M.C. Veranso* 197 (MJG), 20988, MELATHEI10, –, KY284820*, KY284718*; *Melastomastrum theifolium* (G.Don) A.Fern. & R.Fern., Cameroon, NW, *G.F. De Wilde* 7304 (BR), BR0000016884199, MELATHEI83, KX889295*, KY284821*, KY284719*; *Melastomastrum theifolium* (G.Don) A.Fern. & R.Fern., Cameroon, *M.C. Veranso* 204 (MJG), 20987, MELATHEI95, KX889296*, KY284822*, KY284720*; *Osbeckia australiana* Naudin, Australia, *K.G. Brennan* 7008 (NY), JQ730116, JQ730328, JQ730538; *Osbeckia decandra* DC., Guinea, *Bidault & al.* 153 (BR), BR0000016974180, OSBEDECA124, KX889297*, KY284823*, –; *Osbeckia decandra* DC., Liberia, *J.G. Adam* 28699 (BR), BR0000016974197, OSBEDECA125, KX889298*, KY284824*, –; *Osbeckia nepalensis* Hook., China, *D.S. Penneys* 1986 (CAS), JQ730118, JQ730329, JQ730539; *Osbeckia stellata* Buch.-Ham. ex Ker Gawl., China, *D.S. Penneys* 1969 (CAS), JQ730119, JQ730330, JQ730540; *Osbeckia togoensis* Leuenb., Benin, *Akoeginou & al.* 4268 (BR), BR0000016974401, OSBETOGO130, KX889301*, KY284827*, –; *Pseudosbeckia swynnertonii* (Baker f.) A.Fern. & R.Fern., Mozambique, Chimanimani, *B. Wursten* 2235 (BR), BR-SIL-SP-8403, PSEUSWYN4, KX889302*, KY284828*, KY284722*; *Tristemma akeasii* Jacq.-Fél., Guinea, *C.C.H. Jongkind* 10696 (BR), BR000001697668, TRISAKEA147, KX889303*, KY284829*, –; *Tristemma albiflorum* (G.Don) Benth., Guinea, *C.C.H. Jongkind* 10355 (BR), BR0000016975804, TRISALBI158, KX889304*, –; KY284723*; *Tristemma cornifolium* (Benth.) Triana (*Melastomastrum cornifolium*), Liberia, *J.G. Adam* 27383 (WAG), WAG0049684, MELACORN152, KX889292*, KY284817*, –; *Tristemma cornifolium* (Benth.) Triana (*Melastomastrum cornifolium*), Liberia, *J.G. Adam* 27383 (WAG), WAG0049685, MELACORN166, KX889293*, KY284818*, –; *Tristemma coronatum* Benth., Ghana, *H.H. Schmidt* 3386 (CAS), JQ730243, JQ730452, JQ730664; *Tristemma demusei* De Wild., Congo (Brazzaville), Sangha, *D.W. Thomas & al.* 8838 (MO), TRISDEMEW159, KX889306*, KY284831*, KY284724*; *Tristemma hirtum* P. Beauv., Gabon, *S. Smith* 1879 (US), JQ730244, JQ730453, JQ730665; *Tristemma involucreatum* Benth., Liberia, *C.C.H. Jongkind* 12379 (BR), BR0000016976337, TRISINVO154, KX889307*, KY284832*, KY284725*; *Tristemma littorale* Benth., Gabon, *S. Smith* 1725 (US), JQ730245, JQ730454, JQ730666; *Tristemma mauritanum* J.F.Gmel., Madagascar, *F. Almeda* 8021 (CAS), JQ730246, JQ730455, JQ730667; *Tristemma oreophilum* Gilg, Gabon, *F.J. Breteler* 14156 (BR), BR0000017420655, TRISOREO153, KX889308*, KY284833*, KY284726*; *Tristemma sp.*, Gabon, *F.J. Breteler & al.* 15253 (BR), BR0000016975965, TRISDEMEP146, KX889305*, KY284830*, –; *Tristemma vestitum* Jacq.-Fél., Gabon, *Champulvier* 6169 (BR), TRISVEST157, KX889309*, KY284834*, –.