Systematics and biogeography of the Dissochaeta alliance (Melastomataceae)

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CHAPTER 6

Molecular phylogenetics of the *Dissochaeta* alliance (Melastomataceae): Redefining tribe Dissochaeteae

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Molecular phylogenetics of the *Dissochaeta* alliance (Melastomataceae): Redefining tribe Dissochaeteae

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Abstract

The *Dissochaeta* alliance (= subtribe Dissochaetinae) is a group of woody climbing taxa within tribe Dissochaeteae (Melastomataceae) and comprises 90 species mainly distributed in Southeast Asia. The circumscription of the alliance and its genera has been problematic when based on only morphological characters. With a broad sampling of relevant taxa, this study aims at a natural circumscription of and revised generic delimitation within this alliance. A molecular phylogeny based on two nuclear (nrETS, nrITS) and four chloroplast (*ndhF*, *psbK-psbL*, *rbcL*, *rpl16*) markers confirmed the non-monophyly of Dissochaeteae s.l. Taxa traditionally placed in Dissochaeteae are found in three lineages in distant positions within Melastomataceae. The *Medinilla* alliance is resolved within Sonerileae + Oxysporeae, while the monophyletic *Dinophora*/*Ochthocharis* lineage forms a polytomy with Marcetieae, Melastomateae, Microlicieae, and Rhexieae; and the well-supported *Dissochaeta* alliance is sister to the Cambessedesieae. Based on the molecular results, Dissochaeteae is redefined to exclude the *Medinilla* alliance and *Dinophora*/*Ochthocharis*. It consists of six successively branching major clades, which we treat as six genera, *Pseudodissochaeta*, *Creochiton*, *Dalenia* (*Dissochaeta* sect. *Dalenia*), *Diplectria* (*Dissochaeta* sect. *Diplectria*), *Macrolenes* and *Dissochaeta* s.str. To avoid a paraphyletic *Dissochaeta*, *Dalenia* and *Diplectria* are resurrected, *Macrolenes* is expanded to include the *Dissochaeta rostrata* complex, and a narrowly circumscribed *Dissochaeta* s.str. is adopted. A re-investigation of morphological characters based on herbarium material provides support of newly defined taxa. Two sections for *Macrolenes* are newly proposed and two sections of *Dissochaeta* s.str. are maintained. Important morphological traits, such as habit and floral characters are discussed to show the morphological support for each delimited genus and the establishment of a new classification of the tribe.

Keywords

Classification; *Dissochaeta* alliance; Dissochaeteae; Melastomataceae; molecular phylogenetics; Southeast Asia; taxonomy.

Introduction

The species-rich pantropically distributed angiosperm family Melastomataceae Juss. s.l. (incl. Memecylaceae DC., cf. APG III, 2009) is particularly diverse in growth forms. Among the over 5700 species in ca. 177 genera (Renner 1993; Christenhusz & Byng 2016; Michelangeli et al. 2020) are trees, shrubs, subshrubs, geophytes, true epiphytes, perennial and annual herbs, and various forms of woody climbers, such as root climbers and scrambling shrubs. While the former climbing growth forms evolved in various melastome genera, the last is rare and seems to be restricted to the paleotropical subtribe Dissochaetinae (Clausing & Renner 2001a). The majority of melastome species is easily assigned to the family by their acrodromal leaf venation, well-developed hypanthia, bisexual, diplostemonous flowers and poricidal anthers (Clausing & Renner 2001b; Rocha et al. 2016). Although the family ranges among the most diverse tropical angiosperm families and is ubiquitous in lowland to montane tropical forests, it also occurs in savannas as well as in disturbed secondary vegetation of tropical regions (Renner 1993; Clausing & Renner 2001b), Melastomataceae are still understudied especially in the Palaeotropics where ca. one-third of the species are found (Renner 1993; Veranso-Libalah et al. 2018).

Throughout the taxonomic history of Melastomataceae, androecium morphology provided useful characters especially for the delimitation of genera and species (e.g., Triana 1872; Renner 1993; Clausing & Renner 2001b; Goldenberg et al. 2003; Michelangeli et al. 2011; Veranso-Libalah et al. 2020). Naturally, the morphological variability of the androecium in melastomes, especially the elaborate anther appendages and staminodes, is closely linked to the diversity of pollinators. Melastome flowers are predominantly bee pollinated with pollen collected by buzz pollination being the most prevalent pollination syndrome (Renner 1989; Kriebel & Zumbado 2014). The subtribe Dissochaetinae is particularly diverse in androecial morphology ranging from minute flowers with isomorphic unappendaged stamens to large flowers with colorful dimorphic stamen whorls (Fig. 6-1).

Dissochaeteae. — The tribe Dissochaeteae was first proposed by Triana (1866) to accommodate palaeotropical genera previously included in the subtribe Dissochaetinae Naudin of tribe Miconieae DC. (Naudin 1851; Miquel 1855). Traditionally, Dissochaeteae were morphologically defined by stamens with well-developed appendages, an epigynous ovary that develops into a berry, axillary placentation, and cochleate seeds (Triana 1866, 1872; Cogniaux 1891; Krasser 1893; Maxwell 1984; Jacques-Félix 1995). They may be terrestrial or epiphytic, whereby growth forms include erect shrubs, and woody climbers or scrambling shrubs (Triana 1872; Cogniaux 1891; Maxwell 1984; Clausing & Renner 2001a). Dissochaeteae as currently circumscribed (Clausing 1999) are distributed from tropical Africa through Madagascar to tropical Asia and the Western Pacific Islands with the Malesian region as its center of diversity (Triana 1872; Cogniaux 1891; Krasser 1893; Maxwell 1984; Jacques-Félix 1995). The name Dissochaeteae was changed to Medinilleae Hook.f. by Hooker (Bentham & Hooker 1867; Baillon 1877), because the genus name *Medinilla* Gaudich. ex DC. has priority over *Dissochaeta* Blume; however, at the tribal level Dissochaeteae is older and therefore the accepted name. Dissochaeteae was again included inside Miconieae (Renner 1993) because both tribes have berries as fruits but were separated into two groups based on geographical distribution, the Neotropical and Palaeotropical Miconieae.

In the original circumscription of Dissochaeteae, 12 genera were treated in this tribe by Triana (1872), 2 from Africa (*Dicellandra* Hook.f. and *Sakersia* Hook.f.), 9 from Tropical Asia (*Anplectrum* A.Gray [=*Diplectria* (Blume) Rchb.], *Carionia* Naudin, *Creochiton* Blume, *Dalenia* Korth., *Dissochaeta*, *Marumia* Blume [=*Macrolenes* Naudin], *Omphalopus* Naudin, *Pachycentria* Blume, *Pogonanthera* Blume) and 1 widespread palaeotropical genus (*Medinilla*; Table 1). The generic circumscription within Dissochaeteae have changed over the years, with several genera resurrected, synonymized as well as new additions; *Backeria* Bakh.f., *Boerlagea* Cogn., *Catanthera* F.Muell., *Heteroblemma* Camara-Léret et al., *Hypenanthe* Blume, *Medinillopsis* Cogn., *Myrianthemum* Gilg, *Neodissochaeta* Bakh.f., *Orthogoneuron* Gilg, *Phaeoneuron* Gilg, *Preussiella* Gilg, *Pseudodissochaeta* M.P.Nayar and *Tetraphyllaster* Gilg (Cogniaux 1891; Gilg 1898; Bakhuizen van den Brink 1943; Nayar 1969a, 1982; Camara-Léret et al. 2013). The circumscription of the tribe changed several times, sometimes by moving some genera (*Dicellandra*, *Sakersia*) into another tribe, or by adding some other genera such as *Dinophora* Benth., *Kendrickia* Hook.f., *Ochthocharis* Blume and *Plethiandra* Hook.f. (Renner 1993; Jacques-Félix 1995; Clausing & Renner 2001a). Table 6-1 provides an overview and summary of generic classification schemes within Dissochaeteae.

An infratribal classification of Dissochaeteae was first proposed by Maxwell (1980b), who recognized two subtribes, Dissochaetinae and Diplectrinae J.F.Maxwell, based on floral morphology. A new subtribe, Medinillinae J.F.Maxwell was later added on the basis of flower merosity and wood anatomical characters (Van Vliet et al. 1981; Maxwell 1984). Subtribe Dissochaetinae included *Creochiton*, *Dissochaeta*, *Macrolenes*, and *Pseudodissochaeta*; while subtribe Diplectrinae included only *Diplectria*, and subtribe Medinillinae included *Boerlagea*, *Carionia*, *Catanthera*, *Dicellandra*, *Dichaetanthera*, *Medinilla*, *Pachycentria*, *Plethiandra*, and *Pogonanthera* (Maxwell 1984). Jacques-Félix (1995) treated *Dinophora* and *Ochthocharis* in Dissochaeteae due to their indehiscent, berry-like fruits (Table 6-1).

The placement of most genera of Dissochaeteae in their respective subtribes has generally been unequivocal, but the circumscription of some genera is problematic. For example, *Catanthera* is morphologically, especially the floral characters, similar to Medinilla and placed in Medinillinae, but wood anatomy suggests that the genus is part of Dissochaetinae because of the presence of a scandent/lianous habit that seems to resemble *Dissochaeta* (Van Vliet 1981; Van Vliet et al., 1981). Diplectrinae was considered monogeneric and only included *Diplectria* species because of the reduction of the alternipetalous stamens to staminodia, even though all the other characters are similar (or identical) to those of *Dissochaeta*, therefore, *Diplectria* can be classified again in Dissochaetinae (Van Vliet et al. 1981; Clausing & Renner 2001a; Kartonegoro et al. 2018). Most species of *Pseudodissochaeta* are true shrubs, but they have been classified close to the lianas/scramblers inside Dissochaetinae (Nayar 1969a; Maxwell 1984; Clausing & Renner 2001a; Renner et al. 2001b). Morphologically, *Pseudodissochaeta* closely resembles *Medinilla*, and the classification becomes a problem when *Pseudodissochaeta* is considered to be a synonym of *Medinilla*, which is part of the Medinillinae (Chen 1983, 1984; Chen & Renner 2007).

Fig. 6-1. Flowers of representative genera of *Dissochaeta* alliance. **A.** *Pseudodissochaeta septentrionalis*; **B.** *Pseudodissochaeta spirei*; **C.** *Creochiton roseus*; **D.** *Dalenia magnibracteata*; **E.** *Dalenia pulchra*; **F.** *Dalenia glabra*; **G.** *Diplectria conica*; **H.** *Diplectria viminalis*; **I.** *Macrolenes hirsutoidea* (sect. *Terminaliflores*); **J.** *Macrolenes macrosepala* (sect. *Terminaliflores*); **K.** *Macrolenes echinulata* (sect. *Macrolenes*); **L.** *Macrolenes nemorosa* (sect. *Macrolenes*); **M.** *Macrolenes subulata* (sect. *Macrolenes*); **N.** *Dissochaeta bracteata* (sect. *Diplostemones*); **O.** *Dissochaeta pallida* (sect. *Diplostemones*); **P.** *Dissochaeta vacillans* (sect. *Dissochaeta*); **Q.** *Dissochaeta biligulata* (sect. *Dissochaeta*); **R.** *Dissochaeta fallax* (sect. *Dissochaeta*); **S.** *Dissochaeta inappendiculata* (sect. *Dissochaeta*); **T.** *Dissochaeta bakhuizenii* (sect. *Dissochaeta*). — Photos by Y. Liu (A, D, P), L.J. Yezi (B), A. Kartonegoro (C, G, H, L–N, R–T), J. Henrot (E), D.S. Penneys (F, J, Q), Supriyatna (I), C. Ng (K), W.F. Ang (O).

Table 6-1. Classification history of the genera in tribe Dissochaeteae s.l.

Bentham & Hooker 1867	**Triana 1872**	**Cogniaux 1891**	**Gilg 1898**	**Bakhuizen van den Brink 1943**	**Maxwell 1984**	**Jacques-Félix 1995**	**Current Treatment**[1]
Medinilleae	**Dissochaeteae**	**Dissochaeteae**	**Dissochaeteae**	**Dissochaeteae**	**Dissochaeteae**	**Dissochaeteae**	**Dissochaeteae**
Anplectrum	***Anplectrum***	***Anplectrum***		Treated in ***Diplectria***	Treated in ***Diplectria***		Treated in ***Dissochaeta***[10] (*Dissochaeta* alliance)
				Backeria	Treated in ***Diplectria***		Treated in ***Dissochaeta***[10] (*Dissochaeta* alliance)
		Boerlagea		***Boerlagea***	***Boerlagea***		***Boerlagea***[4] (*Medinilla* alliance)
Carionia	***Carionia***	***Carionia***		Treated in ***Medinilla***	***Carionia***		Treated in ***Medinilla***[3,4] (*Medinilla* alliance)
				Treated in ***Medinilla***	***Catanthera***		***Catanthera***[4] (*Medinilla* alliance)
Creochiton	***Creochiton***	***Creochiton***		***Creochiton*** (Astronieae)	***Creochiton***		***Creochiton***[9] (*Dissochaeta* alliance)
Dalenia	***Dalenia***	***Dalenia***		***Dalenia***	Treated in ***Dissochaeta***		Treated in ***Dissochaeta***[10] (*Dissochaeta* alliance)
Dicellandra	***Dicellandra***	***Dicellandra***	***Dicellandra***		***Dicellandra***	***Dicellandra*** (Sonerileae)	***Dicellandra***[5] (Sonerileae)
Dinophora (Osbeckieae)	***Dinophora*** **(**Osbeckieae**)**	***Dinophora*** **(**Osbeckieae**)**	***Dinophora*** **(**Osbeckieae**)**			***Dinophora***	***Dinophora***[5] (*Dinophora* alliance)
Treated in ***Anplectrum***	Treated in ***Anplectrum***	Treated in ***Anplectrum***		***Diplectria***	***Diplectria***		Treated in ***Dissochaeta***[10] (*Dissochaeta* alliance)
Dissochaeta	***Dissochaeta***	***Dissochaeta***		***Dissochaeta***	***Dissochaeta***		***Dissochaeta***[10] (*Dissochaeta* alliance)
Treated in *Medinilla*	Treated in ***Medinilla***	Treated in ***Medinilla***		Treated in ***Medinilla***	***Medinilla* sect. *Heteroblemma***		***Heteroblemma***[8] (*Medinilla* alliance)
Treated in ***Medinilla***	Treated in ***Medinilla***	Treated in ***Medinilla***		***Hypenanthe***	***Hypenanthe***		Treated in ***Medinilla***[3,4] (*Medinilla* alliance)
Kendrickia (Oxysporeae)	***Kendrickia*** (Oxysporeae)	***Kendrickia*** (Oxysporeae)			***Kendrickia*** (Oxysporeae)		***Kendrickia***[4] (*Medinilla* alliance)
Treated in ***Marumia***	Treated in ***Marumia***	Treated in ***Marumia***		***Macrolenes***	***Macrolenes***		***Macrolenes***[11] (*Dissochaeta* alliance)
Marumia	***Marumia***	***Marumia***		Treated in ***Macrolenes***	Treated in ***Macrolenes***		Treated in ***Macrolenes***[11] (*Dissochaeta* alliance)
Medinilla	***Medinilla***	***Medinilla***	***Medinilla***	***Medinilla***	***Medinilla***	***Medinilla***	***Medinilla***[3,4] (*Medinilla* alliance)

Bentham & Hooker 1867	**Triana 1872**	**Cogniaux 1891**	**Gilg 1898**	**Bakhuizen van den Brink 1943**	**Maxwell 1984**	**Jacques-Félix 1995**	**Current Treatment**[1]
		Medinillopsis		Treated in ***Plethiandra***	Treated in ***Plethiandra***		Treated in ***Plethiandra***[7] (*Medinilla* alliance)
			Myrianthemum			Treated in ***Medinilla***	Treated in ***Medinilla***[2] (*Medinilla* alliance)
				Neodissochaeta	Treated in ***Dissochaeta***		Treated in ***Dissochaeta***[10] (*Dissochaeta* alliance)
Ochthocharis (Oxysporeae)	***Ochthocharis*** (Oxysporeae)	***Ochthocharis*** (Oxysporeae)		***Ochthocharis*** (Oxysporeae)		***Ochthocharis***	***Ochthocharis***[5] (*Dinophora* alliance)
Omphalopus	***Omphalopus***	***Omphalopus***		***Omphalopus***	***Dissochaeta*** sect. *Omphalopus*		Treated in ***Dissochaeta***[10] (*Dissochaeta* alliance)
			Orthogoneuron			Treated in ***Gravesia*** (Sonerileae)	Treated in ***Gravesia***[4] (Sonerileae)
Pachycentria	***Pachycentria***	***Pachycentria***		***Pachycentria***	***Pachycentria***		***Pachycentria***[6] (*Medinilla* alliance)
			Phaeoneuron			Treated in ***Ochthocharis***	Treated in ***Ochthocharis***[5] (*Dinophora* alliance)
Plethiandra (Astronieae)	***Plethiandra*** (Astronieae)	***Plethiandra*** (Astronieae)		***Plethiandra***	***Plethiandra***		***Plethiandra***[7] (*Medinilla* alliance)
Pogonanthera	***Pogonanthera***	***Pogonanthera***		***Pogonanthera***	***Pogonanthera***		Treated in ***Pachycentria***[6] (*Medinilla* alliance)
			Preussiella			***Preussiella*** (Sonerileae)	***Preussiella***[5] (Sonerileae)
					Pseudodissochaeta		***Pseudodissochaeta***[12] (*Dissochaeta* alliance)
Sakersia	***Sakersia***	***Sakersia***	***Sakersia***		Treated in ***Dichaetanthera***		Treated in ***Dichaetanthera***[4] (Melastomateae)
			Tetraphyllaster			Treated in ***Tristemma*** (Melastomateae)	Treated in ***Tristemma*** [4] (Melastomateae)

[1] Based on the last account of the generic revision; [2] Jacques-Félix 1977; [3] Regalado 1995; [4] Renner 1993; [5] Jacques-Félix 1995; [6] Clausing 2000; [7] Kadereit 2005; [8] Camara-Léret et al. 2013; [9] Kartonegoro & Veldkamp 2013; [10] Kartonegoro et al. 2018; [11] Kartonegoro et al. 2019; [12] Kartonegoro et al., 2020.

Earlier molecular phylogenetic analyses, based on the combined chloroplast markers *ndhF* and *rpl16*, showed that Dissochaeteae is not monophyletic (Clausing & Renner 2001a, 2001b). This result was later confirmed by other phylogenetic studies of the family that included representatives of the group (Goldenberg et al. 2012; Zeng et al. 2016; Veranso-Libalah et al. 2018; Zhou et al. 2019a, 2019b). The phylogenetic trees from these studies, showed three major lineages within Dissochaeteae, 1) Medinillinae; 2) *Dinophora* + *Ochthocharis*; and 3) Dissochaetinae (Clausing & Renner 2001a, 2001b; Zeng et al. 2016; Veranso-Libalah et al. 2018; Zhou et al. 2019a, 2001b). The Medinillinae is closely related to the Sonerileae DC. complex (Clausing & Renner 2001a; Zeng et al. 2016; Zhou et al. 2019b), while *Dinophora* + *Ochthocharis* are related to the Rhexieae DC. (Veranso-Libalah et al. 2018). Dissochaetinae forms a monophyletic group but its sister group remained unclear. Depending on the study it is sister to either the Sonerileae complex + Medinillinae or to Blakeeae Benth. & Hook.f. (Clausing & Renner 2001a), Cyphostyleae Gleason + Blakeeae (Bacci et al. 2019), or the Cambessedesieae (Penneys et al. 2020). The phylogenetic analyses by Zhou et al. (2019b) also showed that Dissochaetinae is sister to a large clade consisting of Sonerileae-Oxysporeae + Medinillinae. Eventhough the non-herbaceous plants in all genera of Dissochaeteae share berry fruits and cochleate seeds, these characters seem to be rather homoplasious. In general, fruit morphology does not reflect a shared history but is homoplasious and an adaptation to different modes of dispersal (Clausing et al. 2000; Clausing & Renner 2001a; Bacci et al. 2019).

***Dissochaeta* alliance. —** The *Dissochaeta* alliance was first proposed to recognize an informal group of woody climbing or scrambling shrub taxa of Dissochaeteae (Maxwell 1982). It comprises c. 71 species of scrambling shrubs distributed from southern China southward into Indochina, Thailand, and the Malesian region, with Sumatra-Peninsular Malaysia-Borneo as its center of distribution (Kartonegoro et al. 2018, 2019). The *Dissochaeta* alliance is characterized as shrubs having a lianous scrambling habit, growing in open areas or forest edges in Southeast Asia (Maxwell 1984; Kartonegoro et al. 2018, 2019). This scrambling growth form probably evolved only once from a shrubby growth form in Old World Melastomataceae (Clausing & Renner 2001a). Thin branches with long internodes have been suggested as morphological adaptations promoting scrambling growth (Clausing & Renner 2001a). Some species develop interpetiolar outgrowths on the nodes to support the scrambling activity (Clausing & Renner 2001a; Kartonegoro et al. 2018). A lianous growth form is also known for a few New World taxa of Blakeeae, but these usually grow as true epiphytes (Penneys & Judd 2013). Along with the scrambling shrub habit, another apparent synapomorphy for this group is their pattern of flower development (Kartonegoro et al. 2018, 2019). Flowers of the *Dissochaeta* alliance have 4 (haplostemon) equal, or 8 (diplostemon) dimorphic stamens in two whorls with various well-developed appendages (Maxwell 1984; Renner et al. 2001b; Kartonegoro et al. 2018, 2019, 2020). Like all Melastomataceae taxa, stamens are folded in bud. The folding point of the stamens is at the attachment between anthers and filaments for the alternipetalous stamens, while the oppositipetalous ones have a fold in the filaments below the attachment point with the anthers (Maxwell 1984; Kartonegoro et al. 2018). When mature, the stamens will reverse their orientation into curved or straight anthers with varying shape. The number of fertile stamens can be 8 or 4 because either the inner or the outer staminal whorl can be reduced (Kartonegoro et al. 2018).

Previous taxonomic work of the *Dissochaeta* alliance resulted in different generic concepts and was mainly based on morphology and overlooked other important approaches, such as anatomy, cytology and molecular phylogenetics. Genera included by different authors are

Backeria, *Dalenia*, *Diplectria*, *Dissochaeta*, *Macrolenes*, *Neodissochaeta* and *Omphalopus* (Bakhuizen van den Brink 1943; Nayar 1966, 1980; Raizada 1968; Veldkamp et al. 1979; Maxwell 1984; Renner et al. 2001b; Kartonegoro et al. 2018, 2019; see also Table 6-1). In addition, the genera, *Creochiton* and *Pseudodissochaeta* were also treated as part of the alliance (Maxwell 1984; Kartonegoro et al. 2020). The decision whether to include the non-scrambling genera into the alliance was based on similarity of floral characters, such as merosity and stamen dimorphism with distinct connective appendages (Maxwell 1980, 1984). Therefore, the *Dissochaeta* alliance can be generalized as Dissochaetinae and consisting of all genera of the subtribe.

Within the *Dissochaeta* alliance, an infrageneric classification has only been proposed for *Dissochaeta*, the largest genus of the group. In the protologue of *Dissochaeta*, Blume (1831a, 1831b) proposed two sections, *Dissochaeta* sect. *Dissochaeta* and sect. *Diplectria* Blume, based on hypanthium shape and connective appendages. Baillon (1877) further divided the genus into nine sections: *Dissochaeta* sect. *Anoplodissochaeta* Baill., sect. *Anplectrum* (A.Gray) Baill. (≡ sect. *Diplectria*), sect. *Creochiton* (Blume) Baill., sect. *Dalenia* (Korth.) Baill., sect. *Dicellandra* (Hook.f.) Baill., sect. *Eudissochaeta* Blume ex Endl. (invalid name, ≡ sect. *Dissochaeta*), sect. *Omphalopus* (Naudin) Baill., sect. *Oxyotandra* Baill., and sect. *Sakersia* (Hook.f.) Baill. Cogniaux (1891) rejected Baillon’s generic concept of *Dissochaeta* and resurrected some genera such as; *Anplectrum*, *Creochiton*, *Dalenia*, *Dicellandra*, *Omphalopus* and *Sakersia*. He also rearranged the infrageneric classification of *Dissochaeta* and proposed three new sections; *Dissochaeta* sect. *Diplostemones* Cogn., sect. *Dissochaetopsis* Cogn. and sect. *Isostemones* Cogn. An additional section of *Dissochaeta*, *D.* sect. *Disparistemones* Merr. was proposed by Merrill (1917).

An initial molecular phylogenetic study of Dissochaeteae by Clausing & Renner (2001a) showed that the *Dissochaeta* alliance is monophyletic. However, their analyses included only a few species of the *Dissochaeta* alliance and two allied genera (*Creochiton*, *Pseudodissochaeta*) were not sampled. Within the *Dissochaeta* alliance, *Dissochaeta* was resolved as sister to *Diplectria* + *Macrolenes* (Clausing & Renner 2001a). More recent molecular phylogenetic studies strongly support *Pseudodissochaeta*, a non-scrambling taxon, as part of the *Dissochaeta* alliance but unrelated to *Medinilla* (Zeng et al. 2016; Zhou et al. 2019a, 2019b). However, *Creochiton* remains unsampled, and the number of species sampled per genus needs to be improved especially for *Dissochaeta* to ascertain that all the genera and sections are natural lineages.

Aims. — Using sequence data extended to six loci (nrETS, nrITS, *ndhF*, *psbK-psbL*, *rbcL*, *rpl16*) with a much more comprehensive sampling than any previous investigation, this study seeks (1) to confirm the polyphyly of Dissochaeteae as currently circumscribed (Table 1) and identify the position of the lineages within the Melastomataceae; (2) to test the monophyly of the *Dissochaeta* alliance; (3) to resolve phylogenetic relationships among genera and sections within the *Dissochaeta* alliance; and (4) to investigate selected morphological characters as potential synapomorphies for delimiting clades or genera in the alliance.

Material and Methods

Taxon sampling. — For a broad taxon sampling of Dissochaeteae and relevant outgroups we compiled a total of 121 accessions of which 78 represent 63 species and 1 variety of Dissochaeteae (see Appendix 6-1). Within the *Dissochaeta* alliance, 44 of 90 species (50%) were sampled from the following genera: *Creochiton* (4 species sampled/12 species in genus); *Dissochaeta* (28/56); *Macrolenes* (9/17); *Pseudodissochaeta* (3/5). From the *Medinilla* alliance, 16 species belonging to *Heteroblemma* (1/13), *Medinilla* (13/±400) and *Pachycentria* (2/8) were sampled. We also included the African endemic monospecific *Dinophora* (*D. spenneroides* Benth.) and two species of the only disjunct African / Southeast Asian genus *Ochthocharis*, two genera with an unclear phylogenetic placement. As outgroups to test the monophyly of the traditional Dissochaeteae, we selected 44 taxa from Melastomateae (8 species), Miconieae (4), Oxysporeae (5), Kibessieae (4), Merianieae (4), Sonerileae (4), Cambessedesieae (2), Henrietteeae (2), Marcetieae (2), Olisbeoideae (2), and one each from Astronieae, Bertolonieae, Blakeeae, Eriocnemeae, Microlicieae, Rhexieae, and Trioleneae. A complete list of the taxa sampled in this study, their collection localities, voucher information, and Genbank accession numbers are provided in the Appendix 6-1.

Morphological data used for generic delimitations of Dissochaeteae including data on floral morphology that substantiated our floral diagrams were obtained from the literature (Bakhuizen van den Brink 1943; Nayar 1969a, 1982; Veldkamp et al. 1979; Hansen & Wickens 1981; Maxwell 1984; Regalado 1995; Jacques-Félix 1995; Clausing 2000; Kadereit 2005; Cámara-Leret et al. 2013; Kartonegoro & Veldkamp 2013; Kartonegoro et al. 2018, 2019, 2020) and supplemented by the first author during studies of herbarium material and visits to the herbaria BM, BO, E, K, L, SING and U, and through online repositories of AAU (https://www.aubot.dk/search_form.php), HBG (http://www.herbariumhamburgense.de/Data_Spermatophyta/index.php), P (https://science.mnhn.fr/all/search), and PE (http://pe.ibcas.ac.cn/en/#).

DNA extraction, polymerase chain reaction amplification, and sequencing. — Total genomic DNA was extracted, either from silica-gel dried leaves or herbarium specimens, using either the modified CTAB procedure (Doyle & Doyle 1987) using a 96-well Thermo ScientificKingFisher Flex extraction (Thermo Fisher Scientific, Waltham, MA, U.S.A.), following the manufacturer's instructions, or using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany), with modification to the manufacturer's protocol following Goldenberg et 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. Two nuclear ribosomal loci, the internal transcribed spacer (nrITS) and the external transcribed spacer (nrETS) regions, and four plastid loci (*ndhF*, *psbK-psbL*, *rbcL*, and *rpl16*) were amplified and sequenced following the protocols outlined by Clausing & Renner (2001a, 2001b), Fritsch et al. (2004), Rocha et al. (2016), Zeng et al. (2016), Veranso-Libalah et al. (2017, 2018) and Bacci et al. (2019). The nuclear markers have been widely used in phylogenetic studies due to their relatively high rate of nucleotide substitutions providing resolution even at lower taxonomic levels in Melastomataceae (Rocha et al. 2016). Also, the selected plastid loci have proven to be variable at both the tribal and generic levels in the family (Clausing & Renner 2001a, 2001b; Michelangeli et al. 2004, 2013; Goldenberg et al. 2008; Penneys & Judd 2013; Zeng et al. 2016; Veranso-Libalah et al. 2017; Bacci et al. 2019). Amplification and sequencing of ITS and *ndhF* markers were done via two segment regions using overlapping primers. All primers used in this study are shown in Table 6-2.

Polymerase chain reactions (PCR) were performed with a total volume of 25 µl containing the following: template DNA (1-1.5 µL), 10 pMol/µL primers (0.5 µL each), 2.5 nM dNTPs (1.5 µL), 10x Buffer (Qiagen) (2.5 µL), 25 nM MgCl2 (1 µL), DNA Taq polymerase (Qiagen) (0.25 µL) and miliQ water (16-18 µL). Specifically, for ITS 0.25 µL Bovine Serum Albumin (BSA) was added. PCR programs for all markers are shown in Table 6-3. PCR products were run on 1% agarose gels to check the quality of the amplified DNA. Cycle sequencing was carried out either at Baseclear (Leiden, The Netherlands) or StarSEQ (Mainz, Germany) with the same forward and reverse primers used in the amplifications. In addition to the 368 newly generated sequences, 272 were downloaded from GenBank (Appendix 6-1).

Table 6-2. Primers of the six markers used in this study and the sources of primer sequences.

Marker	**Primer name**	**Primer sequence 5’ → 3’**	**Source**
nrETS	ETS NY320 F	AGA CAA GCA TAT GAC TAC TGG CA	Veranso-Libalah & al. (2018)
nrETS	ETS 1428 Mel Spec R	ACG TGT CGC GTC TAG CAG GCT	Veranso-Libalah & al. (2018)
nrITS	ITS1-MEL F	GGA GAA GTC GTA ACA AGG TTT C	Veranso-Libalah & al. (2017)
nrITS	ITS1-MEL R	CTT GCG TTC AAA GAA TTG ATG G	Veranso-Libalah & al. (2017)
nrITS	ITS2-MEL F	CGG CTC TTG CAT CGA TGA AG	Veranso-Libalah & al. (2017)
nrITS	ITS2-MEL R	CCA CCT TCC AGT GAA CTT GG	Veranso-Libalah & al. (2017)
ndhF	*ndhF*-972 F	GTCTCAATTGGGTTATATGATG	Olmstead & Sweere (1994)
ndhF	*ndhF*-1603 R	GCATAGTATTGTCCGATTCATRAGG	Olmstead & Sweere (1994)
ndhF	*ndhF*-1318 F	GGATTAACYGCATTTTATATGTTTCG	Olmstead & Sweere (1994)
ndhF	*ndhF*-1955 R	CGATTATATGACCAATCATATA	Olmstead & Sweere (1994)
psbK	*psbK* F	TTA GCC TTT GTT TGG CAA G	Reginato & al. (2010)
psbL	*psbL* R	AGA GTT TGA GAG TAA GCA T	Reginato & al. (2010)
rbcL	*rbcL*-1 F	ATGTCACCACAAACRGAGACTAAAGC	De Groot & al. (2011)
rbcL	*rbcL*-1361 R	TCAGGACTCCACTTACTAGCTTCACG	De Groot & al. (2011)
rpl16	*rpl16*-71 F	GCTATGCTTAGTGTGTGACTCGTTG	Jordan & al. (1996)
rpl16	*rpl16*-1516 R	CCCTTCATTCTTCCTCTATGTTG	Kelchner & Clark (1997)

Phylogenetic analyses. — Contigs of forward and reverse sequences were assembled and manually edited using either Geneious Prime Sequence Analysis Tools version 2019.2.1 (Biomatters, Auckland, NZ) or Sequencher 4.1.4 (Gene Codes Corporation, Ann Arbor, Michigan, USA). Sequence alignment was done using MAFFT v.7 (Katoh & Standley 2013) implemented in Geneious via plugins with default settings and the results manually checked. Phylogenetic analyses were performed under maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) methods. We separately analysed each of the six individual datasets (nrETS, nrITS, *ndhF*, *psbK-psbL*, *rbcL*, *rpl16*). Later we combined the two nuclear (nrETS, nrITS) and four plastid datasets (*ndhF*, *psbK-psbL*, *rbcL*, *rpl16*) and ran each analysis to check for conflicts between the two matrices. Since no supported conflict was detected a concatenated matrix of all six individual datasets was again analysed. The best-fitting model for each marker was determined using the Akaike information criterion corrected (AICc) in jModelTest v.2.1.6 (Darriba et al. 2012) through the CIPRES portal (www.phylo.org; Miller et al. 2010). The best fit substitution models selected for the datasets are shown in Table 6-4.

Table 6-3. Thermocycler programs for the PCR amplification of all markers.

Marker		**nrETS**	**nrITS**	***ndhF***	***psbK-psbL***	***rbcL***	***rpl16***
Initial denaturation	Temperature (°C)	94	94	94	94	93	94
	Time (m)	4	1	4	2	3	3
Cycle		40	40	40	40	35	35
Denaturation	Temperature (°C)	94	94	94	94	94	94
	Time (s)	30	20	30	30	45	45
Annealing	Temperature (°C)	58	63	54	55	62	58
	Time (s)	30	30	30	30	45	45
Extension	Temperature (°C)	72	72	72	72	72	72
	Time (s)	45	60	60	30	105	75
Final extension	Temperature (°C)	72	72	72	72	72	72
	Time (s)	7	8	7	7	6	7

The MP analyses were carried out in PAUP* v.4.a165 (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 100 trees. All characters were unordered and equally weighted, while gaps were treated as missing data. Bootstrap values (Felsenstein 1985) were calculated from 1000 random replicates using a heuristic search with TBR branch swapping and one random addition-sequence per replicate. The ML trees were generated using RAxML v.8.2.12 using the GTR+I+Γ model and inferred under default settings (Stamatakis 2014). Node support was calculated in RAxML with 1000 bootstrap replicates using a fast bootstrapping algorithm (Stamatakis et al. 2008). Bayesian inference (BI) analyses were carried out using MrBayes v.3.2.7a (Ronquist et al. 2012). The Markov Chain Monte Carlo (MCMC) analyses were carried out with four simultaneous chains of 10 million generations sampling one tree every 1000 generations in two independent runs. The individual output log files were examined using Tracer v.1.7.1 (Rambaut et al. 2018) to assess convergence of both runs. The resultant tree files were combined using LogCombiner v.1.8.4 (Drummond & Rambaut 2007). The first 2500 trees (25%) were discarded as burn-in, and a maximum clade credibility (MCC) tree was constructed using TreeAnnotator v.1.8.4 (Drummond et al. 2012). All analyses (MP, ML and BI) were run through the CIPRES portal (http://www.phylo.org/; Miller et al. 2010).

Results

Out of the total of 640 sequences used in the analyses, 368 were newly generated (Appendix 6-1). The combined data matrix consisted of 77 nrETS sequences, 106 for nrITS, 120 for *ndhF*, 118 for *psbK-psbL*, 112 for *rbcL* and 112 for *rpl16* (Table 4). Gene trees from combined plastid (121 terminals) and nuclear datasets (114 terminals), revealed congruencies in all three analyses without any significant conflicts (Suppl. 6-1 & 6-2). Most of the resolved clades are present in both gene trees (Dissochaeteae; incl. *Dissochaeta* alliance, *Medinilla* alliance and *Dinophora* + *Ochthocharis*), although some clades are poorly supported. The combined dataset contained 121 terminals and 5641 characters from all six loci (nrETS, nrITS, *ndhF*, *psbK-psbL*, *rbcL*, *rpl16*) and showed a similar topology as the individual gene trees but with higher branch support values (Fig. 6-2).

In the parsimony analysis the aligned matrix with all combined regions had 1893 (36%) parsimony informative characters. The Consistency Index (CI) and Retention Index (RI) were 0.47 and 0.76, respectively. Other relevant information of the parsimony analyses is shown in Table 6-4. In general, the nuclear markers produced better resolved trees, probably because of the greater number of informative characters. However, lower CI and RI values for the nuclear markers indicate a greater proportion of homoplasy and less synapomorphies, respectively.

Table 6-4. Summary statistics of genomic regions sequenced for phylogenetic analyses of *Dissochaeta* alliance.

	ETS	**ITS**	***ndhF***	***psbK-psbL***	***rbcL***	***rpl16***	**Nuclear**	**Plastid**	**Combined**
Accession terminals	77	106	120	118	112	112	114	121	121
Aligned characters	693	1057	1001	528	1244	1118	1750	3891	5641
% missing data	36	12	1	2	7	7	6	0	0
Parsimony informative sites	433 (62%)	602 (57%)	298 (30%)	157 (30%)	142 (11%)	256 (23%)	1039 (59%)	854 (22%)	1893 (36%)
Conserved sites	149	340	552	256	1007	665	481	2477	2958
Length of most parsimonius trees	2259	3449	1064	536	472	983	5918	3154	9167
Consistency Index (CI)	0.46	0.38	0.59	0.68	0.59	0.63	0.4	0.6	0.47
Retention Index (RI)	0.76	0.69	0.87	0.88	0.84	0.83	0.71	0.85	0.76
Best substitution model (AICc)	TVM+I+Γ	GTR+I+Γ	TVM+I+Γ	TVM+Γ	TPM1uf+I+Γ	TVM+Γ	GTR+I+Γ	TVM+I+Γ	TVM+I+Γ

Tree topologies from the ML, MP and BI analyses of the complete dataset were overall congruent with a well-resolved backbone. We considered the clades as statistically supported when the bootstrap values from the ML (BS) and MP (PBS) analyses were ≥ 70% and the posterior probabilities (PP) were ≥ 0.95 for the BI analysis. In our analyses, Dissochaeteae s.l. (including *Medinilla* alliance, *Dissochaeta* alliance, *Dinophora* + *Ochthocharis* lineages) was recovered as polyphyletic (Figs. 6-2, 6-3). The *Medinilla* alliance (clade A) is grouped with the Sonerileae + Oxysporeae lineage (PP=1/BS=100/PBS=100). Although a well-supported *Dinophora* + *Ochthocharis* lineage (clade B; PP=1/BS=100/PBS=96) is recovered, it is in a polytomy with Melastomateae, Microlicieae, Marcetieae and Rhexieae

(Fig. 6-2). The species of the *Dissochaeta* alliance form a well-supported monophyletic lineage (clade C; PP=1/BS=100/PBS=100), that is sister to Cambessedesieae (Fig. 6-2).

Three Dissochaeteae genera, *Heteroblemma*, *Medinilla* and *Pachycentria* are recovered within the unresolved *Medinilla* alliance lineage (clade A; Fig. 6-3A). *Medinilla* is recovered as paraphyletic with *Pachycentria* nested within it. Except for the Madagascan *Medinilla* (*M. lophoclada* Baker, *M. chermezonii* H.Perrier and *M. micrantha* Jum. & H.Perrier) which formed a well-supported monophyletic clade (PP=1/BS=92/PBS=92), the remaining *Medinilla* species sampled are unresolved (Fig. 6-3A).

The *Dissochaeta* alliance is composed of six well-supported lineages (clade C; Fig. 6-3B). The well-supported *Pseudodissochaeta* lineage (clade E; PP=1/BS=100/PBS=100) is sister to all other lineages within the *Dissochaeta* alliance. There is little or no resolution between the three *Pseudodissochaeta* species sampled (Fig. 6-3B). *Creochiton* forms the second strongly supported monophyletic lineage (clade F; Fig. 6-3B; PP=1/BS=100/PBS=100) and is sister to the scrambling shrub taxa (clade D). Within *Creochiton*, *C. ledermannii* Mansf. is closely related to *Creochiton* sp. (PP=1/BS=100/PBS=99) but these two are in a polytomy with *C. roseus* Merr. and *C. bibracteatus* (Blume) Blume (Fig. 6-3B).

The scrambling shrubs lineage (clade D; including *Dissochaeta* s.l. and *Macrolenes*), is recovered as well-supported and monophyletic (PP=1/BS=100/PBS=100; Fig. 6-3B), with four well-supported sub-lineages within it (clades G, H, I and J in Fig. 6-3B). Clade G consists of all the species sampled from *Dissochaeta* sect. *Dalenia* and *Dissochaeta* sect. *Disparistemones* (PP=1/BS=97=PBS=77; Fig. 6-3B) and is sister to the well supported clade consisting of clades H, I and J. *Dissochaeta* sect. *Dalenia* consists of *Dissochaeta pubescens* Karton. (*Dalenia beccariana* (Cogn.) M.P.Nayar) and *Dissochaeta beccariana* Cogn. (*Dalenia magnibracteata* Karton.) and it is resolved as sister to *Dissochaeta* sect. *Disparistemones* (*Dalenia glabra* (Merr.) Karton.). Clade H is sister to clade I/J and represents a well-supported lineage comprising the species sampled from *Dissochaeta* sect. *Diplectria* (PP=1/BS=100/PBS=100). Clade I comprises *Macrolenes* (PP=1/BS=100/PBS=100; Fig. 6-3B) and splits into the *Macrolenes* s.str. lineage (Clade L; PP=1/BS=95/PBS=87) and the *Dissochaeta rostrata* complex (clade K; PP=0.99/BS=71/PBS=64). Within *Macrolenes* s.str. (clade L), 9 of the 17 *Macrolenes* species sampled are recovered in this lineage, with the interspecific relationships mostly resolved (Fig. 6-3B). The last lineage recovered within the scrambling shrubs lineage is the well-supported *Dissochaeta* s.str. (clade J; PP=1/BS=99/PBS=92). This lineage comprises two well supported sub-lineages; *Dissochaeta* sect. *Diplostemones* is supported (clade M; PP=1/BS=98/PBS=93) as sister to the other four lineages in clade N (PP=1/BS=99/PBS=100). Clade N consists of *Dissochaeta* sect. *Dissochaeta* + *Dissochaeta* sect. *Isostemones* + *Dissochaeta* sect. *Omphalopus* + *Dissochaeta* sect. *Anoplodissochaeta*. Apart from sect. *Dissochaeta*, which is recovered as paraphyletic, the remaining sections are monophyletic.

Discussion

Redefining Dissochaeteae. — This study represents (1) an expanded molecular phylogenetic study of the tribe Dissochaeteae s.l. with a broad outgroup sampling, and (2) a comprehensive molecular phylogenetic study of the *Dissochaeta* alliance (= subtribe Dissochaetinae). Of the 13 genera currently treated within Dissochaeteae (Table 6-1; one but last column), eight were sampled (*Creochiton*, *Dinophora*, *Dissochaeta*, *Heteroblemma*, *Macrolenes*, *Ochthocharis*, *Pachycentria* and *Pseudodissochaeta*. We were not able to include *Boerlagea* (only known from the type collection), *Catanthera* (PCR failure and incomplete sequences), *Kendrickia* (no material available to us), and *Plethiandra* (incomplete sequences). According to our results, previous classifications of Dissochaeteae s.l. (i.e., Triana 1866, 1872; Cogniaux 1891; Krasser 1893; Gilg 1898; Bakhuizen van den Brink 1943; Van Vliet et al. 1981; Maxwell 1984; Jacques-Félix 1995; Clausing 1999) do not represent a natural, evolutionary unit because the tribe is polyphyletic (Figs. 6-2, 6-3). Our molecular phylogenetic results are similar to those of earlier studies (Clausing & Renner 2001a; Goldenberg et al. 2012; Zeng et al. 2016; Veranso-Libalah et al. 2108; Zhou et al. 2019a, 2019b; Penneys et al. 2020). The berry fruits and the cochleate seeds, used as diagnostic characters for the tribe, are homoplasious and have multiple parallel origins (Clausing et al. 2000). Clausing et al. (2000), suggested that berry fruits may have evolved at least three times within the family. Thus, the berries are a synapomorphy for tribe Dissochaeteae, but not all taxa with berries are Dissochaeteae. Berries are also present in other Melastomataceae lineages: Blakeeae, Henrietteeae, Miconieae, Olisbeoideae and some Old World Melastomateae (Clausing & Renner 2001a; Michelangeli et al. 2004; Penneys et al. 2010; Penneys & Judd 2013; Stone 2014).

The monophyly of the *Dissochaeta* alliance is supported by the following shared morphological characters: thyrsoid inflorescences, tetramerous diplostemonous flowers with unequal/subequal stamens produced in two whorls (alternipetalous and oppositipetalous) and berry fruits (Maxwell 1984). Based on wood anatomy, the *Dissochaeta* alliance have alternate inter-vessel pits, vessel elements with a wide diameter, and rays up to 7 cells wide (Van Vliet 1981). Together with morphology and wood anatomy, our molecular phylogenetic results clearly support a recircumscription of a narrower Dissochaeteae (excluding *Medinilla* alliance, *Dinophora* and *Ochthocharis*) (clades A and B in Figs. 6-2, 6-3). The *Dissochaeta* alliance or subtribe Dissochaetinae clade is thus the only member of Dissochaeteae. With this redefinition, Dissochaeteae (clade C in Fig. 6-2, 6-3B) is only distributed from East Bhutan, Northeast India, Southern China throughout Southeast Asia to New Guinea with no entities in Africa, Madagascar, West and Central India, or Sri Lanka.

Placement of *Medinilla* alliance. — The monophyly of the *Medinilla* alliance (sensu Maxwell 1984; including *Pachycentria* and *Heteroblemma*) is not strongly supported in this study. Its closest relatives are still unknown since it is nested in the still sparsely sampled Sonerileae+Oxysporeae complex (see also Clausing & Renner 2001a; Zeng et al. 2016; Zhou et al. 2019a, 2019b). Except for the Madagascan endemic *Medinilla* species (*M. lophoclada*, *M. chermezonii*, *M. micrantha*; PP=1/BS=92/PBS=92) and *Pachycentria* (PP=1/BS=100/PBS=100), which formed monophyletic lineages and are nested among Southeast Asian *Medinilla*. The genera *Catanthera*, *Kendrickia* and *Plethiandra*, all treated in the *Medinilla* alliance, are unsampled in this study, but were earlier found to be nested inside Sonerileae+Oxysporeae (Clausing & Renner 2001a). *Catanthera* and *Kendrickia* are closely related to *Heteroblemma*, while *Plethiandra* is closely related to *Medinilla* (Clausing & Renner 2001a). The monospecific genus, *Boerlagea* is still unsampled in a phylogenetic context. So far, less than 10% of the species in *Medinilla* alliance have been included in phylogenetic studies. Such confirmation awaits a very broadly sampled study of the putative members of that group, along with a diverse array of Sonerileae+Oxysporeae taxa, as well as genera from across the family. With a comprehensive sampling of the *Medinilla* alliance, intergeneric relationships will be better understood in the future.

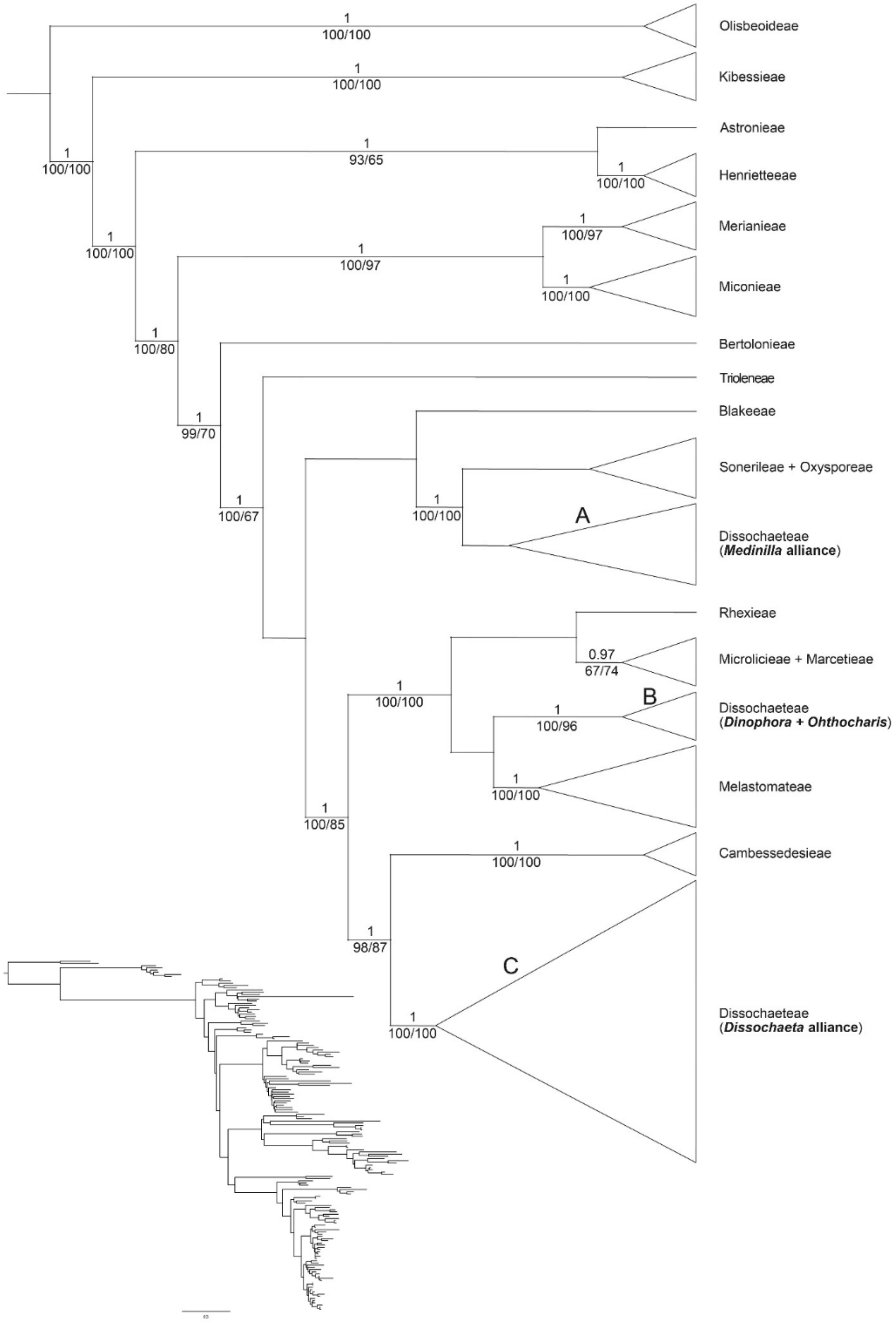


Fig. 6-2. The phylogenetic analyses of Dissochaeteae s.l. plus a broad outgroup sampling reveal the polyphyly of Dissochaeteae with three lineages (A-C) recovered in distinct positions within Melastomataceae. Analyses are based on combined nuclear (nrETS, nrITS) and plastid (*ndhF*, *psbK-psbL*, *rbcL*, *rpl16*) data. Tree resulting from the maximum likelihood (ML) analysis with posterior probabilities above branches, ML bootstrap support values (left) and bootstrap support values resulting from the parsimony analysis (right) below branches. Posterior probabilities below 0.80 and bootstrap values below 50 are not shown. The major clades recognised in Dissochaeteae s.l. in this study are given in bold.

Placement of *Dinophora* and *Ochthocharis*. — Jacques-Félix (1983, 1995) included *Dinophora* and *Ochthocharis* in Dissochaeteae based on the presence of berry fruits. Previously, *Dinophora* was treated in Rhexieae (Bentham 1849), Bertolonieae (Van Tieghem 1891), and Melastomateae (=Osbeckieae) (Triana 1872; Baillon 1877; Cogniaux 1891; Gilg 1898; Renner 1993), and *Ochthocharis* was placed in Oxysporeae (Triana 1872; Cogniaux 1891; Krasser 1893; Bakhuizen van den Brink 1943; Hansen & Wickens 1981; Renner 1993). A previous molecular study suggested that *Dinophora* is not part of Melastomateae (Veranso-Libalah et al. 2017), but instead closely related to *Ochthocharis* and both were found in a polytomy together with Rhexieae, Marcetieae, Microlicieae and Melastomateae (Veranso-Libalah et al. 2018; Zhou et al. 2019b).

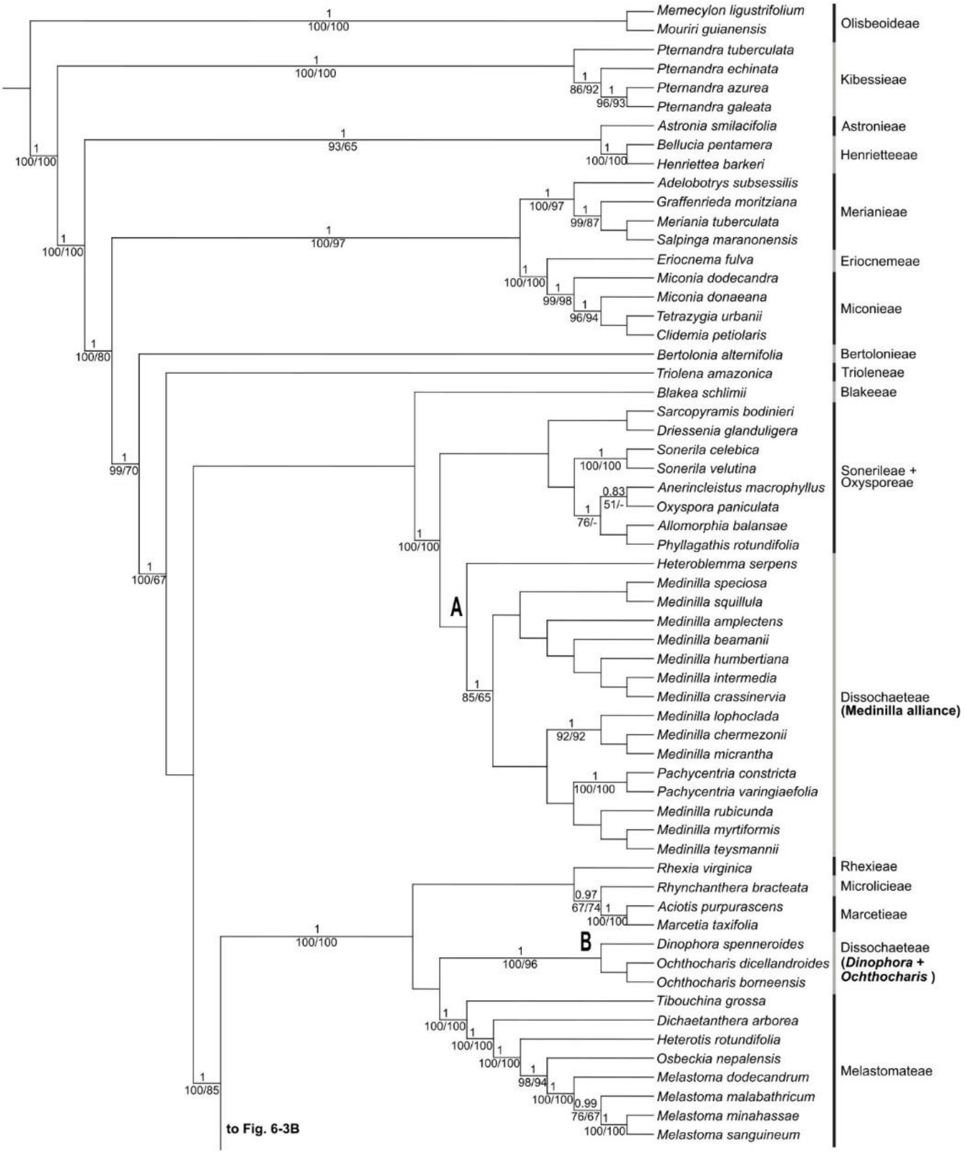
Like previous studies, our phylogenetic results support the monospecific *Dinophora* and the two species of *Ochthocharis* sampled as sister genera (Fig. 6-3A; Clade B), but in a polytomy with several other Melastomataceae tribes. A detailed morphological assessment with better phylogenetic resolution is necessary for the tribal placement of these genera. The type of *Ochthocharis*, *O. javanica* Blume, is still unsampled. Nevertheless, these genera are excluded from the redefined Dissochaeteae.

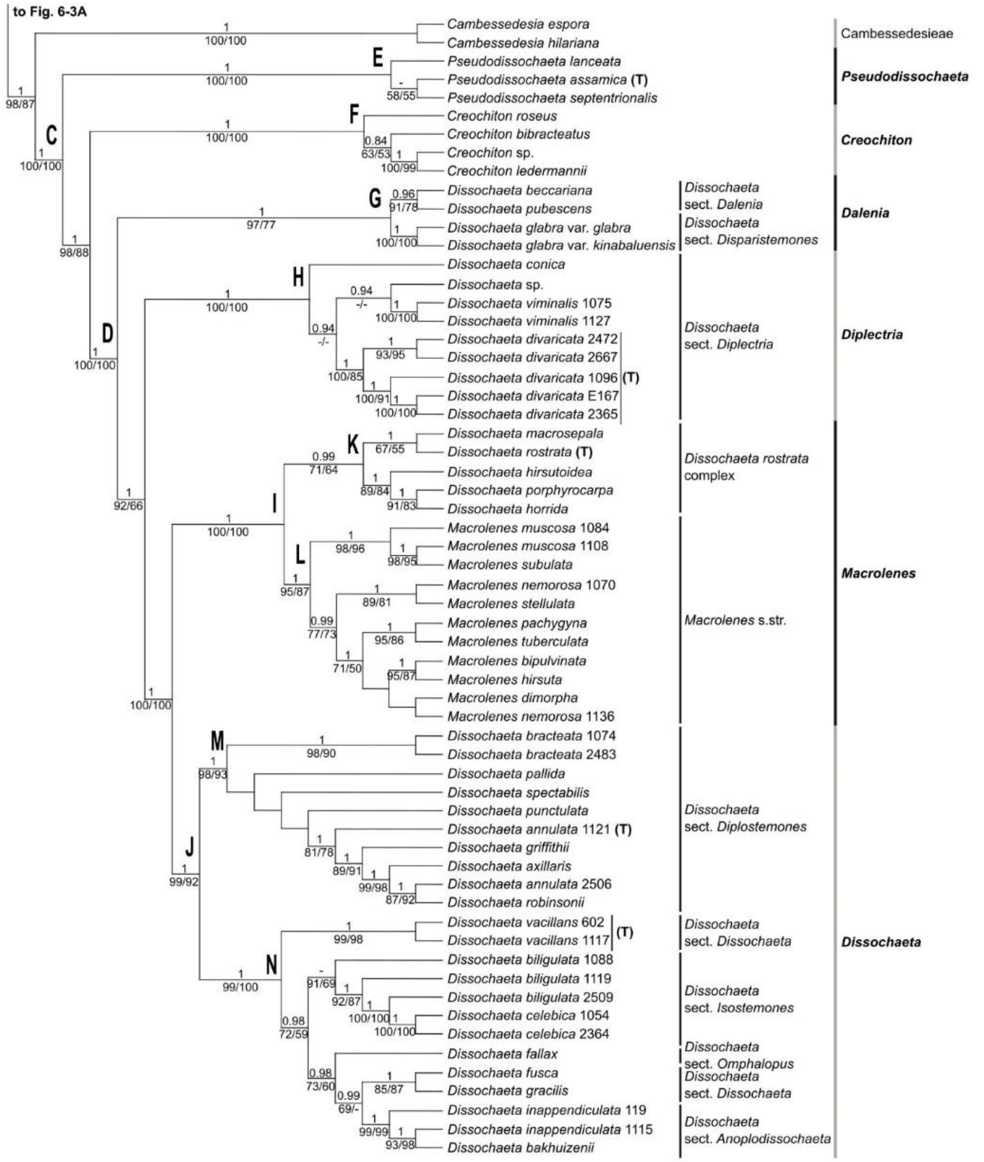
Phylogenetic relationships within Dissochaeteae. — The newly defined Dissochaeteae (*Dissochaeta* alliance) is strongly supported as monophyletic in our BI, ML, and MP analyses (Fig. 6-2, 6-3B; PP=1/BS=100/PBS=100). This confirms earlier phylogenetic studies by Clausing & Renner (2001a), Zeng et al. (2016), Zhou et al. (2019b). The Dissochaeteae are resolved as sister to neotropical tribe Cambessedesieae with strong support values (PP=1/BS=98/PBS=87; Figs. 6-2, 6-3B). *Cambessedesia* and related genera were placed in a new tribe, Cambessedesieae by Bochorny et al. (2019). With a comprehensive sampling including all genera ever treated in the *Dissochaeta* alliance and 44 of putatively 90 species, our results strongly support the monophyly of this lineage (Fig. 6-3B). Six lineages were resolved in the *Dissochaeta* alliance; *Pseudodissochaeta* (clade E), *Creochiton* (clade F), *Dalenia* (clade G), *Diplectria* (clade H). *Macrolenes* (clade I) and *Dissochaeta* s.str. (clade J). Below we discuss in detail each of these lineages.

***Pseudodissochaeta*. —** *Pseudodissochaeta* consists of five species found in east Bhutan, northeast India, upper Myanmar, Indochina, southern China, Hainan, North Thailand (Nayar 1969a; Maxwell 1984; Clausing 1999; Renner et al. 2001b; Kartonegoro et al. 2020). These species are shrubs or small trees with 8 equal stamens, dorsally spurred and ventrally biauriculate (Nayar 1969a; Maxwell 1984; Clausing 1999; Renner et al. 2001b; Zhou et al. 2019b; Kartonegoro et al. 2020; see Figs. 6-1A–B). Morphologically, *Pseudodissochaeta* closely resembles *Medinilla*, which explains why some authors formerly regarded the genus as a synonym of *Medinilla* (Chen 1983, 1984; Chen & Renner 2007). However, in agreement with molecular results (see below), wood anatomy suggests it to be a member of the *Dissochaeta* alliance and not part of the *Medinilla* alliance (Van Vliet 1981; Van Vliet et al. 1981).

Our phylogenetic analyses included three of the five currently recognized *Pseudodissochaeta* species (including the type *P. assamica*; Clade E; Fig. 6-3B). Our results show that *Pseudodissochaeta* is a monophyletic lineage and a member of the *Dissochaeta* alliance and not part of the Medinilla alliance, and thereby confirm previous molecular studies even with more restricted sampling of the *Dissochaeta* alliance (Zeng et al. 2016; Zhou et al. 2019b). *Pseudodissochaeta* is recovered as the sister clade to all remainig Dissochaeteae. The genus is distinguished by its unique leaf features (serrulate margins with oblique base) and terminal (axillary in *P. septentrionalis*) thyrsoid inflorescences. Like the other Dissochaeteae species, *Pseudodissochaeta* has curved stamens arranged in two whorls (Figs. 6-1A–B, 6-4). However, considering the huge variability of stamen morphology in lineage E, this is a rather weak trait.

Fig. 6-3A & 6-3B. Maximum likelihood (ML) phylogenetic cladogram of Dissochaeteae s.l. and *Dissochaeta* alliance with representatives of Asian, African and Madagascan Dissochaeteae, and outgroups derived from the combined data matrix (nrETS, nrITS, *ndhF*, *psbK-psbL*, *rbcL*, *rpl16*). Values above branches refer to posterior probabilities resulting from Bayesian inference (only values ≥0.80), values below branches refer to bootstrap values (only values ≥50) resulting from the ML analysis (left) and parsimony analysis (right). **A.** *Medinilla* alliance; **B.** *Dinophora* + *Ochthocharis*; **C.** *Dissochaeta* alliance; **D.** Scrambling shrub genera; **E.** *Pseudodissochaeta*; **F.** *Creochiton*; **G.** *Dalenia*; **H.** *Diplectria*; **I.** *Macrolenes*; **J.** *Dissochaeta*; **K.** *Macrolenes* sect. *Terminaliflores*; **L.** *Macrolenes* sect. *Macrolenes*; **M.** *Dissochaeta* sect. *Diplostemones*; **N.** *Dissochaeta* sect. *Dissochaeta*.





***Creochiton*. —** *Creochiton* has about 12 species, scattered throughout the Malesian region, and mostly in mountainous areas (Kartonegoro & Veldkamp 2013). They are epiphytic shrubs or lianas with haplostemonous or diplostemonous flowers, 4 alternipetalous or 8 alternipetalous-oppositipetalous equal stamens (Blume 1831a; Veldkamp 1979; Clausing 1999; Kartonegoro & Veldkamp 2013). The dorsally spurred or triangular and ventrally inappendiculate or biligulate appendaged stamens of *Creochiton* are similar to those of *Dissochaeta* (Fig. 6-1C). Some authors treated *Creochiton* in Astronieae based only on the basal placentation present in some species (Mansfeld 1925; Bakhuizen van den Brink 1943), but its habit, wood anatomy, floral morphology, and berry fruits corresponded with other Dissochaeteae genera (Triana 1866, 1872; Cogniaux 1891; Van Vliet 1981; Maxwell 1984;

Renner 1993; Kartonegoro & Veldkamp 2013). Basal placentation evolved in parallel in *Creochiton* and in the tribe Astronieae (Maxwell 1984). *Creochiton* flowers can either have 4 alternipetalous or 8 alternipetalous-oppositipetalous well developed fertile stamens (Kartonegoro & Veldkamp 2013; Fig. 6-4). The variability in stamen number and ventral appendages compelled some authors (Quisumbing & Merrill 1928; Nayar 1970) to recognize two genera, *Eisocreochiton* Quisumb. & Merr. and *Creochiton*. *Eisocreochiton* differed from *Creochiton* by having 4 alternipetalous stamens with ventrally biligulate appendages, and *Creochiton* has 4 alternipetalous and 4 oppositipetalous stamens and is ventrally inappendiculate (Nayar 1970). However, *E. monticola* (Ridl.) M.P.Nayar is morphologically intermediate between the two genera having 8 stamens with the inner whorl stamens distinctly smaller and ventrally inappendiculate (Kartonegoro & Veldkamp 2013). Therefore, *Eisocreochiton* has been treated as a synonym of *Creochiton* (Veldkamp 1979; Kartonegoro & Veldkamp 2013).

Nevertheless, the status of *Eisocreochiton* is still debatable because none of its three species (*E. bracteatus* Quisumb. & Merr., *E. furfuraceus* M.P.Nayar, *E. monticola*) were included in this study. We included only three of the twelve currently recognized species, plus one undescribed species thought to belong in *Creochiton*. Our phylogenetic results support the monophyly of *Creochiton* (clade F) and it is resolved as sister to the scrambling shrubs of Dissochaeteae. Morphologically, this group is also very distinct from the other genera of the Dissochaeteae by having an epiphytic habit, plinerved leaf venation, with fleshy, caducous and concave bracteoles that envelop the flower buds and umbellate inflorescences (Blume 1831; Kartonegoro & Veldkamp 2013).

Scrambling shrubs lineage — We included 37 species of the two previous recognized genera (*Dissochaeta* and *Macrolenes*) of the scrambling shrubs in the molecular phylogenetic analyses (Table 6-1; Kartonegoro et al. 2018, 2019). Our results strongly support monophyly of these scrambling shrubs lineage in all three analyses (clade D; Fig. 6-3B). Within this lineage, *Macrolenes* is monophyletic while *Dissochaeta* s.l. (sensu Kartonegoro et al. 2018) is paraphyletic. Two alternative taxonomic solutions are possible for the scrambling shrubs lineage. The first option would be to recognize a widely circumscribed and large *Dissochaeta* s.l. (including *Dalenia*, *Diplectria* and *Macrolenes*), which would be highly supported by molecular data but defined by only a single morphological character, the scrambling habit. The second option would be to recognize four genera (*Dalenia*, *Diplectria*, *Macrolenes* and *Dissochaeta*) which would each be supported by molecular data and by several diagnostic and good morphological characters. After careful consideration we chose the second option as the more stable and feasible one, and recognize four genera within the scrambling shrub lineage. Below, we discuss these four genera.

***Dalenia* (*Dissochaeta* sect. *Dalenia*). —** The genus *Dalenia* was proposed by Korthals (1844) and accepted by some authors (Cogniaux 1891; Bakhuizen van den Brink 1943; Nayar 1966). Baillon (1877) regarded it as a synonym of *Dissochaeta* because of the distinct calyptriform hypanthium, but treated it as a section, *Dissochaeta* sect. *Dalenia*. In the previous account by Nayar (1966), three species are recognized in this genus; *Dalenia pulchra* Korth. (=*Dissochaeta pulchra* (Korth.) J.F.Maxwell), *Dalenia beccariana* and *Dalenia furfuracea* Ridl. (both =*Dissochaeta pubescens*). *Dalenia beccariana* was sampled in our molecular phylogeny. This species are sister to *Dalenia glabra* (= *Dissochaeta glabra* Merr., type of *Dissochaeta* sect. *Disparistemones*) with which they formed a monophyletic clade (Clade G; PP=1/BS=97/PBS=77; Fig. 6-3B).

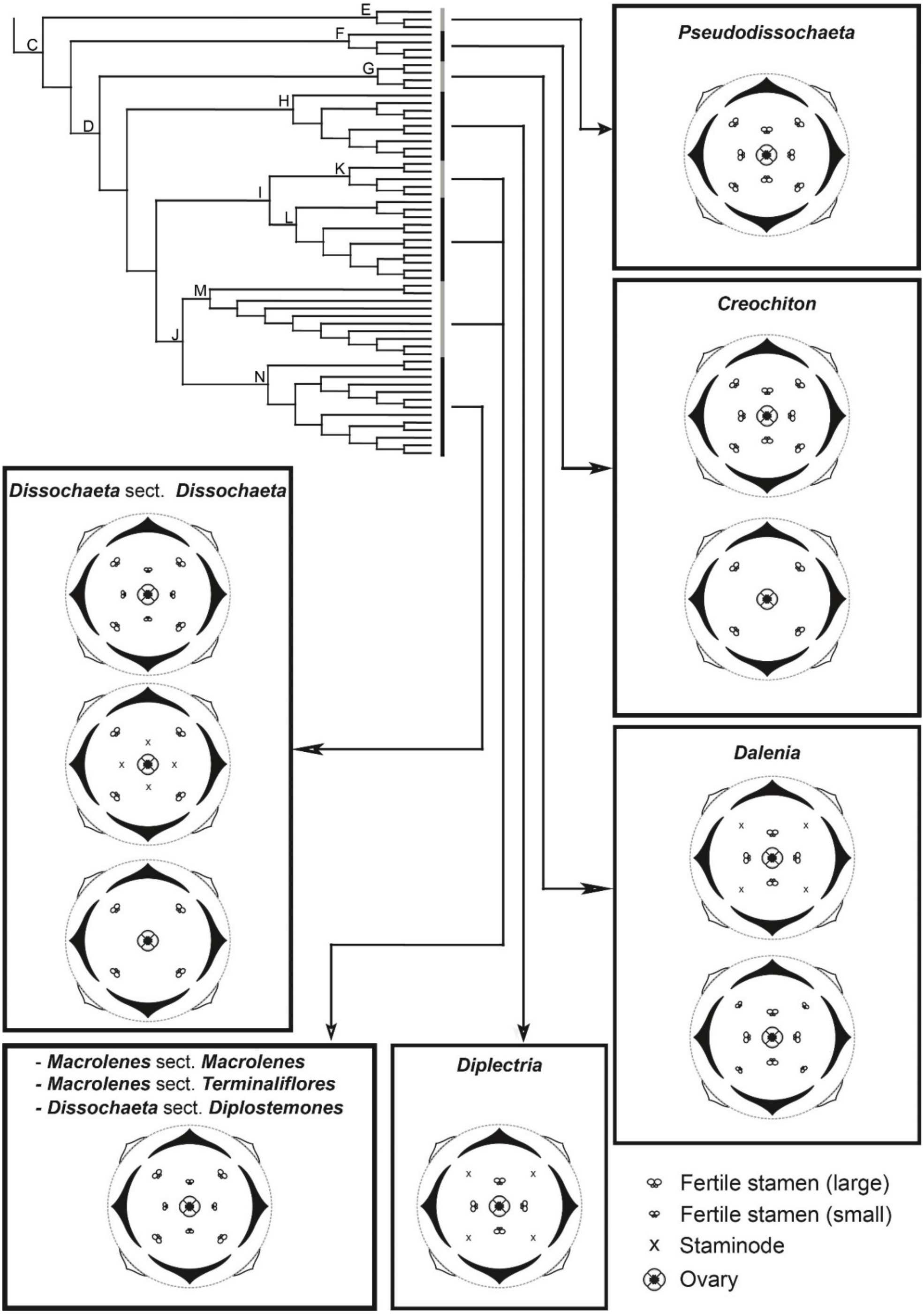


Fig. 6-4. Maximum likelihood (ML) phylogenetic cladogram of *Dissochaeta* alliance with an overview of floral characters including stamen dimorphism and anther fertility. Floral diagram drawn by A. Frenger.

Dalenia (clade G in Fig. 6-3B) can be morphologically distinguished by its interpetiolar growths (lobes, laminar, or pectinate crests) and leaf blade bases with a pair of glandular patches abaxially (Fig 6-5B-E). These interpetiolar growths are suggested to be helpful for climbing and stabilizing onto other plants (Clausing & Renner 2001a; Kartonegoro et al. 2018). The function of the foliar glandular patches in this group is still unknown (Maxwell 1984; Kartonegoro et al. 2018). Several field observations (AK, pers. obs.) indicate that the glands may attract insects like ants, which probably protect against herbivory. Staminal characteristics such as number and shapes of the fertile stamens seem to be variable in this lineage. All species have a fully truncate calyx and 4 well-developed oppositipetalous stamens (Figs. 6-1D–F, 6-4). Alternipetalous stamens vary considerably from forms with reduced and smaller thecae (⅓ of the oppositipetalous ones) to fully undeveloped thecae (staminodes) (Fig. 6-1F). Together with morphology, our molecular phylogenetic results support the reinstatement and expansion of the genus *Dalenia*.

Dissochaeta beccariana (=*Dalenia magnibracteata*) is included in this clade (Fig. 6-1D), even though it is morphologically intermediate between two genera, *Diplectria* and *Dissochaeta* s.str. (Kartonegoro et al. 2018). Although several species (including the type *Dalenia pulchra*; Fig. 6-1E) remain unsampled in a phylogenetic context, their morphology supports the placement in this expanded *Dalenia*. *Dissochaeta glandulosa* Merr., *Dissochaeta laevis* J.F.Maxwell, *Dissochaeta latifolia* (Triana) Karton., *Dissochaeta papuana* (Mansf.) Karton. and *Dissochaeta sarawakensis* (M.P.Nayar) J.F.Maxwell will now be treated in *Dalenia*. *Dissochaeta* sect. *Disparistemones* (Merrill 1917) will be treated as a synonym of *Dalenia*. *Dalenia* will include nine species (see Taxonomic treatment) mainly distributed in Borneo, and one species in New Guinea.

***Diplectria* (*Dissochaeta* sect. *Diplectria*). —** *Diplectria* was first proposed as a section of *Dissochaeta* (Blume 1831a), a view adopted by several authors (Naudin 1851; Miquel 1855). Reichenbach (1841) raised it to the generic rank. The genus was also formerly known as *Anplectrum* (Triana 1872; Cogniaux 1891; Ridley 1922; Merrill 1923), and later considered a synonym of *Diplectria* (Bakhuizen van den Brink 1943; Veldkamp et al. 1979; Maxwell 1980, 1984; Renner 1993). *Diplectria* consists of ca. 11 species distributed in Southeast Asia from Myanmar to New Guinea (Veldkamp et al. 1979). Morphologically, all the species in this genus can be recognized by having tubular or cyathiform hypanthia and (as in *Dalenia*) truncate sepals without any tips (Figs. 6-1G–H, 6-5G). The genus can also be recognized by having a well-developed oppositipetalous stamens with rostrate, thick and oblong anthers, while the alternipetalous whorl is not developed or reduced to staminodes (Figs. 6-1G–H & 6-4; Veldkamp et al. 1979; Maxwell 1984).

Our molecular phylogenetic analyses included three species (with the type *Diplectria divaricata* (Willd.) G.Don) and one undescribed species. The results support monophyly of *Dissochaeta* sect. *Diplectria* (clade H; Fig. 6-3B; PP=1/BS=100/PBS=100). Both morphological and molecular phylogenetic evidence support the reinstatement of the genus *Diplectria* as was earlier suggested (Bakhuizen van den Brink 1943; Veldkamp et al. 1979; Maxwell 1980, 1984; Renner 1993), and it now consists of seven species (see Taxonomic Treatment). The subtribe Diplectrinae (Maxwell 1980, 1984) is not supported in this study, and the undeveloped outer whorl of stamens used to diagnose this subtribe is shared with some species of *Dalenia*.

***Macrolenes*. —** The genus *Macrolenes* comprises ca. 17 species, restricted to west Malesia and Southern Thailand (Kartonegoro et al. 2019). *Macrolenes* has the following diagnostic characters: axillary inflorescences consisting of few-flowered cymes, diplostemonous flowers, robust hypanthia (more than 8 mm long; Kartonegoro et al. 2019), well-developed free calyx lobes, 8 subequal stamens in two whorls (alternipetalous and oppositipetalous) and all fertile (Figs. 6-1K–M, 6-4, 6-5I). Like some *Dissochaeta* species, the stamens of *Macrolenes* also have triangular or hastate dorsal and fimbriate ventral appendages (Bakhuizen van den Brink 1943; Nayar 1980; Kartonegoro et al. 2019). Unlike other allied genera, some species of *Macrolenes*, have hard berries, that are characterized by a persistent endocarp in which the ground tissue of the mesocarp and hypanthium is not fused and parts have a dense ring of sclereids in the ground tissue (Clausing et al. 2000; Kartonegoro et al. 2019). *Macrolenes* species also have a pair of hair cushion domatia near the abaxial leaf base (Fig. 6-5F).

Fig. 6-5. Some morphological characters of *Dissochaeta* alliance: **A-D.** Interpetiolar growth; **A,** ridges (*Dissochaeta annulata*); **B & C,** lobes (**B,** *Dalenia glabra*; **C,** *Dalenia pulchra*); **D,** pectinate (*Dalenia latifolia*); **E & F,** leaf domatia; **E,** glandular patches (*Dalenia glabra*); **F,** hair cushions (*Macrolenes pachygyna*); **G-I,** sepals; **G,** truncate (*Diplectria divaricata*); **H,** semi truncate (*Dissochaeta annulata*); **I,** free lobes (*Macrolenes nemorosa*). — Photographs by D.S. Penneys (A, B, E, G), J. Henrot (C), J.S. Wai (H), A. Kartonegoro (I). D taken from *Lobb s.n.*, F from *Carrick 1563* (both from Kew Herbarium)

We sampled 9 species of *Macrolenes* in our molecular phylogenetic analyses. The results (Fig. 6-3B) showed that *Macrolenes* is a well-supported monophyletic lineage (Clade L; Fig. 6-3B; PP=1/BS=95/PBS=87) and recovered as sister to the *Dissochaeta rostrata* complex

(Clade K; PP=0.99/BS=71/PBS=64). A recognition of *Macrolenes* at genus level would leave *Dissochaeta* paraphyletic. However, extending *Marcolenes* to include the *Dissochaeta rostrata* complex would create monophyletic, well-defined entities. Morphologically, the species of the *Dissochaeta rostrata* complex have terminal inflorescences (not axillary like the remaining *Macrolenes*), but share well-developed sepals, and the size of the hypanthia varies from small (less than 5 mm long) to robust (more than 9 mm long; Fig. 6-1I–J) of which the latter again resembles *Macrolenes*. Apart from these diagnostic features species of these two clades are morphologically similar. Based on our molecular phylogenetic results and morphology, we therefore suggest a broader circumscription of *Macrolenes* to include all the species in the *Dissochaeta rostrata* complex rather than recognize another distinct genus (Clade I; Fig. 6-3B). *Macrolenes*, as defined here, will include the five species of the *Dissochaeta rostrata* complex (clade L), and also another five species which are not included in the molecular analyses, that presumably are part of it based on morphological similarity of free sepals and 8 fertile stamens (*Dissochaeta alstonii* M.P.Nayar, *Dissochaeta atrobrunnea* G.Kadereit, *Dissochaeta floccosa* (J.F.Maxwell) Karton., *Dissochaeta johorensis* Furtado, and *Dissochaeta marumioides* Cogn.). The genus will include 27 species in total (see Taxonomic Treatment). Morphologically, *Macrolenes* has the following diagnostic characters: flowers with well developed free sepals and well developed curved 8 fertile stamens in 2 whorls (Figs. 6-4, 6-5I).

The *Dissochaeta rostrata* complex (clade K) and the *Macrolenes* s.str. clade (clade L) are also individually supported (Fig. 6-3B) and morphologically distinct. *Macrolenes* s.str. (clade L) has a pair of abaxial hair cushion domatia near the leaf base, axillary inflorescences and fimbriate filiform appendages on the connectives of the alternipetalous stamens. On the other hand, the *Dissochaeta rostrata* complex has terminal inflorescences, lacks the hair cushion domatia, and the alternipetalous stamens connectives usually have only biligulate or 4-ligulate appendages (Fig. 6-1I–J). We considered that the character differences between two groups are variability within the genus and not separation on the generic level. With additional evidence from the phylogenetic tree, we propose that *Macrolenes* s.str. and *Dissochaeta rostrata* complex be recognized as *Macrolenes* sect. *Macrolenes* and sect. *Terminaliflores*, respectively (see Taxonomic Treatment).

***Dissochaeta* s.str. —** *Dissochaeta* comprises ca. 40 species distributed from the Nicobar Islands, Myanmar, Indochina, Thailand, and throughout the Malesian Region (Maxwell 1984; Kartonegoro & Veldkamp 2010). The species can be identified by having conspicuous interpetiolar lines or crests (Fig. 6-5A), diplostemonous flowers, semi-truncate sepals with 4 small triangular tips (Fig. 6-5H), terminal inflorescences (except *Dissochaeta acmura* Stapf & M.L.Green and *Dissochaeta axillaris* Cogn., which have axillary inflorescences), and 8 unequal (dimorphic) stamens (Figs. 6-1N–T; Maxwell 1984; Kartonegoro & Veldkamp 2010; Kartonegoro et al. 2018). Similar to *Macrolenes*, the 4 alternipetalous stamens are larger and longer, they are known as the pollinating stamens, and the 4 oppositipetalous ones are smaller and shorter and known as the feeding stamens (Kadereit 2006, Kartonegoro & Veldkamp 2010; see Fig. 6-4). In a few species of *Dissochaeta* sect. *Dissochaeta* the oppositipetalous stamens are reduced to staminodes (<1/3 the size of the alternipetalous ones) or absent, with the flowers appearing to have only the 4 outer whorl stamens (Figs. 6-1Q–S, 6-4). Like in the other Dissochaeteae genera, the base of the stamens and the connective comes with an appendage. The appendages vary in shape and size, the dorsal appendage may be spur-like, triangular, hastate, or ligular, and the ventral one can be bisetose, bifid, or sometimes inappendiculate (Kartonegoro et al. 2018).

Our molecular analyses included 16 species of *Dissochaeta* s.str. (clade J), and some internal relationships were recovered (Fig. 6-3B). The clade contains all species of *Dissochaeta* sect. *Dissochaeta* and four other sections (*Diplostemones*, *Isostemones*, *Omphalopus*, *Anoplodissochaeta*) as well as the type of the genus, *Dissochaeta vacillans* (Blume) Blume (Cogniaux 1891; Maxwell 1980; Kartonegoro & Veldkamp 2010). To avoid the recognition of paraphyletic taxa (see under *Macrolenes*) and to classify into medium sized, well recognizable genera, the circumscription of *Dissochaeta* is narrower here than in previous treatments (see Taxonomic Treatment).

Within *Dissochaeta* s.str. lineage, two well-supported sublineages are evident in the phylogenetic analyses: *Dissochaeta* sect. *Diplostemones* (clade M; PP=1/BS=98/PBS=93) and *Dissochaeta* sect. *Dissochaeta* including three other sections (*Isostemones*, *Omphalopus*, and *Anoplodissochaeta*) (clade N; PP=1/BS=99/PBS=100). Although some other sections were recovered, they were poorly supported and nested within sect. *Dissochaeta*. As a result, we suggest the recognition of the two well-supported lineages as sections (sect. *Diplostemones* and sect. *Dissochaeta*) within *Dissochaeta* s.str.

Morphologically, *Dissochaeta* sect. *Diplostemones* can be distinguished by the robust hypanthia (6–15 mm long). The flowers have 8 slender (lanceolate-ligulate) dimorphic stamens of which the larger, alternipetalous ones are arcuate (Fig. 6-1N–O). The stamens of *Dissochaeta* sect. *Diplostemones* are similar to those of the *Dissochaeta rostrata* complex, which is now considered as part of *Macrolenes* but differ from the latter by having semi-truncate (not fully free) calyx lobes. *Dissochaeta* sect. *Dissochaeta* usually has much smaller hypanthia (2–5 mm long) and the stamens are ovate-oblong and erect (Fig. 6-1P–T). These erect stamens are unique to *Dissochaeta* within the Dissochaeteae. When there are 8 fertile stamens, they are usually subequal and dimorphic. Some species (e.g., *Dissochaeta gracilis* (Jack) Blume and *Dissochaeta inappendiculata* Blume) have the oppositipetalous stamens reduced to staminodes smaller in size (⅓ the size of the alternipetalous ones) (Fig. 6-1S). A few other species (e.g., *Dissochaeta biligulata* Korth., *Dissochaeta celebica* Blume, and *Dissochaeta fallax* (Jack) Blume) have the oppositipetalous stamens completely reduced and only 4 fertile alternipetalous stamens remain (Fig. 6-1Q–R). Most *Dissochaeta* species have ventrally biligulate or bisetose connective appendages, however, a few species (e.g., *Dissochaeta bakhuizenii* Veldkamp, *Dissochaeta fallax*, and *Dissochaeta inappendiculata*) are inappendiculate (Fig. 6-1S–T).

Conclusion

This study clarifies the circumscription of the tribe Dissochaeteae and the six monophyletic genera that it contains, namely; *Creochiton*, *Dalenia*, *Diplectria*, *Dissochaeta*, *Macrolenes*, and *Pseudodissochaeta*. The phylogenetic analyses presented here employed two nuclear ribosomal regions (ETS and ITS), and four chloroplast regions (*ndhF*, *psbK-psbL*, *rbcL*, and *rpl16*). Our results confirm earlier studies (Clausing & Renner 2001a; Zeng et al. 2016; Zhou et al. 2019b) that the Dissochaeteae s.l. is polyphyletic and that more distantly related genera such as the *Medinilla* alliance, *Dinophora*, and *Ochthocharis* should be excluded. As defined here, *Dalenia* and *Diplectria* are resurrected, *Macrolenes* is broadened to include species formerly placed in the *Dissochaeta rostrata* complex, and the core genus of the tribe, *Dissochaeta*, is somewhat narrowed.

Taxonomic Treatment

Tribe **Dissochaeteae** Triana in Bull. Congr. Int. Bot. Hort. Amsterdam 1865: 459. 1866 ≡ [Tribe Miconieae subtribe] Dissochaetinae Naudin, Ann. Sci. Nat., Bot. sér. 3, 14: 67. 1850. – Type: *Dissochaeta* Blume

Shrubs, erect, terrestrial, epiphytic, scramblers, or woody climbers; adventitious roots common; branches terete, glabrous or with stellate hairs and sometimes with simple, soft bristles. Wood vessel elements wide, with alternate inter-vessel pit, rays up to 7 cells wide. Branchlets terete to quadrangular, glabrous or sparsely to densely covered with stellate hairs and sometimes with soft, simple bristles; nodes swollen, with or without a pair of interpetiolar growth lines, ridges, crests, lobes, these laminar or pectinate. Leaves opposite; petioles well-developed or subsessile, terete with a dorsal groove, glabrous or with stellate hairs or bristly; blade thin, chartaceous to coriaceous, ovate to lanceolate or rarely suborbiculate, base cuneate, rounded to slightly cordate, rarely oblique, margin entire, rarely serrulate, apex acuminate; midnerves with 1–3 pairs of basal nerves and a pair of intramarginal nerves; secondary venation pinnate, nerves typically sunken above, slightly raised below; surfaces glabrous to stellately furfuraceous or bristly, indumentum mainly dense on the main nerves, abaxially sometimes with a pair of glandular patches or hair cushion domatia at base. Inflorescences terminal or axillary panicle of cymes, thyrses, rarely umbels, multi- or few-flowered; main axis terete or quadrangular, indumentum similar to branchlets, branching with 2–5 ramifications, cymules 3-flowered at end of branches; bracts and bracteoles paired at each node of the ramifications, thin to subcoriaceous, caducous or persistent, sometimes bracteoles fleshy, enveloping the flower buds. Flowers 4-merous, haplotemonous or diplostemonous; pedicels terete or sometimes not developed. Hypanthium campanulate, tubular, cyathiform, or urceolate, glabrous or with stellate hairs, often with simple glandular or barbed bristles, infrequently tuberculate. sepals completely truncate, with 4 small undulations or teeth, sometimes semi-truncate with 4 triangular tips, or free with well-developed rounded, triangular, or linear lobes; persistent at maturity. Petals elliptic to suborbicular, tip acute to rounded, base clawed, glabrous, generally thin, colourful, reflexed or flat at maturity, caducous after fertilisation. Stamens 8, iso- or dimorphic, equal to unequal, inserted in 2 whorls, outer alternate with the petals, inner opposite with the petals, all fertile or 1 whorl staminodal, sometimes only with 4 stamens; filaments flattened, glabrous; anthers 2-thecate, basifixed, rarely medifixed, smooth, rarely tesselate-reticulate, opening by single terminal pore, straight in bud, inserted in extra-ovarial chambers, slightly curved (sickle- or S-shaped) or straight when mature, ovoid or narrow lanceolate; connective with appendages, dorsally with a spuriform, hastate, or triangular crest, ventrally with a pair of auriculate, ligular to filiform appendages or fimbriate, rarely inappendiculate. Ovary inferior, ¼ to ¾ as long as hypanthium, apex glabrous to pubescent or bristly; locules 4, placenta axillar, rarely basal; style glabrous, curved distally, usually herkogamous; stigma minute, capitate; ovary concrescent with hypanthium with 4 or 8 septae, forming 4 or 8, shallow to deep, extra-ovarial chambers. Fruit a berry, globose to urceolate, exocarp thin, rarely woody, glabrous or with stellate hairs, frequently with barbed bristle hairs, dark purple to blackish when ripe, fleshy; sepals persistent. Seeds numerous, usually cuneate or cochleate, flat-topped, slightly curved, with smooth or papillose testa, hilum black.

Distribution — East Bhutan, northeast India, Southern China (incl. Hainan), Southeast Asia to Papua New Guinea (except eastern part of the Lesser Sunda Islands). Mostly found in the Malesian Region, especially in the everwet triangle of Sumatra, Malay Peninsula and Borneo. Occurring from sea level to ca. 2,000 m elevation.

Key to genera

1 Erect or epiphytic shrubs; interpetiolar ridge indistinct; stamens 8, rarely 4; isomorphic, equal to subequal 2
1 Scrambling shrubs with climbing habit; interpetiolar ridge distinct; stamens 8 or 4; when 8 dimorphic, unequal 3
2 Erect terrestrial shrubs; leaf margin serrulate, lateral nerves basally triplinerved; inflorescences paniculate cymes, thyrsoid; flowers with inconspicuous bracteoles; connective appendages ventrally bi-auriculate or bilobed .... **5. *Pseudodissochaeta***
2 Epiphytic shrubs; leaf margin entire, lateral nerves plinerved (side nerves starting above the base); inflorescences umbels; flowers with a pair of fleshy bracteoles; connective appendages ventrally biligulate or inappendiculate .... **1. *Creochiton***
3 Interpetiolar growth with lobes, laminar, or pectinate; leaves abaxially with a pair of glandular patches at base .... **2. *Dalenia***
3 Interpetiolar growth with lines or ridges; leaves abaxially without glandular patches at base 4
4 Calyx lobes free, distinct rounded, triangular or lanceolate in shape; apex acute or obtuse .... **5. *Macrolenes***
4 Calyx lobes truncate or partly truncate; apex acute or absent 5
5 Calyx lobes fully truncate; alternipetalous stamens staminodal, oppositipetalous fertile .... **3. *Diplectria***
5 Calyx lobes partly truncate; alternipetalous stamens fertile, oppositipetalous fertile or staminodal or absent .... **4. *Dissochaeta***

1. *Creochiton* Blume in Flora 14: 506. 1831 ≡ *Dissochaeta* sect. *Creochiton* (Blume) Baill., Hist. Pl. 7: 15. 1877 – Lectotype: (designated by Kartonegoro & Veldkamp in Blumea 58: 219. 2013): *Creochiton pudibundus* (Blume) Blume.
= *Enchosanthera* Guillaumin in Bull. Soc. Bot. France 60: 341. 1913 ≡ *Anplectrella* Furtado in Gard. Bull. Singapore 20: 106. 1963 – Type: E*nchosanthera anomala* (King & Stapf ex King) Guillaumin [≡ *Creochiton anomalus* (King & Stapf ex King) Veldkamp].
= *Eisocreochiton* Quisumb. & Merr. in Philipp. J. Sci. 37: 177. 1928 – Type: *Eisocreochiton bracteatus* Quisumb. & Merr. [≡ *Creochiton bracteatus* (Quisumb. & Merr.) Veldkamp].

Morphological diagnosis. – Epiphytic shrubs or woody climbers. Leaves subcoriaceous or chartaceous, nervation plinerved. Inflorescences axillary, umbellate, 3-5 flowers, haplo- or diplostemonous, rarely paniculate; bracteoles distinct, coriaceous, concave, enclosing the flower buds; flower with 4 or 8 fertile stamens, equal or unequal, connective dorsally spurred, ventrally biligulate or inappendiculate.

Creochiton anomalus (King & Stapf ex King) Veldkamp in Blumea 24: 438. 1979 ≡ *Anplectrum anomalum* King & Stapf ex King in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 69: 58. 1900 ≡ *Enchosanthera anomala* (King & Stapf ex King) Guillaumin in Bull. Soc. Bot. France 60: 341. 1913 ≡ *Anplectrella anomala* (King & Stapf ex King) Furtado in Gard. Bull. Singapore 20: 106. 1963 – Lectotype (designated by Veldkamp in Blumea 24: 438. 1979): Peninsular Malaysia, Perak, Goping, *King's collector 5779* (CAL; isolectotypes: K barcode K000859588!, K000859589!, K000859590!, L barcode L 0008838!, P barcode P02274804!, P02274805!).
Distribution. – Peninsular Malaysia & Sumatra.

Creochiton bibracteatus (Blume) Blume in Flora 14: 507. 1831 ≡ *Melastoma bibracteatum* Blume in Bijdr. Fl. Ned.-Ind 17: 1071. 1826 ≡ *Dissochaeta bibracteata* (Blume) Baill. in Hist. Pl. 7: 25. 1877 ≡ *Diplectria bibracteata* (Blume) Kuntze in Revis. Gen. Pl. 1: 246. 1891 – Lectotype (designated by Kartonegoro & Veldkamp in Blumea 58: 221. 2013): Java, *Blume s.n.* (L barcode L0008839!; isolectotype: L barcode L0931127!).
Distribution. – Java (West).

Creochiton bracteatus (Quisumb. & Merr.) Veldkamp in Blumea 24: 438. 1979 ≡ *Eisocreochiton bracteatus* Quisumb. & Merr. in Philipp. J. Sci. 37: 177. 1928 – **Lectotype (designated here):** Philippines, Luzon, Nueva Vizcaya, Mt. Alzapan, *Ramos & Edaño BS 45610* (US barcode 00120440 [image!]; isolectotypes: BM barcode BM000944491!, BO!, K barcode K000859580!]).
Distribution. – Philippines (Luzon).
Note. – Kartonegoro & Veldkamp (2013) refered to the holotype of the species in PNH but said that the original collection was lost. Therefore, we selected the lectotype of the extant collection from other herbaria.

Creochiton brevibracteatus Mansf. in Bot. Jahrb. Syst. 60: 135. 1925 – Holotype: New Guinea, East Sepik, April River, main camp, *Ledermann 8660* (B†).
Distribution. – Papua New Guinea.
Note. –No other specimens could be assigned to this taxon and, therefore, no neotype could be selected (Kartonegoro & Veldkamp, 2013).

Creochiton dipterus Elmer in Leafl. Philipp. Bot. 4: 1192. 1911 – **Neotype (designated here):** Philippines, Mindanao, Agusan, Mount Urdaneta, *Elmer 14119* (K barcode K000859581!; isoneotypes: E barcode E00504432!, MO barcode MO-2196137 [No. 748099; image!], US barcode US02927693 [image!]).
Distribution. – Philippines.
Note. – Neither the original type collection of the species (*Elmer 9813*), nor any other associated specimens could be found in any herbaria, because they were probably destroyed during the Second World War when PNH burned down. We hereby designate another specimen (*Elmer 14119*), housed at K and cited by Elmer, as the neotype.

Creochiton furfuraceus (M.P.Nayar) Veldkamp in Blumea 24: 438. 1979 ≡ *Eisocreochiton furfuraceus* M.P.Nayar in J. Bombay. Nat. Hist. Soc. 67: 88. 1970 – Holotype: Borneo, Sarawak, 3rd Division, Kapit District, Belaga Subdistrict, Rejang River, *Jacobs 5293* (K barcode K000859586!; isotypes: CANB, G , L barcode L0008840!, S, SAR, US).
Distribution. – Borneo.

Creochiton ledermannii Mansf. in Bot. Jahrb. Syst. 60: 135. 1925 – Lectotype (designated by Kartonegoro & Veldkamp in Blume 58: 223. 2013): New Guinea, Sepik, Felsspitze, *Ledermann 12943* (B; isolectotype: L barcode L0931128!).
Distribution. – New Guinea.

Creochiton monticola (Ridl.) Veldkamp in Blumea 24: 433. 1979 ≡ *Anplectrum monticola* Ridl. in Kew Bull. 1: 31. 1946 ≡ *Eisocreochiton monticola* (Ridl.) M.P.Nayar in J. Bombay Nat. Hist. Soc. 67: 89. 1970 – Lectotype (designated here): Borneo, Sarawak, Mt. Benkayang, *Brooks 50* (K barcode K000859585!; isolectotype BO!).
Distribution. – Borneo.

Note. – Kartonegoro & Veldkamp (2013) did not select the lectotype of the species from the extant collections. Therefore, we selected one of the lectotypes of the extant collection from K ew herbarium (K).

Creochiton novoguineensis (Baker f.) Veldkamp & M.P.Nayar in Blumea 24: 438. 1979 ≡ *Dissochaeta novoguineensis* Baker f. in J. Bot. 61(Suppl.): 21. 1923 – Lectotype (designated by Veldkamp in Blumea 24: 438. 1979): New Guinea, Central District, Sogeri Region, Mt. Wori-Wori, *Forbes 708* (BM barcode BM000944490!; isolectotypes: BM barcode BM001190923!, E barcode E00288097!, K barcode K000859576!, L barcode L0008844!, L0008845!, L0008847!, P barcode P02274803 [image!]).
Distribution. – New Guinea.

Creochiton pudibundus (Blume) Blume in Flora 14: 506. 1831 ≡ *Melastoma pudibundum* Blume, Catalogus: 71. 1823 ≡ *Diplectria pudibunda* (Blume) Kuntze in Revis. Gen. Pl. 1: 246. 1891 – Lectotype (designated by Kartonegoro & Veldkamp in Blumea 58: 225. 2013): Java, Mt. Salak, Cicalobak, *Blume s.n.* (L barcode L0008850!; isolectotypes: BO!, L barcodes L0537327!, L0008849!).
Distribution. – Java (West).

Creochiton roseus Merr. in Publ. Bur. Sci. Gov. Lab. 29: 32. 1905 – **Lectotype (designated here):** Philippines, Mindanao, Davao District, Todaya, *Copeland 1297* (US barcode US00120527 [image!]; isolectotypes K barcode K000859579!, NY barcode 00221643 [image!]).
Distribution. – N Sulawesi and Philippines (Mindanao).
Note. – Merill (1905) did not specify the holotype of this species, therefore, from among all extant syntype collections, we selected US specimen as the lectotype.

Creochiton turbinatus (J.F.Maxwell) Karton. in Blumea 58: 226. 2013 ≡ *Creochiton ledermannii* var. *turbinata* J.F.Maxwell in Gard. Bull. Singapore 33: 323. 1980 – Holotype: New Guinea, West Papua Province, E of Sorong, Warsamson Valley, Asbakin, *Schram BW 12260* (L barcode L0008841!; isotypes: A, BO!, BRI barcode BRI-AQ0060033 [image!], CANB, K, LAE, MAN).
Distribution. – New Guinea (West Papua).

2. *Dalenia* Korth., Verh. Nat. Gesch. Ned. Bezitt., Bot.: 243. 1844 ≡ *Dissochaeta* sect. *Dalenia* (Korth.) Baill., Hist. Pl. 7: 51. 1877 – Type: *Dalenia pulchra* Korth.
= *Dissochaeta* sect. *Disparistemones* Merr. in J. Straits Branch Roy. Asiat. Soc. 76: 101. 1917 – Type: *Dissochaeta glabra* Merr. [≡ *Dalenia glabra* (Merr.) Karton.].

Morphological diagnosis. – Woody climbers with scrambling growth; nodes swollen with distinct interpetiolar growth, lobes, laminate or pectinate. Leaves at base with pair of glandular patches adaxially. Flowers diplostemonous, with cyathiform or tubular hypanthium, calyx lobes truncate with 4 shallow undulations. Stamens 8, unequal, alternipetalous smaller, fertile or reduced into staminodes, oppositipetalous larger, fertile.

Dalenia beccariana (Cogn.) M.P.Nayar in Kew Bull. 20: 157. 1966 ≡ *Anplectrum beccarianum* Cogn. In Candolle & Candolle, Monogr. Phan. 7: 568. 1891 ≡ *Diplectria beccariana* (Cogn.) Kuntze in Revis. Gen. Pl. 1: 246. 1891 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 126. 2018): Borneo, Sarawak, *Beccari PB 809* (FI

barcode FI008755 [image!]; isolectoypes: BR barcode 000005188895 [image!], K barcode 000859574!, K000859575!).
Distribution. – Borneo.

Dalenia glabra (Merr.) Karton., **comb. nov.** ≡ *Dissochaeta glabra* Merr. in J. Straits Branch Roy. Asiat. Soc. 76: 101. 1917 ≡ *Diplectria glabra* (Merr.) M.P.Nayar in Blumea 24: 421. 1979 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 78. 2018): Borneo, Sabah, Kalabakan, Pinayas River, *Villamil 242* (PNH no. 32349 [image!]; isolectotypes: K!, US barcode US00120530 [image!]).
Distribution. – Borneo.

Dalenia glabra var. ***kinabaluensis*** (Veldkamp) Karton., **comb. nov.** ≡ *Diplectria glabra* ssp. *kinabaluensis* Veldkamp in Blumea 24: 422. 1979 ≡ *Diplectria glabra* var. *kinabaluensis* (Veldkamp) J.F.Maxwell in Gard. Bull. Singapore 33: 313. 1980 ≡ *Dissochaeta glabra* var. *kinabaluensis* (Veldkamp) Karton. in PhytoKeys 107: 81. 2018 – Holotype: Borneo, Sabah, Mount Kinabalu, Sosopodon near Kundasang, *Mikil SAN 46742* (L barcode L 0008869!; isotypes: K barcode K000859551!, L barcode L0008870!, SAN).
Distribution. – Borneo (Sabah).

Dalenia glandulosa (Merr.) Karton., **comb. nov.** ≡ *Dissochaeta glandulosa* Merr. in Univ. Calif. Publ. Bot. 15: 224. 1929 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 85. 2018): Borneo, Sabah, Sandakan, *Elmer 20259* (BO No. BO-1421691!; isolectotypes: BISH barcode BISH1003260 [image!], BM barcodes BM001190924!, BM001190925!, BR barcode 00000522241 [image!], BRI barcode BRI-AQ0023052 [image!], C barcode C10014564 [image!], CAS barcode 0033425 [image!], CM barcode 1527 [image!], F barcode V0063526F [No. 530617, image!], GH barcode 00072204, 00072205 [images!], HBG barcode HB-G514873 [image!], K barcode K000859503!, L barcode L0537261!, MICH barcode 1111782 [image!], NY barcode 00228564 [image!], PH barcode 00009602, 00009603 [images!], S No. S-G-2104 [image!], U barcode U0124130!).
Distribution. – Borneo.

Dalenia laevis (Ohwi ex J.F.Maxwell) Karton., **comb. nov.** ≡ *Dissochaeta laevis* Ohwi ex J.F.Maxwell in Gard. Bull. Singapore 33: 315. 1980 – Holotype: Borneo, East Kalimantan, West Kutai, Long Petah, *Endert 3127* (L barcode L0537281!; isotypes: BO No. BO-1760872!, K barcode K000859490!).
Distribution. – Borneo.

Dalenia latifolia (Triana) Karton., **comb. nov.** ≡ *Anplectrum latifolium* Triana in Trans. Linn. Soc. London 28: 85, t. 7, f. 90d. 1872 ≡ *Diplectria latifolia* (Triana) Kuntze in Revis. Gen. Pl. 1: 246. 1891 ≡ *Dissochaeta latifolia* (Triana) Karton. in PhytoKeys 107 (2018) 105 – Lectotype (designated by Veldkamp et al. in Blumea 24: 412. 1979): Borneo, *Lobb s.n.* (K barcode K000859553!).
Distribution. – Borneo.

Dalenia magnibracteata (Bakh.f.) Karton., **comb. nov.** ≡ *Neodissochaeta magnibracteata* Bakh.f. in Contr. Melastom. 142. 1943 – Holotype: Borneo, West Kalimantan, Sungei Kenepai, *Hallier 2013* (L barcode L0537263!; isotypes BO Nos. BO-1865993!, BO-1865994!, BO-1865995!, K barcode K000859505!).

= *Dissochaeta beccariana* Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 559. 1891 ≡ *Neodissochaeta beccariana* (Cogn.) M.P.Nayar in Kew Bull. 20: 159. 1966 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 45. 2018): Borneo, Sarawak, Santubong, *Beccari PB 2190* (FI barcode FI007928 [image!]; isolectotype: K barcode K000859504!).

Distribution. – Borneo.

Note. – The specific epithet *magnibracteata*, the first available heterotypic synonym, is used here for the new combination because the species name *Dalenia beccariana* already exists.

Dalenia papuana (Mansf.) Karton., **comb. nov.** ≡ *Anplectrum papuanum* Mansf. in Bot. Jahrb. Syst. 60: 115. 1925 ≡ *Diplectria papuana* (Mansf.) Bakh.f. in Contr. Melastom. 202. 1943 ≡ *Diplectria glabra* var. *papuana* (Mansf.) J.F.Maxwell in Gard. Bull. Singapore 33: 313. 1980 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 121. 2018): New Guinea, Papua Province, Siriwo River, *Janowsky 132* (L barcode L0008872!; isolectotype: BO No. BO-1865947!).

Distribution. – New Guinea (Indonesian Papua).

Dalenia pulchra Korth., Verh. Nat. Gesch. Ned. Bezitt., Bot.: t. 58. 1842 ≡ *Dalenia speciosa* Korth., Verh. Nat. Gesch. Ned. Bezitt., Bot. 244. 1844 ≡ *Dalenia korthalsii* Blume, Mus. Bot. 1: 39. 1849 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 129. 2018): Borneo, Central Kalimantan, Tewe River, *Korthals s.n.* (L barcode L0537210!; isolectotypes: L barcodes L0537211!, L0729471!, L0729472!, L0729473!, P barcode P02274827 [image!]).

Distribution. – Borneo.

Dalenia sarawakensis (M.P.Nayar) Karton., **comb. nov.** ≡ *Neodissochaeta sarawakensis* M.P.Nayar in Bull. Bot. Surv. India 11: 195, pl. 1. 1969 ≡ *Dissochaeta sarawakensis* (M.P.Nayar) J.F.Maxwell in Gard. Bull. Singapore 33: 321. 1980 – Holotype: Borneo, Sarawak, Pengkulu Ampat, *Haviland 69* (K barcode K000859625!).

Distribution. – Borneo (Brunei & Sarawak).

3. *Diplectria* (Blume) Rchb., Deut. Bot. Herb.-Buch. 174. 1841 ≡ *Dissochaeta* Blume sect. *Diplectria* Blume in Flora 14: 501. 1831 – Lectotype (designated by Veldkamp et al. in Blumea 24: 410. 1979): *Diplectria cyanocarpa* (Blume) Kuntze [≡ *Diplectria divaricata* (Willd.) Kuntze].

= *Aplectrum* Blume in Flora 14: 502. 1831 ≡ *Anplectrum* A.Gray in U.S. Expl. Exped., Phan. 1: 597. 1854. ≡ *Backeria* Bakh.f., Contr. Melastom.: 130. 1943 – Lectotype (designated by Veldkamp et al. in Blumea 24: 410. 1979): *Aplectrum viminale* (Jack) Blume [≡ *Diplectria viminalis* (Jack) Kuntze].

Morphological diagnosis. – Woody climbers with scrambler growth; nodes swollen with indistinct interpetiolar growth, lines or ridges. Leaves with curved petiole, sometimes pubescent or bristly. Flowers diplostemonous, with cyathiform or tubular hypanthium, calyx lobes truncate with 4 small undulation tips. Stamens 8, unequal, alternipetalous reduced to staminodes, oppositipetalous larger, fertile.

Diplectria barbata (Triana ex C.B.Clarke) Franken & M.C.Roos in Blumea 24: 415, f. 3A. 1979 ≡ *Anplectrum barbatum* Triana ex C.B.Clarke in Hooker, Fl. Brit. India 2: 546. 1879 ≡ *Backeria barbata* (Triana ex C.B.Clarke) Raizada in Indian Forester 94: 435. 1968 ≡ *Dissochaeta barbata* (Triana ex C.B.Clarke) Karton. in PhytoKeys 107: 43. 2018 – Holotype: Burma, Martaban, Chappedong, *Wallich 4082* (K-W barcode K000859568!).
Distribution. – Myanmar, S China, Indochina, N Thailand.

Diplectria conica Bakh. f., Contr. Melastom. 202. 1943 ≡ *Dissochaeta conica* (Bakh.f.) Clausing in Santisuk & Larsen, Fl. Thailand 7: 423. 2001 – Holotype: Sumatra, West Sumatra Province, Agam, Brani, *Bünnemeijer 3094* (L barcode L0537295!; isotypes: BO Nos. BO-1865987!, BO-1865988!, L barcode L0537294!).
Distribution. – Peninsular Malaysia, Sumatra & Java.

Diplectria divaricata (Willd.) Kuntze in Revis. Gen. Pl. 1: 246. 1891 ≡ *Melastoma divaricatum* Willd. in Sp. Pl. 2: 596. 1799 ≡ *Dissochaeta divaricata* (Willd.) G.Don in Gen. Hist. 2: 783. 1832 ≡ *Anplectrum divaricatum* (Willd.) Triana in Trans. Linn. Soc. London 28: 84. 1872 ≡ *Backeria divaricata* (Willd.) Raizada in Indian Forester 94: 435. 1968 – Lectotype (designated by Veldkamp et al. in Blumea 24: 417. 1979): India Orientali, *Klein 2 “8218” in Herb. Rottler* (B-W barcode B -W 08218-01 0 [image!]; isolectotypes C barcodes C10014562, C10014563 [images!], K barcode K000859557!, L barcode L0008867!).
Distribution. – From Myanmar to Papua New Guinea.

Diplectria maxwellii Karton. in Kew Bull. 73, 23: 1. 2018 ≡ *Dissochaeta maxwellii* (Karton.) Karton. in PhytoKeys 107: 114. 2018 – Holotype: Borneo, Sarawak, Kapit, batang Balleh, Nanga Serani, *Runi et al. S.63137* (K barcode K000566618!; isotypes: KEP barcode 43526 [image!], L 2D-code L.3908632!, SAN [images!], SAR).
Distribution. – Borneo (Sarawak).

Diplectria micrantha Veldkamp in Blumea 24: 422, f. 5B. 1979 ≡ *Diplectria glabra* var. *micrantha* (Veldkamp) J.F.Maxwell in Gard. Bull. Singapore 33: 313. 1980 ≡ *Dissochaeta micrantha* (Veldkamp) Karton. in PhytoKeys 107: 115. 2018 – Holotype: Borneo, Sabah, Mount Kinabalu, Sosopodon, *Sario SAN 28959* (L barcode L0008871!; isotypes: K barcode K000859550!, SAN).
Distribution. – Borneo.

Diplectria stipularis (Blume) Kuntze in Revis. Gen. Pl. 1: 246. 1891 ≡ *Melastoma stipulare* Blume in Bijdr. Fl. Ned.-Ind. 17: 1073. 1826 ≡ *Aplectrum stipulare* (Blume) Blume in Flora 14: 503. 1831 ≡ *Anplectrum stipulare* (Blume) Triana in Trans. Linn. Soc. London 28: 84. 1872 ≡ *Backeria stipularis* (Blume) Bakh.f. in Contr. Melastom. 132. 1943 ≡ *Dissochaeta stipularis* (Blume) Clausing in Santisuk & Larsen, Fl. Thailand 7(3): 431. 2001 – Lectotype (designated by Veldkamp & al. in Blumea 24: 424. 1979): Java, Gunung Seribu, *Blume 857* (L barcode L0537306!; isolectotypes L barcodes L0537304!, L0537305!, P barcode P02274923 [image!]).
Distribution. – Thailand, Peninsular Malaysia, Sumatra, Java, Borneo and Philippines (Palawan).

Diplectria viminalis (Jack) Kuntze in Revis. Gen. Pl. 1: 246. 1891 ≡ *Melastoma viminale* Jack in Trans. Linn. Soc. London 14: 16. 1823 ≡ *Aplectrum viminale* (Jack) Blume in Flora

14: 502. 1831 ≡ *Anplectrum viminale* (Jack) Triana in Trans. Linn. Soc. London 28: 84. 1872 ≡ *Backeria viminale* (Jack) Bakh.f., Contr. Melastom. 133. 1943 ≡ *Dissochaeta viminalis* (Jack) Clausing in Santisuk & Larsen, Fl. Thailand 7(3): 433. 2001 – Neotype (designated by Veldkamp & al. in Blumea 24: 427. 1979): Java, West Java, Gunung Seribu, *Blume 856* (L barcode L0008883!; isoneotype L barcode L0008882!).
Distribution. – Thailand, Malay Peninsula, Sumatra, Java, Borneo and New Guinea.

4. *Dissochaeta* Blume in Flora 14: 492. 1831 – Type (designated by Kartonegoro & Veldkamp in Reinwardtia 13: 128. 2010): *Dissochaeta vacillans* (Blume) Blume.
= *Omphalopus* Naudin in Ann. Sci. Nat., Bot. sér. 3, 15: 277. 1851 – Type (designated by Bakhuizen van den Brink in Contr. Melastom. 118. 1943): *Omphalopus fallax* (Jack) Naudin [≡*Dissochaeta fallax* (Jack) Blume].
= *Neodissochaeta* Bakh.f., Contr. Melastom.: 134. 1943 – Type (designated by Kartonegoro & Veldkamp in Reinwardtia 13: 128. 2010): *Neodissochaeta gracilis* (Jack) Bakh.f. [≡*Dissochaeta gracilis* (Jack) Blume].

Morphological diagnosis. – Woody climbers with scrambler growth; nodes swollen with indistinct interpetiolar growth, lines or ridges. Leaves with straight petiole, glabrous, sometimes pubescent or bristly. Flowers haplo- or diplostemonous, with campanulate hypanthia, calyx lobes semi-truncate, united at base with 4 triangular tips. Stamens 4 or 8, unequal, alternipetalous larger, fertile, oppositipetalous smaller, reduced to staminodes or absent.

Dissochaeta sect. ***Diplostemones*** Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 555. 1891 – **Type (designated here):** *Dissochaeta annulata* Hook.f. ex Triana.

Morphological diagnosis. – Inflorescences terminal. Flowers diplostemonous. Hypanthium campanulate or urceolate, densely covered with stellate hairs, infrequently with sparse bristle hairs. Sepals truncate at base, tip triangular. Stamens 8, dimorphic, unequal or subequal; alternipetalous longer, sickle-shaped; oppositipetalous shorter, S-shaped; anthers curved; connective appendages dorsally triangular, ventrally biligulate.

Dissochaeta acmura Stapf & M.L.Green in Bull. Misc. Inform., Kew 1913: 42. 1913 – Lectotype (designated by Kartonegoro & al. in PhytoKeys 107: 27. 2018): Philippines, Luzon, Albay, *Cuming 2838* (K barcode K000859613!).
Distribution. – Philippines.

Dissochaeta annulata Hook.f. ex Triana in Trans. Linn. Soc. London 28: 83, t. 7, f. 89a. 1872 ≡ *Diplectria annulata* (Hook.f. ex Triana) Kuntze in Revis., Gen. Pl. 1: 246. 1891 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 32. 2018): Peninsular Malaysia, Penang, Penang Hill, *Griffith KD 2268* (K barcode K000859545!; isolectotype: K barcode K000859544!).
Distribution. – Sumatra, Malay Peninsula, Borneo.

Dissochaeta axillaris Cogn. in Bot. Jahrb. Syst. 48: 108. 1912 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 38. 2018): Borneo, Central Kalimantan, Semurung, Sungei Tarik, *Winkler 3033* (L barcode L0652534!; isolectotypes: BM barcode BM000944485!, BO!, BR barcode 000005188253 [image!], K barcode K000859508!, WRSL).
Distribution. – Borneo and Philippines (Sulu).

Dissochaeta bracteata (Jack) Blume in Flora 14: 495. 1831 ≡ *Melastoma bracteatum* Jack in Trans. Linn. Soc. London 14: 9. 1823 – Neotype (designated by Kartonegoro & Veldkamp in Reinwardtia 13: 130. 2010): Peninsular Malaysia, Penang, *Wallich 4044* (K-W barcode K000859538!; isoneotypes: BM!, K-W barcode K000859537!).

Distribution. – Thailand, Peninsular Malaysia, Sumatra, Java, Borneo, Philippines and Moluccas.

Dissochaeta griffithii (M.P.Nayar) Karton. in PhytoKeys 107: 91. 2018 ≡ *Macrolenes griffithii* M.P.Nayar in J. Jap. Bot. 55: 47. 1980 ≡ *Dissochaeta annulata* var. *griffithii* (M.P.Nayar) J.F.Maxwell in Gard. Bull. Singpore 33: 313. 1980 – Holotype: Peninsular Malaysia, Malacca, *Griffith KD 2269* (K barcode K001096571!).

Distribution. – Peninsular Malaysia.

Dissochaeta leprosa (Blume) Blume in Flora 14: 494. 1831 ≡ *Melastoma leprosum* Blume in Bijdr. Fl. Ned.-Ind. 17: 1068. 1826 ≡ *Omphalopus leprosus* (Blume) Naudin in Ann. Sci. Nat., Bot. sér. 3, 15: 278. 1851 ≡ *Dissochaeta intermedia* var. *leprosa* (Blume) J.F.Maxwell in Gard. Bull. Singapore 33: 315. 1980 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 107. 2018): Java, West Java, Mount Gede, *Kuhl & Van Hasselt s.n.* (L barcode L0008890!; isolectotypes: K barcode K000859492!, L barcodes L0822675!, L0822676!).

Distribution. – Sumatra (West), Java, Lesser Sunda Islands (Bali).

Dissochaeta malayana Furtado in Gard. Bull. Singapore 20: 110. 1963 ≡ *Dissochaeta rostrata* var. *malayana* (Furtado) J.F.Maxwell in Gard. Bull. Singapore 33: 320. 1980 – Holotype: Peninsular Malaysia, Terengganu, Kemaman, Bukit Kajang, *Corner SFN 30381* (SING barcode SING0051682!).

Distribution. – Peninsular Malaysia (Terengganu).

Dissochaeta nodosa Korth., Verh. Nat. Gesch. Ned. Bezitt., Bot.: 239. 1844 ≡ *Aplectrum nodosum* (Korth.) Blume in Mus. Bot. 1, 3: 37. 1849 ≡ *Anplectrum nodosum* (Korth.) Triana in Trans. Linn. Soc. London 28: 84. 1872 – Lectotype (designated by Kartonegoro & Veldkamp in Reinwardtia 13: 143. 2010): Sumatra, West Sumatra, Indrapura, *Korthals s.n.* (L barcode L0537233!; isolectotype L barcode L0537232!).

Distribution. – Sumatra.

Dissochaeta pallida (Jack) Blume in Flora 14: 500. 1831 ≡ *Melastoma pallidum* Jack in Trans. Linn. Soc. London 14: 12. 1823 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 118. 2018): Peninsular Malaysia, Penang, *Jack 55* (BM barcode BM000944482!).

Distribution. – Malay Peninsula, Sumatra and Borneo.

Dissochaeta punctulata Hook. f. ex Triana in Trans. Linn. Soc. London 28: 83. 1872 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 132. 2018): Peninsular Malaysia, Malacca, *Griffith KD 2291* (K barcode K000859531!; isolectotype: BM!).

Distribution. – Malay Peninsula, Sumatra (Riau Archipelago).

Dissochaeta robinsonii Merr. in Philipp. J. Sci., C 11: 198. 1916 ≡ *Dissochaeta annulata* var. *robinsonii* (Merr.) Bakh. f., Contr. Melastom. 231. 1943 – Lectotype (designated by

Kartonegoro et al. in PhytoKeys 107: 32. 2018): Moluccas, Ambon, Hitumessen, *Robinson 2024* (BO No. BO-1747982!; isolectotypes: BM barcode BM000944486!, GH barcode GH00072242 [image!], K barcode K000859510!, L barcode L0537257!, NY barcode 00228565 [image!], P barcode P02274818 [image!], US barcode US00120532 [image!]).
Distribution. – SE Sulawesi, Moluccas, New Guinea.

Dissochaeta spectabilis J.F.Maxwell in Gard. Bull. Singapore 33: 321. 1980 ≡ *Dissochaeta marumioides* Furtado in Gard. Bull. Singapore 20: 111. 1963, non Cogn. 1891 – Holotype: Peninsular Malaysia, Pahang, Cameron Highlands, Tanah Rata, *Johnston 86* (SING barcode SING0051582!).
Distribution. – Peninsular Malaysia (Pahang, Selangor), Sumatra (West).

Dissochaeta sect. ***Dissochaeta*** – Type: *Dissochaeta vacillans* (Blume) Blume.
= *Omphalopus* Naudin in Ann. Sci. Nat., Bot. sér. 3, 15: 277. 1851. ≡ *Dissochaeta* sect. *Omphalopus* (Naudin) Baill. in Hist. Pl. 7: 51. 1877 – Type: *Dissochaeta fallax* (Jack) Blume.
= *Dissochaeta* sect. *Anoplodissochaeta* Baill. in Hist. Pl. 7: 51. 1877 – Type: *Dissochaeta inappendiculata* Blume.
= *Dissochaeta* sect. *Isostemones* Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 561. 1891 – Type (designated by Kartonegoro & Veldkamp in Reinwardtia 13: 128. 2010): *Dissochaeta monticola* Blume [≡ *Dissochaeta intermedia* Blume].
= *Dissochaeta* sect. *Dissochaetopsis* Cogn. in A.DC. & C.DC, Monogr. Phan. 7: 563. 1891. – Type: *Dissochaeta schumannii* Cogn.

Morphological diagnosis. – Inflorescences terminal. Flowers haplo- or diplostemonous. Hypanthium campanulate, glabrous or densely covered with stellate hairs. Sepals truncate with 4 small triangular tips. Stamens 4 or 8, dimorphic, unequal; alternipetalous fertile; oppositipetalous, shorter, staminodal or absent; anthers straight; connective appendages dorsally triangular, ventrally biligulate or inappendiculate.

Dissochaeta angiensis Kaneh. & Hatus. ex Ohwi in Bot. Mag. (Tokyo) 57: 5. 1943 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 30. 2018): New Guinea, West Papua Province, Arfak Mts., Angi, track Lake Gita from Momi, *Kanehira & Hatusima 13374* (FU; isolectoype: L barcode L0537256!).
Distribution. – Moluccas, New Guinea.

Dissochaeta bakhuizenii Veldkamp in Blumea 24: 443. 1979 – Holotype: Sumatra, West Sumatra Province, Ophir District, Tanang Talu, *Bünnemeijer 1053* (L barcode L0537231!; isotype: BO No. BO-1744599!, BO-1747935!, PNH).
Distribution. – Peninsular Malaysia, Sumatra & Java.

Dissochaeta biligulata Korth., Verh. Nat. Gesch. Ned. Bezitt., Bot.: 240. 1844 ≡ *Anplectrum biligulatum* (Korth.) Triana in Trans. Linn. Soc. London 28: 85. 1872 ≡ *Diplectria biligulata* (Korth.) Kuntze in Revis. Gen. Pl. 1: 246. 1891 ≡ *Neodissochaeta biligulata* (Korth.) Bakh.f., Contr. Melastom. 141. 1943 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 47. 2018): Sumatra, West Sumatra Province, Gunung Paauw, *Korthals s.n.* (L barcode L0537285!; isolectotype: L barcode L0537284!).
Distribution. – Myanmar, Nicobar Islands, Thailand, Indochina, Malay Peninsula, Sumatra, Borneo, and Philippines (Palawan).

Dissochaeta brassii (M.P.Nayar) Karton. in PhytoKeys 107: 55. 2018 ≡ *Neodissochaeta brassii* M.P.Nayar in Kew Bull. 20: 160. 1966 – Holotype: Papua New Guinea, Woodlark Island, Kulumadau, *Brass 28743* (K barcode K000859607!; isotype: L barcode L0537255!).
Distribution. – Papua New Guinea.

Dissochaeta celebica Blume in Mus. Bot. 1, 3: 36. 1849 ≡ *Neodissochaeta celebica* (Blume) Bakh.f. in Contr. Melastom. 141. 1943 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 57. 2018): Sulawesi, North Sulawesi, Tomohon, Mount Mahawu, *Forsten 305* (L barcode L0537287!; isolectotype: L barcode L0625953!).
Distribution. – Philippines (Mindanao), Sulawesi.

Dissochaeta celebica var. ***longilobata*** Karton. in PhytoKeys 107: 59. 2018 –Holotype: Sulawesi, Central Sulawesi, Mount Roreka Timbu, *van Balgooy 3205* (BO; isotypes: K, L barcode L0652533!).
Distribution. – Sulawesi (Central).

Dissochaeta cumingii Naudin in Ann. Sci. Nat., Bot. sér. 3, 15: 75. 1851 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 64. 2018): Philippines, Luzon, Albay Province, *Cuming 1344* (P barcode P02274812 [photo!]; isolectotypes: BM barcode BM001190926!, K barcodes K000859608!, K000859609!, L barcode L0537227!).
Distribution. – Philippines (Luzon).

Dissochaeta densiflora Ridl. in Kew Bull 1: 32. 1946 ≡ *Dissochaeta rostrata* var. *densiflora* (Ridl.) J.F.Maxwell in Gard. Bull. Singapore 33: 319. 1980 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 65. 2018): Borneo, Sarawak, Saribas, Sungei Plandok, *Haviland 1550* (K barcode K000859631!; isolectotype: SAR).
Distribution. – Borneo.

Dissochaeta fallax (Jack) Blume in Flora 14: 493. 1831 ≡ *Melastoma fallax* Jack in Trans. Linn. Soc. London 14: 13. 1823 ≡ *Omphalopus fallax* (Jack) Naudin in Ann. Sci. Nat., Bot. sér. 3, 15: 277. 1851 – Neotype (designated by Kartonegoro & Veldkamp in Reinwardtia 13: 132. 2010): Sumatra, Bengkulu, Ayer Angat, Gunung Kaba, *Forbes 2882a* (L barcode 0822678!; isoneotype: BM!).
Distribution. – Thailand, Peninsular Malaysia, Sumatra, Java, Lesser Sunda Islands (Bali & Lombok) and Papua New Guinea.

Dissochaeta fusca Blume in Flora 14: 497. 1831 ≡ *Neodissochaeta fusca* (Blume) Bakh. f., Contr. Melastom. 136. 1943 – Lectotype (designated by Kartonegoro & Veldkamp in Reinwardtia 13: 143. 2010): Java, *Blume 1791* (L barcode L0729468!; isolectotypes: K barcode K000859621!, L barcode L0537244!, P barcode P05283572!).
Distribution. – Java, Lesser Sunda Islands (Sumbawa).

Dissochaeta glandiformis J.F.Maxwell in Gard. Bull. Singapore 33: 313, f. 1. 1980 – Holotype: Sumatra, Kerinci Region, Gunung Tujuh, *Meijer 7282* (L barcode L0537274!).
Distribution. – Sumatra (Kerinci Range).

Dissochaeta gracilis (Jack) Blume in Flora 14: 498. 1831 ≡ *Melastoma gracile* Jack in Trans. Linn. Soc. London 14: 14. 1823 ≡ *Neodissochaeta gracilis* (Jack) Bakh.f. in Contr. Melastom. 137. 1943 – Neotype (designated by Kartonegoro & Veldkamp in Reinwardtia 13: 134. 2010): Sumatra, Bengkulu, Bukit Daun, Balai, *de Voogd 591* (L barcode L0822677!; isoneotype: BO!),
Distribution. – S Thailand, Malay Peninsula, Sumatra, Java, Borneo.

Dissochaeta inappendiculata Blume in Flora 14: 499. 1831 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 98. 2018): Java, *Blume s.n.* (L barcode L0537236!; isolectotypes: K barcode K000859623!, L barcode L0537235!, P barcode P05283569!).
Distribution. – Peninsular Malaysia, Sumatra, Java.

Dissochaeta intermedia Blume in Flora 14: 439. 1831 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 101. 2018): Java, West Java, Mount Pangrango, Gegerbentang, *Blume 539* (L barcode L0537299!; isolectotypes: K barcodes K000859493!, K000859494!, L barcodes L0537296!, L0537297!, L0537298!, P barcode P05283548!).
Distribution. – Java.

Dissocchaeta rectandra Karton. in PhytoKeys 107: 134. 2018 – Holotype: Peninsular Malaysia, Pahang, Fraser's Hill, *Carrick 1606* (L 2D-code L.2533494!; isotypes: K!, KLU, L 2D-code L.2533495!, SING).
Distribution. – Peninsular Malaysia.

Dissochaeta rubiginosa Stapf in J. Linn. Soc., Bot. 42: 79. 1914 – Holotype: Borneo, Sabah, Mount Kinabalu, Gurulau Spur, *Gibbs 3977* (K barcode K000859491!).
Distribution. – Borneo.

Dissochaeta sagittata Blume in Flora 14: 500. 1831 ≡ *Dissochaeta intermedia* var. *sagittata* (Blume) J.F.Maxwell in Gard. Bull. Singapore 33: 315. 1980 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 140. 2018): Java, Bantam, *Blume 11* (L barcode 0537226!; isolectotype: L barcode L0537228!).
Distribution. – Java.

Dissochaeta schumannii Cogn. in Schumann & Hollrung, Fl. Kais. Wilh. Land: 88. 1889 ≡ *Neodissochaeta schumannii* (Cogn.) M.P.Nayar in Kew Bull. 20: 160. 1966 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 143. 2018): New Guinea, East Sepik, Augusta River, *Hollrung 656* (BO No. BO-1747958!; isolectotypes: BR barcode 000005187904 [image!], K barcode K000859604!, L barcode L0537229!).
Distribution. – New Guinea.

Dissochaeta vacillans (Blume) Blume in Flora 14: 495. 1831 ≡ *Melastoma vacillans* Blume in Bijdr. Fl. Ned.-Ind. 17: 1074. 1826 ≡ *Neodissochaeta vacillans* (Blume) Bakh.f., Contr. Melastom. 144. 1943 – Lectotype (designated by Kartonegoro & Veldkamp in Reinwardtia 13: 143. 2010): Java, West Java, Bogor, Ciawi, *Reinwardt s.n.* (L barcode L0008894!; isolectotype: L barcode L0008895!).
Distribution. – Java.

5. ***Macrolenes*** Naudin in Ann. Sci. Nat., Bot. sér. 3, 15: 311. 1851 – Type: *Macrolenes annulata* (Vent.) Naudin.
= *Marumia* Blume in Flora 14: 503. 1831, non Reinw. (1828). – Type (designated by Kartonegoro et al. in Gard. Bull. Singapore 71: 192. 2019): *Marumia muscosa* (Blume) Blume [≡ *Macrolenes muscosa* (Blume) Bakh.f.].

Morphological diagnosis. – Woody climbers with scrambler growth; nodes swollen with indistinct interpetiolar growth, lines or ridges. Leaves with straight petiole, pubescent or bristly. Flowers diplostemonous, with campanulate or urceolate hypanthium, calyx lobes free with rounded, triangular or lanceolate shape, tips obtuse or acute. Stamens 8, unequal, alternipetalous larger, fertile, oppositipetalous smaller, fertile.

Macrolenes Naudin sect. ***Macrolenes*** – Type: *Macrolenes annulata* (Vent.) Naudin.

Morphological diagnosis. – Inflorescences axillary. Hypanthium campanulate or urceolate, densely covered with stellate hairs or simple bristle hairs or apically stellate bristle hairs, infrequently floccose. Calyx lobes rounded, triangular, apex acute, half as long as hypanthium length. Stamens dimorphic, unequal; anthers curved; alternipetalous longer, sickle-shaped, connective appendages dorsally triangular, ventrally fimbriate; oppositipetalous, shorter, S-shaped, connective appendages dorsally triangular, ventrally biligulate.

Macrolenes annulata (Vent.) Naudin in Ann. Sci. Nat., Bot. sér. 3, 15: 311. 1851 ≡ *Maieta annulata* Vent., Choix Pl. 32. 1803 ≡ *Huberia annulata* (Vent.) DC., Prodr. 3: 167. 1828 ≡ *Marumia annulata* (Vent.) Triana in Trans. Linn. Soc. London 28: 82. 1872 – Holotype: Java, *de Lahaye s.n. "2860"* (G-DC barcode G00341515 [image!]).
Distribution. – Sumatra and Java.

Macrolenes bipulvinata (Korth.) Bakh.f., Contr. Melastom. 218. 1943 ≡ *Dissochaeta bipulvinata* Korth., Verh. Nat. Gesch. Ned. Bezitt., Bot. 239. 1844 ≡ *Marumia bipulvinata* (Korth.) Triana in Trans. Linn. Soc. London 28: 82. 1872 – Lectotype (designated by Bakhuizen van den Brink in Contr. Melastom. 218. 1943): Borneo, SE Borneo, G. Rantau, *Korthals s.n.* (L 2D-code L.2541989!; isolectotypes: BR barcode 00000519595!, P barcodes P05283656!, P05283657!).
Distribution. – Borneo (Kalimantan).

Macrolenes bruneiensis Karton. in Gard. Bull. Singapore 71: 200. 2019 – Holotype: Borneo, Brunei Darussalam, Belait District, Merangking-Buau Road, *Nangkat 246* (BO!; isotypes: BRUN!, K!, L!, SING barcode SING 0157809!).
Distribution. – Borneo (Brunei).

Macrolenes dimorpha (Craib) J.F.Maxwell in Gard. Bull. Singapore 33: 321. 1980 ≡ *Marumia dimorpha* Craib in Bull. Misc. Inform. Kew 1930(7): 320. 1930 – Lectotype (designated by Kartonegoro et al. in Gard. Bull. Singapore 71: 202. 2019): Thailand, Yala, Bannang Sata, *Kerr 7283* (K barcode K000859521!; isolectotypes: AAU [image!], BK barcode 257159 [image!], BM barcode BM000944449!, E barcode E00285930!).
Distribution. – S Thailand, Peninsular Malaysia, Sumatra.

Macrolenes echinulata (Naudin) Bakh.f., Contr. Melastom.: 209. 1943 ≡ *Marumia echinulata* Naudin in Ann. Sci. Nat., Bot. sér. 3, 15: 280. 1851 ≡ *Dissochaeta echinulata*

(Naudin) Clausing in Santisuk & Larsen, Fl. Thailand 7(3): 425. 2001 – Lectotype (designated by Kartonegoro et al. in Gard. Bull. Singapore 71: 204. 2019): Singapore, *Gaudichaud-Beaupré 79* (P barcode P02274823 [image!]; isolectotypes: G barcode G00319903 [image!], P barcodes P P02274821, P02274822, P02274825, P02274826 [images!]).
Distribution. – Malay Peninsula, Sumatra.

Macrolenes esetosa (Craib) Karton. in Gard. Bull. Singapore 71: 208. 2019 ≡ *Marumia rhodocarpa* var. *esetosa* Craib, Fl. Siam. 10: 697. 1931 ≡ *Macrolenes echinulata* var. *esetosa* (Craib.) J.F.Maxwell in Gard. Bull. Singapore 33: 321. 1980 – Lectotype (designated by Kartonegoro et al. in Gard. Bull. Singapore 71: 208. 2019): Thailand, Narathiwat, Sungai Padi, *Bourke s.n.* (K barcode K000859518!; isolectotypes: BK barcode 257157 [image!].
Distribution. – Southern Thailand.

Macrolenes glabrata M.P.Nayar in J. Jap. Bot. 55: 48. 1980 – Holotype: Peninsular Malaysia, Selangor, Ulu Klang Ampang, *Millard 1756* (K!; isotype KLU).
Distribution. – Peninsular Malaysia (Selangor).

Macrolenes hirsuta (Cogn.) J.F.Maxwell in Gard. Bull. Singapore 33: 321. 1980 ≡ *Marumia hirsuta* Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 553. 1891 – Lectotype (designated by Kartonegoro et al. in Gard. Bull. Singapore 71: 210. 2019): Borneo, Kalimantan, Sintang, *Teijsmann HB 8658* (BO No. BO-1859504!; isolectotypes: BO Nos. BO-1859502!, BO-1859503!, FI barcode FI007927 [image!], U).
Distribution. – Borneo.

Macrolenes muscosa (Blume) Bakh.f., Contr. Melastom.: 211. 1943 ≡ *Melastoma muscosum* Blume in Bijdr. Fl. Ned.-Ind. 17: 1070. 1826 ≡ *Marumia muscosa* (Blume) Blume in Flora 14: 504. 1831 ≡ *Dissochaeta muscosa* (Blume) G.Kadereit in Mabb., Pl.-Book, ed. 4: 1101. 2017 – Lectotype (designated by Bakhuizen van den Brink in Contr, Melastom. 212. 1943): Java, *Blume s.n.* (L barcode L0008927!; isolectotypes: K barcodes K000867117!, K000867118!, M , MPU barcodes MPU-013522!, MPU-013523! P barcodes P05283626!, P05283627!, P05283629!).
Distribution. – Sumatra, Java.

Macrolenes neglecta M.P.Nayar in J. Jap. Bot. 55: 46. 1980 – Holotype: Sumatra, Kerinci, Sungei Kumbang, *Robinson & Kloss s.n.* (BM barcode BM000944488; isotype: K barcode K000867115!).
Distribution. – Sumatra (Kerinci Range).

Macrolenes nemorosa (Jack) Bakh.f., Contr. Melastom. 206. 1943 ≡ *Melastoma nemorosum* Jack in Trans. Linn. Soc. London 14: 8. 1823 ≡ *Marumia nemorosa* (Jack) Blume in Flora 14: 505. 1831 – Lectotype (designated by Nayar in J. Jap. Bot. 55: 50. 1980): Peninsular Malaysia, Penang, *Jack 51* (BM barcode BM000944447!).
Distribution. – S Thailand, Peninsular Malaysia, Sumatra and Borneo.

Macrolenes pachygyna (Korth.) M.P.Nayar in J. Jap. Bot. 55: 49. 1980 ≡ *Marumia pachygyna* Korth., Ver. Nat. Gesch. Bed. Bezitt., Bot. t. 59. 1842 ≡ *Dissochaeta pachygyna* (Korth.) I.M.Turner in Taxon 67(3): 628. 2018 – Lectotype (designated by Bakhuizen van

den Brink in Contr. Melastom. 217. 1943 & Turner in Taxon 67: 628. 2018): Borneo, Kalimantan, Kapuas-Barito, Tewe River, *Korthals s.n.* (L barcode L0008936!; isolectotypes K barcode K000867112!, L barcodes L0537218!, L0537219!, P barcodes P05283680! P05283682!, S No. S-G-3965!).
Distribution. – Sumatra, Borneo.

Macrolenes rufolanata (Ridl.) J.F.Maxwell in Gard. Bull. Singapore 33: 321. 1980 ≡ *Marumia rufolanata* Ridl. in Fl. Malay Penins. 5: 310. 1925 – Lectotype (designated by Kartonegoro et al. in Gard. Bull. Singapore 71: 227. 2019): Peninsular Malaysia, Pahang, Kuala Lipis, Ulu Chimeras, *Burkill & Haniff SFN 15661* (K barcode K000867119!; isolectotypes SING barcodes SING0052046!, SING0052047!).
Distribution. – Peninsular Malaysia.

Macrolenes stellulata (Jack) Bakh.f., Contr. Melastom.: 216. 1943 ≡ *Melastoma stellulatum* Jack in Trans. Linn. Soc. London 14: 6. 1823 ≡ *Marumia stellulata* (Jack) Blume in Flora 14: 503. 1831 – Neotype (designated by Kartonegoro et al. in Gard. Bull. Singapore 71: 228. 2019): Sumatra, Jambi, Harapan Rain Forest, Nawai River, *Deden et al. BOHK 239* (BO!; isoneotypes: K barcode K000812315!, KEP).
Distribution. – Peninsular Malaysia, Sumatra, Borneo.

Macrolenes subulata J.F.Maxwell in Gard. Bull. Singapore 33: 321. 1980 – Holotype: Sumatra, Lampung, Mt. Tanggamus, *Jacobs 8028* (L barcode L0537194!; isotypes: BO No. BO-1865976!, K barcode K000867110!, KEP barcode 110313 [image!], SING barcode SING 0052049!).
Distribution. – Sumatra (Lampung).

Macrolenes tuberculata Karton. in Gard. Bull. Singapore 71: 232. 2019 Distribution. – Holotype: Sumatra, North Sumatra, Besitang, Sikundur, *de Wilde & de Wilde-Duyfjes 19573* (BO!; isotypes K barcode K001045168!, L!).
Distribution. – Sumatra (North).

Macrolenes veldkampii Karton. in Gard. Bull. Singapore 71: 236. 2019 – Holotype: Borneo, East Kalimantan, Long Iram, Maruwai, Block Lampunut, *Kessler et al. 2656* (BO!; isotypes: K barcode K000276099! , L barcode L0370302!, WAN).
Distribution. – Borneo.

Macrolenes sect. ***Terminaliflores*** Karton., **sect. nov.** – Type: *Macrolenes rostrata* (Korth.) Karton.

Morphological diagnosis. – Inflorescences terminal. Hypanthium campanulate or urceolate, densely covered with stellate hairs and simple bristle hairs, infrequently floccose. Calyx lobes rounded, triangular or linear lanceolate, apex acute, half to as long as hypanthium length. Stamens dimorphic, unequal or subequal; alternipetalous, longer, oppositipetalous, shorter; anthers curved, sickle-shaped; connective appendages dorsally triangular, ventrally biligulate.

Macrolenes alstonii (M.P.Nayar) Karton., **comb. nov.** ≡ *Dissochaeta alstonii* M.P.Nayar in Bull. Bot. Surv. India 11: 188. 1969 ≡ *Dissochaeta rostrata* var. *alstonii* (M.P.Nayar)

J.F.Maxwell in Gard. Bull. Singapore 33: 318. 1980 – Holotype: Sumatra, Tapanuli, between Sidikalang and Pongkolan, *Alston 14813* (BM barcode BM000944479!).
Distribution. – Sumatra (North).

Macrolenes atrobrunnea (G.Kadereit) Karton., **comb. nov.** ≡ *Dissochaeta atrobrunnea* G.Kadereit in Edinburgh J. Bot. 63: 4, f. 1. 2006 – Holotype: Borneo, Central Kalimantan, Barito Ulu, *Sidiyasa PBU 229* (E barcode E00225106!; isotypes: BO No. BO-0009659!, K barcode K001089634!, L 2D-code L.2542233!, WAN).
Distribution. – Borneo (Central Kalimantan).

Macrolenes floccosa (J.F.Maxwell), Karton., **comb. nov.** ≡ *Dissochaeta rostrata* var. *floccosa* J.F.Maxwell in Gard. Bull. Singapore 33: 319, f. 5. 1980 ≡ *Dissochaeta floccosa* (J.F.Maxwell) Karton. in PhytoKeys 107: 77. 2018 – Holotype: Sumatra, West Coast, Payakumbuh, Pakan Raba, *Maradjo 350* (L barcode L0537273!; isotypes: L barcode L0537271!, PNH No. 59964 [image!], SING barcode SING0051679!).
Distribution. – Sumatra (West).

Macrolenes hirsutoidea (Furtado) Karton., **comb. nov.** ≡ *Dissochaeta hirsutoidea* Furtado in Gard. Bull. Singapore 20: 109, f. 2C. 1963 — Holotype: Borneo, Sabah, Sandakan, Bettotan, *Boden-Kloss SFN 19156* (SING; isotypes: BO!, K barcode K000859626!).
Distribution. – Borneo.

Macrolenes horrida Bakh.f., Contr. Melastom. 208. 1943 ≡ *Dissochaeta rostrata* var. *horrida* (Bakh.f.) J.F.Maxwell in Gard. Bull. Singapore 33: 320. 1980 ≡ *Dissochaeta horrida* (Bakh.f.) Karton. in PhytoKeys 107: 95. 2018 – Holotype: Sumatra, West Coast, Agam, Brani, *Bünnemeijer 3200* (L barcode L0537276!; isotypes: BO Nos. BO-1751324!, BO-1751325!).
Distribution. – Sumatra (West).

Macrolenes johorensis (Furtado) Karton., **comb. nov.** ≡ *Dissochaeta johorensis* Furtado in Gard. Bull. Singapore 20: 110. 1963 – Holotype: Peninsular Malaysia, Johor, Gunong Panti, *Ridley 4185* (SING; isotypes: BM barcode BM000944478!, K barcode K000859526!).
Distribution. – Peninsular Malaysia (Johor), Sumatra (Riau Archipelago).

Macrolenes macrosepala (Stapf) Karton., **comb. nov.** ≡ *Dissochaeta macrosepala* Stapf in J. Linn. Soc., Bot. 42: 80. 1914 ≡ *Dissochaeta rostrata* var. *macrosepala* (Stapf) J.F.Maxwell in Gard. Bull. Singapore 33: 320. 1980 – Holotype: Borneo, Sabah, Mount Kinabalu, ridge above Bundu Tuhan, *Gibbs 3951* (K barcode K000859636!).
Distribution. – Borneo (Sabah).

Macrolenes marumioides (Cogn.) Karton., **comb. nov.** ≡ *Dissochaeta marumioides* Cogn. in Candolle & Candolle, Monogr. Phan. 7: 556. 1891 – Holotype: Sumatra, West Coast, Mount Singgalang, *Beccari s.n.* (FI barcode FI007931 [image!]).
Distribution. – Sumatra (West).

Macrolenes porphyrocarpa (Ridl.) Karton., **comb. nov.** ≡ *Dissochaeta porphyrocarpa* Ridl. in Kew Bull. 1: 32. 1946 ≡ *Dissochaeta rostrata* var. *porphyrocarpa* (Ridl.) J.F.Maxwell in Gard. Bull. Singapore 33: 321. 1980 – Lectotype (designated by Kartonegoro et al. in

PhytoKeys 107: 122. 2018): Borneo, Sarawak, Ulu Tawaran, *Haviland 1287* (K barcode K000859633!).
Distribution. – Borneo.

Macrolenes rostrata (Korth.) Karton., **comb. nov.** ≡ *Dissochaeta rostrata* Korth., Verh. Nat. Gesch. Ned. Bezitt., Bot. 239. 1844 ≡ *Anplectrum korthalsii* Triana in Trans. Linn. Soc. London 28: 85. 1872 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 136. 2018): Borneo, South Kalimantan, Mount Prarawin, *Korthals s.n.* (L barcode L0729470!; isolectotype: L barcode L0729469!).
Distribution. – Borneo.

6. *Pseudodissochaeta* M.P.Nayar in J. Bombay Nat. Hist. Soc. 65(3): 557. 1969 – Type: *Pseudodissochaeta assamica* (C.B.Clarke) M.P.Nayar.

Morphological diagnosis. – Erect or rarely spreading shrubs; nodes swollen with indistinct interpetiolar growth or lines. Leaves with straight petiole or subsessile, glabrous or rarely bristly; base oblique or asymmetric, few symmetric; margin serrulate. Flowers with campanulate or urceolate hypanthium, calyx lobes truncate with four tooth-like tips. Stamens 8, equal to subequal, fertile; connective appendages dorsally spurred, ventrally biauriculate or bilobed.

Pseudodissochaeta assamica (C.B.Clarke) M.P.Nayar in J. Bombay Nat. Hist. Soc. 65(3): 559. 1969 ≡ *Anplectrum assamicum* C.B.Clarke in Hook.f., Fl. Brit. India 2: 546. 1879 ≡ *Diplectria assamica* (C.B.Clarke) Kuntze in Revis. Gen. Pl. 1: 246. 1891 ≡ *Backeria assamica* (C.B.Clarke) Raizada in Indian Forester 94: 435. 1968 ≡ *Medinilla assamica* (C.B.Clarke) C.Chen in Acta Phytotax. Sin. 21: 419. 1983 – Lectotype (designated by Kartonegoro et al. in Phytotaxa 468: 165. 2020): India, Assam, Naga Hills, *Griffith 1445 (KD 2285)* (K barcode K000867403!; isotypes: K barcode K000867404!, L barcode L0009218!, M barcode M0137604 [image!]).
Distribution. – E Bhutan, NE India, N Myanmar.

Pseudodissochaeta lanceata M.P.Nayar in J. Bombay Nat. Hist. Soc. 65(3): 563. 1969 ≡ *Medinilla lanceata* (M.P.Nayar) C.Chen in Acta Phytotax. Sin. 21: 421. 1983 – Holotype: China, Hainan, Hong Ta, *Chinese collector 406* (K barcode K000867414!; isotype: K barcode K000867415!).
Distribution. – S China (Hainan, Yunnan), N Vietnam (Tonkin).

Pseudodissochaeta septentrionalis (W.W.Sm.) M.P. Nayar in J. Bombay Nat. Hist. Soc. 65(3): 565. 1969 ≡ *Oritrephes septentrionalis* W.W.Sm. in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 7: 69. 1911 ≡ *Medinilla septentrionalis* (W.W.Sm.) H.L.Li in J. Arnold Arbor. 25: 38. 1944 – Lectotype (designated by Nayar in J. Bombay Nat. Hist. Soc. 65: 565. 1969): Burma, S. Shan, Kung Lung, *MacGregor 751* (E barcode E00288102 [image!]).
Distribution. – N Mynamar, S China, N Thailand, Indochina.

Pseudodissochaeta spirei (Guillaumin) Veldkamp & J.F.Maxwell in Gard. Bull. Singapore 33: 324. 1980 ≡ *Medinilla spirei* Guillaumin in Bull. Soc. Bot. France 68: 4. 1921 – Lectotype (designated by Veldkamp & Maxwell in Gard. Bull. Singapore 33: 324. 1980): Vietnam, Nghe An, Co Ba, *Chevalier 32408* (P barcode P00700366 [image!]; isolectotypes P barcodes P00700367, P00700368 [images!]).

Distribution. – S China, Vietnam.

Pseudodissochaeta subsessilis (Craib) M.P.Nayar in J. Bombay Nat. Hist. Soc. 65: 561. 1969 ≡ *Allomorphia subsessilis* Craib in Bull. Misc. Inform. Kew 1913: 69. 1913 ≡ *Medinilla subsessilis* M.P.Nayar ex P.H.Hô in Ill. Fl. Vietnam 2, 1: 114. 1992, non Merr., 1912 – Lectotype (designated by Nayar in J. Bombay Nat. Hist. Soc. 65: 561. 1969): Thailand, Chiang Mai, Doi Wao, *Kerr 2427* (K barcode K000867401!; isolectotypes: BM barcodes BM0009444536!, BM000944537!, E barcode E00288101 [image!], K barcode K000867402!).

Distribution. – N Thailand.

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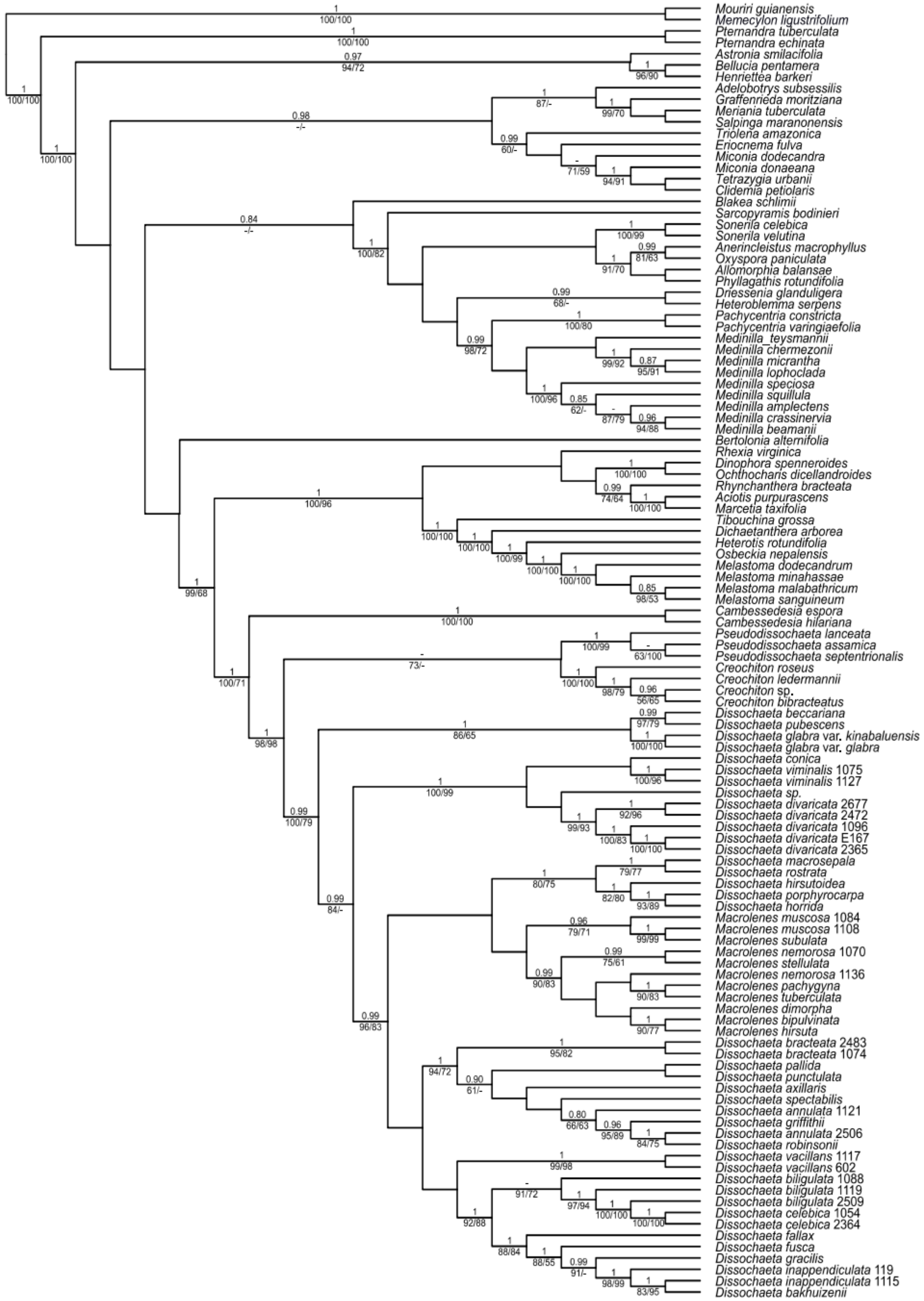
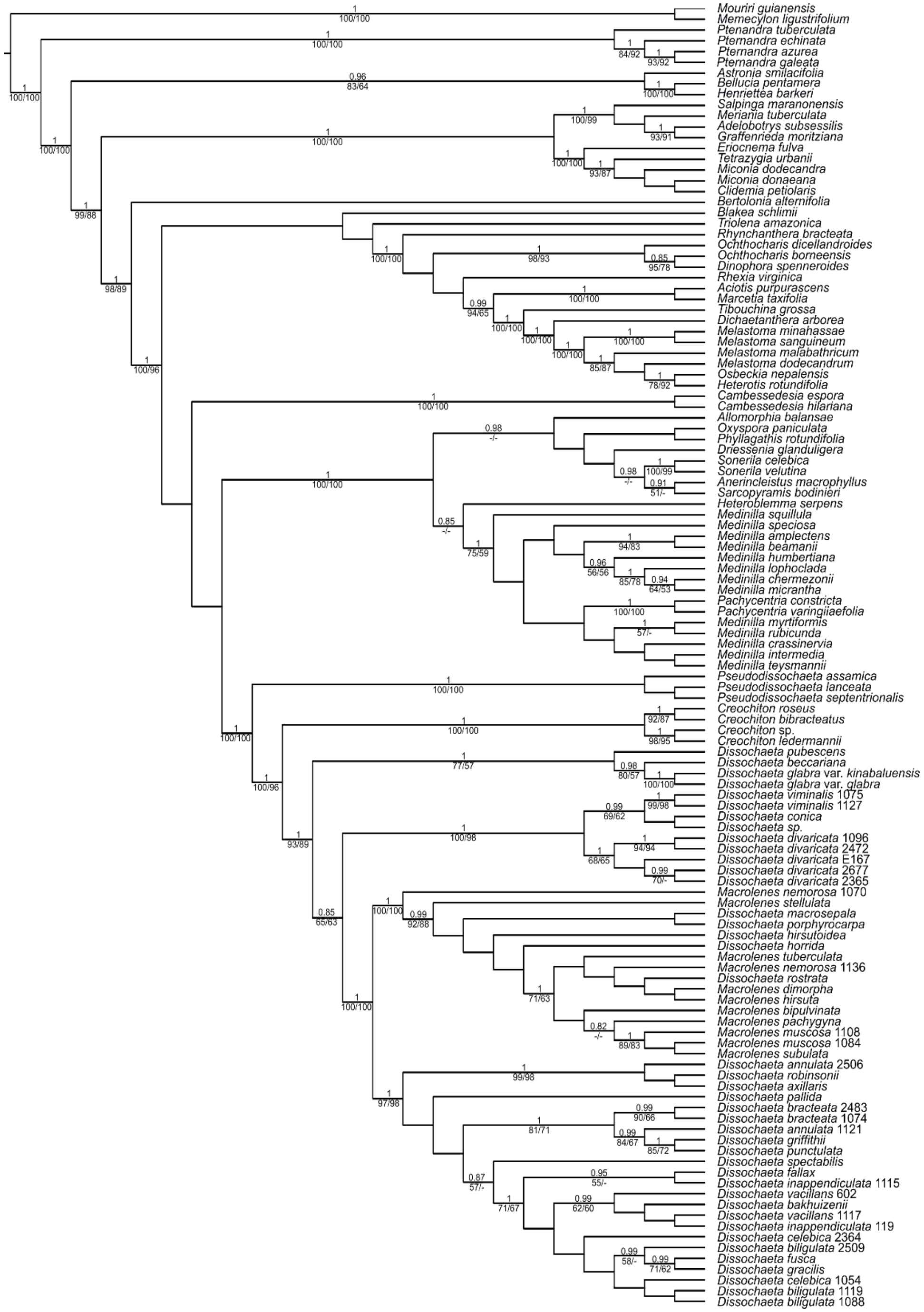
Suppl. 6-1. Maximum likelihood (ML) phylogenetic cladogram of Dissochaeteae *s.l.* with representatives of Asian, African and Madagascan Dissochaeteae, and outgroups derived from the combined nuclear data matrix (nrETS, nrITS). Values above branches refer to posterior probabilities resulting from Bayesian inference (only values ≥0.80), values below branches refer to bootstrap values resulting from the ML analysis (only values ≥50) and bootstrap values resulting from the parsimony analysis (only values ≥50).



Suppl. 6-2. Maximum likelihood (ML) phylogenetic cladogram of Dissochaeteae *s.l.* with representatives of Asian, African and Madagascan Dissochaeteae, and outgroups derived from the combined chloroplast data matrix (*ndhF*, *psbk-psbL*, *rbcL*, *rpl16*). Values above branches refer to posterior probabilities resulting from Bayesian inference (only values ≥0.80), values below branches refer to bootstrap values resulting from the ML analysis (only values ≥50) and bootstrap values resulting from the parsimony analysis (only values ≥50).



Appendix 6-1. *Voucher information. Species name (following a new taxonomic treatment), synonym, country, region, collector and collector number, herbarium code if available. GenBank accessions numbers are given for all nrETS, nrITS, ndhF,* psbK-psbL, rbcL, rpl16 *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 purpurascens*** (Aubl.) Triana, Guyana, *F. Michelangeli 2454* (NY), KU500992, KU501055, AF215561, JQ730461, –, AF322231; ***Adelobotrys subsessilis*** Gleason, Peru, *F. Michelangeli 493* (BH), MH781591, AY966407, MH760283, MH781651, MH747567, AY966419; ***Allomorphia balansae*** Cogn., China, *Y. Liu 451* (SYS), –, MG644470, MK994792, MK994792, MK994792, MK994792; ***Anerincleistus macrophyllus*** Bakh.f., Malaysia, Borneo, *Y. Liu 673* (SYS), –, MN031184, MK994887, MK994887, MK994887, MK994887; ***Astronia smilacifolia*** Triana, Malaysia, Borneo, *Y. Liu 664* (SYS), –, EF683153, MK994883, MK994883, MK994883, MK994883; ***Bellucia pentamera*** Naudin, *D.S. Penneys 1868* (CAS), –, GU968788, AF215578, –, KF781624, AF215615; ***Bertolonia alternifolia*** Baumgratz, Amorim & A.B.Jardim, Brazil, *L.F. Bacci 375* (UEC), MH722270, MH708155, MH729204, MK296663, MH729221, MH722278; ***Blakea schlimii*** (Naudin) Triana, *F. Michelangeli 1227* (NY), –, AY460441, KX826821, KX826821, KX826821, KX826821; ***Cambessedesia espora*** Naudin, *P.J.F. Guimarães 397* (RB), MK165019, JQ730062, JQ899114, JQ730481, JQ899088, JQ899064; ***Cambessedesia hilariana*** DC., *P.J.F. Guimarães 405* (RB), MK165024, JQ730063, JQ899115, JQ730482, JQ899089, JQ899065; ***Clidemia petiolaris*** Triana, *M. Chase 2534* (K), KM893562, KF821452, AM235410, KF821882, AM235643, AM235446; ***Dichaetanthera arborea*** Baker, Madagascar, *A. Razanatsima 823* (MO), –, KX889222, AF272800, KY284742, –, AF294470; ***Driessenia glanduligera*** Stapf, Malaysia, Borneo, *Y. Liu 657* (SYS), –, MN031197, MK994879, MK994879, MK994879, MK994879 ; ***Eriocnema fulva*** Naudin, *F. Almeda 8416* (CAS), KF820735, MH743831, AY553781, MK296694, AY553777, AY553772; ***Graffenrieda moritziana*** Triana, *F. Michelangeli 832* (NY), KF820749, AY460451, EU055944, JQ730504, EU711390, JF832031; ***Henriettea barkeri*** (Urb. & Ekman) Alain, *G. Ionta 2029* (FLAS), –, KJ933957, KX826824, KX826824, KX826824, KX826824; ***Heterotis rotundifolia*** (Sm.) Jacq.-Fél., Dominica, *D.S. Penneys 1304* (FLAS), –, JQ730089, AF215565, –, U26323, AF270745; ***Marcetia taxifolia*** Triana, Venezuela, *F. Michelangeli 680* (BH), KU501041, JQ730102, GU968825**,** JQ730521, **–**, **–**; ***Melastoma dodecandrum*** Lour., China, –, MK292847, MH748092, MH748092, MH748092, MH748092; ***Melastoma malabathricum*** L., *D.S. Penneys 1998* (CAS), –, JQ730105, AF272810, JQ730524, AF270748, AB436376; ***Melastoma minahassae*** Karst.-Mey., Indonesia, Sulawesi, *A. Kartonegoro 1052* (BO), MW462395*, –, MW462472*, MW462324*, MW462634*, MW414599*; ***Melastoma sanguineum*** Sims, Indonesia, Sumatra, *A. Kartonegoro 1099* (BO), MW462396*, JQ730106, MW462473*, MW462325*, MW462635*, MW414600*; ***Memecylon ligustrifolium*** Champ. ex Benth., China, *Y. Liu 726* (SYS), –, KP093034, MK994913, MK994913, MK994913, MK994913; ***Meriania tuberculata*** Triana, Colombia, *P.P. Pedraza 2142* (NY), MH781647, MH819925, MH760361, MH781715, MH747639, –; ***Miconia dodecandra*** Cogn., *F. Michelangeli 758* (NY), KF821020, KF821600, KX826826, KX826826, KX826826, KX826826; ***Miconia donaeana*** Naudin, *F. Michelangeli 727* (NY), KF821024, KY782466, EU056028, KF822206, AM235648, AM235451; ***Mouriri guianensis*** Aubl., FJ792921, FJ792969, AF215575, –, AF215529, AF215610; ***Osbeckia nepalensis*** Hook., *D.S. Penneys 1986* (CAS), –, JQ730118, MH729215, JQ730539, KX527055, MH722991; ***Oxyspora paniculata*** DC., Vietnam, *Y. Liu 523* (SYS), –, MN031212, MK994819, MK994819, MK994819, MK994819; ***Phyllagathis rotundifolia*** (Jack) Blume, Malaysia, *Y. Liu M50* (SYS), –, MG644436, MK994912, MK994912, MK994912, MK994912; ***Pternandra azurea*** (Blume) Burkill, Indonesia, Sumatra, *A. Kartonegoro 1077* (BO), –, –, MW462477*, MW462329*, MW462639*, MW414604*; ***Pternandra echinata*** Jack, Malaysia, *I.J. Chen 542*, –, KF781604, AF215559, –, AF215520, AF270744; ***Pternandra galeata*** Ridl., Indonesia, Sumatra, *A. Kartonegoro 1057* (BO), –, –, MW462478*, MW462330*, MW462640*, MW414605*; ***Pternandra tuberculata*** (Korth.) M.P.Nayar (*Pternandra korthalsiana*), Malaysia, Borneo, *Y. Liu 651* (SYS), –, MW462551*, MK994877, MK994877, MK994877, MK994877; ***Rhexia virginica*** L., *F. Michelangeli 1448* (NY), KF462879, DQ985643, KX826830, KX826830, KX826830, KX826830; ***Rhynchanthera bracteata*** Triana, *F. Zenteno 8801* (NY), KF462880, JQ730137, KX826831, KX826831, KX826831, KX826831; ***Salpinga maranonensis*** Wurdack, *J.L. Clark 6979* (US), MF029372, KY991873, JF831982, MF104983, JF832008, JF832048; ***Sarcopyramis bodinieri*** H.Lév., China, *Y. Liu 502* (SYS), –, MN031206, MK994810, MK994810, MK994810, MK994810; ***Sonerila celebica*** Bakh.f. Indonesia, Sulawesi, *A. Kartonegoro 1027*, MW462398*, MW462552*, MW462479*, MW462331*, MW462641*, MW414606*; ***Sonerila velutina*** Cogn., Malaysia, Borneo, *Y. Liu 683* (SYS), –, MN031224, MK994892, MK994892, MK994892, MK994892; ***Tetrazygia urbanii*** Cogn., *L. Struwe 1166* (NY), KF821374, KF821772, AF270753, KF822547, AF215538, AF215619; ***Tibouchina grossa*** Cogn., *J.C. Zabala 1* (UPTC), KF462935, JQ730192, JF831983, JQ730612, JF832009, JF832050; ***Triolena amazonica*** (Pilg.) Wurdack, *R. Goldenberg 965* (NY), MK165055, –, JF831984, MK296700, NC_031890, JF832051. **— INGROUP:** ***Creochiton bibracteatus*** (Blume) Blume, Indonesia, Java, *A. Kartonegoro 1111* (BO), –, MW462480*, MW462399*, MW462242*, MW462553*, MW290997**;* ***Creochiton ledermannii*** Mansf., Indonesia, Papua, *M. Mambrasar 81* (BO), –, MW462481*, MW462400*, MW462243*, MW462554*, MW290998*; ***Creochiton roseus*** Merr., Indonesia, Sulawesi, *A. Kartonegoro* 1051 (BO), MW462332*, MW462482*, MW462401*, MW462244*, MW462555*, MW290999*; ***Creochiton* sp.**, Indonesia, Sulawesi, *A. Kartonegoro 927* (BO), –, MW462483*,

MW462402*, MW462245*, MW462556*, MW291000*; ***Dalenia beccariana*** (Cogn.) M.P.Nayar (*Dissochaeta pubescens*), Brunei Darussalam, Temburong, *A. Kartonegoro 1118* (BO), –, MW462519*, MW462442*, MW462297*, MW462600*, MW295981*; ***Dalenia glabra*** Merr. var. ***glabra*** (*Dissochaeta glabra* var. *glabra*), Malaysia, Borneo, *D.S. Penneys 2446* (WNC), MW462354*, MW462506*, MW462429*, MW462273*, MW462586*, MW295982*; ***Dalenia glabra*** Merr. var. ***kinabaluensis*** (Veldkamp) Karton. (*Dissochaeta glabra* var. *kinabaluensis*), Malaysia, Borneo, *D.S. Penneys 2542* (WNC), MW462357*, MW462508*, MW462431*, MW462276*, MW462589*, MW295985*; ***Dalenia magnibracteata*** (Bakh.f.) Karton. (*Dissochaeta beccariana*), Malaysia, Borneo, *Y. Liu 676* (SYS), –, MG644477, MK994889, MK994889, MK994889, MK994889; ***Dinophora spenneroides*** Benth., Cameroon, *M.C. Veranso 107* (MJG), MF397951, KX889227, MF398047, KY284746, –, –; ***Diplectria conica*** Bakh.f. (*Dissochaeta conica*), Indonesia, Sumatra, *A. Kartonegoro 1101* (BO), MW462347*, MW462498*, MW462419*, MW462263*, MW462576*, MW414548*; ***Diplectria divaricata*** (Willd.) Kuntze (*Dissochaeta divaricata*), Indonesia, Enggano, *Ardiyani et al. E167* (BO), MW462350*, MW462503*, MW462425*, MW462269*, MW462582*, MW414554*; ***Diplectria divaricata*** (Willd.) Kuntze (*Dissochaeta divaricata*), Indonesia, Sumatra, *A. Kartonegoro 1096* (BO), MW462348*, MW462499*, MW462421*, MW462264*, MW462578*, MW414550*; ***Diplectria divaricata*** (Willd.) Kuntze (*Dissochaeta divaricata*), Philippines, Mindanao, *D.S. Penneys 2365* (WNC), –, MW462500*, MW462422*, MW462266*, MW462579*, MW414551*; ***Diplectria divaricata*** (Willd.) Kuntze (*Dissochaeta divaricata*), Malaysia, Borneo, *D.S. Penneys 2472* (WNC), MW462349*, MW462501*, MW462423*, MW462267*, MW462580*, MW414552*; ***Diplectria divaricata*** (Willd.) Kuntze (*Dissochaeta divaricata*), Thailand, Songkhla, *J.S. Wai 2677* (PSU), –, MW462502*, MW462424*, MW462268*, MW462581*, MW414553*; ***Diplectria* sp.**, Indonesia, Borneo, *A. Kartonegoro 1135* (BO), –, MW462524*, MW462447*, MW462295*, MW462606*, MW414573*; ***Diplectria viminalis*** (Jack) Kuntze (*Dissochaeta viminalis*), Indonesia, Sumatra, *A. Kartonegoro 1075* (BO), MW462377*, MW462528*, MW462451*, MW462299*, MW462610*, MW414577*; ***Diplectria viminalis*** (Jack) Kuntze (*Dissochaeta viminalis*), Indonesia, Borneo, *A. Kartonegoro 1127* (BO), MW462380*, MW462530*, MW462452*, MW462302*, MW462612*, MW414579*; ***Dissochaeta annulata*** Hook.f. ex Triana, Indonesia, Bintan, *A. Kartonegoro 1121* (BO), MW462333*, MW462485*, MW462404*, MW462247*, MW462559*, MW414532*; ***Dissochaeta annulata*** Hook.f. ex Triana, Malaysia, Borneo, *D.S. Penneys 2506* (WNC), MW462335*, MW462486*, MW462405*, MW462249*, MW462560*, MW414533*; ***Dissochaeta axillaris*** Cogn., Indonesia, Borneo, *A. Kartonegoro 1126* (BO), MW462336*, –, –, MW462250*, MW462561*, –; ***Dissochaeta bakhuizenii*** Veldkamp, Indonesia, Java, *A. Kartonegoro 1116* (BO), MW462339*, MW462488*, MW462408*, MW462253*, MW462564*, MW414536*; ***Dissochaeta biligulata*** Korth., Indonesia, Sumatra, *A. Kartonegoro 1088* (BO), MW462340*, MW462489*, MW462409*, MW462254*, MW462565*, MW414537*; ***Dissochaeta biligulata*** Korth., Indonesia, Bintan, *A. Kartonegoro 1119* (BO), MW462341*, MW462490*, MW462410*, MW462255*, MW462566*, MW414538*; ***Dissochaeta biligulata*** Korth., Malaysia, Borneo, *D.S. Penneys 2509* (WNC), MW462343*, MW462492*, MW462411*, MW462257*, MW462568*, MW414540*; ***Dissochaeta bracteata*** (Jack) Blume, Indonesia, Sumatra, *A. Kartonegoro 1074* (BO), MW462344*, MW462494*, MW462413*, MW462258*, MW462570*, MW414542*; ***Dissochaeta bracteata*** (Jack) Blume, Malaysia, Borneo, *D.S. Penneys 2483* (WNC), MW462345*, MW462495*, MW462414*, MW462259*, MW462571*, MW414543*; ***Dissochaeta celebica*** Blume, Indonesia, Sulawesi, *A. Kartoengoro 1054* (BO), –, MW462496*, MW462415*, MW462260*, MW462572*, MW414544*; ***Dissochaeta celebica*** Blume, Philippines, Mindanao, *D.S. Penneys 2364* (WNC), –, MW462497*, MW462417*, MW462261*, MW462574*, MW414546*; ***Dissochaeta fallax*** (Jack) Blume, Indonesia, Java, *A. Kartonegoro 1106* (BO), MW462351*, MW462504*, MW462426*, MW462270*, MW462583*, MW414555*; ***Dissochaeta fusca*** Blume, Indonesia, Java, *A. Kartonegoro 1105* (BO), MW462353*, MW462505*, MW462428*, MW462272*, MW462585*, MW414557*; ***Dissochaeta gracilis*** (Jack) Blume, Indonesia, Java, *A. Kartonegoro 1113* (BO), MW462358*, MW462509*, MW462432*, MW462277*, MW462590*, MW414558*; ***Dissochaeta griffithii*** (M.P.Nayar) Karton., Indonesia, Bintan, *A. Kartonegoro 1122* (BO), MW462359*, MW462510*, MW462433*, MW462278*, MW462591*, MW414559*; ***Dissochaeta inappendiculata*** Blume, Indonesia, Java, *A. Kartonegoro 1115* (BO), MW462364*, MW462515*, MW462438*, MW462283*, MW462596*, MW414564*; ***Dissochaeta inappendiculata*** Blume, Indonesia, Sumatra, *W. Santoso 119* (BO), MW462362*, MW462513*, MW462436*, MW462281*, MW462594*, MW414562*; ***Dissochaeta pallida*** (Jack) Blume, Indonesia, Sumatra, *A. Kartonegoro 1058* (BO), MW462366*, MW462517*, MW462440*, MW462285*, MW462598*, MW414566*; ***Dissochaeta punctulata*** Hook.f. ex Triana, Indonesia, Bintan, *A. Kartonegoro 1123* (BO), MW462369*, MW462520*, MW462443*, MW462289*, MW462601*, MW414568*; ***Dissochaeta robinsonii*** Merr., Indonesia, Moluccas, *Gushilman 382* (BO), MW462372*, MW462522*, MW462444*, MW462292*, MW462603*, MW414569*; ***Dissochaeta spectabilis*** J.F.Maxwell, Indonesia, Sumatra, *A. Kartonegoro 1100* (BO), MW462374*, MW462525*, MW462448*, MW462296*, MW462607*, MW414574*; ***Dissochaeta vacillans*** (Blume) Blume, Indonesia, Java, *Y. Liu 602* (SYS), –, MG644478, MK994856, MK994856, MK994856, MK994856; ***Dissochaeta vacillans*** (Blume) Blume, Indonesia, Java, *A. Kartonegoro 1117* (BO), MW462376*, MW462527*, MW462450*, MW462298*, MW462609*, MW414576*; ***Heteroblemma serpens*** (Stapf) Cámara-Leret, Ridd.-Num. & Veldkamp, Malaysia, Borneo, *Y. Liu 671* (SYS), –, MN031200, MK994886, MK994886, MK994886, MK994886; ***Macrolenes bipulvinata*** (Korth.) Bakh.f., Indonesia, Borneo, *A.*

Kartonegoro 781 (BO), –, MW462532*, MW462453*, MW462304*, MW462614*, MW414580*; ***Macrolenes dimorpha*** (Craib) J.F.Maxwell, Indonesia, Borneo, *A. Kartonegoro 1134* (BO), MW462382*, MW462533*, MW462454*, MW462305*, MW462615*, MW414581*; ***Macrolenes hirsuta*** (Cogn.) J.F.Maxwell, Indonesia, Borneo, *A. Kartonegoro 1139* (BO), MW462383*, MW462534*, MW462455*, MW462306*, MW462616*, MW414582*; ***Macrolenes hirsutoidea*** (Furtado) Karton. (*Dissochaeta hirsutoidea*), Indonesia, Borneo, *A. Kartonegoro 1141* (BO), MW462360*, MW462511*, MW462434*, MW462279*, MW462592*, MW414560*; ***Macrolenes horrida*** Bakh.f. (*Dissochaeta horrida*), Indonesia, Sumatra, *A. Kartonegoro 1073* (BO), MW462361*, MW462512*, MW462435*, MW462280*, MW462593*, MW414561*; ***Macrolenes macrosepala*** (Stapf) Karton. (*Dissochaeta macrosepala*), Malaysia, Borneo, *D.S. Penneys 2512* (WNC), MW462365*, MW462516*, MW462439*, MW462284*, MW462597*, MW414565*; ***Macrolenes muscosa*** (Blume) Bakh.f., Indonesia, Sumatra, *A. Kartonegoro 1084* (BO), MW462384*, MW462535*, MW462456*, MW462307*, MW462617*, MW414583*; ***Macrolenes muscosa*** (Blume) Bakh.f., Indonesia, Java, *A. Kartonegoro 1108* (BO), MW462386*, MW462537*, MW462458*, MW462308*, MW462619*, MW414585*; ***Macrolenes nemorosa*** (Jack) Bakh.f., Indonesia, Sumatra, *A. Kartonegoro 1070* (BO), –, MW462538*, MW462459*, MW462309*, MW462620*, MW414586*; ***Macrolenes nemorosa*** (Jack) Bakh.f., Indonesia, Borneo, *A. Kartonegoro 1136* (BO), MW462387*, MW462541*, MW462462*, MW462310*, MW462623*, MW414589*; ***Macrolenes pachygyna*** (Korth.) M.P.Nayar, Indonesia, Borneo, *A. Kartonegoro 777* (BO), MW462389*, MW462543*, MW462463*, MW462311*, MW462625*, MW414590*; ***Macrolenes porphyrocarpa*** (Ridl.) Karton. (*Dissochaeta porphyrocarpa*), Malaysia, Borneo, *D.S. Penneys 2486* (WNC), MW462367*, MW462518*, MW462441*, MW462286*, MW462599*, MW414567*; ***Macrolenes rostrata*** (Korth.) Karton. (*Dissochaeta rostrata*), Indonesia, Borneo, *R. Susanti 264* (BO), MW462373*, MW462523*, MW462445*, MW462293*, MW462604*, MW414570*; ***Macrolenes stellulata*** (Jack) Bakh.f., Indonesia, Borneo, *R. Susanti 297* (BO), MW462390*, MW462544*, MW462464*, MW462313*, MW462626*, MW414591*; ***Macrolenes subulata*** J.F.Maxwell, Indonesia, Sumatra, *Hughes et al. SUBOE71* (BO), MW462391*, MW462545*, MW462465*, MW462314*, MW462627*, MW414592*; ***Macrolenes tuberculata*** Karton., Indonesia, Borneo, *A. Kartonegoro 1128* (BO), MW462392*, MW462546*, MW462466*, MW462315*, MW462628*, MW414593*; ***Medinilla amplectens*** Regalado, Malaysia, Borneo, *Y. Liu 663* (SYS), –, MN031219, MK994882, MK994882, MK994882, MK994882; ***Medinilla beamanii*** Regalado, Malaysia, Borneo, *Y. Liu 658* (SYS), –, MN031220, MK994880, MK994880, MK994880, MK994880; ***Medinilla chermezonii*** H.Perrier, Madagascar, *Patrice 8570* (MO), MG518536, MG518548, MG702557, MG518563, –, –; ***Medinilla crassinervia*** Blume, Indonesia, Sulawesi, *A. Kartonegoro 1055* (BO), MW462393*, MW462547*, MW462467*, MW462316*, MW462629*, MW414594*; ***Medinilla humbertiana*** H.Perrier, –, –, AF215557, –, AF215517, AF215602; ***Medinilla intermedia*** Blume, Indonesia, Java, *A. Kartonegoro 1109* (BO), –, –, MW462468*, MW462318*, MW462630*, MW414595*; ***Medinilla lophoclada*** Baker, Madagascar, *J.A. Ramahenina 327* (MO), MG518537, –, MG702558, MG518564, –, –; ***Medinilla micrantha*** Jum. & H.Perrier, Madagascar, *J.A. Ramahenina 271* (MO), MG518538, –, MG702559, MG518565, –, –; ***Medinilla myrtiformis*** Triana, Indonesia, Sulawesi, *A. Kartonegoro 924* (BO), –, –, MW462469*, MW462319*, MW462631*, MW414596*; ***Medinilla rubicunda*** (Jack) Blume, Indonesia, Sumatra, *A. Kartonegoro 1072* (BO), –, –, MW462470*, MW462320*, MW462632*, MW414597*; ***Medinilla speciosa*** (Reinw. ex Blume) Blume, Malaysia, Borneo, *Y. Liu 669* (SYS), –, MN031221, MK994885, MK994885, MK994885, MK994885; ***Medinilla squillula*** Veldkamp, Indonesia, Moluccas, *P.P. Lowry II 7287* (MO), MG518539, MG518547, MG702560, MG518566, –, –; ***Medinilla teysmannii*** Miq., Indonesia, Sulawesi, *A. Kartonegoro 934* (BO), MW462394*, –, MW462471*, MW462322*, MW462633*, MW414598*; ***Ochthocharis borneensis*** Blume, Malaysia, Borneo, *Y. Liu 689* (SYS), –, –, MK994895, MK994895, MK994895, MK994895; ***Ochthocharis dicellandroides*** (Gilg) C.Hansen & Wickens, Gabon, *E. Bidault et al. 2116* (BRLU), MG518526, –, MG702562, MG518550, –, –; ***Pachycentria constricta*** (Blume) Blume, Indonesia, Sumatra, *A. Kartonegoro 1076* (BO), MW462397*, MW462548*, MW462474*, MW462326*, MW462636*, MW414601*; ***Pachycentria varingiaefolia*** (Blume) Blume, Indonesia, Sumatra, *S. Barber 76* (E), –, MW462549*, MW462475*, MW462327*, MW462637*, MW414602*; ***Pseudodissochaeta assamica*** (C.B.Clarke) M.P.Nayar (*Medinilla assamica*), China, *Y. Liu 590* (SYS), –, MG644480, MK994848, MK994848, MK994848, MK994848; ***Pseudodissochaeta lanceata*** M.P.Nayar (*Medinilla lanceata*), China, *Y. Liu 593* (SYS), –, MN031232, MK994850, MK994850, MK994850, MK994850; ***Pseudodissochaeta spetentrionalis*** (W.W.Sm.) M.P.Nayar (*Medinilla septentrionalis*), China, *Y. Liu 618* (SYS), –, MN031231, MK994778, MK994778, MK994778, MK994778.