



Universiteit
Leiden
The Netherlands

Systematics and biogeography of the Dissochaeta alliance (Melastomataceae)

Kartonegoro, A.

Citation

Kartonegoro, A. (2021, October 14). *Systematics and biogeography of the Dissochaeta alliance (Melastomataceae)*. Retrieved from <https://hdl.handle.net/1887/3217085>

Version: Publisher's Version

License: [Licence agreement concerning inclusion of doctoral thesis in the Institutional Repository of the University of Leiden](#)

Downloaded from: <https://hdl.handle.net/1887/3217085>

Note: To cite this publication please use the final published version (if applicable).

CHAPTER 7

Historical Biogeography of the Southeast Asian and Malesian tribe Dissochaeteae (Melastomataceae)

Published in: *Journal of Systematics and Evolution*
(Early online Version). 2021

Historical Biogeography of the Southeast Asian and Malesian tribe Dissochaeteae (Melastomataceae)

Abdulrokhman Kartonegoro^{1,2,3}, Sylvia Mota de Oliveira¹,
Peter C. van Welzen^{1,2}

¹ Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands

² Institute of Biology Leiden (IBL), Leiden University, P.O. Box 9505, 2300 RA Leiden, The Netherlands

³ Research Center for Biology, Indonesian Institute of Sciences (LIPI), Jl. Jakarta-Bogor KM.46, Cibinong 16911, Indonesia

Abstract

The region of Tropical Southeast Asia and the Malay Archipelago is a very appealing area for research because of its outstanding biodiversity, being one of the most species-rich areas in the world with high levels of endemism, and because of its complex geological history. The high number of species in tribe Dissochaeteae (Melastomataceae) and their tendency to narrow endemism makes the tribe an ideal group for examining biogeographic patterns. We sampled 58 accessions spread over 42 accepted and two undescribed species of the Dissochaeteae. Two nuclear (ETS, ITS) and four chloroplast regions (*ndhF*, *psbK-psbL*, *rbcL*, *rpl16*) were used for divergence time estimation and ancestral area reconstruction. Results from the molecular dating analysis suggest that the diversity of Dissochaeteae in the Southeast Asian region resulted from a South American ancestor in the late Eocene. The ancestor of the Dissochaeteae might have migrated from South America to Southeast Asia via North America and then entered Eurasia over the North Atlantic land bridge during the Eocene. The origin and early diversification of the Dissochaeteae in Southeast Asia dates back to the middle Oligocene, and most of the genera originated during the Miocene. Indochina and Borneo are most likely the area of origin for the most recent common ancestor of the Dissochaeteae and for many of the early diverging clades of some genera within Southeast Asia.

Keywords

Ancestral area reconstruction, Dissochaeteae, divergence time estimation, historical biogeography, Malesia, Melastomataceae, shrubs, Southeast Asia, tropical rain forests.

Introduction

The region of Tropical Southeast Asia and the Malay Archipelago (Malesia) is a very appealing area for research because of its outstanding biodiversity, being one of the most species-rich areas in the world (Lohman et al. 2011; Grudinski et al. 2014; Atkins et al. 2020), with high levels of endemism, and a complex geological history (Hall 2002, 2009; Grudinski et al. 2014). The area harbours 20–25% of the world's vascular plants and is the meeting point of many biotas from various origins (Woodruff, 2010; van Welzen et al. 2011; Richardson et al. 2012; Zhou et al. 2019b). The vegetation of Southeast Asia has been influenced by the, still continuing, Asian–Australian collision, although the extensive forests of the western part were not substantially invaded by Australian elements (Richardson et al.

2012; De Bruyn et al. 2104). It contains the biodiversity hotspots of Indo-Burma, Sundaland, Wallacea, and Papuasias (Myers et al. 2000; Mittermeier et al. 2003; Brooks et al. 2006; Cannon et al. 2009). The Malesian region, as part of Southeast Asia, extends from the Malay Peninsula eastwards to Papua New Guinea (van Steenis 1950; Raes & van Welzen 2009) and contains an estimated 42,000 plant species of which 70% are endemic (Roos 1993; van Welzen et al. 2005). The high biodiversity is to a high extent the result of the very complex plate tectonic movements and resulting islands and orogenesis during the last 50 million years (Hall 2009; Woodruff 2010; De Bruyn et al. 2014; Atkins et al. 2020). Plant dispersals in Malesia have facilitated the floristic exchange between the continents of Asia and Australia (Crayn et al. 2015; Buerki et al. 2016; Thomas et al. 2017). However, the origins of the region's flora and its biogeographic patterns in this region are still incompletely understood and remain a focus for many botanists (Baker & Couvreur 2012; Richardson et al. 2012). The importance of linking biogeographical patterns to the phylogeny of different taxa lays in the fact that the current flora is the result of evolutionary events that are spread over geological time, and therefore differ among taxa, hampering any generalization.

Phytogeographically, Malesia can be separated into three main subregions, coinciding with three of the biodiversity hotspots: West Malesia or the Sunda Shelf, Wallacea, and east Malesia or the Sahul Shelf (New Guinea) (Raes & van Welzen 2009; van Welzen et al. 2011; Atkins et al. 2020). All areas (except Palawan and a few neighboring islands that rafted from China) originated at some time from the Australian part of Gondwana, whereby west Malesia and parts of Southeast Asia mainland, split off as various terranes, and arrived much earlier at their more or less present position than the Wallacean Islands and the Sahul Shelf. For the distribution patterns of recent groups, the Sunda Shelf is a part of Asia. The Philippines in Wallacea are an amalgamation of island arcs at the edge of the Philippine plate and areas colliding from the east (part of the outer Melanesian Arc) and west (Palawan and Culion) (Hall 2009). Borneo in the west and New Guinea in the east represent the two most important centres of plant species richness and endemism within Malesia (van Welzen et al. 2005; Su & Saunders 2009; De Bruyn et al. 2014; Atkins et al. 2020). The quaternary cycles of glacial and interglacial events together with related changes in the climate affected the sea levels, island connectivity, species occurrences and contractions and expansions in vegetation ranges (Woodruff 2010; van Welzen et al. 2011; Cannon 2012; Morley 2012). Several phylogenetic and biogeographical studies of Malesian plant taxa assumed the three main biogeographic origins of Malesian lineages: (1) Eurasia, with colonization via continental Southeast Asia, e.g. numerous taxa of boreotropical origin (Morley 2003; Li et al. 2017; Zhou et al. 2019; Atkins et al. 2020; Yu & van Welzen 2020) or via the mountain ranges of Taiwan Island and the Philippines (van Steenis 1964); (2) Gondwanan origin via the rafting Indian fragment into continental Southeast Asia (Thomas et al. 2012; Nauheimer et al. 2012) or via migration along the Arabian and south Asian coasts (Sirichamorn et al. 2014; Chen et al. 2019); (3) Australia, with colonization from the Australian continent (Barker et al. 2007; Morley 2003).

The tribe Dissochaeteae (Melastomataceae) comprises six genera and c. 90 species of shrubs, that inhabit the tropical lowland and lower to mid-montane rainforests in Southeast Asia, ranging from Bhutan, NE India, Myanmar, South China, Indochina, Thailand and throughout the Malesian Region (Kartonegoro et al. 2021). The centre of diversity of the group in Southeast Asia is in west Malesia (Malay Peninsula, Sumatra, Borneo) with more than 75% of all species (Maxwell 1984; Kartonegoro et al. 2018, 2019, 2020). Morphologically, the tribe contains shrubs with an erect habit (*Pseudodissochaeta* M.P.Nayar, 5 species), epiphytes or climbers (*Creochiton* Blume, 12 species) and woody scramblers or climbers

(*Dalenia* Korth., 9 species; *Diplectria* (Blume) Rchb., 7 species; *Dissochaeta* Blume, 30 species; *Macrolenes* Naudin, 17 species) (Kartonegoro et al. 2021). Other typical characters of this group are the swollen nodes with distinct interpetiolar lines or growth, thyrsoid inflorescences, 4-merous diplostemonous flowers with iso- or dimorphic stamens, and fleshy berries as fruits (Kartonegoro et al. 2021). The fruits of the species in the Dissochaeteae are likely dispersed by birds or small mammals, like in other Melastomataceae taxa with berries (Renner 2004b), but observations are lacking. Recent molecular phylogenetic studies revealed the monophyly of the tribe Dissochaeteae, from which some genera are excluded as they are part of the *Medinilla* alliance, closely related to the Sonerileae (Zeng et al. 2016; Zhou et al. 2019b; Kartonegoro et al. 2021).

Previous phylogenetic and biogeographical studies have focused on the diversification of the polyphyletic Dissochaeteae s.l., including the *Medinilla* alliance, which are not closely related to the *Dissochaeta* alliance (Renner et al. 2001a; Berger et al. 2016; Veranso-Libalah et al. 2018; Zhou et al. 2019b). The stem age of Dissochaeteae s.l. (including Sonerileae) was estimated to be 38 Ma (Berger et al. 2016), 39.63 Ma (Veranso-Libalah et al. 2018), or 34.78 Ma (Morley & Dick 2003), all in the same range with an expected origin in South America. Two alternative routes of dispersal of (the ancestors of) this large group from South America were hypothesized: (1) Long distance oceanic dispersal of the lineages to the Old World is possible via trans-Atlantic stepping stones during the late Oligocene (Veranso-Libalah et al. 2018); or (2) migration from South America to North America and then to Eurasia via the North Atlantic land bridge and a subsequential spread to SE Asia during the Eocene when the global temperature was still high (Zhou et al. 2019b). The basal clade of Dissochaeteae s.l./Sonerileae is estimated to have originated c. 17.31 Ma and diversified in Southeast Asia following the second scenario (Zhou et al. 2019b). However, the limited samples used in the previous studies are not suitable to accurately describe the biogeographical patterns, diversification rates and dispersal routes within the Dissochaeteae in Southeast Asia, particularly in the Malesian region. Here, we present a broad sampling of the Dissochaeteae from various localities across Southeast Asia that has been used to construct a well-resolved phylogenetic tree based on a combination of nuclear and chloroplast markers. We use these data to estimate divergence times, ancestral ranges, and biogeographical patterns in order to gain insights in the evolutionary history of Dissochaeteae.

Material and Methods

Taxon sampling, DNA sequencing and sequence alignment

A total of 58 accessions from 42 accepted and two undescribed species in the tribe Dissochaeteae were sampled, which is the same set as used for the phylogeny analysis of the group by Kartonegoro et al. (2021). Forty-four species (out of c. 90) and one variety of the tribe represent: *Creochiton* (12 spp. in total/3 species + 1 undescribed species sampled), *Dalenia* (9/3 species + 1 variety), *Diplectria* (7/3 species + 1 undescribed species sampled), *Dissochaeta* (30/16), *Macrolenes* (27/14), and *Pseudodissochaeta* (5/3). As outgroup, 99 species were selected from Astronieae (2), Bertolonieae (3), Blakeeae (3), Cambessedesieae (2), *Dinophora* alliance (3), Eriocnemeae (1), Henrietteae (3), Kibessieae (6), Marcetieae (4), *Medinilla* alliance (16), Melastomateae (17), Merianieae (6), Miconieae (7), Microlicieae (1), Olisbeoideae (2), Oxysporeae (10), Rhexieae (3), Sonerileae (7) and Trioleneae (3). A complete list of the taxa sampled in this study, voucher information, and Genbank accession numbers are provided in Appendix 7-1.

Total genomic DNA was extracted and selected markers were sequenced and aligned as described in Kartonegoro et al. (2021). The selected markers consisted of two nuclear (ribosomal internal transcribed spacers [nrITS] and ribosomal external transcribed spacer [nrETS]) and four plastid loci (*ndhF*, *psbK-psbL*, *rbcL*, *rpl16*). Some of the sequences were downloaded from the nucleotide database of the National Centre for Biotechnology Information (<http://www.ncbi.nlm.nih.gov>).

Divergence time estimation

Four dating priors were utilized to estimate the divergence times, two secondary calibrations from a recent study of Myrtales (Berger et al. 2016) and Asian Sonerileae (Zhou et al. 2019b), and two fossils of Melastomataceae that were widely used in previous biogeographical studies of the family (Renner et al. 2001a; Morley & Dick 2003; Renner 2004a, 2004b; Veranso-Libalah et al. 2018; Zhou et al. 2019b). The Melastomataceae crown node (Fig. 7-1, point a) was calibrated using a secondary calibration to constrain the age estimate for the most recent common ancestor (MRCA) of Melastomataceae at 64.5 Ma (74.8–56.1 Ma; 95% HPD). The age of the Asian Sonerileae (Fig. 7-1, point c) was constrained at 20.25 Ma (15.71–25.24; 95% HPD). The Melastomatoideae (excluding Olisbeoideae and Kibessieae) crown node (Fig. 7-1, point b) was calibrated using the age of *Acrovenia laevis* Hickey, a fossilized leaf from the Eocene (c. 53 Ma) of northwestern North America (Hickey 1977). Another fossil calibration is from the Miocene, Rhexieae seed from Eurasia to constrain the crown node of Rhexieae (Fig. 7-1, point d) (26–23 Ma; Collinson & Pinggen 1992). We selected a normal distribution prior for the secondary calibration with a standard deviation of 6.5 for the Melastomataceae and 3.5 for the Asian Sonerileae crown node, equivalent to the 95% estimated HPD (Berger et al. 2016; Zhou et al. 2019b). For fossil calibrations, we selected a lognormal distribution prior with a mean of 1.5 and standard deviation of 1, with the off-sets (minimum bounds) 53 for Melastomatoideae (point b) and 23 for Rhexieae (point d), allowing the possibility that these nodes are older than the fossils themselves (Sauquet 2013; Berger et al. 2016; Veranso-Libalah et al. 2018; Zhou et al. 2019b).

Bayesian divergence time estimation was performed using BEAST v.2.4.8 (Bouckaert et al. 2014) on the CIPRES Science Gateway 3.3 (<https://www.phylo.org>; Miller et al. 2010), with data partitioned per marker. The best-fitting models for each partition dataset were determined using the Akaike information criterion (AIC) model as incorporated in jModelTest v.2.1.6 (Darriba et al. 2012). Nucleotide substitution models of sequence evolution for each partition were GTR+I+ Γ for ETS, ITS, *ndhF*, *rbcL* and GTR+ Γ for *psbK-psbL*, *rpl16*. The input file was created by BEAUti v.2.6.2 (part of the BEAST package; Bouckaert et al. 2019). We used an uncorrelated lognormal relaxed molecular clock model (Drummond et al. 2006) and the Yule tree prior (Yule 1925; Gernhard 2008), although the birth–death model resulted in a similar topology and divergence times (not shown). Four independent Markov Chain Monte Carlo (MCMC) analyses were run, each of 200 million generations and sampling every 20,000 generations. Output log files were analysed using Tracer v.1.7.1 (Rambaut et al. 2018) to assess the degree of convergence and adequate effective sample sizes (ESS) for each parameter (> 200). As “burn-in”, 10% of the samples of each run were removed prior to combining the independent runs using LogCombiner v.2.6.2 (Bouckaert et al. 2019). The Maximum Clade Credibility (MCC) tree was generated using TreeAnnotator v.2.6.2 (Bouckaert et al. 2019), which was visualized with FigTree v.1.4 (Rambaut 2009).

Ancestral area reconstruction

Bayesian-based statistical dispersal–vicariance analysis (S-DIVA) for ancestral area reconstructions (Yu et al. 2010; based on DIVA by Ronquist 1996a, 1996b, 1997) and likelihood-based analyses under the statistical dispersal-extinction-cladogenesis (S-DEC) model (based on the method by Ree & Smith 2008), implemented in RASP v.3.02 (Reconstruct ancestral State in Phylogenies; Yu et al. 2015), were used to reconstruct ancestral areas at internal nodes. Prior dispersal constraints between the areas in four timeframes (S-DEC) were defined based on the geographical distances at the relevant time of Southeast Asia (Hall 2002, 2009) and is equal to the constraints used by Yu & van Welzen (2020, their table 2, see there). All analyses were based on the output trees and the MCC tree from the BEAST divergence time analyses. For both S-DIVA and S-DEC, the maximum number of ancestral areas at each node was constrained to two as ancestral ranges were assumed to be similar to the ranges of extant species. The MCC tree was pruned from the outgroups to include only the ingroup (Dissochaeteae) to avoid potential bias at the root. For species represented by multiple accessions all but one accession was pruned. The only exceptions are when multiple accessions, representing different morphological forms and different distribution area or islands, were included.

Each taxon was assigned presence in one or more biogeographical area(s) based on its extant distribution in nine geographic regions, based on a combination of geological information of Southeast Asia (Hall 2002, 2012; van Welzen et al. 2011), previous biogeographical studies (Nauheimer et al. 2012; Yu & van Welzen 2020; Atkins et al. 2020; Yu & van Welzen 2020), and current knowledge of species distributions and relationships in the Dissochaeteae (Maxwell 1984; Kartonegoro & Veldkamp 2013; Kartonegoro et al. 2018, 2019). The nine biogeographical areas are: A = East Bhutan, Northeast India and Northwest Myanmar; B = Indo-China (incl. Cambodia, Laos, Central to East Myanmar, South China, Hainan, Thailand and Vietnam); C = Southern Thailand and Malay Peninsula (incl. Riau Archipelago); D = Sumatra and its adjacent islands; E = Java and Lesser Sunda Islands; F = Borneo; G = Sulawesi; H = the Philippine Islands; I = Moluccas and New Guinea (incl. the Bismarck Archipelago). The distribution of sampled taxa based on biogeographical regions assigned above are shown in Table 7-1.

Table 7-1. Distribution of the sampled taxa. The abbreviations in the column ‘distributions’ refer to the biogeographical areas assigned in the ancestral area analyses.

Taxon	Distribution
<i>Creochiton bibracteatus</i> (Blume) Blume	E
<i>Creochiton ledermannii</i> Mansf.	I
<i>Creochiton roseus</i> Merr.	GH
<i>Creochiton</i> sp. “Sulawesi”	G
<i>Dalenia beccariana</i> (Cogn.) M.P.Nayar	F
<i>Dalenia glabra</i> (Merr.) Karton. var. <i>glabra</i>	F
<i>Dalenia glabra</i> (Merr.) Karton. var. <i>kinabaluensis</i> (Veldkamp) Karton.	F
<i>Dalenia magnibracteata</i> Karton.	F
<i>Diplectria conica</i> Bakh.f.	CD
<i>Diplectria divaricata</i> (Willd.) Kuntze “Borneo”	F
<i>Diplectria divaricata</i> (Willd.) Kuntze “Enggano”	D
<i>Diplectria divaricata</i> (Willd.) Kuntze “Mindanao”	H
<i>Diplectria divaricata</i> (Willd.) Kuntze “Sumatra”	D
<i>Diplectria divaricata</i> (Willd.) Kuntze “Thailand”	C
<i>Diplectria viminalis</i> (Jack) Kuntze “Borneo”	F
<i>Diplectria viminalis</i> (Jack) Kuntze “Sumatra”	D
<i>Diplectria</i> sp. “Borneo”	F
<i>Dissochaeta annulata</i> Hook.f. ex Triana “Bintan”	C

<i>Dissochaeta annulata</i> Hook.f. ex Triana “Borneo”	F
<i>Dissochaeta axillaris</i> Cogn.	F
<i>Dissochaeta bakhuizenii</i> Veldkamp	CDE
<i>Dissochaeta biligulata</i> Korth. “Bintan”	C
<i>Dissochaeta biligulata</i> Korth. “Borneo”	F
<i>Dissochaeta biligulata</i> Korth. “Sumatra”	D
<i>Dissochaeta bracteata</i> (Jack) Blume “Borneo”	F
<i>Dissochaeta bracteata</i> (Jack) Blume “Sumatra”	D
<i>Dissochaeta celebica</i> Blume “Mindanao”	H
<i>Dissochaeta celebica</i> Blume “Sulawesi”	G
<i>Dissochaeta fallax</i> (Jack) Blume	CDE
<i>Dissochaeta fusca</i> Blume	E
<i>Dissochaeta gracilis</i> (Jack) Blume	CDEF
<i>Dissochaeta griffithii</i> (M.P.Nayar) Karton.	C
<i>Dissochaeta inappendiculata</i> Blume “Java”	E
<i>Dissochaeta inappendiculata</i> Blume “Simeuleu”	D
<i>Dissochaeta pallida</i> (Jack) Blume	CD
<i>Dissochaeta punctulata</i> Hook.f. ex Triana	C
<i>Dissochaeta robinsonii</i> Merr.	GI
<i>Dissochaeta spectabilis</i> J.F.Maxwell	CD
<i>Dissochaeta vacillans</i> (Blume) Blume	E
<i>Macrolenes bipulvinata</i> (Korth.) Bakh.f.	F
<i>Macrolenes dimorpha</i> (Craib) J.F.Maxwell	C
<i>Macrolenes hirsuta</i> (Cogn.) J.F.Maxwell	F
<i>Macrolenes hirsutoidea</i> (Furtado) Karton.	F
<i>Macrolenes horrida</i> Bakhf.	D
<i>Macrolenes macrosepala</i> (Stapf) Karton.	F
<i>Macrolenes muscosa</i> (Blume) Blume “Java”	E
<i>Macrolenes muscosa</i> (Blume) Blume “Sumatra”	D
<i>Macrolenes nemorosa</i> (Jack) Bakh.f. “Borneo”	F
<i>Macrolenes nemorosa</i> (Jack) Bakh.f. “Sumatra”	D
<i>Macrolenes pachygyna</i> (Korth.) Bakh.f.	F
<i>Macrolenes porphyrocarpa</i> (Ridl.) Karton.	F
<i>Macrolenes rostrata</i> (Korth.) Karton.	F
<i>Macrolenes stellulata</i> (Jack) Bakh.f.	CDF
<i>Macrolenes subulata</i> J.F.Maxwell	D
<i>Macrolenes tuberculata</i> Karton.	D
<i>Pseudodissochaeta assamica</i> (C.B.Clarke) M.P.Nayar	A
<i>Pseudodissochaeta lanceata</i> M.P.Nayar	B
<i>Pseudodissochaeta septentrionalis</i> (W.W.Sm.) M.P.Nayar	B

Results

Divergence time estimation

The Dissochaeteae was estimated to have diverged from its closest South American relative, the Cambessedesieae, in the late Eocene (Fig. 7-1, node A; stem age: 39.32 Ma; 95% HPD: 47.03–31.69 Ma). The origin and early diversification of the Dissochaeteae in Southeast Asia dates back to the middle Oligocene (crown age 25.58 [31.93–19.51] Ma), and most of the genera originated during the Miocene. The Beast MCC tree of the Dissochaeteae including the outgroup, as generated here (Fig. 7-1), has a similar topology as the MrBayes one resulting from phylogenetic analyses by Kartonegoro et al. (2021). The MCC chronogram for the Dissochaeteae crown group is shown as Fig. 7-2 (this figure also contains all node numbers referred to below). The Indo-Burmese *Pseudodissochaeta* (node 116) branched off first from the remaining Dissochaeteae (node 114) (Fig. 7-2). The crown node of *Pseudodissochaeta* is in the late Miocene (node 116; 7.76: 13.66–2.86 Ma). The age of this crown group as found by Zhou et al. (2019b: 6.38: 10.49–2.79 Ma) is within our HPD range. A short internode with unsatisfactory resolution was observed within *Pseudodissochaeta*

(node 113), indicating the onset of speciation in the early Pleistocene (5.78: 10.82–1.74 Ma) (Fig. 7-3; Table 7-2). Next, *Creochiton* (node 111) splits off (Fig. 7-3) and this genus diverges from the scrambling shrubs genera (node 108) around the late Oligocene at stem age 25.71 (32.52–19.45) Ma and a crown age of 10.72 (16.53–5.29) Ma. The group of the scrambling shrubs (*Dalenia*, *Diplectria*, *Dissochaeta* and *Macrolenes*) has a crown age of 21.37 (27.16–16.03) Ma (node 108). The *Dalenia* clade was the first of this group to diversify (node 107) at 14.32 (21.53–6.84) Ma, with subsequent speciation during the late Miocene until Pleistocene (Fig. 7-2). The ancestor of *Diplectria* (node 103) splits off next at 15.04 (19.93–10.59) Ma, followed by the core of of *Dissochaeta* and *Macrolenes* (node 95), which originated during the transition between the middle to the late Miocene (14.37 [18.77–10.36] Ma), and diversified further in the late Miocene. *Macrolenes* (node 94) has as crown age 9.69 (13.12–5.59) Ma. The crown group of *Dissochaeta* (node 79) is from the late Miocene (11.75 [15.70–8.29] Ma). Summaries of divergence time estimates (mean ages and 95% HPD) and PP values of the *Dissochaeteae* stem node and all nodes within the *Dissochaeteae* crown group are presented in Table 7-2.

Table 7-2. Summary of the dated phylogeny and ancestral areas. Shown from left to right are node numbers of figure 2, posterior probabilities, mean ages of the stem age and 95% height of the posterior density intervals (HPD), mean ages of the crown age and 95% height of the posterior density intervals (HPD), most likely S-DEC reconstructions area and relative probability (RP), most parsimonious S-DIVA reconstructions area and marginal probability (MP) and remarks about the corresponding taxonomy. The abbreviations (A–H) indicate the areas.

Node	Posterior	Stem Age	95% HPD	Crown Age	95%HPD	S-DEC	RP	S-DIVA	MP
115	1	39.32	47.03–31.69	28.96	36.28–22.09	BF	0.22	BF	0.73
114	1	28.96	36.28–22.09	7.76	13.66–2.86	AB	0.61	B	0.65
113	0.77	7.76	13.66–2.86	5.78	10.82–1.74	AB	0.69	AB	1
112	1	28.96	36.28–22.09	25.71	32.52–19.45	F	0.31	FG	0.88
111	1	25.71	32.52–19.45	10.72	16.53–5.29	G	0.43	G	0.94
110	0.77	10.72	16.53–5.29	8.44	13.70–3.92	G	0.47	EG	1
109	1	8.44	13.70–3.92	3.66	6.97–1.00	GI	0.85	GI	1
108	1	25.71	32.52–19.45	21.37	27.16–16.03	F	0.58	F	0.91
107	1	21.37	27.16–16.03	14.32	21.53–6.84	F	0.95	F	1
106	0.98	14.32	21.53–6.84	10.07	17.48–3.44	F	1	F	1
105	1	14.32	21.53–6.84	1.72	3.65–0.31	F	1	F	1
104	1	21.37	27.16–16.03	19.3	24.59–14.29	F	0.41	F	0.94
103	1	19.30	24.59–14.29	15.04	19.93–10.59	D=DF	0.37	DF=CF	0.5
102	0.94	15.04	19.93–10.59	12.80	17.34–8.81	DF	0.43	F	0.94
101	0.94	12.80	17.34–8.81	9.21	13.55–5.05	F	0.5	F	0.91
100	1	9.21	13.55–5.05	3.57	6.53–1.15	DF	0.96	DF	1
99	1	12.80	17.34–8.81	9.15	13.09–5.57	DF	0.59	DF	0.91
98	1	9.15	13.09–5.57	5.57	9.26–2.08	CF	0.54	CF	1
97	1	9.15	13.09–5.57	5.71	9.20–2.62	D	0.82	D	1
96	1	5.71	9.20–2.62	1.21	2.55–0.21	DH	0.99	DH	1
95	1	19.30	24.59–14.29	14.37	18.77–10.36	DF	0.43	F	0.87
94	1	14.37	18.77–10.36	9.69	13.12–5.59	DF	0.76	DF	0.5
93	0.99	9.69	13.12–5.59	8.07	11.43–5.06	F	0.75	F	1
92	1	8.07	11.43–5.06	4.15	7.64–1.12	F	1	F	1
91	1	8.07	11.43–5.06	6.19	9.43–3.38	F	0.68	F	1
90	1	6.19	9.43–3.38	3.95	6.76–1.45	DF	0.75	DF	1
89	1	9.69	13.12–5.59	7.72	10.78–5.04	DF	0.63	D=DF	0.5
88	1	7.72	10.78–5.04	5.29	8.11–2.92	D	0.88	D	1
87	1	5.29	8.11–2.92	3.29	5.52–1.32	DE	0.72	DE	1
86	1	7.72	10.78–5.04	5.64	8.24–3.28	DF	0.79	DF	0.46
85	1	5.64	8.24–3.28	3.59	6.04–1.35	D	0.93	D	0.5
84	1	5.64	8.24–3.28	4.18	6.37–2.27	DF	0.51	F	0.65
83	1	4.18	6.37–2.27	2.36	4.10–0.82	F	1	F	1
82	0.29	4.18	6.37–2.27	3.65	5.67–1.78	F	0.49	F	1

81	0.27	3.65	5.67–1.78	3.24	5.44–1.19	F	0.63	F	1
80	1	3.65	5.67–1.78	1.77	3.40–0.41	DF	0.95	DF	1
79	1	14.37	18.77–10.36	11.75	15.70–8.29	D	0.64	EF=F	0.45
78	1	11.75	15.70–8.29	9.49	12.88–6.46	D	0.4	CF	0.96
77	1	9.49	12.88–6.46	4.72	8.25–1.51	DF	0.77	DF	1
76	0.87	9.49	12.88–6.46	8.42	11.53–5.50	CD	0.49	C	1
75	0.77	8.42	11.53–5.50	6.58	9.84–3.24	C	0.64	C	1
74	0.74	8.42	11.53–5.50	7.09	9.90–4.29	C	0.6	C	1
73	1	7.09	9.90–4.29	5.38	7.95–3.02	C	0.78	C	1
72	1	5.38	7.95–3.02	3.64	5.62–1.87	CF	0.84	CF	0.99
71	1	3.64	5.62–1.87	2.29	3.78–0.99	F	0.62	F	0.98
70	1	2.29	3.78–0.99	1.67	2.91–0.70	FG=FI	0.46	FG=FI	0.5
69	1	11.75	15.70–8.29	7.88	11.03–4.98	DE	0.53	E=EF	0.45
68	0.99	7.88	11.03–4.98	6.57	9.17–4.21	DE	0.37	DE	0.19
67	0.63	6.57	9.17–4.21	5.96	8.55–3.62	D	0.48	DG=DH =CD=DF	0.25
66	1	5.96	8.55–3.62	4.61	6.87–2.44	CF	0.16	CH=CF= CG	0.33
65	1	4.61	6.87–2.44	3.21	5.11–1.49	FG=FH	0.31	FH=FG	0.5
64	1	3.21	5.11–1.49	1.64	2.96–0.51	GH	0.9	GH	1
63	0.99	6.57	9.17–4.21	5.07	7.38–2.95	DE	0.36	E	0.82
62	0.99	5.07	7.38–2.95	3.72	5.70–2.01	DE	0.67	E	0.86
61	1	3.72	5.70–2.01	2.13	3.98–0.53	E	1	E	0.82
60	1	3.72	5.70–2.01	1.99	3.36–0.82	DE	0.98	DE	1
59	1	1.99	3.36–0.82	0.63	1.34–0.10	E	0.84	E	0.82

Ancestral area reconstruction

The most probable ancestral area of the Dissochaeteae (Fig. 7-3A, Table 2, node 115) was inferred to be Indo-China and Borneo (area BF) in both the S-DEC and S-DIVA analyses (Relative Probability, RP = 0.22, Marginal Probability, MP = 0.73, respectively). This was followed by ongoing dispersal and vicariance events within the crown Dissochaeteae (clade of node 115; areas BF) into Indo-Burma (the *Pseudodissochaeta* clade, areas AB; node 114) and Borneo (area F; node 112, ancestral node for the other four genera). *Pseudodissochaeta* (crown node 114, Fig. 7-3A) diverged first on mainland Southeast Asia (area AB; RP = 0.61, MP = 0.65) and speciated within Southeast Asia mainland. The other genera of the alliance then speciated on Borneo (F) or dispersed to other Malesian areas with subsequent speciation. *Creochiton* (node 111) diverged and originated on Sulawesi (area G; RP = 0.43, MP = 0.94) and dispersed and speciated within or northwards to the Philippines, westwards to Java and eastwards to New Guinea. Borneo (area F) was estimated to be the most probable ancestral area of the scrambling taxa (node 108, Fig. 7-3A, RP = 0.58, S-DIVA MP = 0.91), from there, via dispersal and speciation and/or vicariance events the group spread over the adjacent islands of Malay Peninsula, Sumatra, Java or eastwards into Sulawesi, the Philippines, the Moluccas and New Guinea. *Dalenia* diverged and originated in Borneo (area F; RP = 0.95, MP = 1.0), followed by *Diplectria* with two possibilities as ancestral areas, Sumatra (D) or Sumatra-Borneo (DF) based on S-DEC (RP = 0.37) and Sumatra-Borneo (DF) or Malay Peninsula-Borneo (CF) based on S-DIVA (MP = 0.50). *Macrolenes* has as ancestral area Sumatra-Borneo (Fig. 7-3B, area DF; RP = 0.76, MP = 0.5) and *Dissochaeta* Sumatra (D) based on S-DEC (RP = 0.64) and Java-Borneo (EF) or Borneo (F) based on S-DIVA (P = 0.45) (Fig. 7-3B). Summaries of ancestral ranges and their relative probabilities of clades within the Dissochaeteae are given in Table 7-2 and Fig. 7-3A & 7-3B.

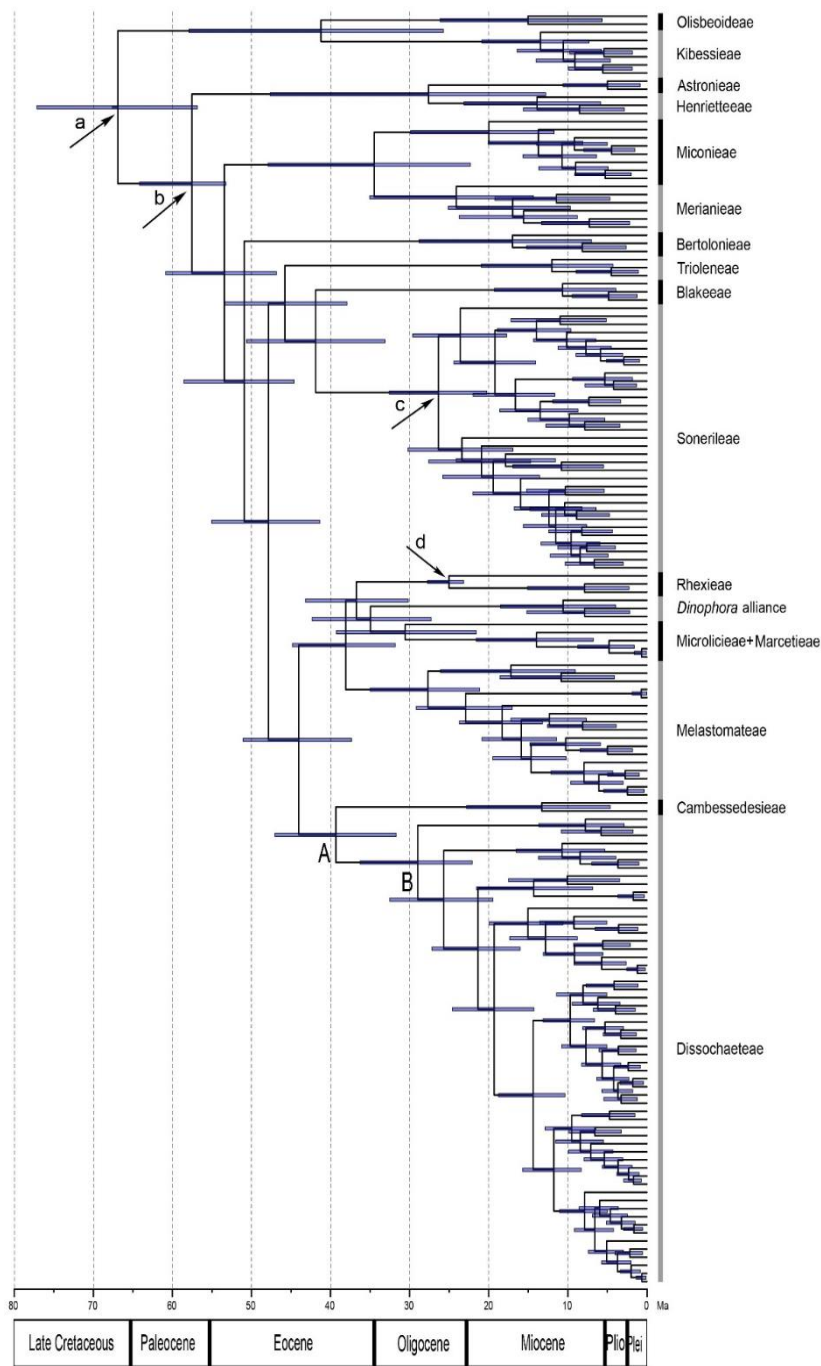


Fig. 7-1. Maximum clade credibility chronogram of the Dissochaeteae and outgroups. The blue node bars represent the 95% Highest Posterior Density intervals (HPD). **A.** Stem age of the Dissochaeteae; **B.** crown age the Dissochaeteae. Arrows refer to the calibration points: **a.** MRCA Melastomataceae; **b.** crown Melastomatoideae (excl. Olisbeoideae + Kibessieae); **c.** crown Asian Sonerileae; **d.** crown Rhexieae. (a & c secondary calibration; b & d fossil calibration). Ma = million years ago; Plei = Pleistocene; Plio = Pliocene.

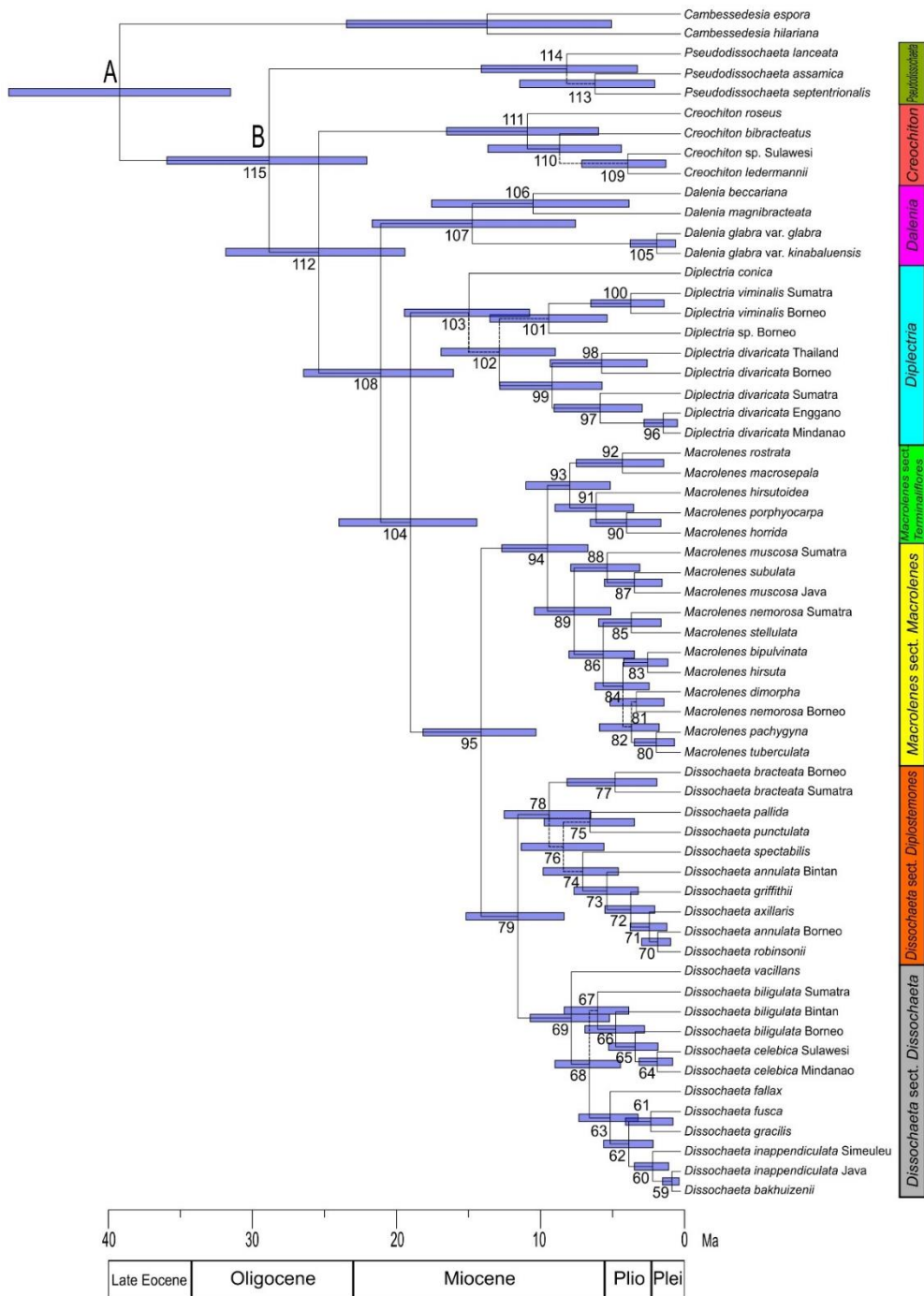


Fig. 7-2. Maximum clade credibility chronogram of the Dissochaeteae (**B**) including the Cambessedesieae as outgroup (**A**); the blue node bars representing the 95% HPD (highest posterior density intervals). Dashed branches lead to nodes with posterior clade probabilities of <0.95. Node numbers correspond to Table 1. Ma = million years ago; Plei = Pleistocene; Plio = Pliocene.

Discussion

Phylogeny

Our Dissochaeteae and outgroup MCC tree (Fig. 7-1) is in general similar to the Melastomataceae MCC tree of Renner et al. (2001a), Berger et al. (2016), Veranso-Libalah et al. (2018) and Zhou et al. (2019b), which describe the same topologies. Most of the previous studies suggested that the origin of Melastomataceae was in the late Cretaceous and the crown age is early Paleocene, which is confirmed here. The crown age of the Melastomataceae here is estimated to be 66.91 (77.14–56.83) Ma. Olisbeoideae and Kibessieae are recognized as the basal clades that diversified within the Melastomataceae, followed by the remaining groups in the family (Fig. 7-1). The MCC tree topology of the Dissochaeteae (clade B) is similar in topology with the other phylogenetic trees of the group (Kartonegoro et al. 2021). The Dissochaeteae s.l., which include the *Medinilla* alliance and *Dinophora-Ochthocharis*, appeared to be not monophyletic. The newly defined Dissochaeteae (s.str.) now only includes the monophyletic *Dissochaeta* alliance with convincing and strong support values (Kartonegoro et al. 2021). The sister group of the newly defined Dissochaeteae is the South American Cambessedesieae (Fig. 7-1). Within the tribe, six distinct and strongly supported clades (genera) are recognized (Fig. 7-2). They are *Creochiton*, *Dalenia*, *Diplectria*, *Dissochaeta*, *Macrolenes* and *Pseudodissochaeta*.

Diversification of Dissochaeteae

The biogeographical reconstructions (Fig. 7-1, 7-2) showed that the Dissochaeteae originated from a South American ancestor in the late Eocene (Fig. 7-1, node A; stem age 39.32 Ma; 95% HPD 47.03–31.69). Two scenarios may likely explain the migration to Southeast Asia. The ancestor of the Dissochaeteae might have migrated from South America to Southeast Asia via North America and then entered Eurasia over the North Atlantic land bridge during the Eocene, when the global temperatures were warmer and tropical forests had expanded northwards and occupied regions from the equator to mid-latitudes across all northern continents (Li et al. 2017; Zhou et al. 2019b). The existence of the boreotropical forests and the North American land bridges connecting the Old and the New Worlds enabled intercontinental biotic exchange of tropical forest taxa in both directions (Brikiatis 2014; Li et al. 2017). This hypothesis is also supported by Eocene Melastomataceae fossils discovered from North America (Hickey 1977). The alternative migration scenario from South America is a direct trans-Atlantic (long distance) dispersal of the lineages to Africa via oceanic stepping stones and dispersal from Africa to Southeast Asia as proposed for tribe Melastomateae by Veranso-Libalah et al. (2018). Our study, in combination with the evidence given by the North American fossils, suggests that the first scenario is more plausible. Also, migration from North America to Asia during middle to late Eocene has been identified in the phylogeny of different plant taxa, such as Annonaceae clade of *Asimina* Adans. / *Disepalum* Hook.f. (Li et al. 2017) and the legume clade *Cladrastis* Raf. (Duan et al. 2020).

The divergence time between the sister groups Cambessedesieae and the Dissochaeteae is estimated at 39.32 Ma (Figs. 7-1, 7-2, Node A; 95% HPD 47.03–31.69) during the late Eocene, with vicariance resulting in two groups, one restricted to the Neotropics (Cambessedesieae) and the other to Southeast Asia (Dissochaeteae), respectively. The decline of global temperatures around the Eocene-Oligocene boundary constricted and fragmented boreotropical forests, resulting in the extinction/disappearance of the northern

mid-latitudinal tropical vegetations and their migration southwards to tropical regions like in Southeast Asia (Morley 2003; Li et al. 2017).

Our result agrees with Zhou et al. (2019b), who also postulated the splitting of the Dissochaeteae from the South American lineage, though based on different phylogenetic data. Therefore, there are also differences with Zhou et al. (2019b). Based on a limited sampling, Zhou et al. (2019b) estimated the crown age of the Dissochaeteae (*Dissochaeta-Pseudodissochaeta*) clade at 17.31 Ma (95% HPD: 24.22–10.72), which is younger than what we found. The slightly older stem age recovered in the present analysis is likely due to the inclusion of a broader ingroup sampling and the inclusion of a more closely related outgroup taxon, Cambessedesieae. This differs from Zhou et al. (2019b), who found the Sonerileae-Oxysporeae to be the sister group.

The pattern of diversification in the late Miocene, mostly the result of speciation in the last 10–5 Ma, is reported in other Southeast Asian genera such as *Artabotrys* R.Br. (Annonaceae; Chen et al. 2019), *Begonia* L. (Begoniaceae; Thomas et al. 2012) and *Cyrtandra* J.R.Forst. & G.Forst (Gesneriaceae; Atkins et al. 2020). There are a number of geological factors, which are likely to have been drivers of diversification during this period. During the late Oligocene to early Miocene, the Sunda and Sahul shelves moved closer together, creating land in the centre of the region for the first time (Hall 2002, 2009). The climate and sea level fluctuations of the Pleistocene glacial periods resulted in cyclic vicariance with frequent habitat fragmentations and amalgamations (Voris 2000; Woodruff 2010; Cannon 2012; Morley 2012). During glacial periods, when due to sea level drops many islands were connected, species may have become widespread, while during interglacials rises in sea level broke up the distributions, which likely resulted in speciations.

Table 7-3. Summary of the crown age and ancestral areas reconstruction from S-DEC and S-DIVA analyses of genera and sections in Dissochaeteae.

Genera/sections	Crown Age (Ma)	95% HPD	Ancestral Area	
			S-DEC	S-DIVA
<i>Pseudodissochaeta</i>	7.76	13.66–2.86	NE India & Indochina	Indochina
<i>Creochiton</i>	10.72	16.53–5.29	Sulawesi	Sulawesi
<i>Dalenia</i>	14.32	21.53–6.84	Borneo	Borneo
<i>Diplectria</i>	15.04	19.93–10.59	Sumatra=Sumatra-Borneo	Sumatra-Borneo =Malay Peninsula-Borneo
<i>Macrolenes</i>	9.69	13.12–5.59	Sumatra-Borneo	Sumatra-Borneo
<i>Macrolenes</i> sect. <i>Terminaliflores</i>	8.07	11.43–5.06	Borneo	Borneo
<i>Macrolenes</i> sect. <i>Macrolenes</i>	7.72	10.78–5.04	Sumatra-Borneo	Sumatra=Sumatra-Borneo
<i>Dissochaeta</i>	11.75	15.70–8.29	Sumatra	Java-Borneo=Borneo
<i>Dissochaeta</i> sect. <i>Diplostemones</i>	9.49	12.88–6.46	Sumatra	Malay Peninsula-Borneo
<i>Dissochaeta</i> sect. <i>Dissochaeta</i>	7.88	11.03–4.98	Sumatra-Java	Java=Java-Borneo

Ancestral range reconstruction

Indochina and Borneo (BF) are most likely the area of origin for the most recent common ancestor of the Dissochaeteae (Fig. 7-3A; node 115) and for many of the early diverging clades of some genera within Southeast Asia based on DEC and S-DIVA analyses. They are also the species richest areas (c. 70% of the species) and show the most abundant

morphological diversity. The combination of Indochina and Borneo represents a large area, long ago emerged (Indochina and south Borneo), and since then with a stable geological history and covered by extensive rainforests, also during glacial maxima; this offers a compelling explanation for the in-situ diversification of the Dissochaeteae (Hall 2012; De Bruyn et al. 2014).

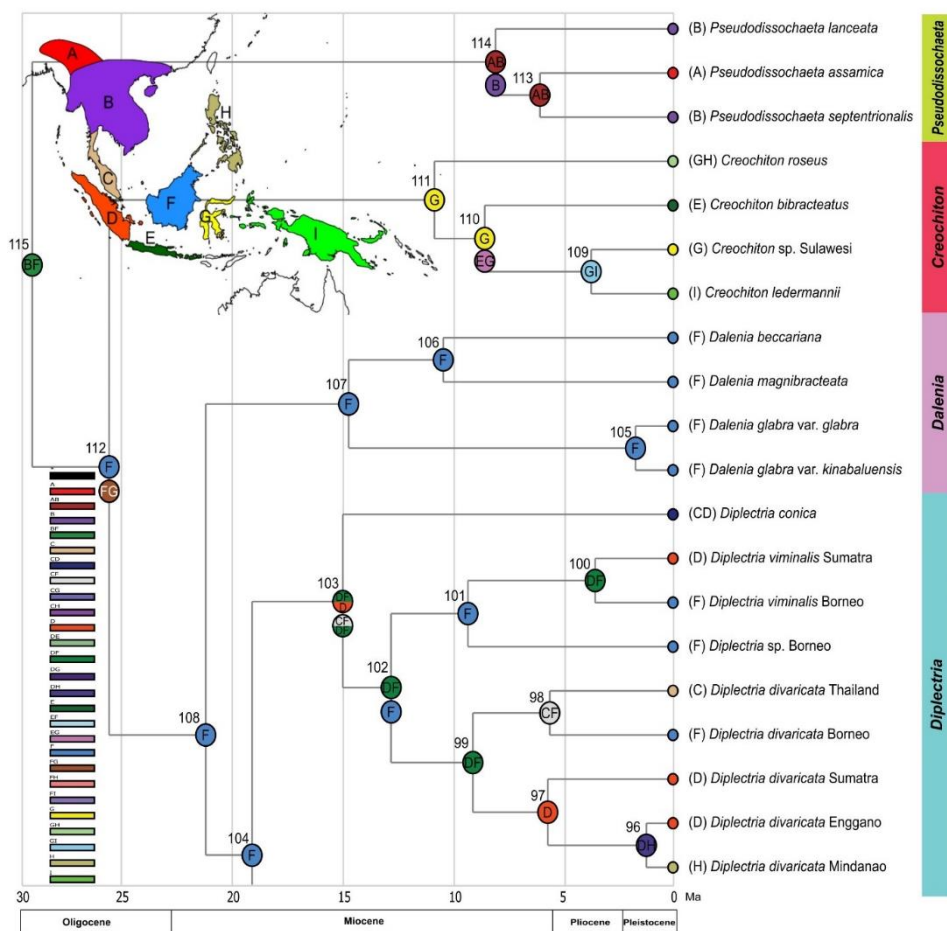


Fig. 7-3A. Ancestral range optimization for the Dissochaeteae. Pie charts at nodes represent optimization under maximum-likelihood S-DEC. When S-DIVA analyses yield a different optimization, then the results are shown below to the relevant nodes. Node numbers indicated next to pie charts correspond to Table 7-2. Colours in the pie charts correspond with geographical areas (see inset map); Ma, million years ago. **A** = E Bhutan, NE India and NW Myanmar; **B** = Indochina, incl. C & E Myanmar, S China, Hainan and Thailand; **C** = S Thailand, Malay Peninsula and Riau Archipelago; **D** = Sumatra and surrounding islands; **E** = Java and Lesser Sunda Islands excl. Sumba, Flores and Timor; **F** = Borneo; **G** = Sulawesi; **H** = Philippines incl. Palawan; and **I** = Moluccas and New Guinea. Map source using DIVA-GIS (<http://www.diva-gis.org/>) with modification.

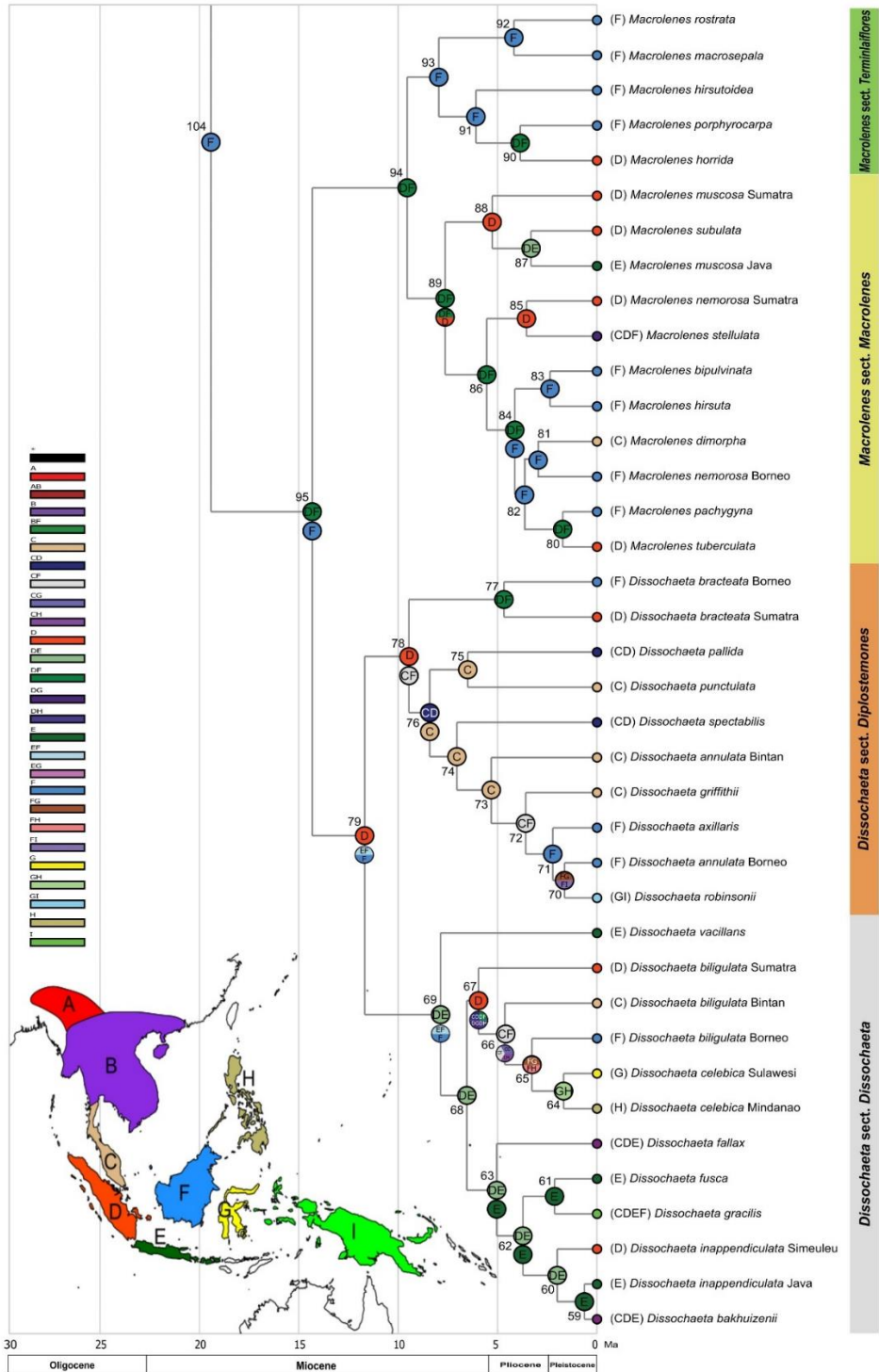


Fig. 7-3B. Continuation of Fig. 7-3A

A split between the basal Indo-Burmese and a predominantly Malesian clade occurred in the Middle Oligocene (clade 115; Figure 7-3A). Dispersal from Indo-China (B) westward into Bhutan, NE India and W Myanmar occurred at the time of at least node 114 (origin of the genus *Pseudodissochaeta*; Fig. 7-3A, Table 7-3: area AB). Colonization of west Malesia and western Wallacea (the Philippines, Sulawesi) by the Dissochaeteae started at the time of the ancestral nodes 115 and 112 (Fig. 7-3A) during the middle Oligocene and early Miocene. The S-DEC analysis indicated Borneo (F) as the origin of Malesian diversification of this group, while the S-DIVA analysis included Sulawesi (FG) as ancestral area (Fig. 7-3A; node 112). Part of west Sulawesi was already close to Borneo, before the east Malesian microplates came close and especially volcanoes could have been colonized early (Hall 2002, 2009). Hall often implied that most east Malesian microplates were submerged when they moved, but dispersal patterns show that it is very likely that more areas were above water than described by Hall (2009), and thus already offered stepping stones for dispersal (van Welzen et al. 2005). After the origin in Borneo, the Malesian taxa started to disperse mainly within west Malesia, but also eastwards, but few crossed Wallace's Line, mainly from Borneo to Sulawesi, passing the narrow, but deep and fast flowing Makassar Strait (*Dissochaeta celebica* Blume, *D. robinsonii* Merr.). Dispersal within the west Malesia region can potentially be explained by overland dispersal when most of extant islands were perhaps still connected (Hall 2009).

Dispersal of some lineages within west Malesia or Wallacea eastwards to the Sahul Shelf (New Guinea) occurred in the late Pliocene and early Pleistocene (nodes 109 and 70; Fig. 7-3A, 7-3B). Initial diversification in Southeast Asia mainland to western Malesia and subsequent dispersal events from western Malesia to eastern Malesia from the early Miocene onwards have been inferred for lineages of several angiosperm genera such as *Aglaia* Lour. (Meliaceae; Grudinski et al. 2014), *Artabotrys* (Annonaceae; Chen et al. 2019), *Begonia* (Begoniaceae; Thomas et al. 2012a), *Cyrtandra* (Gesneriaceae; Atkins et al. 2020), *Goniothalamus* (Blume) Hook.f. & Thomson (Annonaceae; Thomas et al. 2017), *Meiogyne* Miq. - *Fitzalania* F.Muell. (Annonaceae; Thomas et al. 2012b), *Pseuduvaria* Miq. (Annonaceae; Su & Saunders 2009), *Mallotus* Lour. and *Macaranga* Thouars (Euphorbiaceae; van Welzen et al. 2014) and *Trigonostemon* Blume (Euphorbiaceae; Yu & van Welzen 2020). The west to east dispersal appears to have been particularly prevalent from the mid Miocene onwards as warmer and wetter conditions prevailed, rainforest expanded and extant land emerged east of Wallace's Line (Richardson et al. 2012; Grudinski et al. 2014; Crayn et al. 2015). Still, there are examples of dispersal in the opposite direction, such as in Proteaceae (Barker et al. 2007), *Macaranga* (Euphorbiaceae, van Welzen et al. 2014) and Myrtaceae (Sytsma et al. 2004).

Creochiton (Fig. 7-3A; node 111) is the first genus that split off within the Malesian taxa of the Dissochaeteae. Sulawesi is apparently the ancestral area of the genus (Table 7-3), but this may be a sampling artifact as samples of four west Malesian species failed in the molecular analysis. Most likely is that the ancestor might have been on Borneo (before node 112, Fig. 7-2), with dispersal to Sulawesi, perhaps by birds eating the berries. The data used show three dispersal events from Sulawesi to other areas during the late Miocene and Pliocene. Dispersal northward to the southern Philippines (node 111) and eastwards to the Moluccas and New Guinea (node 109) with inter-island dispersal when the Australian plate collided and microplates emerged in Wallacea (Hall 2009). East to west dispersal back from Wallacea into Western Malesia mainly occurred in the late Miocene (8.44; 13.70–3.92 Ma; node 110) when most of the islands within Wallacea started to rise (or sea floors sank) (Hall 2002, 2009).

All species of the scrambling shrubs group, originated on Borneo, (Fig. 7-3A; node 108), have a similar habit and habitat preference. This was followed by dispersal within Borneo (nodes 108, 107, 104) and westward to Sumatra (nodes 103, 95). Within this group, *Dalenia* (node 107) originated first and mainly diversified on Borneo during the late Miocene to Pleistocene (Fig. 7-3A, Table 3). The only species outside Borneo, *Dalenia papuana* (Mansf.) Kartton. from New Guinea, was not sampled in this study, so we cannot comment on this dispersal over Wallace's line. *Diplectria* (Fig. 7-3A, Table 7-3; node 103) most likely originated on Borneo and Sumatra (DF) or Sumatra (D) after dispersal from Borneo (S-DEC optimisation). Alternatively, the S-DIVA analysis showed an origin of the genus on Borneo and Sumatra (DF) or Sumatra and the Malay Peninsula (CF) (Tables 7-2, 7-3). The Philippine *Diplectria divaricata* (Willd.) Kuntze seemingly arrived from Sumatra (nodes 97 and 96) based on both analyses. Three possible dispersal routes might qualify to explain the diversification in the Philippines; whereby all migration routes pass Borneo first and then either via Palawan, the Sulu Archipelago or Sulawesi reaching the Philippines during the Pliocene and Pleistocene. It is also possible that all routes were used as the species occur in all these areas. The migration route through Palawan or the Sulu Archipelago to the main Philippine Islands is also known for the genus *Trigonostemon* (Euphorbiaceae; Yu & van Welzen 2020).

The ancestral area of *Dissochaeta* and *Macrolenes* (splitting at node 95) is estimated to be Sumatra-Borneo (DF) based on S-DEC analysis, while S-DIVA gives Borneo (F) as estimate (Fig. 3B). *Macrolenes* (node 94), which has west Malesia as present distribution, originated on Sumatra-Borneo (DF) (Table 7-3). With several dispersals/vicariance events, *Macrolenes* diversified during the late Miocene to Pleistocene in the Sundaland, favoured by a larger extension of evergreen forest during this period especially between Borneo and Sumatra or within Borneo. Several dispersal events enlarged the distribution to the Malay Peninsula (node 82 from Borneo; node 85 from Sumatra) and to Java (node 88 and 87 from Sumatra) (Fig. 7-3B). The origin of *Dissochaeta* (node 79) is either on Sumatra (D), based on the S-DEC analysis, while S-DIVA gives two possibilities, Java and Borneo (EF) or Borneo (F) (Table 7-2, 7-3; Fig. 7-3B). *Dissochaeta* sect. *Diplostemones* Cogn. (node 78) has its crown group at 8.17 (10.97–5.58) Ma. The S-DEC analysis estimated the origin of the section to be on Sumatra (D), followed by several dispersal events to the Malay Peninsula and Borneo during the late Miocene to Pliocene (these latter two areas were optimised as the area of origin by S-DIVA) (Table 7-3). Dispersals to Borneo from Sumatra are shown at node 78 and 77, or passed via the Malay Peninsula first at node 73 and 72 (Fig. 7-3B). Long distance dispersal to east Malesia (Moluccas and New Guinea) might have been the case on nodes 71 and 70, directed from Borneo via Sulawesi. The age of the crown group of *Dissochaeta* sect. *Dissochaeta* (node 69) is c. 6.79 (9.35–4.41) Ma with an origin either on Sumatra and Java (DE), based on the S-DEC analysis, or Java and Borneo or Borneo according to the S-DIVA analysis (Table 7-3). Diversification within the section occurred during the late Miocene to Pleistocene with dispersal within Sumatra and Java (nodes 69, 68, 63, 62, 61, 60 and 59), dispersal from Sumatra to Malay Peninsula (node 67), followed by dispersal east to Borneo (node 66) and to Sulawesi-Philippines (nodes 65 and 64). Dispersal into the Philippines from Borneo occurred more likely via Palawan rather than via Sulawesi because Palawan forms almost a “bridge” (was connected to Borneo during glacial periods), while Sulawesi was a little more isolated at by the deep Makassar Strait (Fig. 7-3B).

The MCC phylogenetic tree is based on only 44 species out of the 90 species in the Dissochaeteae. Some species are sampled more than once, especially the species with wider distributions, to assess how they originally dispersed. If more species are added to the

analyses, changes in the patterns, dispersal routes, areas of origin may occur. The undersampling showed in the case of *Creochiton* a divergent area of origin, Sulawesi, east of Wallace's line, while all other origins were in West Malesia, which necessitates an unlikely explanation like long-distance dispersal from the western part of Southeast Asia to Sulawesi. The splitting of the clade from its ancestor happened in the Late Oligocene (25.71 Ma) with dispersal from Borneo into Sulawesi (Hall 2009, 2012). Some Sumatran and Bornean species were missing in the analyses and possibly, this can change the date and place of origin of the genus and its dispersal/diversification. A comparable problem appears in *Dissochaeta*, where some eastern Malesian and western Southeast Asian Continental species were not included. The dispersal of the genus into East Malesia or Continental Southeast Asia is, therefore, not resolved.

Biogeographic patterns

Indo-China and Borneo

Indo-China–Borneo was estimated as the most likely ancestral area for the Dissochaeteae. Indochina and Borneo are areas with the longest emergence histories, and they have been major diversification hotspots through time and key sources for lineage dispersal across the region (De Bruyn et al. 2014). Indochina and Borneo have long been recognized as two of the most diverse biodiversity hotspots in Southeast Asia across several taxonomic groups through all time periods (Myers et al. 2000; Lohman et al. 2011; De Bruyn et al. 2014). Of the two areas is it most likely that Indochina was the first area in which the ancestor of the Dissochaeteae settled in Asia, as from here the basal *Pseudodissochaeta* clade developed and dispersed westwards into NE India and Bhutan (Fig. 7-3A). Borneo is the cradle of dispersal events in the remaining part of the Dissochaeteae in Malesia, with many dispersal events to the Philippines, Sulawesi, Sumatra, Malay Peninsula, Java, Moluccas and New Guinea (Fig. 7-3A & 7-3B). The island is not only an important evolutionary hotspot in terms of high species numbers and in situ diversification, but also an important source for subsequent emigration (De Bruyn et al. 2014; Atkins et al. 2020). Borneo represents the original 'heartland' of the group, the area with the highest species numbers and greatest abundance in morphological diversity. High dispersal levels between the islands on the Sunda Shelf, especially between Borneo and nearby islands reflect the shared geological history of these continental islands, which formed continuous land masses during at least some of the glacial maxima (Voris 2000; Hall 2012). At these times there would also have been more extensive areas of rainforest (Cannon et al. 2009, 2012; Raes et al. 2014), facilitating exchange and dispersal in a wet forest group, like the Dissochaeteae.

Wallace Line

Wallace's line divides the floristic region of the Malay Archipelago or Malesia into a western and eastern part (Wallace 1860; van Welzen et al. 2011; Chen et al. 2019; Yu & van Welzen 2020). The tectonic and climatic history of Malesia has resulted in different floras in both areas (van Welzen et al. 2005, 2011; Grudinski et al. 2014). The line runs east of the Philippine islands, between Borneo and Sulawesi, and between Bali and Lombok, which were never connected during the Pleistocene glacial maxima (Voris 2000), possibly hindering dispersal between West Malesia (Sunda shelf) and East Malesia (Sahul shelf). The position of the line was later revised with alternative lines proposed, mostly by zoologists reflecting their taxonomic groups of interest (van Welzen et al. 2011; Crayn et al. 2015). The Merrill-Dickerson or Huxley line in the west and Lydekker's line in the east delimit a zone called Wallacea (the Philippines, Sulawesi, Lesser Sunda Islands and Moluccas). Wallacea

is a good phylogeographic region with many endemic species, especially in the Philippines, but it is also a transition zone between west and east Malesia and plays an important role in the floristic exchanges between the Sunda and Sahul Shelves (van Welzen et al. 2005, 2011). Java has been added to the region because of comparable climatic conditions (yearly dry monsoon on most of the island), resulting in similar floral elements (van Welzen et al. 2005, 2011; van Welzen & Raes 2011). Geologically, Wallacea represents the area of collision between Sundaland and the present-day Indian-Australian plate, whereby west Wallacea is separated from the Sunda Shelf by the deep Makassar Strait, and also during glacial periods the islands (some united) remained at most stepping stones for dispersal, but never formed a continuous land corridor between the Sunda and Sahul Shelves (e.g. Voris 2000; van Welzen et al. 2005; Hall 2009; Lohman et al. 2011). At present, the region generally has a long or brief dry monsoon compared to the everwet Sunda and Sahul Shelves and if this climatic difference was also in place in the Pliocene/Pleistocene, it could have acted as an environmental filter to everwet plant taxa, including Dissochaeteae, causing the number of species to decrease eastwards (Sahul) (van Welzen et al. 2005, 2011). Lianas/woody climbers are mostly restricted to the everwet areas, which is demonstrated here too, only the two non-climbing genera occur in monsonal areas (*Pseudodissochaeta* in Southeast Asia mainland, and *Creochiton* in east Malesia, extending even to the everwet New Guinea). There are few climbing species that also reach Sulawesi and New Guinea/Moluccas. As such one might also state that Weber's line (between Sulawesi and the Moluccas, east of the Lesser Sunda Islands) and Lydekker's line (between the Moluccas and New Guinea, east of the Lesser Sunda Islands) indicate major limits (likely due to monsonal influences) in the dispersal of the Dissochaeteae.

The most probably common migration route from Sundaland across Wallace's line is through Sulawesi or the Philippines to eastern Wallacea/New Guinea (Su & Saunders 2009; Thomas et al. 2012a; Nauheimer et al. 2012; Buerki et al. 2016; Chen et al. 2019; Atkins et al. 2020; Yu & van Welzen 2020). Our biogeographical reconstructions of Dissochaeteae (Fig. 7-3) identified four dispersal events across Wallace's line from West Malesia to Wallacea and East Malesia. Three of them show dispersal from Borneo (node 112 and 111; 71 and 70; 65 and 64) to Sulawesi and Philippines and one, rather oddly, from Sumatra (node 97 and 96) to the Philippines (but more samples may change this view). All dispersal events occurred in the Late Miocene and/or Pliocene and Pleistocene, when marine gaps diminished following convergence of the Sunda and Sahul shelves (Hall 2009). The west to east Malesian dispersal occurring near node 71 likely occurred with Sulawesi as a stepping stone. Most of the west-east dispersal or vice-versa via Wallacea took place during the last 10 Ma (van Welzen et al. 2005). There is one indication of a reverse dispersal from Wallacea to West Malesia on node 110, going from Sulawesi to Java. However, in some analyses, Java is also thought to be part of Wallacea just as Sulawesi (van Welzen et al. 2011). However, the phylogeny is not complete and various east Malesian species are still lacking, thus reversed, east-west dispersals via Wallacea are perhaps still undetected.

Acknowledgements

We thank the Indonesian Ministry of Research and Technology, National Agency for Research and Innovation for the Research and Innovation in Science and Technology Project (RISET-Pro) for the main funding of the project (World Bank Loan No. 8245-ID). Additional funding for this project, including Swaantje Mondt Fund of Leids Universiteits Fonds (LUF), Leiden University and Alberta Mennega Foundation for field work funding. The last author (PvW) thanks the Treub Maatschappij, the Society for the Advancement of Research in the Tropics, for their support of the Ornstein chair in Tropical Plant Biogeography. An earlier version of this article is part of the Ph.D. thesis of AK.

Appendix 7-1. – List of sequences used in this study. Taxa, voucher information, location and GenBank accession numbers for the nuclear and plastid DNA regions.

Taxon	Tribe/ Group	Voucher	Location	ETS	ITS	<i>ndhF</i>	<i>psbK-psbL</i>	<i>rbcl</i>	<i>rpl16</i>
<i>Aciotis paludosa</i>	Marcetieae	Guimarães 317, RB	S America	KF462814	JQ730040	–	JQ730460	–	–
<i>Aciotis purpurascens</i>	Marcetieae	Michelangelo 2454, NY	S America	KU500992	KU501055	AF215561	JQ730461	–	AF322231
<i>Aciotis rubricaulis</i>	Marcetieae	Michelangelo 2542, NY	S America	KU500993	KU501057	–	JQ730462	JQ592644	–
<i>Adelobotrys subsessilis</i>	Merianieae	Michelangelo 493, BH	S America	MH781591	AY966407	MH760283	MH781651	MH747567	AY966419
<i>Allomorpha balansae</i>	Sonerileae	Liu 451, SYS	China	–	MG644470	MK994792	MK994792	MK994792	MK994792
<i>Anerincleistus macrophyllus</i>	Sonerileae	Liu 673, SYS	Malaysia (Borneo)	–	MN031184	MK994887	MK994887	MK994887	MK994887
<i>Astronia meyeri</i>	Astronieae	Fernando 2551	Philippines	–	KF78158	–	–	KF781611	–
<i>Astronia smilacifolia</i>	Astronieae	Liu 664, SYS	Malaysia (Borneo)	–	EF683153	MK994883	MK994883	MK994883	MK994883
<i>Barthea barthei</i>	Sonerileae	Liu 575, SYS	China	–	MG644388	KY873324	KY873324	KY873324	KY873324
<i>Bellucia pentamera</i>	Henrietteae	Penneys 1868, CAS	S America	–	GU968788	AF215578	–	KF781624	AF215615
<i>Bertolonia acuminata</i>	Bertolonieae	Bacci 171, UEC	S America	MK296603	MK258150	KX826820	KX826820	KX826820	KX826820
<i>Bertolonia alternifolia</i>	Bertolonieae	Bacci 375, UEC	S America	MH722270	MH708155	MH729204	MK296663	MH729221	MH722278
<i>Bertolonia mosenii</i>	Bertolonieae	Goldenberg 804, NY	S America	MK296614	MH708156	JF831973	MK296678	JF831998	JF832024
<i>Blakea gracilis</i>	Blakeae	Michelangelo 845, NY	S America	–	AY460445	JF831974	–	JF831999	JF832025
<i>Blakea schlimii</i>	Blakeae	Michelangelo 1227, NY	S America	–	AY460441	KX826821	KX826821	KX826821	KX826821
<i>Blakea trinervia</i>	Blakeae	Penneys 1629, FLAS	S America	–	KY782453	AF215555	–	AF215516	AF215600
<i>Blastus cochinchinensis</i>	Sonerileae	Liu 446, SYS	China	–	MG644467	MK994909	MK994909	MK994909	MK994909
<i>Bredia hirsuta</i>	Sonerileae	Liu 634, SYS	China	–	MN031213	MK994872	MK994872	MK994872	MK994872
<i>Cambessedesia espora</i>	Cambessedesieae	Guimarães 397, RB	S America	MK165019	JQ730062	JQ899114	JQ730481	JQ899088	JQ899064
<i>Cambessedesia hilariana</i>	Cambessedesieae	Guimarães 405, RB	S America	MK165024	JQ730063	JQ899115	JQ730482	JQ899089	JQ899065
<i>Clidemia capillaris</i>	Miconieae	Penneys 1607, FLAS	S America	KF821285	EU055861	EU056121	KF822471	–	–
<i>Clidemia petiolaris</i>	Miconieae	Chase 2534, K	S America	KM893562	KF821452	AM235410	KF821882	AM235643	AM235446
<i>Clidemia umbellata</i>	Miconieae	Judd 8084, FLAS	S America	KF820711	EU055674	EU055929	KF821911	–	–
<i>Creochiton bibracteatus</i>	Dissochaeteae	Kartonegoro 1111, BO	Indonesia (Java)	–	MW462480	MW462399	MW462242	MW462553	MW290997
<i>Creochiton ledermannii</i>	Dissochaeteae	Mambrasar 81, BO	Indonesia (Papua)	–	MW462481	MW462400	MW462243	MW462554	MW290998
<i>Creochiton roseus</i>	Dissochaeteae	Kartonegoro 1051, BO	Indonesia (Sulawesi)	MW462332	MW462482	MW462401	MW462244	MW462555	MW290999
<i>Creochiton</i> sp.	Dissochaeteae	Kartonegoro 927, BO	Indonesia (Sulawesi)	–	MW462483	MW462402	MW462245	MW462556	MW291000
<i>Cyphotheca montana</i>	Sonerileae	Liu 596, SYS	China	–	MG644447	MK994852	MK994852	MK994852	MK994852

Systematics and Biogeography of the *Dissochaeta* alliance

<i>Dalenia beccariana</i>	Dissochaeteae	<i>Kartonegoro 1118</i> , BO	Brunei Darussalam	–	MW4625 19	MW4624 42	MW4622 87	MW4626 00	MW2959 81
<i>Dalenia glabra</i> var. <i>glabra</i>	Dissochaeteae	<i>Penneys 2446</i> , WNC	Malaysia (Borneo)	MW4623 54	MW4625 06	MW4624 29	MW4622 73	MW4625 86	MW2959 82
<i>Dalenia glabra</i> var. <i>kinabaluensis</i>	Dissochaeteae	<i>Penneys 2542</i> , WNC	Malaysia (Borneo)	MW4623 57	MW4625 08	MW4624 31	MW4622 76	MW4625 89	MW2959 85
<i>Dalenia magnibracteata</i>	Dissochaeteae	<i>Liu 676</i> , SYS	Malaysia (Borneo)	–	MG6444 77	MK9948 89	MK9948 89	MK9948 89	MK9948 89
<i>Dichaetanthera arborea</i>	Melastomateae	<i>Razanatsima 823</i> , MO	Madagascar	–	KX8892 22	AF27280 0	KY2847 42	–	AF29447 0
<i>Dichaetanthera articulata</i>	Melastomateae	<i>Ravelonarivo 4320</i> , MO	Madagascar	MF3979 49	KX8892 24	MF3980 44	KY2847 43	–	–
<i>Dinophora spenneroides</i>	Diophora-alliance	<i>Veranso 107</i> , MJG	Africa (Cameroon)	MF3979 51	KX8892 27	MF3980 47	KY2847 46	–	–
<i>Diplectria conica</i>	Dissochaeteae	<i>Kartonegoro 1101</i> , BO	Indonesia (Sumatra)	MW4623 47	MW4624 98	MW4624 19	MW4622 63	MW4625 76	MW4145 48
<i>Diplectria divaricata</i>	Dissochaeteae	<i>Ardiyani et al. E167</i> , BO	Indonesia (Sumatra)	MW4623 50	MW4625 03	MW4624 25	MW4622 69	MW4625 82	MW4145 54
<i>Diplectria divaricata</i>	Dissochaeteae	<i>Kartonegoro 1096</i> , BO	Indonesia (Sumatra)	MW4623 48	MW4624 99	MW4624 21	MW4622 64	MW4625 78	MW4145 50
<i>Diplectria divaricata</i>	Dissochaeteae	<i>Penneys 2472</i> , WNC	Malaysia (Borneo)	MW4623 49	MW4625 01	MW4624 23	MW4622 67	MW4625 80	MW4145 52
<i>Diplectria divaricata</i>	Dissochaeteae	<i>Penneys 2365</i> , WNC	Philippines (Mindanao)	–	MW4625 00	MW4624 22	MW4622 66	MW4625 79	MW4145 51
<i>Diplectria divaricata</i>	Dissochaeteae	<i>Wai 2677</i> , PSU	Thailand	–	MW4625 02	MW4624 24	MW4622 68	MW4625 81	MW4145 53
<i>Diplectria</i> sp.	Dissochaeteae	<i>Kartonegoro 1135</i> , BO	Indonesia (Borneo)	–	MW4625 24	MW4624 47	MW4622 95	MW4626 06	MW4145 73
<i>Diplectria viminalis</i>	Dissochaeteae	<i>Kartonegoro 1075</i> , BO	Indonesia (Sumatra)	MW4623 77	MW4625 28	MW4624 51	MW4622 99	MW4626 10	MW4145 77
<i>Diplectria viminalis</i>	Dissochaeteae	<i>Kartonegoro 1127</i> , BO	Indonesia (Borneo)	MW4623 80	MW4625 30	MW4624 52	MW4623 02	MW4626 12	MW4145 79
<i>Dissochaeta annulata</i>	Dissochaeteae	<i>Kartonegoro 1121</i> , BO	Indonesia (Bintan)	MW4623 33	MW4624 85	MW4624 04	MW4622 47	MW4625 59	MW4145 32
<i>Dissochaeta annulata</i>	Dissochaeteae	<i>Penneys 2506</i> , WNC	Malaysia (Borneo)	MW4623 35	MW4624 86	MW4624 05	MW4622 49	MW4625 60	MW4145 33
<i>Dissochaeta axillaris</i>	Dissochaeteae	<i>Kartonegoro 1126</i> , BO	Indonesia (Borneo)	MW4623 36	–	–	MW4622 50	MW4625 61	–
<i>Dissochaeta bakhuzenii</i>	Dissochaeteae	<i>Kartonegoro 1116</i> , BO	Indonesia (Java)	MW4623 39	MW4624 88	MW4624 08	MW4622 53	MW4625 64	MW4145 36
<i>Dissochaeta biligulata</i>	Dissochaeteae	<i>Kartonegoro 1088</i> , BO	Indonesia (Sumatra)	MW4623 40	MW4624 89	MW4624 09	MW4622 54	MW4625 65	MW4145 37
<i>Dissochaeta biligulata</i>	Dissochaeteae	<i>Kartonegoro 1119</i> , BO	Indonesia (Bintan)	MW4623 41	MW4624 90	MW4624 10	MW4622 55	MW4625 66	MW4145 38
<i>Dissochaeta biligulata</i>	Dissochaeteae	<i>Penneys 2509</i> , WNC	Malaysia (Borneo)	MW4623 43	MW4624 92	MW4624 11	MW4622 57	MW4625 68	MW4145 40
<i>Dissochaeta bracteata</i>	Dissochaeteae	<i>Kartonegoro 1074</i> , BO	Indonesia (Sumatra)	MW4623 44	MW4624 94	MW4624 13	MW4622 58	MW4625 69	MW4145 41
<i>Dissochaeta bracteata</i>	Dissochaeteae	<i>Penneys 2483</i> , WNC	Malaysia (Borneo)	MW4623 45	MW4624 95	MW4624 14	MW4622 59	MW4625 71	MW4145 43

Historical biogeography Dissochaeteae

<i>Dissochaeta celebica</i>	Dissochaeteae	<i>Kartonegoro 1054, BO</i>	Indonesia (Sulawesi)	–	MW4624 96	MW4624 15	MW4622 60	MW4625 72	MW4145 44
<i>Dissochaeta celebica</i>	Dissochaeteae	<i>Penneys 2364, WNC</i>	Philippines (Mindanao)	–	MW4624 97	MW4624 17	MW4622 61	MW4625 74	MW4145 46
<i>Dissochaeta fallax</i>	Dissochaeteae	<i>Kartonegoro 1106, BO</i>	Indonesia (Java)	MW4623 51	MW4625 04	MW4624 26	MW4622 70	MW4625 83	MW4145 55
<i>Dissochaeta fusca</i>	Dissochaeteae	<i>Kartonegoro 1105, BO</i>	Indonesia (Java)	MW4623 53	MW4625 05	MW4624 28	MW4622 72	MW4625 85	MW4145 57
<i>Dissochaeta gracilis</i>	Dissochaeteae	<i>Kartonegoro 1113, BO</i>	Indonesia (Java)	MW4623 58	MW4625 09	MW4624 32	MW4622 77	MW4625 90	MW4145 58
<i>Dissochaeta griffithii</i>	Dissochaeteae	<i>Kartonegoro 1122, BO</i>	Indonesia (Bintan)	MW4623 59	MW4625 10	MW4624 33	MW4622 78	MW4625 91	MW4145 59
<i>Dissochaeta inappendiculata</i>	Dissochaeteae	<i>Kartonegoro 1115, BO</i>	Indonesia (Java)	MW4623 64	MW4625 15	MW4624 38	MW4622 83	MW4625 96	MW4145 64
<i>Dissochaeta inappendiculata</i>	Dissochaeteae	<i>Santoso 119, BO</i>	Indonesia (Sumatra)	MW4623 62	MW4625 13	MW4624 36	MW4622 81	MW4625 94	MW4145 62
<i>Dissochaeta pallida</i>	Dissochaeteae	<i>Kartonegoro 1058</i>	Indonesia (Sumatra)	MW4623 66	MW4625 17	MW4624 40	MW4622 85	MW4625 98	MW4145 66
<i>Dissochaeta punctulata</i>	Dissochaeteae	<i>Kartonegoro 1123, BO</i>	Indonesia (Bintan)	MW4623 69	MW4625 20	MW4624 43	MW4622 89	MW4626 01	MW4145 68
<i>Dissochaeta robinsonii</i>	Dissochaeteae	<i>Gushilman 382, BO</i>	Indonesia (Moluccas)	MW4623 72	MW4625 22	MW4624 44	MW4622 92	MW4626 03	MW4145 69
<i>Dissochaeta spectabilis</i>	Dissochaeteae	<i>Kartonegoro 1100</i>	Indonesia (Sumatra)	MW4623 74	MW4625 25	MW4624 48	MW4622 96	MW4626 07	MW4145 74
<i>Dissochaeta vacillans</i>	Dissochaeteae	<i>Kartonegoro 1117, BO</i>	Indonesia (Java)	MW4623 76	MW4625 27	MW4624 50	MW4622 98	MW4626 09	MW4145 76
<i>Disstotis crenulata</i>	Melastomateae	<i>Goyder 7476, GRA</i>	Africa	MF3979 59	KX8892 36	MF3980 56	KY2847 56	–	–
<i>Disstotis tubulosa</i>	Melastomateae	<i>Veranso 221, MJG</i>	Africa (Cameroon)	MF3979 97	KX8892 71	MF3980 93	KY2847 95	–	–
<i>Driessenia glanduligera</i>	Sonerileae	<i>Liu 657, SYS</i>	Malaysia (Borneo)	–	MN0311 97	MK9948 79	MK9948 79	MK9948 79	MK9948 79
<i>Eriocnema fulva</i>	Eriocnemeae	<i>Almeda 8416, CAS</i>	USA	KF82073 5	MH7438 31	AY5537 81	MK2966 94	AY5537 77	AY5537 72
<i>Fordiophyton longipes</i>	Sonerileae	<i>Liu 610, SYS</i>	China	–	MK7753 01	MK9948 58	MK9948 58	MK9948 58	MK9948 58
<i>Graffenrieda latifolia</i>	Merianieae	<i>Penneys 1303, FLAS</i>	USA	KF82074 4	AY4604 50	EU05594 3	MF1051 19	MF0699 28	AM2354 47
<i>Graffenrieda moritziana</i>	Merianieae	<i>Michelangelo 832, NY</i>	USA	KF82074 9	AY4604 51	EU05594 4	JQ73050 4	EU71139 0	JF83203 1
<i>Henriettea barkeri</i>	Henrietteae	<i>lonta 2029, FLAS</i>	USA	–	KJ93395 7	KX8268 24	KX8268 24	KX8268 24	KX8268 24
<i>Heteroblemma serpens</i>	Sonerileae	<i>Liu 671, SYS</i>	Malaysia (Borneo)	–	MN0312 00	MK9948 86	MK9948 86	MK9948 86	MK9948 86
<i>Heterotis rotundifolia</i>	Melastomateae	<i>Penneys 1304, FLAS</i>	Dominica	–	JQ73008 9	AF21556 5	–	U26323	AF27074 5
<i>Macrolenes bipulvinata</i>	Dissochaeteae	<i>Kartonegoro 781, BO</i>	Indonesia (Borneo)	–	MW4625 32	MW4624 53	MW4623 04	MW4626 14	MW4145 80
<i>Macrolenes dimorpha</i>	Dissochaeteae	<i>Kartonegoro 1134, BO</i>	Indonesia (Borneo)	MW4623 82	MW4625 33	MW4624 54	MW4623 05	MW4626 15	MW4145 81
<i>Macrolenes hirsuta</i>	Dissochaeteae	<i>Kartonegoro 1139, BO</i>	Indonesia (Borneo)	MW4623 83	MW4625 34	MW4624 55	MW4623 06	MW4626 16	MW4145 82
<i>Macrolenes hirsutoidea</i>	Dissochaeteae	<i>Kartonegoro 1141, BO</i>	Indonesia (Borneo)	MW4623 60	MW4625 11	MW4624 34	MW4622 79	MW4625 92	MW4145 60

Systematics and Biogeography of the *Dissochaeta* alliance

<i>Macrolenes horrida</i>	Dissochaeteae	<i>Kartonegoro</i> 1073, BO	Indonesia (Sumatra)	MW4623 61	MW4625 12	MW4624 35	MW4622 80	MW4625 93	MW4145 61
<i>Macrolenes macrosepala</i>	Dissochaeteae	<i>Penneys</i> 2512, WNC	Malaysia (Borneo)	MW4623 65	MW4625 16	MW4624 39	MW4622 84	MW4625 97	MW4145 65
<i>Macrolenes muscosa</i>	Dissochaeteae	<i>Kartonegoro</i> 1084, BO	Indonesia (Sumatra)	MW4623 84	MW4625 35	MW4624 56	MW4623 07	MW4626 17	MW4145 83
<i>Macrolenes muscosa</i>	Dissochaeteae	<i>Kartonegoro</i> 1108, BO	Indonesia (Java)	MW4623 86	MW4625 37	MW4624 58	MW4623 08	MW4626 19	MW4145 85
<i>Macrolenes nemorosa</i>	Dissochaeteae	<i>Kartonegoro</i> 1070, BO	Indonesia (Sumatra)	–	MW4625 38	MW4624 59	MW4623 09	MW4626 20	MW4145 86
<i>Macrolenes nemorosa</i>	Dissochaeteae	<i>Kartonegoro</i> 1136, BO	Indonesia (Borneo)	MW4623 87	MW4625 41	MW4624 62	MW4623 10	MW4626 23	MW4145 89
<i>Macrolenes pachygyna</i>	Dissochaeteae	<i>Kartonegoro</i> 777, BO	Indonesia (Borneo)	MW4623 89	MW4625 43	MW4624 63	MW4623 11	MW4626 25	MW4145 90
<i>Macrolenes porphyrocarpa</i>	Dissochaeteae	<i>Penneys</i> 2486, WNC	Malaysia (Borneo)	MW4623 67	MW4625 18	MW4624 41	MW4622 86	MW4625 99	MW4145 67
<i>Macrolenes rostrata</i>	Dissochaeteae	<i>Susanti</i> 264, BO	Indonesia (Borneo)	MW4623 73	MW4625 23	MW4624 45	MW4622 93	MW4626 04	MW4145 70
<i>Macrolenes stellulata</i>	Dissochaeteae	<i>Susanti</i> 297, BO	Indonesia (Borneo)	MW4623 90	MW4625 44	MW4624 64	MW4623 13	MW4626 26	MW4145 91
<i>Macrolenes subulata</i>	Dissochaeteae	<i>Hughes</i> SUBOE71, BO	Indonesia (Sumatra)	MW4623 91	MW4625 45	MW4624 65	MW4623 14	MW4626 27	MW4145 92
<i>Macrolenes tuberculata</i>	Dissochaeteae	<i>Kartonegoro</i> 1128, BO	Indonesia (Borneo)	MW4623 92	MW4625 46	MW4624 66	MW4623 15	MW4626 28	MW4145 93
<i>Marcetia taxifolia</i>	Marcetieae	<i>Michelangel</i> 680, BH	S America	KU5010 41	JQ73010 2	GU9688 25	JQ73052 1	–	–
<i>Medinilla amplexens</i>	Sonerileae	<i>Liu</i> 663, SYS	Malaysia (Borneo)	–	MN0312 19	MK9948 82	MK9948 82	MK9948 82	MK9948 82
<i>Medinilla beamanii</i>	Sonerileae	<i>Liu</i> 658, SYS	Malaysia (Borneo)	–	MN0312 20	MK9948 80	MK9948 80	MK9948 80	MK9948 80
<i>Medinilla chermesonii</i>	Sonerileae	<i>Patrice</i> 8570, MO	Madagascar	MG5185 36	MG5185 48	MG7025 57	MG5185 63	–	–
<i>Medinilla crassinervia</i>	Sonerileae	<i>Kartonegoro</i> 1055, BO	Indonesia (Sulawesi)	MW4623 93	MW4625 47	MW4624 67	MW4623 16	MW4626 29	MW4145 94
<i>Medinilla humbertiana</i>	Sonerileae		Madagascar	–	–	AF21555 7	–	AF21551 7	AF21560 2
<i>Medinilla intermedia</i>	Sonerileae	<i>Kartonegoro</i> 1109, BO	Indonesia (Java)	–	–	MW4624 68	MW4623 18	MW4626 30	MW4145 95
<i>Medinilla lophoclada</i>	Sonerileae	<i>Ramaheni</i> 327, MO	Madagascar	MG5185 37	–	MG7025 58	MG5185 64	–	–
<i>Medinilla micrantha</i>	Sonerileae	<i>Ramaheni</i> 271, MO	Madagascar	MG5185 38	–	MG7025 59	MG5185 65	–	–
<i>Medinilla myrtiformis</i>	Sonerileae	<i>Kartonegoro</i> 924, BO	Indonesia (Sulawesi)	–	–	MW4624 69	MW4623 19	MW4626 31	MW4145 96
<i>Medinilla rubicunda</i>	Sonerileae	<i>Kartonegoro</i> 1072, BO	Indonesia (Sumatra)	–	–	MW4624 70	MW4623 20	MW4626 32	MW4145 97
<i>Medinilla speciosa</i>	Sonerileae	<i>Liu</i> 669, SYS	Malaysia, Borneo	–	MN0312 21	MK9948 85	MK9948 85	MK9948 85	MK9948 85
<i>Medinilla squillula</i>	Sonerileae	<i>Lowry</i> II 7287, MO	Indonesia (Moluccas)	MG5185 39	MG5185 47	MG7025 60	MG5185 66	–	–
<i>Medinilla teysmannii</i>	Sonerileae	<i>Kartonegoro</i> 934, BO	Indonesia (Sulawesi)	MW4623 94	–	MW4624 71	MW4623 22	MW4626 33	MW4145 98
<i>Melastoma candidum</i>	Melastomateae	–	China	KR8226 64	MK2928 51	KY7458 94	KY7458 94	KY7458 94	KY7458 94
<i>Melastoma dodecandrum</i>	Melastomateae	–	China	–	MK2928 47	MH7480 92	MH7480 92	MH7480 92	MH7480 92
<i>Melastoma malabathricum</i>	Melastomateae	<i>Penneys</i> 1998, CAS	–	–	JQ73010 5	AF27281 0	JQ73052 4	AF27074 8	AB4363 76

<i>Melastoma minahassae</i>	Melastomateae	<i>Kartonegoro</i> 1052, BO	Indonesia (Sulawesi)	MW4623 95	–	MW4624 72	MW4623 24	MW4626 34	MW4145 99
<i>Melastoma sanguineum</i>	Melastomateae	<i>Kartonegoro</i> 1099, BO	Indonesia (Sumatra)	MW4623 96	JQ73010 6	MW4624 73	MW4623 25	MW4626 35	MW4146 00
<i>Memecylon ligustrifolium</i>	Olisbeoideae	<i>Liu</i> 726, SYS	China	–	KP09303 4	MK9949 13	MK9949 13	MK9949 13	MK9949 13
<i>Meriania sanguinea</i>	Merianieae	<i>Fernandez</i> 2215, QCN	S America	–	KY9915 34	MH7603 49	MH7817 03	MH7476 28	–
<i>Meriania tuberculata</i>	Merianieae	<i>Pedraza</i> 2142, NY	S America	MH7816 47	MH8199 25	MH7603 61	MH7817 15	MH7476 39	–
<i>Miconia dodecandra</i>	Miconieae	<i>Michelangelo</i> 758, NY	S America	KF82102 0	KF82160 0	KX8268 26	KX8268 26	KX8268 26	KX8268 26
<i>Miconia donaeana</i>	Miconieae	<i>Michelangelo</i> 727, NY	S America	KF82102 4	KY7824 66	EU05602 8	KF82220 6	AM2356 48	AM2354 51
<i>Miconia hookeriana</i>	Miconieae	<i>Cultivated</i> , M	S America	KF82105 9	EU05578 1	EU05604 0	KF82224 4	–	–
<i>Mouriri guianensis</i>	Olisbeoideae		S America	FJ79292 1	FJ79296 9	AF21557 5	–	AF21552 9	AF21561 0
<i>Ochthocharis borneensis</i>	<i>Dinophora</i> -alliance	<i>Liu</i> 689, SYS	Malaysia (Borneo)	–	–	MK9948 95	MK9948 95	MK9948 95	MK9948 95
<i>Ochthocharis dicellandroides</i>	<i>Dinophora</i> -alliance	<i>Bidault</i> 2116, BRLU	Africa (Gabon)	MG5185 26	–	MG7025 62	MG5185 50	–	–
<i>Osbeckia australiana</i>	Melastomateae	<i>Brenan</i> 7008, NY	Australia	KF46286 8	JQ73011 6	–	JQ73053 8	–	–
<i>Osbeckia chinensis</i>	Melastomateae	–	–	–	–	AF21557 0	–	AF21552 5	AF21037 8
<i>Osbeckia nepalensis</i>	Melastomateae	<i>Penneys</i> 1986, CAS	Asia	–	JQ73011 8	MH7292 15	JQ73053 9	KX5270 55	MH7229 91
<i>Osbeckia stellata</i>	Melastomateae	<i>Penneys</i> 1969, CAS	Asia	–	JQ73011 9	MK3317 13	MK3317 13	MK3317 13	MK3317 13
<i>Oxyspora paniculata</i>	Sonerileae	<i>Liu</i> 523, SYS	Vietnam	–	MN0312 12	MK9948 19	MK9948 19	MK9948 19	MK9948 19
<i>Pachycentria constricta</i>	Sonerileae	<i>Kartonegoro</i> 1076, BO	Indonesia (Sumatra)	MW4623 97	MW4625 48	MW4624 74	MW4623 26	MW4626 36	MW4146 01
<i>Pachycentria varingiaefolia</i>	Sonerileae	<i>Barber</i> 76, E	Indonesia (Sumatra)	–	MW4625 49	MW4624 75	MW4623 27	MW4626 37	MW4146 02
<i>Phyllagathis dispar</i>	Sonerileae	<i>Liu</i> M20, SYS	Malaysia (Borneo)	–	MG6444 29	MK9949 10	MK9949 10	MK9949 10	MK9949 10
<i>Phyllagathis rotundifolia</i>	Sonerileae	<i>Liu</i> M50, SYS	Malaysia	–	MG6444 36	MK9949 12	MK9949 12	MK9949 12	MK9949 12
<i>Plagiopetalum serratum</i>	Sonerileae	<i>Liu</i> 717, SYS	China	–	MN0311 70	MK9949 02	MK9949 02	MK9949 02	MK9949 02
<i>Pseudodissoc haeta assamica</i>	Dissochaeteae	<i>Liu</i> 590, SYS	China	–	MG6444 80	MK9948 48	MK9948 48	MK9948 48	MK9948 48
<i>Pseudodissoc haeta lanceata</i>	Dissochaeteae	<i>Liu</i> 593, SYS	China	–	MN0312 32	MK9948 50	MK9948 50	MK9948 50	MK9948 50
<i>Pseudodissoc haeta septentrionalis</i>	Dissochaeteae	<i>Liu</i> 618, SYS	China	–	MN0312 31	MK9947 78	MK9947 78	MK9947 78	MK9947 78
<i>Pterandra azurea</i>	Kibessieae	<i>Kartonegoro</i> 1077, BO	Indonesia (Sumatra)	–	–	MW4624 77	MW4623 29	MW4626 39	MW4146 04
<i>Pterandra coerulescens</i>	Kibessieae	<i>Chen</i> 543	Malaysia	–	KF78160 2	–	–	KF78163 0	–
<i>Pterandra echinata</i>	Kibessieae	<i>Chen</i> 542, SYS	Malaysia	–	KF78160 4	AF21555 9	–	AF21552 0	AF27074 4
<i>Pterandra galeata</i>	Kibessieae	<i>Kartonegoro</i> 1057	Indonesia (Sumatra)	–	–	MW4624 78	MW4623 30	MW4626 40	MW4146 05
<i>Pterandra multiflora</i>	Kibessieae	<i>Clausing</i> 142, MJG	Malaysia	–	GU9688 01	AF21556 0	–	–	AF21560 3
<i>Pterandra tuberculata</i>	Kibessieae	<i>Liu</i> 651, SYS	Malaysia (Borneo)	–	MW4625 51	MK9948 77	MK9948 77	MK9948 77	MK9948 77
<i>Rhexia aristosa</i>	Rhexieae	<i>Naczi</i> 12065, NY	N America	KF46287 8	JQ73013 4	–	JQ73055 5	–	–

<i>Rhexia mariana</i>	Rhexieae	Ionta 397, FLAS	N America	–	DQ9856 31	AF27281 9	JQ73055 6	KJ77381 7	AF32372 3
<i>Rhexia virginica</i>	Rhexieae	Michelangeli 1448, NY	N America	KF46287 9	DQ9856 43	KX8268 30	KX8268 30	KX8268 30	KX8268 30
<i>Rhynchanthes bracteata</i>	Microlicieae	Zenteno 8801, NY	S America	KF46288 0	JQ73013 7	KX8268 31	KX8268 31	KX8268 31	KX8268 31
<i>Salpinga maranonesis</i>	Meranieae	Clark 6979, US	S America	MF0293 72	KY9918 73	JF83198 2	MF1049 83	JF83200 8	JF83204 8
<i>Sarcopyramis bodinieri</i>	Sonerileae	Liu 502, SYS	China	–	MN0312 06	MK9948 10	MK9948 10	MK9948 10	MK9948 10
<i>Sonerila celebica</i>	Sonerileae	Kartonegoro 1027, BO	Indonesia (Sulawesi)	MW4623 98	MW4625 52	MW4624 79	MW4623 31	MW4626 41	MW4146 06
<i>Sonerila velutina</i>	Sonerileae	Liu 683, SYS	Malaysia (Borneo)	–	MN0312 24	MK9948 92	MK9948 92	MK9948 92	MK9948 92
<i>Sporoxeia calvicarata</i>	Sonerileae	Liu 716, SYS	China	–	MN0311 76	MK9949 01	MK9949 01	MK9949 01	MK9949 01
<i>Tetrazygia urbanii</i>	Miconieae	Struwe 116, NY	S America	KF82137 4	KF82177 2	AF27075 3	KF82254 7	AF21553 8	AF21561 9
<i>Tibouchina grossa</i>	Melastomateae	Zabala 1, UPTC	S America	KF46293 5	JQ73019 2	JF83198 3	JQ73061 2	JF83200 9	JF83205 0
<i>Tibouchina longifolia</i>	Melastomateae	Majure 4277	S America	–	KY7824 69	KX8268 33	KX8268 33	KX8268 33	KX8268 33
<i>Tibouchina urvilleana</i>	Melastomateae	–	–	KR8226 70	AY4604 39	MK7260 30	MK7260 30	MK7260 30	MK7260 30
<i>Tigridiopalm a magnifica</i>	Sonerileae	Zeng G001, SYS	China	–	KM5218 48	MF6637 60	MF6637 60	MF6637 60	MF6637 60
<i>Triolena amazonica</i>	Trioleneae	Goldenberg 965, NY	S America	MK1650 55	–	JF83198 4	MK2967 00	NC0318 90	JF83205 1
<i>Triolena piloides</i>	Trioleneae	Penneys 1626, FLAS	S America	–	KY7825 07	MH7292 19	–	MH7292 38	MH7223 00
<i>Triolena spicata</i>	Trioleneae	Penneys 1726, FLAS	S America	MK2966 27	KY7825 08	–	MK2967 01	MH7292 40	–