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Citation

Kartonegoro, A., Mota De Oliveira, S., & Welzen, P. C. van. (2021). Historical biogeography of the Southeast Asian and Malesian tribe Dissochaeteae (Melastomataceae). *Journal Of Systematics And Evolution*. doi:10.1111/jse.12752

Version: Publisher's Version

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Downloaded from: <https://hdl.handle.net/1887/3250444>

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

Research Article

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

Abdulrohman Kartonegoro^{1,2,3*} , Sylvia Mota de Oliveira^{1,3} , and Peter C. van Welzen^{1,3} ¹Naturalis Biodiversity Center, Leiden 2333 CR, The Netherlands²Research Center for Biology, Indonesian Institute of Sciences (LIPI), Jl. Jakarta-Bogor KM. 46, Cibinong 16911, Indonesia³Institute of Biology Leiden (IBL), Leiden University, Leiden 2333 BE, The Netherlands

*Author for correspondence. E-mail: abdulrohman.kartonegoro@naturalis.nl

Received 25 November 2020; Accepted 12 April 2021; Article first published online 29 April 2021

Abstract The region of Tropical Southeast Asia and the Malay Archipelago is a very appealing area for research due to its outstanding biodiversity, being one of the most species-rich areas in the world with high levels of endemism, and due to its complex geological history. The high number of species in tribe Dissochaeteae (Melastomataceae) and their tendency to narrow endemism make 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.

Key words: ancestral area reconstruction, Dissochaeteae, divergence time estimation, historical biogeography, Malesia, Melastomataceae, shrubs, Southeast Asia, tropical rain forests.

1 Introduction

The region of Tropical Southeast Asia and the Malay Archipelago (Malesia) is a very appealing area for research due to 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 harbors 20%–25% of the world's vascular plants and is the meeting point of many biota from various origins (Woodruff, 2010; van Welzen et al., 2011; Richardson et al., 2012; Zhou et al., 2019). The vegetation of Southeast Asia has been influenced by the, still continuing, Asian–Australian collision; however, the extensive forests of the western part were not substantially invaded by Australian elements (Richardson et al., 2012; De Bruyn et al., 2014). 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 eastward 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

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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 area of Malesia (except Palawan and a few neighboring islands that rafted from China) originated at some time from the Southeast Asian part of Eurasia and Australian part of Gondwana, whereby west Malesia and parts of Southeast Asia mainland, split off as various terranes, 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 centers 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: (i) Eurasia, with colonization via continental Southeast Asia, for example, 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); (ii) Gondwanan origin via the rafting Indian fragment into continental Southeast Asia (Nauheimer et al., 2012; Thomas et al., 2012) or via migration along the Arabian and south Asian coasts (Sirichamorn et al., 2014; Chen et al., 2019); (iii) Australia, with colonization from the Australian continent (Morley, 2003; Barker et al., 2007).

The tribe Dissochaeteae (Melastomataceae) comprises 6 genera and c. 90 species of shrubs, which inhabit the tropical lowland and lower to mid-montane rainforests in Southeast Asia, stretching across E Bhutan, NE India, Myanmar, Southern China, Indochina, Thailand and throughout the Malesian Region (Kartonegoro et al., 2021). The center 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, 27 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., 2019; 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 (Clausing & Renner, 2001; Renner et al., 2001; Berger et al., 2016; Veranso-Libalah et al., 2018; Zhou et al., 2019). 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: (i) Long-distance oceanic dispersal of the lineages to the Old World is possible via trans-Atlantic stepping stones during late Oligocene (Veranso-Libalah et al., 2018); or (ii) 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., 2019). The basal clade of Dissochaeteae s.l./Sonerileae is estimated to have originated c. 17.31 Ma and diversified in Southeast Asia after the second scenario (Zhou et al., 2019). 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 to gain insights into the evolutionary history of Dissochaeteae.

2 Material and Methods

2.1 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), Blakeae (3), Cambesdesieae (2), *Dinophora* alliance (3), Eriocnemeae (1), Henrietteae (3), Kibessieae (6), Marcetieae (4), *Medinilla* alliance (16), Melastomeae (17), Meranieae (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 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 Center for Biotechnology Information (<http://www.ncbi.nlm.nih.gov>).

2.2 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., 2019), and two fossils of Melastomataceae that were widely used in previous biogeographical studies of the family (Renner et al., 2001; Morley & Dick, 2003; Renner, 2004a, 2004b; Veranso-Libalah et al., 2018; Zhou et al., 2019). The Melastomataceae crown node (Fig. 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. 1, point c) was constrained at 20.25 Ma (15.71–25.24; 95% HPD). The Melastomatoideae (excluding Olisbeoideae and Kibessieae) crown node (Fig. 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. 1, point d) (26–23 Ma; Collinson & Pingen, 1992). We selected a normal distribution prior for the secondary calibration with a standard deviation of 6.5 of Melastomataceae and 3.5 for Asian Sonerileae crown, equivalent to the 95% HPD estimated (Berger et al., 2016; Zhou et al., 2019). For fossil calibrations, we selected a lognormal distribution prior with a mean of 1.5 and standard deviation of 1, with the offsets (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., 2019).

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); however, 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 analyzed 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 were removed before 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).

2.3 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 on the basis of the geographical distances at the relevant time of Southeast Asia (Hall, 2002, 2009) and followed constraints build by previous authors (Yu & van Welzen, 2020). 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 accessions were 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 as follows: A = East Bhutan, Northeast India, and Northwest Myanmar; B = Indochina (incl. Cambodia, Laos, Central to East Myanmar, South China [incl. 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 is shown in Table 1.

3 Results

3.1 Divergence time estimation

The Dissochaeteae was estimated to have diverged from its closest South American relative, the Cambessedesieae, in the late Eocene (Fig. 1, node A; stem age: 39.32 Ma; 95% HPD:

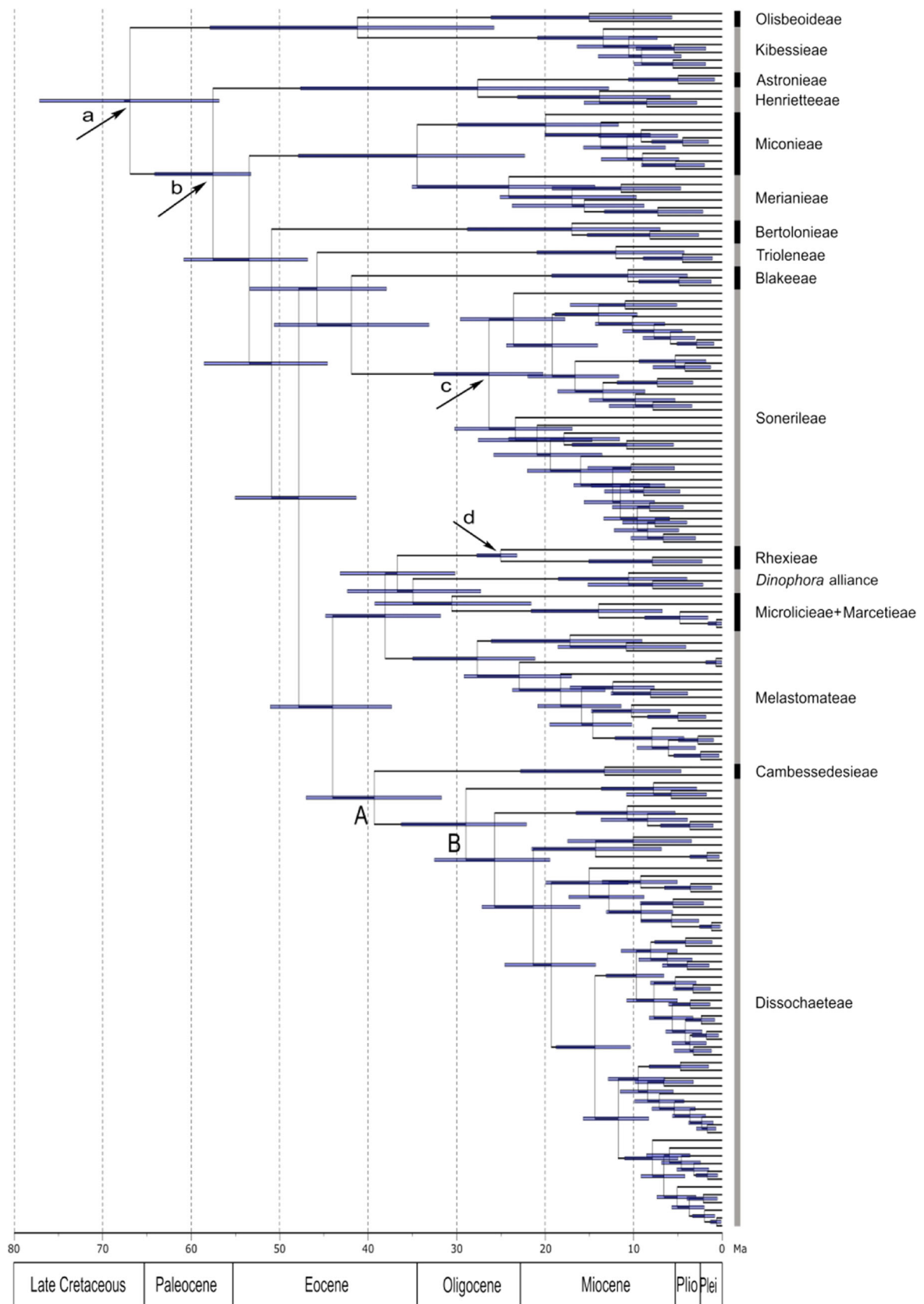


Fig. 1. Continued

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 outgroup generated here (Fig. 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. 2 (this figure also contains all node numbers referred below). The Indo-Burmese *Pseudodissochaeta* (node 116) branched off first from the remaining Dissochaeteae (node 114) (Fig. 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. (2019: 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. 3; Table 2). Next, *Creochiton* (node 111) splits off (Fig. 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. 2). The ancestor of *Diplectria* (node 103) splits off next at 15.04 (19.93–10.59) Ma, followed by the core of *Dissochaeta* and *Macrolenes* (node 95), which originated during the transition from 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). A summary 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 is presented in Table 2.

3.2 Ancestral area reconstruction

The most probable ancestral area of the Dissochaeteae (Fig. 3A; Table 2, node 115) was inferred to be Indochina 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. 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 northward to the Philippines, westward to Java, and eastward to New Guinea. Borneo (area F) was estimated to be the most probable ancestral area of the scrambling taxa (node 108, Fig. 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 eastward into Sulawesi, the Philippines, the Moluccas, and New Guinea. *Dalenia* diverged and originated on 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. 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. 3B). A summary of ancestral ranges and their relative probabilities of clades within the Dissochaeteae is given in Table 2 and Figs. 3A, 3B.

4 Discussion

4.1 Phylogeny

Our Dissochaeteae and outgroup MCC tree (Fig. 1) is in general similar to the Melastomataceae MCC tree of Renner et al. (2001), Berger et al. (2016), Veranso-Libalah et al. (2018), and Zhou et al. (2019), which describes 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. 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 includes 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. 1). Within the tribe, six distinct and strongly supported clades (genera) are recognized (Fig. 2). They are *Creochiton*, *Dalenia*, *Diplectria*, *Dissochaeta*, *Macrolenes*, and *Pseudodissochaeta*.

Fig. 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; Pli, Pliocene.

Table 1 Distribution of the sampled taxa

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

Continued

Table 1 Continued

Taxon	Distribution
<i>Macrolenes muscosa</i> (Blume) Bakh.f. "Java"	E
<i>Macrolenes muscosa</i> (Blume) Bakh.f. "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

The abbreviations in the column "distributions" refer to the biogeographical areas assigned in the ancestral area analyses.

4.2 Diversification of Dissochaeteae

The biogeographical reconstructions (Figs. 1, 2) showed that the Dissochaeteae originated from a South American ancestor in the late Eocene (Fig. 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 northward and occupied regions from the equator to mid-latitudes across all northern continents (Li et al., 2017; Zhou et al., 2019). The existence of the boreotropical forests and the North American land bridges connecting the Old and the New Worlds enabled inter-continental 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 Cambesiedesieae and the Dissochaeteae is estimated at 39.32 Ma (Figs. 1, 2, Node A; 95% HPD 47.03–31.69) during the late Eocene, with vicariance resulting in two groups, one

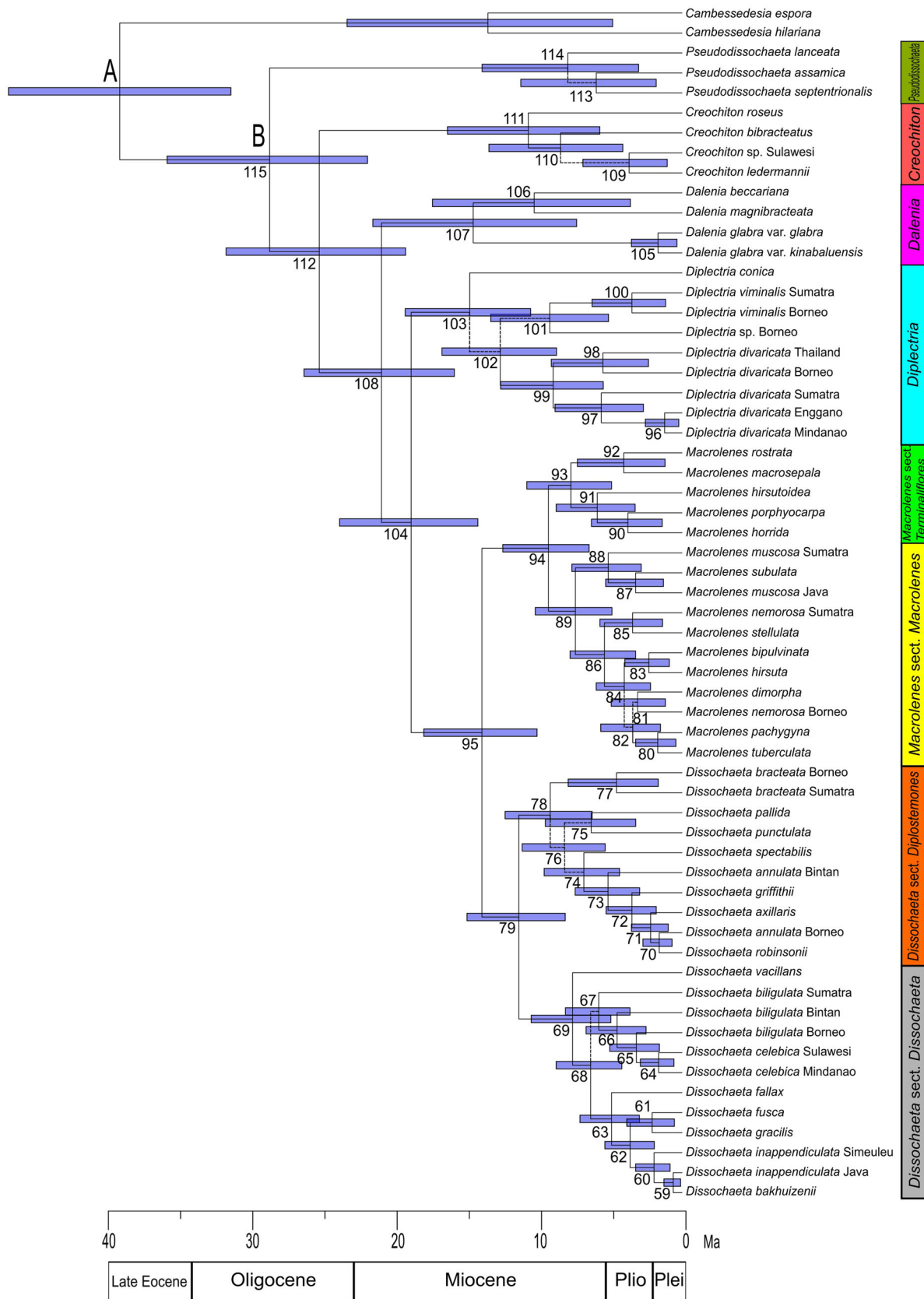


Fig. 2. Maximum clade credibility chronogram of the Dissochaeteae including the Cambessedesieae as outgroup; the blue node bars represent the 95% HPD (highest posterior density intervals). Dashed branches lead to nodes with posterior probabilities of < 0.95. Node numbers correspond to Table 1. Ma, million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

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 southward to tropical regions like in Southeast Asia (Morley, 2003; Li et al., 2017).

Our result agrees with Zhou et al. (2019), 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.

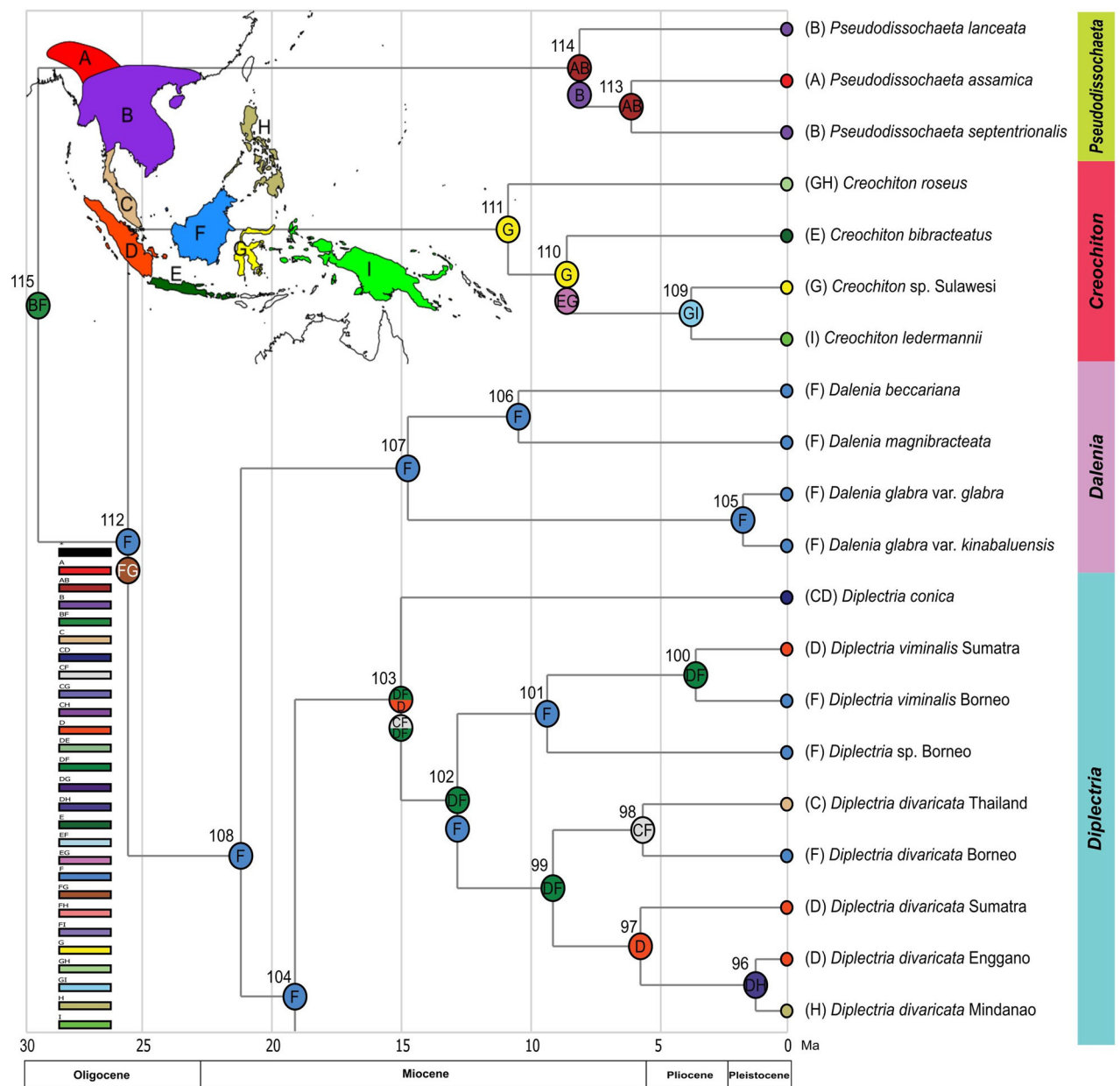


Fig. 3A. Ancestral range optimization for the Dissochaeteae. Pie charts at nodes represent optimization under maximum-likelihood S-DEC. When S-DIVA analyses yield a different optimization, then the results are shown below the relevant nodes. Node numbers indicated next to pie charts correspond to Table 2. Colors 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 [incl. 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.

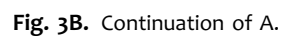


Table 2 Summary of the dated phylogeny and ancestral areas

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

Continued

Table 2 Continued

Node	Posterior	Stem age	95% HPD	Crown age	95% HPD	S-DEC	RP	S-DIVA	MP
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

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.

(2019). On the basis of a limited sampling, Zhou et al. (2019) 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. (2019), 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., 2012a), 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 center 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). When the sea level drops during the glacial periods, many islands were connected and many species may

have become widespread, whereas during interglacial periods, rises in sea level broke up the distributions, which likely resulted speciations.

4.3 Ancestral range estimation

Indochina and Borneo (BF) are most likely the area of origin for the most recent common ancestor of the Dissochaeteae (Fig. 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-rich 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).

A split between the basal Indo-Burmese and a predominantly Malesian clade occurred in the Middle Oligocene (clade 115; Fig. 3A). Dispersal from Indochina (B) westward into E Bhutan, NE India, and W Myanmar occurred at the time of at least node 114 (origin of the genus *Pseudodissochaeta*; Fig. 3A, Table 3: area AB). Colonization of west Malesia and western Wallacea (the Philippines, Sulawesi) by the Dissochaeteae started at the time

Table 3 Summary of the crown node ages 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

of the ancestral nodes 115 and 112 (Fig. 3A) during the middle Oligocene and early Miocene. The S-DEC analysis indicated Borneo (F) as the origin of Malesian diversification of this group, whereas the S-DIVA analysis included Sulawesi (FG) as ancestral area (Fig. 3A; node 112). A 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, and also eastward, 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 eastward to the Sahul Shelf (New Guinea) occurred in the late Pliocene and early Pleistocene (nodes 109 and 70; Figs. 3A, 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* L. (Begoniaceae; Thomas et al., 2012a), *Cyrtandra* (Gesneriaceae; Atkins et al., 2020), *Goniiothalamus* (Blume) Hook.f. & Thomson (Annonaceae; Thomas et al., 2017), *Meiogyne* Miq.-Fitzalanina 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 onward 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. 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 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. 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 eastward 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 (Hall, 2002, 2009).

The scrambling shrubs group (Fig. 3A; node 108), the species of which have a similar habit and habitat preference, originated on Borneo. 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. 3A; Table 3). The only species outside Borneo, *Dalenia papuana* (Mansf.) Kartn. from New Guinea, was not sampled in this study, so we cannot comment on this dispersal over Wallace's line. *Diplectria* (Fig. 3A; Table 3; node 103) most likely originated on Borneo and Sumatra (DF) or Sumatra (D) after dispersal from Borneo (S-DEC optimization). Alternatively, the S-DIVA analysis showed an origin of the genus on Borneo and Sumatra (DF) or Sumatra and the Malay Peninsula (cf.) (Tables 2, 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, whereas 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 3). With several dispersals/vicariance events, *Macrolenes* diversified during the late Miocene to Pleistocene in the Sundaland, favored 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. 3B). The origin of *Dissochaeta* (node 79) is either on Sumatra (D), based on the S-DEC analysis, or on Java and Borneo (EF) or Borneo (F), according to S-DIVA analysis (Tables 2, 3; Fig. 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 optimized as the area of origin by S-DIVA) (Table 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. 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 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, as Palawan formed almost a “bridge,” whereas Sulawesi was a little more isolated by the relatively deeper Makassar Strait (Fig. 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, the 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) from Borneo into Sulawesi, which were not yet in each other's neighborhood (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.

4.4 Biogeographic patterns

4.4.1 Indochina and Borneo

Indochina–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, it is 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 westward into NE India and E Bhutan (Fig. 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 (Figs. 3A, 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.

4.4.2 Wallace line

Wallace's line divides the floristic region of the Malay Archipelago or Malesia into western and eastern parts (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 phytogeographic 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 due to 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 as compared with the everwet climate of 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 eastward (Sahul) (van Welzen et al., 2005, 2011). Lianas/woody climbers are mostly restricted to the everwet areas, which is demonstrated here too, and only the two non-climbing genera occur in monsoonal 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 monsoonal 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. 3) identified four dispersal events across Wallace's line from West Malesia to Wallacea and East Malesia. Three of them show dispersal from Borneo (nodes 112 and 111; 7a and 70; 65 and 64) to Sulawesi and Philippines and one, rather oddly, from Sumatra (nodes 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 after convergence of the Sunda and Sahul shelves (Hall, 2009). The west-to-east Malesian dispersal 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). Nevertheless, 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

The authors 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 includes the Swaantje Mondt Fund of the Leids Universiteits Fonds (LUF), Leiden University, and the Alberta Mennega Foundation, which all supported for field. 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. We are also grateful to Gudrun Kadereit (Munich), Marie Claire Veranso-Libalah (Mainz) and Darin Penneys (Wilmington) for their help and support in terms of providing additional material, data sequences and analyses during this study. An earlier version of this article is part of the Ph.D. thesis of AK.

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Supplementary Material

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