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RESEARCH ARTICLE

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Abstract   Dipterocarpoideae, the largest subfamily in the Meranti family (Dipterocarpaceae) are an ecologically dominant group of trees throughout much of wet tropical Asia. Increasing anthropogenic pressures on this economically important tree family make it essential to resolve their complex evolutionary relationships and understand the distribution of genetic diversity throughout the family and distribution range. Dipterocarpaceae have been the focal group in a wide range of studies, owing to their economic value, importance in historical biogeography and key role in the evolution of the Asian tropical forest biome. Despite this, persistent taxonomic and evolutionary questions remain, ranging from questions on the geographic origin, sequence of dispersal and the identification of diagnostic characters to circumscribe proper evolutionary groups. Here we present a comprehensive phylogenomic hypothesis for Dipterocarpoideae, based on the analyses of plastome and nuclear cistron (NRC) data, and provide an in-depth review on the validity of morphological characters underlying the new tribal classification proposed here for the subfamily. Phylogenomic relationships were inferred using maximum likelihood and Bayesian approaches. Estimates of origin and onset of diversification in major clades and lineages were reconstructed using plastome, nuclear and combined datasets. Results of the separate and combined genomic datasets partly corroborate elements of previous classification systems (with improved support at all levels for major clades) but provide strong support for revising the tribal classification of the subfamily into four main clades: Dipterocarpeae (*Dipterocarpus*), Dryobalanopseae (*Dryobalanops*), Shoreeae (*Hopea*, *Neobalanocarpus*, *Parashorea*, and all parts of a polyphyletic *Shorea*) and Vatieieae (including all other presently accepted Dipterocarpoideae genera). Multi-fossil-dated divergence time estimation suggests Vatieieae first originated in the Late Cretaceous, followed by Dipterocarpeae, with subsequent rise of the Dryobalanopseae and Shoreeae in the Eocene. Diversification of all tribes commenced before the Early Miocene. Our results provide strong support for the position of *Neobalanocarpus heimii*, *Parashorea* and (sub-)sections of the genera *Anisoptera*, *Hopea*, *Shorea* and *Vatica*. Hypotheses on the origin of *Neobalanocarpus heimii* by intergeneric hybridisation between *Anthoshorea* (maternally inherited) and *Hopea* (paternally inherited) species were corroborated. Finally, our study provides support for future revisionary changes: (1) the elevation to generic rank of sections in *Shorea*; and (2) revising the infrageneric classification of *Hopea* as all (sub-)sections were recovered as not monophyletic.

Keywords   classification; Dipterocarpaceae; Dipterocarpoideae; genome skimming; historical diversification; molecular dating; nuclear ribosomal cistrons; phylogenomics; plastomes; tropical Asian rainforest

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

■ INTRODUCTION

Dipterocarpaceae includes nearly 700 species with their centre of diversity in Malesia (Symington, 1943; Ashton, 1982; Whitten & al., 1987; Appanah & Turnbull, 1998; Takhtajan, 2009). They are a major and often dominant structural component of Asian tropical lowland forests (Ghazoul, 2016) and the most important native tree family for timber harvesting in tropical Asia (Tsumura & al., 2011; FAO, 2014; ITTO, 2019). Due to their ecological importance, economic value and increasing anthropogenic pressures on Dipterocarpaceae species and their habitats (IUCN, 2020), studies contributing to

our understanding of the phylogenetic relationships and the distribution of genetic diversity across the family's range are an essential part of the scientific foundation required to establish conservation and restoration priorities.

Dipterocarpaceae have traditionally been classified into three subfamilies: Dipterocarpoideae in Asia, Monotoideae in Africa and South America, and Pakaraimoideae in South America (Maguire & al., 1977; Ashton, 1982; Kostermans, 1985; Londoño & al., 1995; Morton, 1995; Maury-Lechon & Curtet, 1998). Recent molecular phylogenetic studies have suggested that the monospecific genus *Pakaraimaea* (Pakaraimoideae), previously classified in Dipterocarpaceae, may be more closely related to Cistaceae (e.g., Heckenhauer & al., 2017), and the genus was included in this family in APG IV (2016). Heckenhauer & al. (2017) pointed out that the position of *Pakaraimaea* among Cistaceae is not supported by its morphology and ecology (placed among Tiliaceae, close to *Schoutenia* by Kostermans, 1978 and Takhtajan, 1980), and their limited sampling was not sufficient to confirm its position with certainty. The phylogenetic position of Monotoideae is still unclear, and either Sarcolaenaceae (endemic to Madagascar) or Monotoideae have been proposed as sister to Dipterocarpoideae (Takhtajan, 1980, 2009; APG III, 2009; APG IV, 2016; Heckenhauer & al., 2017).

Various classifications have been proposed for the family (see Maury-Lechon & Curtet, 1998; Ghazoul, 2016; and Heckenhauer & al., 2017, for overviews). In his seminal revision of Malesian Dipterocarpaceae, Ashton (1982) recognized 13 genera in Asian Dipterocarpoideae and subdivided the subfamily into two tribes: Dipterocarpeae (*Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Stemonoporus*, *Upuna*, *Vateria*, *Vateriopsis*, *Vatica*), characterized by valvate sepals in fruits, solitary vessels, scattered resin canals, and n = 11; and Shoreeae (*Dryobalanops*, *Hopea*, *Neobalanocarpus*, *Parashorea*, *Shorea*) characterized by imbricate sepals, grouped vessels, resin canals in tangential bands, and n = 7 (Ashton, 1982; Cao & al., 2006; Gamage & al., 2006). Takhtajan (1980, 2009) proposed the classification into four tribes and 13 genera: Dipterocarpeae (*Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Stemonoporus*, *Vateria*, *Vateriopsis*, *Vatica*), Dryobalanopseae (*Dryobalanops*), Parashoreeae (*Parashorea*), and Shoreeae (*Hopea*, *Neobalanocarpus*, *Shorea*, *Upuna*).

Most molecular phylogenetic studies aiming to resolve tribal as well as inter- and infrageneric relationships had taxonomically restricted sampling or employed only standardized low-variable plastome and nuclear DNA loci (Kajita & al., 1998; Kamiya & al., 1998, 2005; Dayanandan & al., 1999; Morton & al., 1999; Gamage & al., 2006; Tsumura & al., 1996, 2011; Yulita & al., 2005; Cao & al., 2006; Heckenhauer & al., 2017). Two recent phylogenomic studies used RADseq-derived SNP (single-nucleotide polymorphism) and plastome data to gain insight into phylogenetic relationships and floral evolution in Shoreeae (Heckenhauer & al., 2018, 2019). The results of these studies have provided valuable information on relationships but also highlighted incongruences in the deeper classification, still largely based on morphological characters.

At tribal level, the circumscriptions of the two tribes by Ashton (1982), Dipterocarpeae (*Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Stemonoporus*, *Upuna*, *Vateria*, *Vateriopsis*, *Vatica*) and Shoreeae (*Dryobalanops*, *Hopea*, *Neobalanocarpus*, *Parashorea*, *Shorea*), were largely corroborated, with the exception of the phylogenetic position of *Dipterocarpus*, which remained unclear and poorly supported in previous molecular phylogenetic studies (e.g., Tsumura & al., 1996; Kajita & al., 1998; Kamiya & al., 1998; Gamage & al., 2003, 2006; Indrioko & al., 2006; Heckenhauer & al., 2017). Morphological characters alone were shown to be unable to resolve the position of *Dryobalanops*, resulting in either inclusion in Shoreeae or as separate tribe (Heckenhauer & al., 2017).

Generic circumscription in Shoreeae has been problematic, and persisting uncertainty in the morphology-based taxonomy of the tribe has been hypothesized to either be the result of a considerable overlap of the morphospaces of the large genera *Shorea* and *Hopea*, intergeneric hybridization, or the presence of ancestral polymorphisms (Ashton, 1982; Murawski & al., 1994; Bawa, 1998; Kamiya & al., 2005; Cao & al., 2006). Molecular data including both cpDNA and RADseq-derived SNPs have corroborated previous studies and showed that *Shorea* sensu Ashton is paraphyletic and that the monophyletic genera *Parashorea* and *Hopea* are nested within (see Ashton, 1982; Heckenhauer & al., 2018, 2019).

The large genus *Shorea* (ca. 200 spp.: Ashton, 2004; ca. 360 spp.: Heckenhauer & al., 2018) is predominantly Malesian and has gone through a remarkable radiation in Borneo (136 species including 96 endemics reported by Ashton, 2004). Previous classifications have segregated *Shorea* into multiple genera based on timber colour, wood anatomy, and morphological features of the flower and embryo, as well as leaf epidermal characters: *Anthoshorea* (White Meranti), *Richetia* (Yellow Meranti) (Heim, 1892; Symington, 1943; Ashton, 1963, 1982; Meijer & Wood, 1964, 1976; Maury, 1978; Maury-Lechon, 1979a,b; Kostermans, 1983, 1984, 1992; Appanah & Turnbull, 1998; Maury-Lechon & Curtet, 1998), *Rubroshorea* (Red Meranti) and *Shorea* s.str. (Balau, Selangan Batu in Borneo). Symington (1943) classified the main genera *Shorea*, *Pentacme* and *Parashorea* into wood groups: Balau, Red, White, and Yellow Meranti. Maury (1978) and Kostermans (1984) introduced *Doona* and *Pentacme* besides the recognized genera *Anthoshorea*, *Shorea*, *Rubroshorea* and *Richetia*. Ashton (1982) recognized 11 sections in *Shorea*: S. sect. *Anthoshorea* (corresponding to White Meranti), sect. *Richetioides* (Yellow Meranti), sect. *Shorea*, sect. *Pentacme* and sect. *Neohopea* (Balau), and sect. *Brachypterae*, sect. *Doona*, sect. *Mutica*, sect. *Ovalis*, sect. *Pachycarpae* and sect. *Rubella* and (Red Meranti).

Geographic distribution of meranti groups varies from widespread (i.e., *Shorea* sect. *Shorea* and sect. *Anthoshorea* occur from Sri Lanka to Malesia) to locally endemic (i.e., Red Meranti sections are restricted to the biogeographic region of western Malesia, while S. sect. *Pachycarpae* and sect. *Rubella* are found only in Borneo and the Philippines) (Symington, 1943; Ashton, 1982; Kamiya & al., 1998, 2005). Heckenhauer

& al. (2018, 2019) concluded that the current infrageneric classification should be abandoned as most sections and subsections are non-monophyletic, and either support recognizing a single wide circumscription of *Shorea* (*Shorea* sensu Ashton) or to recognize *Anthoshorea*, *Doona*, *Richetia*, *Rubroshorea* and *Shorea* s.str. at generic level.

Infrageneric relationships in some other groups have also remained problematic, and Maury-Lechon & Curtet (1998) emphasized the mixed taxa of *Vatica* and *Cotylelobium* have remained poorly understood. *Sunaptea* is placed among *Vatica*, but morphological and anatomical characters in embryos, fruit-seeds and seedlings would suggest a close relationship with *Cotylelobium*.

Hybridization events may have contributed to problematic aspects of the current classification. Nuclear- and plastome-based phylogenies have indicated hard incongruence for the phylogenetic placement of *Parashorea* within *Shorea* (Heckenhauer & al., 2017, 2018, 2019), and a putative hybrid origin of the monotypic genus *Neobalanocarpus* (Shoreeae) has been hypothesized, based on conflicts between phylogenies derived from the nuclear *PgiC* gene and those derived from plastome fragments (Kamiya & al., 2005). However, *Neobalanocarpus* was not included in the recent studies by Heckenhauer & al. (2018, 2019), and the results based on limited DNA data need further corroboration by more extensive phylogenomic analyses.

To address some of these enduring conflicts between historically morphology-based classification systems and lacking genomic data, we employed previously released (Cvetković & al., 2017, 2019) and newly sequenced plastome and nuclear ribosomal cistron (NRC) data for 126 species of Dipterocarpaceae. Our main objectives were: (i) to test the monophyly of the proposed two tribes in Asian Dipterocarpaceae (Ashton, 1982): Dipterocarpeae (*Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Stemonoporus*, *Upuna*, *Vateria*, *Vateriopsis*, *Vatica*) and Shoreeae (*Dryobalanops*, *Hopea*, *Neobalanocarpus*, *Parashorea*, *Shorea*) and clarify the uncertain phylogenetic position of *Dipterocarpus* (Heckenhauer & al., 2017); (ii) to test previous hypotheses on the paraphyly of *Shorea* sensu Ashton and validity of proposed genus-level segregates (Heckenhauer & al., 2019); (iii) to test the monophyly of proposed subsections in *Vatica*; (iv) to test previous hypotheses of ancient hybridization events in the evolution of *Neobalanocarpus* (Kamiya & al., 2005) and *Parashorea* (Heckenhauer & al., 2019) and check for hard phylogenetic incongruence in other groups; (v) to gain insight into molecular divergence age estimates of the main clades and the tempo of diversification of Southeast Asian Dipterocarpaceae.

■ MATERIALS AND METHODS

Sampling. — Leaf material was collected during field work with collected materials frozen in liquid nitrogen or silica gel-dried. Herbarium material in the collections of Naturalis Biodiversity Center (L) were also sampled. Vouchers were deposited in our herbarium (BGT, Brunei Darussalam), Singapore Botanic Gardens herbarium (SING) and Naturalis Biodiversity Center (L, WAG).

New plastome and NRC data was generated for 141 accessions, for 126 species in Dipterocarpaceae with a focus on Southeast Asian taxa (*Anisoptera* 4, *Cotylelobium* 2, *Dipterocarpus* 26, *Dryobalanops* 4, *Hopea* 23, *Neobalanocarpus* 1, *Parashorea* 4, *Shorea* 50, *Vatica* 13). In addition, new genomic data (both the plastomes and NRC sequences) for 23 species in two outgroup families, Malvaceae s.l. and Thymelaeaceae, was added (Cvetković & al., 2021). Finally, we retrieved plastome and ITS data from GenBank to further extend our dataset (Dipterocarpaceae: 6 species; outgroups: 18 species; see Appendix 1).

DNA extraction, sequencing, and phylogenomic analyses. — Total genomic DNA was extracted from frozen and silica-dried leaf material using the Plant Genomic DNA Kit (Tiangen Biotech, Beijing, China), following Hinsinger & Strijk (2015). The NEBNext Ultra II DNA Library Prep Kit (Ipswich, Massachusetts, U.S.A.) was used for construction of 350-bp paired-end libraries at Novogene (Beijing, China). Sequencing was performed on an Illumina HiSeq2500 platform (San Diego, California, U.S.A.) by Novogene (Beijing, China), with a read length of 2 × 150 bp.

Plastome and NRC assembly, annotation and phylogenomic analyses were performed following Cvetković & al. (2019), with DNA matrix assemblies constructed using ECuADOR v.2.0 (Armijos Carrion & al., 2020) (suppl. Appendices S1–S3). Model selection for molecular evolution was performed with ModelTest-NG v.0.1.5 (GTR+I+G4 chosen for plastome, confirmed by both the Akaike information criterion [AIC] and the corrected AIC [AICc]; GTR+I+G4 for combined plastome-NRC datasets, confirmed by the Bayesian information criterion [BIC], AIC and AICc; TIM2+I+G4 for NRC, confirmed by the BIC, AIC and AICc) (Darriba & al., 2020). Likelihood phylogenetic inference was performed using RAxML-NG v.0.9.0 (Kozlov & al., 2019) following Cvetković & al. (2019).

In addition to the likelihood analyses, we performed a coalescent method (ASTRAL) to analyse the rate variation and signal in the plastid protein-coding genes. Coding genes were extracted from assembled plastomes with Geneious R11 v.11.0.4 (http://www.geneious.com) (Kearse & al., 2012). Extracted genes were aligned individually using MAFFT v.7.475 with the FFT-NS-i algorithm and the "--adjustdirectionaccurately" option (suppl. Appendix S4). A maximum likelihood (ML) tree was then built for each gene with IQ-TREE v.1.6.12 (Chernomor & al., 2016), including 1000 replicates for both ultrafast bootstrap and SH-aLRT. Substitution model for each gene was automatically chosen by IQ-TREE, then used for tree building. Resulting ML trees for individual genes were then concatenated and analyzed using ASTRAL v.5.7.4 (Mirarab & al., 2014) with default parameters.

Fossil calibration and molecular divergence time estimation. — Molecular divergence age estimation was performed using four calibrations (Fig. 1). The crown age of the Malvales divergence from Brassicales (102.7 Ma; Magallón & al., 2015)
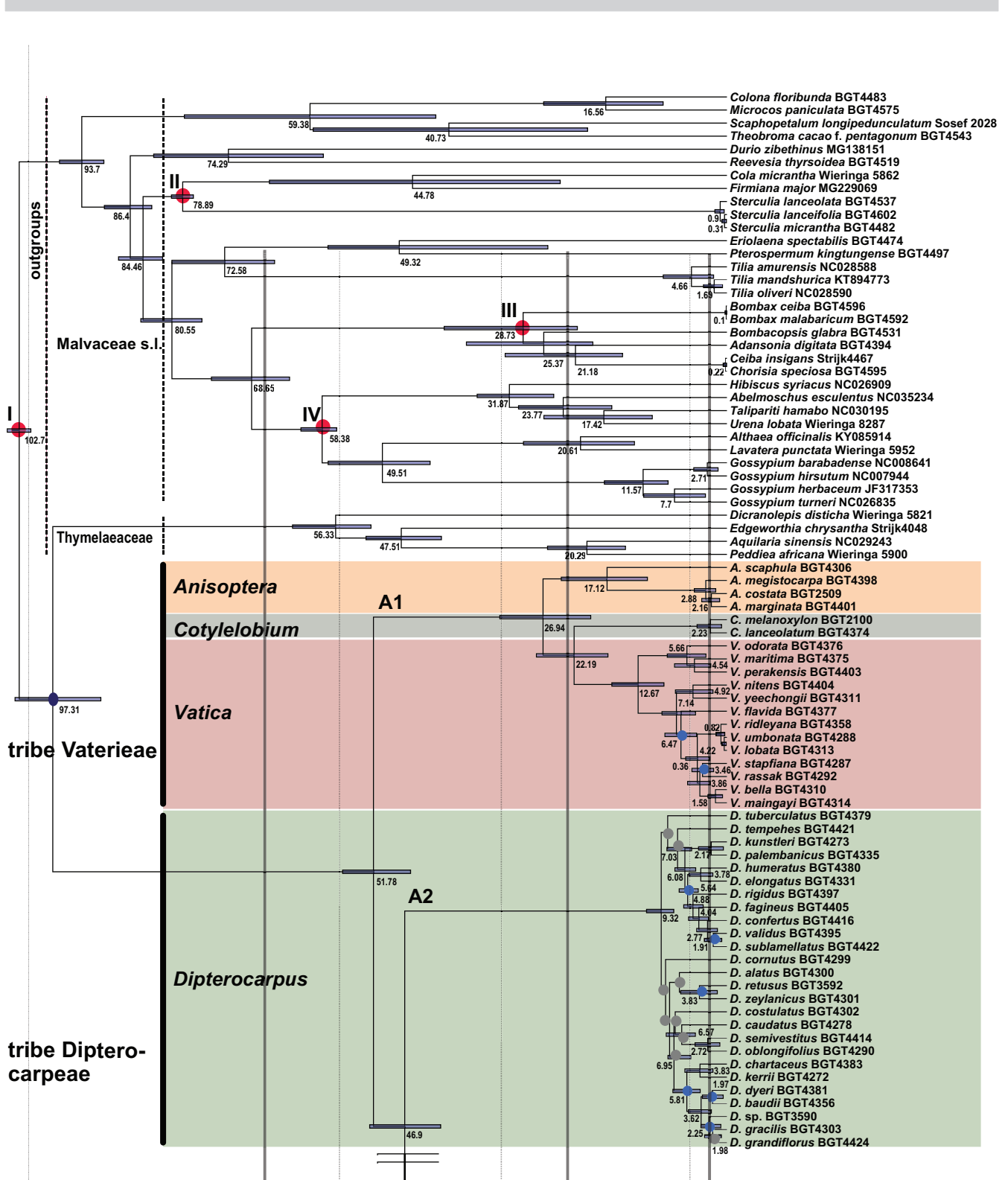
Fig 1. Chronogram of Dipterocarpoideae based on plastome and nuclear sequences (combined dataset) plus outgroups inferred by BEAST 2. Node ages (in Ma) shown at nodes, with the 95% highest posterior density intervals (HPD; blue bars). All nodes with posterior probability (PP) 1, except nodes indicated with blue circles (PP = 0.79–0.99) or grey circles (PP = 0.33–0.69). Overlay with revised tribal classification: A1: Vaterieae; A2: Dipterocarpeae; A3: Dryobalanopseae; A4: Shoreeae; A5: Doona + Anthoshorea + Neobalanocarpus + Hopea clade; A6: *Shorea* sect. *Doona*; A7: *S.* sect. *Anthoshorea*; A8: Richetioides + Parashorea + Shorea + Rubroshorea clade; A9: *S.* sect. *Richetioides*; A10: *S.* sect. *Shorea*; A11: *S.* sect. *Rubroshorea*. Fossils used in this study (red circles): I, the crown age of Malvales divergence from Brassicales (Magallón & al., 2015) (102.7 Ma); II, stem age for the ancestral node leading to Sterculioideae (Hernández-Gutiérrez & Magallón, 2019) (78.89 Mr); III, *Bombacacidites anne* (66–56 Ma) (Van Der Hammen, 1954); IV, *Malvaciphyllum macondicus* (61.6–56 Ma) (Carvalho & al., 2011). Geological time scale shown in millions of years.
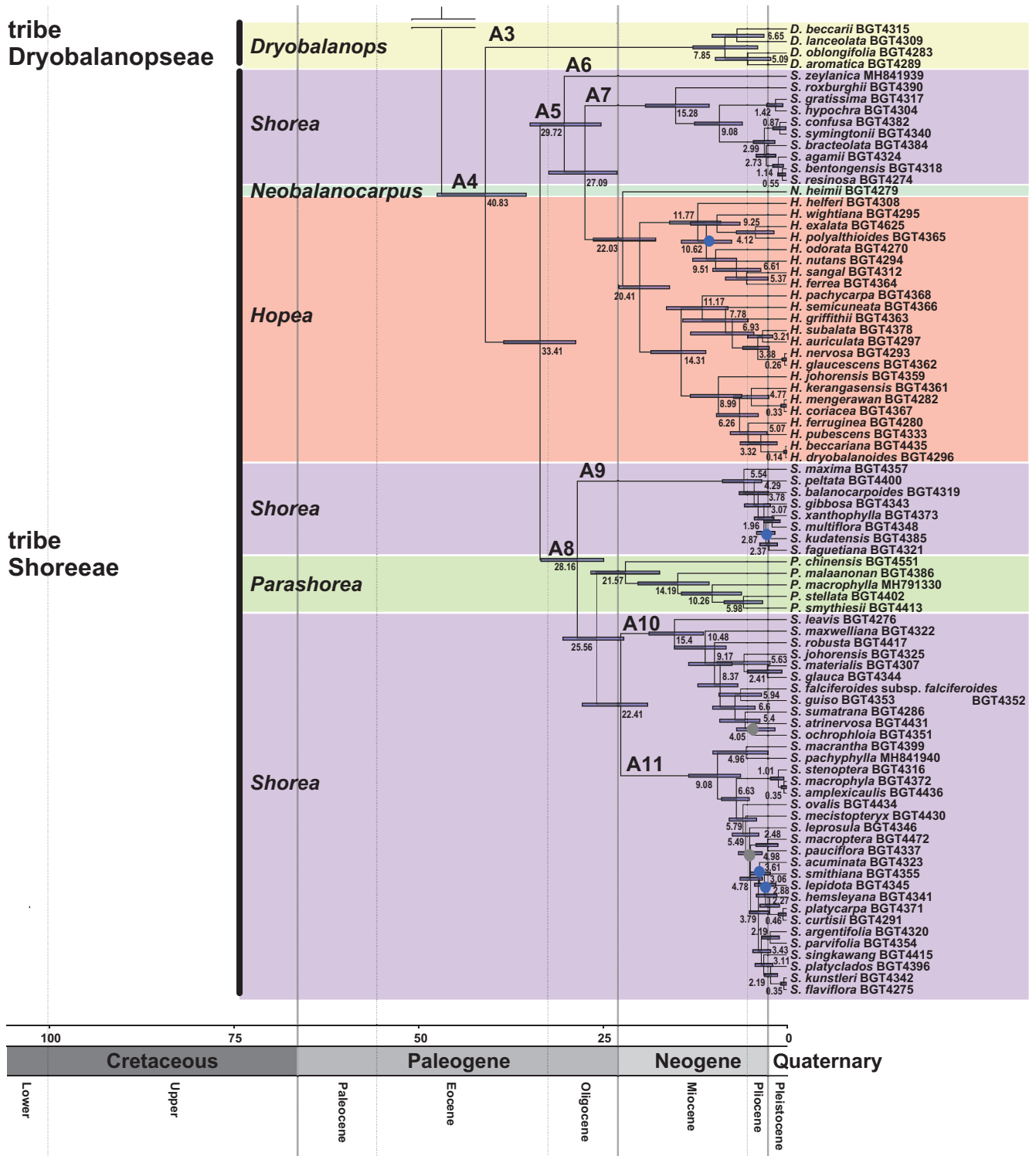
Fig 1. Continued.

was set as a root prior with a normal distribution (95% CI: 100.9–104 Ma, mean 102.7 Ma; node I in Fig. 1). A lognormal prior (95% CI: 76.5–86.5 Ma, mean 80.9 Ma; node II in Fig. 1) was assigned to a stem age for the ancestral node leading to Sterculioideae (81.8 Ma; Hernández-Gutiérrez & Magallón, 2019). *Bombacacidites anne*, a pollen fossil from the Mid-

to Late Palaeocene found in Colombia, was assigned to the crown *Bombax* (66–56 Ma) (Van Der Hammen, 1954). To this node we applied a lognormal prior with a mean of 59.5 Ma (95% CI: 56.0–65.4 Ma; node III in Fig. 1). *Malvaciphyllum macondicus*, a leaf imprint found in Colombian mid- to late Palaeocene deposits was used for the crown eumalvaceae

(61.6–56 Ma) (Carvalho & al., 2011). For the node we used a lognormal prior with a mean of 58.6 Ma (95% CI: 56.0–63.1 Ma; node IV in Fig. 1).

We performed divergence time estimation using plastome, NRC and combined datasets (suppl. Appendices S5–S7) in BEAST v.2.6.1 (Drummond & Rambaut, 2007; Suchard & Rambaut, 2009) on the CIPRES Science Gateway (Miller & al., 2010). We used an uncorrelated relaxed clock with rates obtained from a lognormal distribution (UCLN) (Drummond & al., 2006) and the Yule model (Yule, 1925) as tree prior. The distribution of the two hyperparameters (ucldMean.c: Mean = 10.0; ucldStdev.c: Mean = 0.333) with an exponential distribution were set following Areces-Berazain & Ackerman (2016). For detailed calibration of the priors used in this study see suppl. Table S1.

Here, we have applied the same settings from Cvetković & al. (2021), with the following modifications: two independent MCMC (Drummond & al., 2002) runs were conducted for 515 million generations for the plastome dataset, 200 million generations for the NRC dataset and 470 million generations for the combined dataset, each with the first 80% of tree samples discarded as burn-in. Effective sample size values (ESS), assessed in Tracer v.1.7.1 (Rambaut & al., 2018), were over 150 for plastome, NRC and combined datasets.

■ RESULTS

Plastome and NRC size. — The alignment lengths for the plastome, NRC, and combined datasets were 203,064, 6459 and 209,523 bp, respectively. The reconstructed plastome lengths of Dipterocarpaceae species ranged from 118,091 bp (*Dipterocarpus sublamellatus* BGT4422) to 156,123 bp (*Parashorea smythiesii* BGT4413). The typical plastome organization was confirmed: approximately 85 kbps, 20 kbps and 24 kbps, and overall GC of 35%, 32% and 43% in LSC (large single copy), SSC (small single copy) regions and two IR (inverted repeats) copies, respectively. The NRC lengths ranged from 5769 bp (*Shorea smithiana* BGT4355) to 5832 bp (*Hopea polyalthioides* BGT4365 and *Hopea* cf. *polyalthioides* BGT4360). We presented in detail both the plastome and NRC characteristics of outgroups used elsewhere (Cvetković & al., 2021).

Phylogenomic analyses. — The best-scoring ML tree derived from the plastome data recovered three well-supported clades, representing the Malvales (sub-)families Thymelaeaceae, Malvaceae s.l. and Dipterocarpaceae subfamily Dipterocarpoideae (BS = 100; suppl. Figs. S1–S4).

In Dipterocarpoideae, four main clades were recovered, all with high bootstrap support (BS = 100): Vaterieae (clade A1), Dipterocarpeae (clade A2), Dryobalanopseae (clade A3) and Shoreeae (clade A4) (suppl. Figs. S1–S4).

(1) Clade Vaterieae – Genera *Anisoptera*, *Cotylelobium* and *Vatica* were all strongly supported and recovered as monophyletic (BS = 100; A1, suppl. Figs. S1–S4). *Anisoptera* was recovered as sister to the *Cotylelobium* + *Vatica* clade (BS = 100). The two sections present in our *Anisoptera* sampling

(*A*. sect. *Glabrae*, sect. *Anisoptera*) were supported as monophyletic (BS = 100; A1, suppl. Fig. S2). However, monophyly of *Vatica* sections was not supported with representatives of *V*. sect. *Sunaptea* distributed throughout the *Vatica* clade (BS = 100; A1, suppl. Figs. S1–S3).

(2) Clade Dipterocarpeae was retrieved as monophyletic (BS = 99; A2, suppl. Figs. S1–S4).

(3) Clade Dryobalanopseae was retrieved as monophyletic (BS = 100; A3, suppl. Figs. S1–S4).

(4) Clade Shoreeae: *Hopea*, *Neobalanocarpus*, *Parashorea* and *Shorea* were retrieved as the monophyletic tribe Shoreeae (A4, suppl. Figs. S1–S4). *Shorea* was retrieved as paraphyletic with *Hopea*, *Neobalanocarpus* and *Parashorea* nested within (suppl. Figs. S1–S4).

Clade A5 contains species assigned to *Doona* (A6), *Anthoshorea* (A7), *Neobalanocarpus* and *Hopea*; *Doona* (A6) is sister to an *Anthoshorea* + *Neobalanocarpus* + *Hopea* clade (BS = 100; A5, suppl. Figs. S1–S4). *Hopea* was retrieved as monophyletic (BS = 100); but neither of the two *Hopea* sections (sect. *Hopea*, sect. *Dryobalanoides*) was retrieved as monophyletic group (A5, suppl. Fig. S2). *Neobalanocarpus heimii* was recovered as sister to *Hopea* (BS = 100; A5, suppl. Figs. S1–S3).

Clade A8 is composed of species assigned to *Richetia* (A9), *Parashorea*, *Shorea* s.str. (A10), and *Rubroshorea* (A11); all of these clades are strongly supported. Most sections (*Shorea* sect. *Brachyptereae*, sect. *Mutica*, sect. *Pachycarpae*, sect. *Shorea*) within *Shorea* s.str. and *Rubroshorea* are not supported as monophyletic. *Parashorea* was retrieved as sister to a clade containing *Shorea* s.str. + *Rubroshorea* (BS = 100; A8, suppl. Figs. S1–S3).

Neobalanocarpus heimii was recovered as nested in *Hopea* using the NRC dataset (BS = 93; B10, suppl. Figs. S3, S4), which is incongruent with the position retrieved using the plastome data (i.e., as sister to *Hopea*).

The backbone of Shoreeae received moderate support (B4, BS = 80, suppl. Figs. S3, S4), but some strongly supported clades were recovered: *Richetia* (B5; BS = 100), *Shorea* s.str. (B7; BS = 100), *Rubroshorea* (B8; BS = 99), *Parashorea* (BS = 76), *Anthoshorea* (B9; BS = 100) and *Hopea* (B10; BS = 99). A sister relationship between *Anthoshorea* (including a part of *Shorea* sect. *Mutica*) and *Hopea* was weakly supported (BS = 56).

The RAxML tree constructed using our combined dataset was largely congruent with the topology recovered using the plastome data (suppl. Figs. S5, S6).

Moreover, the four main clades and the placement of genera in Dipterocarpoideae in the ML analyses were additionally supported by Bayesian analysis (for details about the posterior probability values, see Figs. 1 and 2, suppl. Fig. S7).

In addition, the phylogenomic relationships in the ML analyses were confirmed by the concatenated individual species tree inferred by a coalescent method (ASTRAL) (suppl. Fig. S8), but not by the concatenated individual gene tree (suppl. Fig. S9).
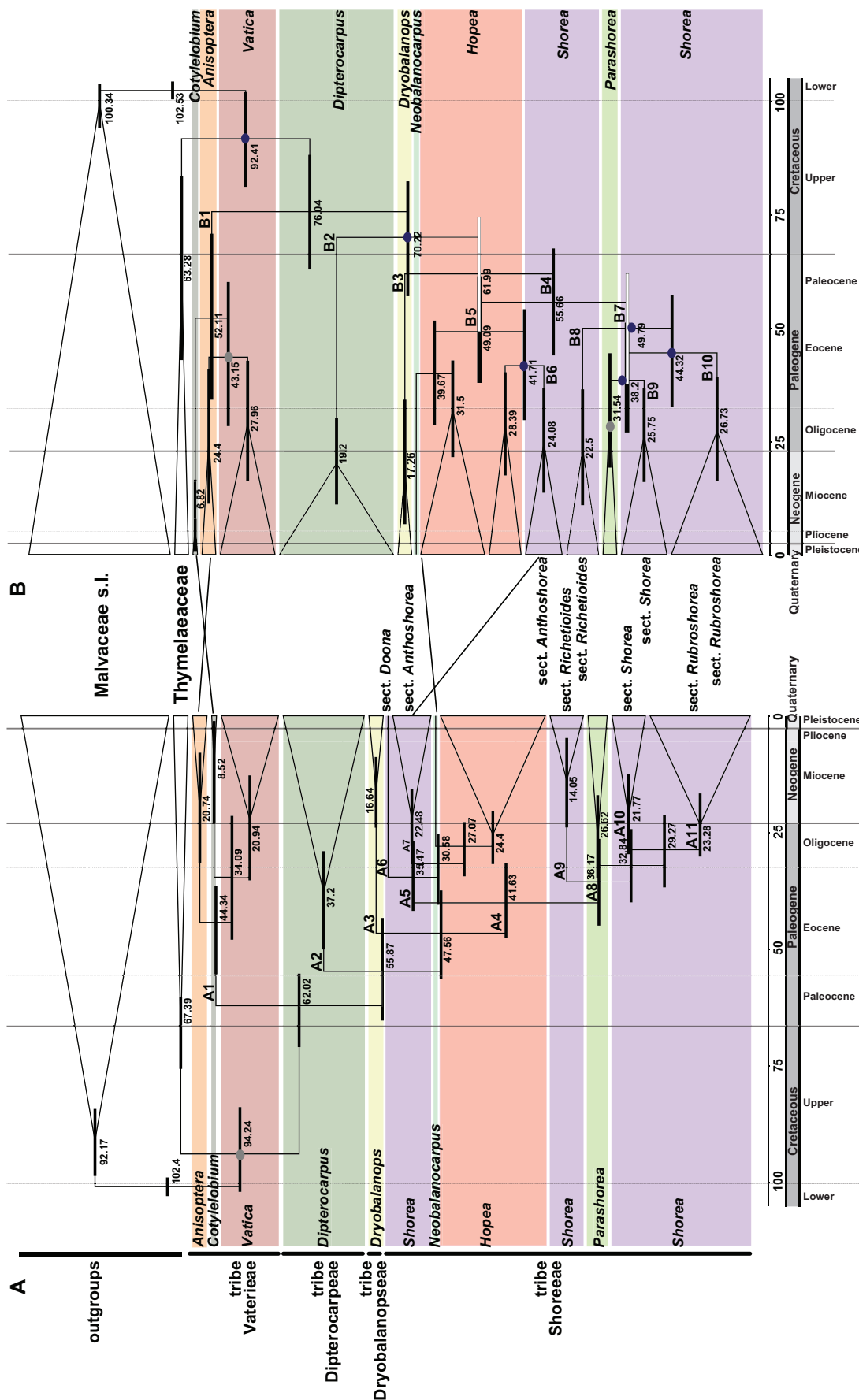
Fig 2. Chronograms of main sections in Dipterocarpoideae based on plastome (**A**) and NRC (**B**) sequences plus outgroups inferred by BEAST 2. Node ages (in Ma) shown at nodes; 95% highest posterior density (HPD) intervals as black bars. All nodes with posterior probability (PP) 1, except nodes with blue circles (PP = 0.83–0.98) and grey circles (PP = 0.56–0.66). Overlay with revised tribal classification: A1: Vaterieae; A2: Dipterocarpeae; A3: Dryobalanopseae; A4: Shoreeae; A5: Doona + Anthoshorea + Neobalanocarpus + Hopea clade; A6: *Shorea* sect. *Anthoshorea*; A8: Richetioides + Parashorea + Rubroshorea clade; A9: *S.* sect. *Richetioides*; A10: *S.* sect. *Shorea*; A11: *S.* sect. *Rubroshorea*; B1: Vaterieae; B2: Dipterocarpeae; B3: Dryobalanopseae; B4: Shoreeae; B5: sect. *Richetioides*; B6: *Shorea* + Rubroshorea + Parashorea + Anthoshorea + Neobalanocarpus + Hopea clade; B7: *S.* sect. *Shorea*; B8: *S.* sect. *Rubroshorea*; B9: *S.* sect. *Anthoshorea*; B10: Neobalanocarpus + Hopea clade. Geological time scale shown in millions of years.

Dating analyses. — An Early Upper Cretaceous origin for all three Malvalean families was retrieved using each of our three datasets (plastome, NRC, combined) [ca. 95 Ma for Malvaceae s.l.; Thymelaeaceae and Dipterocarpaceae, subfamily Dipterocarpoideae] (Figs. 1, 2, suppl. Fig. S7, suppl. Table S1).

Tribe Vaterieae first originated in the Late Upper Cretaceous (ca. 62/76/52 Ma, plastome, NRC and combined datasets, respectively), followed by tribe Dipterocarpeae (ca. 56/71/47 Ma, as before), and tribes Dryobalanopseae and Shoreeae in the Eocene (ca. 48/62/41 Ma, as before). The longest period of relative stasis between origin and onset of diversification occurred in tribe Dryobalanopseae (ca. 30 Myr; plastome data), and tribe Dipterocarpeae (ca. 40–50 Myr; NRC and combined data). The shortest intervals were detected in tribe Shoreeae (ca. 4–7 Myr; all datasets). Plastome and NRC data show divergence of all generic precursors occurring as early as the Early Miocene. Onset of species diversification of all tribes was initiated before the Late Miocene (combined dataset, Fig. 1) or Early Miocene (plastome and NRC data, Fig. 2, suppl. Fig. S7).

Among genera in the tribe Vaterieae, *Anisoptera* and *Vatica* diversified in the Late Oligocene and the Miocene. *Cotylelobium* diverged much later at the end stages of the Miocene (ca. 8.52–6.82 Ma for plastome and NRC datasets, respectively) or Early Pleistocene (ca. 2.23 Ma, combined data) (Figs. 1, 2, suppl. Fig. S7, suppl. Table S1). These estimates are similar to those recovered in tribe Shoreeae, where plastome data suggest a species diversification from the Late Oligocene–Early Miocene (27–21 Ma) (in *Shorea* s.str., *Rubroshorea*, *Anthoshorea*, *Parashorea*, and *Hopea*), except for *Richetioides* (Middle Miocene; 14.05 Ma). As before, nuclear data suggest slightly older age estimates (incl. *Richetioides*, 22–31 Ma; NRC data).

The position of *Neobalanocarpus* varied in our recovered phylogenetic trees, with divergence estimated to have started around 27.07 Ma (Oligocene; 23.34–34.69, plastome), 39.67 Ma (Late Eocene; 28.85–51.46, NRC) and 22.03 Ma (Late Oligocene; 17.76–26.21, combined data) (see Figs. 1, 2, suppl. Fig. S7).

■ DISCUSSION

A revised tribal classification for Dipterocarpoideae and phylogenetic affinities of *Dipterocarpus*. — Our analyses of plastome data resolved the backbone of the Dipterocarpoideae phylogenetic placement and clarified the previously unresolved positions of *Dipterocarpus* and *Dryobalanops* (Heckenhauer & al., 2017). The current tribal classifications of Dipterocarpoideae recognize either the two tribes Dipterocarpeae and Shoreeae (Ashton, 1982; Cao & al., 2006), or the four tribes Dipterocarpeae, Dryobalanopseae, Parashoreeae, and Shoreeae (Takhtajan, 2009), which is not supported by our results. Tribe circumscription here is in partial agreement with that outlined by Brandis (1895), Ashton (1982), Kamiya

& al. (2005), Takhtajan (2009), and Heckenhauer & al. (2018, 2019). Our study recovers the following four strongly supported tribes, and we propose to restructure the tribal classification of Dipterocarpoideae accordingly:

Tribe **Dipterocarpeae** Rchb., Handb. Nat. Pfl.-Syst.: 304. 1837 – Type: *Dipterocarpus* C.F.Gaertn.

Emergent or canopy trees, columnar but hardly buttressed with untidy globose crowns; prominently lenticellate orange–brown massively flaky bark; large leaf buds; amplexicaul bud scales; furnished stipules with diverse species-defining indumenta; plicate venation resulting in corrugation of their coriaceous leaves; thickly geniculate and often long petioles with often complex rings of vascular bundles and resin canals; variously thickened calyx ornamentations (tubercules, simple or folded wings); large flowers bearing a tubular calyx united at base into a smooth, angled, tuberculate or flanged tube enclosing but free from the ovary; two aliform, valvate sepals all along their development; stamens (15–40) are elongate orange anthers and stout tapering connectival appendages; dispersed resin canals in the wood and the largest stamens are the unique characteristic for *Dipterocarpus*; chromosome number $n = 11$ (summarized in Heckenhauer & al., 2017). From India and Sri Lanka to SE Asia.

One genus: *Dipterocarpus* C.F.Gaertn.

Tribe **Dryobalanopseae** Baill., Hist. Pl. 4: 210, 213. 1873 – Type: *Dryobalanops* C.F.Gaertn.

Emergent or canopy; fibres are with bordered pits; scattered resin canals; solitary vessels; fruit sepal is thickened. The subvalvate sepals in fruit (imbricate at first, after only retaining some traces of imbrication) is a unique characteristic for *Dryobalanops*. Chromosome number $n = 7$. Native in W. Malesia.

Note: The name Dryobalanopseae was incorrect and superfluous when published, since it included *Dipterocarpus*, but it was validly published with the correct name on page 213 and the description on 210, and is available for a tribe containing *Dryobalanops* and not *Dipterocarpus*; see Art. 19 Note 3 of the *ICN* (Turland & al., 2018).

One genus: *Dryobalanops* C.F.Gaertn.

Tribe **Shoreeae** Miq., Fl. Ned. Ind. 1(2): 503. 1859 – Type: *Shorea* Roxb. ex C.F.Gaertn.
= [unranked] Hopeae Korth., Verh. Nat. Gesch. Ned. Bezitt., Bot.: 55. 1840.
– "Parashoreeae" Takht., Flowering Pl.: 269. 2009, nom. nud. – Based on *Parashorea* Kurz.

Emergent or canopy, understorey trees; resin canals in tangential bands; thickened sepal base; fruit sepals imbricate at the incrassate-cupped base of the ripe fruit; 3 strata in pollen exine: absent tilioid structure of exine; T and Y columellae shape-type; always grouped vessels with cellular divisions; radial canal formation; 2 or 3 incrassate bases of sepals (and accrescent sepals) in fruits; free bases of fruit sepals; frigid pericarp tissue; circular fruit equatorial section; embryo cotyledons "covering-piled"; inferior or median-inferior hypocotyl; bilobed seedling

cotyledons; 4 root-xylem poles; uni- to tri-lacunar cotyledonary vascular bundles; stomatal types in first leaves paracytic, or para-cyclocytic, or anomo-cyclocytic; elongate stomata, sunken in the epiderm; chromosome number $n = 7$ (summarized in Appanah & Turnbull, 1998). From India and Sri Lanka to Malesia.

Eight genera: *Anthoshorea* Pierre (synonym of *Shorea*), *Doona* Thwaites (synonym of *Shorea*), *Hopea* Roxb., *Neobalanocarpus* P.S.Ashton, *Parashorea* Kurz, *Richetioides* F.Heim (synonym of *Shorea*), *Rubroshorea* (synonym of *Shorea*), *Shorea* Roxb. ex C.F.Gaertn.

Notes: Hopeae, described by Korthals (1839–1842), would have had priority over Shoreeae but was described without explicit rank, which is mandatory before 1887 (Art. 37.1–37.3 of the *ICN*, Turland & al., 2018).

Shoreeae has also been spelled as 'Shoreae'. Given this name has a non-Latin base (named after Sir John Shore), but has been Latinized, where the stem is the single syllable Shore, it seems proper to follow the original spelling of Miquel, who also used 'Shoreeae'. In case we consider this name to have alternative possible genitives, Art. 18.1 (via Art. 17.1) even obliges us to do so. In botanical Latin, double ee's are often avoided, but many recent tribal names based on generic names ending on -ea have also regularly been formed including the double ee. Since *Parashorea* is derived from *Shorea*, a tribe named after it should be spelled with the double ee as well, but so far this name lacks a formal description and is not in alignment with our classification superfluous.

Tribe **Vaterieae** Miq., Fl. Ned. Ind. 1(2): 502. 1859 – Type: *Vateria* L. [see note].
= Anisoptereae Miq., Fl. Ned. Ind. 1(2): 500. 1859 – Type: *Anisoptera* Korth.

Emergent or canopy trees; pollen grains tricolpate and lack endexine; universal presence of intercellular resin canals; valvate base of sepals in calyx of ripe fruit (imbricate at first, after only retain some traces of imbrication); solitary vessels, scattered resin canals; pericarp thickenings; 2 strata in pollen exine; tilioid structure of exine; columellae shape-type V and U; solitary vessels with cellular divisions of canal formation oblique; 0 or 5 incrassate bases of sepals (and accrescent sepals) in fruits; fused bases of fruit sepals; rigid to soft pericarp tissue; circular to 3-symmetric fruit equatorial section; cotyledons in embryo neither covering nor piled; hypocotyl apical or median; seedling cotyledons entire; 6, 8 or 10 root-xylem poles; 3- to multilacunar cotyledonary vascular bundles; stomatal types in first leaves anomocytic or anisocytic; elongate stomata; and sunken in the epiderm (imbricate) or round and raised above the epiderm (valvate); chromosome number $n = 11$ (summarized in Appanah & Turnbull, 1998). From the Seychelles through India and Sri Lanka to SE Asia.

Note: Miquel (1859) seems to have taken up the name from Korthals (1839), who had described the unranked name Vaterieae for a group containing *Vateria* and *Retinodendron* Korth. Subsequently, Blume (1852) used Vaterieae, but as a subfamily name ("subord.") that included both *Vateria* and

Vatica. Miquel was the first to explicitly use the term at tribal level, and provided a new description. Since in this work he only had to deal with some species of *Vatica* (*Vateria* does not occur in Indonesia), it is not immediately apparent here that it is based on *Vateria* instead of *Vatica*. Since Vaterieae is only the correct tribe name when it is based on the generic name *Vateria*, and it likely is a classification following previous works of Korthals and Blume, we consider *Vateria* the type of the tribe, and hence Vaterieae the correct spelling.

Seven genera: *Anisoptera* Korth., *Cotylelobium* Pierre, *Stemonoporus* Thwaites, *Upuna* Symington, *Vateria* L., *Vateriopsis* F.Heim, *Vatica* L.

Resolving power of genomic data and morphological traits, and taxonomic areas requiring additional investigation. — In this revised setup, the chromosome number of $x = 11$ is considered a synapomorphy of Dipterocarpeae, and imbricate flowers as a synapomorphy of Shoreeae (Indrioko & al., 2006). Unique morphological characters of *Dipterocarpus* were summarized in Heckenhauer & al. (2017, 2018). *Stemonoporus*, *Upuna*, *Vateria*, and *Vateriopsis* were not included in this study and will need to be included in an expanded survey. Monophyly of *Stemonoporus* and *Vateriopsis* was confirmed by both morphology (Ashton, 1982) and molecular phylogenetics (Dayanandan & al., 1999; Gamage & al., 2003, 2006; Heckenhauer & al., 2017). However, phylogenetic placement of *Upuna* and *Vateria* remains unresolved (Heckenhauer & al., 2017), and additional genomic data is needed for resolving their placement.

New insights on a hybrid origin of *Neobalanocarpus*. — Various affinities of *Neobalanocarpus heimii* have been suggested using morphological and anatomical data: *N. heimii* was hypothesized to be closely related to *Hopea* sect. *Hopea* on the basis of the inflorescence, fruit embryo and germination mode (Ashton, 1982; Kamiya & al., 1998; Yulita & al., 2005) and *Doona* based on wood anatomy (Parameswaran & Gotwald, 1979). *Neobalanocarpus heimii* shares morphological characters with both *Anthoshorea* and *Hopea* (urceolate corolla and stamens with an acicular connective appendage [Dayanandan & al., 1999], and a linear anther in the flower and sub-equal short woody fruit sepals [Kamiya & al., 2005]).

The placement of *Neobalanocarpus heimii* as sister to *Hopea* (plastome data, Fig. 2A, suppl. Figs. S3A, S4A, S7A, S8) is in concordance with Gamage & al. (2006) and Tsumura & al. (2011); in NRC-derived phylogenetic trees, *Neobalanocarpus* is nested within the *Hopea* clade (Fig. 2B, suppl. Figs. S3B, S4B, S7B), which is not only incongruent with the results of the plastome data, but also with the results from phylogenetic inference based on the nuclear *PigC* gene that indicates that the genus is nested within *Anthoshorea* (White Meranti; Kamiya & al., 2005). Kamiya & al. (2005) hypothesized this incongruence is a likely indicator of an ancient hybridization event involving ancestors of *Anthoshorea* as paternal progenitor and ancestors of the *Hopea* crown group as maternal progenitor. This hypothesis for a hybrid origin is also corroborated by an irregular behaviour during meiosis

in *Neobalanocarpus* (Jong & Lethbridge, 1967; Kamiya & al., 2005). The strong support for inclusion of *Neobalanocarpus* in *Hopea* (Fig. 2B, suppl. Figs. S3B, S4B, S7B) was unexpected and may indicate an additional level of complexity not previously recovered. As the NRC reads in our study are derived from the same read pool as the plastome reads, the latter indicating the expected relationship as sister to *Hopea*, lab artefacts such as sample mix-ups are unlikely. NRC copies can homogenize to either maternal or paternal parent after hybridization (concerted evolution; see Álvarez & Wendel, 2003; Nieto Feliner & Rosselló, 2007). The phylogenetic signal presented by the NRC data may be the result of an additional hybridization event with a species in *Hopea*. This would have occurred after the hybridization event between the *Anthoshorea* crown group species and the ancestor of the *Hopea* crown group that gave rise to *Neobalanocarpus*. Additional nuclear data is clearly required to further disentangle this complex pattern of reticulation.

Paraphyly of *Shorea* and validity of generic segregates of *Shorea*. — Paraphyly of *Shorea* as indicated in previous studies (Kamiya & al., 1998; Heckenhauer & al., 2018, 2019) is corroborated by our results: *Hopea*, *Neobalanocarpus* and *Parashorea* are clearly nested within *Shorea* sensu Ashton (1982).

Hopea is consistently retrieved as sister to *Anthoshorea* (Heckenhauer & al., 2018, 2019, this study), but there are some inconsistencies in the placement of *Parashorea*. Previous analyses of plastome data recovered *Parashorea* as sister to a *Shorea* s.str. + *Rubroshorea* clade, while RADseq-derived SNP data indicated a sister relationship to *Richetia* (Heckenhauer & al., 2019). Our results, with extended taxon sampling in the generic segregates of *Shorea*, corroborate the phylogenetic position in the plastome phylogenetic analysis; the backbone of tribe Shoreeae in the NRC data-derived phylogenetic tree was moderately supported. Heckenhauer & al. (2019) hypothesized that the incongruent placement in the plastome and nDNA phylogenetic analyses may indicate ancient hybridization, and this hypothesis remains plausible given the signals from the extended plastome and NRC data.

Sections of *Shorea* recognized by Maury (1978) and Kostermans (1984) including *S.* sect. *Anthoshorea*, sect. *Doona*, sect. *Richetia*, sect. *Rubroshorea*, and sect. *Shorea* [*Shorea* s.str.] are resolved as separate, well-supported clades in both whole-plastome and NRC phylogenetic analyses, while the monophyly of most subsections (*S.* subsect. *Brachyptereae*, subsect. *Mutica*, subsect. *Pachycarpae*, subsect. *Shorea*) within *S.* sect. *Shorea* s.str. and sect. *Rubroshorea* is not supported, in agreement with recent studies based on plastome and RADseq-derived SNP data by Heckenhauer & al. (2018, 2019). Accessions of species in the genus *Pentacme* (Maury, 1978; Maury-Lechon, 1979a,b) and *Shorea* sect. *Neohopea* and sect. *Rubella* (Ashton, 1977, 1980, 1982) were not included in this study, preventing us from clear conclusions about their placement and relationships within Shoreeae.

Sectional non-monophyly in *Hopea* and *Vatica*. — *Hopea* was retrieved as a monophyletic group in our study

(as in Yulita & al., 2005; Cao & al., 2006; Gamage & al., 2006; Tsumura & al., 2011), but all sections and subsections were non-monophyletic (but *H.* sect. *Dryobalanoides* was monophyletic in Yulita & al., 2005). High levels of morphological diversity within sections and subsections (e.g., variability in ovary, leaf, bark and floral characters; Ashton, 2004) further support this (Heckenhauer & al., 2018; this study).

Monophyly of the genera *Anisoptera*, *Cotylelobium* and *Vatica* among Vaterieae was confirmed by our study (as in Kajita & al., 1998; Gamage & al., 2003, 2006; Indrioko & al., 2006). Two monophyletic sections in *Vatica* (Cao & al., 2006) were not retrieved here. In addition, two entries of *V.* sect. *Sunaptea* were placed among sect. *Vatica* in our study, resolving the previously doubtful position of this group (Maury-Lechon & Curtet, 1998).

Dating analyses. — Here we focused on species in subfamily Dipterocarpoideae and present in detail the origin and divergence of outgroups used elsewhere (Cvetković & al. 2021). Results obtained with our combined dataset (51.78 [45.91–55.77] Ma) partly confirm results from Heckenhauer & al. (2017: 54.9 Ma [39.3–71.6 Ma]) but provide improved phylogenetic resolution. Major clades in Heckenhauer & al. (2017) showed wider range age estimates. A key difference is the position of *Dipterocarpus* forming a monophyletic clade with the rest of species belonging to Vaterieae, in contrast to all our analyses that recovered four tribes in Dipterocarpoideae, including a well-supported Dipterocarpeae. The placement of *Neobalanocarpus* in their study is compatible with our plastome dataset; however, our NRC-based results present an additional previously undetected hybridization event with species in *Hopea*. We agree with Heckenhauer & al. (2017) that calibration remains difficult in the group, despite the large numbers of reported fossils for the family (see discussion further below).

Dipterocarpaceae are an ancient group that evolved slowly and dispersed widely. Evidence for significant increases in speciation rates is absent (Strijk & al., unpub. data) and most extant species are relatively young. Despite many studies in this family, little is known about how this pace of speciation has affected the distribution of genomic diversity or even when this has taken place exactly. A Gondwanan origin is still the more widely accepted theory (i.e., allopatrically evolved from Monotoideae on Deccan and Mascarene Plates) (Ducousso & al., 2004; Dutta & al., 2009; Rust & al., 2010; Beimforde & al., 2011; Shukla & al., 2013; Ghazoul, 2016; Kooyman & al., 2019), but remains contentious. Fossils have been reported from E Africa (Bancroft, 1935), Alaska (Wolfe, 1977) and S and SE Asia (discussed below). Fossils found in the Neogene sediments of India and Nepal (e.g., Prasad, 1990, 1994; Prakash & al., 1994; Prasad & Awasthi, 1996; Khan & Bera, 2010) are absent from the Palaeogene sediments (Bande & Prakash, 1986; Awasthi & Srivastava, 1990; Khan & Bera, 2010; Srivastava & Mehrotra, 2010; Shukla & al., 2013; Kooyman & al., 2019). The Palaeogene fossils in SE Asia (Muller, 1981; Dutta & al., 2011) are presented by several studies to support a SE Asian origin of Dipterocarpaceae

(Lakhanpal, 1970, 1974; Awasthi, 1996; Sasaki, 2006; Shukla & al., 2012, 2013).

The Indian plate (with Madagascar) separated from E Africa 158–160 Ma (Middle Jurassic) moving 15–25 cm/yr (Briggs, 2003; Rust & al., 2010; Ghazoul, 2016). Initial colliding with Eurasia commenced in the early Cenozoic (55–65 Ma; with final suturing 42–55 Ma) (Briggs, 2003), enabling biotic interchange between endemics from both sides (Rust & al., 2010). Nowadays, SE Asia is recognized as having one of the world's most complex and least understood geological histories (Sun & al., 2000). In the Early Palaeogene, the Indian subcontinent witnessed enormous floral diversification as a result of a global rise in temperature and changes in latitudinal position (Zachos & al., 2001; Rana & al., 2004; Sahni & al., 2006; Garg & al., 2008; Shukla & al., 2013; Paul & al., 2015). Modern-type, broad-leaf tropical Dipterocarpaceae forests were spread across the Indian subcontinent from the Eocene (52 Ma) (Van Aarssen & al., 1994; Anderson & Muntean, 2000; Dutta & al., 2009; Mallick & al., 2009; Rust & al., 2010; Rudra & al., 2014; Paul & al., 2015). Our results suggest an early Eocene diversification for Dipterocarpoideae (51.78 Ma), and the origin of all its main tribes during the Middle Eocene (ca. 41–52 Ma). This is remarkable since the origin of the clade has been hypothesized to be of Cretaceous origin (ca. 96 Ma), with a lag in initial divergence for c. 40 Ma (Eocene diversification for Dipterocarpoideae, 51.78 Ma). In contrast, the Legumes have been recently assessed as originating and diversifying around the Cretaceous-Palaeogene Mass extinction event (Vanneste & al., 2014; Koenen & al., 2021), a window in time that the Dipterocarps seem to have passed through without any evidence of major diversification.

Arid climate, uplifting of the Himalaya-Tibetan plateau, monsoon initiation and intensification, and Northern Hemisphere glaciations are thought to have caused complete extirpation of the family in most of parts in the Indian subcontinent during the Cenozoic (Milanković, 1941; Quade & al., 1989; Ruddiman & Kutzbach, 1989; Kroon & al., 1991; Molnar & al., 1993; Derry & France-Lanord, 1996; Ramstein & al., 1997; Dynesius & Jansson, 2000; An & al., 2001; Zheng & al., 2004; Clift & al., 2008; Boos & Kuang, 2010; Shukla & al., 2013; Rudra & al., 2014). In this study, all main sections of Dipterocarpoideae diversified during the Neogene – probably due to irregular annual and mass flowering effects as a result of extended periods of drought (Heckenhauer & al., 2017, 2018). The increased drought during the Neogene is considered to be one of the driving forces behind adaptation and diversification of the family in SE Asia.

Dipterocarpaceae fossils suggest a floristic link between Chinese and Indian palaeofloras and the presence of massive vegetation exchanges between Indian Gondwana and Laurasia (Sun & Wang, 2005; Jacques & al., 2011, 2013, 2015; Feng & al., 2013). Members of the family became adapted to a seasonal climate from the Late Eocene to the Early Miocene (Wolfe, 1994a,b; Zachos & al., 2001; Ho & al., 2003; Mosbrugger & al., 2005; Shi & Li, 2010; Shi & al., 2014a,b; Jacques & al., 2015), and gradually disappeared from SE China

from the Late Miocene (Feng & al., 2013; Jiang & al., 2013; Huang & al., 2016; Liu & Quan, 2017). The family was almost or completely absent from mainland China during the last glacial maximum (LGM) (Ni & al., 2010; Jacques & al., 2015).

In contrast, the SW Chinese Miocene palaeofloras have a different floristic composition without clear Indian affinities (Jiang & al., 2013; Jacques & al., 2015; Huang & al., 2016; Liu & Quan, 2017; Cvetković & al., 2019). The migration route is thought to be through SE Asia, linking India with SE China as opposed to SW China (Jacques & al., 2015). Yunnan has also been affected by a period of aridification since the Miocene (Xia & al., 2009; Jacques & al., 2011; Sun & al., 2011; Xing & al., 2012; Jiang & al., 2013; Huang & al., 2016; Liu & Quan, 2017). The existence and position of the "savanna corridor" across Sundaland during the Neogene and Quaternary, and in which way it affected diversification of the family, remain controversial to this day (Morley & Flenley, 1987; Heaney, 1991; Morley, 2000, 2012; Sun & al., 2000; Gathorne-Hardy & al., 2002; Meijaard, 2003; Bird & al., 2005; Cannon & al., 2009; Wurster & al., 2010; Slik & al., 2011; Iwanaga & al., 2012; Kamiya & al., 2012; Ohtani & al., 2013; Raes & al., 2014). The absence of migration pathways and dispersal capabilities could explain the patterns of narrow endemism in Dipterocarpaceae (Ashton, 1982), but the historical interplay between dispersal and local extirpation, species ecology and adaptive radiations in the family remain less well understood (Kooyman & al., 2019).

■ CONCLUSIONS

Our plastome and NRC datasets confirm some results from previous studies, but also provide novel insights into the tribal classification of Dipterocarpoideae and present strong support for a new tribal classification for the group. Our data resolves the poorly understood phylogenetic relationships of *Dipterocarpus*, establishes non-monophyly of sections in *Hopea*, *Shorea* and *Vatica*, and re-assesses hybridization of *Neobalanocarpus* and *Parashorea*, revealing a previously undetected event. In our study we have focused on the use of a single (extended) nuclear region but in order to fully corroborate this signal, more extensive data, especially from the nuclear genome, is needed. This will aid in ruling out other potential explanations such as incomplete lineage sorting, chloroplast capture and other organism-level processes that can cause phylogenomic discordance (Spooner & al., 2020).

Parashorea is closely related to *Shorea*, and *Neobalanocarpus heimii*'s interspecific hybridisation (Kamiya & al., 2005; Gamage & al., 2006) of *Anthoshorea* (maternally inherited) and *Hopea* (paternally inherited) is supported by its placement between the Anthoshorea and Hopea clades in our plastome-based results, and in the Hopea clade using NRC data.

We propose here the recognition of four tribes in Dipterocarpoideae: Vatierieae (including all genera of presently accepted Dipterocarpeae except for *Dipterocarpus*: *Anisoptera*, *Cotylelobium*, *Stemonoporus*, *Upuna*, *Vateria*, *Vateriopsis*,

Vatica), Dipterocarpeae (*Dipterocarpus*), Dryobalanopseae (*Dryobalanops*), and Shoreeae (*Hopea, Neobalanocarpus, Parashorea, Shorea* s.str. and several generic segregates of *Shorea* s.l. including *Anthoshorea, Doona, Richetioides,* and *Rubroshorea*).

Our molecular results are consistent with previous hypotheses that several *Shorea* sections including *S.* sect. *Anthoshorea,* sect. *Doona,* sect. *Richetia,* sect. *Rubroshorea* and sect. *Shorea* are distinct and could be elevated to the genus rank (Maury, 1978; Maury-Lechon, 1979a,b; Heckenhauer & al., 2018, 2019); this could also resolve the paraphyly of *Shorea* sensu Ashton (1982) in which the genera *Hopea, Neobalanocarpus* and *Parashorea* are nested. Most *Shorea* subsections were shown to be non-monophyletic, indicating that the infrageneric classification at this rank needs to be revised.

■ AUTHOR CONTRIBUTIONS

TC, DDH and DCT performed the experiments and data analyses; TC, DDH, DCT, JJW, EV and JSS collected samples; JSS designed the experiments and provided the funding. All authors contributed to editing, writing and reviewing the manuscript, and approved the final version for submission. The authors alone are responsible for the content and writing of the paper. — TC, https://orcid.org/0000-0002-5981-0134; DDH, https://orcid.org/0000-0001-7459-7610; JJW, https://orcid.org/0000-0003-0566-372X; JSS, https://orcid.org/0000-0003-1109-7015

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Appendix 1. Accession list and voucher information for samples used in this study.

Species name; location data (country, province); voucher information; GenBank accession numbers of cpDNA (complete plastid genome), NRC (nuclear ribosomal cistrons) or ITS (internal transcribed spacer). Newly generated sequences, 151 plastome and 164 NRC, are indicated with *; missing information is indicated by –.

Anisoptera costata Korth., Singapore, *Strijk 4412* (SING), MZ901761*, –, *Anisoptera costata* Korth., Brunei, *Strijk 2509* (BGT), MZ901760*, MZ782371*, *Anisoptera marginata* Korth., Singapore, *Strijk 4401* (SING), MZ901762*, MZ782372*, *Anisoptera megistocarpa* Slooten, Singapore, *Strijk 4398* (SING), MZ901763*, MZ782373*, *Anisoptera megistocarpa* Slooten, Singapore (MacRitchie Reservoir), *Strijk 4429* (SING), MZ901764*, MZ782374*, *Anisoptera scaphula* (Roxb.) Kurz, Singapore (Yishun Park), *Strijk 4306* (SING), MZ901765*, MZ782375*, *Cotylelobium lanceolatum* Craib, Singapore, *Strijk 4374* (SING), MZ901766*, MZ782383*, *Cotylelobium melanoxylon* (Hook.f.) Pierre, Brunei, *Strijk 2100* (BGT), MZ901767*, MZ782384*, *Dipterocarpus alatus* Roxb., Singapore (Yishun Park), *Strijk 4300* (SING), MZ901912*, MZ889121*, *Dipterocarpus baudii* Korth., Singapore, *Strijk 4356* (SING), MZ901768*, MZ782386*, *Dipterocarpus caudatus* Foxw., Singapore, *Strijk 4278* (SING), MZ901769*, MZ782387*, *Dipterocarpus chartaceus* Symington, Singapore, *Strijk 4383* (SING), MZ901770*, MZ782388*, *Dipterocarpus confertus* Slooten, Singapore, *Strijk 4416* (SING), –, MZ782389*, *Dipterocarpus cornutus* Dyer, Singapore (Yishun Park), *Strijk 4299* (SING), –, MZ782390*, *Dipterocarpus costulatus* Slooten, Singapore (Yishun Park), *Strijk 4302* (SING), –, MZ782391*, *Dipterocarpus dyeri* Pierre, Singapore, *Strijk 4381* (SING), –, MZ782392*, *Dipterocarpus elongatus* Korth., Singapore (Chestnut Nature Park), *Strijk 4331* (SING), MZ901771*, MZ782393*, *Dipterocarpus fagineus* Vesque, Singapore, *Strijk 4405* (SING), MZ901772*, MZ782394*, *Dipterocarpus gracilis* Blume, Singapore (Yishun Park), *Strijk 4303* (SING), MZ901773*, MZ782396*, *Dipterocarpus gracilis* Blume, China (Qin Xiu Shan), *Strijk 3593* (BGT), –, MZ782395*, *Dipterocarpus grandiflorus* Blanco, Singapore, *Strijk 4392* (SING), MZ901774*, MZ782397*, *Dipterocarpus grandiflorus* Blanco, Singapore (MacRitchie Reservoir), *Strijk 4424* (SING), MZ901775*, MZ782398*, *Dipterocarpus humeratus* Slooten, Singapore, *Strijk 4380* (SING), MZ901776*, MZ782399*, *Dipterocarpus kerrii* King, Singapore, *Strijk 4272* (SING), MZ901777*, MZ782400*, *Dipterocarpus kunstleri* King, Singapore, *Strijk 4273* (SING), –, MZ782401*, *Dipterocarpus oblongifolius* Blume, Singapore, *Strijk 4290* (SING), MZ901778*, MZ782402*, *Dipterocarpus palembanicus* Slooten, Singapore, *Strijk 4335* (SING), MZ901779*, MZ782403*, *Dipterocarpus retusus* Blume, China (Qin Xiu Shan), *Strijk 3592* (BGT), –, MZ782404*, *Dipterocarpus rigidus* Ridl., Singapore, *Strijk 4397* (SING), MZ901780*, MZ782405*, *Dipterocarpus semivestitus* Slooten, Singapore, *Strijk 4414* (SING), MZ901781*, MZ782406*, *Dipterocarpus* sp., China (Qin Xiu Shan), *Strijk 3590* (BGT), –, MZ782412*, *Dipterocarpus sublamellatus* Foxw., Singapore (MacRitchie Reservoir), *Strijk 4422* (SING), MZ901782*, MZ782407*, *Dipterocarpus tempehes* Slooten, Singapore (MacRitchie Reservoir), *Strijk 4421* (SING), MZ901784*, MZ782409*, *Dipterocarpus tempehes* Slooten, Singapore, *Strijk 4271* (SING), MZ901783*, MZ782408*, *Dipterocarpus tuberculatus* Roxb., Singapore, *Strijk 4379* (SING), MZ901785*, MZ782410*, *Dipterocarpus validus* Blume, Singapore, *Strijk 4395* (SING), –, MZ782411*, *Dipterocarpus zeylanicus* Thw., Singapore (Yishun Park), *Strijk 4301* (SING), MZ901786*, MZ782413*, *Dryobalanops aromatica* C.F.Gaertn., Singapore, *Strijk 4289* (SING), MZ901787*, MZ782414*, *Dryobalanops beccarii* Dyer, Singapore (Yishun Park), *Strijk 4315* (SING), MZ901788*, MZ782415*, *Dryobalanops lanceolata* Burck, Singapore (Yishun Park), *Strijk 4309* (SING), MZ901789*, MZ782416*, *Dryobalanops oblongifolia* Dyer, Singapore, *Strijk 4283* (SING), MZ901790*, MZ782417*, *Hopea auriculata* Foxw., Singapore (Yishun Park), *Strijk 4297* (SING), MZ901805*, MZ782420*, *Hopea beccariana* Burck, Singapore, *Strijk 4435* (SING), MZ901806*, MZ782421*, *Hopea coriacea* Burck, Singapore, *Strijk 4367* (SING), MZ901808*, MZ782423*, *Hopea dryobalanoides* Miq., Singapore (Yishun Park), *Strijk 4296* (SING), MZ901809*, MZ782424*, *Hopea dryobalanoides* Miq., –, –, –, MH791329, *Hopea exalata* W.T.Lin, Y.Y.Yang & Q.S.Hsue, China (Yunnan), *Strijk 4625* (BGT), MZ901810*, MZ782425*, *Hopea ferrea* Laness., Singapore, *Strijk 4364* (SING), MZ901811*, MZ782426*, *Hopea ferruginea* Parijs, Singapore, *Strijk 4280* (SING), MZ901812*, MZ782427*, *Hopea ferruginea* Parijs, Singapore (MacRitchie Reservoir), *Strijk 4425* (SING), MZ901813*, MZ782428*, *Hopea glaucescens* Symington, Singapore, *Strijk 4362* (SING), MZ901814*, MZ782429*, *Hopea griffithii* Kurz, Singapore (MacRitchie Reservoir), *Strijk 4419* (SING), MZ901816*, MZ782431*, *Hopea griffithii* Kurz, Singapore, *Strijk 4363* (SING), MZ901815*, MZ782430*, *Hopea helferi* (Dyer) Brandis, Singapore (Yishun Park), *Strijk 4308* (SING), MZ901817*, MZ782432*, *Hopea johorensis* Symington, Singapore, *Strijk 4359* (SING), MZ901818*, MZ782433*, *Hopea kerangasensis* P.S.Ashton, Singapore, *Strijk 4361* (SING), MZ901819*, MZ782434*, *Hopea mengarawan* Miq., Singapore (Chestnut Nature Park), *Strijk 4330* (SING), MZ901821*, MZ782436*, *Hopea mengarawan* Miq., Singapore, *Strijk 4282* (SING), MZ901820*, MZ782435*, *Hopea nervosa* King, Singapore (Yishun Park), *Strijk 4293* (SING), MZ901822*, MZ782437*, *Hopea nutans* Ridl., Singapore (Yishun Park), *Strijk 4294* (SING), MZ901823*, MZ782438*, *Hopea odorata* Roxb., Singapore, *Strijk 4270* (SING), MZ901824*, MZ782439*, *Hopea pachycarpa* (F.Heim) Symington, Singapore, *Strijk 4368* (SING), MZ901825*, MZ782440*, *Hopea polyalthioides* Symington, Singapore, *Strijk 4365* (SING), MZ901826*, MZ782441*, *Hopea* cf. *polyalthioides* Symington, Singapore, *Strijk 4360* (SING), MZ901807*, MZ782422*, *Hopea pubescens* Ridl., Singapore, *Strijk 4333* (SING), MZ901827*, MZ782442*, *Hopea sangal* Korth., Singapore (Yishun Park), *Strijk 4312* (SING), MZ901828*, MZ782443*, *Hopea semicuneata* Symington, Singapore, *Strijk 4366* (SING), MZ901829*, MZ782444*, *Hopea subalata* Symington, Singapore, *Strijk 4378* (SING), MZ901830*, MZ782445*, *Hopea wightiana* Wall., Singapore (Yishun Park), *Strijk 4295* (SING), MZ901831*, MZ782446*, *Neobalanocarpus heimii* (King) P.S.Ashton, Singapore, *Strijk 4279* (SING), MZ901832*, MZ782449*, *Neobalanocarpus heimii* (King) P.S. Ashton, –, –, MH746730, AY026657, *Parashorea chinensis* Wang Hsie, China (Yunnan), *Strijk 3594* (BGT), https,//doi.org/10.5061/dryad.1512pn3 (previous study), *Parashorea chinensis* Wang Hsie, China (Yunnan), *Strijk 4551* (BGT), MZ901833*, MZ782450*, *Parashorea macrophylla* Wyatt-Sm. ex P.S.Ashton, –, –, –, MH791330, *Parashorea malaanonan* (Blanco) Merr., Singapore, *Strijk 4386* (SING), MZ901834*, MZ782451*, *Parashorea smythiesii* Wyatt-Sm. ex P.S.Ashton, Singapore, *Strijk 4413* (SING), MZ901835*, MZ782452*, *Parashorea stellata* Slooten (1927, non Kurz 1870), Singapore, *Strijk 4402* (SING), MZ901836*, MZ782453*, *Shorea acuminata* Dyer, Singapore (Yishun Park), *Strijk 4323* (SING), MZ901837*, MZ782458*, *Shorea agamii* P.S.Ashton, Singapore (Yishun Park), *Strijk 4324* (SING), MZ901838*, MZ782459*, *Shorea amplexicaulis* P.S.Ashton, Singapore, *Strijk 4436* (SING), MZ901839*, MZ782460*, *Shorea argentifolia* Symington, Singapore (Yishun Park), *Strijk 4320* (SING), MZ901840*, MZ782461*, *Shorea atrinervosa* Symington,

Appendix 1. Continued.

Singapore, *Strijk 4431* (SING), –, MZ782462*, **Shorea balanocarpoides** Symington, Singapore (Yishun Park), *Strijk 4319* (SING), MZ901841*, MZ782463*, **Shorea bentongensis** Foxw., Singapore (Yishun Park), *Strijk 4318* (SING), MZ901842*, MZ782464*, **Shorea bracteolata** Dyer, Singapore, *Strijk 4384* (SING), MZ901843*, MZ782465*, **Shorea confusa** P.S.Ashton, Singapore, *Strijk 4382* (SING), MZ901845*, MZ782467*, **Shorea curtisii** Dyer ex King, Singapore, *Strijk 4291* (SING), MZ901846*, MZ782468*, **Shorea faguetiana** F.Heim, Singapore (Yishun Park), *Strijk 4321* (SING), MZ901847*, MZ782469*, **Shorea falciferoides** subsp. *falciferoides* Foxw., Singapore (The Gallop Arboretum), *Strijk 4352* (SING), MZ901848*, MZ782470*, **Shorea flaviflora** G.H.S.Wood ex P.S.Ashton, Singapore, *Strijk 4275* (SING), MZ901849*, MZ782471*, **Shorea gibbosa** Brandis, Singapore, *Strijk 4343* (SING), MZ901850*, MZ782472*, **Shorea glauca** King, Singapore, *Strijk 4344* (SING), –, MZ782473*, **Shorea gratissima** Dyer, Singapore (Yishun Park), *Strijk 4317* (SING), MZ901851*, MZ782474*, **Shorea guiso** (Blanco) Blume, Singapore (The Gallop Arboretum), *Strijk 4353* (SING), MZ901852*, MZ782475*, **Shorea hemsleyana** (King) King ex Foxw., Singapore, *Strijk 4341* (SING), MZ901853*, MZ782476*, **Shorea hypochra** Hance, Singapore (Yishun Park), *Strijk 4304* (SING), MZ901854*, MZ782477*, **Shorea** cf. *johorensis* Foxw., Singapore (MacRitchie Reservoir), *Strijk 4420* (SING), MZ901844*, MZ782466*, **Shorea johorensis** Foxw., Singapore (Yishun Park), *Strijk 4325* (SING), MZ901855*, MZ782478*, **Shorea kudatensis** G.H.S.Wood ex Meijer, Singapore, *Strijk 4385* (SING), MZ901856*, MZ782479*, **Shorea kunstleri** King, Singapore, *Strijk 4342* (SING), MZ901857*, MZ782480*, **Shorea laevis** Ridl., Singapore, *Strijk 4276* (SING), MZ901858*, MZ782481*, **Shorea lepidota** (Korth.) Blume, Singapore, *Strijk 4345* (SING), MZ901859*, MZ782482*, **Shorea leprosula** Miq., Singapore, *Strijk 4346* (SING), MZ901860*, MZ782483*, **Shorea macrantha** Brandis, Singapore, Strijk 4399 (SING), MZ901861*, MZ782484*, **Shorea macrophyla** (de Vr.) P.S.Ashton, Singapore, *Strijk 4372* (SING), –, MZ782485*, **Shorea macroptera** Dyer, Singapore (MacRitchie Reservoir), *Strijk 4472* (SING), MZ901864*, MZ782487*, **Shorea macroptera** Dyer, Singapore, *Strijk 4339* (SING), MZ901863*, MZ782486*, **Shorea materialis** Ridley, Singapore (Yishun Park), *Strijk 4307* (SING), –, MZ782488*, **Shorea maxima** (King) Symington, Singapore, *Strijk 4357* (SING), MZ901865*, MZ782489*, **Shorea maxwelliana** (King) Symington, Singapore (Yishun Park), *Strijk 4322* (SING), MZ901866*, MZ782490*, **Shorea mecistopteryx** Ridl., Singapore, *Strijk 4430* (SING), MZ901867*, MZ782491*, **Shorea multiflora** (Burck) Symington, Singapore, *Strijk 4348* (SING), MZ901868*, MZ782492*, **Shorea ochrophloia** Strugnell ex Symington, Singapore (The Gallop Arboretum), *Strijk 4351* (SING), MZ901869*, MZ782493*, **Shorea ovalis** (Korth.) Blume, Singapore, *Strijk 4434* (SING), MZ901870*, MZ782494*, **Shorea pachyphylla** Ridl. ex Symington, –, –, –, MH841940, **Shorea parvifolia** Dyer, Singapore (The Gallop Arboretum), *Strijk 4354* (SING), MZ901871*, MZ782495*, **Shorea pauciflora** King, Singapore (MacRitchie Reservoir), *Strijk 4423* (SING), MZ901873*, MZ782497*, **Shorea pauciflora** King, Singapore, *Strijk 4337* (SING), MZ901872*, MZ782496*, **Shorea peltata** Symington, Singapore, *Strijk 4400* (SING), MZ901874*, MZ782498*, **Shorea platycarpa** F.Heim, Singapore, *Strijk 4371* (SING), MZ901875*, MZ782499*, **Shorea platyclados** Slooten ex Foxw., Singapore, *Strijk 4396* (SING), MZ901876*, MZ782500*, **Shorea resinosa** Foxw., Singapore, *Strijk 4274* (SING), MZ901877*, MZ782501*, **Shorea robusta** Gaertn., Singapore, *Strijk 4417* (SING), MZ901878*, MZ782502*, **Shorea roxburghii** G.Don, Singapore, *Strijk 4390* (SING), MZ901879*, MZ782503*, **Shorea roxburghii** G.Don, China (Yunnan), *Strijk 4627* (BGT), MZ901880*, MZ782504*, **Shorea singkawang** (Miq.) Burck, Singapore, *Strijk 4415* (SING), MZ901881*, MZ782505*, **Shorea smithiana** Symington, Singapore (The Gallop Arboretum), *Strijk 4355* (SING), MZ901882*, MZ782506*, **Shorea stenoptera** Burck., Singapore (Yishun Park), *Strijk 4316* (SING), MZ901883*, MZ782507*, **Shorea sumatrana** (Slooten ex Thorenaar) Desch, Singapore, *Strijk 4286* (SING), MZ901884*, MZ782508*, **Shorea symingtonii** G.H.S.Wood, Singapore, *Strijk 4340* (SING), MZ901885*, MZ782509*, **Shorea xanthophylla** Symington, Singapore, *Strijk 4373* (SING), MZ901886*, MZ782510*, **Shorea zeylanica** (Thwaites) P.S.Ashton, –, –, –, MH841939, **Vatica bella** Slooten, Singapore (Yishun Park), *Strijk 4310* (SING), MZ901791*, MZ782518*, **Vatica flavida** Foxw., Singapore, *Strijk 4377* (SING), MZ901792*, MZ782519*, **Vatica lobata** Foxw., Singapore (Yishun Park), *Strijk 4313* (SING), MZ901793*, MZ782520*, **Vatica maingayi** Dyer, Singapore (Yishun Park), *Strijk 4314* (SING), MZ901794*, MZ782521*, **Vatica maritima** Slooten, Singapore, *Strijk 4375* (SING), MZ901795*, MZ782522*, **Vatica nitens** King, Singapore, *Strijk 4404* (SING), MZ901796*, MZ782523*, **Vatica odorata** (Griff.) Symington, Singapore, *Strijk 4376* (SING), MZ901797*, MZ782524*, **Vatica odorata** (Griff.) Symington, Singapore (MacRitchie Reservoir), *Strijk 4426* (SING), MZ901798*, MZ782525*, **Vatica odorata** (Griff.) Symington, China (Yunnan), *Strijk 1594* (BGT), KX966283, –, **Vatica perakensis** King, Singapore, *Strijk 4403* (SING), MZ901799*, MZ782526*, **Vatica rassak** (Korth.) Blume, Singapore, *Strijk 4292* (SING), MZ901800*, MZ782527*, **Vatica ridleyana** Brandis, Singapore, *Strijk 4358* (SING), MZ901801*, MZ782528*, **Vatica stapfiana** (King) Slooten, Singapore, *Strijk 4287* (SING), MZ901802*, MZ782529*, **Vatica umbonata** (Hook.f.) Burck, Singapore, *Strijk 4288* (SING), MZ901803*, MZ782530*, **Vatica yeechongii** Saw, Singapore (Yishun Park), *Strijk 4311* (SING), MZ901804*, MZ782531*, **Outgroups:** **Abelmoschus esculentus** (L.) Moench, U.S.A. (Austin), –, NC035234, KP222461, **Adansonia digitata** L., Gabon (Nyanga, Mayumba), *Wieringa 8465* (WAG8001190), MZ901888*, MZ782370*, **Adansonia digitata** L., Singapore, *Strijk 4394* (SING), MZ901887*, MZ782369*, **Abelmoschus esculentus** (L.) Moench, U.S.A. (Austin), –, NC035234, KP222461, **Althaea officinalis** L., –, –, KY085914, EF679733, **Aquilaria sinensis** (Lour.) Gilg, China (Hainan), –, NC029243, GQ891956, KP222461, **Arabidopsis arenosa** (L.) Lawalrée, –, –, LT161918, DQ528871, **Arabidopsis thaliana** L., U.S.A., –, NC000932, DQ528813, **Arabis alpina** L., –, –, HF934132, AF137559, **Bombacopsis glabra** (Pasq.) A.Robyns, China (Yunnan), *Strijk 4531* (BGT), MZ901889*, MZ782376*, **Bombax ceiba** L., China (Yunnan), *Strijk 4596* (BGT), MZ901890*, MZ782377*, **Bombax ceiba** L., China (Yunnan), –, MG569974, HQ658377, **Bombax malabaricum** DC., China (Yunnan), *Strijk 4592* (BGT), MZ901891*, MZ782378*, **Ceiba insignis** (Kunth) P.E.Gibbs & Semir, China (Qin Xiu Shan), *Strijk 4467* (BGT), MZ901892, MZ782379*, **Chorisia speciosa** A.St.-Hil., China (Yunnan), *Strijk 4595* (BGT), MZ901892*, MZ782380*, **Cola micrantha** K.Schum., Cameroon, –, *Wieringa 5862* (WAG8003629), MZ901894*, MZ782381*, **Colona floribunda** (Kurz) Craib, China (Yunnan), *Strijk 4483* (BGT), MZ901895*, MZ782382*, **Dicranolepis disticha** Planch., Cameroon, *Wieringa 5821* (WAG8003655), MZ901896*, MZ782385*, **Durio zibethinus** L., –, –, MG138151, MF629775, **Edgeworthia chrysantha** Sieb. & Zucc, China (Hangzhou), *Strijk 4048* (BGT), MZ901897*, MZ782419*, **Eriolaena spectabilis** (DC.) Planch. ex Mast., China (Yunnan), *Strijk 4474* (BGT), MZ901898*, MZ782419*, **Firmiana major** (W.W.Sm.) Hand.-Mazz., China (Sichuan), –, MG229069, AF460186, **Gossypium barbadense** L., Japan (Kyoto), –, NC008641, GU935141, **Gossypium herbaceum** L., –, –, JF317353, GQ166629, **Gossypium hirsutum** L., Coker310FR –, NC007944, KC404827, **Gossypium turneri** Fryxell, –, –, NC026835, U12726, **Lavatera punctata** All., Italy, *Wieringa 5952* (WAG8003579), MZ901899*, MZ782447*, **Microcos paniculata** L., China (Yunnan), *Strijk 4575* (BGT), MZ901900*, MZ782448*, **Peddiea africana** Harv., Cameroon, *Wieringa 5900* (WAG8003696), MZ901901*, MZ782454*, **Pterospermum kingtungense** C.Y.Wu ex H.H.Hsue, China (Yunnan), *Strijk 4497* (BGT), MZ901902*, MZ782455*, **Reevesia thyrsoidea** Lindl., China (Yunnan), *Strijk 4519* (BGT), MZ901903*, MZ782456*, **Scaphopetalum longipedunculatum** Mast., Gabon, *Sosef 2028* (WAG8004058), MZ901904*, MZ782457*, **Sterculia lanceifolia** Roxb., China (Yunnan), *Strijk 4602* (BGT), MZ901905*, MZ782511*, **Sterculia lanceolata** Cav., China (Yunnan), *Strijk 4537* (BGT), MZ901906*, MZ782512*, **Sterculia micrantha** Chun & H.H.Hsue, China (Yunnan), *Strijk 4482* (BGT), MZ901907*, MZ782513*, **Theobroma cacao** L., –, –, NC014676, JQ228377, **Theobroma cacao** f. *pentagonum* (Bernoulli) Cuatrec., China (Yunnan), *Strijk 4534* (BGT), MZ901908*, MZ782514*, **Theobroma sp.**, China (Yunnan), *Strijk 4535* (BGT), MZ901909*, MZ782515*, **Tilia amurensis** Kom., China (Heilongjiang), –, NC028588, KF445432, **Tilia mandshurica** Rupr. & Maxim., China (Heilongjiang), –, KT894773, KX062302, **Tilia oliveri** Szyszył., China (Chongqing), –, NC028590, KF897525, **Urena lobata** L., Gabon, *Wieringa 8287* (WAG8001343), MZ901911*, MZ782517*, **Urena lobata** L., China (Yunnan), *Strijk 4494* (BGT), MZ901910*, MZ782516*.