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Phylogenomics and a revised tribal classification of subfamily Dipterocarpoideae (Dipterocarpaceae)

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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. Dipterocarpoideae 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 cistrons (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), Shoreaeae (Hopea, Neobalanocarpus, Parashorea, and all parts of a polyphyletic Shorea) and Vaterieae (including all other presently accepted Dipterocarpoideae genera). Multi-fossil-dated divergence time estimation suggests Vaterieae first originated in the Late Cretaceous, followed by Dipterocarpeae, with subsequent rise of the Dryobalanopseae and Shoreaeae in the Eocene. Diversification of all tribes commenced before the Early Miocene. Our results provide strong support for the position of Neobalanocarpus heimiti, Parashorea and (sub-)sections of the genera Anisoptera, Hopea, Shorea and Vatica. Hypotheses on the origin of Neobalanocarpus heimiti by intergeneric hybridisation between Anthoshoarea (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; Londino & 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 Tillaeaee, 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 sepal 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*), Dryobalanopsea (*Dryobalanops*), Parashoreae (*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 phylogenetic 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; Kamiya & al., 1998; Yulita & 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 nestled 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. *Richetioideae* (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. *Sunapea* 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* (Shoreae) 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 conen (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): *Dipterocarpaceae* (*Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Stemonoporus*, *Upuna*, *Vateria*, *Vateriaispis*, *Vatica*) and Shoreae (*Dyobalanops*, *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 Carrión & al., 2020) (suppl. Appendices S1–S3). Model selection for molecular evolution was performed with ModelTest-NG v.0.1.5 (GRTR+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-aiLRT. 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 (Miraраб & 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: Dryobalanopsaeae; A4: Shoreaeae; A5: Doona + Anthshorea + Neobalanocarps + Hopea clade; A6: Shorea sect. Doona; A7: S. sect. Anthshorea; A8: Richetioideae + Parashorea + Shorea + Rubroshorea clade; A9: S. sect. Richetioideae; A10: S. sect. Shorea; A11: S. sect. Rubroshorea. Fossils used in this study (red circles): I, the crown age of Malvales divergence from Brassicales (Magallon & al., 2015) (102.7 Ma); II, stem age for the ancestral node leading to Sterculioideae (Hernández-Gutiérrez & Magallón, 2019) (78.89 Ma); III, Bombacaccidites anne (66–56 Ma) (Van Der Hammen, 1954); IV, Malviciphyllum maconicus (61.6–56 Ma) (Carvalho & al., 2011). Geological time scale shown in millions of years.
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 Middle 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
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 (BGT4413) to 156,123 bp (BGT4422) to 209,523 bp, respectively. The reconstructed plastome lengths ranged from 5769 bp (NRC, BS = 99; A2, suppl. Figs. S1–S4).

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

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

Clade Shoreae: Hopea, Neobalanocarpus, Parashorea and Shorea were retrieved as the monophyletic tribe Shoreae (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 heimi 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. Brachypetereae, sect. Mutica, sect. Pachycarpaceae, 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 heimi 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 Dipterocarpaceae 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 Dipterocarpaceae 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: Dipterocarpaceae; A3: Dryobalanopseae; A4: Shoreeae; A5: Doona + Anthoshorea + Neobalanocarpus + Hopea clade; A6: Shorea sect. Doona; A7: S. sect. Anthoshorea; A8: Richetioideae + Parashorea + Rubroshorea clade; A9: S. sect. Richetioideae; A10: S. sect. Shorea; A11: S. sect. Rubroshorea; B1: Vaterieae; B2: Dipterocarpaceae; B3: Dryobalanopseae; B4: Shoreeae; B5: sect. Richetioideae; 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 Malvaceous families was retrieved using each of our three datasets (plastome, NRC, combined) [ca. 95 Ma for Malvaceae s.l.; Thymelaeaceae and Dipterocarpaceae, sub-family 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 Dryobalanopsceae 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 Dryobalanopsceae (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. Cotyleloebium 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 (ca. 27–21 Ma) (in Shorea s.str., Rubroshaora, Anthoshorea, Parashoreo, 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 estimates 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, Dryobalanopsceae, 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 vation 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 Dryobalanopsceae 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 sub-valvate 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 Dryobalanopsceae 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 sepal imbricate at the incrase-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 incrase bases of sepal (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, *Richetiodes* 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 *Shoreaee* but was described without explicit rank, which is mandatory before 1887 (Art. 37.1–37.3 of the ICN, Turland et al., 2018).

*Shoreaee* has also been spelled as ‘*Shorea*’. 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 *Miqius*, which is nested within the *Shoreaee* clade (Fig. 2B, suppl. Fig. S2). The placement of *Neobalanocarpus* heimii shares morphological characters with both *Anthoshorea* and *Hopea* (urceolate corolla and stamens with an acicular connective appendage [Dayanandan et al., 1999; Gamage et al., 2003, 2006; Heckenhauer et al., 2017]). However, phylogenetic placement of *Upuna* and *Vateria* remains unresolved (Heckenhauer et al., 2017), and additional genomic data is needed for resolving their placement.

### 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 *Dipterocarpaceae*, and imbricate flowers as a synapomorphy of *Shoreaee* (Indrioko et al., 2006). Unique morphological characters of *Dipterocarpaceae* were summarized in Heckenhauer et 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 et al., 1999; Gamage et al., 2003, 2006; Heckenhauer et al., 2017). However, phylogenetic placement of *Upuna* and *Vateria* remains unresolved (Heckenhauer et 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; Komiya et al., 1998; Yulita et 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 et al., 1999], and a linear anther in the flower and sub-equal short woody fruit sepals [Kamiya et 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 et al. (2006) and Tsumura et 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 et al., 2005). Kamiya & al. (2005) hypothesized this incongruence is a likely indicator of an ancient hybridization event involving ancestors of *Anthoshorea* as maternal 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 artifacts such as sample mix-ups are unlikely. NRC copies can homogenize to either maternal or paternal parent after hybridization (concerted evolution; see Alvarez & 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 Anthoshoarea 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 Anthoshoarea (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. Anthoshoarea, 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. sect. 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 Dipterocarpaceae. 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 Monotoidae on Deccan and Mascarene Plates) (Ducouso & 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 & al., 2006). Two monophyletic sections in Vatica 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).
colliding with Eurasia commenced in the early Cenozoic (Briggs, 2003; Rust & al., 2010; Ghazoul, 2016). Initial Africa 158 & al., 2012, 2013). [57x646](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 Dipterocarpaceae (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 Dipterocarpaceae, 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., 1993; Derry & France-Lanord, 1996; 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 Dipterocarpaceae 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; Wrust & 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 extinction, 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 Dipterocarpaceae 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 heimi’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 Dipterocarpaceae: Vaterieae (including all genera of presently accepted Dipterocarpeae except for Dipterocarpus: Anisoptera, Cotylelobium, Stemonoporus, Upuna, Vateria, Vateriopsis,
were shown to be non-monophyletic, indicating that the infra-
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al., 2018, 2019); this could also resolve the paraphyly of
rank (Maury, 1978; Maury-Lechon, 1979a,b; Heckenhauer &
al., 2018, 2019); this could also resolve the paraphyly of
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Shorea
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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
sect. 
Shorea
sect. and
sect. 
Shorea
are nested. Most
Shorea
subsections were shown to be non-monophyletic, indicating that the infrageneneric 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/0000-0001-7456-372X; 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 cnists) or ITS (internal transcribed spacer). Newly generated sequences, 151 plastome and 164 NRC, are indicated with *; missing information is indicated by –.

Anisoptera costata, Singapore, Strijk 4412 (SING), MZ901761*, –, Anisoptera costata, Korth., Brunel, 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, Kurz. (Roxb.) Singapore, Strijk 4306 (SING), MZ901765*, MZ782375*, Cotylelobium lanceolatum, Crab, Singapore, Strijk 4374 (SING), MZ901766*, MZ782383*, Cotylelobium melanoxylon (Hook.f) Pierre, Brunel, Strijk 2100 (BGT), MZ901767*, MZ782384*, Dipterocarpus alatus, Singapore (Yishun Park), Strijk 4300 (SING), MZ901912*, MZ899121*, Dipterocarpus baudii Korth., Singapore, Strijk 4356 (SING), MZ901768*, MZ782386*, Dipterocarpus caudatus, Fوخ., Singapore, Strijk 4279 (SING), MZ901769*, MZ782387*, Dipterocarpus charchutae, Simington, Singapore, Strijk 4383 (SING), MZ901770*, MZ782388*, Dipterocarpus confertus, Slooten, Singapore, Strijk 4416 (SING), –, MZ782389*, Dipterocarpus corneatus, Singapore (Yishun Park), Strijk 4299 (SING), –, MZ782390*, Dipterocarpus costatus, Slooten, Singapore (Yishun Park), Strijk 4302 (SING), –, MZ782391*, Dipterocarpus dierii, Pierre, Singapore, Strijk 4381 (SING), –, MZ782392*, Dipterocarpus elongatus, Korth., Singapore (Chushtnut Nature Park), Strijk 4331 (SING), MZ901771*, MZ782394*, Dipterocarpus fagineus, Foux., Singapore (MacRitchie Reservoir), Strijk 4342 (SING), MZ901782*, MZ782407*, Dipterocarpus grandiflorus, Blanco, Singapore, Strijk 4392 (SING), MZ901774*, MZ782397*, Dipterocarpus grandiflorus, Blanco, Singapore (MacRitchie Reservoir), Strijk 4424 (SING), MZ901775*, MZ782398*, Dipterocarpus hexamerus, 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 palmenius, Slooten, Singapore, Strijk 4335 (SING), MZ901779*, MZ782403*, Dipterocarpus retusus, Blume, China (Qin Xiu Shan), Strijk 3592 (BGT), –, MZ782404*, Dipterocarpus rigidaus Roxb., 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 submellanetus, Foux., Singapore, (MacRitchie Reservoir), Strijk 4423 (SING), MZ901782*, MZ782407*, Dipterocarpus temephes, Slooten, Singapore (MacRitchie Reservoir), Strijk 4421 (SING), MZ901784*, MZ782409*, Dipterocarpus tuberculatus, Roxb., Singapore, Strijk 4379 (SING), MZ901785*, MZ782410*, Dipterocarpus validus, Blume, Singapore, Strijk 4359 (SING), –, MZ782411*, Dipterocarpus zeylanicus Thw., Singapore (Yishun Park), Strijk 4301 (SING), MZ901786*, MZ782413*, Dryobalanos aromatica C.F. Gaertn., Singapore, Strijk 4289 (SING), MZ901787*, MZ782414*, Dryobalanos beccarii, Dyer, Singapore (Yishun Park), Strijk 4315 (SING), MZ901788*, MZ782415*, Dryobalanos lanceolata, Burck, Singapore (Yishun Park), Strijk 4309 (SING), MZ901789*, MZ782416*, Dryobalanos oblongifolius, Dyer, Singapore, Strijk 4283 (SING), MZ901790*, MZ782417*, Hopea helferi (Dyer) Brandis, Singapore (Yishun Park), Strijk 4308 (SING), MZ901817*, MZ782432*, Hopea honghensis, Singapore, Strijk 4359 (SING), MZ901818*, MZ782433*, Hopea kerangasseri P.S. Ashton, Singapore, Strijk 4366 (SING), MZ901819*, MZ782434*, Hopea koreana, Miq., Singapore (Chushtnut Nature Park), Strijk 4366 (SING), MZ901820*, MZ782435*, Hopea lyrata, King, Singapore, Strijk 4290 (SING), MZ901821*, MZ782436*, Hopea macrophylla, Pax. & Hoffm., Singapore, Strijk 4357 (SING), MZ901822*, MZ782437*, Hopea notunae Rdl., Singapore (Yishun Park), Strijk 4294 (SING), MZ901823*, MZ782438*, Hopea odorata, Roxb., Singapore, Strijk 4270 (SING), MZ901824*, MZ782439*, Hopea pachycarpa, F. Heinm Simington, Singapore, Strijk 4346 (SING), MZ901825*, MZ782440*, Hopea polyallobioides, Simington, Singapore, Strijk 4365 (SING), MZ901826*, MZ782441*, Hopea rosalba, Simington, Singapore, Strijk 4366 (SING), MZ901827*, MZ782442*, Hopea pubescens, Rdl., Singapore, Strijk 4333 (SING), MZ901828*, MZ782443*, Hopea sanguinolenta, Hopea sanguinolenta, Singapore, Strijk 4352 (SING), MZ901829*, MZ782443*, Hopea sanguinolenta, Singapore, Strijk 4359 (SING), MZ901830*, MZ782444*, Hopea subalternata, Simington, 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, –, –, MZ784630, Pachysandra japonica, Wang Hsie, China (Yunnan), Strijk 5394 (BGT), MZ901833*, MZ782450*, Neobalanocarpus macrophylla, Wyatt-Sm. ex P.S. Ashton, –, –, MZ784630, Pachysandra japonica, Wang Hsie, China (Yunnan), Strijk 5394 (BGT), MZ901833*, MZ782450*, Neobalanocarpus macrophylla, Wyatt-Sm. ex P.S. Ashton, –, –, MZ784630, Pachysandra japonica, Wang Hsie, China (Yunnan), Strijk 5394 (BGT), MZ901833*, MZ782450*, Neobalanocarpus macrophylla, Wyatt-Sm. ex P.S. Ashton, –, –, MZ784630, Pachysandra japonica, Wang Hsie, China (Yunnan), Strijk 5394 (BGT), MZ901833*, MZ782450*, Neobalanocarpus macrophylla, Wyatt-Sm. ex P.S. Ashton, –, –, MZ784630, Pachysandra japonica, Wang Hsie, China (Yunnan), Strijk 5394 (BGT), MZ901833*, MZ782450*
