

**CHLOROPLAST DNA VARIATION
IN INDONESIAN DIPTEROCARPACEAE-
PHYLOGENETIC, TAXONOMIC,
AND POPULATION GENETIC ASPECTS**

Dissertation

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To my beloved family...

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1. INTRODUCTION

1.1. Family Dipterocarpaceae

1.1.1. Taxonomy

The placement of family Dipterocarpaceae has been adjusted several times. First, Dipterocarpaceae was grouped in the order Ochnales, then it was moved to the order Theales, and finally to the order Malvales (MAURY-LECHON and CURTET, 1998; APG; 2003).

ASHTON (1982), LONDOÑO (1995), MAGUIRE and ASHTON (1977), VERCOURT (1989) and VILLIERS (1991) described the taxonomical characters of Dipterocarpaceae as follows: **habitus** small or large resinous usually evergreen trees, usually buttressed; **leaves** alternate, simple, margin entire or sinuate, not crenate, terminating \pm abruptly at the \pm prominent geniculate petiole, penninerved, often with domatia in axils between nerves and midrib or along midrib and (rarely) nerves; tertiary nerves scalariform or reticulate; **stipules** paired, large or small, persistent or fugaceous, leaving small to amplexicaul scars; **inflorescence** paniculate, racemose, rarely cymose, \pm regularly, rarely irregularly, branched, terminal or axillary; **bracts** and **bracteoles** paired, small or large, persistent or fugaceous; **flowers** secund or distichous, bisexual, actinomorphic, scented, nodding; **calyx** persistent, five-merous; two to five sepals usually greatly enlarging into wing-like lobes in fruit; **sepals** either free to base, imbricate in bud, remaining so or becoming valvate in fruit, or fused at base, forming a cup or tube \pm enclosing the fruit, adnate to or free from it; **corolla** five-merous, contorted, base connate or free, usually partially or entirely unicellular hairy; **stamens** five to 110, one to three verticillate or irregular, hypogynous or subperigynous, centrifugal; **filaments** compressed or filiform, free or connate, frequently cohering with petals on falling; **anthers** erect, two-celled with (two to) four pollen sacs, introrse or laterally dehiscent; tapetal cells binucleate, pollen grains two-celled at anthesis; connective with short or prominent appendage; **ovary** superior or semi-inferior, three-, rarely two-locular; **style** \pm thickened at base into a stylopodium, entire or trifid towards apex; **stigma** obscure or prominent, three- or six-lobed; ovules two (to three) in each loculus, axile, pendulous, or laterally anatropous, bitegmatic with ventral raphe and superior micropyle; **fruit** indehiscent, one-seeded; with woody pericarp and persistent \pm aliform sepals; embryonic-sac development of **polygonum** type: endosperm of the nuclear type, embryo development normal, ripe seeds with or more usually without endosperm; cotyledons equal or more usually unequal and with one or more

or less enclosing the other, laminar or fleshy, entire or lobed, enclosing the radical; **germination** epigeal or hypogeal; pericarp splitting irregularly or along three sutures.

The family Dipterocarpaceae consists of three subfamilies: Dipterocarpoideae (13 genera, c. 470 spp.) from the Seychelles, Sri Lanka and India northeastwards to southern China and the Batan Islands, and southeastwards to New Guinea and D'Entrecasteaux Island; Monotoideae (three genera, c. 40 spp.) in Africa and South America; Pakaramoideae (one genus, one species) confined to South America (ASHTON, 1982; BANCROFT, 1935; MAURY-LECHON and CURTET, 1998). Based on the observation on Asian dipterocarp species, HALLÉ (1979) found three main architecture models of Dipterocarpaceae, i.e. Roux as the frequent model (*Anisoptera*, *Balanocarpus*, *Hopea*, *Shorea*, *Upuna*, *Vatica*), Rauh (*Dipterocarpus*, *Cotylelobium*), and Massart (*Shorea*, *Dipterocarpus*). Roux's model is characterized by continuous growth of the stem with plagiotrophic branches, while Massart's has rhythmic growth of the stem with plagiotrophic branches, and Rauh's also has rhythmic growth of the stem but with orthotrophic branches (HALLÉ *et al.*, 1978). An African dipterocarp, namely *Monotes kerstingii*, fits Troll's model which does not exist among Asiatic dipterocarps (HALLÉ and NG, 1981). The basic chromosom number of Dipterocarpoideae is $x=11$ in Tribe Dipterocarpeae and $x=7$ in Tribe Shoreae (ASHTON, 1982; JONG and KAUR, 1979; SOMEGO, 1978).

The natural distribution of Dipterocarpaceae in Indonesia comprises (see Figure 1):

- Kalimantan (including insular Malaysia and Brunei Darussalam), with a total of nine genera (*Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Dryobalanops*, *Hopea*, *Parashorea*, *Shorea*, *Vatica*, and *Upuna*), consisting of 267 (ASHTON, 1982) to 274 species (NEWMAN, *et al.*, 1996a, 1998a).
- Sumatra, with a total of eight genera (*Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Dryobalanops*, *Hopea*, *Parashorea*, *Shorea*, and *Vatica*), consisting of 106 (ASHTON, 1982) to 112 species and three sub species (NEWMAN, *et al.*, 1996b, 1998b).
- Java and Nusa Tenggara, with a total of five genera (*Shorea*, *Hopea*, *Dipterocarpus*, *Anisoptera*, and *Vatica*), consisting of 10 species (ASHTON, 1982; NEWMAN, *et al.*, 1998c).

- Sulawesi, with a total of four genera (*Shorea*, *Hopea*, *Anisoptera*, and *Vatica*), consisting of six (ASHTON, 1982) to seven species (NEWMAN, *et al.*, 1998c).
- Maluku, with a total of four genera (*Shorea*, *Hopea*, *Anisoptera*, and *Vatica*), consisting of six (ASHTON, 1982) to seven species (NEWMAN, *et al.*, 1998c).
- Irian (including Papua New Guinea), with a total of three genera (*Hopea*, *Anisoptera*, and *Vatica*), consisting of 15 species (ASHTON, 1982; NEWMAN, *et al.*, 1998c).

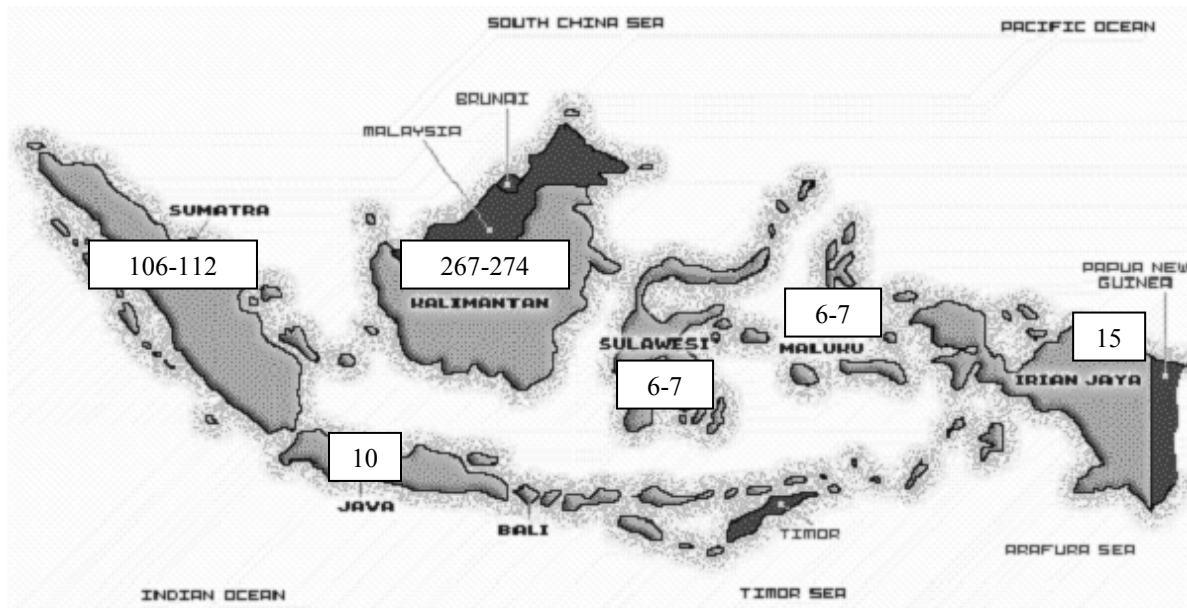


Figure 1. The distribution of Dipterocarpaceae in Indonesia. The total number of species in each island / isles after ASHTON (1982) and NEWMAN *et al.*, (1996a, 1996b, 1998a, 1998b, 1998c) is shown.

1.1.2. Reproductive biology

Dipterocarpaceae have bisexual flowers which are pollinated by a variety of insects as vectors (APPANAH, 1981; APPANAH and CHAN, 1981; CORLETT, 2004; MOMOSE *et al.*, 1998; SAKAI *et al.*, 1999a). Pollen flow of dipterocarps can reach more than 500 m in *Neobalanocarpus heimii* (KONUMA *et al.*, 2000) and approximately 200 m in *Dipterocarpus tempehes* (KENTA *et al.*, 2004). On the basis of controlled pollination, three kinds of breeding systems of dipterocarps are recognized: obligatory outbreeding species in most dipterocarps (BAWA, 1998, CHAN, 1981; SAKAI *et al.*, 1999b); inbreeding species, for example, *Dipterocarpus oblongifolius* (CHAN, 1981); and apomictic species, such as in *Shorea ovalis* ssp. *sericea* and *Shorea agamii* (KAUR *et al.*, 1978). Genetic variation was found in seedlings from a

polyembryonic seed of *Hopea odorata* (WICKNESWARI *et al.*, 1995), which indicated that multiple seedlings may not necessarily involve apomixis (BAWA, 1998).

Outcrossing rates (t_m) of dipterocarps have been estimated using isoenzyme and microsatellite markers in different forest types and species, such as *Dryobalanops aromatica* ($t_m = 0.77$ in logged forest and $t_m = 0.92$ in primary forest; LEE, 2000a), *Shorea megistophylla* ($t_m = 0.71$ in logged forest and $t_m = 0.87$ in primary forest; MURAWSKI *et al.*, 1994b), *Shorea curtisii* ($t_m = 0.52$ in logged forest and $t_m = 0.96$ in primary forest; OBAYASHI *et al.*, 2002), *Shorea congestiflora* ($t_m = 0.87$ in logged forest; MURAWSKI *et al.*, 1994a), *Shorea trapezifolia* ($t_m = 0.54-0.62$ in logged forest; MURAWSKI *et al.*, 1994a), *Shorea leprosula* ($t_m = 0.84$ in primary forest; LEE *et al.*, 2000c) and *Stemonoporus oblongifolius* ($t_m = 0.84$ in primary forest; MURAWSKI and BAWA, 1994). Several factors may influence the outcrossing rate, such as flowering tree density (MURAWSKI and HAMRICK, 1992), density of pollinators (LEE, 2000a), and the types and behavior of pollinators governing the pollen movement (GHAZOUL *et al.*, 1998). In summary, most dipterocarps are predominantly outcrossing, but selfing occurs in many species.

An important character of the family in the non-seasonal region is its flowering behaviour. Flowering time does not occur annually, but at irregular intervals with a mass production in a short (2 – 3.5 weeks) flowering period (ASHTON *et al.*, 1988; CHAN and APPANAH, 1980). They do not flower simultaneously with the different dipterocarp species (LAFRANKIE and CHAN, 1991) or in different elevations (SASAKI *et al.*, 1979). Observations in Kalimantan and Peninsular Malaysia revealed that most dipterocarps flower in March-April and the fruits of most species matured and fell in September-October (CHAN and APPANAH, 1980; WOOD, 1956).

General flowering of Dipterocarpaceae in an aseasonal climate is a supra annual cycle of plant reproduction that takes place at irregular intervals of two to ten years (APPANAH, 1985, 1993; COCKBURN, 1975; NG, 1977; WOOD, 1956, YASUDA *et al.*, 1999). Several environmental factors have been suggested as the floral triggers for general flowering in Dipterocarpaceae, including prolonged drought (APPANAH, 1985; MEDWAY, 1972), increase of photoperiod (NG, 1977; VAN SCHAİK, 1986; WYCHERLEY, 1973), and drop of minimum air temperature at night associated with cloudless weather (ASHTON *et al.*, 1988). Satiation of generalist seed predators has been considered a primary force for general flowering (JANZEN, 1975; SAKAI, 2002).

Seed dispersal of dipterocarps can be divided as follows (ASHTON, 1982; MURAWSKI and BAWA, 1994; SUZUKI and ASHTON, 1996): by wind in most species which have wing-like structure (aliform) sepals, by water in many species which have short sepals and grow in swamps or river banks, and simply by falling on the ground in species without wing-like sepals. Seeds disseminated by water can potentially disperse over longer distances than by wind.

Natural hybridization in dipterocarps has been frequently reported. *Shorea* species flower at the same time and are pollinated by the same insect groups (APPANAH and CHAN, 1981); therefore, the occurrence of interspecific gene exchange is possible. The successful fruit formation resulting from a cross between *Shorea splendida* and *Shorea stenoptera* shows the potential of natural hybridization of closely related species (CHAN, 1981). Putative hybrids between *Shorea acuminata* and *Shorea leprosula* were marked with nucleotide sequences in the *GapC* region (ISHIYAMA *et al.*, 2003). The polyploid condition indicates the possibility of hybridization which might have arisen in several species, such as triploidy in *Hopea beccariana*, *Hopea latifolia*, *Hopea subalata*, *Hopea odorata* and *Shorea resinosa*, and tetraploidy in *Hopea nutans*, *Shorea ovalis* ssp. *sericea* (ASHTON, 1982; JONG and KAUR, 1979; KAUR *et al.*, 1978; SOMEGO, 1978).

1.1.3. Ecology, silviculture and economic importance

Dipterocarpaceae is the most important forest tree family in natural and close-to-nature forests in Southeast Asia. The many different species of dipterocarps have widely varying site requirements, as illustrated by the fact that they can be found on entirely different site types and in nearly all of the different forest types of Southeast Asia (LAMPRECHT, 1989). Dipterocarps usually grow in mixed tropical rain forests, where they often constitute the dominant floristic element (WEIDELT, 1996). The highest species diversity is observed in evergreen rainforests in Peninsular Malaysia, Sumatra and Kalimantan (ASHTON, 1982; SYMINGTON, 1943; WHITTEN *et al.*, 1987). The latter island is the main centre of dipterocarps with the highest number of endemic species (155 species). Approximately one quarter of all trees in most lowland forests of Kalimantan are dipterocarps (ASHTON, 1982; SIST, 1996; SLIK *et al.*, 2003). The greatest richness in terms of abundance of species is attained in the emergent stratum in Sarawak and Brunei, Northwest Kalimantan (WHITMORE, 1975).

The symbiosis with ectomycorrhiza improves the physiological adaptability and is important for the growth of dipterocarps, especially in nutrient poor conditions (SMITS, 1994). Thus, the inoculation of ectomycorrhiza is crucial for the establishment of dipterocarp plantations. Silvicultural treatment, such as liberation thinning, also increases the periodic annual diameter increment (PAI) in larger trees (diameter at breast height / DBH>20 cm) of the Red Meranti group and smaller trees (DBH=10-20 cm) of other *Shorea* spp. and some *Hopea* spp. (KAMMESHEIDT *et al.*, 2003).

The polycyclic silvicultural system has been applied for dipterocarp forest management in Indonesia, namely *Tebang Pilih Indonesia - TPI* (the Indonesian selective cutting system) in 1972, followed by *Tebang Pilih Tanam Indonesia - TPTI* (the Indonesian selective cutting and planting system) since 1989 (DJPH, 1993). Several essentials in the latter system are: stand inventory of all growth stages, limitation of 50 cm minimum of DBH, and maintaining the residual stand with a minimum of 25 nucleus trees per hectare.

Dipterocarpaceae is the pre-eminent timber family in Indonesia, since more than 70% of the world's demand for plywood made from hardwoods has been supplied by Indonesia, principally from dipterocarp species (CHOONG and ACHMADI, 1996). The various wood varieties of dipterocarps are used for veneers and for outdoor and indoor construction (LAMPRECHT, 1989). Additionally, resin is also obtained from various species. Several dipterocarps species, mainly of the genus *Shorea*, produce a nut with an edible fat, identical to that of cocoa, and an excellent substitute for cocoa butter in the manufacture of chocolate and cosmetics (SEIBERT, 1996). The harvesting operation in Indonesia and other countries has a decisive impact on the amount and quality of the residual forest stand. Many of the dipterocarp forest in Southeast Asia have been badly damaged by logging and relogging in the same areas. Several species have been threatened, even coming to the brink of extinction (KORSGAARD, 1985).

Most of dipterocarp species in Indonesia are presently commercial. The vernacular name is usually applied for the timber trading purposes. As a genus consisted of the greatest number of species member, *Shorea* is the most popular timber of Dipterocarpaceae in Indonesia with vernacular name Meranti. Even SYMINGTON (1943) used vernacular name to divide *Shorea* into four groups, namely Balau (Selangan Batu), White Meranti (Meranti Pa'ang), Yellow Meranti (Meranti Damar Hitam) and Red Meranti. NEWMAN *et al.* (1996a, 1996b, 1998a, 1998b, 1998c) described the other common timber names of Indonesian dipterocarps related

to the genus, namely Giam / Merawan (*Hopea*), Keruing (*Dipterocarpus*), Kapur (*Dryobalanops*), Mersawa (*Anisoptera*), White Seraya (*Parashorea*), and Resak (*Vatica*, *Cotylelobium*, and *Upuna*).

1.1.4. Phylogenetics

The taxonomy of Dipterocarpaceae has been studied quite intensively due to their great value in the timber market (ASHTON, 1982), but the phylogenetic relationships among the taxa of Dipterocarpaceae have not been closely studied. Recently, phylogenetic research using molecular markers has been developed because of the simplicity of obtaining large amounts of data and the higher reliability as compared to morphological data for constructing phylogenetic trees (CHASE *et al.*, 1993).

Phylogenetic studies on Dipterocarpaceae have been conducted at various taxonomic levels. A study using nucleotide sequence data of angiosperm taxa showed that Dipterocarpaceae grouped with order Malvales (CHASE *et al.*, 1993; HILU, *et al.*, 2003) and in one clade together with Sarcolaenaceae (ALVERSON *et al.*, 1998; MORTON *et al.*, 1999) supported with a high bootstrap value (80 and 100%). The close relationships of Dipterocarpaceae and Sarcolaenaceae were also supported by DAYANDANAN *et al.* (1999) based on *rbcL* gene sequences. The systematic positions of subfamily Monotoideae and of monotypic *Pakaraimaea dipterocarpea* have been problematic. They were considered to have closer relationships to Tiliaceae (KOSTERMANS, 1978, 1985) or Dipterocarpaceae (ASHTON, 1982). KOSTERMANS (1989) declared Monotaceae to be a new family consisting of three genera, i.e. *Monotes*, *Marquesia* and *Pakaraimaea*. However, molecular data supported the monotypic subfamily Pakaraimoideae (represented by *Pakaraimaea dipterocarpea*) to cluster together with subfamilies Monotoideae and Dipterocarpoideae as a monophyletic clade of Dipterocarpaceae (DAYANANDAN *et al.*, 1999; MORTON *et al.*, 1999).

There are several phylogenetic studies of Asiatic dipterocarps (subfamily Dipterocarpoideae) using various outgroups belonging to subfamily Dipterocarpoideae (KAMIYA *et al.*, 1998; TSUMURA *et al.*, 1996), Monotoideae (GAMAGE *et al.*, 2003), family Bixaceae and Rhopalocarpaceae (DAYANANDAN *et al.*, 1999) and Tiliaceae (KAJITA *et al.*, 1998; LI *et al.*, 2004). Various marker types observing chloroplast DNA variation were investigated, such as PCR-RFLP (TSUMURA *et al.*, 1996), nucleotide sequences of *matK*, *trnL* intron, the *trnL-trnF* intergeneric spacer region (GAMAGE, 2003; KAJITA *et al.*, 1998; KAMIYA *et al.*, 1998; LI,

2004), and *rbcL* (DAYANANDAN *et al.*, 1999; MORTON *et al.*, 1999). The resolution of intergeneric relationships varies greatly but tends to agree with the taxonomic grouping by ASHTON (1982).

The classification of Asian dipterocarps into taxonomically relevant units (tribes, sections, subsections, genera) has recently been reviewed by MAURY-LECHON and CURTET (1998) based on previous work by HEIM (1892), MAURY (1978), MEIJER (1964), SYMINGTON (1943) and ASHTON (1964, 1968, 1982). Many parts of previous classifications are still retained in the present classification. Asian dipterocarps in the present classification have been divided into two tribes, namely Dipterocarpeae and Shoreae (ASHTON, 1982). Furthermore, tribe Dipterocarpeae consists of eight genera with a total of four sections, namely *Dipterocarpus*, *Anisoptera* (two sections), *Upuna*, *Cotylelobium*, *Vatica* (two sections), *Stemonoporus*, *Vateria*, and *Vateriopsis*. Tribe Shoreae consists of five genera with a total of 13 sections and 12 subsections, namely *Hopea* (two sections, four subsections), *Shorea* (11 sections, eight subsections), *Parashorea*, *Neobalanocarpus* and *Dryobalanops*.

1.1.5. Intraspecific variation

Methods to observe genetic variation within dipterocarps have been conducted using various genetic markers, such as isozymes and molecular markers. Microsatellite markers have been developed to observe genetic variation of *Dipterocarpus tempehes* (ISAGI *et al.*, 2002), *Dryobalanops lanceolata* (TERAUCHI, 1994), *Hopea bilitonsis* (LEE *et al.*, 2004a), *Neobalanocarpus heimii* (IWATA *et al.*, 2000), *Shorea cordifolia* and *Shorea megistophylla* (STACY *et al.*, 2001), *Shorea leprosula* and *Shorea parvifolia* (LEE *et al.*, 2004b), *Shorea curtisii* and other dipterocarps species (UJINO *et al.*, 1998). Genetic studies using microsatellite markers revealed high heterozygosity of *Dryobalanops aromatica* ($H_e=0.71$; LIM, *et al.*, 2001) and *Shorea* spp., i.e. $H_e=0.69-0.71$ in *Shorea leprosula* (NAGAMITSU, *et al.*, 2001; NG *et al.*, 2004; RIMBAWANTO and ISODA, 2001), $H_e=0.62-0.67$ in *Shorea ovalis* (NG *et al.*, 2004), $H_e=0.68-0.73$ in *Shorea curtisii* (OBAYASHI *et al.*, 2002), $H_e=0.33-0.85$ in *Shorea parvifolia* and $H_e=0.42-0.76$ in *Shorea acuminata* (TAKEUCHI *et al.*, 2004).

The genetic analysis of dipterocarps found that isozyme variation is low in *Dipterocarpus alatus* ($H_e=0.09$; CHANGTRAGOON, 2001) and *Shorea robusta* ($H_e=0.143$; SUOHEIMO *et al.*, 1999), and exceptionally high in *Stemonoporus oblongifolius* ($H_e=0.34$; MURAWSKI and

BAWA, 1994), *Dryobalanops aromatica* ($H_e=0.46$; LEE, *et al.*, 2000a) and *Shorea leprosula* ($H_e=0.41$; LEE *et al.*, 2000b).

1.2. Genetic properties of chloroplast DNA and its application to phylogenetic and population genetic studies

The genetic information of higher plants is distributed in three types of the genome, i.e. nuclear, mitochondria, and chloroplast. The genes in mitochondrial and chloroplast genomes have become known as extrachromosomal genes, cytoplasmic genes, non-Mendelian genes, organellar genes, or extranuclear genes (RUSSELL, 1994). In angiosperms, Mendelian inheritance is normally assumed for nuclear DNA, whereas uniparental or maternal inheritance is known to be the dominant mode for chloroplast and mitochondria DNA (BIRKY, 1995).

The chloroplast contains not only the enzymes of photosynthesis, but also their own DNA together with the mechanisms needed for DNA replication, DNA transcription and ribosomally catalyzed protein synthesis (DUPRAW, 1970). Therefore, photosynthesis is only one of the many biological functions of chloroplasts; others include protein synthesis, reproduction, and genetic autonomy (SZMIDT, 1991). The chloroplast is only one type of plastid; all plastids (proplastid, chloroplast, chromoplast, amyloplast, etioplast, elaioplast) contain the same cpDNA (DARNELL *et al.*, 1990).

Numerous DNA rings exist in each chloroplast, which are about 120-160 kbps long. Chloroplast DNA (cpDNA) contains genes for rRNA, tRNA, and about 50-100 structure genes (CLEGG *et al.*, 1994; HATTEMER *et al.*, 1993). The cpDNA genome is composed of two regions of single-copy sequences, typically of about 20 and 80 kbps, separated by inverted repeated sequences which are variable in size between species, but typically of about 20 kbps length (KENDREW, 1994). With the help of molecular genetic methods the type of genes and their arrangement on the DNA rings of the chloroplast can be identified in some organisms. The sequences of the chloroplast genomes of some species are already known, like complete sequences in tobacco (SHINOZAKI *et al.*, 1986; WAKASUGI *et al.*, 1998) and rice (HIRATSUKA *et al.*, 1989), the *rbcL* gene in Douglas fir (HIPKINS *et al.*, 1990) and the *trnK-psbA* region of *Pinus contorta*. (LIDHOLM and GUSTAFSSON, 1991).

Phylogenetic and population genetic studies based on cpDNA variation are possible, since cpDNA displays a leisurely pace of sequence evolution (AVISE, 2000). Nonetheless, cpDNA

variation is present and known to be structured geographically in several plant species (SZMIDT, 1991). The comparative analysis of homologous DNA sequences represents an increasingly useful and recognized approach for the definition of taxonomic relationships. Molecular data provide new information for phylogenetic investigations and consequently often clarify the broad connections among taxa (ROSETTO *et al.*, 2000).

The cpDNA lends itself particularly well to phylogenetic studies because: i. the genome is structurally stable; ii. the genome's rate of sequence evolution has been slow, and thus comparisons among species or even genera can be done with ease.; iii. the genome is uniparentally inherited and does not undergo recombination; iv. the small size of cpDNA permits good resolution of most fragments generated by restriction enzymes, so that even alterations of single nucleotides can be detected (CLEGG *et al.*, 1994; RITLAND and CLEGG, 1987).

The chloroplast DNA genome is also useful for population genetic studies. For example, the cpDNA variation in white oak (*Quercus* spp.) species (DUMOLIN-LAPÈGUE *et al.*, 1997a; PETIT *et al.*, 2002a; PETIT *et al.*, 2002b) and *Fagus sylvatica* (DEMESURE *et al.*, 1996) is recognized as being geographically structured at the regional scale in Europe, but in *Prunus spinosa* the cpDNA variations are geographically unrelated (MOHANTY *et al.*, 2002).

1.3. Objectives

1.3.1. Phylogenetic study

The cpDNA variation of dipterocarp species from Indonesia was studied in order to test the following hypotheses:

- Variation of cpDNA is mainly found among species.
- The distinction of two tribes (tribe Shoreae; basic chromosome number $x=7$; tribe Dipterocarpeae; $x=11$) within the subfamily Dipterocarpoideae is reflected in cpDNA variation.
- The differentiation of nine genera and the distinction of sections and sub-sections according to the classification of ASHTON (1982) is well-supported by cpDNA variation.

The results might help to review the intergeneric and interspecies classification of the Dipterocarpaceae (subfamily Dipterocarpoideae).

1.3.2. Population genetic study

The haplotypic diversity within and among populations of four *Shorea* species in Kalimantan and Sumatra was observed using chloroplast DNA. This study is also an initial attempt to present the geographical distribution mapping of cpDNA haplotypes of *Shorea* spp. and to explore the possibility of using molecular markers as a tool to prove the geographical origin of individual trees.

2. MATERIALS AND METHODS

2.1. Materials

2.1.1. Phylogenetic study

The samples consisted of 129 trees belonging to 58 species of all nine genera native to Indonesia, i.e. *Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Dryobalanops*, *Hopea*, *Shorea*, *Parashorea*, *Vatica* and *Upuna* (see Table 1). Samples were collected from one to seven single trees for each species. Trees were sampled in natural and planted forests, arboreta, and botanic gardens in Indonesia. The origin of planted species was also recorded (ANONYMOUS, 1991; DANIMIHardja and NOTODIHARDJO, 2001). A single tree of *Monotes kerstingii* (subfamily Monotoideae) from Benin, Africa, was also included in the phylogenetic study and used as an outgroup for data analysis.

Table 1. Sampled material: species, number of sampled plants (N), location of sampling, origin of the material, section and subsection (according to ASHTON, 1982)

| Species and Section/Subsection | N | Sampling location (*) | Origin |
|--|---|-------------------------|------------|
| <i>Anisoptera</i> | | | |
| Section <i>Anisoptera</i> | | | |
| • <i>Anisoptera costata</i> Korth. | 2 | Arboretum, Haurbentes | Kalimantan |
| • <i>Anisoptera marginata</i> Korth. | 1 | Botanic garden, Bogor | Kalimantan |
| • <i>Anisoptera reticulata</i> Ashton | 1 | Natural forest, Malinau | Kalimantan |
| <i>Cotylelobium</i> | | | |
| • <i>Cotylelobium lanceolatum</i> Craib | 1 | Botanic garden, Bogor | Kalimantan |
| <i>Dipterocarpus</i> | | | |
| • <i>Dipterocarpus grandiflorus</i> Blanco | 3 | Arboretum, Haurbentes | Kalimantan |
| • <i>Dipterocarpus oblongifolius</i> Blume | 1 | Botanic garden, Bogor | Kalimantan |
| • <i>Dipterocarpus retusus</i> Blume | 1 | Botanic garden, Bogor | Java |
| • <i>Dipterocarpus rigidus</i> Ridl. | 1 | Botanic garden, Bogor | Sumatra |
| • <i>Dipterocarpus tempehes</i> Sloot. | 3 | Arboretum, Haurbentes | Kalimantan |

(Continued)

Table 1. Sampled material: species, number of sampled plants (N), location of sampling, origin of the material, section and subsection (according to ASHTON, 1982)

| Species and Section/Subsection | N | Sampling location | Origin |
|---|---|-----------------------|------------|
| <i>Dryobalanops</i> | | | |
| • <i>Dryobalanops aromatica</i> Gaertn.f. | 1 | Botanic garden, Bogor | Sumatra |
| • <i>Dryobalanops lanceolata</i> Burck | 4 | Botanic garden, Bogor | Kalimantan |
| <i>Hopea</i> | | | |
| Section <i>Dryobalanoides</i> , subs. <i>Dryobalanoides</i> | | | |
| • <i>Hopea dryobalanoides</i> Miq. | 3 | Arboretum, Haurbentes | Sumatra |
| • <i>Hopea griffithii</i> Kurz | 1 | Botanic garden, Bogor | Kalimantan |
| • <i>Hopea mengarawan</i> Miq. | 3 | Arboretum, Haurbentes | Sumatra |
| Section <i>Dryobalanoides</i> , subs. <i>Sphaoerocarpae</i> | | | |
| • <i>Hopea nigra</i> Burck | 1 | Botanic garden, Bogor | Kalimantan |
| Section <i>Hopea</i> , subs. <i>Hopea</i> | | | |
| • <i>Hopea bancana</i> (Boerl.) Sloot. | 3 | Arboretum, Haurbentes | Sumatra |
| • <i>Hopea celebica</i> Burck | 1 | Botanic garden, Bogor | Sulawesi |
| • <i>Hopea odorata</i> Roxb. | 3 | Arboretum, Haurbentes | Sumatra |
| • <i>Hopea sangal</i> Korth. | 3 | Arboretum, Haurbentes | Sumatra |
| <i>Parashorea</i> | | | |
| • <i>Parashorea globosa</i> Sym. | 1 | Botanic garden, Bogor | Sumatra |
| • <i>Parashorea lucida</i> (Miq.) Kurz. | 1 | Botanic garden, Bogor | Sumatra |
| <i>Shorea</i> | | | |
| Section <i>Mutica</i> , subs. <i>Mutica</i> | | | |
| • <i>Shorea acuminata</i> Dyer | 7 | Natural forest, Tebo | Sumatra |
| • <i>Shorea leprosula</i> Miq. | 3 | Arboretum, Haurbentes | Kalimantan |
| • <i>Shorea parvifolia</i> Dyer | 2 | Arboretum, Haurbentes | Sumatra |
| • <i>Shorea dasyphylla</i> Foxw. | 3 | Natural forest, Tebo | Sumatra |
| Section <i>Mutica</i> , subs. <i>Auriculatae</i> | | | |
| • <i>Shorea macroptera</i> Dyer ssp. <i>macroptera</i> | 1 | Botanic garden, Bogor | Sumatra |

(Continued)

Table 1. Sampled material: species, number of sampled plants (N), location of sampling, origin of the material, section and subsection (according to ASHTON, 1982)

| Species and Section/Subsection | N | Sampling location (*) | Origin |
|---|---|-----------------------------|------------|
| Section <i>Brachypterae</i> , subs. <i>Brachypterae</i> | | | |
| • <i>Shorea andulensis</i> Ashton | 1 | Natural forest, Muara Teweh | Kalimantan |
| • <i>Shorea balangeran</i> (Korth.) Burck | 1 | Botanic garden, Bogor | Sumatra |
| • <i>Shorea platyclados</i> Sloot. ex Endert | 3 | Arboretum, Haurbentes | Sumatra |
| • <i>Shorea scaberrima</i> Burck | 1 | Botanic garden, Bogor | Kalimantan |
| • <i>Shorea johorensis</i> Foxw. | 2 | Arboretum, Haurbentes | Kalimantan |
| • <i>Shorea palembanica</i> Miq. | 3 | Arboretum, Haurbentes | Kalimantan |
| • <i>Shorea selanica</i> Blume | 3 | Arboretum, Haurbentes | Moluccas |
| • <i>Shorea fallax</i> Meijer | 1 | Botanic garden, Bogor | Kalimantan |
| Section <i>Anthoshorea</i> | | | |
| • <i>Shorea javanica</i> K. & V. | 1 | Botanic garden, Bogor | Java |
| • <i>Shorea montigena</i> Sloot. | 1 | Botanic garden, Bogor | Moluccas |
| • <i>Shorea virescens</i> Parijs | 3 | Arboretum, Haurbentes | Kalimantan |
| Section <i>Pachycarpae</i> | | | |
| • <i>Shorea mecistopteryx</i> Ridl. | 6 | Arboretum, Haurbentes | Kalimantan |
| • <i>Shorea macrophylla</i> (de Vriese) Ashton | 3 | Arboretum, Haurbentes | Kalimantan |
| • <i>Shorea pinanga</i> Scheff. | 6 | Arboretum, Haurbentes | Kalimantan |
| • <i>Shorea splendida</i> (de Vriese) Ashton | 3 | Arboretum, Haurbentes | Kalimantan |
| • <i>Shorea stenoptera</i> Burck | 3 | Arboretum, Haurbentes | Kalimantan |
| Section <i>Ovalis</i> | | | |
| • <i>Shorea ovalis</i> (Korth.) Blume | 3 | Arboretum, Haurbentes | Sumatra |
| Section <i>Richetioides</i> subs. <i>Richetioides</i> | | | |
| • <i>Shorea blumutensis</i> Foxw. | 3 | Natural forest, Tebo | Sumatra |
| • <i>Shorea xanthophylla</i> Sym. | 3 | Natural forest, Tebo | Sumatra |
| • <i>Shorea multiflora</i> (Burck) Sym. | 1 | Botanic garden, Bogor | Sumatra |
| • <i>Shorea acuminatissima</i> Sym. | 1 | Natural forest, Ketapang | Kalimantan |
| • <i>Shorea faguëtiana</i> Heim | 1 | Botanic garden, Bogor | Kalimantan |

(Continued)

Table 1. Sampled material: species, number of sampled plants (N), location of sampling, origin of the material, section and subsection according to ASHTON (1982)

| Species and Section/Subsection | N | Sampling location | Origin |
|--|---|-----------------------|------------|
| Section <i>Shorea</i> subs. <i>Shorea</i> | | | |
| • <i>Shorea seminis</i> (de Vriese) Sloot. | 3 | Arboretum, Haurbentes | Kalimantan |
| • <i>Shorea guiso</i> (Blco) Blume | 2 | Arboretum, Haurbentes | Kalimantan |
| • <i>Shorea materialis</i> Ridl. | 1 | Botanic garden, Bogor | Sumatra |
| <i>Upuna</i> | | | |
| • <i>Upuna borneensis</i> Sym. | 1 | Botanic garden, Bogor | Kalimantan |
| <i>Vatica</i> | | | |
| Section <i>Vatica</i> | | | |
| • <i>Vatica bella</i> Sloot. | 1 | Botanic garden, Bogor | Sumatra |
| • <i>Vatica granulata</i> Sloot. | 2 | Botanic garden, Bogor | Sulawesi |
| • <i>Vatica pauciflora</i> (Korth.) Blume | 6 | Botanic garden, Bogor | Sumatra |
| • <i>Vatica rassak</i> (Korth.) Blume | 2 | Botanic garden, Bogor | Maluku |
| • <i>Vatica venulosa</i> Blume | 1 | Botanic garden, Bogor | Sumatra |
| Section <i>Sunaptea</i> | | | |
| • <i>Vatica bantamensis</i> (Hassk.) B. & H. ex Miq. | 2 | Botanic garden, Bogor | Java |
| <i>Monotes</i> | | | |
| • <i>Monotes kerstingii</i> Gilg | 1 | Benin | Benin |

(*): approximate geographic location (latitude and longitude) of each sampling location:

1. Arboretum Haurbentes, Jasinga, West Java: 6°10'–6°35' S and 106°20'–106°30' E
2. Botanic garden, Bogor, West Java: 6°36'–6°37' S and 106°32'–106°33' E
3. Natural forest, Tebo, Jambi, Sumatra 1°00'–1°45' S and 102°00'–102°45' E
4. Natural forest, Malinau, East Kalimantan: 2°45'–3°21' N and 115°48'–116°34' E
5. Natural forest, Muara Teweh, Central Kalimantan 0°00'–0°20' S and 114°30'–115°10' E
6. Natural forest, Ketapang, West Kalimantan 1°00'–1°15' S and 110°45'–111°00' E

Genera, sections, subsections, and the number of species investigated are described in Table 2 and compared to the total number of dipterocarp species in Indonesia, including insular Malaysia and Brunei Darussalam in Kalimantan Island and Papua New Guinea in Irian Island.

Table 2. Genera, sections, and subsections of dipterocarps in Indonesia, modified after ASHTON (1982)

| Genus | Section | Subsection | Total number of species (*) | Number of species investigated |
|----------------------|------------------------|------------------------|-----------------------------|--------------------------------|
| <i>Anisoptera</i> | <i>Anisoptera</i> | | 7 | 3 |
| | <i>Glabrae</i> | | 1 | 0 |
| <i>Cotylelobium</i> | | | 3 | 1 |
| <i>Dipterocarpus</i> | | | 46 | 5 |
| <i>Dryobalanops</i> | | | 7 | 2 |
| <i>Hopea</i> | <i>Dryobalanooides</i> | <i>Dryobalanooides</i> | 19 | 3 |
| | | <i>Sphaerocarpace</i> | 10 | 1 |
| | <i>Hopea</i> | <i>Hopea</i> | 26 | 4 |
| | | <i>Pierrea</i> | 8 | 0 |
| <i>Parashorea</i> | | | 8 | 2 |
| <i>Shorea</i> | <i>Mutica</i> | <i>Mutica</i> | 21 | 4 |
| | | <i>Auriculatae</i> | 6 | 1 |
| | <i>Brachypterae</i> | <i>Brachypterae</i> | 22 | 8 |
| | | <i>Smithiana</i> | 1 | 0 |
| | <i>Anthoshorea</i> | | 16 | 3 |
| | <i>Pachycarpae</i> | | 10 | 5 |
| | <i>Ovalis</i> | | 1 | 1 |
| | <i>Richetioides</i> | <i>Richetioides</i> | 30 | 5 |
| | | <i>Polyandrae</i> | 1 | 0 |
| | <i>Shorea</i> | <i>Shorea</i> | 22 | 3 |
| | | <i>Barbata</i> | 7 | 0 |
| | <i>Pentacme</i> | | 2 | 0 |
| | <i>Neohopea</i> | | 1 | 0 |
| | <i>Rubella</i> | | 4 | 0 |
| | <i>Upuna</i> | | | 1 |
| <i>Vatica</i> | <i>Vatica</i> | | 19 | 5 |
| | <i>Sunaptea</i> | | 22 | 1 |

(*): Total number species in Indonesia including insular Malaysia and Brunei Darussalam in Kalimantan Island and Papua New Guinea in Irian Island.

Leaf tissue from adult trees was collected by the author from Java and Jambi. Seed samples obtained from Kalimantan were collected by ITTO Project PD 41/00 Rev. 3 (F,M), namely “Model development to establish commercial plantation of dipterocarps”, jointly conducted by Faculty of Forestry, Gadjah Mada University, Yogyakarta, Indonesia and the International Timber Trade Organization (ITTO). Seeds were identified according to the mother trees. Leaf tissue of *Monotes kerstingii* was provided by a colleague from the University of Rostock, Germany.

2.1.2. Population genetic study

Four species of *Shorea* were investigated in the population genetic study, namely *Shorea leprosula* Miq., *Shorea parvifolia* Dyer, *Shorea ovalis* (Korth.) Blume, and *Shorea johorensis* Foxw. These species were chosen due to their broad distribution in Southeast Asia. In Indonesia, these four *Shorea* species are found in Sumatra and Kalimantan (ASHTON, 1982).

The samples were obtained from four sites in Kalimantan and one site in Sumatra (Table 3). Samples originating from Tebo natural forest, Jambi, Sumatra, were collected by the author, whereas samples originating from Kalimantan were collected by ITTO Project PD 41/00 Rev. 3 (F,M), namely “Model development to establish commercial plantation of dipterocarps”, jointly conducted by Faculty of Forestry, Gadjah Mada University, Yogyakarta, Indonesia and the International Timber Trade Organization (ITTO). The sites in Kalimantan are geographically widely separated, as shown in Figure 2. Each species was represented by six single adult trees from every site. Leaf tissue from adult trees was collected from Tebo natural forest, Jambi, Sumatra. Seeds were collected from natural forest in Kalimantan populations and identified according to the mother trees.

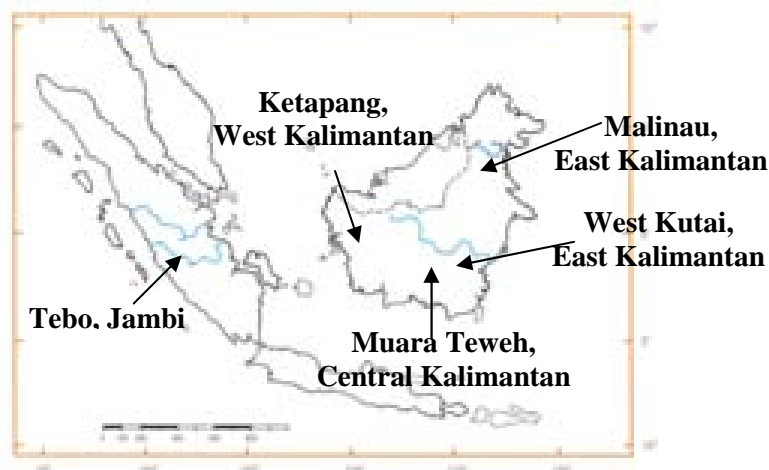


Figure 2. Location map of the sample population sites in Kalimantan and Sumatra

Table 3. The population sites of samples obtained in Kalimantan and Sumatra

| Species and Section/Subsection | Approximate geographic location | |
|---|---------------------------------|-------------------|
| | Latitude | Longitude |
| Section <i>Mutica</i> Subsection <i>Mutica</i> | | |
| <i>Shorea leprosula</i> Miq. | | |
| • West Kutai, East Kalimantan | 0°00'–0°45' S | 115°30'–115°45' E |
| • Muara Teweh, Central Kalimantan | 0°00'–0°20' S | 114°30'–115°10' E |
| • Ketapang, West Kalimantan | 1°00'–1°15' S | 110°45'–111°00' E |
| • Tebo, Jambi, Sumatra | 1°00'–1°45' S | 102°00'–102°45' E |
| <i>Shorea parvifolia</i> Dyer | | |
| • West Kutai, East Kalimantan | 0°00'–0°45' S | 115°30'–115°45' E |
| • Muara Teweh, Central Kalimantan | 0°00'–0°20' S | 114°30'–115°10' E |
| • Ketapang, West Kalimantan | 1°00'–1°15' S | 110°45'–111°00' E |
| • Tebo, Jambi, Sumatra | 1°00'–1°45' S | 102°00'–102°45' E |
| Section <i>Ovalis</i> | | |
| <i>Shorea ovalis</i> (Korth.) Blume | | |
| • Malinau, East Kalimantan | 2°45'–3°21' N | 115°48'–116°34' E |
| • Muara Teweh, Central Kalimantan | 0°00'–0°20' S | 114°30'–115°10' E |
| • Ketapang, West Kalimantan | 1°00'–1°15' S | 110°45'–111°0' E |
| • Tebo, Jambi, Sumatra | 1°00'–1°45' S | 102°00'–102°45' E |
| Section <i>Brachypterae</i> Subsection <i>Brachypterae</i> | | |
| <i>Shorea johorensis</i> Foxw. | | |
| • Malinau, East Kalimantan | 2°45'–3°21' N | 115°48'–116°34' E |
| • Muara Teweh, Central Kalimantan | 0°00'–0°20' S | 114°30'–115°10' E |
| • Ketapang, West Kalimantan | 1°00'–1°15' S | 110°45'–111°00' E |

2.2. Methods

2.2.1. Taxa identification

Species identification was based on field observations and on an independent verification by the analysis of herbarium material. A herbarium was created using twigs with at least five mature, healthy leaves sampled from each tree, registered together with the samples for DNA analysis, dried, and maintained at room temperature in the Institute of Forest Genetics and Forest Tree Breeding, Georg-August University, Göttingen. Species identification was carried out by a dendrologist from the Faculty of Forestry, Gadjah Mada University, Yogyakarta, Indonesia based on the present classification of Dipterocarpaceae (ASHTON, 1982),

2.2.2. Laboratory methods

2.2.2.1. DNA isolation

For DNA analysis, healthy seeds or leaves were collected. DNA was extracted from leaves sampled from germinated seeds or adult trees. The seeds were germinated in a nursery and each mother tree was represented only by one germinated seed for the laboratory and statistical methods. At least one fully developed, healthy leaf from adult trees was air-dried in sealed plastic bags with plenty of silica gel for transportation and kept at $-60\text{ }^{\circ}\text{C}$ until DNA extraction in the laboratory of the Institute of Forest Genetics and Forest Tree Breeding, Georg-August University, Göttingen. The DNA was extracted using the CTAB method and DNA isolation kits. As the preparation in both methods, leaves were ground into a fine powder using a mill apparatus (Retsch, Haan).

2.2.2.1.1. CTAB method

A slightly modified *Hexadecyltrimethylammonium bromide* (CTAB) procedure from CSAIKL *et al.* (1998) and MILLIGAN (1998) was applied to extract dipterocarp samples. Only a few samples could be extracted successfully using this method. It proved to be difficult to develop a universal protocol for DNA extraction using the CTAB method due to species-specific secondary components in dipterocarp leaves inhibiting the extraction, and due to different storage conditions of the sampled material.

2.2.2.1.2. DNA isolation kits

Three DNA isolation kits have been tested to extract the DNA of leaf tissues of dipterocarps, namely DNeasy® Plant Mini Kit (Cat. No. 69104; Qiagen, Hilden), Nucleon PhytoPure Genomic DNA Extraction Kit (Cat. No. RPN 8510; Amersham Pharmacia Biotech, Buckinghamshire), and DNeasy® 96 Plant Kit (Cat. No. 69181; Qiagen, Hilden). The extraction was done following the manufacturer's instructions. However, only the last kit gave the optimum quality and quantity of DNA needed for the next step of genetic analysis (PCR). Most of the samples were extracted using this DNA isolation kit.

2.2.2.2. Electrophoresis

Electrophoresis was carried out on agarose gel to test the quality of DNA isolation results and to estimate the number of base pair of the PCR products and the digestion results of PCR-RFLP of cpDNA. The dilution of cpSSR PCR products for genotyping purposes was also determined based on electrophoretic performance of the samples.

The concentration of agarose gels was adjusted for DNA isolation results, PCR products and digestion results of PCR-RFLP to 0.8%, 2% and 2.5%, respectively. These concentrations depend on the length of the DNA fragments. The quantity of DNA was examined in comparison to a molecular weight standard (Lambda DNA Marker, Cat. No. 745782; Roche, Mannheim). The molecular weight standard XIV (100 bps ladder) DNA Marker (Cat. No. 1721933; Roche, Mannheim) was applied for electrophoresis of the PCR products and digestion results of PCR-RFLP.

Electrophoresis was performed using 1x *Tris-acetate* (TAE) buffer for about 30-150 minutes at 100-220 V. Electrophoresis time needed depends on the length of gels. The electrophoresis buffer solution was composed as follows:

***Tris-acetate* (TAE) electrophoresis buffer (50x concentrated stock solution per liter)**

| | |
|---------------------|----------|
| <i>Tris base</i> | 242.0 g |
| Glacial acetic acid | 57.1 ml |
| 0.5 M EDTA (pH 8.0) | 100.0 ml |

This buffer solution was diluted 50x with distilled water for electrophoresis and stored at room temperature.

After electrophoresis, the agarose gel was stained in 1% of *Ethidium bromide* solution for about 20 minutes at room temperature. The banding patterns of gel were examined using a UV light apparatus in the dark room. Each gel observed was documented using a digital camera.

2.2.2.3. Polymerase chain reaction – restriction fragment length polymorphism (PCR-RFLP) analysis

2.2.2.3.1. Primer test for PCR

Seventeen universal oligonucleotide primers have been tested for the amplification of selected cpDNA gene / intergenic spacer (IS) regions of dipterocarps. All primers have been arranged to amplify the large single copy (LSC) region of chloroplast DNA. The sequences of these primers are described in the following Table:

Table 4. Sequences of primer pairs tested to amplify cpDNA regions (sorted after HIRATSUKA *et al.*, 1989; SHINOZAKI *et al.*, 1986; WAKASUGI *et al.*, 1998)

| Gene / IS | Gene product/position | Forward and reverse primer sequence (5' -- 3') | Note (*) |
|------------------|------------------------------|--|----------|
| <i>trnH-K</i> | tRNA-His (GUG) – | ACG GGA ATT GAA CCC GCG CA | A |
| | tRNA-Lys (UUU) | CCG ACT AGT TCC GGG TTC GA | |
| <i>psbA</i> | PSII 32kd protein | TAC GTT CGT GCA TAA CTT CC CTA GCA CTG AAA ACC GTC TT | B |
| <i>trnK</i> | tRNA-Lys (UUU) | GGG TTG CCC GGG ACT CGA AC | A |
| | | CAA CGG TAG AGT ACT CGG CTT TTA | |
| <i>trnK</i> | tRNA-Lys (UUU) | AAC CCG GAA CTA GTC GGA TG | B |
| | | TCA ATG GTA GAG TAC TCG GC | |
| <i>trnQ-R</i> | tRNA-Gln (UUG) – | GGG ACG GAA GGA TTC GAA CC | C |
| | tRNA-Arg (UCU) | ATT GCG TCC AAT AGG ATT TGA A | |
| <i>rpoC-trnC</i> | RNA polymerase beta' subunit | GCA GTT TCT TGA AAA CTC GC | B |
| | tRNA-Cys (GCA) | TGT ACA CGC GGT AGA AAA AT | |

(Continued)

Table 4. Sequences of primer pairs tested to amplify cpDNA regions (sorted after HIRATSUKA *et al.*, 1989; SHINOZAKI *et al.*, 1986; WAKASUGI *et al.*, 1998)

| Gene / IS | Gene product/position | Forward and reverse primer sequence (5' -- 3') | Note (*) |
|-------------------|---|--|----------|
| <i>trnC-D</i> | tRNA-Cys (GCA) – tRNA-Asp (GUC) | CCA GTT CAA ATC TGG GTG TC GGG ATT GTA GTT CAA TTG GT | A |
| <i>trnD-T</i> | tRNA-Asp (GUC) – tRNA-Thr (GGU) | ACC AAT TGA ACT ACA ATC CC CTA CCA CTG AGT TAA AAG GG | A |
| <i>trnfM-psaA</i> | tRNA-fMet (CAU) – PSI P700 apoprotein A1 | GAA CCC GTG ACC TCA AGG TTA TG ATT CGT TCG CCG GAA CCA GAA GT | C |
| <i>psaA</i> | PSI P700 apoprotein A1 | AAG AAT GCC CAT GTT GTG GC TTC GTT CGC CGG AAC CAG AA | B |
| <i>trnT-L</i> | tRNA-Thr (UGU) – tRNA-Leu (UAA) | CAT TAC AAA TGC GAT GCT CT TCT ACC GAT TTC GCC ATA TC | D |
| <i>trnL-F</i> | tRNA-Leu (UAA) – tRNA-Phe (GAA) | CGA AAT CGG TAG ACG CTA CG ATT TGA ACT GGT GAC ACG AG | D |
| <i>trnT-F</i> | tRNA-Thr (UGU) – tRNA-Phe (GAA) | CAT TAC AAA TGC GAT GCT CT ATT TGA ACT GGT GAC ACG AG | D |
| <i>trnF-V</i> | tRNA-Phe (GAA) – tRNA-Val (UAC) | CTC GTG TCA CCA GTT CAA AT CCG AGA AGG TCT ACG GTT CG | C |
| <i>trnV-rbcL</i> | tRNA-Val (UAC) – RuBisCo large subunit | CGA ACC GTA GAC CTT CTC GG GCT TTA GTC TCT GTT TGT GG | C |
| <i>rbcL</i> | RuBisCo large subunit | TGT CAC CAA AAA CAG AGA CT TTC CAT ACT TCA CAA GCA GC | B |
| <i>petB</i> | Cytochrom b6 | TGG GGA ACT ACT CCT TTG AT CCC GAA ATA CCT TGC TTA CG | B |

(*): A= DEMESURE *et al.* (1995); B= TSUMURA *et al.* (1996); C= DUMOLINE-LAPÈGUE *et al.* (1997b); D= TABERLET *et al.* (1991)

2.2.2.3.2. PCR amplification using selected primer

Out of 17 universal cpDNA primers tested, five primers amplified DNA in all dipterocarp samples, i.e. *petB*, *psbA*, *psaA*, *rbcL* and *trnLF*. The PCR procedures have been optimized for dipterocarps and carried out with the following steps and reaction mixtures of PCR reagents:

Temperature profile of PCR steps

Step 1: initial denaturation for 15 minutes at 95 °C

Step 2: 35 cycles of:

denaturation for 1 minute at 94 °C

annealing for 1 minute at 56 °C (for *trnL-F*) or 50 °C (for the other primers)

extension for 2 minutes at 72 °C

Step 3: final extension for 10 minutes at 72 °C

Reaction mix (15 µL) of PCR reagents

| | |
|---|--------|
| Template DNA (5-10 ng) | 2.0 µl |
| Forward primer (5 pmol/µl) | 1.8 µl |
| Reverse primer (5 pmol/µl) | 1.8 µl |
| Distilled water | 1.9 µl |
| HotStarTaq® Master Mix Kit (Qiagen, Hilden) | 7.5 µl |

The extracted DNA was diluted to 1–10% prior to PCR. Amplification products were analyzed electrophoretically in order to determine the fragment length for each sample.

2.2.2.3.3. Restriction of PCR product using enzymes (PCR-RFLP)

CpDNA fragments amplified with five selected universal primers were then digested with seven restriction endonucleases, i.e. *AluI*, *CfoI*, *HaeIII*, *HinfI*, *MspI*, *RsaI* and *TaqI* (Roche, Mannheim) as described in Table 5. These enzymes recognize specific target sequence of four-base sites (four-cutter).

Table 5. Restriction endonuclease for digesting the amplification product

| Name | Sequence (5'-3') | Incubation Temp. (°C) |
|---------------|-------------------------|------------------------------|
| <i>AluI</i> | AG↓CT | 37 |
| <i>CfoI</i> | GCG↓C | 37 |
| <i>HaeIII</i> | GG↓CC | 37 |
| <i>HinfI</i> | G↓ANTC | 37 |
| <i>MspI</i> | C↓CGG | 37 |
| <i>RsaI</i> | GT↓AC | 37 |
| <i>TaqI</i> | T↓CGA | 65 |

The restriction solution was incubated for at least three hours and at most one night. This solution was made as follows:

Restriction solution (11.5 µl)

| | |
|--------------------------|-----------------|
| Restriction endonuclease | 1.0 µl (1 unit) |
| Enzyme specific buffer | 1.0 µl |
| Amplification product | 5.0 µl |
| Distilled water | 4.5 µl |

The PCR-RFLP products were separated electrophoretically after digestion in order to determine the length of DNA fragments and to reconstruct restriction sites for each sample.

2.2.2.4. Chloroplast simple sequence repeat (cpSSR) analysis

2.2.2.4.1. Primer test for PCR

Ten universal markers, namely consensus chloroplast microsatellite primers (*ccmp*), *ccmp1* to *ccmp10* (WEISING and GARDNER, 1999), were tested in order to analyze the chloroplast microsatellite genome (see Table 6). To this end, only unlabelled forward primers were applied.

Table 6. Sequences of primer pairs tested to amplify cpSSR loci

| cpSSR Locus | Location | Forward and reverse primer sequence (5' – 3') |
|--------------------|---|--|
| <i>ccmp1</i> | <i>trnK</i> intron | CAG GTA AAC TTC TCA ACG GA CCG AAG TCA AAA GAG CGA TT |
| <i>ccmp2</i> | 5' to <i>trnS</i> | GAT CCC GGA CGT AAT CCT G ATC GTA CCG AGG GGT TCG AAT |
| <i>ccmp3</i> | <i>trnG</i> intron | CAG GTA AAC TTC TCA ACG GA CCG AAG TCA AAA GAG CGA TT |
| <i>ccmp4</i> | <i>atpF</i> intron | AAT GCT GAA TCG A(CT)G ACC TA CCA AAA TAT T(GCT)G GAG GAC TCT |
| <i>ccmp5</i> | 3' to <i>rps2</i> | TGT TCC AAT ATC TTC TTG TCA TTT AGG TTC CAT CGG AAC AAT TAT |
| <i>ccmp6</i> | ORF 77 – ORF 82 intergenic spacer | CGA TGC ATA TGT AGA AAG CC CAT TAC GTG CGA CTA TCT CC |
| <i>ccmp7</i> | <i>atpB</i> – <i>rbcL</i> intergenic spacer | CAA CAT ATA CCA CTG TCA AG ACA TCA TTA TTG TAT ACT CTT TC |
| <i>ccmp8</i> | <i>rpl20</i> – <i>rps12</i> intergenic spacer | TTG GCT ACT CTA ACC TTC CC TTC TTT CTT ATT TCG CAG DGA A |
| <i>ccmp9</i> | ORF 74b – <i>psbB</i> intergenic spacer | GGA TTT GTA CAT ATA GGA CA CTC AAC TCT AAG AAA TAC TTG |
| <i>ccmp10</i> | <i>rpl2</i> – <i>rps19</i> intergenic spacer | TTT TTT TTT AGT GAA CGT GTC A TTC GTC G(AGT)C GTA GTA AAT AG |

Source: WEISING and GARDNER (1999)

2.2.2.4.2. PCR amplification using selected primers

Out of ten chloroplast microsatellite primers tested, three primers (*ccmp4*, *ccmp5* and *ccmp9*) showed no amplification product and seven primers amplified DNA from all dipterocarp

samples, i.e. *ccmp1*, *ccmp2*, *ccmp3*, *ccmp6*, *ccmp7*, *ccmp8*, and *ccmp10*. The amplification of cpSSR was applied using fluorescence dyed forward primers (Metabion) for genotyping purpose, namely 6-FAM / blue (for *ccmp2* and *ccmp6*), HEX (for *ccmp1*, *ccmp3*, *ccmp7* and *ccmp10*), and NED (for *ccmp8*). The reaction mix of PCR reagents is the same as for cpDNA. However, the temperature profile is optimized for amplifying the cpSSR locus of dipterocarps and is described as follows:

Temperature profile of PCR steps

Step 1: initial denaturation for 15 minutes at 95 °C

Step 2: 35 cycles of:

denaturation for 1 minute at 94 °C

annealing for 1 minute at 50 °C

extension for 1 minute at 72 °C

Step 3: final extension for 10 minutes at 72 °C

2.2.2.4.3. Genotyping of PCR product

Amplification products were separated by capillar electrophoresis on an automated sequencer ABI Prism 3100® Genetic Analyzer (Applied Biosystems) with polymer 3100 POP-4™ (Applied Biosystems). The length of electrophoresis products (in base pairs = bps) was measured with the help of the internal size standard GS 500 ROX™ (Applied Biosystems). Individual alleles were analyzed using GeneScan© version 3.7 (Applied Biosystems) and genotyped using Genotyper© version 3.7 NT (Applied Biosystems). The reagents for genotyping were described as follows:

Reagent mix for genotyping (for 96 probes)

GS 500 ROX™ (Applied Biosystems) 1 µl

HiDi Formamide (Applied Biosystems) 1.152 ml

The reagent mix was distributed equally for 96 sample tubes, and then 2 µl of amplification product of each sample was added to the tubes.

2.2.3. Statistical methods

2.2.3.1. Generation of the data matrix

The restriction site map data of polymorphic cpDNA regions were transformed to a binary matrix (0, 1) for further analysis. Length variants of restriction fragments and chloroplast

microsatellites were coded as multistate characters (0, 1, 2, ...). Missing and ambiguous data were coded as '-' and '?', respectively.

2.2.3.2. Distance matrix

Genetic distance was calculated in order to describe the genetic differences between two taxa. The numbers of character changes were performed as absolute distances and mean distances (SWOFFORD, 1998). Mean distance was calculated as a ratio between absolute distance and the total number of characters. The value varied between 0 (if two taxa are identical) and 1 (if two taxa do not share any characters). Based on the transformed character matrix, the pairwise genetic distance matrix between samples was computed using PAUP version 4.0 (SWOFFORD, 1998).

2.2.3.3. Phylogenetic analysis

Phylogenetic analysis of dipterocarps was carried out using the equally weighted maximum parsimony and neighbour-joining method of PAUP version 4.0 (SWOFFORD, 1998). *Monotes kerstingii* from Benin was chosen as an outgroup, since it combines many plesiomorphic characters. Alternatively *Upuna borneensis* from Kalimantan was used as an outgroup (TSUMURA *et al.*, 1996). The effect of outgroup selection on tree topology was analyzed using maximum parsimony and neighbour-joining method. The image results (tree files) were presented using TreeView version 1.5.2. (PAGE, 1998).

2.2.3.3.1. Maximum parsimony method

Based on heuristic search algorithms as described by NEI and KUMAR (2000), the maximum parsimony was performed with 1000 bootstrap replications (FELSENSTEIN, 1985). Settings for maximum parsimony method in PAUP included closest addition sequence, tree bisection-reconnection (TBR) branch swapping, steepest descent off, and multrees on. Only groups with a bootstrap value of more than 50% are reported.

2.2.3.3.2. Neighbour-Joining method

Neighbour-joining (NJ) method was carried out based on the matrix of pairwise distances between species (SAITOU and NEI, 1987). The level of support for branches of the NJ tree was determined using the bootstrap method (FELSENSTEIN, 1985) with 1000 replications. Again only groups with a bootstrap value of more than 50% are reported.

2.2.3.4. Measurement of genetic structure within and among population

The genetic structure within and among populations in four *Shorea* spp. was analyzed by means of chloroplast DNA variation. In order to analyse the genetic diversity, the hierarchical analysis of allelic variation among populations is calculated as follows (NEI, 1973):

$$G_{ST} = (H_T - H_S) / H_T$$

where H_T equals the gene diversity $1 - \sum p_i^2$ (p_i is the allele frequency) in the total population of pooled demes and H_S is the average gene diversity within each member of the population.

3. RESULTS

3.1. Phylogenetic study

3.1.1. Polymorphisms of cpDNA

3.1.1.1. PCR-RFLP revealing variation

Out of 17 genes / intergenic spacer regions tested, four genes (*rbcL*, *petB*, *psaA* and *psbA*) and one intergenic spacer region (*trnL-F*) can be applied to amplify the cpDNA of Dipterocarpaceae. The amplification of genomic cpDNA for these gene regions produced fragment length of about 1300 (*rbcL*), 1700 (*petB*), 2500 (*psaA*), 1000 (*psbA*) and 1100 (*trnL-F*) base pairs. Variation was detected for all fragments after digestion with particular restriction enzymes, but the number of enzymes revealing variation varied from one (*psbA*) to seven (i.e., all; *petB* and *rbcL*), as shown in Table 7. There is a total of 23 primer-enzyme combinations showing variation, i.e. restriction site polymorphisms and length differences.

Table 7. PCR-RFLP revealing variation among dipterocarp species

| Gene/IS | Restriction enzyme *) | | | | | | |
|---------------|-----------------------|--------------|----------------|---------------|--------------|--------------|--------------|
| | <i>Alu I</i> | <i>Cfo I</i> | <i>Hae III</i> | <i>Hinf I</i> | <i>Msp I</i> | <i>Rsa I</i> | <i>Taq I</i> |
| <i>rbcL</i> | 8, 8, 0 | 6, 6, 0 | 3, 2, 0 | 5, 7, 0 | 6, 6, 0 | 2, 0, 1 | 2, 3, 0 |
| <i>petB</i> | 5, 4, 1 | 2, 1, 0 | 5, 5, 0 | 14, 16, 0 | 4, 6, 0 | 5, 6, 0 | 8, 11, 0 |
| <i>psaA</i> | - | 4, 6, 0 | 4, 7, 0 | 3, 5, 0 | 5, 8, 0 | 4, 6, 0 | 5, 7, 0 |
| <i>psbA</i> | - | - | - | - | 3, 2, 0 | - | - |
| <i>trnL-F</i> | - | - | - | 9, 0, 5 | - | - | 10, 0, 5 |

*) : Number in each enzyme-primer combination result indicates the number of patterns, restriction site polymorphisms, and amplification length differences, respectively.

Data collected from PCR-RFLP of cpDNA and cpSSR analysis results has been transformed to binary and multistate characters (see Appendix 1). In this phylogenetic part of the study, no variation within species was observed. Restriction patterns were identical for all trees of one species at all primer-enzyme combinations. The taxa groups revealed by PCR-RFLP of cpDNA are described in Appendix 2. PCR-RFLP of individual primer-enzyme combinations

distinguished from two to 14 groups of taxa. The lowest variation with only one different character was revealed by *rbcL* with *Rsa* I (restriction site) and *petB* with *Cfo* I (length difference), whereas *petB* with *Hinf* I showed the highest variation with 16 restriction sites polymorphisms.

Differentiation among genera was possible based on single primer-enzyme combinations. For example, digestion of fragment *petB* with *Cfo* I revealed two patterns and allowed the genus *Dipterocarpus* to be distinguished from all other genera. Likewise, digestion of *psaA* with *Hinf* I revealed differentiation of the genus *Vatica* from all others. However, there is no specific character to identify genus *Shorea* and *Parashorea*.

Digestion using only one primer-enzyme combination resulted in unique, species-specific patterns for 19 definite species, i.e. *Anisoptera marginata*, *Anisoptera reticulata*, *Cotylelobium lanceolatum*, *Dipterocarpus rigidus*, *Dryobalanops aromatica*, *Hopea griffithii*, *Hopea mengarawan*, *Hopea nigra*, *Hopea sangal*, *Monotes kerstingii*, *Shorea blumutensis*, *Shorea fallax*, *Shorea johorensis*, *Shorea leprosula*, *Shorea materialis*, *Shorea seminis*, *Shorea virescens*, *Upuna borneensis* and *Vatica bella*. The highest variation in this regard was generated after digestion of *petB* with *Hinf*I, separating six single different species with unique restriction sites.

Occasionally, a differentiation of single PCR-RFLP patterns was observed which was consistent with the classification of Ashton (1982) grouping species-rich genera into sections or subsections. For example, all species of section *Pachycarpeae* (genus *Shorea*) apart from *Shorea mecistopteryx* were distinguished from all other trees by a particular fragment after digestion of the *trnL-F* fragment with *Hinf* I.

3.1.1.2. CpSSR variation

Out of ten primers (*ccmp1-ccmp10*) applied to amplify cpSSR regions of Dipterocarpoideae, *ccmp4*, *ccmp5* and *ccmp9* showed no amplification product, and four primers (*ccmp1*, *ccmp3*, *ccmp7* and *ccmp8*) did not reveal any variation.

Amplification of cpSSR regions revealed length polymorphisms using *ccmp2* (seven different fragments, 136-155 bps), *ccmp6* (six different fragments, 86-98 bps), and *ccmp10* (nine different fragments, 92-109 bps) as shown in Appendix 3. The amplification revealed intergenera and interspecies variation of dipterocarps, but no variation within species.

The species in each genus *Dipterocarpus*, *Hopea*, and *Shorea* were distributed into 3 different groups with specific length variants in *ccmp2*. Specific characters for *Dipterocarpus* were well supported because this genus did not share identical fragment size with other genera.

Primer *ccmp6* distinguished five different types in genus *Shorea*. Genus *Shorea* section *Shorea* shows the highest variation with four different haplotypes, and genus *Shorea* section *Pachycarpae* has a uniform length of fragment. On the contrary, amplification using *ccmp10* revealed no interspecies variation in genus *Shorea*, whereas *Vatica* and *Hopea* have two and three different amplification lengths, respectively.

Amplification of cpSSRs resulted in new variation which was not detected by PCR-RFLPs. Some species could be identified using only one cpSSR primer, i.e.: *Anisoptera reticulata*, *Dipterocarpus grandiflorus*, *Hopea bancana*, *Hopea odorata*, *Shorea guiso*, and *Vatica granulata*. Thus, addition data from cpSSR regions will provide better information to describe the differentiation of Dipterocarpoideae.

3.1.2. Haplotype variation

The cpDNA and cpSSR variation revealed 116 polymorphic sites and a total of 46 haplotypes as shown in Appendices 1 and 4, respectively. The pairwise distance matrix between species revealed 0-44 % distance variation (see Appendix 5). Some species have the same molecular characters at PCR-RFLP and cpSSR markers resulting in identical haplotypes, namely:

- Haplotype 22: *Shorea acuminata*, *Shorea andulensis*, *Shorea mecistopteryx*, *Shorea platyclados*, and *Shorea xanthophylla*
- Haplotype 23: *Shorea acuminatissima*, *Shorea dasyphylla*, and *Shorea mutiflora*
- Haplotype 32: *Shorea macrophylla*, *Shorea pinanga*, and *Shorea stenoptera*
- Haplotype 34: *Shorea javanica*, *Shorea ovalis*, and *Shorea macroptera*
- Haplotype 46: *Vatica pauciflora*, *Vatica rassak*, and *Vatica venulosa*

As a species belonging to Monotoideae, *Monotes kerstingii* has the highest value (0.325-0.439) for all pairwise distances in comparison to the other taxa. From the indigenous species of the subfamily Dipterocarpoideae, the monotypic species *Upuna borneensis* shows the highest pairwise distance value (0.161-0.415). The results showed no haplotype variation within species, as mentioned above.

3.1.3. Phylogenetic analysis

3.1.3.1. Maximum parsimony method

Heuristic searches using *Monotes kerstingii* as an outgroup resulted in 194,570 most parsimonious trees with a length of 233 steps, a consistency index (CI) of 0.60 and a rescaled consistency index (RC) of 0.53 (Figure 3). The strict consensus tree reveals two major clades with medium to high bootstrap support. The first clade (bootstrap value=71%) comprises tribe Dipterocarpeae (*Anisoptera*, *Upuna*, *Cotylelobium*, *Vatica*, *Dipterocarpus*) and *Dryobalanops* (tribe Shoreae) as a separate group (bootstrap value= 99%; Figure 3). The monophyly of tribe Dipterocarpeae is well-supported (bootstrap value=83%) with genus *Dipterocarpus* as a sister group to the remaining genera of this tribe. *Anisoptera* and *Vatica* form well supported clades (both with bootstrap= 99%).

The second clade consists of *Hopea*, *Shorea* and *Parashorea* (bootstrap value=95%). *Hopea* is a sister group (bootstrap value=85) to *Shorea* and *Parashorea* (bootstrap value=63%). Tribe Shoreae is polyphyletic since *Dryobalanops* groups together with Tribe Dipterocarpeae. The classification of *Shorea* sections and the distinction between *Shorea* and *Parashorea* is not supported by this tree. Well supported clades (bootstrap value=98%), for example clade *Shorea fallax*, *Shorea materialis* and *Shorea virescens* are regarded as members of three different sections (section *Brachypterae*, section *Shorea*, and section *Anthoshorea*, respectively).

The maximum parsimony analysis with *Upuna borneensis* as alternative outgroup resulted in 336,388 equally parsimonious trees with length=193 steps, consistency index=0.60, and rescaled consistency index=0.56 (Figure 4). Tribe Shoreae is monophyletic with *Dryobalanops* basal to other members of this tribe. Members of tribe Dipterocarpeae do not group in one clade. The distinction between *Parashorea* and *Shorea* is also not supported.

(1) Outgroup: *Monotes kerstingii*

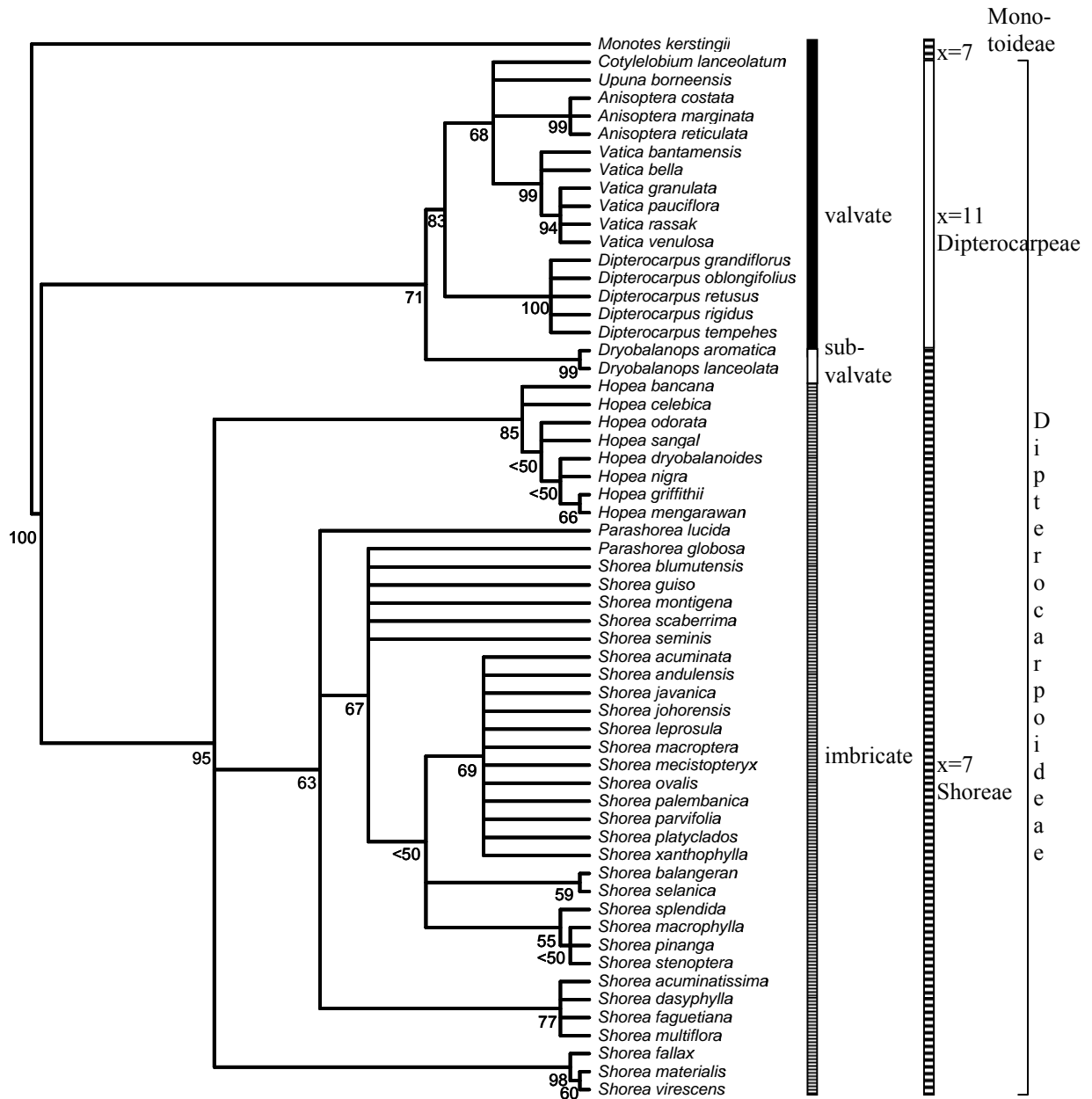


Figure 3. Strict consensus of Dipterocarpoideae (outgroup= *Monotes kerstingii*) retained from 194,570 equally parsimonious trees, length=233 steps, CI=0.60, RC=0.53. Numbers at nodes indicate bootstrap value. Typical characters, tribes and sub family are indicated.

(2) Outgroup: *Upuna borneensis*

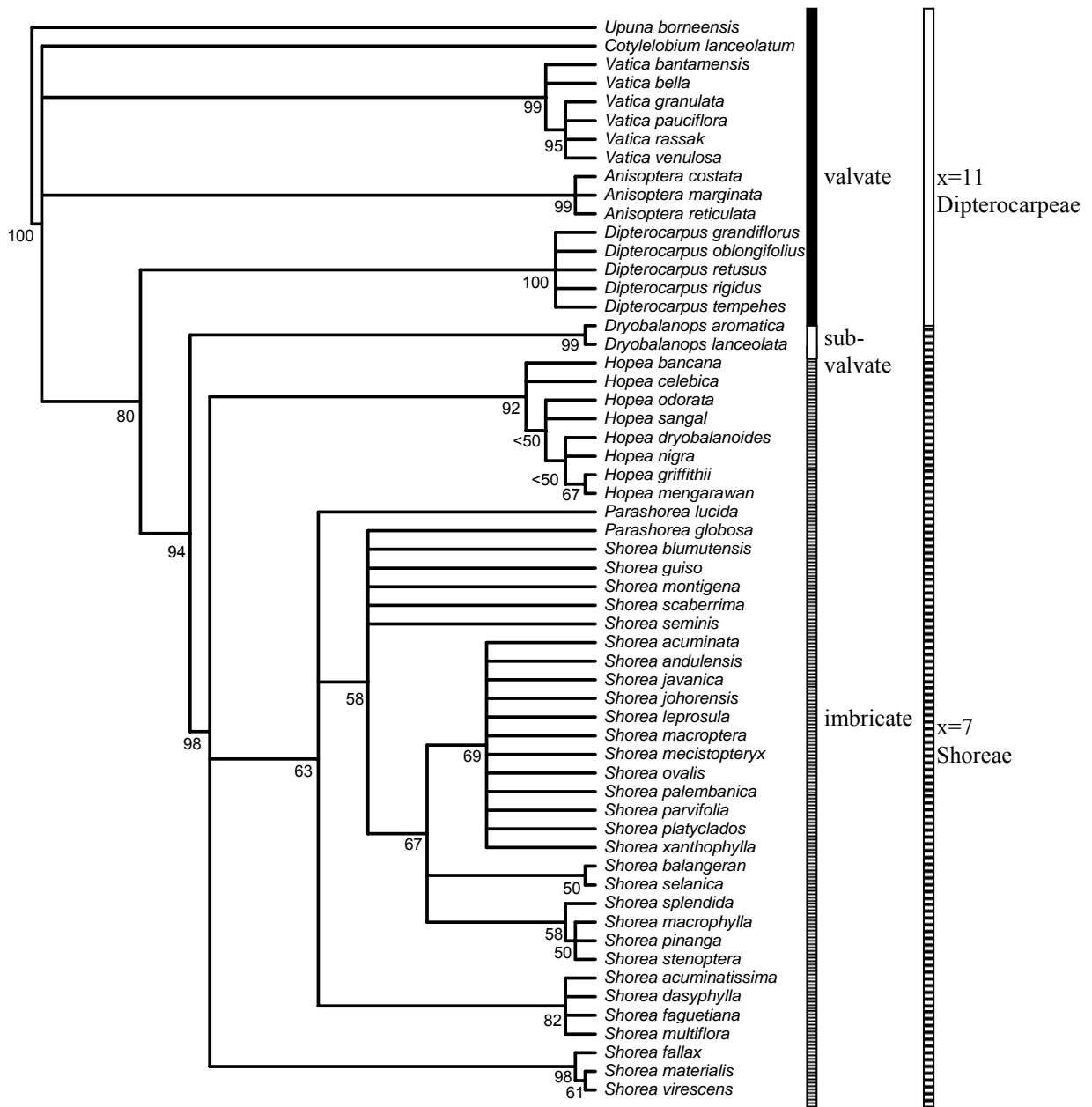


Figure 4. Strict consensus of Dipterocarpoideae (outgroup= *Upuna borneensis*) retained from 336,388 equally parsimonious trees, length=193 steps, CI=0.60, RC=0.56. Numbers at nodes indicate bootstrap value. Typical characters and tribes are indicated.

3.1.3.2. Neighbour-Joining method

With *Monotes kerstingii* as an outgroup, the neighbour-joining method reveals three major clades with high support of bootstrap value (Figure 5). The first clade consists of tribe Dipterocarpeae (bootstrap value=93%). This clade is monophyletic with *Dipterocarpus* as a sister clade to the other genera of tribe Dipterocarpeae (*Cotylelobium*, *Anisoptera*, *Upuna*, and *Vatica*). *Dryobalanops* is placed in the second major clade (bootstrap value=100%). The third major clade consists of tribe Shoreae (bootstrap value=99%) as a monophyletic clade with *Hopea* as a sister clade to *Parashorea* and *Shorea*. The distinction between *Parashorea* and *Shorea* is not supported. *Shorea fallax*, *Shorea materialis* and *Shorea virescens* are in a basal position to other *Shorea* and *Parashorea* species (bootstrap value=99%).

The neighbour-joining tree with *Upuna borneensis* as the outgroup shows that *Vatica* (bootstrap value=99%) rooted to the base with *Upuna borneensis* (Figure 6). The other taxa as one clade rooted also to the base but with lower bootstrap value (51%). Tribe Shoreae is monophyletic with *Dryobalanops* basal to other members of this tribe. Members of tribe Dipterocarpeae do not group in one clade. The distinction between *Parashorea* and *Shorea* is not supported, either.

(1) Outgroup: *Monotes kerstingii*

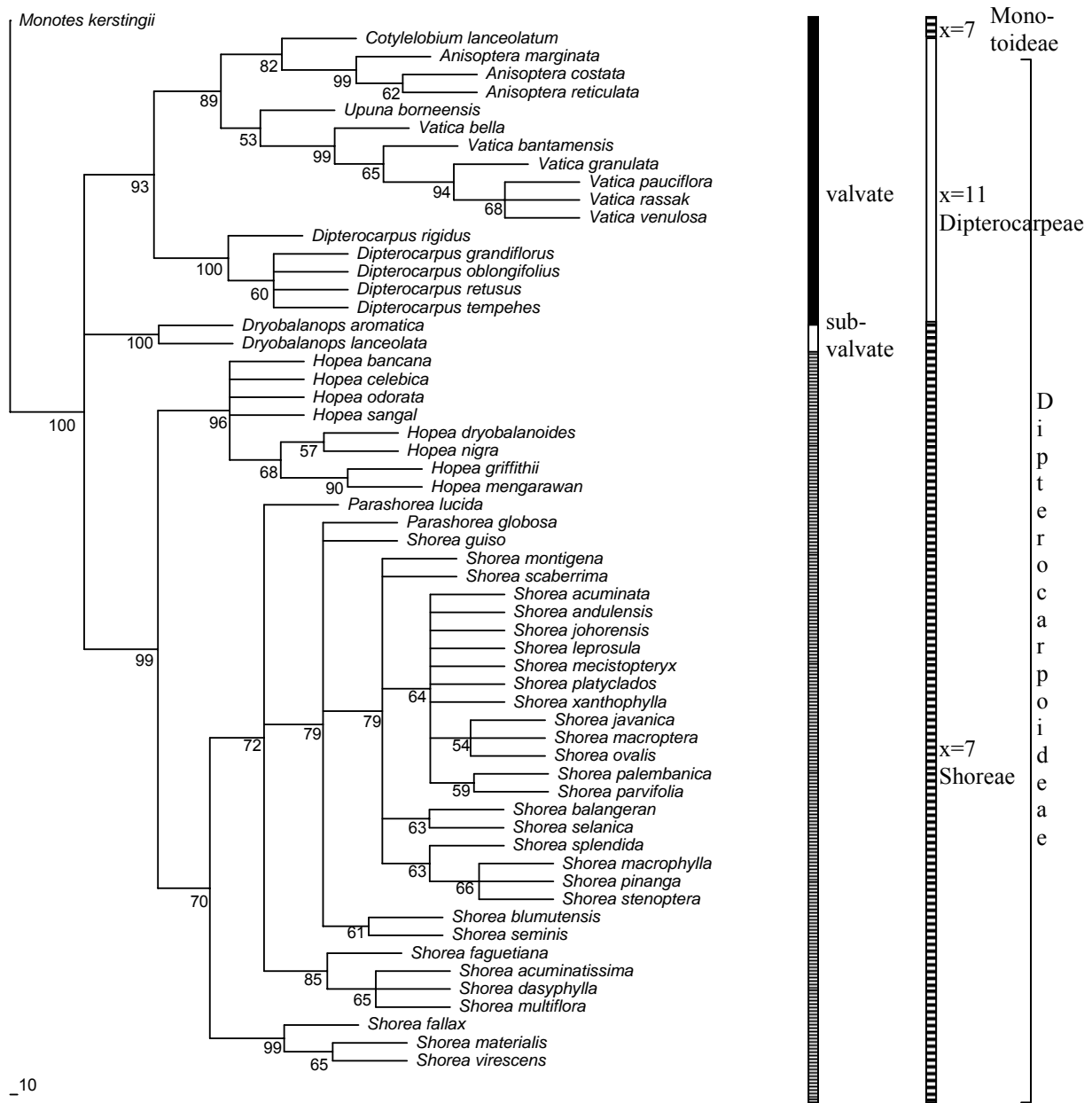
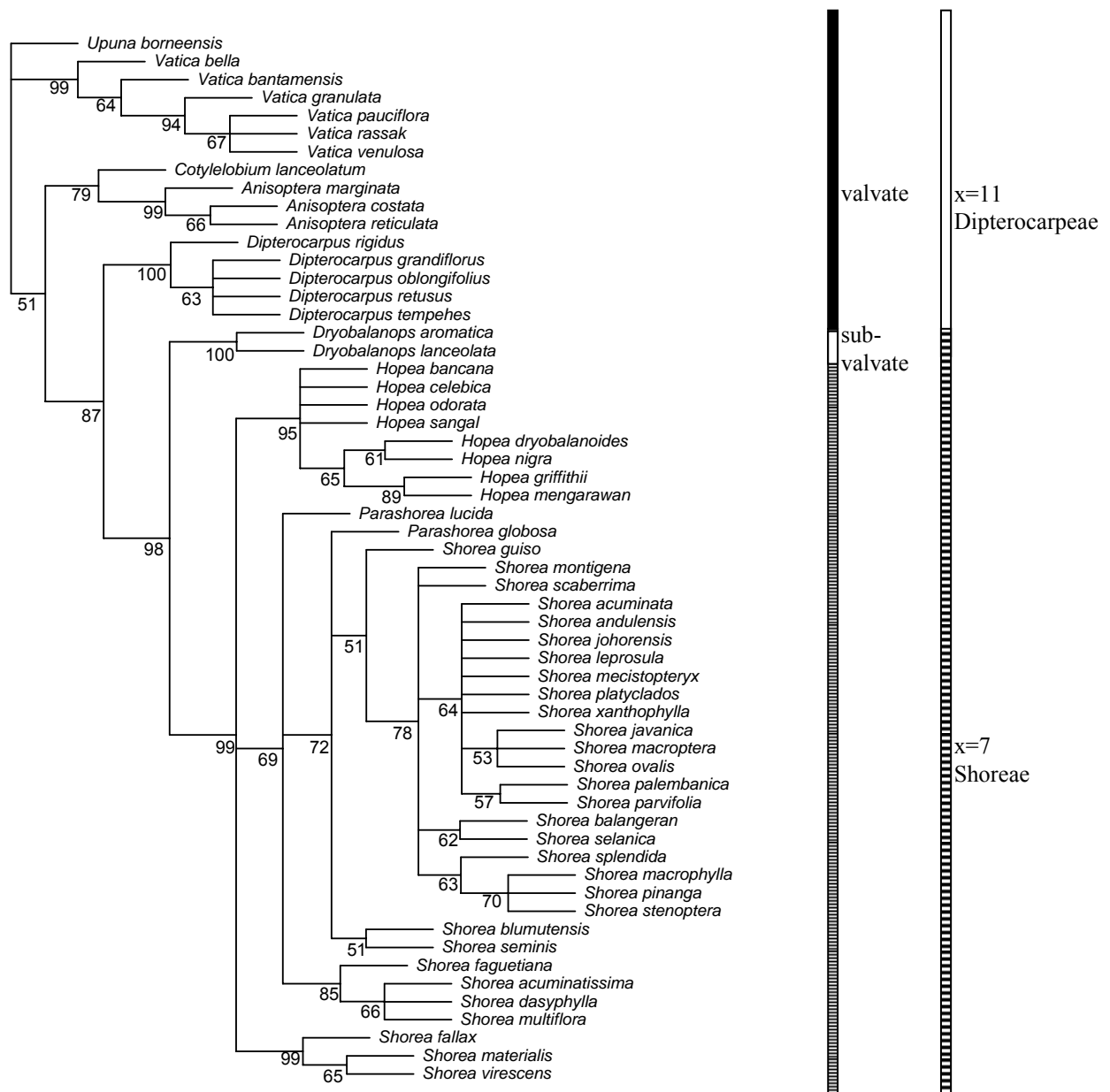


Figure 5. Neighbour-joining tree of Dipterocarpoideae (outgroup: *Monotes kerstingii*). Numbers at nodes indicate bootstrap value. Typical characters and tribes are indicated.

(2) Outgroup: *Upuna borneensis*



_10

Figure 6. Neighbour-joining tree of Dipterocarpoideae (outgroup: *Upuna borneensis*). Numbers at nodes indicate bootstrap value. Typical characters and tribes are indicated.

3.1.4. Diagnostic characters

Out of 137 characters analysed for the phylogenetic analysis, 21 characters are constant for all species, and 71 characters are diagnostic with a consistency index=100% with *Monotes kerstingii* as an outgroup (see Table 8, Figure 7 and Appendix 6). Some taxa or clades are supported by diagnostic characters. These specific molecular characters of the taxa or clades can help to unambiguously identify taxa of Dipterocarpoideae. The major clade tribe Dipterocarpeae+*Dryobalanops* can be identified by three diagnostic characters, while the second clade (*Hopea*, *Parashorea*, *Shorea*) is supported by five diagnostic characters.

A total of 16 species observed in this study are endemic to certain islands, namely Kalimantan (13 species: *Anisoptera reticulata*, *Dipterocarpus tempehes*, *Dryobalanops lanceolata*, *Shorea andulensis*, *Shorea mecistopteryx*, *Shorea scaberrima*, *Shorea macrophylla*, *Shorea pinanga*, *Shorea splendida*, *Shorea stenoptera*, *Shorea acuminatissima*, *Shorea fallax* and *Upuna borneensis*), Sumatra (one species: *Hopea bancana*) and Maluku (two species: *Shorea montigena* and *Shorea selanica*). Four of these endemic species (*Anisoptera reticulata*, *Hopea bancana*, *Shorea fallax* and *Upuna borneensis*) could be unambiguously identified by at least one diagnostic character.

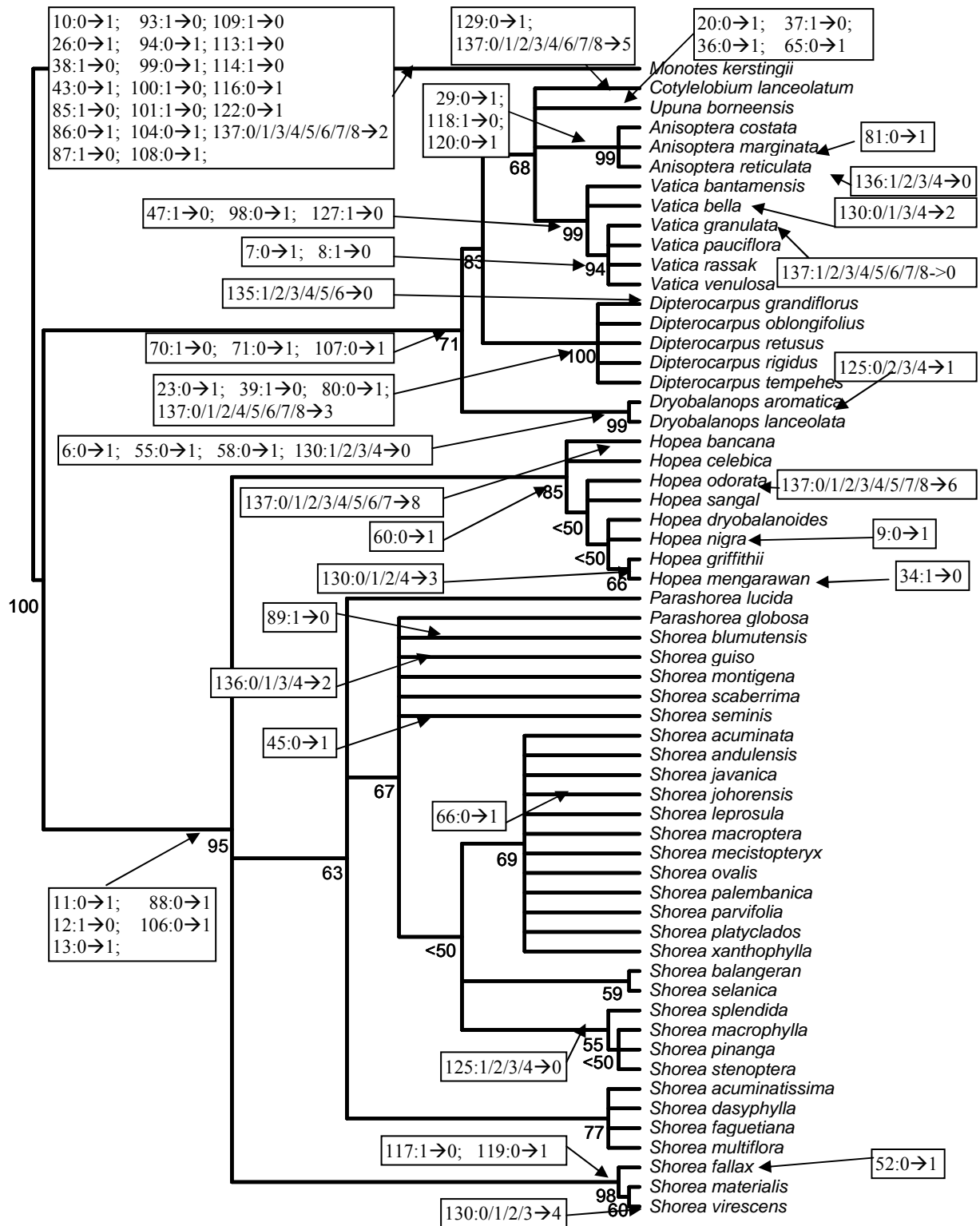


Figure 7. The diagnostic characters (CI=100%) for each taxon / clade revealed by maximum parsimony. The numbers in the boxes show the i^{th} character of the character list and the character changes (see Appendix 1 for details).

Table 8. Diagnostic characters (CI=100%) based on cpDNA and cpSSR

| Taxa | The i th character of the character list (see Appendix 1 for details) | | | | | | | | | | | | | | | | | | | | Total | | | | |
|--|--|-------|--------|-------|--|-------|-------|---------|--------|-------|-------|-------|-------|---------|--------|-------|-------|-------|--------|-------|-------|-------|-------|--------|----|
| | rbcL | | | | | petB | | | | | psaA | | | | | trnLF | | | | | | cpSSR | | | |
| | Alu I | Cfo I | Hinf I | Msp I | | Alu I | Cfo I | Hae III | Hinf I | Msp I | Rsa I | Tag I | Cfo I | Hae III | Hinf I | Msp I | Rsa I | Tag I | Hinf I | Tag I | | cpmp2 | cpmp6 | cpmp10 | |
| <i>Anisoptera</i> | | | | 29 | | | | | | | | | | | | | | 118 | | | | | | | 3 |
| <i>Anisoptera marginata</i> | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| <i>Anisoptera reticulata</i> | | | | | | | | | | | | 81 | | | | | | | | | | | 136 | | 1 |
| <i>Cotylelobium lanceolatum</i> | | | | | | | | | | | | | | | | | | | | | | | | 137 | 2 |
| <i>Dipterocarpeae + Dryobalanops</i> | | | | | | | | | | | | | | | | | | | | | | | | | 3 |
| <i>Dipterocarpus</i> | | | | | | | | | | | | | | | | | | | | | | | | | 4 |
| <i>Dipterocarpus grandiflorus</i> | | | | | | | | | | | | | | | | | | | | | | | | 137 | 4 |
| <i>Dryobalanops</i> | 6 | | | | | | | | | | | | | | | | | | | | | | | | 4 |
| <i>Dryobalanops aromatica</i> | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| <i>Hopea + Parashorea + Shorea</i> | | | | | | | | | | | | | | | | | | | | | | | | | 5 |
| <i>Hopea</i> | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| <i>Hopea bancana</i> | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| <i>Hopea griffithii + Hopea mengarawan</i> | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| <i>Hopea mengarawan</i> | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| <i>Hopea nigra</i> | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| <i>Hopea odorata</i> | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| <i>Monotes kerstingii</i> | | | | | | | | | | | | | | | | | | | | | | | | | 20 |
| | | | | | | | | | | | | | | | | | | | | | | | | | |

(Continued)

Table 8. Diagnostic characters (CI=100%) based on cpDNA and cpSSR

| Taxa | The i th character of the character list (see Appendix 1 for details) | | | | | | | | | | | | | | | | | | | Total | | | | | | |
|--|--|------|-------|------|------|------|--------|-------|------|------|------|------|--------|-------|------|------|------|-------|------|-------|-------|-------|--------|-------|--|--|
| | rbcL | | | | | | petB | | | | | | psaA | | | | | | | | trnLF | | | cpSSR | | |
| | AluI | CfoI | HinfI | MspI | AluI | CfoI | HaeIII | HinfI | MspI | RsaI | TaqI | CfoI | HaeIII | HinfI | MspI | RsaI | TaqI | HinfI | TaqI | | cpmp2 | cpmp6 | cpmp10 | | | |
| <i>Shorea blumutensis</i> | | | | | | 89 | | | | | | | | | | | | | | | | | 1 | | | |
| <i>Shorea fallax</i> | | | | | | | 52 | | | | | | | | | | | | | | | | 1 | | | |
| <i>Shorea. fallax</i> + <i>Shorea.materialis</i> + <i>Shorea virescens</i> | | | | | | | | | | | 117 | | | | | | | | | | | | 2 | | | |
| <i>Shorea guiso</i> | | | | | | | | | | | | | | | | | | | | | 136 | | 1 | | | |
| <i>Shorea johorensis</i> | | | | | | | | | 66 | | | | | | | | | | | | | | 1 | | | |
| <i>Shorea materialis</i> + <i>Shorea virescens</i> | | | | | | | | | | | | | | | | | | | 130 | | | | 1 | | | |
| <i>Shorea. macrophylla</i> + <i>Shorea pinanga</i> + <i>Shorea stenoptera</i> + <i>Shorea splendida</i> | | | | | | | | | | | | | | | | | | | 125 | | | | 1 | | | |
| <i>Shorea seminis</i> | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| <i>Upuna borneensis</i> | | | | | | | | | | | | | | 45 | | | | | | | | | 4 | | | |
| <i>Vatica</i> | | | | | | | | | | | | | | | | | | | | | | | 3 | | | |
| <i>Vatica bella</i> | | | | | | | | | | | | | | 47 | | | | 98 | 127 | | | | 1 | | | |
| <i>Vatica granulata</i> + <i>Vatica pauciflora</i> + <i>Vatica rassak</i> + <i>Vatica venulosa</i> | 7 | | | | | | | | | | | | | | | | | | | | | | 2 | | | |
| <i>Vatica granulata</i> | 8 | | | | | | | | | | | | | | | | | | | | | | 1 | | | |

3.2. Population genetic study

3.2.1. Polymorphisms of cpDNA

Haplotypes were identified based on the restriction site changes and length variations of restriction fragments and chloroplast microsatellites (see subchapter 3.1. Phylogenetic Study). Data collected from cpDNA and cpSSR analyses were transformed into binary and multistate characters. According to previous analyses of the phylogenetic relationships of Dipterocarpaceae three primer-enzyme combinations were selected for further population genetic studies on *Shorea leprosula*, *Shorea parvifolia*, *Shorea ovalis*, and *Shorea johorensis*, i.e. *rbcL* with *Alu* I and *Msp* I, and *petB* with *Rsa* I. Two cpSSR primers, i.e. *ccmp6* and *ccmp10*, are polymorphic for these species.

3.2.2. Haplotype variation

Shorea leprosula and *Shorea ovalis* showed no chloroplast DNA variation. The same haplotypes to the phylogenetic results of these species are found in all 24 investigated trees, namely haplotype 30 and 34, respectively (see Appendix 4). Haplotype variation can be found in *Shorea parvifolia* (three haplotypes: 36 as a common haplotype, 36b and 36c) and *Shorea johorensis* (two haplotypes: 29 as a common haplotype and 29b). The variation among haplotypes in *Shorea parvifolia* has been detected in the *rbcL* gene digested with *Alu* I, and an amplification product with only one base pair difference in *ccmp6* (96-97 bp) and *ccmp10* loci (98-99 bp), with a total of four diagnostic characters. Likewise, haplotype variation in *Shorea johorensis* has been found in *rbcL* digested with *Msp* I and *petB* digested with *Rsa* I, and an amplification product with only one base pair difference in *ccmp6* (96-97 bp), with a total of three diagnostic characters. Haplotypes revealed in this research have low variation with only 0.0073 - 0.0292 mean character distances among haplotypes as shown in Tables 9 and 10.

Table 9. Pairwise distance matrix between haplotypes in *Shorea parvifolia*: total character differences (below diagonal) and mean character differences (above diagonal). Haplotypes are numbered as in Appendix 4.

| Haplotypes | 36 | 36b | 36c |
|------------|----|--------|--------|
| 36 | - | 0.0219 | 0.0073 |
| 36b | 3 | - | 0.0292 |
| 36c | 1 | 4 | - |

Table 10. Pairwise distance matrix between haplotypes in *Shorea johorensis*: total character differences (below diagonal) and mean character differences (above diagonal). Haplotypes are numbered as in Appendix 4.

| Haplotypes | 29 | 29b |
|------------|----|--------|
| 29 | - | 0.0219 |
| 29b | 3 | - |

3.2.3. Genetic variation within and among populations

The species observed, i.e. *Shorea leprosula*, *Shorea ovalis*, *Shorea parvifolia* and *Shorea johorensis* do not share haplotypes among species. The distribution of each haplotype per species in each population is shown in Table 11 and Figures 8-11. *Shorea leprosula* and *Shorea ovalis* did not exhibit chloroplast DNA variation in any population. Differentiation between populations of *Shorea parvifolia* is characterized by a G_{ST} value of 0.15. In West Kalimantan there were three haplotypes, whereas in East Kalimantan there was only one. The separate population in Jambi has two haplotypes. *Shorea johorensis* populations observed in Kalimantan show a G_{ST} value of 0.25. More than one haplotype has been found only in the East Kalimantan population (see Table 11 and Figure 11).

Table 11. Number of samples per geographical origin that contain each haplotype in each species

| Geographical Origin | <i>S. johorensis</i> | | <i>S. leprosula</i> | <i>S. ovalis</i> | <i>S. parvifolia</i> | | |
|---------------------|----------------------|-----|---------------------|------------------|----------------------|-----|-----|
| | 29 | 29b | 30 | 34 | 36 | 36b | 36c |
| East Kalimantan | 4 | 2 | 6 | 6 | 6 | 0 | 0 |
| Central Kalimantan | 6 | 0 | 6 | 6 | 5 | 1 | 0 |
| West Kalimantan | 6 | 0 | 6 | 6 | 3 | 2 | 1 |
| Jambi | - | - | 6 | 6 | 5 | 1 | 0 |

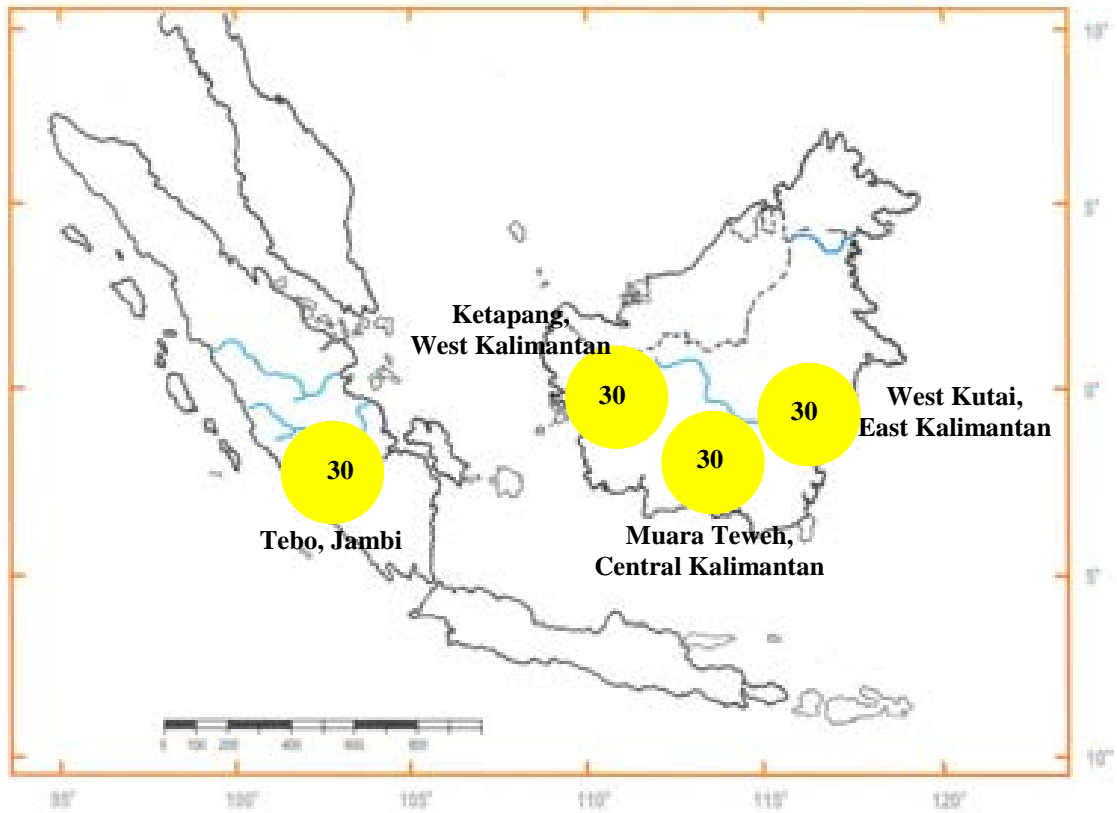


Figure 8. The haplotype distribution in four populations of *Shorea leprosula*

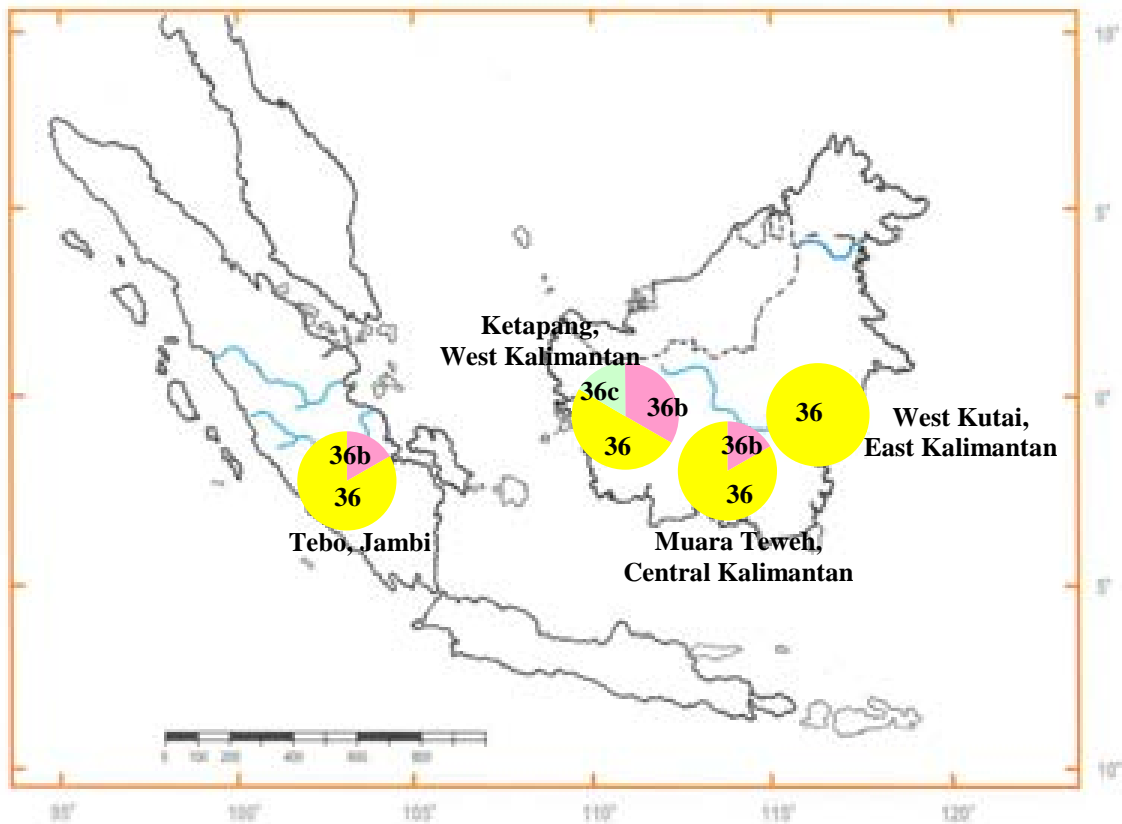


Figure 9. The haplotype distribution in four populations of *Shorea parvifolia*

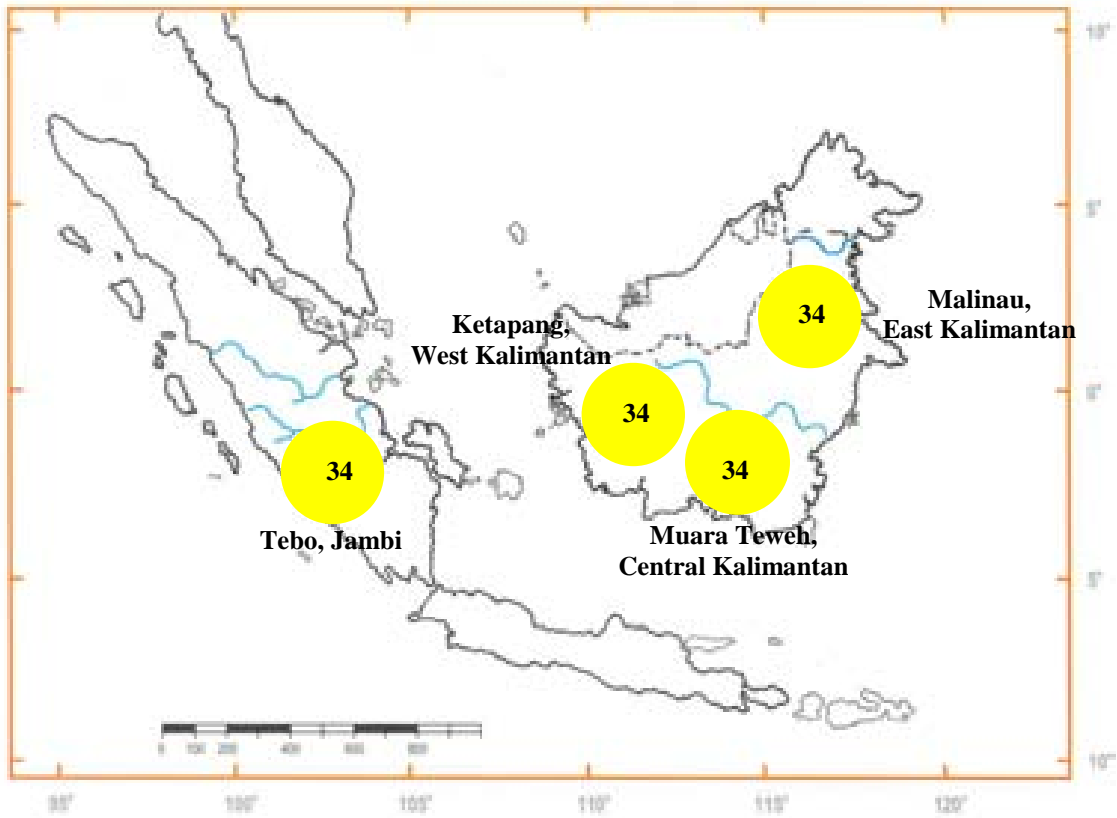


Figure 10. The haplotype distribution in four populations of *Shorea ovalis*

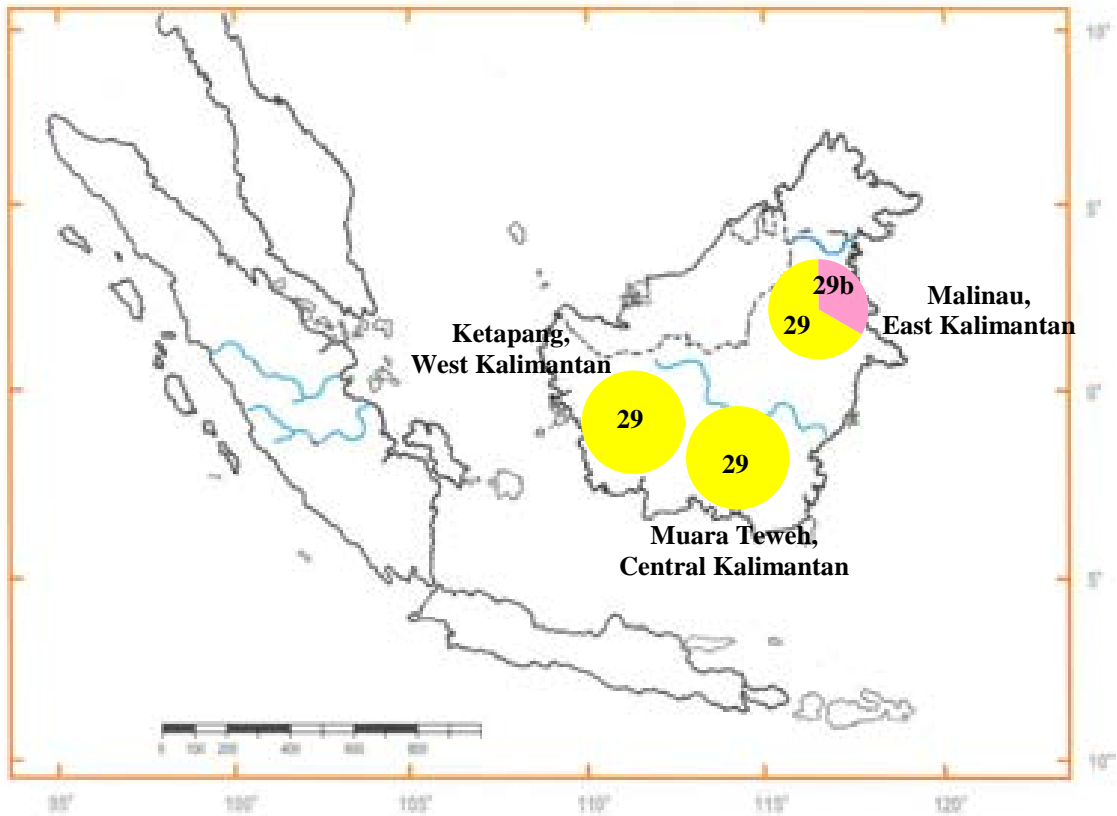


Figure 11. The haplotype distribution in four populations of *Shorea johorensis*

4. DISCUSSION

4.1. Phylogenetic study

4.1.1. Phylogenetic study based on DNA sequences and PCR-RFLP methods

Molecular phylogenetic studies of Dipterocarpaceae have been performed by means of observation of chloroplast DNA by several authors. DNA sequences were studied at the *rbcL* gene (DAYANANDAN *et al.*, 1999; MORTON *et al.*, 1999), non-coding regions of the *trnL* intron and the *trnL-trnF* intergenic spacer region (GAMAGE *et al.*, 2003; KAMIYA *et al.*, 1998) and at the *matK* gene (KAJITA *et al.*, 1998; LI *et al.*, 2004). The PCR-RFLP method has been applied on 11 specific genes by TSUMURA *et al.* (1996) and five genes / intergenic spacer regions with an addition of amplification on three chloroplast microsatellites loci in the present study.

The sequencing method at the chloroplast *rbcL* gene is widely applied for numerous species (CHASE *et al.*, 1993). This gene encodes the large subunit of ribulose-1,5-biphosphate carboxylase, the enzyme that catalyzes CO₂ fixation in the photorespiration process (MIZIORKO and LORIMAR, 1983). However, the sequence of the *rbcL* gene is usually too conservative to generate well-supported phylogenies among closely-related genera and species (RYDIN and WIKSTRÖM, 2002; SAVARD *et al.*, 1993). In comparison with *rbcL* and *atpB* genes, the *matK* gene is considered to evolve approximately three times faster (HILU *et al.*, 2003; WANG *et al.*, 1999).

As the cpDNA genome consist of 120-160 kbps polynucleotides (CLEGG *et al.*, 1994), the DNA sequences of previous observations are considered to represent relatively small parts of the cpDNA genome only, with a total of 890-1265 bps polynucleotides (GAMAGE *et al.*, 2003; KAJITA *et al.*, 1998; KAMIYA *et al.*, 1998; LI *et al.*, 2004). In the present study, the length of genes observed in five genes / intergenic spacer regions in Dipterocarpaceae varied from about 1000 bps (*psbA* gene) up to 2500 bps (*psaA* gene). Thus, the PCR-RFLP method can be applied to observe longer fragments and therefore has better representation than DNA sequencing. However, not all variation at the DNA level can be detected by PCR-RFLPs. On the other hand, DNA sequencing can detect all variation of DNA but is usually applied only to shorter fragments of DNA.

The PCR-RFLP method requires intensive laboratory work, such as multiple screenings and application of numerous genes and restriction endonucleases on each sample in order to detect

as much variation as possible. Out of 17 cpDNA gene / intergenic spacer regions tested, four genes (*rbcL*, *petB*, *psaA* and *psbA*) and one intergenic spacer region (*trnL-F*) can be applied to analyse the genetic variation of dipterocarps. The other primers resulted in unsatisfactory PCR amplifications and could not be used for the next step of genetic analysis. The variation in PCR-RFLP results has been observed by changes in the number and / or size of fragments. Out of five genes / intergenic spacer regions observed in the present study, *petB* and *rbcL* genes revealed more variations and significant results in all seven restriction enzymes employed, whereas the *psbA* gene showed less variation with only one enzyme as shown in Table 7.

Out of ten chloroplast microsatellite primers, namely *ccmp1* to *ccmp10* (WEISING and GARDNER, 1999), three primers, i.e. *ccmp2*, *ccmp6*, and *ccmp10*, were variable. Amplification of cpSSR resulted in new variations which could not be detected by PCR-RFLP studies. Thus, the additional amplification of cpSSR regions allowed for a better description of the differentiation of Dipterocarpoideae.

The observation of cpDNA and cpSSR regions (one to six samples per species) resulted in variation only between species. The absence of variation within species makes them useful for phylogenetic analysis. A total of 71 diagnostic characters (CI=100%) has been found based on PCR-RFLP of cpDNA and amplification products of cpSSR as described in Table 8, Figure 7 and Appendix 6. These characters can be applied robustly to identify unknown dipterocarp samples up to the genus level (except *Shorea* and *Parashorea*) and revealed specific haplotypes for 19 species. Furthermore, the information provided by the present research can be observed as a pre-sequencing selection about the specific informative regions for future phylogenetic analysis using the sequencing method.

4.1.2. Phylogenetic analysis

In order to comprehend the phylogenetic relationships among Indonesian dipterocarps, the analysis has been conducted with two statistical methods (maximum parsimony method and neighbour joining method) and compared using two different outgroups (*Monotes kerstingii* and *Upuna borneensis*). Heuristic searches yielded thousands of equally most parsimonious trees using both outgroups, but fewer trees have been revealed when using *Monotes kerstingii* (194,570 trees) rather than *Upuna borneensis* (336,388 trees) as an outgroup. Both outgroups revealed equal Consistency Indexes (CI=0.60). However, the phylogenetic relationships of the

genera are different. The effect of different outgroups selection is discussed in more detail in the following subchapter (4.1.4. Choice of outgroup). The discussion in this subchapter is based on phylogenetic trees using *Monotes kerstingii* as the outgroup.

Asian dipterocarps are divided into two tribes, namely tribes Dipterocarpeae and Shoreae. Tribe Dipterocarpeae can be identified by an imbricate form of ripe fruit calyx, scattered resin canals, and a basic chromosome number $x=11$, whereas tribe Shoreae has valvate ripe fruit calyx, resin canals in tangential bands, and a basic chromosome number $x=7$ as described particularly in Table 13 (ASHTON, 1982). The strict consensus tree (Figure 3) and neighbour joining tree (Figure 5) revealed that the clade of tribe Dipterocarpeae is separated from tribe Shoreae as a monophyletic clade with high support of bootstrap values, i.e. 83% and 93%, respectively.

Upuna, *Cotylelobium*, *Anisoptera* and *Vatica* are closely related and clustered in a monophyletic clade as a sister clade of *Dipterocarpus* (see Figures 3 and 5). Previous analysis also revealed the same tendency. However, the interrelationships among the genera were variable. *Vatica* has been considered to have the closest relation to *Anisoptera* or *Cotylelobium* (GAMAGE *et al.*, 2003; KAJITA *et al.*, 1998; TSUMURA *et al.*, 1996). The strict consensus tree in the present study showed the equal phylogenetic relationships of *Upuna*, *Cotylelobium*, *Anisoptera* and *Vatica*. The neighbour joining tree (Figure 5) showed that *Upuna boorneensis* is grouped together with *Vatica* with a low support by bootstrap value (53%). The close affinity between *Upuna* and *Vatica* is reflected by the similarity of their wood anatomical characters (i.e. medium-large solitary and partial multiple pores, diffuse resin canals, thick-walled fibres and lack of SiO₂), but the bark anatomy characters do not suggest the affinity (PARAMESWARAN and GOTTWALD, 1979). The classification created by MAURY (1978) also indicated the tendency for close relationships between *Upuna* and *Vatica*, which have been classified together with *Cotylelobium* and other genera of non Malesian dipterocarps in subgroup *Vaticae* (MAURY-LECHON and CURTET, 1998).

The strict consensus trees (Figures 3 and 4) showed that *Dipterocarpus* is in a monophyletic clade with the maximum value of bootstrap (100%). This is supported by four diagnostic characters revealed by primer–enzyme combinations of *rbcL* – *Hinf* I, *petB* – *Cfo* I, *petB* – *Taq* I, and amplification of *ccmp10* cpSSR locus (see Figure 7, Table 8, and Appendix 6). In comparison to other genera within the family, this genus is characterized by abundant content of dipterocarpol (BISSET *et al.*, 1966), dispersed resin canals in the wood, the largest flowers

in the family (up to eight cm across), and in general two-winged fruits (ASHTON, 1982; MEIJER, 1979). Based on anatomical characters *Dipterocarpus* is placed intermediary between the *Vatica-Cotylelobium* group and the *Shorea* group (GOTTWALD and PARAMESWARAN, 1966). This evidence corresponds with present results which placed *Dipterocarpus* in a distinct clade between the rest of the genera of tribe Dipterocarpeae and the genus *Dryobalanops* of tribe Shoreae.

Analysis of the composition of resin sesquiterpene fractions revealed that six groups can be defined in the genus *Dipterocarpus* (BISSET *et al.*, 1966) and based on the character of the fruit calyx tube HEIM (1892) classified Dipterocarpaceae into five sections. However, the overall characters showed that the species member of *Dipterocarpus* should not be divided into subgenera (ASHTON, 1982). Since phylogenetic analysis on the Sri Lankan species showed that *Dipterocarpus* endemic to Sri Lanka grouped separately in the Malesian *Dipterocarpus* cluster (GAMAGE *et al.*, 2003), further studies are needed in order to know the evolutionary history of Sri Lankan Dipterocarpaceae.

In the phylogenetic tree *Dryobalanops* is a sister group to tribe Dipterocarpeae with bootstrap support 71% (see Figure 3), but according to ASHTON (1982) this species belongs to tribe Shoreae. This contradiction is due to the fact that *Dryobalanops* has intermediate characters between tribes Shoreae and Dipterocarpeae. Wood anatomy, palynology and characters of fruit-embryo-seedling locate the genus *Dryobalanops* at an intermediary position between Shoreae-Imbricate and Dipterocarpeae-Valvate groups (MAURY-LECHON and CURTET, 1998). For example, its calyx in ripe fruit is subvalvate, and is thus close to the Valvate group, which has $x=11$ as its basic chromosome number; the basic chromosome number of *Dryobalanops* is $x=7$ as in the Imbricate group. The position of *Dryobalanops* will be discussed in detail below (see 4.1.5. Position of *Dryobalanops*).

The phylogenetic tree showed the closely related genera *Hopea*, *Shorea* and *Parashorea* grouped in one clade. *Shorea* and *Hopea* differ only in a single character, the number of aliform fruit sepals: namely three outer fruit calyx lobes are longer than two inner lobes in *Shorea*, whereas in *Hopea* two outer fruit calyx lobes are longer than three inner lobes or all five fruit calyx lobes are short and subequal (ASHTON, 1982). The occurrence of shoreic acid and oxygenated sesquiterpenes has also been considered to be specific to genus *Shorea* (BISSET *et al.*, 1971). *Parashorea* shows close relationships to *Shorea*. The position of *Parashorea* will be discussed in detail below (see 4.1.6. Position of *Parashorea*).

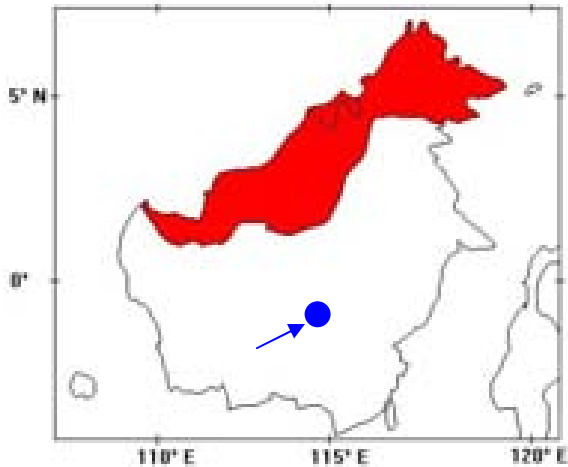
Out of 58 species observed in this study, 16 species are endemic to certain islands, namely Kalimantan (13 species), Sumatra (one species), and the Maluku archipelago (two species). Four endemic species could be identified based on diagnostic molecular genetic markers, namely *Anisoptera reticulata*, *Shorea fallax*, and *Upuna borneensis* (endemic to Kalimantan) and *Hopea bancana* (endemic to Sumatra) as described in Table 12. As the distributions of these species are confined to certain regions on the island, the molecular diagnostic characters can be treated as a basis to develop a suitable method for haplotype mapping of dipterocarps and supporting the certification of timber production by assessment of the origin of wood.

Table 12. Diagnostic characters for species endemic to Indonesia (including insular Malaysia and Brunei Darussalam in Kalimantan Island)

| <i>Natural distribution of each species (after ASHTON, 1982; NEWMANN et al., 1996a, 1998a)</i> | Diagnostic character (the 1 th character of the character list of Appendix 1) |
|--|---|
|--|---|

Anisoptera reticulata

136


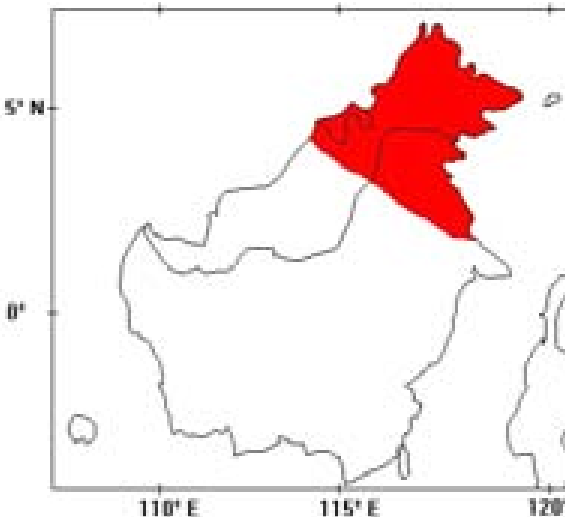


Northeast Sarawak, Brunei, Southwest Sabah

Note: The sampling location of the present study (see the pointer) is not covered by ASHTON (1982) and NEWMANN *et al.* (1996a, 1998a)

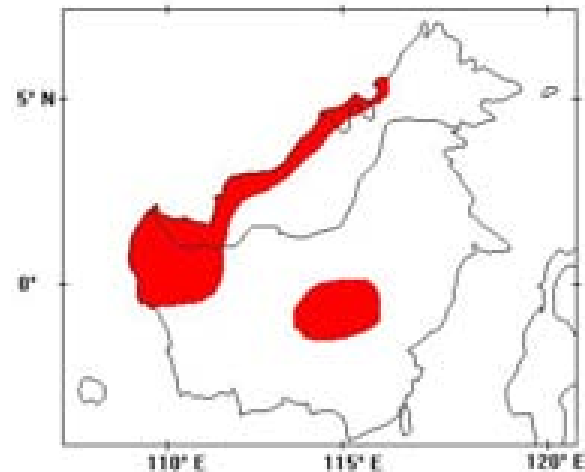
(Continued)

Table 12. Diagnostic characters for species endemic to Indonesia (including insular Malaysia and Brunei Darussalam in Kalimantan Island)

| <i>Natural distribution of each species (after ASHTON, 1982; NEWMANN et al., 1996a, 1998a)</i> | Diagnostic character (the i^{th} character of the character list of Appendix 1) |
|--|---|
| <p data-bbox="175 537 399 582"><i>Hopea bancana</i></p>  <p data-bbox="175 1097 766 1142">Bangka, Central and West Sumatra, Musala</p> | 137 |
| <p data-bbox="175 1187 367 1232"><i>Shorea fallax</i></p>  <p data-bbox="175 1792 766 1825">Northeast Sarawak, Sabah to Berau</p> | 52 |

(Continued)

Table 12. Diagnostic characters for species endemic to Indonesia (including insular Malaysia and Brunei Darussalam in Kalimantan Island)

| <i>Natural distribution of each species (after ASHTON, 1982; NEWMANN et al., 1996a, 1998a)</i> | Diagnostic character (the 1 th character of the character list of Appendix 1) |
|--|---|
| Upuna borneensis | 20, 36, 37, 65 |
|  | |
| South and West Kalimantan, East Kutai, Sarawak, Brunei Darussalam, Southwest Sabah | |

4.1.3. Character evolution

Subfamily Dipterocarpoideae has some vegetative and generative characters which are differentiated from other subfamilies (see Table 13). The species have resin canals which are abundant in many tissues, multiseriate fibers, tricolpate pollen, two to three celled ovaries, five-numerous stamens, and connate sepals. Most of the Asian dipterocarp species occur as trees in primary tropical rain forest.

The three subfamilies of Dipterocarpaceae are widely distributed, namely in Asia, Africa, and South America. As they belong to the same family, however, they should have a shared common ancestor. Therefore, the origin of dipterocarps should have existed in the past when the continents were still interconnected. More data about the historical biogeography and

palaeobotany of dipterocarps are required in order to understand the evolution of their characters and reconstruct the phylogenetic relationships of dipterocarps in detail.

Table 13. Comparison of characters of Dipterocarpaceae

| Character | Dipterocarpoideae | Monotoideae | Pakaraimoideae |
|-------------------------|--|--------------------------------------|--------------------------------------|
| Basic chromosome number | x=11 or x=7 | x=7 | n.a. |
| Sepals | imbricate or valvate, connate | imbricate, not connate | Imbricate, not connate |
| Petals | variously pubescent | variously pubescent | Glabrous |
| Stamens | five – numerous | numerous | Numerous |
| Pollen | tricolpate | tricolporate | tricolporate |
| Ovary | (two) three-celled | three (four)-celled | four (five)-celled |
| Wood anatomy: | | | |
| • Resin canals | present | not present | not present |
| • Fibres | Multiseriate | uniseriate (sometimes biseriate) | biseriate (sometimes uniseriate) |
| Architecture model | Roux, Rauh, or Massart | Troll | n.a. |
| Ecology | trees of primary rain forest and savana woodland | trees of savanna and savana woodland | trees of savanna and savana woodland |
| Geography | tropical Asia, Malesia | tropical Africa and Madagascar | tropical America |

n.a.: the data is not available

Source: ASHTON (1982); HALLÉ (1979); HALLÉ and NG (1981); LONDOÑO, *et al.* (1995); MAGUIRE and ASHTON (1977); MAURY-LECHON and CURTET (1998); VERDCOURT (1989); VILLIERS (1991).

The centre of Asian dipterocarp species diversity is located in Kalimantan, Sumatra and Peninsular Malaysia. This region belongs to Sundaland which is an extension of the Asian continent. In past ice ages, when glacial ice caps restrained water from the sea, reducing the sea level, the Sunda shelf interconnected all of the islands in this region, allowing organisms on the shelf to migrate among the modern islands of Kalimantan, Sumatra, and Java (VORIS, 2000). The facts agreed with an alternative hypothesis that the centre of dipterocarps' origin is

Borneo (MEHER-HOMJI, 1979). AWASTHI (1996) proposed that Dipterocarpaceae originated in Western Malaysia, the Malesian region west of Wallace's line, probably during the late Cretaceous - early Tertiary period.

Wallace's line is an imaginary line postulated by A. R. Wallace as the dividing line between Asian and Australian flora and fauna in the Indonesian archipelago. It passes the Lombok Strait (between Bali and Lombok Islands) and the Makassar Strait (between Kalimantan and Sulawesi), and then continues southward of the Philippines (CAMERINI, 1993). Out of ten dipterocarp genera distributed in the Malesian region, five genera, i.e. *Upuna*, *Cotylelobium*, *Neobalanocarpus*, *Dryobalanops* and *Parashorea*, are confined to west of Wallace's line. Only 31 dipterocarp species of five genera (*Anisoptera*, *Vatica*, *Dipterocarpus*, *Hopea* and *Shorea*) are also distributed east of Wallace's line. The 267 dipterocarp species of Kalimantan contrast with only seven species in Sulawesi (ASHTON, 1982), which is less than 100 km east of Kalimantan at the same equatorial latitude. The present distribution of dipterocarps in Kalimantan has no correlation with the vulnerability of some species to drought (BECKER *et al.*, 1998).

Geological evidence showed that angiosperms did not originate in the Southeast Asia region, but dispersed into the area from other regions (MORLEY, 2000). By the Mesozoic, a region composed of fragments derived from Gondwana formed a Sundaland core, and by the beginning of the Cenozoic era Southeast Asia was a composite mosaic of continental crust, island arc material and oceanic crust (PIELOU, 1979). Many African plant species dispersed into India and many of their descendants subsequently dispersed into Southeast Asia following the collision of the Indian plate with Asia in the middle Eocene (MORLEY, 1998).

Fossil records are valuable resources to trace the origin and evolution of characters of Dipterocarpaceae. But the Dipterocarpaceae fossils from the Cretaceous period seem to be incomplete (BANCROFT, 1933). Dipterocarp fossil records from the Miocene and Plio-Pleistocene epoch found in present-day Ethiopia and Somalia, respectively, are of the monotoid type and not dipterocarpoid, although the fossil's name is *Dipterocarpoxyton* (MAURY-LECHON and CURTET, 1998). Monotoids are presently living in this region, whereas dipterocarpoids are confined to Asia and the Seychelles. The numerous fossils found in the Asian region showed the dipterocarp species richness in the same epoch, namely Miocene and Plio-Pleistocene (AWASTHI, 1971; GOSH and GOSH, 1959; PRAKASH and AWASTHI, 1970). These above facts support the hypothesis that Gondwana is the region of the origin of

dipterocarps and that migration of this family occurred through India to the Malesian region (DAYANANDAN *et al.*, 1999).

The Gondwanaland origin hypothesis suggested that the specific characters of *Monotes kerstingii* are plesiomorph. In the present study, *Monotes kerstingii* is observed as an outgroup in basal position (Figure 3). Based on this phylogenetic tree, the morphological character changes in dipterocarps can be assumed as follows. Since *Monotes kerstingii* possesses several characters postulated as plesiomorph (namely: a base chromosome number of $x=7$, imbricate sepals, tricolporate pollen, uniseriate wood fibers, no resin canals and Troll's architecture model), the common derived characters (synapomorphies) can be interpreted for subfamily Dipterocarpoideae (namely tricoplate pollen, multiseriate wood fibers, presence of resin canals and architecture model of Roux, Massart and Rauh). Tribe Dipterocarpeae has the common derived character of a base chromosome number of $x=11$.

Sarcolaenaceae is a family endemic to Madagascar (CRONQUIST, 1981) and has been claimed as a family which has close affinities with Asian and African dipterocarps (ALVERSON *et al.*, 1998, DUCOUSSO *et al.*, 2004). As in other African regions, in Madagascar monotoid species are present but there are no Asian dipterocarps. Based on histological and molecular methods the last common ancestor of Dipterocarpaceae and Sarcolaenaceae has been proposed to have existed about 88 million years ago, before the separation of India and Madagascar (DUCOUSSO *et al.*, 2004). These facts, therefore, support the Gondwanaland origin hypothesis. As a consequence of this hypothesis, the shared characters of Sarcolaenaceae and Dipterocarpaceae can be proposed to be primitive, namely the absence of resin canals and valvate sepals. This evidence also supports the claim that Monotoideae possesses more plesiomorphic characters than Dipterocarpoideae.

4.1.4. Choice of outgroup

An outgroup is needed in phylogenetic analysis in order to understand the evolution of the ingroup. As the direction of ingroup evolution depends on the outgroup, the choice of the correct outgroup is an important decision. Accuracy of root placement by means of outgroup comparison depends on the plesiomorphy content of the outgroup, especially under the criterion of maximum parsimony (WHEELER, 1990). Comparison of character states in the group under study (ingroup) with homologous character states in a closely related group (outgroup) is important for knowing the descent of the characters. Evidence shows that the

application of distinct outgroups in the phylogenetic analysis can reveal different phylogenetic relationships of Dipterocarpoideae members.

The analysis rooted on *Monotes kerstingii* revealed the consequences for some morphological characters postulated as plesiomorph and the character changes of the results as described above (4.1.3. Character Evolution). Additionally, the pairwise distance matrix revealed the highest character distances of *Monotes kerstingii* to Dipterocarpoideae (see Appendix 5). The greatest total number of 20 diagnostic characters was found for this species. These diagnostic characters can be used to identify *Monotes kerstingii*. They are considered as plesiomorph in comparison with other species.

Alternatively, *Upuna borneensis* has been used as an outgroup. *Upuna borneensis* is considered primitive in several characters in comparison to other genera of tribe Dipterocarpoideae, since it shares a putative aril with *Stemonoporus*, dehiscent pericarp and cymose inflorescence with some *Vatica*, androecium with *Anisoptera*, and gynoecium with *Cotylelobium* (ASHTON, 1982). Acting on this assumption, TSUMURA *et al.* (1986) used this species as the outgroup in the phylogenetic analysis of Asian dipterocarps. In the present study, the strict consensus tree (Figure 3) showed a similar topology as in TSUMURA *et al.* (1986). Tribe Shoreae is monophyletic with *Dryobalanops* basal to other members of this tribe. Members of tribe Dipterocarpeae do not group in one clade. According to this tree, a base chromosome number of $x=7$ can be interpreted as a synapomorphy for tribe Shoreae.

Other non-Asian dipterocarps have been included in previous phylogenetic analyses, i.e. *Pseudomonotes tropenbosii*, a monotoid type occurring in Africa, and *Pakaraimaea dipterocarpea*, from the monotypic subfamily Pakaraimoideae, which is restricted to the Guyana highlands, northern South America (DAYANANDAN *et al.*, 1999; MORTON *et al.*, 1999). The placement of *Pseudomonotes* in subfamily Monotoideae is supported. This species grouped with *Monotes* and as basal for Asian dipterocarps. The phylogenetic study of the order Malvales showed close relationships between Dipterocarpaceae and this order (Alverson *et al.*, 1998), with Sarcolaenaceae basal to dipterocarps. In conclusion, since *Monotes kerstingii* has been suggested to represent more plesiomorphic characters than *Upuna borneensis*, the phylogenetic analysis with *Monotes kerstingii* as outgroup is more likely to reflect the phylogeny of subfamily Dipterocarpoideae.

4.1.5. Position of *Dryobalanops*

In the phylogenetic analysis, outgroup exchange has strong impacts on the position of *Dryobalanops*. If *Monotes kerstingii* is used as the outgroup, *Dryobalanops* groups together with tribe Dipterocarpeae and is supported with a bootstrap value of 71% (see Figure 3). *Dryobalanops* has several morphological characters which correspond to Dipterocarpeae (see Table 14), such as solitary vessels, scattered resin canals, and wood fibres with bordered pits. The alternative analysis using *Upuna borneensis* as the outgroup (Figure 4) reveals that tribe Shoreae is monophyletic with *Dryobalanops* basal to other members of this tribe. Members of tribe Dipterocarpeae do not group in one clade. *Dryobalanops* shares the basic chromosome number $x=7$ with tribe Shoreae.

Table 14. Comparison of characters among tribe Shoreae, tribe Dipterocarpeae and genus *Dryobalanops*

| Character | Tribe Shoreae | Genus <i>Dryobalanops</i> | Tribe Dipterocarpeae |
|-------------------------|----------------------|---------------------------|---|
| Basic chromosome number | $x=7$ | $x=7$ | $x=11$ |
| Sepal aestivation | imbricate | sub valvate | valvate |
| Wood anatomy: | | | |
| • Vessels | grouped | solitary | solitary (<i>Vatica</i> most spp.=grouped) |
| • Resin canals | in tangential bands | scattered | scattered |
| • Fibres | without bordered pit | with bordered pit | with bordered pit |

Source: ASHTON (1982); GOTTWALD and PARAMESWARAN (1966)

The morphological character of sepal aestivation is crucial for an understanding of changes in characters. Tribe Shoreae has imbricate sepals while tribe Dipterocarpeae has valvate sepals. *Dryobalanops* has the intermediate form of sub-valvate sepals. *Dryobalanops* is also located in the intermediary position between the Valvate-Dipterocarpi group (*Vateria*, *Vateriopsis*, *Stemonoporus*, *Vatica*, *Cotylelobium*, *Upuna*, *Anisoptera*, and *Dipterocarpus*) and Imbricate-Shoreae group (*Shorea*, *Parashorea*, *Hopea*, and *Neobalanocarpus*) based on overall morphological characters (MAURY-LECHON and CURTET, 1998). The neighbour-joining tree revealed three major clades (see Figure 5) and supports this view. *Dryobalanops* is located as

an independent clade rooting to basal (bootstrap value=100%) with two sister clades of tribes Dipterocarpeae (bootstrap value=93%) and Shoreae (bootstrap value=99%). This genus appears to build up the connecting bridge between tribe Dipterocarpeae and Shoreae.

In the present study, two *Dryobalanops* species are included, namely *Dryobalanops aromatica* and *Dryobalanops lanceolata*. They are closely related and are grouped together in one clade (bootstrap value=99%). *Dryobalanops lanceolata* has a distinct character, i.e. lanceolate leaf which revolute at the base, while in *Dryobalanops aromatica* the leaf is broadly ovate and its margin does not revolute at the base (ASHTON, 1982). The observation of resin in genus *Dryobalanops* showed that *Dryobalanops aromatica* is chemically distinct from *Dryobalanops oblongifolia* (BISSET *et al.*, 1967). In comparison to other species, *Dryobalanops aromatica* has one diagnostic character (see Table 8 and Appendix 6), namely the specific product of primer-enzyme combination of *trnL-F* and *Hinf I*.

4.1.6. Position of *Parashorea*

Classification up to the genus level of Dipterocarpoideae is well supported, except for genus *Parashorea*, which is located together with *Shorea* in the same great clade with bootstrap value=63% (see Figure 3). Both the maximum parsimony and neighbour-joining methods showed that *Parashorea lucida* is basal to *Parashorea globosa*. Previous phylogenetic studies also found that *Parashorea* is not placed separately from the *Shorea* clade (GAMAGE *et al.*, 2003; KAMIYA *et al.*, 1998; KAJITA *et al.*, 1998; TSUMURA *et al.*, 1996).

In order to distinguish *Parashorea* from *Shorea*, several morphological characters of *Parashorea* are considered to be diagnostic, such as larger lenticels of bark surface, running leaf lateral nerves at a more acute angle to the midrib, glaucous leaf undersurface, smaller stipules, plicate seedling leaves, equal sepals, and globose or verrucose with lenticellate fruit nut (ASHTON, 1982). According to SYMINGTON (1943), however, *Parashorea* has close botanical affinities to *Shorea* and it might be argued that *Parashorea* has a claim to be included in this genus. Using the neighbour-joining method, the low distance between *Parashorea* and *Shorea* species has been demonstrated using 43 and 32 *Shorea* species, respectively (KAMIYA *et al.*, 1998; GAMAGE *et al.*, 2003). The results showed that *Parashorea lucida* did not separate from the *Shorea* clade.

LI *et al.* (2004) included *Parashorea chinensis* in the earlier phylogenetic analysis conducted by KAJITA *et al.* (1998) in order to know the generic relationships of this species to Malesian

dipterocarps. This species is confined to Vietnam and southern China (SMITINAND *et al.*, 1990) and formed the only tropical rain forest in Yunnan Province, China, as the edge of the dipterocarps' distribution toward the north (YUMMING and YUANCHANG, 1996). The topology of the phylogenetic tree was consistent with that of KAJITA *et al.* (1998). *Parashorea chinensis* grouped with *Parashorea lucida* (bootstrap value=80%) as a sister clade to *Shorea ovalis* and *Shorea macroptera* with 96% of bootstrap value (LI *et al.*, 2004), whereas another *Shorea* species, namely *Shorea bracteolata*, claded together with *Hopea* and *Neobalanocarpus*. However, the conclusion about the close generic relationship within *Parashorea* is still debatable, since the analysis included only three *Shorea* species. In addition, an observation on morphological characters of *Parashorea chinensis* revealed that this species has more similarity with *Shorea* than with *Parashorea* (ZHU and WANG, 1992).

The present study analysed 36 *Shorea* species. Strict consensus parsimony trees (Figure 3) showed that *Shorea macroptera* and *Shorea ovalis* are in a distinct clade with other *Shorea* species (bootstrap value=69%), while the neighbour-joining method (Figure 5) revealed the close relationships of *Shorea macroptera* and *Shorea ovalis*, which are in one clade with *Shorea javanica*, although with low bootstrap support (57%). However, *Parashorea* species did not clade with these species.

4.1.7. Infrageneric systematics of *Vatica*

The subdivision of genus *Vatica* has been changed by several authors. Since fruits of *Vatica* are very diverse in form, some species or groups of *Vatica* have been categorized as independent genera or sections, mainly as *Sunaptea*, *Euvatica*, *Isauxis*, *Retinodendron*, and *Pachynocarpus* (MAURY-LECHON and CURTET, 1998). However, the flower, leaf and wood structures of *Vatica* are similar and the generic subdivision is unjustifiable (SYMINGTON, 1943). Later, ASHTON (1982) reduced the infrageneric classification to two sections, mainly based on fruiting calyx lobes, namely section *Vatica* (fruiting calyx lobes equal; included sections *Isauxis*, *Retinodendron*, and *Pachynocarpus*) and section *Sunaptea* (fruiting calyx lobes unequal with two lobes longer than the other three, included section *Euvatica*).

The infrageneric systematics of *Vatica* suggest that they are supported by the grouping of section *Vatica* (except *Vatica bella*) in one clade (bootstrap value=94%) as shown in Figures 3 and 12. *Vatica bantamensis* is represented by section *Sunaptea*. Although this species is endemic in Banten province, West Java, it has close resemblance in molecular structure to the

rest of *Vatica* with only three to five character changes as shown in Appendix 5. The close interrelationships of Malesian *Vatica* are also indicated by other studies which sections *Vatica* and *Sunaptea* in one clade and Sri Lankan *Vatica* in basal position (KAMIYA *et al.*, 1998; GAMAGE *et al.*, 2003).

Only one dipterocarp species, namely *Vatica rassak*, is naturally distributed both in Kalimantan and east of Wallace's line, i.e. Sulawesi and the Maluku archipelago (ASHTON, 1982), although in the early Tertiary period Sulawesi was isolated from Kalimantan by the Makassar strait resulting in strong biogeographic differences between Kalimantan and Sulawesi (MOSS and WILSON, 1998). As this species is abundant in river-bank areas, most likely the seeds were dispersed by water. In the present research, *Vatica rassak* samples originated from Maluku. However, they have identical characters *Vatica venulosa* and *Vatica pauciflora* (see Appendices 1, 4 and 5), which originate in Sumatra (Sundaland).

4.1.8. Infrageneric systematics of *Hopea*

The main diagnostic character for the subdivision of *Hopea* in Malesia is the type of leaf venation, namely section *Dryobalanoides* with truly dryobalanoid type and section *Hopea* with scalariform or subdryobalanoid type (ASHTON, 1982). The strict consensus tree showed that section *Hopea* is basal to section *Dryobalanoides* (see Figures 3 and 12), although with low bootstrap support. However, the neighbour-joining tree revealed that section *Dryobalanoides* (bootstrap value=88%) is monophyletic and rooted to section *Hopea* as shown in Figure 5. Other molecular phylogenetic studies of Dipterocarpoideae also suggest that section *Hopea* diverged earlier than section *Dryobalanoides* (GAMAGE *et al.*, 2003; KAMIYA *et al.*, 1998). However, the infrasection classification is not clearly supported.

Hopea celebica occurs east of Wallace's line and is endemic to Sulawesi Island. However, this species has a high degree of similarity, i.e. only one different characteristic (see Appendix 5) to *Hopea bancana*, an endemic species to Sumatra. *Hopea bancana* has one diagnostic characteristic as shown in Table 12 and Appendix 6, namely the specific amplification product of 109 bps at locus *ccmp10*, whereas the other species have fragment lengths of 92-108 bps.

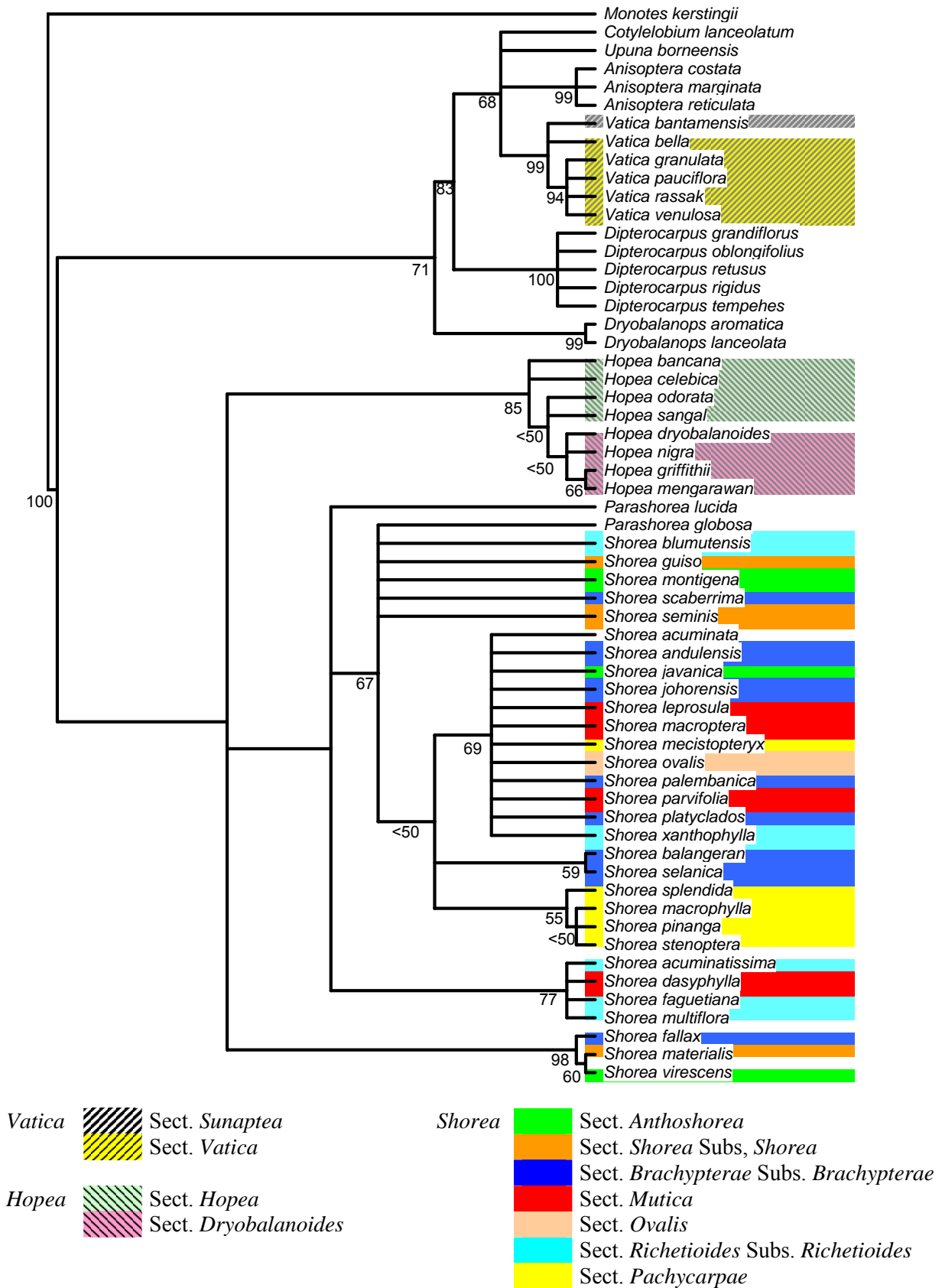


Figure 12. Section and subsection division of Dipterocarpaceae (after Ashton, 1982) mounted in the phylogenetic trees (maximum parsimony method with *Monotes kerstingii* as outgroup).

The chromosome number of some *Hopea odorata* trees is known as triploid / $2n=3x=21$ (ASHTON, 1982; JONG and KAUR, 1979; KAUR *et al.*, 1978; SOMEGO, 1978). However, this species is not placed separately from other, diploid *Hopea* species, possibly since the basic chromosome number is identical to other members of tribe Shoreae ($x=7$).

4.1.9. Infrageneric systematics of *Shorea*

The comparison of previous infrageneric classifications of *Shorea* showed various authors' opinions and revealed variations in groupings which have been reviewed by MAURY-LECHON and CURTET (1998). SYMINGTON (1943) used vernacular names to classify infrageneric relationships of *Shorea*. Furthermore, he separated *Pentacme* as a different genus from *Shorea*. Genus *Shorea* has been classified into four infrageneric groups, i.e. Balau (Selangan Batu), White Meranti (Meranti Pa'ang), Yellow Meranti (Meranti Damar Hitam) and Red Meranti groups. The main diagnostic characters are based on sapwood, bark, resin, flower, and timber properties. Moreover, field and floral characters are used for defining groups according to SYMINGTON (1943). ASHTON (1982) classified the genus *Shorea* into ten sections based on reproductive organs as the main diagnostic characters.

Infrageneric relationships of genus *Shorea* have been observed using cpDNA sequences on 44 (GAMAGE *et al.*, 2003) and 32 (KAMIYA *et al.*, 1998) species. The grouping was compared with the subgenus classification of SYMINGTON (1943) and revealed that the clades of Balau, Yellow Meranti and White Meranti are monophyletic, while the Red Meranti group is polyphyletic. Some *Shorea* species formed independent groups and one endemic to Sri Lanka, section *Doona* sensu ASHTON (1972), did not conform to the grouping and clustered separately as a monophyletic clade, whereas other *Shorea* species endemic to Sri Lanka were grouped with Malesian species (DAYANANDAN *et al.*, 1999; GAMAGE *et al.*, 2003).

Previous analysis using the PCR-RFLP method showed unclear relationships among subsections of *Shorea* (TSUMURA *et al.*, 1996). In the present study, genus *Shorea* is mainly compound of polyphyletic clades. Grouping within this genus did not closely follow the botanical classification at the section and subsection levels. Out of seven sections of *Shorea* sensu ASHTON (1982) included in this study, there is no clear grouping of sections in a single clade. However, several *Shorea* species from the same section are placed in the same clades (see Figure 12), namely:

- *Shorea macrophylla*, *Shorea pinanga*, *Shorea splendida*, *Shorea stenoptera* (Section *Pachycarpae*), with diagnostic characters revealed by PCR-RFLP of primer *trnL-F* and enzyme *Hinf* I (see Figure 7, Table 8, and Appendix 6).
- *Shorea multiflora*, *Shorea acuminatissima*, *Shorea faguetiana* (Section *Richetioides*);
- *Shorea balangeran*, *Shorea selanica* (Section *Brachypterae*).

The previous phylogenetic studies also revealed that genus *Shorea* is not monophyletic and has close affinities to *Hopea*, *Neobalanocarpus* and *Parashorea*. However, grouping pattern of the *Shorea* sections to these genera are not clear. Some *Shorea* species of section *Mutica* grouped with *Parashorea*, whereas the other members of the same section are closely related to *Neobalanocarpus* and *Hopea* (DAYANANDAN *et al.*, 1999; GAMAGE *et al.*, 2003; KAJITA *et al.*, 1998; TSUMURA *et al.*, 1996). As a large genus, *Shorea* has received much attention from systematists. The infrageneric classification of *Shorea* has been problematic, since there are inconsistencies of character grouping in some subgenera (BATE-SMITH and WHITMORE, 1959; PARAMESWARAN and GOTTWALD, 1979).

Shorea ovalis occurs as tetraploid ($2n=4x=28$; ASHTON, 1982; JONG and KAUR, 1979; KAUR *et al.*, 1978; SOMEGO, 1978). In the present study *Shorea ovalis* is not placed separately from other diploid *Shorea* species. The changes of chromosome number in tribe Shoreae, namely diploid to tetraploid (in *Shorea ovalis*) and diploid to triploid (in some *Hopea odorata*) are not clearly reflected in the phylogenetic trees. The close morphological similarity of taxa associated with great differences in the basic karyotype suggests that cytological differences of the species have been by recent fragmentation or translocations (JACKSON, 1971).

4.2. Population genetic study

4.2.1. Geographical distribution of haplotype

In order to reconstruct the geographical origin of species with genetic markers, the analysis of the geographical structure of haplotypes is useful. In the present study, the geographical distribution of haplotype has been observed for four *Shorea* species, i.e. *Shorea leprosula*, *Shorea parvifolia*, *Shorea ovalis*, and *Shorea johorensis*. Based on previous phylogenetic analyses on Dipterocarpaceae, four cpDNA genes (*rbcL*, *petB*, *psaA* and *psbA*) and two cpSSR loci (*ccmp6* and *ccmp10*) are polymorphic in genus *Shorea*. Further analysis in four populations of these *Shorea* species revealed no shared haplotype among the species.

Shorea leprosula and *Shorea ovalis* populations showed no variation and have identical haplotypes as compared to the same species found in the phylogenetic analysis, namely haplotypes 30 and 34, respectively (see Appendix 4). The four populations of *Shorea parvifolia* showed variation with three different haplotypes, i.e. 36 (as the common haplotype), 36b, and 36c. The geographical structure of haplotypes is not clear. Three haplotypes occurred in Kalimantan, whereas only two haplotypes occurred in Jambi, Sumatra. Observation on *Shorea parvifolia* revealed the low variation (4%) in *rbcL* gene digested with *Alu* I, and in loci *ccmp6* and *ccmp10*. Likewise, low variation (3%) in 3 populations of *Shorea johorensis* have been found in the *rbcL* gene digested with *Msp* I, the *petB* gene digested with *Rsa* I and at the locus *ccmp6*. Only 2 haplotypes, i.e. 29 (as the common haplotype) and 29b, have been found in the east Kalimantan population, whereas only one haplotype has been found in west and central Kalimantan populations.

These species have a wide distribution; *Shorea johorensis* and *Shorea ovalis* occur in Kalimantan, Sumatra, and Peninsular Malaysia, whereas *Shorea leprosula* and *Shorea parvifolia* occurred in the same region but also in Thailand. It has been hypothesized that a number of widespread genera and species of Dipterocarpaceae may have originated during the late Cretaceous - early Tertiary period in these regions (AWASTHI, 1996). In Kalimantan, dipterocarps have evolved in all parts of the island between sea level and about 2000 m altitude in all kinds of habitats, and it seems unlikely that speciation can be explained by adaptation to different niches (MEIJER, 1974). Theoretically, it might be assumed that the origin of a series of closely allied species was the result of only a few mutations causing changes directly in a relatively small number of characters, but leading indirectly, through the consequent changes in morphogenesis involving different plant organs, to changes in many other characters (FEDOROV, 1966). Observation of all natural distributions is needed in order to confirm the evolutionary steps of these species, including the chloroplast DNA evolution.

The geographical structure of haplotypes is not always reflected by the natural distribution of certain species. The phylogeographic structure of species observed in white oaks / *Quercus* spp. (DUMOLINE-LAPÈGUE *et al.*, 1997a; PETIT *et al.*, 2002a, 2002b) and *Fagus sylvatica* (DEMASURE *et al.*, 1996) at the regional scale in Europe, showed the interrelationships between haplotype distribution and the origin of the samples. The molecular method for testing the geographic origin of such species has also been developed (DEGUILLLOUX *et al.*, 2003, 2004). On the contrary, observation on *Prunus spinosa* populations revealed

incongruency between the phylogeny of haplotypes and their geographic locations on the European continent (MOHANTY *et al.*, 2002). The colonization history of some tropical species is also indicated by the distribution of haplotypes. *Cedrela odorata*, a tropical tree occurred in Mesoamerica, has five haplotypes and phylogenetically grouped into three distinct lineages (CAVERS *et al.*, 2003), whereas observation of *Cyclobalanopsis glauca* populations in Taiwan and East Asia revealed 13 haplotypes, and it can be concluded that the derived cpDNA variations are confined only to Taiwan (HUANG *et al.*, 2002).

4.2.2. Intraspecific variation

In the phylogenetic study, one to six samples of each *Shorea* species have been observed and no haplotype variation within species has been found. The chloroplast DNA showed low intraspecific variation and only moderate differentiation in two *Shorea* species, i.e. *Shorea parvifolia* ($G_{ST}=0.15$) and *Shorea johorensis* ($G_{ST}=0.25$). The conservative evolution of cpDNA is a factor which tends to limit the amount of useful sequence variation that can be found intraspecifically, or among very closely related species (BIRKY, 1995)

In comparison to the examination of chloroplast DNA, the genetic diversity observation on *Shorea* species showed higher variation using isozyme marker (in multiple populations) with $He=0.41$ in *Shorea leprosula* (LEE *et al.*, 2000b) and nuclear microsatellite markers (in a single population) with $He=0.69-0.71$ in *Shorea leprosula* (NAGAMITSU, *et al.*, 2001; NG *et al.*, 2004; RIMBAWANTO and ISODA, 2001), $He=0.62-0.67$ in *Shorea ovalis* (NG *et al.*, 2004) and $He=0.33-0.85$ in *Shorea parvifolia* (TAKEUCHI *et al.*, 2004).

The spatial genetic structures analysis at allozyme and nuclear microsatellite loci for *Shorea leprosula* and *Shorea ovalis* showed significant spatial genetic structure for short distances in small, medium and big diameter at breast height (dbh)-classes (NG *et al.*, 2004). The decrease of spatial genetic structure was detected from smaller- to larger-diameter classes. Furthermore, isozyme analysis on *Shorea leprosula* revealed that populations in Peninsular Malaysia have low genetic distances (0.14-0.17) to a population in Lambir, Sarawak, but the clustering among populations within Peninsular Malaysia did not reflect geographical proximity and gave few insights into the genetic relatedness of the populations (LEE *et al.*, 2000b).

4.3.Perspective

The present phylogenetic study based on observations of chloroplast DNA resulted in good agreement with the taxonomic division of nine dipterocarp genera in Indonesia. The results might create the opportunity to establish the classification of Dipterocarpoideae also within genera. Therefore, the taxonomic division based on morphological characters should be reviewed together with molecular markers.

Molecular data can make valuable contributions the understanding of the phylogenetic relationships based on present dipterocarp samples in addition to information from fossil records. Fossil records have an important role in tracing the evolutionary steps and past plant distributions which cannot be found using only contemporary taxa. Therefore, efforts to achieve a better understanding of relationships among present taxa would be better served by integrating dipterocarp fossil taxa into comprehensive phylogenetic analyses of Dipterocarpaceae. Ancient DNA can give direct information about the pace and pattern of genetic changes. Since undoubted dipterocarp fossils have been collected from a wide area, i.e. African and Asian regions, the inclusion of fossil materials in the genetic analysis is possible. However, a challenging problem would likely concern the molecular method, namely how to develop a suitable method to analyse an adequate the amount of DNA from dipterocarp fossil materials. Even in the present study the DNA extraction method from dry leaf mature tissues for some samples was problematic in the initial phase and had to be adjusted, since the DNA had probably partially degenerated. In order to solve this problem, molecular methods to recover ancient chloroplast DNA of fossil plants from Holocene and Pleistocene sediments have been improved (SUYAMA *et al.*, 1996; WILLERSLEV *et al.*, 2003). More attention must be paid to fossils and morphological features, with future efforts directed at the integration of fossils into phylogenetic analyses based on both morphological and molecular data.

Variation within species in the phylogenetic study has not been found, whereas the population genetic study of four *Shorea* species (*Shorea leprosula*, *Shorea parvifolia*, *Shorea ovalis* and *Shorea johorensis*) revealed only low haplotype variations. The absence of variation within species makes cpDNA markers useful for phylogenetic analysis. On the other hand, the lack of or low haplotype variation among populations rules out the use of the developed molecular marker as a tool to prove the geographical origin of individual trees. However, the diagnostic characters found in the present study can be used to develop a taxa identification method at

the species level. Furthermore, in this study four endemic species, namely *Anisoptera reticulata*, *Shorea fallax*, and *Upuna borneensis* (endemic to Kalimantan) and *Hopea bancana* (endemic to Sumatra) can be distinguished using diagnostic molecular genetic markers. The relationship between the specificity of the natural distribution and diagnostic characters of these species can be used to develop a suitable method for haplotype mapping of dipterocarps and a marker system that allows identification of the origin of wood or timber products from the various species. The identification of wood or timber products is important to certify that the timber has been legally harvested only from sustainably managed forest areas.

Methods for timber identification and tracking from the logging area through the chain of custody until their conversion into products have been used in the forest products industry for many decades. Conventional labels with barcodes are the leading method for labelling processed wood products but conventional paint, chisel labels, and hammer brands remain more common for labelling logs (DYKSTRA *et al.*, 2003). The use of molecular markers as an alternative identification label is able to solve falsification problems and serve forensic purposes since the identification is based on wood tissues. Therefore, the development of the molecular genetic method for wood and timber products of dipterocarps is indispensable.

SUMMARY

The tropical tree family Dipterocarpaceae is the most important family of forest trees in natural and close-to-nature forests in Southeast Asia. Dipterocarps form dominant elements within the rain forest tree flora in this region. More than 300 dipterocarp species are native to Indonesia. Kalimantan is the diversity centre of the family with more than 260 species, including 155 endemics found only on this island. Chloroplast DNA (cpDNA) variation of dipterocarp species from Indonesia has been studied by means of PCR-RFLP and cpSSR techniques in order to infer a molecular phylogeny of Asian Dipterocarpaceae (subfamily Dipterocarpoideae) and to characterize the haplotypic diversity of four *Shorea* species populations in Kalimantan and Sumatra.

The samples for the phylogenetic study consisted of 129 trees belonging to 58 species in all nine genera of the Dipterocarpaceae native to Indonesia, i.e. *Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Dryobalanops*, *Hopea*, *Shorea*, *Parashorea*, *Vatica* and *Upuna*. Samples were collected from one to seven single trees for each species in natural forests, arboreta and botanical gardens. Preliminary species identification was based on leaf morphological characters. *Monotes kerstingii* (Dipterocarpaceae; Monotoideae) from Benin (Africa) was used as an outgroup. Four genes (*rbcL*, *petB*, *psaA* and *psbA*) and one intergenic spacer region (*trnL-F*) were amplified to analyse the genetic variation of dipterocarps. The amplified regions were digested by seven restriction enzymes, i.e. *Alu* I, *Cfo* I, *Hae* III, *Hinf* I, *Msp* I, *Rsa* I, and *Taq* I. Variation was observed as changes in the number and / or size of fragments (PCR-RFLP technique). Variation was detected for all fragments after digestion with particular restriction enzymes, but the number of enzymes revealing variation varied from one (*psbA*) to seven (i.e. all; *petB* and *rbcL*). Out of ten chloroplast microsatellite primers (cpSSRs) tested, three primers, i.e. *ccmp2*, *ccmp6*, and *ccmp10* were variable. Amplification of cpSSRs resulted in a new variation which was not detected by PCR-RFLP studies.

The cpDNA variation revealed a total of 116 site changes and 46 different haplotypes. In this part of the study, no variation was observed within species. The absence of variation within species makes the technique useful for phylogenetic analysis. A total of 71 diagnostic characters (CI=100%) were found based on PCR-RFLPs of cpDNA and amplification of cpSSRs. These characters can be robustly applied to identify unknown dipterocarp samples up

to the genus level (except *Shorea* and *Parashorea*) and revealed specific haplotypes for 19 species based on a single character only.

The phylogenetic analysis was conducted with two statistical methods, namely maximum parsimony method (MP) and neighbour-joining method (NJ), and using two different outgroups (*Monotes kerstingii* and *Upuna borneensis*). Heuristic searches yielded thousands of equally most parsimonious trees using both outgroups, but fewer trees were revealed when using *Monotes kerstingii* (194,570 trees) rather than *Upuna borneensis* (336,388 trees) as outgroup. Both outgroups revealed an equal Consistency Index (CI=0.60). However, the phylogenetic relationships of the genera were found to be different depending on the outgroup.

The MP and NJ trees using *Monotes kerstingii* as outgroup revealed that a clade of tribe Dipterocarpeae (*Anisoptera*, *Upuna*, *Cotylelobium*, *Vatica*, *Dipterocarpus*) is separated from most genera of tribe Shoreae (*Hopea*, *Parashorea*, *Shorea*) as a monophyletic clade with high support (bootstrap values, 83% and 93%, respectively). Within tribe Dipterocarpeae, genus *Dipterocarpus* is a sister group to the remaining genera of this tribe. *Anisoptera* and *Vatica* form well-supported clades (both MP and NJ trees with bootstrap=99%). The morphological character form of sepal aestivation appears to closely correspond to molecular character changes. Tribe Shoreae has imbricate sepals while tribe Dipterocarpeae has valvate sepals. *Dryobalanops* has an intermediate form (sub-valvate sepals). *Dryobalanops* is also located in the intermediary position between the Valvate-Dipterocarpi group (*Vatica*, *Cotylelobium*, *Upuna*, *Anisoptera*, and *Dipterocarpus*) and the Imbricate-Shoreae group (*Shorea*, *Parashorea*, and *Hopea*). This is most clearly shown by the NJ tree which revealed three major clades: *Dryobalanops* is located as an independent clade rooted to the basis (bootstrap value=100%) with two sister clades of tribes Dipterocarpeae (bootstrap value=93%) and Shoreae (bootstrap value=99%). This genus appears to build up the connecting bridge between tribe Dipterocarpeae and Shoreae. The remaining clade comprises the Imbricate-Shoreae group. *Hopea* is a sister group (bootstrap value MP=85% and NJ=96%) to *Shorea* and *Parashorea* (bootstrap value MP=63% and NJ=70%). Tribe Shoreae is polyphyletic since *Dryobalanops* groups together with Tribe Dipterocarpeae. The classification of *Shorea* sections and the distinction between *Shorea* and *Parashorea* is not supported by the trees. Well-supported clades often belong to different sections according to the most widely accepted classifications. For example, clade *Shorea fallax*, *Shorea materialis* and *Shorea*

virescens is well-supported (bootstrap value MP=98% and NJ=99%), but the species were classified by Ashton in section *Brachypterae*, section *Shorea*, and section *Anthoshorea*, respectively. The analysis rooted on *Monotes kerstingii* suggests some morphological characters to be plesiomorph and morphological character changes in dipterocarps as follows. Important plesiomorph characters are a basic chromosome number of $x=7$, imbricate sepals, tricolporate pollen, uniseriate wood fibers, no resin canals and Troll's architecture model. Therefore, common derived characters (synapomorphies) can be seen in subfamily Dipterocarpoideae such as tricolporate pollen, multiseriate wood fibers, presence of resin canals and the architectural model of Roux, Massart and Rauh. Tribe Dipterocarpeae has the common derived character of a basic chromosome number of $x=11$. The pairwise distance matrix revealed the highest character distances of *Monotes kerstingii* to Dipterocarpoideae. Twenty diagnostic molecular characters, much more than for any other species, were found for this species.

Alternatively, *Upuna boorneensis* was used as an outgroup following previous studies using comparable tools. *Upuna boorneensis* is considered primitive in comparison to other genera of tribe Dipterocarpoideae. The change of the outgroup results in a different topology of the phylogenetic tree. Tribe Shoreae is monophyletic with *Dryobalanops* basal to other members of this tribe. Members of tribe Dipterocarpeae do not group in one clade. The distinction between *Parashorea* and *Shorea* is also not supported. According to the MP tree, a basic chromosome number of $x=7$ can be interpreted as a synapomorphy for tribe Shoreae. In conclusion, since *Monotes kerstingii* has been suggested to represent more plesiomorphic characters than *Upuna borneensis*, the phylogenetic analysis with *Monotes kerstingii* as the outgroup is more likely to reflect the phylogeny of subfamily Dipterocarpoideae.

Out of 16 endemic species observed in this study, four endemic species were identified based on diagnostic molecular genetic markers, namely *Anisoptera reticulata*, *Shorea fallax*, *Upuna borneensis* (endemic to Kalimantan) and *Hopea bancana* (endemic to Sumatra). As the distributions of these species are confined to certain regions on the island, the molecular diagnostic characters can be treated as a basis to develop a suitable method for haplotype mapping of dipterocarps.

The objective of the population genetic study was to observe haplotypic diversity of four *Shorea* species (*Shorea leprosula*, *Shorea parvifolia*, *Shorea ovalis* and *Shorea johorensis*) within and among populations in Kalimantan and Sumatra using chloroplast DNA. Based on

previous analyses (see above), three primer-enzyme combinations were chosen for PCR-RFLP surveys, i.e. *rbcL* with *Alu* I and *Msp* I, and *petB* with *Rsa* I. In addition, two chloroplast primers, i.e. *ccmp6* and *ccmp10*, were investigated. *Shorea leprosula* and *Shorea ovalis* populations did not show any chloroplast DNA variation at the observed markers. However, low variation was observed in *Shorea parvifolia* (three haplotypes, $G_{ST}=0.15$) and in *Shorea johorensis* (two haplotypes, $G_{ST}=0.25$). The haplotype distribution did not reveal a straightforward differentiation between populations from Kalimantan or Sumatra.

This study represents the first molecular phylogeny of the Dipterocarpaceae entirely based on material from the family's diversity centre in Indonesia. The usefulness of cpDNA variation for phylogenetic studies is confirmed, and the conventional taxonomic classification of Indonesian dipterocarps is supported up to the genus level. However, there is in general no close correspondence between the observed molecular variation and the taxonomic distinction of sections and subsections within species-rich genera, in particular the genus *Shorea*. Only low levels of genetic diversity within species were observed in this initial survey.

ZUSAMMENFASSUNG

Die tropische Baumfamilie der Dipterocarpaceen ist die wichtigste Familie von Waldbäumen in natürlichen oder naturnahen Wäldern in Südostasien. Dipterocarpaceen bilden dominante Elemente innerhalb der Regenwälder in dieser Region. Mehr als 300 Arten der Dipterocarpaceen sind in Indonesien natürlich verbreitet. Kalimantan ist das Zentrum mit der größten Diversität mit mehr als 260 Arten, 155 davon sind endemisch. Variation der Chloroplasten-DNA (cpDNA) der Dipterocarpaceen-Arten aus Indonesien wurde mittels PCR-RFLP- und cpSSR- Techniken untersucht, um die molekulare Phylogenie der asiatischen Dipterocarpaceen (Unterfamilie Dipterocarpoideae) herzuleiten, und um die haplotypische Diversität von vier *Shorea*-Arten Populationen in Kalimantan und Sumatra zu charakterisieren.

Die Proben für die phylogenetischen Studien bestanden aus Material von 129 Bäumen, die zu 58 Arten aus allen neun Gattungen der natürlich vorkommenden Dipterocarpaceen in Indonesien gehören, nämlich *Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Dryobalanops*, *Hopea*, *Shorea*, *Parashorea*, *Vatica* und *Upuna*. Die Proben wurden von eins bis sieben Einzelbäumen von jeder Art in natürlichen Wäldern, Aboreten und botanischen Gärten gesammelt. Die vorläufige Artenidentifikation basierte auf den morphologischen Merkmalen der Blätter. *Monotes kerstingii* (Dipterocarpaceen; Monotoideae) aus Benin (Afrika) wurde als Außengruppe herangezogen. Vier Gene (*rbcL*, *petB*, *psaA* und *psbA*) und ein nicht-kodierender Bereich (*trnL-F*) wurden amplifiziert, um die genetische Variation von Dipterocarpaceen zu analysieren. Die vervielfältigten Regionen wurden mit sieben Restriktionsenzymen, *Alu* I, *Cfo* I, *Hae* III, *Hinf* I, *Msp* I, *Rsa* I, und *Taq* I, verdaut. Mit Hilfe der PCR-RFLP Technik wurde die genetische Variation als Veränderungen in der Anzahl und / oder der Größe der Fragmente untersucht. Die Variation aller Fragmente wurden nach Verdau mit den einzelnen Restriktionsenzymen detektiert, aber die Zahl der Enzyme, die Variation zeigten, variierte von einem Enzym für Gen *psbA* zu sieben Enzymen für Gen *petB* und *rbcL*. Von zehn getesteten Chloroplasten-Mikrosatelliten-Primern-Paaren (cpSSRs) waren drei Primer-Paare, *ccmp2*, *ccmp6*, und *ccmp10*, variabel. Die Amplifikation von cpSSRs ergab neue Variation, welche nicht bei PCR-RFLP-Studien entdeckt worden war.

Insgesamt wurden 116 Merkmale (Längen und Schnittstellenunterschiede) als Variationen der cpDNA und 46 verschiedene Haplotypen gefunden. In diesem Teil der Studie konnte keine

genetische Abweichung innerhalb der Arten entdeckt werden. Das Fehlen von Variation innerhalb der Arten macht diese Technik nützlich für phylogenetische Analysen. Insgesamt wurden 71 diagnostische Merkmale (CI=100%) basierend auf PCR-RFLPs von cpDNA und der Amplifikation von cpSSRs gefunden. Diese Marker können sicher angewendet werden, um unbekannte Dipterocarpaceen-Proben bis zum Gattungsniveau (außer *Shorea* und *Parashorea*) zu identifizieren und um spezifische Haplotypen für 19 Arten basierend auf einem einzigen Marker zu zeigen.

Die phylogenetische Analyse wurde mit zwei statistischen Methoden, nämlich "Maximum Parsimony Method" (MP) und "Neighbour-joining Method" (NJ) durchgeführt, wobei zwei verschiedene Außengruppen (*Monotes kerstingii* und *Upuna borneensis*) benutzt wurden. Heuristische Untersuchungen ergaben tausende von gleich langen Bäumen ("equally most parsimonious tree") bei Benutzung von beiden Außengruppen. Weniger Bäume aber wurden gefunden, wenn *Monotes kerstingii* (194.570 Bäume) im Vergleich zu *Upuna borneensis* (336.388 Bäume) gewählt wurde. Beide Außengruppen zeigten den gleichen Konsistenz Index (CI=0,60). Jedoch zeigte sich, dass die phylogenetischen Beziehungen der Genera je nach Außengruppe unterschiedlich waren.

Die MP und NJ Bäume bei Benutzung von *Monotes kerstingii* als Außengruppe zeigten, dass Tribus Dipterocarpeae (*Anisoptera*, *Upuna*, *Cotylelobium*, *Vatica*, *Dipterocarpus*) als monophyletische Gruppe von den meisten Gattungen von Tribus Shoreae (*Hopea*, *Parashorea*, *Shorea*) getrennt ist (Bootstrap-Wert, 83% und 93%). Innerhalb von Tribus Dipterocarpeae, Gattung *Dipterocarpus* ist eine Schwestergruppe zu den verbleibenden Gattungen dieser Tribus. *Anisoptera* und *Vatica* bilden eine gut unterstützte Gruppe (beide MP- und NJ-Bäume zeigen gleichen Bootstrap-Wert=99%). Das morphologische Merkmal der Kelchblattstruktur scheint eng mit den molekularen Merkmalenänderungen zu korrespondieren. Tribus Shoreae hat imbricate Kelchblätter, während die Tribe Dipterocarpeae valvate Kelchblätter besitzt. *Dryobalanops* hat eine Zwischenform (sub-valvate Kelchblätter). *Dryobalanops* ist ebenso in einer intermediären Stellung zwischen der Valvate-Dipterocarpi-Gruppe (*Vatica*, *Cotylelobium*, *Upuna*, *Anisoptera*, und *Dipterocarpus*) und der Imbricate-Shoreae-Gruppe (*Shorea*, *Parashorea*, und *Hopea*) positioniert. Es zeigt sich sehr eindeutig, dass der NJ-Baum drei Hauptgruppen umfasst. *Dryobalanops* gruppiert werde mit Tribus Dipterocarpeae (Bootstrap-Wert=93%) noch mit Tribus Shoreae (Bootstrap-Wert=99%), sondern bildet eine unabhängige Gruppe (Bootstrap-Wert=100%). Diese Gattung

nimmt eine intermediäre Position zum Tribus Dipterocarpeae und Shoreae ein. Die übrig bleibende Gruppe schließt die Imbricate-Shoreae-Gruppe ein. *Hopea* ist eine Schwester-Gruppe (Bootstrap-Werte MP=85% und NJ=96%) zu *Shorea* und *Parashorea* (Bootstrap-Werte MP=63% und NJ=70%). Tribus Shoreae ist polyphyletisch, denn *Dryobalanops* gruppiert zusammen mit Tribus Dipterocarpeae. Die Klassifikation der *Shorea* Sektionen und die Unterscheidung zwischen *Shorea* und *Parashorea* ist nicht unterstützt durch die phylogenetische Analyse. Die gut unterstützten Gruppen gehören oftmals zu verschiedenen Sektionen im Bezug auf die weit verbreitet akzeptierten Klassifikationen. Zum Beispiel, *Shorea fallax*, *Shorea materialis* und *Shorea virescens* gruppieren zusammen (Bootstrap-Wert MP=98% und NJ=99%), aber diese Arten sind von Ashton in die Sektion *Brachypterae*, Sektion *Shorea*, und Sektion *Anthoshorea* eingeordnet. Die Analyse bezogen auf *Monotes kerstingii* schlägt einige morphologische Merkmale als plesiomorph und die Veränderungen der morphologischen Merkmale bei Dipterocarpeen wie folgt vor. Wichtige plesiomorphe Merkmale sind eine Basischromosomenzahl von $x=7$, imbricate Kelchblätter, tricolporate Pollen, uniseriate Holzfasern, keine Harzkanäle und Troll's Architekturmodell. Dafür werden als gemeinsame abgeleitete Merkmale ("synapomorphies") in der Unterfamilie der Dipterocarpoideae als tricolporate Pollen, multiseriate Holzfasern, das Vorhandensein von Harzkanälen und das Architekturmodell von Roux, Massart und Rauh, gefunden. Tribus Dipterocarpeae hat ein gemeinsam abgeleitete Merkmal aufgrund der Basischromosomenzahl von $x=11$. Die paarweisen Distanzmerkmale zeigen die höchsten Merkmaldistanzen von *Monotes kerstingii* zu Dipterocarpoideae. Zwanzig diagnostische molekulare Merkmale, viel mehr als für alle anderen Arten, wurden innerhalb dieser Art gefunden.

Upuna boorneensis wurde alternativ als Außengruppe nach der vorangegangenen Studien bei Verwendung der gleichen statistischen Methoden benutzt. *Upuna boorneensis* stellt sich als primitiver in einigen Merkmalen dar im Vergleich zu anderen Gattungen von Tribus Dipterocarpoideae. Die Veränderung der Außengruppe bewirkt eine unterschiedliche Topologie des phylogenetischen Baumes. Tribus Shoreae ist monophyletisch mit *Dryobalanops* als Basis zu anderen Mitgliedern dieser Tribus. Die Mitglieder von Tribus Dipterocarpeae werden nicht zu einer Gruppe geordnet. Die Unterscheidung zwischen *Parashorea* und *Shorea* ist also nicht unterstützt. Bezüglich des MP Baum kann die Basischromosomenzahl von $x=7$ als eine Synapomorphie für Tribus Shoreae interpretiert werden. Zusammenfassend fällt auf, dass *Monotes kerstingii* mehr plesiomorphe Merkmale als *Upuna boorneensis* aufweist, und somit die phylogenetische Analyse mit *Monotes*

kerstingii als Außengruppe eher geeignet ist, die Phylogenie der Unterfamilie der Dipteroocarpoideae zu reflektieren.

Von 16 in dieser Studie untersuchten endemischen Arten, wurden vier endemische Arten mit Hilfe der diagnostischen molekularen genetischen Marker identifiziert, namentlich: *Anisoptera reticulata*, *Shorea fallax*, *Upuna borneensis* (endemisch in Kalimantan) und *Hopea bancana* (endemisch in Sumatra). Das Vorkommen dieser Arten ist begrenzt auf bestimmte Regionen auf der Insel; die molekularen diagnostischen Merkmale können als Basis für die Entwicklung geeigneter Methoden für die Haplotyp-Kartierung von Dipteroocarpaceen betrachtet werden.

Das Ziel der populationsgenetischen Studie war die haplotypische Diversität der vier *Shorea* Arten (*Shorea leprosula*, *Shorea parvifolia*, *Shorea ovalis* und *Shorea johorensis*) und die Differenzierung innerhalb und zwischen den Populationen in Kalimantan und Sumatra mit Hilfe der Chloroplasten-DNA zu untersuchen. Basierend auf früheren Analysen (siehe oberhalb) wurden drei Primer-Enzyme-Kombinationen für PCR-RFLP-Prüfung ausgewählt, z.B. *rbcL* mit *Alu* I und *Msp* I, sowie *petB* mit *Rsa* I. Zusätzlich wurden auch zwei Chloroplasten-Primer, *ccmp6* und *ccmp10*, untersucht. Die Populationen von *Shorea leprosula* und *Shorea ovalis* zeigten keine Variation in der Chloroplasten-DNA bei den verwendeten Markern. Jedoch konnte geringe Variation bei *Shorea parvifolia* (drei Haplotypen, $G_{ST}=0,15$) und bei *Shorea johorensis* (zwei Haplotypen, $G_{ST}=0,25$) beobachtet werden. Die Haplotyp-Verteilung ergab keine signifikante richtungsweisende Differenzierung zwischen den Populationen von Kalimantan oder Sumatra.

Diese Studie repräsentiert die erste molekulare Phylogenie von Dipteroocarpaceen gänzlich im Diversitätszentrum der Familie in Indonesien. Die Nützlichkeit der cpDNA Variation für phylogenetischen Studien wurde bestätigt, und die konventionelle taxonomische Klassifikation der indonesischen Dipteroocarpaceen wird unterstützt hinauf bis zum Gattungsniveau. Jedoch gibt es insgesamt keinen engen Zusammenhang zwischen der beobachteten molekularen Variation und der taxonomischen Unterscheidung der Sektionen und Untersektionen innerhalb der artenreichen Gattungen, insbesondere innerhalb der Gattung *Shorea*. Nur geringe genetische Diversität wurde innerhalb der Arten beobachtet.

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APPENDICES

Appendix 1. Transformed data from cpDNA and cpSSR analysis results for phylogenetic study

| Species | rbcL | | | | | | | | | | | | | | | | pepB | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|--------------------------------------|------|---|---|---|------|---|---|---|--------|----|----|----|-------|----|----|----|------|----|----|------|----|----|------|----|----|------|----|----|----|----|----|----|----|----|----|----|----|----|---|---|---|---|---|---|---|---|---|
| | AluI | | | | CfoI | | | | HaeIII | | | | HinfI | | | | MspI | | | RsaI | | | TaqI | | | AluI | | | | | | | | | | | | | | | | | | | | | |
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | | | | | | | | | |
| 1 <i>Anisoptera costata</i> | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | | | | | | | | |
| 2 <i>Anisoptera marginata</i> | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | | | | | | |
| 3 <i>Anisoptera reticulata</i> | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | | | | | |
| 4 <i>Coylelobium lanceolatum</i> | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | | | | | |
| 5 <i>Dipterocarpus grandiflorus</i> | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | | | | |
| 6 <i>Dipterocarpus oblongifolius</i> | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | | | | |
| 7 <i>Dipterocarpus retusus</i> | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | | | | |
| 8 <i>Dipterocarpus rigidus</i> | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | | | | |
| 9 <i>Dipterocarpus tempehes</i> | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | | | |
| 10 <i>Dryobalanops aromatica</i> | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | | | |
| 11 <i>Dryobalanops lanceolata</i> | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | | |
| 12 <i>Hopea bancana</i> | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | | |
| 13 <i>Hopea celebica</i> | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | | |
| 14 <i>Hopea dryobalanoides</i> | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | | |
| 15 <i>Hopea griffithii</i> | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | | |
| 16 <i>Hopea mengarawan</i> | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | | |
| 17 <i>Hopea nigra</i> | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | | |
| 18 <i>Hopea odorata</i> | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | |
| 19 <i>Hopea sangal</i> | 1 | 1 | ? | ? | ? | ? | ? | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | |
| 20 <i>Monotes kerstingii</i> | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | |
| 21 <i>Parashorea globosa</i> | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | |
| 22 <i>Parashorea lucida</i> | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | |
| 23 <i>Shorea acuminata</i> | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | |
| 24 <i>Shorea andulensis</i> | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | |
| 25 <i>Shorea acuminatissima</i> | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| 26 <i>Shorea balangeran</i> | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | |
| 27 <i>Shorea blumutensis</i> | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| 28 <i>Shorea dasyphylla</i> | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| 29 <i>Shorea faguetiana</i> | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| 30 <i>Shorea fallax</i> | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |

(Continued)

Appendix 1. Transformed data from cpDNA and cpSSR analysis results for phylogenetic study

| Species | <i>petB</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|--------------------------------------|-------------|---------------|----|----|--------------|----|----|----|----|----|----|----|----|----|-------------|----|----|----|----|-------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|---|
| | <i>Cfol</i> | <i>HaeIII</i> | | | <i>HinfI</i> | | | | | | | | | | <i>RsaI</i> | | | | | <i>MspI</i> | | | | | | | | | | | | | | | |
| | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | |
| 1 <i>Anisoptera costata</i> | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | |
| 2 <i>Anisoptera marginata</i> | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | |
| 3 <i>Anisoptera reticulata</i> | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | |
| 4 <i>Coryleobium lanceolatum</i> | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | |
| 5 <i>Dipterocarpus grandiflorus</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | |
| 6 <i>Dipterocarpus oblongifolius</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | |
| 7 <i>Dipterocarpus retusus</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | |
| 8 <i>Dipterocarpus rigidus</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | |
| 9 <i>Dipterocarpus tempehes</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | |
| 10 <i>Dryobalanops aromatica</i> | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | |
| 11 <i>Dryobalanops lanceolata</i> | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | |
| 12 <i>Hopea bancana</i> | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | |
| 13 <i>Hopea celebica</i> | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | |
| 14 <i>Hopea dryobalanoides</i> | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | |
| 15 <i>Hopea griffithii</i> | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | |
| 16 <i>Hopea mengarawan</i> | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | |
| 17 <i>Hopea nigra</i> | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | |
| 18 <i>Hopea odorata</i> | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | |
| 19 <i>Hopea sangal</i> | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | |
| 20 <i>Monotes kerstingii</i> | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | |
| 21 <i>Parashorea globosa</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 22 <i>Parashorea lucida</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 23 <i>Shorea acuminata</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 24 <i>Shorea andulensis</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 25 <i>Shorea acuminatissima</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 26 <i>Shorea balangeran</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 27 <i>Shorea blumutensis</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 28 <i>Shorea dasyphylla</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 29 <i>Shorea faguetiana</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 30 <i>Shorea fallax</i> | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |

(Continued)

Appendix 1. Transformed data from cpDNA and cpSSR analysis results for phylogenetic study

| Species | <i>petB</i> | | | | | | | | | | <i>psaA</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|--------------------------------------|-------------|----|----|----|----|----|----|----|----|----|--------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|
| | <i>TaqI</i> | | | | | | | | | | <i>HinfI</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 | 101 | 102 | 103 | 104 | 105 | 106 | 107 | 108 | 109 | |
| 1 <i>Anisoptera costata</i> | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | |
| 2 <i>Anisoptera marginata</i> | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | |
| 3 <i>Anisoptera reticulata</i> | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | |
| 4 <i>Coyllobium lanceolatum</i> | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | |
| 5 <i>Dipterocarpus grandiflorus</i> | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 |
| 6 <i>Dipterocarpus oblongifolius</i> | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 |
| 7 <i>Dipterocarpus retusus</i> | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 |
| 8 <i>Dipterocarpus rigidus</i> | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 |
| 9 <i>Dipterocarpus tempehes</i> | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 |
| 10 <i>Dryobalanops aromatica</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | |
| 11 <i>Dryobalanops lanceolata</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | |
| 12 <i>Hopea bancana</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 13 <i>Hopea celebica</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 14 <i>Hopea dryobalanoides</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 15 <i>Hopea griffithii</i> | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 16 <i>Hopea mengarawan</i> | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 17 <i>Hopea nigra</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 18 <i>Hopea odorata</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 19 <i>Hopea sangal</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 20 <i>Monotes kerstingii</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| 21 <i>Parashorea globosa</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 22 <i>Parashorea lucida</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 23 <i>Shorea acuminata</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 24 <i>Shorea andulensis</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 25 <i>Shorea acuminatissima</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 26 <i>Shorea balangeran</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 27 <i>Shorea blumutensis</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 28 <i>Shorea dasyphylla</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 29 <i>Shorea faguetiana</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 30 <i>Shorea fallax</i> | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |

(Continued)

Appendix 1. Transformed data from cpDNA and cpSSR analysis results for phylogenetic study

| Species | psaA | | | | | | | | | | psbA | | trnLF | | | | | | ccmp2 | ccmp6 | ccmp10 | | | | | | | |
|--------------------------------------|------|-----|-----|------|-----|-----|-----|-----|-----|-----|------|------|-------|-----|-----|------|-----|-----|-------|-------|--------|-----|-----|-----|-----|---|---|---|
| | RsaI | | | TaqI | | | | | | | MspI | psbA | HinfI | | | TaqI | | | | | | | | | | | | |
| | 110 | 111 | 112 | 113 | 114 | 115 | 116 | 117 | 118 | 119 | 120 | 121 | 122 | 123 | 124 | 125 | 126 | 127 | 128 | 129 | 130 | 131 | 132 | 133 | 134 | | | |
| 1 <i>Anisoptera costata</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 4 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 3 | 3 | 4 |
| 2 <i>Anisoptera marginata</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 4 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 3 | 3 | 4 |
| 3 <i>Anisoptera reticulata</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 4 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 3 | 0 | 4 |
| 4 <i>Coyllobium lanceolatum</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | - | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 6 | 4 | 5 | |
| 5 <i>Dipterocarpus grandiflorus</i> | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 3 | 3 |
| 6 <i>Dipterocarpus oblongifolius</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 3 | 3 |
| 7 <i>Dipterocarpus retusus</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | 3 | 3 |
| 8 <i>Dipterocarpus rigidus</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 3 | 3 |
| 9 <i>Dipterocarpus tempehes</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | 3 | 3 |
| 10 <i>Dryobalanops aromatica</i> | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 3 | 3 | 4 |
| 11 <i>Dryobalanops lanceolata</i> | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 3 | 3 | 4 |
| 12 <i>Hopea bancana</i> | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 3 | 8 |
| 13 <i>Hopea celebica</i> | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 3 | 7 |
| 14 <i>Hopea dryobalanoides</i> | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 4 | 3 | 7 |
| 15 <i>Hopea griffithii</i> | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 3 | 1 | 0 | 0 | 0 | 4 | 3 | 7 |
| 16 <i>Hopea mengarawan</i> | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 3 | 1 | 0 | 0 | 0 | 5 | 3 | 7 |
| 17 <i>Hopea nigra</i> | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 4 | 3 | 7 |
| 18 <i>Hopea odorata</i> | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 4 | 3 | 6 |
| 19 <i>Hopea sangal</i> | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 4 | 3 | 7 |
| 20 <i>Monotes kerstingii</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 6 | 3 | 2 |
| 21 <i>Parashorea globosa</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 3 | 4 |
| 22 <i>Parashorea lucida</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 3 | 4 |
| 23 <i>Shorea acuminata</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 4 | 4 |
| 24 <i>Shorea andulensis</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 4 | 4 |
| 25 <i>Shorea acuminatissima</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 3 | 4 |
| 26 <i>Shorea balangeran</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 4 | 4 |
| 27 <i>Shorea blumutensis</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 1 | 4 |
| 28 <i>Shorea dasyphylla</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 3 | 4 |
| 29 <i>Shorea faguetiana</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 3 | 4 |
| 30 <i>Shorea fallax</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 5 | 4 | 4 |

(Continued)

Appendix 1. Transformed data from cpDNA and cpSSR analysis results for phylogenetic study

| Species | petB | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|--------------------------------|-------------|---------------|----|----|----|--------------|----|----|----|----|----|----|----|-------------|----|----|----|----|----|----|----|-------------|----|----|----|----|----|----|----|----|----|----|----|----|---|---|---|---|
| | <i>CfoI</i> | <i>HaeIII</i> | | | | <i>HinfI</i> | | | | | | | | <i>RsaI</i> | | | | | | | | <i>TaqI</i> | | | | | | | | | | | | | | | | |
| | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | | | | |
| 31 <i>Shorea guiso</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | | | |
| 32 <i>Shorea javanica</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | |
| 33 <i>Shorea johorensis</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | |
| 34 <i>Shorea leprosula</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | |
| 35 <i>Shorea materialis</i> | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| 36 <i>Shorea macrophylla</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| 37 <i>Shorea macroptera</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | - | - | - | - | - | - | - | - | |
| 38 <i>Shorea mecistopteryx</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | |
| 39 <i>Shorea montigena</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | 1 | 1 | 1 | 0 | 0 | - | - | - | - | - | - | - | - | |
| 40 <i>Shorea multiflora</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| 41 <i>Shorea ovalis</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| 42 <i>Shorea palembanica</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| 43 <i>Shorea parvifolia</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| 44 <i>Shorea pinanga</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| 45 <i>Shorea platyclados</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| 46 <i>Shorea scaberrima</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | 1 | 1 | 1 | 0 | 0 | - | - | - | - | - | - | - | - | - |
| 47 <i>Shorea selanica</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| 48 <i>Shorea seminis</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| 49 <i>Shorea splendida</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| 50 <i>Shorea stenoptera</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| 51 <i>Shorea virescens</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| 52 <i>Shorea xanthophylla</i> | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| 53 <i>Upuna borneensis</i> | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 |
| 54 <i>Vatica bantamensis</i> | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| 55 <i>Vatica bella</i> | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| 56 <i>Vatica granulata</i> | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| 57 <i>Vatica pauciflora</i> | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| 58 <i>Vatica rassak</i> | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| 59 <i>Vatica venulosa</i> | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |

(Continued)

Appendix 1. Transformed data from cpDNA and cpSSR analysis results for phylogenetic study

| Species | <i>petB</i> | | | | | | | | | | | | <i>psaA</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|--------------------------------|-------------|----|----|----|----|----|----|----|----|----|----|----|---------------|----|----|----|----|----|----|----|----|----|----|----|--------------|----|----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-------------|---|---|--|--|--|--|--|--|--|--|--|
| | <i>TaqI</i> | | | | | | | | | | | | <i>HaeIII</i> | | | | | | | | | | | | <i>HinfI</i> | | | | | | | | | | | | <i>MspI</i> | | | | | | | | | | | |
| | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 | 101 | 102 | 103 | 104 | 105 | 106 | 107 | 108 | 109 | | | | | | | | | | | |
| 31 <i>Shorea guiso</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | - | - | - | - | - | - | - | - | - | | | | | | | | | | |
| 32 <i>Shorea javanica</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | - | - | - | - | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | | | | | | |
| 33 <i>Shorea johorensis</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | | | | | | | | | | |
| 34 <i>Shorea leprosula</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | | | | | | | | | | |
| 35 <i>Shorea materialis</i> | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | | | | | | | | | | |
| 36 <i>Shorea macrophylla</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | | | | | |
| 37 <i>Shorea macroptera</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | | | | |
| 38 <i>Shorea mecistopteryx</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | | | | |
| 39 <i>Shorea montigena</i> | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | | | | |
| 40 <i>Shorea multiflora</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | | | | | | | | | | |
| 41 <i>Shorea ovalis</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | | | | |
| 42 <i>Shorea palembanica</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | | | | |
| 43 <i>Shorea parvifolia</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | | | | |
| 44 <i>Shorea pinanga</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | | | | |
| 45 <i>Shorea platyclados</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | | | | |
| 46 <i>Shorea scaberrima</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | | | | |
| 47 <i>Shorea selanica</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | | | | |
| 48 <i>Shorea seminis</i> | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | | | | |
| 49 <i>Shorea splendida</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | | | | |
| 50 <i>Shorea stenoptera</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | | | | |
| 51 <i>Shorea virescens</i> | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | | | | |
| 52 <i>Shorea xanthophylla</i> | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | | | | | | | | | |
| 53 <i>Upuna borneensis</i> | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | | | | | | | | | | |
| 54 <i>Vatica bantamensis</i> | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | | | | | | | | | | |
| 55 <i>Vatica bella</i> | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | | | | | | | | | | |
| 56 <i>Vatica granulata</i> | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | | | | | | | | | | |
| 57 <i>Vatica pauciflora</i> | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | | | | | | | | | | |
| 58 <i>Vatica rassak</i> | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | | | | | | | | | | |
| 59 <i>Vatica venulosa</i> | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | | | | | | | | | | |

(Continued)

Appendix 1. Transformed data from cpDNA and cpSSR analysis results for phylogenetic study

| Species | psaA | | | | | | | | | | psbA | | trnLF | | | | | | | | | | ccmp2 | ccmp6 | ccmp10 | | | |
|--------------------------------|------|-----|-----|-----|-----|------|-----|-----|-----|-----|------|------|-------|-----|-----|-----|-----|------|-----|-----|-----|-----|-------|-------|--------|-----|-----|-----|
| | RsaI | | | | | TaqI | | | | | MspI | MspI | HinfI | | | | | TaqI | | | | | | | | | | |
| | 110 | 111 | 112 | 113 | 114 | 115 | 116 | 117 | 118 | 119 | 120 | 121 | 122 | 123 | 124 | 125 | 126 | 127 | 128 | 129 | 130 | 131 | 132 | 133 | 134 | 135 | 136 | 137 |
| 31 <i>Shorea guiso</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 2 | 4 |
| 32 <i>Shorea javanica</i> | 1 | 1 | 0 | 1 | 1 | 1 | - | - | - | - | - | - | - | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 3 | 4 |
| 33 <i>Shorea johorensis</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 4 | 4 |
| 34 <i>Shorea leprosula</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 4 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 4 | 4 |
| 35 <i>Shorea materialis</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 4 | 1 | 0 | 0 | 0 | 5 | 4 | 4 |
| 36 <i>Shorea macrophylla</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 4 | 4 |
| 37 <i>Shorea macroptera</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 4 | 4 |
| 38 <i>Shorea mecistopteryx</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 4 | 4 |
| 39 <i>Shorea montigena</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 4 | 4 | 4 |
| 40 <i>Shorea multiflora</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 3 | 4 |
| 41 <i>Shorea ovalis</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 3 | 4 |
| 42 <i>Shorea palembanica</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 5 | 4 |
| 43 <i>Shorea parvifolia</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 5 | 4 |
| 44 <i>Shorea pinanga</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 4 | 4 |
| 45 <i>Shorea platyclados</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 4 | 4 |
| 46 <i>Shorea scaberrima</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 4 | 4 |
| 47 <i>Shorea selanica</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 4 | 4 |
| 48 <i>Shorea seminis</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 1 | 4 |
| 49 <i>Shorea splendida</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 4 | 4 |
| 50 <i>Shorea stenoptera</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 4 | 4 |
| 51 <i>Shorea virescens</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 4 | 1 | 0 | 0 | 0 | 5 | 4 | 4 |
| 52 <i>Shorea xanthophylla</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 4 | 4 |
| 53 <i>Upuna borneensis</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 4 | 4 |
| 54 <i>Vatica bantamensis</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 3 | 3 | 1 |
| 55 <i>Vatica bella</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 0 | 2 | 0 | 2 | 0 | 0 | 3 | 3 | 1 |
| 56 <i>Vatica granulata</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 3 | 3 | 0 |
| 57 <i>Vatica pauciflora</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 3 | 3 | 1 |
| 58 <i>Vatica rassak</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 3 | 3 | 1 |
| 59 <i>Vatica venulosa</i> | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 3 | 3 | 1 |

Appendix 2. The groups of taxa revealed by PCR-RFLP of cpDNA

Primer *rbcL*, enzyme *AluI*:

1. *Anisoptera*
2. *Dryobalanops*
3. *Hopea sangal*
4. other *Hopea*
5. *Monotes kerstingii kerstingii*, *Parashorea lucida*, *Shorea fallax*, *Shorea materialis*,
Shorea parvifolia, *Shorea virescens*, *Dipterocarpus tempehes*
6. *Shorea acuminatissima*, *Shorea dasyphylla*, *Shorea faguetiana*, *Shorea multiflora*, *Upuna*
borneensis, *Vatica bantamensis*, *Vatica bella*
7. *Vatica granulata*, *Vatica pauciflora*, *Vatica rassak*, *Vatica venulosa*
8. *Cotylelobium lanceolatum*, other *Dipterocarpus*, *Parashorea lucida*, other *Shorea*

Primer *rbcL*, enzyme *CfoI*:

1. *Monotes kerstingii*
2. *Upuna borneensis*, *Cotylelobium lanceolatum*, *Vatica*, *Anisoptera*
3. *Dipterocarpus*, *Dryobalanops*
4. *Hopea nigra*
5. other *Hopea*
6. *Shorea*, *Parashorea*

Primer *rbcL*, enzyme *HaeIII*:

1. *Monotes kerstingii*, *Upuna borneensis*, *Cotylelobium lanceolatum*, *Vatica*, *Anisoptera*,
Dryobalanops
2. *Dipterocarpus*, *Shorea materialis*, *Shorea fallax*, *Shorea virescens*, *Parashorea*
3. other *Shorea*

Primer *rbcL*, enzyme *HinfI*:

1. *Monotes kerstingii*, *Dryobalanops*, *Hopea*, *Shorea multiflora*, *Shorea dasyphylla*, *Shorea*
acuminatissima
2. *Cotylelobium lanceolatum*, *Anisoptera*, *Vatica*, other *Shorea*, *Parashorea*
3. *Upuna borneensis*
4. *Dipterocarpus rigidus*
5. other *Dipterocarpus*

Primer *rbcL*, enzyme *MspI*:

1. *Monotes kerstingii*
2. *Upuna borneensis*, *Cotylelobium lanceolatum*, *Vatica*, *Shorea johorensis*
3. *Anisoptera*
4. *Dipterocarpus*
5. *Dryobalanops*
6. *Hopea*, other *Shorea*, *Parashorea*

Primer *rbcL*, enzyme *RsaI*:

1. *Monotes kerstingii*, *Dipterocarpus*, *Shorea multiflora*, *Shorea acuminatissima*, *Shorea dasyphylla*, *Shorea faguetiana*
2. *Upuna borneensis*, *Cotylelobium lanceolatum*, *Vatica*, *Anisoptera*, *Dryobalanops*, *Hopea*, other *Shorea*, *Parashorea*

Primer *rbcL*, enzyme *TaqI*:

1. *Monotes kerstingii*, *Upuna borneensis*, *Cotylelobium lanceolatum*, *Vatica*, *Anisoptera*, *Dipterocarpus*, *Dryobalanops*, *Hopea mengarawan*, *Hopea dryobalanoides*, *Hopea griffithii*, *Shorea fallax*, *Shorea multiflora*, *Shorea acuminatissima*, *Shorea virescens*, *Shorea materialis*, *Shorea faguetiana*, *Parashorea globosa*
2. other *Hopea*, other *Shorea*, *Parashorea lucida*

Primer *petB*, enzyme *AluI*:

1. *Monotes kerstingii*
2. *Upuna borneensis*
3. *Hopea mengarawan*
4. *Cotylelobium lanceolatum*, *Vatica bantamensis*, *Vatica bella*, *Anisoptera*, *Dipterocarpus*, *Dryobalanops*, other *Hopea*, *Shorea*, *Parashorea*
5. other *Vatica*

Primer *petB*, enzyme *CfoI*:

1. *Monotes kerstingii*, *Upuna borneensis*, *Cotylelobium lanceolatum*, *Vatica*, *Anisoptera*, *Dryobalanops*, *Hopea*, *Shorea*, *Parashorea*
2. *Dipterocarpus*

Primer *petB*, enzyme *HaeIII*:

1. *Monotes kerstingii*
2. *Upuna borneensis*
3. *Cotylelobium lanceolatum*, *Anisoptera*, *Dipterocarpus*
4. *Vatica*, *Dryobalanops*, *Hopea*, *Shorea fallax*, *Shorea materialis*, *Shorea virescens*
5. other *Shorea*, *Parashorea*

Primer *petB*, enzyme *HinfI*:

1. *Upuna borneensis*
2. *Cotylelobium lanceolatum*
3. *Vatica*
4. *Anisoptera reticulata*
5. *Anisoptera costata*, *Anisoptera marginata*
6. *Dipterocarpus*
7. *Dryobalanops*
8. *Hopea*
9. *Shorea virescens*
10. *Shorea seminis*
11. *Shorea fallax*
12. *Shorea balangeran*, *Shorea selanica*
13. *Shorea acuminatissima*, *Shorea dasyphylla*, *Shorea faguetiana*, *Shorea materialis*, *Shorea multiflora*
14. other *Shorea*, *Parashorea globosa*

n/a: *Monotes kerstingii kerstingii*, *Parashorea lucida*, *Shorea montigena*, *Shorea scaberrima*

Primer *petB*, enzyme *MspI*:

1. *Upuna borneensis*, *Cotylelobium lanceolatum*, *Anisoptera*
2. *Monotes kerstingii*, *Shorea acuminata*, *Shorea andulensis*, *Shorea javanica*, *Shorea johorensis*, *Shorea leprosula*, *Shorea mecistopteryx*, *Shorea ovalis*, *Shorea palembanica*, *Shorea parvifolia*, *Shorea platyclados*, *Shorea xanthophylla*
3. *Vatica*, *Dipterocarpus*, *Dryobalanops*
4. *Hopea*, other *Shorea*, *Parashorea*

n.a: *Shorea scaberrima*, *Shorea macroptera*, *Shorea montigena*

Primer *petB*, enzyme *RsaI*:

1. *Upuna borneensis*
2. *Cotylelobium lanceolatum*, *Anisoptera*, *Dipterocarpus*, *Dryobalanops*
3. *Vatica*
4. *Shorea johorensis*
5. *Monotes kerstingii*, *Hopea*, other *Shorea*, *Parashorea*

Primer *petB*, enzyme *TaqI*:

1. *Upuna borneensis*, *Vatica*
 2. *Anisoptera marginata*
 3. *Cotylelobium lanceolatum*, other *Anisoptera*
 4. *Dipterocarpus*
 5. *Hopea mengarawan*
 6. *Monotes kerstingii*, *Dryobalanops*, other *Hopea*, *Shorea acuminatissima*, *Shorea balangeran*, *Shorea blumutensis*, *Shorea dasyphylla*, *Shorea guiso*, *Shorea multiflora*, *Shorea seminis*, *Parashorea*
 7. *Shorea fallax*, *Shorea materialis*, *Shorea virescens*
 8. other *Shorea*
- n.a: *Hopea griffithii*, *Shorea montigena*

Primer *psaA*, enzyme *CfoI*:

1. *Monotes kerstingii*
2. *Upuna borneensis*, *Cotylelobium lanceolatum*, *Vatica*, *Anisoptera*, *Dipterocarpus*, *Dryobalanops*
3. *Shorea blumutensis*
4. other *Shorea*, *Hopea*, *Parashorea*

Primer *psaA*, enzyme *HaeIII*:

1. *Monotes kerstingii*
 2. *Upuna borneensis*, *Cotylelobium lanceolatum*, *Vatica*, *Anisoptera*, *Dipterocarpus*, *Hopea mengarawan*
 3. *Shorea macrophylla*, *Shorea pinanga*, *Shorea selanica*, *Shorea splendida*, *Shorea stenoptera*
 4. other *Hopea*, other *Shorea*, *Dryobalanops*, *Parashorea*
- n.a: *Shorea javanica*

Primer *psaA*, enzyme *HinfI*:

1. *Monotes kerstingii*
2. *Vatica*
3. *Upuna borneensis*, *Cotylelobium lanceolatum*, *Anisoptera*, *Dipterocarpus*, *Dryobalanops*, *Hopea*, *Shorea*, *Parashorea*

Primer *psaA*, enzyme *MspI*:

1. *Monotes kerstingii*
 2. *Upuna borneensis*, *Cotylelobium lanceolatum*, *Vatica*, *Anisoptera*
 3. *Dipterocarpus*, *Dryobalanops*
 4. *Hopea*, *Shorea acuminatissima*, *Shorea blumutensis*, *Shorea dasyphylla*, *Shorea faguetiana*, *Shorea fallax*, *Shorea materialis*, *Shorea multiflora*, *Shorea seminis*, *Shorea virescens*, *Parashorea*
 5. other *Shorea*
- n.a.: *Shorea platyclados*, *Shorea guiso*

Primer *psaA*, enzyme *RsaI*:

1. *Monotes kerstingii*
2. *Dryobalanops*, *Dipterocarpus grandiflorus*
3. *Upuna borneensis*, *Cotylelobium lanceolatum*, *Vatica*, *Anisoptera*, other *Dipterocarpus*, *Shorea*, *Parashorea*
4. *Hopea*

Primer *psaA*, enzyme *TaqI*:

1. *Monotes kerstingii*
 2. *Shorea fallax*, *Shorea materialis*, *Shorea virescens*
 3. *Shorea acuminatissima*, *Shorea bulumutensis*, *Shorea dasyphylla*, *Shorea faguetiana*, *Shorea guiso*, *Shorea montigena*, *Shoreamultiflora*, *Shorea scaberrima*, *Shorea seminis*
 4. *Upuna borneensis*, *Cotylelobium lanceolatum*, *Vatica*, *Dipterocarpus*, *Hopea*, other *Shorea*, *Parashorea*
 5. *Anisoptera*
- n.a.: *Shorea javanica*

Primer *trnL-F*, enzyme *TaqI*:

1. *Upuna borneensis*
2. *Cotylelobium lanceolatum*
3. *Anisoptera*, *Dipterocarpus*
4. *Dryobalanops*
5. *Vatica bella*
6. *Monotes kerstingii*, other *Vatica*
7. *Hopea griffithii*, *Hopea mengarawan*
8. *Shorea materialis*
9. *Shorea virescens*
10. other *Hopea*, other *Shorea*, *Parashorea*

Primer *trnL-F*, enzyme *Hinf I*:

1. *Cotylelobium lanceolatum*
2. *Vatica*
3. *Anisoptera*
4. *Dipterocarpus*
5. *Dryobalanops aromatica*
6. *Hopea griffithii*
7. *Shorea leprosula*
8. *Shorea macrophylla*, *Shorea pinanga*, *Shorea splendida*, *Shorea stenoptera*
9. *Dryobalanops lanceolata*, other *Hopea*, other *Shorea*, *Parashorea*, *Monotes kerstingii*,
Upuna borneensis

Primer *psbA*, enzyme *MspI*:

1. *Monotes kerstingii*, *Upuna borneensis*, *Cotylelobium lanceolatum*, *Anisoptera*, *Vatica bantamensis*
2. other *Vatica*
3. *Dipterocarpus*, *Dryobalanops* *Hopea*, *Shorea*, *Parashorea*

Appendix 3. Amplification length variation revealed by PCR of cpSSR

Primer ccmp2:

| Length (bp) | Species |
|-------------|--|
| 136 | <i>Dipterocarpus grandiflorus</i> |
| 146 | <i>Dipterocarpus oblongifolius</i> , <i>Dipterocarpus rigidus</i> |
| 147 | <i>Dipterocarpus retusus</i> , <i>Dipterocarpus tempehes</i> |
| 149 | <i>Upuna borneensis</i> , <i>Anisoptera spp.</i> , <i>Vatica spp.</i> , <i>Dryobalanops spp.</i> , <i>Hopea bancana</i> , <i>Hopea celebica</i> , <i>Parashorea</i> , other <i>Shorea</i> |
| 150 | <i>Shorea montigena</i> , <i>Hopea dryobalanoides</i> , <i>Hopea griffithii</i> , <i>Hopea nigra</i> , <i>Hopea odorata</i> , <i>Hopea sangal</i> |
| 151 | <i>Hopea mengarawan</i> , <i>Shorea fallax</i> , <i>Shorea materialis</i> , <i>Shorea virescens</i> |
| 155 | <i>Monotes kerstingii</i> , <i>Cotylelobium lanceolatum</i> |

Primer ccmp6:

| Length (bp) | Species |
|-------------|---|
| 86 | <i>Anisoptera reticulata</i> |
| 90 | <i>Shorea blumutensis</i> , <i>Shorea seminis</i> |
| 91 | <i>Shorea guiso</i> |
| 95 | <i>Monotes kerstingii</i> , <i>Upuna borneensis</i> , <i>Vatica spp.</i> , <i>Anisoptera spp.</i> , <i>Dipterocarpus spp.</i> , <i>Dryobalanops spp.</i> , <i>Hopea spp.</i> , other <i>Shorea spp.</i> , <i>Parashorea spp.</i> |
| 96 | <i>Cotylelobium lanceolatum</i> , <i>Shorea acuminata</i> , <i>Shorea andulensis</i> , <i>Shorea</i> <i>balangeran</i> , <i>Shorea fallax</i> , <i>Shorea johor</i> , <i>Shorea leprosula</i> , <i>Shorea</i> <i>materialis</i> , <i>Shorea macrophylla</i> , <i>Shorea mecistopteryx</i> , <i>Shorea montigena</i> , <i>Shorea pinanga</i> , <i>Shorea platyclados</i> , <i>Shorea scaberrima</i> , <i>Shorea selanica</i> , <i>Shorea splendida</i> , <i>Shorea stenoptera</i> , <i>Shorea virescens</i> , <i>Shorea xanthophylla</i> |
| 97 | <i>Shorea palembanica</i> , <i>Shorea parvifolia</i> |

Primer ccmp10:

| Length (bp) | Species |
|--------------------|--|
| 92 | <i>Vatica granulata</i> |
| 93 | <i>Vatica bantamensis</i> , <i>Vatica bella</i> , <i>Vatica pauciflora</i> , <i>Vatica rassak</i> , <i>Vatica venulosa</i> |
| 94 | <i>Monotes kerstingii</i> |
| 96 | <i>Dipterocarpus spp.</i> |
| 99 | <i>Upuna</i> , <i>Anisoptera</i> , <i>Dryobalanops</i> , <i>Shorea</i> , <i>Parashorea</i> |
| 100 | <i>Cotylelobium lanceolatum</i> |
| 107 | <i>Hopea odorata</i> |
| 108 | <i>Hopea celebica</i> , <i>Hopea dryobalanooides</i> , <i>Hopea griffithii</i> , <i>Hopea mengarawan</i> , <i>Hopea nigra</i> , <i>Hopea sangal</i> |
| 109 | <i>Hopea bancana</i> |

Appendix 4. Haplotype revealed in phylogenetic study and population genetic study

Haplotype revealed in phylogenetic study:

| Haplotype | Species |
|------------------|---|
| 1 | <i>Anisoptera costata</i> |
| 2 | <i>Anisoptera marginata</i> |
| 3 | <i>Anisoptera reticulata</i> |
| 4 | <i>Cotylelobium lanceolatum</i> |
| 5 | <i>Dipterocarpus grandiflorus</i> |
| 6 | <i>Dipterocarpus oblongifolius</i> |
| 7 | <i>Dipterocarpus retusus</i> |
| 8 | <i>Dipterocarpus rigidus</i> |
| 9 | <i>Dipterocarpus tempehes</i> |
| 10 | <i>Dryobalanops aromatica</i> |
| 11 | <i>Dryobalanops lanceolata</i> |
| 12 | <i>Hopea bancana</i> |
| 13 | <i>Hopea celebica</i> |
| 14 | <i>Hopea dryobalanoides</i> |
| 15 | <i>Hopea griffithii</i> |
| 16 | <i>Hopea mengarawan</i> |
| 17 | <i>Hopea nigra</i> |
| 18 | <i>Hopea odorata</i> |
| 19 | <i>Hopea sangal</i> |
| 20 | <i>Parashorea globosa</i> |
| 21 | <i>Parashorea lucida</i> |
| 22 | <i>Shorea acuminata, Shorea andulensis, Shorea mecistopteryx, Shorea platyclados, Shorea xanthophylla</i> |
| 23 | <i>Shorea acuminatissima, Shorea dasyphylla, Shorea mutiflora</i> |
| 24 | <i>Shorea balangeran</i> |
| 25 | <i>Shorea blumutensis</i> |
| 26 | <i>Shorea faguetiana</i> |
| 27 | <i>Shorea fallax</i> |

(Continued)

Haplotype revealed in phylogenetic study:

| Haplotype | Species |
|------------------|--|
| 28 | <i>Shorea guiso</i> |
| 29 | <i>Shorea johorensis</i> |
| 30 | <i>Shorea leprosula</i> |
| 31 | <i>Shorea materialis</i> |
| 32 | <i>Shorea macrophylla, Shorea pinanga, Shorea stenoptera</i> |
| 33 | <i>Shorea montigena</i> |
| 34 | <i>Shorea javanica, Shorea ovalis, Shorea macroptera</i> |
| 35 | <i>Shorea palembanica</i> |
| 36 | <i>Shorea parvifolia</i> |
| 37 | <i>Shorea scaberrima</i> |
| 38 | <i>Shorea selanica</i> |
| 39 | <i>Shorea seminis</i> |
| 40 | <i>Shorea splendida</i> |
| 41 | <i>Shorea virescens</i> |
| 42 | <i>Upuna borneensis</i> |
| 43 | <i>Vatica bantamensis</i> |
| 44 | <i>Vatica bella</i> |
| 45 | <i>Vatica granulate</i> |
| 46 | <i>Vatica pauciflora, Vatica rassak, Vatica venulosa</i> |
| 47 | <i>Monotes kerstingii</i> |

Haplotype revealed in population genetic study:

| Haplotype | Species |
|------------------|--------------------------|
| 29(*), 29b | <i>Shorea johorensis</i> |
| 30 | <i>Shorea leprosula</i> |
| 34 | <i>Shorea ovalis</i> |
| 36(*), 36b, 36c | <i>Shorea parvifolia</i> |

(*): common haplotype found among the populations

Appendix 5. Pairwise distance between species of Dipterocarpaceae: total character differences (below diagonal) and mean character differences (above diagonal)

| No | Species | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
|----|------------------------------------|---|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 1 | <i>Anisoptera costata</i> | - | 0.015 | 0.015 | 0.111 | 0.226 | 0.219 | 0.219 | 0.219 | 0.219 | 0.234 | 0.234 | 0.285 | 0.285 | 0.285 | 0.294 | 0.270 | 0.292 | 0.292 | 0.292 | 0.415 |
| 2 | <i>Anisoptera marginata</i> | | - | 0.029 | 0.126 | 0.241 | 0.234 | 0.234 | 0.234 | 0.234 | 0.234 | 0.234 | 0.285 | 0.285 | 0.285 | 0.294 | 0.285 | 0.292 | 0.292 | 0.292 | 0.415 |
| 3 | <i>Anisoptera reticulata</i> | | | - | 0.119 | 0.241 | 0.234 | 0.234 | 0.234 | 0.234 | 0.248 | 0.248 | 0.299 | 0.299 | 0.299 | 0.310 | 0.285 | 0.307 | 0.307 | 0.307 | 0.423 |
| 4 | <i>Cotylelobium lanceolatum</i> | | | | - | 0.193 | 0.185 | 0.185 | 0.185 | 0.200 | 0.237 | 0.230 | 0.289 | 0.289 | 0.281 | 0.282 | 0.267 | 0.289 | 0.289 | 0.274 | 0.388 |
| 5 | <i>Dipterocarpus grandiflorus</i> | | | | | - | 0.015 | 0.015 | 0.029 | 0.029 | 0.219 | 0.219 | 0.307 | 0.307 | 0.299 | 0.278 | 0.285 | 0.307 | 0.307 | 0.292 | 0.439 |
| 6 | <i>Dipterocarpus oblongifolius</i> | | | | | | - | 0.007 | 0.015 | 0.022 | 0.226 | 0.226 | 0.299 | 0.299 | 0.292 | 0.270 | 0.277 | 0.299 | 0.299 | 0.285 | 0.431 |
| 7 | <i>Dipterocarpus retusus</i> | | | | | | | - | 0.022 | 0.015 | 0.226 | 0.226 | 0.299 | 0.299 | 0.292 | 0.270 | 0.277 | 0.299 | 0.299 | 0.285 | 0.431 |
| 8 | <i>Dipterocarpus rigidus</i> | | | | | | | | - | 0.037 | 0.212 | 0.212 | 0.285 | 0.285 | 0.277 | 0.254 | 0.263 | 0.285 | 0.285 | 0.270 | 0.415 |
| 9 | <i>Dipterocarpus tempelhes</i> | | | | | | | | | - | 0.226 | 0.226 | 0.299 | 0.299 | 0.292 | 0.270 | 0.277 | 0.299 | 0.299 | 0.285 | 0.415 |
| 10 | <i>Dryobalanops aromatica</i> | | | | | | | | | | - | 0.007 | 0.175 | 0.175 | 0.175 | 0.198 | 0.212 | 0.182 | 0.182 | 0.168 | 0.358 |
| 11 | <i>Dryobalanops lanceolata</i> | | | | | | | | | | | - | 0.168 | 0.168 | 0.168 | 0.190 | 0.204 | 0.175 | 0.175 | 0.161 | 0.350 |
| 12 | <i>Hopea bancana</i> | | | | | | | | | | | | - | 0.007 | 0.022 | 0.040 | 0.066 | 0.029 | 0.015 | 0.015 | 0.341 |
| 13 | <i>Hopea celebica</i> | | | | | | | | | | | | | - | 0.015 | 0.032 | 0.058 | 0.022 | 0.015 | 0.007 | 0.341 |
| 14 | <i>Hopea dryobalanoides</i> | | | | | | | | | | | | | | - | 0.016 | 0.051 | 0.007 | 0.015 | 0.007 | 0.333 |
| 15 | <i>Hopea griffithii</i> | | | | | | | | | | | | | | | - | 0.032 | 0.024 | 0.032 | 0.024 | 0.384 |
| 16 | <i>Hopea mengarawan</i> | | | | | | | | | | | | | | | | - | 0.058 | 0.066 | 0.058 | 0.366 |
| 17 | <i>Hopea nigra</i> | | | | | | | | | | | | | | | | | - | 0.022 | 0.015 | 0.341 |
| 18 | <i>Hopea odorata</i> | | | | | | | | | | | | | | | | | | - | 0.007 | 0.341 |
| 19 | <i>Hopea sangal</i> | | | | | | | | | | | | | | | | | | | - | 0.325 |
| 20 | <i>Monotes kerstingii</i> | | | | | | | | | | | | | | | | | | | | - |
| 21 | <i>Parashorea globosa</i> | | | | | | | | | | | | | | | | | | | | 46 |
| 22 | <i>Parashorea lucida</i> | | | | | | | | | | | | | | | | | | | | 45 |
| 23 | <i>Shorea acuminata</i> | | | | | | | | | | | | | | | | | | | | 48 |
| 24 | <i>Shorea andulensis</i> | | | | | | | | | | | | | | | | | | | | 48 |
| 25 | <i>Shorea acuminatissima</i> | | | | | | | | | | | | | | | | | | | | 44 |
| 26 | <i>Shorea balangeran</i> | | | | | | | | | | | | | | | | | | | | 49 |
| 27 | <i>Shorea blumutensis</i> | | | | | | | | | | | | | | | | | | | | 48 |
| 28 | <i>Shorea dasyphylla</i> | | | | | | | | | | | | | | | | | | | | 44 |
| 29 | <i>Shorea faguetiana</i> | | | | | | | | | | | | | | | | | | | | 45 |
| 30 | <i>Shorea fallax</i> | | | | | | | | | | | | | | | | | | | | 47 |

(Continued)

Appendix 5. Pairwise distance between species of Dipterocarpaceae: total character differences (below diagonal) and mean character differences (above diagonal)

| No | Species | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 |
|----|------------------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 1 | <i>Anisoptera costata</i> | 0.292 | 0.276 | 0.336 | 0.336 | 0.299 | 0.299 | 0.307 | 0.299 | 0.307 | 0.292 | 0.295 | 0.331 | 0.336 | 0.328 | 0.307 | 0.328 | 0.305 | 0.336 | 0.274 | 0.299 |
| 2 | <i>Anisoptera marginata</i> | 0.292 | 0.276 | 0.336 | 0.336 | 0.299 | 0.299 | 0.307 | 0.299 | 0.307 | 0.292 | 0.295 | 0.331 | 0.336 | 0.328 | 0.307 | 0.328 | 0.305 | 0.336 | 0.274 | 0.299 |
| 3 | <i>Anisoptera reticulata</i> | 0.307 | 0.285 | 0.343 | 0.343 | 0.314 | 0.307 | 0.314 | 0.314 | 0.321 | 0.299 | 0.302 | 0.347 | 0.343 | 0.336 | 0.314 | 0.336 | 0.321 | 0.343 | 0.274 | 0.314 |
| 4 | <i>Cotylelobium lanceolatum</i> | 0.274 | 0.264 | 0.304 | 0.304 | 0.296 | 0.267 | 0.281 | 0.296 | 0.304 | 0.267 | 0.268 | 0.328 | 0.304 | 0.311 | 0.281 | 0.304 | 0.287 | 0.304 | 0.212 | 0.296 |
| 5 | <i>Dipterocarpus grandiflorus</i> | 0.263 | 0.268 | 0.307 | 0.307 | 0.270 | 0.270 | 0.277 | 0.270 | 0.277 | 0.299 | 0.271 | 0.315 | 0.307 | 0.307 | 0.314 | 0.299 | 0.282 | 0.307 | 0.226 | 0.270 |
| 6 | <i>Dipterocarpus oblongifolius</i> | 0.255 | 0.260 | 0.299 | 0.299 | 0.263 | 0.263 | 0.270 | 0.263 | 0.270 | 0.292 | 0.264 | 0.306 | 0.299 | 0.299 | 0.307 | 0.292 | 0.275 | 0.299 | 0.217 | 0.263 |
| 7 | <i>Dipterocarpus retusus</i> | 0.255 | 0.260 | 0.299 | 0.299 | 0.263 | 0.263 | 0.270 | 0.263 | 0.270 | 0.292 | 0.264 | 0.306 | 0.299 | 0.299 | 0.307 | 0.292 | 0.275 | 0.299 | 0.217 | 0.263 |
| 8 | <i>Dipterocarpus rigidus</i> | 0.255 | 0.260 | 0.299 | 0.299 | 0.248 | 0.263 | 0.270 | 0.248 | 0.255 | 0.292 | 0.264 | 0.306 | 0.299 | 0.299 | 0.307 | 0.292 | 0.275 | 0.299 | 0.217 | 0.248 |
| 9 | <i>Dipterocarpus tempehes</i> | 0.270 | 0.244 | 0.314 | 0.314 | 0.263 | 0.277 | 0.285 | 0.263 | 0.270 | 0.277 | 0.279 | 0.323 | 0.314 | 0.314 | 0.292 | 0.307 | 0.290 | 0.314 | 0.236 | 0.263 |
| 10 | <i>Dryobalanops aromatica</i> | 0.182 | 0.171 | 0.226 | 0.226 | 0.190 | 0.204 | 0.197 | 0.190 | 0.197 | 0.212 | 0.186 | 0.234 | 0.241 | 0.226 | 0.219 | 0.219 | 0.198 | 0.226 | 0.198 | 0.190 |
| 11 | <i>Dryobalanops lanceolata</i> | 0.175 | 0.163 | 0.219 | 0.219 | 0.182 | 0.197 | 0.190 | 0.182 | 0.190 | 0.204 | 0.178 | 0.226 | 0.234 | 0.226 | 0.212 | 0.219 | 0.191 | 0.219 | 0.189 | 0.182 |
| 12 | <i>Hopea bancana</i> | 0.080 | 0.065 | 0.124 | 0.124 | 0.073 | 0.102 | 0.095 | 0.073 | 0.080 | 0.109 | 0.093 | 0.121 | 0.139 | 0.131 | 0.109 | 0.124 | 0.107 | 0.124 | 0.113 | 0.073 |
| 13 | <i>Hopea celebica</i> | 0.080 | 0.065 | 0.124 | 0.124 | 0.073 | 0.102 | 0.095 | 0.073 | 0.080 | 0.109 | 0.093 | 0.121 | 0.139 | 0.131 | 0.109 | 0.124 | 0.107 | 0.124 | 0.113 | 0.073 |
| 14 | <i>Hopea dryobalanoides</i> | 0.080 | 0.081 | 0.124 | 0.124 | 0.088 | 0.102 | 0.095 | 0.088 | 0.095 | 0.117 | 0.093 | 0.121 | 0.139 | 0.131 | 0.117 | 0.124 | 0.107 | 0.124 | 0.094 | 0.088 |
| 15 | <i>Hopea griffithii</i> | 0.103 | 0.107 | 0.143 | 0.143 | 0.111 | 0.127 | 0.119 | 0.111 | 0.111 | 0.127 | 0.119 | 0.142 | 0.159 | 0.151 | 0.119 | 0.143 | 0.125 | 0.143 | 0.113 | 0.111 |
| 16 | <i>Hopea mengarawan</i> | 0.124 | 0.130 | 0.168 | 0.168 | 0.131 | 0.146 | 0.139 | 0.131 | 0.139 | 0.139 | 0.140 | 0.161 | 0.182 | 0.175 | 0.131 | 0.168 | 0.153 | 0.168 | 0.132 | 0.131 |
| 17 | <i>Hopea nigra</i> | 0.088 | 0.089 | 0.131 | 0.131 | 0.095 | 0.109 | 0.102 | 0.095 | 0.102 | 0.124 | 0.101 | 0.129 | 0.146 | 0.139 | 0.124 | 0.131 | 0.115 | 0.131 | 0.104 | 0.095 |
| 18 | <i>Hopea odorata</i> | 0.088 | 0.073 | 0.131 | 0.131 | 0.080 | 0.109 | 0.102 | 0.080 | 0.088 | 0.109 | 0.101 | 0.129 | 0.146 | 0.139 | 0.109 | 0.131 | 0.115 | 0.131 | 0.104 | 0.080 |
| 19 | <i>Hopea sangal</i> | 0.073 | 0.057 | 0.117 | 0.117 | 0.073 | 0.095 | 0.088 | 0.073 | 0.080 | 0.095 | 0.085 | 0.113 | 0.131 | 0.124 | 0.095 | 0.117 | 0.099 | 0.117 | 0.085 | 0.073 |
| 20 | <i>Monotes kerstingii</i> | 0.374 | 0.366 | 0.390 | 0.390 | 0.358 | 0.398 | 0.390 | 0.358 | 0.366 | 0.382 | 0.374 | 0.373 | 0.390 | 0.398 | 0.390 | 0.423 | 0.402 | 0.390 | 0.434 | 0.358 |
| 21 | <i>Parashorea globosa</i> | - | 0.024 | 0.044 | 0.044 | 0.037 | 0.037 | 0.015 | 0.037 | 0.044 | 0.117 | 0.008 | 0.032 | 0.058 | 0.051 | 0.102 | 0.044 | 0.023 | 0.044 | 0.028 | 0.037 |
| 22 | <i>Parashorea lucida</i> | 3 | - | 0.073 | 0.073 | 0.024 | 0.049 | 0.041 | 0.024 | 0.033 | 0.073 | 0.035 | 0.064 | 0.089 | 0.081 | 0.081 | 0.073 | 0.051 | 0.073 | 0.057 | 0.024 |
| 23 | <i>Shorea acuminata</i> | 6 | 9 | - | 0.000 | 0.080 | 0.037 | 0.051 | 0.080 | 0.073 | 0.146 | 0.039 | 0.008 | 0.015 | 0.007 | 0.131 | 0.029 | 0.008 | 0.000 | 0.019 | 0.080 |
| 24 | <i>Shorea andulensis</i> | 6 | 9 | 0 | - | 0.080 | 0.037 | 0.051 | 0.080 | 0.073 | 0.146 | 0.039 | 0.008 | 0.015 | 0.007 | 0.131 | 0.029 | 0.008 | 0.000 | 0.019 | 0.080 |
| 25 | <i>Shorea acuminatissima</i> | 5 | 3 | 11 | 11 | - | 0.073 | 0.051 | 0.000 | 0.007 | 0.109 | 0.047 | 0.073 | 0.095 | 0.088 | 0.095 | 0.080 | 0.061 | 0.080 | 0.066 | 0.000 |
| 26 | <i>Shorea balangeran</i> | 5 | 6 | 5 | 5 | 10 | - | 0.044 | 0.073 | 0.080 | 0.124 | 0.031 | 0.048 | 0.051 | 0.044 | 0.124 | 0.037 | 0.031 | 0.037 | 0.019 | 0.073 |
| 27 | <i>Shorea blumutensis</i> | 2 | 5 | 7 | 7 | 7 | 6 | - | 0.051 | 0.058 | 0.124 | 0.016 | 0.048 | 0.066 | 0.058 | 0.109 | 0.051 | 0.038 | 0.051 | 0.038 | 0.051 |
| 28 | <i>Shorea dasyphylla</i> | 5 | 3 | 11 | 11 | 0 | 10 | 7 | - | 0.007 | 0.109 | 0.047 | 0.073 | 0.095 | 0.088 | 0.095 | 0.080 | 0.061 | 0.080 | 0.066 | 0.000 |
| 29 | <i>Shorea faguetiana</i> | 6 | 4 | 10 | 10 | 1 | 11 | 8 | 1 | - | 0.117 | 0.054 | 0.065 | 0.088 | 0.080 | 0.102 | 0.073 | 0.053 | 0.073 | 0.066 | 0.007 |
| 30 | <i>Shorea fallax</i> | 16 | 9 | 20 | 20 | 15 | 17 | 17 | 15 | 16 | - | 0.124 | 0.145 | 0.161 | 0.153 | 0.029 | 0.146 | 0.145 | 0.146 | 0.094 | 0.109 |

(Continued)

Appendix 5. Pairwise distance between species of Dipterocarpaceae: total character differences (below diagonal) and mean character differences (above diagonal)

| No | Species | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | |
|----|------------------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 1 | <i>Anisoptera costata</i> | 0.328 | 0.336 | 0.336 | 0.328 | 0.326 | 0.282 | 0.314 | 0.299 | 0.321 | 0.328 | 0.299 | 0.336 | 0.175 | 0.168 | 0.182 | 0.197 | 0.197 | 0.197 | 0.197 | 0.197 |
| 2 | <i>Anisoptera marginata</i> | 0.328 | 0.336 | 0.336 | 0.328 | 0.326 | 0.282 | 0.314 | 0.299 | 0.321 | 0.328 | 0.299 | 0.336 | 0.175 | 0.168 | 0.182 | 0.197 | 0.197 | 0.197 | 0.197 | 0.197 |
| 3 | <i>Anisoptera reticulata</i> | 0.343 | 0.343 | 0.343 | 0.336 | 0.333 | 0.282 | 0.321 | 0.307 | 0.328 | 0.336 | 0.307 | 0.343 | 0.190 | 0.168 | 0.182 | 0.197 | 0.197 | 0.197 | 0.197 | 0.197 |
| 4 | <i>Cotylelobium lanceolatum</i> | 0.311 | 0.311 | 0.326 | 0.304 | 0.291 | 0.235 | 0.281 | 0.274 | 0.296 | 0.304 | 0.274 | 0.304 | 0.170 | 0.156 | 0.170 | 0.185 | 0.185 | 0.185 | 0.185 | 0.185 |
| 5 | <i>Dipterocarpus grandiflorus</i> | 0.299 | 0.307 | 0.321 | 0.299 | 0.302 | 0.265 | 0.285 | 0.270 | 0.292 | 0.299 | 0.307 | 0.307 | 0.263 | 0.226 | 0.226 | 0.241 | 0.241 | 0.241 | 0.241 | 0.241 |
| 6 | <i>Dipterocarpus oblongifolius</i> | 0.292 | 0.299 | 0.314 | 0.292 | 0.295 | 0.256 | 0.277 | 0.263 | 0.285 | 0.292 | 0.299 | 0.299 | 0.255 | 0.219 | 0.219 | 0.234 | 0.234 | 0.234 | 0.234 | 0.234 |
| 7 | <i>Dipterocarpus retusus</i> | 0.292 | 0.299 | 0.314 | 0.292 | 0.295 | 0.256 | 0.277 | 0.263 | 0.285 | 0.292 | 0.299 | 0.299 | 0.255 | 0.219 | 0.219 | 0.234 | 0.234 | 0.234 | 0.234 | 0.234 |
| 8 | <i>Dipterocarpus rigidus</i> | 0.292 | 0.299 | 0.314 | 0.292 | 0.295 | 0.256 | 0.277 | 0.263 | 0.285 | 0.292 | 0.299 | 0.299 | 0.241 | 0.219 | 0.219 | 0.234 | 0.234 | 0.234 | 0.234 | 0.234 |
| 9 | <i>Dipterocarpus tempehes</i> | 0.307 | 0.314 | 0.299 | 0.307 | 0.310 | 0.274 | 0.292 | 0.277 | 0.299 | 0.307 | 0.285 | 0.314 | 0.255 | 0.219 | 0.219 | 0.234 | 0.234 | 0.234 | 0.234 | 0.234 |
| 10 | <i>Dryobalanops aromatica</i> | 0.219 | 0.226 | 0.226 | 0.219 | 0.217 | 0.179 | 0.219 | 0.204 | 0.212 | 0.219 | 0.212 | 0.226 | 0.255 | 0.248 | 0.241 | 0.263 | 0.263 | 0.263 | 0.263 | 0.263 |
| 11 | <i>Dryobalanops lanceolata</i> | 0.212 | 0.219 | 0.219 | 0.219 | 0.209 | 0.171 | 0.212 | 0.197 | 0.212 | 0.219 | 0.204 | 0.219 | 0.248 | 0.248 | 0.241 | 0.263 | 0.263 | 0.263 | 0.263 | 0.263 |
| 12 | <i>Hopea bancana</i> | 0.117 | 0.124 | 0.124 | 0.124 | 0.124 | 0.103 | 0.117 | 0.117 | 0.117 | 0.124 | 0.102 | 0.124 | 0.299 | 0.292 | 0.292 | 0.307 | 0.307 | 0.307 | 0.307 | 0.307 |
| 13 | <i>Hopea celebica</i> | 0.117 | 0.124 | 0.124 | 0.124 | 0.124 | 0.103 | 0.117 | 0.117 | 0.117 | 0.124 | 0.102 | 0.124 | 0.299 | 0.292 | 0.292 | 0.307 | 0.307 | 0.307 | 0.307 | 0.307 |
| 14 | <i>Hopea dryobalanoides</i> | 0.117 | 0.124 | 0.124 | 0.124 | 0.124 | 0.103 | 0.117 | 0.117 | 0.117 | 0.124 | 0.109 | 0.124 | 0.299 | 0.292 | 0.292 | 0.307 | 0.307 | 0.307 | 0.307 | 0.307 |
| 15 | <i>Hopea griffithii</i> | 0.135 | 0.143 | 0.143 | 0.143 | 0.144 | 0.123 | 0.135 | 0.143 | 0.143 | 0.143 | 0.111 | 0.143 | 0.294 | 0.286 | 0.278 | 0.302 | 0.302 | 0.302 | 0.302 | 0.302 |
| 16 | <i>Hopea mengarawan</i> | 0.161 | 0.168 | 0.168 | 0.168 | 0.171 | 0.154 | 0.161 | 0.161 | 0.161 | 0.168 | 0.124 | 0.168 | 0.299 | 0.292 | 0.285 | 0.307 | 0.307 | 0.307 | 0.307 | 0.307 |
| 17 | <i>Hopea nigra</i> | 0.124 | 0.131 | 0.131 | 0.131 | 0.132 | 0.111 | 0.124 | 0.124 | 0.124 | 0.131 | 0.117 | 0.131 | 0.307 | 0.299 | 0.299 | 0.314 | 0.314 | 0.314 | 0.314 | 0.314 |
| 18 | <i>Hopea odorata</i> | 0.124 | 0.131 | 0.131 | 0.131 | 0.132 | 0.111 | 0.124 | 0.124 | 0.124 | 0.131 | 0.102 | 0.131 | 0.307 | 0.299 | 0.299 | 0.314 | 0.314 | 0.314 | 0.314 | 0.314 |
| 19 | <i>Hopea sangal</i> | 0.109 | 0.117 | 0.117 | 0.117 | 0.116 | 0.094 | 0.109 | 0.109 | 0.109 | 0.117 | 0.088 | 0.117 | 0.299 | 0.292 | 0.292 | 0.299 | 0.299 | 0.299 | 0.299 | 0.299 |
| 20 | <i>Monotes kerstingii</i> | 0.382 | 0.390 | 0.374 | 0.423 | 0.374 | 0.402 | 0.415 | 0.407 | 0.415 | 0.423 | 0.390 | 0.390 | 0.415 | 0.382 | 0.407 | 0.415 | 0.415 | 0.415 | 0.415 | 0.415 |
| 21 | <i>Parashorea globosa</i> | 0.037 | 0.044 | 0.058 | 0.044 | 0.039 | 0.026 | 0.051 | 0.037 | 0.037 | 0.044 | 0.109 | 0.044 | 0.292 | 0.292 | 0.292 | 0.307 | 0.307 | 0.307 | 0.307 | 0.307 |
| 22 | <i>Parashorea lucida</i> | 0.065 | 0.073 | 0.057 | 0.073 | 0.070 | 0.051 | 0.065 | 0.057 | 0.065 | 0.073 | 0.081 | 0.073 | 0.293 | 0.268 | 0.268 | 0.285 | 0.285 | 0.285 | 0.285 | 0.285 |
| 23 | <i>Shorea acuminata</i> | 0.007 | 0.007 | 0.022 | 0.029 | 0.000 | 0.009 | 0.037 | 0.073 | 0.022 | 0.029 | 0.139 | 0.000 | 0.336 | 0.336 | 0.336 | 0.350 | 0.350 | 0.350 | 0.350 | 0.350 |
| 24 | <i>Shorea andulensis</i> | 0.007 | 0.007 | 0.022 | 0.029 | 0.000 | 0.009 | 0.037 | 0.073 | 0.022 | 0.029 | 0.139 | 0.000 | 0.336 | 0.336 | 0.336 | 0.350 | 0.350 | 0.350 | 0.350 | 0.350 |
| 25 | <i>Shorea acuminatissima</i> | 0.073 | 0.080 | 0.080 | 0.080 | 0.078 | 0.060 | 0.088 | 0.058 | 0.073 | 0.080 | 0.102 | 0.080 | 0.285 | 0.299 | 0.299 | 0.314 | 0.314 | 0.314 | 0.314 | 0.314 |
| 26 | <i>Shorea balangeran</i> | 0.044 | 0.044 | 0.058 | 0.037 | 0.039 | 0.017 | 0.015 | 0.066 | 0.029 | 0.037 | 0.117 | 0.037 | 0.299 | 0.299 | 0.299 | 0.314 | 0.314 | 0.314 | 0.314 | 0.314 |
| 27 | <i>Shorea blumutensis</i> | 0.051 | 0.051 | 0.066 | 0.051 | 0.047 | 0.034 | 0.058 | 0.037 | 0.044 | 0.051 | 0.117 | 0.051 | 0.307 | 0.307 | 0.307 | 0.321 | 0.321 | 0.321 | 0.321 | 0.321 |
| 28 | <i>Shorea dasyphylla</i> | 0.073 | 0.080 | 0.080 | 0.080 | 0.078 | 0.060 | 0.088 | 0.058 | 0.073 | 0.080 | 0.102 | 0.080 | 0.285 | 0.299 | 0.299 | 0.314 | 0.314 | 0.314 | 0.314 | 0.314 |
| 29 | <i>Shorea faguetiana</i> | 0.066 | 0.073 | 0.073 | 0.073 | 0.070 | 0.051 | 0.080 | 0.066 | 0.066 | 0.073 | 0.109 | 0.073 | 0.292 | 0.307 | 0.307 | 0.321 | 0.321 | 0.321 | 0.321 | 0.321 |
| 30 | <i>Shorea fallax</i> | 0.153 | 0.153 | 0.139 | 0.146 | 0.147 | 0.111 | 0.139 | 0.131 | 0.139 | 0.146 | 0.022 | 0.146 | 0.292 | 0.277 | 0.277 | 0.292 | 0.292 | 0.292 | 0.292 | 0.292 |

(Continued)

Appendix 5. Pairwise distance between species of Dipterocarpaceae: total character differences (below diagonal) and mean character differences (above diagonal)

| No | Species | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
|----|-----------------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| 31 | <i>Shorea guiso</i> | 38 | 38 | 39 | 34 | 35 | 34 | 34 | 34 | 36 | 24 | 23 | 12 | 12 | 12 | 14 | 18 | 13 | 13 | 11 | 43 |
| 32 | <i>Shorea javanica</i> | 41 | 41 | 43 | 40 | 39 | 38 | 38 | 38 | 40 | 29 | 28 | 15 | 15 | 15 | 16 | 20 | 16 | 16 | 14 | 41 |
| 33 | <i>Shorea johorensis</i> | 46 | 46 | 47 | 41 | 42 | 41 | 41 | 41 | 43 | 33 | 32 | 19 | 19 | 19 | 20 | 25 | 20 | 20 | 18 | 48 |
| 34 | <i>Shorea leprosula</i> | 45 | 45 | 46 | 42 | 42 | 41 | 41 | 41 | 43 | 31 | 31 | 18 | 18 | 18 | 19 | 24 | 19 | 19 | 17 | 49 |
| 35 | <i>Shorea materialis</i> | 42 | 42 | 43 | 38 | 43 | 42 | 42 | 42 | 40 | 30 | 29 | 15 | 15 | 16 | 15 | 18 | 17 | 15 | 13 | 48 |
| 36 | <i>Shorea macrophylla</i> | 45 | 45 | 46 | 41 | 41 | 40 | 40 | 40 | 42 | 30 | 30 | 17 | 17 | 17 | 18 | 23 | 18 | 18 | 16 | 52 |
| 37 | <i>Shorea macroptera</i> | 40 | 40 | 42 | 37 | 37 | 36 | 36 | 36 | 38 | 26 | 25 | 14 | 14 | 14 | 15 | 20 | 15 | 15 | 13 | 47 |
| 38 | <i>Shorea mecistopteryx</i> | 46 | 46 | 47 | 41 | 42 | 41 | 41 | 41 | 43 | 31 | 30 | 17 | 17 | 17 | 18 | 23 | 18 | 18 | 16 | 48 |
| 39 | <i>Shorea montigena</i> | 29 | 29 | 29 | 22 | 24 | 23 | 23 | 23 | 25 | 21 | 20 | 12 | 12 | 10 | 12 | 14 | 11 | 11 | 9 | 46 |
| 40 | <i>Shorea multiflora</i> | 41 | 41 | 43 | 40 | 37 | 36 | 36 | 34 | 36 | 26 | 25 | 10 | 10 | 12 | 14 | 18 | 13 | 11 | 10 | 44 |
| 41 | <i>Shorea ovalis</i> | 45 | 45 | 47 | 42 | 41 | 40 | 40 | 40 | 42 | 30 | 29 | 16 | 16 | 16 | 17 | 22 | 17 | 17 | 15 | 47 |
| 42 | <i>Shorea palembanica</i> | 46 | 46 | 47 | 42 | 42 | 41 | 41 | 41 | 43 | 31 | 30 | 17 | 17 | 17 | 18 | 23 | 18 | 18 | 16 | 48 |
| 43 | <i>Shorea parvifolia</i> | 46 | 46 | 47 | 44 | 44 | 43 | 43 | 43 | 41 | 31 | 30 | 17 | 17 | 17 | 18 | 23 | 18 | 18 | 16 | 46 |
| 44 | <i>Shorea pinanga</i> | 45 | 45 | 46 | 41 | 41 | 40 | 40 | 40 | 42 | 30 | 30 | 17 | 17 | 17 | 18 | 23 | 18 | 18 | 16 | 52 |
| 45 | <i>Shorea platyclados</i> | 42 | 42 | 43 | 37 | 39 | 38 | 38 | 38 | 40 | 28 | 27 | 16 | 16 | 16 | 17 | 22 | 17 | 17 | 15 | 43 |
| 46 | <i>Shorea scaberrima</i> | 33 | 33 | 33 | 27 | 31 | 30 | 30 | 30 | 32 | 21 | 20 | 12 | 12 | 12 | 13 | 18 | 13 | 13 | 11 | 47 |
| 47 | <i>Shorea selanica</i> | 43 | 43 | 44 | 38 | 39 | 38 | 38 | 38 | 40 | 30 | 29 | 16 | 16 | 16 | 17 | 22 | 17 | 17 | 15 | 51 |
| 48 | <i>Shorea seminis</i> | 41 | 41 | 42 | 37 | 37 | 36 | 36 | 36 | 38 | 28 | 27 | 16 | 16 | 16 | 18 | 22 | 17 | 17 | 15 | 50 |
| 49 | <i>Shorea splendida</i> | 44 | 44 | 45 | 40 | 40 | 39 | 39 | 39 | 41 | 29 | 29 | 16 | 16 | 16 | 17 | 22 | 17 | 17 | 15 | 51 |
| 50 | <i>Shorea stenoptera</i> | 45 | 45 | 46 | 41 | 41 | 40 | 40 | 40 | 42 | 30 | 30 | 17 | 17 | 17 | 18 | 23 | 18 | 18 | 16 | 52 |
| 51 | <i>Shorea virescens</i> | 41 | 41 | 42 | 37 | 42 | 41 | 41 | 41 | 41 | 39 | 29 | 28 | 14 | 14 | 15 | 14 | 17 | 16 | 14 | 48 |
| 52 | <i>Shorea xanthophylla</i> | 46 | 46 | 47 | 41 | 42 | 41 | 41 | 41 | 43 | 31 | 30 | 17 | 17 | 17 | 18 | 23 | 18 | 18 | 16 | 48 |
| 53 | <i>Upuna borneensis</i> | 24 | 24 | 26 | 23 | 36 | 35 | 35 | 33 | 35 | 35 | 34 | 41 | 41 | 41 | 37 | 41 | 42 | 42 | 41 | 51 |
| 54 | <i>Vatica bantamensis</i> | 23 | 23 | 23 | 21 | 31 | 30 | 30 | 30 | 30 | 34 | 34 | 40 | 40 | 40 | 36 | 40 | 41 | 41 | 40 | 47 |
| 55 | <i>Vatica bella</i> | 25 | 25 | 25 | 23 | 31 | 30 | 30 | 30 | 30 | 33 | 33 | 40 | 40 | 40 | 35 | 39 | 41 | 41 | 40 | 50 |
| 56 | <i>Vatica granulata</i> | 27 | 27 | 27 | 25 | 33 | 32 | 32 | 32 | 32 | 36 | 36 | 42 | 42 | 42 | 38 | 42 | 43 | 43 | 41 | 51 |
| 57 | <i>Vatica pauciflora</i> | 27 | 27 | 27 | 25 | 33 | 32 | 32 | 32 | 32 | 36 | 36 | 42 | 42 | 42 | 38 | 42 | 43 | 43 | 41 | 51 |
| 58 | <i>Vatica rassak</i> | 27 | 27 | 27 | 25 | 33 | 32 | 32 | 32 | 32 | 36 | 36 | 42 | 42 | 42 | 38 | 42 | 43 | 43 | 41 | 51 |
| 59 | <i>Vatica venulosa</i> | 27 | 27 | 27 | 25 | 33 | 32 | 32 | 32 | 32 | 36 | 36 | 42 | 42 | 42 | 38 | 42 | 43 | 43 | 41 | 51 |

(Continued)

Appendix 5. Pairwise distance between species of Dipterocarpaceae: total character differences (below diagonal) and mean character differences (above diagonal)

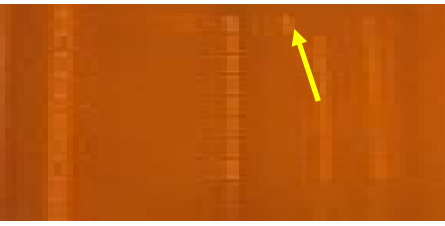
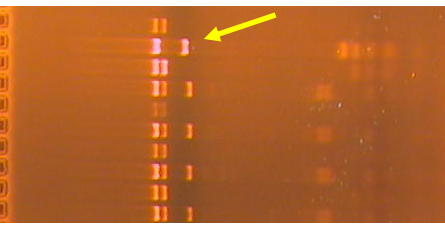
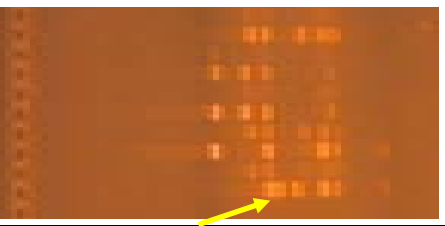
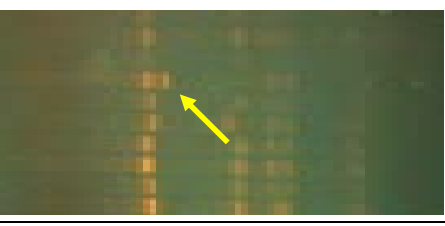
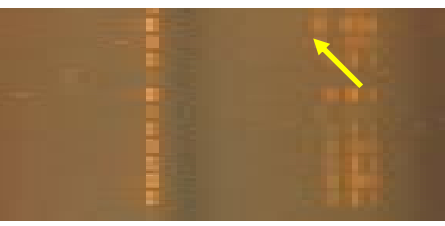

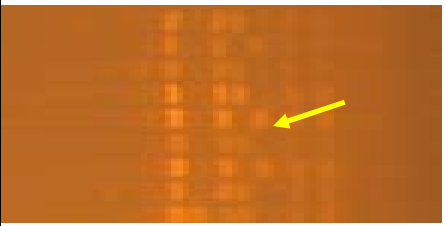
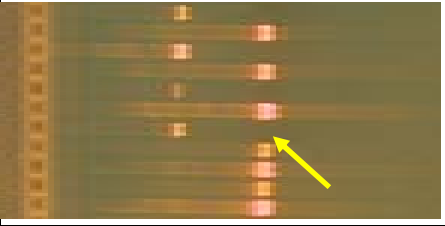
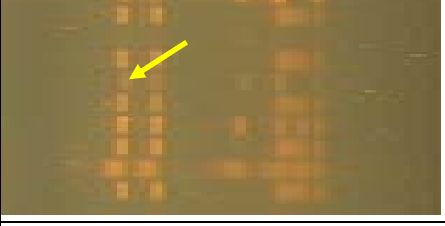
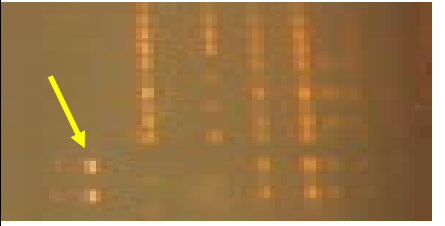
| No | Species | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 |
|----|----------------------------|----|----|----|----|----|----|----|----|----|----|----|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 31 | <i>Shorea guiso</i> | 1 | 4 | 5 | 5 | 6 | 4 | 2 | 6 | 7 | 16 | - | 0.034 | 0.054 | 0.047 | 0.109 | 0.039 | 0.024 | 0.039 | 0.020 | 0.047 |
| 32 | <i>Shorea javanica</i> | 4 | 7 | 1 | 1 | 9 | 6 | 6 | 9 | 8 | 18 | 4 | - | 0.024 | 0.016 | 0.129 | 0.040 | 0.000 | 0.008 | 0.022 | 0.073 |
| 33 | <i>Shorea johorensis</i> | 8 | 11 | 2 | 2 | 13 | 7 | 9 | 13 | 12 | 22 | 7 | 3 | - | 0.022 | 0.146 | 0.044 | 0.023 | 0.015 | 0.038 | 0.095 |
| 34 | <i>Shorea leprosula</i> | 7 | 10 | 1 | 1 | 12 | 6 | 8 | 12 | 11 | 21 | 6 | 2 | 3 | - | 0.139 | 0.029 | 0.015 | 0.007 | 0.028 | 0.088 |
| 35 | <i>Shorea materialis</i> | 14 | 10 | 18 | 18 | 13 | 17 | 15 | 13 | 14 | 4 | 14 | 16 | 20 | 19 | - | 0.131 | 0.130 | 0.131 | 0.104 | 0.095 |
| 36 | <i>Shorea macrophylla</i> | 6 | 9 | 4 | 4 | 11 | 5 | 7 | 11 | 10 | 20 | 5 | 5 | 6 | 4 | 18 | - | 0.023 | 0.029 | 0.038 | 0.080 |
| 37 | <i>Shorea macroptera</i> | 3 | 6 | 1 | 1 | 8 | 4 | 5 | 8 | 7 | 19 | 3 | 0 | 3 | 2 | 17 | 3 | - | 0.008 | 0.028 | 0.061 |
| 38 | <i>Shorea mecistoptyx</i> | 6 | 9 | 0 | 0 | 11 | 5 | 7 | 11 | 10 | 20 | 5 | 1 | 2 | 1 | 18 | 4 | 1 | - | 0.019 | 0.080 |
| 39 | <i>Shorea montigena</i> | 3 | 6 | 2 | 2 | 7 | 2 | 4 | 7 | 7 | 10 | 2 | 2 | 4 | 3 | 11 | 4 | 3 | 2 | - | 0.066 |
| 40 | <i>Shorea multiflora</i> | 5 | 3 | 11 | 11 | 0 | 10 | 7 | 0 | 1 | 15 | 6 | 9 | 13 | 12 | 13 | 11 | 8 | 11 | 7 | - |
| 41 | <i>Shorea ovalis</i> | 5 | 8 | 1 | 1 | 10 | 6 | 7 | 10 | 9 | 21 | 5 | 0 | 3 | 2 | 19 | 5 | 0 | 1 | 3 | 10 |
| 42 | <i>Shorea palembanica</i> | 6 | 9 | 1 | 1 | 11 | 6 | 7 | 11 | 10 | 21 | 5 | 1 | 3 | 2 | 19 | 5 | 1 | 1 | 3 | 11 |
| 43 | <i>Shorea parvifolia</i> | 8 | 7 | 3 | 3 | 11 | 8 | 9 | 11 | 10 | 19 | 7 | 3 | 5 | 4 | 17 | 7 | 3 | 3 | 5 | 11 |
| 44 | <i>Shorea pinanga</i> | 6 | 9 | 4 | 4 | 11 | 5 | 7 | 11 | 10 | 20 | 5 | 5 | 6 | 4 | 18 | 0 | 3 | 4 | 4 | 11 |
| 45 | <i>Shorea platyclados</i> | 5 | 8 | 0 | 0 | 10 | 5 | 6 | 10 | 9 | 19 | 5 | 1 | 2 | 1 | 17 | 4 | 1 | 0 | 2 | 10 |
| 46 | <i>Shorea scaberrima</i> | 3 | 6 | 1 | 1 | 7 | 2 | 4 | 7 | 6 | 13 | 2 | 1 | 3 | 2 | 14 | 3 | 2 | 1 | 1 | 7 |
| 47 | <i>Shorea selanica</i> | 7 | 8 | 5 | 5 | 12 | 2 | 8 | 12 | 11 | 19 | 6 | 6 | 7 | 6 | 19 | 3 | 4 | 5 | 3 | 12 |
| 48 | <i>Shorea seminis</i> | 5 | 7 | 10 | 10 | 8 | 9 | 5 | 8 | 9 | 18 | 5 | 9 | 12 | 11 | 16 | 10 | 8 | 10 | 6 | 8 |
| 49 | <i>Shorea splendida</i> | 5 | 8 | 3 | 3 | 10 | 4 | 6 | 10 | 9 | 19 | 4 | 4 | 5 | 3 | 17 | 1 | 2 | 3 | 3 | 10 |
| 50 | <i>Shorea stenoptera</i> | 6 | 9 | 4 | 4 | 11 | 5 | 7 | 11 | 10 | 20 | 5 | 5 | 6 | 4 | 18 | 0 | 3 | 4 | 4 | 11 |
| 51 | <i>Shorea virescens</i> | 15 | 10 | 19 | 19 | 14 | 16 | 16 | 14 | 15 | 3 | 15 | 17 | 21 | 20 | 1 | 19 | 18 | 19 | 11 | 14 |
| 52 | <i>Shorea xanthophylla</i> | 6 | 9 | 0 | 0 | 11 | 5 | 7 | 11 | 10 | 20 | 5 | 1 | 2 | 1 | 18 | 4 | 1 | 0 | 2 | 11 |
| 53 | <i>Upuna borneensis</i> | 40 | 36 | 46 | 46 | 39 | 41 | 42 | 39 | 40 | 40 | 38 | 43 | 46 | 47 | 42 | 46 | 40 | 46 | 29 | 39 |
| 54 | <i>Vatica bantamensis</i> | 40 | 33 | 46 | 46 | 41 | 41 | 42 | 41 | 42 | 38 | 38 | 43 | 46 | 46 | 40 | 45 | 41 | 46 | 27 | 41 |
| 55 | <i>Vatica bella</i> | 40 | 33 | 46 | 46 | 41 | 41 | 42 | 41 | 42 | 38 | 38 | 43 | 46 | 46 | 39 | 45 | 41 | 46 | 27 | 41 |
| 56 | <i>Vatica granulata</i> | 42 | 35 | 48 | 48 | 43 | 43 | 44 | 43 | 44 | 40 | 40 | 45 | 48 | 48 | 42 | 47 | 43 | 48 | 29 | 43 |
| 57 | <i>Vatica pauciflora</i> | 42 | 35 | 48 | 48 | 43 | 43 | 44 | 43 | 44 | 40 | 40 | 45 | 48 | 48 | 42 | 47 | 43 | 48 | 29 | 43 |
| 58 | <i>Vatica rassak</i> | 42 | 35 | 48 | 48 | 43 | 43 | 44 | 43 | 44 | 40 | 40 | 45 | 48 | 48 | 42 | 47 | 43 | 48 | 29 | 43 |
| 59 | <i>Vatica venulosa</i> | 42 | 35 | 48 | 48 | 43 | 43 | 44 | 43 | 44 | 40 | 40 | 45 | 48 | 48 | 42 | 47 | 43 | 48 | 29 | 43 |

(Continued)

Appendix 5. Pairwise distance between species of Dipterocharaceae: total character differences (below diagonal) and mean character differences (above diagonal)

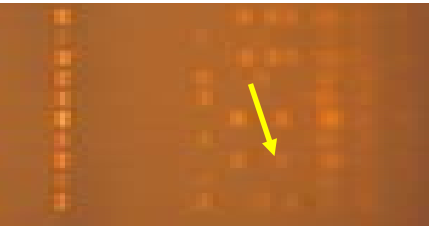
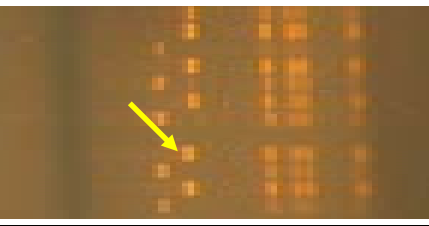
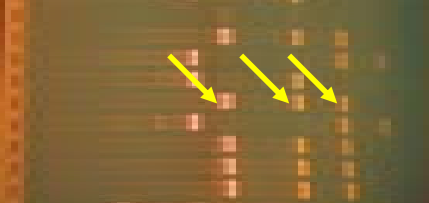
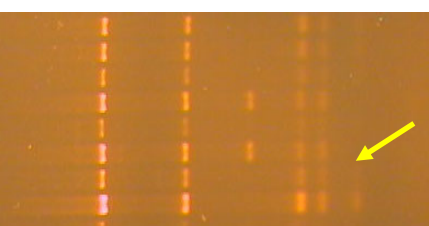
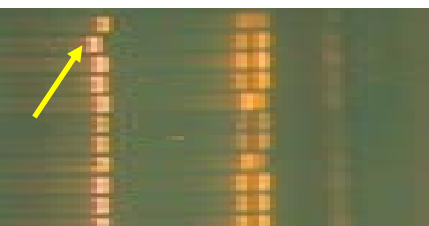
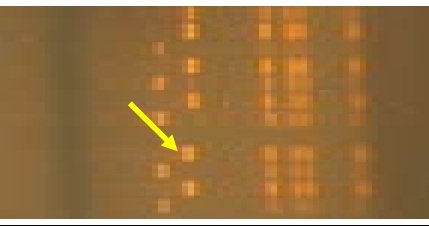
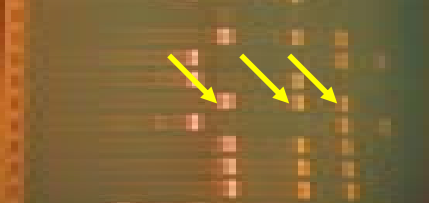
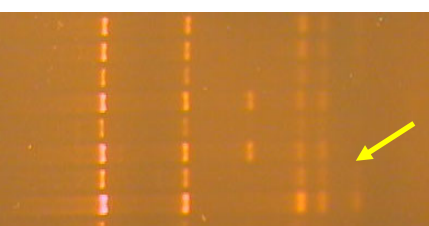
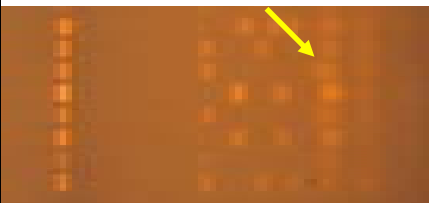
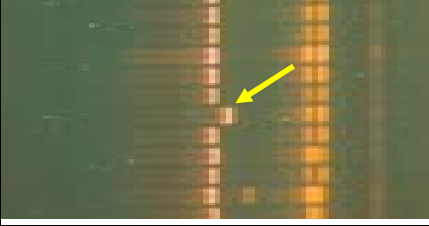

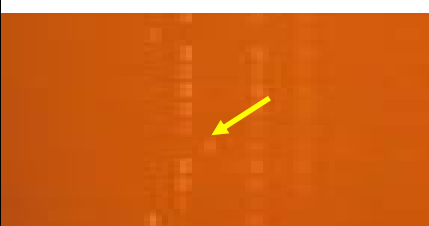

| No | Species | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | | |
|----|-----------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|--------|--------|--------|--------|--------|
| 31 | <i>Shorea guiso</i> | 0.039 | 0.039 | 0.054 | 0.039 | 0.039 | 0.018 | 0.047 | 0.039 | 0.031 | 0.039 | 0.116 | 0.039 | 0.295 | 0.295 | 0.295 | 0.310 | 0.310 | 0.310 | 0.310 | 0.310 | |
| 32 | <i>Shorea javanica</i> | 0.000 | 0.008 | 0.024 | 0.040 | 0.009 | 0.010 | 0.048 | 0.073 | 0.032 | 0.040 | 0.137 | 0.008 | 0.347 | 0.347 | 0.347 | 0.363 | 0.363 | 0.363 | 0.363 | 0.363 | |
| 33 | <i>Shorea johorensis</i> | 0.022 | 0.022 | 0.037 | 0.044 | 0.016 | 0.026 | 0.051 | 0.088 | 0.037 | 0.044 | 0.153 | 0.015 | 0.336 | 0.336 | 0.336 | 0.350 | 0.350 | 0.350 | 0.350 | 0.350 | 0.350 |
| 34 | <i>Shorea leprosula</i> | 0.015 | 0.015 | 0.029 | 0.029 | 0.008 | 0.017 | 0.044 | 0.080 | 0.022 | 0.029 | 0.146 | 0.007 | 0.343 | 0.336 | 0.336 | 0.350 | 0.350 | 0.350 | 0.350 | 0.350 | 0.350 |
| 35 | <i>Shorea materialis</i> | 0.139 | 0.139 | 0.124 | 0.131 | 0.132 | 0.120 | 0.139 | 0.117 | 0.124 | 0.131 | 0.007 | 0.131 | 0.307 | 0.292 | 0.285 | 0.307 | 0.307 | 0.307 | 0.307 | 0.307 | 0.307 |
| 36 | <i>Shorea macrophylla</i> | 0.037 | 0.037 | 0.051 | 0.000 | 0.031 | 0.026 | 0.022 | 0.073 | 0.007 | 0.000 | 0.139 | 0.029 | 0.336 | 0.328 | 0.328 | 0.343 | 0.343 | 0.343 | 0.343 | 0.343 | 0.343 |
| 37 | <i>Shorea macroptera</i> | 0.000 | 0.008 | 0.023 | 0.023 | 0.008 | 0.017 | 0.031 | 0.061 | 0.015 | 0.023 | 0.137 | 0.008 | 0.305 | 0.313 | 0.313 | 0.328 | 0.328 | 0.328 | 0.328 | 0.328 | 0.328 |
| 38 | <i>Shorea mecistopteryx</i> | 0.007 | 0.007 | 0.022 | 0.029 | 0.000 | 0.009 | 0.037 | 0.073 | 0.022 | 0.029 | 0.139 | 0.000 | 0.336 | 0.336 | 0.336 | 0.350 | 0.350 | 0.350 | 0.350 | 0.350 | 0.350 |
| 39 | <i>Shorea montigena</i> | 0.028 | 0.028 | 0.047 | 0.038 | 0.020 | 0.009 | 0.028 | 0.057 | 0.028 | 0.038 | 0.104 | 0.019 | 0.274 | 0.255 | 0.255 | 0.274 | 0.274 | 0.274 | 0.274 | 0.274 | 0.274 |
| 40 | <i>Shorea multiflora</i> | 0.073 | 0.080 | 0.080 | 0.080 | 0.078 | 0.060 | 0.088 | 0.058 | 0.073 | 0.080 | 0.102 | 0.080 | 0.285 | 0.299 | 0.299 | 0.314 | 0.314 | 0.314 | 0.314 | 0.314 | 0.314 |
| 41 | <i>Shorea ovalis</i> | - | 0.007 | 0.022 | 0.037 | 0.008 | 0.017 | 0.044 | 0.073 | 0.029 | 0.037 | 0.146 | 0.007 | 0.328 | 0.328 | 0.328 | 0.343 | 0.343 | 0.343 | 0.343 | 0.343 | 0.343 |
| 42 | <i>Shorea palembanica</i> | 1 | - | 0.015 | 0.037 | 0.008 | 0.017 | 0.044 | 0.073 | 0.029 | 0.037 | 0.146 | 0.007 | 0.336 | 0.336 | 0.336 | 0.350 | 0.350 | 0.350 | 0.350 | 0.350 | 0.350 |
| 43 | <i>Shorea parvifolia</i> | 3 | 2 | - | 0.051 | 0.023 | 0.034 | 0.058 | 0.088 | 0.044 | 0.051 | 0.131 | 0.022 | 0.336 | 0.336 | 0.336 | 0.350 | 0.350 | 0.350 | 0.350 | 0.350 | 0.350 |
| 44 | <i>Shorea pinanga</i> | 5 | 5 | 7 | - | 0.031 | 0.026 | 0.022 | 0.073 | 0.007 | 0.000 | 0.139 | 0.029 | 0.336 | 0.328 | 0.328 | 0.343 | 0.343 | 0.343 | 0.343 | 0.343 | 0.343 |
| 45 | <i>Shorea platyclados</i> | 1 | 1 | 3 | 4 | - | 0.009 | 0.039 | 0.070 | 0.023 | 0.031 | 0.140 | 0.000 | 0.326 | 0.326 | 0.326 | 0.341 | 0.341 | 0.341 | 0.341 | 0.341 | 0.341 |
| 46 | <i>Shorea scaberrima</i> | 2 | 2 | 4 | 3 | 1 | - | 0.017 | 0.051 | 0.017 | 0.026 | 0.120 | 0.009 | 0.299 | 0.282 | 0.282 | 0.299 | 0.299 | 0.299 | 0.299 | 0.299 | 0.299 |
| 47 | <i>Shorea setanica</i> | 6 | 6 | 8 | 3 | 5 | 2 | - | 0.080 | 0.029 | 0.022 | 0.131 | 0.037 | 0.314 | 0.314 | 0.314 | 0.328 | 0.328 | 0.328 | 0.328 | 0.328 | 0.328 |
| 48 | <i>Shorea seminis</i> | 10 | 10 | 12 | 10 | 9 | 6 | 11 | - | 0.066 | 0.073 | 0.124 | 0.073 | 0.299 | 0.285 | 0.285 | 0.299 | 0.299 | 0.299 | 0.299 | 0.299 | 0.299 |
| 49 | <i>Shorea splendida</i> | 4 | 4 | 6 | 1 | 3 | 2 | 4 | 9 | - | 0.007 | 0.131 | 0.022 | 0.328 | 0.321 | 0.321 | 0.336 | 0.336 | 0.336 | 0.336 | 0.336 | 0.336 |
| 50 | <i>Shorea stenoptera</i> | 5 | 5 | 7 | 0 | 4 | 3 | 3 | 10 | 1 | - | 0.139 | 0.029 | 0.336 | 0.328 | 0.328 | 0.343 | 0.343 | 0.343 | 0.343 | 0.343 | 0.343 |
| 51 | <i>Shorea virescens</i> | 20 | 20 | 18 | 19 | 18 | 14 | 18 | 17 | 18 | 19 | - | 0.139 | 0.299 | 0.285 | 0.277 | 0.299 | 0.299 | 0.299 | 0.299 | 0.299 | 0.299 |
| 52 | <i>Shorea xanthophylla</i> | 1 | 1 | 3 | 4 | 0 | 1 | 5 | 10 | 3 | 4 | 19 | - | 0.336 | 0.336 | 0.336 | 0.350 | 0.350 | 0.350 | 0.350 | 0.350 | 0.350 |
| 53 | <i>Upuna borneensis</i> | 45 | 46 | 46 | 46 | 42 | 35 | 43 | 41 | 45 | 46 | 41 | 46 | - | 0.161 | 0.175 | 0.175 | 0.175 | 0.175 | 0.175 | 0.175 | 0.175 |
| 54 | <i>Vatica banitamensis</i> | 45 | 46 | 46 | 45 | 42 | 33 | 43 | 39 | 44 | 45 | 39 | 46 | 22 | - | 0.022 | 0.037 | 0.029 | 0.029 | 0.029 | 0.029 | 0.029 |
| 55 | <i>Vatica bella</i> | 45 | 46 | 46 | 45 | 42 | 33 | 43 | 39 | 44 | 45 | 38 | 46 | 24 | 3 | - | 0.044 | 0.037 | 0.037 | 0.037 | 0.037 | 0.037 |
| 56 | <i>Vatica granulata</i> | 47 | 48 | 48 | 47 | 44 | 35 | 45 | 41 | 46 | 47 | 41 | 48 | 24 | 5 | 6 | - | 0.0073 | 0.0073 | 0.0073 | 0.0073 | 0.0073 |
| 57 | <i>Vatica pauciflora</i> | 47 | 48 | 48 | 47 | 44 | 35 | 45 | 41 | 46 | 47 | 41 | 48 | 24 | 4 | 5 | 1 | - | 0.000 | 0.000 | 0.000 | 0.000 |
| 58 | <i>Vatica rassak</i> | 47 | 48 | 48 | 47 | 44 | 35 | 45 | 41 | 46 | 47 | 41 | 48 | 24 | 4 | 5 | 1 | 0 | - | 0.000 | 0.000 | 0.000 |
| 59 | <i>Vatica venulosa</i> | 47 | 48 | 48 | 47 | 44 | 35 | 45 | 41 | 46 | 47 | 41 | 48 | 24 | 4 | 5 | 1 | 0 | 0 | - | 0 | - |

Appendix 6. Diagnostic characters (CI=100%) revealed by PCR-RFLP. The arrows indicated the presence/absence of bands or the corresponding restriction sites for each primer-enzyme combination and 1th character of the character list described in Appendix 1.

| | | | | |
|--|--|--|--|--|
|  |  |  |  |  |
| <i>rbcL</i> – <i>Msp</i> I (29) | <i>psaA</i> – <i>Taq</i> I (118, 120) | <i>petB</i> – <i>Taq</i> I (81) | <i>trnL-F</i> – <i>Hinf</i> I (129) | <i>petB</i> – <i>Msp</i> I (70, 71) |
| <i>Anisoptera</i> | | | | |
| <i>Dipterocarpeae+Dryobalanops</i> | | | | |
|  |  |  |  |  |
| <i>psaA</i> – <i>Msp</i> I (107) | <i>rbcL</i> – <i>Hinf</i> I (23) | <i>petB</i> – <i>Cfo</i> I (39) | <i>petB</i> – <i>Taq</i> I (80) | <i>rbcL</i> – <i>Alu</i> I (6) |
| <i>Dipterocarpeae+Dryobalanops</i> | | | | |
| <i>Dipterocarpeae</i> | | | | |
| <i>Dryobalanops</i> | | | | |

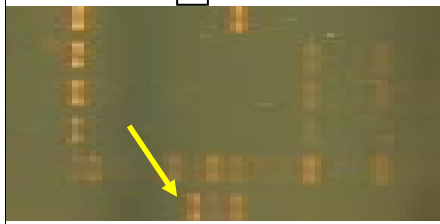
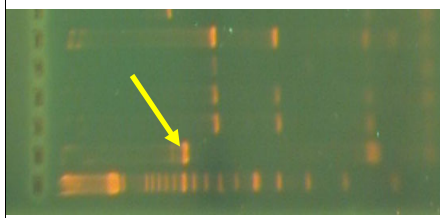
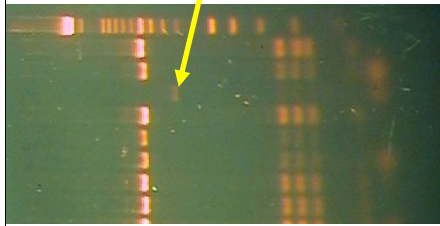

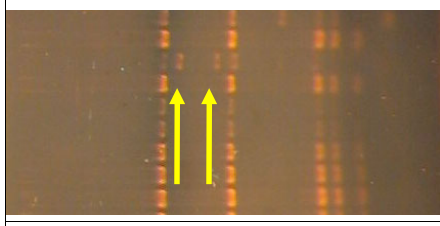
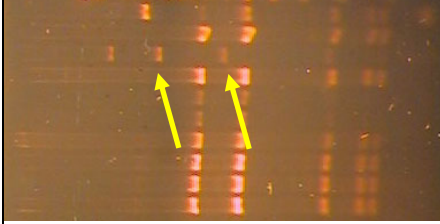
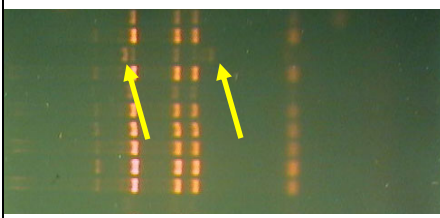
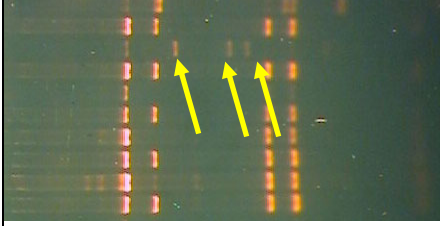
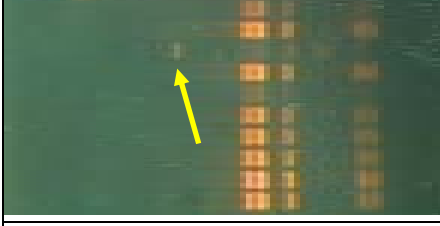
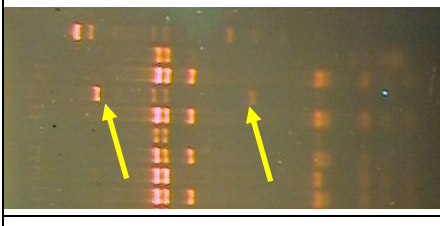
(Continued)

Appendix 6. Diagnostic characters (CI=100%) revealed by PCR-RFLP. The arrows indicated the presence/absence of bands or the corresponding restriction sites for each primer-enzyme combination and 1th character of the character list described in Appendix 1.

| <i>Dryobalanops</i> | | <i>Dryobalanops aromatica</i> | <i>Hopea + Parashorea + Shorea</i> | |
|--------------------------------------|--|---|---|--|
| <i>petB</i> – <i>Hinf</i> I (55, 58) |  180 bp |  380 bp |  750 bp 400 bp 250 bp |  110 bp |
| <i>trnL-F</i> – <i>Taq</i> I (130) |  520 bp |  380 bp |  750 bp 400 bp 250 bp |  110 bp |
| <i>petB</i> – <i>Hinf</i> I (60) | <i>Hopea</i>  140 bp | <i>H. griffithii</i> + <i>H. mengarawan</i>  450 bp | <i>Hopea mengarawan</i>  330 bp | <i>Hopea nigra</i>  600 bp |
| <i>psaA</i> – <i>Msp</i> I (106) | <i>Hopea + Parashorea + Shorea</i>  430 bp | <i>trnL-F</i> – <i>Taq</i> I (130) | <i>petB</i> – <i>Alu</i> I (34) | <i>rbcL</i> – <i>Cfo</i> I (9) |

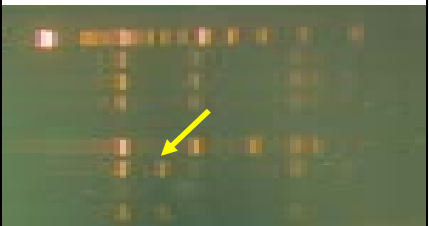
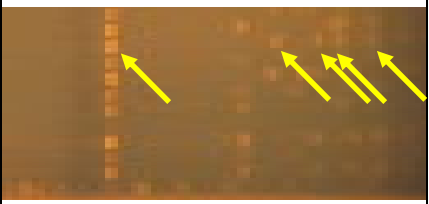
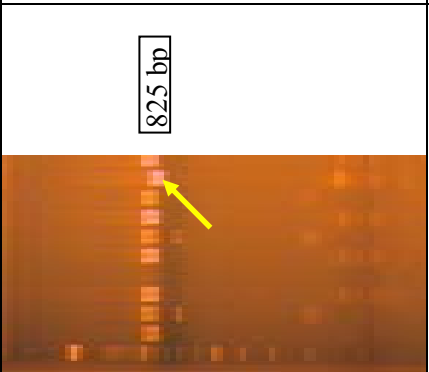


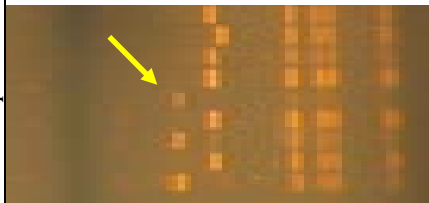
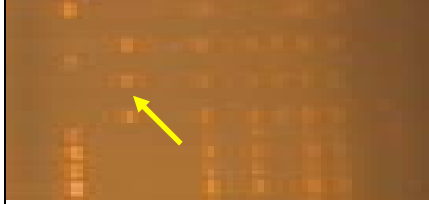
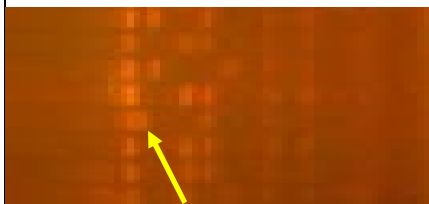

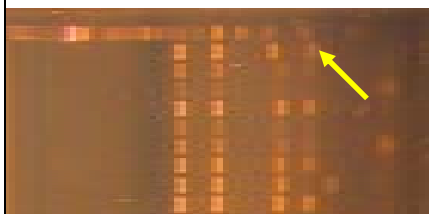
(Continued)

Appendix 6. Diagnostic characters (CI=100%) revealed by PCR-RFLP. The arrows indicated the presence/absence of bands or the corresponding restriction sites for each primer-enzyme combination and 1th character of the character list described in Appendix 1.

| <i>Monotes kerstingii</i> | | | | | |
|--|--|--|--|--|--|
|  |  |  |  |  | <i>rbcL - Cfo I (10)</i> <i>rbcL - Msp I (26)</i> <i>petB - Alu I (38)</i> <i>petB - Hae III (43)</i> <i>psaa - Cfo I (85, 86, 87)</i> |
| <i>Monotes kerstingii</i> | | | | | |
|  |  |  |  |  | <i>psaa - Hae III (93, 94)</i> <i>psaa - Hinf I (99, 100, 101)</i> <i>psaa - Msp I (104, 108, 109)</i> <i>psaa - Rsa I (113, 114)</i> <i>psaa - Taq I (116, 122)</i> |

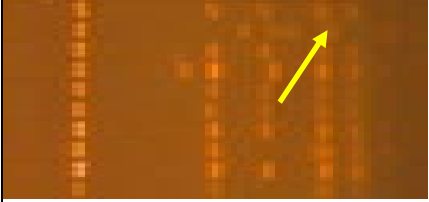
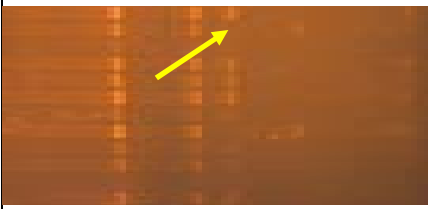
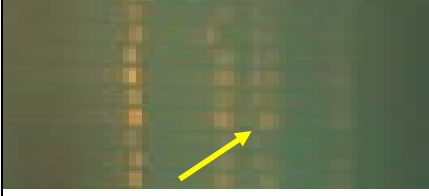
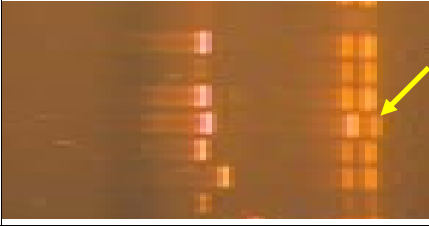
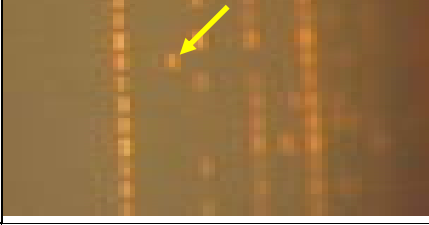
(Continued)

Appendix 6. Diagnostic characters (CI=100%) revealed by PCR-RFLP. The arrows indicated the presence/absence of bands or the corresponding restriction sites for each primer-enzyme combination and 1th character of the character list described in Appendix 1.

| | | | | | | | | | |
|---|--|---|---|--|--|---|--|--|--|
| <i>Shorea blumutensis</i> <i>psaA</i> – <i>Cfo</i> I (89) |  640 bp | <i>Shorea fallax</i> <i>petB</i> – <i>Hinf</i> I (52) |  600 bp 250 bp 160 bp 130 bp 100 bp | <i>S. fallax</i> + <i>S. materialis</i> + <i>S. virescens</i> <i>psaA</i> – <i>Taq</i> I (117, 119) |  825 bp | <i>Shorea johorensis</i> <i>petB</i> – <i>Rsa</i> I (66) |  150 bp | <i>S. materialis</i> + <i>S. virescens</i> <i>trnL-F</i> – <i>Taq</i> I (130) |  360 bp |
| <i>S. macrophylla</i> + <i>S. pinanga</i> + <i>S. stenoptera</i> + <i>S. Splendida</i> <i>trnL-F</i> – <i>Hinf</i> I (125) |  430 bp | <i>Shorea seminis</i> <i>petB</i> – <i>Hinf</i> I (45) |  450 bp | <i>rbcL</i> – <i>Hinf</i> I (20) |  380 bp | <i>petB</i> – <i>Alu</i> I (36, 37) |  180 bp | <i>petB</i> – <i>Rsa</i> I (65) |  180 bp |

(Continued)

Appendix 6. Diagnostic characters (CI=100%) revealed by PCR-RFLP. The arrows indicated the presence/absence of bands or the corresponding restriction sites for each primer-enzyme combination and 1th character of the character list described in Appendix 1.

| <i>Vatica</i> | | <i>Vatica bella</i> | | <i>V. granulata</i> + <i>V. pauciflora</i> + <i>V. rassak</i> + <i>V. venulosa</i> |
|---|---|---|---|---|
|  |  |  |  |  |
| <i>petB</i> – <i>Hinf</i> I (47) | <i>psaA</i> – <i>Hinf</i> I (98) | <i>trnL-F</i> – <i>Hinf</i> I (127) | <i>trnL-F</i> – <i>Taq</i> I (130) | <i>rbcL</i> – <i>Alu</i> I (7, 8) |

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