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Phylogeny and Biogeography of *Dendropanax* (Araliaceae), an Amphi-Pacific Disjunct Genus Between Tropical/Subtropical Asia and the Neotropics

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Abstract—*Dendropanax* (Araliaceae) is a genus of about 80 species disjunctly distributed in tropical to subtropical Asia and the Neotropics, showing an amphi-Pacific tropical disjunction. The phylogeny of the genus was constructed by sampling 95 accessions representing 33 species of *Dendropanax* and 43 closely related taxa using sequences of the nuclear ribosomal internal transcribed spacer (ITS) region and six plastid regions (the *ndhF* gene, the *trnL-trnF* region, the *rps16* intron, the *atpB-rbcL* intergenic spacer, the *rpl16* intron, and the *psbA-trnH* intergenic spacer). Phylogenetic analyses of the combined plastid and ITS data suggested that the monophyly of *Dendropanax* was not supported because the Asian *D. lancifolius* - *D. hainanensis* clade did not group with the main *Dendropanax* clade. Nevertheless, the maximally parsimonious trees (MPTs) from the analysis constraining *Dendropanax* as a monophyletic group were only one step longer than the unconstrained MPTs. The New and Old World *Dendropanax* species except *D. lancifolius* and *D. hainanensis* each formed a robustly supported clade, and the two clades were sister to each other. Based on the biogeographic analyses and fossil-calibrated Bayesian dating, *Dendropanax* was hypothesized to have originated in the Old World and migrated into the New World via the North Atlantic land bridges in the early Tertiary. The amphi-Pacific intercontinental disjunction of *Dendropanax* was dated to be 41.83 mya with a 95% high posterior density [HPD] interval of 28.46−56.15 mya.

Keywords—AmphiPacific tropical disjunction, Araliaceae, biogeography, *Dendropanax*, phylogeny.

The intercontinental disjunctions between eastern Asia and North America have been studied extensively in the last two decades (see reviews by Wen 1999, 2001; Donoghue and Smith 2004; Wen et al. 2010). Most studies so far have focused on temperate elements and have suggested the importance of the Bering land bridge for floristic exchanges between the two continents. Our insights into the evolution of intercontinental disjunctions between Asia and the New World and the regional biodiversity assembly may be hampered by the limited number of analyses on tropical lineages disjunct between the two regions. The tropical Asian-New World disjunction was referred to as the amphi-Pacific tropical disjunction by Thorne (1972). Plant taxa exhibiting such a disjunction occur in both the Neotropics and the subtropical and tropical regions on the western borders of the Pacific Ocean (van Steenis 1962; van Balgooy 1971; Thorne 1972; Wu 1983). Thorne (1972) enumerated 89 genera and eight to eleven families of flowering plants that exhibit the amphi-Pacific tropical distribution. How these taxa achieved their present amphi-Pacific disjunct ranges has long been speculated. van Steenis (1962) postulated various trans-Pacific land bridges to explain the disjunct distributions of the many amphi-Pacific plant genera. The Bering land bridge has been supported as a migration route for many disjuncts, especially those with temperate affinities (Thorne 1972; Raven and Axelrod 1974). The North Atlantic land bridges have been used to explain the migration of tropical lineages (e.g. Davis et al. 2002) in the context of the “boreotropical” hypothesis (Wolfe 1975; Lavin and Luckow 1993). Long-distance dispersal also may be important for at least some of the tropical disjunct genera with fleshy fruits or fruits that can float and remain viable for a longer time in salt water (Thorne 1972; Raven and Axelrod 1974; Givnish and Renner 2004).

Only a few taxa have been examined with molecular phylogenetic and biogeographic methods for the evolution of the disjunction between tropical Asia and the Neotropics, including *Styrax* L. section *Valvatae* Gürke (Styracaceae; Fritsch 2001, 2003), *Symplocos* Jacq. (Symplocaceae; Wang et al. 2004), and *Prunus* L. (Rosaceae; Wen et al. 2008a). An eastern Asian origin through North America to the Antilles and South America is the most likely migration route for the amphi-Pacific tropical *Styrax* section *Valvatae* and *Symplocos* (Fritsch 2001, 2003; Wang et al. 2004). Magnoliaceae contains tropical disjunctions between Asia and the Americas, and such disjunctions have been hypothesized to have resulted from the expansion of the boreotropical flora during the middle to late Eocene (Azuma et al. 2001; Nie et al. 2008). To better understand the evolutionary diversification of the amphi-Pacific tropical disjuncts, we need to evaluate phylogenetic relationships and estimate divergence times in many more lineages disjunct between tropical Asia and the Neotropics.

Dendropanax Decne. & Planch. (Araliaceae) is an excellent model for examining the evolution of the disjunction between tropical Asia and the Neotropics. The fossil record indicates that *Dendropanax* was widely distributed in the early Tertiary, ranging from California, North Dakota and South Dakota in western North America to the Mississippi Embayment area of Tennessee in eastern North America, to Europe (Lesquereux 1883; Knowlton 1911; Reid 1927; Dilcher and Dolph 1970). *Dendropanax* includes ca. 80 species distributed in the Himalaya and eastern and southeastern Asia to western Malesia and Central to South America (Shang and Lowry 2007; Wen et al. 2008b). The genus has the greatest species diversity in northwestern South America and is well developed in the southern part of Central America, Jamaica, and the southern part of eastern Asia and the bordering region of Indochina (also see Merrill 1941; Li 1942; Hoo and Tseng 1965, 1978; Adams 1972; Cannon and Cannon 1989; Mabberley 2008; Wen et al. 2001; Frodin and Govaerts 2003; Shang and Lowry 2007).

Dendropanax demonstrates a high level of morphological diversity. Species of the genus are evergreen trees or small understory shrubs. The stems are unarmed with leaves varying from simple and unlobed to 2− or 3−5-lobed, with margins entire or with a few irregular teeth, often with yellow or red translucent glandular punctae (known as translucent glands). The glands present on the leaves are useful for differentiating species (Harms 1895; Bui 1976). The inflorescence is a simple terminal umbel or a panicle of multiple umbels, or occasionally of multiple heads. The Neotropical species of *Dendropanax* commonly have paniculate or compound umbellate inflorescences, although simple umbels are also known. The Asian species of the genus are more uniform in inflorescence morphology, generally having a solitary terminal umbel, although variation from a simple umbel to a small compound inflorescence within the same species is observed in *D. chevalieri* and *D. dentiger*. Additionally, the ovary is usually 5-carpellate (to rarely 7–9-carpellate, e.g. in *D. umbellatus*, or with three to four carpels, e.g. in *D. oligodontus* and two or three in *D. kwangsiensis*) with the styles distinct or united basally or throughout into a column (Hoo and Tseng 1978; Shang and Lowry 2007). The morphological diversity has made it difficult to detect any synapomorphies for the genus.

The generic name *Dendropanax* Decne. & Planch. (1854) has been widely used by botantists in floras of both the Old and New Worlds (e.g. Li 1942; Smith 1941, 1944; Macbride 1959; Hoo and Tseng 1978; Philipson 1979; Cannon and Cannon 1989; Shang and Lowry 2007). However, in the last century, several workers (e.g. Donnell-Smith 1913; Nakai 1924; Smith 1936; Standley 1938; Paul et al. 1940) followed Harms (1894) and used the older name *Gilibertia* Ruiz & Pavon (1794) for the entire genus *Dendropanax*. These workers apparently overlooked the fact that *Gilibertia* was predated and invalidated by the entirely different *Gilibertia* Gmelin (1791) of Meliaceae (Merrill 1941). Nakai (1927, 1939) reinstated the generic rank of *Textoria* Miq. (Miquel 1863) for the Asian species and assigned taxa with simple umbels to *Textoria* and those with compound inflorescences to *Dendropanax*. However, *Textoria* has not been accepted by later workers (e.g. Merrill 1941; Li 1942; Hoo and Tseng 1978; Philipson 1979; Frodin and Govaerts 2003) because several Old World species possess compound inflorescences.

Two infrageneric classifications of *Dendropanax* have been proposed. Nakai (1924) divided *Gilibertia* into three sections mainly based on inflorescence architecture and number of floral parts: section *Dendropanax* Nakai (with compound umbels and 5-merous flowers), section *Eugilibertia* Nakai (with compound umbels and 6–8-merous flowers), and section *Textoria* (Miq.) Nakai (with simple umbels and 5-merous flowers, distributed in Asia). Based on style morphology, Hoo and Tseng (1965) divided *Dendropanax* into two sections: section *Dendropanax* (with styles distinct, or distinct in upper part or at the apex) and section *Columnistylus* Tseng & Hoo (with styles united throughout into a column) with *Dendropanax brevistylus* Ling as the type species of section *Columnistylus*.

The taxonomic and evolutionary position of *Dendropanax* within Araliaceae has been controversial. Several workers (e.g. Bentham and Hooker 1867; Seemann 1868; Viguier 1906; Hoo 1961; Hutchinson 1967; Tseng and Hoo 1982; Shang and Callen 1988) regarded *Dendropanax* as closely related to *Hedera* L., and this close relationship was supported by the neighbor joining tree of the internal transcribed spacer (ITS) phylogeny of Araliaceae, although only three species of *Dendropanax* and two species of *Hedera* were sampled (Wen et al. 2001). Li (1942) and Hoo and Tseng (1978) suggested that *Dendropanax* may have been derived from *Schefflera* J. R. Forst. & G. Forst. via reduction of the vegetative parts. This relationship has not been supported in recent analyses using nuclear ITS, granule-bound starch synthase I (*GBSSI*) and chloroplast *trnL-trnF* sequences (Wen et al. 2001; Mitchell and Wen 2004; Plunkett et al. 2004). Recent phylogenetic studies using molecular sequence data suggested that *Dendropanax* forms a polytomy with about 20 closely related genera within the Asian Palmate group (Wen et al. 2001, 2008b; Mitchell and Wen 2004; Plunkett et al. 2004). With the limited sampling of these studies, the monophyly of *Dendropanax* has not been assessed and the phylogenetic relationships within the genus remain poorly understood (Wen et al. 2008b).

In this study, we employ a broad taxon and character sampling scheme to (1) test the monophyly of *Dendropanax*; (2) examine phylogenetic relationships within *Dendropanax*; and (3) infer the biogeographic diversification history of *Dendropanax* in tropical Asia and the Neotropics. We employ sequences of the nuclear ribosomal ITS regions and six coding or non-coding plastid regions (the *ndhF* gene, the *trnL-trnF* intergenic spacer, the *rps16* intron, the *atpB-rbcL* intergenic spacer, the *rpl16* intron, and the *psbA-trnH* intergenic spacer), because these sequences have been shown to be useful for inferring relationships at the generic and specific levels of Araliaceae and Apiaceae (e.g. Wen and Zimmer 1996; Wen et al. 1998, 2001, 2003, 2007; Downie et al. 2000; Plunkett et al. 2004; Kadereit et al. 2008). We also used "relaxed clock" analyses and fossil calibrations (Drummond et al. 2006) to obtain age estimates of the main clades of *Dendropanax*.

Materials and Methods

Taxon Sampling—Ninety-five accessions representing 33 species of *Dendropanax* and 43 related taxa were sequenced for the nuclear ribosomal ITS regions, and the plastid *ndhF* gene, the intergenic spacers (*trnL-trnF*, *atpB-rbcL*, *psbA-trnH*), and the intron regions (*rps16*, *rpl16*). All sequences were newly generated in this study and have been deposited in GenBank (Appendix 1). The taxonomy of *Dendropanax* has relied heavily on a few morphological characters, and our sampling covered the morphological diversity, notably presence/absence of translucent dots/glands in the leaves, leaf lobing (lobed vs. unlobed), locule numbers in the ovary (4–5 vs. 6–10), inflorescence structure (compound panicle vs. simple umbel), and style division (free at least at the tip vs. completely united). Geographically, we sampled 13 of about 23 species in Asia, 14 (12 endemic) of the about 27 species in Central America and the Caribbean region, and nine of the approximately 30 species in South America. At present, we only sampled one of the 15 or so endemic Caribbean species, which are mainly confined to Jamaica (Smith 1944; Adams 1972).

We included various taxa in the following genera within the core Asian Araliaceae (Wen et al. 2001) or the Asian Palmate group (Plunkett et al. 2004): *Chengiopanax* C. B. Shang & J. Y. Huang, *Eleutherococus* Maxim., *Fatsia* Decne. & Planch., *Hedera* L., *Kalopanax* Miq., *Macropanax* Miq., *Metapanax* J. Wen & Frodin, *Oplopanax* (Torrey & Gray) Miq., *Oreopanax* Decne. & Planch., *Schefflera* J. R. Forst. & G. Forst., *Sinopanax* H. L. Li, *Tetrapanax* (K. Koch) K. Koch, and *Trevesia* Vis. Species of *Aralia* L., *Panax* L., and *Gastonia* Comm. & Lam. were selected as outgroups because they have been shown to be outside the Asian Palmate group. The wide range of multiple taxa within core Araliaceae was selected to further test the monophyly of *Dendropanax* and to date the divergence times with a broader phylogenetic framework.

DNA Extraction, Amplification, and Sequencing—Total DNA was extracted from about 15 mg silica-gel dried leaf material using the DNeasy plant mini kits (QIAGEN, Mississauga, Ontario) following the manufacturer's protocol or the modified CTAB extraction method (Doyle and Doyle 1987).

The ITS region was amplified and sequenced using primers ITS4 and ITS5 (White et al. 1990). When amplification of the ITS region was unsuccessful, two other primers, Nnc18S10 and C26A, were used (Wen and Zimmer 1996). The *ndhF* gene was amplified and sequenced in three segments with the following primer pairs: 1F and 972R, 803F and 1603R, 1318F and 2110R or 1995R (Olmstead and Sweere 1994; Wen et al. 2003, 2007). The *trnL–trnF* region was amplified and sequenced using primers c and f (Taberlet et al. 1991; Eibl et al. 2001). The *rps16* intron was amplified

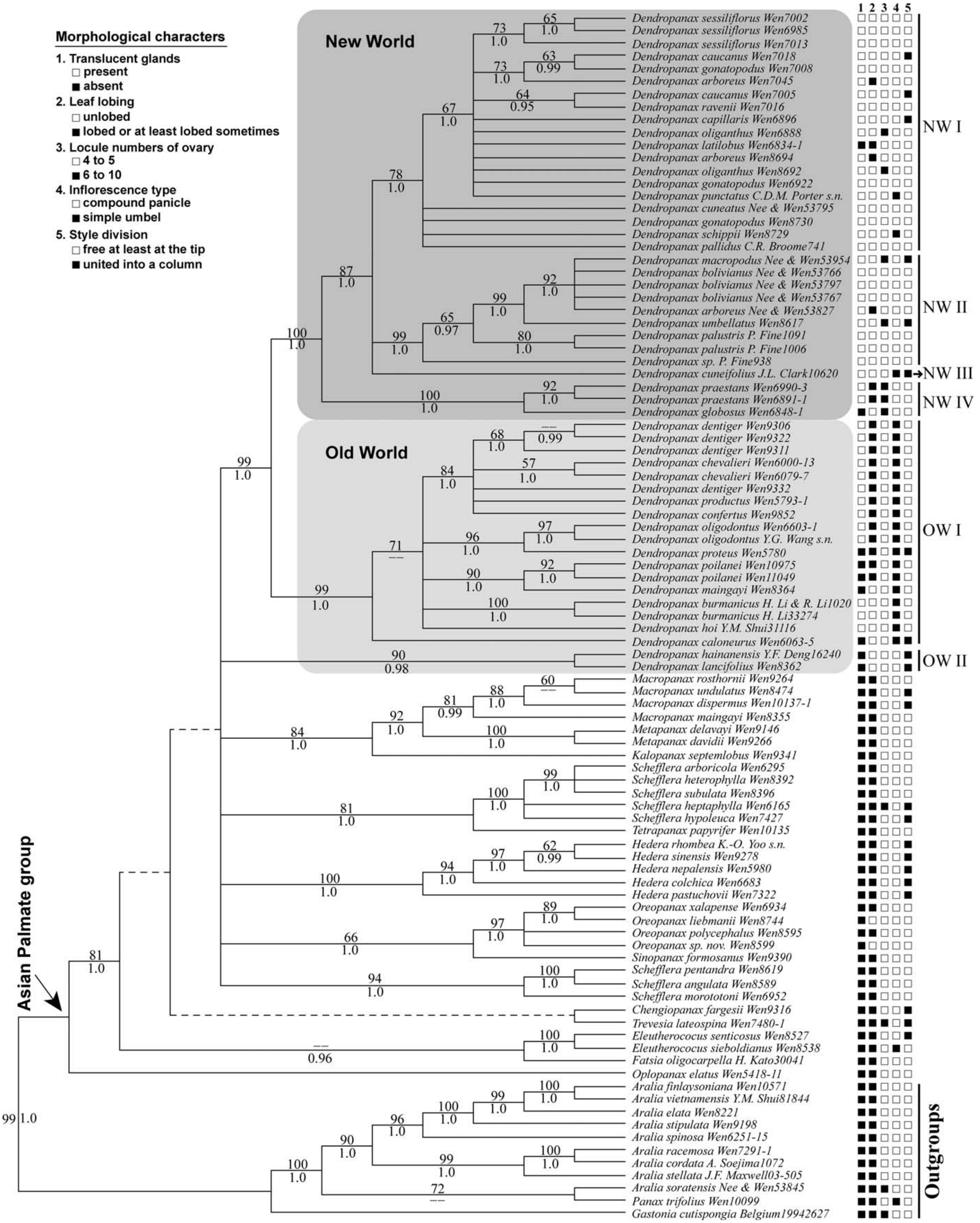

FIG. 1. The parsimony strict consensus tree of *Dendropanax* based on combined plastid and ITS data, with gaps treated as missing data (tree length = 1,856 steps, CI = 0.67, RI = 0.82, and RC = 0.55). Parsimony bootstrap values (BS) for maximum parsimony analysis in 1,000 replicates > 50% are shown above the branches and Bayesian posterior probabilities (PP) ≥ 0.95 are indicated below the branches. Double dash shows that the BS value lower than 50% or the PP value lower than 0.95. Dashed lines indicate the branches that are not supported by both maximum parsimony and Bayesian analysis. Five selected morphological characters of taxonomic importance have been coded and mapped on the parsimony strict consensus tree.

and sequenced using primers F and R2 (Oxelman et al. 1997; Andersson and Rova 1999). The *atpB-rbcL* region was amplified and sequenced following Manen et al. (1994). The *rpl16* intron was amplified and sequenced using primers rpl16_F and R (Asmussen 1999). The *psbA-trnH* region was amplified and sequenced using primers psbA and trnH (Sang et al. 1997; Hamilton 1999). Polymerase chain reaction (PCR) amplifications were performed in a 25 μL volume containing 1.5 mM $MgCl_2$, 0.2 mM of each dNTP, 0.4 mM of each primer, 1 U of *Taq* polymerase (Bioline), and about 10–50 ng of DNA template under the following conditions: 3 min at 95°C, followed by 37 cycles of 20 s at 94°C, 30 s at 50°C, and 40 s at 72°C, and then a final 5 min extension at 72°C.

The PCR products were purified using the polyethylene glycol (PEG) precipitation procedure following the protocol of Sambrook et al. (1989). Cycle sequencing was conducted using BigDye 3.1 reagents and carried out using the following profile: 35 cycles of 97°C for 15 s, 50°C for 5 s, and 60°C for 4 min. The products of cycle-sequencing reactions were cleaned using the Sephadex columns (Amersham Pharmacia Biotech, Piscataway, New Jersey). The sequences were generated on an ABI prism 3730XL capillary sequencer (Applied Biosystems, Foster City, California).

Sequence Alignment and Phylogenetic Analyses—The program Sequencher 4.5 (Gene Codes Corporation, Ann Arbor, Michigan) was used to evaluate chromatograms for base confirmation and to edit contiguous sequences. Sequences were initially aligned with ClustalX version 1.83 (Thompson et al. 1997), followed by manual adjustments on Se-Al v2.0a11 (Rambaut 2007).

Phylogenetic trees were constructed using maximum parsimony (MP) and Bayesian methods (Fig. 1). The MP analyses was conducted using PAUP* version 4.0b10 (Swofford 2002). All characters were weighted equally. Gaps were treated as missing data and coded as binary characters using the "simple gap coding" method (Simmons and Ochoterena 2000). The program GapCoder (Young and Healy 2003) was employed to score the insertions and deletions (indels). The most parsimonious trees were obtained with heuristic searches of 1,000 replicates with random stepwise sequence addition, tree bisection-reconnection (TBR) branch swapping, collapse of zero-length branches, multiple tree option in effect, saving 100 trees from each random sequence addition. Parsimony bootstrap values (BS) for the clades (Felsenstein 1985) revealed in the maximally parsimonious trees (MPTs) were calculated with 1,000 bootstrap replicates. In each replicate, we performed 100 random sequence addition replicates followed by tree bisection-reconnection (TBR) swapping, keeping no more than 10 trees per replicate. Tree statistics, including consistency index and the retention index, were calculated using PAUP*. The sequence alignment and the parsimony strict consensus tree of the combined plastid and ITS data set were deposited in TreeBASE (study number S10629).

Modeltest 3.7 (Posada and Crandall 1998; Posada and Buckley 2004) was used to determine the optimal model of molecular evolution and gamma rate heterogeneity using the Akaike Information Criterion (AIC). Bayesian inference was implemented with MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) using a mixed model Bayesian analysis strategy. We assigned model parameters for each gene partition identified by AIC in Modeltest (Table 1). The Markov chain Monte Carlo (MCMC) algorithm was run for 20,000,000 generations with one cold and three heated chains, starting from random trees. Runs were repeated twice. The resulting log likelihood and number of generations were plotted to determine the point after which the log likelihoods had stabilized. After discarding the trees saved prior to this point as burn-in, the remaining trees were imported into PAUP and a 50% majority-rule consensus tree was produced to obtain posterior probabilities of the clades. Internodes with posterior probabilities (PP) ≥ 0.95 in the consensus trees were considered statistically significant.

The plastid (*ndhF*, *trnL-F*, *rps16*, *atpB-rbcL*, *rpl16*, and *psbA-trnH*) and the ITS data sets were first analyzed separately. To evaluate congruence of the plastid and nuclear data sets, we employed the partition homogeneity test or the incongruence length difference (ILD) test (Farris et al. 1995). The partition homogeneity test was conducted with PAUP* version 4.0b10 (Swofford 2002) with 100 replicates of heuristic searches using the TBR branch-swapping with gaps treated as missing data.

With *Dendropanax* shown to be non-monophyletic in our initial analysis, we performed a constraint analysis using the combined plastid and ITS data set. With *Dendropanax* constrained to be monophyletic, a parsimony analysis was performed with the heuristic search option using 1,000 random sequence additions, TBR, and saving 100 trees from each random sequence addition.

To examine morphological character evolution, we mapped character states onto the parsimony strict consensus tree (Fig. 2) based on the combined plastid and ITS data set using the "trace character history" functions with the program Mesquite version 2.72 (Maddison and Maddison 2009). The coding of morphological characters was based on our examination of herbarium material. In most cases, the same samples used to generate the molecular data were examined for morphological characters.

Estimation of Divergence Times—To estimate divergence times within *Dendropanax*, the combined plastid and ITS data set was used with gaps treated as missing data. Extrapolations of divergence times across separate data sets may be done to avoid the impact of heterogeneity of the plastid and nuclear data set. However, neither the plastid nor the ITS data set provided enough information regarding phylogenetic relationships within the genus to reliably estimate divergence times of clades. We thus followed the procedures suggested by a few workers (Bell et al. 2005; Forest et al. 2007; Inda et al. 2008; Nie et al. 2008) that supported the use of the combined plastid and ITS data set to date the clades, because the combined data sets better resolved phylogenetic relationships within the genus. The Bayesian dating method with a relaxed molecular clock was implemented with the program BEAST 1.5.3 (Drummond and Rambaut 2007) using the strategy of different nucleotide substitution models for each gene region suggested by Modeltest (Table 1). The Yule process for the tree prior model was employed using uncorrelated rates drawn from a lognormal distribution (Drummond et al. 2006). A normal distribution was specified for the priors. Posterior distributions of parameters were approximated using two independent MCMC analyses of 20,000,000 generations with 10% burn-in. Results were checked using the program Tracer 1.5 (Rambaut and Drummond 2007) to ensure that plots of the two analyses were converging on the same area and the value of the effective sample size for each statistic was above 100.

We constrained the ages of two nodes in the phylogeny of *Dendropanax* and its close relatives (Fig. 3). First, the stem lineage of *Metapanax* was constrained to be 44 (+/− 3.2) mya old (node A in Fig. 3) based on the fruit fossil of *Paleopanax oregonensis* Manchester from the Nut Beds flora of the Clarno Formation (north-central Oregon in the middle Eocene). This fossil was comparable to the Asian "*Pseudopanax*" (= *Metapanax*) (Manchester 1994). *Metapanax* is distributed in central and southwestern China and northern Vietnam (Wen and Frodin 2001). Secondly, the crown age of *Aralia elata* was constrained to be 11.2 (+/− 1.56) mya old (node B in Fig. 3) based on fossil seeds of *Aralia* from Stare Gliwice in Upper Silesia of

Table 1. Characters of the plastid and the nuclear ITS data sets.

	Aligned length (bp)	Number of variable sites (%)	Number of informative sites (%)	Model selected by AIC
ndhF	1,959	207 (10.6%)	80 (4.1%)	GTR + I + G
trnL-F	994	129 (13.0%)	47 (4.7%)	K81uf + G
rps16	888	120 (13.5%)	47 (5.3%)	TIM + I + G
atpB-rbcL	778	93 (12.0%)	36 (4.6%)	TIM + G
rpl16	1,013	129 (12.7%)	54 (5.3%)	TIM + I + G
psbA-trnH	510	107 (21.0%)	44 (8.6%)	K81uf + I + G
Combined plastid data matrix	6,142	785 (12.8%)	308 (5.0%)	–
ITS	633	277 (43.8%)	183 (28.9%)	GTR + I + G
Combined plastid and ITS data matrix	6,775	1,062 (15.7%)	491 (7.2%)	–
Within *Dendropanax*	6,429	324 (5.0%)	169 (2.6%)	–
Clade NW I	6,362	68 (1.1%)	20 (0.3%)	–
Clade NW II	6,338	27 (0.4%)	14 (0.2%)	–
Clade OW I	6,389	131 (2.1%)	48 (0.8%)	–

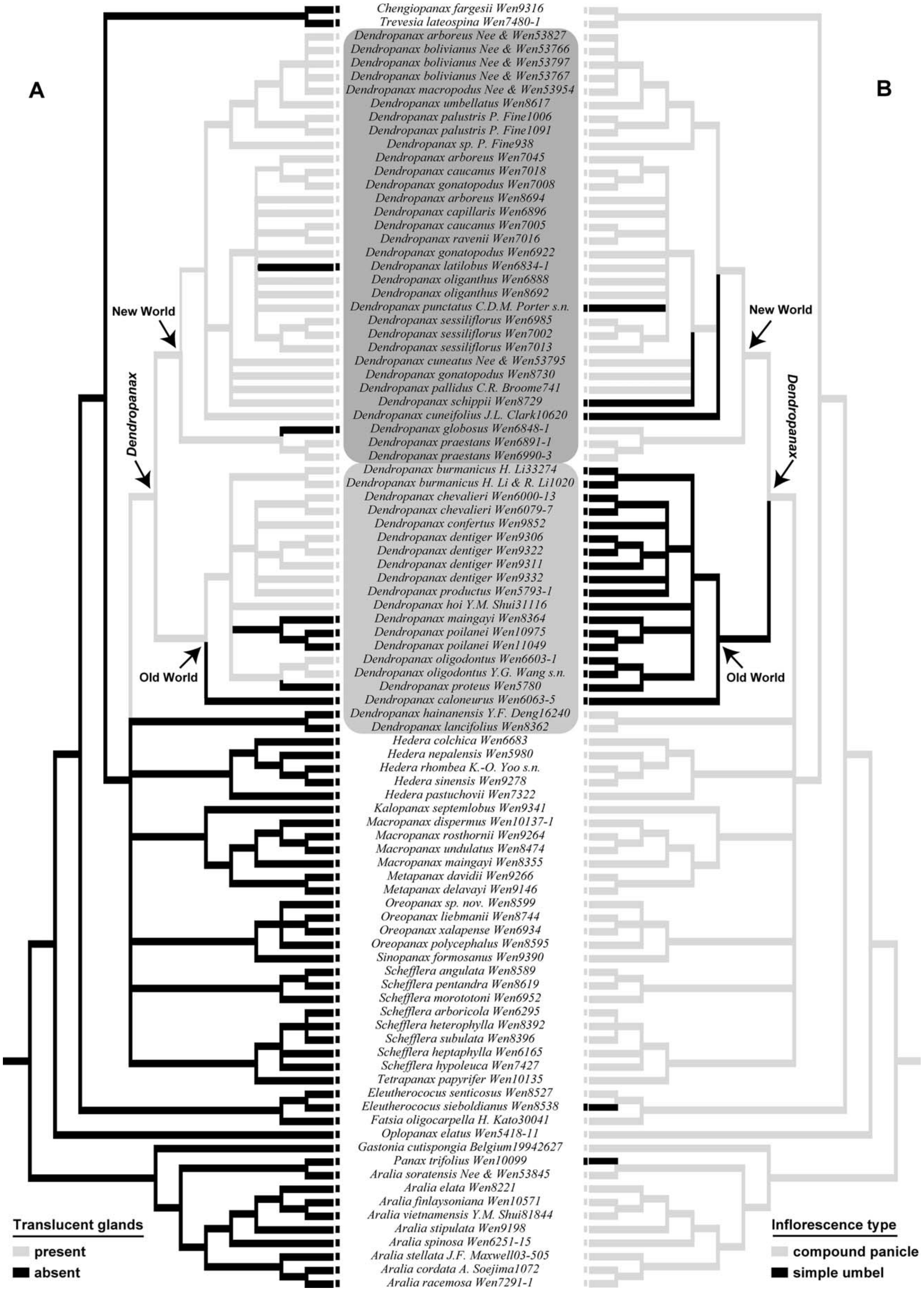

FIG. 2. Ancestral character state reconstructions on the parsimony strict consensus tree of combined plastid and ITS data using parsimony with Mesquite for two characters of *Dendropanax*: (A) translucent glands, and (B) inflorescence type. The species of *Dendropanax* are shaded with gray.

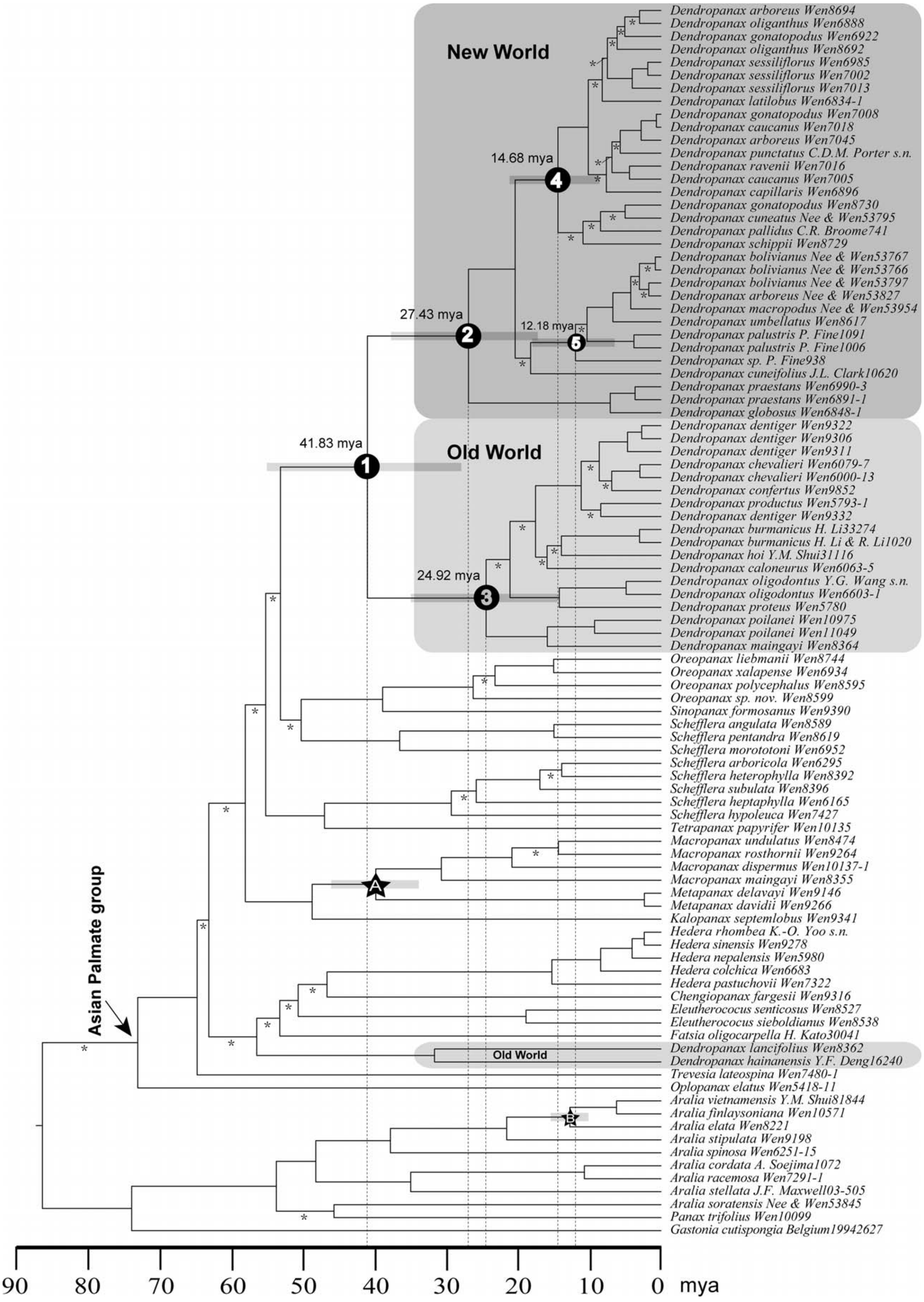

FIG. 3. Chronogram of *Dendropanax* inferred from combined plastid and ITS data using BEAST. Gray node bars indicate 95% highest posterior density intervals. Nodes labeled as 1–5 are indicated with age estimates and are discussed in the text. Asterisks indicate the branches with posterior probabilities < 0.95; all other interior nodes nodes have high support values with the Bayesian posterior probabilities ≥ 0.95.

eastern Europe in the Miocene, which were similar to those of the extant *Aralia elata* (Szafer 1961), a widespread species in the temperate regions of eastern Asia. Our interpretation of geological ages followed the 1999 Geological Time Scale of the Geological Society of America (1999).

Historical Biogeography Reconstructions—The ancestral area distribution of *Dendropanax* was inferred using a maximum likelihood-based method (Lagrange) (Ree et al. 2005; Ree and Smith 2008) and a Bayesian analysis using BayesTraits (Pagel et al. 2004). The two reconstructions of historical biogeography were conducted on the maximum clade credibility (MCC) phylogeny of the combined plastid and ITS data set that resulted from BEAST. The BEAST tree provided the most resolved and best supported topology for *Dendropanax* and its close relatives with nodal ages. Four areas of endemism (the Old World, North America, Central America and the Caribbean region, and South America) were defined based on the taxon distributions and our current interest in understanding the intercontinental amphi-Pacific disjunctions.

The software Lagrange was used to infer geographic range evolution using a likelihood-based approach of historical biogeography. In this method, the transitions between discrete states (ranges) along phylogenetic branches are modeled as a function of time, and thus infer maximum likelihood estimation of the ancestral states (range inheritance scenarios) at cladogensis events (Ree and Smith 2008). The maximum number of areas in ancestral ranges was set to be four in the analyses.

We also used the software BayesTraits (Pagel et al. 2004) to reconstruct the ancestral area using a Bayesian approach. In this analysis, MultiState was selected as the model of evolution and MCMC as the method of analysis. BayesTraits uses reversible-jump MCMC methods to derive posterior probabilities and the values of traits at ancestral nodes of phylogeny. A hyperprior approach was employed with an exponential prior seeded from a uniform on the interval 0–10. The rate deviation was set to 2. A total of 20,000,000 iterations were run for each analysis with the first 10% of samples discarded as burn-in.

RESULTS

ITS Data—The characteristics of the ITS data are shown in Table 1. Treating gaps as missing data, the maximum parsimony (MP) analysis produced 66,701 MPTs of 699 steps, with a consistency index (CI) of 0.56 (CI excluding uninformative characters of 0.47), and a retention index (RI) of 0.82. The 50% majority-rule consensus trees that resulted from the Bayesian analysis were largely congruent with the MPTs except that *Oreopanax* and *Sinopanax* formed a monophyletic group with the posterior probability (PP) value of 0.98; *Oreopanax xalapense* and *O. liebmanii* formed a clade (PP = 0.99) that was sister to the clade composed of *O. polycephalus* and *O. globosus*. Furthermore, the monophyly of *Dendropanax* (except *D. lancifolius* and *D. hainanensis*) was supported (PP = 0.98). Treating the 23 gaps as new characters, the strict consensus tree of the MPTs was identical to that with the gaps treated as missing data. The ITS topology did not resolve the deep nodes within *Dendropanax* well (trees not shown).

Plastid Data—We excluded the poly A, poly T or poly A/T regions from the data sets (*trnL-F*, 4 bp between 700–703; *rps16*, 14 bp between 710–723; *atpB-rbcL*, 3 bp between 569–571 and 13 bp between 579–591; *rpl16*, 9 bp between 630–638; and *psbA-trnH*, 6 bp between 60–65 and 13 bp between 320–332). Because there is no recombination in the plastid DNA, we combined the six plastid data sets in our analysis a priori. The statistics of the plastid data sets are shown in Table 1. Treating gaps as missing data, the maximum parsimony analysis produced 85,700 MPTs of 1,138 steps, with a CI of 0.75, CI excluding uninformative characters of 0.55, a RI of 0.85, and a RC of 0.63. The 50% majority-rule consensus tree resulting from the Bayesian analysis was largely congruent with the trees of the parsimony analysis except that the genera *Oreopanax* and *Sinopanax* formed a monophyletic group with the posterior probability (PP) value of 0.99. Treating the 143 gaps as new characters, the topologies of the MPTs are nearly identical to those generated with gaps treated as missing data. They only differed in that treating gaps as new characters helped resolve *Dendropanax caucauus* (*Wen 7018*) and *D. ravenii* as sister taxa as well as *D. palustris* (*P. Fine 1006*) and an unidentified species from Peru (*P. Fine 938*) within the New World clade. The relationships within *Dendropanax* were not well resolved in the plastid data (trees not shown).

ITS and Plastid Combined Data—Assessments of conflict between the nuclear and the plastid data showed that the two data sets were congruent ($p = 0.07$). We thus performed a combined analysis of all plastid and ITS data (Table 1). Treating gaps as missing data, the maximum parsimony analysis produced 97,300 MPTs of 1,856 steps, with a CI of 0.67, a CI excluding uninformative characters of 0.51, a RI of 0.82, and a RC of 0.55. The parsimony strict consensus tree with parsimony bootstrap (BS) and posterior probability (PP) support is shown in Fig. 1. Treating the 166 gaps as new characters, the topologies of the MPTs were similar to those with the gaps treated as missing data. Nevertheless, the analysis with gaps treated as new characters resolved *Dendropanax burmanicus* as sister to the clade composed of *D. dentiger*, *D. productus*, *D. confertus*, and *D. chevalieri* in the Old World clade, albeit with a low bootstrap value of 56%. In addition, the clade composed of *Dendropanax oligodontus* and *D. proteus* was resolved to be sister to the clade of *D. poilanei* and *D. maingayi* (but with bootstrap support < 50%).

The combined plastid and ITS data strongly supported the monophyly of the Asian Palmate group (BS = 99%, PP = 1.0). *Dendropanax* was part of the Asian Palmate group (Fig. 1). The monophyly of *Dendropanax* was not supported because *D. lancifolius* and *D. hainanensis* formed a polytomy with the main *Dendropanax* clade and other tropical genera (see Fig. 1). Furthermore, *Dendropanax lancifolius* and *D. hainanensis* formed a clade (BS = 90%, PP = 0.98) (clade OW II in Fig. 1). Excluding these two species, the New World and Old World *Dendropanax* each formed robustly supported clades (BS = 100%, PP = 1.0 for the New World clade; BS = 99%, PP = 1.0 for the Old World clade) (Fig. 1).

Within the New World clade, the following clades/relationships were suggested (Fig. 1): (1) the large clade (clade NW I; BS = 78%, PP = 1.0) consisting of species from Central America (Costa Rica and Mexico) with a few exceptions, including *Dendropanax cuneatus* from Bolivia, *D. punctatus* from Peru, and *D. pallidus* from Ecuador; (2) the clade of exclusively South American taxa (clade NW II; BS = 99%, PP = 1.0). Within this clade, *Dendropanax macropodus*, *D. bolivianus*, and the Bolivian accession of *D. arboreus* were well-supported as a subclade sister to *D. umbellatus*. *Dendropanax palustris* is then sister to the clade containing the above-mentioned species; (3) *Dendropanax cuneifolius* (clade NW III) from Cuba forming a trichotomy with clade NW I and clade NW II; and (4) a strongly supported clade of *Dendropanax globosus* and *D. praestans* (clade NW IV; BS = 100%, PP = 1.0) from Costa Rica sister to the large clade of all remaining New World *Dendropanax* species (BS = 87%, PP = 1.0).

Within the Old World clade (clade OW I in Fig. 1), the following clades/relationships were suggested: (1) *Dendropanax caloneurus* sister to the clade of the remaining *Dendropanax* species in the Old World except *D. hainanensis* and *D. lancifolius* (BS = 71%, PP < 0.95); (2) *Dendropanax chevalieri*, *D. confertus*, *D. dentiger*, and *D. productus* forming a clade (BS = 84%, PP = 1.0); (3) *Dendropanax proteus* and *D.*

oligodontus sister to each other (BS = 96%, PP = 1.0); and (4) *Dendropanax maingayi* and *D. poilanei* constituting a clade (BS = 90%, PP = 1.0).

Analyses constraining all *Dendropanax* species into a clade generated MPTs that were only one step longer than the unconstrained MPTs. The *p* value of the Shimodaira-Hasegawa (SH) test is 0.2941.

The ancestral reconstruction of five morphological character states using Mesquite showed that the characters examined were homoplasious. The presence of translucent glands in the leaves was inferred to be synapomorphic for *Dendropanax*, but they have been lost at least five times within the genus (Figs. 1, 2A). Unlobed leaves were plesiomorphic in *Dendropanax*, with lobed leaves evolving independently at least six times (Fig. 1). Five-locular ovaries were ancestral in the genus and pluricarpellate ovaries evolved independently at least four times (Fig. 1). The compound panicle was reconstructed as ancestral in this genus, with simple umbels derived four times independently (Figs. 1, 2B). Free styles were ancestral in *Dendropanax*, yet completely united styles arose independently at least eight times (Fig. 1).

Estimates of Divergence Times and Historical Biogeography Reconstructions—The chronogram and results of divergence time estimation based on the combined plastid and ITS data set from the Bayesian approach are shown in Fig. 3. The disjunction of *Dendropanax* between tropical Asia and the Neotropics was estimated at 41.83 mya (95% high posterior density [HPD] interval of 28.46–56.15 mya) (node 1 in Fig. 3). The crown New World clade was estimated at 27.43 mya (95% HPD: 17.56–38.47 mya) (node 2 in Fig. 3). The crown Old World clade was dated to be at 24.92 mya (95% HPD: 14.75–35.65 mya) (node 3 in Fig. 3).

The maximum likelihood-based analysis using Lagrange (Fig. 4) and the Bayesian estimation (BayesTraits) of ancestral area reconstruction both suggested that the ancestral area of *Dendropanax* was in the Old World.

Discussion

Is Dendropanax Monophyletic?—With the current sampling, the monophyly of *Dendropanax* is not supported. Two Asian species, *Dendropanax lancifolius* and *D. hainanensis,* form a clade, yet this clade does not group with the remainder of the *Dendropanax* species sampled. It is likely that this non-monophyly is due to sampling bias, because our sampling in the Caribbean region and some areas of South America remains poor (e.g. only one species was sampled from the Caribbean region). Furthermore, the MPTs of the analysis constraining *Dendropanax* to monophyly were only one step longer than the unconstrained MPTs. *Dendropanax lancifolius* and *D. hainanensis* are large trees up to 20 m tall and have simple unlobed leaves without punctate glands, a terminal panicle with a conspicuous primary axis, and styles united throughout their length into a single column. It is notable that these two taxa are the only Asian species of the genus consistently possessing a paniculate inflorescence with many umbel units. This inflorescence architecture is similar to that of many Neotropical *Dendropanax* species. It seems likely that *Dendropanax lancifolius* and *D. hainanensis* may be more closely related to the common ancestor of the New/Old World *Dendropanax* species. Monophyly of *Dendropanax* needs to be further examined with additional taxon sampling in the Caribbean and South America.

Dendropanax is defined morphologically by a combination of characters including the habit as evergreen trees or shrubs, simple to palmately lobed leaves, terminal inflorescences, and 5–12-carpellate ovaries with the styles distinct or partially united at the base or united completely into a column (Bentham and Hooker 1867; Seemann 1868; Viguier 1906; Hutchinson 1967; Tseng and Hoo 1982). The leaves of many *Dendropanax* species have yellow or red glandular punctae under transmitted light (or translucent glands). Even though not all *Dendropanax* species possess translucent glands (Merrill 1941; Li 1942; Hoo and Tseng 1965, 1978; Bui 1976; Shang and Lowry 2007), the presence of translucent glands is inferred by our character analysis using parsimony with Mesquite as synapomorphic for the main *Dendropanax* clade and these glands were lost independently in five lineages. Thus far we have not detected any other morphological synapomorphies for the genus, and the defining characters outlined above for *Dendropanax* except the translucent glands on leaves also occur in other genera of Araliaceae. At the family level, many of these morphological characters including habit, inflorescence architecture, leaf shape, and carpel number have been shown to be relatively plastic (see Wen et al. 2001; Plunkett et al. 2004).

Relationships within the New World Clade—The topologies presented here did not resolve the relationships within the large NW I clade (Fig. 1). Species in the clade show only subtle molecular variation (Table 1). The lack of variable molecular characters likely resulted in the polytomy within this clade, suggesting a recent rapid diversification of species in this region. The morphologically unique *Dendropanax sessiliflorus* forms a polytomy with other *Dendropanax* species within this clade. This species is the only member of the genus with heads as the inflorescence units, like those in the genus *Oreopanax*. Nevertheless *Dendropanax sessiliflorus* is morphologically similar in other characters to other *Dendropanax* species in having leaves with translucent glands, 5-merous flowers, and styles free at the apex. The heads of *Dendropanax sessiliflorus* and *Oreopanax* apparently represent convergence rather than shared common ancestry.

The clade of the exclusively South American taxa (clade NW II in Fig. 1) seems to be defined by its geographic distribution, as we have failed to detect any morphological synapomorphies. All species in the clade have leaf blades with translucent glands. Nevertheless, translucent glands are also common in Central American and Asian species of the genus.

Dendropanax cuneifolius (clade NW III in Fig. 1) from Cuba is the only species we sampled from the Caribbean region. This region forms the northern distribution limit of *Dendropanax* in the New World. It has a rich and unique flora as well as a complex geological and environmental history (Fritsch and McDowell 2003; Acevedo-Rodríguez and Strong 2008). Additional sampling of *Dendropanax* species from the West Indies, especially Jamaica, is necessary to assess the phylogenetic position and the diversification history of the Caribbean species of *Dendropanax*.

Dendropanax globosus and *D. praestans* (clade NW IV in Fig. 1) from Costa Rica share the characters of paniculate inflorescences, styles free at the apex, and pluricarpellate ovaries. *Dendropanax praestans* differs from *D. globosus* in the latter having unlobed juvenile leaves (vs. 5–7-lobed), leaf blades without (vs. with) glands, and globose receptacles (vs. subglobose) (Cannon and Cannon 1989; J. Wen, pers. observ.).

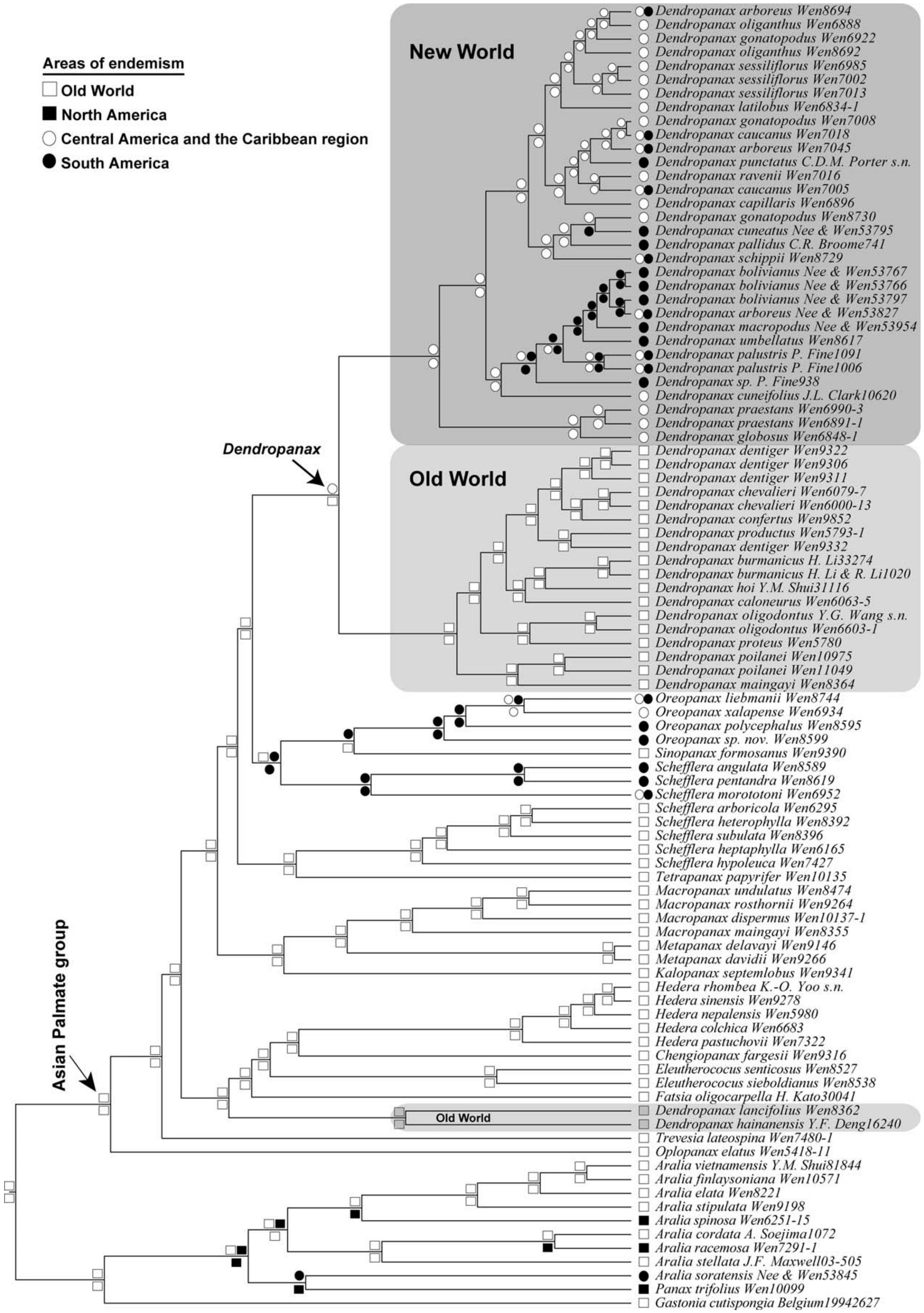

FIG. 4. Ancestral area reconstruction for *Dendropanax* based on a likelihood analysis using Lagrange. Four areas of endemism were defined: Old World (open square), North America (solid square), Central America and the Caribbean region (open circle), and South America (solid circle). The optimal ancestral areas with highest likelihood scores and highest probabilities among the alternatives are shown at each node. Ranges inherited by the daughter lineages are indicated above the nodes for the upper clade and below the nodes for the lower clade.

The widespread *Dendropanax arboreus* is represented by several accessions in our study (Mexico, Costa Rica, and Bolivia) from throughout its distributional range in Central and South America. *Dendropanax arboreus* is morphologically variable in several characters, including a habit ranging from shrubs to trees, unlobed to 3–5-lobed leaves with margins entire to crenate or denticulate, seven to many flowers per umbel, and 5–7-merous flowers. The multiple accessions of this species sequenced here are polyphyletic, suggesting that there may be several cryptic species in this complex as well as in some other species with multiple accessions that are not monophyletic (e.g. *Dendropanax caucanus*, *D. gonatopodus*).

Relationships within the Old World Dendropanax—*Dendropanax caloneurus* from northern Vietnam diverges first (clade OW I in Fig. 1) in the Old World clade. Morphologically, this narrow endemic is similar to *D. proteus* in that both species have solitary umbels, styles united into a column, and leaves without translucent glands. They differ in that *D. caloneurus* has unlobed leaves (vs. lobed leaves in *D. proteus*). In our phylogenetic tree, the two taxa are not closely related.

Dendropanax oligodontus and *D. proteus* (clade OW I in Fig. 1) share the character of dimorphic leaves (unlobed or deeply 2–3-lobed leaves). They differ in that *Dendropanax oligodontus* has styles united 4/5 of their length and leaves with translucent glands. *Dendropanax proteus,* on the other hand, has completely united styles and leaves without glands (Shang and Lowry 2007).

Dendropanax maingayi from the Malay Peninsula and *D. poilanei* from southern Vietnam (clade OW I in Fig. 1) have leaves without translucent glands and styles free in the upper half and are strongly supported as sister taxa. *Dendropanax maingayi* differs from *D. poilanei* in having unlobed (vs. lobed) leaves. Only three species of *Dendropanax* occur in the Malesian region: *D. borneensis* (Philipson) Merr. (not sampled), *D. maingayi*, and *D. lancifolius*. *Dendropanax maingayi* is similar to *D. borneensis* in general leaf and inflorescence morphology. However, *Dendropanax maingayi* does not have pellucid glands in the leaf lamina, whereas *D. borneensis* possesses pellucid glands in the leaf blade. *Dendropanax lancifolius* and *D. maingayi* are sympatric species in tropical montane cloud forests of the Malay Peninsula (J. Wen, pers. observ.), but the phylogenetic analysis suggests that the two taxa are not closely related. *Dendropanax maingayi* is part of clade OW I (Fig. 1), whereas *D. lancifolius* forms a clade with *D. hainanensis* from eastern Asia (clade OW II in Fig. 1). *Dendropanax lancifolius* is a large tree up to 20 m tall, whereas *D. maingayi* is a shrub two to three meters tall.

One well-supported clade is composed of species from southern China (*Dendropanax confertus*, *D. dentiger*, and *D. productus*) and northern Vietnam (*D. chevalieri*) (clade OW I in Fig. 1). These species are morphologically similar. All have lobed leaves with translucent glands, solitary umbels, and styles united into a column. Species of this clade are mostly allopatric and they constitute a polytomy in the phylogenetic tree (Fig. 1). Their morphological resemblance may indicate recent speciation.

Character Evolution—The presence of translucent glands in the leaves is a unique character of *Dendropanax*, yet not all species of the genus possess them. This character has been used to distinguish species within *Dendropanax* by some workers (Li 1942; Hoo and Tseng 1965, 1978; Cannon and Cannon 1989; Shang and Lowry 2007). The presence of translucent glands is inferred to be a synapomorphy of the main *Dendropanax* clade (all *Dendropanax* excluding *D. hainanensis* and *D. lancifolius*). This character was then lost at least five times, in *Dendropanax latilobus* and in *D. globosus* in the New World, and in *D. proteus*, *D. caloneurus*, and the *D. poilanei-D. maingayi* clade in the Old World (Figs. 1, 2A). The ancestor of the *Dendropanax hainanensis-D. lancifolius* clade did not possess translucent glands (Fig. 2A), as inferred by parsimony analysis.

The leaf types in Araliaceae are diverse, varying from simple and entire to simple and variously lobed to compound (either palmately, ternately, or once-, twice-, or thrice-pinnately compound). Simple leaves have been considered plesiomorphic in Araliaceae (Plunkett et al. 1996, 2004; Lowry et al. 2001; Plunkett and Lowry 2001; Wen et al. 2001), and occur in many other core Asian Araliaceae genera, including *Trevesia*, *Fatsia*, *Hedera* (the genus *Hedera* shows dimorphic leaves, with those of the sterile branches usually lobed and those of the fertile branches usually unlobed), *Oplopanax*, *Oreopanax*, and *Tetrapanax*. Leaves of *Dendropanax* are all simple, yet they may be unlobed or 2- or 3 (−5)-lobed. Unlobed leaves are inferred to be ancestral in the genus by parsimony analysis and character mapping using Mesquite (not shown), but lobed leaves evolved at least six times independently, in *Dendropanax arboreus*, *D. latilobus*, and *D. praestans* of the New World clade, as well as in the *D. proteus—D. oligodontus* clade, in the *D. dentiger—D. chevalieri—D. productus—D. confertus* clade, and in *D. poilanei* of the Old World clade (Fig. 1).

The plesiomorphic state for locule number in the ovary in Araliaceae is uncertain, and the polarity of locule number has received some attention. Most workers (Harms 1894; Li 1942; Philipson 1970; Eyde and Tseng 1971; Cronquist 1981) regarded the penta- or pluricarpellate ovary as primitive in Araliaceae. Molecular phylogenetic studies have suggested bicarpellate ovaries as ancestral not only in core Araliaceae (Wen et al. 2001), but also in the Apiales (Plunkett et al. 1996, 1997, 2004; Plunkett 2001; Plunkett and Lowry 2001; Lowry et al. 2001). Most *Dendropanax* species have five (or four to five) locules, but *D. oliganthus* and *D. umbellatus* have seven to nine, *D. praestans* has six to seven, *D. macropodus* has six to eight, and *D. globosus* has eight to 10 locules. The ancestral condition of ovary locule number is inferred to be 5-locular in *Dendropanax* and pluricarpellate (6–10-locular) ovaries evolved independently at least four times in the New World clade (Fig. 1). Nevertheless, some Asian species possess ovaries with fewer locules; for example, *Dendropanax kwangsiensis* H. L. Li and *D. bilocularis* C. N. Ho have two or three locules, and *D. stellatus* H. L. Li has three locules (these three species were not sampled). Inclusion of these few-loculed species in phylogenetic analyses should shed light on evolution of this character in *Dendropanax.*

The basic units of the inflorescence in Araliaceae are mostly umbels, but heads, spikes, or racemes of flowers are also present. The inflorescence units often then aggregate into a paniculate or umbellate structure, and rarely flowers are in a solitary umbel. The evolution of the umbel from a raceme was illustrated by Hutchinson (1967) with reference to *Cuphocarpus* Decaisne & Planchon (1854). A racemose inflorescence unit was also considered to be ancestral in Araliaceae by Philipson (1970). It appears that simple umbels may have evolved four times independently, in *Dendropanax punctatus*, *D. cuneifolius*, and *D. schippii* of the New World clade, and once in the large Old World clade consisting of all *Dendropanax* species except *D. hainanensis* and *D. lancifolius* (Figs. 1, 2B). The simple umbel may be a synapomorphy of the large Asian clade OW I. It is noted that *D. chevalieri* and *D. dentiger* sometimes have an inflorescence with two to five umbels. With the homoplasies in inflorescence structure in the genus as shown here, the previous classifications of *Dendropanax* into three sections based on inflorescence architecture (Nakai 1924) are not supported.

The styles of *Dendropanax* are united basally and free at the tips or united throughout into a column. This character seems to be very labile, but most *Dendropanax* species have styles that are united at the base. The completely united styles may have evolved at least eight times independently, in *D. caucanus*, *D. capillaris*, *D. macropodus*, *D. umbellatus*, and *D. cuneifolius* of the New World clade, and in the *D. hainanensis*-*D. lancifolius* clade, in *D. proteus*, and *D. caloneurus* of the Old World clade (Fig. 1). Based on the style morphology, Hoo and Tseng (1965) split the genus into two sections, sect. *Dendropanax* and sect. *Columnistylus* Tseng & Hoo. Our results clearly do not support their classification, because species with styles completely united into a column are scattered in different lineages in our phylogeny (Fig. 1). For example, *D. proteus* from southern China grouped with other taxa from the same geographic region which have partially united styles, rather than with other species having completely united styles, such as *D. caloneurus* from Vietnam.

Disjunction Between Tropical/Subtropical Asia and the Neotropics and Intracontinental Diversification—Our biogeographic analyses using both Lagrange and BayesTraits suggest that the ancestral area of *Dendropanax* was in the Old World. The divergence time of the main *Dendropanax* clade (excluding *D. hainanensis* and *D. lancifolius*) between tropical and subtropical Asia and the Neotropics was estimated at 41.83 mya (95% HPD 28.46−56.15 mya) in the middle Eocene (node 1 in Fig. 3). The fossil fruits from Brittany of northwestern France (*Dendropanax gallicum* Reid) and the fossil leaves from Tennessee of North America (*D. eocenensis* Dilcher & Dolph) suggested that *Dendropanax* was distributed in Europe and North America in the early Tertiary (Reid 1927; Dilcher and Dolph 1970). The North Atlantic land bridges (NAL) existed in the Paleocene and the early Eocene and have been viewed as a major route for the spread of thermophilic taxa of the boreotropical flora in the early Tertiary (Wolfe 1975; McKenna 1983; Tiffney 1985a, 1985b; Wen 1999; Hably et al. 2000; Tiffney 2000; Tiffney and Manchester 2001). The age estimate and the fossil distribution in Europe and North America suggest that the genus most likely migrated into the New World via the North Atlantic land bridges. The migration via NAL was also favored by the Paleocene-Eocene thermal maximum (Miller et al. 1987; Miller 1992; Zachos et al. 2001; Wing et al. 2003; Lourens et al. 2005). Starting in the early Eocene, the climate cooled in several periods, the most pronounced of which approximately coincided with the Eocene-Oligocene boundary (Miller et al. 1987; Miller 1992; Zachos et al. 2001). The Eocene-Oligocene climatic deterioration perhaps caused the extinction of these taxa or facilitated the southward migration due to the winter temperature extremes in Europe and North America. Fossil pollen of *Dendropanax* was reported from Puerto Rico in the middle Oligocene (Graham and Jarzen 1969), confirming the southward migration of *Dendropanax* taxa in the New World during the Eocene-Oligocene climatic deterioration. Tropical continental Asia has a great diversity of land forms, many of which evolved in the early and mid-Tertiary (Stanley 1999), and the diversity of topography created a wide range of habitats for the southward retreat of *Dendropanax* taxa. The fossil evidence, age estimates, and biogeographic analyses support the hypothesis that *Dendropanax* migrated across the North Atlantic land bridges into Europe and North America from Asia in the early Tertiary, followed by southward migrations and extinctions in the northern regions as climates cooled. This biogeographic pattern was reported by Antonelli et al. (2009) in Rubiaceae, who suggested that Rubiaceae used the corridors of the boreotropical vegetation belt and the North Atlantic land bridges as a pathway to reach North America from the Paleotropics in the late Paleocene/early Eocene.

The crown New World clade and Old World clades of *Dendropanax* were estimated at 27.43 mya (95% HPD: 17.56−38.47 mya) and at 24.92 mya (95% HPD: 14.75−35.65 mya) (nodes 2 and 3 in Fig. 3) in the late Oligocene, respectively. A gradual warming period occurred in the late Oligocene and early Miocene. This warming interval was both short-lived and much cooler than the warm interval of the early and middle Eocene (Tiffney 1985a; White et al. 1997; Tiffney and Manchester 2001). The paleoclimate in the late Oligocene-early Miocene perhaps favored the diversification of *Dendropanax* in both the New and the Old Worlds.

Within the New World, our analyses also suggest two centers of diversification of *Dendropanax* corresponding roughly to Central America (clade NW I) and South America (clade NW II) (Fig. 1). The crown ages of the two major clades are estimated at 14.68 mya (95% HPD: 8.77−21.57 mya) and at 12.18 mya (95% HPD: 6.59−18.34 mya) (nodes 4 and 5 in Fig. 3), respectively. These diversifications may have been driven by the uplift of the northern Andes and the rising of volcanic islands between South and Central America in the late Tertiary, and these islands eventually coalesced into today's lower Central America with a substantial land connection across the Isthmus of Panama (Hammen 1974; Keigwin 1978; Flenley 1979; Zeil 1979; Gentry 1982; Marshall et al. 1982). The events may have provided the conditions responsible for the divergence of *Dendropanax* between Central and South America, followed by the rapid diversification of taxa as the result of adaptation to a wide range of new habitats. The similar diversification pattern was interpreted in the species-rich Neotropical tree genus *Inga* (Fabaceae) by Richardson et al. (2001), who suggested that rapid diversification may have been promoted by the late phases of the Andean orogeny, the land bridge connection of the Panama Isthmus, and Quaternary climatic fluctuations.

In the Old World, the evolutionary diversification of *Dendropanax* in the Miocene was centered in the southern China/Indochina region. This diversification may have been driven by the rising of the Himalaya in the Tertiary (Harrison et al. 1992; An et al. 2001; Spicer et al. 2003). The mountain building processes accompanying the uplift of the Himalaya created regional topographic complexities in continental eastern and South Asia (Shi et al. 1998). The topographic diversity and the east-west oriented mountains in the region created a wide range of habitats. The diverse habitats combined with the climatic changes of the late Tertiary and the Quaternary may have facilitated allopatric speciation in many plant groups (e.g. in *Rhododendron*) (Irving and Hebda 1993).

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Appendix 1. Species name, voucher information, and GenBank accession numbers for taxa used in this study. Herbarium acronyms follow Holmgren et al. (1990). Voucher information is provided alphabetically by taxon name as follows: taxon name, locality, collector and number (herbarium acronym), GenBank accessions numbers (*ndhF*, *trnL-F*, *rps16*, *atpB-rbcL*, *rpl16*, *psbA-trnH*, *ITS*).

Aralia cordata Thunb., Japan, *A. Soejima 1072* (US), GU054744, GU055124, GU055029, GU054554, GU054934, GU054839, GU054649; **Aralia elata** (Miq.) Seem., China: Chongqi, Jinfoshan, *J. Wen 8221* (US), GU054780, GU055160, GU055065, GU054590, GU054970, GU054875, GU054685; **Aralia finlaysoniana** (Wall. ex G. Don) Seem., China: Yunnan, Hekou, *J. Wen 10571* (US), GU054760, GU055140, GU055045, GU054570, GU054950, GU054855, GU054665; **Aralia racemosa** L., U. S. A.: Wisconsin, Menominee, *J. Wen 7291-1* (US), GU054710, GU055090, GU054995, GU054520, GU054900, GU054805, GU054615; **Aralia soratensis** Marchal, Bolivia: Depto. Santa Cruz, Florida, *M. Nee & J. Wen 53845* (US), GU054764, GU055144, GU055049, GU054574, GU054954, GU054859, GU054669; **Aralia spinosa** L., U. S. A.: North Carolina, Avery, *J. Wen 6251-15* (US), GU054794, GU055174, GU055079, GU054604, GU054984, GU054889, GU054699; **Aralia stellata** (King) J. Wen, Thailand: Doichiang Dao, Doi Luang Valley, *J. F. Maxwell 03-505* (US), GU054745, GU055125, GU055030, GU054555, GU054935, GU054840, GU054650; **Aralia stipulata** Franch., China: Xizang, Chayu, *J. Wen 9198* (US), GU054795, GU055175, GU055080, GU054605, GU054985, GU054890, GU054700; **Aralia vietnamensis** Ha, China: Yunnan, Lvchun, *Y. M. Shui 81844* (US), GU054761, GU055141, GU055046, GU054571, GU054951, GU054856, GU054666; **Chengiopanax fargesii** (Franch.) C. B. Shang & J. Y. Huang, China: Hunan, Xinning, *J. Wen 9316* (US), GU054746, GU055126, GU055031, GU054556, GU054936, GU054841, GU054651; **Dendropanax arboreus** (L.) Decne. & Planch. Bolivia: Depto. Santa Cruz, Florida, *M. Nee & J. Wen 53827* (US), GU054779, GU055159, GU055064, GU054589, GU054969, GU054874, GU054684; **Dendropanax arboreus** (L.) Decne. & Planch., Costa Rica: San Jose, Canton de Acosta, *J. Wen 7045* (US), GU054787, GU055167, GU055072, GU054597, GU054977, GU054882, GU054692; **Dendropanax arboreus** (L.) Decne. & Planch. Mexico: Oaxaca, Mpio. Pluma Hidalgo, *J. Wen 8694* (US), GU054765, GU055145, GU055050, GU054575, GU054955, GU054860, GU054670; **Dendropanax bolivianus** Gand., Bolivia: Depto. Santa Cruz, Ichilo, *M. Nee & J. Wen 53766* (US), GU054766, GU055146, GU055051, GU054576, GU054956, GU054861, GU054671; **Dendropanax bolivianus** Gand., Bolivia: Depto. Santa Cruz, Ichilo, *M. Nee & J. Wen 53767* (US), GU054769, GU055149, GU055054, GU054579, GU054959, GU054864, GU054674; **Dendropanax bolivianus** Gand., Bolivia: Depto. Santa Cruz, Ichilo, *M. Nee & J. Wen 53797* (US), GU054767, GU055147, GU055052, GU054577, GU054957, GU054862, GU054672; **Dendropanax burmanicus** Merr., China: Yunnan, Gongshan, *H. Li 33274* (US), GU054781, GU055161, GU055066, GU054591, GU054971, GU054876, GU054686; **Dendropanax burmanicus** Merr., China: Yunnan, Gongshan, *H. Li & R. Li 1020* (US), GU054711, GU055091, GU054996, GU054521, GU054901, GU054806, GU054616;

Dendropanax caloneurus (Harms) Merr., Vietnam: Lao Cai, Sa Pa, *J. Wen 6063-5* (US), GU054712, GU055092, GU054997, GU054522, GU054902, GU054807, GU054617; **Dendropanax capillaries** M. J. Cannon & Cannon, Costa Rica: Cartago, Orosi, *J. Wen 6896* (US), GU054724, GU055104, GU055009, GU054534, GU054914, GU054819, GU054629; **Dendropanax caucanus** Harms, Costa Rica: Puntarenas, Canton de Golfito, *J. Wen 7005* (US), GU054725, GU055105, GU055010, GU054535, GU054915, GU054820, GU054630; **Dendropanax caucanus** Harms, Costa Rica: Puntarenas, Canton de Osa, *J. Wen 7018* (US), GU054726, GU055106, GU055011, GU054536, GU054916, GU054821, GU054631; **Dendropanax chevalieri** (R. Vig.) Merr., Vietnam: Lao Cai, Sa Pa, *J. Wen 6000-13* (US), GU054763, GU055143, GU055048, GU054573, GU054953, GU054858, GU054668; **Dendropanax chevalieri** (R. Vig.) Merr., Vietnam: Lao Cai, Sa Pa, *J. Wen 6079-7* (US), GU054783, GU055163, GU055068, GU054593, GU054973, GU054878, GU054688; **Dendropanax confertus** H. L. Li, China: Jiangxi, Sangqingshan, *J. Wen 9852* (US), GU054793, GU055173, GU055078, GU054603, GU054983, GU054888, GU054698; **Dendropanax cuneatus** Decne. & Planch., Bolivia: Depto. Santa Cruz, Ichilo, *M. Nee & J. Wen 53795* (US), GU054775, GU055155, GU055060, GU054585, GU054965, GU054870, GU054680; **Dendropanax cuneifolius** (Wright) Seem., Cuba: Pinar del Rio, La Palma, *J. L. Clark 10620* (US), GU054762, GU055142, GU055047, GU054572, GU054952, GU054857, GU054667; **Dendropanax dentiger** (Harms) Merr., China: Hunan, Xinning, *J. Wen 9306* (US), GU054749, GU055129, GU055034, GU054559, GU054939, GU054844, GU054654; **Dendropanax dentiger** (Harms) Merr., China: Hunan, Xinning, *J. Wen 9311* (US), GU054709, GU055089, GU054994, GU054519, GU054899, GU054804, GU054614; **Dendropanax dentiger** (Harms) Merr., China: Hunan, Xinning, *J. Wen 9322* (US), GU054789, GU055169, GU055074, GU054599, GU054979, GU054884, GU054694; **Dendropanax dentiger** (Harms) Merr., China: Hunan, Xinning, *J. Wen 9332* (US), GU054713, GU055093, GU054998, GU054523, GU054903, GU054808, GU054618; **Dendropanax globosus** M. J. Cannon & Cannon, Costa Rica: Puntarenas, Monteverde, *J. Wen 6848-1* (US), GU054714, GU055094, GU054999, GU054524, GU054904, GU054809, GU054619; **Dendropanax gonatopodus** (Donn. Sm.) A. C. Sm., Costa Rica: Heredia, *J. Wen 6922* (US), GU054785, GU055165, GU055070, GU054595, GU054975, GU054880, GU054690; **Dendropanax gonatopodus** (Donn. Sm.) A. C. Sm., Costa Rica: Puntarenas, Canton de Golfito, *J. Wen 7008* (US), GU054727, GU055107, GU055012, GU054537, GU054917, GU054822, GU054632; **Dendropanax gonatopodus** (Donn. Sm.) A. C. Sm., Mexico: Chiapas, Mpio, Plaenque, *J. Wen 8730* (US), GU054776, GU055156, GU055061, GU054586, GU054966, GU054871, GU054681; **Dendropanax hainanensis** (Merr. & Chun) Chun, China: Hunan, Mangshan, *Y. F. Deng 16240* (US), GU054750, GU055130, GU055035, GU054560, GU054940, GU054845, GU054655; **Dendropanax hoi** C. B. Shang, China: Yunnan, Maguan, *Y. M. Shui 31116* (US), GU054778, GU055158, GU055063, GU054588, GU054968, GU054873, GU054683; **Dendropanax lancifolius** Ridl., Malaysia: Pahang, Cameron Highlands, *J. Wen 8362* (US), GU054774, GU055154, GU055059, GU054584, GU054964, GU054869, GU054679; **Dendropanax latilobus** M. J. Cannon & Cannon, Costa Rica: Puntarenas, Monteverde, *J. Wen 6834-1* (US), GU054751, GU055131, GU055036, GU054561, GU054941, GU054846, GU054656; **Dendropanax macropodus** (Harms) Harms, Bolivia: Depto. Cochabamba, Chapare, *M. Nee & J. Wen 53954* (US), GU054715, GU055095, GU055000, GU054525, GU054905, GU054810, GU054620; **Dendropanax maingayi** King, Malaysia: Pahang, Cameron Highlands, *J. Wen 8364* (US), GU054728, GU055108, GU055013, GU054538, GU054918, GU054823, GU054633; **Dendropanax oliganthus** (A. C. Sm.) A. C. Sm., Costa Rica: Puntarenas, Santa Maria de Dota, *J. Wen 6888* (US), GU054729, GU055109, GU055014, GU054539, GU054919, GU054824, GU054634; **Dendropanax oliganthus** (A. C. Sm.) A. C. Sm., Mexico: Oaxaca, Mpio. Candelaria, *J. Wen 8692* (US), GU054768, GU055148, GU055053, GU054578, GU054958, GU054863, GU054673; **Dendropanax oligodontus** Merr. & Chun, China: Hainan, *Y. G. Wang s. n.* (US), GU054790, GU055170, GU055075, GU054600, GU054980, GU054885, GU054695; **Dendropanax oligodontus** Merr. & Chun, China: Hainan, Lingshui, *J. Wen 6603-1* (US), GU054784, GU055164, GU055069, GU054594, GU054974, GU054879, GU054689; **Dendropanax pallidus** M. J. Cannon & Cannon, Ecuador, *C. R. Broome 741* (US), GU054791, GU055171, GU055076, GU054601, GU054981, GU054886, GU054696; **Dendropanax palustris** (Ducke) Harms, Peru: Loreto, *P. Fine 1006* (F), GU054753, GU055133, GU055038, GU054563, GU054943, GU054848, GU054658; **Dendropanax palustris** (Ducke) Harms, Peru: Vanillal, *P. Fine 1091* (F), GU054747, GU055127, GU055032, GU054557, GU054937, GU054842, GU054652; **Dendropanax poilanei** Bui, Vietnam: Guangnam, Ba Na Hills, *J. Wen 10975* (US), GU054771, GU055151, GU055056, GU054581, GU054961, GU054866, GU054676; **Dendropanax poilanei** Bui, Vietnam: Lam Dong, Lac Duong, *J. Wen 11049* (US), GU054772, GU055152, GU055057, GU054582, GU054962, GU054867, GU054677; **Dendropanax praestans** Standl., Costa Rica: San Jose, Santa Maria de Dota, *J. Wen 6891-1* (US), GU054754, GU055134, GU055039, GU054564, GU054944, GU054849, GU054659; **Dendropanax praestans** Standl., Costa Rica: Puntarenas, Canton de Golfito, *J. Wen 6990-3* (US), GU054752, GU055132, GU055037, GU054562, GU054942, GU054847, GU054657; **Dendropanax productus** H. L. Li, China: Guangdong, Lianshan, *J. Wen 5793-1* (US), GU054782, GU055162, GU055067, GU054592, GU054972, GU054877, GU054687; **Dendropanax proteus** (Champ. ex Benth.) Benth., China: Guangdong, Heishiding, *J. Wen 5780* (US), GU054716, GU055096, GU055001, GU054526, GU054906, GU054811, GU054621; **Dendropanax punctatus** M. J. Cannon & Cannon, Peru, *Cocle D. M. Porter s. n.* (F), GU054792, GU055172, GU055077, GU054602, GU054982, GU054887, GU054697; **Dendropanax ravenii** M. J. Cannon & Cannon, Costa Rica: Puntarenas, Canton de Osa, *J. Wen 7016* (US), GU054730, GU055110, GU055015, GU054540, GU054920, GU054825, GU054635; **Dendropanax schippii** A. C. Sm., Mexico: Chiapas, Mpio, Ocosingo, *J. Wen 8729* (US), GU054777, GU055157, GU055062, GU054587, GU054967, GU054872, GU054682; **Dendropanax sessiliflorus** (Standl. & A. C. Sm.) A. C. Sm., Costa Rica: Puntarenas, Canton de Coto Brus, *J. Wen 6985* (US), GU054786, GU055166, GU055071, GU054596, GU054976, GU054881, GU054691; **Dendropanax sessiliflorus** (Standl. & A. C. Sm.) A. C. Sm., Costa Rica: Puntarenas, Canton de Golfito, *J. Wen 7002* (US), GU054717, GU055097, GU055002, GU054527, GU054907, GU054812, GU054622; **Dendropanax sessiliflorus** (Standl. & A. C. Sm.) A. C. Sm., Costa Rica: Puntarenas, Canton de Golfito, *J. Wen 7013* (US), GU054731, GU055111, GU055016, GU054541, GU054921, GU054826, GU054636; **Dendropanax sp.**, Peru: Amazon, *P. Fine 938* (F), GU054748, GU055128, GU055033, GU054558, GU054938, GU054843, GU054653; **Dendropanax umbellatus** (Ruiz & Pav.) J. F. Macbr., Peru: Dpto. Pasco, Oxapampa, *J. Wen 8617* (US), GU054770, GU055150, GU055055, GU054580, GU054960, GU054865, GU054675; **Eleutherococcus senticosus** (Rupr. & Maxim.) Maxim., China: Beijing, Baihuashan, *J. Wen 8527* (US), GU054705, GU055085, GU054990, GU054515, GU054895, GU054800, GU054610; **Eleutherococcus sieboldianus** (Makino) Koidz., Japan: Chiba-ken, Narita-shi, *J. Wen 8538* (US), GU054706, GU055086, GU054991, GU054516, GU054896, GU054801, GU054611; **Fatsia oligocarpella** Koidz., Japan, *H. Kato 30041* (US), GU054755, GU055135, GU055040, GU054565, GU054945, GU054850, GU054660; **Gastonia cutispongia** Lam., Cultivated in National Botanical Garden of Belgium, *Belgium 19942627* (US), GU054756, GU055136, GU055041, GU054566, GU054946, GU054851, GU054661; **Hedera colchica** (K. Koch) K. Koch, U. S. A.: California, Los Angeles, *J. Wen 6683* (US), GU054743, GU055123, GU055028, GU054553, GU054933, GU054838, GU054648; **Hedera nepalensis** K. Koch, Vietnam: Lao Cai, Sa Pa, *J. Wen 5980* (US), GU054732, GU055112, GU055017, GU054542, GU054922, GU054827, GU054637; **Hedera pastuchovii** Woronow, U. S. A.: Illinois, Cook, *J. Wen 7322* (US), GU054704, GU055084, GU054989, GU054514, GU054894, GU054799, GU054609; **Hedera rhombea** (Miq.) Bean, Korea, *K.-O. Yoo s. n.* (US), GU054703, GU055083, GU054988, GU054513, GU054893, GU054798, GU054608; **Hedera sinensis** (Tobler) Hand.-Mazz., China: Hunan, Xinning, *J. Wen 9278* (US), GU054718, GU055098, GU055003, GU054528, GU054908, GU054813, GU054623; **Kalopanax septemlobus** (Thunb.) Koidz., China: Hunan, Xinning, *J. Wen 9341* (US), GU054740, GU055120, GU055025, GU054550, GU054930, GU054835, GU054645; **Macropanax dispermus** (Blume) Kuntze, Indonesia: west Java, Bandung, *J. Wen 10137-1* (US), GU054702, GU055082, GU054987, GU054512, GU054892, GU054797, GU054607; **Macropanax maingayi** (C. B. Clarke) Philipson, Malaysia: Langat, Langat, *J. Wen 8355* (US), GU054741, GU055121, GU055026, GU054551, GU054931, GU054836, GU054646; **Macropanax rosthornii** (Harms) C. Y. Wu ex G. Hoo, China: Sichuan, Dujiangyan, *J. Wen 9264* (US), GU054708, GU055088, GU054993, GU054518, GU054898, GU054803, GU054613; **Macropanax undulatus** Seem., China: Yunnan, Jinhong, *J. Wen 8474* (US), GU054719, GU055099, GU055004, GU054529, GU054909, GU054814, GU054624; **Metapanax davidii** (Franch.) J. Wen & Frodin, China: Sichuan, Dujiangyan *J. Wen 9266* (US), GU054720, GU055100, GU055005, GU054530, GU054910, GU054815, GU054625; **Metapanax delavayi** (Franch.) J. Wen & Frodin, China: Yunnan, Lufeng, *J. Wen 9146* (US), GU054707, GU055087, GU054992, GU054517, GU054897, GU054802, GU054612; **Oplopanax elatus** (Nakai) Nakai, China: Jilin, Wusong, *J. Wen 5418-11* (US), GU054757, GU055137, GU055042, GU054567, GU054947, GU054852, GU054662; **Oreopanax** sp. nov., Peru: Dpto. Pasco, Oxapampa, *J. Wen 8599* (US), GU054788, GU055168, GU055073, GU054598, GU054978, GU054883, GU054693; **Oreopanax liebmannii** Marchal, Mexico: Chiapas, Mpio. Palenque, *J. Wen 8744* (US), GU054773, GU055153, GU055058, GU054583, GU054963, GU054868, GU054678; **Oreopanax polycephalus** Harms, Peru: Dpto. Pasco, Oxapampa, *J. Wen 8595* (US), GU054733,

GU055113, GU055018, GU054543, GU054923, GU054828, GU054638; **Oreopanax xalapense** (Kunth) Decne. & Planch., Costa Rica: Heredia, San Jose de La Montana, *J. Wen 6934* (US), GU054734, GU055114, GU055019, GU054544, GU054924, GU054829, GU054639; **Panax trifolius** L., U. S. A.: Maryland, Baltimore, *J. Wen 10099* (US), GU054796, GU055176, GU055081, GU054606, GU054986, GU054891, GU054701; **Schefflera angulata** (Pav.) Harms, Peru: Dpto. Pasco, Oxapampa, *J. Wen 8589* (US), GU054735, GU055115, GU055020, GU054545, GU054925, GU054830, GU054640; **Schefflera arboricola** (Hayata) Merr., China: Yunnan, Baoshan, *J. Wen 6295* (US), GU054721, GU055101, GU055006, GU054531, GU054911, GU054816, GU054626; **Schefflera heptaphylla** (L.) Frodin, Vietnam: Ninh Binh, Mt. Bavi, *J. Wen 6165* (US), GU054736, GU055116, GU055021, GU054546, GU054926, GU054831, GU054641; **Schefflera heterophylla** (Wall. ex G. Don) Harms, Malaysia: Selangor, *J. Wen 8392* (US), GU054737, GU055117, GU055022, GU054547, GU054927, GU054832, GU054642; **Schefflera hypoleuca** (Kurz) Harms, Thailand: Chiang Mai, Doi Intonon, *J. Wen 7427* (US), GU054738, GU055118, GU055023, GU054548, GU054928, GU054833, GU054643; **Schefflera morototoni** (Aubl.) Maguire, Costa Rica: San Jose, Canton de Pérez Zeledón, *J. Wen 6952* (US), GU054742, GU055122, GU055027, GU054552, GU054932, GU054837, GU054647; **Schefflera pentandra** (Pav.) Harms, Peru: Dpto. Pasco, Oxapampa, *J. Wen 8619* (US), GU054722, GU055102, GU055007, GU054532, GU054912, GU054817, GU054627; **Schefflera subulata** R. Vig., Malaysia: Selangor, *J. Wen 8396* (US), GU054739, GU055119, GU055024, GU054549, GU054929, GU054834, GU054644; **Sinopanax formosanus** (Hayata) H. L. Li, China: Taiwan, Kaohsiung, *J. Wen 9390* (US), GU054723, GU055103, GU055008, GU054533, GU054913, GU054818, GU054628; **Tetrapanax papyrifer** (Hook.) K. Koch, Indonesia: west Java, Bogor, *J. Wen 10135* (US), GU054758, GU055138, GU055043, GU054568, GU054948, GU054853, GU054663; **Trevesia lateospina** Jebb, Thailand: Lampang, Muang Bahn, *J. Wen 7480-1* (US), GU054759, GU055139, GU055044, GU054569, GU054949, GU054854, GU054664.