

MOLECULAR PHYLOGENY AND HISTORICAL BIOGEOGRAPHY OF *Dendropanax* (Araliaceae)

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Abstract. Exploring the genetic relationships between plant species as well as their historical evolution can provide important information in science. *Dendropanax* is an excellent model for examining the evolution of the disjunction between tropical Asia and the Neotropics. The study, based on the molecular data of comprehensive taxon sampling of seven DNA regions, supported the relationship within the genus *Dendropanax*. Three clades were recognized in this genus. According to the result of molecular data analyses, the study hypothesized that the genus *Dendropanax* originated in Southeast Asia and South China during the mid-Eocene and then spread to the NKJ region. During the late Eocene, *Dendropanax* was dispersed by birds and mammals in SE Asia, South China, and North America. The genus then migrated to Central America, the Caribbean region, South America, and Europe. Lineages of *Dendropanax* in North America and Europe became extinct due to the major cooling event in the late Eocene to early Oligocene. Thus, at present, no species of *Dendropanax* occurs in North America or Europe.

Keywords: *Dendropanax*, molecular, phylogeny, historical biogeography, SE Asia.

1. INTRODUCTION

The family Araliaceae (the Ginseng family) includes 46 genera and ca. 1500 species with a wide distribution in tropical and subtropical Asia, the Pacific and Indian Ocean basins, and the neotropics, with a few well-known genera from the north and south temperate zones (Wen et al., 2001). The genus *Dendropanax* Decne. & Planch. is a member of the Araliaceae with approximately 90 species from tropical America and East Asia (Xiang & Porter, 2007). Several species of *Dendropanax* are used as traditional medicine for local people in both the Old and New Worlds (Xiang & Porter, 2007; Li & Wen, 2013). The members of *Dendropanax* are characterized by evergreen trees or small understory shrubs. The stems are unarmed, simple leaves with margins that are entire or

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have a few irregular teeth. The inflorescence is a simple terminal umbel or a panicle of multiple umbels, or occasionally of multiple heads (Bui, 1976).

In the study of the historical biogeography of plants, the intercontinental disjunctions between eastern Asia and North America have been of interest to several taxa. *Dendropanax* is an excellent model for examining the evolution of the disjunction between tropical Asia and the Neotropics. Some studies have been conducted to investigate the phylogeny and biogeography of the genus. Li and Wen (2013) performed a phylogeny and biogeography of *Dendropanax* based on the molecular data from seven DNA regions. The result of the study indicated that *Dendropanax* is a non-monophyletic group, and the genus originated in the Old World and then migrated to the New World via the North Atlantic land bridges in the early Tertiary. However, the study did not delve into details about the historical biogeography of *Dendropanax*.

Li and Wen (2016) conducted a study about the phylogeny and diversification of Chinese Araliaceae based on nuclear and plastid DNA sequences. The result showed that the Chinese members of Araliaceae were scattered within the Asian Palmate group, and the Chinese Araliaceae was inferred to have originated in Asia and underwent rapid radiation in its evolutionary history. However, the study only included twelve species of *Dendropanax*, thus the phylogeny and biogeography of the genus is still unclear.

Recently, Balakrishnan et al. (2020) investigated the phytochemistry and pharmacology of some *Dendropanax* species. The study suggests that plants of the *Dendropanax* genus include several active compounds, and they possess a wide range of therapeutic and pharmacological applications, including antifungal, anti-complement, antioxidant, antibacterial, insect antifeedant, cytotoxic, anti-inflammatory, neuroprotective, anti-diabetic, anti-cancer, and anti-hypouricemic properties.

Dendropanax was recorded to be widely distributed in both the Old and New Worlds, thus the determination of the phylogenetic relationship and historical biogeography of the genus is significant. Therefore, the present study aims to (1) clarify the phylogenetic relationship of the genus *Dendropanax*; (2) reconstruct the biogeographical history of *Dendropanax* reconciled with present-day distributions, fossil data, and geological information.

2. MATERIALS AND METHODS

2.1. Taxon sampling, DNA extraction, amplification, sequencing

We sampled 58 species, including 37 species of *Dendropanax*, for molecular data to ensure the representation of all major clades of the genus. 21 species of *Gastonia*, *Panax*, *Aralia*, *Scheffera*, *Hedera*, *Sinopanax*, *Oreopanax*, *Kalopanax*, *Metapanax*, *Macropanax* were used as Outgroups. The molecular matrix was constructed using the seven DNA regions (*ndhF*, *trnL-F*, *rps16*, *atpB-rbcL*, *rpl16*, *psbA-trnH*, and ITS). We downloaded sequences from NCBI and generated sequences from our collections. The voucher information and GenBank accession numbers are listed in Table S1.

The genomic DNA of *Dendropanax* was extracted from silica gel-dried tissues using the CTAB procedure (Doyle & Doyle, 1987). Polymerase chain reactions and sequencing were performed using the primers designed by Li and Wen (2013) and Taberlet et al. (1991).

The PCR amplification reactions used MasterMix from the BioMed company. The PCR program consisted of 5 min at 95 °C, 36 cycles of 30 s at 95 °C, 50 s at 48 °C, and 1 min 30 s at 72 °C, with a final extension of 10 min at 72 °C. We purified the PCR products on a 1.0% agarose gel using BioMed multifunctional DNA fragment purification recovery kits and sequenced them using the amplification primers. The bidirectional sequencing was completed using the ABI 3730 DNA Sequencer (Applied Biosystems, Carlsbad, California, USA). The sequences were aligned in Geneious v.8.0.5 (Kearse et al., 2012).

2.2. Phylogenetic analyses

Both maximum likelihood (ML) and Bayesian inference (BI) were carried out for the phylogenetic analyses of *Dendropanax*. The ML analysis was performed using the program RAxML 8.2.10 (Stamatakis, 2006; Stamatakis et al., 2008) with the GTR + I + G substitution model for each molecular marker and the combined dataset at the CIPRES (Cyber Infrastructure for Phylogenetic Research; www.phylo.org). ML bootstrap analysis was implemented with 1000 replicates. Bayesian inference was conducted in MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003). The best-fitting models for each marker and the combined data set were determined by the Akaike Information Criterion (AIC) as implemented in jModelTest 2.1.6 (Darriba et al., 2012). Bayesian analysis of the combined data set used the GTR + I + G model as determined in jModelTest. The MCMC algorithm was run for 10,000,000 generations with four Markov chain Monte Carlo (MCMC) and trees were sampled every 1000 generations. The program Tracer 1.6 (Rambaut & Drummond, 2007) was used to check that the effective sample size (ESS) for all relevant parameters was well above 200, indicating that stationarity had probably been reached. With the first 25% of sampled generations (2500 trees) discarded as burn-in, a 50% majority-rule consensus tree and posterior probabilities (PP) were obtained using the remaining trees.

2.3. Divergence time estimation

To estimate the origin and divergence times of *Dendropanax*, we used the combined datasets from nuclear (ITS) and plastid (*ndhF*, *trnL-F*, *rps16*, *atpB-rbcL*, *rpl16*, and *psbA-trnH*) sequences for the dating analysis. This adjustment was made to match the markers used in previous phylogenetic studies of *Dendropanax*. The divergence time estimation of *Dendropanax* was conducted by applying the uncorrelated lognormal Bayesian method in BEAST v.1.8.4 (Drummond et al., 2012). We partitioned the combined datasets based on seven DNA regions using the “unlink substitution model” option, and on the other hand, each partition of the combined dataset was run with a substitution model resulting from jModelTest v.2.1.6 (Darriba et al., 2012). All divergence time analyses were run using a Yule process tree prior, while the four

calibration points of the dating analysis applied the lognormal distribution option. The two separate Markov chains in Monte Carlo were run for 150 million generations, with samples taken every 1,500 generations. We used Tracer v.1.6 (Rambaut et al., 2014) to check ESSs and ensure that all relevant parameters are higher than 200 and stationarity has been reached. After discarding the first 25% of trees as burn-in, TreeAnnotator v.1.8.0 (Rambaut & Drummond, 2010) constructed a maximum credibility tree. Figtree v1.4.0 was used to illustrate the outcome (Rambaut, 2009).

2.4. Biogeographic reconstruction

Bayesian approach to dispersal-vicariance analysis (Bayes-DIVA; Nylander et al., 2008) implemented in RASP v.3.2 (Yu et al., 2011) using datasets from the BEAST analysis was utilized to reconstruct the biogeographic history of *Dendropanax*. Using the trees produced by BEAST, the Bayes-DIVA approach can increase phylogenetic certainty (Nylander et al., 2008; Yu et al., 2011). We used 10,000 trees resulting from the dating and removed 25% of the trees to obtain a condensed tree as the final representative tree, with the outgroups pruned. We determined the biogeographic areas for species within the subtribe *Dendropanax* from the distribution information described in the literature and herbarium specimens (PE, K, P, and HN) for extant *Dendropanax* and their relatives. Six biogeographical areas were defined: A, Southeast Asia (SE Asia) and South China (including Assam, East Asia, Indochina, and Malesia); B, North China, the Korean Peninsula, and Japan (NKJ region); C, South America; D, Central America and the Caribbean region; E, North America; and F, North Africa. Although the genus *Dendropanax* is distributed in Asia and America, there are multiple differences in climatic and geographic barriers between the two continents. Thus, this study defined six biogeographical areas following the distribution of extant *Dendropanax* and outgroup species, in which North America and North Africa regions were applied for the outgroups.

3. RESULTS AND DISCUSSION

3.1. Molecular data sets used in the study

The study generated two new sequences of *Dendropanax*. The lengths of individual data sets of *ndhF*, *trnL-F*, *rps16*, *atpB-rbcL*, *rpl16*, *psbA-trnH*, and ITS are 2129, 988, 917, 784, 985, 532, and 699 bps, respectively. The combined dataset included 7034 aligned positions for the ingroups and outgroups. In our molecular data set, some sequences are missing from the species *Dendropanax bahiensis*, *D. morbifer*, *Dendropanax* sp. (LW29), and *D. trifidus*. However, this has no significant influence on the phylogenetic results of *Dendropanax*, and the phylogenetic position of these species is relatively certain (Figure 1). Therefore, we keep them in the molecular data sets to ensure comprehensive sampling coverage.

3.2. Phylogenetic relationships

The combined molecular dataset indicated strong support for most clades. The results from the ML and BI trees were highly congruent, the few differences had low

Figure 1. Majority rule consensus tree of *Dendropanax* based on the combined datasets of seven DNA regions (*ndhF*, *trnL-F*, *rps16*, *atpB-rbcL*, *rpl16*, *psbA-trnH*, and ITS). ML bootstrap values and posterior probabilities (PP) of the BI analysis are presented above the branches. “–” indicates the support values less than 50%.

The *Dendropanax* from the New World, including Central America, the Caribbean region, and South America, form a clade strongly supported by molecular data (Figure 1). The two endemic species of Costa Rica, *Dendropanax globosus* and *D. praestans*, are closely related and placed in the basal of the New World *Dendropanax* clade as sisters to the remaining species of the clade. The two species share the morphological characters of paniculate inflorescences, styles free at the apex, and pluricarpellate ovaries. *D. globosus* can be distinguished from *D. praestans* by unlobed juvenile leaves (vs. 5–7-lobed), leaf blades without (vs. with) glands, and globose receptacles (vs. subglobose) (Cannon and Cannon, 1989). In this clade, the endemic species of South America, including *D. palustris*, *D. bahiensis*, *D. umbellatus*, *D. bolivianus*, *D. arboreus*, and *D. macropodus*, formed a subclade, however, there seems to be no synapomorphy of morphology between the South American endemic species and the New World species. Li and Wen (2013) suggested that the relationship between *Dendropanax* species in the New World is quite complex, and to clarify this question, more investigations are needed in the future.

Clade B includes the Old World *Dendropanax* species (Figure 1). The species *D. caloneurus* from northern Vietnam was supported as the first diverged lineage in this clade by Li and Wen (2013, 2016); however, our study suggests that the molecular relationship of this clade is stable with the polytomy presented in the basal of the clade; this result is also seen in Li and Wen (2013). The two species *D. maingayi* from the Malay Peninsula and *D. poilanei* from southern Vietnam are closely related by molecular data, and they formed a small clade in the basal of clade B (Figure 1). The two species share leaves without translucent glands and styles free in the upper half in morphology. A similar position is held by the two species *Dendropanax oligodontus* and *D. proteus*; their two species are closely related (Figure 1) and placed together in the basal of clade B.

All the *Dendropanax* from Vietnam were placed in clade B except *D. hainanensis*; the Vietnamese species is not a monophyletic group (Figure 1). *D. chevalieri*, *D. confertus*, and *Dendropanax* sp. formed a well-supported clade with some species from China. These species are morphologically similar. All species have lobed leaves with translucent glands, solitary umbels, and styles united into a column. Based on our observation of molecular data, the sequences of the Asian *Dendropanax* species are highly homologous; however, the appearance of polytomy branches and the unstable phylogenetic position of some species indicate the rapid diversification of species in this region.

3.3. Divergence times and historical biogeography of *Dendropanax*

The divergence time estimations for *Dendropanax* are presented in Figure 2. The stem age of *Dendropanax* was estimated to be 46.65 Ma (95 % HPD: 44.14, 47.58 Ma; node 1, Figure 2). The crown age of *Dendropanax* was estimated to be 42.16 Ma (95 % HPD: 39.34, 45.08 Ma; node 2, Figure 2). The two species *D. hainanensis* and *D. lancifolius* split 21.53 Ma (95 % HPD: 15.98, 37.46 Ma, Figure 2). The New World clade diverged 25.61 Ma (95 % HPD: 16.47, 35.17 Ma; node 5, Figure 2), while the Old World clade diverged 26.94 Ma (95 % HPD: 18.57, 35.65 Ma; node 4, Figure 2). These results are congruent with Li and Wen (2013, 2016).

Origin and diversification of *Dendropanax* in SE Asia and South China

Li and Wen (2013) noted that the ancestral area of *Dendropanax* was in the Old World, but the detailed area was not mentioned. Our result suggested that the stem group of *Dendropanax* originated in SE Asia and South China (node 1) ca. 46 Ma during the mid-Eocene, and after the initial origin, *Dendropanax* started to diverge in the Late Eocene at 42.16 Ma (node 2, Figure 2). During the early Eocene, ca. 50–52 Ma, the global climate was optimal (Zachos et al., 2001, 2008). The tropical and subtropical regions consist of most tropical forests in the world, including tropical rainforests, tropical seasonal rainforests, and subtropical evergreen broad-leaved forests (Xiang et al., 2016). *Dendropanax* species have drupe fruit with color when mature (Xiang and Porter, 2007). Similar to the fruit of some plants, such as *Arisaema*, Loranthaceae, and Vitaceae. *Dendropanax* fruit is food for insectivorous birds (blue-headed parrots, saltators, and tanagers) and small mammals (rodents) (Liu et al., 2018; Tran et al., 2022). Therefore, birds and mammals are the main factors in dispersing the seeds of the genus. The combination of the presence and development of the tropical rainforest biome with the warm climate in the Late Eocene could have provided habitats for the origin, survival, and radiation differentiation of *Dendropanax* in SE Asia and South China.

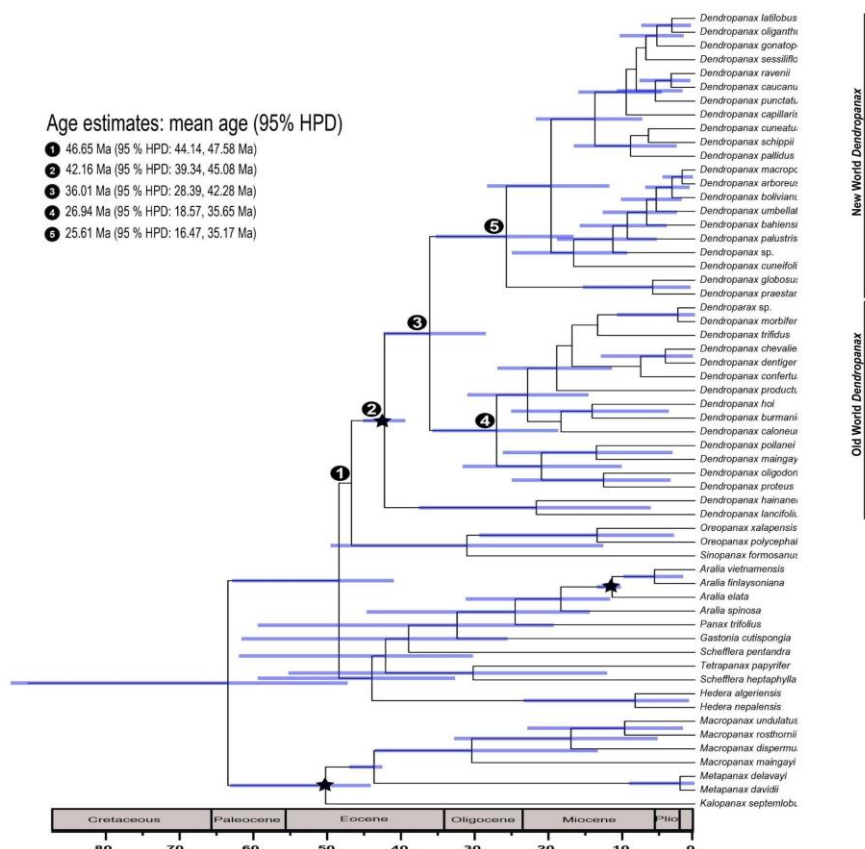


Figure 2. Maximum clade credibility tree inferred from BEAST based on the combined datasets of seven DNA regions. The bars around node ages indicate 95% highest posterior density intervals. Node constraints are indicated with stars. Nodes of interest were marked as 1–5.

The Old World ancestors of *Dendropanax* spread and made the differentiation in SE Asia and then dispersed to the NKJ region two times during the Late Oligocene to Late Miocene (Figure 2). Some angiosperm members like *Arisaema* (Araceae, Tran et al., 2022) and *Loranthus* (Loranthaceae, Liu et al., 2018) have the same situation with *Dendropanax*. Zachos et al. (2001) suggested that the global climate was optimal during the middle Miocene. Moreover, the two areas are very close and always contiguous. Thus, we hypothesize that Southeast Asian *Dendropanax* was dispersed to the NKJ region during a warm climate and via moist forest areas by birds and mammals. The Vietnamese *Dendropanax* species also originated from a SE Asian ancestor via differentiation in this area.

However, we did not find any vice versa dispersal from the NKJ region to SE Asia. This can be explained by the climate cooling after the middle Miocene, and *Dendropanax* in the NKJ region likely adapted to living conditions when dispersing from tropical regions to temperate regions or mountainous forests in high-elevation regions.

Dispersal to the New World from SE Asia and South China

The biogeographical analyses show that the colonization of America by *Dendropanax* from SE Asia and South China has occurred only once (node 5, Figure 3). The disjunction between Asia and America can be explained by the hypothesis of the Bering land bridge. The Bering land bridge was mostly exposed during the Neogene for trans-Pacific floristic changes until about 3.5 Ma (Ickert-Bond et al., 2009; Tran et al., 2022), and it was used to explain the disjunction for angiosperms such as *Pyrularia* (Cervantesiaceae) (Zhou et al., 2019). Li and Wen (2013) suggested that fossil leaves of *D. eocenensis* were reported from Tennessee in North America and fossil fruits of *D. gallicum* from France; thus, *Dendropanax* was distributed in Europe and North America in the early Tertiary (Dilcher & Dolph, 1970). Notwithstanding, in the New World, the genus *Dendropanax* is only found in Central America, the Caribbean region, and South America currently, it seems to be extinct in North America currently. According to West et al. (2015), there was a warm climate in the early Eocene, and forests stretched all the way from North America to modern-day Alaska. Thus, we hypothesized that *Dendropanax* dispersed to North America from SE Asia and South China via the Bering land bridge during the late Eocene (node 3, Figure 3) by birds and mammals. Then, the genus migrated to the contiguous areas of Central America and the Caribbean region during the late Oligocene (node 5, Figure 3) and South America during the mid-Miocene with climate optimums (Zachos et al., 2001) (Figure 3).

The islands that formed when the proto Antilles crashed with the Bahamas plate during the Ypresian (ca. 50 Ma) period can account for the dispersal from North America to South America via Central America and the Caribbean region (Morley, 2003). Based on the dispersal route of Arecaceae (palm family), Baker and Couvreur (2013) proposed a connection between North and South America during the early Eocene.

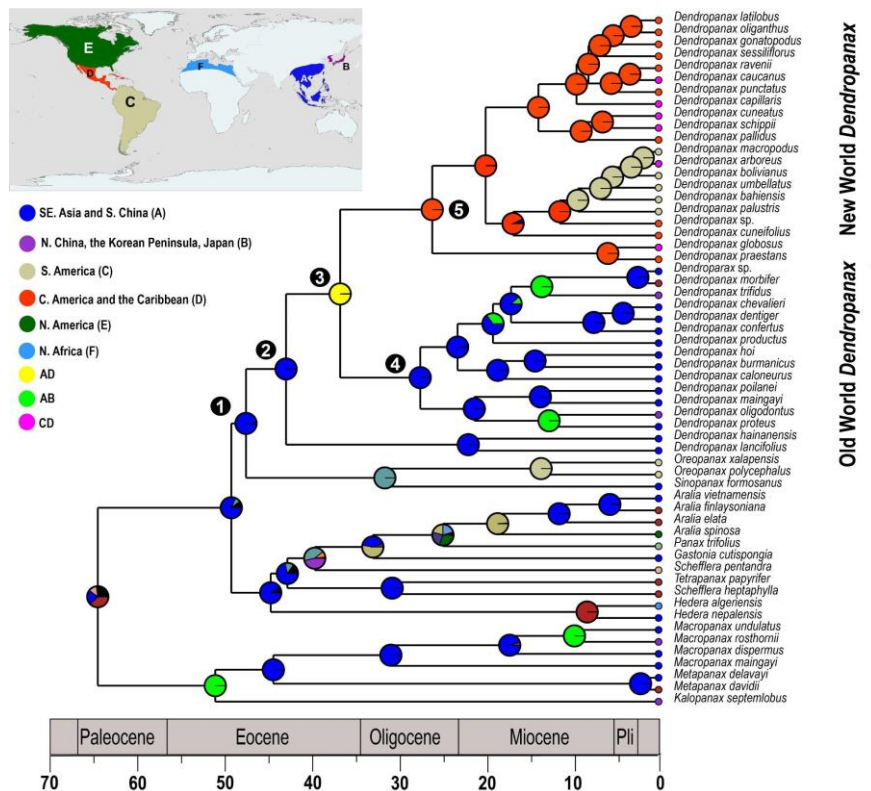


Figure 3. Ancestral area reconstruction of *Dendropanax* by Bayes-DIVA. Geologic time scale is shown at the bottom. Area abbreviations are as follows: A, SE Asia and South China (including Assam, East Asia, Indochina, and Malesia); B, North China, the Korean Peninsula, Japan; C, South America; D, Central America and the Caribbean region; E, North America; F, North Africa.

Li and Wen (2013) also noted that the fossil appearance of *Dendropanax* in Europe can be explained by the North Atlantic land bridges. The North Atlantic land bridges across the north end of the Atlantic Ocean linking northern Canada to Europe via Greenland have been viewed as a principal and most plausible route for the intercontinental spread of thermophilic boreotropical flora between the Old and New Worlds from the early Eocene until the late Miocene (Liu et al., 2018). According to Grímsson et al. (2017), during the late Paleocene to middle Eocene, birds were able to carry the Loranthaceae seed from South America to North America and then via Greenland to Euprosadaro. These movements might have played a major role in enabling the ancestral Loranthaceae to disperse over great distances and hence spread widely. Thus, we suggest that *Dendropanax* likely dispersed to Europe from North America after the late Eocene via the North Atlantic land bridges. However, the major extant lineages of *Dendropanax* differentiated in SE Asia and neotropical between mid-Eocene and mid-Oligocene, but during this time the ancestor of *Dendropanax* in North America and Europe became extinct, which coincides with the major cooling event in the late Eocene to early Oligocene (Zachos et al., 2001, 2008).

4. CONCLUSION

The study based on the molecular data of comprehensive taxon sampling, supported the relationship within the genus *Dendropanax*. Three clades were recognized in this genus. According to the result of molecular data analyses, the study hypothesized that the genus *Dendropanax* originated in SE Asia and South China during the mid-Eocene, and then spread to the NKJ region. During the late Eocene *Dendropanax* was dispersed by birds and mammals in SE Asia, South China, and North America. Then the genus migrated to Central America and the Caribbean region, South America, and Europe. Lineages of *Dendropanax* in North America and Europe became extinct during the major cooling event in the late Eocene to early Oligocene. Thus, at present, no species of *Dendropanax* occurs in North America or Europe.

REFERENCES

- Balakrishnan R., Vijayraja D., Jo S. H., Ganesan P., Su-kim I., Choi D. K., 2020. Medicinal profile, phytochemistry, and pharmacological activities of *murraya koenigii* and its primary bioactive compounds. *Antioxidants*, 9: 101.
- Baker W. J., Couvreur T. L., 2013. Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. *J. Biogeogr.*, 40: 274-285.
- Bui N. S., 1976. Les ponctuations du limbe foliaire dans le genre *Dendropanax* Decne. et Planch. (Araliacées). Bulletin du Muséum National d'Histoire Naturelle Paris, 3^e Série. Botanique., 24: 1-17.
- Cannon M. J., Cannon J. F. M., 1989. Central American Araliaceae - a precursory study for the Flora Mesoamericana. *Bull. Br. Mus. Nat. Hist., Bot.*, 19: 5-61.
- Darriba D., Taboada G. L., Doallo R., Posada D., 2012. jModel Test 2: more models, new heuristics and parallel computing. *Nature Methods*, 9: 772.
- Dilcher D. L., Dolph G. E., 1970. Fossil Leaves of *Dendropanax* from Eocene Sediments of Southeastern North America. *Am. J. Bot.*, 57: 153-160.
- Doyle J. J., Doyle J. L., 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem. Bull.*, 19: 11-15.
- Drummond A. J., Suchard M. A., Xie D., Rambaut A., 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.*, 29: 1969-1973.
- Grimsson F., Kapli P., Hofmann C. C., Zetter R. & Grimm, G.W., 2017. Eocene Loranthaceae pollen pushes back divergence ages for major splits in the family. *PeerJ*, 5: e3373.
- Ickert-Bond S. M., Murray D. F., DeChaine E., 2009. Contrasting patterns of plant distribution in Beringia. *Alaska Park Science*, 8: 26-32.
- Kearse M., Moir R., Wilson A., Stones-Havas S., Cheung M., Sturrock S., Buxton S., Cooper A., Markowitz S., Duran C., Thierer T., Ashton B., Mentjies P., Drummond A., 2012. Geneious basic: an integrated and extendable desktop

- software platform for the organization and analysis of sequence data. *Bioinformatics.*, 28: 1647-1649.
- Li R., Wen J., 2013. Phylogeny and biogeography of *Dendropanax* (Araliaceae), an amphi-pacific Disjunct genus between tropical/subtropical Asia and the neotropics. *Syst. Bot.*, 38: 536-551.
- Li R., Wen J., 2016. Phylogeny and diversification of Chinese Araliaceae based on nuclear and plastid DNA sequence data. *J. Syst. Bot.*, 54: 453-467.
- Liu B., Le C. T., Barrett R. L., Nickrent D. L., Chen Z. D., Lu L. M. & Vidal-Russell R., 2018. Historical biogeography of Loranthaceae (Santalales): Diversification agrees with emergence of tropical forests and radiation of songbirds. *Mol. Phylogent. Evol.*, 124: 199-212.
- Lowry II P. P., Plunkett G. M., Wen J., 2004. Generic relationships in Araliaceae: looking into the crystal ball. *S. Afr. J. Bot.*, 70: 382-392.
- Morley R. J., 2003. Interplate dispersal paths for megathermal angiosperms. Perspectives in Plant Ecology. *Evol. Syst.*, 6: 5-20.
- Nylander J. A., Olsson U., Alstrom P., Sanmartin I., 2008. Accounting for phylogenetic uncertainty in biogeography: a Bayesian approach to dispersal vicariance analysis of the thrushes (Aves: Turdus). *Syst. Biol.*, 57: 257-268.
- Yu Y., Harris A. J., He X., 2011. RASP (Reconstruct Ancestral State in Phylogenies) 2.0 Beta. Available at: < <http://mnh.scu.edu.cn/soft/blog/RASP> >
- Rambaut A., Drummond A. J., 2007. Tracer, Version 1.4. <http://beast.bio.ed.ac.uk/Tracer>.
- Rambaut A., 2009. FigTree v.1.4. Available at: <http://tree.bio.ed.ac.uk/software/figtree/>.
- Rambaut A., Drummond A. J., 2010. TreeAnnotator. Version 1.8, distributed as part of the BEAST Package. Available at: <http://beast.community/installing>.
- Rambaut A., Suchard M. A., Xie D., Drummond A. J., 2014. Tracer v1.6. Available at <http://tree.bio.ed.ac.uk/software/tracer>.
- Ronquist F., Huelsenbeck J. P., 2003. MrBayes 3, Bayesian phylogenetic inference under mixed models. *Bioinformatics.*, 19: 1572-1574.
- Stamatakis A., 2006. RAxML-VI-HPC, maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics.*, 22(1): 2688-2690.
- Stamatakis A., Hoover P., Rougemont J., 2008. A Rapid Bootstrap Algorithm for the RAxML Web Servers. *Syst. Biol.*, 57(5): 758-771.
- Taberlet P., Gielly L., Pautou G., 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Mol. Biol.*, 17: 1105-1109.

- Tran V. T., Hoang T. P. N., Croat T. B., Ma Z., Liu B., Nguyen V. D., & Le C. T., 2022. Reconstruction of the evolutionary biogeography reveals the origin and diversification of *Arisaema* (Araceae). *Acta Bot. Bras.*, 36, e2021abb0253.
- Vidal-Russell R., Nickrent D. L., 2008. Evolutionary relationship in the showy Mistletoe family (Loranthaceae). *Amer. J. Bot.*, 95: 1015-1029.
- Wen J., Plunkett G. M., Mitchell Anthony D., Wagstaff Steven J., 2001. The evolution of Araliaceae: a phylogenetic analysis based on ITS sequences of nuclear ribosomal DNA. *Syst. Bot.*, 26: 144-167.
- Wen J., 2001. Evolution of eastern Asian-Eastern North American biogeographic disjunctions: a few additional issues. *Int. J. Plant Sci.*, 162: S117-S122.
- Wen J., and D. G. Frodin., 2001. Metapanax, a new genus of Araliaceae from China and Vietnam. *Brittonia.*, 53: 116-121.
- Wen J., Nie Z. L. & Ickert-Bond S. M., 2016. Intercontinental disjunctions between eastern Asia and western North America in vascular plants highlight the biogeographic importance of the Bering land bridge from late Cretaceous to Neogene. *J. Syst. Evol.*, 54: 469-490.
- West C. K., Greenwood D. R., Basinge, J. F., 2015. Was the Arctic Eocene ‘rainforest’ monsoonal? Estimates of seasonal precipitation from early Eocene megafloras from Ellesmere Island Nunavut. *Earth Planet. Sci. Lett.*, 427: 18-30.
- Xiang Qibai., Porter P. Lowry II., 2007. Araliacea. In: Wu ZY, Raven PH, Hong DY (eds.). *Flora of China*. Beijing: Science Press & St. Louis: Missouri Botanical Garden Press., 13: 435-491.
- Xiang X. G., Mi X. C., Zhou H. L., Li J. W., Chung S. W., Li D. Z., Huang W. C., Jin W. T., Li Z. Y., Huang L. Q., Jin X. H., 2016. Biogeographical diversification of mainland Asian *Dendrobium* (Orchidaceae) and its implications for the historical dynamics of evergreen broad-leaved forests. *J. Biogeogr.*, 43: 1310-1323.
- Zachos J., Pagani M., Sloan L., Thomas E., and Billups K., 2001. Trends, rhythms and aberrations in global climate 65 Ma to present. *Science.*, 292: 686-693.
- Zachos J. C., Gerald R. D., Richard E. Z., 2008. An early Cenozoic perspective on green house: warming and carbon-cycle dynamics. *Nature.*, 451: 279-283.
- Zhang Y., Dubé M. A., McLean D. D., Kates M., 2003. Biodiesel production from waste cooking oil: Economic assessment and sensitivity analysis. *Bioresour. Technol.*, 90: 229-240.
- Zhou Z., Hu J. J., Wen J., Sun H., 2019. Morphometric, phylogenetic and biogeographic analyses of *Pyrularia* (Santalales), a parasitic disjunct lineage between eastern Asia and eastern North America. *Taxon.*, 64: 47-71.

NGHIÊN CỨU PHÁT SINH LOÀI VÀ LỊCH SỬ ĐỊA LÝ SINH VẬT CỦA CHI *Dendropanax* (Araliaceae)

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Abstract. Khám phá mối quan hệ phát sinh giữa các loài thực vật cũng như lịch sử tiến hóa của chúng đóng góp thông tin quan trọng trong khoa học. *Dendropanax* là một đối tượng điển hình để khám phá sự tiến hóa của các loài tại vùng nhiệt đới châu Á và vùng Trung và Nam Mỹ. Nghiên cứu dựa trên dữ liệu phân tử của bảy vùng DNA từ nhóm mẫu vật đầy đủ nhất đã hỗ trợ mối quan hệ di truyền trong chi *Dendropanax*. Ba nhánh phát sinh được ghi nhận trong chi này. Dựa trên kết quả phân tích dữ liệu phân tử, nghiên cứu giả thuyết rằng chi *Dendropanax* có nguồn gốc từ Đông Nam Á và Nam Trung Quốc trong thời kỳ giữa Eocene và sau đó lan sang khu vực NKJ. Vào cuối thời kỳ Eocene, *Dendropanax* được phát tán bởi chim và động vật có vú ở Đông Nam Á và Nam Trung Quốc tới Bắc Mỹ. Sau đó, chúng di cư đến Trung Mỹ và vùng Caribe, Nam Mỹ và châu Âu. Các dòng dõi của *Dendropanax* ở Bắc Mỹ và châu Âu đã bị tuyệt chủng do hiện tượng lạnh (đóng băng) toàn cầu vào cuối thời kỳ Eocene đến đầu Oligocene. Vì vậy, hiện tại không có loài *Dendropanax* nào được ghi nhận phân bố ở Bắc Mỹ hoặc châu Âu.

Từ khóa: *Dendropanax*, dữ liệu phân tử, phát sinh loài, lịch sử địa lý sinh vật, Đông Nam Á.

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