



Phylogenetic analyses of *Searsia* (Anacardiaceae) from eastern Asia and its biogeographic disjunction with its African relatives



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ABSTRACT

Searsia is an Old World genus in the sumac family Anacardiaceae segregated from the *Rhus* complex. The genus is widely distributed in Africa with three species in eastern Asia, of which *Searsia paniculata* was commonly recognized as *Terminthia paniculata* in China. In this study, we conducted phylogenetic analyses of the eastern Asian *Searsia* to test the relationships to the African relatives, based on both nuclear (ETS and ITS) and chloroplast (*trnL-F* and *ndhF*) sequences. Phylogenetic analyses based on different genomic sequences strongly support that the *Searsia* taxa from eastern Asia are monophyletic. However, topological incongruence is observed between the nuclear and chloroplast data, especially concerning the phylogenetic position of the eastern Asian group. The divergence time of the genus between eastern Asia and Africa was dated to 23.36 Ma (million years ago), with a 95% highest posterior density (HPD) of 14.30–36.31 Ma, using the Bayesian relaxed-clock estimation. It is hypothesized that the closure of the Tethys Sea and the formation of the “*Gomphotherium* Landbridge” likely had enabled the expansion of the *Searsia* lineage between Africa and Asia in the late Oligocene to early Miocene.

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1. Introduction

The sumac group *Rhus* L. is considered the largest and the most heterogeneous taxon and is usually referred to as the *Rhus* complex in the sumac family Anacardiaceae (Barkley, 1937; Young, 1978; Miller et al., 2001; Yi et al., 2004; Pell et al., 2008; Nie et al., 2009; Ren et al., 2013). Bernhardt (1838) suggests the recognition of an Old World genus *Terminthia* Bernh. based on its ternate leaves and pale drupes which can be described as glabrous or tomentose with a resinous mesocarp adhering to the bony endocarp. However, Engler (1881) grouped all these Old World species in his *Rhus* section *Gerontogaeae* Engl., but the section name was shown to be spurious because it was predated by *Rhus* section *Thezera* Raf. (De Candolle, 1825). The genus *Terminthia* was accepted in *Flora Yunnanica* (Wu and Ming, 1979) and *Flora of China* (Min and Barfod, 2008), yet the genus *Searsia* F. A. Barkley, named after Paul B. Sears, was proposed by Barkley as the correct name for this unique Old World group in the *Rhus* complex (Barkley, 1942).

Recent molecular phylogenetic analyses of the *Rhus* complex have shown that the *Searsia* group is monophyletic and should be separated from *Rhus* s. str. (Miller et al., 2001; Yi et al., 2004; Pell et al., 2008). For

example, molecular studies based on the internal transcribed spacer region (ITS) of the nuclear ribosomal DNA sequences of six genera in the *Rhus* complex suggest that *Rhus* s. str. is indeed monophyletic and distinct from the other related genera, including *Actinocheita* F. A. Barkley, *Cotinus* Mill., *Malosma* (Nutt.) Abrams, *Searsia*, and *Toxicodendron* Mill. (Miller et al., 2001). Other phylogenetic analyses of the ITS and chloroplast data confirm that *Searsia* native to Africa is monophyletic and distinct from the *Rhus* s. str. and other groups in the *Rhus* complex (Yi et al., 2004; Pell et al., 2008; Nie et al., 2009; Weeks et al., 2014; Xie et al., 2014).

According to the complete annotation of 111 species and 28 infra-specific taxa of *Searsia* (Moffett, 2007), the genus occurs widely in the tropics and subtropics in the Old World, with most species in continental Africa, especially southern Africa (Fig. 1). *Searsia paniculata* (Wall. ex G. Don) Moffett is one of the three Asian species which occurs along the eastern Himalayas in eastern Asia, and exhibits a limited distribution in NE India, Bhutan, SW China, and N Myanmar. The species is characterized by its entire or shallowly undulate leaflet margin, and the glabrous and lenticellate branchlets. The second Asian species, *Searsia parviflora* (Roxb.) F. A. Barkley exhibits serrate leaflet margins and is distributed across Bhutan, Nepal, N India, and Sri Lanka (Press et al., 2000). The third species *Searsia mysorensis* (G. Don) Moffett exhibits a narrow distributional constraint within the forest of the Chittoor district, A.P., India, and is distinguished by deeply toothed, or lobed leaflets and very spinous branches (Gade et al., 2010). These three Asian species have never been used to test the systematic position and evolutionary

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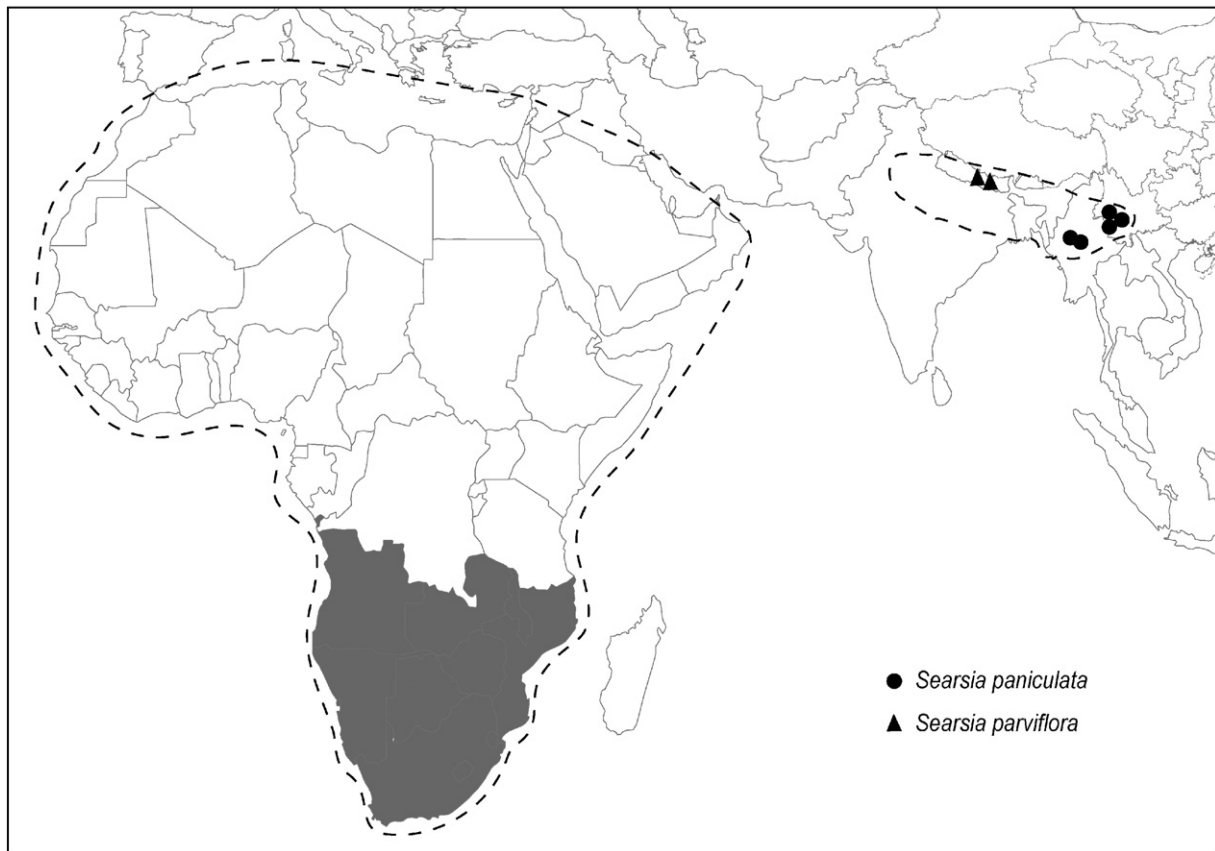


Fig. 1. The major distribution range of *Searsia* (dashed lines) showing the biogeographic disjunction between eastern Asia and Africa. Area in grey indicates the diversity center of the genus and black dots and triangles show the localities of sampled Asian species.

relationships with other taxa in *Searsia* based on phylogenetic analyses of molecular sequence data.

The disjunctive distribution of Asian *Searsia* species with the African relatives is another interesting topic in biogeography. The Old World disjunction between Africa and eastern Asia has been reported from many plant families, such as Annonaceae (Couvreur et al., 2011), Fabaceae (Sirichamorn et al., 2014), Lamiaceae (Yu et al., 2014), Smilacaceae (Chen et al., 2014), Vitaceae (Nie et al., 2012; Liu et al., 2013; Lu et al., 2013), and Papaveraceae (Perez-Gutierrez et al., 2012). Explanations for the wide geographic disjunctions of the Old World taxa between eastern Asia and Africa typically invoke three hypotheses: (1) the tectonic drift of the Indian plate resulted in the collision with the Eurasian plate in the middle Cenozoic (Aitchison et al., 2007; Ali and Aitchison, 2008), which facilitated biotic dispersals between the two plates; (2) the existence of extensive boreotropical forests in the Northern Hemisphere allowed thermophilic taxa to extend their ranges between Africa and Eurasia (Weeks et al., 2005; Muellner et al., 2006; Liu et al., 2013; Meng et al., 2014); and (3) the transoceanic long-distance dispersals, which explain some recent disjunctions (Vatanparast et al., 2013; Müller et al., 2015; Oatley et al., 2015; Yi et al., 2015).

These three explanations can be considered as alternative hypotheses for the *ex situ* origin of species occurrences in the Old World. Recent molecular phylogenetic studies combined with molecular clock inferences have allowed a more precise understanding of the process of dispersal, specifically the dispersal across Arabia and central Asia via the tropical forests that developed during the Miocene climatic optimum (Popp et al., 2008; Zhou et al., 2012). The Old World *Searsia* shows possible inter-continental disjunctive relationships between their African and Asian relatives and provides an ideal model to explore the evolution of the discontinuous distributional pattern and to test the three hypotheses concerning the African–eastern Asian biogeographic disjunctions.

This study reconstructs the evolutionary history of species within *Searsia*, emphasizing the phylogenetic relationships between eastern Asia and Africa, and explores the most likely explanations for the inter-continental disjunctive patterns within the Old World.

2. Materials and methods

2.1. Taxon sampling, DNA extraction, amplification, and sequencing

This study sampled 54 accessions, which included 31 non-*Searsia* taxa as outgroups and 16 *Searsia* species. We sampled eight collections of the two of the three *Searsia* species from eastern Asia: six samples of *S. paniculata* from China and Myanmar and two samples of *S. parviflora* from Nepal (Table 1). Only *S. mysorensis* narrowly distributed from southern India was not sampled in this study. Our sampling of *S. paniculata* and *S. parviflora* represent the major geographic range of the genus in Asia (Fig. 1). We selected 14 *Searsia* species from Africa in our analysis, with their distribution covering most of Africa. We also selected some representatives from Anacardiaceae, including *Anacardium* L., *Drimycarpus* Hook.f., *Fegimanra* Pierre, *Lithraea* Miers ex Hook. & Arn., *Loxopterygium* Hook.f., *Mauria* Kunth, *Poupartia* Comm. ex Juss., *Schinus* L., and *Schinopsis* Engl. as the outgroups (Table 1).

We extracted genomic DNA mainly from silica-gel dried leaf material and a few samples gathered from herbariums, using the Plant Total DNA Extraction Kit (BioTeKe, Beijing, China) following the manufacturer's protocol. We used primers ITS4 and ITS5 to amplify and sequence the nuclear ribosomal DNA (nrDNA) internal transcribed spacer (ITS) (White et al., 1990). To amplify and sequence the nuclear external transcribed spacer (ETS) we used primers ETS1F and 18S-IGS (Pell et al., 2008). We also sequenced the chloroplast *ndhF* gene (Olmstead and Sweere, 1994), the *trnL* intron and *trnL-F* intergenic

Table 1

Information on taxa sampled and corresponding GenBank accession numbers. Accessions beginning with xx are new sequences published in this study; missing data are indicated by a dash. Herbarium acronyms follow <http://sciweb.nybg.org>.

Taxon	Sources	Voucher	ITS	ETS	trnL-F	ndhF
<i>Searsia paniculata</i> (Wall. ex G.Don) Moffett C1	China: Yunnan	Yang 02 (KUN)	KX360039	KX360049	KX360029	KX360023
<i>Searsia paniculata</i> (Wall. ex G.Don) Moffett C2	China: Yunnan	Yang 01 (KUN)	KX360040	KX360050	KX360030	KX360024
<i>Searsia paniculata</i> (Wall. ex G.Don) Moffett C3	China: Yunnan	Yang 19 (KUN)	KX360041	KX360051	KX360031	KX360025
<i>Searsia paniculata</i> (Wall. ex G.Don) Moffett M1	Myanmar: Kyaukpadaung Township	Murata et al. 020827 (KUN)	KX360042	KX360052	KX360032	–
<i>Searsia paniculata</i> (Wall. ex G.Don) Moffett M2	Myanmar: Kyaukpadaung Township	Htwe 032601 (KUN)	KX360043	KX360053	KX360033	–
<i>Searsia paniculata</i> (Wall. ex G.Don) Moffett M3	Myanmar: Kyaukpadaung Township	Htwe 024123 (KUN)	KX360044	KX360054	KX360034	–
<i>Searsia parviflora</i> (Roxb.) F.A.Barkley N1	Nepal	Mikage et al. 9550731 (KUN)	KX360045	KX360055	KX360035	–
<i>Searsia parviflora</i> (Roxb.) F.A.Barkley N2	Nepal	Shrestha KHU-NPCL20121008 (NP)	–	–	KF913496	KF913495
<i>Searsia tenuinervis</i> (Engl.) Moffett	Mozambique: Cuamba	Yang 26 (KUN)	KX360048	KX360058	KX360038	KX360028
<i>Searsia ciliata</i> (Licht. ex Schult.) A.J.Mill.	USA: Arizona (cult.)	Miller 47 (CS)	AY641513	–	AY640464	AY643124
<i>Searsia quartiniana</i> (A. Rich.) A.J.Mill. 1	USA: Phoenix Desert Bot Gard, AZ (acc. # 1,980,007,001)	Miller 51 (CS)	AY641517	KF664513	AY640468	AY643128
<i>Searsia quartiniana</i> (A. Rich.) A.J.Mill. 2	USA: Phoenix Desert Bot Gard, AZ (acc. # 1,980,007,001)	Miller s. n. (CS)	AY641518	–	AY640469	AY643129
<i>Searsia undulata</i> (Jacq.) T.S.Yi, A.J.Mill. & J. Wen	USA: Phoenix Desert Bot Gard, AZ (acc. # 19,800,071)	Miller s. n. (CS)	AY641519	KF664514	AY640470	AY643130
<i>Searsia pyroides</i> (Burch.) Moffett	Kenya: Nairobi	Luke 11,693 (US)	FJ945952	FJ945784	FJ946002	FJ945849
<i>Searsia natalensis</i> (Bernh. ex Krauss) F.A. Barkley	Kenya: Nairobi	Luke 11,694 (US)	FJ945953	FJ945785	FJ946003	FJ945850
<i>Searsia lancea</i> (L.f.) F.A.Barkley	USA: Phoenix Desert Bot Gard, AZ (cult.)	Miller 50 (CS)	AY641514	–	AY640465	AY643125
<i>Searsia glauca</i> (Thunb.) Moffett	South Africa: Western Cape	Wen 10,051 (US)	FJ945962	FJ945800	FJ946017	FJ945865
<i>Searsia lucida</i> (L.) F.A.Barkley	USA: NYBG (South Africa)	Pell 691 (BKL)	EF682851	EF682858	EF682863	–
<i>Searsia dentata</i> (Thunb.) F.A.Barkley	South Africa: KwaZulu Natal	Wen 10,090 (US)	FJ945963	FJ945801	FJ946018	FJ945866
<i>Searsia discolor</i> (E.Mey. ex Sond.) Moffett	South Africa	Wen 10,084 (US)	KX360047	KX360057	KX360037	KX360027
<i>Searsia erosa</i> (Thunb.) Moffett	South Africa	Wen 10,073 (US)	KX360046	KX360056	KX360036	KX360026
<i>Searsia pendulina</i> (Jacq.) Moffett	USA: NYBG (South Africa)	Pell 694 (BKL)	EF089148	EF089163	AY594450	–
<i>Searsia leptodictya</i> (Diels) T.S.Yi, A.J.Mill. & J. Wen	Phoenix Desert Bot Gard, AZ (acc. # 198,007,201)	Miller s. n. (CS)	AY641515	–	AY640466	AY643126
<i>Actinocheita filicina</i> (D.C.) F.A.Barkley	Mexico	Panero s. n. 44 (CS)	AY641509	FJ945802	AY640460	AY643120
<i>Anacardium excelsum</i> Skeels	–	Montiel 32,769 (MO)	KF664193	KF664496	KF664217	KF664343
<i>Anacardium occidentale</i> L.	–	Zhang Ling s. n. (KUN)	KF664192	KF664495	KF664216	KF664342
<i>Baronia taratana</i> Baker	Madagascar	Pell 625 (NY)	EF089149	EF089164	AY594568	–
<i>Rhus thouarsii</i> (Engl.) H.Perrier.	Madagascar	Pell 638 (NY)	EF089150	KP055297	AY594452	–
<i>Cotinus coggygria</i> Scop.	France	Bamps 8753 (LSU)	AY510157	KP055214	AY594545	–
<i>Cotinus obovatus</i> Raf.	USA	Reichard 386 (MOR)	–	KP055215	AY594546	–
<i>Drimycarpus racemosus</i> (Roxb.) Hook.f. ex Marchand	–	Shui 81,748 (KUN)	KF664195	KF664498	KF664219	KF664345
<i>Fegimanra</i> sp.	–	Randrianasolo 843 (MO)	KF664196	–	KF664220	KF664346
<i>Lithraea ternifolia</i> (Gillies) F.A.Barkley	Bolivia	Nee & Wen 53,849	–	FJ945796	FJ946014	FJ945861
<i>Bursera</i> sp.	Mexico	Wen 8,752 (US)	KX426379	KX426378	KX426380	KX426381
<i>Loxopterygium sagotii</i> Hook.f.	Guyana	Polak 309 (E)	AY531208	KP055248	KP055521	–
<i>Loxopterygium grisebachii</i> Hieron. & Lorentz	Bolivia: Santa Cruz	Pendry 678 (E)	AY531207	KP055247	KP055520	–
<i>Malosma laurina</i> (Nutt.) Nutt. ex Abrams	Rancho Santa Ana Bot Gard, USA (cult.)	Miller 34 (CS)	AY641510	FJ945803	AY640461	AY643121
<i>Mauria thummatophylla</i> Loes.	–	Nee & Wen 53,816 (US)	KF664200	KF664503	KF664224	KF664350
<i>Mauria heterophylla</i> Kunth	Bolivia	Nee 53,811 (US)	FJ945958	FJ945795	FJ946013	FJ945860
<i>Metopium brownei</i> Urb.	Belize	Brokaw 295 (NY)	–	KP055258	AY594557	–
<i>Pistacia chinensis</i> Bunge	China	Wen 7,090 (US)	DQ390466	KF664471	DQ390470	DQ390462
<i>Pistacia weinmannifolia</i> J.Poiss. ex Franch	–	Meng 840 (KUN)	KF664191	KF664492	KF664215	KF664341
<i>Pistacia mexicana</i> Kunth	Mexico: Oaxaca	Wen 8,675 (US)	FJ945959	FJ945797	KF664212	FJ945862
<i>Poupartia minor</i> Marchand	Madagascar: Ihosy	Wen 9,481 (US)	FJ945964	FJ945811	FJ946019	KF664351
<i>Rhus integrifolia</i> (Nutt.) Engl.	Rancho Santa Ana Bot Gard, CA (cult.)	Miller 28 (CS)	AY641499	FJ945805	AY640451	AY643111
<i>Rhus sandwicensis</i> A.Gray	Hawaii: Hawaii	Wen 7,052 (US)	AY641491	FJ945806	AY640445	AY643105
<i>Rhus trilobata</i> Nutt.	USA: Colorado	Miller 21 (CS)	AY641497	FJ945807	AY640449	AY643109
<i>Rhus typhina</i> L.	USA: Washington DC	Wen 8,557 (US)	FJ945920	FJ945750	FJ945966	FJ945813
<i>Schinus molle</i> hort. ex Engl.	USA: California, Los Angeles (cult.)	Wen 6,686 (F)	AY641512	FJ945808	AY640463	AY643123
<i>Schinus fasciculata</i> (Griseb.) I.M. Johnst.	Bolivia	Mendoza 2,013 (NY)	–	KP055303	KP055560	–
<i>Schinopsis marginata</i> Engl.	–	Nee & Wen 53,889 (US)	KF664205	KF664510	KF664229	KF664355
<i>Toxicodendron fulvum</i> (Craib) C.Y.Wu & T.L. Ming	China: Yunnan	Nie & Meng 332 (KUN)	FJ945921	FJ945751	FJ945967	FJ945814
<i>Toxicodendron radicans</i> (L.) Kuntze	USA: Virginia	Nie & Meng 530 (KUN)	FJ945946	FJ945775	FJ945993	FJ945840
<i>Toxicodendron striatum</i> Kuntze	Mexico: Chiapas	Wen 8,712 (US)	FJ945948	FJ945778	FJ945996	FJ945843

spacer (Taberlet et al., 1991). All polymerase chain reactions (PCRs) were run in a PTC-100 thermocycler (MJ Research, Ramsey, MN, USA), and we used a BigDye Terminator 3.1 (Applied Biosystems, Foster City, CA, USA) for the sequencing reaction following the manufacturer's instructions. We viewed the sequencing reaction with an ABI PRISM 3730 Sequencer using the same primers as employed for the PCR amplifications. We used Sequencher (version 4.14; Gene Code, Ann Arbor, MI, USA) to edit the resulting sequences. Sequence alignment was done using ClustalX version 1.83 PC version (Thompson et al., 1997), followed by manual adjustment in BioEdit (Hall, 1999).

All sequences were deposited in GenBank with accession numbers provided in Table 1.

2.2. Phylogenetic analysis

The data were analyzed with the maximum likelihood (ML) analysis using RAxML version 7.2.8 (Stamatakis, 2006) and the Bayesian inference (BI) using MrBayes version 3.1.2 (Ronquist and Huelsenbeck, 2003). Nucleotide substitution model parameters were determined for ML and BI using the Akaike Information Criterion (AIC) in Modeltest version 3.7

(Nylander, 2004; Posada and Buckley, 2004). By partitioning the data for analyses into gene regions, we were able to estimate independent parameters on each partition. The ML analysis employed a GTR + I + G model of substitution for ETS, ITS and *ndhF*, and GTR + G for *trnL-F*. A bootstrap analysis of 1000 replicates was performed simultaneously.

Bayesian analyses started from random trees and used four independent Markov chain runs for 10 million Metropolis-coupled generations with average split deviations between parallel runs <0.01 and sampling trees every 1000 generations. The runs were repeated twice to confirm the results. The first 10% of the trees were discarded as burn-in, and the remaining trees were summarized as a maximum clade credibility tree visualized using the program FigTree v.1.4.0 (Rambaut, 2014).

2.3. Dating the divergence times

We estimated the divergence time of the Asian *Searsia*, using a Bayesian relaxed-clock method implemented in the BEAST version 1.8.0 (Drummond et al., 2012) and the combined plastid and nuclear data. BEAST employs a Bayesian Markov Chain Monte Carlo (MCMC) approach to co-estimate topology, substitution rates, and node ages. The GTR + I + G model was used for the ETS, ITS and *ndhF* and the GTR + G model for the *trnL-F* data, based on the results from the Modeltest. The tree prior model (Yule) was implemented in the analysis, with rate variation across branches assumed to be uncorrelated and log-normally distributed (Drummond et al., 2006). We approximated posterior distributions of parameters using two independent MCMC analyses of 60,000,000 generations (sampling once every 1000 generations). Samples from the two chains, which yielded similar results, were combined after a 10% burn-in for each and we examined chain convergence using the program Tracer 1.6 (Rambaut, 2014), with effective sample size (ESS) well over 200 for all categories.

We selected four fossils as calibration points in this study. Wood fossils related to Anacardiaceae and its sister family Burseraceae were reported from the Olmos Formation of late Campanian–early Maastrichtian (Estrada-Ruiz et al., 2010). We set the root age (i.e., the divergence time between Anacardiaceae and Burseraceae) to be 70 ± 5.0 million years ago (Ma). This age is also consistent with the diversification time of Burseraceae hypothesized by De-Nova et al. (2012). Fossils of the cashew nut *Anacardium* were reported from the middle Eocene lake sediments in Messel, Germany (Manchester et al., 2007), and these fossils were used to constrain the minimum age between *Anacardium* and its sister *Fegimanra* to be 47 Ma. Reliable fruit fossils of *Rhus* were found in western North America from the middle Eocene (Manchester, 1994), and they share many characters with the extant *Rhus* including lateral compression, longitudinal vascular bundles forming ribs in the mesocarp, and two or more layers of columnar cells in the endocarp (Manchester, 1994; Miller et al., 2001). The minimum stem age of *Rhus* was thus calibrated to be 44 Ma with a standard deviation of 1.0 Ma. A middle Miocene *Loxopterygium* fruit fossil from the Ecuadorian Andes (Burnham and Carranco, 2004) was used to set the *Loxopterygium* minimum stem age as 10 Ma with the standard deviation as 1.0 Ma.

3. Results

The nrDNA generated a data matrix of 1121 characters, of which 631 were constant, 190 were variable but parsimony-uninformative, and the remaining 300 variable sites were parsimony-informative. BI and ML analyses of the nuclear data yielded similar topologies as well as matching node support values with only the Bayesian consensus tree including the posterior probabilities (PP). These values along with the ML bootstrap (PB) calculations can be seen in Fig. 2, which shows robust support for the eastern Asian *Searsia* group distributed in China,

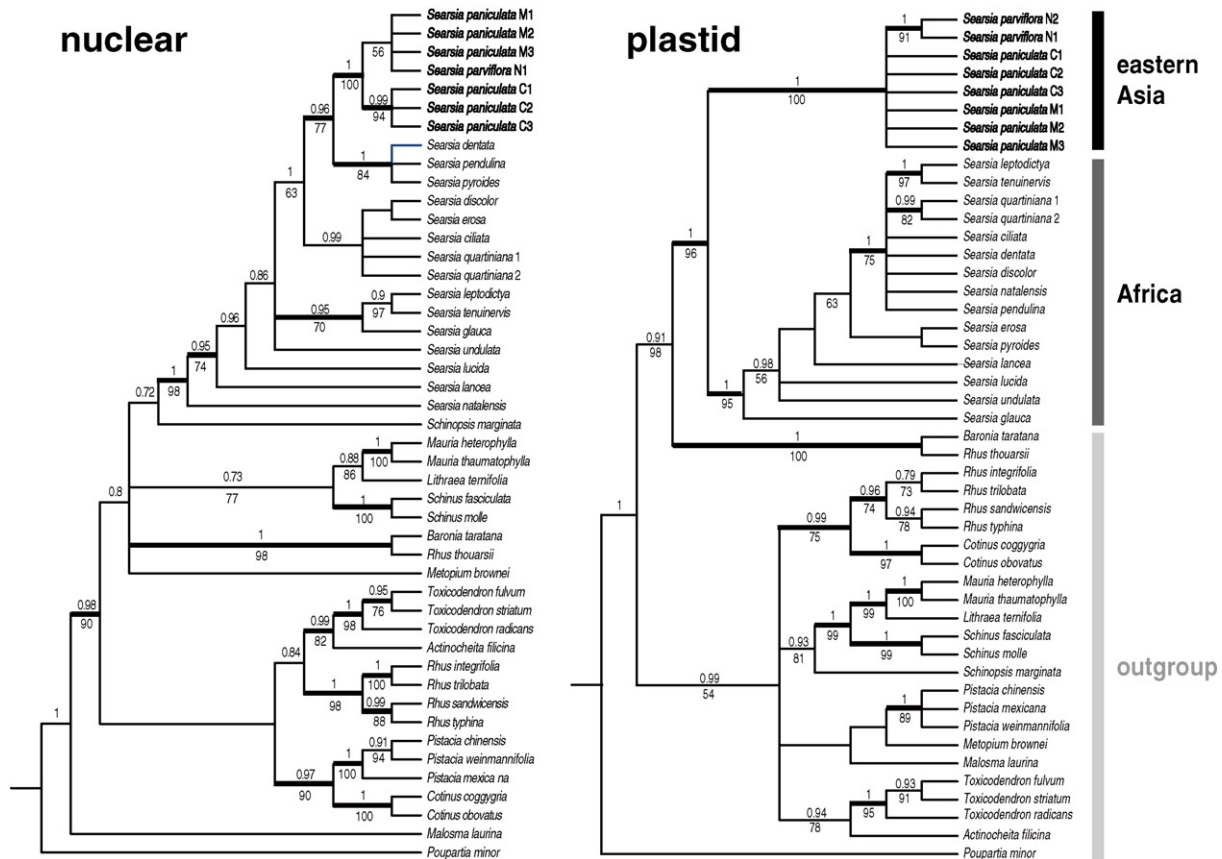


Fig. 2. Bayesian consensus trees of *Searsia* based on nuclear or plastid datasets. Numbers above or below branches are posterior probabilities (≥ 0.7) and bootstrap values ($\geq 50\%$) from Bayesian analysis and Maximum Likelihood, respectively. Branches in bold indicate 95% higher posterior densities and/or 70 higher bootstrap values. Taxa names in bold show samples from eastern Asia.

Myanmar and Nepal as a monophyletic group (PP = 1, PB = 100%). This Asian group was nested within the African *Searsia* clade and was sister to the clade of *S. dentata*, *S. pendulina*, and *S. pyroides* with PP = 0.96 and PB = 77% (Fig. 2).

The plastid sequences generated a data matrix of 3038 characters, with 2651 constant characters, 269 variable but parsimony-uninformative, and 118 variable and parsimony informative. The ML and BI phylogenetic trees are topologically identical, and the Bayesian consensus tree is shown in Fig. 2. Phylogenetic analysis based on the chloroplast data also supported the monophyly of *Searsia* from eastern Asia, but relationships of *S. paniculata* from China and Myanmar remained unresolved based on plastid data. This Asian group (*S. paniculata* and *S. parviflora*) was sister to all other *Searsia* species from Africa (PP = 1, PB = 96%).

The data matrix of the combined sequences contained 4159 characters, comprising 3282 constant, 459 variable but parsimony-uninformative, and 418 variable and parsimony-informative characters. The analysis of this dataset also supported the Asian clade (Fig. 2; PP = 1, PB = 100%). *S. paniculata* from China and Myanmar formed a weakly supported clade (PP = 0.7, PB = 53%), whereas the two samples of *S. parviflora* grouped together with PP = 1 and PB = 92%. This Asian clade was sister to the African clade (Fig. 2; PP = 1, PB = 100%).

The divergence time estimates using the combined data suggested that the Asian *Searsia* diverged from the African *Searsia* clade ca. 23.36 Ma, which is the boundary between the Oligocene and Miocene (95% HPD = 14.30–36.31 Ma) (Fig. 3). Our analysis also showed that *Searsia* diverged from other Anacardiaceae groups at ca. 60.59 Ma in the late Paleocene (95% HPD = 54.27–67.40 Ma).

4. Discussion

Phylogenetic analyses based on different genomic sequences strongly support that the *Searsia* taxa from eastern Asia are monophyletic (Fig. 2). In the combined dataset, samples of *S. paniculata* from China and Myanmar form a weakly supported clade sister to *S. parviflora* sampled from Nepal (Fig. 2). These Asian species are morphologically similar to each other except for the differences in their leaf characters; *Searsia paniculata* is characterized by the entire leaflet margins; *S. parviflora* displays serrate leaflet margins; and *S. mysorensis* shows distinct deeply toothed or lobed leaflets. Our study was aimed at the eastern Asian group in *Searsia*, and was limited in the number of African *Searsia* species sampled. More taxon sampling and more molecular characters are needed to test the phylogenetic relationships of the Asian species within *Searsia*.

Topological incongruence is observed between the nuclear and chloroplast data, especially concerning the phylogenetic position of the eastern Asian group (Fig. 2). Nuclear data suggest that the Asian *Searsia* is nested within the African *Searsia*, sister to a clade including *S. dentata*, *S. pendulina*, and *S. pyroides*, while the chloroplast data place the Asian *Searsia* sister to clade of all the African members included in the study (Fig. 2). Nevertheless, this incongruence may have resulted from the sampling limitation of African species which may have caused the phylogenetic uncertainty.

Chloroplast capture, the replacement of the cytoplasmic genome of one species into the nuclear background of another through hybridization or introgression (Rieseberg and Soltis, 1991; Soltis and Kuzoff, 1995; Yoo et al., 2002), is the most likely explanation for the observed incongruence between nuclear and plastid DNA data in *Searsia*. This kind of phenomenon frequently occurs in species with sympatric distribution and reproductive compatibility (Rieseberg et al., 1991). However, the extant Asian *Searsia* species are well separated from their African relatives without overlap distribution. We suggested that the reticulate evolution of Asian clade could be resulted from a hybrid or introgressed lineage invading Asia from Africa, and the maternal donor may be the common ancestor of the African *Searsia*.

The incongruence between chloroplast and nuclear datasets is common in Anacardiaceae (Barkley, 1937; Brizicky, 1963; Hardin and Phillips, 1985; Burke and Hamrick, 2002; Yi et al., 2004, 2007, 2008; Nie et al., 2009; Xie et al., 2014). For example, Yi et al. (2007) conducted the phylogenetic analysis of *Rhus*, the varying position of the *R. microphylla*–*R. rubifolia* clade made it a problem for the relative relationships of the two subgenera (Subgen. *Rhus* and Subgen. *Lobadium*). They took the discordance between the nuclear and chloroplast datasets as a result of chloroplast capture, which was proved by the geographical sympatry of *R. microphylla* with both the species of subgen. *Lobadium* and Subgen. *Rhus* (Yi et al., 2007). Conflicts between gene trees also recorded in many other plant groups of Anacardiaceae at the species level, have also been explained by hybridization/introgression, e.g., *Toxicodendron* (Nie et al., 2009) and *Pistacia* (Yi et al., 2008).

Topological incongruences caused by reticulate evolution are common in phylogenetic studies using molecular sequences from different genomes (Deng et al., 2015; Mayonde et al., 2015; Ren et al., 2015), and whether conflicting data sets should be analyzed separately or combined in a phylogenetic analysis is a complex and controversial decision (Hipp et al., 2004). Nevertheless, in this study, the incongruence may also probably have resulted from insufficient resolving power of the ITS and ETS data, which suggested the Asian *Searsia* nested in African species. We then combined the nuclear and chloroplast data, which produced a similar topology and phylogenetic relationships to those of the chloroplast data (results not shown). Further reevaluation is necessary to test the reticulate evolutionary status in *Searsia* using extensive sampling and more DNA sequences data.

Based on multiple fossil calibrations and relaxed molecular clocks, the eastern Asian *Searsia* is suggested to have originated approximately 23.36 Ma during the late Oligocene to early Miocene (Fig. 3), too young to be rafted by the Indian tectonic plate. Paleogeographic evidence suggested that India became progressively more isolated from the African landmasses during the Cretaceous and Paleocene. A second possible explanation is that the extensive boreotropical forests distributed across Europe into southern Asia during the early Eocene Climatic Optimum (52–50 Ma) could have facilitated overland expansion of biota between Africa and Asia in both directions (Wolfe and Kaufmann, 1975; Zachos et al., 2001; Davis et al., 2002; Yu et al., 2014). This hypothesis was used to explain biogeographic patterns in several angiosperm families (Weeks et al., 2005; Muellner et al., 2006); however, it seems unlikely to lead to the disjunction of *Searsia* between Asia and Africa since their divergence time is much more recent.

Our results favor the explanation of overland migration between Africa and Asia after the collision of the Afro-Arabian plate with Asia via the expanded tropical forests associated with the Miocene warming trend (Yuan et al., 2005; Kulju et al., 2007; Li et al., 2009). Tectonic collision between the Arabian plate and the Eurasia closed the Tethys Sea connecting Africa and western Asia via the “*Gomphotherium* Landbridge,” and these major palaeogeographic changes coincided with climate changes from the late Oligocene (Rögl, 1998, 1999). The pronounced climate changes from seasonally dry to ever-wet in the southeast Asian region occurred around the Oligocene–Miocene boundary (Guo et al., 2008) and may also be an important factor for plant exchanges between eastern Asia and Africa. Recently, distinctive winged fruit fossils of the Dipterocarpaceae from the middle Miocene found in South Fujian, China, indicates the continuous presence of evergreen forests in southern China and provides evidence for the Miocene floristic affinities between the Indian and South Chinese floras (Jacques et al., 2015).

Therefore, it is likely that the closure of the Tethys Sea and the formation of the “*Gomphotherium* Landbridge” had enabled the expansion of the *Searsia* lineage between Africa and Asia via the expanded tropical forests associated with the early Miocene warming trend. Multiple angiosperm taxa also exhibit this disjunctive pattern, which has been hypothesized to have arisen from the combination of Afro-Arabia–Eurasia continent caused by the Africa–Arabia–Eurasia collision. Popp



Fig. 3. Chronogram of *Searsia* and its relatives from Anacardiaceae based on the plastid and nuclear sequences inferred using Bayesian evolutionary analysis by BEAST. Branches in bold indicate 95% higher posterior densities. Circles A–D at the nodes represent fossil constraints.

et al. (2008) described the dispersal of *Lychnis* L. (Caryophyllaceae) from Eurasia to the Ethiopian highlands via the Arabian Peninsula, which was recognized as an explanation for the “out-of-Africa” dispersal of primates (Fleagle and Gilbert, 2006), and was also invoked in biogeographic studies of *Uvaria* (Zhou et al., 2012). An overland migration from Asia to Africa through Arabia during the early Miocene was also proposed as the most likely explanation for the disjunct distribution of *Isodon* (Yu et al., 2014).

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References

- Aitchison, J.C., Ali, J.R., Davis, A.M., 2007. When and where did India and Asia collide? *Journal of Geophysical Research* 112, B05423.
- Ali, J.R., Aitchison, J.C., 2008. Gondwana to Asia: plate tectonics, paleogeography and the biological connectivity of the Indian subcontinent from the Middle Jurassic through latest Eocene (166–35 Ma). *Earth Science Reviews* 88, 145–166.
- Barkley, F.A., 1937. A monographic study of *Rhus* and its immediate allies in North and Central America, including the West Indies. *Annals of the Missouri Botanical Garden* 24, 265–498.
- Barkley, F.A., 1942. A key to the genera of the Anacardiaceae. *American Midland Naturalist* 28, 465–474.

- Bernhardi, J.J., 1838. Ueber die Gattung *Laurophyllus* Thunb. Oder Botryceras Willdenow. *Linnaea* 12, 129–136.
- Brizicky, G.K., 1963. The genera of Anacardiaceae in the southeastern United States. *Journal of the Arnold Arboretum* 43, 359–375.
- Burke, J.M., Hamrick, J.L., 2002. Genetic variation and evidence of hybridization in the genus *Rhus* (Anacardiaceae). *Journal of Heredity* 93, 37–41.
- Burnham, R.J., Carranco, N.L., 2004. Miocene winged fruits of *Loxopterygium* (Anacardiaceae) from the Ecuadorian Andes. *American Journal of Botany* 91, 1767–1773.
- Chen, C., Qi, Z.C., Xu, X.H., Comes, H.P., Koch, M.A., Jin, X.J., Fu, C.X., Qiu, Y.X., 2014. Understanding the formation of Mediterranean–African–Asian disjunctions: evidence for Miocene climate-driven vicariance and recent long-distance dispersal in the Tertiary relict *Smilax aspera* L. (Smilacaceae). *New Phytologist* 204, 243–255.
- Couvreur, T.L.P., Pirie, M.D., Chatrou, L.W., Saunders, R.M.K., Su, Y.C.F., Richardson, J.E., Erkens, R.H.J., 2011. Early evolutionary history of the flowering plant family Annonaceae: steady diversification and boreotropical geodispersal. *Journal of Biogeography* 38, 664–680.
- Davis, C.C., Bell, C.D., Mathews, S., Donoghue, M.J., 2002. Laurasian migration explains Gondwanan disjunctions: evidence from Malpighiaceae. *Proceedings of the National Academy of Sciences* 99, 6833–6837.
- De Candolle, A.L.P.P., 1825. Terebinthaceae. In: de Candolle, A.L.P.P. (Ed.), *Prodromus Systematis Naturalis Regni Vegetabilis* 2. Sumptibus Sociorum Treuttel & Würtz, Amsterdam, pp. 61–92.
- Deng, T., Nie, Z.L., Drew, B.T., Volis, S., Kim, C., Xiang, C.L., Zhang, J.W., Wang, Y.H., Sun, H., 2015. Does the Arcto-Tertiary biogeographic hypothesis explain the disjunct distribution of Northern Hemisphere herbaceous plants? The case of *Meehania* (Lamiaceae). *PLoS One* 10, e0117171.
- De-Nova, J.A., Medina, R., Montero, J.C., Weeks, A., Rosell, J.A., Olson, M.E., Eguiarte, L.E., Magallón, S., 2012. Insights into the historical construction of species-rich Mesoamerican seasonally dry tropical forests: the diversification of *Bursera* (Burseraceae, Sapindales). *New Phytologist* 193, 276–287.
- Drummond, A.J., Ho, S.Y.W., Phillips, M.J., Rambaut, A., 2006. Relaxed phylogenetics and dating with confidence. *PLoS Biology* 4, e88.
- Drummond, A.J., Suchard, M.A., Xie, D., Rambaut, A., 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* 29, 1969–1973.
- Engler, H.G.A., 1881. Über die morphologische Verhältnisse und die geographische Verbreitung der Gattung *Rhus*, wie der mit ihr verwandten, lebenden und ausgestorbenen Anacardiaceae. *Botanische Jahrbücher* 1, 379–380.
- Estrada-Ruiz, E., Martínez-Cabrera, H.I., Cevallos-Ferriz, S.R.S., 2010. Upper Cretaceous woods from the Olmos Formation (late Campanian–early Maastrichtian), Coahuila, Mexico. *American Journal of Botany* 97, 1179–1194.
- Feagle, J.G., Gilbert, C.C., 2006. The biogeography of primate evolution: the role of plate tectonics, climate and chance. In: Lehman, S.M., Feagle, J.G. (Eds.), *Primate Biogeography*. Springer, New York, pp. 375–418.
- Gade, D.R., Reddy, G.S.K., Reddy Akki, S.N., Reddy, P.V.R., 2010. Hepatoprotective activity of *Rhus soursorensis* against carbon tetrachloride induced hepatotoxicity in albino rats. *International Journal of Pharmaceutical Sciences Review and Research* 4, 46–48.
- Guo, Z.T., Sun, B., Zhang, Z.S., Peng, S.Z., Xiao, G.Q., Ge, J.Y., Hao, Q.Z., Qiao, Y.S., Liang, M.Y., Liu, J.F., Yin, Q.Z., Wei, J.J., 2008. A major reorganization of Asian climate by the early Miocene. *Climate of the Past* 153–174.
- Hall, T.A., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41, 95–98.
- Hardin, J.W., Phillips, L.L., 1985. Hybridization in the eastern North American *Rhus* (Anacardiaceae). *Applied Psychophysiology and Biofeedback* 32, 99–106.
- Hipp, A.L., Hall, J.C., Sytsma, K.J., 2004. Congruence versus phylogenetic accuracy: revisiting the incongruence length difference test. *Systematic Biology* 53, 81–89.
- Jacques, F.M.B., Shi, G.L., Su, T., Zhou, Z.K., 2015. A tropical forest of the middle Miocene of Fujian (SE China) reveals Sino-Indian biogeographic affinities. *Review of Palaeobotany and Palynology* 216, 76–91.
- Kulju, K.K.M., Sierra, S.E.C., Draisma, S.G.A., Samuel, R., Van Welzen, P.C., 2007. Molecular phylogeny of *Macaranga*, *Mallotus*, and related genera (Euphorbiaceae s.s.): insights from plastid and nuclear DNA sequence data. *American Journal of Botany* 94, 1726–1743.
- Li, Y.Q., Dressler, S., Zhang, D.X., Renner, S.S., 2009. More Miocene dispersal between Africa and Asia—the case of *Bridelia* (Phyllanthaceae). *Systematic Botany* 34, 521–529.
- Liu, X.Q., Ickert-Bond, S.M., Chen, L.Q., Wen, J., 2013. Molecular phylogeny of *Cissus* L. of Vitaceae (the grape family) and evolution of its pantropical intercontinental disjunctions. *Molecular Phylogenetics and Evolution* 66, 43–53.
- Lu, L.M., Wang, W., Chen, Z.D., Wen, J., 2013. Phylogeny of the non-monophyletic *Cayratia* Juss. (Vitaceae) and implications for character evolution and biogeography. *Molecular Phylogenetics and Evolution* 68, 502–515.
- Manchester, S.R., 1994. Fruits and seeds of the middle Eocene nut beds flora, Clarno Formation, Oregon. *Palaeontographica Americana* 58, 1–205.
- Manchester, S.R., Wilde, V., Collinson, M.E., 2007. Fossil cashew nuts from the Eocene of Europe: biogeographic links between Africa and South America. *International Journal of Plant Sciences* 168, 1199–1206.
- Mayonde, S.G., Cron, G.V., Gaskin, J.F., Byrne, M.J., 2015. Evidence of *Tamarix* hybrids in South Africa, as inferred by nuclear ITS and plastid trnS–trnG DNA sequences. *South African Journal of Botany* 96, 122–131.
- Meng, H.H., Jacques, F.M.B., Su, T., Huang, Y.J., Zhang, S.T., Ma, H.J., Zhou, Z.K., 2014. New Biogeographic insight into *Bauhinia* s.l. (Leguminosae): integration from fossil records and molecular analyses. *BMC Evolutionary Biology* 14, 181.
- Miller, A.J., Young, D.A., Wen, J., 2001. Phylogeny and biogeography of *Rhus* (Anacardiaceae) based on its sequence data. *International Journal of Plant Sciences* 162, 1401–1407.
- Min, T.L., Barford, A., 2008. Anacardiaceae. In: Wu, Z.Y., Raven, P.H., Hong, D.Y. (Eds.), *Flora of China*. vol. 11. Science Press, Beijing, and Missouri Botanical Garden Press, St. Louis.
- Moffett, R.O., 2007. Name changes in the Old World *Rhus* and recognition of *Searsia* (Anacardiaceae). *Bothalia* 37, 165–175.
- Muellner, A.N., Savolainen, V., Samuel, R., Chase, M.W., 2006. The mahogany family “out-of-Africa”: divergence time estimation, global biogeographic patterns inferred from plastid *rbcL* DNA sequences, extant, and fossil distribution of diversity. *Molecular Phylogenetics and Evolution* 40, 236–250.
- Müller, S., Salomoa, K., Salazar, J., Naumann, J., Jaramillo, M.A., Neinhuis, C., Feild, T.S., Wanke, S., 2015. Intercontinental long-distance dispersal of Canellaceae from the New to the Old World revealed by a nuclear single copy gene and chloroplast DNA. *Molecular Phylogenetics and Evolution* 84, 205–219.
- Nie, Z.L., Sun, H., Meng, Y., Wen, J., 2009. Phylogenetic analysis of *Toxicodendron* (Anacardiaceae) and its biogeographic implications on the evolution of north temperate and tropical intercontinental disjunctions. *Journal of Systematics and Evolution* 47, 416–430.
- Nie, Z.L., Sun, H., Manchester, S.R., Meng, Y., Luke, Q., Wen, J., 2012. Evolution of the intercontinental disjunctions in six continents in the *Ampelopsis* clade of the grape family (Vitaceae). *BMC Evolutionary Biology* 12, 17.
- Nylander, J.A.A., 2004. Bayesian phylogenetics and the evolution of gall wasps. *Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology*, Uppsala.
- Oatley, G., Simmons, R.E., Fuchs, J., 2015. A molecular phylogeny of the harriers (*Circus*, Accipitridae) indicate the role of long distance dispersal and migration in diversification. *Molecular Phylogenetics and Evolution* 85, 150–160.
- Olmstead, R.G., Sweere, J.A., 1994. Combining data in phylogenetic systematics: an empirical approach using three molecular data sets in the Solanaceae. *Systematic Biology* 43, 467–481.
- Pell, S.K., Mitchell, J.D., Lowry, P.P., Randrianasolo, A., Urbatsch, L.E., 2008. Phylogenetic split of Malagasy and African taxa of *Protorhus* and *Rhus* (Anacardiaceae) based on cpDNA *trnL-trnF* and nrDNA ETS and ITS sequence data. *Systematic Botany* 33, 375–383.
- Perez-Gutierrez, M.A., Romero-García, A.T., Salinas, M.J., Blanca, G., Fernandez, M.C., Suarez-Santiago, V.N., 2012. Phylogeny of the tribe Fumarieae (Papaveraceae s.l.) based on chloroplast and nuclear DNA sequences: evolutionary and biogeographic implications. *American Journal of Botany* 99, 517–528.
- Popp, M., Gizaw, A., Nemomissa, S., Suda, J., Brochmann, C., 2008. Colonization and diversification in the African ‘sky islands’ by Eurasian *Lychnis* L. (Caryophyllaceae). *Journal of Biogeography* 35, 1016–1029.
- Posada, D., Buckley, T.R., 2004. Model selection and model averaging in phylogenetics: advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. *Systematic Biology* 53, 793–808.
- Press, J.R., Shrestha, K.K., Sutton, D.A., 2000. Annotated Checklist of the Flowering Plants of Nepal. The Natural History Museum, London, p. 10.
- Rambaut, A., 2014. FigTree 1.4.1. Tree Figure Drawing Tool. <http://tree.bio.ed.ac.uk/>.
- Ren, Z.M., Zhong, Y., Kurosu, U., Aoki, S., Ma, E.B., Von Dohlen, C.D., Wen, J., 2013. Historical biogeography of Eastern Asian–Eastern North American disjunct Melaphidina aphids (Hemiptera: Aphididae: Eriosomatinae) on *Rhus* hosts (Anacardiaceae). *Molecular Phylogenetics and Evolution* 69, 1146–1158.
- Ren, G., Conti, E., Salamin, N., 2015. Phylogeny and biogeography of *Primula* sect. *Armerina*: implications for plant evolution under climate change and the uplift of the Qinghai-Tibet Plateau. *BMC Evolutionary Biology* 15, 161.
- Rieseberg, L.H., Soltis, D.E., 1991. Phylogenetic consequences of cytoplasmic gene flow in plants. *Evolutionary Trends in Plants* 5, 65–84.
- Rieseberg, L.H., Beckstrom-Sternberg, S.M., Liston, A., Arias, D., 1991. Phylogenetic and systematic inferences from chloroplast DNA and isozyme variation in *Helianthus* sect. *Helianthus* (Asteraceae). *Systematic Botany* 16, 50–76.
- Rögl, F., 1998. Palaeogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). *Annalen des Naturhistorischen Museums in Wien* 99, 279–310.
- Rögl, F., 1999. Circum-Mediterranean Miocene paleogeography. In: Rössner, G.H., Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Dr. Friedrich Pfeil, München, pp. 39–48.
- Ronquist, F., Huelsenbeck, J.P., 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19, 1572–1574.
- Sirichamorn, Y., Thomas, D.C., Adema, F., Van Welzen, P.C., 2014. Historical biogeography of *Aganope*, *Brachypterum* and *Derris* (Fabaceae, tribe Millettieae): insights into the origins of Palaeotropical intercontinental disjunctions and general biogeographical patterns in Southeast Asia. *Journal of Biogeography* 41, 882–893.
- Soltis, D.E., Kuzoff, R.K., 1995. Discordance between nuclear and chloroplast phylogenies in the Heuchera group (Saxifragaceae). *Evolution* 49, 727–742.
- Stamatakis, A., 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22, 2688–2690.
- Taberlet, P., Gielly, L., Pautou, G., Bouvet, J., 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17, 1105–1109.
- Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F., Higgins, D.G., 1997. The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 25, 4876–4882.
- Vatanparast, M., Klitgard, B.B., Adema, F.A.C.B., Pennington, R.T., Yahara, T., Kajita, T., 2013. First molecular phylogeny of the pantropical genus *Dalbergia*: implications for infrageneric circumscription and biogeography. *South African Journal of Botany* 89, 143–149.
- Weeks, A., Daly, D.C., Simpson, B.B., 2005. The phylogenetic history and biogeography of the frankincense and myrrh family (Burseraceae) based on nuclear and chloroplast sequence data. *Molecular Phylogenetics and Evolution* 35, 85–101.

- Weeks, A., Zapata, F., Pell, S.K., Daly, D.C., Mitchell, J.D., Fine, P.V., 2014. To move or to evolve: contrasting patterns of intercontinental connectivity and climatic niche evolution in "Terebinthaceae" (Anacardiaceae and Burseraceae). *Frontiers in Genetics* 5, 409.
- White, T.J., Bruns, T., Lee, S., Taylor, J., 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis, M.A., Gelfand, D.H., Sninsky, J.J., White, T.J. (Eds.), *PCR Protocols, A Guide to Methods and Applications*. Academic Press, New York, pp. 315–322.
- Wolfe, A., Kaufmann, R.L., 1975. MHD wave transmission and production near the magnetopause. *Journal of Geophysical Research* 80, 1764–1775.
- Wu, C.Y., Ming, T.L., 1979. *Terminthia paniculata* (Wall, ex G.Don), C.Y.Wu et T.L.Ming. *Flora Yunnan* 2, 408–409.
- Xie, L., Yang, Z.Y., Wen, J., Li, D.Z., Yi, T.S., 2014. Biogeographic history of *Pistacia* (Anacardiaceae), emphasizing the evolution of the Madrean–Tethyan and the eastern Asian–Tethyan disjunctions. *Molecular Phylogenetics and Evolution* 77, 136–146.
- Yi, T.S., Miller, A.J., Wen, J., 2004. Phylogenetic and biogeographic diversification of *Rhus* (Anacardiaceae) in the Northern Hemisphere. *Molecular Phylogenetics and Evolution* 33, 861–879.
- Yi, T.S., Miller, A.J., Wen, J., 2007. Phylogeny of *Rhus* (Anacardiaceae) based on sequences of nuclear *Nia-13* intron and chloroplast *trnC-trnD*. *Systematic Botany* 32, 379–391.
- Yi, T.S., Wen, J., Golan-Goldhirsh, A., Parfitt, D.E., 2008. Phylogenetics and reticulate evolution in *Pistacia* (Anacardiaceae). *American Journal of Botany* 95, 241–251.
- Yi, T.S., Jin, G.H., Wen, J., 2015. Chloroplast capture and intra- and inter-continental biogeographic diversification in the Asian–New World disjunct plant genus *Osmorhiza* (Apiaceae). *Molecular Phylogenetics and Evolution* 85, 10–21.
- Yoo, K.O., Lowry II, P.P., Wen, J., 2002. Discordance of chloroplast and nuclear ribosomal DNA data in *Osmorhiza* (Apiaceae). *American Journal of Botany* 89, 966–971.
- Young, D.A., 1978. Reevaluation of the sections of *Rhus* L. subgenus *Lobadium* (raf.) T. & G. (Anacardiaceae). *Brittonia* 30, 411–415.
- Yu, X.Q., Maki, M., Drew, B.T., Paton, A.J., Li, H.W., Zhao, J.L., Conran, J.G., Li, J., 2014. Phylogeny and historical biogeography of *Isodon* (Lamiaceae): rapid radiation in south-west China and Miocene overland dispersal into Africa. *Molecular Phylogenetics and Evolution* 77, 183–194.
- Yuan, Y.M., Wohlhauser, S., Moller, M., Klackenberg, J., Callmander, M.W., Kupfer, P., 2005. Phylogeny and biogeography of *Exacum* (Gentianaceae): a disjunctive distribution in the Indian Ocean basin resulted from long distance dispersal and extensive radiation. *Systematic Biology* 54, 21–34.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberration in global climate 65 Ma to present. *Science* 292, 686–693.
- Zhou, L.L., Su, Y.C.F., Thomas, D.C., Saunders, R.M.K., 2012. 'Out-of-Africa' dispersal of tropical floras during the Miocene climatic optimum: evidence from *Uvaria* (Annonaceae). *Journal of Biogeography* 39, 322–335.