

RESEARCH ARTICLE

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Biogeography of *Coptis* Salisb. (Ranunculales, Ranunculaceae, Coptidoideae), an Eastern Asian and North American genus

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Abstract

Background: Numerous studies have favored dispersal (colonization) over vicariance (past fragmentation) events to explain eastern Asian–North American distribution patterns. In plants, however the disjunction between eastern Asia and western North America has been rarely examined using the integration of phylogenetic, molecular dating, and biogeographical methods. Meanwhile, the biogeographic patterns within eastern Asia remain poorly understood. The goldthread genus *Coptis* Salisb. includes 15 species disjunctly distributed in North America, Japan, mainland China, and Taiwan. We present a dated phylogeny for *Coptis* under the optimal clock model and infer its historical biogeography by comparing different biogeographic models.

Results: The split of *Coptis* and *Xanthorhiza* Marshall occurred in the middle Miocene (ca. 15.47 Ma). *Coptis* started their diversification in the early late Miocene (ca. 9.55 Ma). A late Miocene vicariance event resulted in the eastern Asian and western North American disjunction in the genus. Within eastern Asia, dispersals from mainland Asia to Japan and from Japan to Taiwan occurred at ca. 4.85 Ma and at ca. 1.34 Ma, respectively.

Conclusions: Our analyses provide evidence that both vicariance and dispersal events have played important roles in shaping the current distribution and endemism of *Coptis*, likely resulting from eustatic sea-level changes, mountain formation processes and an increasing drier and cooler climate from the middle Miocene onwards.

Keywords: Ancestral range evolution, Climate change, *Coptis*, Eastern Asian, Taiwan, Western North America

Background

Understanding the geographical deployment of biodiversity through time is a central theme in historical biogeography [1]. The disjunct distributions of closely related organisms between East Asia and North America have fascinated botanists and biogeographers for over a century and a half [2–5]. In plants, biogeographic studies employing the integration of phylogenetic hypotheses, inference of ancestral ranges, and estimates of divergence times have largely focused on the classic eastern Asian and eastern North American floristic disjunction pattern [5–8]. Few studies have been devoted to investigate the eastern Asian and

western North American disjunction [9, 10]. For these two patterns, the Miocene has been regarded as an important period, in which the Bering land bridge likely acted as a major gateway [5, 11–13].

In the Northern Hemisphere, East Asia is a pivotal biogeographic region as it presents high levels of plant species diversity and endemism [14, 15]. Based on Takhtajan's [16] floristic system, southern East Asia belongs to the Paleotropical Kingdom, whereas northern East Asia is part of the Holarctic Kingdom (Fig. 1). Recent molecular phylogenetic studies also indicate that the Tertiary relict floras within East Asia could be subdivided into two distinct southern and northern regions [17, 18]. The former consists of southern and southeastern China with extending to the Himalayas, while the latter contains Japan, Korea, and northeastern China. Besides, as a continental island

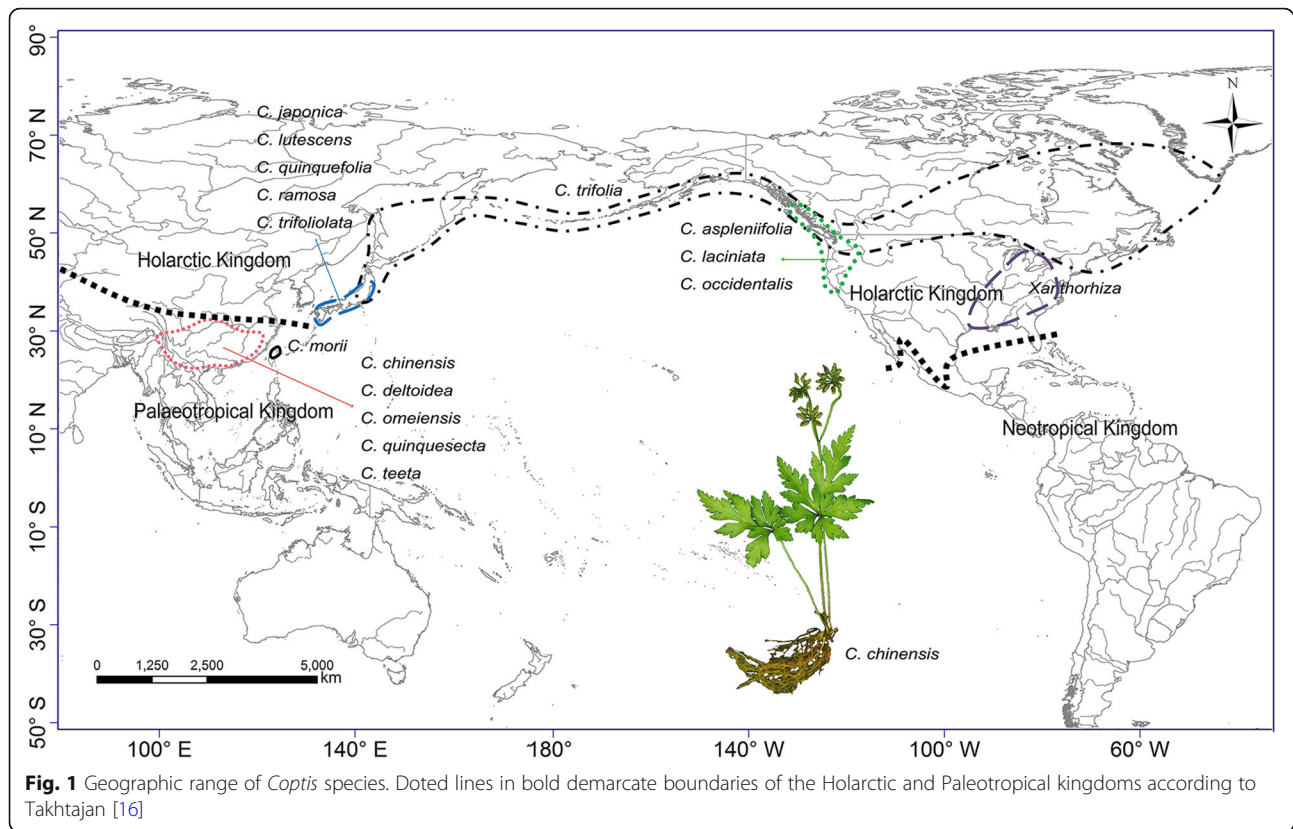
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adjacent to southeastern mainland China, the Ryukyus Islands, and Philippines, the floristic source of Taiwan is not clear [19–21]. To date, biogeographic relationships among southern East Asia, northern East Asia and Taiwan are far from understood.

The goldthread genus *Coptis* Salisb. (Ranunculales, Ranunculaceae, Coptidoideae) is of pharmaceutical and economical importance and is mainly distributed in the warm temperate to the cold coniferous forests of eastern Asia and North America [22, 23]. Among the 15 species recognized by Tamura [22], *C. trifolia* (L.) Salisb. has the widest distribution area (including Japan, the Kurile Islands, Kamchatka, and North America), while the other 14 species are restricted to smaller regions: five species are found in southern and southwestern mainland China with extensions to the Himalayas, five in Japan, one in Taiwan, and three in western North America (Fig. 1). Our recent phylogenetic analysis based on three DNA markers indicates that three western North American species of the genus clustered with five mainland Chinese and two Japanese species, and Taiwanese *C. morii* Hayata and three Japanese species grouped together [23]. The fruits of *Coptis* are dehiscent follicles [22] and seeds may be autochorously dispersed owing to lacking obvious adaptation to wind-dispersal. Seeds are not thereby expected to disperse over long distance or oceanic barriers. Thus, *Coptis* provides a remarkable opportunity for studying the

eastern Asian and western North American distribution pattern, as well as the biogeographic relationships within East Asia.

In this study, first we reconstruct a dated phylogeny for *Coptis* based on six DNA markers, using a Bayesian relaxed clock method. Using the resulting dated-phylogenetic framework, we then infer the ancestral range evolution of *Coptis* by comparing the relative fit of six biogeographic models. Our study contributes to the knowledge on the eastern Asian-western North American distribution pattern and eastern Asian biogeography.

Methods

Samples and sequences

We sampled all 15 species of *Coptis* recognized by Tamura [22]. *Coptis* and the monotypic *Xanthorrhiza* Marshall compose the subfamily Coptidoideae, which is sister to a large clade containing the overwhelming majority of genera of Ranunculaceae [24, 25]. Scoring this large clade for geographic areas is a challenge. Here, we only selected *Xanthorrhiza* as the outgroup. The sampled species and their GenBank accession numbers are listed in Additional file 1: Table S1.

Six DNA markers, including five plastid (*rbcL*, *trnL* intron, *trnL-F* spacers, *trnD-trnT*, and *trnH-psbA*) and one nuclear (ITS) regions were used in this study. We generated new *trnL* sequence for *C. japonica* var. *anemonifolia*

(Siebold & Zucc.) H. Ohba and *trnL* and ITS for *C. morii*. These two samples were collected in public land and no specific permits were required. Other sequences were obtained from GenBank. Laboratory procedures and sequence handling followed Wang and Chen [26]. Three difficult-to-align regions in *trnL-F* (encompassing 20 positions), two difficult-to-align regions in *trnH-psbA* (48 positions), and one difficult-to-align region in *trnD-trnT* (24 positions) were excluded from the analyses. The final dataset included 4288 characters: *rbcL*, 1304 bp; *trnL* intron, 465 bp; *trnL-F*, 426 bp; *trnD-trnT*, 1122 bp; *trnH-psbA*, 289 bp; and ITS, 682 bp.

Phylogeny and divergence time estimates

We first conducted a likelihood ratio test [27] to determine whether our sequence data were evolving in a clock-like fashion. Because rate constancy along all branches of the phylogeny was rejected ($\delta = 146.63$, d.f. = 14, $P < 0.0001$), we used a Bayesian relaxed clock methodology as implemented in BEAST v1.8.2 [28] to generate a dated phylogeny for *Coptis*. Based on our recent broader study of Ranunculaceae [25], the split time between *Coptis* and *Xanthorhiza* was estimated at ca. 16.23 Ma (95% highest posterior density (HPD): 8.51–25.96) and was here used as a secondary calibration point. Following the suggestion of Ho [29], we assigned a prior normal distribution for the calibration, in which a standard deviation of 2 was set.

Following the result of Baele et al. [30], we used Bayes factors [31] calculated by marginal likelihoods derived from path sampling (PS) [32] and stepping-stone sampling (SS) [33] to compare the parametric fit of three clock models: exponential, lognormal and random. Since our sampling included all recognized species of *Coptis* and *Xanthorhiza*, a birth-death tree prior was used.

For all BEAST analyses, data partitioning and nucleotide substitution models were determined using PartitionFinder 2.1.1 [34, 35]. The Markov chain Monte Carlo chains were run for 100 million generations, sampling every 10,000 generations. Tracer v1.6 [36] was used to assess appropriate burn-in and the adequate effective sample size values (> 200). A burn-in of 25% was applied, and the maximum clade credibility (MCC) tree with the mean ages and 95% HPD intervals on nodes were conducted in TreeAnnotator v1.8.2 (part of the BEAST package) and edited in FigTree v1.4.2 (<http://beast.bio.ed.ac.uk/FigTree>).

Ancestral range analysis

Based on the floristic characteristics [16, 18] and distributions of *Coptis* and *Xanthorhiza* [22], we coded five biogeographical areas (Fig. 1): (A) western North America, (B) southern East Asia (including southern and southeastern mainland China and the adjacent Himalayan region), (C) Japan and adjacent islands (including the Kurile Islands and Kamchatka), (D) Taiwan, and (E) eastern

North America. The maximum range size was set to three, as no extant species occurs in more than three biogeographical regions. Because the Bering land bridge was periodically available for exchanges of plants between eastern Asia and western North America until 3.5 Ma [37–39], dispersal probabilities between pairs of areas were specified for two separate time slices (Additional file 1: Table S2).

We used the R package BioGeoBEARS [40] for ancestral range estimation (ARE) on the MCC tree from the BEAST run under the optimal clock model and tree speciation prior. Recently, Ree & Sanmartín [41] demonstrated that the likelihood-based models with the +J parameter are invalid because of errors in the estimation of likelihoods. Here we compared the following three models of biogeographical estimation in the maximum likelihood (ML) framework: dispersal-extinction cladogenesis (DEC) model [42], dispersal–vicariance analysis (DIVA) [43] and BayArea model [44]. The fit for the different models was assessed using the Akaike information criterion scores.

Results

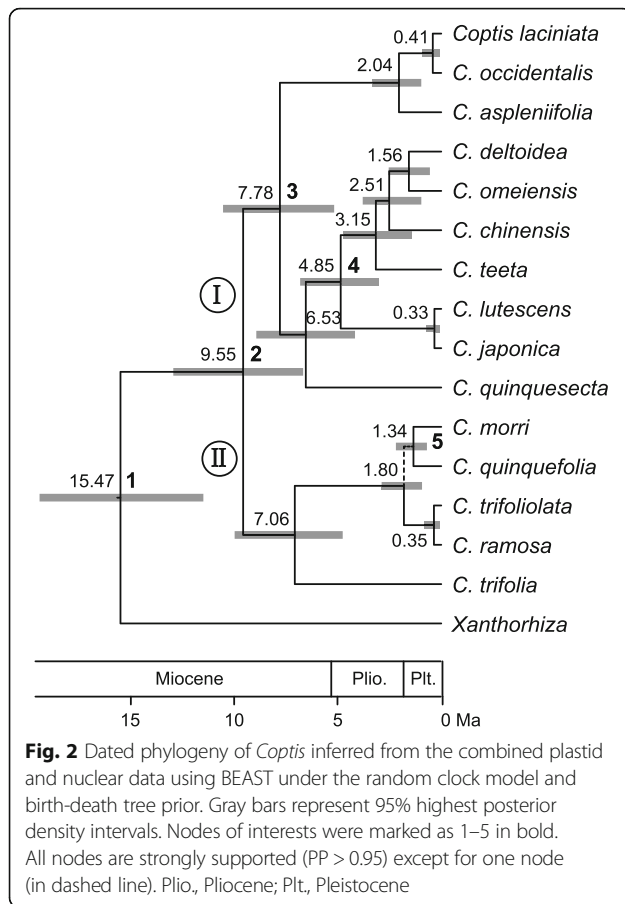
Phylogeny and divergence times

We identified the random clock model as optimal for our data (Table 1). The dated phylogenetic tree generated in the BEAST analysis under the random clock model and birth-death tree prior is indicated in Fig. 2. The relationships among *Coptis* species are well resolved with strong support (PP > 0.95) except for the node defining the sister relationship of *C. quinquefolia* Miq. and *C. morii*. *Coptis* contains two main clades (I and II). Based on our time estimates (Fig. 2), the stem and crown ages of *Coptis* are estimated at ca. 15.47 Ma (95% HPD: 11.47–19.37; node 1) and 9.55 Ma (95% HPD: 6.66–12.92; node 2), respectively. Within clade I, three western North American species clustered together and split from their eastern Asian sister group at ca. 7.78 Ma (95% HPD: 5.16–10.52;

Table 1 Comparison of three clock models in BEAST analyses via Bayes factors

Clock model	Marginal likelihood	Exponential	Lognormal	Random
PS implementation				
Exponential	–8809.70	–	37.44	–32.90
Lognormal	–8828.42	–37.44	–	–70.34
Random	–8793.25	32.90	70.34	–
SS implementation				
Exponential	–8810.29	–	37.62	–33.72
Lognormal	–8829.10	–37.62	–	–71.34
Random	–8793.43	33.72	71.34	–

2ln Bayes factor (BF) was calculated by marginal likelihoods derived from path sampling (PS) and stepping-stone sampling (SS) implementations in BEAST. 2ln BF > 2.0 represents positive evidence, > 6.00 represents strong evidence, and > 10.00 represents very strong evidence [31]



node 3). Japanese *C. japonica* Makino and *C. lutescens* Tamura are nested in the group of mainland Chinese species and the split of these two Japanese species and their sister group occurred at ca. 4.85 Ma (95% HPD: 2.98–6.80; node 4). Within clade II, Taiwanese *C. morii* and Japanese *C. quinquefolia* were grouped together with weak support (PP = 0.73). The split time of *C. morii* and *C. quinquefolia* was estimated to be at ca. 1.34 Ma (95% HPD: 0.69–2.18; node 5).

Ancestral range estimation

A DIVALIKE was found to be the best-fitting model (Table 2). The ARE for *Coptis* using BioGeoBEARS is indicated in Fig. 3 and Additional file 2: Figure S1. Area probabilities of all nodes are high except the root. Our ARE

shows that the ancestral range of *Coptis* and *Xanthorhiza* is unresolved but likely involved eastern North America, western North America and Japan (node 1). The most recent common ancestor of *Coptis* was likely distributed in western North America, southern East Asia and Japan (node 2). Within *Coptis*, two vicariance events and two dispersal events were inferred at the species level (Fig. 3).

Discussion

The phylogenetic relationships in *Coptis* are highly consistent with the results of Xiang et al. [23], but are usually resolved with greater support for clades found therein. Our results do not support Taiwanese *C. morii* as sister to three Japanese species (*C. ramosa* (Makino) Tamura, *C. quinquefolia* and *C. trifoliolata* (Makino) Makino), and instead suggest that *C. morii* is sister to *C. quinquefolia*, although with moderate support (PP = 0.71). Using the split age of ca. 16.23 Ma (95% HPD: 8.51–25.96) between *Coptis* and *Xanthorhiza* [25], we obtained a similar age estimate for the split (ca. 15.47 Ma; 95% HPD: 11.47–19.37; Fig. 2).

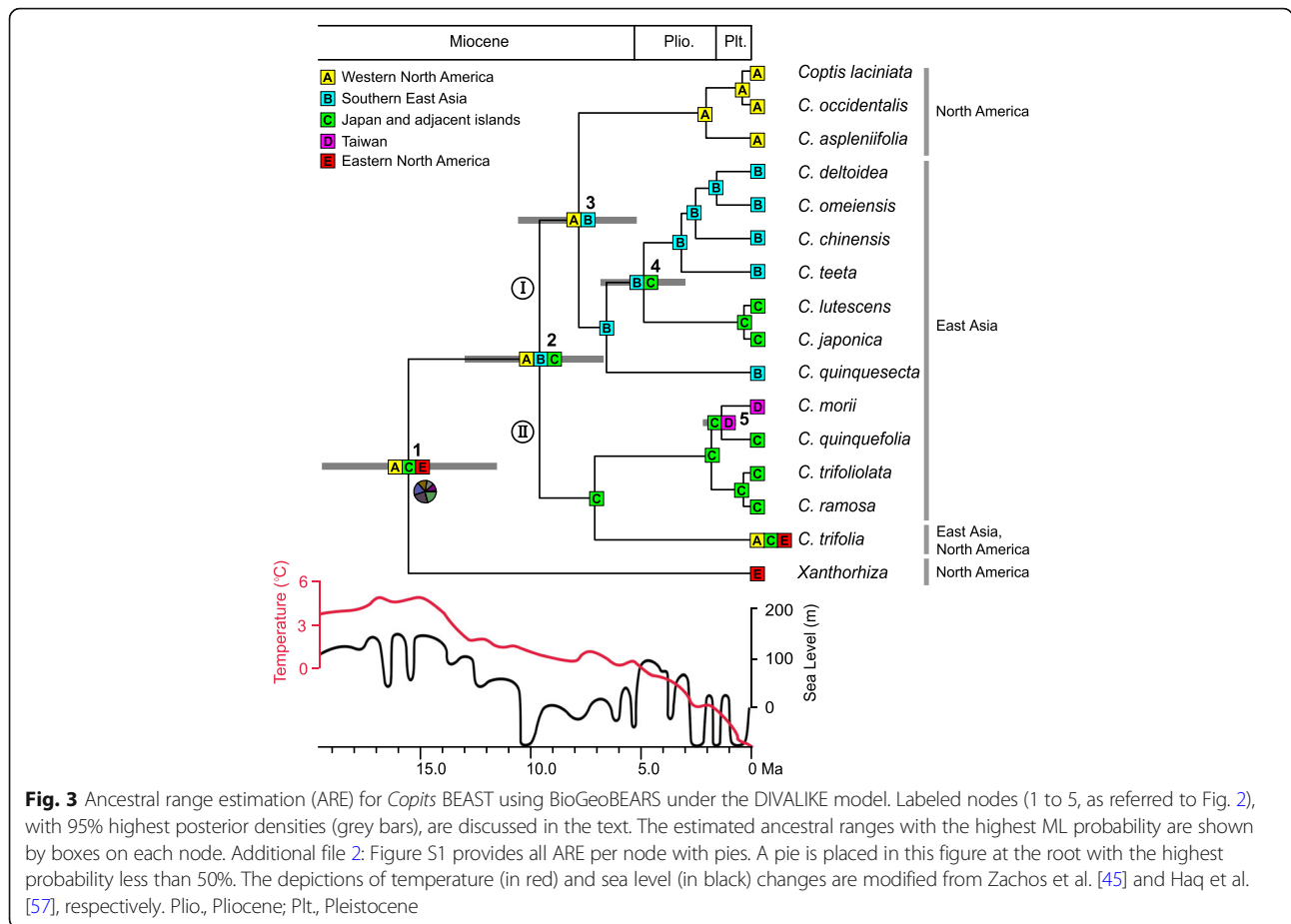
BioGeoBEARS analyses indicate that the crown of *Coptis* and *Xanthorhiza* most likely occurred in a widespread area comprising North America and Japan (Fig. 3; node 1), although other somewhat less likely ARE are possible (Additional file 2: Figure S1). The estimated age for the split of these two genera highly coincides with the mid-Miocene Climatic Optimum (MMCO; ~15–17 Ma; Fig. 3) [45]. During this period, exchange of temperate plants between East Asia and North America could occur via the Bering land bridge [46]. Paleobotanical data indicate that the mixed mesophytic forest of the early and middle Miocene was continuous from Japan through Alaska and into conterminous North America [47, 48].

The American west encompassing the Colorado Plateau, Basin and Range, the High Plains, and the Rocky and Sierra Mountains began to uplift rapidly by 20–15 Ma [49]. A middle Miocene flora from Carson Pass in the central Sierra Nevada suggests uplift of about 2300 m since that time [50]. The uplift is a key factor in creating an increasingly drier climate in the North American interior around that time [49, 51]. Paleobotanical evidence suggests that by the middle Miocene the arid interior has become an effective barrier to biotic interchange between eastern and western North America [52, 53]. After the MMCO, an increasingly drier climate, as well as global

Table 2 Comparison of the fit of three models of biogeographical range evolution and model-specific estimates for the different parameters

Model	LnL	Parameter nb	<i>d</i>	<i>e</i>	AIC	ΔAIC	AIC _C	ΔAIC _C
DEC	−24.06	2	0.03	1.00 × 10 ^{−12}	52.12	3.59	53.04	3.58
DIVALIKE	−22.27	2	0.03	1.00 × 10 ^{−12}	48.53	0	49.46	0
BAYAREALIKE	−28.77	2	0.04	1.04 × 10 ^{−1}	61.55	13.02	52.47	13.01

d = dispersal rate; *e* = extinction rate



cooling (Fig. 3) [45], might thus have resulted in a vicariance event responsible for the divergence of *Coptis* and *Xanthorhiza* (node 1; Fig. 3).

After *Coptis* diverged from *Xanthorhiza*, a subsequent dispersal from Japan to southern East Asia occurred in the early late Miocene (9.55 Ma, 95% HPD: 6.66–12.92; node 2). This time is markedly later than the time of the opening of the Japan Sea (23–15 Ma), which separated the Japanese Islands from the Northeast Asian margins [54–56]. However, during the early late Miocene, a marked drop of sea level occurred (Fig. 3) [57], which might have resulted in East China Sea seafloor exposure between the Eurasian mainland and the Japanese Archipelago. Hence, *Coptis* could have migrated westward into continental Asia via this land bridge. Subsequent sea-level rise might have resulted in the interruption of population exchange of the genus between the Asian mainland and the Japanese Islands. Accordingly, *Coptis* diverged into two clades (I and II).

In clade I, one vicariance episode happened between western North America and southern East Asia in the Late Miocene (ca. 7.78 Ma, 95% HPD: 5.16–10.52; node 3), which overlapped closely with the time of the first opening of the Bering Strait (7.4–5.5 Ma) [58]. Evidence

from sedimentology and foraminifera indicates that uplift of the St. Elias Mts. in Alaska began about 8.5 Ma [59]. Palynological analyses suggest that the trends of temperature decline and increasing canopy openness in Alaska and Yukon Territory occurred between 9.7 and 7.0 Ma, owing to global and local tectonic developments [60]. These events may explain the distribution of *Coptis* between southern East Asia and western North America during the Late Miocene. The split of western North American *Polypodium californicum* Kaulf. (Polypodiaceae) and its eastern Asian relatives (*P. fauriei* (Copel.) Makino & Nemoto and *P. glycyrrhiza* D.C. Eaton) also occurred during the same period (ca. 8.81 Ma, 95% HPD: 5.06–13.08) [61]. Such distribution patterns resulting from orogenic events have been found in some plant lineages and in different biomes, such as Campanulaceae [62], Orchidaceae [63], and Rubiaceae [64].

One dispersal event in clade I occurred in the early Pliocene from southern East Asia to Japan (ca. 4.85 Ma, 95% HPD: 2.98–6.80; node 4). The most recent common ancestor of Japanese *Pseudotsuga japonica* (Shiras) Beissn. and mainland Chinese *P. gaussenii* Flous and *P. sinensis* Dode (Pinaceae) was estimated to occur at ca. 4.64 ± 1.93 Ma [65]. In Eupteleaceae, Chinese *Euptelea pleiosperma* Hook.

f. & Thomson split with Japanese *E. polyandra* Siebold & Zucc. at ca. 6.04 Ma (95% HPD: 2.89–9.36) [66]. The drop of sea level may have resulted in exchanges of plants between mainland Asia and the Japanese Islands via the East China Sea land bridge, and subsequent rise of sea level and global cooling (Fig. 2) [67], as well as an increasingly drier climate in Asia [68], may have caused the interruption of the continuous distribution of ancestral populations of some extant species during the Late Miocene to the Early Pliocene.

Within clade II, one dispersal event from Japan to Taiwan occurred in the Early Pleistocene (ca. 1.34 Ma; 95% HPD: 0.69–2.18; node 5). The eustatic sea-level fluctuation during this period, as well as global cooling (Fig. 2), may have triggered *Coptis* range expansion from Japan to Taiwan via the Ryukyu Islands, and may have subsequently caused range fragmentation. A similar scenario also explains the current distribution of Taiwanese *Chamaecyparis formosensis* Matsum. and *C. taiwanensis* Masam. & Suzuki (Cupressaceae) from hypothetical Japanese ancestors [69]. Our analysis on *Dichocarpum* W.T. Wang & P.G. Xiao indicates that Taiwanese *D. arisanense* (Hayata) W.T. Wang & P.G. Xiao could have originated from mainland China in the Early Pleistocene (ca. 1.26 Ma, 95% HPD: 0.48–2.33) [70]. These studies support the hypothesis that temperate elements of the flora of Taiwan recently migrated from mainland China and Japan [71].

Conclusions

We present a dated phylogeny for all species of *Coptis*, a genus of pharmaceutical and economical importance. Our biogeographical inference indicates that a vicariance event between Japan-western North America and eastern North America occurred in the Middle Miocene, resulting in the split of *Coptis* and *Xanthorhiza*. The most recent common ancestor of *Coptis* occurred in western North America, southern East Asia and Japan. In *Coptis*, two vicariance episodes, involving Japan and western North America-southern East Asian and western North America and southern East Asian, took place at ca. 9.55 Ma and 7.78 Ma, respectively. Two dispersal events happened from mainland Asia to Japan at ca. 4.85 Ma and from Japan to Taiwan at ca. 1.34 Ma, respectively. This study shed light on the past floristic exchanges between East Asia and North America, as well as within East Asia.

Additional files

Additional file 1: Table S1. GenBank accession numbers and vouchers/references for the sequences used in this study. **Table S2.** Manual dispersal multipliers. (PDF 36 kb)

Additional file 2: Figure S1. Raw PDF outputs from biogeographic estimations in BioGeoBEARS. (PDF 358 kb)

Abbreviations

ARE: Ancestral range estimation; BF: Bayes factor; DEC: Dispersal-extinction cladogenesis; DIVA: Dispersal–vicariance analysis; HPD: Highest posterior density; MCC: Maximum clade credibility; ML: Maximum likelihood; MMCO: Mid-Miocene Climatic Optimum; PS: Path sampling; SS: Stepping-stone sampling

Acknowledgements

We sincerely thank Sheng-Xiang Yu for technique assistance and G.H. Harper for carefully reading an early draft of the manuscript. We also thank Gael J. Kergoat and two anonymous reviewers for their comments and suggestions that greatly improved our manuscript.

Funding

This research was partially funded by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDPB0203), the National Basic Research Program of China (2014CB954100), the National Natural Science Foundation of China (31770231, 31270269 and 31470315), the Youth Innovation Promotion Association Foundation of CAS, and the D.I. Mendeleev Scientific Fund Program of Tomsk State University. The funding body had no role in the design, collection and conclusion of this study.

Availability of data and materials

The sequences reported in this paper have been deposited in the GenBank database (accession nos. MG991242–MG991244). The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Authors' contributions

WW designed and managed the project. KLX, ASE, FJ and WW collected the data. KLX, XGX and WW analysed the data. KLX and WW led the writing with contributions from all authors. All authors read and approved the final manuscript.

Ethics approval and consent to participate

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Received: 14 September 2017 Accepted: 17 May 2018

Published online: 24 May 2018

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