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...
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*
Generations. Tracer v1.6 [36] was used to assess appropriate run for 100 million generations, sampling every 10,000. The Markov chain Monte Carlo chains were determined using PartitionFinder v.1.4.2 (http://beast.bio.ed.ac.uk/FigTree). HPD intervals on nodes were conducted in TreeAnnotator 200). A burn-in of 25% was applied, and the maximum burn-in and the adequate effective sample size values (> 10.00 represents very strong evidence [31] – 2ln BF > 2.0 represents positive evidence, > 6.00 represents strong evidence, and > 10.00 represents very strong evidence [31]).

**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 (δ = 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 Xanthorrhiza 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 Xanthorrhiza, 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 v.1.4.2 (http://beast.bio.ed.ac.uk/FigTree).

**Ancestral range analysis**
Based on the floristic characteristics [16, 18] and distributions of Coptis and Xanthorrhiza [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 +I 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; 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].

### 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].
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. ramose* (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

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**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 | d     | e            | AIC  | ΔAIC | AICc  | ΔAICc |
|-------------|------|--------------|-------|--------------|------|------|-------|-------|
| DEC         | −24.06 | 2            | 0.03  | 1.00 x 10^{-12} | 52.12 | 3.59 | 53.04 | 3.58 |
| DIVALIKE    | −22.27 | 2            | 0.03  | 1.00 x 10^{-12} | 48.53 | 0     | 49.46 | 0     |
| BAYAREALIKE | −28.77 | 2            | 0.04  | 1.04 x 10^{-13} | 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* Kauff. (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 Eupeiteaceae, Chinese *Eupeites pleiosperma* Hook.

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**Fig. 3** Ancestral range estimation (ARE) for *Coptis* BEAST using BioGeoBEARS under the DIVALIKE model. Labeled nodes (1 to 5, as referred to Fig. 2), with 95% highest posterior densities (grey bars), are discussed in the text. The estimated ancestral ranges with the highest ML probability are shown by boxes on each node. Additional file 2: Figure S1 provides all ARE per node with pies. A pie is placed in this figure at the root with the highest probability less than 50%. The depictions of temperature (in red) and sea level (in black) changes are modified from Zachos et al. [45] and Haq et al. [57], respectively. Plio., Pliocene; Plt., Pleistocene.
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. taiwannensis* 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 *Xanthorrhiza*. 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)
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