

Research Article

Historical biogeography of the *Angelica* group (Apiaceae tribe Selineae) inferred from analyses of nrDNA and cpDNA sequences

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Abstract Biogeographical patterns and diversification processes of Asia-centered angiosperm groups have been significantly affected by the multistage uplift of the Himalayas–Tibetan Plateau since the Late Tertiary. The divergence time of the largely East Asian *Angelica* group (Apiaceae, subfamily Apioideae, tribe Selineae) was initially analyzed using BEAST and nrDNA internal transcribed spacer sequence data from 96 representatives of tribe Selineae and relatives. Further analyses of the biogeographical history of the *Angelica* group were carried out using BEAST, S-DIVA, RASP, and LAGRANGE on datasets containing all or some of the following loci: nrDNA internal and external transcribed spacers; cpDNA *rps16* intron; and cpDNA *rps16-trnK*, *rpl32-trnL*, and *trnL-trnT* intergenic spacers. The results suggested that the *Angelica* group was originally present in the East Palearctic during the global cooling of the late Middle Miocene (13.6 Mya) and that the *Angelica s.s.* clade originated in the same region at 10.2 Mya. Subsequent diversifications of the *Angelica s.s.* clade intensified in the East Palearctic during the middle Late Miocene (10.0–7.0 Mya) and in the eastern Himalayan Zone during the late Pliocene and Pleistocene (<4.0 Mya). These diversifications likely corresponded with plateau uplift-driven climatic changes. Considering elevational reconstructions, the differential responses to altitude appear to be the primary factor explaining the recent radiation of the group in the eastern Himalayas. The North American species of the *Angelica* group were retrieved as polyphyletic and their migrations involved six independent dispersals to North America at least since the middle Late Miocene, including four times from northeast Asia and twice from Europe.

Key words *Angelica*, biogeography, disjunct distribution, divergence time.

Many angiosperm genera present a disjunctive distribution pattern in the Northern Hemisphere, which was once considered the result of fragmentation of a more widespread ancient flora (reviewed by Xiang & Soltis, 2001). This vicariance-based hypothesis suggested that the ancestors of current disjunct groups should have a wider distribution in the Holarctic prior to the Late Miocene. Vicariance is a simpler explanation accounting for these disjunct distribution patterns than is long-distance dispersal. However, recent dating analyses revealed that the divergence of certain lineages took place much later than the tectonic events accounting for their vicariance (Ronquist, 1997; Wen, 1999, 2001; Xiang & Soltis, 2001). Long-distance dispersal, therefore, should also be considered an important factor shaping the current distribution patterns of plants (e.g., Renner et al., 2001; Yuan et al., 2005; Kadereit et al., 2008; Wen & Ickert-Bond, 2009; Spalik et al., 2010).

Arguably, *Angelica* L. *s.l.* is among the most taxonomically complex groups in Apiaceae subfamily Apioideae. The group comprises approximately 110 species and usually consists of *Angelica s.s.*, *Archangelica* Hoffm., *Coelopleurum* Ledeb., *Czernaevia* Turcz. ex Ledeb., and *Ostericum* Hoffm. (Mathias, 1965; Pimenov, 1968b; Shan & Sheh, 1979; Vasilèva & Pimenov, 1991; Pimenov & Leonov, 1993; Wen, 1999; Pimenov & Kljuykov, 2003; Sheh et al., 2005). Previous molecular systematic studies based on nrDNA internal transcribed spacer (ITS) sequence data have suggested that *Angelica s.l.* is polyphyletic, with the majority of its members occurring in the tribe Selineae. These members include *Angelica s.s.*, *Archangelica*, *Coelopleurum*, *Czernaevia*, and several other relatives including one species of *Ostericum*. In contrast, these same studies also showed that two other species of *Ostericum* (*O. grosseserratum* (Maxim.) Kitag. and *O. scaberulum* (Franch.) R. H. Shan & C. Q. Yuan) were placed in the *Acronema* clade of subfamily Apioideae, and several other species of *Angelica* were placed in either tribe Tordylieae subtribe Tordyliinae (i.e., *A. oncosepala* Hand.-Mazz.) or

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the *Sinodielsia* clade (i.e., *A. paeoniifolia* R. H. Shan & C. Q. Yuan and *A. sinensis* (Oliv.) Diels) (Downie et al., 1998, 2000a, 2000b, 2010; Plunkett & Downie, 1999; Xue et al., 2007; Zhou et al., 2008, 2009; Feng et al., 2009). Our concurrent study of *Angelica s.l.* phylogeny based on an expanded and corrected sampling of the group and using both ITS and cpDNA sequences identified a monophyletic *Angelica* group to comprise the *Angelica s.s.* clade (including *Czernaevia* and two species of *Ostericum*), *Archangelica*, *Coelopleurum*, *Glehnia* F. Schmidt ex Miq., a Littoral *Angelica* clade, a North American *Angelica* clade, and several other species (Liao et al., 2012, unpublished data). This same study also revealed the *Angelica s.s.* clade to comprise five infrageneric lineages and that the North American species of the *Angelica* group were polyphyletic. The complex phylogenetic relationships within the *Angelica* group suggested that a complicated phytogeographical process likely shaped its current distribution pattern.

The *Angelica* group is disjunctively distributed in all continents of the Northern Hemisphere, although its members are particularly concentrated in East Asia (Pimenov, 1968a, 1968b; Pan et al., 1991, 1994; Vasilèva & Pimenov, 1991; Qin et al., 1995; Liao et al., 2012). The climate of Asia has been significantly affected by the extent and height of the Himalayas–Tibetan Plateau. Although the uplift of this region began more than 50 Mya, recent uplift since the late Tertiary has resulted in significant impacts on the climate, ecosystems, and vegetation of East Asia (An et al., 2001; Qiang et al., 2001; Dettman et al., 2003; Fortelius et al., 2006; Harris, 2006; Wang et al., 2006; Eronen et al., 2009). The evolutionary processes affecting most Eurasian plants are inevitably linked to these uplift-driven climatic and environmental changes, especially for certain East Asia-centered floras such as the *Angelica* group (Patterson & Givnish, 2002; Wang et al., 2005).

To date, there have been several studies on the phylogeny and biogeography of Apiaceae subfamily Apioideae (e.g., Spalik et al., 2004, 2010; Spalik & Downie, 2007; Downie et al., 2010; Magee et al., 2010). However, due to a lack of fossil evidence, it has been difficult to reconcile their divergences with the geological history of the Holarctic. Using fossil pollen of basal apioids as calibration points, Spalik et al. (2010) estimated divergence times of the main lineages of Apioideae using a Bayesian approach (BEAST) based on ITS sequence data, and these times were largely congruent to those inferred using a strict molecular clock (Sang et al., 1994; Spalik & Downie, 2006). In the present study, we use ITS, nrDNA external transcribed spacer (ETS), and cpDNA (*rps16* intron, *rps16-trnK*, *rpl32-trnL*, *trnL-trnT*) sequences to explore the biogeographic history of the *An-*

gelica group, particularly focusing on its origination, diversification, and transcontinental dispersals.

1 Material and methods

1.1 Taxon sampling

The three datasets constructed in our concurrent investigation of *Angelica s.l.* phylogeny (Liao et al., 2012, unpublished data) were also considered, with some modification (see Table S1 for a list of all species, including taxonomic authorities). Dataset I (comprising 477 bp of aligned data) contained the ITS1 and ITS2 regions from 96 representatives (16 genera) of tribe Selineae and several closely related major lineages in subfamily Apioideae. *Aegopodium alpestre* Ledeb. (tribe Careae) and *Pimpinella candolleana* Wight & Arn. (tribe Pimpinelleae) were chosen as outgroups based on our previous higher-level investigations (Liao et al., 2012, unpublished data). This dataset was modified from that used previously by excluding distant lineages, such as *Pleurospermum franchetianum* Hemsl. (Pleurospermeae), *Notopterygium forbesii* H. Boissieu (*Physospermopsis* clade), *Conioselinum scopulorum* J. M. Coult. & Rose (*Conioselinum chinense* clade), *Arcuatopterus thalictrioideus* M. L. Sheh & R. H. Shan (*Arcuatopterus* clade), *Sium suave* Walt. (Oenantheae), and four species from tribe Scandiceae. Dataset II was the same as our concurrent paper (Liao et al., unpublished data) and comprised 43 species from the *Angelica* group plus three outgroups. This second dataset (comprising 4779 bp of aligned data) included sequences from the nrDNA ITS1–5.8S–ITS2 and ETS regions and the following cpDNA non-coding loci: *rps16* intron; *rps16-trnK*; *rpl32-trnL*; and *trnL-trnT*. Dataset III (at 2205 bp of aligned data) was similar in composition to that of dataset II, except with the addition of seven species of *Angelica* from North America. This third dataset, representing 50 species, was constructed using sequence data from only the ITS1, ITS2, *rps16* intron, and *trnL-trnT* regions. The trees obtained in datasets II and III were rooted with *Cnidium monnieri* (L.) Spreng., *Peucedanum harry-smithii* Fedde ex H. Wolff and *Peucedanum medicum* Dunn, based on results of analyses of dataset I. All datasets are available from TreeBASE (www.treebase.org, submission No. S11565).

1.2 Divergence dating and biogeographical analyses

The DNA sequences in each dataset were initially aligned using the default pairwise and multiple alignment parameters in CLUSTALX (Jeanmougin

et al., 1998), then rechecked and adjusted manually as necessary using MEGA 4.0 (Tamura et al., 2007). Gaps were positioned to minimize nucleotide mismatches and treated as missing data in the phylogenetic analyses. Uncorrected pairwise nucleotide differences were determined using PAUP* version 4.0b10 (Swofford, 2003).

The general time reversible model with gamma and invariant sites (GTR+I+G) was identified by MrModeltest version 2.2 (Nylander, 2004) as the best-fit model of nucleotide substitution for each nuclear and plastid DNA partition. Estimation of divergence times for each dataset was carried out using BEAST version 1.5.2 (Drummond & Rambaut, 2007), using two independent analyses. The BEAUTi interface was used to create an input file for BEAST, in which the GTR+I+G model was applied. An uncorrelated lognormal model was used to describe the relaxed clock (Drummond et al., 2006; Brown & Yang, 2010; Manen et al., 2010), and a pure birth branching process (Yule model) was chosen as a prior. For dataset I, the split between tribes Selineae and Tordylieae was set to 31.0 Mya (95% highest probability density (HPD) of 41.0–22.5 Mya), in accordance with Spalik et al. (2010), and 40 million generations of the Markov chain Monte Carlo (MCMC) chains were run, with sampling occurring every 1000 generations. The first 8000 trees were discarded as burn-in, and the remaining 32 000 trees were summarized in the maximum clade credibility tree using TreeAnnotator version 1.4.8 (Drummond & Rambaut, 2007), with the posterior probability limit set to 0.5 and summarizing mean node heights. Based on the results obtained from dataset I, the trees derived from datasets II and III were each rooted by the earliest split within the *Angelica* group, at 13.9 Mya (95% HPD = 18.9–8.7 Mya). Twenty million generations of the MCMC chains were run for each analysis, sampling every 1000 generations. From the collected samples, 20% were discarded as burn-in and the rest were summarized. All results were visualized using FigTree version 1.2.3 (Drummond & Rambaut, 2007) and the timescale used was taken from the latest international stratigraphic chart (<http://www.stratigraphy.org/column.php?id=Chart/Time%20Scale>).

To reconstruct the historical biogeography of the *Angelica* group, we applied three methods for inferring the ranges of all ancestral nodes of the phylogeny: S-DIVA (Statistical Dispersal–Vicariance Analysis, Nylander et al., 2008; Yu et al., 2010), RASP (Reconstruct Ancestral State in Phylogenies; <http://mnh.scu.edu.cn/soft/blog/RASP>) and LAGRANGE (Likelihood Analysis of Geographic Range Evolution, Ree et al., 2005; Ree & Smith, 2008). S-DIVA is a com-

plement to DIVA (Ronquist, 1997, 2001; Ronquist & Huelsenbeck, 2003; Yu et al., 2010) and uses a statistical dispersal–vicariance approach to statistically evaluate the alternative ancestral ranges at each node in a tree accounting for phylogenetic uncertainty. Bayesian approaches to ancestral state reconstruction have been applied widely to biogeographical studies (Olsson et al., 2006; Sanmartín et al., 2008). RASP extends the approach to a more generalized method for statistical analysis of biogeography based on phylogenies and distributional data. LAGRANGE is an implementation of the likelihood models for geographic range evolution on phylogenetic trees to infer rates of dispersal, local extinction and ancestral ranges (Ree et al., 2005; Ree & Smith, 2008).

Phylogenetic analysis of each of the three datasets was carried out under Bayesian methods, as implemented by MrBayes version 3.1.2 (Ronquist & Huelsenbeck, 2003). We used the resultant Bayesian trees (available at www.treebase.org, submission no. S11565) to carry out S-DIVA and RASP analyses. In the S-DIVA analysis, the number of ancestral areas was restricted to three. The rationale for such a constraint is that vicariance is a proximate consequence of dispersal and extant taxa used in our analyses rarely occur in more than three individual areas (Sanmartín, 2003; Calviño et al., 2008). The Bayesian analysis with RASP was run for 1 million generations using the model F81+G and the character states were saved every 100 generations. Ten simultaneous MCMC chains were run and the temperature was adjusted to 0.1 in order to keep an appropriate heat range for the 10 chains. The first 2000 states were discarded and ancestral distributions were calculated based on the remaining 8000 states. Parametric maximum likelihood estimation of geographical range evolution was carried out using LAGRANGE on the trees generated by BEAST. The reconstruction for each branch was restricted to a maximum of three areas. The connectivity among the areas was not constrained. We assumed a single dispersal rate and a single extinction rate across the areas and across the phylogeny, with their values estimated to maximize the likelihood of the biogeographical scenario. The following five unit areas were considered: a, East Palearctic (northeast Asia); b, east and central China; c, Sub-Himalayan Zone (the Tibetan Plateau and adjacent areas); d, central Asia and Europe; and e, North America.

The ancestral reconstruction of habitat elevations was mapped onto the Bayesian tree generated from dataset II using Mesquite version 2.71 (Maddison & Maddison, 2009). The optimality criterion selected was maximum parsimony and the following character states were treated as ordered: 0, < 1200 m; 1, 1200–2500 m;

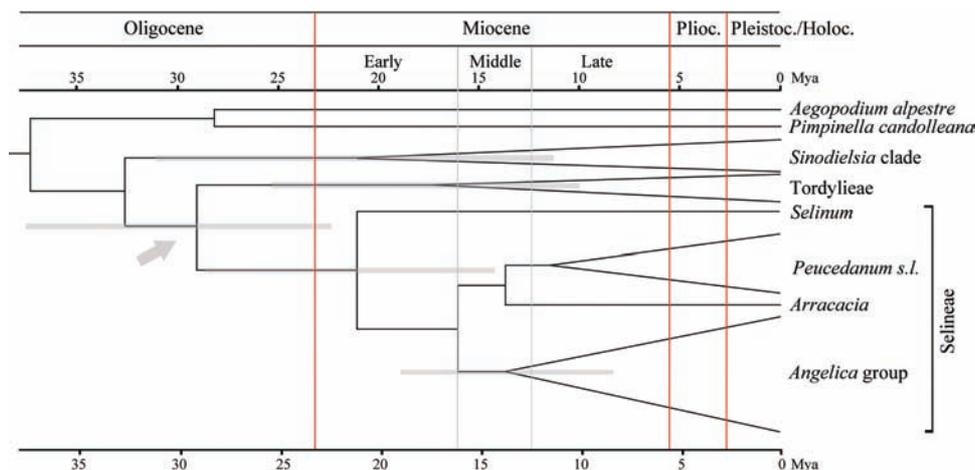


Fig. 1. Phylogenetic dating of the *Angelica* group based on a maximum clade credibility tree obtained from a BEAST analysis of dataset I under an uncorrelated lognormal molecular clock. Node bars reflect 95% highest posterior density of node heights. The node indicated by an arrow was set as 31.0 Mya (95% highest posterior density = 41.0–22.5 Mya), in accordance with Spalik et al. (2010). The names of the main tribes and clades refer to Downie et al. (2010), Zhou et al. (2008, 2009), and our unpublished work (Liao et al., 2012, unpublished data). The width of each clade is roughly approximate to the number of species examined in that clade. Holoc., Holocene; Plioc., Pliocene; Pleistoc., Pleistocene.

2, 2500–3500 m; and 3, 3500–4300 m. Distribution information was taken from Hiroe & Constance (1958), Tutin et al. (1968), Vasiléva & Pimenov (1991), Sheh et al. (2005), and the United States Department of Agriculture National Resources Conservation Service (<http://plants.usda.gov/index.html>).

2 Results

The results of the dating analysis of dataset I are presented in Fig. 1 and suggest that the initial split of the *Angelica* group occurred 13.9 Mya (95% HPD = 18.9–8.7 Mya). Figure 2 presents the results of divergence dating and ancestor-area reconstructions mapped onto the majority-rule consensus Bayesian tree derived from dataset II. Because some species were not sequenced for all loci examined in dataset II, we carried out ancestor-area reconstructions of datasets III and I as complements to the analysis of dataset II. These results are presented in Fig. 3: A and Fig. 3: B, respectively, with the overlapping and congruent topologies omitted. Confidence intervals of node ages were relatively large (Table 1); however, most lineage splits were estimated to have taken place after the Late Miocene. Pie charts at nodes indicate the relative frequencies of ancestral area optimizations generated by RASP. The biogeographical reconstructions by S-DIVA and LAGRANGE are similar to those inferred from RASP, therefore they are not mapped on Fig. 2 or Fig. 3, but are listed in Table 1. The Bayesian posterior probability values are also listed in Table 1. The most significant incongruence

between the results of LAGRANGE and RASP/S-DIVA occurred in node 6, a result of a minor topological difference between the BEAST and Bayesian method at this node.

Our results suggest a complex biogeographical history of the *Angelica* group and especially for the *Angelica s.s.* clade, as we had initially hypothesized. The optimal reconstructions favored that the ancestors of the *Angelica* group were originally present at low elevations in the East Palearctic (a) at 13.6 Mya (Fig. 2, node 1, a: 68.7%, elevation <1200 m). Over millions of subsequent years, a series of sympatric diversifications took place in this region. The initial split within the *Angelica s.s.* clade occurred in the eastern Palearctic during the middle Late Miocene (10.0–7.0 Mya). One descendant stayed there giving rise to Clade I (Fig. 2, node 5), and another descendant subsequently underwent further divergence to account for four other lineages (Clades II–V, Fig. 2). During the Late Pliocene and Pleistocene (approximately 3.6 Mya), accelerated diversifications broke out in the eastern Sub-Himalayan Zone (c). The reconstruction of ancestor habitat elevation suggested that all high-elevation species (>3500 m) occurred quite recently (<4 Mya) and were probably linked to the rapid uplift of the Tibetan Plateau since the late Pliocene. In addition, at least six dispersals to North America were inferred. As examples, the North American *Angelica* clade reached North America in the Late Miocene followed by an initial divergence at the end of the Late Miocene (Fig. 3: A, node 10); *Glehnia littoralis* F. Schmidt and *A. sylvestris* L. colonized there, respectively, at 4.0 and 1.5 Mya (Fig. 3: B, node 15; Fig. 3:

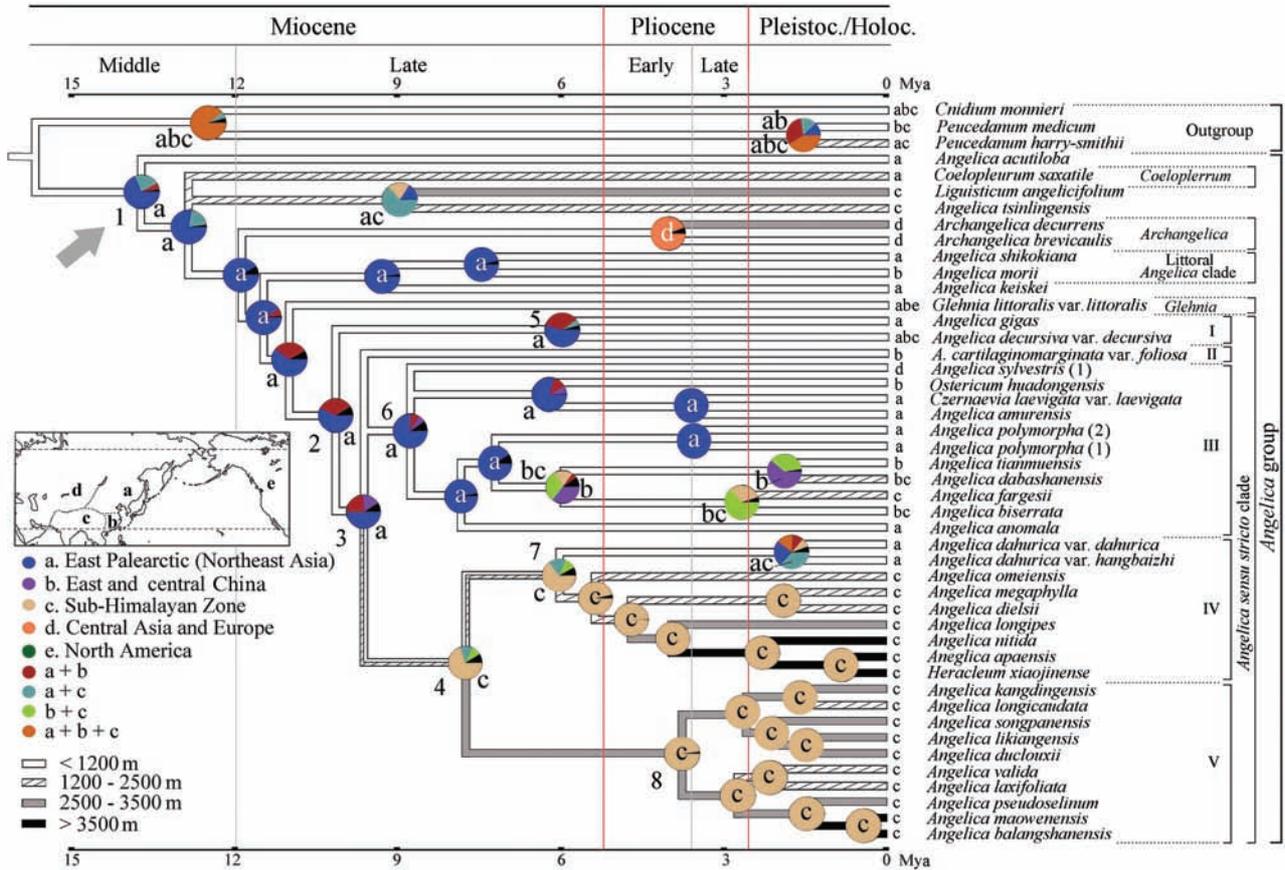


Fig. 2. Combined results of the divergence dating and biogeographical analyses of the *Angelica* group. The ancestor area-reconstruction is based on a Bayesian analysis of dataset II, with branch lengths constrained to reflect estimated ages, as inferred by BEAST. The node indicated by the arrow was set as 13.9 Mya (95% highest posterior density = 18.9–8.7 Mya) according to the results of dataset I. Pie charts at the nodes represent the relative frequencies of ancestral-area reconstructions using RASP; the current species distribution is shown at the terminals. The results of the ancestral habitat elevation reconstruction obtained using Mesquite are also mapped, with the legend indicating the four habitat elevation character states. The frequencies of ancestral-area reconstructions, obtained from RASP, S-DIVA and LAGRANGE analyses, 95% confidence intervals of age, and Bayesian posterior probability values are provided in Table 1. Roman numerals identify lineages within the *Angelica* s.s. clade. Holoc., Holocene; Pleistoc., Pleistocene.

A., node 12); and *A. genuflexa* Nutt. ex Torr. & A. Gray and the genus *Coelopleurum* arrived there no more than 4.3 and 1.2 Mya, respectively (Fig. 3: B, nodes 16 and 14). The origination of *Archangelica* occurred no more than 5.0 Mya, suggesting that its immigration into North America was also a recent event (Fig. 3: A, node 11).

3 Discussion

3.1 Utility of the relaxed clock for divergence dating

An unrooted model of phylogeny and a strict molecular clock model are two extremes of a continuum, but the real evolutionary process could hardly be strictly clocklike and should lie somewhere between these two extremes (Drummond et al., 2006). Drummond et al. (2006) suggested the relaxed-clock anal-

ysis was suitable to both clocklike and non-clocklike datasets, such as a those formed by combined nrDNA and cpDNA data (Zhang et al., 2010). According to Sang et al. (1994), the ITS substitution rate obtained by a study of *Dendroseris* D. Don (Asteraceae) was estimated at 0.39%–0.79% Myr⁻¹. Spalik et al. (2010) revealed that the divergence of the *Sium* L./*Berula* W. D. J. Koch (Apiaceae) alliance was dated at 18.4 Mya, which was within the range based on standard ITS substitution rates (21.7–13.9 Mya). The split between the “*Oreomyrrhis*” clade and the North American species of *Chaerophyllum* L. (Apiaceae) took place at 5.3 Mya with the relaxed-clock analysis, which was close to the strict-clock result using a rate of 0.39% (4.5 Mya). In an analysis of dataset I using a strict-clock model, the initial split within the *Angelica* group was estimated at 9.9 Mya (95% HPD = 12.5–7.5 Mya) using a rate of 0.39%. When we used the relaxed-clock model calibrated with

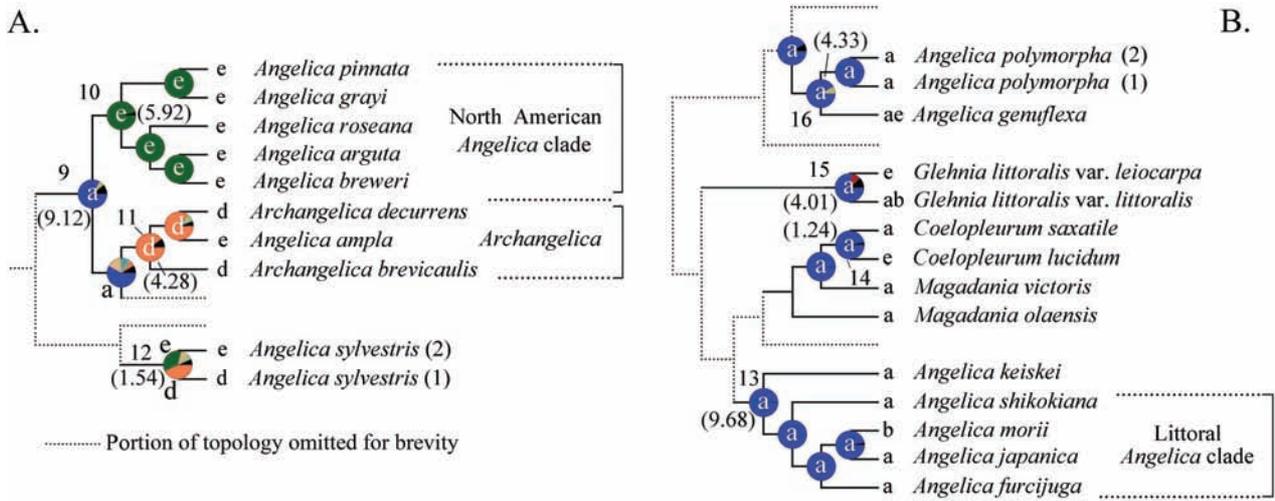


Fig. 3. Results of the divergence dating and biogeographical analyses of datasets III (A) and I (B), with portions of the reconstructions identical to those in Fig. 2 omitted for brevity. The numbers in parentheses represent the node ages (Mya), as estimated by BEAST. Pie charts at the nodes represent the relative frequencies of ancestral-area reconstructions using RASP; the current species distribution is shown at the terminals. The frequencies of ancestral-area reconstructions, obtained from RASP, S-DIVA and LAGRANGE analyses, 95% confidence intervals of age, and Bayesian posterior probability values are provided in Table 1. a, East Palearctic (northeast Asia); b, East and central China; d, Central Asia and Europe; e, North America.

Table 1 Relative frequencies of ancestral-area reconstructions, as obtained from RASP, S-DIVA and LAGRANGE analyses, estimated age, 95% highest probability density (HPD) and Bayesian posterior probability (PP) values of nodes in Fig. 2 and Fig. 3. The proportions less than 10% are not presented.

Node	RASP	S-DIVA	LAGRANGE	Age (Mya)	95% HPD (Mya)	PP
1	a. 68.7% ac. 22.6%	a. 100%	a. 85.4%	13.6	15.6–11.7	1.00
2	a. 56.9% ab. 33.7%	a. 100%	a. 74.1% ab. 10.3%	10.2	12.5–7.8	1.00
3	a. 49.7% ab. 24.1% b. 17.6%	abc. 44.8% ac. 36.7%	a. 48.9% ac. 15.5% ab. 14.0% abc. 11.5%	9.7	11.9–7.4	0.91
4	c. 70.3% ac. 11.8%	c. 50.2% ac. 49.8%	ac. 56.7% c. 28.6%	7.7	9.8–5.5	1.00
5	a. 54.2% ab. 36.0%	a. 100%	a. 73.8% ab. 11.2%	6.1	9.6–2.5	1.00
6	a. 75.4%	ad. 33.3% ae. 33.3% ade. 33.3%	a. 35.7% ab. 11.6% b. 10.5%	8.7	11.1–6.4	0.81
7	c. 64.7% ac. 16.7%	c. 50.2% ac. 49.8%	ac. 51.9% c. 26.9% abc. 13.3%	5.9	7.8–4.2	1.00
8	c. 98.0%	c. 100%	c. 99.6%	3.7	5.6–2.1	1.00
9	a. 83.0%	ade. 45.4% ae. 27.3% ace. 27.3%	ae. 46.7% ade. 18.8% ace. 10.5%	9.1	–	0.67
10	e. 95.6%	e. 100%	e. 97.6%	5.9	9.1–2.9	1.00
11	d. 89.6%	d. 100%	de. 80.7% d. 17.6%	4.3	7.4–1.5	1.00
12	d. 42.9% e. 36.1%	de. 100%	de. 87.9%	1.5	3.3–0.3	1.00
13	a. 99.8%	a. 100%	a. 79.9%	9.6	–	1.00
14	a. 97.1%	ae. 100%	ae. 100%	1.2	2.9–0.2	1.00
15	a. 77.6% ab. 10.4%	ae. 50% abe. 50%	abe. 54.1% ae. 41.5%	4.0	8.8–1.2	1.00
16	a. 91.8%	a. 100%	a. 87.4% ac. 12.4%	4.3	7.4–1.7	0.37

a, East Palearctic (northeast Asia); b, East and central China; c, Sub-Himalayan Zone (the Tibetan Plateau and adjacent areas); d, central Asia and Europe; e, North America. —, node HPD not provided by BEAST.

the split of Selineae and Tordylieae at 31.0 Mya (95% HPD = 41.0–22.5 Mya; Spalik et al., 2010), the age of the crown node of the *Angelica* group was estimated at 13.9 Mya (95% HPD = 18.9–8.7 Mya), a value close to the strict-clock model. Moreover, the ages of the major nodes estimated from the three datasets were roughly consistent with each other. For instance, the estimated ages of node 2 were 11.5, 10.2, and 10.8 Mya; those of node 3 were 10.5, 9.7, and 10.0 Mya; and those of node 4 were 8.7, 7.7, and 8.4 Mya. The ages of the split between the two populations of *A. sylvestris* (node 12) estimated by datasets I and III were 1.92 and 1.54 Mya, respectively. The relaxed-clock model therefore is suitable for combined sequence data.

3.2 Biogeography of the *Angelica* group

Our analyses revealed that at least 60% of the dispersal events within the *Angelica* group occurred in the East Palearctic, implying that this region may be a “cradle for diversification” (Nylander et al., 2008) of these taxa. The climate and vegetation of East Asia have been deeply influenced by the Himalayan orogenesis. Although the uplift of the Tibetan Plateau began approximately 50 Mya, further significant increases in altitude are thought to have occurred over the past 10 Myr. For instance, two main uplifts took place between 10.0 and 7.0 Mya and after 3.6 Mya, respectively (Chung et al., 1998; Ma et al., 1998; Liu et al., 2009; Liu et al., 2010). Palaeogeographic and palaeoclimatic evidence indicated that these two tectonic events constituted a significant factor leading to the development of Asian monsoons and major climatic changes in central and eastern Asia, as well as influencing local environmental patterns (An et al., 2001; Qiang et al., 2001; Dettman et al., 2003; Harris, 2006; Eronen et al., 2009). Thus, the diversification of the *Angelica* group, which is concentrated in East Asia, has been inevitably affected by the climatic and environmental changes driven by the multistage uplift of the Himalayas and Tibetan Plateau since the late Middle Miocene.

In our study, the ancestors of the *Angelica* group originated and underwent initial diversification in the East Palearctic during the climate cooling (approximately 15.0–10.0 Mya) following the Middle Miocene Climatic Optimum. Generally, the Middle Miocene is regarded as a climatic optimal period in East Asia; this period was warmer and more stable than today, as inferred from macrofossil and pollen evidence (Kong, 2000; Tao, 2000; Harris, 2006; Momohara, 2008; Liu et al., 2009). However, the global temperature has decreased since the end of the Middle Miocene and this has been detrimental to thermophilic floras, forcing them to move southward or become extinct. In contrast, these

climatic changes would have also favored the evolution of cold-adapted taxa (Kong, 2000; Tao, 2000; Xiang & Soltis, 2001; Antonelli et al., 2010). Most extant species in the *Angelica* group favor cold and humid conditions, implying that their common ancestors were likely psychrophilic or cold-tolerant. This adaptation to cold provided the opportunity for their prosperity during these climatic changes in East Asia. It is noteworthy that until 10.0 Mya the average elevation of the Tibetan Plateau did not achieve the height necessary to form geographical and ecological barriers between the Sub-Himalayan and East Palearctic regions (average elevation possibly <1500 m; Ma et al., 1998).

The initial diversification within the *Angelica s.s.* clade occurred in the East Palearctic during the middle Late Miocene (10.0–7.0 Mya). Recent research has revealed that this period was a crucial time in the development of the modern East Asian landscape and vegetation. Extensive diversifications during this time period, as examples, have been reported for *Calochortus* Pursh (Liliaceae *s.l.*), Liliaceae *s.s.*, and *Rheum* L. (Polygonaceae) (Patterson & Givnish, 2002; Wang et al., 2005; Liu et al., 2009). Palaeogeographical and palaeoenvironmental evidence suggested that the Tibetan Plateau possibly achieved sufficient elevation to block the penetration of moisture from the Indian and South Pacific Oceans into western China, resulting in the onset of the Indian and East Asian monsoons, a rapid decrease in temperature, and an increasing aridity of the Asian interior, as well as concomitant vegetation changes (Ma et al., 1998; Garzzone et al., 2000; Hoorn et al., 2000; An et al., 2001; Dettman et al., 2003; Clark et al., 2005; Fortelius et al., 2006; Wang et al., 2006; Zheng et al., 2006; Eronen et al., 2009; Liu et al., 2010). During the Late Miocene, the origination of the *Angelica s.s.* clade took place, followed by radiation into five infrageneric lineages in the East Palearctic, East China, and southwest China. Moreover, due to the great geographical and ecological changes occurring in the Sub-Himalayan Zone, the vegetation of this region changed significantly and became different from that of the eastern Palearctic during the middle to the end of the Late Miocene (Hoorn et al., 2000); these changes would account for the occurrence of the Tibetan Plateau lineage (Clades IV and V, Fig. 2, node 4). Concurrently, rapid diversifications within the *Angelica s.s.* clade occurred in the lower regions of the East Palearctic. It is notable that until the Latest Miocene (about 6.2–5.0 Mya) central Asia and the Mongolian Plateau were not as arid as they are today. These regions, therefore, could act as migratory routes for plant exchanges between the East Palearctic and eastern Europe (Guo et al., 2004). Prior to the Latest Miocene, one descendant dispersed westward from the

East Palearctic to central Asia (9.0–8.0 Mya), a dispersal crucial to the origination of the current central Asian and European species of the *Angelica s.s.* clade, such as *A. sylvestris*.

The rapid diversification within the *Angelica s.s.* clade (17 divergence events) since the Late Pliocene (3.6 Mya) coincided roughly with the recent enhanced uplift of the Himalayas–Tibetan Plateau (Hengduan Movement). This increased uplift directly resulted in weaker summer monsoons and stronger winter monsoons across eastern Asia and continuous aridification in central Asia, all of which foreshadowed the Quaternary glacial epoch and changes of the floras (Chen, 1992, 1996; Ma et al., 1998; An et al., 2001; Guo et al., 2004; Zhou & Momohara, 2005; Zheng et al., 2006; Momohara, 2008; Liu et al., 2010). During the Quaternary, the eastern part of the Sub-Himalayan Zone supplied complicated climatic and orographic conditions for organisms. These conditions promoted range fragmentation and population isolation, facilitating accelerated speciation (Patterson & Givnish, 2002; Zhang et al., 2010; Jacques et al., 2011; Qiu et al., 2011). Indeed, the Hengduan Mountains are widely regarded as having provided refugia during the Quaternary; the region is also considered a current biodiversity hotspot (Hao, 1997; Sun, 2002; Sun & Li, 2003). The two Himalayan lineages (Clades IV and V, Fig. 2) rapidly radiated in the eastern Sub-Himalayan Zone (12 diversifications), exhibiting asynchronous diversifications since the Late Pliocene. The significant uplift of this region also brought about cool and humid alpine habitats suitable for cold-tolerant plants. The reconstruction of habitat elevation highlighted an altitudinal species diversity gradient; for example, all high-altitude species of *Angelica* (>3500 m) occurred quite recently. This implies that the evolutionary processes affecting these Himalayan lineages were probably acting in concert with the recent uplift of the region and differential responses to speciation (Fig. 2, nodes 7 and 8; Vetaas & Grytnes, 2002; Zhang & Sun, 2008). *Angelica apaensis* R. H. Shan & C. Q. Yuan and *A. nitida* H. Wolff, growing at more than 3800 m, occur at the highest elevations. We believe that their corky mericarps, easily distinguished from those of other species in the *Angelica s.s.* clade, is an adaptation to prevent freezing. At such high elevations, polyploidization is considered an important aspect of diversification, such as that shown by *Bupleurum* L. and *Heracleum* L. (Wang et al., 2008; Deng et al., 2009). However, few tetraploids have been found in *Angelica*, suggesting that this mechanism is not a key factor for speciation within the group (Pan et al., 1991; Vasilèva & Pimenov, 1991; Zhang et al., 2005).

In North America, at least six independent dispersal events within the *Angelica* group have been inferred, all of which were estimated later than 10.0 Mya. The first of these colonizations was the North American *Angelica* clade that reached North America across the Bering Land Bridge during the middle Late Miocene (Fig. 3: A, nodes 9 and 10); it then radiated in this new geographic region since the Late Miocene (Fig. 3: A, node 10). During the period from 11.5–8.0 Mya, the sea level was much lower than it is today, a condition favorable for the long-distance dispersal of organisms (Renner et al., 2001). The Bering Strait contributed greatly to the exchanges of flora and fauna between eastern Asia and North America, such as the dispersals of *Ilex* L. (Aquifoliaceae) and Felidae from East Asia to North America and the reverse migration of “*Hipparion*” horses (Garcés et al., 1997; Johnson et al., 2006; Manen et al., 2010). The other five intercontinental dispersals occurred more recently and probably were related to climatic shifts during the Pliocene and Quaternary. During the glacial periods, sea levels fell by 85–140 m (Millien-Parra & Jaeger, 1999), providing ample opportunities for intercontinental exchanges across landbridges. The immigration of the “true *Angelica*” (i.e., the *Angelica s.s.* clade) into North America likely involved two pathways: *A. genuflexa* reached the western coastal areas through the Bering/Aleutian Land Bridge no more than 4.3 Mya (Fig. 3: B, node 16), whereas *A. sylvestris* reached the eastern part of North America from across the North Atlantic at 1.5 Mya (Fig. 3: A, node 12). At present, *A. sylvestris* occurs in some North Atlantic islands, such as the British Isles, Ireland, and Greenland, which indicates that those islands could act as a trans-Atlantic pathway for organism exchange during sea level lowering during the Ice Age. *Glehnia littoralis*, which is now distributed in the sandy beaches of eastern Asia and western North America, immigrated to North America at 4.0 Mya (Fig. 3: B, node 15), also possibly by island hopping. Another trans-Pacific event is demonstrated by *Coelopleurum lucidum* Fernald, occurring at 1.2 Mya (Fig. 3: B, node 14) to reach Alaska. This time point implies that this dispersal from northeast Asia to North America probably involved the Quaternary Bering Strait. Although the biogeography of *Archangelica* is still ambiguous because of limited sampling, the genus was revealed as a young group that originated no earlier than the Pliocene. In this sense, the colonization of *Archangelica* in North America must be recent. Considering that *Archangelica* is concentrated in central Asia and East Europe but absent in East Asia at present (Pimenov, 1968b; Tutin et al., 1968), island hopping through the North Atlantic most likely explains the intercontinental dispersal of these taxa.

In summary, the evolutionary history of the *Angelica* group is congruent with the vegetation substitutions resulting from climatic and environmental changes in the eastern Palaeartic since the Middle Miocene. In particular, the divergence of the *Angelica s.s.* clade is closely linked to phases of the Himalayas–Tibetan Plateau uplift. Although it is unclear whether eastern China, Japan, and other coastal regions were seriously affected by Quaternary glaciations, the eastern Tibetan Plateau replaced the eastern Palaeartic in becoming the diversity center of the *Angelica s.s.* clade during the Pliocene and Pleistocene. These conclusions are in stark contrast to hypotheses suggesting either Hengduan Mountains or East Asia–North America origins. This study also suggests that the current distributional disjunction was attributed to complex historical patterns, involving the trans-Pacific and trans-Atlantic pathways in the Late Tertiary and Quaternary. We provide independent evidence supporting the congruence between the multistage uplift of Himalayas–Tibetan Plateau and the diversification of the East Asian modern flora.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1 Taxa and GenBank accessions numbers for the various loci considered in the three datasets examined in this study, together with voucher specimen information or place of original publication if sequence data were published previously. —, region was not sequenced for that taxon.

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