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ORIGINAL ARTICLE

Amphitropic amphiantarctic disjunctions in Apiaceae subfamily Apioideae

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ABSTRACT

Aim Four genera of the plant family Apiaceae subfamily Apioideae – *Apium*, *Chaerophyllum*, *Daucus* and *Lilaeopsis* – are characterized by amphitropic and amphiantarctic distribution patterns, and in Australasia the subfamily is also represented by the tribe Aciphylleae. We infer the molecular ages of achieving amphitropic distribution for these lineages, reconstruct the biogeographical histories of *Apium*, *Chaerophyllum*, *Daucus* and *Lilaeopsis*, and identify the sister group of Aciphylleae.

Location Worldwide, with an emphasis on South America and Australasia.

Methods Divergence times were estimated employing a Bayesian approach (BEAST) with fossil pollen of basal apioids as calibration points and using a data set of nuclear ribosomal DNA internal transcribed spacer (nrDNA ITS) sequences from 284 accessions of Apioideae. Additionally, maximum-likelihood analyses were performed for data subsets comprising *Apium*, *Daucus* and *Lilaeopsis*. For *Chaerophyllum*, maximum-likelihood and BEAST analyses were carried out using combined chloroplast DNA and ITS data. Biogeographical scenarios were inferred using DIVA and LAGRANGE.

Results The sister group to Aciphylleae is the Sino-Himalayan *Acronema* clade and the divergence between these two lineages is dated at 34.8 Ma, whereas the radiation of Aciphylleae started 11.0 Ma. A Northern Hemispheric origin was inferred for *Apium*, *Chaerophyllum* and *Daucus*, whereas *Lilaeopsis* probably originated in South America following a dispersal of its ancestor from North America. *Chaerophyllum*, *Daucus* and *Lilaeopsis* dispersed to the Southern Hemisphere at 5.3, 7.0 and 27.9 Ma, respectively. For *Apium*, two dispersals from Europe were inferred: to South America at 6.3 Ma, and to southern Africa at 3.9 Ma. The taxa migrated along the land masses of North and South America (*Daucus*, *Lilaeopsis*) and Africa (*Apium*) or by direct transoceanic dispersals through the Atlantic (*Apium*) or the Pacific (*Chaerophyllum*). Within the Southern Hemisphere they dispersed both westwards (*Apium*, *Daucus*, *Lilaeopsis*) and eastwards (*Chaerophyllum*, *Lilaeopsis*). For *Chaerophyllum* and *Lilaeopsis*, subsequent dispersal events to the Northern Hemisphere were also inferred.

Main conclusions Similar timing, contrasted with the diversity of migration routes, suggests that the dispersal events of these umbellifer taxa (and many other amphitropic amphiantarctic genera) were facilitated by favourable ecological conditions in the Southern Hemisphere (climatic cooling of the late Palaeogene/early Neogene) rather than by increased dispersal opportunities.

Keywords

Aciphylleae, amphitropic amphiantarctic disjunctions, Apiaceae, *Apium*, calibration, *Chaerophyllum, Daucus, Lilaeopsis,* phylogeny, rDNA ITS.

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INTRODUCTION

Amphitropic (bipolar) distribution patterns are relatively common among diverse groups of temperate-zone organisms, particularly in land masses that extend in geographical latitude, i.e. Africa and North/South America (Raven, 1963). However, many taxa exhibit more complex distributions, including transoceanic disjunctions between Northern and Southern Hemispheres and within the Southern Hemisphere. Such amphitropic and amphiantarctic patterns have been explained by long-distance dispersal (e.g. Raven, 1963, and references therein) or, more commonly, by vicariance resulting from continental drift (for recent examples see Schuettpelz *et al.*, 2002; Schuettpelz & Hoot, 2004). For some time, vicariance biogeography has dominated the field; however, biogeographical studies using molecular phylogenies have suggested that many transoceanic disjunctions, particularly those of plant species, are better explained by long-distance dispersal than by vicariance (Sanmartín *et al.*, 2001; Sanmartín & Ronquist, 2004). Moreover, when examined using dated phylogenies, many of those presumed cases of ancient vicariance are actually relatively recent (e.g. Yuan *et al.*, 2005). Consequently, long-distance transoceanic dispersal has been reinstated as a major factor shaping the distribution of organisms (de Queiroz, 2005). In the Southern Hemisphere, the similarities of moss, liverwort, lichen and pteridophyte floras exhibit a stronger correlation with wind connectivity than with geographical proximities, supporting the hypothesis of anisotropic long-distance dispersal by wind (Muñoz *et al.*, 2004).

Amphitropic amphiantarctic disjunction patterns have been investigated with molecular data in *Euphrasia* (Gussarova *et al.*, 2008), *Rorippa* (Bleeker *et al.*, 2002a), *Plantago sensu lato* (Rønsted *et al.*, 2002; Hoggard *et al.*, 2003), *Lepidium* (Mummenhoff *et al.*, 2001), and other genera. Although unequivocal biogeographical reconstructions and molecular dating are not available for all these genera, they follow a common pattern. First, although several of these genera are much diversified in the Southern Hemisphere, they originated in the north. Second, the molecular ages of achieving bipolarity and of radiation in the Southern Hemisphere are all relatively recent, therefore rejecting a vicariance hypothesis in favour of long-distance dispersal.

In umbellifers, amphitropic disjunctions are relatively common: 11 genera are shared between North and South America, and in Africa 22 genera occur both in the northern and sub-Saharan portions of the continent (Plunkett *et al.*, in press). In contrast, transoceanic disjunctions between Northern and Southern Hemispheres and within the Southern Hemisphere are relatively rare. Only four apioid umbellifer lineages exhibit amphitropic amphiantarctic disjunction patterns [*Apium*, *Chaerophyllum* (including *Oreomyrrhis*), *Daucus* and *Lilaeopsis*]. In the Southern Hemisphere, these genera occur in both South America and Australasia; *Apium* is also found in southern Africa. In Australasia, apioid umbellifers are also represented by a fifth lineage, the endemic tribe Aciphylleae.

The members of tribe Aciphylleae (*Aciphylla*, *Anisotome*, *Gingidia*, *Lignocarpa* and *Scandia*) constitute a morphologically distinct monophyletic group that does not have any close relatives among extant umbellifers; in some molecular analyses, this clade is a sister group to the western Eurasian tribe Smyrnieae (Downie *et al.*, 2000b), and its isolated taxonomic position suggests an ancient split. The remaining four lineages each constitute genera recognized on the basis of the morphological similarity of their included members, suggesting relatively recent divergences. The genus *Chaerophyllum*, as traditionally circumscribed, occurs in Europe, north-western Africa and western Asia, extends to the Himalayas, and has two disjunct species in North America (Schischkin, 1950; Mukherjee & Constance, 1993; Spalik & Downie, 2001), whereas its congeners previously classified in *Oreomyrrhis* are found in Central and South America, Australia, New Zealand and New Guinea, reaching northwards to Taiwan (Mathias & Constance, 1955; Chung *et al.*, 2005; Chung, 2007). A similar disjunction pattern is exhibited by *Daucus*. The endemism centre of *Daucus* is in the Mediterranean, with several species occurring in North America, South America and Australia (Sáenz Laín, 1981). These non-Old World species are members of the same clade, suggesting that a single dispersal from the Mediterranean may have been involved (Spalik & Downie, 2007). Molecular studies of the European members of *Apium* have revealed that the nomenclatural type of the genus, *A. graveolens*, does not have any close relatives in Europe, and that its former congeners should be placed in the restituted genus *Helosciadium* (Hardway *et al.*, 2004; Spalik *et al.*, 2009). However, as revealed by our preliminary analyses, *A. graveolens* is closely related to its putative congeners from the Southern Hemisphere. In the Southern Hemisphere, *Apium* is widely distributed in temperate South America (Johow, 1896; Maticorena & Quezada, 1985; Martinez, 1999), South Africa (van Wyk & Tilney, 2004), and Australasia (Short, 1979; Gardner, 2000). Contrary to the genera *Apium*, *Chaerophyllum* and *Daucus*, which most probably originated in the Old World, the genus *Lilaeopsis* is nested within the North American Endemics clade of tribe Oenantheae (Hardway *et al.*, 2004; Downie *et al.*, 2008). *Lilaeopsis* occurs in North and South America, Australasia, Madagascar and Mauritius (Affolter, 1985; Petersen & Affolter, 1999).

The aim of this paper is to investigate the origins of the amphitropic amphiantarctic disjunction patterns evident in the angiosperm family Apiaceae subfamily Apioideae. We estimate the molecular age of achieving amphitropic distribution for *Apium*, *Chaerophyllum*, *Daucus*, *Lilaeopsis* and tribe Aciphylleae using a nuclear ribosomal DNA internal transcribed spacer (nrDNA ITS) sequence phylogeny. To calibrate the tree, we use pollen data from the French Palaeocene and Eocene pertaining to *Bupleurum* and members of tribe Pleurospermeae: *Pleurospermum*, *Physospermum* and *Trachydium* (Gruas-Cavagnetto & Cerceau-Larrival, 1983/1984). We also infer biogeographical histories of *Apium*, *Chaerophyllum*, *Daucus* and *Lilaeopsis*.

MATERIALS AND METHODS

Taxon sampling

In total, 284 accessions representing nearly all major lineages of Apiaceae subfamily Apioideae were examined for nuclear ribosomal DNA internal transcribed spacer sequence variation; 86 accessions were sequenced specifically for this study (see Appendix S1 in Supporting Information for a list of all study species). For *Chaerophyllum*, *Daucus* and *Lilaeopsis*, we used data from recent extensive studies of these groups (Chung *et al.*, 2005; Spalik & Downie, 2007; Bone *et al.*, unpublished data). The genus *Apium* was also extensively sampled and included 26 accessions from Europe (*A. graveolens*), southern Africa (*A. prostratum*), South America (*A. australe*, *A. chilense*, *A. commersonii*, *A. insulare*, *A. panul*, *A. sellowianum*), Juan Fernández Islands (*A. fernandezianum*), and Australia and New Zealand (*A. prostratum*). We also included members of the South American genus *Niphogeton* that were once classified in *Apium*. In preliminary analyses, the Australasian clade Aciphylleae was a sister group to the *Acronema* clade (the latter comprising mostly Sino-Himalayan endemic species), so we increased sampling of the latter to include other taxa from this region. Because the molecular tree was calibrated with fossil pollen of Pleurospermeae, we added several accessions of some of its included genera: *Aulacospermum*, *Pleurospermum* and *Trachydium*. The tree was rooted with representatives of *Pleurospermopsis* and *Chamaesium* that constitute two early off-shoots of the apioid tree subsequent to the branching of *Bupleurum* (Downie *et al.*, in press). These taxa mark the lower limit of the phylogenetic utility of the ITS region because they are the most distant umbellifer sequences that can be unambiguously aligned with the crown apioids.

DNA extraction, amplification and sequencing

Total genomic DNA was isolated from *c.* 20 mg dried leaf tissue using a DNeasy Plant Mini Kit (Qiagen, Valencia, CA, USA). The DNA samples were amplified by polymerase chain reaction (PCR) using primers ITS4 and ITS5 (White *et al.*, 1990) or N-nc18S10 and C26A (Wen & Zimmer, 1996). For some accessions, the ITS1 and ITS2 regions were each amplified separately using the following pairs of primers: 18S-ITS1-F and 5.8S-ITS1-R for ITS1, and ITS-3N and C26A for ITS2 (Spalik & Downie, 2006). Details of the PCR amplifications are provided by Downie *et al.* (2000a). Each PCR product was electrophoresed in a 1% agarose gel, stained with ethidium bromide, then excised and eluted using a QIAquick Gel Extraction Kit (Qiagen). No obvious polymorphism (multiple bands from a single PCR product) was observed. Cycle sequencing reactions were performed using the purified PCR product, AmpliTaq DNA polymerase (Roche Molecular Systems, Alameda, CA, USA), and fluorescent Big Dye terminators (Applied Biosystems, Foster City, CA, USA). The products were resolved by electrophoresis using an ABI 377A automated DNA sequencer (Applied Biosystems). Simultaneous consideration of both DNA strands permitted unambiguous base determination. The sequences were assembled and edited using SeqMan II ver. 4.0 (DNASTAR, Madison, WI, USA). All newly obtained ITS sequences have been deposited in GenBank (Appendix S1).

Sequence, phylogenetic and biogeographical analyses

The DNA sequences were aligned using Clustal X ver. 2.0 (Larkin *et al.*, 2007), with default parameters for gap penalty and extension. The alignment was then edited where necessary using Mesquite ver. 2.5 (Maddison & Maddison, 2008). Because missing data artificially increase branch lengths, positions containing alignment gaps and the 5.8S rDNA region that was missing in its entirety for many accessions from GenBank were excluded from the distance-based analyses. Phylogenetic analyses included Bayesian inference using MrBayes ver. 3.1 (Ronquist & Huelsenbeck, 2003) and maximum parsimony (MP), maximum likelihood (ML) and neighbour-joining (NJ) methods implemented using paup* ver. 4.0b10 (Swofford, 1998). Substitution models for the ML and Bayesian analyses were selected using the program Modeltest ver. 3.6 (Posada & Crandall, 1998) and the Akaike information criterion (AIC; Akaike, 1974). Bayesian analyses were carried out for 10,000,000 generations with four Monte Carlo Markov chains (MCMC) initiated and a sampling frequency of 100 generations. The initial 30,000 saved trees were discarded and the consensus and posterior probabilities (PP) of particular clades were calculated based on the remaining trees. MP analyses were carried out with gap states treated as missing data, characters unordered, and all character transformations equally weighted. Neighbour-joining analyses were performed using several substitution models available in paup*, including Jukes-Cantor, Kimura 2-parameter, Kimura 3-parameter and general time-reversible (GTR).

The results of the phylogenetic analyses were used to impose topological constraints on molecular dating. To achieve a proper rooting, all accessions but *Physospermopsis sikkimensis* were constrained to form a monophyletic group. Additionally, all sequences that were placed in preliminary phylogenetic analyses in the branch of Pleurospermeae were constrained to form a clade. Estimation of divergence times was performed using beast ver. 1.5.3 (Drummond & Rambaut, 2007). We assumed that substitution rates evolved under the uncorrelated lognormal (UCLN) model (Drummond *et al.*, 2006) and the GTR + I + G model for nucleotide substitution. For the distribution of divergence times, a pure birth branching process (Yule model) was chosen as a prior. As alignment gaps pose difficulty for likelihood estimation (Yang, 2006, pp. 107–108), we removed most of them from the analysis, retaining only some indels that were autapomorphic or occurred at outer branches. We ran two independent Markov chains, each for 300,000,000 generations, initiated with a random starting tree, and sampled every 10,000 generations. From collected samples, 25% were eliminated (treated as burn-in). All log and tree files from independent runs were combined using LogCombiner ver. 1.5.3 (Drummond & Rambaut, 2007).

Two calibration points were used, and both were constrained to a broad lognormal distribution in order to take into account the palaeontological uncertainty (Table 1). On the root of the tree, the lognormal prior was placed with a lower bound (offset) of 55.8 million years ago (Ma) based on the earliest *Bupleurum* pollen record (Gruas-Cavagnetto & Cerceau-Larrival, 1983/1984). The ITS sequence of *Bupleurum* was not included in the analysis because it cannot be unambiguously aligned with those of the core Apioideae; however, the genus constitutes a sister group to those apioids considered in the study (Calviño *et al.*, 2006). An upper bound of distribution (95% quantile) was constrained to 84 Ma, corresponding to the divergence between Apiaceae and Araliaceae (Bremer *et al.*, 2004). For the second calibration point, the pollen record of *Trachydium*, dated to 33.9 Ma, served as a lower bound of a lognormal distribution (Gruas-Cavagnetto & Cerceau-Larrival, 1983/1984). However, because the identification of this pollen as actually pertaining to *Trachydium* is provisional, we considered it as representing tribe Pleurospermeae instead of the genus. As an upper bound, we used the estimated time of divergence between Apiaceae and Araliaceae. We used TreeAnnotator ver. 1.5.3 (Drummond & Rambaut, 2007) to summarize the information from a sample of trees onto a single target tree resulting from the analysis. The maximum clade credibility tree was chosen as a summary tree with mean values for node heights. This tree has the highest product of posterior probabilities on its n-2 internal nodes from all sampled trees. The tree was visualized using FigTree ver. 1.2.3 (Rambaut, 2009).

The removal of gap positions resulted in a decreased resolution of relationships at lower taxonomic levels that could introduce ambiguities in biogeographical reconstructions. Therefore, we performed additional analyses for subsets of the original matrix comprising *Apium*, *Daucus* and *Lilaeopsis* using all ITS1 and ITS2 positions. As the resolution in *Chaerophyllum* in the ITS tree was very low, instead of a subset of our data, we used a matrix from an earlier study comprising the complete nrDNA ITS region and chloroplast DNA (cpDNA) *atp*B–*rbc*L and *trn*S–*trn*G intergenic spacers sampled for 36 species of *Chaerophyllum* and an outgroup (Chung, 2007; TreeBASE study number S1571). These matrices were subject to ML analyses performed with jModelTest ver. 0.1.1 employing phyml and Consense (Guindon & Gascuel, 2003; Felsenstein, 2005; Posada, 2008), with AIC corrected for small sample size, and the results were summarized using a model-averaged majority-rule consensus tree. For *Chaerophyllum*, we also performed additional Bayesian analyses using beast. As the data comprised sequences from two genomes (nuclear and chloroplast) and three loci (ITS, *atp*B–*rbc*L, *trn*S–*trn*G), alternative partitioning strategies were compared using Bayes factors (cf. Brandley *et al.*, 2005). The marginal likelihoods were estimated as natural logarithms of harmonic means of the likelihood values of the MCMC samples obtained using MrBayes with 5,000,000 generations for unpartitioned and partitioned data sets. Values of Bayes factor equal to or greater than 10 were regarded as supporting the alternative hypothesis (Kass & Raftery, 1995). The best division was subsequently employed in molecular dating using beast. To infer absolute divergence times, two secondary calibration points were used representing the root of Scandicinae (*Chaerophyllum* and the outgroup) and root of *Chaerophyllum*; for each of these nodes a normal prior distribution was assumed, with the parameters estimated from the posterior distribution for this node from the analyses of the full data set. Two independent Markov chains, each for 20,000,000 generations, were initiated with a random starting tree, and sampled every 1000 generations; 25% of the trees were treated as burn-in.

Table 1 Temporal constraints used to estimate divergence times for core Apiaceae subfamily Apioideae in the beast analysis. The offset for the prior distribution for the root is based on the earliest record of the pollen of *Bupleurum*, a sister group to the apioid taxa considered in this study, whereas the offset for Pleurospermeae is based on the earliest record of the pollen attributed to *Trachydium*, a member of the tribe.

Taxon/node	Prior distribution	Offset (Ma)	95% quantile (Ma)	μ/σ*
Root	Lognormal	55.8	84	2.517/0.5
Pleurospermeae	Lognormal	33.9	84	3.092/0.5

*Mean and standard deviation of the lognormal distribution.

Biogeographical histories of the genera were inferred using parsimony-based dispersal–vicariance analysis (Ronquist, 1997) and ML inference of geographical range evolution (Ree & Smith, 2008). The dispersal–vicariance analysis was carried out using diva ver. 1.1 (Ronquist, 1996). The optimization was performed with the number of unit areas for each ancestral node restricted to two. The rationale for such a constraint is that with broadly defined unit areas, a dispersal results in immediate genetic isolation (by distance) of the daughter population from its parent. Moreover, none of the extant taxa occurs in more than two unit areas.

Parametric ML estimation of geographical range evolution was conducted using lagrange ver. 20091004 (Ree & Smith, 2008). The same unit areas as in diva were used and the reconstruction for each branch was restricted to a maximum of two areas. The connectivity among the areas was not constrained, allowing dispersal of taxa among them at any time from the root to the tips of the tree. 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 (Ree & Smith, 2008).

RESULTS

Phylogenetic analyses and dating of basal nodes

Upon the removal of identical ITS sequences, the final matrix included 268 terminals and 568 aligned positions, 159 of which comprised gaps or missing data that were subsequently excluded. Of the remaining positions, 30 were constant, 23 were autapomorphic and 356 were parsimony-informative. Modeltest selected the GTR + G + I model of nucleotide substitution as fitting these data best. All phylogenetic analyses using NJ, MP and Bayesian methods resulted in trees (not shown) comprising the same major branches representing hitherto identified monophyletic tribes and informal clades of subfamily Apioideae (Downie *et al.*, in press).

The maximum clade credibility tree resulting from the beast analysis had a similar topology to those trees obtained from the aforementioned phylogenetic analyses, and its outline is presented in Fig. 1. The differences among these trees included some minor rearrangements of their major clades and terminal branches. For instance, in the NJ trees, the *Conioselinum chinense* clade was sister to a branch comprising *Arcuatopterus* clade, Smyrnieae, Aciphylleae, *Acronema* clade and Scandiceae, whereas in the beast analyses it was sister to a much larger clade comprising most apioid umbellifers. The content of the clades is presented in Appendix S1. The basal node of the maximum clade credibility tree was estimated at 75.4 Ma, with 95% highest probability density (HPD) of node height between 60.9 and 94.2 Ma. As in previous analyses, tribe Pleurospermeae constituted the first-branching major clade of core Apioideae. This branch included several newly sequenced accessions from genera *Aulacospermum*, *Korshinskya* and *Trachydium* (Appendix S1); it diverged from the major evolutionary lineage of umbellifers *c.* 66.3 Ma (HPD 52.7–83.4) and subsequently radiated *c.* 45.5 Ma (HPD 38.1–53.8).

Divergence and sister group of Aciphylleae

The Australasian tribe Aciphylleae was placed as a sister group to the Sino-Himalayan *Acronema* clade that also comprised the

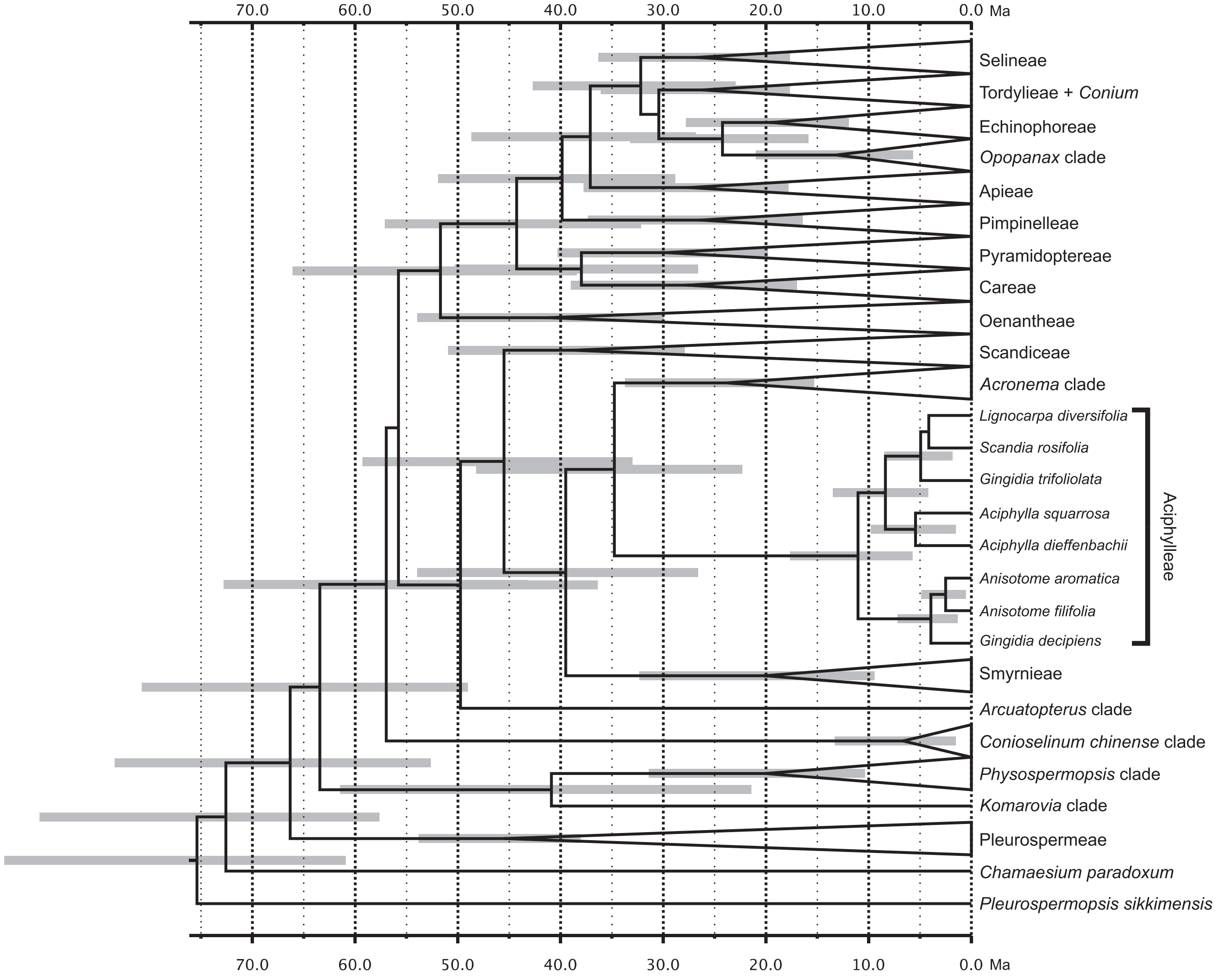

Figure 1 Dated phylogeny for core Apioideae based on a maximum clade credibility tree obtained from a beast analysis of 268 nrDNA ITS1 and ITS2 sequences under an uncorrelated lognormal molecular clock. Node bars reflect 95% highest posterior density of node heights and are given for nodes with posterior probability values > 0.5. The names of monophyletic tribes and informal clades within Apioideae follow Downie *et al.* (in press); the width of each clade is arbitrary, and the content of each clade in given in Appendix S1. The Australasian endemic tribe Aciphylleae is expanded to show intergeneric relationships.

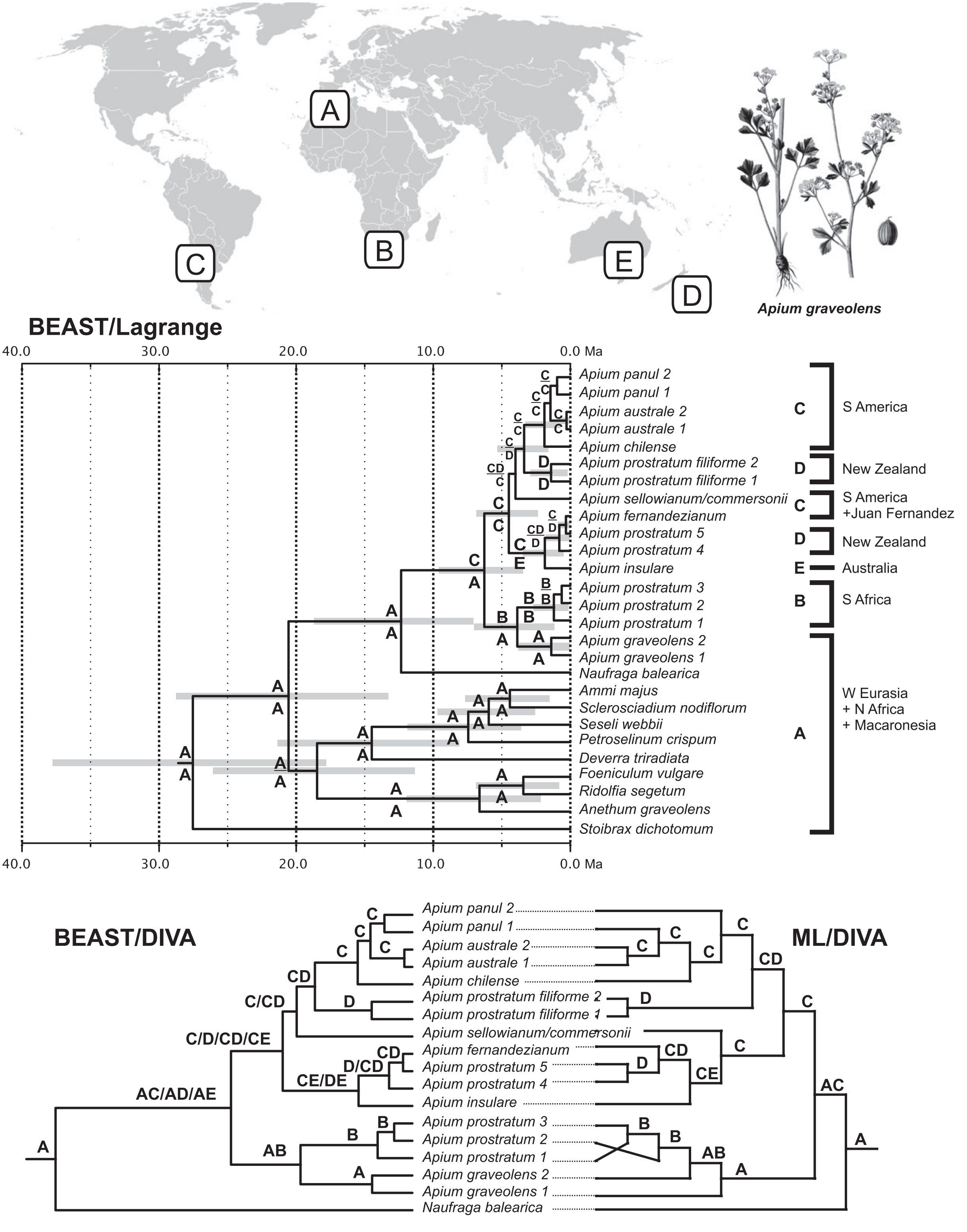

Figure 2 Phylogeny and biogeography of *Apium* and outgroups in Apiaceae tribe Apieae. The upper chronogram corresponds to the branch of Apieae from Fig. 1 with LAGRANGE reconstructions of geographical range evolution. Node bars reflect 95% highest posterior density of node heights and are given for nodes with posterior probability values > 0.5. Below, the topologies of BEAST and model-averaged maximum-likelihood (ML) trees are compared with their respective DIVA reconstructions, with outgroups omitted for simplicity (see text for further details of the analyses). Letters correspond to the areas indicated on the map; additionally, brackets indicate the geographical distribution of taxa. For LAGRANGE inference, letters above and below the branch indicate the inheritance of the area by upper and lower descendant branches, respectively. For DIVA reconstructions, letters along branches indicate ancestral areas. The image of *A. graveolens* is from Thomé (1886), modified.

newly sequenced members of the genera *Pternopetalum*, *Harrysmithia* and *Spuriopimpinella* (Fig. 1). The divergence between these two clades took place 34.8 Ma (HPD 22.3–48.2), whereas the radiation of Aciphylleae in New Zealand and Australia is dated at only 11.0 Ma (HPD 5.7–17.6). The *Acronema* clade, Aciphylleae and Smyrnieae constitute together a sister group to tribe Scandiceae; the radiation of the latter started 38.8 Ma (HPD 27.9–50.9).

Phylogeny, disjunction times and biogeography of *Apium*

Altogether, 17 terminals representing *Apium* and 10 terminals representing the other members of tribe Apieae were analysed using a Bayesian method, as applied in beast, and a model-averaged ML method using jModelTest and phyml. The resulting trees were generally similar to each other (Fig. 2), although they differed with respect to the positions of some species. In all trees, *Naufraga balearica*, an endemic of Baleares, is placed as a sister group to *Apium*. Within the latter, two clades are evident: (1) a clade encompassing European *A. graveolens* and the southern African accessions of a polyphyletic *A. prostratum*; and (2) a clade comprising their South American, Australian and New Zealand congeners. In the second clade, the accessions of the typical variety of *A. prostratum* and of var. *filiforme*, both from New Zealand, did not ally. *Apium graveolens* is a sister group (beast) or is paraphyletic (ML) to its South African cousin. The Bayesian and ML trees also differed with respect to the position of *A. sellowianum/commersonii* (two species with identical ITS sequences treated as one terminal) and some rearrangements within terminal clades. The biogeographical reconstructions using diva are also somewhat different, with five and six dispersal events inferred for ML and beast trees, respectively (Fig. 2). In both reconstructions, Europe was inferred as the ancestral area for *Apium* and the dispersal to southern Africa is independent from the others. In the ML tree, an amphitropic distribution was first achieved through a long-distance dispersal from Europe to South America. Subsequently, three dispersals from South America to Australia and New Zealand took place. No dispersals between New Zealand and Australia were inferred. In contrast, in the beast tree, the reconstruction of the ancestral area for the South American and Australasian clade was equivocal, with South America, Australia or New Zealand inferred as the first foothold of the genus in the Southern Hemisphere. Subsequently, the genus colonized other areas through four dispersal events, including a possible dispersal from Australia to New Zealand and further to the Juan Fernández Archipelago. A similar scenario was inferred using the beast tree and lagrange (Fig. 2). The first dispersal to the Southern Hemisphere was estimated at 6.3 Ma (HPD 3.5–9.6) and the Europe/South America split received a relative probability (RP) of 0.57; an alternative reconstruction (not shown), Europe/New Zealand, received a RP of 0.32 (both reconstructions are within a 2log likelihood interval). New Zealand was colonized twice, but in contrast to the diva scenarios both dispersals occurred from South America instead of from Australia. However, the difference between the most likely scenario and the alternative ones (not shown) was not high. Similarly to the diva reconstructions, southern Africa was colonized from Europe, and this event took place *c.* 3.9 Ma (HPD 1.2–7.0).

Disjunction times and biogeography of *Chaerophyllum*

The relationships among the representatives of *Chaerophyllum* were similar to those obtained from previous studies of ITS sequence variation (Chung *et al.*, 2005), with the Old World members of the genus (excluding those from Taiwan and Borneo) paraphyletic with respect to the clade comprising the two North American congeners and those species from the Southern Hemisphere and Taiwan previously classified in the genus *Oreomyrrhis*.

The results of beast and ML analyses of combined cpDNA and ITS data are presented in Fig. 3. In these trees, the Eurasian members of the genus constitute its early diverging branches, with *C. temulum* sister to a clade comprising the two North American species and all former members of *Oreomyrrhis*. The North American species formed a clade sister group to '*Oreomyrrhis*'. However, the relationships within the latter were different depending upon the method of analysis. In the ML tree, the taxa from New Guinea constituted a basal paraphyly, the New Zealand species formed a clade arising within the Australian/Tasmanian taxa, and the Taiwan endemics comprised a sister group to the congener from Borneo. The former members of *Oreomyrrhis* occurring in North America (Mexico and Guatemala) were distant relatives of North American *C. procumbens* and *C. tainturieri*, yet they were closely related to the Andean *C. andicola*. Together, the American members of '*Oreomyrrhis*' formed a clade within the Australian group. In contrast, in the beast tree, the species from Borneo and Taiwan formed a sister group to the remaining members of the clade, and the taxa from New Guinea formed a monophyletic group.

diva reconstructed 10 dispersal events for the ML tree. *Chaerophyllum* originated in western Eurasia and, successively, colonized North America and New Guinea. From New Guinea, the genus dispersed northwards to Borneo and Taiwan, southwards to Australia and Tasmania, and eastwards to continental South or North America. In a separate dispersal event, it colonized Tierra del Fuego and the Falkland Islands. For the beast tree, the reconstructions for the ancestral area of the '*Oreomyrrhis*' clade were ambiguous and included a combination of North America, New Guinea, Australia, New Zealand, Borneo or Taiwan.

The scenario inferred using lagrange and the beast tree included a transatlantic dispersal from Europe to North America followed by a transpacific dispersal to Taiwan and New Guinea. From New Guinea, the genus colonized Australia and New Zealand; subsequently, it dispersed to Tierra del

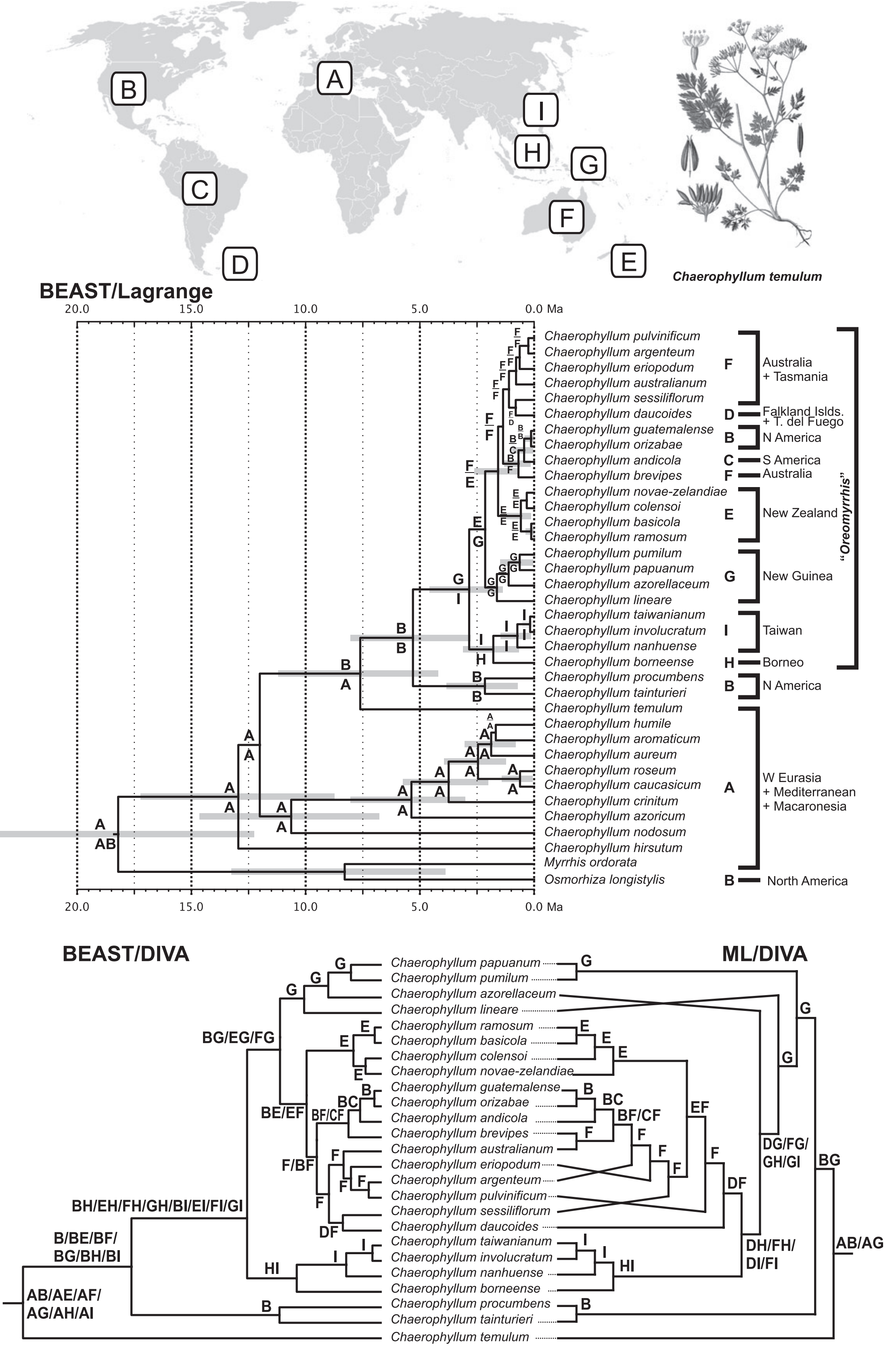

Figure 3 Phylogeny and biogeography of *Chaerophyllum*. Both BEAST chronogram and the maximum-likelihood (ML) tree resulted from the analyses of 36 taxa examined for cpDNA and nrDNA data (see text for further details). Presentation of the results is similar to that in Fig. 2. The image of *C. temulum* is from Thomé (1886), modified.

Fuego and the Falkland Islands, to South America and back to North America. The divergence between the Eurasian *C. temulum* and its sister group (North American *C. procumbens* and *C. tainturieri* and '*Oreomyrrhis*'), that is, the transatlantic dispersal from Europe, occurred at 7.6 Ma (HPD 4.2–11.2), whereas the split between the North American group and '*Oreomyrrhis*', the transpacific dispersal, took place 5.3 Ma (HPD 2.8–8.0). The radiation of the '*Oreomyrrhis*' clade in the Southern Hemisphere began 2.8 Ma (HPD 1.4–4.6).

Disjunction times and biogeography of *Daucus*

Both in the BEAST analysis of the large matrix and in an analysis of a subset of these data using ML (Fig. 4), the members of *Daucus* formed two clades, *Daucus* I and *Daucus* II. The first clade grouped with three Macaronesian endemics and the second clade was sister to the genus *Agrocharis* from tropical Africa, a topology similar to that obtained previously (Spalik & Downie, 2007). The South American and Australian members of *Daucus* were placed in a subclade within the *Daucus* II clade, along with the Old World species *D. arcanus* and *D. durieua*. The clade containing all species of *Daucus* radiated *c.* 19.8 Ma (HPD 13.6–26.6), whereas the *Daucus* II clade diverged from *Agrocharis* *c.* 14.7 Ma (HPD 9.5–20.8). The age of achieving bipolarity in *Daucus*, that is, the divergence of the lineage comprising *D. montanus* and *D. glochidiatus* from *D. durieua*, is 7.0 Ma, whereas the date of achieving an amphiantarctic distribution – the age of divergence between *D. montanus* and *D. glochidiatus* – was estimated at 2.6 Ma (HPD 0.4–5.3).

Despite the differences in topology between the BEAST and ML trees, the biogeographical reconstructions using DIVA and LAGRANGE were generally similar, including two independent long-distance dispersals from Europe to North and South America. The colonization of Australia occurred through a transoceanic dispersal from North or South America.

Disjunction times and biogeography of *Lilaeopsis*

The genus *Lilaeopsis* is nested within the North American endemics clade of tribe Oenantheae (Fig. 5), and it diverged from its sister clade 27.9 Ma (HPD 19.5–37.8). The South American species of *Lilaeopsis* do not form a monophyletic group, but are scattered throughout the genus. The different topologies of the BEAST and ML trees resulted in differences in DIVA reconstruction, although for both trees nine dispersal events were inferred. For the BEAST tree, DIVA reconstructed a South American origin of the genus with subsequent migrations to North America, New Zealand and Mauritius. The colonization of Australia occurred from New Zealand. In contrast, DIVA reconstructions using the model-averaged ML tree were ambiguous. North America, South America, or North and South America together were reconstructed as the ancestral area, from which the genus dispersed to New Zealand and, subsequently, to Australia. The colonization of Mauritius occurred from North or South America; as *L. brasiliensis* is nested within *L. mauritiana*, the origin of the former through a back-dispersal from Mauritius to South America cannot be excluded. Multiple dispersals between North and South America also took place, although the direction of these dispersals cannot be unambiguously inferred.

The most likely scenario inferred using LAGRANGE includes a North American origin of the genus with early migration to South America, from where the genus dispersed to Mauritius, New Zealand and back to North America. As in the DIVA reconstructions, the colonization of Australia occurred from New Zealand. Assuming that the dispersal of the ancestor of *Lilaeopsis* coincided with its divergence from its sister group, it may have occurred as early as 27.9 Ma.

DISCUSSION

Calibrating umbellifer phylogeny

The absolute timing of vicariance and dispersal events is crucial for historical biogeography (Donoghue & Moore, 2003), and its estimation requires calibration with fossil data or with a presumed vicariance event. In previous studies of Apioideae, divergence times were estimated using a strict molecular clock and an ITS substitution rate imported from a study of *Dendroseris* (Asteraceae) estimated to be within a range of 0.39–0.79% Myr^{-1}, with the value of 0.61% considered most probable (Sang *et al.*, 1994). Importing substitution rates from other studies is contentious and should be treated with caution (Ho, 2007); nevertheless, it may be a very rough indicator of divergence timing, permitting a choice between contrasting biogeographical hypotheses such as Gondwanan vicariance and late Tertiary dispersal. For our study group, the estimates obtained from fossil pollen calibration were congruent with those based on a strict molecular clock.

In our previous study of the *Sium*/*Berula* alliance, we estimated the age of its crown node at *c.* 13.9 Ma using a substitution rate of 0.61% Myr^{-1} (Spalik & Downie, 2006). If we had used a rate of 0.39% then we would have obtained the divergence time of 21.7 Ma. In this study, this divergence was dated at 18.4 Ma (not shown), which is within the range based on standard ITS substitution rates. Similarly, Chung *et al.* (2005) estimated the split between the '*Oreomyrrhis*' clade and the North American species of *Chaerophyllum* at 2.2 Ma using a substitution rate of 0.79%; based on our study, this divergence took place 5.3 Ma. Again, when the former estimate is recalculated using a rate of 0.39%, it is 4.5 Ma. These examples demonstrate that the substitution rates along the branches of the tree calibrated with pollen data are close to those hitherto inferred using a strict molecular clock.

Another indirect confirmation of our dating comes from the group of Macaronesian endemics, specifically *Cryptotaenia elegans*, *Melanoselinum decipiens* and *Monizia edulis*. *Cryptotaenia elegans* is an endemic of the Canaries occurring on its four westernmost islands (Tenerife, La Gomera, El Hierro and La Palma), whereas the other two species occur on Madeira

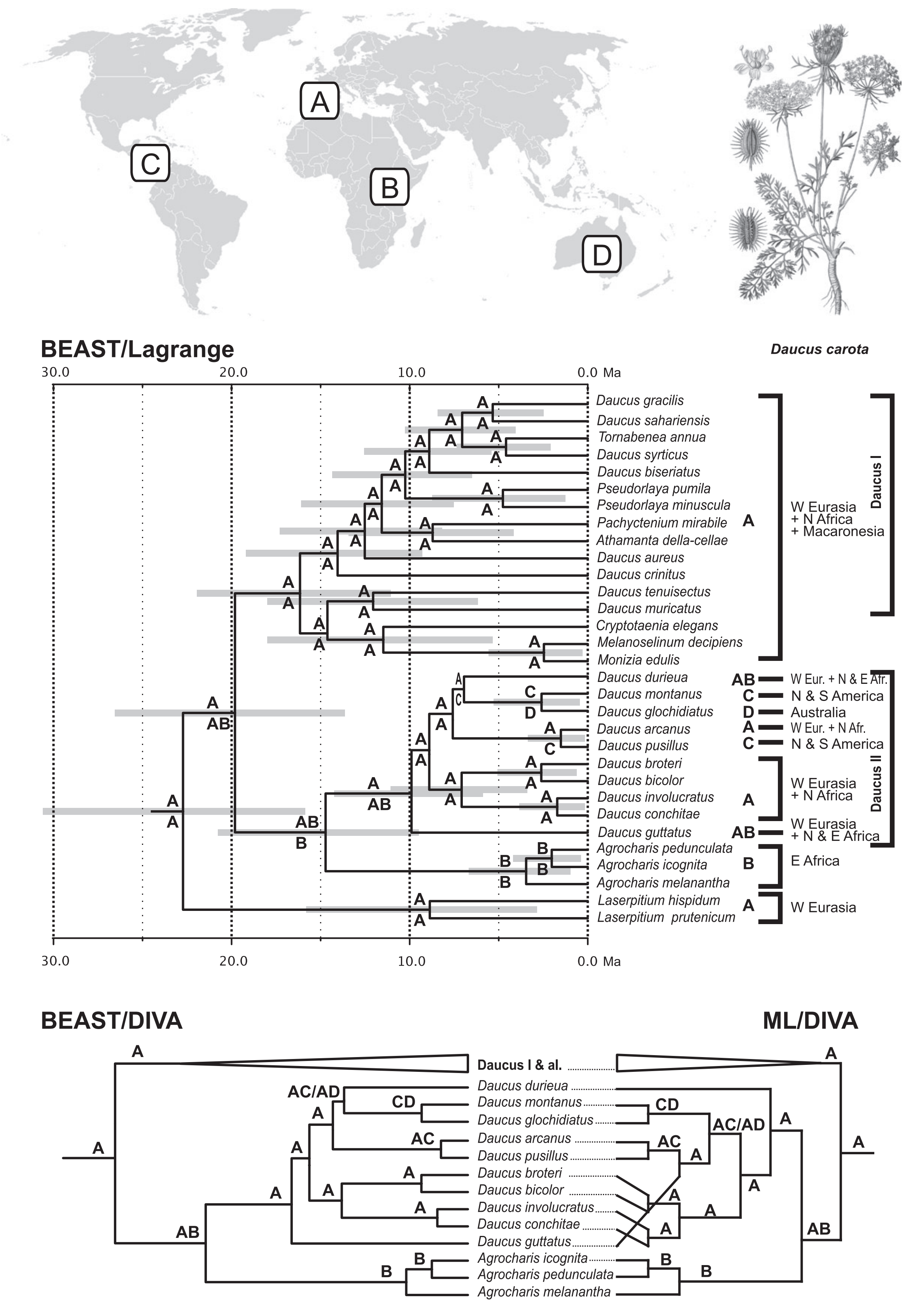

Figure 4 Phylogeny and biogeography of *Daucus* and outgroups. The chronogram represents a subclade (subtribe) Daucinae of the branch of Scandiceae from Fig. 1. Presentation of the results is similar to that in Fig. 2. The image of *D. carota* is from Thomé (1886), modified.

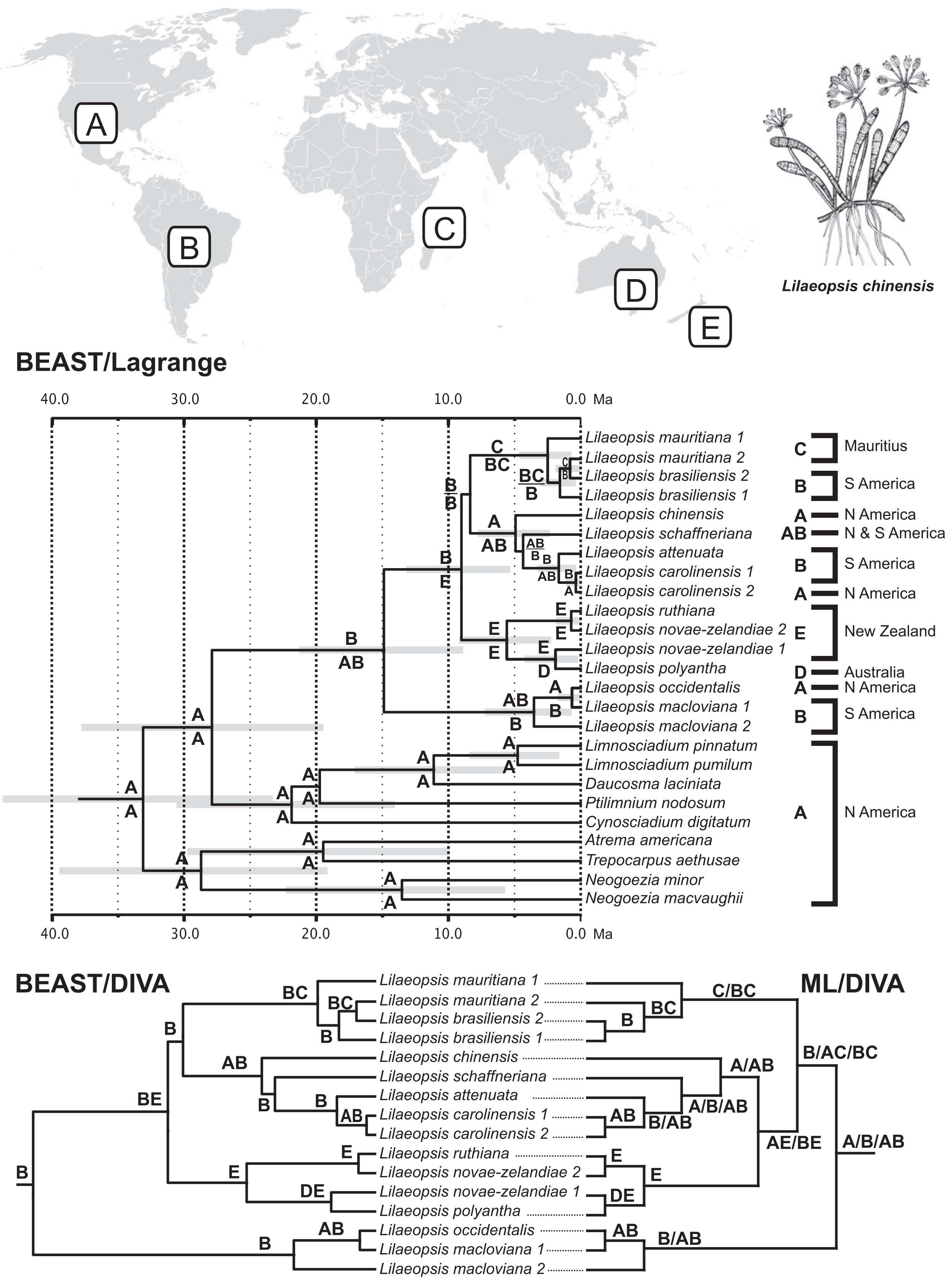

Figure 5 Phylogeny and biogeography of *Lilaeopsis* and outgroups. The chronogram represents a part of the North American endemics clade of tribe Oenantheae from Fig. 1. Presentation of the results is similar to that in Fig. 2. The image of *L. chinensis* is from Britton & Brown (1913), modified.

and are sister taxa. Based on the chronogram (Fig. 4), the separation of this group from its continental cousins occurred 14.6 Ma (HPD 5.3–18.0), which corresponds to the age of La Gomera, the oldest of the four islands, estimated at 14 Ma (Anguita & Hernán, 2000).

The biogeography of amphitropic amphiantarctic apioid umbellifers

The history of Apiaceae in the Southern Hemisphere

The family Apiaceae is generally considered to have originated in the Southern Hemisphere because its early-branching lineages, subfamilies Azorelloideae and Mackinlayoideae, are best represented and diversified there, particularly in temperate South America and Australia (Plunkett *et al.*, in press). For the two remaining subfamilies, Saniculoideae and Apioideae, southern Africa was inferred as their ancestral area (Calviño *et al.*, 2006, 2008). Saniculoideae are very well represented in the Southern Hemisphere, including Australasia. In contrast, Apioideae are mostly diversified in the Northern Hemisphere and, apart from southern Africa, in the Southern Hemisphere they are represented by late-branching lineages. Only five of these apioid lineages exhibit long-distance disjunctions in the Southern Hemisphere, and all were included in this study. Among these taxa, no true disjunctions between southern Africa and other land masses have been inferred, as the putative disjunction in *Apium* is the result of two independent dispersals from the north. In contrast, four of the five lineages exhibit true transpacific disjunctions. This is surprising given the long evolutionary history of apioid umbellifers in southern Africa (Downie & Katz-Downie, 1999; Calviño *et al.*, 2006), whereas the South American and Australasian members of the subfamily represent late-branching lineages. Twenty genera of apioid umbellifers occur in South America; however, only 12 are found in the southern temperate part of the continent (Plunkett *et al.*, in press). Three of these are narrow endemics and nine are characterized by amphitropic disjunctions, including *Apium*, *Chaerophyllum*, *Daucus* and *Lilaeopsis*, which are shared with Australasia. Apart from the genera considered in this study, molecular data are available for South American temperate members of *Osmorhiza*, *Cyclospermum* and *Notiosciadium*, but only *Osmorhiza* has been studied in detail, and its North American–South American disjunction was hypothesized to have originated as a result of a relatively recent dispersal from the north (Wen *et al.*, 2002). The affinity of the monospecific *Notiosciadium* is unclear, although it belongs to the apioid superclade, a crown group of apioid umbellifers (Nicolas & Plunkett, 2009). In a large-scale analysis of ITS sequences of Apioideae (Downie *et al.*, in press), *Cyclospermum* grouped with some accessions of the Old World genus *Scaligeria*, implying another amphitropic transatlantic disjunction; however, taxonomic sampling in Apiaceae is far from being comprehensive and some closer relatives of *Cyclospermum* may be found upon examination of further taxa.

The Sino-Himalayan affinities of Aciphylleae

Tribe Aciphylleae encompasses the Australasian genera *Aciphylla*, *Anisotome*, *Gingidia*, *Lignocarpa* and *Scandia*, which form a highly supported monophyletic group based on molecular data (Mitchell *et al.*, 1998; Downie *et al.*, 2000b), although the boundaries among them are unclear (Radford *et al.*, 2001). In previous molecular analyses, members of Smyrnieae were placed as a sister group to tribe Aciphylleae (e.g. Downie *et al.*, 2000b). Tribe Smyrnieae encompasses only two genera, *Smyrnium* and *Lecokia*, that are distributed in the Mediterranean, therefore making the presumed disjunction between Smyrnieae and Aciphylleae all the more striking. The members of the *Acronema* clade are predominantly Sino-Himalayan alpine species (She *et al.*, 2005), and eastern Asia is a better candidate for the place of origin of the ancestor of Australasian Aciphylleae than the Mediterranean. Many members of Aciphylleae are mountainous plants, and it has been suggested that, similarly to many other New Zealand alpine taxa, these apioids are progenitors of a relatively recent immigrant that has undergone rapid radiation (Winkworth *et al.*, 2005). However, our results only partly confirm this hypothesis. Although the radiation of Aciphylleae is indeed relatively recent (in the Miocene), the ancestor of the tribe colonized New Zealand relatively early, in the Eocene.

Apium: *multiple dispersals to and within the Southern Hemisphere*

Recent molecular studies restricted the genus *Apium* to its nominative section (Hardway *et al.*, 2004; Spalik *et al.*, 2009). This section comprises a single species in Europe, *A. graveolens*, and several species in southern South America (Maticorena & Quezada, 1985; Martinez, 1999), the Juan Fernández Islands (Johow, 1896), Australasia (Short, 1979; Gardner, 2000) and South Africa (Townsend, 1989; van Wyk & Tilney, 2004). Based on the results presented herein, the genus *Apium* originated in Europe and spread to the Southern Hemisphere through two independent dispersals from Europe, followed by several dispersals across the South Pacific. These dispersals occurred in a relatively short period of time, beginning in the late Miocene. A quite unexpected result is the polyphyly of *A. prostratum*, for this taxon comprises three unrelated lineages from South Africa and New Zealand. The overall morphological similarity (or morphological stasis) of those members of *Apium* occurring in South America, Australasia and South Africa suggests that the diversification of this genus in the Southern Hemisphere occurred more as a result of colonization of available habitats than as an adaptation to new habitats.

Chaerophyllum: *the counter-clockwise migration around the Pacific*

Chaerophyllum is the most widespread genus of Apiaceae and therefore poses questions about its origin and spread. Biogeographical analyses clearly indicate a western Eurasian or even a

European origin of the genus, with transatlantic dispersal giving rise to the North American and '*Oreomyrrhis*' branch. This event took place *c.* 7.6 Ma, in the late Miocene. At that time, the continuity of the North Atlantic Land Bridge had long been broken and the harsh climatic conditions limited dispersal through island hopping (Tiffney & Manchester, 2001). Therefore, the colonization of North America by *Chaerophyllum* probably occurred through long-distance dispersal. Successively, in another transoceanic jump, the genus crossed the Pacific during the time of the Miocene/Pliocene boundary. When discussing the origins of the amphitropic disjunctions, Raven (1963) noticed that many disjunct taxa are self-compatible, thereby permitting the colonization of a new area from a single seed. The members of the '*Oreomyrrhis*' clade and the North American congeners are selfers, and this may explain their dispersal abilities. Mathias & Constance (1955) noted that the fruits of '*Oreomyrrhis*' are deprived of any adaptations for long-distance dispersal, so they ruled out transoceanic migration. They considered several places of origin of the genus and various migration routes, including an Antarcto-Tertiary origin or migration through the Antarctic. However, dating the radiation of the '*Oreomyrrhis*' lineage at 2.8 Ma precludes any scenarios involving the Antarctic continent. Moreover, several members of the '*Oreomyrrhis*' clade are characterized by having very small fruits, much smaller than those of their European congeners, and the presence of an indumentum that may facilitate exozoochory.

Despite the ambiguity of the phylogenetic inferences in the '*Oreomyrrhis*' branch and the alternative biogeographical reconstructions, some conclusions may be drawn. The '*Oreomyrrhis*' branch originated in the Southern Hemisphere following a long-distance dispersal from North America to the Malesian Floristic Province (including New Guinea, Borneo and Taiwan), from which the genus dispersed to Australia and colonized the Holantarctic floristic kingdom (including New Zealand, Fuegia and Falkland Islands). The genus appeared in South America due to a dispersal from Australia and it further dispersed to North America. This counter-clockwise migration through the Pacific rim started in the late Pliocene and lasted through the Pleistocene. *Chaerophyllum* represents, therefore, an interesting case of a migration from the Northern Hemisphere to the Southern Hemisphere and successive backward migration to the north. A similar pattern has been found for *Ranunculus* (Ranunculaceae). *Ranunculus* originated in Europe and/or the Mediterranean region and dispersed to the Southern Hemisphere at least three times, with the first dispersal taking place *c.* 4.1. Ma (Paun *et al.*, 2005). One of these Southern Hemispheric lineages includes also several species from Central Asia, North America and Europe, suggesting subsequent dispersals northwards.

Daucus: *Australia colonized from South America*

Despite the economic importance of its nomenclatural type, *Daucus carota* subsp. *sativus* (the cultivated carrot), the phylogenetic relationships within *Daucus* have not yet been satisfactorily resolved. Our previous molecular and biogeographical analyses of Daucinae suggested a single dispersal from the Old World to the New World and, successively, a dispersal from the New World to Australia (Spalik & Downie, 2007), whereas in this study two dispersals to the New World were inferred. However, the relationships within the *Daucus* II clade encompassing all non-Old World species are not well supported, and may change with better taxonomic and molecular sampling. Nevertheless, we conclude that the non-Old World species are recent. Based on our results, the dispersal to South America took place in the late Miocene, whereas the dispersal from South America to Australia occurred during the late Pliocene.

Lilaeopsis: *the demise of the Gondwanan origin hypothesis*

Similar to *Chaerophyllum*, the distribution of the aquatic genus *Lilaeopsis* is not strictly amphitropic because its members also occur in the tropics of South America and in Mauritius and Madagascar, although usually at higher elevations (Affolter, 1985; Petersen & Affolter, 1999). Both Northern and Southern Hemispheric origins for *Lilaeopsis* have been reported. Dawson (1971), for instance, suggested that *Lilaeopsis* originated in the Northern Hemisphere, whereas Hill (1929) regarded *Lilaeopsis* as an originally Antarctic genus that subsequently migrated northwards along two major routes, one leading to New Zealand and Australia, the other leading into and through the Andes of South America into North America. Raynal (1977) described *Lilaeopsis* as a Gondwanan genus, implying not only its southern provenance but also a Cretaceous age.

Based on our results, although the lineage giving rise to *Lilaeopsis* is nested within North American taxa, the South American origin of the genus and successive migrations northwards are very likely. For DIVA and the BEAST tree, four dispersals from South America to North America were inferred. The genus originated in the Oligocene and radiated in the mid-Miocene; this is still much earlier than the other genera considered in this study, but without any doubts it permits the rejection of the Gondwanan hypothesis in favour of more recent long-distance migrations.

A Gondwanan origin was also recently proposed for two genera of Ranunculaceae exhibiting an amphitropic and amphiantarctic distribution. Schuettpelz & Hoot (2004) suggested a mid-Cretaceous origin of *Caltha* in the Northern Hemisphere, late-Cretaceous/early-Palaeogene dispersal from North to South America, and subsequent migration from South America to Australia and New Zealand through Antarctica *c.* 49 Ma. However, the mean ITS sequence divergence between the Australasian species and their South American sister group is merely 4.5%, and with a standard ITS clock it gives a divergence at 3.6–8.3 Ma. For *Anemone*, Schuettpelz *et al.* (2002) suggested an early radiation *c.* 100 Ma and subsequent dispersal to Australasia. However, the ITS sequence divergence between Australasian taxa and their Northern Hemispheric sister group is 4.5%, therefore suggesting a dispersal to the Southern Hemisphere at

3.6–8.3 Ma. For *Caltha* and *Anemone*, the early-vicariance hypothesis should also be rejected in favour of long-distance dispersal.

The timing and origin of the amphitropic amphiantarctic disjunctions

Taxa with transoceanic disjunctions in the Southern Hemisphere, including Australia, New Zealand and South America, were traditionally regarded as representing Gondwanan floristic elements, with their present distributions explained by vicariance resulting from the break-up of this supercontinent and continental drift. However, subsequent biogeographical analyses based on molecular phylogenies have demonstrated that many transoceanic disjunctions, and particularly those of plant species, are better explained by long-distance dispersal instead of vicariance (Sanmartín *et al.*, 2001; Sanmartín & Ronquist, 2004). It is now generally accepted that regional floras, even those developing in isolation, such as the floras of Australia and New Zealand, comprise a mixture of taxa with different histories, including immigrants that managed to cross geographical barriers (Crisp *et al.*, 2004). A question is whether those events of successful dispersal were randomly distributed or structured in space and time. Recent molecular investigations provide evidence for the latter scenario. In amphitropic amphiantarctic genera, the predominant direction of dispersal was from the Northern Hemisphere to the south, and the majority of these genera achieved amphitropic distribution not earlier than in the late Miocene (Table 2). Herein, we concentrate on genera, although we are aware that as units of biodiversity they are arbitrary because they are rarely comparable with respect to their age, number of species and morphological diversity. However, they are still useful morphological units, and molecular studies at the generic level usually provide better and more representative sampling than studies at a higher level, allowing for a better biogeographical inference.

Several recent studies dealing with the origin and diversification of Southern Hemispheric taxa suggested that habitat

Table 2 Molecular dating and biogeographical history of temperate angiosperm genera that exhibit an amphitropic amphiantarctic distribution pattern.

Taxon	Ancestral distribution	Number of dispersals to Southern Hemisphere	Age of bipolarity (Ma)	Reference
Apiaceae				
Apium	Europe	2	6.3	This study
Chaerophyllum	Europe	1	5.3	Chung *et al.* (2005) and this study
Daucus	W Mediterranean	2 (?)	7.0	Spalik & Downie (2007) and this study
Lilaeopsis	South America (?)	1 (?)	27.9	This study
Asteraceae				
Microseris	North America	1	n/a	Vijverberg *et al.* (1999)
Boraginaceae				
Myosotis	N. Hemisphere	1	2.0–14.7	Winkworth *et al.* (2002b)
Brassicaceae				
Lepidium s.l.	Eurasia	2–3	2.1–4.2	Mummenhoff *et al.* (2001)
Cardamine	N. Hemisphere/Africa (?)	2 (?)	n/a	Bleeker *et al.* (2002b)
Rorippa	N. Hemisphere (?)	4	< 3.1	Bleeker *et al.* (2002a)
Coriariaceae				
Coriaria	Eurasia	1	63–59	Yokoyama *et al.* (2000)
Cyperaceae				
Carex sect. *Spirostachyae*	Eurasia	2–4	n/a	Escudero *et al.* (2008)
Caryophyllaceae				
Scleranthus	Equivocal	1 (?)	4.0–7.7	Smissen *et al.* (2003)
Fabaceae				
Trifolium	Mediterranean	4	n/a	Ellison *et al.* (2006)
Gentianaceae				
Gentianella	N. Hemisphere	1	1.6–3.0	von Hagen & Kadereit (2001); Glenny (2004)
Orobanchaceae				
Euphrasia	Eurasia	2	5–7	Gussarova *et al.* (2008)
Plantaginaceae				
Plantago (inc. *Litorella*)	N. Hemisphere (?)	3 (?)	< 5.5	Rønsted *et al.* (2002); Hoggard *et al.* (2003)
Veronica (inc. *Hebe*)	Eurasia	1	9.9	Wagstaff *et al.* (2002)
Ranunculaceae				
Anemone	Holarctic	2	n/a	Schuettpelz *et al.* (2002)
Caltha	Holarctic	1	n/a	Schuettpelz & Hoot (2004)
Ranunculus	Europe/Mediterranean	3 (?)	4.1	Paun *et al.* (2005)

n/a, Estimates of molecular age are not available.

changes, mostly climatic and geological, rather than dispersal opportunities, affect the probability of successful dispersal. Winkworth *et al.* (2005) summarized molecular data for the alpine flora of New Zealand and concluded that most of these taxa reached New Zealand or diversified there in the late Miocene, Pliocene or even Pleistocene, thus confirming an earlier hypothesis formulated by Raven (1973) based on taxonomic and biogeographical data. The Western Wind Drift hypothesis has been proposed to explain several dispersal events within the Southern Hemisphere (Raven, 1973); however, dispersals to and from New Zealand occurred in all directions (Winkworth *et al.*, 2002a). The fossil record indicates that transoceanic dispersals occurred throughout the Tertiary, whereas molecular data suggest that many successful dispersal events have occurred since the Tertiary. This discordance implies that dispersal was limited by the availability of habitats that were suitable for establishment, rather than by opportunities for movement (Winkworth *et al.*, 2002a, 2005). Similarly, the late Tertiary climatic changes in Australia probably constituted the major factor responsible for the establishment of plant immigrants, as well as diversification or extinction of native lineages (Crisp *et al.*, 2004). In the late Palaeogene and early Neogene, the climate of Australia became cooler and drier, therefore promoting rapid radiations in sclerophyll taxa and stasis or extinctions in wet-biome taxa. However, Linder (2008) argued that the conditions promoting diversification in Australia were relatively stable and its floristic diversity is a result of mature radiations rather than recent and rapid radiations.

Although for most studies of amphitropic amphiantarctic genera (see Table 2) formal biogeographical analyses are not available, it seems that the number of transoceanic dispersal events in the Southern Hemisphere was much greater than those events between the Northern and Southern Hemispheres. Such a pattern was also confirmed for the Cape flora. Based on unambiguous molecular phylogenies, almost half of the Cape clades have trans-Indian Ocean (Australasian) disjunct sister taxa. Although many other Cape clades show a relationship with the Eurasian temperate flora, it appears that the Indian Ocean was a less important barrier for plant dispersal than the tropical biomes of Africa (Galley & Linder, 2006).

CONCLUSIONS

This study of amphitropic amphiantarctic members of Apioideae confirms their northern origins and, apart from *Lilaeopsis*, a relatively late migration to the Southern Hemisphere. These taxa followed different migration routes: along the land masses of North and South America (*Daucus*, *Lilaeopsis*) and Africa (*Apium*) or direct transoceanic dispersals through the Atlantic (*Apium*) or Pacific (*Chaerophyllum*) Oceans. Similarly, within the Southern Hemisphere those genera dispersed both westwards (*Apium*, *Daucus*, *Lilaeopsis*) and eastwards (*Chaerophyllum*, *Lilaeopsis*). For *Chaerophyllum* and *Lilaeopsis*, subsequent dispersal events to the Northern Hemisphere were also inferred. A similar pattern – late Tertiary dispersal from the Northern Hemisphere and subsequent dispersals in all directions in the Southern Hemisphere – has also been recorded for many other amphitropic amphiantarctic angiosperm genera. The similar timing contrasted with the diversity of migration routes suggest that these dispersal events were successful due to favourable ecological conditions, probably associated with the climatic cooling of the late Palaeogene/early Neogene, rather than increased movement opportunities.

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REFERENCES

Affolter, J.M. (1985) A monograph of the genus *Lilaeopsis* (Umbelliferae). *Systematic Botany Monographs*, **6,** 1–140.

Akaike, H. (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, **19,** 716–723.

Anguita, F. & Hernán, F. (2000) The Canary Islands origin: a unifying model. *Journal of Volcanology and Geothermal Research*, **103,** 1–26.

Bleeker, W., Weber-Sparenberg, C. & Hurka, H. (2002a) Chloroplast DNA variation and biogeography in the genus *Rorippa* Scop. (Brassicaceae). *Plant Biology*, **4,** 104–111.

Bleeker, W., Franzke, A., Pollmann, K., Brown, A.H.D. & Hurka, H. (2002b) Phylogeny and biogeography of southern hemisphere high-mountain *Cardamine* species (Brassicaceae). *Australian Systematic Botany*, **15,** 575–581.

Brandley, M.C., Schmitz, A. & Reeder, T.W. (2005) Partitioned Bayesian analyses, partition choice, and the phylogenetic relationships of scincid lizards. *Systematic Biology*, **54,** 373–390.

Bremer, K., Friis, E.M. & Bremer, B. (2004) Molecular phylogenetic dating of asterid flowering plants shows Early Cretaceous diversification. *Systematic Biology*, **53,** 496–505.

Britton, N.L. & Brown, A. (1913) *An illustrated flora of the northern United States, Canada and the British Possessions*. C. Scribner, New York.

Calviño, C.I., Tilney, P.M., van Wyk, B.E. & Downie, S.R. (2006) A molecular phylogenetic study of southern African Apiaceae. *American Journal of Botany*, **93,** 1828–1847.

Calviño, C.I., Martinez, S.G. & Downie, S.R. (2008) Morphology and biogeography of Apiaceae subfamily Saniculoideae as inferred by phylogenetic analysis of molecular data. *American Journal of Botany*, **95,** 196–214.

Chung, K.-F. (2007) Inclusion of the South Pacific alpine genus *Oreomyrrhis* (Apiaceae) in *Chaerophyllum* based on nuclear and chloroplast DNA sequences. *Systematic Botany*, **32,** 671–681.

Chung, K.-F., Peng, C.-I., Downie, S.R., Spalik, K. & Schaal, B.A. (2005) Molecular systematics of the trans-Pacific alpine genus *Oreomyrrhis* (Apiaceae): phylogenetic affinities and biogeographic implications. *American Journal of Botany*, **92,** 2054–2071.

Crisp, M.D., Cook, L.G. & Steane, D. (2004) Radiation of the Australian flora: what can comparisons of molecular phylogenies across multiple taxa tell us about the evolution of diversity in present-day communities? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359,** 1551–1571.

Dawson, J.W. (1971) Relationships of the New Zealand Umbelliferae. *The biology and chemistry of the Umbelliferae* (ed. by V.H. Heywood), pp. 43–61. Academic Press, London.

Donoghue, M.J. & Moore, B.R. (2003) Toward an integrative historical biogeography. *Integrative and Comparative Biology*, **43,** 261–270.

Downie, S.R. & Katz-Downie, D.S. (1999) Phylogenetic analysis of chloroplast *rps*16 intron sequences reveals relationships within the woody southern African Apiaceae subfamily Apioideae. *Canadian Journal of Botany*, **77,** 1120–1135.

Downie, S.R., Katz-Downie, D.S. & Spalik, K. (2000a) A phylogeny of Apiaceae tribe Scandiceae: evidence from nuclear ribosomal DNA internal transcribed spacer sequences. *American Journal of Botany*, **87,** 76–95.

Downie, S.R., Katz-Downie, D.S. & Watson, M.F. (2000b) A phylogeny of the flowering plant family Apiaceae based on chloroplast DNA *rpl16* and *rpoC1* intron sequences: towards a suprageneric classification of subfamily Apioideae. *American Journal of Botany*, **87,** 273–292.

Downie, S.R., Katz-Downie, D.S., Sun, F.-J. & Lee, C.-S. (2008) Phylogeny and biogeography of Apiaceae tribe Oenantheae inferred from nuclear rDNA ITS and cpDNA *psbI*-5′*trnK*$^{(UUU)}$ sequences, with emphasis on the North American Endemics clade. *Botany*, **86,** 1039–1064.

Downie, S.R., Spalik, K., Katz-Downie, D.S. & Reduron, J.P. (in press) Major clades within Apiaceae subfamily Apioideae as inferred by phylogenetic analysis of nrDNA ITS sequences. *Plant Diversity and Evolution* (formerly *Botanische Jahrbücher*), **128**.

Drummond, A.J. & Rambaut, A. (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, **7,** 214.

Drummond, A.J., Ho, S.Y.W., Phillis, M.J. & Rambaut, A. (2006) Relaxed phylogenetics and dating with confidence. *PLoS Biology*, **4,** e88.

Ellison, N.W., Liston, A., Steiner, J.J., Williams, W.M. & Taylor, N.L. (2006) Molecular phylogenetics of the clover genus (*Trifolium* – Leguminosae). *Molecular Phylogenetics and Evolution*, **39,** 688–705.

Escudero, M., Valcárcel, V., Vargas, P. & Luceño, M. (2008) Evolution in *Carex* L. sect. Spirostachyae (Cyperaceae): a molecular and cytogenetic approach. *Organisms, Diversity & Evolution*, **7,** 271–291.

Felsenstein, J. (2005) *PHYLIP (Phylogeny Inference Package) version 3.6*. Distributed by the author. Department of Genome Sciences, University of Washington, Seattle, WA. http://evolution.genetics.washington.edu/phylip.html

Galley, C. & Linder, H.P. (2006) Geographical affinities of the Cape flora, South Africa. *Journal of Biogeography*, **33,** 236–250.

Gardner, R. (2000) A variant of the native sea-celery, *Apium prostratum* (Umbelliferae). *Journal of the Auckland Botanical Society*, **55,** 81.

Glenny, D. (2004) A revision of the genus *Gentianella* (Gentianaceae) in New Zealand. *New Zealand Journal of Botany*, **42,** 361–530.

Gruas-Cavagnetto, C. & Cerceau-Larrival, M.-T. (1983/1984) Apports des pollens fossiles d'Ombellifères à la connaissance paléoécologique et paléoclimatique de l'Eocène français. *Review of Palaeobotany and Palynology*, **40,** 317–345.

Guindon, S. & Gascuel, O. (2003) A simple, fast and accurate method to estimate large phylogenies by maximum likelihood. *Systematic Biology*, **52,** 696–704.

Gussarova, G., Popp, M., Vitek, E. & Brochmann, C. (2008) Molecular phylogeny and biogeography of the bipolar *Euphrasia* (Orobanchaceae): recent radiations in an old genus. *Molecular Phylogenetics and Evolution*, **48,** 444–460.

von Hagen, K.B. & Kadereit, J.W. (2001) The phylogeny of *Gentianella* (Gentianaceae) and its colonization of the southern hemisphere as revealed by nuclear and chloroplast DNA sequence variation. *Organisms, Diversity & Evolution*, **1,** 61–79.

Hardway, T.M., Spalik, K., Watson, M.F., Katz-Downie, D.S. & Downie, S.R. (2004) Circumscription of Apiaceae tribe Oenantheae. *South African Journal of Botany*, **70,** 393–406.

Hill, A.W. (1929) *Lilaeopsis* in Tasmania and New Zealand. *Kew Bulletin*, **1929,** 119–121.

Ho, S.Y.W. (2007) Calibrating molecular estimates of substitution rates and divergence times in birds. *Journal of Avian Biology*, **38,** 409–414.

Hoggard, R.K., Kores, P.J., Molvray, M., Hoggard, G.D. & Broughton, D.A. (2003) Molecular systematics and biogeography of the amphibious genus *Litorella* (Plantaginaceae). *American Journal of Botany*, **90,** 429–435.

Johow, F. (1896) *Flora de las Islas de Juan Fernández*. Cervantes, Santiago de Chile.

Kass, R.E. & Raftery, A.E. (1995) Bayes factors. *Journal of the American Statistical Association*, **90,** 773–795.

Larkin, M.A., Blackshields, G., Brown, N.P., Chenna, R., McGettigan, P.A., McWilliam, H., Valentin, F., Wallace, I.M., Wilm, A., Lopez, R., Thompson, J.D., Gibson, T.J. & Higgins, D.G. (2007) Clustal W and Clustal X version 2.0. *Bioinformatics*, **23,** 2947–2948.

Linder, H.P. (2008) Plant species radiations: where, when, why? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363,** 3097–3105.

Maddison, W.P. & Maddison, D.R. (2008) *Mesquite: a modular system for evolutionary analysis. Version 2.5*. Available at: http://mesquiteproject.org

Martinez, S. (1999) Apiaceae. *Catalogo de las plantas vasculares de la Republica Argentina II* (ed. by F.O. Zuloaga and O. Morrone), pp. 46–64. Monographs in Systematic Botany Vol. 74. Missouri Botanical Garden, St Louis, MO.

Mathias, M.E. & Constance, L. (1955) The genus *Oreomyrrhis* (Umbelliferae), a problem in South Pacific distribution. *University of California Publications in Botany*, **27,** 347–416.

Maticorena, C. & Quezada, M. (1985) Catalogo de la flora vascular de Chile. *Gayana, Botanica*, **42,** 1–155.

Mitchell, A.D., Webb, C.J. & Wagstaff, S.J. (1998) Phylogenetic relationships of species of *Gingidia* and related genera (Apiaceae, subfamily Apioideae). *New Zealand Journal of Botany*, **36,** 417–424.

Mukherjee, P.K. & Constance, L. (1993) *Umbelliferae (Apiaceae) of India*. American Institute of Indian Studies and Oxford & IBH Publishing, New Delhi.

Mummenhoff, K., Brüggemann, H. & Bowman, J.L. (2001) Chloroplast DNA phylogeny and biogeography of *Lepidium* (Brassicaceae). *American Journal of Botany*, **88,** 2051–2063.

Muñoz, J., Felicísimo, Á.M., Cabezas, F., Burgaz, A.R. & Martínez, I. (2004) Wind as a long-distance dispersal vehicle in the Southern Hemisphere. *Science*, **304,** 1144–1147.

Nicolas, A.N. & Plunkett, G.M. (2009) The demise of subfamily Hydrocotyloideae (Apiaceae) and the re-alignment of its genera across the entire order Apiales. *Molecular Phylogenetics and Evolution*, **53,** 134–151.

Paun, O., Lehnebach, C., Johansson, J.T., Lockhart, P.J. & Hörandl, E. (2005) Phylogenetic relationships and biogeography of *Ranunculus* and allied genera (Ranunculaceae) in the Mediterranean region and in the European Alpine System. *Taxon*, **54,** 911–930.

Petersen, G. & Affolter, J.M. (1999) A new species of *Lilaeopsis* (Apiaceae) from Mauritius. *Novon*, **9,** 92–94.

Plunkett, G.M., Pimenov, M.G., Reduron, J.P., Kljuykov, E.V., Lee, B.Y., van Wyk, B.E., Tilney, P.M., Watson, M.F., Ostroumova, T.A., Spalik, K., Hart, J.M., Henwood, M.J., Webb, C.J., Pu, F.T., Mitchell, A.D. & Muckensturm, B. (in press) Apiaceae. *The families and genera of vascular plants* (ed. by K. Kubitzky). Springer, Berlin.

Posada, D. (2008) ModelTest: phylogenetic model averaging. *Molecular Biology and Evolution*, **25,** 1253–1256.

Posada, D. & Crandall, K.A. (1998) Modeltest: testing the model of DNA substitution. *Bioinformatics*, **14,** 817–818.

de Queiroz, A. (2005) The resurrection of oceanic dispersal in historical biogeography. *Trends in Ecology and Evolution*, **20,** 68–73.

Radford, E.A., Watson, M.F. & Preston, J. (2001) Phylogenetic relationships of species of *Aciphylla* (Apiaceae, subfamily Apioideae) and related genera using molecular, morphological, and combined data sets. *New Zealand Journal of Botany*, **39,** 183–208.

Rambaut, A. (2009) *FigTree. Tree figure drawing tool version 1.2.2*. Institute of Evolutionary Biology, University of Edinburgh. http://tree.bio.ed.ac.uk.

Raven, P.H. (1963) Amphitropical relationships in the floras of North and South America. *The Quarterly Review of Biology*, **38,** 151–177.

Raven, P.H. (1973) Evolution of the subalpine and alpine plant groups in New Zealand. *New Zealand Journal of Botany*, **11,** 177–200.

Raynal, J. (1977) Le genre *Lilaeopsis* (Ombellifères) à Madagascar. *Adansonia*, **17,** 151–154.

Ree, R.H. & Smith, S.A. (2008) Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, **57,** 4–14.

Ronquist, F. (1996) *DIVA version 1.1*. Computer program and manual available from Uppsala University, http://www.ebc.uu.se/systzoo/research/diva/diva.html.

Ronquist, F. (1997) Dispersal–vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology*, **46,** 195–203.

Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, **19,** 1572–1574.

Rønsted, N., Chase, M.W., Albach, D.C. & Bello, M.A. (2002) Phylogenetic relationships within *Plantago* (Plantaginaceae): evidence from nuclear ribosomal ITS and plastid *trnL-F* sequence data. *Botanical Journal of the Linnean Society*, **139,** 323–338.

Sáenz Laín, C. (1981) Research on *Daucus* L. (Umbelliferae). *Anales Jardín Botánico de Madrid*, **37,** 481–534.

Sang, T., Crawford, D.J., Kim, S.-C. & Stuessy, T.F. (1994) Radiation of the endemic genus *Dendroseris* (Asteraceae) on the Juan Fernandez Islands: evidence from sequences of the ITS regions of nuclear ribosomal DNA. *American Journal of Botany*, **81,** 1494–1501.

Sanmartín, I. & Ronquist, F. (2004) Southern Hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Systematic Biology*, **53,** 216–243.

Sanmartín, I., Enghoff, H. & Ronquist, F. (2001) Patterns of animal dispersal, vicariance, and diversification in the Holarctic. *Biological Journal of the Linnean Society*, **73,** 345–390.

Schischkin, B.K. (1950) *Chaerophyllum* L. *Flora SSSR*, Vol. 16 (ed. by B.K. Schischkin), pp. 94–117. Izdatelstvo Akademii Nauk SSSR, Moskva, Leningrad.

Schuettpelz, E. & Hoot, S.B. (2004) Phylogeny and biogeography of *Caltha* (Ranunculaceae) based on chloroplast and nuclear DNA sequences. *American Journal of Botany*, **91,** 247–253.

Schuettpelz, E., Hoot, S.B., Samuel, R. & Ehrendorfer, F. (2002) Multiple origins of Southern Hemisphere *Anemone* (Ranunculaceae) based on plastid and nuclear sequence data. *Plant Systematics and Evolution*, **231,** 143–151.

She, M., Pu, F., Pan, Z., Watson, M.F., Cannon, J.F.M., Holmes-Smith, I., Kljuykov, E.V., Phillippe, L.R. & Pimenov, M.G. (2005) Apiaceae (Umbelliferae). *Flora of China*, Vol. 14 (ed. by Flora of China Editorial Committee), pp. 1–205. Missouri Botanical Garden, St Louis, MO.

Short, P.S. (1979) *Apium* L. sect. Apium (Umbelliferae) in Australasia. *Journal of the Adelaide Botanic Garden*, **1,** 205–235.

Smissen, R.D., Garnock-Jones, P.J. & Chambers, G.K. (2003) Phylogenetic analysis of ITS sequences suggests a Pliocene origin for the bipolar distribution of *Scleranthus* (Caryophyllaceae). *Australian Systematic Botany*, **16,** 301–315.

Spalik, K. & Downie, S.R. (2001) The utility of morphological characters for inferring phylogeny in Scandiceae subtribe Scandicinae (Apiaceae). *Annals of the Missouri Botanical Garden*, **88,** 270–301.

Spalik, K. & Downie, S.R. (2006) The evolutionary history of *Sium* sensu lato (Apiaceae): dispersal, vicariance, and domestication as inferred from ITS rDNA phylogeny. *American Journal of Botany*, **93,** 747–761.

Spalik, K. & Downie, S.R. (2007) Intercontinental disjunctions in *Cryptotaenia* (Apiaceae, Oenantheae): an appraisal using molecular data. *Journal of Biogeography*, **34,** 2039–2054.

Spalik, K., Downie, S.R. & Watson, M.F. (2009) Generic delimitations within the *Sium* alliance (Apiaceae tribe Oenantheae) inferred from cpDNA *rps16-5′trnK*$^{(UUU)}$ and nrDNA ITS sequences. *Taxon*, **58,** 735–748.

Swofford, D.L. (1998) *PAUP**. Phylogenetic analysis using parsimony (*and other methods). Version 4*. Sinauer Associates, Sunderland, MA.

Thomé, O.W. (1886) *Flora von Deutschland, Österreich und der Schweiz*. F. E. Köhler, Gera.

Tiffney, B.H. & Manchester, S.R. (2001) The use of geological and paleontological evidence in evaluating plant phylogeographic hypotheses in the Northern Hemisphere Tertiary. *International Journal of Plant Sciences*, **162,** S3–S17.

Townsend, C.C. (1989) Umbelliferae. *Flora of tropical East Africa* (ed. by R.M. Polhill), pp. 1–127. AA Balkema, Rotterdam.

Vijverberg, K., Mes, T.H.M. & Bachmann, K. (1999) Chloroplast DNA evidence for the evolution of *Microseris* (Asteraceae) in Australia and New Zealand after long-distance dispersal from western North America. *American Journal of Botany*, **86,** 1448–1463.

Wagstaff, S.J., Bayly, M.J., Garnock-Jones, P.J. & Albach, D.C. (2002) Classification, origin, and diversification of the New Zealand hebes (Scrophulariaceae). *Annals of the Missouri Botanical Garden*, **89,** 38–63.

Wen, J. & Zimmer, E.A. (1996) Phylogeny and biogeography of *Panax* L. (the ginseng genus, Araliaceae): inferences from ITS sequences of nuclear ribosomal DNA. *Molecular Phylogenetics and Evolution*, **6,** 167–177.

Wen, J., Lowry, P.P., Walck, J.L. & Yoo, K.O. (2002) Phylogenetic and biogeographic diversification in *Osmorhiza* (Apiaceae). *Annals of the Missouri Botanical Garden*, **89,** 414–428.

White, T.J., Bruns, T., Lee, S. & Taylor, J. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. *PCR protocols: a guide to methods and applications* (ed. by M.A. Innis, D.H. Gelfand, J.J. Sninsky and T.J. White), pp. 315–322. Academic Press, San Diego, CA.

Winkworth, R.C., Wagstaff, S.J., Glenny, D. & Lockhart, P.J. (2002a) Plant dispersal N.E.W.S. from New Zealand. *Trends in Ecology and Evolution*, **17,** 514–520.

Winkworth, R.C., Grau, J., Robertson, A.W. & Lockhart, P.J. (2002b) The origin and evolution of the genus *Myosotis* L. (Boraginaceae). *Molecular Phylogenetics and Evolution*, **24,** 180–193.

Winkworth, R.C., Wagstaff, S.J., Glenny, D. & Lockhart, P.J. (2005) Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Organisms, Diversity & Evolution*, **5,** 237–247.

van Wyk, B.E. & Tilney, P.M. (2004) Diversity of Apiaceae in Africa. *South African Journal of Botany*, **70,** 433–445.

Yang, Z. (2006) *Computational molecular evolution*. Oxford University Press, New York.

Yokoyama, J., Suzuki, M., Iwatsuki, K. & Hasebe, M. (2000) Molecular phylogeny of *Coriaria*, with special emphasis on the disjunct distribution. *Molecular Phylogenetics and Evolution*, **14,** 11–19.

Yuan, Y.-M., Wohlhauser, S., Möller, M., Klackenberg, J., Callmander, M.W. & Küpfer, P. (2005) Phylogeny and biogeography of *Exacum* (Gentianaceae): a disjunctive distribution in the Indian Ocean resulted from long distance dispersal and extensive radiation. *Systematic Biology*, **54,** 21–34.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Accessions of Apiaceae subfamily Apioideae examined for variation in nuclear ribosomal DNA ITS sequences.

BIOSKETCH

Krzysztof Spalik is a botanist and ecologist whose research studies focus on the molecular phylogeny, biogeography and taxonomy of the family Apiaceae and the evolution of adaptive traits in plants.

Author contributions: K.S. conceived the ideas of the manuscript, provided some data, performed preliminary phylogenetic analyses and wrote the manuscript; M.P. and R.K.-M. performed the analyses; C.A.D. and T.S.B. provided some sequence data; and S.R.D. provided some sequence data and edited the manuscript.

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