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ORIGINAL ARTICLE

The role of the Southern Hemisphere in the evolutionary history of Apiaceae, a mostly north temperate plant family

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ABSTRACT

Aim To estimate the most likely pathways of expansion of the first diverging lineages of the angiosperm family Apiaceae across the Southern Hemisphere and to Eurasia by reconstructing the biogeographical history of the family through space and time.

Location Southern Hemisphere, with emphasis on Africa.

Methods Divergence times were assessed under a penalized-likelihood method (r8s) and a data set of 129 cpDNA *rps16* intron sequences. Confidence intervals were estimated using ABCq, BCa, bootstrap-t and standard normal methods. Biogeographical distributions were reconstructed using DEC analyses over *rps16* intron and/or nrDNA ITS trees.

Results Crown Apiaceae likely originated by the Late Cretaceous in Australasia. Apiaceae subfamilies diverged between 45.9 and 71.2 Ma in the Southern Hemisphere, specifically, Mackinlayoideae in Australasia, Azorelloideae in South America and Apioideae and Saniculoideae in southern Africa. From the Palaeocene to Oligocene, Africa showed connections via transoceanic dispersals as a sink continent with Australasia and as a source continent with South America and Eurasia. These dispersals explain the present intercontinental disjunctions of the subfamilies. The first diverging lineages of Apioideae and Saniculoideae likely originated in Africa and diversified in situ since the Palaeocene, with no input from newcomers until the Miocene. Subsequently, several dispersals mainly from Eurasia are estimated back to northern and eastern Africa.

Main conclusions The Southern Hemisphere has played a key role in the origin and early diversification of Apiaceae, currently a mostly north temperate family. African Apiaceae was likely assembled by Palaeocene lineages that diversified in situ and are now restricted mainly to southern Africa and post Miocene newcomers mostly restricted to northern and eastern Africa by effective environmental barriers.

Keywords

Africa, Apiaceae, Apioideae, Azorelloideae, dispersals, Mackinlayoideae, Madagascar, molecular dating, phylogeny, Saniculoideae

INTRODUCTION

Estimating the pathways of expansion for taxa that show intercontinental disjunctions is essential to understand how and when biota assembled and diversified. The near-cosmopolitan angiosperm family Apiaceae (Umbelliferae) contains *c.* 430 genera and 3780 species treated in four subfamilies: Azorelloideae (*Azorella*), exhibiting its greatest diversity in South America; Mackinlayoideae (*Centella*), exhibiting its greatest diversity in Australasia; and Apioideae (celery, carrot, parsley) and Saniculoideae (*Eryngium*) having their greatest diversity in north temperate regions (Fig. 1; Stevens, 2001 onwards). Currently, over 70% of Apiaceae genera are distributed in the Northern Hemisphere, yet the origin of its first

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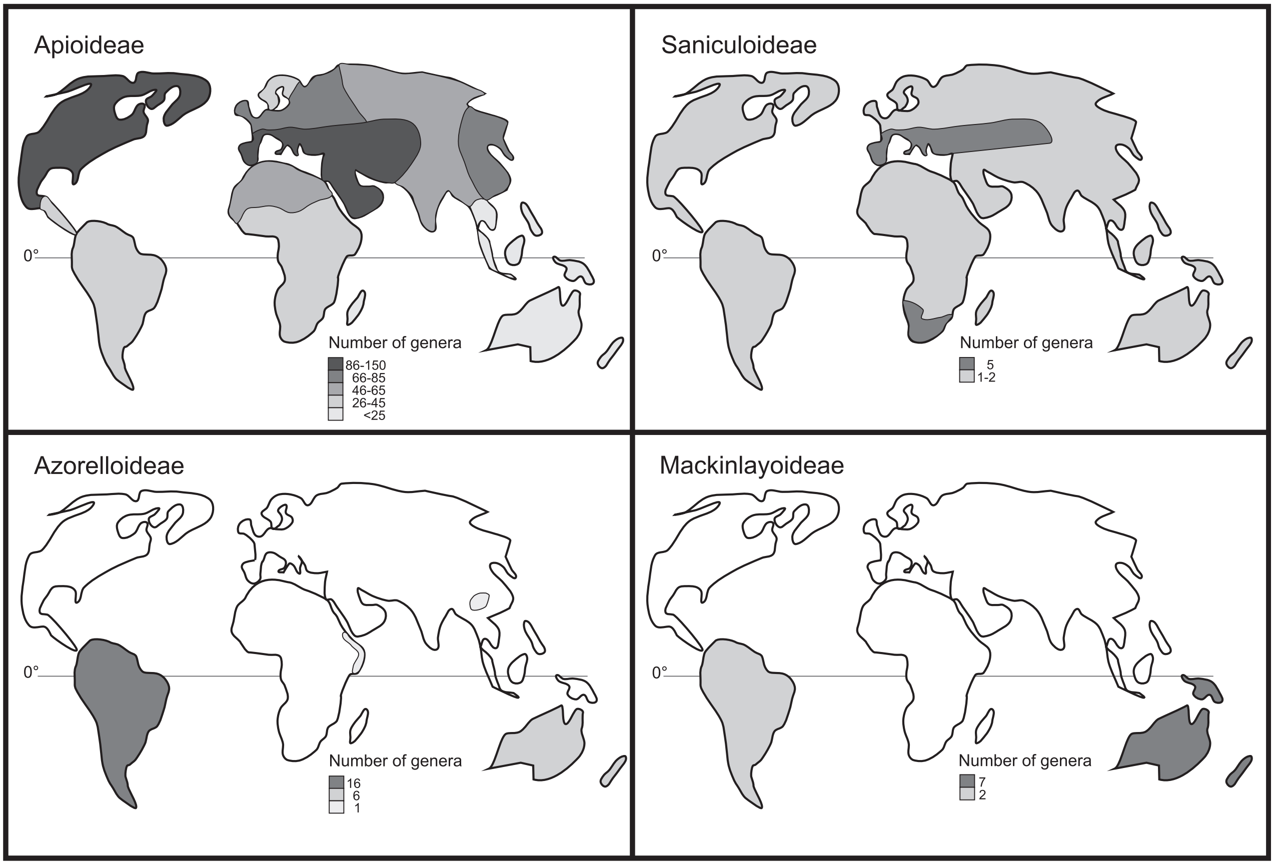


Figure 1 Patterns of distribution of richness of genera for each of the four subfamilies of Apiaceae: Apioideae, Saniculoideae, Azorelloideae and Mackinlayoideae.

diverging lineages (i.e. its four subfamilies) was in the Southern Hemisphere based on molecular phylogenetic and biogeographical studies. Specifically, subfamilies Apioideae and Saniculoideae were inferred to have originated in southern Africa (Calviño *et al.*, 2006, 2008a) and crown Apiaceae was estimated to have originated in Australasia during the Early Palaeogene (54 Ma; highest posterior density: 43–66 Ma; Beaulieu *et al.*, 2013). Questions arise on how the ancestors of Azorelloideae got to South America and those of Apioideae and Saniculoideae got to southern Africa. Apiaceae, therefore, provide an excellent system in which to study pathways of expansion across the Southern Hemisphere after the break-up of West Gondwana and how, when and with what frequency these lineages moved to the Northern Hemisphere.

The intercontinental disjunctions of Apiaceae subfamilies can be explained by either a combination of vicariance and dispersal or dispersals alone based on the palaeogeography of the Southern Hemisphere. By the time of origin of Apiaceae the following routes of expansion existed between Australasia, South America and Africa: (1) a trans-Antarctic route, connecting Australia and South America through Antarctica until the Oligocene (McLoughlin, 2001); (2) a trans-Atlantic route, consisting of islands of considerable size that connected South America and Africa across the Atlantic Ocean (Bandoni de Oliveira *et al.*, 2009); and (3) the Kerguelen plateau, comprised of a submerged area in the Antarctic sector of the Indian Ocean that allowed connections between Africa and Australasia (McLoughlin, 2001). The trans-Antarctic route is the only pathway that involves vicariance, while the other two routes involve dispersals as mechanisms to explain the current intercontinental disjunctions of the subfamilies. Apiaceae fruits have features favouring water dispersal (Calviño *et al.*, 2008a,b) and indeed such a mechanism has already been invoked to explain disjunctions within the family (e.g. Calviño *et al.*, 2008b; Spalik *et al.*, 2010). It has been argued that most plant families and genera are not old enough to be affected by continental drift (e.g. Beaulieu *et al.*, 2013). However, until 28–32 Ma, the trans-Antarctic route was contiguous and only later separated by seas (McLoughlin, 2001; Sanmartín & Ronquist, 2004). Therefore, the relative importance of vicariance and transoceanic dispersals in explaining the current intercontinental disjunctions exhibited by Apiaceae today is unclear, for its subfamilies probably originated when South America-Australia were still connected, but after Africa had already separated.

Africa was isolated from other Gondwanan continents and Laurasia for *c.* 75 Myr, from the Mid-Cretaceous to Early Miocene (Scotese, 2004). However, this isolation was broken intermittently by discontinuous filter routes linking Africa to these other land masses (Gheerbrant & Rage, 2006). In Apiaceae, at least one connection between Africa and South America or Australasia must be invoked to explain the origin of subfamilies Apioideae and Saniculoideae in southern Africa. Moreover, Africa was the source of the vast majority of Eurasian umbellifers recognized today (Calviño *et al.*, 2006, 2008a). Therefore, the connections between Africa and other continents during this period of isolation appear to have had an important impact on the diversification of Apiaceae. Intracontinental disjunctions in Africa have been explained in terms of vicariance by fragmentation of an ancient widespread flora driven by aridification from the Miocene onwards, or by recent dispersal events followed by diversification in situ and restriction of expansion due to the existence of effective environmental barriers, such as hyper arid regions (reviewed in Mairal *et al.*, 2015). Southern African Apiaceae have been considered relicts of a much richer umbelliferan flora, based on their morphological uniqueness (Burtt, 1991), and while Africa was the place of origin of the first ancestors of Apioideae and Saniculoideae, it also received successive lineages that later dispersed back to Africa mainly from Eurasia (Calviño *et al.*, 2006, 2008a). Most of the lineages that dispersed back, however, currently occupy northern or eastern regions of Africa and not the southern African regions as do the descendents of the first diverging lineages of Apioideae and Saniculoideae (e.g. Burtt, 1991; Calviño *et al.*, 2006, 2008a; Spalik *et al.*, 2010). These intracontinental disjunctions appear to reflect an assembly partitioned through time, with those lineages diversifying in Africa for long periods in isolation now restricted mainly to southern Africa through vicariance and extinction, and with post Miocene newcomers from Eurasia that could not expand southwards due to the existence of effective environmental barriers.

The aim of this study was to estimate the most likely pathways of expansion of the first diverging lineages of Apiaceae across the Southern Hemisphere and with Eurasia by reconstructing the biogeographical history of the family. Specifically, we address the following hypotheses: (1) transoceanic dispersals, not vicariance, explain the current intercontinental disjunctions of the subfamilies of Apiaceae; (2) after the break-up of West Gondwana, Africa maintained connections with Australia, South America and/or Eurasia that were important for the later diversification of Apiaceae; and (3) the African Apiaceae assembly is composed of lineages that diversified for a long period of time in situ and are now restricted mainly to southern Africa and of post Miocene newcomers that are mostly restricted to northern and eastern Africa by effective environmental barriers.

MATERIALS AND METHODS

Taxa and outgroup selection

In total, 211 accessions were examined for cpDNA *rps16* intron and/or nrDNA internal transcribed spacer (ITS) sequence variation (see Appendix S1 in the Supporting Information). In the phylogenetic analysis of *rps16* intron sequences, 129 accessions were considered, which included 87 genera and 115 species of Apiaceae and two genera (three species) of Araliaceae. In the ITS phylogenetic analysis, 118 accessions of Apiaceae (representing 77 genera and 107 species) were examined. These Apiaceae accessions are a complete representation of all major lineages of the family, as recognized on the basis of molecular phylogenetic studies that have also taken into consideration its morphological and geographical diversity (Calviño *et al.*, 2006; Calviño & Downie, 2007; Nicolas & Plunkett, 2009; Downie *et al.*, 2010). When selecting taxa, we made sure that the geographical diversity within each major lineage was fully represented. We also ensured that all Malagasy and southern African taxa whose phylogenetic positions were previously unknown were included to better understand the timing and direction of dispersals between Africa and other continents. Although Araliaceae and Apiaceae subfamilies Azorelloideae and Mackinlayoideae were each represented by relatively few accessions, the biogeographical estimations are not likely to be affected (see Biogeographical analyses).

Trees resulting from analyses of *rps16* intron sequences were rooted with *Aralia* L. and/or *Hydrocotyle* L. (Araliaceae; Chandler & Plunkett, 2004). ITS data are too divergent for phylogenetic analyses at deep levels of comparison, such as among members spanning the entire family Apiaceae (Calviño & Downie, 2007), precluding a combined analysis of ITS and chloroplast data across all taxa. Because the results of the Apiaceae *rps16* intron phylogenetic analyses were congruent with studies using other chloroplast or nuclear regions (Chandler & Plunkett, 2004; Calviño & Downie, 2007; Nicolas & Plunkett, 2009; Magee *et al.*, 2010), they were used to partition the taxa of the ITS study into two data sets so that ambiguity of alignment is reduced or avoided and phylogenetic resolution is increased. These two data sets comprised (1) an ITS matrix with a more thorough representation of taxa within the distal apioid tribes Pimpinelleae, Apieae, Tordylieae, Selineae, Echinophoreae, Careae, Pyramidoptereae and Smyrnieae, with representatives of Oenantheae identified as the outgroup, and (2) a combined ITS and *rps16* intron matrix of Annesorhizeae, with four accessions of *Lichtensteinia* selected as the outgroup. For the distal apioids data set our approach was to increase taxon sampling at the expense of reducing commonality between the ITS and *rps16* intron data sets, thereby precluding the possibility of a combined analysis of all data.

Phylogenetic analyses

Strategies used to obtain and align both *rps16* intron and ITS sequences were in accordance with Calviño *et al.* (2006). In the *rps16* intron data matrix, binary-coded indels were added to incorporate length-mutational information into the analysis. In the ITS data matrices, gaps were not scored as additional binary characters because very few were informative among ingroup taxa.

The Apiaceae *rps16* intron, distal apioids ITS and *Annesorhizeae* ITS plus *rps16* intron data matrices were each analysed using maximum parsimony (MP), as implemented by PAUP* (Swofford, 2002) and employing the heuristic search strategies of Calviño *et al.* (2006). Bootstrap values (BS) were calculated from 10,000 replicate analyses using 'fast' stepwise-addition of taxa. Bayesian inference of the three data sets (all without scored gaps) was conducted using MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001). Prior to analysis, MrModeltest 2.3 (Nylander, 2004) was used to select an evolutionary model of nucleotide substitution that best fits these data, as selected by the Akaike information criterion estimator (Posada & Buckley, 2004). The best-fit model selected for all partitions was GTR+I+G. For the *Annesorhizeae* ITS plus *rps16* intron data matrix, the overall mutation rate was allowed to vary between partitions. From different random starting trees, two independent analyses with four chains each were run for 5 million generations; in some instances, the analyses were stopped earlier when the average standard deviation of the split frequencies between runs dropped to less than 0.01 using a relative burn-in of 25% (indicating convergence in topology). Trees and branch lengths were saved to a file every 100 generations. Stationarity and additional convergence search strategies were the same as used in Calviño & Downie (2007). All three data sets (without scored gaps) were also analysed using maximum likelihood (ML), as implemented by RAxML 7.0.3 (Stamatakis, 2006). The best scoring ML tree was searched under a GTR+G model and BS were calculated from 1000 replicate analyses using the rapid BS algorithm in a single run.

Dating analyses

Estimation of divergence times among Apiaceae lineages was assessed using R8S 1.7 under a penalized likelihood (PL) method (Sanderson, 2003) and the truncated Newton algorithm on the *rps16* intron ML tree. The outgroup, *Aralia chinensis*, was pruned prior to analysis. Because terminal zero-length branches can cause problems with the estimation of divergence times (Sanderson, 2003), the accessions *Billburttia capensoides* 3057 and *Tana bojeriana* 3772 were also removed as their sequences were identical to those of *B. capensoides* 3055 and *T. bojeriana* 3067. A previous molecular phylogenetic dating of the asterids estimated the split between Apiaceae and Araliaceae at 70 Ma (Bremer *et al.*, 2004). Other attempts to date this node estimated the same age (Magallón *et al.*, 1999; Davies *et al.*, 2004) or a younger one (41–45 Ma; Wiskström *et al.*, 2001). This younger age, however, was argued to be underestimated (Bremer *et al.*, 2004). Therefore, the age of the root node of the *rps16* intron ML tree was fixed to 70 Ma. This age is also consistent with the earliest Araliaceae fossils from the Maastrichtian (Knobloch & Mai, 1986). An additional calibration point was used to constrain the *Steganotaenia* crown group to a minimum of 1.6 Ma based on a lower Pleistocene wood fossil assigned to *Steganotaenia araliacea* (Dechamps, 1978). Other fossils known from the first diverging lineages of Apiaceae are pollen assumed to be of *Bupleurum*, *Steganotaenia* and *Heteromorpha* (Gruas-Cavagnetto & Cerceau-Larrival, 1984), but because of doubtful identities they could not be assigned unambiguously to particular nodes of the phylogeny and were not included as additional calibration points (Banasiak *et al.*, 2013). The optimal value of smoothing was determined via cross-validation over a range of eight smoothing values, starting with a log-smoothing value of 0 and increasing it by 0.5. The smoothing value with the lowest chi-square value was selected for the final PL analysis (Sanderson, 2003). Ninety-five per cent confidence intervals (CIs) on ages for selected nodes were estimated from 100 *rps16* intron ML trees having the same topology but different branch lengths under the PL method and strategy described above. Some degree of skewing is expected when inferring the distribution of dates using nonparametric bootstraps from a posterior distribution of branch lengths; therefore, methods that account for skewing (i.e. ABCq, BCa, bootstrap-t) were used to correctly estimate CIs (Burbrink & Pyron, 2008). To estimate 95% CIs using these methods and to calculate the ABCq shape parameter of the distribution of dates for all selected nodes, we generated a script based on the spreadsheet available from Burbrink & Pyron (2008).

Biogeographical analyses

We were interested in large-scale biogeographical patterns, so we defined large areas from across the world according to their palaeobiogeographical affinities. To address hypotheses about the assembly of African umbellifers, we subdivided the continent into four areas using physiographic (e.g. climate, vegetation type, landforms) and palaeogeological criteria. The following eight areas were defined: (1) Australasia (including Australia, New Caledonia, New Guinea and New Zealand); (2) southern Africa (i.e. Botswana, Lesotho, Namibia, South Africa and Swaziland); (3) South America; (4) Eurasia; (5) Madagascar; (6) north-eastern Africa and Socotra (i.e. Eritrea, Djibouti, Ethiopia, Somalia, Burundi, Kenya, Malawi, Rwanda, Tanzania, Uganda, east Zambia and the Socotra islands); (7) northern Africa (i.e. Algeria, Egypt, Libya, Morocco and Tunisia); and (8) North America. Within Azorelloideae, each terminal was coded as South America, whereas within Mackinlayoideae and Araliaceae terminals were coded as Australasia because at least the first four diverging lineages within each of these taxa occupy these areas, based on comprehensive sampling (Nicolas & Plunkett, 2009).

Dispersal-extinction-cladogenesis (DEC; Ree & Smith, 2008) analyses were performed using LAGRANGE, using the time-calibrated PL Apiaceae *rps16* intron tree or setting the age of the root node to 36 and 58 Ma in the distal apioids and Annesorhizeae ML trees respectively. The maximum number of ancestral areas was restricted to two because most extant species of Apiaceae are restricted to one, or very rarely two, areas. Also, to analyse the stability of the results with reference to prior knowledge of the geological history of the areas, we ran two analyses: model (M) 1 – single dispersal rates across areas and across time (no prior knowledge); and M2 – three time slices (TS; 60–80 Ma; 30–60 Ma; 0–30 Ma) with transition rates dependent on the geographical connectivity between areas as defined by Buerki *et al.* (2011), except for those between Africa and South America. Buerki *et al.* (2011) disallowed direct movement between South America and Africa from 80 Ma onwards, as a result of the opening of the South Atlantic Ocean *c.* 95 Ma. However, the available geological information indicates the presence of an island chain between Africa and South America across the South Atlantic 40–80 Ma (Bandoni de Oliveira *et al.*, 2009). The results of applying such a strong relative disallowance of dispersals between South America and Africa will likely reconstruct an alternative route artefactually due to the extreme constraint imposed by a model that does not reflect current geological evidence. Therefore, transition rates between Africa and South America for TS 30–80 Ma were coded as 0.5 to be consistent with the coding of other connections that were not continuous.

RESULTS

Phylogenetic analyses

Characteristics of the alignments and results of MP, Bayesian and ML analyses of the Apiaceae *rps16* intron, distal apioids ITS and *Annesorhizeae* ITS plus *rps16* intron data sets are presented in Appendix S2. For each data set, the phylogenies estimated from the different reconstruction methods were highly consistent with each other, and support values for nodes important for biogeographical reconstructions of Apiaceae subfamilies and of dispersals to and from Africa were strong (see Appendix S2). Phylogenetic relationships among the major clades of Apiaceae (Fig. 2; see Appendix S2) are wholly congruent with those inferred by previous studies using ITS and chloroplast markers (e.g. Calviño & Downie, 2007; Nicolas & Plunkett, 2009; Downie *et al.*, 2010; Magee *et al.*, 2010).

Dating analyses

A chronogram showing the estimation of divergence times for the Apiaceae *rps16* intron ML tree is presented in Fig. 2, with 95% ABCq CIs for 17 selected nodes indicated. CIs estimated using alternative methods are presented in Table 1, with the ABCq method favoured for presentation and subsequent discussion because it is the most conservative (i.e. it has the widest CIs). The bootstrap distribution of dates at all selected nodes is asymmetric (a normal distribution of the samples was rejected at a 0.05 significance level and the ABCq shape parameter is different from 1), except at a single node (crown Mackinlayoideae). This indicates that in this study the standard normal method is not appropriate to calculate 95% CIs because it assumes that the bootstrap distribution is symmetric.

Crown Apiaceae was inferred to have originated 65.8 Ma (CI 60.9–71.2). Dates for the crown groups of the four subfamilies of Apiaceae were inferred as follows: Mackinlayoideae, 36.8 Ma (CI 26.5–45.8); Azorelloideae, 58.4 Ma (CI 49.3–68.9); Saniculoideae, 58 Ma (CI 46.8–76.1); and Apioideae, 58.4 Ma (CI 45.9–76.1). The split between Azorelloideae and the rest of Apiaceae (excluding Mackinlayoideae) was immediately followed by the divergence between the *Hermas* clade and the clade of Apioideae plus Saniculoideae, at 63.6 Ma (CI 55.4–72.6) and 63.1 Ma (CI 54.9–72.2) respectively. Expansions out of Africa to Eurasia were estimated between 51.4 and 54.5 Ma (CI 37.2–71.6) for the stem of Chamaesieae to Pimpinelleae, no earlier than 51.2 Ma (max. CI value 78) in Annesorhizeae, and between 27.3 and 41.7 Ma (CI 16.357.8) within subfamily Saniculoideae. Expansions from Africa to Madagascar were estimated no earlier than 20.4 Ma (max. CI value 40). Similarly, all expansions from Eurasia back to Africa were dated no earlier than 23.1 Ma (max. CI value 40).

Biogeographical analyses

Ancestral area reconstructions (including alternative reconstructions within the confidence window of two log-likelihood units) for all data sets and models analysed are presented in Appendix S3. All analyses estimated an expansion from Australasia as the most likely pathway to explain the origin of Saniculoideae and Apioideae in southern Africa (Fig. 2). Crown Azorelloideae is estimated to have originated in South America, most likely by expansion from southern Africa; in an alternative reconstruction, expansion is estimated from Australasia, but this shows a considerably lower relative probability (0.45 vs. 0.26). Therefore, the most likely pathways of expansion of the first diverging lineages of Apiaceae imply two transoceanic dispersals, one between Australasia and southern Africa and the other between Africa and South America (Fig. 3).

Based on all data sets, three expansions from southern Africa to Eurasia were estimated before the collision of Africa with Laurasia; these occurred in tribes Saniculeae and Annesorhizeae and in the stem of Chamaesieae to Pimpinelleae (Fig. 2, see Appendix S3). The Annesorhizeae data set resolves the topological uncertainty apparent in the Apiaceae *rps16* intron data set, and estimates one dispersal from southern Africa to Eurasia and another later from Eurasia to northern Africa to explain the present-day distribution of *Molopospermum* and *Astydamia* (see Appendix S3). From the Miocene onwards, African umbellifers expanded out of the continent to Madagascar and Africa received at least five lineages from Eurasia and one from Madagascar (Figs 2 & 4). Expansions from Africa to Madagascar include at least four dispersals, most likely from southern Africa in

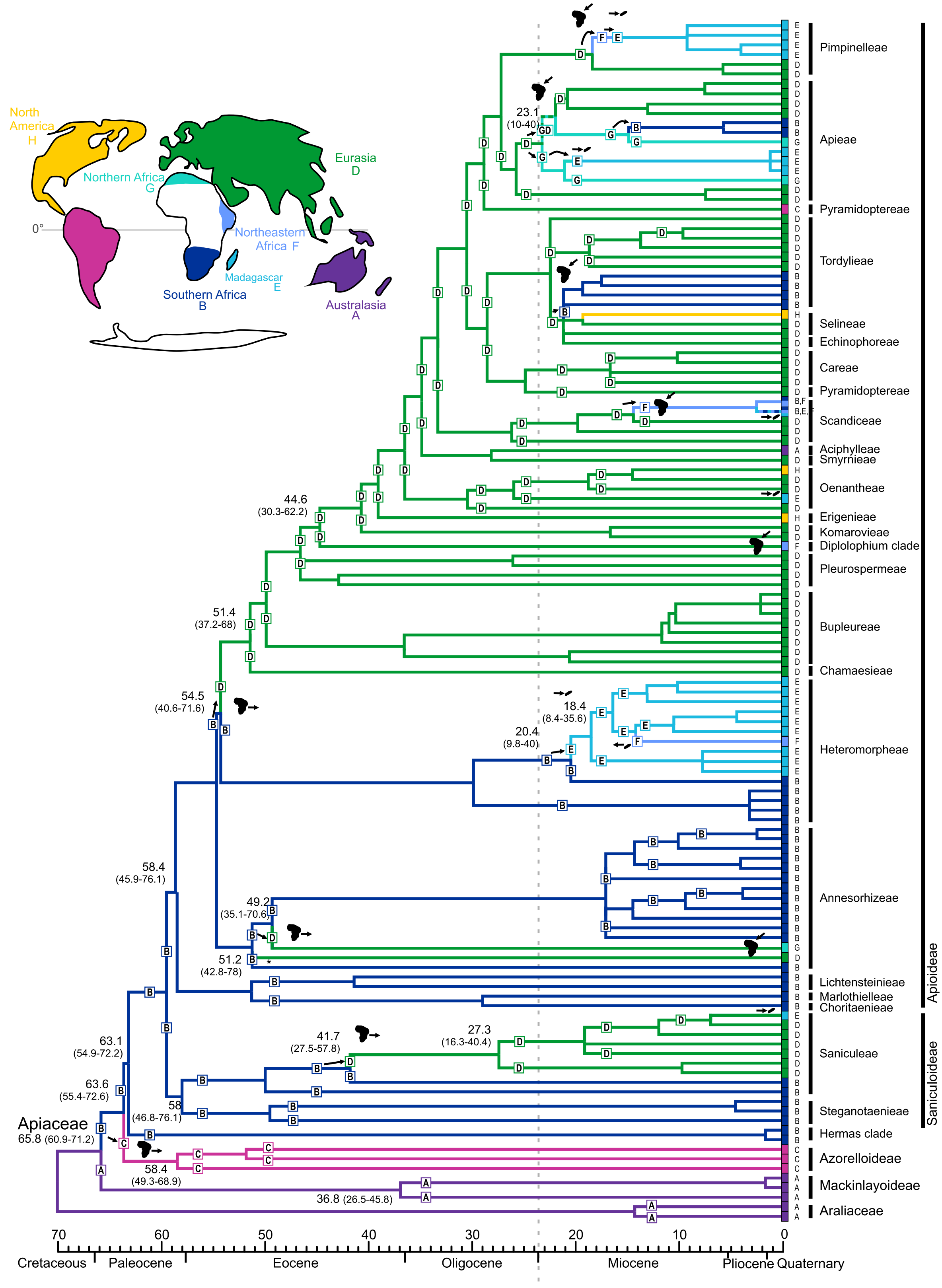


Figure 2 Chronogram showing the estimation of divergence times for the Apiaceae *rps16* intron maximum likelihood tree using penalized likelihood, with 95% ABCq confidence intervals presented for 17 selected nodes. Colours and letters on branches correspond to the areas indicated on the map and represent the most likely ancestral distributions of Apiaceae, its subfamilies, tribes and other major clades, as estimated by dispersal-extinction-cladogenesis (DEC) analyses of all data sets (Appendix S3). The bracketed names are based on Calviño & Downie (2007) and Downie *et al.* (2010). Arrows indicate dispersal events that involve Africa.

Table 1 Point estimate (PE) of divergence times for 17 selected nodes of Apiaceae estimated under a penalized likelihood method, 95% confidence intervals using standard normal (SN), bias corrected and accelerated (BCa), bootstrap-t, approximate bootstrap confidence quadratic (ABCq) methods and the ABCq shape parameter. In column 1, taxa separated by a hyphen indicate the most recent common ancestor between those terminals.

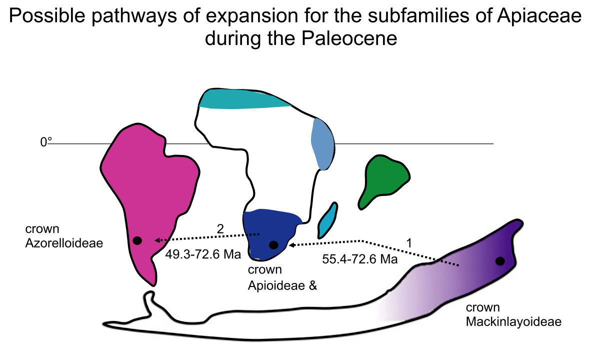
Node	PE (Ma)	SN (Ma)	BCa (Ma)	Bootstrap-*t* (Ma)	ABCq (Ma)	ABCq shape (Ma)
Crown Apiaceae	65.8	64.9–65.6	62.7–64.2	65.6–70.1	60.9–71.2	1.1
Azorelloideae – Apioideae	63.6	61.6–62.7	61.3–62.3	67.5–75.1	55.4–72.6	1.1
Hermas clade – Apioideae	63.1	60.9–62.4	61.4–58.4	65.0–67.8	54.9–72.2	1.1
Crown Azorelloideae	58.4	56.5–57.8	52.6–60.8	58.8–60.4	49.3–68.9	1.2
Crown Apioideae	58.4	53.7–55.9	41.9–57.0	57.9–76.4	45.9–76.1	1.4
Crown Saniculoideae	58.0	53.0–55.5	50.8–57.7	60.8–61.1	46.8–76.1	1.6
Annesorhizeae – Pimpinelleae	54.5	50.4–52.5	51.1–54.4	59.4–73.1	40.6–71.6	1.2
Chamaesieae – Pimpinelleae	51.4	47.4–49.5	46.8–49.4	54.8–64.7	37.2–68.0	1.2
Crown Annesorhizeae	51.2	42.8–46.5	45.8–46.5	52.5–60.4	42.8–78.0	3.2
Itasina – Annesorrhiza (Apioideae Annesorhizeae)	49.2	43.3–46.6	40.4–45.7	45.0–50.6	35.1–70.6	1.5
Diplolophium clade – Pimpinelleae	44.6	40.5–43.1	38.0–49.5	49.4–61.0	30.3–62.2	1.2
Arctopus – Sanicula (Saniculoideae tribe Saniculeae)	41.7	39.0–41.1	46.8–51.7	44.5–56.9	27.5–57.8	1.1
Crown Mackinlayoideae	36.8	37.1–38.4	35.6–39.2	36.8–38.6	26.5–45.8	0.9
Astrantia – Sanicula (Saniculoideae tribe Saniculeae)	27.3	26.0–27.6	24.5–30.0	30.3–37.5	16.3–40.4	1.2
Stoibrax – Petroselinum (Apioideae tribe Apieae)	23.1	19.6–21.9	27.1–30.0	31.1–36.6	10.1–40.0	1.3
Dracosciadium – Tana (Apioideae tribe Heteromorpheae)	20.4	14.8–16.8	4.3–5.7	20.1–36.6	9.8–40.0	1.9
Andriana – Tana (Apioideae tribe Heteromorpheae)	18.4	13.3–15.5	4.9–11.0	22.6–33.4	8.4–35.6	1.7

Heteromorpheae and *Agrocharis* (tribe Scandiceae), from north-eastern Africa in *Phellolophium madagascariense* and *Pimpinella betsileensis* (tribe Pimpinelleae), and from northern Africa in *Billburttia capensoides* (tribe Apieae; Fig. 2, see Appendix S3). Dispersals from Madagascar to north-eastern Africa only included one unambiguous event that took place from within tribe Heteromorpheae (i.e. *Peucedanum eminii*). The five expansions from Eurasia to Africa were estimated to north-eastern Africa in the *Diplolophium* clade, Pimpinelleae and Scandiceae, southern Africa in Tordylieae, and northern Africa in Apieae (Fig. 2, see Appendix S3). Within Apieae, a wider northern African-Eurasian ancestral distribution with later extra dispersals to (and/or from) Eurasia are also estimated. The ratio between overall extinction and dispersal rates was 2.8 for M1 and 1.7 for M2.

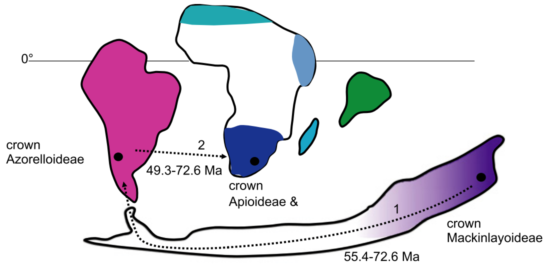
DISCUSSION

Pathways of expansion of Apiaceae subfamilies across the Southern Hemisphere

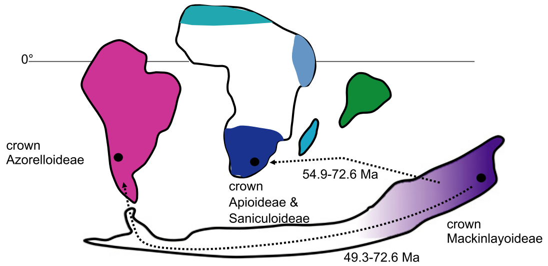
Previous biogeographical studies estimated that crown Apiaceae originated in Australasia 43–66 Ma (Beaulieu *et al.*, 2013). Our studies place its origin between 60.9 and 71.2 Ma, about 10–20 Myr earlier, and estimate that the four subfamilies of Apiaceae diverged during the Late Cretaceous-Palaeocene (45.9–71.2 Ma) in the Southern Hemisphere: stem Mackinlayoideae in Australasia, stem Azorelloideae in South America and stem Apioideae and Saniculoideae in southern Africa. These intercontinental disjunctions are most likely explained by two transoceanic dispersals, possibly involving expansions via the Kerguelen Plateau from Australasia to southern Africa and later via the trans-Atlantic route from southern Africa to South America (Fig. 3a). The Kerguelen Plateau has often been hypothesized to play a role in explaining disjunctions between Australia and Africa (Almeida *et al.*, 2012 and references cited therein). In contrast, it is usually presumed that the Atlantic Ocean was an effective barrier to dispersal, even shortly after its opening (105–135 Ma, McLoughlin, 2001). Dispersal via the trans-Atlantic route is often discarded as a causal explanation for African-South American disjunctions that post-date the break-up of West Gondwana, and many worldwide biogeographical analyses impose very low dispersal rates between Africa and South America from 80 Ma onwards (e.g. Buerki *et al.*, 2011). However, our results add to the growing body of evidence that suggest that biological connections between Africa and South America after their separation were more common than previously thought. Other examples include not only plants and fungi but also insects and vertebrates and some with very poor dispersal capabilities (e.g. 11 examples cited in Ezcurra & Agnolín, 2012; *Manataria* butterflies, *c.* 40 Ma, Price *et al.*, 2011; Sapotaceae, 61–72 Ma, Bartish *et al.*, 2011; Asteraceae, < 50 Ma, Katinas *et al.*, 2013; Asclepiadoideae, 32 Ma, Rapini *et al.*, 2007; Geraniales, 27–67 Ma, Sytsma *et al.*, 2014; and Danthonioideae, 4–21 Ma, Linder *et al.*, 2013). The trans-Atlantic route was not only important for the large number of lineages that crossed it but also for the impact the new arrivals had on the sink continent. The amphisbaenians that crossed the Atlantic Ocean from Africa resulted in a tropical American radiation that now represents one-half of all known amphisbaenian species (Vidal *et al.*, 2008). The Asteraceae, once in Africa from South America, radiated and diversified into other



(a) Most likely based on DEC analyses



(b) Alternative reconstruction with lower relative probability (AppendixS3)



(c) Only recovered when dispersal connectivities between Africa and South America were disallowed (rates=0.01, data not shown)

Figure 3 Possible scenarios for the origin of Apiaceae subfamilies during the Palaeocene. (a) The most likely reconstruction based on this study; (b) alternative reconstruction within the 2-log likelihood, but with lower relative probably (Appendix S3); (c) only recovered when dispersal connectivities between Africa and South America were almost disallowed (discussed under Materials and Methods). Arrows represent range expansions and numbers indicate the sequence of these events. Circles show the estimated places of origin of the ancestors of the crown subfamilies of Apiaceae.

continents and is now a very species-rich family (Katinas *et al.*, 2013). Within Apiaceae, the ancestors that arrived in South America from Africa diversified considerably and now represent major floristic components of many desert and high altitude Andean regions. The arrival of stem Azorelloideae through the trans-Atlantic route (estimated between 20° and 30° S, Bandoni de Oliveira *et al.*, 2009) also implies that the origin of the subfamily was in eastern South America (e.g. Brazil-Uruguay) where the first diverging lineages of the subfamily are currently distributed (Nicolas & Plunkett, 2009). Later, colonization of the rising Andes occurred, as new environments and more arid areas became available (Ortiz-Jaureguizar & Cladera, 2006).

African connections with other continents after its break-up from Gondwana

From the Mid-Cretaceous to Early Miocene, Africa did not have continuous physical connections with any other continent (Scotese, 2004). Despite this solitude, Africa was hypothesized to have had a complex palaeogeographical history composed of isolation coupled with intermittent faunal exchanges with other Gondwanan continents and with Laurasia across discontinuous filter routes (Gheerbrant & Rage, 2006). However, faunal interchanges between Africa and other Gondwanan continents were rare and considered mostly out of Africa (Gheerbrant & Rage, 2006), suggesting that these links had little influence on the evolution of the African fauna per se. In contrast, the biogeographical history of the first diverging lineages of Apiaceae shows links between Africa and Australasia and between Africa and South America. For the latter, Africa likely acted as the source continent, but in the African-Australasian connection, Africa received the ancestors of Apiaceae (save Mackinlayoideae) which diversified on the continent and gave rise to the majority of umbellifers that occur south of the Sahara today (23 endemic genera and 116 species, Burtt, 1991; van Wyk *et al.*, 2013). Similarly, the Asteraceae that arrived in Africa from South America diversified into some 2500 African species of the Carduoideae subfamily (Funk *et al.*, 2009). Therefore, although connections between Africa and other Gondwanan continents were few relative to its long period of isolation, the links that brought lineages to the African continent had a tremendous impact on the evolution of its flora. The high degree of endemicity of the southern African flora (Goldblatt, 1978) underscores its long period of isolation, which is also reflected by the phylogenies presented herein that show the earliest diverging lineages of Apioideae and Saniculoideae originating in Africa and diversifying in situ since the Palaeocene, with no input from newcomers until the Miocene.

The exchange of fauna between Africa and Eurasia prior to their collision (i.e. before the Early Miocene) was numerous and predominantly from Eurasia to Africa (Gheerbrant & Rage, 2006). Our results estimate three expansions between these regions from 27.3 to 54.5 Ma, supporting the hypothesis that dispersals across the Tethys Seaway were effective during this period. Our results also estimate that these dispersals were unidirectional, from southern Africa to Eurasia (Fig. 4a). Dispersals across the Tethys Seaway were facilitated by the Mediterranean Tethyan Sill which consisted of a series of emergent platforms controlled by sea-level changes that connected north-western Africa with Europe and north-eastern Africa with south-eastern Europe and Asia (Gheerbrant & Rage, 2006). It is likely that the first diverging

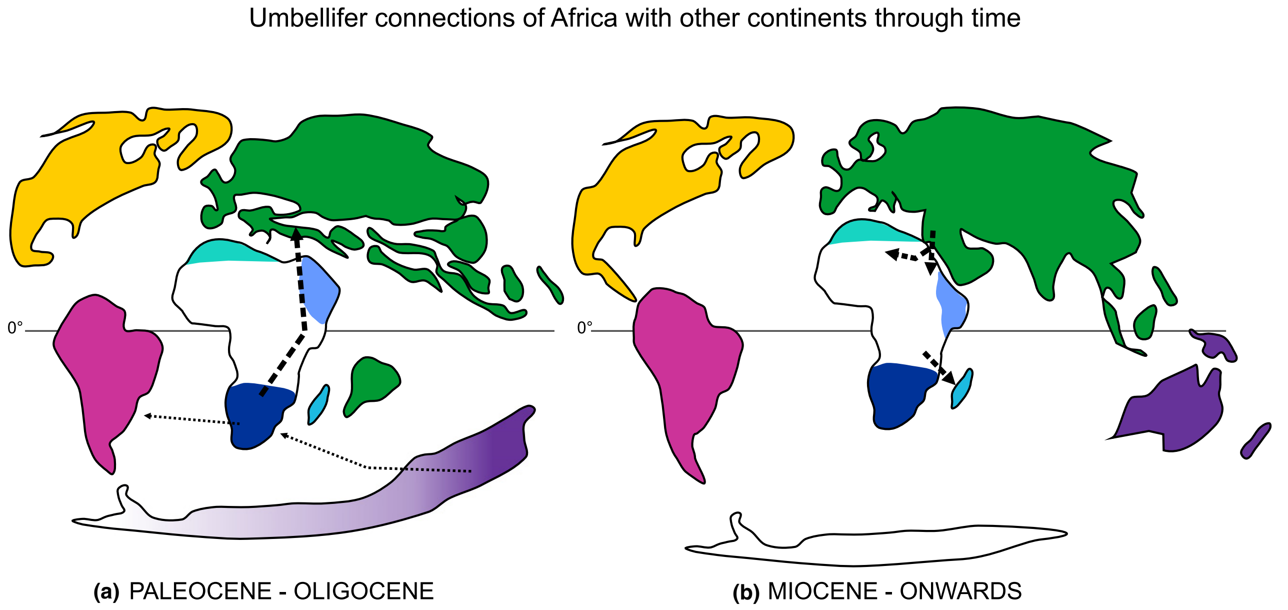


Figure 4 Connectivity of Africa with other continents by umbellifer dispersals through time: (a) from Palaeocene to Oligocene and (b) from Miocene onwards.

lineages of Apioideae and Saniculoideae reached a widespread distribution within Africa, and that many of the southern African-Eurasian disjunctions observed today are the result of extinctions driven by the increasing aridification of Africa from the Miocene onwards (Axelrod & Raven, 1978). Such an idea is supported by the dating analyses that show long intervals (some more than 20 Myr) between the stem and crown of the southern African lineages, by the DEC results that estimate that extinctions were two to three times higher than dispersals, and by the presence of pollen fossils of the Anglo-Parisian basin (Eocene) that are similar to extant African umbellifer endemics (Gruas-Cavagnetto & Cerceau-Larrival, 1984).

From the Miocene onwards, African umbellifers expanded out of the continent to Madagascar, and Africa received umbellifer lineages from Eurasia, with very rare dispersals in other directions. For some species, African-Malagasy dispersals during the Miocene have been explained by bird migrations (e.g. Renner, 2004); however, Apiaceae fruits from those lineages showing African-Malagasy connections do not show any adaptations to zoochory, but rather for wind or water dispersal (Calviño *et al.*, 2008a,b; van Wyk *et al.*, 2013). According to Ali & Huber (2010), water currents of the Indian Ocean flowed eastwards from Africa to Madagascar from the Eocene to the Early Miocene. Many of the umbellifer dispersals estimated from eastern and southern Africa to Madagascar likely occurred at the end of this timeframe and others even post-date these favourable current conditions. Still, the timing of umbellifer dispersals to Madagascar and their African origins coincides with those of many other plant and animal lineages, supporting the hypothesis that the Madagascar biota mainly resulted from diversification in isolation from ancestors that dispersed relatively recently from Africa across the Indian Ocean (Yoder & Nowak, 2006).

The Early Miocene marks the start of major changes in the vegetation of Africa, where rain forests were increasingly restricted and replaced by drier ecosystems, such as savannas and woodlands, that expanded and diversified into more arid types, culminating in the establishment of the Namib (16–17 Ma) and later the Sahara (6–8 Ma) deserts (Axelrod & Raven, 1978; Senut *et al.*, 2009). This coincidence of the arrival of umbellifers from Eurasia at a time when arid habitats were expanding in northern and eastern Africa, together with the capability of umbellifers to disperse across the Tethys in previous times, suggests that dispersal from Eurasia to Africa was limited by the availability of suitable habitats rather than by movement opportunities. The same was concluded for danthonioid grasses (Linder *et al.*, 2013), as well as for other apioid lineages that show intercontinental disjunctions due to Neogene dispersals (Spalik *et al.*, 2010). The fact that umbellifers that dispersed from Eurasia remained in northern and/or eastern Africa suggests that the Namib and later the Sahara deserts acted as effective barriers restricting the expansion of most Neogene-Eurasian umbels to southern Africa.

CONCLUSIONS

The Southern Hemisphere has played a key role in the origin and early diversification of Apiaceae, currently a mostly north temperate family. Given the most probable ages and patterns of ancestral area inheritance, Apiaceae originated in Australasia and likely colonized Africa and South America by two transoceanic dispersals. After the break-up of Gondwana, Africa maintained connections as a sink continent with Australasia and later as a source continent with South America and Eurasia. These transoceanic dispersals, occurring from the Late Cretaceous to Eocene, explain the current intercontinental disjunctions of the subfamilies of Apiaceae and are significant for they ultimately resulted in the diversification of Azorelloideae in South America and of the vast majority of Apioideae and Saniculoideae known today in Eurasia. Exchanges of umbellifers between Africa and Eurasia were largely directional in time, out of Africa during the early Palaeogene and mostly back from Eurasia during the Neogene. The arrival of Eurasian umbellifers in Africa is likely associated with the aridification of the continent from the Miocene onwards and the availability of habitats suitable for establishment. The umbellifer component of the African flora was likely assembled by relicts of Palaeocene lineages currently restricted mainly to southern Africa, together with relatively recently arrived lineages from Eurasia that mostly remained in northern and eastern Africa once environmental barriers were effective.

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SUPPORTING INFORMATION

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

Appendix S1 Accessions of Apiaceae examined for variation in *rps16* intron and/or nrDNA ITS sequences.

Appendix S2 Phylogenetic trees of Apiaceae.
Appendix S3 Ancestral range scenarios of Apiaceae.

BIOSKETCH

Carolina I. Calviño is a plant systematist whose research interests include phylogenetics, historical biogeography and evolution of morphological traits of the family Apiaceae and the flora of the southern Andes.

Author contributions: C.I.C. conceived the ideas for the manuscript, provided data, performed the analyses and wrote the manuscript, F.E.T. wrote the script to obtain 95% confidence intervals of the bootstrap distribution of dates for all nodes, and S.R.D. provided data and edited the manuscript.

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