Intercontinental disjunctions in *Cryptotaenia* (Apiaceae, Oenantheae): an appraisal using molecular data

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ABSTRACT

Aim The angiosperm genus *Cryptotaenia* (family Apiaceae, tribe Oenantheae) exhibits an anomalous distribution pattern, with five of its eight species being narrow endemics geographically isolated from their presumed relatives. We examined the monophyly of the genus and ascertained the phylogenetic placements of its constituent members in order to explain their distribution patterns.

Location Eastern North America, eastern Asia, the Caucasus, southern Italy, Macaronesia and Africa.

Methods In total, 173 accessions were examined for nuclear rDNA ITS sequence variation, representing nearly all major lineages of Apiaceae subfamily Apioideae and seven species of *Cryptotaenia*. Sampling of tribes Oenantheae, Scandiceae and Pimpinelleae was comprehensive. Phylogenetic analyses included Bayesian, maximum parsimony and neighbour-joining methods; biogeographical scenarios were inferred using dispersal–vicariance analysis (DIVA).

Results *Cryptotaenia* is polyphyletic and includes three distant lineages. (1) *Cryptotaenia sensu stricto* (*C. canadensis*, *C. japonica*, *C. flahaultii* and *C. thomasii*) is maintained within tribe Oenantheae; *C. canadensis* and *C. japonica*, representing an eastern North American–eastern Asian disjunction pattern, are confirmed to be sister species. (2) *Cryptotaenia elegans*, endemic to the Canary Islands, is placed within Scandiceae subtribe Daucinae along with two woody endemics of Madeira, *Monizia edulis* and *Melanoselinum decipiens*. The phylogeny of these Canarian and Madeiran endemics is unresolved. Either they constitute a monophyletic sister group to a clade comprising some Mediterranean and African species of *Daucus* and their relatives, or they are paraphyletic to this clade. The herbaceous/woody genus *Tornabenea* from Cape Verde, once included in *Melanoselinum*, is not closely related to the other Macaronesian endemics but to *Daucus carota*. (3) The African members of *Cryptotaenia* (*C. africana*, *C. calycina* and possibly *C. polygama*) comprise a clade with some African and Madagascan umbellifers; this entire clade is sister group to Eurasian *Pimpinella*.

Main conclusions Elucidating the phylogeny of the biogeographically anomalous *Cryptotaenia sensu lato* enabled hypotheses on the biogeography of its constituent lineages. *Cryptotaenia sensu stricto* exhibits a holarctic distribution pattern, with its members occurring in regions that were important glacial refugia. The genus probably originated in eastern Asia and from there dispersed to Europe and North America. For the Macaronesian endemic species – *C. elegans*, *M. edulis* and *M. decipiens* – DIVA reconstructs either a single dispersal event to Macaronesia from the Mediterranean/African region, or a single dispersal followed by a back-dispersal to the mainland. The radiation of *Tornabenea* from Cape Verde followed a second dispersal of Daucinae to Macaronesia. Woodiness

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in *Melanoselinum/Monizia* and *Tornabenea*, therefore, is a derived and independently acquired trait. The African members of *Cryptotaenia* are derived from an ancestor arriving from the Middle East.

Keywords

Apiaceae, *Cryptotaenia*, disjunctions, Macaronesia, phylogeny, rDNA ITS, taxonomy, Umbelliferae.

INTRODUCTION

Cryptotaenia DC. is a small genus of the angiosperm family Apiaceae subfamily Apioideae exhibiting a disjunct distribution that does not correspond to any major disjunction pattern (Fig. 1). Using Thorne's (1972) typology, this distribution pattern is described as anomalous. Three of its eight species, *Cryptotaenia africana*, *Cryptotaenia japonica* and *Cryptotaenia canadensis* (authorities for all species used in this study are given in Appendix S1 in Supplementary Material), are more-or-less widespread and occur in central and western Africa, eastern Asia, and eastern North America, respectively. The remaining members of the genus are narrow endemics. Melchior (1964) and Heywood (1973) noticed this striking distribution pattern, but Heywood warned against drawing any phytogeographical conclusions based on an inadequate taxonomic study of the genus.

Once recognized as conspecific, *C. canadensis* and *C. japonica* are currently treated as closely related but distinct species (Pan & Watson, 2005). Their distribution represents the classic eastern North American–eastern Asian disjunction pattern, which is explained by intensive floristic exchange between Eurasia and North America throughout the Tertiary, and limited by changing geographical links and climatic conditions (reviewed by Tiffney & Manchester, 2001). Biogeographical analyses of other plant groups based on molecular phylogenies have indicated that such disjunct distributions cannot be explained with a simple vicariance model (Wen, 1999; Donoghue *et al.*, 2001; Xiang & Soltis, 2001). Moreover, several traditionally recognized disjunct taxa were demonstrated to be paraphyletic or polyphyletic (Wen, 1999 and references therein). Wen (1999, 2001) summarized evidence from diverse sources, and suggested that these distributions are relics of the maximum development of temperate forests in the northern hemisphere during the Tertiary. Based on palynological evidence and molecular dating, she concluded that although these disjunctions originated throughout the Tertiary, many of them began in the Miocene. Other molecular studies also emphasized a wide range of timing of Asian–North American speciation events (Xiang *et al.*, 1998, 2000; Donoghue *et al.*, 2001).

Western Eurasian *Cryptotaenia thomasii* and *Cryptotaenia flahaultii* are very narrow endemics occurring in Calabria, southern Italy (Pignatti, 1982) and Abkhazia in the Caucasus (Tamamschian, 1967), respectively. The Apennine and Iberian Peninsulas and the Balkans–Greece region were major refugia of Tertiary flora in Europe (Willis, 1996), while the western Transcaucasia (traditionally denoted by its ancient Greek name Colchis) constituted one of two major refugia in the Caucasus (Grossheim, 1948). The affinities of *C. thomasii* and *C. flahaultii* are uncertain. The former is the nomenclatural type of *Lereschia* described by Boissier (1844). *Cryptotaenia flahaultii* was also originally described in *Lereschia* and subsequently recognized as a close relative of *Cryptotaenia* by Koso-Poljansky (1915). Tutin, in his revisions of both *Cryptotaenia* and *Lereschia* for the *Flora Europaea* (Tutin, 1968a,b), regarded *L. thomasii* as more closely related to the genus *Petagnaea* Caruel, another endemic of southern Italy, rather than to *Cryptotaenia*. *Petagnaea* is placed in Apiaceae subfamily Saniculoideae (Downie *et al.*, 2000b), whereas *C. japonica* and *C. canadensis* are members of Apiaceae subfamily Apioideae tribe Oenantheae (Hardway *et al.*, 2004). These contrasting taxonomic treatments suggest different biogeographical scenarios. If the four holarctic species of *Cryptotaenia* are related, then the distribution of this group is relictual. Its members could have originated from a widespread ancestor, exemplifying the mixed mesophytic forest flora that developed from the boreotropical flora during the Oligocene and Miocene through selection of taxa adapted to colder climatic conditions (Wolfe, 1975; Tiffney, 1985a,b). If, however, the putative members of *Lereschia* are closely related to *Petagnaea* rather than to *Cryptotaenia*, then they represent a radiation of a local European lineage rather than relics of a widespread holarctic ancestor.

Among the African members of *Cryptotaenia*, the most widespread is *C. africana*, occurring in montane regions from
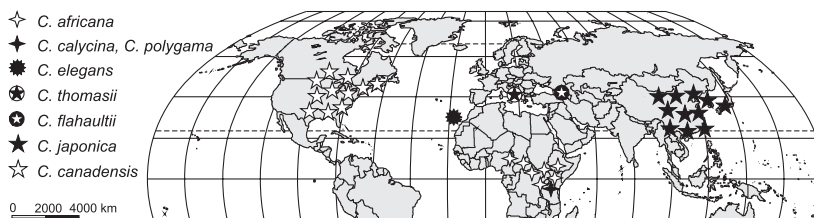

Legend:
- ✧ *C. africana*
- ✦ *C. calycina, C. polygama*
- ✱ *C. elegans*
- ⊛ *C. thomasii*
- ✪ *C. flahaultii*
- ★ *C. japonica*
- ☆ *C. canadensis*

0 2000 4000 km

Figure 1 Distribution of species of *Cryptotaenia*, as the genus is traditionally circumscribed. Symbols indicate approximate geographical range of each species.

northern Nigeria, Cameroon and DR Congo to Ethiopia, Kenya and Tanzania; *Cryptotaenia calycina* and *Cryptotaenia polygama* occur only in Tanzania (Townsend, 1983, 1989). These three species are morphologically similar and are probably closely related; however, their affinity to the other species of *Cryptotaenia* is not clear. Several other African montane plants have their closest relatives in Europe, and sometimes these African and European populations are considered conspecific and indistinguishable (Hedberg, 1957). These are usually widespread species that also occur in the Middle East and Arabia, such as *Arabis alpina* L. (Brassicaceae), that presumably twice colonized the mountains of tropical East Africa (Koch *et al.*, 2006). In contrast, those members of *Cryptotaenia* that are geographically close to the African species are all narrow endemics. Moreover, the African species of *Cryptotaenia* differ significantly from their putative congeners. Townsend (1989) underlined the morphological similarity of these plants to the African representatives of *Pimpinella*, the latter now placed in tribe Pimpinelleae (Downie *et al.*, 2000c, 2001). Therefore the African members of *Cryptotaenia* may have been part of a *Pimpinella* radiation in Africa rather than representing disjunct relatives of their putative congeners.

Although Heywood (1973) proposed a study of *Cryptotaenia elegans* over 30 years ago, the questions he posed about the origin and affinities of this Canary Islands endemic have remained unanswered. Koso-Poljansky (1915) excluded *C. elegans* from *Cryptotaenia*, and although he did not propose an alternative placement he suggested an affinity to such diverse genera as *Carum* L., *Falcaria* L. or *Sphallerocarpus* DC. Within *Cryptotaenia*, he included the Chinese endemic *Cryptotaeniopsis vulgaris* Dunn, currently recognized in *Pternopetalum* Franch. (Pu & Phillippe, 2005). Molecular phylogenetic study confirms that *Pternopetalum* is not a member of tribe Oenantheae (Valiejo-Roman *et al.*, 2002). *Pternopetalum* and *Sphallerocarpus* are eastern Asian endemics and their affinities to *Cryptotaenia elegans* would make the disjunct distribution of the latter even more striking. In contrast, *Carum* and *Falcaria* occur in the Mediterranean, and this region exhibits numerous links with Macaronesia (summarized by Carine *et al.*, 2004).

The aforementioned evidence suggests another explanation for the anomalous distribution pattern observed in *Cryptotaenia*, which is that the genus is polyphyletic and the disjunct taxa are not closely related. In this paper we ascertain the monophyly of *Cryptotaenia*. We infer the molecular phylogeny of the genus and confirm the phylogenetic placements of its disjunct members relative to a broad sampling of taxa from subfamily Apioideae. Additionally, we reconstruct their biogeographical histories using dispersal–vicariance analysis (DIVA; Ronquist, 1997). For phylogenetic analyses, we examine nuclear rDNA internal transcribed spacer (ITS) sequence variation. Although the use of this region in phylogenetic studies has been strongly criticized (Álvarez & Wendel, 2003), phylogenies of Apiaceae inferred from these data are generally congruent with those inferred from chloroplast markers (Downie *et al.*, 2000b, 2001) or the intra-individual ITS

polymorphisms revealed do not interfere with the phylogeny reconstruction (Chung *et al.*, 2005). The advantages of this region are substantial. The presence of multiple copies facilitates PCR amplification even from somewhat degraded DNA samples obtained from herbarium specimens. A relatively small size (*c.* 600 bp in Apioideae, including 5.8S rDNA) facilitates sequencing. A high rate of nucleotide substitution provides reasonable resolution at low taxonomic levels, whereas the vast number of sequences available in data bases allows for immediate comparisons. At present, the ITS region is the best marker for phylogenetic analyses of Apiaceae at low taxonomic levels.

MATERIALS AND METHODS

Taxon sampling

In total, 173 accessions were examined for ITS sequence variation, including seven species of *Cryptotaenia* represented by 15 accessions (Appendix S1). Only *C. polygama* C. C. Towns. was omitted because of a lack of material. We selected a set of accessions representing nearly all major lineages of subfamily Apioideae (Downie *et al.*, 2001). We also added several Eurasian and African taxa that show morphological similarities to *Cryptotaenia* (such as those having loose inflorescences, small fruits and broad-lobed leaves), and which have not hitherto been examined using molecular data. Because sequences of early branching taxa (tribes Heteromorpheae and Bupleureae, and several putatively basal species of uncertain tribal position) cannot be unambiguously aligned with those of the members of the crown clades, we omitted these and used *Physospermum cornubiense*, a member of tribe Pleurospermeae, to root the trees (Downie *et al.*, 2000b,c).

In preliminary phylogenetic analyses, members of *Cryptotaenia* were placed in three branches corresponding to monophyletic tribes Oenantheae (*sensu* Hardway *et al.*, 2004), Pimpinelleae (Downie *et al.*, 2001), and Scandiceae subtribe Daucinae (Downie *et al.*, 2000a; Lee & Downie, 2000). Therefore we sampled additional taxa from these clades. In a previous study of tribe Oenantheae, *C. japonica* and *C. canadensis* formed a clade with members of *Afrocarum* Rauschert, *Berula* W. D. J. Koch, *Helosciadium* W. D. J. Koch, and *Sium* L. (Hardway *et al.*, 2004; Spalik & Downie, 2006), so we included a representative selection of these taxa as well. To infer the phylogenetic position of those accessions of *Cryptotaenia* that grouped with members of Pimpinelleae and Scandiceae subtribe Daucinae, we used nearly all ITS sequences of their constituent taxa available in GenBank.

DNA extraction, amplification and sequencing

ITS sequences from 38 accessions were obtained specifically for this study. Additionally, 43 accessions in GenBank for which only ITS1 and ITS2 data were available through our previous studies were updated with partial or complete 5.8S rDNA sequence data. 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 PCR-amplified 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 across the entire ITS region 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 as contiguous ITS1, 5.8S, and ITS2 data (Appendix S1).

Sequence, phylogenetic and biogeographical analyses

The DNA sequences were aligned using CLUSTALX (Jeanmougin *et al.*, 1998), with default parameters for gap penalty and extension. The alignment was then edited where necessary using GENEDOC ver. 2.6.002 (Nicholas & Nicholas, 1997). The resulting matrix has been deposited with TREEBASE (study accession number S1772, matrix accession number M3237). Phylogenetic analyses included Bayesian inference using MRBAYES ver. 3.1 (Ronquist & Huelsenbeck, 2003) and maximum parsimony (MP) and neighbour-joining (NJ) methods implemented using PAUP* ver. 4.0b10 (Swofford, 1998). The substitution model for the Bayesian analysis was selected using the program MODELTEST ver. 3.6 (Posada & Crandall, 1998) and the Akaike information criterion (Akaike, 1974). The analyses were carried out for 1,000,000 generations with four Monte Carlo Markov chains initiated and a sampling frequency of 100 generations. The initial 10,000 saved trees were discarded, and the consensus and posterior probabilities (PP) of particular clades were calculated based on the remaining trees. Preliminary analyses demonstrated that the

log-likelihood values converged on a stable value by generation 85,000. Maximum parsimony analysis was carried out with gap states treated as missing data, characters unordered, and all character transformations equally weighted. Because in preliminary MP searches the number of shortest trees exceeded 100,000, we employed the 'inverse constraint' approach of Catalán *et al.* (1997). One thousand heuristic searches were initiated with random addition of taxa and tree-bisection-reconnection (TBR) branch swapping, with no more than 200 shortest trees saved per replicate. The strict consensus of these trees was used as a phylogenetic constraint in another round of 10,000 searches. This time, only those trees that did not match the constraint tree were saved. Since all of the saved trees were longer than those obtained from the initial searches, this suggests strongly that the strict consensus tree summarizes all possible shortest tree topologies. Bootstrap support (BS) was estimated using 1000 resampled data sets using TBR branch swapping and simple stepwise addition of taxa, saving no more than 100 trees per replicate. Bremer (1994) support values (or decay indices, DI) were obtained using AUTODECAY 4.0 (Eriksson, 1998). Neighbour-joining analyses were performed using several substitution models available in PAUP*, including Jukes–Cantor, Kimura 2-parameter, and Kimura 3-parameter.

The dispersal–vicariance analysis was carried out using DIVA ver. 1.1 (Ronquist, 1996, 1997). This analysis allows for a reticulate area relationship, which is particularly advantageous for the analysis of Holarctic biogeography. We considered alternative tree topologies resulting from different phylogenetic methods, and focused on those trees that provided reconstructions with fewer dispersals or less ambiguous ancestral areas. DIVA requires a fully resolved tree, therefore polytomies were arbitrarily resolved. Two optimizations were performed: first, with an unconstrained number of unit areas for each ancestral node, and second, with this number restricted to two areas. 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. In other words, vicariance is a proximate consequence of dispersal. Moreover, extant taxa used in the analyses rarely occur in more than two individual areas. DIVA does not assume any area relationships, therefore in the reconstructions long-distance dispersals are equally as probable as colonizations of geographically adjacent areas. Because in fact these are not, we discuss only those ancestral-area reconstructions that contain geographically adjacent areas.

Figure 2 Majority-rule consensus tree obtained from Bayesian analysis of 159 terminals representing *Cryptotaenia* (bold type) and most major clades of Apiaceae subfamily Apioideae using a GTR + G + I substitution model. Percentage posterior probabilities (PP) are given along all branches. For those clades that were supported in the strict consensus of 200,000 minimal-length 2908-step trees obtained from maximum parsimony searches, decay indices (DI) and bootstrap values (BS) are also indicated; bootstrap values < 50% are indicated with hyphens. Numbers following species names refer to those accessions identified numerically in Appendix S1. The terminal '*Daucus carota* subspp.' includes accessions of the following subspecies: *azoricus*, *gadecaei*, *drepanensis*, and both accessions of subsp. *gummifer*.
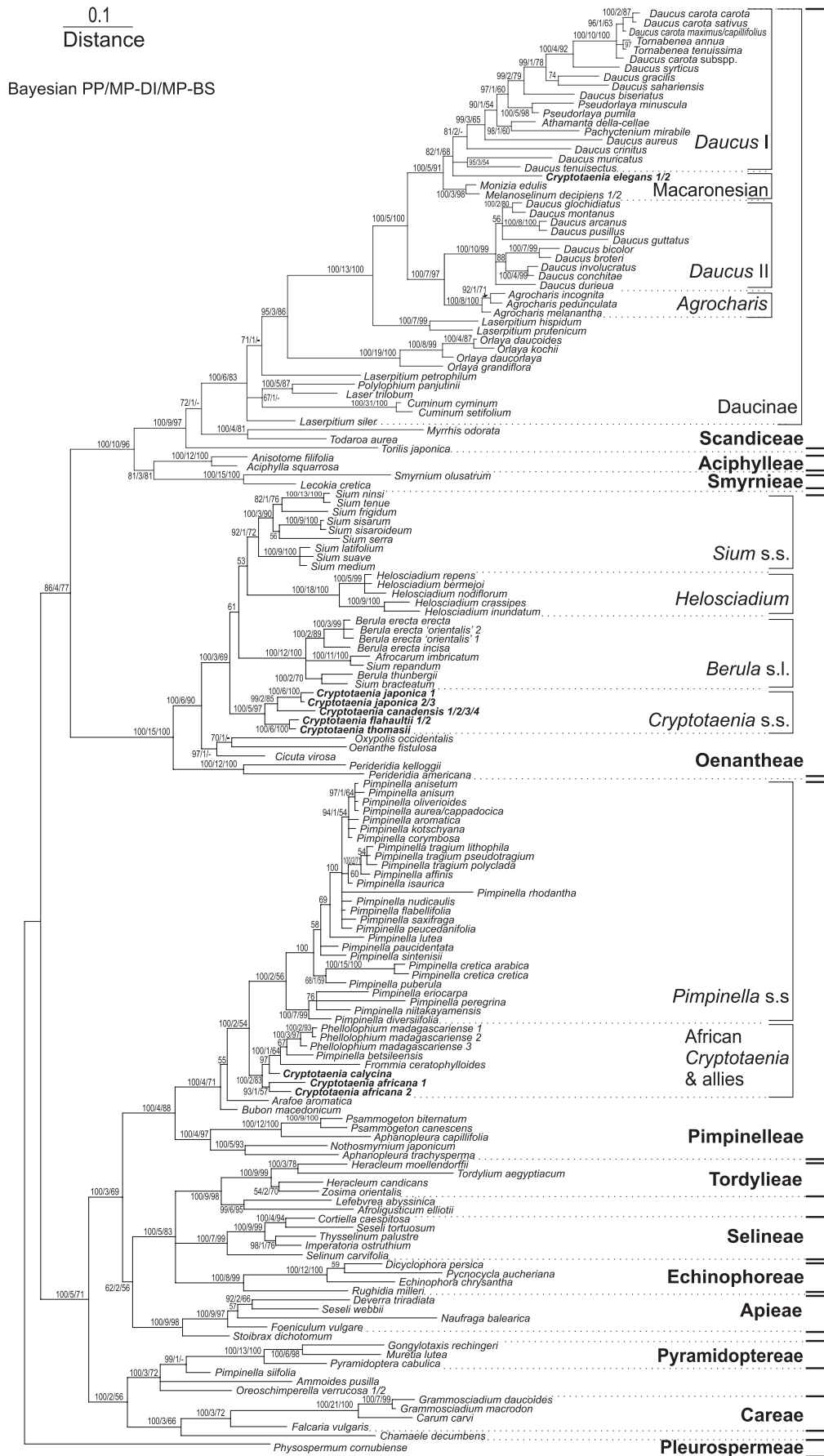
RESULTS

Phylogenetic analyses

Nine groups of accessions each had identical ITS sequences and, as such, each group was represented by a single terminal in the phylogenetic analysis. The final matrix included 159 terminals and 674 aligned positions, 220 of which were constant, 63 autapomorphic, 363 parsimony informative, and 28 of ambiguous alignment; the latter were excluded from the analyses. MODELTEST with the Akaike information criterion selected the GTR + G + I model of nucleotide substitution as fitting these data best. The Bayesian majority rule consensus tree is presented in Fig. 2. Maximum parsimony searches resulted in more than 200,000 shortest trees of 2908 steps each. The strict consensus of these trees has a nearly identical topology to that of the Bayesian consensus tree; differences between them included minor rearrangements among terminal branches. Topologies of NJ trees obtained using different models of nucleotide substitution were generally similar to each other, and contained the same major clades as those obtained from Bayesian and MP analyses. Those clades represent 12 tribes of subfamily Apioideae. The seven species of *Cryptotaenia* examined occur in three distantly related clades. *Cryptotaenia canadensis*, the nomenclatural type of the genus, and three congeners, *C. japonica*, *C. flahaultii* and *C. thomasii*, are grouped with members of tribe Oenantheae. The Oenantheae clade received high support in both Bayesian and MP analyses (PP = 100%, DI = 15, BS = 100%). Within Oenantheae, the four species of *Cryptotaenia* form a monophyletic group (PP = 100%, DI = 5, BS = 97%); hereafter this group is named *Cryptotaenia sensu stricto* (*s.s.*). The western Eurasian *C. thomasii* and *C. flahaultii* are sister species, as are the eastern Asiatic *C. japonica* and eastern North American *C. canadensis*; only the first pair, however, is highly supported (PP = 100%, DI = 6, BS = 100%). *Cryptotaenia s.s.* forms a moderately supported monophyletic group with three other major clades (PP = 100%, DI = 3, BS = 69%): (1) *Helosciadium*, which includes all accessions of this genus; (2) *Berula sensu lato* (*s.l.*) (Spalik & Downie, 2006), which includes all accessions of *Berula*, plus *Afrocarum imbricatum*, *Sium repandum*, and *Sium bracteatum*; and (3) *Sium s.s.* (Spalik & Downie, 2006), encompassing all Eurasian and North American members of *Sium*. Apart from *Sium s.s.*, each of these clades received high support from Bayesian, decay and bootstrap analyses. However, the relationships among these major clades are poorly supported in the Bayesian consensus tree (Fig. 2) and are unresolved in the MP strict consensus tree (not shown). In all NJ trees (not shown), *Cryptotaenia s.s.* is sister group to the clade of *Sium s.s.* plus *Berula s.l.*

Cryptotaenia elegans, an endemic of the Canary Islands, is placed among members of tribe Scandiceae subtribe Daucinae. In the MP strict consensus tree, this species constitutes a separate branch that is sister group to a large clade denoted as '*Daucus* I', comprising members of *Tornabenea* Parl., *Pseudor-*

laya Murb., *Athamanta* L., *Pachyctenium* Maire & Pamp., and several species of *Daucus* L. including the nomenclatural type of the genus, *Daucus carota*. In the Bayesian consensus tree (Fig. 2), the basal node of the '*Daucus* I' clade collapses to form a trichotomy. This entire group, however, is poorly supported (PP = 82%, DI = 1, BS = 68%). *Monizia edulis* and *Melanoselinum decipiens*, both endemic to Madeira, comprise a clade (PP = 100%, DI = 3, BS = 98%) that is sister group to '*Daucus* I' plus *C. elegans* (PP = 100%, DI = 5, BS = 91%). In contrast, in trees resulting from NJ analyses using Jukes–Cantor, Kimura 2-parameter, and Kimura 3-parameter substitution models (not shown), *C. elegans*, *M. decipiens* and *M. edulis* form a clade that is sister group to the '*Daucus* I' clade.

Two representatives of the Cape Verde endemic genus *Tornabenea* ally with several subspecies of *D. carota*, including a subspecies native to the Azores, *D. carota* subsp. *azoricus* (the latter is denoted in Fig. 2 as belonging to the terminal '*D. carota* subspp.'). The *D. carota* plus *Tornabenea* group received strong branch support (PP = 100%, DI = 10, BS = 100%). The remaining members of *Daucus* outside the '*Daucus* I' clade form a well supported group (PP = 100%, DI = 10, BS = 99%), denoted as '*Daucus* II,' that is sister group to the genus *Agrocharis* Hochst. (PP = 100, DI = 8, BS = 100%), endemic to Africa. Collectively, these two clades constitute a sister group to the '*Daucus* I' clade plus Macaronesian endemics group. Similar relationships were inferred by NJ analyses (not shown).

The African species of *Cryptotaenia* found affinity among African members of tribe Pimpinelleae. They formed a moderately supported clade (PP = 100%, DI = 2, BS = 83%) with *Frommia ceratophylloides* and Madagascan endemics *Pimpinella betsileensis* and *Phellolophium madagascariense*. In the Bayesian consensus tree, however, the two African members of *Cryptotaenia* did not group as sister taxa. Instead, *C. calycina* was sister group to *F. ceratophylloides* and the Madagascan endemics (PP = 97%). The Madagascan species formed a clade (PP = 67%) that was sister group to *F. ceratophylloides*. In all trees, the clade of African *Cryptotaenia* and its allies is sister group to a clade encompassing the Eurasian species of *Pimpinella* L., including the nomenclatural type of the genus, *P. peregrina*. Relationships among Eurasian members of *Pimpinella* were mostly unresolved.

Of the remaining newly sequenced Eurasian and African accessions of Apioideae that showed some morphological similarity to *Cryptotaenia*, there are no additions to the genus or to its close relatives. Some species are confirmed as new additions to previously established tribes (their presumed phylogenetic positions are indicated in Appendix S1), while others remain *incertae sedis*.

Biogeographical analyses

Cryptotaenia s.s. *and related members of tribe Oenantheae*

The following unit areas were considered for biogeographical analysis of *Cryptotaenia s.s.* and its allies: Europe (A), western and central Asia (B), eastern Asia (C), North America (D), and

Africa and St Helena (E). We omitted the cultivated *S. sisarum* and replaced the three Eurasian accessions of *Berula erecta* with the single terminal, *B. erecta* var. *erecta*. Two closely related Far East species of *Sium*, *S. ninsi* and *S. tenue*, were also represented by a single terminal taxon. The genera *Oxypolis* Raf. and *Perideridia* Rchb. exemplify two North American clades of tribe Oenantheae (Hardway *et al.*, 2004). For *Oenanthe* L., we assumed a broad distribution in the Old World (ABCE) and omitted its only North American member, *O. sarmentosa* DC., because our preliminary analyses of nuclear rDNA ITS and cpDNA sequences suggested its derived position. Lee & Downie (2006) revealed that the Eurasian *Cicuta virosa* is the sister group to a clade comprising all North American members of this genus, and we considered this information in the biogeographical analysis. For DIVA, we used only the topologies of the Bayesian inference and NJ trees. In the MP strict consensus tree, relationships within Oenantheae were unresolved and the sister group to *Cryptotaenia s.s.* was not identified.

Unrestricted optimal DIVA reconstructions for both tree topologies required 22 dispersal events (not shown). For many ancestral nodes, however, the reconstructions comprised more than two disjunct individual areas, while for the entire group the ancestral distribution included all areas (ABCDE). The reconstruction of the ancestral area for *Cryptotaenia s.s.* was identical for both trees and included almost every combination of individual areas (with the exception of AB and CD), including the entire Holarctic (ABCD). The immediate ancestor of *C. flahaultii* and *C. thomasii* occurred in the western Palearctic (AB), whereas that of *C. japonica* and *C. canadensis* inhabited eastern Asia and North America (CD).

At present, the species analysed rarely occur in more than two individual areas, and if they do, they show a clear genetic pattern suggesting isolation by distance (see Spalik & Downie, 2006 for a detailed analysis of the group). With the maximum number of unit areas set to two, the optimal DIVA reconstructions required 23 dispersals for both the Bayesian (Fig. 3) and NJ (not shown) trees. When only those reconstructions of the ancestral area of *Cryptotaenia s.s.* that include adjacent unit areas are considered, two dispersal scenarios are inferred. The first scenario assumes an eastern Asian origin of the genus and dispersal to western Asia. Subsequent vicariance was followed by two dispersal events: from western Asia (B) to Europe (A), and from eastern Asia (C) to North America (D). In the second scenario, the ancestor of *Cryptotaenia* originated in Europe and dispersed to North America. Subsequently, the North American lineage colonized eastern Asia, whereas the European lineage migrated to western Asia.

The reconstructions for *Sium*, *Berula* and *Helosciadium* are generally congruent with those obtained in our earlier and more detailed analyses of the group (Spalik & Downie, 2006). The ancestral area for *Sium s.s.* was eastern Asia (C), whereas
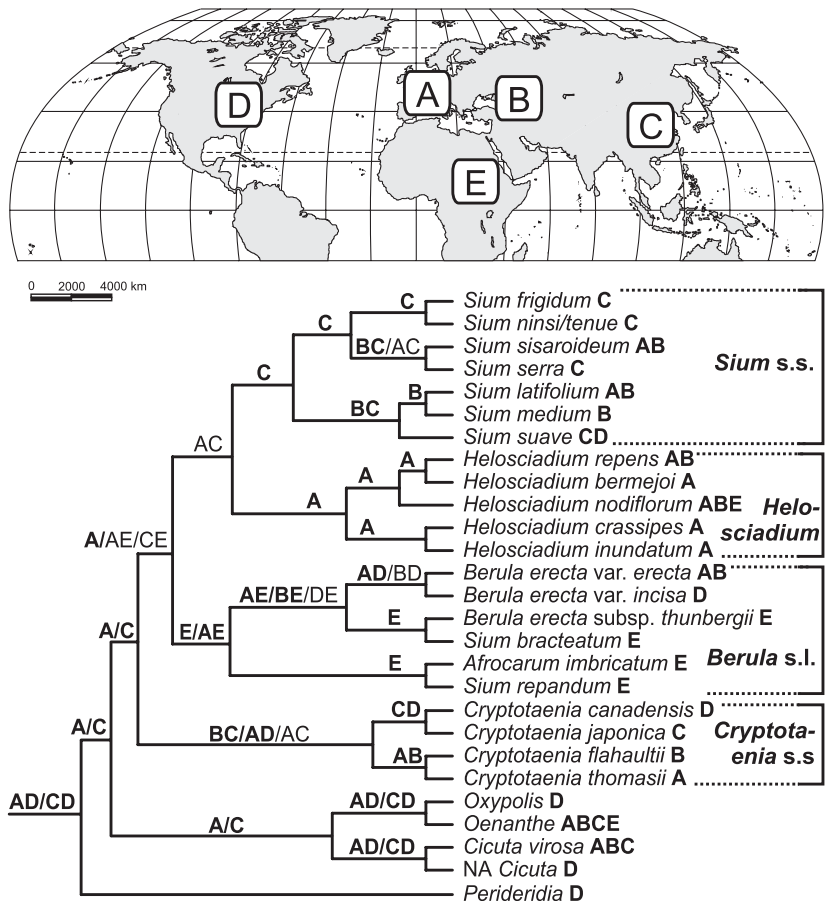

Figure 3 Dispersal–vicariance scenarios for *Cryptotaenia s.s.* and related genera of tribe Oenantheae as reconstructed by dispersal–vicariance analysis (DIVA) optimization with the maximum number of area units set to two, and using the topology of a Bayesian tree with ambiguities resolved arbitrarily. A–E, respective area units (illustrated on map). Ancestral area reconstructions that minimize long-distance dispersal (i.e. comprise geographically adjacent area units or single area units) are in bold type.

Helosciadium originated in Europe (A). The ancestral area for the *Berula s.l.* clade is reconstructed as African (E) or European-African (AE).

Cryptotaenia elegans *and tribe Scandiceae*

For the biogeographical analysis of *C. elegans* and its relatives in tribe Scandiceae, we considered the following unit areas (Fig. 4): north-western Mediterranean and central Europe (A), eastern Mediterranean and Middle East (B), north-western Africa (C), tropical eastern and central Africa (D), Macaronesia (E), North and South America (F), and Australia and

New Zealand (G). The monophyletic genus *Agrocharis* from tropical Africa was reduced to a single terminal. The distributions of those groups of taxa having identical ITS sequences and represented in the analyses by a single terminal taxon (specifically, *Daucus carota* subspp. *gummifer*, *azoricus*, *gadecaei*, and *drepanensis*) were coded as a summary distribution of its included members. For *Daucus durieua*, we assumed that its present occurrence in the Canary Islands is anthropogenic (Kunkel, 1991), therefore we did not include it as belonging to unit area E. We considered two general tree topologies: (1) Bayesian consensus and MP strict consensus trees (with polytomies resolved arbitrarily), showing *C. elegans* sister
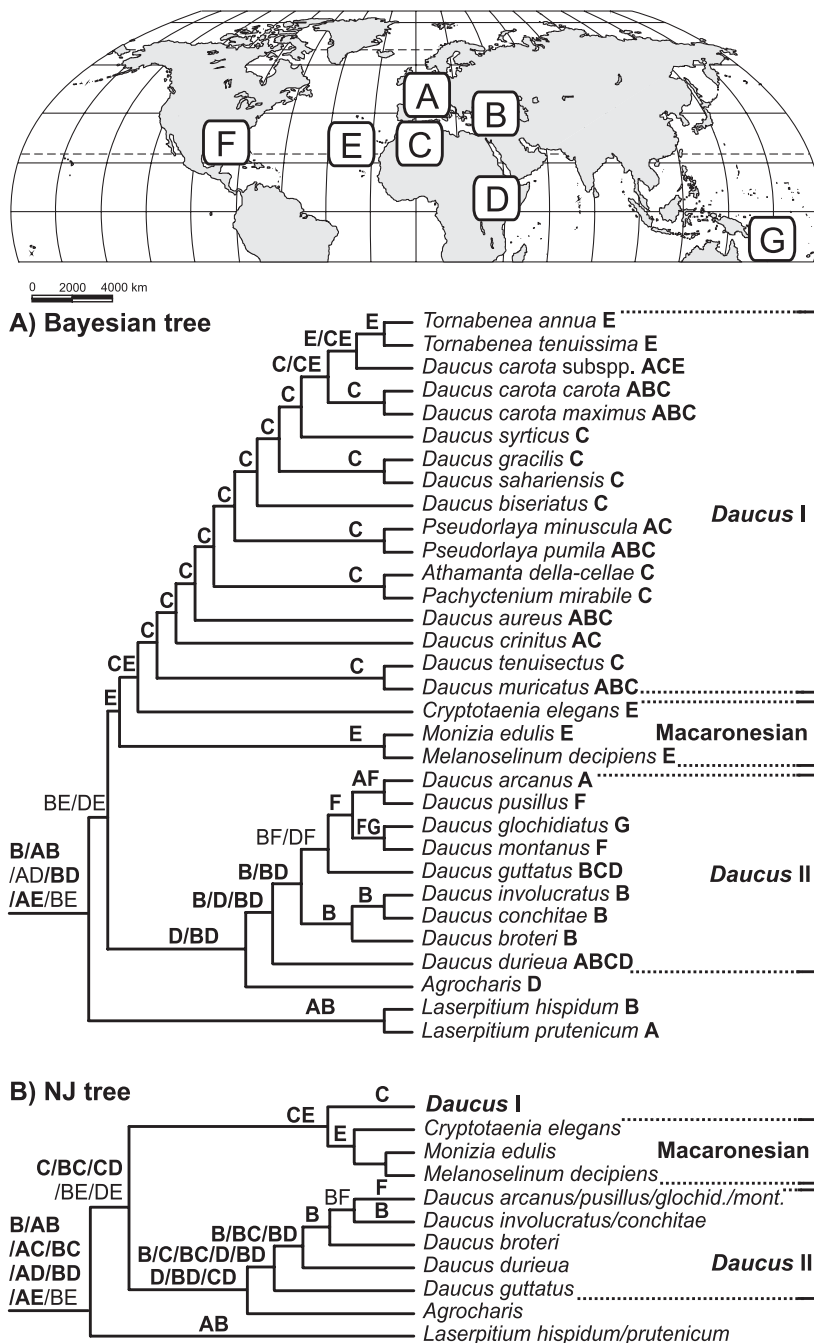

Figure 4 Dispersal–vicariance scenarios for *Cryptotaenia elegans* and related members of tribe Scandiceae as reconstructed by DIVA optimization with the maximum number of area units set to two, and using the topology of (a) a Bayesian tree with arbitrarily resolved ambiguities; (b) a simplified neighbour-joining tree to show the differences between the reconstructions. A–G, respective area units (illustrated on map). Ancestral area reconstructions that minimize long-distance dispersal (i.e. comprise geographically adjacent area units or single area units) are in bold type.

group to the 'Daucus I' clade; and (2) NJ trees, showing *C. elegans* sister group to the clade of *Monizia edulis* and *Melanoselinum decipiens*.

Unconstrained optimal DIVA reconstructions required 25 dispersal events for the Bayesian tree and 24 dispersals for the NJ tree. The ancestral-area reconstructions for most deep nodes in both trees are ambiguous. In both analyses, Macaronesia was always inferred as part of an ancestral area for the entire group. With the maximum number of areas set to two, the optimal DIVA reconstructions required 28 dispersals for both the Bayesian (Fig. 4a) and NJ (Fig. 4b) trees. As before, we focus on those reconstructions that include adjacent areas (if available). Additionally, since Macaronesia (in particular the Canary Islands) has never been connected to the mainland, we considered only those scenarios in which a dispersal to or from Macaronesia is followed by an immediate vicariance. Given these constraints, the scenario inferred using the Bayesian tree (Fig. 4a) postulates two dispersals to Macaronesia and one back-dispersal to northern Africa. The ancestor of both major clades ('Daucus I' + Macaronesian endemics and 'Daucus II' + *Agrocharis*) dispersed to Macaronesia either from eastern Mediterranean or eastern and central Africa (BE/DE). Its continental offspring (D/BD) gave rise to the 'Daucus II' clade and the genus *Agrocharis*, whereas the Macaronesian lineage (E), having produced two Macaronesian offshoots, dispersed back to the mainland (CE). This lineage radiated in north-western Africa (C) and colonized Macaronesia a second

time, giving rise to *Tornabenea*. The 'Daucus II' plus *Agrocharis* clade radiated in the eastern Mediterranean–African region (D/BD). It colonized North and South America by long-distance dispersal (BF/DF) and spread further to Australia and New Zealand (FG). A back-dispersal from America to Europe (AF) is postulated to account for the origin of *Daucus arcanus*. In contrast, the scenario inferred based on results of NJ analyses (Fig. 4b) requires only two dispersals to Macaronesia (without a back dispersal to the mainland). In this scenario, the lineage leading to the 'Daucus I' clade may have originated and continued to evolve in north-western Africa (C). Its first colonization of Macaronesia gave rise to *C. elegans*, *M. edulis* and *M. decipiens*, whereas the second dispersal resulted in the radiation of *Tornabenea*.

African *Cryptotaenia* and tribe Pimpinelleae

We considered the following unit areas for biogeographical analysis of African *Cryptotaenia* and its allies (Fig. 5): Europe (A), western and central Asia (B), eastern Asia (C), tropical Africa (D) and Madagascar (E). The relationships among the members of *Pimpinella s.s.* were unresolved, so most of its representatives were pruned from the trees. All pruned taxa and their relatives retained in the analyses occur in the Middle East, therefore their removal did not affect subsequent biogeographical reconstructions. Because the position of *C. calycina* with respect to *C. africana* and other African and
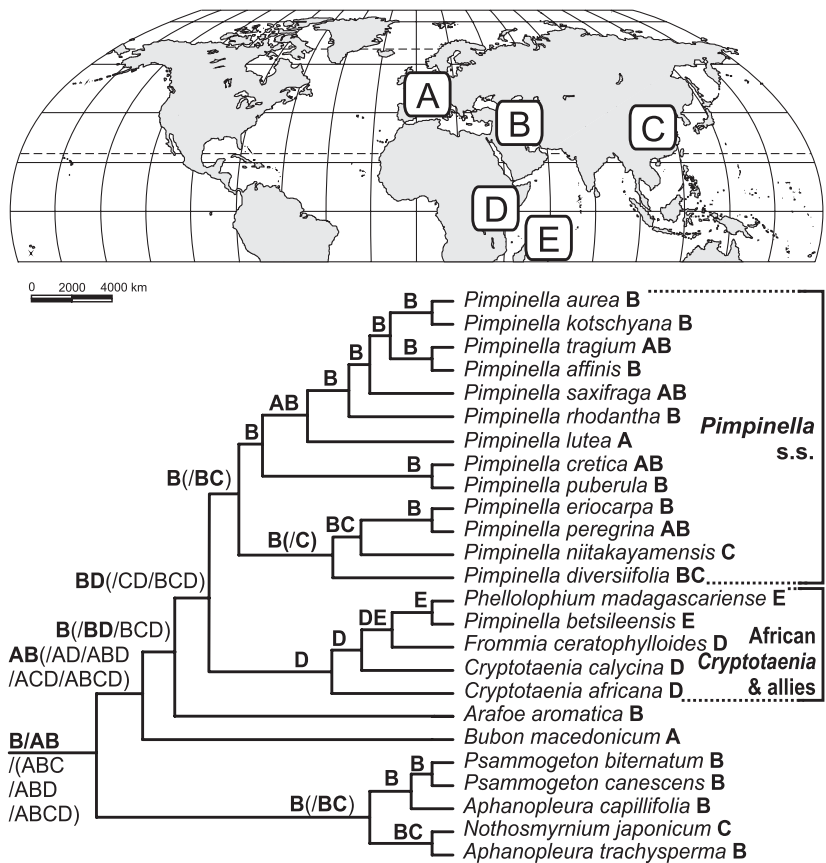

Figure 5 Dispersal–vicariance scenarios for African members of *Cryptotaenia* and related members of tribe Pimpinelleae, as reconstructed by two DIVA optimizations: first unrestricted; second with the maximum number of area units set to two. Reconstructions in parentheses occurred only in the unrestricted optimization, the remainder were inferred in both analyses. Tree topology is based on the results of the Bayesian analysis with ambiguities arbitrarily resolved. A–G, respective area units (illustrated on map). Ancestral area reconstructions that minimize long-distance dispersal (i.e. comprise geographically adjacent area units or single area units) are in bold type.

Madagascan members of this clade was similar in Bayesian, MP and NJ trees, we considered only the results of the Bayesian analyses in DIVA.

Optimal unrestricted DIVA reconstruction required 11 dispersal events. Because several ancestral-area reconstructions included more than two individual areas (whereas extant taxa occur in one or two areas only), we performed an additional DIVA optimization with the maxareas parameter set to two. Similarly to the unrestricted analysis, the optimal reconstruction required 11 dispersals and the ancestral areas constituted a subset of those inferred previously (Fig. 5). The results of the restricted analysis contain only reconstructions that include adjacent unit areas, thus we focus on this scenario. Within this constraint, western Eurasia (B/AB) is reconstructed as the ancestral area of Pimpinelleae, with subsequent dispersals from the Middle East to tropical East Africa and further to Madagascar.

DISCUSSION

Evolution and biogeography of *Cryptotaenia s.s.*

The disjunct pattern shown by *Cryptotaenia s.s.* and many other north temperate genera is generally considered to represent relic distributions of the Tertiary resulting from complex processes of the past, such as migration or dispersal, vicariance and speciation, extinction and morphological stasis (Xiang *et al.*, 1998; Wen, 1999, 2001; Donoghue *et al.*, 2001; Xiang & Soltis, 2001 and references therein). Morphological stasis, exhibited particularly by some eastern Asian and eastern North American disjunct taxa, is explained by the stable environmental conditions of these areas and accompanying stabilizing selection, as well as evolutionary constraints (Wen, 1999, 2001 and references therein). In *Aralia* sect. *Dimorphanthus* Miq. (Araliaceae), north temperate species from these areas of disjunction are more similar to each other than they are to their closest subtropical relatives (Wen, 2000). Geographical and climatic characteristics of eastern Asia–eastern North America disjunct genera (e.g. midpoint latitude, northernmost latitude, latitude range, annual precipitation and mean annual temperature) are significantly correlated between these two regions, suggesting that these disjunct taxa exhibited stable ecological requirements over evolutionary time (Qian & Ricklefs, 2004). *Cryptotaenia s.s.* seems to be just such a genus, trapped in its ecological niche and retaining the basic features of its ancestors, and the morphological differentiation of its members is a simple function of time elapsed since divergence.

The members of *Cryptotaenia s.s.* are very similar to one another, and show characteristics common to other inhabitants of shady mesic to humid forests, in which they occur throughout their entire range. These characteristics include broad, scarcely divided and delicate, almost translucent leaves and loose inflorescences. These species of *Cryptotaenia* differ only slightly in leaf shape and size and inflorescence structure. The morphological similarities and differences among them are paralleled at the molecular level. The sequence divergence

values between *C. flahaultii* and *C. thomasii*, between *C. japonica* and *C. canadensis*, and between these two pairs of species are 0.69%, 3.89% and 4.97%, respectively. *Cryptotaenia flahaultii* and *C. thomasii* are morphologically most similar, whereas *C. japonica* and *C. canadensis* exhibit greater morphological divergence, but nevertheless are more similar to each other than they are to their western palaearctic congeners (K. Spalik & S.R. Downie, unpublished data).

The dispersal abilities of *Cryptotaenia s.s.* are poor. Their fruits are glabrous and do not have any features facilitating dispersal – they are gravity-dispersed. Williams & Guries (1994) examined gene flow among population subdivisions of three sympatric woodland umbellifers, *C. canadensis*, *Osmorhiza claytonii* (Michx.) C. B. Clarke, and *Sanicula odorata* (Raf.) Pryer & Phillippe, the latter two with spiny, animal-dispersed fruits. They concluded that the genetic differentiation among these subdivisions has an inverse relationship with dispersal ability: it is highest in *C. canadensis*, intermediate in *O. claytonii*, and lowest in *S. odorata*. The high dispersal abilities of *Osmorhiza* Raf. and *Sanicula* L. are also reflected in their present distributions and in the morphological divergence of their included taxa. *Osmorhiza* is sympatric with *Cryptotaenia s.s.* throughout most of its range and exhibits a similar disjunction pattern. Its only palaearctic member occurs in the Caucasus and eastern Asia; the remaining species are North American with some extending to South America. Based on morphology, the palaearctic species comprise a monophyletic sister group to two eastern North American congeners, whereas the remaining members of *Osmorhiza* were regarded as their distant cousins (Lowry & Jones, 1984). Based on molecular data, however, the palaearctic and eastern North American taxa do not comprise a sister group, but instead form a paraphyletic group with respect to their congeners (Downie *et al.*, 2000a; Wen *et al.*, 2002; Yoo *et al.*, 2002). Successful dispersal from their refugial area and subsequent exposure to new selection pressures may have accelerated morphological evolution and radiation of the genus. *Sanicula*, a genus of presumed Eurasian origin, radiated in North America and its western North American lineages dispersed to South America and Hawaii. Diversification in lineages that lost dispersal-promoting characteristics was limited compared with those retaining these features (Vargas *et al.*, 1999).

The distribution pattern of *Cryptotaenia s.s.* is somewhat similar to that of *Carpinus* L. (Betulaceae), and *Castanea* Mill. and *Fagus* L. (Fagaceae; Meusel *et al.*, 1965), woody genera occurring alongside *Cryptotaenia* in temperate broad-leaved forests. However, in the western Palaearctic, *Cryptotaenia* is confined to very small regions of Italy and the Caucasus that were important refugial areas. Nevertheless, the Italian refugium did not contribute much to the post-glacial colonization of Europe because the Alps constituted an important physical and ecological barrier to migration, whereas the contribution from the eastern refugia (Hyrcanian and Colchis in the Caucasus) remains undetermined for many species (Hewitt, 2004). For instance, Europe was colonized by oaks coming mostly from the Iberian and Balkan refugia, with only limited

migration from Italy (Petit *et al.*, 2002). Several herbaceous species have a distribution pattern encompassing southern refugial areas and adjacent regions of Italy, the Balkans and the Caucasus. These include *Calamintha grandiflora* Moench (Lamiaceae), *Digitalis ferruginea* L. (Plantaginaceae) and *Salvia glutinosa* L. (Lamiaceae), extending from Italy and adjacent regions of France through the Balkans and the coastal region of the Black Sea to the Caucasus and the Caspian region (Meusel *et al.*, 1978). The Italian–Caucasian disjunction, as exhibited by *C. thomasii* and *C. flahaultii*, may be regarded as an extreme example of this pattern, and at the same time an exceptional one, as the disjunct taxa became trapped in refugia. Their poor dispersal abilities and narrow ecological requirements may have precluded these species from crossing local geographical and ecological barriers. In the case of *C. flahaultii*, the high mountain range of the Greater Caucasus to the north-east may have limited its dispersal from the Colchis refugium. The mountains of southern Italy may have provided a similar barrier for *C. thomasii*.

Xiang & Soltis (2001) recognized four general patterns accounting for the distribution of north temperate taxa, including: (1) origin and speciation in eastern Asia with subsequent dispersal into North America and/or Europe, such as that exhibited by *Aralia* L. sect. *Aralia* (Araliaceae), *Symplocarpus* W. P. C. Barton (Araceae), and possibly *Asarum* L. (Aristolochiaceae), *Aesculus* L. (Sapindaceae) and *Chryso-splenium* L. (Saxifragaceae); and (2) widespread origin in the Northern Hemisphere with subsequent fragmentation by intercontinental vicariance, postulated for *Cornus* L. (Cornaceae) and *Trautvetteria* F. E. Fisch. & C. A. Mey. (Ranunculaceae). Results of the unrestricted DIVA optimization for *Cryptotaenia s.s.* are consistent with the second pattern. The ancestor of *Cryptotaenia* may have been widely distributed in the Holarctic, with its range divided initially into western Palearctic and eastern Asia/North America. Subsequent vicariance events resulted in the present distribution of its four descendants. However, given the low gene flow among local populations of *Cryptotaenia* (Williams & Guries, 1994), the widespread origin of its ancestor in the Holarctic is rather unlikely. With the maximum number of areas restricted to two, DIVA inferred two scenarios including a reconstruction concordant with the first general pattern: an eastern Asian origin of *Cryptotaenia* with subsequent colonization of western Asia (BC). In the first scenario, Europe was colonized from western Asia, while the dispersal to North America occurred from eastern Asia. Dispersal from eastern Asia to North America was the prevailing direction of intercontinental plant exchange between the Old and New Worlds (Xiang & Soltis, 2001). The second scenario for *Cryptotaenia s.s.*, postulating migration from Europe to North America and then from North America to eastern Asia, is less probable because it involves two intercontinental dispersals, whereas the first scenario requires only one. The North Atlantic Land Bridge connected Europe and North America during the early Eocene and may have allowed for migration of warm-temperate taxa; later, occasional stepping-stone dispersal was also possible

(Tiffney, 1985a; Tiffney & Manchester, 2001). However, such a dispersal has been unambiguously inferred for very few disjunct taxa (Donoghue *et al.*, 2001; Tiffney & Manchester, 2001 and references therein); among these is *Berula*, a close relative of *Cryptotaenia s.s.* (Spalik & Downie, 2006; this study). None of those taxa dispersed further to eastern Asia.

Without a fossil record for the group, the dispersal–vicariance scenario for *Cryptotaenia s.s.* cannot be verified. The timing of divergence of the genus also cannot be ascertained. We tested the molecular-clock hypothesis for a smaller matrix comprising only members of tribe Oenantheae, using a likelihood ratio test (Felsenstein, 1988). The molecular-clock hypothesis was rejected and, in the absence of fossils, we could not use any non-clock method of divergence estimation.

Origin and evolution of Macaronesian members of Scandiceae subtribe Daucinae

The endemic flora of Macaronesia, and particularly that of the Canary Islands, was considered to be a relic one with its greatest affinities among the Tertiary floras of the Tethyan-Tertiary region (Meusel, 1953; Takhtajan, 1969; Bramwell, 1972). The evidence for this hypothesis was regarded as very strong and came from biogeography, palaeobotany and ecology (summarized by Bramwell, 1976). These Macaronesian endemics were generally thought to be taxonomically isolated, and several European Tertiary fossil taxa are still extant in Macaronesia. Woodiness, once regarded as an ancestral condition, is very frequent among Macaronesian endemics, accounting for 70% of all taxa. While molecular phylogenetic studies have confirmed the Mediterranean affinity of most Canarian endemics, they also suggested that these taxa are in late- rather than early-branching positions and their sister taxa are still extant in the Mediterranean. Well resolved phylogenies have been obtained for *c.* one-third of all Macaronesian endemic plant species, constituting 56 endemic clades: 71% of these clades have sister clades in the Mediterranean, with over half of these occurring in the western Mediterranean region, including north-western Africa (Carine *et al.*, 2004). Among 37 endemics of the palaeo-islands of Tenerife that were presumed candidates for the oldest lineages in the archipelago, only four represent early-diverging branches (Trusty *et al.*, 2005). Also, woodiness has been shown to be an insular derived trait rather than a mainland ancestral one (Böhle *et al.*, 1996; Panero *et al.*, 1999; Helfgott *et al.*, 2000; Jorgensen & Olesen, 2001; Barber *et al.*, 2002).

The emerging pattern for the flora of Macaronesia is therefore one of a recent rather than relic Mediterranean origin, and the results of our study are generally congruent with this pattern. The examined Macaronesian endemics – *C. elegans*, *M. decipiens*, *M. edulis* and *Tornabenea* – are related to Mediterranean/north-western African members of Scandiceae subtribe Daucinae. *Cryptotaenia elegans*, *M. decipiens* and *M. edulis* represent an early-branching lineage that is sister group or paraphyletic to the entire Mediterranean '*Daucus* I' clade. Because the ITS region in this branch of the phylogenetic

tree does not evolve in a clock-like fashion (the molecular-clock hypothesis was rejected), the estimation of divergence time is not possible. However, ITS sequence divergence (GTR distance) between *C. elegans* and their mainland relatives is relatively low (between 7.4% and 14.4%), suggesting a late Tertiary separation. In contrast, the genus *Tornabenea* from Cape Verde constitutes a late-branching lineage and arises among subspecies of *D. carota*. The sequence divergence between its members and these subspecies of *D. carota* is merely 0.3–1.1%. However, despite its relatively recent arrival in Cape Verde, it has undergone a rapid radiation resulting in six currently recognized species, some of which are polymorphic (Brochmann *et al.*, 1997; Schmidt & Lobin, 1999).

The Madeiran monotypic endemic genera *Melanoselinum* Hoffm. and *Monizia* Lowe comprise woody rosette plants. *Tornabenea tenuissima* is a stout perennial with woody stems (Brochmann *et al.*, 1997). Evidently, woodiness in this branch of Apiaceae was acquired twice – by the common ancestor of *Monizia* and *Melanoselinum* and within *Tornabenea* – and is apparently a derived insular trait because their respective sister groups are each herbaceous. Among Macaronesian umbellifers, the woody habit is also present in *Angelica lignescens* Danton & Reduron, a recently described endemic of the Azores that was once confused with *Melanoselinum* (Danton *et al.*, 1997; Press & Dias, 1998). Based on a molecular phylogeny, this species is a sister group to a clade of several palaearctic herbaceous congeners (Spalik *et al.*, 2004). Nevertheless, the majority of Macaronesian endemic umbellifers are herbaceous, a notable exception considering the high prevalence of woody taxa in the region. Woodiness was generally regarded as ancestral in Apiaceae because its sister family Araliaceae includes predominantly woody plants, while many southern African taxa, regarded as basal lineages in the family, are woody. Early molecular studies suggested that several southern African woody umbellifers constitute sister clades to subfamilies Apioideae and Saniculoideae, supporting this hypothesis (Downie & Katz-Downie, 1996, 1999; Plunkett *et al.*, 1996). However, with expanded sampling of herbaceous southern African umbellifers, woodiness is now thought to be a derived trait within the family (Calviño *et al.*, 2006).

Another interesting parallelism among *Melanoselinum*, *Monizia* and *Tornabenea* is the evolution of wind dispersal. Fruits of members of subtribe Daucinae are usually animal-dispersed due to their prominent spiny secondary ridges; exozoochory is regarded as plesiomorphic for this clade (Lee *et al.*, 2001). Fruits from taxa comprising sister groups to *Melanoselinum/Monizia*, *Tornabenea* and *C. elegans* are each spiny and animal-dispersed. In contrast, the fruits of *Melanoselinum*, *Monizia* and *Tornabenea* have much broader secondary ridges, facilitating wind dispersal. The fruits of *C. elegans* are glabrous and similar in shape to those of *Daucus*, although they are much smaller and do not have secondary ridges or any other appendages facilitating dispersal. These fruits are probably gravity-dispersed. In the absence of dispersing agents, like terrestrial mammals, the insular descendants of zoochoric species have switched to other modes of dispersal.

The phylogenetic position of *C. elegans* with respect to *M. edulis* and *M. decipiens* is enigmatic. In our study, depending on the method of inference, this group is either paraphyletic, with *C. elegans* sister group to the 'Daucus I' clade, or monophyletic, with the entire group sister group to the 'Daucus I' clade. DIVA optimizations reconstruct either a Macaronesian origin for the Macaronesian plus 'Daucus I' clade and back-dispersal to Africa, or a separate origin of the 'Daucus I' clade from African ancestors. Both scenarios assume inter-archipelago dispersal: from Madeira to the Canary Islands, or from the Canary Islands to Madeira. Scenarios with dispersals to the Canary Islands from the mainland and back-dispersals to Africa have already been inferred for several genera from other plant families having members endemic to the islands, such as *Lotus* L. (Fabaceae, Allan *et al.*, 2004), *Tolpis* Adans. (Asteraceae, Moore *et al.*, 2002), *Aeonium* Webb & Berthel. alliance (Crassulaceae, Mort *et al.*, 2002) and *Convolvulus* L. (Convolvulaceae, Carine *et al.*, 2004). Dispersal among the Macaronesian archipelagos has been postulated for *Echium* L. (Boraginaceae, Böhle *et al.*, 1996), *Crambe* L. sect. *Dendrocrambe* DC. (Brassicaceae, Francisco-Ortega *et al.*, 2002) and *Aeonium* (Mort *et al.*, 2002). In each of these cases, the dispersal was from the Canary Islands to Madeira.

Regarding inter-archipelago dispersal, the scenario inferred from the Bayesian tree with a single colonization of Macaronesia and back-dispersal to the mainland appears to be a rather unlikely hypothesis for Madeiran–Canarian Daucinae. First, it requires long-distance dispersal from eastern Mediterranean or eastern Africa to Madeira, colonization of the Canary Islands from Madeira, and dispersal to north-western Africa from the Canaries. For this tree topology, two dispersals from the mainland – to Madeira and to the Canary Islands – provide a simpler explanation. Independent dispersals of closely related (infraspecific) lineages have been inferred for Macaronesian *Olea europaea* L. (Hess *et al.*, 2000). The scenario inferred by the NJ tree requires one dispersal from the mainland to the Canary Islands and then another one from the Canary Islands to Madeira. It postulates the colonization of Macaronesia from north-western Africa, a predominant dispersal route among the endemics of the archipelago (Carine *et al.*, 2004). Many species of *Daucus* are coastal plants, and seeds of the ancestor of the Canarian–Madeiran clade may have been brought to the islands by migrating birds. The Canary Islands may have been the stepping stones for the colonization of Madeira, as inferred for other endemic plants.

Affinity and biogeography of the African members of *Cryptotaenia*

The African species hitherto classified in *Cryptotaenia* are members of tribe Pimpinelleae. Such an affinity is not surprising: Townsend (1989), in his revision of umbellifers for the *Flora of Tropical East Africa*, noted that *Cryptotaenia* is very closely related to *Pimpinella*, with *Pimpinella buchananii* Wolff being most similar to *Cryptotaenia*. Apart from the Madagascan *P. betsileensis*, the African members of *Pimpinella*

have yet to be included in molecular phylogenetic studies. Such a study is necessary, for it is clear that Madagascan *Pimpinella* is unrelated to *Pimpinella* from Eurasia. The genus *Pimpinella*, with some 150 species (Pimenov & Leonov, 1993) is one of the largest genera in the family. Many eastern Asiatic members of the genus are distantly related to the nomenclatural type of the genus (K. Spalik & S.R. Downie, unpublished data), and the group requires a thorough phylogenetic study with extensive sampling throughout its range before any taxonomic changes can be made. Moreover, the generic circumscription of tribe Pimpinelleae is also unclear. Therefore, the biogeographical scenarios resulting from this study as they pertain to African *Cryptotaenia* must be regarded as provisional.

Our study suggests that the African members of tribe Pimpinelleae form a monophyletic branch derived from a common ancestor of Middle Eastern origin. A Middle East–East African track was also hypothesized for *A. alpina* (Koch *et al.*, 2006) and *Crambe* (Brassicaceae; Francisco-Ortega *et al.*, 1999). Among umbellifers, a distribution pattern that suggests a relatively recent use of this track also occurs in *Anthriscus sylvestris* (Spalik, 1997), *Ferula communis* L. (Townsend, 1989), *Helosciadium nodiflorum* (Spalik & Downie, 2006; this study) and *Torilis arvensis* (Huds.) Link (Townsend, 1989). This migration track may have played a crucial role for umbellifers at an early stage of their radiation, although it was used in the opposite direction. Plunkett *et al.* (1996) hypothesized that umbellifers migrated northward from southern Africa, their likely ancestral distribution, to Eurasia through the Middle East. This scenario was confirmed by Calviño *et al.* (2006) based on expanded sampling of African umbellifers. The latter authors also hypothesized a southward migration and subsequent diversification in Africa of several originally Eurasian clades.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

Appendix S1 Accessions of *Cryptotaenia* (*sensu lato*) and major apioid clades (tribes) examined for variation in nuclear ribosomal DNA ITS sequences.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2007.01752.x

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BIOSKETCHES

Krzysztof Spalik has interests in plant molecular phylogenetics, taxonomy and evolution of adaptive traits, particularly in the family Apiaceae.

Stephen R. Downie has interests in the systematics of the Apiaceae.

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