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MORPHOLOGY AND BIOGEOGRAPHY OF APIACEAE SUBFAMILY SANICULOIDEAE AS INFERRED BY PHYLOGENETIC ANALYSIS OF MOLECULAR DATA[1]

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The phylogenetic placements of several African endemic genera at the base of Apiaceae subfamilies Saniculoideae and Apioideae have revolutionized ideas of relationships that affect hypotheses of character evolution and biogeography. Using an explicit phylogeny of subfamily Saniculoideae, we reconstructed the evolutionary history of phenotypic characters traditionally important in classification, identified those characters most useful in supporting relationships, and inferred historical biogeography. The 23 characters examined include those of life history, vegetative morphology, inflorescences, and fruit morphology and anatomy. These characters were optimized over trees derived from maximum parsimony analysis of chloroplast DNA *trnQ-trnK* sequences from 94 accessions of Apiaceae. The results revealed that many of these characters have undergone considerable modification and that traditional assumptions regarding character-state polarity are often incorrect. Infrasubfamilial relationships inferred by molecular data are supported by one to five morphological characters. However, none of these morphological characters support the monophyly of subfamilies Saniculoideae or Apioideae, the clade of *Petagnaea*, *Eryngium* and *Sanicula,* or the sister-group relationship between *Eryngium* and *Sanicula*. Southern African origins of Saniculoideae and of its tribes Steganotaenieae and Saniculeae are supported based on dispersal–vicariance analysis.

Key words: Apiaceae; biogeography; character evolution; molecular phylogeny; morphology; Saniculoideae; southern Africa.

Patterns of morphological character evolution and historical biogeography are important in understanding evolutionary processes. Through a phylogeny, it is possible to infer character state transformations and when and how often these transformations have occurred. Such patterns might indicate what forces promote morphological stasis or drive these changes, including forces arising from other characters (Maddison and Maddison, 2000). Similarly, hypotheses on the historical biogeography might help us understand the processes that have shaped the present-day distribution of organisms.

The interpretation of the phenotypic character evolution and biogeography of Apiaceae has been greatly influenced by the predominant system of classification for the family proposed by Drude (1898) over a century ago. However, the recent phylogenetic placements of several African endemic genera at the base of Apiaceae subfamilies Saniculoideae and Apioideae have changed our inferences on the relationships within Apiaceae and have changed previous hypotheses on morphological character evolution and historical biogeography (Calviño et al., 2006; Calviño and Downie, 2007). Drude recognized three subfamilies (Hydrocotyloideae, Saniculoideae, and Apioideae) that share the following set of distinctive characters: inferior bicarpellate ovaries, reduced calyces, schizocarp fruits with two one-seeded, five-ribbed mericarps, and inflorescences based on simple umbels, compound umbels, or capitules. The subfamilies are distinguished by inflorescence type and several anatomical and morphological features of the fruit, such as the presence of a carpophore, lignification of the endocarp, form and position of calcium oxalate crystals, and the presence of intrajugal oil ducts and vallecular vittae. Subfamily Apioideae has been the focus of much systematic attention, with 11 tribes and seven informally recognized groups confirmed as monophyletic (Downie et al., 2001; Spalik et al., 2004; Calviño et al., 2006). Given the large size of this subfamily and its great taxonomic complexity, however, much additional work is required to resolve its remaining higher-level taxa and their interrelationships. Nevertheless, the research to date has revolutionized ideas of character evolution within Apioideae (Katz-Downie et al., 1999; Downie et al., 2000a, b; Spalik and Downie, 2001; Calviño et al., 2006). In contrast, the morphology of Saniculoideae has yet to be evaluated within the context of an explicit phylogenetic hypothesis, resulting in assumptions of character-state polarity and hypotheses about relationships based on characters that may or may not be synapomorphic. With explicit hypotheses of phylogenetic relationships now available for basal Apioideae (Calviño et al., 2006) and Saniculoideae (Calviño and Downie, 2007), patterns of character evolution within subfamily Saniculoideae and its historical biogeography can be interpreted objectively.

Heretofore, the biogeographic history of subfamily Saniculoideae has not been known. While several authors have speculated about the origins of some of its constituents or groups of putatively allied genera (*Alepidea* F. Delaroche-*Eryngium* L. [Turmel, 1950], *Astrantia* L.-*Actinolema* Fenzl [Wolff, 1913; Ferrarini, 1967], *Sanicula* L. [Shan and Constance, 1951]), there has been no biogeographic study on the origin of the subfamily as a whole. An Asian origin of subfamily Saniculoideae can be assumed simply because this region was hypothesized as the center of origin of the aforementioned genera or groups of genera. Having an explicit hypothesis on the phylogenetic

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relationships for subfamily Saniculoideae (Calviño and Downie, 2007) now makes it possible to reconstruct its biogeographic history.

The major objectives of this study are to (1) reconstruct the evolutionary history of selected morphological characters in Saniculoideae, (2) identify those morphological characters that are most useful in supporting phylogenetic relationships estimated on the basis of molecular data, and (3) estimate the origin of subfamily Saniculoideae and reconstruct its subsequent biogeographic history.

MATERIALS AND METHODS

Accessions examined—Ninety-four accessions, representing 13 genera and 85 species of Apiaceae, were examined. Ninety-one of these accessions were included in a previous molecular phylogenetic study of subfamily Saniculoideae (Calviño and Downie, 2007), and their sequence data were combined with three additional accessions of Old World *Eryngium* (*E. aquifolium* Cav., *E. ilicifolium* Lam., and *E. duriaei* J. Gay ex Boiss.) for which data were available and whose phylogenetic positions were important for the reconstruction of ancestral traits in the genus (Calviño et al., in press). The monotypic genus *Hacquetia* Neck. ex DC. was reduced to synonymy under *Sanicula* (Calviño and Downie, 2007); therefore, the name *Sanicula epipactis* (Scop.) E. H. Krause is used herein to refer to this species. Representatives of all nine monophyletic genera recognized within subfamily Saniculoideae tribes Saniculeae and Steganotaenieae sensu Calviño and Downie (2007) were included. Our revision of tribe Saniculeae corresponds to Drude's (1898) conception of subfamily Saniculoideae, upon the exclusion of *Lagoecia* L. whose affinity to subfamily Apioideae has been previously reported (Plunkett et al., 1996; Downie et al., 2000c; Valiejo-Roman et al., 2002). The accessions of Saniculoideae examined herein were chosen to represent infrageneric morphological diversity. As outgroups, we included basal members of subfamily Apioideae (*Lichtensteinia* Cham. & Schltdl., *Anginon* Raf., and *Annesorhiza* Cham. & Schltdl.), as well as *Hermas* L. from the *Hermas* clade (Calviño et al., 2006). Subfamilies Saniculoideae and Apioideae are monophyletic sister groups (Downie et al., 2001; Calviño and Downie, 2007). The basal members of Apioideae were included to help reconstruct character states for the ancestor of subfamily Saniculoideae. All trees were rooted with *Hermas* because a previous study inferred its sister-group relationship to Apioideae plus Saniculoideae (Calviño et al., 2006). Because the choice of outgroup can greatly affect character reconstruction, we also examined the morphology of members of Apiaceae subfamily Azorelloideae, also estimated as closely related to Apioideae and Saniculoideae (Plunkett et al., 2004).

Morphological data—States for 23 morphological characters were scored based on our experiences working with the group, observations of herbarium specimens, and examination of literature. Herbarium material was obtained from BA, CTES, FCQ, ILL, ILLS, LL, LP, MO, OS, PRE, SI, TEX, UC, US, W, WIS, and WU (herbarium abbreviations are according to Holmgren et al., 1990). The literature examined included all major treatments of the subfamily, as well as revisions of its genera and allies (Grintzesco, 1910; Dümmer, 1913; Wolff, 1913; Weimarck, 1949; Shan and Constance, 1951; Breton, 1962; Froebe, 1964, 1971; Froebe and Ulrich, 1978; Magin, 1980; Mariotti, 1989; Allison and Van Wyk, 1997; Wörz, 1999b; Van Wyk, 2000; Vessio, 2001; Tilney and Van Wyk, 2001). The following floras were also used: *Flora Brasiliensis* (Urban, 1879), *Flora Ibérica* (Nieto Feliner et al., 2003), *Flora Iranica* (Hedge et al., 1987), *Flora of Tropical East Africa* (Townsend, 1989), *Flora of Turkey* (Davis, 1972), *Flora Zambesiaca* (Cannon, 1978), and *North American Flora* (Mathias and Constance, 1944, 1945). Characters of fruit anatomy were based primarily on the studies of Rompel (1895), Tseng (1967), and Liu (2004).

The 23 discrete morphological characters and their respective character states are described in Appendix 1. These characters represent life history and vegetative morphology (characters 1–5), inflorescence morphology and architecture (characters 6–10), and fruit morphology and anatomy (characters 11–23). All characters were treated as unordered; 20 characters were binary, and three were multistate. For a few taxa, some character states could not be assessed because they were absent on the available material and information was not available in the literature; these states were scored as missing. Some characters for some taxa also had to be scored as inapplicable. The data matrix is presented in Appendix 2. Because not all species included herein have been examined for fruit anatomy, we adopted the following criteria to code these characters. When the character is invariant among the analyzed species within a genus, it was assumed that the unexplored species had the same character state as its congeners. If the character is variable within the genus for those species where data are available, then this character was coded as missing for the unexplored species.

Phylogenetic analyses—For phylogenetic analysis, we enhanced the chloroplast DNA (cpDNA) *trnQ-trnK* matrix (and maintained the binary-coded indels) used in Calviño and Downie (2007) by adding *Eryngium aquifolium, E. ilicifolium,* and *E. duriaei*, which required minimal adjustment to the original alignment. The resulting data matrix was analyzed using maximum parsimony (MP) as implemented by PAUP* version 4.0b10 (Swofford, 2002), following the heuristic search strategies suggested by Catalán et al. (1997) and used by Calviño et al. (2006) to ensure that the shortest trees were found when their numbers exceeded the capacity of the computer memory. One thousand heuristic searches were initiated using random addition starting trees with tree-bisection-reconnection (TBR) branch swapping and MulTrees selected, but saving no more than five trees from each search. These trees were subsequently used as starting trees for further TBR branch swapping. In preliminary searches, the maximum number of saved trees exceeded 20 000; this number was set as the maximum number of trees to be saved in subsequent searches and these trees were permitted to swap to completion. The strict consensus of these 20 000 minimal length trees was then used as a topological constraint in another round of 1000 random addition replicate analyses, but in this case, only those trees that did not fit the constraint tree were saved. No additional trees were found at the length of the initial shortest trees, suggesting that the strict consensus tree adequately summarizes the available evidence, even though the exact number of trees at that length is not known. Bootstrap values were calculated from 100 000 replicate analyses using "fast" stepwise-addition of taxa, and only those values compatible with the majority-rule consensus tree were recorded.

Evolution of morphological characters—To assess patterns of evolution of the 23 morphological characters, we optimized each character onto all 20 000 minimal length trees using the computer program T.N.T. version 1.0 (Goloboff et al., 2003) under a parsimony criterion. To identify those morphological characters that support relationships based on molecular data, we recorded all morphological synapomorphies at each node by tracing common synapomorphies over all trees. To further evaluate the utility of morphological characters in delimiting monophyletic groups and their degree of homoplasy, the molecular-based trees were used to infer the number of evolutionary steps of these characters using the program Mesquite version 1.06 (Maddison and Maddison, 2005).

Biogeographic analysis—To reconstruct the distribution of the ancestor of subfamily Saniculoideae, a dispersal–vicariance analysis was carried out with the program DIVA version 1.1 (Ronquist, 1996), using the optimize command and default option settings. We entered the following simplified, fully resolved phylogenetic tree based on the results of the cpDNA *trnQ-trnK* analysis: (*Hermas*, (Apioideae, ((*Steganotaenia* Hochst., *Polemanniopsis* B. L. Burtt), (*Alepidea*, (*Arctopus* L., ((*Actinolema*, *Astrantia*), (*Petagnaea* Caruel, (*Sanicula*, *Eryngium*)))))))). The following unit areas were defined: (1) southern Africa (i.e., Botswana, Lesotho, Namibia, South Africa, and Swaziland); (2) Asia; (3) Europe (excluding the western Mediterranean); and (4) western Mediterranean (Iberian Peninsula and northern Africa). We coded each terminal taxon for its likely ancestral distribution and not for all of the regions in which its members presently occur because if we had, information important for the optimization of ancestral states would be lost (Ronquist, 1996). In most cases, however, ascertaining the ancestral distribution of a terminal taxon was clear because it was endemic to one of the defined unit areas. The likely ancestral distributions of the widespread subfamily Apioideae and of the genus *Eryngium* were determined based on previous phylogenetic studies where southern African (Calviño et al., 2006) and western Mediterranean (Calviño et al., in press) origins were inferred, respectively. Likewise, the origin of the cosmopolitan genus *Sanicula* was scored as Asian, as suggested by a previous study (Vargas et al., 1999). We acknowledge that a formal reconstruction of the ancestral area of *Sanicula* is lacking, and an alternative would be to consider a North American origin of the genus. However, this scenario implies an extra long-distance dispersal between hemispheres. Also, this scenario does not affect the ancestral reconstruction of the basal nodes of Saniculoideae (i.e., ancestors of the subfamily and of its two tribes); thus for simplification, we present only the Asian origin. In *Astrantia*, members of section *Astrantia* are distributed primarily in Asia, while those of section *Astrantiella* occur in Europe. However, the varieties of *A. major*

L. (section *Astrantia*) are distributed in both Europe and Asia. Given these distributions and to determine how each ancestral area affected the reconstruction of the biogeographic history of Saniculoideae, we ran three different analyses assuming that the ancestor of *Astrantia* was distributed only in Asia, only in Europe, or in both places.

RESULTS

Phylogenetic analyses—MP analysis of 4401 unambiguously aligned *trnQ-trnK* nucleotide positions (with 878 informative characters) plus 189 binary-scored informative indels resulted in the preset maximum tree limit of 20 000 trees, each of 2354 steps (CIs = 0.7698 and 0.7083, with and without uninformative characters, respectively; RI = 0.9452). The apioid genera *Lichtensteinia* (five accessions), *Anginon*, and *Annesorhiza* comprise a clade (87% bootstrap) that is a sister group to a monophyletic subfamily Saniculoideae (100% bootstrap). Saniculoideae tribes Steganotaenieae (94% bootstrap) and Saniculeae (99% bootstrap) also comprise monophyletic sister groups. Intergeneric relationships within Saniculoideae are fully resolved and are supported with bootstrap values ranging from 75 to 100%, averaging 95%: ((*Steganotaenia, Polemanniopsis*), (((((*Eryngium, Sanicula*), *Petagnaea*), (*Astrantia, Actinolema*)), *Arctopus*), *Alepidea*)). The strict consensus of these trees is completely consistent with that of our previous analysis (Calviño and Downie, 2007), but with the addition of *Eryngium duriaei, E. ilicifolium*, and *E. aquifolium* positioned as three successive lineages at the base of the "Old World" *Eryngium* clade (supported by 100% bootstrap).

Evolution of morphological characters—The numbers of evolutionary steps for each of the 23 morphological characters optimized over all 20 000 minimal length 2354-step trees are presented in Fig. 1. The total number of steps is 75 for 4725 trees or 76 for the remaining 15 275 trees. This difference in tree length is due to character 3 (palmate leaves) having eight or nine steps across all 20 000 trees (Fig. 2A, B, respectively). Nine of the 23 characters are not homoplastic, with these representing all three classes of characters considered herein. Among the most homoplastic characters are reproductive strategy (character 1), palmate leaves (character 3), length of involucre relative to the basic inflorescence (character 7), and type of fruit wing development (character 15). Patterns in the evolution of each of these characters are presented in the "Discussion" section. Reconstructions of the evolution of palmate leaves, reproductive strategy, leaf margins, flowering unit, sexual system, fruit wings, and crystals scattered in the mesocarp are presented in Figs. 2–8, respectively. When a character reconstruction did not differ among the 20 000 individual MP trees, its pattern of evolution was mapped onto the strict consensus tree (Figs. 3–8); otherwise, alternative reconstructions were mapped onto individual trees (Fig. 2).

The examined morphological characters that support monophyletic groups (i.e., those synapomorphic characters common to all trees) are mapped onto a simplified tree that summarizes the relationships among the genera (Fig. 9). Most clades are supported by one to five morphological synapomorphies, yet no single morphological character state supports the monophyly of subfamilies Saniculoideae or Apioideae or of the clade comprising *Eryngium*, *Sanicula* and *Petagnaea* or the sister group relationship between *Eryngium* and *Sanicula*.

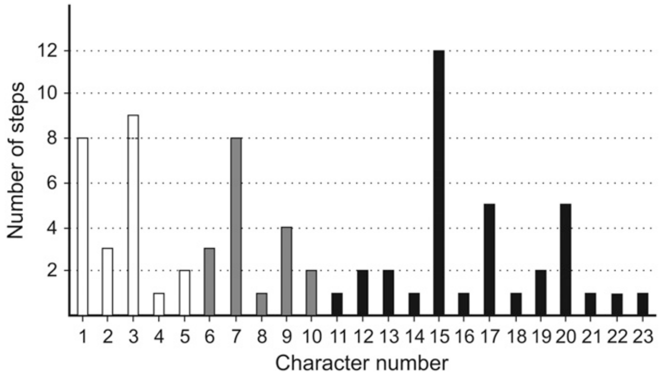

Fig. 1. Number of evolutionary steps of each of the 23 morphological characters when optimized over 20 000 minimal length trees derived from MP analysis of 94 cpDNA *trnQ-trnK* sequences of subfamily Saniculoideae and outgroups. Bars represent the following classes of characters: life history and vegetative morphology (white bars); inflorescence morphology and architecture (gray bars); fruit morphology and anatomy (black bars). Character 3 has eight to nine steps depending upon the reconstruction. Character numbers refer to those presented in Appendix 1.

Biogeographic analysis—The results of the three dispersal–vicariance analyses, assuming that the ancestor of *Astrantia* was distributed only in Europe, only in Asia, or in both places, indicated that the ancestral distribution of subfamily Saniculoideae, as well as that of tribes Steganotaenieae and Saniculeae, was in southern Africa (Fig. 10). When a European origin for *Astrantia* was assumed, four alternative biogeographic scenarios were recovered. Two of these scenarios indicated a dispersal from southern Africa to Asia in the ancestor of the clade of *Arctopus* to *Eryngium* and then either two extra dispersals from Asia to Europe and the western Mediterranean in the ancestor of *Petagnaea* to *Eryngium*, or one dispersal first from Asia to Europe in the latter ancestor and then the other dispersal from Asia or Europe to the western Mediterranean in the ancestor of *Eryngium* plus *Sanicula* (Fig. 10A, B, respectively). The other two scenarios indicated a dispersal event from southern Africa to Europe in the ancestor of *Arctopus* to *Eryngium* and then either two extra dispersals from Europe to Asia and the western Mediterranean in the ancestor of *Petagnaea* to *Eryngium*, or one dispersal first from Europe to Asia in the latter ancestor and then the other from Asia or Europe to the western Mediterranean in the ancestor of *Eryngium* plus *Sanicula* (Fig. 10C, D, respectively). The four alternative scenarios also indicated an extra dispersal event in the ancestor of *Actinolema* plus *Astrantia* to Europe from Asia. The same first two scenarios were recovered when an Asian or Eurasian origin of *Astrantia* was assumed (Fig. 10A, B), but this time the ancestral distribution of *Actinolema* plus *Astrantia* was recovered as Asian, and dispersal to Europe took place in the ancestor of *Astrantia*, or within the genus itself. The first two biogeographic histories infer a northeastern and then a western migration (i.e., from southern Africa to Asia and from there to Europe) of the ancestors, while the last two scenarios imply a northwestern and then an eastern migration of the same ancestors (i.e., from Africa to Europe and from there to Asia).

DISCUSSION

Evolution of morphological characters—*Life history and vegetative morphology*—Reproductive strategy (character 1)—The majority of Saniculoideae species are polycarpic perennials.

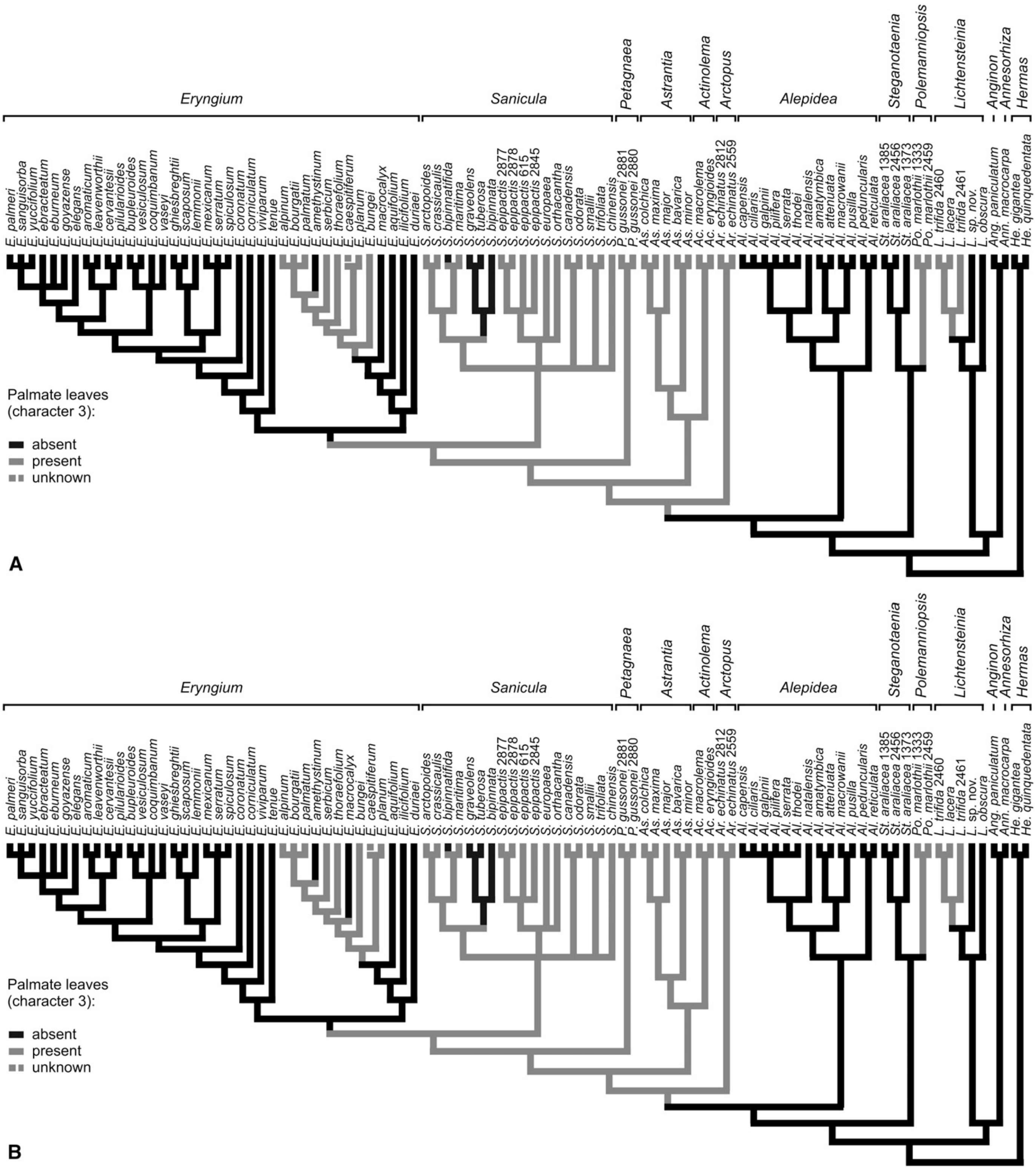

Fig. 2. Evolution of palmate leaves (character 3) when optimized over subsets of the 20 000 minimal length trees derived from MP analysis of 94 cpDNA *trnQ-trnK* sequences of subfamily Saniculoideae and outgroups. In 4725 MP trees, as represented by tree A, character 3 is reconstructed as having eight steps; in the remaining 15 275 MP trees, as represented by tree B, character 3 is reconstructed as having nine steps. This difference in steps is due to the relative placement of *Eryngium macrocalyx*.

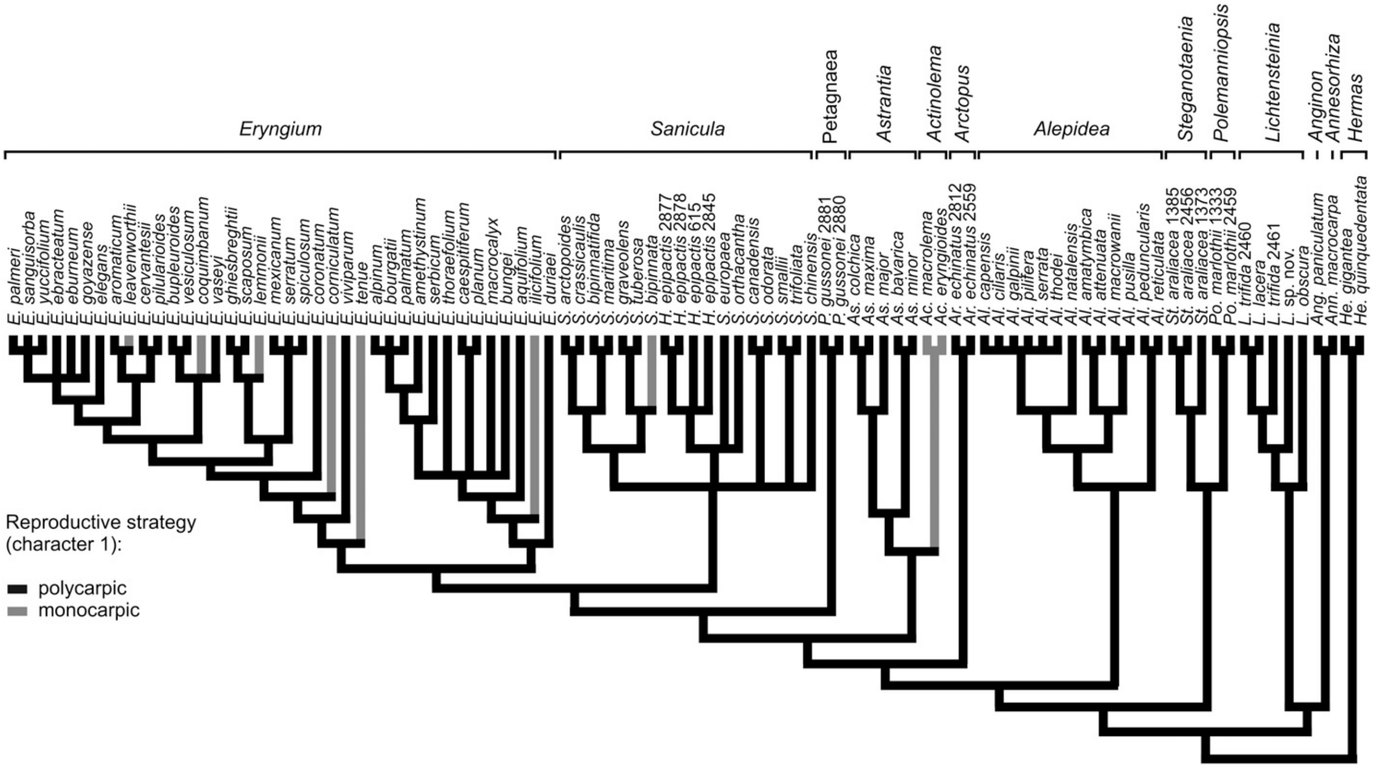

Fig. 3. Evolution of polycarpic vs. monocarpic reproductive strategy (character 1) when optimized over all 20 000 minimal length trees derived from MP analysis of 94 cpDNA *trnQ-trnK* sequences of subfamily Saniculoideae and outgroups. Within Saniculoideae, monocarpy has evolved at least eight times from polycarpic ancestors.

Monocarpic species (annuals or biennials) are present in a few species of *Eryngium* and *Sanicula* and all members of *Actinolema*. This character (usually expressed in literature as perennial vs. annual) is traditionally used to characterize the genus *Actinolema* and to distinguish it from its sister genus *Astrantia*. Optimization of the character reproductive strategy onto all 20 000 minimal length trees shows that monocarpy has evolved at least eight times independently in Saniculoideae from polycarpic ancestors (Fig. 3). The high level of homoplasy for this character is in accordance with other studies that show that this trait is mainly explained by habitat choice rather than phylogeny (Spalik and Downie, 2001; Lososová et al., 2006). Nevertheless, monocarpy is an important synapomorphy for the genus *Actinolema*. In *Eryngium*, the character is homoplastic and according to the reconstruction presented herein, monocarpy has evolved independently in the genus at least six times.

Woody habit (character 2)—Within Saniculoideae, woodiness occurs in *Polemanniopsis, Steganotaenia, Eryngium bupleuroides* Hook. & Arn., *E. fernandezianum* Skottsb., *E. inaccessum* Skottsb., and *E. sarcophyllum* Hook & Arn. Optimization of the character habit onto the phylogenies shows that woodiness occurred two independent times in Saniculoideae from herbaceous ancestors: tribe Steganotaenieae and *Eryngium bupleuroides (E. fernandezianum, E. inaccessum*, and *E. sarcophyllum* were not included in this study). Woodiness has also occurred in *Anginon* of subfamily Apioideae. Tribe Steganotaenieae is mainly distributed in southern Africa, a region where shrubs are dominant mainly because of the nutrient-poor soils that favor this type of growth (Cowling and Hilton-Taylor, 1997). Within subfamily Apioideae, the woody habit originated multiple times independently in this environment, and contrary to earlier ideas of character polarity, it is not plesiomorphic based on its optimization over a phylogeny (Calviño et al., 2006). Similarly, tribe Steganotaenieae exemplifies another independent origin of woodiness in southern Africa from herbaceous ancestors. Despite its high level of homoplasy in Apiaceae, the evidence suggests that woodiness is a synapomorphy for tribe Steganotaenieae. Four species of *Eryngium* are endemic to the Juan Fernandez Islands, Chile, of which only *E. bupleuroides* was included in this investigation. Three of these endemic species (i.e., *E. bupleuroides, E. fernandezianum*, and *E. inaccessum*) examined in a concurrent study (Calviño et al., in press) comprise a monophyletic group, suggesting that woodiness appeared in the ancestor that colonized the islands. The origin of woodiness from herbaceous ancestors is not surprising. The existence of shrubby Asteraceae and *Plantago* L. (Plantaginaceae) species on the Juan Fernandez Islands plus the results of wood anatomy studies of the *Eryngium* endemics (Rodríguez, 1957) suggests that woodiness was secondarily derived and was the result of adaptation to particular local conditions. Oceanic island floras show a high proportion of woody species, with their continental relatives being predominantly herbaceous (Panero et al., 1999). These observations have generated considerable controversy, with an opposing hypothesis suggesting the origin and evolution of woodiness on oceanic islands (Bramwell, 1972; Carlquist, 1974). The *Eryngium* species endemic to the Juan Fernandez Islands clearly exemplify the first hypothesis—a shift from herbaceous continental ancestors to woody insular species.

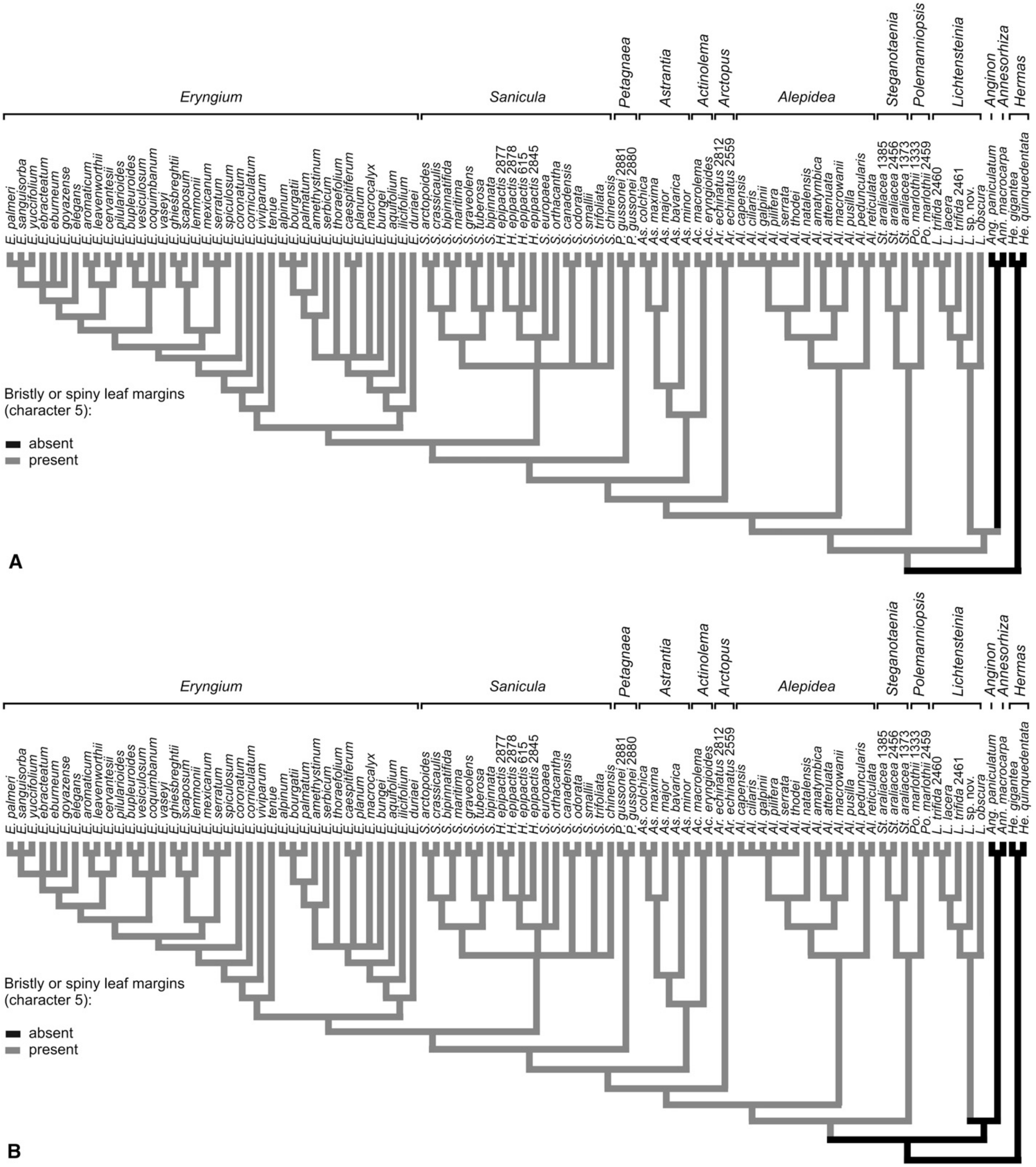

Fig. 4. Evolution of bristly or spiny leaf margins (character 5) when optimized over all 20 000 minimal length trees derived from MP analysis of 94 cpDNA *trnQ-trnK* sequences of subfamily Saniculoideae and outgroups. Two equally most parsimonious patterns of evolution are reconstructed: (A) The presence of bristles or spines is plesiomorphic for subfamilies Saniculoideae and Apioideae. (B) The presence of bristles or spines occurs independently in the ancestors of Saniculoideae and *Lichtensteinia* (Apioideae).

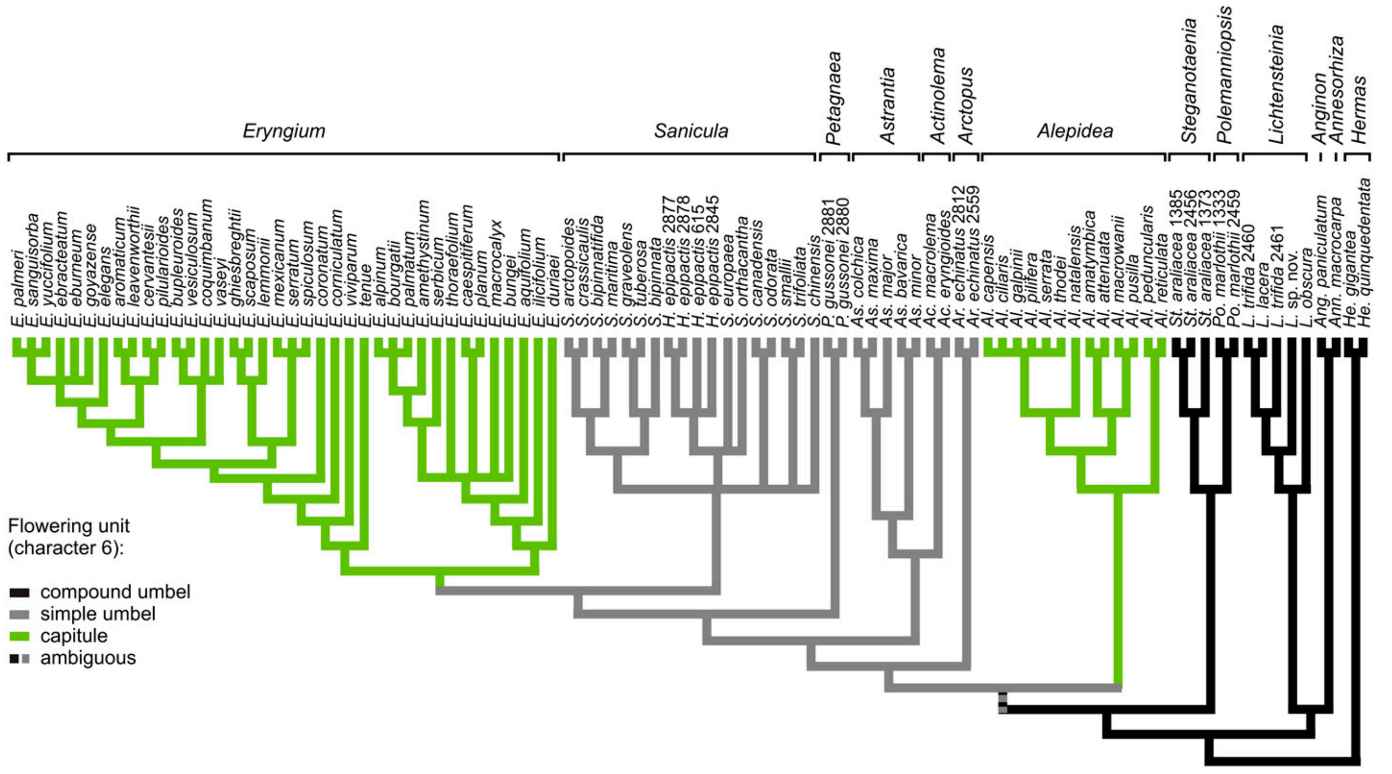

Fig. 5. Evolution of the flowering unit (character 6) when optimized over all 20 000 minimal length trees derived from MP analysis of 94 cpDNA *trnQ-trnK* sequences of subfamily Saniculoideae and outgroups. This character is reconstructed as having three steps within subfamily Saniculoideae. Two equally most parsimonious patterns of evolution are reconstructed, depending on whether the ancestor of tribe Saniculeae had a simple umbel or a capitule.

Leaves (characters 3–5)—Features of the basal leaves are generally considered important for infrageneric classification of Saniculoideae. Palmate leaves (character 3) occur in most genera of Saniculoideae (i.e., *Polemanniopsis*, *Arctopus*, *Actinolema*, *Astrantia*, and *Petagnaea*) and most species of *Sanicula* and Old World *Eryngium*. In general, nonpalmate leaves are envisioned as derivations from palmate ones, as suggested by Shan and Constance (1951) for *Sanicula* and Cerceau-Larrival (1962) for *Eryngium*. Optimization of this character onto the phylogenies indicates that palmate leaves are a synapomorphy for the clade of *Arctopus* to *Eryngium* (Fig. 2). The ancestors of tribes Steganotaenieae and Saniculeae had nonpalmate leaves, a plesiomorphic feature also present in the ancestor of subfamily Saniculoideae, the ancestor of subfamily Apioideae, and their previous common ancestors. The character is quite homoplastic (with eight to nine steps), with most changes occurring within *Eryngium* and *Sanicula*. Palmate leaves occur independently in *Polemanniopsis* and in the ancestor of *Arctopus* to *Eryngium*, and the state reverses to nonpalmate in the ancestor of *Eryngium*. Therefore, in *Alepidea* nonpalmate leaves are plesiomorphic, while in *Eryngium* this feature is a synapomorphy derived from palmate leaves. Within *Eryngium*, nonpalmate leaves are maintained in most species of the New World, while the trait shifts from nonpalmate to palmate in most members of the Old World. The exact number of times this happened in the New and Old World clades cannot be determined because of incomplete sampling.

Simple leaves (entire or with different degrees of margin incision; character 4) are common in Saniculoideae. All members of tribe Steganotaenieae have compound leaves, while those of tribe Saniculeae have simple leaves. Because the sister-group relationship of these two tribes was inferred only recently (Downie and Katz-Downie, 1999; Calviño et al., 2006; Calviño and Downie, 2007), the evolution of this character within the subfamily has heretofore not been determined. The character reconstruction indicates that simple leaves are plesiomorphic in subfamily Saniculoideae and in tribe Saniculeae and that compound leaves are a synapomorphy for tribe Steganotaenieae. Compound leaves are not homoplastic within Saniculoideae. Compound leaves also occur in subfamily Apioideae (e.g., in the genera *Heteromorpha* Cham. & Schltdl. and *Pseudocarum* C. Norman of tribe Heteromorpheae [Apioideae]). Reconstruction of characters 3 and 4 indicates that the palmately compound leaves of *Polemanniopsis* are a derivation from pinnately compound leaves, probably by a reduction of the rachis. Pinnately compound leaves originated in the ancestor of Steganotaenieae and are retained in the genus *Steganotaenia*.

The hair-like bristles or spines at the tips of the marginal teeth (character 5) so common in Saniculoideae also occur in *Lichtensteinia* and *Pseudocarum,* suggestive of their close relationship (Van Wyk, 2001; Van Wyk and Tilney, 2004). Reconstructing the pattern of evolution of this character is equivocal regarding the origin of this feature (Fig. 4). One scenario is that bristles or spines are plesiomorphic in subfamilies Apioideae and Saniculoideae and that these appendages were lost independently in *Hermas* and most members of Apioideae (Fig. 4A). The other scenario is that bristles or spines appeared independently in the ancestors of Saniculoideae and *Lichtensteinia*

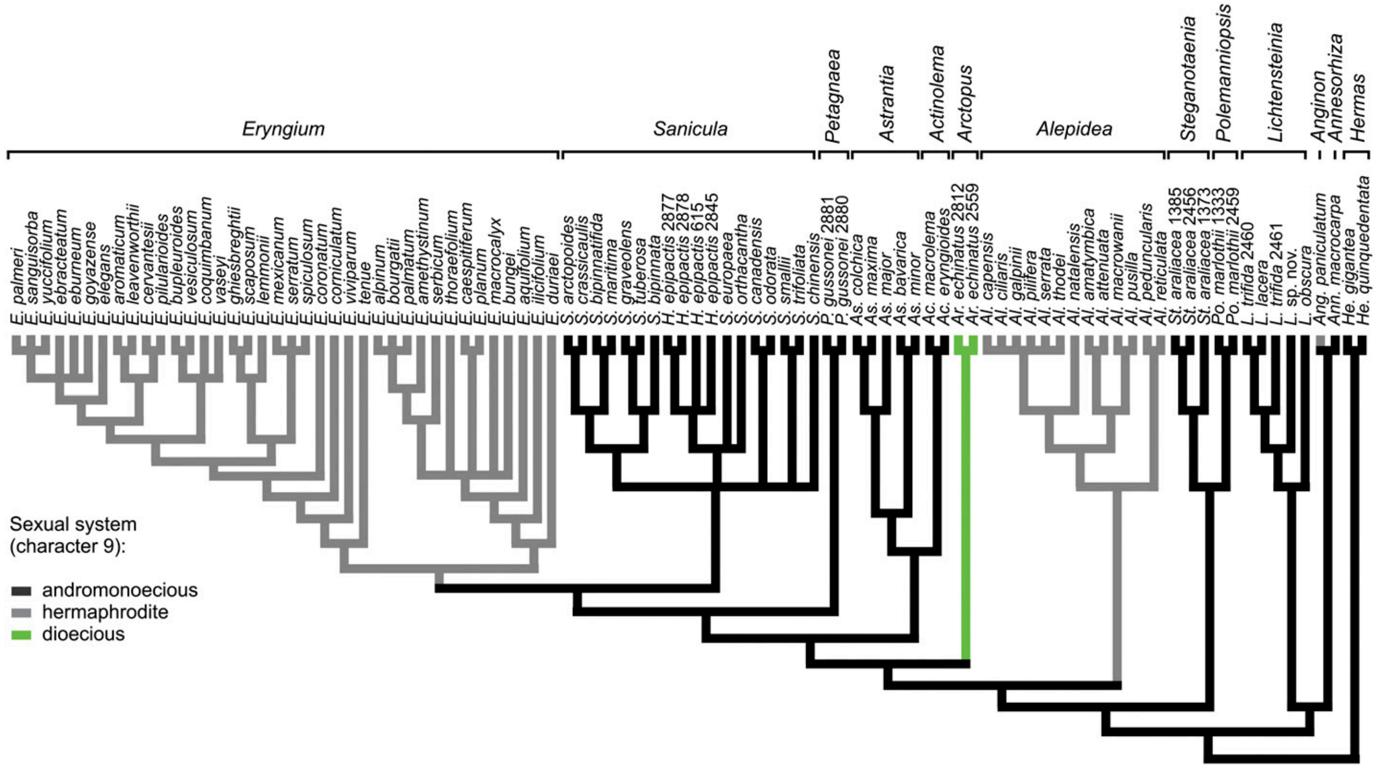

Fig. 6. Evolution of the sexual system (character 9) when optimized over all 20 000 minimal length trees derived from MP analysis of 94 cpDNA *trnQ-trnK* sequences of subfamily Saniculoideae and outgroups. This character is reconstructed as having three steps within subfamily Saniculoideae.

from ancestors lacking this trait (Fig. 4B). To evaluate whether this character is synapomorphic or plesiomorphic for Saniculoideae, we need to understand its reconstruction in the previous ancestors of Apioideae plus Saniculoideae. Unfortunately, this evaluation cannot be done until the positions of *Hermas* and *Klotzschia* Cham. (the latter incertae sedis with respect to subfamily placement, but basal to *Hermas;* Calviño et al., 2006) are corroborated with a broader representation of subfamily Azorelloideae (a putative sister group to Apioideae plus Saniculoideae; Plunkett et al., 2004) and until this character is reconstructed for the ancestor of Azorelloideae. In Azorelloideae, for example, the character is variable; some members of *Eremocharis* Phil., *Azorella* Lam., *Spananthe* Jacq., *Mulinum* Pers. and *Bolax* Comm. ex Juss. clearly display this feature, while others, such as *Huanaca* Cav., do not. In any case, the character does not seem to be of utility to identify affinities with Saniculoideae, given that the relationships suggested previously for *Lichtensteinia* and *Pseudocarum* (Van Wyk, 2001; Van Wyk and Tilney, 2004) are based on symplesiomorphies or convergences.

Inflorescence morphology and architecture—Flowering unit (character 6)—The compound umbel has long been considered the hallmark of subfamily Apioideae, in contrast with the rest of the family where the umbels are simple (Drude, 1898; Wolff, 1913; Spalik and Downie, 2001). Our results indicate that this characteristic feature of Apioideae is plesiomorphic in the subfamily (Fig. 5). Compound umbels are also plesiomorphic in tribe Steganotaenieae. The simple umbel characteristic of Saniculoideae is a derivation from a compound umbel and a synapomorphy of tribe Saniculeae. These results support the hypothesis proposed by Froebe (1964, 1971) that the simple umbels of Saniculeae are formed by the union of various umbellules whose rays and bracteoles (in part) are suppressed. Froebe (1964) suggested that the ancestral umbellules that originated the simple umbel of Saniculeae were andromonoecious, showed centrifugal maturation, and had one central fructiferous flower with several peripherical male flowers. The lack of data for various species, particularly from basal Apioideae and tribe Steganotaenieae, precludes us from including these characters in the analysis. However, umbellules with such characteristics do occur in *Hermas*.

Within Saniculoideae, the capitule identifies *Alepidea* and *Eryngium* and suggests a close affinity between them (Drude, 1898; Wolff, 1913). Turmel (1950) hypothesized that these genera share a recent common ancestor. Our results indicate that capitules evolved independently in the ancestors of each of these genera from plants having simple umbels (or, more appropriately, simplified umbels, as previously discussed). As such, the character state capitule is a synapomorphy for each genus. We acknowledge, however, that in the case of *Alepidea,* the capitule may be a plesiomorphy. Reconstruction of the character floral unit under parsimony optimization is ambiguous about the ancestral trait of Saniculeae, i.e., simple umbels or capitules arose in the ancestor of tribe Saniculeae as a derivation from compound umbels (Fig. 5). We favor the hypothesis of a simple umbel for the ancestor of Saniculeae because it is simpler to explain a derivation of a capitule from a simple umbel, rather than the reverse.

Pedicel of fructiferous flowers (character 10) and length of involucre in relation to the basic inflorescence (character 7)—Saniculoids are often characterized by their "congested,"

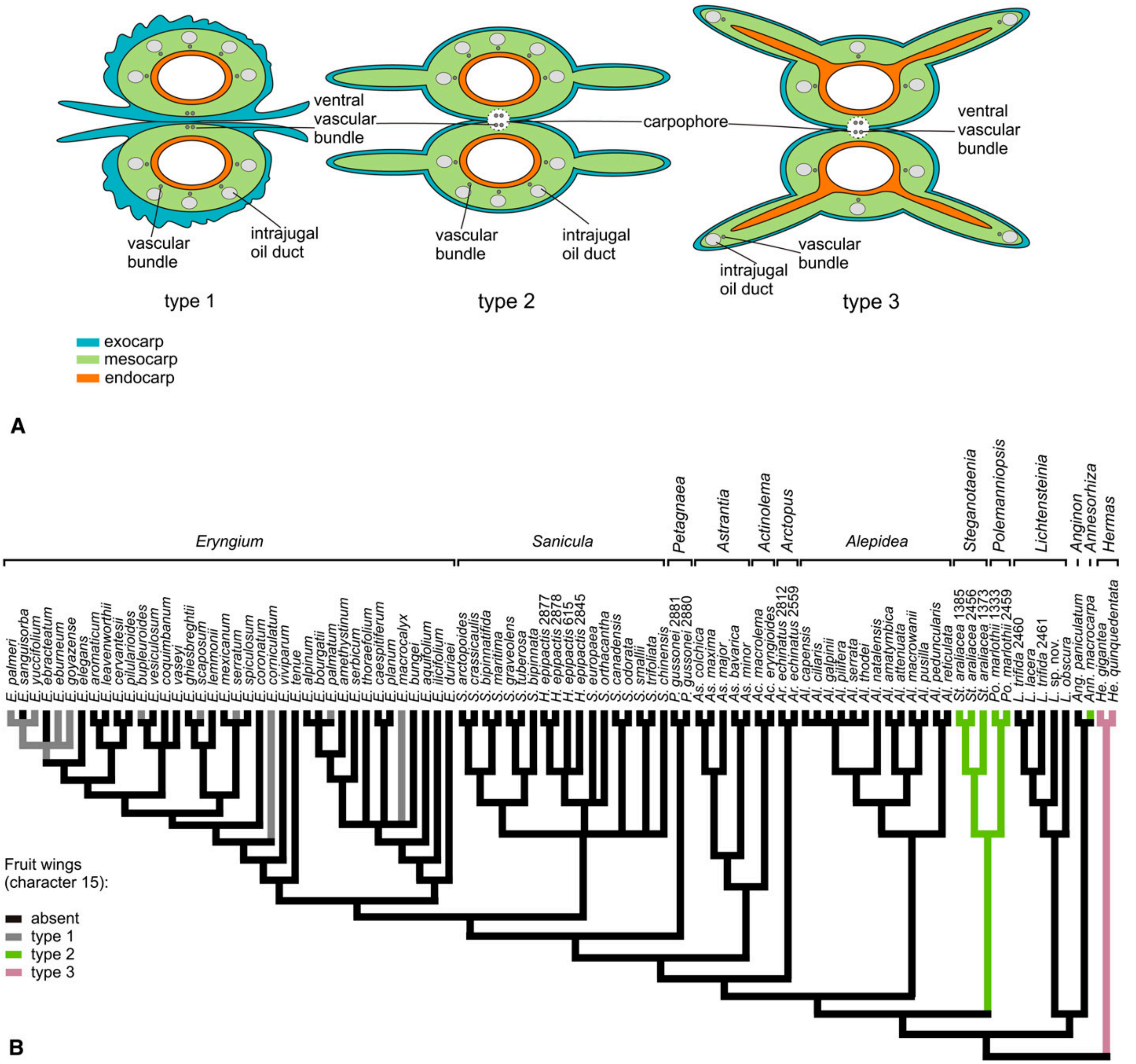

Fig. 7. Evolution of fruit wing type in Apiaceae. (A) Schematic representations of transverse sections of fruits showing wing development of types 1, 2, and 3 (as explained in Appendix 1 and discussed in the text). (B) Evolution of fruit wing type (character 15) when optimized over all 20000 minimal length trees derived from MP analysis of 94 cpDNA *trnQ-trnK* sequences of subfamily Saniculoideae and outgroups. This character is reconstructed as having 12 steps within Saniculoideae and outgroups.

"condensed" or "contracted" inflorescences because of the absence of long pedicellate fructiferous flowers (character 10). The umbels of members of subfamily Apioideae have long pedicellate fructiferous and male flowers, while those of Saniculeae have only long pedicellate male flowers, if they are present. When the fruits mature, the male flowers often fall off enhancing the contracted appearance of the inflorescence. Members of tribe Steganotaenieae have pedicellate flowers, like those of the apioid umbellifers and *Hermas*. Our results indicate that the absence (or shortening) of pedicels of fructiferous flowers is a synapomorphy of tribe Saniculeae, but the character reverts in the ancestor of *Astrantia* to yield pedicellate, fructiferous flowers.

Another characteristic feature of saniculoids is the presence of showy involucral bracts (character 7), and the data indicate that this feature is a synapomorphy of tribe Saniculeae. The character is of value to support the monophyly of tribe Saniculeae; however, there are several reversals in *Eryngium*, *Sanicula,* and *Petagnaea*. The presence of a showy involucre coincides with the congestion of fructiferous flowers and a shift from

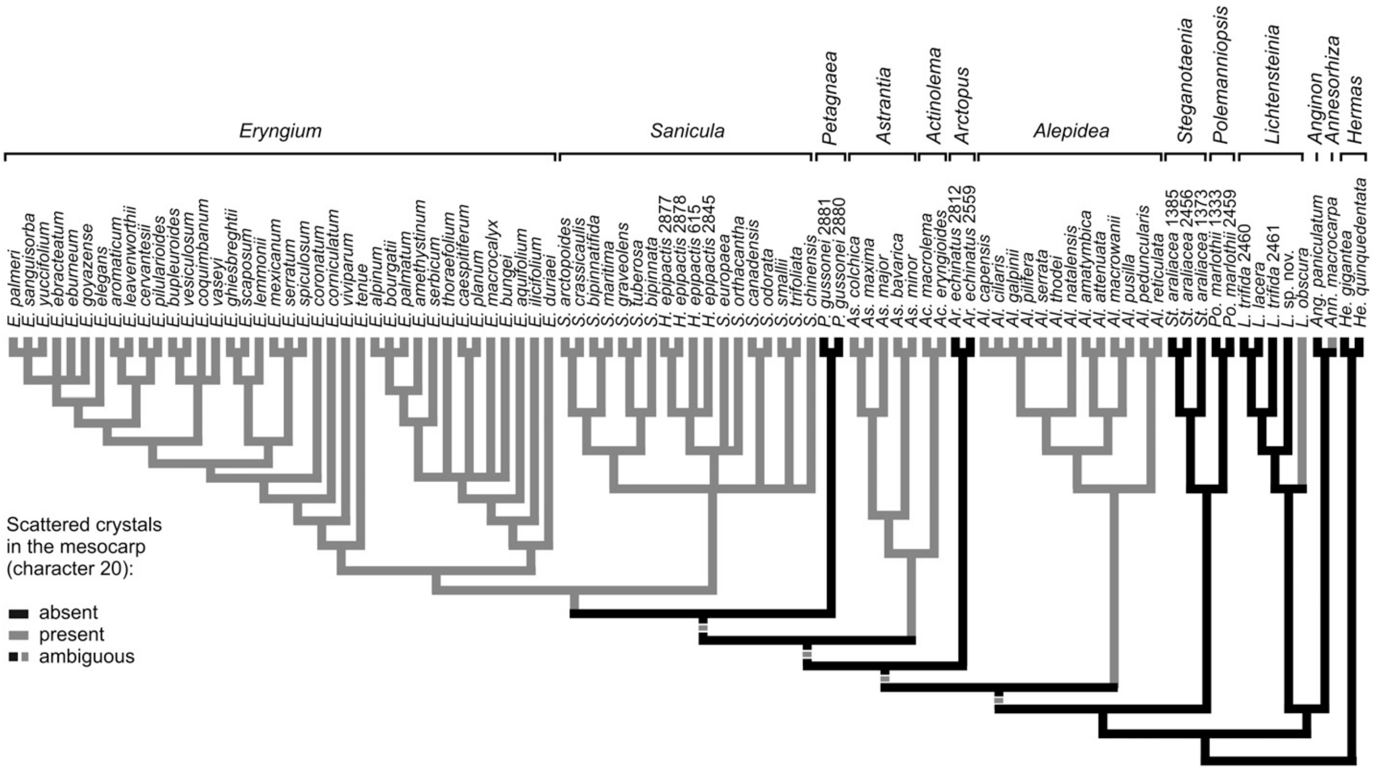

Fig. 8. Evolution of scattered crystals in the mesocarp (character 20) when optimized over all 20 000 minimal length trees derived from MP analysis of 94 cpDNA *trnQ-trnK* sequences of subfamily Saniculoideae and outgroups. This character is reconstructed as having five steps within Saniculoideae and outgroups. Scattered crystals in the mesocarp are ambiguously reconstructed in the ancestor of tribe Saniculeae and those of the next three splits.

compound to simple umbels in the same ancestor, resulting in a radical change of inflorescence structure that gave rise to a pseudanthium.

Floral bracts, one per flower (character 8)—The presence of a single floral bract per flower is characteristic of *Eryngium*, and this feature constitutes a nonhomoplastic synapomorphy for the genus. The character is derived from simple umbels in which floral bracts are absent. This derivation has been difficult to interpret based on classical methods of comparative morphology. Froebe (1964), however, proposed a highly speculative hypothesis for the capitules of *Eryngium*: each flower represents a one-flowered reduced umbellule, so the floral bracts in *Eryngium* are equivalent (homologous) to the involucral bracts of other Saniculeae.

Sexual system (character 9)—Hermaphrodism occurs independently in *Eryngium* and *Alepidea* (Fig. 6). In spite of the apparent similar inflorescences of *Alepidea* and *Eryngium* (both are capitules with hermaphrodite flowers), the capitules differ in the shape of the receptacle (discoid in the former, convex to cylindrical in the latter) and the presence of a single bract per flower (present in *Eryngium*, absent in *Alepidea*). These differences may indicate that the two capitule types are not homologous structures. In Apiaceae, hermaphrodism and andromonoecy are the most common sexual systems (Bell, 1971), whereas dioecy and gynodioecy are less frequent (Webb, 1979). In Saniculoideae, only gynodioecy is absent. Our results indicate that andromonoecy is plesiomorphic in Saniculoideae and that both hermaphrodism and dioecy are derived from andromonoecious ancestors. Dioecy is characteristic of all three species of *Arctopus* (Wolff, 1913) and thus constitutes a synapomorphy for the genus. The evolution of dioecy has generated considerable debate, with its origin mainly explained in terms of the following driving forces: inbreeding avoidance, sexual specialization (i.e., maximizing the production and dissemination of pollen in male individuals and fruits in female individuals), or some combination of both (Freeman et al., 1997; Pannel and Verdú, 2006). In *Arctopus*, dioecy is coupled with changes in morphology of male and female inflorescences (the former having long-petiolated compound umbels with numerous flowers, the latter having sessile umbels surrounded by connate bracts with spines that results in a dispersal unit). Whether such a specialization was a driving force in the evolution of dioecy or a specialization once the state of dioecy was achieved needs further study.

Fruit morphology and anatomy—Number of fertile locules (character 12)—The presence of one fertile locule per ovary in *Lagoecia*, *Arctopus*, and *Petagnaea* was used as a diagnostic character to define Saniculoideae tribe Lagoecieae (Drude, 1898). However, the tribe was considered artificial by many (Koso-Poljansky, 1916; Cerceau-Larrival, 1962; Tseng, 1967; Guyot, 1971; Magin, 1980), and based on molecular phylogenetic studies (e.g., Downie et al., 2000c), *Lagoecia* was transferred to tribe Pyramidoptereae of subfamily Apioideae. Fruits with only one fertile locule per ovary also occur independently in *Arctopus* and *Petagnaea*, corroborating early studies suggesting that tribal designation based on this character is not desirable. This character is an autapomorphy for the monotypic genus *Petagnaea* and a synapomorphy for the three species of *Arctopus*. It is not a reliable character to support suprageneric relationships within Saniculoideae.

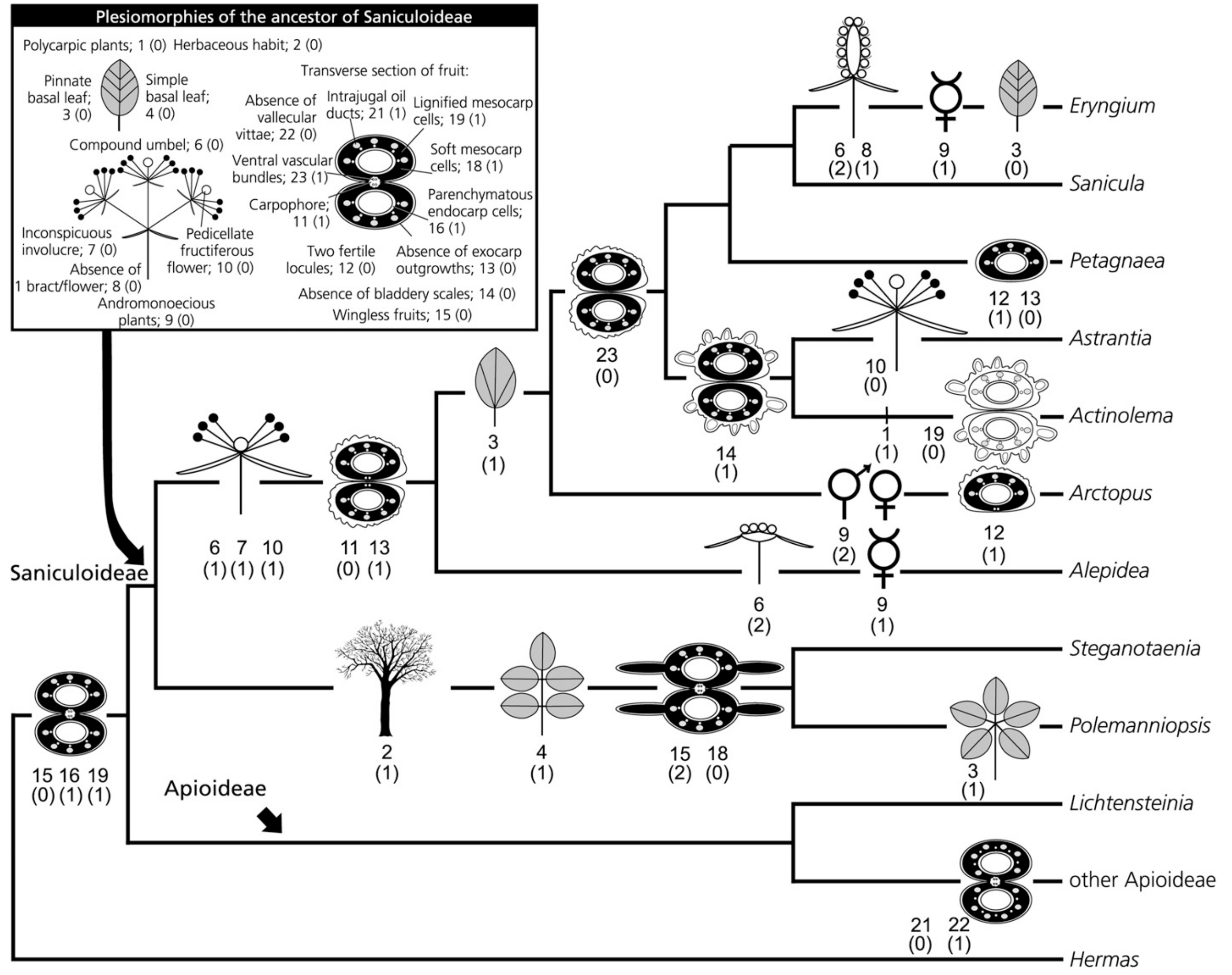

Fig. 9. Examined synapomorphic characters common to all 20 000 minimal length trees derived from MP analysis of 94 cpDNA *trnQ-trnK* sequences of subfamily Saniculoideae and outgroups mapped onto a simplified tree inferred from a strict consensus of these 20 000 trees. Bristly or spiny leaf margins (character 5), lignified parenchymatous cells in the endocarp (character 17), and crystals scattered in the mesocarp (character 20) are not shown because their pattern of evolution is ambiguously reconstructed. Numbers correspond to those characters listed and described in Appendix 1, with states in parentheses. Plesiomorphies of the ancestor of Saniculoideae are provided in the box.

Exocarp covered with scales, bristles, or prickles (character 13) and bladdery fruit scales (character 14)—The presence of scales, bristles, or prickles (character 13) was traditionally used as a diagnostic character of subfamily Saniculoideae. Our results corroborate the value of this character in supporting the monophyly of tribe Saniculeae (Saniculoideae sensu Drude) because it is reconstructed as a synapomorphy for the tribe. Exocarp outgrowths are often interpreted as adaptations that may favor long-distance dispersal by epizoochory, wind, or water (Ridley, 1930; Jury, 1986; Vargas et al., 1999; Calviño et al., in press). It is noteworthy that the occurrence of exocarp outgrowths in the ancestor of Saniculeae coincides with the first dispersal event of subfamily Saniculoideae out of Africa. The character is lost in *Petagnaea* and in a few species of *Sanicula* and *Eryngium* not sampled herein that have naked fruits. Bladdery fruit scales (character 14) develop at the main ribs in *Astrantia* and *Actinolema*. The character was used by Wolff (1913) to separate these two genera from the other members of the tribe Saniculeae. *Actinolema* and *Astrantia* comprise a monophyletic sister group in the molecular-derived phylogenies, and the presence of bladdery vesicles is a synapomorphy for this clade.

Fruit wings (character 15)—Fruit wings in Apiaceae develop in three basic ways: a flattening (and sometimes connation) of lateral scales, with the wing formed by one or a few layers of the exocarp (Fig. 7A, type 1); an expansion of the mesocarp over the vascular bundles, with the wing including the exocarp and mesocarp but not the endocarp and a vascular bundle positioned at the base of each wing in a transverse section of the fruit (Fig. 7A, type 2); and a folding of the carpel (commonly at the lateral ribs), with the wing formed by the exocarp, mesocarp, and endocarp, and the vascular bundle with its associated intrajugal oil

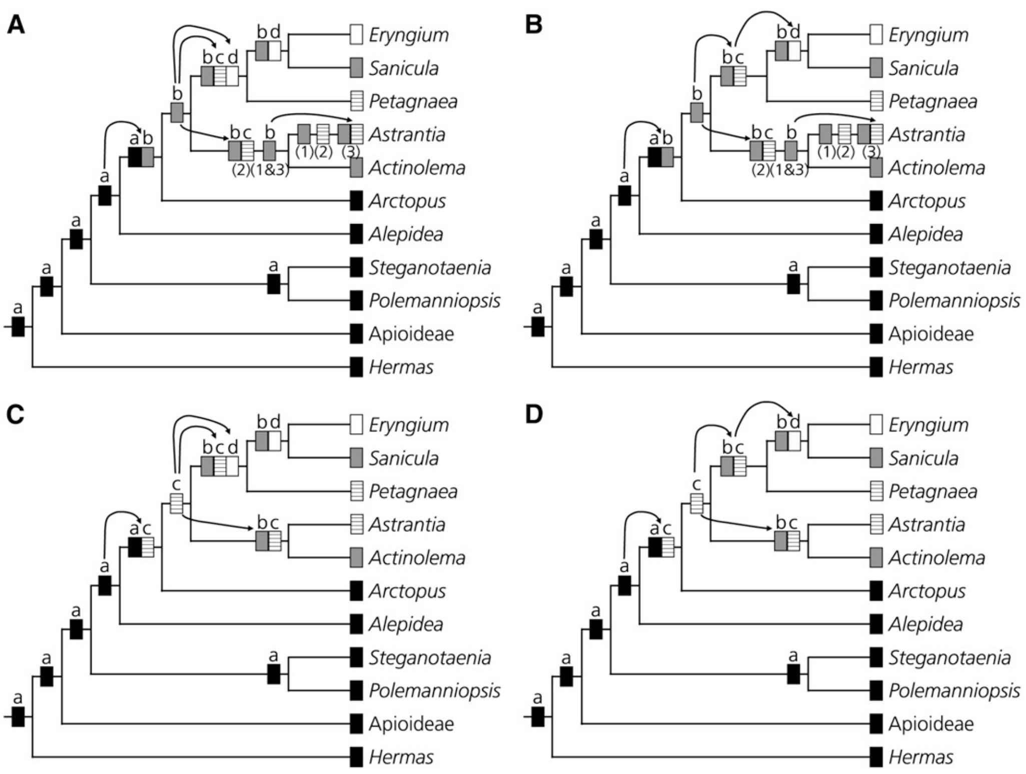

Fig. 10. Optimal reconstructions of the ancestral distributions of Saniculoideae using dispersal–vicariance analysis. (A, B) Alternative biogeographic scenarios inferred when assuming that the ancestor of *Astrantia* was distributed in Asia, in Europe, or in both places. (C, D) Alternative biogeographic scenarios inferred when assuming a European origin of *Astrantia*. The historical biogeography of Saniculoideae was analyzed in terms of four main areas: southern Africa ("a" and solid squares); Asia ("b" and gray squares); Europe ("c" and striped squares); and western Mediterranean ("d" and open squares). Arrows represent dispersal events. At each node, the optimal distribution prior to vicariance is given. Alternative distributions of the ancestor of *Actinolema* plus *Astrantia* are inferred when an (1) Asian, (2) European, or (3) Eurasian origin of *Astrantia* is assumed.

duct positioned at the tip of each wing in a transverse section of the fruit (Fig. 7A, type 3). Wings of type 1 occur in *Eryngium*; those of type 2 are present in *Steganotaenia*, *Polemanniopsis*, some species of *Annesorhiza*, and most apioid umbellifers (see Tseng, 1967); and wings of type 3 are common in the winged-fruited species of Azorelloideae and *Hermas*. Optimization of this character onto the molecular-derived phylogenies reveals that in all cases wings of each type are derived from wingless ancestors and never as a transformation from one type to another (Fig. 7B). This hypothesis corroborates a previous study that considered the anatomical differences observed among the three types of wings as indicative of their independent origins (Tseng, 1967). Therefore, in future studies, these three types of wings can be analyzed as independent characters. In Saniculoideae, wing type is of limited use to delimit monophyletic groups. Excluding wing type 3 because it is only present in the outgroup *Hermas*, wings of type 1 appear independently at least seven times within *Eryngium*, and those of type 2 occur in the ancestors of tribe Steganotaenieae and *Annesorhiza macrocarpa* Eckl. & Zeyh. It is easy to picture the evolution of wing formation as a dispersal mechanism in many independent lineages derived from less specialized types (Tseng, 1967; Theobald, 1971), and previous studies that have analyzed this character (Plunkett et al., 1996; Katz-Downie et al., 1999; Downie et al., 2000c; Spalik et al., 2001) support this idea.

Endocarp: type of cells (character 16) and the presence of lignified parenchymatous cells (character 17)—Lignification of the endocarp was a feature used to distinguish among the three subfamilies of Apiaceae, as traditionally defined (Drude, 1898; Wolff, 1913). Members of subfamily Azorelloideae (Hydrocotyloideae sensu Drude, in part) and the genera *Hermas* and *Klotzschia* have endocarps composed of several layers of fiber-like sclereids (character 16). These fiber-like sclereids are absent in subfamilies Apioideae and Saniculoideae, where the endocarp cells are parenchymatous. Woody endocarps, however, indeed occur in Apioideae and Saniculoideae, but they are the result of a lignification of these parenchymatous cells (character 17). Optimization of the character endocarp cell type (character 16) onto the molecular-derived phylogenies shows that the absence of fiber-like sclereids in the endocarp is a synapomorphy for Apioideae plus Saniculoideae. The shift from fiber-like sclereids to parenchymatous cells in the endocarp supports the sister-group relationship of these subfamilies; the presence of fiber-like sclereids is plesiomorphic in *Hermas*. In *Arctopus, Steganotaenia*, and *Polemanniopsis*, a lignification of the endocarp parenchymatous cells occurs (character 17). Reconstructing the pattern of evolution of this character could not be assessed because it is variable within the outgroup apioid genera. Lignified cells are absent in *Lichtensteinia obscura* (Spreng.) Koso-Pol., but present in *L. lacera* Cham. & Schltdl.; the same situation occurs in *Annesorhiza*. Additional fruit anatomical studies for all species of *Lichtensteinia* and of the *Annesorhiza* clade are required to ascertain the phylogenetic distribution of this character.

Mesocarp: soft parenchymatous cells (character 18) and lignified parenchymatous cells (character 19)—In Saniculoideae, endocarp cells are lignified in several genera (*Arctopus*, *Steganotaenia*, and *Polemanniopsis*; character 17), and mesocarp cells are lignified (character 19) in all genera, save *Actinolema*. Mesocarp cells are also lignified in the apioid outgroups; they are not lignified, however, in *Hermas* or members of Azorelloideae. Therefore, the presence of lignified mesocarp cells constitutes another synapomorphy for the ancestor of Apioideae plus Saniculoideae. The sister-group relationship of Apioideae and Saniculoideae is supported by two synapomorphic morphological characters thus far: the absence of fiber-like sclereids in the endocarp and the presence of lignified parenchymatous cells in the mesocarp. Apparently, the loss of fiber-like sclereids in the endocarp was coupled with mesocarp lignification. Not only did the relative position of woodiness in the fruit change, but also the type of cell that confers protection to the seed. In *Steganotaenia* and *Polemanniopsis*, the mesocarp is formed by lignified parenchymatous cells only, while in the other taxa lignified cells co-occur with soft parenchymatous cells (character 18). Liu (2004) reported that the lignified mesocarp is a synapomorphy for *Steganotaenia* plus *Polemanniopsis*; however, it is more appropriate to say that the lack of soft parenchymatous cells is synapomorphic for the group.

Crystals scattered in the mesocarp (character 20)—Drude's (1898) division of the family into subfamilies Hydrocotyloideae, Saniculoideae, and Apioideae was influenced by the work of Rompel (1895) based on the distribution of calcium oxalate crystals in the pericarp (Constance, 1971). These crystals vary in form and position. In Hydrocotyloideae, they are rhomboidal, whereas in Saniculeae and Apioideae they are druses. Druses are compound crystals formed by many small radially arranged crystals (Tseng, 1967). In most hydrocotyloids, the innermost cells of the mesocarp bear crystals, thus producing a crystalliferous layer surrounding the endocarp. In Saniculeae, these crystals are abundant and scattered throughout the outer mesocarp cells and at the commissure, whereas in most Apioideae, the crystals are distributed at the commissure and around the carpophore. Several basal African apioids (*Annesorhiza*, *Heteromorpha*, and some species of *Lichtensteinia*), however, have crystals scattered in the mesocarp like those of Saniculeae. Rompel (1895) included these genera in his "Sanicula-Typus" and Liu et al. (2003) suggested that *Lichtensteinia* be included within Saniculoideae based on this character (as well as on the shared presence of intrajugal oil ducts, discussed later). Liu et al. (2006) considered the presence of druse crystals in the mesocarp a synapomorphy of Apioideae plus Saniculoideae. Optimization of the character scattered crystals in the mesocarp (character 20) indicates that the presence of mesocarp druse crystals occurs independently in members of Apioideae and Saniculeae (Fig. 8). The ancestor of Apioideae plus Saniculoideae had no crystals in the mesocarp. We consider that the presence of crystals in the mesocarp is not useful to delimit monophyletic groups, given that it is not possible to reconstruct its pattern of evolution unequivocally. In our study, the ancestor of Apioideae does not have crystals scattered in the mesocarp, but this reconstruction may be an artifact of the species sampled for Apioideae or a result of missing data for three accessions of *Lichtensteinia* (Appendix 2). Nevertheless, even if the ancestor of Apioideae had crystals dispersed in the mesocarp, the pattern of evolution of the character would still be ambiguously reconstructed because *Steganotaenia* and *Polemanniopsis* do not have crystals in the mesocarp (Liu et al., 2003; Liu, 2004). Moreover, even if *Steganotaenia* and *Polemanniopsis* did have crystals dispersed in their mesocarps, as implied by Liu et al. (2006), the character is still ambiguously reconstructed in the ancestor of Apioideae plus Saniculoideae. Therefore, the presence of crystals in the mesocarp is either a synapomorphy or a plesiomorphy for Saniculoideae.

Carpophore (character 11) and ventral bundles (character 23)—The carpophore is a specialized structure to which the two mericarps are attached when the fruit splits at maturity. It is formed by the ventral vascular bundles of each mericarp and adjacent tissue in the central part of the fruit, and its function is related to dehiscence of the schizocarp and dissemination. Optimization of this trait (character 11) shows that the presence of a carpophore is plesiomorphic in Saniculoideae and that the structure is lost in the ancestor of tribe Saniculeae. The lack of a carpophore would make the separation of the two mericarps difficult. Tseng (1967), however, has reported that in the absence of a carpophore, as in *Sanicula* and *Eryngium,* the presence of crystals dispersed in the commissure would serve the role of separating the mericarps.

The presence of ventral vascular bundles in the fruits (character 23) does not necessarily imply the presence of a carpophore. Within tribe Saniculeae, carpophores are absent. and while *Alepidea* and *Arctopus* have ventral bundles in their fruits, this trait is not present in *Actinolema*, *Astrantia*, *Petagnaea*, *Sanicula*, or *Eryngium*. The pattern of distribution of ventral vascular bundles is important given that their absence supports the monophyly of *Actinolema* to *Eryngium*. In Saniculoideae, the carpophore was lost first and later, the vascular bundles associated with it. Therefore, within Saniculeae, the vascular bundles can be considered relictual structures of a carpophore once present in previous common ancestors.

Intrajugal oil ducts and vallecular vittae (characters 21–22)—Intrajugal oil ducts and vallecular vittae have been important characters traditionally for defining the three subfamilies of Apiaceae (Drude, 1898). Recently, these characters have been emphasized as useful for resolving phylogenetic relationships (Liu et al., 2003, 2006). However, interpretations about their evolution have been misleading (Calviño et al., 2006). Intrajugal oil ducts is a plesiomorphic character retained in all members of Saniculoideae and the apioid genus *Lichtensteinia*; therefore, the absence of intrajugal oil ducts is synapomorphic for all Apioideae except *Lichtensteinia*. Another synapomorphy for this same group is the presence of vallecular vittae. Among the taxa investigated, these vittae are present only in the apioid genera *Anginon* and *Annesorhiza,* but not *Lichtensteinia*. We hypothesize that the fruits of the ancestor of all apioids, except *Lichtensteinia,* had either a modification in the position of the secretory ducts or the replacement of one type of duct with a different type. No anatomical or developmental studies show the origin of these ducts, but the presence of both types in some apioids favors the second hypothesis. In Apioideae, the loss (or reduction) of intrajugal oil ducts was apparently coupled with the development of vallecular vittae.

Synapomorphic morphological characters in subfamily Saniculoideae—The examined morphological characters supporting the monophyly of the groups inferred by phylogenetic analyses of molecular data are summarized in Fig. 9. Characters of the three classes examined (i.e., life history and vegetative morphology, inflorescence morphology and architecture, and fruit morphology and anatomy) support infrasubfamilial relationships, so the integrative use of all three classes is of value to define groups. Tribe Saniculeae is supported by five characters traditionally used to diagnose subfamily Saniculoideae: simple umbels (6: 1; character: state, respectively), showy involucre (7: 1), sessile (or subsessile) fructiferous flowers (10: 1), absence of a carpophore (11: 0), and fruits with exocarp outgrowths (13: 1). Other characters previously thought to be synapomorphic for this group, such as the presence of bristly or spiny leaf margins (5: 1), the presence of crystals scattered in the mesocarp (20: 1), the presence of intrajugal oil ducts (21: 1), and the absence of vallecular vittae (22: 0) are plesiomorphic or ambiguously reconstructed. The simple umbel of Saniculeae is derived from a compound umbel and the latter is not a synapomorphy of subfamily Apioideae but a plesiomorphy. Tribe Steganotaenieae is supported by four morphological characters: woody habit (2: 1), compound leaves (4: 1), fruit wings of type 2 (15: 2), and absence of soft mesocarp cells (18: 0). The shared presence of enormous cavities in the fruit wings of *Steganotaenia* and *Polemanniopsis*, as reported by Liu et al. (2003), is another synapomorphy for the tribe (but was not examined in our study). Contrary to previous assumptions of character-state polarity, woodiness is not plesiomorphic in Saniculoideae. The woody habit of Steganotaenieae has evolved from herbaceous ancestors (woodiness has also evolved convergently in the species of *Eryngium* from the Juan Fernandez Islands). On the contrary, the presence of lignified cells in the fruit mesocarp (19: 1) is not a synapomorphy of Steganotaenieae but a plesiomorphy. The capitules (6: 2) and pinnate leaves (3: 0) of *Eryngium* and *Alepidea* are not homologous structures as once thought; these characters, together with hermaphrodism (9: 1), evolved independently in both genera.

Most infrasubfamilial relationships inferred by molecular data find support from one to five morphological synapomorphies, yet no single morphological character state examined supports the monophyly of subfamilies Saniculoideae or Apioideae or of the clade comprising *Eryngium*, *Sanicula*, and *Petagnaea*, or the sister-group relationship between *Eryngium* and *Sanicula*. It is interesting to note that some of these clades include relationships that have been hypothesized only on the basis of molecular data (e.g., tribe Steganotaenieae as part of Saniculoideae, and *Petagnaea* as part of Saniculeae). The reconstructions of ancestral character states from subfamilies Apioideae and Saniculoideae require information from southern African umbellifers, and until recently, their importance in the early evolution of the family was not realized. The paucity of comparative morphological studies of these plants, especially when coupled with present-day hypotheses of relationships, may explain why there are so few or no obvious morphological synapomorphies for these newly identified lineages. This lack of morphological support for newly recognized clades is in contrast to, for example, the abundance of morphological synapomorphies inferred for tribe Saniculeae (subfamily Saniculoideae sensu Drude), which has been long recognized as a natural group. However, it is probably unrealistic to assume that morphological synapomorphies can be found for all clades supported by molecular data. The lineages leading to tribes Steganotaenieae and Saniculeae either have evolved independently for a long time or have accumulated many independent morphological changes, thus masking any shared morphological feature that was once present in their common ancestor. Synapomorphies of the latter, however, persist at the molecular level. This hypothesis is supported by the relatively long branches leading to both tribes relative to the branch leading to the ancestor of Saniculoideae (Fig. 6 in Calviño and Downie, 2007). In this study, we did not carry out an exhaustive search of morphological characters that might be synapomorphies within Saniculoideae. Instead, we wanted to better understand the patterns of evolution of those characters traditionally considered important in the classification of the subfamily. Further comparative studies are underway to determine if morphological synapomorphies can indeed be identified for these morphologically unsupported lineages.

Southern African origin of Saniculoideae—No biogeographic hypothesis has been explicitly proposed for subfamily Saniculoideae as a whole. However, because Asia was hypothesized as the center of origin for several genera of Saniculoideae (Wolff, 1913; Turmel, 1950; Shan and Constance, 1951; Ferrarini, 1967; Wörz, 1999a), an Asian origin for the subfamily can be implicitly assumed. In this study, however, all biogeographic reconstructions support a southern African origin of subfamily Saniculoideae and of its two tribes, Steganotaenieae and Saniculeae. Whether tribe Saniculeae subsequently migrated northward into Europe or Asia depends on the ancestral distribution of the genus *Astrantia*. An Asian origin of *Astrantia* (thus, resulting in a migration of Saniculeae into Asia first) is the most likely hypothesis based on morphological and chorological studies of the genus (Ferrarini, 1967, 1987; Wörz, 1999a). However, a European or a widespread Eurasian origin of *Astrantia* is also supported by a dispersal–vicariance analysis of the species sampled herein. While the migration route of tribe Saniculeae cannot be determined unequivocally based on dispersal–vicariance analyses, four alternative scenarios are hypothesized (Fig. 10) that may serve as starting points for further biogeographic studies.

Once more, southern Africa has been implicated as very important in the early evolutionary history of Apiaceae. We have previously inferred that this region was the origin of subfamily Apioideae and of its earliest branching lineages (Calviño et al., 2006). The same pattern is now postulated for subfamily Saniculoideae and its two tribes, suggesting that the ancestor of the two largest (and primarily Eurasian) subfamilies of Apiaceae may have also evolved in southern Africa.

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Appendix 1. Morphological characters and states examined in this study arranged by class, with explanatory comments. The numbers of each character and its character states correspond to those presented in Appendix 2.

Life history and vegetative morphology

1. Reproductive strategy: 0, polycarpic; 1, monocarpic.

In subfamily Saniculoideae, monocarpic species include annuals (*Actinolema* and a few species of *Eryngium*) and biennials (*Sanicula*). Polycarpic species in this subfamily usually have rootstocks.

2. Habit: 0, herbaceous; 1, woody.

Small trees or shrubs with lignified stalks have been coded as having a woody habit.

3. Palmate leaves: 0, absent; 1, present.

Basal leaves were considered palmate when the primary veins or the leaflets diverge from a single point. This character was coded as absent for pinnate- or parallel-veined leaves (the last occurring within *Eryngium*), irrespective of the degree of dissection of the margin.

4. Leaf complexity: 0, simple; 1, compound.

Leaves were coded as simple irrespective of the degree of dissection of the margin. Thus, the simple state includes entire, pinnatipartite/palmatipartite, and pinnatisect/palmatisect leaf margins. Leaves were coded as compound when they were composed of multiple blade units (leaflets), each attached to the rachis by a petiolule.

5. Bristly or spiny leaf margins: 0, absent; 1, present.

This character was coded as present when a spine or bristle projected beyond the margin of the blade. This projection may or may not be associated with a tooth, the latter occurring in some species of *Eryngium*.

Inflorescence morphology and architecture

6. Flowering unit: 0, compound umbel; 1, simple umbel; 2, capitule.

A flowering unit is the minimum possible expression of flowering arrangement in a given species (Sell, 1976). See Rua (1999) for examples and further explanation.

7. Length of involucre in relation to the basic inflorescence: 0, shorter; 1, longer.

In many members of Saniculoideae, the involucral bracts forming the involucre are showy, i.e., they are longer than the umbel or capitule. In other members, as in *Petagnaea*, the involucral bracts are not very developed.

8. Floral bracts, one per flower: 0, absent; 1, present.

The bracts of most saniculoids are restricted to the involucre and the number of involucral bracts is lower than the number of flowers in the basic inflorescence. There is no correspondence between the numbers of bracts and flowers, except in *Eryngium*, where each bract (even involucral bracts) subtends a single flower.

9. Sexual system: 0, andromonoecious; 1, hermaphrodite; 2, dioecious.

Andromonoecious refers to an individual plant that has both hermaphrodite and male flowers. Hermaphrodite refers to a plant that has only monoclinous flowers, and dioecious refers to a plant having only male or female flowers.

10. Pedicel of fructiferous flowers: 0, present; 1, absent.

While male flowers are always pedicellate in umbellifers, fructiferous flowers are pedicellate in most apioids, whereas they are sessile or sub-sessile in most saniculoids. The last condition was coded as absent.

Fruit morphology and anatomy

11. Carpophore: 0, absent; 1, present.

A carpophore is a specialized structure to which the mericarps are attached when the fruit splits at maturity. Carpophores can be entire (*Hermas*, *Huanaca*, *Mulinum*) or bifid (*Steganotaenia*, *Polemanniopsis*, and many apioids). A carpophore was coded as present whether it was entire or bifid.

12. Number of fertile locules per ovary: 0, two; 1, one.

The fruits of umbellifers are schizocarps that comprise two one-seeded mericarps. In most genera, both locules develop at maturity, but in a few genera (*Lagoecia*, *Arctopus*, *Petagnaea*), only one fertile locule develops per ovary.

13. Exocarp covered with scales, bristles, or prickles: 0, absent; 1, present.

This character refers to the outgrowths formed by one or a few layers of the exocarp.

14. Bladdery (inflated) fruit scales: 0, absent; 1, present.

These inflated fruit scales are hollow.

15. Fruit wings: 0, absent; 1, type 1; 2, type 2; 3, type 3.

Three types of fruit wing development are described for Apiaceae (and are illustrated in Fig. 7A): type 1, wing formed by one or a few layers of the exocarp; type 2, wing formed by the exocarp and mesocarp layers, and in a transverse section of the fruit, a vascular bundle is positioned at the base of each wing; and type 3, wing formed by exocarp, mesocarp, and endocarp layers, with a vascular bundle and its associated intrajugal oil duct positioned at the tip of each wing, as seen in transverse section.

16. Type of endocarp cells: 0, fiber-like sclereids; 1, parenchymatous.

Most members of Azorelloideae and *Hermas* have endocarps formed by fiber-like sclereids, while saniculoids and apioids have parenchymatous cells in the endocarp. These parenchymatous cells may have secondary lignified walls. Endocarp cells were coded as parenchymatous irrespective of the presence of lignified walls.

17. Lignified parenchymatous cells in the endocarp: 0, absent; 1, present.

In apioids and saniculoids, the endocarp is formed by parenchymatous cells. In some cases (*Eryngium, Sanicula, Alepidea, Annesorhiza macrocarpa*), these parenchymatous cells have nonlignified secondary cell walls (soft cells), and in other cases, a lignification of the parenchymatous cells is observed (*Polemanniopsis*, *Steganotaenia*, *Arctopus*, *Lichtensteinia*, *Annesorhiza latifolia*).

18. Soft parenchymatous cells in the mesocarp: 0, absent; 1, present.

Soft (nonlignified) parenchymatous cells are present in the mesocarps of the hydrocotyloid lineages and all umbellifers sampled herein, except for *Polemanniopsis* and *Steganotaenia* that have lignified cells only. Soft parenchymatous cells were scored as present irrespective of lignified cells in the mesocarp.

19. Lignified parenchymatous cells in the mesocarp: 0, absent; 1, present.

The mesocarp of most apioids and saniculoids is composed of both lignified and soft parenchymatous cells. *Astrantia*, *Hermas*, and most members of Azorelloideae however, lack lignified cells in the mesocarp. Lignified parenchymatous cells in the mesocarp were scored as present irrespective of soft cells in the mesocarp.

20. Crystals scattered in the mesocarp: 0, absent; 1, present.

Calcium oxalate crystals in umbellifers differ in form and position. The presence of druse crystals dispersed in the mesocarp is typical of many saniculoids but also occurs in *Heteromorpha* and other basal apioids. In *Steganotaenia* and *Polemanniopsis*, crystals dispersed in the mesocarp are absent according to Liu et al. (2003) and Liu (2004). However, in a recent study, Liu et al. (2006) report the opposite for these genera. We scored these taxa as in these first publications, but the alternative is also discussed in the text.

21. Intrajugal oil ducts: 0, absent; 1, present.

Intrajugal oil ducts (also called intrajugal vittae, rib oil ducts, or companion canals) are secretory canals on the dorsal side of each vascular bundle under the ribs (Tseng, 1967). Intrajugal oil ducts are present in the hydrocotyloid lineages, Saniculoideae, and *Lichtensteinia*. In some higher apioids, such as *Echinophora*, *Aciphylla*, *Anisotome*, *Scandia*, *Gingidia*, and *Lignocarpa*, intrajugal oil ducts have also been reported (Liu, 2004); however, in these cases, secretory ducts are on the ventral side of each vascular bundle (or on both the dorsal and ventral sides) but never on the dorsal side only.

22. Vallecular vittae: 0, absent; 1, present.

Vallecular vittae are secretory ducts in the intervals (furrows) between the ribs and are not associated with vascular bundles. These are typical of Apioideae, with the exception of *Lichtensteinia*.

23. Ventral bundles: 0, absent; 1, present.

Ventral vascular bundles face the commissure of the mericarp. These ventral bundles form part of the carpophore, if the latter exists.

APPENDIX 2. Data matrix for the 23 morphological characters and 94 accessions of Apiaceae included in this study. Character numbers refer to those presented in Appendix 1. Voucher information for each accession is presented in Calviño and Downie (2007) and Calviño et al. (in press). Missing data are indicated by a question mark (?), and inapplicable characters are scored with a dash (–).

	Character number																						
Accessions examined	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Actinolema eryngioides	1	0	1	0	1	1	1	0	0	1	0	0	1	1	0	1	0	1	0	1	1	0	0
Actinolema macrolema	1	0	1	0	1	1	1	0	0	1	0	0	1	1	0	1	0	1	0	1	1	0	0
Alepidea amatymbica	0	0	0	0	1	2	1	0	1	1	0	0	1	0	0	1	0	1	1	1	1	0	1
Alepidea attenuata	0	0	0	0	1	2	1	0	1	1	0	0	1	0	0	1	0	1	1	1	1	0	1
Alepidea capensis	0	0	0	0	1	2	1	0	1	1	0	0	1	0	0	1	0	1	1	1	1	0	1
Alepidea ciliaris	0	0	0	0	1	2	1	0	1	1	0	0	1	0	0	1	0	1	1	1	1	0	1
Alepidea galpinii	0	0	0	0	1	2	1	0	1	1	0	0	1	0	0	1	0	1	1	1	1	0	1
Alepidea macrowanii	0	0	0	0	1	2	1	0	1	1	0	0	1	0	0	1	0	1	1	1	1	0	1
Alepidea natalensis	0	0	0	0	1	2	1	0	1	1	0	0	1	0	0	1	0	1	1	1	1	0	1
Alepidea peduncularis	0	0	0	0	1	2	1	0	1	1	0	0	1	0	0	1	0	1	1	1	1	0	1
Alepidea pilifera	0	0	0	0	1	2	1	0	1	1	0	0	1	0	0	1	0	1	1	1	1	0	1
Alepidea pusilla	0	0	0	0	1	2	1	0	1	1	0	0	1	0	0	1	0	1	1	1	1	0	1
Alepidea reticulata	0	0	0	0	1	2	1	0	1	1	0	0	1	0	0	1	0	1	1	1	1	0	1
Alepidea serrata	0	0	0	0	1	2	1	0	1	1	0	0	1	0	0	1	0	1	1	1	1	0	1
Alepidea thodei	0	0	0	0	1	2	1	0	1	1	0	0	1	0	0	1	0	1	1	1	1	0	1

APPENDIX 2. Continued.

Accessions examined	Character number																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Anginon paniculatum	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	1	0	0	1	1
Annesorhiza macrocarpa	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	1	0	1	1	1	0	1	1
Arctopus echinatus 2559	0	0	1	0	1	1	1	0	2	1	0	1	1	0	0	1	1	1	1	0	1	0	1
Arctopus echinatus 2812	0	0	1	0	1	1	1	0	2	1	0	1	1	0	0	1	1	1	1	0	1	0	1
Astrantia bavarica	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	1	0	1	1	1	1	0	0
Astrantia colchica	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	1	0	1	1	1	1	0	0
Astrantia major	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	1	0	1	1	1	1	0	0
Astrantia maxima	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	1	0	1	1	1	1	0	0
Astrantia minor	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	1	0	1	1	1	1	0	0
Eryngium alpinum	0	0	1	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium amethystinum	0	0	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium aquifolium	0	0	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium aromaticum	0	0	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium bourgatii	0	0	1	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium bungei	0	0	1	0	1	2	1	1	1	1	0	0	1	0	?	1	0	1	1	1	1	0	0
Eryngium bupleuroides	0	1	0	0	1	2	1	1	1	1	0	0	1	0	1	1	0	1	1	1	1	0	0
Eryngium caespitiferum	0	0	?	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium cervantesii	0	0	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium coquimbanum	1	0	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium corniculatum	1	0	0	0	1	2	1	1	1	1	0	0	1	0	1	1	0	1	1	1	1	0	0
Eryngium coronatum	0	0	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium duriaei	0	0	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium ebracteatum	0	0	0	0	1	2	0	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium eburneum	0	0	0	0	1	2	0	1	1	1	0	0	1	0	1	1	0	1	1	1	1	0	0
Eryngium elegans	0	0	0	0	1	2	0	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium ghiesbreghtii	0	0	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium goyazense	0	0	0	0	1	2	0	1	1	1	0	0	1	0	1	1	0	1	1	1	1	0	0
Eryngium ilicifolium	1	0	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium leavenworthii	1	0	?	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium lemmonii	1	0	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium macrocalyx	0	0	0	0	1	2	1	1	1	1	0	0	1	0	1	1	0	1	1	1	1	0	0
Eryngium mexicanum	0	0	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium palmatum	0	0	1	0	1	2	1	1	1	1	0	0	1	0	1	1	0	1	1	1	1	0	0
Eryngium palmeri	0	0	0	0	1	2	1	1	1	1	0	0	1	0	1	1	0	1	1	1	1	0	0
Eryngium pilularioides	0	0	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium planum	0	0	1	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium sanguisorba	0	0	0	0	1	2	0	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium scaposum	0	0	0	0	1	2	1	1	1	1	0	0	1	0	1	1	0	1	1	1	1	0	0
Eryngium serbicum	0	0	1	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium serratum	0	0	0	0	1	2	1	1	1	1	0	0	1	0	1	1	0	1	1	1	1	0	0
Eryngium spiculosum	0	0	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium tenue	1	0	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium thoraefolium	0	0	1	0	1	2	1	1	1	1	0	0	1	0	?	1	0	1	1	1	1	0	0
Eryngium vaseyi	0	0	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium vesiculosum	0	0	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium viviparum	0	0	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Eryngium yuccifolium	0	0	0	0	1	2	1	1	1	1	0	0	1	0	1	1	0	1	1	1	1	0	0
Hermas gigantea	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0	–	1	0	0	1	0	1
Hermas quinquedentata	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0	–	1	0	0	1	0	1
Lichtensteinia lacera	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	1	0	1
Lichtensteinia obscura	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	1	0	1
Lichtensteinia sp. nov.	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	?	1	1	?	1	0	1
Lichtensteinia trifida 2460	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1	?	1	1	?	1	0	1
Lichtensteinia trifida 2461	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1	?	1	1	?	1	0	1
Petagnaea gussonei 2880	0	0	1	0	1	1	0	0	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0
Petagneae gussonei 2881	0	0	1	0	1	1	0	0	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0
Polemanniopsis marlothii 1333	0	1	1	1	1	0	0	0	0	0	1	0	0	0	2	1	1	0	1	0	1	0	1
Polemanniopsis marlothii 2459	0	1	1	1	1	0	0	0	0	0	1	0	0	0	2	1	1	0	1	0	1	0	1
Sanicula arctopoides	0	0	1	0	1	1	1	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Sanicula bipinnata	1	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Sanicula bipinnatifida	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Sanicula canadensis	0	0	1	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Sanicula chinensis	0	0	1	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Sanicula crassicaulis	0	0	1	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Sanicula epipactis 615	0	0	1	0	1	1	1	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Sanicula epipactis 2845	0	0	1	0	1	1	1	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Sanicula epipactis 2877	0	0	1	0	1	1	1	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Sanicula epipactis 2878	0	0	1	0	1	1	1	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0

APPENDIX 2. Continued.

	Character number																						
Accessions examined	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Sanicula europaea	0	0	1	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Sanicula graveolens	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Sanicula maritima	0	0	1	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Sanicula odorata	0	0	1	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Sanicula orthacantha	0	0	1	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Sanicula smalii	0	0	1	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Sanicula trifoliata	0	0	1	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Sanicula tuberosa	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0
Steganotaenia araliacea 1373	0	1	0	1	1	0	0	0	0	0	1	0	0	0	2	1	1	0	1	0	1	0	1
Steganotaenia araliacea 1385	0	1	0	1	1	0	0	0	0	0	1	0	0	0	2	1	1	0	1	0	1	0	1
Steganotaenia araliacea 2456	0	1	0	1	1	0	0	0	0	0	1	0	0	0	2	1	1	0	1	0	1	0	1