Evolutionary shifts in fruit dispersal syndromes in Apiaceae tribe Scandiceae

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Abstract

Apiaceae tribe Scandiceae includes species with diverse fruits that depending upon their morphology are dispersed by gravity, carried away by wind, or transported attached to animal fur or feathers. This diversity is particularly evident in Scandiceae subtribe Daucinae, a group encompassing species with wings or spines developing on fruit secondary ribs. In this paper, we explore fruit evolution in 86 representatives of Scandiceae and outgroups to assess adaptive shifts related to the evolutionary switch between anemochory and epizoochory and to identify possible dispersal syndromes, i.e., patterns of covariation of morphological and life-history traits that are associated with a particular vector. We also assess the phylogenetic signal in fruit traits. Principal component analysis of 16 quantitative fruit characters and of plant height did not clearly separate species having different dispersal strategies as estimated based on fruit appendages. Only presumed anemochory was weakly associated with plant height and the flattening of mericarps with their accompanying anatomical changes. We conclude that in Scandiceae, there are no distinct dispersal syndromes, but a continuum of fruit morphologies relying on different dispersal vectors. Phylogenetic mapping of ten discrete fruit characters on trees inferred by nrDNA ITS and cpDNA sequence data revealed that all are homoplastic and of limited use for the delimitation of genera. Spines evolved from wings developing on secondary ribs. We hypothesize that spines cannot form on primary ribs because these contain vascular bundles that may constrain such a transformation. We describe a new subtribe for *Artedia* and propose three new combinations in *Daucus*.

Keywords Apiaceae · Daucinae · Dispersal syndrome · Fruit morphology · Taxonomy · Torilidinae

Introduction

Plant dispersal syndromes describe patterns of covariation of morphological, anatomical and life-history traits that are associated with a particular vector of diaspore dispersal (e.g., wind, water, animals) and its mode (e.g., endozoochory vs. epizoochory). Such patterns may serve as simple phenotypic predictors of dispersal given that the correct set of phenotypic traits explaining a large fraction of variation in effective dispersal is identified and such syndromes are extrapolated to other systems and conditions. This, however, is problematic when patterns of covariation vary themselves continuously across environmental conditions (Ronce and Clobert 2012).

Adaptive shifts toward a particular dispersal vector can affect the entire fruit morphology and anatomy. For example, the selection for lighter diaspores may constrain not only seed size but also endosperm defense structures like a sclerified seed coat. If so, dispersal syndromes in fruit

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multidimensional morphospace are represented by separate clouds of species points. Alternatively, the adaptation to different vectors can affect only a limited number of traits, such as those immediately related to dispersal like fruit appendages (wings, hooks, etc.). If so, the dispersal mode is a poor predictor of fruit morphology and, consequently, its placement in the multidimensional morphospace. To test these hypotheses, we examine fruit evolution in the umbellifer tribe Scandiceae subtribe Daucinae and outgroups. This subtribe is particularly useful for such analyses because our previous study identified several evolutionary switches between anemochory and epizoochory in this group (Banasiak et al. 2016).

In Apiaceae, the fruits are dry schizocarps and the dispersal units are single-seeded mericarps. These diaspores are usually described based on their shape and appendages as anemochorous (dispersed by wind), epizoochorous (carried away on animal fur or feathers), and hydrochorous (floating on water). Fruits without any distinct adaptations to dispersal are regarded as barochorous (gravity dispersed) or autochorous (self-dispersing). Fleshy and thus endozoochorous fruits occur only in *Apiopetalum*, *Mackinalaya*, and *Azorella* sect. *Stilbocarpa* (Grushvitsky et al. 1969).

Anemochorous fruits involve a set of characters including dorsal or, rarely, lateral compression of the mericarps, with wing-like projections of various origins. These fruit types occur in at least 80 genera of umbellifers (Liu et al. 2006). Wind-dispersed fruits are particularly common in tribes Selineae including *Angelica*, *Peucedanum*, and *Lomatium* (Spalik et al. 2004), Scandiceae encompassing *Ferula* (Kurzyna-Młynik et al. 2008), *Thapsia* (Weitzel et al. 2014), and *Laserpitium* (Downie et al. 2010; Lee and Downie 1999), and Tordylieae comprising *Tordylium*, *Heracleum*, and the African ‘peucedanoid’ genera (Winter et al. 2008; Yu et al. 2011). The only study on wind dispersal in winged-fruited umbellifers concluded that its effectiveness as a mode of dispersal is quite low (Jongejans and Telenius 2001).

Adaptations to external animal dispersal (epizoochory) in Apiaceae have not been yet systematically reviewed. Bristles and hooks increase attachment and retention potential on animal fur (Römermann et al. 2005; Tackenberg et al. 2006) and promote gene flow among populations (Williams 1994; Williams and Guries 1994). Stiff bristles occur in several genera of Scandiceae subtribe Scandicinae (Spalik et al. 2001). In several species of *Oenanthe*, *Seseli*, *Magydaris*, and *Hohenackeria*, calyx teeth are extant in fruits and bristle-like (Arenas Posada and García Martín 1993). Spiny fruits developing from secondary ribs occur in former members of tribe Caucalideae; such a development was considered unique among umbellifers and therefore synapomorphic (Heywood 1982; Heywood and Dakshini 1971). However, the results of molecular analyses not only separated these spiny-fruited taxa into

two clades, namely Scandiceae subtribes Torilidinae and Daucinae (Lee and Downie 1999, 2000; Lee et al. 2001), but also demonstrated that Daucinae are closely related to winged-fruited species formerly placed in tribe Laserpitieae (Downie et al. 2000a). Maximum parsimony mapping of secondary ribs characters onto a molecular phylogenetic tree of Daucinae revealed 14 character state changes and at least seven switches between winged and spiny ribs suggesting considerable evolutionary lability of fruit dispersal syndromes in this clade of umbellifers (Banasiak et al. 2016).

When analyzing dispersal syndromes in Apiaceae, it is important to note that fruit appendages are not necessarily the best indicators of dispersal strategy, because fruit morphology and anatomy are also subject to selection pressures other than dispersal. For epizoochory, mericarp mass, width, and length are also important predictors of its attachment and retention potential on animal fur (Römermann et al. 2005; Tackenberg et al. 2006). Therefore, umbellifer fruits may represent a full spectrum of adaptations to diverse dispersing agents rather than distinct dispersal syndromes. If dispersal syndromes do constitute sets of covarying characters, then a change from winged to spiny fruits or the opposite should invoke respective changes in other morphological characters. If there is no morphological covariation, then there are no true, discrete syndromes but a continuum of fruit morphologies in the adaptive landscape. The major aim of this paper is to check whether umbellifer fruits exhibit distinct dispersal syndromes or whether the adaptations to wind or animal dispersal are superficial and do not affect fruit morphology and anatomy. We examine the evolution of fruit morphology and anatomy of tribe Scandiceae in the context of presumed dispersal syndromes, with particular attention to former members of tribes Caucalideae and Laserpitieae—now segregated between subtribes Daucinae and Torilidinae—that represent considerable variation in secondary ribs appendages. We only include representative samples of subtribes Scandicinae and Ferulinae. The former was subject of our earlier studies of fruit evolution (Piwczyński et al. 2015; Spalik et al. 2001) while the latter includes only anemochorous species (Korovin 1947) and therefore does not represent any notable variation in dispersal strategy.

Apart from selection pressure, fruit morphology and anatomy may also reflect a common evolutionary history, i.e., fruit similarity is synapomorphic rather than resulting from convergence. The phylogenetic significance of fruit characters for spiny-fruited taxa placed in the former tribe Caucalideae was evaluated previously by Lee et al. (2001), but their study included only a small sample of winged-fruited taxa. Therefore, a secondary aim of this paper is to assess the phylogenetic signal in fruit morphology and, particularly, to confirm whether the genera

of Daucinae that were recently redefined based solely on molecular data (Banasiak et al. 2016) are also supported with fruit characters.

Materials and methods

Species selection and morphological data

The selection of taxa was based on earlier phylogenetic studies of tribe Scandiceae (Downie et al. 2000a) and its subtribe Daucinae (Banasiak et al. 2016) and the availability of ripe fruits for morphological analyses. Sampled taxa represented a wide array of fruit morphologies occurring in this group. Effectively, 86 species and subspecies were examined for molecular and morphological characters. These included representatives of Scandiceae subtribes Daucinae (39 taxa sampled of approximately 90 in total), Torilidinae (14 of about 20), Scandicinae (22 of about 120), Ferulinae (7 of about 170), and *Artemisia squamata* that does not have a clear subtribal placement. Outgroup taxa included representatives of tribes Smyrniaceae (two species) and Aciphyllaceae (one species).

The external characters of mature fruits were examined using a Nikon SMZ-U dissecting microscope (8–160× magnification). For anatomical studies, the fruits were soaked in water and hand-cut; dissections were stained with phloroglucinol or safranin—fast green and were examined using a Nikon Optiphot 2 optical microscope (40–1000× magnification). Drawings were made using a drawing tube or based on photographs taken using a Nikon Microflex HFX-DX photograph system. Sources of all material examined are provided in Online Resource 1.

Because our aim was not only to assess dispersal syndromes but also to delimit newly redefined genera, we included a variety of fruit morphological and anatomical characters. Some of these characters like fruit size and compression are related to dispersal mode. Other features may result from different selection pressures; for instance, various forms of fruit sclerification or vittae filled with resin may serve as endosperm protection against herbivory. Sixteen quantitative (Nos. 1–16) and ten qualitative (Nos. 18–27, Table 1 and Online Resource 2) fruit characters were considered. We also included approximate plant height (No. 17) and life history (No. 29) because they may affect optimal dispersal mode (Cohen and Plitmann 1997; Harper et al. 1970). Additionally, character No. 28 describes the mode of fruit dispersal as estimated based on fruit appendages. Morphological (external) quantitative characters were scored based on a sample of 3–10 fully ripe fruits (depending on their availability on herbarium specimens), while anatomical characters were usually based on a single dissected fruit

(see Fig. 1 for details of measurements). Approximate plant height and life history were obtained from various floristic accounts.

Molecular data

Four molecular markers were considered: nuclear ribosomal DNA internal transcribed spacer (nrDNA ITS), plastid *rpoB-trnC* intergenic spacer, and introns in plastid *rps16* and *rpoC1* genes. These regions were used in previous studies of Apiaceae phylogeny (Downie et al. 2000b, 2010; Lee and Downie 2000), including Daucinae (Banasiak et al. 2016). Seventy-two sequences were obtained for this study (Online Resource 1).

The laboratory procedures, including PCR and sequencing reactions, followed earlier studies (Banasiak et al. 2016; Panahi et al. 2015). Total genomic DNA was isolated from ca. 20 mg of dried leaf tissue using a DNeasy Plant Mini Kit (Qiagen, Hilden, Germany). For nrDNA ITS, the DNA samples were PCR-amplified using primers N-nc18S10 and C26A (Wen and Zimmer 1996). For some difficult accessions, the ITS 1 and ITS 2 regions were amplified separately using the following pairs of primers: 18S-ITS1-F and 5.8S-ITS1-R for ITS 1, and ITS-3N and ITS4 for ITS 2 (Spalik and Downie 2006).

The *rpoB-trnC* spacer was amplified with primers *rpoB* and *trnC*^{GCA}R (Shaw et al. 2005). Because this region includes long insertions and mononucleotide repeats, three internal primers (*rpoB*400, 400*trnC*, and 400*trnC*2) were additionally used to aid amplification and sequencing (Banasiak et al. 2016). The *rps16* intron was amplified and sequenced using external primers 5*exonC* and 3*exonR* (Calviño et al. 2006) or *s16exF* and *s16exR* (Panahi et al. 2015); additionally, two internal primers, *s16inF* and *s16inR*, were also used to overcome amplification or sequencing difficulties (Panahi et al. 2015). The *rpoC1* intron was amplified and sequenced using external primers *C1exF* and *C1exR*; additionally, two internal primers, *C1inF* and *C1inR*, were also employed for some samples (Panahi et al. 2015). The sequences were assembled and edited using SeqMan Pro v.14 (Dnastar, Madison, Wisconsin, USA). All newly obtained sequences have been deposited in GenBank (Online Resource 1).

Phylogenetic analyses

Sequences were aligned using the G-INS-I algorithm implemented in MAFFT v.7.271 (Kato and Standley 2013) and corrected manually as necessary using Mesquite v.3.51 (Maddison and Maddison 2018). The alignment was trimmed with trimAl v.1.2rev59 (Capella-Gutiérrez et al. 2009). Phylogenetic trees were obtained using maximum likelihood (ML) and Bayesian inference (BI) methods. ML

Table 1 Characters used in the analyses. See Fig. 1 for fruit character explanations

Quantitative characters

1. Ratio of mericarp length to its width 1
2. Ratio of mericarp width 1 to its thickness in dry fruit
3. Ratio of mericarp width 2 to its thickness in soaked fruit
4. Ratio of dorsal bundle width to mericarp perimeter
5. Ratio of dorsal bundle thickness to its width
6. Ratio of lateral bundle width to mericarp perimeter
7. Ratio of lateral bundle thickness to its width
8. Ratio of commissural bundle width to mericarp perimeter
9. Ratio of commissural bundle thickness to its width
10. Ratio of vitta width to mericarp perimeter
11. Ratio of distance between commissural bundles to mericarp width 2
12. Ratio of commissure width to mericarp width 2
13. Ratio of seed (endosperm) width to its thickness
14. Ratio of endosperm groove to endosperm thickness
15. Ratio of minimum to maximum endosperm groove
16. Ratio of cuticle thickness at cell centre to that at cell margin measured in primary ribs epidermis
17. Approximate plant height [m]

Qualitative characters

18. Wings on lateral primary ribs: 0, absent; 1, present
19. Lateral secondary ribs: 0, absent; 1, filiform or keeled; 2, spiny; 3, winged; 4, *Artedia*-type
20. Dorsal secondary ribs: 0, absent; 1, distinctly smaller than lateral secondary ribs; 2, similar to lateral secondary ribs
21. Vallecular vittae: 0, compressed or obsolete; 1, (0–)1 per vallecule; 2, (1–)2 per vallecule; 3, ≥ 3 per vallecule
22. Commissural vittae: 0, absent; 1, (1–)2; 2, > 2
23. Vittae under vascular bundles: 0, absent; 1, present
24. Total number of vittae: 0, 0; 1, 2; 2, 4; 3, 6–10; 4, > 10
25. Rib oil ducts per each primary rib: 0, 0–3; 1, 4–9; 2, > 9
26. Ring of sclerified cells in endocarp: 0, absent; 1, elongated cells around endosperm; 2, one-layered; 3, multilayered
27. Other forms of fruit sclerification: 0, absent; 1, non-elongated cells in endocarp and mesocarp; 2, sclerified exocarp and/or mesocarp; 3, entire fruit sclerified
28. Dispersal mode: 0, barochorous; 1, barochorous or weakly zoochorous (hairs or bristles present); 2, zoochorous; 3, anemochorous
29. Life history: 0, annual; 1, biennial; 2, perennial

analyses were performed with RAXML v.8.2.4 (Stamatakis 2014) employing a GTR + G substitution model with independent estimation of its parameters for nuclear and plastid data. Bootstrap support (BS) was estimated based on 1000 rapid replicate analyses.

Bayesian analyses were performed with MrBayes v.3.2.6 x64 MPI (Ronquist et al. 2012) with GTR + G substitution model with independent estimation of its parameters for nuclear and plastid data. Because in preliminary analyses Ferulinae were paraphyletic with respect to Scandicinae probably due to long-branch attraction, we confined each of the subtribes to monophyly. Two independent runs each of six Monte Carlo Markov chains were initiated and run for 25 million generations with a sampling frequency of 1000 generations. The initial 25% of saved trees were discarded as a burn-in phase; the remaining trees were used to calculate the 50% majority-rule consensus tree and posterior probabilities

(PP) of particular clades. To check the effective sample size (ESS) for the estimated parameters and the convergence of the independent runs, Tracer v.1.6.0 (Rambaut et al. 2014) was used.

Morphological analyses

For a few species, we could not assess some quantitative characters because they were not visible in mature fruits due to tissue compression or because the fruits were not fully ripe. Because missing data are problematic in statistical analyses, we filled these gaps using the *phylopars* function, as implemented in the *Rphylopars* package v.0.2.9 (Bruggerman et al. 2009). To assess whether there are distinct fruit morphotypes, i.e., groups of morphologically similar fruits, we performed principal component analysis (PCA) as implemented in the *R* Stats package v.3.5.1 (R Core Team 2018)

Fig. 1 Mericarp anatomy and characters considered in this study. See Table 1 for character and character state descriptions

for qualitative characters (Nos. 1–17, Table 1). The results were visualized using R packages ggplot2 (Wickham 2016) and ggfortify (Tang et al. 2016). To evaluate the evolution of discrete characters (Nos. 18–27, Table 1), we mapped them onto a ML tree using the maximum parsimony method with Mesquite v.3.51 (Maddison and Maddison 2018).

All matrices of molecular and morphological data and their resulting phylogenetic trees were deposited in TreeBASE, study no. 24058 <http://purl.org/phylo/treebase/phylo/ws/study/TB2:S24058>.

Results

Molecular trees

Trees obtained using ML and BI methods were generally similar, with differences including minor rearrangements among some clades or species within these clades (Fig. 2 and Online Resource 2). Major clades—subtribes and genera—were similar to those apparent in former analyses of Scandicinae (Downie et al. 2000a), Ferulinae (Panahi et al. 2018), and Daucinae (Banasiak et al. 2016).

Within Scandicinae, *Todaroa aurea*, endemic to the Canary Islands and the only anemochorous species in this subtribe, was sister to the barochorous or weakly zoochorous species *Athamanta montana*, another endemic of this archipelago (BS=91%; PP=0.87). *Artedia squamata*, a species with idiosyncratic fruit morphology, was sister to Daucinae in ML analyses albeit with poor bootstrap support (BS<50%) while in BI analyses it was placed sister to Torilidinae (PP=0.71). Most genera of Daucinae that were represented by at least two species or subspecies, i.e., *Thapsia*,

Orlaya, *Silphiodaucus*, and *Daucus*, were each monophyletic. *Laserpitium* included two lineages, with *Laserpitium pseudomeum* placed sister to *Siler montanum* (BS=58%; PP=0.65) rather than with the rest of its congeners. Generally, the relationships among all major clades of Scandiceae were poorly supported with BS<50% and PP≤0.71. The lineages with fruits with secondary ribs—Daucinae, Torilidinae, and *Artedia*—did not form a clade.

Principal component analysis of quantitative traits

In the PCA, the first five components had eigenvalues > 1.0 and together they explained 68.2% of the variance of quantitative morphological characters. The first three principal components (PC1, PC2, and PC3) accounted for 23.2%, 18.8%, and 11.5% of the variance, respectively. The loadings (r) of particular traits for PC1, PC2, and PC3 were low ($|r|<0.5$). Dispersal strategies, as estimated based on fruit appendages, were best resolved with PC1; however, they did not correspond to distinct morphotypes because their convex hulls overlapped considerably (Fig. 3). The characters with highest absolute loadings for PC1 included ratio of endosperm groove to endosperm thickness (No. 14, $r=-0.38$), ratio of mericarp width 2 to its thickness in soaked fruit (No. 3, $r=-0.37$), ratio of mericarp width 1 to its thickness in dry fruit (No. 2, $r=-0.36$), and ratio of commissural bundle thickness to its width (No. 9, $r=-0.36$). The following characters had lower loadings: ratio of minimum to maximum endosperm groove (No. 15, $r=0.29$), ratio of commissure width to mericarp width 2 (No. 12, $r=0.26$), and approximate plant height (No. 17, $r=-0.25$). In summary, anemochorous species tend to have dorsally flattened mericarps with associated changes to their fruit

Fig. 2 Maximum likelihood tree for 86 representatives of Apiaceae tribe Scandiceae and outgroups. Bootstrap support values (≥ 50%) are given along branches; if a particular branch is present in the Bayesian majority-rule consensus tree, posterior probabilities are also indicated

anatomy; they are also somewhat taller than species having other modes of dispersal. This effect is, however, small given low loadings of these traits in PC1 and the low percent of the

variation explained by this component. Moreover, the species with lowest negative eigenvalues for PC1 are representatives of Ferulinae. These species have distinctly flattened

Fig. 3 Ordination plots for PC1 vs. PC2 and PC1 vs. PC3 for 17 quantitative characters of 86 representatives of umbellifers. Different shapes designate groups identified in Fig. 2. Convex hulls with

color shading reflect presumed dispersal strategies estimated based on fruit appendages. Numbers of eigenvectors are the same as numbers of characters in Table 1

mericarps with wings formed by primary commissural ribs (hence their commissural bundles are thicker and narrower). This suggests that the variation explained with PC1 may be phylogenetic rather than resulting from similar adaptive shifts in unrelated species.

The evolution of qualitative traits

Phylogenetic mapping of ten qualitative traits on the best ML tree demonstrated that all fruit characters are homoplastic and of limited use for defining taxa; they may, however, reflect convergent adaptive evolution (Fig. 4). Wings on lateral primary ribs developed in three ingroup lineages: Ferulinae, *Todaroa aurea* (Scandicinae) and *Laser trilobum* (Daucinae). Secondary ribs arose twice, in the ancestor of Torilidinae and the common ancestor of Daucinae and *Arctidia*. However, because basal relationships within Scandiceae are poorly supported, a unique appearance of this character cannot be excluded.

Spiny secondary ribs are ancestral for Torilidinae, while winged ribs are ancestral for Daucinae. In Torilidinae, wings evolved from spines in *Lisaea papyracea*, while in Daucinae spines evolved from wings likely in the common ancestor

of *Orlaya*, *Silphiodaucus*, and *Daucus* with subsequent reversals in *Silphiodaucus*, in the ancestor of *Daucus edulis* and *D. decipiens*, in *D. rouyi*, and in *D. annuus* (but note the ambiguity of reconstruction). Wings of *Arctidia* are idiosyncratic as they occur only on lateral secondary ribs and are divided into broad, round lobes. It is noteworthy that 22 species are annuals and distinctly zoochorous, i.e., have spiny fruits, as opposed to seven annuals without spiny fruits and five spiny-fruited taxa that are biennials or perennials (Fig. 5). However, this co-occurrence is due to common ancestry rather than to convergence or parallel evolution because the ancestors of Torilidinae, *Orlaya*, and *Daucus* are annuals with spiny fruits.

Laserpitium sensu Banasiak et al. (2016) is characterized by the presence of non-elongated sclerified cells in endocarp and mesocarp tissues. This character also occurs in *Ekimia petrophila*, but not in *Laserpitium pseudomeum*. Fruits of *Thapsia* sensu Banasiak et al. (2016) usually have 6–10 or more vittae with some vittae situated under vascular bundles; both characters are, however, highly homoplastic.

Fig. 4 Ancestral state reconstructions for ten qualitative fruit characters (Nos. 18–27, Table 1) for 86 representatives of Scandiceae and outgroups. Tree topology and species order are the same as in Fig. 2

Fig. 5 Ancestral state reconstructions for dispersal strategy and life history (character Nos. 28 and 29, Table 1) for 86 representatives of Scandiceae and outgroups. Tree topology and species order are the same as in Figs. 2 and 4

Discussion

Fruit morphologies and dispersal modes in Apiaceae

The results suggest that there are no clear-cut morphological dispersal syndromes in Apiaceae tribe Scandiceae, but a wide spectrum of fruit morphotypes (Fig. 6) that may reflect diverse and probably mixed dispersal strategies. Due to their small fruit size, Apiaceae are opportunistic dispersers and their actual dispersal mode may depend on local vectors while their fruit morphology may sometimes be misleading. On the other hand, its highly homoplastic nature suggests that fruit morphology in Apiaceae is subject to strong selective pressure.

Experimental studies demonstrate that winged mericarps of umbellifers are carried away by wind a relatively short distance: 90% of fruits reached the ground within five meters from the maternal plant (Jongejans and Teleñius 2001). Therefore, other vectors must be responsible to account for their long-distance dispersal. Our results suggest that winged fruits more often occur in tall, robust umbellifers, such as the several species of *Ferula*, *Laserpitium*, and *Thapsia* examined herein. However, this morphology is better seen as a way to avoid competition of seedlings with the maternal plant than as a means for long-distance dispersal. A study on the presumably wind-dispersed giant hogweed (*Heracleum mantegazzianum*) demonstrated that the maximum distance of seedlings from the maternal plant was 5.3 m, with the highest density of seedlings within the range 0.0–0.5 m (Pergl et al. 2011). Modeling of a regional invasion of *H. mantegazzianum* in the Czech Republic suggested that short-distance dispersal (neighboring dispersal) up to 10 m does not explain its spread; therefore, long-distance dispersal (10–500 m) by other vectors has had to take place

(Nehrbass et al. 2006; Pergl et al. 2011). A study on animal dispersal has shown that some presumed wind-dispersed and gravity-dispersed umbellifer fruits have high attachment potential (AtP) to animal fur (Römermann et al. 2005). Fruit morphology and fruit size were good predictors of attachment potential to sheep fur, with spiny *Daucus carota* and winged *Laserpitium latifolium* having AtP values of 95.7% and 13.7%, respectively. However, the difference disappeared with cattle as dispersing agents (AtP values of 16.7% and 10.3%, respectively) and this time fruit mass alone was the best predictor of attachment potential. Diaspores above a threshold of about 10 mg did not keep attached to cattle hair at all (Römermann et al. 2005). Effectively, spines may serve both epizoochory and anemochory. In a wind-dispersal experiment including fruits of *D. carota* with artificially removed spines, spineless fruits went only two-thirds as far as the intact diaspores even though the former weighed less than the latter (Lacey 1981).

As compared to winged fruits, epizoochorous fruits are generally dispersed at higher distances. In a study modeling seed shade for epizoochorous dispersal by donkeys including the umbellifer *Anthriscus caucalis*, mean dispersal distance for hooked fruits was estimated at 166 m (Couvreur et al. 2008).

A good example of contradictory selection pressures acting on dispersal syndromes is heterocarpy: the presence of different diaspore morphotypes on a single plant reflecting various modes of dispersal. Among umbellifers, barochorous and epizoochorous fruits occur in *Torilis nodosa*, *Lisaea heterocarpa*, *Tordylium aegyptiacum*, *Scandix australis*, and *S. turgida* (Arenas Posada and García Martín 1993; Hedge and Lamond 1972; Jury 1986). It is noteworthy that all of these species are annuals. Barochorous fruits serve therefore to maintain the local population, while epizoochorous diaspores are adapted for long-distance dispersal.

Fig. 6 Fruit morphologies of representatives of Scandiceae with phylogenetic relationships modified from those shown in Figs. 2 and 4

When inferring dispersal strategies from morphology, in some cases the entire plant habit must also be taken into account. For example, 16% of umbellifers native to Israel are tumbleweeds (Cohen and Plitmann 1997); hence, the entire plant is the dispersal unit. In some species of *Daucus*, including *D. carota*, rays of fruiting umbels are bent inward forming a bird's nest structure. These rays bend adaxially with increasing relative humidity and abaxially with decreasing relative humidity, affecting fruit dispersal (Lacey 1980; Lacey et al. 1983). Conventional plant dispersal classification systems based on diaspore appendages are therefore of limited use for addressing ecological questions because the dispersal potential ranges continually (Tackenberg et al. 2003).

Fruit character evolution in Daucinae

In Apiaceae, prominent fruit secondary ribs are unique to three major lineages of Scandiceae—subtribes Daucinae and Torilidinae and the genus *Artemisia*—suggesting that this character is a synapomorphy uniting these three clades. However, these lineages formed a clade neither in our study nor in previously published molecular trees of the group (Downie et al. 2000a; Lee and Downie 1999; Lee et al. 2001). Nevertheless, in all of these analyses, the relationships among major clades were poorly supported and prone to taxon sampling. Most recent RAD-seq analyses of Scandiceae and outgroups strongly supported a sister relationship between Daucinae and Torilidinae and, correspondingly, synapomorphic status of prominent secondary ribs (Marcin Pwiczynski, unpubl.).

Spiny-fruited taxa of Daucinae and Torilidinae were formerly placed in tribe Caucalideae while winged-fruited taxa were classified in tribe Laserpitieae. However, both previous analyses (Banasiak et al. 2016) and this study demonstrated that the morphology of fruit appendages is highly homoplastic. The presence of wings or spines is of limited use at the generic level. Particularly, the genus *Daucus* has been redefined to include winged-fruited *Melanoselinum decipiens* ($\equiv$ *D. decipiens*), *Monizia edulis* ($\equiv$ *D. edulis*), *Rouya polygama* ($\equiv$ *D. rouyi*), and the species of *Tornabenea* that were partly transferred to *Daucus*: *D. annuus*, *D. tenuissimus*, *D. insularis* (Banasiak et al. 2016), with the first included in this study. In fact, the appendages of secondary ribs in *D. annuus* are intermediate between wings and spines. The evolution of winged fruits in these taxa is most likely a reversal, and in some cases, it may be linked to their insular habitat. *Daucus decipiens* and *D. edulis* are endemic to Madeira (Fernandes and Carvalho 2014; Press and Dias 1998), while *Tornabenea* is restricted to Cape Verde (Brochmann et al. 1997). These volcanic Macaronesian archipelagos have never been connected to the mainland, and they lack native large mammals that could have acted as dispersing agents

for epizoochorous species. Particularly interesting are the changes that occurred in '*Tornabenea*,' exemplified in this study by *D. annuus*. This species is nested within the *D. carota* complex, and its evolution was apparently recent. It has spiny or dentate lateral wings indicating that they are derived from spines of *D. carota*. Additionally, its reduced dorsal secondary ribs are similar to the two endemics of Madeira illustrating, therefore, evolutionary parallelism. In our former molecular study, *Tornabenea* was placed under synonymy in *Daucus* (Banasiak et al. 2016); however, some species were not included in that study and thus not formally transferred making the classification system inconsistent. We, therefore, introduce new combinations in *Daucus* below.

Due to numerous homoplasies, fruit characters are of limited utility for delineating generic boundaries in Daucinae as none of the genera is defined based on a synapomorphy. Some genera, however, are defined based on sets of characters, such as the segregates of *Laserpitium*. All species traditionally placed in *Laserpitium* are characterized by the presence of wings at all secondary ridges. However, *Laserpitium* sensu Banasiak et al. (2016) or sensu stricto (s.s.) may be distinguished from its former congeners now placed in *Ekimia*, *Laser*, and *Thapsia* by a suite of characters including the shape of endosperm in transverse section and the fruit sclerification pattern. Particularly interesting are the differences between the species of *Laserpitium* s.s. and *L. pseudomeum*, the latter constituting an isolated lineage that may be sister to *Siler* (this study) or to *Laser* (Banasiak et al. 2016) rather than to its congeners. Fruits of *L. pseudomeum* are superficially similar to *Laserpitium* s.s. in having prominent wings both on dorsal and lateral secondary ribs but are more similar to *Laser* in having distinctly flattened endosperm and non-sclerified exocarp and mesocarp. *Laserpitium pseudomeum* is endemic to the mountain regions of Greece (Hartvig 1986). Additional molecular studies are necessary to firmly establish its phylogenetic position.

The phylogenetic position of *A. squamata* was unstable in previous molecular analyses. Similar to this study, it was placed sister to Daucinae (Lee and Downie 1999, 2000) or Ferulinae (Banasiak et al. 2013) or identified as basal branch in Scandiceae (Valiejo-Roman et al. 2006). Given its peculiar fruit morphology, pollen traits (Cerceanu-Larrival and Roland-Heydacker 1976), and isolated phylogenetic position, it deserves to be placed in a separate subtribe.

Conclusions

Our results suggest that in Scandiceae, and Daucinae in particular, there are no clear-cut dispersal syndromes. Only anemochory is weakly associated with mericarp flattening and concomitant changes in fruit anatomy like endosperm

shape. These associations are weak because fruit appendages facilitating wind dispersal may be of different origins, such as developing from either primary or secondary ribs. It is, however, noteworthy that multiple switches between wings and spines occurred only in taxa where these appendages occur on secondary ribs. To our knowledge, there are no spines—that have to be distinguished from epidermal bristles—developing from primary ribs. Primary ribs contain vascular bundles that may constrain such a transformation.

Similar to previous studies, our study demonstrates that fruit morphology is highly homoplastic in umbellifers and that synapomorphies that are useful for infrafamilial classification rarely occur.

Taxonomic treatment

Daucus bischoffii (J.A.Schmidt) Spalik & Banasiak, **comb. nov.** $\equiv$ *Tornabenea bischoffii* J.A.Schmidt, Beitr. Fl. Cap Verd. Ins. 254. 1852.—LECTOTYPE: Cape Verde, Santo Antão, mountain screes, Mar 1861, *J.A. Schmidt s.n.* (Brochmann et al. 1997, W [n.v.]).

Daucus humilis (Lobin & K.H.Schmidt) Spalik & Wojew., **comb. nov.** $\equiv$ *Tornabenea humilis* Lobin & K.H.Schmidt, Sommerfeltia 24: 83. 1997.—HOLOTYPE: Fogo, 8 Dec 1982, *Lobin 2621* (FR [n.v.]).

Daucus ribeirensis (K.H.Schmidt & Lobin) Spalik & Baczyński, **comb. nov.** $\equiv$ *Tornabenea ribeirensis* K.H.Schmidt & Lobin, Feddes Repert. 110(1–2): 8. 1999.—HOLOTYPE: São Nicolau, 25 Nov 1982, *Lobin 2562* (B [n.v.]).

Artediinae Baczyński, Wojew., S.R.Downie & Spalik **subtrib. nov.** —TYPE: *Artedia* L., Sp. Pl. 1: 242. 1753.

Diagnosis: Inflorescence with central dark florets on elongated stalks; fruits with broadly lobed wings on lateral secondary ribs; pollen distinctly rhomboidal with exceptionally strong apiculation (protrusion) above aperture. Monotypic.

Distribution area: Eastern Mediterranean to Middle East.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Information on electronic supplementary material

Online Resource 1. Accessions of Apiaceae examined for fruit morphology and DNA sequence variation.

Online Resource 2. Bayesian 50% majority-rule consensus tree for 86 representatives of Apiaceae tribe Scandiceae and outgroups.

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