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DELIMITATION OF GENERA IN *APIACEAE* WITH EXAMPLES FROM *SCANDICEAE* SUBTRIBE *SCANDICINAE*

K. Spalik*, A. Wojewódzka* & S. R. Downie†

Of the 455 known genera in *Apiaceae* (*Umbelliferae*), 41% are monotypic and 26% comprise only two or three species each. Similarly, of the 16 genera constituting *Scandiceae* Spreng. subtribe *Scandicinae* Tausch, seven (*Balansaea* Boiss. & Reut., *Kozlovia* Lipsky, *Krasnovia* Schischk., *Myrrhis* Mill., *Myrrhoides* Fabr., *Sphallerocarpus* DC. and *Todaroa* Parl.) are monotypic, and two (*Neoconopodium* Pimenov & Kljuykov and *Tinguarra* Parl.) are bitypic. Phylogenetic analysis of the subtribe, using molecular (rDNA ITS), morphological and anatomical data, indicates that the number of genera may be reduced with only three, *Todaroa*, *Sphallerocarpus* and *Myrrhis*, retained as monotypic. Remaining taxa form eight clades that are supported by high bootstrap values and are morphologically distinct. Four of these clades (*Anthriscus* Pers., *Geocaryum* Coss., *Osmorhiza* Raf. and *Scandix* L.) are equivalent to currently recognized genera. *Kozlovia*, *Krasnovia* and *Neoconopodium* form a well-supported clade that may be recognized as the single genus *Kozlovia*, and *Myrrhoides* is grouped with *Chaerophyllum* L. *Tinguarra* and *Athamanta* L. form a monophyletic group that is well supported by analyses of morphology, fruit anatomy, and combined morphological, anatomical and ITS sequence data; however, this group is not maintained in separate analyses of ITS sequences. Similarly, the group formed by *Conopodium* W. D. J. Koch and *Balansaea* is monophyletic in morphological, anatomical, and combined analyses, but is not supported by the separate analyses of ITS sequence data. All of these groups are well delimited on the basis of fruit characters that have long been regarded as essential in umbellifer taxonomy. One new combination is proposed: *Athamanta montana* (Webb ex H. Christ.) Spalik, A. Wojew. & S. R. Downie.

Keywords. Internal transcribed spacer, morphology, new combination, phylogeny, rDNA, systematics, *Umbelliferae*.

Introduction

Many students of botany regard *Apiaceae* as one of the most notorious families of flowering plants. The reason for this odium is not the dubious infrafamilial classification (which is practically unknown to the non-specialist), but the difficulty in identification of the species resulting partly from their obscure morphology and partly from ambiguous definitions of many genera. The delimitation of genera has not attracted as much attention as studies of higher-level relationships (summarized

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by Downie *et al.*, 2001) and this low profile may give the completely wrong conclusion that most of the work has already been done. Detailed studies reveal that many umbellifer genera are polyphyletic. For instance, extensive research on tribe *Caucalideae* Spreng. (*sensu* Heywood, 1971) resulted in the transfer of one-third of its species from one genus to another (Jury, 1986). Subsequent studies using molecular markers have shown that these changes although substantial are still inadequate because this tribe and some of its constituent genera are not monophyletic (Lee & Downie, 1999). Pimenov & Leonov (1993) indicated that *Peucedanum* L., one of the largest genera in the family, is likely polyphyletic and of its 100–120 species only 8–10 members of sect. *Peucedanum* should be retained. Phylogenetic analysis using a small subset of taxa from this genus confirms its polyphyly (Downie *et al.*, 2000c). Many other species-rich genera of *Apiaceae*, like *Conioselinum* Fisch. ex Hoffm., *Ferula* L. and *Ligusticum* L., are also polyphyletic (Downie *et al.*, 2000b). Therefore, a substantial number of umbellifer species may eventually change their generic placement.

Genera as Tools for Species Identification

For Linnaeus and his followers, the classification system was also an identification key for it was constructed using the Aristotelian rule of logical division (Mayr, 1982). The rank of genus was the cornerstone of classification and was perceived as a real unit of diversity, contrary to suprageneric categories, which were introduced for purely practical reasons (Stafleu, 1971, Mayr, 1982). Today, the genus is recognized simply as the lowest collective category, and the classification is no longer an identification scheme but an index to an information storage and retrieval system. In fact, it would be difficult or even impossible to make an identification key on the basis of a phylogenetic tree, considering the frequencies of parallelism and convergence, and other irregularities of character evolution in flowering plants. It is not surprising then that many classes, subclasses, orders or even families are difficult to delimit using obvious morphological or anatomical synapomorphies (e.g. Angiosperm Phylogeny Group, 1998). Even *Apiaceae*, one of the longest recognized and most distinct families of flowering plants, is not that easy to define, particularly if all of its subfamilies are included with the exception of those hydrocotyloids allied with *Araliaceae* on the basis of molecular evidence (Plunkett *et al.*, 1996, 1997; Downie *et al.*, 1998). Downie *et al.* (2000b), presenting a draft of a new tribal classification system of *Apiaceae* subfamily *Apioideae*, admitted that they could not find any morphological synapomorphies for most of the groups detected on the basis of molecular data.

Although we may eventually agree that in some groups of plants higher taxonomic categories are better delimited by molecular markers rather than morphology and anatomy, most would strongly object to a similar definition of genera. The latter, contrary to tribes or subtribes, still play an important role in species identification and should therefore be well defined morphologically and be visibly distinct from their sister taxa. If they are not, it is difficult to make a good identification key. The advantage of Linnaean names over alternative naming systems (like that of phylogenetic nomenclature, as advocated by Cantino *et al.*, 1999) is that the binomial not only denotes a particular species but also points to its closest relatives, i.e. congeners. These species are usually quite similar and, therefore, may be easy to confuse. The presence of a shared generic name allows one to easily locate specimens in a herbarium or descriptions in a monograph, and compare them when in doubt. Using monophyly as the primary criterion, genera should ideally be of a manageable size. Both monotypic and large genera (the latter, for instance, comprising more than a hundred species) should be avoided. However, large monophyletic genera should not be divided arbitrarily into segregates if these segregates are not indeed morphologically distinct and if this division invokes changing many widely used specific names. In these cases, the introduction of an infrageneric classification is a practical alternative to describing segregate genera. Monotypic genera should only be recognized if they represent isolated lineages with no close relatives (e.g. if their sister group represents a clade of several genera) or if their inclusion into their sister taxa would much worsen the definition of the latter. 'Ideal' genera should be of medium size, of perhaps 10–20 species.

Genera of *Apiaceae*

Forty-five generic names for *Apiaceae* appeared in *Species Plantarum* (Linnaeus, 1753) and are therefore formally attributed to Linnaeus (although he himself coined only a few of these as most were adopted from earlier authors). Actually, Linnaeus's classification of umbellifers was developed by his colleague and friend Petrus Artedi (Constance, 1971). The number of genera in *Apiaceae* rose to 107 in de Candolle's (1830) *Prodromus* and to 195 in Endlicher's (1836–40) *Genera Plantarum*, and was subsequently reduced to 153 by Bentham (1867). Drude (1898) in his influential monograph of the family recognized 231 genera. Constance (1971) outlining the taxonomic history of the group gave an estimate of 300 genera; Pimenov & Leonov (1993) list 455 genera. The circumscriptions of genera have also substantially changed since their original descriptions. For instance, Linnaeus (1753) placed ten species in *Athamanta* L., but now only two of these, *A. cretensis* L. and *A. sicula* L., are retained (Jarvis & Knees, 1988). The type species of *Anthriscus* Pers., *A. caucalis* M. Bieb., was originally described in *Scandix* L. (Linnaeus, 1753) and subsequently recognized in *Caucalis* L., *Chaerophyllum* L., *Myrrhis* Hill. and *Torilis* Adans. until the generic name *Anthriscus* was restored by Persoon (1805). However, the genus owes its present meaning not to this author, but to Sprengel (1813) and Hoffmann (1814), who correctly identified close relatives of its type and removed misplaced species.

When the relations of a distinctive species are not easy to ascertain, the simplest way to resolve the problem is to make it a monotypic genus. Unfortunately, this solution has been used far too often in *Apiaceae*. Of the 455 genera listed by Pimenov

& Leonov (1993), 41% are monotypic and 26% comprise only two or three species each (Fig. 1). As a result, 67% of all genera account for only 13% of all the species. Only 6% of genera have between 10 and 20 species each, and 8% have more than 20 species, but these large genera comprise some 60% of the total number of species (see Watson, 2001: Table 2). Included in this list of large genera are *Conioselinum*, *Ferula*, *Ligusticum*, *Peucedanum* and *Seseli*, all of which have already been shown to be polyphyletic (Katz-Downie *et al.*, 1999; Downie *et al.*, 2000b). The taxonomic confusion surrounding many genera of *Apiaceae*, and their inferred polyphyly, makes their identification a difficult task. The inflation of genus number within the *Apiaceae*, resulting from recognition of many small or monotypic taxa, is also apparent in many other temperate families which include long-recognized edible, medicinal, or poisonous plants (Walters, 1961).

Generic Delimitation in *Scandiceae* Subtribe Scandicinae

Tribe *Scandiceae* Spreng., as revised using molecular markers, includes three subtribes: *Scandicinae* Tausch, *Daucinae* Dumort. and *Torilidinae* Dumort. (Lee & Downie, 1999; Downie *et al.*, 2000a). Subtribes *Daucinae* and *Torilidinae* comprise taxa formerly placed in *Laserpitieae* Benth. and *Caucalideae* (*sensu* Heywood, 1971), the latter including members of *Dauceae* W. D. J. Koch and *Scandiceae* subtribe *Caucalidinae sensu* Drude (1898). Members of subtribes *Daucinae* and *Torilidinae* are characterized by the presence of secondary ridges on the mericarps, this feature is a synapomorphy supporting their putative sister relationship. This affinity, however, is not confirmed in all studies incorporating molecular data; therefore, the order of branching of these three lineages of *Scandiceae* remains unresolved, and is reflected in their recognition at the same taxonomic rank. Recent analyses using nuclear rDNA internal transcribed spacer (ITS) sequences and chloroplast *rps*16

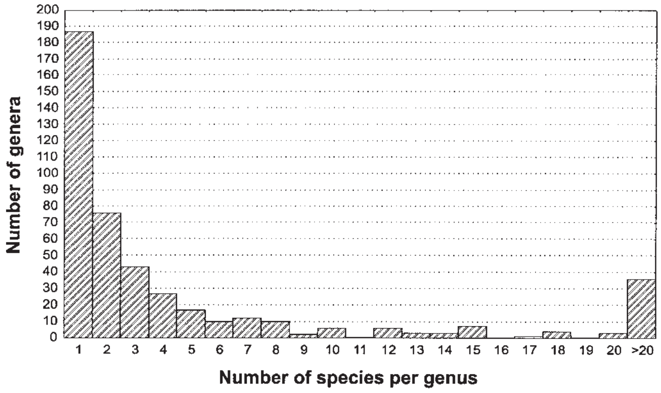

FIG. 1. The distribution of genus size in *Apiaceae* (based on data from Pimenov & Leonov, 1993).

intron data indicate that some species of *Ferula* form a fourth branch of the tribe (Downie *et al.*, 2000c).

From among the 40 genera that were at one time placed in *Scandicinae*, only 16 are confirmed in this subtribe on the basis of phylogenetic analysis of ITS sequence data (Downie *et al.*, 2000a,c). Seven of these genera (*Balansaea* Boiss. & Reut., *Kozlovia* Lipsky, *Krasnovia* Schischk., *Myrrhis* Mill., *Myrrhoides* Fabr., *Sphallerocarpus* DC. and *Todaroa* Parl.) are monotypic, and two (*Neoconopodium* Pimenov & Kljuykov and *Tinguarra* Parl.) are bitypic. Our prior studies using ITS sequences alone (Downie *et al.*, 2000a), ITS sequences plus general morphology (Spalik & Downie, 2001), and ITS sequences plus fruit morphology and anatomy (Spalik *et al.*, unpublished) suggest, however, that some of these monotypic and bitypic genera are not necessary.

In this paper, we present results of a combined analysis of molecular (ITS), morphological and anatomical data sets to address further the question of generic delimitations in *Scandiceae* subtribe *Scandicinae*. Detail of the data used are published elsewhere (Downie *et al.*, 2000a; Spalik & Downie, 2001; Spalik *et al.*, unpublished), and are available from the authors on request. We used a subset of 45 species representing the three subtribes of *Scandiceae*: *Scandicinae* (37 species), *Daucinae* (four species), and *Torilidinae* (three species). *Smyrnium olusatrum* L., a member of the putatively allied tribe *Smyrnieae* Spreng. (Downie *et al.*, 2000c), was used to root the trees. To account for the variable number of states in the morphological and anatomical characters examined, these characters were weighted using the scaling option of PAUP* 4.0 (Swofford, 1998) and employing fractional weights; each ITS position was assigned a weight of 1. Maximum parsimony analysis included heuristic searches with 500 random addition replicates and tree-bisection-reconnection branch swapping. Bootstrap support was estimated using 100 resampled data sets and employing 10 heuristic searches with random addition sequence of taxa for each replicate.

Two minimal-length trees resulted, each 1176.4 steps long, with consistency indices (CIs) of 0.454 and 0.397 (with and without uninformative characters, respectively), and a retention index (RI) of 0.686. The resultant strict consensus tree (Fig. 2) was generally congruent to those inferred from our previous analyses (Downie *et al.*, 2000a; Spalik & Downie, 2001; Spalik *et al.*, unpublished), with bootstrap support for many clades notably higher than in our previous studies which were carried out using fewer characters. Although this new phylogeny confirms the monophyly of all genera of *Scandicinae*, some of these genera are neither well supported by high bootstrap values nor clearly morphologically distinct from their sister taxa. This phylogeny also suggests that members of *Scandicinae* form 11 distinct lineages (identified in Fig. 2) that are also well delimited based on general morphology and fruit characters. We propose to recognize these lineages at generic rank. Three of these lineages (*Myrrhis*, *Sphallerocarpus* and *Todaroa*) represent monotypic genera while further four (*Anthriscus*, *Geocaryum* Coss., *Osmorhiza* Raf. and *Scandix*) are equivalent to currently recognized polytypic genera. The monotypic *Kozlovia* and *Krasnovia*

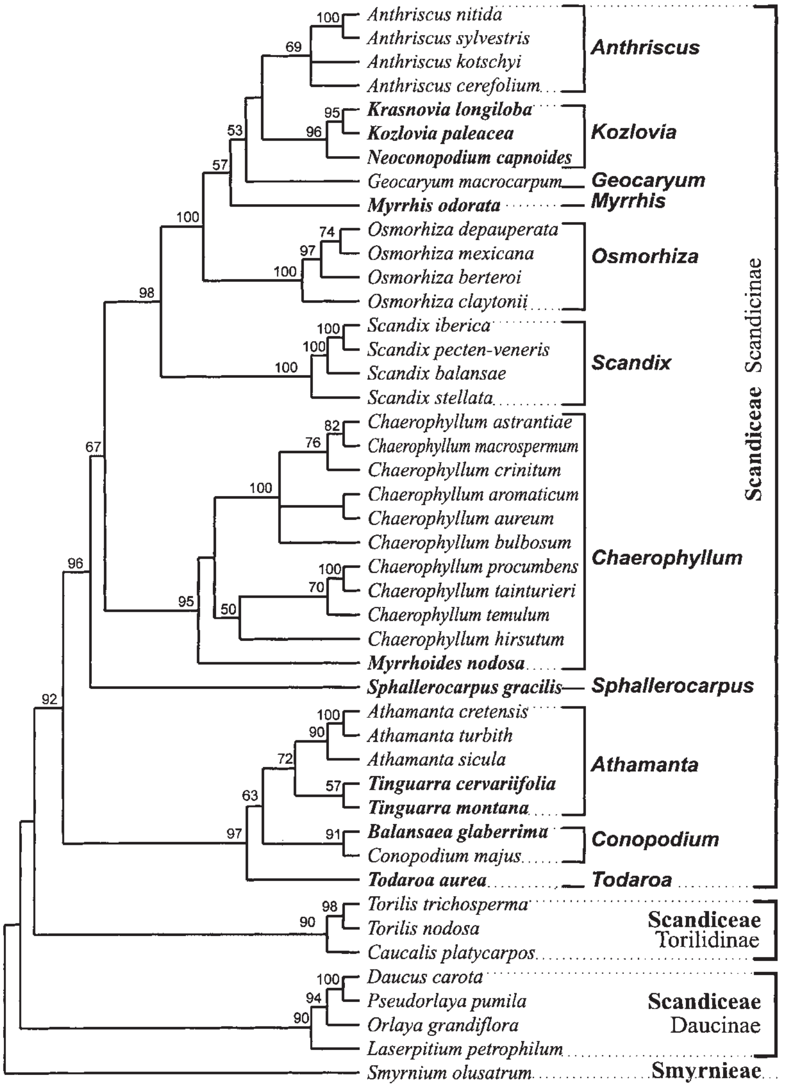

FIG. 2. Strict consensus of two minimal length 1176.4-step trees inferred from maximum parsimony analysis of combined morphological, anatomical, and ITS sequence data for 45 representatives of *Scandiceae* subtribe *Scandicinae* and outgroups (CI = 0.397 without uninformative characters, RI = 0.740). Boldface indicates monotypic and bitypic genera; numbers along nodes denote bootstrap values; only those greater than or equal to 50% are shown. The eleven bracketed taxa in *Scandiceae* subtribe *Scandicinae* are the genera recognized in this study. Authorities for all taxon names are given in Table 1.

and the bitypic *Neoconopodium* (with *N. capnoides* (Decne.) Pimenov & Kljuykov included in this study) may be recognized as the single genus *Kozlovia* whereas the monotypic *Myrrhoides* is included in *Chaerophyllum*. The redefined *Athamanta* unites members of *Athamanta sensu stricto* and *Tinguarra* while the monotypic *Balansaea* is included in *Conopodium* W. D. J. Koch.

The affinity of the *Athamanta* and *Conopodium* groups and *Todaroa aurea* (Sol.) Parl. is strongly supported with a 97% bootstrap value. Fruits of the members of each of these clades are characterized by numerous vallecular vittae (1–3(–4) per vallecula) that sometimes anastomose and are extant at fruit maturity. Such vittae are also present in *Sphallerocarpus*, the next branch up the tree, thus this character may be regarded as plesiomorphic for the subtribe (Spalik *et al.*, unpublished).

The *Athamanta* group includes both species of *Tinguarra*, a genus endemic to the Canary Islands, and representatives of the Mediterranean genus *Athamanta* (Figs 3.3–3.7). Members of these two genera are quite similar and their generic boundaries are unclear: *Tinguarra cervariifolia* (DC.) Parl., the type of the genus, was placed in *Athamanta* by de Candolle (1830) while *A. sicula* L. was also recognized in *Tinguarra* (e.g. Knees, 1996). All species occur in montane habitats and are characterized by hairy fruits with filiform ridges. Based on our prior analysis of general morphology (Spalik & Downie, 2001) and fruit characters (Spalik *et al.*, unpublished) we see no justification for keeping these genera separate. Because both *Athamanta* and *Tinguarra* each seem to be monophyletic, we propose to recognize them at the sectional rank (Table 1). One combination in *Athamanta* is therefore necessary:

Athamanta montana (Webb ex H. Christ) Spalik, A. Wojew. & S. R. Downie, **comb. nov.**
Basionym: *Todaroa montana* Webb ex H. Christ, Bot. Jahrb. Syst. 9: 107 (1888).

The *Athamanta* group is sister to the *Conopodium* group, the latter including a representative of *Conopodium* and the monotypic North African genus *Balansaea* (that was synonymized with *Conopodium* by Engstrand, 1973). Such affinity has not been confirmed by ITS data because *Conopodium* is not monophyletic in these analyses (Downie *et al.*, 2000a). However, analyses using general morphology (Spalik & Downie, 2001), fruit morphology and anatomy (Spalik *et al.*, unpublished), and all available evidence (Fig. 2) support the monophyly of the *Conopodium* group. All members of this group are geophytes and characterized by fruits that are glabrous but otherwise similar to those of ITS sister group *Athamanta* (Figs 3.1, 3.2). According to Pimenov & Leonov (1993), *Conopodium* comprises 20 species; however, Silvestre (1972, 1973) recognizes only five species in the Iberian Peninsula, a region he describes as a centre of diversity of this genus (Table 1).

Sphallerocarpus gracilis (Bess. ex Trevir.) Koso-Pol. traditionally has been described as having no close relatives, and parsimony analysis of ITS sequences, morphology, and fruit anatomy confirms its isolation (Figs 2, 3.8; Downie *et al.*, 2000a; Spalik & Downie, 2001; Spalik *et al.*, unpublished). This species occurs in China and Siberia, while the centre of diversity of *Scandicinae* lies in Europe and the Mediterranean region.

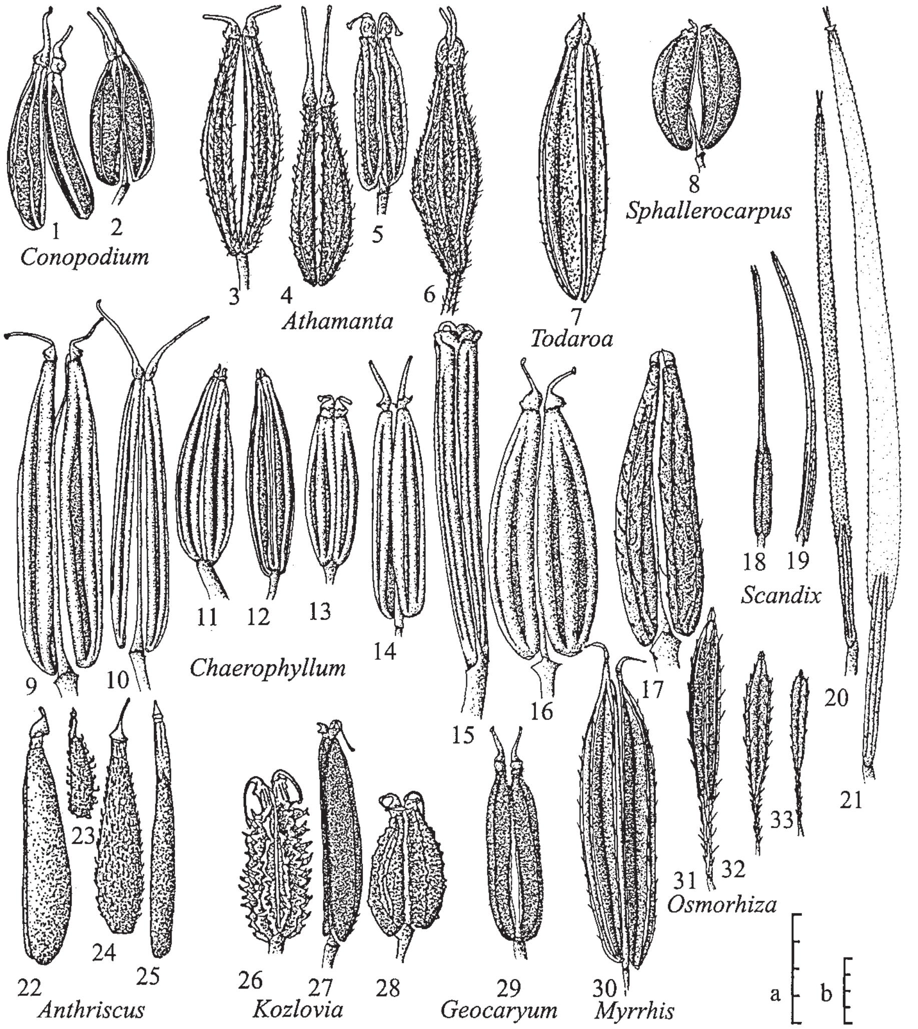

FIG. 3. Fruits of *Scandiceae* subtribe *Scandicinae*: 1, *Conopodium glaberrimum* (*Balansaea glaberrima*); 2, *C. majus*; 3, *Athamanta cretensis*; 4, *A. turbith*; 5, *A. montana* (*Tinguarra montana*); 6, *A. cervariifolia* (*T. cervariifolia*); 7, *Todaroa aurea*; 8, *Sphallerocarpus gracilis*; 9, *Chaerophyllum aromaticum*; 10, *C. hirsutum*; 11, *C. tainturieri*; 12, *C. procumbens*; 13, *C. bulbosum*; 14, *C. astrantiae*; 15, *C. coloratum*; 16, *C. aureum*; 17, *C. nodosum* (*Myrrhoides nodosa*); 18, *Scandix stellata*; 19, *S. australis*; 20, *S. pecten-veneris*; 21, *S. iberica*; 22, *Anthriscus lamprocarpa*; 23, *A. caucalis* var. *caucalis*; 24, *A. sylvestris* subsp. *nemorosa*; 25, *A. cerefolium* var. *cerefolium*; 26, *Kozlovia paleacea*; 27, *K. capnoides* (*Neoconopodium capnoides*); 28, *K. longiloba* (*Krasnovia longiloba*); 29, *Geocaryum macrocarpum*; 30, *Myrrhis odorata*; 31, *Osmorhiza berteroi*; 32, *O. depauperata*, and 33, *O. claytonii*. Scale bars are 4mm: *b* is for *Scandix*, *Myrrhis* and *Osmorhiza*; *a* for remaining taxa. Authorities for all taxon names are given in Table 1. Drawings by A. Wojewódzka.

TABLE 1. Synopsis of *Scandiceae* subtribe *Scandicinae*. For each genus, the source of taxonomic treatment is given in parentheses after the generic name, commonly used synonyms and subspecific taxa are shown in brackets. *, taxa that were confirmed in the subtribe based on phylogenetic analyses of rDNA ITS sequences (Downie *et al.*, 2000a; Spalik *et al.*, unpublished); underlining, types of accepted genera and sections; ?, dubious taxa and uncertain synonymy

Anthriscus Pers. (Spalik, 1997; Spalik & Downie, 2001)

- sect. *Anthriscus*: *A. caucalis M. Bieb., *A. tenerrima* Boiss. & Spruner
- sect. *Cerefolium* (Fabr.) Neilr.: *A. cerefolium (L.) Hoffm.
- sect. *Caroides* Boiss.: *A. kotschyi Boiss. & Balansa, *A. ruprechtii* Boiss.
- sect. *Cacosciadium* (Rchb.) Neilr.: **A. lamprocarpa* Boiss., **A. nitida* (Wahlenb.) Hazsl., **A. schmalhausenii* (Albov) Koso-Pol., A. sylvestris (L.) Hoffm. [*subsp. *sylvestris*, *subsp. *nemorosa* (M. Bieb.) Koso-Pol., *subsp. *fumarioides* (Waldst. & Kit.) Spalik, *subsp. *alpina* (Vill.) Gremli]

Athamanta L. (Tutin, 1968; Knees, 1996; Downie *et al.*, 2000a; and this study). Inc. *Tinguarra* Parl.

- sect. *Athamanta*: *A. cortiana* Ferrarini, *A. cretensis L., *A. densa* Boiss. & Orph., **A. sicula* L., *A. turbith* (L.) Broth. [subsp. *haynaldii* (Borbás & R. Uechtr.) Tutin, subsp. *hungarica* (Borbás) Tutin; inc.: *A. hispanica* Degen & Hervier?, *A. vestina* A. Kern?, *subsp. *turbith*]
- sect. *Tinguarra* (Parl.) Calest.: *A. cervariifolia (DC.) DC. [*Tinguarra cervariifolia* (DC.) Parl.], **A. montana* (Webb ex H. Christ) Spalik, A. Wojew. & S. R. Downie [*Tinguarra montana* (Webb ex H. Christ) A. Hansen & G. Kunkel]

Chaerophyllum L. (Schischkin, 1950; Hedge & Lamond, 1972a, 1987; Czerepanov, 1995; Spalik & Downie, 2001). Inc. *Myrrhoides* Fabr. [*Physocaulis* Tausch (DC.)]

- sect. *Chaerophyllum*: *C. temulum L. [*C. temulentum* L.], **C. procumbens* (L.) Crantz, **C. tainturieri* Hook. & Arn.
- sect. *Physocaulis* DC.: *C. nodosum (L.) Crantz [*Myrrhoides nodosa* (L.) Cannon]
- sect. *Dasypetalon* Neilr.: *C. hirsutum L. [inc. **C. elegans* Gaudin?], **C. magellense* Ten., **C. villarsii* W. D. J. Koch
- sect. *Chrysocarpum* Spalik & S. R. Downie: **C. atlanticum* Coss., **C. aromaticum* L., **C. astrantiae* Boiss. & Balansa, *C. aureum L. [inc. *C. maculatum* Willd. and *C. temuloides* Boiss.], **C. azoricum* Trel., **C. bulbosum* L. [inc. *C. caucasicum* (Fisch.) Schischk., *C. prescottii* DC., and *C. bobrovii* Schischk.], **C. byzantinum* Boiss., **C. crinitum* Boiss., **C. khorassanicum* Czerniak. ex Schischk., **C. libanoticum* Boiss. & Kotschy, **C. macropodum* Boiss., **C. macrospermum* (Spreng.) Fisch. & C. A. Mey. [inc. **C. hakkiaricum* Hedge & Lamond?], **C. meyeri* Boiss. & Buhse, **C. nivale* Hedge & Lamond
- Unclassified[1]: *C. angelicifolium* M. Bieb, *C. borodinii* Albov, *C. coloratum* L., *C. confusum* Woron. ex Grossh., *C. creticum* Boiss. & Heldr., *C. heldreichii* Orph. ex Boiss., *C. humile* Stev. [inc. *C. kiapazi* Woron. ex Schischk.], *C. leucolaenum* Boiss., *C. reflexum* Lindl. [inc. *C. acuminatum* Lindl.], *C. roseum* M. Bieb., *C. rubellum* Albov, *C. villosum* DC.

Conopodium W. D. J. Koch (Silvestre 1972, 1973; Engstrand, 1973; and this study). Inc. *Balansaea* Boiss. & Reut.

- **C. bourgaei* Coss., *C. bunioides* (Boiss.) Calest., **C. glaberrimum* (Desf.) Engstrand [*Balansaea glaberrima* (Desf.) Maire], C. majus (Gouan) Loret [*subsp. *majus*, inc. *C. pyrenaeum* (Loisel.) Miégev.; *subsp. *ramosum* (Costa) S. Silvestre], *C. subcarneum* (Boiss. & Reut.) Boiss. [*C. capillifolium* auct.], *C. thalictrifolium* (Boiss.) Calest.

Geocaryum Coss. (Engstrand, 1977). [*Huetia* Boiss.]

- *G. bornmuelleri* (H. Wolff) Engstrand, G. capillifolium (Guss.) Coss., *G. creticum* (Boiss. & Heldr.) Engstrand [*Huetia cretica* (Boiss. & Heldr.) P. W. Ball], *G. cynapioides* (Guss.) Engstrand [*Huetia cynapioides* (Guss.) P. W. Ball subsp. *cynapioides*], *G. divaricatum*

TABLE 1. (Continued.)

(Boiss. & Orph.) Engstrand ? [*Huetia cynapioides* subsp. *divaricata* (Boiss. & Orph.) P. W. Ball], *G. euboicum* (Rech. f.) Engstrand ?, **G. macrocarpum* (Boiss. & Spruner) Engstrand [*Huetia cynapioides* subsp. *macrocarpa* (Boiss. & Spruner) P. W. Ball], *G. parnassicum* (Boiss. & Heldr.) Engstrand, *G. peloponesiacum* Engstrand, *G. pindicola* (Hausskn.) Engstrand, *G. pumilum* (Sibth. & Sm.) Nyman [*Huetia pumila* (Sibth. & Sm.) Boiss. & Reut.], *G. stylosum* (Boiss.) Engstrand, *G. tuberosum* (W.D.J. Koch) Engstrand

KOZLOVIA Lipsky (Schischkin, 1950; Pimenov & Kljuykov, 1987; Rechinger, 1987; Spalik & Downie, 2001). Inc.: *Krasnovia* Schischk., *Neoconopodium* Pimenov & Kljuykov

**K. longiloba* (Kar. & Kir.) Spalik & S. R. Downie [*Krasnovia longiloba* (Kar. & Kir.) Schischk.], **K. capnoides* (Decne.) Spalik & S. R. Downie [*Neoconopodium capnoides* (Decne.) Pimenov & Kljuykov; *Chaerophyllum capnoides* (Decne.) Benth.], **K. laseroides* (Hedge & Lamond) Spalik & S. R. Downie [*Neoconopodium laseroides* (Hedge & Lamond) Pimenov & Kljuykov; *Chaerophyllum laseroides* Hedge & Lamond], *K. paleacea (Regel & Schm.) Lipsky

MYRRHIS Mill. (Tutin *et al.*, 1968):

*M. odorata (L.) Scop.

OSMORHIZA Raf. (Lowry & Jones, 1984)

**O. aristata* (Thunb.) Rydb., **O. berteroi* DC. (inc. **O. chilensis* Hook. & Arn.), **O. brachypoda* Torr., *O. claytonii (Michx.) C. B. Clarke, **O. depauperata* Phil., *O. glabrata* Phil., **O. longistylis* (Torr.) DC., *O. mexicana* Griseb. [*subsp. *mexicana*, *subsp. *bipatriata* (Constance & Shan) Lowry & A. G. Jones], **O. purpurea* (J. M. Coult. & Rose) Suksd., **O. occidentalis* (Nutt.) Torr.

SCANDIX L. (Tutin *et al.*, 1968; Hedge & Lamond, 1972b)

S. aucheri Boiss., *S. australis* L. [subsp. *australis*, subsp. *brevirostris* (Boiss. & Reut.) Thell., subsp. *grandiflora* (L.) Thell., subsp. *microcarpa* (Lange) Thell.], **S. balansae* Reut. ex Boiss, **S. iberica* M. Bieb., S. pecten-veneris L. [*subsp. *pecten-veneris*, subsp. *brachycarpa* (Guss.) Thell., subsp. *macrorhyncha* (C. A. Mey.) Rouy & E. G. Camus], **S. stellata* Banks & Sol., *S. turgida* (Boiss. & Balansa) Boiss.

SPHALLEROCARPUS DC. (Schischkin, 1950)

*S. gracilis (Bess. ex Trevir.) Koso-Pol.

TODAROA Parl. (Heywood, 1973)

*T. aurea (Sol.) Parl.

[1] Those species of *Chaerophyllum* listed as unclassified were not available for molecular studies and therefore their sectional position is uncertain.

Chaerophyllum, comprising some 30 species (Table 1), is the largest and most diverse genus in the subtribe. Its monophyly is supported by phylogenetic analyses of ITS sequences (Downie *et al.*, 2000a) and, in some trees, by morphological data (Spalik & Downie, 2001). However, in some other trees inferred from general morphology (Spalik & Downie, 2001) or fruit morphology and anatomy (Spalik *et al.*, unpublished) the genus is not maintained as monophyletic. Here, the monotypic *Myrrhoides* allies variously within *Chaerophyllum*, and in the combined analysis presented herein (Fig. 2), it arises as sister to *Chaerophyllum*. *Myrrhoides nodosa* (L.) Cannon was described by Linnaeus (1753) in *Scandix* and transferred to

Chaerophyllum by Crantz (1767). De Candolle (1829) placed it in the monotypic section *Physocaulis* DC. and since 1834 it has been usually recognized as a separate genus (Tausch, 1834), although later the generic name *Physocaulis* (DC.) Tausch was replaced by the overlooked *Myrrhoides* (Dandy & Cannon, 1968). Spalik & Downie (2001) transferred this species back to *Chaerophyllum*. Due to the overall similarity among its constituent species *Chaerophyllum* is easy to distinguish from related genera (Figs 3.9–3.17). Its members are characterized by oblong, straw-yellow to brown fruits with a thin cuticle, vittae single in valleculae and extant at fruit maturity, and much enlarged vascular bundles. None of these characters, however, is unique to the genus. With over 30 members in *Chaerophyllum* it is desirable to divide it into smaller units, possibly at the infrageneric level. The results of our previous molecular analyses do not confirm any of its segregate genera (Koso-Poljansky, 1916) or infrageneric classifications (Koso-Poljansky, 1923; Schischkin, 1950), but instead reveal four distinct lineages (Downie *et al.*, 2000a). These groups, however, are not sufficiently distinct morphologically to justify their recognition at the generic rank (Spalik & Downie, 2001). Moreover, the eventual division of *Chaerophyllum* into smaller genera would result in the renaming of almost all species as the generic name would remain only with a group of three species. These four lineages are formally recognized as sections *Chaerophyllum*, *Physocaulis*, *Dasypetalon* Neilr. and *Chrysocarpum* Spalik & S. R. Downie (Spalik & Downie, 2001; Table 1).

Five lineages (*Anthriscus*, *Geocaryum*, *Kozlovia*, *Myrrhis* and *Osmorhiza*) form a 'crown' clade that is supported by a 100% bootstrap value and is well defined morphologically by the shared presence of fruit with angular primary ribs and a shining aculeate and areolate epidermis (Spalik & Downie, 2001). Some of these characters are also shared by its sister genus *Scandix*, in particular *S. stellata* Banks & Sol. The members of the genus *Scandix* are characterized by fruits with a very long beak (Figs 3.18–3.21), a unique feature among umbellifers. All species are annuals and have similar habit. Their affinity is strongly supported by all sets of data (Downie *et al.*, 2000a; Spalik & Downie, 2001; Spalik *et al.*, unpublished), although their fruit anatomy, particularly the size of the vascular bundles, is much diversified.

Apart from *Osmorhiza*, the lineages forming the 'crown' clade are not supported by high bootstrap values. They are, however, well delimited on the basis of habit and fruit characters.

A pedicel-like fruit appendage is unique for *Osmorhiza* (Figs 3.31–3.33). Its absence in *O. occidentalis* (Nutt.) Torr. (not considered herein) is a reversion when this character is mapped on a tree inferred from ITS data (Spalik & Downie, 2001). Subgenera and sections recognized in *Osmorhiza* by Lowry & Jones (1984) are not supported by analyses of ITS data (Downie *et al.*, 2000a) and of combined morphology and ITS data (Spalik & Downie, 2001). The species of *Osmorhiza* are generally similar to one another and their fruit anatomy is nearly identical. The fruit is pentangular in transverse section, the vascular bundles are small, and the vittae are invisible at fruit maturity. This last feature distinguishes this genus from *Geocaryum*, which also has pentangular fruits but here the vittae are extant at fruit maturity (Spalik *et al.*, unpublished). *Osmorhiza* was once regarded as related to *Myrrhis* (Lowry & Jones, 1984) and such an affinity was also inferred on the basis of combined analysis of ITS and morphological data (Spalik & Downie, 2001). Both genera have a mesic habit and distinctly bristled fruits. However, separate analysis of ITS data suggested that *Myrrhis* is related to *Geocaryum* (Downie *et al.*, 2000a) while in the trees inferred herein from combined data (Fig. 2) it takes an isolated position. It is also morphologically distinct from the other members of the crown clade, advocating its status as a monotypic genus (Spalik & Downie, 2001). *Myrrhis* is readily identified due to its mericarps (Fig. 3.30) which are star-shaped in transverse section.

Geocaryum is a taxonomically difficult genus (Fig. 3.29). Ball (1968) recognized only three species in Europe, while Engstrand (1977) has shown that the most common species, *G. cynapioides* (Guss.) Engstrand (= *Huetia cynapioides* (Guss.) P. W. Ball.), represents two groups of taxa with different chromosome numbers, each comprising reproductively isolated populations. Effectively, he raised the number of species to 13 (with two doubtful species; Table 1). These species are, however, difficult to distinguish one from another. All species share a geophytic habit with globose tubers. Such tubers are also characteristic for members of the *Kozlovia* group and a close relationship between these two groups is inferred from the analysis of morphology as well as the analysis of combined morphological and ITS data (Spalik & Downie, 2001). Their fruit anatomy, however, differs (Spalik *et al.*, unpublished). Mericarps of *Geocaryum* are glabrous, distinctly pentangular, and have vittae persistent at fruit maturity, whereas those of the *Kozlovia* group are bristled or tuberculate, usually rounded at their centre and pentangular at the top, and with compressed vittae.

At quick glance, members of the *Kozlovia* group have fruits that appear dissimilar due to their differing fruit appendages (Fig. 3.26–3.28). Fruits of *Kozlovia paleacea* (Regel & Schm.) Lipsky have bristled ridges, those of *Krasnovia* are tuberculate, while *Neoconopodium* is characterized by smooth fruits with occasional, delicate bristles along its ridges. The bristles of the latter resemble more closely those occurring in *Myrrhis* and *Osmorhiza* rather than those of *Kozlovia*. However, these differences are superficial. In the analyses of data from fruit morphology and anatomy, the taxa comprising the *Kozlovia* group form a well-supported clade (Spalik *et al.*, unpublished). Fruits in this group are usually round in transverse section, and while they show some similarly to those of *Anthriscus* (Spalik, 1996, 1997) they differ in having distinct ridges and styles that are bent at their base at fruit maturity. All four species of the *Kozlovia* group are geophytes and occur in Central Asia. Given these similarities and the results of the ITS analyses, Spalik & Downie (2001) treated these species as the single genus *Kozlovia* (Table 1).

The species constituting the genus *Anthriscus* (Fig 3.22–3.25), despite considerable variation in life history and ecology, are relatively similar to each other and are easy to distinguish from other members of the crown clade due to their distinct fruit morphology and anatomy (Spalik *et al.*, unpublished). Their fruits are round in transverse section, with the ridges apparent only on the beak. They are also characterized by narrowly elliptical commissural bundles that are much bigger than the dorsal circular bundles, with the former situated very close to the carpophore.

Conclusions

Based on phylogenetic analyses of separate and combined ITS sequences, general morphology, and fruit morphology and anatomy, the number of genera in *Scandiceae* subtribe *Scandicinae* may be reduced from 16 to 11. All of these genera are now well delimited on the basis of fruit morphology and anatomy, which greatly facilitates species identification. By extrapolating the results we have obtained for *Scandicinae*, our studies suggest that the large number of small genera recognized in the family *Apiaceae* likely reflect taxonomic practice rather than phylogeny. We hope that the growing evidence from DNA sequences, morphology, anatomy, and phytogeography will bring about not only a new suprageneric classification system for the family but also a reduction in the number of genera, resulting in a more user-friendly classification of this important family of flowering plants.

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