THE UTILITY OF MORPHOLOGICAL CHARACTERS FOR INFERRING PHYLOGENY IN SCANDICEAE SUBTRIBE SCANDICINAE (APIACEAE)[1]

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ABSTRACT

The utility of 44 morphological characters for phylogenetic inference was evaluated against cladograms inferred from nuclear ribosomal DNA internal transcribed spacer (ITS) sequences for 89 representatives of Apiaceae including 58 accessions of Scandiceae subtribe Scandicinae. Distance-based analyses of morphological data confirmed the monophyly of many clades delimited previously on the basis of ITS sequences. However, morphology failed to support the monophyly of Scandicinae and the close affinity between the basally branching *Conopodium* and *Athamanta* groups. The infrageneric divisions in *Anthriscus, Chaerophyllum,* and *Osmorhiza,* traditionally defined on the basis of life history, leaf division, indumentum, and inflorescence architecture, are incongruent with the molecular results as these morphological characters are quite homoplastic. Least homoplastic, and therefore useful for generic delimitation within Scandicinae, are fruit characters such as epidermis morphology and primary ridge shape. *Rhopalosciadium* and *Chaerophyllopsis,* traditionally placed in Scandicinae but not included in the ITS study, do not occur within the subtribe upon analysis of morphological data. The former has affinity to Scandiceae subtribe Torilidinae, whereas the latter allies with the apioid superclade. The following taxonomic changes are suggested: (1) *Krasnovia* and *Neoconopodium* are included in *Kozlovia*; (2) section *Cerefolium* is restored in *Anthriscus* for *A. cerefolium*; and (3) *Myrrhoides* is transferred back to *Chaerophyllum,* with four sections recognized within the latter.

Key words: Apiaceae, morphology, phylogeny, Scandiceae, Scandicinae, taxonomy, Umbelliferae.

The compound umbel is a trademark of subfamily Apioideae and is a feature by which the whole family Apiaceae has earned its traditional name Umbelliferae. Together with other morphological features, such as two one-seeded mericarps joined by a bifurcate carpophore and styles emerging from a more or less flattened floral disc or stylopodium, the compound umbel supports the monophyly of the subfamily and delimits it from the other two subfamilies, Saniculoideae and Hydrocotyloideae. Molecular data corroborate these morphological data in revealing that Apioideae are indeed monophyletic and a sister group to subfamily Saniculoideae (Plunkett et al., 1997; Downie et al., 1998).

Although morphology delimits subfamily Apioideae, it has proved unreliable in demarcating monophyletic groups within the subfamily, and all attempts to generate a useful classification system of umbellifers using this type of evidence have failed (Constance, 1971; Pimenov & Leonov, 1993). The systems of Apiaceae classification, including the most influential system of Drude (1898), are usually based on fruit characters, particularly its shape and compression, the characteristics of ribs, secretory canals, and indumentum, endocarp sclerification, shape of endosperm, and the distribution of calcium oxalate crystals (Koch, 1824; de Candolle, 1830; Tausch, 1834; Bentham, 1867; Drude, 1898; Calestani, 1905; Koso-Poljansky, 1916). The only exception is the classification of Cerceau-Larrival (1962), who underlined the importance of pol len morphology and vegetative features, especially the internal contour of the endexine and shape of the cotyledons. However, characters of the fruit and those used more recently for stomata, pollen, cot yledons, and secondary metabolites (Cerceau-Larrival, 1962, 1963, 1965, 1971; Guyot, 1971; Guy-

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Table 1. Genera included in Scandiceae subtribe Scandicinae based on phylogenetic analysis of nuclear rDNA ITS sequences (Downie et al., 2000a).

Genus	No. of species	Distribution (center)
Anthriscus Pers.	9[a,c]	Eurasia/Africa (NE Mediterranean/Caucasus)
Athamanta L.	5[b]	Europe/N Africa (Italy and Balkans)
Balansaea Boiss. & Reut.	1	SW Mediterranean
Chaerophyllum L.	34[c]	Eurasia/N Africa/N America (Mediterranean/Caucasus)
Conopodium W. D. J. Koch	5[d]	Europe/N Africa (W Mediterranean)
Geocaryum Coss.	3[e]–15[f]	NE Mediterranean (Balkans)
Kozlovia Lipsky	1	Irano-Turanian
Krasnovia Popov ex Schischk.	1	Central Asia
Myrrhis Mill.	1	Central Europe
Myrrhoides Fabr.	1	SE Europe/W Asia
Neoconopodium Pimenov & Kljuykov	2[g]	Irano-Turanian/Himalaya
Osmorhiza Raf.	10[c,h]	Asia/America (N America)
Scandix L.	5–20[i]	Eurasia/Africa (E Mediterranean)
Sphallerocarpus DC.	1	East Asia
Tinguarra Parl.	2[j]	Canaries
Todaroa Parl.[k]	1	Canaries

[a] Spalik (1997). [b] Based on Tutin (1968), but excluding *A. macedonica* and *A. della-cellae*. [c] Table 2. [d] Silvestre (1973). [e] Ball (1968). [f] Engstrand (1977). [g] Pimenov & Kljuykov (1987). [h] Lowry & Jones (1984). [i] Pimenov & Leonov (1993). [j] *T. cervariifolia* and *T. montana*, excluding *T. sicula* transferred back to *Athamanta*. [k] Included based on Downie et al. (2000c).

ot et al., 1980; Harborne, 1971; Nielsen, 1971; Crowden et al., 1969; Harborne et al., 1969; Harborne & Williams, 1972) are homoplastic when optimized onto phylogenies inferred from molecular data (Plunkett et al., 1996; Katz-Downie et al., 1999).

Contrary to those relationships implicit in traditional classifications based on morphology, evolutionary relationships among umbellifers estimated on the basis of various types of molecular markers are generally congruent. Several major lineages have been identified, seven of which have been formally recognized as tribes (Downie et al., 2000b). One tribe, Scandiceae Spreng., is further divided into three subtribes: Scandicinae Tausch, Daucinae Dumort., and Torilidinae Dumort. (Downie et al., 2000a). Although most of these lineages bear traditional tribal or subtribal names, only Echinophoreae and Scandicinae are equivalent to those taxa that have been long recognized under these names (Downie et al., 2000a, c). Moreover, it is difficult to find morphological synapomorphies defining these newly identified lineages (Downie et al., 2000b). It seems therefore that the task of reclassifying umbellifers, at least at higher taxonomic levels, may be accomplished based on molecular rather than on traditional taxonomic data. The latter are, however, crucial for the circumscription and identification of taxa. Evaluating the utility of morphological markers for phylogenetic inference at different taxonomic levels is therefore of great importance.

Subtribe Scandicinae encompasses 16 genera with up to 110 species, with 7 of these genera monotypic (Table 1). Members of Scandicinae are diversified with respect to habit, reproductive strategy, and life history, which makes them a model group to study evolutionary tendencies. Most taxa are perennial polycarpic hemicryptophytes; *Conopodium, Kozlovia, Krasnovia, Neoconopodium,* and *Geocaryum* are geophytes; and *Scandix, Myrrhoides,* and some species of *Anthriscus* and *Chaerophyllum* are annual therophytes ("true" annuals) or hemicryptophytes (winter annuals). The most ecologically diversified genera are *Anthriscus* and *Chaerophyllum,* whose members occur in both primary (montane forests, meadows, and screes) and secondary (ruderal) communities. Members of *Anthriscus, Chaerophyllum,* and *Osmorhiza,* although each united by a similar fruit morphology and anatomy, differ in habit and, as such, infrageneric taxa for each have been recognized (Table 2). Molecular analyses have confirmed that each of these genera is monophyletic but do not support their infrageneric divisions (Downie et al., 2000a). This suggests that, despite criticism, fruit morphology may be a source of taxonomically valuable characters whereas plant habit may not.

In this study, we evaluate the utility of morphological characters in delimiting monophyletic

Table 2. Infrageneric classification of *Anthriscus*, *Chaerophyllum*, and *Osmorhiza* tested in this study using molecular and morphological data. For brevity, taxonomic authorities are omitted if they are provided in Table 3. The source of taxonomic treatment is given in parentheses after each generic name. The treatment of *Chaerophyllum* is taken from Schischkin (1950b) with later changes. Series names enclosed in quotation marks are not validly published. Likewise, infrageneric assignments of Koso-Poljansky (1916) are problematic, lacking designated types.

Anthriscus Pers. (Spalik, 1997)
- section ***Anthriscus***
  - *A. caucalis, A. cerefolium, A tenerrima* Boiss. & Spruner
- section ***Caroides*** Boiss.
  - *A. kotschyi, A. ruprechtii* Boiss.
- section ***Cacosciadium*** (Rchb.) Neilr.
  - *A. lamprocarpa, A. nitida, A. schmalhausenii, A. sylvestris* [subsp. *sylvestris*, subsp. *nemorosa*, subsp. *fumarioides*, subsp. *alpina* (Vill.) Gremli]

Chaerophyllum L. (Schischkin, 1950b; Hedge & Lamond, 1972a, 1987; Czerepanov, 1995)
- Subgenus ***Chaerophyllum***
  - series ***Aromatica*** Koso-Pol.
    - *C. aromaticum, C. aureum*
  - series ***Hirsuta*** Koso-Pol.
    - *C. hirsutum*
  - *series* ***Humilia*** Koso-Pol.
    - *C. humile* Stev.
  - "series ***Rosea*** Schischk."
    - *C. roseum* M. Bieb., *C. rubellum* Albov
  - "series ***Involucrata*** Schischk."
    - *C. astrantiae, C. borodinii*[a] Albov, *C. khorassanicum*
  - "series ***Temula*** Schischk."
    - *C. temulum*
- Subgenus ***Golenkinianthe*** (Koso-Pol.) Schischk.
  - *C. macrospermum*
- Subgenus ***Buniomorpha*** Koso-Pol.
  - series ***Angelicifolia*** Koso-Pol.
    - *C. angelicifolium*[a] M. Bieb., *C. confusum* Woron. ex Grossh., *C. meyeri*
  - series ***Crinita*** Koso-Pol.
    - *C. crinitum*
  - series ***Bulbosa*** Koso-Pol.
    - *C. bulbosum*
- Species not considered by Schischkin (1950b):
  - *C. atlanticum, C. azoricum, C. byzantinum, C. coloratum* L., *C. creticum* Boiss. & Heldr., *C. elegans, C. hakkiaricum* Hedge & Lamond, *C. heldreichii* Orph. ex Boiss., *C. leucolaenum* Boiss., *C. libanoticum, C. macropodum, C. magellense, C. nivale* Hedge & Lamond, *C. procumbens, C. reflexum* Lindl., *C. tainturieri, C. villarsii, C. villosum* DC.

Osmorhiza Raf. (Lowry & Jones, 1984)
- Subgenus ***Osmorhiza***
  - section ***Osmorhiza***
    - *O. aristata, O. claytonii, O. longistylis*
  - section ***Mexicanae*** Constance & Shan ex Lowry & A. G. Jones
    - *O. mexicana* [subsp. *mexicana*, subsp. *bipatriata*], *O. brachypoda, O. glabrata* Phil.
  - section ***Nudae*** Constance & Shan ex Lowry & A. G. Jones
    - *O. berteroi, O. depauperata, O. purpurea*
- Subgenus ***Glycosma*** (Nutt.) Drude
  - *O. occidentalis*

[a] Original spellings *angelicaefolium* and *borodini* are contrary to Art. 60.8 and Art. 60.11 of the Botanical Code (Greuter et al., 2000), respectively.

groups within Scandiceae subtribe Scandicinae in light of the results of our recent molecular systematic study of the group using nuclear ribosomal DNA ITS sequences (Downie et al., 2000a). We are particularly interested in identifying those morphological characters that are most useful in delimiting genera and infrageneric taxa. Similarly, we seek to provide a new circumscription of the subtribe based on morphology which would permit identification of members of this clade. We also confirm the position of two monotypic genera previously placed in Scandicinae, *Rhopalosciadium* Rech. f. and *Chaerophyllopsis* H. Boissieu, that were not available for our earlier ITS study due to a lack of sufficient material.

Materials and Methods

Taxon Sampling

The taxa examined were chosen to achieve nearly complete overlap between morphological and ITS data matrices. In total, 91 taxa were analyzed, with 89 taxa included in both matrices. The ingroup, or subtribe Scandicinae, was represented by 58 accessions belonging to 15 genera. The monotypic *Todaroa* was not included as its affinity to Scandicinae has only recently been confirmed (Downie et al., 2000c). *Anthriscus*, *Chaerophyllum*, and *Osmorhiza* were broadly sampled in order to verify their infrageneric divisions. Subtribes Daucinae and Torilidinae, forming close outgroups, were represented by six and three species, respectively. Additional outgroups represented other major lineages of umbellifers or encompassed taxa that had been previously excluded from Scandicinae based on molecular data, i.e., *Grammosciadium*, *Rhabdosciadium*, and *Bubon*. The genus *Bubon*, formerly recognized in *Athamanta*, was recently reinstated (Downie et al., 2000a). Two species included in the morphological analysis, *Rhopalosciadium stereocalyx* Rech. f. and *Chaerophyllopsis huaui* H. Boissieu, were not sampled in our ITS study (Downie et al., 2000a). The first species is known only from the type gathering, and we have not found any good quality material of the second one.

MOLECULAR DATA

We considered 89 of the 134 accessions from our prior study (Downie et al., 2000a; Table 3), with no additional sequencing of the ITS region undertaken as part of this study. Initially, ITS1 and ITS2 sequences were aligned using the program CLUSTAL V (Higgins et al., 1992) and manually adjusted where necessary. The sequences of the intervening 5.8S subunit were not included as they were incomplete for several taxa and those that were available were not variable enough to justify their inclusion or additional sequencing. GenBank accession numbers of separate ITS1 and ITS2 sequences are provided in Table 3. The aligned matrix is available upon request from either author.

MORPHOLOGICAL DATA

Herbarium material was obtained from the following institutions: B, BC, BM, E, ILL, KRA, KRAM, L, MO, P, W, WA (abbreviations according to Holmgren et al., 1990). Specimen identifications were verified using several keys, the most important being *Flora Europaea* (Tutin et al., 1968), *Flora of Turkey* (Davis, 1972), *Flora Iranica* (Hedge et al., 1987), and *Flora of the USSR* (Schischkin, 1950a). For *Geocaryum, Osmorhiza,* and *Anthriscus,* their respective revisions were used (Engstrand, 1977; Lowry & Jones, 1984; Spalik, 1997).

The morphological matrix comprised 44 discrete characters, including 24 binary, 9 multistate and unordered, and 11 ordinal (Appendices 1 and 2). As ordinal we declared only those characters that can be unambiguously ordered (i.e., those that either coded measurements or, for three-state characters, those in which one state was apparently intermediate between the other two). Chosen characters represented life history and vegetative morphology (1–6), bract and bracteole morphology (7–13), inflorescence architecture (14–20), floral morphology (21–26), and fruit morphology (27–44). Character polymorphisms and uncertainties were distinguished using the "()" versus "{}" coding options available in PAUP* 4.0 (Swofford, 1998).

PHYLOGENETIC ANALYSES

For maximum parsimony analysis of ITS sequences, gaps were treated as missing data and character states were assumed unordered. Heuristic searches, implemented using PAUP* 4.0, employed tree bisection-reconnection (TBR) branch swapping with options MULPARS and STEEPEST DESCENT selected. To locate possible islands of most parsimonious trees, 100 heuristic searches were initiated, saving only five shortest trees from each search. These trees were then used as starting trees for TBR branch swapping. The search was stopped when the number of trees reached the memory limit of 16,000. The strict consensus tree was used as a topological constraint in a subsequent search using the inverse constraint method of Catalán et al. (1997). This time, 1000 heuristic searches were initiated saving only those trees that did not fit the constraint tree (no more than two trees per replicate were saved). Because all trees found were longer than those most parsimonious, this then suggested that the strict consensus tree summarizes all possible topologies of trees at that length, even though their exact number is not known.

Distance trees were obtained from neighbor-joining analyses using PAUP* 4.0, estimated using Kimura's (1980) two- and three-parameter, Jukes-Cantor, and maximum likelihood distance measures. Heuristic searches using the criterion of minimum evolution were also carried out using neighbor-joining trees and a variety of distance measures. Bootstrap analyses were performed using 100 resampled data sets, with 50 best trees per replicate saved.

Morphological data were analyzed using both maximum parsimony and distance methods available in PAUP* 4.0. For the maximum parsimony analysis, TBR branch swapping, with MULPARS and STEEPEST DESCENT, was employed. One hundred heuristic searches were initiated, saving only five shortest trees from each search. These trees were used as starting trees for TBR branch swapping. The search was terminated when the number of trees reached the memory limit of 16,000. Distance trees were constructed using neighbor-joining and minimum evolution methods using mean and total character differences.

In the analysis of the combined ITS and morphological data set, we included morphological data for *Rhopalosciadium stereocalyx* and *Chaerophyllopsis huaui.* Because these species were not included in our prior study (Downie et al., 2000a), ITS data were not available and therefore these characters were scored as missing. For parsimony analysis, the search strategy was the same as for the separate analysis of ITS data. Distance methods comprised neighbor-joining and minimum evolution with mean and total character differences selected.

EVOLUTION OF MORPHOLOGICAL CHARACTERS

To evaluate the utility of morphological characters in delimiting monophyletic groups and to assess the degree of homoplasy in these characters,

Table 3. Accessions of Apiaceae examined for nuclear rDNA ITS sequence variation. Material of uncertain wild origin obtained from botanical gardens is denoted as cultivated. Collection data, locations of voucher specimens, and details on the DNA sequencing are provided elsewhere: (1) Downie and Katz-Downie (1996); (2) Downie et al. (1998); (3) Downie et al. (2000a).

Taxon	Origin	Reference	GenBank accession no.	
			ITS1	ITS2
Anthriscus caucalis M. Bieb.	France (cult.)	2	U79601	U79602
Anthriscus cerefolium (L.) Hoffm.	Spain (cult.)	1	U30532	U30533
Anthriscus kotschyi Boiss. & Balansa	Turkey	3	AF073579	AF073580
Anthriscus lamprocarpa Boiss.	Jordan	3	AF073581	AF073582
Anthriscus nitida (Wahlenb.) Hazsl.	France	3	AF073595	AF073596
Anthriscus schmalhausenii (Albov) Koso-Pol.	Russia	3	AF073587	AF073588
Anthriscus sylvestris (L.) Hoffm. subsp. *sylvestris*	Russia (cult.)	2	U79603	U79604
Anthriscus sylvestris subsp. *fumarioides* (Waldst. & Kit.) Spalik	Yugoslavia [now Serbia]	3	AF073575	AF073576
Anthriscus sylvestris subsp. *nemorosa* (M. Bieb.) Koso-Pol.	Turkey	3	AF073573	AF073574
Apium graveolens L.	France (cult.)	1	U30552	U30553
Athamanta cretensis L.	France	3	AF073685	AF073686
Athamanta della-cellae Asch. & Barbey ex E. A. Durand & Barratte	Libya	3	AF073565	AF073566
Athamanta sicula L.	Morocco	3	AF073683	AF073684
Athamanta turbith (L.) Broth. subsp. *turbith*	Slovenia	3	AF073687	AF073688
Balansaea glaberrima (Desf.) Maire	Algeria	3	AF073689	AF073690
Bubon macedonicum L. subsp. *macedonicum*	Greece	3	AF073541	AF073542
Bunium elegans (Fenzl) Freyn	Iran	3	AF073543	AF073544
Carum carvi L.	Finland (cult.)	2	U78377	U78437
Caucalis platycarpos L.	Germany (cult.)	2	U78364	U78424
Chaerophyllum aromaticum L.	Poland	3	AF073631	AF073632
Chaerophyllum astrantiae Boiss. & Balansa	Turkey	3	AF073653	AF073654
Chaerophyllum atlanticum Coss.	Morocco	3	AF073633	AF073634
Chaerophyllum aureum L.	Turkey	3	AF073655	AF073656
Chaerophyllum azoricum Trel.	Spain	3	AF073657	AF073658
Chaerophyllum bulbosum L.	Turkey	3	AF073659	AF073660
Chaerophyllum byzantinum Boiss.	Turkey	3	AF073635	AF073636
Chaerophyllum crinitum Boiss.	Iran	3	AF073661	AF073662
Chaerophyllum elegans Gaudin	Switzerland	3	AF073663	AF073664
Chaerophyllum hirsutum L.	France	3	AF073665	AF073666
Chaerophyllum khorassanicum Czerniak. ex Schischk.	Turkmenistan	2	U78366	U78426
Chaerophyllum libanoticum Boiss. & Kotschy	Turkey	3	AF073637	AF073638
Chaerophyllum macropodum Boiss.	Iran	3	AF073671	AF073672
Chaerophyllum macrospermum (Willd. ex Spreng.) Fisch. & C. A. Mey.	Turkey	3	AF073651	AF073652

Table 3. Continued.

Taxon	Origin	Reference	GenBank accession no.	
			ITS1	ITS2
Chaerophyllum magellense Ten.	Italy	3	AF073669	AF073670
Chaerophyllum meyeri Boiss. & Buhse	Iran	3	AF073639	AF073640
Chaerophyllum procumbens (L.) Crantz	U.S.A., Indiana	3	AF073643	AF073644
Chaerophyllum tainturieri Hook. & Arn.	U.S.A., Arkansas	3	AF073645	AF073646
Chaerophyllum temulum L.	Poland	3	AF073641	AF073642
Chaerophyllum villarsii W. D. J. Koch	Switzerland	3	AF073667	AF073668
Chaetosciadium trichospermum (L.) Boiss.	Jordan	2	U78363	U78423
Cicuta virosa L.	Finland (cult.)	2	U78372	U78432
Conopodium ramosum Costa	Portugal	3	AF073693	AF073694
Daucus carota L.	Germany (cult.)	1	U27589	U30315
Echinophora tenuifolia L. subsp. *sibthorpiana* (Guss.) Tutin	Turkey	3	AF073529	AF073530
Elaeosticta allioides (Regel & Schmalh.) Kljuykov, Pimenov & V. N. Tikhom.	Turkmenistan	3	AF073547	AF073548
Falcaria vulgaris Bernh.	Russia, Rostov prov.	2	U78378	U78438
Geocaryum macrocarpum (Boiss. & Spruner) Engstrand	Greece	3	AF073607	AF073608
Grammosciadium daucoides DC.	Turkey	3	AF073559	AF073560
Grammosciadium macrodon Boiss.	Turkey	3	AF073553	AF073554
Grammosciadium platycarpum Boiss. & Hausskn.	Turkey	3	AF073551	AF073552
Grammosciadium pterocarpum Boiss.	Turkey	3	AF073557	AF073558
Heracleum sphondylium L.	Finland (cult.)	1	U30544	U30545
Heteromorpha arborescens (Spreng.) Cham. & Schltdl.	Africa (cult. Spain)	1	U27578	U30314
Kozlovia paleacea (Regel & Schm.) Lipsky	Afghanistan	3	AF073597	AF073598
Krasnovia longiloba (Kar. & Kir.) Popov ex Schischk.	Kazakhstan	3	AF073599	AF073600
Laserpitium hispidium M. Bieb.	Russia, Krasnodar prov.	2	U78361	U78421
Laserpitium petrophilum Boiss. & Heldr.	Turkey	3	AF073567	AF073568
Lecokia cretica (Lam.) DC.	Jordan	2	U78358	U78418
Myrrhis odorata (L.) Scop.	Europe (cult. U.S.A.)	1	U30530	U30531
Myrrhoides nodosa (L.) Cannon	Armenia	3	AF073675	AF073676
Neoconopodium capnoides (Decne.) Pimenov & Kljuykov	Himalaya	3	AF073601	AF073602
Neoconopodium laseroides (Hedge & Lamond) Pimenov & Kljuykov	Afghanistan	3	AF073603	AF073604
Orlaya grandiflora (L.) Hoffm.	France (cult.)	1	U30524	U30525

Table 3. Continued.

Taxon	Origin	Reference	GenBank accession no.	
			ITS1	ITS2
Osmorhiza aristata (Thunb.) Rydb.	Japan	3	AF073609	AF073610
Osmorhiza berteroi DC.	U.S.A., California	2	U78365	U78425
Osmorhiza brachypoda Torr.	U.S.A., California	3	AF073617	AF073618
Osmorhiza claytonii (Michx.) C. B. Clarke	U.S.A., Indiana	3	AF073615	AF073616
Osmorhiza depauperata Phil.	U.S.A., Montana	3	AF073611	AF073612
Osmorhiza longistylis (Torr.) DC.	U.S.A., Illinois	2	U79617	U79618
Osmorhiza mexicana subsp. *bipatriata* (Constance & Shan) Lowry & A. G. Jones	Mexico	3	AF073623	AF073624
Osmorhiza mexicana Griseb. subsp. *mexicana*	Mexico	3	AF073621	AF073622
Osmorhiza occidentalis (Nutt.) Torr.	U.S.A., Wyoming	2	U79619	U79620
Osmorhiza purpurea (J. M. Coult. & Rose) Suksd.	U.S.A., Oregon	3	AF073625	AF073626
Pastinaca sativa L.	Germany (cult.)	1	U30546	U30547
Petroselinum crispum (Mill.) A. W. Hill	Germany (cult.)	2	U78387	U78447
Pimpinella peregrina L.	Germany (cult.)	1	U30592	U30593
Pseudorlaya pumila (L.) Grande	Germany (cult.)	1	U30522	U30523
Rhabdosciadium aucheri Boiss.	Iran	3	AF073549	AF073550
Scaligeria moreana Engstrand	Greece	3	AF073545	AF073546
Scandix balansae Reut. ex Boiss.	Germany (cult.)	2	U79621	U79622
Scandix iberica M. Bieb.	Jordan	3	AF073627	AF073628
Scandix pecten-veneris L.	Germany (cult.)	1	U30538	U30539
Scandix stellata Banks & Sol.	Jordan	3	AF073629	AF073630
Sium latifolium L.	Hungary (cult.)	2	U78370	U78430
Smyrnium olusatrum L.	France (cult.)	1	U30594	U30595
Sphallerocarpus gracilis (Bess. ex Trevir.) Koso-Pol.	Russia, Siberia	3	AF073677	AF073678
Tinguarra cervariifolia (DC.) Parl.	Spain, Canaries	3	AF073681	AF073682
Tinguarra montana (Webb ex H. Christ) A. Hansen & G. Kunkel	Spain, Canaries	3	AF073679	AF073680
Torilis nodosa (L.) Gaertn.	France (cult.)	1	U30534	U30535

Table 4. Sequence characteristics of the two nuclear rDNA internal transcribed spacers, separately and combined, for 89 representatives of Apiaceae subfamily Apioideae including 58 accessions of Scandiceae subtribe Scandicinae.

Sequence characteristic	ITS1	ITS2	ITS1 & ITS2
Nucleotide sites			
Spacer length variation (bp)	206–221	203–229	421–444
No. of total aligned positions	249	243	492
No. (and %) of aligned positions ambiguous	10 (4)	6 (2)	16 (3)
No. (and %) of aligned positions constant	64 (26)	41 (17)	105 (21)
No. (and %) of aligned positions autapomorphic	30 (12)	33 (14)	63 (13)
No. (and %) of aligned positions parsimony informative	145 (58)	163 (67)	308 (63)
Sequence divergence (mean and range in %)			
All accessions	18.4 (0–32.8)	19.4 (0–37.3)	19.0 (0–33.6)
Subtribe Scandicinae only	11.8 (0–22.9)	12.5 (0–23.1)	12.2 (0–22.0)

we optimized them onto all ITS-derived trees (whether maximum parsimony or distance) using MacClade 3.07 (Maddison & Maddison, 1992). The tree that best explained the variation in morphology was used to infer the number of evolutionary steps and consistency (CI), retention (RI), and rescaled consistency (RC) indices of these characters. To identify those characters that are most useful for the definition of formally recognized taxa, and of genera in particular, we considered character state changes on the strict consensus tree resulting from parsimony analysis of the combined data set.

Results

Sequence analysis

Due to the exclusion of some Scandicinae and outgroup taxa, the length of the aligned ITS sequences was shorter and the number of ambiguous sites lower than those values presented in our earlier study (Downie et al., 2000a). In this analysis of 89 taxa, the aligned matrix had 492 characters, representing 249 positions from ITS1 and 243 positions from ITS2. The alignment of 10 positions in ITS1 and 6 positions in ITS2 were ambiguous, so these regions were excluded from the analysis. The numbers of constant, autapomorphic, and parsimony-informative positions were similar for both spacers (Table 4), and the ratio of terminal taxa (89) to informative characters across both spacers (308) was 1:3.5. Mean sequence divergence values were also similar for both spacers (18.4 and 19.4% for ITS1 and ITS2, respectively), reaching a maximum of 33.6% pairwise sequence divergence for combined ITS1 and ITS2 data.

Phylogenetic analysis of ITS data

Maximum parsimony analysis of all 476 unambiguously aligned positions resulted in more than 16,000 minimal length trees, each 1746 steps long, with consistency indices of 0.404 and 0.376 (with and without uninformative characters, respectively), and a retention index of 0.748. Despite the high number of trees, the strict consensus tree is well resolved (Fig. 1). At the suprageneric level, most branches are supported by high bootstrap values. The neighbor-joining tree, calculated using Jukes-Cantor distance (Fig. 2), is similar to the parsimony strict consensus tree with few notable differences (discussed below). Trees of nearly identical topology were obtained using other distance measures (not shown).

All resultant parsimony and distance trees were generally congruent to those obtained using a broader sampling of Scandicinae and outgroup taxa (Downie et al., 2000a); the few differences observed comprise minor rearrangements of some weakly supported clades. All major groups are similar to those obtained previously and include four tribes (Scandiceae, Smyrnieae Spreng., Oenantheae Dumort., and Heteromorpheae M. F. Watson & S. R. Downie) and the "apioid superclade" (Downie et al., 2000b). Scandiceae are supported as monophyletic (with bootstrap values of 93% and 95%, in the neighbor-joining and parsimony analyses, respectively) and include three lineages equivalent to subtribes Scandicinae, Daucinae, and Torilidinae (Figs. 1, 2). Within Scandicinae, several additional clades are distinguished, corresponding to approximate generic and infrageneric categories (these informal groups are identified by double quotes in all tree figures presented herein).

Sister to all other Scandicinae is a clade comprising four genera: *Athamanta, Tinguarra, Conopodium,* and the monotypic *Balansaea* (which was synonymized with *Conopodium* by Engstrand, 1973; Figs. 1, 2). Two species formerly recognized in *Athamanta*—*A. macedonica* and *A. della-cel-*

lae—are excluded from this clade. The former is now treated as *Bubon macedonicum,* whereas the latter shows a close relationship with *Daucus* (Downie et al., 2000a). The monophyly of the clade formed by these four genera is strongly supported (with 100% bootstrap values); however, the phylogenetic relationships among its members are somewhat ambiguous. *Athamanta* and *Tinguarra* are each monophyletic and form a weakly supported clade (denoted as the *Athamanta* group) according to the neighbor-joining analysis (Fig. 2), but this relationship is not supported by maximum parsimony (Fig. 1). The *Conopodium* group (i.e., encompassing representatives of *Conopodium* sensu Engstrand, 1973) is not monophyletic.

Within Scandicinae proper, *Sphallerocarpus* forms an isolated branch and is variously placed in Figures 1 and 2. The *Chaerophyllum* group is well supported and also includes the monotypic *Myrrhoides,* although in some distance and maximum parsimony trees (not shown) *Myrrhoides* is sister to *Chaerophyllum.* Those members examined from *Chaerophyllum* form three subclades, denoted as the *C. aureum, C. hirsutum,* and *C. temulum* groups. These groups do not match the subgenera traditionally recognized in *Chaerophyllum* (Table 2), since the *C. aureum* clade includes representatives of subgenera *Chaerophyllum, Golenkinianthe,* and *Buniomorpha,* whereas members of the *C. hirsutum* and *C. temulum* clades are classified in subgenus *Chaerophyllum.* Of the nine series distinguished within *Chaerophyllum* (Schischkin, 1950b), five are monotypic. Of the remaining four, two series, "*Involucrata*" and "*Aromatica,*" were each represented in our study by two species. These series are not supported by ITS data.

Seven genera of Scandicinae belong to a "crown" clade highly supported in both trees (Figs. 1, 2) that is sister to *Scandix.* The relationships among the members of this terminal clade, however, are ambiguous. *Anthriscus* and *Osmorhiza* are each monophyletic, although bootstrap values supporting the *Anthriscus* clade are less than 50%. The infrageneric classification of *Anthriscus* is only partly supported, as section *Anthriscus,* represented by *A. caucalis* and *A. cerefolium,* is not monophyletic. All included members of section *Cacosciadium* (Rchb.) Neilr. form a clade (Figs. 1, 2). Interestingly, Levantine *A. lamprocarpa,* represented by an accession from Jordan, is grouped with European *A. sylvestris* subsp. *sylvestris,* sampled from Russia, and not with the parapatric *A. sylvestris* subsp. *nemorosa,* represented in this study by an accession from Turkey. *Osmorhiza* includes three lineages, with *O. aristata,* the only Asiatic member of the genus, sister to all other *Osmorhiza* species. The two remaining members of section *Osmorhiza* (*O. claytonii* and *O. longistylis*) form the next branch, denoted as the *O. claytonii* group. The *O. berteroi* group comprises most of the species, including *O. occidentalis,* the sole member of subgenus *Glycosma.* This species, clearly distinct from other members of the genus with respect to its leaf division, flower color, and fruit morphology, is allied with *O. depauperata,* although with moderate bootstrap support (54% and 68%, in distance and parsimony analyses, respectively).

The monotypic *Myrrhis* from Central Europe is sister to East Mediterranean *Geocaryum,* although this relationship is not at all supported by high bootstrap values. The *Kozlovia* group is better supported (54% and 71% bootstrap values for distance and parsimony trees, respectively) and includes four Asiatic taxa: Irano-Turanian *Kozlovia,* Central Asiatic *Krasnovia,* and both species of Himalayan *Neoconopodium.*

PHYLOGENETIC ANALYSIS OF MORPHOLOGICAL DATA

Parsimony analysis of morphological data resulted in 9516 trees, each of length 427 steps, and consistency and retention indices of 0.183 and 0.699, respectively. Resolution of its consensus tree (not shown) is poor. *Anthriscus, Chaerophyllum, Geocaryum, Osmorhiza, Myrrhis, Myrrhoides, Scandix,* and the *Kozlovia* group formed a single polytomous clade, with only *Scandix* retained as monophyletic. Neighbor-joining trees (not shown) showed a similar pattern in which the same genera were grouped together, but the monophyly of some was not maintained. The tree obtained using total character differences and minimum evolution (Fig. 3) was most congruent with those trees inferred from ITS sequences. However, in this minimum evolution tree, neither Scandiceae nor any of its three subtribes are retained as monophyletic. The majority of Scandicinae form a clade that is sister to a group comprising representatives of Daucinae and Torilidinae (the latter nested within the former), the *Athamanta* group, the former members of *Athamanta* (*Bubon macedonicum* and *A. della-cellae*), and *Echinophora tenuifolia.* In the ITS analyses, *Bubon macedonicum* and *Echinophora tenuifolia* are placed in the apioid superclade (Figs. 1, 2).

Three genera of Scandiceae subtribe Scandicinae (*Sphallerocarpus, Conopodium,* and *Balansaea*), as circumscribed on the basis of molecular data, fall outside of the tribe when only morphology is considered. *Sphallerocarpus* is placed close to *Smyr-*

nium, the latter a representative of tribe Smyrnieae that in the distance analyses of ITS data is sister to Scandiceae. *Conopodium* and *Balansaea* form a separate clade with no near relatives. The close relationship between the *Athamanta* and *Conopodium* groups, as indicated by the molecular analyses, is not at all apparent.

Two species traditionally placed in Scandicinae that were not included in our earlier molecular analyses (Downie et al., 2000a), *Rhopalosciadium stereocalyx* and *Chaerophyllopsis huaui,* are also placed outside of the subtribe. The first is sister to the clade of *Torilis, Chaetosciadium,* and *Pseudorlaya,* all members of Scandiceae subtribes Torilidinae and Daucinae (Fig. 3), whereas the second is sister to *Petroselinum,* with this clade placed within the apioid superclade.

Phylogenetic analysis of morphological data (Fig. 3) shows that all genera of Scandicinae are monophyletic. However, many of the subclades identified within *Anthriscus, Chaerophyllum,* and *Osmorhiza* on the basis of ITS data (Figs. 1, 2) are not supported upon consideration of morphology. The only exception is the *C. hirsutum* group. None of the clades occurring within *Chaerophyllum* coincide with the subgenera recognized by Schischkin (1950b). In *Anthriscus,* neither section *Cacosciadium* nor section *Anthriscus* (including *A. caucalis* and *A. cerefolium*) are monophyletic. In *Osmorhiza,* morphology supports the isolated position of *O. occidentalis* (subg. *Glycosma*) and the monophyly of the subgenus and section *Osmorhiza.* All species retained in *Athamanta* by Downie et al. (2000a) are grouped together and placed close to *Tinguarra*; however, this clade also encompasses the former members of *Athamanta* (i.e., *Bubon macedonicum* and *A. della-cellae*).

PHYLOGENETIC ANALYSIS OF COMBINED DATA

Maximum parsimony analysis of combined ITS and morphological data resulted in 544 trees, each of length 2272 steps, consistency indices of 0.345 and 0.321 (with and without uninformative characters, respectively), and retention index of 0.717. The topology of their strict consensus tree (Fig. 4) is similar to that obtained using only molecular data (Fig. 1); notable differences include the positions of *Geocaryum* and *Myrrhis,* and of *Balansaea* and *Conopodium* (the *Conopodium* clade). In Figures 1 and 2, *Geocaryum* and *Myrrhis* are sister taxa, whereas in Figure 4 *Geocaryum* is sister to the *Kozlovia* group while *Myrrhis* is sister to *Osmorhiza.* The new addition *Rhopalosciadium* is sister to *Chaetosciadium* (Torilidinae), while the second novel taxon *Chaerophyllopsis* is placed outside of Scandiceae and is sister to *Apium.*

EVOLUTION OF MORPHOLOGICAL CHARACTERS

Of all the trees inferred from ITS data, the neighbor-joining trees obtained using Jukes-Cantor distance or total and mean character differences best explained the morphological variation. Their lengths, as estimated using only morphological data, were each 547 steps (with CI of 0.143 and RI of 0.588). When morphological characters were mapped onto the neighbor-joining trees obtained using Kimura's two- and three-parameter and Tajima-Nei distances, 548 steps were required; mapping these characters onto the maximum parsimony trees required from 549 to 572 steps. Not surprisingly, the tree inferred from analysis of combined ITS and morphological data better explained the variation in morphological characters than any of the trees inferred from ITS data alone. Here, upon the removal of *Chaerophyllopsis* and *Rhopalosciadium,* with no molecular data available for either, only 501 steps were required (with CI of 0.156 and RI of 0.629).

The number of steps and consistency, retention, and rescaled consistency indices of morphological characters estimated on the Jukes-Cantor/neighbor-joining tree inferred from ITS data are presented in Table 5. Most rescaled consistency index values are lower than 0.2, with only six characters having a value greater than 0.3. These six characters all represent fruit morphology, and include the presence/absence of a pedicel-like appendage (character no. 32, Appendix 1), the shape of the primary ridge (35), the presence/absence of secondary ridges (38), the appearance (42) and texture (43) of the cuticle, and the color of the epidermis (44). Among the most homoplastic characters are reproductive strategy (1) and leaf division (3). We point out here that these two characters are often diagnostic at infrageneric levels.

Those 11 characters that are most useful for delimiting certain lineages were mapped onto the consensus tree obtained from the analysis of combined data (Fig. 4). To facilitate mapping, the coding of three ordinal characters was simplified: states "incised" and "pinnate" in character 10 for bracteoles, states "reduced" and "absent" in character 21 for sepal presence, and states "obsolete" and "short" in character 34 for beak length were each combined. The polymorphism exhibited in character 36 for primary ridge indumentum was scored as an additional state. Based on morphology, neither Scandiceae nor any of its three subtribes can be

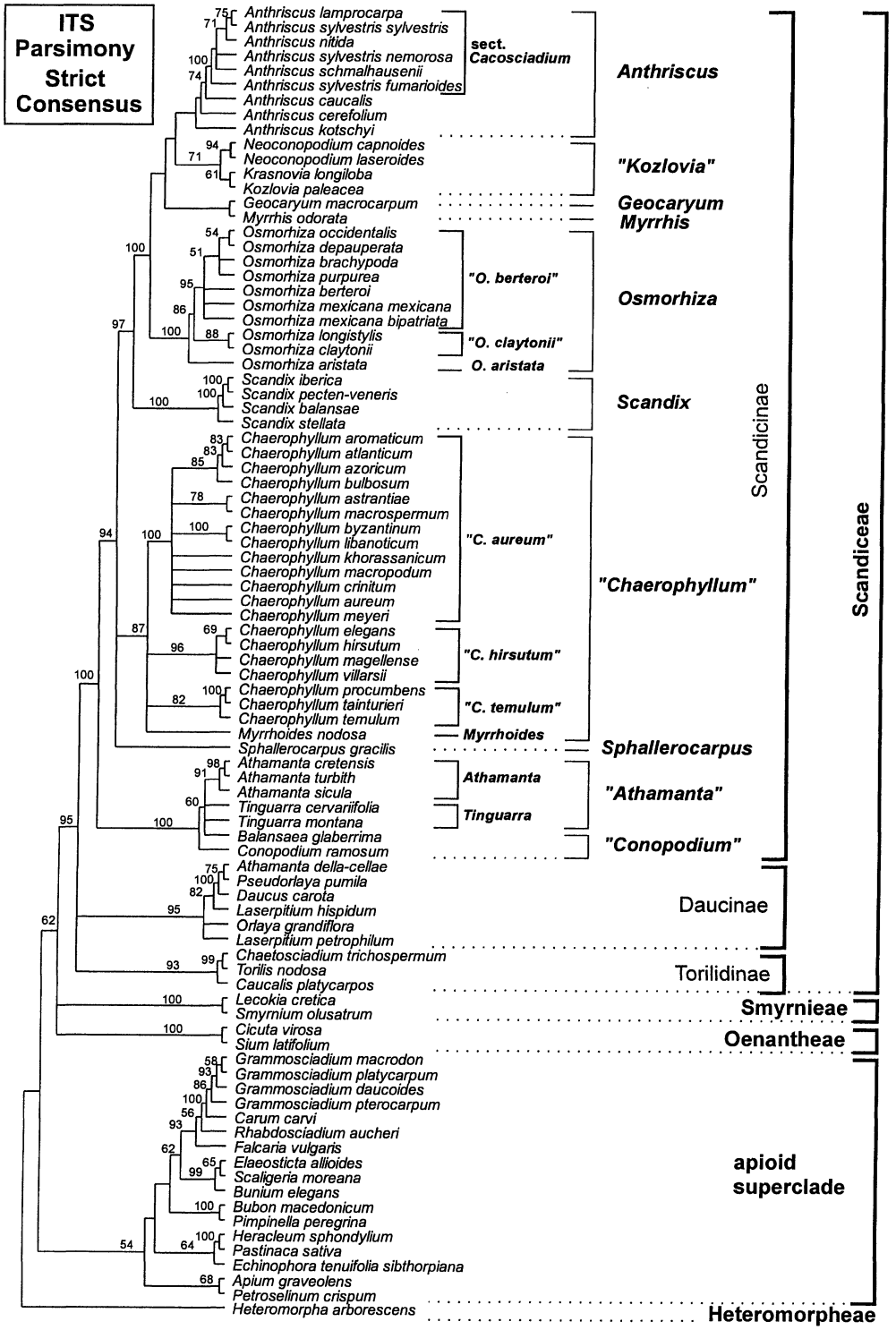

Figure 1. Strict consensus of 16,000 minimal length 1746-step trees derived from equally weighted maximum parsimony analysis of 89 nuclear rDNA ITS sequences from Scandiceae subtribe Scandicinae and outgroups (CI excluding uninformative characters = 0.376; RI = 0.748). Bootstrap values are indicated along respective nodes. Complete taxon names including ranks of infraspecific taxa are provided in Table 3. Bolder brackets at far right indicate

unambiguously defined. Most genera of Scandicinae have reduced sepals, and several genera are also characterized by an areolate fruit epidermis with a shiny aculeate cuticle. Secondary ridges appear twice, in Daucinae and in Torilidinae (Fig. 4); alternatively, they were gained in the common ancestor of Scandiceae and subsequently lost in Scandicinae (not shown). The genera of Scandicinae are usually well delimited although sometimes only on a set of homoplastic characters that may include plesiomorphies. For instance, the *Athamanta* group, which includes representatives of *Athamanta* and *Tinguarra,* is well separated from its sister *Conopodium* group, but only by those characters that have evolved in the latter (e.g., reduced sepals, no primary ridge indumentum, and globose tubers). *Chaerophyllum* may be defined by its broad rounded primary ribs; this character state is, however, homoplastic since it also appears in three species of *Scandix* and in *Carum* and *Grammosciadium,* the last two genera now placed in the apioid superclade, although *Grammosciadium* was once recognized in Scandiceae and regarded as closely related to *Chaerophyllum.* Ribs angular at top of fruit but obsolete below and deprived of distinct indumentum unambiguously delimit *Anthriscus.* A unique feature of *Osmorhiza* is a pedicel-like fruit appendage which is, however, lost in *O. occidentalis.* A long beak is synapomorphic for *Scandix,* which is also characterized by incised or pinnate bracteoles. Similar bracteole types also occur in *Daucus, Pseudorlaya,* and *Grammosciadium.* Apart from the *Conopodium* group, globose tubers also characterize the *Kozlovia* group and *Geocaryum*; outside Scandicinae, they are found in *Bunium* (and several other taxa not considered in this study).

Generally, we have not found any unambiguous character that would define subclades in *Anthriscus, Chaerophyllum,* and *Osmorhiza,* although section *Cacosciadium* and the *C. hirsutum* group each unite species that are so morphologically similar that each is sometimes treated as a single polymorphic species. Members of the *C. hirsutum* group are characterized by ciliate petals (character no. 24); however, single hairs at petal margins also occur in *C. crinitum* and are characteristic for *Osmorhiza* and some members of the *Athamanta* group. The *C. temulum* group includes monocarpic species (1, not shown on the tree) with a predominantly lateral position of umbels (16, not shown); however, these character states are highly homoplastic and are also characteristic for *Myrrhoides nodosa.* There is no single character state that separates the *C. aureum* group from the other members of *Chaerophyllum.*

Discussion

The utility of morphological characters for phylogenetic inference

Our study confirms that morphology is of limited value for estimating phylogenetic relationships in Apioideae, at least at higher taxonomic levels. Such a conclusion is not surprising given the common dissatisfaction among botanists with diagnostic characters used in the taxonomy of umbellifers (e.g., Heywood, 1971, 1982). Katz-Downie et al. (1999) showed that cotyledon shape, pollen morphology, and stomata types that had been evoked to support the classification system of Cerceau-Larrival (1962, 1963, 1965; also Guyot, 1971; Guyot et al., 1980) do not separate major lineages in Apioideae identified using molecular data. Our analyses indicate that those commonly used morphological markers related to habit, life history strategy, and reproductive traits are also highly homoplastic. These characters are all subject to strong selective pressures; hence different lineages may have reached similar adaptive peaks. Bell (1971) pointed out that the inflorescence architecture and floral morphology of umbellifers, generally considered unspecialized, may in fact constitute adaptations to a specific set of pollinators, while Webb (1981) discussed the adaptive significance of andromonoecy and protandry. Jury (1986) underlined similarities in habit, inflorescence, and floral traits of annual members of Caucalideae (i.e., subtribes Torilidinae and Daucinae, in part). Another example of the close connection between morphology and ecology is the diversification of *Anthriscus* (Spalik, 1996, 1997), which fits to Grime's (1988) model of three primary ecological factors, i.e., stress, competition, and disturbance, with the respective strategies being stress resistant, competitive, and ruderal. Different fruit outgrowths such as wings, spines, hairs, etc., are usually explained by different strategies of fruit dispersal. For example, it has been suggested that in heterocarpic members

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tribal and subtribal divisions identified by Downie et al. (2000a, b). Subclades identified in Scandicinae are also bracketed and are further described in the text. Names of informal groups are enclosed with double quotes to distinguish them from formally recognized taxa.

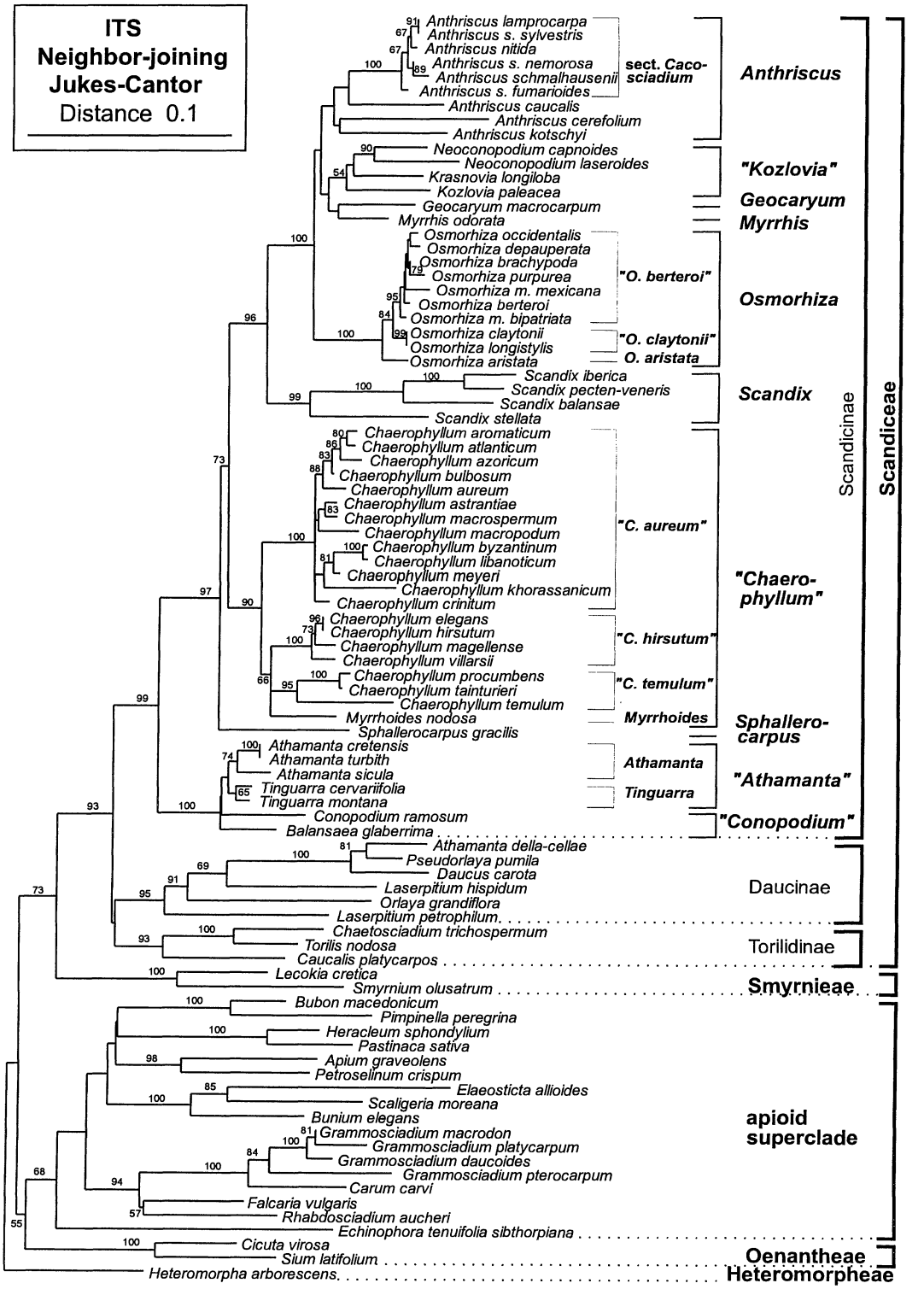

Figure 2. Neighbor-joining tree inferred from 89 nuclear rDNA ITS sequences from Scandiceae subtribe Scandicinae and outgroups. Branch lengths are proportional to distances estimated from the Jukes-Cantor method (note scale bar). Numbers denote bootstrap values for particular nodes; only those > 50% are indicated. Complete taxon names are provided in Table 3. All bracketed groups correspond to Figure 1.

of subtribes Torilidinae and Daucinae, spiny fruits are adapted for long-distance dispersal while naked ones are to maintain the local population (Jury, 1986). Similar heterocarpy has been independently acquired in *Scandix australis* and *S. turgida* in which not only the central fruit may be different from the peripheral ones but the mericarps are heteromorphic, the inner being smooth while the outer is bristled (Hedge & Lamond, 1972c; K. Spalik, pers. obs.).

The traditional emphasis on fruit characteristics for delimiting taxa in Apiaceae has found some confirmation from our analyses. Of the 44 characters examined, 6 from fruit morphology are most congruent with the ITS-derived phylogenies. These include such long-used characters as shape of the primary ribs and the presence of secondary ribs. This result was anticipated as our previous molecular analyses confirmed that most genera of Scandicinae are monophyletic (Downie et al., 2000a), thus suggesting that they were correctly identified as natural groups on the basis of fruit morphology. Other characters have generally appeared unreliable for delimiting taxa. The majority of infrageneric divisions traditionally recognized in *Chaerophyllum* and *Osmorhiza*, erected on the basis of life history, inflorescence architecture, floral morphology, and vegetative characters, are not supported, while newly identified divisions inferred from molecular data find little confirmation from morphology.

The results of the combined analysis, however, show that morphology may be useful at lower taxonomic levels. Adding morphological characters to the molecular data did not substantially change the topology of resulting trees but increased the resolution and bootstrap support for those terminal nodes where molecular data alone were inconclusive (such as within the *Athamanta* and *Conopodium* clades).

Since members of Scandicinae do not share any apomorphic characters, it is surprising that the affinity of its included taxa has been recognized, given that most early botanists were followers of Aristotle's (and Linnaeus's) downward classification by logical division using a limited number of characters rather than Adanson's multi-character upward grouping based on similarity (Mayr, 1982). Their attitude is exemplified by a perfect congruence between their classifications and keys. However, a closer examination of the description and the content of subtribe Scandicinae in different accounts reveals that the rule of logical division was not consistently applied. For instance, Drude (1898) defined Scandiceae based on the presence of calcium oxalate crystals in the aerenchymatic tissue surrounding the carpophore. He placed in subtribe Scandicinae those members of the tribe having oblong fruits with no secondary ridges. However, several species correctly assigned to Scandicinae by Drude, such as some members of *Chaerophyllum*, actually lack these crystals (Calestani, 1905; Koso-Poljansky, 1916). Drude's system, therefore, was probably intuitive and based on multiple characters rather than on single diagnostic characters. It seems that Calestani (1905) tried to follow strictly the rule of logical division, for he separated those species of *Chaerophyllum* that did not have calcium oxalate crystals in the commissure. However, his classification was not much better than that of Drude, and in the case of subtribe Scandicinae much inferior.

Character coding may be another factor leading to poor resolution. Morphological characters can be quite variable, and the typology developed for one taxon is often ineffective for another. When attempting a broader analysis and adding outgroup taxa one has to either mark many characters as inapplicable or exclude them altogether, thus losing resolution at lower taxonomic levels. It is often difficult to establish homologies, hence one gets either a few dubious but potentially more phylogenetically informative states or many unequivocal but often autapomorphic and phylogenetically useless states. For instance, Reduron (1982) developed a detailed typology of petals of umbellifers, but in fact these types were selected from a continuous spectrum of shapes and sizes. Moreover, in species with zygomorphic flowers, several types may occur on a single plant. Similar difficulties arise with fruit and leaf shapes. When adapting such typologies for phylogenetic analysis, there is a danger of "wishful thinking," i.e., unintentional perceiving and consecutive coding character states in such a way as to confirm one's ideas on phylogenetic affinities between taxa. Given the subtle differences seen between some character states in our analysis we may have succumbed to this delusion too. For the morphological analysis of Scandicinae, our departure point was a study of *Anthriscus* (Spalik, 1996, 1997), and this inevitably influenced the choice and coding of characters thereafter.

DEFINITION OF SCANDICINAE

Delimitation of tribes and subtribes on the basis of morphological synapomorphies would significantly speed up the reclassification of umbellifers by allowing preliminary sorting of taxa prior to more costly molecular investigations. However, our anal-

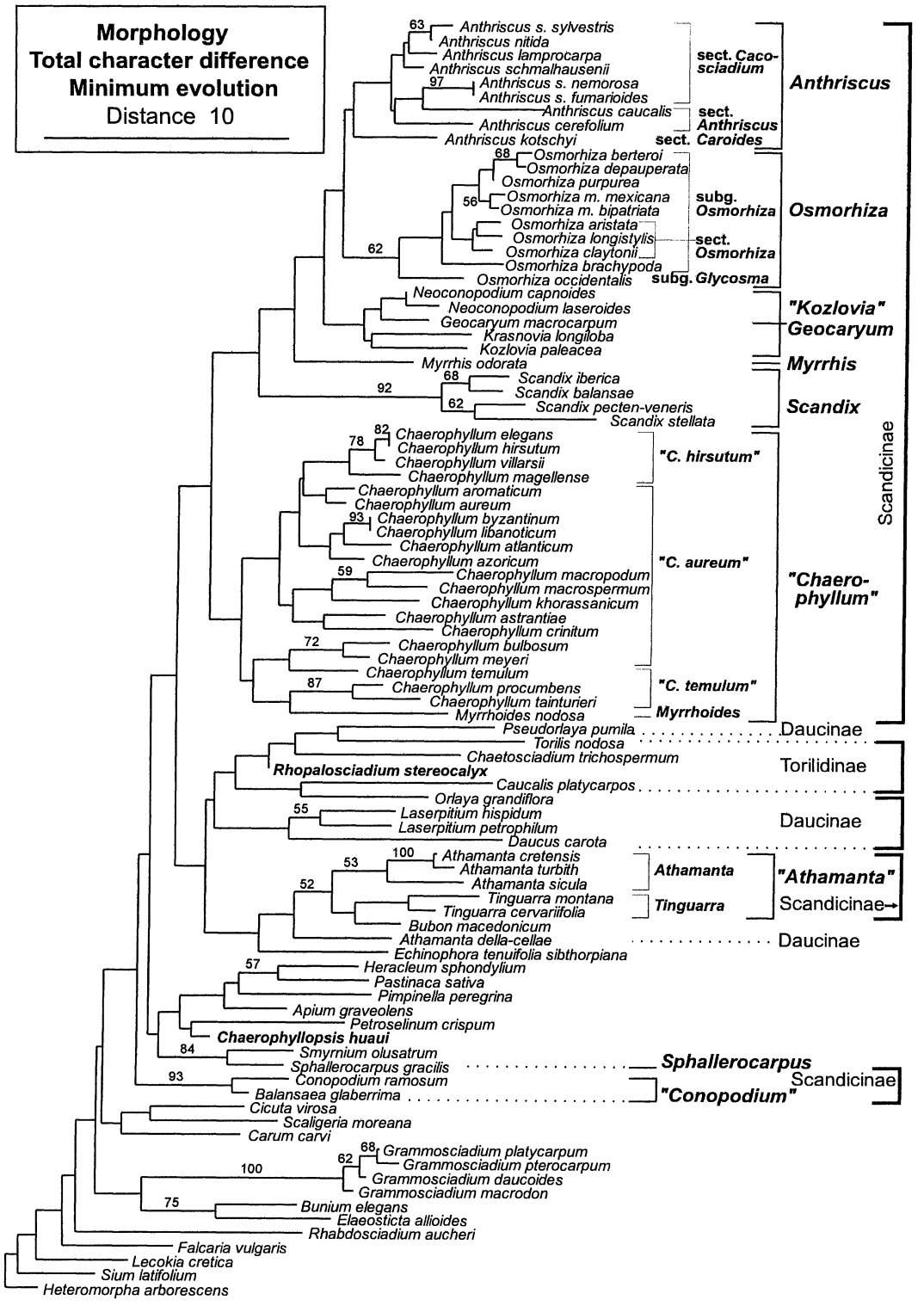

Figure 3. Minimum evolution tree inferred from 44 morphological characters for 91 representatives of Scandiceae subtribe Scandicinae and outgroups. Branch lengths are proportional to distances estimated using total character difference (total branch length = 355.92; note scale bar). Bootstrap values > 50% are indicated along the nodes. Boldface

yses suggest that such an aid for the umbellifer taxonomist is unlikely. None of the morphological characters that we have examined is synapomorphic for Scandicinae, although the taxa included are generally similar and share many common features. Scandicinae may be defined generally by possessing ovate to lanceolate and ciliate bracteoles, and narrowly ovate to linear oblong, laterally compressed, beaked fruits lacking secondary ridges. Several members depart from this definition: for instance *Anthriscus kotschyi* has non-ciliate bracteoles while many species of *Chaerophyllum* do not have a pronounced beak. Additional characters include reduced sepals and the absence of oil ducts in the petals; these characters, however, are not found in basal Scandicinae, i.e., the *Athamanta* and *Conopodium* groups. An aculeate, areolate, and shiny fruit epidermis and angular primary ribs adequately demarcate "crown" Scandicinae (*Anthriscus, Geocaryum, Kozlovia, Krasnovia, Myrrhis, Neoconopodium,* and *Osmorhiza*) from all other umbellifers. *Scandix* may be identified as a close relative to this clade due to its aculeate and areolate fruit epidermis. It seems, therefore, that among potential members of Scandicinae, it would be easy to identify those that belong to the "crown" clade. However, those related to *Sphallerocarpus, Conopodium,* or *Athamanta* may not readily be recognized as the members of the subtribe on the basis of morphology alone.

PHYLOGENETIC AFFINITIES OF *RHOPALOSCIADIUM* AND *CHAEROPHYLLOPSIS*

The monotypic genus *Rhopalosciadium* was described from Iran based on a single gathering and originally placed in Scandicinae, presumably on account of its linear fruits (Rechinger, 1952). Later, based on its fruit indumentum, the genus was transferred to tribe Caucalideae. Its closest relative was thought to be *Torilis,* with which the plant was growing in the wild (Hedge & Lamond, 1980; Rechinger, 1987b). In our combined analysis (Fig. 4), *Rhopalosciadium* was grouped with *Chaetosciadium* in Torilidinae. The type material of *Rhopalosciadium stereocalyx* at W, the data source for this analysis, has only immature fruits with obsolete primary and secondary ridges. These ridges are also inconspicuous in *Chaetosciadium,* a monotypic genus apparently nested within *Torilis* (Lee & Downie, 1999). Bristles covering the ovary of *Rhopalosciadium,* as seen under high magnification of a dissecting microscope, are indeed similar to those of *Torilis,* a member of Torilidinae sensu Downie et al. (2000a), but different from those in Scandicinae. *Rhopalosciadium* should therefore be recognized in subtribe Torilidinae. Given that the only collection of this taxon was found growing with *Torilis,* it may just be an aberrant form of the latter.

Chaerophyllopsis huaui is endemic to China. Herbarium material of this species is very rare in botanical collections, and we have seen only one specimen (Yunnan, 26 July 1906, *Ducloux 4565,* P) but this lacked mature fruits. Based on the analysis of this incomplete specimen, this taxon should be excluded from Scandiceae and transferred to the apioid superclade. Indeed, Pimenov and Leonov (1993) following Sheh and Su (1987) treated it in subtribe Apieae.

THE TAXONOMIC POSITION OF MONOTYPIC GENERA

There is general agreement that all taxonomic categories, with the exception of species, are arbitrary and apart from monophyly there are no universal criteria by which they should be distinguished. The Linnaean hierarchy of names has been a tool for species recognition in which genera play an important role. The binomial not only denotes a particular species but also indicates its closest relatives (i.e., congeners). As an aid to species identification, monotypic genera are therefore useless and taxonomists should avoid creating them unless they indeed represent isolated lineages significantly distinct from their sister taxa. Of the 455 genera of Umbelliferae listed by Pimenov and Leonov (1993), 41% are monotypic and 26% comprise only 2 or 3 species each. Similarly, of the 16 genera constituting Scandiceae subtribe Scandicinae, 7 (44%) are monotypic (Table 1). Based on our combined study, the number of monotypic genera in Scandicinae may satisfactorily be reduced, as only *Sphallerocarpus* and *Myrrhis* represent isolated evolutionary lineages.

Contrary to the molecular analyses, which allied *Myrrhis odorata* with *Geocaryum* (Figs. 1, 2), the combined analysis placed *M. odorata* sister to *Osmorhiza* (Fig. 4) in accordance with the relationship proposed by Lowry and Jones (1984). *Sphallerocarpus gracilis* occurs in the Far East, in contrast to

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marks *Chaerophyllopsis* and *Rhopalosciadium,* which were not available for ITS study. Bracketed names are similar to those provided in Figures 1 and 2; additional detail is provided within the *Anthriscus* and *Osmorhiza* clades.

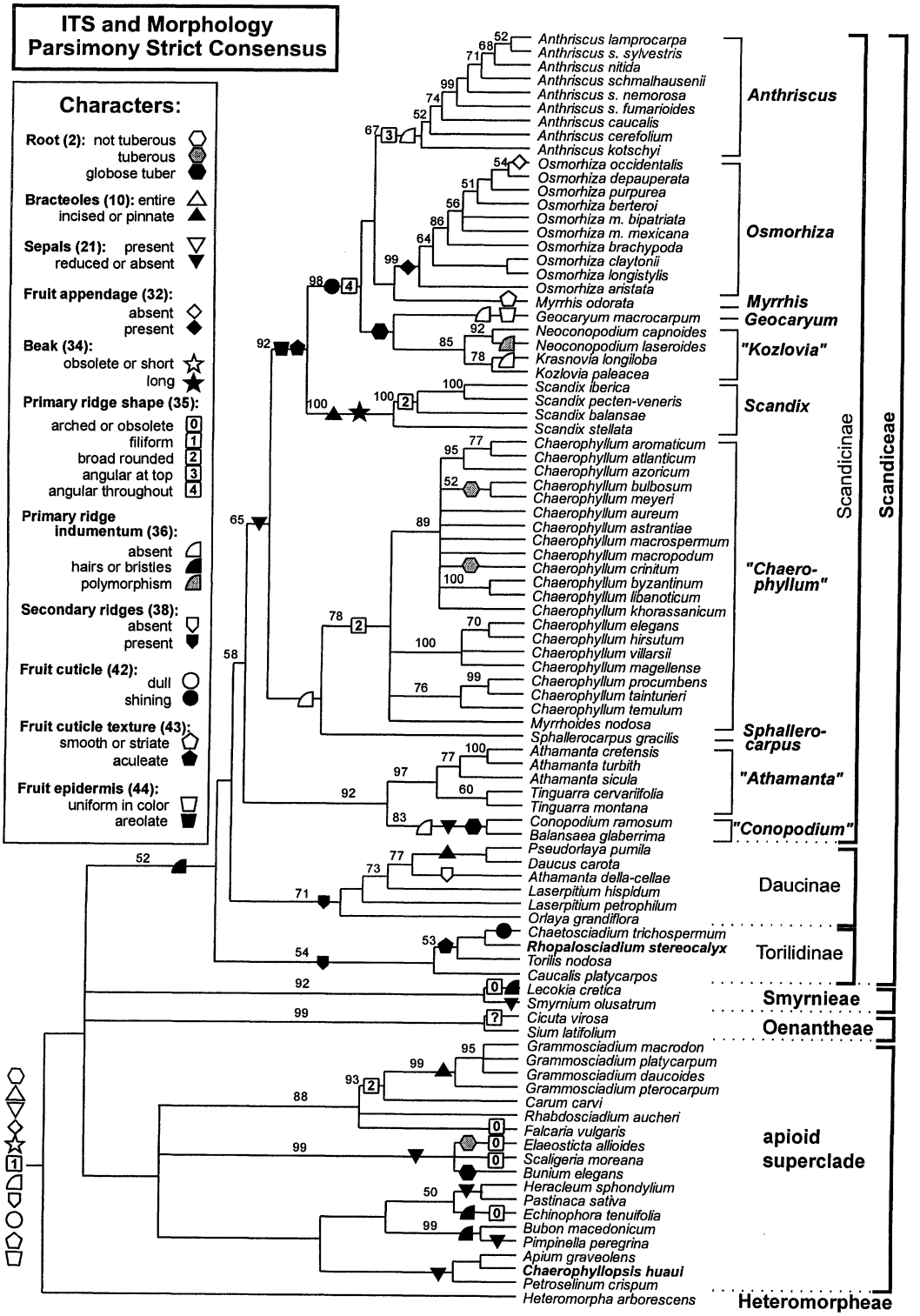

Figure 4. Strict consensus of 544 minimal length 2272-step trees inferred from equally weighted maximum parsimony analysis of combined morphological and ITS sequence data for 91 representatives of Scandiceae subtribe Scandicinae and outgroups (CI = 0.321 excluding uninformative characters, RI = 0.717). Boldface indicates *Chaerophyl-*

Table 5. Number of steps (NS) and consistency (CI), retention (RI), and rescaled consistency (RC) indices of 44 morphological characters estimated by mapping these characters on a Jukes-Cantor/neighbor-joining tree inferred from ITS sequences. Characters are listed according to descending RC values; character numbers refer to those presented in Appendices 1 and 2.

Character	NS	CI	RI	RC
42. Cuticle appearance	2	0.50	0.96	0.48
44. Epidermis coloration	2	0.50	0.96	0.48
32. Fruit appendage	2	0.50	0.88	0.44
38. Secondary ridges	2	0.50	0.86	0.43
35. Primary ridge shape	10	0.40	0.89	0.36
43. Cuticle texture	3	0.33	0.93	0.31
15. Umbel width	2	0.50	0.50	0.25
21. Sepals	7	0.29	0.82	0.23
41. Fruit indumentum	24	0.38	0.58	0.22
10. Bracteole division	7	0.29	0.64	0.18
36. Primary ridge indumentum	9	0.22	0.79	0.18
4. Lobe orientation	8	0.25	0.63	0.16
24. Petal margin	9	0.22	0.71	0.16
37. Mericarp compression	7	0.29	0.50	0.14
8. Bract margin	4	0.25	0.50	0.13
33. Commissure	9	0.11	0.81	0.09
19. Central flower	9	0.11	0.72	0.08
22. Sepal indumentum	6	0.17	0.50	0.08
2. Root	9	0.22	0.30	0.07
26. Oil ducts in petals	9	0.11	0.62	0.07
28. Crown of hairs at fruit base	9	0.11	0.62	0.07
29. Pedicel indumentum	14	0.14	0.48	0.07
31. Fruit shape	25	0.12	0.60	0.07
34. Beak	17	0.12	0.59	0.07
23. Petal incision	12	0.08	0.68	0.06
5. Shape of basal leaf lobes	10	0.10	0.47	0.05
6. Shape of cauline leaf lobes	16	0.13	0.42	0.05
11. Bracteole margin	22	0.09	0.57	0.05
13. Bracteole shape	10	0.10	0.53	0.05
14. No. of umbellets in primary umbel	12	0.08	0.66	0.05
16. Umbel position	15	0.13	0.41	0.05
3. Leaf division	38	0.11	0.37	0.04
7. Bracts	25	0.08	0.44	0.04
20. Outer flowers	15	0.07	0.67	0.04
30. Pedicels of fruit	8	0.13	0.30	0.04
9. No. of bracteoles	35	0.09	0.33	0.03
12. Bracteole indumentum	17	0.06	0.45	0.03
18. Disc male flowers	9	0.11	0.27	0.03
25. Petal indumentum	11	0.09	0.38	0.03
27. Stylopodium shape	29	0.07	0.44	0.03
1. Reproductive strategy	41	0.05	0.38	0.02
17. Peripheral flowers	2	0.50	0	0
39. Secondary ridge appendages	3	0.67	0	0
40. Tubercles at fruit surface	12	0.08	0	0

←

lopsis and *Rhopalosciadium* for which ITS data were not available. Numbers along nodes denote bootstrap values; only those > 50% are indicated. The morphological characters that are most useful for delimiting genera and suprageneric lineages are indicated. Character numbers refer to those presented in Appendices 1 and 2.

other Scandicinae, which have their center of distribution in the Mediterranean region. This East Asiatic lineage may actually be represented by more than one species, with one possible candidate being *Vicatia*, which was included in *Sphallerocarpus* by Koso-Poljansky (1916). In contrast, both molecular (Fig. 2) and morphological (Fig. 3) analyses indicate that *Myrrhoides* is nested within *Chaerophyllum*, although in some trees (not shown) these genera constitute sister taxa. We therefore see no justification for separating these two genera. Such a treatment is not novel. Linnaean *Scandix nodosa* L., the basionym of *Myrrhoides nodosa* (Dandy & Cannon, 1968), was earlier transferred to *Chaerophyllum* by Crantz (1767) and recognized there by de Candolle (1829, 1830). The correct name of this species in *Chaerophyllum* is therefore *C. nodosum* (L.) Crantz.

The relationships among basal Scandicinae are obscure. Phylogenetic analysis of combined data supports the monophyly of each of the *Athamanta* and *Conopodium* groups (Fig. 4), contrary to separate analysis of ITS data (Fig. 2), where the latter is clearly not monophyletic. Based on morphology, the inclusion of *Tinguarra* into *Athamanta* should also be considered but this transfer needs confirmation from fruit anatomy. *Balansaea* was included in *Conopodium* by Engstrand (1973), and although this finds support from morphology (Fig. 3), the monophyly of *Conopodium* is not confirmed by our ITS analyses.

The *Kozlovia* clade encompasses four species (*K. paleacea, Krasnovia longiloba, Neoconopodium capnoides,* and *N. laseroides*) that are similar in habit and closely related based on molecular data. Their geographic distribution also supports their close relationship. *Kozlovia paleacea* and *Krasnovia longiloba* are Central Asiatic, with *Krasnovia* extending northeast to China and *Kozlovia* reaching Afghanistan (Korovin, 1950; Schischkin, 1950c; Rechinger, 1987a). *Neoconopodium* has a Himalayan distribution; *N. laseroides* is western and occurs in Afghanistan and Pakistan, while *N. capnoides* is eastern, occurring in Pakistan, Kashmir, and the Indian Himalayas (Hedge & Lamond, 1980, 1987; Pimenov & Kljuykov, 1987). The combined analysis (Fig. 4) indicates that the East Mediterranean *Geocaryum* (which is also a geophyte) is sister to this group. The morphological variation observed within the *Kozlovia* clade is comparable to that exhibited by *Anthriscus* or *Chaerophyllum* and, consequently, a single genus should be recognized.

Kozlovia Lipsky, Trudy Imp. S.-Peterburgsk. Bot. Sada 23: 146. 1904. TYPE: *Kozlovia paleacea* (Regel & Schmalh.) Lipsky (basionym: *Albertia paleacea* Regel & Schmalh.).

Albertia Regel & Schmalh., Trudy Imp. S.-Peterburgsk. Bot. Sada 5: 603. 1878. Non W. P. Schimper 1837. TYPE: *Albertia paleacea* Regel & Schmalh.

Krasnovia Popov ex Schischk., Flora SSSR 16: 591. 1950. TYPE: *Krasnovia longiloba* (Kar. & Kir.) Popov ex Schischk. (basionym: *Sphallerocarpus longilobus* Kar. & Kir.).

Neoconopodium Pimenov & Kljuykov, Feddes Repert. 98: 377. 1987. TYPE: *Neoconopodium capnoides* (Decne.) Pimenov & Kljuykov (basionym: *Butinia capnoides* Decne.).

1. **Kozlovia paleacea** (Regel & Schmalh.) Lipsky, Trudy Imp. S.-Peterburgsk. Bot. Sada 23: 146. 1904. *Albertia paleacea* Regel & Schmalh., Trudy Imp. S.-Peterburgsk. Bot. Sada 5: 606. 1878. TYPE: Uzbekistan. Between Karasu and Katty Kurgan, 26 Apr. 1869, *O. Fedchenko* (lectotype, designated by Vinogradova (1999), LE not seen).

Even though we have not seen the *Fedchenko* type specimen, we rely on the expert confirmation of its status by V. M. Vinogradova. This lectotype for *Albertia paleacea* was chosen by her among her discussion of Apiaceae types at the Komarov Botanical Institute (Vinogradova, 1999) and later also confirmed to us (Vinogradova, pers. comm.). In the revision of *K. paleacea* for the *Flora Iranica*, Rechinger (1987a) indicated A. Regel as the collector of the type specimen; he did not, however, examine any type collections.

Kozlovia paleacea differs from the other members of this genus in having leaves with broad and deeply lobed ultimate segments, ciliate bracteoles, and ovate fruits with primary ridges covered with prominent hyaline bristles.

2. **Kozlovia capnoides** (Decne.) Spalik & S. R. Downie, comb. nov. Basionym: *Butinia capnoides* Decne., in Jacquem., Voy. Bot. 70: tab. 80. 1844. *Chaerophyllum capnoides* (Decne.) Benth., in Benth. & Hook. f., Gen. Pl. 1: 898. 1867. *Conopodium capnoides* (Decne.) Koso-Pol., Bull. Soc. Imp. Naturalistes Moscou 29: 206. 1916. *Neoconopodium capnoides* (Decne.) Pimenov & Kljuykov, Feddes Repert. 98: 377. 1987. SYNTYPES: India. (Punjab?): between Gereti and Gougoulgaon, 2400 m; Kashmir: Ouri and Nouchaira, banks of the Djhelone, 1980 m, *Jacquemont 308* (K not seen; P not seen), *920* (P not seen).

In their discussion on Asiatic Scandiceae, Hedge and Lamond (1980) revised this species, placing it in *Chaerophyllum*. Both in that revision and in a later treatment for the *Flora Iranica* (Hedge & La-

mond, 1987), they assigned both *Jacquemont* syntypes to *K. capnoides*.

Kozlovia capnoides differs from the other species in having leaves with entire, oblong ultimate segments and oblong-cylindrical glabrous fruits with occasional delicate bristles along primary ridges.

3. **Kozlovia laseroides** (Hedge & Lamond) Spalik & S. R. Downie, comb. nov. Basionym: *Chaerophyllum laseroides* Hedge & Lamond, Notes Roy. Bot. Gard. Edinburgh 38: 252. 1980. *Chaerophyllum aquilegifolium* Rech. f. & Riedl, Dan. Biol. Skr. 13, 4: 44. 1963, nom. illeg., non Koso-Pol. 1916. *Neoconopodium laseroides* (Hedge & Lamond) Pimenov & Kljuykov, Feddes Repert. 98: 378. 1987. TYPE: Afghanistan. Nuristan: Pech (Parun) Valley between Chetras and Wama, *Kerstan 851* (holotype, W not seen; isotype, HAL not seen).

The *Kerstan* holotype was verified by Hedge and Lamond (1980, 1987) for the revision of this species for the *Flora Iranica*.

Kozlovia laseroides differs from its congeners in possessing leaves with ovate and petiolulate ultimate segments and oblong-cylindrical fruits covered with antrorse bristles.

4. **Kozlovia longiloba** (Kar. & Kir.) Spalik & S. R. Downie, comb. nov. Basionym: *Sphallerocarpus longilobus* Kar. & Kir., Bull. Soc. Imp. Naturalistes Moscou 14: 432. 1841. TYPE: Kazakhstan. Tarbagatai Mts., by Dschanybek river, 1840, *Karelin & Kirilov s.n.* (LE not seen, checked by V. M. Vinogradova, pers. comm.).

The identity of the type of this species was confirmed to us by V. M. Vinogradova.

Kozlovia longiloba differs from the other species of this genus in having leaves with linear lobes and ovate, tuberculate fruits.

ANTHRISCUS

Our results show that neither morphology nor ITS data fully support the present classification of *Anthriscus*, as section *Anthriscus* is not monophyletic. Phylogenetic analyses of a data set comprising *Anthriscus* only, based on a larger set of morphological characters than that used here, confirmed the monophyly of each of its three sections (Spalik, 1996). However, the character states that identify these sections, although unique when only *Anthriscus* is considered, are quite common among other umbellifers (Spalik, 1997). For instance, characters that support the monophyly of section *Anthriscus*, such as weak protandry, short and straight styles, and an annual life history strategy, are also typical for other annual monocarpic umbellifers (Jury, 1986), and may be interpreted as adaptations to disturbed habitats (Spalik, 1996). Therefore, section *Anthriscus* is likely polyphyletic, and *A. cerefolium* should be placed in a monotypic section *Cerefolium* (Fabr.) Neilr. (Neilreich, 1859). Based on analysis of partial ITS data, a third member of section *Anthriscus*, *A. tenerrima*, is sister to *A. caucalis* and should therefore be retained in this section (K. Spalik & S. Downie, unpublished data).

Although the monophyly of section *Cacosciadium* has been confirmed (Figs. 1, 2), the affinities among its members are not unambiguously resolved. This section comprises four species (*A. sylvestris*, *A. nitida*, *A. lamprocarpa*, and *A. schmalhausenii*) and all were included in the present study. *Anthriscus sylvestris* is further divided into four subspecies (Reduron & Spalik, 1995; Spalik, 1996, 1997) but two of these, subsp. *nemorosa* and subsp. *fumarioides*, have been previously recognized as good species (Cannon, 1968). In contrast, the specific status of *A. nitida* and *A. lamprocarpa* has been questioned (Thellung, 1926; Hedge & Lamond, 1972b). Spalik (1996) suggested that *A. sylvestris* is paraphyletic with respect to *A. nitida*, *A. lamprocarpa*, and *A. schmalhausenii*, the latter three species likely evolving through speciation of isolated peripheral populations of the former. These three species seem to be well separated from the *A. sylvestris* complex both by qualitative and quantitative characters, while there is no morphological hiatus between other taxa from this group; consequently, the latter are recognized as subspecies or varieties of *A. sylvestris*. Our previous ITS study also encompassed Asiatic and East African representatives of *A. sylvestris*; these were so similar morphologically to the European plants that they all were included in subspecies *sylvestris* (Downie et al., 2000a). However, these ITS data did not confirm this affinity. Instead, a close relationship was suggested among the European smooth-fruited taxa (i.e., *A. sylvestris* subsp. *sylvestris*, *A. sylvestris* subsp. *alpina*, and *A. nitida*), *A. lamprocarpa*, and a representative of *A. sylvestris* from northeastern Asia. Another clade comprised the East African and remaining Asiatic members of the *A. sylvestris* complex, suggesting a primary split of the distribution into northwestern and southeastern populations.

The close affinity between Levantine *A. lamprocarpa*, represented in our molecular study by one accession from Jordan, and the European popula-

tions of *A. sylvestris* is not readily explained, as one would expect the former to be related to either parapatric *A. sylvestris* subsp. *nemorosa* from Turkey or East African representatives of subspecies *sylvestris*. It has been suggested that *A. lamprocarpa* originated from an isolated population of *A. sylvestris* subsp. *sylvestris* that may have reached the Middle East from montane localities in North Africa, which themselves may have originated from Iberian Peninsula stock when this area was covered with forests during the Pleistocene (Spalik, 1996). An analysis of North African *A. sylvestris* could address this hypothesis. One may also postulate a more recent origin of this species by the occasional introduction of *A. sylvestris* into the Middle East in antiquity and its subsequent adaptive evolution. *Anthriscus sylvestris* is a competitive-ruderal species (Grime et al., 1988) that has been recently introduced into North America; given the extensive trade exchange in the Mediterranean region, such a scenario is quite possible.

This study does not answer the question as to how many species there are within the *A. sylvestris* complex. Morphological differences suggest that there are reproductive barriers among *A. nitida, A. lamprocarpa, A. schmalhausenii,* and *A. sylvestris* (Spalik, 1996, 1997). However, other taxa included in the latter, particularly montane populations from Africa and Asia, may also be reproductively isolated and may deserve specific status despite their lack of good diagnostic features. In a biosystematic study of *Geocaryum,* Engstrand (1977) demonstrated by means of hybridization experiments that many populations hitherto regarded as conspecific are partly or entirely reproductively isolated. Consequently, instead of 3 species (Ball, 1968), he recognized as many as 15. However, these taxa are practically indistinguishable based on morphology. *Anthriscus sylvestris* may well represent another such complex of cryptic species with different degrees of reproductive isolation. Contrary to many groups of angiosperms, interspecific hybridization is thought to be exceedingly rare in umbellifers (Bell, 1971). The example of *Geocaryum* suggests, however, that Apiaceae may not be exceptional. Due to their obscure morphology many such cases may simply escape the attention of taxonomists.

CHAEROPHYLLUM

Contrary to *Anthriscus* and *Osmorhiza, Chaerophyllum* has not been revised recently. It is the most diversified genus in the subtribe and includes over 30 species; hence an infrageneric classification would be advantageous. The only modern account containing infrageneric divisions is that of Schischkin (1950b), being mostly based on the work of Koso-Poljansky (1916, 1920, 1923). The names in these treatments, however, are problematic. Koso-Poljansky (1916) did not explicitly indicate nomenclatural types for his subgenera nor did he provide species lists, while the names of series introduced by Schischkin (1950b) were not validly published as he did not provide Latin diagnoses. Additionally, this treatment encompassed only those taxa of the former Soviet Union, and hence some European, Asiatic, and American members of this genus were not considered (Table 2).

Schischkin (1950b) generally based his classification on plant habit, but the content of his divisions occasionally did not coincide with the indicated diagnostic characters. For instance, although his subgenus *Buniomorpha* was defined as encompassing plants with tuberous roots it also included *C. temuloides,* a taxon now included in *C. aureum,* which does not have such a root (Hedge & Lamond, 1972a). His subgenus *Golenkinianthe* was defined by members possessing fruits borne only by central flowers, a feature that is also found in *Grammosciadium* and *Echinophora.* However, central perfect flowers occur practically in all species of *Chaerophyllum,* while in *C. macrospermum,* the only species placed by Schischkin in subgenus *Golenkinianthe,* fruits may also be borne by outer perfect flowers, particularly those of the primary umbels (K. Spalik, pers. obs.). The classification of Schischkin (1950b) has not been confirmed by this study. Instead, both ITS data alone (Figs. 1, 2) and combined molecular and morphological data (Fig. 4) indicate that there are four distinct lineages. We refer to these as (1) the *C. temulum* group, (2) the *C. hirsutum* group, (3) the *C. aureum* group, and (4) *C. nodosum* (≡ *Myrrhoides nodosa*). These groups are not morphologically distinct enough to justify their generic status, so we recognize them as sections of *Chaerophyllum.* Our treatment is incomplete, as not all currently recognized species were available for molecular study. Therefore, we do not attempt a detailed revisionary study of this genus but rather provide a framework for such studies in the future.

Chaerophyllum L., Sp. Pl. 258. 1753. TYPE: *Chaerophyllum temulum* L., Sp. Pl. 258. 1753, *Herb. Linn. 365.3* (lectotype, designated by Reduron & Jarvis (1992), LINN not seen).

Section 1. Chaerophyllum sect. **Chaerophyllum**

Annuals or biennials. Umbels mostly lateral or both lateral and terminal. Male flowers absent or rare. Petals glabrous, non-ciliate. Fruits ovate, glabrous, rarely pilose.

Species included: *C. procumbens, C. tainturieri, C. temulum.*

This section encompasses monocarpic species distributed in Europe (*C. temulum*) and in North America (*C. procumbens, C. tainturieri*). Such a disjunction is generally rare; most groups of vicarious species that occur both in Europe and North America are also found in the Far East (Meusel et al., 1978), supporting the hypothesis that these species diverged from a once widespread common ancestor with circumboreal distribution. The absence of representatives of this clade from Asia suggests that the North American species originated from an incidental dispersion of seeds from European stock, probably by vagrant birds. American species differ from their European cousin in the absence of male flowers and the almost completely reduced corollas, i.e., characters that are typical for self-pollinating species.

Section 2. Chaerophyllum sect. **Dasypetalon** Neilr., Fl. Nied.-Oesterr. 645. 1859. TYPE: *Chaerophyllum hirsutum* L., Sp. Pl. 258. 1753.

Chaerophyllum sect. *Rhynchostylis* (Tausch) Calest., Webbia 1: 188. 1905. *Rhynchostylis* Tausch, Flora 17: 343. 1834. Non Blume 1825. TYPE: *Rhynchostylis hirsutus* Tausch (*Chaerophyllum hirsutum*).

Perennials. Umbels mostly terminal. Male flowers frequent. Petals glabrous, ciliate. Fruits oblong-ovate to oblong.

Species included: *C. hirsutum, C. elegans, C. magellense, C. villarsii.*

The members of this section are morphologically similar, prompting some authors (e.g., Thellung, 1926) to regard these taxa as conspecific. The differences are indeed small and include mostly leaf characters. All taxa are perennials and are characterized by distinctly ciliate petals. The importance of this character was stressed by Neilreich (1859) who divided Austrian species of *Chaerophyllum* into two sections, *Leiopetalon*, with glabrous petals, and *Dasypetalon*, with hairy petals. The first section comprised the type of the genus, and therefore it is synonymous with section *Chaerophyllum*. Neilreich (1859) included two species in section *Dasypetalon, C. hirsutum* and *C. villarsii*, but he did not specify its nomenclatural type. Both species fully conform to the diagnosis of the section. *Chaerophyllum hirsutum* is an older name and has priority when these taxa are treated as conspecific, and therefore it seems to be a better choice.

Chaerophyllum hirsutum has not yet been lectotypified. Of the extant Linnaean specimens of this species, those at LINN and S do not seem to be connected with the entry in the first edition of Linnaeus's (1753) *Species plantarum*. The original material available for lectotypification includes, therefore, two BM specimens (*Herb. Clifford,* 101: *Chaerophyllum 2* and *2*β) and figure 6 (plate 10) from Morison (1699) cited in the protologue (C. E. Jarvis, pers. comm.). Linnaeus (1753) cited also a plate from Haller's (1745) edition of Ruppius's *Flora jenensis.* However, in the second edition of the *Species plantarum* (Linnaeus, 1762), this plate is referred to *C. aureum.* Since we have not had the possibility to examine the original material, we refrain from lectotypification of *C. hirsutum.*

Section 3. Chaerophyllum sect. **Physocaulis** DC., Coll. Mém. 5: 59. 1829. TYPE: *Chaerophyllum nodosum* (L.) Crantz, Class. Umbell. Emend. 76. 1767. Basionym: *Scandix nodosa* L., Sp. Pl. 257. 1753; *Herb. Linn.* 364.6 (lectotype, designated by Hedge & Lamond (1987), LINN not seen).

Densely setose annuals. Umbels mostly lateral. Male flowers scarce. Petals setose, non-ciliate. Fruits ovate, setose.

Chaerophyllum nodosum, the only member of this section, differs from other species of *Chaerophyllum* in having setose fruits with very broad primary ridges. These ridges nearly touch each other, and hence valleculae are inconspicuous and colored similarly to the ridges; in contrast, these regions are often of different color in other species. However, fruit indumentum and broad ridges are not unique to *C. nodosum.* The members of section *Chaerophyllum* may have pubescent fruits (although not setose), while the width of the ridges (as determined by the width of the vascular bundles) is quite variable in the genus (K. Spalik, A. Wojewódzka & S. Downie, unpublished data).

This monotypic section was first recognized by de Candolle (1829, 1830) and raised to generic level by Tausch (1834). Later, the generic name *Physocaulis* (DC.) Tausch was rejected by Dandy and Cannon (1968) in favor of the forgotten but earlier *Myrrhoides.* The ITS and combined analyses place *Chaerophyllum nodosum* either as a sister to remaining members of the genus or nested within it, supporting the treatment of de Candolle (1829).

Section 4. Chaerophyllum sect. **Chrysocarpum** Spalik & S. R. Downie, sect. nov. TYPE: *Chaerophyllum aureum* L., Sp. Pl. ed. 2. 370. 1762, *Herb. Linn. 365.8* (original material, LINN not seen), plate 5 in Haller (1745), (C. E. Jarvis, pers. comm.).

A sectionibus *Chaerophyllo* et *Physocaule* radice perenni vel bienni, a sectione *Leiopetalone* petalis non ciliatis differt.

Biennials or perennials. Umbels mosly terminal or both terminal and lateral. Male flowers usually present. Petals non-ciliate, usually glabrous, rarely hairy. Fruits oblong-ovate to cylindrical, glabrous, rarely pilose.

Etymology. From *chryso-*, golden, and *carpos*, fruit, since many species in this section (including the type species) are characterized by straw-yellow fruits.

Species included: *C. aromaticum, C. astrantiae, C. atlanticum, C. aureum, C. azoricum, C. bulbosum, C. byzantinum, C. crinitum, C. hakkiaricum, C. khorassanicum, C. libanoticum, C. macropodum, C. macrospermum, C. meyeri, C. nivale.* Two of these, *C. hakkiaricum* and *C. nivale,* were not considered herein but are included based on our prior study (Downie et al., 2000a).

Section *Chrysocarpum* is morphologically and ecologically diversified, and we were not able to find any single morphological feature separating it from any other section of *Chaerophyllum.* Its members differ from representatives of sections *Chaerophyllum* and *Physocaulis* in their predominantly perennial habit. Some species are, however, biennials and these may have tuberous roots (*C. bulbosum, C. crinitum*). Several species have pubescent petals with hairs occurring also at the margin. Such petals are superficially similar to those ciliate petals characteristic of members of section *Dasypetalon.*

Maximum parsimony analysis (Fig. 1) did not totally resolve relationships within this clade; however, the affinities inferred from ITS data using distance methods are largely congruent with the geographic distribution of these taxa. Neighbor-joining analysis (Fig. 2) suggests a division into four major lineages; however, only one of these is supported by a high bootstrap value (88%). This lineage encompasses species that have a predominantly European distribution (*C. aureum, C. bulbosum, C. azoricum, C. atlanticum,* and *C. aromaticum*), whereas all other species in the section occur in the Middle East.

The type species of this section, *Chaerophyllum aureum,* has not been properly lectotypified. Although Hedge and Lamond (1987) indicated LINN 365.7 as the type, it is probably not an original element for the name, as Linnaeus did not annotate it as belonging to this species; LINN 365.8 may be original material (C. E. Jarvis, pers. comm.); however, this specimen probably does not represent *C. aureum* as this species is currently recognized (J.-P. Reduron, pers. comm.). In the protologue, Linnaeus (1762) cited also plate 5 from Haller (1745) that is identifiable as *C. aureum.* We refrain from lectotypification of this name until we examine the extant herbarium material. In the first edition of the *Species plantarum* (Linnaeus, 1753), some earlier references that are connected with *C. aureum* as this species is now recognized were included either in *C. sylvestre,* the basionym of *Anthriscus sylvestris* (Reduron & Spalik, 1995), or in *C. hirsutum* (e.g., plate 5 in Haller, 1745).

With no molecular data available, 12 currently recognized species remain outside this new classification. These are *C. angelicifolium, C. borodinii, C. coloratum, C. confusum, C. creticum, C. heldreichii, C. humile, C. leucolaenum, C. reflexum, C. roseum, C. rubellum,* and *C. villosum.* These are either biennials with tuberous roots or perennials; hence it is unlikely that they belong to either section *Chaerophyllum* or section *Physocaulis.* Neither are they likely related to section *Dasypetalon,* since all have non-ciliate petals. The most likely placement may well be in section *Chrysocarpum.* However, some of these species may comprise additional lineages. For instance, on the basis of anatomical characters, three East Mediterranean species were transferred by Calestani (1905) to *Grammosciadium* sect. *Chrysophae* (*C. creticum, C. coloratum*) and section *Heldreichia* (*C. heldreichii*). Based on our preliminary analyses of morphological and anatomical characters of the fruits, such a placement is unlikely (K. Spalik & A. Wojewódzka, unpublished data).

OSMORHIZA

Of all the genera included in Scandicinae, *Osmorhiza* is exceptional in having a predominantly New World distribution. It includes 10 species (with 9 considered herein), of which only *O. aristata* occurs in the Old World (Table 2). *Osmorhiza glabrata* (not considered here) is restricted to the central Andes, while the remaining 8 species are distributed in North and Central America. Western North America is considered the center of origin of the genus (Lowry & Jones, 1984). The taxonomic division developed by Constance and Shan (1948) and later modified by Lowry and Jones (1984) im-

plies that the earliest branch is *O. occidentalis*, which constitutes the monotypic subgenus *Glycosma*. Its distribution includes western North America, thus supporting the American origin of the genus. Subgenus *Osmorhiza* is divided into three sections: *Osmorhiza*, *Mexicanae*, and *Nudae* (Lowry & Jones, 1984; see Table 2). The first encompasses Asiatic *O. aristata* and two closely related species from eastern North America, *O. claytonii* and *O. longistylis*. These three species are so morphologically similar that they are sometimes treated as conspecific (e.g., Gray, 1859; Kuntze, 1891; Boivin, 1968). Lowry and Jones (1979) showed that the two American members of this section are completely separable from each other and that there are no intermediate specimens which would have suggested hybridization.

Three hypotheses have been invoked to explain the similarity between the Asiatic and American members of section *Osmorhiza*. Constance and Shan (1948) suggested that either there had been a relatively recent contact between the Asian and North American populations through Beringia, or these species have differentiated slowly from a once widespread common ancestral population. Li (1972) postulated that these morphological similarities may be the result of parallel evolution due to similar ecological and geographic factors. Lowry and Jones (1984) opted for the second hypothesis arguing that due to more or less stable, mesic conditions in these areas, which constituted the two most important refugia of Tertiary flora in the Northern Hemisphere, the species may have remained relatively unchanged over long periods. The geographic distribution of the members of the remaining sections *Mexicanae* and *Nudae* supports the western North American origin of the genus and its differentiation and dispersion to South America by a step-wise migration through the tropics along a route now marked by members of section *Mexicanae* (Lowry & Jones, 1984). This scenario is also partly supported by the analysis of morphological data that places *O. occidentalis* as sister to the remaining taxa and suggests the monophyly of section *Osmorhiza* (Fig. 3). A different scenario arises from the analyses of ITS (Figs. 1, 2) or combined data (Fig. 4). These results strongly suggest that section *Osmorhiza* is paraphyletic with respect to the other members of the genus as *O. aristata* is sister to all other *Osmorhiza* species. This indicates an Asiatic rather than an American origin of the genus. Therefore, the similarity between *O. aristata*, *O. claytonii*, and *O. longistylis* may be plesiomorphic, which supports the hypothesis of slow morphological change. The eastern North American members of section *Osmorhiza* are a sister group to a clade formed by *O. occidentalis* and representatives of sections *Mexicanae* and *Nudae*. For this clade, southwestern North America seems to be the center of distribution and origin. The results of the ITS (Figs. 1, 2) and combined analysis (Fig. 4), although contradictory to the conclusions inferred from morphology alone (Fig. 3), are no less congruent with the phytogeographic data.

The present subgeneric classification of *Osmorhiza* seems to be untenable. An alternative division of *Osmorhiza* congruent with the phylogenies inferred from molecular and combined data would include three taxa (subgenera or sections) encompassing one, two, and six species respectively (omitting *O. glabrata*, as this species was not available for our molecular studies). Such a division is practically useless as an aid in species recognition. Furthermore, as compared to *Anthriscus* and *Chaerophyllum*, all species of *Osmorhiza* are very similar, hence there is no real justification for infrageneric division.

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Appendix 1. Characters used in the morphological analysis. Arrows indicate ordinal characters, the remaining are multistate or binary.

Life History and Vegetative Morphology

1. Reproductive strategy: 0, always monocarpic ↔ 1, monocarpic or polycarpic ↔ 2, always polycarpic. An ability to switch between monocarpy and polycarpy represents a distinct life history strategy; therefore it was coded as an intermediate state rather than a polymorphism. This feature is often reflected in plant habit. For instance, *Anthriscus sylvestris* subsp. *sylvestris* has monocarpic biennial rosettes but may perennate by buds in the axils of the basal leaves (Grime et al., 1988).
2. Root: 0, not tuberous; 1, tuberous; 2, globose tuber. Geophytes (i.e., plants with globose tubers) can easily be distinguished in herbarium material even if the tuber is not preserved due to the presence of thin, flexuose bases of the leaf stalks and stems. Species with tuberous roots are usually hemicryptophytes and neither their stems nor leaf stalks have flexuose bases.
3. Leaf division: 0, leaf not divided ↔ 1, 1-pinnate ↔ 2, 2-pinnate ↔ 3, 3-pinnate ↔ 4, 4-pinnate. There is variation in leaf division within each species and even on a single plant; therefore, the most common state for each taxon was taken. This character is diagnostic at the infrageneric level; for instance, to separate subgenus *Osmorhiza* from subgenus *Glycosma* or, in *Anthriscus,* to distinguish *A. lamprocarpa* from the closely related *A. sylvestris.*
4. Lobe orientation: 0, leaf ± flat; 1, lobes somewhat spreading; 2, lobes radially spreading around the axis.
5. Shape of basal leaf lobes: 0, ovate to lanceolate; 1, linear-lanceolate to linear.
6. Shape of cauline leaf lobes: 0, ovate to lanceolate; 1, linear; 2, leaves reduced to sheaths. Cauline and basal leaves are usually similar, although the former may have broader lobes. However, in some species (e.g., *Chaerophyllum macrospermum* and *C. macropodum*) the lobes of the cauline leaves, particularly of the uppermost leaves, are morphologically distinct from those of the basal leaves.

Bracts and Bracteoles

7. Bracts: 0, absent or single ↔ 1, few ↔ 2, numerous.
8. Bract margin: 0, entire; 1, pinnate. Bracts and bracteoles are reduced cauline leaves, and hence their morphology often reflects the leaf morphology. If they are reduced to leaf sheaths, they are entire; if the leaf blade is present, they may be incised or pinnate. If bracts are absent, the character was coded as inapplicable.
9. Number of bracteoles: 0, bracteoles absent ↔ 1, 1–3 ↔ 2, 4–5 ↔ 3, more than 5. The number of bracteoles is usually more or less constant, but in *Heteromorpha* there is much variability so this character was coded as missing. If bracteoles are absent, characters 10–13 were coded as inapplicable.
10. Bracteole division: 0, bracteoles entire (not incised) ↔ 1, incised ↔ 2, pinnate.
11. Bracteole margin: 0, deprived of cilia or scales ↔ 1, with minute scales ↔ 2, ciliate. Cilia at bracteole margins are homologous to those at leaf sheath margins and are distinctly longer than hairs that may cover the bracteole. However, in some species with densely hairy bracteoles it was impossible to determine the state of this character and, therefore, it was coded as "0 or 2."
12. Bracteole indumentum: 0, absent; 1, present.
13. Bracteole shape: 0, ovate to narrow lanceolate; 1, linear.

Inflorescence

14. Number of umbellets in primary umbel: 0, less than four; 1, more than four. The number of umbellets (rays) in a primary umbel is variable, but in species with reduced primary umbels it rarely reaches four while in those with well-developed primary umbels it often exceeds ten.
15. Umbel width: 0, more than 2 cm diam.; 1, less than 2 cm diam.
16. Umbel position: 0, mostly terminal ↔ 1, terminal and lateral ↔ 2, mostly lateral. Terminal versus lateral umbel formation is an important element of plant reproductive strategy. Species with terminal umbels are characterized by determinate flowering, and hence the number of consecutive orders of umbels rarely exceeds four (Bell, 1971) and the regulation of reproductive effort is predominantly postgamic (Lloyd, 1980; Lloyd et al., 1980). Lateral formation of umbels allows indeterminate flowering, i.e., further growth of the main axis and the development of additional orders of umbels when resources are abundant. A good example of such a strategy is found in *Anthriscus caucalis,* which may have up to nine orders of umbels permitting a more flexible pregamic regulation of reproductive effort (Spalik, 1996).
17. Peripheral flowers: 0, perfect; 1, male. The majority of umbellifers are andromonoecious, i.e., they have both hermaphrodite and male flowers, the latter usually situated inside the umbellet although the opposite may also be found. Characters 17–20 were determined from primary or secondary umbels. In andromonoecious species umbels of higher orders may bear only male flowers.
18. Disc male flowers: 0, present; 1, absent.
19. Central flower: 0, male or similar to other flowers; 1, perfect, sessile or with distinctly shorter pedicels than other perfect flowers.

20. Outer flowers: 0, actinomorphic or slightly zygomorphic; 1, distinctly zygomorphic.

Floral Morphology

21. Sepals: 0, present; 1, reduced; 2, absent. It is sometimes difficult to determine whether small projections at the fruit top are indeed reduced calyx teeth, as in *Myrrhis*. This character was therefore coded as unordered rather than ordinal.
22. Sepal indumentum: 0, absent; 1, present.
23. Petal incision: 0, absent or shallow; 1, deep. Deeply incised petals were regarded as cut to at least one-third of their length. This character is, however, quite variable since species with zygomorphic flowers have outer petals deeply cut while their inner petals are entire. In such cases, only outer petals were considered.
24. Petal margin: 0, naked ↔ 1, denticulate ↔ 2, ciliate. Small teeth at petal margin seem to be reduced cilia, therefore this character was coded as ordinal.
25. Petal indumentum: 0, absent; 1, present.
26. Oil ducts in petals: 0, present; 1, absent. Since petals were not dissected, it was sometimes difficult to determine whether dark-colored lines seen at the outer sides of petals were oil ducts or veins. Therefore, this character was scored as missing for some species.

Fruit Morphology

27. Stylopodium shape: 0, flat-conic; 1, high-conic; 2, ovoid or rounded. The shape of the stylopodium changes as the fruit matures, and thus its shape was determined at fruit maturity.
28. Crown of hairs (bristles, scales) at fruit base: 0, absent; 1, present. Hairs (bristles, scales) forming the crown on the pedicel at the base of the fruit, if present, are distinctly longer than those that may occur below (character 29). This crown of hairs may be reduced to single scales; if so, the pedicel is usually naked.
29. Pedicel indumentum: 0, absent; 1, pedicels scabrid; 2, pedicels hairy. Scabrid pedicels denote small dents that may occur on their inner sides.
30. Pedicels of fruit: 0, not thickened; 1, thickened. When thickened at fruit maturity, pedicels may obtain the diameter of fruits.
31. Fruit shape: 0, globose ↔ 1, elliptic or ovate to broadly ovate ↔ 2, narrow to oblong ovate ↔ 3, linear-oblong. The order of states reflects the increasing proportion of fruit length to width.
32. Fruit appendage: 0, absent; 1, present. A pedicel-like appendage is formed if the seed does not fill the lower part of the fruit. It is characteristic only for *Osmorhiza*, with the exception of *O. occidentalis*.
33. Commissure: 0, broad; 1, constricted.
34. Beak: 0, obsolete ↔ 1, relatively short ↔ 2, long. A distinct beak is formed when the seed does not fill the top of the fruit. It is sometimes a different color than the rest of the fruit.
35. Primary ridge shape: 0, arched or obsolete; 1, filiform to nearly winged; 2, broad and rounded; 3, angular only at top, obsolete below; 4, angular throughout. As arched we denote broad semicircular ridges that touch each other and are not separated from vallecules—sometimes such ridges are not much pronounced and may be regarded as obsolete. Narrow, filiform ridges are usually of a different color than the vallecules and may form small wing-like projections. Broad and rounded ridges, such as those occurring in *Chaerophyllum*, are also of a different color than the vallecules. Some fruits (their upper portion or throughout) are pentangular or even star-shaped in transverse section.
36. Primary ridge indumentum: 0, absent; 1, hairs or bristles. As primary ridge indumentum we consider only those hairs or bristles that are distinctly lined along the ridges. Therefore, in taxa with hairs or bristles evenly scattered over the fruit surface (e.g., *Anthriscus sylvestris* subsp. *nemorosa*), this character is regarded as absent.
37. Mericarp compression: 0, not compressed (i.e., mericarp as broad as wide) ↔ 1, somewhat dorsally compressed ↔ 2, distinctly dorsally compressed. Fruits lacking compressed mericarps are also described as laterally compressed.
38. Secondary ridges: 0, absent; 1, present.
39. Secondary ridge appendages: 0, wings; 1, spines; 2, hairs. If secondary ridges are absent, this character was coded as inapplicable.
40. Tubercles at fruit surface: 0, absent; 1, present. Tubercles usually constitute the bases of bristles. As these sometimes break away easily, only tubercles can remain on herbarium material, and hence the fruits can be described as tuberculate rather than bristled.
41. Fruit indumentum: 0, absent; 1, hairs; 2, bristles. In *Krasnovia longiloba* tubercles lack normally developed bristles but sometimes end with short hyaline teeth that seem to be homologous with bristles. Therefore, for this species, the character was coded as polymorphic. *Anthriscus caucalis* and *A. cerefolium* include varieties with both naked and bristled fruits.
42. Cuticle appearance: 0, dull; 1, shiny. This character is difficult to determine in badly preserved herbarium material or when the fruits are not fully ripe. However, it does reflect an anatomical basis (i.e., shiny fruits are usually characterized by a thick cuticle while those with a rather dull appearance have a thin cuticle; K. Spalik, A. Wojewódzka & S. Downie, unpublished data).
43. Cuticle texture: 0, smooth or striate; 1, aculeate. Small projections that give an aculeate texture to the cuticle are formed above the centers of the cells. In *Scandix*, they are found only close to the fruit base, while in *Anthriscus lamprocarpa* they may occur only near the commissure.
44. Epidermis coloration: 0, uniform (not areolate); 1, areolate. The areolate appearance of epidermis is due to thickened transverse cell walls (Spalik, 1997).

Appendix 2. Matrix of morphological data. Character numbers refer to those presented in Appendix 1. Question marks denote missing data or polymorphisms that include all character states; hyphens denote inapplicable characters: A, B, and C denote character states "0 or 2," "0 and 1," and "0 and 2," respectively.

	Character number				
	1	1111111112	2222222223	3333333334	4444
Taxon	1234567890	1234567890	1234567890	1234567890	1234
Anthriscus caucalis	0040000020	2000020100	2-00010101	20113000-1	C111
Anthriscus cerefolium	0030000010	2000010001	2-00010000	30113000-1	C111
Anthriscus kotschyi	2030000010	0000000000	2-00010000	20113000-0	0111
Anthriscus lamprocarpa	0020000020	2000000001	2-00010100	20113000-0	0111
Anthriscus nitida	1030000020	2000000001	2-00010100	20113000-0	0111
Anthriscus schmalhausenii	2020000020	2000000001	2-00010100	20113000-0	0111
Anthriscus sylvestris subsp. *sylvestris*	1040000020	2000000001	2-00010100	20113000-0	0111
Anthriscus sylvestris subsp. *fumarioides*	2040000020	2000000001	2-00010100	20113000-1	2111
Anthriscus sylvestris subsp. *nemorosa*	2040000020	2000000001	2-00010100	20113000-1	2111
Apium graveolens	0010000-0-	---1010100	2-00010000	20001000-0	0000
Athamanta cretensis	2031111030	2101000010	0100102020	20111100-0	1000
Athamanta della-cellae	2010002030	A101000000	0110112020	20111100-0	1000
Athamanta sicula	2041101030	2101000000	0102102020	20111100-0	10?0
Athamanta turbith subsp. *turbith*	2031111030	2101000110	0100102020	20111100-0	1000
Balansaea glaberrima	2220010020	0001000010	2-000?2000	20111000-0	0000
Bubon macedonicum subsp. *macedonicum*	2030001020	A111000000	0100102020	10011110-0	1000
Bunium elegans	2220112030	0000000100	2-10001001	20001000-0	0000
Carum carvi	2021000000	0011000001	00100?0000	10102000-0	0000
Caucalis platycarpos	0030100010	2000020000	0010001111	1011110111	2000
Chaerophyllopsis huaui	?030000-0-	---?000000	00000?0000	10101000-0	0000
Chaerophyllum aromaticum	2020000030	2101000011	2-10011000	20012000-0	0000
Chaerophyllum astrantiae	2021110020	2101000011	2-10010000	30012000-0	0000
Chaerophyllum atlanticum	2020001030	2101000010	2-10111000	30002000-0	0000
Chaerophyllum aureum	2030000020	2101000011	2-10011000	20012000-0	0000

Appendix 2. Continued.

Chaerophyllum azoricum	2020000030	2101000011	2-10010000	30002000-0	0000
Chaerophyllum bulbosum	0130010020	0001000011	2-10012000	20012000-0	0000
Chaerophyllum byzantinum	2020001030	2001000011	2-10011000	30002000-0	0000
Chaerophyllum crinitum	0131110020	2001000011	2-11011000	30012000-0	0000
Chaerophyllum elegans	2030000020	2001000011	2-12012000	30012000-0	0000
Chaerophyllum hirsutum	2030000020	2001000011	2-12012000	30012000-0	0000
Chaerophyllum khorassanicum	2040000020	2100000011	2-10111020	30002000-0	1000
Chaerophyllum libanoticum	2020001030	2001000011	2-10011000	30002000-0	0000
Chaerophyllum macropodum	0041010020	2100000011	2-10110001	30002000-0	0000
Chaerophyllum macrospermum	1031010030	1100000011	2-10111000	30002000-0	0000
Chaerophyllum magellense	2020000030	2101000011	2-12011000	30012000-0	0000
Chaerophyllum meyeri	0120000020	0001000011	2-10010000	20012000-0	0000
Chaerophyllum procumbens	0020000020	2000020110	2-00010000	20012000-0	B000
Chaerophyllum tainturieri	0031000020	1000020110	2-00010000	10012000-0	B000
Chaerophyllum temulum	003000Q020	2101010011	2-10012000	20012000-0	B000
Chaerophyllum villarsii	2020000020	2001000011	2-12012000	30012000-0	0000
Chaetosciadium trichospermum	0020000030	2010110000	0110111020	2010110120	1110
Cicuta virosa	2020000030	0011000100	0000010000	0000A000-0	0000
Conopodium ramosum	2220110010	0011000010	2-000?2000	20111000-0	0000
Daucus carota	0020012132	2101000001	0010010110	1001110111	2000
Echinophora tenuifolia subsp. *sibthorpiana*	1020001020	A100011010	01001?202-	20010100-0	1000
Elaeosticta allioides	2121112030	0001000100	2-10001000	00100000-0	0000
Falcaria vulgaris	0010002020	0011000000	0000011000	20100000-0	0000
Geocaryum macrocarpum	2220010020	1001000001	2-00010100	20114000-0	0110
Grammosciadium daucoides	2022112122	0011000001	0010001000	30002010-0	0000
Grammosciadium macrodon	2022112122	1011000001	0010001000	30002010-0	0000
Grammosciadium platycarpum	2022112112	0011000001	0010001000	30002010-0	0000
Grammosciadium pterocarpum	2012112112	0011000001	0010001000	30002010-0	0000
Heracleum sphondylium	1010000010	2111000001	2-00000020	10001020-0	0000
Heteromorpha arborescens	201000207O	A101000000	0000001010	10101000-0	1000

Appendix 2. Continued.

Kozlovia paleacea	1220000020	2001000011	2-10010100	20114100-1	2111
Krasnovia longiloba	2220110020	1001000010	2-00010100	20014000-1	C111
Laserpitium hispidum	1030002030	2101000000	0100010020	1000110100	2000
Laserpitium petrophilum	2020012030	2001000000	0000010010	1000110100	2000
Lecokia cretica	2020001030	0011000000	0000001010	10100000-0	2000
Myrrhis odorata	2030000020	210-000001	1010011020	20114100-0	2101
Myrrhoides nodosa	0020000020	2100020010	2-101?0021	20002000-1	2000
Neoconopodium capnoides	2220000020	1001000001	2-00010000	20114B00-0	C111
Neoconopodium laseroides	2220000020	1001000001	2-00010100	20114100-0	2111
Orlaya grandiflora	0020001010	1001000001	0010000101	1001111110	2000
Osmorhiza aristata	2030000020	2100000001	2-01011100	31114100-0	2111
Osmorhiza berteroi	2030000000	2000000000	2-01012100	31114100-0	2111
Osmorhiza brachypoda	2030001020	2000000000	2-02010000	31114100-0	2111
Osmorhiza claytonii	2030000020	2000000000	2-01011100	31114100-0	2111
Osmorhiza depauperata	2030000000	2001000000	2-01012100	31114100-0	2111
Osmorhiza longistylis	2030001020	2000000001	2-01011100	31114100-0	2111
Osmorhiza mexicana subsp. *bipatriata*	2030000010	2000000000	2-01010100	31114100-0	0111
Osmorhiza mexicana subsp. *mexicana*	2030000010	2000000000	2-01010100	31114100-0	2111
Osmorhiza occidentalis	2020000000	2001000000	2-01010000	30114100-0	0111
Osmorhiza purpurea	203000000-	---0000000	2-01010100	31114100-0	2111
Pastinaca sativa	0010000010	0011000000	2-00010010	10001020-0	0000
Petroselinum crispum	0030001130	0011000000	2-00100000	10001000-0	0000
Pimpinella peregrina	0010010000	A111000100	2-00002020	10001100-0	10?0
Pseudorlaya pumila	0020001111	2100010000	0100101020	1000111110	2000
Rhabdosciadium aucheri	2000021020	0001121010	0000001000	30101000-0	0000
Rhopalosciadium stereocalyx	0020000020	A11?000???	011011102?	30?0?1???0	2???
Scaligeria moreana	0020020020	0011000100	2-10001000	00100000-0	0000
Scandix balansae	0021110021	1000010001	2-00010001	20022100-0	2011
Scandix iberica	0021110021	2100010001	2-10010001	20022100-0	2011
Scandix pecten-veneris	0021110021	2000010001	2-00011001	30022100-1	2011
Scandix stellata	0021110012	2110010100	2-00011001	30021100-1	2011

Appendix 2. Continued.

Sium latifolium	2010002030	0001000000	0000012010	10001000-0	0000
Smyrnium olusatrum	0030000020	1001000011	10000?2010	10101000-0	0000
Sphallerocarpus gracilis	0040000020	2001000001	1000010000	10101000-0	0000
Tinguarra cervariifolia	2030001030	2111000000	0102102020	10111100-0	10?0
Tinguarra montana	2040000030	2111000000	0102102020	10101110-0	1000
Torilis nodosa	0020001010	A110120100	0000112021	1010110111	2-10