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Systematic Botany, Vol. 26, No. 3. (Jul. - Sep., 2001), pp. 622-642.

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Relationships Within the Spiny-Fruited Umbellifers (Scandiceae subtribes Daucinae and Torilidinae) as Assessed by Phylogenetic Analysis of Morphological Characters

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ABSTRACT. Previous molecular systematic studies have indicated that the spiny-fruited umbellifers (Apiaceae tribe Caucalideae sensu Heywood) comprise two major lineages, recently delimited as Scandiceae subtribes Daucinae and Torilidinae, with the former including representation of tribe Laserpitieae sensu Drude. These taxa are allied with the monophyletic Scandiceae subtribe Scandicinae whose members lack spiny fruits. The relationship among these three subtribes is equivocal when nuclear ribosomal DNA internal transcribed spacer sequences are compared. Evidence from plastid DNA, however, suggests that Daucinae and Torilidinae are sister taxa. Herein, we provide results of a phylogenetic study of these spiny-fruited umbellifers based on morphology in order to study the evolution of these characters and to ascertain their utility for resolving relationships by comparison to the results of previous molecular analyses. Maximum parsimony analysis of 56 morphological characters resulted in a paraphyletic Torilidinae (*Astrodaucus*, *Caucalis*, *Glochidotheca*, *Lisaea*, *Szovitsia*, *Torilis*, *Turgenia*, and *Yabea*) from which a monophyletic Daucinae (*Agrocharis*, *Ammodaucus*, *Cuminum*, *Daucus*, *Laserpitium*, *Orlaya*, *Pachyctenium*, and *Pseudorlaya*) are derived. Scandicinae are maintained as monophyletic, sister to Daucinae plus Torilidinae. The genus *Artemisia*, previously attributable to either Daucinae or Torilidinae, shows affinity with the former. The Daucinae plus Torilidinae clade is supported by three fruit synapomorphies—the regular distribution of appendages on both primary and secondary ridges, the presence of primary ridges and hairs on the face of the commissure, and the presence of vittae under the lateral ridges—but each subtribe cannot be circumscribed unambiguously on the basis of morphological data. Characters of the primary appendages exhibit less homoplasy than those of the secondary fruit appendages and support many clades identified in the molecular analyses. Parsimony analysis of combined morphological and ITS data, however, reaffirms the monophyly of subtribe Torilidinae and provides greater resolution of relationships within each of the subtribes than do either of the separate analyses.

Tribe Caucalideae Spreng. was described by Bentham (1867) and Boissier (1872) for those Apiaceae having spines, hooks, tubercles, or bristly hairs on the primary and/or secondary (vallecular) ridges of the fruits. This group reaches its greatest diversity in the Mediterranean region (Heywood 1982b) and includes such economically important members as carrots (*Daucus carota* L.) and cumin (*Cuminum cyminum* L.) and widespread weeds such as hedge-parsley (*Torilis* spp.). Heywood and Jury (in Heywood 1982b) recognized 21 genera and 68 spe-

cies within the tribe, whereas more recent studies incorporating molecular data have removed *Aphanopleura* Boiss., *Kozlovkia* Lipsky, and *Psammogeton* Edgew. (Katz-Downie et al. 1999; Lee and Downie 1999; 2000; Downie et al. 2000). The monotypic *Chaetosciadium* Boiss. has been returned to *Torilis* (as *T. trichosperma* (L.) Spreng.). It was also recommended that the subspecific status of *Daucus maximus* Desf. be resumed (as *D. carota* subsp. *maximus* (Desf.) Ball; Lee and Downie 2000).

The taxonomic history of Caucalideae and a sum-

mary of the multidisciplinary studies the group has received are presented in two symposium volumes (Heywood 1971a; Cauwet-Marc and Carbonnier 1982). More recently, issues of relationship among the spiny-fruited umbellifers and related species have been addressed using a variety of molecular characters. Phylogenetic analyses of nuclear ribosomal DNA (rDNA) internal transcribed spacer (ITS) sequences (Lee and Downie 1999; Downie et al. 2000), chloroplast DNA (cpDNA) restriction sites (Plunkett and Downie 1999; Lee and Downie 2000), and chloroplast *rps16* intron sequences (Lee and Downie 2000) of representative taxa each resulted in three major lineages that were subsequently treated as Scandiceae subtribes Daucinae Dumort., Torilidinae Dumort., and Scandicinae Tausch (Downie et al. 2000). These groups were previously attributable to the "*Daucus*," "*Torilis*," and "*Scandix*" subclades, respectively, within a larger "*Daucus*" clade (Plunkett et al. 1996; Downie et al. 1998; Plunkett and Downie 1999, 2000). Subtribes Daucinae and Torilidinae, with the addition of representatives of Drude's (1898) tribe Laserpitieae in Daucinae (i.e., *Laser* Borkh. ex P. Gaertn., B. Mey. & Schreb., *Laserpitium* L., *Melanoselinum* Hoffm., *Monizia* Lowe, and *Polylophium* Boiss.) and the exclusion of *Aphanopleura*, *Kozlovia*, and *Psammogeton*, coincide approximately with tribe Caucalideae sensu Heywood (1982b) or Dauceae plus Scandiceae subtribe Caucalidinae sensu Drude (1898). Subtribe Scandicinae coincides closely with Scandiceae sensu Heywood (1971b) or Scandiceae subtribe Scandicinae sensu Drude (1898).

In this paper, we compare the results of previous molecular analyses to a phylogeny for tribe Scandiceae as inferred by morphological characters. We place emphasis on the spiny-fruited umbellifers (i.e., Scandiceae subtribes Daucinae and Torilidinae or tribe Caucalideae sensu Heywood); for while we include representation of Scandiceae subtribe Scandicinae, a more thorough analysis of the relationships among its constituent genera, based on molecular, anatomical, and morphological data, are presented elsewhere (Downie et al. 2000; Spalik and Downie 2001; Spalik et al. 2001). Considerable controversy exists as to what features of the fruit are most useful in clade determination, for among the spiny-fruited umbellifers the fruit is extremely variable, both externally and internally (Heywood 1968a, 1982a; Heywood and Dakshini 1971; McNeill et al. 1969; Jury 1982, 1986; Saenz de Rivas et al. 1982). Characters of taxonomic importance have included the form and arrangement of the primary

and secondary ridges and their associated appendages, the shape of the endosperm in transverse section, and the position of the vittae (oil ducts). In addition to improving resolution of relationships within Daucinae and Torilidinae, we identify those morphological characters that are most useful in delimiting genera and infrageneric taxa within each as well as those characters that would permit identification of the subtribes.

MATERIALS AND METHODS

Morphological Analyses. Forty-three accessions representing 38 species and 17 of the 21 genera recognized by Heywood and Jury (Heywood 1982b) in Caucalideae and maintained in Scandiceae subtribes Daucinae and Torilidinae on the basis of phylogenetic analysis of molecular data were examined for morphological character variation. Adequate herbarium material of the rare, monotypic genus *Angosesele* was unavailable for analysis. *Aphanopleura* and *Psammogeton*, included in Caucalideae by Heywood (1982b) but excluded from Scandiceae on the basis of molecular data (Katz-Downie et al. 1999), were retained in this study to confirm if morphology also corroborates their removal from Scandiceae. Also included were seven species (five genera) of Scandiceae subtribe Scandicinae, including the genus *Kozlovia*, which was previously treated in Caucalideae (Heywood 1982b). Three species (two genera) of Drude's tribe Laserpitieae were also considered, as previous molecular analyses placed *Laser* and *Laserpitium* within subtribe Daucinae. *Smyrniun* and *Lecokia* were used to root the trees, as earlier studies indicated that these genera are most appropriate outgroups (Downie et al. 1998; Katz-Downie et al. 1999). In total, 57 accessions were included in the morphological data set (Table 1).

Morphological characters were examined from herbarium material, living plants grown from seed in the greenhouse, or material preserved in ethanol using either an Olympus SZ dissecting microscope (7–40× magnification) or an Olympus BHB optical microscope (100–400× magnification). A list of herbarium specimens examined for each species is available in Lee (1998). Vouchers for greenhouse propagated material are deposited at ILL. For those species where herbarium material was limited (i.e., *Aphanopleura* and *Psammogeton*), supplementary information was obtained from revisionary studies (Clarke 1879; Wolff 1927; Nasir 1972; Leute 1987). Fifty-six characters (seven quantitative and 49 qualitative) were measured or scored for phylogenetic

TABLE 1. Species of Apiaceae tribe Scandiceae and outgroups included in cladistic analysis of morphological data, and source and voucher information for those specific accessions examined for nuclear rDNA ITS sequence variation (Katz-Downie et al. 1999; Lee and Downie 1999). Herbarium acronyms according to Holmgren et al. (1990). UIUC = University of Illinois at Urbana-Champaign.

Species	Source and voucher information for ITS data
<i>Agrocharis incognita</i> (C. Norman) Heywood & Jury	Kenya, Nairobi, DNA supplied by E. Knox (coll. 2578)
<i>Agrocharis melanantha</i> Hochst.	Kenya, Nairobi, DNA supplied by E. Knox (coll. 2579)
<i>Agrocharis pedunculata</i> (Baker f.) Heywood & Jury	Malawi, Limbe, Mpingwe Hill, <i>Hillard & Burt</i> 4131 (E)
<i>Ammodaucus leucotrichus</i> (Coss. & Dur.) Coss. & Dur.	Spain, Canary Islands, Tenerife, <i>Santos-Guerra s.n.</i> (ORT)
<i>Anthriscus caucalis</i> M. Bieb.	cult. UIUC from seeds obtained from Jardin botanique de Caen, France, <i>Lee</i> 44 (ILL)
<i>Anthriscus cerefolium</i> (L.) Hoffm.	cult. UIUC from seeds obtained from Real Jardín Botánico, Spain, <i>Downie</i> 35 (ILL)
<i>Artedia squamata</i> L.	Turkey, Tarsus, Namrun Plateau, <i>Kasapligil</i> 6483 (UC)
<i>Astrodaucus orientalis</i> (L.) Drude	Iran, cult. UIUC from seeds obtained from Research Institute of Forests and Rangelands, Iran, <i>Lee</i> 43 (ILL)
<i>Caucalis platycarpos</i> L.	cult. UIUC from seeds obtained from Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben, Germany, <i>Lee</i> 29 (ILL)
<i>Cuminum cyminum</i> L.	India, cult. UIUC from seeds obtained from grocery store, <i>Lee</i> 120 (ILL)
<i>Cuminum setifolium</i> (Boiss.) Koso-Pol.	Afghanistan, Kandahar, Ispoli, <i>Hedge et al.</i> W7083 (E)
<i>Daucus aureus</i> Desf.	cult. UIUC from seeds obtained from Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben, Germany, <i>Lee</i> 57 (ILL)
<i>Daucus bicolor</i> Sibth. & Sm. subsp. <i>bicolor</i>	Israel, Judean Mtns., Har Herzal, cult. UIUC from seeds obtained from O. Cohen, <i>Lee</i> 270 (ILL)
<i>Daucus bicolor</i> subsp. <i>broteri</i> (Ten.) Okeke	Lebanon, cult. UIUC from seeds obtained from USDA acc. 286611, <i>Lee</i> 185 (ILL)
<i>Daucus carota</i> L. subsp. <i>carota</i>	Kazakhstan, cult. UIUC from seeds obtained from USDA acc. 478882, <i>Lee</i> 167 (ILL)
<i>Daucus carota</i> subsp. <i>gummifer</i> Hook. f.	cult. UIUC from seeds obtained from Jardin botanique de Caen, France, <i>Lee</i> 47 (ILL)
<i>Daucus carota</i> subsp. <i>halophilus</i> (Brot.) Okeke	cult. UIUC from seeds obtained from J.-P. Reduron, Mulhouse, France, <i>Lee</i> 81 (ILL)
<i>Daucus carota</i> subsp. <i>maximus</i> (Desf.) Ball	cult. UIUC from seeds obtained from Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben, Germany, <i>Lee</i> 64 (ILL)
<i>Daucus carota</i> subsp. <i>sativus</i> (Hoffm.) Arcang.	cult. UIUC from seeds obtained from Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben, Germany, <i>Lee</i> 73 (ILL)
<i>Daucus crinitus</i> Desf.	cult. UIUC from seeds obtained from Jardim Botânico de Lisboa, Portugal, <i>Lee</i> 49 (ILL)
<i>Daucus durieua</i> Lange	Israel, Samarian Desert near Sartaba, cult. UIUC from seeds obtained from O. Cohen, <i>Lee</i> 271 (ILL)
<i>Daucus montanus</i> Humb. & Bonpl.	Argentina, cult. Botanical Garden of the University of California, Berkeley 94.0563
<i>Daucus muricatus</i> L.	cult. UIUC from seeds obtained from Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben, Germany, <i>Lee</i> 36 (ILL)
<i>Daucus pusillus</i> Michx.	cult. Botanical Garden of the University of California, Berkeley 92.0891
<i>Glochidotherca foeniculacea</i> Fenzl	Turkey, Adana, <i>Alava</i> 6698 (UC)
<i>Kozlovia paleacea</i> (Regel & Schmalh.) Lipsky	Afghanistan, Baghlan, <i>Podlech</i> 21615 (NY)

TABLE 1. Continued.

Species	Source and voucher information for ITS data
<i>Laser trilobum</i> (L.) Borkh.	Azerbaijan, Caucasus, Vel-Veli-Chai, <i>Pimenov et al. s.n.</i> (MW), cult. Moscow State University Botanical Garden, Russia
<i>Laserpitium hispidum</i> M. Bieb.	cult. UIUC from seeds obtained from Hungarian Academy of Sciences Botanical Garden, Vácrátót, <i>Lee 68</i> (ILL)
<i>Laserpitium siler</i> L.	cult. UIUC from seeds obtained from Johannes Gutenberg University, Germany, <i>Downie 71</i> (ILL)
<i>Lisaea heterocarpa</i> (DC.) Boiss.	Iran, Durud, Luristan, <i>Koelz 15501a</i> (US)
<i>Lisaea papyracea</i> Boiss.	Armenia, <i>Gambarian s.n.</i> (UC)
<i>Lisaea strigosa</i> (Banks & Sol.) Eig	Azerbaijan, Baku to Marand, <i>Lamond 3884a</i> (E)
<i>Myrrhis odorata</i> (L.) Scop.	Europe, cult. Botanical Garden of the University of California, Berkeley 89.1236
<i>Orlaya daucoides</i> (L.) Greuter	cult. UIUC from seeds obtained from Hungarian Academy of Sciences Botanical Garden, Vácrátót, <i>Lee 7</i> (ILL)
<i>Orlaya daucorlaya</i> Murb.	Macedonia, Kuceviste, <i>Edmonston 27</i> (E)
<i>Orlaya grandiflora</i> (L.) Hoffm.	cult. UIUC from seeds obtained from Karl Marx University Botanical Garden, Leipzig, Germany, <i>Lee 41</i> (ILL)
<i>Osmorhiza longistylis</i> (Torr.) DC.	USA, Illinois, Champaign Co., Urbana, <i>Downie 738</i> (ILL)
<i>Pachyctenium mirabile</i> Maire & Pamp.	Libya, E. Shahat, Cyrene, <i>Davis 50249</i> (E)
<i>Pseudorlaya pumila</i> (L.) Grande	cult. UIUC from seeds obtained from Jardim Botânico de Lisboa, Portugal, <i>Lee 59</i> (ILL)
<i>Scandix balansae</i> Reut. ex Boiss.	cult. UIUC from seeds obtained from Karl Marx University Botanical Garden, Leipzig, Germany, <i>Lee 2</i> (ILL)
<i>Scandix pecten-veneris</i> L.	cult. UIUC from seeds obtained from Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben, Germany, <i>Downie 27</i> (ILL)
<i>Szovitsia callicarpa</i> Fisch. & C. A. Mey.	Azerbaijan, Moghan, <i>Lamond 3195</i> (E)
<i>Torilis arvensis</i> (Huds.) Link subsp. <i>arvensis</i>	England, Buckinghamshire, Amersham, <i>Southam s.n.</i> (RNG)
<i>Torilis arvensis</i> subsp. <i>purpurea</i> (Ten.) Hayek	Morocco, Col du Nador, <i>Jury & Wilson s.n.</i> (RNG)
<i>Torilis elongata</i> (Hoffm. & Link) Samp.	Morocco, Col du Nador, <i>Jury & Wilson s.n.</i> (RNG)
<i>Torilis japonica</i> (Houtt.) DC.	not included in molecular analysis
<i>Torilis leptophylla</i> (L.) Rchb. f.	Asia Minor; cult. UIUC from seeds obtained from <i>Anonymous</i> (K), <i>Lee 107</i> (ILL)
<i>Torilis nodosa</i> (L.) Gaertn.	England, Isle of Wight, <i>Linington & Shepard s.n.</i> (K)
<i>Torilis scabra</i> (Thunb.) DC.	Japan, Okinawa, <i>Beauchamp 1217</i> (US)
<i>Torilis tenella</i> (Delile) Rchb. f.	Jordan, Ajlun, Schtafeenah, <i>Lahham & El-Oqlah 1</i> (Yarmouk University Herbarium, Jordan)
<i>Torilis trichosperma</i> (L.) Spreng.	Jordan, Um-Qais, near Irbid, <i>Lahham & El-Oqlah 4</i> (Yarmouk University Herbarium, Jordan) [as syn. <i>Chaetosciadium trichospermum</i> (L.) Boiss.]
<i>Turgenia latifolia</i> (L.) Hoffm.	cult. UIUC from seeds obtained from J.-P. Reduron, Mulhouse, France; <i>Lee 82</i> (ILL)
<i>Yabea microcarpa</i> (Hook. & Arn.) Koso-Pol.	USA, Arizona, Pima Co., <i>Holmgren 6772</i> (WTU)
Outgroups	
<i>Aphanopleura trachysperma</i> Boiss.	not included in molecular analysis
<i>Psammogeton canescens</i> (DC.) Vatke	not included in molecular analysis
<i>Lecokia cretica</i> (Lam.) DC.	Jordan, Ajlun, Schtafeenah, <i>Lahham & El-Oqlah 7</i> (Yarmouk University Herbarium, Jordan)
<i>Smyrniium olusatrum</i> L.	cult. UIUC from seeds obtained from Karl Marx University Botanical Garden, Leipzig, Germany, <i>Lee 113</i> (ILL)

TABLE 2. Morphological characters and character state descriptions used in the cladistic analysis of Apiaceae tribe Scandiceae and outgroup taxa. Ordered characters are indicated.

1. Cotyledon type: round or ovate (0), linear (1).
2. Pollen type: subrhomboidal (0), oval (1), subrectangular (2), equatorially-constricted (3).
3. Stem habit: erect or ascending (0), procumbent or semi-climbing (1).
4. Stem surface or vestiture type: glabrous (0), hispid and spreading (1), retrorsely appressed (2), glochidiate (3), pilose (4).
5. Basal and lower cauline leaf division: ternate (0), 1-pinnate (1), 2-4 pinnate (2), bi-ternate (3).
6. Basal and lower cauline leaf lobe shape: linear-lanceolate (0), filiform (1), oblong-ovate (2).
7. Bracts: absent or rarely one (0), present but caducous (1), present but not caducous (2).
8. Bract shape: simple and linear (0), 3-fid (1), pinnatisect (2).
9. Bract position after anthesis: unchanged (0), strongly curving upwards (1), deflexed (2).
10. Bracteoles: absent (0), present (1).
11. Bracteole division: entire or bifid (0), mostly 3-fid (1), pinnatisect (2).
12. Terminal inflorescence: present (0), absent (1).
13. Ray surface or vestiture type: glabrous (0), hispid and spreading (1), retrorsely appressed (2), glochidiate (3), pilose (4).
14. Ray position after anthesis: unchanged (0), curving upwards (1).
15. Ray number (ordered).
16. Ratio of longest to shortest ray (ordered).
17. Flower sexuality: all flowers perfect (0), perfect and staminate flowers present (1).
18. Central flowers purple: absent (0), present (1).
19. Length of outer petals (ordered).
20. Ratio of longest to shortest petal (ordered).
21. Ratio of style to stylopodium (ordered).
22. Length of style (ordered).
23. Bristles on petal: absent (0), present (1).
24. Stylopodium shape: flat-conic (0), conic (1), depressed (2).
25. Fruit length (ordered).
26. Fruit shape: globose to ovoid (0), elliptic or linear (1).
27. Fruit beak: present (0), absent (1).
28. Fruit compression: compressed laterally or not compressed (0), distinctly dorsally compressed (1).
29. Mature fruit epidermis color: green (0), black (1).
30. Mericarp surface: smooth (0), papillate (1), tuberculate (2), spiny mass (3), peg-like (4).
31. Appendages on fruit surface: absent (0), present (1).
32. Appendage distribution: absent, or infrequent only on primary or secondary ridges (0), regular on both primary and secondary ridges (1).

TABLE 2. Continued.

33. Primary ridge hairs on fruit dorsal surface: absent (0), present (1).
34. Primary ridges and hairs on mericarp commissural face: absent (0), present (1).
35. Primary ridge indumentum: bristles (0), bristles with swollen bases (1), spines (2), spine-like hairs (3).
36. Primary hair apex: straight (0), curved (1).
37. Primary appendage grouping: none (0), multiple (1).
38. Primary hair arrangement: up to biseriate (0), more than tri-seriate (1).
39. Primary hair orientation: spreading laterally, or more or less erect (0), directed toward stylar end (1).
40. Primary hair attachment to mericarp: simple (0), lobed (1).
41. Primary hair surface: striate or smooth (0), tuberculate (1), papillate (2).
42. Development of secondary ridges: not developed (0), developed with broad ridges (1), developed with narrow ridges (2).
43. Secondary ridge appendages: absent (0), present (1).
44. Secondary ridge appendage type: multiple-celled projections (0), long bristles (1), spines (2), undulate wings (3), spatulate plicate (4), dentate wings (5).
45. Secondary ridge appendage arrangement: one row (0), two rows (1), more than two rows (2).
46. Secondary appendage base: free (0), confluent (1).
47. Secondary appendage apex: simple or tapering (0), glochidiate (1), tuberculate (2), rounded (3).
48. Secondary appendage surface: striate or smooth (0), papillate (1), peg-like (2), tuberculate (3), stiff, tiny bristles (4).
49. Mesocarp thickness: thick (0), too thin to tell mesocarp from exocarp (1).
50. Vittae development: very tiny or reduced (0), conspicuously developed (1).
51. Vittae shape: elliptic or oval (0), triangular (1).
52. Number of vittae below secondary ridge: one (0), numerous (1).
53. Number of vittae on commissural face: two (0), four (1), numerous (2).
54. Vittae under lateral ridge: absent (0), present (1).
55. Endosperm shape in cross section: flat (0), curved (1), recurved (2).
56. Chromosome base number: $x = 6$ (0), $x = 7$ (1), $x = 8$ (2), $x = 9$ (3), $x = 10$ (4), $x = 11$ (5).

analysis (Table 2). Thirty-one of these are fruit characters, ten are inflorescence or bract characters, eight are floral characters, and five are vegetative characters. Pollen type and chromosome base number were also considered, with this information obtained from Moore (1971), Constance et al. (1971), and Cauwet-Marc and Jury (1982). Line illustrations of the primary and secondary fruit appendages ex-

amined are presented in Lee (1998); illustrative material and photographs of other characters are available in Cerceau-Larrival (1962), Heywood (1968a, 1973), Okeke (1978, 1982), Jury (1986), Heywood and Dakshini (1971), and Saenz de Rivas et al. (1982). In several instances, however, some published illustrations and descriptions appeared to be inconsistent or in disagreement with our original observations. Our rationale for character and state selection and coding is presented in Lee (1998) and expanded upon in Spalik and Downie (2001). In the present study, the term morphological is used to represent broadly all aspects of the phenotype, including anatomy and chromosome number.

The seven quantitative characters (i.e., characters 15, 16, 19, 20, 21, 22, and 25; Table 2) were coded using the gap-weighting method (Thiele 1993). This coding method divides the range of taxon means for a character into a series of equal segments, each of which corresponds to an ordered state. Each taxon is assigned the state containing the taxon's mean value. Among currently available methods for coding quantitative data, Levin (unpublished data) found gap weighting to be among the best at retaining phylogenetic information. In this study we used 26 character states for each quantitative character, the limit imposed by MacClade (Maddison and Maddison 1992). Raw data for all quantitative characters are presented in Lee (1998). The 49 qualitative characters were treated as non-additive (un-ordered). The resultant data matrix for all 56 characters is presented in Appendix 1. Approximately 10% of all cells in the data matrix were scored as unknown or inapplicable. Because the number of states differed considerably among characters, particularly between quantitative characters with 26 states and qualitative characters with generally fewer than four states, all characters were weighted in inverse proportion to their number of steps using the SCALE option in PAUP version 3.1.1 (Swofford 1993). For the analysis of morphological characters alone, weights were assigned to all characters such that the minimum possible length of each character was as close to 1000 as possible (fractional weights cannot be used in this version of PAUP). Thus binary characters were assigned a weight of 1000, three-state characters a weight of 500, four-state characters a weight of 333, and so on, to the quantitative characters, which have 26 character states and so each received a weight of 40.

The data were analyzed phylogenetically using PAUP version 3.1.1 on a Power Macintosh 8500/120 computer. Heuristic searches were conducted with

100 random addition replicate searches and tree bisection-reconnection branch swapping. The options mulpars, steepest descent, collapse, and acctran optimization were selected. To assess the relative support for each monophyletic group, bootstrap values (Felsenstein 1985) were calculated from 100 replicate analyses using the heuristic search strategy and simple addition sequence of taxa. Also, the weights = simple option was used to assign each character an equal probability of being sampled and to use the weight attached to each character during the following search (Swofford 1993). Decay analyses (Bremer 1988) with tree lengths greater than those most parsimonious were conducted until PAUP ran out of tree storage memory. Measures of character fit in the parsimony analysis were estimated using the consistency (CI; Kluge and Farris 1969) and retention (RI; Farris 1989) indices.

Combined Analysis of Morphological and ITS Data. The spiny-fruited umbellifers were the subject of a previous phylogenetic study using nuclear rDNA ITS 1 and ITS 2 sequences (Lee and Downie 1999). Source and voucher information for the 54 accessions referred to herein is provided in Table 1. ITS data are also available for *Aphanopleura* and *Psammogeton*, but because these genera are clearly excluded from Scandiceae when molecular data are analyzed (Katz-Downie et al. 1999) they were not included in this portion of the investigation. ITS data for *Torilis japonica* were not available. Alignment of all 54 complete ITS 1 and ITS 2 sequences resulted in a matrix of 473 positions, of which 66 positions were excluded because of alignment ambiguities. Of the remaining 407 unambiguously aligned positions, 233 were potentially parsimony informative, 118 were constant, and 56 were autapomorphic. Additional sequence characteristics as well as the phylogenetic hypotheses inferred using these data (which include *Polylophium* and three additional outgroup taxa) are presented in Lee and Downie (1999, 2000).

Phylogenetic analysis of combined morphological and molecular data were carried out in two ways. First, only the 49 qualitative morphological characters were combined with the ITS data and these were analyzed using equally-weighted maximum parsimony, as the seven weighted and ordered quantitative morphological characters cannot be combined with DNA sequence data without considerations of weighting for both partitions. Second, a weight of 1000 was applied to each molecular character while maintaining the weights assigned earlier in the separate analysis of all 56 morphological

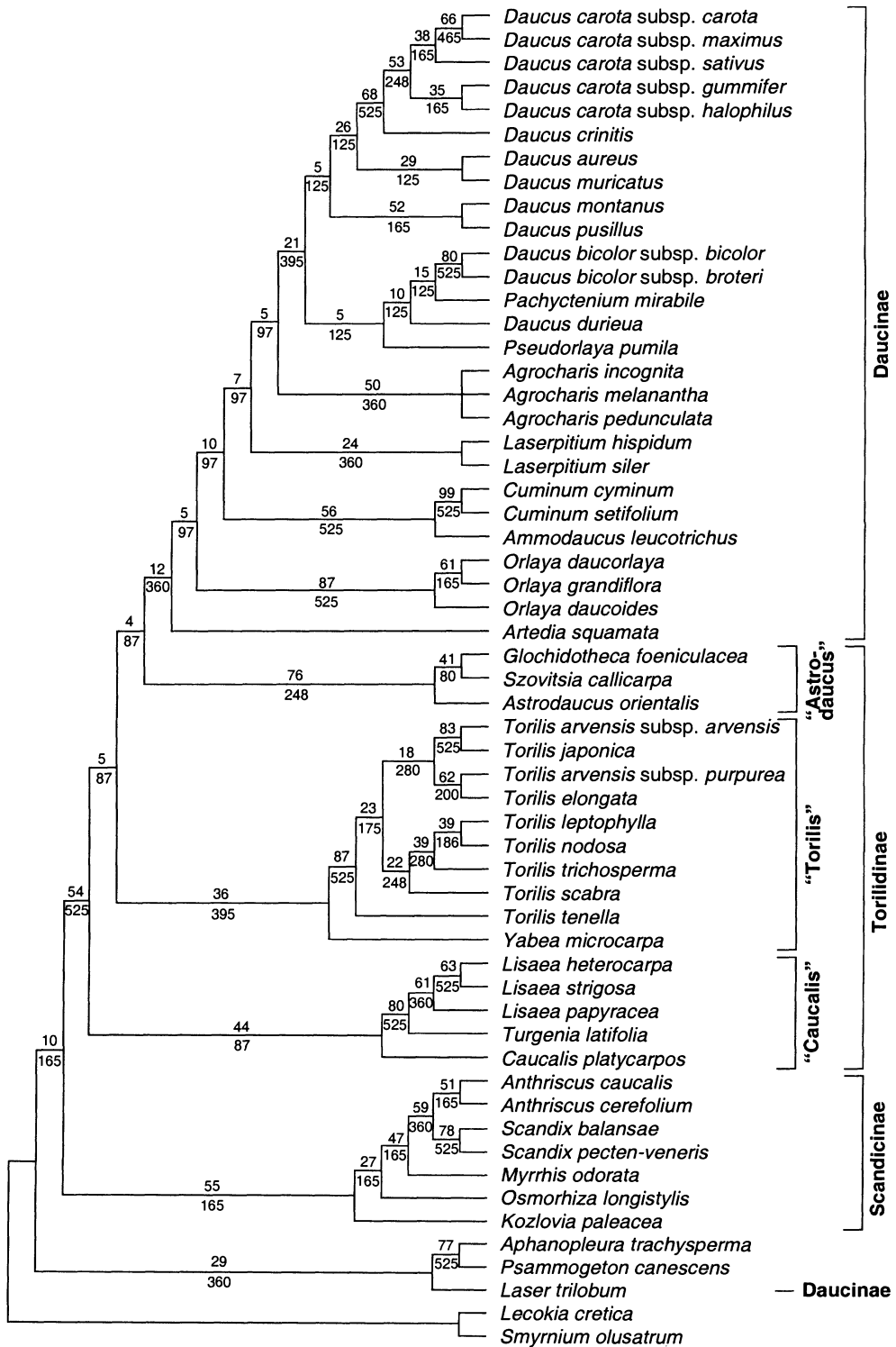


FIG. 1. Strict consensus of three minimal length 160,395 step trees derived from maximum parsimony analysis of 56 weighted morphological characters for 57 accessions of Apiaceae tribe Scandiceae and outgroup taxa (CI = 0.341; RI

characters. Maximum parsimony analysis of these weighted data were carried out as described previously. The strict consensus trees derived from both types of analyses were highly congruent, with the only differences between them being increased resolution of relationships within *Daucus carota* plus *Torilis* in the weighted analysis and the exchange of positions between *Lisaea papyracea* and *L. strigosa* and between *Kozlovkia* and *Myrrhis*. The weighted parsimony analysis, however, did not permit timely completion of the bootstrap and decay analyses, and the branch lengths obtained were highly inflated. Thus, all subsequent discussions of combined morphological and molecular data weight all characters equally and exclude the seven quantitative characters.

RESULTS

Morphological Analyses. Maximum parsimony analysis of the 56 morphological characters resulted in three minimal length trees differing only in the arrangement of the three species of *Agrocharis*. The strict consensus of these trees, with accompanying bootstrap and decay values, is presented in Fig. 1. Each of these trees, constructed with weighted characters, had a length of 160,395 steps, a CI of 0.341, and a RI of 0.739. Decay values ranged from 80 to 525; however, because all characters are weighted, these values are higher relative to those typically obtained when equally-weighted characters are considered. Bootstrap estimates were generally very low, with many basal nodes supported by values $\leq 12\%$.

The previously designated Scandiceae subtribes Daucinae, Torilidinae, and Scandicinae, erected on the basis of phylogenetic analyses of ITS sequences (Downie et al. 2000) and supported by other molecular phylogenetic studies (e.g., Plunkett and Downie 1999; Lee and Downie 2000), are indicated on this tree (and all other trees presented herein). Daucinae, with included *Artemisia*, is monophyletic with a decay value of 360 and a bootstrap value of 12%. Also included within Daucinae are the genera *Agrocharis*, *Ammodaucus*, *Cuminum*, *Daucus*, *Laserpitium*, *Orlaya*, *Pachytenium*, and *Pseudorlaya*. *Daucus* is not monophyletic as the genus includes *Pachy-*

tenium and *Pseudorlaya*. *Daucus carota* is monophyletic, as are *D. bicolor*, *Agrocharis*, *Laserpitium*, *Cuminum*, and *Orlaya*. Torilidinae are paraphyletic. Its paraphyly, however, is only weakly indicated, with its basal branches supported by bootstrap values of either 4 or 5%. Within the previously circumscribed Torilidinae, three major lineages are evident; we refer to these as the "*Astrodaucus*," "*Torilis*," and "*Caucalis*" subclades. The "*Astrodaucus*" subclade comprises the genera *Astrodaucus*, *Glochidotheca* (= *Turgeniopsis* Boiss.), and *Szovitsia*. The "*Torilis*" subclade comprises *Torilis* and *Yabea*, and the "*Caucalis*" subclade comprises *Caucalis*, *Lisaea*, and *Turgenia*. The genus *Torilis*, with seven of its ten species included in this investigation (Heywood 1982b), is monophyletic and supported by a bootstrap value of 87%. Also included within this clade is *Torilis trichosperma*, previously recognized as *Chaetosciadium trichospermum* (Lee and Downie 2000). Scandicinae are maintained as monophyletic but with a bootstrap value of 55% and a decay value of 165. Included within this subtribe are the genera *Anthriscus*, *Kozlovkia*, *Myrrhis*, *Osmorhiza*, and *Scandix*, all members of a "crown" clade with very close affinity (Spalik and Downie 2001). Scandicinae arise as sister to Daucinae plus Torilidinae. The genera *Aphanopleura* and *Psammogeton* are resolved as sister taxa near the base of the tree, and their position there outside of Scandiceae is consistent with the results of earlier molecular studies. However *Laser* groups with *Aphanopleura* and *Psammogeton*; its position there is in contrast to the previous molecular studies where it occurs within Daucinae.

Performance of Morphological Characters. One of the three maximally parsimonious trees was selected arbitrarily in order to show relative branch lengths and the positions of all character state changes for the 49 qualitative characters, as optimized by accelerated transformation (acctrans) in PAUP (Fig. 2). On this tree, 28 nonhomoplastic qualitative character state changes are inferred, and of these, those characters of the fruit (which account for 19 of these unique state changes) appear to be most useful in delimiting clades. For example, the five examined genera of Scandicinae are circumscribed by the presence of beaked fruits (character

←

= 0.739). Bootstrap values, for 100 replicate analyses, are presented above branches; decay values are presented below branches (and are inflated owing to the differential and sometimes large weights assigned to these characters). Scandiceae subtribes Daucinae, Torilidinae, and Scandicinae are indicated based on previous analyses of molecular data.

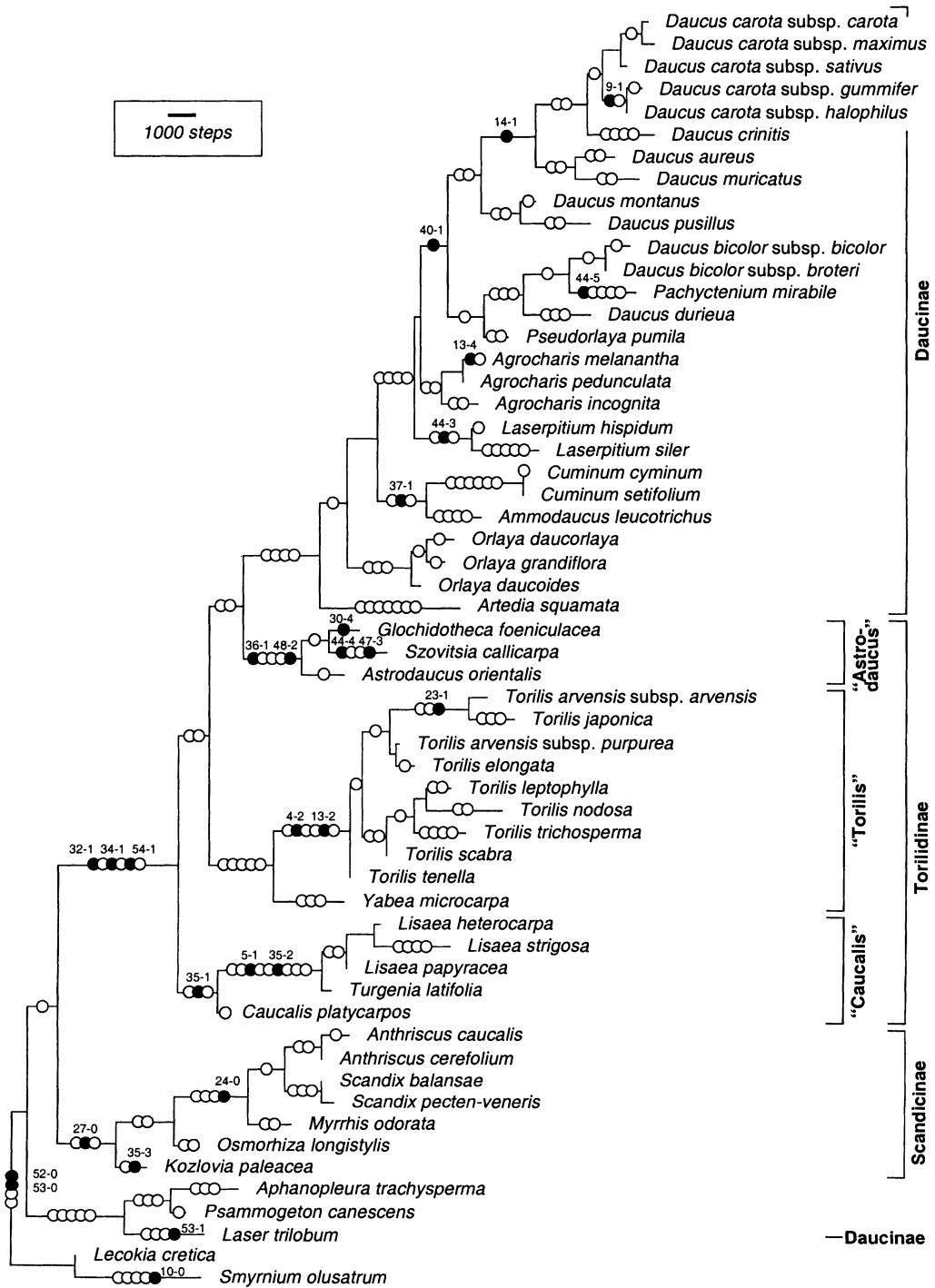


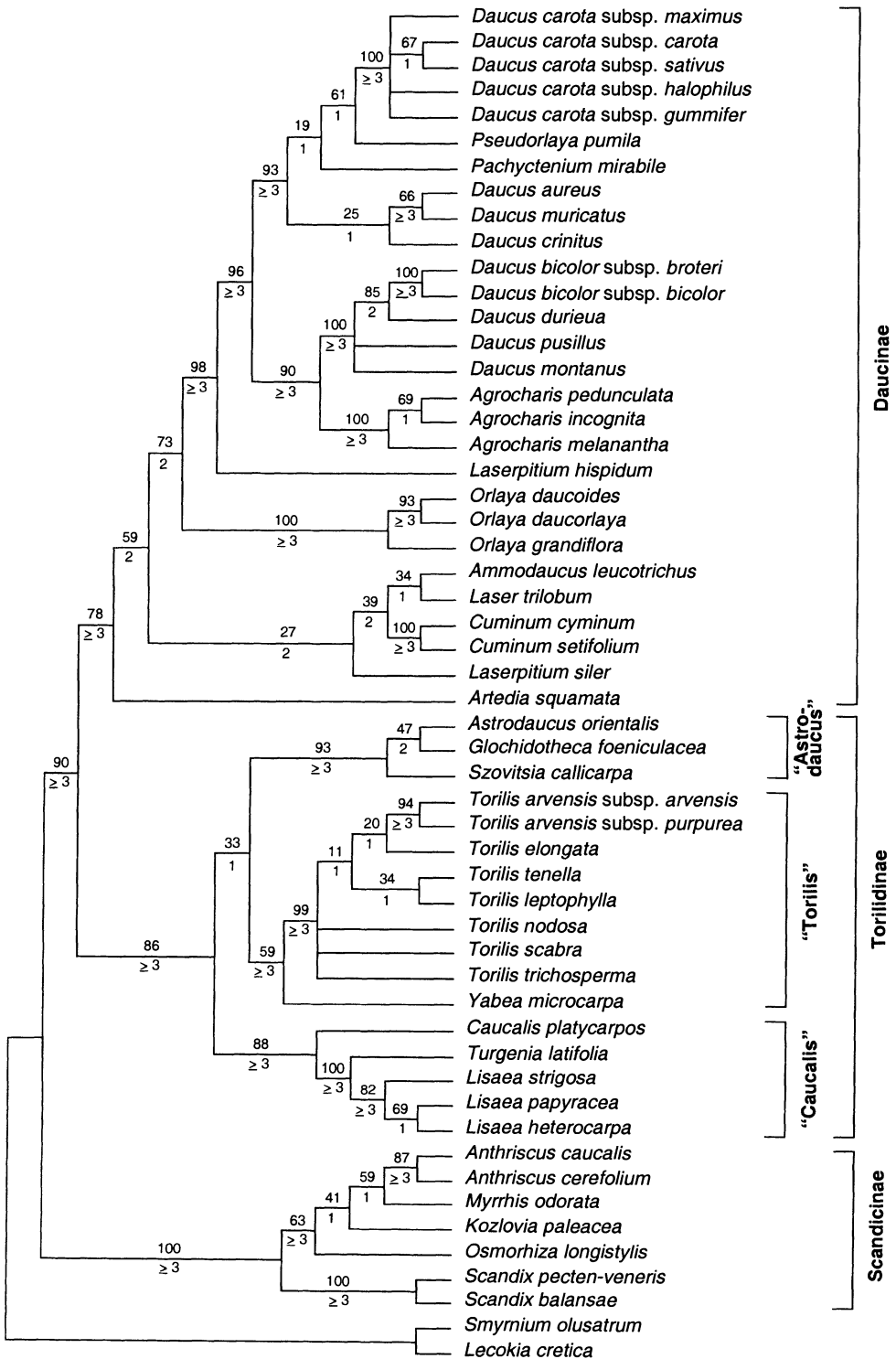
FIG. 2. One of three minimal length 160,395 step trees derived from maximum parsimony analysis of 56 weighted morphological characters for 57 accessions of Apiaceae tribe Scandiceae and outgroup taxa (CI = 0.341; RI = 0.739). Branch lengths are proportional to the number of acctran-inferred character state changes occurring along them (note scale bar); the positions of all character state changes for the 49 qualitative characters are indicated (open and solid circles). Non-homoplastic qualitative character state changes are shown by solid circles, with character and state changes indicated (see Table 2 for descriptions).

27, state 0) whereas the clade of Daucinae plus Torilidinae is defined by the regular distribution of appendages on both primary and secondary fruit ridges (character 32, state 1), the presence of primary ridges and hairs on the commissural face of the mericarp (character 34, state 1), and the presence of vittae under the lateral ridges (character 54, state 1). The "*Astrodaucus*" subclade is defined by primary hairs having a curved apex (character 36, state 1) and the presence of peg-like projections on the surfaces of its secondary appendages (character 48, state 2). Members of the "*Caucalis*" subclade are characterized by having a bristly indumentum on the primary ridges with swollen bases (character 35, state 1). The genus *Daucus* (with *Pachyctenium* and *Pseudorlaya* included) is characterized by a lobed primary appendage base (character 40, state 1), whereas *Laserpitium* is characterized by secondary ridge appendages with undulate wings (character 44, state 3). Scandiceae subtribe Daucinae are characterized by four qualitative and five quantitative character state changes that are each homoplastic, such as the presence of non-caducous bracts, dorsally-compressed fruits with well-developed narrow secondary ridges, and flat endosperm. Similarly, *Torilis* and *Yabea*, comprising the "*Torilis*" subclade of subtribe Torilidinae, also share nine homoplastic state changes (five qualitative and four quantitative) such as tuberculate mericarps and secondary appendages. Considering further the distribution of fruit characters on the tree in Fig. 2, the primary appendage characters (33–41) have higher consistency (range 0.25–1.0; average 0.66) and retention (range 0.4–1.0; average 0.88) indices than those characters of the secondary appendages (42–48). Indeed, five primary appendage characters (34, 35, 36, 37, and 40) each have a RI of 1.0. The seven secondary appendage characters have an average CI of 0.44 (range 0.2–0.83) and an average RI of 0.68 (range 0.43–0.96). Apparently, characters of the primary appendages have greater power to discern clades than do those of the secondary appendages.

CI values for the five vegetative characters ranged between 0.14–0.50 (average 0.42) and their RI values ranged between 0–0.82 (average 0.55). Considering the 10 inflorescence characters, CI and RI values ranged between 0.14–1.0 (average 0.43) and 0.25–1.0 (average 0.61), respectively. The eight floral characters, of which half were quantitative, possessed CIs of 0.14–1.0 (average 0.37) and RIs of 0.27–1.0 (average 0.60). While many floral and vegetative characters have low consistency and retention indices, a few are quite useful in defining

monophyletic groups. As examples, the sister relationship between *Turgenia* and *Lisaea* is supported by the shared presence of a once-pinnate compound leaf (character 5, state 1). The nine examined accessions of *Torilis* are each characterized by a retrorsely appressed stem indumentum (character 4, state 2) and appressed hairs on the rays (character 13, state 2). A major clade within *Daucus* is characterized by a curved ray after anthesis (character 14, state 1). Overall, however, the seven quantitative characters performed relatively poorly, with CI values ranging from 0.14 (character 22) to 0.42 (character 21; average 0.23). CI values for the 49 qualitative characters ranged from 0.14 (characters 6 and 7) to 1.0 (characters 10, 14, 23, 27, 34–37, 40, 52–54; average 0.46).

Phylogenetic Analysis of Combined Data. Maximum parsimony analysis of combined morphological and ITS data for 52 accessions of tribe Scandiceae plus two outgroup genera resulted in 16 minimal length trees. Their strict consensus, with accompanying bootstrap and decay values, is presented in Fig. 3. These trees, constructed with all characters equally weighted, each have a length of 1,200 steps, a CI (excluding uninformative characters) of 0.425, and a RI of 0.754. Major differences between the combined analysis and that of the separate analysis of morphological data include the reaffirmation of the monophyly of subtribe Torilidinae, a sister relationship between the "*Astrodaucus*" and "*Torilis*" subclades (albeit one that is very weakly supported), and the relative placements of *Agrocharis*, *Laser*, *Pachyctenium*, *Pseudorlaya*, and *Scandix*. Relationships among the three genera comprising the "*Astrodaucus*" subclade vary as well, as do those genera within subtribe Scandicinae. Similarly, the position of the New World endemics *Daucus montanus* and *D. pusillus* within the genus *Daucus* differs between the results of the two analyses, as does the position of *D. crinitus*. Subtribe Daucinae (with included *Artemisia*) is maintained as monophyletic and is sister to subtribe Torilidinae. Scandicinae are also retained as monophyletic. Bootstrap support for each of these subtribes (78–100%) as well as each of the three subclades within Torilidinae (59–93%) is much higher than that of the analysis of morphological data alone. Given that all characters were equally-weighted, the decay values are more readily interpretable than those of the previous analysis. Here all three subtribes and all three subclades within Torilidinae, as well as the sister group relationship between Daucinae and Torilidinae, are supported by decay values ≥ 3 .



The results of the combined analysis are highly consistent with those inferred using ITS data alone (Lee and Downie 1999, 2000). While the latter, however, are equivocal in resolving relationships among the three subtribes, the analysis of combined morphological and molecular data clearly supports a sister group relationship between Daucinae and Torilidinae. Indeed, greater resolution of relationships is achieved throughout the entire tree upon simultaneous consideration of both morphology and ITS data than upon separate analysis of either of these two data sets. The results of the combined morphological and ITS analysis are also similar to those inferred upon the basis of phylogenetic analysis of cpDNA restriction sites (Lee and Downie 2000), but again, with greater resolution when combined data are considered. While the restriction site study included only 32 accessions, both the monophyly of Daucinae and Torilidinae and their sister relationship was supported. Similar results were reported upon consideration of chloroplast *rps16* intron sequences (Lee and Downie 2000), with the only notable difference between this and previous studies being the placement of *Artemisia* within Torilidinae and not sister to remaining Daucinae.

DISCUSSION

Most classifications of Apiaceae, including that of Drude (1898), rely on a diverse array of subtle fruit differences to demarcate major taxonomic groups. Such characters include the degree and direction of mericarp compression, the shape of the endosperm, the distribution of sclerenchyma and calcium oxalate crystals in the fruit walls, and various characteristics of the vittae and fruit ridges. Serious doubts have been raised on the phylogenetic utility of these characters (e.g., Theobald 1971; Davis 1972; Cronquist 1982; Jury 1982; Hedge et al. 1987; Shneyer et al. 1992). Indeed, the results of recent phylogenetic analyses of molecular data (Plunkett et al. 1996; Downie et al. 1998; Katz-Downie et al. 1999) provided very little support for Drude's system or for any other non-phylogenetic treatment of the family based largely on anatomical and morpholog-

ical fruit characters. The utility of floral and vegetative features in circumscribing suprageneric groups fares no better, as the former are often quite uniform and the latter differ substantially even among closely related species (Okeke 1982). Considering the spiny-fruited umbellifers, a group characterized by the common possession of spines or other similar appendages on the primary and/or secondary ridges of the mericarps, each genus possesses a unique set of fruit surface features (Heywood and Dakshini 1971; Heywood 1986; Jury 1986; Saenz de Rivas et al. 1982). These characters, while permitting the easy recognition of species, are less useful in providing information on intergeneric relationships.

Previous molecular systematic studies incorporating data from either the chloroplast or nuclear genome (Lee and Downie 1999, 2000; Plunkett and Downie 1999; Downie et al. 2000) and the results of our analysis of combined morphological and ITS data revealed or confirmed three major clades within Apiaceae tribe Scandiceae: subtribes Daucinae, Torilidinae, and Scandicinae (Downie et al. 2000). Each of these clades is often well supported, with bootstrap values generally ranging between 85 and 100%. Subtribes Daucinae and Torilidinae (with the exclusion of those members treated by Drude in Laserpitieae) correspond approximately with Heywood's tribe Caucalideae or Drude's tribe Dauceae plus Scandiceae subtribe Caucalidinae. Subtribe Scandicinae coincides closely with Scandiceae sensu Heywood (1971b) or Drude's Scandiceae subtribe Scandicinae. In the present study, we compared a phylogeny for Scandiceae inferred from 56 morphological characters with those estimated using molecular data. While Daucinae are maintained as monophyletic, it seems to arise from within a paraphyletic Torilidinae when only morphology was considered. Scandicinae are maintained as distinct, sister to Daucinae plus Torilidinae. Within subtribe Torilidinae several smaller clades are evident (i.e., the *Astrodaucus*, *Torilis*, and *Caucalis* subclades), with many of these same clades resolved upon analyses of molecular data.

Traditionally, Caucalideae are circumscribed

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FIG. 3. Strict consensus of 16 minimal length 1,200 step trees derived from maximum parsimony analysis of 49 equally weighted qualitative morphological characters and nuclear rDNA ITS1 and ITS2 sequences for 54 accessions of Apiaceae tribe Scandiceae and outgroup taxa (CI without uninformative characters = 0.425; RI = 0.754). Bootstrap values, for 100 replicate analyses, are presented above branches; decay values are presented below.

largely upon the form and arrangement of the secondary (vallecular) ridges, as these are often more strongly developed than the primary ones. However, our analyses indicate that characters of the secondary appendages are highly homoplastic and that the relationships proposed on the basis of these data do not parallel those inferred using molecular evidence. For example, members of Drude's tribe Laserpitieae (e.g., *Laserpitium*), while lacking spinose fruit ridges, have prominent secondary ridges that are often extended into wings. However, these wings are inferred to have been lost at least twice independently during the evolution of subtribe Daucinae (Lee and Downie 2000). Indeed, within subfamily Apioidae in general, it has been noted that dorsal flattening and the formation of winged secondary appendages has likely evolved as a dispersal mechanism in many independent lineages (Theobald 1971; Plunkett et al. 1996; Downie et al. 1998) and it is not unrealistic to presume that multiple independent losses of wings can also occur. Moreover, anatomical and developmental studies have shown that dorsal flattening and wing formation can occur in a variety of different ways (Theobald 1971). In the present study, other highly homoplastic secondary appendage characters were inferred and include: character 46 (appendage base free or confluent; CI = 0.20); character 47 (appendage apex simple, glochidiate, tuberculate, or rounded; CI = 0.33); and character 45 (appendage arrangement one row, two rows, or more than two rows; CI = 0.33). Some species lack secondary appendages entirely (e.g., *Lisaea strigosa* and *Laser trilobum*). In *Artedia*, only the lateral secondary ridges have developed into expanded wings; the others are slender and filiform.

In contrast to the highly variable and sometimes homoplastic secondary appendage characters, those of the primary appendages provide much support for those clades inferred on the basis of molecular data (Fig. 1 in Lee and Downie 1999). As examples, spiny primary ridges (character 35, state 2) characterize *Turgenia* and *Lisaea*, curved primary hairs (character 36, state 1) are synapomorphic for *Astrodaucus*, *Glochidotheca*, and *Szovitsia*, grouped primary appendages (character 37, state 1) are found in only *Cuminum* and *Ammodaucus*, appressed primary hairs directed towards the styler end of the fruit (character 39, state 1) characterize all examined *Torilis* species, and a lobed primary hair base (character 40, state 1) is synapomorphic for *Daucus*, *Pseudorlaya*, and *Pachyctenium* (but not *Agrocharis*). The clade of Daucinae plus Torilidinae (this study) is

also supported by the presence of hairs on the primary ridges of the mericarp commissural face (character 34, state 1). Retention indices for five of the nine primary appendage characters are 1.0. The distribution and characterization of these primary appendage characters, heretofore underutilized in taxonomic studies of these plants, can offer much insight into evolutionary relationships. However, unlike the larger secondary appendages, which have an obvious role in fruit dispersal, the functional significance of these primary appendage characters is not known. The value of nonfunctional characters in classification has long been appreciated (Darwin 1859).

The clade comprising subtribes Daucinae and Torilidinae is supported by three synapomorphies: the regular distribution of appendages on both the primary and secondary ridges (character 32, state 1), the presence of primary ridges and hairs on the commissural face of the mericarp (character 34, state 1), and the presence of vittae under the lateral fruit ridges (character 54, state 1). Included within this clade are members of Drude's tribe Laserpitieae, a group traditionally recognized by lacking spines on their fruits but by having both primary and prominent secondary ridges and strongly dorsally compressed fruits, features typical of many Daucinae. The separation of Daucinae from Torilidinae, however, is not straightforward. No obvious morphological or anatomical synapomorphy supports either of these clades. Indeed, elsewhere within Apiaceae, morphology is of limited value for estimating phylogenetic relationships, at least at higher taxonomic levels (Downie et al. 1998, 2000). Similarly, such synapomorphies are unavailable for suprageneric groups in other angiosperms delimited on the basis of molecular data (Angiosperm Phylogeny Group 1998). It may be difficult, perhaps impossible, to find unique morphological or anatomical characters supporting the monophyly of each of these two subtribes. Nevertheless, support for their sister-group status is achieved, in accordance with the results of phylogenetic analyses of plastid DNA data (Plunkett and Downie 1999; Lee and Downie 2000).

Phylogenetic Taxonomy. Here we discuss the phylogenetic relationships within Scandiceae subtribes Daucinae and Torilidinae as inferred from morphological characters, with emphasis on those phylogenetic resolutions not discussed in Lee and Downie (1999, 2000). Relationships within Scandiceae subtribe Scandicinae, inferred on the basis of molecular (Downie et al. 2000), morphological

(Spalik and Downie 2001), and anatomical (K. Spalik, A. Wojewódzka, and S. Downie, unpubl. data) evidence, are discussed elsewhere, as is the delimitation of genera within the subtribe (Spalik et al. 2001). Our goal in revising the taxonomy of the spiny-fruited umbellifers is to recognize only those groups that are monophyletic. Some realignments of species and genera have already been made (Katz-Downie et al. 1999; Lee and Downie 1999, 2000; Downie et al. 2000), and others are suggested below upon confirmation of further analysis.

DAUCINAE. Subtribe Daucinae, as sampled herein, comprise the genera *Agrocharis*, *Ammodaucus*, *Cuminum*, *Daucus*, *Laserpitium*, *Orlaya*, *Pachyctenium*, and *Pseudorlaya*. Also included on the basis of phylogenetic analysis of molecular data are *Melanoselinum*, *Monizia*, *Polylophium*, *Thapsia* L., and possibly *Laser* (Lee and Downie 1999, 2000; Downie et al. 2000), all genera previously attributable to Drude's (1898) tribe Laserpitieae. ITS studies also include *Athamanta della-cellae* Asch. & Barbey ex E.A. Durand & Barratte (Downie et al. 2000; Spalik and Downie 2001; Spalik et al. 2001).

The genus *Artedia* is dubiously assigned to this clade. Upon consideration of separate analysis of ITS sequences (Lee and Downie 1999) and morphology, *Artedia* falls sister to all remaining Daucinae. This relationship, however, is very weakly supported with bootstrap values of 12–47%. When these data are combined greater bootstrap support is achieved (78%), but this result is in stark contrast to that inferred using *rps16* intron sequences where *Artedia* is placed well within Torilidinae (Lee and Downie 2000). *Artedia* is clearly anomalous within tribe Scandiceae. Its fruits are strongly dorsally compressed and its lateral secondary ridges have developed into deeply lobed, scaly, expanded wings. Its other secondary ridges, like those of its primary ridges, are slender and filiform. It may very well constitute a separate lineage within the tribe (such as a monotypic subtribe) as its affinities to any other taxon have not yet been well established. The placement of *Artedia* demands further attention.

Laser is another genus of uncertain phylogenetic placement. Our analysis of morphological data positions *Laser trilobum* outside of Scandiceae where it allies weakly with *Aphanopleura* and *Psammogeton*. Both ITS (Lee and Downie 1999) and *rps16* intron analyses, however, place it alongside other Laserpitieae (such as *Laserpitium* and *Polylophium*) in subtribe Daucinae. Similarly, our analysis of combined morphological and ITS data show it allied with *Am-*

modaucus, *Cuminum*, and *Laserpitium siler*, although this union is very poorly supported. While *Laser* has prominent secondary ridges, its fruits (like those of subtribe Scandiceae and the various out-group genera) do not bear primary or secondary appendages; thus many characters had to be scored as "inapplicable," likely accounting for its basal position within the tree. *Laser* is further distinguished from the spiny-fruited umbellifers by having four, not two, apparent vittae on each commissural mericarp face.

Daucus is the largest and most variable genus in the tribe. Heywood (1982b) recognized 21 species in seven sections, of which we have sampled eight species from all sections, including five subspecies of *D. carota* and two subspecies of *D. bicolor*. The results of the analyses presented herein, and those of previous molecular investigations, show a close relationship among *Daucus*, *Pseudorlaya* (3 spp.) and the monotypic *Pachyctenium*. Indeed, in all of these studies, *Pseudorlaya* and *Pachyctenium* arise within *Daucus*, the latter being either polyphyletic or paraphyletic. *Pseudorlaya* is distinguished from *Daucus* in having two rows of fruit secondary spines instead of one (Davis 1972; Zohary 1972), and while we have confirmed that the secondary spines of *Pseudorlaya pumila* are arranged in this same fashion, we have also observed that, within each row, these paired spines alternate with single ones. This pattern appears to be unique to subtribe Daucinae. Another diagnostic character for *Pseudorlaya* is its dome-shaped primary ridges. Otherwise, *Pseudorlaya* is very similar to *Daucus*, both morphologically and chemically (Harborne et al. 1969; Heywood and Dakshini 1971; Williams and Harborne 1972). The Libyan endemic *Pachyctenium* is uniquely distinguished by its secondary appendages having spiny (dentate) wings in the lower half of the fruit yet while being naked above (Jafri 1985). Thus, while it may appear that both *Pseudorlaya* and *Pachyctenium* are distinct morphologically, when compared alongside a large number of *Daucus* species they represent no more than endpoints in a continuum of morphological variation. The genus *Daucus* is highly variable morphologically, phytochemically (Harborne 1967; Crowden et al. 1969; Harborne and Williams 1972; Williams and Harborne 1972), cytologically (Cauwet-Marc and Jury 1982), and palynologically (Cerceanu-Larrival 1962, 1965; Guyot et al. 1980), and thus, it is difficult to define unambiguously, particularly if *Pachyctenium* and *Pseudorlaya* are considered. Some realignment of species and genera may be needed but these will be de-

ferred until all *Daucus* and *Pseudorlaya* species and subspecies have been examined.

The molecular data also suggest a close relationship between *Daucus* and *Agrocharis*. In the ITS trees, *Agrocharis* is sister to the clade of *D. bicolor*, *D. durieua*, *D. pusillus*, and *D. montanus* (Lee and Downie 1999), and a similar position is observed in our analysis of combined data (Fig. 3). *Agrocharis* is the only spiny-fruited umbellifer endemic to tropical Africa (Heywood 1982b), and its close affinity with *Daucus* reflects some similarities in their fruit anatomy and morphology (Heywood 1973). However, *Agrocharis* lacks the lobed primary hair base (character 40) that is characteristic of *Daucus*, *Pachyctenium*, and *Pseudorlaya*. The possible transfer of *Agrocharis* to *Daucus* warrants further investigation.

The precise delimitation of *Daucus carota* is problematic, with some 11–13 wild subspecies described (Heywood 1968b, c, 1983; Okeke 1978). Strong sterility barriers have not developed among the subspecies of *D. carota* nor between *D. carota* and related species, often leading to viable hybrid progeny (McCollum 1975, 1977; Small 1978; DeBonte et al. 1984). Moreover, intermediate forms among subspecies of *D. carota* from European coastal to inland areas make it hard to delimit subspecific boundaries (S. Jury, pers. comm.). In this study, as in the ITS study of Lee and Downie (1999), we have included five subspecies of *D. carota*, including *D. carota* subsp. *maximus* (= *D. maximus* Desf.), and in each of these studies the group unites as a moderately to strongly supported clade. The cpDNA restriction site study of Lee and Downie (2000) also includes *D. carota* subspecies *commutatus*, *hispanicus*, and *maritimus*, and these too unite strongly with the aforementioned assemblage.

The morphological analysis places *Daucus crinitus* sister to *D. carota* (Fig. 1.), in contrast to the molecular studies where *D. carota* and *Pseudorlaya pumila* are sister taxa (Lee and Downie 1999, 2000). The close relationship between *D. crinitus* and *D. carota*, as inferred by Sáenz Laín (1981) on the basis of vittae size and shape, is also supported by the shared presence of purple flowers in the center of the inflorescence and the absence of calyx teeth.

Daucus aureus, treated as the sole member of section *Chrysodaucus* Thell. by Heywood (1982b), is sister to *D. muricatus* (in the monotypic section *Platyspermum* (Hoffm.) DC.). These species share closely located vascular bundles on the commissural surface, reduced elliptic vittae, sclerenchymatous cells between their commissural vittae, and similar leaf

lobing and bract shape. Molecular data also support this union.

Daucus pusillus and *D. montanus*, both native to the New World, are placed in different sections on the basis of vittae shape (Thellung 1926; Sáenz Laín 1981; Heywood 1982b). This is inconsistent with the results of both molecular and morphological analyses where these species arise as closely related (e.g., Fig. 3; Lee and Downie 1999) or sister taxa (e.g., Fig. 1; Lee and Downie 2000). Both species have only perfect flowers and obsolete calyx teeth.

Daucus bicolor can be distinguished from all other *Daucus* species by its bracts, which are trifid rather than pinnatisect or leaf-like, and the unique color of its rays and styles. We have observed that the outer portion of the ray is pink whereas the inner portion is green, the style is pink, the stylopodium cream colored, and the calyx green. In contrast, all other species of *Daucus* (plus *Pseudorlaya* and *Pachyctenium*) have green rays and calyx teeth, and cream colored styles and stylopodia. The two subspecies of *D. bicolor* unite strongly in all analyses, with the only difference between them being the presence of central purple flowers in *D. bicolor* subsp. *bicolor*.

Cuminum also has a complex taxonomic history. On the basis of similarity of fruit bristle structure, Boissier (1872) placed *Cuminum* alongside *Chaetosciadium* and *Psammogeton* in his tribe Caucalideae. In contrast, Drude (1898) treated *Cuminum* in Apieae subtribe Carinae near *Aphanopleura* and *Szovitsia*. *Cuminum* and *Daucus* share similar primary appendage characters (Heywood and Dakshini 1971), whereas *Cuminum* and *Orlaya* share a similar and unique flavonoid chemistry (Harborne and Williams 1972). Both our morphological and molecular analyses confirm the position of *Cuminum* among the spiny-fruited umbellifers and, specifically, within Scandiceae subtribe Daucinae. Furthermore, its sister relationship to *Ammodaucus*, as inferred by the molecular analyses, is also supported by the shared presence of multiple grouping of primary appendages (character 37, state 1). The grouping of *Laser* within this clade is not readily explained on the basis of morphology.

The incorporation of members of Drude's (1898) tribe Laserpitieae (i.e., *Laser*, *Laserpitium*, *Melanose-linum*, *Monizia*, and *Polylophium*) into subtribe Daucinae is consistent, in part, with the classificatory systems of Calestani (1905) and Koso-Poljansky (1916) where a close relationship between *Laserpitium* and *Daucus* (and other taxa) was suggested on the basis of fruit anatomical characters. Laserpitieae

(sensu Drude 1898 or sensu Pimenov and Leonov 1993), however, are not monophyletic with several independent derivations occurring within Daucinae (Lee and Downie 2000). The genus *Laserpitium* may not be monophyletic either, for on the basis of molecular evidence *L. siler* and *L. hispidum* arise in separate clades (Lee and Downie 1999, 2000). The morphological data, on the other hand, unite these *Laserpitium* species, with their undulately winged secondary appendages (character 44) synapomorphic for the group. It is not unrealistic to presume that winged secondary appendages can evolve multiple times. Indeed, in other umbellifers, the presence of wings on the secondary appendages is a highly homoplastic character (Theobald 1971; Downie et al. 1998).

TORILIDINAE. Subtribe Torilidinae, as circumscribed on the basis of molecular data (Lee and Downie 1999; Downie et al. 2000), comprises the genera *Astrodaucus*, *Caucalis*, *Glochidotheca*, *Lisaea*, *Szovitsia*, *Torilis*, *Turgenia*, and *Yabea*. The morphological study, however, fails to support the monophyly of the group. On the basis of phylogenetic analyses of molecular and morphological data, both separately and combined, at least three major lineages are recognized within the subtribe, designated herein as the "*Astrodaucus*," "*Torilis*," and "*Caucalis*" subclades. The genus *Yabea*, however, is only weakly affiliated with the "*Torilis*" subclade and in the ITS study of Lee and Downie (1999) it comprises a fourth major branch within the subtribe.

Astrodaucus, *Glochidotheca*, and *Szovitsia*, comprising the "*Astrodaucus*" subclade, share two synapomorphies: primary hairs having a curved apex (character 36, state 1) and the presence of peg-like projections on the surfaces of the secondary appendages (character 48, state 2). Otherwise, these taxa differ remarkably. *Astrodaucus* has double rows of pyramid-shaped spines on its secondary ridges, which almost conceal the thread-like primary ridges (Heywood 1968d), *Szovitsia* is characterized by unique spatulate pouches for the secondary appendages, and *Glochidotheca* has strongly laterally compressed fruits.

The genus *Torilis* (in the "*Torilis*" subclade) is extremely polymorphic, given the variability seen in its cauline leaf and fruit morphology, and calls for its revision have been put forth by Davis (1972), Al-Attar (1974), Heywood (1982b, 1986), and Jury (1986). Cannon (1968) divided *Torilis arvensis* into four subspecies, all of which have been treated subsequently as separate species (Meikle 1977). On the basis of morphology, *T. arvensis* subsp. *arvensis* and

T. japonica are sister taxa, and while these taxa can be distinguished upon consideration of their bracts (Zohary 1972; Hedge et al. 1987), both share such features as the presence of bristles on the petals (character 23, state 1), styles longer than the stylopodium, numerous rays, and fruit secondary spines in three or four rows. *Torilis arvensis* subsp. *purpurea* and *T. elongata* differ from *T. arvensis* subsp. *arvensis* in having perfect flowers, styles almost sessile, fewer rays, and secondary spines in only two rows. Also, the lower umbels of *T. elongata* are sessile, whereas those of other *Torilis* species are pedunculate (Jury 1996). The separation of *Torilis arvensis* subspp. *arvensis* and *purpurea* is also supported by analysis of cpDNA restriction sites (Lee and Downie 2000) and when *T. japonica* is included in the ITS matrix (B.-Y. Lee, unpubl. data). *Torilis nodosa* clearly belongs within *Torilis* (in spite of their unusual fruit characters), and statements to the contrary (e.g., Davis 1972) are unsupported upon consideration of both morphological and molecular data.

Torilis trichosperma (syn. *Chaetosciadium trichospermum*) can be distinguished from all other species of *Torilis* by its pale pink versus cream colored stamens, larger petals, and multicellular versus simple secondary appendages (Heywood and Dakshini 1971). Also unique within the spiny-fruited umbellifers are its mericarps, which are covered by fine, long bristly hairs made up of a series of tube-like elements. However, *T. trichosperma* shares with other *Torilis* species a similar flavonoid chemistry (Crowden et al. 1969; Harborne and Williams 1972), base chromosome number ($x = 6$; Constance et al. 1971), appressed hairs on their stems and rays, primary hairs directed towards the stylar end of the fruit, and a tuberculate ornamentation on the primary hair surface (Heywood and Dakshini 1971; Zohary 1972; Cauwet-Marc and Jury 1982).

Historically, the placement of *Yabea* among the spiny-fruited umbellifers has been controversial although Saenz de Rivas (1975) agreed with Koso-Poljansky (1917) in the separation of *Yabea* from *Caucalis*, arguing that the former differs in the size of the fruit and its secondary spines, the absence of sclerenchyma in the secondary ridges, its smaller vascular bundles, and a flat versus curved endosperm. While *Yabea* is distinct morphologically, it does have the same base chromosome number as *Torilis*. This number, $x = 6$, is not known for any other genus within the tribe. While the proper placement of *Yabea* within subtribe Torilidinae is still unclear, its separation from *Caucalis* is maintained.

The "*Caucalis*" subclade comprises the genera *Caucalis*, *Lisaea*, and *Turgenia*. *Caucalis* has had a remarkable classificatory history, with many species at one time included within the genus now referable to *Agrocharis*, *Angosesei*, *Astrodaucus*, *Orlaya*, *Torilis*, *Turgenia*, and *Yabea* (Cannon 1967; Heywood and Dakshini 1971; Heywood 1973, 1982b, 1986). *Caucalis* is now treated as monotypic, containing only *C. platycarpus*. *Caucalis* shares with *Turgenia* and *Lisaea* a similar endosperm shape when seen in transverse section, where the inner ends of the endosperm are curved towards the commissural surface and then are recurved back towards the dorsal ridges (character 55, state 2). *Turgenia* and *Lisaea* differ from *Caucalis*, however, in having round and not linear cotyledons (Cerceau-Larrival 1962; Guyot et al. 1980), 1-pinnate versus 2–3 pinnate leaves (character 5; Townsend 1964), castellate spine masses between the tuberculate fruit spines (Heywood and Dakshini 1971), spines on their primary ridges (character 35), and a base chromosome number of $x = 8$ or 9 versus $x = 10$ (Cauwet-Marc and Jury 1982).

In conclusion, Scandiceae subtribes Daucinae and Torilidinae are each supported as monophyletic and are sister taxa upon phylogenetic analyses of cp-DNA restriction sites (Plunkett and Downie 1999; Lee and Downie 2000) and *rps16* intron sequences (Lee and Downie 2000). However, upon ITS sequence comparisons, the relationships among the three subtribes are equivocal, and as such, three clades of equal rank have been recognized (Lee and Downie 1999; Downie et al. 2000). While morphology fails to support the distinction between subtribes Daucinae and Torilidinae, their union is supported by three synapomorphies. As is increasingly becoming apparent in Apiaceae taxonomy, many of those suprageneric taxa recognized on the basis of recent analyses of molecular data cannot be delimited by morphological synapomorphies without homoplasies.

Among the spiny-fruited umbellifers, like the family itself, features of the mature fruit have been traditionally given much importance in delimiting genera and inferring relationships. Indeed, the traditional emphasis on fruit characteristics for delimiting taxa has found some confirmation from our analysis. We have also shown that the primary appendage characters are more useful in delimiting clades than those of the secondary appendages. These primary appendage characters are less homoplastic, although their functional significance is less well known than the more obvious spines,

hooks, hairs, and wings on the well-developed secondary ridges that are usually explained as different strategies of fruit dispersal.

ACKNOWLEDGEMENTS. The authors thank M. Choi, D. S. Katz-Downie, E. Llanas, and S. Ramanath for assistance in the laboratory; S. Jury, G. Plunkett, J.-P. Reduron, and K. Spalik for advice; O. Cohen, L. Landrum, J.-P. Reduron, and A. Santos for providing leaf or seed material; and D. S. Katz-Downie, G. Plunkett, K. Spalik, and one anonymous reviewer for comments on the manuscript. This work was supported by NSF grant DEB 9407712 to SRD, and by a Francis M. and Harlie M. Clark research support grant and a Herbert Holdsworth Ross Memorial award to BYL. This paper represents a portion of a Ph.D. dissertation submitted by BYL to the Graduate College of the University of Illinois. The authors are indebted to the following herbaria for loans of materials: ARIZ, ASU, E, F, HUJ, JEPS, K, MICH, MO, NY, RNG, UC, US, UT, W, and WTU.

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APPENDIX 1. States of the characters indicated in Table 2 for 57 species of Apiaceae tribe Scandiacae and outgroups. Parentheses indicate polymorphisms and “?” indicates unknown or inapplicable data. The quantitative characters (15, 16, 19, 20, 21, 22, and 25) were coded using gap weighting (Thiele 1993) using 26 ordered character states (0–9, A–H, J–N, and P–R).

Taxa	Characters					
	1	11	21	31	41	51
<i>Agrocharis incognita</i>	1111202001	0000??1040	5401A11100	1111000{01}00	2212001001	000115
<i>Agrocharis melanantha</i>	?101202001	0040??10??	??01?11100	1111000{01}00	2212001101	000115
<i>Agrocharis pedunculata</i>	1101202001	00109C1040	EG01C11100	1111000{01}00	2212001001	000115
<i>Ammodaucus leucotrichus</i>	1200202{12}01	{12}000211040	B701E11100	1111001000	2211200401	000112
<i>Anthriscus caucalis</i>	1200220???1	01107??10??	??02?10011	1000? ??????	?00?????10	00001{13}
<i>Anthriscus cerefolium</i>	1200220???1	0110501042	7302A10011	0000? ??????	?00?????10	000?13
<i>Artemisia squamata</i>	1000212221	2000G710MN	B501C11100	1011000000	220? ??????00	000102
<i>Astrodaucus orientalis</i>	120020{01}0?1	0000F510E9	9E01B11000	1111010000	2112111200	000114
<i>Caucalis platycarpus</i>	1301220???1	0000331082	7E01E11100	1111100000	0012000000	000?24
<i>Cuminum cyminum</i>	1200012{01}01	0000430050	6601B11100	1111001000	0210200001	100101
<i>Cuminum setifolium</i>	1200012001	{01}000? ?00??	??01?11100	1111001000	0211200001	100101
<i>Daucus aureus</i>	1201202221	1011N91095	GL01911101	1111000001	2212001100	000105
<i>Daucus bicolor</i> subsp. <i>bicolor</i>	1201202101	{01}010K11A5	AB01E11102	1111000101	2212011300	000105
<i>Daucus bicolor</i> subsp. <i>broteri</i>	1201202101	{01}010??10??	??01?11102	1111000101	2212011300	000105
<i>Daucus carota</i> subsp. <i>carota</i>	12012022{01}1	{01}011PJ11A9	9502511100	1111000001	2212001001	100103
<i>Daucus carota</i> subsp. <i>gummifer</i>	12012222{01}1	{01}011MC11C5	DC02?11100	1111000001	2212001001	100103
<i>Daucus carota</i> subsp. <i>halophilus</i>	12012222{12}1	{01}01???111??	??01?11100	1111000001	2212001001	100103
<i>Daucus carota</i> subsp. <i>maximus</i>	1201202201	{01}011RR1195	B702411100	1111000001	2212001001	100103
<i>Daucus carota</i> subsp. <i>sativus</i>	1201202201	{01}011QD1174	6501?11100	1111000001	2212001001	100103
<i>Daucus crinitus</i>	1200212201	{01}011B911C2	NR01B11100	1111000001	2212000301	100105
<i>Daucus durioua</i>	1201202201	21102F1010	5201?11102	1111000101	2212001300	000105
<i>Daucus montanus</i>	1101202201	{01}000CJ0011	7301?11100	1111000001	2212001001	000105
<i>Daucus muricatus</i>	1201202221	{01}011DR10C8	A902C11100	1111000001	2212011000	000105
<i>Daucus pusillus</i>	1101202201	1010KA0000	6001511100	1111000101	2212011001	100105
<i>Glochidotherca foeniculacea</i>	1200210??{01}	0000011096	0301E11004	1111010000	2112101200	00011?
<i>Kozlovia paleacea</i>	1200020???1	0000D?1086	780?A10001	1040300000	000? ??????10	? ? ?015
<i>Laser trilobus</i>	?2003?0???1	0000? ?10??	??01?11100	0?00? ??????	?20? ??????01	10100?
<i>Laserpitium hispidum</i>	1201222001	0010LA1040	8902D11100	1111000000	221301? ?001	000105
<i>Laserpitium siler</i>	?2003?0???1	0000L410?0	??01F11100	1101? ??????	?21301? ?001	000105
<i>Lisaea heterocarpa</i>	030{13}122001	00308410MD	LP01D11002	1111200000	1012002?00	000?2?
<i>Lisaea papyracea</i>	0303122001	00305310E8	BF01F11002	1111200000	1012002300	000?2?
<i>Lisaea strigosa</i>	030{13}122001	00309510JB	KP01A11000	101?200000	000? ??????00	000?2?
<i>Myrrhis odorata</i>	1200220???1	00109710B5	8C00R10011	0000? ??????	?00? ??????00	? ? ?015
<i>Orlaya daucoides</i>	1300202001	00001110HE	RJ02H11100	1111000000	0212000001	000102
<i>Orlaya daucorlaya</i>	1300202001	00008310NJ	PJ02H11100	1111000000	0212010001	000101
<i>Orlaya grandiflora</i>	1300202001	00008410RR	QL02F11100	1111000000	0212{01}00001	000104
<i>Osmorhiza longistylis</i>	120{04}322001	0000? ?10??	??01?10011	1010000010	000? ??????10	? ? ?01?
<i>Pachyctenium mirabile</i>	?201202001	0010EL1040	J602?11?00	1111000001	221501?100	?0010?
<i>Pseudorlaya pumila</i>	1201222{01}01	{01}0106F1050	2301F11100	1111000101	2212{01}01001	000102
<i>Scandix balansae</i>	120?200???1	0100??10??	??00?10011	0000? ??????	?00? ??????10	00001?
<i>Scandix pecten-veneris</i>	1201200???1	1100101055	ED00G10011	0000? ??????	?00? ??????10	000015
<i>Szovitsia callicarpa</i>	1200210???1	0000611094	C801911000	1111010000	2114003201	00011?
<i>Torilis arvensis</i> subsp. <i>arvensis</i>	1202200???1	0020931063	NF12801002	1111000010	1012201300	000110
<i>Torilis arvensis</i> subsp. <i>purpurea</i>	1202200???1	0020000052	3902B01002	1111000010	1012101300	000110
<i>Torilis elongata</i>	1202200???1	0020210020	4002B01002	1111000010	1012101300	000115
<i>Torilis japonica</i>	1202222001	00209510E8	B712501002	1111000010	1012200300	00011{02}
<i>Torilis leptophylla</i>	1202200???1	01202C0050	2D02A11002	1111000010	1012{01}01300	000110
<i>Torilis nodosa</i>	1212220???1	01202M0010	1802501002	1111000010	1012100300	000110
<i>Torilis scabra</i>	?202220???1	0020? ?00??	??02?11002	1111000010	1012{12}00300	00011?
<i>Torilis tenella</i>	1202200???1	0020? ?00??	??02?11002	1111000010	1012001300	000110
<i>Torilis trichosperma</i>	1302220???1	0120430071	JF02911002	1111000010	1011200400	000110
<i>Turgenia latifolia</i>	0301122001	00103210C6	5901H1100{23}	1111200000	1012002300	000?2{23}
<i>Yabea microcarpa</i>	1201202201	00106A0020	4001911002	1111000100	2012000300	000110
<i>Aphanopleura trachysperma</i>	1204312001	000094?031	9402001000	1000? ??????	?00? ??????01	000005
<i>Psammogeton canescens</i>	1204302001	0010A31070	FC01201000	1000? ??????	?00? ??????01	10000?
<i>Lecokia cretica</i>	??00220???1	0000? ?10??	??01?11000	1000? ??????	?00? ??????00	01201?
<i>Smyrniolum olusatrum</i>	0000220???0	?000A?1040	5F01D01010	0000? ??????	?00? ??????00	012025