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MAJOR LINEAGES WITHIN APIACEAE SUBFAMILY APIOIDEAE: A COMPARISON OF CHLOROPLAST RESTRICTION SITE AND DNA SEQUENCE DATA[1]

GREGORY M. PLUNKETT[2] AND STEPHEN R. DOWNIE

Department of Plant Biology, University of Illinois, Urbana, Illinois 61801

Traditional sources of taxonomic characters in the large and taxonomically complex subfamily Apioideae (Apiaceae) have been confounding and no classification system of the subfamily has been widely accepted. A restriction site analysis of the chloroplast genome from 78 representatives of Apioideae and related groups provided a data matrix of 990 variable characters (750 of which were potentially parsimony-informative). A comparison of these data to that of three recent DNA sequencing studies of Apioideae (based on ITS, *rpoCl* intron, and *matK* sequences) shows that the restriction site analysis provides 2.6–3.6 times more variable characters for a comparable group of taxa. Moreover, levels of divergence appear to be well suited to studies at the subfamilial and tribal levels of Apiaceae. Cladistic and phenetic analyses of the restriction site data yielded trees that are visually congruent to those derived from the other recent molecular studies. On the basis of these comparisons, six lineages and one paraphyletic grade are provisionally recognized as informal groups. These groups can serve as the starting point for future, more intensive studies of the subfamily.

Key words: Apiaceae; Apioideae; chloroplast genome; restriction site analysis; Umbelliferae.

Apioideae are the largest and best-known subfamily of Apiaceae (= Umbelliferae) and include many familiar edible plants (e.g., carrot, parsnips, parsley, celery, fennel, dill, coriander/cilantro, anise, cumin), as well as several deadly poisons (e.g., poison-hemlock, water-hemlock, fool's-parsley). The subfamily is defined by a suite of easily observed and well-known characters, including pinnately lobed or divided leaves with sheathing petioles, herbaceous stems with hollow internodes, compound-umbellate inflorescences, flowers with pentamerous perianths and androecia, and bicarpellate gynoecia that mature into schizocarpic fruits with two ribbed mericarps. These characters make field recognition of most umbellifers a simple task, but the difficulty in identifying these plants to genus and species is renowned. This contrast reflects a complex history of problems in interpreting the phylogeny of Apioideae, and consequently in producing a satisfactory classification system. Much of the difficulty can be attributed to the near uniformity of most floral characters coupled with repeated examples of apparent parallelisms among other features. Leaf-shape changes provide a good illustration of such variation. Many genera, for example, exhibit interspecific transitions from pinnately lobed or divided leaves with broad leaflets at one extreme to decompound leaves with linear or filiform leaflets at the other extreme (e.g., *Ammi*, *Apium*, *Ligusticum*, *Lomatium*, *Seseli*, and *Tauschia*, among many others); in some cases the leaflets are lost altogether (as in the ''rachis-leaf'' species of *Oenanthe*, *Oxypolis*, and *Ptilimnium*). Many other morphological, breeding-system, and biochemical characters exhibit similarly confounding parallelisms (e.g., Bell, 1971; Harborne, 1971; Nielsen, 1971).

Fruit morphology and anatomy were traditionally viewed as the most promising sources of taxonomic characters, exhibiting some (but not excessive) variation in features such as fruit shape, the degree and direction of mericarp compression, modifications of the pericarp ribs (e.g., wings or spines), and the shape of mericarp commissural faces. Thus, most traditional classifications of Apiaceae have relied almost exclusively on fruit characters (Koch, 1824; Bentham, 1867; Boissier, 1872; Drude, 1897–1898; and Koso-Poljansky, 1916; reviewed in Constance, 1971; Plunkett, Soltis, and Soltis, 1996b). Although these systems are now widely regarded as artificial (e.g., Mathias, 1971; Theobald, 1971; Cronquist, 1982; Shneyer et al., 1992; Shneyer, Borschtschenko, and Pimenov, 1995), the lack of acceptable alternatives has led most students of the family to employ the system proposed by Drude (1897–1898) a century ago in *Die Natürlichen Pflanzenfamilian* (Table 1). Present-day modifications of this system (e.g., Heywood, 1993; Pimenov and Leonov, 1993) all retain Drude's basic division of Apiaceae into three subfamilies: Hydrocotyloideae, Saniculoideae, and Apioideae. Hydrocotyloideae and Saniculoideae are much smaller subfamilies (42 genera with ~470 species, and nine genera with ~300 species, respectively; cf. 250–400 genera with 1800–3000 species in Apioideae), and although some questions regarding the relationship of Saniculoideae and Hydrocotyloideae to the apioids persist, recent studies (e.g., Downie et al., 1998; Plunkett, Soltis, and Soltis, 1996b, 1997) suggest that subfamily Apioideae is monophyletic and that phylogenetic problems in this subfamily can be treated as distinct.

Providing robust phylogenetic hypotheses is a crucial precursor to erecting stable classification systems. This goal is especially important for Apioideae, which has

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[2] Author for correspondence, current address: Department of Biology Virginia Commonwealth University, Richmond, VA 23284-2012.

TABLE 1. The subfamilial classification of Apiaceae according to Drude (1897–1898; see also Heywood, 1993); the eight tribes of subfamily Apioideae and the two subtribes of Scandiceae are also provided. Vittae and companion canals are schizogenous oil ducts found in apiaceous fruits (companion canals are associated with vascular bundles; vittae are located between vascular bundles).

Hydrocotyloideae—endocarp sclerified; fruit lacking free carpophore; companion canals present but vittae lacking.
Saniculoideae—endocarp parenchymatous, but containing scattered druses; exocarp bearing scales, prickles, or barbs (rarely smooth); stylopodium ring-like; oil canals or cells variable.
Apioideae—endocarp parenchymatous (fruit sometimes hardened by a woody subepidermal layer); styles emerging from the apex of the stylopodium; vittae and companion cells present.
  Echinophoreae—umbellets with one to a few sessile female flowers enclosed by a crown of male flowers; fruits mostly with a single seed.
  Scandiceae—druse crystals in the parenchyma surrounding the carpophore; seeds curved
    Scandicinae—fruit long-cylindrical and beaked, smooth or with short-prickles
    Caucalidinae—fruit ovoid, strongly bristled over the vallecular ribs.
  Coriandreae—fruit spherical, with sclerified subepidermal layers; parenchyma surrounding the carpophore lacking druse crystals; seeds curved.
  Smyrnieae—fruit ovoid, mericarps rounded outward; seeds curved.
  Apieae (=Ammineae)—fruits terete; lateral and dorsal ribs all alike; seeds straight.
  Peucedaneae—lateral ribs much broader than dorsal ribs, often forming wings; seeds straight; fruits dorsally compressed.
  Laserpitieae—secondary ribs present (in addition to primary ribs), often forming wings.
  Dauceae—secondary ribs present (in addition to primary ribs), armed with spines or prickles.

served as an important system in many evolutionary studies. Most notable among these have been the studies of interactions between umbelliferous host plants and their various insect herbivores (especially the lepidopteran species in the genera *Papilio*, *Depressaria*, and *Greya*; reviewed in Berenbaum, 1983, 1986, 1990; Thompson, 1986, 1994). To the extent that taxonomy in Apioideae is widely held to be inadequate, especially at tribal and generic levels, the absence of a phylogenetic context among and within umbellifer groups greatly hampers the ability to interpret coevolutionary patterns (see Thompson, 1986). Studies of mating systems provide another example where Apioideae have been used as a ‘‘model system.’’ Despite frequent descriptions of the subfamily as being bisexual (e.g., Cronquist, 1981), many taxa are andromonoecious (Bell, 1971; Lovett Doust, 1980; Lovett Doust and Harper, 1980; Webb, 1981,1984). It is often assumed that andromonoecy is a derived adaptation resulting from increased selection for dichogamy to promote outcrossing (see Bell, 1971; Webb, 1979). However, recent studies (Schlessman, Lloyd, and Lowry, 1990; Plunkett, Soltis, and Soltis, 1997) suggest that andromonoecy may represent the ancestral condition in the entire order Araliales (= Apiaceae plus Araliaceae). Correctly interpreting the evolution and adaptive significance of mating systems in Apioideae requires the correct assessment of polarity, which in turn depends on the presence of well-supported phylogenies. Without such phylogenetic hypotheses, these and other evolutionary studies in Apioideae are largely without context.

Recently, several studies have demonstrated the utility of molecular data in examining evolutionary relationships involving Apiaceae, including studies at the interspecific level (Soltis and Kuzoff, 1993; Soltis and Novak, 1997), the tribal level (Lee et al., 1997), subfamilial level (Downie and Katz-Downie, 1996; Downie, Katz-Downie, and Cho, 1996; Downie et al., 1998), as well as intra- and interfamilial levels (Plunkett, Soltis, and Soltis, 1996a, b, 1997). These studies, mostly based on DNA sequence data (from both chloroplast and nuclear markers), have provided insights into the evolutionary history of Apiaceae and hold the promise of producing a framework from which the confusing array of morphological variation can be interpreted. Among the results from these studies are that subfamily Hydrocotyloideae appears to be polyphyletic, but Apioideae and Saniculoideae form monophyletic sister groups. These studies do not, however, support any tribal system of the family, particularly within Apioideae. As a complement to the recent sequencing studies, we undertook an analysis of restriction site data derived from the chloroplast genome of 79 species, with a particular emphasis on subfamily Apioideae. Despite certain limitations, restriction site data confer a number of advantages over sequence data, the most important being that a nearly random sample of the entire chloroplast genome can be surveyed, including data from both rapidly and more slowly evolving sequences (Olmstead and Palmer, 1994). Phylogenetic hypotheses based on restriction site data can be examined for areas of congruence and/or conflict with other data sets in the effort to recognize strongly supported evolutionary lineages.

The earlier molecular studies (Downie and Katz-Downie, 1996, Downie, Katz-Downie, and Cho, 1996; Kondo et al., 1996; Plunkett, Soltis, and Soltis, 1996b, 1997; Downie et al., 1998) have clearly demonstrated the problems inherent in most tribal and intergeneric classifications of Apioideae. Data from chloroplast restriction site analysis confirm these results (see below). In an effort to identify evolutionary lineages within Apioideae, the present study seeks to compare results based on different molecular data sets. Given the size of Apioideae (up to 3000 species), it is impractical to build data sets from the entire subfamily for each new study. We hope that the preliminary groupings presented herein will represent starting points for future, more focused studies within Apioideae.

MATERIALS AND METHODS

Fresh or dried leaf tissue was obtained from 79 species (see Table 2) representing Apiaceae (69 species) and the closely related families Araliaceae (eight species) and Pittosporaceae (two species). The two members of Pittosporaceae were included for outgroup comparison on the basis of previous studies (see Chase et al., 1993; Plunkett, Soltis, and Soltis, 1996a). Because relationships within Apioideae were our primary interest, 63 species were sampled from this subfamily; a smaller number of saniculoids (two species) and hydrocotyloids (four species) were included as reference taxa. Among the apioids sampled, seven of

TABLE 2. Voucher or sources and accession numbers for the 79 species of plants used in the present study (tribal classification of subfamily Apioideae based on Drude, 1897–1898).

Taxon	Voucher or accession
Pittosporaceae	
Hymenosporum flavum F. J. Muell.	Cult., Univ. of Illinois, from seed obtained from North Coast Regional Botanic Garden, Coffs Harbour, N.S.W., Australia (*Downie 836, ILL; Plunkett 1463, ILL*)
Pittosporum revolutum Dryander	Cult., Univ. of Illinois, from seed obtained from North Coast Regional Botanic Garden, Coffs Harbour, N.S.W., Australia (*Downie 829, ILL; Plunkett 1462, ILL*)
Araliaceae	
Aralia spinosa L.	Cult., Missouri Botanical Garden (#895974)
Fatsia japonica Decne. & Planch.	Cult., Royal Botanic Garden Edinburgh (#19687549)
Kalopanax pictus Nakai	Cult., Morton Arboretum (#211-57) (*Downie 522, ILL*)
Polyscias balfouriana (Hort. Sander) L. H. Bailey	Cult., Royal Botanic Garden Edinburgh (#19697330)
Pseudopanax arborus (Murr.) Philipson	Cult., Royal Botanic Garden Edinburgh (#19665059)
Schefflera pueckleri (K. Koch) Frodin	Cult., Missouri Botanical Garden (#897530)
Tetrapanax papyriferus (Hook.) C. Koch	Cult., Royal Botanic Garden Edinburgh (#199696834)
Trevesia sundaica Miq.	Cult., Missouri Botanical Garden (#801619)
Apiaceae: Hydrocotyloideae	
Azorella trifurcata (Gaertn.) Pers.	Cult., Royal Botanic Garden Edinburgh (#19760821)
Bolax gummifera Spreng.	Cult., Royal Botanic Garden Edinburgh (#19361025)
Centella asiatica (L.) Urb.	Cult., Univ. of California Berkeley (L. Constance personal collection #C-1649)
Klotzchia rhizophylla Urb.	Brazil, Minas Gerais, Serra do Cipo (*Pirani 12909, UC*), Cult., Univ. California Botanical Garden, Berkeley; (L. Constance personal collection #C-2414)
Apiaceae: Saniculoideae	
Eryngium cervantesii Delar. f. Eryng.	Cult., Univ. of California Berkeley (L. Constance personal collection #C-2443)
Eryngium variifolium Coss.	Cult., Univ. of California Berkeley
Apiaceae: Apioideae	
Tribe Apieae	
Aciphylla aurea W. R. B. Oliv.	Cult., Royal Botanic Garden Edinburgh (#19712219) (*Downie 146, ILL*)
Aethusa cynapium L.	Cult., Univ. of Oldenberg Botanic Garden
Ammi majus L.	Cult., Jardin botanique de Nancy, France (*Downie 252, ILL*)
Anethum graveolens L.	Cult., Univ. of Oldenberg Botanic Garden (*Downie 157, ILL*)
Anginon rugosum (Thunb.) Raf.	South Africa, West Cape, (*Battten 1018, UC*); Cult., Univ. of California Botanical Garden, Berkeley (L. Constance personal collection #C-2399)
Apium graveolens L.	Cult., Jardin botanique de Belgique, Belgium (*Downie 453, ILL*)
Berula erecta (Huds.) Coville	Cult., Univ. of Oldenberg Botanic Garden (*Downie 150, ILL*)
Bunium elegans	Jordan, Ajlun, near the Community College (*Lanham and El-Oqlah 9,* Yarmouk Univ. Herbarium)
Bupleurum chinense Franch.	Cult., Shanghai Botanic Garden, China (*Downie 409, ILL*)
Carlesia sinensis Dunn	Cult., Univ. of California Berkeley (L. Constance personal collection #C-2401)
Carum carvi L.	Cult. Jardin botanique de Nancy, France (*Downie 243, ILL*)
Cicuta virosa L.	Cult., Univ. of Joensuu, Finland (*Downie 75, ILL*)
Cnidium officinale Malcino	Cult., Univ. of Illinois, from seeds obtained from Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben, Germany (*Downie 830, ILL*)
Cnidium silaefolium (Jacq.) Simonkai	Cult., Urbana, IL, USA (*Plunkett 1470, ILL*)
Coaxana purpurea Coult. & Rose	Mexico, Oaxaca (*Breedlove 72745, UC*; L. Constance personal collection #C-2411)
Conioselinum chinense (L.) B. S. P.	USA, California, San Mateo Co., San Bruno Mtn. (*Raiche 30046, UC*); Cult. Univ. California Botanical Garden, Berkeley (#83.0114)
Crithmum maritimum L.	Cult., Univ. of Illinois, from seeds obtained from Quail Bot. Garden, California (*Downie 345, ILL*)
Cryptotaenia japonica D. Don.	Japan, Honshu Island, Koyosan area (*McNamara et al. 90, UC*), Cult., Univ. California Botanical Garden, Berkeley (#90.0891)
Foeniculum vulgare P. Mill.	Cult., National Botanic Gardens, Glasnevin, Ireland (*Downie 187, ILL*)
Heteromorpha arborescens (Spreng.) Cham. & Schlechtd.	Cult., Univ. of Illinois, from seeds obtained from Real Jardin Botánico, Spain (*Downie 42, ILL*)
Ligusticum scoticum L.	Cult., Shanghai Botanic Garden, China (*Downie 403, ILL*)
Meum athamanticum Jacq.	Cult., Hungarian Acad. Sciences, Vácrátót, Hungary (*Downie 482, ILL*)
Oenanthe fistulosa L.	Cult., Univ. of Oldenberg Botanic Garden (Downie 165, ILL)
Perideridia kelloggii (A. Gray) Mathias	Cult., Univ. of California Berkeley (*Downie 635, ILL*)
Petroselinum crispum (P. Mill.) A. W. Hill	Cult., Akad. der Wissensch., Gatersleben, Germany (*Downie 21, ILL*)
Pimpinella major (L.) Huds.	Cult., Hungarian Acad. Sciences, Vácrátót, Hungary (*Downie 92, ILL*)
Ridolfia segetum (L.) Moris	Jordan, Wadi Al-Yabis, along R. Jordan (*Lahham & El-Oqlah 12,* Yarmouk Univ. Herbarium)
Selinum candollii DC.	Cult., Univ. of California Botanic Garden, Berkeley (#89.2000)
Sium latifolium L.	Cult., Jardin botanique de Caen, France (*Downie 311, ILL*)
Taenidia integerrima (L.) Drude	USA, Illinois, Champaign Co. (*Downie 763, ILL*)
Thaspium pinnatifidum (Buckl.) A. Gray	USA, Kentucky (*Downie 810, ILL*)
Zizia aurea (L.) W. D. J. Koch	Cult., Jardin botanique de Montreal, Canada (*Downie 393, ILL*)

TABLE 2. Continued.

Taxon	Voucher or accession
Tribe Coriandreae	
Coriandrum sativum L.	Cult., Univ. of Illinois, from seeds obtained from Johannes Gutenburg Univ., Germany (*Downie 65, ILL*)
Tribe Dauceae	
Daucus carota L.	Cult., Univ. of Illinois, from seeds obtained from Institut für Pflanzengenetik und Kulturpflanzenschung, Germany (*Lee 73, ILL*)
Pseudorlaya pumila (L.) Grande	Cult., Univ. of Illinois from seeds obtained from Jardin Botaniques Lisboa, Portugal (*Lee 59, ILL*)
Tribe Laserpitieae	
Laserpitium hispidum Bieb.	Cult., Hungarian Acad. Sciences, Vácrátót, Hungary (*Downie 120, ILL*)
Tribe Peucedaneae	
Angelica archangelica L.	Cult., Univ. of Joensuu, Finland (*Downie 78, ILL*)
Angelica polymorpha Maxim.	Japan, Miyazaki, Kyushu (*McNamara et al. 264, UC*), Cult., Univ. of California Botanic Garden, Berkeley (#90.0662)
Coulterophytum laxum Robins.	Cult., Univ. of California Berkeley (L. Constance personal collection #C-1650)
Cymopterus globosus (S. Wats.) S. Wats.	USA, Nevada, Washoe Co., Lyons-Weiler s.n.
Enantiophylla heydeana Coult. & Rose	Cult., Univ. of California Berkeley (L. Constance personal collection #C-2238)
Ferula communis L.	Cult., Hungarian Acad. Sciences, Vácrátót, Hungary (*Downie 112, ILL*)
Levisticum officinale W. D. J. Koch	Cult., Univ. of Oldenberg Botanic Garden (*Downie 161, ILL*)
Lomatium californicum (Nutt.) Mathias & Constance	USA, California, Napa Co. (*Plunkett 1310, WS*)
Mathiasella bupleuroides Constance & Hitchcock	Mexico, Nuevo Leon, Cerro El Viejo (*Hinton et al. 22234. UC*), Cult., Univ. of California Botanical Garden, Berkeley (L. Constance personal collection #C-2447)
Pastinaca sativa L.	Cult., Jardin botanique de Nancy, France (*Downie 244, ILL*)
Prionosciadium acuminatum Robins.	Cult., Univ. of California Berkeley (L. Constance personal collection #C-1871)
Rhodosciadium sp.	Cult., Univ. of California Berkeley (L. Constance personal collection #C-2328)
Tordylium aegyptiacum (L.) Lam. var. *palestinum* (Zoh.) Zoh.	Jordan, Um-Qais, near Irbid, (*Lahham & El-Oqlah 11,* Yarmouk Univ. Herbarium)
Tribe Scandiceae	
Subtribe Caucalidinae	
Astrodaucus orientalis (L.) Drude	Cult., Univ. of Illinois, from seeds obtained from Research Institute of Forests and Rangeland, Iran (*Lee 43, ILL*)
Caucalis platycarpos L.	Cult., Univ. of Illinois, from seeds obtained from Institut für Planzengenetik und Kulturpflanzenforschung, Germany (*Lee 43, ILL*)
Chaetosciadium trichospermum (L.) Boiss.	Jordan, Um-Qais near Irbid (*Lahham & El-Oqlah 4,* Yarmouk Univ. Herbarium)
Torilis arvensis (Hudson) Link	USA, Illinois, Champaign Co. (*Downie 816, ILL*)
Turgenia latifolia (L.) Hoffm.	Cult., Univ. of Illinois, from seeds obtained from J.-P. Reduron, Mulhouse, France (*Lee 82, ILL*)
Subtribe Scandicinae	
Anthriscus cerefolium (L.) Hoffm.	Cult., Akad. der Wissensch., Gatersleben, Germany (*Downie 24, ILL*)
Osmorhiza chilensis Hook. & Arn.	USA, California, Alameda Co., Univ. of California Botanic Garden, Berkeley
Scandix pecten-veneris L.	Cult., Univ. of Illinois, from seeds obtained from Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben, Germany (*Downie 27, ILL*)
Tribe Smyrnieae	
Arracacia brandegei Coult. & Rose	Mexico, Baja California del Sur (*Breedlove 43405, UC*; L. Constance personal collection #C-2045)
Arracacia tolucensis (H. B. K.) Hemsl.	Cult., Univ. of California Berkeley (L. Constance personal collection #C-2124)
Conium maculatum L.	Cult., Jardin botanique de Nancy, France (*Downie 241, ILL*)
Conium maculatum L.	Cult., Akad. der Wissensch., Gatersleben, Germany (Downie 16, ILL)
Lecokia cretica (Lam.) DC.	Jordan, Ajlun, near Schtafeenah (*Lahham & El-Oqlah 7,* Yarmouk Univ. Herbarium)
Smyrnium olusatrum L.	Cult., Quail Botanical Garden, USA (*Downie 343, ILL*)

the eight tribes originally proposed by Drude (Table 1) were represented. Included from the largest two tribes, Apieae and Peucedaneae, were samples from 32 and 13 species, respectively. From the smaller tribes, there were five species from Smyrnieae, eight from Scandiceae (including the segregate tribe Caucalideae), two from Dauceae, and one species each from Laserpitieae and Coriandreae.

Total DNA was extracted from the leaf tissue using the CTAB method of Doyle and Doyle (1987) and purified using cesium chloride/ethidium bromide gradients (Sambrook, Fritsch, and Maniatis, 1989). DNA samples were digested singly with each of the following 14 restriction endonucleases: *Ava* I, *Bam*H I, *Ban* II, *Bcl* I, *Bgl* II, *Cla* I, *Dra* I, *Eco*O109 I, *Eco*R I, *Eco*R V, *Hin*c II, *Hin*d III, *Nci* I, and *Vsp* I. These enzymes recognize 6-bp sequences (except *Nci* I, which has a 5-bp recognition sequence), cut tobacco cpDNA 40–147 times, and have been used successfully in other plant groups. DNA fragments from each digest were separated electrophoretically using 1.0% agarose gels (in which the bromophenol-blue dye marker was run 10 cm) and then bidirectionally transferred to nylon filters (MSI MagnaCharge, Micron Separations, Westborough, Massachusetts) (Southern, 1975). Each of 43 subclones representing the entire tobacco chloroplast genome (described in Olmstead and Palmer [1992] and kindly provided by J. Palmer, Indiana University, Bloomington, Indiana) were labeled with ^{32}P by random priming. The nylon filters were probed with the radiolabeled subclones and then washed in 2×SSC, 0.5% SDS twice for 5 min at room temperature and twice for 60 min at 65°C. Fragment patterns were visualized by autoradiography. Restriction site maps of the entire chloroplast genome were constructed for each of the 14 enzymes. Fragment lengths from each digest were estimated by including two lanes of a size marker (*Eco*R I/*Hin*d III digested lambda phage DNA) and one lane of tobacco DNA (digested with the enzyme of interest). Expected restriction site maps of the entire tobacco chloroplast genome (Shinozaki et al., 1986) were constructed for each enzyme by computer analysis. Because many of the tobacco restrictions sites are conserved among the apioid taxa, a comparison of expected tobacco fragments and observed apioid fragments facilitated map construction.

Phylogenetic analysis of a data matrix based on variable restriction site mutations (available from the authors) was conducted with Wagner parsimony using test version 4.0d63 of PAUP* (D. L. Swofford, Smithsonian Institution, Washington, D.C.). The search options included 1000 replicates (with random addition) of a heuristic search with MULPARS in effect and ACCTRAN optimization. Early trials indicated that the shortest trees were 3038 steps long, but that the analysis was prone to getting stuck on large ''islands'' (sensu Maddison, 1991) of suboptimal trees (3039 steps or longer). For this reason, no more than 500 suboptimal trees were saved per replicate (swapping all saved trees to completion). This search yielded a single island of 84 trees (each of 3038 steps). To test confidence among the nodes of the trees, bootstrap (Felsenstein, 1985) and decay (Bremer, 1988; Donoghue et al., 1992) analyses were carried out. The bootstrap analysis was performed using PAUP*, with 1000 replicates, saving no more than 1000 trees per replicate. To complete the decay analysis, the computer program AutoDecay (Eriksson, 1997) was used with PAUP*, following the converse-constraint method (Baum, Sytsma, and Hoch, 1994). The data sets were examined for phylogenetic signal using the skewness test (generating the g_1 statistic by examining the distribution of 10 000 random trees using the Random Trees function of PAUP*; see Hillis, 1991; Huelsenbeck, 1991; Hillis and Huelsenbeck, 1992; but also Källersjö et al., 1992), and a randomization test (the permutation tail probability or PTP test, performed using the permutation function of PAUP* with 1000 replicates of a heuristic search, saving no more than 100 trees per replicate; see Archie, 1989; Faith and Cranston, 1991). Additionally, PAUP* was used to construct a neighbor-joining tree (for comparison to the parsimony trees) and to generate a distance matrix to examine levels of divergence.

RESULTS

The chloroplast genomes of apioid taxa are colinear in gene arrangement and readily aligned to tobacco cpDNA. However, one probe (2.1 kb in length, corresponding to the location of *trnD*, ORF154, *psbM*, and ORF29 in the large single-copy [LSC] region of tobacco) failed to yield readable fragments, and the fragment patterns from a second probe (2.4 kb long, corresponding to the location of *rp116* and *rps3* in the LSC of tobacco cpDNA) could not be interpreted without ambiguity. The size of the chloroplast genome among apioids ranges from ~140 to 155 kb. This size variation is attributable to major deletions in one of the inverted repeats (IR) at the boundary of the LSC region. Based on our present analysis, there appear to be at least four distinct IR sizes: ~10 kb, ~17 kb, ~23 kb and ~26 kb. The size of the probes used in this study (ranging from 1.06 to 5.49 kb) prevents a more precise mapping of these deletions (or detection of other, very small insertions/deletions), but this issue will be addressed in a subsequent study based on finer scale probes of the IR-LSC region.

TABLE 3. Number, location, and level of homoplasy (HI) for variable restriction sites derived from each of the 14 enzymes used to construct cpDNA maps. Location abbreviations: LSC—large single-copy region of the chloroplast genome; IR—inverted repeat; SSC—small single-copy region (restriction sites from the IR were scored only once).

Enzyme	No. of variable restriction sites LSC	IR	SSC	Total	HI
Ava I	43	8	8	59	0.651
*Bam*H I	34	8	14	56	0.627
Ban II	71	8	18	97	0.655
Bcl I	40	6	10	56	0.663
Bgl II	54	12	8	74	0.693
Cla I	56	11	10	77	0.712
Dra I	40	11	18	69	0.779
*Eco*O109 I	55	9	12	76	0.643
*Eco*R I	63	13	9	85	0.698
*Eco*R V	44	3	11	58	0.589
Hinc II	48	3	7	58	0.525
*Hin*d III	39	7	11	57	0.593
Nci I	84	10	18	112	0.671
Vsp I	46	2	8	56	0.740
Total	717	111	162	990	

Mapping of restriction sites from 79 taxa in Apiaceae and the closely related families Araliaceae and Pittosporaceae yielded a data matrix of 990 characters, of which 750 were potentially parsimony-informative (240 were found in only a single taxon). Of the total 990 characters, 162 were derived from the small single-copy (SSC) region of the chloroplast genome, 111 from the IRs (scored only once), and 717 from the LSC (Table 3). Divergence values, calculated as mean character difference, ranged from 29.9% (between *Scandix* and the outgroup taxon *Hymenosporum*) to 1.0% (between two species of *Arracacia* and between *Anethum* and *Foeniculum*). Within Apiaceae, the range was 27.4% (between *Tordylium* and the hydrocotyloid *Centella*) to 1.0%; the range within Apioideae was 22.7% (between *Bupleurum* and *Pastinaca*) to 1.0% (Table 4). Among the much smaller sample of taxa from Araliaceae, divergence ranged from 9.5% (between *Aralia* and *Tetrapanax*) to 2.4% (between *Pseudopanax* and *Polyscias*). In tests for phylogenetic signal, the skewness test yielded a g_1 statistic of −0.516, and the permutation analysis yielded a PTP value of 0.001. These results are significant above the 99% confidence level and suggest that the data contain significant amounts of nonrandom structure and differ significantly from randomized data.

Cladistic analysis of the restrictions site data set yielded 84 most-parsimonious trees of 3038 steps. Excluding uninformative characters, the tree length was 2798, the consistency index (CI) was 0.268 (homoplasy index [HI] of 0.732), and the retention index (RI) was 0.682. The large difference between the CI and RI suggests that the high levels of homoplasy are due in large part to the size of the data matrix (see below). To examine the relative amount of homoplasy from each of the three major regions of the chloroplast genome, characters derived from the other two regions were excluded and the HI was measured against the shortest trees. The SSC exhibited the highest level of homoplasy (0.707), followed by the LSC (0.674); the slowly evolving IR exhibited the least

TABLE 4. Comparison of chloroplast restriction site data (present study) to three previously published data sets based on DNA sequences from Apioideae (ITS and *rpoC1* intron sequence data, Downie et al., 1998; *matK* sequence data, Plunkett, Soltis, and Soltis, 1996b); abbreviations: HI = homoplasy index; CI = consistency index of most parsimonious trees; RI = retention index (HI, CI, and RI values are based on data sets excluding uninformative characters). Divergence values are provided for comparison, although sequence divergence is not directly comparable to that of restriction sites.

Data set	No. of taxa	No. of parsimony-informative characters	Range of divergence within Apioideae (%)	HI	CI	RI
Restriction sites	79	750	1.0–22.7	0.732	0.268	0.682
rpoCl intron	96	215	0–9.8	0.440	0.560	0.871
matK	53	207	0.1–9.7	0.430	0.570	0.818
ITS	95	294	1.7–34.3	0.686	0.314	0.649

(0.612). A similar comparison was made among the characters derived from each of the 14 enzymes. Characters derived from *Dra* I had the highest levels of homoplasy (0.779), whereas those from *Hin*c II showed the least (0.525). A comparison of these values for each enzyme (Table 3) indicates that homoplasy is not necessarily correlated with the number of characters, and some enzymes providing a large number of variable characters (e.g., *Nci* I, *Ban* II) have lower homoplasy than several other enzymes yielding many fewer characters (e.g., *Dra* I, *Cla* I, *Vsp* I).

The clades in the strict consensus tree (Fig 1) are labeled with group names that were coined in earlier studies (Plunkett, Soltis, and Soltis, 1996b; Downie et al., 1998). Within the monophyletic Apioideae, the largest clade, the ''*Angelica* group,'' is supported by a bootstrap (BS) percentage of 99 and a decay index value (DI) of 10. Other clades include the ''*Aegopodium* group'' (BS = 59%, DI = 2); the ''*Apium* group'' (BS = 39%; DI = 1); the ''*Daucus* group'' (BS = 67%; DI = 3); the ''*Aciphylla*'' group (BS = 79%; DI = 6); the ''*Oenanthe*'' group (BS = 100%; DI = 18); and a basal grade of apioids (*Heteromorpha-Anginon* and *Bupleurum*). Outside Apioideae, the two saniculoids form a monophyletic group (BS = 100%; DI = 41), but the hydrocotyloids form a grade of basally branching lineages within Apiaceae. Although the sampling of araliads was small, the restriction site cladogram suggests that the Araliaceae are monophyletic (BS = 100%; DI = 29). The neighbor-joining (NJ) tree reveals the identical seven groups, although the *Apium* group (rather than the *Aegopodium* group) is sister to the *Angelica* group in the NJ tree (Figs. 1,2).

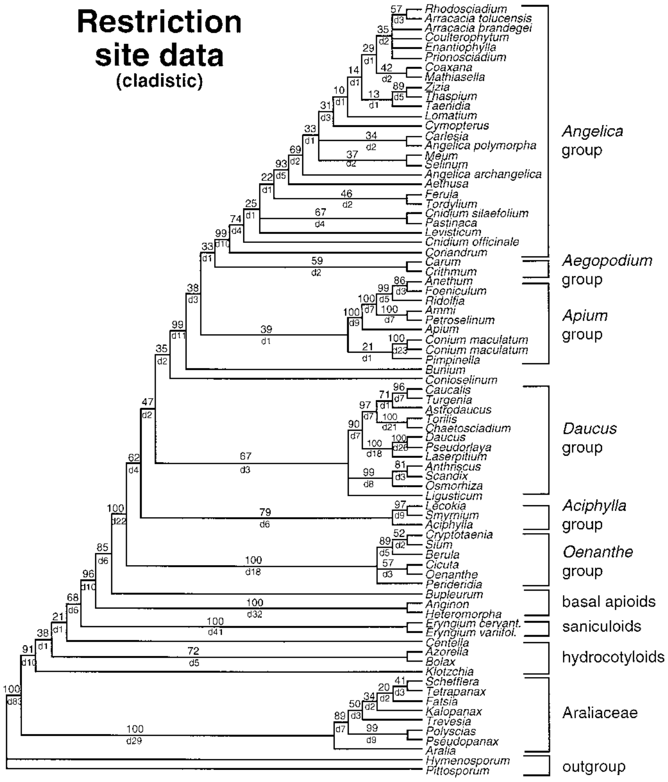

Fig. 1. Strict consensus of the 84 most parsimonious trees resulting from the equally weighted parsimony analysis of cpDNA restriction site data from 79 taxa. Bootstrap percentages are provided above each branch, and decay index values are provided below each branch (preceded by the suffix ''d-'').

DISCUSSION

The utility of restriction site data—Restriction site analysis continues to be an important source of characters for phylogenetic inference in plant groups (e.g., Cota and Wallace, 1997; Luckow, 1997; Olmstead and Palmer, 1997; Panero and Jansen, 1997; Rodriguez and Spooner, 1997; Soltis and Novak, 1997; Steane et al., 1997; Sykes, Christensen, and Peterson, 1997), but to a large degree, this method has been supplanted by DNA sequencing studies. Compared to sequencing methods, restriction site analysis requires relatively large amounts of highly purified DNA and involves more laborious laboratory work. In addition, mapping restriction site data is generally more time consuming and less straightforward than reading gene sequence data. Despite these limitations, however, restriction site analysis can provide many more variable characters than most sequencing studies, and by employing different enzymes and different regions of the chloroplast genome, a study of restriction sites can be adjusted to meet the needs of a range of different taxonomic levels (Olmstead and Palmer, 1994; Jansen, Wee, and Millie, 1998). In the present study, for example, 990 variable characters were scored, of which 750 were potentially parsimony-informative. Compared to three recent sequencing studies of Apioideae (ITS and *rpoCl* intron sequences—Downie et al., 1998; and *matK* sequences—Plunkett, Soltis and, Soltis, 1996b), the restriction site analysis provided 2.6–3.6 times the number of potentially informative characters (see Table 4). When comparing the levels of divergence within Apioideae across

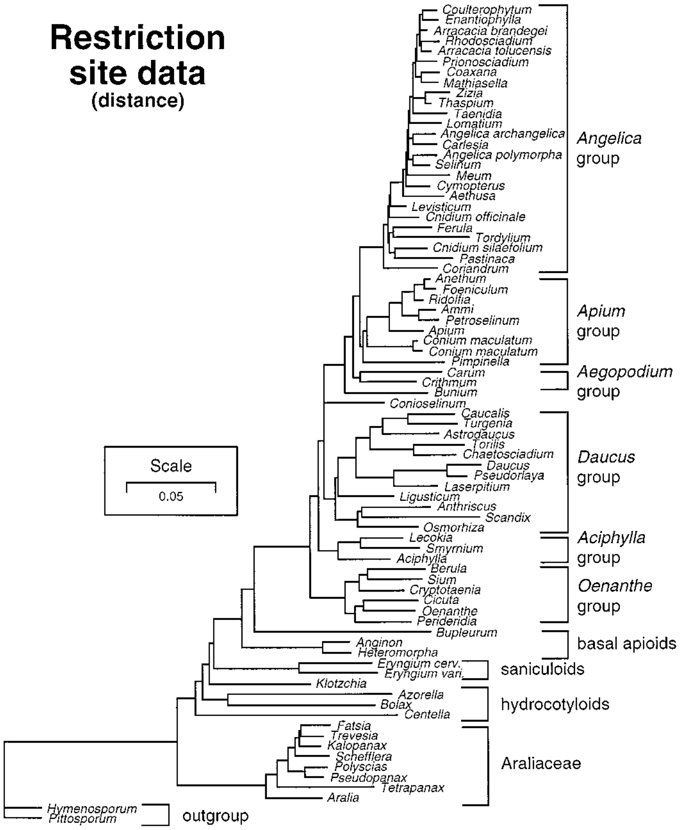

Fig. 2. Neighbor-joining tree resulting from the distance analysis of cpDNA restriction site data from 79 taxa.

these studies, restriction site analysis provides a greater range (1.0–22.7%) than the two chloroplast sequences (*matK* and the *rpoCl* intron, with ranges of 0.1–9.7 and 0–9.8%, respectively). Conversely, restriction site divergence was lower than that found in ITS (1.7–34.3%), where it became difficult to align ITS sequences from taxa of the ‘‘basal grade’’ (*Bupleurum*, *Anginon*, and *Heteromorpha*) to those of the remaining apioids (Downie and Katz-Downie, 1996; Downie et al., 1998). When comparing homoplasy levels of the shortest trees from each study (excluding uninformative characters), the restriction site analysis exhibited the greatest homoplasy (HI = 0.732; CI = 0.268). However, the HI (and conversely the CI) are negatively affected by the number of taxa and the number of characters in a data set (see Archie, 1989). Given the size of the restriction site matrix (79 taxa and 750 informative characters), it is not surprising that homoplasy appears to be high. The retention index (Archie, 1989; Farris 1989), which is less sensitive to increases in the number of taxa and characters, is a better measure for comparing data sets of different sizes. The RI for the restriction site study was 0.682, which is comparable to that of the ITS cladogram (0.649), although both of these data sets exhibit more homoplasy than the chloroplast sequence data (0.871 for the *rpoC1* intron, and 0.818 for *matK*; see Table 4). In general, comparisons of various data-set metrics suggest that restriction site data remain a valuable source of characters for phylogeny reconstruction.

Phylogenetic relationships—The taxonomic problems in Apiaceae are pervasive, ranging from species and generic circumscriptions to the relationship of Apiaceae to its ‘‘sister family,’’ Araliaceae, to the placement of these families among the other dicot groups. This situation makes both ‘‘top-down’’ and ‘‘bottom-up’’ approaches to systematics equally confounding. Simply put, the problem is ‘‘where to jump in.’’ Molecular data are not the panacea of all taxonomic problems, but in troublesome groups like Apiaceae, where the array of ‘‘traditional’’ data is confusing at best, molecular approaches provide the first opportunity of dividing the family into workable units or lineages. Like several previous papers (Downie and Katz-Downie, 1996; Downie, Katz-Downie, and Cho, 1996; Kondo et al., 1996; Plunkett, Soltis, and Soltis, 1996a, b, 1997), the present study suggests that subfamily Hydrocotyloideae is not monophyletic. In the strict consensus of the restriction site trees (Fig. 1), the hydrocotyloids form a paraphyletic grade at the base of the Apiaceae clade. Studies with more intensive sampling of hydrocotyloids and araliads further suggest that Hydrocotyloideae may in fact be polyphyletic, with some taxa (notably *Hydrocotyle*, *Centella*, and *Micropleura*) more closely allied to Araliaceae than to the rest of Apiaceae (discussed in Plunkett, Soltis, and Soltis, 1996a, 1997). Like other recent studies, chloroplast restriction site data also suggest that Apioideae are a well-supported monophyletic group, sister to a monophyletic Saniculoideae. Given that both traditional concepts and molecular data agree that subfamily Apioideae is ‘‘natural’’ or monophyletic, it seems safe to begin a re-evaluation of Apiaceae at this level.

Four data sets with a broad sampling of apioids are now available: chloroplast restriction sites (present study); nuclear ITS sequences and chloroplast *rpoC1* intron sequences (Downie et al., 1998); and chloroplast *matK* sequences (Plunkett, Soltis, and Soltis 1996b) (see Figs. 1, 3–5; hereafter, these data sets will be abbreviated as the ‘‘restriction site,’’ ‘‘ITS,’’ ‘‘*rpoC1*,’’ and ‘‘*matK*’’ studies). Much has been written on the conditions under which data sets can or should be combined (reviewed in de Queiroz, Donoghue, and Kim, 1995). Regardless of these issues, the sampling overlap of the four apioid data sets is not at present sufficient enough to warrant construction of a single combined data set. On the other hand, the overlap is not negligible. Of the total 97 genera sampled across these four studies, 80 were included in at least two of the studies and 50 in at least three. Thus, although combining these data sets is premature, visual comparison of cladogram topologies provides a highly congruent picture of relationships within Apioideae.

Molecular cladograms consistently reveal six major clades (the *Angelica* group, the *Aegopodium* group, the *Apium* group, the *Oenanthe* group, the *Daucus* group, and the *Aciphylla* group) and one basal, paraphyletic grade (the ‘‘basal apioid grade’’). The strict consensus tree based on restriction site data (Fig. 1) is labeled with these informal group names, which were originally proposed on the basis of *matK* data by Plunkett, Soltis, and Soltis (1996b), and later used by Downie et al. (1998). Each group is named after a large and familiar genus found within that clade. The use of informal names for lineages of genera provides flexible descriptors that can be used

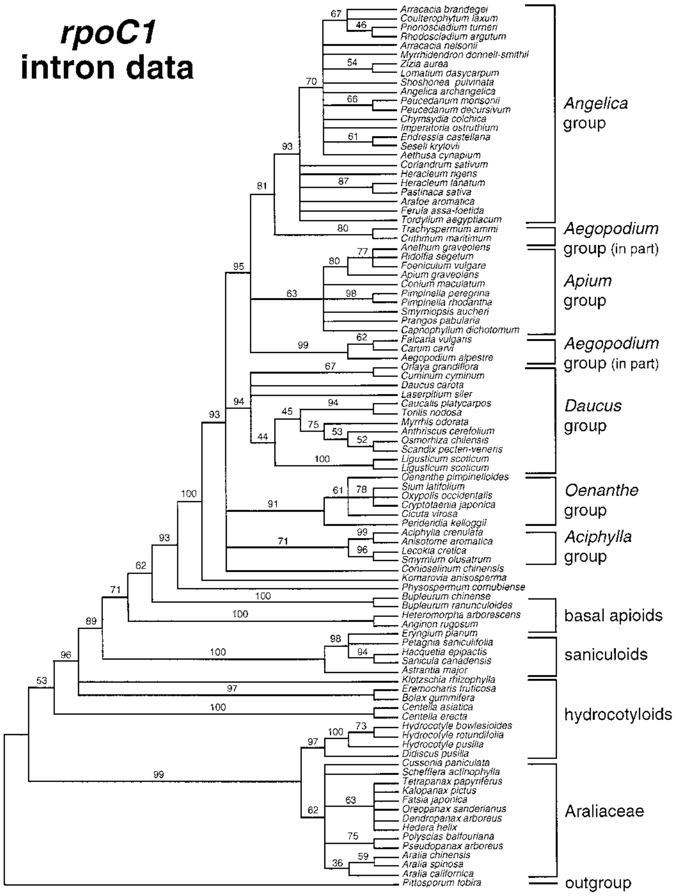

Fig. 3. Strict consensus of 12 000 trees (length = 730 steps) resulting from the equally weighted parsimony analysis of *rpoCl* intron sequences from 96 taxa (redrawn from Downie et al., 1998); CI excluding uninformative characters = 0.560; RI = 0.871. Bootstrap percentages are provided above each branch.

in place of traditional tribal names until a more stable and formal classification system can be erected. Based on comparisons of the four apioid cladograms, we have assigned 90 of the 97 genera in these studies to one of the seven groups (Table 5). Given that many of the larger genera in Apioideae may be paraphyletic (or even polyphyletic), the inclusion of a genus within any informal group may be an oversimplification. Moreover, some genera have been placed in a group on the basis of only a single data set. For these reasons, the groups proposed herein must be viewed as provisional. Appreciating these limitations, we hope the erection of such groups can serve as explicit hypotheses that may be tested at greater length by future studies.

The largest of the seven lineages is the *Angelica* group (see Table 5, Figs. 1, 3–5). Of the four apioid data sets, three (restriction sites, *rpoC1*, *matK*) resolve nearly identical complements of taxa within well-supported clades (BS > 90%). In the ITS cladogram, most members from the *Angelica* group form a single large subclade, but others (e.g., *Heracleum*, *Tordylium*, *Pastinaca*, *Cnidium*, and *Levisticum*) are found in two smaller subclades with genera from the *Apium* group (viz. *Conium*, *Smyrniopsis*, *Prangos*). Branching patterns within the *Angelica* group

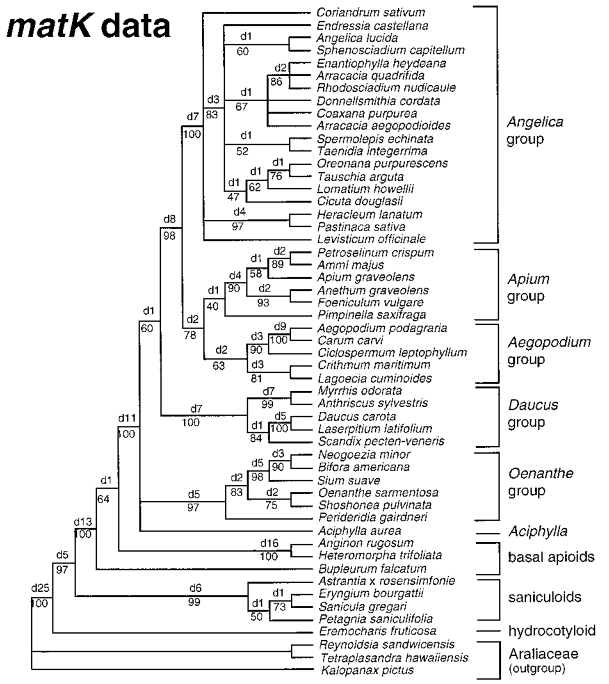

Fig. 4. Strict consensus of 902 trees (length = 709) resulting from the equally weighted parsimony analysis of *matK* sequences from 53 taxa (redrawn from Plunkett, Soltis, and Soltis, 1996b); CI excluding uninformative characters = 0.570; RI = 0.818. Bootstrap percentages are provided below each branch, and decay index values are provided above each branch (preceded by the suffix ''d-'').

vary among the four cladograms, but some groups of taxa are placed together in two or more of the trees. For example, most of the trees suggest a relationship among some of the North American taxa (including *Lomatium-Cymopterus-Tauschia-Oreonana*, and *Zizia-Thaspium-Taenidia-Aletes-Spermolepis*), although problems with resolution or sampling make definition of these subclades difficult. All trees do, however, resolve a subclade geographically centered in meso-America, including *Arracacia*, *Rhodosciadium*, *Coulterophytum*, *Enantiophylla*, and *Prionosciadium*. Some trees include several other meso-American genera, such as *Coaxana*, *Mathiasella*, *Dahliophyllum*, and *Donnellsmithia* within this subclade. The *Angelica* group provides the best evidence of the inadequacy of Drude's intergeneric system, drawing taxa from four of his eight tribes (viz. Apieae, Peucedaneae, Smyrnieae, and Coriandreae). Even so, all but two members of Peucedaneae fall within the *Angelica* group. Thus, although the dorsally compressed, winged fruits diagnostic of this tribe are homoplastic, there may be a developmental predisposition to these fruit types in the *Angelica* group.

The clade originally designated as the ''*Apium* group'' in the *matK* study formed two distinct subclades. On the basis of ITS and *rpoC1* data, Downie et al. (1998) designated each subclade as a distinct group, the *Aegopodium* group and a more narrowly defined *Apium* group. All four data sets reveal nearly identical clades of taxa in the *Apium* group (sensu stricto), except for the ITS tree (which excludes only *Conium*, *Prangos*, *Smyrniopsis*, and *Pimpinella*, all found in small subclades with

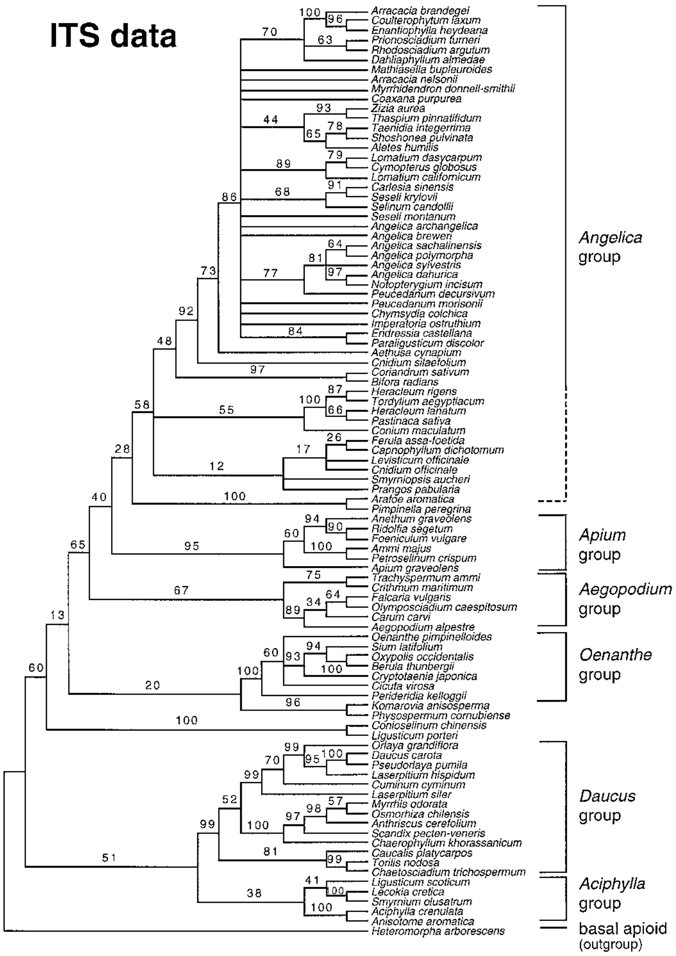

Fig. 5. Strict consensus of 12 000 trees (length = 2107 steps) resulting from the equally weighted parsimony analysis of nuclear ITS sequences from 95 taxa (redrawn from Downie et al., 1998); CI excluding uninformative characters = 0.314; RI = 0.649. Bootstrap percentages are provided above each branch.

members of the *Angelica* group). In comparison to Drude's system, the *Apium* group includes taxa from three tribes: Apieae, Smyrnieae, and Peucedaneae. The resolution of a distinct *Aegopodium* group is based primarily on *matK* and ITS data. It includes *Aegopodium, Carum, Ciclospermum, Crithmum, Trachyspermum, Falcaria*, and *Olymposciadium*. Of these, only *Carum* and *Crithmum* were included in the restriction site data set, but these do form a clade. Intron data from *rpoC1* show two distinct clades of taxa from the *Aegopodium* group (*Trachyspermum-Crithmum*; and *Falcaria-Carum-Aegopodium*), but these do not form a monophyletic group. All taxa from the *Aegopodium* group are from Drude's tribe Apieae, with the exception of *Lagoecia*. The *matK* tree suggests that this monotypic saniculoid genus should be transferred to the *Aegopodium* group in Apioideae, a finding consistent with Koso-Poljanski's (1916) treatment. The transfer of *Lagoecia* is also supported by cotyledon, pollen, stomatal, and floral-development characters (Cerceau-Larrival, 1962, 1971; Guyot, 1966, 1971; Magin, 1980; discussed in Plunkett, Soltis, and Soltis, 1996b).

The *Oenanthe* group is a well-supported clade (BS > 90%) resolved by all four analyses. It includes *Oenanthe, Perideridia, Sium, Berula, Oxypolis, Cicuta*, and probably *Neogoezia*. The *rbcL* study of Kondo et al. (1996) also provides evidence for this lineage. Data from *matK* place *Bifora* and *Shoshonea* in the *Oenanthe* group as well, but in contradiction to the ITS cladogram. In the case of *Bifora*, different species were sampled for each study (the North American species *B. americana* was used for *matK*, whereas the ITS study used the Eurasian *B. radians*), making it difficult to assess the source of the discrepancy. Future studies including both species will be needed to clarify this issue. Conversely, the single species of the monotypic genus *Shoshonea* was used in both the ITS and the *matK* studies and was also included in the *rpoC1* data set. The agreement of the ITS and *rpoC1* cladograms in placing *Shoshonea* in the *Angelica* group (among other western North American endemics) suggests that the *matK* result may be spurious.

The *Daucus* group represents all taxa sampled from Drude's tribes Laserpitieae, Dauceae, and Scandiceae (both subtribes Scandicinae and Caucalidinae; see Table 1). Drude's tribal system differed from those proposed earlier by Bentham (1867) and Boissier (1872), who merged the elements of Drude's Dauceae and subtribe Caucalidinae into a single tribe called Caucalideae (or Caucalineae). This treatment united all taxa with distinctly spiny secondary ribs. As so defined, Caucalideae have been extensively studied by Heywood and colleagues (e.g., Heywood and Dakshini, 1971; Heywood, 1973, 1978, 1983; Jury, 1978, 1986), and have been employed by Pimenov and Leonov (1993). Bentham and Boissier placed Caucalideae near Laserpitieae, which also has secondary ribs (which are winged rather than armed). Molecular data suggest that all of these groups (Drude's Laserpitieae, Dauceae, and Scandiceae including Caucalideae) represent a single evolutionary lineage, the *Daucus* group. Within this group, restriction site and ITS data resolve three very similar subclades. One subclade is roughly equivalent to Drude's subtribe Scandicinae, including *Scandix, Anthriscus, Chaerophyllum, Myrrhis*, and *Osmorhiza*. A second subclade contains only taxa from Drude's subtribe Caucalidinae: *Caucalis, Astrodaucus, Chaetosciadium, Torilis*, and *Turgenia*. The third subclade is drawn from several different tribes and includes *Daucus, Cuminum, Laserpitium, Orlaya*, and *Pseudorlaya*.

The *Aciphylla* group also comprises distinct subclades, one with *Aciphylla* and *Anistome* and a second with *Lecokia* and *Smyrnium*. Geographically, these subclades are well separated: *Lecokia* and *Smyrnium* are native to Eurasia and northern Africa, whereas *Aciphylla* and *Anistome* are restricted to New Zealand and Australia. It is likely that sampling additional taxa may serve to bridge the geographic disjunction between these two subclades. The alliance of the Australasian taxa to largely Eurasian genera, however, does indicate that the distinctive apioids of the South Pacific (e.g., *Aciphylla, Anistome, Scandia, Gingidia*, and *Lignocarpa*; see Dawson, 1971; Dawson and Webb, 1978) may not represent ancient relicts but rather may be derived from Eurasian stock. Thus, although the most ancient extant lineages of the order Apiales (Apiaceae and Araliaceae) appear to persist in Aus-

TABLE 5. Provisional groupings of 98 apioid genera based on molecular data. Taxa followed by an asterisk (*) are placed in groups on the basis of only one data set. Abbreviations for data sets: 1—chloroplast DNA restriction site data (present study); 2—*rpoC1* intron data (Downie et al., 1998); 3—*matK* data (Plunkett, Soltis, and Soltis, 1996b); 4—ITS data (Downie et al., 1998); 5—*rbcL* data (Plunkett, Soltis, and Soltis, 1996a); 6—*rbcL* data (Kondo et al., 1996). Data-set abbreviations followed by a "?" or "x" (e.g., 1 = ?; 1 = X) indicate that a given data set is equivocal or contradicts the inclusion of a genus in a given group, respectively. For comparison, Drude's (1897–1898) tribes are also provided.

Taxon	Data sets	Former tribe
***Angelica* group**		
Aethusa	1, 2, 4	Apieae
*Aletes**	4	Apieae
Angelica	1, 2, 3, 4	Peucedaneae
Arracacia	1, 2, 3,4	Smyrnieae
Carlesia	1, 4	Apieae
Chymsydia	2, 4	Peucedaneae
Cnidium	1,4	Apieae
Coaxana	1, 3, 4	Apieae
Coriandrum	1, 2, 3, 4	Coriandreae
Coulterophytum	1, 2,4	Peucedaneae
Cympoterus	1,4	Peucedaneae
*Dahliophyllum**	4	unknown
*Donnellsmithia**	3	Smyrnieae
Enantiophylla	1, 3, 4	Peucedaneae
Endressia	2, 3, 4	Apieae
Ferula	1, 2; (4=?)	Peucedaneae
Heracleum	2, 3; (4=?)	Peucedaneae
Imperatoria	2,4	Peucedaneae
Levisticum	1, 3; (4=?)	Peucedaneae
Lomatium	1, 2, 3, 4	Peucedaneae
Mathiasella	1, 4	Peucedaneae
*Meum**	1	Apieae
Myrrhidendron	2, 4	Peucedaneae
*Notopterygium**	4	Apieae
*Oreonana**	3	Smyrnieae
*Paraligusticum**	4	Apieae
Pastinaca	1, 2, 3; (4=?)	Peucedaneae
Peucedanum	2, 4	Peucedaneae
Prionosciadium	1, 3, 4	Peucedaneae
Rhodosciadium	1, 2, 3,4	Peucedaneae
Selinum	1, 4	Apieae
Seseli	2, 4	Apieae
Shoshonea	2, 4; (3=X)	Apieae
*Spermolepis**	3	Apieae
*Sphenosciadium**	3	Apieae
Taenidia	1, 3, 4	Apieae
*Tauschia**	3	Smyrnieae
Thaspium	1, 4	Apieae
Tordylium	1, 2; (4=?)	Peucedaneae
Zizia	1, 2,4	Apieae
Aegopodium group		
Aegopodium	2, 3, 4	Apieae
Carum	1, 2, 3, 4	Apieae
*Ciclospermum**	3	Apieae
Crithmum	1, 2, 3,4	Apieae
Falcaria	2, 4	Apieae
*Lagoecia**	3	Lagoecieae (Saniculoideae)
*Olymposciadium**	4	Apieae
Trachyspermum	2, 4	Apieae
***Apium* group**		
Ammi	1, 3, 4	Apieae
Anethum	1, 2, 3, 4	Apieae
Apium	1, 2, 3, 4	Apieae
*Capnophyllum**	2; (4=?)	Peucedaneae
Conium	1, 2; (4=?)	Smyrnieae
Foeniculum	1, 2, 3, 4	Apieae
Petroselinum	1, 3, 4	Apieae
Pimpinella	1, 2, 3; (4=?)	Apieae
*Prangos**	2; (4=?)	Smyrnieae
Ridolfia	1, 2, 4	Apieae
*Silaum**	1	Apieae
*Smyrniopsis**	2; (4=?)	Smyrnieae
***Oenanthe* group**		
Berula	1, 4	Apieae
Cicuta	1, 2, 4, 6; (3=X)	Apieae
Cryptotaenia	1, 2, 4, 6	Apieae
*Neogoezia**	3	Smyrnieae
Oenanthe	1, 2, 3, 4, 6	Apieae
Oxypolis	2, 4	Peucedaneae
Perideridia	1, 2, 3, 4	Apieae
Sium	1, 2, 3, 4, 6	Apieae
***Daucus* group**		
***Scandix* subgroup**		
Anthriscus	1, 2, 3, 4	Scandiceae–Scandicinae
*Chaerophyllum**	4	Scandiceae–Scandicinae
Myrrhis	2, 3, 4	Scandiceae–Scandicinae
Osmorhiza	1, 2, 4	Scandiceae–Scandicinae
Scandix	1, 2, 3, 4	Scandiceae–Scandicinae
***Torilis* subgroup**		
*Astrodaucus**	1	Scandiceae–Caucalinae
Caucalis	1, 2, 4	Scandiceae–Caucalinae
Chaetosciadium	1, 4	Scandiceae–Caucalinae
Torilis	1, 2, 4	Scandiceae–Caucalinae
*Turgenia**	1	Scandiceae–Caucalinae
***Daucus* subgroup**		
Cuminum	2, 4	Apieae
Daucus	1, 2, 3, 4	Dauceae
Laserpitium	1, 2, 3, 4	Laserpitieae
Orlaya	2, 4	Scandiceae–Caucalinae
Pseudorlaya	1, 4	Dauceae
***Aciphylla* group**		
Aciphylla	1, 2, 3, 4	Apieae
Anistome	2, 4	Apieae
Leckockia	1, 2, 4	Smyrnieae
Smyrnium	1, 2, 4	Smyrnieae
Basal apioid grade		
Bupleurum	1, 2, 3, 5	Apieae
Anginon	1, 2, 3, 5	Apieae
Heteromorpha	1, 2, 3, 5	Apieae
Uncertain		
Arafoe	2, 4	Apieae
Bifora	3, 4	Coriandreae
Bunium	1	Apieae
Conioselinum	2, 4	Apieae
Komarovia	2, 4	unknown
Ligusticum	1, 2, 4, 6	Apieae
Physospermum	2, 4	Smyrnieae

tralasia (see Plunkett, Soltis, and Soltis, 1996a, 1997), the four apioid data sets are unified in suggesting that the basal lineages of Apioideae persist in southern Africa. All molecular data reveal a basal paraphyletic grade comprising *Heteromorpha*-*Anginon* and *Bupleurum* ("basal apioid grade" in Figs. 1, 3–5). Data based on *rbcL* sequences (Plunkett, Soltis, and Soltis, 1996a) also support this topology. Both *Heteromorpha* and *Anginon* are woody shrubs or small trees restricted in distribution to southern Africa. *Bupleurum* includes mostly Eurasian herbs, but some species are distinctly woody, and another species is endemic to southern Africa. A more rigorous test of the African origin of Apioideae requires a more intensive study of several other woody African apioids (e.g., *Polemannia*, *Polemanniopsis*, *Steganotaenia*).

Despite the large areas of congruence among the molecular cladograms, several genera are not easily placed. In the case of *Ligusticum*, it appears that differences are due, at least in part, to the polyphyly of this genus. The restriction site, *rpoC1*, and *rbcL* (Kondo et al., 1996) data sets all suggest that *L. scoticum* is allied to the *Daucus* group; ITS data suggest that it belongs to the *Aciphylla* group (which in turn is sister to the *Daucus* group). Two of the data sets (ITS and *rbcL*) included more than one species of *Ligusticum*, and these suggest that *L. scoticum* is not closely related to other species sampled from that genus (*L. porteri*, *L. chuanxiong*, *L. jeholense*, and *L. sinense*). The other ''uncertain taxa'' represent genera that are placed in different groups by two or more of the cladograms. For example, *Arafoe* is placed in the *Angelica* group on the basis of *rpoC1* data, but is placed with *Pimpinella* (of the *Apium* group) by the ITS tree. Finally, some genera (e.g., *Komarovia*, *Physospermum*, and *Conioselinum*) form isolated lineages that are difficult to assign to any of the seven groups. Sampling additional genera may help to stabilize the placement of these genera. Alternatively, these taxa may belong to groups as yet undescribed.

In broader terms, the four apioid cladograms suggest that the *Angelica* group, the *Apium* group, and the *Aegopodium* group form a single large clade (the apioid ''superclade''). Relationships between the superclade and the remaining three monophyletic groups (the *Oenanthe* group, the *Daucus* group, and the *Aciphylla* group) are less clear. Restriction sites and *matK* data suggest that the *Daucus* group is sister to this superclade (Figs. 1, 4), whereas the placement of the superclade in cladograms based on *rpoC1* intron and ITS data is equivocal (Fig. 5). All data sets confirm that *Heteromorpha*, *Anginon*, and *Bupleurum* occupy basally branching positions within Apioideae.

All of the major groups (excluding the basal grade) are monophyletic in at least three of the four apioid cladograms (Figs. 1, 3–5). Of these, the *Angelica* group, the *Oenanthe* group, and the *Daucus* group are each supported by bootstraps of >90% in at least three of the four studies (Table 6). Conversely, the bootstrap support for the *Aciphylla* group, the *Apium* group, and the *Aegopodium* group are low to moderate (ranging from 38 to 79%, 39 to 63%, and 59 to 67%, respectively). Despite such low internal support, clades with nearly identical complements of taxa are resolved by at least three of the four studies. Comparing cladograms from different studies provides an estimate of external support not readily available in studies based on a single source of data. Although three of the four apioid data sets are derived from a single inheritance unit (the chloroplast genome), these represent three different types of data samplings (restrictions sites, intron sequences, and gene sequences). Thus, the four data sets represent not only two independent sources of characters (nuclear and chloroplast DNA), but also four independent samplings. In areas where the four cladograms are largely congruent, we can infer that the data sets from which they were derived contain the same phylogenetic signal. Further, a comparison of the general topologies of each tree and of bootstrap support for individual clade suggests that none of the four data sets excels in its ability to resolve congruent and well-supported clades. These comparisons agree with recent assessments of other groups that multiple data sets will be required before a stable picture of relationships can be discerned. Within Apioideae, we hope that the present grouping of genera into informal groupings can serve as a basic framework in which the complex patterns of morphology, anatomy, biochemistry, and molecular characters can be reinterpreted, and from which a new and more satisfactory classification system can be erected.

TABLE 6. A comparison of bootstrap percentages for the six monophyletic groups resolved by at least three of the four apioid data sets (chloroplast DNA restriction site data—present study; *rpoC1* intron data—Downie et al., 1998; *matK* data—Plunkett, Soltis, and Soltis, 1996b; ITS data—Downie et al., 1998). The apioid ''superclade'' comprises a monophyletic group of the *Angelica* group, the *Apium* group, and the *Aegopodium* group. Symbols: * = not a monophyletic group in a given cladogram (for the ITS tree, values of roughly equivalent subclades are provided in parentheses); † = only a single taxon included from this group.

	Bootstrap values (%)			
Clade	Restriction sites	*rpoC1* intron	*matK*	ITS
Angelica group	99	93	100	*(48)
Apium group	39	63	40	*(95)
Aegopodium group	59	*	63	67
Apioid''superclade''	99	95	98	65
Oenanthe group	100	91	97	100
Daucus group	67	94	100	99
Aciphylla group	79	71	†	38

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