The phylogenetic position of *Peucedanum* sensu lato and allied genera and their placement in tribe Selineae (Apiaceae, subfamily Apioideae)

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Abstract. ITS sequences of members of *Peucedanum* and its segregates (*Cervaria*, *Holandrea*, *Imperatoria*, *Oreoselinum*, *Pteroselinum*, *Thysselinum*, *Tommasinia*, and *Xanthoselinum*), as well as representatives of other members of the previously identified 'Angelica' and 'Arracacia' clades, were analysed using distance, maximum likelihood, and maximum parsimony methods in order to establish their phylogenetic relationships. The 'Angelica' and 'Arracacia' clades comprise a strongly supported monophyletic group that is formally recognised as tribe Selineae. The genus *Holandrea*, expanded to include *Cervaria caucasica* and *Peucedanum achaicum*, is distantly related to the other peucedanoid genera. The remaining segregates are closely related to one another and to *Peucedanum* sensu stricto. The genera *Seseli* and *Selinum* are polyphyletic. Members of the genus *Angelica* form a single clade that also includes representatives of *Selinum* and *Sphenosciadium*. New combinations in *Holandrea* (*H. caucasica*, *H. achaica*) and *Angelica* (*A. capitellata*) are proposed, and *Selinum pyrenaeum* is recognised in *Angelica* (*A. pyrenaea*).

Key words: *Peucedanum*, Apiaceae, Umbelliferae, Selineae, phylogeny, evolution, comb. nov.

Apiaceae (Umbelliferae) include about 450 genera and 3700 species (Pimenov and Leonov 1993). However, these species are not evenly distributed among the genera: 41% of the genera are monotypic and 26% comprise only two or three species each. Sixty percent of the total number of species are placed in a relatively small number of large genera that comprise more than 20 species each (Spalik et al. 2001). These genera include *Ferula* (170 spp.), *Ligusticum* (40–50 spp.), *Seseli* (100–120 spp.), and *Peucedanum* (100–120 spp.), all of which are polyphyletic (Katz-Downie et al. 1999, Downie et al. 2000b). Consequently, they are poorly defined which makes their identification difficult.

The genus *Peucedanum* is distributed in Eurasia and Africa (Pimenov and Leonov 1993). Its members are characterised by flattened fruits with more or less developed lateral wings. It has long been regarded as heterogeneous and several authors have postulated its division into smaller, presumably more natural units (Calestani 1905, Leute 1966, Pimenov 1987, Frey 1989). Pimenov and Leonov (1993)

even suggested that it should be restricted to the 8–10 species comprising sect. *Peucedanum*. Indeed, many species once recognised in *Peucedanum* have found other affinities, sometimes very distant ones. For instance, *P. terebinthaceum* (Fisch. ex Trevir.) Fisch. ex Turcz., along with several other species, were transferred to *Kitagawia* (Pimenov 1986). Based on molecular data, *P. terebinthaceum*—the nomenclatural type of *Kitagawia*—is sister to *Pleurospermum hookeri* (Downie et al. 2000b) that at present is recognised in tribe Pleurospermeae (Downie et al. 2001). Two Socotran species of *Peucedanum* have appeared to be closely related to another Socotran endemic, *Nirarathamnos asarifolius*, the entire clade being a sister group to tribe Echinophoreae (Downie et al. 2000a, b). Moreover, *Peucedanum* sensu Drude (1897–1898) encompassed many North American umbellifers that are now placed in *Lomatium*.

Even the European members of *Peucedanum* are suspected of being distantly related to one another and several species have been treated within segregate genera. For example, in the *Flora Europaea* account (Tutin et al. 1968), a broad concept of *Peucedanum* was adopted, with the exclusion of those species placed in segregate genera *Imperatoria* and *Tommasinia*. In contrast, Reduron et al. (1997) recognised a narrow definition of *Peucedanum* and confirmed restitution of *Cervaria*, *Imperatoria*, *Oreoselinum*, *Pteroselinum*, *Thysselinum*, and *Xanthoselinum*, as well as described the new genus *Holandrea*, with three included species (Table 1). They based their treatment on morphological and phytochemical data; however, they did not perform a formal phylogenetic analysis of these data.

Peucedanum is a member of the '*Angelica*' clade sensu stricto, belonging to the large apioid superclade (Downie et al. 2001). Throughout this paper, names in single quotation marks refer to informal groups, whereas those without quotation marks denote genera or postulated genera. Closely related to the '*Angelica*' clade is the '*Arracacia*' clade, the latter comprising some ten genera of

meso-American distribution. In some analyses, the '*Arracacia*' clade arises within the '*Angelica*' clade (Plunkett et al. 1996, Downie et al. 1998). Downie et al. (2001) suggested that the former may eventually be subsumed within the latter. Both groups comprise many genera that were traditionally placed in Drude's (1897–1898) tribe Peucedaneae subtribes Angelicinae and Ferulinae, or tribes Peucedaneae and Angeliceae in the classification system of Pimenov and Leonov (1993).

The aim of this paper is to verify the taxonomic division of *Peucedanum* sensu lato against a phylogeny inferred from nuclear ribosomal DNA internal transcribed spacer (rDNA ITS) sequences. We include the type species of these segregate genera and a broad representation of the '*Angelica*' and '*Arracacia*' clades in order to find the closest relatives of these segregates.

Material and methods

Taxon sampling. The total number of accessions examined was 107. We included almost all available ITS sequences of members of the '*Arracacia*' clade and Old World members of the '*Angelica*' clade (Table 2). Since the phylogenetic affinities of the North American members of the '*Angelica*' clade were the subject of two recent studies (Downie et al. 2002, Sun et al. in press), we considered only a representative sample of these taxa. To these, we added 30 new accessions including the type species of *Peucedanum* and its segregates, as well as several members of the putatively related genera *Angelica*, *Seseli*, and *Selinum* including their type species. The accessions denoted as *Peucedanum* sp. and *Thysselinum* sp. represent two taxa from France whose affinities are unclear.

Since *Thysselinum palustre* was excluded from the '*Angelica*' clade in an earlier molecular analysis (Katz-Downie et al. 1999), we included a broad representation of outgroup genera from the apioid superclade, such as *Azilia*, *Cnidium*, *Coriandrum*, *Ferula*, *Opopanax*, *Prangos*, *Smyrniopsis*, and *Sphaenolobium*. The trees were rooted with *Krubera peregrina* (= *Capnophyllum dichotomum* in Downie et al. 1998) that in one of the earlier analyses was basal to this part of the apioid superclade (Katz-Downie et al. 1999).

Table 1. Genera segregated from *Peucedanum* sensu lato analysed in this paper and their type species

Genus	Number of species	Type species
Peucedanum L. (sensu stricto)	8–10	*Peucedanum officinale* L.
Cervaria Wolf	4	*Cervaria rivini* Gaertn. (≡*Peucedanum cervaria* (L.) Lapeyr.)
Holandrea Reduron, Charpin et Pimenov	3	*Holandrea carvifolia* (Vill.) Reduron, Charpin et Pimenov (≡*Peucedanum carvifolia* Vill.)
Imperatoria L.	3	*Imperatoria ostruthium* L. (≡ *Peucedanum ostruthium* (L.) W. D. J. Koch)
Oreoselinum Mill.	1	*Oreoselinum nigrum* Delarbre (≡*Peucedanum oreoselinum* (L.) Moench
Pteroselinum Rchb.	2	*Pteroselinum austriacum* (Jacq.) Rchb. (≡*Peucedanum austriacum* (Jacq.) W. D. J. Koch)
Thysselinum Adans.	2	*Thysselinum palustre* (L.) Hoffm. (≡*Peucedanum palustre* (L.) Moench)
Tommasinia Bertol.	1	*Tommasinia verticillaris* (L.) Bertol. (≡*Peucedanum verticillare* (L.) W. D. J. Koch ex DC.)
Xanthoselinum Schur	1	*Xanthoselinum alsaticum* (L.) Schur (≡*Peucedanum alsaticum* L.)

Laboratory procedures. Total DNA was extracted from herbarium specimens using the Plant DNeasy Extraction Kit (Qiagen, Inc., Valencia, CA). Details of PCR amplifications are provided in Downie et al. (2000a). Each PCR product was electrophoresed in a 1% agarose gel, stained with ethidium bromide, then excised and eluted using the QIAEX II Gel Extraction Kit (Qiagen). Cycle sequencing reactions were performed using the purified PCR product, AmpliTaq DNA polymerase, and fluorescent Big Dye terminators (Perkin-Elmer Corp., Norwalk, CT). The products were resolved by electrophoresis using ABI Prism 310 or 377 DNA sequencers. Scans were edited and corrected when necessary.

Data analysis. The DNA sequences were aligned using the program CLUSTAL X (Thompson et al. 1997), and manually adjusted. The aligned data matrix is available from the authors upon request. Phylogenetic analyses included neighbour-joining (NJ), maximum parsimony (MP), and maximum likelihood (ML) methods; all were performed using PAUP* 4.0b10 (Swofford 1998). For the NJ analysis, we used several substitution models available in PAUP*. Bootstrap analysis was performed for 1000 pseudoreplicates. For the MP analysis, the 'inverse constraint' approach was employed (Catalán et al. 1997). One thousand heuristic searches were initiated with random addition and tree-bisection-reconnection (TBR) branch swapping, with no more than ten shortest trees saved per replicate. These trees were then used as starting trees for another search, saving 10 000 shortest trees. The consensus of these trees was used as a phylogenetic constraint in another round of 10 000 searches. This time, only those trees that did not match the constraint were saved. Since all of these saved trees were longer than those obtained from the initial searches, one may suppose that the consensus tree summarises all possible shortest tree topologies. Gaps were treated as missing data; however, the absence/presence of indels was scored as separate binary characters, combined with sequence data, and the MP analyses repeated. Bootstrap support (Felsenstein 1985) was estimated using 1000 resampled data sets, saving no more than 10 trees per replicate. Bremer (1984) support values were obtained using AutoDecay 4.0 (Eriksson 1998).

For the ML analysis, the model of nucleotide substitution was selected using Modeltest 3.0 (Posada and Crandall 1998) and the likelihood ratio test statistic. The values of the model parameters estimated with Modeltest were used in subsequent heuristic searches. Due to time limitation, bootstrap support values were not calculated for the ML trees.

Table 2. Sources of accessions of Apiaceae examined for nuclear ribosomal DNA ITS sequence variation. A single GenBank accession number means that the contiguous sequence of ITS 1, 5.8S rDNA, and ITS 2 is available

Taxon	GenBank accession number		Reference or voucher specimen
	ITS 1	ITS 2	
Aethusa cynapium L.	U30582	U30583	Downie and Katz-Downie (1996)
Aletes humilis J. M. Coult. et Rose	U78401	U78461	Downie et al. (1998)
Angelica acutiloba (Siebold et Zucc.) Kitag.	AB013037	AB013856	GenBank
Angelica ampla A. Nelson	U79597	U79598	Downie et al. (1998)
Angelica archangelica L.	U30576	U30577	Downie and Katz-Downie (1996)
Angelica arguta Nutt. ex Torr. et A. Gray	U79599	U79600	Downie et al. (1998)
Angelica breweri A. Gray	U78396	U78456	Downie et al. (1998)
Angelica cincta H. Boissieu	AF008601	AF009080	Katz-Downie et al. (1999)
Angelica dahurica (Hoffm.) Franch. et Sav.	U78416	U78476	Downie et al. (1998)
Angelica decurrens (Ledeb.) B. Fedtsch.	AF008599	AF009078	Katz-Downie et al. (1999)
Angelica decursiva (Miq.) Franch. et Sav.	U78411	U78471	Downie et al. (1998)
Angelica gigas Nakai	AJ131291		GenBank
Angelica koreana Maxim.	AF455749		GenBank
Angelica lignescens Danton et Reduron	AY179030		Azores, Faial, cultivated in Botanical Conservatory Mulhouse, France, no. 01037, 2 August 2001, *Hildenbrand, Meyer and Reduron s. n.* (ILL)
Angelica polymorpha Maxim.	U78415	U78475	Downie et al. (1998)
Angelica sachalinensis Maxim.	U78413	U78473	Downie et al. (1998)
Angelica sylvestris L.	U78414	U78474	Downie et al. (1998)
Arracacia brandegei J. M. Coult. et Rose	U30570	U30571	Downie and Katz-Downie (1996)
Arracacia nelsonii J. M. Coult. et Rose	U30556	U30557	Downie and Katz-Downie (1996)
Azilia eryngioides (Pau) Hedge et Lamond	AF008620	AF009099	Katz-Downie et al. (1999)
Carlesia sinensis Dunn	U30562	U30563	Downie and Katz-Downie (1996)
Cervaria caucasica (M. Bieb.) Pimenov (≡*Peucedanum caucasicum* (M. Bieb.) K. Koch)	AF008618	AF009097	Katz-Downie et al. (1999)
Cervaria rivini Gaertn. (≡*Peucedanum cervaria* (L.) Lapeyr.)	AF008608	AF009087	Katz-Downie et al. (1999)
Chymsydia colchica (Albov) Woronow ex Grossh.	U78405	U78465	Downie et al. (1998)
Cnidiocarpa alaica Pimenov	AF008615	AF009094	Katz-Downie et al. (1999)
Cnidium silaifolium (Jacq.) Simonk.	U78407	U78467	Downie et al. (1998)
Coaxana purpurea J. M. Coult. et Rose	U30572	U30573	Downie and Katz-Downie (1996)
Coriandrum sativum L.	U30586	U30587	Downie and Katz-Downie (1996)

Table 2 (continued)

Taxon	GenBank accession number		Reference or voucher specimen
	ITS 1	ITS 2	
Cortia depressa (D. Don) C. Norman.	AF008607	AF009086	Katz-Downie et al. (1999)
Coulterophytum laxum B. L. Rob.	U30560	U30561	Downie and Katz-Downie (1996)
Cymopterus globosus (S. Watson) S. Watson	U78398	U78458	Downie et al. (1998)
Dahliaphyllum almedae Constance et Breedlove	U78395	U78455	Downie et al. (1998)
Dystaenia ibukiensis (Y. Yabe) Kitag.	AB013039	AB013873	GenBank
Dystaenia takesimana (Nakai) Kitag.	AB013038	AB013857	GenBank
Enantiophylla heydeana J. M. Coult. et Rose	U30558	U30559	Downie and Katz-Downie (1996)
Endressia castellana Coincy	U30584	U30585	Downie and Katz-Downie (1996)
Exoacantha heterophylla Labill.	AF008617	AF009096	Katz-Downie et al. (1999)
Ferula assa-foetida L.	U78391	U78451	Downie et al. (1998)
Holandrea carvifolia (Vill.) Reduron, Charpin et Pimenov (≡*Peucedanum carvifolia* Vill.)	AF495828	AF495829	France, Isère, mont Bovinant, Chartreuse, 22 August 1989, *Reduron s. n.* (WA)
Holandrea pschawica (Boiss.) Reduron, Charpin et Pimenov (≡*Peucedanum pschawicum* Boiss.)	AF008619	AF009098	Katz-Downie et al. (1999)
Holandrea schottii (Bess. ex DC.) Reduron, Charpin et Pimenov (≡*Peucedanum schottii* Bess. ex DC.)	AF495830	AF495831	France, Alpes-Maritimes, col de Brouis, 30 July 1981, *Reduron s. n.* (WA)
Imperatoria hispanica Boiss. (≡ *Peucedanum hispanicum* (Boiss.) Endl.)	AF495814	AF495815	Cultivated in Botanic Garden Lyon, December 1999, *Baffray s. n.* (WA)
Imperatoria ostruthium L. (≡*Peucedanum ostruthium* (L.) W. D. J. Koch)	U78403	U78463	Downie et al. (1998)
Karatavia kultiassovii (Korovin) Pimenov et Lavrova	AF008612	AF009091	Katz-Downie et al. (1999)
Krubera peregrina (L.) Hoffm. (= *Capnophyllum dichotomum* (Desf.) Lag.)	U78390	U78450	Downie et al. (1998)
Libanotis depressa R. H. Shan et M. L. Sheh	AF164829	AF164854	Downie et al. (2000)
Libanotis pyrenaica Bourg. ex Nyman	AY179026		France, Haut-Rhin, Osenbach, 24 July 2001, *Reduron s. n.* (ILL)
Lomatium dissectum (Nutt. ex Torr. et A. Gray) Mathias et Constance	AF011809	AF011826	Hardig and Soltis (1999)
Lomatium graveolens (S. Watson) Dorn et R. L. Hartm.	AF011810	AF011827	Hardig and Soltis (1999)
Lomatium howellii (S. Watson) Jeps.	AF011800	AF011817	Hardig and Soltis (1999)
Lomatium parvifolium (Hook. et Arnold) Jeps.	AF011801	AF011818	Hardig and Soltis (1999)
Macrosciadium physospermifolium (Albov) V. N. Tichom. et Lavrova (≡*Ligusticum physospermifolium* Albov)	AF008616	AF009095	Katz-Downie et al. (1999)

Table 2 (continued)

Taxon	GenBank accession number		Reference or voucher specimen
	ITS 1	ITS 2	
Myrrhidendron donnell-smithii J. M. Coult. et Rose	U30554	U30555	Downie and Katz-Downie (1996)
Notopterygium incisum C. T. Ting ex H. T. Chang	U78412	U78472	Downie et al. (1998)
Opopanax hispidus (Friv.) Griseb.	AF008624	AF009103	Katz-Downie et al. (1999)
Oreoselinum nigrum Delarbre (≡*Peucedanum oreoselinum* (L.) Moench)	AF495836	AF495837	France, Aveyron, Larzac, August 1977, *Chéron s. n.* (WA)
Paraligusticum discolor (Ledeb.) V. N. Tichom.	U78404	U78464	Downie et al. (1998)
Peucedanum achaicum Halácsy	AF164832	AF164857	Downie et al. (2000)
Peucedanum bourgaei Lange	AF495818	AF495819	Spain, Segovia, Montalbida, cultivated in Botanical Conservatory Mulhouse, France, no. 9406*, 6 December 1999, *Reduron s. n.* (WA)
Peucedanum coriaceum Rchb.	AF495824	AF495825	Cultivated in Botanical Conservatory Mulhouse, France, no. 9515, 8 December 1999, *Reduron s. n.* (WA)
Peucedanum gallicum Latourr.	AF495816	AF495817	France, Loire Atlantique, Séverac, 17 August 1982, *Reduron s. n.* (WA)
Peucedanum japonicum Thunb. ex A. Murray	AF495826	AF495827	Cultivated in Botanical Conservatory Mulhouse, France, no. 97138, 8 December 1999, *Reduron s. n.* (WA)
Peucedanum morisonii Bess. ex Spreng.	U78406	U78466	Downie et al. (1998)
Peucedanum officinale L.	AF495820	AF495821	France, Haut-Rhin, Steinbach, 5 June 1979, *Reduron s. n.* (WA)
Peucedanum sp.	AF495822	AF495823	France, Alpes Maritimes, Tende, cultivated in Botanic Garden Lyon, 28 August 1998, *Reduron s. n.* (WA)
Peucedanum zedelmeyerianum Manden.	AF164834	AF164859	Downie et al. (2000)
Phlojodicarpus popovii Sipliv.	AF008604	AF009083	Katz-Downie et al. (1999)
Prangos pabularia Lindl.	U78409	U78469	Downie et al. (1998)
Prionosciadium turneri Constance et Affolter	U30568	U30569	Downie and Katz-Downie (1996)
Pteroselinum austriacum (Jacq.) Rchb. (≡*Peucedanum austriacum* (Jacq.) W. D. J. Koch)	AF495842	AF495843	France, Haute-Savoie, Onnion, 27 July 1984, *Reduron s. n.* (WA)
Pteroselinum rablense (Wulfen ex Jacq.) Rchb. (≡*Peucedanum rablense* (Wulfen ex Jacq.) W. D. J. Koch)	AF495840	AF495841	Cultivated in Botanical Conservatory Mulhouse, France, no. 8645; 6 December 1999, *Reduron s. n.* (WA)
Rhodosciadium argutum (Rose) Mathias et Constance	U30566	U30567	Downie and Katz-Downie (1996)
Saposhnikovia divaricata (Turcz.) Schischk.	AF495838	AF495839	Cultivated in Botanical Conservatory Mulhouse, France, 23 August 1984, *Reduron s. n.* (WA)

Table 2 (continued)

Taxon	GenBank accession number		Reference or voucher specimen
	ITS 1	ITS 2	
Selinum broteri Hoffmanns. et Link		AY179029	France, Morbihan, Guillac, cultivated in Botanical Conservatory Mulhouse, France, no. 99155A, 2 August 2001, *Hildenbrand, Meyer and Reduron s. n.* (ILL)
Selinum candollei DC.	U30564	U30565	Downie and Katz-Downie (1996)
Selinum carvifolia (L.) L.		AY179028	France, Bas-Rhin, between Herbsheim and Boofzheim, 14 August 2001, *Reduron s. n.* (ILL)
Selinum pyrenaeum Gouan		AY179027	France, Haut-Rhin, Vosges, Markstein, 24 July 2001, *Reduron s. n.* (ILL)
Seseli elatum L.	U79623	U79624	Downie et al. (1998)
Seseli galloprovinciale Reduron		AY179025	France, Vaucluse, Cavaillon, montagne du Luberon, cultivated in Botanical Conservatory Mulhouse, France, no. 98104, 25 June 2001, *Hildenbrand, Meyer and Reduron s. n.* (ILL)
Seseli gracile Waldst. et Kit.	AF008605	AF009084	Katz-Downie et al. (1999)
Seseli gummiferum Pall. ex Sm.		AY179023	Cultivated in Botanical Conservatory Mulhouse, France, no. 9698, ex Bot. Gart. Frankfurt, 25 June 2001, *Hildenbrand, Meyer and Reduron s. n.* (ILL)
Seseli hippomarathrum Jacq. (≡*Hippomarathrum pelviforme* G. Gaertn., B. Mey. et Scherb.)		AY179033	Cultivated in Botanical Conservatory Mulhouse, France, no. 9787, ex Bot. Gart. Aachen, 25 June 2001, *Hildenbrand, Meyer and Reduron s. n.* (ILL)
Seseli krylovii (V. N. Tichom.) Pimenov et Sdobnina	U78402	U78462	Downie et al. (1998)
Seseli libanotis (L.) W. D. J. Koch (≡*Libanotis montana* Crantz)	AF008603	AF009082	Katz-Downie et al. (1999)
Seseli longifolium subsp. *intermedium* (Rupr.) P. W. Ball		AY179032	France, Gard, mont Bouquet, cultivated in Botanical Conservatory Mulhouse, France, no. 99144, 25 June 2001, *Hildenbrand, Meyer and Reduron s. n.* (ILL)
Seseli montanum L.	U30578	U30579	Downie and Katz-Downie (1996)
Seseli mucronatum (Schischk.) Pimenov	AF008606	AF009085	Katz-Downie et al. (1999)
Seseli peucedanoides (M. Bieb.) Koso-Pol.		AY179034	France, Cote d'Or, Darois near Dijon, cultivated in Botanical Conservatory Mulhouse, France, no. 95193, 25 June 2001, *Hildenbrand, Meyer and Reduron s. n.* (ILL)

Table 2 (continued)

Taxon	GenBank accession number		Reference or voucher specimen
	ITS 1	ITS 2	
Seseli praecox (Gamisans) Gamisans	AY179024		France, Corse, Bussaglia, cultivated in Botanical Conservatory Mulhouse, France, no. 9528, 25 June 2001, *Hildenbrand, Meyer and Reduron s. n.* (ILL)
Seseli tortuosum L.	AY179031		Portugal, Lisboa, Sintra Praja das Macas, cultivated in Botanical Conservatory Mulhouse, France, no. 98042, 2 August 2001, *Hildenbrand, Meyer and Reduron s. n.* (ILL)
Seseli webbii Coss.	AY179037		Canaries, Tenerife, cultivated in Botanical Conservatory Mulhouse, France, no. 20117D, 25 June 2001, *Hildenbrand, Meyer and Reduron s. n.* (ILL)
Shoshonea pulvinata Evert et Constance	U78400	U78460	Downie et al. (1998)
Smyrniopsis aucheri Boiss.	U78393	U78453	Downie et al. (1998)
Spermolepis inermis (Nutt. ex DC.) Mathias et Constance	AF008602	AF009081	Katz-Downie et al. (1999)
Sphaenolobium tianschanicum (Korovin) Pimenov	AF008622	AF009101	Katz-Downie et al. (1999)
Sphenosciadium capitellatum A. Gray	AF008600	AF009079	Katz-Downie et al. (1999)
Taenidia integerrima (DC.) Drude	U78399	U78459	Downie et al. (1998)
Thaspium pinnatifidum (Buckley) A. Gray	U78410	U78470	Downie et al. (1998)
Thysselinum lancifolium (Lange) Calest.	AY179036		France, Loire Atlantique, St Lyphard, 10 August 1982, *Reduron s. n.* (WA)
Thysselinum palustre (L.) Hoffm. (≡*Peucedanum palustre* (L.) Moench)	AF008621	AF009100	Katz-Downie et al. (1999)
Thysselinum palustre (L.) Hoffm. (≡*Peucedanum palustre* (L.) Moench)	AY179035		Poland, Warszawa, Bemowo, 23 August 1985, *Kirpluk s. n.* (WA)
Thysselinum sp.	AF495832	AF495833	France, Morbihan, Théhillac, *Reduron and Rivière s. n.* (WA)
Tommasinia verticillaris (L.) Bertol. (≡*Peucedanum verticillare* (L.) W. D. J. Koch ex DC.)	AF008609	AF009088	Katz-Downie et al. (1999)
Xanthogalum purpurascens Avé-Lall. (≡*Angelica purpurascens* (Avé-Lall.) Gilli)	AF008611	AF009090	Katz-Downie et al. (1999)
Xanthogalum tatianae (Bordz.) Schischk. (≡*Angelica tatianae* Bordz.)	AF008610	AF009089	Katz-Downie et al. (1999)
Xanthoselinum alsaticum (L.) Schur (≡*Peucedanum alsaticum* L.)	AF495834	AF495835	France, Haut-Rhin, Westhalten, 21 August 1979, *Reduron s. n.* (WA)
Zizia aurea (L.) W. D. J. Koch	U30574	U30575	Downie and Katz-Downie (1996)

Results

Sequence analysis. The intervening 5.8S rDNA region was not available for most previously published ITS sequences, therefore only the ITS 1 and ITS 2 loci were considered. Complete ITS 1 and ITS 2 sequences for 107 accessions ranged from 424 to 446 base pairs (bp). The aligned matrix included 462 positions, with ITS 1 and ITS 2 each accounting for 226 and 236 positions, respectively. All positions were unambiguous: 210 positions were parsimony informative, 83 variable positions were parsimony uninformative, and 169 positions were constant. Thirty-nine unambiguous gaps were introduced to align these positions. Thirty-three of these were 1-bp in size; single indels ranging from 2 to 14 bp each were also identified. Twenty indels were parsimony informative. Mean uncorrected pairwise distance was 0.075; overall, distance values ranged from identity to 0.219.

Phylogenetic analysis. NJ trees obtained using Jukes-Cantor, Kimura 2-parameter, Tamura-Nei, and GTR models of nucleotide substitutions were generally similar. The tree using the Tamura-Nei model is shown in Fig. 1. In all NJ trees, the formerly identified 'Arracacia' clade is monophyletic (although with bootstrap support < 50%) and nested within the 'Angelica' clade sensu Downie et al. (2001). Several subclades were present in all NJ trees; these subclades are identified in Fig. 1 and are discussed below.

Maximum parsimony searches resulted in the preset limit of 10 000 shortest trees, each 989-steps long, with a retention index of 0.666 and a consistency index of 0.468 (including uninformative characters). The strict consensus of these trees (not shown) yielded a large polytomy, and the relationship between the formerly identified 'Arracacia' and 'Angelica' clades could not be resolved. MP searches of combined ITS sequences and scored indels resulted in 10 000 shortest trees of 1064 steps each, a retention index of 0.672 and a consistency index of 0.483 (including uninformative characters). The strict consensus of these trees (Fig. 2) showed less polytomy and stronger

internal support than in the MP analysis of sequence positions alone. Therefore, from here on, we only refer to the results of MP analyses of combined data. Of the 20 phylogenetically informative indels, 10 were apomorphic and 10 were homoplastic.

Modeltest's likelihood ratio test statistic selected the Tamura-Nei (1993) model of nucleotide substitution, with gamma distribution of substitution rates and a shape parameter of 0.727, for use in the ML analysis. The tree obtained from ML searches (ln L = −6086.77, Fig. 3) had a similar topology to those obtained from the NJ analyses. All major clades and subclades (identified on the Tamura-Nei tree, Fig. 1) had the same composition, with the differences between them including minor rearrangements within these clades or somewhat different affinities among them.

In all analyses, the monophyly of the 'Angelica' clade, with the 'Arracacia' clade included within, was strongly supported (97% and 98% for NJ and MP analyses, respectively). In both the NJ and ML trees, as well as some MP trees, nearly all members of *Peucedanum* and its segregates – i.e., *Peucedanum* sensu stricto, *Imperatoria*, *Thysselinum*, *Oreoselinum*, *Tommasinia*, *Pteroselinum*, and *Xanthoselinum* – occurred in a single clade, denoted as *Peucedanum* sensu lato. This clade also included several taxa that were not hitherto placed in *Peucedanum*, for example *Endressia* and *Xanthogalum*. However, in the NJ tree, this clade received weak bootstrap support (< 50%). Within this clade, several subclades were apparent. These mostly corresponded to the narrowly defined *Peucedanum* segregates, with the notable exception of a more heterogenic 'Xanthoselinum' subclade. Many of these same subclades were also apparent in trees resulting from MP analysis of combined data (Fig. 2).

The *Thysselinum* subclade included three newly sequenced accessions of *Thysselinum* and the accession of *Peucedanum zedelmeyerianum*. The monophyly of *Thysselinum* members was strongly supported by bootstrap

analyses (100% for both NJ and MP trees) and by the presence of one homoplastic deletion.

The accession of *Thysselinum* from France, whose affinity was uncertain, was sister to
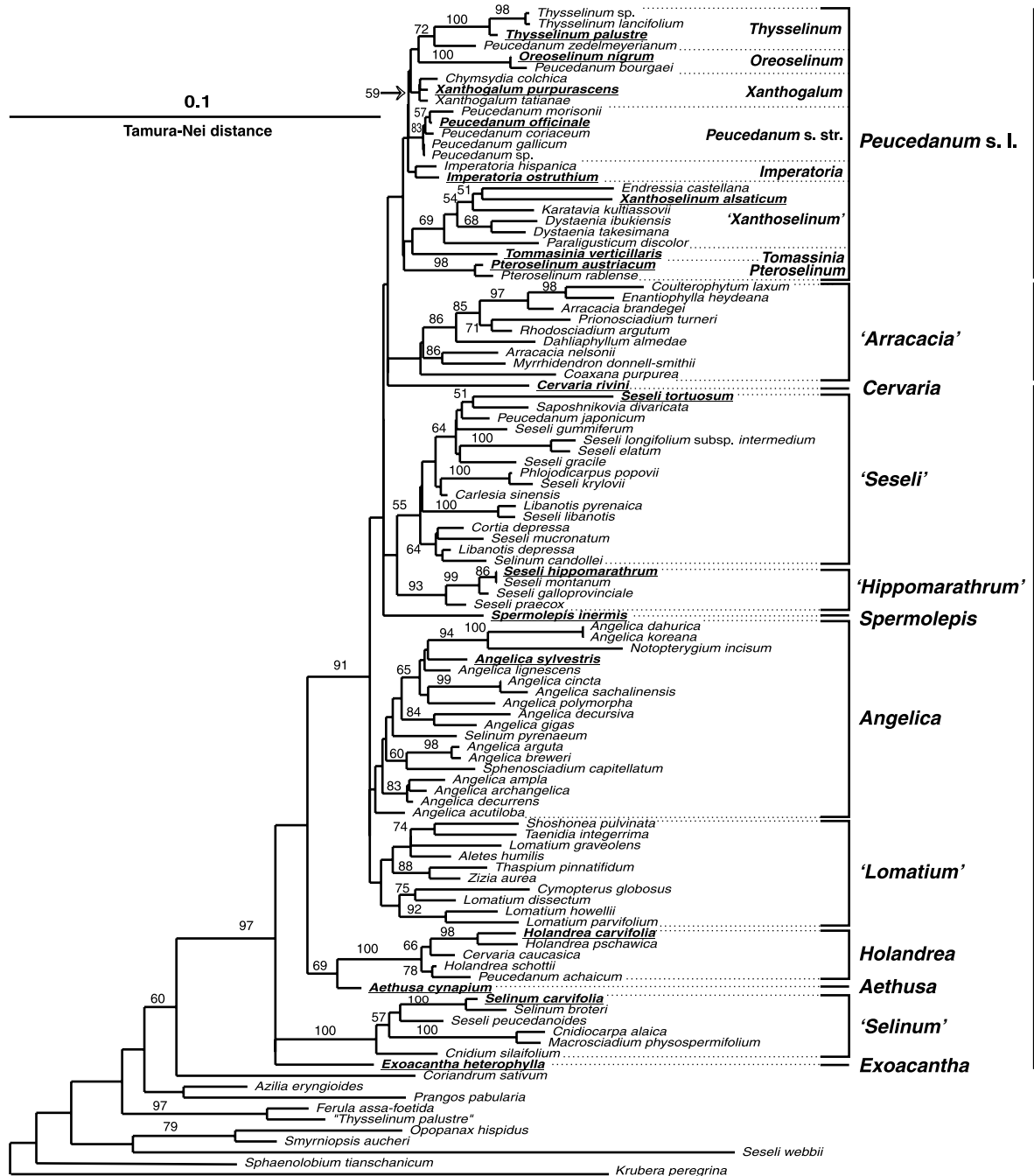

Fig. 1. Neighbour-joining tree obtained using the Tamura-Nei model of nucleotide substitution. Bootstrap support values from 1000 pseudoreplicates are indicated along nodes (those < 50% are omitted). Species that are nomenclatural types of their respective genera are underlined. Brackets indicate groups discussed in the text. Informal names of clades are marked with single quotation marks. Solid and hollow bars denote members of the '*Arracacia*' and '*Angelica*' clades, respectively
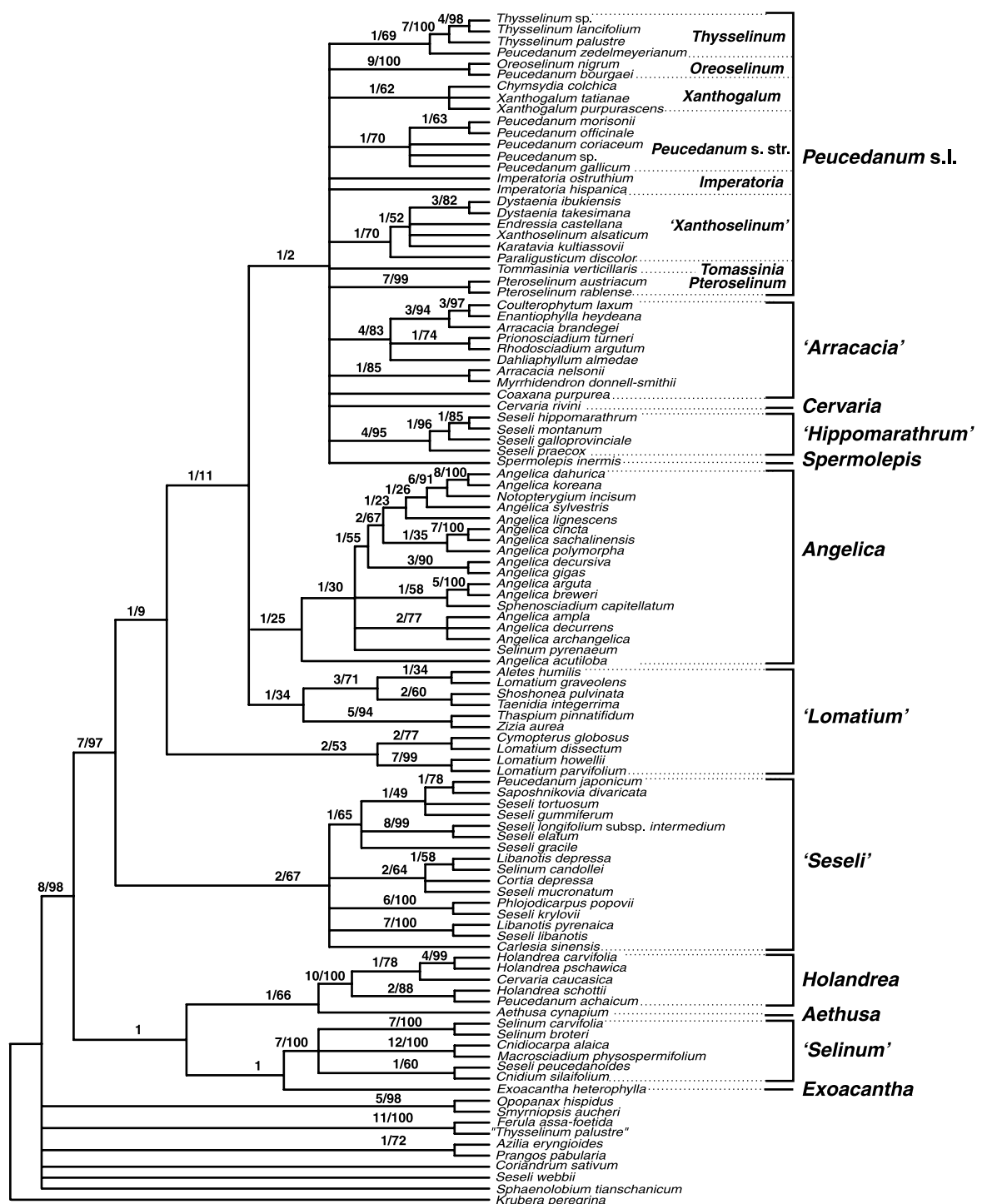
Fig. 2. Strict consensus tree of 10 000 shortest 1064-step trees obtained from maximum parsimony analyses of combined ITS sequences and scored indels (consistency index with uninformative characters = 0.483, retention index = 0.672). Decay indices/bootstrap values from 1000 pseudoreplicates are indicated along nodes (only those consistent with the 50% majority-rule consensus tree are indicated). Group identifiers are the same as in Fig. 1

T. lancifolium. This clade of *Thysselinum* was sister to *Peucedanum zedelmeyerianum*, with this affinity receiving moderate bootstrap support (72 and 69% for NJ and MP trees,

respectively). Interestingly, these newly sequenced accessions did not group with the formerly obtained sequence of *T. palustre* (marked on the trees with double quotation
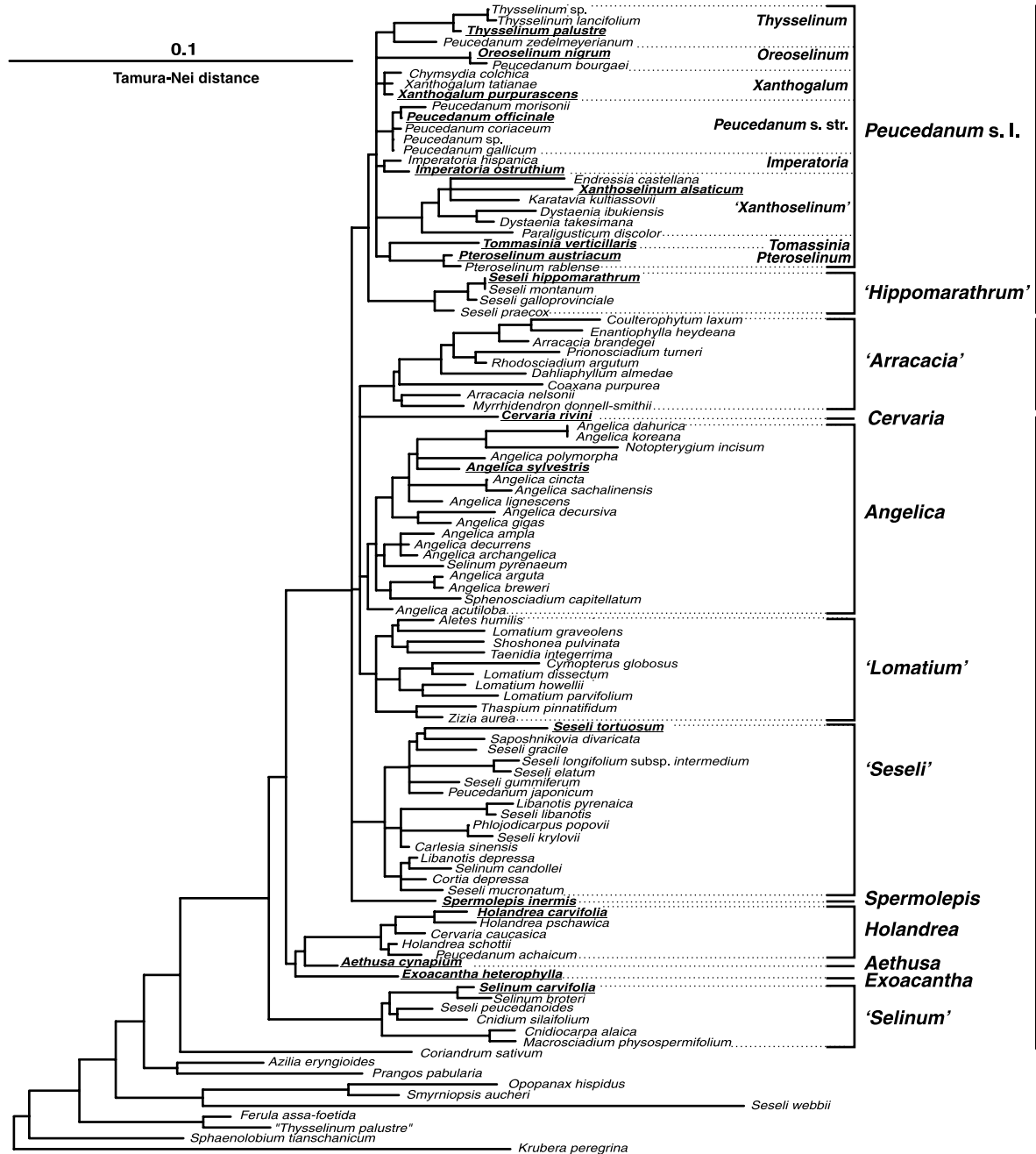
Fig. 3. Maximum likelihood tree obtained using the Tamura-Nei substitution model, with gamma distribution of substitution rates and shape parameter of 0.727 (ln L = −6086.77). Group identifiers are the same as in Figs. 1 and 2

marks) that was sister to *Ferula assa-foetida*, one of several outgroup representatives. The affinity of these two taxa was supported by the presence of three indels, two of them synapomorphic. One of these synapomorphies was also shared by *Sphaenolobium tianschanicum*.

The monotypic genus *Oreoselinum* grouped with *Peucedanum bourgaei* (100% bootstrap support for both MP and NJ trees). The *Xanthogalum* subclade encompassed two species of this genus, as well as the monotypic *Chymsydia*; all three of these species are distributed in the Caucasus. This subclade occurred in all analyses, although its monophyly was weakly supported (bootstrap values 59 and 62% for NJ and MP trees, respectively).

The *Peucedanum* sensu stricto subclade encompassed five accessions that are traditionally placed in sect. *Peucedanum* (bootstrap support 83% and 70% for NJ and MP trees, respectively). Included here is *P. officinale,* the nomenclatural type of the genus. This subclade also included the *Peucedanum* accession (*Peucedanum* sp.) of uncertain affinity from France. Its sequence was identical to that of *P. gallicum*.

Both species of *Imperatoria* grouped together in the NJ and ML trees (Figs. 1 and 3, respectively), although this affinity was poorly supported in the NJ analysis (< 50%). These two species did not always form a monophyletic group in the MP analysis (Fig. 2).

The '*Xanthoselinum*' subclade encompassed the type species of this genus, as well as representatives of *Endressia*, *Karatavia*, *Dystaenia*, and *Paraligusticum*. This clade received moderate bootstrap support (69 and 70% for NJ and MP trees, respectively), albeit the relationships within were poorly supported. In the NJ trees, this subclade was allied weakly with two members of *Pteroselinum* and the monotypic *Tommasinia*. The monophyly of *Pteroselinum* was supported by high bootstrap values (98 and 99% for NJ and MP, respectively) and by one synapomorphic insertion.

The genus *Cervaria* was polyphyletic. The phylogenetic position of *Cervaria rivini*, the nomenclatural type of the genus, was equivocal, although it commonly grouped with the members of *Peucedanum* sensu lato and the '*Arracacia*' clade. The other species, *C. caucasica*, was placed among the members of *Holandrea*. *Holandrea* was distantly related to the other peucedanoid genera. The *Holandrea* clade included the three species hitherto recognised in the genus, plus *C. caucasica* and *Peucedanum achaicum*. This clade was well supported, with 100% bootstrap values in both NJ and MP trees, and was sister to *Aethusa cynapium*. Monophyly of the *Holandrea* clade was also supported by two synapomorphic insertions. These were 1 and 5-bp long and occurred at the beginning of the ITS 1 region and close to the 3' end of ITS 2, respectively.

Most members of *Seseli* and its segregate *Libanotis* Haller ex Zinn, including their type species (*S. tortuosum* for *Seseli* and *S. libanotis* = *Libanotis montana* for *Libanotis*), were placed in a single clade ('*Seseli*'), which however received only moderate bootstrap support (55 and 67% for NJ and MP trees, respectively). This branch also contained several Asiatic umbellifers that are placed in the genera *Saposhnikovia*, *Phlojodicarpus*, *Carlesia*, and *Cortia*. In the NJ trees, the nomenclatural type of *Saposhnikovia*, *S. divaricata*, was sister to *S. tortuosum*, the nomenclatural type of *Seseli*, and both were found to be closely related to *Peucedanum japonicum*. In the MP trees, *S. divaricata* was sister to *P. japonicum*, and this affinity was supported by the presence of one homoplastic insertion. In the ML tree (Fig. 3), *S. tortuosum* and *S. divaricata* were sister taxa, whereas *P. japonicum* formed a branch of a polytomy two nodes away.

Four European members of *Seseli* (*S. hippomarathrum*, *S. galloprovinciale*, *S. montanum*, and *S. praecox*) formed a strongly supported clade (93–95% bootstrap values) that was sister to the '*Seseli*' clade in the NJ analysis (Fig. 1). In the ML tree (Fig. 3), this clade was sister to the *Peuceda-*

Table 3. Generic composition of tribe Selineae Spreng. in Roem. et Schult.

Aethusa L.	*Meum* Mill.
Aletes J. M. Coult. et Rose	*Musineon* Raf.
Angelica L. (inc. *Sphenosciadium* A. Gray)	*Myrrhidendron* J. M. Coult. et Rose
Arracacia Bancroft	*Neoparrya* Mathias
Carlesia Dunn.	*Oreonana* Jeps.
Cervaria Wolf	*Oreoselinum* Mill.
Chamaele Miq.	*Oreoxis* Raf.
Chymsydia Albov	*Orogenia* S. Wats.
Cnidiocarpa Pimenov	*Paraligusticum* V. N. Tikhom.
Cnidium Cusson in Juss. pro parte	*Peucedanum* L.
(= *Katapsuxis* Raf.)	*Phlojodicarpus* Turcz. ex Ledeb.
Coaxana J. M. Coult. et Rose	*Podistera* S. Wats.
Coelopleurum Ledeb.	*Polytaenia* DC.
Cortia DC.	*Prionosciadium* S. Wats.
Coulterophytum B. L. Rob.	*Pseudocymopterus* J. M. Coult. et Rose
Cymopterus Raf.	*Pteroselinum* Rchb.
Dahliaphyllum Constance et Breedlove	*Pteryxia* (Nutt. ex Torr. et A. Gray)
Donnellsmithia J. M. Coult. et Rose	J. M. Coult. et Rose
Dystaenia Kitag.	*Rhodosciadium* S. Wats.
Enantiophylla J. M. Coult. et Rose	*Saposhnikovia* Schischk.
Endressia J. Gay	*Selinum* L.
Exoacantha Labill.	*Seseli* L.
Glehnia F. Schmidt ex Miq.	*Shoshonea* Evert et Constance
Grafia Rchb.	*Spermolepis* Raf.
Harbouria J. M. Coult. et Rose	*Taenidia* (Torr. et A. Gray) Drude
Holandrea Reduron, Charpin et Pimenov	*Tauschia* Schltdl.
Imperatoria L.	*Thaspium* Nutt.
Karatavia Pimenov et Lavrova	*Thysselinum* Adans.
Libanotis Haller ex Zinn	*Tommasinia* Bertol.
Lomatium Raf.	*Xanthogalum* Lallem.
Macrosciadium V. N. Tichom. et Lavrova	*Xanthoselinum* Schur
Mathiasella Constance et C. Hitch.	*Zizia* W. D. J. Koch

num sensu lato clade. In the MP trees, its placement was equivocal, but closer to the *Peucedanum* sensu lato group than to the 'Seseli' clade. Since this group included *Seseli hippomarathrum*, the type species of *Hippomarathrum* G. Gaertn., B. Mey. et Scherb., we therefore refer to it as the '*Hippomarathrum*' clade.

Two members of *Seseli* were placed far away from its other congeners. *Seseli peucedanoides* was included in the '*Selinum*' clade, whereas *S. webbii* was clustered with the outgroup species. Searches in GenBank using BLAST identified ITS sequences of *Ammi*

majus and *Petroselinum crispum* as being most similar to *S. webbii*, and this affinity was confirmed through additional phylogenetic analyses using a larger data set (not shown). Both *Spermolepis inermis* and *Exoacantha heterophylla* appeared to have no close relatives among the taxa included in the analysis.

In all trees, the species of *Angelica* formed a monophyletic group, albeit one that was only poorly supported (< 50% bootstrap values). This clade also included the Asiatic *Notopterygium* and North American *Sphenosciadium*, as well as a species of *Selinum* from Spain and

France. *Sphenosciadium capitellatum* grouped with the two North American representatives of *Angelica* included in this study, whereas *Notopterygium incisum* from China grouped with two *Angelica* species from the Far East (*A. koreana* and *A. dahurica*).

The 'Lomatium' clade included several species endemic to central and western North America. This group was monophyletic in the NJ and ML trees but formed two clades in the MP strict consensus tree.

Discussion

Tribe Selineae. Most of the genera considered in this study are traditionally classified in Drude's (1897–1898) tribe Peucedaneae subtribes Angelicinae and Ferulinae, or tribes Peucedaneae and Angeliceae in the classification system of Pimenov and Leonov (1993). In an outline of a new classification of umbellifers based on molecular data, Downie et al. (2001) placed all of these taxa into two informal groups, named the 'Angelica' clade and the 'Arracacia' clade. However, the phylogenetic position of the 'Arracacia' clade was not clear, for in several previous studies it arose from within the 'Angelica' clade (Plunkett et al. 1996, Downie et al. 1998). Downie et al. (2001) suggested that the 'Arracacia' clade might eventually be subsumed within the 'Angelica' clade. Our study confirms those earlier results indicating that the weakly monophyletic 'Arracacia' clade is indeed nested within the 'Angelica' clade. The monophyly of this expanded 'Angelica' clade is, however, very strongly supported (with 97-98% bootstrap values). Herein, we recognise this expanded clade as a tribe. It includes several nomenclatural types of validly published tribal names of which the earliest is Selineae Spreng. in Roem. et Schult. (Syst. Veg. 6: 46 1820). Table 3 contains the generic composition of tribe Selineae. This table includes 18 additional genera not examined herein; their placement within the tribe is based on Downie et al. (2001).

***Peucedanum* sensu lato vs. *Peucedanum* sensu stricto.** The delimitation of *Peucedanum* as found in most taxonomic monographs is ambiguous. Traditionally, members of this genus are characterised by dorsally compressed orthospermous fruits without prominent dorsal ribs and with a broad commissure. This last character distinguishes *Peucedanum* from *Angelica*, which has a narrow commissure (Ostroumova and Pimenov 1997). Many species of *Peucedanum* have winged fruits. Such a fruit structure is an evident adaptation for wind dispersal and likely evolved independently in several distant lineages of umbellifers (Theobald 1971). Therefore, not surprisingly, *Peucedanum* encompassed taxa that were subsequently found to be distantly related to the type of the genus. For example, *Steganotaenia*, which was synonymised with *Peucedanum* by Drude (1897-1898), is placed close to the subfamily Saniculoideae on the basis of molecular evidence (Downie and Katz-Downie 1999). Apart from these foreign elements, *Peucedanum* sensu amplissimo (i.e. sensu Drude 1897–1898) includes many diverse taxa that are indeed closely related, such as the North American *Lomatium* and *Orogenia*, and the *Peucedanum* segregates from the Old World (i.e. *Cervaria*, *Holandrea*, *Imperatoria*, *Oreoselinum*, *Pteroselinum*, *Thysselinum*, and *Xanthoselinum*). Based on the analysis presented herein, these taxa are scattered among members of tribe Selineae. This finding suggests that the similarity of the former members of *Peucedanum* sensu amplissimo is homoplastic and supports the splitting of the genus into smaller units that may be defined on the basis of apomorphic characters. In spite of the exclusion of the North American taxa that are now placed in *Lomatium* and related genera, *Peucedanum* sensu lato still includes 100-120 species (Pimenov and Leonov 1993).

Based on the results of the NJ and ML analyses, and with the exception of *Holandrea* and *Cervaria*, the segregates of *Peucedanum* sensu lato form a monophyletic group. A subset of the 10 000 MP trees also revealed the same clade. From the point of view of nomenclatural stability, retaining such a delimitation of the genus (but with the exclusion of

Holandrea and *Cervaria*) would be advantageous. However, the monophyly of this group is weakly supported. Moreover, it also includes several taxa that do not conform to the traditional delimitation of *Peucedanum*. For example, *Xanthoselinum alsaticum* is sister taxon to *Endressia castellana*, which is a representative of an Iberian endemic genus encompassing only two species. Contrary to *Peucedanum*, the fruits of *Endressia* are laterally compressed and do not have any wings, and both dorsal and commissural ribs are of the same size (Arenas Posada and García Martín 1993). The 'Xanthoselinum' group, with included genera *Dystaenia*, *Karatavia*, and *Paraligusticum*, is the most heterogeneous among the subclades identified within *Peucedanum* sensu lato, and it is very difficult to find any obvious morphological character that would unite these taxa. Another member of the *Peucedanum* sensu lato clade, *Xanthogalum*, was recognised in *Angelica* by Vasil'eva and Pimenov (1991). While its members are generally similar to those of *Angelica*, they differ in having conspicuous calyx teeth, which are persistent and erect in fruit, and the absence of bracts and bracteoles (Chamberlain 1972). The similarity between *Xanthogalum* and *Angelica* is homoplastic, as these genera are not immediately related (Downie et al. 2000b). In summary, *Peucedanum* sensu lato is too difficult to delimit based on morphology.

The advantage of Linnaean binomials is that the generic name permits the identification of the closest relatives of a species without referring to any external classification system. This is particularly useful for non-taxonomists who deal with species identification, such as in floristic or ecological studies. Therefore, any study that clarifies generic boundaries in the Apiaceae would be very useful. Ideal genera should be monophyletic, clearly delimited based on morphology, and manageable with respect to size (Spalik et al. 2001). Both monotypic and very large genera should be avoided, if possible. However, it seems that if we reject a broad definition of *Peucedanum*, we end up with numerous small genera, each containing only 1–3 species. Sometimes, these species are problematic and often reduced to infraspecific ranks. For instance, *Pteroselinum rablense* is often recognised as a subspecies of *Pteroselinum austriacum*, whereas *Peucedanum bourgaei* is frequently regarded as a subspecies of *Peucedanum oreoselinum* (≡*Oreoselinum nigrum*). *Imperatoria* includes three parapatric species that are morphologically similar: European *I. ostruthium*, Iberian *I. hispanica*, and *I. lowei* from Madeira. *Xanthoselinum* and *Tommasinia* are each monotypic. The *Peucedanum* sensu stricto clade includes taxa that are very similar with respect to their ITS sequences, which suggests that the radiation of this group was recent and thus, included taxa may deserve infraspecific rank rather than that of species. They are very similar in habit, sharing not only fruit characters but also vegetative features, like linear-filiform leaf lobes. The accession denoted as *Peucedanum* sp. represents a population whose members are morphologically very similar to *P. gallicum*. However, this population occurs within the range of *P. coriaceum* rather than of *P. gallicum*. The sequences of *Peucedanum* sp. and *P. gallicum* are identical and somewhat different from *P. coriaceum*, suggesting that *Peucedanum* sp. and *P. gallicum* are conspecific.

The results of the NJ analysis suggests that *Pteroselinum*, *Tommasinia*, and the 'Xanthoselinum' clade are closely related. The affinity among *Pteroselinum austriacum*, *Tommasinia verticillaris*, and *Xanthoselinum alsaticum* was previously revealed by phytochemical data (Hadacek 1989). The relationships among members of *Peucedanum* sensu lato, *Angelica*, and several related genera were recently investigated by Shneyer et al. (2003), using immunological methods. Their study confirmed that species classified in segregate genera *Xanthoselinum*, *Pteroselinum*, *Tommasinia*, and *Oreoselinum* are closely related to one another and to *P. morisonii*, a member of *Peucedanum* sensu stricto. Apparently, more data from DNA sequences, as well as morphology and

phytochemistry, are needed to resolve the taxonomy of *Peucedanum* sensu lato. We therefore refrain from taxonomic changes in this group.

Cervaria and **Holandrea.** The genus *Cervaria* was restored by Pimenov (1987) for the *Flora Iranica*. Pimenov listed several differences between *Peucedanum* sensu stricto and *Cervaria*, including fruit, flower, and leaf characteristics. In contrast to *Peucedanum* sensu stricto, the fruits of *Cervaria* are characterised by the presence of lignified parenchymatic cells in the mesocarp. Calyx teeth are absent and ultimate leaf segments are broad in *Cervaria*, while in *Peucedanum* sensu stricto the calyx is present and the leaf segments are linear-filiform. However, it seems that such a delimitation of *Cervaria* is incorrect.

From among the four species included in *Cervaria*, two – *C. rivini* and *C. caucasica* – were considered in our study. Molecular analyses suggested that these two species were neither closely related to members of *Peucedanum* sensu stricto nor to one another. The placement of the nomenclatural type of the genus, *C. rivini*, was ambiguous and depended on the phylogenetic method used, whereas *C. caucasica* was allied with those former members of *Peucedanum* that we recognise in *Holandrea*.

The genus *Holandrea* was described by Reduron et al. (1997) as comprising three species, all of which have been included in our study. Apart from their general morphological similarity (in habit, leaves, and fruits), they have similar stomata (Guyot 1984). However, they differ from members of *Peucedanum* with respect to their chemical constituents. They all lack coumarins and all have C13-acetylenic compounds (Hadacek 1989). Two members of the *Holandrea* clade, *H. pschawica* and *C. caucasica*, were also included in immunological studies of seed proteins (Shneyer et al. 2003), which confirmed that these species were more closely related to one another than to the other representatives of *Peucedanum* sensu lato. Our data confirm this distant position of *Holandrea*

with respect to the *Peucedanum* segregates. Upon the inclusion of *C. caucasica* and *P. achaicum*, the genus *Holandrea* is monophyletic. Two new combinations are therefore necessary.

Holandrea caucasica (M. Bieb.) Spalik, Reduron et S. R. Downie, comb. nov. ; basionym: *Selinum caucasicum* M. Bieb., Fl. Taur.-Cauc. 1: 213 1808. Type: 'Ex Iberia: in sylvis circa Ananur lectum. a. 1802', *Marschall von Bieberstein* (lectotype, LE, not seen; fide Menitsky 1991).

Holandrea achaica (Halácsy) Spalik, Reduron et S. R. Downie, comb. nov. ; basionym: *Peucedanum achaicum* Halácsy, Suppl. Consp. Fl. Graec. 42 1908. Type: 'in rupibus vallis fluminis Voreikos infra Zachloru Achaiae,' July 1896, *Saint Lager* (WU-Hal-Graec, not seen; G, isotype!).

Thysselinum. The previously obtained ITS sequence of *Thysselinum palustre* allied with *Coenolophium denudatum* and some members of *Ferula*, such as *F. assa-foetida* (Katz-Downie et al. 1999, Downie et al. 2000b). In contrast, the present study indicates that all newly sequenced accessions of *Thysselinum* form a monophyletic group within the *Peucedanum* sensu lato clade. It appears that the newly sequenced *Thysselinum palustre* accession is distantly related to the old accession of the same species; apparently, these two taxa are not conspecific. The results of our analyses confirm the close relationship between *T. palustre* and *T. lancifolium* that was inferred previously from morphology and phytochemistry (Reduron et al. 1997). These species are very similar and differ only in flower colour and shape of the leaf lobes. *Thysselinum lancifolium* is characterised by having greenish flowers and long linear lobes, whereas the flowers of *T. palustre* are white and its leaf lobes are shorter. Therefore, we have no doubt that the correct placement of *Thysselinum* is in the *Peucedanum* sensu lato group of tribe Selineae. The accession denoted as *Thysselinum* sp. comes from a population that occurs at the contact zone of *T. palustre* and *T. lancifolium*, and its members show intermedi-

ate characters between the two species. ITS sequences suggest that this taxon is more closely related to *T. lancifolium* than to *T. palustre*.

Angelica. Phylogenetic analyses using NJ, ML and MP methods confirm the monophyly of the genus *Angelica*. However, internal support for this clade is low. In contrast to our results, Shneyer et al. (2003) found significant differences among the species of *Angelica* included in their immunological study. Particularly, those species that are sometimes placed in the segregate genus *Ostericum* differ considerably from the type of *Angelica* (*A. sylvestris*) and its relatives, as well as from the members of *Peucedanum* sensu lato. Therefore, Shneyer et al. (2003) concluded that *Ostericum* deserved the status of an independent genus. None of the putative members of *Ostericum* has hitherto been included in molecular analyses.

The *Angelica* subclade outlined herein includes three taxa that are usually placed in other genera: *Notopterygium incisum*, *Sphenosciadium capitellatum*, and *Selinum pyrenaeum*. *Notopterygium* H. Boissieu includes five species that occur in Asia, and mostly in China (Pu et al. 2000). The only species included in our analysis, *N. incisum*, grouped with two species of *Angelica* from the Far East (*A. dahurica* and *A. koreana*). Apart from a similar geographic distribution, this relationship obtained strong support from bootstrap and decay analyses. This group belongs to a larger branch that also includes *Angelica sylvestris*, the nomenclatural type of the genus. The position of *Notopterygium* was recently investigated by Valiejo-Roman et al. (2002) using ITS data from the nomenclatural type of the genus, *N. forbesii*, and another accession of *N. incisum* (as *N. weberbauerianum*). Their analyses rejected the close relationship between *Notopterygium* and *Angelica* and suggested that the former was sister to *Hansenia*. Our preliminary analyses of ITS a data from two other accessions of these species confirm the affinity between *Notopterygium* and *Hansenia* (unpublished data).

The placement of *Selinum pyrenaeum* has been the subject of some controversy, as it was also placed in *Seseli*, *Peucedanum*, and *Angelica*. Reduron et al. (1997) regarded this species as related to *Ligusticum* sensu lato and reinstated it in the monotypic genus *Epikeros* Raf. However, they noted that it shared some features with members of *Angelica*, including similar pathogens (Durrieu 1982) and the presence of coumarins (Muckensturm and Diyani 1995). Based on the drawings in Arenas Posada and García Martín (1993), the fruit anatomy of *S. pyrenaeum* is more similar to those winged fruits of *Angelica* than it is to its congener, *S. carvifolia*. Nevertheless, its habit is different from most members of *Angelica*. Our data indicate that the placement of this species is rather in *Angelica* than in *Ligusticum* sensu lato. Since it is nested within the former, it does not deserve the status of a separate genus. The name of this species in *Angelica* is *A. pyrenaea* (L.) Spreng.

Sphenosciadium capitellatum, the only member of *Sphenosciadium* A. Gray, is a striking umbellifer due to its woolly indumentum covering the umbellets. Otherwise, this species is very similar in habit to its closest relatives based on ITS sequences, which are *A. arguta* and *A. breweri*. These three taxa occur in North America, whereas the other members of the *Angelica* clade are from the Old World. Therefore, retaining the monotypic *Sphenosciadium* is not justified. The close relationship between *Sphenosciadium* and *Angelica* was already indicated based on *mat*K sequences (Plunkett et al. 1996), and the transfer of the former into *Angelica* was suggested by Katz-Downie et al. (1999). Therefore, we formally synonymise *Sphenosciadium* with *Angelica*:

Angelica capitellata (A. Gray) Spalik, Reduron et S. R. Downie, comb. nov.; basionym: *Sphenosciadium capitellatum* A. Gray, Proc. Am. Acad. 6: 537 1865. Holotype: 'In the Sierra Nevada, near Ebbett's Pass, Alpine County, California,'' USA, *Brewer 2026* (GH, not seen).

Seseli, Libanotis, Cortia and Hippomarathrum. With 100–120 included species, the

genus *Seseli* is one of the largest in the family (Pimenov and Leonov 1993), and similar to other large genera in Apiaceae, it is polyphyletic (Katz-Downie et al. 1999, Downie et al. 2000b). Several attempts to divide it into smaller units have already been made. For example, Pimenov and Leonov (1993) listed 16 generic names in synonymy. Of these segregates, only *Libanotis* has gained some acceptance. The type of this genus is *Libanotis montana*, a nomenclatural synonym of *Seseli libanotis*. This species was placed in the 'Seseli' clade, thus confirming that *Libanotis* and *Seseli* are closely related. *Seseli libanotis* is sister to *Libanotis pyrenaica*, a taxon that is often included in the former.

Another species described under *Libanotis*, *L. depressa*, is not related to the type of the genus, but rather is sister to *Selinum candollei*, an Asiatic umbellifer, which is also recognised in *Cortia* DC. (as *C. candollei* (DC.) Leute). The type of *Cortia* is *C. lindleyi* DC., a nomenclatural synonym of *C. depressa*, which was grouped in the same subclade. The fourth member of this subclade, *Seseli mucronatum*, is alternatively placed in *Ligusticum* (Flora of China, Umbelliferae, Draft 1: World Umbellifer Database, Royal Botanic Garden Edinburgh, http://rbg-web2.rbge.org.uk/URC/Nomenclature/). Such a placement is not supported by our data. Instead, the results of the phylogenetic analyses suggest that these four species may be either included in a broad genus *Seseli* or in a more narrow genus *Cortia*. Such a decision requires, however, confirmation from independent data, both morphological and molecular. The relationship of this subclade to the other subclades of the 'Seseli' group is also unclear.

Most species recognised in *Seseli* belong to the 'Seseli' clade. Based on additional unpublished ITS data, one may add three other species to this clade: *S. rigidum* Waldst. et Kit., *S. farreynii* Molero et A. Pujadas, and *S. rhodopeum* Velen. Surprisingly, the closest relatives of *Seseli tortuosum*, the nomenclatural type of the genus, are not the other congeners but two species from the Far East:

Saposhnikovia divaricata and *Peucedanum japonicum*. However, the phylogenetic affinities within this clade received very low internal support. Therefore, additional sampling is needed before any definite conclusions are made and taxonomic changes introduced.

The taxonomic history of *Hippomarathrum* is complex. This name was once used for a group of species related to *Cachrys sicula* L., the nomenclatural type of *Hippomarathrum* Link, 1821, Enum. Horti Berol. Alt. 1: 271. However, it is a later homonym of *Hippomarathrum* G. Gaertn., B. Mey. et Scherb. 1799, Oecon. Techn. Fl. Wetterau, 1: 249, 413 typified by *Seseli hippomarathrum*. The proposition to conserve *Hippomarathrum* Link against its earlier homonym was rejected by the Committee for Spermatophyta (cf. *Taxon* 27:385–314, 1978). The group of *Seseli* species denoted on the tree as the '*Hippomarathrum*' clade seems to be distinct from its congeners. Although the NJ analysis suggests its sister relationship with the 'Seseli' clade, such an affinity is not supported by the results of the ML and MP analyses. With additional sampling, it is entirely possible that these two clades of *Seseli* may form a single lineage in all analyses. Therefore, further sampling of members of *Seseli* is required before the restoration of *Hippomarathrum* is considered.

Two species of *Seseli*, *S. peucedanoides* and *S. webbii*, have been placed far away from their congeners. This separation is also supported by morphological characters: those two species have yellow flowers, while in all other *Seseli* species the flowers are white.

Selinum. Only few species are recognised in *Selinum* at present (Pimenov and Leonov 1993), although nearly 300 binomials using this generic name exist (World Umbellifer Database, Royal Botanic Garden Edinburgh, http://rbg-web2.rbge.org.uk/URC/Nomenclature/). These include *S. carvifolia*, *S. pyrenaeum*, and *S. candollei*; the fourth member of this genus included in our study – *S. broteri* – is usually treated as a synonym of *S. carvifolia* or regarded as its subspecies since the differences between them are minor (Arenas Posada and García Martín 1993). With *S. pyrenaeum* and

S. candollei excluded, the genus is practically monotypic. Interestingly, the '*Selinum*' clade also includes several taxa with incorrect generic affiliation. The sister to *Selinum* is a member of *Seseli*, and *Cnidium silaifolium* is sometimes recognised in the monotypic genus *Katapsuxis* Raf. (Reduron et al. 1997). Since the nomenclatural type of *Cnidium*, *C. monnieri* (L.) Cusson, has not been so far included in molecular studies, we are reluctant to accept this placement. The fruits of *Seseli peucedanoides* are generally similar to those of *Cnidium*, supporting the affinity of these species.

There is little doubt that *Ligusticum physospermifolium* is not related to *L. scoticum* L., the nomenclatural type of the genus. Therefore, we recognise this taxon in *Macrosciadium* V.N. Tichom. et Lavrova. Nonetheless, this placement may be provisional since the nomenclatural type of *Macrosciadium*, which is *M. alatum* (M. Bieb.) V. N. Tikhom. et Lavrova, has not been hitherto considered in molecular analyses either. *Macrosciadium physospermifolium* seems to be very closely related to *Cnidiocarpa alaica*, the nomenclatural type of *Cnidiocarpa* Pimenov. Therefore, *Macrosciadium* may eventually appear to be a taxonomic synonym of *Cniodiocarpa*.

Lomatium. This clade was weakly monophyletic in the results of the NJ and ML analyses and formed two clades in the MP trees. Its members are endemic to central and western North America. They are all perennial taxa and are characterised by several non-molecular characters, such as a protogynous breeding system and the lack of a prominent conical-shaped stylopodium. The phylogeny of this group was recently investigated by Downie et al. (2002) and Sun et al. (in press). They demonstrated that upon comprehensive sampling, this group forms a clade, albeit it is still weakly supported.

Conclusions

With increased sampling, resolution within the previously delimited '*Angelica*' and '*Arracacia*' clades, recognised herein as tribe Selineae, increases and several subclades become apparent. Some of these subclades are more or less equivalent to currently recognised genera, while others may eventually be formally recognised as such. Relatively low ITS sequence variation – as compared, for instance, with the high variability exhibited by Apiaceae tribe Scandiceae and its subtribes (Downie et al. 2000a) – coupled with a large number of included taxa makes the reclassification of this branch of umbellifers particularly difficult. Polyphyly of its included genera and low internal support for most hitherto identified clades indicate that this task would require a broader sampling, both with respect to the number of taxa and the sources of data providing information on relatedness.

References

Arenas Posada J. A., García Martín F. (1993) Atlas carpológico y corológico de la subfamilia Apioideae Drude (Umbelliferae) en España peninsular y Baleares. Ruizia 12: 1–245.

Bremer K. (1994) Branch support and tree stability. Cladistics 10: 295–304.

Calestani V. (1905) Conspectus specierum europaearum generis *Peucedani*. Bull. Soc. Bot. Ital. ann. 1905: 193–201.

Catalán P., Kellogg E. A., Olmstead R. G. (1997) Phylogeny of Poaceae subfamily Pooideae based on chloroplast *ndh*F gene sequences. Mol. Phyl. Evol. 8: 150–166.

Chamberlain D. F. (1972). *Xanthogalum* Lallem. In: Davis P. H. (ed.) Flora of Turkey and the East Aegean Islands, vol. 4. Edinburgh University Press, Edinburgh, pp. 432–434.

Downie S. R., Katz-Downie D. S. (1996) A molecular phylogeny of Apiaceae subfamily Apioi-

deae: evidence from nuclear ribosomal DNA internal transcribed spacer sequences. Amer. J. Bot. 83: 234–251.

Downie S. R., Katz-Downie D. S. (1999) Phylogenetic analysis of chloroplast *rps*16 intron sequences reveals relationships within the woody southern African Apiaceae subfamily Apioideae. Canad. J. Bot. 77: 1120–1135.

Downie S. R., Katz-Downie D. S., Spalik K. (2000a) A phylogeny of Apiaceae tribe Scandiceae: evidence from nuclear ribosomal DNA internal transcribed spacer sequences. Amer. J. Bot. 87: 76–95.

Downie S. R., Ramanath S., Katz-Downie D. S., Llanas E. (1998) Molecular systematics of Apiaceae subfamily Apioideae: phylogenetic analyses of nuclear ribosomal DNA internal transcribed spacer and plastid *rpo*C1 intron sequences. Amer. J. Bot. 85: 563–591.

Downie S. R., Watson M. F., Spalik K., Katz-Downie D. S. (2000b) Molecular systematics of Old World Apioideae (Apiaceae): relationships among some members of tribe Peucedaneae sensu lato, the placement of several island endemics, and resolution within the apioid superclade. Canad. J. Bot. 78: 506–528.

Downie S. R., Plunkett G. M., Watson M. F., Spalik K., Katz-Downie D. S., Valiejo-Roman K. M., Terentieva E. I., Troitsky A. V., Lee B.-Y., Lahham J., El-Oqlah A. (2001) Tribes and clades within Apiaceae subfamily Apioideae: the contribution of molecular data. Edinburgh J. Bot. 58: 301–330.

Downie S. R. Hartman R. L., Sun F.-J., Katz-Downie D. S. (2002) Polyphyly of the spring-parsleys (*Cymopterus*): molecular and morphological evidence suggests complex relationships among the perennial endemic genera of western North American Apiaceae. Canad. J. Bot. 80: 1295–1324.

Drude C. G. O. (1897–1898) Umbelliferae. In: Engler A., Prantl K. (eds.) Die natürlichen Pflanzenfamilien, vol. 3. Wilhelm Engelmann, Leipzig, pp. 63–250.

Durrieu G. (1982) Les champignons parasites et leur apport à la systématique des Ombellifères. In: Cauwet-Marc A.-M., Carbonnier J. (eds.) Les Ombellifères "Contributions pluridisciplinaires à la systématique." Actes du 2ème Symposium International sur les Ombellifères. Monographs in Systematic Botany from the Missouri Botanical Garden, vol. 6. Braun-Brumfield, Ann Arbor, Michigan, pp. 525–533.

Eriksson T. (1998) AutoDecay ver. 4.0 (program distributed by the author). Department of Botany, Stockholm University, Stockholm.

Felsenstein J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39: 783–791.

Frey R. (1989) Taxonomische Revision der Gattung *Peucedanum*: Sektion *Peucedanum* und Sektion *Palimbioidea* (Umbelliferae). Candollea 44: 257–327.

Guyot M. (1984) Les types stomatiques dans les espèces françaises du genre *Peucedanum* (Ombellifères). Revue Cytol. Biol. Vég. Bot. 7: 17–30.

Hadacek F. (1989) Vergleichende phytochemische Untersuchungen in der Gattung *Peucedanum* (Apiaceae - Apioideae). Stapfia 18: 1–186.

Hardig T. M., Soltis P. S. (1999) An ITS-based phylogenetic analysis of the *Euryptera* species group in *Lomatium* (Apiaceae). Plant Syst. Evol. 219: 65–78.

Katz-Downie D. S., Valiejo-Roman C. M., Terentieva E. I., Troitsky A. V., Pimenov M. G., Lee B.-Y., Downie S. R. (1999) Towards a molecular phylogeny of Apiaceae subfamily Apioideae: additional information from nuclear ribosomal DNA ITS sequences. Plant Syst. Evol. 216: 167–195.

Leute G.-H. (1966) Die Gattungen *Imperatoria* L. und *Tommasinia* Bertol. (Apiaceae). Ann. Naturhist. Mus. Wien 69: 69–79.

Menitsky G. L. (1991) Konspekt vidov semejstva Apiaceae flory Kakvkaza. Bot. Zhurn. 76: 1749–1764.

Muckensturm B., Diyani F. (1995) Rapport préliminaire sur les constituants volatils de *Selinum pyrenaeum*, *Selinum carvifolia*. Univ. Haute-Alsace, Mulhouse.

Ostroumova T. A., Pimenov M. G. (1997) Carpological diversity of African *Peucedanum* s.l. (Umbelliferae). I. The species of southern Africa. Feddes Repert. 108: 299–318.

Pimenov M. G. (1986) *Kitagawia* – a new Asiatic genus of the family Umbelliferae. Bot. Zhurn. 71: 942–949.

Pimenov M. G. (1987) *Cervaria*. In: Hedge I. C., Lamond J. M., Rechinger K. H., et al. Umbelliferae. In: Rechinger K. H. (ed.) Flora iranica, vol. 162. Akademische Druck- und Verlagsanstalt, Graz, pp. 83–110.

Pimenov M. G., Leonov M. V. (1993) The genera of Umbelliferae. Royal Botanical Gardens, Kew.

Plunkett G. M., Soltis D. E., Soltis P. S. (1996) Evolutionary patterns in Apiaceae: inferences based on *mat*K sequence data. Syst. Bot. 21: 477–495.

Posada D., Crandall K. A. (1998) Modeltest: testing the model of DNA substitution. Bioinformatics 14: 817–818.

Pu F. T., Wang P. L., Zheng Z. H., Wang Y. P. (2000) A reclassification of *Notopterygium* Bossieu (Umbelliferae). [In Chinese]. Acta Phytotax. Sin. 38: 430–436.

Reduron J.-P., Charpin A., Pimenov M. G. (1997) Contribution à la nomenclature générique des Apiaceae (Ombellifères). J. Bot. Soc. bot. Fr. 1: 91–104.

Shneyer V. S., Kutyavina N. G., Pimenov M. G. (2003) Systematic relationships within and between *Peucedanum* and *Angelica* (Umbelliferae-Peucedaneae) inferred from immunological studies of seed protein. Plant Syst. Evol. 236: 175–194.

Spalik K., Wojewódzka A., Downie S. R. (2001) The delimitation of genera in Apiaceae with examples from Scandiceae subtribe Scandicinae. Edinburgh J. Bot. 58: 331–346.

Sun F.-J, Downie S. R., Hartman R. L. (2004) An ITS-based phylogenetic analysis of the perennial, endemic Apiaceae subfamily Apioideae of western North America. Syst. Bot. (in press).

Swofford D. L. (1998) PAUP*. Phylogenetic Analysis Using Parsimony (*and other methods). Version 4. Sinauer Associates, Sunderland.

Tamura K., Nei M. (1993) Estimation of the number of nucleotide substitution in the control region of mitochondrial DNA in humans and chimpanzees. Mol. Biol. Evol. 10: 512–526.

Theobald W. L. (1971) Comparative anatomical and developmental studies in the Umbelliferae. In: Heywood V. H. (ed.) The biology and chemistry of the Umbelliferae. Academic Press, London, pp. 177–197.

Thompson J. D., Gibson T. J., Plewniak F., Jeanmougin F., Higgins D. G. (1997) The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res. 24: 4876–4882.

Tutin T. G., Heywood V. H., Burges N. A., Moore D. M., Valentine D. H., Walters S. M., Webb D. A. (eds.) (1968) Flora Europaea. Vol. 2. Cambridge University Press, Cambridge.

Valiejo-Roman C. M., Terentieva E. I., Samigullin T. H., Pimenov M. G. (2002) nrDNA ITS sequences and affinities of Sino-Himalayan Apioideae (Umbelliferae). Taxon 51: 685–701.

Vasil'eva M. G., Pimenov M. G. (1991) Karyotaxonomical analysis in the genus *Angelica* (Umbelliferae). Plant Syst. Evol. 177: 117–138.

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