Phylogeny of Apiaceae subtribe Daucinae and the taxonomic delineation of its genera

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Abstract Scandiceae subtribe Daucinae encompasses umbellifers that have fruits with prominent secondary ridges projecting into wings (former tribe Laserpitieae) or spines (former tribe Caucalideae pro parte). It comprises several economically or medicinally important genera including *Cuminum*, *Daucus*, *Laser*, *Laserpitium* and *Thapsia* among others. Recent molecular studies, based mostly on nrDNA ITS sequences, revealed that neither *Daucus* nor *Laserpitium* are monophyletic. To address issues of relationships and apply respective nomenclatural changes, we obtained additional ITS sequences as well as independent data from three plastid markers—*rps16* intron, *rpoC1* intron and *rpoB-trnC* intergenic spacer—for a comprehensive sample of the subtribe. We examined data for 260 accessions representing all genera of Daucinae and 81 of its ca. 93 species. Phylogenetic trees were estimated using maximum likelihood and Bayesian inference methods. The results indicate that former Laserpitieae constitute a paraphyletic grade at the base of the spiny-fruited members of Daucinae while traditionally delimited *Daucus* and *Laserpitium* are polyphyletic. To maintain a monophyletic *Daucus*, we suggest including the following genera and species into its synonymy: *Agrocharis*, *Melanoselinum*, *Monizia*, *Pachyctenium*, *Pseudorlaya*, *Rouya*, *Tornabenea*, *Athamanta dellacellae* and *Cryptotaenia elegans*. The species of *Laserpitium* occur in seven clades and only six species of the *Laserpitium* s.str. clade retain the generic name. Several species are transferred to *Ekimia*, *Laser* and *Thapsia*; additionally, a monospecific genus *Siler* is restored and a new genus, *Silphiodaucus*, is established. The inclusion of *Ammodaucus* into *Thapsia* suggested in an earlier study is not supported. The position of *Laserpitium pseudomeum* requires further study.

Keywords cpDNA; *Daucus*; Laserpitieae; *Laserpitium*; nrDNA ITS; Scandiceae; taxonomy

Supplementary Material The Electronic Supplement (Figs. S1–S3; Table S1) is available in the Supplementary Data section of the online version of this article at http://ingentaconnect.com/content/iapt/tax; DNA sequence alignment is available from TreeBase (http://purl.org/phylo/treebase/phylows/study/TB2:S18012).

■ INTRODUCTION

Umbellifers (Apiaceae) have dry fruits (schizocarps) that split into two one-seeded parts (mericarps) acting as dispersal units. These fruits exhibit an array of structural peculiarities, including various appendages that may facilitate fruit dispersal. Winged fruits are generally regarded as adapted to transportation by wind (Theobald, 1971; Jongejans & Telenius, 2001), whereas those with spines and bristles are considered as epizoochorous (Jury, 1982; Williams, 1994; Williams & Guries, 1994; Spalik & al., 2001). Fruit appendages may therefore be subject to strong selective pressure resulting in homoplasy. The diversity of winged fruits in the family is substantial, suggesting, therefore, their independent origins (Theobald, 1971; Liu & al., 2006). Multiple evolution of winged fruits has been demonstrated for several lineages of subfamily Saniculoideae (Calviño & al., 2008).

Schizocarps with prominent secondary ribs that project into broad wings constitute major diagnostic characters for the apioid tribe Laserpitieae Coss. & Germ. sensu Drude (1897–1898). Drude placed nine genera in this tribe, distributing them among three subtribes: Silerinae Tausch, Elaeoselininae Lange in Willk. & Lange and Thapsiinae Coss. & Germ. Silerinae included only *Siler* Crantz, Elaeoselininae incorporated *Elaeoselinum* W.D.J.Koch ex DC. and *Margotia* Boiss., and Thapsiinae encompassed *Guillonea* Coss., *Laserpitium* L., *Melanoselinum* Hoffm., *Polylophium* Boiss., *Thapsia* L., and *Tornabenea* Parl. Since Drude's treatment, the circumscription of Laserpitieae has not generally been changed, although its subtribes are no longer recognized and some modifications at the generic level have been introduced (summarized in Table 1). Four laserpitioid genera have been sunk into *Thapsia* (Weitzel & al., 2014), and *Melanoselinum edule* (Lowe) Drude is usually recognized in

Table 1. Genera of Apiaceae provisionally placed in tribe Daucinae and sampled for this study.

Genus	Nomenclatural type or species placed in Daucinae	No. of species		Reference
		All	This study: all (cpDNA)	
Agrocharis Hochst.	*A. melanantha* Hochst.	4	4 (3)	Townsend (1989)
Ammodaucus Coss. & Durieu[a]	*A. leucotrichus* Coss. & Durieu	2	1 (1)	Reyes-Betancort & al. (2007)
Athamanta L., pro parte, typo excl.[b]	*A. dellacellae* Asch. & Barbey ex E.A.Durand & Barratte	1	1 (1)	Spalik & Downie (2001)
Cryptotaenia DC., pro parte, typo excl.[b]	*C. elegans* Webb ex Bolle	1	1 (1)	Spalik & Downie (2007)
Cuminum L.	*C. cyminum* L.	3	2 (2)	Rechinger (1987a), Czerepanov (1995)
Daucus L.	*D. carota* L.	26	23 (20)	Sáenz Laín (1981), Grzebelus & al. (2011)
Ekimia H.Duman & M.F.Watson	*E. bornmuelleri* (Hub.-Mor. & Reese) H.Duman & M.F.Watson	1	1 (1)	Duman & Watson (1999), Lyskov & al. (2015)
Laser Borkh. ex G.Gaertn. & al.	*L. trilobum* (L.) Borkh. ex G.Gaertn. & al.	1	1 (1)	Rechinger (1987b), Reduron (2007b)
Laserpitium L.	*L. gallicum* L.	19(–35)	18 (14)	Pimenov & Leonov (1993)[c]
Melanoselinum Hoffm.	*M. decipiens* (Schrad. & J.C.Wendl.) Hoffm.	1	1 (1)	Press & Short (1994)
Monizia Lowe	*M. edulis* Lowe	1	1 (1)	Press & Short (1994)
Orlaya Hoffm.	*O. grandiflora* (L.) Hoffm.	3	3 (2)	Jury (2003), Hartvig (1986)
Pachyctenium Maire & Pamp.	*P. mirabile* Maire & Pamp.	1	1 (0)	Lee & al. (2001)
Polylophium Boiss.	*P. orientale* Boiss.	2	2 (1)	Rechinger (1987c)
Pseudorlaya (Murb.) Murb.	*P. pumila* (L.) Murb.	2	2 (0)	Rutherford & Jury (2003)
Rouya Coincy	*R. polygama* (Desf.) Coincy	1	1 (1)	Reduron (2008)
Thapsia L.[d]	*T. villosa* L.	18	15 (8)	Pujadas Salvà & Plaza Arregui (2003), Pujadas Salvà & Rosellò (2003), Weitzel & al. (2014)
*Distichoselinum García-Martín & Silvestre	*D. tenuifolium* (Lag.) García Martín & Silvestre	1	1 (1)	García Martín & Silvestre (1985), García Martín (2003a)
*Elaeoselinum W.D.J.Koch ex DC.	*E. meoides* (Desf.) W.D.J.Koch ex DC.	4(–5)	3 (2)	García Martín & Silvestre (1985), García Martín (2003b), Brullo & al. (2003)
*Guillonea Coss.	*G. scabra* (Cav.) Coss.	1	1 (1)	Montserrat (2003a)
*Margotia Boiss.	*M. laserpitioides* Boiss. (= *M. gummifera* (Desf.) Lange)	1	1 (1)	García Martín & Silvestre (1985), García Martín (2003c)
Tornabenea Parl.	*T. insularis* (Parl. ex Webb.) Parl.	6	3 (1)	Brochmann & al. (1997); Schmidt & Lobin (1999)

[a] *Ammodaucus* was recently synonymized with *Thapsia* based on nrDNA ITS analyses only (Weitzel & al., 2014). However, this placement has little support from morphology while the apparently long branch of this taxon within *Thapsia* makes this assignment problematic.

[b] *Athamanta* and *Cryptotaenia* are polyphyletic with single species placed in Daucinae; therefore, only these species are considered.

[c] Pimenov & Leonov (1993) estimated the number of species in *Laserpitium* at 35. However, upon verification of the local Floras and regional revisions for western Eurasia and the Mediterranean region we have found only 19 currently recognized species.

[d] The genera that are marked with asterisks have been recently sunk into the synonymy of *Thapsia* based on nrDNA ITS analyses only (Weitzel & al., 2014). Because that study did not include all members of the synonymized genera, we also provide their original taxonomic treatment.

the monospecific genus *Monizia* Lowe (Press & Short, 1994). The nomenclatural type of *Siler*, *S. montanum* Crantz, has been returned to *Laserpitium* (as *L. siler* L.), whereas another member of *Siler* sensu Drude, *S. trilobum* (L.) Scop., is at present placed in the monospecific genus *Laser* Borkh. ex G.Gaertn. & al. and usually recognized in tribe Peucedaneae Dumort. (Pimenov & Leonov, 1993). The monospecific genus *Rouya* Coincy has been segregated from *Thapsia*. Additionally, several species have been transferred to or described in *Tornabenea*, *Polylophium* and *Thapsia*. Recently, phylogenetic analyses of ITS sequences suggested that an obscure endemic of Turkey, *Ekimia* H.Duman & M.F.Watson, is closely related to some Anatolian species of *Laserpitium* (Lyskov & al., 2015). Its only member, *E. bornmuelleri* (Hub.-Mor. & Reese) H.Duman & M.F.Watson, was originally placed in *Prangos* Lindl. because of its fruits with wavy wings that are superficially similar to those of the latter (Duman & Watson, 1999).

Drude (1897–1898) suggested that Laserpitieae were allied with his tribe Dauceae W.D.J.Koch, whose members also possess fruits with prominent secondary ribs. In contrast to those in Laserpitieae, the ribs of Dauceae are spiny. Calestani (1905) and Koso-Poljansky (1916) went even further in uniting Laserpitieae and Dauceae. Calestani (1905) synonymized *Thapsia*, *Elaeoselinum*, *Margotia*, and *Guillonea* with *Laserpitium*, recognizing the latter in Ligusticeae Calest. subtribe Daucinae Dumort., although at the same time he included *Siler*, a segregate of *Laserpitium*, in subtribe Peucedaninae Tausch. For *Tornabenea*, he recognized a separate subtribe, although he neither indicated its content nor provided its description because he was concerned with European species only. In his worldwide revision of umbellifers, Koso-Poljansky (1916) followed Calestani's treatment of Daucinae and included all Drude's Laserpitieae in this subtribe: *Elaeoselinum* (including *Margotia*), *Guillonea*, *Laserpitium* s.l. (i.e., including *Laser*, *Melanoselinum*, *Polylophium*, *Rouya*, *Siler*, and *Thapsia*), *Monizia*, and *Tornabenea*. Interestingly, he transferred some species of *Laserpitium*, including *L. prutenicum* L. and *L. hispidum* M.Bieb., to *Daucus* L. placing them in a separate sect. *Silphiodaucus* Koso-Pol.

Spiny or hairy fruits with prominent secondary ribs also occur in those umbellifers that were placed by Drude (1897–1898) in Scandiceae subtribe Caucalidinae Tausch, and the entire tribe Scandiceae Spreng. was circumscribed based on the occurrence of calcium oxalate crystals in the parenchymatic cells surrounding the carpophore. In contrast to Drude's treatment, the revisions of Apiaceae by Bentham (1867) and Boissier (1872) united all spiny-fruited umbellifers in tribe Caucalideae Spreng. Such an approach was also adopted by Heywood & Dakshini (1971), and their treatment served as the basis for a multivariate study of Caucalideae. It resulted in a new circumscription of the tribe (Heywood, 1982) that was generally accepted (Pimenov & Leonov, 1993).

The relationships among Laserpitieae, Caucalideae, and Scandiceae have also been investigated using molecular data. First phylogenetic studies using nuclear rDNA ITS (Downie & Katz-Downie, 1996), plastid *rpoC1* intron (Downie & al., 1996), and plastid *matK* sequences (Plunkett & al., 1996a) suggested

that members of these tribes form a single clade although the relationships among them remained unresolved due to limited sampling. In these analyses, the representatives of *Laserpitium* grouped with some members of Caucalideae forming a *Daucus* clade. Subsequent molecular studies indicated that other members of Laserpitieae—*Thapsia* (Rasmussen & Avato, 1998; Weitzel & al., 2014), *Laser* and *Polylophium* (Katz-Downie & al., 1999), *Monizia* (Downie & al., 2000c), and *Melanoselinum* (Lee & Downie, 2000)—also belong to this clade, treated thereafter as Scandiceae subtribe Daucinae (Downie & al., 2000a, 2001, 2010). Interestingly, these former members of Laserpitieae did not form a monophyletic group within Daucinae (Downie & al., 2000c, 2001; Spalik & Downie, 2007). Moreover, some of them were placed within *Daucus*, making the delineation of this economically important genus problematic. The species of *Daucus* formed two clades with the *Daucus* I clade encompassing the nomenclatural type of the genus, *D. carota* L., which includes the cultivated carrot. This clade was sister to winged-fruited *Melanoselinum* and *Monizia*, while the closest relative of *D. carota* was another laserpitioid genus, *Tornabenea* (Spalik & Downie, 2007). The phylogenetic relationships among the species of *Daucus*, particularly the *D. carota* complex, were recently subject to intense molecular research (Iorizzo & al., 2013; Spooner & al., 2013), but these studies did not result in a new circumscription of the genus due to limited taxonomic sampling. Molecular studies that included more than one member of *Laserpitium* suggested that this genus is polyphyletic (Katz-Downie & al., 1999; Lee & Downie, 1999, 2000; Downie & al., 2000c; Spalik & Downie, 2007; Weitzel & al., 2014).

Among the major clades of umbellifers, subtribe Daucinae is one of the most important from an economical point of view because it includes the cultivated carrot, the most widely grown crop of Apiaceae (Iorizzo & al., 2013). Wild species of *Daucus* constitute an invaluable gene pool for developments in carrot breeding and have also been investigated with respect to the antimicrobial properties of oil components (Grzebelus & al., 2011). Subtribe Daucinae encompasses many taxa with potential medicinal value including *Laser* (Parlatan & al., 2009), *Laserpitium* (Popović & al., 2013) and *Thapsia* (Andersen & al., 2015). Therefore, a classification system congruent with the phylogeny of this group is of considerable practical importance.

In this paper, we examine the phylogenetic relationships within Daucinae (tribe Scandiceae) with a comprehensive sampling of species traditionally classified in tribes Dauceae and Laserpitieae and using phylogenetic markers from nuclear and plastid genomes. Our aim is to provide a new taxonomic treatment of this economically important branch of umbellifers.

■ MATERIALS AND METHODS

Taxon and molecular marker sampling. — Two hundred sixty accessions representing putative members of Scandiceae subtribe Daucineae and outgroups were examined for molecular sequence variation (Appendix 1; Electr. Suppl.: Table S1). Specifically, all genera and 81 of ca. 93 ingroup species were sampled (Table 1). Outgroups included representatives of other

subclades of tribe Scandiceae (Downie & al., 2010). If possible, voucher specimens were examined to confirm their determination (see Appendix 1 and Electr. Suppl.: Table S1 for details).

For all accessions, we obtained the nuclear ribosomal DNA internal transcribed spacer (ITS) region that has already been successfully used in phylogenetic analyses of Apiaceae (Downie & al., 2001). However, our preliminary phylogenetic analyses demonstrated that this marker does not provide adequate resolution among the laserpitioid taxa. Therefore, for a representative set of accessions comprising 18 genera and 59 species of Daucinae we also included three chloroplast markers, the *rpoC1* and *rps16* introns and the *rpoB-trnC* intergenic spacer. These markers have already been employed in phylogenetic analyses of umbellifers (Downie & al., 1996; Downie & al., 2000b; Calviño & al., 2010; Panahi & al., 2015).

DNA extraction, amplification, and sequencing. — Total genomic DNA was isolated from ca. 20 mg of dried leaf tissue using a DNeasy Plant Mini Kit (Qiagen, Hilden, Germany). For the nrDNA ITS sequence, the DNA samples were PCR-amplified using primers ITS4 and ITS5 (White & al., 1990) or N-nc18S10 and C26A (Wen & Zimmer, 1996). For some accessions, the ITS 1 and ITS 2 regions were amplified separately using the following pairs of primers: 18S-ITS1-F and 5.8S-ITS1-R for ITS 1, and ITS-3N and ITS4 for ITS 2 (Spalik & Downie, 2006).

The *rpoB-trnC* intergenic spacer region was amplified with primers rpoB and trnC^{GCA}R from Shaw & al. (2005). Because this region may include long insertions and mononucleotide repeats, three additional internal primers were designed to aid its amplification and sequencing: rpoB400 (AAG ATC AAA TGC CGA ATC CA), 400trnC (ATG GAA TTT TGT ATA GAA TAT CAA) and 400trnC2 (TTT CCT GCT TAA GAG TGG ATT). The pair rpoB and rpoB400 covers ca. 400 bp at the beginning of the spacer, while 400trcC and trnC^{GCA}R were used to amplify the remainder of the region. The reverse primer 400trnC2 located close to the end of the spacer was used together with 400trnC to amplify the middle region for some difficult samples. The *rps16* intron was amplified using external primers 5exonC and 3exonR from Calviño & al. (2006) or s16exF and s16exR from Panahi & al. (2015); additionally, two internal primers, s16inF and s16inR were also used (Panahi & al., 2015). The complete *rpoC1* intron and parts of the flanking

exon regions were amplified using external primers C1exF and C1exR; additionally, internal primers C1inF and C1inR were used to amplify this marker in part and to sequence difficult samples (Panahi & al., 2015). The details of the PCR reactions are provided elsewhere (Panahi & al., 2015).

PCR products were checked on 1% agarose gel with ethidium bromide or Midori Green Advance DNA Stain (Nippon Genetics Europe, Dueren, Germany). Depending on their quality, they were purified using the QIAquick PCR Purification Kit (Qiagen) or gel purified using the QIAEX II Agarose Gel Extraction Kit or QIAquick Gel Extraction Kit (Qiagen). Cycle sequencing reactions were performed using the Big Dye Terminator v.3.1 Cycle Sequencing Kit (Applied Biosystems, Waltham, Massachusetts, U.S.A.) with the same primers as used for PCR amplifications. The products were purified using Sephadex columns or DyeEx 2.0 Spin Kit (Qiagen) and sequenced using an automated DNA sequencer at IBB PAS (Warsaw, Poland). The sequences were assembled and edited using SeqMan II v.4.0 (Dnastar, Madison, Wisconsin, U.S.A.). All newly obtained sequences have been deposited in GenBank (Appendix 1; Electr. Suppl.: Table S1).

Sequence and phylogenetic analyses. — For each marker separately, DNA sequences were aligned using MAFFT v.7.123b (Katoh & Toh, 2008) and the resulting matrix was corrected manually if necessary. The parts of the alignment containing especially large numbers of gaps were identified using trimAl v.1.2rev59 with the "automated1" algorithm (Capella-Gutiérrez & al., 2009) and excluded from the analyses. Accessions with identical sequences (with uncorrected *p* distance = 0) were represented in the analyses by a single terminal (the number of unique and duplicate sequences in each analysis is given in Table 2).

The congruence of the datasets was assessed using a hierarchical likelihood ratio test (hLTR) implemented in Concaterpillar v.1.8a (Leigh & al., 2008). Phylogenetic analyses were performed using the maximum likelihood (ML) method implemented in RAxML v.8.1.18 (Stamatakis, 2014) and the Bayesian inference (BI) method implemented in MrBayes v.3.2.5x64 (Ronquist & al., 2012).

For Bayesian analyses of nrDNA ITS data, the models of nucleotide substitution were chosen with ModelGenerator v.0.85 (Keane & al., 2006). Partition schemes and substitution

Table 2. Characteristics of the datasets used in this study.

	ITS	*rpoB-trnC* spacer	*rpoC1* intron	*rps16* intron	cpDNA	Combined Full	Reduced[a]
No. of unique/duplicate sequences	212/48	34/1	70/5	89/9	106/4	241/19	109/1
No. of aligned positions	649	1643	1139	984	3766	4415	2772
excluded (ambiguous)	49	392	111	129	632	681	289
constant	203	1010	854	672	2536	2739	1753
variable	397	241	174	183	598	995	730
containing gaps and missing data	270	243	503	99	3134	3404	2093
% of gaps and missing data in the matrix	3.4	3.9	1.6	0.4	40.7	62.1	17.5

[a] Combined ITS, *rpoC1* intron and *rps16* intron matrix comprising only accessions, for which both ITS and cpDNA data were available.

models for the analyses of plastid and combined plastid and nuclear data were inferred using PartitionFinder v.1.1.1 (Lanfear & al., 2012, 2014). Bayesian analyses were carried out for 40 million generations with four Monte Carlo Markov chains initiated and a sampling frequency of 1000 generations. Two independent runs were initiated for each analysis. The initial 25% of saved trees were discarded as a burn-in phase and the 50% majority-rule consensus tree and posterior probabilities (PP) of particular clades were calculated based on the remaining 60,000 trees. The effective sample size (ESS) for the estimated parameters and the convergence of the independent runs were checked using Tracer v.1.6.0 (Rambaut & al., 2014).

For ML analyses, we employed the GTR+G substitution model. In RAxML, GTR(+G+I) is the only nucleotide substitution model implemented because according to the author of the program it is better to efficiently implement and optimize this model instead of offering a spectrum of models that are programmed in a generic and thus inefficient way (Stamatakis, 2014). Similarly, GTR+G is preferred over GTR+G+I because the substitution rate heterogeneity is already accounted for with gamma distribution and, therefore, parameters G and I cannot be optimized independently from each other (Stamatakis, 2014). Best ML trees were found based on 200 independent searches starting from distinct randomized maximum parsimony trees. Bootstrap support (BS) was estimated based on 1000 rapid bootstrap replicates. In order to check whether the number of replicates was sufficient, we performed a posteriori bootstopping analysis with the extended majority-rule consensus tree as a convergence criterion. For the analyses of combined data, we used the partition schemes inferred from PartitionFinder.

In order to identify terminals that introduce putative topological conflict, we used the program compat.py that compares bootstrap values for trees inferred from different partitions (Kauff & Lutzoni, 2002). As significantly unstable terminals, we regarded those that occurred in different and well-supported clades (BS ≥ 75) in trees inferred from separate analyses of nrDNA and cpDNA. Then, we excluded these terminals from the matrices, checked again the congruence of the datasets and repeated ML and BI analyses of combined data.

Because the appendages of secondary ribs are principal features delimiting genera, and winged vs. spiny secondary ribs were used to distinguish tribes Dauceae and Laserpitieae in traditional classification systems of umbellifers, we performed maximum parsimony (MP) mapping of this character using a tree from the ML analyses of the combined data. This tree was transformed into a cladogram and pruned such that each taxon was represented by one accession. The reconstruction of character changes was performed using Mesquite v.3.04 (Maddison & Maddison, 2015).

■ RESULTS

Sequence analyses. — For this study, we obtained 119 sequences of ITS, 73 sequences of *rps16* intron, 63 sequences of *rpoC1* intron and 26 sequences of *rpoB-trnC* intergenic spacer from 126 accessions (Appendix 1; Electr. Suppl.: Table S1). The

lower number of cpDNA sequences obtained, particularly of the *rpoB-trnC* intergenic spacer, resulted mostly from unsuccessful PCR amplification of these regions from low-quality DNA samples obtained from herbarium material. Aligned ITS sequences comprised a lower proportion of ambiguously aligned positions than plastid markers: only 7.6% of ITS positions were excluded from the analyses compared to 16.8% of aligned positions deleted from the combined cpDNA matrix (Table 2). Several accessions yielded identical sequences of some markers. For instance, of the 260 ITS sequences only 212 were included in the ITS matrix (Table 2). However, some accessions that had identical ITS sequences provided different cpDNA sequences and vice versa. Therefore, in the full combined matrix only 19 accessions were considered as duplicates.

Five matrices were used in subsequent analyses. First, matching nrDNA ITS and cpDNA matrices with 110 accessions (denoted #1 and #2 with 98 and 106 terminals, respectively) were analysed in order to assess the congruence of markers and to identify accessions introducing topological conflicts. Large ITS matrix (#3) including 260 accessions (212 terminals) was additionally analysed and the results were compared with those from small ITS matrix (#1) in order to evaluate the effect of taxonomic sampling on tree topology. Combined data matrix (#4) with all 260 accessions (241 terminals) was used to identify major highly supported clades that may be recognised as genera. In the combined data matrix we also included those accessions for which only ITS data were available coding respective cpDNA data as missing (Table 2). In effect, this matrix comprised 62.1% missing data. In order to evaluate the impact of those missing data on tree topology, we also analysed a reduced matrix (#5) comprising 110 accessions (109 terminals) and three markers: ITS, *rpoC1* intron and *rps16* intron. This matrix had only 17.5% missing data.

Hierarchical clustering of the markers with Concaterpillar resulted in concatenation of all three plastid loci (Table 3). In contrast, the concatenation of combined cpDNA markers and nrDNA ITS data was rejected with $P < 10^{-6}$. The comparisons of ML bootstrap analyses performed with compat.py identified 13 accessions that may cause a conflict (Figs. 1, 2). After

Table 3. Hierarchical tests of congruence of phylogenetic signal performed with Concaterpillar.

Dataset	*P*-value
All taxa	
rpoB-trnC spacer+*rpoC1* intron	0.367
rpoB-trnC spacer+*rpoC1* intron+*rps16* intron	0.177
rpoB-trnC spacer+*rpoC1* intron+*rps16* intron+ITS	$<10^{-6}$*
Conflicting terminals excluded	
ITS+*rpoB-trnC* spacer	0.610
ITS+*rpoB-trnC* spacer+*rpoC1* intron spacer	0.240
ITS+*rpoB-trnC* spacer+*rpoC1* intron+*rps16* intron	0.199

An asterisk indicates a statistically significant conflict between markers for α = 0.017 corrected for multiple comparisons (with initial α = 0.05).

Fig. 1. Maximum likelihood tree inferred from analyses of 110 nrDNA ITS sequences of Daucinae and outgroups obtained from accessions for which plastid DNA data were also available (dataset #1, see the text for details). Accessions that yielded identical sequences are represented by a single terminal. Bootstrap support and posterior probability (for nodes that also occurred in Bayesian majority-rule consensus tree) are given along the branches. Accessions with significantly different relationships in nrDNA and cpDNA trees are marked with boldface. Major groups are bracketed.
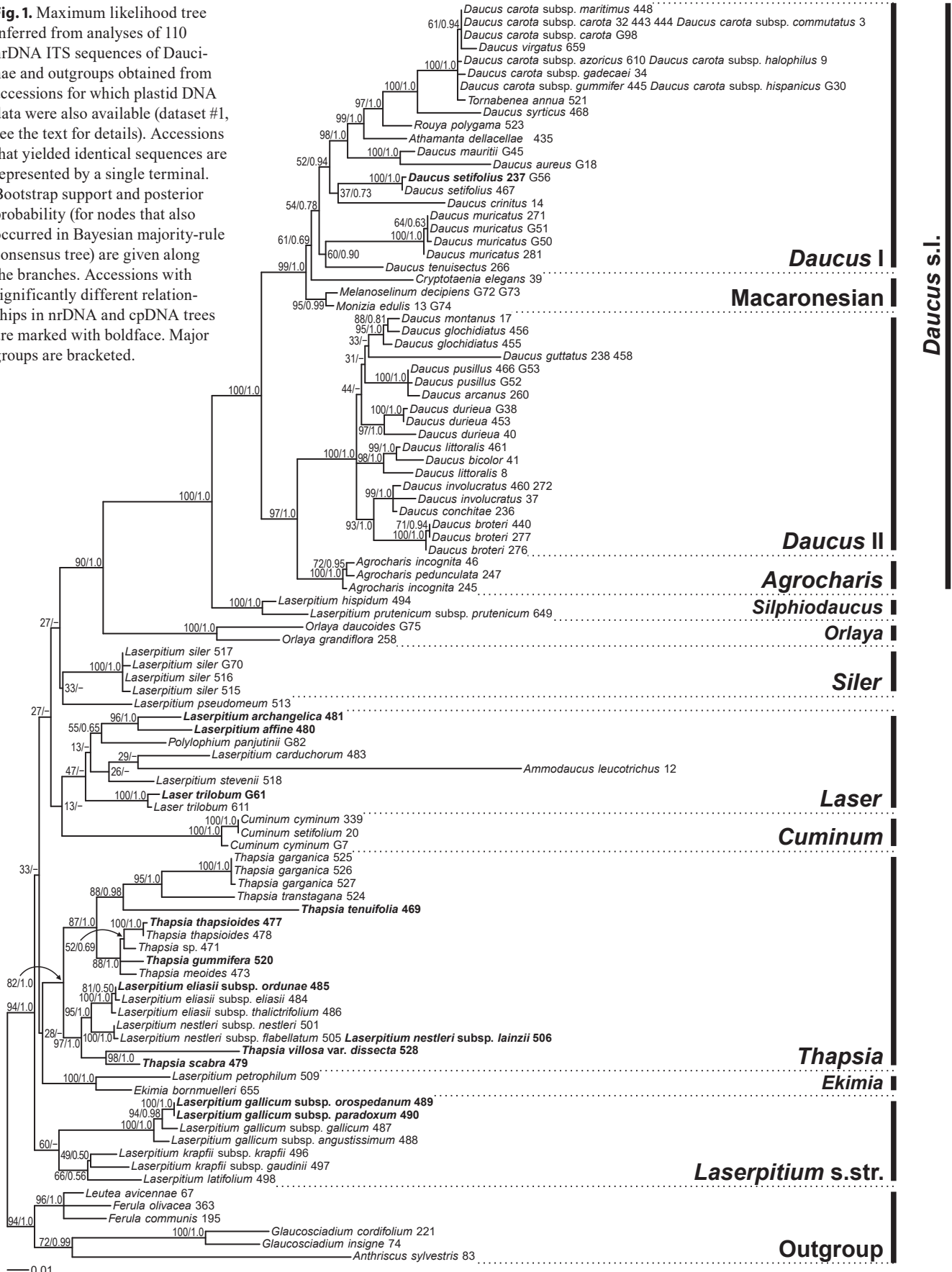
Fig. 2. Maximum likelihood tree inferred from analyses of combined sequences of the *rps16* and *rpoC1* introns and the *rpoB-trnC* intergenic spacer for the same 110 accessions as in Fig. 1 (dataset #2, see the text for details). Accessions that yielded identical sequences are represented by a single terminal. Bootstrap support and posterior probability (for nodes that also occurred in Bayesian majority-rule consensus tree) are given along the branches. Accessions with significantly different relationships in nrDNA and cpDNA trees are marked with boldface. Major groups are bracketed.
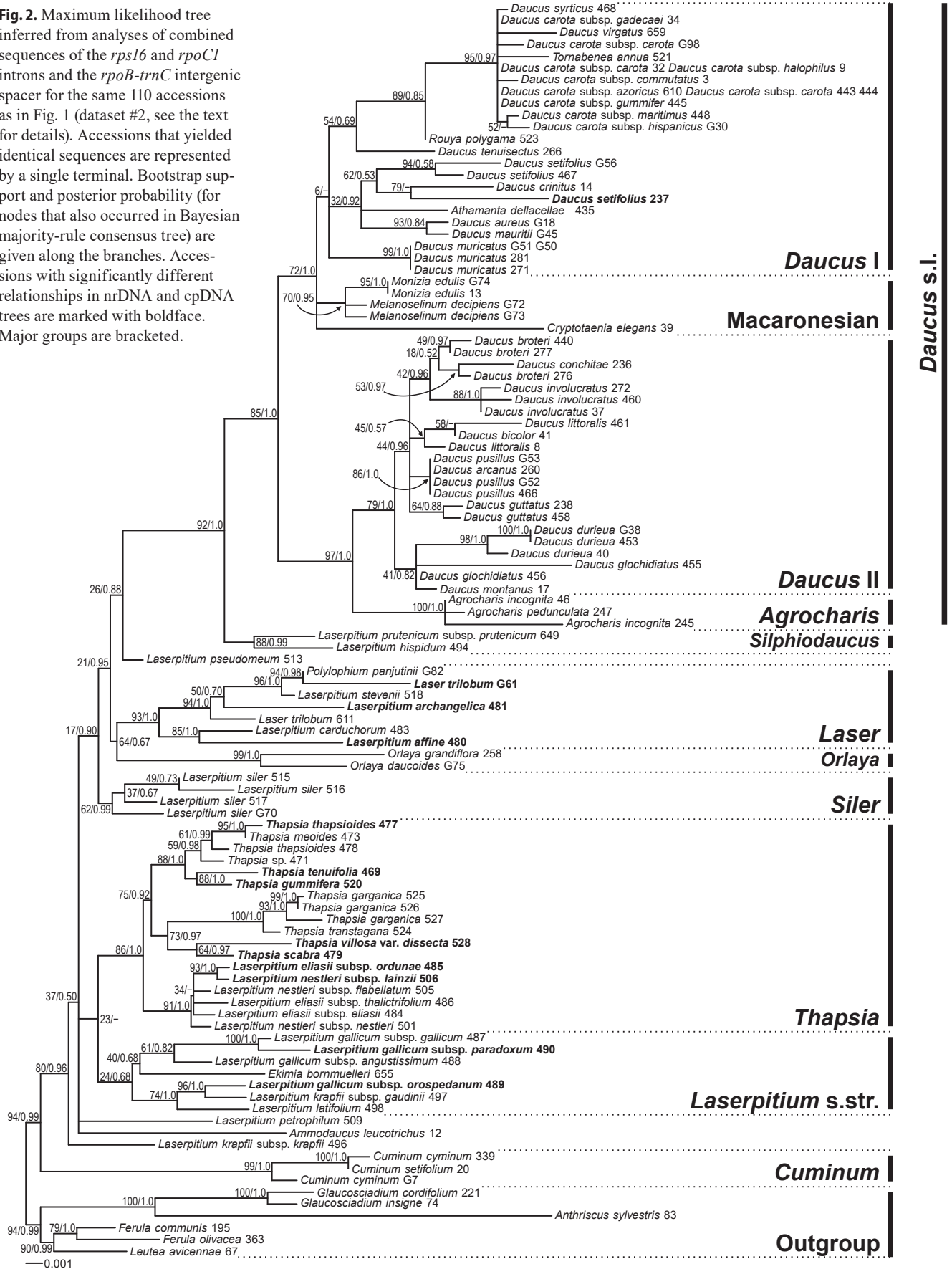
Daucus syrticus 468
Daucus carota subsp. *gadecaei* 34
Daucus virgatus 659
Daucus carota subsp. *carota* G98
Tornabenea annua 521
Daucus carota subsp. *carota* 32 *Daucus carota* subsp. *halophilus* 9
Daucus carota subsp. *commutatus* 3
Daucus carota subsp. *azoricus* 610 *Daucus carota* subsp. *carota* 443 444
Daucus carota subsp. *gummifer* 445
Daucus carota subsp. *maritimus* 448
Daucus carota subsp. *hispanicus* G30
Rouya polygama 523
Daucus tenuisectus 266
Daucus setifolius G56
Daucus setifolius 467
Daucus crinitus 14
Daucus setifolius 237
Athamanta dellacellae 435
Daucus aureus G18
Daucus mauritii G45
Daucus muricatus G51 G50
Daucus muricatus 281
Daucus muricatus 271

Daucus I

Monizia edulis G74
Monizia edulis 13
Melanoselinum decipiens G72
Melanoselinum decipiens G73
Cryptotaenia elegans 39

Macaronesian

Daucus broteri 440
Daucus broteri 277
Daucus conchitae 236
Daucus broteri 276
Daucus involucratus 272
Daucus involucratus 460
Daucus involucratus 37
Daucus littoralis 461
Daucus bicolor 41
Daucus littoralis 8
Daucus pusillus G53
Daucus arcanus 260
Daucus pusillus G52
Daucus pusillus 466
Daucus guttatus 238
Daucus guttatus 458
Daucus durieua G38
Daucus durieua 453
Daucus durieua 40
Daucus glochidiatus 455
Daucus glochidiatus 456
Daucus montanus 17

Daucus II

Agrocharis incognita 46
Agrocharis pedunculata 247
Agrocharis incognita 245

Agrocharis

Laserpitium prutenicum subsp. *prutenicum* 649
Laserpitium hispidum 494

Silphiodaucus

Daucus s.l.

Laserpitium pseudomeum 513
Polylophium panjutinii G82
Laser trilobum G61
Laserpitium stevenii 518
Laserpitium archangelica 481
Laser trilobum 611
Laserpitium carduchorum 483
Laserpitium affine 480

Laser

Orlaya grandiflora 258
Orlaya daucoides G75

Orlaya

Laserpitium siler 515
Laserpitium siler 516
Laserpitium siler 517
Laserpitium siler G70

Siler

Thapsia thapsioides 477
Thapsia meoides 473
Thapsia thapsioides 478
Thapsia sp. 471
Thapsia tenuifolia 469
Thapsia gummifera 520
Thapsia garganica 525
Thapsia garganica 526
Thapsia garganica 527
Thapsia transtagana 524
Thapsia villosa var. dissecta 528
Thapsia scabra 479
Laserpitium eliasii subsp. ordunae 485
Laserpitium nestleri subsp. lainzii 506
Laserpitium nestleri subsp. *flabellatum* 505
Laserpitium eliasii subsp. *thalictrifolium* 486
Laserpitium eliasii subsp. *eliasii* 484
Laserpitium nestleri subsp. *nestleri* 501

Thapsia

Laserpitium gallicum subsp. *gallicum* 487
Laserpitium gallicum subsp. paradoxum 490
Laserpitium gallicum subsp. *angustissimum* 488
Ekimia bornmuelleri 655
Laserpitium gallicum subsp. orospedanum 489
Laserpitium krapfii subsp. *gaudinii* 497
Laserpitium latifolium 498
Laserpitium petrophilum 509
Ammodaucus leucotrichus 12
Laserpitium krapfii subsp. *krapfii* 496

Laserpitium s.str.

Cuminum cyminum 339
Cuminum setifolium 20
Cuminum cyminum G7

Cuminum

Glaucosciadium cordifolium 221
Glaucosciadium insigne 74
Anthriscus sylvestris 83
Ferula communis 195
Ferula olivacea 363
Leutea avicennae 67

Outgroup

0.001

95/0.97
89/0.85
54/0.69
6/–
62/0.53
32/0.92
94/0.58
79/–
93/0.84
99/1.0
52/–
72/1.0
95/1.0
70/0.95
85/1.0
49/0.97
18/0.52
42/0.96
88/1.0
53/0.97
45/0.57
58/–
44/0.96
86/1.0
79/1.0
64/0.88
98/1.0
100/1.0
41/0.82
92/1.0
97/1.0
100/1.0
88/0.99
26/0.88
21/0.95
94/0.98
96/1.0
50/0.70
94/1.0
93/1.0
64/0.67
85/1.0
99/1.0
17/0.90
49/0.73
37/0.67
62/0.99
95/1.0
61/0.99
59/0.98
88/1.0
75/0.92
99/1.0
93/1.0
100/1.0
73/0.97
64/0.97
86/1.0
93/1.0
34/–
91/1.0
23/–
100/1.0
61/0.82
40/0.68
24/0.68
96/1.0
74/1.0
80/0.96
37/0.50
94/0.99
100/1.0
99/1.0
100/1.0
94/0.99
79/1.0
90/0.99

exclusion of these accessions from the matrix, we could not reject the null hypothesis of congruence of all four molecular markers (P = 0.199).

ModelGenerator selected the GTR+G and GTR+G+I models of nucleotide substitution for small (#1) and large (#3) ITS matrices, respectively. PartitionFinder recognized all three cpDNA markers as a single partition and returned the GTR+G+I model. When all markers were combined, ITS was recognized as a separate partition with the SYM+G+I model. These models and partitions were applied in subsequent BI analyses. In ML analyses, these partitions were analysed with the GTR+G model. The data for this study have been deposited with TreeBASE, study No. 18012.

Phylogenetic analyses of separate nrDNA and cpDNA data. — Phylogenetic analyses of small ITS matrix (#1) and cpDNA matrix (#2) with the same accessions resulted in phylogenetic trees with similar major clades, while the discrepancies occurred mostly within those clades or in their relationships to each other (Figs. 1, 2). The species of former Laserpitieae did not form a monophyletic group but most of them constituted a paraphyletic group with respect to the clade of spiny-fruited members of Daucinae, and some winged-fruited species were nested within the latter. Several major groups were apparent within the ITS tree (Fig. 1); with the exception of the *Ekimia* group, these clades also occurred in the cpDNA tree (Fig. 2). The relationships among these clades were equivocal and the internal support for some of them was moderate.

Several species of *Laserpitium* including *L. gallicum* L., the nomenclatural type of the genus, formed the *Laserpitium* s.str. clade that occurred in both the ITS and cpDNA trees with low BS (60% and 24%) and PP support (<0.5 and 0.68). The relationships among the members of this clade differed between the ITS and cpDNA trees. Two accessions of *L. gallicum* were identified as introducing topological conflict, i.e., in each tree their position was different and highly supported with BS > 75% and PP = 1.0. Additionally, the accession of *L. krapfii* Crantz subsp. *krapfii* was included in this clade only in the nrDNA tree but not in the cpDNA tree. However, its position did not receive high support in either of these trees and, therefore, this terminal was not identified as introducing significant topological conflict.

Two Anatolian endemics, *Ekimia bornmuelleri* and *Laserpitium petrophilum* Boiss. & Heldr., formed a highly supported *Ekimia* clade in the ITS trees (BS = 100%, PP = 1.0) while in the cpDNA trees they were placed in separate branches. However, this alternative placement was not highly supported either by ML bootstrap value or by high posterior probability from Bayesian inference.

The species of *Thapsia*, including former members of *Distichoselinum* García Martín & S.Silvestre, *Elaeoselinum*, *Guillonea*, *Margotia*, and two species of *Laserpitium*, *L. eliasii* Sennen & Pau and *L. nestleri* Soy.-Will., formed the *Thapsia* clade. It is noteworthy that *Ammodaucus leucotrichus* Coss. & Durieu, which had been included in this group in previous analyses of ITS data (Weitzel & al., 2014), did not group with *Thapsia* in the trees inferred from the small ITS matrix (#1) and from the cpDNA data (#2). This species was placed in *Thapsia*

only in trees obtained from the analyses of the large ITS matrix (#3, Electr. Suppl.: Fig. S1). Within the *Thapsia* clade, several species took notably different positions in the ITS and cpDNA trees but the support for the entire clade was high (BS > 80%, PP = 1.0) with the exception of the tree from the analyses of all ITS sequence data (Electr. Suppl.: Fig. S1). In this tree, with *Ammodaucus leucotrichus* included in the *Thapsia* clade, its bootstrap support was 30% (as compared to 82% in small ITS tree) and its posterior probability was 0.78 (as compared to 1.0 in small ITS tree).

The accessions of *Cuminum cyminum* L. and *C. setifolium* (Boiss.) Koso-Pol. formed a highly supported clade (BS = 99 or 100%, PP = 1.0) with ambiguous affinities. In the cpDNA trees, this genus was sister to the remaining members of the ingroup and this position received high support from ML bootstrap and BI analyses: BS = 94% and PP = 0.99 for the ingroup and BS = 80% and PP = 0.96 for the sister group relationship of *Cuminum* to the rest of the ingroup. In the ITS trees, *Cuminum* was sister to the *Laser* clade but this relationship had little support (BS = 13%, PP < 0.5).

The *Laser* clade encompassed a monospecific genus *Laser* and some species of *Polylophium* and *Laserpitium*. It was highly supported in the cpDNA trees (BS = 93%, PP = 1.0) but poorly in the ITS trees (BS = 47%, PP < 0.5). In the latter, it also included *Ammodaucus leucotrichus*. In the analyses of the large ITS dataset (#3), with *Ammodaucus* Coss. & Durieu placed outside this clade, its internal support was higher (BS = 55%, PP = 0.95).

All accessions of *Laserpitium siler* formed a clade supported in ITS (BS = 100%, PP = 1.0) and cpDNA trees (BS = 62%, PP = 0.99). Because this species was once placed in the separate genus *Siler*, and it is the generitype of this name, we denote this branch as the *Siler* clade. A single accession of *Laserpitium pseudomeum* Orph., Heldr. & Sart. ex Boiss. constituted a separate lineage and its position differed between the cpDNA and ITS trees. The monophyly of *Orlaya* Hoffm. was strongly supported in both the ITS (BS = 100%, PP = 1.0) and cpDNA trees (BS = 99%, PP = 1.0). This genus with spiny fruits was, however, placed separate from other spiny-fruited taxa: *Agrocharis* Hochst. and *Daucus*.

The core Daucinae were highly supported in all trees (BS ≥ 90%, PP = 1.0). This clade included the *Daucus* s.l. clade and the *Silphiodaucus* clade. The former comprised four groups identified in previous molecular studies: *Agrocharis*, *Daucus* I subclade, *Daucus* II subclade and the Macaronesian endemic group (Lee & Downie, 1999, 2000; Spalik & Downie, 2007). The *Silphiodaucus* clade included two species of *Laserpitium*, *L. prutenicum* and *L. hispidum*, that were placed by Koso-Poljansky (1916) in *Daucus* sect. *Silphiodaucus*. The monophyly of this clade and its sister position to the *Daucus* s.l. clade was strongly supported in all analyses (BS > 85%, PP > 0.95).

The species of *Daucus* were placed in two distinct subclades that received various support: low for the *Daucus* I group (BS = 54%, PP = 0.78 in ITS analyses and BS = 6%, PP < 0.5 in cpDNA analyses) and high for the *Daucus* II group (BS = 100%, PP = 1.0 in ITS analyses and BS = 79%, PP = 1.0 in cpDNA analyses). A group of three Macaronesian endemics

was paraphyletic with respect to the *Daucus* I subclade with the two winged-fruited genera, *Monizia* and *Melanoselinum*, forming a highly supported branch. *Cryptotaenia elegans* Webb ex Bolle, endemic to the Canary Islands, was placed either in a polytomy or sister to the *Daucus* I subclade. The latter also included two other genera of former Laserpitieae: *Tornabenea* and *Rouya*. The species of *Tornabenea* was placed within the *D. carota* complex and this relationship received strong support in both the cpDNA and ITS data analyses. The placement of *Athamanta dellacellae* Asch. & Barbey ex E.A.Durand & Baratte in the *Daucus* I subclade, previously inferred based on ITS data only, has been confirmed with cpDNA data. The monophyly of *Agrocharis* and its sister position to the *Daucus* II subclade were strongly supported in all analyses.

Phylogenetic analyses of combined data. — ML and BI analyses of combined nrDNA ITS and cpDNA sequences (dataset #4) were performed with and without the terminals introducing topological conflict that had been identified with compat.py. Additionally, to assess the impact of missing data on tree topology, we repeated the analyses for a subset of accessions for which both ITS and cpDNA sequences (*rpoC1* intron and/or *rps16* intron) were available (dataset #5). The topologies of trees from all analyses were generally similar with the same major clades identified. Because our major aim is to delimit major clades and provide a new taxonomic treatment for Daucinae, we here present the results of the analyses of all data (matrix #4 with all terminals, Figs. 3, 4), while the trees obtained from the reduced matrices (matrix #4 without the terminals introducing topological conflicts and matrix #5) are provided in the Electronic Supplement (Figs. S2 and S3, respectively).

In the combined analyses, *Cuminum* was placed in a sister position to the remaining Daucinae (Fig. 3). However, this relationship and most relationships among the major clades received very weak BS and PP support. *Ammodaucus* formed a separate branch with no direct relationship to *Thapsia* or *Laser* as in the previous analyses of nrDNA ITS data. The *Ekimia* clade received high support (BS = 100%, PP = 1.0) and it also included *Laserpitium glaucum* Post, another Anatolian endemic, for which only the ITS sequence was available. The *Laserpitium* s.str. clade was well supported in ML analyses (BS = 85%) and in Bayesian inference (PP = 1.0). All accessions of *L. gallicum* formed a clade sister to *L. halleri* Crantz. Two subspecies of *L. krapfii* were not placed as sister taxa but subsp. *gaudinii* was grouped with *L. nitidum* Zanted. and *L. peucedanoides* L., and this relationship was strongly supported (BS = 97%, PP = 1.0).

Several species of *Thapsia* that were represented only by ITS data grouped within the *Thapsia* clade, and the relationships among them were generally well resolved. As in the previous analyses, *L. nestleri* and *L. eliasii* were placed within this group. Noteworthy is the distinct position of *Thapsia* sp. 471, an accession from Corsica of uncertain specific affinity. It was provisionally classified as *Elaeoselinum asclepium* subsp. *meoides* (Desf.) Fiori (Reduron, 2007b) or *Thapsia meoides* Guss. but in our analyses it did not group with conspecific accessions.

The combined analyses confirmed the isolated positions of two species of *Laserpitium*, *L. siler* and *L. pseudomeum*,

which are not related to their congeners. These analyses also supported the sister position of the *Silphiodaucus* clade to the *Daucus* s.l. clade.

The relationships among the major subclades within the *Daucus* s.l. clade were well resolved and highly supported (Fig. 4). They were generally similar to those inferred from the nrDNA ITS analyses. As before, *Cryptotaenia elegans* was placed in sister position to the *Daucus* I subclade rather than to the two endemics from Madeira. Within the *Daucus* I subclade, conspecific accessions usually grouped together, confirming the current delineation of these species. The exception was the *D. carota* complex that also included three species of *Tornabenea* and *Daucus virgatus* (Poir.) Maire. Similar to separate analyses, *Rouya polygama* (Desf.) Coincy was closely related to *D. carota*. A distinct group nested within the *Daucus* I subclade was formed by two species of *Pseudorlaya* (Murb.) Murb. *Athamanta dellacellae* was sister to *Pachyctenium mirabile* Maire & Pamp, the only species of *Pachyctenium* Maire & Pamp. Within the *Daucus* II subclade, two taxa that are usually treated as conspecific, *D. broteri* Ten. and *D. bicolor* Sibth. & Sm., were distantly related. The recently described *D. conchitae* Greuter was placed sister to *D. involucratus* Sm. with very high support (BS = 99%, PP = 1.0).

Morphological analyses. — The morphology of secondary ribs was coded as a discrete unordered character with four states (secondary ribs: obsolete, winged, spiny, keeled). Maximum parsimony mapping of this character onto a pruned cladogram from the ML analyses of combined data inferred 14 character changes (Fig. 5). The reconstruction of the ancestral condition was ambiguous because all character states occurred at basal branches. Throughout the evolutionary history of the group, winged fruits dominated and fruits with spiny secondary ribs are generally derived from the former. However, in the spiny-fruited clade of Daucinae (encompassing the *Daucus* s.l. clade, the *Silphiodaucus* clade and *Orlaya*) the ancestral condition was ambiguous: winged or spiny. Therefore, spiny fruits in *Orlaya*, the *Daucus* I subclade and the *Daucus* II plus *Agrocharis* subclade may have arisen independently from winged fruits; alternatively, winged fruits in the *Silphiodaucus* clade and in the Madeiran endemics subclade are derived from spiny fruits. In contrast, winged fruits in some members of the *Daucus* I subclade represent evolutionary reversions.

■ DISCUSSION

The incongruence between plastid and nuclear data. — Incongruence among molecular markers may result from diverse evolutionary processes such as hybridization, introgression and incomplete lineage sorting. Alternatively, it may be an analytical artefact resulting from lack of phylogenetic signal, i.e., missing data and possible sampling error of characters, taxa, or both (Salichos & al., 2014, and references therein). Discrepancy between cpDNA and nrDNA ITS data has been reported in several studies of Apiaceae (e.g., Lee & Downie, 2006; Spalik & al., 2009; Zhou & al., 2009; Bone & al., 2011; Yi & al., 2015). In this study, 13 accessions
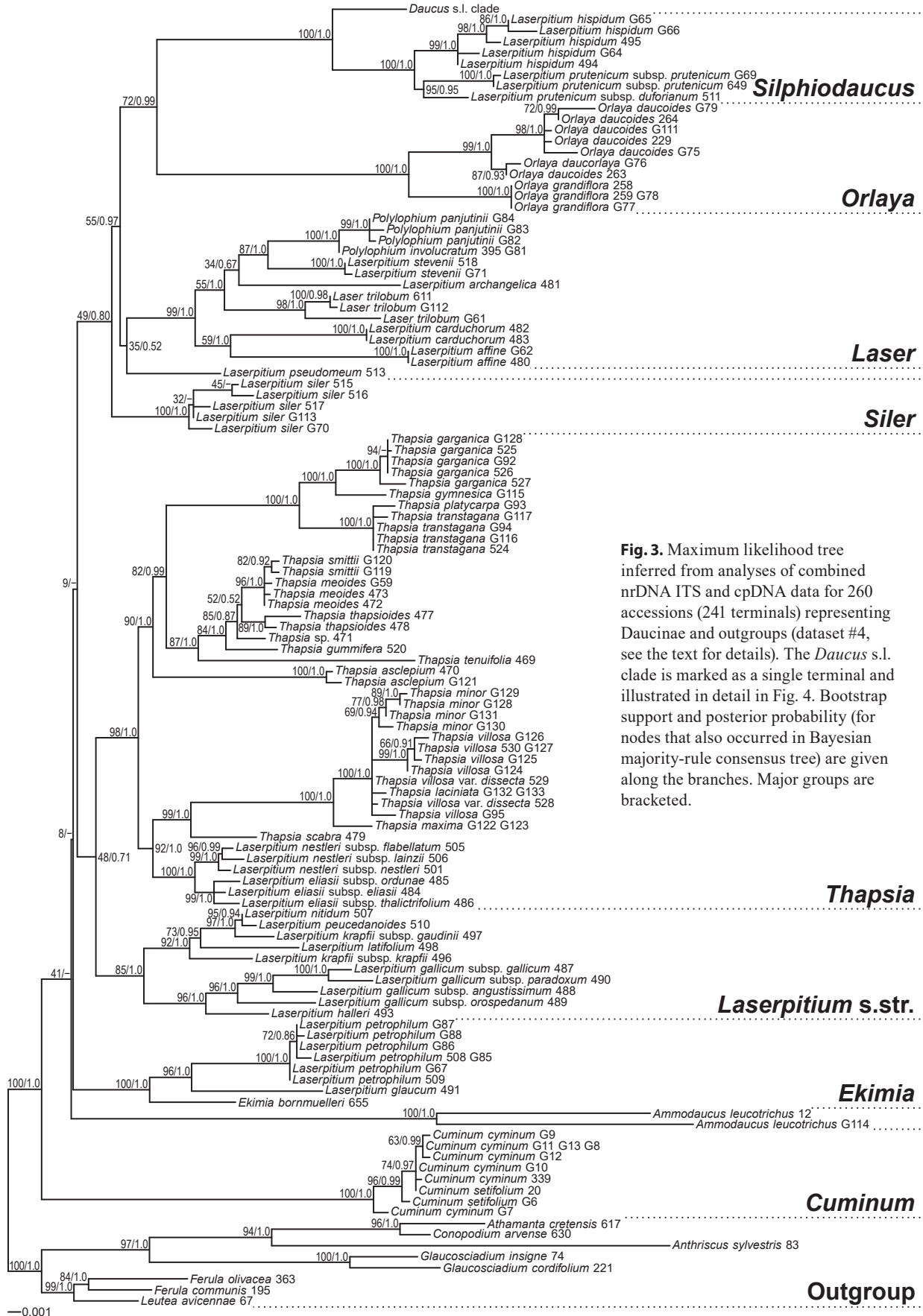
Daucus s.l. clade

Silphiodaucus

Orlaya

Laser

Siler

Thapsia

Laserpitium s.str.

Ekimia

Cuminum

Outgroup

Fig. 3. Maximum likelihood tree inferred from analyses of combined nrDNA ITS and cpDNA data for 260 accessions (241 terminals) representing Daucinae and outgroups (dataset #4, see the text for details). The *Daucus* s.l. clade is marked as a single terminal and illustrated in detail in Fig. 4. Bootstrap support and posterior probability (for nodes that also occurred in Bayesian majority-rule consensus tree) are given along the branches. Major groups are bracketed.

—0.001

Fig. 4. The relationships among the representatives of the *Daucus* s.l. clade inferred from maximum likelihood analyses of combined nrDNA ITS and cpDNA data. See Fig. 3 for details. The asterisk indicates a sequence that was identical to three other sequences obtained from *Daucus carota* subsp. *maximus* 269 and 449, and *Daucus virgatus* 50.
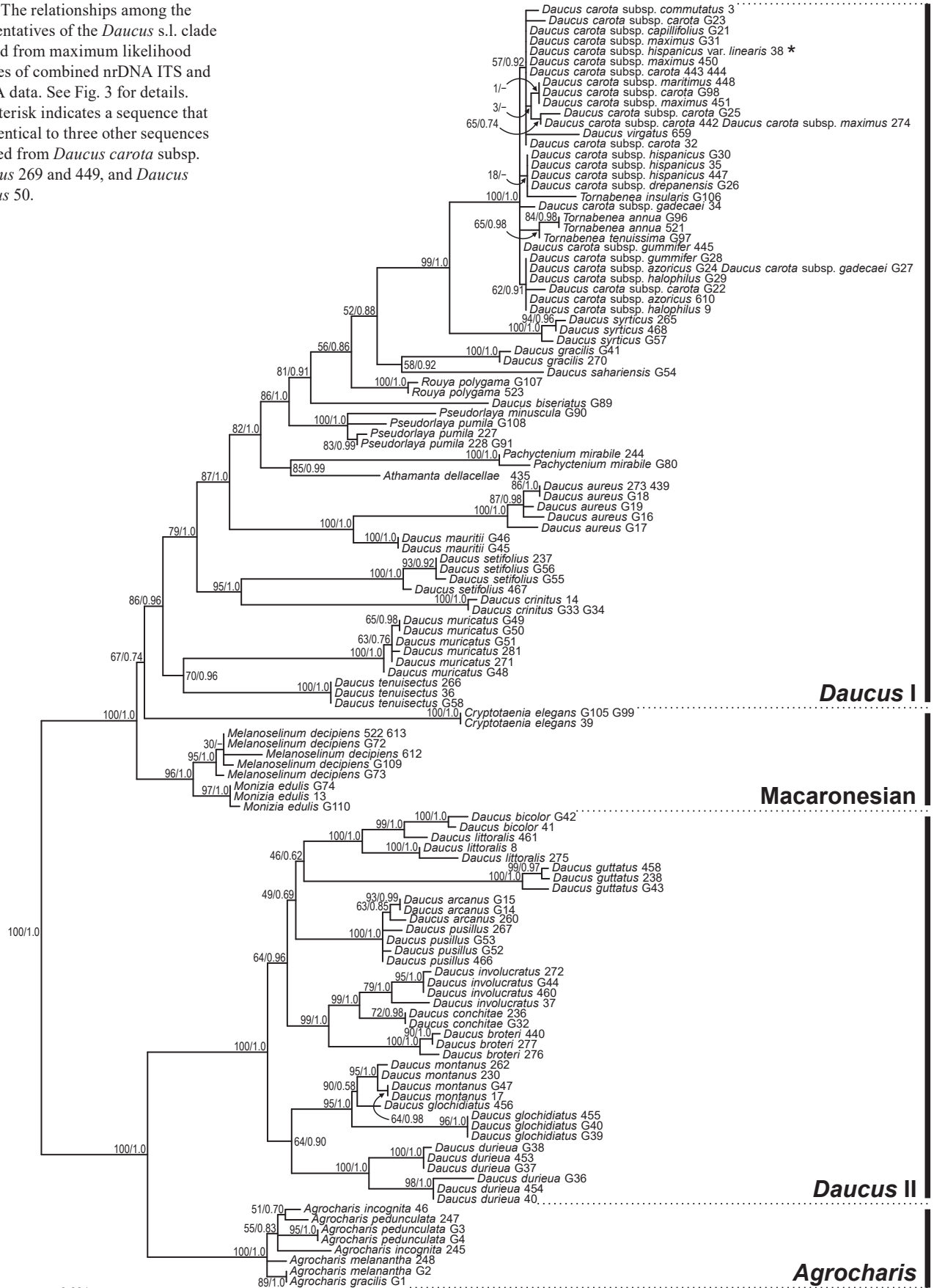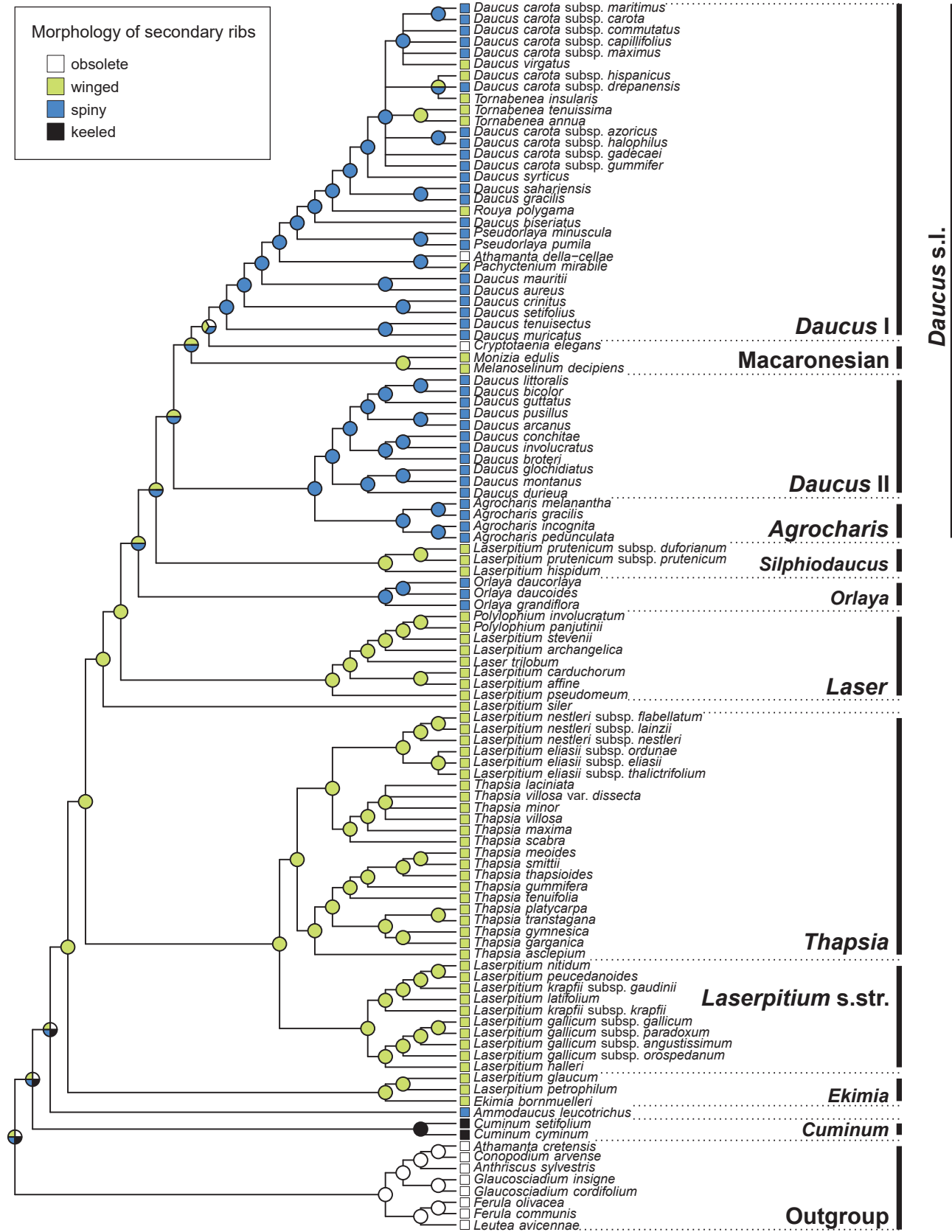
Fig. 5. Maximum parsimony reconstruction of ancestral secondary rib characters for subtribe Daucinae using an ML tree inferred from combined data. This tree was transformed into a cladogram and pruned such that each taxon was represented by one accession. The morphology of secondary ribs was coded as a multistate (unordered) character with four states: obsolete, winged, spiny, keeled.

introducing topological conflict were identified and removal of these terminals from the analyses resulted in a significant decrease in incongruence among the markers. Although these accessions had different positions in ITS and cpDNA trees, they were placed within the same major clades suggesting that this discrepancy may have resulted from reticulation among closely related taxa or from incomplete lineage sorting. Five of them are members of the *Thapsia* clade that comprises diploid and polyploid species; the latter have been recorded in the *T. villosa* L. complex and may represent allopolyploids (Avato & al., 1996). Among the species of *Daucus*, polyploids include tetraploid Australian *D. glochidiatus* (Labill.) Fisch. & al. and hexaploid South American *D. montanus* Humb. & Bonpl. (Grzebelus & al., 2011). These species are closely related in our analyses (Fig. 4).

The homoplasy of fruits with winged secondary ribs. — The fruits of umbellifers are schizocarps that, despite their overall similarity, vary with respect to both their external features, e.g., their shape and compression, the type of appendages and ribs, as well as anatomical characters, including the number and size of vittae, the shape of the endosperm, the form of fruit sclerification, etc. These characters served as basis for nearly all traditional classification systems of the family including the most influential system by Drude (1897–1898). This system had remained almost intact throughout the 20th century until the first molecular phylogenetic studies demonstrated that nearly all tribes recognized by Drude are polyphyletic (Downie & Katz-Downie, 1996; Downie & al., 1996; Plunkett & al., 1996a, b). Subsequent studies of fruit evolution based on molecular phylogenies confirmed that fruit characters in Apiaceae are homoplastic, although less so than other morphological features (Lee & al., 2001; Spalik & Downie, 2001; Spalik & al., 2001; Calviño & al., 2008).

Our study unequivocally demonstrates that umbellifers with secondary ribs projecting into wings do not constitute a single lineage: the majority of species form a grade at the base of Daucinae while some are nested within the clade of spiny-fruited taxa. Therefore, winged fruits are of limited value for the identification of monophyletic groups. Similarly, spiny fruits are homoplastic due to several reversals to winged fruits and they should be used with caution for delimiting genera. In particular, the traditional delineation of *Daucus* and *Laserpitium*, the two largest genera of Daucinae, does not correspond to the phylogenetic relationships in the subtribe.

The phylogeny and taxonomy of *Daucus*. — The cultivated carrot, *Daucus carota* subsp. *sativus*, is one of the most important crops worldwide, and wild species of *Daucus* constitute an invaluable gene pool for improving its cultivars (Grzebelus & al., 2011). A successful example for this was the introduction of resistance to carrot fly (*Chamaepsila rosae*), the most devastating pest of carrot, parsnip, parsley and celery, from wild *D. carota* subsp. *capillifolius* (Gilli) Arbizu (Ellis & al., 1993). The latter taxon was formerly recognized as a separate species but included in *D. carota* based on the analyses of phylogenomic and morphological data (Arbizu & al., 2014a). This case shows the importance of a phylogeny-based taxonomy of *Daucus* for plant breeders.

The separation of *Daucus* into two distinct subclades, subsequently named *Daucus* I and II, was inferred from the analyses of nrDNA ITS (Lee & Downie, 1999) and reassessed with cpDNA data (Lee & Downie, 2000). These studies demonstrated that the *Daucus* I subclade also includes the representatives of *Pachyctenium* and *Pseudorlaya*, while the *Daucus* II subclade is sister to *Agrocharis*. Successive analyses with extended taxonomic sampling added *Athamanta dellacellae* and two species of *Tornabenea* to the *Daucus* I subclade and indicated that this group is sister to a clade of Macaronesian endemics (Spalik & Downie, 2007). The subclades of *Daucus* received very strong support from phylogenomic studies (Arbizu & al., 2014b); however, these analyses did not include representatives of the Macaronesian endemics group and *Agrocharis*, i.e., sister groups to *Daucus* I and II subclades, respectively.

Our study reinforces these previous findings and demonstrates the need for a new taxonomic delineation of *Daucus*. However, the reconciliation of the taxonomy of *Daucus* with its phylogeny is not an easy task because the clades inferred from molecular data lack obvious morphological synapomorphies that facilitate the recognition of their members. Canonical variate analysis and hierarchical cluster analysis based on 40 morphological characters scored for representatives of both *Daucus* clades failed to separate these groups; moreover, none of the characters was diagnostic (Arbizu & al., 2014a). Similarly, the study of fruit anatomy and morphology of Daucinae did not provide any distinctive features for these two lineages (A. Wojewódzka & K. Spalik, unpub. data). In the absence of good diagnostic characters discriminating those two clades, a broad concept of *Daucus* should be considered. In order to maintain the monophyly of the genus, spiny-fruited genera *Agrocharis* and *Pseudorlaya* and the winged-fruited genera *Melanoselinum*, *Monizia*, *Pachyctenium*, *Rouya* and *Tornabenea* must be sunk into synonymy of *Daucus*.

We propose to recognize the major clades within *Daucus* s.l. as sections of the genus. The *Daucus* I clade includes the nomenclatural type of the genus and therefore constitutes sect. *Daucus*. The members of the *Daucus* II clade were traditionally placed in three sections: sect. *Daucus*, sect. *Platyspermum* (Hoffm.) DC. and sect. *Anisactis* DC. (Sáenz Laín, 1981; Heywood, 1982). The genus *Platyspermum* was described by Hoffmann (1814) based on a single species, *D. muricatus* L., which is now placed in the redefined sect. *Daucus*; sect. *Platyspermum* is, therefore, a taxonomic synonym of sect. *Daucus*. Section *Anisactis* was described by Candolle (1830) with four names: *D. brachiatus* Sieber ex DC. (= *D. glochidiatus*), *D. toriloides* DC. (= *D. montanus*), *D. montevidensis* Link ex Spreng. (= *D. pusillus* Michx.), and *D. australis* Poepp. ex DC. (= *D. montanus*). In our analyses, all these taxa are placed in the *Daucus* II clade; therefore, we formally apply the name *Daucus* sect. *Anisactis* to this clade, and designate *D. brachiatus* as the nomenclatural type of this section. The names of the two remaining sections of *Daucus* are based on the generic names *Agrocharis* and *Melanoselinum*, which are here reduced to synonymy under *Daucus*.

***Rouya*. —** This genus includes one species, *Rouya polygama* (Desf.) Coincy that was described in *Thapsia* with the phrase name indicating finely divided leaves as its diagnostic

character (Desfontaines, 1798). It occurs in littoral habitats in the southwest of the Mediterranean region (Algeria, Tunisia) and on the main islands (Corse, Sardinia). In habit it resembles some littoral species of *Daucus*, but differs in having winged rather than spiny fruits (Reduron, 2008). Our results unanimously place this species in *Daucus* and support its formal transfer to this genus. The epithet *polygamus* is not available in *Daucus* because it is occupied by *D. polygamus* Gouan (1773), an unresolved name typified by an illustration in Boccone (1674) that may represent *D. carota* subsp. *drepanensis*. However, both its locus classicus and the only extant herbarium specimen suggest that the name is synonymous with *D. bicolor* (Reduron, 2007a). With the new epithet, *rouyi*, we acknowledge the intention of Coincy, who dedicated the genus to Georges C.C. Rouy, an eminent French botanist and the principal author of the most exhaustive 14-volume *Flore de France*.

***Pseudorlaya.* —** This genus comprises two annual species, *P. pumila* (L.) Grande and *P. minuscula* (Pau ex Font Quer) Laínz, that are morphologically similar to each other (Rutherford & Jury, 2003). The genus supposedly differs from the traditionally delimited *Daucus* in having two rows of spines instead of one on secondary ridges; however, this character is variable in *P. pumila* (Lee & al., 2001). Molecular analyses confirmed the close relationship between the two species and unanimously indicated that the genus is nested within *Daucus*; therefore, Lee & Park (2014) suggested that it should be included in the latter. The names for these species in *Daucus* are therefore *D. pumilus* (L.) Hoffmanns. & Link and *D. minusculus* Pau ex Font Quer.

***Cryptotaenia, Athamanta* and *Pachyctenium.* —** Two species, *Athamanta dellacellae* and *Cryptotaenia elegans*, that are placed in the *Daucus* I clade lack spines or wings on secondary ridges. Therefore, their placement in Daucinae came as a surprise. They are incorrectly classified in their respective genera. *Athamanta dellacellae* has hairy, oblong fruits with a short beak that are superficially similar to those of its congeners; the genus *Athamanta* L., however, is now placed in Scandiceae subtribe Scandicinae (Spalik & al., 2001). The sister species to *A. dellacellae* is *Pachyctenium mirabile* and this affinity is supported by their geographic distribution: both are endemic to the northern African region of Cyrenaica (Quézel, 1978). The placement of *Pachyctenium* in *Daucus* had already been postulated based on phylogenetic analyses of morphological data (Lee & al., 2001). An endemic of the Canary Islands, *Cryptotaenia elegans* has been retained in this genus due to a lack of alternative placement rather than its similarity to distantly related congeners (Spalik & Downie, 2007). Its fruits are glabrous and have no secondary appendages, which is exceptional in Daucinae. Because spiny fruits seem to be plesiomorphic for the *Daucus* clade, Spalik & Downie (2007) speculated that in the absence of dispersing agents, like terrestrial mammals, this insular descendant of epizoochorous species has switched to gravity dispersal.

The winged-fruited endemics of Macaronesia. — *Monizia* and *Melanoselinum* are two monospecific endemics of Madeira characterised by woody stems crowned by a rosette of leaves. *Monizia* was once included in *Melanoselinum* along with the

species of *Tornabenea* (Press & Dias, 1998; Fernandes & Carvalho, 2014). The last genus includes up to six endemics of Cape Verde that are characterised by fruits with narrowly winged secondary ridges with reduced spines. Two species, *T. bischoffii* J.A.Schmidt and *T. tenuissima* (A.Chev.) A.Hansen & Sunding, have slender woody stems at flowering time that make them superficially similar to the Madeiran endemics; however, a relationship of *Tornabenea* to *Daucus* has also been suggested (Brochmann & al., 1997). The results of the molecular phylogenetic studies place the three examined species of *Tornabenea* within the *D. carota* complex. Moreover, experimental crosses between *Daucus carota* subsp. *sativus* (Hoffm.) Arcang. and *Tornabenea tenuissima* (A.Chev.) A.Hansen & Sunding successfully demonstrated that there is no crossing barrier between those species (J.-P. Reduron, unpub. data). The phylogenetic position of the remaining congeners, particularly the woody species, awaits further study.

Recent morphological studies demonstrated that *Monizia edulis* comprises four distinct morphotypes deserving taxonomic recognition at the rank of subspecies (Fernandes & Carvalho, 2014). In fact, morphological differences among those populations are similar to those among the morphological forms of *Tornabenea* that are recognized as separate species (Brochmann & al., 1997). Apparently, detailed morphological and molecular studies are required to assess the status of those insular taxa of *Daucus*.

***Agrocharis.* —** With its spiny fruits, *Agrocharis* is similar to *Daucus* (Lee & al., 2001). The genus comprises up to four species that are distributed in tropical regions of Africa (Townsend, 1989). Until it was revised by Heywood (1973, 1982), most of its species had been recognized in *Caucalis* L. Based on the molecular phylogeny of *Agrocharis* and allied genera, Lee (2002) discussed their morphological delimitation and suggested its inclusion in *Daucus* at the rank of subgenus or section, contingent upon further taxonomic and molecular sampling. Our results justify a formal transfer of *Agrocharis* to *Daucus*. We refrain from a formal recognition of *A. gracilis* Hook.f. in *Daucus* because this species was only represented by one ITS sequence that was identical to that of *A. melanantha* Hochst.

The *Silphiodaucus* clade. — Two species of *Laserpitium*— *L. prutenicum* and *L. hispidum*—form the clade sister to the *Daucus* s.l. clade. Although these species were traditionally placed in *Laserpitium* due to their winged fruits, their similarity to *Daucus* had also been noticed. Koso-Poljansky (1916) included these two species in *Daucus* as *D. prutenicus* (L.) E.H.L.Krause (= *L. prutenicum*) and *D. pilosus* (Willd.) Koso-Pol. (= *L. hispidum*) in sect. *Silphiodaucus* Koso-Pol. He also placed *L. latifolium* L. in this section, but this transfer is not supported by molecular data. With their finely divided leaves and prominent indumentum, *L. prutenicum* and *L. hispidum* resemble the species of *Daucus*, while their winged fruits are somewhat similar to those of *Laserpitium*. We propose to recognize this clade as a new genus based on the section described by Koso-Poljansky. Since this author did not indicate its type, we select *D. prutenicus* as the nomenclatural type of the section and, consequently, the genus.

The *Laser* **clade.** — This clade comprises representatives of three genera, *Laser*, *Laserpitium* and *Polylophium. Laser* is presently recognized as having one species, *L. trilobum* (Pimenov & Leonov, 1993), distributed in Europe and western Asia (Schischkin, 1951a; GBIF, 2013). The fruits of this species are used in traditional medicine and as a condiment with confirmed antimicrobial activity (Parlatan & al., 2009). The other members of this clade have rather narrow distributions. *Laserpitium stevenii* Fisch. & al., *L. affine* Ledeb. and *Polylophium panjutinii* Manden. & Schischk. are all endemics of the Caucasus (Schischkin, 1951b, c), *L. carduchorum* Hedge & Lamond and *P. involucratum* (Pall.) Boiss. are Irano-Turanian elements (Hedge & Lamond, 1972; Rechinger, 1987c), and *L. archangelica* Wulfen occurs in the southeastern part of Central Europe. This clade is supported in molecular analyses and we propose to recognize it as a single genus. Of the two available names, *Laser* Borkh. ex G.Gaertn. & al. 1799 has priority over *Polylophium* Boiss. 1844.

Thapsia. — The phylogeny of *Thapsia* has recently been examined based on ITS sequence variation, resulting in the restoration of a broad Linnaean concept of the genus (Weitzel & al., 2014). Its former segregates, *Elaeoselinum*, *Distichoselinum* and *Margotia*, as well as monospecific *Guillonea* have been sunk into synonymy. The species of *Thapsia* s.l. are characterized by relatively large fruits with broad wings. The clade encompasses species of predominantly western Mediterranean distribution, with the centre of endemism in the Iberian Peninsula. Our results support such a definition of the genus with the addition of two other Iberian endemics, *Laserpitium nestleri* and *L. eliasii*. These species have fruits with relatively small lateral wings that make their fruits externally more similar to the species of *Laserpitium* rather than to the broad-winged fruits of *Thapsia*. However, the fruits of *L. nestleri* and *L. eliasii* have distinct extravallecular vittae that are obsolete in other congeners but occur in some species of *Thapsia* s.l. (Arenas Posada & García Martín, 1993). Both species include several subspecies each (Montserrat, 2003b, c). Some of them were included in our analyses but they were represented only by single accessions. Within each of these species, there seems to be rather low sequence variation suggesting very close relationships among their inclusive taxa. More detailed morphological and molecular studies are required to ascertain whether the recognition of these subspecies is justified.

Within *Thapsia*, there are several species aggregates, including diploid, tetraploid and hexaploid forms that are morphologically hardly distinguishable. However, they are distinguishable based on chemotaxonomy and nrDNA ITS sequences, and some of these chemotypes deserve taxonomic recognition. Recently, one of these was described as a new species, *T. smittii* Simonsen & al., which is a segregate of *T. maxima* Mill. (Weitzel & al., 2014). A detailed morphological and molecular study may unravel new species. The accession from Corsica (No. 471), provisionally determined as *T. meoides*, may represent such a case based on its placement in our molecular trees, where it stands separate from presumably conspecific accessions.

The *Ekimia* **clade.** — *Ekimia bornmuelleri* was originally described in *Prangos* and later transferred to a separate genus of presumed affinity to *Prangos* (Duman & Watson, 1999). However, a detailed comparison of fruit anatomy of *Ekimia* and its presumed relatives (two species of *Prangos*, *P. ferulacea* Lindl. and *P. lophoptera* Boiss., and an Anatolian representative of *Laserpitium*, *L. petrophilum*) demonstrated that *Ekimia* shares several characters with *Laserpitium petrophilum* (Lyskov & al., 2015). Its position in Daucinae is therefore firmly established both by molecular and morphological data. The three members of the *Ekimia* clade are eastern Mediterranean elements but have allopatric distributions: *Ekimia* occurs in southwestern Turkey (Özhatay & al., 2008), *L. petrophilum* inhabits mountains of central southern Anatolia (Hedge & Lamond, 1972), while *L. glaucum* was described from the Nur (Amanus) Mountains in southeastern Turkey (Post, 1891). *Laserpitium petrophilum* was also recognized in *Polylophium* (Pimenov & Leonov, 2004), but our molecular analyses do not confirm this relationship. We propose to include *L. petrophilum* and *L. glaucum* in *Ekimia*.

Laserpitium **s.str.** — Six species, including *Laserpitium gallicum* with four subspecies, and *L. krapfii* with two subspecies, are placed in the *Laserpitium* s.str. clade. This clade is stable and supported in all molecular analyses although only in combined analyses this support is high. Moreover, it is supported by fruit morphology and anatomy: its members differ from former congeners in having non-elongated sclerified cells in the endocarp (A. Wojewódzka & K. Spalik, unpub. data). Because this clade includes the nomenclatural type of the genus, *L. gallicum*, it retains the name *Laserpitium*.

Unstable and isolated lineages. — Several species either formed separate lineages or their phylogenetic positions were unstable. These are *Ammodaucus leucotrichus*, *Laserpitium siler*, *L. pseudomeum* and the genus *Cuminum*. The accessions of *L. siler* included in this study formed a highly supported monophyletic group with a firmly established sister position to the spiny-fruited clade (i.e., *Daucus* s.l., *Silphiodaucus* and *Orlaya*). Therefore, restitution of the genus *Siler* Mill. with a single species, *Siler montanum* Crantz, is justified. This montane species is highly diverse with several infraspecific taxa that are sometimes recognized as species including *L. garganicum* (Ten.) Bertol., *L. ochridanum* Micevski and *L. zernyi* Hayek (Stevanović & al., 1993). Detailed studies are necessary to elucidate their taxonomic status.

Ammodaucus leucotrichus is an annual species distributed in northern Africa. Recently, *A. nanocarpus* (Beltrán) P.Pérez & Velasco has been recognized as a separate species. This taxon was formerly recognized as a subspecies of *A. leucotrichus* and differs from the latter in having smaller fruits; it has a Canarian-Moroccan distribution (Reyes-Betancort & al., 2007). Based on the analyses of ITS sequences only, Weitzel & al. (2014) included *A. leucotrichus* in *Thapsia*. However, our analyses suggest that the position of this species is unstable and that its inclusion in the analyses decreases the support for *Thapsia*. This may be due to the elevated rate of molecular evolution in this species as demonstrated by its long branch in the trees. Moreover, the phylogenetic analyses of cpDNA

do not support a relationship of *A. leucotrichus* to *Thapsia* but place it in an isolated lineage. We therefore propose to retain *Ammodaucus* as a separate genus.

Cuminum includes three species, two of which, *C. cyminum* and *C. setifolium*, were included in this study. The former has glabrous fruits and is widely cultivated but also sometimes occurs adventitiously, while the second has setose fruits and occurs in the wild in the Irano-Turanian region and central Asia (Rechinger, 1987a). Given their low sequence variation, these two species probably represent cultivated and wild varieties of the same species. Due to a high rate of molecular evolution, the phylogenetic position of this clade was unstable. However, it was always placed as a separate lineage among the laserpitioid clades, from which it differs in being annual and in having fruits without prominent secondary ribs. Therefore, its taxonomic status as a separate genus is undisputed.

Laserpitium pseudomeum is endemic to the montane regions of Peloponnesus, Greece (Hartvig, 1986). The species does not seem to have any distinct characters that separate it from other congeners (A. Wojewódzka & K. Spalik, unpub. data). Its isolated phylogenetic position in all analyses suggests that it deserves to be placed in a separate genus. However, more data from morphology are necessary before this genus is established.

■ NOMENCLATURAL CHANGES

The following list contains species with their new generic status. A synopsis of tribe Daucinae with all recognised genera and species is provided in Appendix 2.

Daucus L. sect. ***Daucus*** – Type: *Daucus carota* L.

Daucus annuus (Bég.) Wojew., Reduron, Banasiak & Spalik, **comb. nov.** ≡ *Tornabenea annua* Bég. in Ann. Mus. Civico Storia Nat. Giacomo Doria, ser 3, 8: 39. 1918.

Daucus dellacellae (Asch. & Barbey ex E.A.Durand & Barratte) Spalik, Banasiak & Reduron, **comb. nov.** ≡ *Athamanta dellacellae* Asch. & Barbey ex E.A.Durand & Barratte, Fl. Libyc. Prodr.: 108. 1910.

Daucus elegans (Webb ex Bolle) Spalik, Banasiak & Reduron, **comb. nov.** ≡ *Cryptotaenia elegans* Webb ex Bolle in Braun, Append. Pl. Nov. Hort. Berol. 1861: 9: 1862.

Daucus insularis (Parl. ex Webb) Spalik, Wojew., Banasiak & Reduron, **comb. nov.** ≡ *Tetrapleura insularis* Parl. ex Webb in Hooker, Niger Fl.: 131. 1849 ≡ *Tornabenea insularis* (Parl. ex Webb) Parl. in Hooker's J. Bot. Kew Gard. Misc. 2: 370. 1850.

Daucus mirabilis (Maire & Pamp.) Reduron, Banasiak & Spalik, **comb. nov.** ≡ *Pachyctenium mirabile* Maire & Pamp. in Arch. Bot. (Forlì) 12: 176. 1936.

Daucus rouyi Spalik & Reduron, **nom. nov.** ≡ *Thapsia polygama* Desf., Fl. Atlant. 1: 261, t. 75. 1798 ≡ *Rouya polygama* (Desf.) Coincy in Naturaliste, ser. 2, 15: 213. 1901, non *Daucus polygamus* Gouan, Ill. Observ. Bot.: 9. 1773.

Daucus tenuissimus (A.Chev.) Spalik, Wojew., Banasiak & Reduron, **comb. nov.** ≡ *Melanoselinum tenuissimum* A.Chev. in Bull. Mus. Natl. Hist. Nat., sér. 2. 7: 143. 1935 ≡ *Tornabenea tenuissima* (A.Chev.) A.Hansen & Sunding, Fl. Macaronesia, ed. 2, 1: 92. 1979.

Daucus sect. ***Melanoselinum*** (Hoffm.) Spalik, Wojew., Banasiak & Reduron, **comb. & stat. nov.** ≡ *Melanoselinum* Hoffm., Gen. Pl. Umbell.: 156. 1814, pro gen. – Type: *Selinum decipiens* Schrad. & J.C.Wendl. (≡ *Melanoselinum decipiens* (Schrad. & J.C.Wendl.) Hoffm.).

Daucus decipiens (Schrad. & J.C.Wendl.) Spalik, Wojew., Banasiak & Reduron, **comb. nov.** ≡ *Selinum decipiens* Schrad. & J.C. Wendl., Sert. Hannov. 3: 23, t. 13. 1797 ≡ *Melanoselinum decipiens* (Schrad. & J.C.Wendl.) Hoffm., Gen. Pl. Umbell.: 156. 1814.

Daucus edulis (Lowe) Wojew., Reduron, Banasiak & Spalik, **comb. nov.** ≡ *Monizia edulis* Lowe in Hooker's J. Bot. Kew Gard. Misc. 8: 295. 1856.

Daucus sect. ***Anisactis*** DC. – **Lectotype (designated here):** *Daucus brachiatus* Sieber ex DC. = *Daucus glochidiatus* (Labill.) Fisch., C.A.Mey. & Avé-Lall. (≡ *Scandix glochidiata* Labill.)

Daucus sect. ***Agrocharis*** (Hochst.) Spalik, Banasiak & Reduron, **comb. & stat. nov.** ≡ *Agrocharis* Hochst. in Flora 27: 19. 1844, pro gen. – Type: *Agrocharis melanantha* Hochst.

Daucus incognitus (C.Norman) Spalik, Reduron & Banasiak, **comb. nov.** ≡ *Caucalis incognita* C.Norman in J. Bot. 72: 205. 1934 ≡ *Agrocharis incognita* (C.Norman) Heywood & Jury in Launert, Fl. Zambes. 4: 573. 1978.

Daucus melananthos (Hochst.) Reduron, Spalik & Banasiak, **comb. nov.** ≡ *Agrocharis melanantha* Hochst. in Flora 27: 19. 1844.

Daucus pedunculatus (Baker f.) Banasiak, Spalik & Reduron, **comb. nov.** ≡ *Caucalis pedunculata* Baker f. in Trans. Linn. Soc. London, Bot. 4: 15. 1894 ≡ *Agrocharis pedunculata* (Baker f.) Heywood & Jury in Launert, Fl. Zambes. 4: 573. 1978.

Silphiodaucus (Koso-Pol.) Spalik, Wojew., Banasiak, Piwczyński & Reduron, **stat. nov.** ≡ *Daucus* sect. *Silphiodaucus* Koso-Pol. in Bull. Soc. Imp. Naturalistes Moscou 29: 211. 1916 – **Lectotype (designated here):** *Daucus prutenicus* (L.) E.H.L.Krause ≡ *Laserpitium prutenicum* L.

Silphiodaucus prutenicus (L.) Spalik, Wojew., Banasiak, Piwczyński & Reduron, **comb. nov.** ≡ *Laserpitium prutenicum* L., Sp. Pl.: 248. 1753.

Silphiodaucus hispidus (M.Bieb.) Spalik, Wojew., Banasiak, Piwczyński & Reduron, **comb. nov.** ≡ *Laserpitium hispidum* M.Bieb., Fl. Taur.-Caucas. 1: 221. 1808.

Laser Borkh. ex G.Gaertn., B.Mey. & Scherb., Oekon. Fl. Wetterau 1: 244, 384. 1799 – Type: *Laser trilobum* (L.) Borkh. ex G.Gaertn. B.Mey. & Scherb.

Laser affine (Ledeb.) Wojew. & Spalik, **comb. nov.** ≡ *Laserpitium affine* Ledeb., Fl. Ross. 2: 335. 1844.

Laser archangelica (Wulfen) Spalik & Wojew., **comb. nov.** ≡ *Laserpitium archangelica* Wulfen in Jacquin, Collectanea 1: 214. 1787.

Laser carduchorum (Hedge & Lamond) Wojew. & Spalik, **comb. nov.** ≡ *Laserpitium carduchorum* Hedge & Lamond in Notes Roy. Bot. Gard. Edinburgh 31(1): 76. 1971.

Laser involucratum (Pall. ex Schult.) Spalik & Wojew., **comb. nov.** ≡ *Cachrys involucrata* Pall. ex Schult. in Roemer & Schultes, Syst. Veg. 6: 447–448. 1820 ≡ *Polylophium involucratum* (Pall. ex Schult.) Boiss., Fl. Orient. 2: 1066. 1872.

Laser panjutinii (Manden. & Schischk.) Banasiak, Wojew. & Spalik, **comb. nov.** ≡ *Polylophium panjutinii* Manden. & Schischk. in Bot. Zhurn. (Moscow & Leningrad) 33: 318. 1948.

Laser stevenii (Fisch., C.A.Mey. & Trautv.) Wojew. & Spalik, **comb. nov.** ≡ *Laserpitium stevenii* Fisch., C.A.Mey. & Trautv., Index Sem. Hort. Petrop. 4: 40. 1838.

Thapsia L., Sp. Pl.: 261. 1753 – Type: *Thapsia villosa* L.

Thapsia nestleri (Soy.-Will.) Wojew., Banasiak, Reduron & Spalik, **comb. nov.** ≡ *Laserpitium nestleri* Soy.-Will., Observ. Pl. France: 87. 1828

Thapsia eliasii (Sennen & Pau) Wojew., Banasiak, Reduron & Spalik, **comb. nov.** ≡ *Laserpitium eliasii* Sennen & Pau, Bol. Soc. Aragonesa Ci. Nat. 6: 25. 1907.

Ekimia H.Duman & M.F.Watson in Edinburgh J. Bot. 56: 200. 1999 – Type: *Prangos bornmuelleri* Hub.-Mor. & Reese (≡ *Ekimia bornmuelleri* (Hub.-Mor. & Reese) H.Duman & M.F.Watson).

Ekimia petrophila (Boiss. & Heldr.) Baczyński, Banasiak & Spalik, **comb. nov.** ≡ *Laserpitium petrophilum* Boiss. & Heldr. in Boissier, Diagn. Pl. Orient., Ser. 1, 10: 46. 1849.

Ekimia glauca (Post) Banasiak, Baczyński & Spalik, **comb. nov.** ≡ *Laserpitium glaucum* Post, Pl. Post. 2: 10. 1891.

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Appendix 1. Accessions of Scandiceae subtribe Daucinae and outgroups used in this study with corresponding accession identifiers, voucher information and GenBank reference numbers. Newly generated sequences are identified with an asterisk behind the accession numbers. See Electr. Suppl.: Table S1 for detailed information on vouchers and references.

Taxon name, accession ID, voucher, GenBank accession numbers: ITS, *rpoB-trnC* spacer, *rps16* intron, *rpoC1* intron

Agrocharis gracilis Hook.f., G001, Cameroun, *Letouzey 12123* (K), AY065344/AY065345, –, –, –. *Agrocharis incognita* (C. Norman) Heywood & Jury, 0046, Kenya, DNA supplied by E. Knox (coll. 2578) via S.R. Downie, KT347648*, –, KT347774*, KT347842*; 0245, Tanzania, *Massawe, Gobbo & Mwiga 250* (E), KT347649*, –, KT347775*, –. *Agrocharis melanantha* Hochst, G002, Kenya, DNA supplied by E. Knox (coll. 2579), AF077794, –, –, –; 0248, Yemen Arab Republic, *Miller 286* (E), KT347650*, –, –, –. *Agrocharis pedunculata* (Baker f.) Heywood & Jury, G004, Tanzania, *Gereau & Kayombo 3870* (E), AY065342/AY065343, –, –, –; G003, Malawi, *Hillard Burtt 4131* (E), AF077792/AF077107, –, –, –; 0247, Tanzania, *Gereau & Kayombo 3870* (E), KT347651*, –, KT347776*, –. *Ammodaucus leucotrichus* Coss. & Durieu, 0012, Morocco, cult. Cons. bot. Mulhouse no. F98003, –, KT347642*, KT347762*, KT347831*; G114, Spain, Canary Islands, *Hansen 557* (C), KF160676, –, –, –. *Anthriscus sylvestris* (L.) Hoffm., 0083, France, *Reduron s.n.* (Reduron, pers. coll.), KT347715*, KT347743*, KT347806*, KT347879*. *Athamanta cretensis* L., 0617, Switzerland, *Eckardt 1001* (B), KT347716*, –, –, –. *Athamanta dellacellae* Asch. & Barbey ex E.A. Durand & Barratte, 0435, Libya, *Davis 50209* (E), AF073565/AF073566, –, –, KT347866*. *Conopodium arvense* (Coss.) Calest., 0630, Spain, *Reverchon 1218* (B), KT347717*, –, –, –. *Cryptotaenia elegans* Webb ex Bolle, 0039, Spain, Canary Islands, *Danton s.n.* (Reduron, pers. coll.), KT347674*, –, KT347791*, KT347860*; G099, Spain, *Kunkel 17692* (G), DQ516354, –, –, –; G105, Spain, Canary Islands, *Jarvis 617A* (MO), DQ516355, –, –, –. *Cuminum cyminum* L., G007, cult., *Lee 120* (ILL), U78362, –, U72436, –; 0339, cult. Turkey, (E 00328012), KT347713*, –, KT347804*, KT347878*; G008, HM176650, –, –, –; G009, HM176651, –, –, –; G010, HM176652, –, –, –; G011, HM176653, –, –, –; G012, HM176654, –, –, –; G013, HM176655, –, –, –. *Cuminum setifolium* (Boiss.) Koso-Pol., G006, Afghanistan, *Hedge & al. 7083* (E), AF077796/AF077111, –, –, –; 0020, Iran, *Rechinger 55742* (G), KT347714*, –, KT347805*, –. *Daucus arcanus* García-Martín & Silvestre, G014, Spain, *García & Silvestre s.n.* (E), AY065338/AY065339, –, –, –; G015, Spain (ABH 53887), JQ290118, –, –, –; 0260, Mexico, *Davis & Lightowlers 66231* (E), KT347671*, –, –, KT347858*. *Daucus aureus* Desf., G017, *Reading Univ./B.M.Exped. 1076* (RNG), HE602378, –, –, –; G016, cult., *Lee 57* (ILL), AF077784/AF077099, –, –, –; G018, Spain, *Triano & Castro s.n.* (ABH 55117), JQ290119, –, –, JQ290131; G019, Algeria, *Juan s.n.* (ABH 57786), JQ290120, –, –, –; 0273, Tunisia, *Davis & Lamond 57901* (E), KT347685*, –, –, –; 0439, Algeria, *Reverchon 203* (B), KT347686*, –, –, –. *Daucus bicolor* Sibth. & Sm., G042, Israel, *Lee 270* (ILL), AF077791/AF077106, –, –, –; 0041, Israel, *Cohen s.n.* (WA), KT347652*, –, KT347777*, KT347843*. *Daucus biseriatus* Murb., G089, Algeria, cult. Univ. of California no. C-958, AY065328/AY065329, –, –, –. *Daucus broteri* Ten., 0276, Turkey, *Coode & Jones 2575*

Appendix 1. Continued.

(E), KT347653*, –, KT347778*, KT347844*; 0277, Turkey, *Alava & Bocquet 4988* (E), KT347654*, –, KT347779*, KT347845*; 0440, Turkey, *Bornmüller & Bornmüller 14160* (B), KT347655*, –, –, KT347846*. **Daucus carota** subsp. **azoricus** Franco, G024, Morocco (RNG), AY065312/AY065313, –, –, –; 0610, Portugal, Azores, *Danton s.n.* (Cons. bot. Mulhouse no. 08-092A, Reduron, pers. coll.), KT347693*, –, –, KT347869*. **Daucus carota** subsp. **capillifolius** (Gilli) Arbizu, G021, Libya (E), AY065318/AY065319, –, –, –. **Daucus carota** L. subsp. **carota**, G098, Germany, *Downie 164* (ILL), U27589/U30315, –, U36290, –; G022, *Jury 17848* (RNG), HE602376, –, –, –; G025, Kazakhstan, *Lee 167* (ILL), AF077779, –, –, –; G023, AY552527, –, –, –; 0032, France, *Reduron s.n.* (Cons. bot. Mulhouse no. 08-114A, Reduron, pers. coll.), KT347694*, –, KT347798*, KT347870*; 0443, Greece, *Böhling 10118* (B), KT347695*, –, –, KT347871*; 0444, Romania, *Paucă 2255* (B), KT347696*, –, –, KT347872*; 0442, Iran, *Wojewódzka & Zych s.n.* (WABG), FJ415158, –, –, –. **Daucus carota** subsp. **commutatus** (Paol.) Thell., 0003, France, *Bocquet 16283* (G), KT347697*, –, KT347799*, KT347873*. **Daucus carota** subsp. **drepanensis** (Arcang.) Heywood, G026, Portugal, AY065314/AY065315, –, –, –. **Daucus carota** subsp. **gadecaei** (Rouy & Camus) Heywood, G027, France, cult. Univ. of Reading, AY065316/AY065317, –, –, –; 0034, France, *Reduron s.n.* (Reduron, pers. coll.), KT347698*, –, KT347800*, –. **Daucus carota** subsp. **gummifer** Hook.f., G028, cult. UIUC from seeds from France, *Lee 47* (ILL), AF077782/AF077097, –, –, –; 0445, France, *Kohlmeyer 1448* (B), KT347699*, –, –, KT347874*. **Daucus carota** subsp. **halophilus** (Brot.) Okeke, G029, cult. UIUC from seeds from France, *Lee 81* (ILL), AF077781/AF077096, –, –, –; 0009, Portugal, cult. Cons. bot. Mulhouse no. 9305*, KT347700*, –, KT347801*, KT347875*. **Daucus carota** subsp. **hispanicus** (Gouan) Thell., G030, Spain, *Llorenç Saéz s.n.* (ABH 53270), JQ290121, –, –, JQ290132; 0035, France, *Reduron, Dumet & Le Clerc s.n.* (Reduron, pers. coll.), KT347701*, –, –, –; 0447, Spain, *Benedi & Molero 28* (B), KT347703*, –, –, –. **Daucus carota** subsp. **hispanicus** var. **linearis** Reduron, 0038, France, *Reduron s.n.* (Reduron, pers. coll.), KT347702*, –, –, –. **Daucus carota** subsp. **maritimus** (Lam.) Batt., 0448, France, *Mory s.n.* (B), KT347704*, –, –, KT347876*. **Daucus carota** subsp. **maximus** (Desf.) Ball., G031, cult., *Lee 64* (ILL), AF077778/AF077093, –, –, –; 0269, Algeria, *Davis 52992* (E), KT347705*, –, –, –; 0274, Turkey, *Davis 47038* (E), KT347706*, –, –, –; 0449, Turkey, *Kehl s.n.* (B), KT347707*, –, –, –; 0450, Algeria, *Reverchon 45* (B), KT347708*, –, –, –; 0451, Greece, *Shay 80-394* (B), KT347709*, –, –, –. **Daucus conchitae** Greuter, G032, Turkey, *Jury & Warren 366* (RNG), AY065332/AY065333, –, –, –; 0236, Turkey, *Gardner, Knees, Barker-Mill & Layman 8120* (E), KT347656*, –, KT347780*, KT347847*. **Daucus crinitus** Desf., G033, *Ait Lafkih & al. 70* (RNG), HE602443, –, –, –; G034, Spain, *Martínez-Flores s.n.* (ABH 52065), JQ290122, –, –, –; 0014, cult. UIUC from seeds from Portugal, *Lee 49* (ILL), KT347675*, –, KT347792*, KT347861*. **Daucus durieua** Lange, G037, *Díez 3482/94* (RNG), HE602377, –, –, –; G036, Israel, cult. UIUC, *Lee 271* (ILL), AF077790/AF077105, –, –, –; G038, Spain, *Navarro Reyes s.n.* (ABH 53919), JQ290123, –, –, JQ290133; 0040, Israel, *Cohen s.n.* (WA), KT347657*, –, KT347781*, KT347848*; 0453, Spain, *Valdés & al. 256/88* (B), KT347658*, –, –, KT347849*; 0454, Israel, *Danin s.n.* (B), KT347659*, –, –, –. **Daucus glochidiatus** (Labill.) Fisch., C.A.Mey. & Avé-Lall., G039, New Zealand (AK 297601), EU331132, –, –, –; G040, Australia, New South Wales, *Lepschi 449* (CANB), AY065340/AY065341, –, –, –; 0456, Australia, New South Wales, *Eichler 22856* (B), KT347660*, –, KT347851*. 0455, Australia, North West Plains, *Blaylock 938* (KRAM), FJ415160*, KT347740*, KT347782*, KT347850*. **Daucus gracilis** Steinh., G041, Algeria, *Davis 52098* (RNG), AY065322/AY065323, –, –, –; 0270, Algeria, *Davis 52098* (E), KT347687*, –, –, –. **Daucus guttatus** Sm., G043, Greece, *Jury & Warren 209* (RNG), AY065336/AY065337, –, –, –; 0238, Greece, *Gardner, Knees & Amor 8226* (E), KT347661*, –, KT347783*, –; 0458, Greece, *Risse 2101* (B), KT347662*, –, KT347784*, KT347852*. **Daucus involucratus** Sm., G044, Greece, *Bowen 8896* (E), AY065334/AY065335, –, –, –; 0037, Greece, *Charpin 25294* (G), KT347663*, –, KT347785*, KT347853*; 0272, Turkey, *Davis 41352* (E), KT347664*, –, KT347786*, –; 0460, Greece, *Greuter & Matthäs 19630* (B), KT347665*, –, KT347787*, KT347854*. **Daucus littoralis** Sm., 0008, Israel, cult. Cons. bot. Mulhouse no. 99080*, *Reduron s.n.* (Reduron, pers. coll.), KT347666*, –, KT347788*, KT347855*; 0275, Egypt, *Mashaly s.n.* (E), KT347667*, –, –, –; 0461, Iran, *Wojewódzka & Zych s.n.* (WABG), FJ415159*, KT347741*, –, KT347856*. **Daucus mauritii** Sennen, G045, Morocco, *Crespo & al. s.n.* (ABH 55659), JQ290124, –, –, JQ290134; G046, Morocco, *Crespo & al. s.n.* (ABH 55656), JQ290125, –, –, –. **Daucus montanus** Humb. & Bonpl., G047, Argentina, cult. Botanical Garden of the University of California, Berkeley 94.0563, AF077789/AF077104, –, –, –; 0017, Chile, cult. Cons. bot. Mulhouse no. 98050, *Reduron s.n.* (Reduron, pers. coll.), KT347668*, –, KT347789*, KT347857*; 0230, Mexico, *Gardner & Knees 5108* (E), KT347669*, –, –, –; 0262, Peru, *Hutchinson 1659* (E), KT347670*, –, –, –. **Daucus muricatus** L., G049, *Jury 16748* (RNG), HE602379, –, –, –; G048, cult. UIUC, *Lee 36* (ILL), AF077785/AF077100, –, –, –; G050, Morocco, *Crespo & al. s.n.* (ABH 55634), JQ290126, –, –, JQ290135; G051, Spain, *Meneses Sores s.n.* (ABH 53894), JQ290127, –, –, JQ290136; 0271, Algeria, *Davis 58080* (E), KT347676*, –, KT347793*, KT347862*; 0281, Portugal, *Gibbs 69.148* (E), KT347677*, –, –, KT347863*. **Daucus pusillus** Michx., G052, cult. Botanical Garden of the University of California, Berkeley 92.0891, AF077788/AF077103, –, –, AF123729; G053, Argentina, *Camadro s.n.* (ABH 57683), JQ290128, –, –, JQ290137; 0267, USA, California, *Thorne, Wallace & Haefs 48769* (E), KT347672*, –, –, –; 0466, Argentina, *Leuenberger & Arroyo 3867* (B), KT347673*, –, KT347790*, KT347859*. **Daucus sahariensis** Murb., G054, Algeria, *JGR & AA 129-108* (RNG), AY065320/AY065321, –, –, –. **Daucus setifolius** Desf., G055, *Jury 17514* (RNG), HE602375, –, –, –; G056, Spain, *Aparicio s.n.* (ABH 53906), JQ290129, –, –, JQ290138; 0237, Spain, *Gardner, Knees & Read 4837* (E), KT347678*, –, KT347794*, –; 0467, Algeria, *Reverchon 234* (B), KT347679*, –, –, KT347864*. **Daucus syrticus** Murb., G057, Libya (RNG), AY065324/AY065325, –, –, –; 0265, Libya, *Davis 49612* (E), KT347688*, –, –, 0468, Libya, *Bornmüller 711* (B), KT347689*, –, KT347797*, KT347867*. **Daucus tenuisectus** Coss. ex Batt., G058, Morocco, *Jury & Springate s.n.* (RNG), AY065326/AY065327, –, –, –; 0266, Morocco, *Balls 2504* (E), KT347681*, –, KT347795*, –; 0036, Morocco, *Charpin 27029* (G; Reduron, pers. coll.), KT347680*, –, –, –. **Daucus virgatus** (Poir.) Maire, 0050, Algeria, *Maire (Duffour 4456)* (G), KT347710*, –, –, –; 0659, Algeria, *Véla s.n.* (Reduron, pers. coll.), KT347711*, –, KT347802*, –. **Ekimia bornmuelleri** (Hub.-Mor. & Reese) H. Duman & M.F. Watson, 0655, Turkey, *Duman & Karaveliogullari 5071* (E), KT347640*, –, –, KT347810*. **Ferula communis** L., 0195, Spain, *Sánchez-Gómez s.n.* (Univ. of Zaragoza, Spain), DQ379392, KJ660616, KJ660477, KJ698369. **Ferula olivacea** (Diels) H. Wolff, 0363, China, *Chamberlain, Ming, Yuan & al. 229* (E), KJ660802, KJ660688, KJ660547, KJ660382. **Glauocosciadium cordifolium** (Boiss.) B.L. Burtt & P.H. Davis, 0221, Cyprus, cult. Cons. bot. Mulhouse no. 98112, *Reduron s.n.* (WA), DQ379459, KJ660745, KJ660458, KJ660439. **Glauoscosciadium insigne** (Pimenov & Maassoumi) Spalik & S.R. Downie, 0074, Iran, *Mozaffarian 77099* (TARI), KJ660839, KJ660746, KJ660405, KJ660440. **Laser trilobum** (L.) Borkh. ex G. Gaertn., B. Mey. & Scherb., G061, Azerbaijan, cult. Moscow State University Botanical Garden, Russia, *Pimenov & al. s.n.* (MW), AF008644/AF009123, –, –, AF123735; 0611, France, cult. Cons. bot. Mulhouse no. 98020B, *Reduron s.n.* (Reduron, pers. coll.), KT347638*, –, KT347744*, KT347807*; G112, Jelitto Staudensamen GmbH, Schwarmstedt, Germany, 2011, Lot-No. 70016019AA1AA0s. LA017, KF160678, –, –, –. **Laserpitium affine** Ledeb., G062, Georgia, *Pimenov 1454* (MW), JQ305145, –, –, –; 0480, Georgia, *Shreter & Pimenov 394* (LE), FJ415151*, KT347718*, KT347745*, KT347808*. **Laserpitium archangelica** Wulfen, 0481, Slovenia, *Mayer 63416* (KRAM), FJ415153, KJ832093, KJ832098, KJ832103. **Laserpitium carduchorum** Hedge & Lamond, 0482, Turkey, *Davis & Polunin 24567* (E 00042009), FJ415116*, –, –, –; 0483, Turkey, *Davis & Polunin 22551* (E), FJ415117, KJ832094, KJ832099, KJ832104. **Laserpitium eliasii** Sennen & Pau subsp. **eliasii**, 0484, Spain, *Alejandre s.n.* (VIT 27070), FJ415118*, –, –, KT347823*. **Laserpitium eliasii** subsp. **ordunae** P. Monts., 0485, Spain, *Montserrat s.n.* (JACA 733483), FJ415119, KJ832095, KJ832100, KJ832105. **Laserpitium eliasii** subsp. **thalictrifolium** (Samp.) P. Monts., 0486, Spain, *Rico s.n.* (JACA ex SALA 41460), FJ415120*, KT347727*, KT347755*, KT347824*. **Laserpitium gallicum** L. subsp. **gallicum**, 0487, France, *Reduron s.n.* (Reduron, pers. coll.), FJ415128*, KT347722*, KT347749*, KT347816*. **Laserpitium gallicum** subsp. **angustissimum** (Willd.) Lange, 0488, Morocco, *Jury & al. 17635* (E 00065531), FJ415129*, KT347723*, KT347750*, KT347817*. **Laserpitium gallicum** subsp. **orospedanum** M.B. Crespo & al., 0489, Spain, *Crespo & al. s.n.* (isotype, ABH 43500), FJ415126*, KT347724*, KT347751*, KT347818*. **Laserpitium gallicum** subsp. **paradoxum** (O. Bolòs & Font Quer) P. Monts., 0490, Spain, *Viñas s.n.* (HGI 15292), FJ415127*, KT347725*, KT347752*, KT347819*. **Laserpitium glaucum** Post, 0491, Turkey, *Darrah 552* (E 00042002), FJ415115*, –, –, –. **Laserpitium halleri** Crantz, 0493, France, *Reverchon s.n.* (KRAM), FJ415130*, –, –, –. **Laserpitium hispidum** M. Bieb., G064, Russia, Krasnodar, *Pimenov 316* (MW), JQ305142, –, –, –; G065, Turkey, *Pimenov & Kljuykov s.n.* (MW), JQ305143, –, –, –; G066, Russia, Krasnodar, *Ostroumova 19* (MW), AF077898, –, –, –; 0494, Turkey, *Davis, Coode & Yaltirik 38795* (E 00042016), FJ415154*, –, KT347772*, –; 0495, Ukraine, Crimea, *Werblan-Jakubiec & al. s.n.* (WABG), FJ415155*, –, –, –. **Laserpitium krapfii** Crantz subsp. **krapfii**, 0496, Romania, *Nyárády 976* (WA), FJ415124*, –, –, KT347821*. **Laserpitium krapfii** subsp. **gaudinii** (Moretti) Thell., 0497, Italy, *Charpin s.n.* (G), FJ415125*, KT347726*, KT347753*, KT347820*. **Laserpitium latifolium** L., 0498, Poland, *Sudnik s.n.* (WA), FJ415131*, –, KT347754*, KT347822*. **Laserpitium nestleri** Soy.-Will. subsp. **nestleri**, 0501, Italy, *Fabregat & Udias 2007* (BCC), FJ415123, KJ832097, KJ832102, KJ832107. **Laserpitium nestleri** subsp. **flabellatum** var. **tensinum** P. Monts., 0505,

Appendix 1. Continued.

Spain, *Montserrat s.n.* (JACA R265475), FJ415121*, KT347728*, KT347756*, KT347825*. **Laserpitium nestleri** subsp. **lainzii** P. Monts., 0506, Spain, *Garcia s.n.* (JACA 466085), FJ415122*, KT347729*, KT347757*, KT347826*. **Laserpitium nitidum** Zanted., 0507, Italy, *Cobau 2715* (KRA), FJ415132*, –, –, –. **Laserpitium petrophilum** Boiss. & Heldr., 0508, Turkey, *Southam s.n.* (RNG), FJ415114*, –, –, –; 0509, Turkey, *Davis 18412* (E), KT347641*, –, KT347747*, KT347811*; G067, Turkey, *Spalik & Żochowska s.n.* (WA), AF073567, –, –, –; G085, Turkey, *Eren s.n.* (B), JQ305150, –, –, –; G086, Turkey, *Davis 18412* (E), JQ305151, –, –, –; G087, Turkey, *Hartvig 23613* (EGE), JQ305152, –, –, –; G088, Turkey, *Kotschy 186/242* (MW), JQ305153/JQ305154, –, –, –. **Laserpitium peucedanoides** L., 0510, Montenegro, *Zarzycki s.n.* (KRAM), FJ415133*, –, –, –. **Laserpitium prutenicum** L. subsp. **prutenicum**, 0649, Poland, *Nowak s.n.* (WA), AF336374, –, KT347773*, KT347841*; G069, Russia, *Maiorov s.n.* (MW), JQ305144, –, –, –. **Laserpitium prutenicum** subsp. **duforianum** (Rouy & Camus) Braun-Blanq., 0511, Spain, *Montserrat s.n.* (JACA 701083), FJ415156*, –, –, –. **Laserpitium pseudomeum** Orph., Heldr. & Sart. ex Boiss., 0513, Greece, *Gustavsson 9672* (G), FJ415134*, –, KT347748*, KT347812*. **Laserpitium siler** L., 0515, Italy, *Davis & Sutton D 65739* (E), FJ415111*, –, –, KT347813*; 0516, Spain, *Gardner & Gardner 781* (E 00043183), FJ415112*, KT347720*, –, KT347814*; 0517, Montenegro, *Gardner & Gardner 2455* (E 00043177), FJ415113*, KT347721*, –, KT347815*; G070, Germany, cult. Johannes Gutenberg University (no. 1112), *Downie 71* (ILL), U30528/U30529, –, U36296, AF123734; G113, Jelitto Staudensamen GmbH, Schwarmstedt, Germany, 2011, Lot-No. 8001018100g. LA021, *Simonsen 2013-09* (C), KF160679, –, –, –. **Laserpitium stevenii** Fisch. & Trautv., 0518, Georgia, *Muibaniani & al. s.n.* (LE), FJ415152*, KT347719*, KT347746*, KT347809*; G071, Georgia, *Pimenov 886* (MW), JQ305146, –, –, –. **Leutea avicennae** Mozaff., 0067, Iran, *Mozaffarian 65041* (TARI), KJ660830, KJ660736, KJ660449, KJ660430. **Melanoselinum decipiens** (Schrad. & J.C. Wendl.) Hoffm., G109, cult. Botanical Garden, Copenhagen, Denmark, *Hansen 13407* (C), KF160680, –, –, –; 0522, Portugal, Madeira, cult. Cons. bot. Mulhouse no. 2027, *Reduron s.n.* (Reduron, pers. coll.), FJ415161, –, –, –; 0612, Seeds from Botanischer Garten der Universität Kiel, Univ. of Warsaw Bot. Garden nos. KS 124/97, 163/245 (WA), KT347682*, –, –, –; 0613, Portugal, Madeira, cult. University of Oslo Botanical Garden, seeds no. 447, garden no. 257, KT347683*, –, –, –; G072, Portugal, Madeira, cult. University of Reading, England, APE 605, plant A EF016755, –, –, AF123737; G073, Portugal, Madeira, cult. University of Reading, England, APE 605, plant B, EF016756, –, –, AF123738. **Monizia edulis** Lowe, 0013, Portugal, Madeira, cult. Cons. bot. Mulhouse no. 98141, KT347684*, –, KT347796*, KT347865*; G074, Madeira, cult. Madeira Botanic Garden, *F. & O. Baets 08655* (E), AF073569, –, –, AF123739; G110, Portugal, Madeira, *Hansen 2478* (C), KF160681, –, –, –. **Orlaya daucoides** (L.) Greuter, 0229, Greece, *Gardner, Knees & Amor 8225* (E), KT347643*, –, –, –; 0263, Italy, *Davis & Sutton 65766* (E), KT347644*, –, –, –; 0264, Spain, *Galiano, Gibbs, Silvestre & Valdes 1284.69* (E), KT347645*, –, –, –; G075, cult. UIUC form seeds from Hungarian Academy of Sciences, Vácrátót, *Lee 7* (ILL), AF077797, –, –, AF123733; G079, Germany, cult., *Downie 20* (ILL), U30526/U30527, –, –, –; G111, Greece, *Strid 42072* (C), KF160682, –, –, –. **Orlaya daucorlaya** Murb., G076, Macedonia, *Edmonston 27* (E), AF077798/AF077113, –, –, –. **Orlaya grandiflora** (L.) Hoffm., 0258, Slovakia, *Smejkal & Vicherek 1544* (E), KT347646*, –, KT347771*, KT347840*; 0259, Italy, *Davis & Sutton 65886* (E), KT347647*, –, –, –; G077, France, cult. Jardin botanique de Caen (no. 1474), *Downie 309* (ILL), U30524/U30525, –, –, –; G078, Spain, *Lopes & Javier s.n.* (ABH 55673), JQ290130, –, –, –. **Pachyctenium mirabile** Maire & Pamp., 0244, Libya, *Davis 50249* (E), KT347690*, –, –, –; G080, Libya, *Davis 50249* (E), AF077787/AF077102, –, –, –. **Polylophium involucratum** (Pall. ex Schult.) Boiss., 0395, Iran, *Klein 3699* (W 06547), KT347639*, –, –, –; G081, Iran, *Mozaffarian s.n.* (TARI), JQ305147, –, –, –. **Polylophium panjutinii** Manden. & Schischk., G082, Georgia, *Daushkevich. s.n.* (MW), AF008645/AF009124, –, –, AF123736; G083, Georgia, *Arzinba s.n.* (AA), JQ305148, –, –, –; G084, Georgia, *Ostroumova s.n.* (MW), JQ305149, –, –, –. **Pseudorlaya minuscula** (Pau ex Font Quer) Laínz, G090, Spain (RNG), AY065330/AY065331, –, –, –. **Pseudorlaya pumila** (L.) Grande, G091, cult. University of Oldenburg Botanic Garden (no. 20), *Downie 138* (ILL), U30522, –, –, –; 0227, Algeria, *Davis 51712* (E), KT347691*, –, –, –; 0228, Tunisia, *Davis 56740b* (E), KT347692*, –, –, –; G108, Greece, *Strid 38276* (C), KF160683, –, –, –. **Rouya polygama** (Desf.) Coincy, 0523, France, cult. Cons. bot. Mulhouse no. 99143, 9 September 2000, FJ415157, –, –, KT347868*; G107, Italy, *Greuter 9736* (C), KF160684, –, –, –. **Thapsia asclepium** L., G121, Greece, *Strid 39066* (C), KF160685, –, –, –; 0470, Italy, *Optima Iter VIII* (RNG), FJ415135, –, –, –. **Thapsia garganica** L., G092, Italy, AJ007930, –, –, –; G128, Greece, *Strid 26821* (C), KF160688, –, –, –; 0525, Algeria, *Davis 53034* (E), FJ415143*, KT347730*, KT347758*, KT347827*; 0526, Tunisia, *Davis & Lamond D 56827* (E), FJ415144*, KT347731*, KT347759*, KT347828*; 0527, Greece, *Edmonson & McClintock E 2579* (E), FJ415145*, KT347732*, KT347760*, KT347829*. **Thapsia gummifera** (Desf.) Spreng., 0520, Portugal, cult. Cons. bot. Mulhouse no. 9309, FJ415139, KT347733*, KT347761*, KT347830*. **Thapsia gymnesica** Rosselló & A. Pujadas, G115, Spain, *Smitt 94-01* (C), KF160693, –, –, –. **Thapsia laciniata** Rouy, G132, France, *Smitt 90-01* (C), KF160694, –, –, –; G133, Spain, *Smitt 87-12* (C), KF160696, –, –, –. **Thapsia maxima** Mill., G122, Spain, *Smitt 87-31* (C), KF160698, –, –, –; G123, Portugal, *Smitt 88-19* (C), KF160699, –, –, –. **Thapsia meoides** Guss., 0472, Morocco, *Jury s.n.* (RNG), FJ415137*, –, –, –; 0473, Morocco, *Davis 54321* (E), FJ415138*, –, KT347763*, KT347832*; G059, *Jury & Upson 20572* (RNG), HE602456, –, –, –. **Thapsia minor** Hoffmanns. & Link, G128, Portugal, *Smitt 81-v-10* (C), KF160701, –, –, –; G129, Portugal, *Smitt 88-17* (C), KF160702, –, –, –; G130, Portugal, *Smitt 88-25* (C), KF160703, –, –, –; G131, Portugal, *Smitt 88-30* (C), KF160704, –, –, –. **Thapsia platycarpa** Pomel, G093, *Jury 15837* (RNG), HE602373, –, –, –. **Thapsia scabra** (Cav.) Simonsen, Rønsted, Weitzel & Spalik, 0479, Spain, *Aran & Tohá s.n.* (VAL 118242), FJ415150, –, KT347764*, KT347833*. **Thapsia smittii** Simonsen, Rønsted, Weitzel & Spalik, G119, Morocco, *Montserrat FC-9169* (C), KF160706, –, –, –; G120, Portugal, *Smitt 81-v-11* (C), KF160708, –, –, –. **Thapsia tenuifolia** Lag., 0469, Portugal, cult. Cons. bot. Mulhouse no. 9372, FJ415140*, KT347735*, KT347766*, KT347835*. **Thapsia thapsioides** (Desf.) Simonsen, Rønsted, Weitzel & Spalik, 0477, Tunisia, *Davis & Lamond D 57768* (E 00040997), FJ415141*, KT347736*, KT347767*, KT347836*; 0478, Algeria, *Davis 53419* (E), FJ415142*, KT347737*, KT347768*, KT347837*. **Thapsia transtagana** Brot., 0524, Morocco, *Davis & Davis D 48431* (E), FJ415146*, KT347738*, KT347769*, KT347838*; G094, *Jury 16325* (RNG), HE602372, –, –, –; G116, Portugal, *Smitt 81-t-16* (C), KF160714, –, –, –; G117, Spain, *Smitt 87-15* (C), KF160719, –, –, –. **Thapsia villosa** L., 0530, Portugal, *Bowen s.n.* (RNG), FJ415149*, –, –, –; G095, *Lambinon 94/Ma/350* (RNG), HE602371, –, –, –; G124, Portugal, *Smitt 88-33* (C), KF160723, –, –, –; G125, Portugal, *Smitt 88-32* (C), KF160726, –, –, –; G126, Spain, *Smitt 87-11* (C), KF160730, –, –, –; G127, Portugal, *Weitzel 2011-10* (C), KF160734, –, –, –. **Thapsia villosa** var. **dissecta** Boiss., 0528, Morocco, *Davis & King D 68336* (E), FJ415147*, KT347739*, KT347770*, KT347839*; 0529, Spain, *Davis 61691* (E 00042013), FJ415148*, –, –, –. **Thapsia** sp., 0471, France, Corsica, cult. Cons. bot. Mulhouse no. 98138, FJ415136*, KT347734*, KT347765*, KT347834*. **Tornabenea annua** Bég., 0521, Cape Verde Islands, cult. Cons. bot. Mulhouse no. 99145, KT347712*, KT347742*, KT347803*, KT347877*; G096, Cape Verde Islands, *Hildenbrand, Meyer & Reduron 01007* (ILL, Reduron, pers. coll.), DQ516356, –, –, –. **Tornabenea insularis** (Parl. ex Webb.) Parl., G106, cult. Botanical Garden, Copenhagen, Denmark, *Hansen 53* (C), KF160739, –, –, –. **Tornabenea tenuissima** (A. Chev.) A. Hansen & Sunding, G097, Cape Verde Islands, *Hildenbrand, Meyer & Reduron 2036* (ILL, Reduron, pers. coll.), DQ516357, –, –, –.

Appendix 2. Synopsis of tribe Scandiceae subtribe Daucinae. The arrangement of genera and species reflects their phylogenetic position in the combined-data tree (see Figs. 3 and 4). For the species that have changed their generic position, their previous (commonly used) name is also given. Species, which were not checked for molecular markers, are indicated with asterisks.

Daucus L.

    sect. ***Daucus***: *D. carota* L., *D. annuus* (Bég.) Wojew. & al. [≡ *Tornabenea annua* Bég.], *D. insularis* (Parl. ex Webb) Spalik & al. [≡ *Tornabenea insularis* (Parl. ex Webb) Parl.], *D. tenuissimus* (A.Chev.) Spalik & al. [≡ *Tornabenea tenuissima* (A.Chev.) A.Hansen & Sunding], *D. virgatus* (Poir.) Maire, *D. syrticus* Murb., *D. gracilis* Steinh., *D. sahariensis* Murb., *D. rouyi* Spalik & Reduron [≡ *Rouya polygama* (Desf.) Coincy], *D. biseriatus* Murb., *D. pumilus* (L.) Hoffmanns. & Link [≡ *Pseudorlaya pumila* (L.) Grande], *D. minusculus* Pau ex Font Quer [≡ *Pseudorlaya minuscula* (Pau ex Font Quer) Laínz], *D. mirabilis* (Maire & Pamp.) Reduron & al. [≡ *Pachyctenium mirabile* Maire & Pamp.], *D. dellacellae* (E.A.Durand & Barratte) Spalik & al. [≡ *Athamanta dellacellae* E.A.Durand & Barratte], *D. aureus* Desf., *D. mauritii* Sennen, *D. setifolius* Desf., *D. crinitus* Desf., *D. muricatus* L., *D. tenuisectus* Coss. ex Batt., *D. elegans* (Webb ex Bolle) Spalik & al. [≡ *Cryptotaenia elegans* Webb ex Bolle];

    sect. ***Melanoselinum*** (Hoffm.) Spalik & al.: *D. decipiens* (Schrad. & J.C.Wendl.) Spalik & al. [≡ *Melanoselinum decipiens* (Schrad. & J.C.Wendl.) Hoffm.], *D. edulis* (Lowe) Wojew. & al. (≡ *Monizia edulis* Lowe);

    sect. ***Anisactis*** DC.: *D. bicolor* Sibth. & Sm., *D. littoralis* Sm., *D. guttatus* Sm., *D. arcanus* García-Martín & Silvestre, *D. pusillus* Michx., *D. involucratus* Sm., *D. conchitae* Greuter, *D. broteri* Ten., *D. montanus* Humb. & Bonpl., *D. glochidiatus* (Labill.) Fisch., C.A.Mey. & Avé-Lall., *D. durieua* Lange;

    sect. ***Agrocharis*** (Hochst.) Spalik & al. : *D. incognitus* (C.Norman) Spalik & al. [≡ *Agrocharis incognita* (C.Norman) Heywood & Jury], *D. melananthos* (Hochst.) Reduron & al. [≡ *Agrocharis melanantha* Hochst.], *D. pedunculatus* (Baker f.) Banasiak & al. [≡ *Agrocharis pedunculata* (Baker f.) Heywood & Jury];

    Incertae sedis: **Tornabenea bischoffii* J.A.Schmidt, **T. humilis* Lobin & K.H.Schmidt, **T. ribeirensis* K.H.Schmidt & Lobin, *Agrocharis gracilis* Hook.f., **Daucus jordanicus* Post, **D. microscias* Bornm. & Gauba, **D. reboudii* Coss.

Silphiodaucus (Koso-Pol.) Spalik & al.

    S. prutenicus (L.) Spalik & al. [≡ *Laserpitium prutenicum* L.], *S. hispidus* (M.Bieb.) Spalik & al. [≡ *Laserpitium hispidum* M.Bieb.].

Orlaya Hoffm.

    O. daucoides (L.) Greuter, *O. daucorlaya* Murb., *O. grandiflora* (L.) Hoffm.,

    Laser Borkh. ex G.Gaertn. & al.

    L. panjutinii (Manden. & Schischk.) Banasiak & al. [≡ *Polylophium panjutinii* Manden. & Schischk.], *L. involucratum* (Pall. ex Schult.) Spalik & Wojew. [≡ *Polylophium involucratum* (Pall. ex Schult.) Boiss.], *L. stevenii* (Fisch., C.A.Mey. & Trautv.) Wojew. & Spalik [≡ *Laserpitium stevenii* Fisch., C.A.Mey. & Trautv.], *L. archangelica* (Wulfen) Spalik & Wojew. [≡ *Laserpitium archangelica* Wulfen], *L. trilobum* (L.) Borkh. ex G.Gaertn. & al., *L. carduchorum* (Hedge & Lamond) Wojew. & Spalik [≡ *Laserpitium carduchorum* Hedge & Lamond], *L. affine* (Ledeb.) Wojew. & Spalik [≡ *Laserpitium affine* Ledeb.].

Siler Mill.

    Siler montanum Crantz [≡ *Laserpitium siler* L., inc. *L. garganicum* (Ten.) Bertol., *L. zernyi* Hayek, *L. ochridanum* Micevski].

Thapsia L.

    T. garganica L., *T. gymnesica* Rosselló & A.Pujadas, *T. platycarpa* Pomel, *T. transtagana* Brot., *T. smittii* Simonsen & al., *T. meoides* Guss., *T. thapsioides* (Desf.) Simonsen & al., *T. gummifera* (Desf.) Spreng., *T. tenuifolia* Lag., *T. asclepium* L., *T. minor* Hoffmanns. & Link, *T. villosa* L., *T. laciniata* Rouy, *T. maxima* Mill. [= *T. nitida* Lacaita?], *T. scabra* (Cav.) Simonsen & al., *T. nestleri* (Soy.-Will.) Wojew. & al. [≡ *Laserpitium nestleri* Soy.-Will.], *T. eliasii* (Sennen & Pau) Wojew. & al. [≡ *Laserpitium eliasii* Sennen & Pau], **T. cinerea* A.Pujadas., **T. foetida* L.

Laserpitium L.

    L. nitidum Zanted., *L. peucedanoides* L., *L. krapfii* Crantz, *L. latifolium* L., *L. gallicum* L., *L. halleri* Crantz.

    Ekimia H.Duman & M.F.Watson

    E. bornmuelleri (Hub.-Mor. & Reese) H.Duman & M.F.Watson, *E. petrophila* (Boiss. & Heldr.) J.Baczyński & al. [≡ *Laserpitium petrophilum* Boiss. & Heldr.], *E. glauca* (Post) Banasiak & al. [≡ *Laserpitium glaucum* Post].

Ammodaucus Coss. & Durieu

    A. leucotrichus Coss. & Durieu, **A. nanocarpus* (Beltrán) P.Pérez & Velasco.

Cuminum L.

    C. cyminum L., *C. setifolium* (Boiss.) Koso-Pol.,

Incertae sedis: **Cuminum borsczowii* (Regel & Schmalh.) Koso-Pol., **Elaeoselinum tunetanum* Brullo, Minissale & Terrasi, *Laserpitium pseudomeum* Orph., Heldr. & Sart. ex Boiss., **L. longiradium* Boiss.