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Redefined generic limits of *Carum* (*Umbelliferae*, *Apioideae*) and new systematic placement of some of its taxa

Abstract

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A phylogenetic analysis of nuclear ribosomal DNA internal transcribed spacer (nrDNA ITS) sequences of the species of *Carum* (*Umbelliferae*, *Apioideae*) in its traditional circumscription is provided. The sampling includes also a wide spectrum of taxa across subfamily *Apioideae*, to identify the relationships of the various disparate elements so far united in *Carum*. The molecular analysis has been supplemented by an analysis of fruit and petal morphology of several critical species of *Carum* and beyond. *Carum* in its traditional interpretation is confirmed to be polyphyletic; it includes at least seven independent evolutionary lines. *C. carvi*, which provides the type of the generic name, and only four Caucasian and Near Eastern species, *C. caucasicum*, *C. meifolium*, *C. grossheimii*, *C. porphyrocoleon*, make up *Carum* s.str., while their relationship to *Grammosciadium*, *Chamaesciadium* and *Fuernrohrria* in the same clade needs further studies. The rare Caucasian *Carum komarovii* as well as the W Asian *Pimpinella anthriscoides* and the Japanese *Chamaele decumbens* are closely related to and united here with *Aegopodium*. *Carum verticillatum*, for which a sister group relationship to the *Oenantheae* clade is revealed, is restored as the monotypic genus *Trocdaris*. The previous transfer of the S Siberian and Middle Asian *Carum atosanguineum* to *Vicatia* is confirmed. *Pimpinella cruciata* clusters with and is included in the genus *Tamamschjanella*. Three new nomenclatural combinations, *Aegopodium decumbens*, *A. komarovii* and *Tamamschjanella cruciata*, are published.

Additional key words: *Apiaceae*, *Aegopodium*, *Pimpinella*, *Tamamschjanella*, *Trocdaris*, taxonomy, systematics, molecular phylogenetics, nrITS, fruit anatomy, petal morphology

Introduction

At present, generic classification and relationships within the tribe *Apieae* in its traditional circumscription (*Ammineae* in Drude's classification of *Umbelliferae* subfam. *Apioideae*, Drude 1897–98) have remained complicated and largely unresolved. According to molecular phylogenetic analyses in the *Apioideae*, the larger genera appear nearly all non-monophyletic (Downie & al. 2001, 2010). In the corresponding classifications of the *Apioideae*, most of these larger genera are members of the so-called “apioid superclade”, which is analogous to the *Apieae* of the Drude and post-Drude morphological classifications.

Carum L. is one of these larger, traditional genera and was established at an early stage of scientific plant systematics, primarily on the basis of common European species. The nomenclatural type of *Carum* is *C. carvi* L. (caraway), the only Linnean species of the genus. Later, numerous species from different countries and continents were described within or attributed to *Carum*, because of similarities in the general habit and a rather simple fruit structure, mainly characterised by a glabrous pericarp with almost equal ribs and solitary or coupled vascular vittae. Today, about 200 validly published species names are known in *Carum*, according to the International Plant Names Index (IPNI 2012). However, further

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morphological investigations showed the genus to be largely polyphyletic and many species already have been transferred from *Carum* to other, sometimes new genera, after more detailed morphological analysis (Boissier 1872; Drude 1897–98; Korovin 1927; Wolff 1927; Handel-Mazzetti 1933; Kljuykov 1985, 1986). *Carum*, in its narrower sense includes 22–25 (Drude 1897–98; Wolff 1927) to 30 (Mabberley 1987; Pimenov & Leonov 1993) species, which are distributed in Europe, Africa, Asia and North America; *C. carvi* is widely cultivated. A broader concept of *Carum*, with dozens of genera merged (Koso-Poljansky 1916; Hiroe 1979) does not seem to be popular in current *Umbelliferae* systematics. The accepted number of *Carum* species varies in different Floras: USSR (Schischkin 1950: 10 species), Europe (Tutin 1968: 5 species), Caucasus (Tamamschjan 1967: 8 species), Turkey (Hedge & Lamond 1972: 5 species).

Comparative carpological studies (Zakharova 2010) are available for the majority of the currently accepted species (except for some N African ones). According to these, several European and E Asian species (*C. heldreichii* Boiss., *C. appuanum* (Viv.) Grande, *C. verticillatum* (L.) W. D. J. Koch, *C. diversifolium* (DC.) C. B. Clarke) had been demonstrated to be morphologically alien to *Carum*; of these *C. diversifolium* was shown to be member of *Trachyspermum* Link.

Also molecular phylogenetic studies by Papini (2006), Papini & al. (2007) and Degtjareva & al. (2009) indicated that *Carum* is polyphyletic, although their samplings usually included only few species of the genus. Downie & al. (2010) in their classification based on the phylogenetic analyses of nrDNA sequences, classified the diverse elements of *Carum* in their two, newly circumscribed tribes *Careae* (including the generitype) and *Pyramidoptereae*.

The objective of the present study has been (1) to assess through a molecular phylogenetic analysis of nrITS sequences the extent of polyphyly of *Carum* in its current circumscription; (2) to identify, supplemented by an analysis of the fruit and petal morphology of several critical taxa, the relationships of the various elements of current *Carum*; (3) to provide a revised generic classification of the elements to be excluded from *Carum*. The species included in our sampling represent current *Carum* in its entire geographical range except N Africa.

Materials and methods

Taxon sampling for the molecular phylogenetic analyses — A total of 41 new sequences of the nuclear ribosomal DNA internal transcribed spacer (nrDNA ITS) were generated for this study, including 30 sequences for 16 taxa currently classified in or not unanimously excluded from *Carum*, and 6 sequences for *Aegopodium* species, one sequence for *Chamaele*, three sequences for species of *Pimpinella*, and one for *Chamaescidium*. In

the light of the apparent polyphyly of *Carum*, the initial set of samples was increased, based on previous studies (Papini 2006; Papini & al. 2007; Spalik & Downie 2007; Degtjareva & al. 2009; Downie & al. 2008; Downie & al. 2010; Magee & al. 2010; Zhou & al. 2008) and a BLAST search in GenBank, to include representatives of all genera to which closer affinities of species currently classified in *Carum* could be detected. In this way, representatives of the tribes *Careae*, *Pimpinelleae*, *Pyramidoptereae*, *Oenantheae*, *Selineae* and of the *Physospermopsis* clade according to the classification by Downie & al. (2010), were added. A member of the genus *Physospermum*, *P. cornubiense*, was selected as outgroup based on previous higher-level studies (e.g., Valiejo-Roman & al. 1998, Downie & al. 2010). The final sampling included 146 accessions of 134 species from 49 genera (see Appendix).

DNA isolation, amplification and sequencing — Total genomic DNA was isolated from fruits and leaf tissue using the NucleoSpin Plant isolation kit (Macherey-Nagel, Düren, Germany) following the manufacturer's instructions. PCR amplification and sequencing strategies (including primer locations and characteristics) followed the protocols given previously (Valiejo-Roman & al. 2002). PCR products were purified using the DNA cleaning kit (Evrogen, Moscow, Russia) following the manufacturer's instructions. Direct sequencing was performed on the ABI PRISM 3100 Genetic Analyzer (Applied Biosystems), with the use of the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit for cycle sequencing reactions following the manufacturer's instructions. Forward and reverse strands of all ITS samples were sequenced. The resulting sequences were checked with the CHROMAS 1.45 software (www.technelysium.com.au/chromas.html). The ITS sequences were edited and manually aligned using the BioEdit program, version 5.0.9 (Hall 1999). Sequences of the 5.8S rRNA gene were also obtained but excluded from the analysis because in many published sequences this region is not represented. Gap-rich columns of the alignment were excluded from the analysis in order to avoid tree topology deformation due to misinterpretation of missing characters (Lemmon & al. 2009). The aligned data matrices are available upon request from the corresponding author.

Molecular phylogenetic analyses — Maximum Parsimony (MP) analysis was carried out with PAUP* (version 4.0b8, Swofford 2000) using the heuristic search with TBR branch swapping, all character states specified as equally weighed and all gaps treated as missing data. One hundred replicates with random addition of sequences were performed and all shortest trees were saved. Bootstrap analysis (Felsenstein 1985) was performed to assess the degree of support for particular branches of the tree. Bootstrap support (BS) values were calculated from 100 replicate analyses with TBR branch swapping and random addition sequence of taxa. One

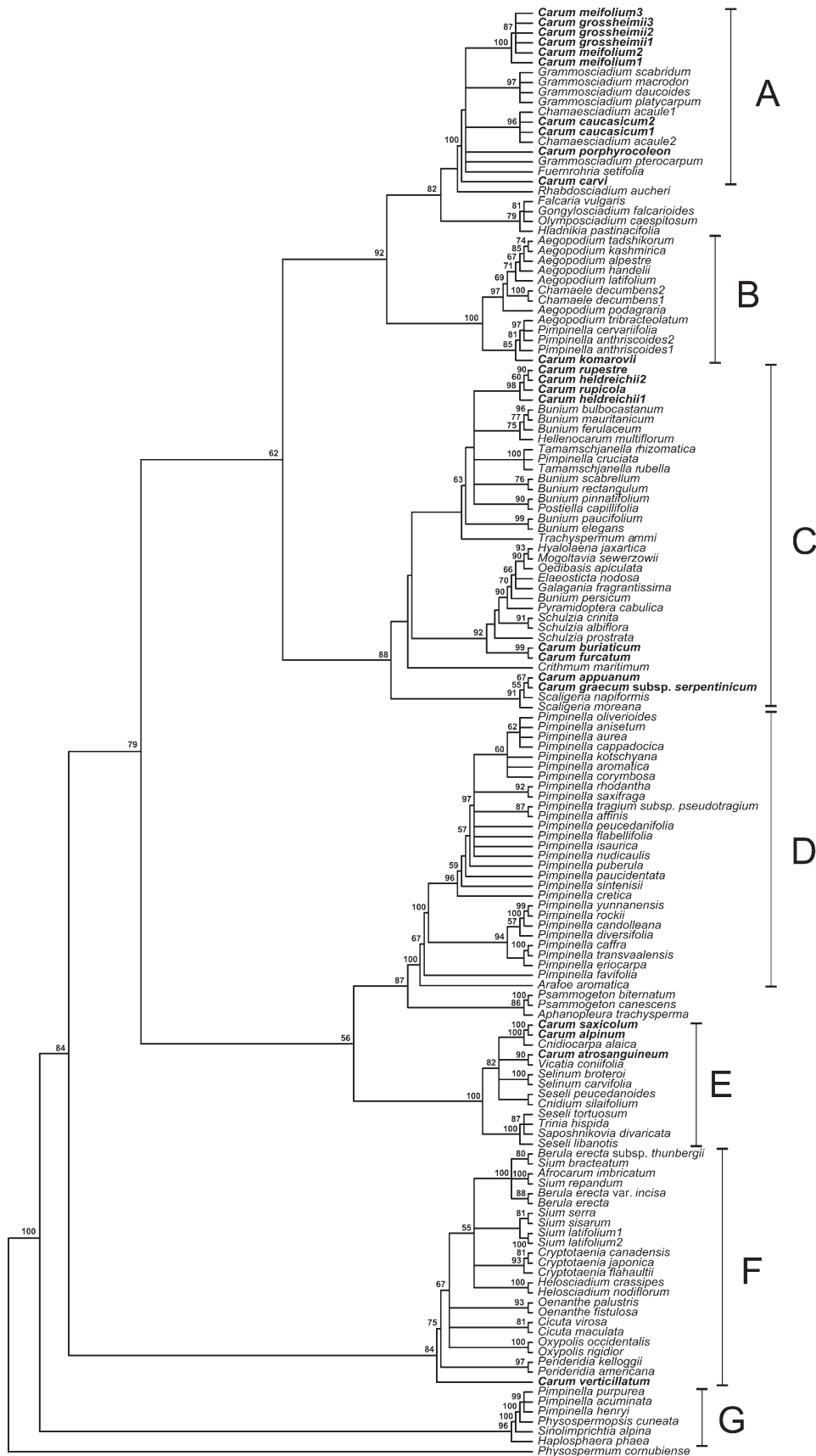


Fig. 1. Maximum Parsimony (MP) analysis of the ITS dataset; strict consensus tree of 100 000 shortest trees. Major clades are denoted by vertical bars to the right. Numbers above the branches are the bootstrap support values > 50 % from MP bootstrapping. *Carum* species are shown in bold.

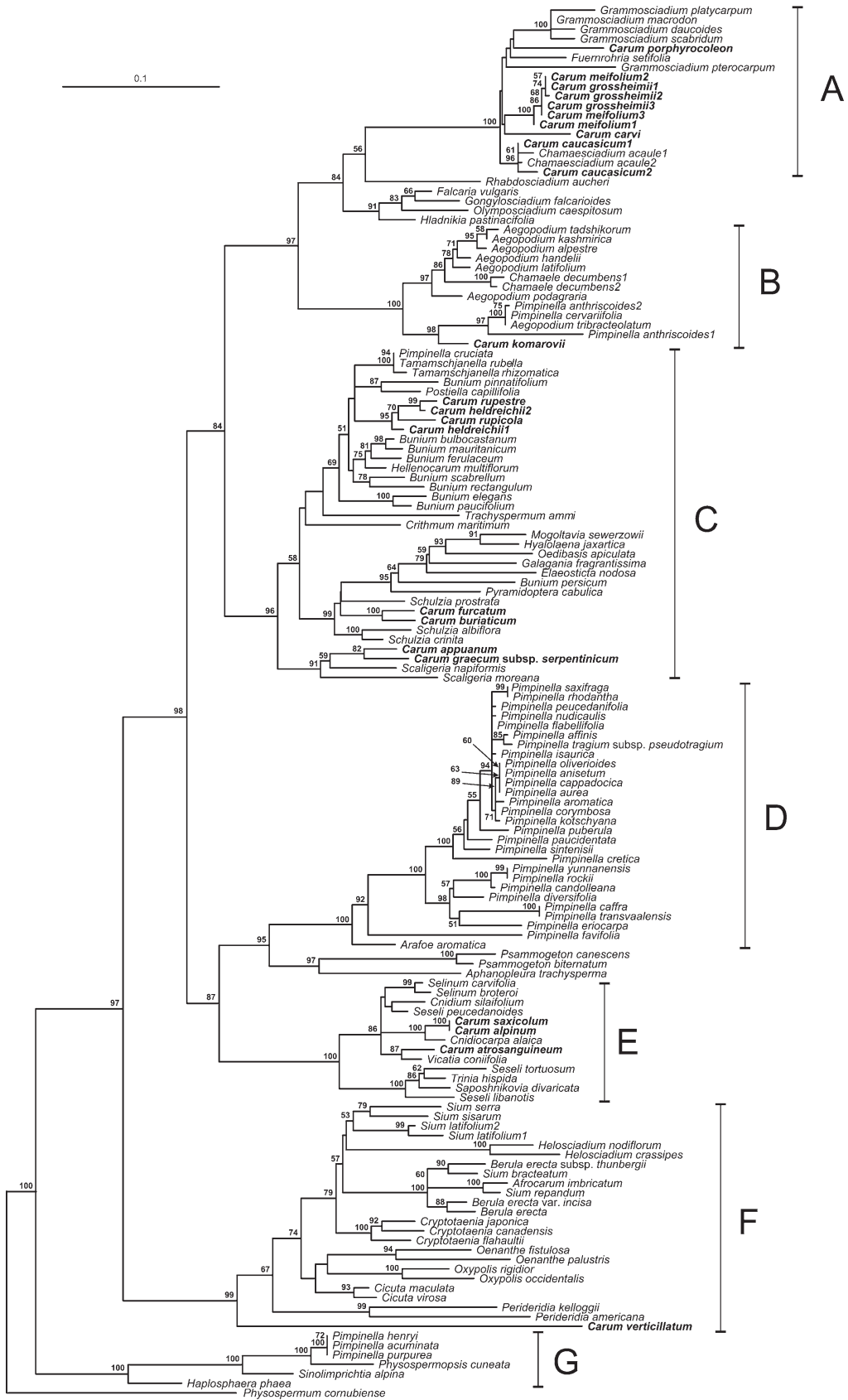


Fig. 2. Phylogenetic Maximum Likelihood (ML) tree inferred from the ITS dataset with RAxML under a GTRGAMMA nucleotide substitution model approximation. Major clades are denoted by vertical bars to the right. Branch lengths are proportional to the number of the expected nucleotide substitutions. Numbers above the branches are the bootstrap support values > 50 % from ML bootstrapping. *Carum* species are shown in bold.

thousand most parsimonious trees from each replicate were saved.

Maximum Likelihood (ML) analysis was carried out with RAxML (version 7.2.6, Stamatakis 2006) using the GTRGAMMA model. The model was selected by the Akaike Information Criterion in the Modeltest program (Posada & Crandall 1998). Bootstrapping was made using the rapid bootstrapping algorithm implemented in RAxML with 100 replicates. Bootstrap support (BS) values were then drawn onto the best-known likelihood tree.

Morphological analysis — The material for morphological studies had been obtained from the herbaria B, IRK, LD, LE, MHA, MW and WU (abbreviations according to Thiers 2008+) and is given in the figure captions. Morphological characters significant in *Umbelliferae* systematics (Kljuykov & al. 2004) were studied and compared using a reflected-light microscope. Fruit anatomy was examined under a light microscope, the sections being made in the middle of the mericarps, with a hand razor. Before sectioning, the fruits had been kept for three days in a mixture of equal parts of glycerine, ethyl alcohol and water. The sections were treated with phloroglycine and hydrochloric acid and then mounted in glycerine.

Results

ITS data set — To check the infraspecific variability of ITS sequences, for some species of the genera *Carum* L., *Chamaele* Miq., *Pimpinella* L. and *Vicatia* DC., samples from several populations were sequenced. No infraspecific ITS variation has been found in *Carum buriaticum* Turcz., *C. carvi*, *C. graecum* subsp. *serpentinicum* Hartvig, *C. komarovii* Karjag., *C. porphyrocoleon* (Freynt & Sint.) Woronow ex Schischk., *Pimpinella anthriscoides* Boiss., *P. cruciata* Bornm. & H. Wolff, *Carum atosanguineum* Kar. & Kir. (≡ *Vicatia atosanguinea* (Kar. & Kir.) P. K. Mukh. & Pimenov) and *Carum verticillatum*. Consequently, only a single accession was included in the phylogenetic analyses. Different accessions of *Carum caucasicum* (M. Bieb.) Boiss., *C. grossheimii* Schischk., *C. heldreichii*, *C. meifolium* (M. Bieb.) Boiss., *Chamaele decumbens* (Thunb.) Makino and *Pimpinella anthriscoides* Boiss., in contrast, possessed slightly different ITS sequences and were therefore subject to the phylogenetic analyses.

Among the species investigated, the length of ITS1 ranges from 209 bp to 221 bp and that of ITS2 from 209 bp to 225 bp. Seventy three gap-rich columns of the alignment were excluded from the analysis. The alignment (ITS1+ITS2) comprised 72.8 % parsimony informative characters.

MP analyses yielded 100 000 shortest trees, with a length of 2108 steps (CI = 0.342, RI = 0.808). The strict consensus tree is shown in Fig. 1. The ML tree (Fig. 2) is

remarkably similar to the MP strict consensus tree (Fig. 1) in recovering the same major groups. Within the major clades, the differences between ML and MP trees are localised to parts, where the MP tree is unresolved or the ML tree contains subclades with low bootstrap support (BS) values.

Phylogenetic relationships — Seven major clades have been resolved. Our largely representative sampling of the species of *Carum* is found dispersed over five of these seven major clades and represents at least seven independent evolutionary lines.

Clade A (100 % MP BS; 100 % ML BS) comprises the generitype *Carum carvi* plus *C. porphyrocoleon*, *C. caucasicum*, *C. meifolium* and *C. grossheimii*, as well as species of the genera *Chamaescidium* C. A. Mey., *Grammoscadium* DC. and *Fuernrohria* K. Koch. All taxa are distributed in the Caucasus and adjacent countries.

Clade B (100 % MP BS; 100 % ML BS) comprises the genera *Aegopodium* L. and *Chamaele*, two species of *Pimpinella* and the rare Transcaucasian *Carum komarovii*.

Clade C (88 % MP BS; 96 % ML BS) comprises eight *Carum* species scattered among three well supported subclades.

Clade D (100 % MP BS; 100 % ML BS) comprises 27 species of *Pimpinella* and *Arafoe aromatica* Pimenov & Lavrova, which is sister to the *Pimpinella* group.

Clade E (100 % MP BS; 100 % ML BS) comprises *Carum alpinum* (M. Bieb.) Benth. and *C. saxicolium* Albov as well as *C. atosanguineum*, which recently has been included in *Vicatia*.

Clade F (84 % MP BS; 99 % ML BS) comprises *Carum verticillatum*, being sister to the remainder of this clade.

Clade G (96 % MP BS; 100 % ML BS) comprises three *Pimpinella* species, *Physospermopsis cuneata* H. Wolff, *Sinolimprichtia alpina* H. Wolff and *Haplo-sphaera phaea* Hand.-Mazz.

Morphology and anatomy of fruits — Below we provide a detailed description of fruit morphology and anatomy as analysed for some critical species:

Carum carvi (Fig. 3A). Fruit of ovoid or ellipsoid mericarps, with the carpophore bifid to the base; mericarps homomorphic, glabrous, 3–3.5 mm long, 0.8–1.2 mm broad, terete, primary ribs equal, keeled, straight, with entire margin; calyx teeth very short or obsolete; stylopods low-conical, styles recurved; mericarps in transverse section slightly compressed laterally; exocarp cells small; commissure narrow, exocarp almost reaching carpophore; mesocarp parenchyma not lignified; vascular bundles compact, situated in primary rib bases; vallecular vittae solitary, two on the commissural side; rib secretory ducts solitary, small; endocarp not lignified, its cells tubular; endosperm flat on the commissural side.

Carum verticillatum (Fig. 3B). Fruit of ellipsoid mericarps, with the carpophore bifid in the upper part; mericarp homomorphic, glabrous, 2.5–2.7 mm long, 0.5–0.7 mm broad, primary ribs approximately equal, keeled, straight, with entire margin; calyx teeth very short or obsolete; stylopods low-conical, styles recurved; mericarps in transverse section slightly compressed laterally; commissure narrow, exocarp almost reaching carpophore; mesocarp parenchyma not lignified; vascular bundles compact, situated in primary rib bases; vallecular vittae solitary, two on the commissural side; rib secretory ducts solitary, small; endosperm on the commissural side flat.

Aegopodium podagraria (Fig. 3C). Fruit of ovoid or ellipsoid mericarps, with the carpophore bifid to the base; mericarps homomorphic, glabrous, 3–6 mm long, 1–2 mm broad, terete, primary ribs equal, filiform, straight; calyx teeth obsolete; stylopodia conical, styles recurved; mericarps in transverse section almost rounded; exocarp cells small; commissure narrow, exocarp almost reaching carpophore; mesocarp parenchyma not lignified, with dark yellow content; vascular bundles compact, situated in primary rib bases; vallecular and commissural vittae small and sometimes invisible, 3–5 in each furrow, 4–7 on the commissural side, rib secretory ducts solitary, small; endocarp slightly lignified, its cells rectangular, big; endosperm flat on the commissural side.

Carum komarovii (Fig. 3D). Fruit of ovoid or ellipsoid mericarps, with the carpophore bifid to the base; mericarps homomorphic, glabrous, 4–6 mm long, 1–1.2 mm broad, terete, primary ribs equal, keeled (or short-winged), straight (or sometimes slightly wavy), with entire margin; calyx teeth obsolete; stylopodia conical, styles recurved; mericarps in transverse section almost rounded; exocarp cells small; commissure narrow, exocarp almost reaching carpophore; mesocarp parenchyma not lignified, with dark yellow content; vascular bundles compact, situated in primary rib bases; vittae vallecular and commissural, small and sometimes invisible, 3–5 in each furrow, 4–6 on the commissural side, rib secretory ducts solitary, small; endocarp slightly lignified, its cells rectangular, big; endosperm flat on the commissural side.

Pimpinella anthriscoides (Fig. 3E). Fruit of ovoid or ellipsoid mericarps, with the carpophore bifid to the base; mericarps homomorphic, glabrous, 3–4 mm long, 1–1.5 mm broad, terete, primary ribs equal, filiform, straight, sometimes slightly wavy, with entire margin; calyx teeth obsolete; stylopodia conical, styles recurved; mericarps in transverse section almost rounded; exocarp cells small; commissure narrow, exocarp almost reaching carpophore; mesocarp parenchyma not lignified, with dark yellow content; vascular bundles compact, situated in primary rib bases; vittae vallecular and commissural, small and sometimes invisible, 5–7 in each furrow, 4 on the commissural side, rib secretory ducts solitary, small; endocarp slightly lignified, its cells rectangular, big; endosperm flat on the commissural side.

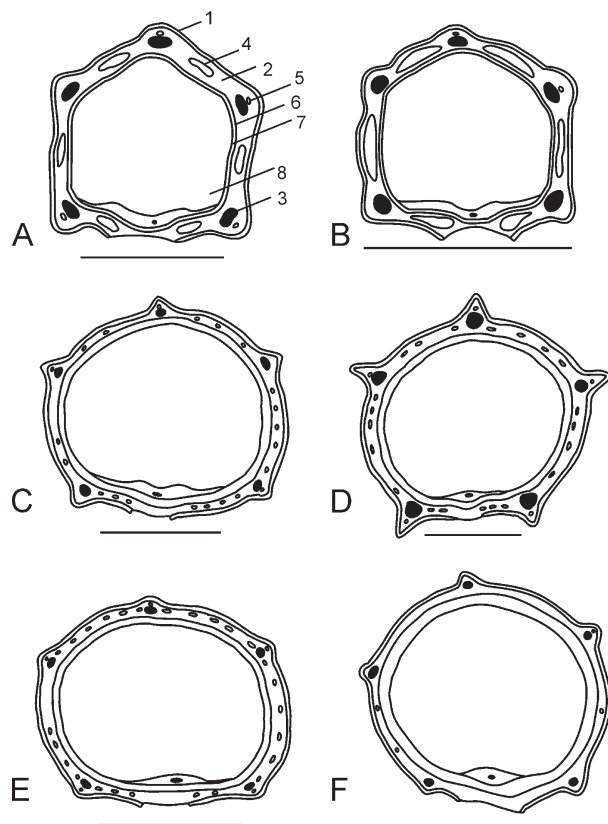


Fig. 3. Schematic transects of mericarps – A: *Carum carvi* [Russia, Vladimir region, 9.7.2002, Seryogin & Privalova 1433 (MW)]; B: *Carum verticillatum* [Pampilhosa, Valdoiro, 5.7.1950, Matos & Matos s.n. (MHA)]; C: *Aegopodium podagraria* [Russia, Moscow, 29.8.2011, Zakharova s.n. (MW)]; D: *Carum komarovii* [Armenia, 8.7.1977, Pimenov & al. 1274 (MW)]; E: *Pimpinella anthriscoides* [Armenia, 4.6.1977, Pimenov & al. 164 (MW)]; F: *Chamaele decumbens* [Japan, Shikoko, Tokushima, 1919, Krug s.n. (B)]. – 1 = exocarp, 2 = mesocarp, 3 = vascular bundles, 4 = vallecular vittae, 5 = rib secretory ducts, 6 = endocarp, 7 = seed coat, 8 = endosperm; scale bars = 1 mm.

Chamaele decumbens (Fig. 3F). Fruit of ellipsoid mericarps, with the carpophore bifid to the middle or the base; mericarps homomorphic, glabrous, 2.4–2.6 mm long, 0.7–0.8 mm broad, terete, primary ribs equal, filiform, straight (or sometimes slightly wavy), with entire margin; calyx teeth obsolete; stylopodia low conical, styles recurved; mericarps in transverse section almost rounded; exocarp cells small; commissure narrow, exocarp almost reaching carpophore; mesocarp parenchyma not lignified, with dark yellow content, vittae vallecular and commissural, obsolete in mature fruit; rib secretory ducts obsolete; endocarp slightly lignified, its cells rectangular, extending in radial direction, big; endosperm flat on the commissural side.

Chamaescidium acaule. Fruit of ovoid mericarps, with the carpophore bifid to the middle; mericarps homomorphic, glabrous, 3.5–4 mm long, 0.9–1.1 mm broad, terete, primary ribs equal, keeled, straight, with entire margin; calyx teeth obsolete; stylopodia flat or

low conical, styles recurved; mericarps in transverse section slightly compressed laterally; exocarp cells small; commissure narrow, almost reaching carpophore; mesocarp parenchyma not lignified; vascular bundles compact, situated in primary rib bases; vittae vallecular and commissural, 2–4 in each furrow, 4 on the commissural side; rib secretory ducts solitary, small, present in all ribs; endocarp not lignified; endosperm flat on the commissural side.

Morphology of petals — The number of petal secretory ducts varies in the taxa studied (Fig. 4). Within *Carum* it ranges from 1 to 7 (*C. carvi* has 1 secretory duct, *C. buriaticum* 7, *C. komarovii* 4–5), within *Aegopodium* from 1 to 7 too (*Aegopodium kashmiricum* and *A. tadshikorum* have 6–7 secretory ducts, *A. alpestre* and *A. latifolium* 1 as was noted by Vinogradova (1991), *A. podagraria* has 4–5). *Pimpinella anthriscoides* has 5–7 secretory ducts.

Discussion

When compared with the major clades recognised as tribes within *Apioideae* by Downie & al. (2010), our Clade A + Clade B correspond to *Careae*, Clade C to the deeply reformed *Pyramidoptereae*, Clade D to the expanded *Pimpinelleae*, Clade E to the *Selineae*, Clade F to the *Oenantheae*, and the species of Clade G partly to the E Asian *Physospermopsis* clade.

Carum in its current wide sense is heavily polyphyletic and represents at least seven independent evolutionary lines spread over five of these major *Apioideae* clades. This confirms in a much more detailed way the preliminary findings in previous molecular phylogenetic analyses including members of *Carum* (Papini 2006, Papini & al. 2007, Degtjareva & al. 2009).

***Carum carvi* and its allies** — Clade A, containing *Carum carvi*, which corresponds to *Carum sensu strictissimo*, is taxonomically heterogeneous. Besides *C. carvi*, it includes *C. porphyrocoleon*, *C. caucasicum*, *C. meifolium* and *C. grossheimii*, but also representatives of the genera *Chamaescidium*, *Grammoscadium* and *Fuernrohrria*.

As far as the four *Carum* species clustering with *C. carvi* in this clade are concerned, their position and af-

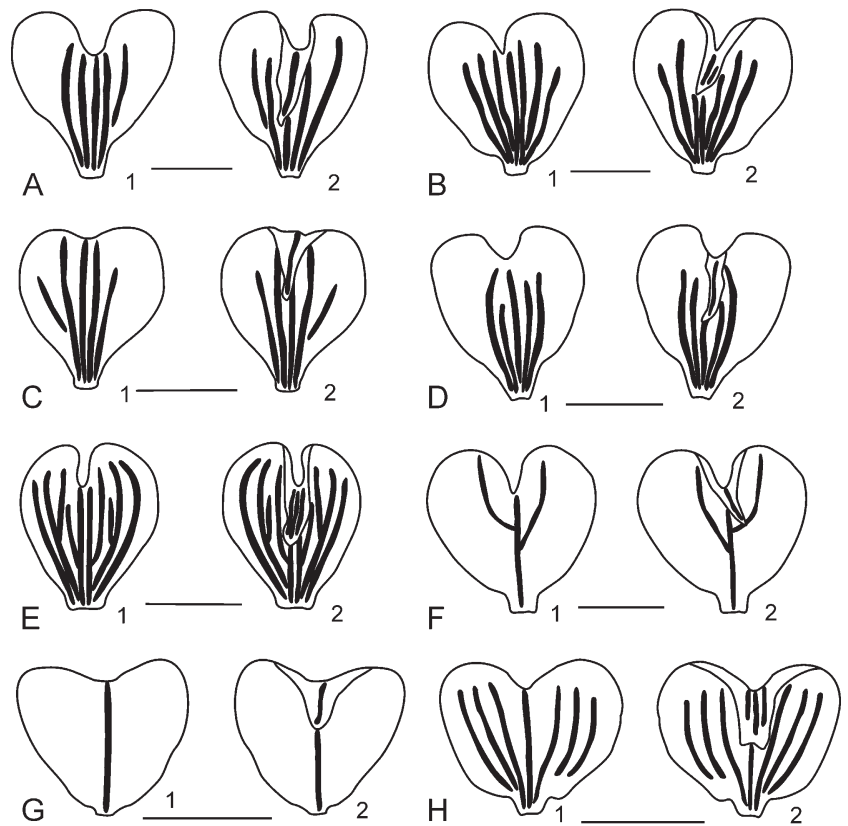


Fig. 4. Secretory ducts of petals – A: *Aegopodium podagraria* [Russia, Moscow, 6.7.2006, Zakharova s.n. (MW)]; B: *Aegopodium kashmiricum* [Kazakhstan, Lepsinsk, 1.8.1974, Pimenov & al. s.n. (MW)]; C: *Carum komarovii* [Armenia, 8.7.1977, Pimenov & al. 1274 (MW)]; D: *Pimpinella anthriscoides* [Armenia, Takerlu, 4.6.1977, Pimenov & al. 164 (MW)]; E: *Aegopodium tadshikorum* [Tajikistan, 19.6.1973, Pimenov & Baranova 956 (MW)]; F: *Aegopodium latifolium* [Russia, Irkutsk region, Lake Baikal, 14.8.1992, Pimenov & Kljuykov 83 (MW)]; G: *Carum carvi* [Russia, Vladimir region, 18.6.1972, Tikhomirov & al. 7031 (MW)]; H: *Carum buriaticum* [Russia, Buryatia, 28.8.2003, Pimenov s.n. (MW)]. – 1 = external side of petal, 2 = internal side of petal; scale bars = 1 mm.

finity to each other is not surprising. All are distributed in the Caucasus and adjacent territories of the Near East, only *C. carvi* exceeds this range very considerably. In the ML tree, *C. caucasicum*, *C. meifolium*, *C. grossheimii* and *Chamaescidium acaule* (M. Bieb.) Boiss. form two subclades. *C. meifolium* clusters with *C. grossheimii*, while *C. caucasicum* with *Chamaescidium acaule*. Not only are the members of each subclade closely related, but they are also almost indistinguishable in their ITS sequences. The accessions of *C. caucasicum* and *Chamaescidium acaule* show moderate infraspecific variation. Specific independence and correct morphology-based identification of *C. meifolium* and *C. grossheimii* are beyond question.

Chamaescidium is regarded by some botanists (Drude 1897–98; Koso-Poljansky 1914, 1916; Rechinger 1987) as a close relative or even a part of *Carum*, although Wolff (1927), Schischkin (1950) and Peşmen (1972) placed it near *Pimpinella*, and Heywood (1971) in *Apiaceae* subtribe *Seselineae*. The fruits of *Chamaescia-*

dium acaule (see Pimenov & Kljuykov 1995) are rather similar to those of *Carum carvi* (Fig. 3A), the main difference being the number of vallecular and commissural vittae.

Based on morphology, the two other genera, *Grammosciadium* and *Fuernrohria*, clustered in Clade A, were usually attributed to other tribes, *Grammosciadium* to *Scandiceae* and *Fuernrohria* to *Coriandreae*. Hedge & Lamond (1987) and Vinogradova (1995), however, doubted the placement of *Fuernrohria* in *Coriandreae*. Previous molecular analyses (Katz-Downie & al. 1999; Downie & al. 2000a, b, 2001; Valiejo-Roman & al. 2006b; Terentjeva & al. 2008) all supported the affinity of *Fuernrohria* and *Grammosciadium* to each other. The fruits of *F. setifolia* K. Koch are similar to those of *G. pterocarpum* Boiss. in style, stylopods and calyx teeth structure, and to *G. conferum* Hub.-Mor. & Lamond in some characters of mechanic and secretory systems (Vinogradova 1995).

Morphologically, the inferred affinity of the two genera with *Carum* is surprising and they could by no means be united with the latter. Unlike *C. carvi*, *Grammosciadium daucooides* DC. (the nomenclatural type of that genus) is a polycarpic perennial with leaves with filiform terminal segments having acute apices, numerous pinnate bracts and 5–7 pinnate, or ternate, or entire bracteoles, linear to oblong fruits with filiform calyx teeth and broad commissure. Other species of *Grammosciadium* have winged marginal ribs and a mesocarp with sclerenchyma cell groups. *Fuernrohria setifolia* differs from *C. carvi* in its life form (polycarpic perennial), filiform terminal leaf segments having acute apices, numerous ternate bracts and entire filiform or ternate bracteoles, not prominent fruit ribs, a continuous sclerenchyma layer in mesocarp, cyclic vittae, broad commissure. Further studies are needed to assess the relationship between the genera of this clade.

The rare Transcaucasian *Carum komarovii* — The most interesting result obtained in our molecular phylogenetic appraisal of *Carum* concerns the rare *C. komarovii*. The species is only known from a few localised Transcaucasian occurrences, in Armenia and Azerbaijan (Karjagin 1944; Tamamschjan 1967). The ITS sequences of its two accessions were identical. Distant from *Carum* s.str., *C. komarovii* is nested in Clade B together with six species of *Aegopodium*, a species of the monotypic genus *Chamaele* and *Pimpinella anthriscoides*, whose four accessions (kept in herbaria under the names of *P. anthriscoides*, *P. cervariifolia* Freyn & Sint. and *Aegopodium tribracteolatum* Schmalh.) form a separate subclade in both the MP and ML trees, despite their low infraspecific variability. *C. komarovii* is sister to the latter subclade and both are in turn sister to the subclade containing the six *Aegopodium* and the *Chamaele* species.

Aegopodium is a genus of seven species, widely distributed in the Palearctic (Europe, temperate Asia, N

Africa, adventive in North America). The distinguishing features of *Aegopodium* are glabrous fruits without prominent ribs, inconspicuous vallecular and commissural vittae sometimes invisible in mature fruits (3–5 in each furrow and 4–9 on the commissural side), big, slightly lignified endocarp cells and broad ultimate leaf blade segments; some of the species have long horizontal rhizomes. *A. tadshikorum* Schischk. is an *Aegopodium* species with short rhizomes. The fruit structure of *A. podagraria* L. (Fig. 3C), the generitype, well represents carpological peculiarities of the genus.

Chamaele decumbens is an endemic genus and species of the Japanese flora, spread on all main islands of Japan, with best known localities in the mountains of Honshu (Hiroe & Constance 1958). *Chamaele* was regarded as a subgenus of *Aegopodium* by Yabe (1902), as a part of *Carum* by Koso-Poljansky (1916) and as an independent genus by most other researchers (Wolff 1927; Ohwi 1953; Hara 1954; Hiroe & Constance 1958; Kitagawa 1960, 1982; Hiroe 1979; Ohba 1999). The fruits of *C. decumbens* (Fig. 3F) resemble those of *Aegopodium*. The species has short rhizomes and adventive roots; it differs from *A. podagraria* by the absence of horizontal rhizomes and is similar in that feature to *A. tadshikorum*. The morphological data are fully consistent with the molecular data, so that *Chamaele decumbens* can safely be transferred to *Aegopodium*.

Pimpinella anthriscoides appears in our ITS tree far from the Clade D, where the bulk of the species of *Pimpinella* and also its generitype *P. saxifraga* L. is placed. In an earlier study by Tabanca & al. (2005), *P. anthriscoides* appeared as sister taxon to all other *Pimpinella* species. This is, however, clearly due to their sampling strategy, which a priori assumed monophyly of *Pimpinella* by including only species of that genus and a single remote outgroup taxon. Its position in our ITS tree, forming with *Carum komarovii* the sister group to the *Aegopodium* clade, is in good agreement with the morphological data. *P. anthriscoides* is similar to *Aegopodium* in fruit morphology (Fig. 3E) and rhizome structure (thick elongated horizontal black rhizomes), and Zakharova (2010) already noted the morphological similarity between *C. komarovii* (Fig. 3D) and *P. anthriscoides*. Fruit structure of *C. komarovii*, in contrast, differs considerably from the core of *Carum*. Moreover, *C. komarovii* and *P. anthriscoides*, like *A. podagraria* and most other *Aegopodium* species but in contrast to *C. carvi* (Fig. 4), have several petal secretory ducts.

Hence, both molecular analysis and morphological data provide support for a unification of *Carum komarovii*, *Pimpinella anthriscoides* and *Chamaele* with *Aegopodium*.

According to current taxonomy, *Pimpinella anthriscoides* is represented by two varieties, i.e. the type variety and var. *cruciata* (Bornm. & H. Wolff) Matthews. Matthews (1972: 363) supposed that the two differ from each other in the number of rays (6–10 in var. *cruciata*, 12–20

in var. *anthriscoides*) and flowers in umbels (8–15 in var. *cruciata*, 15–25 in var. *anthriscoides*). Var. *cruciata* was initially described as an independent species, *P. cruciata* Bornm. & H. Wolff (Bornmüller & Wolff 1921), which was together with *P. anthriscoides* attributed to *P.* subsect. *Saxifragae* H. Wolff (i.e. *P.* subsect. *Pimpinella* according to the Code) and the series *Anthriscioideae* H. Wolff. Wolff (1927: 289, 306) distinguished the two species by the presence (*P. anthriscoides*: “involucris phylla 4–5 lineari-lanceolata, radiis pluries breviora”) versus absence (*P. cruciata*: “involucrum nullum”) of involucral bracts. Absence of involucral bracts is a usual feature of *Pimpinella*, whereas their presence is not. Wolff (1927) qualified *P. cervariifolia* Freyn & Sint. as a synonym of *P. anthriscoides*. In our ITS tree, *P. cruciata* appears as sister to *Tamamschjanella* in Clade C, which represents the *Pyramidoptereae* by Downie & al. (2010), distant from *P. anthriscoides* s.str., whereas *P. cervariifolia* is situated in the same terminal clade as the latter. Two conclusions can be drawn: (1) *P. anthriscoides* and *P. cruciata* are two “good” independent species and can by no means be regarded as varieties of one species. (2) *P. anthriscoides* and *P. cruciata* have to be excluded from *Pimpinella* and belong to different genera: *P. anthriscoides* to *Aegopodium*, whereas *P. cruciata* to *Tamamschjanella* (including the former *Ligusticum rhizomaticum* Hartvig).

Carum atosanguineum* and *Vicatia — *Carum atosanguineum* Kar. & Kir., described from S Siberian mountains and also distributed in Middle Asia and the W Himalaya, was recognised as a species closely related to *Vicatia* by Pimenov (1977) and later included in that genus as *V. atosanguinea* (Kar. & Kir.) P. K. Mukh. & Pimenov (Pimenov & al. 1991). With the inclusion of *V. atosanguinea*, the small genus *Vicatia*, formerly regarded as an E Asian (Sino-Himalayan) taxon, became a S Siberian-Himalayan genus (Pimenov & al. 1991).

We tested this relationship hypothesis by including *Carum atosanguineum* (the two accessions showed identical ITS sequences) and *Vicatia conifolia* DC., the generic type of *Vicatia*, in our molecular analysis. The analysis revealed a sister group relationship of both species far from *Carum* s.str. in Clade E, which corresponds to the clade identified by Downie & al. (2010) as tribe *Selineae*. Our analysis thus provides full support for the classification of *C. atosanguineum* as a member of the genus *Vicatia*.

Carum alpinum* and *C. saxicolum — Two Caucasian species, *Carum alpinum* (M. Bieb.) Benth. and *C. saxicolum* (Albov) Pimenov, are placed remotely from *Carum* s.str. in Clade E. The ITS sequences of *C. alpinum* and *C. saxicolum* are identical. This increases the doubt on the specific independence of *C. saxicolum*, because the two species are morphologically very similar. Pimenov (1978) revised their generic position and returned (*C. alpinum*) or transferred (*C. saxicolum*) them to *Seseli* as

S. alpinum M. Bieb. and *S. saxicolum* (Albov) Pimenov, respectively.

To test the conflicting hypotheses on the taxonomic affinity of these species (*Carum* versus *Seseli*), we included in our analysis also *S. tortuosum* L., the nomenclatural type of *Seseli*, and *S. libanotis*, the nomenclatural type of *S.* sect. *Libanotis*. The ITS tree clearly supports the exclusion of the two species from *Carum* s.str. They are nested in a statistically well supported major clade with *Seseli* and representatives of the genera *Cnidiocharpa* (*C. alaica* Pimenov), *Gasparrinia* (*G. peucedanoides* (M. Bieb.) Thell. ≡ *Seseli peucedanoides* M. Bieb.), *Katapsuxis* (*K. silaifolia* (Jacq.) Reduron & al. ≡ *Cnidium silaifolium* (Jacq.) Simonk.), *Saposhnikovia* (*S. divaricata* (Turcz.) Schischk.), *Selinum* (*S. carvifolia* (L.) L., *S. broteroi* Hoffmanns & Link), *Trinia* (*T. hispida* Hoffm.) and *Vicatia* (see above). Our ITS tree, however, neither supports their placement in *Seseli*. Within Clade E, the two species appear as sister group to *Cnidiocharpa alaica*, but further investigations with a denser sampling and, perhaps more markers, appear necessary.

For the time being, *Carum alpinum* might best be treated in the tradition of Fischer & Meyer (1840) in a genus of its own, *Lomatocarum* Fisch. & C. A. Mey., as *L. alpinum* (M. Bieb.) Fisch. & C. A. Mey.

Carum buriaticum* and *C. furcatum — The first species has a large distribution area, including S Siberia (from Altai Mts to Transbaicalia), Mongolia and China (the N, NE and central Asian parts to the Tibetan Plateau), the second was described from China and is now treated as a synonym of the first (Pu FaTing 1985). Molecular data have never been published before. The three accessions from different parts of the area show no variation in their sequences and the species is nested in Clade C of the ITS tree, which corresponds to the *Pyramidoptereae* of Downie & al. (2010). Within Clade C, *C. buriaticum* appears as sister to (MP tree, Fig. 1) or part of (ML tree, Fig. 2) a statistically well supported subclade including *Bunium persicum* and some other geophilic taxa, mainly of Mediterranean (s.l.) origin and distribution, namely *Elaeosticta*, *Galagania*, *Hyalolaena*, *Mogoltavia*, *Oedibasis*, as well as the non-geophilic *Pyramidoptera* and *Schultzia*. According to the ITS trees, *C. buriaticum* is nearest to *Schultzia*, in the ML tree (Fig. 2) it is even nested among the samples of that genus. The taxa of this subclade are morphologically rather dissimilar, making this placement surprising.

Carum buriaticum differs from *C. carvi* in its life form as a polycarpic perennial, in the presence of numerous bracts and bracteoles, in the number of secretory ducts in the petals (Fig. 4G, H) and in a medium-sized commissure. However, compared with the Caucasian species closely related to *C. carvi* according to our ITS tree, the commissure width is the only character separating *C. buriaticum* from them. Hence, the distant position in the ITS tree of *C. buriaticum* from *Carum* s.str. does

not correspond to any apparent morphological difference.

Further investigations appear necessary prior to a revised classification of *Carum buriaticum*.

Eastern Mediterranean *Carum* species — This group includes in our view *Carum heldreichii* Boiss., *C. rupestre* Boiss & Heldr., *C. appuanum* (Viv.) Grande, *C. graecum* Boiss. & Heldr. and *C. rupicola* Hartvig & Strid.

The taxonomy of the group is rather controversial. Tutin (1968) regarded *Carum graecum* as a synonym of *C. appuanum* and *C. rupestre* as a synonym of *C. heldreichii*. Hartvig (1986), in contrast, accepted *C. graecum*, *C. appuanum*, *C. heldreichii* and *C. rupestre* as independent species. *C. graecum* differs from *C. appuanum*, according to Hartvig (1986), in leaf lobes being 2–5(–8) mm long, bracts up to 8 and petals with 3–7 secretory ducts, while *C. rupestre* differs from *C. heldreichii* in yellowish petals and leaf lobes 5–20 mm long.

All E Mediterranean species are nested in Clade C of the ITS tree (Fig. 1–2) like *C. buriaticum*, but in two other subclades. The first, composed of *Carum graecum* subsp. *serpentinicum* Hartvig and *C. appuanum* together with *Scaligera napiformis* and *S. moreana*, is statistically well supported and sister to all other subclades of Clade C. The second subclade with badly resolved internal relationships and lacking sufficient statistical support, includes the SE European *C. heldreichii*, *C. rupestre* and the S Anatolian *C. rupicola* in a well supported terminal clade, together with taxa of *Bunium*, *Hellenocarum*, *Postiella*, *Tamamschjanella* and *Trachyspermum*.

The data clearly support (1) the exclusion of the E Mediterranean members of *Carum* from that genus, and (2) indicate that they represent two different evolutionary lines, confirming the preliminary results of analyses by Papini & al. (2007) and Degtjareva & al. (2009).

Carum verticillatum — The W European *Carum verticillatum*, morphologically being considerably different from *C. carvi*, never before has been included in a molecular phylogeny (so far only cp *matK* and *rbcL* sequences published). In our ITS trees (Fig. 1–2) it is the only species of *Carum* placed in Clade F. *C. verticillatum* branches at the very base of Clade F, being sister to all its other members. Clade F includes taxa with different morphology but rather similar ecology, all being hydrophilous or hygrophilous plants. The long branch leading to *Carum verticillatum* in the ML tree corresponds to the higher rates of nucleotide substitution in the ITS region.

Carum verticillatum is characterised by unusual leaf structure with transversal orientation of the subdivisions of paired first-order pinnae (Rutishauser & Isler 2001). The pinnae along the main rachis are arranged as if they were verticillate leaves along the stem. The attribution of the species to *Carum* (Koch 1824 and the majority of later workers) is based mainly on considerable carpological similarity with *C. carvi*. Like the latter, *C. verticillatum*

(Fig. 3B) has glabrous fruits, divided into two homomorphic mericarps, with approximately equal, keeled dorsal and marginal primary ribs, narrow commissure, non-lignified parenchyma, commissural solitary vallecular vitta and two commissural vittae, and the endosperm flat on the commissural side. However, from the cladistic viewpoint, such a fruit structure must be regarded as plesiomorphic, thus not informative for relationship clarification. It is represented widely in subfamily *Apiioideae*, being found in *Bunium*, *Bupleurum* L., *Cnidiocarpa* Pimenov, *Falcaria* Fabr., *Gasparrinia* Bertol., *Geocaryum* Coss., *Paulita* Sojak, *Physospermopsis*, *Rupiphila* Pimenov & Lavrova, *Seseli*, *Visnaga* P. Gaertn. and some other Eurasian genera. The very distant positions in the ITS tree of this species and *C. carvi* correlates with morphological dissimilarity in the life form and the root, leaf, involucre, involucl and pollen morphology. The roots of *C. verticillatum* are fusiform, thickened downwards; its leaves are narrowly oblong in outline, pinnatisect, with numerous pairs of deeply palmatisect verticillately arranged filiform segments, markedly diminishing towards the leaf base; bracts and bracteoles are 5 to 10, linear to lanceolate, acute, deflexed. The palynological differences between *C. verticillatum* and *C. carvi* were shown by Cerceau-Larrival (1959) and El Alaoui-Faris (2005) and include pollen grain shape (P/E >2–2.5, pollen constricted in the equatorial area in *C. carvi* versus P/E = 2, pollen not constricted in the equatorial area in *C. verticillatum*), endoaperture structure and size (prominent, 4 × 3 μm in *C. carvi* and plane, 6 × 2.4 μm in *C. verticillatum*), exine thickness (in the equatorial area 2.4 μm, in the polar area 1.6 μm in *C. carvi*, equal in the equatorial and polar areas, 2.5 μm in *C. verticillatum*) and longer columellae in *C. carvi* as compared with *C. verticillatum*.

The taxonomic history of *C. verticillatum* reflects its critical taxonomic position: it was classified in *Sison* L. (basonym by Linnaeus 1753), *Seseli* (Crantz 1767; independently Desfontaines 1798), *Sium* (Lamarck 1779), *Trocdaris* (Rafinesque 1840), *Bunium* (Godron 1848), *Pimpinella* (Jessen 1879), *Apium* (Caruel 1886) and *Selinum* (Krause 1904).

Taxonomic conclusions

(1) ***Carum* s.str.** — Among the species here investigated only four are truly closely related to *C. carvi*, the nomenclatural type of *Carum*. Therefore we conclude that *Carum* s.str. is composed only of *C. carvi*, *C. meifolium*, *C. caucasicum*, *C. grossheimii* and *C. porphyrocoleon*. All these species are distributed in Caucasus and adjacent countries of the Near East.

(2) ***Carum alpinum*** — *C. alpinum* (M. Bieb.) Benth (incl. *C. saxicolum* (Albov) Pimenov) is to be excluded

from *Carum*. The species is nearer to *Seseli*, but has some differences from the species of that genus. For the time being, the best solution is probably to treat it as member of the separate, monotypic genus *Lomatocarum* Fisch. & C. A. Mey. as *L. alpinum* (M. Bieb.) Fisch. & C. A. Mey. in Index Seminum [St Petersburg]: vi. 59. 1840.

(3) *Carum atrosanguineanum* — The molecular analysis, in accord with the morphological data (Pimenov & al. (1991), provide evidence for the placement the species in *Vicatia* DC. (Pimenov & al. 1991).

(4) *Carum verticillatum* — This species deserves the status of an independent genus, whose name was proposed by Rafinesque in 1840. According to molecular and morphological data, *C. verticillatum* differs considerably from other *Carum* species. After its attribution to *Carum* (Koch 1824), which is currently generally accepted, it was regarded as a member of seven other *Umbelliferae* genera. However, nowadays these generic attributions are solely of historical interest. The only exception is *Trocdaris* Raf., Good Book: 50. 1840, being a validly published generic name, if *C. verticillatum* is regarded as a separate monotypic genus:

Trocdaris verticillatum (L.) Raf., Good Book: 50. 1840 ≡ *Sison verticillatum* L., Sp. Pl.: 253. 1753 ≡ *Seseli verticillatum* (L.) Crantz, Cl. Umbel. Emend.: 92. 1767 ≡ *Sium verticillatum* (L.) Lam., Fl. Franç. 3: 460. 1767 ≡ *Carum verticillatum* (L.) W. D. J. Koch in Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12(1): 122. 1824 ≡ *Bunium verticillatum* (L.) Gren. & Godr., in Genier, Fl. France 1: 729. 1848 ≡ *Pimpinella verticillata* (L.) Jess., Deut. Excurs.-Fl.: 191. 1879 ≡ *Apium verticillatum* (L.) Caruel in Parlatore, Fl. Ital. 8: 430. 1886 ≡ *Selinum verticillatum* (L.) E. H. L. Krause in Sturm, Deutschl. Fl., ed. 2, 12: 48. 1904. – Lectotype (designated by Reduron & Jarvis in Jarvis & al. 2006): France, “Habitat in Gallia, Pyrenaeis”, *Burser VII*(2): 35 (UPS).

Ref. (all sub *Carum verticillatum*) — Reichenbach 1863: pl. 31; Coste 1902: 209; Thellung 1926: 1187; Tutin 1968: 354; Tutin 1980: 150, fig. 57; Cook 1983: 551, fig. 8; Valdés & al.: 1987: 319; Arenas & Garcia 1993: 151, fig. 65(2), 66(3); Villar & al. 1997: 573; Gómez 2003: 300; Reduron 2007: 742

Distribution. — Morocco, Portugal, Spain, France, Belgium, Netherlands, Germany (extreme W, probably extinct), W Great Britain (northwards to Scotland), Ireland. See map in Cook (1983: fig. 8).

(5) *Carum segregates nested in the Pyramidoptereae clade* — Three separate evolutionary lines to be excluded

from *Carum* s.str. (a) *Carum heldreichii* Boiss., *C. rupestre* Boiss & Heldr. and *C. rupicola* Hartvig & Strid, (b) *Carum buriaticum* (incl. *C. furcatum*), and (c) *C. apuanum* (Viv.) Grande and *C. graecum* Boiss. & Heldr. have each still uncertain positions in the *Pyramidoptereae* sensu Downie & al. (2010).

(6) *Carum komarovii* and recircumscription of *Aegopodium* — *C. komarovii* has to be excluded from *Carum* s.str. and to be united with *Aegopodium*. The genus has also to be enlarged by two species, currently treated as *Chamaele decumbens* and *Pimpinella anthriscoides*, see clade B. After these transfers, *Aegopodium* contains 10 species.

Aegopodium decumbens (Thunb. ex J. A. Murray) Pimenov & Zakharova, **comb. nov.** ≡ *Sium decumbens* Thunb. ex J. A. Murray, Syst. Veg., ed. 14: 284. 1784; Thunb., Fl. Jap.: 118. 1784 ≡ *Chamaele decumbens* (Thunb.) Makino in Bot. Mag. (Tokyo) 17: 14. 1903. – Holotype: Japan, “in insula Nipon, prope Iedu et Faknam, Thunberg” (L).

= *Chamaele tenera* Miq. in Ann. Mus. Bot. Lugduno-Batavi 3: 60. 1867 ≡ *Aegopodium tenerum* (Miq.) Yabe in J. Coll. Sci. Imp. Univ. Tokyo 16, 2 [Rev. Umbell. Jap.]: 46, t. 1, fig. 22, 23. 1902 ≡ *Carum tenerum* (Miq.) Koso-Pol. in Bull. Soc. Imp. Naturalistes Moscou, ser. 2, 29: 199. 1916, nom. illeg. [non Franch. 1894]. – Type: “Japan”.

= *Aegopodium tenerum* var. *japonicum* Yabe in J. Coll. Sci. Imp. Univ. Tokyo 16, 2 [Rev. Umbell. Jap.]: 47. 1902 ≡ *Chamaele decumbens* var. *japonica* (Yabe) Makino in Inuma, Somoku-dzusetsu, ed. 3, 1: 364, t. 16. 1907 ≡ *Chamaele japonica* (Yabe) Makino ex Yabe in J. Coll. Sci. Imp. Univ. Tokyo 16: 47. 1902 ≡ *Chamaele decumbens* f. *japonica* (Yabe) Ohwi, Fl. Jap.: 849. 1953. – Holotype: Japan, “in horto botanico Tokyoensis culta, 2.5.1899, Makino” (TI!).

= *Chamaele decumbens* var. *gracillima* H. Wolff in Engler, Pflanzenreich 90: 333. 1927. – Type: Japan, “Shikoko, in Wäldern des Berges Tsungsi, Faurie 3985.

= *Chamaele decumbens* var. *micrantha* Masamune in J. Soc. Trop. Agric. Taiwan 4: 76. 1932. – Type: Japan, “Insl. Yaku, near Miyanoura, 1.9.1931, Masamune 1432”.

= *Chamaele decumbens* f. *flabellifoliolata* Y. Kimura in J. Jap. Bot. 16: 59. 1940. – Lectotype (designated here): Japan, “Shinryo-mura, Nanishi-gun, prov. Awa, 1.5.1938, Abe 2” (TI!); paralectotype: “Sikoku, Prov. Awa, Myosaigun, Zinryo-mura, 23.5.1937, Abe 40” (TI).

= *Chamaele decumbens* f. *dilatata* Satake & Okuyama in J. Jap. Bot. 18: 661. 1942. – Holotype: Japan, “Mt. Ibuki, prov. Ohmi, 23.5.1942, Satake & Okuyama” (TNS!).

Ref. — Thunberg 1784: 285 (sub *Sium decumbens*); Candolle 1830: 126 (sub *Sium decumbens*); Linnaeus 1753: fig. 15 (sub *Carum tenera*); Makino 1907: 363, t. 15; Wolff 1927: 332; Ohwi 1953: 848; Hara 1954: 304; Hiroe & Constance 1958: 35, fig. 17; Kitagawa 1960: 14; Hiroe 1979: 990; Kitagawa 1982: 281, t. 256–3; Ito & al. 1994: 371; Ohba 1999: 281.

Distribution. — Japan (Hokkaido; Honshu; Shikoku; Kyushu).

Aegopodium komarovii (Karjagin) Pimenov & Zakharova, **comb. nov.** ≡ *Carum komarovii* Karjagin in Izv. Azerb. Fil. Akad. Nauk SSSR 10: 48. 1944. – Syntypes: “Azerbaidzhan, distr. Dostaffjur, ad pedes m-tis Koschkar dagh, c. 2200 m alt., 27.5.1928, *Doluchanov*” (BAK, TBI); “Azerbaidzhan, ad pedes m-tis Koschkar-Dagh, c. 2200 m, 14.7.1928, *Serdjukov*” (BAK, TBI); “Azerbaidzhan, in faucibus fl. Koschkar-tschaj, 19.7.1928, *Serdjukov*” (BAK, TBI); “Armenia, distr. Nor-Bajazet, in m-bus supra pag. Schich-keja, c. 2000 m alt., 19.7.1923, *Grossheim*” (BAK!).

Ref. (all sub *Carum komarovii*) — Schischkin 1950: 352; Akhundov 1955: 444; Tamamschjan 1967: 76, map. 82; Mandenova 1973: 353.

Distribution. — Armenia, Azerbaidzhan.

Aegopodium tribracteolatum Schmalh. in Ber. Deutsch. Bot. Ges. 10: 289. 1892 [non *Aegopodium anthriscoides* (H. Boissieu) H. Boissieu 1909]. – Holotype: Georgia, “Transcaucasia, prope Borshom, 2800', 6.6.1887, *Akinfev* (LE!).

= *Pimpinella anthriscoides* Boiss., Fl. Orient. 2: 874. 1872 ≡ *Pseudopimpinella anthriscoides* (Boiss.) F. Gharem. & al. in Flora, Morphol. Distrib. Funct. Ecol. Pl. 205: 353. 2010. – Lectotype (designated here by Pimenov & Jacquemoud): Iran, “M. Avroman et Schahu Persiae occid. ad rivulos, 4000–6000' [Montes Avroman et Schahu], 7.1867, *Hausknecht 507*” (G-BOIS!; isolectotypes: JE!, LE!, W); paralectotypes: [Lebanon], “Libanus supra Eden et Cedros et in Caelesyria prope Balbek, in humidiusculis regionis alpinae, 8.–19.5.1867, *Blanche 717, 727*” (G-BOIS!); Turkey, “Mons Amanus supra Arsus, 1862, *Kotschy*” (G-BOIS!)

= *Pimpinella cervariifolia* Freyn & Sint. in Bull. Herb. Boissier 3: 303. 1895. – Holotype: [Turkey], “Armenia turcica, Szandschak Gumuschakhane, Tempede, in fruticetis, 22.8.1894, *Sintenis 7541* (LD!; isotypes: B!, G!, WU!).

Note. — When *Pimpinella anthriscoides* is transferred to *Aegopodium*, the epithet *anthriscoides* cannot be used, as the resulting combination is already in use for a different, Chinese species (Boissieu 1909). The second oldest

available name is *A. tribracteolatum* Schmalh.

Ref. (sub *Pimpinella anthriscoides* unless otherwise stated) — Akinfev 1893: 22; Post 1896: 350; Lipsky 1899: 318; Sommier & Levier 1900: 179; Wolff 1927: 306; Wolff 1927: 331; Grossheim 1932: 161 (sub *P. cervariifolia*); Post 1932: 520; Thiebaut 1936: 144; Parsa 1948: 730; Schischkin 1950: 432; Karjagin 1955: 456; Rechingner 1959: 313; Townsend 1964: 429; Tamamschjan 1967: 86, map 93; Mouterde 1970: 609, tab. 274, fig. 1; Matthews 1972: 363, map 55; Mandenova 1973: 365; Mozaffarian 1983: 51; Engstrand 1987: 330, tab. 262, 488; Menitski 1991: 1757; Heller & Heyn 1993: 26; Mozaffarian 2007: 338; Menitski 2008: 85.

Distribution. — Iran (W: W Azarbayjan, Kordestan, Hamadan, Lorestan; N: Mazandaran; C: Tehran, Chaharmahal va Bakhteyari), Azerbaidzhan, Georgia, Armenia, Turkey (N (Pontic) Anatolia: Kastamonu, Ordu, Giresun, Çoruh; C Anatolia: Ankara, Çankiri, Sivas, Bilecik, Eskişehir, Konya, Kayseri; S Anatolia: Antalya; E Anatolia: Gümüşhane, Erzincan, Malatya, Tunceli, Bitlis, Van, Hakkari), Iraq, Lebanon, Syria.

(7) *Pimpinella cruciata* — This species is to be excluded from *Pimpinella* and transferred to *Tamamschjanella*; *T. rubella* (based on *Eleutherospermum rubellum*) appears to be conspecific.

Tamamschjanella cruciata (Bornm. & H. Wolff) Pimenov & Zakharova, **comb. nov.** ≡ *Pimpinella cruciata* Bornm. & H. Wolff in Repert. Spec. Nov. Regni Veg. 17: 44. 1921 ≡ *Pimpinella anthriscoides* var. *cruciata* (Bornm. & H. Wolff) V. A. Matthews in Davis, Fl. Turkey 4: 364. 1972 ≡ *Pseudopimpinella anthriscoides* var. *cruciata* (Bornm. & H. Wolff) F. Gharem. in Ann. Naturhist. Mus. Wien, B, 112: 501. 2011. – Lectotype (designated here by Pimenov): [Turkey], “Turkish-Armenien, Gumuschkhane, Tempede, in frutices, 19.7.1894, *Sintenis 7255*” (B!; isolectotypes: BM, E!, G!, JE!, K!, LD!, LE!); paralectotypes: Turkish-Armenien: Koesoedagh, *Sintenis 1311* (LD!); Turkish-Armenien, Sipikordagh, Pirin baghre, *Sintenis 3193* (B!, JE!, LD!); Pontus: Amasia, Ak Dagh, *Bornmüller 374* (B!).

= *Eleutherospermum rubellum* E. A. Busch in Trudy Bot. Muz. Akad. Sci. URSS 23: 229. 1931 ≡ *Pleurospermum rubellum* (E. A. Busch) Flerov, Spisok Rast. Severn. Kavkaza & Daghest.: 396. 1938 ≡ *Tamamschjanella rubella* (E. A. Busch) Pimenov & Kljuykov in Bot. Zhurn. 81(8): 76. 1996 ≡ *Ligusticum rubellum* (E. A. Busch) Menitsky, Konspekt Fl. Kavkaza 3,1: 95. 2008. – Lectotype (designated by Pimenov & Kljuykov in Bot. Zhurn. 81(8): 76. 1996): [Georgia], “Ossetia austr., fauces Sba, latus dextrum, Fageto-Piceetum supra pagum Sba interior, 2000 m, 19.7.1929, *E. Busch & N. Busch*” (LE!).

Ref. — Wolff 1927: 306 (sub *Pimpinella cruciata*); Grossheim 1932: 141 (sub *Eleutherospermum rubellum*); Schischkin 1950: 237, p.p. (sub *E. lasicum* auct. non Boiss. & Balansa); Tamamschjan 1967: 54, map 58 (sub *E. lasicum* auct. non Boiss. & Balansa); Mandenova 1973: 320; Mandenova 1984: 180 (sub *E. lasicum* auct. non Boiss. & Balansa); Engstrand 1987: 330 (sub *P. anthriscoides* var. *cruciata*); Zernov 2006: 417 (sub *Tamamschjanella rubella*).

Distribution. — Russia (N Caucasus: Adygea, Karachai-Cherkessia, Kabardino-Balkaria, N Ossetia), Azerbaidzhan, Iran (N: Mazandaran), Georgia, Armenia, Turkey (N (Pontic) Anatolia: Çoruh, Ordu, Çoruh; C Anatolia: Amasya; E Anatolia: Gümüşhane, Erzincan).

Note. — *Pimpinella cruciata* cannot be regarded as a variety of *P. anthriscoides*. Moreover, it belongs to another genus, not closely related to *Aegopodium*, where *P. anthriscoides* has been transferred in the present revision. *P. cruciata* has true affinity with the Balkan - Near Eastern - Caucasian genus *Tamamschjanella*. Both previously known species of *Tamamschjanella* (*T. rubella* and *T. rhizomatica*) have, like *Aegopodium*, horizontal rhizomes, differing, however, in the presence of bracts.

According to initial descriptions (Bornmüller & Wolff 1921; Busch 1931), *P. cruciata* differs from *Eleutherospermum rubellum* (basionym of *T. rubella*) in petal colour (*albida* = somewhat white in *P. cruciata* versus red in *T. rubella*), all other features in the two species are the same. However, our investigation of type material in both Lund (LD) and St-Petersburg (LE) herbaria revealed that the petals of *P. cruciata* are whitish (pale) only after drying, whereas initially they seem to be red, what can be confirmed by examining better preserved plants. So, the two species are regarded here as conspecific.

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Appendix

Voucher information and GeneBank accession numbers for plants used in the present study.

Aegopodium alpestre Ledeb.: U78436, U78376 (Downie & al. 1998). *A. decumbens* (Thunb. ex J. A. Murray) Pimenov & Zakharova [= *Chamaele decumbens* Makino]: (1) DQ516364 (Spalik & Downie 2007); (2) Japan, Honshu, Tochigi pref., Nikko national park, near Chezeng lake, 27.5.1956, *Hedberg 6222* (UPS), JQ792194. *A. handelii* H. Wolff: China, Hunan prov., Mt. Yün-schan, 7.8.1917, *Handel-Mazzetti 11146* (WU), JQ792195. *A. kashmirica* (R. R. Stewart ex Dunn) Pimenov: cult. Moscow State University Botanical Garden, Russia, JQ792197. *A. komarovii* (Karjagin) Pimenov & Zakharova [= *Carum komarovii* Karjag.]: (1) Armenia, eastern slope of Khustup Mt., Kafan distr., 8.7.1977, *Pimenov & al. 1274* (MW), JQ792198; (2) Azerbaijan, Khanlar prov., Kjapaz Mt., 8.6.1971, *Gogina 1882* (MHA), JQ792199. *A. latifolium* Turcz.: Russia, Irkutsk prov., Lake Baikal, near Utulik, 14.8.1992, *Pimenov & Kljuykov 83* (MW), JQ792196. *A. podagraria* L.: cult. Moscow State University Botanical Garden, Russia, JQ792200. *A. tadshikorum* Schischk.: cult. Moscow State University Botanical Garden, Russia, JQ792201. *A. tribracteolatum* Schmalh.: (1) [= *Pimpinella anthriscoides* Boiss.] AY581783 (Tabanca & al. 2005); (2) [= *Pimpinella anthriscoides* Boiss.] Armenia, Takerlu, 4.6.1977, *Pimenov & al. 164* (MW), JQ792203; (3) [= *Pimpinella anthriscoides* Boiss.] Azerbaijan, Dzhimi, 11.8.1978, *Pimenov & al. 338* (MW), JQ792204; (4) [= *Pimpinella cervarifolia* Freyn & Sint.] Turkey, Turkish-Armenien, Szandshak Gümüşchakhane, Tempede, 22.8.1894, *Sintenis 7541* (LD), JQ792234; (5) Georgia, Transcaucasia, near Borshom, 6.6.1887, *Akinfiiev s.n.* (LE), JQ792202. — *Af-rocarum imbricatum* (Schinz) Rauschert: AY360228 (Hardway & al. 2004). — *Aphanopleura trachysperma* Boiss.: AF009108 (Katz-Downie & al. 1999). — *Arafoc aromaticum* Pimenov & Lavrova: U78443 (Downie & al. 1998). — *Berula erecta* (Huds.) Coville: DQ005656 (Spalik & Downie 2006). *B. erecta* var. *incisa* (Torr.) Cronquist: DQ005648 (Spalik & Downie 2006). *B. erecta* subsp. *thunbergii* (DC.) B. L. Burt: AY353976 (Hardway & al. 2004). — *Bunium bulbocastanum* L.: DQ443722, DQ443724 (Degtjareva & al. 2009). *B. elegans* (Fenzl) Freyn AF073543, AF073544 (Downie & al. 2000a). *B. ferulaceum* Sm.: DQ435219, DQ435258 (Degtjareva & al. 2009). *B. mauritanicum* Batt.: DQ435226, DQ435265 (Degtjareva & al. 2009). *B. paucifolium* DC.: DQ435229, DQ435268 (Degtjareva & al. 2009). *B. persicum* (Boiss.) B. Fedtsch.: DQ435230, DQ435269 (Degtjareva & al. 2009). *B. pinnatifolium* Kljuykov: DQ435231, DQ435270 (Degtjareva & al. 2009). *B. rectangulum* (Boiss. & Hausskn.) H. Wolff: DQ435232, DQ435271 (Degtjareva & al. 2009). *B. scabrellum* Korovin: DQ435234, DQ435273 (Degtjareva &

al. 2009). — *Carum alpinum* (M. Bieb.) Benth. [= *Seseli alpinum* M. Bieb.]: Russia, Krasnodar Terr., Republic of Adygea, the Caucasian reserve, 19.7.1936, *Pimenov & al. 409* (MW), JQ792205. *C. appuanum* (Viv.) Grande: AY840985, AY840984 (Papini & al. 2007). *C. buriaticum* Turcz.: (1) Russia, Chita prov., Olovjanninsky distr., near Olovjannaya, 20.8.1993, *Pimenov & Vassilieva 97* (MW), JQ792206; (2) Russia, Altay region, Teletsky lake reserve, 30.7.1959, *Kurganskaja & Kurchenko s.n.* (MW), JQ792207; (3) Russia, Burjatia, Lake Salty, 16.8.2006, *Kazanovsky s.n.* (IRK), JQ792208. *C. carvi* L.: (1) Kirghizia, Issyk Kul region, Kadzhi-Say, 42°7'N, 77°12'E, 14.8.2010, *Ukrainskja & Zakharova 16* (MW), JQ792209; (2) Armenia, Megrinsky ridge, N slope of Chignovar Mt., 6.7.1977, *Pimenov & al. 1209* (MW), JQ792210; (3) Russia, Karachai-Cherkessia, Zelenchuk region, Zelenchukskaja, 3.6.2007, *Zernov & Mitin s.n.* (MW), JQ792211. *C. caucasicum* Boiss.: (1) Russia, Kabardino-Balkaria, 21.8.1970, *Pimenov & al. 428* (MW), JF510478; (2) Georgia, Kazbek district, Krestovaja Mt., near Gudauri, 10.8.1966, *Gogina 2039* (MHA), JQ792212. *C. furcatum* H. Wolff: China, Shansi, Chieh hesiuh distr., Mien-Shan, Sung-lin-miao, 18.6.1924, *Smith 5838* (UPS), JQ792213. *C. graecum* subsp. *serpenticum* Hartvig: (1) Greece, Grevena, Vourinos mountain range, eastern from Exarhos, 19.8.1983, *Hegenenn & al. s.n.* (LD), JQ792214; (2) *Hartvig & Christsansen 8332* (C), JQ792215. *C. grossheimii* Schischk.: (1) Abkhazia, 23.7.1987, *Ostroumova & al. 133* (MW), JF510479; (2) Georgia, Svanetia, upper part of Devry river, Hida pass, 25.8.1965, *Pimenov 1152* (MW), JQ792216; (3) Georgia, South Ossetia, upper part of Great Liakhvi river, 21.7.1956, *Gogina s.n.* (MHA), JQ792217. *C. heldreichii* Boiss.: (1) AY840989, AY840988 (Papini & al. 2007); (2) Greece, Sterea Ellas, Phokidhos, Vardousia Mt., E-ENE from Artotina, 26.8.1982, *Hartvig & al. 10471* (C), JQ792218. *C. meifolium* (M. Bieb.) Boiss.: (1) Russia, Krasnodar Terr., 18.7.1976, *Pimenov 392* (MW), JF510480; (2) Georgia, Megrel ridge, upper part of Tekhuri river, 11.7.1971, *Rusanovich s.n.* (MHA), JQ792219; (3) Russia, Karachay-Cherkessia, Teberda Reserve, 9.7.1976, *Pimenov & al. 332* (MW), JQ792220. *C. porphyrocoleon* (Freyn & Sint.) Woronow ex Schischk.: (1) Georgia, Trialeti ridge, near Bakuriani, 15.7.1977, *Pimenov & al. 1374* (MW), JF510481; (2) NE Turkey, Arsian ridge, Artvin, 6.7.1984, *Pimenov & al. 232* (MW), JQ792221. *C. rupestre* Boiss. & Heldr.: Greece, Kozani, Siniatsikon Mt., 6 km SSE of Vlasti, 30.8.1980, *Franzén 229* (LD), JQ792222. *C. rupicola* Hartvig & Strid: Turkey, 50 km SW Antalya, Tantalı, 17.7.1984, *Gork & al. 23604* (B), JQ792223. *C. saxicolum* Albov: Georgia, Svanetia, upper part of Tshenistskali river, 15.8.1973, *Pimenov 743* (MW), JQ792224. — *Chamaescidium acaule* C. A. Mey.: (1) GQ379318 (Spalik & al. 2010); (2) Russia, Karachai-Cherkessia, upper part of Mahar river, 4.8.2006, *Zernov & al. s.n.* (MW), JQ792225. — *Cicuta maculata* L.:

- AY524741 (Lee & Downie 2006). *C. virosa* L.: AY524764 (Lee & Downie 2006). — *Cnidiocarpa alai-*
ca Pimenov: AF008615, AF009094 (Katz-Downie & al. 1999). — *Cnidium silaifolium* Fiori & Paol.: U78407,
 U78467 (Downie & al. 1998). — *Crithmum maritimum*
 L.: U30541, U30540 (Downie & Katz-Downie 1996). — *Cryptotaenia canadensis* DC.: U79613 (Downie & al.
 1998). *C. flahaultii* Koso-Pol.: DQ516349 (Spalik &
 Downie 2007). *C. japonica* Hassk.: AY360236 (Hardway
 & al. 2004). — *Elaeosticta nodosa* Boiss.: AY941271,
 AY941299 (Valiejo-Roman & al. 2006a). — *Falcaria*
vulgaris Bernh.: AF077888 (Valiejo-Roman & al. 1998).
 — *Fuernrohrria setifolia* K. Koch: AF009112, AF008633
 (Katz-Downie & al. 1999). — *Galagania fragrantissima*
 Lipsky: DQ422820, DQ422839 (Degtjareva & al. 2009).
 — *Gongylosciadium falcarioides* (Bornm. & Wolff)
 Rech. f.: EU169272 (Ajani & al. 2008). — *Grammoscia-*
dium daucoides DC.: AF073559 (Downie & al. 2000a).
G. macrodon Boiss.: AF073553 (Downie & al. 2000a).
G. platycarpum Boiss. & Hausskn. ex Boiss.: AF073551,
 AF073552 (Downie & al. 2000a). *G. pterocarpum*
 Boiss.: AF073557, AF073558 (Downie & al. 2000a). *G.*
scabridum Boiss.: AF073555, AF073556 (Downie & al.
 2000a). — *Haplosphaera phaea* Hand.-Mazz.:
 EU236167 (Zhou & al. 2008). — *Hellenocarum multi-*
florum H. Wolff: AY840986, AY840987 (Papini & al.
 2007). — *Helosciadium crassipes* W. D. J. Koch:
 AY360239 (Hardway & al. 2004). *H. nodiflorum* (L.) W.
 D. J. Koch: AY360240 (Hardway & al. 2004). — *Hlad-*
nikia pastinacifolia Rchb.: EU169287 (Ajani & al. 2008).
 — *Hyalolaena jaxartica* Bunge: DQ422823, DQ422842
 (Degtjareva & al. 2009). — *Mogoltavia sewerzowii* (Re-
 gel) Korovin: DQ422827, DQ422846 (Degtjareva & al.
 2009). — *Oenanthe fistulosa* L.: DQ005664 (Spalik &
 Downie 2006). *O. palustris* (Chiov.) C. Norman:
 EU233941 (Spalik & al. 2009). — *Oxypolis occidentalis*
 J. M. Coult. & Rose: AY360254 (Hardway & al. 2004).
O. rigidior (L.) Raf.: EF177743 (Downie & al. 2008).
 — *Oedibasis apiculata* (Kar. & Kir.) Koso-Pol.:
 DQ422828, DQ42284 (Degtjareva & al. 2009). — *Olym-*
posciadium caespitosum Sibth. & Sm.: Turkey, Pimenov
 & al. s.n. (MW), JQ792226. — *Perideridia americana*
 (Nutt. ex DC.) Rchb. ex Steud.: AY246909 (Downie & al.
 2004). *P. kelloggii* (A. Gray) Mathias: AY246967 (Down-
 ie & al. 2004). — *Physospermopsis cuneata* H. Wolff:
 FJ385055 (Zhou & al. 2009). — *Physospermum cornu-*
biense (L.) DC.: AF077904 (Valiejo-Roman & al. 1998).
 — *Pimpinella acuminata* C. B. Clarke: EU236193
 (Zhou & al. 2008). *P. affinis* Ledeb.: AY581780 (Tabanca
 & al. 2005). *P. anisetum* Boiss. & Balansa: AY581781
 (Tabanca & al. 2005). *P. aromatica* M. Bieb.: AY581784
 (Tabanca & al. 2005). *P. aurea* DC.: AY581785 (Tabanca
 & al. 2005). *P. caffra* D. Dietr.: FM986447 (Magee & al.
 2010). *P. candolleana* Wight & Arn.: EU236194 (Zhou
 & al. 2008). *P. cappadocica* Boiss. & Balansa: AY581786
 (Tabanca & al. 2005). *P. corymbosa* Boiss.: AY581787
 (Tabanca & al. 2005). *P. cretica* Poir.: AY581789 (Ta-
 banca & al. 2005). *P. diversifolia* DC.: DQ516369 (Spalik
 & Downie 2007). *P. eriocarpa* Banks & Sol.: AY581790
 (Tabanca & al. 2005). *P. favifolia* C. Norman: FM986458
 (Magee & al. 2010). *P. flabellifolia* (Boiss.) Benth. &
 Hook.: AY581791 (Tabanca & al. 2005). *P. henryi* Diels:
 EU236195 (Zhou & al. 2008). *P. isaurica* Matthews:
 AY581792 (Tabanca & al. 2005). *P. kotschyana* Boiss.:
 DQ516373 (Spalik & Downie 2007). *P. nudicaulis*
 Trautv.: AY581794 (Tabanca & al. 2005). *P. oliverioides*
 Boiss. & Hausskn.: AY581795 (Tabanca & al. 2005). *P.*
paucidentata V. A. Matthews: AY581796 (Tabanca & al.
 2005). *P. peucedanifolia* Fisch. ex Ledeb.: AY581798
 (Tabanca & al. 2005). *P. puberula* (DC.) Boiss.:
 AY581799 (Tabanca & al. 2005). *P. purpurea* H. Bois-
 sieu: EU236197 (Zhou & al. 2008). *P. rhodantha* Boiss.:
 AY581800 (Tabanca & al. 2005). *P. rockii* H. Wolff:
 FJ385057 (Zhou & al. 2009). *P. saxifraga* L.: AY581801
 (Tabanca & al. 2005). *P. sintenisii* H. Wolff: AY581802
 (Tabanca & al. 2005). *P. tragium* subsp. *pseudotragium*
 (DC.) Matthews: AY581805 (Tabanca & al. 2005). *P.*
transvaalensis H. Wolff: FM986449 (Magee & al. 2010).
P. yunnanensis H. Wolff: FJ385058 (Zhou & al. 2009).
 — *Postiella capillifolia* (Post ex Boiss.) Kljuykov:
 DQ422829, DQ422848 (Degtjareva & al. 2009). —
Psammogeton biternatum Edgew.: AF164839,
 AF164864 (Downie & al. 2000b). *P. canescens* (DC.)
 Vatke: AF009109, AF008630 (Katz-Downie & al. 1999).
 — *Pyramidoptera cabulica* Boiss.: AF008631,
 AF009110 (Katz-Downie & al. 1999). — *Rhabdoscia-*
dium aucheri Boiss.: AF073549, AF073550 (Downie &
 al. 2000). — *Saposhnikovia divaricata* (Turcz.)
 Schischk.: AF495838, AF495839 (Spalik & al. 2004). —
Scaligeria moreana Engstrand: AH008893 (Downie &
 al. 2000). *S. napiformis* (Willd. ex Spreng.) Grande:
 DQ422830, DQ422849 (Degtjareva & al. 2009). —
Schulzia albiflora (Kar. & Kir.) Popov: DQ422831,
 DQ422850 (Degtjareva & al. 2009). *S. crinita* (Pall.)
 Spreng.: AY328949, AY330515 (Valiejo-Roman & al.
 2006b). *S. prostrata* Pimenov & Kljuykov: HM229406.
 — *Selinum broteroi* Hoffmanns. & Link: AY179029
 (Spalik & al. 2004). *S. carvifolia* (L.) L.: AY179028
 (Spalik & al. 2004). *S. libanotis* W. D. J. Koch: AF009082,
 AF008603 (Katz-Downie & al. 1999). *S. peucedanoides*
 Hayek: AF008613, AF009092 (Katz-Downie & al.
 1999). *S. tortuosum* L.: AY179031 (Spalik & al. 2004).
 — *Sinolimprichtia alpina* H. Wolff: GQ379336 (Spalik
 & al. 2010). — *Sium bracteatum* (Roxb.) Cronk:
 AY353982 (Hardway & al. 2004). *S. latifolium* L.: (1)
 DQ005669 (Spalik & Downie 2006), (2) DQ005671
 (Spalik & Downie 2006). *S. repandum* Welw. ex Hiern:
 DQ005680 (Spalik & Downie 2006). *S. serra* (Franch. &
 Sav.) Kitag.: DQ005681 (Spalik & Downie 2006). *S. si-*
sarum L.: AY360262 (Hardway & al. 2004). — *Tamam-*
schjanella cruciata (Bornm. & H. Wolff) Pimenov &
 Zakharova [= *Pimpinella cruciata* Bornm. & H. Wolff]:
 (1) Turkey, Turkish-Armenien, Koesoedagh, 17.7.1889,
Sintenis 1311 (LD), JQ792232; (2) Turkey, Turkish-Ar-

- menien, Gümüşchakhane, Tempede, 19.7.1894, *Sintenis* 7255 (LD), JQ792227; (3) Turkey, Turkish-Armenien, Sipikordagh, Pirin baghre, *Sintenis* 3193 (LD), JQ792233. — *Tamamschjanella rhizomatica* (Hartvig) Pimenov & Kljuykov: DQ422826, DQ422845 (Degtjareva & al. 2009). — *Tamamschjanella rubella* (E. Busch) Pimenov & Kljuykov: DQ422833, DQ422852 (Degtjareva & al. 2009). — *Trachyspermum ammi* (L.) Sprague: U78380, U78440 (Downie & al. 1998). — *Trinia hispida* Hoffm.: EU169330 (Ajani & al. 2008). — *Trocdaris verticillatum* (L.) Raf. [= *Carum verticillatum* (L.) W. D. J. Koch]: (1) United Kingdom, Scotland, 30–40 km to NW from Glasgow, 56°14'50"N, 4°43'10"W, 5.7.2003, *Seregin & Naikatini E-270* (MW), JQ792228; (2) United Kingdom, Wales, 51°52'N, 3°50'W, 13.7.1980, *Jury & Rumsey 1409* (MHA), JQ792229. — *Vicatia atrosanguinea* (Kar. & Kir.) P. K. Mukh. & Pimenov: (1) Kirghizia, Chujsky region, Ak-Tjuz, 2700 m, 42°53'N, 76°10'E, 12.8.2010, *Ukrainskaja & Zakharova 3* (MW), JQ792230; (2) Kazakhstan, Altai Mts., Burkhat pass, 14.8.1972, *Pimenov 451* (MW), JQ792231. *V. conifolia* DC.: EU169331 (Ajani & al. 2008).