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Research

Molecular data to elucidate the taxonomy of *Seseli* sect. *Seseli* (Apiaceae) in east Mediterranean and southern Europe

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The taxonomy of the type section of the genus *Seseli* is revised based on newly obtained molecular data. The type species of the genus, *Seseli tortuosum*, is shown to be a polyphyletic taxon and is split into two species: the western Mediterranean *S. tortuosum* and the eastern Mediterranean *S. arenarium*. The Turkish endemics *S. hartvigii*, *S. serpentinum* and *S. andronakii*, and the Transcaucasian *S. grandivittatum* form a complex of closely related species together with *S. arenarium*. The results of the molecular analysis confirm the specific rank of *S. corymbosum*, *S. phrygium* and *S. paphlagonicum* and the status of *S. gummiferum* as distinct from either of these three. The latter species is strictly endemic to Crimea and does not occur in Turkey.

Keywords: Crimea, nrDNA, plant taxonomy, *Seseli tortuosum*, Turkey, Umbelliferae

Introduction

The genus *Seseli* L. (Apiaceae, Apioideae) is represented by numerous species (more than 135) distributed in the Old World from western Europe and northwestern Africa to China and Japan (Pimenov and Leonov 1993). The majority of the species of this genus are narrow endemics, growing in arid conditions, in calcareous rocks and on rocky slopes.

The composition of the type section of *Seseli*, i.e. of the species closely related to the type species *S. tortuosum* L., has not been clearly outlined to date. This is due to the imperfection and incompleteness of the supraspecific classification of *Seseli* species, most of which are regional endemics, and to controversies about the lectotypification of the genus. Drude (1898) attempted to classify all known species of the genus. He distinguished four subgenera, one of them typical ('*Eu-Seseli*'), containing five sections. Section II ('Seselia genuina') includes *S. tortuosum* and some other species, some of which are now sometimes treated in other sections. Calestani (1905) recognized five sections for the European species, with *S.* sect. '*Euseseli*' being the most speciose (32 species). In Flora Europaea (Ball 1968) however, a different classification of European species of *Seseli* was proposed: they were divided into two subgenera,

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Libanotis (Hill) Drude and *Seseli*, the latter containing 31 species, without further classification.

Other attempts to classify the species of *Seseli* have been undertaken mainly for the species known from the former Soviet Union (Schischkin 1950, Pimenov and Sdobnina 1975, Pimenov 1978), where, in spite of the enormous area, some infrageneric groups are absent. Schischkin (1950) divided *S.* sect. '*Euseseli*' into ten series; their names remained *nomina illegitima* being described only in Russian. Later, Pimenov and Sdobnina (1975), Pimenov (1978) and Pimenov and Ostroumova (2012) raised some of these series at the sectional level, and ser. *Peucedanoides* even as a separate genus, i.e. *Gasparrinia* Bertol. Among the species of the former Soviet Union, nine belong to *S.* sect. *Seseli* (Pimenov and Sdobnina 1975, Pimenov 1978), namely *S. petraeum* M. Bieb., *S. dichotomum* Pall., *S. alexeenkoi* Lipsky, *S. rupicola* Woronow, *S. tortuosum* (incl. *S. campestre* Besser), *S. leptocladum* Woronow, *S. gummiferum* Pall. ex Sm., *S. lehmannii* Degen, and *S ponticum* Lipsky.

In Turkey, according to Hedge and Lamond (1972), with additions by Davis et al. (1988) and Duman (2000), the genus is represented by ten species, including *S. gummiferum*, which was treated in the broad sense, with a single Turkish subsp. *corymbosum* (Boiss. & Heldr.) P.H. Davis. Some corrections to the taxonomy of the Turkish *Seseli* species were also made later. Hartvig and Strid (1987) described a new species, *S. ramosissimum* Hartvig & Strid from Toros Dağlari, but this name appears to be a latter homonym of *S. ramosissimum* (Port. ex Spreng.) Ces. Thus, the combination of Hartvig & Strid was subsequently replaced by *S. hartvigii* Parolly & Nordt (Parolly and Nordt 2001). Southam (1999) attempted to revise *S. rubellum* Post, for which he found a new locality between Fethiye and Köyceğiz in Muğla Province. Southam (1999) compiled an updated description of *S. rubellum* and attributed to the species another collection from Hatay Province. The plant described by him, however, does not correspond to characters of the type collection of *S. rubellum* from 'Bithynia' stored in G [G00359703]. Then, Pimenov and Kljuykov (2010) described two species related to *S. gummiferum*; they treated the latter as a narrow endemic of the southern shore of the Crimean Peninsula, absent from Turkey. These two new species are *S. paphlagonicum* Pimenov & Kljuykov from Kastomonu Province and *S. phrygium* Pimenov & Kljuykov from Eskişehir Province. Doğan Güner and Duman (2013) published a revision of Turkish species of *Seseli*, with descriptions of two new species, *S. marashicum* E.Doğan & H.Duman (as '*marashica*') from the Kahramanmaraş and Kayseri Provinces, and *S. serpentinum* B.L.Burtt ex H.Duman & E.Doğan (2013) (as '*serpentina*') from Muğla Province. *Seseli serpentinum* seems to be a legitimate name for '*S. rubellum*' in the sense of Southam (1999).

As some issues remain controversial, we decided to combine our efforts for elucidating the taxonomy of Turkish and Mediterranean species of *Seseli* by comparison of plant material from adjacent countries. Taking into consideration that all previous taxonomic treatments were based only on morphological data and, on the other hand, that the molecular approach is becoming a common aspect of taxonomic studies of plants at various levels (Blockeel et al. 2017, Fedosov et al. 2017, Ignatova et al. 2017, Krinitsina et al. 2017, Lyskov et al. 2017a, b, Yurtseva et al. 2017), we also aimed to undertake molecular analysis of the Mediterranean taxa of the type section of the genus *Seseli* and related species, with special emphasis on the eastern Mediterranean.

Seseli sect. *Seseli* s.str. includes two clearly distinguished species groups: the '*S. tortuosum* complex' and the '*S. gummiferum* complex'. In both taxonomic groups there are some controversies in the treatment of species.

In the '*S. tortuosum* complex', the unresolved problem is the composition and borders (taxonomic and phytogeographical) of *S. tortuosum*, which is polymorphic. Some additional species and infraspecific taxa have been recognized in this complex, including *S. arenarium* M. Bieb. (Table 1). These taxa have either been included in or excluded from *S. tortuosum*, and consequently the range of the latter has been considered limited to the western and central Mediterraneen, or wider, including Turkey and European Russia (Euro+Med Plantbase) <www.emplantbase.org/home.html>.

Doğan Güner and Duman (2013) reported that *S. tortuosum* is more widely distributed in Anatolia, while *S. campestre* has a narrow distribution range close to the Sea of Marmara. However, the status of the circum-Marmara populations, identified as *S. campestre* by Doğan Güner and Duman, deserves further attention, as they seem to have constant morphological differences from the *S. campestre* type specimens originated from Ukraine.

Similar taxonomic problems and controversies exist in the '*Seseli gummiferum* complex'. The central species *S. gummiferum* was described from Tauria (Crimea), and has usually treated as a Crimean narrow endemic. However, de Candolle (1830) described a new variety within this species, *S. gummiferum* var. *crithmifolium* DC., from the Aegean island of Karpathos, later treated by Boissier (1872) and his followers as a separate species, but by P. H. Davis (1953) as a subspecies of *S. gummiferum*. Davis also included within *S. gummiferum* two more subspecies, one previously known as a separate species, *S. corymbosum* Boiss. & Heldr. (= *S. gummiferum* subsp. *corymbosum*), from central and southern Turkey, and a new *S. gummiferum* subsp. *aegeum* P.H. Davis from the Aegean Islands. Pimenov and Kljuykov (2010) described two species of the same group from Turkey: *S. paphlagonicum* and *S. phrygium*. The first species was later regarded by Doğan Güner and Duman (2013) as a synonym of the Crimean *S. gummiferum*, and the second one as a subspecies of *S. corymbosum*: *S. corymbosum* subsp. *phrygium* (Pimenov & Kljuykov) E. Doğan & H. Duman. Interestingly, *S. paphlagonicum* was described from the same area (Mt Ilgaz) by Çetin et al. (2015) as *S. gummiferum* subsp. *ilgazense* A. Duran, O. Çetin & M. Öztürk. Çetin et al. (2015) mention a collection of '*S. gummiferum*' from central Anatolia (Ankara Province); this might be the second locality of *S. paphlagonicum*. In addition to the above-mentioned taxa,

Table 1. Species of *Seseli* sect. *Seseli* distributed in eastern Europe and Asia Minor; species included in the present study are in bold.

Taxon	Synonyms	Distribution range
S. alexeenkoi Lipsky (1902)		southwest Russia
S. andronakii Woronow ex Schischk. (1950)		Turkey
S. arenarium M. Bieb. (1820)	*S. peucedanifolium* Besser (1822) *S. tauricum* Link ex Spreng. (1824) *S. puberulum* DC. (1830) *S. pauciradiatum* Schischk. (1950) *S. tenderiense* Kotov (1955) *S. aroanicum* Hartvig (1984) *S. tortuosum* subsp. *thracicum* Delipavlov (2000)	eastern Europe and southwest Asia
S. campestre Besser (1822)	*S. rubellum* Post (1985)	Ukraine, western Turkey
S. corymbosum Boiss. & Heldr. (1849)	*S. gummiferum* subsp. *corymbosum* (Boiss. & Heldr.) P.H. Davis (1953)	Turkey
S. dichotomum Pall. (1795)		Crimea
S. gummiferum subsp. *gummiferum* Pall. ex Sm. (1824)		Crimea
S. gummiferum subsp. *crithmifolium* (DC.) P.H. Davis (1952)		east Aegean Islands (Rodos), Karpathos
S. gummiferum subsp. *aegeum* P.H. Davis (1953)		Crete, Cyclades
S. halkensis C.Catt., Kit Tan & Biel (2016)		east Aegean Islands (Halki)
S. hartvigii Parolly & Nordt (2001)	*S. ramosissimum* auct. non (Port. ex Spreng.) Ces. (1836)	Turkey
S. lehmannii Degen (1898)		Crimea
S. leptocladum Woronow (1933)		Armenia
S. marashicum E.Doğan & H.Duman (2013)		Turkey
S. paphlagonicum Pimenov & Kljuykov (2010)	*S. gummiferum* subsp. *ilgazense* A.Duran, O.Çetin & M.Öztürk (2015)	Turkey
S. petraeum M. Bieb. (1808)		southwest Russia, Turkey
S. phrygium Pimenov & Kljuykov (2010)	*S. corymbosum* subsp. *phrygium* (Pimenov & Kljuykov) E.Doğan & H.Duman (2013)	Turkey
S ponticum Lipsky (1884)		southwest Russia
S. resinosum Freyn & Sint. (1894)		Turkey
S. rupicola Woronow (1905)		Abkhazia
S. serpentinum B.L.Burtt ex H.Duman & E.Doğan (2013)	*S. rubellum* auct. Southam, non Post (1895)	Turkey
S. tortuosum L. (1753)	*S. littoraee* Willk. (1851) *S. massiliense* Bubani (1899) *S. tortuosum* subsp. *maritimum* (Guss.) C. Brullo, Brullo, Giusso & Sciandr (2011)	western Europe and northern Africa (Portugal, Spain, France, Italy, Croatia, Slovenia , Tunisia, Algeria, Lybia)

the closest relatives of *S. gummiferum*, all of them calcareous chasmophytes, there are some other species belonging to the '*S. gummiferum* complex': *S. ponticum*, *S. dichotomum* and *S. lehmannii*, all from the Pontic basin.

The purposes of this study are 1) to investigate the molecular affinity among species of *Seseli* sect. *Seseli*, 2) to investigate the taxonomic and phylogenetic relationships within the '*S. tortuosum* complex', paying special attention to *S. tortuosum* in relation to taxa currently regarded as conspecific with it and, 3) to perform a similar investigation within the '*S. gummiferum* complex'.

Material and methods

DNA extraction, amplification and sequencing

Total DNA was extracted from fruits from herbarium specimens using a NucleoSpin Plant II kit following the protocol of the manufacturer. Detailed information about the ITS primers and PCR conditions have previously been provided by Valiejo-Roman et al. (2002). Primers for ETS sequence and conditions of amplification and sequencing were described by Logacheva et al. (2010). PCR products were purified using a DNA cleaning kit (Evrogen, Moscow, Russia) following instructions provided by the manufacturer. Determinative cycle sequence analysis was performed using an ABI Prism BigDye Terminator 3.1 sequencing kit followed by analysis of products on an automated DNA sequencer ABI Prism 3100-Avant. Newly obtained sequences were deposited in the GenBank (Appendix 1).

Alignment and phylogenetic analysis

ITS and ETS sequences were aligned using MUSCLE 3.6 (Edgar 2004) and manually adjusted in BioEdit 7.2.5 (Hall 1999). To infer phylogenetic relationships, Maximum Parsimony and Bayesian analyses were performed using a

set of ITS sequences from 48 samples of *Seseli*, *Angelica* L., *Bifora* Hoffm., *Coriandrum* L. and *Ferulago* W.D.J.Koch (Appendix 1). *Bifora testiculata* DC. was used as an outgroup based on the results of previous higher-level phylogenetic study of the subfamily Apioideae (Valiejo-Roman et al. 2006).

Maximum Parsimony (MP) analyses were performed using PAUP* 4.0.b08 (Swofford 2003) with TBR branch swapping and equal weighing of characters; gaps were treated as missing data. For each heuristic search, 1000 random sequence additions replicates were run and 1000 shortest trees were saved. Bootstrap values were calculated using 100 replicates with TBR branch swapping and random addition of taxa (Felsenstein 1985), saving the 1000 most parsimonious trees from each replicate. For assessment of bootstrap support (BS), we considered 85–100% as strong, 75–84% as moderate, and 50–74% as weak support (Kress et al. 2002).

Bayesian phylogenetic inference was performed using MrBayes 3.2.5 (Ronquist et al. 2012) with the GTR+G model of nucleotide substitutions, which was selected by AIC in MrModeltest 2.3 (Nylander 2004). The algorithm consisted of two independent runs with four chains for 15 000 000 generations, sampling one tree per 1000 generations. The first 50 (0.33%) trees were discarded as a burn-in, and a majority-rule consensus tree was constructed from the remaining trees. Because PP in Bayesian analyses are not equivalent to BS and are generally much higher (Ericson et al. 2003), we considered PP > 0.95 as well supported. In all analyses, gaps (indels) were treated as missing data. Visualisation of the trees was made in TreeView (Page 1996).

Results

The nrDNA data set of two intragenic spacer regions includes 1020 aligned characters; 51 ambiguous and gap-rich positions were excluded. Of these, 669 characters were constant and 159 characters were parsimony-uninformative. The number of (included) parsimony-informative characters is 195. Analysis of this data set resulted in one MP tree (tree length 585 steps; consistency index 0.728; retention index 0.799). Trees generated for the nrITS and nrETS regions are congruent between themselves and the combined tree. The trees generated for the nrITS region by different methods (MP and BI) have a similar topology; therefore we only present a Bayesian tree with the posterior probabilities and bootstrap percentages for the maximum parsimony provided (Fig. 1).

The topologies of both MP and BI trees strongly confirm two well-supported unequal clades of *Seseli* specimens: one small clade of three species (*S. montanum* L., *S. polyphyllum* Ten. and *S. bocconei* Guss.) and a large clade of the other studied *Seseli* species. The second clade splits into two large groups with strong support (PP 0.92): the first one is the '*Seseli tortuosum* complex', the second one is the '*Seseli gummiferum* complex' with some additional species, such as *S. petraeum*, *S. rigidum*, *S. marashicum*, *S. transcaucasicum* (Schischk.) Pimenov & Sdobnina and *S. libanotis* W.D.J.Koch (Fig. 1). The above-mentioned group has weak support (PP 0.6). The '*Seseli tortuosum* complex' includes *S. tortuosum*, *S. hartvigii*, *S. grandivittatum* Schischk., *S. serpentinum*, *S. andronakii*, *S. globiferum* Vis., *S. alexeenkoi* and *S. leptocladum*. *Seseli tortuosum* appears to be a non-monophyletic taxon and splits into two well-supported clades. *Seseli gummiferum* shows affinity to *S. corymbosum*, *S. paphlagonicum*, *S. phrygium*, *S. resinosum*, *S. lehmannii*, *S. rupicola*, *S. ponticum* and *S. dichotomum*, but this clade also contain some morphologically distant species, i.e. *S. transcaucasicum* and *S. libanotis*.

Discussion

Relationships within *Seseli* sect. *Seseli*

As revealed by our molecular analysis, the type species of *Seseli* sect. *Seseli*, viz *S. tortuosum*, forms a clade with *S. arenarium*, *S. hartvigii*, *S. andronakii*, *S. sepentinum*, *S. globiferum*, *S. alexeenkoi*, *S. grandivittatum* and *S. leptocladum*. This clade has moderate support (PP 0.8). A sister clade to *S. tortuosum* is the *S. gummiferum* clade, including the members of the '*S. gummiferum* complex' as well as *S. petraeum*, *S. rigidum*, *S. transcaucasicum*, *S. marashicum* and *S. libanotis*. This clade has only weak support (PP 0.6). Most of the species of this clade have previously been included in *S.* sect. *Seseli* based on morphological data (Pimenov 1978). However, this clade also contains two species previously placed in *S.* sect. *Libanotis* on the basis of morphological data (Pimenov and Sdobnina 1975): *S. transcaucasicum* and *S. libanotis*. We decided to include in *S.* sect. *Seseli* all aforementioned species except *S. transcaucasicum* and *S. libanotis*. In the present analyses, the two latter species together form a clade with strong support (PP 1.00). Although this small clade appears nested within the larger clade formed by the '*Seseli gummiferum* complex', this clade as a whole has only weak support (PP 0.6). Thus, we consider it is premature to transfer *S. transcaucasicum* and *S. libanotis* to *S.* sect. *Seseli*, in particular in light of the morphological differences documented by previous studies (Pimenov and Sdobnina 1975). Further study of these species is needed. However, in any case, the genus *Libanotis* may not be accepted as a separate genus.

The non-monophyletic nature of *Seseli tortuosum* sensu lato

This study includes, among others, numerous samples of the type species of the genus *Seseli,* viz *Seseli tortuosum*, and these were divided between two distinct groups in both the nrITS and nrETS analyses (Fig. 1). One clade is composed of *S. tortuosum* samples from the western Mediterranean region (clade A), while the other clade includes samples from the eastern Mediterranean and southwest Asia regions, the Turkish species *S. hartvigii*, *S. andronakii* and *S. serpentinum*, and the Transcaucasian species *S. grandivittatum* (clade B) (Fig. 2). Both clades have strong support (PP 1.0). Within each of these clades, the sequences are almost completely identical.

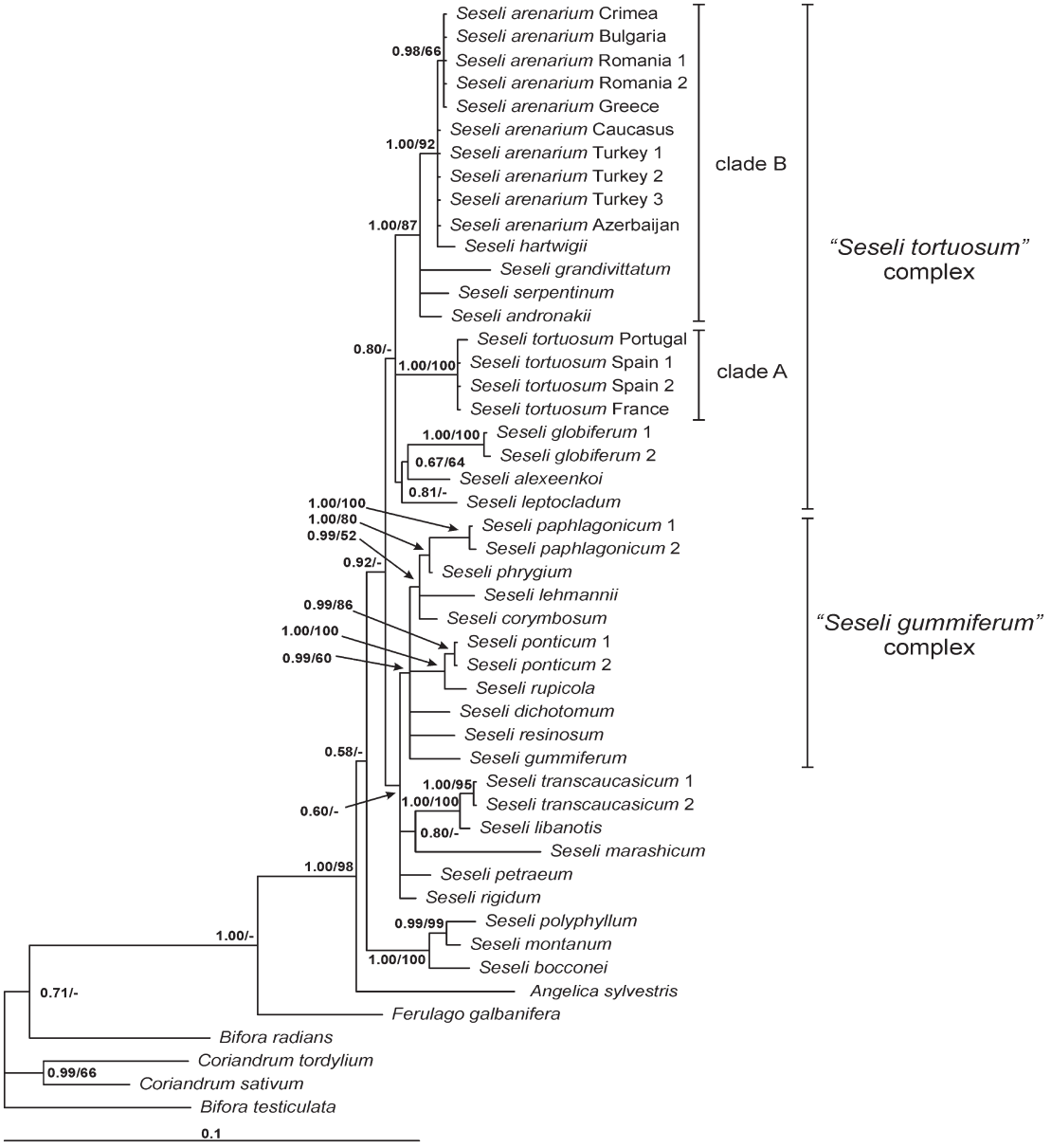

Figure 1. Bayesian analysis phylogenetic tree of nrITS/ETS nucleotide sequences. Posterior probability values and bootstrap values of a maximum parsimony analysis with similar topology are shown.

This division suggests a non-monophyletic nature of the polymorphic *S. tortuosum*, but does not confirm the existence of additional species. Only *S. hartvigii*, *S. andronakii* and *S. serpentinum* show differences from other specimens of clade B. The type specimen of *S. tortuosum* was collected from western Europe; therefore, this name is valid for the specimens of clade A. The specimens of *S. tortuosum* in clade B have been identified by the collectors as several different species: *S. tortuosum*, *S. pauciradiatum*, and *S. arenarium*. According to the International Code of Nomenclature for Algae, Fungi and Plants we have chosen the earliest of them, *S. arenarium* as the name of this species; the other combinations are treated by us as synonyms.

The third clade of the '*Seseli tortuosum* complex' consists of three species: *S. globiferum*, *S. alexeenkoi* and *S. leptocladum* (Fig. 1). These species are part of *S.* sect. *Seseli* according to morphological features, but they do not constitute an homogenous group. *Seseli globiferum* shows some affinities to the '*Seseli gummiferum* complex', while the other two species are closer to *S. tortuosum*. Further investigation of this group is needed to clarify its position in the '*Seseli tortuosum*' complex. Thus, according to our results, the '*Seseli tortuosum* complex' consists of the following species: *S. tortuosum*, *S. arenarium*, *S. hartvigii*, *S. andronakii*, *S. serpentinum*, *S. grandivittatum*, *S. serpentinum*, *S. globiferum*, *S. alexeenkoi* and *S. leptocladum*. The existence

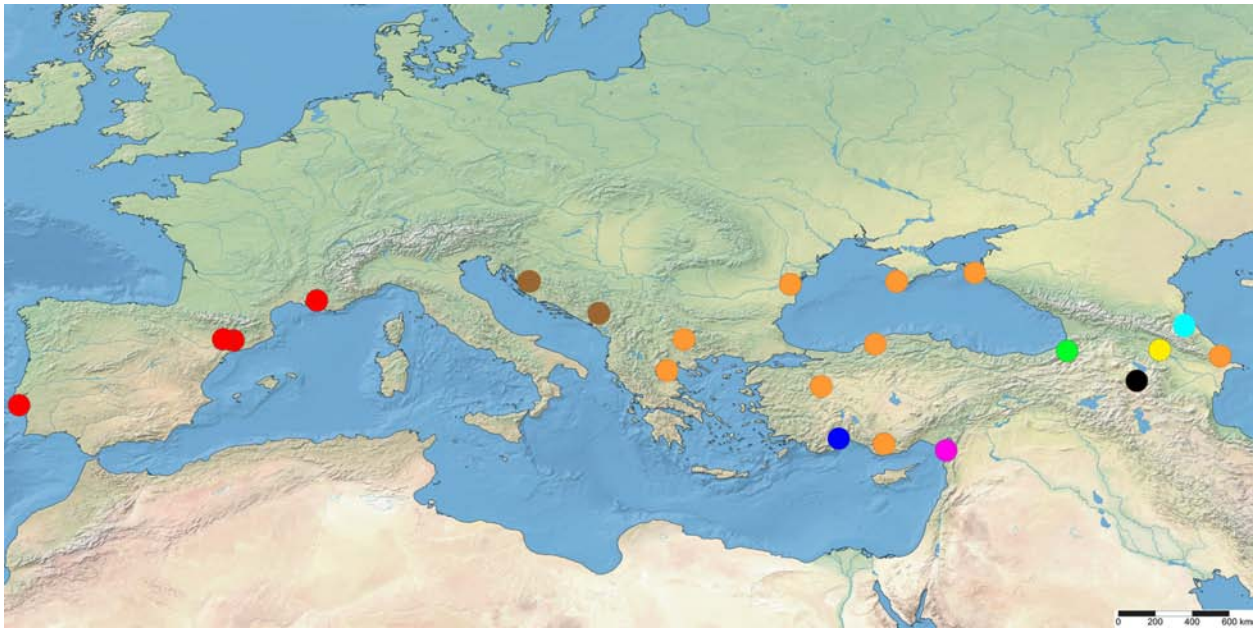

Figure 2. Distribution of *Seseli* specimens: *S. alexeenkoi* (light blue), *S. andronakii* (green), *S. arenarium* (orange), *S. globiferum* (brown), *S. grandivittatum* (yellow), *S. hartvigii* (blue), *S. leptocladum* (black), *S. serpentinum* (purple), *S. tortuosum* (red).

of two independent species in western Mediterranean and southwest Asia was also confirmed by analysis of coumarine composition since Muckensturm in Reduron (2008) noted that plants from Azerbaijan studied by Abyshev and Abyshev (1984) differ from Portuguese plants of *S. tortuosum* in this respect. These two species are also very similar in morphological features. However, as illustrated by of Reduron (2008) and Pignatti (1982), *S. tortuosum* does not have tumbleweed form, which is usual for *S. arenarium*. In addition, umbels of *S. tortuosum* are larger and the terminal segments of the leaves are shorter.

Relationships within the '*Seseli gummiferum* complex'

The specimens of the '*S. gummiferum* complex' form a clade with strong support (PP 0.99). Such controversial taxa as *S. corymbosum*, *S. paphlagonicum* and *S. phrygium* are nested in the clade with *S. lehmannii* with strong

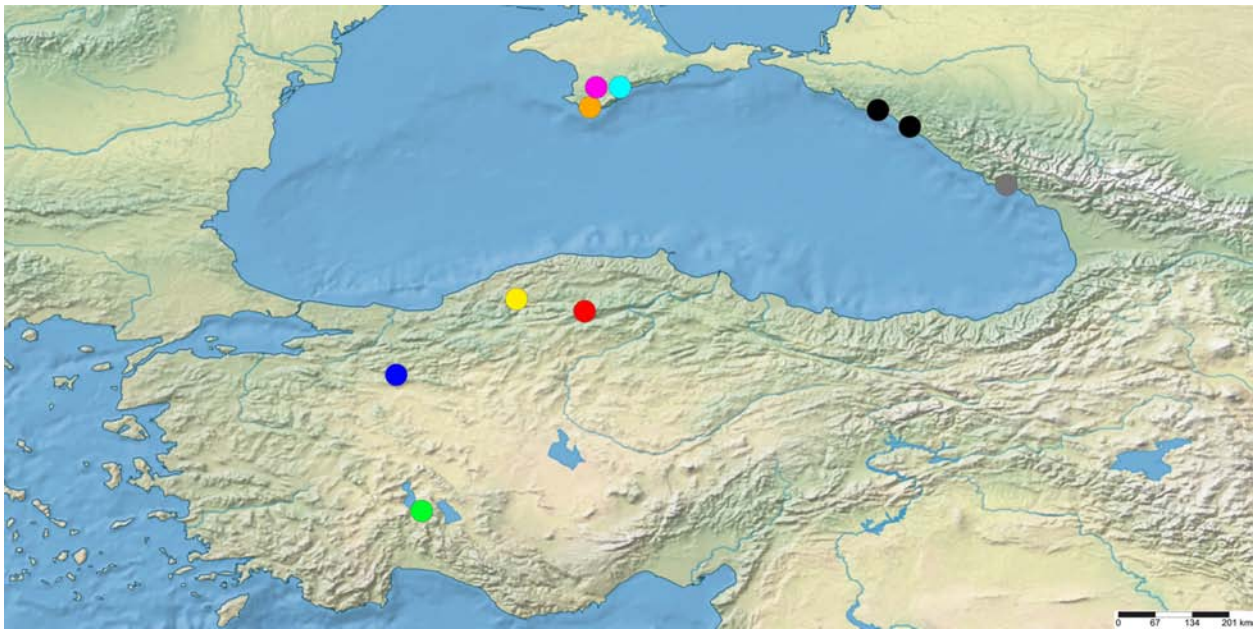

Figure 3. Distribution of *Seseli* specimens: *S. ponticum* (black), *S. rupicola* (grey), *S. gummiferum* (orange), *S. lehmannii* (purple), *S. dichotomum* (light blue), *S. paphlagonicum* (red), *S. phrygium* (blue), *S. resinosum* (yellow), *S. corymbosum* (green).

support (PP 0.99). The other clade in the '*S. gummiferum* complex' is formed by the Caucasian species *S. rupicola* and *S. ponticum*. *Seseli gummiferum*, *S. resinosum* and *S. dichotomum* do not form any clade. Thus, our results support the recognition of most species belonging to '*S. gummiferum* complex' as distinct taxonomic entities. However, molecular data do not confirm the presence of *S. gummiferum* in Turkey. *Seseli paphlagonicum*, which has been treated as a synonym (Doğan Güner and Duman 2013) or subspecies (Çetin et al. 2015) of *S. gummiferum*, appears to be a distinct species. *Seseli corymbosum* and *S. phrygium* are also independent species. Thus, *S. gummiferum* should be considered as a narrow endemic of the Crimean Mountains (Fig. 3).

Conclusions

A total of 12 species of *S.* sect. *Seseli* are distributed in southwest Asia: *S. andronakii*, *S. arenarium*, *S. corymbosum*, *S. grandivittatum*, *S. hartvigii*, *S. leptocladum*, *S. marashicum*, *S. paphlagonicum*, *S. petraeum*, *S. phrygium*, *S. resinosum* and *S. serpentinum*. Six more species are east Mediterranean and southeastern European: *S. alexeenkoi*, *S. dichotomum*, *S. globiferum*, *S. gummiferum*, *S. lehmanii*, *S. ponticum*, *S. rigidum* and *S. rupicola*. *Seseli tortuosum* s. str. is not distributed in these regions and is known only from western Europe. *Seseli gummiferum* is a strict endemic of Crimea and is not distributed in Turkey. The independent specific ranks of *S. marashicum*, *S. paphlagonicum*, *S. phrygium* and *S. serpentinum* are confirmed.

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Appendix 1

List of the plant material used in the study

Angelica sylvestris L.: HQ256681, HQ256688; *Bifora radians* M.Bieb.: JF807570, JF807550, JF807505; *B. testiculata* (L.) Spreng.: JF807571, JF807551, JF807506; *Coriandrum sativum* L.: JF807575, JF807555, JF807513; *C. tordylium* Bornm.: JF807576, JF807556, JF807514; *Ferulago galbanifera* W.D.J. Koch: AF077889, JF807520; *Seseli alexeenkoi* Lipsky: Russia, Dagestan, Pimenov, MW0699634 (MW) MG697118, MG697160; *S. andronakii* Woronow ex Schischk.: Turkey, Artvin Province, Pimenov et al., MW0744433 (MW) MG697135, MG697177; *S. arenarium* M.Bieb.: Russia, Krasnodar Krai, Kuvaeva & Chertikov, MW0700004 (MW) MG697123, MG697165; *S. arenarium*: Russia, Crimea, Seregin & Privalova, MW0621316 (MW) MG697124, MG697166; *S. arenarium*: Azerbaijan, Absheron District, Pimenov, MW0700014 (MW) MG697125, MG697167; *S. arenarium*: Turkey, Bursa Province, Pimenov & Kljuykov, 27 (MW) MG697144, MG697186; *S. arenarium*: Turkey, Bartın Province, Pimenov & Kljuykov, 124 (MW) MG697145, MG697187; *S. arenarium*: Turkey, Karaman Province, Pimenov & Kljuykov, 56 (MW) MG697146, MG697188; *S. arenarium*: Greece, Central Macedonia, Kljuykov & Ukrainskaya, 15 (MW) MG697149, MG697191; *S. arenarium*: Romania, Constanţa County, Paun & Popescu, 450a (MHA) MG697150, MG697192; *S. arenarium*: Bulgaria, Blagoevgrad Province, Khokhryakov & Mazurenko, s.n. (MHA) MG697153, MG697195; *S. arenarium*: Romania, Constanţa County, Paun & Popescu, 450b (MHA) MG697154, MG697196; *S. bocconei* Guss.; Italy, Sicilia, Pimenov, 7 (MW), MG697139, MG697181; *S. corymbosum* Boiss. & Heldr.: Turkey, Isparta province, Pimenov & Kljuykov, s.n. (MW) MG697129, MG697171; *S. dichotomum* Pall.: Russia, Crimea, Alexandrova & Belianska, MW0621247 (MW) MG697116, MG697158; *S. globiferum* Vis.: Croatia, Lotzel, s.n. (S) MG697137, MG697179; *S. globiferum*: Montenegro, Grebenscikov, 15919, (BEO) MG697147, MG697189; *S. grandivittatum* Schischk.: Georgia, Kostyleva, MW0699712 (MW) MG697120, MG697162; *S. gummiferum* Pall. ex Sm.: Russia, Crimea, Lavrova et al., MW0621255 (MW) MG697127, MG697169; *S. hartvigii* Parolly & Nordt: Turkey, Antalya Province, Duman, 6839 (GAZI) MG697138, MG697180; *S. lehmannii* Degen: Russia, Crimea, Vylezheanina, MW0621293 (MW) MG697114, MG697156; *S. leptocladum* Woronow: Armenia, Vayots Dzor Province, Pimenov, MW0699722 (MW) MG697117, MG697159; *S. libanotis* W.D.J.Koch: Russia, Dagestan, Maytulin, MW0699771 (MW) MG697128, MG697170; *S. marashicum* E.Doğan & H.Duman: Turkey, Kahramanmaraş Province, Doğan Güner, MW0595662 (MW) MG697143, MG697185; *S. montanum* L.: Italy, Liguria, Galosso, s.n. (MHA) MG697141, MG697183; *S. paphlagonicum* Pimenov & Kljuykov: Turkey, Kastamonu Province, Pimenov & Kljuykov, MW0593871 (MW) MG697130, MG697172; *S. paphlagonicum*: Turkey, Kastamonu Province, Pimenov & Kljuykov, 105, (MW) MG697133, MG697175; *S. petraeum* M.Bieb.: Russia, Karachay-Cherkessia, Zernov, MW0699861 (MW) MG697122, MG697164; *S. phrygium* Pimenov & Kljuykov: Turkey, Eskişehir Province Pimenov & Kljuykov, MW0593874 (MW) MG697131, MG697173; *S. polyphyllum* Ten.: Italy, Campania, Khokhryakov & Golovin, s.n. (MW) MG697136, MG697178; *S. ponticum* Lipsky: Russia, Krasnodar Krai, Khokhryakov & Mazurenko, MW0699967 (MW) MG697115, MG697157; *S. ponticum* Lipsky: Russia, Krasnodar Krai, Kozhin, MW0699983 (MW) MG697119, MG697161; *S. resinosum* Freyn & Sint.:Turkey, Karabük Province, Pimenov & Kljuykov, s.n. (MW) MG697132, MG697174; *S. rigidum* Waldst. & Kit.: Greece, Makedonia, Raus et al., 21939 (MHA) MG697140, MG697182; *S. rupicola* Woronow: Abkhazia, Gogina, MW0699986 (MW) MG697126,

MG697168; *S. serpentinum* B.L.Burtt ex H.Duman & E.Doğan: Turkey, Hatay Province, Duman, MW0595661 (MW) MG697142, MG697184; *S. tortuosum* L.: Portugal, Setúbal District, Santos, 196014 (LISU) MG697148, MG697190; *S. tortuosum*: France, Provence-Alpes-Côte d'Azur, Martin, 9498 (MHA) MG697151, MG697193; *S. tortuosum*: Spain, Catalonia, Monsterrat, 13377 (MHA) MG697152, MG697194; *S. tortuosum*: Spain, Catalonia, Monsterrat, 10489 (MHA) MG697155, MG697197; *S. transcaucasicum* (Schischk.) Pimenov & Sdobnina: Armenia, Aragatsotn Province, Pimenov, MW0699812 (MW) MG697134, MG697176; *S. transcaucasicum*: Armenia, Aragatsotn Province, Khokhryakov, MW-0699804 (MW) MG697121, MG697163.