

Redefining the phylogenetic relationships of European *Angelica* (Apiaceae) species

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4 **(Apiaceae) species**
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Redefining the phylogenetic relationships of European *Angelica* (Apiaceae) species

Angelica (Apiaceae) is a large complex genus with high morphological diversity. The many taxonomic treatments explain the controversy regarding the number of European species, which range from 4 to 10. Molecular methods have unraveled the complicated Asian and American taxonomies; however, no comprehensive molecular study has been conducted on the European taxa. We aim to determine the number of different European *Angelica* s. l. taxa and their relationship within the Selineae tribe by conducting Maximum Likelihood (ML) and Bayesian Inference (BI) analyses based on the nuclear Internal Transcribed Spacer (ITS) and haplotype networks by TCS and neighbor-net based on the plastid trnL. Three separate Iberian species (*A. angelicastrum*, *A. razulii*, and *A. pyrenaea*) formed the new Iberian Angelica clade, which is sister to the *Archangelica* clade. Although morphologically different, *A. pachycarpa* cannot be differentiated from *A. angelicastrum* by molecular methods, casting new doubts the existing taxonomies. Molecular evidences suggest that *A. heterocarpa* should be considered an estuary forma of *A. sylvestris*. The East and West *A. sylvestris* subclades support the subspecies *A. sylvestris* ssp. *elatior* and *A. sylvestris* ssp. *villosa* (including *A. heterocarpa*). Our evidences support the classification of *A. palustris* as *Ostericum palustre*.

Keywords: *Angelica*, *Archangelica*, Europe, Iberian Peninsula, Internal Transcribed Spacer (ITS), *Ostericum*, trnL

Introduction

Apiaceae Lindl. (1836) (=Umbelliferae nom. cons.) is a large family formed by 300-466 genera and 3000-3820 species (Constance 1971; Pimenov and Leonov 1993; Downie et al. 2001; Plunkett et al. 2018) which are systematized into four monophyletic subfamilies: Apioideae Drude, Azorelloideae G.M.Plunkett & Lowry (2004) (Hydrocotyloideae Link in part), Mackinlayoideae G.M.Plunkett & Lowry (2004) (Hydrocotyloideae Link in part) and Saniculoideae (Chandler and Plunkett 2004; Plunkett et al. 2004, 2018). The large monophyletic Apioideae subfamily has been

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3 traditionally divided by Drude (1898) into a group of tribes and subtribes that have been
4 often subjected to morphological (e.g. Downie et al. 2000; Downie et al. 2001; Calviño
5 and Downie 2007), serological (e.g. Shneyer et al. 1991) and molecular studies (e.g.
6 Katz-Downie et al. 1999), which have found the tribes not to be monophyletic.
7
8 Nevertheless, the comprehensive molecular studies of Downie et al. (2001) and Downie
9 et al. (2010) on the Apoid superclade found 10 monophyletic tribes based on nuclear
10 and plastid data: *Aciphyllae* M.F. Watson & S.R. Downie (2000), *Bupleureae* Spreng.
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12 (1820) (=*Bupleurum* L. (1753) clade), *Careae* Baill. (1879), *Echinophoreae* Benth.
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14 (1867), *Heteromorpheae* M. F. Watson & S. R. Downie (2000), *Oenantheae* Dumort.
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16 (1827), *Pleurospermeae* M. F. Watson & S. R. Downie (2000), *Pyramidoptereae* Boiss.
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18 (1872), *Scandiceae* Spreng. (1820) and *Smyrniaeae* Spreng. (1820).
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Within tribe Selineae (Apoid superclade), the genus *Angelica* L. (1753) *sensu lato* (s.l.) is the most taxonomically complex and includes approximately 90–120 species with high fruit diversity distributed throughout the temperate regions of the North hemisphere with a centre of differentiation in Japan and East Asia (Hiroe and Constance 1958; Pimenov 1978; Gutiérrez Bustillo 1981; Downie et al. 2001; She et al. 2005; Liao et al. 2012, 2013; Plunkett et al. 2018). *Angelica* s.l. has been subjected to recurrent changes in systematics (e.g. Drude 1898; Koso-Poljansky 1916; Feng et al. 2009) due to both the difficulties in discriminating this genus from others of its family without using fruit morphology and the existence of many synonyms as a consequence of the different conceptions of this genus and its species (Gutiérrez Bustillo 1981; Liao et al. 2020). Hence, taxa from other genera such as *Archangelica* Hoffm. (1814), *Coeloleurum* Ledeb. (1844), *Czernaevia* Turcz. ex Ledeb. (1844), or *Ostericum* Hoffm. (1816), which were historically considered *Angelica* species, have been reclassified by some authors based on features of fruits, pollen and other structures

(see Downie et al. 2000; Deyu et al. 2004; Spalik et al. 2004; Feng et al. 2009; Liao et al. 2013).

In this context, the phylogenetic studies based on the nuclear marker Internal Transcribed Spacers (ITS) and other plastid marker conducted by Feng et al. (2009) and Xue et al. (2007) shed some light on the polyphyletic character of *Angelica*, first on the Asian *Angelica* sensu stricto (s.s.) species (Xue et al. 2007; Feng et al. 2009) and later on a broader sample of species including American and some European representatives (Downie et al. 2010; Liao et al. 2012; Liao et al. 2020). These analyses revealed that even when some taxa included in genera such as *Coelopleurum*, *Czernaevia*, *Ostericum* Hoffm. pro parte, *Sphenosciadium* A. Gray (1865), *Melanosciadium* H. Boissieu (1902) or *Pimpinella* L. (1753) are reclassified as *Angelica* L., this would be a polyphyletic genus, since some of the taxa classically considered as *Angelica* were found in at least four major clades (the Acronema and Sinodielsia Clades and the Selineae and Tordyliinae tribes) (Downie et al. 2010).

The number of European genera and species within the Apiaceae family has been much discussed throughout history (see Table 1, Figure 1 and Table 2). More specifically, the number of *Angelica* different species ranges from 6 to 10 depending on the number of synonymies and satellite genera considered by some authors (e.g. Lange 1880; Cannon 1968; Gutiérrez Bustillo 1981; Castroviejo and Gutiérrez Bustillo 2003; Hand 2011). Thus, the two most relevant sources who treated all the European taxa, Cannon (1968) and The Euro+Med Plantbase Project (Hand 2011) are only coincidental in the recognition of 6 European species, 2 of which are distributed exclusively in the Iberian Peninsula. These differences in part are due to synonymies of 3 Iberian and 1 Pyrenean taxa: The Euro+Med Plantbase Project (Hand 2011) considers the taxa *Angelica angelicastrum* (Hoffmanns. & Link) Coutinho (1913) (= *Selinum*

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3 *angelicastrum* Hoffmanns. & Link (1834)) and *Angelica laevis* J.Gay ex Fisch. &
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5 C.A.Mey (1843) synonyms of *Angelica major* Lag. (1816), meanwhile Cannon (1968)
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7 does not even treat *A. major*, hence considering the latter two taxa as independent
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9 species. Moreover, Cannon (1968) and Flora Iberica (Gómez 2003) systematize
10 *Angelica pyrenaea* (L.) Spreng. (1813) within *Selinum* L. (1762), which would then be
11 homotypically synonymous to *Epikeros pyrenaeus* (L.) Raf. (1840) and *Seseli*
12 *pyrenaeum* L. (1753). Another source of discordance is the rare species *Angelica*
13 *palustris* Hoffm. (1814), which is endemic to eastern Europe and western Asia
14 (Dittbrenner et al. 2005). This species, which exhibits a wetland preference (Dittbrenner
15 et al. 2005), is classified within *Ostericum* Hoffm. (1816) as *Ostericum pratense* Hoffm.
16 (1816) (=*Ostericum palustre* (Besser) Besser (1822)) by The Euro+Med Plantbase
17 Project and other authors (e.g. Gutiérrez Bustillo 1981; Hand 2011; Liao et al. 2020),
18 but not by Cannon (1968). Conversely, the French endemic species of the Atlantic coast
19 estuaries of Loire, Charente, Gironde, and l'Adour et de la Nive, *Angelica heterocarpa*
20 J.Lloyd (1860), has been consistently considered a separated species from *Angelica*
21 *sylvestris* L. (1753) despite their morphological resemblance (Cannon 1968; Reduron
22 2007; Hand 2011; Cianfaglione and Bioret 2018).

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24 Besides *O. pratense* and *A. pyrenaea*, the Iberian and Pyrenean *Angelica* taxa
25 are an important source of disagreement as Lange (1880) listed 3 endemisms (*A. razulii*
26 Gouan (1773), *A. major* and *A. pachycarpa* Lange (1864) (Table 2)), while Cannon
27 (1968) cited only 4 *Angelica* species (*A. angelicastrum*, *A. razulii*, *A. laevis*, and *A.*
28 *pachycarpa*) and posterior morphological studies of herbarium samples by Gutiérrez
29 Bustillo (1981) and Castroviejo and Gutiérrez Bustillo (2003) referred to only 3 species
30 as they consider *A. angelicastrum*, *A. laevis* and *A. reuteri* Boiss. (1856) as synonymous
31 to *A. major*.

All these different classifications and synonymies based on morphological studies suggest that the diversity and systematics of the European *Angelica* s. l. species would benefit from molecular phylogenetic studies, especially the Iberian *Angelica*. However, up to this date, despite the demonstrated utility of these kinds of analyses in clarifying the taxonomy and phylogenetic relationships in the east Asian and North American *Angelica* taxa (Liao et al. 2013; Liao et al. 2020), no comprehensive molecular focus on the European *Angelica* species has been conducted. In this context, we aim to conduct the first comprehensive phylogenetic molecular study of the European *Angelica* s.l. taxa to determine the real number of European species and their phylogenetic relationships within the Selineae tribe by performing phylogenetic analyses based on nuclear and plastid molecular markers.

Material and Methods

Sample collection, DNA extraction and amplification

Leaf tissue from 51 samples of 10 *Angelica* s. l. taxa and 1 sample of *Sanicula europaea* L. (1753) from the Iberian Peninsula and Central and East Europe was collected for this study (see Table 3 and Figure 2). The leaf material was preserved in silica gel during transportation and before DNA extraction. DNA extraction was conducted using the Qiagen DNeasy® Plant Minikit (Qiagen Inc., Valencia, CA, USA), after which samples were kept at -20°C before amplification.

The nuclear molecular marker Internal Transcribed Spacer (ITS) and the plastid marker trnL were amplified by Polymerase Chain Reaction (PCR). The nuclear sequences of ITS1, 5.8 S and ITS2 were amplified using the pairs of primers ITS1 and ITS4 (White et al. 1990) and 17SE and 26SE (Sun et al. 1994), while the plastid sequence intron trnL (UAA) was amplified with the Lc and Ld primers (Taberlet et al.

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3 1991). The PCR mix consisted in a total volume of 25 µL containing 2.5 µL of 10x PCR
4 buffer (Biotoools), 2mM of MgCl₂, 0,2 mM of each dNTP (Biotoools), 0,5 µM of
5 primers, 1 U of Taq polimerase (Biotoools) and 10-20ng of DNA. The PCR consisted in
6 an initial denaturalization at 95°C for 2 minutes, followed by 35 cycles formed by a
7 denaturalization phase at 95°C during 1 minute, an annealing phase at 55°C for 1 minute
8 and an elongation phase at 72°C during 2 minutes, followed by a final elongation of 12
9 minutes at 72°C. Amplicons were sequenced using the Sanger method in the facilities of
10 Macrogen Inc. (Netherlands).

21 22 ***Phylogenetic analyses***

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25 The obtained new sequences were reviewed and edited in Geneious 2019 1.3. (Kearse et
26 al. 2012). Double peaks were considered to be “real” when it occurred in both forwardly
27 and reversely amplified sequences and the lower peak reached at least a third of the
28 height of the higher peak. Bases and ambiguities were coded following the International
29 Union of Pure and Applied Chemistry (IUPAC) criteria (International Union of Pure
30 and Applied Chemistry (IUPAC) 2020).

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33 Two different ITS data sets were created for this study: the European ITS dataset
34 and the Apioideae ITS dataset. The phylogenetic relationships among the recognized
35 European *Angelica* s. l. species was inferred by analysing the newly obtained ITS
36 sequences of the sampled individuals plus sequences from *Angelica* sequences from
37 previous studies (e.g. Liao et al. 2020) available at GenBank of taxa considered to be
38 European species (see Appendix for more detail). This dataset included sequences of the
39 type of *Angelica* (*A. sylvestris*), the sequences of 10 species with European distribution
40 and the Saniculoideae species *Sanicula europaea* L. (1753) as outgroup. *Sanicula*
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42 *europaea* was chosen as outgroup for this dataset since this included species from
43 genera that have been previously found in the Selineae tribe and in the Acronema clade
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(e.g. Liao et al. 2013; Liao et al. 2020) and a species from this genus has been successfully used in a similar phylogenetic analysis focusing on East Asia species, which comprised *Angelica* and *Ostericum* species (Huajie et al. 2007). In a wider context, the Apioideae ITS dataset was created so as to infer the relations of the European Angelica species with the rest of *Angelica* and Apioideae taxa. This dataset was formed by the sequences of the nuclear regions ITS1, 5.8 S and ITS2, whenever available, of the type species of the genera of the Apioideae subfamily sensu Downie et al. (2001). The Apioideae ITS dataset included sequences of taxa belonging to the Selineae tribe and the Acronema, the Arracacia and the Perennial Endemic North American Apiod (P.E.N.A) clades as described in previous studies (e. g. Downie et al. 2010; Liao et al. 2013), since these have been included in previous studies focused on the genera *Angelica* and *Ostericum* (e.g. Liao et al. 2013) (see Appendix 1 for sequences details). The inclusion of various sequences of the same species generated in different studies was favoured to detect potential misidentification among Genbank sequences and minimize the risk of extracting incorrect conclusions. Whenever a sequence of the type species of one genus was not available or was too short, sequences of several species of that genus where included in the analyses. Finally, the intron trnL (UAA) dataset (hereinafter called trnL dataset) consisted in 44 new intron trnL (UAA) sequences of the sampled taxa plus sequences of the European taxa available at Genbank from previous studies (see Appendix 1).

These datasets were aligned using the MUSCLE alignment method in Jalview 2.11.1.3 (Edgar 2004; Barton et al. 2009). The obtained alignments of the ITS and trnL datasets were manually edited before the diagnosis of best fitting nucleotide substitution model by the corrected Akaike Information Criterion (cAIC) using jModelTest 2.1.10 (Akaike, 1974; Darriba et al. 2012). The best fitting model for the Apioideae ITS

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3 dataset was the Symmetrical model with Gamma distribution (SYM+G) (Zharkikh
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5 and the General Time Reversible with Gamma distribution (GTR+G) (Tavaré
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7 1986; Yang 1994) for the European ITS dataset, while the best model for the trnL
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9 alignment was Felsenstein 1981 with Gamma distribution (F81+G) (Felsenstein 1981;
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11 Yang 1994).
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15 The phylogenetic relationships of the European *Angelica* between them and with
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17 the rest of Apiaceae were inferred by two different methods: Bayesian Inference (BI)
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19 and Maximum Likelihood (ML). The BI analyses consisting of 2 MCMC runs of 6
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21 chains (5 hot chains and 1 cold chain) for 10000000 generations with a temperature of
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23 0.1 and a burn-in fraction of 0.25 were performed in Mr. Bayes 3.2. (Tuffley and Steel
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25 1997; Yang and Rannala 1997; Larget and Simon 1999; Mau et al. 1999; Huelsenbeck
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27 and Ronquist 2001; Altekar et al. 2004; Ronquist et al. 2012). The posterior probability
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29 (PP) was calculated to infer the statistical support of the branches of the obtained
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31 topologies (Metropolis et al. 1953; Hastings 1970; Geyer 1991). On the other hand,
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33 ML analysis performed in IQtree (Saitou and Nei 1987; Nguyen et al., 2015;
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35 Trifinopoulos et al. 2016) consisted of an heuristic Tree Bisection Reconnection (TBR)
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37 search, Nearest-Neighbor Interchange (NNI) full-tree rearrangements and 10000
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39 ultrabootstrap (BT) replications in the case of the European ITS dataset and 5000
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41 ultrabootstrap replications in the case of the Apioideae ITS dataset for the branch
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43 support analysis of the obtained topologies (Robinson 1971; Moore et al. 1973; Minh et
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45 al. 2013; Chernomor et al. 2016; Hoang et al. 2018). Branches with less than 50% of
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47 support by PP or BT were collapsed in the final consensus tree.
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52 Phylogenetic relationships among the European species were also inferred by
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54 plastid-based haplotype network analyses. A phylogenetic network based on distances
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56 was generated using the neighbour-net analysis of Splitstree 14.4.4 (CBOL Plant
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Working Group et al. 2006). The statistical branch support was of this network was calculated by 10000 bootstrap repetitions. The Fitness of the model was estimated by the index Fit. A gene genealogy was estimated by the generation of a genealogy based on Templeton, Crandall and Sing (TCS) cladistics method in PopART 1.7 (Clement et al. 2002).

Results

The main features of the European and Apioideae ITS and trnL dataset alignments (excluding the outgroup taxa) used for this study are resumed in Table 4. The trnL dataset of the European *Angelica* species presented substantially less parsimomious-informative sites (17) than the ITS European *Angelica* species dataset (114), although it should be noted that the former presents 1 less *Angelica* taxa and included less sequences of the studied taxa. On the other hand, the Apioideae ITS dataset presented 410 parsimomious-informative sites and included 67 *Angelica* taxa.

The topology obtained after the phylogenetic analyses of the European ITS dataset (Figure 3) shows two major clades (PP: 100, BT: 100): the clade A (PP: 100, BT: 95) formed by *A. sylvestris* (ASYL1-8 and An 334-555), *A. razulii* (ARAZ 1-6), *A. reuteri* (AREU1), *A. laevis* (ALAE 1-8), *A. pyrenaea* (APYR 1-2), *A. major* (AMAJ 1-4), *A. archangelica* (AARC1), *A. decurrens*, *A. heterocarpa* (AHET 1-3), *A. lignescens* and *A. pachycarpa* (APA 1-8) and clade O (PP: 100, BT: 100) formed exclusively by *O. pratense* and *O. palustre* (APAL 1-4) sequences. The major clade A is subdivided into four subclades: the subclade AS (PP: 100, BT: 99), formed by sequences of *A. sylvestris* (ASYL1-8 and An 334-555) and *A. heterocarpa* (AHET 1-3); the subclade AIB (PP: 94, BT: 87), which comprises the subclade AI (PP: 96, BT: 88) formed by the Iberian endemisms (*A. razulii* (ARAZ 1-6), *A. reuteri* (AREU1), *A. laevis* (ALAE 1-8), *A. pyrenaea* (APYR 1-2), *A. major* (AMAJ 1-4) and *A. pachycarpa* (APA 1-8)) and the

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3 subclade AR (PP: 100, BT: 97), formed by samples of *A. archangelica* (AARC1) and *A.*
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5 *decurrens*; the subclade AL1 (PP: 74, BT: 71), which comprises sequences of *A.*
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7 *lignescens* from the Azoric islands of Pico and Terceira; and the subclade AL2 (PP: 55),
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9 formed by sequences of *A. lignescens* from the azoric islands of Flores, Faial and Sao
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11 Miguel. The subclade AI is subdivided into 3 clades of Iberian endemism. The
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13 individuals of *A. razulii* (ARAZ 1-6) grouped in their own highly-supported
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15 independent clade (PP: 100, BT: 95). Similarly, the individuals of *A. pyrenaea* (APYR
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17 1-2) generated their own clade (PP: 81, BT: 57), whereas the individuals of *A. reuteri*
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19 (AREU1), *A. laevis* (ALAE 1-8), *A. major* (AMAJ 1-4) and *A. pachycarpa* (APA 1-8)
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21 grouped in a single highly-supported subclade (PP: 100, BT: 98), in which our
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23 individual of *A. reuteri* (AREU1) formed a highly-supported subclade (PP: 98, BT: 96)
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25 with samples of cultivated *A. pachycarpa*. The subclade AR was formed one single
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27 clade comprising samples of *A. archangelica* (AARC1) and *A. decurrens*, which did not
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29 form species-exclusive inner subclades. The *A. sylvestris* subclade AS is divided into
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31 two different sister subclades: the ASH subclade (PP: 100, BT: 99) and the AEC
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33 subclade (PP: 99, BT: 78). The ASH subclade grouped together samples from
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35 individuals of *A. heterocarpa* (AHET1-3 and Genbank sequences) and from individuals
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37 of *A. sylvestris* sampled in the East Pyrenees (ASYL7-9), the Cantabrian Mountains
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39 (ASYL1-2 and ASYL4) and Central France (ASYL3). On the other hand, the AEC
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41 subclade is formed by individuals of *A. sylvestris* from Central and East Europe.
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48 The phylogenetic relationships of these species within Apioideae were clarified
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50 by the results of the analysis of the Apioideae ITS dataset (see Figure 4-8). The
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52 European samples were distributed in the Eurasian *Angelica* clade (PP: 99, BT: 72; see
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54 Figure 4), in the Archangelica-Iberian clade (PP: 90, BT: 81; see Figure 5) and in the
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56 Acronema (PP: 100, BT: 100; see Figure 7). The sampled *A. sylvestris* and *A.*
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3 *heterocarpa* (AHET 1-3) individuals were found in the *A. sylvestris* clade (PP: 100, BT:
4 100; see Figure 5) of the Eurasian *Angelica* clade. Within the *A. sylvestris* clade, the
5 highly-supported sister subclades which grouped together on the one side the *A.*
6
7 *heterocarpa* (AHET 1-3) and the Iberian *A. sylvestris* samples (PP: 100, BT: 100) and
8 on the other side the Central-East Europe *A. sylvestris* samples (PP: 99, BT: 100) can
9 also be found. The *A. sylvestris* clade is also sister to many other clades of the Eurasian
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11 *Angelica* Clade (PP: 72, BT: 94), including the two *A. lignescens* clades (AL1 PP: 96,
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13 BT: 100 and AL2 PP: 100, BT: 100).
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17 The Iberian endemic species and the sampled *A. archangelica* were found in the
18 Archangelica-Iberian clade (see Figure 5), which is sister (PP: 65, BT: 79) to the
19 Eurasian *Angelica* Clade and the North American Clade. This clade is subdivided in two
20 highly-supported sister clades: the Iberian clade (PP: 100, BT:100) and the
21 Archangelica clade (PP:95, BT:99). The Archangelica clade comprised European (i. e.
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23 *A. archangelica*), Asian (i. e. *A. decurrens* B. Fedtsch. (1909), *A. brevicaulis* B.
24
25 Fedtsch. (1909) and *Angelica tschimganica* V.N. Tikhom. (1967)) and American
26 species (i. e. *A. ampla* A. Nelson (1898) and *A. atropurpurea* L. (1753)), while the
27
28 Iberian clade was formed exclusively by Iberian endemism (*A. razulii* (ARAZ 1-6), *A.*
29
30 *reuteri* (AREU1), *A. laevis* (ALAE 1-8), *A. pyrenaea* (APYR 1-2), *A. major* (AMAJ 1-
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32 4) and *A. pachycarpa* (APA 1-8)). Within the Archangelica clade, the American species
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34 *A. ampla* and *A. atropurpurea* formed a moderately-supported clade (PP: 55, BT: 78),
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36 which comprised two species-exclusive highly supported clades: the *A. ampla* clade
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38 (PP: 81, BT: 100) and the *A. atropurpurea* clade (PP: 99, BT: 100). Nevertheless, it
39
40 should be noted that the partial *A. ampla* sequence AH006065 did not form part of any
41
42 of those clades. The sequences of *A. archangelica* and *A. decurrens* did not form
43
44 species-exclusive clades, neither the *A. brevicaulis* and *A. tschimganica* sequences,
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which were related with moderate support (PP: 63, BT: 66) to the rest of the clade. The *O. pratense* (=*A. palustris*) (APAL 1-4) samples were located in the *Ostericum* group (PP: 99, BT: 90, see Figure 7) within the Acronema clade, together with other *Ostericum* species and *A. anomala* Avé-Lall. (1999).

The haplotype networks obtained from the analyses of the European trnL dataset analyses present similar topologies (Figure 9 A and B). The neighbournet analysis reflects a well-fitting model (Fit: 92.685) which shows the Iberian clade is clearly separated (BT: 74.5) from the *A. sylvestris* and the *Ostericum palustre* clades and the *A. archangelica* sequence. In both analyses, the *Ostericum palustre* clade (BT: 99.4) is the most divergent clade, consistently with the nuclear data. The *A. sylvestris* clade included most of the *A. heterocarpa* sequences, as AHET2 (BT: 99.9) and ASYL1 (BT: 100) are separated from the rest of the group. A similar result was obtained with some Genbank sequences labelled as *A. sylvestris* in the TCS analysis (i.e. *A. sylvestris* GQ25456 and KF18351). Interestingly, the *A. archangelica* sequence is most closely related to the *A. sylvestris* clade than to the Iberian clade in both networks, in contrast with the results obtained with the nuclear data.

Discussion

The complicated taxonomic history of the genus *Angelica* is closely related to the morphology of these plants (Gutiérrez Bustillo 1982; Liao et al. 2020). The European taxa, particularly the Iberian taxa, have been subject to various systematic treatments based on their morphology (e.g. Cannon 1968; Liao et al. 2020), some of which propose different generic and subgeneric ascriptions for the same taxon. Our molecular analyses based on ITS and plastid markers have shed some light on the systematics of the European taxa, as they support the coexistence in Europe of an *Ostericum* taxon and 5 *Angelica* taxa belonging to two different highly supported clades within *Angelica* s.s.:

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2
3 the “*A. sylvestris* clade” and the “Archangelica-Iberian clade”.
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5 The phylogenetic analyses of the *A. sylvestris* clade based on nuclear markers
6 allowed greater resolution than the cpDNA analyses as it revealed the existence of two
7 clear geographical subclades within the European *A. sylvestris*, the East clade and the
8 West clade, and a group of undefined samples belonging to the North of Europe (i.e.
9 Finland, Russia, Iceland and Poland), the North group. The West subclade of the *A.*
10 *sylvestris* clade comprised two taxa which are closely related which inhabit Europe and
11 the Macaronesia (Bensettiti et al. 2002; Intuition Adour 2010; Cianfaglione and Bioret
12 2018) and have been traditionally considered as separated species. *A. sylvestris* L.
13 (1753) and *A. heterocarpa* Lloyd (1860). The samples of *A. heterocarpa* from the
14 French Loire-Atlantic region were genetically indistinguishable from the *A. sylvestris*
15 individuals of the East Pyrenees, the Cantabrian Mountains and Central France,
16 although there exist evident morphological differences, such as the fruit morphology the
17 presence of wide folioles and large umbel in *A. heterocarpa* (Bensettiti et al. 2002;
18 Reduron 2007). In addition, the nuclear marker results are further supported by the
19 plastid network, in which *A. heterocarpa* and *A. sylvestris* formed the same group.
20 Given our results based on molecular evidence in which *A. heterocarpa* individuals are
21 neither separated from the rest of *A. sylvestris*, nor they group in a *A. heterocarpa-*
22 exclusive inner subclade, we believe the morphological differences do not support the
23 consideration of *A. heterocarpa* as a distinct specie endemic to the French estuaries, but
24 rather support the consideration of a forma of *A. sylvestris* associated to the estuaries of
25 Loire, Charente, Gironde, and l'Adour et de la Nive. Moreover, the consideration of *A.*
26 *heterocarpa* as a forma and the inclusion of this taxon within *A. sylvestris* concurs with
27 both the intermediate *A. heterocarpa*- *A. sylvestris* forms observed by Metais et al.
28 (2008) and the experimental generation of hybrids by Bernard (1991).
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The existence of a West and an East *A. sylvestris* clade, which includes material collected in Central and East Europe, together with the observation about *A. sylvestris* variability (Gutiérrez Bustillo 1981; Reduron 2007) are compatible with the existence of at least two European subspecies of *A. sylvestris* that could correspond to the varieties *A. sylvestris* L. var. *villosa* (Lag.) Willkomm & Lange (1880) *A. sylvestris* L. var. *elatior* Wahlenb. (1814) as defined by Lange (1880). These authors specified that *A. sylvestris* var. *villosa* would occur in Asturias—North Iberian Peninsula—however, our data suggest that this subspecies occupies a broader range including not only Asturias, but also the French Atlantic coast, the Pyrenees and at least Central France. Furthermore, this distribution could be wider given the observation of Lagasca y Segura (1826) regarding the similarity between his *A. villoso* Lag. (1816) (=*A. sylvestris* var. *villosa* (Lag.) Willkomm & Lange (1880)) and the *A. sylvestris* of the British Islands and the report of this subspecies in the Basque Country (Reduron 2007). It should also be noted that according to our phylogenetic analyses based on molecular data, *A. heterocarpa* should be included within this subspecies. In this sense, the clade of *A. sylvestris* subp. *villosa* (the West *A. sylvestris* clade) could not correspond to the subspecies defined by Reduron (2007) *Angelica sylvestris* ssp. *bernardiae* Reduron (2007), as this taxon is supposed to show adaptations to the mountainous regions of Pyrenees and Jura and to be different from *A. heterocarpa*. On the other hand, the East *A. sylvestris* clade suggests the existence of *A. sylvestris* ssp. *elatior* in Central and Eastern Europe. However, we depend on limited samples to draw consistent conclusions about this clade, as the sequences from previous studies native to the same region were generated from cultivated individuals, therefore should be taken with caution. Hence, taking into account our results and the observation of Bernard (1991) about the caryology in this species, a more comprehensive study of these two taxa would be

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2 required to understand the observed morphological differences and their taxonomic
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4 consistency.
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7 Compellingly, the individuals of *A. sylvestris*, seem from a different taxon from
8 the morphologically similar Macaronesian endemism *Angelica lignescens* Reduron &
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10 Danton (1998) found in Madeira and Azores Islands (Danton et al. 1997; Press and Dias
11
12 1998) thus, supporting the separation into two species made by Danton et al. (1997).
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14 Moreover, the sequences from *A. lignescens* generated two independent clades—the
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16 Flores, Faial and Sao Miguel Clade and the Pico and Terceira Clade—within *Angelica*
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18 s.s., bringing further support to the remarks of Schaefer et al. (2011) about the need of
19
20 more in-depth studies to understand the biodiversity and origin of *A. lignescens*.
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24 The Archangelica-Iberian clade presents the inner clade of Archangelica and the
25 inner Iberian clade, retrieving thus a similar topology to that of Liao et al. (2020),
26 although these authors only included two *A. pachycarpa* (APA 1-8) samples and a *A.*
27
28 *razulii* (ARAZ 1-6) sample and did not describe an Iberian clade. This topology also
29 revealed new insights into the subgeneric position of the Iberian endemisms, which has
30 been treated differently through the years. De Candolle (1830) considered *Angelica*
31 Hoffm. (1814) and *Archangelica* Hoffm. (1814) as separate genera and subdivided
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33 *Angelica* Hoffm. (1814) into the sections Euangelica and Pseudoangelica, belonging *A.*
34
35 *razulii* and *A. sylvestris* to the former, and *A. pyrenaea* to the latter. On the other hand,
36 Cannon (1968) systematised the Iberian endemisms, together with *A. sylvestris* (for this
37 author =*A. major* (AMAJ 1-4) and *A. reuteri* (AREU1)) and *A. heterocarpa*, as part of
38 the subgenus *Angelica*, while *A. archangelica* would belong to the subgenus
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40 *Archangelica* (Hoffm.) Maxim. Our results revealed that all Iberian endemisms have a
41 close phylogenetic relationship with the Archangelica clade taxa, thus contradicting
42 both De Candolle (1830) and Cannon (1968) regarding the subgeneric adscription of
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3 these taxa. These results also suggest that the Iberian taxa could belong to the subgenus
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5 *Archangelica* (Hoffm.) Maxim; however, more research involving more genetic
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7 markers and more *Angelica* s. s. taxa is needed to verify this hypothesis and to clarify
8
9 the subgeneric classification of this genus.
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12 The Archangelica clade was similar to the Archangelica clade obtained by Liao
13 et al. (2012). Within this group, the *A. archangelica* L. (1753) and the *A. decurrens*
14 (Lebdeb.) B. Fedtsch (1909) sequences were not genetically distinguishable, as they
15 formed part of the same clade. Thus, this topology supports the hypothesis of Cannon
16 (1968), who argued that *A. decurrens* (Lebdeb.) B. Fedtsch (1909) was not a separate
17 entity and should be systematised as *A. archangelica* ssp. *archangelica*. Nevertheless, it
18 should be noted that most of the material from which the *A. archangelica* and the *A.*
19
20 *decurrens* sequences were obtained, was cultivated, not natural. Therefore, although the
21 current evidences are enough to determine that *Angelica tschimganica* (Klokov)
22 V.N.Tikhom. (1967) is not synonymous to *A. decurrens*, more samples belonging to
23 natural populations of are required to determine the taxonomic status of *A. archangelica*
24 and *A. decurrens* species. Thus, we take a conservative approach and consider them to
25 be closely related separate species.
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28 The Iberian Clade, supported by ITS and cpDNA evidence, comprised 6
29
30 *Angelica* endemic taxa which have been defined through the years—*A. razulii* Gouan
31 (1773), *A. reuteri* Boiss. (1856), *A. laevis* Gay ex Fisch., Mey. & Avé-Lall (1843), *A.*
32
33 *major* Lag. (1816), *A. pachycarpa* Lange (1864) and *Angelica pyrenaea* (L.) Spreng
34 (1813)—, but none of the *A. sylvestris* individuals collected in the Iberian Peninsula.
35 Nevertheless, the ITS results indicate that only 3 of the 6 *Angelica* endemic taxa could
36 be considered as separate species. The ITS phylogenies revealed that the Iberian taxa *A.*
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38 *reuteri*, *A. laevis*, *A. major* and *A. pachycarpa* form part of the same species, hence
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2 supporting the hypothesis of Gutiérrez Bustillo (1981) and Castroviejo and Gutiérrez
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4 Bustillo (2003) who, based on morphological data, considered *A. laevis* and *A. reuteri*
5 synonymous to *A. major* Lag. (1816) and contradicting that of Cannon (1968), who
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7 considered *A. major* and *A. reuteri* synonymous to *A. sylvestris*. However, it should be
8
9 considered that *A. major* Lag. (1816) has been found to be an invalid name as *Angelica*
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11 *major* Gilib. (1782) is a posterior homonym of *A. archangelica* L. (1753) (Fernández
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13 Prieto et al. 2020), consequently, *A. reuteri* and *A. major* should be considered as
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15 synonyms of *Angelica angelicastrum* (Hoffmanns. & Link) Coutinho, Fl. Portugal: 455
16
17 (1913) as that is the valid name (Castroviejo 2002).

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19 In addition to this pre-existing hypothesis, our phylogenetic topologies indicate
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21 that *A. pachycarpa* Lange (1864) is genetically indistinguishable from the *A.*
22
23 *angelicastrum* group, which is rather surprising since *A. pachycarpa* has always been
24
25 considered a separated taxon. The Iberian endemisms present similar leaf morphology,
26
27 the *A. pachycarpa* leaves being completely glabrous and “slightly fleshy” with a bright
28
29 green colouration, while *A. angelicastrum* group present dull green leaves with hairy
30
31 nerves at the underside (Castroviejo and Gutiérrez Bustillo 2003; Reduron 2007).
32
33 Moreover, *A. pachycarpa* can be found at coastal cliffs and lowlands of North West
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35 Iberian Atlantic coast, whereas the *A. angelicastrum* group taxa inhabit wet meadows
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37 up to 2100 m, mainly with siliceous substrates, of the Central and West Iberian
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39 Peninsula (Gutiérrez Bustillo 1981; Castroviejo and Gutiérrez Bustillo 2003). This
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41 information, together with the phylogenetic data, suggest that *A. pachycarpa* could be a
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43 subspecies of *A. angelicastrum* adapted to the specific conditions of coastal areas.
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45 Nonetheless, neither the possibility of the ITS marker being incapable to distinguish two
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47 separated taxa, nor the possibility of *A. pachycarpa* being a coastal forma of *A.*
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49 *angelicastrum* can be ruled out given the current knowledge of these two taxa. We
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3 favour the conservative approach and consider that *A. pachycarpa* should be systemised
4 as a separated species. Compellingly, the ITS sequences of *A. pachycarpa* by Liao et al.
5 (2020), which were obtained from cultivated samples in New Zealand—where
6 naturalised *A. pachycarpa* populations have been reported (Constance 1967; Webb
7 1978)—, generated a subclade with our *A. reuteri* sample within the Iberian clade. *A.*
8 *reuteri* Boiss. (1856) was first identified by Reuter as *A. laevis* J. Gay (1836) and later
9 separated into two taxa by Boissier (Gutiérrez Bustillo 1981). A posterior
10 morphological study by Gutiérrez Bustillo (1981) agreed with Reuter as this author
11 considered *A. reuteri* a synonym of *A. major* (*A. angelicastrum*). This hypothesis is also
12 supported by the phylogenetic position of *A. reuteri*, which conflict with the World
13 Flora Online databases, which considers *A. reuteri* a synonym of *A. sylvestris* (World
14 Flore Online (WFO) 2021).

15
16 The ITS-based analyses indicates that two other Iberian taxa, *A. razulii* Gouan
17 (1773) and *Angelica pyrenaea* (L.) Spreng (1813), should be considered distinct species
18 separated from the *A. angelicastrum* group. These results are unsurprising in the case of
19 *A. razulii*, as this Pyrenean endemism found in wet meadows up to 2000–2600 m is
20 easily distinguished from the rest of the Iberian endemism by the morphology of its
21 folioles and has been recognised as a separate species by many authors (Lange 1880;
22 Gutiérrez Bustillo 1981; Bernard 1991; Castroviejo and Gutiérrez Bustillo 2003;
23 Reduron 2007). The case of the Iberian mountainous endemism *A. pyrenaea* is more
24 surprising, since this taxon has been considered in the past as part of other genera like
25 *Selinum* L. (1753) or *Peucedanum* L. (1753) (e.g. Lange 1880; Cannon 1968). Our
26 results contradict the former hypothesis as the samples of this taxon are found in a
27 different clade from that of *Selinum carvifolia* L. (1762), type-species of *Selinum*, thus
28 suggesting that this taxon should not be classified as *Selinum pyrenaeum* (L.) Gouan
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(1773). Therefore, our results contradict the current taxonomy of Flora Iberia (Gómez 2003) and the World Flora Online databases (WFO 2021) on the one hand, while giving further support to the findings of Spalik et al. (2004), who argued that this species should be included in *Angelica*. Additionally, our analyses revealed that *A. pyrenaea*, a high-mountain endemism (1400–2700 m) found in acid substrate of wet grassland of the North and Central Iberian mountainous systems (from the Pyrenees to the Central System) (Gómez 2003), has a close phylogenetic relationship with another two Iberian taxa with preferences for different habitats: the *A. angelicastrum* group—whose members can be found from seaside altitudes to 2100 m (Castroviejo and Gutiérrez Bustillo 2003)— and *A. razulii*, another Pyrenean endemism found at altitudes ranging from 700 m to 2600 m (Castroviejo and Gutiérrez Bustillo 2003).

The taxonomy of *A. palustris* (Besser) Hoffm. (1814) is complex, as this species has been ascribed to genera such as *Imperatoria* Besser, *Ostericum* Hoffm. and *Angelica* L., being to this date considered to belong in *Angelica* by The Euro+Med Plantbase Project and World Flore Online (Hand 2011; WFO 2022). Our ITS results do not support the current treatment of this species, as this taxon seems to be closely related to other species belonging to *Ostericum* (*Ostericum* clade sensu Liao et al. (2013)) placed in the Acronema clade, which is robustly separated from Selineae tribe. Hence, our ITS results support the hypothesis of Gutiérrez Bustillo (1981) and Liao et al. (2020) of including this taxon within *Ostericum* Hoffm. (1816) as synonymous to the type of this genus *Ostericum palustre* (Besser) Besser (1822).

The molecular studies conducted on American and Asian *Angelica* taxa based on ITS and plastid markers such as rps16, trnL-trnT or psbM-psbD has allowed to clarify their taxonomy (Huajie et al. 2007; Feng et al. 2009; Liao et al. 2012; Liao et al. 2013; Liao et al. 2020). The application of a similar methodology to the European *Angelica*

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3 taxa has revealed that the Iberian endemic taxa are more closely related among them
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5 than with more widespread European taxa, even when their morphology suggests
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7 otherwise (e. g. *A. sylvestris* and *A. retueri*). Furthermore, the Iberian taxa are more
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9 closely related to the Asian, European and North American members of the
10
11 Archangelica clade than to the taxa with a Euroasian distribution found in *A. sylvestris*
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13 clade (e.g. *A. heterocarpa*), opening new questions regarding the process of
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15 colonization of the European continent. At a more specific level, an similarly to what
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17 has been observed in the American and Asian taxa (Liao et al. 2012; Liao et al. 2013;
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19 Liao et al. 2020), the Iberian-Archangelica and the *A. sylvestris* clades aggregate an
20
21 heterogeneous group of taxa with different foliar morphologies that have been
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23 considered separate, although the use of morphological characters has raised
24
25 controversies long before the molecular methods were (e.g. Lange 1880; Cannon, 1968;
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27 Gutiérrez Bustillo 1981). This morphologically heterogeneous clades suggests that (1)
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29 new and further morphological and ecological analyses must be conducted on these
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31 species, especially on taxa belonging to the *A. angelicastrum* and *A. sylvestris* groups
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33 and (2) more molecular analyses must be conducted in order to determine whether ITS
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35 and the used cpDNA sequences have enough resolution to solve this genus or other
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37 nuclear and plastid markers are more adequate.

46 Taxonomic treatment of European *Angelica* s.l. taxa

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48 • *Angelica archangelica* L., Sp. Pl.: 250 (1753)

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51 =*Angelica officinalis* Moench, Methodus (Moench): 81 (1794)

52
53 =*Archangelica archangelica* H.Karst., Deut. Fl. (Karsten): 843 (1882)

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55 =*Selinum archangelica* (L.) Vest Man. Bot. [Vest]: 501 (1806)

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3 • *Angelica angelicastrum* (Hoffmanns. & Link) Coutinho, Fl. Portugal: 455
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5 (1913)
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9 ≡*Selinum angelicastrum* Hoffmanns. & Link, Fl. Portug. 2: 428 (1834)
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11 = *Angelica angelicastrum* (Hoffmanns. & Link) Coutinho, Fl. Portugal: 455
12
13 (1913)
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15 = *Angelica hermini* Mariz, Bol. Soc. Brot. 12: 214 (1895)
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17 = *Angelica major* Gilib., Fl. Lit. Inch. ii. 24 (1782), nom. illeg.
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19 = *Angelica major* Lag., Gen. Sp. Nov. 13 (1816)
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21 = *Angelica laevis* J.Gay ex Fisch. & C.A.Mey., Index Sem. Hort. Petrop. 9: 58
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23 (1843)
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25 = *Angelica reuteri* Boiss., Diagn. Pl. Orient., ser. 2, 3: 87 (1856)
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33 • *Angelica decurrens* B.Fedtsch., Conspl. Fl. Turkestanicae [O.A. Fedchenko
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35 & B.A. Fedchenko] 3: 99 (1909)
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38 ≡ *Archangelica decurrens* var. *tschimganica* Klokov, Sched. Herb. Fl. As. Med.
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40 10: 12 (1826)
41
42 = *Archangelica decurrens* Ledeb., Fl. Altaic. 1: 316 (1829)
43
44 = *Archangelica decurrens* var. *alpina* Regel & Herder, Bull. Soc. Imp.
45
46 Naturalistes Moscou 39(II): 76 (1866)
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49 = *Angelica decurrens* B.Fedtsch., Beih. Bot. Centralbl., Abt. 2. 28(2): 44 (1911)
50
51 = *Angelica archangelica* var. *decurrens* (Ledeb.) Weinert, Feddes Repert. 84(4):
52
53 309 (1973)
54
55 = *Angelica archangelica* subsp. *decurrens* (Ledeb.) Kuvaev, Bot. Zhurn.
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57 (Moscow & Leningrad) 66(7): 952 (1981).
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7 • *Angelica lignescens* Reduron & Danton, Acta Bot. Gallica 144(1): 186
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9 (1998)
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- *Angelica lignescens* Reduron & Danton, Acta Bot. Gallica 144(1): 186
(1998)

- *Angelica pachycarpa* Lange, Descr. Icon. Pl. Nov.: 7, pl. 9 (1864)

- *Angelica pyrenaea* (L.) Spreng., Umb. 62. (1813)

≡*Seseli pyrenaeum* L., Sp. Pl.: 261 (1753)

=*Epikeros pyrenaicus* (L.) Raf., Good Book: 51 (1840)

=*Micrangelia pyrenaea* Fourr., Ann. Soc. Linn. Lyon sér. 2, 16: 388 (1868)

=*Oreoselinum pyrenaeum* Hoffm., Gen. Pl. Umbell.; 155 (1814)

=*Selinum pyrenaeum* (L.) Gouan, Obs. Bot.: 11 (1773)

- *Angelica razulii* Gouan, Ill. Observ. Bot.: 13. t. 6. (1773)

=*Angelica diversicolor* Dulac, Fl. Hautes-Pyrénées: 345 (1867)

=*Angelica ebulifolia* Lapeyr., Suppl. Hist. Pl. Pyrénées 1: 156 (1818)

=*Angelica flavesrens* Besser, Prim. Fl. Galic. 1: 213 (1809)

=*Angelica montana* Schleicher in Sprengel, Pl. Umb. Prodr.: 16 (1813)

=*Angelica tournefortiana* Cusson ex Steud., Nomencl. Bot. [Steudel] 50 (1821)

=*Imperatoria razoulii* Hort. Vindob. ex Schult., Syst. Veg., ed. 15 bis [Roemer & Schultes] 6: 602 (1820)

=*Selinum razulii* (Gouan) Link, Enum. Hort. Berol. Alt. 1: 269 (1821)

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6 • *Angelica sylvestris* L., Sp. Pl.: 251 (1753)
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9 ≡ *Imperatoria sylvestris* Lam., Fl. Franç. (Lamarck) 3: 417 (1779)
10
11 = *Angelica apiifolia* Sennen, Bull. Soc. Bot. France 63: 127 (1916)
12
13 = *Angelica heterocarpa* J.Lloyd, Bull. Soc. Bot. France 6: 709 (1860)
14
15 = *Angelica macrophylla* Schur, Enum. Pl. Transss.: 262 (1866)
16
17 = *Angelica montana* Brot., Fl. Lusit. 1: 426 (1804)
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19 = *Angelica montana* Gaudin, Fl. Helv. 2: 341 (1828)
20
21 = *Angelica nemorosa* Ten., Fl. Neapol. Syll.: t. 231, 561 (1831)
22
23 = *Angelica pratensis* J. Presl «fe K. Presl, Fl., Cech. 61 (1819)
24
25 = *Angelica sylvestris* ssp. *bernardiae* Reduron, Ombellif. France 1: 340-343, fig.
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30 41 (2007)
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32 = *Peucedanum angelica* Caruel in Parí., Fl. Ital. 8: 28 (1888)
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34 = *Selinum angelica* Roth, Tent. Fl. Germ. 1: 133 (1788)
35
36 = *Selinum sylvestre* Crantz, Stirp. Austr. Fase. 1: 177 (1762)
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43 • *Angelica sylvestris* L. ssp. *villosa* (Lag.) González-Toral, Nava, Cires &
44
45 Fern.Prieto comb. nov.
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48 ≡ *Angelica villosa* Lag., Gen. Sp. Nov.: 12 (1816)
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54 • *Angelica sylvestris* L. ssp. *elatior* (Wahlenb.) González-Toral, Nava,
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56 Cires & Fern.Prieto comb. nov.
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59 ≡ *Angelica sylvestris* L. var. *eliator* Wahlenb. Fl. Caarpat.: 84 (1814)
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6 • *Angelica sylvestris* L. ssp. *elatior* f. *heterocarpa* (J.Lloyd) González-Toral,
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8 Nava, Cires & Fern.Prieto comb. nov.

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21 ≡*Imperatoria palustris* Besser, Prim. Fl. Galiciae Austriac. 1: 214 (1809)
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23 =*Angelica palustris* Hoffm., Gen. Pl. Umbell. 162 (1814)
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25 =*Angelica pratensis* M.Bieb. ex Fisch., Cat. Jard. Pl. Gorenki (1812), nom.
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27 inval.
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30 =*Ostericum pratense* Hoffm., Gen. Pl. Umbell., ed. 2. 164 (1816)
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32 =*Selinum ostericum* E.H.L.Krause, Deutschl. Fl. (Sturm), ed. 2., 12: 119 (1904)
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38
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42 by the University of Oviedo.
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46 **Data availability statement**
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48 The data that support the findings of this study are openly available in Genbank
49 at <https://www.ncbi.nlm.nih.gov/genbank/>. The reference number of each sequence are
50
51 specified in Table 3.
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57 **Disclosure statement**
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59 The authors declare no conflict of interest.
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APPENDIX 1

List of Apoidae taxa used in the ITS phylogenetic analysis. The associated data have been gathered from previous studies. The order of the displayed data corresponds to the following information: taxon name, collection site, collector, voucher and GenBank accession numbers.

Acronema atrantiifolium H. Wolff, Shudu Lake (Yunnan, China), voucher KUN:J03 ZJ0526: EU236155; *Acronema paniculatum* (Franch.) H. Wolff, Ma'er Mt., Heqing, (Yunnan, China), voucher KUN:J030 :FJ385031; *Acronema schneideri* H. Wolff, Shangri-La, Tiansheng Bridge, (Yunnan, China), voucher ZJ810826 (KUN):EU236156; *Aethusa cynapium* L., Cultivated in Jardin Botanique de Caen, no. 1424 (France), Downie, voucher Downie 337 (ILL): AH003541 (=U30582 and U30583); *Aethusa cynapium* L., Cultivated in Jardin Botanique de Caen, no. 1424 (France), Downie, voucher Downie 337 (ILL): GQ862376; *Aletes acaulis* (Torr.) J.M.Coult. & Rose, Canyon of the Big Thompson, Larimer Co. (Colorado, U.S.A.), Hartman, voucher Hartman 24386 (RM): AF358528 and AF358461. *Aletes acaulis* (Torr.) J. M. Coult. & Rose, Boulder Co. (Colorado, U. S. A.), T. Hogan, voucher T. Hogan 1739 (RM 577080): KF619603; *Ammi majus* L., Sevilla, Andalucía (Spain), P. Jiménez-Mejías, voucher P. Jiménez-Mejías 54PJM06, UPOS: KJ473864; *Ammi majus* L., Cervognano-Montepulciano, province of Siena, Tuscany (Italy), voucher WU:W. & S.Till s.n.: MT513148; *Anethum graveolens* L., Cultivated in Jardin Botanique de Caen (no. 1980) (France), Downie, voucher Downie 326 (ILL): AH003470 (=U30550 and U30551); *Anethum graveolens* L., voucher MP 519:MN257763; *Angelica acutiloba* (Siebold & Zucc.) Kitag: AB569093; *Angelica ampla* A. Nelson, Flat Tops-White River Plateau, Garfield Co. (Colorado, U.S.A.), voucher Hartman 25821 (RM): AH006065 (=U79597 and U79598). *Angelica ampla* A. Nelson, Medicine Bow Mts., Carbon Co. (Wyoming, U.S.A.), voucher Nelson 74945 (RM 915607): MT735408. *Angelica ampla* A. Nelson, Laramie, Albany Co. (Wyoming, U.S.A.), voucher Lukas 8251 (RM 915615): MT735409. *Angelica amurensis* Schischk., Dailing, Liangshui Nature Reserve (Helongjiang, China), voucher Liao & Zhang 2016082806 (SZ): MT735424; *Angelica amurensis* Schischk., voucher NHW 200404: DQ263581; *Angelica anomala* Avé-Lall., GAP depot, Chuanshan County (GAP) (China), voucher CDCM:20100613: HQ699461; *Angelica anomala* Avé-Lall., voucher NHW 200403: DQ263582; *Angelica apaensis* R.H. Shan & C.Q. Yuan, voucher its-yy1: EU001364; *Angelica archangelica* L., Findland from material cultivated in University of Joensuu Botanical garden, Joensuu (North Karelia, Finland), Downie, voucher Downie 79 (ILL) (nº 33): AH003539 (=U30576 and U30577); *Angelica archangelica* L., Kanas, Xinjiang (China), Wang, voucher Wang CB 727249 (SZ); GU395171; *Angelica archangelica* L., cultivated in cultivated in University of Illinois Urbana-Champaign (UIUC) (U. S. A) from Matrial of University of Joensuu Botanical Garden (Finland), Downie, voucher Downie 79 (ILL): MT735410. *Angelica archangelica* L., cultivated in University of Illinois Urbana-Champaign (UIUC) (U. S. A) from material of University of Botanical Garden (Finland), Downie, voucher Downie 79 (ILL): MT735410. *Angelica archangelica* L., cultivated in cultivated in University of Illinois Urbana-Champaign (UIUC) (U. S. A) from material of University of Turku (Finland), Downie Downie 419 (ILL): MT735411. *Angelica archangelica* L., cultivated in University of Illinois Urbana-Champaign (UIUC) (U. S. A) from material of University of Kuopio (Finland), Downie, voucher Downie 435 (ILL): MT735412. *Angelica archangelica* L., cultivated in

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3 cultivated in the University of California Botanical Garden (UC Botanical Garden), Berkeley (California,
4 U.S.A) from material of Moscow (Russia), voucher C-1693 (ISU 13350): MT735413; *Angelica arguta*
5 Nutt. ex Torr. & A. Gray: AH006066; *Angelica atropurpurea* L., White Pine State Park, Ogle Co.
6 (Illinois, U.S.A), Phillippe, Phillippe et al. 40690 (ILLS 242713): MT735421; *Angelica atropurpurea* L.,
7 Kinney's Ford Seep., Vermilion Co. (Illinois, U.S.A), Phillippe, voucher Phillippe 18763 (ILLS
8 176702.1): MT735422; *Angelica balangshanensis* R.H. Shan & F.T. Pu, Sichuan (China), Liao CY,
9 voucher 742598 (SZ): HQ896671; *Angelica biserrata* R.H. Shan & C.Q. Yuan, Anhui (China), Liao CY,
10 voucher 666796 (SZ): GU395180; *Angelica biserrata* R.H. Shan & C.Q. Yuan, Tianmu Mountain, Linan
11 Co. (Zhejiang, China), Liao CY et al., Liao et al. 2014111001 (SZ): MT735572; *Angelica brevicaulis* B.
12 Fedtsch., Houxia, Xinjiang (China), Wang, voucher Wang CB 727248 (SZ): GU395170; *Angelica*
13 *brevicaulis* B. Fedtsch., Taragay River (Issyk-Kul Region, Kyrgyzstan) Phillippe, voucher Phillippe et al.
14 30918 (ILLS 204789): MT735423; *Angelica brevicaulis* B. Fedtsch., Tianshan, Fukang Co., (Xinjiang,
15 China), Bartholomew, Bartholomew et al. 8540 (MO 5724329): MT735417; *Angelica brevicaulis* B.
16 Fedtsch., voucher SZ727248: GU395170; *Angelica breweri* A. Gray, Diamond Mtn., Lassen Co.,
17 (California, U.S.A), Ertter, voucher Ertter 7869 (RM 567616): MT735440; *Angelica breweri* A. Gray,
18 Bucks Lake, Plumas Co., (California, U.S.A), Taylor and Foster, voucher Taylor & Foster 3896 (MO
19 3209901): MT735441; *Angelica californica* Jeps., Natalie Coffin Greene Park, Marin Co. (California,
20 U.S.A), Smith and Follette, voucher Smith & Follette s.n. (CAS 1115946): MT735508; *Angelica*
21 *californica* Jeps., Lucas Valley road, Marin Co. (California, U.S.A), Smith, voucher Smith s.n. (CAS
22 1202614): MT735509; *Angelica callii* Mathias & Constance, Greenhorn Mtn, Kern Co., (California,
23 U.S.A), Shevock, voucher Shevock 10775 (CAS 1170580): MT735531; *Angelica callii* Mathias &
24 Constance, Mill Creek, Sequoia National Forest, Fresno Co. (California, U.S.A), York and Tenneboe,
25 York & Tenneboe 2329 (CAS 1118158): MT735532; *Angelica canbyi* J.M. Coulter. & Rose, Wenatchee,
26 Chelan Co. (Washington, U.S.A), Whited, voucher Whited 1410 (OSC 7586): MT735547; *Angelica*
27 *canbyi* J.M. Coulter. & Rose, Bingham Springs, Western Blue Mtn, Umatilla Co. (Oregon, U.S.A), Cusick,
28 Cusick 3288a (OSC 634459): MT735548; *Angelica capitellata* (A. Gray) Spalik, Reduron & S. R.
29 Downie, voucher DM12_719 18S: KF619735; *Angelica capitellata* (A. Gray) Spalik, Reduron & S. R.
30 Downie, Anderson Creek and Wood River, Blaine Co., (Idaho, U.S.A) Warnock & Sternner, voucher
31 Warnock & Sternner 1970 (ILL): MT735497; *Angelica capitellata* (A. Gray) Spalik, Reduron & S. R.
32 Downie, Grizzly Valley Quad., Plumas Co. (California, U.S.A), Taylor, voucher Taylor 4120 (MO
33 4016388): MT735496; *Angelica cartilaginomarginata*.var.*foliosa* C.Q. Yuan & R.H. Shan, Jiangsu
34 (China), Liao CY, voucher 667428 (SZ): GU395177; *Angelica cartilaginomarginata* (Makino ex Y.
35 Yabe) Nakai, Tonghua (Jilin, China), Huasheng Peng, voucher Huasheng Peng 055-02: JX022901;
36 *Angelica cartilaginomarginata* var. *matsumurae* (H. Boissieu) Kitag., Muyuzi, Huanren Co. (Liaoning,
37 China), Liao, Liao et al. 2015072809 (SZ) MT735573; *Angelica cincta* H. Boissieu, cultivated in
38 Moscow State University Botanical Garden (Russia), Katz-Downie, voucher Katz-Downie et al., 1999:
39 AF008601 and AF009080; *Angelica cincta* H. Boissieu, East of Vityaz, Gamov Peninsula, Khasansky
40 District (Primorsky Krai, Russia), Solomon and Barkalov, voucher Solomon & Barkalov 19580 (MO
41 4629223): MT735425; *Angelica czernaevia* (Fisch. & C.A. Mey.) Kitag., Dailing suburb (Helongjiang,
42 China), Liao, Liao et al. 2016082802 (SZ): MT735553; *Angelica czernaevia* (Fisch. & C.A. Mey.)

Kitag., Muyuzi, Huanren Co. (Liaoning, China), Liao, Liao et al. 2015072813 (SZ): MT735554; *Angelica dabashanensis* C.Y. Liao & X.J. He, voucher SZ666959: HQ896670; *Angelica dahurica* (Hoffm.) Benth. & Hook.f. ex Franch. & Sav.: AB569095; *Angelica dahurica* (Hoffm.) Benth. & Hook.f. ex Franch. & Sav., China, cultivated in the University of California Botanical Garden (UC Botanical Garden), Berkeley (California, U.S.A), voucher No. 88.0678: MT735565; *Angelica dawsonii* S. Watson, North West of Hoodoo Pass, Lolo National Forest, Mineral Co. (Montana, U.S.A.), Stickney, voucher Stickney 1875 (RM 404596): MT735551; *Angelica dawsonii* S. Watson, East of Hamilton, Skalkaho Pass Road, Ravalli Co. (Montana, U.S.A.), Hitchcock, voucher Hitchcock 23956 (RM 277277): MT735552; *Angelica decurrens* B. Fedtsch., voucher KUN:ZJ0738: FJ385033; *Angelica decurrens* B. Fedtsch, voucher SZ727249: GU395171; *Angelica decurrens* B. Fedtsch, Irkutsk Region (Siberia, Russia) cultivated in Moscow State Univ. Botanical Garden (Russia), Pimenov, voucher Pimenov et al. s.n. (MW): MT735414; *Angelica decurrens* B. Fedtsch, Altay (Xinjiang, China), Li, voucher Li et al. 20160716 -04 (SZ): MT735415; *Angelica decurrens* B. Fedtsch, Fuyun Co. (Xinjiang, China), Li, voucher Li et al. 20160718-04 (SZ): MT735416; *Angelica decursiva* (Miq.) Franch. & Sav.: AJ131293; *Angelica decursiva* (Miq.) Franch. & Sav., Siming Mtn., Yuyao City, (Zhejiang, China), Liao, voucher Liao et al. ZHQH2014 (SZ): MT735549; *Angelica dentata* (Chapm. ex Torr. & A. Gray) J.M. Coulter. & Rose, Wakulla Co.- León Co. (Florida, U.S.A.), Kral, voucher Kral 64448 (MO 5990771): MT735519; *Angelica dentata* (Chapm. ex Torr. & A. Gray) J.M. Coulter. & Rose, Wright Lake, León Co. (Florida, U.S.A.), Kral, voucher Kral 52412 (MO 4271710): MT735520; *Angelica dielsii* H. Boissieu, Daba Mtns (Shaanxi, China), Liao CY, voucher 666961 (SZ): GU395154; *Angelica duclouxii* Fedde ex H. Wolff, Dongchuan (Yunnan, China), Liao CY, voucher 674189 (SZ): GU395155; *Angelica edulis* Miyabe ex Y. Yabe, Tohoku Univerty Experimental Forest (Miyagi Pref., Japan) Kuriyama, voucher Kuriyama s.n. (MO 4365802): MT735463; *Angelica fargesii* H. Boissieu, Daba Mtns. (Shaanxi, China), Liao CY, voucher 673574 (SZ): GU395181; *Angelica furcijuga* Kitag.: DQ278164; *Angelica genuflexa* Nutt. ex Torr. & A. Gray: DQ263566; *Angelica genuflexa* Nutt., Haines airport, Skagway Quad. (Alaska, U.S.A.), Parker, voucher Parker et al. 9882 (ALA V130563) MT735469; *Angelica genuflexa* Nutt., Hanna Lake, Malaspina Coastal Plain, Bering Glacier Quad. (Alaska, U.S.A.), Barker and Pratt, voucher Barker & Pratt s.n. (ALA V136716): MT735470; *Angelica gigas* Nakai, cultivated in Missouri Botanical Garden Saint Louis City (Missouri, U.S.A.), Klinger and Lievens, voucher Klinger & Lievens 279 (MO 5079406): MT735477; *Angelica gigas* Nakai, Jingbai Road, Jingyu Co. (Jili, China), Liao, voucher Liao et al. 2015073002 (SZ): MT735478; *Angelica gigas* Nakai: AJ131290; *Angelica grayi* J.M. Coulter. & Rose, Blair Mountain-North West of Glenwood Springs, Garfield Co. (Colorado, U.S.A.), Vanderhorst and Palaci, voucher Vanderhorst & Palaci 4490 (RM): AY146825 and AY146891; *Angelica grayi* J.M. Coulter. & Rose, Medicine Bow Mountains Forest Road-West of Centennial, Albany Co. (Wyoming, U.S.A.), Lukas, voucher Lukas 3408 (RM 915628): MT735560; *Angelica grayi* J.M. Coulter. & Rose, Arapaho National Forest- North of boundary with Pike National Forest, Clear Creek Co. (Colorado, U.S.A.), Nye, voucher Nye et al. 256 (MO 6608950): MT735561; *Angelica grosseserrata* Maxim., Shihu, Kuandian Co. (Liaoning, China), Liao, voucher Liao et al. 2015072703 (SZ): MT735398; *Angelica hakonensis* Maxim., Fuji Mountain, Shizuoka Pref. (Honshu, Japan), Murata, voucher Murata 37194 (MO 2665957) MT735574; *Angelica hendersonii* J.M. Coulter. & Rose, Beards Hollow, Pacific Co.

(Washington, U.S.A.), Heckard, voucher Heckard 1648 (ISU 1402): MT735456; *Angelica hendersonii* J.M. Coulter & Rose, North of Lucia, Monterey Co. (California, U.S.A.), Constance and Chuang, voucher Constance & Chuang 3771 (ISU 13441): MT735457; *Angelica heterocarpa* M.J. Lloyd, cultivated in the Conservatoire Botanique d'Alsace, Mulhouse (Alsace, France) from material of Couëron (Loire-Atlantic, France), Hildenbrand, voucher No. 9508B, Hildenbrand s.n. (ILL) MT735579; *Angelica heterocarpa* M.J. Lloyd, cultivated in the Conservatoire Botanique d'Alsace, Mulhouse (Alsace, France) from material of Couëron (Loire-Atlantic, France), Reduron, voucher No. 97.214B, Reduron s.n. Reduron Loriot s.n. (ILL): MT735581; *Angelica heterocarpa* M.J. Lloyd, South Atlantic National Botanical Conservatory, Génissac (Gironde, France), Loriot, voucher Loriot s.n. (ILL): MT735581; *Angelica heterocarpa* M.J. Lloyd, La Basse-Indre-Indret (Loire-Atlantic, France), Dupont, voucher Dupont et al. s.n. (ILL): MT735582; *Angelica hirsutiflora* S.L. Liou, C.Y. Chao & T.I. Chuang, chromosome vouchers cultivated in the University of California Botanical Garden (UC Botanical Garden), Berkeley (California, U.S.A) from material of Shimen, Taipei Co. (Taiwan, China), Chuang, voucher Chuang 3979, C-401 (ISU 1134): MT735570; *Angelica hirsutiflora* S.L. Liou, C.Y. Chao & T.I. Chuang, Santiaochiao Lighthouse, Taipei Co. (Taiwan, China), Leong, voucher Leong et al. 2758 (MO 5749038): MT735571; *Angelica hirsutiflora* S.L. Liou, C.Y. Chao & T.I. Chuang, Taiwan (China), Yand, voucher Yang TY 0091455 (KUN): HQ256683; *Angelica japonica* A. Gray, Osaka University of Pharmaceutical Sciences, Osaka (Pref. Osaka, Japan): DQ278166; *Angelica kangdingensis* R.H. Shan & F.T. Pu ex W.T. Wang, Szechuan Kang ding (China), voucher NHW 200421: DQ263584; *Angelica keiskei* Koidz., cultivated in Zhongshan Botanical Garden, Jiangsu (Nanjing, China) form material of Japan, Liao and Tang, voucher Liao & Tang 2015111502 (SZ): MT735563; *Angelica keiskei* Koidz., Oshima (Pref. Tokyo, Japan), voucher NHW 200421: DQ263561; *Angelica kingii* (S. Watson) J.M. Coulter & Rose, Leidy Creek, White Mountains, Mono Co. (California, U.S.A.), Morefield and McCarty, voucher Morefield & McCarty 4151 (dupl. m) (RM 551984): MT735503; *Angelica kingii* (S. Watson) J.M. Coulter & Rose, East Creek-Forest Service Campground, Schell Creek Range, White Pine Co. (Nevada, U.S.A.) Tiehm 9765 (RM 367590): MT735504; *Angelica koreana* Maxim (=*Ostericum grosseserratum*): AF455749; *Angelica laxifoliata* Diels, Zheguo Mts., Kangding, (Sichuan, China), voucher SZ2006071804: EU647210; *Angelica lineariloba* A. Gray, White Mountain Ranger District, Inyo National Forest, Mono Co. (California, U.S.A.), Meyer and Townesmith, voucher Meyer & Townesmith 223 (MO 6146685): MT735445; *Angelica lignescens* Reduron & Danton, cultivated in the Conservatoire Botanique d'Alsace, Mulhouse (Alsace, France) from material of Falial (Azores, Portugal), voucher no. 01037, 2 August 2001, Hildenbrand, Meyer & Reduron s.n.: AY179030; *Angelica lignescens* Reduron & Danton, Terceira (Azores, Portugal), H. Schaefer and M. Carine, voucher H. Schaefer & M. Carine T2 (BM): HQ202018; *Angelica lignescens* Reduron & Danton, Pico(Azores, Portugal), M. Carine, voucher M. Carine et al. 107 (BM, AZB): HQ202022, *Angelica lignescens* Reduron & Danton, Flores (Azores, Portugal), H. Schaefer, voucher H. Schaefer 2008/437 (BM): HQ202034; *Angelica lignescens* Reduron & Danton, Flores (Azores, Portugal), H. Schaefer, voucher H. Schaefer 2008/437 (BM): HQ202035; *Angelica lignescens* Reduron & Danton Portugal, Azores, Island of Faial (Azores, Portugal), Danton and Reduron, voucher Danton & Reduron 01037 (ILL): MT735498; *Angelica likiangensis* H. Wolff, Lijiang (Yunnan, China), Minhui Li, voucher Minhui Li 049-01 HLQA10049-01(KUN): JX022921; *Angelica longicaudata* C.Q.

Yuan & R.H. Shan (), Emei Mtn. (Sichuan, China), Liao, voucher Liao CY 673421 (SZ): GU395160;
Angelica longipes H. Wolff, China, Tibet, Nielamu (Tibet, China), Yu, voucher Yu Y 802447 (SZ): HQ256679; *Angelica lucida* L, Carter Bay, Kuskokwim Bay, Goodnews Bay Quad. (Alaska, U.S.A.), Parker, voucher Parker 15706 (ALA 150217): MT735489; *Angelica lucida* L, Petit Manan Point, Washington Co. (maine, U.S.A.), Hill and Renda, voucher Hill & Renda 30467 (MO 4925887) MT735490; *Angelica maowenensis* C.Q. Yuan & R.H. Shan, Szechwan Xiao jin (China), voucher NHW 200413: DQ263585; *Angelica megaphylla* Diels, Chongqing Jin fu san (China), voucher NHW 200304: DQ263568; *Angelica morii* Hayata, Fujian Wu yi san (China): DQ263573; *Angelica morrisonicola* Hayata, Jade Mountain (Taiwan, China), Li, voucher Li et al. 2014080302 (SZ): MT735517; *Angelica muliensis* C.Y. Liao & X.G. Ma, China, Sichuan, Muli Co. Ma et al. 2010092905 (SZ): MT735567; *Angelica nelsonii* J.M. Coulter. & Rose, cultivated in the University of California Botanical Garden (UC Botanical Garden), Berkeley (California, U.S.A) from material of Paraje Matsab., Tenejapa (Chiapas, Mexico), Breedlove, voucher Breedlove 15173, chromosome voucher Berkeley. C-175 (ISU 1132): MT735499; *Angelica nelsonii* J.M. Coulter. & Rose, Chenpil, Oxchuc (Chiapas, Mexico), Gómez Santiz., voucher Gómez Santiz 274 (MO 4268951): MT735500; *Angelica nitida* H. Wolff, Qinghai (China), voucher ZLX 483: DQ263592; *Angelica omeiensis* : Szechwan E Mei (China): DQ263571; *Angelica on cosepala* Handel-Mazzetti, voucher SZ 2006071803: EU418382; *Angelica pachycarpa* Lange, in the Conservatoire Botanique d'Alsace, Mulhouse (Alsace, France) from material of Couëron (Loire-Atlantic, France), Hildenbrand, voucher No. 2009 Hildenbrand s.n. (ILL): MT735505; *Angelica pachycarpa* Lange, cultivated in the University of California Botanical Garden (UC Botanical Garden), Berkeley (California, U.S.A) from material cultivated in Riccarton (Christchurch, New Zealand), Healy voucher Healy 143831, Chromosome Vouchers C-567, 596 (ISU 1129): MT735506; *Angelica palustris* Hoffm. (=*Ostericum palustre*), Olomouc (Moravia, Czech Republic), Otruba, voucher Otruba 447 (MO 2497627): MT735404; *Angelica palustris* Hoffm. (=*Ostericum palustre*), Tartu near the Emajõgi River (Estonia), Skvortsov, voucher Skvortsov et al. s.n. (MO 4252778): MT735405; *Angelica paeoniifolia* R.H. Shan & C.Q. Yuan, Lingzhi (Tibet, China), voucher MNH 2008072404: FJ237533; *Angelica pinnata* S. Watson, Commissary Ridge, Lincoln Co. (Wyoming, U.S.A.), Hartman, voucher Hartman 41500 (RM):AF358465 and AF358532; *Angelica pinnata* S. Watson, Beartooth Mtns., Shoshone National Forest, Park Co. (Wyoming, U.S.A.), Elliott and Kuhn, voucher Elliott & Kuhn 7239 (RM 860686): MT735515; *Angelica pinnata* S. Watson, Douglas Creek Trail, Platte River Wilderness, Medicine Bow Mtns., Albany Co. (Wyoming, U.S.A.), Lukas, voucher Lukas 3890 (RM 915622): MT735516; *Angelica pinnatiloba* R.H. Shan & F.T. Pu, Huanglong, Songpan Co. (Sichuan, China), Liao, voucher Liao 2019081909 (SZ): MT735568; *Angelica polymorpha* Maxim., Gwangdeog-san (Korea), BY Lee, BYLee 090823-13 (KB): JN603223; *Angelica polymorpha* Maxim., cultivated in the University of California Botanical Garden (UC Botanical Garden), Berkeley (California, U.S.A) from material of Kyushu (Pref. Miyazaki, Japan), McNamara, voucher McNamara et al. 264 (UC) No. 90.0662: MT735473; *Angelica polymorpha* Maxim., China, Liaoning, Huanren Co., Huangai Road, Huanren Co. (Liaoning, China), Liao, voucher Liao et al. 2015072803 (SZ): MT735474; *Angelica pseudoselinum* H. Boissieu China, Sichuan, Ma'erkang (Sichuan, China), Mozi ditch, voucher ZJ0629 (KUN): EU236158; *Angelica pseudoselinum* H. Boissieu, Wuxi Co., Hongchiba, (Chongqing, China),

Liao, Liao 2019091903 (SZ): MT735569; *Angelica pubescens* Maxim., Hakitani (Pref. Osaka, Japan), voucher NHW 200431: DQ263567; *Angelica pubescens* Maxim., Nagase, Shikoku, (Pref. Kochi, Japan), Yamaoka, voucher Yamaoka et al. FOK-059077 (MO 5960420): MT735475; *Angelica purpureifolia* (nom. illeg.), AY548229; *Angelica razulii* Gouan ex Avé-Lall., Llaurenti massif, (Aude, France) Reduron, voucher Reduron s.n. (ILL): MT735491; *Angelica roseana* L.F. Hend., Blue Miner Lake, Teton Co. (Wyoming, U.S.A.), Hartman, voucher Hartman 50090 (RM): AF358466 and AF358533; *Angelica roseana* L.F. Hend., Trout Creek-Cookstove Basin, Big Horn Mtns., Big Horn Co. (Wyoming, U.S.A.), Nelson, voucher Nelson 4583 (RM 347468): MT735536; *Angelica roseana* L.F. Hend., Rendevous Mtn., Teton Range, Bridger-Teton National Forest, Teton Co. (Wyoming, U.S.A.), Hartman and Scott, voucher Hartman & Scott 86481 (RM 837529): MT735537; *Angelica sachalinensis* Maxim., Hamatonbetsu (Pref. Hokkaido, Japan), voucher NHW 200428: DQ263564; *Angelica sachalinensis* Maxim., cultivated in Moscow State University Botanical Garden, Moscow (Russia) from material of Sakhalin Oblast, Sakhalin Island, Chekhov Mtn., Sakhalin Island (Sakhalin Oblast, Russia), Pimenov and Kljuykov, voucher Pimenov & Kljuykov s.n. (MW): MT735427; *Angelica sachalinensis* Maxim., Kuki, Honshu (Wakayama Pref., Japan), Mimoro, voucher Mimoro et al. 4161 (MO 2687393): MT735428; *Angelica shikokiana* Makino ex Y. Yabe, : AB697610; *Angelica sinensis* (Oliv.) Diels: AF393784; *Angelica songpanensis* R.H. Shan & F.T., Pu, Songpan (Sichuan, China), voucher Ma XG 714746 (SZ): GU395167; *Angelica stenoloba* Kitag., Bozuyama (Hokkaido Pref., Japan), Tsugaru, voucher Tsugaru 5086 (MO 3009426): MT735471; *Angelica sylvestris* L.: HQ2566681; *Angelica sylvestris* L., Bavarian Swabia (Germany), German-Chinese Exped., voucher German-Chinese Exped. 0562104 (KUN): HQ256681; *Angelica sylvestris* L., voucher Peu53: KP682411; *Angelica sylvestris* L., cultivated in University of Illinois Urbana-Champaign (UIUC) (U. S. A) from material of University of Turku Botanic Garden, Turku (Finland), Downie, voucher Downie 428 (ILL): MT735575; *Angelica sylvestris* L., cultivated in Moscow State University Botanical Garden, Moscow (Russia) from material of Oka Valley (Moscow, Russia), Ostroumova, voucher Ostroumova et al. 1463 (MW): MT735576; *Angelica sylvestris* L., NE of Canton Neuchatel (Switzerland), Kohler, voucher Kohler s.n. (MO 6271139): MT735583; *Angelica sylvestris* L., Stokksnes (Iceland) Balogh, voucher Balogh 64 (ILL): MT735577; *Angelica sylvestris* L., cultivated in University of Illinois Urbana-Champaign (UIUC) (U. S. A) from material of Krosno (Poland), Liao, voucher NPGS (PI 654393) Liao 2018022601 (SZ): MT735578; *Angelica taiwaniana* S.S. Ying 1496 China, cultivated in University of Illinois Urbana-Champaign (UIUC) (U. S. A) from material of Shanghai Botanical Garden (China), Downie, voucher Downie 1496 (ILL): MT735566; *Angelica tarokoensis* Hayata, Shakatang Forest- Chingshuishan Mtn., Hsiulin Hsiang, Hualian Co. (Taiwan, China), Huang, voucher Huang et al. 586 (MO 5765518): MT735564; *Angelica tianmuensis* Z.H. Pan & T.D. Zhuang, Tianmu Mtn. (Zhejiang, China), Liao CY, voucher Liao CY 667442 (SZ): GU395178; *Angelica tianmuensis* Z.H. Pan & T.D. Zhuang, Tianmu Mtn., Linan Co. (Zhejiang, China), Liao, voucher Liao et al. 2014111002 (SZ): MT735562; *Angelica tomentosa* S. Watson, Forest Ranch Fire Control Station, Paradise Quad., Butte Co. (California, U.S.A.), Taylor, voucher Taylor 3335 (MO 4014289): MT735453; *Angelica tomentosa* S. Watson, Big Bend Post Office, Shasta Co. (California, U.S.A), Bacigalupi and Heckard, voucher Bacigalupi & Heckard 6057 (ILL): MT735447; *Angelica triquinata* Michx., Mount Mitchell State Park, Yancey Co. (North Carolina,

U.S.A.), Schwarzkopf, voucher Schwarzkopf 0084 (MO 2474283): MT735461; *Angelica triquinata* Michx., Franklin-Reddish Knob Mtn., Pendleton Co. (West Virginia, U.S.A.), Boufford, voucher Boufford et al. 21358 (MO 3026411): MT735462; *Angelica tschimganica* V.N. Tikhom., Tashkent, (Ahangaran District, Uzbekistan), Tojiboev and Mamarahimov, voucher Tojiboev & Mamarahimov UPL00087 (ILLS 240857): MT735418; *Angelica tsinlingensis* K.T. Fu, Shanxi Hua san (China): DQ263572; *Angelica ursina* Maxim., Hamatonbetsu (Pref. Hokkaido, Japan), voucher NHW 200429: DQ263565; *Angelica ursina* Maxim., Utka River (Kamchatka, Russia), Eriksen and Töpel, voucher Eriksen & Töpel 1416B (ALA V161632): MT735476; *Angelica valida* Diels, Chongqing Jin fu san (China), voucher NHW 200306: DQ263569; *Angelica venenosa* (J. Greenway) Fernald, Little Black Slough, Wildcat Bluff Area, Johnson Co. (Illinois, U.S.A.), Basinger, voucher Basinger 3924 (ILLS 192155): MT735527; *Angelica venenosa* (J. Greenway) Fernald, Elizabethtown Ranger District, Shawnee National Forest, Pope Co. (Illinois, U.S.A.), Shimp and Basinger, voucher Shimp & Basinger 1987 (ILLS 270350.1): MT735528; *Angelica wheeleri* S. Watson, Right Fork Indian Creek, Uinta National Forest, Utah Co. (Utah, U.S.A.), Hannan and Leinbach, voucher Hannan & Leinbach s.n. (BRY 617170): MT735541; *Angelica wheeleri* S. Watson, Oak Basin, Tushar Mtns., Piute Co. (Utah, U.S.A.), Taye, voucher Taye 4230 (BRY 331456): MT735542; *Angelica yakusimensis* H. Hara, Yudomari Mtn., Yakushima Island, Kyushu, (Kagoshima Pref., Japan) Yahara and Akiyama, voucher Yahara & Akiyama 877012 (MO 4381570): MT735472; *Aphanopleura capillifolia* Lipsky: DQ516368; *Aphanopleura trachysperma* Boiss: Vedi, Ararat (Armenia), V. Manakian, voucher V. MANAKIAN s.n. (MO): AF008629 and AF009108; *Apium graveolens* L., Cultivated in Conservatoire et Jardins Botaniques de Nancy (France), Downie, Downie 258 (ILL): AH003471(=U30552 and U30553); *Apium graveolens* L., voucher PS0319MT01: MZ191026; *Arafoe aromaticata* Pimenov & Lavrova, cultivated in Moscow State University Botanical Garden, Moscow (Russia) from material of Lagonaki, Caucasian Reserve, Krasnodar (Russia), voucher Pimenov 403 (MW): U78383 and U78443; *Arafoe aromaticata* Pimenov & Lavrova: AF077874; *Arracacia aegopodioides* J. M. Coul. & Rose, D. Anderson, voucher Anderson 13082 (UC): GQ862378; *Arracacia nelsonii* Coul. & Rose, Breed/ove 72434 Mexico, Oaxaca (Mexico), Constance, voucher Constance 2410 (UC): AH003472 (=U30556 and U30557); *Arracacia xanthorrhiza* Bancr., Blas, voucher Blas 1 (COL): GQ862445; *Athamanta macedonica* (L.) Spreng., Greece, Ioannina, Koukouli, Ioannina (Greece), Dudley, voucher Dudley et al. 18205 (RNG): AF073541; *Carlesia sinensis* Dunn (1902), Cultivated in Hort. Nanjing (China), Constance, voucher Constance 2401 (UC): U30563 and U30562; *Cervaria cervariifolia* (C.A. Mey.) Pimenov, Iran, Ajani, voucher Ajani 2058 (TUH) (No. 3130): EU169250; *Chamaele decumbens* Makino, Ishikawa-gun, Yoshinodani-mura, Yoshino, Ishikawaken (Honshu, Japan), Tsugaru, voucher Tsugaru 14314 (MO): DQ516364; *Chymsydia colchica* (Albov) Woronow ex Grossh., Downie, voucher Downie et al. (1998): U78405 and U78465; *Chymsydia colchica* (Albov) Woronow ex Grossh.: AF077882; *Chymsidia colchica* (Albov) Woronov ex Grossh: HQ256685; *CnidioCARPA alaica* Pimenov, cultivated in Moscow State University Botanical Garden (Moscow, Russia) from material of Kichik-Karamyk (Tadzhikistan), M. G. Pimenov, voucher M. G. PIMENOV & al. 1332 (MW): AF008615 and AF009094; *Cnidium monnierii* (L.) Cuss., China, Yunnan, Songming (Yunnan, China), voucher ZJ0676 (KUN): EU236164; *Cnidium monnierii* (L.) Cuss., Sichuan (China), Liao CY, voucher 802525 (SZ): HQ316168; *Cnidium monnierii* (L.) Cuss., voucher SZ802525: HQ256685;

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3 *Cnidium monnierii* (L.) Cuss., Hebei (China), X.J. Ge, voucher 24-Sep-2013 Ge131194: MH712671;
4 *Coaxana bambusoides* Mathias & Constance, Breedlove, voucher Breedlove 61980 (CAS): GQ862448;
5 *Coelopleurum lucidum*, Hokkaido hamatonbetsu (Japan), voucher NHW 200332: DQ270196;
6 *Coelopleurum saxatile* Drude, Jilin (China), Liao CY, voucher 706634 (SZ): GU395172; *Coelopleurum*
7 *saxatile* (Tuecz.) Drude, Jiling Chang bai san (China), voucher NHW 200406: DQ270195; *Cortia*
8 *depressa* (D. Don) Leute, cultivated in the Royal Botanic Garden Edinburgh, Edinburgh (Scotland, U.K.),
9 voucher no. 19892739: AF009086 and AF008607; *Conioselinum tataricum* Hoffm.: Baidula Gorge,
10 Ottuk, Kirghizia from cultivated in Moscow State University Botanical Garden (Moscow, Russia), M. G.
11 Pimenov, voucher M. G. PIMENOV & al. s.n. (MW): AF008623 and AF009102; *Conioselinum*
12 *pacificum* (Watson) Coulter. & Rose, Cape Perpetua, Siuslaw National Forest, Lincoln County (Oregon,
13 U.S.A) Lincoln Co., Applequist and Bradley, voucher Applequist & Bradley 98(MO): MK694936;
14 *Conioselinum vaginatum* (Spreng.) Thell., voucher P19(KUN): MG745193; *Cortiella hookeri*
15 (C.B.Clarke) C.Norman, Lauribina Yak-Gosainkunda, basin of Trisuli Khola, National Park, Langtang
16 (Central Nepal, East Himalaya), Pimenov and Kljuykov, voucher Pimenov & Kljuykov 51 (MW):
17 AY328932 and AY330498; *Coulterophytum jaliscense* McVaugh, Zarzamora (Las Joyas), Sierra de
18 Manantlán, Las Joyas (Jalisco, Mexico) from material cultivated in UC Berkeley, Berkeley (California,
19 U. S. A.), Iltis and L. Constance, voucher Iltis et al. 1299 (UC), L. Constance pers. coll. C-2236:
20 AF358473 and AF358540; *Coulterophytum laxum* Robins., Michoacán (Mexico), Iltis, Cochrane and
21 Contance, Iltis 298 & Cochrane (=Contance 2411 (UC): AH003542 (=U30560 and U30561);
22 *Coulterophytum pubescens* J.M.Coult.& Rose, Rzedowski, voucher Rzedowski 26206 (MICH):
23 GQ862450; *Cymopterus glomeratus* var. *concinna* (Osterh.) Mathias Delta Co. (Colorado, U.S.A.), C.
24 E. Hinchliff, voucher C. E. Hinchliff 1323 (CIC 041348): KF619643; *Dahliaphyllum almedae* Constance
25 & Breedlove, Puerto El Gallo-Atoyac (Guerrero, Mexico) from aterial cultivated in Univervisty of
26 California Botanical Garden, Berkeley (California, U. S. A.), L. Constance voucher Breedlove 61970
27 (UC) L. Constance 2328: U78395 and U78455; *Deverra aphylla* DC., Cape (South Africa), S.
28 Castroviejo, voucher S. Castroviejo 14915SC, MA: KJ47387; *Dichoropetalum schottii* (Besser ex DC.)
29 Pimenov & Kljuykov (=Peucedanum schottii Besser ex DC.), col de Brouis (Alpes-Maritimes, France),
30 Reduron, voucher Herb. Reduron 30 July 1981: AH012695; *Dimorphosciadium gayoides* Pimenov:
31 AY328935 and AY330501; *Donnellsmithia juncea* (Spreng.) Mathias & Constance, Saynes, voucher
32 Saynes 717 (MO): GQ862459; *Donnellsmithia juncea* (Spreng.) Mathias & Constance, Paredes, voucher
33 Paredes 10 (MO):GQ862458; *Dystaenia takesimana*, voucher um13: AY548224; *Enantiophylla*
34 *heydeana* Coult. & Rose, Mantlán (Jalisco, Mexico), Iltis, voucher Iltis et al. 3187: AH003475 (=U30558
35 and U30559); *Enantiophylla heydeana* Coult. & Rose, Flores-Franco, Calzada and Solis, voucher Flores-
36 Franco, Calzada, & Solis 2840 (MO): GQ862468; *Endressia castellana* Coincy., from material cultivated
37 in Institute of Botany of the University of Neuchâtel, Neuchâtel (Canton of Neuchâtel, Switzerland),
38 Constance, voucher Constance 2184 (UC): AH003545 (=U30584 and U30585); *Exoacantha*
39 *heterophylla* Labill, South of Mevo-Hamma (Golan, Israel), A. Liston, voucher A. LISTON 535/1:
40 AF008617 and AF009096; *Ferulopsis hystrix* (Bunge ex Ledeb.) Pimenov, Russia from material
41 cultivated in Royal Botanic Garden Edinburgh, Edinburgh (Scotland, U. K.), voucher cult. RBGE
42 19932301A DNA No. 3215: EU169271; *Foeniculum vulgare* L. Canakkale (Turkey): AY581806;

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3 *Foeniculum vulgare* L. voucher nrITS_LH7218_99: MW366656; *Glehnia littoralis* F.Schmidt ex Miq.:
4 EU164928; *Glehnia littoralis* F.Schmidt ex Miq., South Korea, voucher gl-02: KX757779; *Glehnia*
5 *littoralis* F.Schmidt ex Miq., voucher 71: MK961278; *Halosciastrum melanotilingia* (H.Boissieu)
6 Pimenov & V.N.Tikhom.:AY328937 and AY330503; *Hansenia forbesii* (H.Boissieu) Pimenov &
7 Kljuykov, voucher QH8: KJ999465; *Hansenia mongholica* Turcz., Karakol Lakes (Altai, Russia) from
8 material cultivated in Moscow State University Botanical Garden (Moscow, Russia), M. G. Pimenov,
9 voucher M. G. PIMENOV & al. 18 (MW): AF008643 and AF009122; *Hansenia weberbaueriana* (Fedde
10 ex H.Wolff) Pimenov & Kljuykov, voucher PS2005MT16: JQ936558; *Harbouria trachypleura* (A.
11 Gray) J.M. Coulter. & Rose, Philmont Scout Ranch, Colfax Co. (New Mexico, U.S.A.), Embry, voucher
12 Embry 56 (RM): AF358493 and AF358560; *Harrysmithia heterophylla* H. Wolff, GQ379321, China,
13 Sikiang: Kangting (Tachienlu), Smith, voucher Smith 10804 (MO) (29-VII-1934): GQ379321;
14 *Heracleum sphondylium* L., findland, cultivated in University of Koupio Botanical Garder, Downie,
15 voucher Downie 433 (ILL): AH003484 (=U30546 and U30547); *Heracleum sphondylium* L., Piwniczna
16 Zdrój, Małopolskie voivodeship (Poland), Piwcyński, voucher Piwcyński KEIB_AP_00052 (cultivated
17 from seeds): MK050079; *Imperatoria ostruthium* L.: AF077896; *Johrenia aromatica* Rech.f., Ajani,
18 voucher Ajani s.n. (Hb. Akhani): EU169288; *Kadenia dubia* (Schkuhr) V.N. Tikhom. & Lavrova, Aktau
19 Mtns. (Dzheskasgan province, Kazakhstan), Pimenov and Kljuykov, voucher Pimenov & Kljuykov 117
20 (MW): AY328950 and AY330516; *Karatavia kultiassovii* (Korovin) Pimenov & Lavrova, cultivated in
21 Moscow State University Botanical Garden (Moscow, Russia) from material of Mynzhilke, Syrdariinsky
22 Karatau Gorge (Kazakhstan), M. G. Pimenov, M. G. PIMENOV & al. 164 (MW): AF008612 and
23 AF009091; *Komarovia anisosperma* Korovin: AF077897; *Komarovia anisosperma* Korovin, Urgut,
24 Zeravshan Mtns. (Uzbekistan) from material cultivated in Moscow State University Botanical Garden
25 (Moscow, Russia), Pimerov, voucher Pimenov et al. 178 (MW): U78381 and U78441; *Komarovia*
26 *anisosperma* Korovin, voucher 2019-06-23#08: MN832991; *Ledebouriella multiflora* H.Wolf
27 :FJ489337 and FJ489368; *Libanotis eriocarpa* Schrenk, Tian Mt., Fukang (Xinjiang, China), voucher
28 ZJ0708 (KUN): FJ385045; *Libanotis pyrenaica* Bourg. ex Nyman, Haut-Rhin (France), Osenbach,
29 Reduron, voucher 24 July 2001, Reduron s. n. (ILL): AY179026; *Libanotis schrenkiana*, voucher
30 SschrA94: MG920273; *Libanotis seseloides* (Fisch. & C.A. Mey. Ex Ledeb) Turcz, Dunhua City,
31 Hancogling (Jilin, China), Liao, voucher Liao et al. 2015073006 (SZ): MT707544; *Libanotis sibirica*
32 (L.) C.A. Mey., Xinjiang, TieLieKe, Habahe (Xinjiang, China), voucher ZJ0741 (KUN): FJ385046;
33 *Ligusticum daucoides*(Franch.) Franch., Bowa Mtn., Daocheng (Sichuan, China), voucher ZJ0556
34 (KUN): EU236173; *Ligisticopsis dielsianaei* (H. Wolff) Pimenov & Kljuykov, Ranwu-Shanranwu
35 (Sichuan, China) Pimenov, voucher Pimenov et al. 416 (MW): AY328945 and AY330511; *Ligisticum*
36 *mucronatum* (Schrenk) Leute, voucher J110 (XAU): FJ385047; *Ligisticum oliverianum* (H. de
37 Boissieu) Shan, Geka Country, Daofu (Sichuan, China), voucher KUN 201606127: MK036610;
38 *Ligisticum physospermifolium* Albov, cultivated Moscow State University Botanical Garden (Moscow,
39 Russia) from material of Teberdinsky Reserve (Stavropol Region, Russia), M. G. Pimenov, voucher M.
40 G. PIMENOV & al. s.n. (MW): AF008616 and AF009095; *Ligisticum pteridophyllum* Franch. Rewu
41 Country, Xiangcheng (Sichuan, China), voucher KUN Z15177: MK036612; *Ligisticum scapiforme* H.
42 Wolff, Kalatz Mt., Litang (Sichuan, China), voucher KUN Z15162: MK036614; *Ligisticum scoticum* L.,
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3 cultivated in University of Illinois at Urbana-Champaign (UIUC) (Illinois, U.S.A.) from material of the
4 Jardin Botanique de Montréal (Quebec, Canada), Downie, voucher Downie 3 (ILL): AH006062
5 (=U79591 and U79592), *Ligusticum scoticum* L., voucher RBGE6: KX167844; *Ligusticum scoticum*
6 **subsp. *hultenii*** (Fern.) Calder & Taylor, East of Montague Island (Alaska, U.S.A.), Lewis, voucher Lewis
7 *ALA V110933*: MK694948; *Ligusticum sikiangense* Hiroe, Yanyuan, (Sihuan, China), voucher KUN
8 20160636: MK036619; *Ligusticum physospermifolinum* Albov, Teberdinsky Reserve (Stavropol
9 Region, Russia) from material cultivated in Moscow State University Botanical Garden (Moscow,
10 Russia), M. G. Pimenov, voucher M. G. PIMENOV & al. s.n. (MW): AF008616 and AF009095;
11 *Ligusticum thomsonii* C. B. Clarke, Daofu-Bamei, (Sichuan, China), voucher KUN 201606132:
12 MK036623; *Ligusticum weberbauerianum* H. Wolff, Jianziwan Mt., Yajiang (Sichuan, China), Feiyong
13 and Liliangqian, voucher Feiyong&Liliangqian2969 (KUN): MK036626; *Lomatocarpa albomarginata*
14 (Schrenk) Pimenov & Lavrova, Usunmurun river, Karamyk, Alai Mts. (Kirghyzia), Pimenov and
15 Kljuykov, voucher Pimenov & Kljuykov, 427 (MW): AY328954 and AY330520; *Lomatium bicolor* var.
16 *leptocarpum*, Flattop Butte, Owyhee Co. (Idaho, U.S.A.), voucher CIC:D3434: HQ426089; *Lomatium*
17 *brandegeei* (J. M. Coulter & Rose) J. F. Macbr, Kittitas Co. (Washington, U.S.A.), D. Mansfield, voucher
18 D. Mansfield 11-477, (CIC 041532): KF619632; *Lomatium californicum* (Nutt.) Mathias & Constance,
19 Josephine Co. (Oregon, U.S.A.), R. Helliwell, voucher R. Helliwell 3949 (CIC 039924): KF619636;
20 *Lomatium grayi* (J. M. Coulter & Rose) J. M. Coulter & Rose, Malheur Co. (Oregon, U.S.A.), E. George,
21 voucher E. George 050 (CIC 039901): KF619669; *Lomatium grayi* (J. M. Coulter & Rose) J. M. Coulter &
22 Rose, Yakima Co. (Washington, U.S.A.), C. E. Hinchliff, voucher C. E. Hinchliff 1240 (CIC 041459):
23 KF619670; *Lomatium foeniculaceum* (Nutt.) J. M. Coulter & Rose var. *macdougalii* (J. M. Coulter &
24 Rose) Cronquist, Canyon Co. (Idaho, U.S.A.), D. Mansfield, voucher D. Mansfield 07-001 (CIC 034364):
25 KF619660; *Lomatium nevadense* (S. Watson) J. M. Coulter & Rose, Page Springs Campground, Harney
26 Co. (Oregon, U.S.A.), voucher CIC:0344242: HQ426096; *Lomatium nevadense* (S. Watson) J. M. Coulter.
27 & Rose var. *parishii* (J. M. Coulter & Rose) Jeps., Apache Co. (Arizona, U.S.A.), C. E. Hinchliff, voucher
28 C. E. Hinchliff 1283 (CIC 040914): KF619681; *Lomatium nudicaule* (Pursh) J. M. Coulter & Rose,
29 Washington Co. (Idaho, U.S.A.), E. George, voucher E. George 065 (CIC 039895): KF619685;
30 *Lomatium ochocense* Helliwell & Constance, Crook Co. (Oregon, U.S.A.), R. Helliwell, voucher R.
31 Helliwell 3961 (CIC 044308): KF619688, *Lomatium pastoralis* D. H. Wagner ex M. E. Darrach & D. H.
32 Wagner, Umatilla Co. (Oregon, U.S.A.), M. Darrach, voucher M. Darrach 675 (CIC 042000). KF619691;
33 *Lomatium salmoniflorum* (J. M. Coulter & Rose) Mathias & Constance, Whitman Co. (Washington,
34 U.S.A.), C. E. Hinchliff, C. E. Hinchliff 1209 (CIC 041450): KF619698; *Lomatium trternatum* (Pursh)
35 J. M. Coulter & Rose var. *trternatum*, Río Arriba Co. (New Mexico, U.S.A.), C. E. Hinchliff, voucher C.
36 E. Hinchliff 1280 (CIC 040913): KF619714, *Lomatium trternatum* (Pursh) J. M. Coulter & Rose var.
37 *trternatum*, Benton Co. (Washington, U.S.A.), M. Darrach, voucher M. Darrach 630 (CIC 042001):
38 KF619702; *Lomatium trternatum* (Pursh) J. M. Coulter & Rose var. *trternatum*, Harney Co. (Oregon,
39 U.S.A.), D. Mansfield, voucher D. Mansfield 11-007 (CIC 040127): KF619715; *Magadania victoris*
40 (Schischk.) Pimenov & Lavrova, Russia, Magadan prov., near Magadan (Magadan prov., Russia), H. E.
41 Grosset, voucher H. E. Grosset (MW): AY328947 and AY330513; *Malabaila aurea* Boiss., Veles
42 (Macedonia), Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of
43 Macedonia, Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of
44 Macedonia, Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of
45 Macedonia, Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of
46 Macedonia, Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of
47 Macedonia, Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of
48 Macedonia, Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of
49 Macedonia, Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of
50 Macedonia, Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of
51 Macedonia, Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of
52 Macedonia, Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of
53 Macedonia, Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of
54 Macedonia, Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of
55 Macedonia, Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of
56 Macedonia, Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of
57 Macedonia, Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of
58 Macedonia, Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of
59 Macedonia, Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of
60 Macedonia, Mayer, voucher Mayer 50567 (KRAM): EU594919; *Malabaila aucheri* Boiss., East of

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3 Bedehan (Iran), Davis and Bokhari, Davis & Bokhari 55816: EU185665; *Malabaila dasyantha* (C. Koch)
4 Grossh., Turkey, Menemen and Hamzaoglu, voucher Menemen & Hamzaoglu 60 (ADO) DNA No. 1862:
5 EU169296; *Malabaila involucrata* Boiss. & Spruner, Greece, Cghanson, Cghanson s.n.: EU185669;
6 *Malabaila pastinacifolia* Boiss. & Bal., Turkey, voucher Duran & al. 5498 (ADO) DNA No. 1861:
7 EU169297; *Mathiasella bupleuroides* Constance & Hitchcock, Cerro El Viejo, (Nuevo León, Mexico)
8 from material cultivated in University of California Botanical Garden, Berkely (California, U. S. A.),
9 Hinton et al. 22234 (UC), L. Constance, voucher L. Constance 2447: U78394 and U78454;
10 *Myrrhidendron donnellsmithii* Coulter. & Rose, Province of San José (Costa Rica) from material
11 cultivated int UC Botanical Garden, Berkely (California, U. S. A.), Grantham and Parso, voucher
12 Grantham and Parsons 0433-90 (nº. 90.2637): AH003480 (=U30554 and U30555); *Myrrhidendron*
13 *donnellsmithii* Coulter. & Rose, Alfaro, voucher Alfaro 1727 (MO): GQ862471; *Meeboldia yunnanensis*
14 (H.Wolff) Constance & F.T.Pu ex S.L.Liou, voucher GB0005MT01: KF725057; *Meum athamanticum*
15 Jacq.: AF077900; *Meum athamanticum* Jacq., Murias Longas, Somiedo (Asturias, Spain), T. Sánchez
16 Corominas, V.M. Vázquez and J.A. Fernández Prieto, voucher FCO:32709: KC676174; *Musineon*
17 *divaricatum* (Pursh) Nutt. ex Torr. & A. Gray var. *divaricatum*, north-west of Chugwater Platte Co., NW
18 of Chugwater (Wyoming, U.S.A.), Nelson, voucher Nelson 30905 (RM): AF358506 and AF358573;
19 *Musineon divaricatum* (Pursh) Nutt., White Pine Co. (Nevada, U.S.A.), C. E. Hinchliff, voucher C. E.
20 Hinchliff 1311 (CIC 041346): KF619722; *Musineon divaricatum* (Pursh) Nutt., Horstmann Peak,
21 Sawtooth Mnts., Sawtooth National Forest (Idaho, U.S.A.), voucher August 7, 2012 Zion 2012-038 ID:
22 MK802451; *Musineon lineare* (Rydb.) Mathias, Bear Lake Co. (Idaho, U.S.A.), D. Mansfield, voucher
23 D. Mansfield 12-692: KF619723; *Musineon vaginatum* Rydb., Missoula Co. (Montana, U.S.A.), P.
24 Lesica, voucher P. Lesica 10620 (CIC 041462): KF619724; *Naufraga balearica* Constance & Cannon,
25 Majorca (Balearic Islands, Spain), P. Vargas, voucher P. Vargas 81PV11, MA Balearic Islands, Majorca:
26 KJ473894; *Naufraga balearica* Constance & Cannon, Cala de Sant Vicenc., Port de Pollenca, Majorca
27 (Balearic Islands, Spain) from material cultivated in Royal Botanic Garden Edinburgh, Edinburgh
28 (Scotland, U.K.) McBeath, voucher McBeath 2760 (E) (no. 19943095): AF073563; *Neoparrya lithophila*
29 Mathias, Upper Saguache Forest Service Station, Saguache Co. (Colorado, U.S.A., Colorado), Hartman,
30 voucher Hartman 17360 (RM): AF358576 and AF358509; *Neoparrya lithophila* Mathias,Taos Co. (New
31 Mexico, U.S.A.), C. E. Hinchliff, voucher C. E. Hinchliff 1275 (CIC 040908): KF619725;
32 *Notopterygium incisum* Ting ex H.T. Chang, KIB nursery (Yunnan, China), voucher ZJ0697:
33 EU236180; *Notopterygium incisum* Ting ex H.T. Chang, Szechwan Kang ding (China): DQ278168;
34 *Notopterygium incisum* Ting ex H.T. Chang, China, voucher Ho et al. 258 23-VII-1993 (MO):
35 GQ379335; *Oreocomopsis stelliphora* (Cauwet & Farille) Pimenov & Kljuykov, Farille, voucher Farille
36 81-421 18-IX-1981 (G): GQ379322; *Oreonana clementis* (M.E. Jones) Jeps., Guyot Mtn., Tulare County
37 (California, U.S.A.), Howell, voucher Howell 25604 (UTC): AY146857 and AY146923; *Oreonana*
38 *purpurascens* Shevock & Constance, Slate Mountain, Sequoia National Forest, Tulare Co. (California,
39 U.S.A.), Shevock, voucher 26 Apr 1977 Shevock 5428 (BRY): AY146858 and AY146924; *Oreonana*
40 *vestita* (S. Watson) Jeps., Mt Harwood-Mt San Antonio Peak, San Gabriel Mtns, Angeles National Forest,
41 San Bernardino Co. (California, U.S.A.), Shevock, voucher 4 May 1977 Shevock 5433 (BRY):
42 AY146859 and AY146925; *Oreoselinum nigrum* Delarbre (=*Peucedanum oreoselinum* (L.) Moench),
43 San Bernardino Co. (California, U.S.A.), Shevock, voucher 4 May 1977 Shevock 5433 (BRY):
44 AY146859 and AY146925; *Oreoselinum nigrum* Delarbre (=*Peucedanum oreoselinum* (L.) Moench),
45 San Bernardino Co. (California, U.S.A.), Shevock, voucher 4 May 1977 Shevock 5433 (BRY):
46 AY146859 and AY146925; *Oreoselinum nigrum* Delarbre (=*Peucedanum oreoselinum* (L.) Moench),
47 San Bernardino Co. (California, U.S.A.), Shevock, voucher 4 May 1977 Shevock 5433 (BRY):
48 AY146859 and AY146925; *Oreoselinum nigrum* Delarbre (=*Peucedanum oreoselinum* (L.) Moench),
49 San Bernardino Co. (California, U.S.A.), Shevock, voucher 4 May 1977 Shevock 5433 (BRY):
50 AY146859 and AY146925; *Oreoselinum nigrum* Delarbre (=*Peucedanum oreoselinum* (L.) Moench),
51 San Bernardino Co. (California, U.S.A.), Shevock, voucher 4 May 1977 Shevock 5433 (BRY):
52 AY146859 and AY146925; *Oreoselinum nigrum* Delarbre (=*Peucedanum oreoselinum* (L.) Moench),
53 San Bernardino Co. (California, U.S.A.), Shevock, voucher 4 May 1977 Shevock 5433 (BRY):
54 AY146859 and AY146925; *Oreoselinum nigrum* Delarbre (=*Peucedanum oreoselinum* (L.) Moench),
55 San Bernardino Co. (California, U.S.A.), Shevock, voucher 4 May 1977 Shevock 5433 (BRY):
56 AY146859 and AY146925; *Oreoselinum nigrum* Delarbre (=*Peucedanum oreoselinum* (L.) Moench),
57 San Bernardino Co. (California, U.S.A.), Shevock, voucher 4 May 1977 Shevock 5433 (BRY):
58 AY146859 and AY146925; *Oreoselinum nigrum* Delarbre (=*Peucedanum oreoselinum* (L.) Moench),
59 San Bernardino Co. (California, U.S.A.), Shevock, voucher 4 May 1977 Shevock 5433 (BRY):
60 AY146859 and AY146925; *Oreoselinum nigrum* Delarbre (=*Peucedanum oreoselinum* (L.) Moench),

Larzac (Aveyron, France) Aveyron, Chéon, voucher Chéon s. n. (WA): AH012698 (=AF495836 and AF495837); *Oreoxis alpina* (A. Gray) J.M. Coulter & Rose subsp. *alpina*, Pyramid Peak, Río Blanco Co. (Colorado, U.S.A.) Vanderhorst, voucher 27 June 1991 Vanderhorst 2806 (RM): AF358510 and AF358577; *Oreoxis alpina* (A. Gray) J.M. Coulter & Rose, Larimer Co. (Colorado, U.S.A.), S. Nunn, voucher S. Nunn 2078 (RM 765899): KF619726; *Oreoxis bakeri* J.M. Coulter & Rose, Lake Peak, Santa Fe Co. (New Mexico, U.S.A.) Hartman voucher 19 June 1980 Hartman 11725 (RM): AF358511 and AF358578, *Oreoxis humilis* Raf., Pikes Peak Road, Teller Co. (Colorado, U.S.A.), Hartman, voucher Hartman 11718 (RM): AF358579 and AF358512; *Oreoxis trotteri* S.L. Welsh & S., North West of Moab, Grand Co. (Utah, U.S.A.), Neese and Welsh, voucher 4 Jun 1985 Neese & Welsh 16984 (BRY): AY146861 and AY146927; *Ormosolenia alpina* (Sieber ex Schultes) Pimenov, Mtn. Pachnes, Lefka Ori (Crete, Greece), voucher Pimenov Brullo & Giusso del Galdo 2061 (CAT): HQ269391; *Orogenia fusiformis* S. Watson., Jackson Co. (Oregon, U.S.A.) J. T. Duncan, voucher J. T. Duncan 7A (CIC 041668): KF619727; *Orogenia linearifolia* S. Watson, Hams Fork Plateau, Lincoln Co. (Wyoming, U.S.A.), Hartman, voucher Hartman 37557 (RM): AF358513 and AF358580; *Orogenia littariaefolia* S. Watson, Hornet Cr. - Bear, Adams Co. (Idaho, U.S.A.), voucher CIC:034349: HQ426099; *Ostericum citriodorum* (Hance) R.H. Shan & C.Q. Yuan, China, Guangxi, Luzhai (Guangxi, China), Liao CY, voucher Liao CY 908277 (SZ): JX312701; *Ostericum grosseserratum* (Maxim.) Kitag., Jinzhai (Anhui, China), Liao CY, voucher Liao CY 667435 (SZ): GU390409; *Ostericum huadongensis* Z.H. Pan & X.H. Li, Jinzhai (Anhui, China), Liao CY, Liao CY 667429 (SZ): GU395175; *Ostericum maximowiczii* (F. Schmidt) Kitag., China, Jilin, Changbai Mtn. (Jilin, China), Liao CY, voucher Liao CY 744114 (SZ): GU390410; *Ostericum scaberulum* (Franch.) R.H. Shan & C.Q., Yuan, China, Yunnan, Shangri-la (Yunnan, China), Liao CY, voucher Liao CY 703013 (SZ): GU390411; *Ostericum scaberulum* (Franch.) R.H. Shan & C.Q., Muli County (Sichuan, China) Mianya Liao and Tang, voucher Mianya Liao & Tang 2014101202 (SZ): MT735406; *Ostericum sieboldii* (Miq.) Nakai, Changbai Mtn. (Jilin, China), Liao CY, voucher Liao CY 667568 (SZ): GU390412; *Ostericum sieboldii* (Miq.) Nakai, Iwaki-shi (Fukushima Prefecture, Honshu, Japan), Yonekura and Ishiguri, voucher Yonekura & Ishiguri 3573 (MO 4987936): MT735403; *Ostericum viridiflorum* (Turcz.) Kitag., Yichun (Heilongjiang, China), Wang CB 674185 (SZ): GU390413; *Ostericum viridiflorum* (Turcz.) Kitag., Sifongshan, Kiamusze (Helongjiang, China), Liao and Zhang, voucher Liao & Zhang 2016082905 (SZ): MT735402; *Pachypleurum alpinum* Ledeb, Mongolia, Caddick, voucher Caddick 172 (E): KJ660840; *Pachypleurum mutellinoides* (Crantz) Holub, Col du Gd. St. Bernard, les Alpes Pennines (canton Valais, Suisse), Pimenov, voucher Pimenov et al. S96-13 (MW): AY330506 and AY328940; *Paraligusticum discolor* (Ledeb) V.N. Tichom., cultivated in Moscow State University Botanical Garden, (Moscow, Russia) from material of Lepsinsk, Dzhungar Alatau Mtns. (Kazakhstan), Kljuykov, voucher Kljuykov 119 (MW): U78404 and U78464; *Paraligusticum discolor* (Ledeb) V.N.Tichom., Lepsinsk, Dzhungar Alatau Mtns. (Kazakhstan) from material Cultivated in Moscow State Univ. Botanical Garden (Moscow, Russia), Kljuykov, voucher Kljuykov 119 (MW): AF077902; *Parasilaus afghanicus* (Gilli) Leute, China, Wendelbo, voucher Wendelbo et al. 8509(E): MK088003; *Parasilaus asiaticus* (Korovin) Pimenov, Nikolayevsky Spusk (Tadzhikistan) from material cultivated in Moscow State University Botanical Garden (Moscow, Russia), M. G. Pimenov, voucher M. G. PIMENOV & al. s.n. (MW): AF008642 and AF009121; *Pastinaca sativa*

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2
3 L., material cultivaed in Johannes Gutenberg University, Mainz (Rhineland Palatinate, Germany),
4 Downie, voucher Downie 70 (ILL) (no. 1597): AH003484 (=U30546 and U30547); *Pastinaca sativa* L.,
5 Musala, Rila Planina (Sofia, Bulgaria), Gardner and Gardner, voucher Gardner & Gardner 3202 (E):
6 EU185666; *Petroselinum crispum* (Mill.) Fuss., S. Downie, voucher S. Downie 21 (ILL): GQ148800;
7 *Petroselinum crispum* (Mill.) Fuss., voucher PS0325MT01: MZ191031; Peucedanum officinale L.,
8 Steinbach (Haut-Rhin, France), Reduron, voucher 5 June 1979, Reduron s. n. (WA): AH012690
9 (=AF495820 and AF495821); Peucedanum officinale L., voucher C:Simonsen 2013-4: KF160673,
10 Peucedanum officinale L., voucher Peu10: KP682404; *Phlojodicarpus popovii* Sipliv., from material
11 cultivated in the Royal Botanic Garden of Edinburgh (Edinburgh, U. K.) voucher (no. 19932315):
12 AF009083 and AF008604; *Physospermopsis delavayi* H.Wolff, YuLong Snow Mtn. (Yunnan, China),
13 voucher KUN:J033; FJ385056; *Physospermopsis delavayi* (Franch.) H. Wolff, Yulongxue Shan Mtns.,
14 Lijiang County (Yunnan, China), Pimenov, voucher Pimenov et al. 532 (MW): FJ625831 and FJ483501;
15 *Pimpinella afinis* Ledeb, Mesudiye, Ordu (Turkey), voucher June 2001 ESSE 13890: AY581780;
16 *Pimpinella austriaca* Mill.: KX982512; *Pimpinella brachycarpa* Nakai: AY548230, *Pimpinella major*,
17 Santiago de Arenas, Siero, (Asturias, Spain), Herminio S. Nava, voucher FCO 37750-37751-37752:
18 MH377862; *Pimpinella lutea* Desf., cultivated in the Conservatoire Botanique d'Alsace, Mulhouse
19 (Alsace, France) from material of Corsica (France), Hildenbrand, voucher Hildenbrand/C.B.M. 9564
20 (ILL): DQ516374; *Pimpinella niitakayamensis* Hayata, Tunyuan-Yunhai, Jenai Hsiang, Nantou Hsien
21 (Taiwan, China), Chi-Chen Liao, voucher Chi-Chen Liao et al. 1276 (MO): DQ516375; *Pimpinella*
22 *olivieroides* Boiss. & Hausskn., Beynam woods (Ankara, Turkey), voucher June 2000 ESSE 13928:
23 AY581795 *Pimpinella peucedanifolia* Fischer, Solhan (Mus, Turkey), voucher July 2001 ESSE 13913:
24 AY581798; *Pimpinella puberula* (DC.) Boiss., Hakkari-Van road (Hakkari, Turkey), voucher July 2001
25 ESSE 13909: AY581799; *Pimpinella rhodantha* Boiss., Turkey: Giresun: Tamdere (Giresun, Turkey),
26 August 2001 ESSE 13932: AY581800; *Pimpinella saxifraga* L., Sarikamis (Kars, Turkey), July 2001
27 ESSE 13924: AY581801; *Pimpinella saxifraga* L., cultivate in University of Oldenburg Botanic Garden,
28 Oldenburg (Bayern, Germany) Downie, voucher (no. 19) Downie 137 (ILL): AH003548; *Pimpinella*
29 *tibetanica* H.Wolff, voucher G2010070709: JF831528; *Pimpinella smithii* H.Wolf, Wolong, Wenchuan
30 (Sichuan, China), voucher ZJ0643: EU236196; *Pimpinella smithii* H. Wolff, voucher wzx09092212:
31 JF831526; *Pimpinella smithii* H. Wolff, China, Smith, voucher Smith 6931 20-VIII-1924 (MO):
32 GQ379272; *Pimpinella valleculosa* K.T.Fu, voucher wzx2010101002: JF831529; *Pimpinella sintenisii*
33 Wolff, Turkey: Mardin: Zafran (Mardin, Turkey), voucher Kew: AY581802; *Pimpinella tragium* Vill.
34 subsp. *pseudotragium* (DC.) Matthews, Kicilahamam (Ankara, Turkey), June 2001 ESSE 13874:
35 AY581805; *Pilopleura goloskokovii* (Korov.) Pimenov, M.G.Pimenov, voucher M.G.Pimenov et al.
36 No.512 (MW): FJ489384 and FJ489353; *Pleurospermum hookeri* var. *thomsonii* C.B. Clarke, Ma'an
37 Mtn. (Sichuan, China) voucher ZJ0545: EU236199; *Podistera nevadensis* (A. Gray) S. Watson, Frell
38 Peak, Lake Tahoe Basin Management Unit, El Dorado Co. (California, U.S.A.), Matson, voucher 27 Jul
39 2002 Matson 634 (ILL): AY146865 and AY146931; *Polytaenia nuttallii* DC. U.S.A., Illinois, Rock
40 Island Co., North of Cordova, Rock Island Co. (Illinois, U.S.A.), Evers, voucher Evers 110464 (ILLS):
41 AF358516 and AF358583; *Polytaenia nuttallii* DC., McLellan Co. (Texas, U.S.A.), F. R. Barrie, voucher
42 F. R. Barrie 1406 (RM 529215): KF619728; *Polytaenia texana* (J.M. Coulter & Rose) Mathias &
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Shoshonea pulvinata Evert & Constance, Logan Mtn., Park County (Wyoming, U.S.A.), Evert, voucher Evert 10623 (RM): U78460 and U78400; **Shoshonea pulvinata** Evert & Constance, Park Co. (Wyoming, U.S.A.), W. Fertig, voucher W. Fertig 15327 (RM 613328): KF619734; **Sinocarum coloratum** (Diels) H. Wolff ex R.H. Shan & F.T. Pu, YuLong Snow Mtn. (Yunnan, China), voucher KUN:YL561: FJ385063; **Spermolepis inermis** (Nurr. ex DC.) Mathias & Constance, USA, Illinois, Rock Island Co., Cordova Rock Island Co. (Illinois, U.S.A.), R. A. Evers, voucher R. A. EVER 80062 (ILLS): AF008602 and AF009081; **Sphenosciadium capitellatum** A. Gray, Oregon (U.S.A.), G. Mason, voucher G. MASON 7531 (ILL): AF008600 and AF009079; **Spuriopimpinella calycina** (Maxim.) Kitag., Japan, Ohwi, voucher Ohwi 126 4-IX-1950 (G): GQ379330; **Stenocoelium athamantoides** Ledeb., M. G. Pimenov, voucher M.G.Pimenov et al. No.447 (MW): FJ489385 and FJ489354; **Taenidia integerrima** (L.) Drude, Lake View Park (Illinois, U.S.A.), Downie, voucher Downie 763 (ILL): U78399 and U78459; **Tauschia texana** A. Gray, Gonzales County (Texas, U.S.A.), Barrie, voucher Barrie 1435 (RM) :AF358592 and AF358525; **Thaspium barbinode** (Michx.) Nutt., North of Tolono, Champaign Co. (Illinois, U.S.A.), Ulaszek, voucher 12 June 1990 Ulaszek 1484 (ILLS): AF358526 and AF358593; **Thaspium barbinode** (Michx.) Nutt., Ozark Trail, Mark Twain Forest, Wayne Co. (Missouri, U.S.A.), Brant, voucher Brant 3900 (MO 4900599): MT707549; **Thaspium pinnatifidum**, voucher Wofford et al. THA-11-13, 5/23/2000 (TENN): MK355979; **Thaspium trifoliatum**(L.) A. Gray, Urbana (Illinois, U.S.A.), Downie, voucher Downie 744 (ILL): U78410 and U78470.1; **Thecocarpus meifolius** Boiss., Jasuj, Zagros Mts. (Boyerahmad va Kohgiluye, Iran), M. G. Pimenov, E. V. Kluykov, A. K. Sytin and F. G haremandinejad, voucher MW 211: AY941290 and AY941318; **Thecocarpus meifolius** Boiss., voucher 97167-TARI: MT254224; **Thyselinum palustre** (L.) Hoffm. (=*Peucedanum palustre* (L.) Moench), Bemowo (Warszawa, Poland), Kirpluk, voucher 23 August 1985 Kirpluk s. n. (WA): AY179035; **Tilingia ajanensis** Regel & Til., Cheshov Mtn. (Saghaliens, Russia), Pimenov and Kljuykov, voucher Pimenov & Kljuykov 139 (MW): AY328939 and AY330505; **Tilingia ajanensis** Regel & Til., voucher M16-5: LC554281; **Tommasinia verticillaris** Bertol., cultivated in Moscow State University Botanical Garden, Moscow (Russia): AF008609 and AF009088; **Tordylium aegyptiacum** (L.) Lam., Lahham & El-Oqlah , Jordan, cultivated in Yarmouk University Herbarium (Irbid, Jordania), Lahham and El-Oqlah, voucher Lahham & El-Oqlah 11 :EU169328; **Tordylium apulum** L., Izmri (Turkey), Davis, Davis 41835: EU185679; **Tordylium elegans** (Boiss. & Balansa) Alava & Hub.-Mor., Adan (Turkey), Alava 6694 :EU185664; **Tordylium maximum** L. Georgia, between Ambrolauri-Oni, Georgia, M. G. Pimenov, voucher 15.08.1973. M. G. Pimenov 744 (MW): DQ996585; **Tetraena canescens** Lindl.,Nainital, Uttar Pradesh (India), Pimenov and Kljuykov voucher Pimenov and Kljuykov (MW): KY851299; **Tetrataenium nepalense** (D.Don) Manden: HQ686493; **Tetrataenium nepalense** (D.Don) Manden: DQ427036; **Trinia hispida** Hoffm., Russia, Botschkin, voucher Botschkin & al. 70 (MO 04985260) DNA No. 2127:EU169330 ; **Vicatia coniifolia** Woll ex DC, King, voucher King 1132 (E 00059551): EU169331; **Xanthoselinum alsaticum** (L.) Schur (=*Peucedanum alsaticum* L.), Westhalten (Haut-Rhin, France), Reduron, voucher 21 August 1979 Reduron s. n. (WA): AH012697 (=AF495834 and AF495835); **Zizia aurea** (L.) Koch., cultivated in ther Jardin Botanique de Montréal, Downie, voucher (no. 60) Downie 8 (ILL): AH003554 (=U30574 and U30575); **Zizia aurea** Koch. Kansas: Cherokee Co. (Kansas, U.S.A.), R. L. McGregor, voucher R. L. McGregor 32898 (RM 527763): KF619741; **Zizia**

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3 *aurea* (L.) Koch., voucher DPP61: MT610976, *Zosima orientalis* Hoffm., Tortum-Erzerum (Turkey)
4 from material cultivated in Moscow State University Botanical Garden (Moscow, Russia), M. G.
5 Pimenov, voucher M. G. PIMENOV & al. s.n. (MW): AF008628 and AF009107.
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10 List of *Angelica* taxa and sequences generated in previous studies used in the trnL phylogenetic analysis.
11 The order of the displayed data corresponds to the following information: taxon name, collection site,
12 collector, voucher and GenBank accession numbers.
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15 *Angelica sylvestris* L., from material cultivated of UIUC from Shanghai Botanic Garden (Shanghai,
16 China), Downie, voucher Downie 428 (ILL): AY379236; *Angelica sylvestris* L.: GQ244572; *Angelica*
17 *sylvestris* L., voucher isolate 0760g: GQ244569; *Angelica sylvestris* L., voucher isolate P28: KF718351.
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Table 1. Number of European genera of *Angelica* s.l. proposed by different authors. Genera considered treated as different from *Angelica* in the reference are indicated with a plus sign (+), while untreated taxa are indicated by a dot (.). Gray squares indicates that the taxon has been considered as synonymous of other species, the Synonyms species are indicated in brackets.

Genus	Linnaeus (1753)	Cannon & Tutin (1968)	EURO+MED (2011)	Liao et al. (2020)
<i>Angelica</i> L. (1753)	+	+	+	+
<i>Archangelica</i> Wolf (1776)	<i>Angelica archangelica</i> L. (1753)	<i>Angelica archangelica</i> L. (1753)	<i>Angelica</i> <i>archangelica</i> L. (1753)	<i>Angelica archangelica</i> L. (1753)
<i>Ostericum</i> Hoffm. (1816)	.	<i>Angelica palustris</i> (Besser) Hoffm. (1814)	+	+

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Table 2. European species of *Angelica* proposed by different authors. Species treated in the reference are indicated with a plus sign (+), while untreated taxa are indicated by a dot (.). Gray squares indicate that the taxon has been considered as synonymous to other species (synonyms are indicated in brackets). Iberian or Pyrenean endemic taxa are indicated with an asterisk (*).

	Lange (1874-1880)	Cannon & Tutin (1968)	Gutiérrez Bustillo (1981), <i>Flora Iberica</i>	Reduron (2007)	EURO+MED (2011)
<i>Angelica angelicastrum</i> (Hoffmanns. & Link)	.	+	[<i>Angelica major</i> Lag. (1816)]*	.	[<i>Angelica major</i> Lag. (1816)]*
Cout. (1913)*
<i>Angelica archangelica</i> L. (1753)	.	+	.	+	+
<i>Angelica decurrens</i> (Lebdeb.) B. Fedtsch (1909)	.	[<i>Angelica archangelica</i> ssp. <i>archangelica</i> L. (1753)]	.	.	+
<i>Angelica heterocarpa</i> J. Llyod (1860)	.	+	.	+	+
<i>Angelica laevis</i> Gay ex Fisch. & C.A.Mey (1843)*	.	+	[<i>Angelica major</i> Lag. (1816)]*	.	[<i>Angelica major</i> Lag. (1816)]*
<i>Angelica major</i> Lag. (1816)*	+	[<i>Angelica sylvestris</i> L. (1753)]	+	[<i>Angelica archangelica</i> L. (1753)]	+
<i>Angelica palustris</i> (Besser) Hoffm. (1814)	.	+	[<i>Ostericum pratense</i> Hoffm. (1816)]	.	[<i>Ostericum pratense</i> Hoffm. (1816)]
<i>Angelica pachycarpa</i> Lange (1864)	+	+	+	+	+

	[<i>Selinum pyrenaeum</i> (L.) Gouan. (1773)]*	[<i>Selinum pyrenaeum</i> (L.) Gouan. (1773)]*	[<i>Selinum pyrenaeum</i> (L.) Gouan. (1773)]*	[<i>Epikeros pyrenaicus</i> (L.) Raf. (1840)]*	+
<i>Angelica pyrenaea</i> (L.) Spreng (1813)*					
<i>Angelica razulii</i> Gouan. (1773)*	+	+	+	+	+
<i>Angelica reuteri</i> Boiss. (1856)*	.	[<i>Angelica sylvestris</i> L. (1753)]	[<i>Angelica major</i> Lag. (1816)]*	.	.
<i>Angelica sylvestris</i> L. (1753)	+	+	+	+	+

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Table 3. Samples of *Angelica*, *Ostericum* and *Sanicula europaea* collected for this study.

Taxon	Code	Genbank Accession number	Site of collection / Voucher	Coordinates (latitude, longitude)	Collector
<i>Angelica archangelica</i> L. (1753)	AARC1	ITS: OQ064632 <i>trnL</i> :OQ060687	Cultivated in Jardín Botánico Atlántico (JBA) de Gijón (Asturias, Spain) / FCO: 40961	43.521509, -5.615900	A. Bueno
	AHET1	ITS: OQ064633 <i>trnL</i> :OQ060688	Right riverbank of Adour river, Bayonne-Lartigue, Atlantic Pyrenees (Pyrénées-Atlantiques, France) / FCO: 40962	43.498830, -1.140511	M. Ceballos de Horna, M. Fdez. Ceballos & J.A. Fdez. Prieto
<i>Angelica heterocarpa</i> Lloyd (1860)	AHET2	ITS: OQ064634 <i>trnL</i> :OQ060689	Right riverbank of Adour river, Bayonne-Lartigue, Atlantic Pyrenees (Pyrénées-Atlantiques, France) / FCO: 40963	43.497533, -1.378182	M. Ceballos de Horna, M. Fdez. Ceballos & J.A. Fdez. Prieto
	AHET3	ITS: OQ064635 <i>trnL</i> :---	Right riverbank of Adour river, Bayonne-Lartigue, Atlantic Pyrenees (Pyrénées-Atlantiques, France) / FCO: 40964	43.50174, -1.346874	M. Ceballos de Horna, M. Fdez. Ceballos & J.A. Fdez. Prieto
<i>Angelica laevis</i> , J.Gay ex Fisch. & C.A.Mey (1843)	ALAE1	ITS: OQ064636 <i>trnL</i> :OQ060690	Port of Pajares, between Arbás del Puerto and el Brañilín (León, Castilla y León, Spain) / FCO: 40965	42.990768, -5.752714	A. Fdez. Ceballos & J.A. Fdez. Prieto
	ALAE2	ITS: OQ064637 <i>trnL</i> :OQ060691	Port of Pajares, between Busdongo and Arbás del Puerto (León, Spain) / FCO: 40966	42.992095, -5.743954	A. Fdez. Ceballos & J.A. Fdez. Prieto

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6	ALAE3	ITS: OQ064638 <i>trnL</i> :OQ060692	Port of Leitariegos, nearby la Venta de la Farruquita (Asturias, Spain) / FCO: 40967	43.022144, -6.449024	V. Vázquez & J.A. Fdez. Prieto	
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10	ALAE4	ITS: OQ064639 <i>trnL</i> :OQ060693	Near the port of Leitariegos (Asturias, Spain) / FCO: 40968	42.995874, -6.415972	V. Vázquez & J.A. Fdez. Prieto	
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14	ALAE5	ITS: OQ064640 <i>trnL</i> :OQ060694	De Suares al Plano, Bimenes (Asturias, Spain) / FCO: 40969	43.338852, -5.594057	H.S. Nava	
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18	ALAE6	ITS: OQ064641 <i>trnL</i> :OQ060695	Pereda de Ancares-Tejeda de Ancares (León, Spain) / FCO: 40970	42.834291, -6.755010	M. Ceballos de Horna & J.A. Fdez. Prieto	
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22	ALAE7	ITS: OQ064642 <i>trnL</i> :OQ060696	C. Sabugo River, Fonsagrada (Lugo, Spain) / FCO: 40971	43.22526, -7.160381	A. Bueno & J.A. Fdez. Prieto	
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25	ALAE8	ITS: OQ064643 <i>trnL</i> :OQ060697	La Garganta, Villanueva de Oscos (Asturias, Spain) / FCO: 40972	43.346486, -7.012432	M. Ceballos de Horna, M. Fdez. Ceballos & J.A. Fdez. Prieto	
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33	<i>Angelica major</i> Lag. (1816)	AMAJ1	ITS: OQ064644 <i>trnL</i> :OQ060698	Portillo de la Sía (Cantabria-Burgos, Spain) / FCO: 40973	43.176908, -3.573379	M. Ceballos de Horna, M. Fdez. Ceballos & J.A. Fdez. Prieto
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1	AMAJ2	ITS: OQ064645 <i>trnL</i> :OQ060699	Portilla de Lunada (Cantabria, Spain) / FCO: 40974	43.153010, -3.573156	M. Ceballos de Horna, M. Fdez. Ceballos & J.A. Fdez. Prieto
2	AMAJ3	ITS: OQ064646 <i>trnL</i> :OQ060700	Covaleda (Soria, Castilla y León, Spain) / FCO: 40975	41.941408, -2.887904	A. Bueno & J.A. Fdez. Prieto
3	AMAJ4	ITS: OQ064647 <i>trnL</i> :OQ060701	Villoslada de Cameros-Lumbrales (La Rioja, Spain) / FCO: 40976	42.114866, -2.641459	A Bueno & J.A. Fdez. Prieto
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5	APAC1	ITS: OQ064648 <i>trnL</i> :OQ060702	Cabo de Peñas, Gozón, cultivated in JBA de Gijón (Asturias, Spain) / FCO: 40977	43.640622, -5.840844	A. Bueno
6	APAC2	ITS: OQ064649 <i>trnL</i> :OQ060703	Punta de Morás (Lugo, Galicia, Spain) / FCO: 40978	42.105777, -7.511960	M. Ceballos de Horna & J.A. Fdez. Prieto
7	APAC3	ITS: OQ064650 <i>trnL</i> :---	Oleiros Beach, Cudillero (Asturias, Spain) / FCO: n.d.	43.586386, -6.225475	M. Ceballos de Horna & J.A. Fdez. Prieto
8	APAC4	ITS: OQ064651 <i>trnL</i> :---	Navia Beach (Asturias, Spain) / FCO: n.d.	43.555887, -6.720303	M. Ceballos de Horna y J.A. Fdez. Prieto

Angelica pachycarpa
Lange (1864)

1	APA5L	ITS: OQ064675 <i>trnL</i> :---	West of Luarca's lighthouse, Luarca (Asturias, Spain) / FCO: 40832	43.549658, -6.532500	H.S. Nava
2	APA6C O	ITS: OQ064676 <i>trnL</i> :---	Near the lighthouse of Cabo de San Agustín Cape, Ortiguera, Coaña (Asturias, Spain) / FCO: 40833	43.564134, -6.732477	H.S. Nava
3	APA8GI	ITS: OQ064677 <i>trnL</i> :---	Campa torres, Gijón (Asturias, Spain) / FCO: 40831	43.566078, -5.705356	H.S. Nava
4	APAL1	ITS: OQ064652 <i>trnL</i> :OQ060704	Uckermark-Randowbruch (Brandenburg, Germany) / FCO: n.d.	53.383329, 13.916668	J.A. Fdez. Prieto & E. Cires
5	APAL2	ITS: OQ064653 <i>trnL</i> :OQ060705	Wroclaw (Breslavia, Poland) / FCO: n.d.	51.127800, 16.997423	J.A. Fdez. Prieto & E. Cires
6	APAL3	ITS: OQ064654 <i>trnL</i> :OQ060706	Havelgebiet (Brandenburg, Germany) / FCO: n.d.	52.533331, 13.033327	J.A. Fdez. Prieto & E. Cires
7	APAL4	ITS: OQ064655 <i>trnL</i> :OQ06070	Leipziger (Saxony-Anhalt, Germany) / FCO: n.d.	51.449991, 12.049991	J.A. Fdez. Prieto & E. Cires

Ostericum palustre
(Besser) Besser (1822)

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6		APYR1	ITS: OQ064656 <i>trnL</i> :OQ060708	Sorteny (Andorra) / FCO: n.d. 42.620530, 1.580750
7				J.A. Fdez. Prieto & E. Cires
8		<i>Angelica pyrenaea</i> Spreng. (1813)		
9				
10		APYR2	ITS: OQ064657 <i>trnL</i> :OQ060709	Formiguères -Mirepoix, Eastern Pyrenees, (Pyrénées-Orientales, Occitania, France) / FCO: n.d. 42.731764, 1.988900
11				J.A. Fdez. Prieto & E. Cires
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14		ARAZ1	ITS:--- <i>trnL</i> :OQ060710	Ortzansurieta-Orbaiceta (Navarra, Spain) / BIO: 24466 43.004015, -1.227571
15				J. Loidi, J.A. Campo, A Berastegui & A. Darquistade
16				
17				
18		ARAZ2	ITS: OQ064658 <i>trnL</i> :OQ060711	Ibón Baños Balneario, pie Argualas (Huesca, Aragón, Spain) / JACA: 237500 42.752156, -0.238632
19				P. Montserrat
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22		<i>Angelica razulii</i> Gouan (1773)	ARAZ3	ITS: OQ064659 <i>trnL</i> :OQ060712 Balneario de Panticosa, riverbanks near Bachimaña (Huesca, Aragón, Spain) / JACA: 265366 42.767509, -0.231155
23				L. Villar
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28		ARAZ4	ITS: OQ064660 <i>trnL</i> :OQ060713	Arinsal, riverbanks of Truites river (Andorra) / JACA: 184492 42.577466, 1.476947
29				P. Montserrat, D. Gómez & J.L. Benito
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33		ARAZ5	ITS: OQ064661 <i>trnL</i> :OQ060714	La Rivereta, Pinar dels Clots, San Juan de Plan (Huesca, Aragón, Spain) / JACA: 273390 41.904224, 1.394644
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6		ARAZ6	ITS: OQ064662 <i>trnL</i> : OQ060715	Valle de Literola, Benasque (Huesca, Aragón, Spain) / JACA: 359497	42.656908, 0.532517
7					J.V. Ferrández
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10	<i>Angelica reuteri</i> Boiss. (1856)	AREU1	ITS: OQ064663 <i>trnL</i> : OQ060716	La Covatilla, Sierra de Béjar (Salamanca, Castilla y León, Spain) / FCO: 40979	40.353159, -5.684065
11					M. Ceballos de Horna, M. Fdez. Ceballos & J.A. Fdez. Prieto
12					
13					
14		ASYL1	ITS: OQ064664 <i>trnL</i> : OQ060717	Cultivated in the alder grove of the JBA de Gijón (Asturias, Spain) / FCO: 40982	43.520343, -5.618540
15					A. Bueno
16					
17		ASYL2	ITS: OQ064665 <i>trnL</i> : OQ060718	Covadonga, Cangas de Onís (Asturias, Spain) / FCO: 40983	43.307292, -5.053215
18					V. Vázquez & J.A. Fdez. Prieto
19					
20	<i>Angelica sylvestris</i> L. (1753)	ASYL3	ITS: OQ064666 <i>trnL</i> : OQ060719	Pas de Peyrol, Puy Mary, Massif Central (Cantal, France) / FCO: 40984	45.133531, 2.717557
21					M. Ceballos de Horna, M. Fdez. Ceballos & J.A. Fdez. Prieto
22					
23		ASYL4	ITS: OQ064667 <i>trnL</i> : OQ060720	Trubia-Oviedo (Asturias, Spain) / FCO: 40985	43.347476, -5.889873
24					M. Ceballos de Horna, M. Fdez. Ceballos & J.A. Fdez. Prieto
25					
26		ASYL5	ITS: OQ064668 <i>trnL</i> : OQ060721	Upper Lusatia, village Dürrbach (Saxony, Germany) / FCO: 40986	51.355955, 14.626202
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5	6	7	8	ASYL6	ITS: OQ064669 <i>trnL</i> :OQ060722	Mosset -La Moulinasse, Eastern Pyrenees (Pyrénées-Orientales, Occitania, France) / FCO: 40987	42.503182, 2.099611
9	10	11	12	ASYL7	ITS: OQ064670 <i>trnL</i> :OQ060723	Cabanasse-Bolquere, Eastern Pyrenees (Pyrénées-Orientales, Occitania, France) / FCO: 40988	42.503180, 2.099611
13	14	15	16	ASYL8	ITS: OQ064671 <i>trnL</i> :OQ060724	Arán-Bagneres de Luchon (Lérida, Cataluña, Spain) / FCO: 40989	42.761294, 0.658172
17	18	19	20	An 334	ITS:--- <i>trnL</i> :OQ060725	Kepsha, near Sochi (Krasnodar Krai, Russia) / MW: 0700334	43.613888, 40.063888
21	22	23	24	An 523	ITS: OQ064673 <i>trnL</i> :---	Near Mamai, Baikal lake (Buryatia, Russia) / MW: 0159523	51.492000, 104.841662
25	26	27	28	An 001	ITS: OQ064672 <i>trnL</i> :---	Pskov Oblast (Russia) / MW: 0459001	57.121565, 30.365512
29	30	31	32	An 555	ITS:--- <i>trnL</i> :OQ060726	Murmansk Oblast (Terskii, Russia) / MW: 0458555	66.677570, 33.881620
33							Polina A. Volkova
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5 *Sanicula europaea* L.
6 (1753) SEU ITS: OQ064674
7 *trnL*:--- Covadonga, Cangas de Onís (Asturias,
8 Spain) / FCO: 37746 43.31235,
9 -5.059108 V. Vázquez & J.A.
10 Fdez. Prieto
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Table 4. Main features of the European ITS, Apioideae ITS and *trnL* alignments used for the phylogenetic analyses. Variable sites are positions in the alignment containing a minimum of two different nucleotides, they were considered to be parsimonious-informative sites when each of the nucleotides had at minimum frequency of two in the alignment.

	European ITS	Apioideae ITS	<i>trnL</i>
Analyzed <i>Angelica</i> taxa	12	67	11
Number of sequences	78	478	44
Range of length of sequences (pb)	537-606	398-611	274-510
Alignment length (pb)	633	699	518
(C+G) %	56.1	55.7	34.9
Conserved sites	476	185	446
Variable sites	136	494	64
Parsimonious-informative sites	114	410	17
Singletons**	22	76	47

**Here singletons are considered following the MEGA X criteria (Kumar et al., 2018), when ambiguities are located at a particular site by at least 3 different sequences.

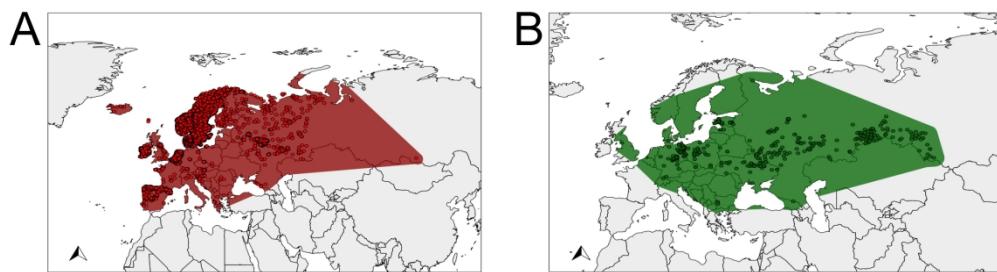


Figure 1. Global distribution of the *Angelica* s. l. genera *Angelica* (A) and *Ostericum* (B) taxa occurring in Europe based on this study's occurrences and the occurrences available at GBIF (<https://www.gbif.org/>).

167x44mm (600 x 600 DPI)

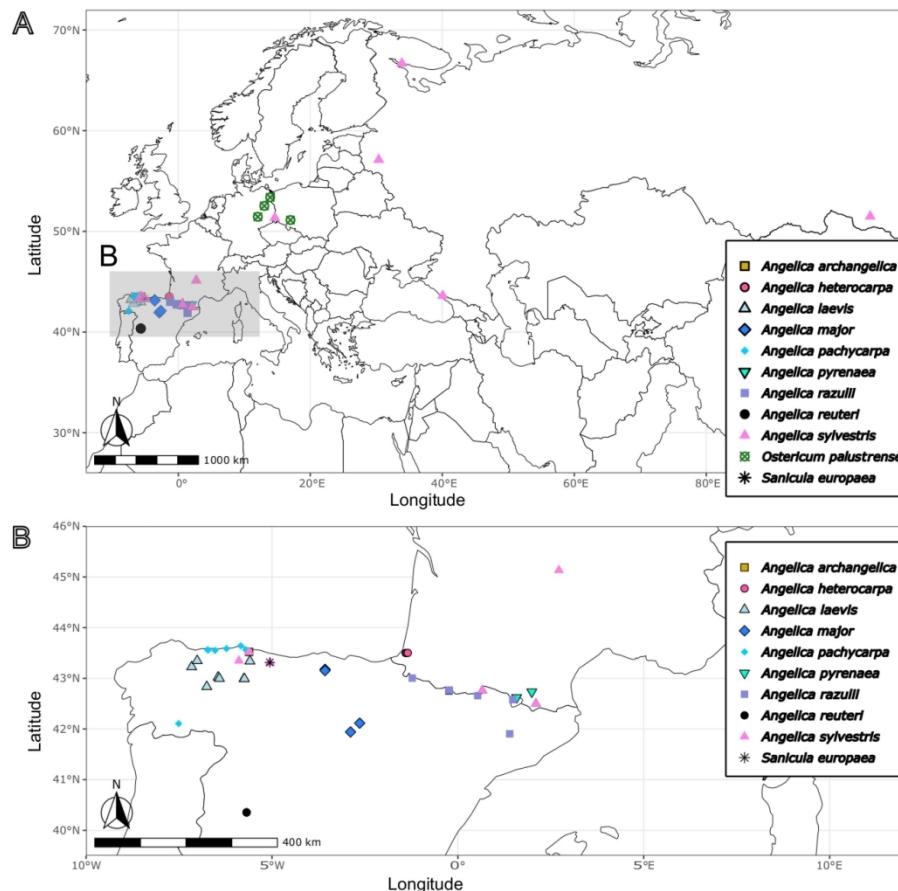


Figure 2. A). Sampling sites of *Angelica*, *Ostericum* and *Sanicula europaea* samples in Europe. B). detailed sampling sites of the Iberian Peninsula and France (B).

123x118mm (300 x 300 DPI)

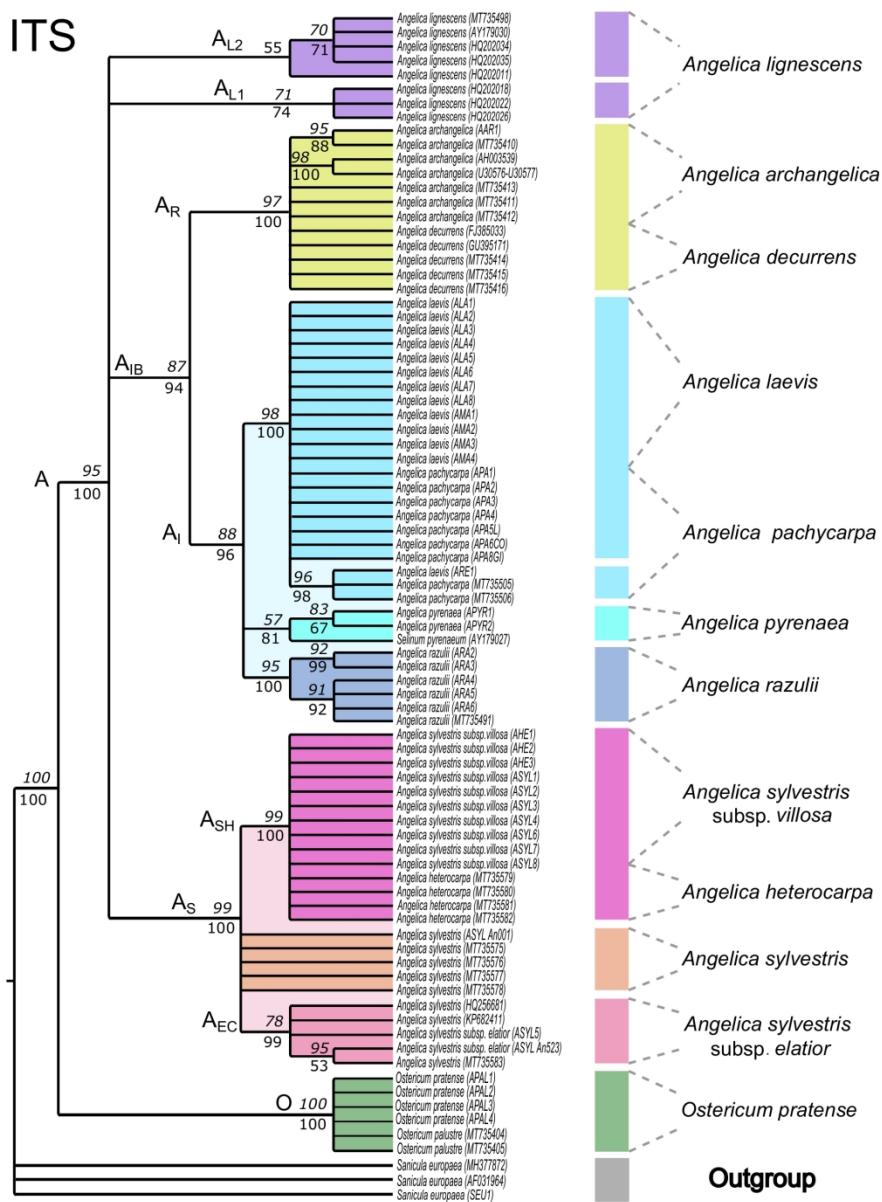


Figure 3. Consensus tree obtained from the ML and BI analyses of the European ITS dataset. Branch support values are displayed in italics over the branches which correspond to bootstrap value (BT) from the ML analysis ranging from 0 to 100, while the numbers under the branches correspond to the posterior probability (PP) of the BI analysis ranging from 1 to 100. Abbreviations correspond to *Angelica archangelica* (AARC), *Angelica heterocarpa* (AHET), *Angelica laevis* (ALAE), *Angelica major* (AMAJ), *Ostericum palustre* (=*Angelica palustris*) (APAL), *Angelica pachycarpa* (APAC), *Angelica pyrenaea* (APYR), *Angelica razulii* (ARAZ), *Angelica reuteri* (AREU), *Angelica sylvestris* (ASYL) and *Sanicula europaea* (SEU).

175x229mm (600 x 600 DPI)

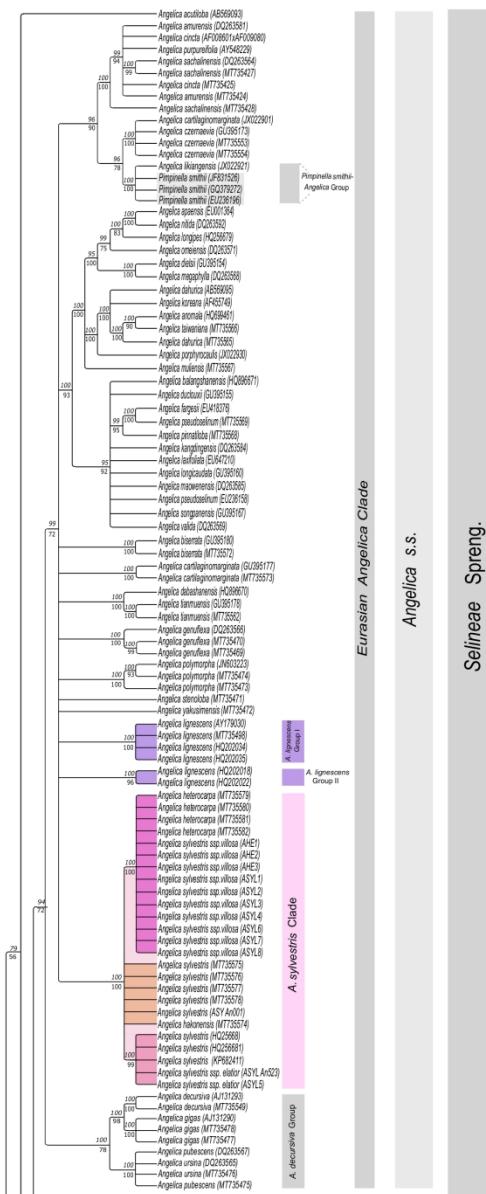


Figure 4. Part I of the consensus tree obtained from the BI and ML analyses of the Apioideae dataset. The numbers under the branches correspond to PP values obtained in the BI analysis, while numbers over the branches correspond to the BT values obtained in the ML analysis. The clades comprising the samples of *Angelica sylvestris* have been highlighted in pink-orange, while clades comprising *Angelica lignescens* have been highlighted in purple. Abbreviations correspond to *Angelica heterocarpa* (AHE) and *Angelica sylvestris* (ASYL).

210x297mm (600 x 600 DPI)

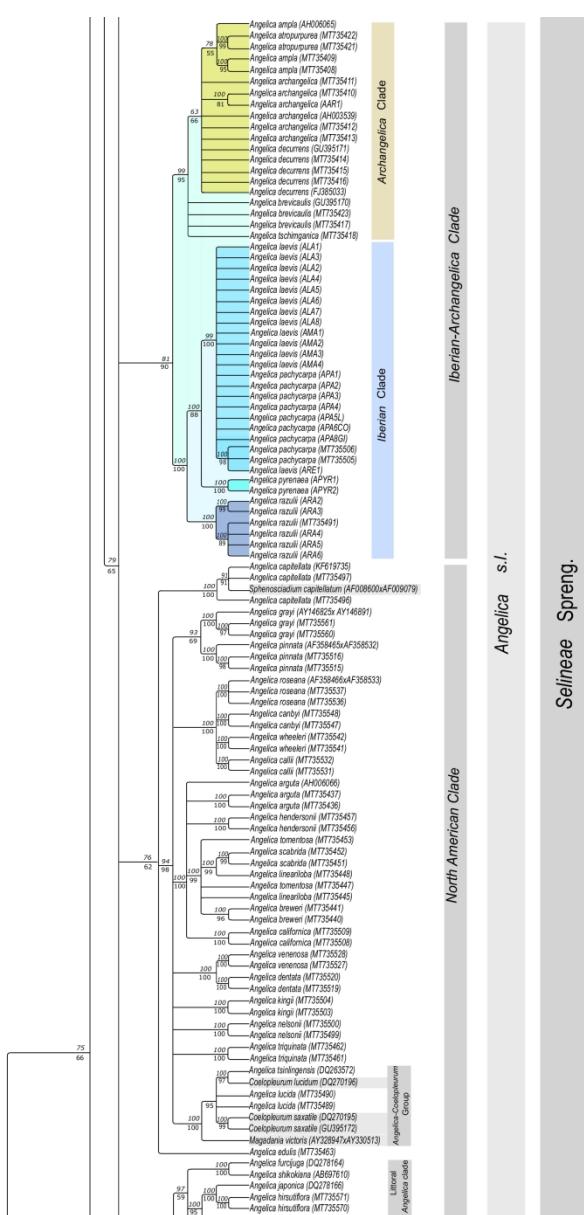


Figure 5. Part II of the consensus tree obtained from the BI and ML analyses of the Apioideae dataset. The numbers under the branches correspond to PP values obtained in the BI analysis, while numbers over the branches correspond to the BT values obtained in the ML analysis. The clades comprising the samples the Iberian endemic species of *Angelica* have been highlighted in blue, while the Archangelica clade has been highlighted in yellow. Abbreviations correspond to *Angelica archangelica* (AAR), *Angelica laevis* (ALA), *Angelica major* (AMA), *Angelica pachycarpa* (APAC), *Angelica pyrenaea* (APYR), *Angelica razulii* (ARA) and *Angelica reuteri* (ARE).

210x297mm (600 x 600 DPI)

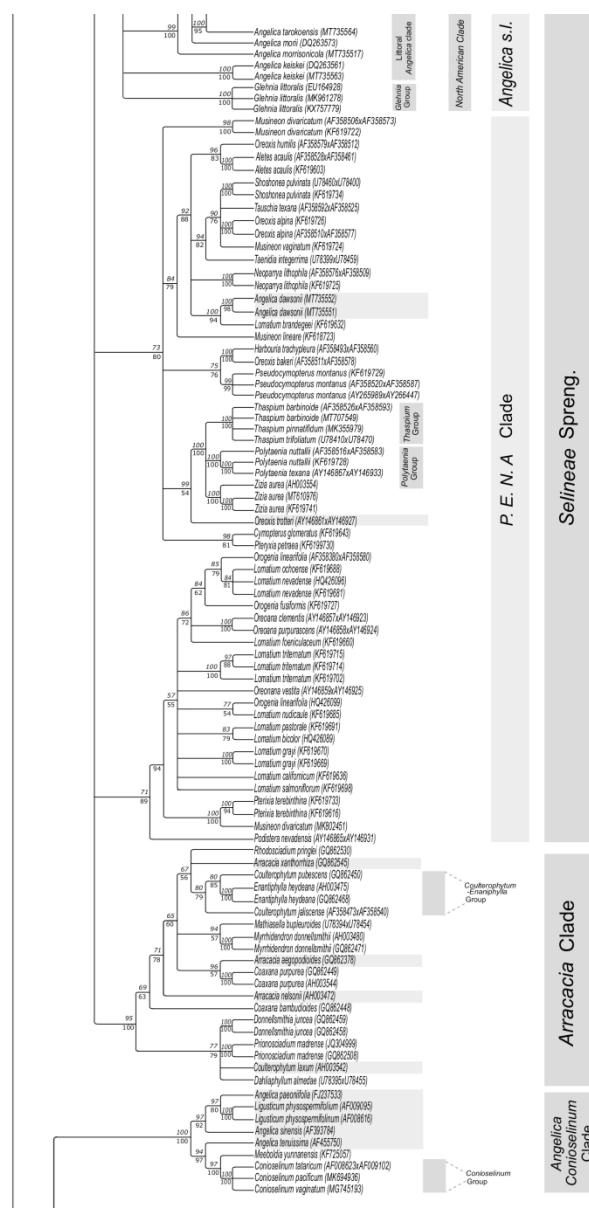


Figure 6. Part III of the consensus tree obtained from the BI and ML analyses of the Apioidae dataset. The numbers under the branches correspond to PP values obtained in the BI analysis, while numbers over the branches correspond to the BT values obtained in the ML analysis.

210x297mm (600 x 600 DPI)

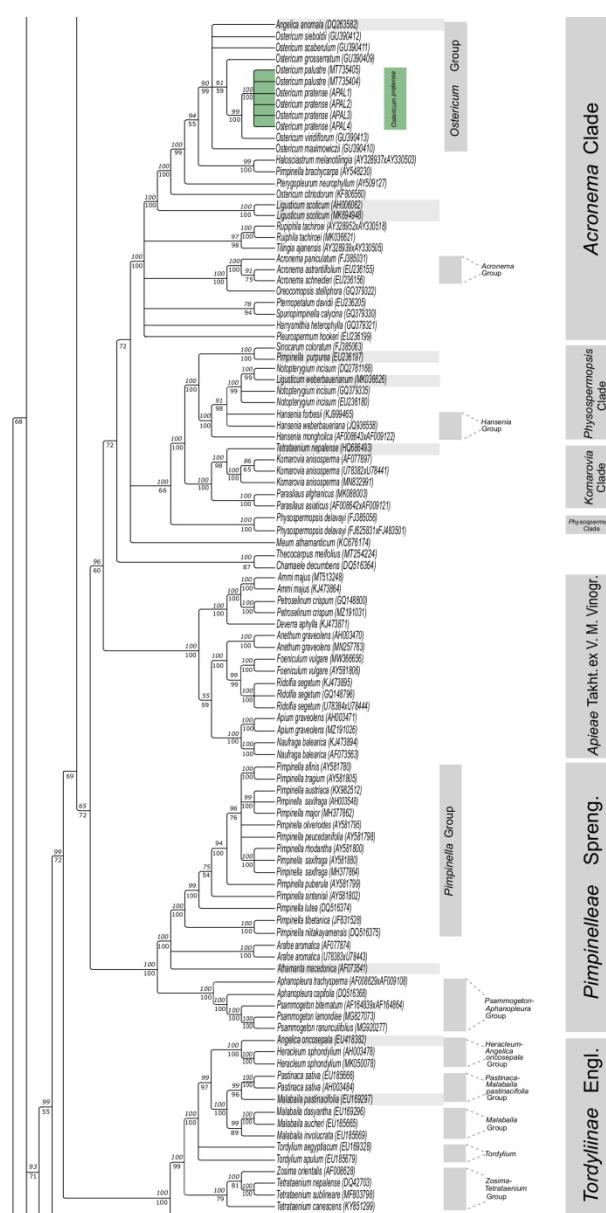


Figure 7. Part IV of the consensus tree obtained from the BI and ML analyses of the Apioideae dataset. The numbers under the branches correspond to PP values obtained in the BI analysis, while numbers over the branches correspond to the BT values obtained in the ML analysis. The clade comprising the samples of *Ostericum palustre* (=*Angelica palustris*) samples APAL1-4, have been highlighted in green.

210x297mm (600 x 600 DPI)

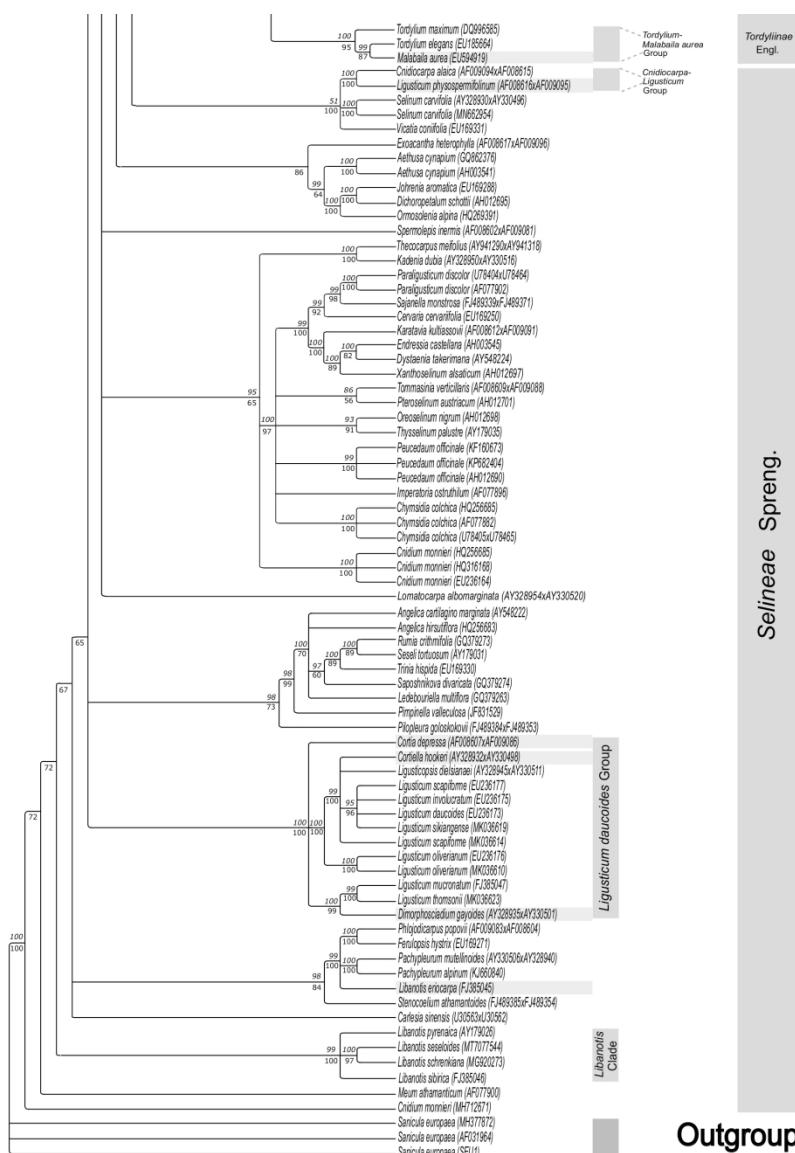


Figure 8. Part V of the consensus tree obtained from the BI and ML analyses of the Apioideae dataset. The numbers under the branches correspond to PP values obtained in the BI analysis, while numbers over the branches correspond to the BT values obtained in the ML analysis.

210x241mm (600 x 600 DPI)

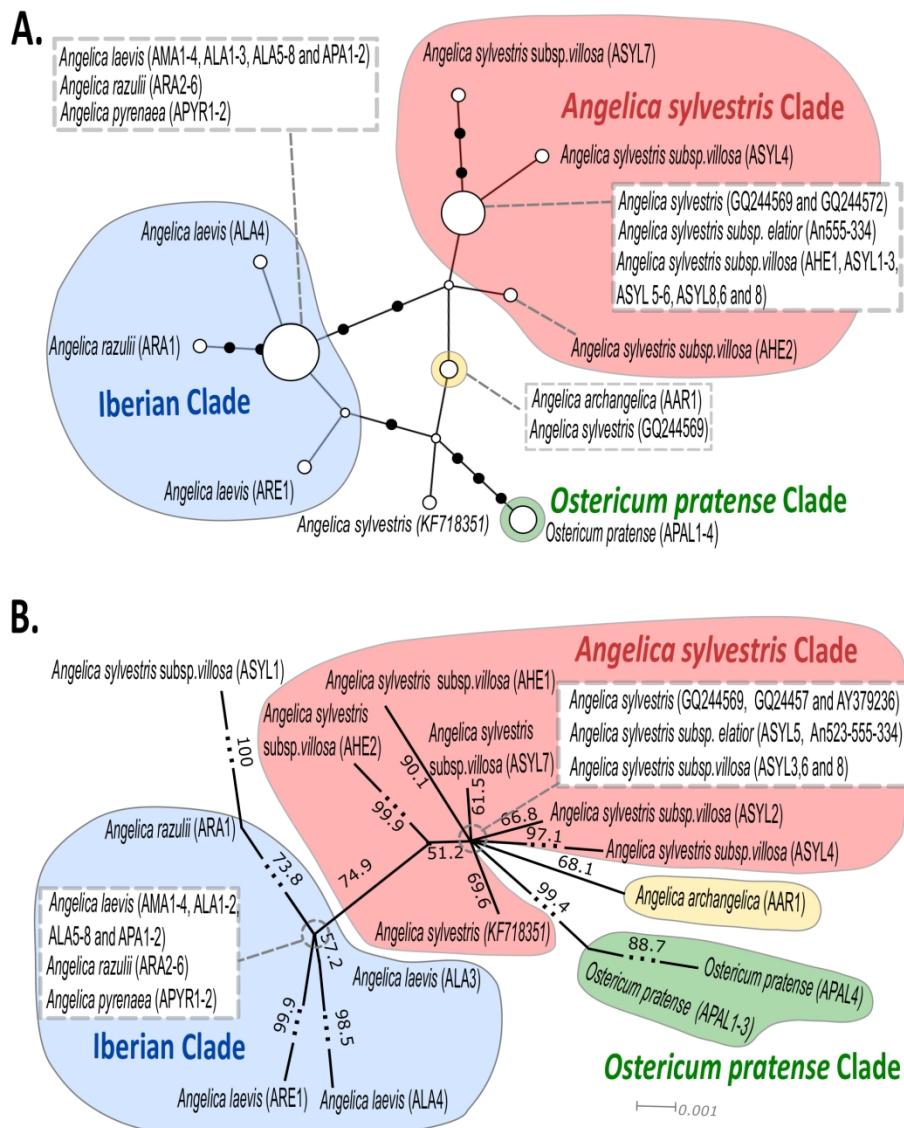
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Figure 9. A). European *Angelica* species haplotype network obtained from *trnL* sequences by TCS, where black dots represent mutations and white circles represents nodes, their size being proportional to the number of individuals found in it. B). Gene genealogy by Neighbor-Net obtained from the *trnL* sequences of European *Angelica* and *Ostericum* samples. Bootstrap values, ranging from 0 to 100 (%), are shown over the branches.

175x229mm (600 x 600 DPI)