Siculosciadium, A New Monotypic Genus of Apiaceae from Sicily

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SICULOSCIADIUM, A NEW MONOTYPIC GENUS OF APIACEAE FROM SICILY[1]

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ABSTRACT

The results of a morphological and molecular systematic investigation of the poorly known Sicilian endemic species *Peucedanum nebrodense* (Guss.) Nyman (Apiaceae subfam. Apioideae) are presented in order to better characterize the species and clarify its phylogenetic position. Morphological, karyological, anatomical, and ontogenetic studies indicate that this species is taxonomically distinct. Phylogenetic analysis of combined morphological and nuclear ribosomal DNA (nrDNA) ITS sequence data suggests an affinity with *Dichoropetalum* Fenzl, whereas an unweighted pair group method with arithmetic mean (UPGMA) analysis, based on 36 morphological characters, suggests that *P. nebrodense* is similar to *Ormosolenia* Tausch. Given its unusual life cycle; distinct suffruticose, evergreen, and dwarf habit; and peculiar fruit anatomy, we recognize *P. nebrodense* as distinct from *Ormosolenia* and *Dichoropetalum*, and we treat it as the new monotypic genus *Siculosciadium* C. Brullo, Brullo, S. R. Downie & Giusso based on *S. nebrodense* (Guss.) C. Brullo, Brullo, S. R. Downie & Giusso [≡ *Pteroselinum nebrodense* Guss.], which is lectotypified herein.

Key words: Apiaceae, IUCN Red List, *Peucedanum*, Sicily, *Siculosciadium*.

The genus *Peucedanum* L., as traditionally defined within the Apiaceae, contains more than 100 species of Eurasian and African distribution (Pimenov & Leonov, 1993). However, the genus has long been regarded as an unnatural group, and the need for its reduction into smaller, monophyletic units has been proposed by many (Pimenov, 1987, 1992; Burtt, 1991; Pimenov & Leonov, 1993; Ostroumova & Pimenov, 1997; Reduron et al., 1997; Shneyer et al., 2003; Pimenov et al., 2007). Indeed, the subdivision of the large polymorphic genus *Peucedanum* into natural groups is "among the most urgent challenges" facing the realization of a modern classification of the family Apiaceae (Winter et al., 2008: 347). The results of molecular systematic investigations have confirmed the polyphyletic nature of *Peucedanum* s.l., and, as a consequence, the genus is now reduced to only a few species allied to the type species, *P. officinale* L., and several segregates of *Peucedanum* are now recognized as distinct genera (Downie et al., 1998, 2000; Spalik et al., 2004; Winter et al., 2008; Magee et al., 2009). The results of these investigations also placed *Peucedanum* s. str. and other segregates in the revised Apiaceae tribe Selineae (Spalik et al., 2004; Downie et al., 2010).

[1] The authors thank the curators of the herbaria cited in the text for the loan of herbarium materials. We are also very grateful to M. C. Terrasi for help with the karyological investigations and to G. Venora for help with the fruit anatomy.

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One species of *Peucedanum* whose biology and phylogenetic placement have yet to be investigated is *P. nebrodense* (Guss.) Nyman. This species was first referred to *Imperatoria chabraei* Spreng. by Gussone (1827), based on specimens from the Madonie Massif (northern Sicily), which still represents its sole locality. Gussone (1844) later attributed the population from Madonie to a new species, namely *Pteroselinum nebrodense* Guss., and highlighted its morphological differences from *Pteroselinum chabraei* (Spreng.) Rchb. Nyman (1855) later ascribed this species to the genus *Peucedanum*, a transfer supported by both Cesati et al. (1884) and Strobl (1886). Subsequently, Paoletti (1900) and Fiori (1925) considered this taxon a variety of *Peucedanum carvifolia* (L.) Vill. Pignatti (1982), however, stressed the unclear and still unsolved taxonomic position of *P. nebrodense*, and Banfi et al. (2005) attributed this species to the genus *Holandrea* Reduron, Charpin & Pimenov, although without substantiating evidence. It is likely that the classification proposed by Banfi et al. (2005) was based on the transfer of *Peucedanum carvifolia* into the genus *Holandrea* by Reduron et al. (1997).

Because of their rarity and extreme localized distribution, specimens of *Peucedanum nebrodense* are not commonly found in major European herbaria, and the species is usually not treated in European floras. The plant does have a very unusual habit, however, when compared with the other known species of *Peucedanum*, which are commonly hemicryptophytes. *Peucedanum nebrodense* is characterized by a dwarf shrubby habit with many woody branches and persistent leaves. As such, the species appears taxonomically well isolated, showing a morphological affinity only with *P. alpinum* (Sieb. ex Schult.) B. L. Burtt & P. H. Davis from Crete, a taxon recently attributed by Pimenov (1992) to the restored genus *Ormosolenia* Tausch. The morphological similarities between these species include their branched rootstocks, well-developed caudices, and polycarpic life form. To better characterize the poorly known species *P. nebrodense* and to address its taxonomic position, we conducted morphological, karyological, and anatomical studies, and present herein the results of a phylogenetic analysis of this species and its closest allies, using morphological and molecular evidence.

Materials and Methods

general morphology

Morphological investigations of *Peucedanum nebrodense* were based on an examination of living material collected from the type locality. In order to understand its ontogeny and phenology, fruits, seedlings, and mature plants were cultivated at the Botanical Garden of Catania, Italy, for several years. Additional characters considered were those of leaves and other vegetative organs, inflorescences, flowers, and fruits. Specimens of *P. nebrodense* were examined from herbaria B, CAT, FI, G, M, NAP, PAL, RO, W, and WU. Specimens from *Dichoropetalum* Fenzl, *Johrenia* DC., *Ormosolenia*, *Peucedanum* s. str., and *Zeravschania* Korovin were also included in this comparative examination of general morphology, with emphasis placed on *P. nebrodense* and *Ormosolenia*. Recently, Pimenov et al. (2007) considered *Holandrea*, *Johreniopsis* Pimenov, and some species of *Johrenia* and *Peucedanum* as belonging to the genus *Dichoropetalum*.

karyology

Mitotic metaphase plates were obtained from squashed root tips of cultivated plants of *Peucedanum nebrodense*, pretreated with 0.3% colchicine water solution for three hours and fixed in ethanol-acetic acid (3:1) for six hours, then hydrolyzed in 1N HCl for seven minutes and stained, according to the Feulgen method. Metaphase observations and chromosome measurements were made using the image analysis systems IKAROS 4.6 (Metasystem, Altlussheim, Germany) and Zeiss (Oberkochen, Germany) AxioVision 5.1. Karyotyping was done with the software Cromolab 1.1 (Brullo, 2002–2003), which was used to recognize homologues, to order chromosomes by size, and to classify them according to morphology and centromere position (Levan et al., 1964). Ten mitotic plates from five individuals were used to determine the karyotype.

anatomy

Fruit and leaf petiole anatomy was examined from living material collected from the type locality, fixed in Karpechenko solution, and then embedded in paraffin. Transverse sections were double stained with ruthenium red and light green. Comparisons in leaf petiole anatomy were made between *Peucedanum nebrodense* and a putative ally, *Ormosolenia alpina* (Sieber ex Schultes) Pimenov.

phenetic analysis of morphological characters

We supplemented and slightly modified the morphological data matrix provided by Pimenov et al. (2007) in their comparative multivariate analyses of *Holandrea*, *Johrenia*, *Johreniopsis*, *Peucedanum* s.l., and *Zeravschania* by including the species *Ormosolenia alpina*, *O. pisidica* Boiss. & Heldr., and *P.*

nebrodense and two additional characters (i.e., leaf persistence and rootstock habit). In total, the data matrix comprised 36 morphological characters (Appendix 1) and 41 species. The importance of these characters in distinguishing among these putatively related taxa has been highlighted by Pimenov et al. (2007). No data cells in the matrix were scored as missing. Our rationale for including a phenetic analysis in this paper was to comprehensively compare those diagnostic characters across all included taxa to ascertain what species might be most similar morphologically to *P. nebrodense*. The resultant data matrix is presented in Appendix 2. Cluster (unweighted pair group method with arithmetic mean [UPGMA]) analysis of these data was implemented by using the NTSYSpc package (Rohlf, 2000).

DNA SEQUENCING

Total genomic DNAs of *Ormosolenia alpina*, *O. pisidica*, and *Peucedanum nebrodense* were extracted from approximately 20 mg of dried leaf tissue using a DNeasy Plant Mini Kit (Qiagen, Valencia, California, U.S.A.). The nuclear ribosomal DNA (nrDNA) ITS region in each of these species was polymerase chain reaction (PCR)-amplified by using the protocol described in Downie and Katz-Downie (1996). For template purification, the QIAquick PCR Purification Kit (Qiagen) was used. Sequencing reactions were carried out using a BigDye Terminator Cycle Sequencing Kit (version 3.1; Applied Biosystems, Foster City, California, U.S.A.) and sequenced with an ABI 3730xl sequencer (Applied Biosystems). The simultaneous consideration of both DNA strands across the entire ITS region permitted unambiguous base determination. ITS sequence heterogeneity, as evidenced by polymorphisms at single bases in otherwise perfect chromatograms, was not detected for any accession. GenBank accession numbers and specimen voucher information for *O. alpina*, *O. pisidica*, and *P. nebrodense* are presented in Table 1.

PHYLOGENETIC ANALYSES OF MOLECULAR AND MORPHOLOGICAL DATA

To ascertain the phylogenetic positions of *Ormosolenia alpina*, *O. pisidica*, and *Peucedanum nebrodense*, their ITS sequences were first analyzed with 40 additional ITS sequences from other members of the Apiaceae, tribe Selineae. These sequences were obtained from GenBank and represented most major clades of the tribe. Included here were representatives of Eurasian *Peucedanum* and its segregates, including *P. officinale* (the type for *Peucedanum*), *Imperatoria* L., and *Pteroselinum* Rchb., and *Zeravschania* Korovin and *Pimpinella* L. (both in tribe Pimpinelleae) were used to root the trees. These sequence data were analyzed using maximum parsimony as implemented by PAUP* version 4.0b.10 (Swofford, 2003), and the resultant strict consensus tree revealed that *Ormosolenia* and *P. nebrodense* comprised a well-supported clade along with representatives of *Holandrea*, *Johrenia*, and *Johreniopsis* (many of which have been treated as species of *Dichoropetalum*, according to Pimenov et al., 2007). Sister group to this clade was *Aethusa cynapium* L. Subsequently, another data matrix was produced to include all species of *Holandrea*, *Johrenia*, and *Johreniopsis* for which ITS data were available in GenBank. Thirteen species comprised this matrix, including *Ormosolenia* and *P. nebrodense*, and *A. cynapium* was used to root the resulting phylogenetic trees. GenBank accession numbers and voucher information for these species are presented in Table 1. This reduced matrix was analyzed by using heuristic maximum parsimony searches and 1000 replicate analyses, random stepwise addition of taxa, and tree bisection-reconnection (TBR) branch swapping. Bootstrap values were calculated from 1000 replicate analyses, using TBR branch swapping and simple stepwise addition of taxa. In the phylogenetic analysis of morphological data, 17 parsimony-informative morphological characters were considered, representing both vegetative and reproductive structures (Appendix 3). Eleven characters were binary, the remaining multistate; all characters were unordered and equally weighted. The taxa included in this portion of the study corresponded to those included in the 13-species ITS matrix, and the data matrix of morphological characters is presented in Appendix 4. These ITS and morphological data were analyzed separately and combined, with only the results of the combined analysis presented herein. Separate maximum parsimony analysis of each data set resulted in highly consistent yet generally poorly resolved and weakly supported trees, whereas analysis of the combined matrix yielded trees of greatest resolution and highest branch support overall. The data matrix of combined morphological and ITS sequence data, as well as the resulting strict consensus tree, is available from TreeBase (<http://purl.org/phylo/treebase/phylows/study/TB2:S12922>).

Results and Discussion

KARYOLOGY

According to Solov'eva et al. (1985) and Pimenov et al. (2003), species of *Peucedanum* s.l. are usually

Table 1. Accessions of Apiaceae examined for nuclear ribosomal DNA ITS sequence variation, with specimen voucher information and GenBank accession numbers. Two GenBank accession numbers for a taxon refer to ITS-1 and ITS-2 data only, with no data available for the intervening 5.8S region; a single GenBank accession number indicates that 5.8S data were available and used in the phylogenetic analysis. With the exception of data for the two *Ormosolenia* species and *Siculosciadium nebrodense*, all ITS data were previously published by others and obtained from GenBank. Nomenclature follows Pimenov et al. (2007).

Taxon	Voucher information	GenBank accession number(s)
Aethusa cynapium L.	Germany. Cult. at UIUC from seeds, Univ. Oldenburg Bot. Gard., Germany, *Downie 127* (ILL)	GQ862376
Dichoropetalum achaicum (Halácsy) Pimenov & Kljuykov	Greece. N. Pelóponnisos, Vouraikos Gorge, *Southam s.n.* (E), cult. Royal Bot. Gard. Edinburgh (no. 19912669)	AF164832, AF164857
D. aromaticum (Rech. f.) Pimenov & Kljuykov	Iran. *Ajani s.n.* (Herb. Hossein Akhani, Univ. Tehran)	EU169288
D. carvifolia (Vill.) Pimenov & Kljuykov	France. Isère, mont Bovinant, Chartreuse, 22 Aug. 1989, *Reduron s.n.* (WA)	AF495828, AF495829
D. golestanicum (Rech. f.) Pimenov & Kljuykov	Iran. *Ajani 2053* (TEH)	EU169289
D. paucijugum (DC.) Pimenov & Kljuykov	Iran. *Ajani 852* (Herb. Hossein Akhani, Univ. Tehran)	EU169290
D. pschawicum (Boiss.) Pimenov & Kljuykov	Russia. S. Ossetia, Bad, *Pimenov et al. 112* (MW), cult. Moscow State Univ. Bot. Gard.	AF008619, AF009098
D. schottii (Besser ex DC.) Pimenov & Kljuykov	France. Alpes-Maritimes, col de Brouis, 30 July 1981, *Reduron s.n.* (WA)	AF495830, AF495831
D. scoparium (Boiss.) Pimenov & Kljuykov	Iran. Arak Prov., Zalion Pass betw. Arak & Borujet, 33°53′N, 49°00′E, 17 June 2001, *Pimenov et al. 406* (MW)	AY941274, AY941302
D. seseloides (C. A. Mey.) Pimenov & Kljuykov	Iran. Tehran Prov., *Ajani 2057* (TEH)	EU169291
Ormosolenia alpina (Sieber ex Schult.) Pimenov	Greece. Crete, Lefka Ori, Mt. Pachnes, 1 Sep. 2006, *Brullo & Giusso del Galdo 2061* (CAT)	HQ269391
O. pisidica Boiss. & Heldr.	Turkey. Davraz Dag, 20 June 1998, *Brullo & Pavone s.n.* (CAT)	HQ269392
Siculosciadium nebrodense (Guss.) C. Brullo, Brullo, S. R. Downie & Giusso	Italy. Sicily, Madonie, Pizzo Carbonara, Fosse di S. Gandolfo, 24 July 2002, *Brullo & Giusso del Galdo s.n.* (CAT)	HQ269390

diploid ($2n = 2x = 22$), a feature common in the subfamily Apioideae. *Peucedanum nebrodense* has a diploid chromosome count $2n = 22$ (Fig. 1A, part 1), as previously reported by Duro et al. (2003), and has a karyotype characterized by five metacentric pairs of chromosomes, by five pairs of chromosomes approximate to the submetacentric type, and by one subtelocentric pair (Fig. 1A, part 2). Two chromosome pairs have microsatellites. This karyotype differs from those of other examined *Peucedanum* species, including those species recently transferred to *Dichoropetalum* (i.e., *D. carvifolia* and *D. pschawicum*), and from those of genera segregated from *Peucedanum* s.l. (i.e., *Imperatoria* and *Thysselinum* Adans.; Solov'eva et al., 1985). The karyotype of *Peucedanum* s.l. is characterized by at least seven pairs of metacentric chromosomes, while telocentric chromosomes have never been detected. Similarly, in *Peucedanum* s.l., microsatellites are absent or, if present, occur in one pair of chromosomes only. Karyological data are currently unavailable for other species of *Dichoropetalum* and *Johrenia*, as well as for *Ormosolenia* and many other Apiaceae. Nevertheless, the karyotype of *P. nebrodense* appears to be unique, bolstering its possible isolated taxonomic position within the Apiaceae.

LEAF MORPHOLOGY AND PETIOLE ANATOMY

Peucedanum nebrodense has 2-pinnate leaf blades, occasionally 1-pinnate in the cauline leaves, with sessile or subsessile leaflets (Fig. 1B, part 1). The basal leaves are always long-petiolate, although in the cauline ones the petiole tends to reduce progressively upward until disappearing; in such cases, the leaf blades are inserted directly on the sheaths. The petioles in cross section are falcate, with an adaxial groove, and have five collenchymatous ribs in the abaxial face and two in the adaxial face. Vascular bundles are five, all arranged in the peripheral part of the parenchyma, and interpose with four secretory

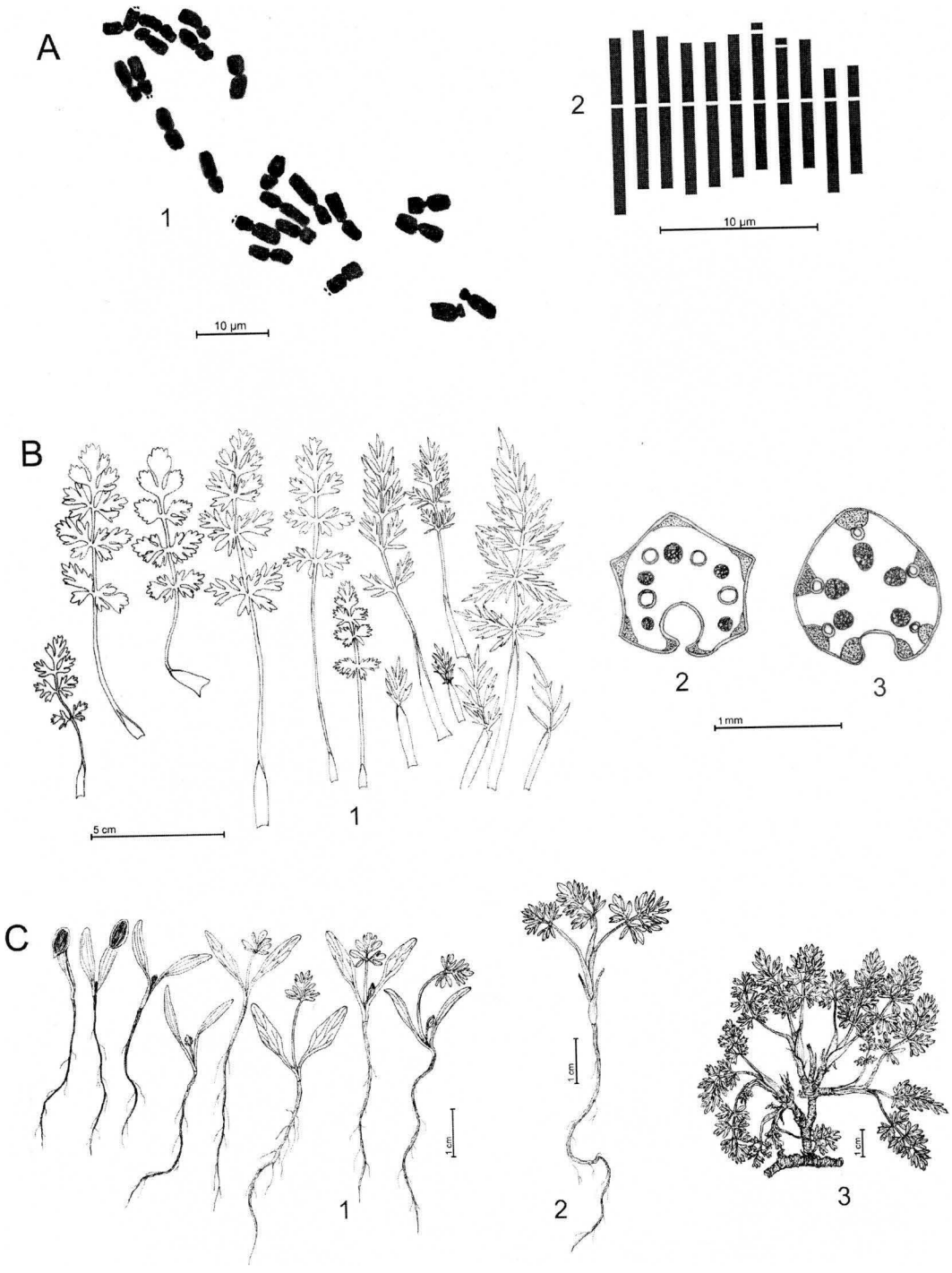


Figure 1. —A. Mitotic chromosome number of *Siculosciadium nebrodense*. —Part 1. Somatic metaphase plate. —Part 2. Karyotype ($2n = 22$). Root tip preparations from the 24 July 2002 collection, *S. Brullo*, *G. Giusso del Galdo & S. Sciandrello s.n.* (CAT). —B. Leaf variability of *S. nebrodense*. —Part 1. Living material from Madonie (Sicily). —Part 2. Petiole cross section of *S. nebrodense*. —Part 3. Petiole cross section of *Ormosolenia alpina*. —C. Vegetative stages of *S. nebrodense* (all living material taken from Madonie, Sicily). —Part 1. Seedlings. —Part 2. Juvenile plant. —Part 3. Adult sterile plant.

ducts (Fig. 1B, part 2). The petiole anatomy of *Ormosolenia alpina* is rather different from that of *P. nebrodense*. The petiole cross section of *O. alpina* shows that its collenchymatous ribs are not prominent (Fig. 1B, part 3). Interposed among the collenchymatous ribs and vascular bundles are five secretory ducts that unlike in *P. nebrodense* are directly in contact with the collenchyma. The leaf morphology of *P. nebrodense* suggests an affinity to some species of *Dichoropetalum* (Pimenov et al., 2007), whereas the petiole anatomy of *P. nebrodense* is unusual within the group.

FRUIT MORPHOLOGY AND ANATOMY

The mericarps of *Peucedanum nebrodense* are subrounded to elliptical, dorsally compressed, with distinctive spongy wings. The stylopodium is conical-flattened and the curved stylodium is much longer than the stylopodium (Fig. 2A, parts 1, 2). The exocarp is single-layered, interrupted near the ventral portion of the wings, and followed by an irregularly stratified parenchyma interspersed with thin-walled cells in the outer mesocarp and thickened in the ribs; the vascular bundles and secretory ducts are sunken in this parenchyma (Figs. 2B, 2C). The inner layer of the mesocarp consists of one row of tangentially elongated prosenchymatous cells with slightly lignified walls. The endocarp consists of one row of collenchymatous cells. Five of 11 oil ducts are associated with as many vascular bundles, four are vallecular and two are commissural, but do not reach the mericarp base. According to Pimenov (1992) and our own observations, the aforementioned features are quite different from those of *Ormosolenia alpina* and *O. pisidica* (Figs. 2A, parts 3–6; 2C, parts 2, 3). The latter two species are characterized by a more flattened stylopodium, a stylodium shorter than the stylopodium, three to six vittae per vallecula, and four to eight commissural vittae (secretory ducts associated with vascular bundles are not always present). The inner layer of the mesocarp of both species consists of three to five rows of elongated prosenchymatous cells and the single-layered endocarp also has tangentially elongated cells. The mericarp anatomy of *Dichoropetalum*, *Johrenia*, and *Zeravschania* is rather variable, but is always well differentiated from that of *P. nebrodense* (Pimenov et al., 2007). In summary, the peculiar fruit morphology and anatomy of *P. nebrodense* do not suggest any close taxonomic ally.

LIFE CYCLE

Both field and greenhouse observations reveal that *Peucedanum nebrodense* is characterized by a life cycle quite different from that known for other species of *Peucedanum* and *Ormosolenia*. The mericarps of *P. nebrodense* reach maturity between early September and October, when they gradually become loose and fall. These mericarps remain for about four months (December to early April) under the snow bed and only after the snow melts do they start to germinate (late April to May). The seedlings are characterized by well-developed roots, two oblanceolate to ovate-oblanceolate cotyledons that abruptly narrow into a 3-nerved petiole (0.5–0.8 mm), and a null hypocotyl (Fig. 1C, part 1). The blade is 8–13 × 1.5–4 mm, 3-nerved, with secondary nervation at maturity. The primordial leaf is 1- to 2-pinnate, long-petiolate, and subequal or longer than the cotyledons. Afterward, the seedling produces other leaves and, after this stage, it develops rhizomes bearing new leaves at its apex (Fig. 1C, part 2). During the second year, the rhizomes grow and branch, producing a well-developed rootstock (Fig. 1C, part 3). From June to early September, the caudices produce flowering stems from the center of the leaf rosette. Therefore, *P. nebrodense* is a perennial, polycarpic, and evergreen plant because its leaves persist through the winter (under the snow bed), a feature we observed on both wild and cultivated plants. *Peucedanum* s. str., *Dichoropetalum*, *Johrenia*, and *Zeravschania* are characterized by mono- or polycarpic plants with well-developed taproots, and basal leaves arranged in deciduous rosettes, usually with the remains of petioles at the stem base, while *Ormosolenia* is polycarpic with branched rootstocks, only basal leaves that are entire or 1-pinnate, with blades reniform to orbicular. *Peucedanum nebrodense* possesses an unusual life cycle and its suffruticose, evergreen, and dwarf habit is distinctive within the group.

PHENETIC ANALYSIS OF MORPHOLOGICAL CHARACTERS AND COMPARATIVE MORPHOLOGY

Peucedanum nebrodense has been considered morphologically similar to *P. carvifolia* (Paoletti, 1900; Fiori, 1925; Banfi et al., 2005), the latter recently included by Pimenov et al. (2007) in *Dichoropetalum* sect. *Holandrea*. In contrast, the unweighted pair group method with arithmetic mean (UPGMA) phenogram (Fig. 3A) revealed that *P. nebrodense* clustered with *Ormosolenia alpina* and *O. pisidica* and was separate from any species attributable to *Dichoropetalum* (including *Holandrea*), *Johrenia*, or *Zeravschania*. There are, however, remarkable morphological differences between *Ormosolenia* and *P. nebrodense*, such that the inclusion of the latter species into *Ormosolenia* is difficult to

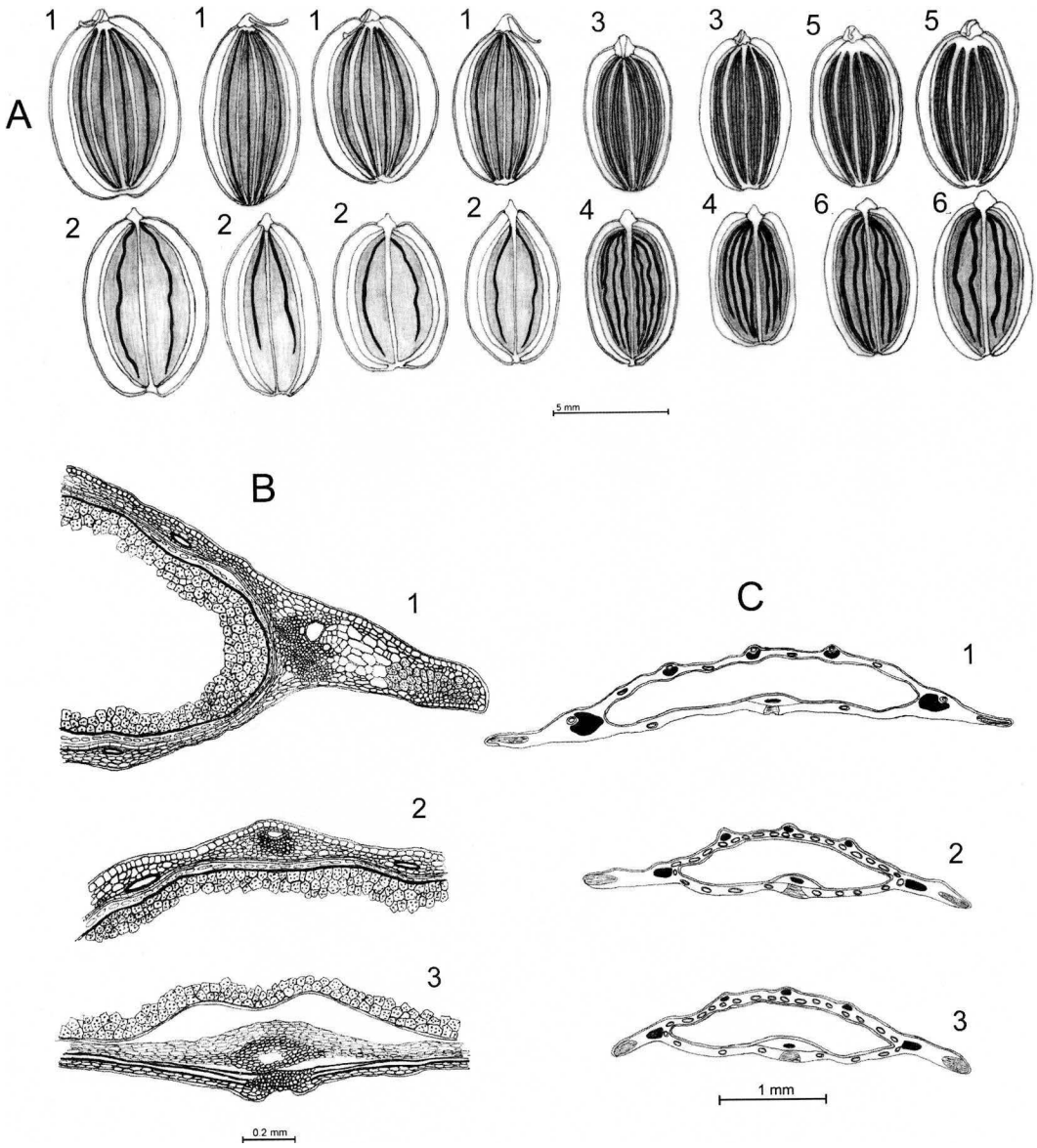
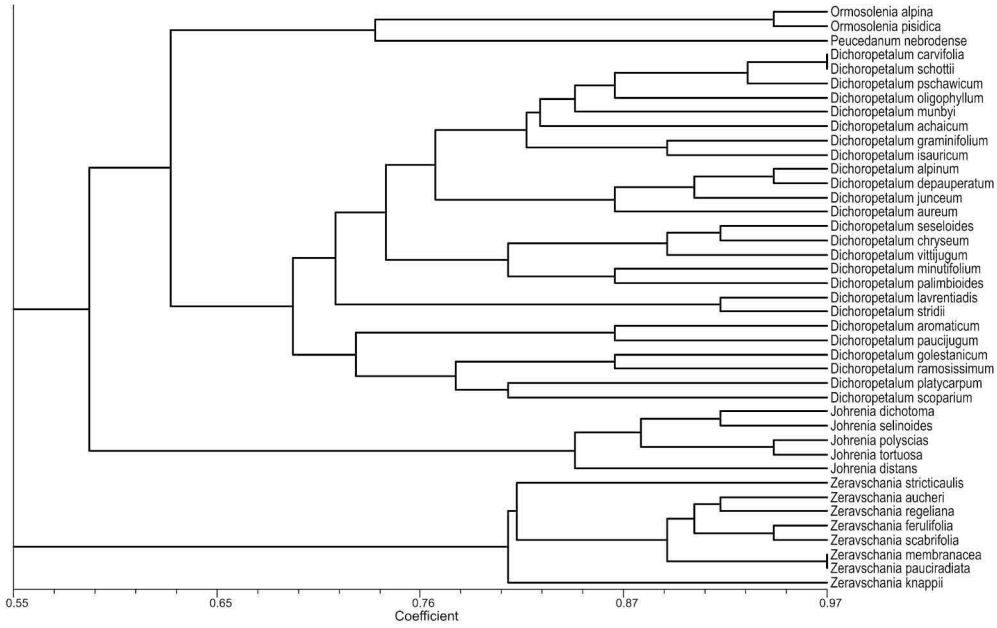
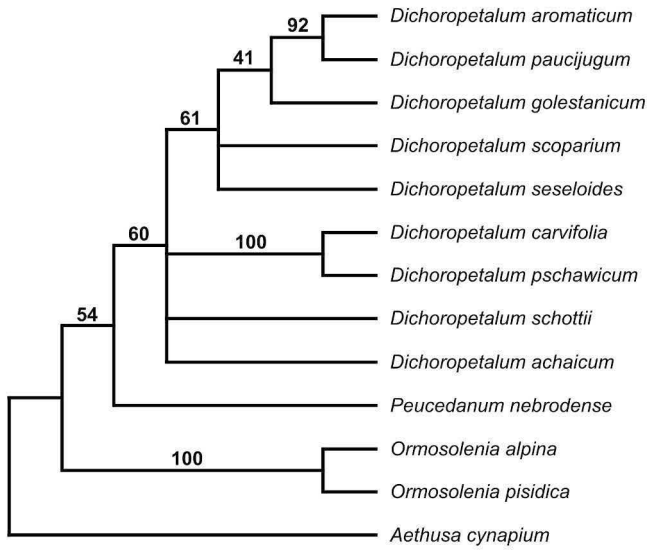


Figure 2. —A. Mericarp variability in *Siculosciadium* and *Ormosolenia*. —Part 1. Mericarp, dorsal view, *S. nebrodense* (30 Sep. 2009, *Brullo et al. s.n.*, CAT). —Part 2. Mericarp, commissural view, *S. nebrodense* (30 Sep. 2009, *Brullo et al. s.n.*, CAT). —Part 3. Mericarp, dorsal view, *O. alpina* (1 Sep. 2006, *Brullo & Giusso 2061* CAT). —Part 4. Mericarp, commissural view (1 Sep. 2006, *Brullo & Giusso 2061*, CAT). —Part 5. Mericarp, dorsal view *O. pisidica* (20 June 1998, *Brullo & Pavone s.n.*, CAT). —Part 6. Mericarp, commissural view (20 June 1998, *Brullo & Pavone s.n.*, CAT). —B. Mericarp cross sections of *S. nebrodense* (all living material from Madonie, Sicily). —Part 1. Mericarp, lateral view. —Part 2. Mericarp, dorsal central view. —Part 3. Mericarp, commissural central view. —C. Mericarp cross sections of *Siculosciadium* and *Ormosolenia*. —Part 1. Mericarp, *S. nebrodense* (30 Sep. 2009, *Brullo et al. s.n.*, CAT). —Part 2. Mericarp, *O. alpina* (1 Sep. 2006, *Brullo & Giusso 2061*, CAT). —Part 3. Mericarp, *O. pisidica* (20 June 1998, *Brullo & Pavone s.n.*, CAT).

accept upon the basis of these characters, several of which were not included in the phenetic analysis. These differences chiefly concern their ontogenetic cycle, life form, leaf shape, and petiole and fruit anatomy (Table 2). The genus *Ormosolenia* is characterized by a nonsuffruticose rootstock and basal leaves that are deciduous, reniform to ovate in outline, entire to 1-pinnate, and with up to one pair of leaflets. Its cauline leaves are usually absent. The petiole has five secretory ducts between the collenchyma and vascular bundles, the petals are yellowish green, the mericarps have three to six



A



B

Figure 3. —A. UPGMA phenogram showing the morphological relationships among the genera *Ormosolenia*, *Dichoropetalum*, *Johrenia*, *Zeravschania*, and *Siculosciadium*. —B. Strict consensus tree of ten 129-step trees resulting from maximum parsimony analysis of 17 parsimony informative morphological characters and DNA sequence data from the nrDNA ITS region. The numbers above the branches are bootstrap values.

Table 2. Comparative scheme of the distinguishing morphological characters of *Siculosciadium*, *Ormosolenia*, *Peucedanum*, *Dichoropetalum*, *Johrenia*, and *Zeravschania*.

Character	*Siculosciadium*	*Ormosolenia*	*Peucedanum* s. str.	*Dichoropetalum*	*Johrenia*	*Zeravschania*
Life form	polycarpic	polycarpic	polycarpic or monocarpic	polycarpic or monocarpic	monocarpic	polycarpic
Taproot	no	no	yes	yes	yes	yes
Leaf persistence	evergreen	deciduous	deciduous	deciduous	deciduous	deciduous
Rootstock	suffruticose	not suffruticose	not suffruticose	not suffruticose	not suffruticose	not suffruticose
Caudices	well developed	well developed	absent	absent	absent	absent
Fibrous collar	absent	absent	present	present	present	present
Basal leaves, insertion	apex of caudices	apex of caudices	apex of taproot	apex of taproot	apex of taproot	apex of taproot
Basal leaf blade, in outline	oblong to oblong-ovate	reniform to ovate	ovate to semicircular	triangular to lanceolate	triangular to ovate	triangular to ovate
Basal leaf shape	2-pinnate	entire to 1-pinnate	ternate to multisect	1- to 3-pinnate	2-pinnate	1- to 3-pinnate
Pairs of leaflets, number	3 to 4	absent to 1	3 to 5	1 to 6	1 to 6	1 to 3
Leaflet shape	ovate to deltoid	reniform to ovate	linear	linear to ovate	linear to lanceolate	ovate to ovate-oblong
Cauline leaves	present	usually absent	present	present	present or strongly reduced	present
Umbel rays, number	4 to 8	3 to 6	10 to 45	3 to 20	3 to 20	3 to 12
Bracts	absent	absent	absent to 3	absent	absent	(1)3 to 8
Bracteoles, number	1 to 5	absent to 2	2 to 10	1 to 5	1 to 5	2 to 8
Bracteoles, texture	herbaceous	setaceous	herbaceous	herbaceous	herbaceous	herbaceous
Bracteoles, relative to umbellulae	subequal to shorter	shorter	shorter	usually shorter	shorter	subequal to shorter
Calyx teeth	absent	inconspicuous	developed	inconspicuous	inconspicuous	inconspicuous to triangular
Petal color	white	yellowish green	yellow	white, yellow, pink	yellow	white (rarely yellowish white?)
Stylopodium	conical-flattened	conical-flattened	conical	flat to conical	flat to shortly conical	shortly conical
Mericarp wings	developed	short	developed	short to well developed	absent	short
Dorsal ribs	keeled	indistinguishable	filiform	filiform to inflated	indistinguishable	filiform
Vittae, per vallecula	1	3 to 6	1 to 3	absent to 3	absent to 3	1
Commissural vittae	2	4 to 8	2	absent to 4	absent to 4	2
Secretory ducts associated with vascular bundles	5	usually absent	absent	absent to 5	absent to 5	absent

vittae per vallecula and four to eight commissural vittae, the secretory ducts associated with vascular bundles are not always present, and the stylodium is shorter than the stylopodium. *Peucedanum nebrodense*, in contrast, has a suffruticose rootstock, basal leaves that are evergreen, oblong to oblong-ovate in outline, and 2-pinnate with three to four pairs of leaflets. Its cauline leaves are present. The petiole has four secretory ducts interposed among the vascular bundles, the petals are white, the mericarps have only a single vitta per vallecula and two commissural vittae, five secretory ducts are associated with its vascular bundles, and the stylodium is much longer than the stylopodium. Remarkable morphological differences are also apparent between *P. nebrodense* and other genera included in our comparative study, namely *Dichoropetalum* (including *Holandrea*), *Johrenia*, and *Zeravschania*. These differences are presented in Table 2, but are also reflected in the groupings of the UPGMA tree (Fig. 3A).

Ormosolenia pisidica is considered by Boissier (1849) as distinct from *O. alpina* by its better developed stems, nonthickened umbel rays, and yellow flowers. Subsequently, Boissier (1872) transferred both species to the genus *Peucedanum*, while more recently Chamberlain (1972), Hartvig (1986), and Pimenov (1992) treated *O. pisidica* as a synonym of *O. alpina*. In this study, both morphological and anatomical characters support the separation of *O. pisidica* from *O. alpina*. In particular, *O. pisidica* is characterized by stems 10–20(–30) cm tall, leaves 2–4 cm, umbels 3- to 4-rayed, umbellules 3- to 6-flowered, petals yellow, fructiferous pedicels thin and subequal to the fruit, and mericarps with filiform ribs and four(six) commissural vittae. *Ormosolenia alpina*, on the other hand, has stems 3–10(–15) cm tall, leaves 2–10 cm, umbels 4- to 7-rayed, umbellules up to 10-flowered, petals greenish white (often violet in bud), fructiferous pedicels thickened and shorter than the fruit, as well as mericarps with slightly inflated ribs and six to eight commissural vittae.

PHYLOGENETIC ANALYSES OF MOLECULAR AND MORPHOLOGICAL DATA

The data matrix of combined ITS sequence and morphological data for 13 species comprised 544 invariant, 43 autapomorphic, and 41 informative positions, the latter including 17 parsimony-informative morphological characters. Maximum parsimony analysis of these combined data resulted in ten 129-step trees (consistency indices = 0.7442 and 0.6071, including and excluding uninformative characters; retention index = 0.6452). Differences among these trees were restricted to the relative placements of several *Dichoropetalum* species. The strict consensus of these 10 trees is presented in Figure 3B. The results of this analysis support the recognition of *Dichoropetalum* as a monophyletic group (albeit the clade is weakly supported, with a 60% bootstrap value). The two species of *Ormosolenia* unite as a strongly supported clade (100% bootstrap value). *Peucedanum nebrodense* is sister to the *Dichoropetalum* clade, although this relationship is also weakly supported (54% bootstrap value), with only four or five molecular characters supporting this relationship, depending upon the tree. Constraining both species of *Ormosolenia* and *P. nebrodense* to monophyly and repeating the maximum parsimony analysis resulted in trees just one step longer than those without the constraint invoked. These results are inconclusive in establishing whether *P. nebrodense* is more closely related to *Dichoropetalum* or to *Ormosolenia*; indeed, *P. nebrodense* may actually comprise an isolated lineage separate from these two taxa upon the collapse of a single node. Further molecular data will be required to elucidate unequivocally the phylogenetic position of *P. nebrodense*.

CONCLUSIONS

The results of this study, incorporating data from morphology, karyology, fruit and petiole anatomy, and ontogeny, as well as results of both phenetic analysis of morphological data and phylogenetic analysis of combined morphological and molecular data, strongly support the recognition of *Peucedanum nebrodense* as a distinct taxon, closely allied to *Dichoropetalum* and *Ormosolenia*. An affinity to *Peucedanum* s. str. is not supported, nor is a close relationship to segregate taxa such as *Imperatoria* and *Pteroselinum*. Instead, maximum parsimony analysis of combined data suggests an affinity with *Dichoropetalum*, whereas the UPGMA tree, based largely upon characters selected by Pimenov et al. (2007) to discern among species of *Dichoropetalum*, *Johrenia*, and *Zeravschania*, suggests that *P. nebrodense* is more similar morphologically to *Ormosolenia*. Of these two analyses, we favor the maximum parsimony trees as indicating true relationship, but we acknowledge that branch support is weak and that further molecular studies incorporating chloroplast DNA will be necessary to confirm phylogenetic relationships among these taxa. Nevertheless, *Peucedanum nebrodense* can clearly be distinguished from *Ormosolenia* and *Dichoropetalum* upon a variety of characters, with many of these characters supporting its isolated position within the group. Furthermore, *P. nebrodense*

presents an isolated geographic distribution, known only from one population exclusively localized in a high mountain doline of the Madonie Massif. No other species examined herein occur in Sicily or in southern Italy. Therefore, we recognize *P. nebrodense* as comprising the new genus *Siculosciadium*. In order to highlight the morphological differences between this new genus and its putatively allied genera, the following analytical key is provided.

Key to the Closely Related Genera of *Siculosciadium*

1a. Rootstock not well developed with numerous long caudices, without fibrous collar; basal leaves inserted at apex of caudices.
  2a. Basal leaves 2-pinnate, with 3 to 4 pairs of ovate to deltoid leaflets; cauline leaves present; mericarps with 1 vitta per vallecula and 2 commissural vittae, with secretory ducts associated with vascular bundles ..... *Siculosciadium*
  2b. Basal leaves entire or 1-pinnate, with up to 1 pair of reniform to ovate leaflets; cauline leaves usually absent; mericarps with 3 to 6 vittae per vallecula and 4 to 8 commissural vittae, without secretory ducts associated with vascular bundles ..... *Ormosolenia*

1b. Rootstock robust without caudices, covered at the top by a fibrous collar; basal leaves inserted directly at apex of the rootstock.
  3a. Calyx teeth developed; leaf petiole round in cross section; leaf blade ternate-multisect, tridimensional, with primary segments long petiolate and ultimate segments entire, 2–9 cm ..... *Peucedanum* s. str.
  3b. Calyx teeth inconspicuous or very short; leaf petiole falcate in cross section with a ventral groove; leaf blade once to 3-pinnate, plane, with primary segments sessile or short petiolate and ultimate segments dentate or lobate (rarely entire), 0.5–2 cm.
    4a. Bracts (1 to)3 to 8; mericarps dorsally convex without occurrence of secretory ducts associated with vascular bundles ..... *Zeravschania*
    4b. Bracts absent; mericarps dorsally compressed usually with secretory ducts associated with vascular bundles.
      5a. Leaf sheath very long; mericarps with dorsal ribs indistinguishable and wings absent ..... *Johrenia*
      5b. Leaf sheath rather short; mericarps with dorsal ribs filiform to inflated (keeled) and wings more or less developed ..... *Dichoropetalum*

Taxonomic Treatment

I. Siculosciadium C. Brullo, Brullo, S. R. Downie & Giusso, gen. nov. TYPE: *Siculosciadium nebrodense* (Guss.) C. Brullo, Brullo, S. R. Downie & Giusso

Genus novum *Ormosoleniae* Tausch affine, a qua caudice suffruticoso sempervirenti, foliis basalibus bipinnatis segmentis lateralibus ambitu oblongis vel oblongo-ovatis segmento terminali laterales subaequenti vel quam eis minore, foliis caulinis praesentibus, bracteolis umbellularum 1 ad 5 herbaceis margine hyalinis, dentibus calycinis nullis, petalis albis colore roseo-purpurascenti suffusis apice truncatis, strato interno mesocarpii ex cellularum prosenchymatarum serie una et cellularum collenchymatarum serie una constanti, quaque vallecula vitta valleculari solitaria et vittis commissularibus duabus praedita, canaliculis jugalibus solitariis atque stylodio in fructu bene evoluto reflexo quam stylopodio per anthesin multo longiore differt.

Evergreen polycarpic dwarf shrub; rootstock branched, covered by a thin rhytidome, without fibrous collar; stems numerous, leafy, erect to ascending, usually with umbels at the nodes. Basal leaves petiolate, inserted in the terminal part of the caudices; sheath linear, whitish; blade 2-pinnate, with 3 to 4 pairs of leaflets, terminal leaflet subequal or smaller than the lateral ones; lobes oblong to ovate, rounded at apex; cauline leaves becoming increasingly smaller upward, petiolate to sessile; blade 1- or 2-pinnate; lobes linear to linear-lanceolate. Inflorescence composed of long pedunculate compound umbels, unequally rayed; bracts absent; umbellule with 1 to 5 bracteoles, herbaceous with hyaline margin, subequal to or shorter than rays. Flowers hermaphrodite or masculine, pedicellate; calyx teeth absent; petals white, tinged with pink purplish outside, inflexed, thick, truncate at apex; stylopodium conical-flattened. Mericarps lenticular, shallowly compressed dorsally with well-distinct spongy wings, 5-ribbed, 3 of which are dorsal and 2 marginal; exocarp 1-layered; mesocarp 2-layered, its outer layer consisting of parenchymatous cells; inner layer of mesocarp consisting of 1 row of prosenchymatous cells and 1 row of collenchymatous cells; vascular bundles 5; five secretory ducts associated with vascular bundles, 4 more are vallecular and 2 commissural not reaching the base. Stylodium in fruit well developed, reflexed, and much longer than the stylopodium in flower.

1. Siculosciadium nebrodense (Guss.) C. Brullo, Brullo, S. R. Downie & Giusso, comb. nov. Basionym: *Pteroselinum nebrodense* Guss., Fl. Sicul. Syn. 1: 336. 1844. *Imperatoria chabraei* Guss., Fl. Sic. Prodr. 1: 368. 1827, nom. illeg., non *Imperatoria chabraei* Spreng., Sp. Umbell.: 64. 1818. *Peucedanum nebrodense* (Guss.) Nyman, Syll. Fl. Eur.: 153. 1855. *Peucedanum nebrodense* (Guss.) Strobl, Flora 69(36): 567. 1886. *Peucedanum carvifolia* (L.) Vill. var. *nebrodense* (Guss.) Paol. in Fiori & Paol., Fl. Anal. Ital. 2: 179. 1900.

Holandrea nebrodensis (Guss.) Banfi, Galasso & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civ. Stor. Nat. Milano 146(2): 233. 2005. TYPE: [Italy, Sicily. Palermo:] Sub *Pteroselinum nebrodense*, Madonie, alle Fosse di S. Gandolfo, julio [manu Gussone], (lectotype, designated here, NAP-GUSS!; isolectotype, FI!). Figure 4.

Dwarf glabrous perennial, polycarpic, suffruticose, rhizomatous, evergreen, with a well-developed creeping and branched rootstock, 4–12 cm, 2–5 mm diam., covered by a thin, pale brown rhytidome; fibrous collar absent; stems numerous, leafy, erect to ascending, 15–30 cm tall, usually with umbels at the nodes. Basal leaves green, glaucous, 5–15 cm, inserted in the terminal part of the caudices; sheath long linear, whitish, 1–2.5 cm × 3–5 mm; petiole slightly striate, 1.5–7 cm; blade oblong to oblong-ovate in outline, flat, 1.5–6 × 1–3 cm, 2-pinnate, with 3 to 4 pairs of leaflets, ovate to deltoid, ± incised, terminal leaflet subequal or smaller than the lateral ones; lobes oblong to ovate, rounded at apex with hyaline mucro; primary lobes 6–17 mm and secondary lobes 3–11 mm; cauline leaves becoming increasingly smaller upward with petiole 0–25 mm; sheath 2–5.5 cm × 2–4 mm; blade lanceolate to triangular in outline, 1- or 2-pinnate; lobes linear to linear-lanceolate, primary ones 5–22 mm and secondary ones 5–13 mm, usually acute at apex. Inflorescence composed of long pedunculate compound umbels, unequally 4- to 8-rayed, rays 0.5–1.5 cm; bracts absent; flexuous when flowering, rigid when fruiting; umbellule with 1 to 5 bracteoles, subulate, herbaceous with hyaline margin, subequal to or shorter than rays. Flowers hermaphrodite or masculine, 4 to 8 per umbellule, 2–2.2 mm diam., pedicellate; calyx teeth absent; petals ovate, 1.5 mm, white tinged with pink purplish outside, inflexed, thick, truncate at apex; stamens long exserted, inrolled, wholly white; staminal filament 1.7 mm; anther 0.5 mm; stylopodium conical-flattened; stylodium ca. 1 mm long, cylindrical, erect; ovary subcylindrical to obovoid, 1–1.2 mm. Mericarps subrounded to elliptical, lenticular, 6–8.5 × 4–5 mm, shallowly compressed dorsally with well-distinct spongy wings, 0.5–0.8 mm wide, 5-ribbed, 3 of which are dorsal and 2 marginal; exocarp 1-layered, interrupted near the ventral part of the wings; mesocarp 2-layered, its outer layer consisting of parenchymatous cells with thin walls; in the distal part of the wings these cells have slightly lignified walls with chinked pores; the inner layer of mesocarp consisting of 1 row of tangentially elongated prosenchymatous cells with slightly lignified walls; endocarp consisting of 1 row of collenchymatous cells; vascular bundles 5 (3 small and dorsal and 2 big and at the wing base); 5 secretory ducts associated with the vascular bundles, 4 more are vallecular and 2 commissural not reaching the base; endocarp 1-layered; endosperm ventrally flat. Stylodium in fruit elongating to ca. 2 mm, slender, reflexed, curved, and much longer than the stylopodium.

Distribution and ecology. This Italian species is exclusively found in the Madonie Massif on the island of Sicily, where it grows on the southern slopes of a dolina near Pizzo Carbonara, locally known as Fosse di S. Gandolfo. It grows at an altitude of about 1870 m.s.m. on Mesozoic carbonatic substrates, within a dwarf shrubby plant community characterized by several endemic chamaephytes and hemicryptophytes (Brullo et al., 2005), e.g., *Astragalus nebrodensis* (Guss.) Strobl (Fabaceae), *Erysimum bonannianum* C. Presl (Brassicaceae), *Acinos alpinus* (L.) Moench subsp. *nebrodensis* (Kerner & Strobl) C. Brullo & Brullo (Lamiaceae), *Minuartia verna* (L.) Hiem subsp. *grandiflora* (C. Presl) Hayek (Caryophyllaceae), *Petrorhagia saxifraga* (L.) Link subsp. *gasparrini* (Guss.) Greuter & Burdet (Caryophyllaceae), *Centaurea parlatoris* Heldr. (Asteraceae), *Cerastium tomentosum* L. (Caryophyllaceae), *Herniaria microcarpa* C. Presl (Illecebraceae), and *Silene sicula* Ucria (Caryophyllaceae).

Phenology. *Siculosciadium nebrodense* has been observed in flower from July to August, and in fruit from August to October.

Etymology. *Siculosciadium* comes from the Greek words "siculo," referring to "Sicilian," and "sciadion," referring to "umbel."

IUCN Red List category. *Siculosciadium nebrodense* is represented by few individuals, usually forming a thick layer and occupying a surface area of about 1000 m^2. For this reason, we propose to include this species in the Red List of Threatened Species as Critically Endangered (CR). Based on the criteria adopted by IUCN (2001, 2003, 2005), we herein proposed its inclusion in the following categories: CR B2ab(ii, iii, iv, v), C1.

Additional specimens examined. ITALY, SICILY. **Palermo:** Madonie, Fosse di S. Gandolfo, s.d., manu Gussone, sub *Pteroselinum nebrodense* (NAP-GUSS); in pascuis montosis Madonie, July, *Citarda 1450* (FI, PAL), 1 Sep. 1881, *Lojacono 223* (FI); Madonie, Fosse di S. Gandolfo e Vallone Reale, *Tineo* (FI); Madonie, Pizzo Carbonara, Fosse di S. Gandolfo, 9 Sep. 2001, *S. Brullo, G. Giusso del Galdo & S. Sciandrello s.n.* (CAT); Madonie, Pizzo Carbonara, Fosse di S. Gandolfo, 24 July 2002, *S. Brullo, G. Giusso del*

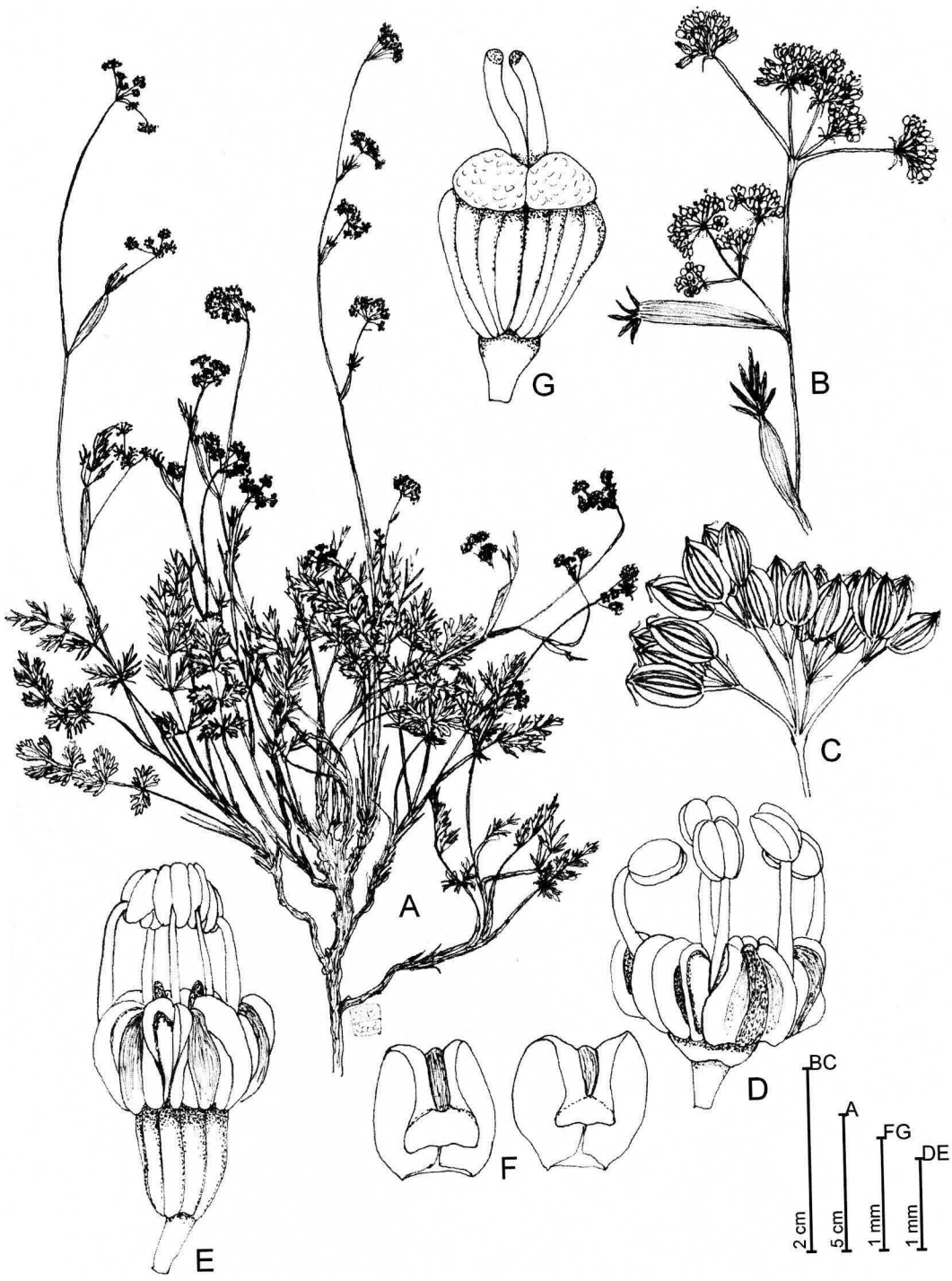


Figure 4. *Siculosciadium nebrodense*. —A. Flowering plant habit. —B. Inflorescence. —C. Fructified umbel. —D. Male flower. —E. Hermaphrodite flower. —F. Two petals, internal view. —G. Pistil. Living material taken from Madonie, Sicily, and drawn from the collection, 9 Sep. 2001, *S. Brullo, G. Giusso & S. Sciandrello s.n.* (CAT).

Galdo & S. Sciandrello s.n. (CAT), 30 Sep. 2009, *C. Brullo, S. Brullo & G. Giusso del Galdo s.n.* (CAT).

Specimens examined for Ormosolenia alpina. GREECE. **Crete:** in summis montibus Sphacioticas [Stravopodia] Creta, 10 July 1846, *Heldreich*, sub *Peucedamum creticum* (WU); in summis alpinis Sphakiottleis, s.d., *Sieber*, sub *P. creticum* (G-DC); in Crete, s.d., *Sieberus*, sub *Sison alpina* (B); n. M. altis Sphakiott, s.d., *Sieber*, sub *S. alpinum* (G); Creta, inter lapidis summi inter Stravopodia, 10 July 1846, *Heldreich*, sub *Ormosolenia cretica* (G-BOISS, G); Crete, hautes montagnes de Sphakia, June 1845, *Raulin 485* (G-BOISS); Creta, Distr. Sphakia, Levka Ori, in glareosis calc. montis Pachnes, 16 June 1942, *Rechinger 13848* (G); Crete, Ep. Sphakia, 20 Sep. 1966, *Greuter 7551* (G); Crete, Sfakia, 20 km above Anopoli to top of Mt. Pachnes, 12 July 1993, *Bergmeier & Matthas 3416* (B); Griechenland, Nomos Hanion, Eparchia Sfakion, Lefka Ori, Pahnes-Gipfel, 7 Aug. 1998, *Böhling 8750* (B); Crete, Lefka Ori, Trocharis, 26 Aug. 2003, *Bacchetta & Brullo* (CAT); Crete, Lefka Ori, Mt. Pachnes, 1 Sep. 2006, *Brullo & Giusso del Galdo 2061* (CAT).

Specimens examined for Ormosolenia pisidica. TURKEY. Dans la region alpine de Mt. Stravros près d'Isparte, 10 Aug. 1845, *Boissier* (G-BOISS); Davraz Dag, 20 June 1998, *Brullo & Pavone s.n.* (CAT). **C2:** Mugla, Koycegeiz, Sandras Da. Besparmak Tepesi, 5 Sep. 1978, *N. & E. Ozhatay 41501* (G). **C3:** Pisidien, Isparta, 2 July 1948, *Renz 8704* (G); Anatolia, Distr. Kemer, Tahtali Dag, 16 Aug. 1947, *Davis 14196* (G); Anatolia, Tahtali Dag (ca. 50 km SW Antalya), W side, (ascent from village of Yukari Beycik) rocky slope & scree, 17 July 1984, *Gork, Hartvig & Strid 23599* (B, G).

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Appendix 1. List of 36 morphological characters and character states included in the morphological matrix used in the phenetic analysis.

1. Habit: 0, monocarpic with unbranched rootstock; 1, polycarpic with branching rootstock.
2. Leaf petioles at stem base: 0, present (at least as dense remnants); 1, absent.
3. Stem height: 0, 7–40 cm; 0.5, 41–100 cm; 1, exceeding 100 cm.
4. Stem ribs: 0, without prominent ribs; 1, with ± prominent ribs.
5. Stem pubescence: 0, glabrous; 1, pubescent.
6. Leaf shape: 0, linear to lanceolate; 0.5, subrounded to reniform; 0.75, oblong to oblong-ovate; 1, ovate to triangular.
7. Leaf sheath relative length: 0, long; 1, short.
8. Leaf sheath shape: 0, linear; 1, triangular.
9. Leaf basal primary segments: 0, sessile; 0.5, with petiole less than 5 mm; 1, with petiole exceeding 5 mm.
10. Shape of terminal leaf lobes: 0, filiform or linear; 0.5, lanceolate; 1, ovate.
11. Terminal leaf lobes: 0, clustered; 1, not clustered.
12. Upper cauline leaves: 0, absent; 1, present.
13. Bracts: 0, present; 1, absent.
14. Mininum number of rays per umbel: 0, fewer than 5; 1, equal to or more than 5.
15. Maximum number of rays per umbel: 0, < 10; 1, > 10.
16. Umbel rays, relative proportions: 0, very unequal; 0.5, slightly unequal; 1, almost equal.
17. Bractlet texture: 0, completely herbaceous, 1, with narrow white margins.
18. Bractlet shape: 0, subulate to linear; 0.5, linear-lanceolate; 1, lanceolate to broadly lanceolate.
19. Bractlets/umbellules, relative proportions: 0, bractlets longer than umbellules, 1, shorter than umbellules.
20. Calyx teeth: 0, present; 1, absent.
21. Petals color: 0, white; 1, yellow.
22. Stylopodium shape: 0, flat; 0.5, short-conical; 1, conical.
23. Mericarps shape: 0, dorsally convex; 1, dorsally compressed.
24. Dorsal mericarp ribs: 0, indistinguishable; 0.5, filiform; 0.75, keeled or slightly inflated; 1, strongly spongy inflated.
25. Marginal mericarp ribs: 0, not developed; 1, ± developed.
26. Mericarp parenchyma (commissural side): 0, with destroyed parenchyma near carpophore; 1, commissural parenchyma not destroyed.
27. Parenchyma cells with lignified pitted walls on dorsal mericarp side: 0, developed; 1, absent or sometimes only under vascular bundles.
28. Marginal ribs inflated: 0, composed of large mesocarp cells with lignified pitted walls; 1, without lignified pitted walls.
29. Inner lignified layer of mesocarp (hypendocarp): 0, absent; 0.5, faintly marked; 1, strongly expressed.
30. Secretory ducts (vittae) in mericarp furrows, presence: 0, absent or inconsistent, not visible in each furrow; 1, always developed.
31. Secretory ducts (vittae) in mericarp furrows, organization: 0, solitary; 1, several in each furrow.
32. Commissural secretory ducts (vittae): 0, absent; 0.5, two in each mericarp; 1, more than two per mericarp.
33. Rib secretory ducts: 0, absent; 1, present.
34. Mericarp vascular bundle organization and number: 0, compact; 1, consisting of several groups of vascular elements.
35. Leaf persistence: 0, deciduous; 1, evergreen.
36. Rootstock habit: 0, not suffruticose; 1, suffruticose.

Appendix 2. Data matrix of the 36 morphological characters used for the phenetic analysis. Character and coding character states correspond to those in Appendix 1.

Taxa	Character states for characters 1–36																																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Dichoropetalum achaicum (Halácsy) Pimenov & Kljuykov	1	0	0	0	0	1	1	0	0	1	1	0	1	1	1	0	0	0	1	1	1	1	1	0.5	1	1	1	0	1	1	0	1	1	0	0	0
Dichoropetalum alpinum Fenzl	1	0	0	0	0	1	1	0	0	1	1	1	1	0	0	0	0	0	1	1	1	0.5	1	0.75	1	1	1	0	1	1	0	0.5	1	0	0	0
Dichoropetalum aromaticum (Rech. f.) Pimenov & Kljuykov	0	0	0.5	1	0	0	1	1	0	1	1	1	1	1	0	0	0	0	1	1	1	0.5	1	1	1	1	0	0	0.5	0	0	0	1	0	0	0
Dichoropetalum aureum (Boiss. & Balansa) Pimenov & Kljuykov	1	0	0	0	0	1	1	0	0	0.5	0	1	1	0	0	0	0	0	1	1	1	0.5	1	0.75	1	1	1	0	1	1	0	0	1	0	0	0
Dichoropetalum carvifolia (Vill.) Pimenov & Kljuykov	1	0	0.5	0	0	1	1	0	0	0.5	1	0	1	1	1	0	0	0	1	1	0	0.5	1	0.5	1	1	1	0	1	1	1	1	1	0	0	0
Dichoropetalum chryseum (Boiss. & Heldr.) Pimenov & Kljuykov	0	0	0.5	1	0	0	1	0	0	0.5	1	1	1	1	1	0	0	0	1	1	1	0.5	1	0.5	1	1	1	0	0.5	1	0	0.5	1	0	0	0
Dichoropetalum depauperatum (Boiss. & Balansa) Pimenov & Kljuykov	1	0	0.5	0	0	1	1	0	0.5	1	1	1	1	0	0	0	0	0	1	1	1	0.5	1	0.75	1	1	1	0	1	1	0	0.5	1	0	0	0
Dichoropetalum golestanicum (Rech. f.) Pimenov & Kljuykov	0	0	0.5	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	1	1	1	1	1	0.5	1	1	0	0	1	1	0	0	1	0	0	0
Dichoropetalum graminifolium (Boiss.) Pimenov & Kljuykov	0	0	0.5	0	0	1	1	0	0	0.5	1	0	1	1	1	0	0	0	1	1	0	0.5	1	0.75	1	1	1	0	1	1	0	0.5	1	0	0	0
Dichoropetalum isauricum (Parolly & Nordt) Pimenov & Kljuykov	0	0	0.5	0	0	1	1	0	0	1	1	0	1	0	0	0	1	0	1	1	0	0.5	1	0.75	1	1	1	0	1	1	0	0.5	1	0	0	0
Dichoropetalum junceum (Boiss.) Pimenov & Kljuykov	1	0	1	0	0	1	1	0	0.5	1	1	1	1	0	0	0	0	0	1	1	1	0.5	1	0.5	1	1	1	0	1	1	0	0.5	0	0	0	0
Dichoropetalum lavrentiadis (Strid & Papan.) Pimenov & Kljuykov	1	0	0	1	0	1	1	0	0	0.5	1	1	1	1	0	0.5	0	0	1	1	0	0.5	1	0.75	1	1	1	0	0.5	1	0	0.5	1	0	0	0
Dichoropetalum minutifolium (Janka) Pimenov & Kljuykov	0	0	0.5	0	1	0	1	0	0	1	1	1	1	1	1	0	0	0	1	1	1	0	1	0.5	1	1	1	0	1	1	1	1	1	0	0	0
Dichoropetalum munbyi (Boiss.) Pimenov & Kljuykov	1	0	1	0	0	1	1	0	0	0.5	1	0	1	0	0	0	0	0	1	1	0	0.5	1	0.5	1	1	1	0	1	1	0	0	1	0	0	0
Dichoropetalum oligophyllum (Griseb.) Pimenov & Kljuykov	0	0	0	0	0	1	1	0	0	0.5	1	0	1	1	0	0	0	0	1	1	0	0.5	1	0.5	1	1	1	0	1	1	1	0.5	1	0	0	0
Dichoropetalum palimbioides (Boiss.) Pimenov & Kljuykov	0	0	0.5	0	1	0	1	0	0	1	1	1	1	1	1	0.5	0	0.5	1	1	1	0.5	1	0.75	1	1	1	0	0.5	1	1	1	1	0	0	0
Dichoropetalum paucijugum (DC.) Pimenov & Kljuykov	0	0	0	1	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	1	1	0	1	1	1	1	0	0	0.5	0	0	0	1	0	0	0
Dichoropetalum platycarpum (Boiss.) Pimenov & Kljuykov	1	0	0.5	0	1	0	1	0	0	0.5	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0
Dichoropetalum pschawicum (Boiss.) Pimenov & Kljuykov	1	0	0.5	0	0	1	1	0	0	0.5	1	0	1	1	1	1	0	0	0	1	0	0.5	1	0.5	1	1	1	0	1	1	1	1	1	0	0	0
Dichoropetalum ramosissimum (Mozaff.) Pimenov & Kljuykov	0	0	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	1	1	1	0.5	1	0.5	1	1	0	0	1	0	0	0	0	0	0	0

Appendix 2. Continued.

Taxa	Character states for characters 1–36																																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Dichoropetalum schottii (Bess) Pimenov & Kljuykov	1	0	0.5	0	0	1	1	0	0	0.5	1	0	0	1	1	0	0	0	1	1	0	0.5	1	0.5	1	1	1	0	1	1	1	1	1	0	0	0
Dichoropetalum scoparium (Boiss.) Pimenov & Kljuykov	1	0	1	0	1	0	1	0	0	0.5	1	0	1	0	0	0	0	0	1	1	1	1	1	0.5	1	1	1	0	0.5	1	1	0	1	0	0	0
Dichoropetalum seseloides (C. A. Mey.) Pimenov & Kljuykov	0	0	0.5	0	0	0	1	0	0	0.5	1	1	1	1	1	0	0	0	1	1	1	1	1	0.5	1	1	1	0	1	1	0	0.5	1	0	0	0
Dichoropetalum stridii (Hartvig) Pimenov & Kljuykov	1	1	0	1	0	1	1	0	0	0.5	1	1	1	1	0	0.5	0	0	1	1	0	0.5	1	0.75	1	1	1	0	0.5	0	0	0	1	0	0	0
Dichoropetalum vittijugum (Boiss.) Pimenov & Kljuykov	0	0	1	0	0	0	1	0	0	1	1	1	1	1	1	0	0	0	1	1	1	0	1	0.5	1	1	1	0	1	1	0	0.5	1	0	0	0
Johrenia dichotoma DC.	0	1	1	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0.5	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Johrenia distans (Griseb.) Halácsy	0	1	0.5	0	0	1	0	0	0	0.5	1	1	1	0	0	0	0	0	1	1	1	0.5	0	0	0	0	0	0	1	0	1	1	1	0	0	0
Johrenia polyscias Bornm.	0	1	0.5	0	0	1	0	0	0.5	0.5	1	1	1	1	0	0	0	0	1	1	1	0.5	1	0	0	0	0	0	1	0	0	0	1	0	0	0
Johrenia selinoides Boiss. & Balansa ex Boiss.	0	1	1	0	0	1	0	0	1	1	1	1	1	1	1	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Johrenia tortuosa (Fisch. & C. A. Mey.) Chamberlain	0	1	1	0	0	1	0	0	0.5	0.5	1	1	1	1	0	0	0	0	1	1	1	0.5	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Ormosolenia alpina (Sieber ex Schult.) Pimenov	1	1	0	1	0	0.5	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0.5	1	0	1	1	1	0	0.5	1	1	1	1	0	0	0
Ormosolenia pisidica Boiss. & Heldr.	1	1	0	1	0	0.5	0	0	0	1	1	1	1	0	0	0	0	0	1	0	1	0.5	1	0.5	1	1	1	0	0.5	1	1	1	1	0	0	0
Peucedanum nebrodense (Guss.) Nyman	1	1	0	1	0	0.75	0	0	0	1	1	0	1	0	0	0	1	0	1	1	0	0.5	1	0.75	1	1	1	0	0.5	1	0	0.5	1	0	1	1
Zeravschania aucheri (Boiss.) Pimenov	1	0	0.5	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0.5	0	0.5	1	1	1	1	1	1	0	0.5	0	0	0	0
Zeravschania ferulifolia (Gilli) Pimenov	1	0	0.5	0	0	1	1	1	1	1	1	1	0	0	0	1	1	1	1	0	0	1	0	0.5	1	1	1	1	1	1	0	0.5	0	0	0	0
Zeravschania knappii (Bornm.) Pimenov & Kljuykov	1	0	1	0	0	1	1	0	1	0	1	1	0	0	0	1	0	0	1	1	1	0.5	0	0.5	1	1	1	1	1	1	0	0.5	1	0	0	0
Zeravschania membranacea (Boiss.) Pimenov	1	0	1	0	0	1	1	1	1	0	1	1	0	0	0	1	1	1	1	1	1	0.5	0	0.5	1	1	1	1	1	1	0	0.5	0	0	0	0
Zeravschania pauciradiata (Tamamsch.) Pimenov	1	0	1	0	0	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	0.5	0	0.5	1	1	1	1	1	1	0	0.5	0	0	0	0
Zeravschania regeliana Korovin	1	0	0.5	0	0	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	0	0.5	0	0.5	1	1	1	1	1	1	0	0.5	1	0	0	0
Zeravschania scabrifolia Pimenov	1	0	0	0	0	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	0	1	0	0.5	1	1	1	1	1	1	0	0.5	0	0	0	0
Zeravschania stricticaulis (Rech. f.) Pimenov & Kljuykov	1	0	0.5	0	1	1	1	0	0	0.5	1	1	0	0	0	1	1	1	1	0	1	0.5	0	0.5	1	1	1	1	1	1	0	0.5	0	0	0	0

Appendix 3. List of 17 morphological characters and associated character states used in the phylogenetic analysis

1. Habit: 0, monocarpic with unbranched rootstock; 1, polycarpic with branching rootstock.
2. Stem base: 0, densely covered by remains of leaf petioles; 1, without remains of petioles.
3. Stem height (in cm): 0, 7–40; 1, 41–100; 2, more than 100.
4. Stem ribs: 0, without prominent ribs; 1, with ± prominent ribs.
5. Leaf shape: 0, linear to lanceolate; 1, subrounded to reniform; 2, oblong to oblong-ovate; 3, ovate to triangular.
6. Leaf sheath length: 0, long; 1, short.
7. Leaf sheath shape: 0, linear; 1, triangular.
8. Shape of terminal leaf lobes: 0, filiform to linear; 1, lanceolate; 2, ovate.
9. Calyx teeth: 0, absent; 1, present.
10. Petal color: 0, more white; 1, more yellow.
11. Stylopodium shape: 0, flat; 1, short-conical; 2, conical.
12. Dorsal mericarp ribs: 0, indistinguishable; 1, filiform; 2, keeled or slightly inflated; 3, strongly spongy inflated.
13. Marginal mericarp ribs: 0, not developed; 1, ± developed.
14. Parenchyma cells with lignified pitted walls on dorsal mericarp side: 0, developed; 1, absent or sometimes only under vascular bundles.
15. Secretory ducts (vittae) in mericarp furrows: 0, absent or inconsistent, not visible in each furrow; 1, always developed.
16. Commissural secretory ducts (vittae): 0, absent; 1, two in each mericarp; 2, more than two per mericarp.
17. Rib secretory ducts: 0, absent; 1, present.

Appendix 4. Data matrix of the 17 morphological characters used for the phylogenetic analysis. Characters and the coding of character states correspond to those in Appendix 3.

	Character states for characters 1–17																
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Aethusa cynapium	0	1	2	1	3	1	0	2	0	0	1	3	0	1	1	1	0
Dichoropetalum achaicum	1	0	0	0	3	1	0	2	0	1	2	1	1	1	1	2	0
D. aromaticum	0	0	1	1	0	1	1	1	0	1	1	3	0	0	0	0	1
D. golestanicum	0	0	1	0	0	1	1	1	0	1	2	1	1	0	1	0	0
D. paucijugum	0	0	0	1	0	1	0	1	0	1	0	3	0	0	0	0	1
D. pschawicum	1	0	1	0	3	1	0	0	0	0	1	1	1	1	1	2	0
D. schottii	1	0	1	0	3	1	0	0	0	0	1	1	1	1	1	2	0
D. scoparium	1	0	2	0	0	1	1	0	0	1	2	1	1	1	1	0	0
D. seseloides	0	0	1	0	0	1	0	0	0	1	2	1	1	1	1	1	1
D. carvifolia	1	0	1	0	3	1	0	0	0	0	1	1	1	1	1	2	0
Ormosolenia alpina	1	1	0	1	1	0	0	2	1	0	1	0	1	1	1	2	0
O. pisidica	1	1	0	1	1	0	0	2	1	1	1	1	1	1	1	2	0
Peucedanum nebrodense	1	1	0	1	2	0	0	2	0	0	1	2	1	1	1	1	0