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Source: Willdenowia, 50(1) : 39-63

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: https://doi.org/10.3372/wi.50.50105

Willdenowia

Annals of the Botanic Garden and Botanical Museum Berlin

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Delimitation of Iranian species of *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* (*Asteraceae*, *Cichorieae*) based on morphological and molecular data

Version of record first published online on 6 March 2020 ahead of inclusion in April 2020 issue.

Abstract: *Scorzonera* L. is represented by 57 species in Iran including three subgenera: *S.* subg. *Scorzonera*, *S.* subg. *Podospermum* and *S.* subg. *Pseudopodospermum*. Species of *S.* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* in Iran are morphologically similar, which limits species delimitation. In order to clarify intersubgeneric and interspecific delimitation in Iran, we carried out extensive sampling of the two subgenera in Iran. We conducted phylogenetic analyses based on the nuclear Internal Transcribed Spacer (nrITS), detailed morphological studies, and we evaluated the systematic value of achene features. Our results showed that *Scorzonera* s.l. is polyphyletic, and both *S.* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* are monophyletic. The monophyly of *S.* subg. *Podospermum* morphologically corresponds to a combination of characters containing pinnatifid leaves, phyllaries with black corniculate projections, and the presence of a swollen carpopodium on the achenes. A comparison of the topology observed in the nrITS phylogeny with achene features indicates that a sculptured achene wall surface in members of *S.* subg. *Pseudopodospermum* provides a synapomorphy for this lineage. This study supports a broader circumscription of *S.* subg. *Pseudopodospermum* with the addition of *S. calyculata* (*S.* sect. *Incisae*), *S. ovata*, *S. papposa* and *S. paradoxa* (*S.* sect. *Papposae*). Finally, we provide a taxonomic treatment, including an identification key and species diagnoses and distributions, with nomenclature of Iranian species.

Key words: achene surface, *Asteraceae*, carpopodium, *Cichorieae*, *Compositae*, diagnoses, Iran, morphology, nrITS, phylogeny, *Podopermum*, *Pseudopodospermum*, *Scorzonera*, *Scorzonerinae*, species, taxonomy

Article history: Received 4 July 2019; peer-review completed 29 October 2019; received in revised form 19 November and 17 December 2019; accepted for publication 17 December 2019.

Citation: Hatami E., Mirtadzadini M., Bordbar F. & Jones K. E. 2020: Delimitation of Iranian species of *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* (*Asteraceae*, *Cichorieae*) based on morphological and molecular data. – Willdenowia 50: 39–63. doi: https://doi.org/10.3372/wi.50.50105

Introduction

Scorzonera L. (*Asteraceae*, *Cichorieae*, *Scorzonerinae*) with 160–175 species, depending on the circumscription and species concepts, has a distribution spanning Europe and the Mediterranean region, N Africa and SW and C Asia, with a particularly high concentration of species in SW Asia (Bremer 1994; Rechinger 1977; Mabberley 2008; Norouzi & al. 2016; Kilian & al. 2009b+). In its widest circumscription, *Scorzonera* is characterized by simple or pinnatifid leaves, multiseriate and unequal phyllaries, glabrous or entirely lanate achenes, and plumose pappus bristles with soft and interwoven fimbriae (Lipschitz 1964; Rechinger 1977; Mavrodiev & al. 2004; Kilian & al. 2009a). The other unanimously recognized genera of subtribe *Scorzonerinae* are readily distinguished from *Scorzonera* in its widest sense: *Tragopogon* L., the only other large genus of the subtribe (c. 150 species), by its uniseriate involucre; *Koelpinia* Pall. by its scorpioid achenes without a pappus but with hooked pro-

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jections; *Epilasia* (Bunge) Benth. & Hook. f. by its leafy outer series of phyllaries usually as long as or longer than the inner series; the monotypic *Tourneuxia* Coss. by its pappus laterally situated at the achene apex; and the monotypic *Pterachaenia* Benth. by its winged achenes (Mavrodiev & al. 2004; Kilian & al. 2009a).

Starting with Candolle (1805), who described the genus *Podospermum* DC., attempts have been made to segregate *Scorzonera* into separate genera; the most recent was by Nazarova (1990), who distinguished the monotypic *Takhtajaniantha* Nazarova from all other species in the genus. *Podospermum* was characterized by Candolle (1805) at generic rank by the combination of pinnatifid leaves and a well-expressed carpopodium, which is the sterile abscission zone at the base of the achene, attached to the receptacle and composed of one or more rows of cells that are distinct from the rest of the achene wall (Mukherjee & Nordenstam 2004). Due to this attractive diagnosis, the recognition of *Podospermum* at generic rank has been widely accepted (Candolle 1805, 1838; Cassini 1827; Dumortier 1827; Lessing 1832; Endlicher 1841; Grossheim 1949; Kuthatheladze 1978; Pignatti 1982; Tzvelev 1988; Nazarova 1997; Mavrodiev & al. 2004; Winfield & al. 2006; Greuter 2006+; Kilian & al. 2009a, 2009b+; Makbul & al. 2016). Instead of splitting *Scorzonera* into different genera, some workers (Lipschitz 1964; Rechinger 1977; Safavi 2013; Coşkunçelebı & al. 2015) recognized three subgenera: *S.* subg. *Scorzonera*, *S.* subg. *Podospermum* (DC.) Lipsch. and *S.* subg. *Pseudopodospermum* (Lipsch. & Krasch.) Lipsch., a treatment first established by Lipschitz (1935–1939) in his monograph of the genus. Lipschitz (1964) described the three subgenera based on the presence of a carpopodium with simple leaves (*S.* subg. *Pseudopodospermum*), the presence of a carpopodium with pinnatifid leaves (*S.* subg. *Podospermum*) and the absence of a carpopodium with simple leaves (*S.* subg. *Scorzonera*). Rechinger (1977) recognized that the carpopodium is sometimes inconspicuous in species of *S.* subg. *Pseudopodospermum*. He therefore considered other morphological characters, including a tuberous root, simple leaves, and a sculptured achene surface (lamellate, muricate, tuberculate or verrucose) to separate *S.* subg. *Pseudopodospermum* from *S.* subg. *Scorzonera* and *S.* subg. *Podospermum.* Morphological studies of achene features by Coşkunçelebı & al. (2016) confirmed that achene surface patterns are valuable for distinguishing between *S.* subg. *Pseudopodospermum* and *S.* subg. *Podospermum* (Coşkunçelebı & al. 2016). Those studies focused on Turkish species and they only sampled one and three species of *S.* subg. *Pseudopodospermum* and *S.* subg. *Podospermum* from Iran, respectively.

Previous molecular phylogenetic studies have sampled broadly across subtribe *Scorzonerinae*. The genus *Scorzonera* was resolved as polyphyletic, based on the nuclear ribosomal Internal Transcribed Spacer (nrITS; Mavrodiev & al. 2004) and a combined nrITS and external transcribed spacer (ETS) analysis and Amplified Fragment Polymorphisms (AFLPs) by Winfield & al. (2006). Intergeneric nodes in those analyses were, however, statistically unsupported. Both studies revealed that the "*Lasiospora* clade", named after the *Scorzonera* segregate *Lasiospora* Cass. based on *S. hirsuta* (Gouan) L., represents a lineage that is far from the core of *Scorzonera*, in the sense of its type *S. humilis* L. Mavrodiev & al. (2004) showed that the *Lasiospora* clade can also be distinguished from *Scorzonera* based on chromosome number (6 and 7, respectively; see also Nazarova 1977; Diaz De La Guardia & Blanca 1987; Martin & al. 2012). The morphological distinction of *Lasiospora* species from *Scorzonera* is, however, unclear. Importantly, both studies confirmed that *S.* subg. *Podospermum* is monophyletic, but with *S. purpurea* L. resolved as sister to the *Podospermum* clade.

Zaika & al. (2020) recently provided a taxonomic reassessment of *Scorzonera* s.l. based on broad taxonomic sampling, carpological (including anatomical) data, and nrITS and two plastid markers (partial *rbcL* and *matK*) molecular phylogenetic analyses (Zaika & al. 2020). That study confirmed the polyphyly of *Scorzonera* and proposed a revised classification of the subtribe. As a result of their analyses, the following seven genera were confirmed: *Gelasia* Cass.; *Pseudopodospermum* (Lipsch. & Krasch.) Kuth.; *Pterachaenia* (including *S. codringtonii* Rech. f.); *Scorzonera* (including four major clades: *Podospermum*, *Scorzonera* s. str., *S. albicaulis* Bunge and *S. purpurea*); *Takhtajaniantha*; and the newly described *Lipschitzia* Zaika & al. (*S. divaricata* Turcz. clade) and *Ramaliella* Zaika & al. (*S. polyclada* Rech. f. & Köie clade). Therefore, the authors proposed a narrow circumscription of *Scorzonera* (containing the *Podospermum* clade) and accepted *Pseudopodospermum* as a separate genus. At present, we are uncertain of the most appropriate taxonomic concept for the clades *Podospermum* and *Pseudopodospermum*. Therefore, for the purpose of this study, we follow the wider circumscription of genus *Scorzonera* that recognizes these lineages at subgeneric rank: *S.* subg. *Podospermum*, and *S.* subg. *Pseudopodospermum*. This taxonomic concept is in accordance with the following studies: Lipschitz (1964), Rechinger (1977), Safavi (2013), and Coşkunçelebı & al. (2015). In contrast to Zaika & al. (2020), who investigated generic-level relationships within *Scorzonera* s.l. Our study focuses on the shallower taxonomic levels and aims to clarify the morphological delimitation among Iranian species within *S.* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* and compare it with the nrITS tree.

Currently, the genus *Scorzonera* is represented by 57 species in Iran; of which 33% (20 species) are considered endemic to the country (Rechinger 1977; Safavi 2013; Safavi 2016; Safavi 2019). Of the 57 species in Iran, 36 belong to *S.* subg. *Scorzonera* (137 worldwide), nine to *S.* subg. *Pseudopodospermum* (20 worldwide) and 12 (21 worldwide) to *S.* subg. *Podospermum* (Kamelin & Tagaev 1986; Rechinger 1977; Safavi 2013; Safavi 2016; Safavi

2019). In Iran, *S.* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* contain closely related species that are currently difficult to distinguish based on morphological characters, which limits species identification. With the exception of leaf-anatomical studies of Iranian species of *S.* subg. *Pseudopodospermum* and *S.* subg. *Podospermum* (Norouzi & al. 2016), and karyological analyses of a limited number of species from Iran (Safavi 1999; Bordbar & al. 2019; Hatami & al. 2019), no comprehensive study has been carried out to date to clarify the nomenclature and intergeneric and interspecific diagnostic characters of these subgenera in Iran. In order to clarify the circumscription of *S.* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* and give stronger insight into these lineages in Iran, we conducted extensive sampling of the two subgenera in Iran for detailed morphological studies. We also sampled representatives of all major clades across *Scorzonerinae* for phylogenetic analysis based on nrITS. Therefore, the aims of the present study are to:

1. Conduct phylogenetic analyses using nrITS sequence data to test the monophyly of *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* in Iran and evaluate the phylogenetic relationship between species. We sampled representatives from across subtribe *Scorzonerinae* and the two subgenera with a focus on Iranian species.
2. Investigate morphological characters of species of *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* to understand the morphological boundaries and diagnostic characters both between the subgenera and among their species in Iran.
3. Assess the systematic value of achene features for distinguishing between taxa and to compare the patterns of achene features with the inferred topology from phylogenetic analyses of the nrITS region.
4. Provide a taxonomic treatment, including diagnoses and distributions, with a clarified circumscription and nomenclature of all species of *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* in Iran. We also provide an identification key for the two subgenera and their species in Iran.

Material and methods

Sampling — For nrITS analyses, the sampling approach for *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* was guided by treatments in *Flora iranica* (Rechinger 1977). Refer to Appendix 1 for a list of all samples included in the nrITS analyses with voucher information and GenBank numbers for newly generated sequences in this study. See Table 1 for classifications of *Scorzonera* species based on previous studies. In order to include representatives from the major clades across *Scorzonerinae* in the molecular analyses, we also incorporated already published nrITS sequence data of members outside of the focus subgenera. Therefore, the ingroup comprised extensive sampling from Iranian *S.* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* (Rechinger 1977), and sampling outside of those subgenera: species from *S.* subg. *Scorzonera* and from the genera *Epilasia*, *Koelpinia*, *Pterachaenia* and *Tragopogon* guided by the clades in subtribe *Scorzonerinae* in the nrITS analyses of Mavrodiev & al. (2004; Appendix 1). Sequences of nrITS for 29 accessions were newly generated in this study: 11 from species of *S.* subg. *Podospermum*, seven from species of *S.* subg. *Pseudopodospermum* and one species of the *Lasiospora* clade distributed in Iran. In some cases, there were multiple accessions per species. It was not possible to generate nrITS data for *S. turkeviczii* Krasch. & Lipsch. or *S. syriaca* Boiss. & Blanche (*S.* subg. *Pseudopodospermum*); however, these species were included in the morphological analyses and taxonomic treatment (see below; Table 1). *Scorzonera lachnostegia* (Woronow) Lipsch. (*S.* subg. *Podospermum*) is very rare in Iran (Safavi 2013); therefore, it was not possible to locate specimens for morphological or molecular studies. Sequences of 22 species from NCBI were included, corresponding to the three subgenera of *Scorzonera* and other related genera in subtribe *Scorzonerinae*. In total, nrITS sequences for 44 species of *Scorzonerinae* were included in the phylogenetic analyses. Sequences for *Cichorium intybus* L., *Lactuca sativa* L. and *Scolymus maculatus* L. from NCBI were included as outgroup species to *Scorzonerinae* (Appendix 1).

Phylogenetic reconstruction — Genomic DNA was extracted from leaf material using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) according to the manufacturer's protocol. For amplification of the nrITS region, primers ITS-A and ITS-B were used (Blattner 1999). The PCR reaction mixture consisted of 20 µl deionized water, 7 µl 2×Taq DNA polymerase master mix Red (Amplicon, Cat. No.180301), 0.75 µl of each primer (50 pmol/µl), and 1.5 µl template DNA. PCR amplification consisted of an initial denaturation step of 3 minutes at 94°C, followed by 38 cycles of 30 seconds denaturation at 94°C, 40 seconds annealing at 53°C and 1-minute extension at 68°C, and a final extension step at 70°C for 10 minutes. Sequencing reactions were performed at Macrogen Inc. (Seoul, Korea) using the same PCR primers.

Sequences were initially aligned using MAFFT v. 6.0 (Katoh & Toh 2008) and checked manually using the program PhyDE v. 0.9971 (Müller & al. 2005). Indels were coded as binary characters using the simple indel coding approach, according to Simmons & Ochoterena (2000) in SeqState v. 1.4.1 (Müller 2005). Phylogenetic analyses were conducted using Maximum Parsimony (MP), Maximum Likelihood (ML) and Bayesian Inference (BI). Maximum Parsimony analyses were performed using heuristic searches in PAUP* v. 4.0b10 (Swofford 2003) in combination with parsimony Ratchet (Nixon 1999) in PRAP (Müller 2004). Ratchet settings included 200 iterations with 25% of the positions randomly unweighted (weight = 2), and 100 random additional cycles. Jackknife

Table 1. *Scorzonera* species included in this study and their subgeneric classification based on previous literature (in column 2: Lipschitz 1964; Rechinger 1977; Kamelin & Tagaev 1986; Mavrodiev & al. 2014; Safavi 2013; Zaika & al. 2020) compared to results of phylogenetic analyses (Fig. 1) and the taxonomic treatment of this study (in column 3).

Scorzonera species included in this study	Treatment based on previous literature (Lipschitz 1964b [Lip]; Rechinger 1977 [Rech]; Kamelin & Tagaev 1986 [KT]; Mavrodiev & al. 2004 [Mav]; Safavi 2013 [Saf]; Zaika & al. 2020 [Za])*	Clade name according to the phylogeny in this study (if sampled; Fig. 1) / *S.* subg. (*Podospermum* or *S.* subg. *Pseudopodospermum* only) according to taxonomic treatment of this study**
S. hirsuta (Gouan) L.	*S.* subg. *Scorzonera* (Lip, Saf, KT); *Lasiospora* clade (Mav); genus *Gelasia* (Za)	*Lasiospora* clade**
S. cinerea Boiss.	*S.* subg. *Scorzonera* (Lip, Rech, KT, Saf); genus *Gelasia* (Za)	*Lasiospora clade***
S. litwinowii Krasch. & Lipsch.	*S.* subg. *Scorzonera* (Lip, Rech, Saf); *Lasiospora* clade (Mav); genus *Gelasia* (Za)	*Lasiospora clade***
S. pseudolanata Grossh.	*S.* subg. *Scorzonera* (Rech, KT); genus *Gelasia* (Za)	*Lasiospora clade***
S. rigida Aucher ex DC.	*S.* subg. *Scorzonera* (Lip, Rech, KT, Saf); *Lasiospora* clade (Mav); genus *Gelasia* (Za)	*Lasiospora clade***
S. seidlitzii Boiss.	*S.* subg. *Scorzonera* (Lip, Rech, KT, Saf); *Lasiospora* clade (Mav); genus *Gelasia* (Za)	*Lasiospora clade***
S. aristata Ramond ex DC.	*S.* subg. *Scorzonera* (KT); *Scorzonera* s. str. Clade (Za)	*S. humilis* clade**
S. humilis L.	*S.* subg. *Scorzonera* (Lip, KT, Saf); *Scorzonera* s.str. Clade (Za)	*S. humilis* clade**
S. intricata Boiss.	*S.* subg. *Scorzonera* (Lip, Rech, Saf); genus *Ramaliella* (Za)	*S. intricata* clade**
S. tortuosissima Boiss.	*S.* subg. *Scorzonera* (Lip, Rech, Saf); genus *Ramaliella* (Za)	*S. intricata* clade**
S. purpurea L.	*S.* subg. *Scorzonera* (Lip, Saf); *S.* subg. *Podospermum* (KT); *Scorzonera purpurea* clade (Za)	*S. purpurea*, sister to *S.* subg. *Podospermum*
S. armeniaca (Boiss. & A. Huet) Boiss.	*S.* subg. *Podospermum* (Rech, KT); genus *Podospermum* (Mav); *Podospermum* clade (Za)	*S. cana* clade / *S.* subg. *Podospermum*
S. cana (C. A. Mey.) O. Hoffm.	*S.* subg. *Podospermum* (Rech, KT); genus *Podospermum* (Mav); *Podospermum* clade (Za)	*S. cana* clade / *S.* subg. *Podospermum*
S. grossheimii Lipsch. & Vassilcz.	*S.* subg. *Podospermum* (Rech, KT); *Podospermum* clade (Za)	*S. cana* clade / *S.* subg. *Podospermum*
S. kandavanica Rech. f.	*S.* subg. *Podospermum* (Rech, KT)	*S. cana* clade / *S.* subg. *Podospermum*
S. luristanica Rech. f.	*S.* subg. *Podospermum* (Rech, KT); *Podospermum* clade (Za)	*S. cana* clade / *S.* subg. *Podospermum*
S. meyeri (K. Koch) Lipsch.	*S.* subg. *Podospermum* (Rech); genus *Podospermum* (Mav); *Podospermum* clade (Za)	*S. cana* clade / *S.* subg. *Podospermum*
S. persepolitana Boiss.	*S.* subg. *Podospermum* (Rech, KT)	*S. cana* clade / *S.* subg. *Podospermum*

* Some species were not included in all literature.

** Species outside of the monophyletic clades corresponding to *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* in Fig. 1 were not included in the morphological analyses or taxonomic treatment. Furthermore, *S.* subg. *Scorzonera* is polyphyletic and taxonomic studies for this group are beyond the scope of this study. Therefore, we provide subgeneric names only for species that we treat as *S.* subg. *Podospermum* or *S.* subg. *Pseudopodospermum*.

S. radicosa Boiss.	*S.* subg. *Podospermum* (Rech, KT); *Podospermum* clade (Za)	*S. cana* clade / *S.* subg. *Podospermum*
S. laciniata L.	*S.* subg. *Podospermum* (Rech, KT); genus *Podospermum* (Mav); *Podospermum* clade (Za)	three samples unresolved within *S.* subg. *Podospermum* / *S.* subg. *Podospermum*
S. meshhedensis (Rech. f.) Rech. f.	*S.* subg. *Podospermum* (Rech, KT); *Podospermum* clade (Za)	*S. songorica* clade / *S.* subg. *Podospermum*
S. songorica (Kar. & Kir.) Lipsch. & Vassilcz.	*S.* subg. *Podospermum* (Rech, KT); *Podospermum* clade (Za)	*S. songorica* clade / *S.* subg. *Podospermum*
S. leptophylla (DC.) Krasch. & Lipsch.	*S.* subg. *Pseudopodospermum* (Lip, Rech, Saf)	*S. mollis* clade / *S.* subg. *Pseudopodospermum*
S. mollis M. Bieb. subsp. *mollis*	*S.* subg. *Pseudopodospermum* (Lip, Saf); genus *Pseudopodospermum* (Za)	*S. mollis* clade / *S.* subg. *Pseudopodospermum*
S. mucida Rech. f. & al.	*S.* subg. *Pseudopodospermum* (Rech); *S.* subg. *Podospermum* (KT); genus *Pseudopodospermum* (Za)	*S. mollis* clade / *S.* subg. *Pseudopodospermum*
S. phaeopappa (Boiss.) Boiss.	*S.* subg. *Pseudopodospermum* (Lip, Rech, Saf); genus *Pseudopodospermum* (Za)	*S. mollis* clade / *S.* subg. *Pseudopodospermum*
S. raddeana C. Winkl.	*S.* subg. *Pseudopodospermum* (Lip, Rech, Saf); *S.* subg. *Podospermum* (KT); genus *Scorzonera* (Mav); genus *Pseudopodospermum* (Za)	*S. mollis* clade / *S.* subg. *Pseudopodospermum*
S. semicana DC.	*S.* subg. *Pseudopodospermum* (Lip, Saf); *S.* subg. *Podospermum* (KT)	*S. mollis* clade / *S.* subg. *Pseudopodospermum*
S. stenocephala Boiss.	*S.* subg. *Pseudopodospermum* (Rech, KT)	*S. mollis* clade / *S.* subg. *Pseudopodospermum*
S. szowitzii DC.	*S.* subg. *Pseudopodospermum* (Lip, Rech, Saf)	*S. mollis* clade / *S.* subg. *Pseudopodospermum*
S. tunicata Rech. f. & Köie	*S.* subg. *Pseudopodospermum* (Rech); *S.* subg. *Podospermum* (KT)	*S. mollis* clade / *S.* subg. *Pseudopodospermum*
S. papposa DC.	*S.* subg. *Scorzonera* (Lip, Rech, KT, Mav, Saf); genus *Pseudopodospermum* (Za)	*S. papposa / S.* subg. *Pseudopodospermum*
S. calyculata Boiss.	*S.* subg. *Scorzonera* (Rech, Lip, Mav, Saf); *S.* subg. *Podospermum* (KT); genus *Pseudopodospermum* (Za)	*S. calyculata / S.* subg. *Pseudopodospermum*
S. ovata Trautv.	*S.* subg. *Scorzonera* (Lip, Rech, KT, Saf)	not in phylogeny / *S.* subg. *Pseudopodospermum*
S. paradoxa Fisch. & C. A. Mey. ex DC.	*S.* subg. *Scorzonera* (Rech, KT)	not in phylogeny / *S.* subg. *Pseudopodospermum*
S. syriaca Boiss. & Blanche	*S.* subg. *Pseudopodospermum* (Rech); *S.* subg. *Podospermum* (KT); genus *Pseudopodospermum* (Za)	not in phylogeny / *S.* subg. *Pseudopodospermum*
S. turkeviczii Krasch. & Lipsch.	*S.* subg. *Pseudopodospermum* (Lip, Rech, Saf); *S.* subg. *Podospermum* (KT)	not in phylogeny / *S.* subg. *Pseudopodospermum*

(JK) support was estimated in PAUP by conducting a single heuristic search within each 10 000 replicates using the Tree Bisection and Re-connection branch-swapping algorithm and a deletion of 36.79% characters in each replicate. A strict-consensus tree was constructed from all saved trees. The symmetrical (SYM) nucleotide substitution model was selected as the best-fit model using JModelTest v.2.1.6 (Darriba & al. 2012), according to the Akaike Information Criterion (AIC). The neighbour-joining algorithm BIONJ was used for the initial tree search (Gascuel 1997; Saitou & Nei 1987). Maximum Likelihood analyses were conducted using the graphical user interface of RAxML v. 1.5b1 (Silvestro & Michalak 2012). Bootstrap support was estimated based on the majority-rule consensus tree from 1000 replicates with 200 searches and the final tree topology was evaluated under the GTR GAMMA algorithm because the SYM model is not available in RAxML. Bayesian Inference was conducted in

MrBayes v. 3.2 (Ronquist & Huelsenbeck 2003) on the CIPRES science gateway (Miller & al. 2010). Four runs each with four chains were performed for 30 million generations, sampling every 2000 generations. After removing 10% of the sampled trees as burn-in, a 50% majority-rule consensus tree was constructed. Final tree visualization was carried out using TreeGraph v. 2.13.0-748 beta (Stöver & Müller 2010). Final DNA sequences were submitted to ENA (https://www.ebi.ac.uk/ena) using the software tool annonex2embl (Gruenstaeudl 2019).

Morphological and taxonomic studies — Collections of *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* were made between 2015 and 2018 across a broad geographic range in Iran in order to sample the maximum diversity of each taxon. Specimens from those field trips were deposited at MIR (see Appendix 2 for a list of specimens examined for the morphological and taxonomic studies). Live plants in the field and herbarium specimens in B, FMUH, HSHU, IRAN, JE, MIR and W were examined (herbarium codes according to Thiers 2019+; Appendix 2). Digitized specimens were examined via virtual herbarium catalogues at E (https://data.rbge.org.uk/search/herbarium/), G (http://www.ville-ge.ch/musinfo/bd/cjb/chg/), LINN (http://linnean-online.org/linnaean_herbarium.html), P (https://science.mnhn.fr/institution/mnhn/search) and via JSTOR Global Plants (https://plants.jstor.org/). Where possible, type specimens were examined by E.H. in the herbaria B, JE and W, from images provided by LE for types in that herbarium, and via virtual herbarium catalogues and JSTOR Global Plants for types in G and LINN. Descriptions of morphological characters were based on our observations and measurements (life cycle, plant height, root, stem, leaves, flowering capitula, fruiting capitula, achenes, pappus; Appendix 4) with comparisons to previous relevant studies (Lipschitz 1964; Rechinger 1977; Safavi 2013). Terminology for vegetative and reproductive morphological characters follows Beentje (2010). For each species the general distribution, updated nomenclature, and synonyms are given based on *Flora iranica*, *Flora of Iran*, and the *Cichorieae* portal (Rechinger 1977; Safavi 2013; Kilian & al. 2009+).

Macro photographs of achenes from species belonging to *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* were made using a stereomicroscope (Olympus SZX16) equipped with DP72 (a 12.5 megapixel digital colour camera), connected to cellSens Standard programme with an extended focus imaging function, at the Botanic Garden and Botanical Museum Berlin.

Results

Molecular analyses — The aligned nrITS data matrix comprised of 55 sequences and 826 characters including 126 coded indels, 291 parsimony informative sites and 156 parsimony uninformative sites (see alignment in Appendix 3). Maximum Parsimony analyses resulted in 16 most parsimonious trees with a length of 1096, a consistency index of 0.615, and a retention index of 0.863.

Bayesian Inference, ML, and MP analyses of the nrITS dataset produced identical topologies. The MrBayes 50% majority-rule consensus tree is presented in Fig. 1. Here, we report statistical support values that are well-supported (>0.95 posterior probability [PP], and >80% BS and JK) in parentheses (Fig. 1). Subtribe *Scorzonerinae* received full statistical support (1 PP, 100 JK, 100 BS; Fig. 1). The *Lasiospora* clade was resolved as monophyletic (1 PP, 100 JK, 100 BS) and as sister to a clade (1 PP, 99 JK, 97 BS) containing a polytomy that consisted of the rest of subtribe *Scorzonerinae*. This polytomy comprised five clades; one clade (1 PP, 92 BS) included in two subclades that contained the genera *Epilasia* (1 PP, 100 JK, 100 BS) and *Tragopogon* (1 PP, 100 JK, 100 BS), respectively. A second lineage in the polytomy corresponded to a single accession representing the monotypic genus *Pterachaenia*. The third clade in the polytomy (1 PP, 93 JK, 94 BS) contained the genus *Koelpinia*, sister to a clade consisting of *Scorzonera intricata* Boiss, and *S. tortuosissima* Boiss. (*S. intricata* clade; 1 PP, 100 JK, 100 BS). In a fourth clade (1 PP, 91 JK, 84 BS), *S. humilis* and *S. aristata* Ramond ex DC. (*S. humilis* clade; 1 PP, 99 JK, 99 BS) and a single accession of *S. purpurea* were resolved as consecutive sisters to a clade uniting the members of *S.* subg. *Podospermum* (1 PP, 100 JK, 100 BS). The relationships within the *S.* subg. *Podospermum* clade were largely unresolved, with the exception of the *S. songorica* (Kar. & Kir.) Lipsch. & Vassilcz. clade (1 PP, 100 JK, 100 BS) and the *S. cana* (C. A. Mey.) O. Hoffm. clade (0.99 PP, 91 JK, 80 BS). The fifth clade included *S.* subg. *Pseudopodospermum* (1 PP, 100 JK, 100 BS). Within *S.* subg. *Pseudopodospermum*, an accession of *S. calyculata* Boiss. was resolved as sister to *S. papposa* DC., which was sister to the *S. mollis* M. Bieb. clade (13 samples of nine species; 1 PP, 87 JK, 95 BS). The *S. mollis* clade contained a polytomy consisting of an accession of *S. mollis*, one clade (0.99 PP, 64 JK, 71 BS) containing three accessions of *S. szowitzii* DC. and another clade (1 PP) with the three samples of *S. raddeana* C. Winkl. (1 PP, 93 JK, 94 BS) in one subclade that was sister to a subclade containing *S. phaeopappa* (Boiss.) Boiss., *S. semicana* DC., *S. mucida* Rech. f. & al., and *S. tunicata* Rech. f. & Köie (0.93 PP).

Morphology — Images of achenes of 22 species are presented in this study (Fig. 2; Fig. 3). A summary of the achene surface pattern, pubescence, carpopodium and pappus bristles of species in *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* from Iran is provided in Table 2. Our observations revealed that, in *S.* subg. *Podospermum*, outer achenes are smooth, subterete to sulcate, glabrous or lanate, with a conspicuous carpopodium, and the pappi are apically scabrous with plumose bristles for most of the length. In contrast, in *S.* subg. *Pseudopodospermum*, the outer achenes are lamellate, muricate,

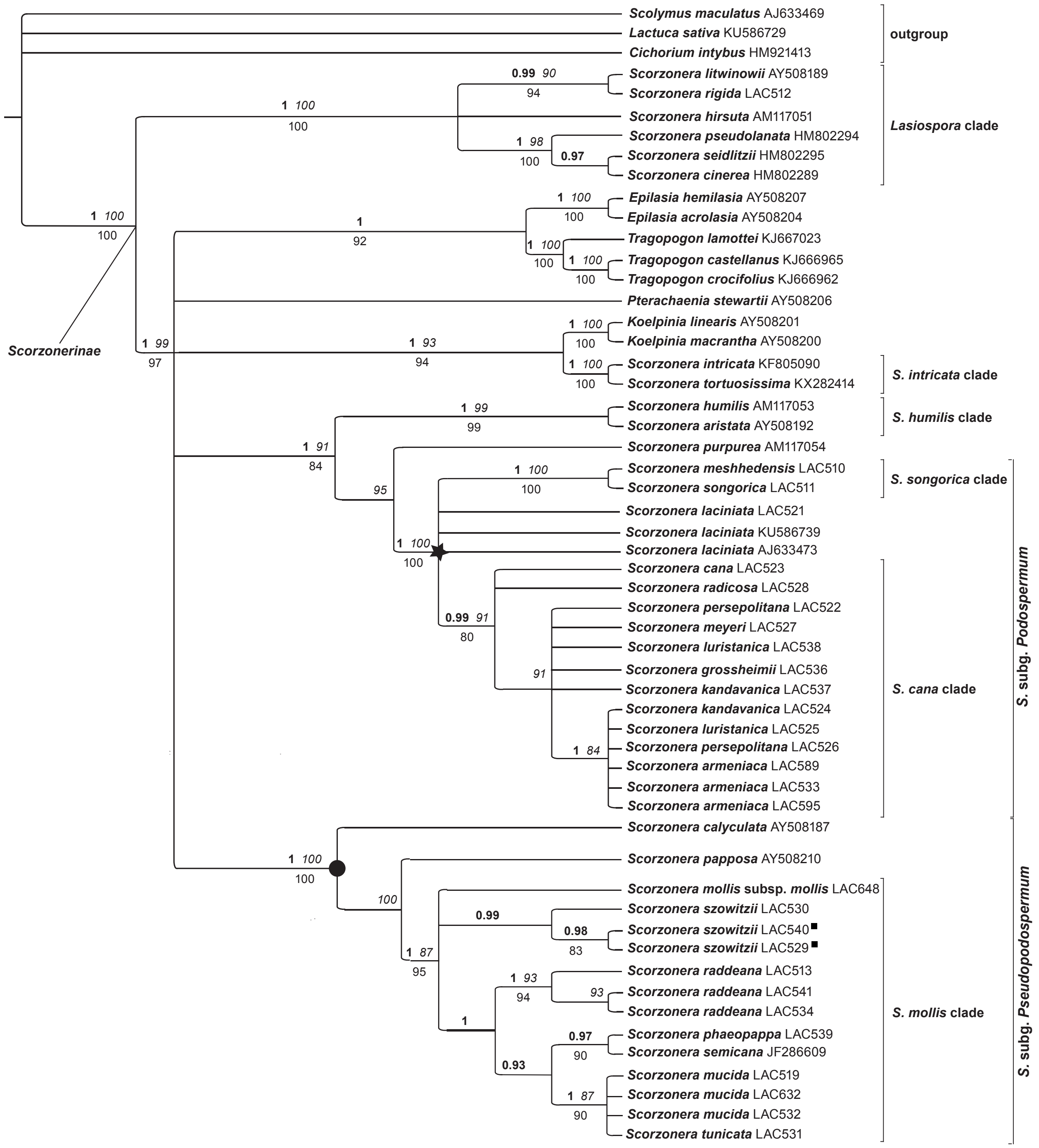

Fig. 1. Bayesian 50% majority-rule consensus tree inferred from the nuclear Internal Transcribed Spacer dataset. Values above nodes indicate posterior probability (bold) and jack-knife support (italic), and values below nodes indicate bootstrap support. Tip names correspond to species names and GenBank numbers or DNA numbers for newly generated sequences; see Appendix 1 for specimen details and Appendix 3 for the alignment). Clade names are indicated to the right of the phylogenetic tree. The star corresponds to the monophyletic *Scorzonera* subg. *Podospermum* and the circle corresponds to *S.* subg. *Pseudopodospermum*. Squares next to two tip names correspond to accessions of species names that are newly synonymized with *S. szowitzii* in this study (LAC540 *S. leptophylla*; LAC529 *S. stenocephala*; see the taxonomic treatment for details).

or verrucose, with or without a conspicuous carpopodium, glabrous, and the pappi either consist of bristles that are plumose for the entire length or for most of the length, and are apically scabrous, sometimes with five obvious longer scabrous bristles. More detailed characteristics of achenes for each species are given in Table 2.

In addition to achene morphology, a range of morphological features was examined for the identification key and taxonomic treatment below. Voucher information for specimens examined are provided for all species in Appendix 3; and the summary of morphological features (life cycle, plant height, root, stem, leaves, flowering

Table 2. Comparisons of achene features (achene surface, pubescence, carpopodium and pappus features) of representative species within *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum*.

Subgeneric classification (this study)	**Species**	**Achene surface**	**Achene pubescence**	**Carpopodium**	**Pappus bristles**
S. subg. *Podospermum*	*S. armeniaca*	smooth	sparsely lanate	present, conspicuously swollen, one third of achene length	plumose for most of length, scabrous above
	S. cana	smooth	glabrous	present, conspicuously swollen, one third of achene length	plumose for most of length, scabrous above
	S. grossheimii	smooth	glabrous	present, conspicuously swollen, one fifth to one fourth of achene length	plumose for most of length, scabrous above
	S. kanadavanica	smooth	sparsely lanate	present, conspicuously swollen, one fourth to one third of achene length	plumose for most of length, scabrous above
	S. laciniata	smooth	glabrous	present, conspicuously swollen, one third to half of achene length	plumose for most of length, scabrous above
	S. luristanica	smooth	glabrous	present, conspicuously swollen, one fifth to one fourth of achene length	plumose for most of length, scabrous above
	S. meshhedensis	smooth	glabrous	present, conspicuously swollen, one fourth of achene length	plumose for most of length, scabrous above
	S. meyeri	smooth	glabrous	present, conspicuously swollen, one fourth of achene length	plumose for most of length, scabrous above
	S. persepolitana	smooth	sparsely lanate	present, conspicuously swollen, one third of achene length	plumose for most of length, scabrous above
	S. songorica	smooth	glabrous	present, conspicuously swollen, one fifth to one fourth of achene length	plumose for most of length, scabrous above
S. subg. *Pseudo-podospermum*	*S. calyculata*	verrucose	glabrous	absent	plumose for most of length, scabrous above
	S. papposa	dentate-muricate	glabrous	absent	entirely plumose. with five conspicuous longer naked bristles
	S. mucida	lamellate-muricate	glabrous	present, not conspicuously swollen	plumose for most of length, scabrous above
	S. mollis subsp. *mollis*	lamellate-muricate	glabrous	present, conspicuously swollen, one sixth to one fifth of achene length	plumose for most of length, scabrous above. with five longer scabrous bristles
	S. ovata	dentate-muricate	glabrous	absent	entirely plumose
	S. phaeopappa	lamellate-muricate	glabrous	present, conspicuously swollen, one ninth to one seventh of achene length	plumose for most of length, scabrous above. with five longer scabrous bristles
	S. raddeana	lamellate-muricate	glabrous	present, not conspicuously swollen	plumose for most of length, scabrous above
	S. semicana	lamellate-muricate	glabrous	present, conspicuously swollen, one fifth to one fourth of achene length	plumose for most of length, scabrous above, with five longer scabrous bristles
	S. szowitzii	lamellate-muricate	glabrous	present, not conspicuously swollen	plumose for most of length, scabrous above
	S. tunicata	lamellate-muricate	glabrous	present, not conspicuously swollen	plumose for most of length, scabrous above
	S. turkeviczii	lamellate-muricate	glabrous	present, not conspicuously swollen	plumose for most of length, scabrous above
outside of these two subgenera	*S. purpurea**	smooth	glabrous	absent	plumose for most of length, scabrous above

* Sister to the *Scorzonera* subg. *Podospermum* clade in analyses of nuclear ribosomal Internal Transcribed Spacer (Fig. 1) and, based on morphological studies here, not treated as *S.* subg. *Podospermum* in the taxonomic treatment of this study.

capitula, fruiting capitula, achenes, pappus) for selected species in *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* are provided in Appendix 4.

Discussion

Relationships within subtribe Scorzonerinae — The topology inferred in our phylogenetic analyses (Fig. 1) confirms the results of previous studies that showed *Scorzonera* s.l. is polyphyletic (Mavrodiev & al. 2004; Winfield & al. 2006; Zaika & al. 2020). Based on our molecular analysis, the *Lasiospora* clade is well-resolved as a lineage that is remote from the core of *Scorzonera*, in the sense of its type *S. humilis*, in accordance with Mavrodiev & al. (2004), Winfield & al. (2006) and Zaika & al. (2020). However, Zaika & al. revealed that *S. villosa* Scop. is included in this lineage, and they proposed the oldest generic name: *Gelasia*. Our molecular analysis showed a sister-group relationship between the genus *Koelpinia* (*K. linearis* Pall. and *K. macrantha* C. Winkl.) and the *S. intricata* clade (*S. intricata* and *S. tortuosissima* here) from *S.* sect. *Intricatae* (Boiss.) Lipsch. within *S.* subg. *Scorzonera.* Our findings are in agreement with Zaika & al (2019), who revealed a sister relationship between the *S. polyclada* clade (including *S. intricata*, *S. longipapposa* Rech. f. and *S. polyclada* from *S.* sect. *Intricatae* of *S.* subg. *Scorzonera*) and *Koelpinia* proposing the generic name *Ramaliella* for *S. polyclada*. The sister relationship between *Epilasia* and *Tragopogon* in Fig. 1 is also congruent with previous studies (Mavrodiev & al. 2006; Zaika & al. 2020).

The remainder of the ingroup forms two major well-supported clades: one including the *Scorzonera humilis* clade, *S. purpurea* and *S.* subg. *Podospermum* and the other including *S.* subg. *Pseudopodospermum*. Our phylogenetic analyses incorporated some rare species of *S.* subg. *Podospermum* (*S. kandavanica* Rech. f., *S. persepolitana* Boiss.) and *S.* subg. *Pseudopodospermum* (*S. szowitzii*, *S. tunicata*) that had never been sampled before. *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* are monophyletic according to our nrITS tree (Fig. 1). Based on our nrITS phylogenetic tree, the *S. humilis* clade containing *S. humilis*, the type of *Scorzonera*, was resolved as sister to a clade containing *S. purpurea* and *S.* subg. *Podospermum*. This supports the treatment of *S.* subg. *Podospermum* as a subgenus within the genus *Scorzonera* (Lipschitz 1964; Rechinger 1977; Kamelin & Tagaev 1986) in contrast to previous treatments that considered it as an independent genus (Candolle 1805; 1838; Cassini 1827; Dumortier 1827; Lessing 1832; Endlicher 1841; Grossheim 1949; Kuthatheladze 1978; Pignatti 1982; Tzvelev 1988; Nazarova 1997; Mavrodiev & al. 2004; Winfield & al. 2006; Greuter 2006+; Kilian & al. 2009a, 2009b+; Makbul & al. 2016). *Scorzonera humilis*, *S. purpurea* and species of *S.* subg. *Podospermum* are morphologically distinct. However, based on morphological observations by E.H., they share the following morphological characters: woody cylindric root (non-tuberous) and the presence of basal leaves with few and small cauline leaves.

Lipschitz and Krascheninnikov (Lipschitz 1935) described *Scorzonera* subg. *Pseudopodospermum* as a section within the genus *Scorzonera* containing 14 species. Later, Lipschitz (1964) changed its taxonomic rank to subgenus, which is widely accepted in the following floras: *Flora URSS* (Lipschitz 1964), *Flora iranica* (Rechinger 1977), and *Flora of Iran* (Safavi 2013). We took the descriptions of species within this subgenus from different regional Floras into account: *Flora URSS* (Lipschitz 1964), *Flora iranica* (Rechinger 1977), *Flora of Iran* (Safavi 2013) and from recent studies (Coşkunçelebı & al. 2015; Coşkunçelebı & al. 2016; Norouzi & al. 2016; Hatami & al. 2019), which included additional species that were not considered members of *S.* subg. *Pseudopodospermum* by Lipschitz (1964): *S. aksekiensis* A. Duran & M. Öztürk, *S. elata* Boiss., *S. inaequiscapa* Boiss., *S. mucida*, *S. pachycephala* Podlech & Rech. f., *S. syriaca* and *S. tunicata*. The topology inferred by our molecular analyses and morphological observations, in particular of the achene surface, supports a broader circumscription of *S.* subg. *Pseudopodospermum*, to include *S. calyculata* and *S. papposa*. Zaika & al. (2020) also included members of *S.* sect. *Incisae* Lipsch. and *S.* sect. *Papposae* Lipsch. & Krasch. in *S.* subg. *Pseudopodospermum*, which was treated at generic level, based on their analyses of nrITS and plastid data and carpological features.

The monophyly of clades corresponding to *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* was confirmed based on broad taxonomic sampling in Zaika & al. (2020) similar to previous studies that had less sampling (Mavrodiev & al. 2004). In the nrITS and plastid phylogenetic trees in Zaika & al. (2020), there is limited phylogenetic resolution within the *Podospermum* and *Pseudopodospermum* clades. Therefore, the fact that we did not include all species that were sampled in the phylogenetic analyses in Zaika & al. (2020) does not cause a bias in our phylogenetic analyses. Furthermore, we broadened the taxonomic sampling compared to Zaika & al. (2020): three species in *S.* subg. *Pseudopodospermum* (*S. semicana*, *S. szowitzii* and *S. tunicata*) and two species in *Podospermum* (*S. kandavanica* and *S. persepolitana*). Below, we discuss the results of our morphological analyses of Iranian species of *S.* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* in the context of our nrITS tree (Fig. 1).

Scorzonera subg. *Podospermum* — The monophyly of *Scorzonera* subg. *Podospermum* (Fig. 1) morphologically corresponds to a combination of morphological characters containing pinnatifid leaves, phyllaries with a black corniculate projection (Fig. 4A), and the presence of a swollen carpopodium (Fig. 2A–J; Fig. 4B). Species of *S.* subg. *Podospermum* are mostly distributed in

Fig. 2. Macro photographs of achenes of species within *Scorzonera* subg. *Podospermum* (A–J), *S. purpurea* (K, L), and *S.* subg. *Pseudopodospermum* (M–T). – Scale bar lengths are given in parentheses after figure letters. – Voucher locality, collection date, collector(s) and number, and herbarium code for each sample are given in parentheses after species names. – *Scorzonera* subg. *Podospermum*: **A** (2 mm) and **B** (1 mm): *S. cana* (Greece, Grevena, 2.1 km NE of Paliouria, 31 May 1990, *Laubwald & al. 8941*, B). – **C** (2 mm) and **D** (1 mm): *S. kandavanica* (Iran, N Iran, 6 km from Lowshan to Jirandeh, 20 May 2016, *Mirtadzadini 2212*, MIR). – **E** (2 mm) and **F** (2 mm): *S. laciniata* (Iran, Zanjan to Bijar, 22 May 2016, *Mirtadzadini 2216*, MIR). – **G** (5 mm) and **H** (1 mm): *S. persepolitana* (Iran, Esfahan, near Delijan on clay hill, 20 May 2010, *Mirtadzadini 2218*, MIR). – **I** (2 mm) and **J** (1 mm): *S. songorica* (Iran, Kerman, Sardu, 24 Jun 2017, *Hatami & al. 2247*, MIR). – **K** (2 mm) and **L** (1 mm): *S. purpurea* (Germany, Frankenhausen, Jun 1994, *W. Becker s.n.*, B). – *S.* subg. *Pseudopodospermum*: **M** (5 mm) and **N** (1 mm): *S. papposa* (Palestine, Shefela, 23 Mar 2010, *Ristow 34/10*, B). – **O** (5 mm) and **P** (2 mm): *S. phaeopappa* (Iran, Kordestan, Marivan, *Mirtadzadini 2162*, MIR). – **Q** (5 mm) and **R** (2 mm): *S. raddeana* (Iran, Fars, between Estahban and Niriz, 3 May 2016, *Mirtadzadini & al. 2157*, MIR). – **S** (5 mm) and **T** (2 mm): *S. calyculata*, Iran, Between Karaj and Qazvin, 22 Jun 2011, *Mirtadzadini 2219*, MIR). – Macro photographs produced using a stereomicroscope (Olympus SZX16) equipped with DP72 (a 12.5 megapixel cooled digital colour camera) at the Botanic Garden and Botanical Museum Berlin.

the Euro-Siberian region in the north of Iran, and in the Irano-Turanian region, particularly the Kurdo-Zagrosian zone in the west of Iran (Zohary 1973; Rechinger 1977; Safavi 2013). This subgenus is most common in highland regions (>1000 m a.s.l) of more or less wet meadows, ruderal sandy or gravelly soils, stony slopes, or wet corners of agricultural fields (based on observations by E.H. and M.M.; Fig. 4D–F).

All species of *Scorzonera* subg. *Podospermum* that are distributed in Iran (Rechinger 1977; Safavi 2013) are included in our phylogenetic analyses, with the exception of *S. lachnostegia*, a rare species, which was sampled by Zaika & al. (2020) and resolved in a polytomy within the *Podospermum* clade in their nrITS tree. In spite of sampling multiple accessions of different species in our phylogenetic studies, the interspecific relationships were poorly resolved based on nrITS sequences, similar to Zaika & al. (2020) (Fig. 1). However, morphological characters, particularly achene features, were informative for clarifying the interspecific circumscription of this subgenus; see taxonomic treatment below (Table 2; Fig. 2A–J).

Within the *Scorzonera songorica* clade (Fig. 1), *S. meshhedensis* (Rech. f.) Rech. f. and *S. songorica* are morphologically similar to each other in possessing basal or cauline simple leaves (see Fig. 4E for *S. meshhedensis*). The pappus of these two species can be easily detached; a characteristic that is unique to this lineage among all *Scorzonera* species sampled in this study. The type of *S.* subg. *Podospermum* is *S. laciniata* L. (Lipschitz 1964). It is morphologically distinctive in having the longest carpopodium (6–7 mm) with the highest ratio of carpopodium length to total achene length among all species of *S.* subg. *Podospermum* (Table 2; Fig. 2E, F). The *S. cana* clade received strong statistical support (0.99 PP, 91 JK, 80 BS), but its internal relationships are unresolved due to the low variation of the nrITS region. However, species within the *S. cana* clade can be distinguished based on diagnostic morphological characters (Fig. 4C, D; Appendix 4); see taxonomic treatment below.

Previous treatments placed *Scorzonera purpurea* in *S.* subg. *Podospermum* (Candolle 1838; Kamelin & Tagaev 1986), whereas others treated it as a member of *S.* subg. *Scorzonera* sect. *Purpureae* Lipsch. (Lipschitz 1964; Zaika & al. 2020). The achenes of *S. purpurea* possess pale and tube-like swollen bases (Lipschitz 1964; Chater 1976), which is morphologically similar to the carpopodium of species in *S.* subg. *Podospermum* (Fig. 2K, L). However, the swollen bases are entirely fertile in *S. purpurea* compared to infertile carpopodia in species of *S.* subg. *Podospermum*. Furthermore, members of *S.* subg. *Podospermum* differ from *S. purpurea* in having pinnatifid leaves and phyllaries with corniculate projections (Fig. 4A); in contrast, *S. purpurea* has simple leaves and no corniculate projections. Although a sister relationship between *S. purpurea* and *S.* subg. *Podospermum* is well-supported in our nrITS analyses (95 PP; Fig. 1), we propose to maintain the treatment of this species outside of *S.* subg. *Podospermum* based on morphological differences observed here and in accordance with previous studies (Lipschitz 1964; Zaika & al. 2020).

Scorzonera subg. *Pseudopodospermum* — Our nrITS analyses included all species of *S.* subg. *Pseudopodospermum* distributed in Iran (Rechinger 1977; Safavi 2013; except *S. syriaca* and *S. turkeviczii*); as well as *S. mollis*, which represents the type of this subgenus (Lipschitz 1964). Members of this subgenus are widely distributed in dry to humid areas of the Irano-Turanian region (Zohary 1973; Rechinger 1977; Safavi 2013) and mostly grow in highland regions (>1000 m a.s.l) on sandy, clay or gravelly steppe hills, stony and rocky slopes, limestone hills in grassy steppes, stony semi-deserts, and open grassland (based on observations by E.H. and M.M.).

Scorzonera subg. *Pseudopodospermum* is monophyletic based on our nrITS phylogeny (Fig. 1) and the morphological observations in this study suggest that a sculptured (as opposed to smooth) achene-wall surface provides an exclusive synapomorphy for this lineage (Table 2). Within *S.* subg. *Pseudopodospermum*, the type of sculpturing on the achene surface is variable among species, and can be muricate, tuberculate, lamellate or verrucose (Table 2; Fig. 2M–T). Moreover, we include sequences of species from Iran that also have sculptured achenes from *S.* sect. *Incisae* and *S.* sect. *Papposae* to clarify their phylogenetic position and compare their morphological characters with members of *S.* subg. *Pseudopodospermum*. The *S. mollis* clade in our nrITS tree (Fig. 1) represents *S.* subg. *Pseudopodospermum* in its traditional circumscription (Lipschitz 1964; Rechinger 1977; Fig. 1). Based on our nrITS tree, *S. calyculata* (*S.* subg. *Scorzonera* sect. *Incisae*) and *S. papposa* (*S.* subg. *Scorzonera* sect. *Papposae*) are sister to the *S. mollis* clade with full statistical support and together they form a monophyletic clade. In Iran, *S.* sect. *Incisae* is represented by *S. calyculata*, and *S.* sect. *Papposae* by *S. ovata* Trautv., *S. papposa* and *S. paradoxa* Fisch. & C. A. Mey. ex DC.; we include all species in our morphological studies and the taxonomic treatment (see below). Morphological comparisons revealed that the sculptured achene surface supports a close relationship between the *S. mollis* clade and *S. calyculata* and all members of *S.* sect. *Papposae* in Iran, in support of the close relationship observed in the nrITS tree (Table 2; Fig. 1). We therefore propose a broader circumscription of *S.* subg. *Pseudopodospermum* to include members of *S.* sect. *Incisae* and *S.* sect. *Papposae* (*S. calyculata* and *S. papposa*, *S. ovata* and *S. paradoxa*; Table 1). Members of *S.* sect. *Incisae* and *S.* sect. *Papposae* outside of Iran also have sculptured achene surfaces (Lipschitz 1964; Rechinger 1977); it would therefore be beneficial incorporate all members of these sections and *S.* subg. *Pseudopodospermum* into future phylogenetic studies. Based on previous treatments (Lipschitz 1964; Rechinger 1977), members of *S.* sect. *Incisae* and *S.* sect. *Papposae* were morphologically distinguishable within *S.* subg. *Scorzonera* according to the absence of a carpopodium. Furthermore, we found that the carpopodium is only sometimes swollen among members of the *S. mollis* clade. The newly circumscribed *S.* subg. *Pseudopodospermum* in our study contains species either without a carpopodium or with a carpopodium that may be conspicuous or inconspicuous. Our study therefore suggests that the presence or absence of carpopodia is not a diagnostic character for intersubgeneric classification within the genus *Scorzonera*, in accordance with Haque & Godward (1984) and Zaika & al. (2020).

The *Scorzonera mollis* clade within *S.* subg. *Pseudopodospermum* (Fig. 1) contains a number of well-supported subclades, which we now discuss. In the nrITS analyses, we include sequences of an accession that we identified as *S. szowitzii* (LAC530) and accessions that corresponded of *S. leptophylla* (DC.) Krasch. & Lipsch. (LAC540) and *S. stenocephala* Boiss. (LAC529) according to species descriptions in *Flora iranica* (Fig. 1; Rechinger 1977). All three accessions were resolved in a strongly supported clade (0.99 PP; Fig. 1). We also studied morphological characters of multiple populations of *S. leptophylla*, *S. stenocephala* and *S. szowitzii* from several geographic regions in the field and herbaria (Appendix 1; Appendix 2). We observed extreme phenotypic plasticity among these species in vegetative characters including plant height, leaf width, possessing an entire or undulate leaf margin, and glabrous or tomentose indumentum (Appendix 4). All species are indistinguishable according to capitula length, number of florets in each capitulum, and achene and pappus features (Table 2; Appendix 4). Based on overlapping morphological characters and nomenclatural priority, we treat them as *S. szowitzii* (see taxonomic treatment below).

Three accessions of *Scorzonera raddeana* in the nrITS analyses show intraspecific variation, which is consistent with morphological variation; length and width of fruiting capitula and width of leaves are variable between individuals; LAC540 and LAC534 were distinct from LAC513 (see taxonomic treatment below). However, all individuals of *S. raddeana* samples in the nrITS tree have the typical *S. raddeana* achene and pappus type (Table 2). *Scorzonera phaeopappa* is resolved as sister to *S. semicana* with high statistical support (Fig. 1). Based on our observations, a combination of the following characters represents the synapomorphy for the *S. phaeopappa* and *S. semicana* subclade: achenes with a swollen carpopodium and five conspicuously long scabrous bristles in the pappus (Table 2; Fig. 2O; Fig. 3Q; Appendix 4). Another strongly supported clade (1 PP, 87 JK, 90 BS) contains *S. mucida* and *S. tunicata* with similar morphological characters (Table 2; Appendix 4). We consider them as separate species based on differences in achene and phyllary characters (see Notes under *S. mucida*). Hatami & al. (2019) recently found that chromosome number and ploidy are also different between these species: tetraploid and $2n = 28$ in *S. mucida* in contrast to diploid and $2n = 14$ in *S. tunicata*. The placement of the diploid *S. tunicata* in a clade with the tetraploid *S. mucida* in the nrITS tree may suggest that *S. tunicata* represents a parent of *S. mucida*. Further studies are required to determine if *S. mucida* is an auto- or allotetraploid. It was not possible to include other species from *S.* subg. *Scorzonera* that have sculptured achenes in our molecular studies because they are rare in Iran, including *S. helodes* Rech. f. and *S. limnophila* Boiss. (*S.* sect. *Dimophopapposae* Lipsch.) and *S. nivalis* Boiss. & Hausskn. (*S.* sect. *Foliosae* (Boiss.) Lipsch.) (Rechinger 1977; Kamelin & Tagaev 1986). It would be beneficial to include these rare *Scorzonera* species that also have sculptured achenes in future studies, in order to explore their relationships with members of *S.* subg. *Pseudopodospermum*.

Taxonomic treatment of *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* in Iran

Habit — Most taxa in *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* are perennial, possessing a taproot or tuberous root with developed lateral roots (Appendix 4). Morphology and placement of tubers are not used here as diagnostic features because they are highly variable within species depending on the ecological conditions. Tubers may be cylindric or spherical and can be deep underground or near to the surface. Some species within *S.* subg. *Podospermum* possess a caudex, which is the persisting woody axis of the (former) rosette shoot (Beentje 2010) that may be branched or unbranched, characterized by densely set leaf scars or leaf remains; it is often dark brown and transversely rough with numerous dry and membranous scales at the apex. With the exception of two species in *S.* subg. *Podospermum*, all species of *S.* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* are perennial herbs with either a caespitose, subcaespitose or caulescent habit (Fig. 4: Fig. 5). In caespitose perennials, the flowering stems arise from radical rosettes and are often scape-like, thus leafless or bearing few reduced leaves or bracts (Fig. 4C, F; Fig. 5A, D, E). Caulescent perennials usually have developed cauline leaves and a branched flowering stem (Fig. 4D; Fig. 5B). Two species (*S. laciniata* and *S. songorica* from *S.* subg. *Podospermum*) are biennial with a thin taproot, typically lacking remains of previously withered leaves.

Leaves — Basal and cauline leaves vary from undivided to deeply pinnatisect among species of *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* (Fig. 4; Fig. 5). Undivided leaves may be linear, lanceolate or ovate and the leaf margin may be flat or undulate (Fig. 5F, G). Pinnatifid leaves are pinnately divided but not all the way down to the rachis, whereas pinnatisect leaves (Fig. 4C, D) are deeply divided reaching the rachis (Allaby 1992). Leaf segments may be linear, oval-lanceolate or orbicular. The leaves can be sessile or with a long petiole-like portion usually with an enlarged base.

Capitula and phyllaries — The length and width of full-flowering and fruiting capitula were examined from herbarium samples. Length of capitulum was measured from the base of the longest innermost phyllary to the apex (Appendix 4). Phyllaries are always herbaceous, usually with a scarious margin; the width of the margin varies depending on the species. Small black spiny appendages occur on the apex of phyllaries only in members of *Scorzonera* subg. *Podospermum* (Fig. 4A).

Achenes — Achenes are sometimes ribbed and the ribbing depth varies ranging from subterete to sulcate. The ribs are either smooth (*Scorzonera* subg. *Podospermum*; Fig. 2A–J) or with tuberculate, lamellate or verrucose sculptures (*S.* subg. *Pseudopodospermum*; Fig. 2M–T).

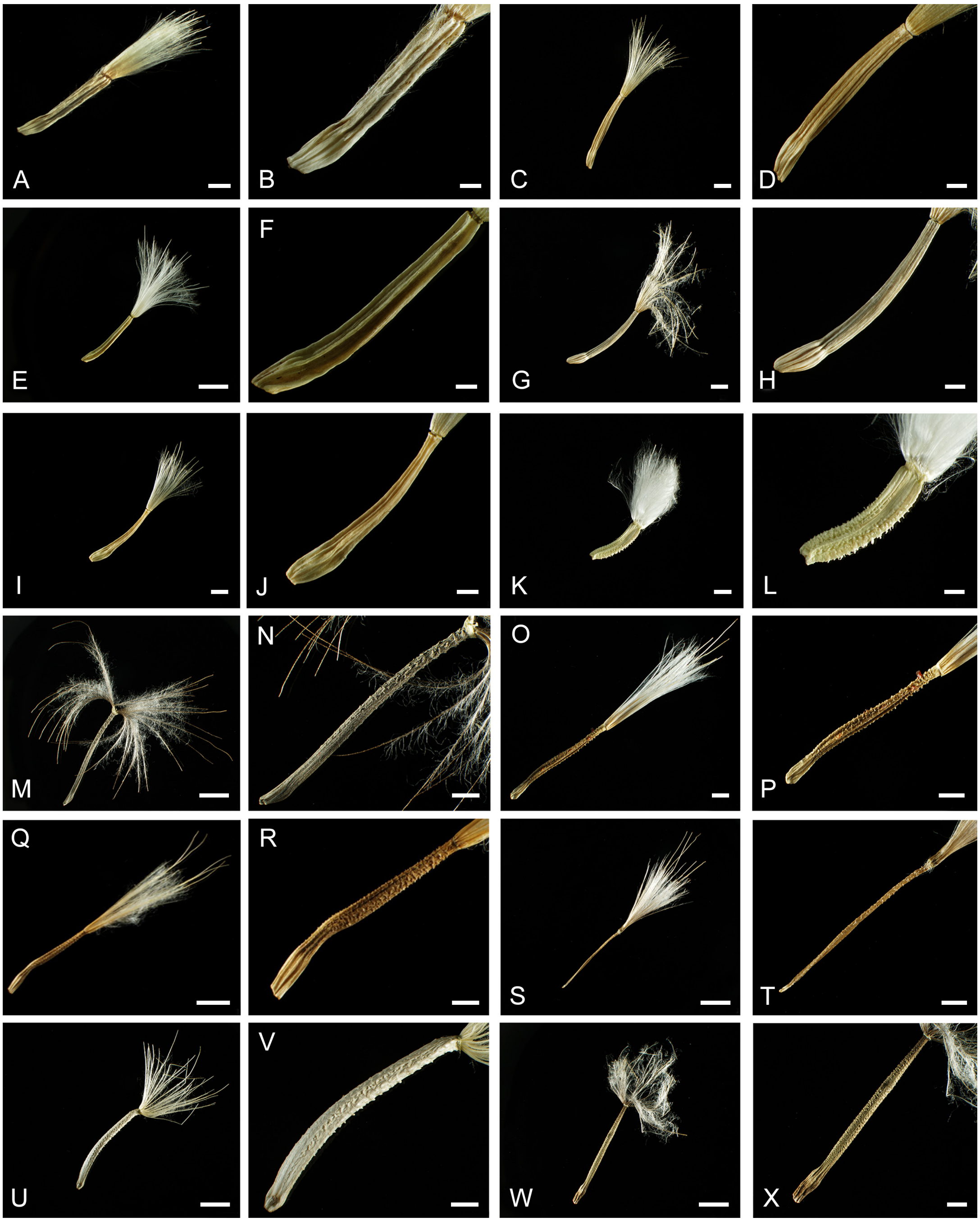

Fig. 3. Macro photographs of achenes of species within *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum*. – Scale bar lengths are given in parentheses after figure letters. – Voucher locality, collection date, collector(s) and number, and herbarium code for each sample are given in parentheses after species names. – **A** (2 mm) and **B** (1 mm): *S. armeniaca* (Iran, Azerbaijan, 36 km from Ahar to Tabriz, alt. 1554 m, 18 Jun 2015, *Mirtadzadini 2239*, MIR). – **C** (2 mm) and **D** (1 mm): *S. grossheimii* (Iran, Gorgan, Almeh, alt. 1500–1800 m, 8–10 Jun 1975, *Rechinger 53108*, B). – **E** (5 mm) and **F** (1 mm): *S. luristanica* (Iran, Kermanshah, between Quriqala and Paweh, 34°57'28.9"N, 46°26'46.5"E, alt. 1246 m, *Mirtadzadini & al. 2213*, MIR). – **G** (2 mm) and **H** (1 mm): *S. meshhedensis* (Iran, Kerman to Bam road, Golbaf, near Abolfazl mosque, 14 Apr 2016, *Samareh 2244*, MIR). – **I** (2 mm) and **J** (1 mm): *S. meyeri* (Iran, Khorassan, SW of Bojnurd, Salook mt., 11 Aug 1994, *Zangooei & al. 24493*, FUMH). – **K** (2 mm) and **L** (1 mm): *S. ovata* (Iran, Baluchistan, NE of Bazman, Siah Band mt. range, 28 Apr 2017, *Mirtadzadini 2322*, MIR). – **M** (5 mm) and **N** (2 mm): *S. mucida* (Iran, Kerman, Deh Bala, *Bordbar 3000*, MIR). – **O** (2 mm) and **P** (2 mm): *S. mollis* subsp. *mollis* (Greece, Kilkis, E of Polykastro 41°00'21"N, 22°38'12"E, 21 Apr 2006, *Willing 153 107*, B). – **Q** (5 mm) and **R** (2 mm): *S. semicana* (Turkey, Mardin, 5 km E of Mardin, 1100 m, 25 May 1957, *Davis & Hedge D.28603*, W). – **S** (2 mm) and **T** (2 mm): *S. szowitzii* (Iran, East Azerbaijan, N of Tabriz, Eynali mountain, 10 Jun 2013, *Ebrahimi 2989*, MIR). – **U** (5 mm) and **V** (2 mm): *S. tunicata* (Iran, Khorassan, 32 km from Birjand to Qa'en, alt. 1991 m, 7 May 2015, *Mirtadzadini 2158*, MIR). – **W** (5 mm) and **X** (2 mm): *S. turkeviczii* (Iran, 7 km NE of Karaj toward Tschalus, after Sarv-e Dar village, 18 May 2016, *Mirtadzadini 2160*, MIR). – Macro photographs produced using a stereomicroscope (Olympus SZX16) equipped with DP72 (a 12.5 megapixel cooled digital colour camera) at the Botanic Garden and Botanical Museum Berlin.

Fig. 4. Photographs of representatives of *Scorzonera* subg. *Podospermum* in the field. For each image the locality and date of the photograph are given, and where applicable voucher data are given (collector and number, herbarium code). – A: black corniculate appendages on phyllaries (see voucher under E); B: swollen carpopodium on achenes (see voucher under D); C: *S. armeniaca*, NW Iran, Tabriz, Varzeqan, 5 Jun 2017; D: *S. persepolitana*, Iran, Esfahan, near Delijan on clay hill, 20 May 2010, *Mirtadzadini* 2218, MIR; E: *S. meshhedensis*, Iran, Kerman, Golbaf, 14 Apr 2016, *Mirtadzadini* 2244, MIR; F: *S. meyeri*, Iran, Zanjan to Abbar, May 2017. – Photographs by M. Mirtadzadini (A, B, D), A. Ebrahimi (C, F; Tehran university, Tehran, Iran), M. Samareh (E; Shahid Bahonar University of Kerman, Kerman, Iran).

Species in *S.* subg. *Pseudopodospermum* always have glabrous achenes, however in *Podospermum* they can be glabrous or hairy (Fig. 2). The achene features are often not fully expressed in the innermost achenes of a capitulum; therefore, we only examine the outermost achenes in this study.

Fig. 5. Photographs of representatives of *Scorzonera* subg. *Pseudopodospermum* in the field. For each image the locality and date of the photograph are given. – A: *S. raddeana*, Iran, Kerman, Sirch, 22 Apr 2015; B: *S. phaeopappa*, Iran, Kordestan, Baneh, May 2019 (B1: habit; B2: inflorescence); C: *S. calyculata*, N Iran, Gilan, Lowshan, May 2016 (C1: habit; C2: inflorescence); D: *S. ovata*, SE Iran, Baluchistan, between Iranshahr and Sarbaz; E: *S. paradoxa*, Iran, Fars, Eqlid, Apr 2007; F: *S. mucida*, Iran, Kerman, Mahan, May 2019 (F1: habit; F2: inflorescence); G: *S. mucida*, Iran, Kerman, Kuhbanan, Jun 2017. – All photographs by M. Mirtadzadini.

Carpopodium — The carpopodium refers to the basal prolongation of the achene wall forming a hollow tube-like sterile foot, which may be swollen or not in comparison to the fertile portion (Mukherjee & Nordenstam 2004). Species within *Scorzonera* subg. *Podospermum* almost always have a conspicuous carpopodium (Fig. 2A–H). In contrast, within *S.* subg. *Pseudopodospermum*, the carpopodium may be absent (e.g. *S. calyculata*

[Fig. 2S, T], *S. ovata*, *S. papposa* [Fig. 2M, N] and *S. paradoxa*), or inconspicuous to conspicuous (Fig. 2O–R; Fig. 3K, L). The size and presence of the carpopodium is important for interspecific delimitation but not informative at intersubgeneric level.

Pappus — Within *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum*, the setaceous pappus is typically persistent, but in two cases (*S. meshhedensis* and *S. songorica*) the bristles can be easily detached (*S. songorica* in Fig. 2J). Pappus bristles are entirely plumose in *S. ovata* (Fig. 3K, L) and *S. papposa* (Fig. 2M), in contrast to pappus bristles that are plumose in the proximal part and naked or scabrous at the distal part for all other species in both subgenera (Table 2; Fig. 2; Fig. 3). The pappus bristles on a single achene can be of equal or unequal lengths. Some species have only five bristles that are conspicuously longer and darker than the others (e.g. *S. phaeopappa*; Fig. 2O).

Key to species of *Scorzonera* subg. *Podospermum* and *S.* subg. *Pseudopodospermum* in Iran

1. Leaves entire (but at least some lobed or pinnately divided in *S. calyculata*); phyllaries without a corniculate projection; achene surface ridged, muricate, tuberculate, verrucose or rugulose, with or without longitudinal ribs . . . . ***S.*** subg. ***Pseudopodospermum***
– Leaves pinnatifid to pinnatisect; phyllaries always with a corniculate projection; achene surface always smooth with longitudinal ribs . . . . . . ***S.*** subg. ***Podospermum***

Scorzonera **subg.** ***Pseudopodospermum***

1. Leaves pinnatifid to pinnatisect, or rarely entire but with at least one leaf lobed; achene surface verrucose . . . . **1. *S. calyculata***
– Leaves all entire; achene surface not verrucose . . . **2**
2. Radical leaves lanceolate or linear; achenes terete, mostly with a hollow swollen carpopodium at base **3**
– Radical leaves elliptic or oblong-elliptic; achenes angulate, always without a hollow swollen carpopodium at base **9**
3. Plants 20–40(–60) cm tall; stems branched up to apex, with well-developed cauline leaves **4**
– Plants (2–)5–15(–20) cm tall, reaching maximum height in fruit; stems mostly branched and leafy only in lower part, sometimes with one or two reduced leaves reaching apex, without well-developed cauline leaves **5**
4. Radical leaves 1.5–2.7(–3) cm wide; outer phyllaries in fruit 1–1.2 cm wide; ligules entirely violet . . . . **2. *S. phaeopappa***
– Radical leaves 0.4–1.2(–2) cm wide; outer phyllaries in fruit 0.4–0.7 cm wide; ligules yellow, sometimes with red or purple stripes . . . . **3. *S. syriaca***
5. Capitula with 9–12 florets, fruiting capitula narrowly cylindric, 0.5–0.6 cm in diam. at base . . . . **4. *S. szowitzii***
– Capitula with 14–24 florets, fruiting capitula broadly cylindric, 0.8–2 cm in diam. at base **6**
6. Achenes with a conspicuously swollen carpopodium; pappus with five bristles that are longer and darker than rest . . . . **5. *S. turkeviczii***
– Achenes with an inconspicuous carpopodium; pappus bristles of more or less equal lengths **7**
7. Flowering stems erect, thickened especially just below fruit; leaves 1–3(–5) mm wide, margin almost flat . . . . **6. *S. raddeana***
– Flowering stems ascending or flexible, not thickened in fruit; leaves 0.4–0.8(–1.2) cm wide, margin undulate **8**
8. Outer phyllaries in fruiting capitula 8–10 mm wide, often with purple scarious margin; achenes creamy white, glabrous . . . . **7. *S. tunicata***
– Outer phyllaries in fruiting capitula 5–7 mm wide, with white scarious margin; achenes almost dark brown, with farinose hairs . . . . **8. *S. mucida***
9. Plant (2–)3–5 cm tall, stems ascending or flexible; leaves green-violet . . . . **9. *S. paradoxa***
– Plant 10–15(–20) cm tall, stems erect; leaves green or yellow-green **10**
10. Florets yellow, sometimes with violet veins . . . . **10. *S. ovata***
– Florets completely violet . . . . **11. *S. papposa***

Scorzonera **subg.** ***Podospermum***

1. Alpine plants, caespitose, always with branched woody caudex; stems 1–8(–10) cm long, rarely with cauline leaves **2**
– Plants of lower and middle altitudinal zones, predominately caulescent, rarely subcaespitose, with or without a branched woody caudex; stems 10–40(–80) cm long, always with cauline leaves **3**
2. Plants cushion-forming; stems 1–3(–4) cm long; phyllaries 8–10 mm long at flowering; achenes 6–7 mm long . . . . **12. *S. radicosa***
– Plants not cushion-forming; stems 5–10(–15) cm long; phyllaries 15–18 mm long at flowering; achenes 9–10 mm long . . . . **13. *S. meyeri***
3. Radical leaves entire to pinnatisect, phyllaries (6–)8–10 cm long at full flowering, pappus easily detachable on touching **4**
– Radical leaves always pinnately divided; phyllaries (10–)12–20 mm long at full flowering; pappus persistent on touching **5**
4. Halophyte, perennial herbs, 5–12 cm high; leaf margin yellow, cartilaginous dentate . . . **14. *S. meshhedensis***
– Hygrophyte, biennial herbs, 15–40 cm high; leaf margin not yellow, entire . . . . **15. *S. songorica***
5. Biennial; fully developed florets less than 1.5 times as long as phyllaries; carpopodium 3–5 mm long, one third to one half of achene length . . . **16. *S. laciniata***

– Perennial; fully developed florets 1.5–2 times as long as phyllaries; carpopodium 2–3 mm long, one fifth to one third of achene length **6**
6. Achenes glabrous **7**
– Achenes hairy **9**
7. Plants 40–80 cm tall; radical leaves 14–22 cm long . . . . **17.** ***S. luristanica***
– Plants 8–25 cm tall; radical leaves 6–12 cm long **8**
8. Carpopodium 3–4 mm long, 3–4 mm wide, about one third of achene length . . . . **18.** ***S. cana***
– Carpopodium <3 mm long, <3 mm wide, about one fourth of achene length . . . . **19.** ***S. grossheimii***
9. Radical leaves mostly pinnatifid, rarely pinnatisect with leaf rachis 4–8 mm wide; outer achenes sulcate, angulate . . . . **20.** ***S. kandavanica***
– Radical leaves always pinnatisect with leaf rachis 1–3 mm wide, outer achenes subterete, not angulate **10**
10. Plants subscapigerous, 10–15 cm tall; outer achenes as long as inner ones, pappus about as long as achenes . . . . **21.** ***S. armeniaca***
– Plants caulescent, 20–45 cm tall; outer achenes shorter and thicker than inner ones, pappus about two times as long as achenes . . . . . . **22.** ***S. persepolitana***

Scorzonera subg. ***Pseudopodospermum*** (Lipsch. & Krasch.) Lipsch. in Komarov, Fl. URSS 29: 48. 1964 ≡ *Scorzonera* sect. *Pseudopodospermum* Lipsch. & Krasch. in Lipschitz, Fragm. Monogr. Scorzonera 1: 70. 1935 ≡ *Pseudopodospermum* (Lipsch. & Krasch.) Kuth., Kavk. Predst. Scorzonerineae: 85. 1978. – Type: *Scorzonera mollis* M. Bieb.

Diagnosis — Members of *Scorzonera* subg. *Pseudopodospermum* can be identified by the following combination of characters: tuberous root, entire leaves (except *S. calyculata* with pinnatifid to pinnatisect leaves), phyllaries without corniculate projections at the apex, and glabrous achenes with their sculptured (muricate, tuberculate, verrucose or denticulate) surfaces even with or without carpopodia. See comparison with *S.* subg. *Podospermum* under the diagnosis for *S.* subg. *Podospermum* below.

1. ***Scorzonera calyculata*** Boiss., Diagn. Pl. Orient., ser. 1, 11: 42. 1849. – Syntypes: Iran, Tehran, in collibus occidentalibus Syach Palas ad radices mt. Damavand, 21 Mar 1843, *Kotschy 341-a* (P00720135 [image!]), *Kotschy 324* (P00720136 [image!]).

Diagnosis — *Scorzonera calyculata* can be distinguished from other species of *S.* subg. *Pseudopodospermum* in Iran based on a combination of the presence of pinnatifid leaves, ligules that are mostly yellow, but the ligule base and entire tube are black-purple (Fig. 5C2), and verrucose achene surfaces without a carpopodium.

Distribution — Armenia, Iran (north, northwest, west, central, south) and Iraq.

Notes — Leaf shape within *Scorzonera calyculata* varies from undivided to pinnatisect in different populations or even in one individual (Fig. 5C). Achenes are sometimes with a swollen part due to insect galls. This species is morphologically similar to the following species, which do not occur in Iran: *S. incisa* DC., *S. lacera* Boiss. & Balansa and *S. violacea* D. F. Chamb. Based on Lipschitz (1935), the floret colour is a diagnostic character to distinguish *S. calyculata*. Individuals with entirely violet florets correspond to *S. incisa*, *S. lacera* and *S. violacea* whereas those with florets that are a combination of yellow and black-purple correspond to *S. calyculata*. The morphological differences between *S. calyculata*, *S. incisa*, *S. lacera* and *S. violacea* were not sufficiently resolved in Lipschitz (1935) and Chamberlain (1975). Further molecular and morphological studies are required to examine the delimitation of these species.

2. ***Scorzonera phaeopappa*** (Boiss.) Boiss., Fl. Orient. 3: 764. 1875 ≡ *Podospermum phaeopappum* Boiss., Diagn. Pl. Orient., ser. 1, 7: 5. 1846. – Syntypes: Turkey, Kurdistan, inter Diarbekir et Mardin, 10 Jun 1841, *Kotschy 237.251* (K000797177 [image!], K000797178 [image!], W0009727!, W0033701!).

Diagnosis — *Scorzonera phaeopappa* can be distinguished by its entirely violet florets based on our observations of live plants and herbarium specimens (Fig. 5B), which is in agreement with previous literature (Boissier 1875; Coşkunçelebı & al. 2015).

Distribution — Iran (northwest, west, central), Iraq, Palestine, Saudi Arabia, Syria and Turkey.

Notes — In contrast with our study, Rechinger (1977) described this species with both yellow florets and entirely violet florets. Therefore, it is possible that individuals with yellow florets, which may be *Scorzonera syriaca* or *S. turkeviczii*, could be erroneously determined as *S. phaeopappa*.

3. ***Scorzonera syriaca*** Boiss. & Blanche, Diagn. Pl. Orient., ser. 2, 3: 93. 1856 ≡ *Scorzonera mollis* var. *longifolia* Boiss., Fl. Orient. 3: 762. 1875. – Holotype: Syria, in rupestribus Libani inter Scanderouna et Jumalie prope Saida, 19 Mar 1953, *C. I. Blanche* (G00780148 [image!]; isotype: W0209864!).

Diagnosis — *Scorzonera syriaca* can be identified by the following combination of characters: branched stems from base to middle, the presence of cauline leaves on the stem up to the apex, yellow florets and achenes with a conspicuous carpopodium.

Distribution — Iran (northwest, west, central, east, south), Iraq, Lebanon, Oman, Palestine, Saudi Arabia, Sinai, Syria and Turkey.

4. ***Scorzonera szowitzii*** DC., Prodr. 7: 117. 1838 ≡ *Scorzonera mollis* subsp. *szowitzii* (DC.) D. F. Chamb. in Notes Roy. Bot. Gard. Edinburgh 33: 433. 1975 ≡ *Pseudopodospermum szowitzii* (DC.) Kuth., Kavk. Predst. *Scorzonerinae*: 92. 1978. – Holotype: Iran, Azerbaijan, in collibus argillosis salsis circa Deliman et Distr. Khoi, 4 May 1828, *Szowitz s.n.* (G00498242 [image!]; isotype: LE01051867 [image!]).

= *Scorzonera mollis* var. *leptophylla* DC., Prodr. 7: 122. 1838, **syn. nov.** ≡ *Scorzonera leptophylla* (DC.) Krasch. & Lipsch. in Lipschitz, Fragm. Monogr. Scorzonera 1: 78. 1935 ≡ *Pseudopodospermum leptophyllum* (DC.) Kuth., Kavk. Predst. *Scorzonerinae*: 88. 1978. – Holotype: Iran, Azerbaijan, Deliman in collibus argillosis, 4 Apr 1828, *Szowitz 48* (LE01053003 [image!]).

= *Scorzonera stenocephala* Boiss., Diagn. Pl. Orient., ser. 1, 7: 6. 1846, **syn. nov.** ≡ *Scorzonera mollis* var. *stenocephala* (Boiss.) Boiss., Fl. Orient. 3: 762. 1875. – Syntypes: Iran, Fars, in alpe Kuh-Delu, 11 Jun 1842, *Kotschy 481* (FI006753 [image!], G00301816 [image!], G00301837 [image!], K000797182 [image!], MO-149527 [image!], W0051305 [image!]).

Description — *Herb* perennial, 3–12 cm tall at flowering, 6–12(–15) cm tall at fruiting. *Root* thickened into tuber, placed in deep part of soil, or near soil surface below root collar; root collar covered with remnants of leaf sheaths. *Stems* scape-like, one to seven (sometimes <10), more or less tomentose, becoming glabrescent, slightly bent, leafy mainly in lower part, sometimes with one to three reduced cauline leaves. *Leaves* narrowly linear, 1–3(–6) mm wide, glaucous or green, pubescent or farinose when young, later becoming glabrous, bent, usually folded lengthwise, less often flat, with plane or undulate margins. *Capitula* narrow cylindric; phyllaries pubescent, becoming glabrescent; outer phyllaries ovate-lanceolate, obtuse, 0.3–0.4 cm wide at flowering, 0.5–0.6 mm wide at fruiting; inner phyllaries linear-lanceolate, usually acuminate, 1.5–1.8 (–2) cm long at flowering, 2.5–3.5(–4) cm long at fruiting, 3–4 times longer than outer phyllaries. *Ligulate florets* yellow with violet stripes. *Achenes* glabrous, narrowly terete, without conspicuous carpopodium, 12–14 mm long, with longitudinal ribs, ribs muricate. *Pappus* 14–20 mm long, white to greyish, bristles of unequal lengths, plumose proximally, scabrous distally.

Diagnosis — *Scorzonera szowitzii* can be distinguished from other species of *S.* subg. *Pseudopodospermum* in Iran based on the narrower cylindric fruiting capitula (0.5–0.6 cm in diam. in *S. szowitzii* compared to 0.8–2.5 cm in others) and fewer florets in flowering capitula (9–12 florets in *S. szowitzii* compared to 14–28 in others).

Distribution — Armenia, Azerbaijan, Iran (north, northeast, northwest, west, southwest, central), Palestine, Syria and Turkey.

Notes — Specimens from different localities across the distribution of *Scorzonera leptophylla*, *S. stenocephala* and *S. szowitzii*, including Armenia, Iran, Palestine, Syria and Turkey, were examined in herbaria and in the field (in Iran). According to *Flora iranica* (Rechinger 1977) and *Flora of Iran* (Safavi 2013), individuals of *S. leptophylla*, *S. stenocephala* and *S. szowitzii* can be differentiated from one another by leaf width, undulate or entire leaf margins and density of hairs of the indumentum. Our field and herbarium observations showed, however, that these characters were very variable, even within the same population, and overlap between species. By comparing the original descriptions of *S. leptophylla*, *S. stenocephala* and *S. szowitzii* (Boissier 1846; Lipschitz 1935), we noted that they also overlap considerably. Lipschitz (1935) also commented on the similarities between *S. leptophylla* and *S. szowitzii*, and he differentiated them by the more undulate leaf margin and the tuber located near the surface for individuals of *S. leptophylla* in contrast to the plane leaf margin and deeper position of the tuber in individuals of *S. szowitzii*. Based on our observations, these characters are in fact very plastic in nature. Therefore, we conclude that *S. leptophylla* and *S. stenocephala* are conspecific with *S. szowitzii* and they are synonymized here. The characters are poorly represented on the holotype of *S. szowitzii* at G (G00498242), but an isotype at LE (LE01051867) shows all relevant characteristics for its delimitation.

5. ***Scorzonera turkeviczii*** Krasch. & Lipsch. in Lipschitz, Fragm. Monogr. Scorzonera 1: 83. 1935 ≡ *Pseudopodospermum turkeviczii* (Krasch. & Lipsch.) Kuth., Kavk. Predst. *Scorzonerinae*: 98. 1978. – Holotype: Turkey, Anatolia boreo-orientalis, Kars. Kagisman, in declivibus argillosis, *Turkevicz 65* (LE01053004 [image!]).

Diagnosis — *Scorzonera turkeviczii* is similar to *S. phaeopappa* in Iran in the presence of a swollen carpopodium on the achenes and a pappus with five conspicuous scabrous bristles, which are longer than the rest (Table 2; Fig. 3W). However, the two species differ according to the width of the fruiting capitula (1.2–1.5 cm in *S. turkeviczii* vs. 1.5–2 cm in *S. phaeopappa*), basal leaf width (0.4–1.2 cm in *S. turkeviczii* vs. 1.5–2.7 cm in *S. phaeopappa*; see Appendix 4) and floret colour (yellow with red or purple stripes in *S. turkeviczii* vs. completely violet in *S. phaeopappa*).

Distribution — Iran (north, northwest, southwest, west), Iraq, Palestine, Russia (northern Caucasus) and Turkey.

Notes — In *Flora of Turkey* (Chamberlain 1975), *Scorzonera turkeviczii* was considered a synonym of *S. semicana*. Chamberlain (1975) considered *S. semicana* an

Irano-Turanian element that varies markedly in the length of stem, width and shape of leaves; its morphological characteristics overlap with those of *S. turkeviczii*. However, in *Flora iranica* (Rechinger 1977) and the *Flora of Iran* (Safavi 2013), only *S. turkeviczii* (not *S. semicana*) was included in the treatment of *Scorzonera*. Therefore, there are inconsistencies between Floras from different countries. More field and herbarium observations, as well as molecular and morphological studies including samples from both species across the distribution range, are needed in order to compare populations of the species from Iran and Turkey and to clarify species delimitations. We did not include *S. semicana* in this study because its occurrence in Iran has not been reported, with the exception of *Flora of Turkey* (Chamberlain 1975).

6. *Scorzonera raddeana* C. Winkl. in Trudy Imp. S.-Peterburgsk. Bot. Sada 11: 150. 1889. – Syntypes: Turcomania, Inter Chodscha Kala et Bami, May 1886, *Radde 402* (LE00050804 [image!], LE00050805 [image!]).

= *Scorzonera turcomanica* Krasch. & Lipsch. in Lipschitz, Fragm. Monogr. Scorzonera 1: 80. 1935. – Holotype: Turcomania, Kopet Dagh mountains, Vannovskoje-Czuly, 18 Apr 1912, *Lipsky s.n.* (LE [image!]).

= *Scorzonera afghana* Rech. f. in Österr. Bot. Z. 97: 264. 1950. – Holotype: Afghanistan, Bandar-e Amir, 30 Jun 1940, *Codrington s.n.* (BM000996291 [image!]).

Diagnosis — *Scorzonera raddeana* is morphologically similar to *S. mucida* and *S. tunicata*. See diagnoses of all three species under *S. mucida* below.

Distribution — Afghanistan, Iran (northeast, east, southeast, central), Pakistan, Tajikistan and Turkmenistan.

Notes — *Scorzonera raddeana* (Fig. 5A) is morphologically very variable (Appendix 4) and we observe geographic structuring of the morphological variation. The populations from eastern Iran are similar to the holotype of this species, which was collected in Turkmenistan to the northeast of Iran. Individuals from the eastern range of *S. raddeana* have linear basal leaves 1–3(–5) mm wide with a bent apex and an entire margin, few or no cauline leaves, and fruiting capitula 2–2.5 cm long and 1.5–2 cm wide. In contrast, individuals in southwestern and central Iran have wider leaves (5–8 mm wide) and wider and longer fruiting capitula (3.5–4[–4.5] cm long and 2.5–3[–4] cm wide) compared to individuals in the eastern populations. However, individuals across the distribution of this species are similar in achene and pappus features, they all have yellow florets with violet or red stripes, muricate achenes without a conspicuous swollen carpopodium, and a pappus with bristles of unequal lengths; see further discussion under *S. mucida* below (Appendix 4; Table 2; Fig. 2Q, R).

7. *Scorzonera tunicata* Rech. f. & Köie in Biol. Skr. 8(2): 196. 1955. – Holotype: Afghanistan, Farah-Shin Dand, Jija, 1200 m, 12 Apr 1949, *Köie 3710* (W19560000506!; isotype: W19560003033 [image!]).

Diagnosis — *Scorzonera tunicata* is morphologically similar to *S. mucida* and *S. raddeana*. See diagnoses of all three species under *S. mucida* below.

Distribution — Afghanistan, Iran (east, northeast, southeast) and Pakistan.

Notes — Based on our morphological observations, the height of the holotype of *Scorzonera tunicata* (c. 20 cm tall) is not typical compared to that of most individuals of this species, which are typically 5–10 cm tall and rarely reach 20 cm tall, in accordance with Rechinger (1977) (Appendix 4).

8. *Scorzonera mucida* Rech. f. & al. in Österr. Bot. Z. 97: 264. 1950 ≡ *Scorzonera mollis* var. *mucida* (Rech. f. & al.) Parsa, Fl. Iran 10: 187. 1980. – Holotype: Iran, Kerman, Inter Kerman et Saidabad (Sirdjan), Inter Mashiz, 2000 m, et jugum Khan-e Sorck, 2580 m, 27 Apr 1948, *Rechinger 3052-a* (W0004704!).

Diagnosis — *Scorzonera mucida* (Fig. 5F, G) is morphologically very similar to *S. tunicata*, but individuals of the two species can be distinguished from each other by the width of the outer phyllaries (5–7 mm in *S. mucida* vs. 8–10 mm in *S. tunicata*; Appendix 4), colour of the phyllary margins (white or pale in *S. mucida* vs. purple in *S. tunicata*) and colour and indumentum of the achenes (grey with farinose hairs in *S. mucida* vs. light cream and glabrous in *S. tunicata*; see images of achenes in Fig. 3M, N for *S. mucida* and Fig. 3U, V for *S. tunicata*). *Scorzonera mucida* is also morphologically similar to *S. raddeana*, but *S. mucida* possesses achenes with a white ring between the pappus and the fertile part that is not present in *S. raddeana* (see images in Fig. 2R vs. Fig. 3N for *S. raddeana* and *S. mucida*, respectively). In *S. raddeana*, the stems are erect and thickened in the fruiting stage whereas in *S. mucida* and *S. tunicata* they are procumbent to ascending and not thickened.

Distribution — Iran (west, central, northeast, southeast).

Notes — *Scorzonera mucida* is endemic to Iran, where its geographical distribution overlaps with Iranian populations of the more widespread species *S. raddeana* and *S. tunicata* (see above).

9. *Scorzonera paradoxa* Fisch. & C. A. Mey. ex DC., Prodr. 7: 119. 1838. – Lectotype (designated by Rechinger 1977: 62): Iran, Azerbaijan, Ad lacum Urmia, *Szowitz s.n.* (G).

Diagnosis — *Scorzonera paradoxa* (Fig. 5E) is morphologically very similar to *S. ovata*; see under diagnosis for *S. ovata* below.

Distribution — Afghanistan, Iran (northeast, east, southeast, central, south) and Pakistan.

10. *Scorzonera ovata* Trautv. in Trudy Imp. S.-Petersburgsk. Bot. Sada 1: 275. 1872. – Syntypes: Turkmenistan, near Krasnowodsk, 20 May 1870, *Maloma s.n.* (LE00050806 [image!], LE00050807 [image!]).

Diagnosis — *Scorzonera ovata* (Fig. 5D) is similar to *S. paradoxa* in having yellow florets with red stripes, but differs from the latter in having 10–20(–30) cm long branched flowering stems and green or green-yellow leaves compared to (2–)5–8 cm long simple flowering stems and violet-green leaves in *S. paradoxa*.

Distribution — Afghanistan, Iran (northeast, east), Kyrgyzstan, Tajikistan, Turkmenistan and Uzbekistan.

11. *Scorzonera papposa* DC., Prodr. 7: 119. 1838. – Holotype: Turkey, Gazi Antep, Antab, 1837, *Aucher-Eloy 3316* (G00498266 [image!]).

= *Scorzonera kurdica* Boiss. & Noë in Boissier, Diagn. Pl. Orient., ser. 2, 3: 93. 1856. – Type: Iraq, in subalpinis Persiae in Kurdistania prope Mendeli, *Noë s.n.* (not traced).

Diagnosis — *Scorzonera papposa* differs from *S. ovata* in floret colour (florets entirely violet in *S. papposa* vs. entirely yellow or sometimes yellow with red stripes in *S. ovata*) and pappus characters (pappus with five conspicuous scabrous bristles longer than the rest in *S. papposa* vs. without five conspicuously longer bristles in *S. ovata*; Fig. 2M vs. Fig. 3K, L, respectively). Furthermore, they have different geographic distributions in Iran: *S. papposa* is distributed in western Iran, whereas *S. ovata* is known only from eastern Iran.

Distribution — Iran (northwest, west, southwest, central), Iraq, Palestine, Saudi Arabia, Sinai, Syria and Turkey.

Notes — We could not locate a type specimen of *Scorzonera kurdica* for this study, and we therefore follow Rechinger (1977) in treating it as a heterotypic synonym of *S. papposa*.

Scorzonera subg. ***Podospermum*** (DC.) Lipsch., Fragm. Monogr. Scorzonera 1: 7. 1935 ≡ *Podospermum* DC. in Lamarck & Candolle, Fl. Franç., ed. 3, 4: 61. 1805 ≡ *Scorzonera* sect. *Podospermum* (DC.) Benth. & Hook. f., Gen. Pl. 2: 532. 1873. – Type: *Scorzonera laciniata* L.

Diagnosis — Members of *Scorzonera* subg. *Podospermum* can be distinguished from *S.* subg. *Pseudopodospermum* by a combination of characters. Species of *S.* subg. *Podospermum* have pinnatifid leaves, phyllaries with corniculate projections at the apex (Fig. 4A) and glabrous or sparsely lanate achenes with smooth surfaces and conspicuous carpopodia. In contrast, species of *S.* subg. *Pseudopodospermum* do not possess pinnatifid leaves (with the exception of *S. calyculata*), the phyllaries do not have corniculate projections at the apex, and thr achenes are always glabrous with sculptured surfaces, which may be with or without conspicuous carpopodia.

12. *Scorzonera radicosa* Boiss., Diagn. Pl. Orient., ser. 1, 11: 43. 1849 ≡ *Scorzonera cana* var. *radicosa* (Boiss.) D. F. Chamb. in Notes Roy. Bot. Gard. Edinburgh 33: 433. 1975. – Syntypes: Iran, Mazandaran, in glareosis alpium Hasartschal in partibus occidentalibus montis Elbours, 3000 m, 12 Aug 1843, *Kotschy 492* (FI006751 [image!], G00418597 [image!], G00418598 [image!], G00780179 [image!], K000797190 [image!], MO-149526 [image!], P00720073 [image!], P00720074 [image!], US00119832 [image!], W0009728!).

Diagnosis — *Scorzonera radicosa* can be distinguished from other species in *Scorzonera* subg. *Podospermum* by being an alpine cushion-forming perennial, growing at high altitudes (>2500 m), with a branched thickened woody caudex. It has scapose flowering stems up to 3 cm long with only basal simple to pinnatisect leaves.

Distribution — Iran (north, northwest, central, northeast), Iraq and Turkey.

13. *Scorzonera meyeri* (K. Koch) Lipsch. in Karjagin, Fl. Azerbaijan 8: 518. 1961 ≡ *Podospermum meyeri* K. Koch in Linnaea 23: 659. 1851 ≡ *Podospermum canum* var. *glabratum* DC., Prodr. 7: 111. 1838. – Syntypes: ad Guriel Persiae, *Szowitz s.n.* (G00473936 [image!], LE01053014 [image!]); in regione alpine Caucasi, 1832, *Meyer s.n.* (G00473935 [image!]).

Diagnosis — *Scorzonera meyeri* (Fig. 4F) is a perennial species of mountainous regions (2000–3000 m). It has a branched caudex, which is covered with remnants of old basal leaves, and scapose flowering stems (5–20 cm long) with basal and cauline simple to pinnatisect leaves. It can be distinguished from *S. radicosa* by not having the cushion form characteristic of that species.

Distribution — Armenia, Azerbaijan, Georgia, Iran (north, northwest, northeast, central), Russia (northern Caucasus) and Turkey.

14. *Scorzonera meshhedensis* (Rech. f.) Rech. f., Fl. Iran. 122: 25. 1977 ≡ *Podospermum meshhedense* Rech. f. in Ann. Naturhist. Mus. Wien 55: 289. 1944. – Holotype: Iran, Khorassan, inter Mashhad et Torbat-e

Heydariyeh, in salsis l.d. Sahahtari, 10–11 Jul 1937, *Rechinger 1504* (W0011955!; isotype: US00119831 [image!]).

Diagnosis — *Scorzonera meshhedensis* is morphologically similar to *S. songorica*; see the diagnosis under *S. songorica* for a comparison of these two species.

Distribution — Afghanistan and Iran (northwest, northeast, east, west, central).

15. *Scorzonera songorica* (Kar. & Kir.) Lipsch. & Vassilcz. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 22: 301. 1963 ≡ *Podospermum laciniatum* var. *songoricum* Kar. & Kir. in Bull. Soc. Imp. Naturalistes Moscou 15: 396. 1842 ≡ *Podospermum songoricum* (Kar. & Kir.) Tzvelev, Rast. Tsentral. Azii 14b: 104. 2008. – Syntypes: in arenosis Songariae ad fluv. Lepsa circa radicem M. Alatau, 1841, *Karelin & Kirilov 1672* (G390183 [image!], G390223 [image!], LE00050800 [image!], LE00050801 [image!], LE00050802 [image!], LE00050803 [image!]).

Diagnosis — *Scorzonera songorica* (Fig. 4E) is morphologically close to *S. meshhedensis* but a number of characters can be used to distinguish them. *Scorzonera meshhedensis* is perennial with a plant height of 5–10 cm and leaf margins cartilaginous dentate; in contrast, *S. songorica* is biennial with a plant height of 15–40 cm and leaf margins not cartilaginous dentate. *Scorzonera songorica* is hygrophytic, often growing in disturbed areas of fields and gardens, whereas *S. meshhedensis* is halophytic.

Distribution — Afghanistan, Iran (northeast, southeast, east, central), Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan and Uzbekistan.

16. *Scorzonera laciniata* L., Sp. Pl. 2: 791. 1753 ≡ *Podospermum laciniatum* (L.) DC. in Lamarck & Candolle, Fl. Franç., ed. 3, 4: 62. 1805. – Lectotype (designated by Alavi 1983: 363): Herb. Linn. No. 947.8 (LINN [image!]).

Diagnosis — *Scorzonera laciniata* is similar to *S. songorica*, but it can be distinguished from the latter species by leaf and pappus characters. In individuals of *S. laciniata*, all leaves are pinnatifid, in contrast to individuals of *S. songorica*, which can have both pinnatifid and simple leaves. The pappus of *S. songorica* can be easily detached by touch but is persistent in *S. laciniata*.

Distribution — Widespread in Africa, Asia and Europe (Kilian & al. 2009+).

17. *Scorzonera luristanica* Rech. f. in Anz. Österr. Akad. Wiss., Math.-Naturwiss. Kl. 88: 266. 1951 ≡ *Scorzonera laciniata* var. *luristanica* (Rech. f.) Parsa, Fl. Iran 10: 184. 1980. – Holotype: Iran, Luristan, Durud, 1670 m, 21 May 1940, *Köelz 15621* (W0003543!; isotype: US00119831 [image!]).

Diagnosis — *Scorzonera luristanica* is morphologically similar to *S. laciniata*, but they differ from each other in the following morphological characters: *S. luristanica* is perennial with a branched caudex, the outer achenes are sulcate and the length of the carpopodium is one fifth to one fourth of the achene length. In contrast, *S. laciniata* is biennial without a branched caudex, the outer achenes are subterete and the length of carpopodium is one third to half of the achene length (Fig. 3E, F; Appendix 4).

Distribution — Iran (northwest, west, southwest) and Iraq.

18. *Scorzonera cana* (C. A. Mey.) O. Hoffm. in Engler & Prantl, Nat. Pflanzenfam. IV(5): 365. 1893 ≡ *Podospermum canum* C. A. Mey., Verz. Pfl. Casp. Meer.: 62. 1831. – Syntypes: Azerbaijan, in collibus prope Baku, *Meyer s.n.* (LE01042946 [image!], LE01042947 [image!]).

Diagnosis — *Scorzonera cana* is morphologically similar to *S. grossheimii*; see the diagnosis under *S. grossheimii* for a comparison of these two species.

Distribution — Armenia, Azerbaijan, Cyprus, Georgia, Iran (northwest, west, central), Iraq, Palestine, Russia (northern Caucasus), Syria, Turkey and widespread in Europe (Kilian & al. 2009+).

Notes — *Scorzonera cana* is a perennial species with high morphological variation within and between populations, in particular in plant height (8–25 cm) and indumentum (canescent to glabrous). Individuals of this species can be distinguished from *S. meyeri* based on the capitula length (10–15 mm in *S. cana* vs. 15–18 mm in *S. meyeri*; Appendix 4).

19. *Scorzonera grossheimii* Lipsch. & Vassilcz. in Komarov, Fl. URSS 29: 718. 1964 ≡ *Podospermum grossheimii* (Lipsch. & Vassilcz.) Kuth., Kavk. Predst. *Scorzonerinae*: 117. 1978. – Holotype: Azerbaijan, Talish, in declivibus glareosis montis Sibirdu, 9 Jul 1931, *N. Schipzinsky 733* (LE01053017 [image!]).

Diagnosis — *Scorzonera grossheimii* is a perennial species that is morphologically similar to *S. cana*. However, these two species can be distinguished based on their carpopodium (<3 mm long, one fifth to one fourth of achene length in *S. grossheimii* vs. 3–4 mm long, about one third of achene length in *S. cana*; Fig. 3C, D vs. Fig. 2A, B) and leaves (both simple and pinnatisect in *S. grossheimii* vs. only pinnatisect in *S. cana*; Appendix 4).

Distribution — Azerbaijan and Iran (northwest, west, central).

20. ***Scorzonera kandavanica*** Rech. f., Fl. Iran. 122: 30. 1977. – Holoype: Iran, Mazandaran, in declivibus borealibus jugi Kandavan, 2400 m, 21 Jun 1974, *Rechinger 48310* (W0001082!; isotypes: B-10-0097174!, E00385284 [image!], G00301821 [image!], GZU000272963 [image!], K000797262 [image!], M0030724 [image!], MA496672 [image!], MO-277012 [image!]).

Diagnosis — *Scorzonera kandavanica* is morphologically similar to *S. armeniaca* and *S. persepolitana*; see the diagnosis under *S. persepolitana* for the distinguishing characters of these three species.

Distribution — Iran (north, northwest).

Notes — Different populations of this species vary in lamina indumentum from densely tomentose to glabrous.

21. ***Scorzonera armeniaca*** (Boiss. & A. Huet) Boiss., Fl. Orient. 3: 760. 1875 ≡ *Podospermum armeniacum* Boiss. & A. Huet in Boissier, Diagn. Pl. Orient., ser. 2, 3: 92. 1856. – Holotype: Armenia, prope Kochaponar, inter Baibout et Erzeroum, May 1853, *Pavillon s.n.* (G00418595 [image!]; isotypes: K000797186 [image!], P00720133 [image!]).

Diagnosis — *Scorzonera armeniaca* (Fig. 4C) is a subscapigerous perennial species with a branched or undivided caudex. It is similar to *S. cana* and *S. meyeri* in vegetative characters, but *S. armeniaca* has lanate achenes, whereas *S. cana* and *S. meyeri* have glabrous achenes (Table 2). *Scorzonera armeniaca* is also similar to *S. kandavanica* and *S. persepolitana*; see under *S. persepolitana* for a comparison.

Distribution — Iran (north, northwest), Armenia, Azerbaijan and Turkey.

22. ***Scorzonera persepolitana*** Boiss., Fl. Orient. 3: 760. 1875 ≡ *Podospermum eriospermum* Boiss., Diagn. Pl. Orient., ser. 1, 7: 5. 1846 [non *Scorzonera eriosperma* Gouan, Ill. Observ. Bot.: 52. 1773]. – Syntypes: Iran, in rupestribus et in arenosis apricis pr. Ruinas u. Persepolis, 21 Apr 1842, *Kotschy 275* (G00390186, G00390187, G00780184, JE00012061!, K000797187 [image!], K000797188 [image!], K000797189 [image!], L.3671120 [image!], W29556!, W29557!, WAG0004210 [image!], WAG0004211 [image!]).

= *Podospermum canum* var. *murdabadense* Rech. f. in Ann. Naturhist. Mus. Wien 55: 289. 1944. – Holotype: Iran, montes Elburz, in ditione oppidi Keredj, in montibus Helkedar ad Mardabad, 1300 m, 15 Jun 1937, *Rechinger 1054* (W0011943!).

Diagnosis — *Scorzonera persepolitana* (Fig. 4D), *S. armeniaca* and *S. kandavanica* are morphologically similar in possessing lanate achenes (Fig. 2G, H). *Scorzonera armeniaca* can, however be distinguished from those species because the inner and outer achenes have similar lengths and widths. In contrast, in *S. kandavanica* and *S. persepolitana*, the inner achenes are thinner and longer than the outer achenes (see key above and measurements in Appendix 4). *Scorzonera kandavanica* and *S. persepolitana* can be distinguished based on the width of the mid-rachis on the leaves, which is wider in *S. kandavanica* (4–9 mm) compared to *S. persepolitana* (1–3 mm) (Appendix 4). Furthermore, based on our morphological observations, *S. persepolitana* leaves have an accumulation of white lanate hairs at the apex of the segments; this character was not present in any individuals of *S. kandavanica* examined in this study.

Scorzonera persepolitana is also similar to *S. luristanica*, but differs in the presence of lanate achenes in contrast to glabrous achenes in *S. luristanica*. *Scorzonera luristanica* does not have the accumulation of white lanate hairs at the apex of the leaf segments that is characteristic of *S. persepolitana*. *Scorzonera persepolitana* varies in the width of the lateral segments of the pinnatisect leaves (1–5 mm) and the glabrous to tomentose indumentum of the plants.

Distribution — Iran (west, southwest, central).

Acknowledgements

This paper is part of the PhD thesis of Elham Hatami; funding for lab work and nrITS sequencing was supported by the Iranian National Science Foundation (INSF). We are grateful to the herbarium curators and staff at B, FMUH, HSHU, IRAN, JE and W. Visits to the herbaria JE and W were supported by the Research Group *Asterales* (BGBM). We are grateful to Fereshteh Alifarsangi, Dúban Canal, Targol Chatrenoori, Julia Dietrich, Atefeh Ebrahimi and Nana Silakadze for their help during this study. We also thank Evgeny V. Mavrodiev (Florida Museum of Natural History) and an anonymous reviewer for their comments on an earlier version of this paper. Special thanks are due to Norbert Kilian (Research Group *Asterales*; BGBM) for valuable comments and suggestions to improve the manuscript and his general support during this study.

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Appendices

See the Supplemental Content in the online edition at https://doi.org/10.3372/wi.50.50105

Appendix 1

Taxon sampling and GenBank accession numbers of examined specimens included in nuclear ribosomal Internal Transcribed Spacer phylogeny of the present study. Data are arranged in the following order: taxon name in bold (in alphabetical order); voucher data (country, locality, collecting date, collector[s], collecting number, herbarium code, accession number).

Appendix 2

Selected specimens examined for taxa in the taxonomic treatment of this study. For each specimen, we provide the following voucher information: country, locality, collecting date, collector(s), collecting number, herbarium code.

Appendix 3

Alignment of sequences of the nuclear ribosomal Internal Transcribed Spacer (nrITS) region analysed in this study (phyDE format).

Appendix 4

Summary of morphological features of all taxa in this study. The following characters are included: life cycle, plant height, root, stem, leaves, flowering capitula, fruiting capitula, achenes, pappus. Terminology of vegetative and reproductive traits is according to Allaby (1992) and Beentje (2010).

Willdenowia
Open-access online edition bioone.org/journals/willdenowia
Online ISSN 1868-6397 · Print ISSN 0511-9618 · 2018 Journal Impact Factor 1.156
Published by the Botanic Garden and Botanical Museum Berlin, Freie Universität Berlin