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

Introduction

*Scorzonera* L. (*Asteraceae, Cichorieae, Scorzonerae*) 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. 2009a). In its widest circumscription, *Scorzonera* is characterized by simple or pinnatifid leaves, multisieriate 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 *Scorzonerae* are readily distinguished from *Scorzonera* in its widest sense: *Tragopogon* L., the only other large genus of the subtribe (c. 150 species), by its uninseriate involucre; *Koelpinia* Pall. by its scorpoid achenes without a pappus but with hooked pro-
ectations: 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 Cass. by its pappus laterally situated at the achene apex; and the monotypic Pterachaeция 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 Taktajaniantha 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; Tzevelk 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; Coskuncelebi & 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 Coskuncelebi & al. (2016) confirmed that achene surface patterns are valuable for distinguishing between S. subg. Pseudopodospermum and S. subg. Podospermum (Coskuncelebi & 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 Scorzonerae. 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 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.; Pterachaeция (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. & Köe 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 Coskuncelebi & 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
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 & 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 Scorzonerinae 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 Scorzonerinae 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 Scorzonerinae 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 Scorzonerinae 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 Scorzonerinae 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). Scorzonerinae 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 Scorzonerinae 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 (Ambiclon, 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 (Swoford 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).

<table>
<thead>
<tr>
<th>Species included in this study</th>
<th>Treatment based on previous literature</th>
<th>Clade name according to the phylogeny in this study (if sampled; Fig. 1)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. hirsuta</em> (Gouan) L.</td>
<td>S. subg. <em>Scorzonera</em> (Lip, Saf, KT); Lasiospora clade (Mav); genus Gelasia (Za)</td>
<td>Lasiospora clade**</td>
</tr>
<tr>
<td><em>S. cinerea</em> Boiss.</td>
<td>S. subg. <em>Scorzonera</em> (Lip, Rech, KT, Saf); genus Gelasia (Za)</td>
<td>Lasiospora clade**</td>
</tr>
<tr>
<td><em>S. litwinowii</em> Krasch. &amp; Lipsch.</td>
<td>S. subg. <em>Scorzonera</em> (Lip, Rech, KT, Saf); Lasiospora clade (Mav); genus Gelasia (Za)</td>
<td>Lasiospora clade**</td>
</tr>
<tr>
<td><em>S. pseudolanata</em> Grossh.</td>
<td>S. subg. <em>Scorzonera</em> (Rech, KT); genus Gelasia (Za)</td>
<td>Lasiospora clade**</td>
</tr>
<tr>
<td><em>S. rigida</em> Aucher ex DC.</td>
<td>S. subg. <em>Scorzonera</em> (Rech, KT, Saf); Lasiospora clade (Mav); genus Gelasia (Za)</td>
<td>Lasiospora clade**</td>
</tr>
<tr>
<td><em>S. seidlitzii</em> Boiss.</td>
<td>S. subg. <em>Scorzonera</em> (Lip, Rech, KT, Saf); Lasiospora clade (Mav); genus Gelasia (Za)</td>
<td>Lasiospora clade**</td>
</tr>
<tr>
<td><em>S. aristata</em> Ramond ex DC.</td>
<td>S. subg. <em>Scorzonera</em> (KT); <em>Scorzonera</em> s. str. Clade (Za)</td>
<td>S. humilis clade**</td>
</tr>
<tr>
<td><em>S. humilis</em> L.</td>
<td>S. subg. <em>Scorzonera</em> (Lip, KT, Saf); <em>Scorzonera</em> s.str. Clade (Za)</td>
<td>S. humilis clade**</td>
</tr>
<tr>
<td><em>S. intricata</em> Boiss.</td>
<td>S. subg. <em>Scorzonera</em> (Lip, Rech, KT, Saf); Lasiospora clade (Mav); genus Gelasia (Za)</td>
<td>S. intricata clade**</td>
</tr>
<tr>
<td><em>S. tortuosissima</em> Boiss.</td>
<td>S. subg. <em>Scorzonera</em> (Lip, Rech, KT, Saf); Lasiospora clade (Mav); genus Gelasia (Za)</td>
<td>S. intricata clade**</td>
</tr>
<tr>
<td><em>S. purpurea</em> L.</td>
<td>S. subg. <em>Scorzonera</em> (Lip, Saf); S. subg. <em>Podospermum</em> (KT); <em>Scorzonera</em> purpurea clade (Za)</td>
<td>S. purpurea, sister to S. subg. <em>Podospermum</em></td>
</tr>
<tr>
<td><em>S. armeniaca</em> (Boiss. &amp; A. Huet) Boiss.</td>
<td>S. subg. <em>Podospermum</em> (Rech, KT); genus <em>Podospermum</em> (Mav); <em>Podospermum</em> clade (Za)</td>
<td>S. cana clade / S. subg. <em>Podospermum</em></td>
</tr>
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<td><em>S. cana</em> (C. A. Mey.) O. Hoffm.</td>
<td>S. subg. <em>Podospermum</em> (Rech, KT); genus <em>Podospermum</em> (Mav); <em>Podospermum</em> clade (Za)</td>
<td>S. cana clade / S. subg. <em>Podospermum</em></td>
</tr>
<tr>
<td><em>S. grossheimii</em> Lipsch. &amp; Vassilcz.</td>
<td>S. subg. <em>Podospermum</em> (Rech, KT); <em>Podospermum</em> clade (Za)</td>
<td>S. cana clade / S. subg. <em>Podospermum</em></td>
</tr>
<tr>
<td><em>S. luristanica</em> Rech. f.</td>
<td>S. subg. <em>Podospermum</em> (Rech, KT); <em>Podospermum</em> clade (Za)</td>
<td>S. cana clade / S. subg. <em>Podospermum</em></td>
</tr>
<tr>
<td><em>S. meyeri</em> (K. Koch) Lipsch.</td>
<td>S. subg. <em>Podospermum</em> (Rech, KT); genus <em>Podospermum</em> (Mav); <em>Podospermum</em> clade (Za)</td>
<td>S. cana clade / S. subg. <em>Podospermum</em></td>
</tr>
</tbody>
</table>

* 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. pseudolanata Grossh. S. subg. *Podospermum* (Rech, KT); Lasiospora clade (Mav); genus Gelasia (Za) Lasiospora clade**
S. rigida Aucher ex DC. S. subg. *Scorzonera* (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, KT, Saf); Lasiospora clade (Mav); genus Gelasia (Za) S. intricata clade**
S. tortuosissima Boiss. S. subg. *Scorzonera* (Lip, Rech, KT, Saf); Lasiospora clade (Mav); genus Gelasia (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*
<table>
<thead>
<tr>
<th>Species</th>
<th>Subgroup(s) and Clade(s)</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. radicosa</em> Boiss.</td>
<td><em>S. subg. Podospermum</em> (Rech, KT); <em>Podospermum</em> clade (Za)</td>
<td><em>S. cana</em> clade / <em>S. subg. Podospermum</em></td>
</tr>
<tr>
<td><em>S. laciniata</em> L.</td>
<td><em>S. subg. Podospermum</em> (Rech, KT); <em>Podospermum</em> clade (Mav); <em>Podospermum</em> clade (Za)</td>
<td>three samples unresolved within <em>S. subg. Podospermum</em></td>
</tr>
<tr>
<td><em>S. meshhedensis</em> (Rech. f.) Rech. f.</td>
<td><em>S. subg. Podospermum</em> (Rech, KT); <em>Podospermum</em> clade (Za)</td>
<td><em>S. songorica</em> clade / <em>S. subg. Podospermum</em></td>
</tr>
<tr>
<td><em>S. songorica</em> (Kar. &amp; Kir.) Lipsch. &amp; Vassilcz.</td>
<td><em>S. subg. Podospermum</em> (Rech, KT); <em>Podospermum</em> clade (Za)</td>
<td><em>S. songorica</em> clade / <em>S. subg. Podospermum</em></td>
</tr>
<tr>
<td><em>S. mollis</em> M. Bieb. subsp. mollis</td>
<td><em>S. subg. Pseudopodospermum</em> (Lip, Saf); <em>genus Pseudopodospermum</em> (Za)</td>
<td><em>S. mollis</em> clade / <em>S. subg. Pseudopodospermum</em></td>
</tr>
<tr>
<td><em>S. mucida</em> Rech. f. &amp; al.</td>
<td><em>S. subg. Pseudopodospermum</em> (Rech); <em>S. subg. Podospermum</em> (KT); <em>genus Pseudopodospermum</em> (Za)</td>
<td><em>S. mollis</em> clade / <em>S. subg. Pseudopodospermum</em></td>
</tr>
<tr>
<td><em>S. phaeopappa</em> (Boiss.) Boiss.</td>
<td><em>S. subg. Pseudopodospermum</em> (Lip, Rech, Saf); <em>genus Pseudopodospermum</em> (Za)</td>
<td><em>S. mollis</em> clade / <em>S. subg. Pseudopodospermum</em></td>
</tr>
<tr>
<td><em>S. raddeana</em> C. Winkl.</td>
<td><em>S. subg. Pseudopodospermum</em> (Lip, Rech, Saf); <em>S. subg. Podospermum</em> (KT); <em>genus Scorzonera</em> (Mav); <em>Scorzonera</em> (Za)</td>
<td><em>S. mollis</em> clade / <em>S. subg. Pseudopodospermum</em></td>
</tr>
<tr>
<td><em>S. semicana</em> DC.</td>
<td><em>S. subg. Pseudopodospermum</em> (Lip, Saf); <em>S. subg. Podospermum</em> (KT)</td>
<td><em>S. mollis</em> clade / <em>S. subg. Pseudopodospermum</em></td>
</tr>
<tr>
<td><em>S. stenocephala</em> Boiss.</td>
<td><em>S. subg. Pseudopodospermum</em> (Rech, KT)</td>
<td><em>S. mollis</em> clade / <em>S. subg. Pseudopodospermum</em></td>
</tr>
<tr>
<td><em>S. szovitzii</em> DC.</td>
<td><em>S. subg. Pseudopodospermum</em> (Lip, Rech, Saf)</td>
<td><em>S. mollis</em> clade / <em>S. subg. Pseudopodospermum</em></td>
</tr>
<tr>
<td><em>S. tunicata</em> Rech. f. &amp; Köie</td>
<td><em>S. subg. Pseudopodospermum</em> (Rech); <em>S. subg. Podospermum</em> (KT)</td>
<td><em>S. mollis</em> clade / <em>S. subg. Pseudopodospermum</em></td>
</tr>
<tr>
<td><em>S. papposa</em> DC.</td>
<td><em>S. subg. Scorzonera</em> (Lip, Rech, KT, Mar, Saf); <em>genus Pseudopodospermum</em> (Za)</td>
<td><em>S. papposa</em> / <em>S. subg. Pseudopodospermum</em></td>
</tr>
<tr>
<td><em>S. calyculata</em> Boiss.</td>
<td><em>S. subg. Scorzonera</em> (Rech, Lip, Mar, Saf); <em>S. subg. Podospermum</em> (KT); <em>genus Pseudopodospermum</em> (Za)</td>
<td><em>S. calyculata</em> / <em>S. subg. Pseudopodospermum</em></td>
</tr>
<tr>
<td><em>S. ovata</em> Trautv.</td>
<td><em>S. subg. Scorzonera</em> (Lip, Rech, KT, Saf)</td>
<td>not in phylogeny / <em>S. subg. Pseudopodospermum</em></td>
</tr>
<tr>
<td><em>S. paradoxa</em> Fisch. &amp; C. A. Mey. ex DC.</td>
<td><em>S. subg. Scorzonera</em> (Rech, KT)</td>
<td>not in phylogeny / <em>S. subg. Pseudopodospermum</em></td>
</tr>
<tr>
<td><em>S. syriaca</em> Boiss. &amp; Blanche</td>
<td><em>S. subg. Pseudopodospermum</em> (Rech); <em>S. subg. Podospermum</em> (KT); <em>genus Pseudopodospermum</em> (Za)</td>
<td>not in phylogeny / <em>S. subg. Pseudopodospermum</em></td>
</tr>
</tbody>
</table>

(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_search/herbarium/), 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, life cycle, fruiting capitula, achenes, pappus; Appendix 4) with comparisons to previous relevant studies (Lipschitz 1964; 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). Subtree Scorzoneraeinae 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 Scorzoneraeinae. 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. szowitzi 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. & Köe (0.93 PP).

Morphology — Images of achenes of 22 species are presented in this study (Fig. 2; Fig. 3). A summary of the achenes shape pattern, pubescence, carpodipodium 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, suberete to sulcate, glabrous or lanate, with a conspicuous carpodipodium, 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,
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.

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

* 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 Scorzonerae — 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. tortuosisima* 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 & Tgaev 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; Kuthathelahde 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-tuberos) 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 (Coşkunçelebi & al. 2015; Coşkunçelebi & 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 phyllogenetic 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 carpodopodium (Fig. 2A–J; Fig. 4B). Species of *S.* subg. *Podospermum* are mostly distributed in...
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

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, Sardas, 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, Ristov 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 Estabban 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.

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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 cauleine 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 carpodium 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 carpodium of species in S. subg. Podospermum (Fig. 2K, L). However, the swollen bases are entirely fertile in S. purpurea compared to infertile carpodia in species of S. subg. Podospermum. Furthermore, members of S. subg. Podospermum differ from S. purpurea in having pinnatifid leaves and phyllaries with coriaceous projections (Fig. 4A); in contrast, S. purpurea has simple leaves and no coriaceous 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. turkevitzii); 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, tuberculare, 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 carpodium. Furthermore, we found that the carpodium 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 carpodium or with a carpodium that may be conspicuous or inconspicuous. Our study therefore suggests that the presence or absence of a carpodium 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. stenoecephala* 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. stenoecephala* 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 carpodium 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 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. Dimophopappae 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 cylindrical 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 cauleine 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 cauleine 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 scarios 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 tuberculae, 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. luriatanica* (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, Shah 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.28693, W). – S (2 mm) and T (2 mm): *S. szowitzii* (Iran, East Azerbaijan, N of Tabriz, Eynali mountain, 10 Jun 2013, Ebruhimi 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 Tscharis, 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.
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.
Carpododium — The carpododium 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 carpododium (Fig. 2A–H). In contrast, within S. subg. Pseudopodospermum, the carpododium may be absent (e.g. S. calypculata...
5. Capitula with 9–12 florets, fruiting capitula narrowly cylindric, 0.5–0.6 cm in diam. at base .......................... 4. S. szowitsii
- 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 .................. 9
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. meshedensis
- 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

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

<table>
<thead>
<tr>
<th>Key</th>
<th>Description</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Leaves entire (but at least some lobed or pinnately divided in <em>S. calyculata</em>); phyllaries without a corniculate projection; achene surface ridged, muricate, tuberculate, verrucose or rugulose, with or without longitudinal ribs</td>
<td><em>S. calyculata</em></td>
</tr>
<tr>
<td>2.</td>
<td>Radical leaves lanceolate or linear; achenes terete, mostly with a hollow swollen carpopodium at base</td>
<td><em>S. calyculata</em></td>
</tr>
<tr>
<td>3.</td>
<td>Radical leaves elliptic or oblong-elliptic; achenes angulate, always without a hollow swollen carpopodium at base</td>
<td><em>S. calyculata</em></td>
</tr>
<tr>
<td>9.</td>
<td>Plants 20–40(–60) cm tall; stems branched up to apex, with well-developed cauline leaves</td>
<td><em>S. calyculata</em></td>
</tr>
<tr>
<td>4.</td>
<td>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</td>
<td><em>S. calyculata</em></td>
</tr>
<tr>
<td>5.</td>
<td>Radical leaves 1.5–2.7(–3) cm wide; outer phyllaries in fruit 1–1.2 cm wide; ligules entirely violet</td>
<td><em>S. calyculata</em></td>
</tr>
<tr>
<td>2.</td>
<td>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</td>
<td><em>S. calyculata</em></td>
</tr>
<tr>
<td>3.</td>
<td>Radial leaves all entire; achene surface not verrucose</td>
<td><em>S. calyculata</em></td>
</tr>
<tr>
<td>4.</td>
<td>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</td>
<td><em>S. calyculata</em></td>
</tr>
</tbody>
</table>

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**Pappus** — Within *Scorzonera subg. Podospermum* and *S. subg. Pseudopodospermum*, the setaceous pappus is typically persistent, but in two cases (S. meshedensis and *S. songorica*) the bristles can be easily detached (*S. songorica* in Fig. 2t). 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).
– 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. turistanica
– 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


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 carpopodium. Sc. m. under the diagnosis for S. subg. P. p. below.


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. 5C), and verrucose achenes 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. lacerca 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. lacerca 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. lacerca 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.


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; Coşkunçelebi & 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.


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.


**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 cauleine 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 – 1.5 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, scabrulous 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).
Irano-Turanian element that varies markedly in the length of stem, width and shape of leaves; its morphological characteristics overlap with those of *S. turkevicii*. However, in *Flora iranica* (Rechinger 1977) and the *Flora of Iran* (Safavi 2013), only *S. turkevicii* (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).


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 cauleine 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 carpodium, and a pappus with bristles of unequal length; see further discussion under *S. mucida* below (Appendix 4; Table 2; Fig. 2Q, R).


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).


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).

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.


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.


Diagnosis — *Scorzonera papposa* differs from *S. ovata* in floret colour (florets entirely violet in *S. papposa* vs. entirely yellow or sometimes yellow 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*.


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.


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.


**Diagnosis** — *Scorzonera songorica* is similar to *S. songorica*; see the diagnosis under *S. songorica* 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).


**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+).


**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 suberete and the length of carpopodium is one third to half of the achene length (Fig. 3E, F; Appendix 4).

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


**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+).

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.


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.


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).

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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).