

## DIVERSIFICATION OF THE OLD WORLD SALSOLEAE s.l. (CHENOPODIACEAE): MOLECULAR PHYLOGENETIC ANALYSIS OF NUCLEAR AND CHLOROPLAST DATA SETS AND A REVISED CLASSIFICATION

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A first comprehensive phylogenetic analysis of tribe Salsoleae s.l. (Salsoloideae: Chenopodiaceae) is presented based on maximum parsimony and maximum likelihood analysis of nuclear ribosomal internal transcribed spacer and chloroplast *psbB-psbH* DNA sequences. Our data strongly support (1) the sister relationship of Camphorosmeae to the Salsoleae s.l.; (2) splitting of Salsoleae s.l. into two monophyletic tribes, Salsoleae s.s. and Caroxyloneae tribus nova; (3) the current status of most monotypic or oligotypic genera in Salsoleae; and (4) polyphyly of the Botschantzev and Freitag (among others) circumscriptions of *Salsola*, which falls into 10 (on average) monophyletic genera/lineages. Three well-supported genera are described as new (*Pyankovia*, *Kaviria*, and *Turania*), and four previously described genera are resurrected (*Caroxylon*, *Climacoptera*, *Kali*, and *Xylosalsola*). *Salsola* s.s. include a group of central and southwest Asian and north African species that consists of *Salsola* sect. *Salsola* s.s., *Salsola* sect. *Caroxylon* subsect. *Coccosalsola*, *Salsola* sect. *Obpyrifolia*, *Fadenia*, *Hypocylix*, *Seidlitzia*, and *Darniella*. All species of tribe Caroxyloneae investigated so far have C<sub>4</sub> photosynthesis of the NAD-malic enzyme subtype, while the majority of the species of Salsoleae s.s. are known to be of the NADP-malic enzyme subtype.

**Keywords:** Caroxyloneae, Chenopodiaceae, classification, molecular phylogeny, Salsoleae, Salsoloideae.

### Introduction

Chenopodiaceae is a cosmopolitan, eudicot lineage especially diverse in arid, semiarid, saline, and hypersaline ecosystems (Kühn et al. 1993; Hedge et al. 1997). The family is extremely variable in its ecomorphological and anatomical types and modes of photosynthesis (Carolin et al. 1975, 1978; Gamaley and Voznesenskaya 1986; Pyankov et al. 1992, 1997, 2001*b*, 2002; Akhani et al. 1997, 2005; Jacobs 2001; Voznesenskaya et al. 2001*b*, 2002; Kadereit et al. 2003; Schütze et al. 2003; Edwards et al. 2004; Akhani and Ghasemkhani 2007). Many members of this family are succulent and late flowering and fruiting, which has historically made collections difficult to identify, with many specimens lacking the necessary characters for species identification. Additionally, the high levels of diversity in the deserts of central Asia and the Middle East have created a limitation on investigation and collection activities because of poor representation in Western herbaria. The diversity of photosynthetic types and leaf anatomies in this family, particularly the discovery of two anatomical types that perform C<sub>4</sub> photosynthesis without Kranz anatomy in one species of *Suaeda* (*Borszczowia*) and two species of *Bienertia* (Freitag and Stichler 2000, 2002; Voznesenskaya et al. 2001*b*, 2002; Akhani et al. 2003, 2005), has attracted considerable interest in this intriguing group.

The classification of Chenopodiaceae and its phylogenetic relationships with other families have been explored by a

number of researchers using morphological and molecular markers (Scott 1977*a*, 1977*b*, 1978; Cuénoud et al. 2002; Kadereit et al. 2003, 2006; Pratt 2003; Schütze et al. 2003; Müller and Borsch 2005; Shepherd et al. 2005; Kapralov et al. 2006). The Salsoloideae subfamily has been circumscribed variously, but in recent years it has either included tribes Sarcobateae, Suaedeae, and Salsoleae (Kühn et al. 1993) or been restricted to the tribes Camphorosmeae, Sclerolaeneae, and Salsoleae (Kadereit et al. 2003). The Salsoloideae, here defined as including the Salsoleae s.l. and Camphorosmeae (including Sclerolaeneae) clades (Kadereit et al. 2003; Pratt 2003; Kapralov et al. 2006), has been demonstrated to be monophyletic (Kapralov et al. 2006). The monophyly of the two Salsoleae clades in relation to the Camphorosmeae, however, has been both questioned and poorly supported in past studies (Pyankov et al. 2001*a*; Kadereit et al. 2003; Kapralov et al. 2006).

Tribe Salsoleae includes one-third of all known genera currently recognized in the family Chenopodiaceae (32 of 98 genera; *sensu* Kühn et al. 1993), but it is a poorly understood lineage. Species concepts in the tribe have varied widely among researchers, with some recognizing a large number of species separated by relatively minor morphological differences (the Russian “splitters”; Botschantzev 1970, 1972, 1974*a*, 1975*b*, 1976, 1977, 1981*a*, 1982, among others; Pratorov 1986) and others circumscribing fewer “metaspecies” (the European “lumpers”; Freitag 1997), resulting in between 300 and 400 species accepted in the tribe (Botschantzev 1969*a*, 1969*b*, 1969*c*, 1970, 1971, 1972, 1974*a*, 1974*b*, 1975*a*, 1975*b*, 1975*c*, 1975*d*, 1976, 1977, 1980, 1981*a*, 1981*b*, 1982, 1986, 1989; Kühn et al. 1993; Freitag 1997). It is unclear

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which school might better reflect phylogenetic relationships and monophyletic lineages, but we here test several of these concepts by sampling multiple individuals/populations within some of these species groups. However, several of these groups will require more detailed population genetic and morphological studies for an understanding of species boundaries.

This tribe is Old World in distribution, with its main center of diversity in central Asian and Middle Eastern deserts and subdeserts, with radiations into the Mediterranean, north and south Africa, and Australia. Some species have also been introduced into the New World. They are mostly leaf- and stem-succulent halophytic, xerohalophytic, xerophytic, and ruderal plants with diverse traits, particularly in photosynthetic pathways and concurrent anatomical structures (Butnik et al. 1991, 2001; Akhani et al. 1997; Pyankov et al. 1997, 2001b, 2002; Voznesenskaya et al. 1999, 2001a, 2001b; Akhani and Ghasemkhani 2007). The potential synapomorphies for the tribe are the presence of scarios winged perianth segments in fruit, with possible loss in some species, and utricule with a spiral embryo. Apparently, the winged fruiting perianth is a most successful device for wind dispersal in desert areas. However, the presence of a wing does not occur in all genera and may be replaced by small protuberances or may be completely absent. In this latter group, zoochory and hydrochory dispersal mechanisms seem likely.

Generic boundaries in Salsoleae have been the subject of a long-standing controversy (Meyer 1829; Moquin-Tandon 1840, 1849; Bunge 1862; Bentham and Hooker 1880; Volkens 1893; Iljin 1936; Kühn et al. 1993; Hedge et al. 1997). *Salsola* has had a controversial subgeneric classification, and its monophyly has been questioned, as has the recognition of such genera as *Climacoptera* (Botschantzev 1956, 1969b; Prato 1986), *Halothamnus* (= *Aellenia*) (Iljin 1936; Botschantzev 1981b), *Darniella* (Brullo 1984), *Fadenia* (Aellen and Townsend 1972), and *Xylosalsola*, *Nitrosalsola*, and *Newcaspia* (Tzvelev 1993). Tables 1 and 2 summarize the complicated historical nomenclature of Salsoleae and the genus *Salsola*, at least for those species included here. In the first phylogenetic analysis of Salsoleae using internal transcribed spacer (ITS) sequences, Pyankov et al. (2001a) revealed that *Salsola* is likely to be polyphyletic, and similar results were found using *rbcL* sequences (Kadereit et al. 2003). The limited sampling of Salsoleae in both of these studies, however, leaves many questions regarding phylogenetic relationships and generic circumscription in the tribe unanswered.

We use maximum parsimony and maximum likelihood analyses of nrDNA ITS and cpDNA *psbB-psbH* spacer sequences to elucidate phylogenetic relationships in Salsoleae to test generic monophyly. Further, we suggest a new generic classification of the Salsoleae to more closely reflect phylogenetic relationships.

## Material and Methods

### Sampling

Most of the studied plants were collected by H. Akhani during intensive collections since 1988 from Iran, Turkmenistan, Turkey, and the United Arab Emirates. Some collections were dried in silica gel during field studies, and additional

specimens were obtained from the herbaria GAZ (Gazy Herbarium, Ankara, Turkey) K, LE, M, and MSB (Ludwig-Maximilians-Universität, München, Germany) (table B1). Other sources of samples included cultivated species in the greenhouse of Washington State University (table B1) and nine ITS sequences previously published (Pyankov et al. 2001a; Kadereit et al. 2003). Outgroups were chosen from representatives of major lineages of the Suaedoideae and Salicornioideae (six species in total); these lineages together have been demonstrated to be the sister group to the Salsoloideae s.l. (Kadereit et al. 2003; Kapralov et al. 2006). Because of amplification failure or lack of material, we could not include the following monotypic Salsoleae s.l. genera: *Sevada* Moq. (Moquin-Tandon 1849), *Iljinia* Korovin ex V. Komarov (Iljin 1936), *Halarchon* Bunge (1862), *Physandra* Botsch. (Botschantzev 1956), *Traganopsis* Maire et Wilczek, *Nucularia* Battand, and *Lagenantha* Chiov. We also could not include the ditypic genus *Choriptera* Botsch. (= *Gyroptera*). Further studies will be necessary to resolve the phylogenetic position of these genera.

New sequences have been deposited in GenBank (accessions EF453380–EF453632). The data matrix and resultant trees have been deposited in TreeBase (accession S1737).

### DNA Sequencing

DNA was isolated using a modified 2× CTAB buffer method (Doyle and Doyle 1987). Templates of the nrDNA ITS region were prepared using the primers ITS5HP (5'-AGG TGA CCT GCG GAA GGA TCA TT-3'; Suh et al. 1993) and ITS4 (5'-TCC TCC GCT TAT TGA TAT GC-3'; White et al. 1990). Polymerase chain reaction (PCR) amplifications followed the procedures described by Roalson et al. (2001). The chloroplast *psbB-psbH* spacer region was amplified using the primers *psbB-psbH-f* (5'-AGA TGT TTT TGC TGG TAT TGA-3') and *psbB-psbH-r* (5'-TTC AAC AGT TTG TGT AGC CA-3'; Xu et al. 2000). PCR amplifications followed the procedures described by Schütze et al. (2003).

The PCR products were electrophoresed using a 0.8% agarose gel in a 0.5× TBE (pH 8.3) buffer, stained with ethidium bromide to confirm a single product, and purified using the PEG precipitation procedure (Johnson and Soltis 1995). Sequencing was performed using an ABI Prism 3730 genetic analyzer. Direct-cycle sequencing of purified template DNAs followed manufacturer's specifications, using the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (PE Biosystems).

The two ITS sequencing primers provide sequences for overlapping fragments that collectively cover the entire spacer and 5.8S rDNA regions along both strands. The two *psbB-psbH* sequencing primers provide near-complete overlap along both strands. Sequencing of ITS and *psbB-psbH* used the same primers that were used for amplification.

Automated DNA sequencing chromatograms were proofed and edited and contigs were assembled using Sequencher 4.0 (Gene Codes). The ITS sequences were truncated to include only ITS1, 5.8S, and ITS2. The *psbB-psbH* sequences were truncated to include the 3' end of the *psbB* coding region, the *psbB-psbT* intergenic spacer, the *psbT* coding region, the *psbT-psbN* intergenic spacer, the *psbN* coding region, and the *psbN-psbH* intergenic spacer. Identification of the terminal ends and spacer boundaries of ITS1, 5.8S, ITS2, and the *psbB-psbH*

Table 1

Historical Classifications of Salsoleae s.l. from 1829 to Present

	Meyer 1829	Moquin-Tandon 1840, 1849	Bunge 1862 <sup>a</sup>	Hooker 1880	Volkens 1893	Boissier 1879	Ulbrich 1934	Ilijin 1936	Kühn et al. 1993	This article
Anabaseae	Anabaseae	Anabaseae	Anabaseae	Salsoleae	Salsoleae	Salsoleae	Nuculariaceae	Salsoleae	Salsoleae	Salsoleae
<i>Brachylepis</i>	<i>Ofaiston</i>	<i>Ofaiston</i>	<i>Ofaiston</i>	(A) Horizontal seeds	<i>Traganum</i>	<i>Traganum</i>	<i>Traganum</i>	<i>Salsola</i>	<i>Traganum</i>	<i>Anabasis</i>
<i>Anabasis</i>	Noaea	Noaea	Noaea	seeds	<i>Arthropophytum</i>	<i>Traganum</i>	<i>Nucularia</i>	Noaea	<i>Sympegma</i>	<i>Arthropophytum?</i>
Salsoleae	<i>Girgensohnia</i>	<i>Girgensohnia</i>	<i>Girgensohnia</i>	<i>Traganum</i>	<i>Horaninovia</i>	<i>Horaninovia</i>	Salsoleae	<i>Aellenia</i>	Noaea	“Canarosalsola”
<i>Halogoeton</i>	<i>Anabasis</i>	<i>Anabasis</i>	<i>Anabasis</i>	<i>Cornulaca</i>	<i>Horaninovia</i>	<i>Arthropophytum</i>	Sodinae	<i>Rhaphidophyton</i>	<i>Salsola</i>	“Collinosalsola”
<i>Halimocnemis</i>	<i>Brachylepis</i>	<i>Brachylepis</i>	<i>Brachylepis</i>	<i>Seidlitzia</i>	<i>Seidlitzia</i>	<i>Haloxylon</i>	<i>Seidlitzia</i>	<i>Horaninovia</i>	<i>Halothamnus</i>	<i>Cornulaca</i>
<i>Salsola</i>	<i>Nanophyton</i>	<i>Nanophyton</i>	<i>Nanophyton</i>	<i>Arthropophytum</i>	<i>Salsola</i>	<i>Seidlitzia</i>	<i>Seidlitzia</i>	<i>Ofaiston</i>	<i>Cyatobasis</i>	<i>Cornulaca</i>
<i>Schanginia</i>	<i>Petrosimonia</i>	<i>Petrosimonia</i>	<i>Petrosimonia</i>	<i>Horaninovia</i>	<i>Haloxylon</i>	<i>Salsola</i>	<i>Seidlitzia</i>	<i>Girgensohnia</i>	<i>Girgensohnia</i>	<i>Cornulaca</i>
<i>Schoberia</i>	<i>Halocharis</i>	<i>Halocharis</i>	<i>Halocharis</i>	<i>Haloxylon</i>	<i>Helicilla</i>	Anabaseae	<i>Aellenia</i>	<i>Halogoeton</i>	<i>Halogoeton</i>	<i>Halogoeton</i>
	<i>Halimocnemis</i>	<i>Halimocnemis</i>	<i>Halimocnemis</i>	<i>Salsola</i>	Anabaseinae	Noaea	<i>Lagenantha</i>	<i>Seidlitzia</i>	<i>Halothamnus</i>	<i>Halothamnus</i>
	<i>Halarchon</i>	<i>Halarchon</i>	<i>Halarchon</i>	<i>Helicilla</i>	<i>Ofaiston</i>	[Noaea]	<i>Arthropophytum</i>	<i>Arthropophytum</i>	<i>Haloxylon</i>	<i>Haloxylon</i>
	<i>Halanthium</i>	<i>Halanthium</i>	<i>Halanthium</i>	(B) Vertical seeds	Noaea	<i>Girgensohnia</i>	<i>Haloxylon</i>	<i>Ilijinia</i>	<i>Hammada?</i> p.p.	<i>Hammada?</i> p.p.
	<i>Gamanthus</i>	<i>Gamanthus</i>	<i>Gamanthus</i>	<i>Ofaiston</i>	<i>Girgensohnia</i>	<i>Anabasis</i>	<i>Haloxylon</i>	<i>Nanophyton</i>	<i>Hammada</i>	<i>Hammada</i>
	<i>Cornulaca</i>	<i>Cornulaca</i>	<i>Cornulaca</i>	Noaea	<i>Anabasis</i>	<i>Brachylepis</i>	Anabaseidae	<i>Girgensohnia</i>	<i>salicornica</i>	<i>salicornica</i>
	<i>Agathophora</i>	<i>Agathophora</i>	<i>Agathophora</i>	<i>Girgensohnia</i>	<i>Nanophyton</i>	<i>Petrosimonia</i>	Anabaseidae	<i>Halocharis</i>	<i>Horaninovia</i>	<i>Horaninovia</i>
	<i>Halogoeton</i>	<i>Halogoeton</i>	<i>Halogoeton</i>	<i>Anabasis</i>	<i>Petrosimonia</i>	<i>Halocharis</i>	<i>Ofaiston</i>	<i>Halanthium</i>	<i>Ilijinia?</i>	<i>Ilijinia?</i>
				<i>Nanophyton</i>	<i>Halocharis</i>	<i>Halimocnemis</i>	Noaea	<i>Fadenia</i>	<i>Kali</i>	<i>Kali</i>
				<i>Halocharis</i>	<i>Halimocnemis</i>	<i>Halotus</i>	<i>Girgensohnia</i>	<i>Sevada</i>	<i>Lagenantha?</i>	<i>Lagenantha?</i>
				<i>Halimocnemis</i>	<i>Piptoptera</i>	<i>Piptoptera</i>	<i>Halotus</i>	<i>Choriptera</i>	Noaea	Noaea
				<i>Halanthium</i>	<i>Halanthium</i>	<i>Halarchon</i>	<i>Fredlia</i>	<i>Rhaphidophyton</i>	<i>Nucularia?</i>	<i>Nucularia?</i>
				<i>Halanthium</i>	<i>Halarchon</i>	<i>Halarchon</i>	<i>Brachylepis</i>	<i>Halanthium</i>	“Oreosalsola”	“Oreosalsola”
				<i>Piptoptera</i>	<i>Halarchon</i>	<i>Gamanthus</i>	Halimocnemideae	<i>Gamanthus</i>	<i>Rhaphidophyton</i>	<i>Rhaphidophyton</i>
				<i>Halogoeton</i>	<i>Halarchon</i>	<i>Halanthium</i>	Nanophytum	<i>Cornulaca</i>	<i>Salsola</i> s.s.	<i>Salsola</i> s.s.
				<i>Sympegma</i>	<i>Agathophora</i>	<i>Cornulaca</i>	<i>Petrosimonia</i>	<i>Traganum</i>	<i>Sympegma</i>	<i>Sympegma</i>
				Suaedaceae	<i>Halogoeton</i>	<i>Halogoeton</i>	<i>Halocharis</i>	<i>Traganopsis</i>	<i>Traganum</i>	<i>Traganum</i>
				<i>Hypocylax</i>	<i>Sympegma</i>	<i>Sevada</i>	<i>Halimocnemis</i>	<i>Nucularia</i>	<i>Traganum</i>	<i>Traganum</i>
								<i>Horaninovia</i>	<i>Traganopsis?</i>	<i>Traganopsis?</i>
								<i>Piptoptera</i>	<i>Turania</i>	<i>Turania</i>
								<i>Gamanthus</i>	<i>Xylosalsola</i>	<i>Xylosalsola</i>
								<i>Halarchon</i>	<i>Caroxyloneae</i>	<i>Caroxyloneae</i>
								<i>Petrosimonia</i>	<i>Caroxylon</i>	<i>Caroxylon</i>
								<i>Halimocnemis</i>	<i>Climacoptera</i>	<i>Climacoptera</i>
								<i>Halotus</i>	<i>Halarchon?</i>	<i>Halarchon?</i>
								<i>Lagenantha</i>	<i>Halimocnemis</i>	<i>Halimocnemis</i>
									<i>Halocharis</i>	<i>Halocharis</i>
									<i>Kaviria</i>	<i>Kaviria</i>
									<i>Nanophyton</i>	<i>Nanophyton</i>
									<i>Ofaiston</i>	<i>Ofaiston</i>
									<i>Piptoptera</i>	<i>Piptoptera</i>
									<i>Petrosimonia</i>	<i>Petrosimonia</i>
									<i>Physandra?</i>	<i>Physandra?</i>
									<i>Pyankovia</i>	<i>Pyankovia</i>

Note. Classification of *Salsola* and its segregates is given separately in table 2. Other tribes are mentioned only when a member of Salsoleae was classified under that tribe. Genera marked with a question mark are genera of questionable status, as dealt with in this article. Several other infratribal units are not listed here. Other authors: Botschantzev (1967, 1975a, 1975b, 1975c, 1975d: Salsoleae, subtrib. Sevadiinae [Sevada, *Lagenantha*, *Fadenia*, *Choriptera*, *Gyroptera*], 1977: *Agathophora* [= *Halogoeton* subgen. *Agathophora*]).  
<sup>a</sup> The monograph dealt only with Anabaseae.

**Table 2**  
**Historical Classification of *Salsola* and Segregate Genera**

Ilijin 1936	Botschantzev (various articles) <sup>a</sup>	Tzvelev 1993	Freitag 1997	Hedge 1997; Rilke 1999	Freitag 1997; Rilke 1999	This article
Sect. <i>Kali</i>	<i>Climacoptera</i> (1956) <sup>3</sup>	<i>Salsola</i>	Sect. <i>Belanthera</i>	Sect. <i>Belanthera</i>	Sect. <i>Belanthera</i>	1 "Canarosalsola"
<i>S. kalfi</i> <sup>6</sup>	<i>Halothammus</i> (1981b) <sup>5</sup>	Sect. <i>Kali</i> (Mill.)	Sect. <i>Kali</i> (Mill.)	Sect. <i>Coccosalsola</i> <sup>10</sup>	<i>S. gossypina</i> <sup>7</sup>	2 <i>Caroxylon</i>
<i>S. paulsenii</i> <sup>6</sup>	Sect. <i>Caroxylon</i> subsect. <i>Caroxylon</i> <sup>2</sup> (1974a, 1974b)	Dumort. <sup>6</sup>	(No species included in our analysis)	<i>S. drummondii</i> <sup>10</sup>	<i>S. brachiata</i> <sup>9</sup>	3 <i>Climacoptera</i>
<i>S. soda</i> <sup>10</sup>	Sect. <i>Caroxylon</i> subsect. <i>Caroxylon</i> <sup>2</sup> (1974a, 1974b)	Sect. <i>Salsola</i>		<i>S. kernerii</i> <sup>10</sup>	<i>S. vvdenskii</i> <sup>7</sup>	4 "Collimosalsola"
<i>S. aperta</i> <sup>6</sup>	<i>S. zeyheri</i> <sup>2</sup>	<i>Climacoptera</i>	Sect. <i>Belanthera</i>	Sect. <i>Arbuscula</i>	<i>S. canescens</i> <sup>2</sup>	5 <i>Halothammus</i>
<i>S. deserticola</i> <sup>11</sup>	<i>S. araneosa</i> <sup>2</sup>	Sect. <i>Heterotricha</i>	(1968, 1980)	<i>S. richteri</i> <sup>12</sup>	<i>S. aucheri</i> <sup>7</sup>	6 <i>Kali</i>
Sect. <i>Physurus</i>	<i>S. dendroides</i> <sup>2</sup>	Ilijin ex Prato <sup>9</sup>	<i>S. canescens</i>	<i>S. montana</i> <sup>8</sup>	<i>S. rubescens</i> <sup>7</sup>	7 <i>Kaviria</i> gen. nov.
<i>S. lanata</i> <sup>3</sup>	<i>S. glabrescens</i> <sup>2</sup>	Sect. <i>Climacoptera</i> <sup>3</sup>	(as <i>S. boissieri</i> ) <sup>9</sup>	<i>S. arbuscula</i> <sup>12</sup>	<i>S. lachnantha</i> <sup>7</sup>	8 "Oreosalsola"
<i>S. crassa</i> <sup>3</sup>	<i>S. cyclophylla</i> <sup>2</sup>	Sect. <i>Brachyphylla</i>	<i>S. carpatha</i> <sup>2</sup>	<i>S. arbusculiformis</i> <sup>4</sup>	<i>S. tomentosa</i> <sup>7</sup>	9 <i>Pyankovia</i> gen. nov.
<i>S. turcomanica</i> <sup>3</sup>	Sect. <i>Caroxylon</i> subsect. <i>Vermiculatae</i> <sup>2</sup> (1975a, 1975b, 1975c, 1975d)	Ilijin ex Prato <sup>5</sup>	<i>S. rubescens</i> <sup>7</sup>	Sect. <i>Salsola</i>	Sect. <i>Physurus</i> <sup>3</sup>	10 <i>Salsola</i> s.s.
Sect. <i>Heterotricha</i> <sup>9</sup>	<i>S. aucheri</i> <sup>7</sup>	<i>Nitrosalsola</i> <sup>2</sup> (= <i>Salsola</i> )	<i>S. tomentosa</i> <sup>7</sup>	<i>S. soda</i> <sup>10</sup>	<i>S. lanata</i> <sup>3</sup>	11 <i>Turania</i> gen. nov.
<i>S. brachiata</i> <sup>9</sup>	<i>S. tomentosa</i> <sup>7</sup>	sect. <i>Nitraria</i> Ulbr.)	<i>S. vvdenskii</i> <sup>7</sup>	<i>S. aperta</i> <sup>11</sup>	<i>S. crassa</i> <sup>3</sup>	12 <i>Xylosalsola</i>
Sect. <i>Anchophyllum</i>	<i>S. nitraria</i> <sup>2</sup>	<i>Caroxylon</i> <sup>2</sup>	<i>S. gossypina</i> <sup>7</sup>	Hedge 1997	Hedge 1997	
<i>S. arbuscula</i> <sup>12</sup>	<i>S. vermiculata</i> <sup>2</sup>	Sect. <i>Belanthera</i>	<i>S. vvdenskii</i> <sup>7</sup>	<i>S. paulsenii</i> <sup>6</sup>	<i>S. paulsenii</i> <sup>6</sup>	
<i>S. arbusculiformis</i> <sup>4</sup>	<i>S. larinata</i> <sup>2</sup>	(Ilijin) Tzvel.	<i>S. gossypina</i> <sup>7</sup>	<i>S. kalfi</i> <sup>6</sup>	<i>S. kalfi</i> <sup>6</sup>	
<i>S. montana</i> <sup>8</sup>	<i>S. orientalis</i> <sup>2</sup>	Sect. <i>Caroxylon</i> <sup>2</sup>	Sect. <i>Malpigipila</i> <sup>2</sup>	<i>S. griffithii</i> <sup>6</sup>	<i>S. griffithii</i> <sup>6</sup>	
<i>S. chiwensis</i> <sup>12</sup>	<i>S. dzhungarica</i> <sup>2</sup>	Sect. <i>Caroxylon</i> <sup>2</sup>	Sect. <i>Malpigipila</i>	Sect. <i>Caroxylon</i> <sup>2</sup>	Sect. <i>Salsola</i> <sup>10</sup>	
<i>S. richteri</i> <sup>12</sup>	Sect. <i>Caroxylon</i> subsect. <i>Coccosalsola</i> (1976, 1989)	(Botsch.) Tzvel. <sup>2</sup>	(1969a, 1969b, 1969c)	<i>S. nitriaria</i> <sup>2</sup>	Sect. <i>Sogdiana</i>	
Sect. <i>Spiragidanthus</i>	<i>S. divaricata</i> <sup>1</sup>	<i>Xylosalsola</i> <sup>12</sup>	(1969a, 1969b, 1969c)	<i>S. dendroides</i> <sup>2</sup>	<i>S. sogdiana</i> <sup>11</sup>	
<i>S. subaphylla</i> <sup>5</sup>	<i>S. kernerii</i> <sup>10</sup>		<i>S. inermis</i> <sup>2</sup>	<i>S. abarghuensis</i> <sup>2</sup>	<i>S. aperta</i> <sup>11</sup>	
<i>S. glauca</i> <sup>5</sup>	<i>S. drummondii</i>		<i>S. forcipitata</i> <sup>2</sup>	<i>S. vermiculata</i> <sup>2</sup>	Sect. <i>Androssovia</i>	
Sect. <i>Caroxylon</i> <sup>2</sup>	(sub <i>S. schweinfurthii</i> ) <sup>10</sup>		<i>S. chorassanica</i> <sup>2</sup>	<i>S. orientalis</i> <sup>2</sup>	<i>S. androssout</i> s.l. <sup>11</sup>	
<i>S. larinata</i> <sup>2</sup>	<i>S. foliosa</i> <sup>10</sup>		<i>S. jordanicola</i> <sup>2</sup>	Sect. <i>Malpigipila</i> <sup>2</sup>	<i>S. kalfi</i> <sup>6</sup>	
<i>S. dendroides</i> <sup>2</sup>	<i>S. zygophylla</i> <sup>10</sup>		<i>S. turkestanica</i> <sup>2</sup>	<i>S. gemmascens</i> <sup>2</sup>	<i>S. griffithii</i> <sup>6</sup>	
<i>S. dzhungarica</i> <sup>2</sup>	Sect. <i>Caroxylon</i> subsect. <i>Arbusculae</i> (1976)		Sect. <i>Obpyrifolia</i> <sup>10</sup>	<i>S. yezdiana</i> <sup>2</sup>	<i>S. tragus</i> <sup>6</sup>	
Sect. <i>Aleuranthus</i> <sup>2</sup>	<i>S. arbusculiformis</i> <sup>4</sup>		(Botschantzev and Akhmi 1989)	Sect. <i>Cardiandra</i> <sup>2</sup>	<i>S. kalfi</i> <sup>6</sup>	
<i>S. sclerantha</i> <sup>2</sup>	<i>S. montana</i> <sup>8</sup>		<i>S. drummondii</i> <sup>10</sup>	<i>S. chorassanica</i> <sup>2</sup>	<i>S. paulsenii</i> <sup>6</sup>	
Sect. <i>Belanthera</i>	<i>S. masenderanica</i> <sup>8</sup>		(sub <i>S. obpyrifolia</i> )	<i>S. forcipitata</i> <sup>2</sup>		
<i>S. gemmascens</i> <sup>2</sup>	<i>S. arbuscula</i> <sup>12</sup>		Sect. <i>Irania</i> (1986)	<i>S. jordanicola</i> <sup>2</sup>		
<i>S. aucheri</i> <sup>7</sup>	<i>S. richteri</i> <sup>12</sup>		Subtribe <i>Sevadinae</i> (1975c)	<i>S. turkestanica</i> <sup>2</sup>		
<i>S. vvdenskii</i> <sup>7</sup>	Sect. <i>Caroxylon</i> subsect. <i>Tetragona</i> (1972) <sup>2</sup>		<i>Fadenia zygophylloides</i> <sup>10</sup>	<i>S. inermis</i> <sup>2</sup>		
<i>S. gossypina</i> <sup>7</sup>	(No species included in our analysis)					
Sect. <i>Coccosalsola</i>						
<i>S. foliosa</i> <sup>10</sup>						
<i>Allenia</i> <sup>5</sup>						
<i>A. auriculata</i> <sup>5</sup>						

Note. Only those taxa that were used in our phylogeny are listed. For a full checklist, see appendix A and references. Superscript numbers correspond to the numbers of the accepted genera in this article (right column). Other classifications not listed included Brullo (1984); *Darniella*; <sup>10</sup> Galushko (1976); *Caspia*; and Woloszczak (1885); *Hypocylix*.<sup>10</sup>

<sup>a</sup> References are given by section. Publication years of the relevant Botschantzev articles are given in parentheses.

gene regions was based on comparisons with other species of Chenopodiaceae (Kapralov et al. 2006). Sequences were aligned using Clustal X (Thompson et al. 1997) with gap opening penalty of 10.00 and gap extension penalty of 1.00 for both pairwise and multiple comparisons. The resultant alignment was then checked by eye for necessary minor corrections. Alternate alignment parameters did not result in significantly different topologies (data not shown). Gaps were not coded as binary characters because of the complex nature of the gaps in these data sets and the additional problem that they cannot be integrated into the maximum likelihood analyses.

### Phylogenetic Analyses

ITS and *psb-psbH* regions were analyzed separately and in combination with both maximum parsimony (MP) and maximum likelihood (ML) analyses. All analyses were performed using PAUP\* 4.0b10 (Swofford 2001). MP analyses of the individual and combined data sets used heuristic searches (ACCTRAN; 1000 random addition cycles, tree-bisection-reconnection [TBR] branch swapping, limit of 10,000 rearrangements per addition sequence replicate). Swapping was run to completion for all random addition replicates. Clade support was estimated using 1000 heuristic bootstrap replicates (100 random addition cycles per replicate, TBR branch swapping, limit of 10,000 rearrangements per addition sequence replicate; Felsenstein 1985; Hillis and Bull 1993).

ML analyses employed heuristic searches (TBR branch swapping). Clade support was estimated using 100 heuristic bootstrap replicates (10 random addition cycles and 100 total rearrangements per replicate, TBR branch swapping; Felsenstein 1985; Hillis and Bull 1993). ML analysis of the ITS data set employed the general time-reversible model with proportion of invariant sites (*I*) and gamma shape ( $\Gamma$ ) parameters and empirical base frequencies (six substitution types: A/C = 1.4064, A/G = 2.5332, A/T = 1.7413, C/G = 0.7280, C/T = 3.5703, G/T = 1.0000; *I* = 0.2193;  $\Gamma$  = 0.9803; A = 0.2084, C = 0.2519, G = 0.2849, T = 0.2548). ML analysis of the *psbB-psbH* genetic region employed a five-rate class transversion model with *I* and  $\Gamma$  parameters and empirical base frequencies (five substitution types: A/C = 0.9657, A/G = 1.3422, A/T = 0.2773, C/G = 0.7521, C/T = 1.3422, G/T = 1.0000; *I* = 0.2417;  $\Gamma$  = 0.9036; A = 0.2982, C = 0.1616, G = 0.1794, T = 0.3608). ML analysis of the combined data set employed a four-rate class transition model with *I* and  $\Gamma$  parameters and empirical base frequencies (four substitution types: A/C = 1.0000, A/G = 1.9407, A/T = 0.8031, C/G = 0.8031, C/T = 2.5593, G/T = 1.0000; *I* = 0.2700;  $\Gamma$  = 0.7111; A = 0.2613, C = 0.2239, G = 0.2239, T = 0.2909). These models were chosen based on the results of analysis using DT\_ModSel (Minin et al. 2003). The DT\_ModSel analysis uses a Bayesian information criterion to select a model using branch-length error as a performance measure in a decision theory framework that also includes a penalty for model overfitting.

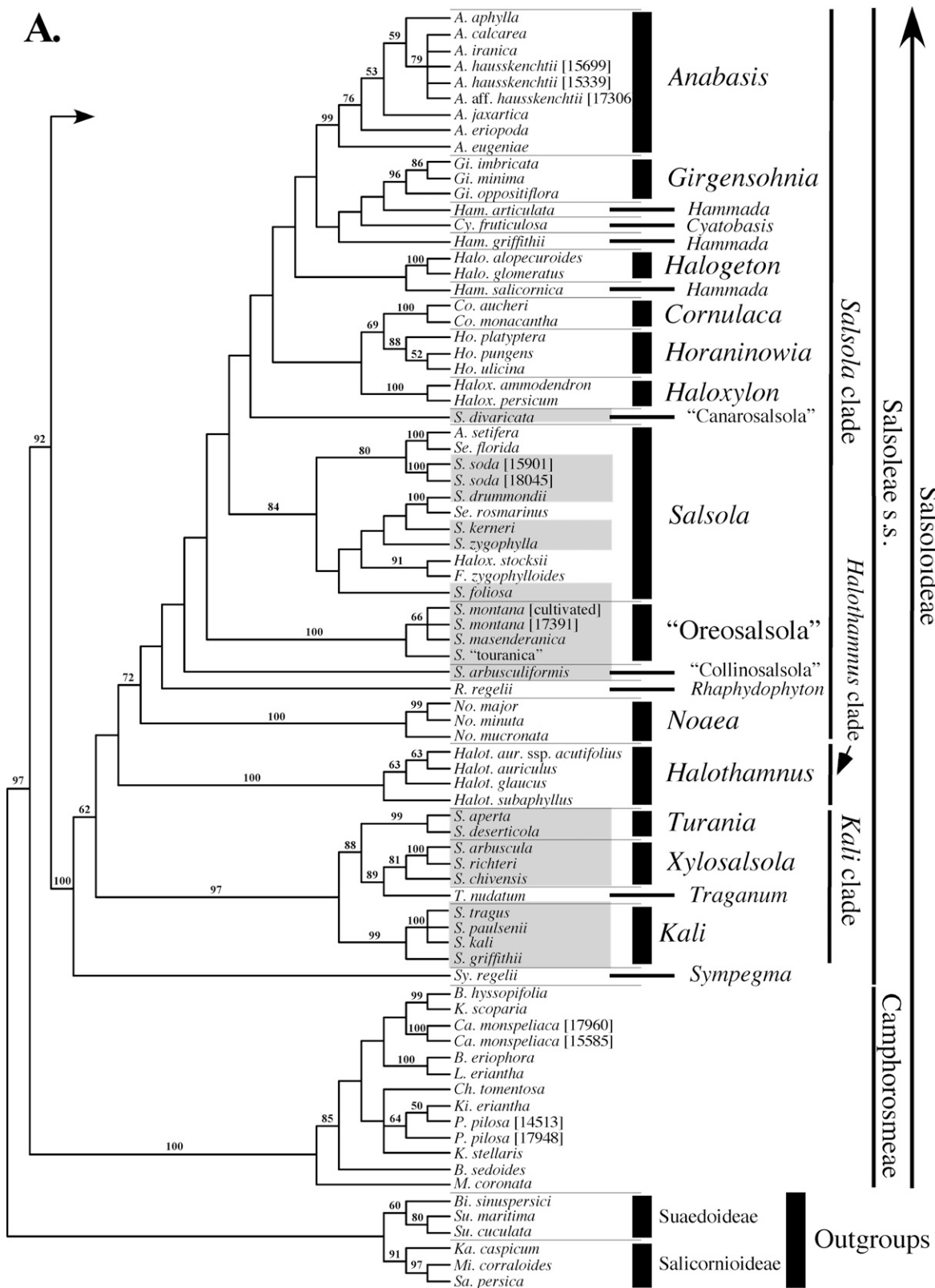
### Results

New ITS and *psbB-psbH* sequences were obtained for 132 species/accessions belonging to tribe Salsoleae s.l. and six

species of Salicornieae and Suaedeae as outgroups. The aligned ITS data matrix was 743 base pairs (bp) long with 511 variable sites (68.8%), of which 400 (53.8%) were parsimony informative. Because of poor sequencing reads of some regions, three sequences are missing a portion (104–182 bp) of the 5' end of the ITS 1 spacer, eight sequences are missing a portion (92 bp) of the 5' end of the ITS 2 spacer, and 14 sequences are missing a portion (4–82 bp) of the 3' end of the ITS 2 spacer. The aligned *psbB-psbH* data matrix was 741 bp long with 270 variable sites (36.4%), of which 144 (19.4%) were parsimony informative. Because of poor sequencing reads of some regions, nine sequences are missing a portion (1–113 bp) of the 5' end of the *psbB-psbH* spacer region, and 21 sequences are missing a portion (1–121 bp) of the 3' end of the *psbB-psbH* spacer region.

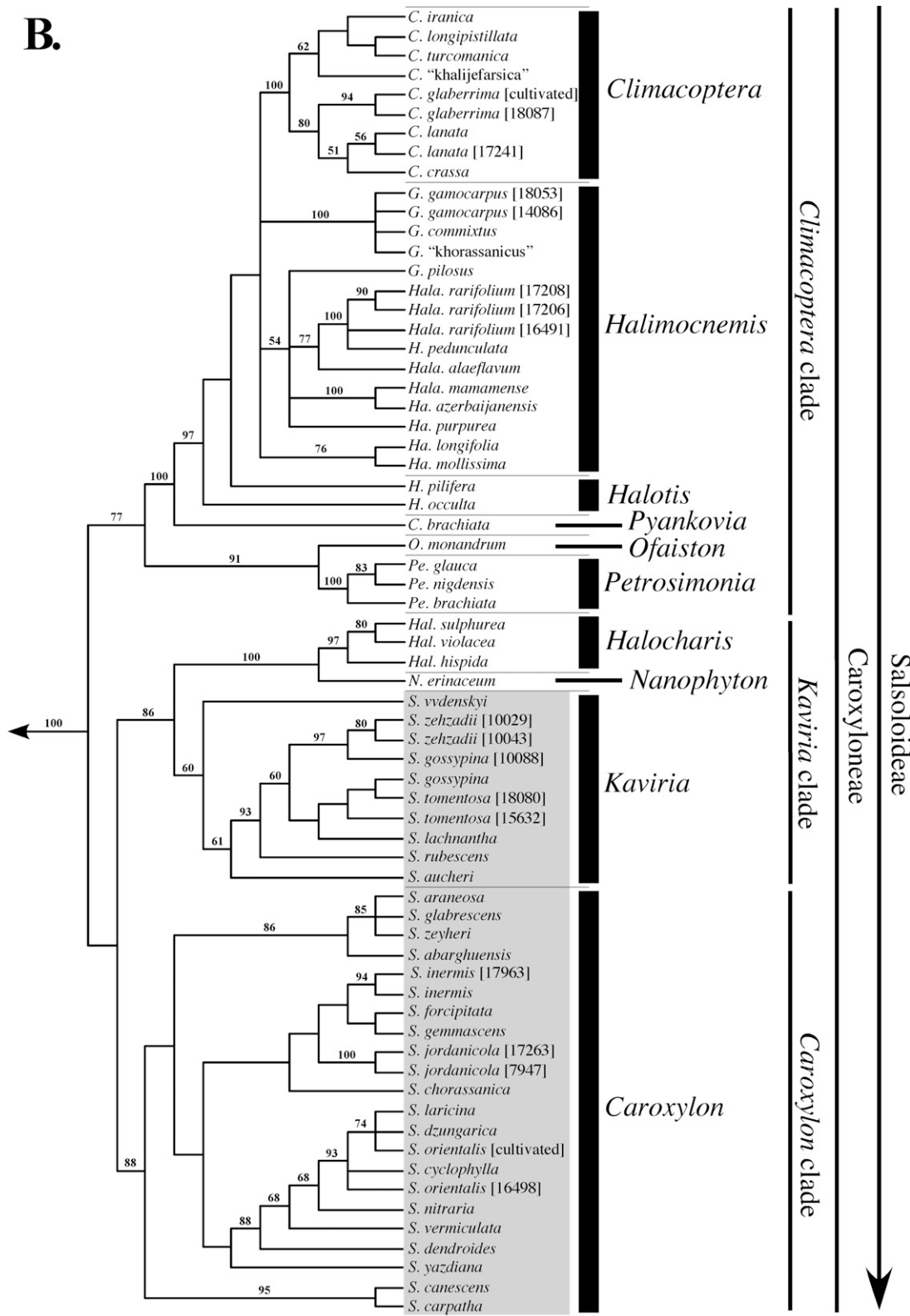
MP analysis of the ITS Salsoleae data set resulted in 1451 most parsimonious trees (length = 3445 steps, consistency index [CI] = 0.303, retention index [RI] = 0.741, rescaled consistency index [RC] = 0.224). The ITS ML analysis resulted in a single tree ( $-\ln L = 17800.03435$ , where *L* = likelihood). MP analysis of the *psbB-psbH* data set resulted in 11,122 most parsimonious trees (length = 600 steps, CI = 0.595, RI = 0.766, RC = 0.456). The *psbB-psbH* ML analysis resulted in two tied trees ( $-\ln L = 4783.22431$ ). Strict consensus trees of the MP individual data set analyses and the ML trees of individual data set analyses are available from the corresponding authors. MP analysis of the combined data set resulted in 231 most parsimonious trees (length = 4067 steps, CI = 0.343, RI = 0.740, RC = 0.254; fig. 1). The combined ML analysis resulted in a single tree ( $-\ln L = 23216.90496$ ; fig. 2).

Analyses of individual data sets resulted in congruent estimates of relationships, with slight differences associated with unresolved branches and short branches with low bootstrap support, particularly in the *psbB-psbH* analysis. Combined analyses reflect the well-resolved portions of individual data set analyses, and all branches are better supported in the combined analysis than in either of the individual data set analyses (trees from individual analyses in TreeBase). Given our results that multiple alignments of individual data sets produced congruent topologies and that there were no well-supported conflicting branches, as well as the fact that the clades we found are generally supported by morphological characters, we do not consider the high levels of ITS variability or alignment issues to reduce the ability of our analyses to reconstruct robust phylogenetic hypotheses. MP and ML analyses of the combined data result in congruent inferences of relationships, with differences in resolution resulting in slightly different placement of some species (figs. 1, 2). These differences, however, are associated with branches with low bootstrap support in one or both analysis types. In all analyses, *Salsola* s.l. is clearly polyphyletic, with *Salsola* species present in seven to 13 lineages or different clades, depending on the resolution of the phylogenetic hypotheses (figs. 1, 2). Several other genera are not monophyletic as currently circumscribed, namely, *Anabasis*, *Halanthium*, *Halimocnemis*, *Hammada*, *Gamanthus*, and *Climacoptera* (figs. 1, 2). In some cases, this is due to the misclassification of one or a small number of species (e.g., *Climacoptera brachiata*; figs. 1B, 2B), whereas other cases, such as the polyphyly and

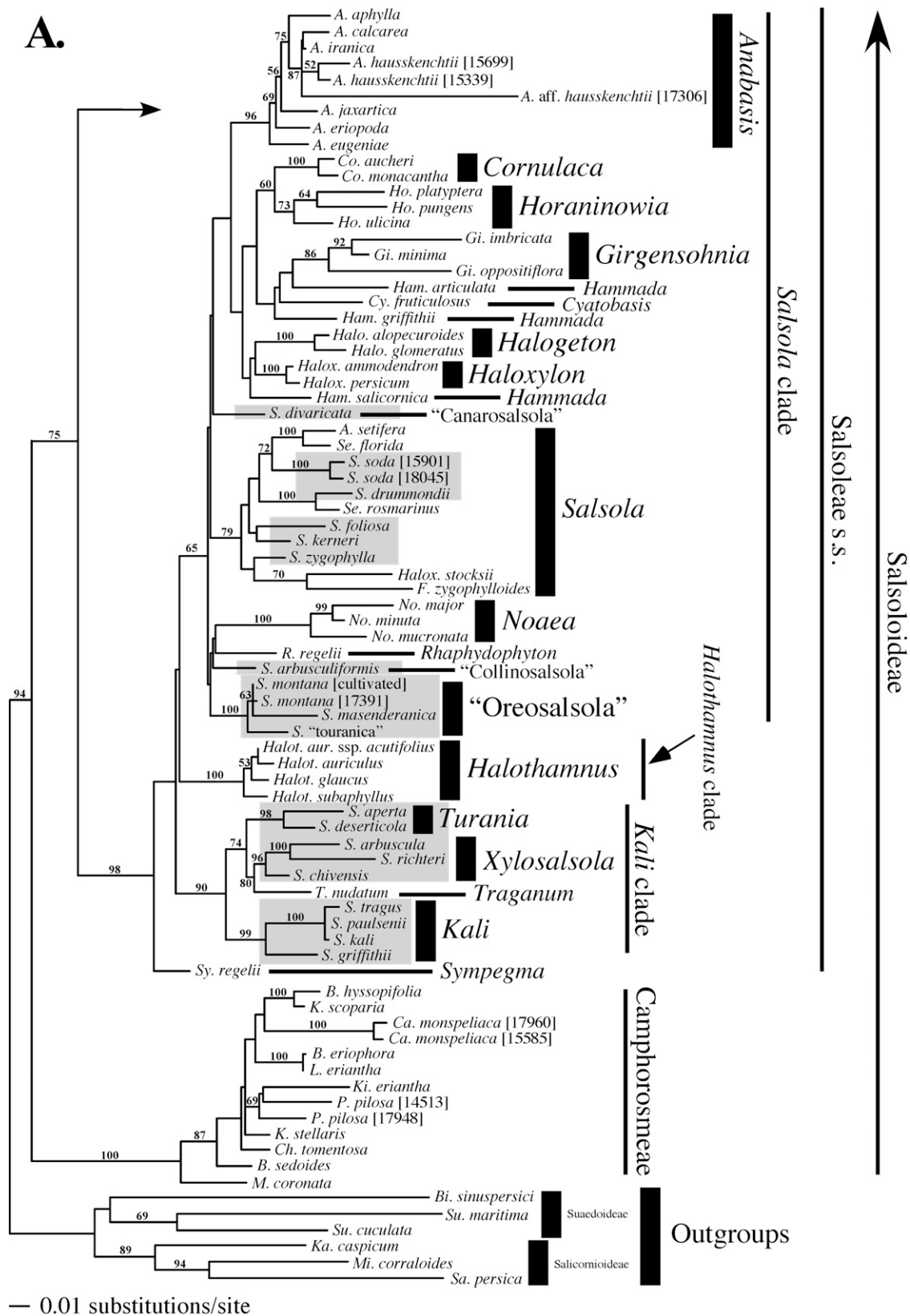


**Fig. 1** Maximum parsimony combined data analysis strict consensus tree of 231 shortest trees (length = 4067; consistency index = 0.343; retention index = 0.740; rescaled consistency index = 0.254). A, Outgroups and clades of Camphorosmeae and Salsoleae s.s. tribes. B, Caroxyloneae tribe clade. Numbers above branches reflect maximum parsimony bootstrap numbers. Shaded boxes refer to species traditionally placed in the genus *Salsola*. Generic abbreviations are as follows: A. = *Anabasis*, B. = *Bassia*, Bi. = *Bienertia*, C. = *Climacoptera*, Ca. =

**B.**



*Camphorosma*, *Ch.* = *Chenoleoides*, *Co.* = *Cornulaca*, *Cy.* = *Cyatobasis*, *F.* = *Fadenia*, *G.* = *Gamanthus*, *Gi.* = *Girgensobnia*, *H.* = *Halotis*, *Ha.* = *Halimocnemis*, *Hal.* = *Halocharis*, *Hala.* = *Halanthium*, *Halo.* = *Halogeton*, *Halot.* = *Halothamnus*, *Halox.* = *Haloxylon*, *Ham.* = *Hammada*, *Ho.* = *Horaninowia*, *K.* = *Kochia*, *Ka.* = *Kalidium*, *Ki.* = *Kirilowia*, *L.* = *Londesia*, *M.* = *Maireana*, *Mi.* = *Microcnemum*, *N.* = *Nanophyton*, *No.* = *Noaea*, *O.* = *Ofaiston*, *P.* = *Panderia*, *Pe.* = *Petrosimonia*, *R.* = *Rhaphidophyton*, *S.* = *Salsola*, *Sa.* = *Salicornia*, *Se.* = *Seidlitzia*, *Su.* = *Suaeda*, *Sy.* = *Sympegma*, *T.* = *Traganum*.



**Fig. 2** Maximum likelihood combined data analysis tree ( $-\ln L = 23216.90496$ ). A, Outgroups and clades of Camphorosmeae and Salsoleae s.s. tribes. B, Caroxyloneae tribe clade. Numbers above branches reflect maximum likelihood bootstrap numbers. Shaded boxes refer to species traditionally placed in the genus *Salsola*. Generic abbreviations follow those in fig. 1.





interdigitation of *Halanthium* and *Halimocnemis*, are more difficult (figs. 1B, 2B).

## Discussion

### Tribal Classification

Because individual analyses were congruent with, although less resolved than, the combined analyses, we will generally refer to the combined MP and ML results in our discussion. It seems clear from the analyses presented here that the Salsoloideae is a monophyletic group with the Camphorosmeae tribe the sister clade to Salsoleae s.l. (figs. 1, 2) and is well supported by maximum parsimony bootstrap (mpbs = 92%) and maximum likelihood bootstrap (mlbs = 75%). This relationship has been previously found (Kadereit et al. 2003; Kapralov et al. 2006), although this branch was weakly supported by *rbcl*, and the multigene analysis of Kapralov et al. (2006), while providing strong support (mlbs = 86%), did not have sufficiently extensive sampling to allow confidence in this relationship. One previous study placed the Camphorosmeae as sister to a portion of the Salsoleae s.l. (our Caroxyloneae), creating a paraphyletic Salsoleae s.l., but this result was weakly supported (mpbs < 50%; Pyankov et al. 2001a). Furthermore, the traditional Salsoleae is clearly composed of two strongly supported clades, here referred to as the Salsoleae s.s. (mpbs = 100%; mlbs = 100%) and the Caroxyloneae (mpbs = 98%; mlbs = 98%; figs. 1, 2; see taxonomic revision in app. A). The occurrence of two well-supported clades in Salsoleae s.l. has been found with analyses of ITS sequences from 34 species (Pyankov et al. 2001a) and 12 species in *rbcl* analysis (Kadereit et al. 2003). The latter authors referred to these two clades as Salsoleae I and Salsoleae II. Both clades are well distinguished by a number of characters

(table 3). A particularly distinguishing characteristic of the Caroxyloneae clade is the vesicular and disjunct anther appendage, which seems to occur in most groups and may be involved in attracting insect pollinators, which have been observed frequently in nature (H. Akhiani, personal observation). These connectives are absent or very small in members of Salsoleae and have been noted as a minute appendage in *Halothamnus*, *Noaea*, and *Halogeton* (Kothe-Heinrich 1993; Hedge 1997); they are rarely large as those found in *Raphy-dophytum* (Iljin 1936). The two clades are also distinguishable based on C<sub>4</sub> photosynthesis subtypes: all known species of Caroxyloneae are of the NAD-malic enzyme subtype (table 3), and except for one doubtful case (H. Akhiani, unpublished data), all Salsoleae are known to be of the NADP-malic enzyme subtype (see also Pyankov et al. 2001a, 2001b).

### Classification and Relationships in Clade Salsoleae

The Salsoleae s.s. tribe is more diverse than Caroxyloneae, both morphologically and physiologically. In this tribe, C<sub>4</sub>, C<sub>3</sub>, and C<sub>3</sub>-C<sub>4</sub> intermediate species occur, with strong morphological features separating the tribe from Caroxyloneae (table 3). Four primary lineages or clades in Salsoleae s.s. can be distinguished: *Sympegma*, the *Halothamnus* clade, the *Kali* clade, and the *Salsola* clade (figs. 1A, 2A). The monotypic *Sympegma* is sister to a clade composed of the rest of the lineages of the Salsoleae s.s., although its separation is only weakly supported (mpbs = 62%; mlbs < 50%). The ordering of the other three clades is not strongly supported (mpbs < 50%; mlbs < 50%), but both analyses suggest that the *Kali* clade is sister to a clade composed of the *Halothamnus* and *Salsola* clades.

The monotypic *Sympegma* is restricted to central Asia and is unique in the family in having terminal glomerate

Table 3

Comparison of the Characters of the Two Major Clades of Salsoleae s.l.

Character	Caroxyloneae	Salsoleae s.s.
Life form	Mostly annual, with some hemicryptophytes and subshrubs	Mostly shrubby, subshrubby and even tree; rarely annual
Branches and leaves	Alternate (except <i>Pyankovia</i> and one species of <i>Petrosimonia</i> )	Alternate in basal genera, opposite in most advanced lineages
Assimilation organs	Leaves and sometimes stems by age, never articulated	Leaves and stems, often articulated
Spines at leaf apex	Mostly obtuse, rarely with spine or mucro at apex	Mostly with mucro or spine at apex, rarely obtuse
Cotyledon leaves	Flat, linear, oblong, ovate	Mostly terete and filiform (flat in <i>Anabasis</i> and <i>Halothamnus</i> )
Indumentum	Stem, leaves, and perianths with long multicellular hairs, at least when young	Plants mostly glabrous, with a tuft of flexuose hairs in nodes or axil of leaves and flowers
Type of indumentum	Hairs various; mostly articulate, spinulose, flattened, bladderlike, basifixed, or medifixed	Hairs papillose, unicellular; axial hairs flexuose and multicellular, always basifixed
Anther appendage	Present and mostly separated from theca and vesiculose, discolor with anthers	Mostly absent; if present, small and nonvesiculose, color usually concolor with anthers
Wing on fruiting perianths	Wings mostly present; absent in some genera	Wings always present
Photosynthetic type	Exclusively C <sub>4</sub>	C <sub>4</sub> with a few C <sub>3</sub> and C <sub>3</sub> -C <sub>4</sub> intermediates
C <sub>4</sub> subtype	NAD-malic enzyme	NADP-malic enzyme (with few exceptions)
Ecology	Plants with concentration in temperate deserts on nitrified soil and ruderalized habitats	Plants concentrated mostly in hot deserts rich in sand, gravel, and gypsum
Geography	Mostly central and southwest Asia, northern and southern Africa	As for Caroxyloneae but absent in southern Africa

inflorescence consisting of several flowers surrounded by two or more bracts. This species is most likely to be  $C_3$ , as suggested by its Kranz-less sympegmoid leaf anatomy (Carolin et al. 1975) and a  $-21.6\text{‰}$  carbon isotope ratio. However, the carbon isotope ratio is more positive than is typical for  $C_3$  species, which suggests that more studies on living plants are necessary to exclude the possibility of it functioning as a  $C_3$ - $C_4$  intermediate.

The monophyletic *Halothamnus* clade probably includes 21–23 species, although only four taxa are included here. Most species are concentrated in southwest Asia (Iran and Afghanistan) but also occur widely in central Asia, and one species is found in east Africa (Somalia, Ethiopia, and Djibouti) (Kothe-Heinrich 1993). The monophyly of this genus is well supported (figs. 1A, 2A; mpbs = 100%; mlbs = 100%). This genus can be defined by green annual branches, speciform inflorescence, indurated fruiting perianths that are pitted in the abscission zone, presence of a hypogenous disk, horizontal seeds, absence of Kranz anatomy in cotyledon leaves, and presence of a short anther appendage clearly not separated from the theca. All known species are  $C_4$  with a leaf anatomy lacking a hypodermis layer (Pyankov and Vakhrusheva 1989; Kothe-Heinrich 1993; Akhani et al. 1997).

The *Kali* clade is strongly supported in all analyses (mpbs = 97%; mlbs = 90%). This clade assembles four previously separate taxa in Salsoleae: the genus *Traganum*, *Salsola* sect. *Kali*, *Salsola* sect. *Sogdiana* (sensu Rilke 1999), and *Salsola* sect. *Caroxylon* subsect. *Arbusculae* p.p. (sensu Botschantzev 1976) or *Salsola* sect. *Arbuscula* p.p. (sensu Freitag 1997). Besides sharing similar habitats in sandy deserts or coastal sands, members of this clade can be defined by the combination of morphological characteristics including succulent leaves, nonjointed stems, apiculate to spiny leaf and bract apices, winged fruiting perianths in most species (except *Traganum*), and a cupulate or cylindrical corona above the wings of fruiting perianths. The clade is divided into two well-supported subclades (figs. 1A, 2A). The first of these is the *Kali* subclade, previously classified as *Salsola* sect. *Kali* (sensu Rilke 1999) or *Salsola* sect. *Salsola* s.l. p.p. (Iljin 1936), and is strongly supported (mpbs = 99%; mlbs = 99%). Included here are annual or perennial species with spiny leaf tips that lack a leaf hypodermis. The most important feature characterizing this clade is the green cortex of annual shoots, which are associated with longitudinal striae. The striate lines are chlorenchymotous tissue interrupted by cholenchyma tissue (Rilke 1999). Because the genus *Kali* Miller is validly published (Miller 1754), it is here used for this subclade. We here designate *Kali soda* Moench (Methodus 331, 1794) as the lectotype of *Kali* (see app. A) against two other possibilities: *Kali tragus* (L.) Scop., Fl. Carniol. 1: 775, 1772 (= *Salsola tragus* L., Cent. Pl. 2: 13, 1756) and *Kali rosacea* (L.) Moench, suppl. Meth. Plant. 115, 1804 (= *S. rosacea* L., Sp. Pl. 222, 1753). *Kali soda* was validly described under *Salsola kali* L., Sp. Pl.: 222, 1753, 1 yr earlier than the description of the genus *Kali* in 1754 (Rilke 1999), and it is among the oldest names of species in this genus (1753).

The second subclade of the *Kali* clade is a heterogeneous assemblage of small trees, shrubs, subshrubs, and annual species distributed in extreme deserts of central Asia and north Africa, primarily as components of sandy ecosystems. Its

monophyly is well supported (mpbs = 89%; mlbs = 80%); it is composed of species previously placed in *Salsola* sect. *Sogdiana* (Iljin) Rilke, *Salsola* sect. *Androssowia* Rilke (sensu Rilke 1999), *Salsola* sect. *Caroxylon* subsect. *Arbusculae* p.p. (sensu Botschantzev 1976), and the monotypic genus *Traganum*. Based on the topology of the tree and distribution of morphological features in the group, three well-supported genera are here distinguished: *Xylosalsola*, *Traganum*, and *Turania*. *Xylosalsola* Tzvelev includes  $C_4$  species of *Salsola* sect. *Caroxylon* subsect. *Arbuscula* p.p. (Botschantzev 1976) or *Salsola* sect. *Arbuscula* p.p. (sensu Freitag 1997). These are shrubby species of central Asia characterized by long terete linear leaves, solitary flowers, milky white and shining young stems, overlapping fruiting perianths that form a corona-like structure above the winged fruiting perianths, and presence of a minute anther appendage (Botschantzev 1976; Freitag 1997).

The small genus *Traganum* includes two north African/eastern Mediterranean species, one of which is sampled here. These are small shrubs with woolly nodes and semiterete leaves. The fruiting perianths are indurated throughout, have two hornlike teeth, and lack a wing. The leaves reportedly lack a hypodermis layer (Carolin et al. 1975), which separates this genus from other lineages in this subclade of the *Kali* clade.

The third lineage of this subclade includes species previously classified in *Salsola* sect. *Salsola* (Iljin 1936) or *Salsola* sect. *Sogdiana* (Iljin) Rilke and *Salsola* sect. *Androssowia* Rilke (Rilke 1999). These central Asian annual species have succulent flat or semiterete leaves with a short (0.5 mm) or long (5 mm) spine at the apex, a leaf hypodermis layer, and cupulate fruiting perianths that are somewhat connate at the base and give the ovary a false-inferior appearance. Furthermore, they have filiform stigmas that are very long, up to three to five times as long as the style. Given the clear morphological circumscription of these species, we are here recognizing this clade as the genus *Turania* (see app. A).

The *Salsola* clade is a complex assemblage of genera in Salsoleae but is moderately supported in the phylogenetic hypotheses presented here (mpbs = 72%; mlbs = 65%). This lineage includes taxa occurring from central and southwest Asia to the north African and Mediterranean areas. The monophyly of the clade is supported by several morphological features including presence of a spine or mucro on leaf tips that sometimes appears as a caducous bristle and most species being completely glabrous or having papillose or tubercle-like hairs. Many groups are represented by opposite leaves or branches, and stamens have no or very short anther appendages. Many genera have been previously described in this clade, and most of them are supported by the phylogenetic hypotheses (figs. 1A, 2A).

The genus *Salsola* was typified by *Salsola soda* (Jarvis et al. 1993; see Rilke 1999 for details), which is nested within a homogenous group of species that have been variously placed in several genera in previous classifications. The monophyly of this clade is well supported (mpbs = 84%; mlbs = 79%). In spite of the morphological synapomorphies that strongly support this clade, species of this clade have been placed by various authors in several sections of *Salsola*, including sect. *Salsola* (Rilke 1999), sect. *Obpyrifolia* (Botschantzev

and Akhani 1989), sect. *Caroxylon* subsect. *Coccosalsola* (Botschantzev 1976, 1989), and sect. *Coccosalsola* (Freitag 1997), or have been classified into other genera, including *Seidlitzia* Bunge ex Boiss. (Iljin 1954), *Hypocylix* Woloszczak (Woloszczak 1885), *Darniella* Maire & Weiller (Brullo 1984), *Neocaspi* Tzvelev (Tzvelev 1993), *Caspia* (Galushko 1976), *Fadenia* (Aellen and Townsend 1972), and *Anabasis* p.p. The most obvious synapomorphy of *Salsola* s.s. as treated here is the presence of clusters of two to six flowers (or, rarely, one) in the axil of each floral leaf. Further characters include absence or presence of a very minute anther appendage, presence of a hypogynous disk or staminode (much reduced in *S. soda*), presence of a leaf hypodermis, cylindrical and obtuse leaves (more often obpyriform, at least in the juvenile state or in bracts) that are opposite in most species, and fruiting perianths with well-developed wings (reduced in *S. soda*). A surprising result is the inclusion of the tropical African monotypic genus *Fadenia* in *Salsola* (Aellen and Townsend 1972). *Fadenia zygophylloides* is known from Kenya, Ethiopia, and Somalia and was previously separated from all other species of Salsoloideae by the fruiting perianths having longitudinal membranous crests. This species has been previously classified in subtribe Sevadinae (Botschantzev 1967, 1975c; Boulos et al. 1991). Although we have not sampled all species of the complex, there is little doubt that all species treated under the genus *Darniella* by Brullo (1984) and the genus *Seidlitzia* by Iljin (1954) belong to *Salsola* s.s.

With the exclusion of *Anabasis setifera*, the rest of the genus *Anabasis* forms a well-supported monophyletic group (mpbs = 99%; mlbs = 96%). The monophyly of this clade is supported by the combination of several morphological features, including a perennial and shrubby habit, a thick basal caudex (mostly woolly), opposite leaves and branches, vertical seeds, fleshy utricle that resembles a berrylike fruit in several species, articulated branches, vestigial leaves in most species (in *Anabasis eugeniae*, the leaves are developed), and the presence of a multilayered epidermis and sunken stomata (Bokhari and Wendelbo 1978). Ecologically, most species are extreme xerohalophytic species and frequently grow on halogypsum soils. The genus *Anabasis* is distributed from southwest Europe and north Africa to the Red Sea coast (Ethiopia) and southwest and central Asia.

The monophyly of the genus *Halogeton* is strongly supported by all analyses (mpbs = 100%; mlbs = 100%). This is a small genus of approximately five species, including both annual (in temperate salines and ruderal places) and perennial species (in warm and hot deserts). The genus is well defined by the combination of fleshy cylindrical leaves terminating in a persistent or caducous bristle, presence of three to several flowers in the axil of each floral leaf, presence of a papillose staminodial disk, presence of five wings on fruiting perianths, and membranous perianth segments. Some authors have removed the perennial species to the genus *Agathophora* (Botschantzev 1977; Hedge 1997). Our results support a monophyletic clade including both annual and perennial species; however, because only one of each is sampled here, future studies will be necessary to explore whether the two growth forms form monophyletic sister lineages.

*Girgensohnia*, *Cyatobasis*, and two species of *Hammada* form a clade in the analyses presented here, although it is

weakly supported. The central Asian and Persian genus *Girgensohnia* includes approximately four or five species, three sampled in this study, and forms a monophyletic well-supported group (mpbs = 96%; mlbs = 86%). Morphologically, the genus is well defined by an annual life form, opposite leaves and branches, presence of an indumentum of scabrid papillae, semiamplexicaule leaves with a scariosus base and spine-tipped apex, and vertical seeds. The species of *Girgensohnia* are ruderal and sometimes weedy species on low salty soils in the deserts of central Asia and Iran. The monotypic central Anatolian genus *Cyatobasis* was described by Aellen (1949), who distinguished it from *Girgensohnia* by characters such as elongate styles, a noncapitate stigma, and connate leaf base. Our analyses suggest that this species, together with *Hammada articulata* and *Hammada griffithii*, forms a grade leading to *Girgensohnia* s.s. These results and shared morphological characters suggest that a wider circumscription of the genus *Girgensohnia*, including *Cyatobasis* and *Hammada* p.p. and probably the other species of *Arthrophytum*, is appropriate.

Analysis of two of the approximately six species of *Cornulaca* reveals a strongly monophyletic group (mpbs = 100%; mlbs = 100%). The genus is characterized by a sturdy habit, alternate branches, decurrent strongly spiny leaves and bracts, presence of a dense white tuft of hairs among and at the base of flowers, membranous perianth segments that become indurated and coalescent in fruit, one (sometimes two) terminal perianth spine, filaments connating into a tube, and vertical seeds. *Cornulaca* species occur in central and southwest Asia and northern Africa on sandy or dry soils and can tolerate long periods of drought (H. Akhani, personal observation). The genus is sister to *Horaninowia*, another spiny genus, but is clearly separated by other morphological characteristics (see next paragraph).

*Horaninowia* is a well-supported monophyletic genus in our analyses (mpbs = 88%; mlbs = 73%). There are approximately seven spiny annual species that are characterized by a green cortex, the presence of unicellular papillae, spiny-tipped leaves and bracts, solitary flowers in hairy leaf axils, exappendiculate anthers, perianths in fruit becoming hardened in the upper middle, capitate or clavate stigmas, and horizontal seeds (Carolin et al. 1975). Species of *Horaninowia* are restricted in their range to central Asia and Iran, growing on sandy dunes or gravelly deserts. The phylogenetic analyses and morphological features clearly support a close relationship with *Cornulaca* (figs. 1A, 2A).

The traditional circumscription of *Haloxyton* (Iljin 1936) includes only tall shrub to small tree species and is well supported in these analyses (mpbs = 100%; mlbs = 100%). The two species, *Haloxyton ammodendron* and *Haloxyton persicum*, are found in central and southwest Asia and occur on sandy dunes or dry salty habitats close to the margins of playas, where their long roots have access to underground salty water (Léonard 1991; Akhani et al. 2003; Akhani 2004). The combination of unique tree life form with articulated branches, horizontal seeds, occurrence of an arista at the scalelike leaf apex, presence of a hypodermis layer in assimilating shoots, and the isopalisade cotyledon leaves without Kranz anatomy (Pyankov et al. 1999), characterizes the genus. Bunge (1879) and Hedge (1997) proposed a broader circumscription of this

genus, including species from other genera such as *Arthrophytum* and *Hammada*, but this is not supported by the phylogenetic hypotheses presented here (figs. 1A, 2A).

The genera *Hammada* and *Arthrophytum* have been interpreted differently by different authors. Hedge (1997) and Boulos (1996) considered them congeneric with *Haloxylon*. The three species we have analyzed (*Hammada salicornica*, *Hammada articulata*, and *Hammada griffithii*) are not closely associated with *Haloxylon* and may form early lineages of the *Girgensohnia/Cornulaca/Horaninowia* clade (fig. 2A), although these relationships are not well supported and are placed differently by the MP strict consensus (fig. 1A) but, again, with little support.

The phylogenetic hypotheses presented suggest a possible clade including the C<sub>3</sub> *Salsola montana* complex, *Salsola arbusculiformis*, *Raphydophytum regelii*, and the genus *Noaea* (fig. 2A). This clade, however, is not strongly supported and is not present in the MP strict consensus (fig. 1A). The placement of the C<sub>3</sub>-C<sub>4</sub> intermediate *Salsola arbusculiformis* (Voznesenskaya et al. 2001a) between *Salsola montana* and *Noaea*, a C<sub>4</sub> genus, might demonstrate an interesting case of transition in photosynthetic pathway across a clade. Given the weak phylogenetic placement of *S. arbusculiformis* in the phylogenetic hypotheses presented here, we are only informally recognizing this species as “Collinosalsola” and will await further evidence of its phylogenetic position before formally placing the species. The small subshrub *Raphydophytum* is characterized by stiff and spinescent leaves that are acicular and three-angular in cross section, with scabrid margins and a dilated base. The perianths bear wings near the base, and the filaments produce a staminal tube with well-developed semiorbicular lobes on the hypogynous disk.

All known species of *Noaea* are included in our phylogenetic analyses, and its monophyly is well supported (mpbs = 100%; mlbs = 100%). This genus is characterized by alternate branches, leaves spiny tipped or cuspidate at the base with broad white membranous margins, and vertical seeds. All three species grow in temperate and cold-temperate deserts or montane and submontane steppe vegetation, which is not typical for C<sub>4</sub> species.

The *S. montana* complex was classified in *Salsola* sect. *Anchophyllum* by Iljin (1936), sect. *Caroxylon* subsect. *Arbusculae* by Botschantzev (1976), and sect. *Arbuscula* by Freitag (1997). The complex includes subshrubby species that differ from species of previously mentioned *Salsola* s.l. groups in having not only green young stems but also a sympegmoid leaf anatomy (Akhani and Ghasemkhani 2007), filaments attached to the disk without staminodes, and anthers divided only to two-thirds of their length. The precise phylogenetic position of this strongly supported clade (mpbs = 100%; mlbs = 100%) is not clear, and we are therefore here treating this complex as the informal taxonomic entity “Oreosalsola” (see app. A).

The *S. montana* species complex represents an assemblage of microspecies (*Salsola maracandica* Iljin, *Salsola oreophila* Botsch., *Salsola masenderanica* Botsch., *Salsola botschantzevii* Kurbanov, *Salsola flexuosa* Botsch., *Salsola tianschanica* Botsch., *Salsola lipschitzii* Botsch., *Salsola junatovii* Botsch., and *S. montana* Litw.), which are collectively included in a broadly defined *S. montana* by Freitag (1997). We have here examined three populations in this complex, one from Golestan

National Park (*S. montana*), one from the Alborz mountains (*S. masenderanica*), and “*Salsola touranica*,” an undescribed but likely distinct entity from the Touran Protected Area of Iran. Members of this species complex need to be studied further in order for us to understand where species boundaries lie and whether one or eight or more species should be recognized.

*Salsola divaricata* was included in *Salsola* sect. *Caroxylon* subsect. *Coccosalsola* by Botschantzev (1976, 1989). This shrubby species is endemic to the Canary Islands and is distinctive in having opposite leaves, mature leaves that are triangular in cross section, and leaves with one layer of hypodermis, two layers of palisade parenchyma, scattered peripheral vascular bundles, and a central aqueous tissue. Morphologically, it is very similar to species of *Salsola* s.s., but this species does not strongly group with *Salsola* s.s. Given its unclear phylogenetic position and the need to sample the similar C<sub>3</sub> Mediterranean/north African/central Asian species *Salsola genistoides*, *Salsola webbii*, and *Salsola pachyphylla*, no nomenclatural changes are here proposed.

#### Classification and Relationships in Clade Caroxyloneae

Three major clades can be distinguished in Caroxyloneae, which are here labeled as the *Caroxylon* clade (mpbs = 88%; mlbs = 93%), the *Kaviria* clade (mpbs = 86%; mlbs = 87%), and the *Climacoptera* clade (mpbs = 77%; mlbs = 83%). Two of the three clades can be divided further into two or more monophyletic lineages, which in most cases correspond with traditional classifications of Salsoleae genera. However, the relationship and generic circumscription of several closely related annual genera in this clade, including *Halanthium*, *Halimocnemis*, *Halotis*, *Gamanthus*, *Climacoptera*, *Piptoptera*, *Halocharis*, *Halarchon*, *Petrosimonia*, and *Physandra*, has been controversial (Pratov 1986; Akhani 1996; Hedge 1997; Assadi 2001; Ghobadnejhad et al. 2004). These euhalophytic and xerohalophytic species are endemic to the Irano-Turanian area, primarily in temperate deserts of central Asia, Afghanistan, and Iran. Except *Petrosimonia*, with connate cagelike anther appendages, all species are characterized by large, often showy and colorful (white, yellow, or purple) vesiculate anther appendages, which apparently act as an attractor for insect pollinators and may also contribute as a wind-dispersal device for anthers and pollen grains, depending on the species.

The *Caroxylon* clade includes a large group of species traditionally classified as *Salsola* sects. *Caroxylon* p.p. (subsect. *Caroxylon*, subsect. *Vermiculatae*), *Cardiandra*, *Irania*, and *Malpigipila* and two species of sect. *Belanthera* (*Salsola canescens* and *Salsola carpatha*). The monophyly of this clade is well supported (figs. 1B, 2B). This is the most widespread lineage of Salsoleae s.l., with ca. 140 described species, being found in central Asia, Arabia, and northern and southern Africa (Botschantzev 1968, 1969a, 1969c, 1970, 1972, 1974a, 1974b, 1975b, 1975d, 1980, 1986; Freitag 1997). Our phylogeny includes 19 species covering most known lineages and geographic areas. The clade is morphologically heterogeneous, although the presence of an acute anther appendage, winged perianth segments, a gibbous leaf base, and a staminal disk provides a combination of characters that distinguishes the clade. The oldest generic name for species in this clade is *Caroxylon* Thunb. It was reduced to a section of *Salsola* by several

subsequent authors (Fenzl 1851; Iljin 1936) but recognized at the generic level by Tzvelev (1993), which is supported by our data. Relationships within *Caroxylon* are generally weakly supported (figs. 1B, 2B) and will require further study to clarify.

The *Kaviria* clade includes species traditionally classified in *Salsola* sect. *Belanthera* (excluding *S. canescens*, *S. carpatha*, and other microspecies classified in subsect. *Kochioides* by Botschantzev [1968, 1980]), the oligotypic genus *Halocharis*, and the monotypic genus *Nanophyton* (figs. 1B, 2B). The combination of the C<sub>3</sub> cotyledon leaves, the absence of a leaf hypodermis, and the presence of an acute triangular anther appendage that is separated from the thecae circumscribes this clade well, and morphological and ecological features clearly separate each of these three lineages from each other (table 4). *Salsola* sect. *Belanthera* is here named *Kaviria* (see app. A) after the Persian term “Kavir,” a name used to refer to the Iranian Great Desert.

The *Climacoptera* clade is composed of a lineage including *Petrosimonia* and *Ofaiston*, which is sister to the remainder of the clade (figs. 1B, 2B). This is an exclusively Irano-Turanian species group that predominantly occurs in annual halophytic and xerohalophytic communities of central and southwest Asia. *Petrosimonia* and *Ofaiston* are quite distinct morphologically, and *Petrosimonia* is supported as monophyletic in all analyses. *Ofaiston* is characterized by having only one or two stamens and three to five perianth parts (tepals), strongly keeled bracteoles, and small wings on two tepals (Iljin 1936). In *Petrosimonia*, the anther appendages are connate at the apex, creating a cagelike structure, and wings are completely absent from the membranous tepals.

The remainder of the *Climacoptera* clade is strongly supported (mpbs = 100%; mlbs = 100%). All of the genera within this clade are para- or polyphyletic, including *Climacoptera*, *Gamanthus*, *Halanthium*, and *Halimocnemis* (figs. 1B, 2B). The majority of the members of several genera form strongly supported clades, and clear lineages can be defined in several cases. If *Climacoptera brachiata* is excluded from the rest of the genus, *Climacoptera* forms a strongly supported monophyletic genus (mpbs = 100%; mlbs = 100%). *Climacoptera* was segregated from *Salsola* by Botschantzev (1956); however, it was considered as *Salsola* sect. *Physurus* by Freitag (1997). The presence of five winged perianths in fruit, strongly fleshy, glaucous, and mostly decurrent floral leaves, a main central erect stem, and an interrupted Kranz layer on the adaxial leaf surface define the genus. The number of species in this lineage is unclear, as different authors have recognized from as many as 42 species (Pratov 1986) to as few as six (Freitag 1997). Preliminary evidence from Iran (H. Akhani, unpublished data) suggests that approximately eight to 10 species are distinguishable, as opposed to only two species recognized in *Flora Iranica* by Freitag (1997).

*Climacoptera brachiata* has been variously treated as a member of *Salsola* sect. *Heterotricha* Iljin (Iljin 1936), *Climacoptera* (Botschantzev 1956), *Climacoptera* sect. *Heterotricha* Iljin ex Pratov (Pratov 1986), and *Salsola* sect. *Belanthera* (Freitag 1997). Based on the characteristic opposite leaves (except uppermost floral leaves), small obtuse anther appendage, and presence of a spinulose indumentum with long smooth articulate hairs, it is well separated from the other genera of the *Climacoptera*

Table 4

Morphological and Anatomical Comparison of Genera in the *Kaviria* Clade

Character	<i>Kaviria</i>	<i>Halocharis</i>	<i>Nanophyton</i>
Habit	Undershrub, rarely annual, erect to ascending	Annual, prostrate	Pulvinate undershrub, with stout woody base, erect
Inflorescence (flowers in each floral leaf axis)	Solitary	Solitary to several	Solitary
Indumentum	Spinulose, branched, scabrid, articulated	Articulated, scabrid hairs, multicellular flexuous hairs on axil of flowers	Multicellular, smooth flexuous hairs in leaf and flower axils
Leaf shape	Terete to semiterete, succulent, hairy or glabrous throughout	Terete, strongly succulent, with one or a few bristlelike hairs at apex	Semiterete to triangular in section, spiny tipped
Leaf base	Slightly gibbous	Gibbous	Not gibbous
Hypodermis	Absent	Absent	Present
Central vascular bundle (VB)	VB associated with sclerenchymatous tissue	VB lacking sclerenchymatous tissue	VB associated with sclerenchymatous tissue
Fruiting perianth	Winged or with small transversal line	Scarious, wingless	Enlarged and inflated in fruit but without wing
Seeds	Horizontal, rarely vertical	Vertical	Vertical
Hypogynous disc	Hypogynous disk present, without or with short interstaminal lobes	Filaments not narrowed to base, hypogynous disk absent	Filament not narrowed to base, located at hypogynous disk with staminode lobes
Anther	Triangular, appendage scabrous	Appendage divided to the base, appendage vesiculous or triangular, papillose	Anthers divided to the apex, appendage triangular, smooth
Stigma	Flat, shortly dentate	Terete, not dentate	Terete, not dentate
Ecology	Dry gravelly and slightly salty soils	High salty clay soils	Xerophytic communities

clade. Given the isolated phylogenetic position of this species and its distinctive combination of characteristics, we feel it is best treated as a monotypic genus, here named *Pyankovia* (see app. A) in honor of the late professor Vladimir Pyankov.

The remainder of the species in the *Climacoptera* clade belong to four genera: *Gamanthus*, *Halanthium*, *Halotis*, and *Halimocnemis*. The relationships and generic boundaries of these genera have been debated (Akhani 1996; Hedge 1997; Assadi 2001; Ghobadnejhad et al. 2004). The phylogenetic results presented here suggest the possibility of four lineages, although the relationships among these lineages and clade membership are generally poorly supported (figs. 1B, 2B), and whether there are consistent morphological characters by which to define these clades is unclear. Further, there are entanglements of the types of some genera (e.g., *Gamanthus pilosus* nested within the *Halanthium* clade, separate from the rest of *Gamanthus*). While a case could be made for either rejecting the current lectotype of *Gamanthus* or renaming the rest of the *Gamanthus* clade under a new name (given its strong support), we consider the recognition of all of these species within *Halimocnemis* to be the best option at this time, at least until the generic boundaries and nomenclatural problems can be untangled. While this group is not present in the MP strict consensus, it is present in the most likely tree, albeit with low support (58%). Because *Halimocnemis* and *Halotis* are very similar morphologically and were previously merged by Hedge (1997), and the phylogenetic hypotheses places *Halimocnemis purpureum* and *Halotis pedunculata* among *Halanthium* species (see Akhani 1996; Hedge 1997), we feel the combination of these genera to be a reasonable compromise, despite the low branch support.

The monotypic genus *Piptoptera* was amplified only for *psbB-psbH*, confirming that it is not a well-supported member of any of the clades described above, which corresponds with its morphological isolation. It is weakly placed among *Halanthium* and *Gamanthus* species. This might suggest its inclusion in the more broadly circumscribed *Halimocnemis*, but formal inclusion in that genus will require further data, particularly given the peculiar features of this genus of sturdy habit with adpressed indumentum and development of two large, circular perianth wings.

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## Appendix A

### A Revised Classification of Salsoleae s.l.

Here we present a synopsis of generic circumscriptions and new combinations resulting from this study, where both strong molecular and morphological support necessitate changes. To save space, we have included only the most necessary nomenclatural data. Therefore, most synonyms and citations are not included in this article. A detailed morphological, taxonomical, and anatomical assessment of tribes Camphorosmeae, Caroxyloneae, and Salsoleae awaits future publication.

#### Tribe Salsoleae s.s.

*Anabasis* L., Sp. Pl. 223, 1753. Type: *Anabasis aphylla* L.

Includes *Anabasis aphylla* L., *A. aretioides* Moq. & Coss., *A. articulata* (Forssk.) Moq., *A. brevifolia* C. A. Mey., *A. brachiata* Fisch. & C. A. Mey., *A. calcarea* (Charif & Aellen) Bokhari & Wendelbo, *A. cretacea* Pall., *A. ebracteolata* Korov. ex Botsch., *A. ehrenbergii* Schweinf. ex Boiss., *A. elatior* (C. A. Mey.) Schrenk, *A. eriopoda* (Schrenk) Benth. ex Volkens, *A. eugeniae* Iljin, *A. ferganica* Drob., *A. gypsicola* Iljin, *A. haussknechtii* Bunge ex Boiss., *A. iranica* Iljin, *A. jaxartica* (Bunge) Benth. ex Volkens, *A. lachmantha* Aellen & Rech. f., *A. paucifolia* M. Pop. ex Iljin, *A. pelliottii* Danguy, *A. macroptera* Moq., *A. prostrata* Pomel., *A. oropediorum* Maire, *A. salsa* (C. A. Mey.) Benth. ex Volkens, *A. syriaca* Iljin, *A. tianschanica* Botsch., *A. truncata* (Schrenk) Bunge, *A. turkestanica* Iljin & Korov., and *A. turgaica* Iljin & Krasch.

*Arthrophytum* Schrenk, Bull. Phys. Math. Acad. Petrop. 3: 211, 1845. Type: *A. subulifolium* Schrenk.

Includes *Arthrophytum gracile* Aellen, *A. iliense* Iljin, *A. balchaschense* (Iljin) Botsch., *A. lehmannianum* Bunge, *A. pulvinatum* Litv., *A. subulifolium* Schrenk, *A. longibracteatum* Korov., *A. korovinii* Botsch., and *A. betpakdalense* Korov. (Korovin and Mironov 1935).

*Cornulaca* Delile, Flore d'Egypte—explic. des planches 72, 1813. Type: *Cornulaca monacantha* Delile.

Includes *Cornulaca alaschanica* C. P. Tsien & G. L. Chu, *C. aucheri* Moq., *C. ehrenbergii* Asch., *C. korshinskyi* Litv., *C. monacantha* Delile, and *C. setifera* (DC.) Moq. (Aellen 1950; Boulos 1992).

*Girgensohnia* Bunge ex Fenzl in Ledeb., Fl. Ross. 3: 835, 1851. Type: *Girgensohnia oppositiflora* (Pall.) Fenzl.

Includes *Girgensohnia diptera* Bunge, *G. imbricata* Bunge, *G. minima* E. Korov., and *G. oppositiflora* (Pall.) Fenzl.

*Halogeton* C. A. Mey. in Ledeb., Icon. Pl. Fl. Ross. 1: 10, 1829. Type: *Halogeton glomeratus* (M. Bieb.) C. A. Mey. Synonyms: *Agathophora* (Fenzl) Bunge, *Micropeplis* Bunge.

- Includes *Halogeton alopecuroides* (Delile) Moq., *H. arachnoideus* Moq., *H. glomeratus* (M. Bieb.) C. A. Mey., *H. sativus* (L.) Moq., and *H. tibeticus* Bunge (Bunge 1862; Botschantzev 1977).
- Halothamnus* Jaub. & Spach, Illustr. Pl. Or. 2: 50, tab. 136, 1845. Type: *Halothamnus bottae* Jaub. & Spach. Synonym: *Aellenia* Ulbr.
- Includes *Halothamnus beckettii* Botsch., *H. somalensis* (N. E. Br.) Botsch., *H. bottae* Jaub. & Spach, *H. iranicus* Botsch., *H. hierochunticus* (Bornm.) Botsch., *H. iliensis* (Lipsky) Botsch., *H. auriculus* (Moq.) Botsch., *H. kermanensis* Kothe-H., *H. afghanicus* Kothe-H., *H. lancifolius* (Boiss.) Kothe-H., *H. cinerascens* (Moq.) Kothe-H., *H. glaucus* (M. Bieb.) Botsch., *H. bamianicus* (Gilli) Botsch., *H. shurabi* Botsch., *H. turcomanicus* Botsch., *H. ferganensis* Botsch., *H. sistanicus* (De Marco & Dinelli) Kothe-H., *H. oxianus* Botsch., *H. seravschanicus* Botsch., *H. iraqensis* Botsch., and *H. subaphyllus* (C. A. Mey.) Botsch. (Aellen 1950; Botschantzev 1981b; Kothe-Heinrich 1993).
- Haloxydon* Bunge, Rel. Lehm. in Mém. Sav. Etrang. Petersb. 7: 468, 1851. Type: *Haloxydon ammodendron* (C. A. Mey.) Bunge ex Fenzl.
- Includes *Haloxydon ammodendron* (C. A. Mey.) Bunge and *H. persicum* Bunge ex Boiss.
- Hammada* Iljin, Bot. Zhurn. 33: 582, 1948. Type: *Hammada leptoclada* (M. Popov) Iljin.
- Includes *Hammada articulata* (Moq.) O. Bolós & Vigo, *H. eigii* Iljin, *H. griffithii* (Moq.) Iljin, *H. multiflora* (Moq.) Iljin, *H. negevensis* Iljin & Zoh., *H. ramosissima* (Boiss.) Iljin, *H. salicornica* (Moq.) Iljin, *H. schmittiana* (Pomel) Botsch., *H. scoparia* (Pomel) Iljin, *H. thomsoni* (Bunge) Iljin, and *H. tamariscifolia* (L.) Iljin, and *H. wakhanica* (Paulsen) Iljin (Iljin 1948).
- Horaninowia* Fisch. & C. A. Mey., Enum. Pl. Nov. Schrenk 1: 10, 1841. Type: *Horaninowia ulicina* Fisch. & C. A. Mey.
- Includes *Horaninowia anomala* (C. A. Mey.) Moq., *H. excellens* Iljin, *H. minor* Fisch. & C. A. Mey., *H. platyptera* Charif & Aellen, *H. pungens* (Gilli) Botsch., and *H. ulicina* Fisch. & C. A. Mey. (Aellen 1950).
- Kali* Mill., Gard. Dict. Abr. Ed. 4, 1754. (= *Salsola* sect. *Kali* Dumort; Rilke 1999). Type (lectotype selected here): *Kali soda* Moench, Method 331, 1794. = *Salsola kali* L., Sp. Pl.: 222, 1753.
- Kali australis* (R. Br.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola kali* R. Br. Prodr. 411, 1810.
- Kali griffithii* (Bunge) Akhani & E. H. Roalson, comb. nov. Basionym: *Noaea griffithii* Bunge, Mém. Acad. Imp. Sci. St. Pétersb., Sér. 7, 4, 11: 22–23, 1862.
- Kali tamariscina* (Pall.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola tamariscina* Pall., Illustr. Pl. 33, 1803.
- Kali collina* (Pall.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola collina* Pall., Illustr. Pl.: 34, 1803.
- Kali zaidamica* (Iljin) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola zaidamica* Iljin, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 17: 122–124, 1955.
- Kali tamamschjanae* (Iljin) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola tamamschjanae* Iljin, Trudy Bot. Inst. Akad. Nauk. SSSR, ser. 1: 161, 1936.
- Kali jacquemontii* (Moq.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola jacquemontii* Moq. in DC. Prodr. 13, 2: 188, 1849.
- Kali komarovii* (Iljin) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola komarovii* Iljin, Bot. Zhurn. SSSR 18, 2: 276, 1933.
- Kali ikonnikovii* (Iljin) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola ikonnikovii* Iljin, Izv. Glavn. Bot. Sada Akad. Nauk SSSR 30: 748, 1931.
- Kali paulsenii* (Litv.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola paulsenii* Litv., Izv. Turkestansk. Otd. Imp. Russk. Geogr. Obshch. 4, 5: 28, 1905 and in Sched. Herb. Fl. Ross. 5: 29, No. 1431, 1905.
- Other species recognized include *Kali soda* Moench (= *Salsola kali* L.), *K. tragus* (L.) Scop., and *K. rosacea* (L.) Moench.
- Noaea* Moq. in DC., Prodr. 13, 2: 207 (1849). Type: *Noaea mucronata* (Forssk.) Aschers. & Schweinf.
- Includes *Noaea major* Bunge, *N. minuta* Boiss. & Bal., and *N. mucronata* (Forssk.) Aschers. & Schweinf.
- Rhaphidophyton* Iljin, Tr. Bot. Inst. Akad. Nauk SSSR I, Fl. Sist. Vyss. Rast. 3: 157, 1936. Type: *Rhaphidophyton regelii* (Bunge) Iljin.
- Includes *Rhaphidophyton regelii* (Bunge) Iljin.
- Salsola* L., Sp. Pl. ed. 1: 222, 1753. Type: *Salsola soda* L. Synonyms: *Darneilla* Maire & Weiller, *Fadenia* Aellen & Townsend, *Neocaspiya* Tzvelev, *Hypocylix* Wol., *Seidlitzia* Bunge ex Boiss., *Salsola* sect. *Coccosalsola* Fenzl subsect. *Coccosalsola*, and *S.* sect. *Obpyrifolia* Botsch. & Akhani (Woloszczak 1885; Iljin 1954; Aellen and Townsend 1972; Botschantzev 1976; Brullo 1984; Botschantzev 1989; Botschantzev and Akhani 1989; Tzvelev 1993; Rilke 1999).
- Salsola setifera* (Moq.) Akhani, comb. nov. Basionym: *Anabasis setifera* Moq., Chenopod. Monogr. 164, 1840.
- Salsola rosmarinus* (Ehrenb. ex Boiss.) Akhani, comb. nov. Basionym: *Seidlitzia rosmarinus* Ehrenb. ex Boiss., Fl. Or. 4: 951, 1879.
- Salsola zygophylloides* (Aellen & Townsend) Akhani, comb. nov. Basionym: *Fadenia zygophylloides* Aellen & Townsend, Kew Bull. 27: 501, 1972.
- Other species recognized include *Salsola acutifolia* (Bunge.) Botsch., *S. cruciata* Chevall. ex Batt. & Traubert, *S. cyrenaica* (Maire & Weiller) Brullo, *S. drummondii* Ulbr., *S. florida* (M. Bieb.) Poir, *S. foliosa* (L.) Schrad., *S. grandis* Freitag, Vural & N. Adigüzel, *S. glomerata* (Maire) Brullo, *S. gymnomaschala* Maire, *S. kernerii* (Wol.) Botsch., *S. longifolia* Forssk., *S. makranica* Freitag, *S. melitensis* Botsch., *S. oppositifolia* Desf., *S. papillosa* Willk., *S. schweinfurthii* Solms-Laub., *S. sinaica* Brullo, *S. soda* L., *S. stocksii* Boiss., *S. tunetana* Brullo, *S. verticillata* Schousboe, and *S. zygophylla* Batt. & Traub.
- Sympegma* Bunge, Bull. Acad. St. Pétersb. 25: 351, 371, 1879. Type: *Sympegma regelii* Bunge.
- Includes *Sympegma regelii* Bunge.
- Traganum* Del., Fl. Égypte: 204, 113–1814. Type: *Traganum nudatum* Del.
- Includes *Traganum nudatum* Del. and *T. moquini* Webb.
- Traganopsis* Maire et Wilczek, Bull. Soc. Hist. Nat. Afr. N. 27: 67, 1936. Type: *Traganopsis glomerata* Maire & Wilczek.
- Includes *Traganopsis glomerata* Maire & Wilczek.
- Turania* Akhani & E. H. Roalson, gen. nov. Type: *Turania sogdiana* (Bunge) Akhani; basionym: *Salsola sogdiana* Bunge, Mém. Acad. Imp. Sci. St. Pétersb. Divers Savans 7: 473, 1852. Synonyms: *Salsola* sect. *Sogdiana* (Iljin) Rilke, Rev. Sect. *Salsola* Gatt. *Salsola* 69, 1999; *S.* sect. *Androssowia* Rilke, Rev. Sect. *Salsola* Gatt. *Salsola* 77, 1999.
- Plantae annuae. Foliae, bracteeae bracteolaeque spina terminatae. Antherae per 3/4 vel 4/5 longitudinem incisae, minute appendiculatae. Stigmata 2 quam stylus multo (3–4 x) longiora. Flores in axilibus singulae. Tepala fructificantia alata; tubus patelliformis, induratus; semina valde complanata. A *Kali* caule non striato, antheris per 3/4 vel 4/5 longitudinem (nec usque medium tantum) incis differt.
- Turania sogdiana* (Bunge) Akhani, comb. nov. Basionym: *Salsola sogdiana* Bunge, Mém. Acad. Imp. Sci. St. Pétersb. Divers Savans 7: 473, 1852.



*Turania aperta* (Paulsen) Akhani, comb. nov. Basionym: *Salsola aperta* Paulsen, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn. 6, 5: 197, 1903.

*Turania androssowii* (Litw.) Akhani, comb. nov. Basionym: *Salsola androssowii* Litw., Sched. Herb. Fl. Ross. 6: 111, No. 1890, 1908.

*Turania deserticola* (Iljin) Akhani, comb. nov. Basionym: *Salsola deserticola* Iljin, Bot. Zhurn. SSSR 18: 277, 1933.

*Xylosalsola* Tzvelev in Ukr. Bot. Zhurn., 50 (1): 81, 1993. Type: *Salsola arbuscula* Pall. Synonym: *Salsola* section *Coccosalsola* Fenzl subsection *Arbuscula* (Ulbrich) Botsch. p.p.

*Xylosalsola richteri* (Moq.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola arborescens* L. fil. var. *richteri* Moq. in DC., Prodr. 13, 2: 185, 1849; *S. richteri* (Moq.) Karel. ex Litw.

*Xylosalsola paletzkiiana* (Litw.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola paletzkiiana* Litw., Sched. Herb. Fl. Ross. 50: no. 2569, 1914.

*Xylosalsola chiwensis* (M. Pop.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola chiwensis* M. Pop. in Pochv. Issl. V Bass. R. Syr-Dar'i i Amu-Dar'i, 1, 1915; 49; in O. et B. Fedtsch. Consp. Fl. Turk. 7: 355, 1916.

Other species recognized include *Xylosalsola arbuscula* (Pall.) Tzvelev.

Tribe Salsoleae incertae sedis

“Canarosalsola”: *Salsola divaricata* Masson ex Link.

“Collinosalsola”: *Salsola arbusculiformis* Drob. and *S. laricifolia* Turcz. ex Litw.

“Oreosalsola”: *Salsola abrotanoides* Bunge, *S. botschantzevii* Kurbanov, *S. flexuosa* Botsch., *S. junatovii* Botsch., *S. lipschitzii* Botsch., *S. maracandica* Iljin, *S. masenderanica* Botsch., *S. montana* Litw., *S. oreophila* Botsch., and *S. tianschanica* Botsch.

Others: *Salsola genistoides* Juss. ex Poir., *S. pachyphylla* Botsch., and *S. webbii* Moq.

Tribe Caroxyloneae Akhani & E. H. Roalson, tribus nov. Type: *Caroxylon* Thunb.

A tribu Salsoleae planta plerumque tota pilosa, caulibus et foliis pilos articulatos atque interdum etiam pilos medifixos ferentibus differt. Antherae vario modo appendiculatae, disjunctae, plerumque vesiculosae. Caules numquam articulati. Folia alterna (rarissime opposita).

For details of the differences between Salsoleae s.s. and Caroxyloneae, see table 3.

*Caroxylon* Thunb. Nov. Gen. ii. 37, 1782. Type: *Caroxylon aphyllum* (L. f.) Tzvelev (= *Salsola aphylla* L.). Synonyms: *Salsola* sect. *Caroxylon* (Thunb.) Fenzl, *Salsola* sect. *Irania* Botsch., *Salsola* sect. *Malpighipila* Botsch., *Salsola* sect. *Cardiandra* Aellen, and *Nitrosalsola* Tzvelev (Botschantzev 1970, 1974a, 1974b, 1975b, 1975d, 1981a, 1986; Freitag 1997).

*Caroxylon abarghuense* (Assadi) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola abarghuensis* Assadi, Iranian J. Bot. 2: 136, 1984.

*Caroxylon aegeum* (Rech. f.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola aegaea* Rech. f., Denksch. Akad. Wiss. Wien, Math.-Nat. 105, 2, Abt. 1: 67, 1943.

*Caroxylon arabicum* (Botsch.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola arabica* Botsch. in Bot. Zhurn. 60(4): 499, 1975.

*Caroxylon araneosum* (Botsch.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola araneosa* Botsch. in Bot. Zhurn. 58(6) 818, 1973.

*Caroxylon canescens* (Moq.) Akhani & E. H. Roalson, comb. nov. Basionym: *Noaea canescens* Moq. in DC., Prodr. 13, 2: 208, 1849.

*Caroxylon carpathum* (P. H. Davis) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola carpatha* P. H. Davis, Notes Roy. Bot. Gard. Edinb. 21: 139, 1953.

*Caroxylon chorassanicum* (Botsch.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola chorassnica* Botsch., Bot. Mat. Gerb. Inst. Bot. Akad. Nauk Uzbek. SSR 18: 6, 1969.

*Caroxylon cyclophyllum* (Baker) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola cyclophylla* Baker in Bull. Misc. Inform. (Kew Bull.) 1894: 340, 1894.

*Caroxylon dzhungaricum* (Iljin) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola dzhungarica* Iljin in Trudy Bot. Inst. Akad. Nauk SSSR, ser 1, 2: 129, 1936.

*Caroxylon ericoides* (M. Bieb.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola ericoides* M. Bieb., Mém. Soc. Imp. Naturalites Moscou 1: 141, 1806.

*Caroxylon forcipitatum* (Iljin) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola forcipitata* Ljin, Bot. Zhurn. 18: 275, 1933.

*Caroxylon gaetulum* (Maire) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola foetida* Delile var. *gaetula* Maire, Bull. Soc. Hist. Nat. Afriq. Nord, 27, 7: 257, 1936.

*Caroxylon glabrescens* (B. Davy) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola glabrescens* B. Davy, in Man. Fl. Pl. & Ferns Pt. 1. 50: 177, 1926.

*Caroxylon imbricatum* (Forssk.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola imbricata* Forssk., Fl. Egypt.-Arab.: 57, 1775.

*Caroxylon incanescens* (C. A. Mey.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola incanescens* C. A. Mey. in Eichw., Pl. Casp.-Cauc. 2: 35, 1833.

*Caroxylon inermis* (Forssk.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola inermis* Forssk., Fl. Egypt.-Arab. 57, 1775.

*Caroxylon implicatum* (Botsch.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola implicata* Botsch., in Bot. Mater. Gerb. Bot. Inst. Akad. Nauk Uzbeksk. SSR, 13: 6, 1952.

*Caroxylon jordanicola* (Eig) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola jordanicola* Eig, Palest. Journ. Bot., Jerusalem Ser. 3, 3: 130, 1945.

*Caroxylon littoralis* (Moq.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola littoralis* Moq., in DC. Prodr. 13, 2: 180, 1849.

*Caroxylon nitrarium* (Pall.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola nitraria* Pall., Illustr. Pl.: 25, 1803. Synonym: *Nitrosalsola nitraria* (Pall.) Tzvelev, in Ukr. Bot. Zhurn. 50(1): 80, 1993.

*Caroxylon passerinum* (Bunge) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola passerina* Bunge, Linnaea 17: 4, 1843.

*Caroxylon persicum* (Bunge ex Boiss.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola persica* Bunge ex Boiss., Fl. Or. 4: 964, 1879.

*Caroxylon pulvinatum* (Botsch.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola pulvinata* Botsch., Bot. Mat. Gerb. Bot. Inst. Akad. Nauk SSSR 22: 96, 1963.

*Caroxylon scleranthum* (C. A. Mey.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola sclerantha* C. A. Mey., in Eichw., Pl. Nov. Casp.-Cauc. 2: 35, 1835.

- Caroxylon spinescens* (Moq.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola spinescens* Moq., in DC., Prodr. 13(2): 179, 1849.
- Caroxylon stenopterum* (Wagenitz) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola stenoptera* Wagenitz, in Ber. Deutsch. Bot. Ges. 72: 155, 1959.
- Caroxylon tetrandrum* (Forssk.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola tetrandra* Forssk., Fl. Aegypt.-Arab. 58, 1775.
- Caroxylon turkestanicum* (Litw.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola tukestanica* Litw., Trudy Bot. Muz. Akad. Nauk, 7: 78, 1910.
- Caroxylon vermiculatum* (L.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola vermiculata* L., Sp. Pl. 223, 1753.
- Caroxylon villosum* (Schult.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola villosa* Schult., Syst. Veg. 6: 232, 1820.
- Caroxylon volkensis* (Aschers & Schweinf.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola volkensis* Aschers & Schweinf., in Ill. Fl. Égypte 130, 1887.
- Caroxylon yazdianum* (Assadi) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola yazdiana* Assadi, Iranian J. Bot. 2, 2: 140, 1984.
- Caroxylon rosbevitzi* (Iljin) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola rosbevitzi* Iljin, in Journ. Bot. URSS, 18: 277, 1933.
- Other species include *Caroxylon aphyllum* (L.f.) Tzvelev, *C. dendroides* (Pall.) Tzvelev, *C. foetidum* Moq., *C. gemmascens* (Pall.) Tzvelev, *C. imbricatum* Moq., *C. laricinum* (Pall.) Tzvelev, *C. orientale* (S. G. Gmel.) Tzvelev, *C. tetragonum* (Delile) Moq., *C. verrucosum* Moq., and *C. zeyheri* Moq.
- Climacoptera* Botsch., Sborn. Posv. Akad. Sukachevu: 111, 1956. Type: *Climacoptera lanata* (Pall.) Botsch.
- Climacoptera maimanica* (Freitag) Akhani, comb. nov. Basionym: *Salsola maimanica* Freitag, in Fl. Iranica 172: 254, 1997.
- Includes *Climacoptera affinis* (C. A. Mey.) Botsch., *C. afghanica* Botsch., *C. amblyostegia* Botsch., *C. aralensis* (Iljin) Botsch., *C. botschantzevii* Prатов, *C. bucharica* (Iljin) Botsch., *C. chorassanica* Prатов, *C. crassa* (M. Bieb.) Botsch., *C. czelekenica* Prатов, *C. ferganica* (Drob.) Botsch., *C. glaberrima* Botsch., *C. intricata* (Iljin) Botsch., *C. iranica* Prатов, *C. iraqensis* Botsch., *C. kasakorum* (Iljin) Botsch., *C. khalisica* Botsch., *C. korsbinskyi* (Drob.) Botsch., *C. lachnophylla* (Iljin) Botsch., *C. lanata* (Pall.) Botsch., *C. longipistillata* Botsch., *C. longistylota* (Iljin) Botsch., *C. malyginii* (Korov. ex Botsch.) Botsch., *C. merkulowitschii* (Zakir.) Botsch., *C. minkwitzae* (Korov.) Botsch., *C. narynensis* Prатов, *C. obtusifolia* (Schrenk) Botsch., *C. olgae* (Iljin) Botsch., *C. oxyphylla* Prатов, *C. pjataevae* Prатов, *C. ptiloptera* Prатов, *C. roborowskii* (Iljin) Grub., *C. subcrassa* (M. Pop.) Botsch., *C. sukaczewii* Botsch., *C. susamyrica* Prатов, *C. tyshchenkoi* Prатов, *C. transoxana* (Iljin) Botsch., *C. turcomanica* (Litv.) Botsch., *C. turgaica* (Iljin) Botsch., *C. ustjurtensis* Prатов, and *C. vachschi* Kinz. & Prатов (Botschantzev 1982; Prатов 1986).
- Halarchon* Bunge, Mém. Acad. Imp. Sc. Pétersb. 7. sér., 4, 11: 75, 1862. Type: *Halarchon vesiculosum* (Moq.) Bunge.
- Includes *Halarchon vesiculosum* (Moq.) Bunge.
- Halimocnemis* C. A. Mey. in Ledeb., Fl. Alt. 1: 381, 1829. Type (lectotype selected here): *Halimocnemis sclerosperma* (Pall.) C. A. Mey., Fl. Alt. 1: 387, 1829; basionym: *Polycnemum sclerospermum* Pall., Reise Versch. Prov. Russ. Reich 3: 725, Tab. M, Fig. 2E, e. 1776. Synonyms: *Gamanthus* Bunge, Mém. Acad. Imp. Sc. Saint Pétersbourg 7. sér., 4, 11: 76, 1862; *Halanthium* C. Koch, Linnaea 17: 313, 1843; *Halotis* Bunge, Mém. Acad. Imp. Sc. Pétersb. 7. sér., 4, 11: 73, 1862.
- Halimocnemis alaeiflava* (Assadi) Akhani, comb. nov. Basionym: *Halanthium alaeiflavum* Assadi, Iranian J. Bot. 5, 2: 58, 1992.
- Halimocnemis commixtus* (Bunge) Akhani, comb. nov. Basionym: *Gamanthus commixtus* Bunge, Mém. Acad. Imp. Sc. Pétersb. 7. Sér., 4, 11: 76, 1862.
- Halimocnemis ferganica* (Iljin) Akhani, comb. nov. Basionym: *Gamanthus ferganicus* Iljin, in Acta Inst. Bot. Acad. Sc. URSS, sér. 1, 2. 1936.
- Halimocnemis leucophysa* (Botsch.) Akhani, comb. nov. Basionym: *Gamanthus leucophysus* Botsch., Not. Syst. Herb. Inst. Bot. Acad. Sci. URSS 12: 97, 1963.
- Halimocnemis pedunculata* (Assadi) Akhani, comb. nov. Basionym: *Halotis pedunculatus* Assadi, Iranian J. Bot. 5, 2: 60, 1992.
- Halimocnemis pilosa* (Pall.) Akhani, comb. nov. Basionym: *Salsola pilosa* Pall., Illustr. Pl. 28, tab. 20, 1803.
- Halimocnemis rarifolia* (C. Koch) Akhani, comb. nov. Basionym: *Halanthium rarifolium* C. Koch, Linnaea 17: 314, 1844.
- Halimocnemis rosea* (Trautv.) Akhani, comb. nov. Basionym: *Halanthium kulpianum* var. *roseum* Trautv., in Trudy Imp. S.-Petersburgsk. Bot. Sada 4: 1, 1876.
- Includes *Halimocnemis aequipila* Iljin, *H. beresinii* Iljin, *H. gamocarpus* Moq., *H. glaberrima* Iljin, *H. karelinii* Moq., *H. kulpiana* C. Koch, *H. lasiantha* Iljin, *H. latifolia* Iljin, *H. longifolia* Bunge, *H. macrantha* Bunge, *H. mamamensis* (Bunge) Assadi, *H. mironovii* Botsch., *H. mollissima* Bunge, *H. occulta* (Bunge) Hedge, *H. pilifera* Moq., *H. purpurea* Moq., *H. sclerosperma* (Pall.) C. A. Mey., *H. smirnovii* Bunge, and *H. villosa* Kar. & Kir. (Botschantzev 1971; Ghobadnejhad et al. 2004).
- Halocharis* Moq. in DC., Prodr. 13, 2: 201, 1849. Type: *Halocharis sulphurea* Moq.
- Includes *Halocharis clavata* Bunge, *H. gossypina* Korov. & Kinz., *H. lachnantha* E.Korov., *H. hispida* (Schrenk) Bunge, *H. sulphurea* (Moq.) Moq., *H. turcomanica* Iljin, and *H. violacea* Bunge (Iljin 1949).
- Kaviria* Akhani & E. H. Roalson, gen. nov. Type: *Kaviria tomentosa* (Moq.) Akhani; basionym: *Halimocnemis tomentosa* Moq. Synonym: *Salsola* section *Belanthera* Iljin, Trudy Bot. Inst. Nauk SSSR 1, 3: 158, 1937, p.p. (Revised by Botschantzev 1968, 1980).
- Genus novum ad *Halocharem* approximatum, sed seminibus saepius horizontalibus (nec verticalibus), stigmatibus planis (nec teretibus) ± denticulatis, perianthio non scarioso, appendice antherarum non vesiculosa, perianthio fructicanti plerumque alato, flore solitari (nec floribus saepe pluris) differt. Planta plerumque fruticosa raro tantum annua pilis articulatis spinulosissimis vel ramosis immixtis ornata.
- Kaviria aucheri* (Moq.) Akhani, comb. nov. Basionym: *Noaea aucheri* Moq. in DC., Prodr. 13, 2: 207, 1849.
- Kaviria cana* (C. Koch) Akhani, comb. nov. Basionym: *Salsola cana* C. Koch, Linnaea 22: 190, 1849.
- Kaviria futilis* (Iljin) Akhani, comb. nov. Basionym: *Salsola futilis* Iljin, Bot. Mat. Gerb. Bot. Inst. Akad. Nauk SSSR, 7: 210, 1938.
- Kaviria gossypina* (Bunge) Akhani, comb. nov. Basionym: *Salsola gossypina* Bunge in Boiss. Fl. Or. 4: 956, 1879.
- Kaviria lachnantha* (Botsch.) Akhani, comb. nov. Basionym: *Salsola tomentosa* (Moq.) Spach subsp. *lachnantha* Botsch., Bot. Zhurn. 53: 1448, 1968.
- Kaviria pycnophylla* (Brenan) Akhani, comb. nov. Basionym: *Salsola pycnophylla* Brenan, Kew Bull. 3: 433, 1953.
- Kaviria rubescens* (Franch.) Akhani, comb. nov. Basionym: *Salsola rubescens* Franch., in Révoil, Faune Fl. Çomalis: 60, 1882.
- Kaviria tomentosa* (Moq.) Akhani, comb. nov. Basionym: *Halimocnemis tomentosa* Moq., Hist. Mém. Acad. Sci. Toulouse 5: 180, 1839.
- Kaviria vudenskyi* (Iljin & M. Pop.) Akhani, comb. nov. Basionym: *Salsola vudenskyi* Iljin & M. Pop. in Fl. URSS 6: 876, 1936.

- Kaviria zehzadii* (Akhani) Akhani, comb. nov. Basionym: *Salsola zehzadii* Akhani, Sendtnera 3: 6, 1996.  
*Nanophyton* Less., Linnaea 9: 197, 1834–1835. Type: *Nanophyton erinaceum* (Pall.) Bunge.  
 Includes *Nanophyton erinaceum* (Pall.) Bunge.  
 The identities of nine additional taxa described by Botschantzev (1975a) and Pratov (1975, 1982, 1985) need to be clarified. They include *N. botschantzevii* Pratov, *N. erinaceum* (Pall.) Bunge subsp. *karataviense* Pratov, *N. erinaceum* (Pall.) Bunge subsp. *subulifolium* Pratov, *N. grubovii* Pratov, *N. iliense* Pratov, *N. mongolicum* Pratov, *N. narynense* Pratov, *N. pulvinatum* Pratov, and *N. saxatile* Botsch.  
*Ofaiston* Raf., Fl. Tell. 3: 46, 1837. Type: *Ofaiston monandrum* (Pall.) Moq.  
 Includes *Ofaiston monandrum* (Pall.) Moq.  
*Petrosimonia* Bunge, Mém. Acad. Imp. Sci. St. Pétersb. 7. sér., 4, 11: 19, 52, 1862. Type: *Petrosimonia monandra* (Pall.) Bunge.  
 Includes *Petrosimonia brachiata* (Pall.) Bunge, *P. brachyphylla* (Bunge) Iljin, *P. glauca* (Pall.) Bunge, *P. glaucescens* (Bunge) Iljin, *P. hirsutissima* (Bunge) Iljin, *P. litwinowii* Korsh., *P. nigdeensis* Aellen, *P. monandra* (Pall.) Bunge, *P. oppositifolia* (Pall.) Litv., *P. sibirica* (Pall.) Bunge, *P. squarrosa* (Schrenk) Bunge, and *P. triandra* (Pall.) Simonk.  
*Piptoptera* Bunge Trudy Glavn. Bot. Sada 5: 644, 1877. Type: *Piptoptera turkestanica* Bunge.  
 Includes *Piptoptera turkestanica* Bunge.  
*Physandra* Botsch., Sborn. Posv. Akad. Sukachevu: 114, 1956. Type: *Physandra halimocnemis* (Botsch.) Botsch.  
 Includes *Physandra halimocnemis* (Botsch.) Botsch.  
*Pyankovia* Akhani & E. H. Roalson, gen. nov. Type: *Pyankovia brachiata* (Pall.) Akhani & E. H. Roalson; basionym: *Salsola brachiata* Pall.  
 Synonym: *Climacoptera* section *Heterotricha* Iljin ex Prato, in Rod *Climacoptera* 24, 1986.  
 Planta annua, erecta, pilos longos articulatos atque pilos breviores spinulissimos immixtos ferentes; folia superiora floralibus exceptis opposita, ad apicem cuspidata. Stylus brevis, ad maturitatem conicus, stigma subulata. Stamina 5; antherae lineares, per 1/3 vel 2/5 longitudinem partitae appendicibus sessilibus albis obtusis ornatae. Perianthia fructificantia horizontalia omnia alata. Semina verticalia. Genus novum a *Climacoptera* foliis oppositis, pilis spinulissimis, seminibus verticalibus differt.  
*Pyankovia brachiata* (Pall.) Akhani & E. H. Roalson, comb. nov. Basionym: *Salsola brachiata* Pall., Illustr. 30, tab. 22, 1803.  
 Lectotype (Pratov 1986): In siccis squalidis salsis deserti australoris Volgum frequens, P. S. Pallas (LE).

## Appendix B

Table B1

List of Sampled Taxa with Their Respective Vouchers and GenBank Accession Numbers

Subfamily, tribe, and species	Voucher of DNA source	GenBank no.	
		ITS	<i>psbB-psbH</i>
Salsoloideae:			
Camphorosmeae:			
<i>Bassia hyssopifolia</i> (Pall.) O. Kuntze	H. Akhani 18064. Iran: Golestan, Alagol Lake, 37°21'8"N, 54°34'13"E, 10 m, 8.10.2004.	EF453390	EF453527
<i>Bassia eriophora</i> (Schrad.) Aschers.	H. Akhani 8381. Iran: Ilam, Mehran, 3.5.1992.	EF453391	EF453528
<i>Bassia sedoides</i> Aschers.	Kadereit et al. 2005.	AY489199	...
<i>Camphorosma monspeliaca</i> L.	H. Akhani & M. Ghabadnejhad 15585. Iran, E Azerbaijan: 55 km NE of Tabriz toward Ahar, 38°15'39"N, 46°52'53"E, 1571 m, 4.9.2001.	EF453392	EF453529
<i>Camphorosma monspeliaca</i> L.	Akhani et al. 17960. Turkey: Aksaray: S of Tuz Gölü Lake, 17 km from Yenikent toward Sultanhani, 38°15'56"N, 33°38'51"E, 938 m, 27.8.2004.	EF453393	EF453530
<i>Chenoleoides tomentosa</i> (Lowe) Botsch.	H. Akhani 16440. Canary Islands: Gran Canaria, southeastern coasts, Faro de Arinaga, sea level, 22.9.2002.	EF453394	EF453531
<i>Kirilowia eriantha</i> Bunge	D. Podlech 18952 (M). Afghanistan: Ghorat, Panjao to La'l, Asgharat to Khargol, 3120 m, 29.7.1970.	EF453445	EF453574
<i>Kochia scoparia</i> (L.) Schrad.	H. Akhani & Zangui 10114. Iran: Khorassan, 17.8.1994.	EF453446	...
<i>Kochia stellaris</i> Moq.	Kadereit et al. 2005.	AY489219	...
<i>Londesia eriantha</i> Fisch. & C. A. Mey.	Kadereit et al. 2005.	AY489220	...
<i>Maireana coronata</i> (J. M. Black) P. G. Wilson	Based on cultivated plant from Royal Botanical Gardens, Kew (origin Australia).	EF453447	EF453575
<i>Pandertia pilosa</i> Fisch. & C. A. Mey.	H. Akhani 14513. Iran, Tehran: 35 km E of Eshtahard, ca. 8 km W of Mardabad, Rude Shur, 35°42'44"N, 50°44'26"E, 1163 m, 8.12.2000.	EF453454	EF453582
<i>Pandertia pilosa</i> Fisch. & C. A. Mey.	H. Akhani et al. 17948. Turkey: Ankara, eastern side of Tuz Gölü Lake, 62 km S of Sereflikochisar, 5–7 km W of Ulukisla, 38°29'1"N, 33°44'17"E, 921 m, 27.8.2004.	EF453455	EF453583
Salsoleae s.l.:			
<i>Anabasis aphylla</i> L.	H. Akhani 18072. Iran: Khorassan, easternmost parts of Golestan National Park, near Mirzabaylu Protection Station, 37°19'59"N, 56°14'20"E, 1756 m, 9.10.2004.	EF453380	EF453517
<i>Anabasis calcarea</i> (Charif & Aellen) Bokhari & Wendelbo	H. Akhani 14372. Iran: Tehran, Kavir Protected Area, near Qasre Bahram, 34°44'N, 52°10'E, 1200 m, 27.10.2000.	EF453381	EF453518

Table B1

(Continued)

Subfamily, tribe, and species	Voucher of DNA source	GenBank no.	
		ITS	<i>psbB-psbH</i>
<i>Anabasis eriopoda</i> (C. A. Mey.) Benth.	H. Akhani & M. Ghobadnejhad 15812. Iran: Semnan, Touran Biosphere Reserve, 19 km SW of Biarjmand toward Daqe Biar, 35°56'28"N, 55°42'48"E, 1260 m, 4.10.2001.	EF453383	EF453520
<i>Anabasis eugeniae</i> Iljin	T. Eftekhari 10219. Iran: Semnan, ca. 28 km NW of Semnan, W of Aftar, Khonar Forbidden Hunting, 1980 m, 11.10.1999.	EF453384	EF453521
<i>Anabasis hausskenchtii</i> Bunge ex Boiss.	H. Akhani & M. Salimian 15339. Iran: Semnan, 19 km NW of Damghan toward Cheshmeh Ali, 1420 m, 36°14'58"N, 54°9'57"E, 14.7.2001.	EF453386	EF453523
<i>Anabasis hausskenchtii</i> Bunge ex Boiss.	H. Akhani & M. Ghobadnejhad 15699. Iran: Yazd: ca. 10 km W of Taft toward Abarkuh, 31°56'28"N, 54°15'23"E, 1233 m, 18.9.2001.	EF453387	EF453524
<i>Anabasis</i> aff. <i>hausskenchtii</i> Bunge	H. Akhani & M. R. Joharchi 17306. Khorassan: 65 km SE of Birjand, near Sarbisheh, at the beginning of the road toward Doroh, 32°34'26"N, 59°48'35"E, 2.9.2003.	EF453388	EF453525
<i>Anabasis iranica</i> Iljin	H. Akhani & M. Ghobadnejhad 15700. Iran: Yazd: ca. 10 km W of Taft toward Abarkuh, 31°56'28"N, 54°15'23"E, 1233 m, 18.9.2001.	EF453382	EF453519
<i>Anabasis jaxartica</i> (Bunge) Benth. ex Volkens	H. Akhani 14078. Iran, Golestan: Southern border of Golestan National Park, 37°17'50"N, 55°55'36"E, 1240 m, 4.6.2000.	EF453385	EF453522
<i>Anabasis setifera</i> Moq.	H. Akhani 14519. Iran, Tehran: Tehran-Qom highway, Heuze Soltan Lake, 34°59'2"N, 50°51'22"E, 840 m, 22.12.2000.	EF453389	EF453526
<i>Climacoptera brachiata</i> (Pall.) Botsch.	Akhani 17356. Iran: Golestan: Golestan National Park, 2 km S of Dasht, 37°19'26"N, 55°57'24"E, 1403 m, 13.10.2003.	EF453403	EF453536
<i>Climacoptera crassa</i> (M. Bieb.) Botsch.	H. Akhani & al. 18005. Turkey: Aksaray, 10 km E of Eskil toward southern saline shores of Tuz Gölü Lake, 38°25'5"N, 33°29'52"E, 914 m, 28.8.2004.	EF453401	EF453534
<i>Climacoptera glaberrima</i> Botsch.	H. Akhani 18087. Golestan: 5 km E of Maraveh Tappeh, along Atrak river, 37°54'23"N, 56°00'36"E, 230 m, 11.10.2004.	EF453396	EF453532
<i>Climacoptera glaberrima</i> Botsch.	Based on cultivated plant originated from the same population as above Akhani 18087.	EF453400	EF453533
<i>Climacoptera iranica</i> Prатов	Voucher lost. Iran: Golestan, 5 km E of Maraveh Tappeh, along Atrak river, 37°54'23"N, 56°00'36"E, 230 m, 11.10.2004.	EF453395	...
<i>Climacoptera</i> "khalijefarsica"	H. Akhani et al. 18118. Iran: Khuzestan, Persian Gulf coasts near Bandare Imam, 30°34'52"N, 49°1'59"E, 10.12.2004.	EF453402	EF453535
<i>Climacoptera lanata</i> (Pall.) Botsch.	H. Akhani & M. R. Joharchi 17241. Khorassan: between Torbate-Heydarieh and Gonabad, ca. 35 km N of Gonabad, Kal Shur River, 34°40'21"N, 58°47'10"E, 856 m, 31.8.2003.	EF453404	EF453537
<i>Climacoptera lanata</i> (Pall.) Botsch.	H. Akhani & M. R. Joharchi 16510. Iran: Khorassan, ca. 35 km E of Torbat-e Jam near Malu, 35°12'19"N, 61°1'17"E, 820 m, 20.11.2002.	EF453398	...
<i>Climacoptera longipistillata</i> Botsch.	H. Akhani 18092. Golestan: 28 km W of Maraveh Tappeh, near Ghara-Gol, 37°54'56"N, 55°39'43"E, 140 m, 11.10.2004.	EF453397	...
<i>Climacoptera turcomanica</i> (Litv.) Botsch.	H. Akhani 17207. Iran: Tehran, ca. 60 km W of Tehran, Mardabad, salt flats near Rude Shur, 35°43'N, 50°44'E, 1164 m, 8.8.2003.	EF453399	...
<i>Cornulaca aucheri</i> Moq.	H. Akhani 7964. Iran: Bushehr, 13 km after Cheghadak toward Delvar, near Gar Gur village, sea level, 20.11.1991.	EF453405	EF453538
<i>Cornulaca monacantha</i> Delile	H. Akhani & M. R. Joharchi 17297. Iran: Khorassan, ca. 50 km S of Birjand, Mokhtaran, 32°28'25"N, 59°23'8"E, 1506 m, 1.9.2003.	EF453406	EF453539
<i>Cyatobasis fruticulosa</i> (Bunge) Aellen	Turkey, M. Vural, H. Duman, Z. Aytac 8012 (GAZ). Kayseri: Dortyol-Develi, Tuzlu Topraklar, 1080 m, 19.9.1997.	EF453516	...
<i>Fadenia zygophylloides</i> Aellen & Townsend	I. Friis, K. Vollesen & A. S. Hassan 4768 (K). Somalia: Gedo Region, ca. 36 km S of Lung, 3°33'N, 42°42'E, ca. 200 m, 25.5.1987.	EF453513	...
<i>Gamanthus commixtus</i> Bunge	V. Botschantzev 15 (LE). Uzbekistan, Surkhandarja province, between Shirabad and Zarabag, 8.10.1970.	EF453410	EF453543
<i>Gamanthus gamocarpus</i> (Moq.) Bunge	H. Akhani 14086. Iran: Golestan, southern border of Golestan National Park, NW of Dasht village toward Yelaq, 37°18'41"N, 55°58'43"E, 1200 m, 5.6.2000.	EF453407	EF453540
<i>Gamanthus gamocarpus</i> (Moq.) Bunge	Cultivated based on H. Akhani 18053. Iran: Golestan, between Aghghala and Dashliborun, 38 km N of Aghghala, 37°20'43"N, 54°33'E, 16 m, 8.10.2004.	EF453408	EF453541
<i>Gamanthus</i> "khorassanicus"	H. Akhani & M. R. Joharchi 17237. Khorassan: between Torbate-Heydarieh and Gonabad, 55 km N of Gonabad, 34°50'26"N, 58°51'18"E, 908 m, 31.8.2003.	EF453411	EF453544
<i>Gamanthus pilosus</i> (Pall.) Bunge	Akhani & Ghobadnejhad 15551. Iran: E Azerbaijan, 52 km S of Aslanduz in the road toward Ardabil, 39°9'N, 47°38'37"E, 1200 m, 3.9.2001.	EF453409	EF453542
<i>Girgensobnia imbricata</i> Bunge	H. Akhani & M. R. Joharchi 17291. Iran: Khorassan, ca. 40 km S of Birjand, 13 km E of Majhan toward Giv, 32°33'25"N, 59°7'54"E, 1492 m, 1.9.2003.	EF453412	EF453545
<i>Girgensobnia minima</i> K. Korov.	H. Akhani & Zangooei 10109. Iran: Khorassan, 10–11 km E of Chahchaheh along Turkmenistan border, 700–850 m, 17.8.1994.	EF453413	EF453546
<i>Girgensobnia oppositiflora</i> (Pall.) Fenzl	H. Akhani & M. Ghobadnejhad 15701. Iran: Yazd, ca. 27 km W of Taft toward Abarkuh, 31°41'54"N, 53°55'19"E, 2179 m, 18.9.2001.	EF453414	EF453547

Table B1

(Continued)

Subfamily, tribe, and species	Voucher of DNA source	GenBank no.	
		ITS	<i>psbB-psbH</i>
<i>Halanthium alae flavum</i> Assadi	H. Akhani & M. Ghobadnejhad 15610. Iran: E Azerbaijan, 1 km W of Maraqeh toward Bonab, 37°21'11"N, 46°8'58"E, 1383 m, 7.9.2001.	EF453416	EF453548
<i>Halanthium mamamense</i> Bunge	H. Akhani & M. Ghobadnejhad 15531. Iran: E Azerbaijan, 10 km E of Mianeh, near Maman, 37°27'18"N, 47°52'3"E, 1095 m, 2.9.2001.	EF453417	...
<i>Halanthium rarifolium</i> C. Koch	H. Akhani 16491. Iran: Semnan, SW of Touran Protected Area, ca. 15 km from Razeh toward Torud, 35°24'29"N, 55°15'51"E, 1320 m, 14.11.2002.	EF453419	EF453550
<i>Halanthium rarifolium</i> C. Koch	H. Akhani 17206. Iran: Tehran, ca. 60 km W of Tehran, Mardabad, salt flats near Rude Shur, 35°43'N, 50°44'E, 1164 m, 8.8.2003.	EF453418	EF453549
<i>Halanthium rarifolium</i> C. Koch	H. Akhani 17208. Iran: Tehran: ca. 60 km W of Tehran, Mardabad, salt flats near Rude Shur, 35°43'N, 50°44'E, 1164 m, 29.8.2003.	EF453415	...
<i>Halimocnemis azarbaijanensis</i> Assadi	H. Akhani & M. Ghobadnejhad 15550. Iran: E Azerbaijan, 52 km S of Aslanduz in the road toward Ardabil, 39°9'N, 47°38'37"E, 1200 m, 3.9.2001.	EF453420	EF453551
<i>Halimocnemis longifolia</i> Bunge	H. Akhani & M. R. Joharchi 17245. Iran: Khorassan, between Torbate-Heydarieh and Gonabad, ca. 33 km N of Gonabad, 34°39'51"N, 58°45'53"E, 871 m, 31.8.2003.	EF453421	EF453552
<i>Halimocnemis mollissima</i> Bunge	H. Akhani 17208. Iran: Tehran, ca. 60 km W of Tehran, Mardabad, salt flats near Rude Shur, 35°43'N, 50°44'E, 1164 m, 8.8.2003.	EF453422	EF453553
<i>Halimocnemis purpurea</i> Moq.	H. Akhani 9036. Iran: Ilam, ca. 25–28 km N of Mehran, Konjanham river margin, 300 m, 16.10.1993.	EF453426	EF453557
<i>Halocharis hispida</i> (Schrenk) Bunge	H. Akhani 10179-T. Turkmenistan, 2 km N of Ashghabad, 16.9.1994.	EF453429	EF453560
<i>Halocharis sulphurea</i> (Moq.) Moq.	H. Akhani & M. Ghobadnejhad 15841. Iran: Semnan, 47 km W of Shahrud toward Damghan, 36°15'51"N, 54°39'40"E, ca. 1140 m, 6.10.2001.	EF453427	EF453558
<i>Halocharis violacea</i> Bunge	H. Akhani & M. R. Joharchi 17288. Khorassan: 143 km E of Qaen toward Afghanistan border, W of Daqe Petergan, 33°31'29"N, 60°39'12"E, 644 m, 31.8.2003.	EF453428	EF453559
<i>Halogeton alopecuroides</i> (Delile) Moq.	Originated from Arabia, cultivated in WSU.	EF453430	EF453561
<i>Halogeton glomeratus</i> (M. Bieb.) C. A. Mey.	Voucher unknown, the same specimen used in Pyankov et al. 2001a.	EF453431	EF453562
<i>Halothamnus auriculus</i> (Moq.) Botsch.	H. Akhani 15164. Iran: Qom, at the beginning of Qom-Tehran highway, 34°41'15"N, 50°53'20"E, 962 m, 24.5.2001.	EF453433	EF453564
<i>Halothamnus auriculus</i> (Moq.) Botsch. subsp. <i>acutifolius</i> (Moq.) Kothe-Heinr.	Akhani & Salimian 15444. Iran: Semnan, 28 km E of Shahrud toward Sabzevar, 36°26'42"N, 55°14'21"E, 1375 m, 20.7.2001.	EF453432	EF453563
<i>Halothamnus glaucus</i> (M. Bieb.) Botsch.	A. Ghorbani 56. Iran: Golestan, N of Golestan National Park, between Lohondor and Soolegerd, 8.7.2002.	EF453434	EF453565
<i>Halothamnus subaphyllus</i> (C. A. Mey.) Botsch.	H. Akhani & M. Salimian 15445. Iran: Semnan, 28 km E of Shahrud toward Sabzevar, 36°26'42"N, 55°14'21"E, 1375 m, 20.7.2001.	EF453435	EF453566
<i>Halotis occulta</i> Bunge	H. Akhani & M. R. Joharchi 17202. Khorassan: ca. 42 km SE of Birjand, 3 km NE of Mokhtaran toward Razgh, 32°28'42"N, 59°24'7"E, 1558 m, 1.9.2003.	EF453423	EF453554
<i>Halotis pedunculata</i> Assadi	H. Akhani 17217. Iran: Hormozgan, 9 km SW of Goshoon toward Tadroyeh, 27°21'25"N, 54°49'10"E, 584 m, 21.8.2003.	EF453424	EF453555
<i>Halotis pilifera</i> (Moq.) Botsch.	H. Akhani et al. 17692. Iran: Esfahan, 12 km E of Golpayegan in the Muteh road, near Vedagh, 33°30'23"N, 50°26'1"E, 1819 m, 9.6.2004.	EF453425	EF453556
<i>Haloxylon ammodendron</i> (C. A. Mey.) Bunge ex Fenzl	H. Akhani 17398. Iran: Khorassan, eastern parts of Golestan National Park, 6 km W of Mirzabaylu toward Alameh, 37°21'N, 56°11'E, 1384 m, 15.10.2003.	EF453436	EF453567
<i>Haloxylon persicum</i> Bunge ex Boiss. & Buhe	H. Akhani & M. Ghobadnejhad 15832. Iran: Semnan, Touran Biosphere Reserve, 4 km E of Ahmadabad, 35°47'N, 56°39'E, ca. 1000 m, 5.10.2001.	EF453438	EF453569
<i>Haloxylon stocksii</i> (Boiss.) Benth. & Hook.	H. Akhani s.n. Sistan va Baluchestan, 5 km S of Negur, 25°22'15"N, 61°10'31"E, 140 m, 28.11.2005.	EF453512	...
<i>Hammada articulata</i> (Moq.) O. Bolòs & Vigo	Based on cultivated plant from Royal Botanical Gardens, Kew.	EF453440	EF453571
<i>Hammada griffithii</i> (Moq.) Iljin	D. Podlech 32707 (MSB). Afghanistan: Samangan, Tang-I Tashqurghan, 7 km S of Tashqurghan, 520 m, 11.11.1978.	EF453437	EF453568
<i>Hammada salicornica</i> (Moq.) Iljin	H. Akhani 16004. Iran: Hormozgan, northern parts of Mehregan saline, 26°45'49"N, 54°46'46"E, 30 m, 21.12.2001.	EF453439	EF453570
<i>Horaninowia platyptera</i> Charif & Aellen	H. Akhani & M. Salimian 15442. Iran, Semnan, 28 km E of Shahrud toward Sabzevar, 36°26'42"N, 55°14'21"E, 1375 m, 20.7.2001.	EF453441	EF453572
<i>Horaninowia pungens</i> (Gilli) Botsch.	D. Podlech 19662 (MSB). Afghanistan: Kandahar, Banks of Helmand river at Girishk, 840 m, 18.09.1970.	EF453442	...

Table B1

(Continued)

Subfamily, tribe, and species	Voucher of DNA source	GenBank no.	
		ITS	<i>psbB-psbH</i>
<i>Horaninowia ulicina</i> Fisch. & C. A. Mey.	H. Akhani & M. Ghobadnejhad 15833. Iran: Semnan, Touran Biosphere Reserve, sand dunes 4 km E of Ahmadabad, 35°47'N, 56°39'E, ca. 1000 m, 5.10.2001.	EF453443	EF453573
<i>Nanophyton erinaceum</i> (Pall.) Bunge	(LE). Central Asia: southwest Kyzylkum, 2.11.96. Data on collector unavailable.	EF453449	EF453577
<i>Noaea major</i> Bunge	Neubauer 4768 (M). Afghanistan: Kabul, Bande Kargha, 2000 m.	EF453450	EF453578
<i>Noaea minuta</i> Boiss. & Ball	Cultivated specimen based on H. Akhani 18095. Iran: Hamadan, 9 km NE of Hamadan in the road toward Noubaran, 1729 m, 34°54'26"N, 48°3'7"E, 8.12.2004.	EF453451	EF453579
<i>Noaea mucronata</i> (Forssk.) Asch. & Schweinf.	H. Akhani 13761. Iran: Mazandaran, ca. 5 km E of Doab (Chalus road) toward Kojur, 36° 28'28"N, 51°25'13"E, 657 m, 12.9.1999.	EF453452	EF453580
<i>Ofaiston monandrum</i> (Pall.) Moq.	V. I. Vasilevich et al. 3008 (LE). Kazakhstan: Semipalatinsk, 90 km W of Ajaguza, by the road to village Chubartau, 26.7.1965.	EF453453	EF453581
<i>Petrosimonia brachiata</i> (Pall.) Bunge	H. Akhani & M. Salimian 14238. Iran: E Azerbaijan, northern side of Orumiye Lake, W of Bandar-e Sharafkhaneh, 38°11'23"N, 45°27'41"E, 1300 m, 3.9.2000.	EF453457	EF453585
<i>Petrosimonia glauca</i> (Pall.) Bunge	H. Akhani & M. Ghobadnejhad 15535. Iran: E Azerbaijan, 13 km E of Maman, near salt mine, 37°25'28"N, 47°55'58"E, 1378 m, 2.9.2001.	EF453456	EF453584
<i>Petrosimonia nigdeensis</i> Aellen	H. Akhani et al. 17925. Turkey: Ankara, 28 km N of Sereflikochisar toward Ankara, N of Tuz Gölü Lake, Mogan Gol Lake, 39°8'50"N, 33°19'4"E, 895 m, 27.8.2004.	EF453458	EF453586
<i>Piptoptera turkestanica</i> Bunge	H. Akhani 5775. Iran: Esfahan, ca. 30 km ESE of Kashan, 2 km N of Abu-Zeid abad, 9.9.1989, ca. 900 m.	...	EF453631
<i>Rhaphidophyton regelii</i> (Bunge) Iljin	V. Botschantzev & Litvinova N. P. 477 (LE). Kazakhstan: Chimkent province, Karatau mountain range, 2 km NE of village Leontjevka, valley of river Ulkan- Burul, 17.7.1980.	EF453459	EF453587
<i>Salsola abarghuensis</i> Assadi	H. Akhani 16492. Iran: Semnan, SW of Touran Protected Area, 8 km after Razeh toward Sahl, around Cheshmeh Morra, 35°35'38"N, 55°20'1"E, 1227 m, 14.11.2002.	EF453464	EF453591
<i>Salsola aperta</i> Paulsen	Chopanov & Seifulin 27.8.1976. Turkmenistan: Kunya-Urgench Region, on sand dunes between Daryalyk and Butentau.	EF453466	...
<i>Salsola arbuscula</i> Pall.	H. Akhani & M. Ghobadnejhad 15826. Iran: Semnan, Touran Biosphere Reserve, 85 km SW of Biarjmand toward Torud, river bed 6 km S of Sahl, 35°35'40"N, 55°20'4"E, 1230–1240 m, 4.10.2001.	EF453467	EF453592
<i>Salsola arbusculiformis</i> Drob.	H. Akhani 17397. Iran: Khorassan, eastern parts of Golestan National Park, 5–6 km W of Mirzabaylu toward Almelh, 37°21'16"N, 56°12'6"E, 1350 m, 15.10.2003.	EF453468	EF453593
<i>Salsola araneosa</i> Botsch.	Merxmüller and Giess 28372 (M). Namibia: S Lüderitz, 23 km S of Grillental, 12.09.1972.	EF453461	EF453588
<i>Salsola aucheri</i> (Moq.) Bunge	H. Akhani 17190. Iran: Golestan, southern parts of Golestan National Park, between Sharlegh and Cheshmeh Khan, 37°18'13"N, 56°5'1"E, 1154 m, 3.8.2003.	EF453469	EF453594
<i>Salsola canescens</i> (Moq.) Boiss.	H. Akhani 13185. Iran: Tehran, N Tehran, Golabdareh, 35°50'10"N, 51°26'23"–48"E, 3.9.1998.	EF453503	EF453623
<i>Salsola carpatha</i> P. H. Davis	W. Greuter 7835 (K). Greece, Dragonára Island, 31.10.1966.	EF453514	...
<i>Salsola chivensis</i> M. Pop.	Pyankov et al. 2001a.	AF318642	...
<i>Salsola chorassanica</i> Botsch.	H. Akhani & M. R. Joharchi 17281. Iran: Khorassan, 143 km E of Qaen toward Afghanistan border, W of Daqe Petergan, 33°31'29"N, 60°39'12"E, 644 m, 31.8.2003.	EF453487	EF453609
<i>Salsola cyclophylla</i> Baker	H. Akhani 15998. Iran: Hormozgan, 10 km W of Bandar Khamir, 26°, 26°56'40"N 55°29'5"E, 50 m, 20.12.2001.	EF453471	EF453596
<i>Salsola dendroides</i> Pallas	H. Akhani 18090. Iran: Golestan, 5 km E of Maraveh Tappeh, along Atrak river, 37°54'23"N, 56°00'36"E, 230 m, 11.10.2004.	EF453472	EF453597
<i>Salsola deserticola</i> Iljin ( <i>S. androssowii</i> Litv. subsp. <i>deserticola</i> [Iljin] Rilke)	Chopanov & Seifulin 1.9.1976. Turkmenistan: Dargan-Ata region, on the hills nearby southern lake Soltansardzhar.	EF453473	EF453598
<i>Salsola divaricata</i> Masson ex Link	Based on cultivated plant originated from H. Akhani 16469. Canary Islands: Gran Canaria, western coasts, near Agaete, 23.9.2002.	EF453474	EF453599
<i>Salsola drummondii</i> Ulbr.	H. Akhani 17234. Iran: Hormozgan, 36 km W of Bandar Abbas, at the beginning of Gachin village, 27°4'32"N, 55°54'45"E, 22.8.2003.	EF453475	EF453600
<i>Salsola dzhungarica</i> Iljin	The same herbarium material cited in Pyankov et al. 2001a (no voucher available).	EF453476	EF453601
<i>Salsola foliosa</i> (L.) Schrad.	Pyankov et al. 2001a.	AF318652	...
<i>Salsola forcipitata</i> Iljin	D. Podlech 17012 (MSB). Afghanistan: Baghlan, 8 km E of Kotal-i-Mirza Atbili, between Aybak and Pul-i-Khumri, 1100 m, 08.10.1969.	EF453477	...
<i>Salsola gemmascens</i> Pall.	D. Podlech 32697 (MSB). Afghanistan: Samangan, 8 km N of road Mazar-i-Sharif to Tashkurghan, at road to Termez, 320 m, 11.11.1978.	EF453478	...
<i>Salsola glabrescens</i> B. Davy	R. Story 2083 (M). South Africa: Cape, Aliwal North, banks of Orange River, 1300 m, 10.03.47.	EF453479	EF453602
<i>Salsola gossypina</i> Bunge	Herbarium material from Pyankov et al. 2001a.	EF453480	EF453603
<i>Salsola gossypina</i> Bunge	H. Akhani & Zangooi 10088. Iran: Khorasan, 24 km from Chahchaheh toward Kalat-e Naderi, 700–720 m, 17.8.1994.	EF453481	EF453604

Table B1

(Continued)

Subfamily, tribe, and species	Voucher of DNA source	GenBank no.	
		ITS	<i>psbB-psbH</i>
<i>Salsola griffithii</i> (Bunge) Freitag & Khani	H. Akhani et al. 17823. Iran: Kerman, ca. 7 km N of Faryab, sandy dunes near Hoore Olia village, 28°9'18"N, 57°16'3"E, 674 m, 14.6.2004.	EF453482	EF453605
<i>Salsola inermis</i> Forssk.	H. Akhani 5561. Iran: Ilam, 5 km SW of Dehloran, 170 m, 6.8.1989.	EF453465	...
<i>Salsola inermis</i> Forssk.	H. Akhani et al. 17963. Turkey: Aksaray, salt flats S of Tuz Gölü Lake, 17 km from Yenikent toward Sultanhani, 38°15'56"N, 33°38'51"E, 938 m, 27.8.2004.	EF453483	...
<i>Salsola jordanicola</i> Eig	H. Akhani 7947. Iran: Fars, 11 km in the road from Konartakhteh toward Borazjan, 300–400 m, 20.11.1991.	EF453484	EF453606
<i>Salsola jordanicola</i> Eig	H. Akhani & M. R. Joharchi 17236. Iran: Khorassan, between Torbate-Heydariyeh and Gonabad, 55 km N of Gonabad, 34°50'26"N, 58°51'18"E, 908 m, 31.8.2003.	EF453485	EF453607
<i>Salsola kali</i> L.	Pyankov et al. 2001a; Kapralov et al. 2006.	AF318646	DQ499431
<i>Salsola kernerii</i> (Wol.) Botsch.	H. Akhani 15045. Iran: Tehran, 20 km S of Behesht-e Zahra toward Hasanabad, 35°24'N, 51°19'E, 1300 m, 3.5.2001.	EF453486	EF453608
<i>Salsola lachnantha</i> (Botsch.) Botsch.	H. Akhani 9022. Iran: Ilam, ca. 25 km from Salehabad in the road toward Mehran, 16.10.1993.	EF453488	EF453610
<i>Salsola laricina</i> Pallas	H. Akhani et al. 17966. Turkey: Aksaray, ruderal places near Sultanhani, 39°15'40"N, 33°32'21"E, 956 m, 28.8.2004.	EF453470	EF453595
<i>Salsola masenderanica</i> Botsch.	H. Akhani 17403. Iran: Mazandaran, 169 km to Tehran, 5 km after Veresk toward Amol, 35°56'53"N, 53°00'20"E, 1201 m, 16.10.2003.	EF453504	EF453624
<i>Salsola montana</i> Litw.	H. Akhani 17391. Iran: Golestan, southern parts of Golestan National Park, near Sharlegh, 15.10.2003.	EF453489	EF453611
<i>Salsola montana</i> Litw.	Cultivated based on seeds originated from Iran: Golestan National Park.	EF453490	EF453612
<i>Salsola nitraria</i> Pallas	H. Akhani et al. 17946. Turkey: Ankara, eastern side of Tuz Gölü Lake, 14 km S of Sereflikochisar, 38°48'13"N, 33°36'40"E, 919 m, 27.8.2004.	EF453491	EF453613
<i>Salsola orientalis</i> S. G. Gmelin	H. Akhani 16498. Iran: Semnan, 38 km E of Khors toward Chajam, S of Kavire Haj Ali Qoli, 35°48'22"N, 54°57'10"E, 1098 m, 14.11.2002.	EF453492	EF453614
<i>Salsola orientalis</i> S. G. Gmelin	Cultivated plant originated from central Asia.	EF453493	EF453615
<i>Salsola paulsenii</i> Litw.	Pyankov et al. 2001a.	AF318647	...
<i>Salsola richteri</i> (Moq.) Karel. ex Litw.	Cultivated from a central Asian origin.	EF453494	EF453616
<i>Salsola rubescens</i> Franch.	H. Akhani 9117. United Arab Emirates: ca. 23 km S of Al-Ain, near Jebel Haft (Haft Mont), 350 m, 15.12.1990.	EF453495	...
<i>Salsola soda</i> L.	H. Akhani 15901. Iran: Tehran, Tehran-Saveh, Rude Shur, 9.11.2001.	EF453496	EF453617
<i>Salsola soda</i> L.	H. Akhani 18045. Iran: Golestan, N Gomishan, 37°10'14"N, 54°3'4"E, 13 m, 8.10.2004.	EF453497	EF453618
<i>Salsola tomentosa</i> (Moq.) Spach	H. Akhani & M. Ghobadnejhad 15632. Iran: E Azerbaijan, 10 km SW of Sarab in the road toward Asbforoushan, 37°52'7"N, 47°30'30"E, 1700 m, 8.9.2001.	EF453499	EF453620
<i>Salsola tomentosa</i> (Moq.) Spach	H. Akhani 18080. Iran: Golestan, 70 km S of Maraveh Tappeh, near Golidagh, 37°41'43"N, 56°4'19"E, 979 m, 11.10.2004.	EF453500	EF453621
<i>Salsola</i> "touranica"	H. Akhani & M. Ghobadnejhad 15808. Iran: Semnan, Touran Biosphere Reserve, above Qaaleh Bala, 36°00'15"N, 56°00'41"E, 1350 m, 4.10.2001.	EF453505	EF453625
<i>Salsola tragus</i> L. (published under <i>S. australis</i> R. Br.)	Pyankov et al. 2001a.	AF318648	...
<i>Salsola turkestanica</i> Litw.	H. Akhani & M. Ghobadnejhad 15821. Iran: Semnan, Touran Biosphere Reserve, 80 km SW of Biarjmand toward Torud, river bed near Sahl, 35°39'1"N, 55°18'24"E, 1351 m, 4.10.2001.	...	EF453632
<i>Salsola vermiculata</i> L.	H. Akhani 18102. Iran: Kermanshah, 35 km from Gilanegharb toward Sumar, 33°57'6"N, 45°56'55"E, 630 m, 9.12.2004. ITS based on cultivated plant from the same collection.	EF453501	EF453622
<i>Salsola vudenskyi</i> Iljin & M. Popov	D. Podlech 17001 (M). Afghanistan: Mazar-i Sharif, 2 km NW of Ghaznigak, near the road to Haibak (Aybak), 700 m.	EF453462	EF453589
<i>Salsola yazdiana</i> Assadi	H. Akhani & M. Dehghani s.n. Esfahan: 32 km S of Jandagh toward Chupanan, 33°47'12"N, 54°25'18"E, 1004 m, 27.10.2005.	EF453515	...
<i>Salsola zehzadii</i> Akhani	H. Akhani, 10029. Iran: Khorassan: ca. 35 km E of Torbat-e Jam near Malu, 35°12'19"N, 61°1'17"E, 15.8.1994.	EF453463	EF453590
<i>Salsola zehzadii</i> Akhani	H. Akhani & Zangui 10043. Khorasan: ca. 38 km E of Torbat-e Jam, 11 km after Mohammad-abad toward Maloo, gypsum hills, 720–740 m, 15.8.1994.	EF453498	EF453619
<i>Salsola zeyheri</i> (Moq.) Bunge	Giess, Volk & Bleissner 5349a (M). Namibia: S Luederitz; Farm Zebrafontein, LU 87, 21.02.1963.	EF453502	...
<i>Salsola zygophylla</i> Batt. et Trab. <i>Seidlitzia florida</i> (M. Bieb.) Bunge ex Boiss.	Pyankov et al. 2001a.	AF318651	...
	H. Akhani & M. Ghobadnejhad 15630. Iran: E Azerbaijan, 10 km SW of Sarab in the road toward Asbforoushan, 37°52'7"N, 47°30'30"E, 1700 m, 8.9.2001.	EF453507	EF453627
<i>Seidlitzia rosmarinus</i> Ehrenb. ex Boiss.	H. Akhani, s.n. Iran: Tehran, between Tehran and Qom, W of Heuz-Soltan Lake, 35°2'6"N, 50°51'47"E, 861 m, 23.7.2003.	EF453506	EF453626
<i>Sympegma regelii</i> Bunge	V. Bochantzev et al. 5229 (LE). Kyrgyzstan: Issykkulj province, Gionskij region, Mountain range Terskej Alatau, northern slopes around village Kadanisaj.	EF453510	EF453629

Table B1

(Continued)

Subfamily, tribe, and species	Voucher of DNA source	GenBank no.	
		ITS	<i>psbB-psbH</i>
<i>Traganum nudatum</i> Del.	S. Chaudhary 8644 (LE). Saudi Arabia: Haayer, 16.4.1984.	EF453511	EF453630
Salicornioideae:			
Salicornieae:			
<i>Kalidium caspicum</i> (L.) Ungern-Sternb.	H. Akhani 15329. Iran: Semnan, Alborz mountains, 67 km W of Damghan in the road toward Cheshmeh Ali, 1822 m, 36°6'19"N, 53°47'27"E, 14.7.2001.	EF453444	...
<i>Microcnemum corraloides</i> (Loscos & Pardo) Buen	H. Akhani & M. Ghobadnejhad 15491. Iran: Arak (Ostan-e Markazi), northwestern parts of the Kavir-e Meyghan, near Deh-e Namak, 33°55'N, 49°19'E, 1688 m, 19.8.2001.	EF453448	EF453576
<i>Salicornia persica</i> Akhani	H. Akhan & M. Ghobadnejhad 15719. Iran: Fars, N of Tashk lake, high salty soils near Gomban, 29°48'N, 53°28'E, 1590 m, 20.9.2001.	EF453460	...
Suaedoideae:			
Bienertiaeae:			
<i>Bienertia sinuspersici</i> Akhani	H. Akhani 17433. Iran: Khuzestan, 17 km N of Bandare Mahshahr, 30°39'5 N, 49°15'51"E, 28 m, 31.10.2003.	DQ499349	DQ499434
Suaedeae:			
<i>Suaeda cuculata</i> Aellen	H. Akhani et al. 17920. Turkey: Ankara, 28 km N of Sereflikochisar toward Ankara, N of Tzu Gölü Lake, 39°8'50"N, 33°19'4"E, 895 m, 27.8.2004.	EF453509	...
<i>Suaeda maritima</i> (L.) Dum.	H. Akhani & M. Ghobadnejhad 15492. Iran: Arak (Ostan-e Markazi), northwestern parts of the Kavir-e Meyghan, near Deh-e Namak, 33°55'N, 49°19'E, 1688 m, 19.8.2001.	EF453508	EF453628

Note. The vouchers, unless otherwise indicated, are deposited in TUH and the School of Biology, University of Tehran, Research Laboratory of Plant Systematics and Plant Geography (H. Akhani). Herbarium abbreviations: GAZ = Gazy Herbarium, Ankara, Turkey; K = Royal Botanic Gardens, Kew, United Kingdom; LE = V. L. Komarov Botanical Institute, St. Petersburg, Russia; M = Botanische Staatssammlung München, München, Germany; MSB = Ludwig-Maximilians-Universität, München, Germany. ITS = internal transcribed spacer.

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