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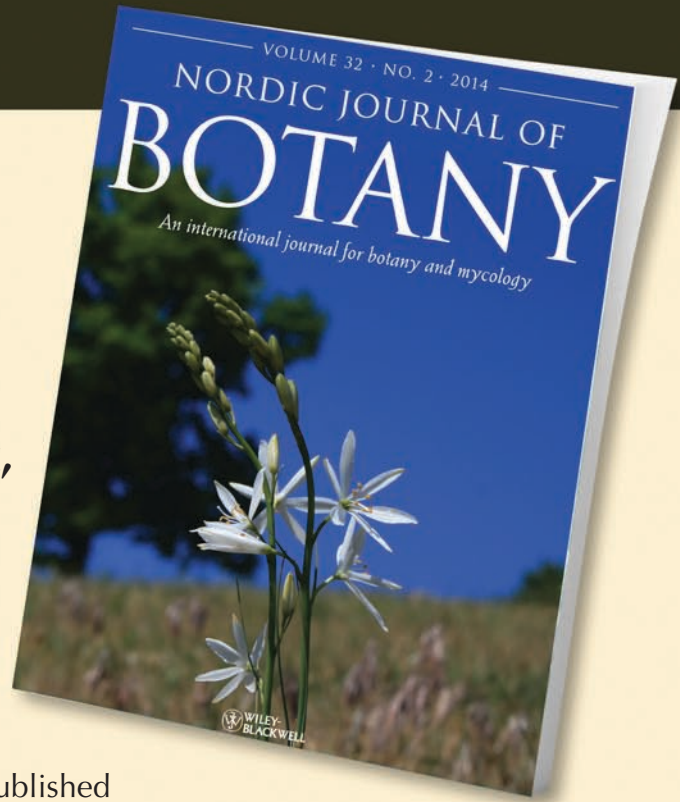
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Salsola arbusculiformis and *S. laricifolia* (Chenopodiaceae) in China

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To examine diagnostic characters and test phylogenetic relationships between *Salsola arbusculiformis* and the closely similar *S. laricifolia*, characters were examined from previous reports and herbarium specimens, and sequences of nrDNA ITS and cpDNA *psbB-psbH* were compared for these species as well as other representative taxa of Salsoleae. Our results 1) confirm most of the morphological differences highlighted in previous studies, such as those of leaf size, bracts, bracteoles, style, fruiting perianth, and anther appendages; 2) show that *S. arbusculiformis* is a typical Irano-Turanian species, mainly distributed from Iran and Turkmenistan to westernmost China (Tacheng, Ili, and Bole regions, Xinjiang), while *S. laricifolia* is a central Asian floristic element mainly distributed from east Kazakhstan and Kyrgyzstan to northern China (north Xinjiang, inner Mongolia, Ningxia and Gansu provinces), and Mongolia; and 3) strongly support their sister relationship, with samples from five different populations clustering together for each of the two species.

Salsola arbusculiformis Drob. is closely related to *S. laricifolia*, with which it has sometimes been confused or considered conspecific (Nikitina 1955, Goloskokov 1960, Kinzikayeva 1968). It was therefore necessary to study both species in detail (Freitag and Rilke 1997).

Salsola arbusculiformis and *S. laricifolia* are closely similar not only in habitat and ecology, but also in morphological features (Drobow 1927, Iljin 1936, Freitag and Rilke 1997, Grubov 1999, Zhu et al. 2003) and anatomical structure (Wen and Zhang 2011). They are small shrubs with non-decurrent semiterete leaves, having bracteoles shorter than the perianth, spicate inflorescences, and with a portion of the perianth segments above the wing joined to form a cone. They have a similar leaf anatomy, with two to three layers of palisade mesophyll cells and distinctive Kranz-like innermost layer of chlorenchyma cells, and with more numerous chloroplasts and mitochondria than Sympegmoid species (Voznesenskaya et al. 2001, Wen and Zhang 2011). *Salsola arbusculiformis* and *S. laricifolia* have previously been classified in *Salsola* sect. *Arbuscula* (Ulbrich 1934, Liu 1991, Freitag and Rilke 1997, Grubov 1999, Huang 2005), *Salsola* sect. *Anchophyllum* series *Arbusculae* (Iljin 1936), *Salsola* sect. *Cocosalsola* subsect. *Arbusculae* (Botschantzev 1976), and in the tentatively proposed genus '*Collinosalsola*' (Akhani et al. 2007).

Since the description of *S. arbusculiformis* by Drobow in 1916, comparison of characters of *S. arbusculiformis* and *S. laricifolia* have been made by several taxonomists (Table 1). Their treatments can be grouped into two kinds.

In several treatments the species were accepted as separate entities, although based on different morphological characters by different authors, with anther appendage as the most widely used feature, then bracts and bracteoles. In several other treatments, because of their similarities, *S. arbusculiformis* has been treated as a synonym of *S. laricifolia*, e.g. by Nikitina (1955) in 'Flora Kirghizskaya SSR', Goloskokov (1960) in 'Flora of Kazakhstan SSR', and Kinzikayeva (1968) in 'Flora of Tadzhikistan SSR'. Although Iljin (1936) distinguished the two species, he thought that *S. arbusculiformis* might represent an ecological variety of *S. laricifolia*.

The distribution of these two species is summarized in Table 1. For *S. laricifolia*, records of its distribution have gradually increased, from initially including only Kazakhstan and Mongolia (Drobow 1916), to eastern Kazakhstan, parts of China (the Dzungarian region, inner Mongolia), and Mongolia (Botschantzev 1976), and finally a more complete distribution in China (northern Xinjiang, inner Mongolia, Ningxia, and northern Gansu Provinces), as well as Mongolia, and central Asia (not mentioning individual countries in central Asia) (Zhu et al. 2003). With regards to *S. arbusculiformis*, compared to records of its distribution outside China, those inside China have been more consistent, mainly focusing on the Dzungarian region and the northern Tian Shan Mountains. 'Flora Xinjiangensis' (Mao et al. 1994) stated that the distribution of *S. arbusculiformis* in China was narrow, only including Wenquan county (the Bole region, Xinjiang) and the Ili region (Xinjiang).

Table 1. Historical comparison of diagnostic characters and accepted distribution of *S. arbusculiformis* and *S. laricifolia* (since 1916).

	Characters	<i>S. laricifolia</i>	<i>S. arbusculiformis</i>
Drobow (1916)	Flowers	smaller	larger
Drobow (1916, 1927)	Perianth	wide-oval	oval-ovoid
	Stigma apex	sharp	obtuse
	Anther appendage	acute	obtuse
Drobow (1927)	Style	divided up to 1/3	divided up to 3/4
Iljin (1936)	General distribution	Kazakhstan, Mongolia	Kyrgyzstan, Uzbekistan, Kazakhstan
	Height	dwarf plant, 10–30 cm	taller plant, 20–50 cm
	Leaves	5–20mm long, pale green	10–35mm long, green
	Flowers	smaller, surpassing the bracteoles	larger, greatly exceeding the bracteoles
	General distribution	Dzungaria-Kashgar region, Mongolia	Dzungaria-Kashgar region
Botschantzev (1963)	Color of Perianth	smoky	bright
	General distribution	Kazakhstan, China (Dzungarian region), Mongolia	central Asia (Kazakhstan), from Kopet Dagh and Ust-Urt in the west to Dzungarian region (China)
Botschantzev (1963, 1976)	Bract base	decurrent	not decurrent
	Anther appendage	acute	obtuse
	Bracteoles	acuminate, not scarious-edged at apex	obtuse, scarious-edged at apex
Botschantzev (1976)	General distribution	east Kazakhstan, China (Dzungarian regions, Gansu, inner Mongolia provinces), Mongolia	Iran, USSR (Turkmenistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan), China (Dzungarian region)
Grubov (1966, 1999)	Bract base	decurrent	not decurrent
	Bracteoles	terminal bracteoles with fleshy green cusp or short and thick process, scarious only on sides	without cusp, sinuately scarious on sides and apex, green only along back
	Anthers	mainly yellow	mainly red
	General distribution	Balkhash region	Aral-Caspian, Balkhash region, Nor. Tian Shan, Iran
Freitag and Rilke (1997)	General distribution	—	west Kopet Dagh and Ust-Urt plateau eastwards to the Tian Shan and Kazakhstan, southwards to Khorasan and S Tadjikistan
Zhu et al. (2003)	Bract base	decurrent	not decurrent
	Bracteoles	margin membranous laterally, but apex herbaceous, acute	margin membranous throughout, apex obtuse
	Anther appendage	pungent	obtuse
	General distribution	China (north Xinjiang, inner Mongolia, Ningxia and north Gansu Provinces), Mongolia, central Asia	China (north Xinjiang), central Asia
This article	Color	light brown	brownish green
	Leaves	longer, 1–2 cm long	shorter, 1.0–1.5 cm long
	Bract	decurrent	not decurrent
	Bracteoles	with fleshy green cusp, scarious only at the lateral margins	without cusp, margin scarious throughout
	Fruiting winged perianth	8–12 mm in diameter	8–14 mm in diameter
	Style	divided up to 1/3	divided up to 3/4
	Anther appendage	acute	obtuse
	General distribution	from east Kazakhstan and Kyrgyzstan to northern China (north Xinjiang, inner Mongolia, Ningxia and Gansu provinces) and Mongolia	from Iran and Turkmenistan to westernmost China (Tacheng, Ili and Bole regions, Xinjiang)

Table 2. Sampled taxa, vouchers, and Genbank accession numbers in this study.

Species	Voucher	Source	Genbank Accession no.	
			ITS	psbB-psbH
<i>Salsola</i> s.l.				
<i>Anabasis aphylla</i> L.	Wen et al. (2010)		HM131608	HM131677
<i>Anabasis elatior</i> (C. A. Mey.) Schischk.	Wen et al. (2010)		HM131612	HM131681
<i>Anabasis eriopoda</i> (Schrenk) Benth. ex Volkens	Wen et al. (2010)		HM131613	HM131682
<i>Anabasis truncata</i> (Schrenk) Bunge	Wen et al. (2010)		HM131615	HM131684
<i>Climacoptera affinis</i> (C. A. Mey.) Botsch.	Wen et al. (2010)		HM131617	HM131686
<i>Climacoptera brachiata</i> (Pall.) Botsch.	Wen et al. (2010)		HM131618	HM131687
<i>Climacoptera lanata</i> (Pall.) Botsch.	Wen et al. (2010)		HM131621	HM131690
<i>Climacoptera obtusifolia</i> (Schrenk) Botsch.	Wen et al. (2010)		HM131622	HM131691
<i>Climacoptera subcrassa</i> (M. Pop.) Botsch.	Wen et al. (2010)		HM131624	HM131693
<i>Cirgensohnia oppositiflora</i> (Pall.) Fenzl	Wen et al. (2010)		HM131626	HM131695
<i>Halogeton arachnoideus</i> Moq.	Wen et al. (2010)		HM131630	HM131699
<i>Halogeton glomeratus</i> (M. Bieb.) C. A. Mey.	Wen et al. (2010)		HM131631	HM131700
<i>Horaninowia ulicina</i> Fisch. et. C. A. Mey.	Wen et al. (2010)		HM131634	HM131703
<i>Ilijinia regelii</i> (Bunge) Korov.	Wen et al. (2010)		HM131635	HM131704
<i>Halimocnemis karelinii</i> Moq.	Wen et al. (2010)		HM131627	HM131696
<i>Halimocnemis villosa</i> Kar. et Kir.	Wen et al. (2010)		HM131629	HM131698
<i>Nanophyton erinaceum</i> (Pall.) Bunge	Wen et al. (2010)		HM131639	HM131708
<i>Petrosimonia glaucescens</i> (Bunge) Ilijin	Wen et al. (2010)		HM131640	HM131709
<i>Petrosimonia squarrosa</i> (Schrenk) Bunge	Wen et al. (2010)		HM131642	HM131711
<i>Salsola arbuscula</i> Pall.	Wen et al. (2010)		HM131645	HM131714
<i>Salsola arbusculiformis</i> Drob.	Wen Z. B. and Meng H. H. W003 (XIBI)	Longkou, Xinyuan county, Xinjiang, China	KC310715	KC310707
	Wen Z. B. and Meng H. H. W006 (XIBI)	On the road from Xinyuan county to Yili city, Xinjiang, China	KC310716	KC310708
	Wen Z. B. and Meng H. H. W013 (XIBI)	Tiechanggou town, Toli county, Xinjiang, China	KC310717	KC310709
	Wen et al. (2010)		HM131646	HM131715
	Akhani et al. (2007)		EF453468	EF453593
<i>Salsola chinghaiensis</i> A. J. Li	Wen et al. (2010)		HM131647	HM131716
<i>Salsola dzhungarica</i> Ilijin	Wen et al. (2010)		HM131650	HM131719
<i>Salsola foliosa</i> (L.) Schrad.	Wen et al. (2010)		HM131651	HM131720
<i>Salsola implicata</i> Botsch.	Wen et al. (2010)		HM131653	HM131722
<i>Salsola junatovii</i> Botsch.	Meng H. H. 2010-11 (XIBI)	Wuqia county, Kashi city, Xinjiang, China	KC310718	KC310710
<i>Salsola laricifolia</i> Turcz. ex Litv.	Wen Z. B. and Meng H. H. W008 (XIBI)	Near overpass of Bole city, Xinjiang, China	KC310719	KC310711
	Wen Z. B. and Meng H. H. W015 (XIBI)	Tiechanggou town, Toli county, Xinjiang, China	KC310720	KC310712
	Wen et al. (2010)		HM131655	HM131724
	Zhang M. L., Wen Z. B., Zhu G. L. 082135 (XIBI)	At 4649 km of 312 national highway, near Bole city, Xinjiang, China	KC310721	KC310713
	Zhang M. L., Wen Z. B., Zhu G. L. 082116 (XIBI)	On the road from Hebukesaiter to Emin county, Xinjiang, China	KC310722	KC310714
<i>Salsola micranthera</i> Botsch.	Wen et al. (2010)		HM131656	HM131725
<i>Salsola nitraia</i> Pall.	Wen et al. (2010)		HM131661	HM131729
<i>Salsola paulsenii</i> Litv.	Wen et al. (2010)		HM131663	HM131731
<i>Salsola pellucida</i> Litv.	Wen et al. (2010)		HM131664	HM131732
<i>Salsola praecox</i> Litv.	Wen et al. (2010)		HM131665	HM131733
<i>Salsola rosacea</i> L.	Wen et al. (2010)		HM131666	HM131734

(Continued)

Table 2. (Continued).

Species	Voucher	Source	Genbank Accession no.	
			ITS	<i>psbB-psbH</i>
<i>Salsola zaidamica</i> Iljin	Wen et al. (2010)		HM131669	HM131737
<i>Sympegma regelii</i> Bunge	Wen et al. (2010)		HM131676	HM131744
Outgroup				
Salicornieae				
<i>Kalidium cuspidatum</i> (Ung.-Stemb.) Grub.	Wen et al. (2010)		HM131637	HM131706
<i>Kalidium foliatum</i> (Pall.) Moq.	Wen et al. (2010)		HM131638	HM131707
Suaedeae				
<i>Suaeda microphylla</i> (C. A. Mey.) Pall.	Wen et al. (2010)		HM131671	HM131739
<i>Suaeda physophora</i> Pall.	Wen et al. (2010)		HM131673	HM131741
<i>Suaeda pterantha</i> (Kar. et Kir.) Bunge	Wen et al. (2010)		HM131675	HM131743

The phylogenetic relationship between *S. arbusculiformis* and *S. laricifolia* has also been studied using molecular methods. Both species have been well separated in all published dendrograms (Pyankov et al. 2001, Wen et al. 2010, Kadereit and Freitag 2011). *Salsola arbusculiformis* and *S. laricifolia* were resolved as a sister pair by Wen et al. (2010) using three molecular markers (ITS, *psbB-psbH*, and *rbcL*), and by Kadereit and Freitag (2011) using *ndhF* gene sequences with Beast analysis (Fig. S3 in Kadereit and Freitag 2011), or on separate branches as in the analyses of Pyankov et al. (2001) based on ITS sequences only (incomplete, with at least 80 base pairs of the ITS 2 region missing), and Kadereit and Freitag (2011) using *ndhF* gene sequences with the Maximum likelihood analysis (Fig. S4 in Kadereit and Freitag 2011).

In this study, we checked specimens of *S. arbusculiformis* and *S. laricifolia* in the main herbaria in China, and sequenced nrDNA ITS and cpDNA *psbB-psbH* of these and other species of the Salsoleae. We focused on the following aims: 1) to identify diagnostic characters of *S. arbusculiformis* and *S. laricifolia* throughout their distribution in China; and 2) to test the phylogenetic relationship between *S. arbusculiformis* and *S. laricifolia*.

Material and methods

Plant sampling

During field work from 2008 to 2011, we collected numerous specimens of Salsoleae, and examined specimens of *S. arbusculiformis* and *S. laricifolia* in the following herbaria: PE, CAS, SHI, XJA, XJBI.

For the phylogenetic analysis, the species of Salsoleae included are listed in Table 2. We sampled *S. arbusculiformis* and *S. laricifolia* from five different populations each in order to search for consistent differences in their sequences, including one population of *S. arbusculiformis* from Iran, referenced in Akhiani et al. (2007). Five species from Salicornieae and Suaedeae were chosen as outgroups. New sequences (accession no. KC310707–KC310722 in Table 2) have been deposited in GenBank. Previously reported sequences were also employed (Akhiani et al. 2007, Wen et al. 2010).

DNA amplification and sequencing

Isolation of total DNA followed the modified 2 × CTAB buffer method (Doyle and Doyle 1987). The internal transcribed spacer (ITS) was amplified with primers ITS1 (5'-AGA AGT CGT AAC AAG GTT TCC GTA GC-3') (Kang et al. 2003) and ITS4 (5'-TCC TCC GCT TAT TGA TAT GC-3') (White et al. 1990). The *psbB-psbH* 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). Polymerase chain-reaction (PCR) amplification followed the procedures described by Schütze et al. (2003). After PCR, products were purified using the PEG precipitation procedure (Johnson and Soltis 1995) and sequencing was performed with an ABI Prism 3730 Genetic Analyzer.



Figure 1. Morphological characters of *S. laricifolia* (A)–(F) and *S. arbusculiformis* (G)–(L). (A) and (G) branchlet, (B) and (H) anther, (C), and (I) bracteole, (D) and (J) bract, (E) and (K) fruiting perianth, (F) and (L) fruit.

Alignment and phylogenetic analysis

The identification of terminal ends and spacer boundaries of all sequences was based on comparisons with other species of Salsoleae (Kapralov et al. 2006, Akhani et al. 2007). Forward and reverse sequences were aligned using Clustal X (Thompson et al. 1997). Gaps were scored as missing data in the phylogenetic analyses. Finally, two datasets consisting of ITS, and ITS + *psbB*–*psbH* were assembled. Bayesian inference (BI) was employed for phylogenetic analyses, using MrBayes, ver. 3.0b4 (Huelsenbeck and Ronquist 2001, Huelsenbeck and Rannala 2004). Four chains were run, beginning with a random tree and saving a tree every 100 generations for 2 million generations. For Bayesian analyses, the appropriate model of DNA substitution was estimated using Modeltest 3.06 (Posada and Crandall 1998). The variable sites of sequences for *S. arbusculiformis* and *S. laricifolia* were estimated using DnaSP 5.0 (Rozas et al. 2003).

Results

Salsola arbusculiformis is characterized by leaves ca 1.0–1.5 cm long; bracteoles without a cusp and margins membranous throughout; fruiting perianth 8–14 mm in diameter; style divided for up to 3/4; yellow anthers with an appendage with obtuse apex (Fig. 1G–L). It occurs on rocky slopes and in deserts at altitudes of 500–900 m. *Salsola laricifolia* has leaves ca 1–2 cm long; bracteoles with a fleshy green cusp and margins that are membranous only along the sides; fruiting perianth 8–12 mm in diameter; style divided for up to 1/3; yellow anthers with an appendage with acute apex (Fig. 1A–F). It is distributed on rocky slopes, dunes, and in deserts at altitudes of 100–2000 m a.s.l.

According to our survey and herbarium specimens, the distribution of *S. arbusculiformis* in China is mainly in the westernmost part of the country, and consists of the Bole region (Wenquan county), the Ili region (Yining city, Xinyuan county), and the Tacheng region (Tacheng

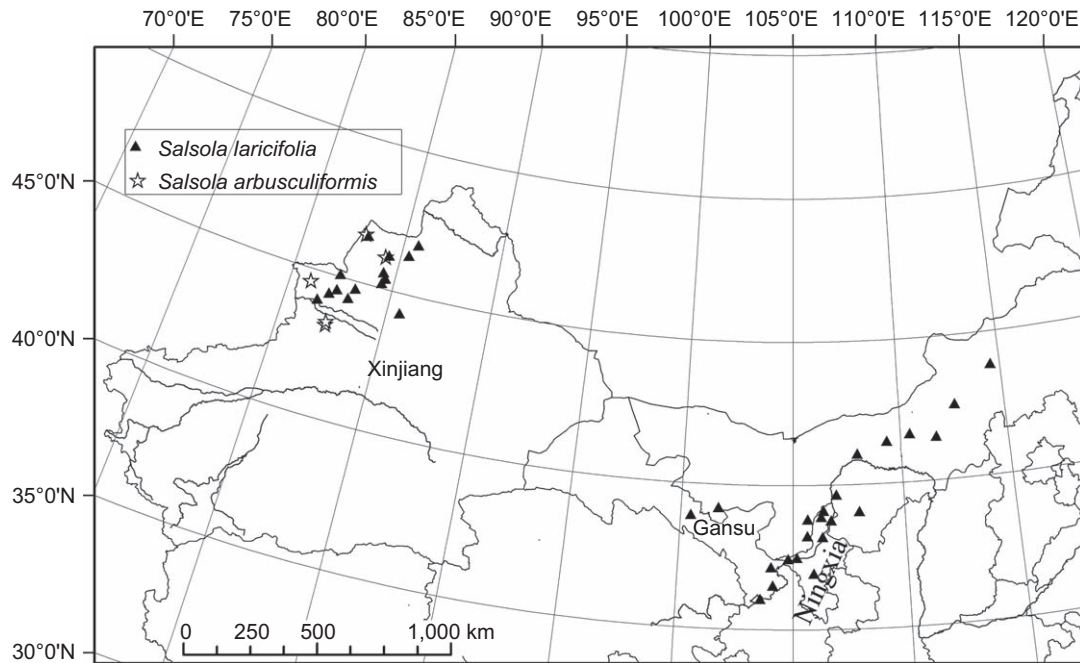


Figure 2. Distributions of *S. arbusculiformis* and *S. laricifolia* in China.

city, Toli county) (Fig. 2). The Chinese distribution of *S. laricifolia* is mainly in northern Xinjiang, inner Mongolia, Ningxia, and Gansu provinces (Fig. 2).

Phylogenetic trees based on ITS and ITS + *psbB-psbH* had the same topology. Here we show only the tree from the combined sequences (Fig. 3). In this tree, the samples of *S. arbusculiformis* from five different populations (one from Iran, the others from China) forms a separate clade ($pP = 100\%$), and samples of *S. laricifolia* from five different populations (all from China) form another well supported clade ($pP = 100\%$). *Salsola arbusculiformis* and *S. laricifolia* are resolved as a sister pair ($pP = 99\%$). The distribution of the sites variable in these two species is compared in Table 3. There were 40 variable sites in *S. arbusculiformis* and *S. laricifolia* in the ITS and *psbB-psbH*, with 24 in ITS and 16 in *psbB-psbH*. Among these 40 variable sites, there were 3 indels, 2 transitions, and 11 transversions, of which 1 indel and 1 transversion were in the *psbB-psbH* sequence, with all others in ITS.

Discussion

Diagnostic characters of *S. arbusculiformis* and *S. laricifolia*

The morphological characteristics of *S. arbusculiformis* and *S. laricifolia* revealed in this study are listed in Table 1. *Salsola arbusculiformis* resembles *S. laricifolia*, but even from a distance *S. arbusculiformis* can be recognized by its brownish green color. *Salsola arbusculiformis* can also be distinguished from *S. laricifolia* based on six morphological characters in bracts, bracteoles, and anther appendages. Our study confirmed most of the characters

highlighted in previous studies (Drobow 1916, 1927, Iljin 1936, Botschantzev 1963, 1976, Freitag and Rilke 1997, Grubov 1999, Zhu et al. 2003), but indicated that some of the characters given as diagnostic by previous authors are less useful, such as perianth shape (Drobow 1916), height (Iljin 1936), perianth color (Botschantzev 1963), and anther color (Grubov 1966).

As for their distributions, *S. arbusculiformis* is found from Iran and Turkmenistan to westernmost China. Its distribution in China is mainly in the Tacheng, Ili, and Bole regions in Xinjiang (Fig. 2), which expands the distribution area given by Mao et al. (1994). *Salsola laricifolia* is distributed in northern and northwestern China, Mongolia, eastern Kazakhstan and Kyrgyzstan. Its distribution in China is mainly in northern Xinjiang, inner Mongolia, Ningxia, and Gansu provinces (Fig. 2). Remarkably, a large gap is present between the western and eastern localities of *S. laricifolia* in China (Jiang and Ni 2005, Wu 2010), which might have been caused by ecological factors, because it is bridged by localities in the south Mongolian Omnogobi Aimak (Rilke 2012). From the distribution areas we conclude that *S. arbusculiformis* is a typical Irano-Turanian species while *S. laricifolia* is a central Asian floristic element.

Phylogenetic relationship of *S. arbusculiformis* and *S. laricifolia*

As mentioned above, *S. arbusculiformis* and *S. laricifolia*, each represented by samples from five different populations, were perfectly resolved in our phylogenetic analyses based on data from two genes (Fig. 3). Our analysis strongly supports a sister pair relationship between these species, as previously found by Wen et al. (2010) and in the *ndhF* tree of Kadereit

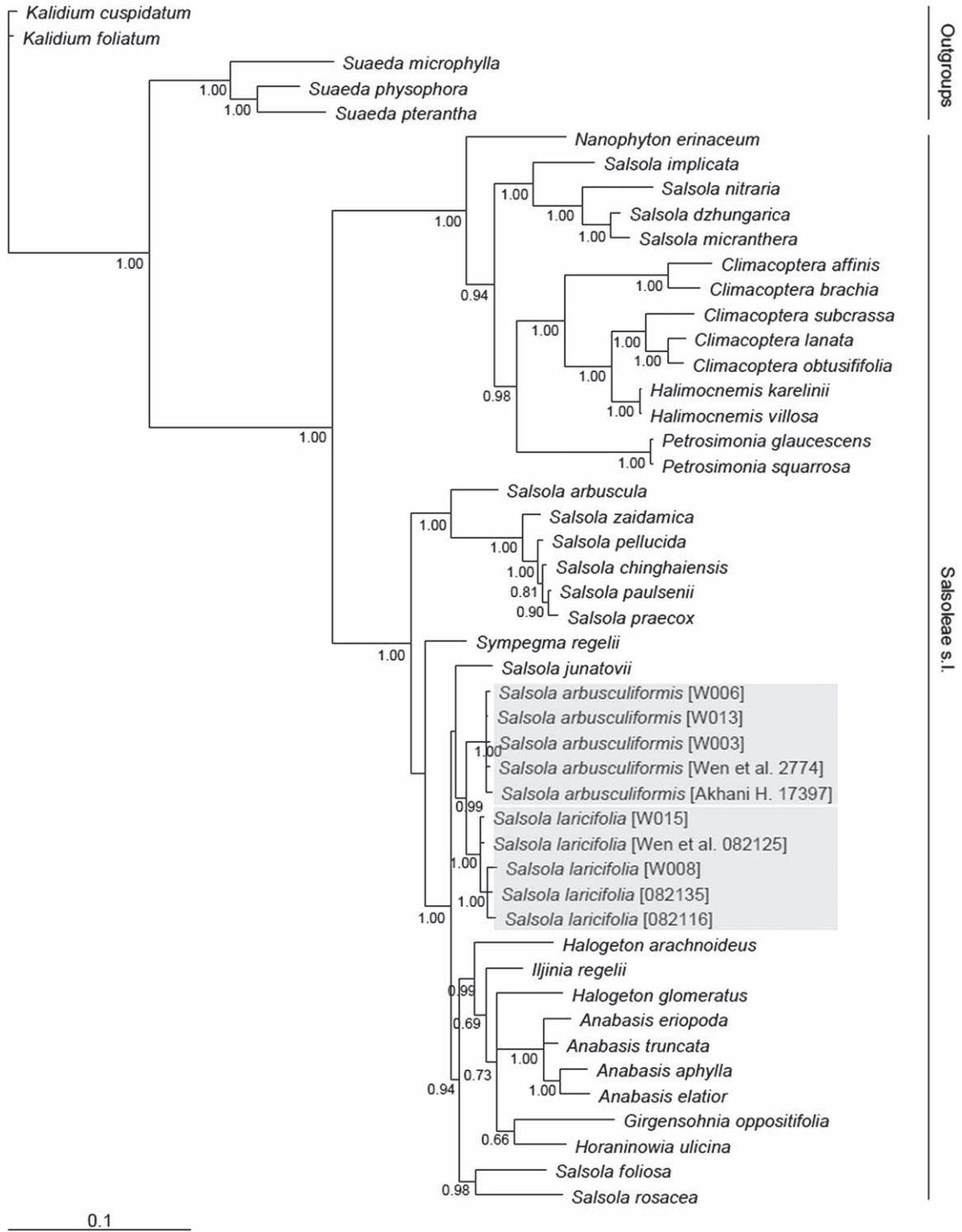


Figure 3. Phylogenetic tree of Salsoleae s.l. based on Bayesian inference analysis of ITS + *psbB-psbH* data. Bayesian posterior probabilities are given below the branches.

Table 3. Distributions of variable sites in ITS and psbB-psbH sequences of *S. arbusculiformis* and *S. laricifolia*.

aNo.	ITS										psbB-psbH									
	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
W003	3	5	6	7	0	8	8	8	8	9	1	1	1	1	1	1	1	1	1	5
W006	3	2	7	A	T	A	C	T	T	C	2	4	6	2	3	5	9	0	1	5
W013	G	T	A	A	T	T	T	T	T	C	2	4	6	2	3	5	9	0	1	5
Wen et al. 2774	G	T	A	A	T	T	T	T	T	C	2	4	6	2	3	5	9	0	1	5
H. Akhani 17397	G	T	A	A	T	T	T	T	T	C	2	4	6	2	3	5	9	0	1	5
W008	T	C	A	T	C	C	T	A	C	2	4	6	2	3	5	9	0	1	5	5
W015	G	C	C	T	C	C	T	A	C	2	4	6	2	3	5	9	0	1	5	5
Wen et al. 082125	G	C	A	T	C	C	T	A	C	2	4	6	2	3	5	9	0	1	5	5
082135	T	C	A	T	C	C	T	A	C	2	4	6	2	3	5	9	0	1	5	5
082116	T	C	A	T	C	C	T	A	C	2	4	6	2	3	5	9	0	1	5	5

^aNumbers W003, W006, W013, Wen et al. 2774, and H. Akhani 17397 are *S. arbusculiformis*; subsequent numbers are *S. laricifolia*.

and Freitag (2011). This relationship is consistent with their close resemblance in morphology. At the same time, the consistent sequence differences revealed between *S. arbusculiformis* and *S. laricifolia* are in line with the morphological distinctions they exhibit.

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