
A TAXONOMIC SYNOPSIS OF THE GENUS *SALSOLA* (CHENOPODIACEAE) IN NORTH AMERICA¹

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ABSTRACT

A key and synopsis of the genus *Salsola* L. (Chenopodiaceae) in North America north of Mexico are presented, including the taxonomy and distribution of six recognized species. A new combination is proposed: *Salsola kali* L. subsp. *pontica* (Pallas) Mosyakin.

The genus *Salsola* L. sensu lato, which includes the segregate genera *Caroxylon* Thunberg, *Climacoptera* Botschantsev, *Hypocylix* Woloszczak = *Darniella* Maire, *Neocaspia* Tzvelev, *Nitrosalsola* Tzvelev, and *Xylosalsola* Tzvelev, comprises 130–150 species, which are especially numerous in the arid and coastal zones of Eurasia, including Central Asia (all sections of the genus), the Middle East, and the Mediterranean region. Some species, mostly representatives of *Salsola* sect. *Salsola* (including sect. *Kali* Dumortier), also occur in other regions of the world as introduced synanthropic weeds, including in North America.

The considerable biological diversity of arborescent and shrubby species of *Salsola* sect. *Caroxylon* (Thunberg) Fenzl (or the separate genus *Caroxylon*) is confined also to northern (Mediterranean), southern, and eastern parts of Africa (see Botschantsev, 1969, 1975a, b). Some “satellite” genera closely related to *Salsola* (*Aellenia* Ulbrich, *Physandra* Botschantsev, *Horaninivia* Fischer & Meyer, *Girgensohnia* Bunge) are widely recognized by botanists, while some others are not. However, in most cases the latter segregate genera, usually treated as synonyms of *Salsola* sensu lato or recognized as infrageneric taxa, are not less distinct from *Salsola* sensu stricto, than, for example, such readily accepted pairs of genera as *Kochia* Roth and *Bassia* Allioni, *Salicornia* L. and *Arthrocnemum* Moquin-Tandon, *Corispermum* L. and *Anthochlamys* Fenzl,

Atriplex L. and *Halimione* Aellen. It means that the generic boundaries of *Salsola* and related taxa are in need of a systematic revision. It is also evident that *Salsola* in the traditional sense should be regarded as a group of genera, rather than as a natural genus. The taxonomic problems related to forming a generic concept within this group have been discussed recently by Tzvelev (1993). He accepted several quite distinct genera, including *Caroxylon*, which is represented in North America by only one alien species, usually referred to as *Salsola vermiculata*; all other North American taxa belong to *Salsola* sensu stricto.

As noted above, all species of North American *Salsola* should be regarded as naturalized or casual aliens native to Eurasia.

In the course of preparing a taxonomic treatment of the genus for the *Flora of North America* it has become evident that the taxonomy, nomenclature, and distribution of some species need clarification. Extensive herbarium collections from MO, GH, NY, and US served as the base for this study. Comparative Eurasian material from LE, KW, MHA, and some other Russian and Ukrainian herbaria was also examined. Types of *Salsola australis* R. Br. and *S. caroliniana* Walt. sent on loan to MO from BM were also consulted, as were photographs of Linnaean specimens from LINN.

Following is a brief synopsis of the *Salsola* species occurring in North America north of Mexico,

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with some notes on their taxonomy and distribution. Unfortunately, it is impossible to present a complete account of the North American distribution for all *Salsola* species, mostly due to taxonomic confusion (especially for species of the *S. kali* aggregate) in the literature. The distribution statements in this account are based on reliably identified herbarium specimens seen in the course of this study. For more or less common species only states, provinces, and territories are cited in the following synopsis, while for the rare aliens more detailed information is presented.

This article does not pretend to solve all problems concerning distribution and ecology of introduced species of *Salsola* in North America. Its primary aim is to provide a more reliable taxonomic background for further studies.

TAXONOMY OF *SALSOLA* IN NORTH AMERICA

Salsola L., Sp. Pl. 1: 222. 1753. TYPE: *Salsola soda* L. (lectotype, selected by Britton & Brown, 1913).

Annual herbs, or subshrubs [in the Old World also shrubs and small trees], glabrous or \pm pubes-

cent or hispid. Stems branched (very rarely simple), erect, ascending or prostrate. Leaves mostly alternate (occasionally lower ones subopposite), sessile, semiterete, lanceolate, linear, or filiform, margin entire. Inflorescences spicate. Flowers normally bisexual, solitary (rarely in twos or threes, but in this case lateral flowers poorly developed) in axils of bracts, with 2 bracteoles. Perianth segments 5, at maturity covering the fruit and in most species developing a transverse dorsal membranous or almost coriaceous wing (sometimes only 2 or 3 perianth segments winged, or all wingless). Stamens 5. Styles and stigmas 2 (3). Seeds usually horizontal; pericarp adherent; embryo spiral.

The name is derived from Latin sal, salt; or sal-sus, salty. The name *Salsola* was first used by Cesalpino (1519–1603) for a plant that is now known as *Halogeton sativus* (L.) Moquin-Tandon (basionym: *Salsola sativa* L., published in 1762).

Vernacular names. Saltwort, Russian-thistle (English); Soude, Salsovie (French); Salzkraut (German); Kali, Soda (Italian); Solyanka (Russian), Solyanka, Kurai (Ukrainian); Solanka (Polish); Slanobyl (Czech).

ARTIFICIAL KEY TO *SALSOLA* TAXA IN NORTH AMERICA

- 1a. Annual herbs, glabrous or papillose-hispid; leaves and bracts with spinose (or at least mucronulate) apex; perianth segments completely glabrous, or indistinctly papillose (occasionally ciliate at margin).
- 2a. Leaves (especially lower ones) mostly opposite, with apex mucronulate, not spinose; bracts distinctly swollen at base, alternate or subopposite; perianth segments normally with crenate or pectinate-ciliate apex; plants always glabrous..... 5. *S. soda*
- 2b. Leaves all alternate (sometimes only 1–3 pairs of lower ones subopposite), with spinose or spinescent (rarely almost mucronulate) apex; bracts not swollen, or in some species indistinctly swollen at base, normally alternate; perianth segments with acute entire apex (sometimes papillose at margins, but never crenate or pectinate-ciliate); plants papillose-hispid or occasionally glabrous.
- 3a. Leaves fleshy (in living plants), linear, in herbarium specimens mostly 1–2 mm broad, \pm gradually narrowed into rather firm apical spine; bracts reflexed at maturity.
- 4a. Perianth segments with long-acuminate or long-subulate spinose apex, at maturity forming a slender columnar beak above the broad wings; fruiting perianth 7–12 mm diam.; plants of open sands and inland saline habitats..... 3. *S. paulsenii*
- 4b. Perianth segments with short-acuminate or triangular apex, never forming a columnar beak at maturity; wings absent or shorter; fruiting perianth 6–7(10) mm diam. or less; plants of maritime saline habitats (seashores, tidal marshes, etc.)..... 1. *S. kali*
- 5a. Perianth segments with rigid, subspinose apex and distinct midvein; bracteoles not swollen, free..... 1a. *S. kali* subsp. *kali*
- 5b. Perianth segments with weak apex and obscure midvein; bracteoles swollen, connate at least at base..... 1b. *S. kali* subsp. *pontica*
- 3b. Leaves normally not fleshy (occasionally somewhat fleshy in plants growing in saline and alkaline habitats), narrowly linear to filiform, in herbarium specimens mostly less than 1 mm broad, in most cases abruptly narrowed into weak apical spine (mucro); bracts reflexed or appressed at maturity.
- 6a. Bracts appressed and strongly imbricate at maturity, gradually narrowed into subulate spinose apex; inflorescence narrowly spicate, rather dense, not interrupted at maturity; perianth segments wingless or rarely with narrow (usually less than 1 mm) erose wing; plants normally erect, branched above the base, or with a few slender branches near the base..... 4. *S. collina*
- 6b. Bracts reflexed, not imbricate at maturity, in most cases \pm abruptly narrowed into spinose or submucronulate apex; inflorescence spicate, at maturity interrupted at least in lower half; perianth segments normally with membranous wing; plants erect or ascending, branched from the base.

- 7a. Perianth segments with long-acuminate spinose apex, at maturity forming a slender columnar beak above the wings; fruiting perianth 7–12 mm diam. 3. *S. paulsenii*
7b. Perianth segments with obtuse to weakly acuminate or reflexed apex, at maturity not forming a columnar beak; fruiting perianth normally less than 8–10 mm diam. 2. *S. tragus*

1b. Perennial subshrubs covered with glabrous (smooth) and minutely denticulate hairs (sometimes becoming glabrous at maturity); leaves and bracts obtuse, without spinose apex; perianth segments with \pm pubescent (not papillose) apex. 6. *S. vermiculata* sensu lato

1. *Salsola kali* L., Sp. Pl.: 222. 1753. TYPE:
Herb. Burser XVI(2): 24 (lectotype, selected by Jonsell & Jarvis (1994), UPS not seen).

See discussion below. The species is described from Europe: "Habitat in Europae litoribus maris."

Annual herbs, 5–50 cm tall, papillose-hispid or glabrous. Stems branched from the base, erect, rarely ascending; branches arcuate or sometimes prostrate. Leaves alternate, linear, fleshy, in herbarium specimens mostly 1–2 mm broad, semiterete, normally not swollen at base; apex \pm gradually narrowed into rather firm spine. Inflorescence spicate, interrupted at maturity. Bracts reflexed, not imbricate at maturity, alternate, narrowing into subulate spinose apex. Flowers normally solitary in axils of bracts or reduced upper leaves. Perianth segments glabrous, with weak or firm apex, at maturity wingless or with comparatively narrow wing (in subsp. *pontica* sometimes prominently winged), becoming connate and united with bracteole bases, or bracteoles free. Fruiting perianth ca. 3–5 (rarely up to 8) mm diam.

Chromosome number. $2n = 36$ (Bassett & Crompton, 1970).

Distribution. Native to maritime coastal areas of Europe, northern Africa, southwestern Asia; introduced and naturalized in many other coastal regions of the world, including North America. This species is represented by two (or possibly three) subspecies.

Note on lectotypification. The specimen LINN 315.1 was selected as the lectotype of *Salsola kali* by Jafri and Rateeb (1978). This specimen represents a typical form of the species. However, it lacks a Species Plantarum number, and probably was added to the Linnaean collection after 1753. Because of that this lectotypification was superseded by Jonsell and Jarvis (1994) in favor of the Burser specimen cited above. The second Linnaean specimen identified as *S. kali*, LINN 315.2, also lacks a Species Plantarum number; moreover, it seems to be identical to *S. collina* Pallas.

1a. *Salsola kali* L. subsp. *kali*

Stems normally papillose-hispid (var. *kali*), or rarely glabrous (var. *polysarca* G. F. W. Meyer). Bracteoles free, not swollen. Perianth segments with rigid, almost spinose apex and distinct midvein.

Habitats. Seashores, salt marshes, sandy places in coastal regions and other saline maritime habitats, very rarely in ruderal inland habitats; 0–100 m.

Distribution. Herbarium specimens were examined from the following states, provinces, and territories: FRANCE (overseas department): St. Pierre et Miquelon. CANADA: New Brunswick, Newfoundland, Nova Scotia, Prince Edward Island, Quebec. U.S.A.: Connecticut, Delaware, Maine, Maryland, Massachusetts, New Hampshire, New Jersey, New York, North Carolina, Pennsylvania, Rhode Island, South Carolina, Virginia. This subspecies possibly also occurs in the District of Columbia, U.S.A. It is native to coastal maritime regions of western and northern Europe and is naturalized in many coastal regions of the world.

1b. *Salsola kali* L. subsp. *pontica* (Pallas) Mosyakin, comb. nov. Basionym: *Salsola kali* var. *pontica* Pallas, Illustr. Pl.: 37. 1803. *Salsola pontica* (Pallas) A. Degen, Flora Velebitica 2: 47. 1937. TYPE: authentic specimens in BM, lectotype not selected; see discussion below.

Stems in most cases glabrous (var. *glabra* Forsskal = *Salsola pontica* var. *glabra* Tzvelev, Ukrayins'k. Bot. Zhurn. 50(1): 82. 1993), or sometimes papillose-hispid (var. *pontica*). Bracteoles swollen, connate at base. Perianth segments with weak apex and obscure midvein.

Habitats. Seashores, salt marshes, sandy places in coastal regions, rarely in ruderal inland habitats; 0–100 m.

Distribution. Herbarium specimens were examined from the following states of the U.S.A.: Alabama, California (one locality: San Nicolas Island, Lat. 33°15'N; Long. 119°30'W, U.S. Naval Radiological Defense Laboratory, near road above sand spit at 100 ft. elevation, R. E. Foreman (No. 42),

E. C. Evans III, S. C. Rainey), Delaware, District of Columbia, Florida, Georgia, Louisiana, Massachusetts, Maryland, Mississippi, North Carolina, New Jersey, New York, Oregon (only one locality: on ballast grounds of Albine, Portland, 29 Sep. 1910, *W. N. Suksdorf s.n.*), South Carolina, Texas, and Virginia; this subspecies also occurs in Mexico and seems to be common in coastal regions of South America. It is native to coastal maritime regions of southern Europe, northern Africa, and southwestern Asia, northward to Great Britain, eastward to the Caspian Sea, and is locally naturalized in many coastal regions of the world.

This subspecies is closely related to *S. kali* subsp. *kali*, and in Eurasia replaces the latter on seashores of the Mediterranean, Black, Azov, and Caspian Seas. Its nomenclature is complicated and still unresolved. For a long time it was known in European botanical literature under the misapplied names *S. tragus* (sensu auct., non L.) or *S. kali* subsp. *tragus* (L.) Čelakovský (in part, excluding the type of the basionym). According to Botschantzev (1974), the southern maritime taxon of the *S. kali* aggregate is conspecific with *S. caroliniana* Walter (type at BM), which seems to be the earliest valid name at the species level. Tzvelev (1993), however, regarded *S. caroliniana* as a synonym of *S. tragus* sensu stricto. I have studied a small fragment of the type specimen of *S. caroliniana* sent as a loan to MO. This immature plant evidently belongs to *S. kali*, not to *S. tragus* sensu stricto. However, it is impossible to assign it with certainty to any subspecies of *S. kali*. Moreover, in American literature the name *S. caroliniana*, or *S. kali* var. *caroliniana* (Walter) Nuttall, was sometimes applied to other taxa of the *S. kali* aggregate. Because of this uncertainty in the proper identity of *S. caroliniana*, I selected as a basionym for the subspecies the name given by Pallas (1803) to the coastal Eurasian race of the *S. kali* aggregate. At least, this name refers to the native Eurasian taxon, as it was noted by Degen (1937) and Tzvelev (1993). When describing his *Salsola kali* var. *pontica*, Pallas (1803) had at his disposal specimens from coastal habitats of the Black Sea in the Crimea near modern Sevastopol (“... in littore Chersonesi Tauricae crescentes pro distincta specie habuisssem, nisi lectae circa Maeotin et in mediterraneis Tauriae,” Pallas, 1803: 37), and probably some additional specimens from adjacent coasts of the Black and Azov Seas, where only one littoral taxon of the *S. kali* aggregate is known to occur. The description and illustration in the protologue are also diagnostic. I did not have a chance to select the lectotype among Pallas's specimens deposited at BM; however, if

there are any obstacles for selecting a particular specimen at BM, the lectotypification could be based on the illustration in Pallas (1803).

In their secondary, anthropogenous areas of distribution (particularly, in North America) both subspecies of *S. kali* are often represented by convergent or deviate forms and seem to be less morphologically and geographically separated from each other than in their native Eurasian areas (e.g., North American specimens of *S. kali* subsp. *pontica* often approach *S. tragus* in having quite broad wings, a character that is not as common in Eurasian littoral plants). Due to this peculiarity of introduced plants, it would be reasonable for the purpose of nomenclatural stability to abandon some uncertain names of taxa described within the *S. kali* aggregate from various parts of the world (including *S. caroliniana* and *S. australis*; see also discussion below, under *S. tragus*).

When immature, subspecies *pontica* is almost indistinguishable from *S. kali* subsp. *kali*. Unfortunately, many specimens of *S. kali* sensu lato are represented in American herbaria by immature plants. More detailed studies using fruiting material are needed to clarify the distribution of both taxa in North America. However, *S. kali* subsp. *pontica* is certainly a more southern subspecies (in both North America and Europe), and seems to be the only race of *S. kali* occurring in littoral habitats from South Carolina to coastal Texas. It is also known from scattered localities as far north as Massachusetts. From New Hampshire to Newfoundland only subspecies *kali* seems to occur, and it is quite common as far south as Virginia, being gradually replaced southward (in Virginia and North Carolina) by subspecies *pontica*.

Both subspecies of *S. kali* were probably the first taxa of *Salsola* introduced to North America (evidently, on ship ballasts) shortly after the establishment of the first European settlements and the beginning of colonization of the continent.

Salsola kali is confined mostly to coastal saline habitats; however, it rarely occurs as introduced in ruderal inland habitats, but usually not far away from the coast.

2. *Salsola tragus* L., Cent. Pl. 2: 13. 1756. *Salsola kali* L. subsp. *tragus* (L.) Čelakovský, Prodr. Fl. Boehmen 2: 155. 1871 (see discussion under *S. kali* subsp. *pontica*). TYPE: LINN 315.3 (lectotype, selected here; see also Degen, 1937; Tzvelev, 1993).

Salsola australis R. Brown, Prodr. Fl. Nov. Holl. 1: 412. 1810 (emend. Botschantzev, Kew Bull. 29: 614. 1974). TYPE: “S. Australia: Nuyts Archipelago, Pe-

- treil Bay, Isle St. Francis, 8 Feb. 1802 (fl. & fr.) *Good & Bauer*" (lectotype, selected by Botschantzev (1974), BM, "planta dextra").
- Salsola kali* L. var. *tenuifolia* Moquin-Tandon, *Chenopodiarum Monographica Enumeratio*: 136. 1840. TYPE locality: southwestern Ukraine: "Ad Baltam [sphalm. "Balkam" -S. M.] (Besser in herb. DC.)" (holotype, probably at P not seen; isotype in the Besser memorial collection at KW).
- Salsola kali* L. var. *angustifolia* Fenzl in Ledebour, *Fl. Ross.* 3, 2: 798. 1851. TYPE: no reference to the type in the protologue; original specimens annotated by Fenzl at LE, lectotype not selected.
- Salsola kali* L. var. *leptophylla* Bentham, *Fl. Austral.* 5: 207. 1870. TYPE locality: "Queensland and N. S. Wales." TYPE: not designated.
- Salsola tragus* subsp. *iberica* Sennen & Pau, *Bull. Acad. Intern. Geogr. Bot. (Le Mans)*, ser. 3, 18: 476. 1908. *Salsola iberica* (Sennen & Pau) Botschantzev, *Bot. Zhurn. (Leningrad)* 54: 991. 1969, cum auct. "Sennen et Pau" (comb. invalid.). *Salsola iberica* (Sennen & Pau) Botschantzev ex Czerepanov, *Svod Dopolneniy i Izmeneniy k "Flore SSSR"*: 192. 1973, cum auct. "Sennen et Pau." TYPE: "Hab. Castille: Miranda de Ebro (Elias); Logroño, terrains vagues, près la station (Sennen)" (holotype, not seen; isotype, US).
- Salsola kali* L. var. *pseudotragus* G. Beck in Reichenbach, *Icon. Fl. Germ. Helv.* 25: 172. 1909. TYPE: not designated; described from Germany, "Inprimis in terris interioribus."
- Salsola pestifer* A. Nelson in Coulter's *New Manual Bot. Centr. Rocky Mountains*, ed. 2: 169. 1909. TYPE: "The now widely distributed Russian Thistle" (no collection cited in protologue; authentic specimens at GH, NY, US; lectotype not selected).
- Salsola ruthenica* Iljin in B. A. Keller et al., *Sornye Rasteniya SSSR (Weeds of the USSR)*, 2: 137. 1934, nom. illegit. *Salsola kali* L. subsp. *ruthenica* Soó in Soó et Jávorka, *Magyar Növ. Kéz.* 2: 786. 1951. TYPE: not designated.
- Salsola kali* L. var. *austroafricana* P. Aellen, *Mitteilungen der Botanischen Staatssammlung München* 4: 27. 1961. TYPE: Südwestafrika: Distr. Lüderitz-Süd, weed in dry riverbed near farmhouse farm "Klein Aus," 28.6.1949, *Kinges 2297* (M not seen). [I follow the synonymy of Botschantzev, *Kew Bull.* 29: 614. 1974].

Annual herbs, (5-)10-100 cm, glabrous or sparsely papillose-hispid. Stems profusely branched from the base or near the base (rarely simple in underdeveloped specimens), erect, rarely ascending; branches normally arcuate. Leaves alternate, filiform or narrowly linear, in herbarium specimens normally less than 1 mm broad, semiterete, not swollen at base; apex rather soft, subspinescent. Inflorescence spicate, interrupted at maturity (at least in lower part). Bracts at maturity reflexed, not imbricate; alternate, \pm abruptly narrowing into mucronulate-spinose apex. Bracteoles free, or occasionally connate at base in lower flowers. Flowers solitary or rarely 2 or 3 (in the last case lateral flowers mostly abortive) in axils of bracts or reduced upper leaves. Perianth segments glabrous,

with weak apex; at maturity distinctly winged; fruiting perianth ca. 4-10 mm diam.

Chromosome number. $2n = 36$ (Mulligan, 1961; Bassett & Crompton, 1970).

Vernacular names. Russian-thistle (English); soude roulante (French).

Habitats. Waste places, roadsides, cultivated fields, disturbed natural and semi-natural plant communities (e.g., coastal and riparian sands, semi-deserts and deserts, eroded slopes); 0-2500 m.

Distribution. Herbarium specimens were examined from the following states and provinces: CANADA: Alberta, British Columbia, Manitoba, New Brunswick, Nova Scotia, Ontario, Prince Edward Island, Quebec, Saskatchewan. U.S.A.: Alabama, Arizona, Arkansas, California, Colorado, Connecticut, Delaware, Georgia, Idaho, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana, Nebraska, Nevada, New Hampshire, New Jersey, New Mexico, New York, North Carolina, North Dakota, Ohio, Oklahoma, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Texas, Utah, Vermont, Virginia, Washington, West Virginia, Wisconsin, Wyoming. Judging from the limited number of herbarium specimens available from Alabama, Georgia, Louisiana, and Mississippi, this species seems to be rare (or undercollected) in the southeastern part of the United States. *Salsola tragus* probably also occurs in Newfoundland, the District of Columbia (it is known from the adjacent part of Maryland), and Florida; native to inland arid regions of southeastern Europe and Central Asia, and occasionally occurs as an introduced alien in some other regions of the world (naturalized in South Africa, Australia, and South and Central America).

Salsola tragus may have been first introduced to the United States in South Dakota in 1873 or 1874 in flax seed imported from Russia (Piper, 1898; Beatley, 1973; Crompton & Bassett, 1985). This noxious weed now occupies almost all its potential range in North America. However, young plants are considered to be an additional forage source for livestock in arid rangelands (Welsh, 1984).

The mature plant may break off at the stem base to form a tumbleweed (also called Rolly-polly in Australia).

The synonymy of *S. tragus* is complicated, and the correct use of some names applied to this taxon is still uncertain. For example, Botschantzev (1974), who had selected the lectotype of *S. aus-*

tralis R. Brown (deposited in BM), considered it to be conspecific with *S. pestifer* and *S. ruthenica*. Crompton (pers. comm.; see also note in Clemants, 1992), who had also studied the type, claimed it to be conspecific with *S. kali* sensu stricto. I have also studied the type of *S. australis* sent on loan to MO. The herbarium sheet contains several fragments. In my opinion, four of these fragments belong to *S. kali* subsp. *pontica*, a southern maritime race of the *S. kali* aggregate (see discussion above). However, the lectotype of *S. australis* selected by Botschantzev (1974) is the fifth fragment, which is mounted at the right side of the herbarium sheet. This fragment represents a form morphologically intermediate between *S. kali* subsp. *pontica* and *S. tragus*.

The combination *S. kali* subsp. *tragus* (L.) Čelakovský was constantly misapplied in Europe to the littoral taxon treated here as *S. kali* subsp. *pontica* (see discussion under that taxon). The authorship of the former combination was often incorrectly attributed to Nyman (Consp. Fl. Europ.: 631. 1881), who in fact validated it 10 years after Čelakovský.

In North America, this taxon was subsequently treated as *S. kali* var. *tenuifolia* (with the authorship incorrectly attributed to Tausch, who published only the name, nomen nudum), *S. pestifer*, *S. iberica* (with its authorship incorrectly attributed to Sennen & Pau, who published their taxon as a subspecies), and *S. australis*. In Europe this taxon was also known as *S. ruthenica* and *S. kali* subsp. *ruthenica* (Iljin) Soó. *Salsola ruthenica* is an illegitimate name, because, when describing his species, Iljin cited in its synonymy *S. pestifer*, the earlier valid name of the same rank. The subspecific name proposed by Soó is legitimate, but, since its basionym was illegitimate, it should be regarded as a new name (not a new combination; see ICBN article 58, Greuter et al., 1994).

Recently Tzvelev (1993) confirmed that the correct name for the widespread narrow-leaved weedy representative of the *S. kali* aggregate is *S. tragus* L., a name that had already been accepted for this taxon by Degen (1937). Judging from the photographs of the Linnaean specimen of *S. tragus* (LINN 315.3), which I selected as the lectotype, this point of view is correct. This change of a name seems to be desirable, because it would guarantee more stable nomenclature for this taxon in the future. The name *S. tragus* was used for this species by some American botanists in the 19th century, but unfortunately, most North American botanists did not resist the temptation to accept the common European misapplication of the name.

3. *Salsola paulsenii* D. I. Litvinov, Izv. Turkestansk. Otd. Russk. Geogr. Obshch. 4, 5: 28. 1905. TYPE: "Turkestan. Dominium Buchara. In arenosis subsalsis pr. Farab (ad fl. Amu-darja). 14 Sept. 1903. Legit N. Androssow et M. Kolow" (LE).

Salsola pellucida D. I. Litvinov, Herb. Fl. Ross. 49: No 2434. 1913. TYPE: "Dominium Buchara, in arenosis pr. Farab. 14 Sept. 1903 [sphalm. 1913—S. M.]. Leg. N. Androssow" (LE).

Annual herbs, 10–80(–100) cm, glabrous or sparsely papillose-hispid. Stems profusely branched from the base or near the base (rarely simple in underdeveloped specimens), erect, rarely ascending or prostrate; branches straight or arcuate, often almost perpendicular to the stem. Leaves alternate, filiform or linear, in herbarium specimens normally ca. 1 mm broad, but occasionally slightly broader, semiterete, not swollen at base; apex spinose. Inflorescence spicate, distinctly interrupted at maturity. Bracts at maturity strongly reflexed, not imbricate; alternate, narrowing into spinose apex. Bracteoles free or connate near the base, spreading, spinescent. Flowers solitary, or rarely 2 or 3 (in the last case lateral flowers mostly abortive) in axils of bracts or reduced upper leaves. Perianth segments glabrous, with long-acuminate spinose apex, at maturity forming a slender columnar beak above the wings, prominently winged. Fruiting perianth 7–12 mm diam.

Chromosome number. $2n = 36$ (Semiotrocheva, 1983; see fig. 3).

Vernacular name. Barbwire Russian-thistle.

Habitats. In sandy soil in disturbed natural and semi-natural plant communities (e.g., open sands, sand dunes, sandy waste places, semi-deserts and deserts, eroded sandy slopes, etc.); 0–1900 m.

Distribution. Herbarium specimens were examined from the following states: Arizona, California, Colorado, Nevada, Utah. *Salsola paulsenii* is native to southeasternmost Europe and Central Asia.

This species is confined mostly to open sands, and rarely to saline sandy habitats. It may be expected in the future in New Mexico and Texas, as well as in some Great Plains states. It was first reported from North America by Munz (1968), and the determination was made by Botschantzev. Additional details of distribution and morphology of this species have been discussed by Beatley (1973) and Fuller (1986).

Salsola paulsenii is weakly differentiated from its

allied taxon, *S. tragus* sensu stricto. The intermediate forms between them seem to be quite rare in Central Asia, but more common in southeasternmost Europe, western Kazakhstan, secondary synanthropic localities in East Europe, as well as in the United States.

4. *Salsola collina* P. S. Pallas, Illustr. Pl.: 34. 1803. TYPE: "in tractu collium cotaceorum inter Rhyminum et Samaram fl. a jugo Uralensi descendendum" (holotype, BM not seen).

Annual herbs, 10–100 cm, sparsely to densely papillose or hispid (rarely almost glabrous). Stems branched above the base (occasionally with slender branches near the base), erect, rarely ascending; branches straight or slightly arcuate. Leaves alternate, filiform or narrowly linear, semiterete, sometimes semi-amplexicaul at base; apex with rather soft bristle (rarely spinescent). Inflorescence narrowly spicate, not interrupted. Bracts at maturity appressed and imbricate, alternate, gradually narrowing into a subulate spinose apex. Flowers solitary or rarely 2 or 3 in axils of bracts or reduced upper leaves (sometimes flowers are also present at axils of lower leaves and branches, at maturity forming gall-like caducous balls). Perianth segments glabrous, with weak, flaccid apex; at maturity wingless or with narrow erose wing, becoming connate and united with bracteole bases; fruiting perianth ca. 3–5(7) mm diam.

Chromosome number. $2n = 18$ (Pohl & Gillespie, 1959).

Habitats. Waste places, roadsides and railway areas, cultivated fields, disturbed natural and seminatural plant communities; 100–2000 (?) m.

Distribution. Herbarium specimens were examined from the following states in the U.S.A.: Arizona, Colorado, Iowa, Kansas, Michigan, Minnesota, Missouri, Montana, Nebraska, New Mexico, North Dakota, Texas, Utah, and Vermont.

The species is also reported from additional localities in Iowa (Schapaugh, 1958), Utah (S. L. Welsh, pers. comm.), and Canada: Ontario (possibly also in Quebec) and Saskatchewan (Crompton & Bassett, 1985). *Salsola collina* is native to southeasternmost Europe, southern Siberia, and arid regions of Central Asia; it is known as a naturalized or casual alien in some other regions of Europe and Asia.

This Asian species was reported for the first time for North America from Minnesota by Moore (1938). However, it had been collected in Kansas in 1923 (Brooks et al., 1976), but was misidenti-

fied. Later it spread to Colorado, Iowa, and Missouri (Cory, 1948; Schapaugh, 1958; Muhlenbach, 1979).

At present this species is known in North America mostly from the Great Plains region and scattered localities in other states. Recently it was also discovered in Canada (Crompton & Bassett, 1985). However, its actual distribution seems to be underestimated due to the common and constant confusion with deviate forms of *S. tragus*, which occasionally resemble *S. collina* in having narrow inflorescences and gall-like caducous flowers/fruits at the axils of lower and middle branches. In the future *S. collina* may be expected to occur within the present range of *S. tragus* throughout North America.

It was also reported as a casual alien from several countries of western and central Europe and is regarded to be established or even completely naturalized in eastern Europe (see map of its secondary distribution in Baranova & Khilova, 1990).

5. *Salsola soda* L., Sp. Pl. 1: 233. 1753. *Kalisoda* (L.) Scopoli, Fl. Carn., ed. 2, 1: 175. 1772. TYPE: LINN 315.7 (lectotype, selected by I. Hedge in Jarvis et al., 1993). [The species described from southern Europe: "Habitat in Europae australis salsis."]

Annual herbs, 5–70 cm, glabrous. Stems branched from the base or nearly so, erect or ascending; branches straight or slightly arcuate (lower ones sometimes almost prostrate). Leaves (especially lower ones) mostly opposite, linear, semiterete, fleshy, in herbarium specimens usually more than 1.5 mm broad, distinctly swollen or ovate at base; apex mucronulate, non-spinose. Inflorescence spicate, distinctly interrupted. Bracts at maturity horizontally reflexed, alternate or almost opposite, abruptly narrowing into mucronulate non-spinose apex. Flowers mostly solitary in axils of bracts or reduced upper leaves. Perianth segments glabrous, with crenate to pectinate-ciliate apex, at maturity wingless or with rudimental triangular tubercles, not connate to bracteoles. Fruiting perianth ca. 3–6(7) mm diam.

Chromosome number. $2n = 18$ (Zakhar'yeva, 1985).

Habitats. Coastal and disturbed saline habitats; 0–50 m.

Distribution. Herbarium specimens were examined from California: San Mateo Co., Palo Alto Yacht Harbor near airport, altitude about sea level, 6 Oct. 1974, J. H. Thomas 17615 (MO); Santa Clara Co., Palo Alto Yacht Harbor, near E end of yacht

basin, edge of disturbed area along salt marsh, 7 Dec. 1975, *J. H. Thomas 18062* (US). *Salsola soda* is native to Eurasia (mostly Atlantic Europe, the Mediterranean region, and southwestern Asia) and northern Africa.

Salsola soda is known from several localities in central California, near San Francisco Bay (Thomas, 1975). It can be expected to spread in California, or to appear in inland or coastal saline habitats in other southern states.

6. *Salsola vermiculata* L., Sp. Pl.: 223. 1753.

TYPE: LINN 315.20 (lectotype, selected by Botschantzev, 1975b). [The species described from Spain: "Hispania."]

Subshrubs, 20–70(–100) cm, densely pubescent (especially when young) with smooth and minutely denticulate hairs; sometimes becoming glabrous at maturity. Stems branched at the woody base, branches erect or ascending, virgate. Leaves 5–8 × 0.5–1 mm, semiterete, usually pubescent, expanding into ovate base, bearing in their axils several reduced leaves ca. 1–4 mm long; apex obtuse. Inflorescence spicate but its primary axis sometimes paniculately branched. Bracts normally densely pubescent, obtuse. Bracteoles free. Flowers solitary or rarely 2–3 in axils of bracts or reduced upper leaves. Perianth segments sparsely pubescent above wings (especially at apex), sometimes becoming glabrous, with conical apex, winged at maturity. Fruiting perianth (including wings) 7–12 mm diam.

Chromosome number. $2n = 18$ (Sankary, 1986; the record for "*S. vermiculata* L. var. *villosa* (Del.) Moq.>").

Habitats. Rocky slopes, clay soils, disturbed places; ca. 1000 m.

Distribution. Herbarium specimens were examined from California: San Luis Obispo Co., Recruit Grade Pass, 5.2 km W of Kern Co. line, Temblor Range, elev. 979 m, 3 Oct. 1978, *J. L. Johnson & G. D. Barbe 2448* (US); Temblor Range, ridge top and E slope at Crocker Grade, S of Crocker Springs Rd., ca. 2 mi. W of the county line and 7.5 mi. (airline) SW of McKittrick, elev. 3200 ft., 31 Oct. 1989, *Don Pendleton s.n.* (MO). *Salsola vermiculata* is native to the Mediterranean region.

Salsola vermiculata sensu lato is known in North America only from California, as a locally persistent escaped weed. It is naturalized near an abandoned experimental plot, Recruit Grade Pass, Temblor Range, San Luis Obispo Co. (possibly also in Kern Co.), where it was previously tested as a po-

tential forage plant introduced from Syria in 1969. *Salsola vermiculata* is designated as a Federal Noxious Weed by the United States Department of Agriculture (Westbrooks, 1993). It is so far the only perennial species of *Salsola* sensu lato introduced to North America. Together with other related Eurasian and African taxa, it should probably be segregated into a separate genus, *Caroxylon*.

Salsola vermiculata sensu lato is a taxonomically complicated and morphologically polymorphic complex represented in Eurasia (mostly in the Mediterranean region, western and Central Asia) by several closely related races usually treated as subspecies or distinct species (Botschantzev, 1975a, b; Greuter et al., 1984). *Salsola vermiculata* sensu stricto is a western Mediterranean species occurring in southwestern Europe and northwestern Africa. Numerous records of *S. vermiculata* from Syria and other countries of the Middle East refer to other closely related species and/or subspecies, which replace it in the eastern Mediterranean region. North American material most probably belongs to *S. damascena* sensu stricto. It fits the protologue and the type specimen deposited at LE, but additional study and comparison with other Eurasian "microspecies" are necessary. Some of these taxa remain little-known and poorly understood taxonomically. Because of that I prefer provisionally to place the North American plant of Syrian origin in *S. vermiculata* sensu lato until further clarification of its taxonomic identity.

The nomenclatural citation for *Salsola damascena* and its basic synonymy are provided below.

Salsola damascena Botschantzev, Bot. Zhurn. (Leningrad) 60(4): 500. 1975. TYPE: "Syrie: Tallus pierreux du jardin Boustan el Nashé a Mezzé près de Damas, 9 Aug. 1856, *C. Gaillardot 1627*" (holotype, LE).

According to Botschantzev (1975a, b), the synonymy of *Salsola damascena* includes *S. rigida* Pallas var. *tenuifolia* Boissier (Flora Orient. 4, 2: 968. 1879, in part) and *S. vermiculata* subsp. *tenuifolia* (Boissier) Botschantzev (Novosti Sist. Vyssh. Rast. (Leningrad) 1: 375. 1964). The names *Salsola villosa* Delile (Fl. Aegypt. Illustr.: 57, No. 309. 1813, in part, excluding the type) and *S. vermiculata* subsp. *villosa* (Delile) Eig (Palest. J. Bot., ser. J, 3, 3: 132. 1945, in part, excluding the type of the basionym) were misapplied to *S. damascena* sensu stricto.

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