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Source: Willdenowia, 38(1) : 81-109

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

URL: <https://doi.org/10.3372/wi.38.38105>

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Abstract

Lomonosova, M., Brandt, R. & Freitag, H.: *Suaeda corniculata* (Chenopodiaceae) and related new taxa from Eurasia. – Willdenowia 38: 81-109. – ISSN 0511-9618; © 2008 BGBM Berlin-Dahlem. doi:10.3372/wi.38.38105 (available via <http://dx.doi.org/>)

The name of the hitherto widely circumscribed species *Suaeda corniculata* is lectotypified by a specimen from the Altai and the species subdivided into two subspecies, with the new subsp. *mongolica* being tetraploid and restricted to SE Siberia and C Asia. Based on morphological, Caryological and molecular data, the three new species *S. tuvinica*, *S. kulundensis* and *S. sibirica* are separated from *S. corniculata* and discussed with regard to their origin. *S. tuvinica* ($2n = 54$) is endemic to northern C Asia and southernmost Siberia; *S. kulundensis* ($2n = 72, 90$), from SE Europe to W Siberia, has arisen by allopolyploidy from *S. corniculata* ($2n = 36, 54$) and *S. salsa* ($2n = 36$); *S. sibirica* ($2n = 72$), from C to E Siberia and northern C Asia, is an allopolyploid offspring of *S. corniculata* and an extinct taxon related to *S. heteroptera* ($2n = 18$). Dot maps for the total distribution of the new taxa and a new key for all taxa of the *S. corniculata* group in Eurasia are provided.

Additional key words: allopolyploidy, lectotypification, phylogeny, reticulate evolution, taxonomy.

Introduction

The hitherto widely circumscribed *Suaeda corniculata* (C. A. Mey.) Bunge is an annual halophyte that grows in forest-steppe, steppe and semidesert areas on soda or chloride solonchaks flooded in spring and drying out at various degrees during summer and autumn. The respective plant communities are mainly formed by a few annual chenopod species. The area of *S. corniculata* extends from SE European Russia to E Siberia, Kazakhstan, Mongolia, W, C and NE China (see, e.g., Iljin 1936a for the former USSR; Tzvelev 1996 for E Europe; Lomonosova 1992 for Siberia; Prатов 1972 for Middle Asia; Grubov 1982 for C Asia; Zhu 1979, 2003 for China). Reports of localities from further west in the Pannonian lowlands (Aellen 1971) refer to the closely related *S. pannonica* (Beck) Graebn. (in Ascherson & Graebner 1913: 202). Inclusion of the high-mountain *S. olufsenii* Paulsen from the Pamir and S Tibet as subspecies into *S. corniculata* by Zhu (1979)

and Li (1983) was recently questioned by Zhu (2003) himself. By its annual habit, stems with alternating green and whitish or purplish lines, leaves with C_3 anatomy, and pistils with a gradually attenuated ovary carrying two stigmas, the plants easily can be identified as belonging to *S.* subg. *Brezia* sect. *Brezia* (= sect. *Heterosperma* Iljin 1936b; Schütze & al. 2003). For separation from related species, in most keys the unequal tepals are cited, with one or more of them protruding into veritable horns (name!). Identification is hampered by the fact that this character is most conspicuous only near to fruiting stage when the tepals are specifically enlarged but usually it can be stated already at flowering time. In fully mature fruits or when immature plants are herborized, the tepals change their shape, often dramatically, by shrinkage in the strongly succulent tissues but usually by careful soaking they can be restored, at least to some extent.

The early descriptions of the species already refer to the remarkable morphological diversity of the plants identified as *Suaeda corniculata*. Thus, the protologue of Meyer (1829) contains the statement “*planta spontanea erecti, in culta partim erecti, partim assurgentes*”. Bunge, who during his journeys in the Altai Mts (Bunge in Ledebour 1830a) collected some of the material used by Meyer, separated them later, when he had gained more experience with plants collected in S Siberia and Middle Asia, as var. *prostrata* and var. *erecta*, respectively (Bunge 1852). Bunge (1852: 290) emphasized the identity of his var. *erecta* and t. 195 in Ledebour (1830b) and suspected that it might be a separate species (“*Nonne potius species distinctae*”). An analysis of a type specimen of Bunge’s var. *erecta* (A. Lehmann 224 from Lake Inder, preserved in P) has shown that in fact it does not belong to *S. corniculata* but to the *S. prostrata* group instead.

The concept of two intraspecific groups (informally named *lusus* 1 and 2, respectively), based on differing growth forms and associated with narrower and wider leaves in the inflorescence was overtaken by Fenzl (1851) though it is very difficult to trace them to the taxa as they are defined today. Since long, obvious variation also is known from the shape of the fruiting perianth, which is determined by the postfloral growth of the individual tepals. This refers to the apical and basal parts of the tepals as well as to the extent of their fusion and is fully considered in the extensive description given by Fenzl (1851). Conflicting statements on the perianth structure in *S. corniculata* and widely differing determinations in the herbaria go back to the earlier authors including Bunge and Meyer himself. Later, a few species with slightly different tepals in fruiting stage and with rather limited distribution were described, namely *S. olufsenii* Pauls., *S. arctica* Jurtz. & Petrovsky and *S. tschujensis* Lomon. & Freitag, but the wide concept of *S. corniculata* remained almost untouched.

Although botanists with ample field experience repeatedly suspected that different taxa might be hidden among *Suaeda corniculata* (e.g., Kamelin, pers. comm.), even the earlier infraspecific classification was given up in more recent flora accounts, maybe due to the high degree of environmentally induced variability and the partly sympatric occurrence of different forms. Only in the first comprehensive molecular study of *Suaedoideae* (Schütze & al. 2003) it was shown that two different samples from E Kazakhstan technically keying out as *S. corniculata* belong to rather different genotypes: in the ITS tree (nuclear genome), the erect form holds a position in the *S. maritima/salsa* subclade close to the likewise erect *S. salsa* (L.) Pall., whereas the prostrate plant proves to be a member of the *S. corniculata* subclade and is more closely allied to species with a likewise prostrate or ascending habit, as *S. pannonica*, *S. tschujensis* and *S. patagonica* Speg. Another puzzling result was that in the parallel *atpB-rbcL* tree (chloroplast genome) both samples appear side by side in the *S. corniculata* subclade. Due to the limited sampling and to the focus of the paper on higher classificatory and evolutionary units in *Suaedoideae*, the authors restrained from any interpretation of the problems around *S. corniculata*.

In the present paper, we aim to detect the taxonomic units that are hitherto summarized in the collective species *Suaeda corniculata*. In order to reach this goal, we studied the *S. corniculata* group all over its distributional area by applying an integrated morphological, cytological and molecular approach, including extensive fieldwork, cultivation experiments and study of type material.

Material and methods

Material. – On several expeditions we studied populations of *Suaeda corniculata* in the field to record the distribution of the various taxa, to observe their morphological variability along gradients of salinity and soil moisture, and to collect herbarium specimens and wet-conserved fruiting material for detailed investigations in the laboratory as well as seeds for cultivation and subsequent cytological and molecular studies. The more extensive journeys were undertaken to Kazakhstan in 1992 (H. Freitag, abbreviated in the following as HF), together with S. Rilke & W. Wucherer), 2000 (M. Lomonosova, abbreviated in the following as ML, together with A. Sukhorukov), 2001 (ML, together with A. Korolyuk), the Caspian Lowlands in 1996 (HF, together with V. Golub & N. Yuritzina), to the Altai Mts 1990 (ML, together with D. Shaulo & A. Krasnikov), 2002 (ML), to S Siberia from Novosibirsk to Chita provinces including Tuva in 2003 (HF, ML, together with P. Schütze), to C Siberia from Krasnoyarsk to Tuva in 1989 (ML, together with D. Shaulo & O. Zhdanova), to Novosibirsk region in 1991, 1997, 2001 (ML), 1999 (ML, together with A. Krasnikov), 2000 (ML, together with A. Sukhorukov), Irkutsk region in 2002 (ML), Khakass' region in 2004 (ML) and Kurgan region in 2005 (ML).

Besides, relevant herbarium collections (abbreviations according to Holmgren & Holmgren 1998-) were evaluated, in particular from AA (by ML), ALTB (by ML), BM (by HF), GOET (by HF), IRK, IRKU (by ML), KRAS (by ML), Kurgan (by ML), LE (by HF & ML), MHA, MW (by ML), NS, NSK (by ML), P (by HF & ML), TASH (by HF & ML) and TK (by ML).

Morphological methods. – Traditional morphological investigations were carried out with a particular focus on plants collected from diverse habitats including individuals from cultivation. Seeding took place in March or April in protected indoor (Novosibirsk) or greenhouse conditions (Kassel), and plants were transferred to the garden in May. Most studies were carried out parallel in Novosibirsk and Kassel with regular binocular preparatory microscopes and by using herbarium or wet-conserved material. As far as possible they were extended to living plants. If for assessment of the important characters in the fruiting perianth living or wet-conserved material was not available, suitable herbarium material was soaked in water for about 5-10 minutes and finally heated up to boiling point. By that procedure at least some fruits approximately regained their original shape.

In addition to the results from light microscopy, SEM micrographs were taken from the seed surface of selected specimens. The investigations were carried out by means of the scanning electron microscope LEO 420 (Carl Zeiss) in the Institute of Hydrodynamics in Novosibirsk. The dry seeds were transferred to an aluminium holder with the universal glue Moment (Henkel), and covered with carbon (c. 5-10 nm) in the sputter coater VUP 2 (made in USSR).

Cytological methods. – Altogether 143 chromosome counts were carried out in samples from different localities belonging to all taxa recognized in the text, most of them by ML and a few by HF. For chromosome counts in Novosibirsk, root tips were cut in the morning (between 9 and 12 a.m.), pretreated in 0.2 % colchicine for two hours, fixed in ethanol-acetic acid (3 : 1) for 24 hours, stained in 4 % ferric ammonium sulfate 20 minutes, heated in 1 % acetic hematoxylin and squashed in a drop of saturated solution of chloral hydrate (Smirnov 1968; Pausheva 1988). The procedure applied in Kassel differed in the following points: pretreatment in 0.1 % colchicine followed up by maceration in a mixture of 1N HCl and 45 % acetic acid (2 : 1) for 10 minutes at 60 °C, staining in 2 % aceto-orcein for 25 minutes at room temperature and subsequent squashing (Chouhdry 1984). Due to the extremely small size and often high number of chromosomes in some cases the data obtained may be slightly inaccurate.

Molecular methods. – Since the publication of the first molecular study in *Suaedoideae* (Schütze & al. 2003) the ITS phylogeny (nuclear ribosomes) was refined by a greatly enlarged sampling, including 86 samples of the *Suaeda salsa/maritima* clade, 37 samples of the *S. prostrata/spicata* clade and 29 samples of the *S. corniculata* clade. Represented are now all Old World species except for some Far Eastern taxa restricted to Japan, Korea and E China (Schütze, unpubl.). In ad-

dition, we analysed a set of three intergenic chloroplast markers. They were recently designed (S. Gorke & H. Schumacher unpubl. protocol for a laboratory course in molecular systematics; S. Möller unpubl. diploma thesis on the speciation and biogeography of *Suaeda* species on the European coast) in the Botany Department of Kassel University on base of the completely known sequence data of *Spinacia oleracea* chloroplasts. However, so far the coverage is almost complete only for the *S. salsa/maritima* clade, again with 86 samples, whereas the other two groups are represented only by few species. DNA was isolated from CTAB samples or from suitable herbarium specimens. With regard to the procedures used for isolation, amplification and sequencing of DNA as well as to the methods for data analysis we refer to Schütze & al. (2003) and to forthcoming papers.

General results

Assessment of morphological characters

In face of the great amount of environmentally induced variation, an abbreviated discussion of the characters that proved to be useful in the subdivision of the *Suaeda corniculata* group is given below (see also Table 1):

Growth form. – The taxa differ considerably in growth form. Whereas the new species *Suaeda kulundensis* and *S. sibirica* grow strictly erect in normal conditions, in both subspecies of *S. corniculata* the stem system is ascending to prostrate, and in the new *S. tuvinica* it is distinctly prostrate. However, some overlap occurs. In particular, trampling or other mechanical factors may impose prostrate habit on erect growing species, and very dense stands can inversely lead to limited erect growth in taxa that normally have an ascending habit. Besides, judgements on growth form in the herbarium requires particular caution because many specimens contain only fragments of the shoot system, and in species with prostrate or ascending habit, in particular when grown with ample water and nutrient supply, the separated upper parts of individual branches may look like being erect. In such cases, usually the original orientation can be deduced from the orientation of side branches, which is strictly erect in upright growing species but tends to be spreading in species with prostrate or ascending habit. Also dwarfed plants with suppressed branching sometimes loose their original prostrate habit by herborization procedures. Several species differ in branching density, which is essentially determined by the length of internodes in the stem and the number of axillary buds producing side branches of first and higher orders.

Leaves. – The leaves show some diagnostic features but unfortunately they are often superimposed by modifications induced by habitat conditions, and even on the same stem they vary with the sequence from basal to upper leaves and bracts. Most obvious are differences in colour, size, outline, shape of apex and in the degree of succulence. The colour is comparatively constant and can be best judged from the appearance of the living plant. It is glaucous in *Suaeda kulundensis* and *S. sibirica*, green in *S. corniculata* and bright green in combination with a distinctly shiny appearance in *S. tuvinica*. In fruiting stage and when the plants grow under stress conditions, the colour usually changes toward purplish or pinkish. In most species, completely desiccated plants are black or blackish but they turn to olive green in *S. tuvinica* and to pale green in species that grow in cooler climates such as *S. tschujensis* and *S. arctica*. The leaves are moderately succulent and flat to semiterete in most species, but almost cylindrical by strong succulence in *S. tuvinica*. The outline varies from linear to narrowly lanceolate and the apex from obtuse to acuminate and acute. For further details see Table 1. Leaf orientation differs among species in accordance with their habit: in species with prostrate habit the leaves are usually spreading, and in those with erect stems and branches they are ascending. Often the leaves are more or less incurved but that tendency is enhanced in dried specimens.

Flowers. – The floral characters are rather similar in all species of the group. Flowers are arranged in cymose axillary clusters (glomerules) and in the same species the number of flowers per cluster differs widely from (1-3 to 7(-17)). They are essentially bisexual, but by progressive

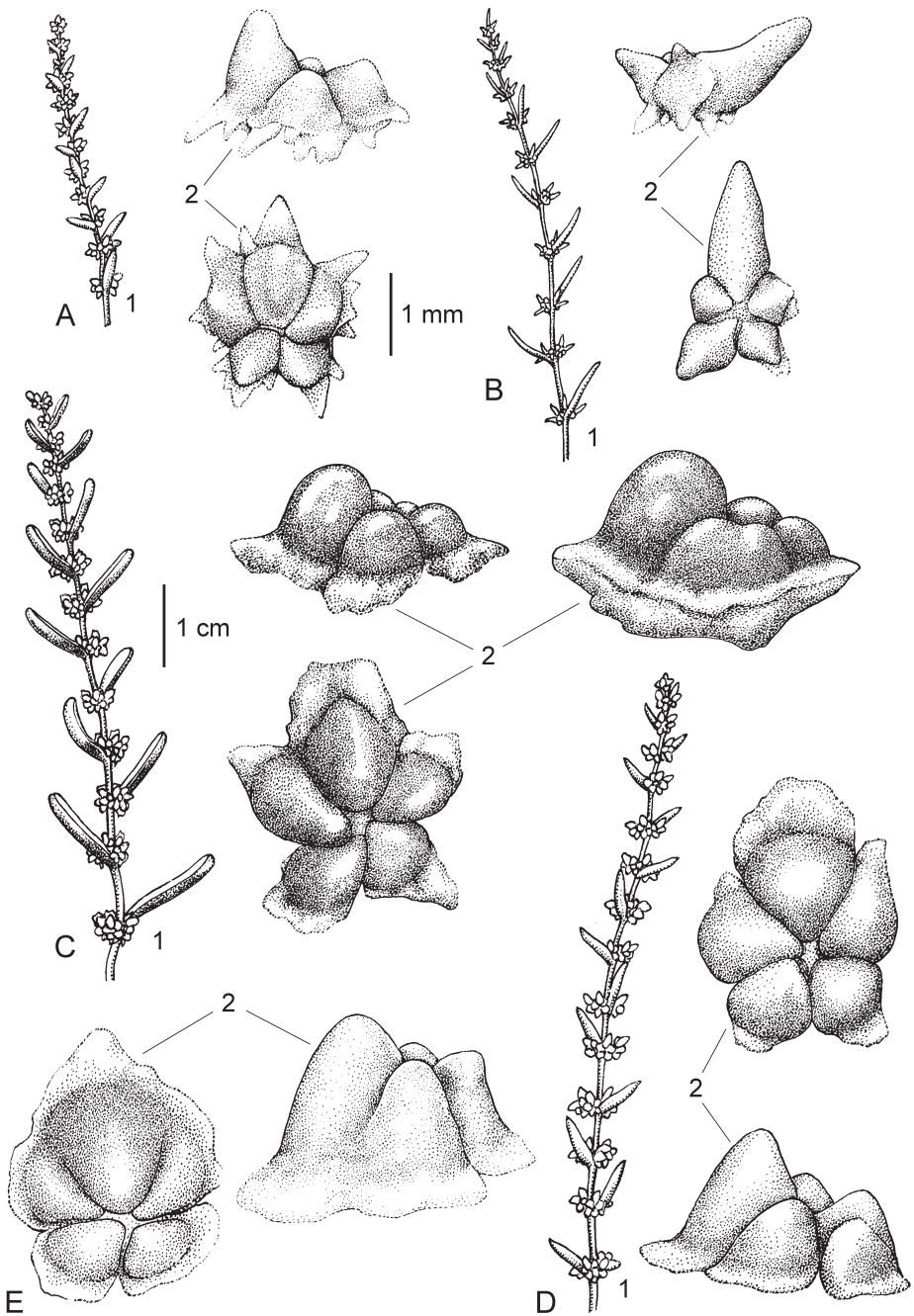


Fig. 1. Fruiting branches (1) and fruits with tepals (2) in species of the *Suaeda corniculata* group – A: *S. corniculata* subsp. *corniculata* (from *M. Lomonosova* 241, NS); B: *S. corniculata* subsp. *mongolica* (from the holotype); C: *S. tuvinica* (from the holotype); D: *S. kulundensis* (from *V. Golub* 762, NS, cultivated in Novosibirsk in 2006); E: *S. sibirica* (from the holotype). – Drawings by N. Prijdak.

reduction in the number of functional stamens (from 5 to 0) the outermost flowers in the individual cymes are usually female. Often the uppermost clusters and those on the latest accessory branches only contain female flowers. The 5 tepals are usually connate in their lower part and differ significantly in size and later on (see below) also in shape. The filaments are narrow, band-shaped and inserted near the tepal bases, and the small subglobular anthers show a basal split up to $1/3-1/2$ of their length. The ovary is uniformly depressed and bears apically two thin, diverging or slightly reflexed stigmas covered all around by short, delicate papillae.

Fruiting perianth. – The fruiting perianth shows most important characters (Fig. 1). However, their expression differs significantly according to the position of the individual flower in the axillary cluster and to the formation of the regular blackish or the irregular brown seeds (see paragraph below). The characters can best be assessed in young fruits with regular seeds, and even then the first (central) axillary flower and the latest lateral flowers may deviate in shape. The tepals of the fruiting perianth are distinctly unequal, with one or, more rarely, two of them becoming much larger than the others. However, the larger tepal differs among the 5 taxa by shape and orientation from very long, narrow and almost horizontally spreading, as in *Suaeda corniculata* subsp. *mongolica*, to subglobular and upright as in *S. tuvinica*. The fusion of tepals is either restricted to their basal (horizontal) parts (*S. kulundensis*, *S. corniculata*) or it reaches slightly (*S. sibirica*) or significantly higher up (*S. tuvinica*). In the latter taxon two smaller tepals often fuse almost completely. The degree of tepal fusion is also reflected in the structure of the outgrowths that are formed after pollination around the girdle line of the perianth, which is defined here as the area where the tepals change their orientation to cover the seed on its upper side: *S. kulundensis* has 5 separate, short, horizontally arranged, wing-like gibbositities, in *S. sibirica* usually three of them are united, in *S. tuvinica* either three and two or all five are united in a continuous ring-like manner and in addition a few short gibbositities are arranged below them, whereas in *S. corniculata* a ring of more or less numerous smaller and larger acute, membranous outgrowths is formed. Sometimes the shape of tepals and the evolution of basal outgrowths may be influenced by external factors. In *S. corniculata* we observed that increased succulence led to shorter and thicker (almost balloon-shaped) “horns”, which run parallel with a suppression of the basal outgrowths. Rather often such structures were found without seeds.

Seeds. – Only the characters of ‘regular’ seeds are considered. They are lens-shaped and furnished with a hard, blackish testa. As in many other species of *Suaeda* sect. *Brezia* heterospermy is common and a second type of seeds/fruits has been observed. These ‘irregular’ seeds are significantly larger, disc-shaped and have a thin, brownish testa, which replicates the shape of the coiled embryo. The ‘irregular’ seeds are not included in the descriptions and in the key because of their uniform appearance. The regular seeds differ in size from 0.8×0.7 mm in *S. corniculata* to 2×1.85 mm in *S. kulundensis* var. *macrocarpa*, but infra-individual and infra-specific variation is considerable. In seed coat ornamentation, which can be recognized already by a hand lens, *S. sibirica* can be separated easily from related taxa of the area by its almost smooth surface (Fig. 2 I, J).

Caryological data

The results of the numerous chromosome counts (included into the taxonomy part, see also Fig. 1 and Table 1) clearly show that the traditional *Suaeda corniculata* consists of a number of cytologically different populations, which represent a ploidy series that starts from the tetraploid ($2n = 4x = 36$) level and leads through the hexaploid ($2n = 6x = 54$) to the octoploid ($2n = 8x = 72$) and decaploid ($2n = 10x = 90$) levels. However, not any of the different ploidy levels is restricted to a single taxon. *S. corniculata* subsp. *mongolica* is the only unit that is exclusively tetraploid (7 samples), but a few tetraploids were also found in the typical subspecies, which has proven to be hexaploid in the overwhelming majority of samples (3 and 63 samples, respectively). Hexaploid conditions were detected also in *S. tuvinica* (2 samples) but due to uncertainties in counting, octoploid conditions can not be ruled out. Octoploidy was constantly

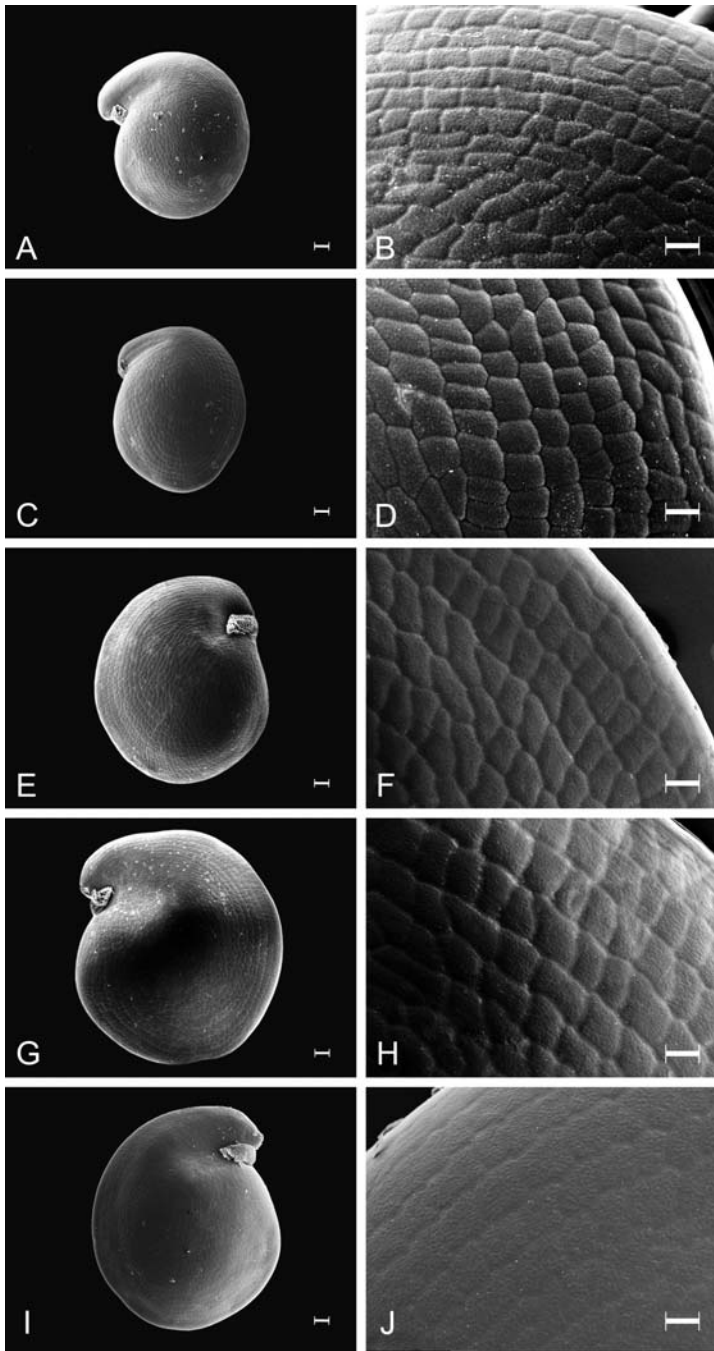


Fig. 2. SEM micrographs of *Suaeda* seeds – A-B: *S. corniculata* subsp. *corniculata* (from *M. Lomonosova* 79, NS); C-D: *S. corniculata* subsp. *mongolica* (from the holotype); E-F: *S. tuvinica* (from the holotype); G-H: *S. kulundensis* (from the holotype); I-J: *S. sibirica* (from *M. Lomonosova* 299, NS). – Scale bars: A, C, E, G, I = 100 μ m, B, D, F, H, J = 30 μ m; micrographs by M. Lomonosova and Y. Lukyanov. In most figures, below the radicle a remainder of the broken funiculus can be seen.

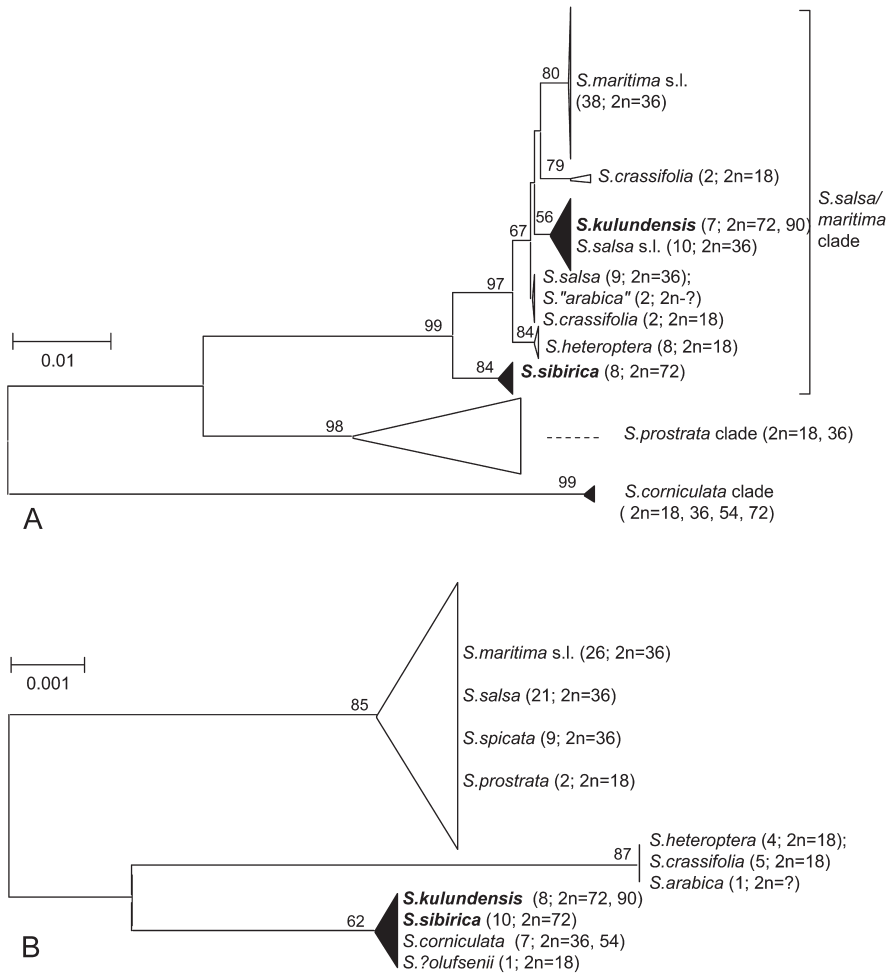


Fig. 3. Condensed neighbour-joining trees of Eurasian *Suaeda* species obtained from nuclear and chloroplast sequences – A: tree based on the nuclear ribosomal ITS region; B: tree based on the intergenic chloroplast *atpH-atpI* region. – Numbers on branches refer to bootstrap values higher than 50 %. Behind the species names, the number of samples and number of chromosomes are given in parentheses. Groups of particular interest are highlighted by black triangles.

found in *S. sibirica* (38 samples), whereas in *S. kulundensis* (31 samples) the majority is likewise octoploid but with a few decaploid populations in the eastern part of the species range. Until its recent description (Lomonosova & Freitag 2003) the diploid species ($2n = 2x = 18$) *S. tschujensis* also was included into *S. corniculata*.

Molecular data

The complete set of results will be published in a revised paper on the phylogeny of *Suaedoideae* (Schütze, in prep.) and in forthcoming papers by Brandt & al. Here only the parts related to the relatives of *Suaeda corniculata* are presented and discussed by use of two condensed neighbour-joining trees from the diploma thesis on the phylogeography of the *S. maritima/salsa* group by Brandt (unpubl. 2007).

The condensed ITS tree of the nuclear genome (Fig. 3A) shows three major clades as in Schütze & al. (2003). Again in agreement with the previous ITS tree, the basally diverging *Suaeda corniculata* clade consists of *S. corniculata* samples and *S. pannonica*. The more extended ITS tree in Schütze (unpubl., not shown) also includes the new taxa *S. tuvunica* and *S. corniculata* subsp. *mongolica*, with both of them being identical or differing by one mutation only from *S. corniculata* subsp. *corniculata*. The *S. salsa/maritima* clade branches first and with high statistical support into *S. sibirica*, which is sister to all other species. A subsequent branch with a likewise high bootstrap value leads to *S. heteroptera*, which also shows sister position to the remaining taxa. Among them, the samples of *S. kulundensis* are weakly separated from different accessions of *S. salsa*, *S. crassifolia* and an hitherto undescribed *S. "arabica"*, whereas the crown group is made up of different taxa summarized here as *S. maritima* s.l.

Essential results with regard to the new species described here are: (1) *Suaeda sibirica* and *S. kulundensis*, despite of approaching *S. corniculata* in their perianth characters, do not belong to the *S. corniculata* clade but to the *S. salsa/maritima* clade instead. (2) *S. sibirica* and *S. kulundensis* are so widely separated from each other in the ITS tree that treating them as species appears to be appropriate. (3) Among the extant species, *S. sibirica* takes a rather isolated position, with its nearest relative being *S. heteroptera*. (4) Regarding the nuclear genome, *S. kulundensis* is intimately related to or even identical with *S. salsa*.

The chloroplast tree (Fig. 3B) based on the scmp 14 section of the *atpH-atpI* region (two other sections deliver similar results) shows a topology that deviates considerably from the ITS tree. Although again three clades can be identified, they include different sets of species, and resolution among species is very low. The species under discussion in the present paper except for *Suaeda tuvunica*, which was not analysed so far, appear side by side in the *S. corniculata* clade, whereas a second clade is formed by *S. heteroptera*, *S. crassifolia* and *S. "arabica"*, and a third by *S. maritima* s.l., *S. salsa*, *S. prostrata* and *S. spicata*. The most important conclusion in the present context is the similarity in the investigated chloroplast genome region of *S. corniculata*, *S. sibirica* and *S. kulundensis* and their wide genetical distance to the *S. heteroptera/S. crassifolia/S. "arabica"* and *S. maritima/S. salsa/S. prostrata/S. spicata* groups.

Taxonomy

Suaeda corniculata (C. A. Mey.) Bunge in Acta Horti Petropol. 6(2): 429. 1879

Annual, (3-)6-40(-70) cm in height and up to 1 m in diameter, very variable in habit, prostrate or ascending, very rarely erect, primary stem usually surpassed by basal laterals, living plants fresh green or purplish, turning brownish or blackish when dried or remaining purplish. *Stem* at base up to 2.5 mm thick, 1 or 2(-3) times loosely branched from the base; branches ascending or spreading; younger axes with alternating green and purplish or whitish lines. *Leaves* ascending to spreading, flat to semiterete, moderately to strongly succulent, with *Brezia* type C₃ anatomy, 10-40 × 1-2 mm, almost linear, obtuse to subacute. *Inflorescences* terminal, simple or branched, spike-like, 1-15 cm long; internodes in lower part of spikes (1.5-)3-10(-15) mm long, becoming shorter towards the top. *Bracts* spreading, the lower similar to the leaves, 2-3 times longer than the glomerules, the upper gradually smaller, lanceolate to narrowly ovate, at base somewhat sheathing, apiculate, only slightly longer than the glomerules. *Bracteoles* 0.5-0.7 mm long, narrow-ovate or obovate, acute or acuminate, the margins in upper part erose-dentate. *Glomerules* axillary, 3-7(-17)-flowered, loosely or densely arranged, in fruiting stage usually resembling spinous spheres. *Flowers* bisexual, the central flower protandrous, the laterals usually protogynous, bowl-shaped, 1.3-1.7 mm in longer diameter. *Tepals* fused for c. 1/2, the outermost much longer and wider. *Stamens* 5, or less in lateral flowers, filaments up to 0.75 mm long; anthers 0.15-0.2 × 0.2-0.3 mm, divided for c. 1/2. *Ovary* superior, depressed-ovoid, apically narrowed; the two stigmas 0.25-0.5 mm long, ascending to spreading, very thin, with short papillae. *Fruiting perianth* considerably enlarged, 2-2.3(-2.7) mm in longer diameter, the outermost tepal conically elongated into an obtuse or acutish horn-like structure 1.5-3 × longer than wide, held in oblique to almost horizontal position; other tepals with much shorter apical elongations or with evenly



Fig. 4. *Suaeda corniculata* subsp. *corniculata*, M. Lomonosova 234 at NS. – Photograph by M. Lomonosova.

cupula-shaped apex; around the girdle with a ring of \pm numerous smaller and larger acute, membranous, usually red-coloured outgrowths. *Seeds* horizontal, dimorphic; black seeds (0.8-)1.1 (-1.35) mm long, (0.7-)0.9(-1.2) mm wide, 0.45-0.6 mm thick, flattened; testa dull to somewhat shining, distinctly sculptured.

Two subspecies are recognized:

1. Larger tepal in the fruiting perianth 1.5-2 \times longer than other tepals, broadly conical, arranged vertically or somewhat obliquely; plants usually robust, 6-70 cm high subsp. *corniculata*
- Larger tepal in the fruiting perianth 2-3 \times longer than other tepals, narrowly conical, arranged almost horizontally or at an angle up to 45°; plants usually delicate, 3-30 cm high subsp. *mongolica*

a. subsp. *corniculata*

\equiv *Schoberia corniculata* C. A. Mey., Fl. Altaic. 1: 399. 1829. – Lectotype (designated here): Altai, in locis salsis, C. A. Meyer (LE [left and central branches only, see Fig. 7]); paratypes: Flora altaica, Meyer (GOET); Flora altaica, herb. Al. de Bunge (P); see paragraph Typification, below.

\equiv *Schoberia corniculata* α *prostrata* Bunge, Reliq. Lehmann.: 289. 1847 \equiv *Suaeda corniculata* var. *prostrata* (Bunge) Krylov, Fl. Zap. Sib. 4: 941. 1930.

lc. – Fig. 1A, 2A-B, 4, 7. – For published figures see Freitag & al. 1996: 351, fig. 2C1, C2; Iljin 1936a: t. IX, fig. 7a-b (poor); Moquin-Tandon 1831: t. 22B (with reconstructions of perianth that lost its typical shape).

Chromosome numbers. – $2n = 54$ (hexaploid) from 63 localities, $2n = 36$ (tetraploid) from 3 localities only: S Kazakhstan (Freitag 26.290, see Freitag & al. 1996), middle Volga area (Freitag 28.200) and Altai distr. (Krasnoborov 80).

Distribution. – Forest steppe, steppe and semidesert zones of Eurasia from southern European Russia to Kazakhstan, Mongolia, N China and Sakha (Yakutiya) – Fig. 5.

Habitat. – In open plant communities on solonchaks that dry out during summer and are often temporarily covered by snow-like efflorescences of soda or sodium chloride, often dominating a certain belt or on slightly lower patches in denser stands of moderately halophytic plants (Mirkin & al. 1992; Freitag & al. 2001, pp. Camphorosmo-Suaedion, Suaedetum corniculatae); up to c. 2000 m in the Altai Mts.

Selected specimens. – RUSSIA: [SE EUROPE]: Samara obl.: 20 km N Tolyatti, Nizhn. Sanchi-leyevo, Freitag 28.012 (KAS, NS). Saratov obl.: Yeruslan valley near Dyakovka, Freitag 28.312a (KAS, NS). Volgograd obl.: Sarepta, 1864, Becker (LE); 1881, Becker (GOET); Lake El'ton, SE shore near Ozerneye, Freitag 28.258 (KAS, NS). Astrakhan obl.: 65 km SE Akhtyubinsk near Sagotovki, Freitag 28.200 (KAS, NS). Orenburg obl.: Near Orenburg, Gorodkova-Selinova 1123 (LE). – [WEST SIBERIA]: Chelyabinsk obl.: near Yuzhnoural'sk, 26.8.1955, Ezhov (NS). Kurgan obl.: Kurtamysh, Lomonosova & Zhdanova 25 (NS). Omsk obl.: Isil-Kul distr., Krasnogorka, Lomonosova & Zhdanova 34 (NS). Novosibirsk obl.: Ust-Tara distr., Pokrovka, Krasnoborov & al. 123 (NS); Zdvinsk distr., Chulym, Shaulo 213 (NS); Altaisk. krai: Loktevsk distr., between Novenkoye & Gornyyak, Korolyuk 371 (NS); Barnaul distr., Kalmanka, Saltykova (TK). Altai Republic: Kosh-Agach distr., 4 km E Chegan-Uzun, Lomonosova 251 (NS, KAS); Onguday distr., Eloman, 17.7.1927, Malakhova (TK). Kemerovo obl.: Dagino near Kuznetsk, Kuznetsov 1539 (LE). – [CENTRAL SIBERIA]: Khakass Republic: Ust-Abakan distr., Krasnoye lake, Lomonosova 619 (NS). Tuva Republic: Cheder lake 45 km SSE Kyzyl, Freitag 33.025 (KAS, NS); Barum-Khemchik distr., 27 km from Ak-Dovurak to Abaza, 19.8.1971, Shreter (MW). – [EAST SIBERIA]: Irkutsk obl.: Olkhon distr., Tazhiranskaya steppe, Lomonosova

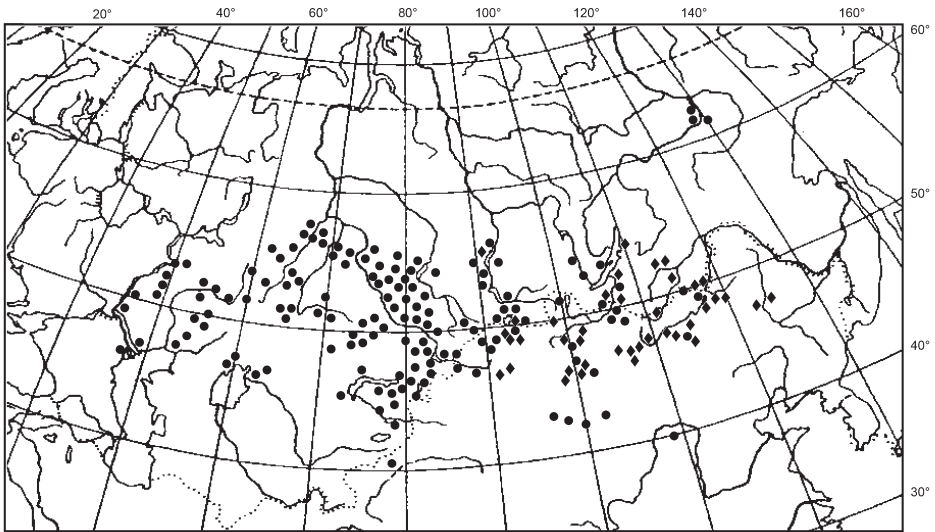


Fig. 5. Distribution of *Suaeda corniculata* subsp. *corniculata* (●) and *S. corniculata* subsp. *mongolica* (◆).

295 (NS, KAS); Cheremkhovo distr., Kuchirskaya 30.7.1926, *Epova* (IRKU). Buryat Republic: Sosново-Ozersk, 11.8.1953, *Gorshkova & Andreyeva* (NSK). Chita obl.: Nerchinsk, *Karo 300* (BM, P), Borzya distr., near Zagan-Olui, 15.8.1953, *Sakovich* (TK). Onon distr., Barun-Torei lake, *Lomonosova 490* (NS). Sakha Republic (Yakutia): Olekminsk distr., near Neruktei, 16.8.1935, *Kuminova & Sobolevskaya* (TK); near Amga, *Nikolin 80* (NS).

KAZAKHSTAN: Ural'sk obl.: Chelkar lake c. 100 km SSE Ural'sk, *Freitag 28.073* (KAS, NS); betw. Kalmykovo and Sacharnaya, *A. Lehmann 225* (P). Turgai obl.: Kustanai distr., Dzhakso-Dzhar-Kul lake, *Korotkiy & Lebedeva 1339* (LE). Kzyl-Orda obl.: 47 km E Kazalinsk, *Freitag 26.503* (KAS, NS). Akmolinsk [Astana] obl.: Balykty lake, 63 km S Petropavlovsk, *Drobov 1381* (TASH); near Karatal, *Goncharova & Borisova 1705* (LE). S-Kazakhstan obl.: West Betpak-Dala, Semen'-Kum Sands, 2.9.1946, *Kubanskaya* (AA). Dzhambul obl.: northern border of Chu vall. near Gory Dzhambul, *Freitag 26.339* (KAS, NS). Almaty obl.: 102 km W A. at road to Otar, *Freitag 26.290* (KAS, NS). East-Kazakhstan obl.: Noor-Zaysan lake, *Karelin & Kirilov 1000* (BM, LE, P).

MONGOLIA: Bayan-Ölgyi aimak, Saksai, *Krasnoborov & al. 11* (NS); Uvs aimak, 20 km N Ulangom, *Gubanov 4724* (MW); Bayankhongor aimak, Batsagad, 1.9.1949, *Kuznetsov* (LE); Dornogovi aimak, 25 km SW Khatan-Bulak, *Gubanov 5593* (MW).

b. subsp. *mongolica* Lomon. & Freitag, subsp. nov.

Holotypus: Russia, Buryat Republic, Dzhida district, 2 km SE Beloozersk village, 50°37'N, 105°48'E, gentle stony slopes covered by red salty soils, c. 630 m, 4.9.2003, *M. Lomonosova 439* (NS; isotypi: B, K, KAS, LE).

A subspecies *corniculata* differt habitu humiliori, post anthesin cornu in tepalo majori graciliori 2-3 × longiori disposito fere horizontaliter differt.

lc. – Fig. 1B, 2C-D, 6. – For published figures (poor), sub *Suaeda corniculata*, see: Mao 1994: 66, fig. 1, 2; Liu 1985: 401, fig. 1-4; Zhu 1979: 133, fig. 8-10.

Chromosome numbers. – $2n = 36$ (tetraploid) from 7 localities (*Lomonosova 439, 445, 455, 508, 512, 638, 642*).

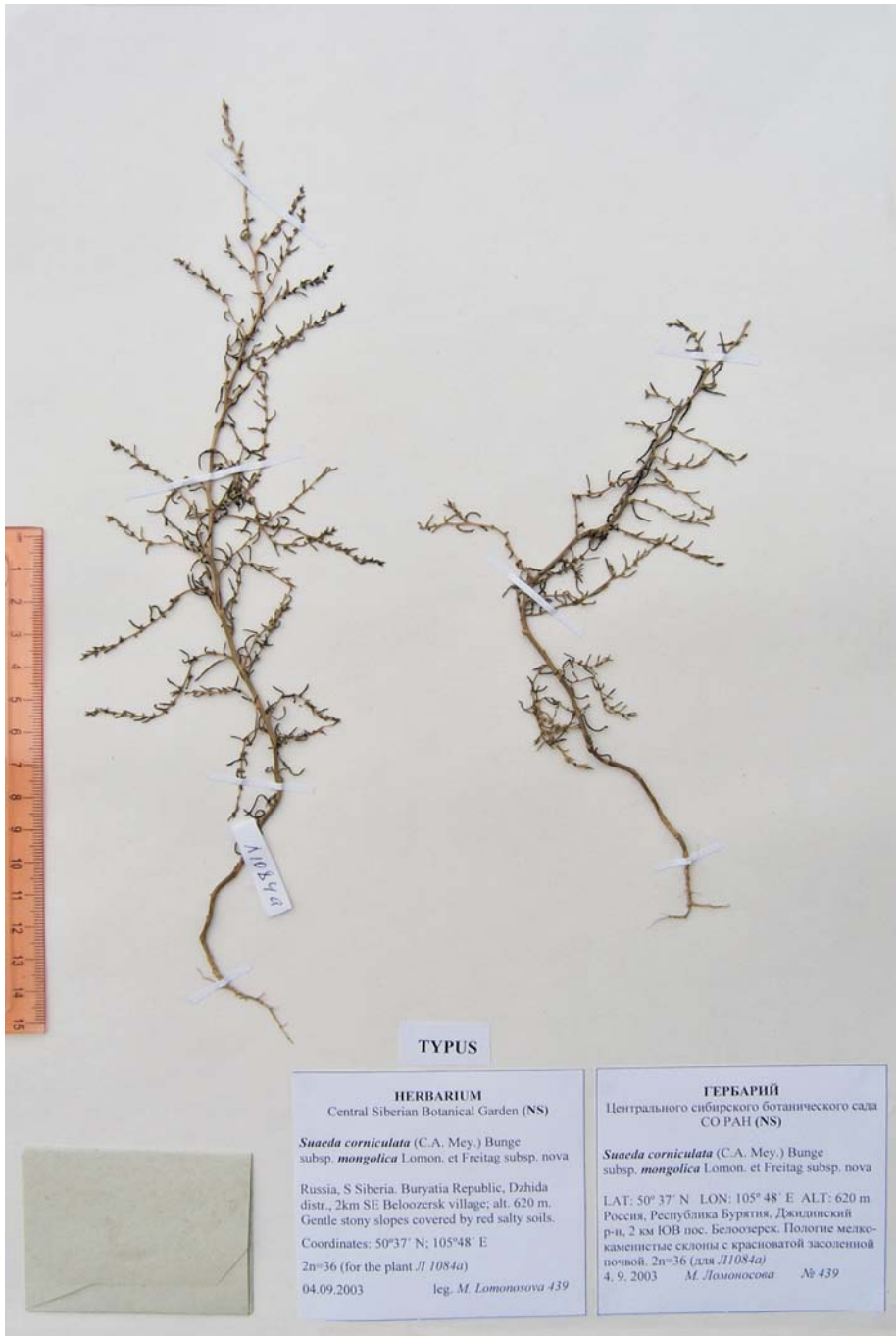


Fig. 6. Holotype of *Suaeda corniculata* subsp. *mongolica* at NS. – Photograph by M. Lomonosova.

Distribution. – Steppe and semidesert zones of central S Siberia (Tuva to Chita), Mongolia and N China – Fig. 5.

Habitat. – Widely the same as in subsp. *corniculata* but seemingly avoiding solonchaks rich in chlorides and also colonizing drier habitats; up to c. 1400 m.

The new subspecies is named after Mongolia where it is rather common on saline habitats in the northern parts.

Remarks. – Beside of the characters given in the key and in the diagnosis, the new taxon also differs from subsp. *corniculata* by the tetraploid genome, thinner glomerules, slightly smaller seeds, a more delicate habit, and by usually not turning blackish on drying. Taken together, these features might well justify species rank if not several intermediates were seen and the distribution widely overlapped. Not even the tetraploid genome is strictly confined to our plants because we found it, though very scattered, also in the typical subspecies. On the other hand, one could speculate that the respective populations represent just an ecotype but the limited distributional area and the uniform chromosome number suggest that it is a separate evolutionary unit.

Selected specimens. – RUSSIA: [CENTRAL SIBERIA]: Tuva Republik: Tes-Khem river valley, above Erzin, *Lomonosova* 82 (NS); Shara-Nur lake 40 km W Erzin, *Freitag* 33.053 (KAS). Khakass Republic: Ust-Abakan distr., Kamizyak steppe, Ulug-Khol lake, *Lomonosova* 638 (NS). – [EAST SIBERIA]: Irkutsk obl.: Sagonur lake, N Kuitun, *Korotkij & Nikolaev* 939 (LE). Buryat Republic: Baikal lake, east shore, mouth of Barguzin valley, *Sukachev & Bryzshev* 1726 (LE); Barguzin vall., near Suvo, *Lomonosova* 445 (NS); Mukhorshibir distr., near Sharaldai, *Lomonosova*, 455 (NS); Selenginsk distr., Sulphatnoye lake, 18.9.2002, *Badmayeva* (NS); Verchneudinsk distr., Zolotuchino post station, *Poplavskaya* 2534 (LE); Sosново-Ozersk distr., near Konstantinovka, *Korotkij & al.* 367 (LE). Chita obl.: Nerchinsk distr., between Nerchya and Kuenga, *Sukachev & Poplavskaya* 2476 (LE); Zabaikal'sk distr., 10 km from Kharanur, *Lomonosova* 508 (NS); 10 km from Zabaikalsk to Abagaitui, *Lomonosova* 512 (NS); Dauriya Biosphere Res., Gashkoy lake, 40 km SW Nizhn. Tsasuchey, *Freitag* 33.129 (KAS); 40 km SE Aginskoye near road to Nizhn. Tsasuchey, *Freitag* 33.127b (KAS).

MONGOLIA: Gobi Altai aimak, 43 km SSE Delger Somon, *Grubov* 6072 (LE); Bayan-Hongor aimak, Dolon-Gol river vall. NE Erdeni-Uzu, *Prochanov* 648 (LE); Archangai aimak, 50 km NW Tevirulekh, *Gubanov* 1552 (MW); Hentiy aimak, Muringol river (Kerulen tributary), 14.8.1924, *Polynov* (LE).

CHINA: Heilongjiang prov., Taikan, *Skvortsov* 1008 (LE); Sukhebaatar aimak, Dariganga, 10-12 km SSW Khabirga-Bulak, *Yunatov* 15.697 (LE).

Typification of *Suaeda corniculata*

Typification of the binomial *Suaeda corniculata* rendered difficult due to ambiguous or conflicting phrases in the protologue and corresponding heterogeneous elements in the original material. The statement in the protologue “Calyx ... dorso bicorniculatis: corniculis terminalibus saepe inaequalibus; uno alterove obsoleto” (Meyer 1829: 399) contradicts Ledebour (1830b: t. 195), which shows almost equally and only moderately enlarged tepals. A corresponding statement was given also in an earlier draft of the protologue on one of the putative syntypes in LE (“304. prope Loktjew. legit A. Ledebour”) with the phrase “Calyx 5 fidus, demum dorso in corniculos (calyptraeformis) 5 crassos breves definens”. This discrepancy was recognized already by Moquin-Tandon (1840: 133) as he stated “... Icon florum Altaicae haud rite cornicula indicat”. The Icones (Ledebour 1830b) are formally published one year later, but the reference is made in the protologue to the plate, which therefore represents an original element.

Iijin (1936a) and Grubov (1966) quoted type material in St Petersburg (LE) for *S. corniculata* without giving further details. In search for relevant specimens, we detected the collection “Herb. Ledebour, *Schoberia corniculata* m., Altai” (without coll.) with the label “typus” attached by V. Botschanzev, without date. Obviously it was selected because of its similarity to



Fig. 7. Lectotype of *Suaeda corniculata*, Altai, C. A. Meyer, at LE (left and central branches only) – Photograph by E. Punina.

t. 195 in Ledebour (1830b), but in fact it belongs to *Suaeda salsa* (L.) Pall. as defined by Freitag & Lomonosova (2006). Fortunately, this misleading typification was never published.

All specimens in LE collected, labelled and identified by Ledebour and Meyer with full indication of the type localities "Loktewsk" (Ledebour) and "Semipalatinsk" (Meyer) were named *Schoberia maritima* L. or *S. salsa*, respectively, and do not belong to *S. corniculata*. Only one unnamed specimen from "Loktewsk" perhaps belongs to *S. corniculata*, but the plant is too young to allow determination. The third type locality, "Tschuja" (Bunge), is not represented on any label.

From six more sheets that are putative candidates for a suitable lectotype because being named *Schoberia corniculata* either by Meyer, Ledebour or Bunge, three belong to *Suaeda salsa*, one to *S. acuminata* (C. A. Mey.) Moq., one to *S. prostrata* Pall., and only one contains *S. corniculata* as defined in this paper (Fig. 7). In fact, the plants mounted on the sheet look somewhat different: both the richly branched stem at the left side (with flowers only) and the longer stem in the centre (with flowers and fruits) clearly belong to *S. corniculata*, whereas the complete but much smaller plant on the right side with flowers differs by wider leaves and could well belong to the related *S. tschujensis* Lomon. & Freitag. A first label, written most likely by C. A. Meyer himself, reads as "*Schoberia corniculata* C. A. Mey., Altai, in locis salsis, C. A. Meyer". A second (later) label carries the printed words "Herbarium proprium Turczaninowii".

In GOET another sheet was found that can be traced to the original material. It carries two fruiting branches of *Suaeda corniculata* and a pocket with a considerable number of fruits. One richly branched stem is very similar to the left one in the LE specimen, whereas the second is much smaller. According to the two labels mounted above each other in the left lower corner, probably they came from different herbaria: The upper label was written by Meyer himself and reads, obviously for the purpose of distribution, as "2. *Schoberia corniculata* m. (mihi), Fl. Altaica I p. 399, Meyer". The pocket also is labelled by Meyer as "*Schoberia corniculata*". The lower label carries the data: "2. *Schoberia corniculata* C. A. M., In Siberia Altaica, bot. Mis. C. A. Meyer. Herb. Philipp 1846".

Both specimens equally fulfill the requirements to serve as lectotype. Here we have chosen the specimen in LE (only the left and the central branches of Fig. 7) because it is more easily accessible to the botanists of the area. Consequently, the specimen in GOET remains a paratype though probably being an isolectotype.

Another specimen from Bunge's collection in P also should be considered as belonging to the original material. It carries an original white label "*Schoberia corniculata*, Flora Altaica, Herb. Al. de Bunge" and a later addition on an overlapping blue label "Nr. 434 fl. alt., Prodrum. 304b, 305b". The sheet consists of 9 individual plants: 8 are blackish, of prostrate habit, and represent typical *Suaeda corniculata*, whereas one light-coloured delicate plant (second from the right in upper row) most likely belongs to *S. olufsenii* Pauls. That specimen (restricted to the 8 *S. corniculata* plants) should be considered as paratype.

***Suaeda tuvunica* Lomon. & Freitag, sp. nov.**

Holotypus: Russia, Tuva Republic, Tes-Khem Distr., Shara-Nur lake 42 km W Erzin, S side, flat runnels in *Achnatherum splendens* comm., 24.9.2003, Freitag & Lomonosova 33.054 (NS; isotypi: B, K, KAS, LE, MW, TK).

A proxima *Suaeda corniculata* foliis laete viridibus, valde succulentis, nitentibus, tepalis fructiferis distincte alatis (alis horizontalibus cingulum constituentibus), a dimidio ad tres partes longitudinis connatis (saepe tepalis duobus minutissimis complete coalitis), nec non seminibus magnis 1.5-1.7 mm in diam. differt. A simili *S. kossinskyi* habitu et tepalis alatis inaequalibus convexissimis succulentis differt.

Annual, in prostrate mats up to 5 cm in height and 40 cm in diameter, branched from the very base; living plants bright green, shining, turning dark-, brown- or olive-green, never blackish. *Stem* at base up to 2 mm thick, 1 to 2 × spreadingly branched; with alternating, light green and pale lines



Fig. 8. Holotype of *Suaeda tuvinica* at NS. – Photograph by M. Lomonosova.

throughout, later turning light brown. *Leaves* spreading, highly succulent, mostly subterete but more convex beneath, with *Brezia* type C₃ anatomy, 10–25 mm long, up to 3 mm wide, with parallel margins, at the apex rounded and sometimes with very short hyaline point. Inflorescences hardly separated, internodes in lower and middle parts 7–25 mm long, becoming shorter towards the top. *Bracts* leaf-like, 6–11 mm long, spreading or ascending, usually ± incurved, the lower c. 3 × longer than fruiting clusters, the upper successively shorter, narrowly ovate and not surpassing the glomerules. *Bracteoles* up to 0.5 mm long, lanceolate, acute, entire. *Glomerules* 5–9-flowered, widely spaced almost from the base onwards. *Flowers* bisexual, mostly perfect, protogynous, irregular in shape, 1.3–1.5 mm in diameter. *Tepals* 5 or 4 by fusion, unequal, fused for 1/2–3/4. *Stamens* usually less than 5, often 1; filaments up to 0.7 mm long, band-shaped, inserted at base of tepals; anthers 0.25–0.4 mm long, divided for 1/3. *Ovary* superior, depressed; the 2 stigmas 0.3–0.5 mm long, erect or somewhat recurved, with short papillae. *Fruiting perianth* up to c. 3.5 mm in longest diameter; tepal lobes highly succulent, the upper parts almost semiglobular but the outermost much bigger, two smaller lobes often almost completely fused, around the girdle line transversally winged, with 3 and 2 or all 5 wings ± fused, below the wings often with one or two short oblique outgrowths. *Seeds* horizontal, dimorphic; black seeds lenticular, oval in outline, radicle area short and rounded, (1.45–)1.65(–2.05) × (1.25–)1.4(–1.6) × 0.5–0.8 mm; testa dull, sculptured; brown seeds immature in the investigated specimens.

lc. – Fig. 1C, 2E–F, 8. – For a published figure see Zhu 1979: 29, fig. 9–11 (sub *Suaeda prostrata*).

Chromosome number. – $2n = 54$ (hexaploid), from 2 localities (*Artemov & Shaulo 103*; *Shaulo & Doduk 109*).

Distribution. – Dry steppe and semidesert areas from Altaiskiy Krai to Tuva Republic in central S Siberia, N Mongolia and China – Fig. 9.

Habitat. – In depressions and around moderately salty lakes on solonchaks, usually together with *Suaeda corniculata* subsp. *corniculata* in open patches of tall *Achnatherum splendens* or *Leymus pubescens* communities; at altitudes from c. 800 to 1100 m.

Etymology. – The epithet of the new species refers to the Tuva Republic where it was detected first.

Remarks. – With the very pronounced and widely fused wings and the strictly prostrate habit, the new species is similar to *Suaeda kossinskyi* Iljin, which was described from the southern Caspian Lowlands and extends up to the foothills of the Altai in NW China. Therefore we were first inclined to follow Grubov (1966), who named some specimens from Mongolia *S. kossinskyi*. However *S. tuvinica* differs from *S. kossinskyi* in the following characters: leaves bright green, brilliantly shining versus greyish green, ± dull; tepals distinctly unequal versus ± equal; tepals strongly thickened throughout versus remaining thin; fruiting perianth knobby, with irregular, somewhat star-like outline versus strongly flattened from both sides, with ± circular outline. Both species also differ in their distribution, with *S. kossinskyi* being an element of the semideserts of the Caspian Lowlands and northern Middle Asia and *S. tuvinica* replacing it in the corresponding habitats in western C Asia. Obviously, the new species also occurs in China as can be concluded from Zhu (1979: t. 29, fig. 9–11), where a typical fruit of *S. tuvinica* is shown under the erroneous name *S. prostrata*.

Selected specimens. – RUSSIA: [WEST SIBERIA]: Altaisk. Krai: Uglovsk distr., 4 km from Lyapunovo to Shadruckha, 51°17'N 80°04'E, 13.9.1999 *Artemov & al.* (NS); Mikhailovsk distr., Malinovoye lake, *Lomonosova & Zhdanova 22* (KAS, NS); *ibid.*, *Lomonosova & Zhdanova 32* (NS); Blagoveshchensk distr., Kulundinskoye lake, *Lomonosova 16* (NS). – [CENTRAL SIBERIA]: Tuva Republic: Bai-Khol lake 15 km NW Erzin, *Lomonosova 368* (NS), Freitag 33.064 (KAS); Tes-Khem river valley, *Lomonosova & Zhdanova 82* (KAS, NS); Tere-Khol' lake, *Lomonosova & Krasnikov 935* (NS), *Lomonosova & Rozhizina 953* (NS), *Shaulo & Doduk 109* (NS), *Artemov*

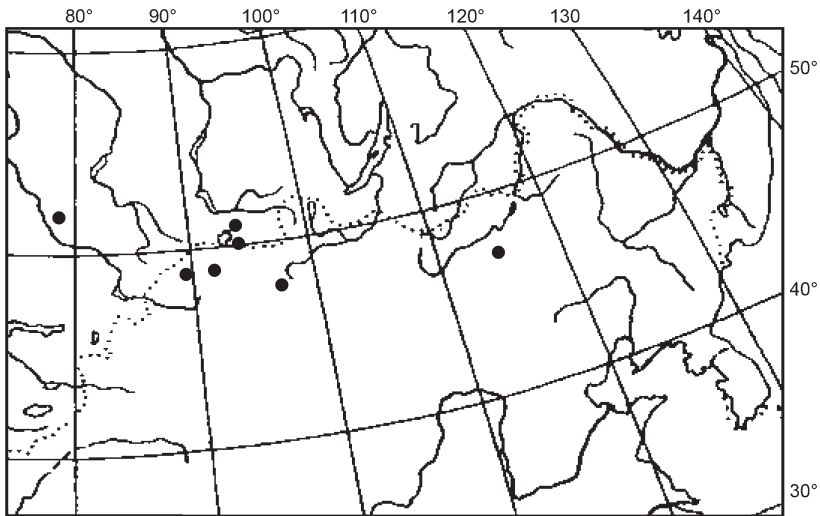


Fig. 9. Distribution of *Suaeda tuvinica*.

& *Shaulo* 103 (KAS, NS); Tandinskiy distr., Khadyn lake, *Lomonosova & al.* 51 (NS), *Lomonosova & al.* 95 (NS).

MONGOLIA: Uvs aimak: Achit-Nur lake, *Klemenz* 162, 162a (LE); Naran-Bulak Somon, Khirgis-Nuur lake, *Gubanov* 9106a (MW, NS). Dzavkhan aimak: Buren Somon, 20 km SSW Ulyasatui, *Gubanov* 5520 (MW). Central aimak: Baga-Urgo mountain, Baishintinskaya depression, *Shastin* 1147 (LE).

***Suaeda kulundensis* Lomon. & Freitag, sp. nov.**

Holotypus: Russia, Kurgan obl., Petukhovo distr., northern shore of Medvezhye lake, solonchak along the road, 14.9.2005, *M. Lomonosova* 755 (NS; isotypi: ALTB, B, K, KAS, LE, MW, TK).

Species nova inter *Suaeda salsam* et *S. corniculatam* quasi intermedia et verosimiliter ex hybridatione et allopolyploidisatione harum specierum orta, a prima tepalis valde inaequalibus difert, a secunda habitu strictissime erecto, foliis basi dilatatis et tepalis alatis diversa est. Ab affini *S. sibirica* alis tepalorum liberis, projectione tepalorum maxima conica, nec non seminibus manifeste sculpturatis differt.

Annual, (4-)10-60(-90) cm in height and up to 20(-40) cm in width, usually strictly erect with dominant primary stem, living plants green, somewhat glaucescent, often turning dark brown to black when dried. *Stem* at base up to 5 mm thick, unbranched or with several short vegetative laterals, higher up 2-3 × branched, with numerous spike-like ascending or spreading generative branches, rarely branched from the base; younger axes with alternating green and whitish lines. *Leaves* ascending, flat to semiterete, moderately succulent, with *Brezia* type C₃ anatomy, 10-20(-30) × 1-2 mm, linear-lanceolate, widest near the base, gradually narrowing toward the acute or apiculate apex. *Inflorescences* terminal, spike-like, usually interrupted, more rarely ± condensed, (2-)3-8(-12) cm long; internodes in lower part of the spikes usually 3-5 mm long, gradually shorter towards the top. *Bracts* ascending, leaf-like, 2-7 mm long, the lower 2-4 × longer than the internodes, the upper gradually shorter, equalling the glomerules. *Bracteoles* 0.5-1 mm long, very variable in shape, from narrow-ovate to obovate, acuminate, subentire, erose-dentate or ciliate. *Glomerules* (3-)5-11-flowered. *Flowers* bisexual, protogynous, bowl-shaped, up to 2 mm in longer diameter. Tepals 5, fused for about 1/2, the outermost distinctly longer and wider. *Stamens* 5 or less by abortion in lateral flowers, filaments up to 0.4 mm, narrow,



Fig. 10. Holotype of *Suaeda kulundensis* at NS. – Photograph by M. Lomonosova.

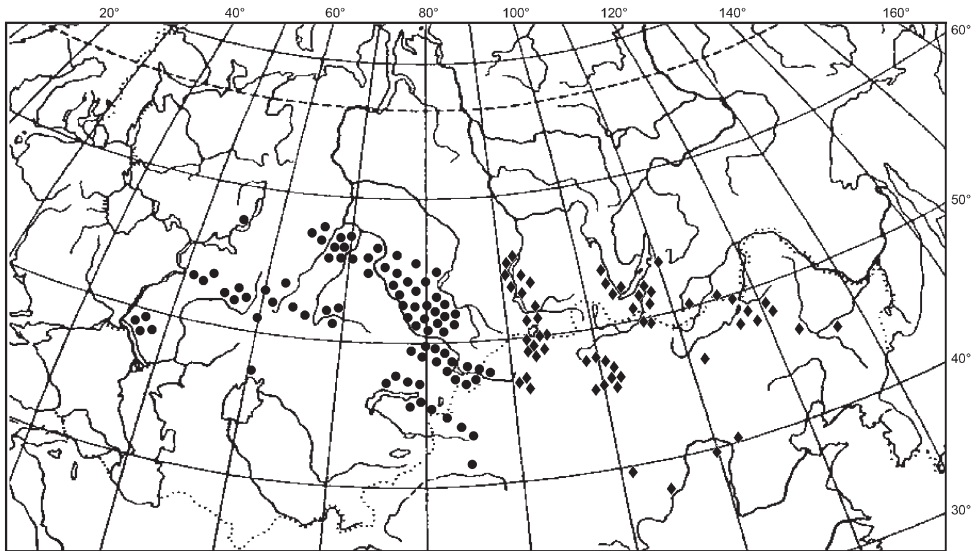


Fig. 11. Distribution of *Suaeda kulundensis* (●) and *S. sibirica* (◆).

band-shaped, anthers 0.15-0.2 × 0.2-0.35 mm, divided for $\frac{1}{2}$ - $\frac{2}{3}$. Ovary superior, depressed ovoid, apically narrowed; stigmas 2, rarely 3, 0.25-0.8(-1) mm long, straight or slightly recurved, with short papillae. *Fruiting perianth* enlarged, 2-4.5 mm in longest diameter; outermost tepal horn-shaped, 1.3-2 × longer and 1.5-3 × wider than the others, more or less upright, somewhat conical, the tepals at the girdle line thickened and forming unequal, separate, up to 0.6 mm wide wing-like horizontal outgrowths with rounded or distantly crenate margins, more rarely outgrowths poorly developed. *Seeds* horizontal, dimorphic; black seeds (1.15-)1.35(-1.55) mm long, (1-)1.2(-1.4) mm wide, 0.5-0.9 mm thick, lens-shaped, flattened, beaked; testa somewhat shining, distinctly sculptured.

Ic. – Fig. 1D, 2G-H, 10.

Chromosome numbers. – Two ploidy levels were found in samples from 31 localities throughout the area. The majority proved to be octoploid, with $2n = 72$, whereas in the eastern part of the area alongside with octoploids also decaploid plants with $2n = 90$ were detected.

Distribution. – Forest-steppe and steppe zones in SE European Russia, W Siberia, N, C and E Kazakhstan, NW China – Fig. 11.

Note. – In the flora accounts of Siberia (Krylov 1930; Lomonosova 1992), *Suaeda kulundensis* is dealt with under the name *S. corniculata* var. *erecta* Bunge and *S. corniculata* subsp. *erecta* (Bunge) Lomon. p.p., respectively, but the type of Bunge's name does not belong to the species complex of *S. corniculata* (see above, Introduction, second paragraph).

Habitat. – In depressions, around salt lakes and in river valleys on solonchaks temporarily flooded in spring and remaining moist during summer, usually in dense stands and forming a plant community of its own behind the *Salicornia* belt; usually up to 400 m in altitude, but in China reaching c. 1000 m.

Etymology. – The new species is named after the Kulunda steppe, which extends from NE Kazakhstan to the northwestern foothills of the Altai in S Siberia.

Remarks. – *Suaeda kulundensis* differs from *S. corniculata* in two conspicuous features: (1) erect with densely arranged ascending branches versus prostrate with \pm spreading branches; (2) each tepal in the fruiting perianth with one rounded or erose-dentate wing-like outgrowth versus outgrowths deeply divided or numerous with acutish apices. In the first character, the new species is very similar to *S. salsa*, and from the lower Volga area to W Siberia both species are sympatric, with *S. kulundensis* being rather rare in SE Europe but becoming dominant towards the East. However, even when growing in the same plant community, from flowering stage onwards they can be discerned by the different structure of the fruiting perianth. Furthermore, numerous chromosome counts have shown that *S. salsa* is invariably tetraploid. From *S. sibirica*, which likewise shows an erect habit and replaces *S. kulundensis* from Tuva and the Middle Yenisey areas to the East, it can be distinguished, beside the usually somewhat denser branching system, by the complete lack of fusion between adjoining wings and by the distinctly sculptured testa.

Variation. – *Suaeda kulundensis* is a variable species. Several populations, in particular from the Kulunda steppe, have larger black seeds (1.5–2 mm in diameter). However, as we have observed a gradual variation and as they agree in all other characters including chromosome numbers, nuclear (ITS) and chloroplast (scmp 14, 16, 20) sequences, they are considered as a minor variety. This is supported by the fact that similar variation is also known from *S. maritima* as var. *macrocarpa* Moq. (Moquin 1840) and from *S. salsa* described under the name *S. prostrata* subsp. *macrocarpa* (Moq.) Iljin (1936a), which was also listed in previous papers under the working name *S. "elegans"* (Schütze & al. 2003; Freitag & Lomonosova 2006). Conspicuous variation also occurs in the rather different size of the horn-like enlarged tepal, in the shape and size of the wing-like outgrowths, and in the elongated or condensed spikes. See, also below, discussion, under *S. kulundensis*.

We treat the specimens from the Kulunda steppe to E Kazakhstan with larger seeds, thinner and unwinged tepals and longer internodes in the inflorescence as *Suaeda kulundensis* var. *macrocarpa*:

var. *macrocarpa* Lomon. & Freitag, **var. nov.**

Holotypus: Russia, Altaiskiyi krai: Kulunda distr., near Mirabilit village, salty lake (shore), meadow on solonchak, 5.10.1999, *I. Krasnoborov* & *D. Shaulo* 135 (NS; isotypus KAS).

A *Suaeda kulundensis* var. *kulundensis* seminibus magnis 1.5–2 mm in diam. plerumque atris, tepalis fructiferis tenuibus sine alis, internodiis inflorescentiarum elongatis differt.

In the specimen list below the respective collections are marked by an asterisk.

Selected specimens. – RUSSIA: [SE EUROPE]: Samara obl.: 20 km N Tolyatti, Nizhn. Sanchileyevo, *Golub* 762 (NS). Bashkir Republic: Argalash distr., between Alabuga and Kirpichiki, *Lind* 681 (LE). Volgograd obl.: Lake El'ton, near Ozerneye, *Freitag* 28.262 (KAS). Orenburg Region: Orsk distr., between Briski and Kulmskiy, *Fedchenko* 540 (LE). Chelyabinsk obl.: Uvel'ska distr., 1.5–2 km SE Duvankul', 25.8.1951, *Samarin* (LE). – [WEST SIBERIA]: Kurgan obl.: Makushino, *Lomonosova* 742 (NS). Omsk obl.: Isil-Kul distr., Ebeiti lake, *Lomonosova & Zhdanova* 34 (NS). Novosibirsk obl.: Kochki distr., c. 232 km WSW Novosibirsk at road to Karasuk, *Freitag* 33.084 (KAS, NS); Karasuk distr., 2 km N Troitskoe, *Lomonosova & Sukhorukov* 79 (NS); Baraba, Itkulskoye, 8–12.8.1890, *Krylov* (TK). Altaisk. Krai: Aleisk distr., Urzhum, 21.8.1996, *Shmakov & al.* (ALTB); Burla distr., Novopeschanoye, *Artemov & al.* 303 (NS)*; Slavgorod distr., Bursol, Burlinskoye lake, 6.9.1996, *Kupriyanov & Chusovlyanov* (ALTB)*.

KAZAKHSTAN: Kustanai obl.: Kustanai distr., Zatobolsk, 9.1924, *Rusanov* (LE); Kulimurun lake, 7.1999, *Nuriukhaibetova* (KAS). Semipalatinsk obl., Dzhapan-Bish-Cheku mts., *Iljin* 734 (TASH). Dzhambul obl.: N border of Chu valley, source at foot of Dzhambul Mts, *Freitag* 26.339 (KAS). Taldy-Kurgan obl.: lower reaches of Aksu river, *Pavlov* 1162 (AA); near Ush-Tobe, *Lomonosova & Sukhorukov* 53a (NS). East-Kazakhstan obl.: Kurchum distr., Darstvennoye, *Lomonosova* 125 (NS); Ust'-Kamenogorsk distr., Sary-Abay river valley, *Ovchinnikov* 2614 (LE).



Fig. 12. Holotype of *Suaeda sibirica* at NS. – Photograph by M. Lomonosova.

***Suaeda sibirica* Lomon. & Freitag, sp. nov.**

Holotypus: Russia, Chita oblast', Onon district, Khuduktui lake, 645 m, solonchak, 50°20'N, 115°28'E, 14.9.2003, *M. Lomonosova 521* (NS; isotypi: ALTB, B, IRK, K, KAS, LE, MW, TK)

Species nova inter *Suaedam heteropteram* et *S. corniculatam* quasi intermedia et verosimiliter ex hybridisatione et allopolyploidisatione harum specierum orta, a prima tepalis valde inaequalibus differt, a secunda habitu strictissime erecto, tepalis alatis et foliorum forma diversa est. *S. kulundensi* primo aspectu similis, sed inflorescentiis laxe ramosis, alis tepalorum partim connatis, tepalis maximis apice cupuliformibus, nec non seminibus nitentibus indistincte sculpturatis differt.

Annual, in vegetative and some generative characters similar to *Suaeda kulundensis* but differing by: *Branching* usually more sparsely, mostly with laterals of first order only from near the base. *Glomerules* more loosely arranged due to 5-10(-15) mm long internodes in lower and middle parts. *Bracts* longer, usually 5-10(-15) mm in lower part of inflorescences. *Fruiting perianth* with at least three (rarely two) larger tepals fused in the wing area and somewhat higher up, the outermost, biggest tepal of obtusely conical shape. *Black seeds* (1.15-1.3-1.5(-1.65) mm long, 1-1.2(-1.45) mm wide; testa only obscurely sculptured, almost smooth, more shining.

Ic. – Fig. 1E, 2I-J, 12

Chromosome number. – Counts in plants from 38 habitats in different parts of the area including the type revealed an octoploid chromosome complement of $2n = 72$.

Distribution. – C and E Siberia from the upper reaches of the Yenisey river (Krasnoyarsk area and Tuva) to Chita, Mongolia and NE China (Manchuria) – Fig. 11.

Habitat. – In depressions and around salt lakes on solonchaks temporarily flooded in spring and remaining moist during summer, usually in dense stands and forming a plant community of its own behind the *Salicornia* belt, up to 1450 m.

Selected specimens. – RUSSIA: [CENTRAL SIBERIA]: Khakass Republic: Ust-Abakan distr., Krasnoye lake, *Lomonosova 621* (NS); Uzur distr., Kornilovskoye, *Cherepin 2547* (KRAS); Bograd distr., Gor'koye lake, 10.9.1934, *Tarchevskiyi* (LE). Tuva Republic: Tes-Khem distr., Dus-Khol' lake, 17 km NW Erzin, *Lomonosova 366* (NS), *Freitag 33.062* (KAS). – [EAST SIBERIA]: Irkutsk obl.: near Ust-Ordynskoye, *Lomonosova 299* (NS); Balagansk distr., Bazheyevskoye, 25.8.1905, *Maltsev* (IRKU); Nukuty, Zalarinka river valley, *Peshkova & Petrochenko 1839* (NSK). Buryat Republic: Dzhida distr., Borgoiszkaya steppe, 1951, *Reshchikov* (NSK); Barguzin distr., Suvo, *Lomonosova 445* (NS), *Freitag 33.126* (KAS); Mukhor-Shibir distr., Olon-Shibir lake, 27.8.1998, *Azovskiy* (IRK). Chita obl.: Onon distr., Barun-Torei lake, *Lomonosova 489* (NS).

MONGOLIA: Uvs Aimak, SE shore of Uvs-Nuur lake, *Gubanov 8148* (MW, NS); Central aimak, Ukhtal-Tsaidam somon, 60 km W Dzhartalandy, *Yunatov 18921* (LE); Bayan Hongor aimak, 45°05'39"N, 100°48'47"E, *Hurka & Neuffer 12.145* (KAS).

CHINA: [MANCHURIA]: Heilongjiang prov., Anda distr., Sartu station, *Chao 766* (LE); Ningxia prov., Gaoshavo region, Chagan' lake, 27.8.1884, *Potanin* (LE); Zhekhe Prov., Chiphyn distr., *Fuh 5222* (LE).

Exsiccata. – Herb. Fl. Ross. 1237 (sub *Suaeda corniculata*), Irkutsk prov., Balagansk distr., Alar, 21.8.1903, *Maltsev* (LE, TASH); Herb. Fl. Ross. 5009b (sub *S. corniculata*), Buryat Republic: Barguzin distr.: Alga, 3.9.1964, *Siplivinskiy* (TASH) – another specimen with the same number in LE belongs to *S. heteroptera* Kitag.

Discussion – relationships of the new taxa

Combining the morphological, caryological and molecular data (Fig. 3 and Table 1) allows to draw the following conclusions on the relationships of the taxa dealt with in the present contribution.

Suaeda corniculata is considered to be the “core” species of the *S. corniculata* clade because in terms of geographical range and representation in the plant communities of saltmarshes in Eurasia it is the most successful species. Furthermore, the most conspicuous morphological characters of the clade, the presence of one (or more) greatly enlarged, horn-like tepal, together with a prostrate or ascending habit are particularly well expressed. Despite of high uniformity in the nuclear ITS and the chloroplast *atpH-atpI* sequences, genetically it is heterogenous by different chromosome numbers reaching from tetraploid ($2n = 36$) to hexaploid ($2n = 54$) levels. Obviously, the higher numbers originated by autopolyploidy, because allopolyploidy most likely would have left molecular signals either in the nuclear or in the chloroplast genome. However, the great morphological variation is only loosely associated with the ploidy level. Tetraploid plants, like those classified under the new subsp. *mongolica*, are always delicate, but individuals with similar habit also have been found among the hexaploids. As the tetraploid level represents an earlier evolutionary stage, subsp. *mongolica* either represents an ancestral form, or it has evolved in tetraploid populations of the typical subspecies. Interestingly, in the distantly related *S. tschujensis*, which has a more basal position in the topology of the *S. corniculata* clade (Fig. 1 and 2 in Schütze & al. 2003), even the diploid condition has been conserved (Lomonosova & Freitag 2003). On the other hand, the closely related Pannonian endemic *S. pannonica* (Beck) Graebn. shows the octoploid ($2n = 72$) chromosome complement (Krahlucová & Tomšovic 1997).

Suaeda tuvinica. – The morphological characters equivocally indicate relationships to *S. corniculata* (unevenly enlarged fruiting tepals) and to *S. kossinskyi* Iljin (wing formation is most obviously expressed in the *S. prostrata/spicata* clade). In fact, before recognizing its independent position, several collections of *S. tuvinica* were named *S. kossinskyi* by us. However, the identity of the ITS sequences with those of *S. corniculata* (Schütze, unpubl.) clearly underlines its placement in the *S. corniculata* clade. The very peculiar wing formation at the fruiting perianth and the shiny and highly succulent leaves indicate a separate position despite of the identical ITS sequences. Most likely the hexaploid ($2n = 54$) *S. tuvinica* has arisen in northern C Asia from a likewise hexaploid form of *S. corniculata*. Unfortunately, chloroplast sequences are not known so far.

Suaeda kulundensis. – In morphological respect, this new species combines characters typical for the *S. salsa* clade (strictly erect habit) and the *S. corniculata* clade (unevenly enlarged tepals in the fruiting perianth). As the three taxa *S. salsa*, *S. corniculata* and *S. kulundensis* are for the most part sympatric, a hybrid origin appears conceivable. However, a simple hybrid nature of *S. kulundensis* can be excluded for the following reasons: (1) Neither in nature nor in cultivation a split of the offspring into the parental forms has been observed. (2) The chromosome complements of *S. kulundensis* ($2n = 72, 90$) differ from both *S. salsa* ($2n = 36$) and *S. corniculata* ($2n = 36, 54$), which is highly suggestive of an origin by allopolyploidisation. This latter hypothesis is strongly supported by the molecular results (Fig. 3A, B). They show that characters of both putative parental species are combined in the genome of *S. kulundensis*, with *S. salsa* sequences in the nuclear ribosomes (ITS) and *S. corniculata* sequences in the chloroplast *atpH-atpI* sequences. By that, *S. kulundensis* proves to be a fine example of reticulate evolution. Most likely, the presence of geographically slightly separated octoploid and decaploid populations in *S. kulundensis* can be explained by parallel allopolyploidisation events, with participation of tetraploid and hexaploid individuals of *S. corniculata*. As the genetic material was essentially the same in both cases, the resulting chromosome races do not show clear morphological differences.

Suaeda sibirica. – Obviously, *S. sibirica* displays a similar case of reticulate evolution. It also shows striking combinations of morphological and molecular characters of the otherwise widely differing *S. salsa* and *S. corniculata* clades. Once more, the greatly enlarged outermost tepal and the chloroplast sequences (Fig. 3B) are markers of *S. corniculata*, which is widely sympatric with the putative parents. However, tracing the second ancestor is more difficult because neither the specific morphological characters nor the topology of the ITS tree allow clear-cut sugges-

Table 1. Diagnostic characters of the Eurasian *Suaeda* species belonging to the *S. corniculata* group of *S. subg. Brezia*.

	<i>S. corniculata</i> subsp. <i>corniculata</i>	<i>S. corniculata</i> subsp. <i>mongolica</i>	<i>S. tavinnica</i>	<i>S. kulundensis</i>	<i>S. sibirica</i>	<i>S. tschujensis</i>	<i>S. pannonica</i>	<i>S. arctica</i>
Growth form in normal conditions	ascending or prostrate	prostrate or ascending	strictly prostrate	strictly erect	strictly erect	strictly prostrate, forming mats	ascending	prostrate
Colour living plants	fresh green or purplish	fresh green or purplish	bright green, shining	glaucous or purplish	glaucous or purplish	pale green or pinkish	dark green	pale green
dried plants	blackish or purplish	brown or blackish	olive-green or brown	dark brown or black	dark brown or black	pale green	black	pale green
Branching	loose, spreading	loose, spreading	loose, spreading	dense, erect	loose to moderately dense, erect	loose to moderately dense, spreading	loose, spreading	almost absent
Flowers per glomerule	3-7(-17)	5-7(-9)	5-9	(3-)5-11	5-10(-15)	(1-)3-5(-7)	3-7(-9)	3-5
Leaves orientation	(ascending to) spreading	(ascending to) spreading	spreading	ascending	ascending	ascending (to appressed)	(ascending to) spreading	ascending (to appressed)
size [mm]	10-40 × 1-2	10-30 × 1-1.5	10-25 × 1.5-3	10-30 × 1-2	10-30 × 1-2	9-18 × 1.5-2	10-40 × 1.5-2.5	3-5 × 1
succulence	++	+ + + +	+++	+ + + +	+ + + +	+ + + +	++	+ + + +
apex	obtuse to acutish	obtuse to acutish	obtuse	acuminate to acutish	acuminate to acutish	obtuse to acutish	obtuse	obtuse
Seeds ¹ size ² [mm]	(0.8-)1.08(-1.35) × (0.7-)0.92(-1.17)	(0.85-)1.05(-1.25) × (0.7-)0.87(-1)	(1.45-)1.64(-2.05) × (1.25-)1.4(-1.6)	(1.15-)1.35(-1.5) × (1-)1.2(-1.4) ³	(1.15-)1.39(-1.65) × (1-)1.2(-1.45)	(0.78-)0.89(-1) × (0.68-)0.78(-0.9)	(1.2-)1.4(-1.6) × 1-1.2	(1-)1.15(-1.23) × (0.95-)1(-1.1)
surface ⁴	distinctly sculptured	distinctly sculptured	distinctly sculptured	distinctly sculptured	obscurely sculptured	distinctly sculptured	obscurely sculptured	distinctly sculptured
2n =	54(36)	36	54	72(90)	72	18	72	?

¹ The data refer to regular seeds, which are lens-shaped and furnished with a hard, blackish testa; be careful to avoid the larger, disc-shaped seeds with a thin, brownish testa.

² Minimum, mean and maximum values are given, based on $n = 100$ seeds except for *S. tavinnica* ($n = 56$) and *S. arctica* ($n = 20$). For the measurements, 10 seeds per plant were randomly selected, and the plants were chosen to represent the total geographical distribution. The data for *S. pannonica* are overtaken from Freitag & al. (1996).

³ var. *macrocarpa*: (1.5-)1.74(-2) × (1.25-)1.54(-1.85).

⁴ See also SEM micrographs in Fig. 2.

tions. In the latter (Fig. 3A), *S. sibirica* holds a somewhat isolated position. The sympatric *S. heteroptera* Kitag. comes closest, but more likely the second ancestor of *S. sibirica* became extinct.

Identification of taxa belonging to the *Suaeda corniculata* group occurring in Eurasia

For facilitating the determination of plants that belong to the taxa described here or to other Eurasian species of the *Suaeda corniculata* group, a key and a synoptic table (Table 1) are provided:

1. Annuals; young stems with alternating green and whitish or reddish lines; leaves with C_3 anatomy, ovary with 2 stigmas at its acutish apex *Suaeda* sect. *Brezia* 2
 - Perennials or annuals; young stems whitish or greenish throughout; leaves with C_4 or C_3 anatomy; ovary with 3(-4) stigmas arising from a depression at its apex *Suaeda*, other sections
2. Tepals in flowering stage moderately, in fruiting stage strongly unequal, the bigger with dome-shaped or conical (horn-like) upper part *Suaeda corniculata* group 3
 - Tepals in flowers and in fruits almost equal *Suaeda*, other species of sect. *Brezia*
3. Fruiting perianth, at least some tepals, distinctly winged. 4
 - Fruiting perianth unwinged, but often with unequal teeth like outgrowths at the girdle line 6
4. Plants strictly prostrate, bright green; leaves and bracts highly succulent, terete, obtuse, sometimes apiculate; fruiting perianth very fleshy, with bulged apices and fused wings, in addition often with scattered short conical outgrowths below the wing; $2n = 54$ *S. tuvinica*
 - Plants erect or ascending, glaucous-green, later often turning black; leaves and bracts semiterete, acuminate; fruiting perianth not as above 5
5. Fruiting perianth with at least the wings of 3 tepals fused; the bigger tepal with dome-shaped apex; black seeds obscurely sculptured; $2n = 72$ *S. sibirica*
 - Fruiting perianth with all wings free from each other; the bigger tepal with conical apex; black seeds distinctly sculptured; $2n = 72$ (90) *S. kulundensis*
6. Plants minute, less than 2 cm, with leaves up to 8 in number and 6 mm in length; the bigger tepal with short conical erect horn; only in the NE Siberian Arctic; $2n = ?$ *S. arctica*
 - Plants bigger, with more and larger leaves 7
7. Plants up to 10 cm, lower internodes 5-10 mm long; inflorescence very dense; fruiting perianth without or with minute outgrowths at the girdle line; only in mountain semideserts of the Altai and Mongolian Altai; $2n = 18$ *S. tschujensis*
 - Plants usually larger, lower internodes at least 10 mm long; inflorescences lax; fruiting perianth with or without teeth-like outgrowths at the girdle line. 8
8. Plants delicate; upper part of bigger tepal narrowly conical, 2-3 × longer than wide, almost horizontally spreading; $2n = 36$ *S. corniculata* subsp. *mongolica*
 - Plants more robust; upper part of bigger tepal broadly conical or dome-shaped, up to 1.5 (-2) × longer than wide, more or less vertically arranged 9
9. Upper part of bigger tepal conical, more rarely dome-shaped; teeth-like outgrowths at the girdle line usually present; seeds distinctly sculptured; $2n = 54(36)$
 - Upper part of bigger tepal dome-shaped, teeth-like outgrowths absent; seeds almost smooth; only in the Pannonian Lowlands, also reported from Ushgorod in W Ukraine, $2n = 72$ *S. corniculata* subsp. *corniculata*
 - Upper part of bigger tepal dome-shaped, teeth-like outgrowths absent; seeds almost smooth; only in the Pannonian Lowlands, also reported from Ushgorod in W Ukraine, $2n = 72$ *S. pannonica*

Acknowledgements

We are most thankful to the curators of the herbaria AA, ALTB, BM, GOET, IRK, IRKU, KRAS, KURGAN, LE, MW, MHA, NS, NSK, P, TASH and TK for the opportunity to study their specimens at the spot or for sending them on loan. We are also indebted to Ms N. Prijdak for the drawings, to Ms E. Punina for processing the photo of the lectotype of *S. corniculata*, to A. Sennikov

for linguistically improving the diagnoses, and to the referees A. Sukhorukov and M. Piirainen for commenting on the manuscript. We are grateful for funding of the field work by the Deutsche Forschungsgemeinschaft (DFG) and the RFBR [Kazakhstan 1992, grant Fr 438.111/16/92; Caspian Lowland 1998, grant Fr 222/14-1, Uzbekistan 2000, grant We 1830/2-1; S Siberia 2003, grant We 1830/2-3; Tuva 2003 grant RFBR 03-04-63147]. By the same institutions financial support was granted for visiting some herbaria: DFG to HF - Fr 220/10-1; RFBR to ML - 04-48778, 07-04-01414 and 08-04-01021a.

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