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Typification and identity of *Suaeda crassifolia*, *S. prostrata* and *S. salsa*, three often confused species of *Suaeda* sect. *Brezia* (*Chenopodiaceae*, *Suaedoideae*)**Abstract**

Freitag, H. & Lomonosova, M.: Typification and identity of *Suaeda crassifolia*, *S. prostrata* and *S. salsa*, three often confused species of *Suaeda* sect. *Brezia* (*Chenopodiaceae*, *Suaedoideae*). – Willdenowia 36 (Special Issue): 21-36. – ISSN 0511-9618; © 2006 BGBM Berlin-Dahlem. doi:10.3372/wi.36.36102 (available via <http://dx.doi.org/>)

The nomenclatural history of the three common and often confused species *Suaeda crassifolia*, *S. salsa* and *S. prostrata*, distributed from Europe to S Siberia and Middle Asia, is outlined, their identity is critically discussed and the three names are typified. The differential characters of the three species are presented in a table.

Key words: Peter Simon Pallas, halophytes, Eurasia, taxonomy, lectotypification.

1. Introduction

Suaeda sect. *Brezia* (Moq.) Volkens (= *Heterosperma* Iljin) is represented in Europe by about nine species and in Eurasia, including N Africa, by about 20 species (Schütze & al. 2003a). They are obligate halophytes and important components of coastal and inland salt marshes. A few of these species were already treated in previous papers (Freitag & al. 1996, Lomonosova & Freitag 2003), but most are still insufficiently known with regard to their nomenclature, delimitation, distribution and ecology. The present paper deals with three notoriously confused species of *S.* sect. *Brezia*, viz. *S. crassifolia* Pall., *S. salsa* (L.) Pall. and *S. prostrata* Pall., all described from around the Caspian Sea. They share some features that separate them from the other species of this section in the area, in particular the absence of horns or wings on the fruiting perianth. Widely differing circumscriptions and misapplied names are found in the Floras and on labels in herbaria. Authors from W and Central Europe preferably treated *S. salsa*, and sometimes also *S. prostrata*, as subspecies of a broadly defined and widespread *S. maritima* (L.) Dumort. (e.g., Aellen 1960-61, Greuter & al. 1984, Ball & Akeroyd 1993), as did many Russian authors from Meyer (1829) to Iljin (1930), or included both in *S. maritima* subsp. *maritima* (e.g., Jalas & Suominen 1980). The diverging treatments are mainly caused by the difficulties to delimit the annual taxa of *S.* sect. *Brezia*. They show only few and inconspicuous characters, some of which are present only after flowering, and vary with salinity, water and nutrient supply as observed in

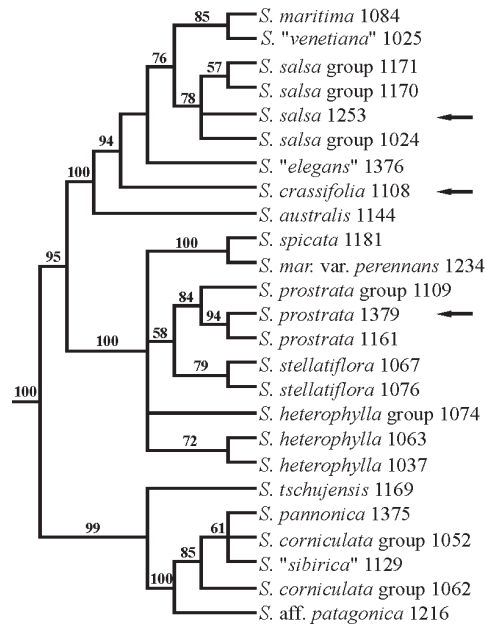


Fig. 1. *Suaeda* sect. *Brezia*, strict consensus tree of the 72 equally most parsimonious trees of 1580 steps resulting from the combined analyses of one nuclear marker (ITS) and two chloroplast markers (*atpB-rbcL*, *psbB-psbH*), with bootstrap values. – Adapted from Schütze & al. 2003a; samples collected in the Aralo-Caspian area are indicated by arrows.

the field and in cultivation experiments (e.g., Schütze & al. 2003a). A further reason is the lack of knowledge about the types of the names and ignoring material from the type localities.

Some phytocoenological and ecological results concerning *Suaeda prostrata* and *S. salsa* were included in a previous contribution (Freitag & al. 2001). First molecular results of a project on the phylogeny and taxonomy of the genus *Suaeda* in the Old World (Fig. 1, a slightly modified version of Schütze & al. 2003a: fig. 7) based on material from the type localities collected and identified by the first author have shown that the species dealt with here are, in spite of their morphological similarity, not particularly closely related to each other.

Aiming at a better understanding of these species, our integrated studies dealt with the following topics: (1) search for and designation of types; (2) complementary herbarium studies; (3) field studies at and around the type localities; (4) cultivation experiments; (5) chromosome counts.

Here we report on the typification of *Suaeda crassifolia*, *S. salsa*, and *S. prostrata* and some nomenclatural problems associated with the application of these names. Data on the identity of species also are given and shortly discussed. In the case of *S. salsa* and *S. prostrata* we considered it expedient to confine relevant statements to the populations from the Aralo-Caspian area to SW Siberia because further east and west they are replaced by populations that somewhat differ in morphology and in nuclear and chloroplast sequences. They may or may not belong to the same species. Molecular and morphological studies to clarify their relations are still ongoing. However, their results will not impair the taxonomic problems dealt with in this paper but for that reason we refrain from presenting a new key to all Eurasian species of *Suaeda*.

2. Materials and methods

Herbarium studies were carried out in AA, ALTB, BM, K, LE, MHA, MW, NS, P, TASH, TK, and W (abbreviations following Holmgren & Holmgren 1998-). To detect the common misapplications of names in publications, emphasis was given on identifications by the pertinent au-

thors, in particular in LE. Field work to study the variability and ecology was carried out in the northern Caspian Lowlands, parts of Siberia and Middle Asia, including visits of the type localities. From many localities flowering and fruiting material was fixed in alcohol to avoid shrinking of the highly succulent tepals and leaves.

Seeds from several proveniences of all three species were cultivated during 1997-1999 in the greenhouse of the Institute of Biology in Kassel and from 2000-2004 outdoor in the Central Siberian Botanical Garden in Novosibirsk. In Kassel an experimental setting with varying nutrient and salinity conditions was applied in order to distinguish between environmentally and genetically induced variation, and *S. maritima* from the shores of the North Sea and from inland Germany was included for comparison. In Novosibirsk the plants received a weekly addition of a 1 % NaCl solution. For chromosome counts in Kassel, the classical orcein technique of Le Cour (Böck 1989) was used with the following specifications: root tips cut in the morning (10:00 a.m.), put in iced water for 24 hours, fixed in an 3 : 1 ethanol/acetic acid solution, macerated for 10 min. at 60 °C, transferred into an orcein staining solution for about 30 min., and squashed. Chromosome counts in Novosibirsk used root tips that were pretreated in 0.2 % colchicine solution for two hours, fixed in ethanol-acetic acid (3 : 1), stained in 4 % ferric ammonium alum, treated in 1 % acetic hematoxylin, and squashed in a drop of saturated solution of chloral hydrate (Smirnov 1968, Barykina & al. 2004).

3. Results and discussion

3.1. Typification

Suaeda crassifolia Pall., Ill. Pl.: t. 54, fig. 46. 1803 ≡ *Echinopsilon crassifolium* (Pall.) Moq., Chenop. Monogr. Enum.: 89. 1840. – Lectotype (designated here): [Iran], Gilan, S. G. Gmelin (LE!).

= *Schoberia obtusifolia* Bunge, Beitr. Fl. Russl.: 290. 1852 ≡ *Suaeda obtusifolia* (Bunge) Trautv. in Bull. Soc. Imp. Naturalistes Moscou 40: 62. 1867. – Lectotype (designated here): [Kazakhstan], “E deserto trans-Uralensi, in salinis Ustjurtensibus, Sept. 1840”, *Cederholm* (P!; isotypes: P!, LE 3×!).

= *Suaeda corniculata* var. *drepanophylla* Litv., Sched. Herb. Fl. Ross. 6: 108. 1908 ≡ *Suaeda drepanophylla* Litv., Sched. Herb. Fl. Ross. 6: 109. 1908 [Iljin in Komarov, Fl. SSSR 6: 196, t. 9, fig. 10a-c. 1936]. – Lectotype (designated here, based on the unpubl. selection by Grubov of 11.3.1964): [Uzbekistan], “Bukharsk. vlad., solonchak bliz st. Farab’, 1.-12.10.1901”, *N. Androssov* (LE!; isotypes: LE 4×!, MHA!).

Ic. – Fig. 2, 6A, 7A.

Notes on the typification. – In addition to the diagnosis “*S. annua* erecta glabra, caulibus subsimplicibus, foliis oblongo ovatis, calycibus quinque-angulatis”, Pallas described the leaves as “crassissima, cylindracea, in ramulis floridis oblongo-ovata, carnosa, glabra”, and the flowers as “ad singula folia duo sessiles; calyx rubens, depressus et quinquangulatus, ut in precedente [*Suaeda albida* = *Bassia hirsuta*], angulis minus prominulis. Semen non vidi maturum”. Regarding the material on which the protologue is based he quoted “Specimina huius plantae in littore Turcomanico et Persico maris Caspii legit S. G. Gmelin, in nostra ora non occurrit”.

Obviously, t. 46 in Pallas was drawn from the type specimen, as was already noticed by Litvinov (in sched. 22.2.1907). In studying the type more carefully, we noted that the leaves are up to 12 × 2 mm, and the bracts 6-3 × 2.5-1.5 mm. However, instead of being cylindrical, they are flat on the adaxial side. Leaves and bracts are incurved, and the axillary clusters contain 3-5 flowers. Despite Pallas’ comment “semen non vidi maturum”, a few nearly mature seeds were found; they measure c. 1.05 × 0.95 mm and have a weakly reticulate surface.

The only synonym cited by Pallas, with a question mark, is Buxbaum’s *Chenopodium maritimum* Cent. 1 : 21, t. 31, fig. 1. 1728. Buxbaum’s figure has indeed some superficial similarity with *S. crassifolia*, but obviously belongs to *Bassia hirsuta*, as confirmed by the descriptive phrase (for further discussion of Buxbaum’s taxon see under *S. salsa*).

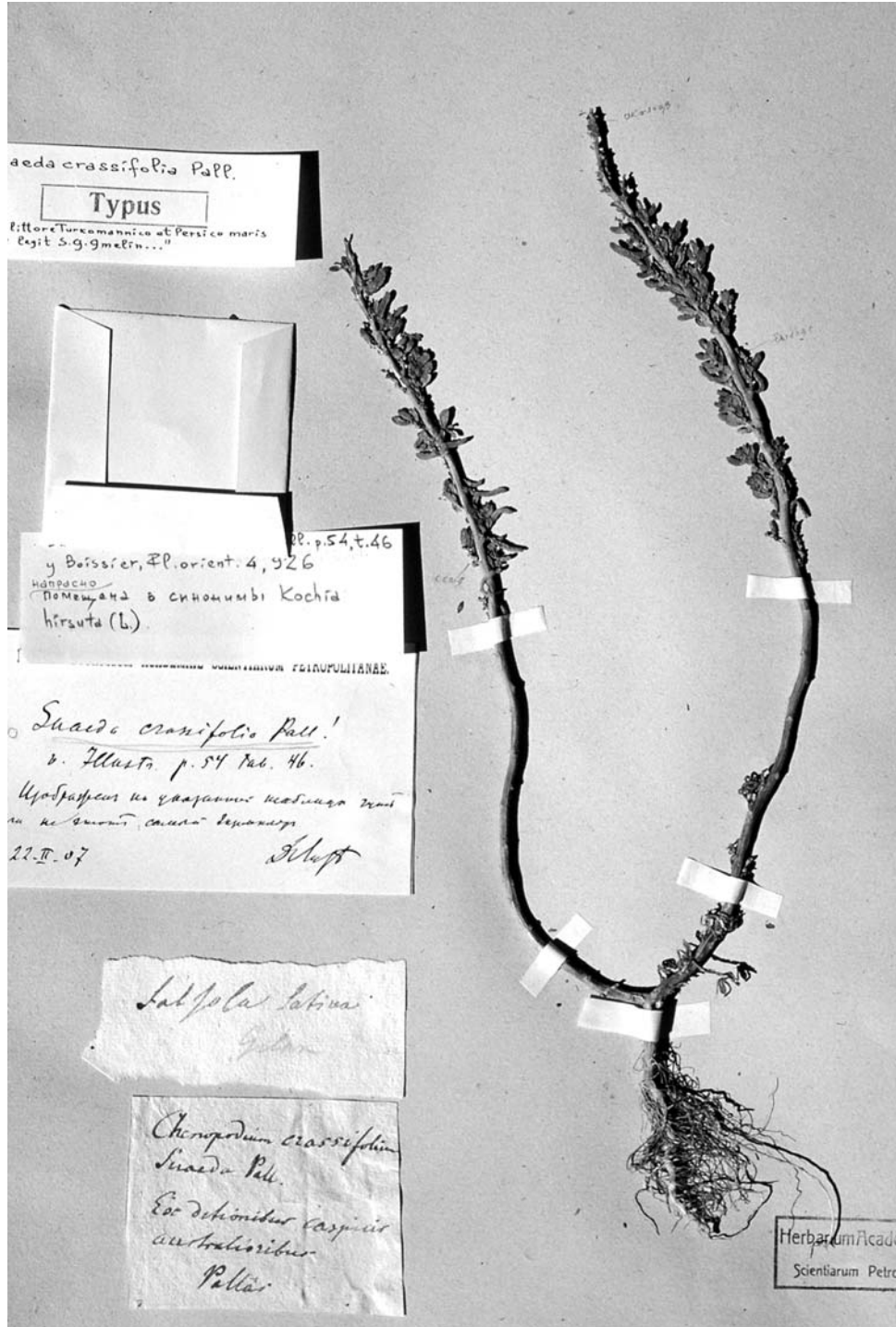


Fig. 2. Lectotype of *Suaeda crassifolia* at LE. – Photograph by H. Freitag.

Notes on the synonymy. – The types of *Schoberia obtusifolia* and *Suaeda corniculata* var. *drepanophylla* agree in their essential characters. However, in the latter the leaves and bracts are more incurved and more strongly succulent. The perianth shows unequal tepals, described in the protologue as corniculate and by Iljin (1936) as “with unequal corniculate protuberances resembling those of *S. corniculata*”. In studying a great number of specimens we found all intermediates between slightly and distinctly unequal tepals. During field work and in cultivated plants we observed that the degree of succulence in all leaf-like organs is intimately related to salinity and/or permanent shortage of water supply. The highest degree of succulence occurs in the lower three to four tepals. They can reach 2-4 times the size of the uppermost tepal and have a wide, rounded (semi-globular or dome-shaped) apical part when fresh, quite different from the horn-shaped apex of tepals in *S. corniculata*. While comparing fresh with dried fruiting perianths of the same individuals, we recognized that the corniculate appearance of the earlier descriptions is an artefact resulting from shrinking of the very succulent lower tepals during desiccating: the upper part of the succulent tepals forms a vertical crest, and the lowermost sometimes shrinks to a horizontal wing-like structure.

The LE material of *Schoberia obtusifolia* was labelled as holotype and isotypes by Grubov on 20.2.1964. However, the specimens from Bunge’s personal herbarium in Paris are better suited because their original labels contain more information, and the one selected here as lectotype carries an additional label with a draft of the diagnosis written by Bunge himself.

Soon after Pallas, the name *Suaeda crassifolia* was misapplied for *S. salsa* (see below) and pertinent plants were cited under the superfluous names *S. obtusifolia* and *S. drepanophylla*. It was properly used only by Grubov (1966), Soskov (1968) and Pratorov (1972). More recent Floras (e.g. Tzvelev 1996) recognize *S. crassifolia* but the diagnostic characters are confused with those of *S. salsa*.

Suaeda salsa (L.) Pall., Ill. Pl.: 46. 1803 ≡ *Chenopodium salsum* L., Sp. Pl.: 221. 1753 ≡ *Salsola salsa* (L.) L., Sp. Pl., ed. 2: 324. 1762 ≡ *Suaeda maritima* var. *salsa* (L.) Moq., Chenop. Monogr. Enum.: 128. 1840 ≡ *Chenopodium salsa* (L.) Moq. in Candolle, Prodr. 13(2): 160. 1849 ≡ *Suaeda maritima* subsp. *salsa* (L.) Soó in Soó & Javorka, Magyar Növ. Kézik. 2: 785. 1951. – Lectotype (designated here): “Habitat ad Astracanam”, herb. Linnaeus no. 315.12 (LINN!). – Epitype (designated here): Russia, Astrakhan prov., northern part of Astrakhan city, near bus station Novostroi, solonchak in small depression together with *Salicornia perennans* and *Tamarix* spp., 7.10.2004, *M. Lomonosova* 716 (NS; isoepitypes: AA, ALTB, B, C, E, G, GB, JE, K, KAS, LD, LE, MHA, MW, NS, TK, W).

Ic. – Fig. 3, 4, 6B, 7B.

Notes on the typification. – The confusion about *Suaeda salsa* started with Linnaeus himself because two different elements were included in the protologue of the basionym *Chenopodium salsum*. It contains the diagnosis “*Chenopodium foliis linearibus obtusis: subtus convexis, caule ramoso: ramis deflexis*”, the provenance “ad Astracanam”, the symbol for annual growth form, and the two references “Hort. ups. 55”, and “Buxb. Cent. 1, p. 21, t. 31, f. 1” with “*Chenopodium maritimum, foliis sedi teretibus*”. In the first reference, he used a phrase very similar to the later diagnosis (“*Chenopodium foliis linearibus planis obtusis, caule ramoso, ramis deflexis*”), and again Buxbaum was cited. The full phrase of Buxbaum is “Est kali parvum hirsutum [!] J. B. Fructus fert Chenopodii instar in singula folii ala singulum, tota planta glauca est”. The related figure shows a glabrous plant with highly succulent, obtuse leaves, single axillary flowers and flexuous, partly pendent (obviously a wilting effect), upper branches. These data conflict with all *Suaeda* species of section *Brezia* because these are always glabrous and the axillary clusters contain at least three flowers. Furthermore, *Suaeda salsa* and their closer relatives have acute to subacute leaves. Instead, the characters given by Linnaeus and Buxbaum apply to *Bassia hirsuta* (L.) Asch., which occurs in “Species Plantarum” as 20 *Chenopodium hirsutum*, just after *C. salsum* and also grows in the surroundings of Astrakhan. In view of this confusion, a rejection of the Linnaean *Chenopodium salsum* seemed to be appropriate.

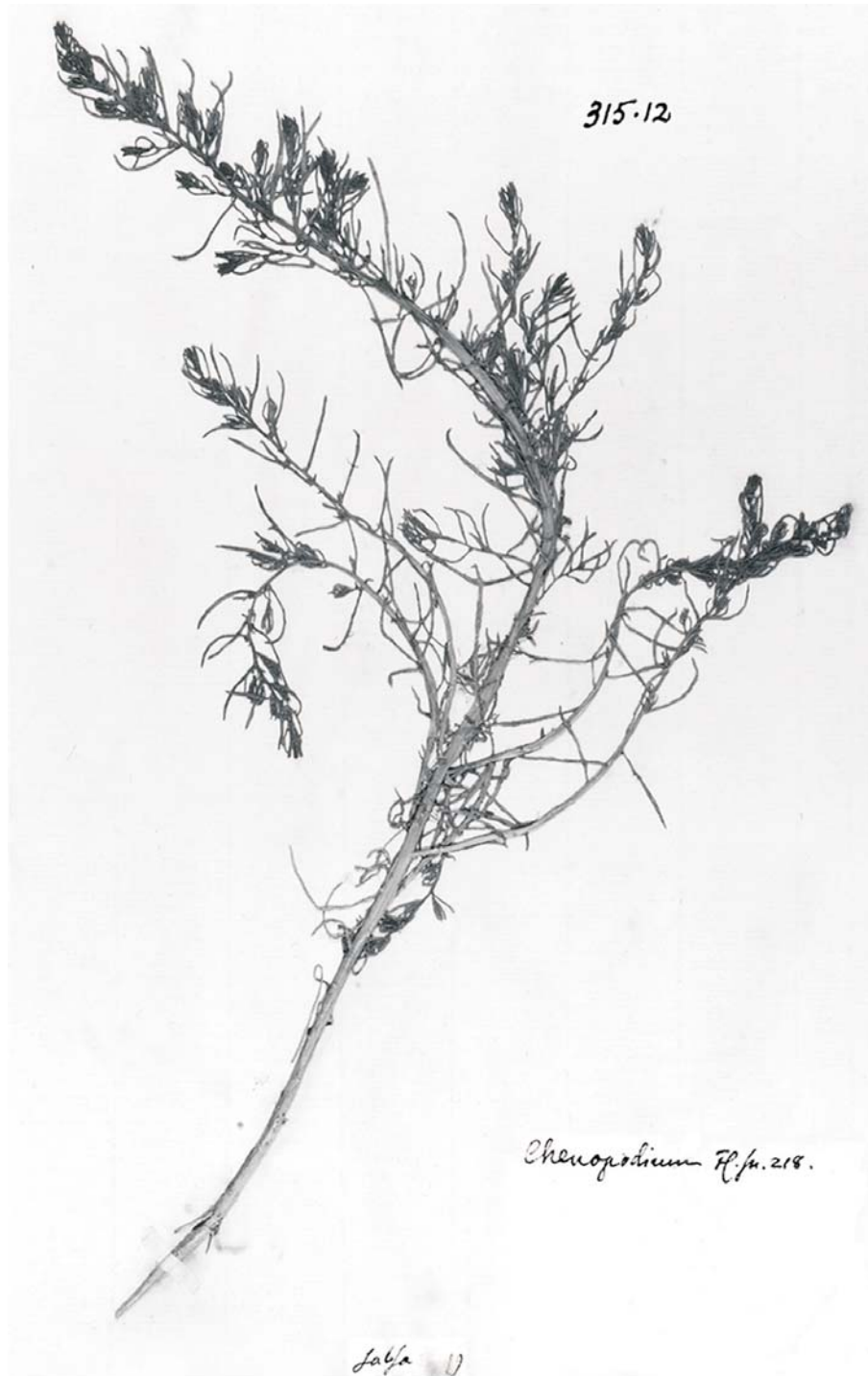


Fig. 3. Lectotype of *Chenopodium salsum* L. (LINN 315.12). – Photograph by the Linnean Herbarium.

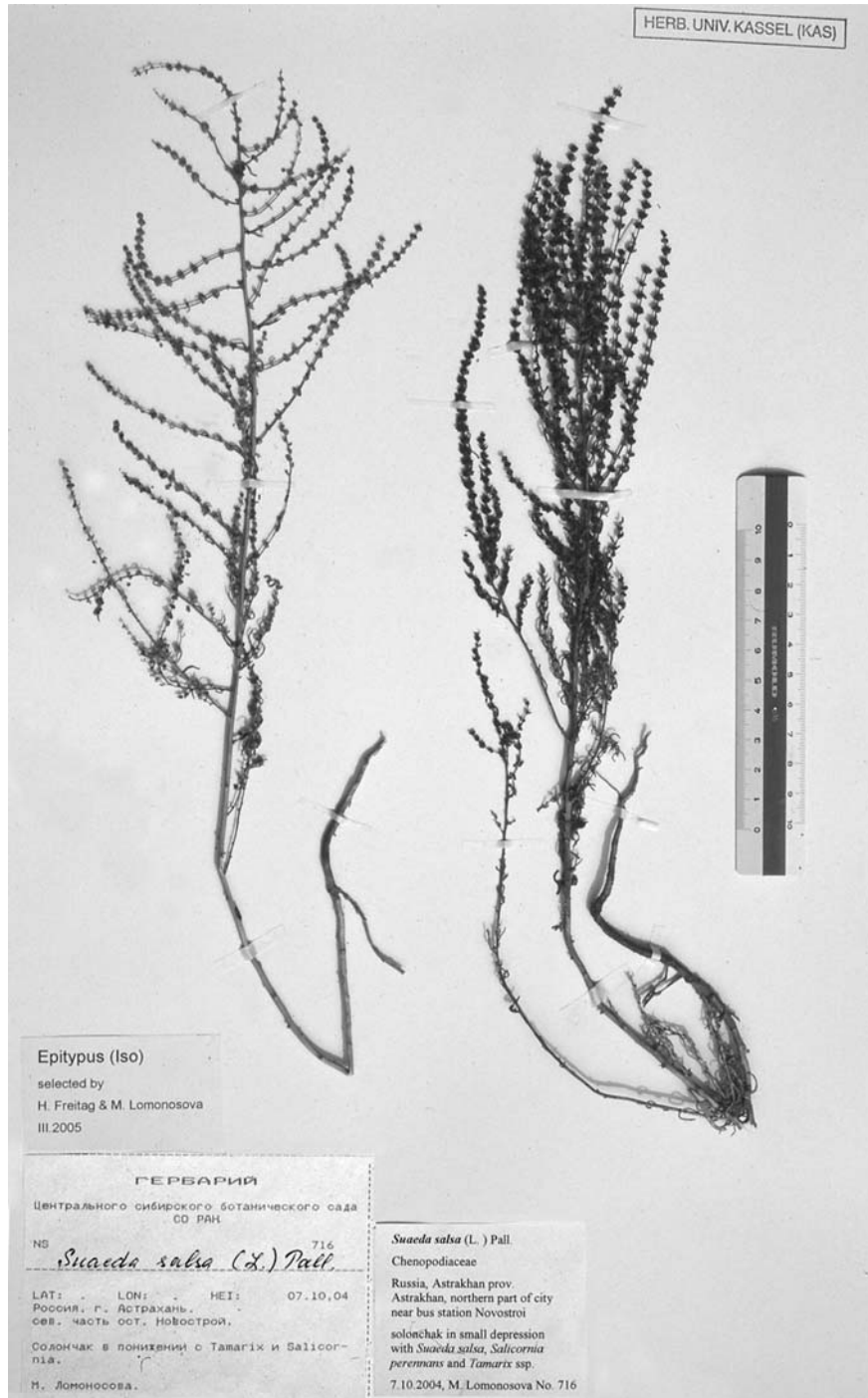


Fig. 4. Isoepitype of *Suaeda salsa* (L.) Pall., M. Lomonosova 716 (KAS). – The left plant is thinned out by shedding most of the ripe fruits. – Photograph by H. Freitag.

However, during our search for original material in the Linnaean Herbarium we found the sheet 315.12, which perfectly fits *Suaeda salsa* in the circumscription of Pallas (1803). The specimen is annotated by Linnaeus as “*Chenopodium salsum* 19”. As this number corresponds to the entry in “Species Plantarum”, the specimen represents an original element of *C. salsum*. It is chosen here as lectotype. The sheet carries an additional label “*Chenopodium* Fl. Su. 218”, probably in Loeffling’s handwriting. That label number refers to the entry in “Flora Suecica” (Linnaeus 1745) and suggests that the specimen should be associated with *C. maritimum* L., which is listed as no. 16 in “Species Plantarum” and the only *Suaeda* species occurring in Sweden. However, the latter label must have been attached to this sheet in error because it contradicts Linnaeus’s annotation and most likely has nothing to do with the plant mounted on it. Savage (1945) questioned that the specimen would have come from Loeffling, and this is also unlikely because it would imply a provenance from Spain where *S. salsa* does not occur.

The specimen of sheet 315.12 was probably not collected in Astrakhan as the protologue suggests, but taken from cultivation in the Uppsala Botanic Garden. This can be concluded from the remark in Hort. Ups. “Habitat ad Astracan. Hospitatur sub dio, annua”. Probably it has been grown from seeds collected near Astrakhan either by J. J. Lerche or J. F. Gmelin. The lectotype consists of one young plant (25 cm) that had just started flowering, so that diagnostically important characters as the shape of the inflorescence/infructescence and of the fruiting perianth are not yet developed. However, the long, narrow leaves and the comparatively short internodes distinguish the specimen clearly from the closely related *Suaeda maritima* L. The plant has a few drooping branches, like in the figure in Buxbaum and in agreement with the diagnosis. The early phenological stage represented by the lectotype seems also significant. As a species of the SE European and S Siberian steppe and semidesert areas, *S. salsa* requires higher temperatures and stronger insolation than *S. maritima*. From our cultivation in central Germany we concluded that *S. salsa* is unable to complete its life cycle in an average Scandinavian summer. There is another specimen of *S. salsa* preserved in the Linnaean herbarium of Stockholm, with an added annotation “*Chenopodina salsa* Moq.” by an unknown hand. It has an almost identical appearance (sheet 110.13) and may have come from the same cultivation, but is without any annotation by Linnaeus.

Another strong argument for maintaining Linnaeus’s name is the early correction of his contradictory concept. In the second (1762) and almost unchanged third edition (1764: 324) of “Species Plantarum”, *Chenopodium salsum* was treated as *Salsola salsa*, but in Syst. Nat. 2: 312. 1767 Linnaeus changed the diagnosis to “herbacea erectiuscula, fol. linearibus subcarnosis muticis, calyc. succulentis diaphanis” and added an extended description. Pallas (1771: 420) was the first to express doubt about its classification in *Salsola*. Willdenow (1797: 1312-1313), who gave an enlarged but still ambiguous description, obviously became aware of Linnaeus’ mistake and recognized the close affinity of *S. salsa* to *S. maritima*. He omitted the wrong description of the leaf apex and added the new statement “flores axillares, sessiles, terni”, which excludes *Bassia*; nevertheless, he still quoted the Buxbaum reference.

Pallas (1803) transferred Linnaeus’ *Salsola salsa* to *Suaeda* with a diagnosis and description fitting the specimen 315.12. The diagnosis reads: “S. biennis multicaulis ascendens ramosa, foliis hemicylindricis acutis, floribus glomeratis, glomerulis distantibus”. Pallas cited *S. salsa* as a most common species on saline localities from Europe to Siberia. He explicitly excludes the Buxbaum reference but wrongly cited *Salsola spicata* Willd. as a synonym, a W Mediterranean species somewhat similar in habit to *Suaeda salsa*. There are several indications that Pallas also mixed up other species with *S. salsa*, e.g., the plant figured on t. 39 associated with Pallas’ description, which looks very much like *S. altissima* (L.) Pall. by its branching pattern (compare t. 42), density of inflorescence and length of bracts. Fortunately, the four specimens of Pallas’ collection preserved in LE are correctly identified by himself.

Considering the juvenile stage of the lectotype, we recognized the need to select an epitype to serve as an interpretative type. The first candidates for epitypification would have been the Pallas specimens, but they also lack fruits or have been collected far from the type locality. Therefore the second author collected new material with abundant duplicates near the type locality to serve that purpose.

Up to now, the species is completely or partly confused both with *Suaeda crassifolia* and *S. prostrata*. For differentiation, see Table 1.

Suaeda prostrata Pall., Ill. Pl.: 55, t. 47. 1803

Lectotype (designated here): [icon] Pall., Ill. Pl.: t. 47. – Epitype (designated here): SE European Russia, Saratov prov., Yeruslan river valley near Dyakovka, c. 7 km below mouth of river Solyanka, alkaline meadows, in eroded patches with *Camphorosma songorica* community, 27.9.1996, H. Freitag 28312 (KAS; isoeatypes: B, C, E, G, JE, K, KAS, LD, LE, MHA, MW, NS, TK, W).

= *Schoberia parviflora* Less. in Linnaea 9: 201. 1835 ≡ *Suaeda parviflora* (Less.) Moq., Chenop. Monogr. Enum.: 131. 1840.

Ic. – Fig. 5, 6C, 7C.

Notes on the typification. – The diagnosis, description and figure of Pallas are very precise and leave no doubt about the identity of *Suaeda prostrata*. The most unequivocal statements are: “... humifusa ramosissima ..., elegantissima et tenera species ...; caules prostrati, in plano ramosi ...; flores minutissimi, grano papaveris minores”. The species is reported only from “circa rivum Solenka [Solyanka] in Jeruslan fluv. tendentem, et inter fortalitia Zarizyn [Volgograd] et Tschernojarsk”. Because we did not find any original material, and as the illustration does not show the essential flower and fruit characters, we recollected the species near the first locality and design the material here as epitype.

Later authors determined individuals of *Suaeda prostrata* usually correctly but extended the species concept to include a large part of the variation of *S. salsa*. Today, we know that *S. prostrata* often also grows as a somewhat bushy or even erect plant, especially in denser vegetation. Stunted or impoverished specimens of *S. corniculata* and juvenile prostrate forms of *S. salsa* sometimes look similar. However, the former are unmistakable by their unequal and variously horned fruiting perianth, whereas the latter differ by longer internodes in the inflorescence, more numerous and larger flowers per cluster, and larger seeds.

Notes on the synonymy. – The type material of *Schoberia parviflora* is probably lost. However, because so many characters of *Suaeda prostrata* are cited in the description, inclusion in the latter species seems justified (“Annuā, ramosissima Flores ... minutissimi, terni in axillis bractearum singulārum glomerati iisque multo supercoti ... Folia pellucido-mucronulata”).

3.2. On the history of the nomenclatural confusion

The confusion about naming the three taxa started with Meyer (1829), who defined his *Schoberia salsa* with two characters highly diagnostic for *Suaeda crassifolia*, viz “foliis semicylindricis obtusiusculis, seminibus laevibus” (p. 401). He referred both to Linnaeus and Pallas despite the conflicting descriptions. Besides, he recognized *Schoberia maritima* with the description “... foliis acutis ... seminibus punctulatis”, which fits Pallas’ *S. salsa*. This double misnaming was followed by many Russian authors.

Moquin-Tandon (1831) listed *Suaeda crassifolia*, *S. salsa* and *S. prostrata* under “unknown or doubtful species”. Regarding *S. salsa*, he described the problem of conflicting concepts but finally followed Meyer (1829) in distinguishing *S. salsa* from *S. maritima* by the same characters (leaves obtuse, seeds almost smooth). Later, Moquin-Tandon (1840) transferred *S. crassifolia* to *Echinopsilon* (= *Bassia*) and many authors including Iljin (1936) followed him. *S. salsa* was reduced to *S. maritima* β *salsa*, which differs from the type variety by “foliis saepius obtusiusculis, fructibus parvulis” (Iljin 1936: 128). He quoted both Linnaeus and Pallas and referred to a specimen collected by Meyer from Loktevsk. Moquin-Tandon referred to it as *Chenopodina salsa* with the description “foliis ... saepius obtusis, ... semine... laeviusculo, nitido” (Moquin-Tandon 1849: 160), based on the same specimen. *S. prostrata* was cited from Pallas and its difference from *S. maritima* questioned.

Fenzl (1851: 785-786) mentioned *Suaeda salsa* with “semine ... nitido, laevissimo, nunc omnino epunctato, nunc marginem versus obsoletissime striolato” and divided it into two variet-

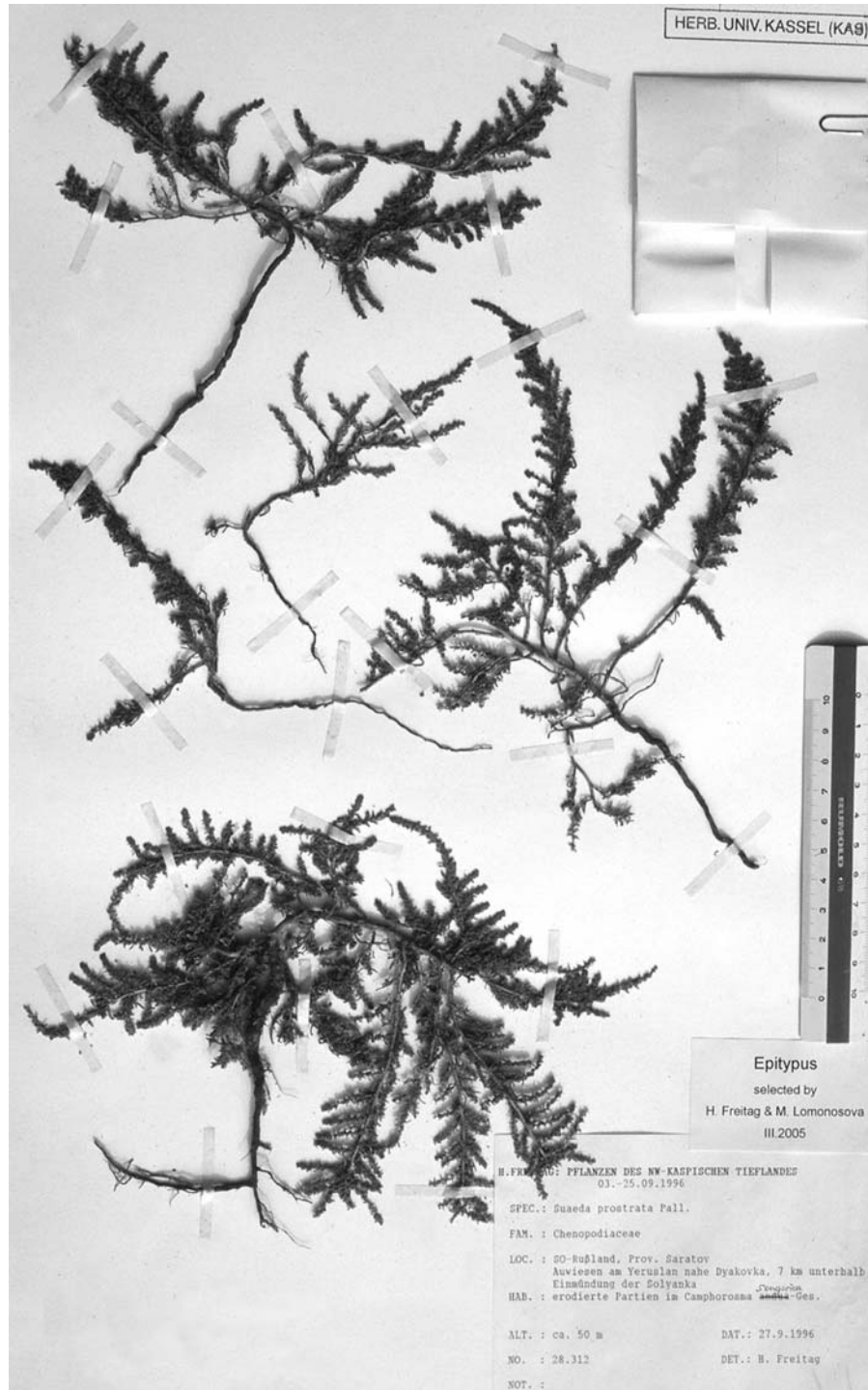


Fig. 5. Epitype of *Suaeda prostrata* Pall., *H. Freitag* 28312 (KAS). – Photograph by H. Freitag.

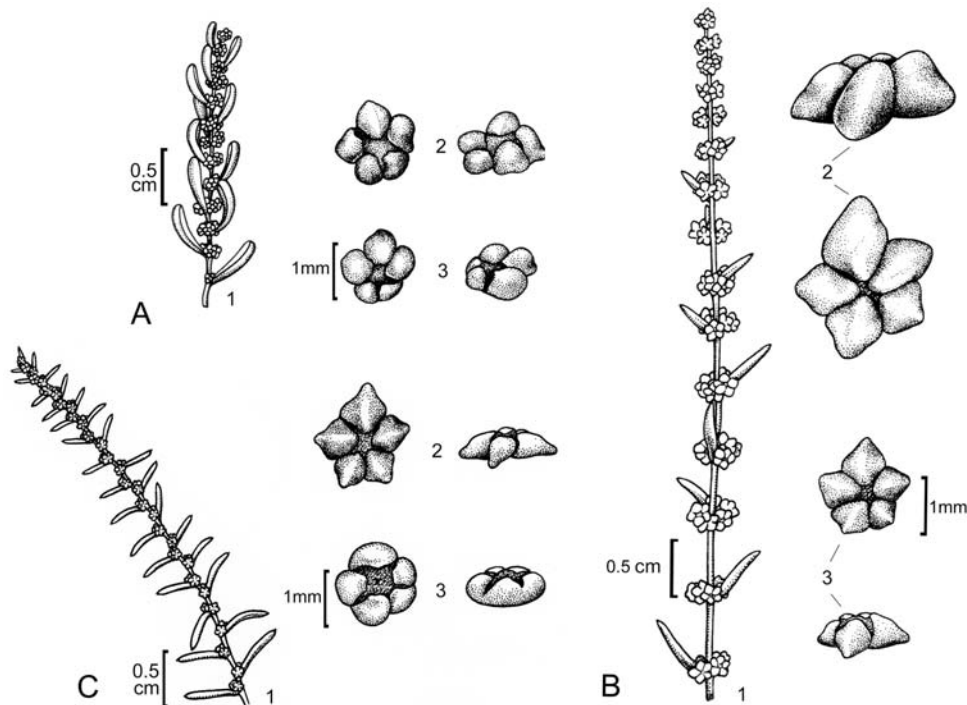


Fig. 6. Fruiting branches and fruits (with tepals) of *Suaeda* – A: *S. crassifolia* (Turkmenistan, island Cheleken, 4.10.1928, E. Bobrov 2169, LE); B: *S. salsa* (M. Lomonosova 716, NS); C: *S. prostrata* (H. Freitag 28312, NS). – 1 = fruiting branch, 2 = brown-seeded fruits, 3 = black-seeded fruits. – Drawing by N. Prijdak.

ies, viz α *crassifolia*: “foliis carnosis majoribus ad minimum $\frac{3}{4}$ lin., plerumque 1-1½ lin. latis obtusis”, and β *angustifolia*: “foliis caulinis majoribus $\frac{1}{2}$ lin. vix crassioribus”. From these descriptions, Fenzl’s corresponding determinations (in LE) and distribution data, it becomes clear that the first variety is identical with *S. crassifolia*, whereas the identity of the second (no specimens in LE) remains obscure. He also described *S. maritima* sensu Meyer with “semina ... concentric punctato-striato”, which corresponds to *S. salsa*, and added that only cultivation experiments will give clear evidence if *S. salsa* and *S. maritima* are different species.

Bunge (1852) also contributed to the confusion. In the key on p. 464 he mentioned for some species including *Schoberia salsa* “semina laevissima ... folia obtusa semicylindrica linearia” (p. 288). In addition, he described *Schoberia obtusifolia* with “folia ... basi parum attenuata, superne crassiora, omnia obtusissima ... semina ... nitido-nigra, vix tenuissime rugulosa, fere omnino laevia”. As earlier authors, he considered *S. crassifolia* Pall. to belong to *Kochia hirsuta* (L.) Nolte (= *Bassia hirsuta*) which obviously refers to Linnaeus’ mistake in the protologue of *S. salsa* but not to the description of Pallas. *S. prostrata* does not appear in the account. Later Bunge maintained *S. salsa* and *S. maritima* in the sense of Meyer and Fenzl. In addition, he explicitly excluded the description of Pallas with the remark “ad *Suaedam corniculatam* spectante” (Bunge 1879: 428-429) and added in a comment on *S. corniculata* “Vix credible hanc speciem tam late diffusam et haud infrequentem oculatissimum Pallasium effugisse, qui sine ulla dubitatione illam sub nomine *S. salsae* describit” (p. 429).

Iljin recognized only *Suaeda maritima* for SE European Russia, including “*S. salsa* ex parte” but, from the description of the seeds as “distinctly flattened, with acute borders and distinctly reticulate” (Iljin 1930: 198), it becomes clear that he meant the real *S. salsa*. Later, in Flora SSSR (Iljin 1936) he changed his view. On the one hand, he recognized that *S. maritima* is restricted to

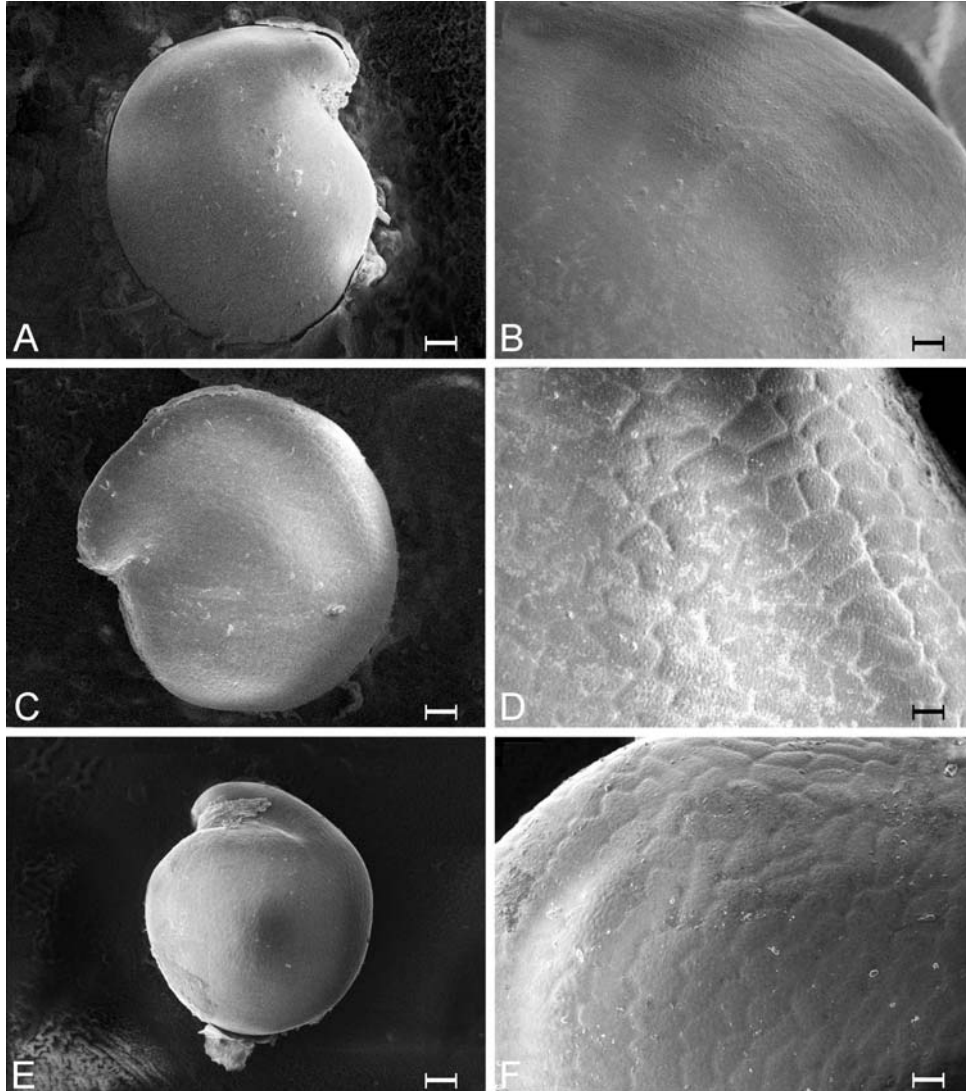


Fig. 7. SEM photographs of *Suaeda* seeds – A-B: *S. crassifolia* (from the lectotype); C-D: *S. salsa* (from the epitype); E-F: *S. prostrata* (from the epitype). – Scale bars A, C, E = 100 μ m, B, D, F = 20 μ m; photographs by M. Lomonosova and Y. Lukjanov.

the shores of the Baltic Sea, but on the other hand he returned to Meyer's misapplication of the name *S. salsa* to plants that belong to *S. crassifolia* ("seeds obscurely reticulate, leaves obtuse, plants conspicuously glaucous"). Furthermore, he revived the name *S. drepanophylla* and used it for some specimens that differ from his *S. salsa* by "fruiting perianth with unequal corniculate outgrowths" (see above for evaluation of that character). Unfortunately, he even added a new concept of *S. prostrata*, which embraced all continental populations of his former *S. maritima*. In fact, *S. prostrata* sensu Iljin includes both *S. prostrata* and *S. salsa*. Iljin's concept of these species is clearly illustrated (Iljin 1936: t. 9) and his account became most influential, almost all *Chenopodiaceae* authors of the former Soviet Union having followed his treatment.

Grubov (1966) was the first who returned to the correct use of the name *Suaeda crassifolia* and included both *S. obtusifolia* and *S. drepanophylla* as synonyms of it. He also mentioned *S. salsa*, but combined it with *S. heteroptera* Kitag., a species described from Manchuria and also widely distributed in Central Asia and SE Siberia.

Several later accounts followed Grubov (1966) with regard to *Suaeda crassifolia* (Soskov 1968, Pratov 1972), but in most of them the confusion of the three species persisted (e.g., Skripnik 1987, Lomonosova 1992, Tzvelev 1996). This also holds true for the Flora of Iran (Akhani & Podlech 1997). In contrast, in the Flora of Turkey, Aellen (1967) listed only *S. prostrata* (correctly identified), confirmed by Freitag (2000).

3.3. Delimitation of *Suaeda crassifolia*, *S. salsa* and *S. prostrata*

Table 1 gives the differentiating characters, supplemented by Fig. 6 and 7, referring to the populations of the Aralo-Caspian and SW Siberian areas. In adjacent areas deviating populations exist, which also differ somewhat in molecular respect (see, e.g., the position of the different accessions of *Suaeda salsa* and *S. prostrata* in Fig. 1). However, the molecular trees in Schütze & al. (2003a) fully support the species rank of the three taxa discussed here as well as of *S.*

Table 1. Diagnostic characters of the treated *Suaeda* species, applicable to well-developed plants from the Aralo-Caspian region and SW Siberia.

	<i>S. crassifolia</i>	<i>S. salsa</i>	<i>S. prostrata</i>
Size [cm]	(5-)15-30(-50)	(5-)15-40(-75)	(2-)5-10(-20)
Growth form	usually erect	usually erect	usually prostrate
Plant colour	glaucous	greyish green	bright to yellowish green
Branching	loose, paniculate	loose, paniculate	dense, usually feathery
Leaves and bracts			
succulence	very high	usually moderate	low to moderate
apex	obtuse	acutish to acute	apiculate
bundle arrangement	peripheral, in u-shaped semicircle	median, in slightly curved plane	median, in slightly curved plane
Flowers per cluster	usually 3-7(-9)	usually 5-9(-11)	usually 3
Seed ¹ surface			
reticulation ²	+	++	+++
punctulation	0	++	+++
brightness	+++	++	+
flattening	moderate	strong	strong
length [mm] ³	0.9-1.1 (<i>n</i> = 10)	1.0-1.4 (<i>n</i> = 29)	0.8-1.0 (<i>n</i> = 10)
Geographical distribution	NE Black Sea coast to SW Iran and C China	Pannonian lowlands to SW Siberia	Pannonian lowlands to SE Siberia
Biome	semidesert	forest steppe and northern steppe	steppe and northern semidesert
Chromosome number	$2n = 18^4$	$2n = 36^5$	$2n = 18^6$

¹ The data refer to regular seeds which are clearly lens-shaped, furnished with perisperm and a hard, blackish testa; be careful to avoid the larger, disc-shaped seeds lacking perisperm and with a thin, brownish testa; for seed ornamentation see also fig. 6.

² The reticulate pattern is caused by the \pm sunken anticlinal walls of the testa cells, the punctulation is shown when the centre of the testa cells is distinctly arched.

³ Mean values from *n* seeds per sample.

⁴ Sources: Ebrahimzadeh & al. (1994), Lomonosova & al. (2003), one original count by M. Lomonosova.

⁵ Sources: three original counts by H. Freitag and 46 counts by M. Lomonosova.

⁶ Sources: Lomonosova & al. (2001, 2003), three original counts by H. Freitag and nine by M. Lomonosova.

maritima and *S. corniculata*, two related species which are likewise involved in the nomenclatural history of the three species. *S. maritima* is related to *S. salsa* and differs mainly by wider leaves and bracts, much longer internodes, and by its W to Central European distribution (coasts of the N Atlantic, North Sea, Baltic Sea, N and central Germany). *S. corniculata*, being sympatric with the species dealt with, belongs to a different clade in *S. sect. Brezia* and can be easily recognized by its strongly unequal tepals, even in buds. In fruiting stage, one or more tepals carry conspicuous horn-like outgrowths at the apex and unequal short wing-like outgrowths near the base. The other two *Suaeda* species of the area belonging to *S. sect. Brezia*, viz *S. heterophylla* (Kar. & Kir.) Bunge and *S. kossinskyi* Iljin, are characterized by distinct wings while the apical parts of the tepals remain unchanged in the first species and enlarge somewhat vertically in the second. We refrain from presenting a key to all species of *S. sect. Brezia* awaiting the results of ongoing studies which will include the definition of at least one new species from the area ("*Suaeda elegans*" in Fig. 1).

It should be noted that the confusion is not restricted to the three *Suaeda* species treated here. In particular in LE we found many sheets of *S. salsa* misidentified, even by reputed experts, as *S. acuminata* (C. A. Mey.) Moq. In habit and in leaf shape, both species often look alike. However, as a member of *S. sect. Schoberia* the latter can be recognized by a number of distinct characters: (1) leaves of dried specimens white-margined, resulting from a peculiar C₄ leaf anatomy (*Schoberia* type, see Schütze & al. 2003a); (2) styles three, long, arising from a central depression in the collar-like top of the ovary; (3) seeds smooth, shiny and almost globular.

Acknowledgements

We are most thankful to the curators of the herbaria AA, ALTB, BM, K, LE, MHA, MW, NS, P, TASH, TK and W for the opportunity to study their material and to have specimens on loan. Particular thanks are due to Dr Charlie Jarvis, Natural History Museum London, for his advice in evaluating specimens in the Linnean Herbarium and providing the photograph of LINN 315.12, and to Peter Schütze, Kassel, for modifying the molecular tree of *Suaeda sect. Brezia*. We are also indebted to Ms N. Pridak for the drawings, and to Ms Hage and Ms Müller for processing photographs. With gratitude, we acknowledge linguistic suggestions by Ian Hedge, Royal Botanic Garden Edinburgh, and valuable comments by two unknown reviewers. Finally, we are most thankful to the Deutsche Forschungsgemeinschaft (DFG) for financial support to the first author, which allowed field work in Kazakhstan (1992, grant Fr 438.111/16/92), in the Caspian Lowland (1998, grant Fr 222/14-1), in Uzbekistan (2000, grant We 1830/2-1), in S Siberia (2003, grant We 1830/2-3) and herbarium visits (1994, grant Fr 220/10-1), and to the RFBR for financial support to the second author (2005, grant 05-04-48778).

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