



Restoration of *Suaeda* sect. *Helicilla* (Chenopodiaceae) and typification of its related taxa

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Abstract

Suaeda glauca is separated off from sect. *Schanginia* and classified in the revived monotypic sect. *Helicilla*. Morphologically it is characterized by dimorphic fruits and seeds, with the fruits bearing flat seeds being strongly carinate and obconical, and the sub-spherical seeds of the globular fruits having a prominent honeycomb-like pattern caused by sunken lines above the anticlinal cell walls of the testa which are bordered by distinct narrow ridges that are unique in *Suaeda*. The separate position of *S. glauca* is also clearly confirmed in the ITS and the combined *atpB-rbcL* / *psbB-psbH* trees. For nomenclatural purposes, the synonymous names *S. stauntonii* and *Helicilla altissima* are lectotypified, while the typification of *Salsola asparagoides* is corrected. Finally the inclusion of sect. *Macrosuaeda* into sect. *Salsina* is advocated.

Key words: nomenclature, lectotypification, phylogeny

Introduction

Based on phylogenetic studies by Schütze *et al.* (2003), Kapralov *et al.* (2006) and Schütze (2011), the traditional classifications of genus *Suaeda* Forsskål ex J.F. Gmelin (1776: 797) (Suaedeae, Suaeodoideae, Chenopodiaceae Vent. / Amaranthaceae Juss. *sensu* APG (1998: 549) and APG IV (2016) as more recently modified by Schenk & Ferren (2001) had somewhat changed. Currently, *Suaeda* is subdivided into the subgenera *Brezia* (Moquin-Tandon 1849: 167) Freitag & Schütze (2003: 282) with the single section *Brezia* (Moquin-Tandon 1849: 167) Volkens (1893: 80) and *Suaeda* with the sections *Borszczowia* (Bunge 1878: 643) Freitag & Schütze (2003: 283), *Schanginia* (Meyer 1829: 394) Volkens (1893: 80), *Suaeda*, *Salsina* Moquin-Tandon (1840: 121), *Physophora* Iljin (1936a: 44), *Schoberia* (Meyer 1829: 395) Volkens (1893: 80) and *Alexandra* (Bunge 1843: 120) Kapralov, Akhani & Roalson (2006: 582) (see Fig. 1). In addition, more recently also sect. *Macrosuaeda* Tzvelev (1993: 84) was separated from *Salsina*. However, so far not all species were included in the ongoing molecular analyses, and not all taxonomic conclusions were drawn.

Suaeda glauca (Bunge 1833: 56) Bunge (1879: 362) is traditionally placed in sect. *Schanginia* subsect. *Spermacocca* Iljin (1936a: 44) together with *S. linifolia* Pallas (1803: 47) and *S. paradoxa* Bunge (Bunge 1852: 462) (Bunge 1880: 427). The subsection was defined as having solitary or clustered flowers usually borne on the petiole of bracts at some distance from the axil, and by the often prominently granular seeds. Schenk & Ferren (2001) restricted the section *Schanginia* to these three species, and so they were listed in Schütze *et al.* (2003) who did not include *S. glauca* into their sampling. The molecular analyses of nuclear rDNA ITS and of plastid *psbB-psbH* sequences by Lee *et al.* (2007) were the first who detected that *S. glauca* forms a separate and well supported clade. That was confirmed by Schütze (2011) who used the same markers and in addition also *atpB-rbcL* sequences, as well as by Kucev and Brandt (unpublished data). Schütze (2011: 114) informally suggested that *S. glauca* should be placed in a section of its own based on molecular data, its peculiar leaves and pistil morphology that clearly separate it from the more closely related sects. *Brezia* and *Schanginia*. The separate position of *S. glauca* was also corroborated in comparative studies of seed micromorphology by Lomonosova (2009). Subsequently Lomonosova (2012: 104) placed *S. glauca* provisionally in the new section “*Glaucæ*” (*nom. inval.*, Art. 36.1c). But so far all taxonomists dealing with the sectional subdivision of *Suaeda* overlooked the fact that Baillon (1887: 195) had already established the section *Helicilla* (Moquin-Tandon 1849: 169) Baillon just to fit *S. glauca* though with arguments which do not hold up.

In this study, we combine all the available evidence in favour of a separate position of *S. glauca*, discuss the re-establishment of the forgotten sect. *Helicilla*, provide an improved diagnosis, and lectotypify the synonyms of *S. glauca*, viz. *S. stantonii* Moquin-Tandon (1840: 131) and *Helicilla altissima* Moq. in Candolle (1849: 170). Furthermore, we discuss the inclusion of sect. *Macrosuaeda* into sect. *Salsina*.

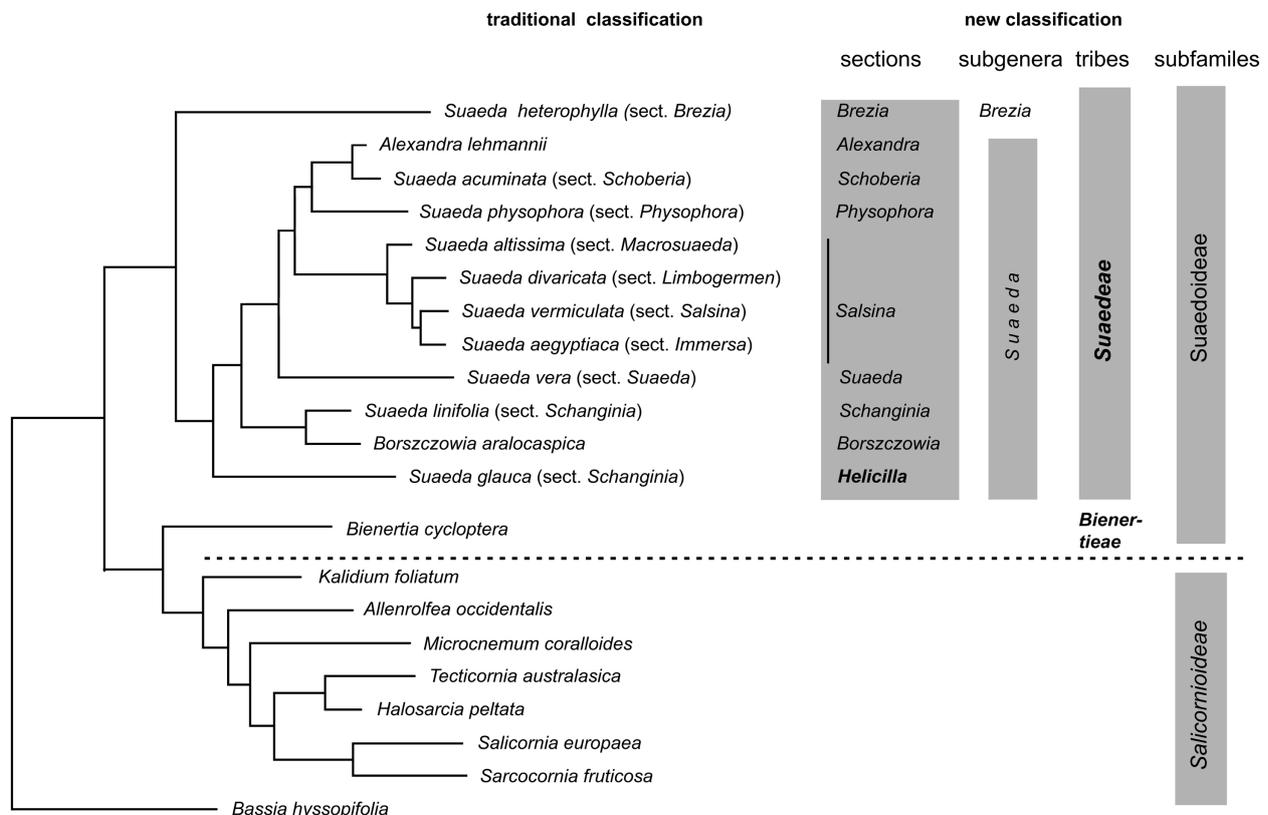


FIGURE 1. Abbreviated ITS maximum likelihood tree of Suaedoideae / Salicornioideae including key species of the different sections, based on Schütze *et al.* (2003), Kapralov *et al.* (2006) and Schütze (2011). Tree computed by R. Brandt.

Material and methods

In addition to the literature data, morphology and distribution of *Suaeda glauca* were studied based on herbarium material preserved in KAS, LE, MHA, MW, TK, P, and VLA (acronyms according to Thiers 2017+), as well as by field studies conducted in Russian Far East (by ML) and in South Korea (by HF). Leaf anatomy was checked by manual cuts as described in Freitag & Kadereit (2014). Concerning the stem anatomy, routine manual cuts were made and photographed without staining under microscope Axioscop 40 (Carl Zeiss). SEM micrographs from the seed surface were taken by scanning electron microscope LEO 420 (Carl Zeiss). The data obtained through these studies were checked against species of the most closely related sects. *Schanginia* and *Brezia*. The original molecular trees were compared and an abbreviated ITS tree was generated based on data of Schütze *et al.* (2003), Lee *et al.* (2007) and Schütze (2011), taken from GenBank.

Results

Morphological data

Suaeda glauca is a stiffy erect annual of 20–100 cm growing along sandy and pebbly shores of the Sea of Japan in the Primorye province of Russian Far East (Fig. 2A) around the Korean Peninsula (Fig. 2 B) and around the Honshu island of Japan, as well as in interior salt-marshes of SE-Siberia, E- and S-Mongolia and E-China. For the first time we provide a distribution map covering all these areas (Fig. 3E). Most morphological data as given in *Flora*



FIGURE 2. *Suaeda glauca*. **A.** Habitat on sandy shore of the Sea of Japan, Southern Primoriye (Russian Far East), the species grows scattered among the predominant *Phragmites australis* var. *humilis* (De Not) Tzvelev. **B.** Habit and habitat (sandy pockets among lava rocks) near Seogwipo, Jeju island (S Korea). **C.** Flowering branch, note the carinate tepals; from greenhouse in Novosibirsk. **D.** Fruiting branches, note strongly carinate, flattened fruits bearing disc-shaped seeds; from Southern Primoriye. **E.** Cross section of stem. **F.** Cross section of a leaf. Photos by H. Freitag (B, F); M. Lomonosova (A, C, E); molbiol.ru (D).

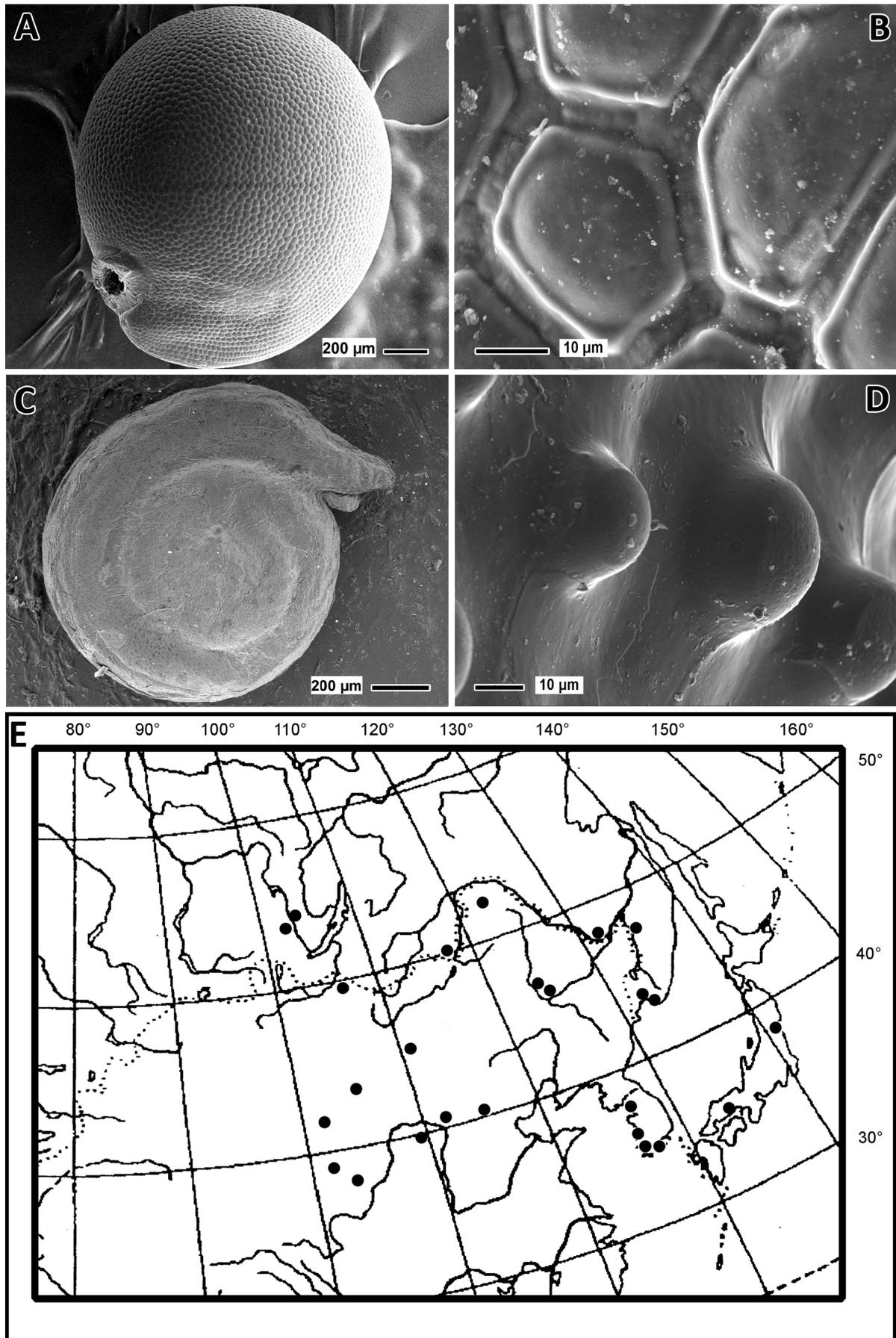


FIGURE 3. *Suaeda glauca*, SEM micrographs. **A.** A regular, sub-spherical seed. **B.** Detail of seed coat. **C.** An irregular, disc-shaped seed. **D.** *S. linifolia*, detail of seed coat. **E.** *S. glauca*, distribution map: Most Chinese records from Qin Hai-Ning & Ma Ke-Ping (2016). Photos and map by M. Lomonosova.

U.S.S.R. (Iljin 1936b), *Plantae Asiae Centralis* (Grubov 1966, 2000), *Flora of China* (Zhu *et al.* 2003) and *Flora of Japan* (Clemants 2006) are confirmed. However, several traits were not studied in detail so far or not fully used for appropriate classification. While in general appearance, in particular by the loose structure of the inflorescence and the solitary or clustered flowers borne not precisely in the axil but usually on the petiole of leaf-like bracts (Fig. 2C–D) it is similar to the two species of sect. *Schanginia*, it differs from them by stem and leaf anatomy, number of stigmas, fruit and seed morphology.

Suaeda glauca displays stems distinctly ribbed with massive strands of collenchyma in the more prominent ridges and chlorenchymatous cortex tissue in between (Fig. 2E). The narrow, linear leaves are biconvex and their mesophyll is subdivided into an outer palisade parenchyma, a central water storage tissue made up of polyhedral cells lacking chloroplasts, and an intermediate tissue of enlarged, radially arranged cells containing few chloroplasts (Fig. 2F). In contrast, the species belonging to the sects. *Brezia* and *Schanginia* the stems do not have that massive collenchymatic ribs and only appear striate by alternating chlorenchymatic and collenchymatic areas in the cortex. Their leaves are wider, less succulent and flattened at least adaxially. A distinct water-storage tissue devoid of chloroplasts might be absent (*Schanginia* type) or present (*Brezia* type of Schütze *et al.* 2003).

The flowers, fruits and seeds of *Suaeda glauca* are prominently dimorphic, even more so than in the related sects. *Brezia* and *Schanginia*. The flowers that produce regular seeds possess a more or less cupular perianth with a pyriform ovary containing a vertical ovule and topped by two (rarely three) slightly flexuose stigmas, (0.3–)0.5–1.0 mm long, which are densely covered by long papillae. The fruits are almost spherical and enclose subglobose seeds which are 1.5–2.0 mm in diameter. Their surface looks delicately granular under a loupe (Fig. 3A) but the SEM reveals a prominently reticulate, honeycomb-like pattern unique in *Suaeda* and described as *Glauca* type by Lomonosova (2009). It shows a very clear network of pentagonal or hexagonal units caused by sunken lines above the anticlinal cell walls of the seed coat which are bordered by distinct narrow ridges, while the area above the periclinal walls is slightly bulging and smooth (Fig. 3B).

The flowers and fruits bearing irregular seeds obconic in shape, with prominently carinate tepals giving them a stellate appearance when seen from the flattened top (Fig. 2C, and D). The stigmas are shorter, stiff and spreading (Fig. 2C). The seeds are flat, disc-shaped, also about 1.5–2.0 mm in diameter and equipped with a thin, smooth, brownish testa (Fig. 3C). The sect. *Schanginia* has similar regular flowers and fruits, but the ovary is globular and carries three stigmas. The seeds also correspond in shape and size, but their surface is completely different: the course of the anticlinal wall is not marked, and the periclinal walls show one prominent semi-globular, papilla-like bulge restricted just to the central part of the cell surface (Fig. 3D). This pattern was described by Lomonosova (2009) as *Schanginia* type. In *Brezia* the regular flowers and fruits are plate-like to saucer-shaped. They include a depressed ovary topped by two stigmas, and finally a lens-shaped seed with a seed coat that shows an indistinct reticulate pattern, and is clearly sculptured on the surface of the slightly bulged periclinal cell wall areas, named *Brezia* type by Lomonosova (2009).

Molecular data

All the molecular trees cited in the introduction, which were generated from nuclear and chloroplast sequences, agree in placing *S. glauca* as the first branch following the *Brezia* clade and being sister to all other lineages of *Suaedaeae*, with the sects. *Schanginia* and *Borszczowia* at the next split being sisters to all other sections. We abstain here from reproducing one of the rather large trees (e.g. with 50 species of *Suaedoideae* in Schütze 2011). Instead, we give an abbreviated phylogenetic tree based on ITS sequences from GenBank. We used a selection of key species representing all currently known sections of *Suaeda*. Thereby, our tree (Fig. 1) reflects the current classification and in addition it indicates the separate and well-resolved branch formed by *S. glauca*. It should be emphasized, that in the original trees the relevant species are represented by more or less numerous samples, e.g., up to eight from *S. glauca* in Lee *et al.* (2007). Furthermore, we want to emphasize that most likely no other species of the *Glauca* clade is to be expected because the wider area is well collected, and *S. stauntonii* from China as well as *S. asparagoides* (Miquel 1866: 194) Makino (1894: 382) as defined in the Japanese literature are synonyms of *S. glauca* only (see below).

Taxonomic treatment

The data obtained from literature and from our morphological studies, and in particular the phylogenetic trees resulting from nuclear and chloroplast sequences (Lee *et al.* 2007, Schütze 2011, our Fig. 1) clearly indicate the separate position of *Suaeda glauca* from the sect. *Schanginia*. They do not only justify but beyond they require its recognition as representative of a section differing from sect. *Schanginia* in order to have all sections of *Suaeda* monophyletic.

Here we restore the name *Helicilla* which was proposed by Moquin-Tandon (1849) to accommodate his *S. stauntonii*, a taxon identical with *S. glauca*. By error *Helicilla* was originally placed as a genus under *Salsoleae* but afterwards transferred by Baillon (1887) as section to *Suaeda* with the slightly changed diagnosis (“*floribus omnino Schoberiae in spicas terminales lateralesque graciles dispositis, in axilla bractearum minorum solitariis v. 2, 3-nis; bracteoles minutis 2; embryonis horizontalis spiralis (viridis) radícula laterali*”). As these attributes are either not specific for *S. glauca* or even inaccurate (position of flowers), below an improved diagnosis is given.

Suaeda* sect. *Helicilla (Moq.) Baillon in Baillon (1887: 195).

≡ *Helicilla* Moquin-Tandon (1849: 169).

Type:—*Suaeda glauca* (Bunge) Bunge

– “*Suaeda* sect. *Glaucæ*” in Freitag & Lomonosova (2012: 104), *nom. inval.* (Art. 36.1c).

Improved diagnosis:—The sect. *Helicilla* differs from the similar sect. *Schanginia* by stems with marked collenchymatic ridges, leaves being narrow, biconvex and containing distinct water-storage mesophyll, flowers with usually 2 stigmas, irregular fruits which are apically flattened and strongly carinate, and regular (spherical) seeds having a prominently reticulate seed coat pattern attributable to sunken lines above the anticlinal cell walls aligned with narrow ridges. Also the nuclear ITS and plastid *psbB-psbH* and *atpB-rbcL* sequences widely deviate.

Species richness:—A monotypic section.

Suaeda glauca (Bunge) Bunge (1879: 362) ≡ *Schoberia glauca* Bunge (1833: 56) ≡ *Chenopodina glauca* Moquin-Tandon (1849: 162).

Lectotype (designated by Lomonosova & Freitag 2011: 226):—CHINA. Chin. bor., 1831, *Bunge s.n.* (LE!).

= *Suaeda stauntonii* Moquin-Tandon (1840: 131) ≡ *Helicilla altissima* Moquin-Tandon (1849: 170), *nom. illeg. et superfl.* (Arts. 52.1, and 52.2).

Lectotype (designated here):—CHINA. G. Staunton, Pl. Sinensis *ex itin.* [sine loco] (FI-017377!, see also Fig. 4; image available at parlatore.msn.unifi.it/types/search.php); isolectotype P-00799028!, image available at https://plants.jstor.org/search?filter=name&so=ps_group_by_genus_species+asc&Query=Suaeda+stauntonii).

= *Salsola asparagoides* Miquel (1866: 194) ≡ *Schoberia maritima* (Linnaeus (1753: 221) C.A. Meyer (1829: 400) var. *asparagoides* Franchet & Savatier (1879: 470) ≡ *Suaeda asparagoides* (Miq.) Makino (1894: 382).

Lectotype (see Ohba *et al.* 2005: 43)¹:—JAPON. *Japonia* [sine loco] (L-0329072!); isotype (L-9329072, image available at https://plants.jstor.org/search?filter=free_text&so=ps_group_by_genus_species+asc&Query=%28Salsola+asparagoides).

Phylogenetic relationship:—According to the phylogenetic trees cited in the introduction, the monotypic sect. *Helicilla* has the most basal position in subg. *Suaeda*. In the chronogram of Schütze (2011) it branched off from subg. *Brezia* already in the late Oligocene, between 24.5 and 26.7 mya. Probably, the predominant presence of two stigmas can be interpreted as a plesiomorphic trait because it is shared by the numerous species of subg. *Brezia* and the monotypic *Bienertia* placed at the base of *Suaeda*, while the most closely related sects. *Schanginia* and *Borszczowia* as all other more derived clades of *Suaeda* have three (or more) stigmas.

Comments and typification of synonyms:—The type material of *Suaeda stauntonii* is represented by fragments of branches carrying the unique and unmistakable star-like irregular fruits borne on the bract petioles. *S. stauntonii* was later raised by Moquin-Tandon (1849) to the monotypic genus *Helicilla* and named *H. altissima*, by overtaking the specific epithet from the first incorrect identification of the specimen by Dryander as *Salsola altissima* L. [≡ *Suaeda altissima* (L.) Pall.]. However, though stating that in habit and attributes it somewhat (*paululum*) resembles to *Suaeda* (*Schoberia*), he erroneously placed the new genus in *Salsoleae* because he was not aware yet that horizontally coiled and thereby *Salsola*-like seeds also occur in some groups of *Suaeda*. The genus *Helicilla* was still maintained by Ulbrich (1934) though Baillon (1887) had already restored it to *Suaeda*. Iljin (1936b) recognized that it is identical with *S. glauca*.

1 Ohba *et al.* (2005: 43) designated the L specimen as the holotype. However Miquel (1866: 194) did not define a holotype. According to the Art. 9.9, Ohba’s statement has to be corrected and interpreted as a lectotypification.

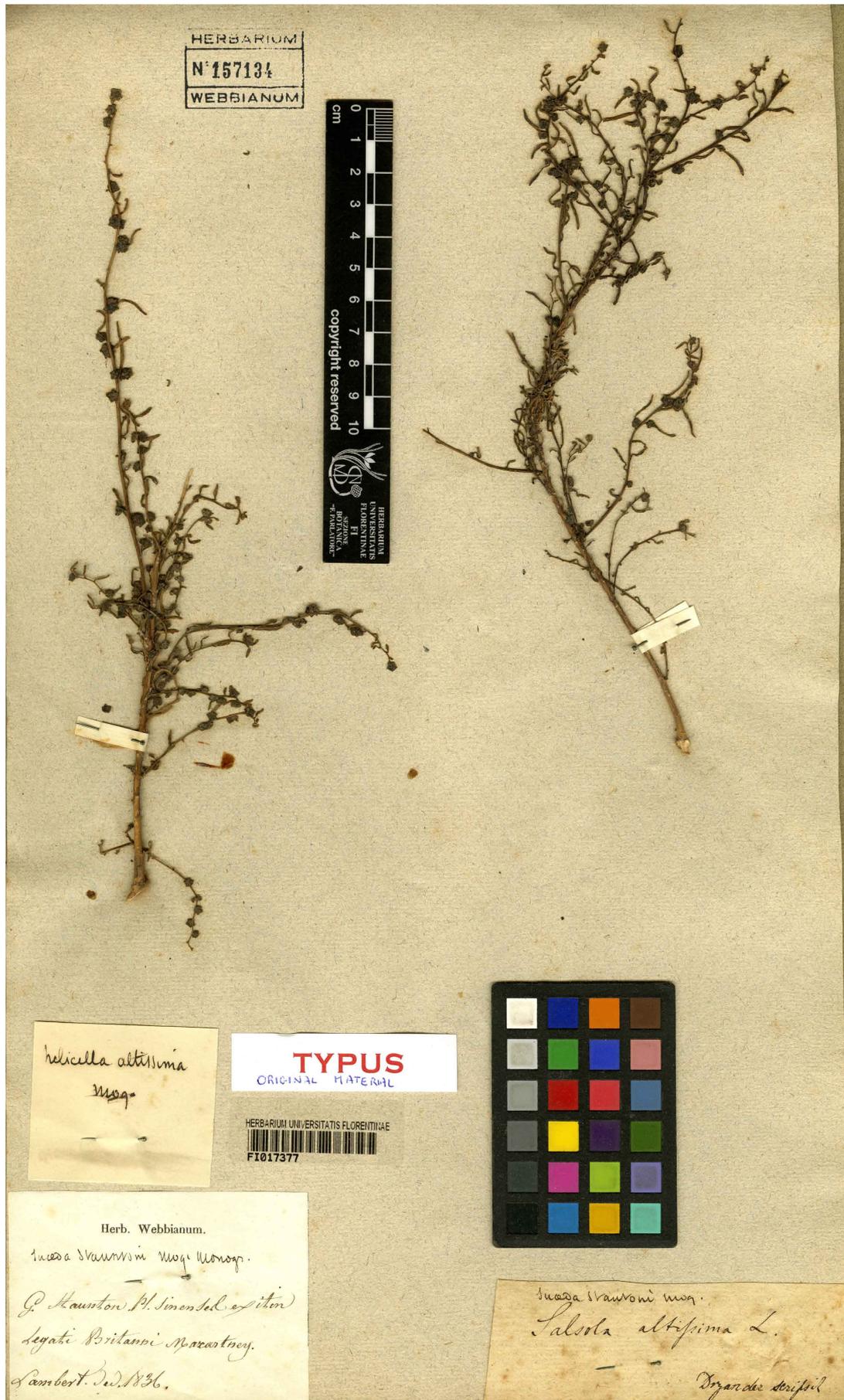


FIGURE 4. Lectotype of *Suaeda stauntonii* Moq., Herbarium Firenze (FI-017377, herb. Webb no. 157134). Photo by courtesy of the Herbarium Firenze.

Concerning *Suaeda stauntonii*², we traced two specimens at FI and P, which are part of the original material. Both these specimens are labeled as types, but any effective publication was found and the typification is necessary. The sheet at FI (code 017377, Herb. Webb ; Fig. 4) contains two fruiting branches which are 27.5 and 22.5 cm long, respectively. The two labels bear on the sheet report the name *Suaeda stauntoni*. The oldest label (bottom-right of the sheet) reads as “*Salsola altissima* L. / Dryander *scripsit*“ that agrees with the protologue (Dryander was the curator of the Banks herbarium). The second label, from Herb. Webbianum (bottom-left of the sheet), reads as “G. Staunton Pl. Sinenses ex itin / Legati Britannici Macartney. / Lambert ded. 1836”. The Stauntons (father George Leonard and son George Thomas) took part in Lord Macartneys mission to China in 1792. Since no location is given on the label, the specimen must have been collected either around a former capital of the Xia dynasty in central eastern China (in today’s Shaanxi or Henan provinces), or on the way from or to the British embassy in Beijing. A third label reports the name *Helicilla altissima* only (Moquin’s hand), indicating that he had seen the specimen a second time.

The sheet at P is made up of 3 branchlets 10–13 cm long and contains three labels. The oldest (left-side, middle) is an abbreviated compilation of the data given on the labels in FI, but without a note from Moquin’s hand. The second label (left-side, bottom), from the Herbarium Moquinianum, reads as “*Helicilla altissima* Moq. [in his handwriting] / *Salsola altissima* Linn. non / Chine / Staunton”. The third label contains rough sketches of a flower, ovule, anther, ovary and a horizontally coiled seed (most likely drawn by Moquin) with the notes “*embryo cochleatus* “ and “[unreadable]...*annulose*”.

Preference as lectotype is given to the FI specimen because it is much larger and contains the name *Suaeda stauntoni* in Moquin’s handwriting. Comparison of the plants and the labels indicate that most likely the branchlets of the P specimens were separated from the FI specimen after the description of *S. stauntoni*. The drawing and the note of the horizontal seed were later added on the P specimen because in the protologue of *S. stauntoni* (sic!, non *stauntonii*) the seed shape was explicitly left open. A 3 cm long fragment likewise belonging to the original material of *S. stauntonii* was found by HF in P (herb. Bunge) in a capsule attached to the isotype of *S. glauca*.

As regards the name *Helicilla altissima*³, the ticketed drawings on the P specimen indicate that they were used for the description of *Helicilla altissima*, while Moquin-Tandon probably only later added his replacement name to the FI specimen. Nevertheless, as he cited the earlier *Suaeda stauntonii* as synonym, according to Art. 7.4 of ICN (McNeill *et al.* 2012) *Helicilla altissima* is typified by the type of the replaced synonym *Suaeda stauntonii*. Moreover the name *Helicilla altissima* is superfluous and illegitimate according to Arts. 52.1, and 52.2 of ICN.

Comment on *Suaeda* sect. *Macrosuaeda* Tzvelev:—The name *Macrosuaeda* was proposed by Tzvelev (1993: 83) including a single species, *S. altissima*, and the diagnosis “*Plantae annuae, vulgo magnae. Folia subfiliformia. Glomerulae et bractae in pedunculis brevissimis positae (“extraaxillares”). Perianthium ad demidiam coalescens*”. This section was accepted by Schenk & Ferren (2001) and Kapralov *et al.* (2006), however already included in sect. *Salsina* by Schütze *et al.* (2003) where it takes a well supported position at the base of the *Fruticosa* subclade in their cp and ITS trees. Morphologically, the traits cited by Tzvelev also occur in other species of sect. *Salsina*, e.g., the annual habit in *S. aegyptiaca* (Hasselquist 1757: 460) Zohary (1957: 635) and *S. arcuata* Bunge (1852: 461), and the extraaxillary position of flower clusters in *S. asphaltica* (Boissier 1853: 98) Boissier (1879: 938), and in *S. microphylla* Pallas (1803: 52) beside of the species of sect. *Schanginia*. Thus they indicate that both traits have originated several times. Obviously by the presence of these conspicuous traits the *S. glauca* material of Miquel was at first inaccurately identified by Dryander as *S. altissima*. Consequently, we argue once again for including *Macrosuaeda* in sect. *Salsina*.

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2 Moquin-Tandon (1840: 131) validly published the name *Salsola stauntonii*, also listing as synonym “*Salsola altissima* Dryander! *Mss. in herb. Staunton* (V.s. in herb., Webb)”. Since the latter name was firstly published by Moquin-Tandon (l.c.) but placed as synonym, it is invalid (Art. 36.1c).

3 Moquin-Tandon (1849: 170) validly published the name *Helicilla altissima*, also listing as synonym “*Salsola altissima* Dryander! *mss. in herb. Lamb.*”. Since the latter name was firstly published by Moquin-Tandon (l.c.) but placed as synonym, it is invalid (Art. 36.1c).

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References

- APG (1998) An ordinal classification for the families of flowering plants. *Annals of the Missouri Botanical Garden* 85: 531–553.
<https://doi.org/10.2307/2992015>
- APG IV (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* 181: 1–20.
- Baillon, H.E. (1887) *Histoire des plantes, vol. 9*. Librairie Hachette, Paris, 491 pp.
- Boissier, E. (1853) *Diagnoses plantarum orientalium novarum, sér. 1, vol. 2(12)*. Published by the author, Geneva, 115 pp.
- Boissier, E. (1879) *Flora Orientalis, vol. 4*. H. Georg, Basel & Genève, 1276 pp.
- Bunge, A.A. (1833) *Enumeratio plantarum, quas in China boreali collegit Dr Al. Bunge anno 1831*. Without place, 73 pp.
- Bunge, A.A. (1843) Novum genus Chenopodearum. *Linnaea* 17: 120.
- Bunge, A.A. (1852) Beitrag zur Kenntnis der Flora Russlands und der Steppen Central-Asiens. *Mémoires de l'académie impériale des sciences de St.-Petersbourg, Divers Savants* 7: 177–535.
- Bunge, A.A. (1878) *Salsolacearum novarum in Turkestania indigenarum descriptiones. Trudy Imperatorskago S.-Peterburgskago Botanicheskago Sada* 5: 642–646.
- Bunge, A.A. (1879) Enumeratio *Salsolacearum* omnium in Mongolia hucusque collectarum. *Bulletin de l'académie impériale des sciences de Saint-Petersbourg, Sér. 3* 25: 349–371.
- Bunge A.A. (1880) Enumeratio *Salsolacearum* centrasiatricarum. *Acta Horti Petropolitani* 6 (2): 403–459.
- Clemants, S.E. (2006) Chenopodiaceae Vent. In: Iwatsuki, K., Boufford, D.E. & H. Ohba (Eds.) *Flora of Japan, vol. 2a*. Kodansha, Tokyo, pp. 211–222.
- Franchet, A. & Savatier, L. (1879) *Enumeratio plantarum in Japonia sponte crescentium, vol. 1*. F. Avy, Paris, 789 pp.
- Freitag H. & Kadereit G. (2014) C₃ and C₄ leaf anatomy types in Camphorosmeae (Camphorosmoideae, Chenopodiaceae). *Plant Systematics and Evolution* 300: 665–687.
<https://doi.org/10.1007/s00606-013-0912-9>
- Gmelin, J.F. (1776) *Onomatologia botanica complete, oder vollständiges botanisches Wörterbuch, vol. 8*. J.F. Gaum, Frankfurt & Leipzig, 856 pp.
- Grubov, V.I. (1966) *Plantae Asiae Centralis, vol. 2*. Izdatel'stvo Akademii Nauk, Moskva/Leningrad. 134 pp.
- Grubov, V.I. (2000) *Plantae Asiae Centralis, vol. 2*. Science Publishers Plymbridge House, Plymouth, 164 pp.
- Hasselquist, F. (1757) *Fredric Hasselquists Iter Palaestinum eller resa til hetil heliga landet, foerraetad ifr an ar 1749 til 1752*. Salvi, Stockholm, 619 pp.
- Iljin, M.M. (1936a) On the systematics of genus *Suaeda* Forssk. and tribe Suaedeae Rchb. *Sovetskaya Botanika* 5: 39–49. [in Russian]
- Iljin, M. (1936b) *Suaedeae*. In: Komarov, V.L. (Ed.) *Flora U.S.S.R., vol. 6*. Izdatel'stvo Akademii Nauk, Moskva/Leningrad, pp. 174–200.
- Kapralov, M.V., Akhani, H., Voznesenskaya, E.V., Edwards, G., Franceschi, V. & Roalson, E.H. (2006) Phylogenetic relationships in the Salicornioideae / Suaedoideae / Salsoloideae s.l. (Chenopodiaceae) clade and clarification of the phylogenetic position of *Bienertia* and *Alexandra* using multiple DNA sequence datasets. *Systematic Botany* 31 (3): 571–585.
- Lee, J.-S., Park, D.S., Ihm, B.-S. & Lee, W.J. (2007) Taxonomic reappraisal on *Suaeda australis* (Chenopodiaceae) in Korea based on the morphological and molecular characteristics. *Journal of Plant Biology* 50 (6): 605–614.
<https://doi.org/10.1007/BF03030603>
- Linnaeus, C. (1753) *Species plantarum, vol. 1*. L. Salvi, Stockholm, 560 pp.
- Lomonosova, M.N. (2009) Morphology and ultrastructure of the seed surface in the subfamily *Suaedoideae* (Chenopodiaceae). *Botanicheskii Zhurnal* 94 (5): 736–744.
- Lomonosova, M.N. (2012) *Chenopodiaceae* Vent. In: Baikov, K.S. (Ed.) *Conspectus florum Rossiae Asiaticae: plantae vasculares*, Izdatel'stvo Sibirskogo otdeleniya Rossiiskoi akademii nauk, Novosibirsk, pp. 90–104.
- Lomonosova, M. & Freitag, H. (2011) Typification of plant names in *Suaedoideae* (Chenopodiaceae) published by P. Pallas, C. A. Meyer and A. Bunge. *Willdenowia* 41 (2): 217–229.
- Makino, T. (1894) Miscellaneous notes on the plants of “Yôjôshô-oku”. *Botanical Magazine (Tokyo)* 8: 377–383. [in Japanese]
- McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, Greuter, D.L., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prud'homme van Reine, W.F., Smith, G.F., Wiersema, J.H. & Turland, N.J. (2012) *International Code of Nomenclature for algae*,

- fungi, and plants (Melbourne Code)*. [Regnum Vegetabile 154.] Koeltz Scientific Books, Königstein.
- Meyer, C.A. (1829) Chenopodeae. In: Ledebour C.F. (Ed.) *Flora Altaica, vol. 1*. G. Reimer, Berlin, pp. 370–417.
- Miquel, F.A.W. (1866) *Annales musei botanici lugduno-batavi, vol. 2, 7*. Van der Post, Amsterdam, pp. 181–212.
- Moquin-Tandon, A. (1840) *Chenopodearum monographica enumeratio*. Loss, Paris, 183 pp.
- Moquin-Tandon, A. (1849) Salsolaceae [Chenopodiaceae]. In: Candolle, A. (Ed.) *Prodromus systematis naturalis regni vegetabilis, vol. 13(2)*. Typ. Masson, Paris, pp. 43–219.
- Ohba, H., Akiyama, S. & Thijsse, G. (2005) Miquel's new taxa of the vascular plants described from Japan in Prolusio Florae Japonicae and some other works. *Bulletin, university museum, university of Tokyo* 41: 43.
- Pallas, P.S. (1803) *Illustrationes plantarum imperfecte vel nondum cognitarum, cum centuria iconum*. G. Martini, Lipsiae, 68 pp. + 59 tab.
- Qin, H.-N. & Ma, K.-P. (2016) *Chinese Virtual Herbarium(CVH). A National Taxonomic Database*. Available from: www.codata.info/06conf/abstracts/K2/QINHaining.htm (accessed 12 January 2017)
- Schenk, H.J. & Ferren, W.R. (2001) On the sectional nomenclature of *Suaeda* (Chenopodiaceae). *Taxon* 50 (3): 857–873.
<https://doi.org/10.2307/1223715>
- Schütze, P. (2011) *Molekulare Systematik der Gattung Suaeda (Chenopodiaceae) und Evolution des C₄-Photosynthesesyndroms*. Thesis Kassel University. Available from: <https://kobra.bibliothek.uni-kassel.de/bitstream/urn:nbn:de:hebis:34-2011121940085/3/DissertationPeterSchuetze.pdf> (accessed 20 October 2016)
- Schütze, P., Freitag, H. & Weising, K. (2003) An integrated molecular and morphological study of the subfamily *Suaedoideae* Ulbr. (Chenopodiaceae). *Plant Systematics and Evolution* 239: 257–286.
<https://doi.org/10.1007/s00606-003-0013-2>
- Thiers, B. (2017) [continuously updated] *Index herbariorum: A global directory of public herbaria and associated staff*. New York Botanical Garden, Bronx, NY. Available from: <http://sweetgum.nybg.org/science/ih/> (accessed 26 October 2016)
- Tzvelev, N.N. (1993) Notes on Chenopodiaceae of Eastern Europe. *Ukrains'kyi Botanichnyj Zhurnal* 50: 78–85.
- Ulbrich, E. (1934) Chenopodiaceae. In: Engler, A. & Prantl, K. (Eds.) *Die natürlichen Pflanzenfamilien ed. 2, vol. 16c*. Engelmann, Leipzig, pp. 379–584.
- Volkens, G. (1893) Chenopodiaceae. In: Engler, A. & Prantl, K. (Eds.) *Die natürlichen Pflanzenfamilien ed. 1, Teil 3, Abt. 1a*. Engelmann, Leipzig, pp. 36–91.
- Zhu, Gelin, Mosyakin, S.L. & Clemants, S.E. (2003) Chenopodiaceae Vent. In: Wu, Z.Y. & Raven, P. (Eds.) *Flora of China, vol. 5*. Science Press, Beijing and Missouri Botanical Garden Press, St. Louis, pp. 351–414.
- Zohary, M. (1957) A contribution to the flora of Saudi Arabia. *The Journal of the Linnean Society of London, Botany* 55: 632–643.
<https://doi.org/10.1111/j.1095-8339.1957.tb00026.x>