A taxonomic nightmare comes true: phylogeny and biogeography of glassworts (*Salicornia* L., Chenopodiaceae)

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In this study we analysed ETS sequence data of 164 accessions belonging to 31 taxa of *Salicornia*, a widespread, hygrohalophytic genus of succulent, annual herbs of Chenopodiaceae subfam. Salicornioideae, to investigate phylogenetic and biogeographical patterns and hypothesise about the processes that shaped them. Furthermore, our aim was to understand the reasons for the notorious taxonomic difficulties in *Salicornia*. *Salicornia* probably originated during the Miocene somewhere between the Mediterranean and Central Asia from within the perennial *Sarcocornia* and started to diversify during Late Pliocene/Early Pleistocene. The climatic deterioration and landscape-evolution caused by orogenetic processes probably favoured the evolution and initial diversification of this annual, strongly inbreeding lineage from the perennial *Sarcocornia* that shows only very limited frost tolerance. The further diversification of *Salicornia* was promoted by at least five intercontinental dispersal events (2× to South Africa, at least 3× to North America) and at least two independent polyploidization events resulting in rapidly expanding tetraploid lineages, both of which are able to grow in lower belts of the saltmarshes than their diploid relatives. The diploid lineages of *Salicornia* also show rapid and effective range expansion resulting in both widespread genotypes and multiple genotypes in a given area. Reproductive isolation through geographical isolation after dispersal, inbreeding, and comparatively young age might be responsible for the large number of only weakly differentiated lineages. The sequence data show that the taxonomic confusion in *Salicornia* has two major reasons: (1) in the absence of a global revision and the presence of high phenotypic plasticity, the same widespread genotypes having been given different names in different regions, and (2) striking morphological parallelism and weak morphological differentiation led to the misapplication of the same name to different genotypes in one region.

KEYWORDS: annual habit, diversification, ecological and morphological parallelism, inbreeding, Miocene, Pleistocene, polyploidization

INTRODUCTION

Among botanists in temperate regions of the northern hemisphere, *Salicornia* L. (glasswort, saltwort, samphire) is well-known for two reasons: firstly, because of its unusual appearance with succulent, apparently articulated and leafless stems and branches (Fig. 1) and flowers aggregated in dense terminal, spike-like thyrses (Fig. 2), and secondly because of its notoriously difficult taxonomy which makes it almost impossible for non-specialists to determine most species, not to mention microspecies, subspecies, varieties and putative hybrids. Frequently the names *Salicornia europaea* or *S. herbacaea* are used in a very broad sense to include most of the species in the genus. This greatly complicates the assignment of published information to taxa of the genus.

According to a molecular phylogenetic study by Kadereit & al. (2006), *Salicornia* is monophyletic and nested within the morphologically and ecologically closely related *Sarcocornia*. *Salicornia* and *Sarcocornia* differ from all other Salicornioideae by seeds that lack perisperm (Ulbrich, 1934; Shepherd & al., 2005). *Salicornia* split from *Sarcocornia* during the Middle Miocene (14.2–9.4 mya), but its extant lineages started to diversify only in the Early Pleistocene (1.4–1.8 mya; Kadereit & al., 2006). The genus is distinguishable from *Sarcocornia* by two characters. These are the annual life form of *Salicornia* versus the perennial life form of *Sarcocornia*, and the flowers forming a characteristic triangle with a larger central and two smaller lateral flowers in *Salicornia* versus being arranged in a horizontal row in *Sarcocornia*.

Salicornia grows in periodically wet saline coastal and inland habitats such as salt marshes, salt lake shores, mud flats and salt pans (Fig. 1). The genus currently comprises ca. 25 to 30 species (Table 1). This is a rough estimate because no general agreement exists on the number of accepted species. *Salicornia* is widely distributed in boreal, temperate and subtropical regions of the northern

Fig. 1. Photo plate illustrating different habitats and species of *Salicornia*. A, B, *Salicornia meyeriana*, South Africa, Western Cape, Overberg, Cape inland salt pans (photo L. Mucina, 5 Apr. 2006); C, D, *S.* aff. *perennans* (chen 865), West Kazakhstan, Kambash lake 30 km E of Small Aral lake (photo W. Wucherer, Oct. 2004); E, F, *S. pojarkovae*, Norway, East Finnmark, Porsanger, Caskilnjarga (photo M. Piirainen, 15 Jul. 1989); G, H, *S. europaea*, Sweden, Gotland, Burgsviken, Näsudden, type locality (photo M. Piirainen, 16. Sep. 1999); I, *S. dolichostachya* comm., Germany, Lower Saxony, Jadebusen, foreland of dike near Varel (photo H. Freitag, Sep. 1996); J, *S. procumbens* (right) with the short-spiked *S. ramosissima* (left), other data as in I; K, L, *S. emerici*, Southeast Turkey, Seyhan prov., lagoon Ömer Gölü, ca. 35 km SE Adana (photo H. Freitag, Oct. 1997).

hemisphere and in South Africa (Figs. 1, 3). It is considered as absent from South America and Australia.

In their treatment of *Salicornia* for *Flora Europaea*, Ball & Akeroyd (1993) pointed out that local accounts can not be correlated either taxonomically or nomenclaturally, even in NW Europe. These taxonomic difficulties have five main reasons:

(1) Paucity of morphological characters. — *Salicornia* has a greatly simplified morphology (Figs. 1, 2). The plants have green, succulent, articulated stems when young, and the leaves and bracts are reduced to small, scarious rims (Fig. 2B–E). Flowers consist of 3–4 fused tepals, (0–)1–2 stamens, an ovary with one ovule and a style that is apically divided into 2–3 stigmatic lobes (Fig. 2A, E). The flowers are sessile and mostly arranged in 3-flowered cymes per bract. The bracts are opposite, connate and the flowers are tightly embedded in cavities of the main axis and partly hidden by the bracts (Fig. 2B–E).

Further fusions within the inflorescence can be observed in the recently described *Salicornia heterantha*. This species shows a total fusion of the tepals of the central flower with the main axis of the inflorescence (Fig. 2C; Beer & Demina, 2005). Reduction of the inflorescence to one flower per cyme can be observed occasionally in a few species (P. Ball, S. Beer, pers. obs.), but this character seems to be genetically fixed in *Salicornia pusilla* (probably identical with *S. disarticulata* (Moss, 1912), *S. uniflora* (Tölken, 1967) and in an unpublished taxon preliminarily called *S. "knysnaensis"* (L. Mucina & G. Kadereit, unpulished data).

This highly reduced leaf and flower morphology provides relatively few taxonomic characters. Some of these are quantitative and applicable only to "well"-grown individuals. Characters traditionally used to delimitate *Salicornia* species are growth form, angle of branching, shape of sterile and fertile segments, length of the inflorescence, shape of bracts, size relation of central and lateral flowers, shape of central flower, anther length and anther dehiscence and occurrence of spirally thickened cells in the cortex (e.g., Ball, 1964; Géhu, 1989; Ball & Akeroyd, 1993; Iberite, 1996; Davy & al., 2001; Ball, 2003; Lahondère, 2004).

(2) Inadequacy of dried material for taxonomic studies. — The difficulties caused by scarcity of diagnostic characters and the importance of quantitative and growth form characters are aggravated by the inadequacy of dried and pressed plant material to represent the details of the succulent growth form of *Salicornia* (Davy & al., 2001; Ball, 2003). In herbarium specimens, some of the diagnostic characters, such as segment shape and length, bract shape and length, relation of central flower to lateral flowers and shape of central flower and anther length are no longer reliably measurable. Fortunately, most *Salicornia* species were described on the basis of fresh material while few *Salicornia* taxonomists worked with herbarium material only. A critical example of the latter is *S. borysthenica* which was described by Tzvelev (1993) on the basis of only one herbarium specimen (Russia, Prov. Cherson, Aleschki, 1901, *N. Egorov s.n.*, LE). The only difference between *S. borysthenica* and *S. dolichostachya* is the length of the anthers. Measurements of this, however, are not strictly comparable in dried and fresh material and anther size is quite variable in *S. dolichostachya* even on one plant and certainly in one population.

If identification keys were based on fresh material, the identification of dried specimens can be very difficult if not impossible. Already Ball & Tutin (1959) stated that to key out *Salicornia* it is necessary to take a sample of ten

Fig. 2. A, central flower of *S. pojarkovae* with simultaneously emerging anther and stigma, cultivated at Botanical Garden (BG) Mainz (photo P. Teege); B, inflorescence of *S. pojarkovae*, cultivated at BG Mainz (photo P. Teege); C, inflorescence of *S. heterantha*, cultivated at BG Mainz (photo P. Teege); D, inflorescence of *S. bigelovii* (chen 896), U.S.A., Massachusetts, South Wellfleet (photo P. Teege); E, inflorescence of *S. perennans* (photo S. Beer).

to twelve individuals from a (homogeneous) population, excluding any damaged or apparently abnormal plants.

(3) Phenotypic plasticity. — The habitats of *Salicornia* are characterized by diurnal and/or seasonal dynamics where duration of submergence, tidal scour, waterlogging and salinity vary locally as well as within or between seasons. Especially salinity fluctuates greatly due to different factors such as tidal cycles, evapotranspiration, precipitation and availability of fresh groundwater. These fluctuations require high physiological plasticity and cause strong phenotypic variation. The latter is also caused by differences in soil texture and nutrient supply (e.g., König, 1960).

It has been indicated that considerable phenotypic plasticity exists in *Salicornia* and that the genetic basis of diagnostic characters has to be tested experimentally (Dalby, 1955; Ball & Tutin, 1959; Langlois & Ungar, 1976; Rozema & al., 1987). Morphometric studies using all phenotypic differences available irrespective of whether they have a genetic basis or not could not reveal distinct taxa even on a small regional scale (Ingrouille & Pearson, 1987; Ingrouille & al., 1990). The density of populations also is important and can vary greatly (Dalby, 1955; Ungar & al., 1979; Jefferies & al., 1981; Beeftink, 1985; Ungar, 1987; Davy & al., 2001). *Salicornia* seeds may accumulate in depressions, below algal mats or around silted mother plants, or remain attached to the buried stems of the mother plants. In dense populations, *Salicornia* – like most plant species – tends to be less branched, remains smaller, has fewer and smaller inflorescences and sometimes larger numbers of sterile segments especially in the shaded, basal branches (G. Kadereit & P. Teege, pers. obs.). In contrast, in open stands and particularly on nutrient-rich places plants tend to be larger, with a more elaborate branching pattern and root system.

Disentangling phenotypic plasticity and genetically determined morphological differences is most difficult without experimental approaches or long-term observations. For example, some diagnostic features such as prostrate growth may disappear in cultivation (Dalby, 1955; Ball & Tutin, 1959). However, transplantation experiments have shown that transplanted individuals normally retain their specific morphology (Jefferies & al., 1981; Davy & Smith, 1985, 1988; Smith, 1985; A. Davy, pers. comm.; H. Freitag, pers. obs.; P. Teege, G. Kadereit & J. Kadereit, unpublished data) indicating the genetic distinctness of certain morphotypes.

However, the identification of stable and genetically determined morphotypes does not automatically imply that these belong to one evolutionary unit. They may well represent several lineages that show morphological parallelism.

(4) Breeding system and hybridization. — Inbreeding seems to play a dominant role in the reproduction of *Salicornia* (Dalby, 1962; Ferguson, 1964). This is more evident in the diploid species studied so far as their anthers usually dehisce before they are exserted, and several individuals in a population have been observed to be entirely cleistogamous (Ball & Tutin, 1959; Ball, 1960, 1964; P. Teege, pers. obs.). In contrast, anthers of tetraploid species normally dehisce after they have been exserted but stigmatic lobes and anthers are always in close contact which makes inbreeding also very likely (Fig. 2A; P. Teege, pers. obs.). Potentially there is a small chance of outbreeding by wind-pollination at least in the slightly protogynous tetraploid taxa (Dalby, 1962; Davy & al., 2001) and maybe through pistillate flowers which can for example be observed in the diploid *Salicornia ramosissima* (P. Ball, pers. obs.).

Population genetic studies using isozymes found individuals of diploid populations to be homozygous while in individuals of tetraploid populations a homozygous and fixed heterozygotic profile has been observed. For both ploidy levels genetic differentiation was observed between groups of populations (Jefferies & Gottlieb, 1982; Wolff & Jefferies, 1987b). In their RFLP analysis of 38 maternal plants and 2,112 F1 progeny, Noble & al. (1992) found no instance of genetic divergence between parent and offspring. These molecular results imply near 100% inbreeding in *Salicornia* which certainly contributes greatly to the taxonomic difficulties in the group by resulting in inbreedings lines with minute but fixed phenotypic differences.

Although the strong inbreeding seems to preclude hybridization, several putative hybrids have been described (e.g., Tölken, 1967; Dalby, 1975; Lahondère, 2004). A prominent example may be *S. pusilla* × *S. ramosissima* which can be identified with some certainty by the occurrence of one, two and three flowers per cyme in one individual and which occurs together with the parents (Dalby, 1975). In no case has the existence of hybrids been clearly verified by molecular evidence. So far two molecular studies (Murakeözy & al., 2007; M. Kaligaric, B. Bohanec, B. Simonovik & N. Sajna, unpublished data) found some molecular evidence for reticulate evolution in *Salicornia* (see below). Probably mainly due to technical problems nobody has succeeded in producing definite hybrids experimentally in *Salicornia* (although two of us, P. Ball and P. Teege, tried hard). However, in many places two or even more species of *Salicornia* grow sympatrically, and often patches of plants or individual plants look odd and seem to represent intermediate morphotypes which can not be clearly assigned to any of the species present.

(5) Regional treatments. — Possibly caused by the difficulties outlined above, a cosmopolitan revision of *Salicornia* has never been published. The large number of regional treatments and flora accounts (Table 1) offer conflicting information, or by accepting only one or two polymorphic species evade the problematic taxonomy of the genus. In most cases the treatments are not comparable because of the inconsistency of the few diagnostic characters available, and uncertainties about the identity of the respective taxa. Additional confusion was caused by authors who are famous for outstanding knowledge of their regional *Salicornia* species, but did not always pay due attention to the rules of botanical nomenclature (e.g., König, 1960; Lahondère, 2004). Therefore, also the attempts to treat the genus over larger areas, as in *Flora Europaea* (Ball & Akeroyd, 1993) could not solve the taxonomic problems. An example to illustrate this problem is material from the English Channel. Depending on which of the keys is considered one ends up with different names for the same specimen. One specimen (P. Teege chen 968, MJG) collected at La Gran Vey (Normandie, France), for example, is keyed out as *S. europaea* subsp. *europaea* (Rothmaler, 2002), *S. europaea* (Stace, 1997), *S. brachystachya* (König, 1960; Lahondère, 2004) and *S. ramosissima* (Ball & Akeroyd, 1993).

There are three regional studies of *Salicornia* that were based on molecular data (Papini & al., 2004; Murakeözy & al., 2007; M. Kaligaric, B. Bohanec, B. Simonovik & N. Sajna, unpublished data). Papini & al. (2004) found that diploid and tetraploid accessions of *Salicornia* resolved as sister clades. The study was based on ITS sequences of twelve samples of *Salicornia* (all but one from Italy) representing four species (three tetraploid, one diploid). Another regional study was done by Murakeözy & al. (2007) investigating *Salicornia* native to the Atlantic coast of France. The 28 populations included were carefully identified as eight different species according to Lahondère (2004) and analysed using sequence data (ITS, cp *trnL-F*, cp *matK*) and RAPD fingerprints. Here also diploid and tetraploid accessions were found to belong to sister clades in the ITS tree. The cp DNA tree, however, showed a conflicting result for two tetraploid accessions (referred to as *S. fragilis*) which were placed among the diploid accessions. Murakeözy & al. (2007) offer hybridization and allopolyploidisation as likely explanation for the conflicting topologies. A similar incongruency between nuclear and cp trees was found in *Salicornia* populations from the Gulf of Trieste (M. Kaligaric, B. Bohanec, B. Simonovik & N. Sajna, unpublished data). This study was based on 14 populations (seven tetraploid, seven diploid), relative nuclear DNA content measured by flow cytometry, a morphometric survey as well as ITS and cp *trnT*-*trnL* spacer sequences. As in the previous two studies, ITS sequences separated the populations according to ploidy level. In this study, however, two diploid samples (referred to as *S. patula*) showed the same *trnT-trnL* spacer sequences as the tetraploid samples again indicating hybridization, albeit with a tetraploid mother.

Aims of this study. — The taxonomic difficulties hamper the formulation of testable hypotheses about phylogenetic relationships and the biogeography of *Salicornia*. The aim of this study is to identify evolutionary units within *Salicornia* using External Transcribed Spacer (ETS) sequence data, to understand the patterns of morphological and geographical diversification, and perhaps to identify the main reasons for the taxonomic difficulties in the genus.

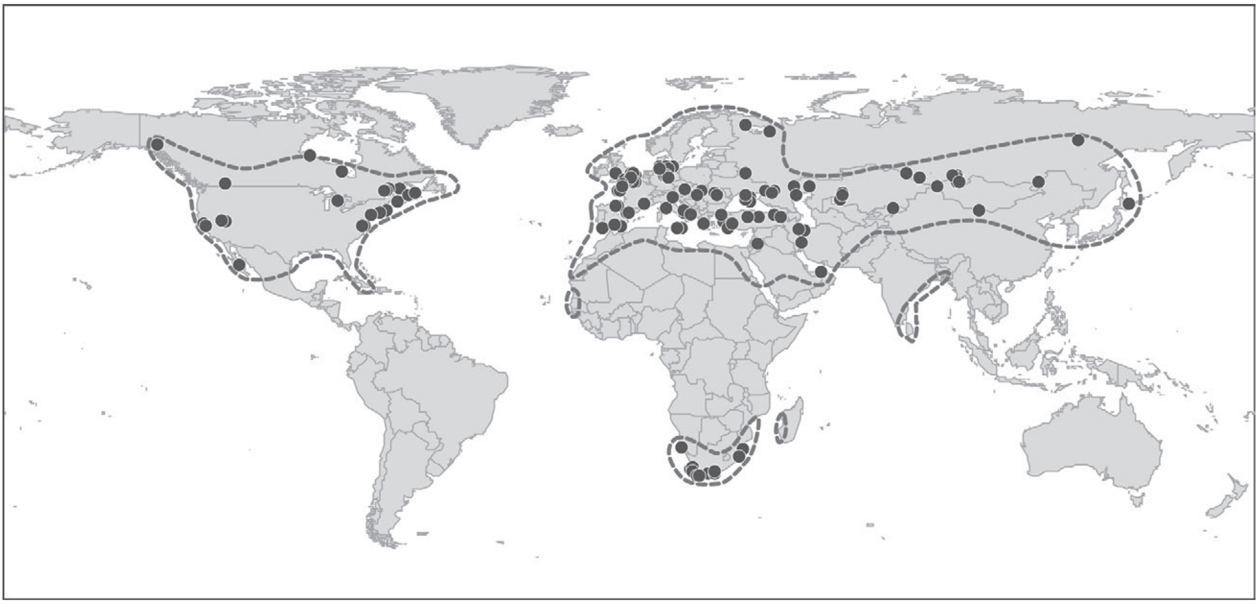

Fig. 3: Distribution map of *Salicornia* with location of accessions included in the ETS analysis.

MATERIAL AND METHODS

Plant material. — Altogether, 164 accessions of *Salicornia* were sampled. The accessions are located throughout the distribution area of *Salicornia* except for North Africa and South Asia (Fig. 3). They include 23 out of a total of ca. 30 recognized taxa, and about 8 putative new species. Some areas are more densely sampled than others, thus reflecting the availability of material. We tried to handle the identification problems by using the most recent treatments of the specific regions (Table 1) as far as they appear to be taxonomically reliable, and our own knowledge which is still fragmentary. It must be emphasised that in many cases the naming remains tentative. Then, we simply added "aff." to the respective species name, or—in case of putative new taxa—by giving them working names which are set in quotation marks. The sampled plant material was of different quality, ranging from living specimens to relatively old herbarium vouchers.

The ingroup sampling also included 17 species of *Sarcocornia* representing the major clades of the genus as found by Kadereit & al. (2006) and two species of the Australian Salicornieae (*Halosarcia indica* and *Tecticornia australasica*) which are sister to the *Salicornia*/*Sarcocornia* lineage. *Microcnemum coralloides* and *Arthrocnemum macrostachyum* served as outgroup (all according to Kadereit & al., 2006).

The taxa sampled, their voucher information and GenBank accession numbers are listed in the Appendix.

DNA isolation, amplification, and sequencing. — Total DNAs were isolated either from fresh parts of the plants (stem and/or inflorescence), with 50–100 mg samples preserved in saturated NaCl-CTAB solution supplemented with 200 mM sodium ascorbate (Thomson, 2002), or silica gel dried material, or herbarium material using ca. 20–50 mg. The plant material was in most cases ground in mortars using liquid nitrogen only rarely with sand directly in the Eppendorf tubes. For DNA extraction the NucleoSpin plant DNA extraction kit (Macherey-Nagel) or DNeasy Plant Mini Kit (QIAGEN) was used following the manufacturers' specifications.

The Internal and External Transcribed Spacers (ITS and ETS) are part of the 18S-5.8S-26S region of the nuclear ribosomal DNA. ETS was choosen in this study because it is known to evolve faster than ITS (e.g., Baldwin & Markos, 1998; Markos & Baldwin, 2002; Linder & al., 2000; Álvarez & Wendel, 2003; Vander Stappen & al., 2003). The resolution within *Salicornia* gained by ITS is rather limited (Papini & al., 2004; Kadereit & al., 2006; Murakeözy & al., 2007). For *Salicornia*, ETS shows ca. thrice as many informative sites as ITS.

The entire IGS (Intergenic Spacer) was amplified with the 18S-II rev (5′-CTC TAA CTG ATT TAA TGA GCC ATT CGC A-3′) and the 26S-II for (5′-TGC AGA CGA CTT AAA TAC GCG ACG GGG T-3′) primers (Ochsmann, 2000) for a few representatives of *Salicornia*. The 25 µl PCR reaction contained the following: 10x Buffer (supplied with the *Taq* polymerase), 2.25 mM $MgCl_2$, 50 pmol forward and reverse primers, 0.6 U *Taq* polymerase. A PTC-100 cycler (MJ Research, Inc., MA, U.S.A.) was programmed as follows: 95°C for 4 min; 30 cycles of 95°C for 30 s, 50.5°C for 45 s, 72°C for 4 min; 50.5°C for 1.2 min, 72°C for 8 min; 4°C forever. With a five-fold diluted 18S-II rev-primer ca. 800 bp of the 3′ ETS-region were sequenced (sequencing reaction and alignment see below). To determine the correctness of the obtained ETS sequences, these were initially aligned to the overlapping 5′ end of the18S rDNA of *Celosia argentea* (Amaranthaceae, GenBank accession AF206883). The ETS region ended after ca. 550 bp. One new internal primer was designed specifically to amplify and sequence the 3′ ETS region of the IGS, namely, ETS-*Salicornia*-5′-GTC CCT ATT GTG TAG ATT TCA T-3′. Successive amplifications of the 3′ ETS were done using the primer combination ETS-*Salicornia* and 18S-II rev.

Reactions for the amplification of the 3′ ETS fragment were prepared in 25 µl aliquots containing 10x Buffer (supplied with the *Taq* polymerase), 2.25 mM $MgCl_2$, 50 pmol forward and reverse primers, 0.6 U *Taq* polymerase and 4% DMSO. A PTC-100 cycler (MJ Research, Inc., MA, U.S.A.) or a Biometra® T gradient thermocycler was used according to the following protocol for the 3' ETS, 95°C for 3 min; 30 cycles of 95°C for 30 s, 50.5°C for 45 s, 72°C for 2 min; 72°C for 8 min. PCR products were subsequently visualized on a 0.8% agarose gel, then purified using a PCR extraction kit (QiaGen GmbH, Hilden, Germany).

Sequencing reactions were prepared using ABI's Big Dye Terminator Kit following the manufacturer's protocol. Sequences were obtained using an ABI 373A DNA Sequencer. DNA chromatograms were edited and aligned using Sequencher. The alignment was straightforward.

Phylogeny inference. — The ETS data matrix was analyzed using the Maximum Likelihood (ML) and Maximum Parsimony (MP) implemented in PAUP*4.10b (Swofford, 2002) for Apple Computers. Heuristic search settings were set to 100 (MP) and 10 (ML) random addition of taxa and tree-bisection-reconnection (TBR) branch swapping.

Furthermore, we used Bayesian inference with Markov chain Monte Carlo simulation implemented in MrBayes v.3 (Ronquist & Huelsenbeck, 2003) for phylogenetic reconstructions. The nucleotide sequence evolution model needed for this analysis was identified using Modeltest (Posada & Crandall, 1998). Maximum likelihood analysis was performed using the GTR+G (general time reversal) model of sequence evolution. The

Table 1. Important treatments of *Salicornia*, ploidy levels, synonymy, and distribution.

Area, reference	**Listed species**	**Ploidy level 2n =**	**Synonyms, as given by the authors (selected)**	**Species names accepted in this account (partly provisional)**	**Distribution**
Europe (*Fl. Eur.* 1, ed. 2; Ball & Akeroyd, 1993)	***S. europaea*** L.	18	*S. stricta* Dumort., *S. patula* Duval-Jouve, *S. brachystachya* (G.F.W. Meyer) D. König, *S. simonkaiana* (Soó) Soó	***S. europaea*** L.	NW Europe
	S. obscura P.W. Ball & Tutin	18		***S. obscura*** P.W. Ball & Tutin	W Europe
	S. prostrata Pall.	18		***S. perennans*** Willd.	SE & E Europe, ?Siberia
	S. pusilla Woods	18		***S. pusilla*** Woods	N & NW France, S Britain, S Ireland
	S. ramosissima Woods	18		***S. ramosissima*** Woods	W Europe, W Mediterranean,
	S. dolichostachya Moss subsp. ***dolichostachya***	36	*S. oliveri* Moss, *S. pojarkovae* Semenova	***S. dolichostachya*** Moss	N Europe (except Baltic Sea)
	subsp. ***strictissima*** (Gram) P.W. Ball	36	*S. strictissima* Gram	***S. procumbens*** Sm. in Sowerby	North Sea, Baltic Sea
	S. fragilis P.W. Ball & Tutin	36	*S. emerici* Duval-Jouve, *S. stricta* subsp. *decumbens* Aellen (S. *stricta* subsp. *procumbens* sensu D. König), *S. veneta* Pignatti & Lausi, *S. lutescens* P.W. Ball & Tutin	***S. emerici*** Duval-Jouve	W & S Europe
	S. nitens P.W. Ball & Tutin	36		***S. nitens*** P.W. Ball & Tutin	W Europe
Scandinavia (*Fl. Nord.* 1; Piirainen, 2001)	***S. europaea*** L.	18	*S. herbacea* L., *S. ramosissima* Woods, *S. brachystachya* (G.F.W. Meyer) D. König	***S. europaea*** L.	Coasts up to 70°
	S. dolichostachya Moss subsp. ***dolichostachya***	36		***S. dolichostachya*** Moss	W Denmark
	subsp. ***pojarkovae*** (Semenova) Piirainen		*S. pojarkovae* Semenova	***S. pojarkovae*** Semenova	N Norway
	subsp. ***strictissima*** (Gram) P.W. Ball		*S. strictissima* Gram, *S. leiosperma* Gram	***S. procumbens*** Sm. in Sowerby	Denmark, SW Sweden, S Norway
British Isles (Davy & al., 2001)	***S. europaea*** L.	18		***S. europaea*** L.	All coasts up to 54° (scattered)
	S. obscura P.W. Ball & Tutin	18	(?var. of *S. europaea* L.)	***S. obscura*** P.W. Ball & Tutin	Up to 55°30′
	S. pusilla Woods	18	(?var. of *S. europaea* L.)	***S. pusilla*** Woods	All coasts
	S. ramosissima Woods	18		***S. ramosissima*** Moss	All coasts
	S. dolichostachya Moss	36		***S. dolichostachya*** P.W. Ball & Tutin	Up to 56°

Table 1. Continued.

Area, reference	Listed species	Ploidy level 2n =	Synonyms, as given by the authors (selected)	Species names accepted in this account (partly provisional)	Distribution
	S. fragilis P.W. Ball & Tutin	36		***S. fragilis*** P.W. Ball & Tutin	Up to 55°40′
	S. nitens P.W. Ball & Tutin	36		***S. nitens*** P.W. Ball & Tutin	Up to 55°30′ (scattered)
France (Lahondère, 2004)	***S. brachystachya*** D. König	18	*S. pusilla* Moss, *S. stricta* Dumort.	***S. ramosissima*** Woods	N coast up to Bretagne
	S. disarticulata Moss	18	*S. pusilla* Woods	***S. disarticulata*** Moss	N & W coasts
	S. obscura P.W. Ball & Tutin	18	*S. stricta* (G.F.W. Meyer) D. König p.p., etc.	***S. obscura*** P.W. Ball & Tutin	W & N coasts
	S. patula Duval-Jouve	18		***S. patula*** Duval-Jouve	S coast, Corse
	S. ramosissima Woods	18	*S. procumbens* Sm. in Sowerby, *S. appressa* Dumort.	***S. ramosissima*** Woods	W and N coasts, Corse
	S. dolichostachya Moss	36	*S. procumbens* Sm. in Sowerby var. *stricta*	***S. dolichostachya*** Moss	W and N coasts
	S. emerici Duval-Jouve	36	*S. nitens* P.W. Ball & Tutin, *S. veneta* Pignatti & Lausi	?***S. emerici*** Duval-Jouve	S coast, W coast up to Bretagne
	S. fragilis P.W. Ball & Tutin	36	*S. lutescens* P.W. Ball & Tutin	***S. fragilis*** P.W. Ball & Tutin	W and N coasts
Mediterranean Region (Greuter & al., 1984)	***S. europaea*** L.		*S. brachystachya* (G.F.W. Meyer) D. König, *S. europaea* subsp. *duvalii* (A. Chev.) Maire, *S. obscura* (P.W. Ball & Tutin, *S. patula* Duval-Jouve, *S. stricta* Dumort., *S. appressa* Dumort., *S. fragilis* P.W. Ball & Tutin, *S. lutescens* P.W. Ball & Tutin	***S. patula*** Duval-Jouve, and ?	Around the Mediterranean except from Algeria to Sinai
	S. prostrata Pall.			***S. perennans*** Willd.	Bulgaria, Asian Turkey
	S. pusilla Woods		*S. disarticulata* C.E. Moss	***S. pusilla*** Woods	France
	S. ramosissima Woods			?	Spain to Italy, Bulgaria
	S. procumbens Sm. in Sowerby			?	Portugal, France, Italy, Asian Turkey
	?*S. emerici* Duval-Jouve			***S. emerici*** Duval-Jouve	France
	?*S. nitens* P.W. Ball & Tutin			***S. nitens*** P.W. Ball & Tutin	Portugal
	?*S. oliveri* Moss			?	France
	?*S. veneta* Pignatti & Lausi			***S. veneta*** Pignatti & Lausi	Italy
	S. deserticola A. Cheval.			***S. deserticola*** A. Cheval.	Algeria (N Sahara)

Table 1. Continued.

Area, reference	Listed species	Ploidy level 2n =	Synonyms, as given by the authors (selected)	Species names accepted in this account (partly provisional)	Distribution
Iberian Pen. (*Fl. Ib* 2; Valdés & Castroviejo, 1990)	***S. ramosissima*** Woods	18	*S. nitens* sensu Franco	***S. ramosissima*** Woods (? also ***S. patula*** Duval-Jouve)	All coasts incl. Balearic Isl., more rarely inland
	S. emerici Duval-Jouve	36		***S. emerici*** Duval-Jouve	Coasts of NE Spain and S France
	S. dolichostachya Moss	36		***S. dolichostachya*** Moss	Coasts of N Spain
Iberian Pen. (Rivas-Martinez & Herrera, 1996)	***S. obscura*** P.W. Ball & Tutin	18	*S. decumbens* (Aellen) Rivas-Mart. (? *S. procumbens* Sm.)	? ***S. obscura*** P.W. Ball & Tutin	Coats from S Scandinavia to N Spain
	S. patula Duval-Jouve	18		***S. patula*** Duval-Jouve	Strait of Gibraltar, Medit. coasts and inland Spain
	S. ramosissima Woods	18	*S. appressa* Dumort.	***S. ramosissima*** Moss	S England to Portugal (Algarve)
	S. dolichostachya Moss	36	*S. stricta* sensu D. König	***S. dolichostachya*** Moss	Coasts from Britain to S Portugal, probably also along NW Morocco and SE Spain
	S. lutescens P.W. Ball & Tutin	36	*S. fragilis* P.W. Ball & Tutin	***S. nitens*** P.W. Ball & Tutin	Atlantic coasts
	S. emerici Duval-Jouve s.l.	36	*S. veneta* Pignatti & Lausi, *S. vicensis* J. Duvign., *S. nitens* P.W. Ball & Tutin,	***S. emerici*** Duval-Jouve	Atlantic and Medit. coasts from Britain to Corse and Sardinia
Italy (Iberite, 1996)	***S. patula*** Duval-Jouve	18		***S. patula*** Duval-Jouve	All Italian coasts, incl. islands
	S. emerici Duval-Jouve	36		***S. emerici*** Duval-Jouve	All Italian coasts, incl. Sicily & Sardinia
	S. dolichostachya Moss	36		***S. dolichostachya*** Moss	Tyrrhenian coast (S Latium)
	S. veneta Pignatti & Lausi	36		***S. veneta*** Pignatti & Lausi	NW Adriatic coast, endemic
Turkey (*Fl. Turk*. 2; Ball, 1967)	***S. europaea*** L.		*S. stricta* Dumort.	?	?
	S. prostrata Pall.		*S. ramosissima* auct.	***S. perennans*** Willd.	Inland Turkey
	S. fragilis P.W. Ball & Tutin		*S. stricta* auct., *S. lutescens* P.W. Ball & Tutin	***S. patula*** Duval-Jouve	Coastal W Turkey
Egypt (Boulos, 1999)	***S. europaea*** L. s.l.		*S. obscura* P.W. Ball & Tutin	?	N & C Egypt, Sinai
Arabian Pen. (Boulos, 1996)	***S. europaea*** L.			?	Arabian Gulf: Kuwait to Bahrein

Table 1. Continued.

Area, reference	Listed species	Ploidy level 2n =	Synonyms, as given by the authors (selected)	Species names accepted in this account (partly provisional)	Distribution
Libanon/Syria (Mouterde, 1966)	***S. europaea*** L.			?	SW Syria (near Damascus), NE Syria (Lake Khatouniye)
Iraq (Aellen & Hillcoat, 1964)	***S. herbacea*** L. s.l.			?	Iraq (Western Desert)
Middle East (*Fl. Ir.* 172, Hedge, 1997)	***S. europaea*** L. s.l.		*S. prostrata* Pall.	?	N & C Iran, Turkmenistan, NE Afghanistan
(described afterwards)	***S. persica*** Akhani	36		***S. persica*** Akhani	C Iran
East Europe (*Fl. Eur. Or.* 9; Tzvelev, 1996)	***S. europaea*** L.	18	*S. acetaria* Pall.	***S. europaea*** L.	White Sea coast, Baltic Sea coast
	S. perennans Willd.	18	*S. prostrata* Pall	***S. perennans*** Willd.	S Ukraine, SE European Russia
	? *S. ramosissima* Woods			?	S Crimea and S Russia (Rostov prov.)
	S. borysthenica Tzvelev	36		***S. borysthenica*** Tzvelev	Black Sea coast near lower Dnepr river
	S. pojarkovae Semenova	36	*S. herbacea* L. subsp. *pojarkovae* (Semenova) V.G. Sergienko, *S. dolichostachya* Moss subsp. *pojarkovae* (Semenova) Piirainen	***S. pojarkovae*** Semenova	Northern European Russia: White Sea coast
Former U.S.S.R (Czerepanov, 1995)	***S. europaea*** L.			***S. europaea*** L.	European Russia (northern)
	S. perennans Willd.		*S. prostrata* Pall.	***S. perennans*** Willd.	Widespread
	S. borysthenica Tzvelev			***S. borysthenica*** Tzvelev	European Russia (southern)
	S. pojarkovae Semenova		*S. dolichostachya* auct.	***S. pojarkovae*** Semenova	European Russia (northern)
(described afterwards)	***S. heterantha*** S.S. Beer & Demina			***S. heterantha*** S.S. Beer & Demina	SE European Russia
Siberia (*Fl. Sib.* 5; Lomonosova, 1992)	***S. europaea*** L.			?	W, C & E Siberia
(described afterwards)	***S. altaica*** Lomon.			***S. altaica*** Lomon.	S Siberia (Altai)
Central Asia (*Pl. Centr. Asia* 2; Grubov, 2000)	***S. europaea*** L.				Mongolia, W China
	subsp. ***acetaria*** Pall.			?	
	subsp. ***prostrata*** Pall.			***S. perennans*** Willd. (p.p.)	

Table 1. Continued.

Area, reference	Listed species	Ploidy level 2n =	Synonyms, as given by the authors (selected)	Species names accepted in this account (partly provisional)	Distribution
China (*Fl. China* 5; Zhu Gelin, 2003)	***S. europaea*** L.		Prob. *S. prostrata* Pall.	?	W, C and NE China, coastal China down to 31° N
North America (*Fl. North Am.* 4; Ball, 2003)	***S. maritima*** S.L. Wolff & Jefferies	18	*S. prostrata* sensu Standl.	**? *S. maritima*** S.L. Wolff & Jefferies	Coastal SE Canada, northeastern U.S.A., S Alaska
	S. rubra A. Nelson	18	*S. borealis* S.L. Wolff & Jefferies	**? *S. rubra*** A. Nelson**,** **? *S. borealis*** S.L. Wolff & Jefferies	Central U.S.A. and Canada, Subarctic Canada
	S. bigelovii Torrey	36		***S. bigelovii*** Torr.	Gulf of Mexico, Atlantic coast up to Maine, S California
	S. depressa Standl.	36	*S. virginica* L**.**	***S. depressa*** Stando.	Pacific coast from Alaska to California, Atlantic coast from Canada to S Carolina
Western Trop. Africa (Brenan, 1954, 1966)	***S. praecox*** A. Chev.			***S. praecox*** A. Chev.	W Senegal
	S. senegalensis A. Chev.			***S. senegalensis*** A. Chev.	W Senegal
Eastern Trop. Africa (*Fl. Zamb.* 9; Brenan, 1988)	***S. perrieri*** A. Chev.		*S. pachystachya* sensu Toelken p.p.	***S. perrieri*** A. Chev.	E African coast: Mozambique to Natal, Madagascar, poss. Tanzania and Zanzibar
	S. pachystachya Bunge ex Ungern-Sternb.			***S. pachystachya*** Bunge ex Ungern-Sternb.	E African coast: S Kenia to Natal, Madagascar
South Africa (Tölken, 1967)	***S. meyeriana*** Moss		Incl. *S. perrieri* A. Chev.	***S. meyeriana*** Moss	S African coasts, Vanrhynsdort to Durban
	S. pachystachya Bunge ex Ungern-Sternb.			***S. pachystachya*** Bunge ex Ungern-Sternb.	E African coast to Natal
	S. uniflora Toelken			***S. uniflora*** Toelken	SW Namibia (Lüderitz), Northwest S Africa (Darling)
South Asia (*Rev. Handb. Ceylon* 9; Boulos, 1995)	***S. brachiata*** Roxb.			***S. brachiata*** Roxb.	Coastal Ceylon, E coast of India up to Bengal

detailed ML settings were: base frequencies A = 0.3235, C = 0.2886, G = 0.1969, T = 0.1910, γ-shape parameter: 0.7555, rate matrix: 0.534, 2.989, 1.327, 0.224, 2.989. A total of 10,000,000 generations were simulated, sampling the chain every 100 generations. The first 4,000 trees were discarded in the burn-in phase and the remaining 16,000 were used to estimate Bayesian posterior probabilities. The posterior probabilities derived from the Bayesian inference served as measure of support.

RESULTS

The ETS data matrix comprises 185 individuals and 507 characters. Of these, 279 are invariable, 76 are parsimony uninformative and 152 (30%) parsimony informative. Within *Salicornia* (164 individuals), 431 characters are invariable, 22 are parsimony uninformative and 54 (10.7%) parsimony informative.

In the MP analysis a total of 3,937 shortest trees of 437 steps were found on one island with a consistency index (CI) of 0.705 and a retention index (RI) of 0.936. Figure 4 shows the ML tree with number of character changes above branches and posterior probabilities resulting from the Bayesian analysis below branches. The strict consensus tree derived from the parsimony analysis and the cladogram derived from the Bayesian inference were identical.

DISCUSSION

Origin of *Salicornia*. — The ETS tree clearly resolves *Salicornia* as monophyletic (Fig. 4A). This supports the results of previous studies (Kadereit & al., 2006; Murakeözy & al., 2007) which were based on a much smaller sample of ITS and *atpB-rbcL* spacer sequences (Kadereit & al., 2006) and ITS, *matK*, *trnL/F* (Murakeözy & al., 2007), respectively.

The annual habit and the size difference between larger central and smaller lateral flowers together forming a triangle (Fig. 2A–E) which were used by Scott (1977) as diagnostic characters to delimit *Salicornia* from *Sarcocornia* thus prove to be autapomorphies of the genus. The latter character, however, needs to be qualified: In most species of *Sarcocornia* the lateral flowers are also slightly smaller than the central flower (comparable to some tetraploid *Salicornia*, especially *Salicornia* "*freitagii*") and in a few species of *Sarcocornia* lateral flowers are distinctly

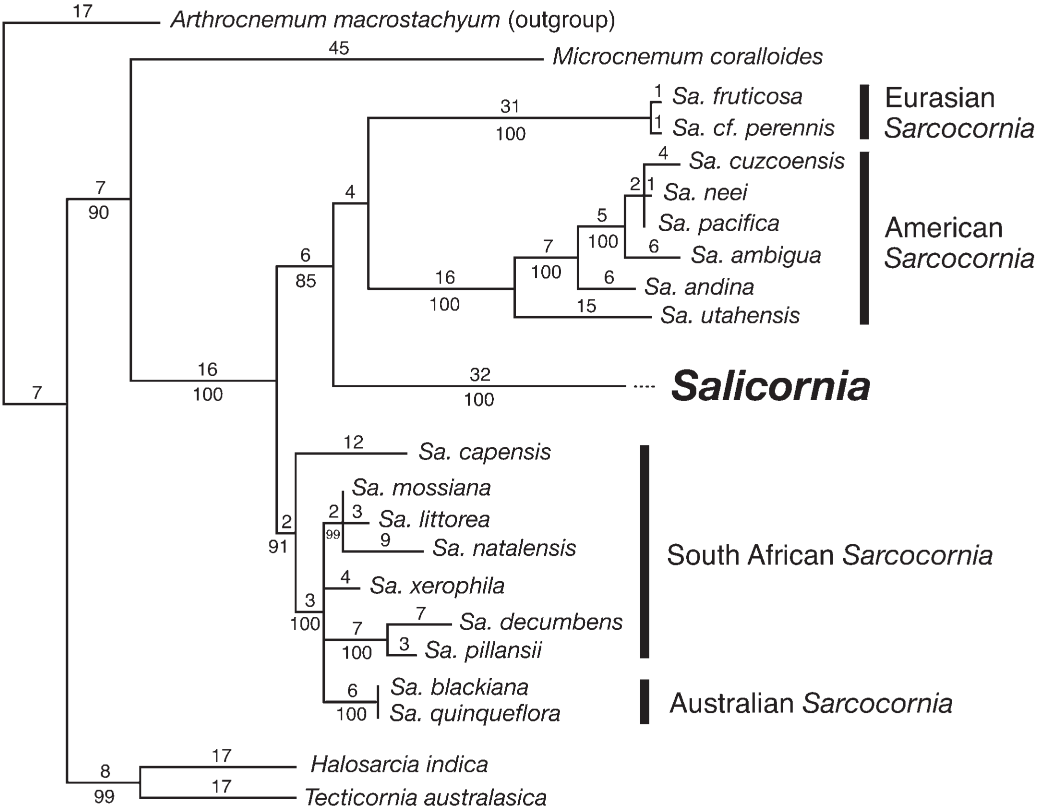

Fig. 4A–C. Maximum likelihood tree based on 185 ETS sequences; 164 sequences represent the genus *Salicornia*; number of character changes above branches, posterior probabilities (>75) resulting from the Bayesian analysis below branches.

smaller (e.g., *Sarcocornia freitagii* S. Steffen, L. Mucina & G. Kadereit, ined.). But the flowers in *Sarcocornia* are always arranged in a row and the lateral flowers are never in contact beneath the central flower as is usually the case in *Salicornia* (but see Moss, 1912).

The ITS and *atpB-rbcL* spacer data for the *Salicornia*/*Sarcocornia* lineage (Kadereit & al., 2006) and our findings for ETS (Fig. 4A) congruently support three major clades: (1) American/Eurasian *Sarcocornia*, (2) *Salicornia*, and (3). South African/Australian *Sarcocornia*. Of these, the former two are well-supported by molecular data while the latter receives relatively low BS support and is not resolved by *atpB-rbcL* spacer data. The molecular data are contradictory with respect to the position of *Salicornia*. In the ETS tree, *Salicornia* is sister to a clade comprising Eurasian and North American *Sarcocornia* (Fig. 4A), in the ITS tree it originates from within South African/Australian *Sarcocornia*, and in the *atpB-rbcL* spacer tree it originates from within the American/Eurasian *Sarcocornia*. None of these topologies receives convincing statistical support. The changing position of *Salicornia* might be an artefact caused by its relatively long branch in combination with short basal branches within the *Sarcocornia*/*Salicornia* lineage. In addition to the morphological differences between the two genera (see above), these results substantiate the separation of *Salicornia* and *Sarcocornia* though this eventually might leave the latter genus paraphyletic.

The intrageneric topology of the ETS tree implies an Eurasian origin of *Salicornia* because the early branching *Salicornia* "*crassa*" group is distributed in Eurasia, and most American as well as the two South African lineages originate from within Eurasian clades (Fig. 4B). This in turn suggests that *Salicornia* is most closely related to Eurasian/American *Sarcocornia* as found here. In Eurasia, *Sarcocornia* is restricted to the Mediterranean and the Atlantic coast. *Sarcocornia perennis*, a species with creeping branches, extends northwards up to the British Channel with a few outposts in coastal South Ireland, Wales and Scotland (Davy & al., 2006). The distribution area of *Sarcocornia* usually does not exceed the 1°C January isotherm in the northern hemisphere (although according to Davy & al., 2006 in case of the populations on the British Isles its distribution corresponds more closely with the July isotherm). Obviously *Sarcocornia* is frost-susceptible, and its distribution also thins out in the Northeast Mediterranean towards the Black Sea coast. In North America only the erect growing *Sarcocornia ambigua* reaches southern New England where mean low temperatures reach –5°C. In severe winters the growth of the current season dies back but the stouter woody branches survive (P. Ball, pers. obs.). We deduce, therefore, that many local *Sarcocornia* lineages might have gone extinct during the Pleistocene glaciations. Especially in the northern hemisphere the genus is species-poor with only two species in Eurasia and three to four species occurring in North America. In contrast, the South African and South American *Sarcocornia* lineages comprise 11 to 15 species (Kadereit & al., 2006) and 6 to 7 species (Alonso & Crespo, in press). For South Africa this would constitute an indirect corroboration of the hypothesis that the climatically stable regions support and preserve rich cladogenesis (Dynesius & Jansson, 2000; Jansson & Dynesius, 2002).

Large-scale extinctions in northern *Sarcocornia* lineages might have also played a role in shaping the unresolved relationships among the major clades of *Sarcocornia* and *Salicornia*, and they might explain the relatively long and late diverging clades supporting the Eurasian and American *Sarcocornia* species, in constrast to the early and more extensively diverging South African clade.

The annual *Salicornia* species have a much wider distribution in the Northern hemisphere than *Sarcocornia* (see Fig. 3). They extend into adjacent areas with severe frost during winter, and even into the boreal and subarctic zones. The northernmost species are *Salicornia pojarkovae* which occurs at the White Sea (northern European Russia) and at the Norwegian Sea (northern Norway) coasts including the area beyond the Polar Circle (Semenova-Tyan-Shanskaya, 1956; Piirainen, 2001) and *S. borealis* which is distributed in North Canada (James Bay, Hudson Bay and southern Yukon). This area expansion of *Salicornia* in contrast to *Sarcocornia* indicates that likely the annual life form was the key innovation which enabled *Salicornia* to colonize hygro-halophytic habitats in environments susceptible to severe frost. In warm temperate and Mediterranean climates, *Salicornia* and *Sarcocornia* grow in close sympatry but in ecological respect they are usually well separated. *Salicornia* often dominates coastal lagoons and—most conspicuously—saline inland depressions of the semiarid and arid parts of the Mediterranean region which are flooded for weeks or months by the winter rains. Therefore, the annual life form was possibly also a key innovation which enabled *Salicornia* to colonize less stable and seasonally flooded habitats.

The annual life form in *Salicornia* arose some time between the Middle Miocene and the beginning of the Pleistocene (9.4–1.4 mya; Kadereit & al., 2006). Based on the ecology and distribution of extant species of Eurasian *Sarcocornia* and *Salicornia* two alternative hypotheses can be formulated: (1) The annual life form evolved from a perennial lineage in marginal habitats where probably increasing frost was the driving selective force, possibly through selection for shorter generation cycles as consequence of reaction to cold stress. Simultaneously or later it invaded suitable habitats in areas with warmer climates. (2) The annual life form evolved from an ancestral Mediterranean perennial lineage under a warm-temper-

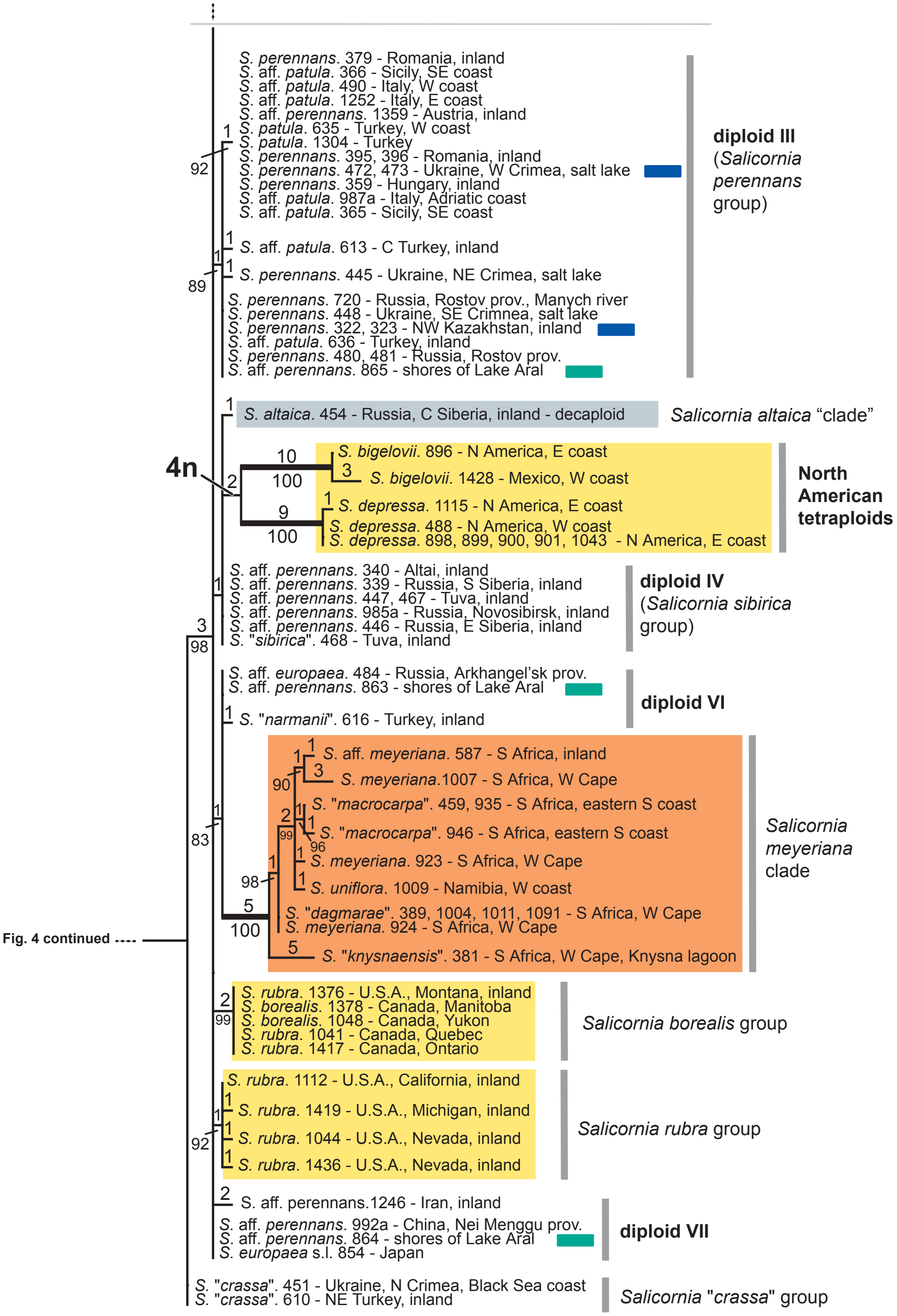

Fig. 4B. Monophyletic *Salicornia* lineage resolved in the ML tree based on ETS sequences (see Fig. 4A); numbers after species names indicate different accessions from the same region (compare Appendix for exact localities of each sample); colour labelling: yellow – American samples; orange – South African samples; samples without underlying colour are from Eurasia; red bars – Baltic Sea; green bars – Lake Aral (both examples for multiple arrival of different ETS genotypes); blue bars mark two samples where prostrate and erect growth forms were analysed from the same locality (see text for further explanations).

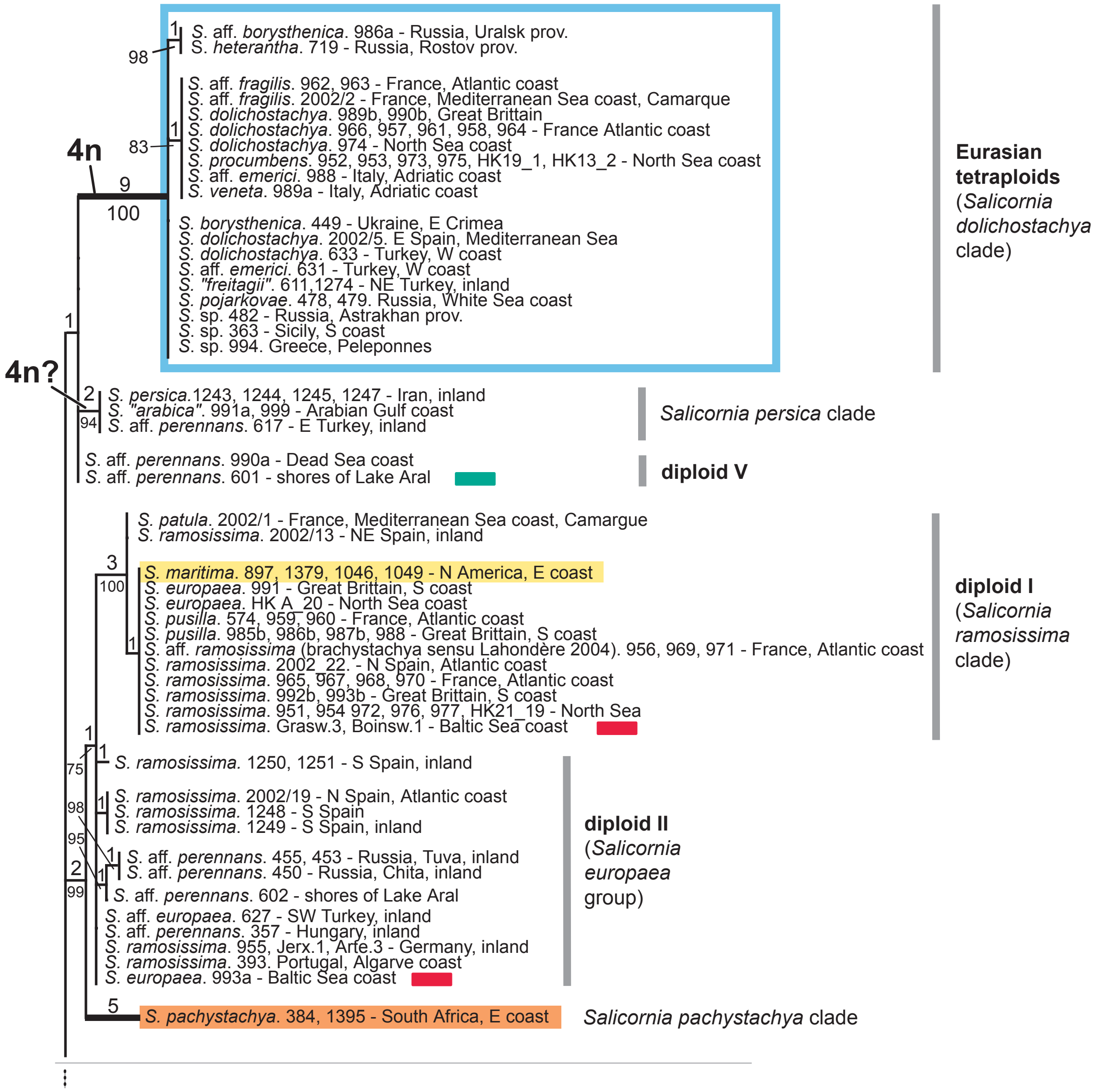

Fig. 4 continued

Fig. 4C. Monophyletic *Salicornia* lineage resolved in the ML tree based on ETS sequences (see Fig. 4A); numbers after species names indicate different accessions from the same region (compare Appendix for exact localities of each sample); colour labelling: yellow – American samples; orange – South African samples; samples without underlying colour are from Eurasia; red bars – Baltic Sea; green bars – Lake Aral (both examples for multiple arrival of different ETS genotypes); blue bars mark two samples where prostrate and erect growth forms were analysed from the same locality (see text for further explanations).

ate (subtropical) climate. The annual habit enabled the first *Salicornia*s to colonize seasonally flooded habitats in large parts of the *Sarcocornia* area and subsequently it proved also to be an appropriate adaptation to habitats exposed to severe frost. However, neither hypothesis can be tested.

When the *Salicornia* lineage split from the *Sarcocornia* lineages some time in the Middle or Late Miocene, about 9.4–4.2 Mya (Kadereit & al., 2006), globally the climate was much warmer, and large areas from Southeast Europe across the Black Sea, the Caspian Sea and beyond to the Aral Sea were covered by the Paratethys, a northern remnant of the former Tethys Sea, which in the process of the alpine orogenies stepwise disintegrated into isolated basins still present today (see, e.g., Rögl & Steininger, 1983; Steininger & Rögl, 1984; Ricou, 1996; Dineley, 2004). Fossil evidence of *Sarcocornia* from the Paratethys area is lacking, but the genus probably was present there because many fossil terrestrial floras from the Central and Eastern Paratethys contain evergreen laurophyllous and sclerophyllous frost-sensitive trees and shrubs through Ukraine and the Caucasus up to Turkmenia and West Kazakhstan (Palamarev, 1989; Mai, 1995 and ref. therein), and near to its arid easternmost section microfossils document the formation of steppes and semideserts (see, e.g., Song & al., 1981 and ref. therein). The Paratethys area with predominance of shallow coasts, absence of tides and arid conditions in the eastern section probably offered suitable conditions for the origin of *Salicornia*. The presence of the most ancestral *Salicornia* "*crassa*" group just near the northern and the southern shores of the Black Sea which represents the residual of the Central Paratethys is well in accordance with our opinion that *Salicornia* might have originated somewhere between the East Mediterranean and the eastern Paratethys.

In summary, the evolution of the annual habit (maybe together with predominant inbreeding) was a key innovation that enabled *Salicornia* to colonize cold temperate and boreal regions as well as seasonally flooded and highly dynamic habitats. Two main selective forces might have driven the evolution of the annual life form, regular severe frost and/or long-lasting flooding. Possibly, the area of origin was located between the East Mediterranean and the Central or eastern Paratethys.

Diversification within *Salicornia*. — The tree topology within Salicornia reveals the following overall pattern (Fig. 4B, C): A basal split separates the *S.* "*crassa*" group from the remainder of the genus. The latter shows a large number of only weakly differentiated lineages, most of them having a Mediterranean and/or Eurasian distribution. Five long branches (branches with five or more character changes marked by bold lines in Fig. 4B, C) are nested among these lineages. These long-branched lineages show either polyploidization or they are distributed in geographically remote areas, or both. However, there are two lineages in North America and two polyploid lineages that do not have a long branch. Most likely, they are of more recent origin. This topology shows that both polyploidization and long-distance dispersal which often were followed by radiation have played a major role in the evolution of the genus.

Initial diversification. — Diversification of extant lineages probably started in the late Pliocene/early Pleistocene, about 1.8–1.4 mya (Kadereit & al., 2006) with the split of the *S.* "*crassa*" group (Fig. 4B). It consists of two accessions, one from Crimea and one from Northeast Turkey. The plants were collected in areas where no particular attention has been given to *Salicornia* so far. The molecular data and also morphological differences, the most prominent being the extremely robust appearance of the specimens suggest that they likely represent a new species which is awaiting a detailed study. From their morphology we concluded that these two specimens represent diploids. This and the distribution of tetraploid clades within *Salicornia* (compare Fig. 4B, C) imply that tetraploid and diploid *Salicornia* are not monophyletic sister groups as suggested by previous studies (Papini & al., 2004; Murakeözy & al., 2007) but that tetraploid *Salicornia* originated more than once from within diploid *Salicornia* lineages.

The polyploid clades. — It has long been known (e.g., König, 1939), that diploid ($2n = 18$) and tetraploid ($2n = 36$) karyotypes occur in *Salicornia* (see review given by Shepherd & Yan, 2003), and recently a decaploid species (*S. altaica*, $2n = 90$) was discovered (Lomonosova, 2005). Polyploidization marks at least three widespread, long-branched clades within *Salicornia*, the *Salicornia dolichostachya*, S. *bigelovii* and *S. depressa* clades (North American tetraploids) with the latter two being sister to each other and probably one short-branched clade, the *Salicornia persica* clade (Fig. 4B, C).

Surprisingly, almost all known Eurasian tetraploids (*S. dolichostachya*, *S. emerici*, *S. fragilis*, *S. pojarkovae*, *S. procumbens*, and *S. veneta* [probably a synonym of *S. emerici*]) together with a few species of unknown ploidy level (*S. borysthenica*, *S.* "*freitagii*", *S. heterantha*) form a well-supported, monophyletic group (*Salicornia dolichostachya* clade) with very little variation among the 32 accessions included. Our sampling covers most of the distribution area of these species (Fig. 5A) and represents all recognized species except *S. nitens* which maybe is a synonym of *S. emerici* (Lahondère, 2004), or a microspecies of the latter (Rivas-Martinez & Herrera, 1996). Only one species, *S. persica* (Akhani, 2003), represents an independent Eurasian tetraploid lineage, its ITS sequence being identical to accessions from Turkey and the Arabian Peninsula with unknown ploidy level (Fig. 4C). The ETS tree suggests that both the *S. dolichostachya* clade and the *S. persica* clade are most closely related to Southwest and Central Asian diploids. We are lacking sufficient material from SW Asia (except for Turkey), East Asia and North Africa from where the occurrence and distribution of tetraploid species is not known. Probably, as can be judged from the illustration in Berhaut (1974: 302), also *S. senegalensis* from Senegal belongs to the *Salicornia dolichostachya* clade, and likewise maybe *S. deserticola* (Maire, 1962). An improved sampling might reveal further origins of Eurasian polyploid lineages such as the decaploid *S. altaica*.

The low genetic variation found within the *Salicornia dolichostachya* clade points to a recent and rapid expansion into its present day distribution area. The clade is distributed more or less continuously along the sandy and muddy coasts of Europe from Portugal to South Scandinavia and the Kattegat. It has a more scattered distribution around North Norway up to the White Sea (*S. pojarkovae*), along the coasts of the Mediterranean and the Black Sea, from where sometimes it enters inland salt marshes. This

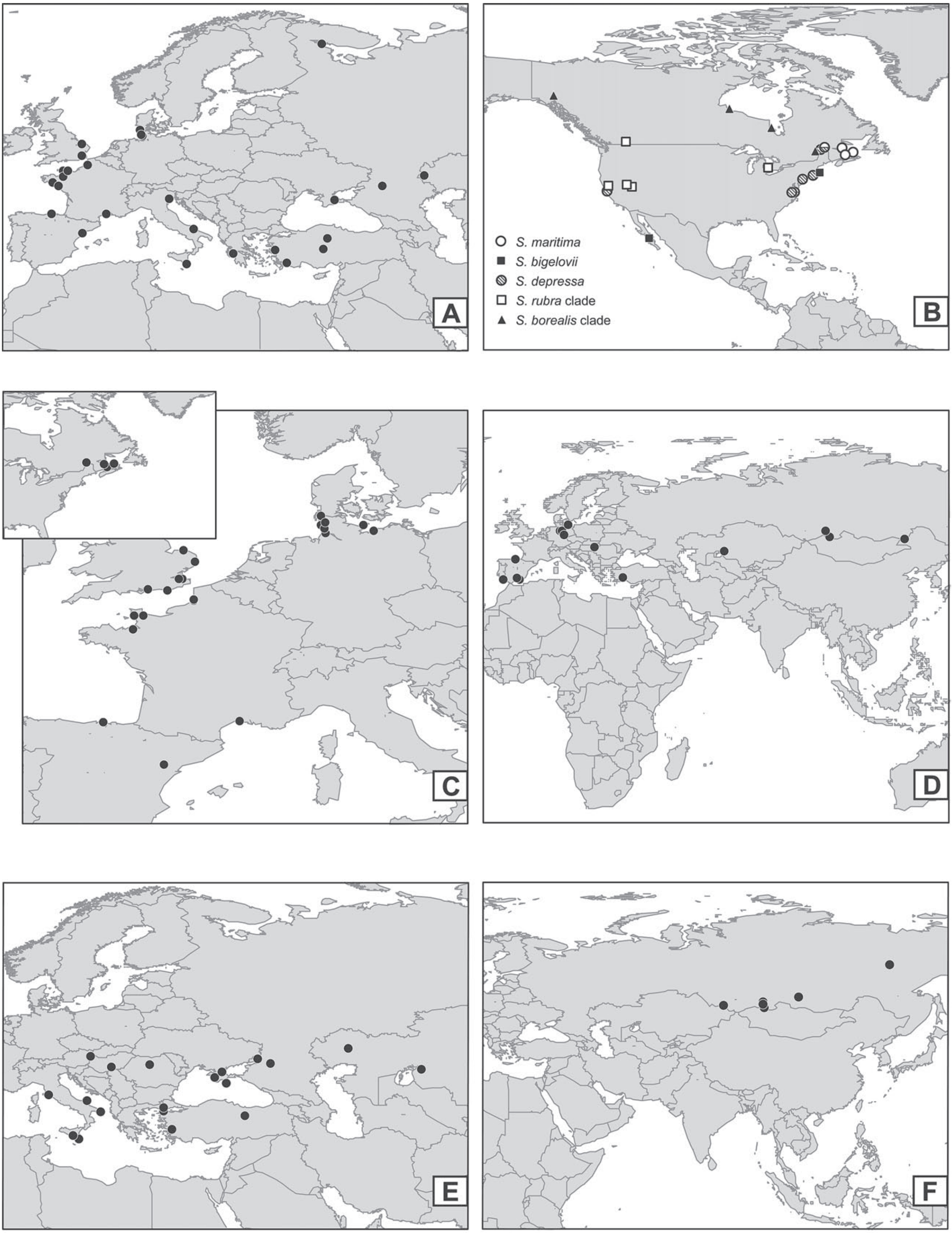

Fig. 5. A, distribution of examined specimens of Eurasian tetraploid *Salicornia* species; B, distribution of the different North American ETS genotypes; C, distribution map of the *S. ramosissima* clade; D, distribution map of the *S. europaea* group; E, distribution of the *S. perennans* group; F, distribution of the *S. sibirica* group.

shows that this lineage is able to tolerate a span of climatic conditions ranging from the warm-temperate Mediterranean to subarctic climates. Most species of the *Salicornia dolichostachya* clade grow in the lower belts of intertidal salt marshes which are exposed to daily flooding for several hours while only a few grow in the middle salt marsh that is not flooded for several weeks in summer.

Although the species of the *Salicornia dolichostachya* clade are molecularly very uniform, at least some show considerable morphological and ecological differentiation. This applies in particular to *S. pojarkovae*, a dwarfed subarctic species with a very short life cycle (Semenova-Tyan-Shanskaya, 1956; Piirainen, 2001), *S. heterantha* (Beer & Demina, 2005; Fig. 2C) in which the tissues of the central flower tepals and the inflorescence axis are completely fused, and *S.* "*freitagii*", an inland tetraploid with conspicuous scarious leaf and bract margins and subequal flowers in one cyme.

Most species of the *S. dolichostachya* clade (*S. borysthenica, S. dolichostachya, S. emerici*, *S. fragilis*, *S. nitens, S. procumbens*, *S. veneta*), however, are more difficult to separate morphologically and ecologically. *Salicornia dolichostachya* seems to be a low level pioneering species of the Atlantic coast with high tidal amplitudes, whereas *S. emerici* seems to be confined to coastal lagoons of the Mediterranean with very weak tides. The other species, however, are somewhat intermediate. Since also their distribution ranges at least partly overlap, a more detailed study of the *S. dolichostachya* clade is needed to disentangle the phylogenetic relationships within this group. An ongoing AFLP analysis of this clade may result in better phylogenetic resolution and may show the genetic distinctness of some species (S. Beer, A.E. Yaprak & G. Kadereit, unpublished data).

Two North American tetraploids, *S. depressa* and *S. bigelovii,* form a monophyletic group that includes two long-branched tetraploid sister clades (*Salicornia bigelovii* clade and *Salicornia depressa* clade, Fig. 4B). This clade forms a polytomy with the decaploid *S. altaica* and seven accessions from Central Asia of unknown ploidy level. This relationship, however, received little statistical support (posterior probability 60; Fig. 4B).

In contrast to the Eurasian tetraploids, these two North American tetraploid species are well separated. When directly compared they show 13 base mutations and two indels of 10 and 6 nucleotides, respectively. While *S. bigelovii* is morphologically very distinct, *S. depressa* could well be taken for an Eurasian tetraploid, e.g., *S. fragilis.* The monophyly of the *S. depressa*/*S. bigelovii* clade receives only weak support (Fig. 4B). Probably the two species separated shortly after their arrival in North America.

Salicornia bigelovii is distributed on the Atlantic and Gulf of Mexico coasts of the U.S.A., the Caribbean and the coast of South California and adjacent Mexico and can be distinguished from all other species of *Salicornia* by its acute and sharply mucronate leaf and bract tips (Ball, 2003). According to *Flora of North America* (Ball, 2003), *Salicornia depressa* is widespread along the Atlantic and Pacific coasts of North America. While the seven accessions of *S. depressa* are identical in their ETS sequences, the two accessions of *S. bigelovii* (one from the East and one from the West coast) differ substantially. *Salicornia bigelovii* and *S. depressa* grow—like the Eurasian tetraploids—in more frequently flooded lower and middle zones of salt marshes.

Apart from the karyotype, the decaploid *Salicornia altaica* is distinct in that the spike length—as in *S. pojarkovae*—exceeds the sterile part of the stem, in growth form and in ecology. It grows on solonchaks at 1800 m above sea level (Lomonosova, 2005). Surprisingly, it shows very little sequence divergence from some Central Asian accessions which were provisionally identified as *S.* aff. p*erennans* and may contain hidden polyploids as well. Chromosome counts and a more detailed sampling in the distribution area of *S. altaica* might give a clearer picture of its origin.

In conclusion, the polyploid lineages are very successful in terms of range expansion. Like their diploid relatives, the polyploid species were able to rapidly spread along the coasts. Most polyploid species found their ecological optimum in lower and middle belts of salt marshes and occupy these habitats often in monospecific stands under widely differing climatic conditions. Possibly more polyploid lineages will be found when sampling is increased.

The diploid Eurasian clades and groups. — The diploid Eurasian accessions fall into seven clades/groups of more or less similar ETS genotypes. Only some of these clades/groups receive considerable statistical support and the relationships among them remain largely unresolved. All seven diploid Eurasian clades/groups are widespread with overlapping distribution ranges (Figs. 4, 5C–F).

The *Salicornia ramosissima* clade (diploid I, Fig. 4C) is a clearly monophyletic, well supported lineage of 33 accessions distributed in the West Mediterranean, the Atlantic coasts of West, Northwest and Central Europe, the westernmost Baltic Sea and in eastern North America (*S. maritima*, see above, Fig. 5C). The *Salicornia ramosissima* clade originates from within the *Salicornia europaea* group. Except for the two accessions from the West Mediterranean which represent *S. patula* and *S. ramosissima*, the accessions of the *Salicornia ramosissima* clade show identical ETS sequences although several species are included, *S. ramosissima* (locally often called *S. brachystachya*), *S. europaea, S. pusilla* and *S. maritima*.

The *Salicornia europaea* group (diploid II, Fig. 4C) consists of 16 accessions which form a polytomy of similar

ETS genotypes that show a wide geographical distribution (Fig. 5D). Like the *Salicornia ramosissima* clade it comprises several species, viz. *S. ramosissima*, *S. europaea* and *S.* aff. *perennans*. The latter is not represented in the *Salicornia ramosissima* clade. The *Salicornia europaea* group plus the *Salicornia ramosissima* clade are sister to the presumably also diploid South African *Salicornia pachystachya* clade (see below).

The *Salicornia perennans* group (diploid III, Fig. 4B) comprises 24 accessions of similar ETS genotypes. It is an only weakly supported widespread lineage occurring from South Europe to Central Asia (Fig. 5E). This lineage contains mainly samples that were identified as *S. perennans* but also samples morphologically close to *S. patula* and *S. europaea* are included in this group. The group also includes two samples where an erect and a prostrate form of *S. perennans* were collected at the same place near the type locality (marked by blue bars in Fig. 4B, compare also Appendix). In both cases the ETS sequences showed no differences indicating that prostrate growth is probably not or not always genetically fixed in *Salicornia*. The same observation has been made in cultivation experiments where the prostrate growth was usually not maintained (P. Ball, pers. obs.).

The *Salicornia* "*sibirica*" group (diploid IV, Fig. 4B) consists of seven accessions with identical ETS sequences that were identified as *S.* aff. *perennans* and as a new morphological entity here provisionally named *S.* "*sibirica*" (Fig. 4B). The group is distributed from Central to East Asia (Fig. 5F). Despite of a distinct eastern range, the distribution area of this clade overlaps with that of the widespread *S. europaea* and *S. perennans* groups (Fig. 5D–F).

The remaining Eurasian diploid groups (diploid V–VII, Fig. 4B, C) comprise only a few accessions that have been identified as *S.* aff. *perennans* or *S.* aff. *europaea*. These three rather fragmentary groups are distributed from North Europe to Western and Eastern Asia.

To understand the phylogenetic pattern found for the Eurasian diploids, the following considerations are important: (1) The extant lineages of *Salicornia* are comparatively young (1.8–1.4 Mya) as is reflected in the generally very short branches. (2) Diploid *Salicornia* species that have been investigated are predominantly homozygous inbreeders. This, together with the high dispersal abilities of the genus outlined below means that we are likely dealing with a large number of widespread inbreeding lines as has been suspected by Dalby (1955).

(3) The biogeography of these lineages in northern temperate and boreal regions was greatly affected by repeated range displacements during the Pleistocene ice ages. In previous interglacial periods and in the Holocene, like other coastal plants (Kadereit & al., 2005), *Salicornia* recolonized the northern areas. In this more or less linear system along the coast or patchy-disjunct system via suitable inland locations retreat and recolonization might have taken place along the same routes several times. For example, the *S. ramosissima* clade probably has originated from within the *S. europaea* clade during the later Pleistocene somewhere in Southwest or West Europe and migrated northward finally reaching the Baltic Sea. Even glaciated areas could have been recolonized by more than one remigrating lineage. The Baltic Sea coast was reached at least two times (marked by red bars in Fig. 4C), (1) from the West by migration along the coast (*S. ramosissima* clade) and (2) from the Southeast by long-distance dispersal from inland saltmarshes of Southeast Europe (*S. europaea* clade). Irrespective of the route, the recolonization of the Baltic Sea by halophytes could not have started earlier than 8,000 years ago when the former freshwater lake became reconnected with the oceans (Björck, 1995), again indicating the effective range expansion abilities of *Salicornia*. A similar bifurcate recolonization was recently found in the halophytic *Triglochin maritimum* L. (Juncaginaceae) which in its present day distribution is similar to *Salicornia* (Lambracht & al., 2007).

The presence of five *Salicornia* genotypes in the Aral Lake basin (marked by green bars in Fig. 4B, C) most likely also can be explained by multiple historical immigration events. In contrast to Europe, there the driving force during the Pleistocene and Holocene certainly was not as much the change in summer temperatures but the repeated dramatic change in the size of lakes (sometimes connected with the Caspian Sea) and in its salinity that resulted in large-scale displacement of halophytes. Obviously these events started in earlier periods of the Pleistocene and they are still highly active today (Dumont, 1998; Ferronskii & al., 2003).

In southern temperate and Mediterranean regions where the climatic oscillations of the Pleistocene were less severe, *Salicornia* had the possibility to continuously colonize suitable habitats. Here the distribution of genotypes observed (Fig. 5C–F) was probably shaped by the multiple arrival and persistence of different lineages in the same region. Turkey being a link between Mediterranean, Eurosiberian and Irano-Turanian floristic regions seems to be exceedingly diverse in *Salicornia*. The Turkish diploid accessions are represented in five different clades/groups, viz. *S. europaea* gr., *S. perennans* gr., diploid V and VI gr. and *S.* "*crassa*" group. We predict that in other regions which were continuously inhabited by *Salicornia*, dense sampling also would reveal the presence of multiple lineages (ETS genotypes).

Intercontinental dispersal. — Altogether at least five intercontinental dispersal events can be inferred from the tree indicating the high ability for long-distance dispersal in the genus. However, seeds of *Salicornia* lack conspicuous devices for dispersal over long distances.

Instead, they show little buoyancy and sink more or less immediately (Hilton, 1975 cited in Davy & al., 2001; P. Teege, pers. obs.) or within the first day after being shed (Koutstaal & al., 1987). Therefore, it is not surprising that 50% of the seeds can be found within a distance of 10 cm from their mother plant (Ellison, 1987). Only small numbers of seeds can be dispersed considerable distances in coastal habitats (Smith, 1985) mainly by rolling along the sediment surface by tidal currents (Brereton, 1971; Hilton, 1975; Costa, 1992 cited in Davy & al., 2001). However, most seeds are trapped by sediment depressions, algae and marsh vegetation and remain within a few metres of their mother plant. *Salicornia* has mucilage and hooked hairs on its testa. These may support anchoring to the substrate and avoid seeds being washed away and dispersed to greater distances. Stormy tides, however, which are common from late autumn to early spring and hit the coasts at an acute angle, might disperse seeds with other loose material over greater distances along the coastline.

When the seeds are dispersed in broken infructescences (e.g., *S. dolichostachya*, König, 1960, sub *S. stricta*), partial infructescences (e.g., *S. pusilla*, Dalby, 1963) or within the persistent perianth (e.g., *S. patula*, Berger, 1985), they are able to float for several months and might also be dispersed over long distances. In *S. heterantha*, ca. one third of seeds is dispersed with parts of infrutescences (see Beer & Demina, 2005). Also, seedlings of *Salicornia* are able to float in sea water and remain alive for at least three months (Petch & Swann, 1968; Hilton, 1975). They are still able to establish when they arrive in suitable habitats. This floating ability of seeds attached to the perianth or infructescences and eventually also uprooted seedlings offer an additional potential for long-distance dispersal.

A further mode of dispersal in *Salicornia* might be epi- or endozoochory by migrating birds which often use estuaries or inland salt lakes as resting and feeding places. Seeds of *Salicornia* might be dispersed either in guts of water fowl (Figuerola & al., 2003; Chang & al., 2005), wigeon (Durant & al., 2006; Van Eerden, 1984; Drent & Prins, 1987), barnacle geese (Ebbinge & al., 1975), brent geese (Summers & al., 1993; Rowcliffe & al., 1998) or by the mud sticking to the feet of birds as has been observed in case of other organisms bound to (semi)aquatic habitats (Figuerola & Green, 2002).

From Eurasia to North America. — In the history of *Salicornia* at least three migrations from Eurasia to North America took place (yellow boxes in Figs. 4B, C and Fig. 5B). These are (1) the relatively early immigration of the *Salicornia bigelovii*/*S. depressa* clades, (2) at least one (maybe two) independent immigration(s) of the North American inland species (*Salicornia rubra*/*S. borealis* groups, and (3) a very recent immigration of *Salicornia maritima*. Of these only the *Salicornia bigelovii* and *S. depressa* clade have long branches while the remaining American groups show two, one or zero character changes, respectively, indicating that they might represent more recent immigrations or synanthropic introductions.

The closest relatives of the *S. bigelovii* clade are distributed in Central and East Asia. This might indicate that this clade immigrated from Central or East Asia either by long distance dispersal or via Beringia during an interglacial period. The members of the *S. borealis* clade seem to be distributed distinctly further North than the members of the *S. rubra* clade (Fig. 5B). The question whether *S. borealis* and *S. rubra* represent one monophylectic lineage or two distinct lineages and the identification of their area of origin in East Eurasia requires further sampling. The accessions of *Salicornia maritima* are genetically identical with those of the *S. ramosissima* clade. The latter is distributed along the coasts of West and Northwest Europe and most likely *S. maritima* is a recent arrival in North America (Fig. 5C). The samples of *S. maritima* are distributed along the Canadian east coast, from the St. Lawrence River estuary to New Brunswick and Nova Scotia, and as far as known, the taxon is restricted to East Canada (Ball, 2003, Fig. 5B, C).

As regards North American *Salicornia*, our analysis certainly has raised more questions than provided answers. Our sampling is far too fragmentary (compare Fig. 5B) to allow us to say much about the distinctness and distribution of the species in question. Detailed phylogeographic studies and a morphological survey with a fresh look at the immigrated lineages are needed to circumscribe North American *Salicornia* species morphologically and geographically.

From Eurasia to South Africa. — Our ETS analysis revealed two migrations from Eurasia to South Africa (orange boxes in Fig. 4B, C). These are represented by (1) the *Salicornia pachystachya* clade which contains two accessions of *S. pachystachya* and (2) the *Salicornia meyeriana* clade which contains 13 accessions of *S. meyeriana*, *S. uniflora* and several other, so far undescribed taxa.

We assume that *Salicornia perrieri*, which was not studied here also belongs to the *Salicornia pachystachya* clade because both species are found in estuaries of (sub) tropical summer-rainfall regions of the Indian Ocean seaboards of East and South Africa and Madagascar. Because of their morphological similarity (especially in dry herbarium material) Tölken (1967) considered both taxa conspecific (using the name *S. pachystachya*). He has, however, admitted that two “forms“ may be distinguished within his broadly-conceived *S. pachystachya*. Later, Brenan (1988), interpreting a number of differences in architecture (growth-form, ramification) and thickness of the inflorescences, reinstated both taxa as separate species. The taxonomic status of both species remains, however, an open issue (as also admitted by Brenan, 1988) although O'Callaghan (1992) accepted them as two distinct species. The closest relatives of the *Salicornia pachystachya* clade seem to be distributed mainly in western and northern Europe, and not (as might have been expected) in the Eastern Mediterranean or in the Arabian Gulf. This could, however, be a sampling artefact due to the limited sample size from North Africa and the Middle East at our disposal.

The three closest relatives of the *Salicornia meyeriana* clade are distributed in Turkey, northern European Russia and the Aral lakes. The *Salicornia meyeriana* clade is distributed on the West and South Coasts of South Africa and the coast of the Namib Desert (Namibia). These regions have either winter-rainfall (West Coast), or transitional winter-rainfall to summer-rainfall and in places all-year rainfall (South Coast) or erratic and sparse rainfall boosted partly by frequent fog incidence (Namib Desert coast). The lineage shows considerable variation in ETS which might be indicative of substantial diversification and the presence of several sublineages. The clade is not resolved satisfactorily to clearly substantiate the presence of new South African *Salicornia* species, but the deviating morphology of local lineages tentatively called *S.* "*dagmarae*", *S.* "*macrocarpa*" and *S.* "*knysnaensis*", indicates that a complex of evolutionarily young taxa could be singled out. A more detailed study into molecular phylogeny and taxonomy of this clade is underway and will be published elsewhere (G. Kadereit & L. Mucina, in prep.).

Taxonomic difficulties in *Salicornia* and the apparent polyphyly of species. — A serious problem in understanding and interpreting the ETS tree as well as using it for an improved classification of *Salicornia* is the incongruency of taxon names. Plants named as the diploid species *S. europaea*, *S. perennans* and *S. ramosissima* occur in many different clades or groups. If there was a clear morphological circumscription of these three species we would have to conclude that they are highly polyphyletic and their diagnostic characters had evolved several times independently. However, *S. europaea*, *S. ramosissima* and *S. perennans* are notorious for the paucity of reliable morphological characters and the considerable amount of phenotypic plasticity found in these taxa is very difficult to disentangle. This means that lack of diagnostic characters together with misleading phenotypic plasticity are responsible for misidentifications and misapplication of existing names.

Apart from the confusion caused by phenotypic plasticity, the taxonomic difficulties are further aggravated by minute but fixed phenotypic changes that likely resulted in repeated morphological parallelisms in *Salicornia*. One example is the dwarf habit and branching at the cotyledonary node in the subarctic taxa *Salicornia borealis* (diploid) and *S. pojarkovae* (tetraploid). The same characters, however, can be observed in subarctic populations of *S. dolichostachya* and *S. europaea* (M. Piirainen, pers. comm.; S. Beer & D. Sokoloff, pers. obs.) where they are not genetically fixed but environmentally induced. Another example is the reduction of the number of flowers from three to one per cyme which seems to be genetically fixed in *S. uniflora*, *S. pusilla* and *S.* "*knysnaensis*". However, this trait also occurs occasionally in other species such as *S. pojarkovae* (S. Beer, pers. obs.). These examples show that defining *Salicornia* taxa by conspicuous morphological characters could also be misleading even when they are genetically fixed. Other morphological parallelisms are certainly less obvious and even more difficult to detect, especially when they appear in characters related to growth form, branching angle, segment and flower shape.

It is therefore very difficult to realize in the field that plants occurring in the same region and sharing a similar morphology possess different genotypes, such as for instance *S. ramosissima* and *S. europaea* from the Baltic Sea and the five genotypes of *S.* aff. *perennans* found around the Aral lakes, all placed in different groups/clades.

One objection could be that at least in some cases ETS might not be variable enough to resolve morphologically distinct evolutionary units, as, e.g., *S. pusilla* in the *S. ramosissima* clade, *S. heterantha, S. freitagii* and *S. pojarkovae* in the *S. dolichostachya* clade, *S. uniflora* in the *S. meyeriana* clade and *S. borealis* in the *S. rubra* group. Here, fingerprint data might show the monophyly of these taxa. However, in the case of *S. pusilla* an equally plausible hypothesis is that it is an ecotype adapted to colonize the uppermost drift lines in a marsh or on a shore evolving easily and repeatedly from within *S. ramosissima*. *Salicornia ramosissima* and *S. pusilla* appear to form fertile hybrids which means that it is not genetically isolated.

CONCLUSIONS

The ETS data revealed a number of major factors that shaped the phylogeny and biogeography of *Salicornia*. (1) The climatic deterioration from the later Miocene to the early Pleistocene and associated changes in coastal configuration might have favoured the evolution of an annual, strongly inbreeding, diploid lineage from within the perennial *Sarcocornia* in the Paratethys area of Eurasia and triggered the initial diversification of *Salicornia*, with probable remnants detected in inland Crimea and Turkey. (2) Independent polyploidization events resulted in at least two well differentiated and widespread tetraploid lineages which both colonized the lower and middle belts of the saltmarshes in the northern hemisphere and expanded rapidly. (3) At least five intercontinental dispersal events occurred and were in two cases (*S. meyeriana* clade, *S.*

bigelovii/*S. depressa* clades) followed by radiation and rapid expansion in the newly colonized areas. (4) In Eurasia, during the Pleistocene climatic cycles with repeated large-scale range displacements, rapid and effective range expansion of *Salicornia* resulted in widespread inbreeding lines and multiple arrivals of slightly different genotypes especially in non-glaciated regions.

The major reasons for the taxonomic confusion that can be deduced from the sequence data are the young age of the extant lineages, the rampant dispersal of *Salicornia* which led to widespread genotypes with high phenotypic plasticity being given different names in different regions, and morphological parallelism resulting in the fact that different genotypes were given the same name in one region.

A taxonomical perspective. — The problems discussed above are a challenge for further taxonomical studies in *Salicornia*. From this study, the following suggestions for future research in the genus can be derived: (1) Extension of the molecular studies by sampling more individuals especially in the so far missing or poorly represented areas of North Africa, parts of Southwest Asia, East Asia and North America; (2) morphological and cytological investigation of the new, divergent genotypes found in the area from Southwest Asia to East Asia, supplemented by additional sampling to elucidate their respective distribution; (3) verifying the identity of the hitherto described taxa, in particular those from Europe, by typification and careful comparison including molecular data of material collected at type localities; (4) eventually applying a wider species concepts for taxa that are extremely difficult to disentangle, to meet the problems caused by inbreeding lines and satisfy the needs of field biologists and laymen; (5) new species should only be accepted or described when they are morphologically and/or ecologically clearly distinct and when their monophyly has been shown by molecular evidence.

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Appendix. Taxa sampled, vouchers, and GenBank accession numbers; names given in quotation marks are putative new taxa.

Taxon, lab number, voucher specimen (herbaria), collection locality, GenBank accession (more than one entry after a species name indicates multiple accessions for that species)

Outgroups[1]: ***Arthrocnemum macrostachyum*** (Moric.) K. Koch: chen 353; *H. Freitag & N. Adıgüzel 28.846* (KAS, GAZI); Turkey, Seyhan Prov., SE of Adana; EF433587/ ***Halosarcia indica*** (Willd.) Paul G. Wilson subsp. *bidens* (Nees) Paul G. Wilson: chen 558; *S. Jacobs 9135* (NSW); Western Australia, Mortlock River; EF433588/ ***Microcnemum coralloides*** (Loscos & Pardo) Buen subsp. *coralloides*: chen 2002/15; *G. Kadereit 2002/15* (MJG); Spain, Aragón, Laguna de Guallar; EF433589/ ***Tecticornia australasica*** (Moq.) Paul G. Wilson: chen 260; *S. Jacobs 8685* (NSW); Australia, Queensland, N of Townsville; EF433590.

Sarcocornia*: *Sa. ambigua*[2]** (Michx.) M.A. Alonso & M.B. Crespo: chen 894; *P. Teege 05-US-004* (MJG); U.S.A., Massachusetts, Chatham; EF433591/ ***Sa. andina*[2]** (F. Phil.) Freitag, M.A. Alonso & M.B. Crespo: chen 313; *E. García, St. Beck & R. de Michel 600* (LPB, KAS); Bolivia, Oruro Prov., 10 km N of Challapata; EF433592/ ***Sa. blackiana (Ulbr.) A.J. Scott: chen 534; *S. Jacobs 9136* (NSW); Western Australia, Mortlock River; EF433593/ ***Sa. capensis*** (Moss) A.J. Scott: chen 311; *L. Mucina 7202/2* (MJG, STEU); South Africa, Western Cape Prov., Gansbaai, Uilkraalsmond; EF433596/ ***Sa. cuzcoensis*[2]** Freitag, M.A. Alonso & M.B. Crespo (ined.): chen 921; *P. Gutte & G. Müller 9461ab* (LZ); Peru, Dpto. Cuzco, Huacarpay; EF433595/ ***Sa. decumbens*** (Toelken) A.J. Scott: chen 312; *L. Mucina 7205/1* (MJG, STEU); South Africa, Western Cape Prov., Gansbaai, Uilkraalsmond; EF433596/ ***Sa.***

Appendix. Continued.

fruticosa (L.) A.J. Scott: chen 2002/20; *G. Kadereit 2002/20* (MJG); Spain, Cantabria, Noja; EF433597/ ***Sa. littorea*** (Moss) A.J. Scott: chen 382; *L. Mucina 7209/1* (MJG, STEU); South Africa, Western Cape Prov., Gansbaai, Uilkraalsmond; EF433598/ ***Sa. mossiana*** (Toelken) A.J. Scott: chen 593; *Walter & L. Mucina 5060* (MJG, STEU); South Africa, Western Cape, Klein Langkloof; EU000541/ ***Sa. natalensis*** (Bunge ex Ung.-Sternb.) A.J. Scott var. *natalensis*: chen 597; *L. Mucina 260200/1–5* (MJG, STEU); South Africa, Western Cape, Kalbaskraal; EF433600/ ***Sa. neei***[2] (Lag.) M.A. Alonso & M.B. Crespo: chen 329; *F.G. Schröder s.n.,* 12.02.2003 (KAS); Argentine, Patagonia, Chubut Prov., Cabo dos Bahias, Camarones; EF433599/ ***Sa. pacifica*** (Standl.) A.J. Scott: chen 487; *D. Stone 2570* (UC); U.S.A., California, Napa Valley near Vallejo; EF433602/ ***Sa.* aff. *perennis*** (Miller) A.J. Scott: chen 572; *P. Teege chen-572* (MJG); France, Loire-Atlantique, St-Nazaire; EF433603/ ***Sa. pillansii*** (Moss) A.J. Scott: chen 385; *L. Mucina 210901/19S* (MJG, STEU); South Africa, Northern Cape Prov., Namaqualand, Kamieskroon; EF433604/ ***Sa. quinqueflora*** (Bunge ex Ung.-Sternb.) A.J. Scott: chen 331; *N. Schmalz 32* (MJG); Australia, New South Wales, Karuah; EF433601/ ***Sa. utahensis*** (Tidestr.) A.J. Scott: chen 585; *E.H. Zacharias 855* (UC); U.S.A., Utah, Utah County; EF433605/ ***Sa. xerophila*** (Toelken) A.J. Scott: chen 390; *L. Mucina 230901/8* (MJG, STEU); South Africa, Western Cape Prov., Knersvlakte, Vanrhynsdrop, Quaggaskop; EF433606.

Salicornia*: *S. altaica Lomon.: chen 454; *H. Freitag 19.09.03* (KAS); Russia, C Sib. Bot. Gard., seeds from Altai Mts. near Kosh Agach (M. Lomonosova 239/2002); EF433607/ ***S.* "*arabica*"**, ined.: chen 991a; *B. Böer s.n.* (21.09.1992) (KAS); Saudi Arabia, Arabian Gulf, Abu-Ali Island; EF433608/ ***S. bigelovii*** Torrey: chen 896; *P. Teege 05US/021* (MJG); U.S.A., Massachusetts, South Wellfleet; EF433609/ chen 1428; *Moran 19740* (CAS 597787); Mexico, Baja California, NW of Abreojos; EU000542/ ***S. borealis*** Wolff & Jefferies: chen 1048; *Calder 28101* (CAS 469354); Canada, Yukon, between Whitehorse and Haines Junction; EF433610/ chen 1378; *S. Wolff s.n.* (TRT 243075, syntype); Canada, Manitoba, La Perouse Bay; EU000543/ ***S. borysthenica*** Tzvelev: chen 449; *H. Freitag 33.235* (KAS); Ukraine, E Crimea, Arabat'skaya Strelka; EF433611/ ***S.* "*crassa*"**, ined.: chen 610; *A.E. Yaprak 2004-1* (ANK); Turkey, Çorum, Sungurlu, Bahsili; EF433613/ chen 451: *H. Freitag 33.286* (KAS); Ukraine, N Crimea, Krasne Lake near Krasnoperekopsk; EF433614/ ***S.* "*dagmarae*"**, ined.: chen 1091; *S. Steffen & V. Koecke 190406/25* (MJG); South Africa, Western Cape, West Coast, Velddrif, Berg River estuary; EF433615/ chen 1011; *L. Mucina 090306/01* (STEU, MJG); South Africa, Western Cape, Vredenburg, at road to Velddrif; EF433615/ chen 1004; *S. Steffen & V. Koecke 170506/04* (STEU, MJG); South Africa, Western Cape Prov., Velddrif, Berg River estuary; EF433617/ chen 389; *L. Mucina 091200/6-2* (MJG); South Africa, Western Cape Prov., Velddrif, Dwarskersbos; EF433618/ ***S. depressa*** Standley: chen 898; *P. Teege 05US/011* (MJG); Canada, Québec, St. André; EF433619/ chen 899; *P. Teege 05US/032* (MJG); U.S.A., Rhode Island, Wakefield; EF433620/ chen 488; *D. Stone 2571* (UC); U.S.A., California, Napa Valley, San Francisco Bay; EF433621/ chen 1043; *P.W. Ball 94235ter; plant A* (TRTE, Ball); U.S.A., Virginia, Gloucester Co., E of Williamsburg; EF433622/ chen 1115; *P.W. Ball 94235ter; plant D* (TRTE, Ball); U.S.A., Virginia, Williamsburg E of Williamsburg; EF433623/ chen 901; *P. Teege 05US/029* (MJG); U.S.A., New Jersey, Highlands, Sandy Hook; EF433624/ chen 900; *P. Teege 05US/026* (MJG); Canada, Québec, Trois Pistoles; EF433625/ ***S. dolichostachya*** Moss: chen 957; *P. Teege 04F/0050* (MJG); France, Morbihan, Riantec; EF433630/ chen 961; *P. Teege 04F/0059* (MJG); France, Manche, Sainte-Marie-du-Mont; EF433631/ chen 964; *P. Teege 04F/0048*_2 (MJG); France, Îlle-et-Vilaine, Le-Vivier-sur-Mer; EF433632/ chen 966; *P. Teege 04F/0098* (MJG); France, Somme, St-Valerie-sur-Somme; EF433633/ chen 633; *A.E. Yaprak 2004-85* (ANK); Turkey, Izmir, Çamalti saltworks; EF433634; chen 958; *P. Teege 04F/0046* (MJG); France, Loire-Atlantique, La Turballe; EF433635/ chen 974; *P. Teege 04/chen 974* (MJG); Germany, North Sea, Schleswig-Holstein, Büsum; EF433636/ chen 989b; *P. Teege 04GB/0034* (MJG); Great Britain, Kent, Isle of Sheppey; EF433637/ chen 990b; *P. Teege 04GB/0016* (MJG); Great Britain, Kings Lynn & West Norfolk, Brancaster Staithe; EF433638; chen 2002/5; *G. Kadereit 2002/5* (MJG); Spain, Delta del Ebro, Punta del Falgar; EF433639/ ***S.* aff. *emerici*** Duval-Jouve: chen 988a; *H. Freitag 30.012* (KAS); Italy, Adriatic coast, Puglia, saltworks of Trinitapoli; EF433640/ chen 631; *A.E. Yaprak 2004-81*(ANK); Turkey, Aydın, Söke, Doganbey; EF433641/ ***S. europaea*** L.: chen 993a; *H. Freitag 34.076* (KAS); Germany, Mecklenburg-Vorpommern, Zingst; EF433642; chen HK A_20; *P. Teege HK* A_20 (MJG); Germany, North Sea Schleswig-Holstein, Büsum; EF433643/ chen 991b; *P. Teege 04GB/0061* (MJG); Great Britain, East Sussex, Seaford; EF433644/ chen 999; *B. Böer s.n.*, 1996 (KAS); United Arab Emirates, Ras-al-Khaimah; EF433645/ chen 854; *Y.S. Momonoki s.n.*, July 2005 (no voucher); Japan, Hokkaido, Abashiri, Lake Notoro; EF433646/ ***S.* aff. *europaea*** L.: chen 627; *A.E. Yaprak 2004-64b* (ANK); Turkey, Denizli, Çardak, Acı Göl; EF433647/ chen 484; *S. Pankova (Beer) 7* (MW); Russia, Arkhangel'sk Prov., Primorsk region; EF433648/ ***S.* aff. *fragilis*** P.W. Ball & Tutin: chen 2002/2; *G. Kadereit 2002/2* (MJG); France, Camargue, Le-Grau-du-Roi; EF433649/ chen 962; *P. Teege 04F/0060* (MJG); France, Manche, St-Marie-du-Mont; EF433650/ chen 963; *P. Teege 04F/0100* (MJG); France, Somme, St-Valerie-sur-Somme; EF433651/ ***S.* "*freitagii*"** ined.: chen 611; *A.E. Yaprak 2004-5* (ANK); Turkey, Çorum, Sungurlu, Bahsili; EF433652/ chen 1274; *A.E. Yaprak 2006-73* (ANK); Turkey, Ankara,Sereflikoçhisar; EU000544; ***S. heterantha*** S.S. Beer & Demina: chen 719; *Pankova & Demina 8.1* (MW); Russia, Rostov Prov., Proletarsk, Manych river vall.; EF433653/ ***S.* "*knysnaensis*"** ined.: chen 381; *J. Walter & L. Mucina 5050* (MJG, STEU); South Africa, Western Cape Prov., Knysna Lagoon, George Rex Drive; EF433654/ ***S.* "*macrocarpa*"** ined.: chen 459; *L. Mucina 6937/2* (MJG, STEU); South Africa, Eastern Cape Prov., Jefferey's Bay, Paradise Beach; EF433655/ chen 946; *L. Mucina 5025* (MJG, STEU); South Africa, Eastern Cape Prov., Cape St. Francis, Kromme River estuary; EF433656/ chen 935; *L. Mucina 6928/3* (MJG, STEU); South Africa, Eastern Cape Prov., Gamtoos River mouth; EF433657/ ***S. maritima*** Wolff & Jefferies: chen 897; *P. Teege 05US/008* (MJG); Canada, Québec, St. André; EF433658/ chen 1049; *M J. Oldham 21044* (TRTE 63962); Canada, Prince Edward Island, SW of Summerside; EF433659/ chen 1046; *M.J. Oldham 21164* (TRTE 63963); Canada, Québec, Magdalen Islands, Ile du Havre Aubert; EF433660/ chen 1379; *S. Wolff 1984* (TRT 243066); Canada, Quebec, Rimouski; EU000545/ ***S. meyeriana*** Moss: chen 1007; *S. Steffen & V. Koecke 200406/13* (STEU, MJG); South Africa, Western Cape, Cape Town, Milnerton, Rietvlei Nature Reserve (loc. class.); EF433661/ chen 923; *J. Walter & L. Mucina 5103* (MJG, STEU); South Africa, Western Cape Prov., Gansbaai, Uilkraalsmond; EF433662/ chen 924; *J. Walter & L. Mucina 5097* (MJG, STEU); South Africa, Western Cape Prov., Struisbaai, De Mond Nat. Res.; EF433663/ ***S.* aff. *meyeriana*** Moss: chen 587; *L. Mucina 6917/1* (STEU); South Africa, Western Cape Prov., Agulhas Plain,

Appendix. Continued.

Elim; EF433664/ ***S. "narmanii"*** ined.: chen 616; *A.E. Yaprak 2004-16* (ANK); Turkey, Erzurum, Narman, Narman to Oltu; EF433665/ ***S. pachystachya*** Bunge ex Ung.-Sternb.: chen 384; *L. Mucina 080701/2* (MJG, STEU); South Africa, Kwa Zulu-Natal Prov., St. Lucia Wetland Park; EF433666/ chen 1395; *S. Naidoo 080207/02* (MJG, STEU); Kwa Zula-Natal, Elephant Coast, Richards Bay; EU000546/ ***S. patula*** Duval-Jouve: chen 2002/1; *G. Kadereit 2002/1* (MJG); France, Camargue, Le-Grau-du-Roi; EF433667/ chen 1304; *A.E. Yaprak 2006/31* (ANK); Turkey, Izmir, Selçuk, Pamucak, Pamucak to Ephessus; EU000561/ chen 635; *A.E. Yaprak 2004-96* (ANK); Turkey, Çanakkale, Gelibolu, Kavak Çoragı; EF433668/ ***S.*** **aff.** ***patula*** Duval-Jouve: chen 636; *A.E. Yaprak 2004-98* (ANK); Turkey, Edirne, Kesan, Erikli; EF433669/ chen 366; *H. Freitag 31.308* (KAS); Italy, SE Sicily, near Pachino; EF433670/ chen 490; *G. Kadereit s.n.*, 06.2004 (no voucher); Italy, Toscana, Marina di Grosseto; EF433671/ chen 613; *A.E. Yaprak 2004-12*; Turkey, Sivas, Zara, Tödürge Gölü; EF433672/ chen 987a; *H. Freitag 30.018* (KAS); Italy, Adriatic coast, Puglia, Gargano Peninsula, Vieste; EF433673/ chen 365; *H. Freitag 31.313* (KAS); Italy, S Sicily, near Gela; EF433674/ chen 1252; *H. Freitag 20.10.06* (KAS); Italy, Apulien, Cileste; EU000547/ ***S. perennans*** Willd.: chen 445; *H. Freitag 33.242* (KAS); Ukraine, NE Crimea, S Kazantip Peninsula, Aktas'ke lake; EF433675/ chen 323; *H. Freitag 28.130a* (KAS), erect form; NW Kazakhstan, Ural'sk Prov., near Kalmykovo (loc. class.); EF433676/ chen 322; *H. Freitag 28.130b* (KAS); prostrate form; NW Kazakhstan, Ural'sk Prov., near Kalmykovo (loc. class.); EF433677/ chen 359; *G. Kadereit 2003/5* (MJG); Hungary, Kecskemét, Kiskunsági Nemzeti Park; EF433678/ chen 448; *H. Freitag 33.220* (KAS); Ukraine, SE Crimea, Barakol' lake near Koktebel'; EF433679/ chen 472; *H. Freitag 33.272* (KAS); Ukraine, W Crimea, Saks'ke Lake near Saki; EF433680/ chen 480; *S. Pankova (Beer) 3* (MW); Russia, Rostov Prov., Rostov-on-Don environs; EF433681/ chen 481; *S. Pankova (Beer) 4* (MW); Russia, Rostov Prov., Manych river valley; EF433682/ chen 395; *M. Höhn s.n.* (MJG); Romania, Mures, Reghin, Ideci Bai; EF433683/ chen 396; *M. Höhn s.n.* (MJG); Romania, Mures, Sovata, Praid; EF433684/ chen 379; *A.-M. Csergo s.n.*, 2003 (MJG); Romania, Northern Transsylvania, EF433685/ chen 473; *H. Freitag 33.272* (KAS), prostrate form; Ukraine, W Crimea, Saks'ke lake near Saki; EF433686/ chen 865; *W. Wucherer, sample 3*; 09.2004 (no voucher); W Kazakhstan, Kambash Lake near Small Aral Lake; EF433687/ ***S.*** **aff.** ***perennans*** Willd.: chen 1359; *B. Neuffer 10195* (OSBU); Austria, Neusiedler See, near Ilmitz; EF433755/ chen 601; *W. Wucherer sample 1; 09.2003* (no voucher); W Kazakhstan, Small Aral Lake, Aralsk Bay; EF433688/ chen 720 (and chen 856); *Pankova & Demina 9.1* (MW); Russia, Rostov Prov., Proletarsk, Manych River vall.; EF433689/ chen 467; *H. Freitag 33.030* (KAS); Russia, Tuva, Cheder lake SSE of Kyzyl; EF433690/ chen 455; *H. Freitag 33.055a* (KAS); Russia, Tuva, Shara-Nur lake W of Erzin; EF433691/ chen 450; *H. Freitag 33.151* (KAS); Russia, Chita Prov., NE of Zaibaikal'sk, Khara-Nur lake; EF433692/ chen 357; *G. Kadereit 2003/1* (MJG); Hungary, Hortobágyi Nemzeti Park; EF433693/ chen 339; *M. Lomonosova 277* (NS); Russia, S Siberia, Irkutsk Prov., near Usol'e Sibirskoye; EF433694/ chen 863; *W. Wucherer*, *sample 3a*; 09. 2004 (no voucher); W Kazakhstan, shore of Small Aral Lake, W Amanotkel'; EF433695/ chen 864; *W. Wucherer*, ditto, *sample 2a* (no voucher); ditto; EF433696/ chen 602; *W. Wucherer*, ditto, *sample 3a* (no voucher); W Kazakhstan, Kambash Lake near Small Aral Lake; EF433697/ chen 990a; *H. Freitag 30.166* (KAS); Jordania, Dead Sea, S of Wadi el Mujib; EF433698/ chen 617; *A.E. Yaprak 2004-19* (ANK); Turkey, Igdır, Tuzluca; EF433699/ chen 992a; *H. Kürschner & M. Sonnentag 00–626* (BSB, KAS); China, Nei Menggu Prov., 5 km S of Ejin Qi; EF433700/ chen 340; *B. Neuffer& H. Hurka 13624* (NS, OSBU, KAS); Russia, Altai Republic, NE of Aleysk at river Chaplaya; EF433701/ chen 446; *V. Zacharova 09.2003* (CTAB sample only); Russia, E Siberia, Yakutsk; EF433702/ chen 453; *H. Freitag 33.073* (KAS); Russia, Tuva, Uyuk Valley near Arzhaan; EF433703/ chen985a; *H. Freitag 33.101* (KAS); Russia, Novosibirsk Prov., Karasuk distr., 20 km N of K.; EF433704/ chen 447; *H. Freitag 33.061* (KAS); Russia, Tuva, Duz-Khol NW of Erzin; EF433705/ chen 1246; *I. Mehregan s.n.*, 19.10.2006 (MJG); Iran, Fars, N Tash, lake between Neiriz & Arsenjan; EU000548/ ***S. persica*** Akhani: chen 1247; *I. Mehregan s.n.*, 19.10.2006 (MJG); Iran, Fars, N Tash; 1590 m; lake between Neiriz & Arsenjan; EF433706/ chen 1243; *Moazzeni 35040* (MJG); Iran, Fars, Shiraz, Pol-e Fasa; EU000549/ chen 1244; *Moazzeni s.n.* (MJG); Iran, Fars, Shiraz, Maharlu Lake; EU000550/ chen 1245; *Moazzeni s.n.* (MJG); Iran NW of Tehran, Karaj, Mardabad; EU000551/ ***S. pojarkovae*** Semenova: chen 478; *S. Pankova 1* (MW); Russia, Karelia, White Sea, Kandalaksha Bay, Monastyrski Island; EF433707/ chen 479; *S. Pankova 2* (MW); Russia, Karelia, Loukhi distr., Peninsula Kindo; EF433708/ ***S. procumbens*** Sm. in Sowerby: chen HK 19_1; *P. Teege HK 1*9_1 (MJG); Germany, North Sea, Schleswig-Holstein, Büsum; EF433709/ chen HK 13_2; *P. Teege HK 1*3_2 (MJG); Germany, North Sea, Schleswig-Holstein, Büsum; EF433710/ chen 952; *P. Teege s.n.*, 2005 (MJG); Germany, North Sea, Schleswig-Holstein, Marne; EF433711/ chen 953; *P. Teege s.n.*, 2005 (MJG); Germany, North Sea, Schleswig-Holstein, Meldorf; EF433712/ chen 973; *P. Teege 04/*chen 973; Germany, North Sea, Schleswig-Holstein, Klanxbül; EF433713/ chen 975; *P. Teege 01.1/*chen 975; Germany, North Sea, Schleswig-Holstein, Büsum; EF433714/ ***S. pusilla*** J. Woods: chen 985b; *P. Teege 04/GB0046* (MJG); Great Britain, Kent, Chellness; EF433715/ chen 986b; *P. Teege 04/GB0010* (MJG); Great Britain, Suffolk Coastal Walberswick; EF433716/ chen 987b; *P. Teege 04/GB0007* (MJG); Great Britain, Hampshire, Hayling Island; EF433717/ chen 988b; *P. Teege 04/GB0006* (MJG); Great Britain, North Norfolk; EF433718/ chen 959; *P. Teege 04F/0080* (MJG); France, Manche, Portbail; EF433719/ chen 960; *P. Teege 04F/0039* (MJG); France, Somme, Le Crotoy; EF433722/ chen 574; *P. Teege 04F/0064* (MJG); France, Îlle-et-Vilaine, Hirel; EF433721/ ***S. ramosissima*** J. Woods: chen 951; *P. Teege s.n., 2005* (MJG); Germany, North Sea, Schleswig-Holstein, Marne; EF433725/ chen 954; *P. Teege s.n., 2005* (MJG); Germany, North Sea, Schleswig-Holstein, Helmsand; EU000552/ chen 972; *P. Teege 04/chen 972* (MJG); Germany, North Sea, Schleswig-Holstein, Klanxbül; EF433726/ chen 976; *G. Kadereit 200*3_H*K1* (MJG); Germany, North Sea, Schleswig-Holstein, Büsum; EF433727/ chen 977; *G. Kadereit* 2003_WL4 (MJG); Germany, North Sea, Schleswig-Holstein, Westerhever; EF433728/ chen HK 21_19; *P. Teege HK 2*1_1*9* (MJG); Germany, North Sea, Schleswig-Holstein, Büsum; EF433729/ chen Grasw.3; *G. Kadereit s.n.*, 2001 (MJG); Germany, Baltic Sea, Schleswig-Holstein, Heiligenhafen, Graswarder; EF433730/ chen Boinsw.1; *G. Kadereit s.n.*, 2001 (MJG); Germany, Baltic Sea, Mecklenburg-Western Pomerania, Boiensdorf; EF433731/ chen 955; *P. Teege s.n.*, 2005 (MJG); Germany, Lower Saxony, Ilten; EF433732/ chen Jerx.1; *G. Kadereit s.n.*, 2001 (MJG); Germany, Lower Saxony, Jerxheim; EF433733/ chen Arte.3; *G. Kadereit s.n.*, 2001 (MJG); Germany, Thuringia, Artern; EF433734/ chen 968; *P. Teege 04F/0061* (MJG); France, Manche, St-Marie-du-Mont; EF433735/ chen 970; *P. Teege 04F/0097* (MJG); France, Somme, St-Valerie-sur-Somme; EF433736/ chen 992b; *P. Teege 04GB/0058* (MJG); Great Britain, East Sussex,

Appendix. Continued.

Seaford; EF433737/ chen 993b; *P. Teege 04GB/0040* (MJG); Great Britain, Kent, Isle of Sheppey; EF433738/ chen 967; *P. Teege 04F/0084* (MJG); France, Manche, Portbail; EF433739/ chen 2002/22; *G. Kadereit 2002/22* (MJG); Spain, Delta del Anson, Marisma de Santona; EF433740/ chen 1248; *G. Kadereit 2006/30* (MJG); Spain, Almeria, Cabo de Gata; EU000553/ chen 393; *F. Sales & I. Hedge 00/108* (KAS); Portugal, Algarve, Tavira, Olhao, Park of Ria Formosa; EF433741/ chen 2002/19; *G. Kadereit 2002/19* (MJG); Spain, Cantabria, Noja, Playa de Ris; EF433742/ chen 1249; *G. Kadereit 2006/31* (MJG); Spain, Granada, El Hondo, Laguna del Fondo; EU000554/ chen 1250; *G. Kadereit 2006/35* (MJG); Spain, Granada, Laguna de Piedra; EU000555/ chen 2002/13; *G. Kadereit 2002/13* (MJG); Spain, Alcaniz, Salada Grande; EF433743/ chen 965; *P. Teege 04F/0048*_1 (MJG); France, Îlle-et-Vilaine, Le-Vivier-sur-Mer; EF433744/ chen 1251; *G. Kadereit 2006/40* (MJG); Spain, Granada, Laguna Dulce; EU000556/ ***S.* aff. *ramosissima*** J. Woods[3]: chen 971; *P. Teege 04F/0036* (MJG); France, Somme, Le Crotoy; EF433722/ chen 969; *P. Teege 04F/0106* (MJG); France, Somme, St.-Valerie-sur-Somme; EF433723/ chen 956; *P. Teege 04F/0063* (MJG); France, Manche, Sainte-Marie-du-Mont; EF433724/ ***S. rubra*** Nelson: chen 1044; *A. Tiehm 11561* (CAS 766229); U.S.A., Nevada, Nye County, Little Fish Lake (alt. 1970m); EF433745/ chen 1044; *A. Tiehm 11561* (CAS 766229); U.S.A., Nevada, Nye County, Little Fish Lake (alt. 1970m); EF433745/ chen 1436; *A. Tiehm 10022* (CAS 814829); U.S.A., Nevada, Elko County, Tecoma valley; EU000557/ chen 1112; *Mason 713* (CAS 418046); U.S.A., California, Redwood City; EF433746/ chen 1041; *S. Hay 88375* (TRTE 44820); Canada, Québec, Laprairie (introduced); EF433747/ chen 1419; *Reznicek 7456* (TRTE 47234); U.S.A., Michigan, Wayne County; EU000558/ chen 1376; *B. Heidel 1750* (TRT 256287); U.S.A., Montana, Gallatin County, Three Forks; EU000559/ chen 1417; *Ringius & al. 977* (MT); Canada, Ontario, Western James Bay; EU000560/ ***S.* "*sibirica*"** ined.: chen 468; *H. Freitag 33.074* (KAS); Russia, Tuva, 70 km NW Kyzyl, near Arzhaan; EF433748/ ***S. uniflora*** Toelken: chen 1009; *L. Mucina 061205/14* (STEU, MJG); Namibia, Lüderitz, Second Lagoon; EF433749/ ***S. veneta*** Pignatti & Lausi: chen 989a; *H. Freitag 27.169* (KAS); Italy, Prov. Venezia, Lido di Jesolo; EF433750/ ***S.* sp.**: chen 994; *H. Freitag 19.812* (KAS); Greece, Peleponnissos, Patras, Varda Lagoon; EF433751/ chen 363; *H. Freitag 31.302* (KAS); Italy, SE Sicily, near Pachino; EF433752/ chen 482; *S. Pankova (Beer) 5* (MW); Russia, Astrakhan Prov., Narimanov; EF433753.

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[1] According to Kadereit & al. 2006.

[2] The combinations *Sarcocornia ambigua*, *S. andina*, *S. neei* and the new species *S. cuzcoensis* will be published in forthcoming papers (Alonso, Crespo & Freitag, in prep.; Alonso & Crespo, in press).

[3] aff. *Salicornia brachystachya* sensu Lahondére 2004.