Taxonomic status of diploid Salicornai europaea (s.L.) (Chenopodiaceae) in northeastern North America.

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ABSTACT

The taxonomic status of diploid Salicornia europaea L. (s.1.) in northeastern North America has been evaluated based on morphological and electrophoretic variation within and between populations. Populations of two European diploid micro- species, S. ramosissima J. Woods and S. europaea (s.s.), and populations of the midwestern diploid, S. rubra A. Nels., were also examined, affording a comparison between North American S. europaea (s.1.) and recognized species. Anther length, width of the scarious border of the fertile segment, and floral perianth shape were used to subdivide North American diploid populations into two groups. These groups were morphologically distinct from S. rubra and the European microspecies. The electrophoretic profile was unique in each morphologically distinct group of populations of S. europaea (s.1.) in northeastern North America. Based on morphological, geographical, and electrophoretic differences, diploid populations of S. europaea (s.1.) from this region are assigned to one of the following two new species: S. maririma Wolff & Jefferies, sp.nov., and S. borealis Wolff & Jefferies, sp.nov. The tetraploids are retained in S. europaea (s.1.).

INTRODUCTION

Salicomia europaea L. (s.1.) (Chenopodiaceae), an annual halophyte, is a colonizer of bare sediments in coastal and inland salt marshes. Identification and description of taxa at the species level are extremely difficult because of a reduced vegetative and floral morphology and an autogamous breed- ing system. Few constant characters are available to delimit species, and these are often obscured by the marked pheno- typic plasticity of individuals (Dalby 1962; Ball and Brown 1970; Ungar et al. 1979; Jensen and Jefferies 1984).

Present-day classifications of European members of Sali- comia emphasize ploidy level (Ball and Tutin 1959; Konig 1960; Ball 1964a, 19646; Hansen and Pedersen 1968; Scott 1977), with diploid taxa described as microspecies. Morphological characters, such as anther length (Ball and Brown 1970), width of

the scarious border (Ball 1964a), and shape of the fertile segment (Ball and Tutin 1959), aid in delimitation.

Recent research concerning New World members of the genus (Wolff and Jefferies 1987) has shown that three distinct morphological groups exist within S. europaea (s.1.) in north- eastern North America. These groups, differing in chromo- some number and geographical location, are Atlantic coast tetraploids, Atlantic coast diploids, and Hudson Bay diploids. Anther length, width of the scarious border of the fertile seg- ment, length and width of the fertile segment, and lengths and widths of the central and lateral perianth are the primary morphological characters used to separate the groups from each other and from inland midwestern diploid populations of S. rubra A. Nels. (Wolff and Jefferies 1987).

Evidence of electrophoretic variation between two diploid microspecies of S. europaea (s.1.) in England provided support for the taxonomic scheme of Ball (1 9 6 4 ~) .Jefferies and Gottlieb (1982) found that S. europaea (s.s.) and S. ramosissima differed completely in electrophoretic profile at six enzyme loci, which exhibited allelic variation. The electro- phoretic mobilities of 24 other enzymes were identical in all plants. Individuals of the two microspecies were easily distinguished from each other by their electrophoretic banding patterns: each microspecies exhibited a unique set of alleles for the six loci. Similarly, the electrophoretic profiles of S. euro-

paea (s.1.) in northeastern North America provided qualitative criteria for identification of the three morphological groups (Wolff and Jefferies 1987).

In this study, morphological and electrophoretic comparisons were made among the diploid members of S. europaea (s.1.) from North America, ***S.*** rubra from inland midwestern North America, and two European diploid microspecies, S. europaea (s.s.) and S. ramosissima. Based on morpho- logical and electrophoretic divergences, a formal description at the species level is given for each of the two diploid groups present within S. europaea (s.1.) in northeastern North America.

METHOD

Salicornia europaea (s.1.) was collected from 31 sites in northeastern North America during the late spring and summer of 1983,1984, and 1985 (Wolff 1985; Wolff and Jefferies 1987). Plants from 16 diploid populations were sampled. In August 1985, plants were also collected from 12 populations of the inland diploid, ***S.*** *rubra* (Wolff 1985; Wolff and Jefferies 1987). During August 1984 and 1985, six populations of S. *europaea* (s.s.) and eight populations of S. *ramosissima* were sampled from locations in southern

England and Jutland, Denmark (Table 1).

At each site at least 30 plants were collected. Mature plants (those that had set seed in the lower fertile segments of the spicate inflorescences, with upper segments still in flower) were obtained. All plants were washed free of sediment, refrigerated, and transported to the University of Toronto. The interval of time between collection of plants and anival in Toronto was 10 days or less.

TABLE 1. *Salicornia europaea* L. (s.s.) and *S. ramosissima* J. Woods: collection sites in England and Jutland, Denmark

Collection no.	Microspecies	Location	Latitude	Longitude
*EN1	*S. ramosissima*	Upper marsh, Hayling Island, Hampshire, United Kingdom	50°50′ N	0°58′ W
EN2	*S. ramosissima*	Shingle St., River Orwell, Essex, United Kingdom	52°02′ N	1°57′ E
ST1	*S. ramosissima*	Upper marsh, Stiffkey, Norfolk, United Kingdom	52°57′ N	0°56′ E
ST2	*S. europaea*	Upper marsh, Stiffkey, Norfolk, United Kingdom	52°57′ N	0°56′ E
ST6	*S. ramosissima*	Upper marsh, Stiffkey, Norfolk, United Kingdom	52°57′ N	0°56′ E
ST7	*S. europaea*	Lower marsh, Stiffkey, Norfolk, United Kingdom	52°57′ N	0°56′ E
ST9	*S. europaea*	Lower marsh, Stiffkey, Norfolk, United Kingdom	52°57′ N	0°56′ E
KA1	*S. ramosissima*	Kalo, Jutland, Denmark	56°17′ N	10°29′ E
KA2	*S. ramosissima*	Kalo, Jutland, Denmark	56°17′ N	10°29′ E
KA3	*S. ramosissima*	Kalo, Jutland, Denmark	56°17′ N	10°29′ E
RO1	*S. europaea*	Rømø, Jutland, Denmark	55°08′ N	8°31′ E
RO2	*S. europaea*	Rømø, Jutland, Denmark	55°08′ N	8°31′ E
SK1	*S. europaea*	Skallingen, Jutland, Denmark	55°30′ N	8°17′ E
SK3	*S. ramosissima*	Skallingen, Jutland, Denmark	55°30′ N	8°17′ E
SK5	*S. europaea*	Skallingen, Jutland, Denmark	55°30′ N	8°17′ E

*Type locality of *S. ramosissima* J. Woods.

Morphometric analysis

A series of measurements of 20 continuous morphological characters (i.e., lengths and widths of vegetative and floral structures; Wolff and Jefferies 1987) was obtained from 20 plants of each population, along with descriptions of five discrete and qualitative characters: the presence of exerted anthers, shape of the central perianth, habit, branch angle, and branch shape. The measures for each continuous character were grouped according to population and log-transformed. All statistical analyses were run using a statistical computing package, SPSS (Nei *et al*. 1975). Heteroscedastic characters (determined by one-way analysis of variance and Cochran's C test for homogeneity of variance) were excluded from further statistical analysis. The following 10 characters were homoscedastic: anther length, width of the scarious border, length and width of the central perianth, length and width of the lateral perianth, length of the fertile segment, and three widths of the fertile segment measured at top, middle, and bottom of the segment. These characters were included in subsequent statistical analyses.

The reduced data set was subjected to a Pearson's correlation analysis. No character pairs equalled or exceeded a Pearson product- moment correlation of 0.90 (P.

W. Ball, personal communication). Each of the 10 characters, again grouped by population, was subjected to a one-way ANOVA and a least significant difference (LSD) *a posteriori* test. The LSD test was used to determine if morphological characters could be used singly to group or separate populations.

Two discriminant analyses were performed on the morphological data, one comparing the two European microspecies morphologically and one comparing all diploid populations measured in North America and Europe. Populations served as the *a priori* grouping. Canonical variates were derived from variance-covariance matrices. A Wilks' lambda stepwise procedure was used in the computation on the canonical variates (Klecka 1980). Classification procedures based upon the derived canonical variates assigned individuals to the popu- lation to which they had the highest morphological affinity. Discriminant analyses of North American populations have been documented previously (Wolff and Jefferies 1987).

Electrophoretic analysis

Sample preparation and electrophoretic analysis followed the methods described in Wolff and Jefferies (1987). Initially 21 enzymic systems were screened electrophoretically; 16 systems exhibited no variation either within or between populations of the different species. At least 20 individuals from each population were screened for the five enzyme systems that showed isozymic variation within the genus (Wolff and Jefferies 1987). The five systems were phosphoglucomutase (PGM, EC 5.4.2.2). asoartate aminotransferase (AAT. EC 2.6.1'. 1) , malic enzyme (ME, 'EC 1.1.1.40), alcohol dehydro: genase (ADH, EC 1.1.1. 1) , and malate dehydrogenase (MDH, EC 1.1.1.37) .

Results

Based on univariate tests of least significant difference, five characteristics examined, anther length, width of the scarious border, and length to width ratios of the fertile segment (width measured at midsegment), of the central perianth and of the lateral perianth, resulted in a separation of North American and European populations into a number of groups (Table 2).

TABLE 2. Means (mm), standard errors, *F*-values, and results of LSD tests for five morphological characters measured in North American *Salicornia europaea* (s.l.), *S. rubra*, *S. europaea* L. (s.s.), and *S. ramosissima*

	Atlantic coast diploids (n = 240)		Hudson Bay diploids (n = 80)		*S. rubra* (n = 240)		*S. europaea* L. (s.s.) (n = 115)		*S. ramosissima* (n = 134)		
Character	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	*F*-value
Anther length	0.206*a*	0.002	0.342*c*	0.005	0.328*b*	0.003	0.711*e*	0.006	0.472*d*	0.007	1938.95
Width of scarious border	0.236*b*	0.003	0.152*a*	0.003	0.235*b*	0.002	0.289*c*	0.004	0.296*c*	0.004	231.7
Length to width ratio											
Central perianth	1.04*a*	0.007	1.03*a*	0.012	1.02*a*	0.008	1.38*c*	0.025	1.10*b*	0.010	141.9
Lateral perianth	1.17*b*	0.006	0.998*a*	0.013	1.02*a*	0.008	1.43*d*	0.028	1.30*c*	0.015	158.8
Fertile segment	1.33*c*	0.014	0.916*a*	0.011	1.21*b*	0.012	1.58*d*	0.025	1.53*d*	0.018	173.0

NOTE: Group means followed by different letters were significantly different ($p \leq 0.05$) in the LSD test. Degrees of freedom for all characters: 4, 804; all *F*-values were highly significant ($p \leq 0.001$). n, number of plants. ANOVA and LSD tests based on log-transformed data.

Both S. *ramosissima* and *S. europaea* (s.s.) exhibited significantly longer anthers than their North American counterparts. Indi- viduals of S. *europaea* (s.s.) had the largest anthers of any group. Width of the scarious border separated diploid and tetraploid plants of S. *europaea* (s.1.) from northeastern North America into three significantly different groups (Wolff and Jefferies 1987). In the present analyses, both European micro- species contained individuals with wider scarious borders than those observed within the North American groups. Although width of the scarious border was shown to be different between North American and European diploids and among North American diploids, this character afforded no separation of the European microspecies.

Four significant groups were formed when the length to width ratio of the fertile segment was examined (Table 2). Hudson Bay diploids exhibited the smallest ratio. This was the only group composed of individuals with segments wider than long. The two European microspecies were placed together into one significant subset; individuals had the largest ratio values, as fertile segments were much longer than wide. *Sali- comia rubra* and Atlantic coast diploids exhibited ratios inter- mediate in value.

Analysis of length to width ratios of the central and also of the lateral perianth resulted in the separation of North American diploids from the European microspecies (Table 2). The ratios for the three North American groups, Atlantic coast diploids, Hudson Bay diploids, and *s.-rubra,* were signifi- cantly smaller than those of either European microspecies. Values for each of the two ratios were significantly different between the two European microspecies.

In the discriminant analysis of populations of *S. europaea* (s.~.a)nd *S. rarnosissima,* the total set of six canonical variates (CVl -CV6) was highly

significant (chi-squared conversion of Wilks' lambda = 27.825, DF = 9, $p <$ 0.001). The first three canonical variates explained 90.1% of the variation encountered between populations. Anther length (CV 1, stand- ardized canonical variate coefficient (SCVC) = 0.91), width at the top of the fertile segment (CV2, SCVC = 0.65), and length of the lateral perianth (CV3, SCVC = 1.73) were the three characters thatcontributed most strongly to the separa- tion of populations. Discrimination among populations by the stepwise analysis resulted in the formation of two clusters of individuals, one composed of members of *S. europaea* (s.s.) and the other of members of *S. ramosissima*.

The assignment of individuals to populations of the correct microspecies was high, 100.0% in *S, europaea* (s.s.) and 99.3% in *S. rarnosissima*. Only one individual of *S. ramosis- sima* was placed into a *S. europaea* population by the classi- fication procedure. The large percentage of correct assignment of individuals to microspecies illustrated the high level of morphological divergence between the microspecies.

The second discriminant analysis examined morphological similarity and divergence among North American diploid populations of *S. europaea* (s.l.), *S. rubra,* and the two Euro- pean microspecies. The set of six canonical variates was highly significant (chi-squared = 246.1, D F = 3 7 , p $<$ 0.0001). The first three canonical variates accounted for 91.5% of the total variation. The morphological characters that contributed most strongly to the discriminating power of the analysis were anther length (CV1, SCVC = 0.92), width at midsegment (CV2, SCVC = 0.68), width of the scarious border (CV2, SCVC = -0.68), and length of the lateral perianth (CV3, SCVC = -0.85). Five clusters of individuals were formed.

These clusters were identifiable as diploid *S. europaea* (s.1.) from the Atlantic coast, diploid *S. europaea* (s.1.) from Hudson Bay, *S. rubra, S. ramosissima,* and *S. europaea* (s . ~ .) .

The results of the classification procedure are given in Table 3. Classification of individuals into their original geographic group or microspecies was greater than 92.0% in all five cases. At most, 17 individuals (7.1 %) from a specific group were placed with groups other than their group of origin. No member of the North American *S. europaea* (s.1.) was classi- fied with the diploid European microspkcies.

TABLE 3. Classification results of the discriminant analysis of North American diploid populations of *S. europaea* (s.l.) and populations of *S. rubra*, *S. europaea* (s.s.), and *S. ramosissima*. Individuals grouped *a priori* by population

Group	No. of individuals	% assigned to original group	% assigned to other groups				
			ACD	HB	RUB	EUR	RAM
Diploid *S. europaea* (s.l.)							
Atlantic coast and James Bay (ACD)	240	97.1	–	–	2.9(8)	–	–
Hudson Bay (HB)	80	92.5	–	–	7.5(6)	–	–
S. rubra (RUB)	240	92.9	5.0(12)	0.4(1)	–	0.4(1)	1.3(3)
S. europaea (s.s.) (EUR)	115	100.0	–	–	–	–	–
S. ramosissima (RAM)	134	96.3	–	0.7(1)	1.5(2)	1.5(2)	–

NOTE: Numbers in parentheses are number of individuals placed in group.

Electrophoretic results

Isozyme banding patterns and the relative mobilities of bands are given in Table 4. Anodal band migration was observed in all systems. The number of loci and alleles present in each enzyme system was inferred from the banding patterns and the currently accepted number of loci coding specific enzyme systems in vascular plants (Gottlieb 1981). The homology of bands was inferred from banding patterns, as attempts to cross individuals of *Salicornia* have not been successful because of their small autogamous flowers. Loci were all homozygous, except *Aat-I,* in which a heterozygous pattern was observed in a number of diploid individuals from Denmark.

Within each population of *S. europaea* (s.1.) and *S. rubra,* no variation in electrophoretic profile was observed. All indi- viduals within a population were fixed for identical allozymic patterns at all seven loci (Table 4). Within each of the two major groups of populations of *S. europaea* (s.l.), Atlantic coast diploids and Hudson Bay diploids, no variation in multi- locus phenotype was observed between the populations at the seven loci (Wolff and Jefferies 1987). The variation observed within the diploid members of *S. europaea* (s.1.) was among groups of populations, not within populations. With the exception of the James Bay population, morphological characters and patterns of geographical distribution were used to recognize these same groups in both the current study and in an earlier morphometric study (Wolff and Jefferies 1987). The morphometric analysis indicated that although the James Bay population is electrophoretically identical with the Hudson Bay population, its morphological affinity lies with the Atlantic coast populations.

TABLE 4. Observed allelic frequencies and relative electrophoretic mobilities at seven isozyme loci in *Salicornia*

Group	No. of individuals	*Pgm*				*Aat*†			*Me-1*			*Adh-1*		*Mdh-1*†
		*1a**	*1b*	*2a*	*2b*	*1a*	*1b*	*2b*	*a*	*b*	*c*	*a*	*b*	*2c*
Diploid *S. europaea* (s.l.)														
Atlantic coast	220	–	1.00	1.00	–	–	1.00	1.00	–	1.00	–	1.00	–	1.00
James Bay	20	–	1.00	–	1.00	–	1.00	1.00	1.00	–	–	–	1.00	1.00
Hudson Bay	80	–	1.00	–	1.00	–	1.00	1.00	1.00	–	–	–	1.00	1.00
S. rubra	240	–	1.00	0.08*a*	0.92	–	1.00	1.00	1.00	–	–	–	1.00	1.00
S. europaea (s.s.)	115	1.00	–	–	1.00	0.73	0.27*c,d*	1.00	1.00	–	–	–	1.00	1.00
S. ramosissima	130	–	1.00	0.97	0.03*b*	–	1.00	1.00	–	0.68	0.3*d*	1.00	–	1.00
Relative electrophoretic mobilities (mm)‡		38	35	35	31	54	50	39	25	22	17	22	16	41

NOTE: *a*, all members of one population only (20 individuals); *b*, all members of one population only (4 individuals); *c*, *Aat-1b* allele is only present in a heterozygous state, a heterodimer (*1ab*) is also present in heterozygous individuals; *d*, the *Aat-1b* and *Me-1c* alleles were present in Danish populations only; *e*, front migration distance equals 100 mm.

*Loci and alleles are labelled from front to origin.

†*Aat-2a*, *Mdh-2a*, and *Mdh-2b* are present in tetraploid populations of *S. europaea* (s.l.) (Wolff and Jefferies 1987).

‡Front migration distance equals 100 mm.

Certain allozymes, or combinations thereof, were unique to each group. This enabled differentiation and identification of the groups based on multilocus phenotypes (Table 4). All diploid populations from the Atlantic coast were fixed for the following alleles: *Pgm-lb, Pgm-2a, Aat-lb, Aat-2b, Me-lb, Adh-la,* and *Mdh-2c*. Diploid populations from both Hudson Bay and James Bay were fixed for alleles identical with those observed in Atlantic coast diploids at the *Pgm-I, Aat-I, Aat-2,* and *Mdh-2* loci. However, the northern populations could be distinguished from the Atlantic coast diploids at the *Pgm-2, Me-I,* and *Adh-l* loci. These populations exhibited the *Pgm-2b, Me-la,* and *Adh-lb* alleles.

All individuals of *S. rubra* were monomorphic for the same allele at 6 of the 7 loci examined (Table 4). The observed multilocus phenotype was identical with that recorded for plants from Hudson Bay and James Bay *(Pgm-lb, Aat-lb,*

Aat-2b, Me-la, Adh-lb, and *Mdh-2c).* Eleven of the 12 *S. rubra* populations were also fixed for *Pgm-2b*. The remain- ing population was fixed for *Pgm-2a*.

Variation within microspecies and within populations was observed in both *S. ramosissima* and *S. europaea* (s.s.) (Table 4). Most (65%) individuals identified as *S. ramosis- sima* exhibited a multilocus phenotype identical with that observed in all diploid *S. europaea* (s.1.) from the Atlantic coast of northeastern North America: *Pgm-lb, Pgm-2a, Aat-lb, Aat-2b, Me-lb, Aat-2b, Me-lb, Adh-la,* and *Mdh-2c*. All individuals (four) examined from one population, collected in Stiffkey, United Kingdom, were fixed for the *Pgm-2b* allele and not *Pgm-2a* (3% of total *S. ramosissima* individuals screened). The *Me-lc* allele was observed in 32% of the *S. ramosissima* individuals screened in the study. Individuals with the *Me-lc* allele were only observed in several populations collected from Jutland, Denmark.

The multilocus phenotypes exhibited by individuals of *S. europaea* (s.s.) were unlike any phenotype observed in the North American *Salicornia,* differing at the *Pgm-1* and *Aat-1* loci (Table 4). All individuals were monomorphic for the following alleles: *Pgm-la, Pgm-2b, Aat-la, Aat-2b, Me-la, Adh-lb,* and *Mdh-2c*. Twenty-seven percent of the individuals were heterozygous at the *Aat-1* locus, exhibiting *Aat-la, Aat-lb,* and the interallelic heterodimer *Aat-la,b*. This pattern was observed in individuals belonging to several Danish populations. These populations also contained individuals homozygous for the *Aat-la* allele. However, no individuals homozygous for the *Aat-lb* allele were observed in any of the Danish populations.

Discussion

Based on the morphological and electrophoretic results pre- sented in this study and two previous investigations (Wolff and Jefferies 1987), the two major groups of diploid *S. europaea* (s.1.) present in northeastern North America are recognized as distinct taxonomic entities at the species level. Based on a combination of morphological characters, the two groups are readily separated from the European diploid microspecies, *S. europaea* (s . ~ .)and *S. ramosissima,* and from the inland midwestern diploid, *S. rubra* (Table 2). Overall morphological separation among these five taxa is clearly indicated by univariate and multivariate analysis of characters (Tables 2 and 3). This separation is further supported by the observed electrophoretic variation (Table 4).

Fernald (1907) placed the North American members of *S. europaea* (s.1.) into two species: *S. europaea* and *S. rubra* A. Nels. Three varieties of *S. europaea* were described, based primarily on thickness of spikes and branching habit. *Sali- comia europaea* L. var. *pachystachya* (Koch) was described as having thicker spikes than *S. europaea* var. *europaea*. *Sali- cornia europaea* var. *prostrata*

(Pallas) was described as having horizontally spreading or drooping branches, with the lowermost much elongated and decumbent.

Standley (1916) described three annual species of *Salicornia* from northeastern North America: *S. bigelovii* Torr., *S. europaea,* and *S. prostrata*. *Salicornia bigelovii* differed from all other annual taxa in having fertile segments at least twice as wide as long and mucronate "leaf tips." Branching habit was used to separate *S. prostrata* from *S. europaea*. Standley (1916) also described *S. rubra* as a strictly inland midwestern species with two primary distinguishing characters: segments as wide as long and a bright red coloration of both fertile and sterile segments prior to senescence. Gleason (1952) followed Standley's (1916) treatment of *S. europaea* (s.1.) but placed *S. prostrata* within *S. europaea,* although Fernald (1950) again described three varieties of *S. europaea* (var. *europaea,* var. *simplex,* var. *prostrata)* based on branch- ing habit. Both Fernald (1907) and Standley (1916) relied pri- marily on branching habit, general shape of branches, and relative thickness of fertile segments in their descriptions of *S. europaea*. Often these were the only characters measurable on herbarium specimens, as many characters were lost or dis- torted when *Salicornia* plants were preserved or dried and mounted. Subsequently, branching characteristics have been shown to be plastic and of little use in describing taxa within *Salicomia* (Ball and Tutin 1959; Ungar *et al*. 1979).

Salicomia prostrata Pallas was originally described from the northwest coast of the Caspian Sea (Pallas 1803). The species is present in southeast Europe (Ball 19646). Moss (191 1) and Tutin (1952) included west European plants in the species *(S. prostrata* auct.). Work by Ball and Tutin (1959) showed, however, that the progeny of *S. prostrata* auct. remain erect in cultivation and most closely resembled *S. ramosissima*. The west European members of *S. prostrata* were subsequently reassigned to *S. ramosissima,* with *S. prostrata* Pallas defined as an eastern European species (Ball 1964a, 19646). The *S. europaea* var. *prostrata* and *S. prostrata* described by Fernald (1907) and Standley could not have belonged to the species originally described by Pallas (1803).

In light of the findings of this study and the various taxo- nomic revisions of European *Salicornia* (Ball and Tutin 1959; Ball 1964a, 1964b), the present treatment of *S. europaea* (s.1.) in northeastern North America is uninformative, as all morphological groups, diploid and tetraploid, are identified only as *S. europaea* (s.1.). A comparison of diploid and tetra- ploid members of *S. europaea* L. (s.1.) (Wolff and Jefferies 1987) has shown that in northeastern North America the two ploidy levels are separable on the basis of morphological differences. Diploids and tetraploids can also be distinguished based on multilocus phenotypes (Wolff and Jefferies 1987). Formal descriptions of the two diploid taxa present within *S. europaea* (s.1.) in northeastern North America are now given. As comparison has

not been made between tetraploid *S. europaea* (s.1.) from North America and Europe, the taxo- nomic status of the North American members cannot be fully evaluated and they are retained within *S. europaea* (s.1.).

Key to species of *Salicornia* in northeastern North America

1. Leaf tips and bracts mucronate, cymes completely hidden by bracts, fertile segments approximately twice as wide as long..... ..... *S. bigelovii* Torr.
1. Leaf tips and bracts blunt or rounded, central flower of cyme visible above bract, fertile segments less than twice as wide as long..2

2. Terminal spike and branches cylindrical to extremely tapered, fertile segments tubular in shape, (5–)7–23(–25) fertile segments in the terminal spike, profuse exsertion of stamens, scarious border 0.3–0.4 mm wide..... tetraploid *S. europaea* L. (s.l.)
2. Terminal spike and branches swollen and rounded at tip, fertile segments distinctly widest from the midsegment to the top, 2–10(–14) fertile segments in the terminal spike, exsertion of stamens rare, scarious border of less than 0.3 mm wide.....3

3. Central and lateral perianths longer than wide, suborbicular above cuneate base, fertile segments conspicuously longer than wide, anthers (0.1–)0.2–0.3 mm long..... *S. maritima* Wolff & Jefferies
3. Central and lateral perianths as wide or wider than long, fertile segments approximately as long as wide, anthers (0.2–)0.3–0.5 mm long 4

4. Plant 1.0–10 cm long, often prostrate, branching at the cotyledonary node only. Fertile segment wider than long, central perianth distinctly orbicular, scarious border 0.1–0.2 mm wide; distributed along the Hudson Bay..... *S. borealis* Wolff & Jefferies
4. Plant 4.0–20–(–25) cm, erect, with regular decussate branching. Fertile segment almost as wide as long, central perianth sub-orbicular to orbicular, scarious border 0.2–0.3 mm wide; strictly western inland distribution..... *S. rubra* A. Nels.

1. ***Salicornia maritima*** Wolff & Jefferies, sp.nov. Fig. 1

HOLOTYPE: Quebec, Rimouski, 2 **km** east. 1984. S. L. Wolff (TRT).

Rami ad apicem rotundati; ramificatio regularis decussata; segmenti fertiles et perianthii longiores quam latiores; perian- thium centralis suborbicularis; margo scariosus latus; raro staminum exsertis; antherae breves.

Plant (4.5-)6.0-26 cm, erect or occasionally prostrate, with few to many short primary and often secondary branches. Tertiary branching occurs rarely. Branches are short, thin, sausage-shaped, and rounded at the tip. Subsequent to flower- ing, both fertile and sterile segments colour red to purple, colour originating directly below the scarious border, around margins of floral perianths, and at base of segment. The ter- minal spike contains (3-)5 - lo(- 14)fertile

segments. Lower fertile segments are 2.9-5.2 x 2.4-4.0(-4.3) mm, bulging, widest between scarious border and top of central perianth, with a conspicuous scarious border, 0.2-0.3 mm wide. Central flower 1.3-2.6 x 1.5-2.4 mm, longer than wide and suborbicular to orbicular above cuneate base. Distance between the central flower and top of segment is variable, normally less than one-third the length of the segment. Lateral flower 1.3-2.3 x 1.3- 1.9 mm, slightly smaller than the central flower, often visually obscured by reduced leaf. Stamens are rarely exerted, and if so, after dehiscence.

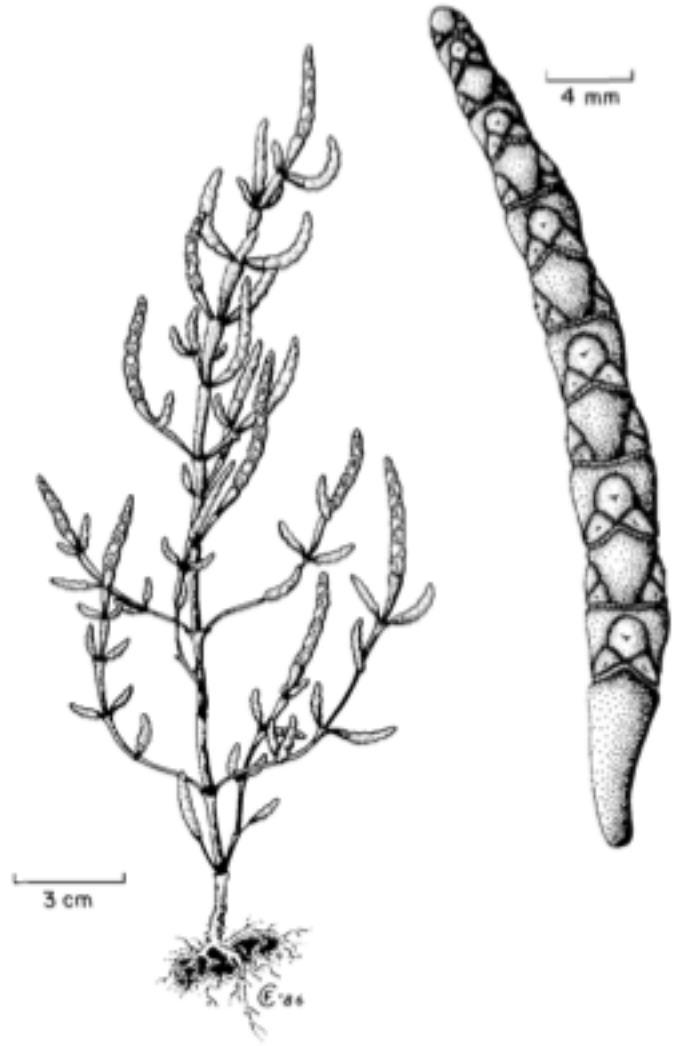

FIG. 1. *Salicornia maritima* Wolff & Jefferies, sp.nov. (A) habit; (B) fertile spike.

Anthers (0.1-)0.2-0.3 mm in length. Flower: August and September. Fruit: September and October.

DISTRIBUTION A N D HABIT A T: Widely distributed above the mean high tide level in salt marshes along the northeastern coast of Canada. Populations also present in the southern region of James B anIges from Newfoundlandand St. Lawrence estuary in the north to southern coasts of New Brunswick. Restricted to high marsh zone. In open areas, shallow depressions, or around periphery of marsh pans. No inland populations known. Typical specimens include plants from St. Omer, Que. (E43); Rimouski, Que. (E45); Trois Pistoles, Que.

(E46); Conrad Beach, N .S. (E20A). Collection numbers are those of S. L. Wolff. Voucher specimens depos- ited in TRT.

2. ***Salicorniu borealis*** Wolff & Jefferies, sp.nov.

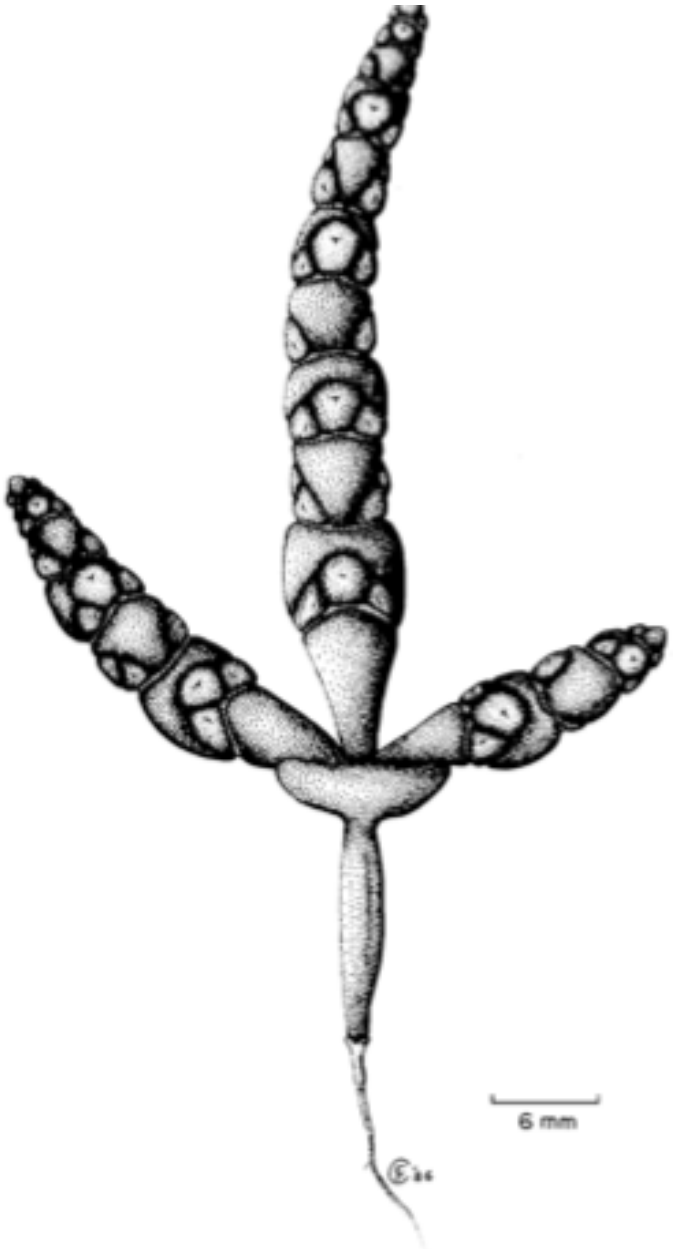

FIG. 2. *Salicornia borealis* Wolff & Jefferies, sp.nov.

HOLOTYPE: Manitoba, La PCrouse Bay, 30 km east of Churchill. 1985. R. L. Jefferies (TRT).

Rami ad apicem acuti, ad nodum cotyledonium restricti; segmenti fertiles et peranthii latiores quam longiores; perian- thium centralis orbicularis; margo scariosus angustus; raro staminum exsertis; antherae longae.

Plant 1.0-10 cm, prostrate or erect, branches absent or simple and primary. Branching occurs only at the cotyledonary node (rarely a second sterile internode is present, accompanied by a second set of branches), and main axis terminates immediately in an inflorescence. Branches are short, fat, sausage-shaped, and pointed. Subsequent to flowering, both fertile and sterile

segments become dark red to deep purple in colour, colour originating directly below the scarious border, around margins of floral perianths, at base of segment. Ter- minal spike contains 2 -5(- 10) fertile segments. Lower fertile segments 2.4-3.6 x (1.5)2.3-3.3 mm, concave, with narrow scarious border 0.1-0.2 mm wide. Central flower 1.2-2.3 x 1.3-2.1 mm, as wide as or wider than long and distinctly orbicular, often extending to the top of the segment. Lateral flower 1.0-1.7 x 1.3-1.6 mm. as wide as or wider than long. Stamens are rarely exserted, and if so, exsert following dehiscence. Anthers (0.2 -)0.3 -0.4 mm in length. 2N = 18. Flower: July and August. Fruit: August. Distribution and Habitat: Distributed above mean hightide level in salt marshes and estuaries along coasts of Hudson Bay in the region of Churchill, Man. Northern limit of dis- tribution follows the 10°C isotherm for July. Commonly found growing around periphey of small marsh pools and on open flats in high marsh. Typical specimens are plants from Churchill, Man. (E19), and La PCrouse Bay, Man. (E49, E50, E51). Collection numbers are those of S. L. Wolff. Voucher specimens deposited in TRT.

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References

BALL,P. W. 1964a. Salicornia. In Flora Europaea. Vol. 1. Edited by T. G. Tutin, V. H. Heywood, N. A. Burgess, D. H. Valentine, S. M. Walters, and D. A. Webb. Cambridge University Press, London, pp. 101-102.

----1964b.A taxonomic review of Salicornia in Europe.Feddes Repert. **69:** 1-8.

BALL,P.W.,andBROWNK,.G.1970.A biosystematics and ecological study of Salicornia in the Dee Estuary. Watsonia, **8:** 27-40. BALL,P. W., and TUTIN,T. G. 1959. Notes on annual species ofSalicornia in Britain. Watsonia, **4:** 193-205.

DALBYD, . H. 1962. Chromosome number, morphology and breeding behaviour in the British Salicorniae. Watsonia, **5:** 150- 162. FERNALDM,. L. 1907. Salicornia europaea and its representatives in eastern America. Rhodora, **9:** 204 -207.

-----1950. Gray's manual of botany. 8th ed. American Book Co.,New York. p. 599.

GLEASONH,.A. 1952.ThenewBrittonandBrownillustratedfloraof the northeastern United States and adjacent Canada. Hafner Press, MacMillan Publishing Co. Inc., New York. p. 98.

GOTTLIEBL,. D. 1981. Electrophoretic evidence and plant populations. Prog. Phytochem. **7:** 1-45.

HANSENA, ,, and PEDERSENA,. 1968. Chenopodiaceernes og Amaranthaceernes udbredelse i Danmark. Bot. Tidsskr. **63:** 205-288.

JEFFERIERS,. L., and GOTTLIEBL,. D. 1982. Genetic differentiation of the microspecies Salicornia europaea L. (sensu stricto) and S. ramosissi~naJ. Woods. New Phytol. **92:** 123- 129.

JENSENA, and JEFFERIESR,. L. 1984. Fecundity and mortality in populations of Salicornia europaea agg. at Skallingen, Denmark. Holarct. Ecol. **7:** 399-412.

KLECKAW, . R. 1980. Discriminant analysis. Quantitative applica- tions in the social sciences. No. 19. Sage Publications, Beverly Hills, CA.

KONIG,D. 1960. Beitrage zur Kenntnis der deutschen Salicor~lien. Mitt. Florist. Soziol. Arbeitsgem. **8:** 5-58.

Moss, C. E. 1911. Some species of Salicornia. J. Bot. **49:** 177- 185.

Nei, N. G., Hull, C. H., Jenkinsj., G., Stenibrennker, ,and Bent,D. H. (Editors). 1975. Statistical package for social sciences. 2nd ed. McGraw-Hill Book Co., New York.

Pallasp,. S. 1803. Illustrationes plantarium imperfecte vel nondum cognitarum. Leipzig.

Scott,A. J. 1977. Reinstatement and revision of Salicorniaceae J.Agardh (Caryophyllales). Bot. J. Linn. Soc. **75:** 357-374. STANDLEYP,. C. 1916. Chenopodiales, Chenopodiaceae. In North American flora. Vol. 21, part 1. New York Botanical Garden, NewYork. pp. 81-85.

TUTINT,.G.1952.Salicornia.InFloraoftheBritishIsles.Editedby A. R. Clapham, T . G. Tutin, and E. F . Warburg. Cambridge UniversityPress,London.pp.285-289.UNGARI,. K., BENNERD,. K., and MCGRAWD, . C. 1979. The dis-

tribution and growth of Salicornia europaea on an inland salt pan.

Ecology, **60:** 329 -336.WOLFF,S. L. 1985. Morphological and genetic variation in Salicornia eruopaea agg. in northeastern North America. M.Sc. thesis,University of Toronto, Toronto.

WOLFF,S. L., and JEFFERIESR, . L. 1987. Morphological and isozyme variation in Salicornia europaea (s.1.) (Chenopodiaceae) in northeastern North America. Can. J. Bot.

This issue.