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Taxonomy and evolutionary diversification of the Central European endemic *Spergularia echinosperma* (Caryophyllaceae)

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Abstract

The patterns of morphological variation and distribution of the rare Central European endemic *Spergularia echinosperma* were investigated. Morphometric analyses revealed the existence of two distinct morphotypes differing each other mainly in seed color, which is either brown or black. Other differences are in density of the seed surface papillae, height and shape of the papillae, seed width, pedicel/capsule and internode/leaf ratios, and leaf length. A geographic separation of the morphotypes also exists. The black-seeded morphotype occurred nearly exclusively in drained fishponds in the south-western part of the Czech Republic, the brown-seeded morphotype was found in drained fishponds in the eastern part of the Czech Republic and in alluvial pools and river deposits of the Elbe River (Germany). We hypothesize that the black-seeded morphotype may have been indigenous in former natural lakes which were widespread in the SW-Czech Republic and they were frequently transformed into fishponds. The brown-seeded morphotype may have its origin in river alluvia of the Elbe (Germany) and possibly also of other rivers in the Czech Republic. Since the two morphotypes are morphologically and geographically well separated, we propose to describe the brown-seeded morphotype as a new subspecies for science, *S. echinosperma* subsp. *albensis subsp. nov*.

Keywords: discriminant analysis, endemism, hierarchical classification, morphometrics, *Spergularia*

Introduction

Vascular plants, which are endemic to Central Europe outside high mountains, are few. Among them is *Spergularia echinosperma* (Čelakovský 1881: 867) Ascherson & Graebner (1893: 517) (see e.g., Čelakovský 1881, Friedrich 1979, Dvořák 1990) which is a species confined to the threatened vegetation of annual wetland herbs bound to exposed bottoms of freshwater reservoirs (phytosociological class Isoëto-Nano-Juncetea Br.-Bl. et Tüxen ex Br.-Bl. *et al.* 1952). *S. echinosperma* has two main centers of distribution: Germany where it grows in alluvial pools and river banks along the Elbe (Friedrich 1979, Jäger 2011, Brück *et al.* 2012), and the Czech Republic where it grows exclusively in secondary habitats, especially drained fishponds (Friedrich 1979, Dvořák 1990, Kaplan *et al.* 2016). It also marginally occurs in Austria (Fischer *et al.* 2008), and Slovakia (Dvořák 1979, Goliašová 2012).

Spergularia echinosperma has been long considered a taxonomically critical species (Jage 1974, Dvořák 1990, Suda *et al.* 2007) due to its morphological similarity to a widespread congener *S. rubra* (Linnaeus 1753: 423) Presl & Presl (1819: 94), and the two species were frequently confused. Recent studies by Kúr *et al.* (2012, 2016) demonstrated that although an interspecific hybrid between *S. echinosperma* and *S. rubra* exists [it is named *S. kurkae* Dvořák (1989: 320)], it is a stable hybrid species reproductively isolated from the parents. It was also showed that all the three species are morphologically well delimited.

The main morphological characters discriminating *S. echinosperma* from the other species refer to the seeds (Kúr *et al.* 2012). However, there has been contradictory information in the literature as for the actual values of some seed characters in *S. echinosperma*. The most conspicuous is the difference in the indicated seed color. Czech authors describe *S. echinosperma* as displaying black seeds (Dostál 1989, Dvořák 1990, Kúr *et al.* 2012), including the

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description of this taxon by Čelakovský (1881). German plants, on the other hand, are characterized by (dark) brown seed color (Jage 1974, Friedrich 1979). Our study of the herbarium material of *S. echinosperma* indeed confirmed the presence of two groups differing in seed color.

The taxonomic value of this character in *S. echinosperma* remains unknown. In the genus *Spergularia*, seed characters are usually important from the taxonomical point of view (see e.g., Monnier & Ratter 1993, Hartman & Rabeler 2005). It is therefore possible the varying seed morphology in *S. echinosperma* may reflect an unrevealed taxonomic structure of this Central European endemic.

The aims of the present study are to investigate correlations of seed color with other morphological characters and to map the distribution of particular morphotypes. Specifically, we asked the following questions: (1) what is the pattern of morphological variation in *S. echinosperma*? (2) Is the morphological variation correlated with different environmental conditions and/or geographical regions?

Materials and Methods

Plant material from 21 herbaria (B, BRNM, BRNU, CB, CBFS, DR, GAT, HAL, JE, LIM, LIT, MJ, MNVD, OLM, OP, PL, PR, PRA, PRC, STU, and ZMT; acronyms according to Thiers 2016+) and 7 personal herbaria, not listed in the *Index Herbariorum* (H. Jage, J. Komárek, J. Zámečník, L. Čech, P. Kúr, R. Paulič, Z. Kaplan), from the Czech Republic and Germany was revised. The habitat types derive from the herbarium labels.

A subset of 114 plants from 15 populations were used for the morphometric analyses [1–19 individuals per population (see Table 1 for the exact localities and acronyms of the populations used in the text)]. Only mature plants with ripe capsules were used.

TABLE 1. List of the populations of *Spergularia echinosperma* used for the morphometric analyses. The geographic coordinates are based on the WGS84 datum.

Label	Locality	Lat.	Long.	Number of plants	Date	Coll.
Bleddin	Distr. Wittenberg, Bleddin: oxbow lake called "Bleddiner Riß", exposed margin	51.79411	12.79542	7	26.6.1982	H. Jage
Gallin	Distr. Wittenberg, Gallin: scour upstream the ferry in the village, the right bank of the Elbe	51.83680	12.75619	4	11.9.1967	H. Jage
Hodemysl	Dist. Příbram, Hoděmyšl: bare bottom of the Velký hoděmyšlský fishpond	49.61600	13.87864	7	21.6.2011	P. Kúr
Hrachoviste	Dist. Jindřichův Hradec, Hrachoviště: bare bottom of the Hrachovišťský fishpond	48.92864	14.76408	10	26.6.2011	P. Kúr
Kojatin	Dist. Třebíč, Kojatín: bare bottom of the Kojatínský fishpond	49.24172	16.00847	6	6.6.2011	P. Kúr
KWurf	Distr. Roßlau, Klieken: oxbow lake called "Kurzer Wurf" WSW of the town	51.88031	12.32558	7	9.9.1989	H. Jage
Malobor	Dist. Strakonice, Sedlice: bare bottom of the Malobor pond	49.36678	13.97556	7	25.6.2008	P. Kúr
Mlynhor	Dist. Strakonice, Drahonice: bare bottom of the Mlýnský horní fishpond	49.19467	14.08694	7	25.6.2011	P. Kúr
Parezny	Dist. Žďár Nad Sázavou, Bohdalov: bare bottom of the Pařezný fishpond	49.47744	15.85317	1	4.6.2011	P. Kúr
Pratau	Distr. Wittenberg, Pratau: oxbow lake N of the town, E of the F2 road (near the "Bude 100")	51.85115	12.64539	7	7.10.1963	H. Jage
Priesitz	Distr. Wittenberg, Priesitz: the Old Elbe ca 1 km NE of the town; sandy-muddy margin of the oxbow lake	51.70727	12.83715	7	12.10.1971	H. Jage
Skopec	Dist. Písek, Nová Ves u Protivína: bare bottom of the Skopec fishpond	49.23108	14.25231	10	25.6.2011	P. Kúr
Svihov	Dist. Chrudim, Švihov: bare bottom of the Švihov fishpond	49.84264	15.85931	10	5.6.2011	P. Kúr
Tangermunde	Distr. Stendal, Tangermünde: right bank of the Elbe opposite the town, under the road bridge.	52.56491	11.98564	5	14.10.1963	H. Jage
Terlicko	Dist. Karviná, Těrlicko: exposed margin of the Těrlicko water reservoir	49.74336	18.49515	19	25.10.2012	H. Jage

TABLE 2. List of the morphological characters used in the morphometric analyses and summary of their values for the black-seeded (41 individuals) and brown-seeded (73 individuals) morphotypes. The numbers denote (minimum–)10th percentile/**mean**/90th percentile(–maximum). Characters log-transformed prior to the multivariate analyses are marked with an asterisk.

Acronym	Character [units]	Seed color group	
		brown	black
Cap-K	capsule-sepal length ratio	(1.00–)1.13/**1.26**/1.56(–1.41)	(1.07–)1.13/**1.21**/1.39(–1.33)
CapsLeng	capsule length [mm]	(2.4–)3.0/**3.2**/4.1(–3.5)	(2.6–)2.8/**3.1**/3.7(–3.5)
FrPedLen*	length of the fruit pedicel adjacent to the capsule [mm]	(1.7–)2.4/**4.1**/9.1(–6.7)	(3.8–)4.1/**5.6**/11.1(–7.5)
InterLen*	length of the internode adjacent to the measured leaf [mm]	(3.33–)6.47/**11.43**/21.27(–16.83)	(5.43–)7.90/**11.94**/25.07(–18.97)
Int-Leaf*	internode length/leaf length ratio	(0.43–)0.77/**1.02**/1.65(–1.34)	(0.72–)0.91/**1.39**/3.42(–1.87)
KLength*	sepal length [mm]	(2.1–)2.3/**2.6**/3.4(–2.8)	(2.1–)2.3/**2.6**/3.2(–3.0)
LeafLeng*	leaf length [mm]	(5.3–)6.4/**11.5**/21.0(–17.6)	(5.0–)5.7/**9.1**/15.6(–12.7)
LeafRat*	leaf length/width ratio	(10.4–)15.6/**22.8**/38.5(–32.5)	(13.2–)14.8/**21.5**/62.0(–26.9)
LeafWidt	leaf width [mm]	(0.2–)0.4/**0.5**/0.8(–0.6)	(0.1–)0.2/**0.5**/0.8(–0.7)
LengSeed	seed length [μm] (Fig. 7)	(323–)377/**412**/507(–467)	(336–)357/**397**/473(–448)
PapHei	papilla height [μm] (Fig. 7)	(12–)15/**18**/23(–21)	(16–)17/**19**/24(–21)
PapNum	number of papillae on one quarter of the seed circumference (papillae density)	(5–)8/**12**/19(–15)	(10–)13/**15**/20(–18)
PapRat	ratio of the papilla upper part ("head") width and papilla lower part ("neck") width (papilla shape)	(1.01–)1.10/**1.24**/1.55(–1.42)	(1.04–)1.08/**1.21**/1.50(–1.35)
Ped-Cap*	pedicel/capsule length ratio	(0.57–)0.73/**1.27**/2.28(–2.10)	(1.21–)1.39/**1.80**/3.25(–2.34)
PlHeight*	height of the longest stem [cm]	(4–)5/**8**/16(–12)	(5–)6/**8**/12(–10)
SeedRat	seed length/width ratio	(1.09–)1.22/**1.29**/1.51(–1.38)	(1.23–)1.26/**1.34**/1.48(–1.42)
StemWidth*	stem width [mm]	(0.4–)0.4/**0.6**/1.3(–0.7)	(0.2–)0.3/**0.5**/0.8(–0.6)
StpLt	stipule length [mm]	(0.9–)1.1/**1.3**/1.8(–1.6)	(0.9–)1.1/**1.2**/1.5(–1.4)
StpRT	stipule length/width ratio	(0.48–)0.60/**0.72**/1.01(–0.86)	(0.58–)0.63/**0.74**/0.90(–0.83)
StpWd	stipule width [mm]	(1.3–)1.6/**1.9**/2.5(–2.2)	(1.3–)1.5/**1.7**/2.0(–1.8)
WidtSeed	seed width [μm] (Fig. 7)	(242–)289/**321**/383(–358)	(252–)265/**297**/341(–338)

14 quantitative and 7 derived ratio characters were measured (Table 2). Seed color was used as an ordinary variable. All the individuals could be unambiguously classified into two groups, one possessing black and the other brown seeds (Fig. 1). Special caution was given to evaluating well-developed seeds only.

The data were processed by multivariate statistical analyses. Quantitative characters that deviated most from a normal distribution in each of the pre-defined groups were log-transformed to improve normality (Table 2). Principal component analysis (PCA) was used to visualize the overall pattern of morphological variation in the data (CANOCO 5; Šmilauer & Lepš 2014). To find out which characters significantly separated the seed color groups, canonical discriminant analysis (CDA) was applied. The significance of individual characters was tested using both marginal effects (i.e., when a character is alone in the model) and unique contributions of the characters (i.e., the addition of each character into the model with all other characters) (Koutecký 2015). Forward selection of characters was employed to detect the combination of characters most contributing to the separation of the groups. The threshold significance level was set to $\alpha = 0.05$ and a Monte-Carlo permutation test (1000 permutations) used. The predictive ability of the selected characters was tested by classificatory discriminant analysis based on the posterior group membership probabilities and cross-validation using whole populations as leave-out units. The percentage of misclassified samples in each group served as a measure of the predictive ability. The discriminant analyses were computed using the MorphoTools scripts (Koutecký 2015) in R 3.2.3 (R Development Core Team 2015).

We also reanalyzed the data by classification trees that create a hierarchical classification based on univariate splits that can then be visualized as an easily interpretable tree diagram (Breiman *et al.* 1984). The function rpart (package rpart) in R 3.2.3 (R Development Core Team 2015) was used. The minimum split parameter (minsplit) was set to 1 and

the initial complexity parameter (cp) to 0.001. A cross-validation using the populations as the leave-out subsamples was used to assess the optimal tree complexity, instead of random subsamples as implemented in the original method (Venables & Ripley 2002). The resulting tree was selected on the basis of the 1-SE rule (Venables & Ripley 2002).

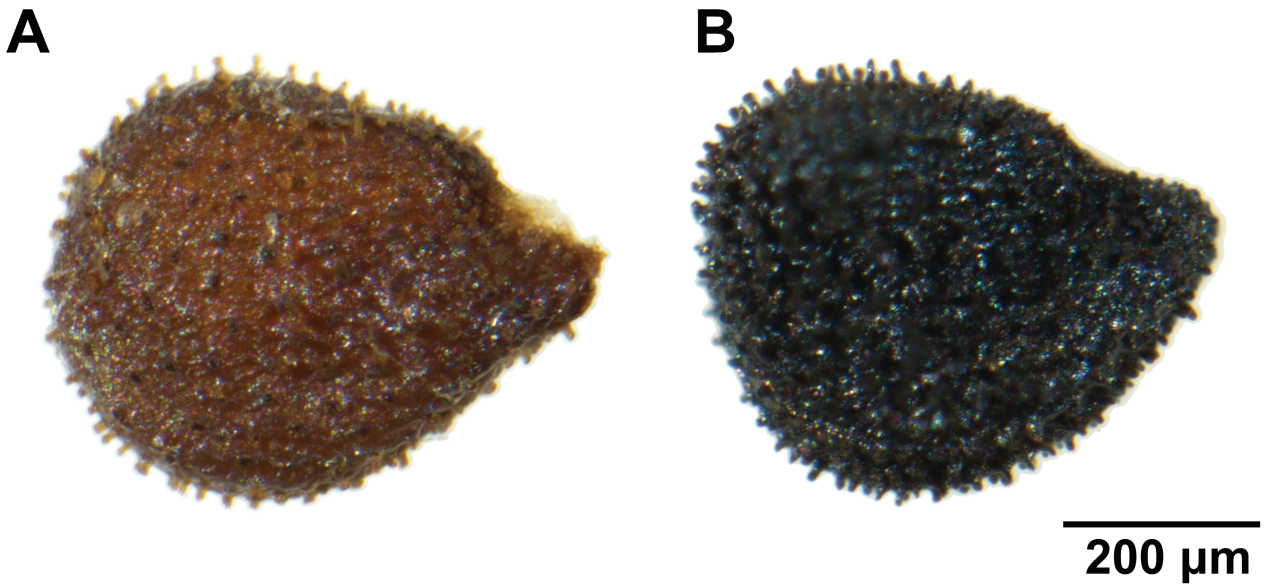

FIGURE 1. A typical seed of the brown-seeded (A) and black-seeded (B) morphotypes of *Spergularia echinosperma*.

Results

By using all 21 morphological characters, PCA did not produce any clear and distinct clusters of plants. However, the black-seeded and brown-seeded plants separated slightly along the second ordination axis (Fig. 2).

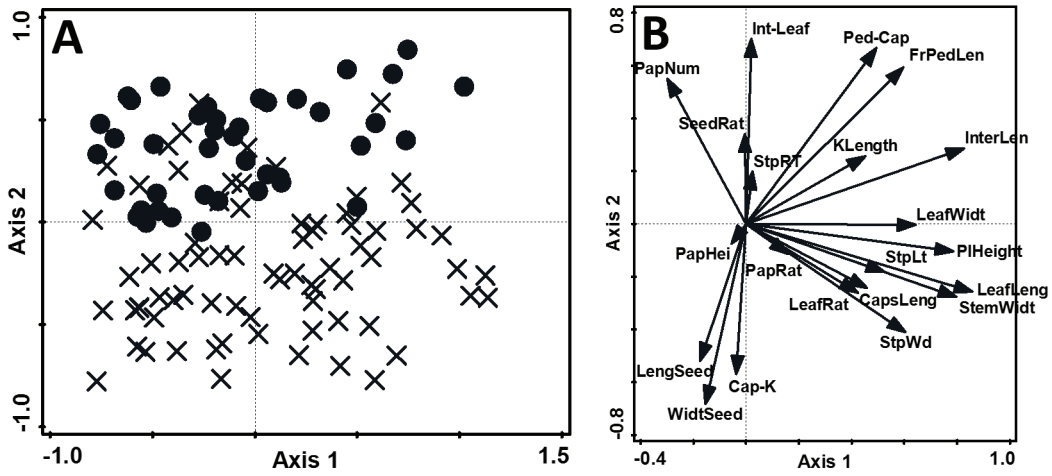

FIGURE 2. PCA analysis: (A) distribution of individuals in the ordination space (circles – black-seeded plants, X-marks – brown-seeded plants), (B) fit of the 21 morphological characters to the ordination axes. The first and the second ordination axes explain 24.3% and 16.4% of the total variation, respectively.

On the contrary, CDA highlighted some characters which significantly separate the groups (Table 3). The 7 best predictors were mainly seed characters (papillae density, papilla head/neck ratio, papilla height, seed width) plus other characters referred to the vegetative parts (i.e. pedicel/capsule length ratio, stipule width, and internode/leaf length ratio). The predictive ability of the selected characters was 84% of correctly classified samples (Fig. 3, Table 4).

TABLE 3. Morphological characters tested in the forward selection with their conditional and marginal effects, unique contributions, and their contributions to the canonical axis (biplot scores).

Character	Conditional effects		Marginal effects		Unique contributions		Biplot scores
	F	p	F	p	F	p	
PapNum	60.8	0.005	60.8	0.005	17.1	0.001	0.426
Ped-Cap	30.8	0.005	36.9	0.005	7.4	0.005	0.332
StpWd	19.7	0.005	23.3	0.005	2.3	0.146	-0.263
PapRat	13.7	0.005	2.0	0.200	12.6	0.001	-0.077
WidtSeed	8.8	0.005	18.8	0.005	3.4	0.064	-0.237
PapHei	6.3	0.015	7.8	0.005	22.3	0.001	0.152
Int-Leaf	4.9	0.020	30.2	0.005	0.3	0.639	0.300
FrPedLen	n. s.		25.9	0.005	7.9	0.003	0.278
StemWidth	n. s.		12.9	0.005	3.2	0.071	-0.196
SeedRat	n. s.		11.3	0.005	2.2	0.141	0.183
LeafLeng	n. s.		10.6	0.005	0.0	0.972	-0.178
StpLt	n. s.		8.0	0.015	0.4	0.539	-0.154
Cap-K	n. s.		7.5	0.010	0.0	0.920	-0.149
CapsLeng	n. s.		6.5	0.020	3.4	0.065	-0.139
LeafWidt	n. s.		5.4	0.030	0.0	0.925	-0.127
LengSeed	n. s.		4.7	0.035	2.2	0.140	-0.118
StpRT	n. s.		1.2	0.275	0.8	0.384	0.060
LeafRat	n. s.		1.0	0.305	0.4	0.568	-0.056
InterLen	n. s.		0.5	0.505	0.1	0.785	0.038
PlHeight	n. s.		0.2	0.690	6.3	0.011	-0.023
KLength	n. s.		0.0	0.940	0.0	1.000	-0.002

TABLE 4. Summary of the classification matrices of the black-seeded and brown-seeded morphotypes of *Spergularia echinosperma* resulting from the classificatory discriminant analysis and classification trees.

Classificatory discriminant analysis				Classification trees			
observed	black	brown	Total	observed	black	brown	Total
predicted				predicted			
black	37 (90.2%)	14 (19.2%)		black	24 (58.5%)	23 (31.5%)	
brown	4 (9.8%)	59 (80.8%)		brown	17 (41.5%)	50 (68.5%)	
Percent correct	90.0%	80.8%	84.2%	Percent correct	58.5%	68.5%	64.9%

The final classification tree selected had 3 terminal nodes (complexity parameter cp = 0.1). It confirmed the high discrimination power of pedicel/capsule length ratio. The second character selected was leaf length, contrary to the CDA forward selection (Fig. 4). The overall predictive power of this model was lower with 65% of correctly classified samples (Table 4).

The revision of herbarium specimens showed that the black-seeded morphotype is, with two exceptions, restricted to the southwestern part of the Czech Republic (especially the South Bohemian fishpond basins). The exceptions were one locality in Germany (Rathenow) and one locality in the eastern part of the Czech Republic (Kadolecký fishpond near Křižanov). The brown-seeded morphotype, on the other hand, occurs in the eastern part of the Czech Republic (especially in the Bohemian-Moravian Highlands) and Germany (along the Elbe) only (Fig. 5).

Four distinct types of habitats were found: fishponds, river reservoirs, alluvial pools, and river banks (Table 5). Nearly all localities from the Czech Republic came from drained fishponds. An exception was one population from an exposed margin of a river reservoir. In Germany, *S. echinosperma* occurred nearly exclusively in alluvial pools or river banks along the Elbe River. An exception was the only German locality of black-seeded *S. echinosperma* which was located in the vicinity of the river Havel, ca. 20 km off the Elbe. The type of habitat was unfortunately not specified on the herbarium label.

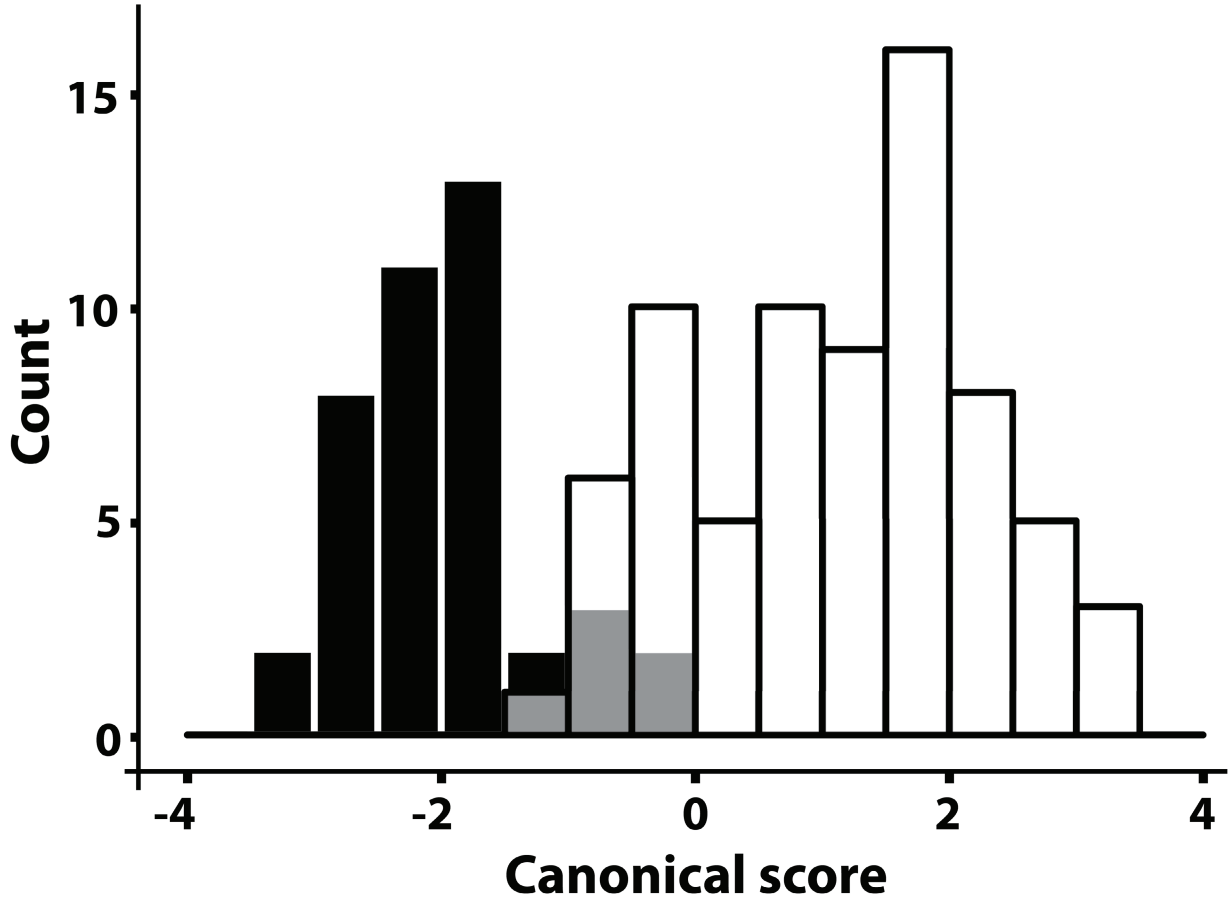

FIGURE 3. Distribution of the canonical scores from CDA for the black-seeded (black) and brown-seeded (white) morphotypes of *Spergularia echinosperma*.

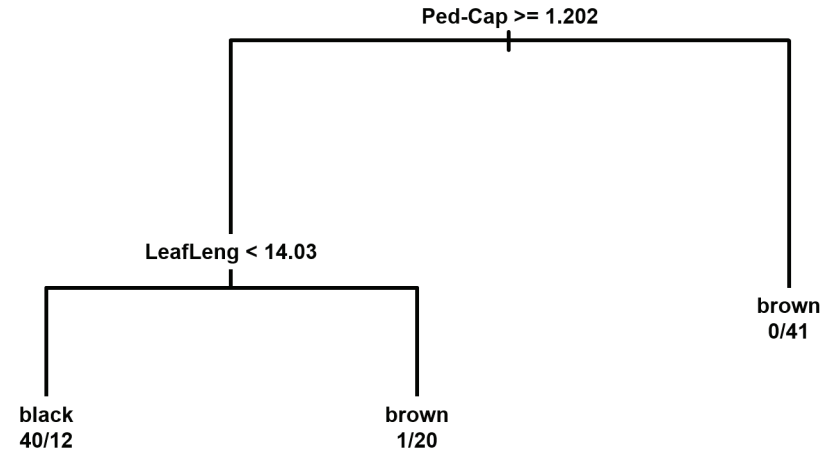

FIGURE 4. Classification tree of the individuals of the black-seeded and brown-seeded morphotype of *Spergularia echinosperma*. If a character value matches the classification rule, the determination continues to the left branch, otherwise to the right branch. Lengths of the branches correspond to the relative discriminatory powers of the respective rules. The group names at the terminal nodes indicate the predicted classification of a particular node, whereas the numbers separated by slashes indicate actual membership of samples classified to a particular node (black/brown).

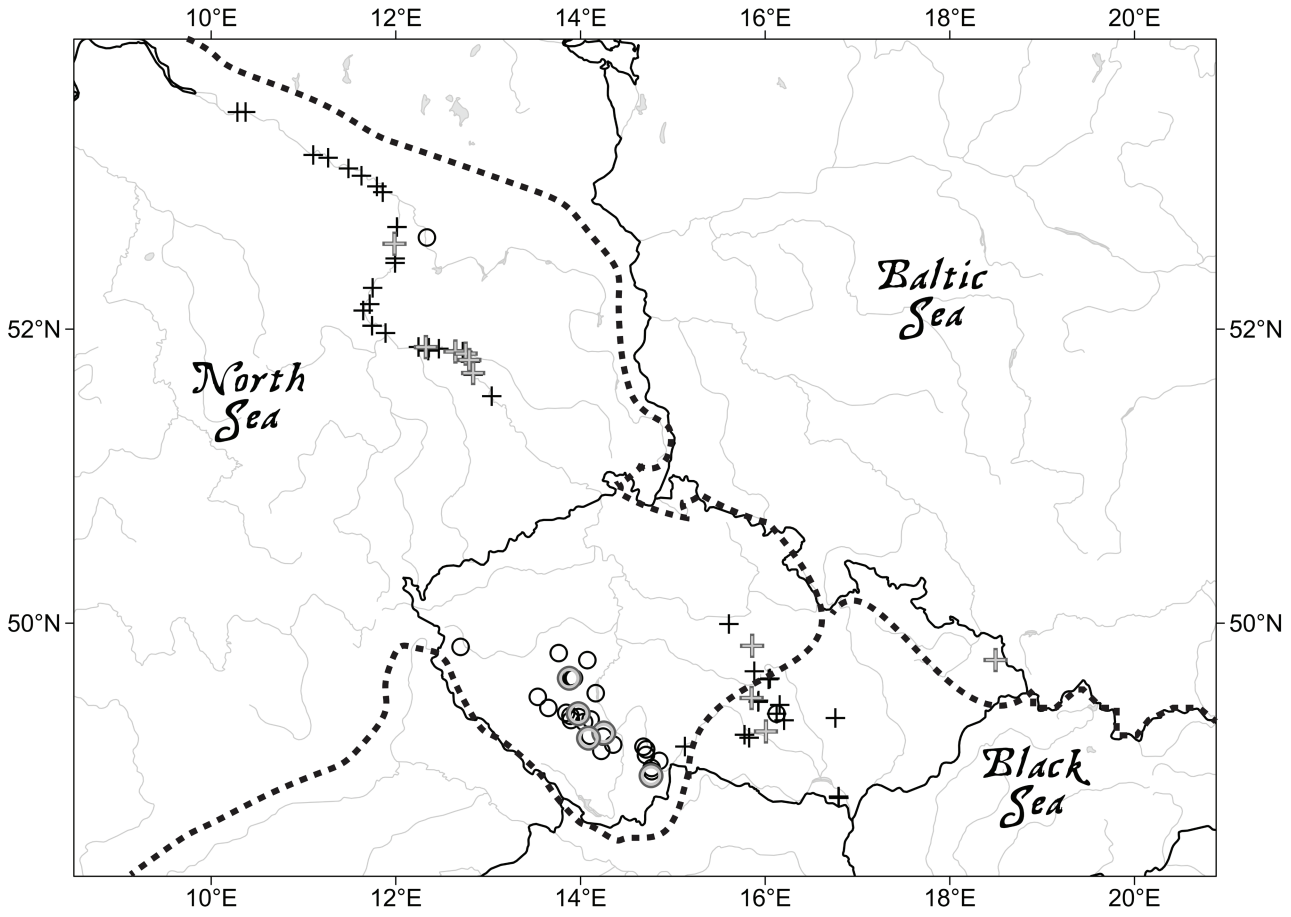

FIGURE 5. Distribution map of the black-seeded (circles) and brown-seeded (crosses) morphotypes of *Spergularia echinosperma*. Populations used for morphometric analyses are highlighted in gray. The dashed lines denote the main European drainage divides.

TABLE 5. Absolute frequencies of habitat types in which *Spergularia echinosperma* was recorded, summarized across morphotypes and countries.

Country	**Czech Republic**		**Germany**	
Seed color	black	brown	black	brown
fishpond	47	63	.	.
reservoir	.	1	.	.
alluvial pool	.	.	.	31
river bank	.	.	.	34
unknown	.	.	1	.

Discussion

We confirmed that the observed differences in seed color in *Spergularia echinosperma* are related with the differences in some other morphological characters. Most of them are related to seed morphology, but there are also some well-discriminating vegetative characters. Even if the determination of the morphotypes without the information about the seed color is not fully reliable, their morphological separation seems to be well supported.

The morphotypes display also a clearly vicariant distribution. The occurrence of brown-seeded *S. echinosperma* in Germany is in accordance with the descriptions of this species by German authors (Jage 1974, Friedrich 1979). From the Czech Republic, however, only the black-seeded morphotype has been reported so far (Dostál 1989, Dvořák 1990, Kúr 2012).

We can now only speculate about the origin and migration history of the different lineages of *S. echinosperma*. The black-seeded morphotype may have its origin in natural lakes which existed in South and South-West Bohemia

and were frequently transformed into fishponds during the Middle Ages and the Early Modern Age (Chvojka *et al.* 2010, Pokorný 2015). The brown-seeded morphotype, on the other hand, may be indigenous to periodically exposed substrates in river alluvia. This is easily conceivable in the case of the Elbe where the species still grows in this type of habitats. The same may hold true for the populations of brown-seeded *S. echinosperma* in the eastern part of the Czech Republic. In the latter region, natural lakes were not common (Chlupáč *et al.* 2002, Břízová 2009), and alluvial pools seems to be a more probable primary habitat for *S. echinosperma*. Periodically exposed alluvial pools still occur in this region (especially along the Morava River), but they were vastly destroyed in the 20th century. Unfortunately, there are no historical records of *S. echinosperma* from these habitats in this region to corroborate its indigenous status here.

Even if the two morphotypes of *S. echinosperma* have probably evolved in different regions, they nearly complete vicariance is surprising. As the Bohemian populations of black-seeded *S. echinosperma* lie within the Elbe river catchment, one would expect their occurrence at the lower reaches of the Elbe too. This could be explained by different ecological adaptations of the morphotypes. The black-seeded morphotype may be adapted to the management of the South Bohemian fishponds where there is only a relatively short and unpredictable period of substrate exposure during the spring, which makes a strong selection pressure on shortening life cycle and the presence of primary seed dormancy (Šumberová *et al.* 2005). In contrast, alluvial pools in river floodplains are usually exposed for a longer period in late summer and fall, and their water regime is more predictable probably relaxing existing selection pressures (Šumberová 2011). Differences in seed dormancy may also be the direct cause of different seed morphology. Seeds of the black-seeded morphotype probably have thicker testa than those of the brown-seeded morphotype, which is a trait that is related to increased seed dormancy (Bewley *et al.* 2012).

The absence of the black-seeded morphotype in the eastern part of the Czech Republic as well as the absence of the brown-seeded morphotype in south-western part of the Czech Republic are harder to explain as it is the same type of habitats, i.e. fishponds. This may be the result of dispersal limitation. As the majority of the populations of the black-seeded morphotype lie within a different drainage basin than do the populations of the brown-seeded morphotype, a limited diaspore exchange between the two regions seems logical. In addition, there may also exist some sort of environmental filtering. As far as we know, fishponds in the Bohemian-Moravian Highlands, where most of the Czech localities of the brown-seeded morphotype lie, are usually dried for a longer period than the South-Bohemian fishponds (K. Šumberová, pers. comm.). This may create ecological conditions more similar to those of exposed substrates in river alluvia.

Clearly, further studies, including macrofossil analyses and the study of dormancy and germination biology, are needed to elucidate the evolution history of *S. echinosperma*. Partial insight should be provided by an ongoing genetic study (based on published microsatellite markers; Kúr *et al.* 2014).

Based on the obvious geographic and ecological differentiation of the two morphotypes, as well as the morphological differences, their taxonomic treatment as separate subspecies seems justified. Since the type of *S. echinosperma* belongs to the black-seeded morphotype (deposited in the herbarium PR, No. 374981; Kúr *et al.* 2012), we decided to describe the brown-seeded morphotype as the new subspecies.

Taxonomic treatment

Spergularia echinosperma (Čelak.) Ascherson & Graebner (1893: 517) subsp. ***echinosperma*** ≡ *Spergularia rubra* subsp. *echinosperma* Čelakovský (1881: 867)

Lectotype (designated by Kúr *et al.* 2012: 921):—"*Spergularia echinosperma* n. sp. forma *pallens*, u Švarcenberského rybníka u Protivína se *Scirpus Michelianus*, Aug 1876 leg. Čelak.", PR 374981, left bottom individual.

Specimina Visa:—Czech Republic: U Švarcenberského rybníka u Protivína se Scirpus Michelianus, 49.20507, 14.2445 (±100 m), August 1876, *Čelakovský* (PR); Bei dem St. Stephans Teiche unweit von Zbirow, 49.79192, 13.76418 (±500 m), September 1902, *Domin* (B, JE, PRC); Zbirožské Brdy, m demolatis ad piscinam Sv. Štěpánský rybník prope Mýto divulgata., 49.79192, 13.76418 (±500 m), August 1902, *Domin* (PRC, PR); Jižní Povltaví: dno bývalého rybníka U Bulana u Vorlíka v množství, 49.51097, 14.16476 (±1000 m), August 1902, *Domin* (PRC); Vorlík, 49.51097, 14.16476 (±1000 m), August 1902, *Domin* (PRC); Suché dno rybníka Sv. Štěpánského u Zbiroha, 49.79192, 13.76418 (±500 m), September 1903, *Domin* (PRC); Bohemia merid., distr. Písek, nudofundo piscinae emmissae Dolní Luskovec prope Albrechtice apud Protivín, 425 m, 49.21083, 14.1031 (±100 m), 03 October 1943, *Hejný* (PRC); Třeboňsko, obnaž. dno ryb. Opatovického u obory u Třeboně, 48.98308, 14.77017 (±500 m), 10 July 1956, *Kurka*

(CB); Bohemia meridionalis - distr. Strakonice: ad ripam piscinae Horní Mlýnecký inter pagos Drahonice et Skočice, haud procul ab opp. Vodňany, 49.19467, 14.08694 (±100 m), 26 July 1967, *Pučelíková* (LIM); Horažďovicko, Jámský rybník u Kvášňovic, 49.40762, 13.652 (±100 m), 14 August 1968, *Vaněček* (CB); jižní Čechy, pánev Třeboňská, SZ okraj ryb. Ponědražského S od Lomnice n. Luž., 49.11521, 14.71102 (±500 m), 04 July 1972, *Kurka* (CB); Třeboňsko, Ponědrážka, obnažený S břeh Ponědrážkovského rybníka Z od obce, 49.11521, 14.71102 (±500 m), 09 July 1972, *Slaba* (CB); Jižní Čechy, Třeboňská pánev, Veselí nad Lužnicí, na obnaženém dně rybníka u obce Ponědráž, na písku, 49.11521, 14.71102 (±1500 m), 09 July 1972, *Deyl* (OLM); Česká republika: 39. Třeboňská pánev, Jindřichův Hradec, Ponědrážka. Třeboň: dno Veselského (Ponědrážkovského) rybníka Z obce Ponědrážka, 49.11521, 14.71102 (±500 m), *Čejka* 9 July 1972 (PL); Bohemia australis, distr. Lomnice nad Lužnicí, ad ripam piscinae Ponědrážkovský rybník prope pagum Ponědraž., 49.11521, 14.71102 (±500 m), 09 July 1972, *Deylová* (PR); Flora bohemica. Třeboňská pánev: jihovýchodní okraj Ponědrážkovského rybníka jižně od Veselí nad Lužnicí. S. m. ca 410 m, 49.11521, 14.71102 (±500 m), 20 September 1979, *Kurka* (BRNU); Flora bohemica. Třeboňská pánev: jihovýchodní okraj Ponědrážkovského rybníka jižně od Veselí nad Lužnicí. S. m. ca 410 m, 49.11521, 14.71102 (±500 m), 20 September 1979, *Kurka* (BRNU); Flora bohemica. Třeboňská pánev: jihovýchodní okraj Ponědrážkovského rybníka jižně od Veselí nad Lužnicí. S. m. ca 410 m, 49.11521, 14.71102 (±500 m), 20 September 1979, *Kurka* (BRNU); Flora bohemica. Třeboňská pánev: jihovýchodní okraj Ponědrážkovského rybníka jižně od Veselí nad Lužnicí. S. m. ca 410 m, 49.11521, 14.71102 (±500 m), 22 August 1979, *Dvořák* (BRNU); Pičín u Příbrami. Rybník Pilka. Dno zaplavovaného rybníka , 49.74266, 14.07421 (±200 m), 27 June 1981 (LIT); Veselí nad Lužnicí, Ponědrážka, obnažený rybník Hliníř, 49.1336, 14.68207 (±200 m), 04 July 1984, *Kučera* (CB); Příbram - Vranovice. Strýčkovy; dno rybníka, 49.61687, 13.92982 (±1000 m), 07 July 1985, *Zelenka* (OLM); Distr. Příbram: Nesvačily. Podhlubocký rybník, obnažené dno, 0.5 km SSZ obce, 49.61313, 13.91118 (±200 m), 07 July 1985, *Grulich* (PR); Distr. Jindřichův Hradec: Ponědrážka, vypuštěný rybník Hliníř 1.2 km Z obce, 49.1336, 14.68207 (±200 m), 09 July 1988, *Grulich* (PR); Bohemia, distr. Strakonice. Černěves: jihovýchodní část Černěveského rybníka, 1,2 km JV od středu obce; písčitý okraj letněného rybníka; 420 m s. m., 49.10472, 14.22555 (±200 m), 24 July 2000, *Šumberová* (BRNU); Dist. Strakonice, Lažany: bare bottom of the Cky pond, 49.35192, 13.89136 (±4 m), 25 June 2008, *Kúr* (CBFS); Dist. České Budějovice, Dříteň: bare pond bottom of the Kočínský rybník pond, 49.14892, 14.35417 (±4 m), 25 June 2008, *Kúr* (CBFS); Dist. Písek, Písek: bare bottom of the Jenšovský rybník pond, 49.32661, 14.10972 (±4 m), 25 June 2008, *Kúr* (CBFS); Dist. Strakonice, Sedlice: bare bottom of the Malobor pond, 49.36678, 13.97556 (±4 m), 25 June 2008, *Kúr* (CBFS); Bohemia, distr. Písek, Písecko. Dobešice: rybník Jenšovský jižně obce, za silnicí E49. S. m. 380 m, 49.32661, 14.10972 (±200 m), 17 June 2008, *Šumberová* (BRNU); Ditr. Písek, In fundo piscinae emmisae Jenšovský rybník inter vicos Dobešice et Oldřichov, 49.32661, 14.10972 (±200 m), 12 August 2009, *Paulič et Nedvědová* (CB); Dist. Strakonice, Záboří: bare bottom of the Hůrka pond, 49.37306, 13.84564 (±4 m), 21 June 2009, *Kúr* (CBFS); Dist. Strakonice, Velká Turná: bare bottom of the Babák fishpond, 49.34353, 13.9785 (±4 m), 26 June 2010, *Kúr* (CBFS); Dist. Příbram, Hoděmyšl: bare bottom of the Velký hoděmyšlský fishpond, 49.616, 13.87864 (±4 m), 21 June 2011, *Kúr* (CBFS); Dist. Jindřichův Hradec, Hrachoviště: bare bottom of the Hrachovišťský fishpond, 48.92864, 14.76408 (±4 m), 26 June 2011, *Kúr* (CBFS); Dist. Strakonice, Radomyšl: bare bottom of the Chválovec fishpond, 49.32208, 13.89681 (±4 m), 22 June 2011, *Kúr* (CBFS); Dist. Strakonice, Drahonice: bare bottom of the Mlýnský horní fishpond, 49.19467, 14.08694 (±4 m), 25 June 2011, *Kúr* (CBFS); Dist. Příbram, Vranovice: bare bottom of the Podhůrecký fishpond, 49.62389, 13.89206 (±4 m), 21 June 2011, *Kúr* (CBFS); Dist. Písek, Nová Ves u Protivína: bare bottom of the Skopec fishpond, 49.23108, 14.25231 (±4 m), 25 June 2011, *Kúr* (CBFS); Distr. Písek. Dobev - obnažené břehy polovypuštěného rybníka Stašov severně od obce, písčité dno, hojně., 49.30818, 14.03891 (±100 m), 26 June 2012, *Paulič* (R. Paulič); Dist. Jindřichův Hradec, Lomnice nad Lužnicí: exposed bottom of the Služebný fishpond, 49.07507, 14.70887 (±4 m), 16 June 2012, *Kúr* (CBFS); Dist. Písek, Stará Dobev: exposed bottom of the Stašov fishpond, 49.30818, 14.03891 (±4 m), 23 June 2012, *Kúr* (CBFS); Dist. Jindřichův Hradec, Stříbřec: exposed bottom of the Stolec fishpond, 49.03375, 14.85335 (±4 m), 08 June 2012, *Kúr* (CBFS); Dist. Jindřichův Hradec, Branná: exposed bottom of the Tobolky fishpond, 48.96055, 14.7718 (±4 m), 16 June 2012, *Kúr* (CBFS); Kadolecký rybník u Křižanova, 49.36663, 16.12426 (±4 m), 20 June 2012, *Čech* (L. Čech); Distr. Tachov, Nahý Újezdec: bare margin of the Sítina fishpond, at the end of the manipulation road, 49.83501, 12.70116 (±4 m), 08 July 2016, *Kúr* (P. Kúr); Nepomucko. Rybník Nový vypuštěný. Velmi hojná na poněkud oschlém bahně dna., 49.48527, 13.53709 (±200 m), s.d., *Mencl* (PL); **Germany:** Flora von Brandenburg, Rathenow, 52.60601, 12.33664 (±2000 m), 15 September 1899, *Kirschstein* (B).

Spergularia echinosperma subsp. ***albensis*** Kúr, Amarell, Jage & Štech, *subsp. nova*

Type:—GERMANY. Distr. Wittenberg, Priesitz: oxbow lake 1 km East by North of the church in the village; lat.: +51.7047, long.: +12.8393; 12. 10. 1971; leg. H. Jage (holotype GLM-0168069!, (Fig. 6), isotypes PR-878041!, BRNM-792025!, LI-802800!, B-100673696!).

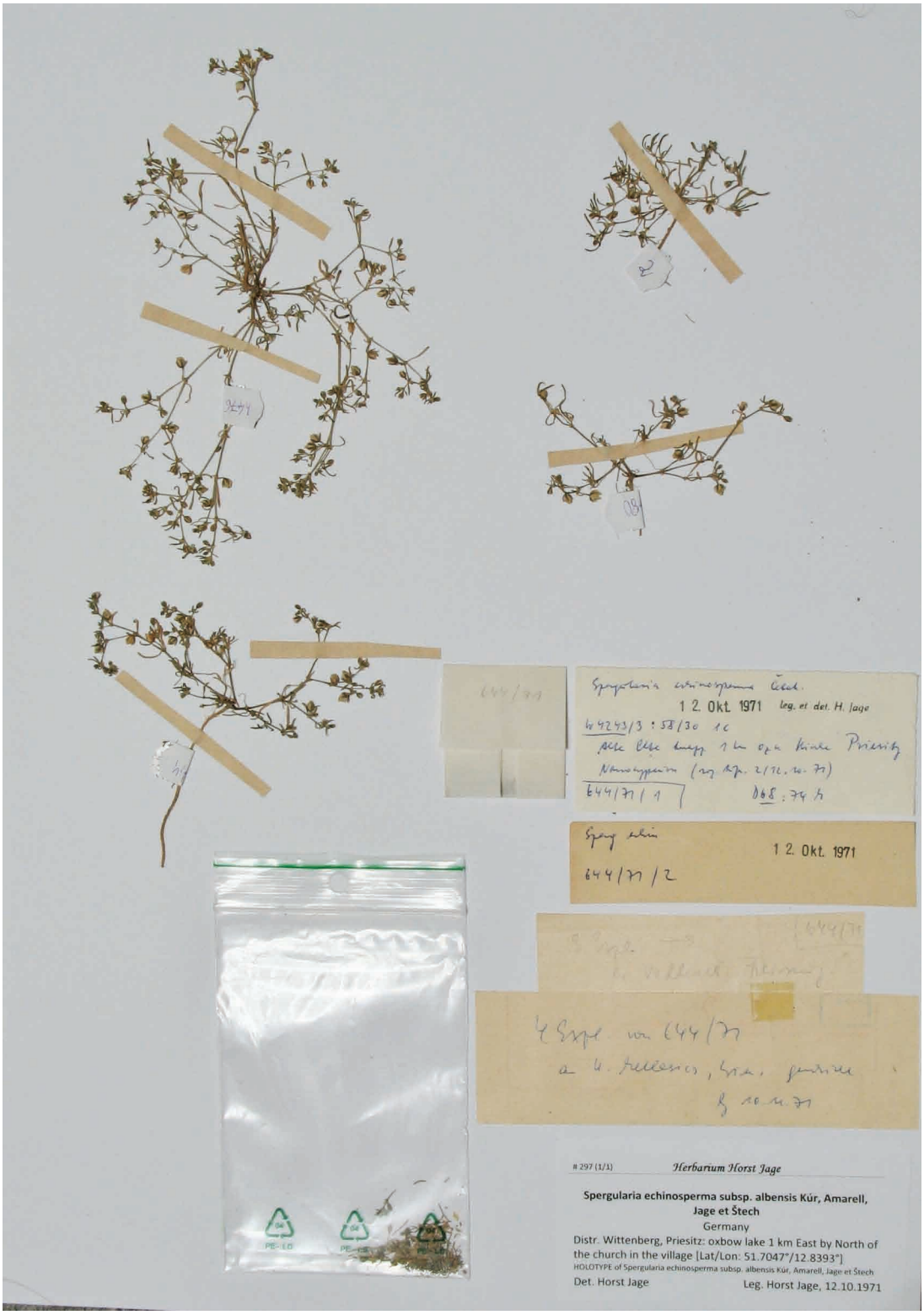

FIGURE 6. Holotype of *Spergularia echinosperma* subsp. *albensis* (GLM-0168069).

Diagnosis:—*Spergularia echinosperma* subsp. *albensis* differs from *S. echinosperma* subsp. *echinosperma* in having seeds with brown to dark-brown testa. In addition, the subsp. *albensis* has, on average, shorter fruit pedicels, lower pedicel length / fruit length ratio and longer leaves than *S. echinosperma* subsp. *echinosperma*.

Etymology:—This subspecies is named after the river Elbe where it has its main center of distribution.

Distribution and habitat:—*Spergularia echinosperma* subsp. *albensis* is currently known only from Germany and the Czech Republic. In Germany, it grows on exposed margins of alluvial pools and river banks of the Elbe, while in the Czech Republic it occurs on drained bottoms of fishponds and river reservoirs. We expect it to occur also in the neighboring countries (Austria, Slovakia, Poland).

Phenology:—Flowering time May–October, fruiting time June–November.

Conservation status:—*Spergularia echinosperma* subsp. *albensis* currently occurs in 176 known localities, in 39 of which it has been reported after 2000. Its estimated extent of occurrence (EOO) is about 20000 km^2, and its area of occupancy (AOO) is about 200 km^2. Following the recommendations of IUCN (2016), we propose treating the taxon as endangered [EN, B2b(iv)c(iii)].

Taxonomic notes:—On the basis of recent phylogenetic analyses (Smissen *et al.* 2002, Fior 2006) and the alleged lack of reliable discriminatory characters between the genera *Spergularia* and *Spergula* (López González 2010), some authors accept to merge them in a single genus (see e.g., López González 2010, Raab-Straube & Raus 2013). In our opinion, however, reliable arguments justifying the union of these two genera are still lacking as there has been no study focusing on the phylogeny and biosystematics of the *Spergula*/*Spergularia* clade yet. In addition, the genus *Spergularia* is accepted in most of the recent floras and checklists (e.g. Danihelka *et al.* 2012, Goliašová 2012, Peruzzi *et al.* 2015, Kaplan *et al.* 2016, Lorite 2016, Villaseñor 2016). We therefore use the name *Spergularia* in the present study.

Specimina Visa:—Czech Republic: Flora Moravica. Jedovnice., 49.33658, 16.76052 (±1000 m), July 1918, *Vitek* (BRNM); U Steklého rybníka u Třebíče, 49.21847, 15.77636 (±400 m), 17 September 1924, *Krajina* (PRC); Flora moravica. Třebíč: ad ripam piscinae Zteklý rybník pr. Starč, 49.19746, 15.82644 (±1000 m), September 1924, *Krajina* (BRNU); Flora moravica. Třebíč: ad ripam piscinae Zteklý rybník pr. Starč, 49.19746, 15.82644 (±1000 m), September 1924, *Krajina* (BRNU); Flora moravica. Třebíč: ad ripam piscinae Zteklý rybník pr. Starč, 49.19746, 15.82644 (±1000 m), September 1924, *Krajina* (BRNU); Flora moravica, na břehu Steklého rybníka u Hvězdoňovic (okres Třebíč), 49.21847, 15.77636 (±400 m), 16 August 1925, *Jičínský* (ZMT); Flora moravica: Osová Bítýška: Vlkovský rybník, v písku. S. m. 500 m, 49.32056, 16.20528 (±500 m), 07 September 1928, *Vybíralová* (BRNU); Flora moravica, Lednice, obnažené dno Středního rybníka. S. m. 165 m, 48.78028, 16.79556 (±300 m), 25 June 1931, *Zapletálek* (BRNU); Flora moravica, Lednice, obnažené dno Středního rybníka. S. m. 170 m, 48.78028, 16.79556 (±300 m), 25 June 1931, *Zapletálek* (BRNU); Jedousov, okr. Pardubice, obnažené dno rybníka v čistém porostu, 49.99432, 15.60735 (±200 m), 01 July 1934, *Hadač* (PR); Brno: Jedovnice, ad finstune niccum pisc. Olšovec; 500 m, 49.33658, 16.76052 (±500 m), 06 October 1943, *Podpěra* (PR); Flora moravica, Vojnův Městec: Malé Dářko., 49.66472, 15.88222 (±200 m), 26 June 1948, *Podpěra* (BRNU); Morava: Nové Město, dno letněného rybníka Medlova u Tří Studní, 49.61395, 16.05096 (±300 m), 14 July 1951, *Smejkal* (BRNM); Flora moravica. Nové Město na Moravě: ad fundum (sicaum) piscinae Medlov dictae prope pagum Tři Studně. S. m. 700 m, 49.61395, 16.05096 (±300 m), 30 July 1951, *Smejkal* (BRNU); Moravia occid., Nové Město na Moravě: ad fundum piscinae dict. Medlov apud pag. Tři Studně. S. m. cca 710 m, 49.61395, 16.05096 (±300 m), 14 July 1951, *Smejkal* (BRNU); Flora moravica, Nové Město na Moravě: na dně letněného rybníka Medlova u Tří Studní v masách. S. m. 715 m, 49.61395, 16.05096 (±300 m), 14 July 1951, *Smejkal* (BRNU); Flora moravica, Nové Město na Moravě: v masách na dně letněného rybníka Medlova u Tří Studní. S. m. 700 m, 49.61395, 16.05096 (±300 m), 14 July 1951, *Smejkal* (BRNU); Moravia occid., Nové Město na Moravě: ad fundum piscinae Medlov dict. ap. pag. Tři Studně. S. m. 710 m, 49.61395, 16.05096 (±300 m), 14 July 1951, *Smejkal* (BRNU); Flora moravica, Nové Město na Moravě: na dně letněného rybníka Medlova u Tří Studní /v masách/. S. m. 710 m, 49.61395, 16.05096 (±300 m), 14 July 1951, *Smejkal* (BRNU); Žďár nad Sázavou, Sykovec ad pagum Tři Studně, 720 m, 49.60871, 16.03817 (±200 m), 14 July 1961, *Smejkal* (BRNM, HAL, JE, MJ, OP, PRC); Moravia occidentalis, distr. Žďár nad Sázavou: in fundo paludoso piscinae aestate vacuefactae Sykovec dictae ad pagum Tři Studně. S. m. cca 720 m, 49.60871, 16.03817 (±200 m), 14 July 1961, *Smejkal* (BRNU); Flora Moravica: Nové Město na Moravě: ad fundum piscinae vacuefactae Sykovec dictae prope pagum Tři Studně. S. m. cca 720 m, 49.60871, 16.03817 (±200 m), 14 July 1961, *Smejkal* (BRNU); Flora Moravica: Nové Město na Moravě: ad fundum piscinae vacuefactae Sykovec dictae prope pagum Tři Studně. S. m. cca 720 m, 49.60871, 16.03817 (±200 m), 14 July 1961, *Smejkal* (BRNU); Distr. Lednice: Allahovy rybníčky /prostřední/ mezi Valticemi a Lednicí., 48.76986, 16.79811 (±100 m), 23 July 1962, *Hejný* (PRA); Flora moravica. Vlkov u obce Velká Bíteš, okraj Vlkovského rybníka. S. m. ca 490 m, 49.32056, 16.20528 (±500 m), 05 August 1969, *Dvořák* (BRNU); Žďárské vrchy - Tři studně, dno vypuštěného Medlov. rybníka, uprostřed, 49.61395, 16.05096 (±300 m), 10 September 1970, *Pospíšil* (BRNM); Flora moravica: Nové město na Moravě: na dně vypuštěného (letněného) rybníka Medlov u Tří Studní, masově., 49.61395, 16.05096 (±300 m), 22 July 1970, *Smejkal* (MJ); Flora moravica. Moravia occident., distr. Žďár nad Sázavou: in fundo piscinae aestatae vacuefactae Medlov dictae prope pag. Tři Studně. S. m. cca 720 m, 49.61395, 16.05096 (±300 m), 22 July 1970, *Smejkal* (BRNU); Distr. Jižní Morava: Lednické rybníky (rybn. Aloch IV), 48.7775, 16.79456 (±100 m), 13 June 1971, *Husák* (PR); Flora moravica, dist. Břeclav, Lednice, obnažená rybničná půda rybníčka Alah 4, řídce. S. m. ca 160 m, 48.7775, 16.79456 (±100 m), 18 September 1973, *Vicherek* (BRNU); Flora moravica, dist. Břeclav, Lednice, obnažená rybničná půda rybníčka Alah 4, řídce. S. m. 160 m, 48.7775, 16.79456 (±100 m), 18 September 1973,

Vicherek (BRNU); Distr. Žďár nad Sázavou: na jižním obnaženém písčitém okraji rybníka Sykovec u obce Tři Studně. cca 720 m, 49.60871, 16.03817 (±200 m), 22 July 1975, *Smejkal* (MJ); Flora moravica. Moravia occident., Nové Město na Moravě: locis paludosis arenosis que ad marginem oriental. piscinae Sykovec dictae prope pagum Tři Studně. S. m. cca 720 m, 49.60871, 16.03817 (±200 m), 22 July 1975, *Smejkal* (BRNU); Flora moravica. Moravia occident., Nové Město na Moravě: locis paludosis arenosis que ad marginem oriental. piscinae Sykovec dictae prope pagum Tři Studně. S. m. cca 720 m, 49.60871, 16.03817 (±200 m), 22 July 1975, *Smejkal* (BRNU); Flora moravica. Moravia occident., Nové Město na Moravě: locis paludosis arenosis que ad marginem oriental. piscinae Sykovec dictae prope pagum Tři Studně. S. m. cca 720 m, 49.60871, 16.03817 (±200 m), 22 July 1975, *Smejkal* (BRNU); Flora moravica. Moravia occident., Nové Město na Moravě: locis paludosis arenosis que ad marginem oriental. piscinae Sykovec dictae prope pagum Tři Studně. S. m. cca 720 m, 49.60871, 16.03817 (±200 m), 22 July 1975, *Smejkal* (BRNU); Flora moravica. Moravia occident., Nové Město na Moravě: locis paludosis arenosis que ad marginem oriental. piscinae Sykovec dictae prope pagum Tři Studně. S. m. 720 m, 49.60871, 16.03817 (±200 m), 22 July 1975, *Smejkal* (BRNU); Flora moravica. Moravia occident., Nové Město na Moravě: locis paludosis arenosis que ad marginem oriental. piscinae Sykovec dictae prope pagum Tři Studně. S. m. 720 m, 49.60871, 16.03817 (±200 m), 22 July 1975, *Smejkal* (BRNU); Flora moravica. Moravia occident., Nové Město na Moravě: ad marginem oriental. piscinae Sykovec dictae prope pagum Tři Studně, locis paludosis arenosisque. S. m. 720 m, 49.60871, 16.03817 (±200 m), 22 July 1975, *Smejkal* (BRNU); Flora moravica. Moravia occident., distr. Žďár nad Sázavou: in fundo piscinae aestatae vacuefactae Medlov dictae prope pag. Tři Studně, copiose! S. m. 720 m, 49.61395, 16.05096 (±300 m), 22 July 1975, *Smejkal* (BRNU); Flora Moravica. Lednice: obnažené dno Valachovského ryb. II [Alah 2]. S. m. ca 170 m, 48.76986, 16.79811 (±100 m), 03 July 1980, *Zapletálek* (BRNU); Flora moravica. Hills Žďárské vrchy, the pond Sykovec near the village Tři Studně, 5 km NNW from the Nové Město na Moravě. The locality no. 14 (Dvořák 1979: 115). S. m. ca 720 m, 49.60871, 16.03817 (±200 m), 26 October 1982, *Dvořák* (BRNU); Flora moravica. Distr. Žďár nad Sázavou, obec Tři Studně: obnažené dno vypuštěného rybníka Sykovec severně od Nového Města na Mor. S. m. ca 720 m, 49.60871, 16.03817 (±200 m), 26 October 1982, *Dvořák* (BRNU); Flora moravica. Distr. Žďár nad Sázavou, obec Tři Studně: obnažené dno vypuštěného rybníka Sykovec. S. m. ca 720 m, 49.60871, 16.03817 (±200 m), 26 October 1982, *Dvořák* (BRNU); Flora moravica. Distr. Žďár nad Sázavou, obec Tři Studně: obnažené dno vypuštěného rybníka Sykovec severně od Nového Města na Mor. S. m. ca 720 m, 49.60871, 16.03817 (±200 m), 26 October 1982, *Dvořák* (BRNU); Flora moravica. Distr. Žďár nad Sázavou, obec Tři Studně: obnažené dno vypuštěného rybníka Sykovec severně od Nového Města na Mor. S. m. ca 720 m, 49.60871, 16.03817 (±200 m), 26 October 1982, *Dvořák* (BRNU); Flora moravica. Distr. Žďár nad Sázavou, obec Tři Studně: obnažené dno vypuštěného rybníka Sykovec severně od Nového Města na Mor. S. m. 720 m, 49.60871, 16.03817 (±200 m), 26 October 1982, *Dvořák* (BRNU); Flora moravica. Distr. Žďár nad Sázavou, obec Tři Studně: obnažené dno vypuštěného rybníka Sykovec. S. m. ca 720 m, 49.60871, 16.03817 (±200 m), 26 October 1982, *Dvořák* (BRNU); Flora moravica. Distr. Žďár nad Sázavou, obec Tři Studně: obnažené dno vypuštěného rybníka Sykovec. S. m. ca 720 m, 49.60871, 16.03817 (±200 m), 26 October 1982, *Dvořák* (BRNU); Flora moravica. Hills Žďárské vrchy, the pond Sykovec near the village Tři Studně, 5 km NNW from the Nové Město na Moravě. The locality no. 14 (Dvořák 1979: 115). S. m. ca 720 m, 49.60871, 16.03817 (±200 m), 26 October 1982, *Dvořák* (BRNU); Flora moravica. Distr. Žďár nad Sázavou, obec Tři Studně: obnažené dno vypuštěného rybníka Sykovec. S. m. ca 720 m, 49.60871, 16.03817 (±200 m), 26 October 1982, *Dvořák* (BRNU); Distr. Nové Město na Moravě, rybník Sykovec, obnažené břehy rybníka. S. m. ca 650 m, 49.60871, 16.03817 (±200 m), 18 September 1985, *Smejkal* (BRNU); Pavlov, 12 km J od Žďáru nad Sázavou: obnažené dno při S břehu rybníka Podvesník V od obce., 49.45019, 15.92491 (±200 m), 12 July 2001, *Čech* (L. Čech); Okr. Žďár nad Sázavou: Rudolec: obnažené a právě znovu zaplavované dno rybníka Pařezný 1 km V od obce, J od silnice do Bohdalova., 49.47744, 15.85317 (±200 m), 04 July 2005, *Kaplan* (Z. Kaplan); Dist. Třebíč, Kojatín: bare bottom of the Kojatínský fishpond, 49.24172, 16.00847 (±4 m), 06 June 2011, *Kúr* (CBFS); Dist. Žďár Nad Sázavou, Bohdalov: bare bottom of the Pařezný fishpond, 49.47744, 15.85317 (±4 m), 04 June 2011, *Kúr* (CBFS); Dist. Chrudim, Švihov: bare bottom of the Švihov fishpond, 49.84264, 15.85931 (±4 m), 05 June 2011, *Kúr* (CBFS); Dist. Jindřichův Hradec, Malý Ratmířov: bare bottom of the Vosecký fishpond, 49.13522, 15.13089 (±4 m), 07 June 2011, *Kúr* (CBFS); Dist. Žďár Nad Sázavou, Kadolec: bare bottom of the Kadolecký fishpond, 49.36663, 16.12426 (±4 m), 18 June 2012, *Kúr* (CBFS); Dist. Žďár nad Sázavou, Radkov: bare bottom of the Nohavice fishpond, 49.42881, 16.15753 (±4 m), 19 June 2012, *Kúr* (CBFS); Dist. Karviná, Těrlicko: exposed margin of the Těrlicko water reservoir, 49.74336, 18.49515 (±4 m), 25 October 2012, *Kúr* (CBFS); Distr. Žďár nad Sázavou, Znětínek: bare bottom of the Znětínecký fishpond., 49.4592, 15.92774 (±4 m), 21 August 2014, *Kúr* (P. Kúr); Moravia, Pavlov (dist. Žďár nad Sázavou): hojně na obnaženém dně rybníku Podvesník, přibližně 1017 m východně kostela svatého Filipa a Jakuba v centru Pavlova., 49.45019, 15.92491 (±200 m), 11 September 2015, *Zámečník et Ducháček* (J. Zámečník); **Germany:** Magdeburg, 52.12388, 11.64658 (±20000 m), 17 October 1898

(POZ); Magdeburg: An der Elbe nahe Pratau. 2n, mit Corrigiola., 52.12388, 11.64658 (±20000 m), October 1898 (POZ); Flora von Anhalt, Elbstrand beim Sieglitzer und weiter an der Elbe beim niedrigen Wasserstrand, 51.85718, 12.35127 (±500 m), 01 August 1908, *Zobel* (MNVD); Flora der Altmark, Sandiges Elbufer bei Arneburg im Kreis Stendal (Provinz Sachsen), 52.67469, 12.01255 (±1000 m), September 1909, *Schuster* (GAT, DR); Wittenberg, Elbufer, 51.85968, 12.6326 (±2000 m), 24 August 1911, *Matthies* (GAT); Elbestrand r[echtes]. Ufer oberhalb Schönebeck., 52.0229, 11.74255 (±2000 m), 17 September 1911 (GAT); Flora der Altmark, Schlickbuhne an der Elbe bei Arneburg im Kreise Stendal., 52.67469, 12.01255 (±1000 m), August 1911, *Schuster* (GAT, DR); Sachsen. Elbstrand bei Schönebeck, 52.0229, 11.74255 (±2000 m), 10 August 1911, *Meißner* (MNVD); Anhalt. Elbstrand Sieglitzer – Vockerode, 51.85718, 12.35127 (±500 m), 19 August 1911, *Zobel* (MNVD); Anhalt. Elbstrand beim Sieglitzer, 51.85718, 12.35127 (±500 m), 09 August 1911, *Zobel* (MNVD); Alte Elbe bei Magdeburg (Strand), 52.16631, 11.71703 (±500 m), 10 August 1911, *Meißner* (MNVD); Elbstrand zw. Roßlau und Brambach, 51.88124, 12.24526 (±2000 m), 12 August 1911, *Zobel* (MNVD); Elbstrand bei Schönbeck, auch an der alten Elbe bei Magdeburg, 52.0229, 11.74255 (±2000 m), 10 August 1911, *Meißner* (MNVD); Strand der Elbe von Schönbeck bis Magdeburg, 52.12388, 11.64658 (±20000 m), 10 August 1911, *Meißner* (MNVD); Strand der Elbe bei Barby, 51.97425, 11.88841 (±1000 m), 03 August 1911, *Meißner* (MNVD); Strand der Elbe bei (Barby) Roßlau, 51.88124, 12.24526 (±2000 m), August 1911, *Meißner* (MNVD); Strand der Elbe oberhalb Schönbeck, rechtes Ufer., 52.0229, 11.74255 (±2000 m), 17 August 1911, *Meißner* (MNVD); Strand der Elbe oberhalb Schönbeck, rechtes Ufer., 52.0229, 11.74255 (±2000 m), 17 August 1911, *Meißner* (MNVD); Elbstrand bei Barby, 51.97425, 11.88841 (±1000 m), *Meißner* 03 September 1911, *Meißner* (MNVD); Sachsen, Wittenberg, Elbe-Ufer, 51.85968, 12.6326 (±2000 m), 24 August 1911, *Mayer* (STU); Elbe, südl. Hamburg, Winsen, bei Elbstorf., 53.42157, 10.28427 (±500 m), 24 August 1916, *Junge* (STU); Elbe, südl. Hamburg, Winsen, bei Marschhacht., 53.42215, 10.37284 (±500 m), 10 September 1916, *Junge* (STU); Elbufer bei Rosslau (Anhalt), 51.88124, 12.24526 (±2000 m), 06 September 1928, *Linstow* (B); Flora Germanica, Eldeufer bei Kl[ein] Schmölen, 53.12642, 11.26686 (±1000 m), 16 July 1960, *Bisse* (JE); Kreis Roßlau: Rechtes Elbufer im Luch bei Coswig, auf Elbschlick, selten, 51.86963, 12.46612 (±1000 m), 08 October 1962, *Jage* (H. Jage); Rechtes Elbufer südlich an Wittenberg, stark sandiger Schlick, selten, 51.85968, 12.6326 (±2000 m), 10 October 1962, *Jage* (H. Jage); Kreis Stendal: rechtes Elbufer gegenüber Tangermünde, wenig unterhalb der Straßenbrücke, 52.56491, 11.98564 (±500 m), 14 October 1963, *Jage* (B, H. Jage); Kreis Wittenberg: Altwasser nördlich Pratau (östlich der Fernverkehrsstraße Nr. 2), sandiger Teichschlamm, 51.85115, 12.64539 (±500 m), 07 October 1963, *Jage* (HAL, H. Jage); Kreis Wittenberg: Dorfteich Bleddin (Altwasserrest), Teichschlamm, 51.79411, 12.79542 (±500 m), 30 July 1963, *Jage* (H. Jage); Kreis Wittenberg: Nordende des Bleddiner Risses (Elbaltwasser) östlich Wartenburg, Sandbank, massenhaft!, 51.79411, 12.79542 (±500 m), 07 September 1963, *Jage* (H. Jage,); Kreis Wittenberg: Mühlanger: Südlich am Ortsteil Hohndorf, Mündungsgebiet des Mühlgrabens in die Alte Elbe, fetter Teichschlamm, 51.85029, 12.72451 (±500 m), 13 September 1963, *Jage* (H. Jage); Kr. Wittenberg: N Pratau, Altwasser östl. F2 (nahe Bude 100), 51.85115, 12.64539 (±500 m), 07 October 1963, *Jage* (H. Jage); Kreis Wittenberg: oso Wartenburg am Bleddiner Riß (Elbaltwasser), fetter Teichschlamm, 51.79411, 12.79542 (±500 m), 05 November 1963, *Jage* (H. Jage); Altkreis Roßlau: wenig oberhalb Autobahnbrücke bei Vockerode, 3. Buhne am rechten Elbufer, 51.85718, 12.35127 (±500 m), 06 September 1964, *Jage* (H. Jage); Fundort: Elbtal, Kurzer Wurf am Matzwerder, 51.88031, 12.32558 (±500 m), 05 September 1965, *Jage* (MNVD); Mittelelbegebiet zwischen Wittenberg u. Dessau: trockengefaller Uferschlamm eines Elbarmes westl. Vorwerk Werder sw Klieken. Nanocyperion; Schlamm - Sand, 51.87596, 12.3582 (±500 m), 10 September 1967, *Hilbig* (HAL); Kreis Wittenberg: Kolk oberhalb Fähre Gallin, rechts der Elbe, 51.8368, 12.75619 (±200 m), 11 September 1967, *Jage* (H. Jage); Verlandungssaum des Dorfteiches von Bleddin, 51.79411, 12.79542 (±500 m), 22 September 1968, *Zenker* (MNVD); Altkreis Roßlau: Kurzer Wurf WSW Klieken, 51.88031, 12.32558 (±500 m), 09 September 1968, *Jage* (H. Jage); Mittleres Elbtal 14 km südöstlich von Wittenberg. Bleddin: Schluft (alter Elbarm), 51.79411, 12.79542 (±500 m), 25 September 1969, *Werner et Günther* (HAL); Im Teich Die Schluft, Bleddin b. Trebitz (Elbe), 51.79411, 12.79542 (±500 m), 13 September 1970 (HAL); Flora von Anhalt, Wittenberg: Bleddin, Schluff (= Bleddiner Dorfteich), 51.79411, 12.79542 (±500 m), 13 September 1970, *Manitz* (JE); Kurzer Wurf (Elbaltwasser) reichl. 3 km WSW Klieken, 51.88031, 12.32558 (±500 m), 08 November 1971, *Jage* (H. Jage); Altkreis Torgau. Alte Elbe wenig OSO Werdau, 51.55185, 13.03868 (±300 m), 06 November 1971, *Jage* (H. Jage); Deutschland, mittleres Elbtal: Kreis Wittenberg, Alte Elbe knapp 1 km ozn Priesitz; sandig-schlammiges Ufer eines Elbatwassers, häufig im Cypero-Limoselletum (Nanocyperion), 51.70727, 12.83715 (±200 m), 12 October 1971, *Jage* (H. Jage); NNO Sachau: Kolk zwischen Elb-Damm u. Alte Elbe, 51.69527, 12.8375 (±300 m), 09 September 1972, *Jage* (H. Jage); Deutschland (DDR): Elbtal bei Wittenberg, Bleddiner Riß, 1 km nördl. Bleddin., 51.79411, 12.79542 (±500 m), 16 September 1973, *Diholz* (B); Mittleres Elbtal: Elbe-Altwasser zwischen Wittenberg u. Pratau, 51.85115, 12.64539 (±500 m), 10 June 1973, *Rauschert* (HAL); Altwasser bei Bude 100 nördl. Pratau, 51.85115, 12.64539 (±500 m), 22 October 1973, *Jage*

(H. Jage); Kreis Wittenberg: ca 1.5 km NNO Sachau, Elbaltwasser, 51.69527, 12.8375 (±300 m), 13 September 1973, *Jage* (H. Jage); Lüchow-Dannenberg: bei Gartow, Elbholz, sand. Buhnenschotter., 53.057, 11.48683 (±500 m), 30 August 1982, *Ketelhut/Meyer* (B); Kr. Wittenberg: Bleddiner Riß, Uferschlamm, 51.79411, 12.79542 (±500 m), 26 June 1982, *Jage* (H. Jage); Flora von Sachsen-Anhalt, Wittenberg, 2 km N Bleddin, Sandufer eines Elbaltarmes, 51.79411, 12.79542 (±500 m), 31 October 1990, *Korsch* (JE); Mecklenburg, Dömitz, auf Sandbänken der Elbaue bei Strachau in Menge mit Sp. rubra vergesellschaftet, 53.14466, 11.10518 (±500 m), 02 October 1990, *Henker* (LI); Sachsen-Anhalt, Kreis Stendal. Shore of r. Elbe E Grieben., 52.4387, 11.9919 (±2000 m), 18 October 1992, *Müller* (JE); Sachsen-Anhalt, Kreis Wittenberg. Bleddiner Riß NE Bleddin., 51.79411, 12.79542 (±500 m), 30 August 1992, *Müller* (JE); Sachsen-Anhalt, Kreis Wolmirstedt. Elbe meadows S Heinrichsberg., 52.2741, 11.74874 (±1000 m), 18 October 1992, *Müller* (JE); Sachsen-Anhalt, Kreis Stendal. Shore of r. Elbe SSE Schelldorf, 52.46844, 11.99283 (±1000 m), 10 October 1993, *Müller* (JE); Krs. Wittenberg, OSO Wartenburg, Bleddiner Riß nahe N-Ende, Sandbank, 51.79411, 12.79542 (±500 m), 25 September 1998, *Jage* (H. Jage); Kreis Wittenberg: östl. Priesitz, Altwasser Schluft bei Kote 77,8, auf getrockenen Sand, 51.70727, 12.83715 (±200 m), 24 August 2003, *Jage* (H. Jage); Altkreis Jessen: W Schützberg, Klödener Riß, rechtes Ufer, Sand, 51.78215, 12.8079 (±300 m), 26 August 2003, *Jage* (H. Jage); Kreis Wittenberg: OSO Wartenburg, Bleddiner Riß N-Teil (Angelgewässer Falkenweiden), ausgedehnte Sandbank, 51.79411, 12.79542 (±500 m), 07 August 2003, *Jage* (H. Jage); Elbufer / Sand NO Klein Wanzer, 53.00946, 11.62762 (±1000 m), 20 September 2003, *Frank* (H. Jage); Brandenburg, Deich: exposed shore of the oxbow lake Haken, 52.90258, 11.85815 (±4 m), 16 July 2012, *Kúr* (CBFS); Saxony-Anhalt, Beuster: exposed shore of an oxbow lake 600 m E of the village, 52.94019, 11.79487 (±4 m), 16 July 2012, *Kúr* (CBFS).

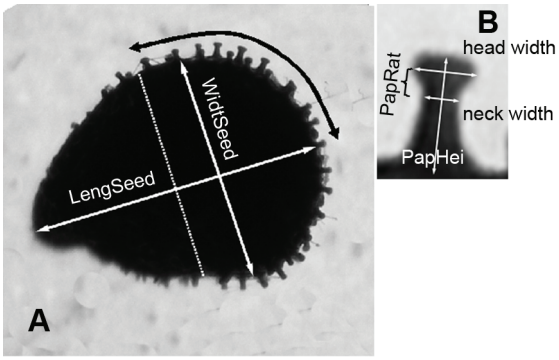

FIGURE 7. Characters measured on the seeds (A) and surface papillae (B). The black curved line specifies the part of the seed circumference where the density of papillae was determined. The longitudinal border of this part is a plane halving the vector of maximal seed length and perpendicular to it (indicated by a dotted line). The character PapRat was computed by dividing the width of the papilla head by the width of the neck.

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