The differentiation of subspecies in *Bolboschoenus maritimus* based on the inflorescence structure

Rozlišení subspecií *Bolboschoenus maritimus* na základě stavby květenství

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The importance of inflorescence structure as a diagnostic feature was studied to distinguish *Bolboschoenus maritimus* (L.) Palla subsp. *maritimus* and *B. maritimus* subsp. *compactus* (Hoffm.) Hejný in Dostál. The subspecies were determined using characters in the fruits and the level of agreement with inflorescence characters was compared. The following characters were recorded: the length of spikelets and of peduncles of the inflorescence, the number of peduncles of the inflorescence, the number of sessile and peduncled spikelets. From these primary characters, relative characters were derived. Plants from field populations and cultivated plants collected from localities throughout the Czech and Slovak Republics were studied, as well as changes in inflorescence morphology after transplanting. Significant differences were found between both subspecies in most of the characters measured in the field populations as well as in the cultivated plants. The number of peduncles of the inflorescence, the ratio between the number of sessile and peduncled spikelets and the length ratio of sessile spikelets and peduncles of the inflorescence were found to be most suitable to use for the determination of both subspecies. Plants of subsp. *compactus* were found to be more variable in most characters compared with subsp. *maritimus*. The field populations of subsp. *maritimus* were homogeneous in most characters (negligible intrapopulation variation), and the influence of habitat was found to be significant only in some characters. The populations of subsp. *compactus* showed greater variation in most characters within populations and were not significantly influenced by habitat.

Keywords: *Bolboschoenus maritimus*, subsp. *maritimus*, subsp. *compactus*, inflorescence morphology, intraspecific variation, diagnostic features

Introduction

Bolboschoenus maritimus (L.) Palla (= *Scirpus maritimus* L.) represents a non-homogeneous taxonomic unit. In Europe, two types have been recognized within this species, differing in the inflorescence structure, in the shape of the fruits and in their ecology (relationship to salinity): *B. maritimus* subsp. *maritimus* and *B. m.* subsp. *compactus* (Foerster 1972, Casper & Krausch 1980). They have been classified at various taxonomic levels by different authors: varieties or forms (Reichgelt 1956 – f. *compactus*, Schultze-Motel 1980), paramorphs (Robertus-Koster 1969) or species (Smirenskij 1952, Dobročaeva et al. 1987). In other cases these two types within *B. maritimus* have not been considered as separate taxonomic units, or intraspecific variation has not been mentioned (Norlindh 1972, Rothmaler 1982, Kukkonen 1984, Tutin et al. 1980).

The areas of distribution of both subspecies are not well known; the saline subspecies *compactus* prevails in coastal regions of western and northern Europe, while both taxa were found in The Netherlands, France, Germany, Czech Republic, Poland, Slovakia, Hungary, Ukraine (Hroudová et al. 1998). The intraspecific variation of *Bolboschoenus maritimus* seems to increase eastwards across Europe, which may reflect the taxonomic classification: the concept of separate species in eastern Europe, subspecies in Central Europe and mostly lower taxonomic units or no intraspecific differentiation in western Europe.

Two types found in the Czech and Slovak Republics have been recently considered as subspecies (Soják 1958, Hejný 1960, Dostál 1958, 1982, 1989, Dykyjová 1986). While bearing in mind that there are nomenclatural problems in *Bolboschoenus maritimus* at specific and intraspecific levels, the solution of nomenclatural problems and taxonomic classification is beyond the scope of our study. We follow the intraspecific division according to Casper & Krausch (1980) because the characteristics of both subspecies described there correspond best with the characteristics of plants found in our country. Thus, the type of saline, more eutrophic habitats is called subsp. *compactus* (Hoffm.) Hejný in Dostál, and the non-saline type is called subsp. *maritimus*.

The basic diagnostic features leading to the determination of the two subspecies within *B. maritimus* are the characters of the fruits (shape, colour and anatomy), and the structure of the inflorescence. The characters of the fruits are very suitable for the determination of *Bolboschoenus* taxa (Soják 1958, Browning & Gordon-Gray 1993, Browning et al. 1995, 1997) and appear to be stable and reliable. The inflorescence structure may be more influenced by habitat conditions and thus be more variable; however, it is the only character available when plants are flowering and is very useful for field determination.

The aim of this paper is to evaluate the variation in inflorescence structure in both subspecies, to test the reliability of the determination based on inflorescence characters compared with the determination using characters of the fruits and to determine which characters in the inflorescence are the most efficient and suitable to distinguish both subspecies. We studied variations in field populations of *B. m.* subsp. *maritimus* and *B. m.* subsp. *compactus* in the Czech and Slovak Republics, in clones cultivated in the experimental garden and changes in inflorescence structure after transfer into cultivation.

Material and methods

Plants

Plant material was sampled in field habitats throughout the whole of the Czech and Slovak Republics, from as many localities as possible, mostly in the period 1983 to 1992 (see List of localities). In each flowering population of *B. maritimus*, 25 flowering shoots randomly chosen were sampled, dried and measured. Only inflorescences which had finished flowering or with unripe fruits could be used for further measurements. In addition, plants for cultivation were sampled in all localities and transplanted into the experimental garden in Průhonice. One plant consisting of one or several underground tubers connected by rhizomes and forming aboveground shoots was sampled in each locality. The plants were cultivated for one to several years under conditions favourable for both subspecies (water level 0.1 to 0.2 m, humus-rich garden soil with sand, mineral fertilizer used in each growing season). Each

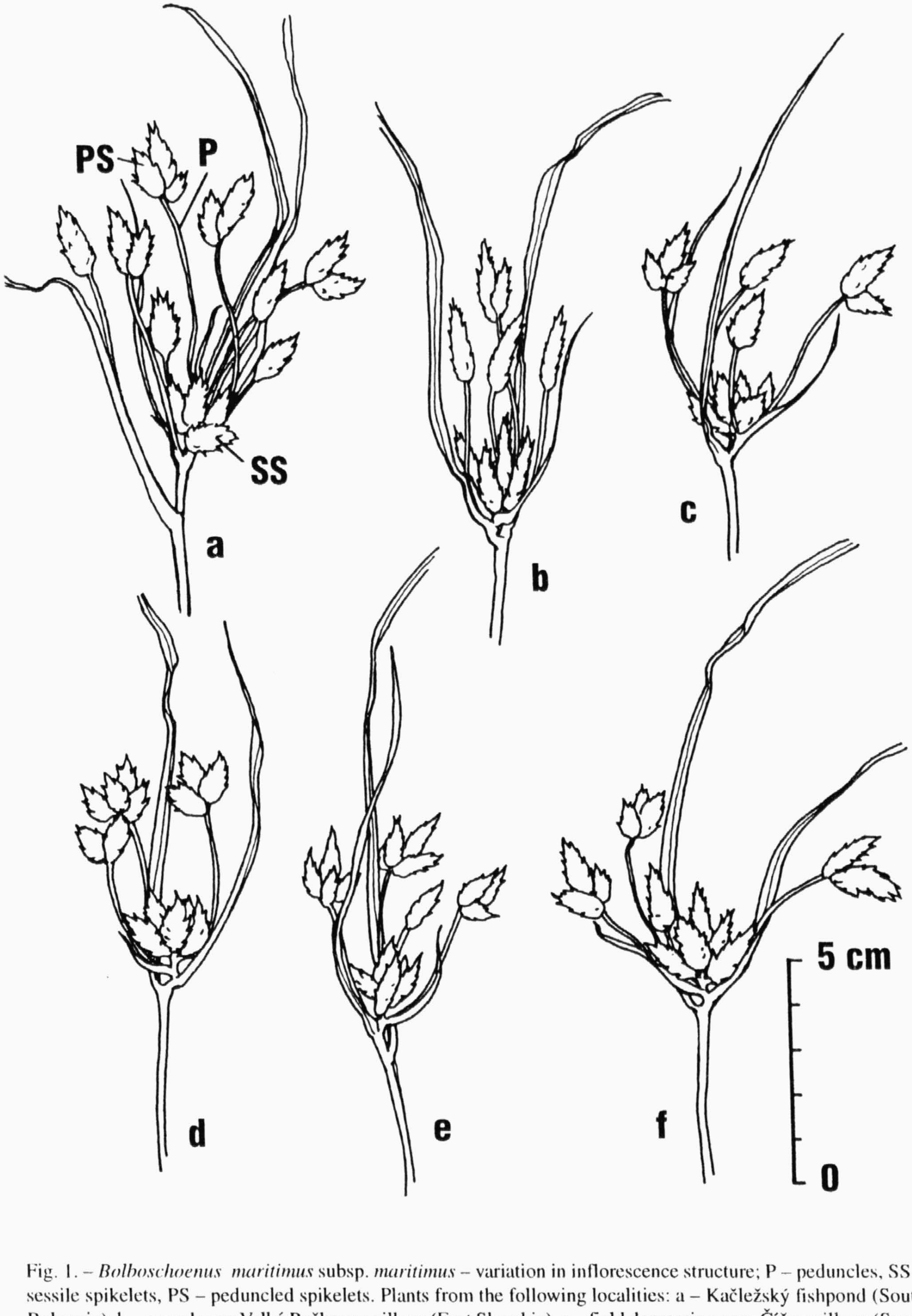


Fig. 1. – *Bolboschoenus maritimus* subsp. *maritimus* – variation in inflorescence structure; P – peduncles, SS – sessile spikelets, PS – peduncled spikelets. Plants from the following localities: a – Kačležský fishpond (South Bohemia), b – a pool near Velké Raškovce village (East Slovakia), c – field depression near Číčov village (South Slovakia), d – Bruksa oxbow in Břeclav (South Moravia), e – fish hatchery near Jistebník railway station (North Moravia), f – field depression near Vehlovice village (Central Bohemia).

plant multiplied vegetatively forming clones in which genetic heterogeneity could be excluded. In the following text we use the term "population" for all plants occurring in one field locality, and the term "clone" for cultivated plants originating from one locality. Plants were measured in 34 field populations, cultivated clones from 57 localities and the plants from 24 localities were measured both in the field population and after transplanting.

The subspecies of *B. maritimus* were determined using only characters in fruit as follows:
(i) subsp. *maritimus*: achenes triangular in cross section (with the edge on the dorsal side), dark brown to black, with mostly persistent perigon bristles;
(ii) subsp. *compactus*: achenes concave or nearly flat on the dorsal side, ochre, light- to rusty-brown, mostly without perigon bristles. This taxon corresponds with *B. planiculmis* sensu Egorova (1967, 1976).

Measurements

The following primary characters were recorded (see Fig. 1):
1. P-L: length of the peduncles of the inflorescence,
2. PS-L: length of peduncled spikelet,
3. SS-L: length of sessile spikelet,
4. P-No: number of peduncles per inflorescence,
5. PS-No: number of spikelets on all peduncles per inflorescence,
6. SS-No: number of sessile spikelets per inflorescence.

From these primary characters, the relative characters were derived:
7. PS/P-No: number of peduncled spikelets per peduncle of the inflorescence,
8. SS/P-L ratio: length of sessile spikelet/mean length of a peduncle in the same inflorescence,
9. PS/P-L ratio: length of peduncled spikelet/mean length of a peduncle in the same inflorescence,
10. SS/PS-L ratio: length of sessile spikelet/mean length of peduncled spikelet in the same inflorescence,
11. SS/PS-No ratio: number of sessile spikelets within one inflorescence/number of spikelets on all peduncles within that inflorescence,
12. SS/P-No ratio: number of sessile spikelets/number of peduncles in the same inflorescence.

The same variables were measured in plants in the field (25 inflorescences in each population) as in plants cultivated in the experimental garden in Průhonice. In the cultivated plants, flowering shoots were sampled from each flowering clone. The number of inflorescences differed between plants; we sampled all (maximum 25) inflorescences from each clone in the same growing season.

Statistical treatment

Variations in the characters measured were tested within natural populations and in cultivated plants separately. In those localities where both data (field and cultivated plants after transplanting) were available, changes after transplanting were tested. The program SOLO (BMDP) was used for the statistical analysis. The data measured were analysed as follows:

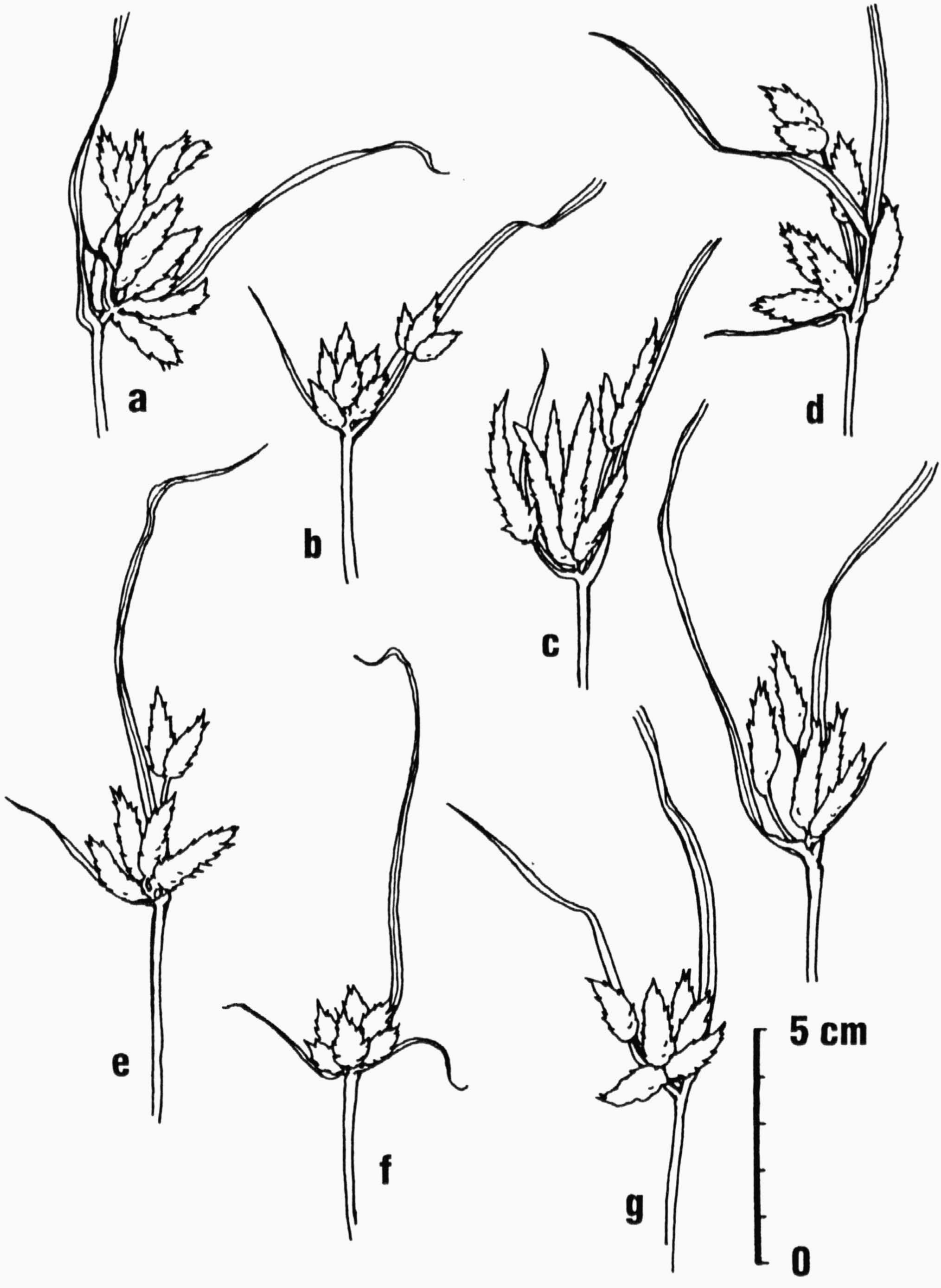


Fig. 2. – *Bolboschoenus maritimus* subsp. *compactus* – variation in inflorescence structure. Plants from localities: a – field depression near Sekule railway station (West Slovakia), b – field depression on the border of Lanžhot village (South Moravia), c – field depression near Dobré Pole village (South Moravia), d – Dobroměřický fishpond near Louny (North-West Bohemia), e – the ditch on the border of Velký Kamenec village (East Slovakia), f – field depression near the road in Přerov (North Moravia), g – field depression near the shore of Nesyt fishpond near Valtice (South Moravia), h – field depression near Kucany village (East Slovakia).

1. Mean values of all characters of each inflorescence were calculated (data set No. 1).
2. Mean and coefficient of variation of subspecies were calculated using data set No. 1.
3. Log-transformation of the data set No. 1 was used (non-normal distribution of the data).
4. Nested analysis of variance (with clones resp. populations as a nested factor) of the log-transformed data was used for the evaluation of differences between subspecies and the influence of transplanting.
5. Discriminant efficiency of individual characters was compared using discriminant analysis of the data set No. 1.
6. For discriminant analyses of sets of primary and relative characters, characters with F-values significant at the level p = 0.001 were chosen. To find the reliability of distinguishing characters, agreement of the original determination based on fruit characters with the determination resulting from discriminant function was compared.

Table 1. – Comparison of characters of *Bolboschoenus maritimus* subsp. *maritimus* and *B. m.* subsp. *compactus* measured in plants from field populations and in cultivated plants. Mean and sample size are given for each character. Significance level of difference between subspecies is given for each character (*** = P < 0.001, ** = P < 0.01, * = P < 0.05, n. s. = not significant). Tested by nested ANOVA.

Character		Field			Culture		
		maritimus	*compactus*	signif.	*maritimus*	*compactus*	signif.
1	mean	26.41	15.58	***	29.84	16.74	***
P-L (mm)	n	392	362		587	218	
2	mean	11.49	13.44	*	10.23	12.63	***
PS-L (mm)	n	393	366		587	218	
3	mean	12.06	14.26	*	11.17	13.45	***
SS-L (mm)	n	384	590		584	499	
4	mean	4.28	0.92	***	4.07	0.61	***
P-No	n	395	590		593	499	
5	mean	7.85	1.66	***	8.04	0.88	***
PS-No	n	395	590		593	499	
6	mean	3.71	5.24	***	3.95	4.76	***
SS-No	n	395	590		593	499	
7	mean	0.50	1.15	***	0.37	0.89	***
PS/P-L	n	392	362		587	218	
8	mean	0.53	1.26	***	0.40	1.02	***
SS/P-L	n	381	362		587	218	
9	mean	1.06	1.12	**	1.10	1.16	n. s.
SS/PS-L	n	382	366		578	218	
10	mean	1.87	1.72	n. s.	1.88	1.38	***
PS/P-No	n	392	362		587	218	
11	mean	1.13	4.15	***	1.13	3.97	***
SS/P-No	n	392	362		587	218	
12	mean	0.67	2.86	***	0.73	3.20	***
SS/PS-No	n	393	366		587	218	

Results

Differences between subspecies

Significant differences were found between the two subspecies in most characters in the field populations as well as in cultivated clones (Table 1). Plants of subsp. *maritimus* were distinguished especially by the more numerous and longer peduncles of the inflorescence and by the more numerous peduncled spikelets, which correspond with highly significant differences in some derived (relative) characters: length ratio of peduncle or sessile spikelets and peduncles, ratio of the number of sessile spikelets and peduncles or peduncled spikelets. The overall structure of inflorescence of both subspecies is shown in Fig. 1, 2.

Table 2. – Variation in all characters measured in cultivated plants of *Bolboschoenus maritimus* subsp. *maritimus* and *B. m.* subsp. *compactus*. Total variation includes genetic (G) and residual (Rc) variation and is expressed as coefficient of variation based on all data for each subspecies. Genetic variation represents interclonal variation and is expressed as coefficient of variation of mean values of clones. Significance of differences in variation between subspecies and between total and genetic variation was tested by F-test. Level of significance is given (** = P < 0.01, * = P < 0.05, n. s. = not significant). c. v. = coefficient of variation, n = sample size, m = *maritimus*, c = *compactus*.

Character	Cultivated plants							
	Total variation G + Rc			Genetic (interclonal) variation G			Genetic × total	
	maritimus c. v. (n)	*compactus* c. v. (n)	signif. m × c	*maritimus* c. v. (n)	*compactus* c. v. (n)	signif. m × c	signif. m × total	signif. c × total
1 P-L	0.310 (587)	0.403 (218)	**	0.219 (59)	0.322 (32)	**	**	n. s.
2 PS-L	0.193 (587)	0.287 (218)	**	0.140 (59)	0.263 (32)	**	**	n. s.
3 SS-L	0.205 (587)	0.282 (499)	**	0.158 (59)	0.241 (35)	**	*	n. s.
4 P-No	0.377 (593)	1.289 (499)	**	0.318 (59)	0.835 (35)	**	n. s.	**
5 PS-No	0.667 (593)	1.640 (499)	**	0.503 (59)	0.979 (35)	**	**	**
6 SS-No	0.398 (593)	0.373 (499)	n. s.	0.259 (59)	0.291 (35)	n. s.	**	*
7 PS/P-L	0.316 (587)	0.556 (218)	**	0.238 (59)	0.369 (32)	**	*	**
8 SS/P-L	0.307 (578)	0.583 (218)	**	0.241 (59)	0.374 (32)	**	*	**
9 SS/PS-L	0.153 (578)	0.206 (218)	**	0.088 (59)	0.097 (32)	n. s.	**	**
10 PS/P-No	0.494 (587)	0.381 (218)	**	0.311 (59)	0.346 (32)	n. s.	**	n. s.
11 SS/P-No	0.606 (587)	0.485 (218)	**	0.478 (59)	0.297 (32)	**	*	**
12 SS/PS-No	0.840 (587)	0.548 (218)	**	0.658 (59)	0.330 (32)	**	*	**

Table 3. – Variation in all characters measured in plants of *Bolboschoenus maritimus* subsp. *maritimus* and *B. m.* subsp. *compactus* from field populations and differences between interpopulation and interclonal variation. Total variation includes genetic (G), habitat (H) and residual (Rf) variation and is expressed as coefficient of variation based on all data for each subspecies. Interpopulation variation includes genetic and habitat variation and was counted as coefficient of variation of mean values of populations. Significance of differences in variation between subspecies, between total and interpopulation variation and between interclonal and interpopulation variation was tested by F-test. Level of significance is given (** = P < 0.01, * = P < 0.05, n. s. = not significant). c. v. = coefficient of variation, n = sample size, m = *maritimus*, c = *compactus*.

Character	Field								Culture × field	
	Total variation H + G + Rf			Interpopulation variation H + G			Interpopulation × total		Interclonal × interpopulation	
	maritimus c. v. (n)	*compactus* c. v. (n)	signif. m × c	*maritimus* c. v. (n)	*compactus* c. v. (n)	signif. m × c	signif. m × total	signif. c × total	signif. m	signif. c
1 P-L	0.365 (392)	0.516 (366)	**	0.297 (16)	0.408 (23)	n. s.	n. s.	n. s.	*	n. s.
2 PS-L	0.197 (393)	0.295 (366)	**	0.134 (16)	0.217 (23)	*	n. s.	*	n. s.	n. s.
3 SS-L	0.217 (384)	0.282 (590)	**	0.157 (16)	0.221 (23)	n. s.	n. s.	n. s.	n. s.	n. s.
4 P-No	0.429 (395)	0.992 (590)	**	0.335 (16)	0.603 (23)	**	n. s.	**	n. s.	n. s.
5 PS-No	0.652 (395)	1.307 (590)	**	0.473 (16)	0.822 (23)	*	n. s.	**	n. s.	n. s.
6 SS-No	0.558 (395)	0.331 (590)	**	0.425 (16)	0.242 (23)	**	n. s.	*	**	n. s.
7 PS/P-L	0.475 (392)	0.727 (362)	**	0.368 (16)	0.404 (23)	n. s.	n. s.	**	**	n. s.
8 SS/P-L	0.514 (381)	0.689 (362)	**	0.414 (16)	0.402 (23)	n. s.	n. s.	**	**	n. s.
9 SS/PS-L	0.155 (382)	0.167 (366)	n. s.	0.074 (16)	0.062 (23)	n. s.	**	**	n. s.	*
10 PS/P-No	0.587 (392)	0.554 (362)	n. s.	0.424 (16)	0.37 (23)	n. s.	n. s.	*	*	n. s.
11 SS/P-No	0.940 (392)	0.520 (362)	**	0.688 (16)	0.368 (23)	**	n. s.	*	*	n. s.
12 SS/PS-No	0.930 (393)	0.545 (366)	**	0.567 (16)	0.285 (23)	**	*	*	n. s.	n. s.

Variation in most characters was higher within subsp. *compactus* than within subsp. *maritimus* (more frequently in cultivated plants – Table 2, 3). Plants of subsp. *maritimus* were more variable in the characters concerning numbers of some organs (ratio in number of sessile spikelets and peduncles and in number of sessile and peduncled spikelets). Similar differences between subspecies were found in interclonal resp. interpopulation variation (Table 2, 3).

Discriminant efficiency of an individual character indicates how the determination of subspecies based on this character corresponds with the determination using fruits. The highest efficiency appeared in the number of peduncles, the ratio of the number of sessile spikelets and peduncles, the ratio in number of sessile and peduncled spikelets, length ratio of sessile spikelets and peduncles and peduncled spikelets and peduncles (Table 4). The determination was in general more correct in cultivated plants, probably due to the higher variation in field populations.

Relatively high efficiency was found in the determination of the two taxa using both primary and relative characters (Table 5). When comparing discriminant efficiency for each subspecies separately, the determination was more reliable in subsp. *maritimus* using primary characters, while derived (relative) characters appeared to be more efficient for the determination of subsp. *compactus*.

The characters most suitable for the determination of both subspecies are those with high discrimination efficiency and low variation (Fig. 3, 4). In general, the most suitable appeared to be: the number of peduncles, ratio of number of sessile spikelets to peduncles, ratio of number of sessile to peduncled spikelets, length ratio of sessile spikelets to peduncles.

Table 4. – Discriminant efficiency of individual characters, expressed as agreement of the value of discriminant function based on each inidividual character with the original determination of the plants of *Bolboschoenus maritimus* subsp. *maritimus* and *B. m.* subsp. *compactus*.

Character	Proportion of agreement (%)	
	Field	Culture
P-L	76	78
PS-L	62	72
SS-L	59	63
P-No	91	93
PS-No	82	79
SS-No	70	59
PS/P-L	77	88
SS/P-L	77	90
SS/PS-L	54	57
PS/P-No	50	57
SS/P-No	81	90
SS/PS-No	83	89

Table 5. – Discriminant efficiency of set of characters, expressed as agreement of the value of discriminant function based on these characters with the original determination of the plants of *Bolboschoenus maritimus* subsp. *maritimus* and *B. m.* subsp. *compactus*. Primary characters are those based on linear measures, those based on ratios are termed relative characters.

	Proportion of agreement (%)			
	Characters 1–6 (primary characters)		Characters 7–12 (relative characters)	
	maritimus	*compactus*	*maritimus*	*compactus*
Field	94.3	84.1	78.2	93.5
Culture	99.2	78.1	90.9	95.8

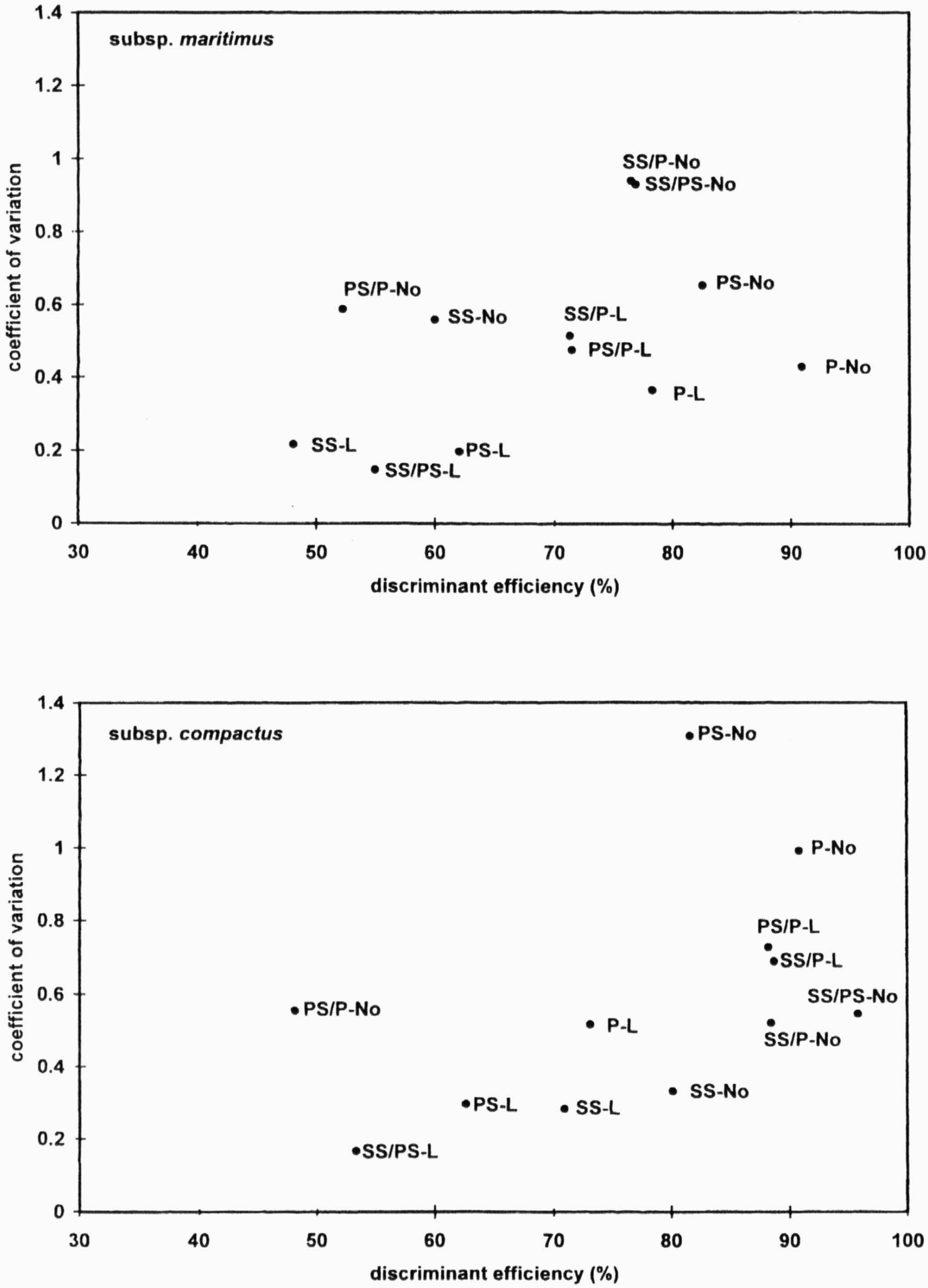
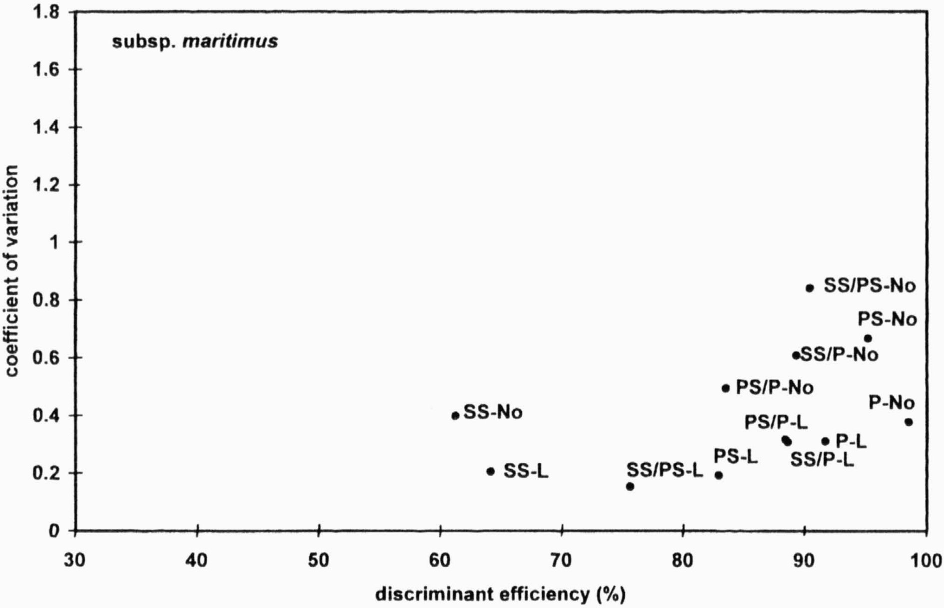
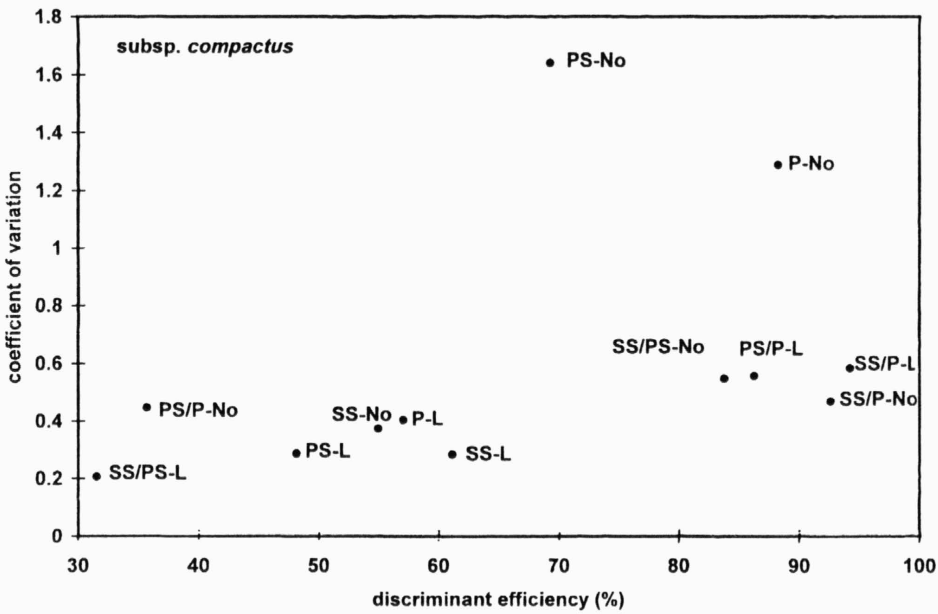


Fig. 3. – Discriminant efficiency plotted against coefficient of variation of characters. All characters were measured in plants from field populations of the two subspecies of *Bolboschoenus maritimus*.





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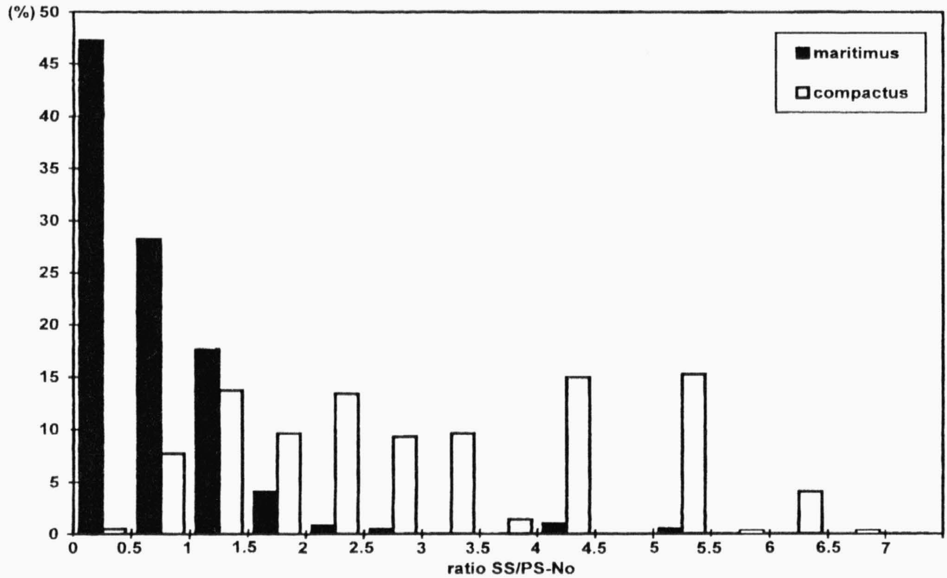

Fig. 5. – Frequency distribution of *Bolboschoenus maritimus* subsp. *maritimus* and *B. m.* subsp. *compactus* in ratio of number of sessile spikelets to peduncled spikelets; n = 393 for subsp. *maritimus*, n = 366 for subsp. *compactus*.

Descriptive statistics of the selected characters provided a basis for the definition of the value ranges distinguishing both subspecies: number of peduncles – subsp. *maritimus*: median 4, 10–% tile 2, 90–% tile 7; subsp. *compactus*: median 1, 10–% tile 0, 90–% tile 2; ratio of length of sessile spikelets and peduncles – subsp. *maritimus*: median 0.47, 10–% tile 0.29, 90–% tile 0.85; subsp. *compactus*: median 1.02, 10–% tile 0.53, 90–% tile 2.07. The distribution of the ratio of the number of sessile spikelets to peduncled spikelets shows the difference between the subspecies (Fig. 5): subsp. *maritimus* has mostly a low ratio, while a wide range in this character in subsp. *compactus* is influenced by the frequent occurrence of one peduncled spikelet to 3 to 6 sessile spikelets.

Proportion of habitat and genetic variation

In cultivated plants, total variation included genetic (interclonal) variation and residual variation caused by non-specific influences (genetic heterogeneity within clones and the influence of different habitat conditions were excluded) (Table 2). In most cases, significant differences were found between total and genetic variation, which indicates the important influence of residual variation.

In field populations the total variation included the influence of habitat conditions, genetic variation (forming together interpopulation variation) and residual variation containing possible genetic heterogeneity within populations and micro-habitat heterogeneity within one locality.

When comparing the proportion of interpopulation (genetic + spatial) variation and total variation (Table 3), mostly non-significant differences were found in subsp. *maritimus*. This indicates that in most characters a small proportion of total variation remained for residual variation (variation within populations), i.e., the populations were found to be homogeneous. In subsp. *compactus* significant differences between interpopulation and total variation were found in most characters.

The interpopulation variation in field populations of subsp. *maritimus* was higher in 6 characters compared with interclonal variation in culture. No similar differences were found for plants of subsp. *compactus* (Table 3). This indicated that a small proportion remained for spatial (habitat) variation among field populations, namely in subsp. *compactus*.

On the basis of the data in Table 2 or 3, the sources of variation were mutually related and the role of habitat variation and remaining residual variation were derived for individual characters (Table 6). Only in the first group of characters (6 characters of subsp. *maritimus*) did the important role of habitat variation appear. In addition, a significant influence of residual variation in culture was found. On the other hand, most of the characters in subsp. *compactus* were included within group 2, with a significant proportion of the residual variation occurring in culture and in the field, but not being influenced by habitat. In other groups the role of genetic variation prevailed and other sources of variation were frequently not significant.

Table 6. – Proportion of habitat (H) and residual (Rc, Rf) variation in individual characters of *Bolboschoenus maritimus* subsp. *maritimus* and *B. m.* subsp. *compactus* based on mutual relationships of sources of variation. These relationships were derived from the significance differences in Table 2,3 (non-significant differences are marked =): 1. differences between interclonal and total variation in cultivated plants; 2. differences between interpopulation and total variation in field populations; 3. differences between interclonal and interpopulation variation. Characters are grouped according to significant proportions of habitat and residual variation. Rc = residual variation in cultivated clones, Rf = residual variation in field populations

	H	Rc	Rf	mutual relationships of sources of variation	*maritimus*	*compactus*
Group 1	signif.	signif.	n. s.	1) G < G+Rc	P-L	
				2) H+G = H+G+Rf	SS-No	
				3) G < H+G	PS/P-L	
					SS/P-L	
					PS/P-No	
					SS/P-No	
Group 2	n.s	signif.	signif.	1) G < G+Rc	SS/PS-L	P-No
				2) H+G < H+G+Rf	SS/PS-No	PS-No
				3) G = H+G		SS-No
						PS/P-L
						SS/P-L
						SS/PS-L
						SS/P-No
						SS/PS-No
Group 3	n. s.	n. s.	n. s.	1) G = G+Rc	P-No	P-L
				2) H+G = H+G+Rf		SS-L
				3) G = H+G		
Group 4	n. s.	signif.	n. s.	1) G < G+Rc	PS-L	
				2) H+G = H+G+Rf	SS-L	
				3) G = H+G	PS-No	
Group 5	n. s.	n. s.	signif.	1) G = G+Rc		PS-L
				2) H+G < H+G+Rf		PS/P-No
				3) G = H+G		

Table 7. - Differences in characters measured in field populations and in cultivated plants of *Bolboschoenus maritimus* subsp. *maritimus* or *B. m.* subsp. *compactus* originating from the same localities. Mean, sample size and significance level are given (* = P < 0.05, n. s. = not significant). Tested by nested ANOVA.

Character		*maritimus*			*compactus*		
		Field	Culture	Signif.	Field	Culture	Signif.
1	mean	26.54	30.01	n. s.	14.58	17.53	n. s.
P-L (mm)	n	268	147		215	166	
2	mean	11.69	10.06	n. s.	13.80	13.13	n. s.
PS-L (mm)	n	269	147		218	166	
3	mean	12.19	10.73	n. s.	14.38	14.13	n. s.
SS-L (mm)	n	261	145		359	297	
4	mean	4.05	4.23	n. s.	0.89	0.79	n. s.
P-No	n	270	148		359	297	
5	mean	7.26	7.43	n. s.	1.43	1.10	n. s.
PS-No	n	270	148		359	297	
6	mean	3.84	3.63	n. s.	5.21	4.46	n. s.
SS-No	n	270	148		359	297	
7	mean	0.48	0.36	*	1.30	0.87	*
PS/P-L	n	224	99		191	120	
8	mean	0.50	0.39	n. s.	1.44	0.98	n. s.
SS/P-L	n	219	97		191	120	
9	mean	1.05	1.08	n. s.	1.12	1.14	n. s.
SS/PS-L	n	219	97		194	120	
10	mean	1.88	1.73	n. s.	1.59	1.31	n. s.
PS/P-No	n	268	147		215	166	
11	mean	1.24	1.06	n. s.	4.10	3.68	n. s.
SS/P-No	n	268	147		215	166	
12	mean	0.76	0.77	n. s.	2.89	3.10	n. s.
SS/PS-No	n	260	144		218	166	

Table 8. – Features distinguishing the two subspecies of *Bolboschoenus maritimus*. Value ranges are based on descriptive statistics and frequency distribution of the selected characters.

Character	subsp. *maritimus*	subsp. *compactus*
Number of peduncles	(2) – 4 – (7) peduncles	0–2 peduncles, frequently none
Ratio in number of sessile and peduncled spikelets	more peduncled spikelets than sessile spikelets (mutual ratio may be close to 1)	fewer (up to 5 times) peduncled spikelets than sessile spikelets, frequently no peduncled spikelets
Ratio of length of sessile spikelets and peduncles	peduncles approx. twice as long as length of sessile spikelets	peduncles (if present) less than twice as long as sessile spikelets

When comparing measurements of plants collected in field populations with cultivated plants originating from the same localities, significant differences appeared only in one character – length ratio of peduncled spikelets and peduncles (Table 7). All other characters did not change significantly after transplanting into cultivation, which demonstrates their high genotypically-fixed stability.

Discussion

For the determination of both taxa studied and their possible taxonomic classification, the following questions need to be answered:

Which distinguishing characters are reliable and easy to use?

The inflorescence of *Bolboschoenus maritimus* was morphologically characterized as follows (Kukkonen 1984): "Terminal on leafy shoot; the terminal and main florescence is a sessile spike in the centre of a group of other sessile spikes, arranged spirally; a further lower spike with a long peduncle, in ± pseudoterminal position; the rest of the inflorescence, with a short internode, being slightly bent to the side." This description (and also the accomparying figure) evidently concerned the halophytic type with a predominance of sessile spikelets, close to subsp. *compactus*. The inflorescence of subsp. *maritimus* differs in the presence of numerous long peduncles bearing bundles of several spikelets; the basic arrangement of the inflorescence is the same as mentioned above.

When comparing the determination of both taxa by various authors (Ascherson & Graebner 1904, Drobov 1913, Podpěra 1928, Robertus-Koster 1969, Foerster 1972, Casper & Krausch 1980, Dobročaeva 1987, Dostál 1989), the most frequent distinguishing characters are: presence/absence of peduncles in the inflorescence and their number, number of peduncled spikelets, length of peduncles. This is in agreement with the results of our measurements. Owing to the higher variation in quantitative characters (length of spikelets and peduncles), the relative characters appeared to be more efficient. Considering the variation (Table 2, 3), the discriminant efficiency (Table 4, Fig. 3, 4) and the stability in a changing environment (Table 7) of individual characters, and also their suitability for the determination of plants in the field, the two subspecies may be distinguished by features given in Table 8.

In general, greater variation was found within subsp. *compactus*, corresponding to the variation in the fruits (Robertus-Koster 1969). This author also found differences in the number of peduncles in the inflorescence between coastal saline and inland freshwater plants corresponding with fruit shape; the differences appeared to be genotypical (Browning et al. 1997). The number of peduncles of subsp. *maritimus* appeared to be a stable character with high discriminant efficiency; this corresponds to the variation of *B. maritimus* subsp. *maritimus* in Rozkoš reservoir (Krahulec et al. 1996) – the number of peduncles was strongly determined by the genotype, with a low proportion of unexplained variation. The length ratio of sessile spikelets to peduncles was the second character with a low proportion of unexplained variation, but with considerably higher temporal variation. This indicates greater plasticity in this character as a reaction to changed habitat conditions and may correspond to interpopulation variation in field populations. Nevertheless, high discriminant efficiency makes this determination character reliable. The ratio of the number of sessile spikelets to peduncles and the number of sessile spikelets to peduncled spikelets are the other characters which are highly discriminant efficient. They are mutually correlated especially in subsp. *maritimus*; the ratio of the number of sessile to peduncled spikelets is easier to use as a diagnostic feature for determination practice.

What is the role of individual sources of variation?

The genotype influences considerably the variation in both subspecies, in some characters no other sources of variation were significant. This is in accordance with the study of variation of *B. m.* subsp. *maritimus* in the Rozkoš reservoir (Krahulec et al. 1996), where year-to-year variation in individual clones was lower than the differences among the clones. Genetic variation maintains variation within subspecies (interclonal variation), but distinguishing characters which are genetically fixed are reliable and their stability provides a good basis for taxonomic classification.

The influence of habitat was found to be surprisingly low, as indicated by the non-significant differences between interpopulation and interclonal variation (Table 3). Habitat significantly influenced a group of characters in subsp. *maritimus*, while in subsp. *compactus* the proportion of habitat variation was low.

Residual variation was found to be negligible in most characters in field populations of subsp. *maritimus*. While the residual variation represents variation within populations (genetic heterogeneity caused by possible multiple origin, micro-habitat heterogeneity within one locality, influence of animals and other unexplained variation), field populations of subsp. *maritimus* were more homogeneous. Higher residual variation was found in the field populations of subsp. *compactus*. This fact can be explained by the more heterogeneous habitat conditions within a locality owing to the more frequent occurrence of subsp. *compactus* in non-flooded habitats. In littoral habitats typical of subsp. *maritimus* the aquatic environment is uniform. A higher proportion of residual (unexplained) variation and a higher total variation may reduce the correct determination of subsp. *compactus*.

Conclusions

The types of *Bolboschoenus maritimus* investigated (*B. m.* subsp. *maritimus* and *B. m.* subsp. *compactus*) differed significantly in the structure of their inflorescence in all the characters measured. Corresponding differences between both subspecies were found in natural populations as well as in cultivated plants. The transfer of plants from field populations into cultivation had no influence on most of the characters measured and the differences between the subspecies maintained.

The highest discriminant efficiency (80–90 %) was found in several characters, which were found to be suitable and easy to use for determination of both subspecies: number of peduncles, ratio between the number of sessile and peduncled spikelets, length ratio of sessile spikelets to peduncles.

Higher variation was found in most characters within subsp. *compactus* than within subsp. *maritimus*. The strong influence of genotype on variation appeared in both subspecies. The influence of habitat was relatively low; a significant proportion of spatial (habitat) variation was found only in several characters of subsp. *maritimus*, while residual (intrapopulation) variation was negligible. A low influence of habitat and higher residual variation were found in most characters in subsp. *compactus*.

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Souhrn

Proměnlivost květenství *Bolboschoenus maritimus* byla studována na rostlinách z přírodních populací v České republice a na Slovensku, a rovněž na rostlinách pěstovaných v kultuře. Byly srovnávány počty a délky klásků i stopek v květenství a z nich odvozené poměrné znaky a testována jejich účinnost ve srovnání s prvotním určením subspecií podle znaků na plodech.

Výsledky byly využity pro odlišení dvou u nás se vyskytujících typů, nazývaných podle práce Casper & Krausch z r. 1980 *B. m.* subsp. *maritimus* a *B. m.* subsp. *compactus*. Oba tyto taxony se lišily průkazně ve všech měřených znacích, a to jak u rostlin z přírodních stanovišť, tak u rostlin z kultury. Jako rozlišovací znaky se osvědčily zejména některé poměrné znaky. Pro určování obou subspecií je možno doporučit jako vhodné a snadno použitelné tyto znaky: počet stopek v květenství, poměr počtu přisedlých klásků a stopkatých klásků, poměr délky přisedlých klásků a stopek.

V rámci souboru rostlin *B. m.* subsp. *compactus* byla u většiny znaků větší variabilita než u rostlin *B. m.* subsp. *maritimus*. Variabilita u obou subspecií byla zřetelně fixována geneticky, což se projevilo jak u rostlin v přírodních populacích, tak i po přenesení rostlin do kultury. Překvapivě nízký byl vliv stanoviště, který byl významný jen u skupiny znaků subsp. *maritimus*; zde byla zároveň zanedbatelná residuální (vnitropopulační) variabilita, což ukazuje na značnou homogenitu uvnitř populací. U subsp. *compactus* byla u většiny znaků významná residuální variabilita a nevýznamný vliv stanoviště, což snižuje rozdíly mezi lokalitami; to může souviset s větší heterogenitou uvnitř populací na terestrických stanovištích.

References

Ascherson P. & Graebner P. (1904): Synopsis der mitteleuropäischer Flora Vol. 2/2. – Engelmann, Leipzig, 530 pp.

Browning J. & Gordon-Gray K. D. (1993): Studies in *Cyperaceae* in southern Africa. 21: The taxonomic significance of the achene and its embryo in *Bolboschoenus*. – S. Afr. J. Bot., Pretoria 59: 311–318.

Browning J., Gordon-Gray K. D. & Smith S. G. (1995): Achene structure and taxonomy of North American *Bolboschoenus (Cyperaceae)*. – Brittonia, New York, 47: 433–445.

Browning J., Gordon-Gray K. D., Smith S. G. & van Staden J. (1997): *Bolboschoenus maritimus* s. l. in The Netherlands: a study of pericarp anatomy based on the work of Irene Robertus-Koster. – Ann. Bot. Fennici, Helsinki, 34: 115–126.

Casper S.J. & Krausch H.-D. (1980): Süsswasserflora von Mitteleuropa. 1. Teil: *Lycopodiaceae* bis *Orchidaceae*. – Gustav Fischer Verlag, Jena.

Dobročaeva D. N. et al. (ed.) (1987): Opredelitel vysšich rastenij Ukrainy [The determination key of vascular plants of Ukraine]. – Naukova Dumka, Kiev.

Dostál J. (1958): Klíč k úplné květeně ČSR [The determination key to the flora of Czechoslovakia]. – Nakl. ČSAV, Praha.

Dostál J. (1982): Seznam cévnatých rostlin květeny československé [List of vascular plants of the Czechoslovak flora]. – Pražská bot. zahrada, Praha-Troja.

Dostál J. (1989): Nová květena ČSSR 2 [New flora of Czechoslovakia. Vol. 2]. – Academia, Praha.

Drobov V. P. (1913): K sistematike roda *Bolboschoenus* Palla (*Scirpus* L. ex parte) i jego rasprostranenie v Sibiri [On the systematics of the genus *Bolboschoenus* Palla (*Scirpus* L. ex parte) and its distribution in Siberia]. – Trudy Bot. Muz. Akad. Nauk, St. Peterburg, 11: 86–96.

Dykyjová D. (1986): Production ecology of *Bolboschoenus maritimus* (L.) Palla (*Scirpus maritimus* L. s. l.). – Folia Geobot. Phytotax., Praha, 21: 27–64.

Egorova T. V. (ed.) (1967): Rastenija Centralnoj Azii [Plants of Central Asia]. Vol. 3. – Nauka, Leningrad.

Egorova T. V. (1976): *Bolboschoenus*. – In: Fedorov A. A. (ed.), Flora Evropejskoj časti SSSR [Flora of the European part of the USSR], 2: 93–96. Nauka, Leningrad.

Foerster E. (1972): *Bolboschoenus maritimus* (L.) Palla. – Göttingen Flor. Rundbriefe 6: 101.

Hejný S. (1960): Ökologische Charakteristik der Wasser- und Sumpfpflanzen in den Slowakischen Tiefebenen. – Vyd. SAV, Bratislava, 492 pp.

Hroudová Z., Moravcová L. & Zákravský P. (1998): Differentiation of the Central European *Bolboschoenus* taxa based on fruit shape and anatomy. – Thaiszia, J. Bot., Košice (in press).
Krahulec F., Frantík T. & Hroudová Z. (1996): Morphological variation of *Bolboschoenus maritimus* population over a ten year period. – Preslia, Praha, 68: 13–21.
Kukkonen I. (1984): On the inflorescence structure in the family *Cyperaceae*. – Ann. Bot. Fennici, Helsinki, 21: 157–264.
Norlindh T. (1972): Notes on the variation and taxonomy in *Scirpus maritimus* complex. – Bot. Notiser, Lund, 125: 397–405.
Reichgelt Th. J. (1956): *Cyperaceae*. – In: Weevers Th., Danser B. H. & Heimens J., Flora Neerlandica 1 (4): *Cyperaceae* excl. *Carex*, p. 16–18, Koninklijke Nederlandse botanische Vereniging, Amsterdam.
Robertus-Koster E. I. (1969): Differentiatie van *Scirpus maritimus* L. in Nederland. – Gorteria, Leiden, 4: 193–200.
Rothmaler (1982): Exkursionsflora für die Gebiete der DDR und BRD. 4. Kritischer Band. – Volk und Wissen Volkseig. Verl., Berlin.
Schultze-Motel W. (1980): 3. *Scirpus maritimus*. – In: Hegi G., Illustrierte Flora von Mitteleuropa, Ed. 3, 2/1: 18–20, Verlag Paul Parey, Berlin.
Smirenskij A. A. (1952): Vodnye kormovye i zaščitnye rastenia v ochotničje-promyslovych chozjajstvach [Water feed and protecting plants in hunting-industrial management]. – Moskva.
Soják J. (1958): Klíč k určení plodů našich *Cyperaceí* (excl. *Carex*) [The key to determination of the fruits of our *Cyperaceae* (excl. *Carex*)]. – Preslia, Praha, 30: 43–58.
Tutin et al. (eds.) (1980): Flora Europaea. Vol. 5. – Cambridge Univ. Press, Cambridge.

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Appendix 1. – List of localities of *Bolboschoenus maritimus* where plants for this study were sampled. (f – plants sampled in field populations, c – cultivated plants).

B. maritimus subsp. *maritimus*

Central Bohemia

Mělník district: 1. field depression on the S border of Vehlovice village, 1 km NNW of Mělník, alt. 160 m, f, c; 2. the channel near Netřeba village, about 6 km W of Neratovice, alt. 175 m, c.
Nymburk district: 3. the fishpond in Nouzov village, 6 km SE of Rožďalovice, alt. 205 m, f, c; 4. Krtský fishpond 2 km NW of Městec Králové, near the road to Dymokury village, alt. 209 m, c; 5. Kněžský Dolní fishpond on the S border of Hasina village, 1 km N of Rožďalovice, alt. 203 m, c; 6. reservoir near the brook on the SW border of Starý Vestec village, 6 km S of Lysá nad Labem, alt. 185 m, c; 7. the brook near the road on the S border of Úmyslovice village, 6 km NNE of Poděbrady, alt. 185 m, c.
Kutná Hora district: 8. the channel in fields on the S border of Svobodná Ves village, 6 km NE of Čáslav, alt. 210 m, c.

South Bohemia

Strakonice district: 9. Zadní Svinětický fishpond, 1 km N of Svinětice village, 4 km W of Vodňany, alt. 413 m, f.
Písek district: 10. Ražický fishpond on the NE border of Ražice village, 4 km SW of Písek, alt. 369 m, c.
Jindřichův Hradec district: 11. Káčležský fishpond 6 km SE of Jindřichův Hradec, alt. 529 m, f, c; 12. Děkanec fishpond between the villages of Branná and Domanín, 4.5 km S of Třeboň, alt. 442 m, f; 13. Frajmarek fishpond 3 km SW of Kardašova Řečice village, alt. 447 m, f, c; 14. Služebný fishpond on the S border of Lomnice n. Lužnicí, alt. 424 m, f, c; 15. Velký Dubovec fishpond below the dam of Velký Tisý fishpond, 1.5 km S of Lomnice nad Lužnicí, alt. 424 m, c; 16. Medenice fishpond 1 km WNW of Žíteč village, 10 km E of Třeboň, alt. 457 m, c; 17. Ostrý fishpond 5 km E of Lomnice nad Lužnicí, alt. 425 m, c; 18. Velký Roch (Rochovský) fishpond 2 km NNW of Jindřichův Hradec, alt. 480 m, c; 19. Tobolky fishpond 1 km SW of Branná village, 4 km S of Třeboň, alt. 442 m, c; 20. Stružky fishpond 2.5 km NW of Třeboň, alt. 445 m, c.

East Bohemia

Jičín district: 21. Pilský fishpond 4 km N of Rožďalovice, alt. 209 m, f, c.
Pardubice district: 22. the sand pit 1 km SE of Staré Ždánice village, alt. 222 m, c; 23. Tichý fishpond near the road from Lázně Bohdaneč to Bukovka village, 2 km NW of Lázně Bohdaneč, alt. 225 m, c; 24. flooded meadow between the fishponds Ředický and Mordýř, N of Horní Ředice village, 11 km ENE of Pardubice, alt. 240 m, c.

North Moravia

Nový Jičín district: 25. fish hatchery 1 km NE of the railway station at Jistebník, alt. 220 m, f.
Karviná district: 26. the fishpond on the N border of Orlová, alt. 215 m, c; 27. the fishpond on the S border of Rychvald village, NE of Ostrava, alt. 215 m, c.

South Moravia

Žďár nad Sázavou district: 28. Velké Dářko fishpond 8 km NNW of Žďár nad Sázavou, alt. 614 m, c.
Břeclav district: 29. Bruksa oxbow on the W border of Břeclav, alt. 157 m, f; 30. field depression in meadow near Bruksa oxbow, on the W border of Břeclav, alt. 160 m, f, c; 31. Allah VI fishpond 2.5 km NE of Valtice, alt. 187 m, c; 32. field depression on the NE border of Lanžhot village near Kyjovka river, between the highway and the railway line, 5 km SE of Břeclav, alt. 156 m, c; 33. eastern shore of Nesyt fishpond, 1.5 km WSW of Hlohovec village, alt. 175 m, c; 34. former sand pit near the transfer pump station on the bank of the middle Nové Mlýny reservoir, 2 km SE of Iváň village, alt. 169 m, c; 35. field depression on the SW border of Pasohlávky village on the bank of the upper Nové Mlýny reservoir, 8 km S of Pohořelice, alt. 165 m, c.
Hodonín district: 36. the fishpond near the road between Lužice village and Hodonín, 1 km SW of Hodonín, alt. 162 m, c.

South Slovakia

Komárno district: 37. field depression along the way between Číčov village and Jazero Lion oxbow, 1 km W of Číčov village, alt. 110 m, f, c.

East Slovakia

Trebišov district: 38. the channel on the NW border of Strážné village, 3 km E of Velký Kamenec village, alt. 100 m, f, c; 39. a pool in a meadow near Velké Raškovce village, 10 km W of Velké Kapušany, alt. 103 m, f, c.

B. maritimus subsp. *compactus*

Central Bohemia

Prague city: 40. the fishpond at the E border of Vinoř district, NE part of Prague city, alt. 235 m, c.
Beroun district: 41. field depression on the SW border of Zdice, alt. 265 m, f, c.

North-West Bohemia

Louny district: 42. field depression in a meadow below the dam of Lenešický fishpond on the W border of Lenešice village, 3 km NW of Louny, alt. 185 m, f, c; 43. small fishpond in the Nový Dvůr settlement, near the road between Lenešice and Břvany villages, 5 km NW of Louny, alt. 190 m, f; 44. Dobroměřický fishpond 3 km N of Louny, alt. 195 m, f.
Most district: 45. field depression in Čepirohy suburb on the SSE border of Most, alt. 240 m, c.

North Moravia

Přerov district: 46. field depression near the road in the NE part of Přerov, alt. 220 m, f, c

South Moravia

Břeclav district: 47. field depression in meadow near the Bruksa oxbow, on the W border of Břeclav, alt. 160 m, f, c; 48. field depression on the NE border of Lanžhot village near Kyjovka river, between the highway and the railway line, 5 km SE of Břeclav, alt. 156 m, f; 49. field depression near the highway 1 km NE of Rakvice village, 4 km NNW of Podivín, alt. 165 m, c; 50. field depression between the SW border of Dobré Pole village and the railway line, 6 km W of Mikulov, alt. 185 m, f, c; 51. field depression near the shore of the third of the Nové Mlýny reservoirs, 7 km SSE of Hustopeče, alt. 170 m, f; 52. field depression on the SE shore of Nesyt fishpond, near the mouth of the Valtická stoka brook into the fishpond, 2 km SW of Hlohovec village, alt. 175 m, c, f; 53. field depression at the SW border of Pasohlávky village on the bank of the upper Nové Mlýny reservoir, 8 km S of Pohořelice, alt. 165 m, c; 54. the oxbow of Dyje river, 1 km NE of Nejdek village, 2 km NW of Lednice, alt. 162 m, c; 55. Eda fishpond on the NW border of Hlohovec village, alt. 172 m, c

Hodonín district: 56. the fishpond near the road between Lužice village and Hodonín, 1 km SW of Hodonín, alt. 162 m, c.

South-West Slovakia

Senica district: 57. flooded field depression near the railway station at Sekule, 16 km SE of Břeclav, alt. 163 m, f, c; 58. drainage channel about 500 m SE of Kúty village, 12 km SE of Břeclav, alt. 157 m, f, c.

Bratislava-vidiek district: 59. the sand pit on the SW border of Jakubov village, 6 km SW of Malacky, alt. 145 m, f; 60. field depression near the road from Jakubov village to Záhorská Ves village, 7 km SW of Malacky, alt. 145 m, f, c.

South Slovakia

Nové Zámky district: 61. field depression near the road between Gbelce and Kamenín villages, 10 km NW of Štúrovo, alt. 120 m, f, c.

East Slovakia

Trebišov district: 62. field depression near Kucany village, 14 km WSW of Velké Kapušany village, alt. 100 m, f, c; 63. the Velká Karčava oxbow about 2 km SE of Velký Kamenec village, alt. 99 m, f, c; 64. the ditch near Růžový Dvůr farm, on the E border of Velký Kamenec village, alt. 105 m, f, c; 65. field depression 1 km W of Vojany village, 6 km W of Velké Kapušany village, alt. 104 m, f, c; 66. field depression on the NE border of Streda nad Bodrogom village near "Čárda" pub, alt. 100 m, f, c