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Morphometric comparison of diploid populations of *Cardamine amara* (Brassicaceae) from Central Europe and the Balkan Peninsula.

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ABSTRACT: A multivariate morphometric study of three diploid Central European and Balkan subspecies of *Cardamine amara* (Brassicaceae), namely *C. amara* subsp. *amara*, *C. amara* subsp. *opicii* and the recently described *C. amara* subsp. *balcanica* is presented. Cluster, principal components and discriminant analyses (both canonical and classificatory ones) confirmed good morphological separation of these taxa using mostly quantitative characters.

KEYWORDS: Brassicaceae, Bulgaria, *Cardamine*, Carpathians, Cruciferae, Greece, multivariate morphometrics, Sudety Mts.

Introduction

In Central Europe and the Balkan Peninsula *Cardamine amara* is represented by diploid and tetraploid populations. In a recent paper (MARHOLD et al. 1996) a new diploid subspecies, namely *C. amara* subsp. *balcanica* MARHOLD et al., was described from the mountains of SW Bulgaria and NE Greece. The other two previously known subspecies, *Cardamine amara* L. subsp. *amara* and *C. amara* subsp. *opicii* (J. PRESL & C. PRESL) ČELAK. have been dealt with in several papers by MARHOLD (e.g. MARHOLD 1992, 1995). *Cardamine amara* subsp. *amara* is widespread throughout most of Europe, while *C. amara* subsp. *opicii* is restricted to the upper montane to alpine belt of the Sudety Mts. (Czech Republic and Poland) and the Carpathians. The tetraploid populations of *C. amara*, having its main distribution area in the Eastern Alps in Austria, extending northwards to the Czech Republic and Germany, southwards to Slovenia and north Italy and westwards to Switzerland, most probably represent separate subspecies as well (MARHOLD 1993). The aim of this paper is to present the detailed morphological comparison of the diploid populations of *C. amara* subsp. *balcanica* with the two other, above-mentioned diploid subspecies using the methods of multivariate morphometrics (cluster analysis, principal components analysis and discriminant analysis).

Material and methods

The morphometric analyses were based on 55 population samples of *C. amara* subsp. *amara* and *C. amara* subsp. *opicii* from the Carpathians and Sudety Mts., listed by MARHOLD (1992: 134-135), together with samples of three populations of *C. amara* subsp. *amara* from South Bohemia and Austria, and 11 populations of *C. amara* subsp. *balcanica* from Bulgaria (see Appendix). The population samples comprise altogether 1457 plants of *C. amara* subsp. *amara*, 753 plants of *C. amara* subsp. *opicii* and 338 plants of *C. amara* subsp. *balcanica*, mostly 30-40 plants per population. Chromosome number counts of plants from all localities studied confirmed the diploid level, 2n=16 (cf. MARHOLD 1994, MARHOLD et al. 1996).

The following 10 characters were measured or scored for each plant: width of stem (WS), mm; branching of the stem (BS): branched (1), not branched (0); number of stem leaves (NL); maximum number of leaflets of the leaves in the upper 4/5 of stem (NLL); degree of congestion of leaves beneath the inflorescence, expressed by the number of leaves reaching the base of the uppermost stem leaf (NLR); number of flowers (including buds) in the main inflorescence (NF); length of petals (LP), mm; width of petals (WP), mm; length of sepals (LS), mm; length of filaments of the longer stamens (LF), mm. The sizes of the petals, sepals and filaments were measured on fresh floral parts attached on adhesive tape and dried, so as to preserve their original size as much as possible. These include characters traditionally used for the identification of taxa within *Cardamine amara* (or the *C. amara* group) (e.g., by JONES 1964 and MARKGRAF 1958-1963) and those which proved to be useful in previous study of *C. amara* in the Carpathians and Sudety mountains (MARHOLD 1992).

Morphometric analyses included the following steps (for general notes to these methods see also MARHOLD 1992):

- Exploratory data analysis (SAS INSTITUTE 1990a): basic statistics for all three subspecies, including the test of normality (the Shapiro-Wilk statistic with associated probability).
- Correlation coefficients (Pearson coefficient and non-parametric, rank Spearman coefficient) for the characters for all three subspecies and for the pooled matrix of all material.

- Cluster analysis (average linkage with standardised characters; EVERITT 1986) of populations (OTU's), characterised by the mean values of characters.
- Principal components analyses, based on correlation matrices (KRZANOWSKI 1990, SNEATH & SOKAL 1973) and populations as OTU's, characterised by the mean values of characters.
- Canonical discriminant analyses (KLECKA 1980, KRZANOWSKI 1990) and classificatory discriminant analysis (KLECKA 1980, SAS INSTITUTE 1990b) of the individual plants as OTU's and the three above mentioned subspecies as groups were performed. Both analyses assume a multivariate normal distribution of characters, but considerable robustness to violation of these assumptions has been demonstrated (cf. SNEATH & SOKAL 1973, KLECKA 1980). Because the distribution of the characters within the groups more or less deviated from a normal distribution, the option of a non-parametric analysis offered by the SAS package was used for the classificatory discriminant analysis. For this analysis the k-nearest neighbours method was used and discriminant power was determined by crossvalidation.
- Canonical discriminant analyses on the individual plants as OTU's and (a) *C. amara* subsp. *amara* and *C. amara* subsp. *balcanica*, and (b) *C. amara* subsp. *opicii* and *C. amara* subsp. *balcanica* as groups; the purpose of these analyses was to reveal the characters that are most useful in the differentiation of *C. amara* subsp. *balcanica* from the other two diploid taxa.

Cluster analyses were performed using the SYN-TAX 5.02 package (PODANI 1993, 1994). Remaining numerical analyses were computed on the mainframe computer of the University of Vienna, Austria, using procedures CANDISC, CORR, DISCRIM, PRINCOMP, and UNIVARIATE, available in the SAS package (SAS INSTITUTE 1990a,b).

Voucher specimens of all collections are deposited in the herbarium SAV.

Results

Results of the exploratory data analysis presented in Tabs. 1 and 2 indicate that *Cardamine amara* subsp. *balcanica* differs from *C. amara* subsp. *amara* especially in characters NL and WS, and from *C. amara* subsp. *opicii* in characters NLL and to a lesser extent in BS. Certain differences can also be seen in various other characters. However, extreme values of all characters for these three subspecies overlap at least to a certain degree and it is clear that *C. amara* subsp. *balcanica* is not easily and completely distinguishable from either of the other two subspecies by any single character.

Values of Pearson and Spearman correlation coefficients differ only slightly. The maximum value is 0.826 (Spearman coefficient of NL-NLR) for the pooled matrix of all plants, and 0.763 (Spearman coefficient of LF-LP for *C. amara* subsp. *balcanica*) for the three individual matrices of different subspecies; thus there are no very highly correlated characters and all characters can be used in subsequent analyses.

Tab. 1. Results of the exploratory data analysis of three diploid subspecies of *Cardamine amara*. CB - *C. amara* subsp. *balcanica*, CA - *C. amara* subsp. *amara*, CO - *C. amara* subsp. *opicii*.

Character	Mean	St. dev.	Percentiles 1% (5%)	99% (95%)
width of stem - WS (mm)				
CB	4.20	1.29	2.0 (2.5)	7.5 (6.5)
CA	2.27	0.85	1 (1)	4.5 (4)
CO	4.42	1.79	2 (2.5)	11 (7.5)
length of filaments of the longer stamens - LF (mm)				
CB	6.17	0.82	3.5 (4.9)	7.8 (7.5)
CA	5.67	0.70	3.8 (4.7)	7.3 (7.0)
CO	5.68	0.73	3.3 (4.5)	7.3 (6.8)
length of sepals - LS (mm)				
CB	3.79	0.43	2.9 (3.1)	4.7 (4.5)
CA	3.59	0.38	2.8 (2.9)	4.5 (4.2)
CO	4.20	0.48	3.1 (3.5)	5.2 (5.0)
width of petals - WP (mm)				
CB	3.13	0.39	2.3 (2.6)	4.2 (3.8)
CA	4.49	0.71	2.9 (3.5)	6.2 (5.7)
CO	3.80	0.64	2.6 (2.8)	5.4 (4.9)
length of petals - LP (mm)				
CB	7.52	0.80	5.9 (6.4)	9.2 (8.8)
CA	8.25	0.93	6.1 (6.8)	10.2 (9.7)
CO	8.14	0.94	5.7 (6.6)	10.2 (9.7)
number of flowers (including buds) in the main inflorescence - NF				
CB	22.26	8.32	6 (9)	42 (37)
CA	14.42	5.91	3 (5)	28 (24)
CO	17.03	5.90	5 (8)	33 (28)
maximum number of leaflets of the leaves in the upper 4/5 of stem - NLL				
CB	8.10	1.28	5 (7)	11 (10)
CA	8.28	1.78	5 (5)	13 (11)
CO	14.24	2.19	9 (11)	19 (17)
number of stem leaves - NL				
CB	26.24	5.23	15 (18)	38 (35)
CA	8.16	3.12	3 (4)	17 (14)
CO	24.14	7.69	9 (13)	49 (38)
degree of congestion of leaves beneath the inflorescence, expressed by the number of leaves reaching the base of the uppermost stem leaf - NLR				
CB	3.39	1.27	1 (2)	6 (6)
CA	1.21	0.93	0 (0)	4 (3)
CO	5.97	2.42	1 (2)	13 (10)

Tab. 2. Frequency of the states of character BS (branching of stem) in three diploid subspecies of *Cardamine amara*. CA - *C. amara* subsp. *amara*, CO - *C. amara* subsp. *opicii*, CB - *C. amara* subsp. *balcanica*.

	number of plants with	
	BS = 1 (stem branched)	BS = 0 (stem not branched)
CB	49	289
CA	949	508
CO	43	710

Tab. 3. Total canonical structure (correlation coefficients) of two canonical discriminant axes from the canonical analysis of three diploid subspecies of *Cardamine amara* (CAN1 and CAN2), and from the canonical analyses of *C. amara* subsp. *amara* vs. *C. amara* subsp. *balcanica* (CANAB) and *C. amara* subsp. *opicii* vs. *C. amara* subsp. *balcanica* (CANOB) (coefficients exceeding arbitrary level 0.6 are marked in bold).

Character	CAN1	CAN2	CANAB	CANOB
WS	**0.699**	0.000	**0.667**	0.070
LF	0.105	-0.248	0.278	-0.316
LS	0.550	0.267	0.213	0.424
WP	-0.577	0.346	**-0.670**	0.531
LP	-0.161	0.256	-0.325	0.341
NF	0.321	-0.308	0.461	-0.376
NLL	**0.708**	**0.634**	-0.044	**0.915**
BS	**-0.630**	-0.020	-0.427	-0.162
NL	**0.923**	-0.147	**0.954**	-0.152
NLR	**0.842**	0.302	**0.696**	0.544

Tab. 4. Results of the non-parametric classificatory discriminant analysis of three diploid subspecies of *Cardamine amara*. CA - *C. amara* subsp. *amara*, CO - *C. amara* subsp. *opicii*, CB - *C. amara* subsp. *balcanica*.

Actual group	Predicted group membership (number of observations and percent classified into groups)		
	CA	CO	CB
CA	1449/99.45	7/0.48	1/0.07
CO	24/3.19	725/96.28	4/0.53
CB	1/0.30	2/0.59	335/99.11

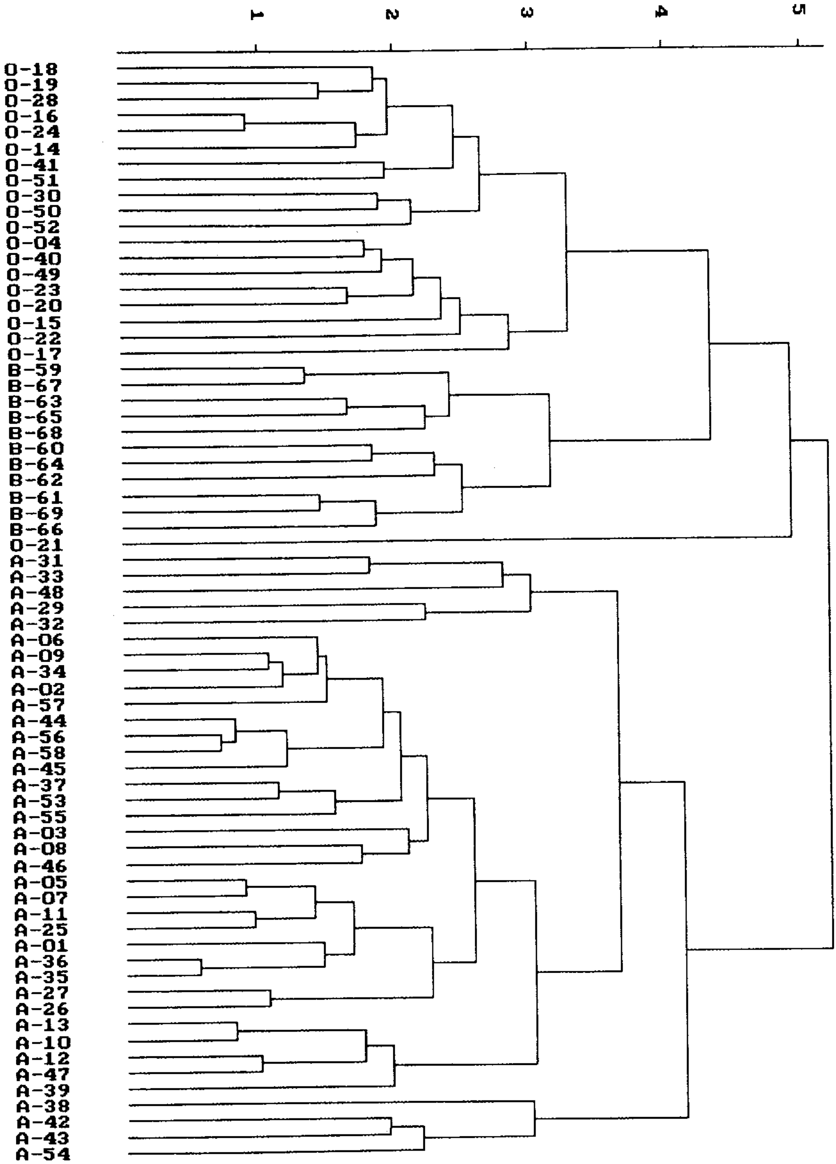

Fig. 1. Average linkage (UPGMA) clustering dendrogram of 69 population samples of *Cardamine amara*. A - *C. amara* subsp. *amara*; O - *C. amara* subsp. *opicii*; B - *C. amara* subsp. *balcanica*; for numbers of populations and their localities see Appendix.

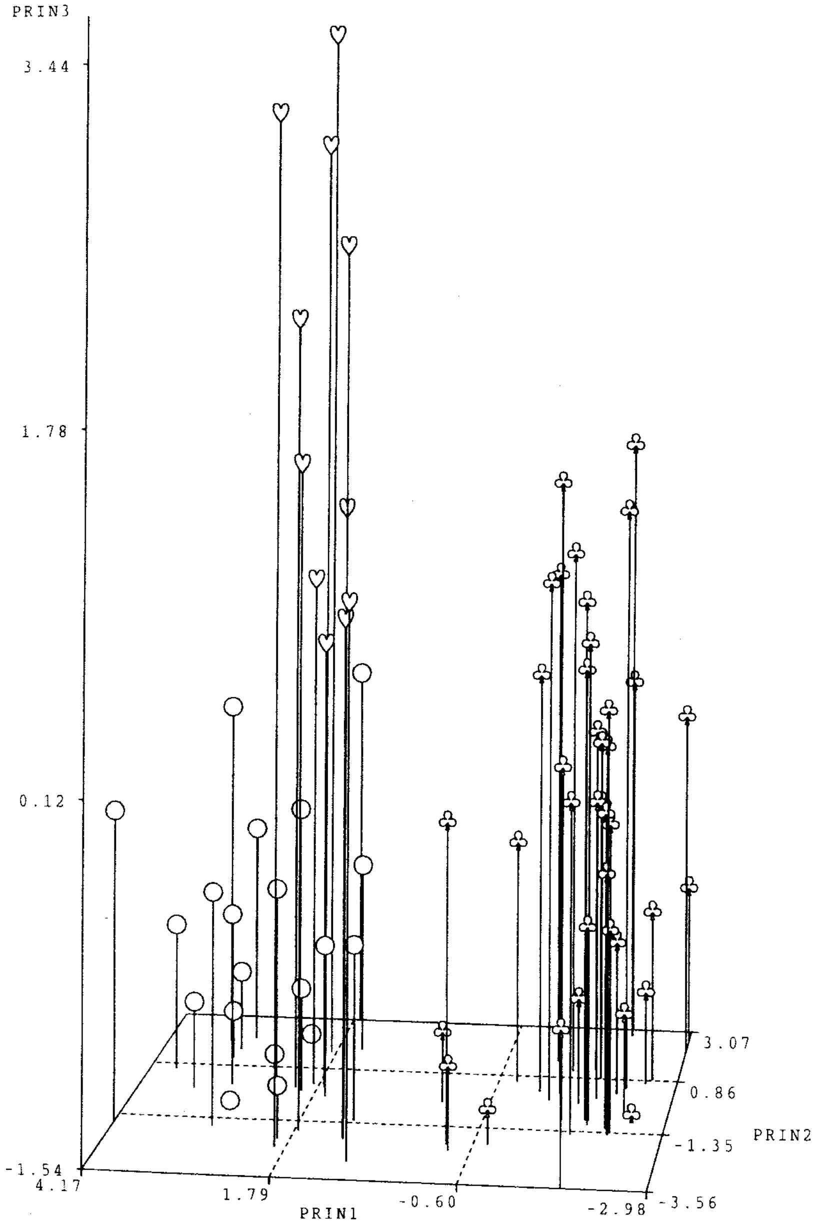

Fig. 2. Ordination diagram of the principal components analysis of 69 population samples of *Cardamine amara*. Club - *C. amara* subsp. *amara*; ball - *C. amara* subsp. *opicii*; heart - *C. amara* subsp. *balcanica*. The first three axes account for 47.13, 22.06 and 13.13 % of the variability respectively.

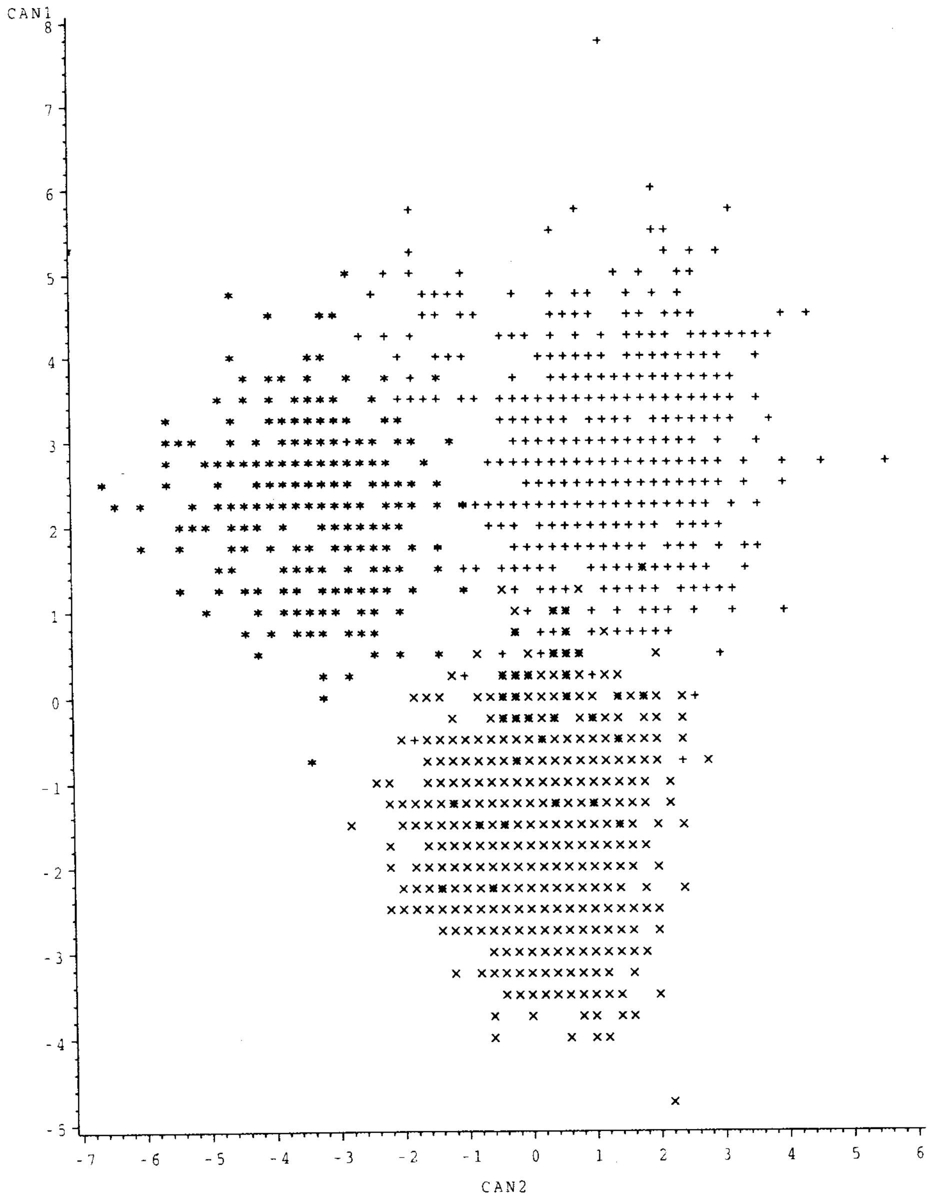

Fig. 3. Ordination diagram of the canonical discriminant analysis of the individual plants of *Cardamine amara*. × - *C. amara* subsp. *amara*; + - *C. amara* subsp. *opicii*; * - *C. amara* subsp. *balcanica*.

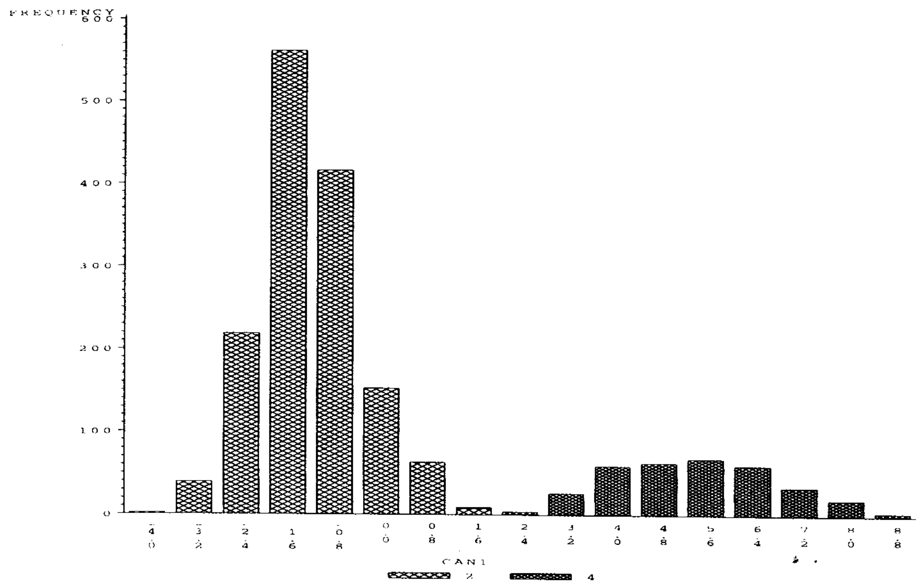

Fig. 4. Ordination diagram of the canonical discriminant analysis of the individual plants of *Cardamine amara* subsp. *amara* (2) and *C. amara* subsp. *balcanica* (4).

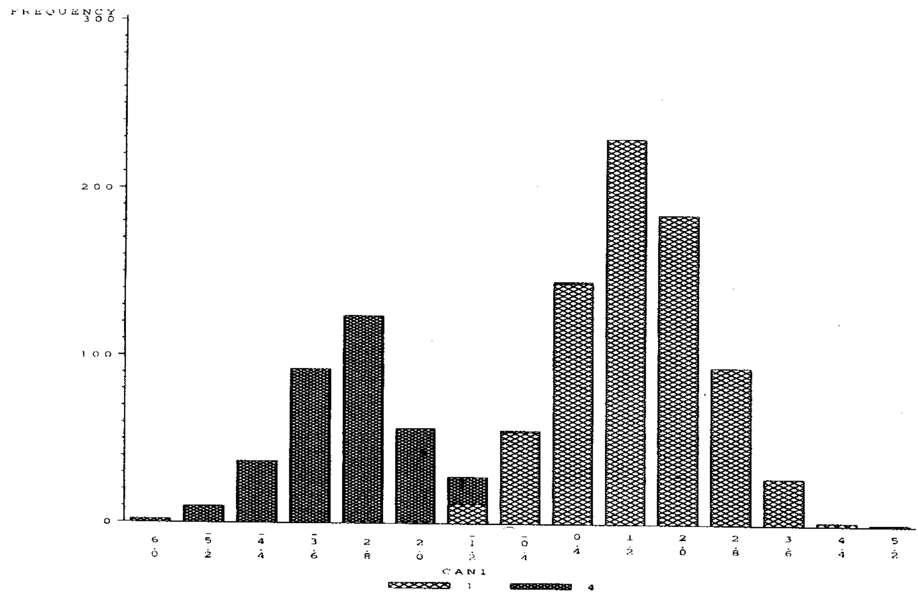

Fig. 5. Ordination diagram of the canonical discriminant analysis of the individual plants of *Cardamine amara* subsp. *opicii* (1) and *C. amara* subsp. *balcanica* (4).

The results of both the cluster analysis and principal components analysis of the populations, based on the average values of characters confirmed three groups in the material studied. On the dendrogram of the cluster analysis (Fig. 1) three main clusters, corresponding to the three subspecies of *C. amara* are clearly visible. Only one population of *C. amara* subsp. *opicii* is separated from the main cluster of this taxon. Plants of this population (no. 21, Vysoké Tatry Mts., Veľká Studená dolina Valley) are unusually tall with a large amount of leaves, but otherwise correspond to *C. amara* subsp. *opicii* quite well. The same picture is visible on the three dimensional ordination diagram of the principal components analysis (Fig. 2). *C. amara* subsp. *amara* is separated from both *C. amara* subsp. *opicii* and *C. amara* subsp. *balcanica* along the first component axis, while the latter two subspecies are separated along the third one. The first three component axes account for 82.32% of the variation among the studied plants.

Discriminant analyses were performed as hypothesis testing methods. The purpose of their application was to test how successfully individual plants of the three taxa could be identified using the above mentioned set of characters. Ordination graphs of the canonical discriminant analysis (Figs. 3-5) revealed that in spite of slight overlap in several specimens (which is also reflected in the classificatory analysis) the three studied subspecies form well separated groups which must be treated as separate taxa. The total canonical structure (Tab. 3), which expresses the correlations of the individual characters with canonical axes, show that characters NL, NLR, WS and WP are important for the separation of *C. amara* subsp. *amara* and *C. amara* subsp. *balcanica*, while *C. amara* subsp. *opicii* and *C. amara* subsp. *balcanica* strongly differ in the character NLL.

The results of non-parametric classificatory discriminant analysis (Tab. 4) are similar to those of the canonical analysis. They indicate a good separation of *C. amara* subsp. *balcanica* - less than one percent of plants were wrongly classified either into *C. amara* subsp. *amara* or *C. amara* subsp. *opicii*.

Discussion

The results of the multivariate morphometric study of the Central European and Balkan diploid taxa of *Cardamine amara* confirmed the fact that *C. amara* subsp. *balcanica*, recently described from the mountains of SW Bulgaria and NE Greece is morphologically a well separated taxon. *Cardamine amara* subsp. *balcanica* was distinguished mostly by the number of leaves from *C. amara* subsp. *amara* and by the maximum number of leaflets on the stem leaves from *C. amara* subsp. *opicii* (although several other characters contributed to the separation of these taxa as well). Character BS (branching of stem) also contributed to the separation of both *C. amara* subsp. *balcanica* and *C. amara* subsp. *amara* (stem simple or branched) from *C. amara* subsp. *opicii* (stem usually simple). Branched individuals of *C. amara* subsp. *opicii* were found in a few populations only (more than half of them were found in population no. 17, Nízke Tatry Mts., Ďurková) and the presence of this character might indicate an influence of *C. amara* subsp. *amara*. In addition to the quantitative and binary characters there is also one qualitative character, which was not included in the analysis, namely indument of stem. MARHOLD (1992) pointed out that while stems of *C. amara* subsp. *amara* are most often only slightly hairy at the base, those of *C. amara* subsp. *opicii* are either completely glabrous or densely hairy (both types often occurring within the same population). *C. amara* subsp. *balcanica* nearly invariably has densely hairy stems. Out of the 338 plants studied only one individual had a completely glabrous stem (from the locality no. 60, Demjaniška poljana).

Cardamine amara subsp. *balcanica* and *C. amara* subsp. *opicii* represent a good example of geographic vicariancy. Both are restricted to certain mountain ranges and occupy localities with similar ecological conditions, namely stream banks and springs; they are often dominant in the vegetation forming associations *Brachythecio rivularis-Cardaminetum opicii* (KRAJINA 1933) HADAČ 1983 and vicariant *Brachythecio rivularis-Cardaminetum balcanicae* (MARHOLD & VALACHOVIČ, in prep.) both very similar in their species composition. While *Cardamine amara* subsp. *opicii* occupies the upper montane to alpine belt of the Carpathians and Sudety mountains, *C. amara* subsp. *balcanica* is concentrated in the montane belt reaching its maximum distribution altitude in the lower part of the subalpine belt of the Balkan mountains.

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Appendix

List of localities of population samples of *Cardamine amara* [for detailed analysis of populations no. 1-55 see MARHOLD (1992: 134-135)]:

Cardamine amara subsp. *amara*

1 Slovakia, Malé Karpaty Mts., Bratislava, Železná studnička, 200 m
2 Slovakia, Malé Karpaty Mts., Horné Orešany, near the stream Parná, 290 m
3 Slovakia, Kremnické vrchy Mts., Kremnica, Keslo, 750 m
5 Slovakia, Slovenské rudohorie Mts., Klenovec, 360 m
6 Slovakia, Muránska planina Plain, Tisovec, 440 m
7 Slovakia, Muránska planina Plain, Zbojská, near the railway station, 725 m
8 Slovakia, Slanské vrchy Mts., Kokošovce, 0.5 km NE of the water reservoir, 500 m
9 Slovakia, Krivánska Malá Fatra Mts., Strečno, E of the railway station, 440 m
10 Slovakia, Veľká Fatra Mts., Gaderská dolina Valley, near the lower forester's house, 550 m
11 Slovakia, Veľká Fatra Mts., Ľubochnianska dolina Valley, below the forester's house Raková, 820 m
12 Slovakia, Veľká Fatra Mts., Gaderská dolina Valley, the beginning of the Dedošova dolina Valley, 860 m
13 Slovakia, Veľká Fatra Mts., Dedošova dolina Valley, 900 m
25 Slovakia, Spišské vrchy Mts., Starina, NE of the village, 460 m
26 Slovakia, Čergov Mts., Tarnov, near the Topľa River, 320 m
27 Slovakia, Bukovské vrchy Mts., Starina, bottom of the new water reservoir, 320 m
29 Czech Republic, Hrubý Jeseník Mts., Malá Morávka, Mt. Temná, E slope, 950-1000 m
31 Czech Republic, Jizerské hory Mts., Malá Jizerská Louka, Mt. Bukovec, 850 m
32 Czech Republic, Mt. Králický Sněžník, Nad Vilemínou, 1000 m
33 Czech Republic, Krkonoše Mts., Obří důl Valley, 880 m
34 Poland, Wyżina Krakowsko-Częstochowska Lowland, Krzesowice, Tenczynek, 300 m
35 Poland, Pieniny Mts., Valley of the Dunajec River, Zawiasy, near the village, 430 m
36 Poland, Beskid Makowski Mts., N slope of Mt. Sularzówka, ca. 2 km of the village of Stróża, 450 m
37 Poland, Gorce Mts., Szczawa, valley of the Kamienica River, 500 m
38 Poland, Gorce Mts., valley of the Łopuszna River, 650 m
39 Poland, Gorce Mts., Huba, N slope of Mt. Kotelnica, 800 m
42 Ukraine, Prykarpattja Mts., Nyžnij Synovydnyj, 380 m
43 Ukraine, Prykarpattja Mts., Teršiv, 370 m
44 Ukraine, Prykarpattja Mts., Pidbuž, Zolokot', near the stream Bystrycja, 467 m
45 Ukraine, Schidni Beskydy j Nyz'ki Polonyny Mts., between the villages of Huklyvyj and Podobovec, 750 m
46 Ukraine, Opol'e Lowlands, Mikolajiv, Trostjanec, 250 m

47 Ukraine, Svydovec' Mts., near the road to the Polonyna Drahobrat, 850-900 m
48 Ukraine, Čornohora Mts., Cybul'nik, 1350 m
53 Romania, Depresiunea Sibiului, Sibiu, forest Pădurea Dumbrava, 420 m
54 Romania, Depresiunea Făgăraşului, Cîrţa, in the village, 400 m
55 Romania, Depresiunea Sibiului, Tălmaciu, Valea Sadu Valley, 400 m
56 Austria, Lower Austria, Purkersdorf, Baunzen, NW of the village, 300 m
57 Austria, Lower Austria, Gablitz, near the rivulet Gablitz Bach, NW of the village, 290 m
58 Czech Republic, Střední Povltaví, Bečice, NW of the village, the valley of the Lužnice River, 370 m

Cardamine amara subsp. *opicii*
4 Slovakia, Poľana Mts., Mt. Predná Poľana, near the way to the tourist chalet, 1000 m
14 Slovakia, Nízke Tatry Mts., Lomnistá dolina Valley, NE of the Struhárske sedlo Saddle, 1080-1120 m
15 Slovakia, Veľká Fatra Mts., Ľubochnianska dolina Valley, above the forester's house Raková, 850-900 m
16 Slovakia, Nízke Tatry Mts., Železnô, near the stream Tlstý potok, 1200 m
17 Slovakia, Nízke Tatry Mts., Mt. Ďurková, S slope, Šifrová dolina Valley, 1100-1150 m
18 Slovakia, Nízke Tatry Mts., Štiavnica Valley, S of Mt. Konský grúň, 1080 m
19 Slovakia, Nízke Tatry Mts., Štiavnica Valley, E of the Bocianske sedlo Saddle, 1400 m
20 Slovakia, Nízke Tatry Mts., Mt. Kráľova hoľa, Martalúzka Valley, near the Hnilec River, 1480-1500 m
21 Slovakia, Vysoké Tatry Mts., Veľká Studená dolina Valley, 1580 m
22 Slovakia, Vysoké Tatry Mts., Velická dolina Valley, near the Dlhé (Kvetnicové) pleso Lake, 1750 m
23 Slovakia, Vysoké Tatry Mts., Mlynická dolina Valley, near the right-side tributary stream of the Mlynica River, 1600 m
24 Slovakia, Západné Tatry Mts., Látaná dolina Valley, the margin of the protected nature area "Kotlov žľab", 1250 m
28 Czech Republic, Hrubý Jeseník Mts., Velká kotlina Cirque, Šmardova stěna, 1340 m
30 Czech Republic, Mt. Králický Sněžník (locus classicus), SW slope, above the saddle between Mt. Králický Sněžník and Mt. Malý Sněžník, 1350-1370 m
40 Poland, Tatry Zachodnie Mts., Dolina Kondratowa Valley, NW of Mt. Myślenickie Turnie, 1200 m
41 Poland, Tatry Wschodnie Mts., near the Litworowy Staw Lake, 1620 m
49 Ukraine, Čornohora Mts., Mt. Hoverla, NW slope, 1700 m
50 Ukraine, Čornohora Mts., valley of the stream Arendarčyk, 1400 m
51 Ukraine, Čornohora Mts., Mt. Turkul, NE slope, 1600 m
52 Ukraine, Čornohora Mts., between Mt. Velyky Kozol and Mt. Maly Kozol, 1650 m

Cardamine amara subsp. *balcanica*
59 Bulgaria, Vitoša region, Mt. Vitoša, "Aleko", 1800 m
60 Bulgaria, Pirin Mts., Demjaniška poljana, 1620 m
61 Bulgaria, Pirin Mts., near Demjanica chalet, 1850 m
62 Bulgaria, Rila Mts., between Borovec and Sitnjakovo, 1600 m
63 Bulgaria, Rila Mts., Borovec, 1300 m
64 Bulgaria, Rila Mts., Kostenec, Jurukova poljana, Inčov most, on the slope of Mt. Sokolovec, 1500 m

65 Bulgaria, Rila Mts., Kostenec, Jurukova poljana, on the slope of Mt. Sokolovec, 1500 m
66 Bulgaria, Rila Mts., Kompleks Maljovica, 1750 m
67 Bulgaria, Rhodope Mts., West Rhodope, Beglika, Semsiza River, near Kolarova poljana, 1600-1650 m
68 Bulgaria, Rhodope Mts., West Rhodope, Beglika, natural reserve, near the right tributary of Semsiza River, 1600-1650 m
69 Bulgaria, Rhodope Mts., West Rhodope, Beglika, Toškovo dere, 1600-1650 m

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