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Low level of inter-populational differentiation in *Juniperus excelsa* M. Bieb. (Cupressaceae)

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Abstract: The intra- and inter-population variation in three populations of *Juniperus excelsa*, two from Crimea and one from the Balkan Peninsula, were analyzed biometrically. Fourteen morphological characters of cones, seeds, shoots and leaves were used. The number of seeds per cone appears to be the most variable character. The others were more stable. Differences among particular individuals within the samples were slight, as well as between populations compared. The Crimean samples were very close to each other, while the more geographically distant sample from the Balkan Peninsula appears also to be morphologically more separate. This suggests that the Balkan populations originated from another Pleistocene refugium. The Crimean populations did not show the reduction of variability, which could have resulted from their geographical isolation and their considerably restricted numbers of individuals.

Additional key words: plant variation, plant taxonomy, juniper, numerical taxonomy, biometrics

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Introduction

The Grecian juniper – *Juniperus excelsa* M. Bieb. is a monoecious tree which occurs in south-eastern Europe and south-western Asia (Fig. 1). It is a mountain species and in Europe grows at elevations of 500–1500 m. Only at the northern limit of the range does it come down to an altitude of about 50–100 m, as for example in the Crimea. In the mountain regions of the Asiatic parts of its distribution and in the Balkan Peninsula in Europe it forms forests, which can even locally cover extensive areas (Stoyanov 1963, Horvat et al. 1974, Browicz 1982; Boratyński et al. 1992, Didukh 1992).

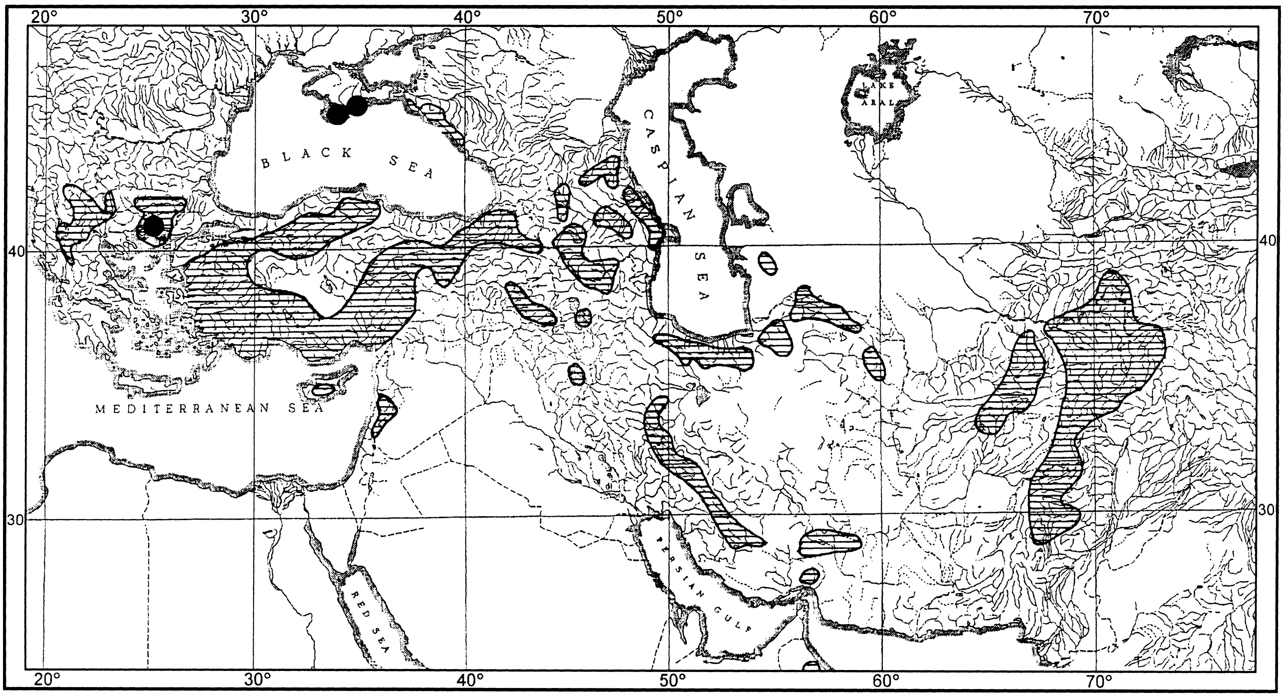

Fig. 1. Range of *Juniperus excelsa sensu lato* (including *J. procera*, *J. seravshanica* and *J. semiglobosa*) (after Browicz 1982; Boratyński et al. 1992, supplemented)

The morphological polymorphism and occurrence over an extended area, as also in populations isolated from each other, resulted in the description of several juniper species closely related to *Juniperus excelsa* (Komarov 1934, Maleev 1949), lately treated mostly as synonyms (see Coode and Cullen 1965, Riedl 1968, Greuter et al. 1984, Farjon 1992, 2001). The closely related, Transcaucasian – Central-Asian *J. polycarpos* K. Koch. was also included within *J. excelsa* (Cood and Cullen 1965; Riedl 1968, Browicz 1982; Greuter et al. 1984; Kerfoot and Lavranos 1984; Christensen 1997) or treated at the subspecific rank (Farjon 1992). The RAPDs and the leaf essential oils analyses, however, rather suggest a specific rank of that taxon (Adams 2001).

In spite of the description of several intraspecific or closely related taxa, the variation of *Juniperus excelsa* has not been examined in details. Only diameter of cones, ratio length/diameter of cones and number of seeds per cone were analysed for 44 individuals from 3 populations from Turkey, in comparative study of *J. excelsa* and *J. thurifera* (Barbero et al. 1994).

The distribution of the taxa included within *Juniperus excelsa* (see Fig. 6 in Farjon 1992), suggest that the Crimean population could be closer to *J. polycarpos*, while the Balkan ones are separated from this taxon and probably represent the most typical *J. excelsa*. The latter were also formed from the other Pleistocene refugium during the Holocene (Reinig, after Kostrowicki 1999 and Kornaś and Medwecka-Kornaś 2002), which can be a reason of possible differences.

Juniperus excelsa and *J. polycarpos* differ each other mostly in the diameter of the ultimate branchlet, length of the scale leaves and diameter of cones (Farjon 1992, 2001), but these differences have not been studied biometrically. The main goal of the present study was a biometrical comparison of three populations of *J. excelsa*, two isolated ones from the northern limit of the range in the Crimea and one from the more common occurrence on the Balkan Peninsula. Our specific aims were: (1) to verify the hypothesis that the intra-population variability of the isolated, northernmost Crimean populations is at a lower level than in populations from the more dense species occurrence in the Balkans and, (2) to check that the populations from the Crimea are morphologically more closely related to each other than to the geographically more distant one from the Balkan Peninsula.

Material and methods

Plant material and measurement procedures

The material for the study was sampled in 2001 (Table 1). The samples of mature cones and parts of twigs of latest ramifications were gathered separately from different individuals, from the south-facing (including south-eastern and south-western) exposures of the tree-like individuals, at a height of about 1.0–2.5 m above ground level. Totally 66 individuals

Table 1. Sampled populations of *Juniperus excelsa*

No.	Locality	Acronym	Number of specimens	Longitude	Latitude	Altitude [m]
1	Bulgaria, The Struma river valley, near Gara Pirin, on the slopes	Balkan	18	23°12'	41°43'	400–500
2	Ukraine, Crimea, S slopes above Yalta NE of Uchansu Falls	Crimea 1	25	34°07'	44°29'	450–600
3	Ukraine, Crimea, Karadag Nature Reserve	Crimea 2	23	35°13'	44°55'	150–250

Table 2. Morphologic characters of *Juniperus excelsa* cones, seeds and leaves analysed in the study (adopted from Mazur et al. 2003)

No.	Character	Accuracy and measure
1	Number of recta (4 or 6)	Specimen
2	Length of cone	0,1 mm
3	Width of cone	0,1 mm
4	Thickness of cone	0,1 mm
5	Cone scale number	Specimen
6	Number of seeds	Specimen
7	Length of seeds	0,1 mm
8	Width of seeds	0,1 mm
9	Number of leaves on the 5 mm of the last ramification shoot	Specimen
10	Thickness of the last ramification shoot with leaves	0,1 mm
11	Ratio of cone length/wide (2/3)	
12	Ratio of cone length/thickness (2/4)	
13	Ratio of seed length/width (7/8)	
14	Ratio of cone width/number of seeds (3/6)	

were sampled, 48 from the Crimea (Ukraine) and 18 from Struma river valley (Bulgaria) (Table 1).

Measuring was performed on dry material by means of the method used for variation testing of *Juniperus phoenicea* (Mazur et al. 2003). Seven characters of the cones and seeds, three of shoots and leaves, and four ratios were examined (Table 2).

Data analyses

The data were standardized before statistical analyses to remove the influence of variation resulting from various types of characters used (Łomnicki 2000). The normality of distribution of variables was verified using Shapiro-Wilk's test (Zar 1999) to assess the possibility of proceeding statistical analyses. The interactions between characters were examined using Pearson's correlation coefficient to avoid the most closely correlated, possibly redundant variables and to verify the possibility of discrimination analysis (Tabachnik and Fidell 1996, Underwood 1997, Zar 1999). The Tukey *T*-test was used to verify the significance of differences between mathematic means of particular characters from separate populations (Zar 1999). The variation coefficients of particular characters of three populations were compared using *t*-Student test to verify the hypothesis that the intra-populational variability of isolated populations is at a lower level than in populations from the more dense species occurrence.

The stepwise discriminant function analysis (Marek 1989; Morrison 1990; Tabachnick and Fidell 1996; Moczko et al. 1998) was used to: a) identify the discriminant power of characters, b) eliminate the possible redundant variables, c) determine the intra-populational, and d) the inter-populational variation.

The dendrograms on the basis of the shortest Euclidean distances between populations were constructed to check their affinities revealed in discriminating analysis (Underwood 1997; Moczko et al. 1998, Zar 1999).

Results

Variation of morphological characters

The frequency distribution of the examined characters was unimodal, or at least very close to unimodal. This enables the further statistical analyses.

Several, mostly dimensional characters, correlated statistically significantly at level $p=0.01$. Numbers of statistically significant correlations and the correlated characters were not always the same in the particular populations. The cone width (character 3) and the cone thickness (character 4) were the strongest correlated features in all populations. The seed length (character 7) and the seed width (character 8) also correlated statistically significantly in all samples, but not so strongly as the cone characters. Besides, the cone length (character 2) was statistically strongly significantly correlated with the cone width (character 3) and with the cone thickness (character 4). Only two significant at level $p=0.05$ correlation between characters of cone/seed and shoot thickness were found (Tables 3, 4 and 5).

Differences between populations in particular characters

The population from the Balkans differs statistically significantly in 9 of analysed characters from both populations from Crimea, while the latter are more similar, differing significantly only in 3 characters (Fig. 2). The statistically significant differences between both Crimean and Balkan population showed

Table 3. Correlation coefficients between characters of *Juniperus excelsa* from population Balkan

3	0.85**							
4	0.85**	0.98**						
5	0.25	0.09	0.04					
6	0.38	0.45	0.46	0.18				
7	0.63**	0.61**	0.56*	0.04	0.02			
8	0.52*	0.70**	0.68**	–0.15	–0.03	0.62**		
9	0.18	0.25	0.29	–0.25	–0.19	0.22	0.58*	
10	0.25	0.25	0.28	–0.23	–0.15	0.04	0.40	0.25
Characters	2	3	4	5	6	7	8	9

* – significance at level p = 0.05; ** – significance at level p = 0.01 (charakter numbers as in Table 2)

Table 4. Correlation coefficients between characters of *Juniperus excelsa* from population Crimea 1

3	0.45*							
4	0.41*	0.98**						
5	0.04	0.17	0.16					
6	0.32	0.30	0.27	0.44*				
7	0.44*	0.49*	0.52**	–0.32	–0.37			
8	0.05	0.49*	0.54**	–0.09	–0.35	0.61**		
9	–0.28	–0.12	–0.11	0.17	0.45*	–0.46*	–0.35	
10	–0.11	0.35	0.34	–0.13	0.08	–0.06	–0.11	0.08
Characters	2	3	4	5	6	7	8	9

* – significance at level p = 0.05; ** – significance at level p = 0.01 (charakter numbers as in Table 2)

Table 5. Correlation coefficients between characters of *Juniperus excelsa* from population Crimea 2

3	0.67**							
4	0.69**	0.97**						
5	0.19	0.01	0.04					
6	0.21	0.38	0.31	0.26				
7	0.39	0.31	0.23	–0.36	0.18			
8	0.37	0.48*	0.48*	–0.36	0.01	0.57**		
9	–0.10	0.07	0.02	–0.31	–0.22	–0.08	0.01	
10	0.07	0.21	0.30	–0.12	0.02	–0.12	0.22	0.27
Characters	2	3	4	5	6	7	8	9

* – significance at level p = 0.05; ** – significance at level p = 0.01 (charakter numbers as in Table 2)

the length of cone, diameter of cone, the thickness of branchlets, ratio of cone length/width and ratio of cone width/number of seeds (characters 2, 3, 4, 10, 11 and 14, respectively). The number of recta, number of seeds in cone and number of seed length/width (characters 1, 6 and 13, respectively) did not differentiate samples statistically significantly.

The cones of *Juniperus excelsa* sampled in Bulgaria were larger than in both Crimean populations (char-

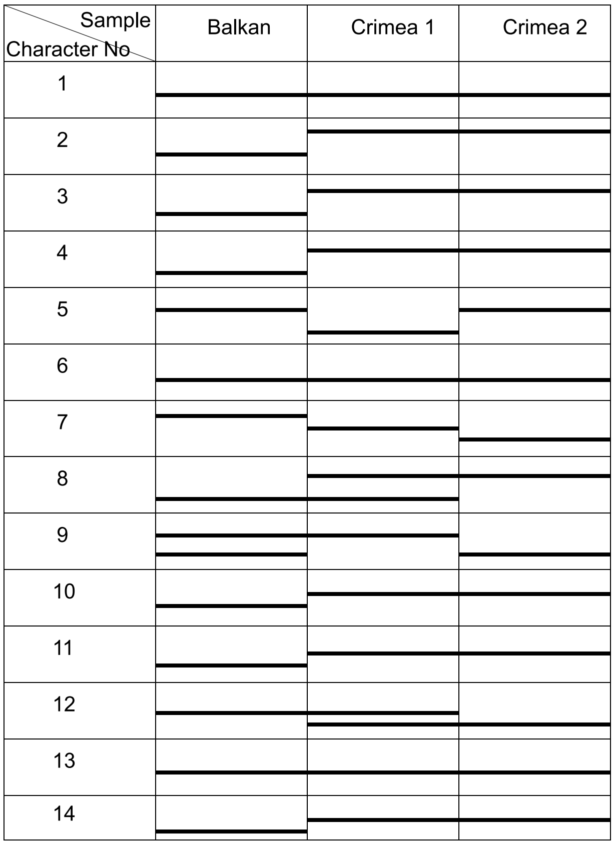

Fig. 2. Tukey's T-test of differences between three populations of compared *Juniperus excelsa*

acters 2, 3 and 4), but contained less seeds (character 6). The leaves within populations had a similar length, but the diameter of shoots of the last ramification (character 10) and the ratio of cone width/number of seeds (character 14) were higher in Bulgarian sample (Table 6).

Results of discriminant analysis

The analysis of discriminating function for all populations showed that the most important aspects in the distinguishing of individuals from particular populations were the width of cone (character 3) and ratio cone width/number of seeds (character 14) with partial Wilks' lambda values of 0,839 and 0.850, respectively (Table 7). Both these characters differentiated samples at a level below p=0.01. All other characters were less statistically significant, or insignificant (Table 7). Generally, the compared samples differed from each other in cone and shoot characters, while the scale characters did not differentiate them in a statistically significant way.

All specimens from the three examined populations formed one group in the area of two main discriminant variables, responsible for 100% of the total variation. The first main variable (U_1) covered 76% of total variability and was determined mostly by the width of cone, ratio of cone width/number of

Table 6. Statistical description of the 14 analysed characters of *Juniperus excelsa* (characters numbers 1–14 as in Table 2)

Statistics	Sample	Character													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Mean	Balkan	4.00	9.07	9.50	8.95	6.92	5.51	4.98	3.08	20.61	0.76	0.96	1.02	1.64	1.83
	Crimea 1	4.00	8.44	8.36	7.98	7.33	6.13	4.63	2.93	19.47	0.69	1.01	1.06	1.60	1.46
	Crimea 2	4.03	8.53	8.19	7.78	7.16	6.05	4.37	2.75	21.02	0.70	1.04	1.10	1.62	1.43
	All samples	4.01	8.64	8.61	8.17	7.16	5.93	4.63	2.91	20.30	0.71	1.01	1.06	1.62	1.55
Minimum	Balkan	4.0	6.8	6.6	6.3	6.0	2.0	3.1	2.1	14.0	0.6	0.7	0.8	1.1	1.0
	Crimea 1	4.0	6.1	5.4	5.1	6.0	2.0	3.0	1.9	14.0	0.5	0.8	0.9	1.1	0.8
	Crimea 2	4.0	6.6	6.2	5.8	6.0	2.0	2.4	1.7	14.0	0.4	0.9	0.9	0.7	0.8
	All samples	4.0	6.1	5.4	5.1	6.0	2.0	2.4	1.7	14.0	0.4	0.7	0.8	0.7	0.7
Maximum	Balkan	4.0	13.7	14.0	13.8	8.0	11.0	6.4	4.3	34.0	1.2	1.2	1.2	2.3	3.8
	Crimea 1	6.0	10.6	10.4	10.1	10.0	13.0	6.4	4.4	28.0	1.0	1.3	1.3	2.3	3.1
	Crimea 2	6.0	11.4	11.2	10.1	12.0	11.0	5.6	4.1	30.0	1.0	1.3	1.3	2.4	3.4
	All samples	6.0	13.7	14.0	13.8	12.0	13.0	6.4	4.4	34.0	1.2	1.3	1.3	2.4	3.8
Standard deviation	Balkan	0.0000	0.9053	1.1324	1.2011	0.9998	1.5592	0.5679	0.4258	3.3462	0.1073	0.0724	0.0864	0.2284	0.4693
	Crimea 1	0.0632	0.8225	0.8107	0.7644	1.0009	1.7003	0.5362	0.4590	2.6844	0.0964	0.0829	0.0891	0.2223	0.3765
	Crimea 2	0.1137	0.8844	0.8589	0.7531	1.0539	1.5363	0.5496	0.4388	2.4984	0.1144	0.0732	0.0737	0.2569	0.3640
	All samples	0.0777	0.9056	1.0750	1.0212	1.0309	1.6248	0.5962	0.4615	2.8691	0.1091	0.0837	0.0886	0.2366	0.4353
Variation coefficient	Balkan	0.00	9.98	11.92	13.42	14.44	28.28	11.39	13.83	16.24	14.09	7.55	8.46	13.93	25.59
	Crimea 1	3.16	9.75	9.70	9.58	13.65	27.75	11.59	15.67	13.79	13.88	8.19	8.40	13.88	25.86
	Crimea 2	5.65	10.36	10.48	9.68	14.73	25.40	12.37	15.98	11.89	16.37	7.00	6.71	15.85	25.42
	All samples	3.87	10.48	12.48	12.49	14.40	27.38	12.87	15.88	14.14	15.33	8.29	8.33	14.62	28.08

seeds, and the length of seeds and cones (characters 3, 14, 7 and 2, respectively). The second main discriminant variable (U_2) covered less than 19% of total variability and was determined by seed length, seed width and ratio of cone length/thickness (characters 7, 3 and 12, respectively).

Table 7. Discriminant power testing for the characters of *Juniperus excelsa*

Characters	F statistics
1. Number of recta	0.772
2. Length of cone	2.292
3. Width of cone	5.444**
4. Thickness of cone	0.518
5. Cone scale number	4.038*
6. Number of seeds	0.884
7. Length of seeds	4.493*
8. Width of seeds	2.284
9. Number of leaves on the 5 mm of the last ramification shoot	1.052
10. Thickness of the last ramification shoot with leaves	0.718
11. Ratio of cone length/wide (= traits 2/3)	0.837
12. Ratio of cone length/thickness (= traits 2/4)	2.277
13. Ratio of seed length/width (= traits 7/8)	1.119
14. Ratio of cone width/number of seeds (= traits 3/6)	5.048**

* – value statistically significant at level p = 0.05; ** – value statistically significant at level p = 0.01

The individuals from three different populations did not form separate groups (Fig. 3). The individuals from the Balkan population differed slightly from the individuals from the two Crimean populations in the distance determined by the first main variable (U_1), which was responsible for almost 76% of total variation. The Crimean populations were much more

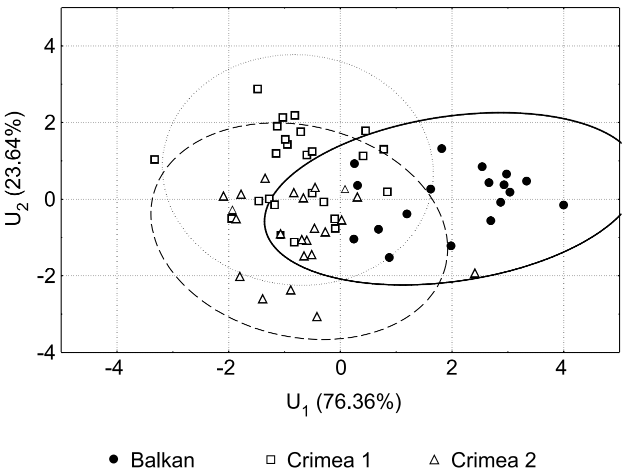

Fig. 3. Result of discriminant analysis based on characters of cones and needles of two populations from Ukraine (Crimea 1, Crimea 2) and one population from Bulgaria (Balkan) plotted along the two first discriminant variables U_1 and U_2, which accounted for 100% of the total variation

weakly differentiated from each other, mostly in the distance determined by the second main variable (U_2), responsible for more than 23% of total variation (Fig. 3). The 0.95 ranges of confidence of particular populations overlap each other at least in part. More than 60% of individuals from the Balkan sample were outside the ranges of confidence of both Crimean samples, but only 20% and 4% of individuals from Crimea 1 and 2, respectively, were separate from the confidence ranges of other samples (Fig. 3).

Results of clustering

The closest Euclidean distances between individuals did not agglomerate them in three separate groups. However, the cluster analysis conducted on the basis of mean values for 3 analyzed populations (Fig. 4) showed a closer relationship between the two populations of *J. excelsa* from Crimea than between *J. excelsa* from Bulgaria and the same taxon from Crimea. This confirms the results of the discrimination analysis.

Intra-populational variation

Among all the features the most variable was the ratio of cone width to the number of seeds (character 14) with a variation coefficient of more than 28%, but about 25% for particular populations, and the number of seeds per cone (character 6), with a variation coefficient of more than 27% for all three populations and about 25–28% in particular populations. The most stable feature was the shape of cone, exposed in cone length/width (character 11) and length/thickness (character 12) ratios, with the variation coefficients of about 8.29 and 8.33%, respectively (Table 6).

The intra-population variability of all three samples has a similar pattern, reflected in values of the coefficients of variation (Table 6). The differences among the populations in the variation coefficients of the same characters did not show statistically significant differences (Student's *t*-test) (Table 8).

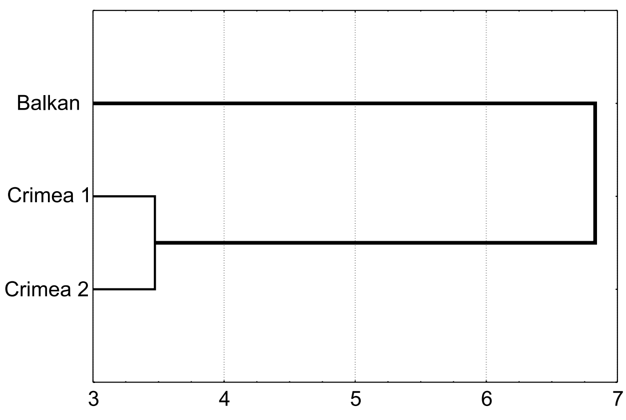

Fig. 4. Dendrograms constructed on the shortest Euclidean distances according to Ward's method, showing the connections among studied populations of *Juniperus excelsa*

Table 8. Values of t-Student's test evaluating the differences between variability coefficients of characters from three samples compared

Compared samples	*df*	*t* calculated	*t* critical value
Balkan – Crimea 1	13	0.377	3.012
Balkan – Crimea 2	13	0.377	3.012
Crimea 1 – Crimea 2	13	0.310	3.012

The intra-population variation of individuals within the samples in the discriminant analysis was also generally weak. Only two individuals from sample Crimea 2 stand out from the centroid of population crossing the 0.95 range of confidence (Fig. 2). The isolated, marginal populations of the species from Crimea appears to be variable at a similar level to population from Bulgaria, from the main part of the species range.

Discussion and conclusion

The 5 from 10 measured characters of the three populations of *Juniperus excelsa* were positively related to each other, with Pearson's correlation coefficient statistically significant at p=0.01, forming 13 positive correlations. In the population of *J. phoenicea* from the Iberian Peninsula (Mazur et al. 2003), analyzed on the basis of the same characters, the 7 characters correlated strongly significantly, forming 10 positive and 11 negative correlations (Mazur et al. 2003). This indicates another type of morphological construction of both species.

The evaluation of intra-population variability on the basis of distribution of individuals in the space of the first two main components of discrimination analysis (Fig. 3) shows a differentiation of individuals of *J. excelsa* similar to that found among individuals of *J. phoenicea* from the Iberian Peninsula, analyzed on the same characters (see Fig. 8 in: Mazur et al. 2003). The ranges of dispersion of individuals of particular samples along the two main discriminant variables were also similar (Fig. 3). The lack of significant differences between values of the variation coefficient of the same characters confirm the similar level of variability of *J. excelsa* in the isolated Crimean populations and in the main part of the species range on the Balkan Peninsula. These indicate that populations of *J. excelsa* in the Crimea, in spite of their marginal geographic position (Browicz 1982) and restricted numbers of individuals (about 400 and 800 individuals in Crimea 1 and Crimea 2, respectively) (Didukh 1992; Mosyakin and Fedoronchuk 1999), do not exhibit a significant loss of their variation.

Values of features from all three sampled populations of *Juniperus excelsa* placed them directly into characteristic for the species. The cone and shoot diameters, also the number of seeds in our study, are very close to values reported for Grecian juniper (not for *J. polycarpos*) (compare with Komarow 1934, Farjon 1992, 2001). *J. excelsa* from Crimea appeared not to be closer to *J. polycarpos*, as we expected. Surprisingly, the Crimean populations of Grecian juniper have values of cone and shoot diameters and number of seeds in the cone more similar to typical *J. excelsa* than the Balkan one (compare table 6 with data by Komarow 1934 and Farjon 1992, 2001).

The differences between individuals representing the three analyzed populations of *Juniperus excelsa* do not allow us to distinguish them in the field, as was the case with the three distant populations of *Juniperus phoenicea* from the Iberian Peninsula (Mazur et al. 2003). The interpopulation variation of the latter species was found to be much larger than the *J. excelsa* populations. The individuals of all analyzed populations of Greek juniper form one group as a result of discrimination analysis (Fig. 3), with weak, but visible separateness of those from the Balkan Peninsula. The larger distance between Crimean and Balkan populations than between the Crimean ones was also confirmed in the agglomeration on the shortest Euclidean distances (Fig. 4). This dependence can be explained by the large geographic distance between Crimea and the Balkans. The gene flow by seed transport between the two distant populations compared is probably impossible, and by means of pollen at least strongly restricted. The pollen grains of the species of *Juniperus* are relatively small and characterized by slow setting velocity (Moore et al. 1991), but their production is relatively not too high and for this reason the possibility of transportation and pollination across the distance between Crimea and the Balkan Peninsula (about 1000–1100 km) is minimal.

The geographic isolation of the Crimean populations of *Juniperus excelsa* and their origin from a different Pleistocene refugium than that of the Balkan population (Reinig, after Kostrowicki 1999 and Kornaś and Medwecka-Kornaś 2002) may be a reason for the ongoing speciation process, visible in the differences among populations studied. The greater distances, even taxonomic ones, between populations developed from separate Pleistocene refugia, were described in other plant species (e.g. Staszkiewcz 1968, Mazur et al. 2003, Carrión et al. 2003, Palme et al. 2003).

The tree-like *Juniperus* species of Section *Sabina* are suggested to have originated from one ancestral taxon, widespread in Europe during the Tertiary (Kvaček 2002). Their suppression to the Mediterranean region in the late Tertiary and early Quaternary was suggested to be a reason for the development of *J. excelsa* in the East- and *J. thurifera* in the West-Mediterranean (Barbero et al. 1994, Jiménez et al. 2003). If we accept this opinion, the long-time geographic isolation of the Crimean and Balkan populations of *J. excelsa* is not in itself a reason for their significant morphological differentiation.

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