International Journal of Applied Environmental Sciences
ISSN 0973-6077 Volume 10, Number 1 (2015), pp. 163-187

http://www.ripublication.com

Morphological Variability Of *Bembidion Articulatum* (Coleoptera, Carabidae) Populations: Linear Dimensions Depend On Sex, While Morphological Indices Depend On Ecosystems

Viktor V. Brygadyrenko and Viktorija O. Slynko

Department of Zoology and Ecology, Oles' Honchar Dnipropetrovsk National University, pr. Gagarina, 72, 49010 Dnipropetrovsk, Ukraine; e-mail: brigad@ua.fm

Abstract

Bembidion (Trepanes) articulatum (Panzer, 1796) is distributed from Great Britain in the west to Japan in the east, is very common on moist to wet loamy water margins, from lowlands to mountains. The objective of our research is the evaluation of the populational and sexual variability of this species in central Ukraine. Beetles were studied in 9 ecosystems differing by mechanical composition of the soil, mineralization of soil solution, pH of aqueous extract, plant cover, degree of litter development, type and intensity of anthropogenic impact. 8 linear characteristics, one angular characteristic, density of pores and contrast of spots on the beetles' elytra were measured, and 6 morphometric indices were calculated. The results of Manova show the absence of a statistically significant effect of ecosystem on the body length, elytra length, head width, maximal prothorax width and elytra width. Sexual differences were found for all studied linear characteristics of *B. articulatum*. The Manova test for the influence of the ecosystem factor showed significant variation in the prothorax length, prothorax width between the front angles and the back angles, density of pores and degree of contrast of the humeral spot on the elytra. In distinction to the linear characteristics, according to the Manova results, sex showed no statistically significant influence on any of the six studied morphometric indices of *B. articulatum*, while ecosystem defines the variability of half (3 of the 6) studied morphometric indices. Results of PCA analysis show that sex is the most important factor (52.6% of dispersion) determining the variability of linear body dimensions of *B. articulatum*.

Key words: sexual dimorphism, population variability, morphometrics, Coleoptera, Carabidae, *Bembidion articulatum*

Introduction

Bembidion (Trepanes) articulatum (Panzer, 1796) is a Transpalearctic species which is distributed from Great Britain in the west to Japan in the east (LINDROTH, 1985). In Europe *B. articulatum* is distributed in Albania, Austria, Belgium, Bosnia, Bulgaria, Belarus, Croatia, the Czech Republic, Denmark, Estonia, Finland, France, Great Britain, Germany, Greece, Herzegovina, Hungary, Italy, Latvia, Liechtenstein, Lithuania, Luxembourg, Macedonia, Moldavia, the Netherlands, Norway, Poland, Portugal, Romania, Russia (north, central and south European Territory), Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, Ukraine; in Asia – in Armenia, Azerbaijan, China, Georgia, Japan, Kazakhstan, Kyrgyzstan, Russia (west and east Siberia, the Far East) and Turkey (NETOLITZKY, 1942, 1943; TURIN et al., 1977; KRYZHANOVSKY et al., 1995; LOBL, SMETANA, 2003).

According to the data of LINDROTH (1985), in Denmark the species is recorded in all districts, being well distributed and quite common in the eastern Jutland and on the islands. In Sweden it is quite common, not rare, being especially well established in the lowlands around the great lakes in central Sweden; in Norway it is locally common in the south (LINDROTH, 1985).

Peak activity of imagoes of *B. articulatum* in the Netherlands is recorded in May and June, with lower activity from March to October and occasional observations till December (TURIN et al., 1977). LINDROTH (1985) also states that most observations of this species are in spring. In the territory of Ukraine we also recorded the same periodicity of seasonal activity: numbers increased from the end of March to mid-May and decreased from early June to early July; in the latter half of summer and in autumn the numbers of this species on various sampling plots is 5–15 times lower than in spring.

In the Czech and Slovak Republics *B. articulatum* is very common on unshaded or partly shaded, moist to wet loamy water margins, from lowlands to mountains (HURKA, 1996). In the Polish fauna (ALEKSANDROVICH, 2004), *B. articulatum* is a common, mainly predatory species, with an affinity for wet places, tyrphobiont (inhabiting peatlands), ripicolous (living on the banks of rivers, lakes, streams), pratinicolous (living in grassland and meadowland).

KARPOVA and MATALIN (1993), when studying fauna in the south of Moldova, refer this species to the riparian ecological group (of banks of rivers, streams) and state that at night imagoes fly towards ultraviolet light, and occur mainly on clay soils. LINDROTH (1974) mentions that this species is often abundant in England as far north as Derby, and also in S. Wales, on sterile, moist clay of sandy mud near fresh water, often hidden in cracks. In Belarus (ALEKSANDROWICZ, 2002) *B. articulatum* is a stenobiont peat bog species. In the forest-steppe zone of Ukraine (KRYSHTAL, 1956) this species occurs more rarely, mainly on shore drift. KIRICHENKO and KRAVCHENKO (2006) point out that in Ukraine *B. articulatum* is very common on unshaded or partly shaded, moist to wet loamy and sandy shores from lowlands to mountains. According to our data (BRYGADYRENKO, 2003), in the central and southern parts of Ukraine *B. articulatum* prefers a neutral reaction of soil solution, however it is also rather abundant on sub-saline areas, as well as in habitats with acid reaction of the soil solution. *B. articulatum* is found in equal numbers both in riparian areas with sandy soil and in areas with sandy loam, clay loam and heavy soil. This species is common on river shore drift, areas without clusters of dead organic matter, ecosystems with dense grass stands and in areas barren of plant life.

The morphological variability of *B. articulatum* has not been studied so far. Studies have been conducted on some other species of the genus, notably on the variability (SLINKO et al., 2008) of *B. varium*, which is a common species in most semi-aquatic ecosystems of Eurasia. LANGOR and LARSON (1983) present data on variability of *B. lampros*. However, a general evaluation of the morphological variability of species of the *Bembidion* genus based on a sufficiently large sample of the diverse set of ecosystems has not been performed yet. Similar studies for large-size wingless South-American ground beetles revealed new mechanisms of responses of populations to various ecological parameters of the habitat (BENÍTEZ et al., 2010, 2011, 2013). Therefore, the main objective of this article is evaluation of general sexual and interpopulation variability of *B. articulatum* populations.

Material and Methods

B. articulatum imagoes were collected from 9 populations in Pavlograd (ecosystems 1–4), Sinelnikovo (ecosystem 5), Novomoskovsk (ecosystems 6 and 7), and Magdalinovka (ecosystems 8 and 9) districts of the Dnipropetrovsk region, Ukraine (Table 1).

Table 1. Brief characteristic of ecosystems (Dnipropetrovsk region, Ukraine) where *B. articulatum* was collected

Ecosystem	Administrative region	Ecosystem coordinates	Mechanical composition of soil	Salt content in soil solution, g/l	pH of soil solution	Dominating plant species (density of herb layer), composition of litter	Degree of anthropogenic impact	Prevailing type of anthropogenic impact
1	Pavlograd	48°28’40’’N 36°01’22’’E	clay loam	4.42	7.98	*Chenopodium album* L. (30%), *Poa sp.* (5%), no litter	Medium	watering of livestock, domestic wastes
2	Pavlograd	48°30’33’’N 36°04’44’’E	sand	0.87	8.66	*Xanthium albinum* (Widd.) Scholz (50%), *Chenopodium album* L. (30%), *Bolboschoenus maritimus* (L.) Palla (10%), no litter	High	watering of livestock, domestic wastes
3	Pavlograd	48°34’24’’N 35°52’13’’E	sand clay	1.63	7.98	No grass stand and no litter	Low	domestic wastes
4	Pavlograd	48°34’18’’N 35°51’57’’E	sand	4.40	7.75	No grass stand and no litter	Medium	watering of livestock, birds, domestic wastes
5	Sinelnikovo	48°29’33’’N 35°21’49’’E	clay loam	1.12	8.22	No grass stand, shore drift of water macrophytes 4 cm thick	High	watering of livestock
6	Novomos-kovsk	48°40’21’’N 35°21’19’’E	clay loam	3.48	7.99	*Typha angustifolia* L. (90%), litter of dead roots of cattail 2 cm thick	High	domestic wastes
7	Novomos-kovsk	48°40’01’’N 35°21’56’’E	clay loam	0.49	7.98	*Phragmites australis* (Cav.) Trin. ex Steud. (95%), litter of dead roots of reed 5 cm thick	High	domestic wastes
8	Magdali-novka	48°43’46’’N 35°00’31’’E	clay loam	1.58	8.10	No grass stand, shore drift of water macrophytes 4 cm thick	Low	domestic wastes
9	Magdali-novka	48°47’47’’N 34°59’27’’E	clay loam	1.74	8.91	*Bolboschoenus maritimus* (L.) Palla (5%), no litter	High	watering of livestock, birds, domestic wastes

In order to prepare the aqueous extracts, 30 g soil samples (weighed to the nearest 1 mg) were placed into flasks into which 150 ml of distilled water was poured. The soil and water were mixed for 3 minutes and kept for 5 minutes to settle. The pH of the aqueous extract was determined by the probe of portable pH-meter PH-03 (II) with the automatic temperature compensator from 0 to 50 °C and accuracy of ±0.1 pH units. After each measurement the probe was washed with distilled water.

Determination of total dissolved salts in the aqueous extract was carried out by the probe using COM-100, with the accuracy of ±2% and function of automatic temperature compensation. Measurements were made on a ppm (parts per million) scale with the calibration by *NaCl*. Sodium chloride is used for measurements in water with prevailing content of *NaCl* ions or with properties close to *NaCl* (for example, sea water or sub-saline water). After each measurement, the probe was thoroughly washed with distilled water.

The ecosystems differed (Table 1) in mechanical composition of the soil (ecosystems 2 and 4 – sandy soil, 3 – sandy loam, ecosystems 1 and 5–9 – loam), salt content in the soil solution (low – 2 and 7, medium – 3, 5, 8 and 9 and high – 1, 4 and 6). The pH of the aqueous extract from all areas examined was slightly alkaline (from 7.75 to 8.91).

Specimens of *B. articulatum* were collected by soil traps, beetles were killed by freezing at –15 ºC during 24 hours in a cooling chamber, laid onto cotton mats, having been previously spread out (to maintain proportions, orientation of the head and prothorax was followed). Photographs of the dried out insects were taken through binocular MBS-10 with the use of digital camera of 5 megapixel resolution. Each beetle was assigned a serial number including the number of the ecosystem it was collected from and its sex (female, male). Measurements were made by digital photos in the software package TpsDig 2.17 (2013, Rohlf F.J., Ecology & Evolution, SONY at Stony Brook). 8 linear characteristics, 1 angular characteristic, density of pores on elytra, contrast of the front and rear light spots of elytra (Table 2) were measured.

The following linear characteristics were measured: length of body (Lb), prothorax (Lp), elytra (Le), width of head with eyes (Sc), width of prothorax between front angles (Sp1) and back angles (Sp3), maximum width of prothorax (Sp2), maximum width of elytra (Se). Linear characteristics were evaluated by photographs with an accuracy of ±1 pixel (0.0016 mm).

In order to eliminate the influence of the position of each beetle when the photographs were taken, the back angles of the prothorax (B) were measured on the right and left parts of the body, for the further calculations their arithmetic mean value was used. Accuracy of photographic measurement of angles was equal to ±0.1º.

Density of elytra puncturing (P) was assessed from photographs by counting the quantity of pores on the area of 0.135 mm^2 between the back edge of the scutellar groove and the first groove of the elytra. For each beetle the hairs on the right and left elytra were counted; for the further processing the arithmetic mean values of the above were taken.

Indices (body proportions) were calculated taking into account the methods we used earlier (SHAROVA, 1981; FALY and BRYGADYRENKO, 2007; BRYGADYRENKO and FEDORCHENKO, 2008; BRYGADYRENKO AND KOROLEV, 2014; BRYGADYRENKO AND

RESHETNIAK, 2014). 6 morphometric indices were calculated, that is: ratio of arithmetic mean value of the width of head, prothorax and elytra to body length ((Sc+Sp+Se)/3Lb), ratio of prothorax length to its maximum width (Lp/Sp2), ratio of elytra length to prothorax length (Le/Lp), ratio of maximum width of elytra to maximum prothorax width (Se/Sp2), ratio of maximum prothorax width to its width at the back edge (Sp2/Sp3), and ratio of elytra length to their width (Le/Se).

The results were processed by standard methods of variation statistics (with the calculation of: x – mean value, SD – standard deviation, Min–Max – minimum and maximum values, D – characteristics' variation range, As – asymmetry, Ex – excess) using Statistica software (version 8, StatSoft, USA). The most important parameters of morphological variability were determined with the use of the PCA method. The effect of sex and ecosystem on the morphological characteristics and indices was evaluated using MANOVA. Significance of variations between samples was assessed by one-way ANOVA, for multiple comparisons of samples the Tukey test was used (StatGraphics Plus v5.1 package). Data in the text and tables is represented as the mean value ± standard deviation.

Results

Effect of sex and ecosystem on morphometric characteristics and indices of *B. articulatum*

Following the result of Manova (Table 2) for the morphometric characteristics of the studied *B. articulatum* populations, no significant effect of ecosystem on body length (Lb), elytra length (Le), head width (Sc), maximum prothorax width (Sp2) and elytra width (Se) was revealed. Sex has an influence on all morphometric characteristics of *B. articulatum*.

Under the influence of the ecosystem factor in Manova (Table 2) the values for prothorax length (Lp), prothorax width between front (Sp1) and back (Sp3) angles, density of pores on the elytra (P), degree of contrast of humeral spot on the elytra (K1) vary significantly. Among the indices (Table 3) a significant influence of the ecosystem factor was observed for the ratio of prothorax length to its maximum width (Lp/Sp2), elytra length to prothorax length (Le/Lp), maximum prothorax width to its width between back angles (Sp2/Sp3). There is good reason to use these characteristics of *B. articulatum* imago morphology in bio-indication studies in future.

According to the results of Manova (Table 3), sex has no significant influence on any of the six studied morphometric indices of *B. articulatum*, while ecosystem determines variability of half (3 of the 6) the studied morphometric indices.

Sexual differences in morphometric characteristics and indices of *B. articulatum*

The variability of morphometric characteristics (coefficient of variation, CV, %) for linear characteristics varies from 3.4% to 5.8% (Table 4): in males it is equal to 4.21 ± 0.69%, in females it is 4.63 ± 0.33% ($P = 0.151$, $F = 2.31$, $F_{0.05(1, 14)} = 4.60$). Variability of morphometric indices, in contrast, is much lower than for linear measurements, varying from 1.9% to 4.3% (Table 4): in males CV is equal on average to 3.54 ± 1.10%, in females it is 2.98 ± 0.93% ($P = 0.359$, $F = 0.92$, $F_{0.05(1, 10)} = 4.97$).

Significant differences between males and females ($P < 10^{-8}$) were obtained on all morphometric characteristics analyzed (Lb, Lp, Le, Sc, Sp1, Sp2, Sp3, Se, Table 4). This shows the smaller absolute size of males and lower range of fluctuations in the linear morphometric characteristics of males.

Table 2. Manova results of morphometric characteristics of studied populations of *B. articulatum* (n = 213)

Characteristic	Factor	*Beta* ± *SE*	*B* ± *SE*	$t_{(210)}$	*P*
Lb	Ecosystem	0.066 ± 0.059	0.005 ± 0.004	1.11	0.267
	Sex	–0.504 ± 0.059	–0.190 ± 0.023	–8.46	<0.001
	Ecosystem * Sex	–	23.215 ± 2.304	10.08	<0.001
Lp	Ecosystem	–0.147 ± 0.063	–0.003 ± 0.001	–2.32	0.021
	Sex	–0.411 ± 0.063	–0.038 ± 0.006	–6.50	<0.001
	Ecosystem * Sex	–	4.711 ± 0.597	7.89	<0.001
Le	Ecosystem	0.017 ± 0.061	0.001 ± 0.003	0.28	0.776
	Sex	–0.485 ± 0.061	–0.122 ± 0.015	–7.97	<0.001
	Ecosystem * Sex	–	14.816 ± 1.564	9.47	<0.001
Sc	Ecosystem	–0.010 ± 0.061	–0.001 ± 0.001	–0.17	0.867
	Sex	–0.472 ± 0.061	–0.042 ± 0.005	–7.69	<0.001
	Ecosystem * Sex	–	5.279 ± 0.563	9.37	<0.001
Sp1	Ecosystem	0.191 ± 0.061	0.003 ± 0.001	3.13	0.002
	Sex	–0.418 ± 0.061	–0.036 ± 0.005	–6.84	<0.001
	Ecosystem * Sex	–	4.432 ± 0.540	8.21	<0.001
Sp2	Ecosystem	0.036 ±0.060	0.001 ± 0.001	0.59	0.557
	Sex	–0.489 ± 0.060	–0.043 ± 0.005	–8.08	<0.001
	Ecosystem * Sex	–	5.372 ± 0.549	9.78	<0.001
Sp3	Ecosystem	0.129 ± 0.062	0.002 ± 0.001	2.10	0.037
	Sex	–0.426 ± 0.062	–0.028 ± 0.004	–6.89	<0.001
	Ecosystem * Sex	–	3.427 ± 0.410	8.36	<0.001
Se	Ecosystem	0.014 ± 0.059	0.001 ± 0.002	0.24	0.807
	Sex	–0.527 ± 0.059	–0.079 ± 0.009	–8.91	<0.001
	Ecosystem * Sex	–	9.598 ± 0.909	10.56	<0.001
B	Ecosystem	0.077 ± 0.069	0.166 ± 0.149	1.12	0.265
	Sex	–0.052 ± 0.069	–0.594 ± 0.798	–0.74	0.458
	Ecosystem * Sex	–	152.48 ± 81.84	1.86	0.064
P	Ecosystem	–0.142 ± 0.068	–0.942 ± 0.449	–2.10	0.037
	Sex	0.163 ± 0.068	5.805 ± 2.407	2.41	0.017
	Ecosystem * Sex	–	–424.5 ± 246.9	–1.72	0.087
K1	Ecosystem	0.447 ± 0.061	0.085 ± 0.012	7.27	<0.001
	Sex	–0.099 ± 0.061	–0.101 ± 0.063	–1.60	0.110
	Ecosystem * Sex	–	13.262 ± 6.437	2.06	0.041
K2	Ecosystem	–0.007 ± 0.070	–0.002 ± 0.015	–0.11	0.913
	Sex	–0.023 ± 0.070	–0.028 ± 0.082	–0.33	0.738
	Ecosystem * Sex	–	4.535 ± 8.456	0.54	0.592
Acari	Ecosystem	0.011 ± 0.070	0.001 ± 0.008	0.15	0.878
	Sex	–0.016 ± 0.070	–0.010 ± 0.042	–0.23	0.820
	Ecosystem * Sex	–	1.047 ± 4.313	0.24	0.809

Note: names of characteristics are given in section Materials and Methods.

No significant differences between males and females on the values of morphometric indices were recorded (Table. 4), i.e. absolute size in males is less; however, body proportions remain unchanged.

There are no sexual differences on the value of back angles of the prothorax (B), though density of pores on the elytra (P) in males is significantly higher ($P < 0.01$). The score of contrast of the rear light spot of elytra (K2) does not significantly differ in specimens of different sex (Table 4), whereas the front light spot of elytra (K1) in males is significantly more contrasting.

Table 3. Manova results of morphometric indices of the studied populations of *B. articulatum* (n = 213)

Index	Factor	*Beta ± SE*	*B ± SE*	*t(210)*	*P*
(Sc + Sp + Se)/3Lb	Ecosystem	–0.134 ± 0.069	–0.001 ± 0.001	–1.94	0.053
	Sex	0.051 ± 0.069	0.001 ± 0.001	0.73	0.463
	Ecosystem * Sex	–	0.238 ± 0.088	2.71	0.007
Lp/Sp2	Ecosystem	–0.213 ± 0.068	–0.003 ± 0.001	–3.14	0.002
	Sex	–0.008 ± 0.068	–0.001 ± 0.006	–0.12	0.901
	Ecosystem * Sex	–	0.960 ± 0.576	1.67	0.097
Le/Lp	Ecosystem	0.221 ± 0.068	0.010 ± 0.003	3.26	0.001
	Sex	–0.051 ± 0.068	–0.012 ± 0.016	–0.76	0.451
	Ecosystem * Sex	–	4.072 ± 1.641	2.48	0.014
Se/Sp2	Ecosystem	–0.038 ± 0.069	–0.001 ± 0.001	–0.55	0.583
	Sex	–0.119 ± 0.069	–0.011 ± 0.006	–1.72	0.087
	Ecosystem * Sex	–	2.701 ± 0.640	4.22	<0.001
Sp2/Sp3	Ecosystem	–0.161 ± 0.069	–0.003 ± 0.001	2.34	0.020
	Sex	–0.016 ± 0.069	–0.002 ± 0.007	–0.23	0.817
	Ecosystem * Sex	–	1.713 ± 0.718	2.39	0.018
Le/Se	Ecosystem	0.006 ± 0.070	0.000 ± 0.001	0.09	0.926
	Sex	0.028 ± 0.070	0.002 ± 0.006	0.40	0.690
	Ecosystem * Sex	–	1.345 ± 0.570	2.36	0.019

Note: names of indices are given in section Materials and Methods.

Apart from absolute values, the pattern of distribution of characteristics has a significant ecological importance. This distribution can be considered normal at insignificant values of excess and asymmetry. Normal distribution (Table 4) both in males and females is typical for the width of prothorax and elytra in males and females (Sp1, Sp2, Sp3, Se).

Negative asymmetry in males and females was recorded for head width (Sc, Fig. 1) and prothorax length (Lp, Fig. 2): specimens with high values of characteristics (Table 4) prevail in the population. Negative asymmetry in females is present for total body length (Lb, Fig. 1) and elytra length (Le, Fig. 3): females with longer abdomen (and, accordingly, body), which reflects a high reproductive capacity, gain the advantage.

Oppositely directed changes in *B. articulatum* occur in the value of back angle of prothorax (B, Table 4, Fig. 3): the males have positive asymmetry (specimens with lower values of humeral angle are the most widespread), and asymmetry in females is negative (specimens with blunter humeral angle dominate).

Among six morphometric indices in males and females significant positive asymmetry is found only for the ratio of elytra width to maximum width of prothorax (Se/Sp2, Table 4, Fig. 5): specimens with lower value of the index, i.e. with narrower elytra in relation to prothorax, prevail.

Table 4. Variability of morphometric characteristics and indices in males and females of the studied populations of *B. articulatum*

Characteristic	Sex	*x ± SD*	*Ex*	*As*	*CV*	*D*	*Min – Max*	F ($F_{0.05}$ = 3.89, *df1* = 1, *df2* = 211)	*P*
Lb	male	3.661 ± 0.140	–0.22	0.04	3.8	0.684	3.359 – 4.043	75.28	$1.1•10^{-15}$
	female	3.854 ± 0.172	–0.13	–0.45*	4.5	0.901	3.302 – 4.203		
Lp	male	0.799 ± 0.045	0.83	–0.43*	5.6	0.279	0.643 – 0.922	38.29	$3.1•10^{-9}$
	female	0.835 ± 0.040	1.33***	–0.54**	4.7	0.240	0.669 – 0.909		
Le	male	2.298 ± 0.095	0.16	0.23	4.2	0.473	2.116 – 2.589	65.54	$4.5•10^{-14}$
	female	2.420 ± 0.116	0.06	–0.37*	4.8	0.624	2.043 – 2.667		
Sc	male	0.926 ± 0.034	0.99**	–0.72**	3.7	0.185	0.817 – 1.002	60.12	$3.7•10^{-13}$
	female	0.969 ± 0.042	2.41***	–1.00***	4.3	0.272	0.777 – 1.049		
Sp1	male	0.737 ± 0.034	–0.01	–0.23	4.6	0.167	0.647 – 0.814	51.34	$1.3•10^{-11}$
	female	0.775 ± 0.041	–0.44	–0.01	5.3	0.206	0.674 – 0.880		
Sp2	male	0.919 ± 0.031	–0.36	0.05	3.4	0.144	0.849 – 0.994	67.85	$1.8•10^{-14}$
	female	0.962 ± 0.042	0.16	–0.38	4.4	0.221	0.838 – 1.059		
Sp3	male	0.601 ± 0.027	–0.15	0.09	4.5	0.127	0.542 – 0.670	51.36	$1.3•10^{-11}$
	female	0.630 ± 0.030	0.54	–0.29	4.7	0.170	0.550 – 0.720		
Se	male	1.461 ± 0.058	0.67	0.25	3.9	0.350	1.314 – 1.664	81.77	$1.0•10^{-16}$
	female	1.541 ± 0.066	0.20	–0.27	4.3	0.364	1.364 – 1.728		
B	male	92 ± 5	0.72	0.56*	5.6	27	82 – 108	0.80	0.371
	female	93 ± 6	3.11***	–0.40*	6.5	42	66 – 108		
P	male	168 ± 19	1.98***	0.68**	11.0	110	133 – 244	7.21	0.008
	female	162 ± 16	–0.94**	0.06	10.1	59	133 – 192		
K1	male	3.37 ± 0.55	–0.01	–0.57*	16.4	2.0	2.0 – 4.0	5.30	0.022
	female	3.53 ± 0.46	–0.72	–0.43*	13.0	2.0	2.0 – 4.0		
K2	male	1.68 ± 0.63	–0.08	0.58*	37.1	2.5	1.0 – 3.5	0.10	0.746
	female	1.71 ± 0.56	–0.35	0.31	32.5	2.0	1.0 – 3.0		
(Sc+Sp+Se)/3Lb	male	0.301 ± 0.007	0.64	0.34	2.2	0.035	0.287 – 0.322	0.97	0.324
	female	0.300 ± 0.006	–0.31	0.26	1.9	0.028	0.289 – 0.316		
Lp/Sp2	male	0.870 ± 0.045	3.14***	0.02	5.2	0.339	0.704 – 1.042	0.08	0.780
	female	0.869 ± 0.037	1.00**	–0.03	4.3	0.245	0.749 – 0.994		
Le/Lp	male	2.881 ± 0.129	1.66***	0.55*	4.5	0.730	2.592 – 3.321	1.35	0.246
	female	2.900 ± 0.107	1.13***	0.31	3.7	0.688	2.531 – 3.219		
Se/Sp2	male	1.591 ± 0.051	11.68***	2.23***	3.2	0.391	1.491 – 1.882	2.78	0.097
	female	1.601 ± 0.039	2.83***	0.75***	2.4	0.277	1.506 – 1.784		
Sp2/Sp3	male	1.529 ± 0.051	–0.22	0.17	3.3	0.239	1.421 – 1.660	0.01	0.942
	female	1.528 ± 0.050	11.03***	1.74***	3.3	0.447	1.383 – 1.829		
Le/Se	male	1.573 ± 0.045	0.46	–0.18	2.9	0.251	1.428 – 1.679	0.15	0.696
	female	1.571 ± 0.035	–0.16	–0.01	2.2	0.182	1.484 – 1.665		

Note: x – mean value, SD – standard deviation, Ex – excess, As – asymmetry, CV – coefficient of variation (%), D – range of characteristic or index variation, Min – Max – minimum and maximum values, F – value of F-criterion of Fisher, P – significance of differences in characteristics or indices in males and females; names of morphometric characteristics and indices, see sections Materials and Methods; for As and Ex * – P < 0.05, ** – P < 0.01, *** – P < 0.001; n_{male} = 87, n_{female} = 126.

Positive asymmetry and excess are revealed for the ratio of maximum prothorax width to its width between back angles (Sp2/Sp3, Table 4, Fig. 5). This proves the predominance in the studied populations of females with the lower value of the given index, i.e. with more parallel lateral sides of the prothorax.

In males and females significant values of excess on indices Lp/Sp2 (Fig. 4), Le/Lp (Fig. 4), Se/Sp2 (Fig. 5), in females – also on index Sp2/Sp3 (Fig. 5) were revealed. This indicates the lower variability of body proportions compared with linear characteristics (Table 4).

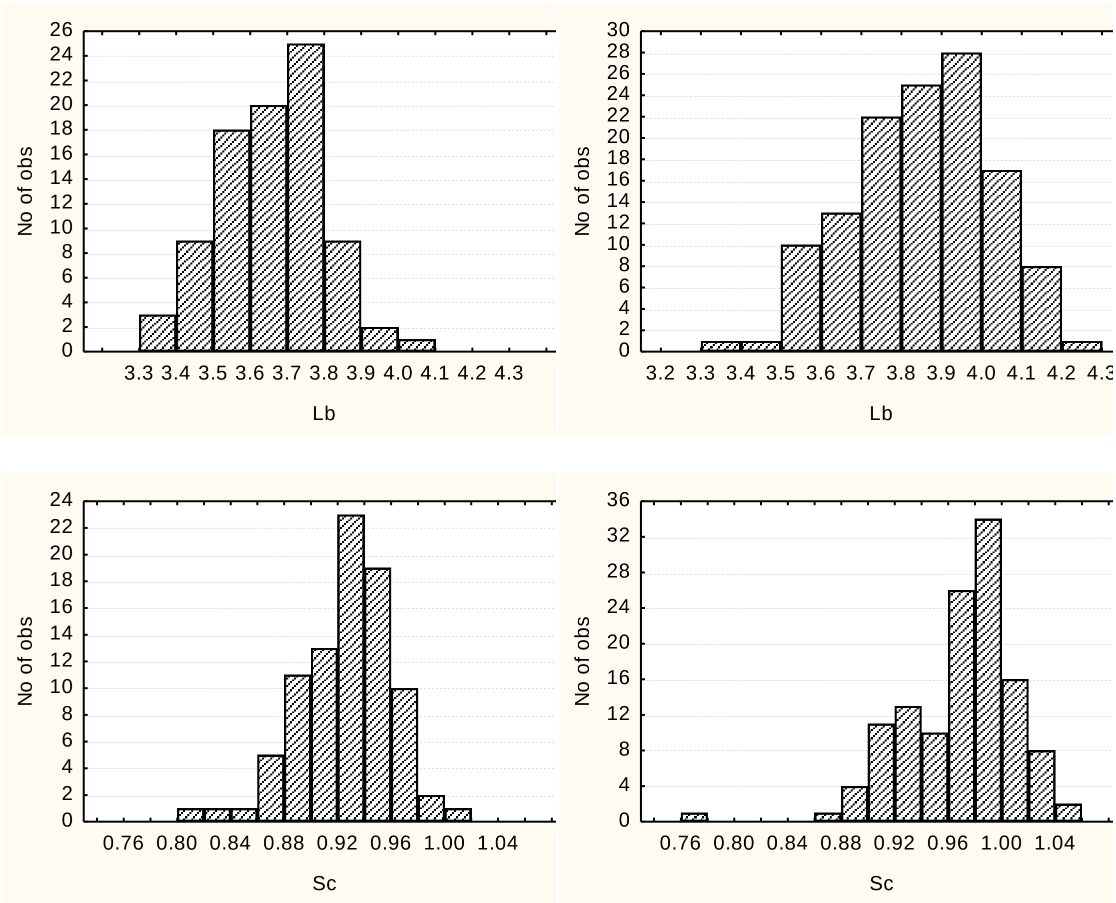
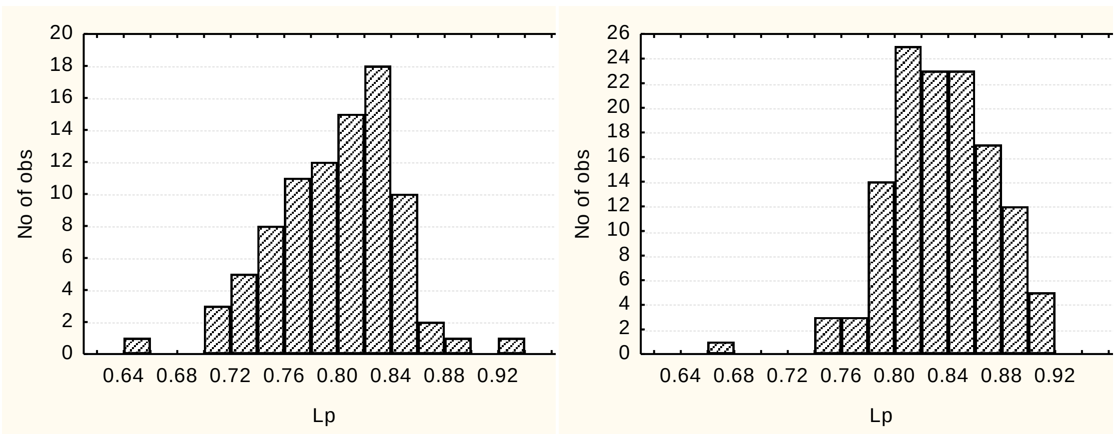


Fig. 1. Variability of body length (Lb) and head width (Sc) in *B. articulatum*: on the left – males (n = 87), on the right – females (n = 126); on X-axis – value of characteristics in millimeters, on Y-axis – number of specimens.



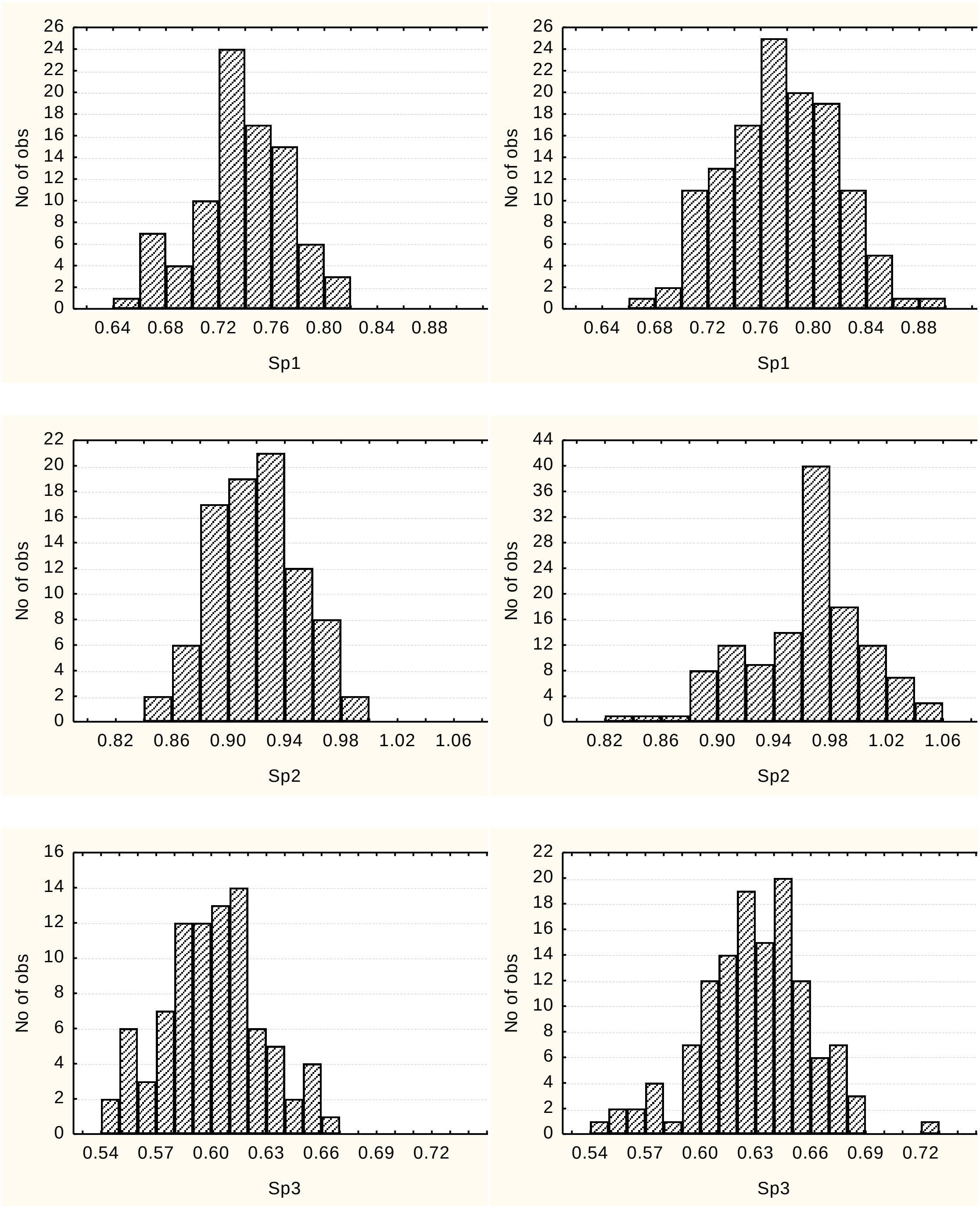
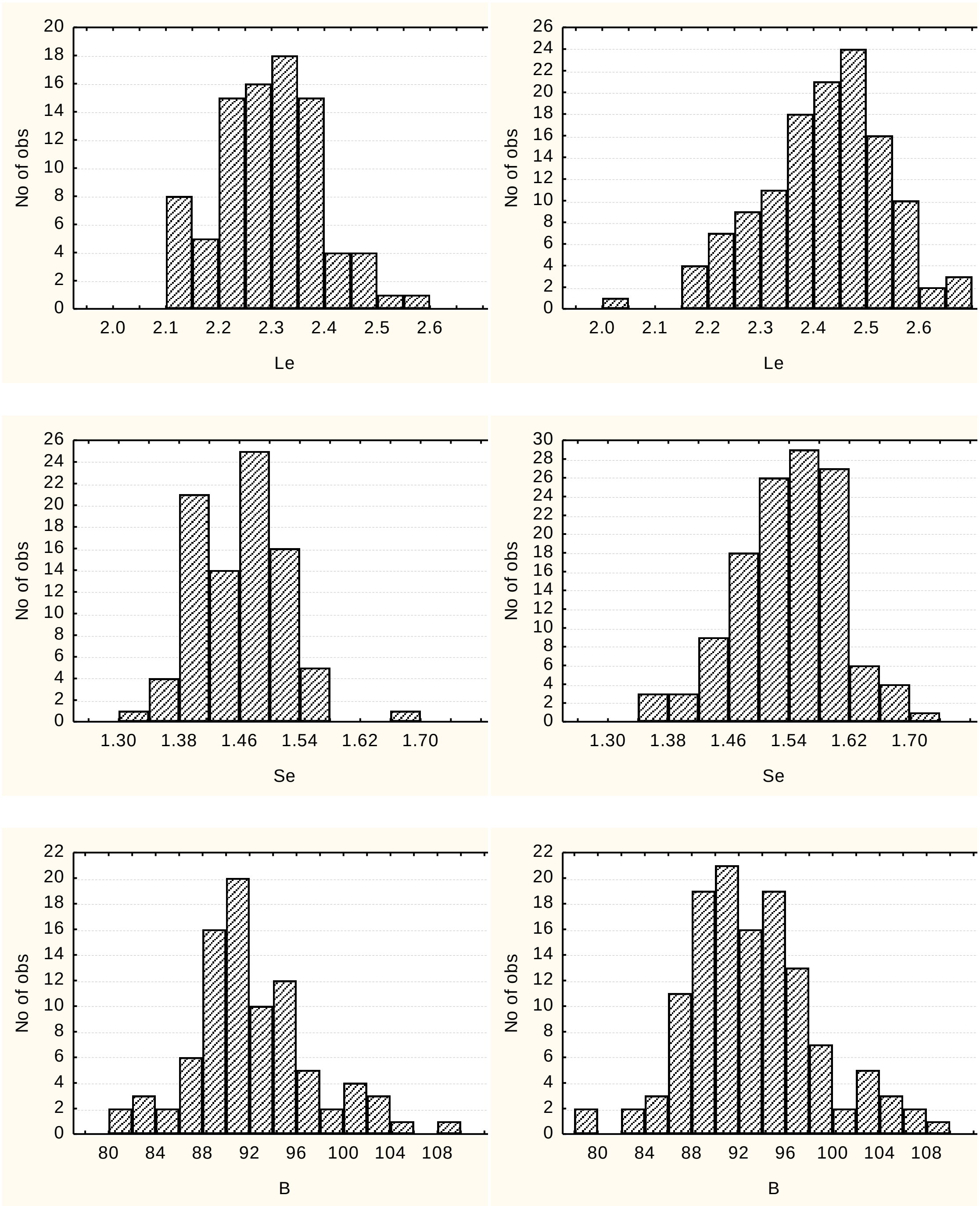


Fig. 2. Variability of prothorax width (Lp), maximum prothorax width (Sp2), its width at the front (Sp1) and back edge (Sp3) in *B. articulatum*: on the left – males (n = 87), on the right – females (n = 126); on X-axis – value of characteristics in millimeters, on Y-axis – number of specimens.


No of obs
Le
No of obs
Le
No of obs
Se
No of obs
Se
No of obs
B
No of obs
B

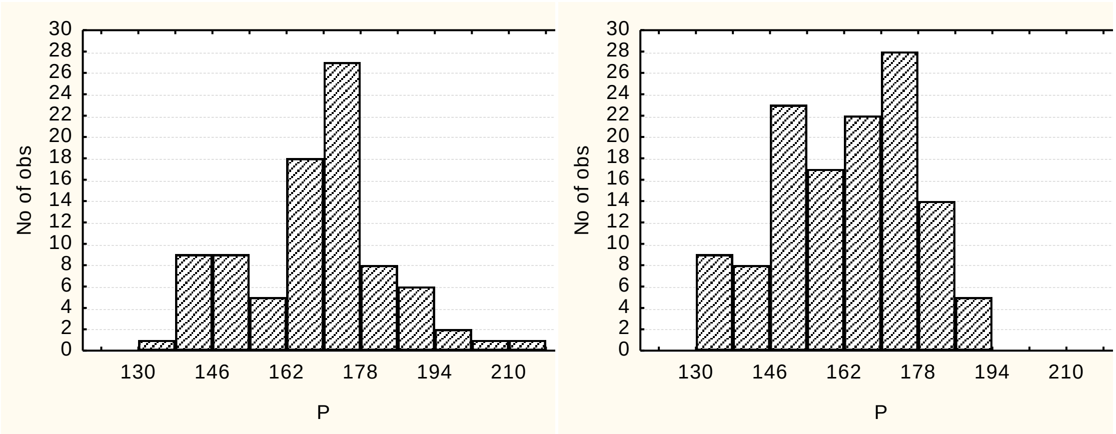
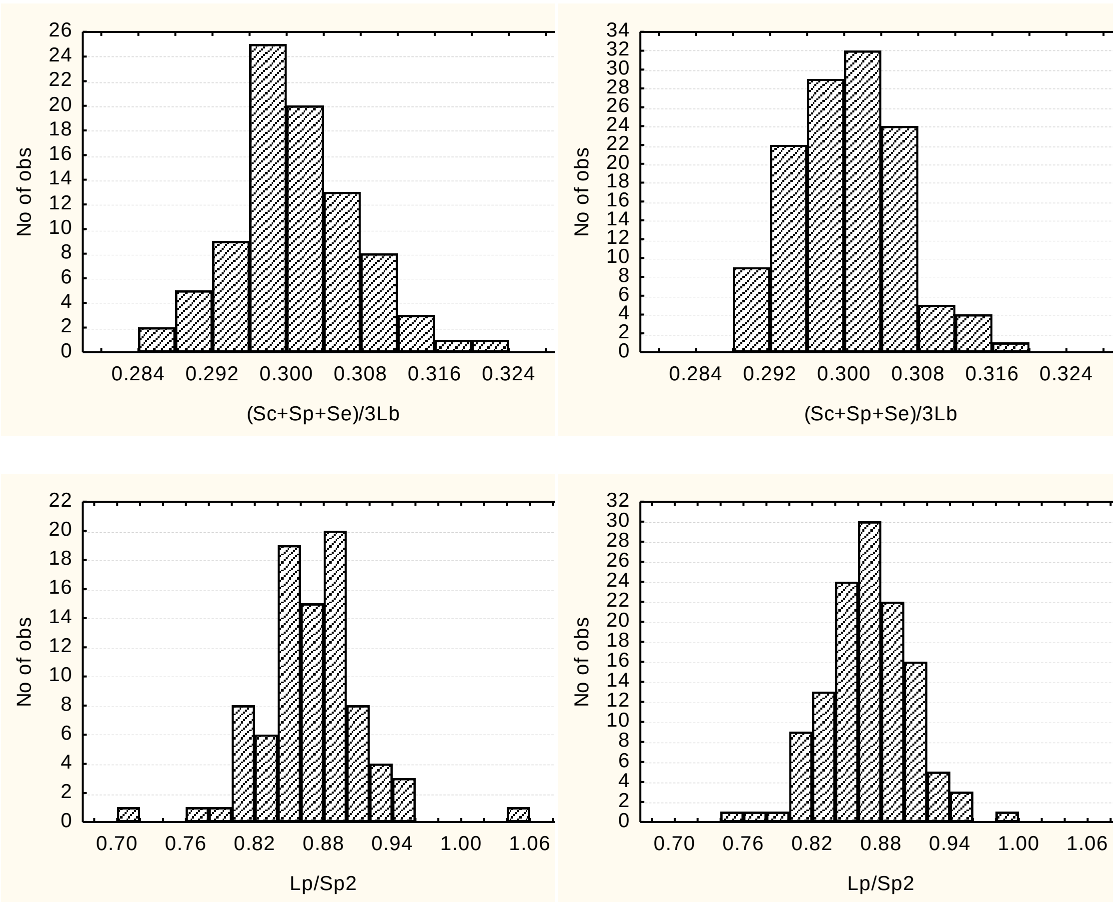


Fig. 3. Variability of length (Le, mm) and elytra width (Se, mm), back angle of prothorax (B, degrees) and quantity of pores on elytra (P, pores/mm^2) in *B. articulatum*: on the left – males (n = 87), on the right – females (n = 126); on X-axis – value of characteristic, on Y-axis – number of specimens.



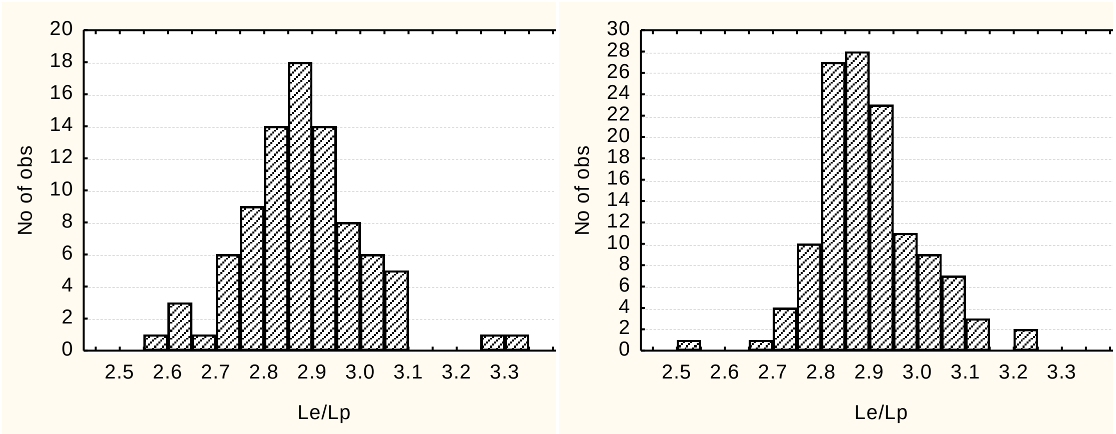
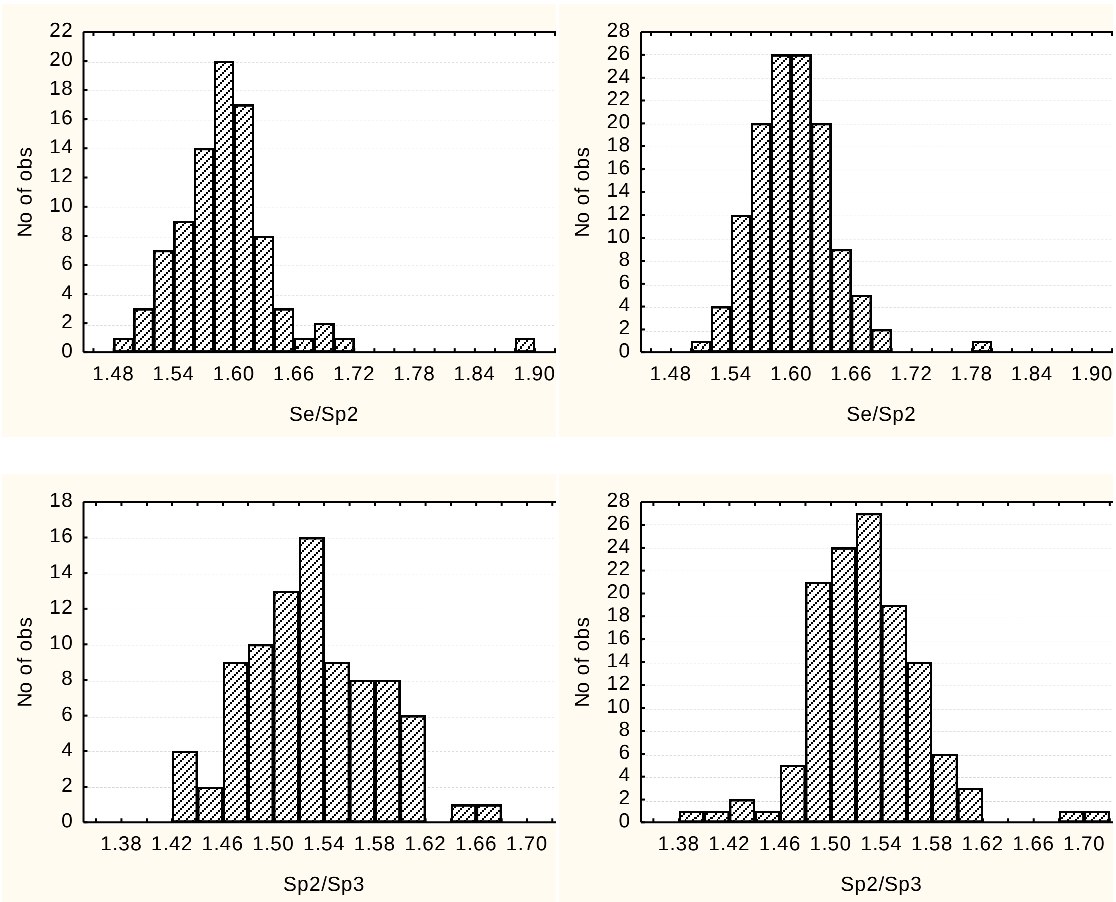


Fig. 4. Variability of morphometric indices of *B. articulatum*: (Sc + Sp + Se)/3Lb – ratio of arithmetic mean value of width of the head, prothorax and elytra to body length, Lp/Sp2 – ratio of prothorax length to its maximum width, Le/Lp – ratio of elytra length to prothorax length; on the left – males (n = 87), on the right – females (n = 126); on X-axis – index value, on Y-axis – number of specimens.



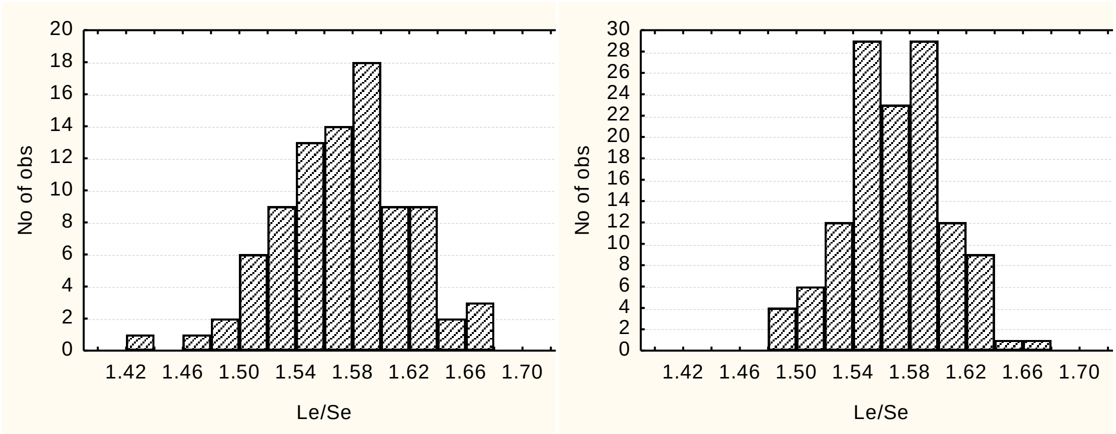


Fig.5. Variability of morphometric indices of *B. articulatum*: Se/Sp2 – ratio of maximum elytra width to maximum prothorax width, Sp2/Sp3 – ratio of maximum prothorax width to its width at back edge, Le/Se – ratio of elytra length to their width; on the left – males (n = 87), on the right – females (n = 126); on X-axis – index value, on Y-axis – number of specimens.

Variability of individual populations of *B. articulatum*

Sexual dimorphism between males and females was absent only in population 5 only (Table 5). Sexual dimorphism in body length was expressed to the maximum extent in populations 7, 8 and 3. Interpopulation differences within specimen groups of the same sex, were not found for body length (Table 5).

Table 5. Variability of body length (Lb) in studied populations of *B. articulatum*

Ecosystem	*n*	male $x \pm SD$, mm	*n*	female $x \pm SD$, mm	*F*	$F_{0.05}$ (*df1*, *df2*)	*P*
1	13	3.681 ± 0.175	11	3.870 ± 0.162	7.46	4.30 (1, 22)	0.012
2	6	3.610 ± 0.151	3	3.855 ± 0.031	7.21	5.59 (1, 7)	0.031
3	6	3.519 ± 0.119	6	3.836 ± 0.063	32.99	4.96 (1, 10)	$1.9 \cdot 10^{-4}$
4	5	3.629 ± 0.168	14	3.784 ± 0.167	3.15	4.45 (1, 17)	0.094
5	8	3.653 ± 0.128	8	3.769 ± 0.311	0.95	4.60 (1, 14)	0.347
6	8	3.752 ± 0.116	15	3.885 ± 0.311	4.61	4.32 (1, 21)	0.044
7	10	3.666 ± 0.092	10	3.964 ± 0.118	39.82	4.41 (1, 18)	$6.0 \cdot 10^{-6}$
8	20	3.653 ± 0.124	39	3.867 ± 0.181	22.42	4.01 (1, 57)	$1.5 \cdot 10^{-5}$
9	11	3.704 ± 0.142	20	3.829 ± 0.145	5.38	4.18 (1, 29)	0.028
F	1.59		1.23		–		
$F_{0.05}$ (*df1*, *df2*)	2.06 (8, 78)		2.02 (8, 117)				
P	0.143		0.289				

Note: see numbers of ecosystems and their brief characteristic in Table 1; x – mean value, SD – standard deviation; F – value of F-criterion of Fisher, P – significance of differences in characteristics

Significant differences between sexes in prothorax length (Lp) were also recorded for populations 8, 3, 7 and, besides, for populations 11 and 1. Interpopulation sexual differences of males (Table 6) on this index are significant (P = 0.018, minimum values are found in populations 3–5 and 8), and no significant differences are revealed in females (P = 0.122).

Table 6. Variability of prothorax length (Lp) of studied populations of *B. articulatum*

Ecosystem	*n*	male *x* ± *SD*, mm	*n*	female *x* ± *SD*, mm	*F*	$F_{0.05}$ (*df1*, *df2*)	*P*
1	13	0.829 ± 0.042[a]	11	0.862 ± 0.030	4.99	4.30 (1, 22)	0.036
2	6	0.827 ± 0.031[a]	3	0.849 ± 0.030	1.05	5.59 (1, 7)	0.341
3	6	0.781 ± 0.040[b]	6	0.842 ± 0.032	8.33	4.96 (1, 10)	0.016
4	5	0.774 ± 0.044[b]	14	0.817 ± 0.041	3.97	4.45 (1, 17)	0.063
5	8	0.774 ± 0.061[b]	8	0.812 ± 0.072	1.26	4.60 (1, 14)	0.281
6	8	0.819 ± 0.034[a]	15	0.845 ± 0.037	2.57	4.32 (1, 21)	0.124
7	10	0.799 ± 0.038[ab]	10	0.841 ± 0.035	6.64	4.41 (1, 18)	0.019
8	20	0.782 ± 0.044[b]	39	0.833 ± 0.037	21.65	4.01 (1, 57)	$2.0 \cdot 10^{-5}$
9	11	0.805 ± 0.035[ab]	20	0.833 ± 0.032	5.24	4.18 (1, 29)	0.030
F	2.50		1.64		–		
$F_{0.05}$ (*df1*, *df2*)	2.06 (8, 78)		2.02 (8, 117)				
P	0.018		0.122				

Note: see Table 5; the same letters designate ecosystems for the males, differences between which are insignificant according to results of Tukey test (P < 0.05).

Sexual differences on width of prothorax between back angles (Sp3) are also significant for populations 8, 7, 6, 1 and 3 (Table 7). However, within the specimen groups of the same sex the pattern is different: males demonstrate insignificant differences (P = 0.178), while they are significant in females (P = 0.008, population 2 is characterized by minimum values).

Table 7. Variability of prothorax width between back angles (Sp3) of the studied populations of *B. articulatum*

Ecosystem	*n*	male *x* ± *SD*, mm	*n*	female *x* ± *SD*, mm	*F*	$F_{0.05}$ (*df1*, *df2*)	*P*
1	13	0.607 ± 0.032	11	0.638 ± 0.017[b]	8.42	4.30 (1, 22)	0.008
2	6	0.585 ± 0.028	3	0.592 ± 0.039[a]	0.33	5.59 (1, 7)	0.583
3	6	0.577 ± 0.027	6	0.613 ± 0.021[ab]	6.44	4.96 (1, 10)	0.029
4	5	0.594 ± 0.010	14	0.610 ± 0.033[ab]	1.08	4.45 (1, 17)	0.313
5	8	0.603 ± 0.024	8	0.632 ± 0.031[b]	4.22	4.60 (1, 14)	0.059
6	8	0.598 ± 0.020	15	0.639 ± 0.033[b]	10.38	4.32 (1, 21)	0.004
7	10	0.606 ± 0.027	10	0.652 ± 0.026[b]	14.87	4.41 (1, 18)	$1.1 \cdot 10^{-3}$
8	20	0.603 ± 0.027	39	0.629 ± 0.028[b]	12.04	4.01 (1, 57)	$1.0 \cdot 10^{-3}$
9	11	0.615 ± 0.027	20	0.633 ± 0.027[b]	3.15	4.18 (1, 29)	0.086
F	1.48		2.74		–		
$F_{0.05}$ (*df1*, *df2*)	2.06 (8, 78)		2.02 (8, 117)				
P	0.178		0.008				

Note: see Table 5; the same letters designate ecosystems for the females, differences between which are insignificant according to results of Tukey test (P < 0.05).

Significant differences between males and females for three analyzed body proportions (Lp/Sp2, Le/Lp and Sp2/Sp3, Table 8, 9 and 10) was not found in any of the populations under study. Within specimen groups of the same sex, differences of morphometric indices between males and females are expressed for the ratio of elytra length to prothorax length (Le/Lp, Table 9) and ratio of maximum prothorax width to its width at the backward edge (Sp2/Sp3, Table 10).

Table 8. Variability of ratio of prothorax length to its maximum width (Lp/Sp2) for the studied populations of *B. articulatum*

Ecosystem	*n*	male *x* ± *SD*	*n*	female *x* ± *SD*	*F*	$F_{0.05}$ (*df1*, *df2*)	*P*
1	13	0.897 ± 0.054	11	0.887 ± 0.027	0.32	4.30 (1, 22)	0.577
2	6	0.897 ± 0.028	3	0.925 ± 0.066	0.91	5.59 (1, 7)	0.372
3	6	0.884 ± 0.033	6	0.880 ± 0.020	0.09	4.96 (1, 10)	0.769
4	5	0.852 ± 0.048	14	0.864 ± 0.046	0.27	4.45 (1, 17)	0.612
5	8	0.841 ± 0.064	8	0.863 ± 0.058	0.49	4.60 (1, 14)	0.494
6	8	0.880 ± 0.047	15	0.866 ± 0.033	0.71	4.32 (1, 21)	0.409
7	10	0.856 ± 0.032	10	0.851 ± 0.042	0.09	4.41 (1, 18)	0.764
8	20	0.859 ± 0.042	39	0.964 ± 0.034	0.24	4.01 (1, 57)	0.628
9	11	0.872 ± 0.028	20	0.872 ± 0.025	0.00	4.18 (1, 29)	0.985
F	1.86		1.74		–		
$F_{0.05}$ (*df1*, *df2*)	2.06 (8, 78)		2.02 (8, 117)				
P	0.078		0.097				

Note: see Table 5.

Table 9. Variability of ratio of elytra length to prothorax length (Le/Lp) of the studied populations of *B. articulatum*

Ecosystem	*n*	male *x* ± *SD*	*n*	female *x* ± *SD*	*F*	$F_{0.05}$ (*df1*, *df2*)	*P*
1	13	2.802 ± 0.118^{ab}	11	2.831 ± 0.120^{c}	0.359	4.30 (1, 22)	0.555
2	6	2.753 ± 0.121^{a}	3	2.893 ± 0.076^{cd}	3.23	5.59 (1, 7)	0.115
3	6	2.829 ± 0.091^{ab}	6	2.845 ± 0.105^{c}	0.07	4.96 (1, 10)	0.791
4	5	2.923 ± 0.065^{b}	14	2.912 ± 0.101^{cd}	0.06	4.45 (1, 17)	0.811
5	8	2.990 ± 0.169^{b}	8	2.933 ± 0.112^{cd}	0.63	4.60 (1, 14)	0.440
6	8	2.881 ± 0.055^{b}	15	2.893 ± 0.104^{cd}	0.10	4.32 (1, 21)	0.759
7	10	2.891 ± 0.095^{b}	10	2.972 ± 0.130^{d}	2.58	4.41 (1, 18)	0.125
8	20	2.927 ± 0.144^{b}	39	2.919 ± 0.110^{cd}	0.06	4.01 (1, 57)	0.811
9	11	2.881 ± 0.096^{b}	20	2.864 ± 0.058^{cd}	0.34	4.18 (1, 29)	0.562
F	3.09		2.03		–		
$F_{0.05}$ (*df1*, *df2*)	2.06 (8, 78)		2.02 (8, 117)				
P	0.004		0.049				

Note: see Table 5; the same letters designate ecosystems for both sexes, differences between which are insignificant according to results of Tukey test (P < 0.05).

Table 10. Variability of maximum prothorax width to its width at back edge (Sp2/Sp3) of the studied populations of *B. articulatum* (n = 213)

Ecosystem	*n*	male *x* ± *SD*	*n*	female *x* ± *SD*	*F*	$F_{0.05}$ (*df1*, *df2*)	*P*
1	13	1.528 ± 0.060	11	1.526 ± 0.031^{ab}	0.01	4.30 (1, 22)	0.922
2	6	1.577 ± 0.076	3	1.539 ± 0.076^{ab}	0.52	5.59 (1, 7)	0.493
3	6	1.533 ± 0.043	6	1.563 ± 0.074^{a}	0.76	4.96 (1, 10)	0.403
4	5	1.531 ± 0.018	14	1.555 ± 0.087^{a}	0.38	4.45 (1, 17)	0.548
5	8	1.526 ± 0.044	8	1.489 ± 0.060^{b}	1.97	4.60 (1, 14)	0.182
6	8	1.559 ± 0.046	15	1.527 ± 0.044^{ab}	2.58	4.32 (1, 21)	0.123
7	10	1.541 ± 0.045	10	1.517 ± 0.022^{ab}	2.31	4.41 (1, 18)	0.146
8	20	1.511 ± 0.048	39	1.533 ± 0.032^{ab}	3.52	4.01 (1, 57)	0.058
9	11	1.502 ± 0.038	20	1.511 ± 0.039^{ab}	0.42	4.18 (1, 29)	0.522
F	1.95		2.03		–		
$F_{0.05}$ (*df1*, *df2*)	2.06 (8, 78)		2.02 (8, 117)				
P	0.064		0.048				

Note: see Table 5; the same letters designate ecosystems for the females, differences between which are insignificant according to results of Tukey test (P < 0.05).

General parameters of variability

The results of PCA analysis illustrate a pattern of influence of ecological factors on the morphological variability of *B. articulatum* specimens which has been shown to be typical (Fig. 6) in similar studies. The sex of the specimen is the leading factor (52.6% of dispersion) defining variability of body size (Fig. 6, 7a, 8). In Fig. 8 males predominantly correspond to positive values of factor 1, and females mostly meet the negative ones. Linear characteristics vary depending on the sex of the specimen (Fig. 7a). Factors 2, 3 and 4 (Fig. 7a, b), jointly accounting for 27.1% of dispersion, reflect variability of the values of the back angles of the prothorax, density of pores on the elytra and contrast of the front and rear light spots on the elytra. Factors 5 and 6 (Fig. 7c) jointly accounting for 11.0% of the sample dispersion are determined by prothorax length and its width at the forward edge, as well as by the contrast of the front and rear spots on the elytra. Factor 7 (accounting for 3.3% of dispersion, Fig. 7d) is determined by prothorax width (Sp1, Sp2 and Sp3), while factor 8 (accounting for 2.1% of dispersion, Fig. 7d) is determined by length of the body (Lb), elytra (Le), prothorax (Lp) and width of elytra (Se). Therefore, the results of PCA analysis confirm the joint variability of linear characteristics of *B. articulatum* and their relationship with the sex of the beetle.

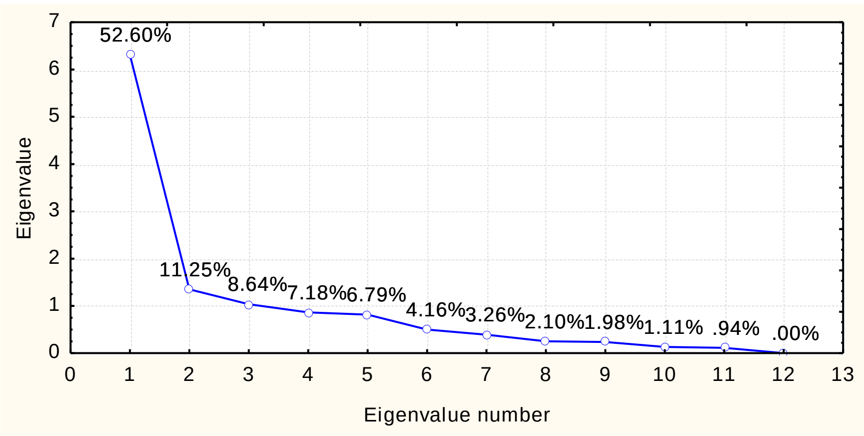


Fig. 6. Eigenvalues of correlation matrix of PCA analysis in the studied populations of *B. articulatum*

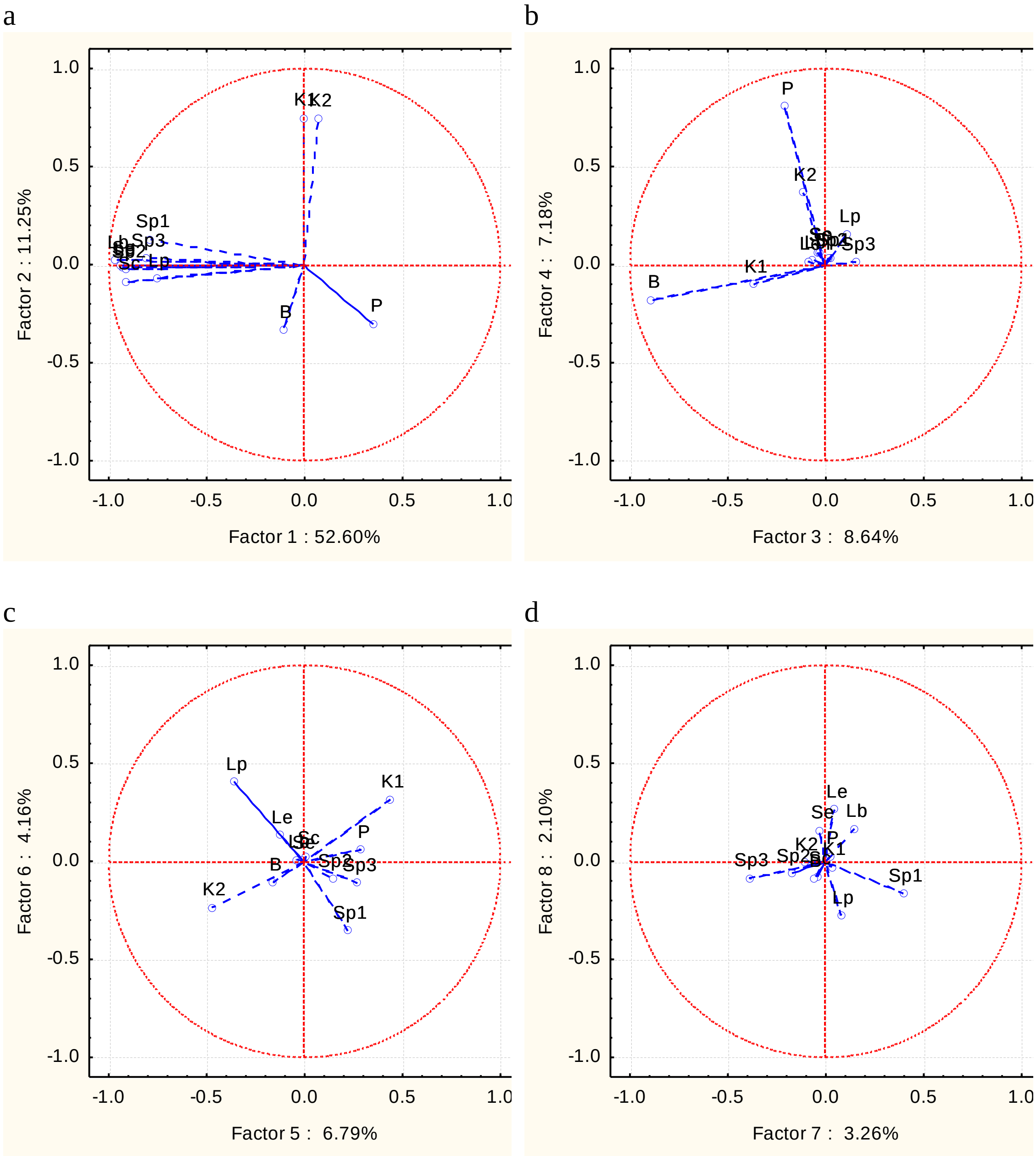


Fig. 7. Results PCA analysis of studied populations of *B. articulatum* in the factor space (a–d) of 8 most significant factors

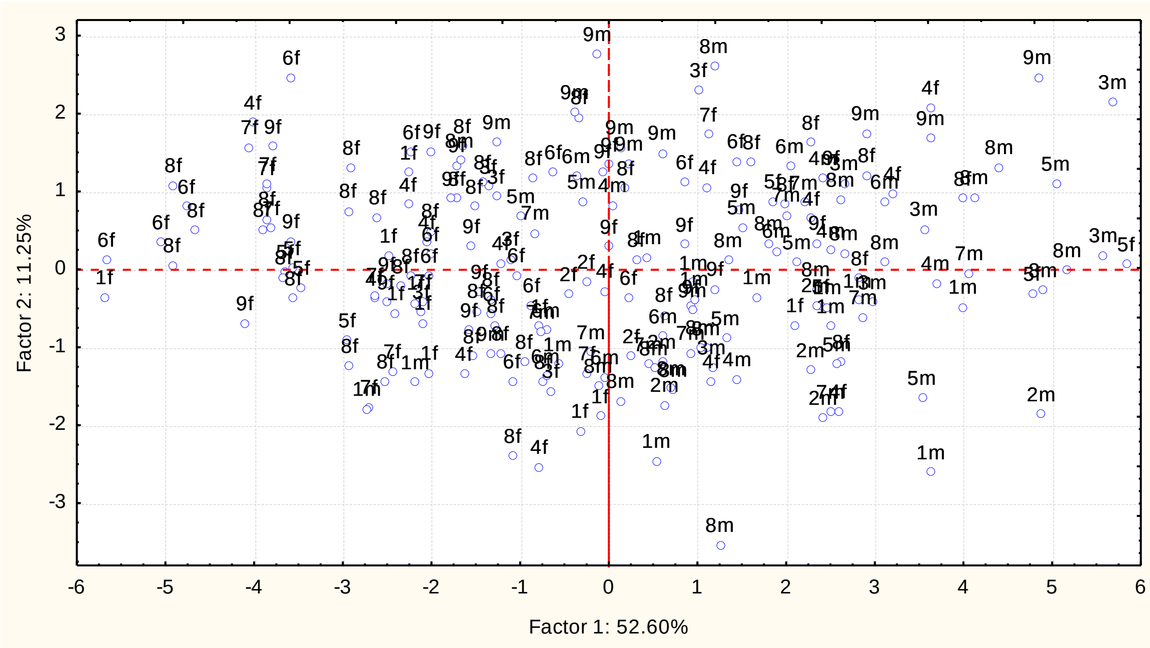


Fig. 8. Distribution of *B. articulatum* specimens in the factor space of factors 1 and 2: m – males (mainly positive values of factor 1), f – females (mainly negative values of factor 1)

Discussion

Data in the literature data on morphometric characteristics of the studied species contains limited information on the body length of *B. articulatum*. The information about *B. articulatum* body length given in various sources is rather lacking in variety: LINDROTH (1974, 1985) – 2.9–3.9 mm, FREUDE et al. (2004) – 3.0–3.9 mm, HABERMAN (1968) – in males 3.32 ± 0.03, in females 3.54 ± 0.04 mm (n = 15), HURKA (1996) – 2.7–3.9 (mean value – 3.4) mm. Mean body length values obtained in our study for the various ecosystems varied from 3.52 ± 0.12 to 3.75 ± 0.12 mm (in males), and from 3.78 ± 0.17 to 3.96 ± 0.12 mm (in females). Compared with the data of HABERMAN (1968) for Estonia, in the steppe zone of Ukraine imagoes of *B. articulatum* are larger by 9.0% (male specimens) and by 9.3% (female specimens).

All authors mention that *B. articulatum* is macropterous species (LINDROTH, 1985; KARPOVA, MATALIN, 1993; HURKA, 1996). All specimens collected by us also belonged to the macropterous form.

The most interesting fact, that ecosystem has no significant influence on the linear characteristics of *B. articulatum* can be attributed to the well-developed wing apparatus, though, flight migration activity of any individual specimen cannot exceed several kilometers (LOVEI, 1996; HENDRICKX et al., 2013). The ecosystems under study are located within a few dozen kilometers from each other, and they belong to basins of different rivers, so it is reasonable to consider the given groups of *B. articulatum* as separate populations.

Stabilization of morphological indices should be characteristic for the center of the range of widely distributed species, while variability should increase on its periphery (SCHLUTER, 2000; SCHÄUBLE, 2004). The species studied by us is not an invasive carabid species, so the variability of its linear morphometric characteristics does not exceed 4.2–4.6%, which is lower than for species extending their range (LAPARIE et al., 2010). Competition with related species has its effect on the morphological variability of populations (OKUZAKI et al., 2010; TALARICO et al., 2011). Long-term variations in environmental conditions may also lead to changing of the range and growth of morphological variability, seasonal fluctuations of reproduction and duration of ground beetle development (LINDROTH, 1972; DEN BOER, 1985; MATALIN 2007; SVANBÄCK et al., 2009; BOBYLIOV et al., 2014).

The Manova results showing the absence of significant influence of ecosystem on body length, elytra length, head width, maximum prothorax width and elytra width, as well as sexual differences for all morphometric characteristics of *B. articulatum*, and absence of spatial heterogeneity of populations in the species under study is compensated by pronounced sexual dimorphism.

Significant variation of prothorax length, prothorax width between the front and back angles, density of pores and degree of contrast of humeral spot on elytra under the influence of ecosystem suggests higher ecological plasticity of the linear dimensions of the prothorax and the colour characteristics of this species.

Body proportions, as opposed to linear characteristics, insignificantly differ in males and females for all six morphometric indices of *B. articulatum* under study, i.e. isometric increase in body size is observed in most *B. articulatum* females. Ecosystem determines variability of half (3 of the 6) studied morphometric indices, compared with 3 of the 8 linear measurements of this species.

Analysis of properties of soil, plant cover and anthropogenic impact in ecosystems under study did not reveal any significant influence on the morphology of *B. articulatum*, however the influence of these factors has been recorded for other species of ground beetles (BLAKE et al., 1994; GIGLIO et al., 2011; SUKHODOLSKAYA, 2013). It is probable that this abundant, widely distributed and ecologically plastic species which is adapted to multi-species communities of ground beetles on the banks of water bodies is far less subject to influence from soil and vegetation, than from its food objects, predators and parasites (ANDERSEN, 1988; MATTHIEU et al., 1997; PAETZOLD et al., 2005; RUEFFLER et al., 2006). Studying of these types of effects on populations of *B. articulatum*, requires much finer experimental methods (HODKINSON and JACKSON, 2005).

The isometric variability revealed in this study (absence of significant changes of morphometric indices) for males and females of *B. articulatum*, is not typical for many other ground beetle species, where elytra in females become longer and wider than in males (BRYGADYRENKO and FEDORCHENKO, 2008; BENITEZ et al., 2010, 2013; SUKHODOLSKAYA and EREMEEVA, 2013; BRYGADYRENKO and RESHETNIAK, 2014). Possibly, this is connected to the smaller body size of the species of ground beetles studied earlier. The results of this study supplement the data obtained earlier for *Bembidion varium* (SLIN'KO et al., 2008) on the influence of population variability of this species of ground beetles.

Morphometric studies allow the norms of plasticity of ground beetle shape and size to be evaluated, in order to reveal the forms of response of individual species to ecologically unsuitable conditions of existence (RAINIO and NIEMELÄ, 2003; FALY and BRYGADYRENKO, 2007; KOTZE et al., 2011). Morphometric studies of ground beetles are undergoing intensively development in several directions, which should lead to deeper understanding of stability of population systems (ALIBERT et al., 2001; SASAKAWA and KUBOTA, 2007; BENÍTEZ, 2013).

Conclusions

Particular interest should be given to further studying of the morphological variability, on the one hand, of locally distributed stenotopic species with a narrow range, which are in need of protection, and on the other hand, of rather "successful" abundant species, whose numbers are not diminishing in changing, contrasting habitat conditions. Concurrent research into variations of the linear characteristics and metric indices for such species will allow the causes and mechanisms of stabilization for the species to be identified with various degree of "success" in both natural and anthropogenically transformed ecosystems.

References

[1] ALEKSANDROVICH, O.R. 2004. Wykaz gatunków – Coleoptera: Carabidae. In: Bogdanowicz W., Chudzicka E., Pilipiuk I., Skibińska E. (eds). Fauna Polski – charakterystyka i wykaz gatunków. MiIZ PAN, Warszawa, 1: 32–42.

[2] ALEKSANDROWICZ, O.R. 2002. Changes in the carabid fauna of Polesie peat-bog due to drainage, ploughing and agricultural development. In: J. Szyszko et al. (Eds) How to protect or what we know about Carabid Beetles. Warsaw Agricultural University Press, Warsaw, pp. 171–184.

[3] ALIBERT, P., MOUREAU, B., DOMMERGUES, J.-L., DAVID, B. 2001. Differentiation at a microgeographical scale within two species of ground beetle, *Carabus auronitens* and *C. nemoralis* (Coleoptera, Carabidae): A geometrical morphometric approach. *Zool. Scripta*, 30(4): 299–311.

[4] ANDERSEN, J. 1988. Resource partitioning and interspecific interactions among riparian *Bembidion* species (Coleoptera: Carabidae). Entomol. Gen. 13(1–2): 47–60.

[5] BENITEZ, H., FUENTE, D.L., VIDAL, M., BRIONES, R., JEREZ, V. 2010. Sexual dimorphism and morphological variation in populations of *Ceroglossus chilensis* (Eschscholtz, 1829) (Coleoptera: Carabidae). *J. Entomol. Res. Soc.*, 12(2): 87–95.

[6] BENÍTEZ, H.A. 2013. Assessment of patterns of fluctuating asymmetry and sexual dimorphism in carabid body shape. *Neotrop. Entomol.*, 42: 164–169.

[7] BENÍTEZ, H.A., AVARIA-LLAUTUREO, J., CANALES-AGUIRRE, C.B., JEREZ, V., PARRA, L.E., HERNANDEZ, C.E. 2013. Evolution of sexual size dimorphism

and its relationship with sex ratio in carabid beetles of genus *Ceroglossus* Solier. *Curr. Zool.*, 59(6): 769–777.

[8] BENÍTEZ, H.A., BRIONES, R., JEREZ, V. 2011. Intra- and inter-population morphological variation of shape and size of the Chilean magnificent beetle, *Ceroglossus chilensis* in the Baker River Basin, Chilean Patagonia. *J. Insect Sci.*, 11: 94.

[9] BLAKE, S., FOSTER, G.N., EYRE, M.D., LUFF, M.L. 1994. Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. *Pedobiologia*, 38: 502–512.

[10] BOBYLIOV, Y.P., BRYGADYRENKO, V.V., BULAKHOV, V.L., GAICHENKO, V.A., GASSO, V.Y., DIDUKH, Y.P., IVASHOV, A.V., KUCHERIAVYI, V.P., MALIOVANYI, M.S., MYTSYK, L.P., PAKHOMOV, O.Y., TSARYK, I.V., SHABANOV, D.A. 2014. Ekologija [*Ecology*]. Folio, Kharkiv 672 pp. (in Ukrainian).

[11] BRYGADYRENKO, V.V. 2003. Fauna zhuzhelic (Coleoptera, Carabidae) Dnepropetrovskoj oblasti [Ground beetle (Coleoptera, Carabidae) fauna of Dnipropetrovsk region]. *Problems of Ecology and Nature Conservation of the Technogenic Region* 3: 78–88 (in Russian).

[12] BRYGADYRENKO, V.V., FEDORCHENKO, D.O. 2008. Morfologichna minlyvist populjacii *Carabus hungaricus scythus* (Coleoptera, Carabidae) v umovakh ostrova Khortytsia (Zaporizka oblast) [Morphological variability of populations of *Carabus hungaricus scythus* (Coleoptera, Carabidae) on Khortitsa Island (Zaporizhzhya region)]. *Vìsn. Dnìpropetr. Unìv. Ser. Bìol. Ekol.*, 16(1): 20–27 (in Ukrainian).

[13] BRYGADYRENKO, V.V., RESHETNIAK, D.Y. 2014. Morphological variability among populations of Harpalus rufipes (Coleoptera, Carabidae): What is more important – the mean values or statistical peculiarities of distribution in the population? Folia oecol., 41: in press.

[14] DEN BOER, P.J. 1985. Fluctuations on density and survival of carabid populations. *Oecologia*, 67: 322–330.

[15] FALY, L.I., BRYGADYRENKO, V.V. 2007. Morfologichna minlyvist osobyn u populjacii *Philonthus decorus* (Coleoptera, Staphylinidae) [Individual morphological variability in *Philonthus decorus* (Coleoptera, Staphylinidae) populations]. *Scientific Bulletin of the Uzhgorod University. Biology*, 20: 66–71 (in Ukrainian).

[16] FREUDE, H., HARDE, K.-W., LOHSE, G.A. 2004. Die Kafer Mitteleuropas. Band 2. Adephaga. 1. Carabidae (Laufkafer). Elsevier Gmbh, Spektrum Akademischer Verlag, Heidelberg, 521 p.

[17] GIGLIO, A., GIULIANINI, P.G., ZETTO, T., TALARICO, F. 2011. Effects of the pesticide dimethoate on a non-target generalist carabid, *Pterostichus melas italicus* (Dejean, 1828) (Coleoptera: Carabidae). *Ital. J. Zool.*, 78(4): 471–477.

[18] HABERMAN, H. 1968. Eesti jooksiklased (Coleoptera, Carabidae). Valgus, Tallinn, 598 pp.

[19] HENDRICKX, F., PALMER, S.C.F., TRAVIS, J.M.J. 2013. Ideal free distribution of fixed dispersal phenotypes in a wing dimorphic beetle in heterogeneous landscapes. Ecology 94(11), 2487–2497.

[20] HODKINSON, I.D., JACKSON, J.K. 2005. Terrestrial and aquatic invertebrates as bioindicators for environmental monitoring, with particular reference to mountain ecosystems. Environmental Management. 35(5): 649– 666.

[21] HURKA, K. 1996. *Carabidae of the Czech and Slovak Republics*. Kabourek, Zlin. 565 p.

[22] KARPOVA, V.E., MATALIN, A.V. 1993. Аннотированный список жужелиц (Coleoptera, Carabidae) юга Молдовы. An annotated check list of carabids (Coleoptera, Carabidae) of Moldova Энтомологическое обозрение 72(3): 570–585.

[23] KIRICHENKO, M.B., KRAVCHENKO, O.M. 2006. An annotated list of the tiger-beetles and ground beetles (Coleoptera: Cicindelidae, Carabidae) of Shatski National Nature Park and adjacent territories. The Kharkov Entomological Society Gazette, 14: 9–18.

[24] KOTZE, D.J., BRANDMAYR, P., CASALE, A., DAUFFY-RICHARD, E., DEKONINCK, W., KOIVULA, M.J., LÖVEI, G.L., MOSSAKOWSKI, D., NOORDIJK, J., PAARMANN, W., PIZZOLOTTO, R., SASKA, P., SCHWERK, A., SERRANO, J., SZYSZKO, J., TABOADA, A., TURIN, H., VENN, S., VERMEULEN, R., ZETTO, T. 2011. Forty years of carabid beetle research in Europe – from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation. ZooKeys 100: 55–148.

[25] KRYSHTAL, O.P. 1956. Ентомофауна ґрунту та підстилки в долині середньої течії р. Дніпро. Entomo-fauna of soil and litter in the valley of Dnipro river midstream. Kyiv State University, Kyiv, 423 c.

[26] KRYZHANOVSKY, O.L., BELOUSOV, I.A., KABAK, I.I., KATAEV, B.M., MAKAROV, K.V., SHILENKOV, V.G. 1995. *A checklist of the ground-beetles of Russia and adjacent lands (Insecta, Coleoptera, Carabidae).* Pensoft Publishers, Sofia – Moscow, 272 p.

[27] LANGOR, D.W., LARSON, D.J. 1983. Alary polymorphism and life history of a colonizing ground beetle, Bembidion lampros Herbst (Coleoptera: Carabidae). The Coleopterists Bulletin 37(4) 365–377.

[28] LAPARIE, M., LEBOUVIER, M., LALOUETTE, L., RENAULT, D. 2010. Variation of morphometric traits in populations of an invasive carabid predator (Merizodus soledadinus) within a sub-Antarctic island. Biol. Invasions 12: 3405–3417.

[29] LINDROTH, C.H. 1972. Changes in the Fennoscandian ground-beetle fauna (Coleoptera, Carabidae) during the twentieth century. Ann. Zool. Fennici. 9: 49–64.

[30] LINDROTH, C.H. 1974. *Handbooks for the identification of British insects. Vol. 4, part 2. Coleoptera, Carabidae*. Royal Entomological Society of London, London, 150 pp.

[31] LINDROTH, C.H. 1985. *The Carabidae (Coleoptera) of Fennoscandia and Denmark*. No. 1. Brill Academic Pub., 497 p.

[32] LOBL I., SMETANA A. 2003. Catalogue of Palaearctic Coleoptera. Vol. 1. Apollo Books, 574 pp.

[33] LOVEI, G.L. 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annu. Rev. Entomol.*, 41: 231–256.

[34] MATALIN, A.V. 2007. Typology of the life cycles of ground beetles (Coleoptera, Carabidae) of the Western Palearctic. *Entomol. Rev.*, 87(8): 947–972.

[35] MATTHIEU, G., MICHEL, L., TANGUY, D. 1997. Relationships between the regional distribution of carabid beetles (Coleoptera, Carabidae) and the abundance of their potential prey. Acta Oecologica 18(4): 465–483.

[36] NETOLITZKY, F. 1942. Bestimmungstabelle der Bembidion-Arten des palaarktischen Gebietes. Koleopterologische Rundschau 28: 29–124.

[37] NETOLITZKY, F. 1943. Bestimmungstabelle der Bembidion-Arten des palaarktischen Gebietes. Koleopterologische Rundschau 29: 1–70

[38] OKUZAKI, Y., TAKAMI, Y., SOTA, T. 2010. Resource partitioning or reproductive isolation: The ecological role of body size differences among closely related species in sympatry. *J. Anim. Ecol.*, 79: 383–392.

[39] PAETZOLD, A., SCHUBERT, C., TOCKNER, K. 2005. Aquatic terrestrial linkages along a Braided-River: Riparian arthropods feeding on aquatic insects. Ecosystems 8(7): 748–759.

[40] RAINIO, J., NIEMELÄ, J. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodivers. Conserv.*, 12: 487–506.

[41] RUEFFLER, C., VAN DOOREN, T.J.M., LEIMAR, O., ABRAMS, P.A. 2006. Disruptive selection and then what? *Trends Ecol. Evol.*, 21(5): 238–245.

[42] SASAKAWA, K., KUBOTA, K. 2007. Utility of external morphometrics for cryptic species identification: A case study of two species in Poecilus 'samurai' (Coleoptera: Carabidae). Appl. Entomol. Zool. 42(3), 353–365.

[43] SCHÄUBLE, C.S. 2004. Variation in body size and sexual dimorphism across geographical and environmental space in the frogs Limnodynastes tasmaniensis and L. peronii. Biological Journal of the Linnean Society 82, 39–56.

[44] SCHLUTER, D. 2000. *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford, UK, 296 p.

[45] SHAROVA, I.C. 1981. Zhiznennye formy zhuzhelic (Coleoptera, Carabidae) [Life forms of ground beetles (Coleoptera, Carabidae)]. Nauka Publishers, Moscow, 360 p. (in Russian).

[46] SLIN'KO, V.O., BRYGADYRENKO, V.V., PAKHOMOV, O.Y. 2008. Morfologicheskaja izmenchivost' *Bembidion varium* (Carabidae, Coleoptera) v uslovijah antropogennogo vozdejstvija [Morphological variability of *Bembidion varium* (Carabidae, Coleoptera) in the conditions of anthropogenic pressure]. *Proceedings of the National Academy of Sciences of Azerbaijan (Biological Sciences)*, 64(5–6): 200–206 (in Russian).

[47] SUKHODOLSKAYA, R. 2013. Intraspecific body size variation in ground beetles (Coleoptera, Carabidae) in urban – suburban – rural – natural gradient. *Acta Biol. Univ. Daugavp.*, 13(1): 121–128.

[48] SUKHODOLSKAYA, R.A., EREMEEVA, N.I. 2013. Body size and shape variation in ground beetle *Carabus aeruginosus* F.–W., 1822 (Coleoptera, Carabidae). *Contemp. Probl. Ecol.*, 6(6), 609–615.

[49] SVANBÄCK, R., PINEDA-KRCH, M., DOEBELI, M. 2009. Fluctuating population dynamics promotes the evolution of phenotypic plasticity. *Am. Nat.*, 174(2): 176–189.

[50] TALARICO, F., BRANDMAYR, P., GIGLIO, A., MASSOLO, A., BRANDMAYR, T.Z. 2011. Morphometry of eyes, antennae and wings in three species of *Siagona* (Coleoptera, Carabidae). *ZooKeys*, 100: 203–214.

[51] TURIN, H., HAECK, J., HENGEVELD, R. 1977. Atlas of the carabid beetles of the Netherlands. North-Holland Publishing Company, Amsterdam, 230 pp.