

Morphometric diversity of *Zabrus morio* (Coleoptera: Carabidae) in relation to sex and altitude in Uzbekistan's mountain ecosystems

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Manuscript received: 10 June 2025. Revision accepted: 27 September 2025.

Abstract. Zokirova DF, Kudratov JA, Khamzaev RA, Khamidova AB, Otakulov B, Urinova G, Zohidova I, Abdllaev E, Rayimova F, Pazilov A, Tursunova S, Bakhrillayeva M, Khalimov FZ. 2025. Morphometric diversity of *Zabrus morio* (Coleoptera: Carabidae) in relation to sex and altitude in Uzbekistan's mountain ecosystems. *Biodiversitas* 26: 4730-4745. *Zabrus morio* is the only representative of the genus *Zabrus* in Uzbekistan, considered a potential pest and widely distributed in mountainous and foothill ecosystems. Studying its morphometric characteristics is important for understanding population traits and adaptive responses. A total of 115 individuals (50 females, 65 males) from 10 sites along an altitudinal gradient were examined. Sites above 1,200 masl were represented by mountain steppes, subalpine meadows, juniper woodlands, and alpine meadows. Sites below 1,200 m were characterized by arid ephemeral-grass steppes, sagebrush-ephemeral steppes, and shrub-steppe communities. Ten morphometric traits were measured using a binocular microscope. Head length was the most variable trait (CV = 10.2%), while elytral width was the least variable (CV = 5.5%); in general, body length parameters were more variable than widths. The strongest correlation was found between elytra length and total body length ($r = 0.93$), while head length and pronotum length were the most independent traits ($r = 0.49$). Females showed greater variability in head dimensions and pronotum length, while males exhibited higher variability in elytral width and interocular distance. In females, elytra length correlated most strongly with total body length ($r = 0.92$), whereas in males, head width closely correlated with pronotum width ($r = 0.95$), which may indicate a relationship between head size and pronotum size. Overall, trait variability decreased with increasing altitude, with only male head length showing a statistically significant reduction. These findings emphasize the adaptive morphometric variability of *Z. morio* depending on sex and ecological conditions, as well as the potential implications of these correlations for the species' ecology and evolution.

Keywords: Altitudinal gradients, coefficient of variation, morphometrics, sexual dimorphism, *Zabrus morio*

INTRODUCTION

Body shape is a fundamental metric of animal diversity, as similarities and differences in morphological traits can be related to sex, geography, and ecological conditions (Lorenz et al. 2017). Morphological variability helps clarify adaptation processes and ecological interactions. Recently, morphometric analysis has become a common approach in studying insect population structure (Bulgarella et al. 2015; Rusynov and Brygadyrenko 2017). Phenotypic traits expressed at the morphometric level reflect both developmental plasticity within populations and adaptive plasticity among populations (Kawano 2016). Morphological variability is also influenced by genetic, biochemical, and physiological factors (Luzyanin et al. 2022a,b). Evidence shows that traits can undergo rapid adaptive changes when exposed to new environmental conditions (Favé et al. 2015; Yadav et al. 2019; Zhang et al. 2023).

Intraspecific trait variation (ITV) arises from adaptive microevolution, plasticity, or sexual dimorphism (Moran et al. 2016; Andereg 2023). ITV is typically measured with

coefficients of variation (Yang et al. 2020) and reflects the capacity of populations to adapt to diverse environments (Muscarella and Uriarte 2016). Traits linked to dispersal, thermoregulation, and fecundity respond rapidly to environmental change, including body size and wing morphology (Montejo-Kovacevich 2021; Kaspari et al. 2024).

Geographic gradients, especially altitude, are often used as proxies for environmental influences on morphology (Stillwell 2010). Yet ground beetles remain understudied in this context (Venn 2007; Koivula 2011). Some species show size reductions in urban landscapes (Sukhodolskaya and Savelyev 2014). Morphometric traits are also affected by soil chemistry, including Mg, Mn, N content, and pH (Sun et al. 2023), or salinity (Komlyk and Brygadyrenko 2020). Variations in head or elytra length have been reported in *Nebria kratteri*, *Pterostichus melanarius*, and *Carabus odoratus* across different elevations and regions (Ananina and Sukhodolskaya 2019; Talarico et al. 2020; Luzyanin et al. 2022). Similar patterns are noted in dung beetles (Bui et al. 2020) and *Helophorus aquaticus* (Polat 2023). Some traits, such as body or abdomen length, tend

to vary most, while head length is often stable, though exceptions occur (Zokirova et al. 2022).

Sexual dimorphism further influences variability. Female morphometrics may respond more strongly to anthropogenic pressures, often with reduced body size (Komlyk and Brygadyrenko 2019). In some beetles, such as tiger beetles, head size differs markedly between sexes (Koçak et al. 2025). Studies on *Bembidion minimum* also showed higher elytra and body length variability in females, although both sexes contribute equally to polymorphism (Parhomenko et al. 2022).

The genus *Zabrus* includes 15 subgenera and 117 extant species (Löbl and Löbl 2017). In Uzbekistan, the only representative is *Zabrus morio*, an eastern Mediterranean wheat beetle (Abdurakhmanov and Klicheva 2010). Although widely recognized as a cereal pest in other regions (Dudarova and Abdurakhmanov 2009; Abdurakhmanov and Kassem 2013), in Uzbekistan, its pest status is not fully established, though it dominates mountain and foothill beetle communities (Khalimov 2020, 2023; Khalimov et al. 2023). The subspecies *Zabrus morio* subsp. *klapperichi* also occurs in gerbil burrows, feeding on seeds (Sazhnev et al. 2024).

Uzbekistan's mountain ecosystems are highly distinctive, with recent faunal surveys highlighting their unique invertebrate diversity (Rakhimov 2023; Kudratov et al. 2024; Mamanov et al. 2024; Naydenov et al. 2025; Medetov et al. 2025). However, morphometric studies are still limited, and results vary among species. More study is essential to understand morphological variability and its ecological or pest-management implications. Morphometric traits can serve as bioindicators of environmental disturbance (Magura and Lövei 2020, 2021). For potential pests such as

Z. morio, this knowledge is especially important for assessing population dynamics and adaptive strategies.

This study, therefore, aims to: (i) identify morphometric trait variations in *Z. morio*, (ii) analyze the correlations between size parameters, (iii) reveal sexual dimorphism related to morphometric features, and (iv) evaluate the influence of altitudinal gradient on morphometric indicators. These objectives provide scientific basis for understanding the population characteristics and potential pest status of *Z. morio* in Uzbekistan's mountain ecosystems.

MATERIALS AND METHODS

Study area

Specimens of *Zabrus morio* were collected from various altitudinal zones across the Zeravshan, Turkestan, and Gissar mountain ranges (Table 1). These three ranges are parts of a single mountain system — the Pamir-Alay. They share similarities in altitudinal zonation, fauna and flora, as well as climatic characteristics. Two primary methods were employed: pitfall trapping and manual collection.

Pitfall traps of the Barber-Geideman type were used for systematic sampling. These consisted of 0.5-L glass jars with an opening diameter of 72 mm, following the methodology described by Karpova (1992). The jars were buried flush with the soil surface to allow beetles to fall in naturally. Traps were arranged in linear transects of 10 units, spaced 5 meters apart. Sampling was conducted every 10-12 days. Additionally, material from the entomological collection of Samarkand State University was used for the research. All beetle specimens were collected during the spring and summer seasons between 2021 and 2024.

Table 1. Sampling sites and their brief characteristics

Name of collection points	Height (masl)	Coordinates	Climate and vegetation of sampling sites
Zarafshan range			
Kamangaron	1,200	39°23'08" N, 67°12'01" E	Warm, dry summers, mild winters; 300-500 mm of precipitation; ephemeral-grass steppe, dry steppe, juniper stands on high slopes.
Tahtakoracha	1,500	39°18'17" N, 66°56'17" E	Moderately warm summers, cold winters; 400-550 mm of precipitation; mountain steppe, juniper forests.
Etty uilli	1,060	39°26'07" N, 66°59'04" E	Dry steppe climate; 300-400 mm of precipitation; ephemeral-grass steppes, shrubs.
Ohaliksay	900	39°30'45" N, 66°52'51" E	Arid low-mountain climate; hot summers, mild winters; sagebrush-ephemeral vegetation.
Hazrati Dovud	1,150	39°29'23" N, 66°37'11" E	Semi-arid climate, moderate precipitation; steppe with sparse shrubs.
Ingichka	900	39°45'46" N, 65°54'13" E	Dry low-mountain climate; hot summers, mild winters; ephemeral-grass steppes, shrub vegetation.
Turkestan range			
Nurata National Reserve	1,050	40°31'24" N, 66°45'30" E	Arid continental climate; 250-350 mm of precipitation; shrub steppes, pistachio groves.
Zhum-zhumsoy	1,700	39°41'12" N, 67°50'58" E	Cooler summers, snowy winters; 450-600 mm of precipitation; juniper forests, mountain meadows.
Gissar range			
Gissar National Reserve: Tamshush River	1,800	38°59'23" N, 67°21'59" E	Cool summers, snowy winters; 500-800 mm of precipitation; juniper forests, alpine meadows.
Gissar National Reserve: Tankhozdaryo River	1,580	38°53'15" N, 67°17'24" E	Moderately warm summers, snowy winters; juniper forests, subalpine meadows.

Data collection

A total of 115 specimens of *Z. morio* (50 females and 65 males) were studied. To assess the impact of the altitudinal gradient on the examined morphological parameters, the study sites were conditionally divided into two groups (A and B). Group A included sites at 900-1,150 meters above sea level (masl) (Etty uilli, Ohaliksay, Hazrati Dovud, Ingichka, Nurata National Reserve), while Group B comprised sites above 1,200 masl (Kamangaron, Tahtakoracha, Zhum-zhumsay, Tamshush River, and Tankhozdayo River). From Group A, 28 females and 37 males were sampled, and from Group B, 22 females and 28 males were studied. Mountain steppes, subalpine grasslands, juniper woodlands, and, in some areas, ephemeral grass steppes and alpine meadows dominate the sites located above 1,200 masl. In contrast, the sites situated below 1,200 masl are characterized by a more arid climate and support ephemeral-grass steppe, sagebrush-ephemeral steppe, and arid shrub-steppe communities. For morphometric measurements, 10 beetle specimens were collected from each site, except for Etty Uilli and Ohaliksay, which included 18 and 17 specimens, respectively. At these sites, the population density of *Z. morio* was considerably higher compared to the other locations.

The study of morphometric parameters was conducted manually using a binocular microscope MVS-9 equipped with a measuring scale, without the aid of software. The following morphometric parameters were measured: HL - head length, HW - head width, DI - distance between the eyes, PL - pronotum length, PW - pronotum width, EL - elytra length, EW - elytra width, and BL - total body length (HL + PL + EL) (Figure 1). Additionally, ratios of different body parts were analyzed: HL/BL, HW/BL, DI/BL, PL/BL, PW/BL, EL/BL, EW/BL, PW/PL, and EW/EL.

Data analysis

The standard Statistica 10 package was used for statistical analysis (Mukhtorova et al. 2024). The arithmetic mean, standard deviation, coefficient of variation, and correlation coefficients between the sizes of different body parts were calculated. Analysis of variance (ANOVA) and principal component analysis (PCA) were used to compare morphometric measurements across samples.

RESULTS AND DISCUSSION

The total body length of *Zabrus morio* individuals ranged from 12.7 to 17.9 mm, with a mean length of 15.6 mm and a coefficient of variation of 5.9%. Variation in the studied morphometric traits within the population was generally low, indicating relative stability of these characteristics. Statistical analysis revealed that head length (HL) was the most variable trait, with a coefficient of variation (CV) of 10.2%. At the same time, elytra width (EW) showed the least variability, with a CV of 5.5% (Table 2).

In general, aside from head length, most body part measurements demonstrated comparable levels of variation. Additionally, length-related traits (HL, PL, EL) exhibited greater variability than width-related traits (HW, PW, EW), suggesting that longitudinal dimensions are more sensitive to environmental or developmental influences in *Z. morio*. It is well known that the sizes of different organs are closely related. However, the strength of the relationship between the sizes of various organs may differ. To assess these connections, a correlation analysis was performed on the morphometric parameters of the measured body parts of the beetles.

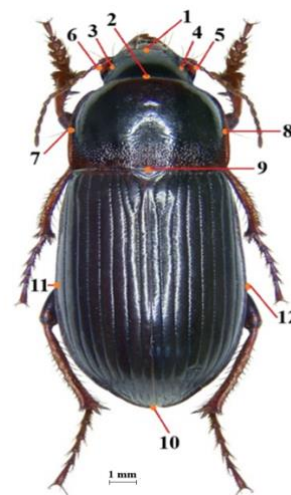


Figure 1. Morphometric measurements scheme: 1-2: head length - HL, 3-4: distance between the eyes - DI, 5-6: head width - HW, 7-8: width of the pronotum - PW, 2-9: length of the pronotum - PL, 9-10: length of the elytra - EL, 11-12: width of the elytra - EW

Table 2. Morphometric parameters of the beetle *Zabrus morio* and their variation

Body parts	Max.	Min.	Arithmetic mean, M	Standard deviation, sd	Standard error, m	The coefficient of variation (Cv, %)
HW	3.6	2.5	3.2±0.21	0.21	0.02	6.6
HL	4.3	2.1	3.3±0.34	0.34	0.04	10.2
DI	2.9	2.1	2.6±0.16	0.16	0.02	6.2
PW	5.6	4.2	5.1±0.3	0.30	0.03	5.9
PL	3.8	2.9	3.5±0.21	0.21	0.02	6.1
EW	7.1	5.2	6.1±0.35	0.35	0.04	5.8
EL	9.8	7.1	8.8±0.52	0.52	0.06	5.9
BL	17.9	12.7	15.6±0.92	0.92	0.10	5.9

Note: HW: head width, HL: head length, DI: interocular distance, PW: pronotum width, PL: pronotum length, EW: elytral width, EL: elytral length, BL: body length. All measurements are in millimeters (mm)

Table 3. Correlation dependence (r) between the sizes of different body parts in *Zabrus morio*

Body parts	HW	HL	DI	PW	PL	EW	EL	BL
HW	1							
HL	0.57	1						
DI	0.77	0.58	1					
PW	0.90	0.63	0.77	1				
PL	0.84	0.49	0.66	0.85	1			
EW	0.84	0.61	0.69	0.86	0.77	1		
EL	0.79	0.53	0.64	0.86	0.78	0.77	1	
BL	0.83	0.78	0.72	0.90	0.84	0.82	0.93	1

Note: HW: head width, HL: head length, DI: interocular distance, PW: pronotum width, PL: pronotum length, EW: elytral width, EL: elytral length, BL: body length. All measurements are in millimeters (mm)

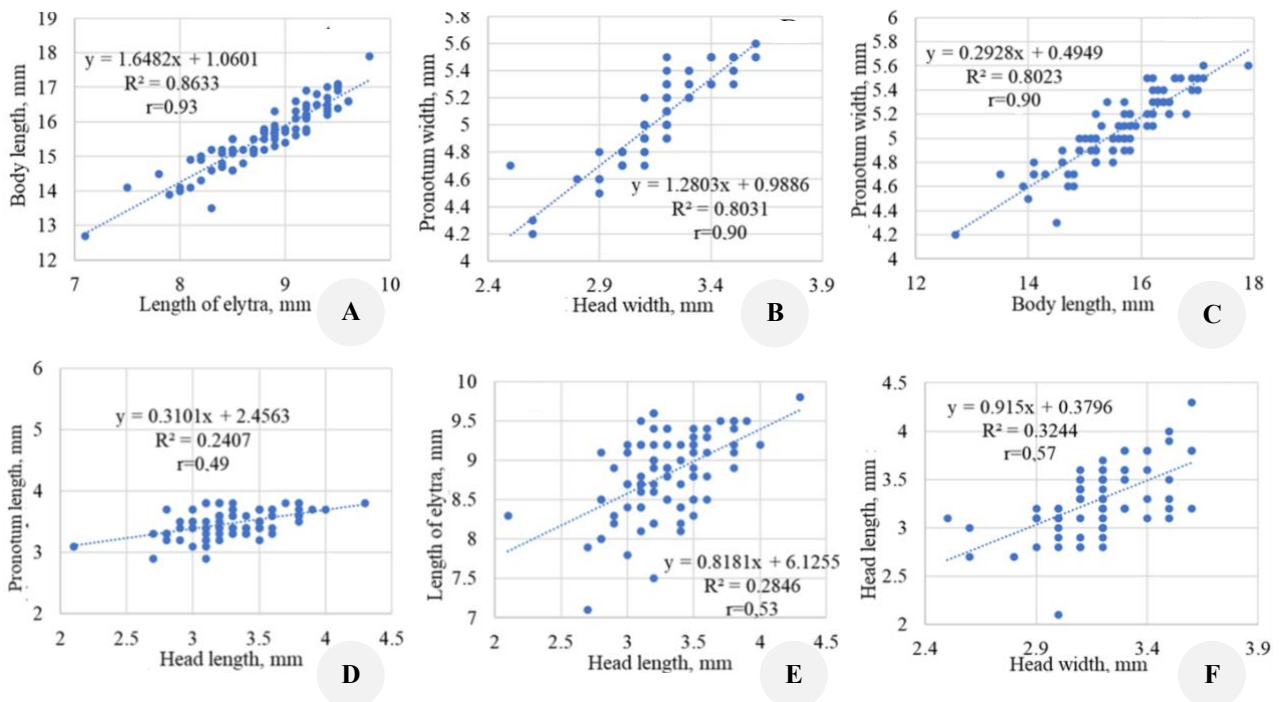


Figure 2. Regression analysis of morphometric relationships among body parts in *Zabrus morio*. A. Body length vs. elytra length, B. Pronotum width vs. head width, C. Pronotum width vs. body length, D. Pronotum length vs. head length, E. Elytra length vs. head length, F. Head length vs. head width. Dotted lines indicate linear regression; regression equations, coefficients of determination (R^2), and Pearson correlation coefficients (r) are shown

The correlation analysis of morphometric parameters in *Z. morio* revealed that most measured body traits are in a strong positive relationship with one another (Table 3; Figure 2). This indicates coordinated growth and proportional enlargement of the main body parts in this species. A strong positive correlation was observed between elytra length (EL) and total body length (BL) ($r = 0.93$), as well as between pronotum width (PW) and head width (HW), and between pronotum width (PW) and total body length (BL) ($r = 0.90$) (Figures 2.A-2.C). Conversely, the lowest correlation was found between head length (HL) and pronotum length (PL) ($r = 0.49$). Weak correlations were also observed between elytra length (EL) and head length (HL), and between head length (HL) and head width (HW) ($r = 0.57$) (Figures 2.D-2.F).

Head parameters

Head width (HW) showed strong positive correlations with interocular distance (DI) ($r = 0.77$), pronotum width (PW) ($r = 0.90$), pronotum length (PL) ($r = 0.84$), elytra width (EW) ($r = 0.84$), elytra length (EL) ($r = 0.79$), and body length (BL) ($r = 0.83$). These results demonstrate that increases in head size are accompanied by proportional enlargement of both the pronotum and elytra, as well as the overall size of the beetle. Head length (HL) showed slightly weaker, though still significant, correlations with DI ($r = 0.58$), PW ($r = 0.63$), EW ($r = 0.61$), and EL ($r = 0.53$). The highest correlation for HL was observed with BL ($r = 0.78$), suggesting that head length is closely linked to overall body size.

Pronotum parameters

Pronotum width (PW) and length (PL) exhibited strong interdependence ($r = 0.85$) and also showed high associations with most other traits. PW positively correlated with EW ($r = 0.86$), EL ($r = 0.86$), and BL ($r = 0.90$). Similarly, PL correlated with EW ($r = 0.77$), EL ($r = 0.78$), and BL ($r = 0.84$). These findings indicate that pronotum dimensions are tightly linked to elytra size and total body length, reflecting a general tendency for proportional enlargement across major body sections.

Elytra parameters

Elytra width (EW) and length (EL) were strongly correlated with each other ($r = 0.77$). In addition, both traits showed high correlations with BL ($r = 0.82$ for EW and $r = 0.93$ for EL), as well as with pronotum and head measurements. The particularly strong relationship between EL and PW ($r = 0.86$) highlights the proportional development of protective body structures.

Overall body length

BL, as an integrative indicator, showed strong associations with nearly all measured traits. The highest coefficients were found for BL-EL ($r = 0.93$), BL-PW ($r = 0.90$), BL-PL ($r = 0.84$), and BL-EW ($r = 0.82$). This suggests that overall body length is primarily determined by elytra and pronotum dimensions. Correlations of BL with head parameters were also high: HW ($r = 0.83$), HL ($r = 0.78$), and DI ($r = 0.72$).

Table 3 demonstrates a high degree of morphometric concordance in *Z. morio*. The strongest correlations were observed among traits associated with the pronotum, elytra, and total body length, while head parameters showed slightly weaker but still significant relationships. This indicates that size variation in this species is driven primarily by changes in thoracic and elytral dimensions, while head proportions remain fairly consistent.

Comparison of morphometric parameters of females and males

No significant differences in overall body size were found between females and males (Table 4). However, differences in the variability of certain morphometric parameters were observed. In females, both the length and width of the head, as well as the length of the pronotum, exhibited higher variability. The highest coefficient of variation (CV) in females was found for head length (10.6%), while the variation in head width and pronotum length was equal at 6.8%. In males, head length was also the most variable trait (CV = 9.9%), but greater variability was observed in the distance between the eyes and the width of the elytra. Overall, head dimensions and pronotum length showed greater variation in females compared to males, whereas males exhibited higher variability in the distance between the eyes and elytra width. Variation in total body length and pronotum width was similar in both sexes.

The analysis of the reliability of differences in morphometric parameters between males and females of *Z. morio* (Table 5) showed that most of the studied traits do not exhibit statistically significant differences between sexes. The obtained F-values in all cases were lower than the critical threshold, and all P-values exceeded 0.05, indicating the absence of pronounced sexual dimorphism in the main morphological parameters.

The traits closest to the significance level were head width (HW) ($F = 3.47$; $P = 0.066$), interocular distance (DI) ($F = 3.59$; $P = 0.062$), and elytra width (EW) ($F = 3.14$; $P = 0.080$). Although these indicators did not reach the conventional level of statistical significance ($p < 0.05$), a tendency toward more noticeable differences can be observed precisely in these parameters. It is likely that head width and elytra width are more closely associated with overall body proportions and may display sex-related features, which, however, do not manifest strongly enough in the analyzed sample.

Table 4. Morphometric parameters of females and males of *Zabrus morio* and their variation

Body parts	Gender	Max.	Min.	Arithmetic mean, M	Standard deviation, sd	Standard error, m	The coefficient of variation, Cv, %
HW	Male	3.6	2.6	3.2±0.20	0.20	0.03	6.3
	Female	3.6	2.5	3.1±0.21	0.21	0.03	6.8
HL	Male	4.3	2.7	3.3±0.33	0.33	0.05	9.9
	Female	4	2.1	3.2±0.34	0.34	0.06	10.6
DI	Male	2.9	2.1	2.6±0.17	0.17	0.02	6.4
	Female	2.8	2.1	2.6±0.15	0.15	0.02	5.8
PW	Male	5.6	4.2	5.1±0.30	0.30	0.04	5.9
	Female	5.5	4.3	5.0±0.30	0.30	0.05	5.9
PL	Male	3.8	2.9	3.5±0.19	0.19	0.03	5.5
	Female	3.8	2.9	3.4±0.23	0.23	0.04	6.8
EW	Male	7.1	5.2	6.1±0.37	0.37	0.05	6.1
	Female	6.5	5.3	6.0±0.31	0.31	0.05	5.1
EL	Male	9.8	7.1	8.8±0.51	0.51	0.07	5.8
	Female	9.6	7.5	8.8±0.53	0.53	0.09	6.0
BL	Male	17.9	12.7	15.7±0.92	0.92	0.13	5.9
	Female	17	13.5	15.5±0.91	0.91	0.15	5.9

Note: HW: head width, HL: head length, DI: interocular distance, PW: pronotum width, PL: pronotum length, EW: elytral width, EL: elytral length, BL: body length. All measurements are in millimeters (mm)

Other traits, such as head length (HL), pronotum width and length (PW, PL), elytra length (EL), and total body length (BL), showed even lower F-values and higher P-values (0.14-0.61). This indicates a complete overlap in the ranges of variation between males and females and further supports the absence of sexual dimorphism in these morphological features.

Thus, the results demonstrate that *Z. morio* does not possess distinct sexual dimorphism in linear morphometric traits. The borderline tendencies noted for head width, interocular distance, and elytra width require further investigation on a larger dataset, which would allow a more precise evaluation of whether these parameters may play a role in sex differentiation of the beetles. Overall, it can be concluded that the morphometric structure of this species is characterized by a high degree of uniformity between sexes, reflecting the similarity of their morphological proportions and, most likely, associated with the ecological adaptations and lifestyle of *Z. morio*.

A similar pattern was observed for the body proportion indices (Table 6). The analysis of morphometric indices in males and females of *Z. morio* showed that the relative sizes of different body parts are generally characterized by low variability and weak sexual dimorphism. The coefficients of variation for most indices did not exceed 7-8%, indicating stability of body proportions within the population.

The index of head width relative to body length (HW/BL) was 0.21 in males with a coefficient of variation of 5.27%, and 0.20 in females with Cv = 4.76%. The differences between sexes were statistically insignificant (F = 1.09; p = 0.299). A similar pattern was observed for the head length index (HL/BL): the values were identical in both sexes (0.21), with slightly higher variability in females (7.76%), but without significant differences.

Indices related to pronotum proportions demonstrated the lowest variability. Thus, PW/BL was 0.33 in males and 0.32 in females, with very low Cv (2.67-2.87%). The ratio

of pronotum length to body length (PL/BL) was the same for both sexes (0.22) with low variability (3.09-3.81%). Such low coefficients of variation indicate that pronotum dimensions in *Z. morio* are among the most stable morphological traits. Elytral proportions (EW/BL and EL/BL) were also similar in males and females. The width of the elytra relative to body length was 0.39 in both groups, while elytral length was 0.56 in males and 0.57 in females. Variability in these indices ranged between 2% and 3.5%. Although differences between sexes were statistically insignificant, there was a slight trend toward larger relative elytral length in females. The interocular distance index (DI/BL) was 0.17 in both groups with similar variability (4.58-4.77%). Despite a relatively higher F value (2.16), the differences did not reach statistical significance (p = 0.145). However, this parameter may be of interest in further studies on larger samples. Analysis of combined indices (PW/PL and EW/EL), reflecting pronotum and elytral proportions, showed almost no differences between males and females of *Z. morio*. PW/PL was 1.45 in males and 1.46 in females, while EW/EL was 0.69 and 0.68, respectively. In both cases, coefficients of variation did not exceed 4%, indicating high conservatism of these traits.

Table 5. Reliability of differences in morphometric parameters of females and males of *Zabrus morio*

Parameters	F	P-value	F critical
Head width	3.46838	0.066091	
Head length	1.713918	0.194091	
Distance between eyes	3.592183	0.061533	
Pronotum width	1.781635	0.185599	3.955961
Pronotum length	2.184702	0.143173	
Elytra width	3.135607	0.080271	
Elytra length	0.259774	0.611628	
Body length	1.101347	0.297017	

Table 6. Variability of morphometric indices of females and males of *Zabrus morio*

Indices	Gender	Index value	Variation, Cv, %	F at F _{0,05} =3.955961	p
HW/BL	Male	0.21±0.002	5.27%	1.094051	0.298612
	Female	0.20±0.002	4.76%		
HL/BL	Male	0.21±0.002	6.03%	0.32837	0.56817
	Female	0.21±0.003	7.76%		
PW/BL	Male	0.33±0.001	2.67%	0.715566	0.400034
	Female	0.32±0.002	2.87%		
PL/BL	Male	0.22±0.001	3.09%	0.931817	0.337196
	Female	0.22±0.001	3.81%		
EW/BL	Male	0.39±0.002	3.55%	1.364396	0.246121
	Female	0.39±0.002	3.46%		
EL/BL	Male	0.56±0.002	1.99%	0.941557	0.334697
	Female	0.57±0.002	2.56%		
DI/BL	Male	0.17±0.002	4.58%	2.164645	0.144999
	Female	0.17±0.002	4.77%		
PW/PL	Male	1.45±0.01	3.29%	0.152561	0.697101
	Female	1.46±0.01	3.51%		
EW/EL	Male	0.69±0.004	4.04%	2.366626	0.127758
	Female	0.68±0.004	4.00%		

Note: HW: head width, HL: head length, DI: interocular distance, PW: pronotum width, PL: pronotum length, EW: elytral width, EL: elytral length, BL: body length. All measurements are in millimeters (mm)

Thus, the results demonstrate that morphometric indices of *Zabrus morio* are characterized by low variability and an absence of statistically significant sexual differences. The highest stability was observed in indices related to pronotum and elytral proportions, which likely reflects their importance in maintaining body shape and adaptation to the environment. Weak trends of sexual differentiation were found in interocular distance and relative elytral length, which require further verification on larger samples.

The correlation analysis revealed noticeable differences in the structure of morphometric trait relationships between males and females of *Z. morio* (Table 7; Figures 3 and 4). In females, head width (HW) showed stronger associations with body size compared to males. For instance, the HW-PW correlation in females was 0.95, whereas in males it was 0.83; HW-BL was 0.90 versus 0.74, respectively. This indicates that in females, head enlargement is proportionally accompanied by an increase in pronotum size and overall body length, while in males this dependence is less pronounced. Head length (HL) played a more significant role in the morphometric organization of males. The HL-BL correlation reached 0.81 in males, compared to 0.73 in females. Moreover, HL showed stronger associations with other traits in males (e.g., HL-PW = 0.66 versus 0.56 in females). Thus, in males, head length contributes more substantially to variation in body size and proportions.

The distance between eyes (DI) exhibited stronger correlations in females. For example, DI-PW was 0.82 in females and 0.68 in males, while DI-PL was 0.71 versus 0.60. This reflects a tighter integration between the ocular region and pronotum in females compared to males. Pronotum dimensions in both sexes were closely linked to body length, but these correlations were generally higher in males. For instance, PL-BL was 0.85 in males and 0.82 in females; PW-BL was equally high (0.90) in both sexes, but PL-HL was higher in males (0.56) than in females (0.40). This suggests that the pronotum in males is more strongly involved in proportional body changes.

Elytral traits also displayed sex-related differences. Elytra length (EL) in males showed a stronger dependence on body length (EL-BL = 0.94) compared to females (0.92). In addition, EL-HL correlation was higher in males (0.60 versus 0.45 in females), underlining the connection between head development and elytra size. In females, however, elytra width was more tightly associated with the pronotum (EW-PW = 0.87 versus 0.85 in males).

Overall, in males, the head (especially its length) and elytra significantly influence overall body size, whereas in females, head width and its integration with the pronotum and elytra are more crucial. These differences emphasize sex-specific patterns of morphological organization: in males, body length depends more on longitudinal measurements, while in females, it is more affected by transverse dimensions.

The influence of the altitudinal zone on morphometric parameters

Morphometric analysis of *Z. morio* populations from two altitudinal belts (Group A: 900-1,150 masl, Group B:

1,200-1,800 masl) showed that the mean values of most traits were similar between samples, although in all measured parameters males from Group A were slightly larger than females, whereas in Group B males were larger than females only in pronotum length and width. However, the coefficient of variation (Cv) in high-altitude populations was lower in many cases (Table 8; Figure 5). The coefficient of variation for seven of the eight parameters was higher in beetles from Group A. The only exception was head length in females, which showed a markedly higher coefficient of variation in Group B. This indicates greater stability of morphometric traits in beetles from mountain habitats compared to lowland ones.

Mean head width (HW) values were nearly identical in all groups (≈ 3.1 - 3.2 mm). Analysis of variance revealed no statistically significant differences either at the species level or between sexes ($p > 0.23$; Table 9). This confirms that HW is a conservative trait unaffected by altitude. Head length (HL) showed the most pronounced effect of the altitudinal gradient. At the species level, the differences were close to statistical significance ($F = 3.72$; $p = 0.056$). In males, a significant difference was found ($F = 7.55$; $p = 0.0078$), with lowland populations showing larger and more variable HL values, whereas highland males had smaller and more stable values. In females, no significant differences were observed ($p = 0.95$).

As for interocular distance (DI), all comparisons were non-significant ($p > 0.10$ - 0.66). The lowest variability was recorded in females of high-altitude populations ($Cv = 3.4\%$), indicating strong stabilizing pressure on this sensory trait.

Although variation in pronotum width and length (PW, PL) was lower in the high-altitude group (≈ 4.6 - 4.9% vs. 6.1 - 7.2% in lowland beetles), no statistically significant differences in mean values were detected ($p > 0.20$ - 0.83).

Table 7. Comparison of correlation coefficients of morphometric traits between females and males of *Zabrus morio*

Pair of traits	Females	Males	Stronger correlation in
HW - PW	0.95	0.83	Females
HW - BL	0.90	0.74	Females
HL - BL	0.73	0.81	Males
HL - PW	0.56	0.66	Males
DI - PW	0.82	0.68	Females
DI - PL	0.71	0.60	Females
PL - BL	0.82	0.85	Males
PL - HL	0.40	0.56	Males
EW - PW	0.87	0.85	Females
EL - BL	0.92	0.94	Males
EL - HL	0.45	0.60	Males

Note: HW: head width, HL: head length, DI: interocular distance, PW: pronotum width, PL: pronotum length, EW: elytral width, EL: elytral length, BL: body length. All measurements are in millimeters (mm)

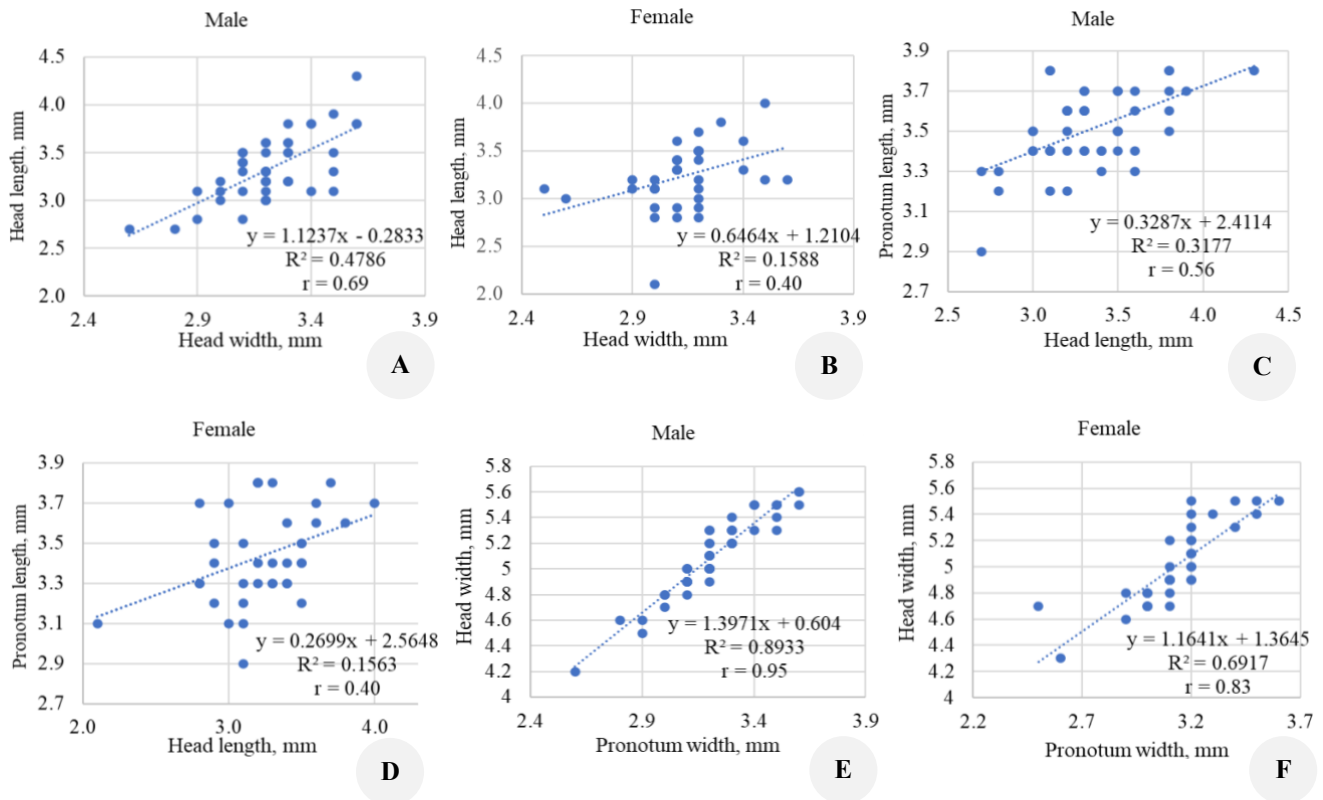


Figure 3. Correlations of morphometric traits in males and females of *Zabrus morio*. A-B. Head length vs. head width, C-D. Pronotum length vs. head length, E-F. Head width vs. pronotum width. Left panels (A, C, E) represent males; right panels (B, D, F) represent females. Dotted lines indicate linear regression; regression equations and coefficients of determination (R^2) are shown

For elytra width (EW), no differences were detected at the species level ($p = 0.39$). In males, a weak tendency toward differentiation was observed ($F = 3.44$; $p = 0.068$), which may reflect a potential influence of altitude. In females, no significant differences were found ($p = 0.24$). No significant differences were found in elytra length (EL) either ($p \approx 0.37-0.99$). Nevertheless, females from Group B showed slightly higher mean values and markedly lower variation ($Cv = 3.7\%$ vs. 6.4% in Group A), suggesting morphological stabilization in the absence of statistically significant mean differences.

Mean total body length (BL) values were almost identical across groups ($\approx 15.4-15.7$ mm), but the coefficient of variation was lower in high-altitude populations ($4.3-4.6\%$) compared to lowland ones ($6.2-6.3\%$). At the same time, analysis of variance confirmed the absence of statistically significant differences ($p = 0.25-0.67$).

Thus, among all traits, significant differences between altitudinal groups were revealed only in head length of males (HL, $p < 0.01$). In elytra width of males (EW) and HL at the species level, a tendency toward significance was observed, but without crossing the $p < 0.05$ threshold. All other traits showed no statistically significant differences in mean values; however, the reduction in the coefficient of variation for most morphometric parameters in the high-altitude group indicates the action of stabilizing selection in mountain ecosystems.

The results of the principal component analysis (PCA) provide a detailed characterization of the structure of morphometric variability in *Z. morio* (Figure 6). On the PC1-PC2 plane, it is clearly visible that individuals from low-mountain populations (group A) and high-mountain populations (group B) are partially separated along the PC1 axis, which primarily reflects overall body size. Traits such as body length (BL), pronotum width and length (PW, PL), as well as elytral dimensions (EW, EL), contribute substantially to PC1. The vectors of these variables are oriented in approximately the same direction and are relatively long, indicating their strong covariation and high contribution to the overall variance. Thus, PC1 can be interpreted as the "axis of general body size".

The second principal component (PC2) explains a smaller portion of the variance but reflects finer differences. The main contribution to PC2 comes from head length (HL), whose vector is clearly oriented along the PC2 axis. This indicates that HL is a key trait that differentiates individuals not only by altitude but also by sex. Indeed, males and females occupy somewhat different positions along PC2: males tend to shift towards positive values, whereas females are located closer to negative values. This pattern confirms the presence of moderate sexual dimorphism in head length. It is worth noting that interocular distance (DI) and head width (HW) show shorter vectors, which indicates their smaller contribution to the overall variability and their relative stability.

Particularly notable is HW, which remains a conservative trait across all groups, a finding that is also supported by the results of the dispersion analysis. PCA demonstrates that morphological variability in *Z. morio* is defined by two main axes: (i) overall body size (PC1), associated with altitudinal differences, and (ii) head length (PC2), related to sexual dimorphism.

Discussion

Different body parts of animals may respond differently to changing environmental conditions (Shelomi 2023). Ornaghi et al. (2023) suggest that the most variable morphometric features in ground beetles are head width and elytra width, especially when habitats change. Other authors report that in many ground beetle species, the most variable traits are body length and abdomen length, while head length tends to be the least variable (Stachewicz et al. 2021). However, our findings differ from these reports. Our study shows that in *Zabrus morio*, the most variable morphometric feature is the head length, while the elytra width is the least variable. Similar data on head parameters were obtained for *Pterostichus melanarius* (Illiger),

although in this species, elytral width also appears to be the most variable trait (Luzyanin et al. 2022). Notably, the length measurements of all studied body parts were generally more variable than their widths.

The present analysis demonstrates a consistently low level of morphological variability in *Z. morio* across all traits examined, as reflected by coefficients of variation (CV) not exceeding 11%. The narrow standard deviations and low standard errors for each trait further indicate a pronounced morphological uniformity within the studied sample. This pattern likely reflects ecological specialization or the action of stabilizing selection. Notably, body length (BL; mean = 15.6 mm, CV = 5.9%) exhibits a high degree of stability, potentially conferring selective advantages associated with habitat-specific constraints or predator avoidance strategies. These findings suggest a morphologically conserved phenotype, yet further investigations involving multiple populations across a range of environmental conditions are essential to determine whether this morphological stability is a species-wide characteristic or a population-specific phenomenon.

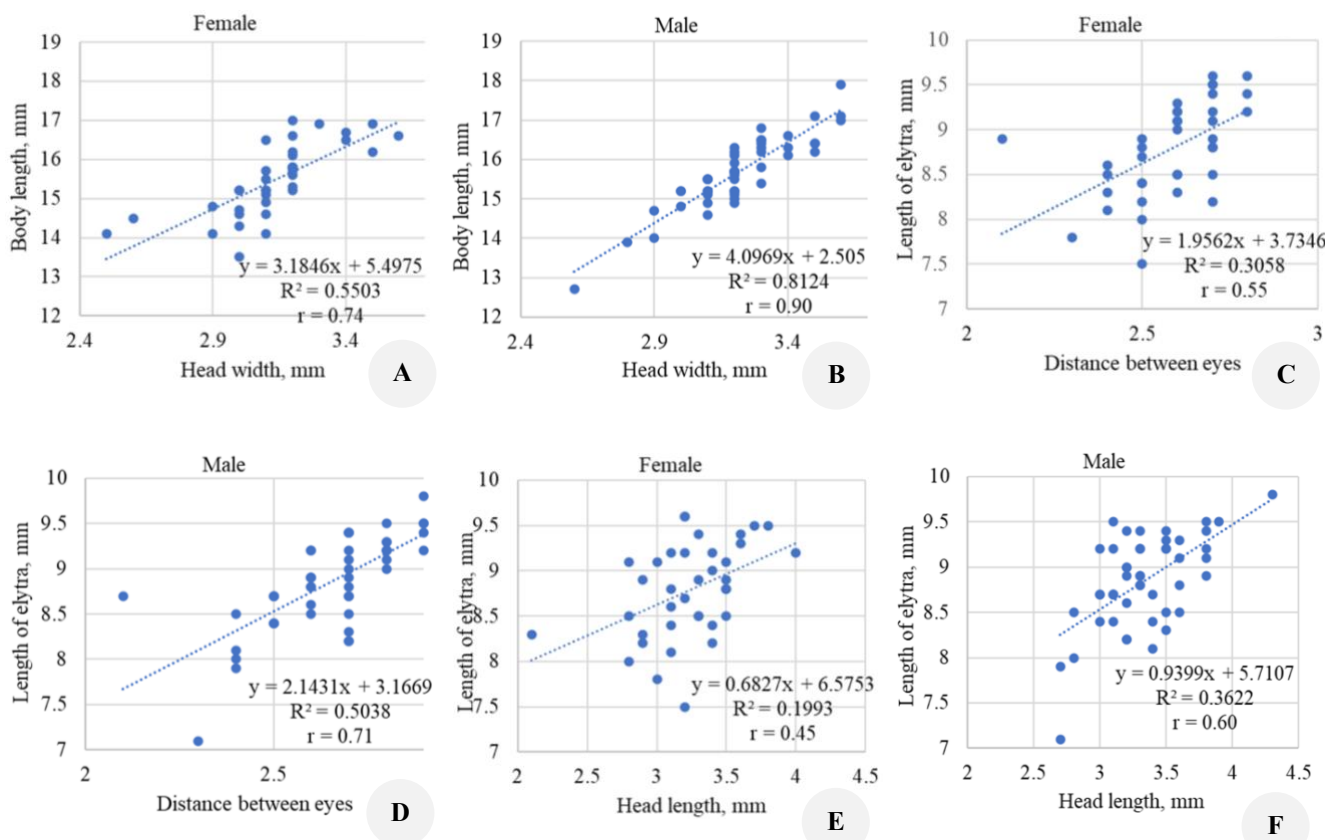


Figure 4. Correlations of morphometric traits in males and females of *Zabrus morio*. A-B. Body length vs. head width, C-D. Elytra length vs. interocular distance, E-F. Elytra length vs. head length. Left panels (A, C, E) represent females; right panels (B, D, F) represent males. Dotted lines indicate linear regression; regression equations and coefficients of determination (R^2) are shown

Table 8. Morphometric parameters of females and males of *Zabrus morio* and their variation at different altitudes

Body parts	Sites	Gender	Max	Min	Arithmetic mean, M	The coefficient of variation, Cv, %
HW	Group A	Male	3.6	2.6	3.2±0.21	6.4%
		Female	3.6	2.5	3.1±0.23	7.4%
	Group B	Male	3.5	2.8	3.2±0.19	5.8%
		Female	3.5	3	3.2±0.15	4.6%
HL	Group A	Male	4.3	2.7	3.4±0.34	10.1%
		Female	3.8	2.1	3.2±0.35	10.7%
	Group B	Male	3.5	2.7	3.2±0.25	7.8%
		Female	4	2.8	3.2±0.39	12.1%
DI	Group A	Male	2.9	2.1	2.7±0.18	6.7%
		Female	2.8	2.1	2.6±0.16	6.3%
	Group B	Male	2.8	2.4	2.6±0.15	5.7%
		Female	2.8	2.5	2.6±0.09	3.4%
PW	Group A	Male	5.6	4.2	5.1±0.31	6.1%
		Female	5.5	4.3	5.0±0.31	6.1%
	Group B	Male	5.5	4.6	5.1±0.25	4.9%
		Female	5.5	4.8	5.0±0.24	4.7%
PL	Group A	Male	3.8	2.9	3.5±0.20	5.7%
		Female	3.8	2.9	3.4±0.25	7.2%
	Group B	Male	3.8	3.3	3.6±0.17	4.8%
		Female	3.7	3.3	3.5±0.16	4.6%
EW	Group A	Male	7.1	5.2	6.2±0.37	6.1%
		Female	6.5	5.3	6.0±0.33	5.5%
	Group B	Male	6.6	5.4	6.0±0.37	6.2%
		Female	6.5	5.7	6.1±0.23	3.8%
EL	Group A	Male	9.8	7.1	8.9±0.53	6.0%
		Female	9.6	7.5	8.7±0.56	6.4%
	Group B	Male	9.5	7.9	8.8±0.47	5.4%
		Female	9.2	8.3	8.9±0.33	3.7%
BL	Group A	Male	17.9	12.7	15.7±0.98	6.2%
		Female	17	13.5	15.4±0.97	6.3%
	Group B	Male	16.4	13.9	15.5±0.72	4.6%
		Female	16.9	14.6	15.6±0.67	4.3%

Note: Group A: points located at 900-1,150 masl, Group B: points located at 1,200-1,800 masl

Table 9. Significance criteria for differences in the morphometric parameters of *Zabrus morio* between sites of groups A and B

Parameters	Gender	F	P-value	F critical
Head width	For the species	0.02917146	0.86468918	3.92507562
	Female	1.47078098	0.23115757	4.04265213
	Male	0.66119472	0.41920092	3.99336492
Head length	For the species	3.71689686	0.05637397	3.92507562
	Female	0.00314808	0.95548885	4.04265213
	Male	7.54519917*	0.00783551	3.99336492
Distance between eyes	For the species	0.32019388	0.57261312	3.92507562
	Female	2.70316924	0.10668378	4.04265213
	Male	0.19231192	0.66249954	3.99336492
Pronotum width	For the species	0.15465297	0.69486886	3.92507562
	Female	0.04738304	0.82860392	4.04265213
	Male	0.46549106	0.49756978	3.99336492
Pronotum length	For the species	2.95693846	0.08824758	3.92507563
	Female	1.62547346	0.20846722	4.04265213
	Male	1.43276291	0.23579887	3.99336492
Elytra width	For the species	0.73889363	0.39183546	3.92507562
	Female	1.39453806	0.24345873	4.04265213
	Male	3.43601248	0.06847275	3.99336492
Elytra length	For the species	0.00010019	0.99203129	3.92507562
	Female	0.82837575	0.36729052	4.04265213
	Male	0.53280163	0.46813689	3.99336492
Total body length	For the species	0.17282726	0.67839967	3.92507562
	Female	0.50868526	0.47916191	4.04265213
	Male	1.31563640	0.25571420	3.99336492

Note: *significant differences

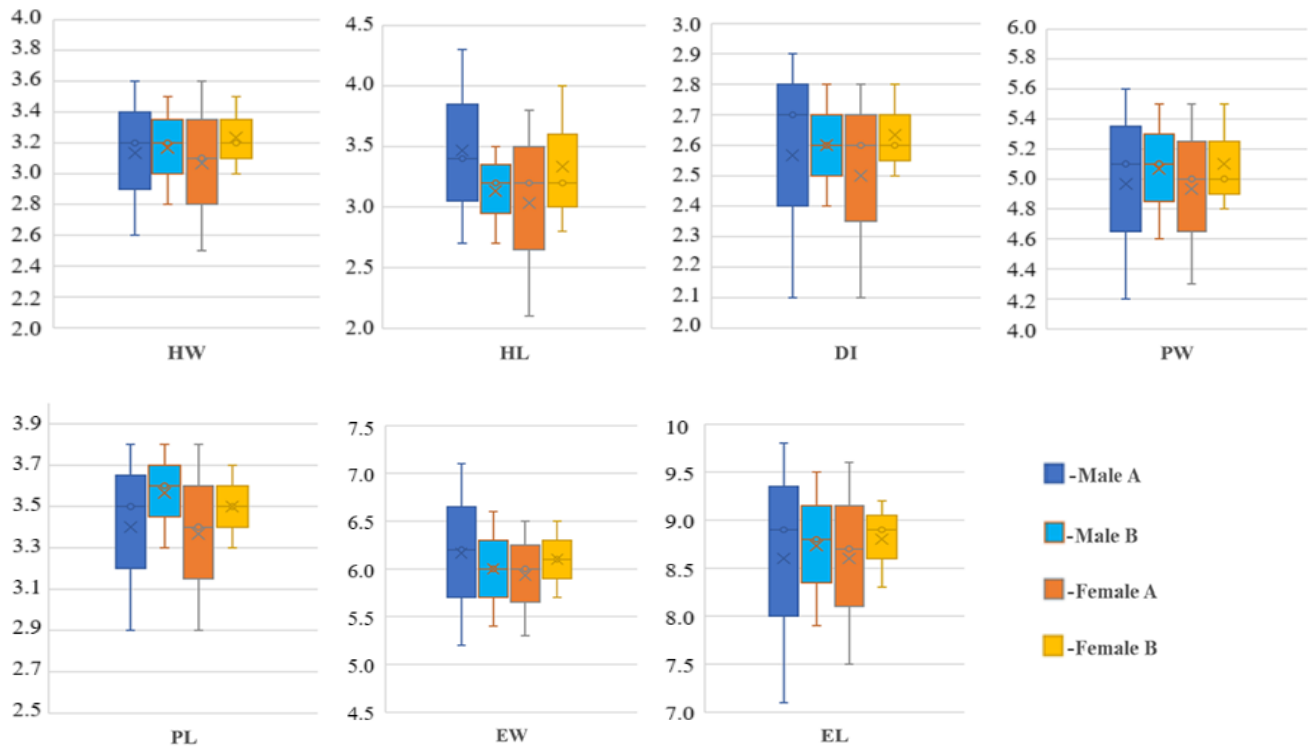


Figure 5. Variation in morphometric traits of male and female *Zabrus morio* collected at different elevations in the mountains. Notes: HW: head width, HL: head length, DI: interocular distance, PW: pronotum width, PL: pronotum length, EW: elytral width, EL: elytral length, BL: body length. Color coding: Male A (dark blue) - males from 900-1,150 masl; Male B (light blue) - males from 1,200-1,800 masl; Female A (orange) - females from 900-1,150 masl; Female B (yellow) - females from 1,200-1,800 masl; unit of measurement: mm

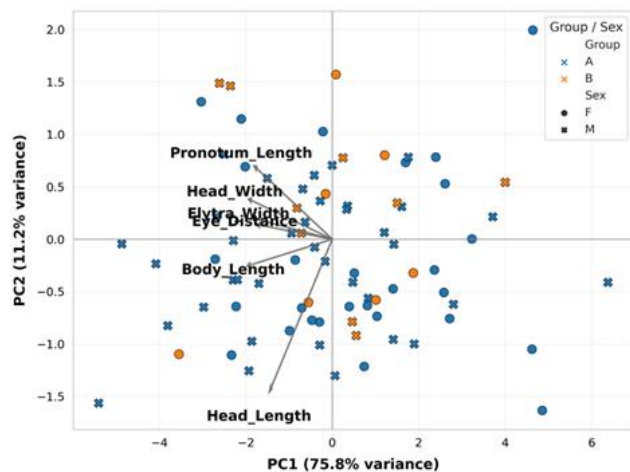


Figure 6. Results of principal component analysis (PCA) based on morphometric data of *Z. morio* (each point represents an individual, where color indicates elevation group (A: 900-1,150 m, B: 1,200-1,800 m), and shape denotes sex). Trait vectors (arrows) indicate the direction and strength of each morphological variable's contribution in the PC1-PC2 space. The longer the vector, the greater the variable's influence. PC1 reflects overall body size variation and most clearly separates individuals by elevation, while PC2—primarily influenced by head length—may reflect sexual dimorphism

The strongest correlation was observed between elytra length and total body length. The most independent traits were head length and pronotum length. This pattern of morphological trait interdependence appears to be characteristic of many ground beetles (Carabidae), as similar findings were obtained in our studies of other species, such as *Acinopus laevigatus* and *Machozetus lehmanni* (Zokirova and Khalimov 2022; Zokirova et al. 2022).

Sexual dimorphism in morphometric parameters varies among beetle species. For example, in the burying beetle (*Nicrophorus vespilloides*), males have wider heads, attributed to more developed jaws (Smith et al. 2024). In *Carabus granulatus*, females are larger than males across all studied traits (Sukhodolskaya and Savelyev 2017). Sexual dimorphism has also been documented in *Nebria germarii* and *Nebria castanea*, where females are significantly larger than males (Ornaghi et al. 2023). This is a common pattern, the ecological significance of which lies in the more intensive biomass accumulation by females, which is essential for egg production (Marshall et al. 2013).

In our study, no pronounced differences in morphometric traits between male and female *Z. morio* were found. However, the pattern of trait variability differed between the sexes. In females, head parameters and pronotum length were more variable compared to males. Males, on the other hand, showed greater variability in elytral width and interocular distance. As noted by Sukhodolskaya (2013),

under the influence of various environmental factors, the pronotum and elytra are more variable in males, whereas head parameters show greater variability in females (Sukhodolskaya 2013). However, in *Nebria castanea* (Bonelli), females exhibited greater morphometric variation in elytral width, which the authors attribute to fluctuations in the abundance of collembolan prey (Ornaghi et al. 2023).

Correlation analysis of morphometric traits in males and females of *Z. morio* revealed a number of features that confirm the presence of sex-specific patterns in the morphological organization of the species. Overall, the correlation structure is similar in both sexes: almost all parameters demonstrate positive associations, which is consistent with data on the high integrativity of morphological traits in ground beetles (Carabidae) (Lövei and Sunderland 1996; Kotze et al. 2011). However, differences are manifested in the strength and character of these relationships.

In females, correlation coefficients are generally higher, indicating more coordinated development of morphological structures. This aligns with findings for other Carabidae species, where females often show less variability in body size and stronger trait correlations (Sukhodolskaya and Saveliev 2014). Such a trend is believed to be connected to the need to maintain stable body proportions, which is crucial for successful reproduction.

Males, in contrast, display greater variability in the structure of correlation networks: some parameters show strong dependencies, while more moderate relationships characterize others. A similar pattern has been reported in beetles of the genus *Carabus* (Sukhodolskaya and Saveliev 2017), where male morphometric traits demonstrated higher variability than those of females. This may reflect the influence of sexual selection, which enhances variability in male traits associated with mobility, competition, and mate searching.

A notable difference exists in which groups of traits form more stable correlation blocks. In females, width-related traits (head, pronotum, and elytra width) develop more consistently, while in males, longitudinal parameters (head, pronotum, and elytra length) are more strongly interconnected. A similar pattern has been observed in other ground beetle species (e.g., *Pterostichus melanarius*), where female elytra and pronotum dimensions varied in a coordinated manner. At the same time, males showed stronger associations among longitudinal parameters (Desender 1986).

Thus, the results show that *Z. morio* females are characterized by a more stable and balanced system of morphological proportions, while males exhibit a more variable correlation structure. These differences fit well into the general picture of sexual dimorphism in ground beetles, where females tend to display conservative traits related to reproduction, while males are more variable, being influenced by behavioral factors and sexual selection.

Due to the high adaptive capacity of arthropods to local environments, the same species undergoes corresponding trait modifications along elevational gradients in order to adapt to varying local conditions (Messier et al. 2017). It

has been shown that carrion beetles (Silphidae) exhibit a decrease in body length with increasing elevation (Nishikawa et al. 2010; Baranovská and Knapp 2018; Ji et al. 2024). A reduction in the average body size of populations with increasing altitude has also been observed in dung beetles and ground beetles (Stanbrook et al. 2021; Sukhodolskaya and Ananina 2015). In *Acinopus laevigatus*, a statistically significant effect of altitudinal zonation on morphometric traits was identified across eight studied parameters (Zokirova and Khalimov 2022).

A comparative analysis of morphometric parameters between *Z. morio* populations from groups A and B revealed no statistically significant differences for the majority of measured traits. According to the results of the analysis of variance (Table 9), F-values did not exceed their respective critical thresholds, and the significance levels (P-values) generally remained above the conventional alpha level of 0.05. These findings indicate a high degree of morphometric similarity between the two populations, both in the overall dataset and when analyzed separately by sex.

The only trait showing a statistically significant difference was head length in males ($F = 7.55$; $P = 0.0078 < 0.05$), where the F-value considerably exceeded the critical value ($F_{critical} = 3.99$). This suggests the presence of meaningful intergroup variation in this trait among males, potentially resulting from local adaptation, sexual selection, or environmentally mediated morphological divergence specific to males. No such differences were observed in females or in the pooled dataset, pointing to a sex-specific pattern of morphological variability.

Other traits, including pronotum dimensions, elytral measurements, and total body length, showed no significant variation between groups under any analytical framework. This supports the overall morphological similarity of *Z. morio* across the studied populations, which may reflect ongoing gene flow between them or convergent phenotypic responses to similar environmental conditions.

It is worth noting that although male head length was the only trait reaching statistical significance, several other traits—such as pronotum length and elytral width in males—exhibited P-values approaching the threshold for significance ($P = 0.068$ – 0.088). These borderline results may indicate emerging trends that could become statistically significant with increased sample sizes.

The present findings contrast with those reported by several authors (Sukhodolskaya and Ananina 2015; Stanbrook et al. 2021; Ji et al. 2024) as well as with our previous results (Zokirova and Khalimov 2022). These discrepancies highlight that altitudinal gradients may exert species-specific influences on body size in ground beetles. For example, studies by Baranovská et al. (2019) and Liu et al. (2024) found that body size in most ground beetle species exhibited no clear response to elevation. In contrast, a subset of species showed size reduction with increasing altitude.

As the results showed, in *Z. morio*, the variation in all studied morphological parameters was lower in high-altitude individuals compared to low-altitude ones (Figure 6). The only exception was head length in females, which exhibited greater variability than in low-altitude individuals.

It seems that head length is one of the most functionally important traits in these beetles, contributing to adaptation to environmental conditions. Head and thorax size in ground beetles has been used to define their ecological niche, as these morphological traits influence their ability to move across different substrate types and access various resources (Fountain-Jones et al. 2015).

The differences revealed by PCA reflect the influence of both ecological and evolutionary factors. The main separation along PC1 is associated with the altitudinal gradient: beetles from low-mountain habitats tend to exhibit larger body sizes, whereas in high-mountain populations, morphological stabilization and reduced trait variation are observed. Such patterns are consistent with Bergmann's rule and its interpretations for insects, where altitude and temperature play key roles in determining body size (Shelomi 2012; Alcantara et al. 2024).

Stabilizing selection in high-altitude environments is likely linked to harsher ecological constraints—lower temperatures, shorter vegetation periods, and limited resources. These conditions promote the formation of more homogeneous morphometric characteristics within populations, a phenomenon previously reported for several beetle species and other insects (Hodkinson 2005).

Head length (HL) has particular importance, as it emerges in our analysis as a key trait defining the second principal component. This parameter showed statistically significant differences between altitudinal groups in males and, as indicated by the PCA, serves as an important factor in sex differentiation. Similar results have been reported in studies of ground beetles and other predatory insects, where head and mandible morphology are closely related to sexual and trophic differences (Budilov 2013).

Overall, the PCA results highlight the dual nature of morphological variability in *Z. morio*: on the one hand, the altitudinal gradient shapes differences in body size; on the other, the expression of sexual dimorphism in certain traits (particularly HL) enhances within-population differentiation. This interplay of ecological and biological factors makes *Z. morio* a convenient model for studying beetle adaptations to mountain ecosystems.

However, it should not be overlooked that, besides geographic gradients, insect morphology is also influenced by factors such as population density (Sugahara and Tanaka 2018), environmental pollution (Li et al. 2024), seasonal fluctuations (Zhang et al. 2023), and biotic pressures such as predation (Wos et al. 2023; Khojakulov et al. 2024). Therefore, more detailed research is required to disentangle the effects of individual factors as well as their combined impact on morphological diversity within insect populations.

In conclusion, this study is the first to reveal unique patterns of morphological variability in *Zabrus morio* from mountain ecosystems of Central Asia. Unlike most previous findings on other ground beetles, head length proved to be the most variable trait in this species, whereas elytral width showed the lowest variability. Furthermore, we demonstrate for the first time that the correlation structure of morphometric traits differs substantially between sexes: females exhibit a more stable and balanced system of body proportions, while males are characterized

by greater variability, likely associated with sexual selection and behavioral factors.

The results indicate that *Z. morio* can be considered a promising model species for studying ground beetle adaptations to altitudinal gradients and ecological constraints. The novelty of this work lies in its integrative approach, combining interpopulation, sexual, and ecological levels of analysis. This has allowed us to identify previously unknown patterns of morphological plasticity and stability, contributing significantly to the development of morpho-ecological research on ground beetles and providing a basis for further studies of microevolutionary processes in insects under the conditions of mountain ecosystems in Central Asia.

ACKNOWLEDGEMENTS

The authors express their gratitude to the staff of the Department of Zoology and the Zoological Museum of Samarkand State University, Uzbekistan, for the provided collection material.

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