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ОРИГИНАЛЬНЫЕ СТАТЬИ

DIFFERENTIATION DEGREE AND DEVELOPMENTAL STABILITY OF *CHIONOMYS GUD* (RODENTIA: CRICETIDAE) BY NONMETRIC CRANIAL TRAITS

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The work describes the results of assessing developmental stability and the degree of differentiation in *Chionomys gud* within Protected Areas of the Central and Western Caucasus. We characterised developmental stability in *Chionomys gud* in different eco-geographical conditions by means of fluctuating asymmetry levels (FA_{nm}) in a series of cranium phenes in four geographical populations. Thus we estimated the effect of environmental factors on FA_{nm} levels. We registered the highest FA_{nm} value for the sample from middle mountains of the Central Caucasus, i.e. the vicinities of the village Elbrus. The environment conditions of the given sample were the most stressful for the species (annual average temperature below 5°C and annual average precipitation below 1000 mm). Two-way ANOVA for factors «annual average temperature» and «annual average precipitation» verified a correlation between FA_{nm} levels and complex effects of the two climatic factors. We evaluated the levels of interpopulation phenetic distances by the analysis of frequencies of phenes of nonmetric cranial traits in *Chionomys gud* populations. Maximum phenetic distances were revealed between geographically distant (over 300 km) populations of the Central and Western Caucasus. The degree of morphological differentiation of the samples from the Central Caucasus, which are apart at the absolute distance of 20–60 km, was less pronounced. Our results suggest that the level of phenetic distances is determined not only by the effect of territorial isolation, but also by climatic peculiarities of a particular locality.

Key words: endemic, fluctuating asymmetry, morphological differentiation, middle mountains, nonmetric bilateral traits, Protected Area

Introduction

Morphological assessment of the state of living organisms which is based on fluctuating asymmetry is one of the commonly used methods for ecological monitoring by both national and foreign scientists (Zakharov, 1987; Gileva & Kosareva, 1994; Zakharov et al., 2000; Gileva & Nokhrin, 2001; Vasil'ev, 2005; Gileva et al., 2007; Vasil'eva et al., 2003; Yalkovskaya et al., 2016; Pankakoski et al., 1992; Markowski, 1993; Graham et al., 2000; Oleksyk et al., 2004; Veličković, 2004; Vishalakshi & Singh, 2008; Allenbach, 2011; Coda et al., 2016, 2017; Benítez et al., 2018). The assessment of the state of animal populations is essential in itself as a parameter of biodiversity (Ryadinskaya & Kokhonov, 2016). In view of the foregoing, it is no less important to study the species adaptation to mountain conditions at different levels of organisation in terms of a latitudinal gradient.

In this context Protected Areas, which are under maximum protection and represent model plots, are of significant interest as test areas for long-term studies and monitoring of the nature population state. According to Zakharov et al. (2000), besides the assessment of anthropogenic impact, it is necessary to monitor natural changes of environment. Corresponding monitoring is essential for the understanding of general trends of environment changes on both local and global scales, and also for integral estimation of the environment quality and state under the combination of effects.

Priority objects under monitoring are sensitive and fragile elements of biological assemblages, i.e. rare and endemic species as their restricted distribution makes them extremely vulnerable to unfavourable natural and anthropogenic effects. Besides, endemics are often small in numbers and found as isolated populations; they prefer specific habitats, and that is probably the reason of their extinction. *Chionomys gud* Satunin, 1909 refers to the abovenamed species. *Chionomys gud* is a typically mountain mammal and endemic within a mountain area in the Caucasus; it is also a stenoecic species which occupies rocky biotopes of middle mountains.

Relevant data on the given species in the Caucasus apply to systematics, ecology, distribution and hematology of the species (Emelyanov et al., 1983; Mezhzherin et al., 1990; Nadachowski, 1991; Kryštufek, 1999; Khulamkhanova et al., 2004; Khulamkhanova & Dzuev, 2005; Okulova et al., 2005, 2007; Khulamkhanova, 2006, 2007; Buzan & Kryštufek, 2008; Sizhazheva & Dzuev, 2011; Dzuev et al., 2011; Yannic et al., 2012; Bannikova et al., 2013; Bottaeva et al., 2016; Balakirev et al., 2017), whereas much less attention has been focused on morphology of the species.

The aim of the present work is to study the levels of fluctuating asymmetry (FA) in nonmetric cranial traits of *Chionomys gud* and reveal environmental factors, which determine FA, and also to assess the relative state of individual populations according to the quality of their habitats under different eco-geographical conditions of the North Caucasus.

Material and Methods

We collected the material in the Western Caucasus within Shaposhnikov Caucasus biosphere reserve (Adygea, the vicinities of the Lago-Naki Plateau) and in the Central Caucasus within the Kabardino-Balkar State High-Mountain Nature Reserve (vicinities of the village Bezengi, Ushtulu Landmark Area) and National Park «Prielbrusye» (vicinities of the village Elbrus) (Fig. 1). According to typification of altitudinal zonal spectra which was developed by Tembotov (Sokolov & Tembotov, 1989; Tembotov et al., 2001), these localities refer to different variants of altitudinal zonation and vary in climatic conditions. The Lago-Naki Plateau refers to the Kuban variant of altitudinal zonation, the village Elbrus – to the Elbrus variant of altitudinal zonation, and the village Bezengi and Ushtulu landmark area – to the Tersk variant of altitudinal zonation. Differences between variants of altitudinal zonation are determined by orographic peculiarities of the given areas, presence and location of mountain ranges which influence on distribution of arid and humid air masses, which, in turn, form typical climatic conditions of each variant of altitudinal zonation. So, air masses of the Mediterranean and Black Sea basin, and of the Atlantic Ocean determine the more humid, warm and mild climate of the Kuban variant of altitudinal zonation. The Elbrus variant is more arid and continental as compared to other variants involved, and that is due to the structure of front ranges. In the Tersk variant, the overall elevation of the front ranges is higher, and they represent a barrier to hot winds of the Caspian Depression, thus reducing the influence of the north-eastern hot winds on mountain landscapes. The Tersk variant of altitudinal zonation is correspondingly characterised by more humid and milder climate compared to the Elbrus variant.

The sampling localities are within the subalpine belt. Table 1 shows certain physiographic sampling localities. As follows from Table 1, within the studied areas the background gamma-radiation level is low (under 0.5 μ Sv/h), and normal for humans as it offers no pathological effect.

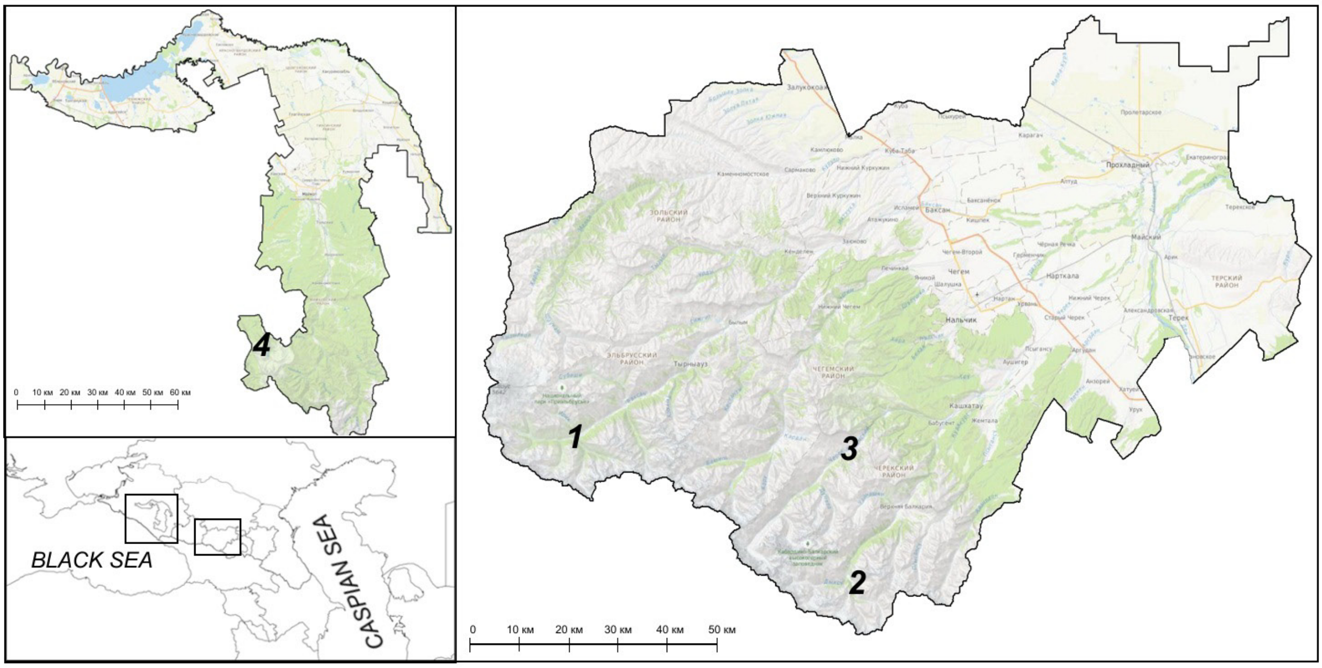

Fig. 1. *Chionomys gud* sampling localities in the Central and Western Caucasus: 1 – village Elbrus; 2 – Ushtulu Landmark Area; 3 – village Bezengi; 4 – Lago-Naki Plateau.

Table 1. Certain climatic characteristics, background gamma-radiation and altitude of *Chionomys gud* sampling localities in the Central (CC) and Western Caucasus (WC)

Locality	Altitude, m a.s.l.	Annual average temperature, °C	Annual average precipitation, mm	Gamma-radiation background, μ Sv/h
1. Village Elbrus (CC)	1800	3.8	917	0.20
2. Ushtulu landmark area (CC)	1737	3.8	1018	0.31
3. Village Bezengi (CC)	1500	5.2	926	0.20
4. Lago-Naki Plateau (WC)	1756	5.7	1485	0.15

We studied 115 *Chionomys gud* skulls and classified them according to 27 phenes of nonmetric threshold traits.

We analysed nonmetric variations of the skull structure under a Stemi 2000C microscope (Carl Zeiss, Germany). For the analysis we applied most of the phenes from the published data (Vasil'ev et al., 1996; Peskov & Emelyanov, 2000; Vasil'eva et al., 2003), and code-named the phenes by means of the system which was developed by Vasil'ev & Vasil'eva (2009).We calculated the correlation of phene expression with animal sex and age and between the phenes from the values of nonparametric Spearman correlation coefficient. Thereafter we excluded several phenes which showed significant correlation with the above factors, from further analysis (Vasil'ev, 2005). Fig. 2 presents the locations of 27 remaining phenes and their description.

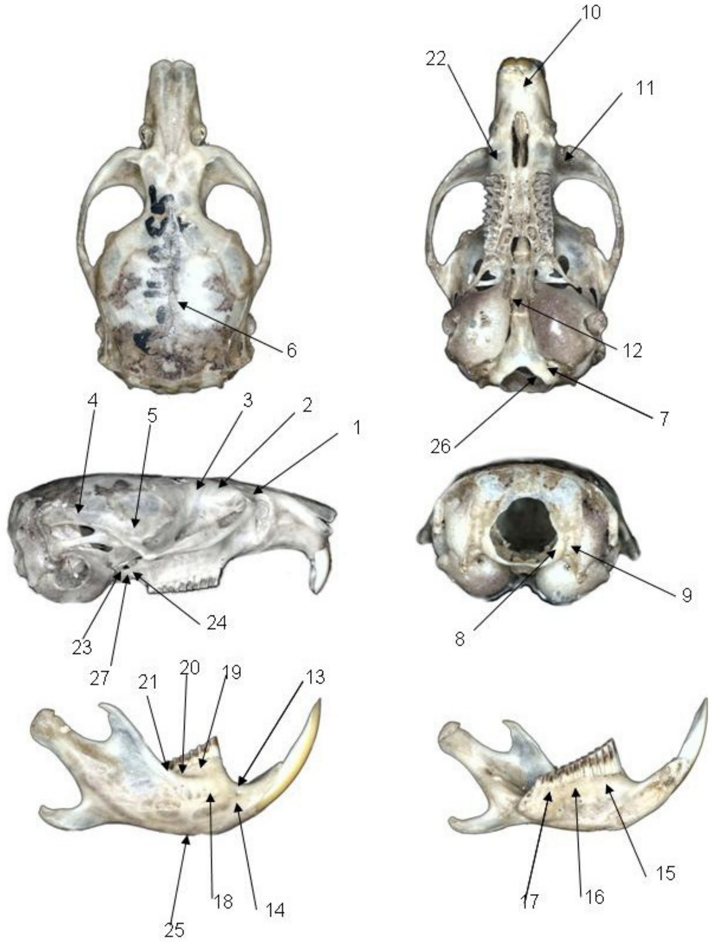

Fig. 2. Phenes of nonmetric cranial traits in *Chionomys gud*: 1 – duplicate preorbital foramina (FPodu); 2 – accessory anterior frontal foramen (FFracan); 3 – the absence of frontal foramen (FFracan (–)); 4 – foramen temporal (FTm); 5 – singular accessory anterior temporal foramen (FTmacan); 6 – ossiculum interparietale (OcPa); 7 – duplicate hypoglossal foramina (FHgdu); 8 – condylar foramen (FCn); 9 – multiplex foramina in the occipital fossa (FFsOc(mx)); 10 – foramen praemaxillare medium (FPmme); 11 –foramen maxillare zygomaticum orale (FMxzmor); 12 – lateral foramina on the ventral surface of the basisphenoid (FBsla); 13 – foramen mentale accessorium anterius (FMtacan); 14 – foramen mentale accessorium posterius (FMtacpo); 15 – multiplex foramina on the lingual side of M_1 alveolus (FMtlgmx); 16 – duplicate foramina on the lingual side of M_2 alveolus (FMblgdu); 17 – singular foramen on the lingual side of M_3 alveolus (FMblg); 18 – foramen massetericum (FMas); 19 – foramen in the region of M_1 on the internal surface (FPC (M_1)); 20 – duplicate foramina in the region of M_2 on the internal surface (FPC (M_2)); 21 – foramen in the region of M_3 on the internal surface (FPC (M_3)); 22 – foramen maxillary (FMx); 23 – foramen columellatum (FCm); 24 – foramen rotundum accessorium inferius (FRtacif); 25 – multiplex foramina on the mandibular body (FOMmx); 26 – lateral hypoglossal foramen (FHgla); 27 – stylus alisphenoideus medialis (Stasme).

We calculated phenetic distances as mean measures of divergence (MMD) within and between populations, and their mean standard deviations (MSD) according to Hartman. The differences were statistically significant at $p < 0.05$ when MMD > 2 MSD. We also used the index of mean measure uniqueness (Vasil'ev et al., 2000).

Assessing phenetic diversity of populations we applied standard indices of resemblance and identity according to Zhivotovskiy (1982). We estimated sampling resemblance by *r* index, and identity index *I* to consider significances of deviation between the pairs of samples. The *I* value distribution is approximately the same as χ^2 value with m-1 degrees of freedom under null-hypothesis which testifies that both samples refer to the united sampled population. We applied the table χ^2 values for assessing differences between the samples.

To determine the level of FA we calculated the average population index of FA in nonmetric skull traits (FA_{nm}) as the average proportion of asymmetrically expressed bilateral traits per individual (Zakharov, 1987; Markowski, 1993).

We processed the results statistically with PHEN 3.0 (Vasil'ev, 1995), PAST (Hammer et al., 2001) and STATISTICA 10 software packages. We estimated the significance of differences between the samples by the nonparametric Kruskal-Wallis test which is an alternative to one-way ANOVA (Vasil'ev, 2005). Two-way ANOVA was applied for revealing the effects of the factors.

Results and Discussion

Sex differences by FA level were insignificant, but in all the samples FA_{nm} was higher in females than in males, suggesting that females are more responsive to the environment. As there were no significant differences, we had to pool female and male samples for further analysis.

Table 2 and Table 3 present higher FA values in the animals from the vicinities of the village Elbrus in the Central Caucasus (CC) and Lago-Naki Plateau in the Western Caucasus (WC).

Among all the studied areas the first sampling locality (village Elbrus) is characterised by severe climatic conditions (annual average temperature of 3.8°C, and annual average precipitation – 920 mm). On the contrary, the second sampling locality (Lago-Naki Plateau) is the warmest and with maximum precipitation (annual average temperature of 5.7°C, and annual average precipitation – 1485 mm).

We registered the lowest FA_{nm} values in *Chionomys gud* from Ushtulu landmark area. As FA_{nm} values serve to make an indirect assessment of the conditions required for animal development, so we can suggest from the data obtained that *Chionomys gud* habitat is more favourable within Ushtulu Landmark Area (Table 1).

On the whole, we revealed statistically significant differences by FA_{nm} level only between a pair of samples Elbrus – Ushtulu (Table 3). The FA_{nm} level in the sample from the vicinity of the village Elbrus shows higher stress load on the individuals.

It is our opinion that in absence of the anthropogenic factor insignificant differences of the value of this parameter in the studied samples are determined by climatic factors. Based on two-way ANOVA we calculated the impact of climatic factors: annual average temperature (factor gradation: below or above 5°C) and annual average precipitation (below or above 1000 mm).

Table 2. Levels of fluctuating asymmetry (FA_{nm}, %) in *Chionomys gud* populations of the Central and Western Caucasus

Samples	N	FA_{nm} ± SE	CV, %
1. Village Elbrus	39	32.0 ± 1.31	25.7
2. Ushtulu Landmark Area	19	26.5 ± 1.21	20.0
3. Village Bezengi	19	27.6 ± 2.00	31.7
4. Lago-Naki Plateau	38	28.9 ± 1.21	25.8

Note: *N* – sample size, SE – standard error, CV, % – coefficient of variation.

Table 3. Significance of differences in the level of fluctuating asymmetry between *Chionomys gud* samples of the Central and Western Caucasus (above the diagonal) according to Tukey-Kramer post hoc pairwise Q-test (q values below the diagonal)

Samples	1	2	3	4
1. Village Elbrus		*	ns	ns
2. Ushtulu landmark area	3.65		ns	ns
3. Village Bezengi	2.92	0.73		ns
4. Lago-Naki Plateau	2.05	1.60	0.87	

Note: significance level of intergroup variations: ns – not significant; *$p < 0.05$.

Table 4 presents that neither the factor «annual average temperature» nor the factor «annual average precipitation» affects FA_{nm} levels. We revealed significant correlation only within interaction of the given factors.

Thus, among the given localities the climatic conditions of the village Elbrus (annual average temperature below 5°C and annual average precipitation less than 1000 mm) present a stressing environment for *Chionomys gud*.

When assessing the FA_{nm} level of the skull in the authochton from the middle mountains of the Caucasus, it is pertinent to show the results which we obtained in the same localities for such a widespread species of the Caucasus as *Apodemus uralensis* Pallas, 1811 (Tembotova & Amshokova, 2018). It is notable that in *A. uralensis* a minimum FA_{nm} accounts for 21.9, and the maximum FA_{nm} is 25.8, whereas in *C. gud* these values are 26.5 and 32.0 correspondingly. It is evident that the FA_{nm} is higher in *C. gud*. An important point is that in *A. uralensis*, under the absence of significant differences between the samples, the maximum FA_{nm} is in the animals from Ushtulu, and the minimum FA_{nm} is in the animals from Bezengi. On the contrary, *C. gud* sample from Ushtulu is characterised by the lowest FA_{nm} value, and its sample from the village Elbrus has the highest FA_{nm} value. We can suggest that ecological preferences of the species determine the revealed interspecific differences, and correspondingly, different responses to the same environment.

The second task of the work is to assess the degree of phenetic differentiation in *C. gud* samples of different geographical distance. Such an assessment is also essential as we conduct the studies on an authochton of middle mountains and a stenoecic species which occupies rocky habitats of subalpine meadows. To do this, we calculated mean phenetic distances between the samples. The comparison of individuals by sex revealed a slight, but statistically significant difference ($p < 0.05$) only in two populations from the vicinities of the village Elbrus and Lago-Naki Plateau. As there were no significant differences in other populations, we pooled male and female samples for further analysis. Table 5 and Table 6 present the results of interpopulation comparison.

The comparison of three *C. gud* samples from the Central Caucasus showed that distances varied from 0.034 to 0.108. We revealed a minimum distance (MMD = 0.034 ± 0.016, $p < 0.05$) between the populations of Ushtulu – Bezengi, which are about 20 km apart (absolute distance) in two adjacent gorges (Fig. 1). The differences between the given samples were registered in the frequency of 4 traits out of 27. Table 6 shows that the animals had a high frequency of traits 2 and 26 from the vicinities of the village Bezengi; a high frequency of traits 9 and 15 was found in the animals from Ushtulu landmark area.

We revealed a maximum distance MMD = 0.108 ± 0.012 ($\chi^2 = 101.8$; df = 26; $p < 0.001$) between the samples of Elbrus – Bezengi, which are from two adjacent gorges (Fig. 1) and about 50 km apart. The given samples were distinguished in the frequency of 8 traits (FFracan, FTmacan, FCn, FOcsimx, FMblgmx, FMas, FPC (M_3), Stasme) (Table 6). We registered seven traits, excepting FFracan, significantly often in the animals from the village Elbrus. The similar comparison of the animals from the vicinities of the village Elbrus with the animals from Ushtulu showed significant differences in the frequency of 4 traits, i.e. FTmacan, FCn, FPC (M_3), FMx, which were more often in the sample from the village Elbrus (Table 6). In this case the phenetic distance was MMD = 0.042 ± 0.012, $p < 0.001$, and the samples were 62 km apart.

Table 4. Results of two-way ANOVA for the effect of climatic factors (annual average temperature and annual average precipitation) on FA_{nm} levels in *Chionomys gud* populations of the Central and Western Caucasus

Factor (variation source)	Sum of squares	Number of degrees of freedom, df	Mean square	Fisher test, *F*	Significance level, *p*
Temperature (A)	86.39	1	86.39	1.478	0.227
Precipitation (B)	174.5	1	174.5	2.987	0.087
Factor interaction (A × B)	320.8	1	320.8	5.49	0.020
Within-group variation	6487	111	58.44	–	–
Total variation	6985	114	–	–	–

Table 5. Phenetic distances (MMD) (superdiagonal matrix), mean standard deviations (MSD) (subdiagonal matrix), and values of mean measure of uniqueness (MMU) between *Chionomys gud* samples of middle-mountains in the Central and Western Caucasus

Samples	1	2	3	4	MMU
1. Village Elbrus (CC)	–	0.042	0.108	0.084	0.078
2. Ushtulu landmark area (CC)	0.012	–	0.034	0.096	0.057
3. Village Bezengi (CC)	0.012	0.016	–	0.148	0.097
4. Lago-Naki Plateau (WC)	0.008	0.012	0.012	–	0.109

Table 6. Frequencies of cranial nonmetric variations (phenes) in *Chionomys gud* populations of the Central and Western Caucasus, %

Samples / Nonmetric variations (phenes)	1	2	3	4	1–2	1–3	1–4	2–3	2–4	3–4
	N = 78	N = 38	N = 38	N = 76	χ^2					
1. FPodu	5.13	7.89	13.2	6.76						
2. FFracan	3.85	2.63	15.8	14.5		*	*	*	*	
3. FFracan (-)	88.5	76.3	86.8	92.1					*	
4. FTm	80.8	89.5	84.2	80.3						
5. FTmacan	83.3	63.2	44.7	95.9	*	***	*		***	***
6. OcPa	5.13	0	0	2.6						
7. FHgdu	35.9	31.6	36.8	14.5			*		*	**
8. FCn	71.8	29.0	42.1	65.8	***	**			***	*
9. FOcsimx	55.1	39.5	13.2	32.9		***	**	*		*
10. FPmm*	84.6	84.2	68.4	89.5						
11. FMxzmor	42.3	47.4	36.8	35.5						
12. FBsla	25.6	29.0	15.8	36.0						*
13. FMtacan	6.41	0	0	2.63						
14. FMtacpo	41.0	26.3	39.5	5.26			***		**	***
15. FMblgmx	35.9	39.5	10.5	32.9		**		**		*
16. FMblg(M_2)	23.1	13.2	23.7	35.5					*	
17. FMblg(M_3)	32.1	34.2	29.0	43.4						
18. FMas	71.8	65.8	47.4	55.3		*	*			
19. FPC(M_1)	25.6	15.8	29.0	25.0						
20. FPC(M_2)	37.2	29.0	31.6	47.4						
21. FPC(M_3)	39.7	18.4	10.5	31.6	*	***				*
22. FMx	20.5	2	7.89	2.6	**		***			
23. FCm	16.7	13.2	21.1	21.1						
24. FRtacif	29.5	23.7	18.4	15.8			*			
25. FOMmx	55.1	60.5	63.2	46.1				*		
26. FHgla	6.41	5.3	13.2	31.6			***		***	*
27. Stasme	96.2	97.4	84.2	98.7		*				**

Note: 1 – vicinities of village Elbrus, 2 – Ushtulu Landmark Area, 3 – vicinities of village Bezengi, 4 – Lago-Naki Plateau. N – number of the studied sides of the skull; significance levels of intergroup differences: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

From the above, we can suggest that in the Central Caucasus the factor of geographical distance (absolute distance of 20–60 km) has a slight effect on the phenetic distance between the samples, although three samples are from different gorges.

We estimated the effect of geographical distance (absolute distance of 240–310 km) by comparison of *C. gud* samples of the Central Caucasus with samples of the Western Caucasus. The data obtained are indicative of significant isolation of the Lago-Naki sample from all the samples of the Central Caucasus (Table 5). We found a maximum phenetic distance MMD = 0.148 ± 0.012 (χ^2 = 127.0; df = 26; $p < 0.001$) by comparison the Lago-Naki population with the Bezengi population. In this case we registered differences in the frequency of 10 traits, 8 of which were more often in the Lago-Naki population. Phenetic distances between pairs of samples from Lago-Naki – village Elbrus and Lago-Naki – Ushtulu were less significant, and accounted for MMD = 0.084 and MMD = 0.096, correspondingly. Compared to the samples of the Central Caucasus, the sample of the Western Caucasus is characterised by a higher frequency of the following traits: FFracan (–), FTmacan, FBsla, FMblg (M_2), FMblg (M_3), FPC (M_2), FHgla (Table 6). The correlation analysis between phenetic distances of all four samples, one of which is from the Western Caucasus, and with an absolute distance of 20–300 km, showed a mean positive correlation (Spearman 0.54), but the value is insignificant.

The comparison of populations by index of resemblance and criterion of identity (Table 7) is consistent with the data obtained. We revealed maximum values of index of resemblance between the populations of the village Elbrus–Ushtulu and Ushtulu – Bezengi in the Central Caucasus. It is evident that values of index of resemblance gradually decrease under comparison of the populations from the Central Caucasus with the population from the Western Caucasus.

The criterion of identity revealed significant differences in all pairwise comparisons, and maximum values, which essentially exceeded the table χ^2 values (Table 7), were registered under comparison of the Central Caucasus populations with the Western Caucasus population.

Table 7. Values of index of resemblance *r* (superdiagonal matrix) and criterion of identity *I* (subdiagonal matrix) for *Chionomys gud* samples in the Central and Western Caucasus

Samples	1	2	3	4
1. Village Elbrus	–	0.988 ± 0.003	0.979 ± 0.004	0.985 ± 0.003
2. Ushtulu Landmark Area	61.4 ($p < 0.001$)	–	0.988 ± 0.003	0.981 ± 0.003
3. Village Bezengi	109.4 ($p < 0.001$)	48.9 ($p < 0.01$)	–	0.975 ± 0.004
4. Lago-Naki Plateau	120.7 ($p < 0.001$)	99.7 ($p < 0.001$)	131.8 ($p < 0.001$)	–

The assessment of correlation between presence/absence of qualitative cranial traits and climatic factors (temperature and precipitation) of *C. gud* habitat is as follows: there is a significant negative correlation of moderate strength between temperature and precipitation. Fig. 3 presents the strength level of significant correlation ($p < 0.05$) between expression of all threshold cranial traits of four samples and climatic characteristics. The presence of 41% of traits correlates with temperature factor (strength of the relationship is moderate for 7 traits, and it is weak for 4 traits). 33% of the traits correlates with precipitation (strength of the relationship is maximum for 1 trait, it is strong for 1 trait, it is moderate for 1 trait, and it is weak for 6 traits).

We also assessed the differences of phene presence in the gradient of temperature and precipitation. There were no differences in the proportion of phenes registered in less humid habitats of *C. gud* (village Elbrus and village Bezengi, 47% of phene presence) and more humid habitats (Ushtulu and Lago-Naki Plateau, 48% of phene presence). The proportion of phenes in colder biotopes (village Elbrus and Ushtulu, 51% of phene presence) is significantly higher ($p = 0.005$) than in warmer habitats (village Bezengi and Lago-Naki Plateau, 43% of phene presence).

Conclusions

The studies on population differentiation of *Chionomys gud* in the Central and Western Caucasus by means of phenetics present the following data.

The range of phenetic distances in *C. gud* accounted for 0.034–0.148. In the Central Caucasus, despite the fact that all three samples are from three parallel gorges, the distance factor has a minimal effect on the phenetic distance between the samples (absolute distance of 20–60 km). The phenetic distances are more pronounced between geographically distant (over 300 km) populations of Lago-Naki Plateau and the village Elbrus. According to the published data, such values of phenetic distances are common in populations which were isolated by landscape-ecological barriers over prolonged periods (Vasil'ev et al., 2000).

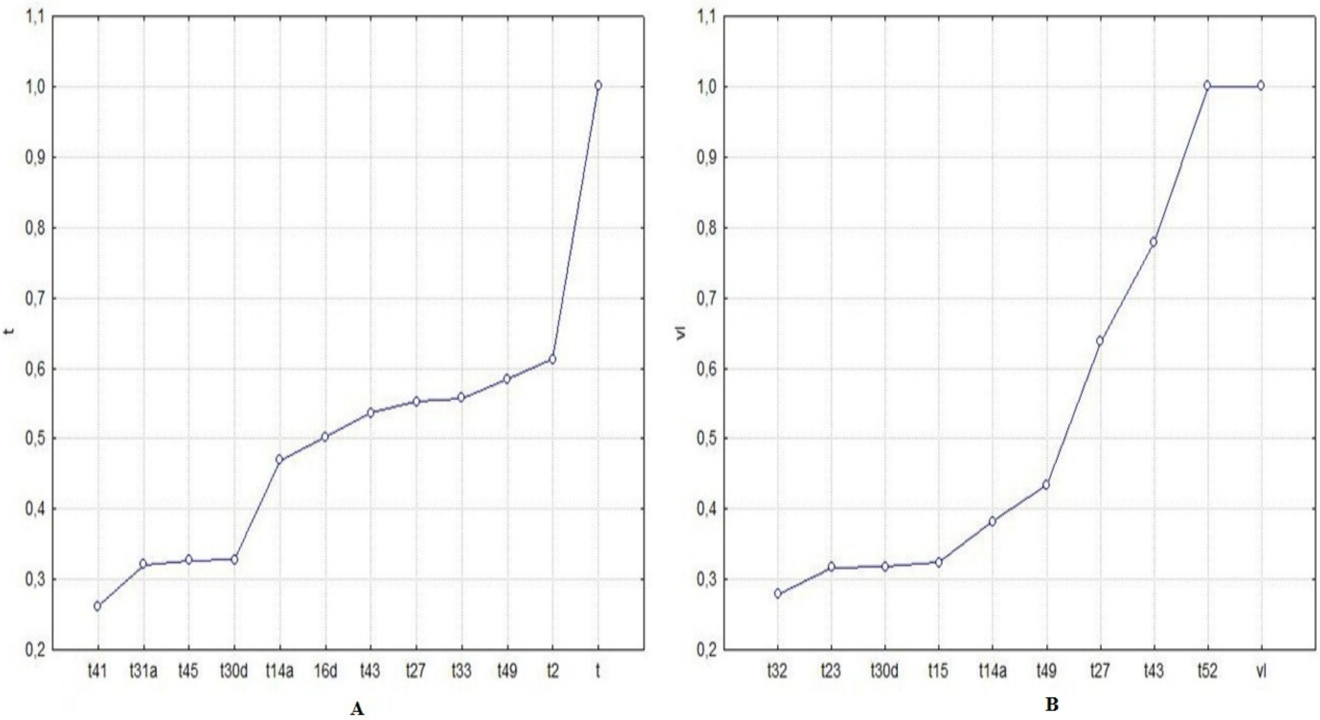

Fig. 3. Gamma correlation of phenes of nonmetric cranial traits with temperature (A) and precipitation (B) in *Chionomys gud* populations of the Central and Western Caucasus.

The correlation analysis of phenetic distances of four samples which are located 20–300 km apart, and one of them is from the Western Caucasus, revealed the presence of a moderate positive correlation (Spearman 0.54), although it was insignificant.

However, we suppose that not only the factor of territorial isolation but also climatic characteristics exert influence on the level of phenetic distances. So, the village Elbrus has more severe climatic conditions with an annual average temperature below 5°C and an annual average precipitation below 1000 mm, whereas Lago-Naki Plateau is characterised by an annual average temperature above 5°C and an annual average precipitation above 1000 mm. The data on fluctuating asymmetry provide support for this view.

The level of fluctuating asymmetry in *C. gud* populations from different eco-geographical conditions of the Caucasus accounted for 26.5–32.0%, which is significantly higher than in *Apodemus uralensis* (21.9–25.8%) (Tembotova & Amshokova, 2018), which is a widespread species of the North Caucasus, and the middle mountains of the Central Caucasus represent stress conditions for it.

We revealed the highest values of fluctuating asymmetry in *C. gud* from the village Elbrus, suggesting that development of animals in the given population is under definite stress. The climate of the village Elbrus is the most severe of all the studied localities. Two-way ANOVA showed that neither the annual average temperature nor the annual average precipitation, when taken separately, had a significant effect on the FA_{nm} level, but the FA_{nm} was correlated at a statistically significant level under the interaction between the factors «annual average temperature» and «annual average precipitation». The conditions for *C. gud* habitats are the most optimal in Ushtulu landmark area as the lowest FA_{nm} values were registered at this locality. So, we suggest that the conditions with an annual average temperature below 5°C and an annual average precipitation within 1000–1100 mm are optimal for the species.

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СТЕПЕНЬ ДИФФЕРЕНЦИАЦИИ И СТАБИЛЬНОСТЬ РАЗВИТИЯ *CHIONOMYS GUD* (RODENTIA: CRICETIDAE) ПО НЕМЕТРИЧЕСКИМ ПРИЗНАКАМ ЧЕРЕПА

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Представлены результаты по оценке стабильности развития и степени дифференциации гудаурской полевки *Chionomys gud* на ООПТ Западного и Центрального Кавказа. Стабильность индивидуального развития *C. gud* в различных эколого-географических условиях характеризовалась по флуктуирующей асимметрии (*FA*nm) проявления фенов черепа в четырех географических популяциях, что позволило оценить влияние комплекса факторов среды на уровни *FA*nm. Самое высокое значение флуктуирующей асимметрии обнаружено в выборке из среднегорий Центрального Кавказа, окрестности п. Эльбрус, условия обитания которой можно характеризовать как наиболее стрессовые для вида при среднегодовой температуре ниже 5°C и среднегодовым количеством осадков меньше 1000 мм. Двухфакторным анализом подтверждена связь показателя флуктуирующей асимметрии с комплексным влиянием двух климатических факторов – среднегодовой температурой и среднегодовым количеством осадков. Анализ частот неметрических признаков черепа в популяциях *C. gud* позволил оценить уровни межпопуляционных фенетических различий. При этом наибольшие фенетические дистанции выявлены между пространственно разобщенными (более чем на 300 км) популяциями Центрального и Западного Кавказа. Степень морфологической дифференциации центрально-кавказских выборок, находящихся на абсолютном расстоянии в пределах 20–60 км выражена слабее. Предполагается, что уровень фенетических различий обусловлен не только влиянием фактора территориальной изолированности, но и климатическими особенностями каждой географической точки.

Ключевые слова: морфологическая дифференциация, неметрические билатеральные признаки, ООПТ, среднегорья, флуктуирующая асимметрия, эндемик