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CRANIOLOGY OF *NEOGALE VISON* IN AREAS OF INTRODUCTION: ANALYSIS OF SAMPLES FROM UKRAINE

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Key words

American mink, craniological analysis, geometric morphometrics, introduction, river basins of Ukraine

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Abstract

The article presents the results of a comprehensive craniological analysis of the American mink (*Neogale vison* Schreber 1777) based on skulls from three different geographic samples: 1) Upper Dnipro (Kyiv Oblast) and its first-order tributary (Desna, Chernihiv Oblast); 2) animal farm of the Cherkasy Oblast Consumer Union within the territory of the Sosnovsky hunting ground; and 3) the Siversky Donets River basin (Luhansk and Donetsk oblasts). The research included standard analysis based on craniometric measurements of 19 parameters, analysis of the shape of skulls by geometric morphometrics separately for the dorsal and ventral sides of the skull and buccal surface of the left mandible. The total sample comprised 29 specimens. The study showed that, according to the average values, skulls from the Siverky Donets River basin are the smallest in size, while the skulls of the American mink from Cherkasy Oblast are the largest among the studied samples. The analysis by geometric morphometrics showed the presence of inter-population differences, which is expressed between geographically distant samples. The most important features that distinguish the studied samples include the shape of the nasal and frontal bones, the braincase region on the dorsal side of the skull, as well as the shape of structures associated with the diastema and the proximal part of the hard palate, and the shape of the occipital bones of the skull. The differences in the shape of the mandible are related to the position of the coronal process in relation to the jaw base and articular process. In the majority of specimens from the Siversky Donets and Upper Dnipro basins, the coronal and articular processes are closer to each other than in specimens from Cherkasy Oblast. The identified features and the results of the comparison of samples from Ukraine and other territories suggest that in the case of natural populations of *Neogale vison*, the leading role in the variability of geographically separated populations is played by such factors as origin (founder effect), trophic adaptations, and population status. Comparison of the results of our study with studies from other countries indicates that skull dimensions are larger in those regions where stable and powerful populations have formed as a result of the introduction, but in regions where the species is still spreading or forming populations, skull sizes were smaller.

Cite as

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Краніологія *Neogale vison* в зонах інтродукції: аналіз матеріалів з України

Денис Лазарєв

Резюме. Представлено результати комплексного краніологічного аналізу зразків черепів візона річкового (*Neogale vison* Schreber 1777) за трьома вибірками: 1) Верхній Дніпро (Київська обл.) та його притоку першого порядку (р. Десна, Чернігівська обл.), 2) Звірогосподарство Черкаської облспоживспілки на території Сосновського мисливського господарства, 3) басейн річки Сіверський Донець (Луганська і Донецька обл.). Дослідження, включає в себе стандартний аналіз на основі краніометричних промірів по 19 параметрах, аналіз форми черепів методами геометричної морфометрії окремо для дорсальної і вентральної сторони черепа та щічної сторони лівої нижньої щелепи. Загальна вибірка склала 29 зразків. Дослідження показало, що за середніми значеннями, черепи з басейну річки Сіверський Донець є найменшими за розмірами, в той час як черепи візона річкового з Черкащини є крупнішими серед досліджених вибірок. Аналіз методами геометричної морфометрії показав наявність міжпопуляційних відмінностей, що виражена між географічно віддаленими вибірками. Найбільш важливі ознаки, які розрізняють досліджені вибірки включають форму носових і лобових кісток, форму мозкової капсули на дорсальній стороні черепа, а також форму структур, пов'язаних з діастемою та проксимальною частиною твердого піднебіння, формою потиличних кісток черепа. Розбіжності у формі нижньої щелепи пов'язані з положенням вінцевого відростку по відношенню до основи щелепи та суглобового відростку. У більшості зразків з басейну Сіверського Дінця та верхнього Дніпра вінцевий та суглобовий відростки більш наближені один до одного ніж у зразків з Черкаської області. Виявлені особливості та результати порівняння зразків з України та інших територій дозволяють припустити, що у випадку з природними популяціями *Neogale vison*, провідну роль у мінливості географічно відділених популяцій мають такі чинники як походження (ефект засновника), трофічні адаптації, та стан популяцій. Порівняння результатів нашого дослідження з дослідженнями з територій інших країн вказують на те, що розміри черепів є більшими саме в тих регіонах де в результаті інтродукції сформувалися стійкі та потужні популяції, проте в регіонах де досі триває поширення виду або формування популяції, розміри черепів виявились меншими.

Ключові слова: візон річковий, краніологічний аналіз, геометрична морфометрія, інтродукція, річкові басейни України.

Introduction

The American mink (*Neogale vison* Schreber, 1777) is an alien species in the Ukrainian fauna. It appeared in the early 20th century as a commercial species kept in captivity, which then accidentally entered the natural environment and formed natural populations [Pavlov *et al*. 1973]. In Ukraine, no large-scale measures were taken to specially release the American mink into the nature [Koslov & Lavrov 1968], thus the species appeared as a result of escapes from breeding sites. The first native populations of this mammal species in Ukraine were formed in 1960–1980 [Panov 2002]. The appearance of this animal in the mammal fauna of Ukraine caused considerable concern in the field of nature conservation, and significantly affected populations of other native species of the Mustelidae family [Zagorodniuk 2006].

Several studies of the morphology of this alien mammal species from neighbouring territories indicate that the shape of the animal's skull acquires certain changes over time, which may be the result of its adaptation to changing environmental conditions [Stepanova *et al.* 2023]. There are several works on the study of cranial morphometry of the species in other countries [Sedalishchev & Odnokurtsev 2012; Korablev *et al*. 2013; Taraska *et al*. 2016; Stepanova *et al*. 2023; etc.], but such analysis has not yet been carried out on materials from different river basins of Ukraine, particularly by using methods of geometric morphometrics. A similar craniological analysis was carried out earlier in relation to *Ondatra zibethicus* [Lazariev & Barkasi 2023].

The aim of the present study is to investigate the morphological differences between *Neogale vison* specimens from the river basins of the Upper and Middle Dnipro and Siversky Donets.

Fig. 1. Map of origin of the studied samples. (1) Upper Dnipro: (1*a*) specimens from the city of Kyiv and Kyiv Oblast, (1*b*) Chernihiv Oblast, (1*c*) Zhytomyr Oblast; (2) Middle Dnipro, Cherkasy Oblast; (3) Siversky Donets River basin: (3*a*) Lyman, Donetsk Oblast, (3*b*) Starobilsk, Luhansk Oblast, (3*c*) Slovianoserbsk, Luhansk Oblast.

Рис. 1. Карта походження зразків. (1) Верхній Дніпро: (1*a*) зразки з Києва та Київської обл., (1*b*) Чернігівська обл., (1*c*) Житомирська обл.; (2) Середній Дніпро, Черкаська обл.; (3) Басейн Сіверського Дінця: 3*a* – Лиман, Донецька обл., (3*b*) Старобільськ, Луганська обл., (3*c*) Слов'яносербськ, Луганська обл.

Materials and Methods

The studied specimens are housed in the collections of the Department of Zoology (NMNHU–z), and the Department of Palaeontology (NMNHU–p) at the National Museum of Natural History of the National Academy of Sciences of Ukraine (NMNHU, Kyiv, Ukraine), as well as of the Zoological Museum of Taras Shevchenko National University of Kyiv (ZMKU, Kyiv, Ukraine), the Zoological Museum of Luhansk Taras Shevchenko National University (ZMLG, Luhansk, Ukraine) and the State Museum of Nature of V. N. Karazin Kharkiv National University (MNKhU, Kharkiv, Ukraine). Acronyms for these museums are given after [Zagorodniuk & Shydlovskyy 2014]. Some specimens were collected by the author and are kept in his personal collection, which is described in more detail below. All sampling localities are presented in Fig. 1.

In total, 29 skulls of adult American minks from three geographical regions of Ukraine were used in the analysis:

(1) Upper Dnipro River basin:

Kyiv Oblast, n = 13 (ZMKU, No. 7546; 7559–7563; NMNHU–z, No. 16546–16552, Troieshchyna, mouth of the Desna River, leg. Shevchenko, collected in 2011; one specimen from the author's personal collection, Kyiv, collected in 2024).

Chernihiv Oblast, n = 4 (ZMKU, No. 7562; NMNHU–p, No. 6809, leg. V. Smagol, collected in 2003; two specimens from the author's personal collection, Mena Raion, collected in 2023).

Due to the geographical proximity, a specimen from Babynichi, Zhytomyr Oblast was also included, n = 1 (NMNHU–z, No. 2010, leg. A. Volokh, collected in 2015).

(2) Middle Dnipro River basin:

Animal farm of the Cherkasy Oblast Consumer Union within the territory of the Sosnovsky hunting ground, n = 5, NMNHU–p, No. 6810–6814, leg . Lebid Y. O, collected in 1986.

(3) Siversky Donets River basin:

Luhansk Oblast, n = 4 (ZMLG, No. M–00117, leg. S. Litvinenko, det. I. Zagorodniuk; M–00133, Slovianoserbsk, det. I. Zagorodniuk, collected in 2009; M–00136; M–00138, Starobilsk, det. I. Zagorodniuk);

Donetsk Oblast, Lyman, n = 2 (MNKhU, No. M–1720–1721, collected in 1986).

Some of the specimens stored in NMNHU-p were previously identified by other scientists as *Mustela lutreola* (NMNHU-p, no. 6809) or were assigned only to the family Mustelidae (NMNHU-p, no. 6810-6814). We re-identified these specimens as *Neogale vison*.

In total, 19 craniometrical characters were analysed [after Zagorodniuk 2012]:

CBL—condylobasal length; CRH—cranial height; CRB—braincase width; ZYG—zygomatic width; IOR—interorbital width; POR—postorbital width; ROH—rostral height; FIL—incisive foramina length; BUL—auditory bulla length; BUB—auditory bulla width; DMM—greatest palatal width; DIM—upper tooth row length; JUG—jugular width; OCC—occipital width; DCM—upper canine–molar length; MAL—mandible length; MAH—mandible height; dcm—lower canine–molar length; dim—lower tooth-row length.

Measurements were taken by calliper with an accuracy of 0.1 mm.

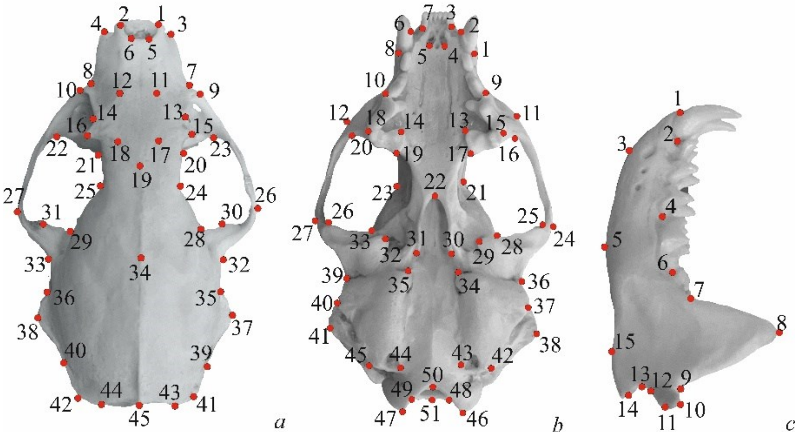

Fig. 2. Landmarks on the dorsal (*a*) and ventral (*b*) surfaces of the skull and on the buccal surface of the left mandible (*c*) used in geometric morphometrics analysis.

Рис. 2. Мітки на дорсальній (*a*) та вентральній (*b*) поверхні черепа та на щічній поверхні лівої нижньої щелепи (*c*), аналізовані методами геометричної морфометрії.

Basic descriptive statistics were calculated, including minimum (min), maximum (max), and mean (M) values, standard deviation (SD), and coefficient of variation (CV), for each of the three geographic samples. The Shapiro–Wilk test was applied to analyse the distribution of the datasets; the null hypothesis was rejected at a significance level of $p < 0.05$. Consequently, the characters POR ($p = 0.0057$), BUL ($p = 0.0002$), OCC ($p = 0.0252$), CRH ($p = 0.0256$), DCM ($p = 0.0105$), and dim ($p = 0.0022$) were excluded from further analyses. The equality of means of the samples was tested by MANOVA; uncorrected p-values were considered for the acceptance or rejection of the null hypothesis. The variation of linear characters was also analysed by multivariate ordination methods (principal component analysis, PCA and canonical variate analysis, CVA). All calculations were carried out in PAST 4.16c [Hammer *et al.* 2001].

The shape variation of the American mink skulls was analysed using methods of geometric morphometrics [Klingenberg & McIntyre 1998]. For each geographic sample, three sets of landmarks were studied. On the dorsal surface, 45 landmarks were analysed, of which landmarks 1–6 describe the nasal bones, 11–19 the marginal points and points on the sutures of the frontal bones, 7–10, 29–33 the zygomatic bones, and 34–45 the neurocranium (Fig. 2*a*). Of the landmarks on the ventral surface (51), 1–3, 6–11, 13–15, and 17–19 describe the position of the teeth, 4–5 the incisive foramina, 20, 21, 23–28, and 33 the zygomatic bones, 34–42 and 45 the auditory bulla, 43–44 the jugular holes, and 46–51 the occipital bones (Fig. 2*b*). On the mandible, of the 15 landmarks 1–7 describe the alveolar process of the mandible, 7–9 the coronoid process, 9–13 the articular process, and 13–15 the angular process (Fig. 2*c*).

The software tpsUtil32 and tpsDig232 were used to generate the corresponding landmark datasets based on the digital images of skulls. The analysis of skull shape variation was carried out in MorphoJ [Klingenberg 2011]. Due to the incompleteness of some skulls, one specimen from the Siversky Donets basin (No. M-00138) was excluded from the ventral surface analysis. Also, the specimens M-00136 and M-00117 were excluded from the analysis of the mandible shape due to the absence of this cranial element.

Shape variation of the American mink skulls were analysed using principal component analysis (PCA) and canonical variate analysis (CVA) in MorphoJ. The first three principal components were retained for detailed analysis. Differences between samples from different river basins were tested using the non-parametric multivariate analysis of variance (PERMANOVA) of Anderson [2001] with Euclidean distances between scores on the retained principal components, using 9999 replicates in PAST 4.16c [Hammer *et al.* 2001]. Uncorrected p-values were considered for the acceptance or rejection of the null hypotheses.

Most specimens were collected in 2000–2024. Collections of *Neogale vison* specimens in Ukrainian museums are poor compared to other alien species (*Ondatra zibethicus*, *Nyctereutes procyonoides*), which might be due to the relatively later formation of natural populations of the species and the ongoing process of the species' expansion [Lazariev 2023].

Results and Discussion

Linear morphometrics

Among the studied samples the highest size indices are observed in samples from the Cherkasy Oblast, which, in our opinion, indicates the likely origin of these samples from farm-raised animals, as the skulls of such animals are in most cases significantly larger [Taraska *et al*. 2016; Tamlin *et al*. 2009], and the general body parameters of farmed animals of this species are also significantly larger [Mucha *et al*. 2021].

The animals from the Upper Dnipro and Siversky Donets basins are noticeably smaller, but these samples also differ slightly from each other. Specimens from Kyiv, Chernihiv, and Zhytomyr oblasts are somewhat larger than those from the Siversky Donets basin, which were the smallest among the studied material, but some parameters in specimens from the Donets are still slightly higher, in particular DMM, MAL, and dcm. Such indicators as FIL are the same for Dnipro and Donets. However, no significant differences were found between the three samples (MANOVA, $p > 0.05$).

The largest coefficients of variation are characteristic of such features as FIL, MAH for all samples. In addition, ROH, dcm, and dim are among the most variable traits in the Dnipro sample, and BUL, BUB, JUG, and OCC are among the most variable traits in the Donets sample. In specimens from Cherkasy Oblast, the most variable traits are MAL and IOR (Table 1).

It is worth noting that the Siversky Donets is a smaller river, in terms of basin area, length, and water content, compared to the Dnipro River basin. In this regard, we suggest that animal size can be explained by the 'hydrobiont rule', according to which body size is larger in animals associated with large river floodplains and high ecosystem productivity [Panteleev 1996, 2001].

The principal component analysis (PCA) of American mink craniometric traits showed that the first three components describe 86% of the total variance, of which PC1 describes 65% and PC2 12% (Table 2). All traits have a positive score on PC1, and the highest loadings have the characters CBL, MAL, ZYG, and CRB, which describe the main dimensions of the skull. DIM and dcm, which describe the dimensions of the dentition, also have relatively high scores.

Table 1. Results of measurements of *Neogale vison* skulls in three samples from the territory of Ukraine

Таблиця 1. Результати вимірів черепів *Neogale vison* із трьох вибірок із території України

Characters	Upper Dnipro (wild)			Siversky Donets (wild)			Cherkasy Oblast (farm)		
	min–max	M ± SD	CV	min–max	M ± SD	CV	min–max	M ± SD	CV
CBL	59.8–76.0	66.2 ± 4.0	6.1	59.0–68.5	64.0 ± 4.0	6.2	66.0–72.5	70.0 ± 2.7	3.8
CRB	29.7–39.4	33.9 ± 2.5	7.3	28.1–36.0	32.5 ± 2.9	9.0	36.0–40.5	37.0 ± 2.0	5.3
ZYG	33.4–43.0	38.7 ± 2.9	7.6	32.6–40.0	36.3 ± 2.9	7.9	38.7–44.2	40.9 ± 2.2	5.4
IOR	13.1–18.7	15.7 ± 1.3	8.3	12.0–15.7	14.1 ± 1.4	9.7	13.8–17.5	15.2 ± 1.4	9.1
POR	11.2–17.1	13.2 ± 1.3	9.8	11.5–14.0	13.0 ± 1.0	7.9	11.4–13.9	12.7 ± 0.9	7.4
FIL	2.0–3.6	2.8 ± 0.4	16.0	2.0–2.6	2.2 ± 0.3	11.5	2.2–3.0	2.7 ± 0.4	13.6
DMM	19.7–24.3	22.2 ± 1.4	6.1	20.0–23.2	21.6 ± 1.3	5.8	22.1–24.0	22.8 ± 0.7	3.2
DIM	21.3–30.1	24.0 ± 2.0	8.5	21.0–26.0	23.2 ± 1.8	7.9	24.5–26	25.3 ± 0.6	2.6
BUL	15.5–18.6	17.4 ± 0.7	4.2	13.0–18.0	16.3 ± 1.9	11.8	16.8–18.7	18.0 ± 0.8	4.5
BUB	10.0–13.1	11.7 ± 0.8	6.8	9.2–13.0	11.1 ± 1.5	13.8	11.0–12.4	11.5 ± 0.6	5.4
JUG	11.1–16.1	13.8 ± 1.3	9.3	10.0–13.0	11.3 ± 1.3	11.6	13.4–15.0	14.0 ± 0.6	4.3
OCC	15.0–19.0	17.1 ± 1.1	6.6	13.0–16.3	14.8 ± 1.7	11.3	16.9–18.2	17.7 ± 0.6	3.3
CRH	22.5–29.2	24.4 ± 1.6	6.6	21.2–25.0	23.8 ± 1.6	6.7	24.0–27.0	25.4 ± 1.2	4.6
ROH	15.0–22.7	17.7 ± 2.1	11.7	13.0–16.4	15.0 ± 1.3	8.5	16.8–18.8	17.6 ± 0.8	4.3
DCM	19.0–27.5	21.5 ± 1.9	9.1	19.0–23.0	20.7 ± 1.5	7.5	22.1–25.6	23.2 ± 1.4	6.0
MAL	33.1–48.9	39.6 ± 3.9	9.9	33.4–42.0	38.8 ± 3.7	9.6	36–45.3	42.0 ± 3.6	8.5
MAH	15.8–21.8	18.8 ± 1.8	9.3	15.3–24.0	19.3 ± 3.6	18.5	19.8–27	21.7 ± 3.1	14.1
Dcm	18.1–33.0	22.5 ± 3.6	16.2	22.0–24.1	23.1 ± 1.5	6.4	26.0–27.8	26.5 ± 0.7	2.8
Dim	22.2–34.0	25.4 ± 2.6	10.3	22.2–24.4	23.3 ± 1.6	6.7	26.5–27.8	27.2 ± 0.5	2.0

Table 2. Factor loadings of the linear craniometrical characters on the first three principal components

Таблиця 2. Факторні навантаження лінійних краніометричних ознак на перші три головні компоненти

Character	PC 1	PC 2	PC3	Character	PC 1	PC 2	PC3
CBL	0.5365	0.1132	0.0324	BUB	0.0729	-0.0254	0.1292
CRB	0.3006	0.2287	0.2638	JUG	0.0934	-0.0061	0.3262
ZYG	0.3637	0.0677	0.4002	ROH	0.1706	0.0035	0.2187
IOR	0.1443	-0.0096	0.1925	MAL	0.4901	-0.7494	-0.2724
FIL	0.0089	0.0319	0.0286	MAH	0.1690	0.4710	-0.0865
DMM	0.1512	0.0524	0.0983	Dcm	0.2900	0.3618	-0.6805
DIM	0.2226	0.1057	-0.0760	Variance, %	65.38	12.05	8.85

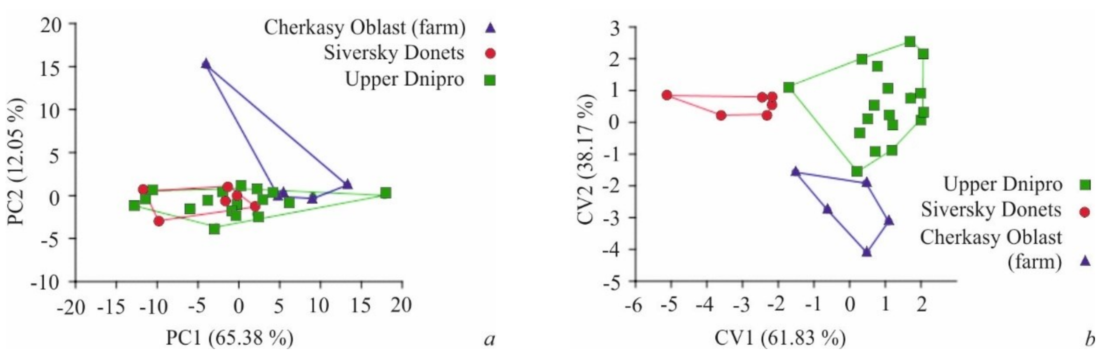

Fig. 3. The distribution of American mink samples in the space of the first two principal components (*a*) and canonical variates (*b*) based on linear craniometrical characters.

Рис. 3. Розподіл вибірок візона річкового у просторі перших двох головних компонент (*a*) та канонічних змінних (*b*) за лінійними краніометричними ознаками.

All traits have a positive score on PC1, and the highest loadings have the characters CBL, MAL, ZYG, and CRB, which describe the main dimensions of the skull. DIM and dcm, which describe the dimensions of the dentition, also have relatively high scores.

In the space of PC1 and PC2, the Siversky Donets and Cherkasy samples tend to separate along PC1 (Fig. 3*a*). Specimens from Cherkasy Oblast have the highest positive loads on PC1 (respectively, higher length, width, and height of the skull, and higher jaw height). Along PC2, specimens from Cherkasy Oblast also have higher scores, related to the width and length of the dentition. Despite the similarities between the samples by absolute values of craniometrical characters, canonical variate analysis (CVA) shows their discrimination in the multivariate morphospace, particularly the Siversky Donets sample along CV1 and the Cherkasy sample along CV2 (Fig. 3*b*).

The comparison with samples from other territories showed that founder effect, natural conditions, and population status and ecosystem productivity are most likely to be responsible for the size differences between geographically separated samples. For example, samples with smaller sizes are found in large river basins, such as the Omolon and Anadyr river basins in Russia (Table 3).

Specimens from central Canada are also noticeably smaller, despite the fact that this area is the natural distribution range of the species. Some researchers have pointed out that *Neogale vison* released from farms could have a negative impact on the natural population of American mink, in particular, causing a decrease in their numbers due to outbreeding depression and the introduction of new diseases into natural populations [Bowman 2007]. This suggests a deterioration in the condition of the American mink populations in some areas of its natural range and a decrease in the overall and skull size in wild populations. In general, the largest specimens were reported from the West Pomeranian Voivodeship of Poland, while the smallest from the Anadyr River basin in the Chukotka. Curiously, a repeated measurement of the size of wild minks from Yakutia with a difference of 40 years (1980–2020) may indicate the possibility of an increase in the size of *Neogale vison* in the areas of introduction in the process of development and formation of natural populations.

Table 3. Mean values (mm) of craniometrical characters of American mink from different countries and regions
Таблиця 3. Середні значення (мм) краніометричних ознак візона річкового із різних країн і регіонів

Region	Sex	n	CBL	ZYG	POR	CRH	MAL	MAH	References
Ukraine	♂	14	67.0	39.3	13.4	24.6	40.8	19.7	this study
	♀	9	62.5	35.5	12.8	23.2	36.2	17.1	
	total	29	65.4	37.9	13.2	24.1	39.2	18.8	
Poland, West Pomeranian Voivodeship	♂	20	69.0	40.2	13.2	21.4	40.1	19.8	Taraska *et al*. 2016
	♀	12	61.9	34.8	11.8	18.9	35.0	16.8	
	total	32	66.4	38.2	12.7	20.5	38.2	18.7	
Canada, Ontario	♂	65	64.3	—	12.5	—	—	—	Tamlin *et al*. 2009
	♀	35	58.1	—	11.9	—	—	—	
	total	100	61.9	—	12.1	—	—	—	
Russia, Republic of Sakha, 1980	♂	18	65.8	38.9	—	23.7	—	—	Sedalishchev & Odnokurtsev 2012
	♀	12	58.8	33.6	—	21.5	—	—	
	total	30	62.3	36.2	—	22,6	—	—	
Russia, Republic of Sakha, 2020	♂	54	67.1	38.6	12.5	23.5	38.3	18.7	Stepanova *et al*. 2023
	♀	31	59.4	33.3	11.8	22.2	32.9	15.6	
	total	85	63.4	35.9	12.1	22.9	35.6	17.1	
Russia, Altai Republic	♂	16	66.4	37.1	—	—	—	—	Ternovsky 1958
	♀	9	59.3	32.8	—	—	—	—	
	total	25	62.8	34.9	—	—	—	—	
Russia, Bashkortostan	♂	16	66.4	37.8	—	—	—	—	Pavlinin 1962
	♀	5	59.0	33.0	—	—	—	—	
	total	21	62.7	70.8	—	—	—	—	
Russia, Omolon River basin	♂	14	66.0	37.7	—	23.6	39.9	—	Chernyavsky 1984
	♀	10	59.2	32.9	—	21.4	34.6	—	
	total	24	62.6	35.3	—	22.5	37.2	—	
Russia, Anadyr River basin	♂	17	66.5	38.1	—	23.6	40.3	—	Chernyavsky 1984
	♀	15	57.0	31.6	—	19.9	33.0	—	
	total	32	61.7	34.8	—	21.4	36.6	—	

Geometric morphometrics

The shapes of the dorsal and ventral surfaces of the skull, as well as the buccal surface of the mandible, were analysed using the tools of landmark-based geometric morphometrics. According to the results of the analysis of the dorsal surface, 83% of the variance is described by the first eight principal components, of which 34.45% is described by PC1 and 17.15% by PC2. The highest negative scores on PC1 were recorded for the points x17–x19, describing the proximal edges of the frontal bones, whereas the highest positive loadings were recorded for the points describing the external contours and structures of the skull at y5–y6, y7–y8, y26–y27, y39–y40, and x22–x23 (Fig. 4*a*). The letters 'x' and 'y' refer to the respective Procrustes shape coordinates of the analysed landmarks.

Most specimens from the Dnipro sample are characterised by narrower braincases and frontal bones, while the specimens from the Donets and Cherkasy samples are characterised by having generally wider skulls, moderately widened and elongated braincases, and narrowed and shortened frontal and nasal bones. In this case, the exception is the specimens from Donetsk Oblast, which are closer to the negative end of PC2 (Fig. 4*b*): the braincase is shorter, but they have longer frontal and nasal bones, and the skull is narrower than in most specimens.

Principal component analysis demonstrates that the specimens largely overlap in the space of PC1 and PC2, although specimens from Cherkasy Oblast tend to form a clear cluster closer to the positive end PC1 (Fig. 5*a*). Canonical variate analysis showed that the samples are well discriminated in the morphospace. The Cherkasy and the Donets samples separate from the Upper Dnipro along CV1, while the latter has an intermediate position along CV2 (Fig. 5*b*).

The most distant are the Upper Dnipro and Cherkasy samples, and the differences between them are significant ($p < 0.05$; Table 4). According to the results of the analysis of the ventral surface of the skull, 82% of the variance is described by the first nine principal components, among which PC1 accounts for 30.14% and PC2 for 14.39%. The highest positive factor loadings on PC1 have the points x25, x26, x29, x32, with relatively high values also y11, y12, x24, x27, x28, and x33.

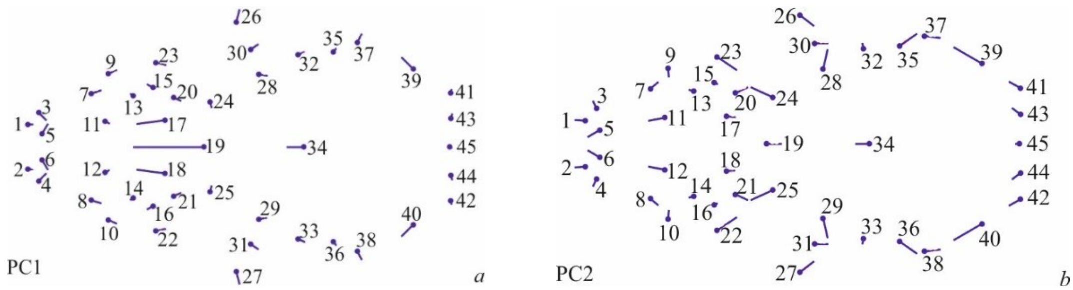

Fig 4. Variation of the shape of the dorsal surface of the skull along PC1 (*a*) and PC2 (*b*).

Рис 4. Зміни форми дорсальної поверхні черепа за ГК1 (*a*) та ГК2 (*b*).

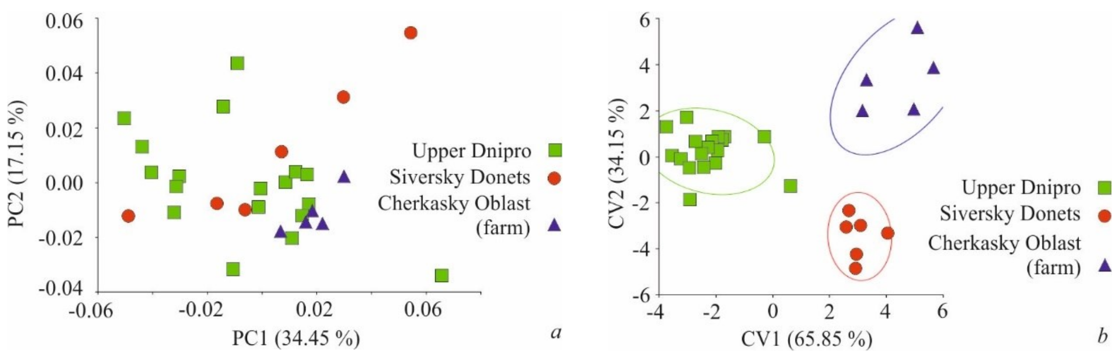

Fig. 5. Distribution of American mink specimens from different regions of Ukraine according to the shape of the dorsal surface of the skull: (*a*) in the space of the first two principal components; (*b*) in the space of the first two canonical variates.

Рис. 5. Розподіл зразків візона річкового із різних регіонів України за формою дорсальної поверхні черепа: (*a*) у просторі перших двох головних компонент; (*b*) у просторі перших двох канонічних змінних.

Table 4. Mahalanobis distances (D_M) among the samples and uncorrected p-values of pair-wise one-way PERMANOVA based on PC scores

Таблиця 4. Відстані Махаланобіса (D_M) між вибірками та некореговані p-значення попарного однофакторного PERMANOVA на основі навантажень на ГК

Group	Samples	Upper Dnipro	Siversky Donets	Cherkasy Oblast
Dorsal ($F = 2.3309$; $p = 0.0042$)	Upper Dnipro	—	6.470	7.359
	Siversky Donets	0.174	—	6.905
	Cherkasy Oblast	**0.005**	0.101	—
Ventral ($F = 2.0932$; $p = 0.0028$)	Upper Dnipro	—	5.100	5.590
	Siversky Donets	0.211	—	6.358
	Cherkasy Oblast	**0.029**	**0.0163**	—
Mandible ($F = 3.3202$; $p = 0.0001$)	Upper Dnipro	—	9.1122	11.441
	Siversky Donets	0.192	—	9.195
	Cherkasy Oblast	**0.000**	0.056	—

Note: $p < 0.05$ are given in bold.

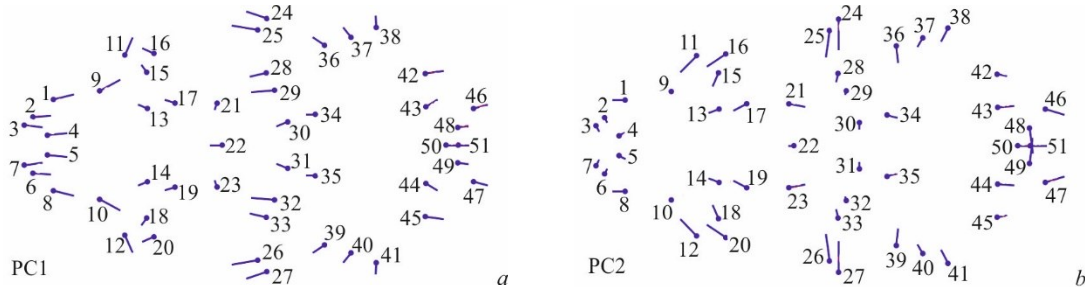

Fig. 6. Variation of the shape of the ventral surface of the skull along PC1 (*a*) and PC2 (*b*).

Рис. 6. Зміни форми вентральної поверхні черепа за ГК1 (*a*) та ГК2 (*b*).

These landmarks are mostly related to the shape of the zygomatic bones. The largest negative scores on PC1 have the points x1–x10, x42, and x45, which describe the shape of the nasal bones and the occipital region of the skull (Fig. 6*a*). On PC2, the highest positive factor loadings have the points x11 and y48, and relatively high scores have x14, y15, y24–y35, y46, and y47. The highest negative loadings have the points y11, y12, y21, and y23, with relatively high negative values of y13–y15, y18, y24–y27, y29–y32, y34, y35, y46, and y47, indicating variation in the outline of various skull structures. (Fig. 6*b*).

The analysis of the ventral surface showed that samples from the Cherkasy region generally have longer skulls, correspondingly elongated nasal bones, bones forming the rostrum and structures in the area of the brain capsule, in contrast to samples from the Upper Dnipro and Siverskyi Donets.

According to the shape of the ventral surface of the skull, there are more noticeable differences between the samples. While specimens from all three samples overlap in the space of PC1 and PC2, especially so the ones from the Upper Dnipro, specimens from Cherkasy and the Siversky Donets tend to separate along PC1 (Fig. 7*a*). Canonical variate analysis shows that each sample forms a separate clouds in the morphospace. The Upper Dnipro sample, as in the case as in the case with the dorsal surface, separates along CV1 from the other two samples. On the other hand, the Cherkasy sample separates along CV2 (Fig. 7*b*). It is the most distant from the Upper Dnipro sample and differs significantly from both the Upper Dnipro and the Siversky Donets samples ($p < 0.05$; Table 4).

The analysis of the buccal side of the mandible showed that 83.36% of the variance is described by the first six principal components, of which PC1 describes 24.90% and PC2 describes 22.48%. The highest positive scores on PC1 have the points x8, x14, y11, and y15, and relatively high values have x6, x7, and x10. The highest negative loadings on PC1 have the points y8, x11, and x14.

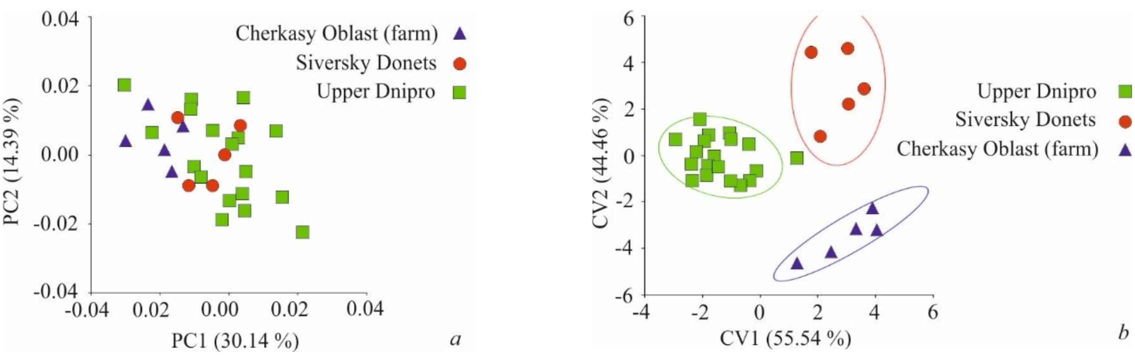

Fig. 7. Distribution of American mink specimens from different regions of Ukraine according to the shape of the ventral surface of the skull: (*a*) in the space of the first two principal components; (*b*) in the space of the first two canonical variates.

Рис. 7. Розподіл зразків візона річкового із різних регіонів України за формою вентральної поверхні черепа: (*а*) у просторі перших двох головних компонент; (*б*) у просторі перших двох канонічних змінних.

All these coordinates are related to the extreme points of coronoid, articular and angular processes of the mandible (Fig. 8*a*). On PC2, the highest positive loadings have the points x5, y5, y6, y7, and y8, describing the height of the base of the mandible in the area of the tooth row. Whereas the most negative scores have x1, x2, x10, x11, x14, y1, and y11 which generally describe the length of the mandible, and the shape of the jaw in the canine area and articular, angular process (Fig. 8*b*).

In the morphospace of the first two principal components, the specimens demonstrate a great overlap, similarly to the analysis of the dorsal and ventral sides of the skull, although the Cherkasy specimens tend to aggregate at the negative end of PC1 and also tend to slightly separate along PC2 (Fig. 9*a*). Nevertheless, canonical variate analysis shows that all three samples are well separated in the space of CV1 and CV2, particularly the Upper Dnipro and Cherkasy samples along CV1 and the Siversky Donets sample from the other two along CV2 (Fig. 9*b*). The Cherkasy sample is the most distant and significantly differs from the Upper Dnipro sample ($p < 0.05$), although it also differs notably from the Siversky Donets sample as well (see: Table 4).

Results of the geometric morphometric analysis of the skull of American minks indicate that the most substantial differences are characteristic for the sample from Cherkasy Oblast. These are specimens of farmed minks, which also have larger cranial dimensions. The Mahalanobis distances also demonstrate that the samples that came from natural environments (i.e. the Upper Dnipro and Siversky Donets samples) are the closest according to all three analyses of shape variation of the skull

In the course of this study, there was no significant correlation between skull shape or size and geographical distance of the populations, so when considering possible causes of differences in skull shape and size, it should be noted that the condition of the populations studied, natural conditions, and the founder effect may have played a significant role. The study also confirms the high value of geometric mophometrics analysis in exploring the variability of the shape of skull of the studied species, particularly in samples that come from different geographic regions as well as different conditions of existence, both natural habitats and fur farms.

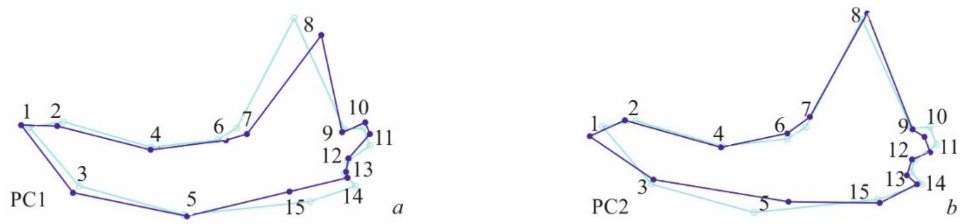

Fig. 8. Variation of the shape of the buccal surface of the left mandible PC1 (*a*) and PC2 (*b*).

Рис. 8. Зміни форми щічної поверхні лівої нижньої щелепи за ГК1 (*а*) та ГК2 (*b*).

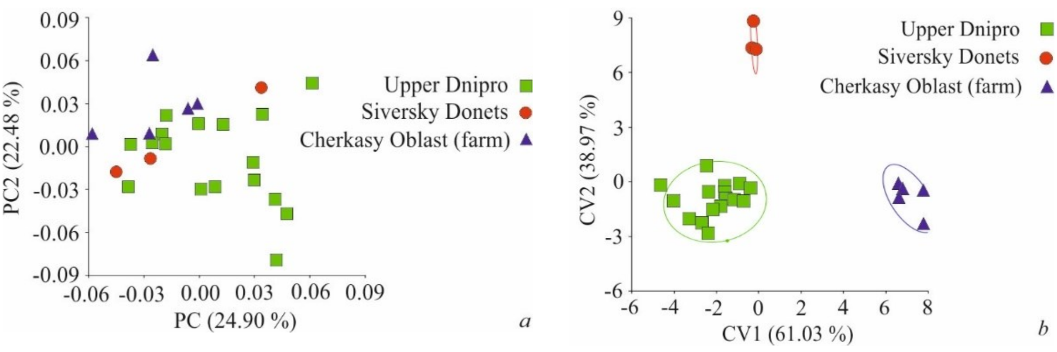

Fig. 9. Distribution of American mink specimens from different regions of Ukraine according to the shape of buccal surface of the left mandible: (*a*) in the space of the first two principal components; (*b*) in the space of the first two canonical variates.

Рис. 9. Розподіл зразків візона річкового із різних регіонів України за формою щічної поверхні лівої нижньої щелепи: (*а*) у просторі перших двох головних компонент; (*б*) у просторі перших двох канонічних змінних.

Conclusions

Based on the results of this study, the following conclusions can be drawn:

1. According to the results of the measurements of the three samples from Ukraine and their statistical analysis, the largest American mink specimens were those from Cherkasy Oblast, whose size and shape analysis confirms that these samples originated from farms. Specimens from the Donets River basin were the smallest, but they did not differ significantly in size from the Upper Dnipro sample. This is explained by the different conditions and resources in which these populations exist.

2. Comparing the results of our study with the literature from other areas, we find the following features: skulls from the area of natural distribution of the species are smaller than in several countries that are part of introduction range of this species. We assume that this phenomenon is another result of outbreeding depression and the fact that farmed American minks introduce new diseases into natural populations. At the same time, as populations develop in the areas of introduction, the size of animals and their skulls can increase, as shown by repeated studies in Sakha Republic.

3. Geometric morphometric analysis showed that minks from natural populations (Upper Dnipro, Siversky Donets) and from farms (Cherkasy Oblast) are morphologically the most distant. Less pronounced but statistically significant or close to significant differences are also observed between samples from natural populations: between the Upper Dnipro and Siversky Donets samples by the shape of the ventral surface of the skull and the shape of the mandible.

4. The most significant differences are related to the shape of the frontal bones and sutures, nasal bones, the shape of the braincase and related structures of the ventral surface of the skull. The most variable was the shape of the mandible, particularly the height of the mandible body, the position of the coronoid process relative to the jaw base and articular process, and the size of the articular process.

5. Based on the identified features, it can be assumed that the main factors affecting the shape and size of the skull and its structures are the environmental conditions in which the animals live, the origin of these natural populations (founder effect), and the state of natural populations.

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Declarations

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Conflict of interests. The author has no conflicts of interest to declare that are relevant to the content of this article.

Handling of materials. Collection specimens were handled according to the regulations of the respective housing institutions.

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