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CRANIOLOGICAL ANALYSIS OF THE MUSKRAT (*ONDATRA ZIBETHICUS*) FROM DIFFERENT RIVER BASINS OF UKRAINE

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Key words

muskrat, craniological analysis, geometric morphometrics, introduction, river basins of Ukraine

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Abstract

The paper presents the results of a comprehensive craniological analysis of muskrats (*Ondatra zibethicus* Linnaeus, 1766) from five river basins of Ukraine: Dnipro (Lower Dnipro, Kherson Oblast), Snihurivka (irrigation canal, Mykolaiv Oblast), Danube (Lower Danube, Odesa Oblast), Dnister (Middle Dnister, Lviv and Ternopil oblasts), and Donets (Siversky Donets, Luhansk and Kharkiv oblasts). In total, 72 skulls were analysed using methods of traditional and geometric morphometrics. The craniometrical analysis included 14 measurements that describe general dimensions of the skull and its elements, whereas shape analysis was carried out separately for the dorsal and ventral surfaces of the skull and the buccal surface of the left mandible. The study revealed that muskrats from the Donets basin have the smallest skulls, whereas the other four samples greatly overlap. According to the results of multivariate analyses (PCA, CVA), the length and height of the mandible contribute the most into the differentiation of the samples. Geometric morphometrics showed that the most important distinguishing features include the shape of the nasal and parietal bones on the dorsal side, and of structures mainly related to the diastema and proximal part of the hard palatine on the ventral side. The most significant differences between the five samples, however, depend on the shape and relative orientation of the elements of the ascending ramus of the jaw—the coronoid, condylar, and angular processes, as well as the shape of bights between them and of the adjacent curvatures on the dorsal and ventral sides of the ascending ramus. The revealed features allow suggesting that the main contributing factors into the variation of geographically distinct populations include diet and feeding adaptations on the one hand, and possible spatial relationships and origin on the other. The Ukrainian sample also notably differs from muskrats from geographically distant regions by the mean values of several craniometrical characters, also indicating that animals in areas of secondary introduction have smaller cranial dimensions.

Cite as

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Краніологічний аналіз ондатри (*Ondatra zibethicus*) з різних річкових басейнів України

Денис Лазарєв, Золтан Баркасі

Резюме. У статті представлено результати комплексного краніологічного дослідження ондатр (*Ondatra zibethicus* Linnaeus, 1766) з п'яти річкових басейнів України: Дніпро (Нижній Дніпро, Херсонська обл.), Снігурівка (іригаційний канал, Миколаївська обл.), Дунай (Нижній Дунай, Одеська обл.), Дністер (Середній Дністер, Львівська і Тернопільська обл.) та Донець (Сіверський Донець, Луганська і Харківська обл.). Усього проаналізовано 72 черепи методами традиційної та геометричної морфометрії. Краніометричний аналіз проведено на промірах 14 ознак, що характеризують загальні розміри черепа та його окремих елементів, а аналіз форми черепа проведено окремо для дорсальної і вентральної сторони черепа та щічної сторони лівої нижньої щелепи. Дослідження показало, що ондатри із басейну Дінця мають найменші черепи, тоді як інші чотири вибірки значно перекриваються. За результатами багатовимірних методів аналізу (ГК та КЗ), довжина і висота нижньої щелепи найбільше впливає на диференціацію вибірок. Геометрична морфометрія показала, що найбільш важливі ознаки, що розрізняють досліджені вибірки включають форму носових та тім'яних кісток на дорсальній стороні черепа, а також форму структур, переважно пов'язаних з діастемою та проксимальною частиною твердого піднебіння на вентральній стороні черепа. Найбільш значимі відмінності між п'ятьма вибірками, однак, залежать від форми та відносної орієнтації елементів висхідної гілки нижньої щелепи — вінцевого, виросткового та кутового відростків, а також форми вирізок між ними та прилеглих країв з дорсальної та вентральної сторони відростка. Виявлені особливості дозволяють припустити, що провідну роль у мінливості географічно відділених популяцій мають, з одного боку, раціон та трофічні адаптації, а з іншого — можливі просторові взаємини та походження. Вибірка з України помітно відрізняється від ондатр із географічно віддалених регіонів за середніми значеннями низки краніометричних ознак, що також вказує на те, що для тварин із ареалів вторинної інтродукції характерно менші розміри черепа.

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

Introduction

Craniological analysis allows estimating the morphological variation between animal populations that are isolated or geographically distant. Muskrat skull specimens present a particularly intriguing subject for such investigations, given that the species was introduced and is non-native to the Eurasian continent. Morphological traits of animals from distant geographic or isolated populations may manifest distinct features, which are available to study and characterisation through morphometric analysis of their skulls.

In the territory of Ukraine, muskrats were introduced in 1945 to 1966. The history of fauna enrichment by means of introduction of this rodent is documented in several works by both Ukrainian and foreign researchers [Lavrov 1957; Kolosov & Lavrov 1968]. The introduction of muskrats to Ukraine was secondary. Animals for the introduction were sourced from the Kurgan region of Russia [Pavlov *et al.* 1973], where this species had been introduced earlier. The release of these animals in Ukraine in 1944–1945 resulted in the formation of the first stable populations. In the lower reaches of the Dnipro River, 1677 muskrats were released from the Arkhangelsk region of Russia, leading to the rapid establishment of a large population [Volokh 2014].

Since their introduction to Ukraine, muskrats have established stable populations in various river basins across the country, colonising even the most remote rivers. Over time, these populations have reached their peak numbers, demonstrating a certain stabilisation in population dynamics, with some regions experiencing a notable decline in muskrat numbers. Several studies have been conducted on muskrat habitats and population sizes in different regions of Ukraine [Panov 2002; Volokh 2014; Lazariev 2023].

Studies of muskrat skulls from geographically distant populations have revealed distinct variation patterns among representatives of different regions. Particularly noteworthy are the differences in size and shape observed in skulls or their discrete elements, which have proven to be crucial aspects of the analysis [Skyriene & Paulauskas 2014; Otgonbaatar & Shar 2019; Chueva *et al.* 2020 and others].

The aim of this study is to carry out a detailed craniological analysis of muskrats originating from various river basins of Ukraine using methods of linear and geometric morphometrics.

Materials and Methods

In total, 72 skulls of adult muskrats from five river basins of Ukraine were used for analyses:

(1) Lower Dnipro River, Kherson Oblast: n = 19, leg. O. Gizenko, 1960–1961, collections of NMNH;

(2) Snihurivka irrigation canal (Inhulets River), Mykolaiv Oblast: n = 15, leg. D. Berestennikov, 1963, collections of NMNH;

(3) Danube river basin, Odesa Oblast: n = 15: leg. V. Samosh (n = 10), 1962–1963, collections of NMNH; leg. M. Heheniuk (n = 4), 1973, collections of ZM KNU;

(4) Dnister river basin: n = 19: leg. K. Tatarynov (n = 16), Lviv Oblast, 1949–1950, collections of SMNH; leg. Govda (n = 3), Ternopil Oblast, 1962–1963, collections of ZM LNU;

(5) Siversky Donets river basin, n = 4: leg. O. V. Kondratenko (n = 2), Luhansk Oblast, Serebrianka forestry, 1995–1996, collections of NMNH; leg. G. Tkach, O. Zorya (n = 2), Pechenihy Reservoir, Kharkiv Oblast, 01.09.1995, collections of KhNU.

The studied specimens are housed in the collections of the Department of Zoology at the National Museum of Natural History of the National Academy of Sciences of Ukraine (NMNH, Kyiv, Ukraine), the State Museum of Natural History of the National Academy of Sciences of Ukraine (SMNH, Lviv, Ukraine), the Zoological Museum of Taras Shevchenko National University of Kyiv (ZM KNU, Kyiv, Ukraine), the Zoological Museum of Ivan Franko National University of Lviv (ZM LNU, Lviv, Ukraine), and the Department of Zoology and Animal Ecology at V. N. Karazin National University of Kharkiv (KhNU, Kharkiv, Ukraine). The majority of muskrat skulls, including those in the collections of SMNH and NMNH, were collected during two periods: 1949–1950 and 1960–1963, respectively. By this time, large populations of these animals had already emerged in many regions of Ukraine, and expansion was ongoing, although efforts on animal resettlement continued to be undertaken.

In total, 14 craniometrical characters were analysed [after Zagorodniuk 2012]: CBL—condylobasal length; CRH—cranial height; CRB—braincase width; ZYG—zygomatic width; IOR—interorbital width; ROH—rostral height; FIL—incisive foramina length; BUL—auditory bulla length; BUB—auditory bulla width; DBM—upper molars alveolar length; dbm—lower molars alveolar length; DIA—diastema length; MAL—mandible length; and MAH—mandible height (Fig. 1). Measurements were taken by calliper with an accuracy of 0.1 mm.

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 five 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 BUL ($p = 0.005$) and dbm ($p = 0.002$) were excluded from further analyses. The equality of means of the samples was tested by MANOVA; uncorrected p-values have been 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 muskrat skulls was analysed using methods of geometric morphometrics [Klingenberg & McIntyre 1998]. For each geographic sample, three sets of landmarks were selected on the dorsal (50 landmarks) and ventral surface (50) of the skull and on the buccal surface of the left mandible (25) (Fig. 2). Most of the analysed landmarks were selected based on previous studies of cranial shape variations (see Table 1).

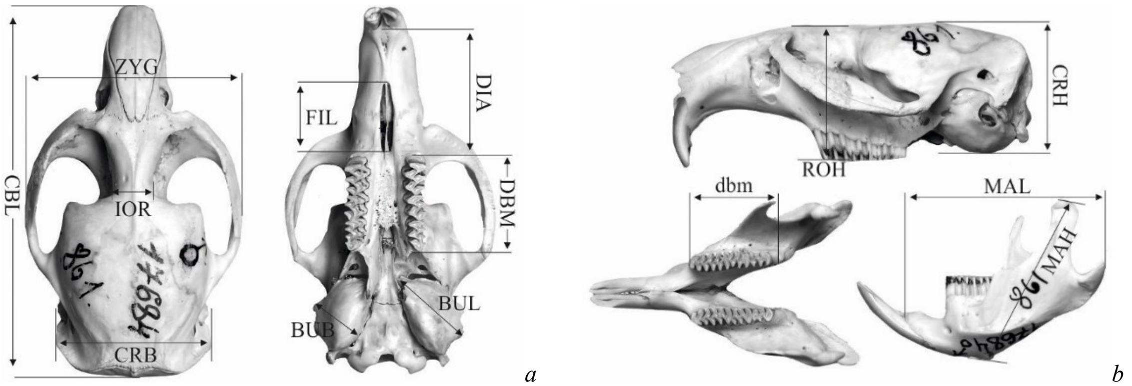


Fig. 1. Skull measurements of *Ondatra zibethicus* analysed in this study: (*a*) dorsal and ventral sides of the skull; (*b*) lateral side of the skull, dorsal and lateral sides of the mandible.

Рис. 1. Досліджені проміри черепа *Ondatra zibethicus*: (*a*) дорсальна і вентральна сторони черепа; (*b*) латеральна сторона черепа, дорсальна і латеральна сторони нижньої щелепи.

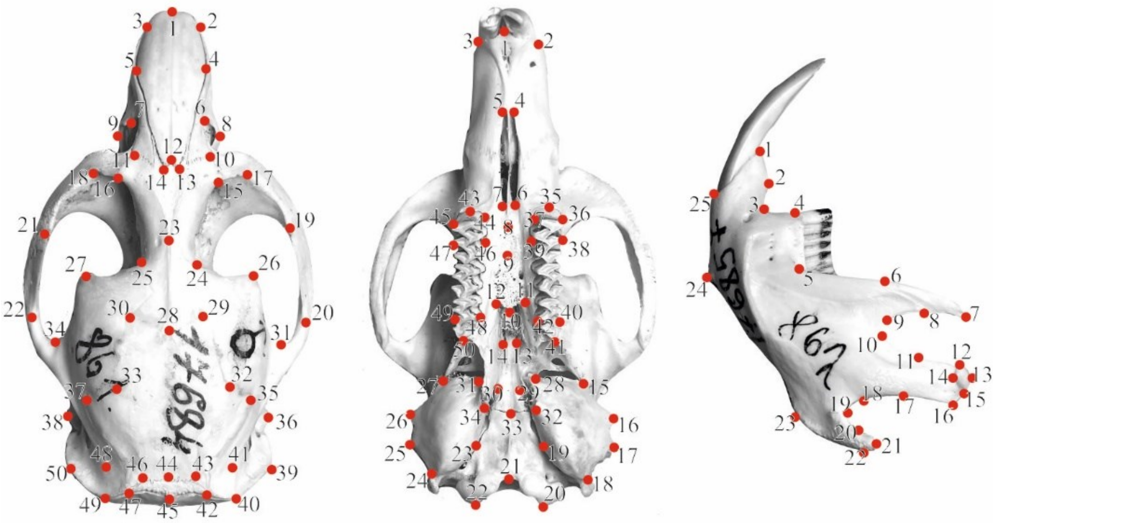


Fig. 2. Landmarks on the dorsal and ventral surfaces of the skull and on the buccal surface of the left mandible used in geometric morphometrics analysis.

Рис. 2. Орієнтири на дорсальній та вентральній поверхні черепа та на щічній поверхні лівої нижньої щелепи, аналізовані методами геометричної морфометрії.

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 skull from the Donets dataset was excluded from all analyses, and two skulls from the Dnister dataset basin were excluded from the ventral surface analysis.

Shape variation of the muskrat 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.

Table 1. Landmarks selected for shape analysis of the skull and mandible

Таблиця 1. Орієнтири, вибрані для аналізу форми черепа та нижньої щелепи

Surface	Description of landmarks
Dorsal surface of the skull (50)	1[1], 2, 3, 4[1], 5[1], 6, 7, 8[2], 9[2], 12[1], 13[1], 14[1]—points on the edges and at the junction of the nasal bone sutures; 10[3], 11[3]—midpoints of the sutures between the zygomatic bones and nasal bones; 15[1], 16[1], 17[2, 6], 18[2, 6], 19[3], 20[3], 21[3], 22[4], 24[4], 25[4], 26[4], 27[4], 31[1, 6], 34[1, 6]—marks at the angles and sutures around the orbits; 23, 24[4], 25[4], 26[4], 27[4], 28[1, 4]—points on the edges of the axial suture; 29[4], 30[4], 32, 33, 35, 37—marks indicating the angles of the parietal bones; 43, 44[4, 6], 46—points in the middle and edges of the suture between the occipital and parietal bones; 36, 38—extreme lateral points of the auditory bullae; 39, 40, 41[4], 42[1], 45[1], 47[1], 48[4], 49, 50—points on the edges and dots marking the angles of the occipital bones.
Ventral surface of the skull (50)	1[1, 2, 5], 2[1], 3[1]—lateral and midpoints of the incisor base; 4[1], 5[1], 6[1], 7[1]—points on the edges of the incisive foramina; 8[5], 9, 10[1, 5], 11[3], 12[1, 3]—points on the edges, axis, and sutures of the palatine bone, 13[1], 14[1]—points on the edges of the palatine bone; 15[6], 16, 17[1, 6], 18[6], 19[1, 6], 28[1], 32[1, 6], 23[6], 24[6], 25[1, 6], 26, 27[1, 6] , 31[1], 34[1, 6]—points on the edges and angles of the auditory bullae; 29, 30[1]—points on the edges of the narrowest space between the auditory bullae; 33[1]—midpoint between the auditory bullae; 20[1], 21[1, 5], 22[1, 2]—points on the edges and angles of the occipital bones in the area of the foramen magnum; 35[1], 36, 37, 38, 39, 40, 41[1], 42[1], 43[1], 44, 45, 46, 47, 48, 49, 50[1]—extreme points of the upper molar alveoli.
Buccal surface of the left mandible (25)	1[6], 2[6], 3[6]—points on the edges and angles of the diastema; 4[6]—the point between the jaw and the first molar; 5[6], 6[6], 7[6], 8, 9—coronoid process; 10, 11, 16[6], 17[6], 18[6]—condyloid process; 12[6], 13, 14, 15—points on the edges of the joint; 19[6], 20[6], 21[6], 22[6], 23[6]—points on the edges of the angular process; 24[6], 25[6]—points on the edges of the mandible body.

References: (1) Lalis *et al*. 2009; (2) Quintela *et al*. 2016; (3) Maga *et al*. 2015; (4) Chueva *et al*. 2020; (5) Cox *et al*. 2013; (6) Ge *et al*. 2015.

Results of Linear Morphometrics

According to the absolute values of the 14 craniometrical characters studied, muskrats of all the five geographical samples have rather similar dimensions (Table 2). The Donets sample is characterised by smaller values of characters that are related to the general dimensions of the skull, both the rostral and neurocranial parts, such as condylobasal length (CBL), cranial height (CRH), braincase width (CRB), diastema length (DIA), and incisive foramina length (FIL), as well as mandible length (MAL). The other four samples are characterised by rather similar values of these characters, except for the Dnipro sample that demonstrate larger values of auditory bulla width (BUB).

The highest coefficients of variation (CV) are shown for such characters as incisive foramina length (FIL) and auditory bulla length (BUL). The most variable characters also include diastema length (DIA) in the Snihurivka and Danube samples, zygomatic width (ZYG) in the Snihurivka and Dnipro samples, and interorbital width (IOR) in the Dnipro and Donets samples.

However, in general, even these small differences appear to be significant ($p < 0.05$) between most of the analysed samples. Despite having smaller general dimensions of the skull, the Donets sample demonstrates no significant differences ($p > 0.05$) from the other four samples. Similarly, the Danube sample also does not differ significantly from the Dnister population ($p = 0.08$).

Principal component analysis (PCA) of the craniometrical characters of muskrats revealed that the first two components describe 81% of total variance, of which PC1 describes 74% (Table 3). All characters score positively on the first principal component and the highest loadings have the characters CBL and ZYG, which describe the general length and width of the skull.

The characters MAL, ROH, DIA, MAH, and CRB also score relatively largely, which are also related to general cranial dimensions. Accordingly, only the Donets sample separates along PC1, whereas the other samples largely overlap (Fig. 3 *a*). They demonstrate some degree of variation along PC2, the highest loadings on which have the characters of the mandible, i.e. MAL and MAH. The characters CBL, ZYG, and MAL also have the highest loadings on PC3.

On the other hand, canonical variates analysis (CVA) also confirms the differences between the Snihurivka, Danube, Dnipro, and Dnister samples, between the Danube and Dnipro samples, and between the Dnipro and Dnister samples (Fig. 3 *b*).

Table 2. Results of measurements of *Ondatra zibethicus* skulls in five samples from the territory of Ukraine

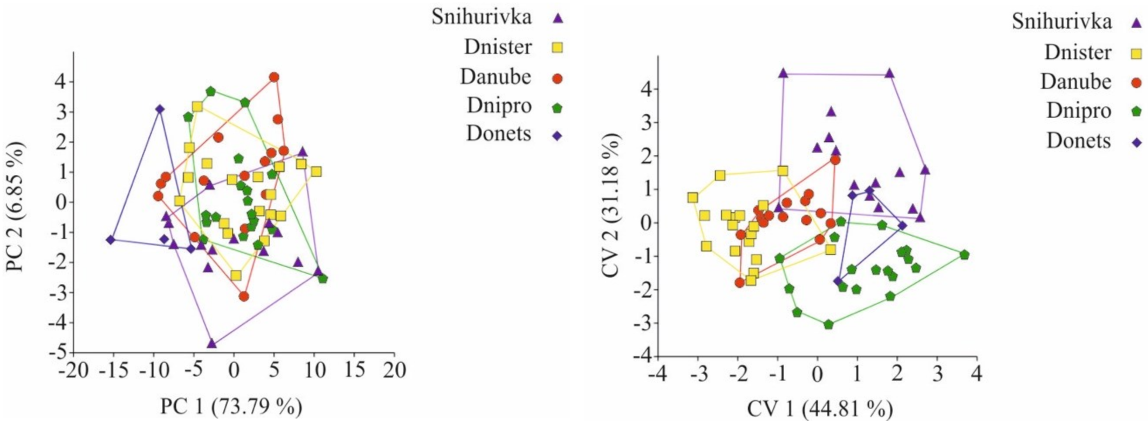
Таблиця 2. Результати вимірів черепів *Ondatra zibethicus* із п’яти вибірок із території України

Characters	Dnipro, n = 19		Snihurivka, n = 15		Danube, n = 15		Dnister, n = 19		Donets, n = 4	
	min–max M±SD	CV	min–max M±SD	CV	min–max M±SD	CV	min–max M±SD	CV	min–max M±SD	CV
CBL	57.4–66.9 61.2±2.3	3.7	54.5–67.0 60.9±3.6	5.9	54.2–63.0 60.0±2.9	4.8	56.6–66.6 62.1±2.9	4.7	52.2–60.0 56.1±3.3	5.9
CRH	20.5–24.9 22.1±1.0	4.6	20.0–23.2 21.7±1.0	4.7	20.0–24.2 22.0±1.5	6.8	21.0–25.4 22.5±1.3	5.6	18.0–20.0 19.1±0.9	4.5
CRB	24.7–28.0 26.6±0.9	3.3	24.0–28.2 25.9±1.3	4.9	23.9–30.1 26.9±2.1	7.8	24.8–28.1 27.0±1.0	3.6	22.0–24.2 23.4±1.0	4.2
ZYG	31.1–42.5 37.1±2.4	6.5	31.0–41.5 36.5±3.4	9.2	32.1–41.3 37.0±2.9	7.7	33.1–41.6 37.3±2.0	5.4	29.6–34.0 32.8±2.1	6.5
IOR	5.5–7.1 6.3±0.5	7.3	5.5–6.5 6.1±0.2	3.8	6.0–6.9 6.4±0.2	3.9	6.2–7.2 6.8±0.3	4.0	5.0–6.5 6.1±0.7	11.8
ROH	20.9–26.0 23.2±1.2	5.3	22.0–28.0 24.1±2.0	8.4	20.2–25.4 23.2±1.6	7.0	21.2–27.1 23.7±1.5	6.1	19.0–21.5 20.0±1.2	6.0
FIL	10.0–14.0 12.5±1.1	9.0	10.0–15.8 12.3±1.7	13.8	10.0–14.3 12.3±1.3	10.8	11.3–15.5 13.7±1.1	7.7	9.4–11.5 10.5±1.0	9.4
BUL	11.0–14.3 13.5±0.7	5.0	12.3–16 13.4±0.9	6.9	12.0–17.2 14.1±1.5	10.7	12.5–15.0 13.3±0.6	4.9	11.5–17.0 13.4±2.5	18.7
BUB	10.0–12.0 11.6±0.6	5.4	9.0–12.0 10.6±0.8	7.9	9.3–11.0 10.0±0.5	4.7	9.1–11.1 10.3±0.6	6.0	9.9–10.7 10.7±0.4	3.6
DBM	14.0–16.0 15.0±0.5	3.4	14.0–16.0 15.2±0.8	5.2	13.8–16.5 14.9±0.9	6.1	14.1–17.0 15.3±0.7	4.4	13.9–14.5 14.2±0.3	1.9
dbm	14.0–16.0 15.4±0.5	3.1	14.0–15.8 15.0±0.5	3.0	13.8–18.0 15.1±1.0	6.7	13.7–15.5 14.7±0.5	3.5	13.3–14.0 13.8±0.4	2.5
DIA	19.0–25.4 22.2±1.3	5.8	18.0–25.0 21.8±1.9	8.6	17.6–23.5 21.6±1.7	8.1	19.8–24.0 21.7±1.4	6.3	17.6–20.0 18.7±1.1	5.8
MAL	31.7–41.8 36.8±2.3	6.2	33.0–42.0 37.2±2.6	7.1	31.2–39.1 36.2±2.3	6.3	30.3–39.0 37.2±2.3	6.1	31.0–35.0 33.3±2.0	6.1
MAH	30.0–35.8 32.4±1.3	3.9	28.4–36.0 30.9±2.2	7.0	29.2–37.0 32.3±2.5	7.7	29.8–36.0 32.6±1.8	5.7	27.2–31.3 29.6±1.7	5.8

Table 3. Factor loadings of the linear craniometrical characters on the first three principal components

Таблиця 3. Факторні навантаження лінійних краніометричних ознак на перші три головні компоненти

Character	PC 1	PC 2	PC3	Character	PC 1	PC 2	PC3
CBL	0.5318	-0.1739	-0.6925	DBM	0.0829	-0.0663	-0.0570
ZYG	0.4601	0.1925	0.4007	DIA	0.2758	-0.0722	-0.1159
IOR	0.0042	0.0810	-0.0271	ROH	0.2905	0.0035	0.0066
FIL	0.1847	0.0767	-0.2331	BUB	0.0380	-0.0371	-0.0363
CRB	0.2421	0.1858	0.2505	MAL	0.3680	-0.6450	0.4413
CRH	0.1848	0.1493	0.1678	MAH	0.2729	0.6595	0.0337
				Variance, %	73.79	6.85	4.80



a *b*

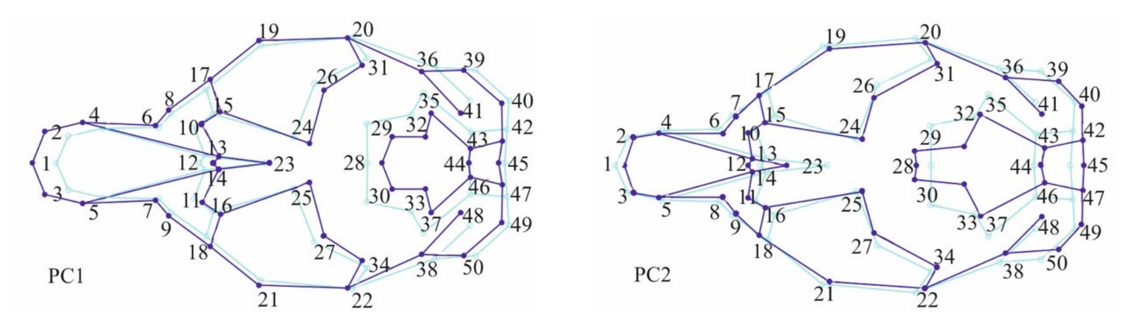
Fig. 3. The distribution of muskrat samples in the space of the first two principal components (*a*) and canonical variates (*b*) based on linear craniometrical characters.

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

Results of Geometric Morphometrics

Variation of the shape of cranial elements on the dorsal and ventral surfaces of the skull and on the buccal surface of the left mandible was analysed by utilising tools of landmark-based geometric morphometrics. The results revealed that, contrary to variation by linear characters, shape variation is more substantial between the samples, even between those that do not differ significantly by cranial dimensions.

In case of the dorsal surface of the skull, 80% of the variance is described by the first ten principal components, of which 34.81% is described by PC1 and 10.98% by PC2. The coordinates x1, x2, x3, and y32 have the highest negative scores on PC1, whereas x29, x30, and y33 have the highest positive scores. These points mark the distal end of the nasal bones and the distal and lateral ends of the parietal bones (Fig. 4 *a*). Meanwhile, the coordinate x23, which is on the interfrontal suture, and the coordinates y29, y30, y32, y33, and y37, which mark the lateral edges of the right and left parietal bones, have the highest loadings on PC2 (Fig. 4 *b*). Thus, variation of specimens along both PC1 and PC2 is mainly related to the variation of the shape of the nasal and parietal bones and of the interorbital suture, although all five samples greatly overlap (Fig. 5). Coordinates marking the lateral edges of the parietal bones (x32, x33) have the highest loadings also on PC3.



a *b*

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*).

When analysing the differences between the samples from different river basins, each sample tend to form its own cloud in the space of the first two canonical variates (Fig. 6). There can also be seen a trend of variation along a geographical gradient, and animals from neighbouring river basins tend to be more similar. In particular, the lowest values of Mahalanobis distances were obtained for the samples of Snihurivka–Dnipro, Danube–Dnister, and Danube–Snihurivka basins, whereas the Donets sample is the most distant from the other four (Table 4).

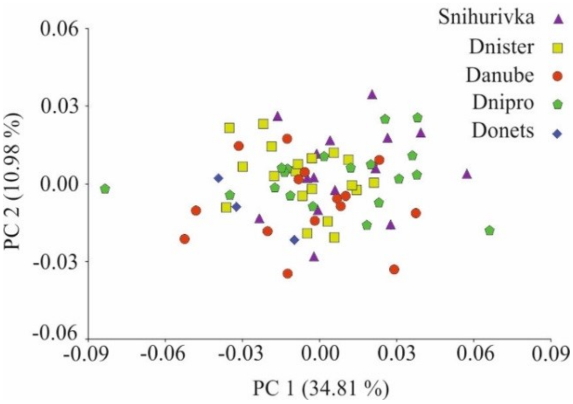


Fig. 5. Distribution of muskrat specimens from different river basins of Ukraine in the space of the first two principal components according to the shape of the dorsal surface of the skull.

Рис. 5. Розподіл зразків ондатр із різних річкових басейнів України у просторі перших двох головних компонент за формою дорсальної поверхні черепа.

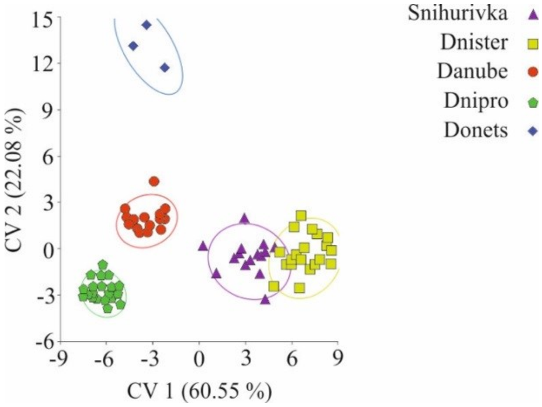


Fig. 6. Distribution of muskrat samples from different river basins of Ukraine in the space of the first two canonical variates according to the shape of the dorsal surface of the skull.

Рис. 6. Розподіл вибірок ондатр із різних річкових басейнів України у просторі перших двох канонічних змінних за формою дорсальної поверхні черепа.

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

p \ D_M	Donets	Danube	Dnipro	Snihurivka	Dnister
Dorsal (F = 3.29; p = 0.0001)					
Donets	—	13.8748	17.5960	16.2777	16.3975
Danube	**0.1155**	—	11.3034	8.8818	7.4282
Dnipro	0.0016	0.0022	—	6.5816	13.3616
Snihurivka	0.0046	0.0191	0.0003	—	10.5509
Dnister	0.0215	0.0124	0.0007	0.0140	—
Ventral (F = 3.09; p = 0.0001)					
Donets	—	11.5919	10.9412	9.5842	13.1642
Danube	**0.1063**	—	10.4214	6.9716	11.4761
Dnipro	0.0008	0.0246	—	8.4002	12.7166
Snihurivka	0.0287	**0.1298**	**0.1711**	—	9.8682
Dnister	0.0009	0.0006	0.0001	0.0024	—
Mandible (F = 2.92; p = 0.0001)					
Donets	—	11.6421	11.7009	12.6879	10.9933
Danube	0.0409	—	7.6189	6.6431	6.3762
Dnipro	0.0030	0.0395	—	4.8541	5.6558
Snihurivka	0.0014	0.0236	0.0018	—	7.1056
Dnister	0.0082	0.0009	0.0060	0.0006	—

Note: p > 0.05 are given in bold.

Despite these close distances among the samples, they differ significantly except for the pair of the Donets–Danube samples, although it may be related to the small size of the Donets sample given that there is a relatively large geographical distance between these two populations.

The analysis of landmarks on the ventral surface of the skull revealed that, similarly to the dorsal surface, 80% of variance is described by the first ten principal components, of which 26.66% is described by PC1 and 13.58% by PC2. The coordinates x39 and x46 have the highest negative scores on PC1, whereas x1, x2, and x3 have the highest positive scores. These points mark the mesial edge of alveoli at the distal part of M1 and the distal end of premaxillae, respectively (Fig. 7 *a*). Relatively high loadings on PC1 have also the coordinates x40–x42 and x48–x50 that mark the edges of alveoli around the proximal part of M3. The variation of placement of points that mark certain alveoli also indirectly denotes the variation in the shape of the distal and proximal parts of the hard palatine.

Coordinates that have the highest loadings on PC2 include x1, x40–x42, and x48–x50, which are related to the suture between the most distal points of the premaxillae at the base of the incisors, and to the edges of alveoli around the proximal part of the right and left M3, which indirectly denote the variation of the proximal part of the hard palatine as well (Fig. 7 *b*). Relatively high scores on PC2 have also the coordinates y16–y18 and y24–y26 that describe the shape of the posterolateral edges of auditory bullae. Additionally, coordinates x6 and x7 that mark the proximal end of incisive foramina have the highest loadings on PC3.

Similarly to the case with the dorsal surface of the skull, variation of specimens along PC1 and PC2 tends to be similar and all five samples greatly overlap, although specimens from the Snihurivka sample demonstrate a wide range of variation along both principal components (Fig. 8).

Canonical variates analysis showed that samples from different river basins form separates clouds in the space of CV1 and CV2 (Fig. 9). A trend of geographical variation can also be seen among the groups. In particular, the sample from the Dnister basin is the most distant from the Donets, Dnipro, and Danube samples and the differences are significant ($p < 0.05$). On the other hand, the sample from Snihurivka is the closest to the samples from the neighbouring Dnipro and Danube basins and does not differ significantly from them (see: Table 3).

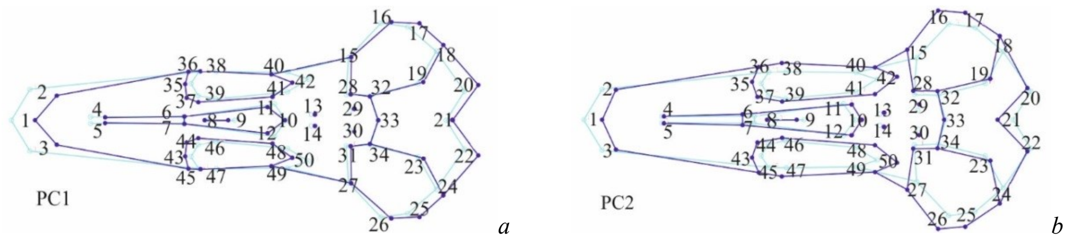


Fig. 7. Variation of the shape of the ventral surface of the skull along PC1 (*a*) and PC2 (*b*).

Рис. 7. Зміни форми вентральної поверхні черепа за ГК1 (*a*) та ГК2 (*b*).

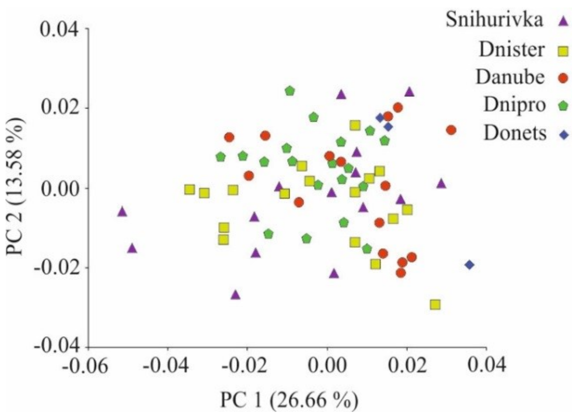


Fig. 8. Distribution of muskrat specimens from different river basins of Ukraine in the space of the first two principal components according to the shape of the ventral surface of the skull.

Рис. 8. Розподіл зразків ондатр із різних річкових басейнів України у просторі перших двох головних компонент за формою вентральної поверхні черепа.

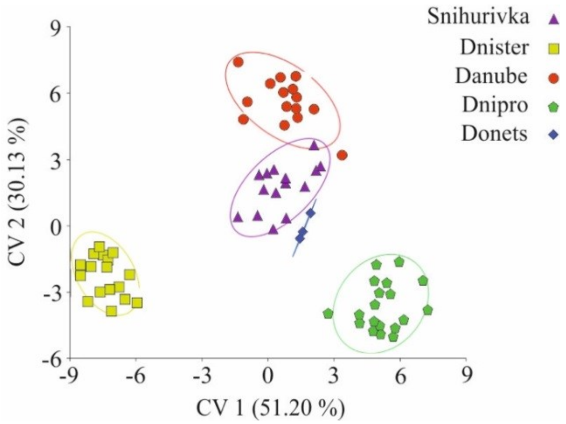


Fig. 9. Distribution of muskrat samples from different river basins of Ukraine in the space of the first two canonical variates according to the shape of the ventral surface of the skull.

Рис. 9. Розподіл вибірок ондатр із різних річкових басейнів України у просторі перших двох канонічних змінних за формою вентральної поверхні черепа.

Considering that the mandible is heavily involved in feeding, its morphology may reflect adaptive traits related to the food sources a particular locality provides. The principal component analysis of landmarks on the buccal surface of the mandible showed that 83% of variance is described by the first nine principal components, of which 27.07% is described by PC1 and 15.16% by PC2.

Variation in the shape of the mandible is mainly related to the changes in angles and shapes of the elements of the ascending ramus, and, to a lesser extent, in the shape of the distal end of the corpus (Fig. 10). In particular, the highest positive loadings on PC1 have coordinates x18–x20 and y20–y22 that are related to the bight between the condylar and angular processes and the general shape of the angular process, respectively. The highest negative scores on PC1 have coordinates y7, x2, x13, x15, and x25, which, respectively, mark the tip of the coronoid process, the most convex part of the diastema, the tip of the condylar process, and the lower distal end of the mandibular body.

Similarly, coordinates x6–x8 and y18–21 have the highest positive and y1, y2, x19, x20, x23, and x25 have the highest negative scores on PC2—all these points are related to the shape of the coronoid, condylar, and angular processes of the mandible and the shape of the bight between the condylar and angular processes. Meanwhile, landmarks that describe the shape of the anterior edge of the coronoid process and the lower edge of the angular process have the highest loadings on PC3.

Overall, the lower mandible demonstrates a relatively high degree of shape variation, particularly in the masseteric region. It is the part of the mandible where large masticatory muscles attach and through which the mandible itself attaches to the cranium. Such a high degree of shape variation might be influenced with a varying quality of feeding resources provided in the estuarine lower (Danube, Dnipro, and Snihurivka) and less productive middle (Dnister, Donets) reaches of rivers. Nonetheless, specimens from various river basins greatly overlap in the space of the first two principal components, although muskrats from the Snihurivka, Danube, and Donets basins tend to separate along PC2 (Fig. 11).

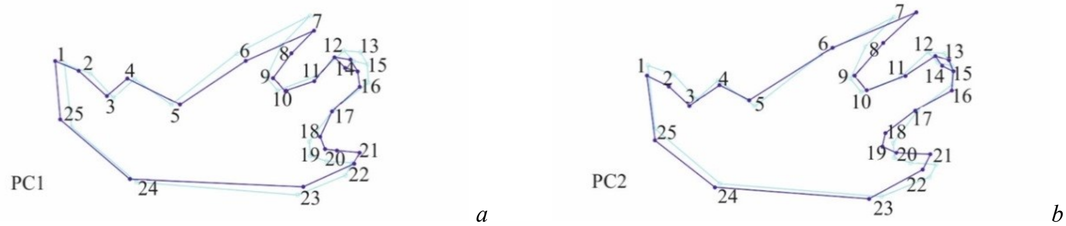


Fig. 10. Variation of the shape of the buccal surface of the left mandible PC1 (*a*) and PC2 (*b*).

Рис. 10. Зміни форми щічної поверхні лівої нижньої щелепи за ГК1 (a) та ГК2 (b).

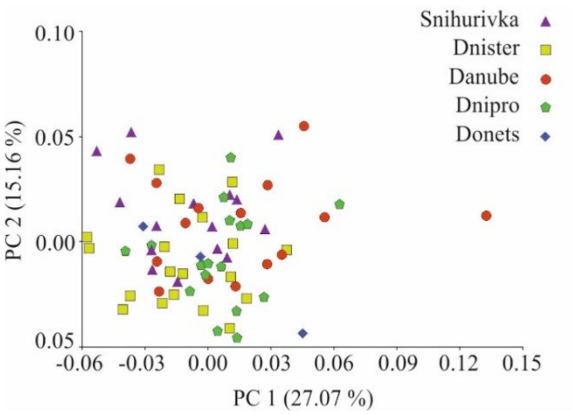


Fig. 11. Distribution of muskrat specimens from different river basins of Ukraine in the space of the first two principal components according to the shape of the buccal surface of the left mandible.

Рис. 11. Розподіл зразків ондатр із різних річкових басейнів України у просторі перших двох головних компонент за формою щічної поверхні лівої нижньої щелепи.

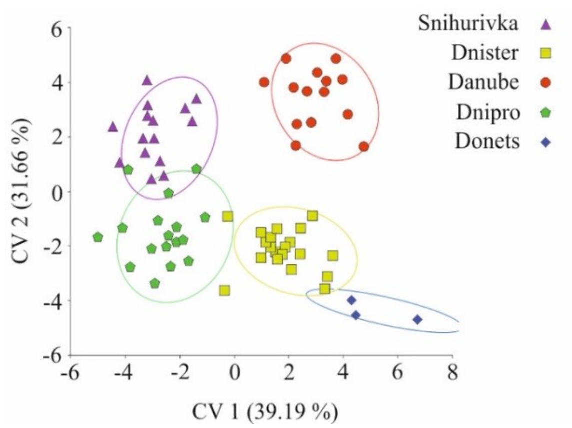


Fig. 12. Distribution of muskrat samples from different river basins of Ukraine in the space of the first two canonical variates according to the shape of the buccal surface of the left mandible.

Рис. 12. Розподіл вибірок ондатр із різних річкових басейнів України у просторі перших двох канонічних змінних за формою щічної поверхні лівої нижньої щелепи.

On the other hand, canonical variates analysis showed that samples from different river basins form well-separated clouds in the space of CV1 and CV2 (Fig. 12). In particular, the Snihurivka–Dnipro, Danube–Dnister, and Donets samples form separate groups along CV1, whereas separation along CV2 can be observed between the groups of Snihurivka–Danube, Dnister–Dnipro, and Donets. In both cases, variation is related to the shape of the condylar and angular processes and adjacent curvatures of the mandible. Based on the mandible shape, the differences between each sample are statistically significant (Table 3).

Discussion

The muskrat is a Nearctic element in the Eurasian mammal fauna and has demonstrated a relatively large scale of morphological differentiation across the continent depending on local habitat features (e.g. [Ruprecht 1974; Pankakoski & Nurmi 1986; Otgonbaatar & Shar 2019; Chueva *et al.* 2020] and references therein).

In Ukraine, as well as in other countries of the former USSR, muskrats were introduced with a declared aim to enrich the fauna of local game and 'industrially important' (particularly fur-bearing) species, and the animals were brought from previously established populations in various regions of Russia [Pavlov *et al.* 1973; Volokh 2014]. Shortly, muskrats have established stable populations and their dynamics have been subject to a number of studies (e.g. [Panov 2002; Volokh 2014; Lazariev 2023]). However, research into the morphological variation of muskrats that inhabit different river basins of Ukraine has not been carried out before and this is the first analysis of such kind employing a variety of analytical approaches.

Traditional morphometric analysis included the study of variation of 14 craniometrical characters by using both univariate and multivariate methods. Despite the fact that the Donets sample included only four specimens, general trends of geographical variation of muskrats can be inferred.

In particular, muskrats from the Donets basin demonstrate smaller skull dimensions, whereas the other four samples are characterised by similar sizes of the rostral and neurocranial regions.

Principal component analysis revealed that condylobasal length and zygomatic length contribute the most into the variation between the Donets and the other four samples, whereas the latter demonstrate some degree of differentiation along PC2, on which mandible length and mandible height have the highest factor loadings. Geographical differences between muskrats therefore appear to manifest in the morphology of the mandible, which is functionally closely related to feeding and diet.

Geometric morphometrics allows for a more detailed analysis of differences between cranial morphologies and it was shown to yield fairly accurate results even when relatively small samples are available [Cardini *et al*. 2021], which is the case with the Donets sample. Using this approach, shape-related variation was revealed on both sides of the skull as well as on the buccal side of the lower jaw.

On the dorsal surface, the shape of the nasal and parietal bones and related sutures are the most contributing characters into the variation between the samples. On the ventral surface, those characters include the shape of alveoli around the proximal end of M3, of the most distal end of the praemaxillae, and of the proximal end of the incisive foramina, which also describe the shape of the elements of the hard palatine and diastema. The shape of the auditory bullae also seems to be an important contributing factor. Although the samples from different river basins greatly overlap in the space of the first two principal components, a trend of geographic variation can also be inferred in that animals from neighbouring river basins tend to have more similar features.

The most important differentiation, however, is by the shape of the lower jaw, as predicted by the analysis of metric characters, particularly by the shape and spatial relations of the elements of the ascending ramus. These include not only the coronoid, condylar, and angular processes, but also the shape of bights between them as well as adjacent curvatures on the dorsal and ventral edges of the ramus. All five samples differ significantly from one another by the shape of the mandible making it the most variable element of the muskrat skull.

The revealed features allow suggesting that the main contributing factors into the variation of geographically distinct populations include diet and feeding adaptations on the one hand and possible spatial relationships and origin on the other. For instance, muskrats in the Danube basin could have been originated from both introduction and expansion from already established populations at upper sections of the river. The same applies to the Dnister River basin.

Similarly, morphological features of muskrats from the Donets sample can also be explained by several factors, including geographical remoteness, relative isolation, and different natural conditions. Different sources of introduction is a less likely reason for such substantial differences of this sample, as it is known from the literature that the main centre of introduction of muskrats here was Kreminna Raion in Luhansk Oblast [Lavrov 1957], particularly the Serebrianka forestry and other areas in the middle reaches of the Donets. In addition, the samples from the Donets River basin were collected much later than the rest of the samples studied, so they may possess characteristics acquired as a result of their long existence in relatively isolated locations. Averaged Mahalanobis distances also reflect a geographical pattern in the craniological variation of muskrats (Fig. 13)

When comparing our results with data reported from geographically distant regions, they are practically in line with and further confirm the so-called 'hydrobiont rule' [Panteleyev *et al*. 1990], according to which the size and weight of animals are larger in large river basins due to the excessive heat loss during swimming. This pattern is observed both in the natural range of the muskrat and in areas where the species was introduced (Table 5).

Thus, the size of animals tends to be larger in floodplains of large rivers, as demonstrated by the sample from Louisiana (Mississippi River basin) [Latimer & Riley 1934], and, conversely, smaller in smaller rivers, as seen in the sample from Texas (Texas River basin) [Gould & Kreeger 1948]. This trend is evident by most of the main craniological measurements, except for interorbital width, which is likely to decrease with age [Otgonbaatar & Shar 2019] and depending on the size and productivity of the ecosystem in which the animals exist.

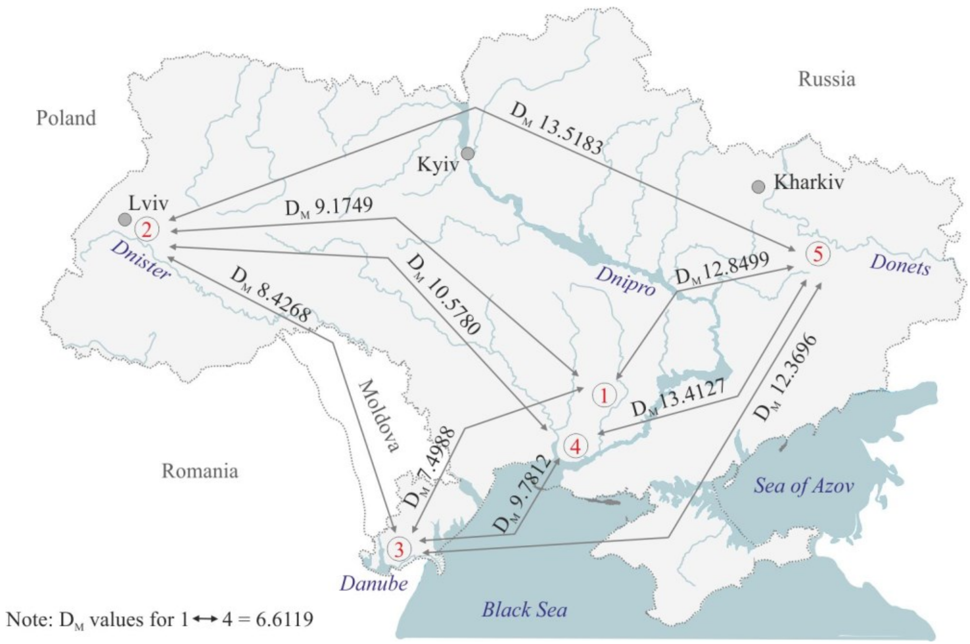


Fig. 13. Averaged Mahalanobis distances (D_M) between the studied samples (based on Table 4). Samples: (1) Snihurivka; (2) Dnister; (3) Danube; (4) Dnipro; and (5) Donets.

Рис. 13. Усереднені значення відстаней Махаланобіса (D_M) між дослідженими вибірками (на основі табл. 4). Вибірки: (1) Снігурівка; (2) Дністер; (3) Дунай; (4) Дніпро; (5) Донець.

Table 5. Mean values (mm) of craniometrical characters of muskrats from different countries and regions

Таблиця 5. Середні значення (мм) краніометричних ознак ондатр із різних країн і регіонів

Region	n	CBL	ZYG	IOR	DIA	DBM	References
USA, Kansas	124	62.4	38.3	6.6	22.5	15.0	Latimer & Riley 1934
USA, Louisiana	357	65.5	40.9	6.3	22.5	15.9	Gould & Kreeger 1948
Finland (regional mean)	580	62.8	38.7	6.8	21.8	15.5	Pankakoski & Nurmi 1986
Lithuania (regional mean)	–	60.3	36.6	6.6	20.7	15.4	Skyriene & Paulauskas 2014
Poland (regional mean)	62	62.3	37.3	6.3	22.0	15.6	Ruprecht 1974
Germany (regional mean)	78	60.6	11.5	6.8	20.4	15.1	Otgonbaatar & Shar 2019
Mongolia, Khar-Us Lake	208	64.0	36.4	6.1	23.1	15.9	Otgonbaatar & Shar 2019
Russia, Kurgan & Chelyabinsk	69	63.4	38.5	6.1	22.5	15.3	Sokolov & Lavrov 1993
Russia, Komi	9	63.6	39.5	6.0	24.3	16.8	Estafiyeva 1994
Russia, Arkhangelsk	3	63.4	38.1	6.2	21.7	17.1	Estafiyeva 1994
Russia, Nizhny Novgorod	15	63.2	38.8	6.2	23.2	15.8	Chueva *et al*. 2020
Kazakhstan, Ili river	21	64.3	38.8	6.0	23.6	15.9	Chueva et al. 2020
Ukraine (regional mean)	72	60.7	36.7	6.4	21.6	15.0	this study

No substantial differences were found among the measurements of muskrat skulls from Finland, Russia, Kazakhstan and Mongolia, even when compared to samples from the species' natural range (USA). However, the samples from Germany, Lithuania and Ukraine, which are smaller, exhibit notable differences.

The Lithuanian sample includes animals of secondary introductions [Lavrov 1957; Prūsaitė *et al*. 1988], and the same applies to the Ukrainian sample [Pavlov *et al*. 1973; Volokh 2014].

Researchers of the Lithuanian sample focus on the distinction between populations formed as a result of primary and secondary introductions, where the primary (Finland, Germany, etc.) ones are larger and the secondary (Lithuania) ones are smaller [Skyriene & Paulauskas 2014].

The skulls of muskrats from the territory of Ukraine are also smaller compared to those from populations from which animals were selected for introduction in Ukraine (Kurgan and Arkhangelsk regions of Russia, Fig. 14) [Pavlov 1973; Volokh 2014].

Muskrats from the Ukrainian part of the Danube basin are also notably smaller than the average for other Danube countries [Skyriene & Paulauskas 2014; Otgonbaatar & Shar 2019]. The Danube population was likely formed as a combined result of expansion from already established European populations and local introductions.

Several studies have also repeatedly emphasised the dependence of animal skull size on climatic conditions, temperature, nutrition, and isolation, which can lead to differences between populations [Cerevitinov 1970; Ruprecht 1974]. The map of Eurasia (Fig. 14) shows the similarity of close and distant samples in terms of size (CBL). In addition, the difference between the zones of primary and secondary introduction is confirmed, in particular, for Poland and Finland, CBL values fluctuate within 62 mm, while for Germany, Ukraine, and Lithuania they are within 60 mm. The size increases with the size of the water area—the largest muskrat skulls are found in large rivers in Russia (primary introduction zone), Kazakhstan, and lakes in Mongolia.

Based on the above, we suggest that the contribution of the area of water bodies and the productivity of ecosystems in which populations were formed into the patterns of geographical variation is equally important as the factor of origin via primary or secondary introduction.

Conclusions

The morphometric study of skulls of the introduced muskrat from five different river basins of Ukraine has revealed several variation patters that can be summarised as follows:

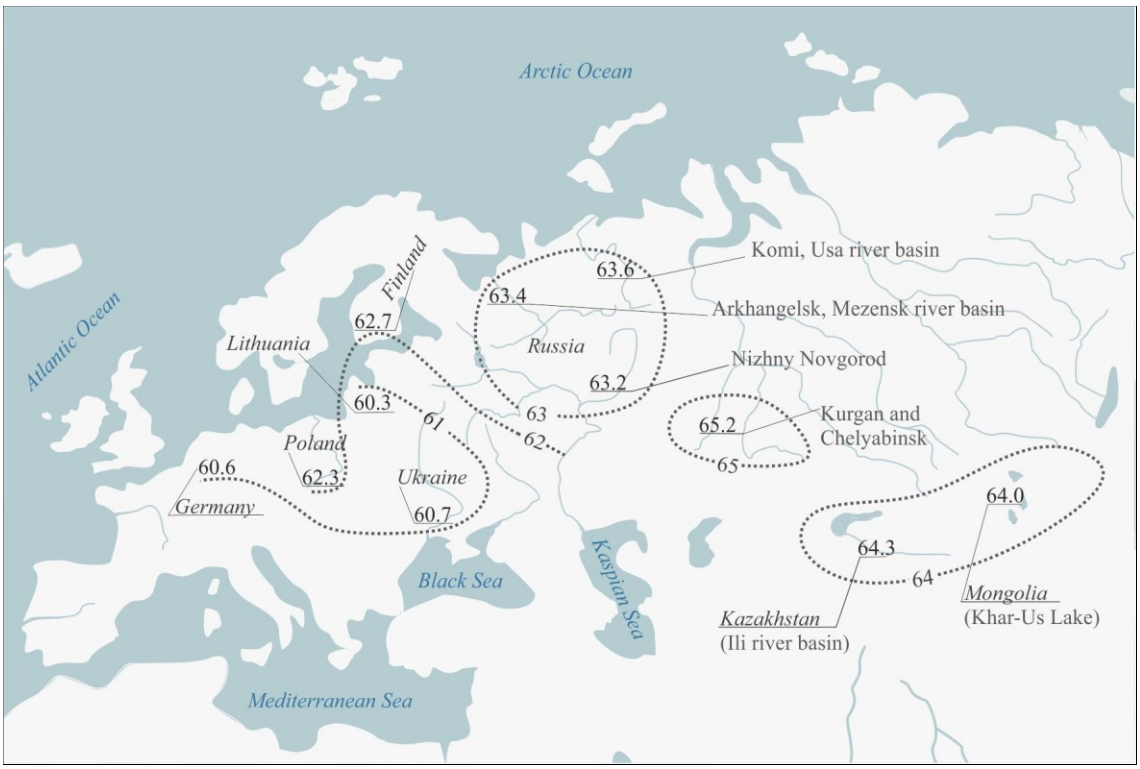


Fig. 14. Average values of the condylobasal length (CBL) of the muskrat skull in geographically distant populations on the map of Eurasia (based on Table 1). Dotted lines combine values rounded to whole numbers.

Рис. 14. Середні значення кондилобазальної довжини (CBL) черепа ондатри у географічно віддалених популяціях на карті Євразії (за даними табл. 1). Пунктирами об’єднано значення в округленні до цілих чисел.

1. Among the five muskrat samples, specimens from the Donets basin have the smallest skulls. Muskrats in the samples from the Snihurivka irrigation canal (Mykolaiv Oblast), the lower reaches of the Dnipro (Kherson Oblast), and the upper reaches of the Dnister (Lviv and Ternopil oblasts) are characterised by similar values of craniometrical characters. Animals from the Danube basin (Odesa Oblast) tend to be larger.

2. Multivariate methods (PCA, CVA) revealed that condylobasal length (CBL) and zygomatic width (ZYG) are the characters that contribute the most into the differences between the Donets and the other four samples, whereas mandible length (MAL) and mandible height (MAH) contribute the most into the differentiation among the latter.

3. Geometric morphometrics analysis indicates that geographic distance and the level of isolation contribute to differences between various samples by the shape of the skull and its structures. The most important distinguishing features include the shape of the nasal and parietal bones and related sutures on the dorsal surface of the skull, as well as the shape of alveoli around the proximal end of M3, the most distal end of the praemaxillae, the auditory bullae, and the relative placement of the proximal end of the incisive foramina, i.e. the shape of structures mainly related to the diastema and proximal part of the hard palatine.

4. The most significant differences between the five samples are related to the shape of the lower jaw, particularly the shape and relative orientation of the elements of the ascending ramus—the coronoid, condylar, and angular processes, as well as the shape of bights between them and of the adjacent curvatures on the dorsal and ventral edges of the ramus.

5. The revealed features allow suggesting that the main contributing factors into the variation of geographically distinct populations include diet and feeding adaptations on the one hand and possible spatial relationships and origin on the other.

6. The comparison of mean values of the most important craniometrical characters of the Ukrainian sample with mean values reported from other countries and regions revealed notable differences in size variation between populations within the natural geographic range and regions of primary and secondary introductions. In areas of secondary introduction, the animals have notably smaller cranial dimensions.

7. Differences revealed by methods of both traditional and geometric morphometrics are likely attributable to environmental conditions, water area, habitat productivity, and the level of isolation and geographic distance between different populations.

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