Theriologia Ukrainica, **28**: 55–68 (2024)
p-ISSN 2616-7379 • e-ISSN 2617-1120
DOI: 10.53452/TU2805

CRANIOLOGY OF *NYCTEREUTES PROCYONOIDES* (CARNIVORA) BASED ON MATERIALS FROM UKRAINE

Denys Lazariev

Key words

common raccoon dog, craniological analysis, geometric morphometrics, introduction, river basins of Ukraine

doi

http://doi.org/10.53452/TU2805

Article info

submitted 02.10.2024
revised 27.12.2024
accepted 30.12.2024

Language

English, Ukrainian summary

Affiliations

I. I. Schmalhausen Institute of Zoology, NAS of Ukraine (Kyiv, Ukraine); National Museum of Natural History, NAS of Ukraine (Kyiv, Ukraine)

Correspondence

Denys Lazariev; I. I. Schmalhausen Institute of Zoology, NAS of Ukraine; 15 Bogdan Khmelnitsky Street, Kyiv, 01054, Ukraine; Email: lazarevden@ukr.net; orcid: 0000-0002-8663-747X

Abstract

The article presents the results of a comprehensive craniological analysis of the common raccoon dog (*Nyctereutes procyonoides* Gray 1834) based on adult skulls from four samples, three of which comprise materials from Ukraine: 1) central and northern oblasts of Ukraine (Kyiv, Chernihiv, and Cherkasy oblasts); 2) eastern oblasts of Ukraine (Luhansk, Zaporizhzhia, and Poltava oblasts); 3) southern oblasts of Ukraine (Kherson Oblast). Additionally, a sample that includes materials from the native range of the species (Khabarovsk Krai, Primorsky Krai, and Chita Oblast of Russia) was also analysed. The research included standard analysis based on craniometric measurements of 19 parameters, and analysis of the skull shape by tools of geometric morphometrics separately for the dorsal and ventral sides of the skull and the buccal surface of the left mandible. The total sample comprised 62 specimens. The results of the analysis of linear characters showed that specimens from the northern, central, and southern oblasts of Ukraine differ from those from the eastern oblasts of Ukraine and from specimens from the Far East, which are characterised by larger dimensions. The analysis of shape differences using MorphoJ demonstrates the greatest morphological distance between the samples from the territory of Ukraine and the sample from the species' native range. The analysis of the dorsal and ventral surfaces of the skulls showed that the specimens from the native range of the common raccoon dog have more elongated and broader nasal bones, while the braincase is narrowed from the sides, but elongated towards the occipital bones. The greatest level of shape variation is characteristic of the mandible. Specimens from the territory of Ukraine have a more elongated mandibular ramus and a larger area of the coronal, articular, and angular processes, while skulls from the species' native range have a larger angle between the mandibular ramus and the coronal process, which in turn has a greater inclination relative to the articular process and a smaller area of the angular process. Skull size is often larger in animals in introduced populations, but it also depends on environmental conditions, nutrition, and interspecific competition.

Cite as

Lazariev, D. 2024. Craniology of *Nyctereutes procyonoides* (Carnivora) based on materials from Ukraine. *Theriologia Ukrainica*, **28**: 55–68. [In English, with Ukrainian summary]

Краніологія *Nyctereutes procyonoides* (Carnivora) за матеріалами з України

Денис Лазарєв

Резюме. Представлено результати комплексного краніологічного аналізу черепів дорослих особин єнота уссурійського (*Nyctereutes procyonoides* Gray 1834) за чотирма вибірками три з яких представлені матеріалами з України: 1) центральні та північні області України (Київська, Чернігівська, Черкаська обл.); 2) східні області України (Луганська, Запорізька, Полтавська обл.); 3) південні області України (Херсонська обл.), а також вибіркою, що сформована матеріалами з території аборигенного ареалу єнота уссурійського (Хабаровський та Приморський край та Читинська обл. росії). 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 62 зразки. Результати аналізу лінійних ознак показали, що зразки з північних, центральних та південних областей України відрізняються від зразків зі східних областей України та зразків з Далекого Сходу, які характеризуються більшими розмірами. Аналіз відмінностей форми засобами MorphoJ демонструє найбільшу морфологічну дистанцію між вибірками з території України та вибіркою сформованою на основі зразків з аборигенного ареалу. Аналіз дорсальної та вентральної поверхні черепів показав, що зразки з території природного ареалу єнота уссурійського мали більш видовжені та широкі носові кістки, в той же час мозкова капсула була звужена з боків, проте видовжена в напрямку потиличних кісток. Найбільший рівень варіативності форми характерний для нижньої щелепи. Всі вибірки з території України характеризуються менш видовженою основою нижньої щелепи та більшою площею вінцевого, суглобового та кутового відростків, в той час як черепи аборигенних єнотів з регіонів природного поширення виду мали більший кут між основою щелепи та вінцевим відростком, який в свою чергу мав більший нахил відносно суглобового відростку і меншу площу кутового відростка. Часто розмір черепів є більшим у тварин в інтродукованих популяціях, проте це також залежить від природних умов, харчування та міжвидової конкуренції.

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

Introduction

The common raccoon dog (*Nyctereutes procyonoides* Gray 1834) is an alien species in the fauna of Ukraine. Work on the introduction of this species began in 1928 with the release of animals in Poltava Oblast. The mass introduction of the species in Ukraine began in 1935 and covered the territories of Luhansk and Kharkiv oblasts, and in the following years spread to the rest of Ukraine, primarily to the eastern and central oblasts. After the Second World War, the common raccoon dog was also released in the western oblasts [Kolosov & Lavrov 1968]. Today, the common raccoon dog is found in most oblasts of Ukraine: the highest population levels (according to the State Statistics Service of Ukraine) are in the northern oblasts, while in mountainous areas the species is completely absent or its population is insignificant [Zagorodniuk & Lazariev 2024].

Specimens of introduced mammal species available in museum collections allow us to assess craniological differences between geographically distant samples both within Ukraine and from other regions. The level of morphological variability of introduced mammals is influenced by their geographical remoteness, isolation of populations, the founder effect, and the productivity of the ecosystems in which they live [Lazariev & Barkaszi 2023; Lazariev 2024].

A number of scientific papers [Haidaka *et al*. 1998; Jurgelėnas & Daugnora 2005; Haba *et al*. 2008; Ansorge *et al*. 2009; Asahara 2013] have been devoted to craniological studies of the common raccoon dog, in particular the description of morphological variability between different populations, emphasising intraspecific and interspecific differences based on craniological data. The aim of this study is to determine the level and direction of morphological variation between common raccoon dog specimens from Ukraine, to present the results of comparison with materials from other countries, and to identify the possible causes of morphological variation.

Materials and Methods

As material for craniological analysis, samples of adult skulls of the common raccoon dog were taken from different museums in Kyiv: the Department of Zoology (NMNHU-z) and the Department of Palaeontology (NMNHU-p) of the National Museum of Natural History, National Academy of Sciences of Ukraine, the Zoological Museum of Taras Shevchenko National University of Kyiv (ZMKU). A total of 62 specimens were included for morphological analysis using MorphoJ (dorsal and ventral skull surfaces).

Despite the fact that the common raccoon dog is often confined to river floodplains, its distribution is not limited to river basins, so when forming samples for the analysis, not the basin principle was used (as in the case of muskrat [Lazariev & Barkaszi 2023]), but the principle of dividing into groups of oblasts of Ukraine (Fig. 1*a*) and regions of Russia (Far East) in the area of natural distribution of the common raccoon dog (Fig. 1*b*).

Skulls of adult individuals were selected for analysis, among which there are samples of individuals of different ages, but samples with obvious signs of juvenile and subadult individuals were not included in the work.

Four samples were formed (taking into account geography and taxonomy)

Introduced populations:

(1) Central and northern oblasts of Ukraine (18 specimens): • Cherkasy Oblast, near Liashchivka village, collector M. Klestov: specimen in NMNHU–p collection No. 6410 (11.1996) and two specimens in NMNHU-z collection, No. 8602 (2008–2009) and No. 8603 (2011). • Chernihiv Oblast: one specimen in the NMNHU-z collection, No. 11594 (23.03.1973, L. Shevchenko), and a specimen in the ZMKU collection, without data on the number and collector (7.01.2001). • Kyiv Oblast: two specimens in the NMNHU-z collection, No. 11611 (3.02.1977, K. Mykhailov) and No. 11610 (10.1982, K. Mykhailov). Seven specimens are in the ZMKU collection, No. 4387 (2.12.1954, D. Borzakovskyi), No. 3893 (16.10.1955, D. Borzakovskyi), No. 3354 (2.10.1952, O. Korneev), No. 446 (10. 09.1946, no data on the collector), No. 3305 (27.05.1952, no data on the collector), No. 3345 (8.11.1949, no data on the collector) and No. 4004 (10.08.1953). Four specimens are from the NMNHU-p collection, No. 6435 (4.05.1937, no collector's data), No. 6413 (10.1997, I. Leheida), No. 6415 (10.1997, I. Leheida) and No. 4789 (1937, no collector's data).

(2) Eastern oblasts of Ukraine (12 specimens): • Luhansk Oblast: one specimen in the collection NMNHU-z, No. 11608 (08.1958, no data on the collector), two specimens in the collection NMNHU-p: No. 6420 (12.02.1938, no data on the collector) and No. 6808 (05.2002, O. Kondratenko). One specimen is kept in the working collection of I. Zagorodniuk (no date and no data on the collector). • Zaporizhzhia Oblast: two specimens from the collection NMNHU-z, No. 14472 (25.12.1993, A. Volokh) and No. 2017 (08.2005, A. Volokh). • Poltava Oblast, six specimens in the ZMKU collection: No. 3351 (1952, M. Havrylenko), No. 3356 (12.12.1952, M. Havrylenko), No. 3357 (03.1953, O. Kornieiev), No. 4297 (1.11.1953, M. Havrylenko), No. 3306 (24.11.1952, Kyshchynskyi) and No. 3355 (9.12.1952, M. Havrylenko).

Fig. 1. Places of capture of individuals on the basis of which the samples were formed: from the territory of Ukraine (*a*) and from the Far East (*b*).

Рис. 1. Місця відлову особин на основі яких сформовано вибірки: з території України (*a*) та з Далекого Сходу (*b*).

(3) Southern oblasts of Ukraine (26 specimens): • Kherson Oblast, Black Sea Reserve, 12 specimens in the collection NMNHU-z (1967): No. 1706, 11612, 12423, 12424, 12425, 12426, 12428, 12429, 12430, 12431, 12432 and 16059. 14 specimens in the NMNHU-p collection: No. 6421, 6422, 6423, 6425, 6426 (1960, O. Gizenko); 6411 and 6412 (09.1997, V. Tkach); 6727, 6428 (7.01.1961, S. Mylynskyi); 6429, 6430, 6431 (03.1962, O. Gizenko); 6432 and 6434 (1961, S. Mylynsky).

Native populations:

(4) Far East, Russia (6 specimens): • Khabarovsk Krai, one specimen from the collection NMNHU-z: No. 5273 (22.11.1959, V. Yahontov). • Primorsky Krai, one specimen from the collection NMNHU-z: No. 11075 (05.1987, O. Zykov), and three specimens in the NMNHU-p collection, No. 1186, 1187 and 1988 (Primorsky Krai, 1930s, M. Shcherbyna). • Chita Oblast: one specimen from the ZMKU collection, No. 7478 (05.1988, no data on the collector).

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

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

To compare the size of the skulls of the common raccoon dog from the territory of Ukraine with the results of studies from other countries [Haidaka *et al*. 1998; Jurgelenas & Daugnora, 2005; Kim *et al*. 2012; Korablev & Szuma 2014], we calculated the average values of individual craniometric traits based on the samples of animals captured in Ukraine. Average values for males, females and average values for all individuals are presented.

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 $p < 0.05$. Therefore, only the characters CRB, IOR, POR, BUL, OOC, FIL, and MAH were used in the subsequent analysis.

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].

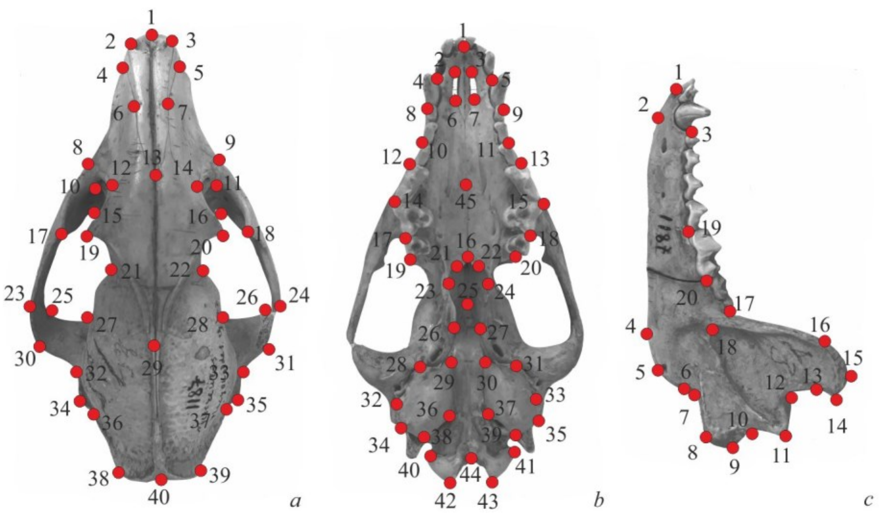


Fig. 2. Landmarks on the dorsal (*a*) and ventral (*b*) surfaces of the skull and on the buccal surface of the left mandible (*c*) used in geometric morphometrics analysis.

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

Variations in skull shape were analysed using geometric morphometry [Klingenberg & McIntyre 1998]. For each sample, three sets of landmarks were selected (Fig. 2) on the dorsal (40 landmarks) and ventral (45 landmarks) surfaces of the skull and on the buccal surface of the left mandible (20 landmarks).

On the dorsal surface, landmarks 1–7 and 13 describe the shape of the nasal bones, landmarks 6–11, 17, 18, 23–28 and 30–33 describe the shape of the zygomatic bones, landmarks 12, 14–16 and 19–22 describe the shape of the interorbital and postorbital zones, landmarks 29 shows the growth of sutures on the neurocranium, 34–37 describe the width of the neurocranium, and 38–40 describe the extreme and middle points of the occipital bones.

On the ventral surface, point 1 shows the midpoint at the base of the anterior teeth of the maxilla, points 2, 3, 6, and 7—the incisive foramina, 4, 5, 8, and 9—the canines, 10–15 and 17–20—points between the teeth of the maxilla, 16 and 21–27—the opening and sutures of the sphenoid bone, 28–39—the extreme points of the left and right auditory bulla, 40–44—points on the occipital bones, 45—point on the suture in the middle part of the palatine bone.

On the buccal side of the left mandible, points 1–6, 19, and 20 are the points at the ramus of the mandible, 7–10 are the points describing the shape of the angular process, 10–12 are the articular process, 12–17 are the coronal process.

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 specimens (lack of mandible), 54 specimens were included in the morphological analysis of the buccal side of the left jaw in MorphoJ.

Shape variation of the common raccoon dog 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 regions 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.

Results

Linear morphometrics

According to the results of the analysis of linear morphometry based on 19 craniological features, all four samples (three from the territory of Ukraine and one from the Far East) have quite similar sizes (Table 1). The sample based on samples from the native area (the Far East) is characterised by larger skull sizes and most of their structures compared to the samples from the territory of Ukraine. Among the three samples from the territory of Ukraine, the samples from the central and northern oblasts are smaller, while the samples from the eastern and southern oblasts do not differ significantly from each other.

The highest coefficients of variation (CV) were observed for the zygomatic width (ZYG) and interorbital width (IOR) in the sample from the central oblasts of Ukraine, the width of the auditory bulla (BUB) and jugular width (JUG) in the central and southern oblasts, and the length of the incisive foramina (FIL) in most samples. However, the differences between the analysed samples are statistically insignificant ($p > 0.05$).

The principal component analysis (PCA) of the craniometric characters of the common raccoon dog showed that the first three components describe 81.8% of the total variance, of which PC1 describes 53.0% (Table 2). All the traits in PC1 have a positive score. The highest loadings are for MAH, CRB and IOR, which describe the mandibular height, the width of the brain capsule and the interorbital space.

The relatively high values observed for BUL and OOC are associated with the overall cranial dimensions. In the space of PC1 and PC2 (Fig. 3*a*), all samples show considerable overlap.

Table 1. Results of measurements of *Nyctereutes procyonoides* skulls in three samples from the territory of Ukraine and one sample from Far East

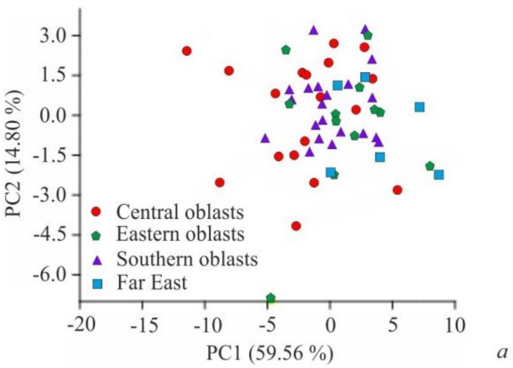
Таблиця 1. Результати вимірів черепів *Nyctereutes procyonoides* із трьох вибірок із території України та однієї вибірки з Далекого Сходу

Characters	Central oblasts, n = 18		Eastern oblasts, n = 12		Southern oblasts, n = 26		Far East, n = 6	
	min–max M ± SD	CV	min–max M ± SD	CV	min–max M ± SD	CV	min–max M ± SD	CV
CBL	96.2–125.0 116.3 ± 6.6	5.7	97.6–128.0 118.7 ± 8.3	7.0	113.5–130 121.0 ± 3.7	3.1	113,3–127.7 121.6 ± 4.9	4.0
ZYG	36.6–74.1 63.9 ± 8.3	13.1	61.7–75 68.7 ± 3.5	5.1	60.1–73.3 66.6 ± 2.9	4.3	66.7–79.1 71.0 ± 4.4	6.2
CRB	39.2–45.2 42.0 ± 1.9	4.6	36.0–46.5 43.5 ± 2.8	6.5	39.0–46.0 42.7 ± 1.5	3.6	41.4–46.2 44.7 ± 1.7	3.8
CRH	41.0–49.0 44.0 ± 2.2	5.1	38.0–46.2 44.2 ± 2.3	5.2	34.0–49.5 44.6 ± 2.9	6.6	42.9–48.0 45.0 ± 2.0	4.5
IOR	17.4–26.0 21.9 ± 2.5	11.2	21.7–25.3 23.3 ± 1.2	5.3	20.4–26.8 22.8 ± 1.6	6.9	21.1–26.8 23.3 ± 2.0	8.4
POR	18.0–23.0 20.1 ± 1.2	6.0	18.0–22.9 20.6 ± 1.4	6.8	17.0–22.1 19.8 ± 1.3	6.7	18.4–22.0 20.5 ± 1.4	7.0
BUL	15.0–22.0 19.5 ± 1.8	9.4	15.8–20.7 19.2 ± 1.4	7.4	17.8–23.0 20.5 ± 1.3	6.4	19.2–21.5 20.2 ± 0.9	4.4
BUB	12.0–18.7 14.7 ± 2.1	14.0	11.7–16.0 14.0 ± 1.2	8.4	12.3–19.9 14.5 ± 1.9	13.2	14.0–16.0 15.0 ± 0.7	4.5
JUG	9.2–12.8 11.2 ± 1.2	10.6	10.0–13.0 11.7 ± 1.0	8.9	9.9–18.1 11.7 ± 1.7	14.3	11.1–13.0 11.7 ± 0.7	6.2
BOC	18.5–26 22.5 ± 1.7	7.6	19.8–25.0 23.0 ± 1.7	7.5	20.5–24.8 23.4 ± 1.1	4.5	21.2–25.7 23.9 ± 1.6	6.6
ROH	28.8–36.1 32.8 ± 1.9	5.8	28.5–36.2 33.9 ± 2.0	6.0	30.8–35.0 33.6 ± 1.2	3.5	33–37.2 34.7 ± 1.7	4.8
DCM	38.6–47.0 44.1 ± 2.5	5.7	37.3–52.0 44.7 ± 3.8	8.4	15.1–47.2 42.7 ± 7.5	17.5	44.8–47.1 46.1 ± 0.8	1.8
DIM	49.2–59.4 55.1 ± 3.0	5.5	45.7–63.1 56.6 ± 4.5	7.9	44.0–59.7 56.4 ± 3.6	6.4	57.9–61.2 59.2 ± 1.3	2.2
DMM	32.4–48.9 36.3 ± 3.6	9.9	31.1–38.0 35.8 ± 2.3	6.4	32.4–38.8 36.3 ± 1.6	4.5	35.3–38.8 36.8 ± 1.5	4.1
FIL	5.1–8.3 6.9 ± 0.7	10.6	6.8–8.8 7.5 ± 0.6	7.4	6.0–8.9 7.2 ± 0.7	9.5	6.1–8.8 7.8 ± 1.0	13.4
MAL	76.0–95.4 88.9 ± 5.2	5.9	85.0–97.2 92.1 ± 4.4	4.8	86.2–97.4 92.2 ± 2.7	2.9	90.0–101.0 93.6 ± 4.0	4.3
MAH	38.0–53.0 46.1 ± 3.6	7.7	43.2–55.0 48.8 ± 3.4	6.9	44.2–51.2 47.6 ± 2.0	4.2	48.1–55.2 51.2 ± 2.9	5.7
dcm	44.6–54.5 50.3 ± 2.9	5.7	47.0–55.1 52.0 ± 2.7	5.2	39.0–56.2 53.0 ± 3.7	6.9	51.0–57.8 54.1 ± 2.4	4.4
dim	48.2–59.6 55.4 ± 2.9	5.3	51.9–60.8 56.9 ± 2.9	5.1	45.3–60.0 56.5 ± 3.4	6.0	55.8–62.4 59.0 ± 2.3	3.8

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	PC 3	Character	PC 1	PC 2	PC 3
CRB	0.4016	0.5775	-0.2803	OOC	0.2398	0.3494	-0.0124
IOR	0.3810	0.0493	0.6819	FIL	0.0749	-0.0171	-0.0376
POR	0.1374	0.0524	0.6084	MAH	0.7501	-0.5845	-0.2640
BUL	0.2206	0.4441	-0.1220	Variance, %	59.565	14.801	10.827



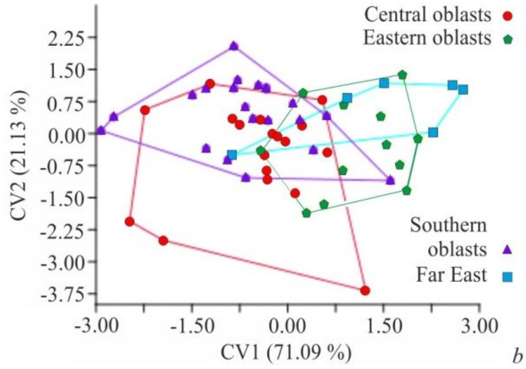


Fig. 3. The distribution samples in the space of the first two principal components (*a*) and canonical variates (*b*) based on linear craniometrical characters.

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

However, the sample from the Far East distinctly shifts toward extreme positive values in PC1. The analysis of canonical variables (Fig. 3*b*) indicates that the samples differ significantly along CV1: the sample from the Far East and eastern Ukraine aligns closely with the extreme negative values of CV1, while the samples from southern and central Ukraine predominantly occupy the range of positive values.

The sample from the east of Ukraine (a sample from the working collection of I. Zagorodniuk) took the most negative values for PC2, separating from the total set of samples due to its smaller size (Fig. 3 *a*). Similarly, specimens No. 6413, 6415, 6435 have negative values for CV2, which also deviate from the general cloud of specimens (Fig. 3 *b*) due to their small size, in particular the size of the postorbital constriction (POR).

We analysed the size of skulls from introduced populations and the native range according to the traits characterising the length and width of the skull and mandible (Table 3). There are some differences between the populations, such as the small size of skulls from the Kagoshima Prefecture in Japan [Haidaka *et al*. 1998]. In general, the size of skulls in introduced populations often tends to be larger than in native populations. Animal size is influenced by factors that may be local in nature, as skull size can vary even within a single small administrative unit (Tver Oblast, Russia).

It can be assumed that factors such as the founder effect, food availability, or interspecific competition have an impact on animal size. As an example, researchers cite a high proportion of skull injuries in eastern Poland, which are likely to be the result of intra- and interspecific competition [Korablev & Szuma 2014] and the cause of smaller animal sizes in this population.

Geometric morphometrics

The analysis by methods of geometric morphometrics in the MorfoJ software package was carried out for the dorsal and ventral surfaces of the skulls and for the lateral side of the mandible. According to the results of the analysis of the dorsal surface of the skull, 71.4% of variance is described by the first 6 components, where PC1 accounts for 25.8% and PC2 for 16.8% (Fig. 4; 5a).

The highest positive values for PC1 were recorded for coordinates y19, y21, describing postorbital narrowing and coordinates x32, x33, x34, x35, describing the elongation of the brain capsule. The most negative values are at point x29, which describes the junction of the sutures on the brain capsule, as well as at coordinates x15, x16, y19, x19, y20, x20, which describe the orbital narrowing. Such signs most often describe the degree of skull development and are related to the age of the animal. In PC2, the most negative values were found at coordinates y19, x19, y20, x20, x22, x21, describing the expansion of the interorbital part of the skull, and the most positive values were found at points x1, x2, x3, x4, x5, x6, x7, describing the elongation of the nasal bones.

Table 3. Mean values (mm) of craniometrical characters of common raccoon dog from different countries and regions
Таблиця 3. Середні значення (мм) краніометричних ознак єнота уссурійського із різних країн і регіонів

Region	Sex	n	CBL	ZYG	POR	CRH	MAL	MAH	References
Introduced population									
Ukraine	♂	16	120.9	67.5	20.1	44.6	91.4	48.3	this study
	♀	16	118.6	63.8	20.0	44.5	91.0	46.8	
	total	51	119.7	66.4	20.1	44.6	91.2	47.5	
Lithuania	♂	10	120.2	67.9	20.8	—	90.6	38.9	Jurgelenas & Daugnora, 2005
	♀	5	122.8	69.2	21.3	—	88.8	38.5	
	total	15	121.5	68.5	21.0	—	89.7	38.7	
East Poland*	♂	33	118.3	68.1	—	—	87.4	50.5	Korablev & Szuma, 2014
	♀	31	117.6	66.5	—	—	86.3	49.5	
	total	82	*117.9*	*67.3*	—	—	*86.8*	*50.1*	
Northest Tver*	♂	40	121.7	69.3	—	—	89.3	50.9	Korablev & Szuma, 2014
	♀	41	121.0	68.3	—	—	88.6	50.0	
	total	81	*121.3*	*68.8*	—	—	*88.9*	*50.4*	
West Tver*	♂	59	120.8	68.5	—	—	88.7	50.9	Korablev & Szuma, 2014
	♀	51	119.9	68.4	—	—	87.6	50.5	
	total	110	*120.3*	*68.4*	—	—	*88.1*	*50.7*	
Central Tver*	♂	18	119.5	68.0	—	—	88.9	50.5	Korablev & Szuma, 2014
	♀	33	117.0	66.8	—	—	86.1	48.4	
	total	51	*118.2*	*67.4*	—	—	*87.5*	*49.4*	
South Vologda*	♂	13	120.5	69.7	—	—	90.1	51.1	Korablev & Szuma, 2014
	♀	13	117.6	67.0	—	—	86.5	50.0	
	total	26	*119.0*	*68.3*	—	—	*88.3*	*50.5*	
Native populations									
Amur*	♂	83	118.6	67.8	—	—	66.7	48.6	Korablev & Szuma, 2014
	♀	74	116.9	66.2	—	—	65.5	47.6	
	total	157	*117.7*	*67.0*	—	—	*66.1*	*48.1*	
Japan, Kagoshima Prefecture	♂	35	106.7	60.6	—	—	82.7	41.8	Haidaka *et al.* 1998
	♀	45	105.6	59.1	—	—	81.1	41.3	
	total	80	106.1	59.8	—	—	81.9	41.5	
South Korea	♂	37	118.7	67.0	—	43.7	86.6	46.8	Kim *et al.* 2012
	♀	26	119.5	66.3	—	43.5	87.3	47.1	
	total	63	119.1	66.6	—	43.6	86.9	46.9	
Khabarovsk*	♂	10	119.8	67.8	—	—	86.7	49.0	Korablev & Szuma, 2014
	♀	9	118.5	66.5	—	—	87.9	49.2	
	total	19	*119.1*	*67.1*	—	—	*87.3*	*49.1*	

*Note: italics indicate the average values calculated by the author of this study on the basis of data from the source indicated in the table.

In the space of the first two principal components, the samples largely overlap, but a large number of specimens from the central oblasts have higher values than PC2 (Fig. 5 *a*).

The analysis of canonical variates (Fig. 5 *b*) shows that each sample forms a separate cloud of points in the space of CV1 and CV2, but there is an overlap between samples from the east and south of Ukraine. The sample from the Far East is the most distant from the three Ukrainian samples, with negative values on CV1. In general, samples from the Far East were more likely to have wider and more elongated nasal bones, and an elongated and smaller braincase.

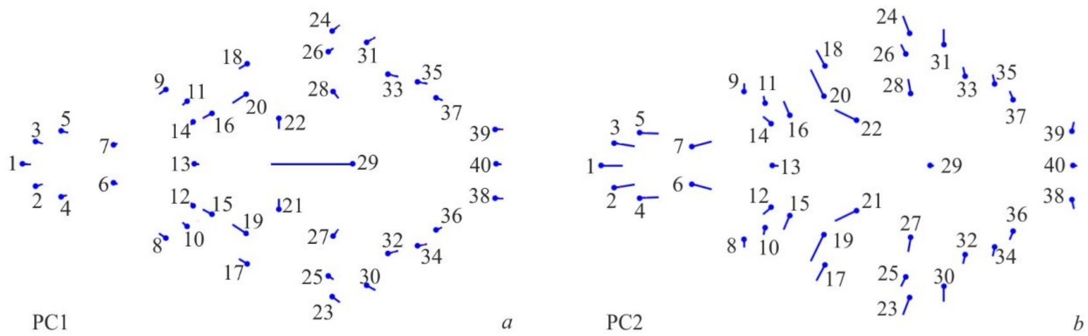


Fig 4. Variation of the shape of the dorsal surface of the skull along PC1 (*a*) and PC2 (*b*).

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

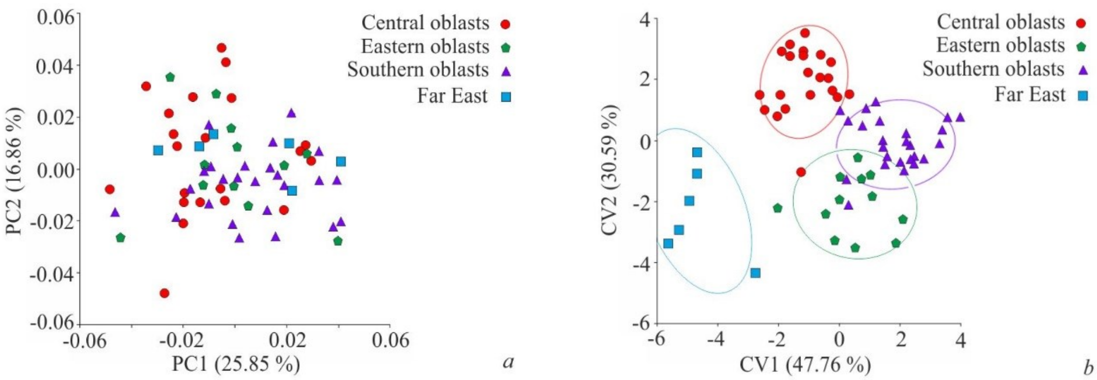


Fig. 5. Distribution of common raccoon dog specimens from different regions of Ukraine according to the shape of the dorsal surface of the skull: (*a*) in the space of the first two principal components; (*b*) in the space of the first two canonical variates.

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

The analysis of the ventral surface of the skull showed that 72.0 % of variance is described by the first seven principal components, where PC1 describes 22.01 % and PC2 describes 15.90 % (Fig. 6 *a*; 7). The most positive values on PC1 were recorded for coordinates x21, x22, x17, x18, x23, x24, which characterise the position of the carnassial and the sphenoid bone, the most positive values were recorded for coordinates x1, x2, x3, x4, x5, x6, x7, which characterise the position of the anterior teeth and incisive foramina. Thus, PC1 is more characterised by elongation of the upper jaw and narrowing of the skull structures in the area of the auditory bulla and at the attachment point of the atlas. On PC2, the most positive values were recorded for coordinates x25, x21, x22, x16, x23, x24, x26, x27, which characterise the position of the sphenoid bone. The most negative values have the coordinates x14, x15, x17, x18, x19, x20, which characterise the position of the jaw in the area of the carnassial, which generally describes the elongation of the skull in the area of the sphenoid bone and the molars.

The analysis of the canonical variates (Fig. 6 *b*) shows differences between the three samples of materials from Ukraine, but at the same time, the sample from the Far East overlaps with the sample from the central oblasts, which, in turn, overlaps with the sample from the south of Ukraine in the direction of negative values along CV2, where the sample from the eastern oblasts also occupies a position within the negative values. Along CV1, the eastern Ukrainian sample is also located in the negative range; the sample from the south is located in the positive range, while the samples from the central oblasts of Ukraine and Far East regions occupy the middle range between the east and south of Ukraine. Thus, among the specimens from the east of Ukraine, the maxilla was more often longer, but the structures of the braincase were located closer to its base, while the rest of the samples had the opposite shape: the rostral part was narrower and located closer to the braincase, and the structures of the braincase were located closer to its lateral borders.

The position of the sample from the Far East along CV2 confirms the direction of shape described for the dorsal surface of this sample: they had a wider braincase, while the auditory bulla and occipital bones were not as elongated as in the other samples. The rostral part of the skull was closer to the braincase, and the anterior part of the upper jaw was wider than in the other samples.

The analysis of differences between the samples based on the buccal side of the left mandible demonstrated that 75.6% of variance was explained by the first four principal components, with PC1 accounting for 42.1% and PC2 for 19.7% (Fig. 8 *a*).

The most positive values on PC1 (Fig. 9 *a*) were recorded for coordinates x9, y14, y16, y15, x2, x1, while the most negative for coordinates y7, y14, y6, y16, y15, y8, which characterise the position of the angular and coronal processes and their deviation from the articular process, as well as an increase or decrease in the angle between the mandibular ramus and the coronal process.

On PC2 (Fig. 9 *b*), the most positive values were recorded for y1, y3, x8, y2, x4, x5. The most positive values had the points x1, x2, x14, y16, x16, x15. This principal component describes the length of the mandibular ramus and the height of the coronal process.

In the space of canonical variates (Fig. 7 *b*), the sample from the native range of the species is the most distant from the other samples, having the most positive values on CV2 and the most negative values on CV1. Differences between samples from the territory of Ukraine are more noticeable only along CV2. Thus, specimens from the Far East (with greater expression) and eastern Ukraine more often had coronal, articular, and angular processes closer to each other, and were characterised by a more elongated mandibular ramus.

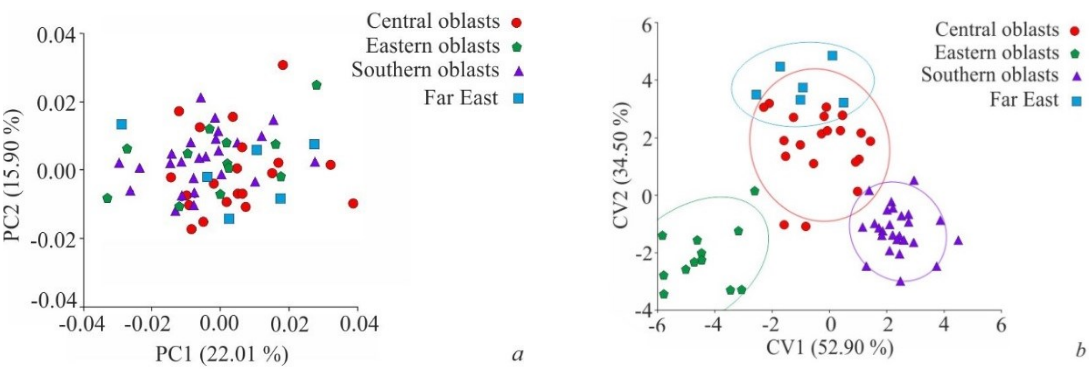


Fig. 6. Distribution of common raccoon dog specimens from different regions of Ukraine according to the shape of the ventral surface of the skull: (*a*) in the space of the first two principal components; (*b*) in the space of the first two canonical variates.

Рис. 6. Розподіл зразків єнота уссурійського з різних регіонів України за формою вентральної поверхні черепа: (*a*) у просторі перших двох головних компонент; (*б*) у просторі перших двох канонічних змінних.

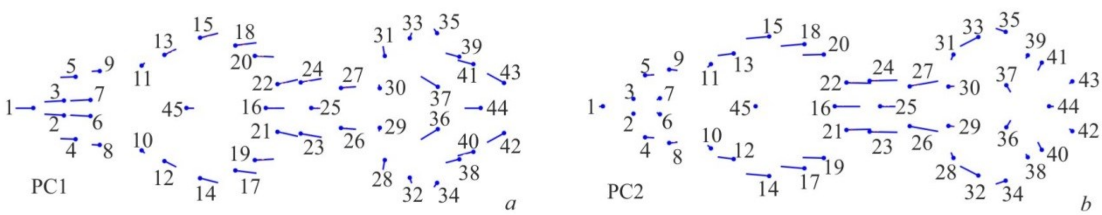


Fig. 7. Variation of the shape of the ventral surface of the skull along PC1 (*a*) and PC2 (*b*).

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

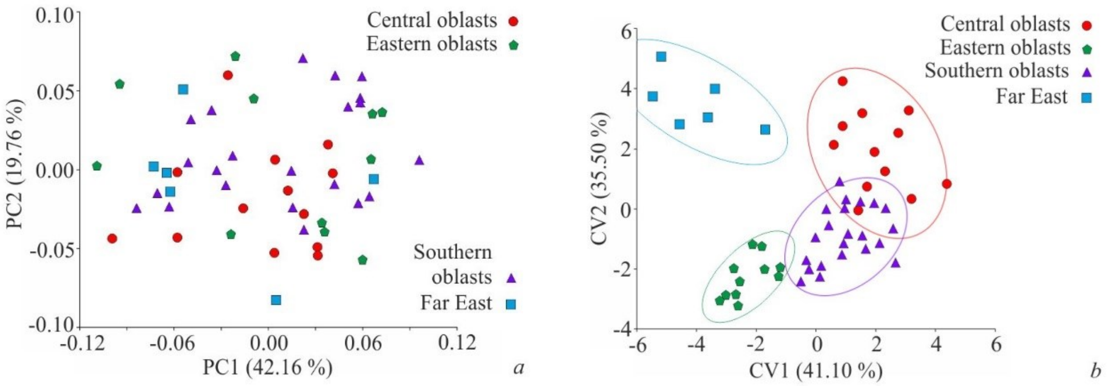


Fig. 8. Distribution of common raccoon dog specimens from different regions of Ukraine according to the shape of the buccal surface of the left mandible: (*a*) in the space of the first two principal components; (*b*) in the space of the first two canonical variates.

Рис. 8. Розподіл зразків єнота уссурійського 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.

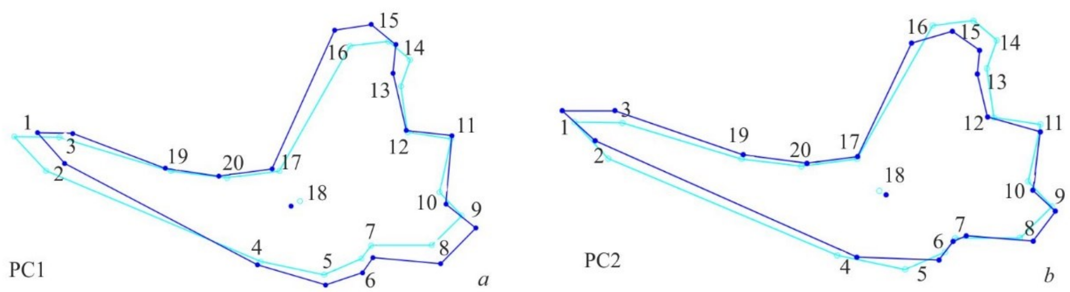


Fig. 9. Variation of the shape of the buccal surface of the left mandible along PC1 (*a*) and PC2 (*b*). The blue lines indicate the starting shape. The light blue lines show the direction and magnitude of shape changes between the baseline and the altered configuration.

Рис. 9. Зміни форми щічної поверхні лівої нижньої щелепи за ГК1 (*а*) та ГК2 (*b*). Сині лінії позначають вихідну форму. Блакитні лінії вказують напрямок і величину змін форми між базовою та зміненою конфігурацією.

Specimens from eastern and southern Ukraine differ from those from central Ukraine and the Far East in the height of the coronoid and angular processes: specimens from eastern and southern Ukraine show a larger angle, while specimens from central Ukraine and the Far East have larger coronoid and angular processes, often with the coronoid rounded in relation to the joint (Fig. 10).

Such changes in shape can often be explained by age-related variability, but in the material studied, these differences are observed between specimens of the same age group, which are also similar in size but come from different populations (Kherson Oblast, Ukraine and the Far East).

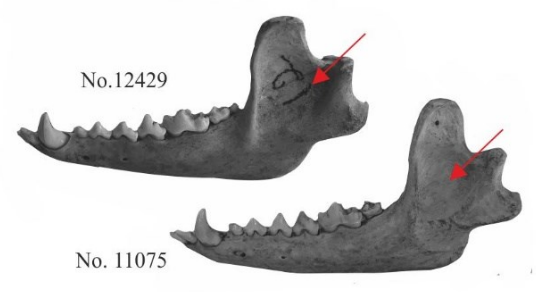


Fig. 10. Differences in the shape of the buccal surface of the left lower jaw as exemplified by the sample from the Kherson region (No. 12429) and the Primorsky Krai (No. 11075). Arrows indicate the part of the jaw that, in most cases, demonstrates differences between the samples.

Рис. 10. Відмінності форми щічної поверхні лівої нижньої щелепи на прикладі зразка з Херсонської області (№ 12429) та Приморського краю (№ 11075). Стрілками показано частину щелепи яка в більшості випадків демонструє відмінності між зразками.

Samples from the central part of Ukraine and its southern regions differ from each other to the least extent, but at the same time, the largest significant differences were recorded between Ukrainian samples and the sample from the native range of the common raccoon dog (Table 4).

Discussion

The natural conditions in the areas of introduction are quite diverse, which has led to differences in animal size in different areas of the European part of the common raccoon dog's range. Animal sizes are larger in the north of the European range and smaller in the south, and the size of animals depends on natural conditions, in particular the availability of food resources and interspecific competition.

Since most of skulls of the common raccoon dog were collected in the first half to mid-twentieth century, we can say that in the first decades after the formation of the Ukrainian population, the animals acquired certain adaptive features in the shape of the skull, primarily in those structures responsible for feeding.

Thus, the most significant differences between the Ukrainian population and the specimens from the native range of the species were recorded in the shape of the mandible, which in the Far Eastern population is characterised by a larger mandibular ramus area, smaller areas of the coronal, articular, and angular processes. The coronal process has an inclination towards the articular process, but this feature was more pronounced in the eastern Ukrainian sample.

The morphological similarity of the eastern Ukrainian sample to the native population in the Far East can be explained by the fact that eastern Ukraine was the area of initial introduction in 1928–1936. After that, the range of the common raccoon dog expanded to other regions of Ukraine, in particular through introduction in the regions of Ukraine and expansion to European countries [Kolosov & Lavrov 1968], which could have contributed to changes in their morphology due to the founder effect and the influence of natural conditions in new habitats and interspecific competition.

Linear morphometric analysis revealed differences in skull size between the three Ukrainian samples and the sample from the Far East, where the Ukrainian samples are characterised by smaller skull sizes. Animal size is influenced by environmental conditions, feeding, and interspecific competition. A review of data from different remote areas of the common raccoon dog's range showed that, in general, skulls in introduced populations were more likely to be larger than in the native range.

Table 4. Mahalanobis distances (D_M) between 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 р-значення попарного однофакторного PERMANOVA на основі навантажень на ГК

Group	Samples	Central oblasts	Eastern oblasts	Southern oblasts	Far East
Dorsal (F = 1.8867 p = 0.0084)	Central oblasts	—	4.6664	4.0055	5.9977
	Eastern oblasts	0.3196	—	4.0920	6.5994
	Southern oblasts	**0.0017**	0.0792	—	6.9085
	Far East	0.2339	0.5625	0.0989	—
Ventral (F = 1.7984 p = 0.0073)	Central oblasts	—	6.0117	4.4086	4.7632
	Eastern oblasts	0.1062	—	6.9723	7.8388
	Southern oblasts	**0.0049**	**0.0065**	—	6.6029
	Far East	0.8645	0.2155	**0.0488**	—
Mandible (F = 1.2915 p = 0.1999)	Central oblasts	—	5.9568	4.3513	6.9568
	Eastern oblasts	0.4351	—	4.7818	6.7995
	Southern oblasts	0.0909	0.5327	—	6.7108
	Far East	0.3972	0.3840	0.0830	—

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

Based on the results of the analysis of linear and geometric morphometrics, it can be concluded that the skulls of animals from the introduced population of the species in Ukraine and the native population in the Far East have significant differences that are reflected in the overall dimensions of the skull (length, width of the skull and its structures), and the most significant are differences in the shape of the mandible.

Conclusions

Based on the morphological study of common raccoon dog skulls from Ukraine and the Far East, the following conclusions can be drawn:

1. The animals from the Ukrainian population exhibit morphological differences from the Far Eastern (native) population in terms of skull size and shape. The most significant differences are observed in the structures of the skull associated with feeding functions.

2. Skulls from the Far Eastern population are generally larger compared to those from the Ukrainian population. They have longer and wider nasal bones, elongated brain capsule, extended mandibular ramus, and smaller area of the coronoid, articular, and angular processes. Additionally, skulls from the Far Eastern population and eastern Ukraine more often feature a coronoid process tilted toward the articular process.

3. The combination of traditional and geometric morphometric approach allowed for a detailed analysis of differences between introduced and native populations of the common raccoon dog. Geometric morphometrics revealed the most significant shape differences between the Ukrainian and Far Eastern populations.

Acknowledgements

The author sincerely thanks Y. M. Ulyura (National Museum of Natural History, Kyiv) and Z. V. Rozora (Zoological Museum of Taras Shevchenko National University of Kyiv) for their guidance and assistance in searching for collection specimens, and D. V. Ivanov (National Museum of Natural History, Kyiv) for providing materials from the Department of Palaeontology, consultations, and copies of scientific works. Thank you to the reviewers for their consideration of the manuscript and for the valuable comments that helped to improve the work, Z. Barkaszi for help in mastering the methods of working with MorphoJ software and editing the text, and supervisor I. Zagorodniuk for the idea of the article, methodological and editorial support at all stages of this study.

Declarations

Funding. The study was carried out as part of the research project supported by the National Museum of Natural History, NAS of Ukraine (No. 0124U000572) and as part of DL's doctoral thesis titled 'Introduced mammal species in the river basins of left-bank Ukraine: morphological variability and chorological analysis.'

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.

References

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**: 32–46. CrossRef

Ansorge, H., M. Ranyuk, K. Kauhala, R. Kowalczyk, N. Stier. 2009. Raccoon dog, Nyctereutes procyonoides, populations in the area of origin and in colonised regions — the epigenetic variability of an immigrant. *Annales Zoologici Fennici*, **46**: 51–62. CrossRef

Asahara, M. 2013. Shape variation in the skull and lower carnassial in a wild population of raccoon dog (Nyctereutes procyonoides). *Zoological Science*, **30** (3): 205–210. CrossRef

Asahara, M. 2014*a*. Shape variation in the skull within and between wild populations of the raccoon dog (Nyctereutes procyonoides) in Japan. *Mammal Study,* **39**: 105–113. CrossRef

Asahara, M. 2014*b*. Evolution of relative lower molar sizes among local populations of the raccoon dog (Nyctereutes procyonoides) in Japan. *Mammal Study,* **39**: 181–184. CrossRef

Haba, C., T. Oshida, M. Sasaki, H. Endo, H. Ichikawa, Y. Masuda. 2008. Morphological variation of the Japanese raccoon dog: implications for geographical isolation and environmental adaptation. *Journal of Zoology*, **274** (3): 239–247. CrossRef

Hammer, Ø., D. A. T. Harper, P. D. Ryan. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, **4** (1): a04.

Hidaka, S., M. Matsumoto, H. Hiji, S. Ohsako, H. Nishinakagawa. 1998. Morphology and morphometry of skulls of raccoon dogs, Nyctereutes procyonoides and badgers, Meles

meles. *Journal of Veterinary Medical Science*, **60** (2): 161–167. CrossRef

Jurgelėnas, E., L. Daugnora. 2005. Osteometrical analysis of skulls in red foxes and raccoon dogs. *Veterinarija ir zootechnika*, **32** (54): 11–15 [Lithuanian]

Kauchala, K., E. Helle. 1990. Age determination of the raccoon dog in Finland. *Acta Theriologica*, **35** (3–4): 321–329. CrossRef

Kim, S. I., S. Suzuki, G. Oh, D. Koyabu, T. Oshida, H. Lee, [et al.]. 2012. Sexual dimorphism of craniodental morphology in the raccoon dog Nyctereutes procyonoides from South Korea. *Journal of Veterinary Medical Science*, **74** (12): 1609–1616. CrossRef

Kim, S. I., T. Oshida, H. Lee, M. S. Min, G. Kimura. 2015. Evolutionary and biogeographical implications of variation in skull morphology of raccoon dogs (Nyctereutes procyonoides, Mammalia: Carnivora). *Biological Journal of the Linnean Society*, **116**: 856–872. CrossRef

Klingenberg, C. P., G. S. McIntyre. 1998. Geometric morphometrics of developmental instability: Analyzing patterns of fluctuating asymmetry with procrustes methods. *Evolution*, **52** (5): 1363–1375. CrossRef

Klingenberg, C. P. 2011. MorphoJ: an integrated software package for geometric morphometrics. *Molecular Ecology Resources*, **11**: 353–357. CrossRef

Kolosov, A. M., N. P. Lavrov. 1968. *Enrichment of the Commercial Fauna of the USSR.* Publishing 'Forest industry'. Moskva, 1–256. [In Russian]

Korablev, N. P., E. Szuma. 2014. Variability of native and invasive raccoon dogs' Nyctereutes procyonoides populations: looking at translocation from a morphological point of view. *Acta Theriologica*, **59**: 61–79. CrossRef

Korablev, N. P., M. P. Korablev, P. N. Korablev. 2012. Craniometrical variability of raccoon dog — Nyctereutes procyonoides Gray (Carnivora, Canidae) in Tver Region: from reintroducents to modern populations. *Bulletin of Moscow Society of Naturalists*, **117**(1): 15–25. [Russian]

Korablev, N. P., E. Szuma, P. N. Korablev, A. V. Zinoviev. 2017. Dental polymorphism of the raccoon dog in indigenous and invasive populations: internal and external causation. *Mammal Research,* **62**: 163–177. CrossRef

Korablev, N. P., P. N. Korablev, M. P. Korablev. 2018. *Microevolutionary Processes in Populations of Introduced Species: Eurasian Beaver, Common Raccoon Dog, American Mink.* KMK, Moskva, 1–402. [Russian]

Lazariev, D., Z. Barkaszi. 2023. Craniological analysis of the muskrat (Ondatra zibethicus) from different river basins of Ukraine. *Theriologia Ukrainica*, **26**: 71–86. CrossRef

Lazariev, D. 2024. Craniology of Neogale vison in areas of introduction: analysis of samples from Ukraine. *Theriologia Ukrainica*, **27**: 36–47. CrossRef

Nowicki, W., W. Brudnicki, B. Skoczylas. 2011. Studies of interdependences between characteristics in raccoon dog (Nyctereutes procyonoides Gray). *Electronic Journal of Polish Agricultural Universities*, **14** (2): art17.

Zagorodniuk, I., D. Lazariev. 2024. Dynamics of distribution of introduced mammals in Ukraine and factors influencing them. *Biosystems Diversity*, **32** (4): 522–542. CrossRef