Theriologia Ukrainica, **22**: 63–68 (2021)
p-ISSN 2616-7379 • e-ISSN 2617-1120
DOI: 10.15407/TU2207

THE INCISIVE FORAMEN AS CHARACTER IN DISTINGUISHING MORPHOLOGICALLY SIMILAR SPECIES OF MAMMALS

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Key words

morphologically similar species, incisive foramen, interspecific differences

doi

http://doi.org/10.15407/TU2207

Article info

submitted 29.05.2021
revised 25.07.2021
accepted 22.12.2021

Language

English, Ukrainian summary

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Abstract

An analysis of the morphology and variability of the size and shape of a key morphological structure in the rostral part of the skull—the incisive foramen—has been carried out. It is shown that incisive foramina are variable morphological structures, the features of which are group-specific (at the level of genera and families), and in some cases also species-specific. At both these levels, the shape and size of the incisive foramen have features that can serve as criteria for species identification by osteological patterns. Their location is important for diagnosis because these structures are preserved in most specimens that have suffered various kinds of damage (e.g. in fodder residues of carnivorous mammals or in owl pellets), and their placement in the anterior part of the bony palate as well as them being protected from the sides with rows of teeth makes these structures invulnerable to trauma-related variation. It is shown that there is a specific structure (size, location, and shape) of incisive foramina at the level of taxonomic groups of all ranks, from orders to species. The analysis was performed mainly on the examples of different groups of rodents as an order, represented by the largest number of pairs of close species. Examples with several different groups, in particular with different pairs of species of voles, mice, mole rats, ground squirrels, and others are considered. Examples with differences in close pairs of species in other groups (white-toothed shrews, polecats, roe deer, etc.) are also known. In all pairs of related species, a pattern was found, according to which species that are restricted to steppe ecosystems have the smallest incisive foramina, while species from wetland habitats have large ones. In many cases, groups of genera and families well differ in the shape and location of incisive foramina, and close pairs of species differ well in the size of these structures (primarily in length), although it is important to always consider the ontogenetic age of specimens: in young individuals, the incisive foramina are naturally small, similar to incisive foramina in other species, which are characterized by small incisive foramina in general. Based on the known data on the role of incisive foramina and the Jacobson organ in the life of mammals, hypotheses have been considered that may explain the differences in species and genera by the structure (size, location, and shape) of incisive foramina.

Cite as

Zagorodniuk, I. 2021. The incisive foramen as character in distinguishing morphologically similar species of mammals. *Theriologia Ukrainica*, **22**: 63–68. [In English, with Ukrainian summary]

Різцеві отвори як ознака при розрізненні морфологічно близьких видів ссавців

Ігор Загороднюк

Резюме. Проведено аналіз морфології та мінливості розмірів і форми ключової морфологічної структури в ростральному відділі черепа — різцевих отворів. Показано, що різцеві отвори є мінливою морфологічною структурою, особливості якої є групоспецифічними (на рівні родів і родин), а в низці випадків і видоспецифічними. На обох цих рівнях— форма і розміри різцевих отворів мають особливості, що можуть слугувати критеріями для ідентифікації видів за остеологічними зразками. Їхнє розташування є важливим для діагностики, оскільки ці структури зберігаються в більшості зразків, що зазнали тих чи інших руйнувань (напр. в поїдях хижих ссавців або в пелетках сов) — розміщення їх в передній частині кісткового піднебіння і до певної міри захист з боків зубними рядами робить цю частину рострума непідвладною травматичній мінливості. Показано, що існує специфіка будови (розміри, розташування й форма) різцевих отворів на рівні таксономічних груп всіх рангів — від рядів до видів. Аналіз проведено переважно на прикладів різних груп гризунів як ряду, що представлений найбільшою кількістю пар близьких видів. Розглянуто приклади з кількома різними групами, зокрема з різними парами видів щурових (полівки, щурі), мишевих (миші, мишаки), сліпакових, вивіркових тощо. Відомими також є приклади з відмінностями близьких пар видів у інших груп (білозубки, тхори, сарни тощо). У всіх парах близьких видів виявлено закономірність, за якою види, що обмежено поширені в степових екосистемах, мають найбільш малі різцеві отвори, натомість види з вологих біотопів — великі. У багатьох випадках родові і родинні групи добре розрізняються формою і розміщенням різцевих отворів, а близькі пари видів добре розрізняються за розмірами (насамперед, довжиною), проте тут важливо завжди враховувати онтогенетичний вік зразків, оскільки у молодих особин різцеві отвори закономірно малі, подібні до різцевих отворів інших видів, для яких характерні малі розміри *incisive foramen*. На основі відомих даних про роль різцевих отворів і якобсонова органу в житті ссавців розглянуто гіпотези, що можуть пояснювати відмінності видів і родів за будовою (розміри, розташування й форма) різцевих отворів.

Ключові слова: морфологічно близькі види, різцеві отвори, міжвидові відмінності.

Introduction

The incisive foramen (*foramen incisivum*) is a morphological structure, the most noticeable in the rostral part of the skull. Its role is specific and is primarily related to the functions of the vomeronasal organ (VNO), also known as the Jacobson organ described in 1811, an ancient amniotic sense organ well known in mammals [Bhatnagar & Smith 2003; Mendoza 1993]. One of the names of the Jacobson organ is 'water olfactory organ' (Wassergeruchsorgan), which is located in the nasal cavity and has access to the oral cavity through the incisors [Broman 1920]. These sensory organs in mammals are associated with chemoreception, and especially, as shown later, with the analysis of pheromones and the formation of sexual behaviour [Wysocki & Lepri 1991]. Due to the development of the hard palate in mammals, this sense organ has anatomical limitations and a clear localization: the incisive foramina are small paired openings located behind the incisors.

The practice of identifying mammalian taxa by osteological features demonstrates the importance of such features as size, shape, and location of incisive foramina to determine genera and species in many mammalian groups [e.g. Pucek 1984], including when comparing morphologically similar species belonging to the same genus [Zagorodniuk 1991; Zagorodniuk *et al.* 1992; Barkaszi 2017]. In a number of cases, the usual metrics are important—the length (LFI) and width (BFI) of incisive foramina—, which has repeatedly been discussed in detail by the author in a series of special publications [e.g. Zagorodniuk 1993, 2004].

The purpose of this work is to analyse the diagnostic significance of incisive foramina (size, shape, and location) in the study of differences between morphologically similar species of mammals, mainly on the example of rodents of the fauna of Ukraine.

General morphological characteristics

Incisive foramina are one of the most notable morphological characters of the rostral part of the skull of most mammals, and due to their location they are one of the most available morphological feature for comparison. This is a paired morphological structure, which is normally represented by two openings in the bone of oval or other shape, usually located closer to the anterior edge of the skull, often at the level of premolars or mid-diastema. From the incisive foramina dorsally on the surface of the bony palate often extend two channels, which in some species (e.g. voles) extend to the posterior edge of the palate. Along the central line is a bony septum that separates these two openings. There are groups in which incisive foramina are very specific, such as bats, in which upper incisors are reduced and the incisive foramina open anteriorly as a maxillary notch [Giannini & Simmons 2007; Thier & Stefen 2020].

The incisive foramina are highly variable morphological structures (Fig. 1), the features of which are group-specific (at the level of genera and families), and in some cases they are species-specific. At both levels, the levels of superspecific groups and pairs of related species, the shape and size of incisive foramina have features that can be used as morphological criteria to identify osteological materials. Their topography also makes them important for diagnosis, as these structures are preserved in most specimens that have suffered some kind of destruction (e.g. in fodder residues of carnivorous mammals or in owl pellets): their location in the anterior part of the hard palate and also, to some extent, them being protected on the sides by the upper dentition makes this part of the rostrum essentially invulnerable to traumatic variability. Therefore, this feature is often one of the best preserved and most accessible for analysis.

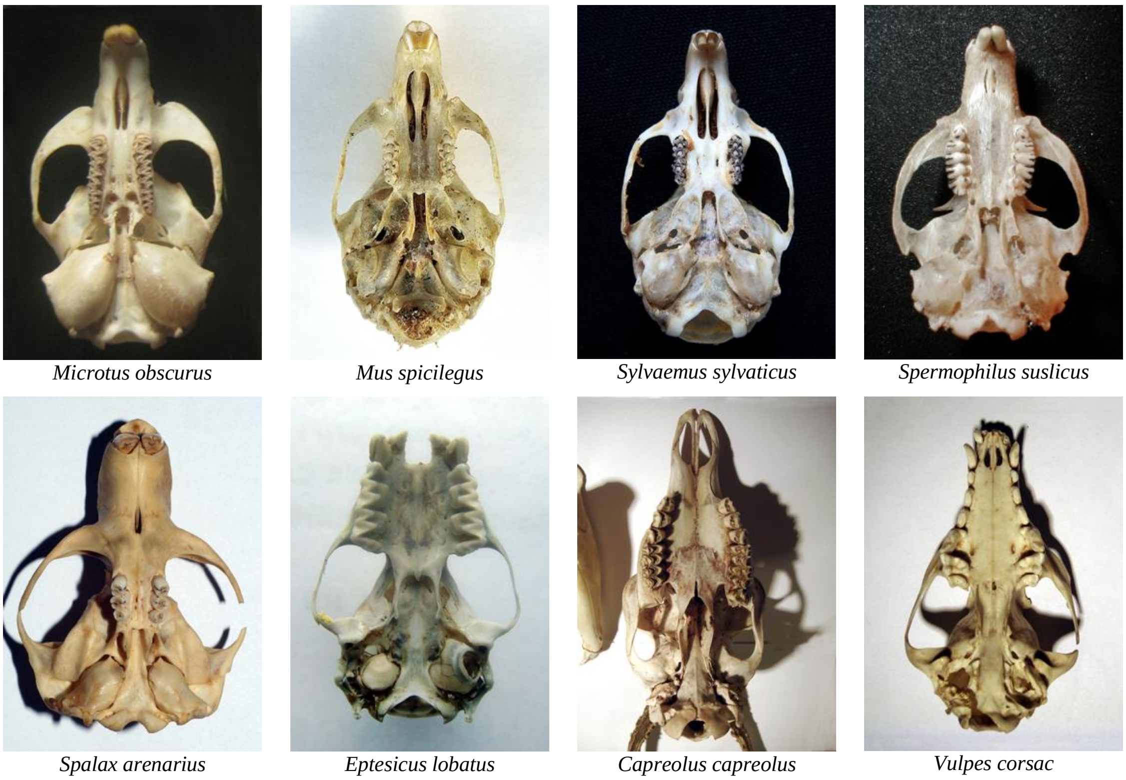

Fig. 1. Variants of appearance (size, position, and shape) of incisive foramina in different groups of mammals: muroid (*Microtus obscurus*, *Mus spicilegus*, and *Sylvaemus sylvaticus*) and non-muroid rodents (*Spermophilus suslicus*, *Spalax arenarius*), bats (*Eptesicus lobatus*), ungulates (*Capreolus capreolus*), and carnivorans (*Vulpes vorsac*).

Рис. 1. Варіанти зовнішнього вигляду (розміри, положення і форма) різцевих отворів у різних груп ссавців: мишовидих (*Microtus obscurus, Mus spicilegus, Sylvaemus sylvaticus*) та немишовидих гризунів (*Spermophilus suslicus, Spalax arenarius*), кажанів (*Eptesicus lobatus*), ратичних (*Capreolus capreolus*), хижих (*Vulpes vorsac*).

Examples of differences in close species

Comparisons of craniometrical characters in a series of 12 pairs of morphologically similar species revealed three groups of species in which the dimensions of incisive foramina are among the five most significant[1]: 1) *Mus musculus* and *M. spicilegus*, 2) *Sylvaemus sylvaticus* and *S. uralensis*; 3) *Microtus levis* and *M. arvalis–M. obscurus* [Zagorodniuk 2004]. Subsequently, significant differences were found in the group of close species of ground squirrels, in which the length of incisive foramina (LFI) is also included in the CD5 group [Zagorodniuk 2019].

***Microtus* (sensu lato).** Voles are the first group of species considered here, for which the leading role of the size and shape of incisive foramina in the identification of close species has been established—*Microtus arvalis* and *M. levis* [Zagorodniuk 1991 et al.]. Thus, in *M. arvalis*, incisive foramina are elongated and narrow, clearly narrowed in the proximal part, while in *M. levis* they are short and wide, usually almost equally wide along the entire length (Fig. 2*a–b*). Examples are shown in Fig. 2; metric features were published earlier [Zagorodniuk 2004]. Similar differences were found by the author in the pair of *Microtus subterraneus–M. tatricus*, but these differences are almost exclusively related to the measurement of length: LFI = 3.5–4.1 mm in *M. subterraneus* and LFI = 4.1–4.4 in *M. tatricus*. Differences between the pair of species *M. arvalis–M. agrestis* based on craniometrical data are described by Barkaszi [2021]: the efficiency of diagnostics by the combination of such characters as upper molars length vs incisive foramina length is shown.

Fig. 2. Incisive foramina in close species of grey voles and wood mice, *Microtus arvalis–M. levis* and *Sylvaemus sylvaticus–S. uralensis.*

Рис. 2. Різцеві отвори у близьких видів сірих полівок та мишаків, *Microtus arvalis–M. levis* та *Sylvaemus sylvaticus–S. uralensis.*

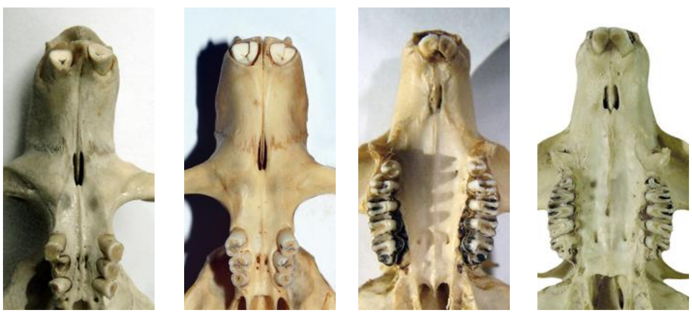

Fig. 3. Examples of relative size and shape of incisive foramina in pairs of close species of mole rats and ground squirrels, *Spalax zemni–S. arenarius* and *Spermophilus odessanus–S. suslicus.*

Рис. 3. Приклади відносного розміру і форми різцевих отворів у близьких видів сліпаків і ховрахів, *Spalax zemni–S. arenarius* та *Spermophilus odessanus–S. suslicus.*

Fig. 4. Examples of relative size and shape of incisive foramina in the pair of similar species of fox *Vulpes vulpes–V. corsac* and two related species of minks *Mustela lutreola–M. vison.*

Рис. 4. Приклади відносного розміру і форми різцевих отворів у парі близьких видів мишей *Mus musculus–M. spicilegus* та у двох близьких видів норок, *Mustela lutreola–M. vison.*

[1] To the CD5 group the author includes 5 metric features having the largest values of the coefficient of divergence.

Table 1. Dimensions of incisive foramina in samples of *Microtus* ex gr. '*arvalis*' [Zagorodniuk 2007], *Sylvaemus sylvaticus*–*S. uralensis* [Zagorodniuk 2004], and *Mus musculus*–*M. spicilegus* [Zagorodniuk 2002]

Таблиця 1. Виміри різцевих отворів у вибірках *Microtus* ex gr. "*arvalis*" [Zagorodniuk 2007], *Sylvaemus sylvaticus*–*S. uralensis* [Zagorodniuk 2004] та *Mus musculus*–*M. spicilegus* [Zagorodniuk 2002]

Character	'Maternal' species	Value, mm	'Daughter' species	Value, mm	CD
LFI	*Microtus arvalis* (n = 28)	4.94 ± 0.23	*levis* (n = 34)	4.43 ± 0.20	2.37
BFI	*Microtus arvalis* (n = 28)	1.27 ± 0.10	*obscurus* (n = 42)	1.11 ± 0.09	1.68
BFI	*Microtus levis* (n = 34)	1.30 ± 0.10	*obscurus* (n = 42)	1.11 ± 0.09	2.00
LFI	*Sylvaemus sylvaticus* (n = 94)	5.34 ± 0.27	*uralensis* (n = 92)	4.57 ± 0.26	2.91
BFI	*Sylvaemus sylvaticus* (n = 94)	1.77 ± 0.12	*uralensis* (n = 92)	1.51 ± 0.11	2.26
LFI	*Mus musculus* (n = 27)	5.07 ± 0.32	*spicilegus* (n = 34)	4.61 ± 0.32	1.40
LFI	*Spermophilus odessanus* (n = 13)	3.07 ± 0.33	*suslicus* (n = 13)	2.65 ± 0.28	1.39

Sylvaemus. All species of wood mice in the fauna of Ukraine have significant differences in the size of incisive foramina. They are the largest in *S. tauricus* and *S. sylvaticus.* The absolute dimensions of incisive foramina in these two species are rather similar, although the relative size of these structures are much larger in *S. sylvaticus*, in which they clearly extend beyond the line of the anterior faces of M1. In the second pair of species, *S. uralensis* and *S. witherbyi*, these foramina are small and rounded at the ends. The most noticeable differences characterize the pair of species *S. sylvaticus*–*S. uralensis* (Fig. 2*c*–*d*). An important coordinate in the descriptions of these features is the line of the anterior edge of M1, which is intersected or not by the incisive foramina.

Spalax. In mole rats, an example is the pair of *S. zemni*–*S. arenarius*, in which the incisive foramina are located more proximally than the 'rostral' suture (suture between the intermaxillary and maxillary bones), and their anterior edges are relatively wide and rounded; in *S. arenarius*, the anterior edge of the incisive foramina are acute and located above this suture (Fig. 3*a*–*b*).

Spermophilus. In the pair of allospecies of ground squirrels, *S. odessanus*–*S. suslicus*, incisive foramina are small, with weak but noticeable differentiation in size (Fig. 3*c*–*d*; Table 1).

Vulpes. Differences in the size, position, and shape of incisive foramina were found in the pair of the red and the steppe foxes, *V. vulpes*–*V. corsac*: the incisive foramina in the latter species are shortened, narrowed at the front, and do not reach the posterior edges of the canines (Fig. 4*a*–*b*).

Mustela. Several pairs of close species are in this group, including polecats and minks [Gálvez-López *et al.* 2021]. Photos in Fig. 4*c*–*d* demonstrate differences between incisive foramina of the European and American minks by size and position.

Patterns

When analysing the variability of incisive foramina in different groups of mammals, some general patterns can be noted related to their diagnostic value, differences in close species, and ontogenetic growth rates. Of these, it is important to highlight the following three:

1) Incisive foramina have significant differences in size, location, and shape at the level of families and genera, and are important characters in the identification of osteological specimens; clear differences are usually found at the level of genera, and such features are often qualitative and can be easily described in morphological terms (e.g. large, wide, and extended posteriorly in hares and birch mice, short and narrow in mole rats, mole voles, and ground squirrels);

2) There are distinct differences in the size of incisive foramina in all pairs of sibling species, especially in length and less so in width, or in the degree of development of the septum between them; moreover, in pairs of related species, the differences are regular—in steppe species they are the smallest, in species of wetter habitats are the largest (examples are given above);

3) Incisive foramina in the studied species have a pronounced age-related variability: in young individuals they are short, pointed, but with age they increase markedly, which generally coincides with the time of maturation. This has been noted before [Balčiauskienė *et al*. 2015]. It is known that the role of the VNO is especially important during maturation, and later it is lost [Meredith 1986].

Discussion

The incisive foramina are morphological structures that actually represent a duct to the vomeronasal organ (VNO). Among their key functions is their role in chemical sensation and communication, in particular in the perception of pheromones and the formation of mating behaviour [Wysocki & Lepri 1991]. In particular, as shown in experiments with mice, male VNOs detect the pheromone of the female primer, which subsequently causes the release of testosterone [Wysocki *et al*. 1983]. Obviously, such features should affect not only the interaction of sexes, but also the relationship of related species, ensuring the protection of populations from unjustified reproductive efforts.

Based on the role of VNOs in chemical communication and differences in the morphology of incisive foramina in close species, we can assume the important role of these structures in semiotics, that is, in the 'friend-foe' recognition system. Such system is a safeguard against interspecific hybridization [Kuhl 2016]. Obviously, the differences in functions and ways of its implementation are determined by differences in the size, shape, and position of incisive foramina.

Thus, incisive foramina are an informative system of features when comparing species, and most pairs of close species show differences in the size, position, and shape of these structures.

Acknowledgement

The author sincerely thanks colleagues who contributed to the development of this study, in particular O. Savarin and S. Teslenko. My thanks to K. Ocheretna and T. Postawa for their advice on anatomical terminology. The reviewers are also acknowledged for their helpful comments on the contents of the manuscript.

References

Balčiauskienė, Laima., L. Balčiauskas, V. Vitkauskas, S. Podėnas. 2015. Indoor small mammals in Lithuania: some morphometrical, body condition, and reproductive characteristics. *Zoology and Ecology*, **25** (4): 305–313. CrossRef

Barkaszi, Z. 2017. Diagnostic criteria for identification of Microtus s. l. species (Rodentia, Arvicolidae) of the Ukrainian Carpathians. *Vestnik zoologii*, **51** (6): 471–486. CrossRef

Bhatnagar, K. P., T. D. Smith. 2003. The human vomeronasal organ. V. An interpretation of its discovery by Ruysch, Jacobson, or Kölliker, with an English translation of Kölliker (1877). *The Anatomical Record*, **270B** (1): 4–15. CrossRef

Broman, I. 1920. Das Organonvomero-Nasale Jacobsoni Ein Wassergeruchsorgan. *Anatomische Hefte (Abteilung I. Heft 174)*, **58** (1): 143–188. CrossRef

Gálvez-López, E., B. Kilbourne, P. G. Cox. 2021. Cranial shape variation in mink: Separating two highly similar species. *Journal of Anatomy*, **240** (2): 210–225. CrossRef

Giannini, N. P., N. B. Simmons. 2007. The chiropteran premaxilla: a reanalysis of morphological variation and its phylogenetic interpretation. *American Museum Novitates*, **3585**: 1–44. CrossRef

Kull, K. 2016. The biosemiotic concept of the species. *Biosemiotics*, **9** (1): 61–71. CrossRef

Mendoza, A. S. 1993. Morphological studies on the rodent main and accessory olfactory systems: the regio olfactoria and vomeronasal organ. *Annals of Anatomy*, **175**: 425–446. CrossRef

Meredith, M. 1986. Vomeronasal organ removal before sexual experience impairs male hamster mating behavior. *Physiology & Behavior*, **36** (4): 737–743. CrossRef

Pucek, Z. (ed.). 1984. *Klucz do oznaczania ssaków Polski*. Państwowe Wydawnictwo Naukowe, Warszawa, 1–383.

Thier, N., C. Stefen. 2020. Morphological and radiographic studies on the skull of the straw-coloured fruit bat Eidolon helvum (Chiroptera: Pteropodidae). *Vertebrate Zoology*, **70** (4): 601–613. CrossRef

Wysocki, C. J., Y. Katz, R. Bernhard. 1983. Male vomeronasal organ mediates female-induced testosterone surges in mice. *Biology of reproduction*, **28**: 917–922. CrossRef

Wysocki, C. J., J. J. Lepri. 1991. Consequences of removing the vomeronasal organ. *The Journal of Steroid Biochemistry and Molecular Biology*, **39** (4B): 661–669. CrossRef

Zagorodniuk, I. V. 1991. Systematic position of Microtus brevirostris (Rodentiformes): materials to the taxonomy and diagnostics of the "arvalis" group. *Vestnik zoologii*, (3): 26–35. [In Russian]

Zagorodniuk, I. V., N. N. Vorontsov, V. N. Peskov. 1992. Tatra vole (Terricola tatricus) in the Eastern Carpathians. *Zoologicheskii zhurnal*, **71** (6): 96–105. [In Russian]

Zagorodniuk, I. V. 1993. Identification of East European forms of Sylvaemus sylvaticus (Rodentia) and their geographic occurrence. *Vestnik zoologii*, **27** (6): 37–47. [In Russian]

Zagorodniuk, I. V. 2002. Taxonomic revision and diagnostics of the rodent genus Mus from Eastern Europe. 2. *News Biosphere reserve Askania-Nova*, **4**: 130–140. [In Russian]

Zagorodniuk, I. 2004. Levels of morphological differentiation in closed species of mammals and the concept of hiatus. *Visnyk of the Lviv University. Series Biology*, **38**: 21–42. [In Ukrainian]

Zagorodniuk, I. 2007. Coordinated genetic, biogeographical and morphological differentiation in evolutionary young species: analysis of the group Microtus "arvalis" (Mammalia). *Reports of the National Academy of Sciences of Ukraine*, (3): 175–181. [In Ukrainian]

Zagorodniuk, I. 2019. Close non-murid rodent species in the Ukrainian fauna: differences, biogeography, ecomorphology. *Theriologia Ukrainica*, **17**: 8–27. [In Ukrainian] CrossRef