Vestnik zoologii, **49**(6): 419–528, 2015
DOI 10.1515/vzoo-2015-0062

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UDC 569.322/3(477)

BEAVERS OF THE GENUS *TROGONTHERIUM* (CASTORIDAE, RODENTIA)FROM THE LATE MIOCENE OF UKRAINE

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Beavers of the Genus *Trogontherium* (Castoridae, Rodentia) from the Late Miocene of Ukraine. Apoltsev, D. A., Rekovets, L. I. — The description of teeth and cranial fragments of extinct beavers, belonging to the genus *Trogontherium* Fischer von Waldheim, 1809 from Late Miocene strata of Ukraine, is presented in this paper. Their comparison with contemporaneous remains from localities in Europe and Asia is conducted. New data on systematics and paleogeography of *Trogontherium* (*Euroxenomys*) *minutum minutum* Meyer, 1938 and *T.* (*Euroxenomys*) *minutum rhenanum* Franzen, Storch, 1975, and also about their possible phylogenetic connections with the most ancient representatives of the family Castoridae are presented.

Key words: extinct beavers, tooth morphology, systematics, Late Miocene, Eastern Europe.

Бобры рода *Trogontherium* (Castoridae, Rodentia) из позднего миоцена Украины. Апольцев Д. А., Рековец Л. И. — В статье представлено детальное описание морфологии зубов и фрагментов черепа вымерших бобров рода *Trogontherium* Fischer von Waldheim, 1809 из отложений позднего миоцена Украины. Осуществлено их сравнение с близкими по возрасту остатками из местонахождений на территории Европы и Азии. Приводятся новые данные о систематике и палеогеографии *Trogontherium* (*Euroxenomys*) *minutum minutum* Meyer, 1938 и *T.* (*Euroxenomys*) *minutum rhenanum* Franzen, Storch, 1975, а также об их возможных филогенетических связях с более древними представителями семейства Castoridae.

Ключевые слова: вымершие бобры, морфология зубов, систематика, поздний миоцен, Восточная Европа.

Introduction

Fossil remains of beavers of the genus *Trogontherium* (Castoridae, Rodentia) were firstly described from the late Pliocene strata of the Azov region — vicinities of Taganrog, Russia (Fischer von Waldheim, 1809). Nearly fifteen species of this genus have been described over the last 200 years (Stefen, 2011). However, a clear revision of the extinct taxa for the ascertainment of their systematic affiliation is not fully carried out until now (Motuzko, 1972; Franzen, Storch, 1975; Mayhew, 1978; Hugueney, 1999; Stefen, Rummel, 2003; Rekovets, 2006; Rekovets et al., 2009; Giersch et al., 2010; Hugueney, Duranthon, 2012). Issues regarding the taxonomic status, systematics and geological distribution of the smallest members of the *Trogontherium* (*T. minus*, *Euroxenomys minutus*, *T. minutum*) still remain controversial. It is assumed that existence of *T. minutum* can be restricted by MN 3-11 zones (Hugueney, Duranthon, 2012), *T. minus* — MN 13–17, and *T. cuvieri* — from MN 16 to the middle Pleistocene (Hugueney et al., 1989).

Remains of about ten species of extinct beavers belonging to different genera (e. g., *Steneofiber*, *Monosaulax*, *Palaeomys* = *Chalicomys*, *Trogontherium*, *Dipoides*, and *Castor*) have been previously identified on the territory of Ukraine (Topachevsky et al., 1987; Dema, 2000; Rekovets, 2006; Rekovets et al., 2009; Casanovas-Vilar, Alba, 2011; Rekovets, Nowakowski, 2013; Prieto et al., 2014). Material of *Trogontherium*-like beavers from Late Miocene localities of Ukraine have allows characterizing morphological features of remains and obtaining new data on their taxonomy and geological distribution, which are presented in this paper.

Material and methods

The material under study is mostly represented by molar series from the late Miocene (Sarmatian, Maeotian, and Pontian) localities of Ukraine. These items are housed in the Department of Paleontology of the Na-

tional Museum of Natural History, National Academy of Sciences of Ukraine (Kyiv). Ninety eight teeth (molars and incisors), as well as several fragments of upper and lower jaws have been morphometrically processed. Specific amount of the investigated material is indicated in the text. The specimens were measured with aid of a binocular microscope with an ocular micrometer. All measurements are given in millimeters with 0.01 mm precision. The following measurements were taken: L — length, W — width. W/L ratio is counted and expressed as a percentage (table 1). The metric data for comparison are derived from other late Miocene localities outside of Ukraine (table 1), e. g. Catakbagyaka (Ünay, 1975), Dorn-Dürkheim (Franzen, Storch, 1975), Petersbuch (Stefen, Rummel, 2003), Höwenegg (Giersch et al., 2010), and Höwenegg (Hugueney, Duranthon, 2012). Osteological material has been processed in accordance with conventional techniques. Tooth terminology follows Stirton (1935), correlation of the Eastern Paratethys stages with European Mammal Neogene zones — Topachevsky et al. (1997), and also Nesin, Nadachowski (2001).

Results and discussion

The genus *Trogontherium* is conditionally divided into two informal groups: "*minutum*", which includes small representatives, and "*cuvieri*", uniting larger beavers. This separation can be also considered as a stratigraphic: fossil remains of the small forms have been found in sediments, dated as late Miocene — late Pliocene, as well as large beavers — from late Pliocene-middle Neopleistocene strata (Hugueney et al., 1989; Hugueney, Duranthon, 2012).

The most important diagnostic features for the **genus** *Trogontherium* are (1) cement absence on molars (2) convex front part of incisors with smooth enamel (3) the third upper molar is always elongated and triangular, with a larger number of inflections or fossettes (4) poorly developed roots. Metric values of the teeth do not overlap and clearly distinguish large (**subgenus** *Trogontherium*) and small (**subgenus** *Euroxenomys*) beavers. Premolars are one of the most diagnostic teeth for *Trogontherium*. Length of P_4 in small forms is 5.0–6.5, width — 4.0–4.8 mm; P^4 — 6,0–6,5 × 5,0–5,5 mm. P_4 size in large representatives of the genus is 10.0–15.0 × 8.0—10.0 mm; P^4 — 10.0–12.0 × 12.0–14.0 mm, respectively. Furthermore, the degree of stretch marks, development of striids and roots, formation time of facets and fossetids, as well as tooth enamel ultrastructure are important additional diagnostic features (Koenigswald, Mörs, 2001).

Genus ***Trogontherium*** Fischer von Waldheim, 1809

Type species: *Trogontherium cuvieri* Fischer von Waldheim, 1809.

Type locality: Taganrog (Sea of Azov).

Geological age: late Pliocene — early Pleistocene.

Distribution: Europe, Asia.

Generic composition: subgenera *Trogontherium* Fischer von Waldheim, 1809 (large forms), *Euroxenomys* Samson, Radulescu, 1973 (small forms).

Trogontherium is represented in the fossil record of Ukraine by the three species (Schreuder, 1929): *T. minutum* Meyer, 1838 (Late Miocene), *T. minus* Newton, 1890 (Pliocene), and *T. cuvieri* (late Pliocene — Pleistocene).

Subgenus ***Euroxenomys*** Samson, Radulescu, 1973

Detailed synonymy is presented in Hugueney, 1999; Hugueney, Duranthon, 2012.

Composition of the subgenus: *T. minutum* Meyer, 1838; *T. minus* Newton, 1890.

Trogontherium minutum on the territory of Ukraine is reliably detected from the Grytsev locality (MN 9), while the remains of *Trogontherium minus* have been found on the numerous Pliocene localities of Ukraine (MN 14–17). Some of these remains were identified earlier as *Monosaulax savinovi* Lytchev, 1977 (label definitions: G. F. Lychev).

Trogontherium* (*Euroxenomys*) *minutum Meyer, 1838

Monosaulax sp.: Topachevsky et al., 1987; *Trogontherium minutum*: Rekovets et al., 2009; Kovalchuk, Apoltsev, 2013; *Euroxenomys minutus*: Hugueney, Duranthon, 2012.

Type locality: Elgg (Braunkohle), Switzerland.

Geological age: middle Miocene.

Species composition: *Trogontherium minutum minutum* Meyer, 1938, *Trogontherium minutum rhenanum* Franzen, Storch, 1975, *Trogontherium minutum ozansoyi* (Ünay, 1975) and *Euroxenomys minutus minutus* from Sansan (Hugueney, Duranthon, 2012) described earlier as a separate genus.

Remains of the nominative subspecies are known from the early Late Miocene (MN 9) of the Grytsev locality in Western Ukraine. Remains of *Trogontherium* (*Euroxenomys*) *minutum rhenanum* have been collected from the Late Miocene in the range of MN 10 (late Vallesian) — MN 13 (Turolian), i. e. during the time of existence of the Sarmatian-Pontian sea basins in the south of Eastern Europe. The subspecies *Trogontherium minutum ozansoyi* (= *Steneofiber minutus ozanzoyi*) was found in the Late Miocene (MN 12) strata of Catakbayaka, Turkey (Ünay, 1975).

Morphometric parameters, separating these three subspecies of the genus *Trogontherium* based mainly on differences in the length of dentition, although they are also based on some other features. E. g., the length of the lower P_4–M_3 dentition in *Trogontherium* (*Euroxenomys*) *minutum minutum* from Petersbuch is in the range of 11.0–13.0 mm, while it averages 13.0 mm (restored) in the subspecies *Trogontherium* (*Euroxenomys*) *minutum rhenanum* (Franzen, Storch, 1975). The restored length of the lower dentition P_4–M_3 in *Trogontherium minutum ozansoyi* may be in the range of 10.0–11.0 mm. Special morphology of the P_4 also is a hallmark for this subspecies (Ünay, 1975).

Trogontherium* (*Euroxenomys*) *minutum minutum Meyer, 1938

Investigated material. Grytsev: 1 skull fragment with maxillary part and P^4–M^3 (fig. 1, *1*), a fragment of the mandible with P_4 and M_1 (fig. 1, *2*), an incisor fragment, 4 P^4, 1 $M^{1\text{-}2}$, 4 M^3, 4 P_4, 5 $M_{1\text{-}2}$, 3 M_3.

Geological age: MN 9, middle Sarmatian (Vallesian).

According to Lychev (1973, 1983), fossil remains of *T.* (*Euroxenomys*) *minutum* from the Late Miocene of Ukraine, including the material from Grytsev, are belonging to *Monosaulax savinovi*, typical North American and Asian species. Molars from Grytsev (fig. 1, *3*) have relatively smaller crowns and less-developed roots than those in *Monosaulax savinovi*, which was described from the Miocene of Kazakhstan.

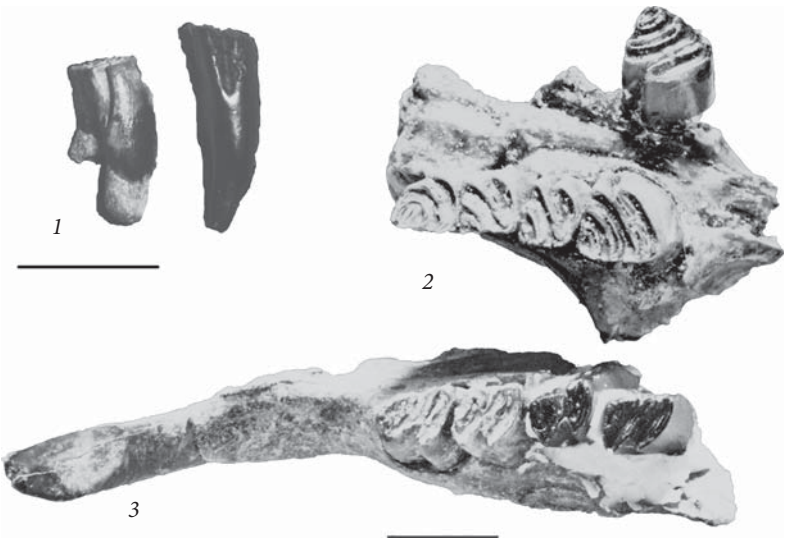

Fig. 1. Chewing surface of upper (*1*) and restored lower (*2*) dentition, character of the molar roots development (*3*) of *Trogontherium* (*Euroxenomys*) *minutum minutum* from the Grytsev locality. Scale bar 5 mm.

Description and comparison. Skull fragment has full dentition — 2 P^4 and M^{1-3}. Palate without expressed median crest, its posterior part is broken; the smallest palatal width between the P^4 alveoli — 2.3 mm, and between the M^1 alveoli — 4.5 mm. Alveolar length of the P^4–M^3 is 12.4 mm, coronary length — 12.2 mm. Teeth without cement have well-developed roots, hypostriae and hypoflexus. Mesofossette is convex, other fossettes are nearly straight. There is a fourth fossette on M^3. P_4, M_1, and incisor are preserved in front of the mandible. Coronoid process and the back part of the mandible are broken down to M_2. Teeth with greatly developed hypostriids and hypoflexids do not have cement; length of diastema is 9.1 mm, the restored height at P4 — 13.0 mm. For comparison, these values on material from Petersbuch are 8.87 and 20.05 mm, respectively (Stefen, Rummel, 2003).

The fragment of triangular lower incisor has a weak curvature; the enamel slightly covers the lateral surface. Enamel anterior side is convex. Incisor width is 3.4 mm, anteroposterior diameter — 3.9 mm. Average length of the P^4 is 4.1 mm, width — 4.5 mm (the length ratio — 109 %). The tooth is medium-worn. Para- and hypoflexi are straight and contrasted (not shifted) at the middle part of the tooth. Mesoflexus crosses the entire width of the chewing surface and has a slight bend. According to these features, P^4 from Grytsev is inferior in size compared to teeth from Petersbuch, and *Trogontherium minutum ozansoyi* (Ünay, 1975) from the Late Miocene of Turkey.

Length of M^{1-2} is 2.4 mm, width — 2.9 mm (W/L ratio is 120 %). Parafossette is small, shifted to edge of the chewing surface and opposed to the hypoflexus. Metaflexus is under closure into fossette. The subspecies from Petersbuch has a markedly larger size of these teeth with a W/L ratio of 159.0 %. Perhaps, this is due to different degrees of the tooth wear (Stefen, Rummel, 2003).

Length of M^3 is 3.1 mm, width — 2.9 mm (W/L ratio — 93 %). The teeth are shaped like an elongated triangle, which distinguishes the genus *Trogontherium* from others. Paraflexus is in the process of circuit into a fossette, slightly shifted in direction to the hypoflexus. Mesofossette is straight, stretched out over the entire tooth width. Dimensional parameters of the M3 from Grytsev are less than those from Petersbuch, as well as from the Late Miocene of Turkey. At the same time its W/L ratio remains almost in the range of 75–93 % (table 1).

Length of P_4 is 4.0 mm, width — 3.0 mm, W/L ratio — 75.0 %. Anterior part of the tooth is trapezoidal (not rectangular) unlike *Trogontherium minutum ozansoyi*, and the hypoflexus is not parallel to the labial side of the tooth.

Four M_{1-2} with weak roots belong to adult individuals (fig. 1, *3*); maximum crown height — 6.7; 7.0; 7.0; 7.3 mm, hypostriid height — 3.3; 3.4; 3.5; 3.6 mm, mesostriid height — 1.3; 1.4; 1.4; 1.6 mm. There are well-developed meso- and paraflexids, metafossetids on the chewing surfaces. The length exceeds the width (3.4 × 2.7 mm, W/L ratio — 79.4 %; 3.4 × 3.0 mm, W/L — 88.2 %; 3.5 × 2.7 mm, W/L — 77.1 %).

Two M_3 with well-marked four half-fused roots belong to adult individuals. Tooth height is 6.0 and 5.3 mm; hypostriid (2.4 and 2.0 mm) is well expressed, the mesostriid length is 0.9 and 1.7 mm. There are meta- and parafossetids on the crown surface; mesoflexid is weak (narrow and short) unlike the hypoflexid. Tooth length is 3.2 and 2.8 mm, width — 3.2 and 2.8 mm, W/L ratio is 100 %.

Remarks. P^4 from Petersbuch are on average about 5–7 % larger than those from Grytsev. M^{1-2}, conversely, are larger in Grytsev versus those from Petersbuch. P_4 and M^3 from Petersbuch are larger than those from Grytsev. M_{1-2} from Grytsev are longer and less wide than those from Petersbuch. M_3 are not represented in materials from Petersbuch, thus it is not possible to compare these teeth.

Trogontherium* (*Euroxenomys*) *minutum rhenanum Franzen, Storch, 1975

Monosaulax sp.: Topachevsky et al., 1987, 1992, 1997; *Steneofiber* sp.: Nesin, Nadachowski, 2001; *Euroxenomys minutus rhenanus* (comb. n.): Casanovas-Vilar, Alba, 2011.

Type locality. Dorn-Dürkheim, Germany.

Investigated material. Mikhailovka 2 (MN 11): 1 M_{1-2}, dP^4; Popovo 3 (MN 12): 1 dP_4; Cherevichnoe 3 (MN 12): 1 P_4, 1 dP_4, 1 mandible with P_4-M_2 (fig. 2), 2 M_{1-2}, 1 P_4 (fig. 3, *8*), 5 M^{1-2}, 3 M^3; Belka (MN 12): 1 M^3; Nikomarovka: 1 M_{1-2}; Novoelizavetovka 2: 1 M_{1-2}; Vinogradovka 1: M^{1-2} — 5, M^3 — 2, P_4 — 3, M_{1-2} — 7; Pontian lectostratotype: P^4 — 5, M^{1-2} — 2, M^3 — 3, P_4 — 3, M_{1-2} — 5; Andreevka: P^4 — 1, M^{1-2} — 2, M^3 — 2, P_4 — 2, M_{1-2} — 4.

Geological age: MN 10–13, Late Miocene (Turolian).

The earliest representatives of the *T.* (*Euroxenomys*) *minutum rhenanum* in Ukraine are known from the Mikhailovka 1 and 2 locality.

Description and comparison. P^4 from the numerous localities on the territory of Ukraine (fig. 3, *1*) are characterized by a somewhat larger size as compared to the nominative subspecies and those from Dorn-Dürkheim. The height of the tooth crown is on average 4.2 mm (maximum — up to 8.0 mm), length — within the range of

Fig. 2. Right mandible of *Trogontherium* (*Euroxenomys*) *minutum rhenanum*. Cherevichnoe 3 locality: *1* — labial view; *2* — view on the point of chewing surface. Scale bar 5 mm.

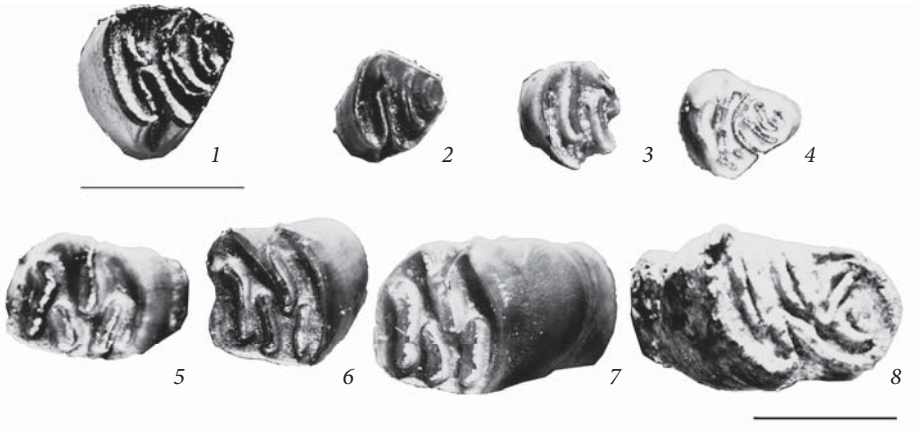

Fig. 3. Chewing surface of upper (*1–4*) and lower (*5–8*) dentition of *Trogontherium* (*Euroxenomys*) *minutum rhenanum*: *1* — P^4, Cherevichnoe 3; *2–3* — M^{1-2}, Andreevka; *4* — M^3, Andreevka; *5* — M_3, Andreevka; 6–7 — M_{1-2}, Cherevichnoe 3; *8* — P_4, Cherevichnoe 3. Scale bar 5 mm.

3.6–5.3 mm, width — 4.1–6.1 mm, and W/L ratio is 110 % (table 1). The widest teeth are observed in materials from Mikhailovka on Bug 2 and Verkhnya Krynitsa 2 (W/L ratio — 115.0 %). Hypostria usually reach the crown bottom, mesostria is long; flexus closed into the fossettes in early stages of wear; parafossette and metafossette are insular-shape. Tooth size of the subspecies from Dorn-Dürkheim is similar, but the latter have almost the same length and width (W/L ratio — 98 %). Length of the dP^4 from Vinogradovka 1 is 2.9 mm, width — 3.0 mm (W/L = 103 %), the height of the tooth crown is 4.6 mm. Paraflexus tends to branching, mesoflexus crosses the entire width of the chewing surface, metafossette is circular. Apex of the hypoflexus reaches the middle part of the chewing surface, para- and mesostriae are weak, hypostria reaches the crown bottom.

Height of M^{1-2} from Andreevka, Vinogradovka 1 and Pontian lectostratotype is on average 8.0 mm, length — near 3.5 mm, width is 4.0 mm (W/L ratio — 114 %). Parafossette and mesofossette are well-expressed (fig. 3, *2*, *3*); hypofossette is shifted to the labial edge, while its lingual side docks with the labial edge. Parafossette is sometimes small and short in buccal-lingual direction, hypostria ends below half of the crown height. Insular-shape hypofossette is often small, slightly elongated, and located parallel with the parafossette. Paraflexus reaches half of the chewing surface width in contact with hypoflexus. Lingual edge of mesoflexus almost reaches the edge of the chewing surface. Metafossette is oval. Meso- and metastries are weak and hardly noticeable. One M^{1-2} from Frunzovka 2 is slightly different in size and morphology: L = 5.5 mm, W = 3.8 mm (W/L ratio — 69.1 %), i. e. the tooth is longer than wider.

Elongated M^3 with well-developed roots from Belka, Andreevka (fig. 3, *4*), Pontian lectostratotype are relatively large (L in the range of 4.0–5.5 mm, W = 3.3–4.0 mm, the average index — 75 %). Parafossette is located transversely with hypostriid, mesostria is long, ends by less than half of the crown height. Metafossette is Y-shaped; there are two small additional fossetids. There is a small additional fossette under the parafossette, from the labial tooth side; mesoflexus is not closed, there are two small fossettes at the bottom of metaflexus. Hypostria reaches extends about nearly 2/3 of the crown height. Teeth from the Pontian lectostratotype have an oblong parafossette and a long arched mesofossette. Metafossette disposed substantially parallel to the longitudinal axis of the chewing surface. There is an additional (fourth) fossette inside the bend of metafossette.

M^3 from Belka is shorter and wider than those from Dorn-Dürkheim, while inferior in the size of the teeth from the Pontian lectostratotype. M^3 from Andreevka is smaller than those from the Pontian lectostratotype and Dorn-Dürkheim. M^3 length from Vinogradovka 1 is 3.0 mm, width — 2.2 mm, crown height is 6.4 mm. The tooth is slightly worn; paracone is insular (isolated). Parafossette in the teeth from the Pontian lectostratotype is located on the labial tooth side; mesofossette is expressed across the entire width of the chewing surface and permanently bonded to the front part of the tooth. The metafossette is slightly curved. Additional fossettes, different in form, are located down. Hypostria reaches 1/3 of the crown height.

P_4 morphology of the studied subspecies from the Late Miocene localities are divided into two groups — early or small, including the remains from MN 11–12, and late or larger — MN 13. Differences between them are stored mainly in terms of size. Tooth length of the early Maeotian (MN 11–12) populations is in the range of 5.1–5.7 mm, width — 4.1–4.6 mm, W/L ratio is 80 %. The larger tooth size is characteristic for the populations, dated by the Pontian (MN 13) : 6.0 × 4.3 mm in average, W/L ratio — 71.5 %. Beavers from Andreevka, Vinogradovka 1 and Pontian lectostratotype have less broad teeth and reflect a general trend to P_4 elongation in time. The population from Dorn-Dürkheim takes an intermediate position: under size (6.2 × 4.8 mm) it is closer to those from the Pontian lectostratotype; however under the W/L ratio (77 %) it is similar to Maeotian populations. Height of the tooth crown is in the range of 8.0–9.0 mm, roots are moderately developed. Parafossetid is elongated and slightly curved, mesoflexid is

Table 1. Tooth measurements of *Trogontherium* (*Euroxenomys*) *minutum* from the Late Miocene of Ukraine and localities in Europe and Asia

Taxa and localities	P^4			M^{1-2}			M^3			P_4			M_{1-2}			M_3		
	L	W	%	L	W	%	L	W	%	L	W	%	L	W	%	L	W	%
T. minutum Vinogradovka 1	–	–	–	7.5 5.8	7.5 5.8	100 100	3.0	2.2	73	5.0 4.9	3.4 3.0	68 61	3.0	2.8	93	–	–	
T. minutum Pontian lectostratotype	5.3 4.9	5.1 5.1	96 100	3.9	3.6	92	5.5 4.8	3.9 3.5	70 72	6.4 5.7	4.3 4.3	67 75	3.2	4.5	141	–	–	–
T. minutum Andreevka	6.1	5.0	81	3.5 3.4	4.0 3.9	114 110	4.6 4.0	4.0 3.3	86 82	5.3 6.7	4.2 4.5	79 67	4.1	4.0	97	–	–	–
T. minutum Novoukrainka	–	–	–	–	–	–	–	–	–	5.7	4.1	71	3.9	3.9	100	–	–	–
T. minutum rhenanum Nikomarovka	–	–	–	–	–	–	–	–	–	–	–	–	3.5	3.4	97	–	–	–
T. minutum rhenanum Dorn-Dürkheim	5.4	5.3	98	3.3	3.5	101	5.5	3.9	70	6.2	4.8	77	3.5	4.3	122	–	–	–
T. minutum rhenanum Belka	–	–	–	–	–	–	5.0	3.9	78	–	–	–	–	–	–	–	–	–
T. minutum rhenanum Cherevichnoe 3	–	–	–	–	–	–	–	–	–	5.1	4.6	90	–	–	–	–	–	–
T. minutum rhenanum Verkhnya Krynitsa	3.6	4.1	113	–	–	–	–	–	–	–	–	–	3.4	3.3	97	–	–	–
T. minutum rhenanum Mikhailovka 2	5.3	6.1	115	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
T. minutum ozansoyi Catakbagyaka	4.6	4.2	91	–	–	–	3.4	3.0	88	4.5	3.6	80	2.9	3.6	124	–	–	–
T. minutum minutum Grytsev	4.1	4.5	109	2.8 2.4	2.4 2.9	103 120	3.1	2.9	93	4.1	2.8	67	3.6	3.1	85	3.2	2.8	87
T. minutum minutum Petersbuch	4.7 4.3	4.5 4.9	105 105	2.2	3.5	159	4.5 4.9	3.4 3.7	75 75	5.3	3.9	73	2.8 3.1	3.8 4.0	133 133	–	–	–
T. minutum minutum Höwenegg	–	–	–	–	–	–	–	–	–	4.45	3.93	88.3	2.85	3.85	135	3.11	3.38	108
Euroxenomys minutus Sansan	5.0	4.8	96.0	3.1	4.0	129	3.2	4.0	80	4.4	4.2	95	3.0	3.7	123	2.3	3.2	139

straight, and metafossetid is located on the labial tooth side and similar in shape and size to parafossetid. Hypoflexid abuts by the labial edge into the lingual edge of metafossetid. Mesostriid reaches 2/3 of the crown height. Occasionally there is an additional rounded fossetid between para- and mesoflexids. A slightly different P_4 morphology is peculiar for the remains from Andreevka (fig. 3, *5*). Tooth length is 6.7 mm, width — 4.5 mm (W/L index — 67 %). There is an additional fossetid in the front part of the tooth; other fossetids have approximately the same shape. Hypoflexus comes on the chewing surface between the mesofossetid and metafossetid; hypostriid reaches the bottom of the crown, and the height of the crown is 5.2 mm. Tooth roots are greatly developed, exceeding the crown height.

M_{1-2} of this subspecies from the Maeotian localities of Ukraine belongs to adult individuals (fig. 3, *6*, *7*). They have poorly developed roots; there is no cement at the crown base. Crowns are slightly curved, their average height is 8.0 mm, hypostriid length — 3.9 mm, parastriid height is 0.1 mm, mesostriid — 1.2 mm. Metafossetid is somewhat curved and well-expressed. There is a fourth (additional) fossetid that distinguishes it from other Palearctic subspecies. The tooth crown is almost square (W/L ratio is in the range of 97–100 %). Parafossetid on individual teeth, e. g. from the Verkhnya Krynitsa 2, shifted leftwards, mesoflexid comes under the lingual edge of the hypoflexid, metafossetid is well-expressed. Hypostriid lowered on ¾ of the crown height. Mesoflexid and metaflexid formed two (lingual and labial) striids in the process of crown wear. There is a small rounded fossetid below the metaflexid, in the middle part of the lower edge of hypoconid. Labial edge of the mesostriid is weakly expressed, lingual edge is very small. Metastriids and metaflexies are also hardly expressed. Hypostriid reaches more than half of the crown height.

Remains of *T. minutum minutum* from Grytsev (MN 9) are similar to those from the Höwenegg locality in Germany (Giersch et al., 2010) in size of the lower molars as well as tooth proportions. Subspecies of Grytsev locality also has similar size with *Euroxenomys minutus minutus* from Sansan, but differs by narrower teeth, especially in the lower jaw, and relatively broader and shorter P_4 (109 % against 96.0 % for the subspecies from Sansan). Remains of *T. minutum ozansoyi* are closest to subspecies from Sansan in size and proportions of P^4 and M_{1-2} (table 1). This group of remains includes the most ancient and most minor forms of the nominative subspecies; they differ from the later and larger subspecies *T. minutum rhenanum*.

All teeth from the Maeotian localities are somewhat smaller as compared to those from Dorn-Dürkheim, Andreevka, Vinogradovka 1 and Pontian lectostratotype (table 1). Besides, typical series has wider teeth (W/L index — 122.0 %) unlike the Maeotian forms. M_{1-2} are smaller in Maeotian localities (average length is 3.4 mm, width — 3.35 mm, W/L ratio is 97.0 %), i. e. teeth are clearly square. Teeth from the late Maeotian and Pontian localities (Andreevka, Vinogradovka 1, Pontian lectostratotype) are larger (average length is 3.5 mm, width — 4.4 mm, W/L ratio is 140 %), i. e. width is much greater than length. It is an important indicator, especially for the remains from the Vinogradovka 1. Height of the crowns is in the range of 6.0–8.0 mm. *T.* (*Euroxenomys*) *minutum rhenanum* from Ukraine differs under the marked morphological features from the type series of Dorn-Dürkheim, which is closer to the Pontian populations. M_{1-2} from Andreevka are longer, but narrower than those from the Pontian lectostratotype. Besides, they are larger than those from Novoukrainka, Nikomarovka, and Verkhnya Krynitsa 2. M_{1-2} from Andreevka is bigger than those from Dorn-Dürkheim, and wider than longer.

Conclusions

Beavers from the Late Miocene localities of Ukraine are represented by the genera *Castor*, *Palaeomys* (= *Chalicomys*) and *Trogontherium*. The latter is the dominant group, although it is represented by only one species *Trogontherium* (*Euroxenomys*) *minutum*. This species is

divided into two allochronous subspecies — nominative (*minutum*), as well as *rhenanum*. These forms differ in size and stratigraphic range. The nominative subspecies is characterized by the small size and existed during the early stages of the late Miocene (Sarmatian, MN 9). *T. minutum rhenanum* was larger and existed in the second half of the Late Miocene (Pontian, MN 10–13). The changes of features took place in ontogeny and time: increase in size and hypsodonty, loss of the roots, earlier formation of fossettes in the genus *Trogontherium* from the Sarmatian to Pontian. Such morphological changes in strict relation to stratigraphic units formed the basis for taxonomic grades — subspecies. Remains from the late Maeotian and Pontian (MN 13) localities (Andreevka, Pontian lectostratotype and Vinogradovka 1) have noticeably larger size as compared to other Late Miocene beavers from Ukraine (table 1). They can qualify for special taxonomic status provided a more detailed study and on the more abundant material. Obtained results allow us to characterize the place of studied taxa in the evolution of this genus in Eastern Europe. *Trogontherium* probably is phylogenetically associated with the more ancient genus *Steneofiber*, and its appearance at the beginning of the Late Miocene on the south of the studied region was a result of prochoresis from the Asian continent. Since that time, these forms developed in the region were autochthonous and represented in the Miocene and Pliocene by two species changing in time — *T. minutum* and *T. minus*. Remains of the latter have been identified in materials from numerous localities throughout the Pliocene of Ukraine.

We are grateful to Prof. Dr. T. Mörs (Swedish Museum of Natural History, Stockholm, Sweden) and Prof. Dr. C. Stefen (Senckenberg Naturhistorische Sammlungen Dresden, Germany) for their important comments. We thank to Dr. M. V. Sinitsa, Dr. O. M. Kovalchuk and S. V. Neofitny (National Museum of Natural History, National Academy of Sciences of Ukraine, Kyiv) for their help in the preparation of the manuscript.

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Received 2 0ctober 2014
Accepted 29 0ctober 2015