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Taxonomic diversity and spatio-temporal distribution of late Cenozoic beavers (Castoridae, Rodentia) of Ukraine

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> Abstract. For the first time, data on distribution in time and space of fossil beavers (Castoridae) from the late Miocene (early Sarmatian) to Pleistocene of Ukraine are presented. The faunal list comprises: *Palaeomys castoroides, Steneofiber jaegeri, Trogontherium minutum* (Miocene), *T. minus, T. cuvieri, Dipoides sigmodus, Castor praefiber* (Pliocene), *C. tamanensis, C. fiber, T. minus* and *T. cuvieri* (Pleistocene). Many forms have been designated as sp. (species). Taxonomic problems and synonymy of extinct genera of Castoridae (from Miocene and Pliocene) of Europe are briefly discussed. The remains of the genus *Monosaulax* have not been identified to the species level. Faunistic lists of particular localities were supplemented, palaeoecological conditions and stratigraphic problems are also discussed.

Key words: Fossil beavers, Ukraine, Pleistocene, Pliocene, Miocene, stratigraphy.

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I. INTRODUCTION

Beavers (Castoridae) as members of Rodentia are an important and characteristic group of the upper Cenozoic fauna of the Holarctic Region. Their remains from the Oligocene till present are often excavated. Although the taxonomy of fossil Castoridae was relatively well-studied, a reanalysis and revision of this group is required. This applies, first of all, to the well-known groups of Castoridae from the Nearctic Region and Western Europe, as a high number of extinct taxa were described from these areas. The evolution of this group in Eastern Europe, including the Ukraine, has been poorly investigated.

Brief synopses of fossil beavers from Miocene and Pliocene localities were given by TOPACHEVSKY (1965) and TOPACHEVSKY et al. (1987). However, to date no qualitative or quantitative analyses of beaver assemblages, including morphological analysis, have been conducted in particular localities nor stratigraphic levels.

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The main aim of this study was to determine beaver species diversity, to supplement faunal lists and to identify stratigraphic levels in which beaver fossils were deposited. Further studies will be devoted to the taxonomic revision of Castoridae from the Ukraine, the diagnosis of particular taxa, a detailed description of teeth and bone morphology, and kin relationships between particular taxa.

II. AN OUTLINE OF THE HISTORY OF RESEARCH

Beaver remains from the Ukraine were described for the first time as *Trogontherium cuvieri*, FISCHER VON WALDHEIM 1809. They originated from Pliocene-Pleistocene sediments in the area around the Azov Sea in Ukraine. Later, EICHWALD (1830), NORDMANN (1858) and WOLDRICH (1887) described beavers among other mammal remains mainly from the Miocene sediments of Odessa. In the 20th century, LINSTOW (1908), ALEKSEEV (1933) and DJOZHKIN and SAFONOV (1972) have summed up these findings from southern Russia. They also gave data on beaver evolution since the Oligocene both in the Old and in the New World, but they failed to provide important data on morphology and taxonomy of this group. SCHREUDER (1929) provided morphological and taxonomic data on one genus only (*Trogontherium*). Later, several other species of this genus were described from other regions of Europe from Miocene-Pliocene deposits. FRANZEN and STORCH (1975), HUGUENEY (1999), MAYHEW (1978) and other authors partially revised this genus.

Based on material from Romania, Ukraine and Russia, a partial revision of Castoridae, with descriptions of new genera, species and subspecies, was undertaken by SIMIONESCU (1930), ALEK-SEEV (1933), VERESTCHAGIN (1951), MOTUZKO (1972), and RADULESCU and SAMSON (1967, 1972). Recently, studies on beaver remains from the Plio-Pleistocene deposits of the Ukraine were published by DEMA (2000), REKOVETS (2006), REKOVETS and KOPIJ (2007). In the last years, the taxonomy and systematics of Castoridae in Europe were analyzed in detail. The results were published in works of XU (1994), KORTH (2001), STEFEN and RUMMEL (2003), RYBCZYNSKI (2007) and other writers.

Since C. LINNAEUS published a short description of the current species *Castor fiber* in 1758, many other extinct beaver genera and species have been described from the Holarctic Region, including over 20 genera from North America and 30 genera from Europe and Asia, including synonyms. According to MCKENNA and BELL (1997) 30 extinct genera (including the genus *Rhizospalax*) are included in the infraorder Castorimorpha. The first attempt to revise this group has been undertaken by STIRTON (1935). Later, the group was a subject of LYCHEV's (1983) and HUGUENEY's (1999) revisions. Despite this, the taxonomy of fossil beavers both at the species and generic level is still in a stage of flux. If the taxonomy is not comprehensive, the origin of species and species groups is also not explicit.

Although most remains were excavated in the Oligocene and Miocene deposits of Western Europe, others were excavated in the Pliocene and Pleistocene deposits of Eastern Europe. A comparative analysis of such stratigraphically unequal material is very difficult to conduct. The diagnoses of beaver species were based on tooth structure, especially on enamel pattern, but this appeared to be almost identical in various species which occurred under similar ecological conditions. In other words, beavers went through a so called parallel transformation of traits (especially dentition) in their evolution. Based solely on these traits, it is difficult to identify species or to resolve phylogenetic lineages (LYCHEV 1983). These difficulties may be linked to stratigraphic distances and to a high level of tooth homoplasy.

Such transformations also led to a high level of specialization among the beaver species in different phylogenetic lineages, especially apparent in genera such as *Anchitheriomys* ROGER, 1898, (= ?*Amblycastor* MATTHEW, 1918) and *Asiacastor* LYCHEV, 1971. According to LYCHEV (1983) such morphological transformations were characteristic for four phylogenetic lineages equivalent to the subfamilies Castoroidinae TROUESSART, 1880, Trogontheryinae LYCHEV, 1973, Asiacastorinae LYCHEV, 1973 and Castorinae GRAY, 1875. Only one lineage: *Propalaeocastor* – (*Steneofi*- *ber?*) – *Monosaulax* (?) – *Castor* led to the origin of the current genus *Castor*, which includes two species *Castor fiber* LINNAEUS, 1758 and *C. canadensis* KUHL, 1820. The systematics of Castoridae proposed by LYCHEV is not comprehensive because it does not take into account the tooth cement and the W/L molar index, which constitute important taxonomic traits.

KORTH (2001) and RYBCZYNSKI (2007) provide data to support the division of Castoridae into four groups (subfamilies): Agnotocastorinae, Palaeocastorinae, Castoridinae, Castorinae, and their further division into tribes. According to MCKENNA and BELL (1997), the family Castoridae comprises two subfamilies: Castoridinae (14 genera) and Castorinae (10 genera).

III. MATERIAL AND METHODS

A total of 200 items of taxonomic value were examined. All these items were excavated from various localities of the late Miocene, Pliocene and Pleistocene of Ukraine and neighboring countries (Fig. 1). These items are represented mainly by teeth (including incisors), rarely by mandibles and maxilla fragments and fragments of the postcranial bones. The following traits were taken for the identification of Castoridae remains: the presence or lack of cement, and root, fossete and hypsodonty development, the cross-section of incisors, relationships between lateral-medial section (LM), the thickness of the anterior-posterior section (AP) and other mandible and maxilla traits. To date, the presence or lack of tooth cement has been badly neglected in taxa diagnosis. However, this trait seems to be important in dividing the family into subfamilies and genera, and therefore is used in our investigation of the beaver family. In species determination, we have also used other details of tooth structure, i.e. dimensions; degree and developmental peculiarities of flexus (id), fossete (id), strie (id) undulation of the enamel; the presence or lack of the root; the height of the tooth crown and other traits.

An almost complete skull of the genus *Palaeomys* from the Cherevichne locality (hipparion fauna) as well as 30 premolars and molars, 1 mandible and 1 incisor belonging to this genus were collected from various localities of late Miocene age. The species *Trogontherium minutum* was represented by 43 teeth (premolars and molars), 2 mandibles and 2 incisors in localities from the late Miocene. For the species *Trogontherium minus* from Pliocene localities, 60 premolars and molars, 2 maxillae, 5 mandibles and 11 incisors were studied. The species *Trogontherium cuvieri* from the Pliocene and Pleistocene was represented by 6 teeth and 2 incisors. The genus *Steneofiber* in Miocene localities was represented by 36 premolars and molars, 1 maxilla, 2 mandibles and 3 incisors. The genus *Castor* from the Pliocene and Pleistocene was represented by 25 teeth, 2 mandibles and 1 incisor.

A detailed description of this material will be provided in another paper on the taxonomic revision of Castoridae of the Ukraine. The material is deposited in the Department of Paleontology in the National Museum of Natural History in Kiev. In this paper, the status of particular species is discussed, however no attempt is taken to analyze relationships between these species.

IV. RESULTS AND DISCUSSION

The morphological comparison of all remains of beavers listed above reveals that at least 15 beaver species represented by 5 genera existed in various geological periods of the late Neogene and Anthropogene of the Ukraine and neighboring areas (Table I). The genera include *Palaeomys* KAUP, 1832 (1-2 species), *Steneofiber* GEOFFROY, 1833 (1-2 species), *Trogontherium* FISCHER VON WALDHEIM, 1809 (3-4 species), *Dipoides* GERVAIS, 1859 (single species) and *Castor* LINNAEUS, 1758 (3-4 species). The presence of the genus *Monosaulax* STIRTON, 1935 (one species) has not been confirmed to date (TOPACHEVSKY et al. 1987).

The oldest remains belong to the genus *Palaeomys* KAUP, 1832 (REKOVETS 2006; REKOVETS & KOPIJ 2007). The analysis of fossil material and literature data support the view that the genus *Pa*-



Fig. 1 Distribution of Late Miocene, Pliocene and Pleistocene Castoridae sites (localities) in Ukraine.
Miocene: 1. Grytsev, 2. Mikhailovka, 3. Frunzovka, 4. Novoelizavetovka, 5. Novoukrainka, 6. Cherevichne, 7. Andreevka, 8. Vinogradovka.
Michailovka, 3. Frunzovka, 10. Obukhovka, 11. Kotlovina, 12. Odessa catacombs, 13. Shirokino, 14. Zhevakhova Gora, 15 Kryzhanovka, 16. Kuyalnik.
Pliocene: 9. Kuchurgan (complex localities), 10. Obukhovka, 11. Kotlovina, 12. Odessa catacombs, 13. Shirokino, 14. Zhevakhova Gora, 15 Kryzhanovka, 16. Kuyalnik.
Pliocene: 17. Tiligul, 18. Berdjansk, 19. Nogaisk, 20. Kairy, 21. Luzanovka, 22. Bolshevik, 23. Tikhonovka, 24. Krasnoselka, 25. Morozovka, 26. Medzhybozh. 27. Gunki,

laeomys is valid, as shown by FRANZEN and STORCH (1975). Based on the material deposited in the Senckenberg Museum, we can show that the description of *Palaeomys plassi* was based on teeth of young specimens and that the species is a synonym of *Palaeomys castoroides* KAUP, 1832.

These remains were excavated from calcareous sediments of the late Miocene (Sarmatian, MN 9) at Grytsev (= Gryciv, Gritev, Gritsiv), they therefore go back to ca. 12 million years (Table I). Members of this genus were widespread in the Miocene of Western Europe. For the first time their remains were excavated in the Western Ukraine, which constituted the eastern boundary of the range of this species. Remains from Grytsev (12 teeth), Frunzovka 2 (2 teeth), Cherevichne 3 (4 teeth) belong to *P. castoroides* KAUP, 1832. This species has a primitive dentition and was a characteristic member of the late Miocene fauna of Western Europe. The teeth had well-developed roots, cement, fossets at early tooth stage and relatively large dimensions. This species was characteristic for faunistic complexes from the Sarmatian-Grytsevian (MN 9), possibly Kalfian (MN 10), Beryslavian (MN 11) and Maeotian-Belkian (MN 12). These are faunas from the late Vallesian and early Turolian (NESIN & NADACHOWSKI 2001).

Remains of the species *Palaeomys* sp. were excavated from the Miocene (Maeotian-Pont) of the following localities: Cherevichne-excavation, Andreevka (= Andriyvka) and Novoukrainka 1. This species was of relatively large body size, had a high teeth crown, underdeveloped roots and cemented strie and striids, and also incisors, flat from the anterior end, and the W/L index is 100%. Through analysis of the faunistic complex containing *Palaeomys* it can be concluded that this genus was ecologically associated with humid conditions prevailing in Europe in that time.

The genus *Steneofiber* GEOFFROY, 1833 was a characteristic member of older epochs (Oligocene, early Miocene) of Europe (SCHLOSSER 1885; HUNNERMANN 1966; UNAY 1977; KOWALSKI 1967, 1997; SACH & HEIZMANN 2001; STEFEN 2005). However, the validity of genera such as *Steneofiber, Palaeomys* and *Chalicomys* require further support (KOTSAKIS 1989; KUBIAK & WOLSAN 1986). In order to precisely confirm the generic position of *Chalicomys minutus* MEYER, 1838 to *Steneofiber* or *Trogontherium* (FRANZEN & STORCH 1975; UNAY 1977) further studies are needed. A similar uncertainty of relationships pertains to *Chalicomys* and *Steneofiber jaegeri* KAUP, 1832. The synonymy and taxonomic relationship among *Monosaulax, Euroxenomys, Boreofiber, Steneofiber*, and especially the position of *Chalicomys minutus* (= minutum) are also unclear.

In the Ukraine, the presence of the species *Steneofiber jaegeri* from the locality Cherevichne 3 (MN 12) has been documented. Tooth morphology indicates its close relationship with the species from the locality Reisenburg of the upper Miocene. Very small teeth of *Steneofiber* (?) sp. were also excavated from the locality Grytsev (MN 9). Most probably there were two forms which differed from one another by the W/L index, i.e. one group of molars has a W/L index less than 100%, and the other – more than 100%. There are also other morphological differences.

The genus *Trogontherium* FISCHER VON WELDHEIM, 1809 was the most common in the late Neogene and early Anthropogene of the Palearctic Region. At least 4 species of this genus from the Sarmatian (MN 9) – Likhvin (MQR 3) were recorded. Representatives of this genus had incisors rounded on the frontal surface. The breadth of $M^{1.2}$ and $M_{1.2}$ was greater than their length. M^3 was elongated and triangular in shape, with unusual structure of the occlusion, and lack of cement. At least three species belonging to this genus were described from the Ukraine. They were also associated with wet ecosystems of the steppe zone in the Ukraine and mezophilic areas of Western Europe.

Trogontherium (Euroxenomys?) minutum (= minutus) MEYER, 1838 was a widespread species from the late Miocene to the early Pliocene (MN 9-13) (STEFEN & RUMMEL 2003). Its remains were excavated in Miocene localities such as Grytsev, Mikhailovka 1, 2; Frunzovka 2, Cherevychne 3; Cherevichne-excavation, Novoelizavetovka, Novoukrainka, Vinogradovka-Pontian. The remains belong to faunistic complexes from the Sarmatian, Maeotian and Pontian. In total, 80 teeth and some fragments of maxillae and mandibles were excavated from these localities.

Trogontherium minus NEWTON, 1890 was a characteristic species of the Pliocene fauna, mainly in Western Europe. In the Ukraine, its remains were excavated at Cherevichne 2, Kotlovina 2, 3,

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Table I

Distribution of the late Miocene, Pliocene and Pleistocene species of Castoridae in localities of Ukraine Mammal (MN+MQR) Zones Genera Eastern Paratethys Stages opean Land Mamn Mega-Zones Epoch Faunal complexes and subcomplexes Investigated Species localities Novgorod- Severski Karangat+ New Euxin Late Weichselian Judinovo Sungirian 1 Shkurlatian Neopleistocene 0.13 Gunki Steinheimian Singilian+ Khazarian Medzhybozh Morozovka 2 Khazarian Pleistocene Uzunlar 3-2 Singilian 0.5 Krasnoselka Bolshevik 2(1) Tikhonovka 1 Tiraspolian late Chauda 7-4 early Luzanovka **3 iharian** Cherevichne-1 1.0 Kairy Nogaisk Eopleistocene Tamanian Tamanian Gurij= Apsheron 11-7 Zevakhova Gora 5 Odessian Tiligul Kotlovina 2, 3 1.7 17 late Kuyalnikian =Akchagylian Khaprovian Villanyian Cherevichne 2 middle Kryzhanovka 2 Zhevakhova Gora 11, 15 16 Obukhovka 2 Shirokino early Pliocene 3.4 Odessa-catacombs late Vinogradovka 3 Moldavian Kotlovina 1 middle 15 Ruscinian Kimmerian Obukhovka 1 early Krasnopol, Velikomikhailovka, Novopetrovka, Frunzovka 1, Voinichevo, Trudomirovka, 14 Kuchurganian Trostianets 5.4 Vinogradovkian Vinogradovka 1 (Pont) Pontian Fontanian Odessa (lectostratotype of Pontian) 13 7.1 Cherevichne-excavation Cherevichnian Andreevka Novoukrainka 1 Maeotian Miocene Belkian Novoelizavetovka 3 **Furolian** 12 Belkian Novoukrainka 2 Cherevichne 3 Novoelizavetovkian 9.88 Grebenikian Novoelizavetovka 2 Khersonian Late 11 Berislavian Frunzovkian Frunzovka 2 Sarmatian s.l. (=Berislavian) Mikhailovka 2 (Southern Bug River) 11.0 <u>Mikhailovka 1 (Southern Bug River)</u> Kalfa Buzhor

Mikhailovkian

Kalfian

Grytsevian

Grytsev

Bessarabian

Vallesian

10

Table I ctd

	Dipoides	Stenofiber		Trogontherium					Castor			
Palaeomys		jægeri	sp. (small)	minutum	ex.gr.minus							
castoroides sp.	sigmodus				minus	sp.(small)	cuvieri	ssp.?	sp. (large)	præfiber	tamanenis	fiber
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Obukhovka 1, Kairy, Kuchurgan and Odessa-catacombs from the Pliocene (MN 14-17). These faunas belong to the Kuchurganian, Moldavian and Khaprovian faunistic complexes (NESIN & NADACHOWSK12001). In total, almost 70 teeth and fragments of maxillae and mandibles were excavated from these localities. The taxonomic position of this species is still not resolved (FRANZEN & STORCH 1975; HUGUENEY et al. 1989).

A distinct species, *Trogontherium cuvieri* FISCHER VON WALDHEIM, 1809, was characteristic for the late Pliocene and early Pleistocene (FOSTOWICZ-FRELIK 2008). In the Ukraine, few remains (10 teeth) belonging to this species were excavated from the early Kuyalnik, Khaprovian (MN 16-17), at Shirokino, Zhevakhova Gora 11, 15, Kairy, Berdyansk, Kryzhanovka 2, Nogaisk, Tiligul and other localities. Rather doubtful is information on its occurrence in the middle Pleistocene of Ukraine (locality at Medzhybozh). The preservation of one tooth in this locality could have resulted rather from redeposition than from the real existence of this species. However, it is important to point out that remains (teeth are small) belonging probably to *Trogontherium* cf. *boisvilletti* LAUGEL, 1862, were excavated at the Medzhybozh locality. In our opinion, the great morphological diversity of *Trogontherium cuvieri* in time and space allows for the identification of several subspecies (MAYHEW 1978). In Western Europe *Trogontherium cuvieri* occurred since the middle Pleistocene. This very large species had well-developed incisors, with frontal surface rounded, and there was no cement on its teeth. This species existed under wet steppe conditions in the Ukraine and in more mezophilic ecosystems in Western Europe.

Large body size was also a characteristic feature of other beaver forms. For example, overall teeth length from P_4^4 to M_3^3 reached 100 mm in *T. cuvieri*, as compared with only 35 mm in the recent *Castor fiber*. These species differ in incisor size (in horizontal section). The breadth (lateral-medial section – LM) and thickness (anterior-posterior section – AP) of the incisors are 15 x 12 mm in the genus *Trogontherium cuvieri* (LM/AP index = 125%). These dimensions are 8.5 x 7.7 mm and the LM/AP index = 110% in *Castor fiber*. The length between P_4^4 and M_3^3 (overall teeth length) is 60 mm and dimensions of incisors are 18 x 15 mm respectively (LM/AP index = 120%) in *Youn-gifiber sinensis* YOUNG, 1955. These few giant species support hypertrophy as a distinct evolutionary trend. In addition to beavers, hypertrophy is also known in other rodent families, e.g. Arvicolidae. Two genera in this family, the extinct *Kislangia* and the recent *Ondatra* reached especially large body size. Hypertrophy can also be observed in other rodent families such as Muridae and Sciuridae.

The genus *Dipoides* SCHLOSSER & JAEGER, 1902 is extremely rare in East European localities, but it is widespread in the Pliocene of West Europe and Asia. *Dipoides* ex. gr. *sigmodus* GERVAIS, 1859 was excavated only at the locality Kotlovina 2 from the late Pliocene (MN 17). It is important to point out that remains of this genus were found in East Europe for the first time (DEMA 2000). It had a small body size, high-crown cemented teeth, relatively underdeveloped undulating of the enamel and well-developed strie and undeveloped roots, ecologically associated with riparian ecosystems.

According to many authors, the oldest remains of the genus *Castor* from Europe are known from the late Miocene (FRANZEN & STORCH 1975; GROMOV & BARANOVA 1981; HUGUENEY 1999; REK-OVETS 2006). During this time the genus was represented by two species, morphologically resembling the genus *Palaeomys*, which could have been an ancestor of the genus *Castor* (LYCHEV 1983). Representatives of the genus *Castor* were of relatively large body size, they had cement on teeth, undeveloped roots, and incisors with a flat frontal surface. They differ from *Palaeomys* by having elongated molars M_{1-2}^{1-2} (their W/L index is always less than 100%). An almost complete castorid skull has been excavated at Cherevichne-excavation (= Cherevichne, hipparion fauna, MN 13) and has been placed into the genus *Palaeomys*, not into *Castor neglectus*, as previously suggested.

After careful examination of the material from the Senckenberg Museum and literature data, *Castor neglectus* SCHLOSSER, 1902 can be regarded as a synonym of *Trogontherium (Euroxeno-mys?)* ex. gr. *minutum* (= *minutus*). This is supported by type material M_3 (according to FRANZEN & STORCH 1975 and, in our opinion, also by P⁴) from the locality Melchingen – upper Miocene

(SCHLOSSER 1902). These teeth have no cement, and the pattern of loops is much like in *Tro-gontherium*.

Among remnants of *Castor neglectus* from Dorn-Durkheim described by FRANZEN & STORCH (1975, fig. 24), two teeth belong to *Palaeomys*, and two others with a complex pattern of enamel and the presence of cement, cannot be *Castor neglectus* (a similar structure is shown by the genus *Eucastor*?).

Fossil remains of Castoridae from the Miocene of the Ukraine show probable morphological similarities between *Castor* and *Palaeomys*. They differ in molar shape: these are broad and short in the genus *Palaeomys* while elongated in the genus *Castor*. A revision of this material and validation of the species *Castor neglectus* will be conducted in the near future.

The Ukrainian remains of the genus *Castor* (*C. praefiber* DEPERET, 1897) (15 molars and premolars) appeared for the first time in the early Pliocene and were only excavated at localities in the Kuchurgan river valley of the Kuchurganian faunal complex (MN 14). In the early Kimmerian (MN 15), the species was rare and seldomly encountered at the locality Obukhovka 1 (basin of the Don River). However, it was a common species in the Pliocene of Western Europe. *Castor praefiber* is regarded as an intermediate form in the evolution of *Castor fiber*.

Castor tamanensis VERESTCHAGIN, 1951 was very rare in early Pleistocene sediments of southern Ukraine and East Europe. Its remains were identified in the Tamanian faunistic complex (locality Taganrog and older locality Tiligul [MQR 11]). Some characteristic features in the skull of this species allow a designation as a possible ancestral form of *Castor fiber*. However, detailed examination of tooth morphology in *Castor tamanensis* is needed to support this premise. The holotype of this species is deposited in the Institute of Paleontology in Moscow and will be re-examined in the near future.

Remains of *Castor tamanensis* are difficult to identify because no data on tooth morphology are available. Remains of *Castor fiber* are very rare in Pleistocene localities of the Ukraine and neighbouring areas, probably because it was a rare species during Pleistocene glaciations. It was not recorded at all in periglacial fauna with specific tundra-steppe conditions. Because of the lack of suitable material, the evolution of the recent *Castor fiber* is therefore still unclear. Single remains, in most cases identified as *Castor* sp., were found in Pleistocene localities of Ukraine, such as Luzanovka, Bolshevik 2, Tikhonovka, Krasnoselka, Morozovka 2, Gunki, Medzhybozh (REKOVETS 1994; REKOVETS et al. 2007). Most probably they all belong to *Castor fiber*, with some intraspecific temporal variants.

V. CONCLUSIONS

It should be underlined that there is a lack of remains of the genus *Monosaulax* in the Miocene-Pliocene sediments. Distinct species belonging to this genus are widespread in this epoch in the Holarctic Region, except for the Ukraine. There are several explanations for this situation: 1 - this species was not present in the dry climate of southeastern Europe; 2 - there is a lack of diagnostic remains for well-known forms of this genus in sediments in the Ukraine; 3 - localities have taphonomic peculiarities, therefore associated remains are rare in sediments.

A similar situation pertains to the genus *Dipoides*. Apparently, identification of remains as belonging to this species was rather uncertain. The species occurred almost in the whole Holarctic Region, but was almost unrecorded in the Ukraine. This and similar questions regarding family relationships in extinct beavers of the Ukraine should be subjects of further investigations.

Special attention should be paid to the stratigraphic locations of various genera of Castoridae. This constitutes a good indication of the dynamics of various groups of this family from the late Miocene (Sarmatian) to the Holocene. On the other hand, it is possible to determine the stratigraphic role of beavers in geological dating, and to determine a succession and progression of faunistic changes and correlations of sediments and locations.

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Castor (*C. praefiber*) and *Trogontherium minus* were characteristic for the early Pliocene (Kuchurgan, early Ruscinian). The genus *Trogontherium* was common in the middle Pliocene (Kimmerian-Ruscinian fauna). Remains of *Castor* from that period were not recorded to date. However, remains belonging probably to the genus *Castor* were excavated at the locality Obukhovka 1. *Trogontherium* (both large and small forms) and *Castor* (very rarely recorded) were characteristic for the upper Pliocene (Kuyalnik-Villanian fauna).

Species included in *Trogontherium* (a large form – *T. cuvieri*) and *Castor (C. tamanensis)* were rare in the lower Pleistocene (Tamanian and partly Tiraspolian faunistic complex, Biharian fauna). This beaver species assemblage was probably characteristic for the next epoch, the Likhvin (Singilian faunistic complex, Holstein). The *Castor* forms (probably chrono-subspecies of the recent species *C. fiber*) existed from the beginning of this epoch till the Holocene (the second half of the Neopleistocene).

VI. SUMMARY

Members of Castoridae were relatively diverse taxonomically at localities from the late Neogene and Pleistocene of the Ukraine; about 15 species from 5 genera are known to date.

Qualitative and quantitative comparison of beaver assemblages shows a decline in taxa frequency (mainly genera) from the late Miocene till present.

The occurrence and stratigraphic succession of beavers was determined for each locality in the Ukraine; sediments have been aged from MN 9 till present.

There was a rapid decline in the number of beaver taxa (3-4 species of 2 genera) caused by cyclic climate cooling in the Pleistocene.

All extinct beaver species were ecologically associated with a riparian ecosystem in the steppe zone of southeastern Europe and mezophilic areas of Western Europe.

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