



Bats (Chiroptera, Mammalia) from the Turolian of the Ukraine: phylogenetic and biostratigraphic considerations

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With 3 figures and 5 tables

Abstract: The fossil bats from five riverine and lacustrine localities of the Ukraine are described. The biostratigraphic correlations of the examined faunas are MN 11 and MN 12 (Early Turolian). Six taxa were identified, all belonging to Vespertilionidae. A new species, *Pipistrellus semenovi* nov. sp., close to basal clades of the extant genus, is described from Altestovo 5 (MN 12). The records of *Pipistrellus* from Altestovo 5 and Egorovka 1 and 2 (MN 12) are at present the earliest findings of this genus in Europe. The *Nyctalus* sp. from Palievo (MN 11) is one of the rarest records of this genus in the Neogene of Europe. The records of *Vespertilio* sp. from Palievo and Egorovka 1 morphologically are similar to Recent *V. murinus*. Recognition of *Eptesicus* aff. *campanensis* from Novoelizavetovka 3 (MN 12) is, at present, the youngest known record of this species. *Eptesicus* aff. *kowalskii* from Egorovka 1 and 2 differs from the nominotypical taxon in being smaller and in having a less reduced m3. The bat assemblages from Turolian localities of the Ukraine are most similar to those from Bernardière, Lobrieu and Dionay (MN 11) of France. The peculiar aggregation of bat taxa in the studied taphocenosis is consistent with avian pellet origin.

Key words: Chiroptera, systematics, Vespertilionidae, Lower Turolian, Southern Ukraine, taphonomy, *Pipistrellus semenovi* sp. nov.

1. Introduction

Late Miocene bats are well-known from the territory of modern Europe (FORTELIUS 2003), but Turolian localities including fossil bats are relatively rare. Such localities are found in France (Dionay, Bernardière and Lobrieu, MN 11, Lissieu, MN13), Austria (Kohfidisch and Eichkogel, MN 11), Italy (Brisighella, MN 13), Spain (Los Mansuetos, MN 12) and Hungary (Csakvar, MN 11 and Polgardi, MN 13). Single records of Turolian bats are also available from Germany, Kazakhstan and Russia (FORTELIUS 2003). Most Turolian localities with fossil bats are karstic while alluvial localities are comparatively rare. The locality Morskaya 2 (the Sea of Azov region of Russia) is one of the latter (TITOV et al. 2006). Among numerous fossil bones of

mammals from this locality was found a single skeletal fragment of the bat *Vespertilio* cf. *villanyiensis* (ROSSINA et al. 2006). The Early Turolian localities in France – Dionay, Bernardière and Lobrieu, containing comparatively rich records of bats, – also have a non-karstic genesis and are found in fluvial sands (MEIN 1999). In Ukraine, the new Early Turolian localities Egorovka 1, 2, Palievo and Altestovo 5 were found in the Odessa region in riverine and lacustrine sediments by M. V. Sinita who described the rich vertebrate faunas from there (SINITA 2008, 2009, 2012). Among numerous fossil bones, remains of bats of good preservation appear and these are for the first time reported in the present paper. Some fossil bats we described here from another Early Turolian locality of the Ukraine Novoelizavetovka 3, reported by TOPACHEVSKII

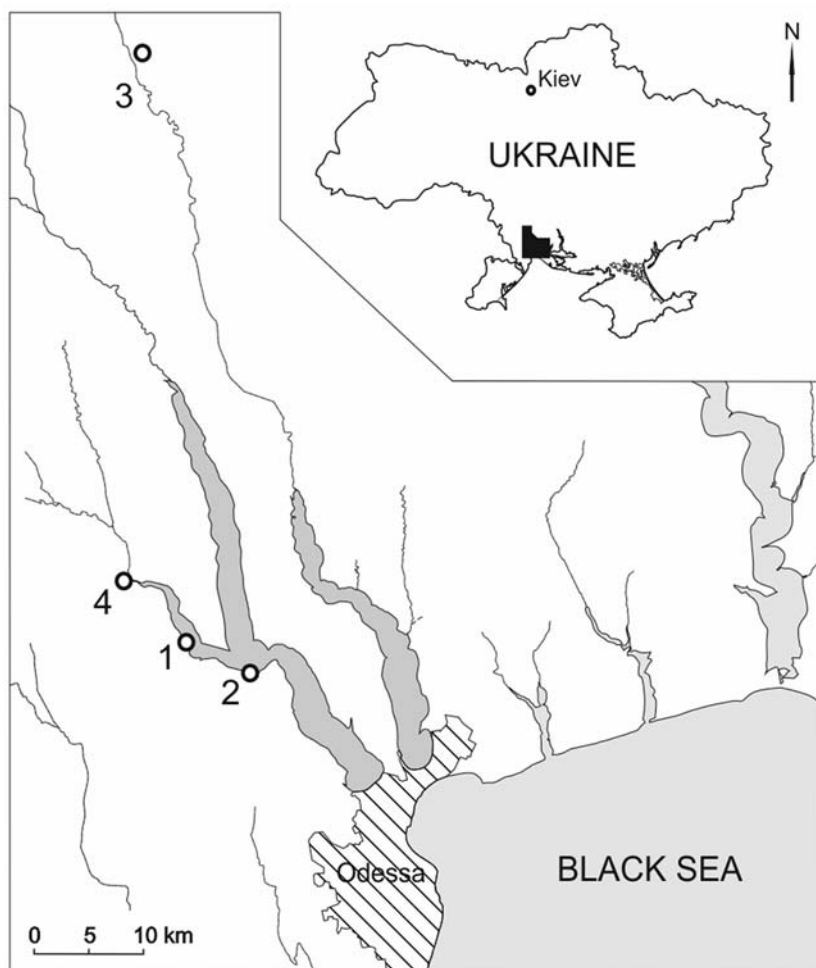


Fig. 1. The Turolian sites of the Ukraine in the study (for details see the text): 1 – Palievo; 2 – Altestovo 5; 3 – Novoelizavetovka 3; 4 – Egorovka 1 and Egorovka 2 localities.

et al. (2000). The bat records from the Turolian of the Ukraine extend the distributional span of the reported taxa both in geographical and stratigraphical respects.

The Palievo locality is an exposure in the steep river bank of the Khadzhibeiskii “liman” (here and hereafter the “liman” is a near-mouth riverine lake) between the villages of Palievo and Otradovo (Razdel’nyanskii District, Odessa Region, Ukraine (Fig. 1: point 1). The thin alluvial layer yielded most of the fossil bones. The overlying deposits are represented by oolitic limestones and greenish-clays which are Upper Sarmatian (Khersonian) in age. The presence of brackish limestones and the heterogeneity of the facies pattern suggest alluvial-riverine genesis of this locality, which

occurred in an unstable transitional zone of the Sarmatian Paratethys Sea. The Palievo mammalian fauna includes *Schizogalerix* cf. *moedlingensis* (RABEDER, 1973), *Archaeodesmana* aff. *vinea* (STORCH, 1978), *Gerhardstorchia* cf. *biradicata* (ZIEGLER, 2006), “*Paenelimnoecus*” *reppeningi* (BACHMAYER & WILSON, 1970), *Pliopetaurista* cf. *bressana* MEIN, 1970, *Lophocricetus complicidens* TOPACHEVSKI, SCORIK & REKOVETS, 1984, *Apodemus barbarae* (VAN DE WEERD, 1976), *Apodemus* aff. *lugdunensis* (SCHAUB, 1938), *Kowalskia progressa* TOPACHEVSKI & SCORIK, 1992, and *Stylocricetus*, among others. This complex shows a gliroid-insectivore community, the dominant groups of which were composed of dwarf hamsters (*Kowal-*

skia) and mice (*Apodemus*). Insectivores, pikas and glirids are very common. The vertebrate fauna from Palievo is similar to the Early Turolian (MN 11) faunas of Germany (Dorn-Dürkheim 1) and Austria (Eichkogel) (SINITSA 2009).

The Egorovka 1 and 2 localities are situated on the right river bank of the Svinaya River near the village of Egorovka (Razdel'nyanskii District, Odessa Region, Ukraine) (Fig. 1: point 4). Several layers of clays and gravels yielded most of the fossils. The bones of small mammals from the Egorovka 1 locality were scattered in a layer of light grey clay. This locality represents lacustrine environments, which is different from most Late Neogene localities of Eastern Europe, often associated with alluvial and paleokarst deposits. Supposedly, the lacustrine nature of the bone-bearing layer explains the very good preservation of the fossils, including remains of bats. Cricetids such as *Pseudocricetus orienteuropaeus* TOPACHEVSKI & SCORIK, 1992 and mice of the genus *Apodemus* KAUP, 1929 (*A. schaubi* (PAPP, 1947), *A. aff. lugdunensis*, *A. dominans* KRETZOI, 1959) dominate the mammalian fauna of the Egorovka 1 locality, which is very typical for the second half of the Middle Turolian (MN12) of the south of Eastern Europe. The Egorovka 2 locality is represented by a thick lens of clay with gravel. The small mammal community is very similar to Egorovka 1 with both being characterized by the total predominance of *Pseudocricetus orienteuropaeus* and *A. schaubi*. Nonetheless, the presence of the latest *Vasseuromys* BAUDULOT & BONIS 1966 (Rodentia, Gliridae) and an earlier evolutionary stage of *P. orienteuropaeus* implies a somewhat older age for Egorovka 2 within MN 12 compared to Egorovka 1 (SINITSA 2008, 2009).

The Altestovo 5 locality represents one of many layers of the Late Miocene streamflow alluvium, which is exposed in the right river bank of the Khadzhibeiskii liman near the village of Altestovo (Belyaevskii District, Odessa Region, Ukraine) (Fig. 1: point 2). The gravels bearing fossil bones are interlaid with sands and overlie Late Sarmatian marly limestones and clays. The bones were probably accumulated in an ancient delta. The mammalian fauna of the Altestovo 5 locality includes *Catromys nadachowskii* NESIN & STORCH, 2004 and *Pseudocricetus antiquus* TOPACHEVSKI & SCORIK, 1992, which are very typical for the early half of the Middle Turolian (MN 12) of the south of Eastern Europe.

The Novoelizavetovka 3 locality is located in the left river bank of the Kuyal'nitskii liman near the vil-

lage Novoelizavetovka (Shiryayevskii District, Odessa Region, Ukraine) (Fig. 1: point 3). Two layers of gravel with fossils apparently formed in alluvial-lacustrine conditions in an area of an unstable transitional zone of the Sarmatian Paratethys Sea. The mammalian fauna of the Novoelizavetovka 3 locality includes *Schizogalerix* sp., *Amblycoptus* sp., *Zelceina* sp., *Alilepus* sp., *Pliopetaurista* sp., "*Sciurotamias*" cf. *gromovi* TOPACHEVSKI, 1971, *Trogontherium (Euroxenomys) minutum* (v. MEYER, 1838), *Myomimus* sp., *Muscardinus* sp., *Apodemus alae* NESIN, 2011, *Apodemus schaubi*, *Kowalskia* sp., *Pseudocricetus orienteuropaeus* TOPACHEVSKI & SCORIK, 1992, *Stylocricetus meoticus* TOPACHEVSKI & SCORIK, 1992, and others. Because *Apodemus schaubi* and *Pseudocricetus orienteuropaeus* are found in Novoelizavetovka 3 together, the age of the locality is established as Middle Turolian (MN12) (TOPACHEVSKII et al. 2000; NESIN & NADACHOWSKI 2000; NESIN & STORCH 2004).

2. Material and methods

The material of the fossil bats is represented mostly by dentary fragments and isolated teeth. Occasionally there are almost undamaged lower jaws, rostral parts of skulls in varying degrees of integrity and humeri fragments. Dental terminology follows MILLER (1907) and HUTCHINSON (1974). The tribe taxonomy follows SIMMONS (2005). The specimens were measured in a standard way using a binocular microscope MBS-10 with ocular micrometer. All measurements are given in millimeters with 0.01 mm precision. Lengths of individual teeth and tooth-rows were taken as the maximal distances between the posterior and anterior crown edges of the respective teeth. Lengths of the upper molars are measured parallel to the labial side, the widths parallel to the mesial side (see SIGÉ 1968: 72, fig. 4). Tooth widths were taken as the maximal distances between the lingual and buccal crown edges. The heights of the C sup. and C inf. are measured lingually.

The following measurements were taken:

- length (L) × width (W) × height (H) of C inf., C sup., p2, p3, p4, P2, P3 and P4 (in the case of p4 – the maximal width of the p4 crown);
- length × width of the molar trigonid (Wtr) × width of the molar talonid (Wtl) of m1,2,3;
- length of the m3 talonid (Ltm3);
- length × width of M1,3;
- lengths of the tooth-row: Lp2-p4, Lc-p4, Lc-m1, Lp4-m3, Lm1-3, Lm1-2, Lm2-3;
- Hmdm1 – the height of a mandibular corpus measured from the lingual side below m1;
- Hmdm3 – the height of a mandibular corpus measured from the lingual side below m3;
- Lorb – the length of the bony bridge between a lacrimal foramen and infraorbital foramen;
- Hiorb – the dorso-ventral height of an infraorbital foramen;
- Wiorb – the lateral weight of an infraorbital foramen;

Wdep – the maximal width of a distal epiphysis of the humerus (see ROSINA & SEMENOV 2012: 200, fig. 4A);

Lep – the maximal length of a lateral epicondyle in a cranio-caudal direction (see ROSINA & SEMENOV 2012: 200, fig. 4A);

Ltr – the maximal length of the trochlea humeri and capitulum humeri (see ROSINA & SEMENOV 2012: 200, fig. 4A).

The following abbreviations and abridgements were used in a text: mnd – mandibular bone; sin. – sinister (from lat. “sinistrum”), left; dex. – dexter (from lat. “dextrum”), right; al. – alveole; sup. – superior; inf. – inferior.

All fossil material is stored in the Palaeontological Museum of the National Museum of Natural History, National Academy of Sciences of the Ukraine (NMNHU-P). The osteological collections of Recent Chiroptera, deposited in the Palaeontological Museum and in the Zoological Museum of the NMNHU, in the Zoological Museum of Moscow University (Moscow, Russia), in the Bavarian State Collection of Zoology (Munich, Germany) and in the Senckenberg Research Institute (Frankfurt am Main, Germany), have been used for comparison of the fossil specimens with Recent bats. Photographs have been taken with a scanning electron microscope at the Borissiak Paleontological Institute of the Russian Academy of Science.

3. Systematic palaeontology

Order Chiroptera BLUMENBACH, 1779

Suborder Microchiroptera DOBSON, 1875

Family Vespertilionidae GRAY, 1821

Subfamily Vespertilioninae s. str.

Tribe Pipistrellini TATE, 1942

Pipistrellus semenovi sp. nov.

Fig. 2A

Etymology: The specific name is given in honour of Dr. YURI A. SEMENOV, an eminent Ukrainian vertebrate paleontologist, who enthusiastically supports the research of fossil bats from the Neogene localities of the Ukraine.

Holotype: Ch/379, a left maxillary fragment with P2, P4 and M1, the proximal part of I2 alveolus and alveoli of the canine and M2 are preserved (Fig. 2A).

Type locality: Altestovo 5, near the village Altestovo, Belyevskii district of the Odessa region, Ukraine.

Age: MN 12, the Middle Turolian.

Measurements of the holotype: C sup. (al.) 1.00×0.70 ; P2 0.42×0.39 ; P4 0.97×0.94 ; M1 1.38×1.48 ; Lorb 0.38 ; Hiorb 0.56 ; Wiorb 0.38 .

Diagnosis: A vespertilionid bat with a single small premolar in upper jaw corresponding in size to *P. kuhlii* and like

this species has para- and metaloph and evident paraconule on the upper M1. Fossil species differs from *P. kuhlii* in having a larger P2 that is not dislocated lingually from the tooth-row; in having a larger I2 that is not dislocated buccally from the tooth-row; in having a longer P4 that has a poorly-developed posterolingual talon and a small cuspid at the anterolingual side of the crown; in having a poorly-developed metacingulum of M1. It differs from the extant species of *P. pipistrellus* group and from *P. rueppelii* in being considerably larger and in having an evident paraconule on the upper M1 and a poorly-developed anterolingual cuspid on P4.

Description of the holotype: The left half of the maxilla is broken at the incisor alveolus. The P2, P4 and M1 and alveolus of canine are present. The infraorbital foramen is rounded and opens at the level of the anterior root of the M1. The front wall of the orbit forms a quite wide bony ridge. The alveolus of the last incisor is broken. There is a noticeable diastema between the upper incisors and canine. The preserved alveolus of the canine is oval. The conical P2 is small, shaped by well-developed cingulum, and has a distinct cuspid at the anterolingual side of the crown. The crown has a distinct distal crest, anteroposteriorly compressed in occlusal view and displaced lingually. The trapeziform P4 has a low degree of molarization and is shaped by a thin cingulid which forms a small cuspid at the anterolingual side of the crown. The M1 has a distinct paraconule, paraloph and hypocone. The metaloph extends anteriorly from the base of the metacone to the small hypocone, where it runs into the postprotocrista. Thus, the trigon basin of the upper molar is closed.

Comparison: According to the morphology of the upper teeth (the poorly-developed posterolingual talons of P4 and molar and a well-developed cingulum) the fossil specimen belongs to the family Vespertilionidae. There are many vespertilionid bats which have only one small premolar in the upper jaws, for example, *Plecotus*, *Barbastella*, *Murina*, *Nyctalus* or *Miostrellus*. But only some species of *Myotis* and *Pipistrellus* have at the same time the para- and metalophs and well-developed paraconules on the upper molars. However, as opposed to the fossil specimen from Altestovo 5, species of *Myotis* usually have two small premolars in the upper and lower jaws. And from *Pipistrellus* only the Recent *P. kuhlii* has well-developed para-, metalophs, paraconules and hypocones simultaneously on the upper molars like the fossil bat from Altestovo 5. In size the fossil form corresponds to the Recent *P. kuhlii* (Table 1), the largest of extant West Palearctic species of the genus (HORÁČEK, written communication). Further both *P. kuhlii* and the fossil specimen from Altestovo 5 have distinct cuspids at the anterolingual side of the P4 crowns, however that of *P. kuhlii* is appreciably smaller. Thus, the fossil specimen from Altestovo 5 definitely belongs to the genus *Pipistrellus* but it shows further clear differences from the *P. kuhlii*: the P2 is larger and only slightly displaced lingually so that the crowns of C sup. and P4 have no contact on the buccal side; the crown of the P4 is not so compact and compressed like that of *P. kuhlii*, but is more elongate in anteroposterior direction (Table 1); the anterolingual cuspid of P4 is small and the pos-

Table 1. Comparison of different fossil and Recent species of *Pipistrellus* (in mm, the size difference between maximum and minimum values, an arithmetic mean is in brackets; n: number of specimens).

Species	<i>P. semenovi</i> nov. sp.	<i>Pipistrellus</i> sp.	<i>Pipistrellus</i> sp.	<i>P. kuhlii</i>	<i>Nyctalus leisleri</i>
Measur.	Altestovo 5 (Ukraine) holotype	Egorovka 1, 2 (Ukraine) n = 5	Palievo (Ukraine) n = 1	(Recent, Ukraine, Sicily, Armenia) n = 7	(Recent, Germany) n = 1
LC	1.00 (al.)	–	–	0.89-1.21 (1.06)	1.25
WC	0.70 (al.)	–	–	0.88-0.96 (0.92)	1.25
LP4	0.97	–	–	0.88-1.00 (0.91)	1.04
WP4	0.94	–	–	0.96-1.13 (1.06)	1.42
LM1	1.38	–	–	1.29-1.40 (1.33)	1.50
WM1	1.48	–	–	1.29-1.58 (1.43)	1.83
		n = 1			(Recent, Ukraine, Germany) n = 5
Lc	–	0.85	–	0.63-0.92 (0.79)	0.80-0.90 (0.86)
We	–	0.77	–	0.74-0.88 (0.80)	0.83-0.92 (0.89)
Hc	–	1.30	–	1.17-1.58 (1.41)	1.23-1.42 (1.30)
Lm2	–	1.31	1.19	1.25-1.35 (1.30)	1.50-1.58 (1.52)
Wtrm2	–	0.73	0.66	0.75-0.91 (0.83)	0.92-1.04 (0.99)
Wtlm2	–	0.88	0.78	0.83-0.96 (0.90)	1.00-1.10 (1.06)
Wtlm3	–	0.55	–	0.58-0.62 (0.60)	0.71-0.80 (0.75)
Ltlm3	–	0.55	–	0.54-0.63 (0.60)	0.62-0.71 (0.68)
Hmdm1	–	1.70	1.38	1.58-1.67 (1.64) (n = 3)	1.50-1.80 (1.69)
Hmdm3	–	1.50-1.55 (n = 2)	–	1.50 (n = 3)	1.43-1.60 (1.51)

terolingual talon is poorly-developed; the diastema between C sup. and I2 is evident. The preserved distal side of the I2 alveolus of the *Pipistrellus* from Altestovo 5 suggests that this tooth was situated in the midline of the tooth-row and apparently was not very reduced in size. The I2 of *P. kuhlii* on the contrary is reduced in size and displaced lingually. The metacarpal on M1 of the *Pipistrellus* from Altestovo 5 is not so strongly developed as in *P. kuhlii*. In some characters, particularly in shape of the protoconal complex of M1, the *Pipistrellus* from Altestovo 5 resembles rather the situation in the *P. pipistrellus* group or even in *P. rueppelli*, the North-African and Middle East form which is considered as basal clade of the Western radiation of the genus (Koubinova et al. 2013). Nevertheless these Recent species are significantly smaller and have no evident paraconule on M1. Furthermore the P4 of these Recent species has a well-developed anterolingual cuspid. Thus, the morphological peculiarities of the fossil form from Altestovo 5 convincingly support its independent taxonomical status.

Remarks: The Quaternary records of the genus *Pipistrellus* are relatively common. Pleistocene finds of *P. pipistrellus* sp. are reported from Austria (Hundsheim, RABEDER 1973), Germany (Gröbern bei Gräfenhainichen, BENECKE et

al. 1990), Spain (Las Grajas, SEVILLA 1988, 1989; SESE & SEVILLA 1996), Malta (Ghar-Dalam cave, STORCH 1974) and Hungary (Beremend 15, TOPAL 1985). They are also known from France, Romania, Serbia, Bulgaria, Italy, Poland (in detail see HORÁČEK & JAHELKOVÁ 2005; SALARI & CANZIO 2009) and Russia (Caucasus, ROSSINA et al. 2006). Records of this species are very common in the Holocene deposits of Europe (HORÁČEK 1984, 1995). Records of fossil *P. kuhlii* are known from the Middle Pleistocene of France (Aldène locality, SEVILLA & CHALINE 2011) and from the Late Pleistocene of Central Italy (Grotta Barbara 1, SALARI & KOTSAKIS 2011). In the Late Pleistocene deposits of the Matuzka cave (Caucasus, Russia) were found remains of *P. cf. kuhlii* (ROSSINA et al. 2006). The Holocene record of *P. kuhlii* is known from the locality Breitenberghöhle in Germany (BRUNNER 1958; HORÁČEK & JAHELKOVÁ 2005). The Neogene records of *Pipistrellus* are quite exceptional (MEIN 1999) and unfortunately they never been described in detail. *Pipistrellus* indet. has been listed in assemblages of the Late Miocene localities Bernardière and Dionay (MN 11, France, MEIN, 1999). Thus, the new species *P. semenovi* from Altestovo 5 and *Pipistrellus* sp. from Palievo, Egorovka 1 and 2 (see below) represent the earliest reliable records of the genus.

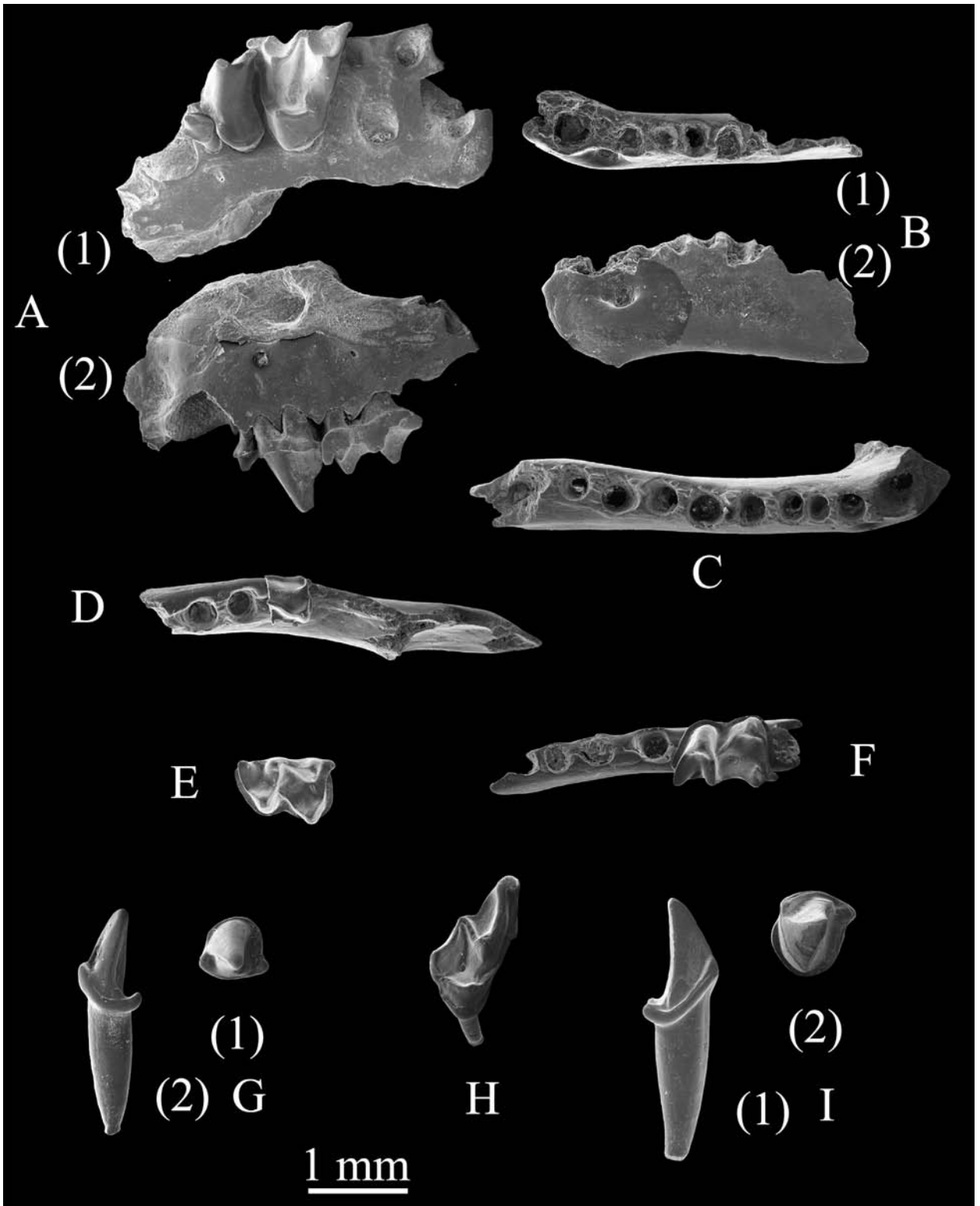


Fig. 2. **A** – *Pipistrellus semenovi* nov. sp., maxillary fragment sin. with P2, P4 and M1, holotype, Alttestovo, Ch/379, (1) ventral view, (2) lateral view; **B–G** – *Pipistrellus* sp.; **B**: dentary fragment sin., Egorovka 1, Ch/339 (1) ventral view, (2) lateral view; **C**: dentary fragment dex., Egorovka 1, Ch/337, ventral view; **D**: dentary fragment sin. with preserved talonid of m3, Egorovka 1, Ch/338, ventral view; **E**: m1 sin., Egorovka 1, Ch/340, occlusal view; **F**: dentary fragment dex. with m2, Palievo, Ch/376, ventral view; **G**: C inf. dex., Egorovka 2, Ch/344, (1) occlusal view, (2) lingual view; **H** – *Nyctalus* sp., M3 dex., Palievo, Ch/378, occlusal view; **I** – *Vespertilio* sp., C inf. sin., Palievo, Ch/377, (1) lingual view, (2) occlusal view.

Pipistrellus sp.

Fig. 2B-G

Material: Egorovka 1: Ch/337 mnd dex. p2 (al.) 0.40×0.40 , Hmdm1 = 1.70, Hmdm3 = 1.55, Ch/338 mnd sin. with a talonid of m3 Wtlm3 = 0.55, Ltlm3 = 0.55, Hmdm3 = 1.50; Ch/339 mnd sin. WC inf. (al.) = 0.65, p2 (al.) 0.40×0.40 , Hmdm1 = 1.50; Ch/340 m1 sin. $1.31 \times 0.73 \times 0.88$; Egorovka 2: Ch/344 C inf. dex. $0.85 \times 0.77 \times 1.30$; Palievo: Ch/376 mnd dex. with m2 $1.19 \times 0.66 \times 0.78$ Hmdm1 = 1.38.

Description: Only dentary fragments from an undetermined *Pipistrellus* species are preserved. The mental foramen is rounded and situated at the midline of the mandible below c/p2 (specimens Ch/337 and Ch/339). The lower canine is crescent-shaped in occlusal view, is surrounded by a well-developed cingulum with two distinct cingular cusps – mesolingual and distolingual. The mesolingual cuspid is not high and does not fit closely to the body of the tooth (specimen Ch/344). The preserved alveoli of p2 and p3 suggest that both teeth were single-rooted, close in size and situated in the midline of the tooth-row (specimens Ch/337 and Ch/339). The preserved anterior alveolus of p4 is appreciably smaller than the posterior one. Both alveoli are somewhat compressed in anteroposterior direction, thus suggesting that the crown of the p4 was short and compressed in the anteroposterior direction (specimen Ch/337). Lower molars are nyctalodont. In comparison with m1 (specimen Ch/340) the trigonid of m2 has a wider angle between the paraconid and metaconid (specimen Ch/376). The m3 has a small but well-defined hypoconulid (specimen Ch/338).

Comparison: The following features suggest that the fossils examined are members of the family Vespertilionidae: a well-developed cingulum, especially on the buccal sides of the tooth crowns; the slightly curved para- and metalophids of the lower molars; a well-developed cingulum and the presence of a notable mesolingual cingular cuspid on the crown of the lower canine; alveoli of p3 and p2 are close in size and situated in the midline of the tooth-row. Among vespertilionid bats only *Nyctalus*, *Miniopterus*, *Barbastella* and *Pipistrellus* have nyctalodont molars. As opposed to the lower canines in *Miniopterus*, *Barbastella* and *Nyctalus* the fossil lower canine from the Ukraine is more rounded in occlusal view and has a low mesolingual cingular cuspid which is partially detached from the main cusp of the tooth. Moreover, *Miniopterus* has two small lower premolars and p3 is double-rooted. In contrast to *Miniopterus* and to *Barbastella*, the fossil molars are shorter and more compacted; the trigonids are considerably narrower than the talonids. Unlike in *Barbastella*, the paralophids of the fossil molars are not curved. As opposed to *Nyctalus*, the talonids of the fossil molars are close in width with the trigonids. By the form and size the fossils belong to the genus *Pipistrellus*, in particular to *P. kuhlii* (Table 1).

Remarks: These fossil dentary fragments could belong to the newly described form from Altestovo 5 or even to *P. kuhlii* (Table 1). However, none of the available fragments can be assigned to an exact species.

Nyctalus sp.

Fig. 2H

Material: Palievo: Ch/378 M3 dex. 0.95×1.95 .

Description: The M3 has a clearly defined paraloph but no paraconule. The well-developed stylocone is rounded. The metacone is somewhat reduced in size and the tooth crown is moderately compressed in the anteroposterior direction.

Comparison: The form of the tooth crown, which has a well-developed cingulum, suggests that it represents a member of the family Vespertilionidae. Among vespertilionid bats only some species of *Pipistrellus*, *Myotis*, *Nyctalus* and *Vespertilio* have M3 with a distinct paraloph. The fossil M3 has a slightly reduced metacone and its crown is appreciably compressed in the anteroposterior direction which is typical for the M3 of *Nyctalus*. The size of the fossil M3 from Palievo is smaller than *N. noctula* (n = 4: WM3 = 2.45-2.50) and compares well with *N. leisteri* (n = 3: LM3 = 0.92-0.96 \times WM3 = 1.83-1.92).

Remarks: Records of *N. noctula* are not found in deposits older than the Early and Middle Pleistocene (RABEDER 1972; TATA & KOTSAKIS 2005). The larger species *N. lasiopterus* (= *N. maximus* (FATIO, 1869) is known from the Early Pleistocene of Germany (Breitenberghöhle, BRUNNER 1958), and the Late Pleistocene of Italy (Punta Padrebello-Omo Morto, KOTSAKIS 1987) and Spain (LÓPEZ-GARCÍA et al. 2009). The *N. kormosi* from the Breitenberghöhle (BRUNNER 1958) is indeed *Eptesicus serotinus* (HORÁČEK 2001). The Early Miocene *N. storchi* HORÁČEK, 2001 from Merkur-north and Ahníkov (MN 3, Czech Republic, HORÁČEK 2001) is similar in size to Recent *N. noctula* and significantly larger than the *Nyctalus* sp. from Palievo. Thus the fossil *Nyctalus* sp. from Palievo adds a new record to this extremely rare genus in the Neogene of Europe.

Tribe Vespertilionini GRAY, 1821

Vespertilio sp.

Figs. 2A-B, E-F, H

Material: Egorovka 1: Ch/341 C sup. dex. $1.55 \times 1.32 \times 2.40$, Ch/331 C sup. sin. 1.60×1.40 , Ch/332 C sup. sin. 1.71×1.42 ; Palievo: Ch/373 C sup. sin. $1.52 \times 1.30 \times 2.60$; Ch/374 m1 sin. $1.75 \times 0.93 \times 1.02$; Ch/375 m2 dex. $1.60 \times 0.92 \times 1.10$; Ch/377 C inf. sin. $0.91 \times 1.00 \times 1.56$.

Description: The crown of the upper canine has a well-developed concave disto-lingual face and only lingual and distal crests (specimens Ch/331, Ch/332, Ch/341, Ch/373). Its crown is triangular in cross-section and at the anterolingual side has a well-developed cingulum which forms a narrow talon with small cusps (Fig. 2A1, B1).

The crown of the lower canine is compressed and has a poorly-defined mesolingual cingular cuspid which merges into the main crown cone (specimen Ch/377, Fig. 2H). The lower molars (specimens Ch/374 and Ch/375) are myoto-

dont with somewhat curved paralophids. The m1 and m2 are similar in size but the m1 has a wider angle between the paraconid and metaconid, and a more curved paralophid. The metalophid of m1 (specimen Ch/374) is convex in the anterior direction.

Comparison: A well-developed cingulum and simple cone-shaped forms of the upper and lower canines suggest that the fossils examined are members of the family Vespertilionidae.

The typical feature of the upper canines of most *Vespertilio* and *Nyctalus* species is a considerable expansion of the anterolingual part of the cingulum which forms a narrow thickening with small cuspids. Moreover, the upper canines of many Recent species of *Vespertilio* and *Nyctalus* are triangular in occlusal view and have wide concave distolingual faces and as a rule, only lingual and distal crests. All these morphological features are present on the crowns of the fossil upper canines from Egorovka 1 and Palievo. On the contrary, the upper canines of the most Recent *Eptesicus* species are diamond-shaped in occlusal view, and besides lingual and distal crests, they also have visible labial and mesial crests, their disto-lingual faces being comparatively narrow, the anterolingual thickening of the cingulum with its small cuspids is absent. In comparison with *Vespertilio* the upper canines of *Nyctalus* have a more developed anterolingual thickening of the cingulum and frequently tend to have second tips on the cutting edges of their crowns. Because the fossil upper canines (specimens Ch/341, Ch/331-332 and Ch/373) have no second tips on the cutting edges of their crowns and have all the above-listed morphological features of *Vespertilio* they are assigned to *Vespertilio* sp.

The fossil lower canine (specimen Ch/377) from Palievo is compressed in the anteroposterior direction to the same degree as the lower canines of *Eptesicus* or *Vespertilio*. However as opposed to *Eptesicus* it has a poorly-defined mesolingual cingular cuspid which merges into the main cone of the lower canine. This is a typical feature of *Vespertilio*. There are only a limited number of *Eptesicus* species (such as *E. nilssoni*, *E. bottae* and *E. anatolicus*) which share with *Vespertilio* this feature of having a mesolingual cingular cuspid of the lower canine. The fossil lower canine from Palievo is appreciably larger than *E. nilssoni* and *E. anatolicus* (Table 2). *Eptesicus bottae*, closer in size to the fossil canine from Palievo, differs from them in being more compressed and having a visible posterolingual cingular cuspid which is absent on the crown of Recent species.

The para- and metalophids of the fossil lower molars (specimens Ch/375 and Ch/374) are only somewhat curved, which is typical for the species of *Myotis* and *Vespertilio*. However, the metalophids of the fossil lower molars from Palievo are convex in the anterior direction (to the talonid), so that the tips of the metaconids are directed backwards instead of forward, as with *Myotis*. On the basis of these morphological features the fossil lower molars from Palievo are defined as *Vespertilio* sp.

All specimens of *Vespertilio* sp. from Egorovka 1 and Palievo are significantly larger than the Recent *V. murinus* (Table 2). Moreover, in contrast to the Recent *V. murinus* the upper canines of the fossil *Vespertilio* sp. are less compressed and more elongate. The angle between the lingual

Table 2. Comparison of different fossil and Recent species of *Vespertilio* (in mm, the size difference between maximum and minimum values, an arithmetic mean is in brackets; n: number of specimens). The measurements for *V. cf. villanyiensis* are quite approximate because the specimen was reconstructed after damage (details see in ROSSINA et al. 2006).

Species	n	LC	WC	Lc	Wc	Lm1	Wtrm1	Wtlm1	Lm2	Wtrm2	Wtlm2	Reference
<i>Vespertilio</i> sp., Egorovka 1, Ukraine	3	1.55-1.71 (1.62)	1.32-1.42 (1.38)	-	-	-	-	-	-	-	-	own data
<i>Vespertilio</i> sp., Palievo, Ukraine	1	1.52	1.30	0.91	1.00	1.75	0.93	1.02	1.60	0.92	1.10	own data
<i>V. villanyiensis</i> , holotype, Hungary	1	-	-	0.88	-	1.54	0.90	1.04	1.45	0.90	1.04	ROSSINA et al. 2006; HORÁČEK 1997
<i>V. cf. villanyiensis</i> , Morskaya 2, Russia	1	-	-	-	-	1.60	0.82	0.90	1.65*	-	-	own data
<i>V. sinensis</i> , Bilike, Mongolia	1	1.40	1.30	-	-	-	-	-	-	-	-	QIU & STORCH 2000
<i>V. sinensis</i> , Recent, Russia, China	10	1.30-1.60 (1.43)	-	-	-	-	-	-	-	-	-	own data
<i>V. murinus</i> , Recent, Russia	11	1.10-1.35 (1.19)	-	-	-	1.35-1.45 (1.41)	0.80-0.90 (0.88)	0.85-0.95 (0.92)	1.30-1.45 (1.39)	0.85-0.90 (0.88)	0.90-1.00 (0.93)	own data

and distal crests of the upper canines of the fossil *Vespertilio* sp. is wider than that of the Recent *V. murinus*. In size, the fossil specimens of *Vespertilio* sp. from Egorovka 1 and Palievo are also larger than the Recent *V. sinensis* and fossil *V. sinensis* from the Early Pliocene site Bilike (~MN 14, Inner Mongolia, China, QIU & STORCH 2000, Table 2). The *Vespertilio* sp. from Egorovka 1 and Palievo is most similar in size to *V. villanyiensis* HORÁČEK, 1997 (= *V. majori* KORMOS, 1934) from the Late Pliocene site Villány-Kalkberg (Villány 3, MN 17, Hungary) and to the *V. cf. villanyiensis* from the Late Turolian vertebrate fauna of Morskaya 2 (MN12-13, Russia, ROSSINA et al. 2006). Nevertheless, the *Vespertilio* sp. from Egorovka 1 and Palievo is somewhat larger than *V. villanyiensis* (Table 2), which morphologically is very close to the Recent *V. murinus* and most likely is its synonym (HORÁČEK 1997).

Remarks: Many records of *Vespertilio*, in particular *V. murinus*, are known from the Holocene and the Late Pleistocene deposits of Central Europe (HORÁČEK & JAHELKOVÁ 2005). *V. murinus* is also known from Pleistocene localities in Russia (BARYSHNIKOV 2002; ROSSINA et al. 2006; ROSINA 2012). A reference to fossil material belonging to this genus in Western Europe is found in the faunal list of the Late Pliocene locality of Valdeganga 2 (MN 16, Spain, MEIN et al. 1978) but without a morphological description or figures that might make comparisons possible. Apparently all known fossil species *Vespertilio* s.l. from Europe, including *Vespertilio* sp. from Egorovka 1 and Palievo, morphologically bear a resemblance to each other and are similar to Recent *V. murinus*.

Tribe Eptesicini VOLLETH & HELLER, 1994

Eptesicus aff. *campanensis* BAUDELLOT, 1970

Fig. 3H

Material: Novoelizavetovka 3: Ch/382 C sup. dex. 2.25 × 2.00 × 4.00.

Description: This isolated right upper canine is very large and robust. It is diamond-shape in occlusal view and has a well-developed undulating cingulum and a distinct mesiolingual cingular caspid. There are distinct lingual and distal crests which delimit a narrow lingual concave surface of the crown. The front side of the crown is convex.

Comparison: A well-developed cingulum and simple cone-shaped form of the fossil upper canine suggest that the specimen examined is a member of the family Vespertilionidae. The fossil canine from Novoelizavetovka 3 is morphologically somewhat similar to the Late Miocene molossid *Meganycteris monslapidis* RACHL, 1983 (Steinberg, Goldberg, MN 6, Germany) which is also very large in size. Nevertheless, the fossil canine from Novoelizavetovka 3 is smaller (*M. monslapidis*: LC = 3.43-3.80, WC = 2.75-2.85, RACHL 1983) and differs from *M. monslapidis* in having more rounded cross-sections of root and tooth crown and in hav-

ing more developed mesiolingual and distolingual cingular cusps.

Among vespertilionid bats, the enlarged curved upper canines with a well-developed sharp cutting edge are typical for the genera *Ia*, *Vespertilio*, *Nyctalus* and *Eptesicus*. Like the typical upper canine of most *Eptesicus* species the fossil canine from Novoelizavetovka 3 is diamond-shaped in the occusal view and does not have an anterolingual thickening of the cingulum (as *Vespertilio*) and a second tip on the cutting edge of the crown (as *Nyctalus*). From the upper canine of *Ia io* THOMAS, 1902 it differs in being smaller and diamond-shaped in the occusal view, in having a clearly defined mesiolingual cingular caspid.

The fossil canine from Novoelizavetovka 3 is somewhat similar to that of the Recent *E. serotinus* but is considerably larger in size and is not compressed in the buccolingual direction. Moreover, the crown of the fossil specimen has a clearly defined mesiolingual cingular caspid (whereas it is absent at the crown of *E. serotinus*). Morphologically the fossil canine from Novoelizavetovka 3 is very similar to that of the Recent *E. fuscus miradorensis* (H. ALLEN, 1866) from Mexico, which nevertheless is considerably smaller in size (LC = 2.00-2.08, WC = 1.67-1.75).

The fossil forms of *Eptesicus* related to the Recent species *E. serotinus* SCHREBER, 1774 group are reported from many Pleistocene sites of Europe. Some of them are morphologically close in some degree to the fossil from Novoelizavetovka 3. Such fossil form defined as *E. cf. serotinus* is known from the Middle Pleistocene locality Kozi Grzbiet (Poland, WOŁOSZYN 1987). Another form defined as *E. cf. praeglacialis* is described from the Early and Middle Pleistocene of Hungary (Beremend 15, Tarkó and Csarnóta 2, TOPAL 1985). All these fossil *Eptesicus* are very large in size and have upper canines which are similar in length but significantly shorter than the fossil canine from Novoelizavetovka 3 (the ratio LC/WC×100% is more than 120, Table 3). Unfortunately the nominotypical *E. praeglacialis* from the Late Pliocene Hungarian site Villány-Kalkberg (= Villány 3, MN 17, KORMOS 1930) is described by a lower jaw fragment, thus its comparison with the the fossil upper canine from Novoelizavetovka 3 is impossible.

The closest similarity of the fossil upper canine from Novoelizavetovka 3 has been found in *E. campanensis* from the Late Middle Miocene of Petersbuch 6 and Petersbuch 10 (MN 7/8, Germany, ZIEGLER 2003: Fig. 3.1, p. 462). In spite of the fact that the fossil upper canine from Novoelizavetovka 3 is slightly larger, the ratio of LC/WC×100% is less than 120 and corresponds to that of the fossil forms related to the *E. campanensis* (see Table 3). But because of the marked difference in morphology and scarcity of fossil bats at Novoelizavetovka 3 it is designated as "affinis".

Remarks: *Eptesicus campanensis* is well-known from the localities of Europe but everywhere it is both scarce and rare. This species was first described from the Sansan locality (MN 6, France, BAUDELLOT 1972), the deposits of which correspond to ancient swamps or a small lake (BONIS et al. 1999). Later this species was also found in the karstic sites Petersbuch 6 and 10 (MN 7/8, Germany, ZIEGLER 2003) and Petersbuch 28 (MN 3, Germany, ROSSINA & RUMMEL 2012). A single upper canine of *E. campanensis* is known from

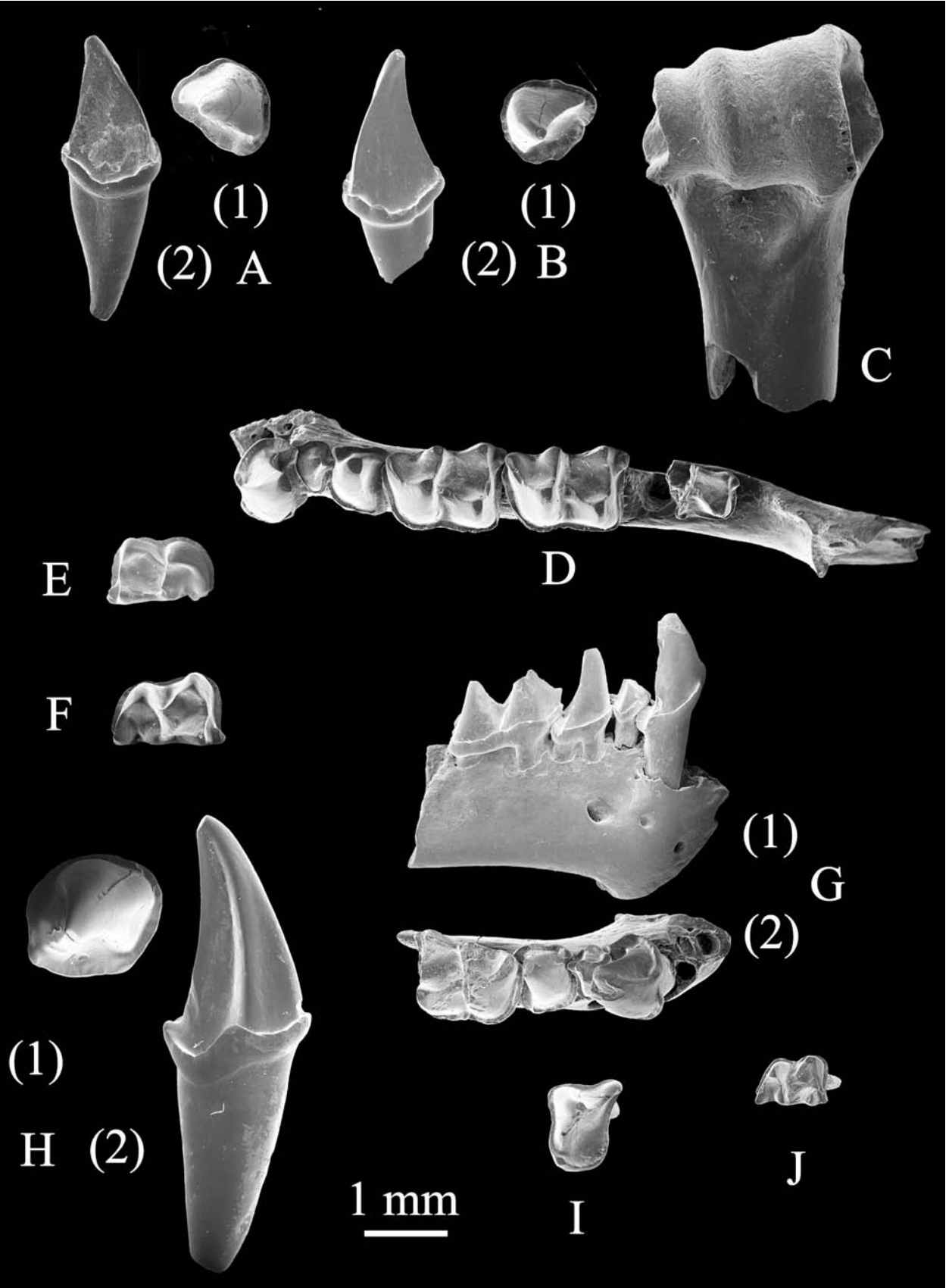


Fig. 3.

Table 3. Comparison of upper canines of different fossil and Recent species of *Eptesicus* (in mm, the size difference between maximum and minimum values, an arithmetic mean is in brackets; n: number of specimens).

Species	n	LC	WC	HC	LC/ WC×100%	Reference
<i>E. aff. campanensis</i> Novoelizavetovka 3, Ukraine	1	2.25	2.00	4.00	112.5	own data
<i>E. campanensis</i> Petersbuch 28, Germany	1	1.95	1.70	3.40	114.7	ROSINA & RUMMEL 2012
<i>E. campanensis</i> Petersbuch 6, Germany	1	2.07	1.77	>2.95	116.9	ZIEGLER 2003
<i>E. campanensis</i> Petersbuch 10, Germany	2	2.10-2.13	1.93	3.62	110.4	ZIEGLER 2003
<i>E. campanensis</i> Sansan, France	2	2.01-2.10	1.87-1.96	3.55	107.2-107.5	GINSBURG & MEIN 2012; BOUDELLOT 1972
<i>E. campanensis</i> Póvoa de Santarém, Portugal	1	1.97	1.73	-	113.9	ANTUNES & MEIN 1977
<i>E. serotinus</i> Ukraine, Yugoslavia	2	2.08-2.10	1.58	3.50	131.6-132.9	own data
<i>E. cf. serotinus</i> Kozi Grzbiet, Poland	3	2.31-2.39	1.69-1.85	-	124.9-141.4	WOŁOSZYN 1987
<i>E. cf. praeglacialis</i> Beremend 15, Hungary	1	2.18	1.68	-	129.8	TOPAL 1985
<i>E. cf. praeglacialis</i> Tarkó, Hungary	-	1.68-2.13	1.45-1.63	-	-	TOPAL 1985
<i>E. cf. praeglacialis</i> Csarnóta 2, Hungary	-	1.86-2.27	1.50-1.72	-	-	TOPAL 1985

the alluvial locality Póvoa de Santarém (MN 6, Portugal, ANTUNES & MEIN 1977). This species was also reported in the faunal list from the Late Miocene locality Lobrieu (MN 11, France, MEIN 1999). The record of *E. campanensis* s. l. in Novoelizavetovka 3 (MN12) is thus the youngest representative of this taxon at present.

Eptesicus aff. kowalskii WOŁOSZYN, 1987

Fig. 3C-D, G

Material: Egorovka 1: **Ch/324** mnd with c-m2, talonid m3 sin., C inf. $0.90 \times 1.20 \times 1.90$, Lc-p4 = 2.40, Lc-m1 = 3.72,

Lp2-m3 = 6.37, p2 0.65×0.71 , Lp2-p4 = 1.60, p4 1.00×0.90 , Lp4-m3 = 6.00, Lm1-3 = 5.15, Lm1-2 = 3.42, Lm2-3 = 3.50, m1 $1.80 \times 0.95 \times 1.10$, m2 $1.80 \times 1.00 \times 1.15$, Wtlm3 = 0.80, Ltlim3 = 0.70, Hmdm1 = 2.25, Hmdm3 = 1.90; **Ch/325** mnd with c-m1 dex., C inf. 1.05×1.19 , Lc-p4 = 2.50, Lc-m1 = 4.00, p2 0.62×0.77 , Lp2-p4 = 1.65, p4 1.10×0.97 , m1 $1.80 \times 1.10 \times 1.20$, Hmdm1 = 2.20; **Ch/326** mnd dex., Hmdm1 = 2.20; **Ch/327** mnd with p2 dex., p2 0.70×0.70 , Hmdm1 = 2.36; **Ch/328** mnd dex., Hmdm3 = 1.90; **Ch/329** m2 dex. $1.88 \times 1.00 \times 1.20$; **Ch/330** m2 dex. $1.85 \times 1.00 \times 1.10$; **Ch/333** mnd dex., Hmdm3 = 1.90; **Ch/334** mnd dex., Hmdm1 = 2.00; **Ch/335** m1 dex. $1.77 \times 0.90 \times 1.00$; **Ch/342** distal epiphysis of the left humerus Wdep = 3.40, Lep = 1.60, Ltr = 2.40. Egorovka 2: **Ch/343** m2 sin. $1.85 \times 0.99 \times 1.11$.

Fig. 3. A-B, E-F – *Vespertilio* sp.; A: C sup. dex., Egorovka 1, Ch/341, (1) occlusal view, (2) lingual view; B: C sup. sin., Palievo, Ch/373, (1) occlusal view, (2) lingual view; E: m1 sin., Palievo, Ch/374, occlusal view; F: m2 dex., Palievo, Ch/375, occlusal view; **C-D, G** – *Eptesicus aff. kowalskii*; C: distal epiphysis of the humerus sin., Egorovka 1, Ch/342, anterior view; D: dentary fragment sin. with C inf.-m2 and a preserved talonid of m3, Egorovka 1, Ch/324, ventral view; G: dentary fragment sin. with C inf.-m1, Egorovka 1, Ch/325, (1) lateral view, (2) ventral view; **H** – *Eptesicus aff. campanensis*, C sup. dex., Novoelizavetovka 3, Ch/382, (1) occlusal view, (2) lingual view; **I** – *Eptesicus* sp., P4 sin., Novoelizavetovka 3, Ch/381, occlusal view; **J** – *Vespertilionidae* indet., m2 sin., Egorovka 2, Ch/345, occlusal view.

Description: The lower incisor row is very short. The preserved alveoli of i1-3 are equal in size. They suggest that the teeth stood very close to each other so that the i3 was buccally displaced and the i2 lingually displaced from the tooth-row (specimen Ch/325). The alveole of i2 is considerably compressed in the anteroposterior direction; evidently the i2 was the smallest of the incisors. The high lower canine is crescent-shaped in occlusal view and has a high mesiolingual tubercle on the cingulum (specimens Ch/324 and Ch/325). The single-rooted conical p2 is shaped by a well-developed cingulid and has visible anterior and posterior cusplules on the crown. The crown is strongly compressed in the anteroposterior direction. The p4 is conical and quadrangular in occlusal view. It has distinct small anterior and posterior tubercles at the lingual side of the crown and is encircled by a well-developed cingulid. The lower molars are myotodont. The m1 and m2 are similar in size, but m1 has a wider trigonid angle (specimen Ch/324). The talonid of m3 is appreciably reduced and has a well-defined hypoconulid (specimen Ch/324).

The styloid process of the distal epiphysis of the humerus is broken off (specimen Ch/342). The olecranon fossa is well-marked but not deep. The humeral condyle is divided into a small capitulum and a larger trochlea. The medial ridge of the capitulum is well-developed and more massive than the lateral ridge. The lateral and medial epicondyles are well-developed. A Lep/Ltr $\times 100\%$ = 66.66. The radial fossa is deep.

Comparison: The strong reduction of the lower incisive row, a high lower canine anteroposteriorly compressed, myotodont lower molars and a considerable reduction of the m3 talonid are the typical features of the *Eptesicus* and *Vespertilio* species. Moreover, because the fossil lower canines from Egorovka 1 (Ch/324 and Ch/325) have well-developed mesolingual cingular cusplids of the crowns which are detached from the main cones, they are defined as *Eptesicus*. The distal epiphysis of the fossil humerus from Egorovka 1 (specimen Ch/342) is most similar to that of the Recent *Eptesicus* (FELTEN et al. 1973: 296, figs. 13-14) in having a shallow, but well-marked, olecranon fossa and a deep radial fossa. Among the Recent *Eptesicus* species the fossil *Eptesicus* from Egorovka 1 and 2 is morphologically most similar to *E. bottae* (PETERS, 1869), *E. anatolicus* FELTEN, 1971 and to a certain degree to *E. serotinus*.

The fossil *Eptesicus* from Egorovka 1 and 2 differs from *E. serotinus* s. l. in being considerably smaller (Table 4) and in having a more marked and high posterolingual cingular cusplid on the lower canine. However, the talonid of the m3 is reduced to the same degree as in *E. serotinus*. Further the tooth row of the fossil *Eptesicus* from Egorovka 1 and 2 is still more compressed because of a more reduced p2 and more closely packed p2-p4 than in Recent *E. serotinus*. The preserved alveoli of i1-3 (specimen Ch/325) suggest that the alveole of i2 is strongly compressed and displaced lingually and the incisors were still closer to each other than in Recent *E. serotinus*. The fossil *Eptesicus* from Egorovka 1 and 2 also differs from the other large Recent *E. fuscus* BEAUVOIS, 1796 by all these features.

The fossil *Eptesicus* from Egorovka 1 and 2 closely resembles Recent *E. bottae* and *E. anatolicus* both in the size

and reduction of the m3 talonid. However, it differs from *E. bottae* in having larger p2, lower canine and lower molars (Table 4). In addition, the incisors of the fossil *Eptesicus* were more closely packed than in Recent *E. bottae*, in which they are more loosely located and the alveole of i2 is only slightly displaced lingually. On the other hand, the fossil *Eptesicus* from Egorovka 1 and 2 differs from Recent *E. anatolicus* in having a more reduced p2, the crown of which is clamped between the lower canine and the p4.

When compared with other *Eptesicus* species, the fossil *Eptesicus* from Egorovka 1 and 2 is larger (Table 4) than both fossil *E. mossoczyi* WOŁOSZYN, 1987 (MN 14, Podlesice, Poland) and Recent *E. nilssonii* KEYSERLING & BLASIUS, 1839 and has a more reduced talonid of the m3.

The greatest morphological similarity of the fossil *Eptesicus* from Egorovka 1 and 2 has been found with *E. kowalskii* WOŁOSZYN, 1987 from Podlesice (MN 14, WOŁOSZYN 1987: Fig. 6, Pl. 12, p. 327). However, because the fossil *Eptesicus* from Egorovka 1 and 2 is somewhat smaller (Table 4) and differs in having a less reduced talonid of the m3, it is designated as *E. aff. kowalskii*.

Remarks: The morphology of *E. aff. kowalskii* from Egorovka 1 and 2 combines plesiomorphic and apomorphic features. The apomorphic characters are: a very short tooth row because of the reduction of the incisive row and p2-p4, a compressed C inf. and a strong reduction of the talonid of the m3. On the other hand, a well-developed mesolingual cingular cusplid on the lower canine, which is detached from the main cone, can be considered as a distinct plesiomorphy by which the *E. aff. kowalskii* from Egorovka 1 and 2 differs from Recent taxa of *Eptesicus*.

Eptesicus sp.

Fig. 31

Material: Novoelizavetovka 3: Ch/381 P4 sin. 1.19 \times 1.44.

Description: The crown of P4 is wider than its length in occlusal view, it has a short postparacrista, slightly curved labially, and a distinct talon on the posterolingual side of the crown. The tooth is shaped by a well-developed cingulid which forms a distinct cusplid at the anterolingual side of the crown.

Comparison: A well-developed cingulum and a distinct cusplid at the anterolingual side of the crown suggest that the fossil examined is a member of the family Vespertilionidae. The square form of the crown with WP4 \geq LP4 is a typical feature of the *Eptesicus* and *Vespertilio* species. Similar to the P4 of *Eptesicus*, the fossil P4 from Novoelizavetovka 3 has a well-developed cusplid at the anterolingual side of the crown which nevertheless is not as high as, for example, on the crown of P4 of the Recent *Vespertilio murinus*. The fossil P4 from Novoelizavetovka 3 is larger than the P4 of Recent *E. nilssonii* and has a more compacted rectangular form of the crown in occlusal view. The P4 of the *E. nilssonii* has a more graceful form and has a wider stylar shelf (ectoflexus). The fossil P4 from Novoelizavetovka 3

Species	n	LC inf.	WC inf.	Lc-p4	Lp2	Wp2	Lp2-p4	Lp4	Wp4	Lm1-3	Lm1	Lm2	Ltlm3	Wtlm3	Reference
<i>E. serotinus</i> Recent, Ukraine, Yugoslavia	2	1.50		3.33-3.50	0.83-1.00		2.17-2.30	1.33-1.40		5.68-5.85	2.08-2.30	2.08-2.20	0.75	0.79-0.80	own data
<i>E. kowalskii</i> Podlesice, Poland	8	-	-	2.82	-	-	2.09	1.04-1.27 (1.18)	0.98-1.10 (1.04)	5.53	1.92-2.02 (1.98)	1.92-2.05 (1.98)	-	0.83	WOŁOSZYN 1987
<i>E. kowalskii</i> holotype Podlesice, Poland	1	1.16	1.46	-	0.81	0.81	-	1.24	1.06	-	1.92	-	-	-	WOŁOSZYN 1987
<i>E. aff. kowalskii</i> Egorovka 1, Ukraine	10	0.90-1.05 (0.98)	1.19-1.20 (1.195)	2.40-2.50 (2.45)	0.62-0.70 (0.66)	0.70-0.77 (0.73)	1.60-1.65 (1.63)	1.00-1.10 (1.05)	0.90-0.97 (0.94)	5.15	1.77-1.80 (1.79)	1.80-1.88 (1.84)	0.70	0.80	own data
<i>E. aff. kowalskii</i> Egorovka 2, Ukraine	1	-	-	-	-	-	-	-	-	-	-	1.85	-	-	own data
<i>E. bottae</i> Recent, Azerbaïdjan	2	1.00	1.04-1.08 (1.06)	2.42	0.54-0.67 (0.60)	0.67-0.75 (0.71)	1.58-1.63 (1.60)	1.00-1.04 (1.02)	0.83	4.63	1.71-1.75 (1.73)	1.67-1.75 (1.71)	0.50-0.58 (0.54)	0.54-0.63 (0.58)	own data
<i>E. mossoczyi</i> Podlesice, Poland	2	-	-	-	0.55	0.60	1.30	0.85-0.87 (0.86)	0.75-0.77 (0.76)	≈ 3.80	1.46	1.41-1.44 (1.43)	-	0.62-0.68 (0.65)	WOŁOSZYN 1987
<i>E. nilssonii</i> Recent, Central Europe	2	0.88	0.63	-	0.64	0.67-0.83	1.52	0.90	0.82	3.60-4.10 (3.79)	1.30-1.50 (1.43)	1.25-1.50 (1.33)	-	0.75	own data, WOŁOSZYN 1987

morphologically corresponds well to the P4 of *E. kowalskii* (WOŁOSZYN 1987: p. 275) but the latter one is considerably larger (LP4 = 1.44, WOŁOSZYN 1987). In size and other morphological characters the fossil P4 from Novoeliazavetovka 3 is most similar to the P4 of the Recent *E. bottae* and *E. anatolicus*. However, it differs in having a more developed talon on the posterolingual side of the crown.

Remarks: Because the morphology of the fossil *Eptesicus* sp. from Novoeliazavetovka 3 corresponds well to that of *E. bottae*, it could not be ruled out that this P4 belongs to the *E. aff. kowalskii* from Egorovka 1 and 2.

Vespertilionidae indet.

Fig. 3J

Material: Egorovka 2: Ch/345 m2 sin. 1.09 × 0.70 × 0.72.

Description: The m2 is myotodont, para- and metalophids are slightly curved.

Comparison: A well-developed cingulum and only slightly curved para- and metalophids suggest that the molar belong to a member of the family Vespertilionidae. The myotodonty and relatively small size of the tooth exclude its belonging to any of the above surveyed species.

Remarks: The myotodont type and an intermediate size of the m2 characterize many species of the family Vespertilionidae, so an accurate identification of such an isolated molar is extremely difficult.

4. Discussion

4.1. Composition of the Turolian bat associations from the Ukraine and biostratigraphic considerations

Until now from the Ukraine only the Late Miocene locality Gritsev (MN 9) provided a very rich fossil bat fauna, including a newly described genus *Eptenonnis* ROSINA & SEMENOV, 2012 (Vespertilionidae) with a new species *E. gritsevensis* ROSINA & SEMENOV, 2012 and the largest Neogene *Myotis* – *M. korotkevichae* ROSINA & SEMENOV, 2012. The present paper provides the first data on Turolian bats in Ukraine. In total six taxa, all belonging to the Vespertilionidae were identi-

Table 4. Comparison of different fossil and Recent species of *Eptesicus* (in mm, the size difference between maximum and minimum values, an arithmetic mean is in brackets; n: number of specimens).

fied (Table 5). In many cases, the fragmentary nature and poor preservation of some of the fossil bats from these Turolian sites did not allow an exact species identification (e.g., *Vespertilio* sp. or *Nyctalus* sp.).

The fossil remains of bats are rare in all sites considered in this paper. In the taphocenosis of Palievo they composed 0.63% of all small mammal remains, in Novoelizavetovka 3 - 0.76%, in Altestovo 5 - 1.82%, in Egorovka 2 - 0.51%, and only in the taphocenosis of Egorovka 1 are bats more abundant, representing 5.83% of all examined material. Such situations are typical for localities from lacustrine and fluvial deposits and contrast with those from karstic sediments where bat remains often are quite abundant. All examined localities differ appreciably from each other by composition and diversity of bat taxa (Table 5). The richest bat assemblages were found in the sites Egorovka 1 and Palievo.

Thus, fossil remains of *Pipistrellus* s.l. are the most constant component in these taphocenosis but never in high numbers. The sites with fossil *Vespertilio* and *Eptesicus* s.l. are appreciably rarer but fossil remains of these bats can be abundant. *Nyctalus* and *Eptesicus* aff. *campanensis* fossils are very rare in all taphocenosis considered in this paper and both are represented by a single specimen only.

It is very difficult or almost impossible to compare the examined fossil assemblages of bats with those from the West-European karstic sites of the same age, such as Kohfidisch etc. As a rule, the bat assemblages of the karstic sites are dominated by Rhinolophidae and cave-dwelling forms of Vespertilionidae, such as *Myotis* and *Miniopterus*, which are absent in the examined material. The fossil assemblages from the Ukraine most resemble those from non-karstic sites of France (Bernardière, Lobrieu and Dionay, MN 11) and of the Southern European area of Russia (Morskaya 2, MN 12). In both Altestovo 5 in Ukraine and Bernardière in France only one bat species *Pipistrellus* s.l. was found (MEIN 1999). The fossil bat assemblage of Novoelizavetovka 3 is very similar to that of the Lobrieu (MN 11), nevertheless the latter is of a bit older age. In both sites the remains of the *Eptesicus* s. l., in particular *E. campanensis* s. l., were found (MEIN 1999). A rich mammal assemblage from the Dionay locality provided remains of three species of bats (*Rhinolophus csakvarensis* KRETZOI 1951, *Myotis boyeri* MEIN 1964, *Pipistrellus* sp., MEIN 1999). The appearance of *Pipistrellus* s.l., corresponding to that in Altestovo 5, Palievo and Egorovka 1, 2, is particularly worthy of mentioning as these records represents the earliest

Miocene records of the genus *Pipistrellus*, one of the most diversified clade of extant vespertilionids (HULVA et al. 2004, BENDA et al. 2004, KOUBÍNOVÁ et al. 2013). In contrast to the French sites, the fossil taphocenosis from the Ukraine include also other clades of non-cave dwelling bats: *Nyctalus* s.p., *Vespertilio* s.p. and *Eptesicus* ssp. (Table 5).

Until now the records of *E. kowalskii* were known only from the type locality Podlesice in Poland (MN 14, WOŁOSZYN 1987). The discovery of *Eptesicus* aff. *kowalskii* in Egorovka 1 and 2 which are related to the nominotypical taxon from Poland appreciably extend the area of distribution of this species group to the east. Of course, the fauna of Podlesice differs considerably from those of Egorovka 1 and 2, it is enormously rich and includes numerous species of *Myotis*, *Plecotus*, *Miniopterus* and *Rhinolophus* (KOWALSKI 1956) and other taxa not appearing in Ukrainian taphocenosis, such as *E. mossoczyi* (WOŁOSZYN 1987).

Similar to the Egorovka 1 and Palievo sites, the fossil records of *Vespertilio* s.l. are known from the locality Morskaya 2 in the Sea of Azov region of Russia (ROSSINA et al. 2006). The Morskaya 2 locality is associated with alluvial deposits and includes rich material of vertebrate remains (TITOV et al. 2006), but only a single fragment of a bat was found there (ROSSINA et al. 2006). The bat faunas from the Egorovka 1 and Palievo are much richer.

The locality Lufeng (the age is generally equivalent to the European Turolian, c. MN 12) known from South China is associated with marsh deposits rich with lignites (QIU et al. 1984). It contains a rich and abundant Late Miocene small mammal assemblage including some fossil bats (Table 5). Fossils of *Pipistrellus* sp. are the most abundant in this taphocenosis (QIU et al. 1984) resembling somewhat the Turolian bat assemblage from the Ukraine, in particular Egorovka 2. Unfortunately, description of the respective taxon from Lufeng is too brief (QIU et al. 1984) to enable any comparison and the above mentioned records of *Pipistrellus* sp. from France are just items in species list of the respective sites (MEIN 1999). Thus, the remains of *Pipistrellus* ssp. described in this paper are to be looked upon as the first reliable data concerning the early history of that widely distributed genus.

4.2. Phylogenetic considerations

Three bat species which morphologically differ from all known Recent and fossil bats are in the examined taphocenosis from the Turolian sites of the Ukraine.

Table 5. Taxonomical compositions of bat assemblages from of the examined Turolian sites from the Ukraine and their biostratigraphic comparison with some Late Miocene sites (after KORMOS 1930; MEIN et al. 1978; MEIN 1999; KOWALSKI 1956; WOŁOSZYN 1987; QUI et al. 1985; ROSSINA et al. 2006). Designations and notes: “+” species was recorded (the percentage of each bat species from the total bat records are in brackets); * the age is generally equivalent to the European Turolian, c.a. MN 12 (QIU et al. 1984).

Sites	MN zone	Location	Deposits	<i>Pipistrellus</i>	<i>Nyctalus</i>	<i>Vespertilio</i>	<i>Eptesicus campanensis</i> s. l.	<i>Eptesicus kowalskii</i> s. l.	<i>Eptesicus</i>	Other bat taxa
Palievo	11	Ukraine	alluvial-riverine	+ (16.7%)	+ (16.7%)	+ (66.7%)				
Egorovka 1	12	Ukraine	lacustrine	+ (22.2%)		+ (16.7%)		+ (61.1%)		
Egorovka 2	12	Ukraine	lacustrine	+ (33.3%)				+ (33.3%)		Vespertilionidae indet. (33.3%)
Novoelizavetovka 3	12	Ukraine	alluvial-lacustrine				+ (50%)		+ (50%)	
Altestovo 5	12	Ukraine	alluvial	+ (100%)						
Dionay	11	France	fluviatile	+						<i>Myotis</i> , <i>Rhinolophus</i>
Bernardière	11	France	fluviatile	+						
Lobrieu	11	France	fluviatile				+		+	
Morskaya 2	12	Russia	lacustrine			+				
Podlesice	14	Poland	palaeokarst					+	+	<i>Rhinolophus</i> , <i>Myotis</i> , <i>Plecotus</i> , <i>Miniopterus</i>
Villány 3	17	Hungaria	palaeokarst			+				<i>Myotis</i>
Valdeganga 2	16	Spain	riverine			+				
Lufeng	12*	China	Marsh deposits	+					+	<i>Plecotus</i> , <i>Myotis</i> , Hipposideridae, Pteropodidae

Pipistrellus semenovi nov. sp. from Altestovo 5 undoubtedly is a member of the Recent genus, but differs from most of the Recent species, such as *P. kuhlii* or *P. rueppellii*, in having a more primitive morphology. So the P2 of *P. semenovi* is less reduced, the crown of P4 is more elongated in anteroposterior direction and has a weakly marked anterolingual tubercle and a poorly-developed posterolingual talon. The P4 of the Recent *P. kuhlii* is more advanced: it has a short compressed crown with well-developed anterolingual tubercle and posterolingual talon. Apparently in the evolution of *Pipistrellus* occur the reduction of the I2 and a shortening of a diastem between C sup. and the upper inci-

sors. A poor development of the metacarpal on the M1 crown of the *P. semenovi* is also a primitive feature which retained only in the basal clades of the genus such as in *P. rueppellii* or partly in the *P. pipistrellus* group. Such combination of plesiomorphic characters with relatively larger body size characterizes (Table 1) the unique and basal phylogenetic position of *P. semenovi* sp. nov. quite convincingly.

Eptesicus aff. *kowalskii* from Egorovka 1 and 2 is morphologically close to the Pliocene *E. kowalskii*. However, *E. aff. kowalskii* has a more primitive morphology because it has a less reduced m3 talonid and it is smaller than the nominotypical taxon. *Eptesicus*

aff. *kowalskii* from Egorovka 1 and 2 is probably an ancestral form of the Pliocene *E. kowalskii*. Further, *E. aff. kowalskii* exhibits a set of characters typical for a greatly derived group of the genus represented in the Recent fauna by species of *E. bottae-anatolicus* group, widely distributed in the Middle East, Transcaucasia and Central Asia (JUSTE et al. 2013). Meanwhile, in spite of the above listed primitive characters of the *E. aff. kowalskii* from Egorovka 1 and 2, it was a very specialized form. It differs from the highly specialized Recent and fossil *E. serotinus* s. l. in having more advanced features: the tooth row is shorter because of a more reduced p2 and a constricted location of p2-p4, the lower incisive row is also shorter because of a greater reduction of i2 which is considerably displaced lingually. Thus the phyletic branch of *E. kowalskii* s.l. is apparently separate and independent from the evolutionary branch of *E. serotinus* s.l.

The single upper canine of *E. aff. campanensis* from Novoelizavetovka 3 is much larger than that of all known fossil and Recent *Eptesicus*. Morphologically it is very close to the Early and Middle Miocene species of *E. campanensis*. Apparently it suggests their close phyletic relationship; the upper canines of these species display a trend towards increasing size during their Miocene evolution. The phyletic branch of *E. campanensis* s. l. is also independent of the group taxa *E. praeglacialis* s.l. and *E. serotinus* s.l. which had considerably smaller upper canines up to the beginning of the Pleistocene.

4.3. Taphonomical and paleoecological aspects

Pipistrellus, *Vespertilio*, *Nyctalus* and *Eptesicus* are the only bat taxa in the examined taphocenosis from the Turolian sites of the Ukraine. The modern species of these genera as a rule live in large colonies and make seasonal migrations, they are often fairly large taxa (except *Pipistrellus* species), that all together apparently made them accessible prey for owls, hawks and falcons. Extant *Vespertilio*, *Eptesicus*, *Nyctalus* and *Pipistrellus* species fall prey to nocturnal predators and their remains are often found in pellets of these flying avian predators (OBUCH 1989; STUBBE et al. 1989; RUPRECHT 1990, 2005; KOWALSKI 1995; KAWAGUCHI & YAMAMOTA 2003; CHIBA et al. 2005; ROSSINA et al. 2006; ROSINA & SHOKHRIN 2011). Thus, a pellet origin of the bat bones from the examined taphocenosis is most probable. Perhaps the ancient pellets accumulated and subsequently were fossilized near the roost sites of predatory birds, frequently near the

water. Of course, it is not excluded that some remains can be accumulated and fossilized following natural deaths of bats foraging above the water surface. However the pellet origin of the fossil material in the examined taphocenosis from the Ukraine is defined also by a high portion of bones and teeth of small mammals with characteristic marks from exposure to digestive enzymes. About 14% of all examined fossil remains from Palievo have marks of such corrosion produced by digestion (SINITSA 2012).

Vespertilio, *Eptesicus*, *Nyctalus* and *Pipistrellus* are absent or very rare in numerous Neogene localities associated with paleokarst deposits such as Kohfidisch in Austria or Lissieu in France, suggesting that in the Neogene these bats roosted in other refuges besides caves. Modern *Pipistrellus*, *Vespertilio* and *Eptesicus* are opportunists in terms of their roosting ecology; they have generalized roosting habits and wide geographic distributions. More recently these species roost often or almost exclusively in man-made structures (KUNZ 1982; AVERY 1991; JENKINS et al. 1998) but they often inhabited cavities of trees, especially during maternity periods (VIERHAUS 2004; ZAHN et al. 2004; NAÑO et al. 2011, own data) or hibernation (NAGY & POSTAWA 2010; BÜCS et al. 2012). *Nyctalus* species are one of the typical forest-dwelling bats in Europe (GEISLER et al. 1979; BOONMAN 2000; RUCZYŃSKI & BOGDANOWICZ 2005). Mainly Neogene remains of *Pipistrellus*, *Vespertilio* and *Nyctalus* in Europe are found in localities associated with riverine and lacustrine deposits (SIGÉ & LEGENDRE 1983, Table 5). In many cases, the Neogene finds of *Eptesicus* s.l. are also made at sites which have an alluvial-riverine genesis (ibid.). These facts also support the notion that these bats seldom roosted in karstic caves.

Contrary to the Neogene, the Pleistocene remains of *Pipistrellus*, *Vespertilio*, *Eptesicus* and *Nyctalus* become numerous and very common in paleokarstic sites in Europe (e.g., HORÁČEK & JAHELKOVÁ 2005; ROSSINA et al. 2006). The earliest find of *Vespertilio* in paleokarstic deposits is dated to the Late Pliocene (Villány 3, MN 17, Hungary). At present *Nyctalus*, *Pipistrellus*, *Vespertilio* and *Eptesicus* inhabit karstic roosts usually during hibernation (NAGY & POSTAWA 2010; NAGY & SZANTO 2003; BÜCS et al. 2012; own data). Remains of bats in karstic deposits frequently accumulate as the result of natural deaths occurring in animals forming big colonies, more often during hibernation (e.g., HORÁČEK & JAHELKOVÁ 2005; ROSSINA et al. 2006; ROSINA 2012). Thus, it becomes obvious that from the end of the Neogene some forest-dwelling

bats began using karstic caves as roosting sites, apparently during hibernation. The general deterioration of the climatic situation in the territory of Eurasia at the end of the Neogene could be the possible reason for such changes in roosting ecology of these bats. The cooling trend in the Miocene of Europe starts at c. 14 Ma as is described from the continental areas of Western Eurasia (e.g., Lower Rhine Basin, Germany; UTESCHER et al. 2000) and is connected to the expansion of polar ice-sheets (e.g., ZACHOS et al. 2001). In particular the climate of the territory of the Recent southeastern Ukraine became more arid and colder at the end of the Middle Miocene (SYABRYAJ et al. 2007). As indicated for Central European Cenozoic climate evolution (UTESCHER et al. 2000; MOSBRUGGER et al. 2005), this cooling is dominantly controlled by decreasing winter temperatures and increased seasonality of climate. Thus, climate change could be a probable cause for why *Pipistrellus*, *Vespertilio*, *Eptesicus* and *Nyctalus* began to prefer karstic cavities for winter hibernation, the microclimate of which is more stabile. This also can be an explanation as to why, up the end of the Neogene, the fossil remains of these bat species became more abundant and more numerous in karstic sites.

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References

- ANTUNES, M.T. & MEIN, P. (1977): Contributions à la paléontologie du Miocène moyen continental du bassin du Tage. III. Mammifères. Póvoa de Santarém, Pero Filho et chões (secorio). Conclusions générales. – *Ciências da Terra (U.N.L.)*, **3**: 143-165.
- AVERY, M.I. (1991): *Pipistrellus pipistrellus*. – In: CORBET, G.B. & HARRIS, S. (Eds.): *The Handbook of British Mammals*, 124-128; Oxford (Oxford University Press).
- BARYSHNIKOV, G.F. (2002): Local biochronology of Middle and Late Pleistocene mammals from the Caucasus. – *Russian Journal of Theriology*, **1** (1): 61-67.
- BAUDELLOT, S. (1972): Étude des Chiroptères, Insectivores et Rongeurs du Miocène de Sansan (Gers). – Thèse Université Toulouse. – 496 pp.
- BENDA, P., HULVA, P. & GAISLER, J. (2004): Systematic status of African populations of *Pipistrellus pipistrellus* complex (Chiroptera: Vespertilionidae), with a description of a new species from Cyrenaica, Libya. – *Acta Chiropterologica*, **6**: 193-217.
- BENECKE, N., BÖHME, G. & HEINRICH, W.-D. (1990): Wirbeltierreste aus interglazialen Beckensedimenten von Gröbern (Kr. Gräfenhainichen) und Grabschütz (Kr. Delitzsch). – *Altenburger Naturwissenschaftliche Forschungen*, **5**: 231-281.
- BONIS, L. DE, BOUVRAIN, G. & KOUFOS, G.D. (1999): Palaeoenvironments of late Miocene primate localities in Macedonia, Greece. – In: AGUSTÍ, J., ROOK, L. & ANDREWS, P. (Eds.): *The evolution of Neogene terrestrial ecosystem in Europe. Hominoid evolution and climatic change in Europe*. 413-435; Cambridge (Cambridge University Press).
- BOONMAN, M. (2000): Roost selection by noctules (*Nyctalus noctula*) and Daubenton's bats (*Myotis daubentonii*). – *Journal of Zoology*, **251** (3): 385-389.
- BRUNNER, G. (1958): Nachtrag Breitenberghöhle bei Gössweinstein (Ofr.). – *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1958**: 500-517.
- BÜCS, S., JÉRE, C., CSÓSZ, I., BARTI, L. & SZODORAY-PARÁDI, F. (2012): Distribution and conservation status of cave-dwelling bats in the Romanian Western Carpathians. – *Vespertilio*, **16**: 97-113.
- CHIBA, A., ONOJIMA, M. & KINOSHITA, T. (2005): Prey of the long-eared owl *Asio otus* in the suburbs of Niigata City, central Japan, as revealed by pellet analysis. – *The Ornithological Society*, **4**: 169-172.
- FELTEN, H., HELFRICHT, A. & STORCH, G. (1973): Die Bestimmung der europäischen Fledermäuse nach der distalen Epiphyse des Humerus. – *Senckenbergiana biologica*, **54** (4-6): 291-297.
- FORTELIUS, M. (2003): *New and Old Worlds Database of Fossil Mammals (NOW)*. – University of Helsinki. <http://www.helsinki.fi/science/now/>
- GAISLER, J., HANAK, V. & DUNGEL, J. (1979): A contribution to the population ecology of *Nyctalus noctula* (Mammalia: Chiroptera). – *Acta Scientiarum Naturalium Academiae Scientiarum Bohemicae Brno*, **13** (1): 1-38.
- GINSBURG, L. & MEIN, P. (2012): Les Chiroptera de Sansan. – In PEIGNÉ, S. & SEN, S. (Eds.): *Mammifères de Sansan*, 13-28; Paris (Muséum national d'Histoire naturelle).
- HORÁČEK, I. & JAHELKOVÁ, H. (2005): History of the *Pipistrellus pipistrellus* group in Central Europe in light of its fossil record. – *Acta Chiropterologica*, **7**: 189-204.
- HORÁČEK, I. (1984): Remarks on causality of population decline in European bats. – *Myotis*, **21-22**: 138-147.
- HORÁČEK, I. (1995): Postglacial development of the mid-

- European bat fauna [Postglaciální vývoj středoevropské netopýří fauny]. – In: UHRIN, M. (Ed.): Netopiere I. Správa slovenských jaskýň, B. Bystrica, 93-98 [in Czech, with English summary].
- HORÁČEK, I. (1997): Comments on *Vespertilio majori* KORMOS, 1934. – *Vespertilio*, **2**: 131-133.
- HORÁČEK, I. (2001): On the early history of vespertilionid bats in Europe: the Lower Miocene record from the Bohemian Massif. – *Lynx*, n. s., **32**: 123-154.
- HULVA, P., HORÁČEK, I., STRELKOV, P.P. & BENDA, P. (2004): Molecular architecture of *Pipistrellus pipistrellus/Pipistrellus pygmaeus* complex (Chiroptera: Vespertilionidae): further cryptic species and the Mediterranean origin of the divergence. – *Molecular Phylogenetics and Evolution*, **32**: 1023-1035.
- HUTCHISON, J.H. (1974): Notes on type specimens of European Miocene Talpidae and a tentative classification of old world Tertiary Talpidae (Insectivora: Mammalia). – *Geobios*, **7** (3): 211-256.
- JENKINS, E.V., LAINE, T., COLE, K.R. & SPEAKMAN, J.R. (1998): Roost selection in the pipistrelle bat, *Pipistrellus pipistrellus* (Chiroptera Vespertilionidae), in northeast Scotland. – *Animal Behaviour*, **56** (4): 909-917.
- JUSTE, J., BENDA, P., GARCIA-MUDARRA, J.L. & IBÁÑEZ, C. (2013): Phylogeny and systematics of Old World serotine bats (genus *Eptesicus*, Vespertilionidae, Chiroptera): an integrative approach. – *Zoologica Scripta*, **42**: 441-457.
- KAWAGUCHI, S. & YAMAMOTA, T. (2003): Food item found in pellets of Long-eared owls wintering in Ehime, Japan. – *Japanese Journal of Ornithology*, **52** (1): 29-31 [in Japanese, with English summary].
- KORMOS, T. (1930): Diagnosen neuer Säugetiere aus der oberpliozänen Fauna des Somlyóberges bei Püspökördö. – *Annales Musei Nationalis Hungarici*, **27**: 237-246.
- KOTSAKIS, T. (1987): Les chiroptères du Pléistocène supérieur des environs de Alghero. (Sardaigne, Italie). – *Geologica Romana*, **26**: 103-108.
- KOUBINOVÁ, D., IRWIN, N., HULVA, P., KOUBEK, P. & ZIMA, J. (2013): Hidden diversity in Senegalese bats and associated findings in the systematics of the family Vespertilionidae. – *Frontiers in Zoology*, **2013**: 10-48.
- KOWALSKI, K. (1956): Insectivores, bats and rodents from the early Pleistocene bone breccia of Podlesice near Kroczyce (Poland). – *Acta Palaeontologica Polonica*, Warsaw, **1** (4): 331-394.
- KOWALSKI, K. (1995): Taphonomy of bats (Chiroptera). – *Geobios, Mémoires spéciaux*, **18**: 251-256.
- KUNZ, T.H. (1982): Roosting ecology. – In: KUNZ, T.H. (Ed.): *Ecology of Bats*. – 1-55; New York (Plenum Press).
- MADEYSKA, T. (2002): Evidence of climatic variations in loess and cave Palaeolithic sites of southern Poland and western Ukraine. – *Quaternary International*, **91**: 65-73.
- MEIN, P. (1999): The Late Miocene small mammal succession from France, with emphasis on the Rhône valley localities. – In: AGUSTÍ, J., ROOK, L. & ANDREWS, P. (Eds.): *The evolution of Neogene terrestrial ecosystem in Europe. Hominoid evolution and climatic change in Europe*, 140-164; Cambridge (Cambridge University Press).
- MEIN, P., MOISSENET, E. & TRUC, G. (1978): Les formations continentales du Néogène supérieur des vallées du Jucar et du Cabriel au NE d'Albacete (Espagne). *Biostratigraphie et environnement*. – Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon, **72**: 99-147.
- MILLER, G.S. (1907): The families and genera of bats. – *Smithsonian Institute U.S. National Museum Bulletins*, **57**.
- MOSBRUGGER, V., UTESCHER, T. & DILCHER, D.L. (2005): Cenozoic continental climatic evolution of Central Europe. – *Proceedings of the National Academy of Sciences*, **102** (42): 14964-14969.
- NAGY, Z.L. & SZANTO, L. (2003): The occurrence of hibernating *Pipistrellus pipistrellus* (SCHREBER, 1774) in caves of The Carpathian Basin. – *Acta Chiropterologica*, **5**: 155-160.
- NAGY, Z.L. & POSTAWA, T. (2010): Seasonal and geographical distribution of cave-dwelling bats in Romania: implications for conservation. – *Animal Conservation*, **2010**: 1-13.
- NAÑO, L., CELUCH, M., ŠEVČÍK, M. & KAŇUCH, P. (2011): Tree roosts and competitors of *Nyctalus noctula* in the Sihot' town park, Nitra, Slovakia. – *Vespertilio*, **15**: 71-77.
- NESIN, V.A. & NADACHOWSKI, A. (2001): Late Miocene and Pliocene Small Mammal Faunas (Insectivora, Lagomorpha, Rodentia) of Southeastern Europe. – *Acta Zoologica Cracovensia*, **44** (2): 107-135.
- NESIN, V.A. & STORCH, G. (2004): Neogene Murinae of Ukraine (Mammalia, Rodentia). – *Senckenbergiana lethaea*, **84** (1/2): 351-365.
- OBUCH, J. (1989): Chiropteran thanatocenoses in rocky fissures. – In: HANAK, V., HORACEK, I. & GAILSER, J. (Eds.): *European Bat Research 1987*. Praha (Charles University Press); 453 pp.
- QIU, Z. & STORCH, G. (2000): The early Pliocene micromammalian fauna of Bilike, Inner Mongolia, China (Mammalia: Lipotyphla, Chiroptera, Rodentia, Lagomorpha). – *Senckenbergiana lethaea*, **80** (1): 137-229.
- QUI, Z., HAN, D., QI, G. & YUFEN, L. (1985): A preliminary report on a micromammalian assemblage from the hominoid locality of Lufeng Co. Yunnan Province. – *Acta Anthropologia Sinica*, **4** (1): 13-32.
- RABEDER, G. (1972): Die Insectivoren und Chiropteren (Mammalia) aus dem Altpleistozän von Hundsheim (Niederösterreich). – *Annalen des Naturhistorischen Museums Wien*, **76**: 375-474.
- RACHL, R. (1983): Die Chiroptera (Mammalia) aus den mittelmiozänen Kalken des Nördlingers Rieses (Süd-Deutschland). – Ph.D. thesis, University of Munich (unpublished).
- ROSINA, V.V. & RUMMEL, M. (2012): The bats (Chiroptera, Mammalia) from the Early Miocene of Petersbuch (Bavaria, Southern Germany). – *Geobios*, **45** (5): 463-478.
- ROSINA, V.V. & SEMENOV, Y.A. (2012): New taxa of vespertilionid bats (Chiroptera, Mammalia) from the Late Miocene of Ukraine. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **264**: 191-203.
- ROSINA, V.V. & SHOKHRIN, V.P. (2011): Bats (Chiroptera) in the diet of owls (Strigiformes) of the Russian Far East, Southern Sikhote Alin. – *Hystrix*, n. s., **22** (1): 205-213.
- ROSINA, V.V. (2012): *Myotis* cf. *schaubi* and other bats from

- the Pleistocene of the Central Altai Mts., Russia. – *Vespertilio*, **16**: 271-278.
- ROSSINA, V.V., BARISHNIKOV, G.F. & WOŁOSZYN, B.W. (2006): Dynamics of the Pleistocene bat fauna from the Matuzka Paleolithic site (Northern Caucasus, Russia) (*Chiroptera*) – *Lynx*, n. s., **37**: 229-240.
- ROSSINA V.V., KRUSKOP, S.V., TESAKOV, A.S. & TITOV, V.V. (2006): The first record of Late Miocene bat from European Russia. – *Acta Zoologica Cracoviensia*, **49A** (1-2): 125-133.
- RUCZYŃSKI, I. & BOGDANOWICZ, W. (2005): Roost Cavity Selection by *Nyctalus noctula* and *N. leisleri* (*Vespertilionidae*, *Chiroptera*) in Białowieża Primeval Forest, Eastern Poland. – *Journal of Mammalogy*, **86** (5): 921-930.
- RUPRECHT, A.L. (1990): Bats (*Chiroptera*) in the food of owls in the Nadnotecka Forest. – *Przegląd zoologiczny*, **34**: 349-358 [in Polish, with English summary].
- RUPRECHT, A.L. (2005): Some aspects of myself research on bats (*Chiroptera*) of Poland in 1964-1990. – *Leśne Prace Badawcze*, **2**: 107-119.
- SALARI, L. & DI CANZIO, E. (2009). Bats of the Late Pleistocene and Early Holocene from some caves of Central and Southern Italy [I chiropteri del Pleistocene superiore e Olocene antico di alcune grotte dell'Italia centro-meridionale] – *Bollettino del Museo Civico di Storia Naturale di Verona*, **33**: 3-25.
- SALARI, L. & KOTSAKIS, T. (2011): Late Pleistocene and Holocene bats of Latium (Central Italy). – *II Quaternario, Italian Journal of Quaternary Sciences*, **24** (1): 121-129.
- SESE, C. & SEVILLA, P. (1996): Los micromamíferos del Cuaternario peninsular español. Cronostratigrafía e implicaciones bioestratigráficas. – *Revista Española de paleontología* (Nº Extraordinario): 278-287.
- SEVILLA, P. & CHALINE, J. (2011): New data on bat fossils from middle and upper Pleistocene localities of France. – *Geobios*, **44**: 289-297.
- SEVILLA, P. (1988): Estudio paleontológico de los Quirópteros del Cuaternario español. – *Paleontologia i Evolució*, **22**: 113-233.
- SEVILLA, P. (1989): Quaternary fauna of bats in Spain: Paleoeologic and biogeographic interest. – In: HANAK, V., HORÁČEK, I. & GAISLER, J. (Eds.): *European bat research 1987*, 349-355; Praha (Charles University Press).
- SIGÉ, B. & LEGENDE, S. (1983): L'histoire des peuplements de chiroptères du bassin méditerranéen: l'apport comparé des remplissages karstiques et des dépôts fluviolacustres [History of chiroptera populations in Mediterranean Basin: comparison between karst fillings and fluviolacustrine depositions]. – *Mémoires de biospéologie*, **10**: 209-225.
- SIGÉ, B. (1968): Les chiroptères du Miocène inférieur de Bouzigues. I. Étude systématique. – *Palaeovertebrata*, **1** (3): 65-133.
- SIMMONS, N.B. (2005): Order *Chiroptera*. – In: WILSON, D.E. & REEDER, D.M. (Eds.): *Mammal species of the world: a taxonomic and geographic reference* (3rd ed.), 312-529; Baltimore (Johns Hopkins University Press).
- SINITSA, M.V. (2008): Meotian small mammals from the Egorovka locality [Mikroteriofauna meoticheskikh otlozhenii mestonakhozheniya Egorovka]. – In: GOZHNIK, P.F. (Ed.): *Biostratigraphic fundamentals of creating the stratigraphic schemes of the Phanerozoic of Ukraine*. Proceedings of the Institute of Geological Sciences of the NAS of Ukraine, 285-89; Kyiv (Nora-print) (in Russian, with English summary).
- SINITSA, M.V. (2009): A new small mammal fauna from the Lower Turolian (MN 11) of the Southern Ukraine. – In: CODREANU, I. (Ed.): *Materialele simpozionului jubiliar internațional "Mediul și dezvoltarea durabilă"*, 181-182; Chișinău (Labirint).
- SINITSA, M.V. (2012): *Cricetids* (Mammalia, Rodentia) from the Late Miocene Locality Palievo, Southern Ukraine. [Khomyakoobraznie (Mammalia, Rodentia) iz pozdnemiocenovogo mestonakhozheniya Palievo na yuge Ukraine]. – *Vestnik zoologii*, **46** (2): 137-147.
- STORCH, G. (1974): Quartäre Fledermaus-Faunen von der Insel Malta. – *Senckenbergiana lethaea*, **55**: 407-434.
- STUBBE, M., ANSORGE, H., PIECHOCKI, R., LANCE, U., SAMJAA, R. & BARTU, D. (1989): Weitere Beiträge zur Ernährung des Uhus *Bubo bubo* (L., 1758) in der Erntmongolei. – *Erforschung der Biologischen Ressourcen der MVR, Halle Saale*, **6**: 25-32.
- SYABRAJ, S., UTESCHER, T., MOLCHANOFF, S. & BRUCH, A.A. (2007): Vegetation and paleoclimate in the miocene of Ukraine. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **253**: 153-168.
- TATA, C. & KOTSAKIS, T. (2005): Italian fossil chiropteran assemblages: a preliminary report. – *Geo.Alp*, **2**: 53-60.
- TITOV, V.V., TESAKOV, A.S., DANILOV, I.G., DANUKALOVA, G.A., MASHCHENKO, E.N., PANTELEEV, A.V., SOTNIKOVA, M.V. & SYCHEVSKAYA, E.K. (2006): The First Representative Vertebrate Fauna from the Late Miocene of Southern European Russia. – *Doklady Biological Sciences*, **411**: 508-509.
- TOPACHEVSKII, V.A., NESIN, V.A., CHEPALYGA, A.L. & TOPACHEVSKII, I.V. (2000): Biostratigraphy of small mammal assemblages of Maeotian and Upper Sarmatian age in Novoelizavetovka section [Biostratigraficheskoe raspredelenie mestonakhozhenii ostatkov mlekopitayushchikh (Mammalia) v meotise i verkhnm sarmate novoelizavetovskogo razreza] – *Dopovidi Natsionalnoy Akademii Nauk Ukraini*, **11**: 213-217 (in Russian, with English summary).
- TOPAL, G. (1985): Bats from the lowermost Pleistocene Locality 15 at Beremend, Hungary (*Mammalia*, *Chiroptera*). – *Fragmenta Mineralogica et Palaeontologica*, **12**: 51-57.
- UTESCHER, T., MOSBRUGGER, V. & ASHRAF, A.R. (2000): Terrestrial climate evolution in Northwest Germany over the last 25 million years. – *Palaios*, **15**: 430-449.
- VIERHAUS, H. (2004): *Pipistrellus nathusii* (KEYSERLING und BLASIUS 1839) *Rauhautfledermaus*. – In: KRAPP, F. (Ed.): *Handbuch der Säugetiere Europas*. Band 4: *Fledertiere*. Teil II: *Chiroptera* II. *Vespertilionidae* 2, *Molossidae*, *Nycteridae*, 825-873; Wiebelsheim (Aula-Verlag).
- WOŁOSZYN, B.W. (1987): Pliocene and Pleistocene bats of Poland. – *Acta Palaeontologica Polonica*, **32**: 207-325.
- ZACHOS, J.C., PEGANI, M., STONE, L., THOMAS, E. & BILLUPS, K. (2001): Trends, rhythms, and aberrations in global climates 65 Ma to present. – *Science*, **292**: 293-686.
- ZAHN, A., MESCHEDÉ, A. & RUDOLPH, B.U. (2004): *Abend-*

segler (*Nyctalus noctula*). – In: Bayerisches Landesamt für Umweltschutz (Ed.): Fledermäuse in Bayern, 232-252; Stuttgart (Ulmer-Verlag).

ZIEGLER, R. (2003): Bats (Chiroptera, Mammalia) from Middle Miocene karstic fissure fillings of Petersbuch near Eichstätt, Southern Franconian Alb (Bavaria). – Geobios, **36**: 447-490.

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