PALÆO VERTEBRATA

New Late Miocene plecotine bats (Chiroptera, Vespertilionidae: Plecotini) from Gritsev, Ukraine

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Abstract: The Late Miocene site of Gritsev (MN 9, Ukraine) has yielded a very rich bat fauna, the remains of which are well preserved. Compared to other Neogene bat assemblages of Europe, the Gritsev bat community is unique in preserving plecotine bats, which are rare from Neogene sites. Some peculiar and new bat species, including a large plecotin *Otonycteris*, already were described from the Gritsev mammal site. Here we report new records of small plecotin bats from Gritsev, including a new taxon, *Barbastella maxima* nov. sp. This is the earliest reliable fossil record of this genus and it differs from more recent species of *Barbastella* in being considerably larger. The evolutionary patterns in the odontology within the tribe Plecotini, supported by biostratigraphical distribution of fossil records of *Plecotus* are discussed. The morphological peculiarities of the new fossils of plecotine bats from Gritsev are discussed in connection with its possible taxonomical affinity.

Keywords: Mammalia, bats, late Neogene, *Plecotus*, *Barbastella*

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INTRODUCTION

The Late Miocene taphocoenosis from the Gritsev site of Ukraine is well known for different vertebrate remains (Topachevsky *et al.,* 1996; Nesin & Kowalski, 1997; Rzebik Kowalska & Topachevsky, 1997; Morlo & Semenov, 2004). The Gritsev fauna is referred to the transitional period between the Astaracian and Vallesian; it belongs to the Zone MN 9 and corresponds to the Bessarabian regional stage of the middle Sarmatian (Fig. 1; Korotkevich, 1988; Topachevsky *et al.,* 1996; Vangengeim *et al.,* 2006). Although remains of reptiles and amphibians predominate in the Gritsev taphocoenosis, the mammalian fauna is also quite abundant. The faunal dominance of the insectivores over rodents and lagomorphs represents a special character of the Gritsev fauna (Nesin & Nadachowski, 2001). Among many other mammals the Gritsev site yielded a rich bat fauna, the specimens of which are well preserved. The latter circumstance led to a description of several new and peculiar bat species, namely: *Eptenonnus gritsevensis* Rosina & Semenov, 2012, *Myotis korotkevichae* Rosina & Semenov, 2012, and *Otonycteris rummeli* Rosina, 2015 (Rosina & Semenov, 2012; Rosina, 2015).

Currently, members of tribe Plecotini occur widely throughout the temperate and subtropical zones of the Northern Hemisphere, and include at least five and probably six living genera: *Barbastella, Plecotus* and probably, *Otonycteris* in Palearctic and *Corynorhinus, Idionycteris* and *Euderma* in Nearctic (Simmons, 2005; Benda & Gvoždík, 2010; Roehrs *et al.*, 2010).

The first and most ancient bat associated with the plecotine clade is the Early Oligocene species *Quinetia misonnei* (Quinet, 1965) from Hoogbutsel (MP 21), Belgium (Quinet, 1965). This fossil has several very peculiar morphological features, retaining the *Myotis*-like dentition and nyctalodonty like the recent genus *Barbastella*. Nevertheless, it cannot be assigned to the genus *Barbastella*, but could possibly represent its ancestral grade (Horáček, 2001). The earliest fossil record of the genus *Plecotus* is represented by *P. schoepfelii* Rosina & Rummel, 2012, known from the Early Miocene site Petersbuch 62 (MN 3) in Germany (Rosina & Rummel, 2012). Until now, only one extinct *Barbastella* species, *B. schadleri* Wettstein-Westersheim, 1923, was described from the Late Pleistocene site Mixnitz in Austria (Wettstein-Westersheim, 1923). However, a single dentary fragment (specimen 7343C1) with m1, putatively allocated to aff. *Barbastella*, was described from the Miocene site Dolnice 1 (MN5) in Hungary (Horáček, 2001). Taking into account the estimated time of basal divergence within the tribe and the genus *Plecotus* in particular (Datzmann *et al.*, 2012; Amador *et al.*, 2016), the presence of variable plecotines in Miocene deposits is considered to be highly probable. In this paper, we discuss the morphological peculiarities of fossil plecotine bats from Gritsev in connection with their possible taxonomical affinity, and describe the earliest reliable fossil record of the genus *Barbastella*.

MATERIAL AND METHODS

The fossil material of this study is represented mostly by dentary fragments and isolated teeth. Occasionally there are almost completed lower jaws and humeri fragments. 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. The tribe taxonomy here follows Simmons (2005).

The designation of the measurements and their definitions for:
p4 are the maximal length (L) × width (W) of the crown, in the case of P2, p2 and p3 – the measurements of the alveoli of the crowns;

m1,2,3 are length (L) × width of the molar trigonid (Wtr) × width of the molar talonid (Wtl);

M1,2,3 are length (L) × width (W) of the crowns;

Lc-m3, Lc-m1, Lm1-3, Lm1-2, Lm2-3 – accordingly the lengths of the corresponding tooth-row;

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;

Worb – 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 width of an infraorbital foramen;

Bd – the maximal width of a distal epiphysis of the humerus.

Due to damage, only very limited number of measurements were taken from suitable amount of specimens, and vice versa only very few specimens were measured for significant numbers of measurements in statistical analyses. No more than ten specimens of the Gritsev *Plecotus* were considered simultaneously in analysis. For this reason, only the Principal Component analysis was performed, using PCA and Classification modules of STATISTICA for Windows version 7.0 (StatSoft, Inc., 2004), to compare Gritsev specimens with morphologically similar putative *Plecotus* species from other fossil-bearing sites. The Gritsev specimens were compared with *P. schoepfelii* from Petersbuch 28, 62 (one to three specimens per analysis), *P. rabederi* Wołoszyn, 1987 (up to five specimens), individual specimens of *P. crassidens* Kormos, 1930 and *P. atavus* Topál, 1987, and with type specimens of *P. atavus, P. crassidens* and *P. schoepfelii*. To optimize the number and composition of specimens being analyzed, from eleven to four measurements were used in different variants of PC analyses.

The abbreviations of the usual biometric parameters in the tables are: n = number of specimens, R = range of measurements, i.e. the difference between maximum and minimum values, m = arithmetic mean, S = standard deviation. The following abbreviations and abridgements were used in a text: mxl – maxillary bone; mnd – mandibular bone; sin. – sinistral (from lat. “sinistrum”); dex. – dextral (from lat. “dextrum”); al. – alveolus; sup. – superior; inf. – inferior.

All the fossil bat material from the Gritsev locality (the collection series Ch/G) is preserved in the Palaeontological Museum of the National Museum of Natural History, National Academy of Sciences of Ukraine (NNPM). The osteological collections of recent and fossil Chiroptera, deposed in Zoological Museum of Moscow University (ZMMU, Moscow, Russia), and in the Natural Museum of city of Augsburg (NMA, Germany) have been used for comparisons of the investigated specimens with the recent and fossil bats. The photographs have been taken by a scanning electron microscope of the Borissiak Paleontological Institute Russian Academy of Science.

SYSTEMATIC PALAEONTOLOGY

Order Chiroptera Blumenbach, 1779
Suborder Microchiroptera Dobson, 1875
Family Vespertilionidae Gray, 1821
Subfamily Vespertilioninae s. str.
Tribe Plecotini Gray, 1866
Genus ***Plecotus*** Geoffroy, 1818
Type species: *Vespertilio auritus* Linnaeus, 1758
Plecotus* aff. *atavus Topál, 1987
Fig. 2 B, 3 C-F, 4 A-D, 5

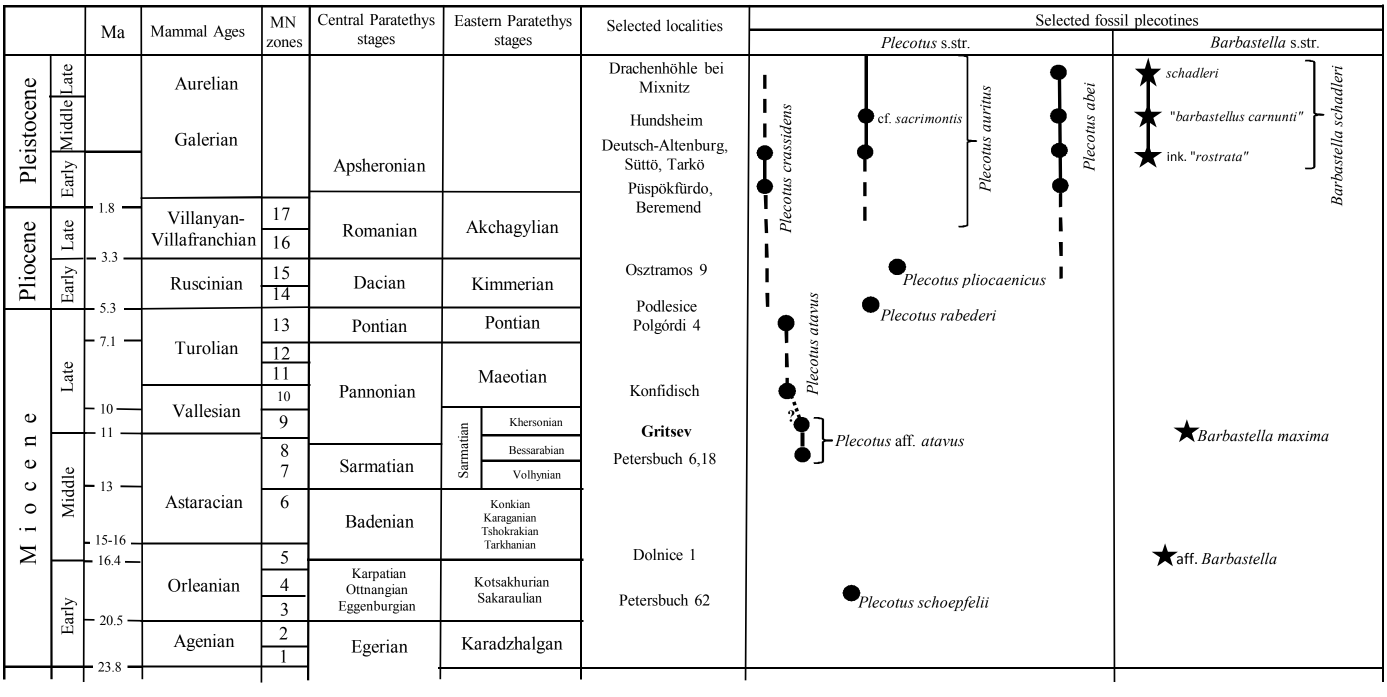

Figure 1. The chronostratigraphic position of the Gritsev site with correlation of some other Miocene-Quaternary mammal fossiliferous sites of Europe and the biochronology of the European plecotine bats. Vertebrate biostratigraphy (MN zones modified after Jones, 1999; Rögl, 1999).

Material and measurements (see Table 1**)**. Ch/G-014 right maxillary fragment with alveoli of cheek teeth; Ch/G-023, Ch/G-221-223 mnd, dex. without teeth; Ch/G-096 mnd, dex. with p4-m3; Ch/G-097, Ch/G-099 mnd, dex. with m2-3; Ch/G-098, Ch/G-109 mnd, dex. with m1-3; Ch/G-100 M2 dex.; Ch/G-103, Ch/G-112 mnd, sin. with m2; Ch/G-104, Ch/G-153 mnd, sin. with m2-3; Ch/G-105 mnd, sin. with p4-m3; Ch/G-107, Ch/G-224, Ch/G-225, Ch/G-227 mnd, sin. without teeth; Ch/G-108 mnd, dex. with p4; Ch/G-110, Ch/G-113, Ch/G-186 mnd, sin. with m1-3; Ch/G-111 mnd, dex. with m1-2; Ch/G-137 mnd, dex. with m3; Ch/G-139, Ch/G-231-232 M2 sin.; Ch/G-151 mnd, sin. with p4-m2; Ch/G-154 mnd, dex. with m2; Ch/G-175 M1 sin.; Ch/G-176, Ch/G-177, Ch/G-188 mnd, dex. with m2-3; Ch/G-179, Ch/G-184 mnd, dex. with m1; Ch/G-180 m1 sin.; Ch/G-181, Ch/G-183 m1 dex.; Ch/G-182, Ch/G-233 M3 sin.; Ch/G-226, Ch/G-228 mnd, sin. with m1-2; Ch/G-234 M3 dex.; Ch/G-253 mnd, dex. with p4-m2; Ch/G-368, Ch/G-012, Ch/G-370-371 distal epiphyses of the humerus, sin.; Ch/G-369 distal epiphysis of the humerus, dex (Bd: n = 4, 3.22 – 3.39, m = 3.29, s = 0.072).

Description. In the Gritsev fossil material there are eight isolated upper molars and one fragile portion of a right maxillary, broken on the level of the canine alveolus, with preserved cheek teeth alveoli. On the maxillary (specimen Ch/G-014), the infraorbital foramen is rounded and located above P4/M1 (Fig. 2 B). The area of the lacrimal foramen is broken but there is a long bony bridge between the anteriormost wall of the orbit and the infraorbital foramen (Worb = 0.6 mm, Table 1). The zygomatic arch originates above M2/M3 crowns (Fig. 2 B). The alveolus of P2 is oval and a bit compressed in the anteroposterior direction, but lies in line with the tooth-row (Fig. 2 B). The location of the root alveoli of P4 (Fig. 3 D) indicates that the tooth crown was not as elongated in the anteroposterior direction as in the Quaternary *Plecotus* species, but most likely had a form with a developed heel and shortened paracrista as in the Miocene *P. atavus* (Polgárdi 4; Topál, 1989 a: fig. 1, p. 79) and *P.* aff. *atavus* from Petersbuch 6 and 18 (Ziegler, 2003: figs. 5.7, p. 472). The area of the paraconule and the preprotocrista of the only preserved M1 (specimen Ch/G-175; Fig. 3 F) is damaged. The postprotocrista of the tooth does not reach the base of the metacone, and thus the trigon basin is open. The metaloph and hypocone are absent (Fig. 3 F). In the M2 (e.g., specimen Ch/G-139; Fig. 3 E) the preprotocrista is continuous with the paracingulum and the postprotocrista nearly reaches the base of the metacone and disappears here. Thus, strictly speaking, the trigon basin of M2 is also open. The paraloph, metaloph and hypocone are absent. The preserved alveoli of M3 in the maxillary fragment (specimen Ch/G-014; Fig. 3 D) suggest that the M3 was slightly reduced in length, the ratio LM3/WM3*100% being about 51.4%. The crowns of the preserved isolated M3 (e.g., specimen Ch/G-182; Fig. 3 C) is slightly reduced in length, indeed, with the ratio LM3/WM3*100% being from 50.98-55.56%. The stylocones of M3 are markedly large and have a shape of rounded knobs (Fig. 3 C). All upper molars are surrounded by a well-developed cingulum, which is thicker at the lingual side of the crowns.

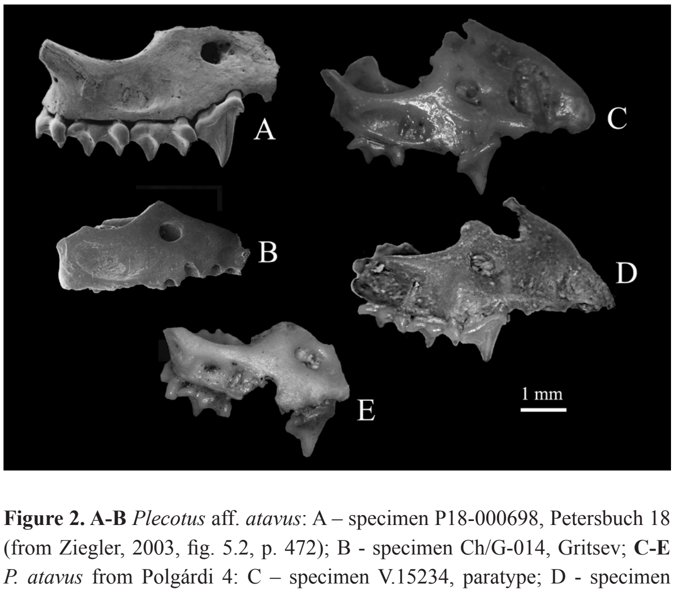

Figure 2. A-B *Plecotus* aff. *atavus*: A – specimen P18-000698, Petersbuch 18 (from Ziegler, 2003, fig. 5.2, p. 472); B - specimen Ch/G-014, Gritsev; **C-E** *P. atavus* from Polgárdi 4: C – specimen V.15234, paratype; D - specimen V.15228 (VT.138), holotype; E - specimen V.15230, paratype; lateral view.

In most specimens only the horizontal ramus is preserved. Only one specimen (Ch/G-099) has a damaged ascending ramus with a narrow masseteric fossa (Fig. 4 A). The small and rounded mental foramen is situated at the middle line of the mandible, below and between p2/3 (e.g., specimens Ch/G-098-099 and Ch/G-104; Fig. 4) or between p2 and the canine (specimen Ch/G-096; Fig. 4 D). The preserved alveoli of i1-3 in the dentary fragments (e.g., specimen Ch/G-096; Fig. 4 D) suggest that the tooth crowns stand side by side with considerable overlapping: the alveolus of i3 is labially displaced and the alveolus of i2 is lingually displaced (Fig. 4 C-D and specimen Ch/G-098; Fig. 4 C). The alveolus of the canine (e.g., specimens Ch/G-096 and Ch/G-098; Fig. 4) is rounded and not compressed. The one-rooted p2-3 have rounded alveoli located in line the tooth-row (Fig. 4). The alveolus of p3 is somewhat

Table 1. Comparison of the *Plecotus* aff. *atavus* from Gritsev with *Plecotus* species from Petersbuch 6 and 18 (own data, after Ziegler, 2003), and the nominative taxon of *P. atavus* from Polgárdi 4 (after Topál, 1989 a), sample statistics of the teeth and jaws.

Species	*Plecotus* aff. *atavus* Gritsev				*P. atavus* Polgárdi 4		*P.* aff. *atavus* Petersbuch 6, 18			
Measur.	n	R	m	S	R	m	n	R	m	S
Lc al. Wc al.	8 7	0.63 – 0.78 0.63 - 0.70	0.70 0.65	0.063 0.034	–	–	–	–	–	–
Lc-m1	1	3.35	–	–	–	–	–	–	–	–
Lc-m1 al.	1	3.30	–	–	–	–	–	–	–	–
Lc-m3	2	5.90 – 5.95	5.93	0.035	5.85 - 6.07	5.96	–	–	–	–
Lc-m3 al.	1	5.90	–	–	–	–	–	–	–	–
Lp2 al. Wp2 al.	23 22	0.34 – 0.43 0.38 - 0.50	0.37 0.46	0.024 0.034	–	–	–	–	–	–
Lp3 al. Wp3 al.	24 23	0.28 – 0.41 0.35 - 0.48	0.35 0.40	0.029 0.034	–	–	–	–	–	–
Lp4 Wp4	5 5	0.75 – 0.88 0.69 - 0.73	0.81 0.70	0.057 0.015	0.68 - 0.77 0.65 – 0.72	0.73 0.69	–	–	–	–
Lm1-3	6	3.85 – 4.10	3.95	0.123	3.66 - 3.7	3.73	–	–	–	–
Lm1-2	13	2.60 – 3.09	2.79	0.150	–	–	–	–	–	–
Lm2-3	8	2.35 – 2.91	2.56	0.160	–	–	–	–	–	–
Lm3 Wtrm3 Wtlm3	13 14 12	1.15 – 1.38 0.70 - 0.85 0.60 - 0.72	1.25 0.77 0.67	0.069 0.058 0.036	–	–	–	–	–	–
Lm2 Wtrm2 Wtlm2	22 21 21	1.30 – 1.63 0.72 - 0.91 0.78 - 1.00	1.41 0.81 0.87	0.086 0.058 0.055	1.37 0.95	–	–	–	–	–
Lm1 Wtrm1 Wtlm1	17 17 16	1.35 – 1.66 0.75 - 0.90 0.81 - 1.00	1.49 0.82 0.89	0.081 0.041 0.050	1.36 0.95		–	–	–	–
Hmdm1	25	1.35 - 1.94	1.57	0.159	1.45 - 1.68	1.55	–	–	–	–
Hmdm3	4	1.38 - 1.66	1.50	0.147	1.31 – 1.5	1.41	–	–	–	–
LP2 al. WP2 al.	1	0.50 0.55	–	–	–	–	1	0.45 0.5	–	–
LM1 WM1	1	1.38 1.66	–	–	1.4 – 1.45 1.65 – 1.77	1.43 1.7	3	1.45 - 1.5 1.8 - 1.9	1.47 1.84	0.025 0.055
LM2 WM2	4	1.31 - 1.47 1.72 - 1.88	1.40 1.80	0.069 0.065	1.29 – 1.45 1.65 - 1.79	1.36 1.74	3	1.45 1.89 - 1.95	1.45 1.91	– 0.032
LM3 WM3	3	0.81 - 0.94 1.59 - 1.70	0.88 1.66	0.063 0.058	0.81 1.68 – 1.72	– 1.7	3	0.95 - 0.97 1.85 - 1.87	0.96 1.86	0.012 0.012
LM1-M3 al.	1	3.50	–	–	–	–	–	–	–	–
LP4-M3 al.	1	4.60	–	–	–	–	–	–	–	–
Worb	1	0.60	–	–	0.5 – 0.68	0.63	3	0.77 – 1.00	0.91	0.121
Hiorb	1	0.65	–	–	–	–	–	–	–	–
Wiorb	1	0.60	–	–	–	–	–	–	–	–

smaller than that of p2 (Fig. 4). However, the alveolus of p2 could be slightly compressed (e.g., specimens Ch/G-096 and Ch/G-104; Fig. 4). The triangular p4 is shaped by a distinct cingulid and has small anterior and posterior tubercles on the lingual side of the crown (Fig. 4). Usually, the broad trigonid of m1 overlaps the distal part of p4 (e.g., specimens Ch/G-096 and Ch/G-104, Fig. 4). The length relation among the lower molars is consistently m1 ≈ m2 > m3. The m1 has a wider trigonid than that of the m2. Typical of *Plecotus*, the paralophids of the lower molars are distinctly curved, most noticeable in the m1 (Fig. 4). The m1 could be either nyctalodont (e.g., specimens Ch/G-096 and Ch/G-104; Fig. 4) or submyotodont (e.g., specimens Ch/G-098), when the additional posterior branch of the postcristid runs to the hypoconulid (Fig. 4). In most cases the m2 is myotodont (e.g., specimens Ch/G-098-099 and Ch/G-104; Fig. 4), but sometimes could be also submyotodont (e.g., specimen Ch/G-096; Fig. 4). Usually the m3 is myotodont and its talonid is slightly smaller than the trigonid, with a well-defined hypoconulid (Fig. 4).

The distal epiphysis of the humerus of *Plecotus* from Gritsev (Fig. 5) is similar to that of representatives of moden *Plecotus*, in particular to *P. auritus* (Felten *et al.*, 1973: figs. 15-16, p. 296). Both, fossils and modern species have a poorly marked and shallow olecranon fossa, and massive but very short styloid process which does not protrude beyond the trochlea (Fig. 5).

Comparisons. The dental formula, the shape of the molars and p4, the reduced talonid of m3 and the compressed lower incisors almost undoubtedly allocate this Gritsev material to the genus *Plecotus*. The long bony bridge between the infraorbital foramen and the anterior wall of the orbit is similar to that of *P. atavus* Topál, 1987 (Wołoszyn, 1987; Topál, 1989 a, b). The presumed crown shape of the P4, estimated from the location of the alveoli, is more similar to that of the Late Miocene species *P. atavus*, as well as to the modern *Corynorhinus*, and differs significantly from the crown shape of the P4 of the modern species of *Plecotus* (see Fig. 3).

Currently, there are only two Miocene species of *Plecotus* s. str. known in Europe: the Early Miocene *P. schoepfelii* from Petersbuch 62 and the Late Miocene *P. atavus* from Polgárdi 4 (MN 13, Hungary) and Kohfidisch (MN 10, Germany; Storch, 1999). One maxillary fragment of *P.* aff. *atavus* has been described from the late Middle Miocene site Petersbuch 6 (MN 7/8, Germany; Ziegler, 2003). However, there are two more maxillary fragments (specimens P18-000706 and P18-000698) from the Petersbuch 18 site, which were previously described as *Myotis reductus* (Ziegler, 2003). Both maxillary fragments possess only one small premolar (P2) and an alveolus of a larger tooth located anteriorly of the P2 (Ziegler, 2003: figs. 2-3, p. 472). The depth of the alveolus of this tooth, as well as its estimated diameter, determined from the curvature of the preserved proximal wall, indicate that it is most probably the alveolus of a canine, and not that of the second small premolar. Accordingly, the dental formula of both specimens includes only one small upper premolar that corresponds to *Plecotus,* rather than *Myotis*. Moreover, similar to the modern *Plecotus*, the upper molars of both fossil specimens P18-000706 and P18-000698 show neither para- and metaloph nor any trace of hypocone. However, the postprotocrista in upper molars of both fossil specimens from Petersbuch reaches the base of the metacone, so that the trigon basin is closed. The shape of the P4 crowns in these specimens is more similar to that of the Late Miocene *P. atavus* (Fig. 3) and to *P.* aff. *atavus* from Petersbuch 6 (compared with Ziegler, 2003: fig. 7 and figs. 2-3, p. 472). The moderate but obvious reduction of the M3 in both specimens from Petersbuch 18 additionally supports their assignment to *Plecotus*. Both specimens P18-000706 and P18-000698 correspond well in size to the specimen of *P.* aff. *atavus* (P6-01044) from Petersbuch 6 (Table 1). Morphologically *Plecotus* from Gritsev is similar to *Plecotus* specimens from Petersbuch 6 and 18 but a little bit smaller (Figs. 2-3, Table 1) and differs in having an opened trigon basin in upper molars (Fig. 3 E, F; Ziegler, 2003: fig. 5 (2, 7), p. 472). In addition, the M3 of *P.* aff. *atavus* from Petersbuch is somewhat wider (LM3/WM3*100% = 51.87; Ziegler, 2003: fig. 5 (7), p. 472) than the M3 of *Plecotus* from Gritsev.

There is a visible but incomplete morphological resemblance between *Plecotus* from Gritsev and the nominative species of *P. atavus* from Polgárdi 4 (Figs. 2-3; Topál, 1989 b: figs. 7-8, plate. 1, p. 52). They are similar in the shape of the upper molars and the position of the infraorbital foramen, and are close in size (Table 1).

In comparison with other species of *Plecotus,* both the Miocene *P.* aff. *atavus* from Gritsev and *P. atavus* from Polgárdi 4 have a less reduced p3, which is situated in the tooth-row (Topál, 1989 a: figs. 2-3, p. 79; Topál, 1989 b: figs. 1-2, plate 2, p. 52). The size of the mandible of these two species is close

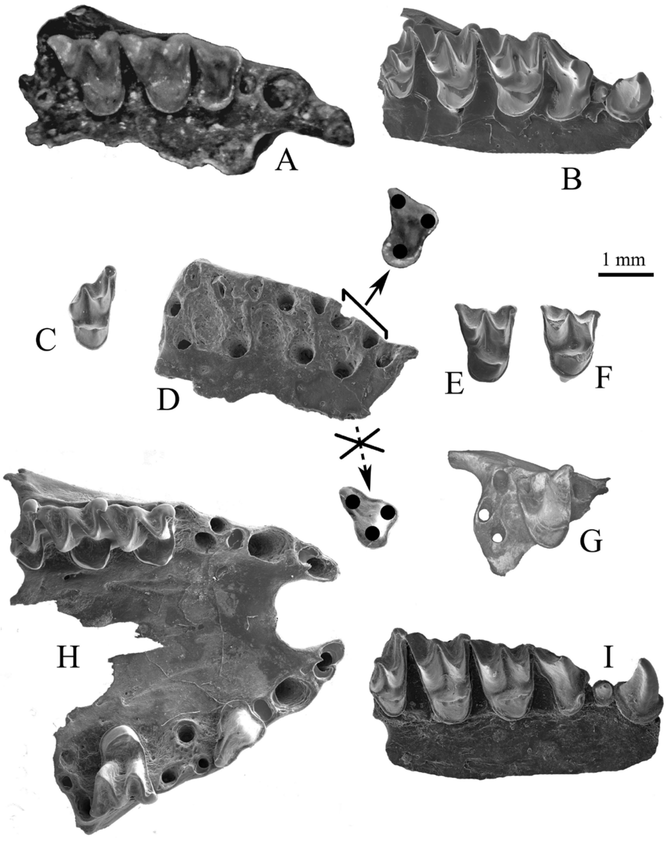

Figure 3. Upper jaws and upper dentition of modern and fossil plecotine bats used for illustrating the presumed crown shape of the P4 of *Plecotus* aff. *atavus* from Gritsev, estimated from the location of the alveoli. **A** – *P. atavus,* V.15228 (VT.138), holotype, Polgárdi 4; **B** - *Corynorhinus townsendii,* Cooper, 1837, ZMMU S-105677, Recent, USA; **C-F** *P.* aff. *atavus* from Gritsev: C - specimen Ch/G-182, isolated M3; D - specimen Ch/G-014, right maxillary fragment with alveoli of cheek teeth; E - specimen Ch/G-139, isolated M2; F - specimen Ch/G-175, isolated M1; **G** – *P. schoepfelii*, P62/0114, paratype, Petersbuch 62; **H** – *P. ognevi* Kishida, 1927, specimen H81-(1-2), Holocene, Altai, Russia; **I** – *P. auritus* ZMMU S-174773, Recent; ventral view.

but *Plecotus* from Gritsev has a somewhat longer p4 (Table 1). In *P. atavus* from Polgárdi 4, the foramen mentale is located between the canine and the alveolus of p2 (Topál, 1989 a: figs. 2-3, p. 79; Topál, 1989 b: fig. 2, plate 2, p. 52), whereas only one Gritsev specimen of *P.* aff. *atavus* (Ch/G-096) has such a position of the foramen mentale. In most cases the foramen mentale of *Plecotus* from Gritsev is between p2/3 (Fig. 4).

The preserved alveoli of lower small premolars (e.g., specimen Ch/G-096, Ch/G-099; Fig. 4) suggest that the p3 of the Late Miocene *Plecotus* from Gritsev was only slightly smaller than the p2; both are situated in the tooth-row. In contrast, the Early Miocene *P. schoepfelii* has a greatly reduced p3 (less than half the size of the p2), which is displaced lingually (Rosina & Rummel, 2012: fig. 5 I, J, p. 471). However, in *Plecotus* from Gritsev the posterior part of the p4 crown is under the anterior part of the m1 crown that caused a considerable shortering of the premolar-row (e.g., specimen Ch/G-096, Ch/G-104; Fig. 4). Also, the *Plecotus* from Gritsev differs from *P. schoepfelii* in having a less reduced talonid of the m3 (Fig. 4; Rosina & Rummel, 2012: fig. 5 I, p. 471).

All three molars of *P. schoepfelii* have a submyotodont crown structure (Rosina & Rummel, 2012: fig. 5 I, J, p. 471). In contrast, the m1 in *Plecotus* from Gritsev is usually nyctalodont (e.g., specimen Ch/G-096, Ch/G-104; Fig. 4), but sometimes it could be submyotodont (e.g., specimen Ch/G-098; Fig. 4); the m2 is usually myotodont (e.g., specimens Ch/G-104, Ch/G-098, and Ch/G-099; Fig. 4) and only rarely is it submyotodont (e.g., specimen Ch/G-096; Fig. 4); the m3 usually has a myotodont crown structure (e.g., specimens Ch/G-104, Ch/G-098, Ch/G-099, and Ch/G-096; Fig. 4).

The lower molars of *P. rabederi* from the Early Pliocene site of Podlesice near Kroczyce (MN 13/14, Poland; Kowalski, 1956; Wołoszyn, 1987) also have a submyotodont crown structure. Similar to *P. rabederi* (Wołoszyn, 1987: fig. 4., plate 12, p. 327), *Plecotus* from Gritsev has a quite large p3, which is not displaced lingually from the tooth-row, and a talonid of the m3, which is only slightly narrower than the trigonid (Fig. 4). However, the *Plecotus* from Gritsev differs from *P. rabederi* in having a shortened lower incisor row: the alveolus of i3 is labially displaced and that of i2 is lingually displaced (specimens Ch/G-096, Ch/G-098; Fig. 4). In contrast, the alveoli of *P. rabederi* suggest that the i1-3 were only slightly different in size and stood in more or less a straight row (Wołoszyn, 1987: fig. 4., plate 12, p. 327).

There are some additional Pliocene and Pleistocene *Plecotus* species: *P. crassidens* (MN17/MQ 1, Püspökfürdó, Romania; Kormos, 1930; Beremend 17, Hungary; Topál, 1989 b), *P. abeli* Wettstein, 1923 (MN17/MQ 1, Beremend 16, 17, Hungary; Topál, 1989 b) and *P. pliocaenicus* Topál, 1988 (MN 15b, Osztramos, Loc. 9, Hungary; Topál, 1989 b), which all differ significantly from the *Plecotus* from Gritsev.

Both *P. crassidens* from Beremend 17 and *Plecotus* from Gritsev have a quite long bony bridge between the infraorbital foramen and the anterior wall of the orbit (Worb = 0.6; Fig. 2; Topál, 1989 b: fig. 6, plate 1, p. 53). However, *Plecotus* from Gritsev differs from *P. crassidens* in being larger (Kowalski, 1956: p. 360, compare with Table 1), in having a less reduced p3, which is not displaced lingually (Fig. 4; compared with Topál, 1989 b: figs. 3-4, plate 2, p. 52). Moreover, *Plecotus* from Gritsev and *P. crassidens* differ in their mandibule proportions, e.g., *P. crassidens* has a shorter anterior part of the mandible

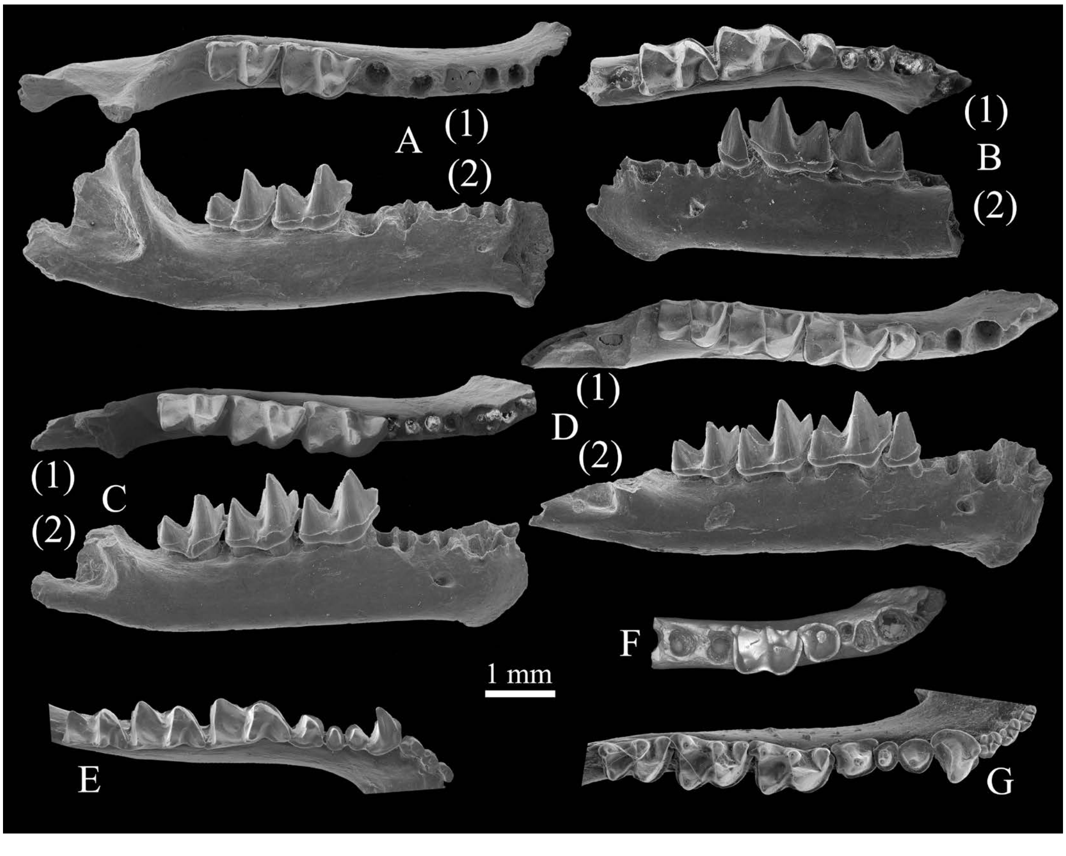

Figure 4. A-D *Plecotus* aff. *atavus* from Gritsev: A - specimen Ch/G-099; B – specimen Ch/G-104; C - specimen Ch/G-098; D - specimen Ch/G-096; **E** - *Corynorhinus townsendii*, ZMMU S-105677, Recent, USA; **F** - *P. schoepfelii*, P28/0478, Petersbuch 28; G - *P. auritus* ZMMU S-174773, Recent; (1) ventral view, (2) lateral view.

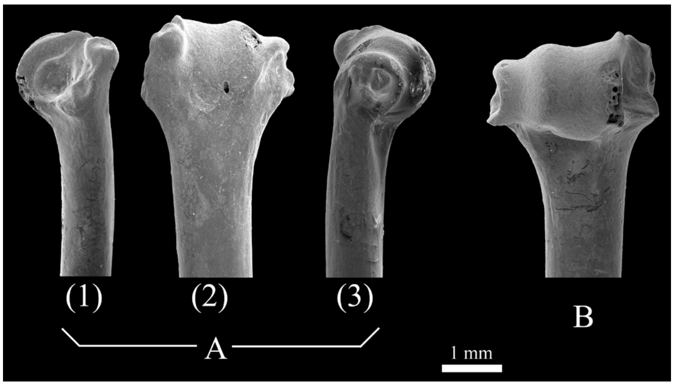

Figure 5. The distal epiphyses of the humerus *Plecotus* aff. *atavus* from Gritsev: **A** - specimen Ch/G-368, (1) medial view, (2) posterior view, (3) lateral view; **B** - specimen Ch/G-371, anterior view.

Table 2. The factor loadings and eigenvalues for four variants of the Principal Component analysis (see "Material and methods" for the measurement explanations). A-D correspond to the different analyses performed, and represented on the Figure 6. The significant factor loadings (≥ 0.8) are typed in bold.

	A			B			C			D	
Characters	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2
LP2 al.	0.551	-0.415	-0.552	–	–	–	–	–	–	–	–
LP3 al.	-0.563	-0.683	-0.402	–	–	–	–	–	–	–	–
LM3	-0.579	0.442	**-0.833**	-0.774	-0.049	-0.550	–	–	–	-0.780	-0.526
LM2	**-0.923**	-0.059	-0.148	**-0.882**	-0.009	0.121	**-0.954**	-0.020	0.194	**-0.912**	0.346
LM1	–	–	–	–	–	–	**-0.819**	0.214	0.523	-0.769	0.610
Wtlm1	–	–	–	–	–	–	**-0.916**	0.127	-0.253	–	–
Wtrm2	**-0.841**	-0.157	0.217	-0.759	0.163	0.567	–	–	–	–	–
Wtlm2	**-0.977**	-0.083	0.003	**-0.922**	0.046	0.218	**-0.847**	-0.182	-0.475	–	–
Wtrm3	**-0.819**	0.511	0.015	**-0.894**	-0.084	-0.105	–	–	–	–	–
Wtlm3	-0.685	0.540	0.186	-0.788	-0.351	-0.207	–	–	–	-0.739	-0.507
WP3 al.	-0.359	-0.676	-0.305	–	–	–	–	–	–	–	–
WP2 al.	-0.594	-0.710	0.573	–	–	–	–	–	–	–	–
Hmdm1	-0.190	0.225	-0.076	-0.249	**0.930**	-0.226	-0.121	**-0.975**	0.167	–	–
Eigenvalue	5.128	2.433	1.691	4.284	1.026	0.791	3.152	1.047	0.628	2.579	1.025
% of total variance	46.617	22.123	15.376	61.204	14.655	11.301	63.036	20.932	12.565	64.470	25.632

(Lc-m3 is less but Lm1-3 is equal), and a much shorter p4, but a wider p2 (Table 1; compared with Kowalski, 1956: p. 360).

Both *Plecotus abeli* from Beremend 16, 17 and *P. pliocaenicus* from Osztramos Loc. 9, clearly differ from the *Plecotus* from Gritsev in having a narrower bony bridge between the infraorbital foramen and the anterior wall of the orbit (0.12-0.28 mm in *P. abeli* and 0.16-0.36 mm in *P. pliocaenicus* according to Topál, 1989 b: table 3, p. 45, character AB). Furthermore, *Plecotus* from Gritsev and *P. abeli* differ in their mandibule proportions, e.g., *Plecotus* from Gritsev has a shorter lower dentition (Lc-m3), a much smaller p2 length and width, but a longer p4 (see Topál, 1989 b: table 4, p. 47). *Plecotus pliocaenicus* differs from the Gritsev *Plecotus* in having a shorter maxillary dentition (LM1-3<; Topál, 1989 b: table 5, p. 48) and a distinctly reduced M3 (Topál, 1989 b: fig. 11, plate 2, p. 52). *Plecotus pliocaenicus* also differs in showing a wider lower canine and m1-3 crowns and a much larger p2 and p3; moreover, its p3 is displaced lingually (Topál, 1989 a: fig. 8, p. 85; Topál, 1989 b: table 6, p. 49, fig. 9, plate 2, p. 52).

Statistical approach. As previously mentioned, the small number of well-preserved fragments and the incompleteness of the material as the whole gave no possibility of analyzing large samples or including all the available samples in a single analysis. It is noteworthy, however, that analyzing data seems to be informative: the cumulative variance covered by the first two Principal Components (Table 2) varies from ca. 54 to 71%, usually exceeding 60%. The first Factor (PC I) in all cases highly correlates with the length of M2, in some cases - also with the width of M2-3 and/or with the length of M1. The second Factor (PC II) correlates with the size of the P3 alveoli (in case of large set of measurements) or with the height of mandible. The third Factor (PC III), in case of largest measurement set, highly correlates with the length on M1, and have no significantly high correlations in other cases. Exact factor loadings are represented on Table 2.

A comparison of *Plecotus* from Gritsev with the specimens of *P. schoepfelii* from Petersbuch 62 and 28 has shown only a slight overlap between these two samples (Fig. 6 A-B). Unfortunately, no more than three Petersbuch specimens (besides the *P. schoepfelii* holotype) have enough measurements for comparison. Therefore, the results of the analyses cannot be considered as definitive. The type specimen of the *P. schoepfelii* (specimen NMA P62/0117) is almost always plotted apart from the Gritsev sample, independently from the number of analyzed variables (Fig. 6 A-D). This can be considered as an argument in favor of the assumption that the Gritsev specimens do not represent *P. schoepfelii*.

Using only a reduced set of five measurements, we were able to compare the Gritsev sample with samples of three Neogene species of *Plecotus*. In the space of the first two Factors, the type of *P. schoepfelii* plots far apart from the Gritsev cluster, while the type specimens of *P. crassidens* and *P. atavus* seemingly demonstrate similarities with it. However, they also plot far apart from this cluster using the third Factor (Fig. 6 C). Only a much reduced number of variables let us compare Gritsev specimens with *P. rabederi*. Two samples show only a very slight overlap (Fig. 6 D), suggesting that they are most probably not identical. In summary, we may conclude that according to the PC analyses of the skull and dental features, *Plecotus* from Gritsev may be considered similar to some material from Petersbuch 62 or 28, but cannot be definitely correlated to any of the other named European fossil species of this genus. Due to the low reliability, these results do not provide ultimate arguments for a taxonomic conclusion. However, at least the results of these analyses do not show a significant similarity of the Gritsev specimens to any named taxon and thus do not contradict the taxonomic isolation of *Plecotus* from Gritsev.

Given the statistical results, the biostratigraphic distribution of the analysed fossils and the general but not definitive, morphological similarities of the Gritsev specimens with *P. atavus* and *P.* aff. *atavus* from Petersbuch 6 and 18 (see above), we assign the Gritsev *Plecotus* to *P.* aff. *atavus*.

Barbastella Gray, 1821

Fig. 7

Type species. *Vespertilio barbastellus* Schreber, 1774.

Included species. *B. barbastellus* (Schreber, 1774), *B. leucomelas* (Cretzschmar, 1830), *B. caspica* Satunin, 1908, *B. darjelingensis* (Hodgson, 1855), *B. beijingensis* (Zhang, Han, Jones, Lin, Zhang, Zhu, Huang & Zhang, 2007), *B. schadleri* Wettstein, 1923.

Range and distribution. The genus has a modern distribution ranging from the Canary Islands and westernmost Europe to Japan, Taiwan and Northern Indochina (Kruskop, 2015: fig. 1, p. 51).

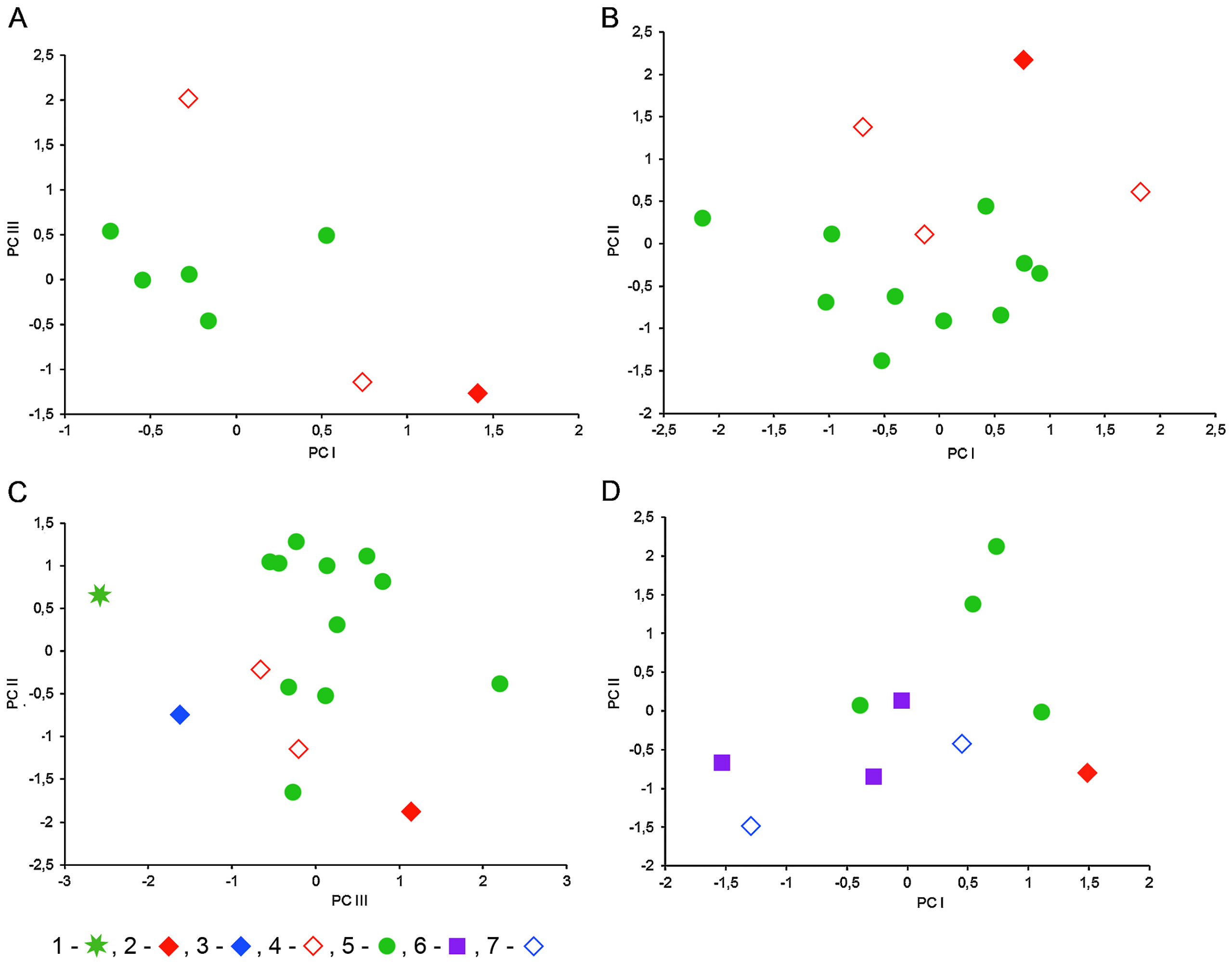

Figure 6. The bivariate scatterplots for the factors calculated in the Principal Component analyses of the dental measurements of selected fossil *Plecotus*. **A** – the first and third factors, calculated for 11 variables, comparing the Gritsev sample (*P.* aff. *atavus*) with *P. schoepfelii*; **B** – the first and second factors, calculated for seven variables, comparing the Gritsev sample with *P. schoepfelii*; **C** – the second and third factors, calculated for five variables, comparing the Gritsev sample with *P. schoepfelii*, *P. atavus* and *P. crassidens*; **D** – the first and second factors, calculated for four variables, comparing the Gritsev sample with *P. schoepfelii*, *P. crassidens* and *P. rabederi*. Selected fossil *Plecotus* species*:* 1 - *P. atavus,* V.15228 (VT.138), holotype, Polgárdi 4; 2 - *P. schoepfelii*, P62/0117, holotype, Petersbuch 62; 3 - *P. crassidens*, No. 4727, holotype, Püspökfürdó; 4 - *P. schoepfelii,* Petersbuch 28; 5 - *P.* aff. *atavus*, Gritsev; 6 - *P. rabederi,* Podlesice; 7 - *P. crassidens,* Beremend 17. See Table 2 for the factor loadings; see "Materials and methods" for the measurements used.

Diagnosis. These are small to medium sized vespertilionid bats, which are unmistakable among European chiropterans due to their short, broad ears that face forward and join across the forehead (Rydell & Bogdanowicz, 1997). The skull is lightly built (Rydell & Bogdanowicz, 1997: fig. 2, p. 2) and similar to that of *Plecotus*, with slender teeth. Facial part of the skull is proportionally short, and the brain case is usually somewhat inflated and rounded, with poorly developed crests. Zygomatic arches are delicate and the zygomatic width does not exceed the width across mastoids. The dental formula is i 2/3 c 1/1 pm 2/2 m 3/3, total 34. Upper small premolars (P2) are highly reduced and displaced from the tooth-row lingually; in some cases, P2 can be absent on one or both sides. The upper molars of modern species have neither paraconule nor para- or metaloph. The hypocone is absent. The postprotocrista in M1-2 is very weak on the distal part of the crown but, it joins the postcingulum, and thus the trigon basin is closed. M3 is slightly reduced, with developed metacone and mesostyle. Lower molars are nyctalodont.

Barbastella maxima nov. sp.

lsid:zoobank.org:act:EFCA1FAD-3E4C-4149-9E6A-924360D1AE6E

Holotype. Ch/G-001, right maxillary fragment with M1-3, holotype (Fig. 7 A)

Hypodigm. only the holotype.

Measurements of the holotype. M1: 1.80 × 1.90; M2: 1.50 ×2.00; M3 ≈ 0.90 × 1.88; LM1-3 ≈ 3.88.

Type locality. Gritsev, near the village of Hrytsiv, Shepetivskii district of the Khmelnitskii region, Ukraine.

Age. MN 9, the Bessarabian regional stage of the Late Miocene.

Etymology. After Latin *Maximus* for "greatest" or "largest".

Differential diagnosis. Differs from the recent species of *Barbastella* in being considerably larger and in having its M3 more compressed anteroposteriorlly; M2 is more compressed anteroposteriorlly; and M1 with the distinctly closed trigon basin. Differs from the Pleistocene *B. schadleri* Wettstein, 1923 in its larger size.

Description. The upper molars are without paraconule but with small paraloph, their preprotocrista is continuous with the paracingulum. In M1-2 the postprotocrista reaches the postcingulum and there is a distinct metaloph that links the base of the metacone to the postprotocrista. The hypocone is absent. The trigon basin of M1-2 is closed. The molars are surrounded by a well-developed cingulum, which is thicker at the lingual side of the crowns. The stylocones of the upper molars are large and have a rounded knob shape. Despite the fact that the metacone of the M3 is broken, it was likely reduced in length, the ratio LM3/WM3*100% being above 47.87%.

Comparison. There is no doubt in the allocation of the mentioned Gritsev specimen to the family Vespertilionidae because of the molar shape with a well-developed cingulum, the presence of lophs and the lack of talon and hypocone. In contrast to species of *Myotis*, which also have upper molars with para- and metalophs, the lophs of the Gritsev fossil are weak, the paraconule and hypocone are absent, and the M3 is appreciably reduced (Fig. 7 A). Morphologically the specimen from Gritsev is most similar to *Barbastella.* Some morphological similarities of the M2 of the examined fossils with that of *Plecotus* also justify its allocation to the tribe Plecotini (see below). Horáček (2001) recorded the presence of a single dentary fragment (specimen 7343C1) from the Middle Miocene site Dolnice 1 (MN 5, Hungary) that was preliminarily identified as aff. *Barbastella* (Horáček, 2001: p. 127). This specimen is the only Miocene fossil tentatively associated with *Barbastella*. Unfortunately, direct comparison of our fossil with this specimen was not possible.

The genus *Barbastella* currently comprises at least five modern species: *B. barbastellus*, *B. leucomelas*, *B. caspica*, *B. darjelingensis* and *B. beijingensis*, which show morphological similarities but considerable genetic divergence over their range (Zhang *et al.*, 2007; Benda *et al.*, 2008; Kruskop, 2015). In fact, all the barbastelles are quite similar in skull morphology and dental pattern but differ mostly in body size, pelage and skin coloration, shape of the ear pinna and baculum, and sometimes in echolocation call parameters (Zhang *et al.*, 2007; Benda *et al.*, 2008). Although all modern species differ in skull size, this difference is not very important and the limits of size variation often overlap (Zhang *et al.*, 2007; Kruskop, 2015, see also Table 2).

The largest modern representative of the genus is most probably *B. beijingensis* from China (Zhang *et al.*, 2007); the next smaller is *B. caspica* from Transcaucasia and Central Asia (Table 3; Kruskop, 2015). We did not have an opportunity to examine *B. beijingensis*. However, according to its morphological description and published measurements (Zhang *et al.*, 2007: table 4, p. 1401), it is markedly smaller in size than the Miocene *Barbastella* from Gritsev. Both the middle-Asian *B. caspica* and European *B. barbastellus* are much smaller than the Gritsev specimen (Fig. 8 A-C; Table 2). Moreover, in contrast to the living species, the M3 and M2 of the fossil specimen are more compressed anteroposteriorly (Fig. 7).

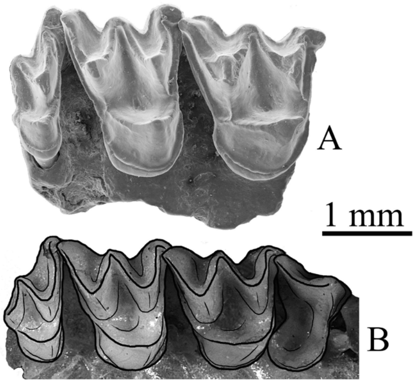

Figure 7. A - *Barbastella maxima* nov. sp., Ch/G-001, holotype, Gritsev; **B** – *B. caspica*, ZMMU S-90966, Recent, Turkmenistan; ventral view.

Up to the present time, only one extinct *Barbastella* species has been described – *B. schadleri* from the Late Pleistocene site Mixnitz (Austria; Wettstein-Westersheim, 1923). The Middle Pleistocene subspecies of *B. barbastellus carnunti* Rabeder, 1972 from Hundsheim (Austria; Rabeder, 1972) and the Early Pleistocene species *B. rostrata* Topál, 1970 from Tarkö (Hungary; Topál, 1970) actually most probably should be considered as junior synonyms of *B. schadleri* (Rabeder, 1974). Remains of *B. schadleri* are also known from the Early Pleistocene sites Deutsch-Altenburg and Süttö 7 (Topál, 1981). Morphologically, *B. schadleri* is very similar to the recent barbastelle bats (Rabeder, 1972: plate 12, figs. 40-44) and differs only in its somewhat large size (details see Rabeder, 1974: p. 176-181).

Fossil *B. barbastellus* s. str. and *B. leucomelas* s. str., which demonstrate morphology of the living species, are very common in the Pleistocene and Holocene sites of Europe, in particular in Poland, Hungary and the Czech Republic (e.g., Kowalski, 1962; Topál, 1970; Wołoszyn, 1987 etc.). Thus, the Miocene *Barbastella* from Gritsev is considerably larger in size than all currently known exant and extinct barbastelle bats, including *B. schadleri* (Table 3; Fig. 8 A-C).

species	Locality	n	LM1	WM1	LM2	WM2	LM3	WM3	LM1-3	references
Barbastella maxima nov. sp., holotype, Ch/G-001	Gritsev, Ukraine	1	1.80	1.90	1.50	2.00	≈0.90	1.88	≈3.88	new data
B. schadleri, holotype, UWPI 1947/5	Drachenhöhle von Mixntiz, Austria	1	1.31	1.51	-	-	-	-	-	Rabeder, 1972
B. schadleri	Drachenhöhle von Mixntiz, Austria	12	1.31-1.42 (1.36)	1.57-1.70 (1.65)	1.29-1.40 (1.34)	1.66-1.73 (1.69)	0.67-0.76 (0.72)	1.48-1.57 (1.55)	3.24-3.40 (3.32)	Rabeder, 1974
B. schadleri (=*B. b. carnunti*)	Hundsheim, Austria	10	1.28-1.39 (1.34)	1.51-1.63 (1.57)	1.25-1.36 (1.30)	1.60-1.76 (1.66)	0.67-0.75 (0.71)	1.48-1.60 (1.54)	3.00-3.70 (3.27)	Rabeder, 1972
B. schadleri (= *B. rostrate)*	Tarköi, Hungary	19	1.27-1.41 (1.34)	1.54-1.72 (1.63)	1.29-1.41 (1.35)	1.54-1.77 (1.69)	0.64-0.77 (0.70)	1.43-1.69 (1.52)	-	Topál, 1970
B. caspica	Central Asia	11	1.34-1.42 (1.40)	1.61-1.72 (1.65)	1.32-1.39 (1.35)	1.58-1.68 (1.62)	0.63-0.84 (0.69)	1.50-1.68 (1.57)	3.26-3.53 (3.41)	new data
B. darjelingensis, ZMMU S-164496	Nepal	1	1.37	1.44	1.32	1.47	0.58	1.47	3.26	new data
B. barbastella	Europe	26	1.13-1.26 (1.20)	1.38-1.63 (1.53)	1.08-1.25 (1.19)	1.43-1.74 (1.61)	0.51-0.69 (0.59)	1.28-1.53 (1.38)	-	Topál, 1970
B. barbastella, ZMMU S-171543	Southern Russia	1	1.26	1.50	1.21	1.47	0.63	1.47	3.11	new data

Table 3. Comparison of the *Barbastella maxima* nov. sp. from Gritsev with some recent and fossil *Barbastella* species (in mm). The numbers in brackets correspond to the averages.

DISCUSSION

Implications on systematics of the Plecotini tribe inferred with fossil evidence

The tribe Plecotini itself was established on its morphological basis (Tate, 1942); its five "core" genera have reliable similarities in external and dental morphology, followed by certain karyological traits (Fedyk & Ruprecht, 1983; Frost & Timm, 1992).

In the meantime, gene-based phylogenies on plecotine remain so far controversial and insufficient. Though Hoofer & Van Den Bussche (2003) once obtained some support for the monophyly of the five "core" plecotines, further studies (Hoofer & Van Den Bussche, 2001; Roehrs *et al.*, 2010) failed to recover similar results. Combined and independent analyses of mitochondrial and nuclear markers in the latter study leave the monophyly of the Plecotini neither supported nor rejected. For this reason, estimates for phylogenetic splits within the Plecotini, based on a "molecular clock", are also highly controversial.

There are two competing views among the authors who discussed this subject. One of them is based on the view that both *Plecotus* and *Corynorhinus* occurred in the Late Pliocene in Europe, marking the possible time for the split of these genera at about 6 Myr ago (Topál, 1989 b). This event was taken as a calibrating point by Juste *et al.* (2004), who estimated the speed of variation in the mtDNA of plecotines as 3.5% per 1 Myr. Such opinion was shared by Paggio & Perkins (2005) in connection with the evolution of *Corynorhinus*.

This point of view, however, was criticized by Spitzenberger *et al.* (2006), who proposed that such an evolutionary rate is too high (about twice as high as that was supposed for mammalian mtDNA (Talbot & Shields, 1996; Lopez *et al.*, 1997). Spitzenberger *et al.* (2006) nonetheless avoid any estimate, believing that the available data is not sufficient for an adequate assessment. However, evolutionary rates of ca. 2% per Myr were used later by Dazmann *et al.* (2012) who supposed that the basal divergence within the genus *Plecotus* (between "*auritus*" and "*austriacus*" lineages) took place in the lower Miocene, at about 20 Myr ago. If so, all the Miocene finds date back to the time when modern evolutionary lineages already existed, and therefore could not add anything substantial to our knowledge about the evolution of modern groups and the real time of their divergence.

Such a situation could really be caused by the insufficient data both from molecular and paleontological sides. Studies on Plecotini phylogeny were based on limited and not always a successful set of markers. It is known currently that the evolutionary rates of mt-genes could vary widely (Ho *et al.*, 2005; Peterson & Masel, 2009) and in certain situations could be even much higher than 3.5% (Herman *et al.*, 2014). Moreover, some of these markers lose their informative value after 12-15% of substitutions because of saturation. More reliable phylogenetic studies on higher bat taxonomic groups suggest basal divergence within the Vespertilionidae in the Late Oligocene or Lower Miocene (Teeling *et al.*, 2005; Lack *et al.*, 2010). This suggests the basal divergence within the Vespertilioninae later than the lower Miocene. Roehrs *et al.* (2010) proposed that the separation of the Plecotini tribe occurred very close to the basal vespertilionine diversification, thus we also may date it back to the lower Miocene.

In the latter case, one could state that during the first half of the Miocene, modern genera were emerging, and therefore all the Miocene records acquire special significance. The Miocene record of *Barbastella* in Gritsev more or less corresponds to the possible time of the diversification of the genus (Fig. 1; see above). In this case, *B. maxima* nov. sp. should be an important calibration point for plecotine evolution and its

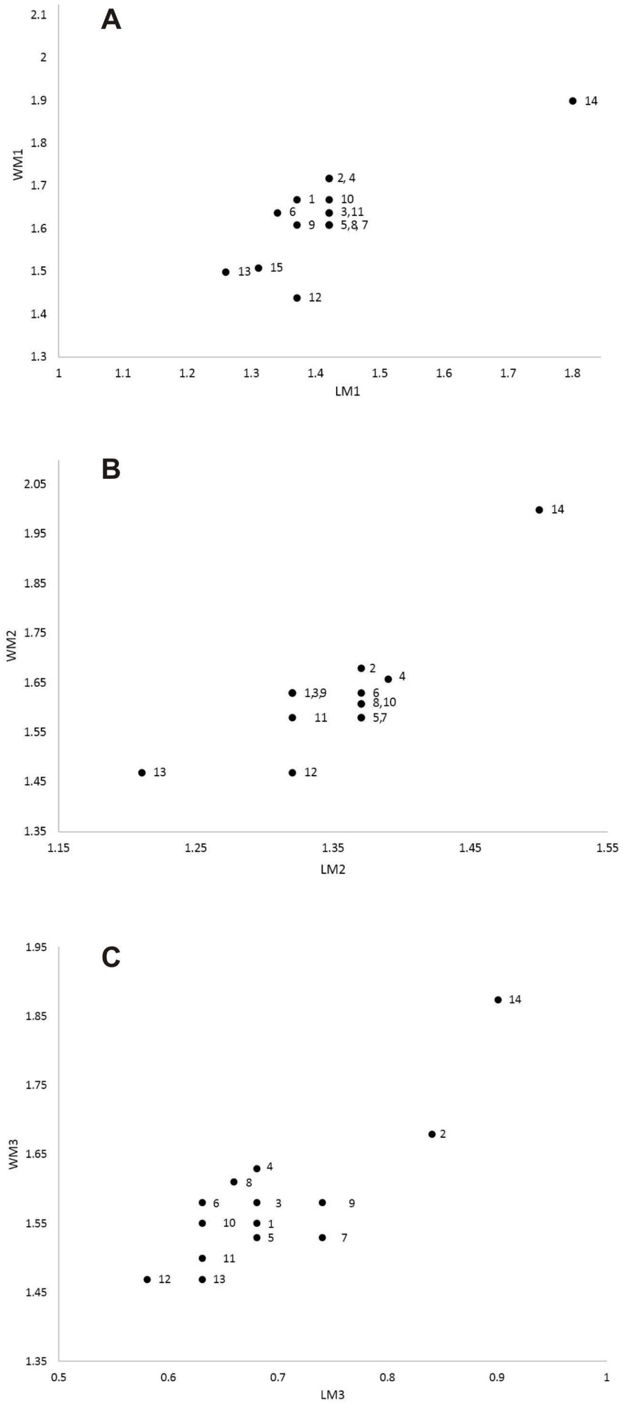

Figure 8. Scatter diagrams of the upper molars measurements of fossil and some recent *Barbastella* species: **A** – LM1 × WM1, **B** – LM2 × WM2, **C** – LM3 × WM3 for specimens: 1-11 *Barbastella caspica* from Middle Asia (Uzbekistan, Kyrgyzstan, and Turkmenistan); 12 - *B. darjelingensis* from Nepal (ZMMU S-164496); 13 - *B. barbastella* , Central Russia, S- 171543); 14 – *B. maxima* nov. sp., Ch/G-001, holotype, Late Miocene, Gritsev, (Ukraine); 15 - *B. schadleri*, UWPI 1889/28/11, holotype, Late Pleistocene site of Mixnitz (Austria, values are from Rabeder, 1972).

time of diversification. As we suggest that all the modern plecotine genera diversified at almost the same time (except for *Euderma/Idionycteris* split; Roehrs *et al.*, 2010), the presence of *Barbastella* in the Gritsev layers implies that both *Plecotus* and *Corynorhinus* already occured at that time period. Topál (1989 b) proposed that both *Plecotus* s. str. and *Corynorhinus* (interpreted by him as a subgenus) once co-occurred in Europe, and few European fossil long-eared bats were described as *Corynorhinus* (Zeigler, 2003). However, Arita *et al*. (2014), analysing patterns of the New World bat endemism, concluded that *Corynorhinus* most probably evolved in North America. This agrees with the absence of *Plecotus* in Pleistocene-Holocene deposits of North America and of *Corynorhinus* in the same-aged deposits of Eurasia. Therefore, we suggest that the most ancient *Plecotus* of Europe, including *P.* aff. *atavus* from Gritsev, just share some common features with the Recent New World genus. The presence of some peculiar features, like nyctalodont first lower molars, also corroborates that these fossil species are not *Corynorhinus*. Actually, the Miocene *Plecotus* appearance may represent some ancestral evolutionary stage of the Old World *Plecotus* species or an independent evolutionary lineage, which was later (probably in Pliocene) replaced by *Plecotus* s. str.

Clarification of this subject requires further parallel studies in two directions: more precise studies of the morphological traits of extant and extinct plecotines to determine the taxonomic delimitation, and molecular studies of the modern species with use of an expanded set of nuclear DNA markers to obtain a well-supported phylogeny and a reliable base for evolutionary split estimates.

Dental pattern of Palearctic plecotine bats: implications on the phylogeny of the tribe

Long-eared bats of the genus *Plecotus* are widespread in the Palearctic region from Ireland to Japan, including North Africa and Macaronesia (Spitzenberger *et al.*, 2006). Based on molecular and morphological analyses, five European modern species of *Plecotus* are currently recognized: *P. auritus, P. austriacus, P. kolombatovici* Dulic, 1980, *P. macrobullaris* Kuzjakin, 1965, and *P. sardus* Mucedda, Kiefer, Pidinchedda & Veith, 2002. All of these species show a broad overlap in most of the external features and are therefore difficult to identify using morphological characters alone (Juste *et al.*, 2004). Their identification is possible with certainty mostly through molecular methods (Spitzenberger *et al.*, 2006; Ashrafi *et al.*, 2010). Thus, *Plecotus* species are almost identical in dental morphology and their dental formulas differ from the most complete and generalized dentition of *Myotis* only in the absence of one upper premolar. However, the dental morphology of modern *Plecotus* is characterized by the following derived dental features: 1) a reduced i3 and a rather compressed lower incisor row, 2) a shortened p4, the anterior root of this tooth is often more reduced than the posterior root, 3) a markedly reduced talonid of m3, and 4) a reduced crown of M3. In comparison to *Myotis*, tooth crowns of *Plecotus* show higher and sharp (cutting) cristids with noticeably curved paralophids of the lower molars. Upper molars of *Plecotus* have neither para- and metaloph nor hypocone. The crown of M3 in *Plecotus* is highly compressed with a markedly reduced third commissure. Moreover, like the vast majority of *Myotis*, all modern *Plecotus* have myotodont lower molars.

Fossil records of *Plecotus* are not very rare in Europe, including records of some fossil species from the Miocene (Table 1). The earliest species *P. schoepfelii* is currently known from the Early Miocene of South Germany (Rosina & Rummel, 2012). Another fossil species *P. atavus* s.str. was recorded from different Late Miocene sites of Europe (Fig. 1; Topál, 1989 b; Storch, 1999; Ziegler, 2003; also see below for details). At least three species of *Plecotus* are known from the Pliocene and Pleistocene sites (Table 1). Holocene records of this genus sometimes are abundant in karstic sites of Europe (e.g., Postawa, 2004; Obuch, 2012; Hutterer *et al.*, 2012).

The Miocene fossils of *Plecotus* display even more advanced dental features in comparison to the modern species. Thus, the low incisor rows of *Plecotus atavus* s. str. and *P. schoepfelii* are more compressed due to a strongly reduced i3, which is displaced in a labial direction. The talonid of the m3 in the Miocene *Plecotus* is usually strongly reduced. Therefore, currently known Miocene species of *Plecotus* cannot be considered as ancestral taxa for younger genus members, and often the phylogenetic position of extinct species remains unclear. Only in some cases, the possible relationship between the Miocene forms can be assumed. Thus, a noticeable morphological similarity between the nominative form of *P. atavus* from the Pliocene locality Polgórdi 4 (MN 13, Hungary) and forms of *P.* aff. *atavus* from the Late Miocene sites Petersbuch 6 and 18 (MN 7/8, Germany) and Gritsev (MN 9, Ukraine) provides even more support to their close phylogenetic relationships (Fig. 1).

Unlike the modern and Late Quaternary species of *Plecotus*, the Miocene and some Pliocene species of *Plecotus* are characterized by not only myotodont but also submyotodont or nyctalodont lower molars. All three lower molars of *P. schoepfelii* have a submyotodont crown structure (Rosina & Rummel, 2012: fig. 5 I, J, p. 471). In contrast, in *Plecotus* from Gritsev, the m1 is usually nyctalodont (e.g., specimens Ch/G-096 and Ch/G-104; Fig. 4 B 1, D 1) and only sometimes submyotodont (e.g., specimen Ch/G-098; Fig. 4 C 2); the m2 is usually of myotodont type (e.g., specimens Ch/G-104, Ch/G-098, and Ch/G-099; Fig. 4 A-C) and only rarely submyotodont (e.g., specimen Ch/G-096; Fig. 4 D 1); the m3 has a myotodont talonid structure (e.g., specimens Ch/G-104, Ch/G-098, Ch/G-099, and Ch/G-096; Fig. 4). A similar transition from nyctalodonty to myotodonty through submyotodonty in a similar sequence of change of the lower molars is observed, for example in *Lasionycteris noctivagans* and in the extinct and extant representatives of the genus *Submyotodon* (the Late Miocene *S. petersbuschensis* and Recent *S. caliginosus).* It is noteworthy that the submyotodonty is not very rare in the fossil species of *Plecotus.* The lower molars of the Early Pliocene *P. rabederi* from Podlesice site also have a submyotodont crown structure.

The lower molar types in fossil species of *Plecotus* may document the evolutionary change from nyctalodonty (as the probable ancestral state of the Plecotini; Horáček, 2001) to myotodonty through the transitional state, submyotodonty, no later than between the Early Miocene up to the Early Pliocene. Since the beginning of the Pliocene, the morphological state of dentition, typical of the modern representatives of the species groups "*auritus*" and "*austriacus*", has appeared. Subsequent species (e.g., *P. abeli* and *P. pliocaenicus*) already have only myotodont lower molars, and the shape of their P4 is the same as in modern *Plecotus* (Fig. 3). Noteworthy is that starting from the beginning of the Pliocene, several different species of *Plecotus,* morphologically similar to the living lineages of the genus, have appeared (Fig. 1). Some of them apparently represent derived phylogenetic lineages and cannot be attributed to ancestral forms of the modern *Plecotus*. For example, *P. pliocaenicus* (Fig. 1) possesses a very robust and obvious specialized morphological type. The smaller and more gracile species *P. crassidens* has P4 with a crown shape similar to that of the Miocene *Plecotus*, modern *Corynorhinus* or *Barbastella.* Therefore, *P. crassidens* also cannot be treated as an ancestor of any modern members of the genus. Other small species, e.g., *P. abeli,* which is almost indistinguishable from the modern *Plecotus,* only appeared at the beginning of the Pleistocene (Fig. 1).

Unlike *Plecotus,* the tooth-row of *Barbastella* is characterized by the presence of only one small premolar, both in the upper and lower tooth-rows, and the nyctalodont type of the lower molars. Nevertheless, morphologically, *Barbastella* shows a close similarity to *Plecotus* due to: 1) a strongly curved paralophid on m1-2; the paralophid on m1 is more curved than that on m2; 2) the upper molars have neither paraloph nor paraconule; the preprotocrista smoothly connects to the anterocingulum at the base of the paracone; 3) the hypocone is absent and the postprotocrista smoothly joins the postcingulum at the base of the metacone, like in some Miocene *Plecotus* species; and 4) the crown of M3 is markedly compressed in the anteroposterior direction and displays a rounded stylocone. Such morphological similarity suggests a close affinity of *Barbastella* with *Plecotus,* and strenghtens support for their monophyly within the Plecotini tribe of the Palaearctic.

It is noteworthy that *Barbastella* is similar to both the Nearctic genus *Corynorhinus* and the Miocene species of *Plecotus* in the shape of the P4 crown (Figs. 3, 6). The marked morphological similarity between the modern North American *Corynorhinus* and the Miocene species of the European *Plecotus* has already been noted by researchers (Kowalski, 1956), who assumed the phylogenetic relationships of these two genera (Wołoszyn, 1987; Topál, 1989 a, b; Spitzenberger *et al.*, 2006). Obviously, the discussion about the true taxonomic status of fossil European species of *Plecotus* and their phylogenetic relationships to North American *Corynorhinus* is still far from being complete, and requires additional researches and fossil evidence.

The new species *Barbastella maxima* nov. sp. shows some rather advanced traits, e.g., a markedly reduced M3, and cannot be considered as an ancestral taxon for the genus. Moreover, there is a huge gap in the history between this Late Miocene fossil and the Pleistocene species of *Barbstella* (Fig. 1). Morphologically, *B. maxima* is very similar to modern barbastelles, but is significantly larger in size, and possesses a more reduced M3 and a more compressed M2 crown. The Late Miocene *B. maxima* from Gritsev represents the earliest reliable record of this genus, since all other fossil records are Pleistocene or Holocene in age (e.g., Wettstein-Westersheim, 1923; Kowalski, 1962; Topál, 1970; Wołoszyn, 1987; Rabeder, 1972, 1974).

CONCLUSION

Paleontological records of the vespertilionid tribe Plecotini are quite scarce and sporadic in space and time; this is especially true for pre-Pliocene records. In this respect, any new materials from the Miocene are important since they fill one of numerous gaps in the evolutionary history of this group. We reported here new records of *Plecotus* aff. *atavus* and a new species of the genus *Barbastella* from the Late Miocene site Gritsev (MN 9, Ukraine), which provide new data on the phylogeny and biostratigraphy of the tribe. The Miocene *Plecotus*, including *P.* aff. *atavus* from Gritsev, show more advanced dental features with respect to modern species. Therefore, they cannot be considered as ancestral taxa for younger members of the genus. A noticeable morphological similarity between the nominative form of *P. atavus* from the Early Pliocene of Hungary and the Late Miocene *P.* aff. *atavus* from Gritsev (MN 9, Ukraine) yield even more support for their close phylogenetic relationships. The Miocene *Plecotus* from Europe, including *P.* aff. *atavus* from Gritsev, share some common features with Recent New World *Corynorhinus*, which they evidently developed independently. The Miocene record of *Barbastella maxima* nov. sp. in Gritsev is the earliest reliable fossil record of this genus, and it morphologically differs from the Recent species of *Barbastella* in being considerably larger. It more or less corresponds to the possible time of diversification of the genus and should be considered as an important calibration point for plecotine evolution and its time of diversification.

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