V E R T E B R A T A   H U N G A R I C A

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Tertiary and Early Quaternary remains of Corynorhinus and Plecotus from Hungary (Mammalia, Chiroptera)

By

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Abstract: Plecotus (Corynorhinus) atavus from the Upper Miocene (MN 13) of Polgárdi Loc. 4, Hungary and Plecotus (Plecotus) pliocaenicus, from the Lower Pliocene of Osztramos Loc. 9, Hungary are reviewed. These species are compared with recent Plecotus (Corynorhinus) townsendii, Plecotus (C.) sp. from Osztramos Loc. 9 and with the holotype (Betfia) and the recently found specimens of Plecotus (C.) crassidens from the Lower Pleistocene of Beremend Loc. 17 on the one hand, and with Plecotus (P.) cf. abeli from Osztramos Loc. 9, Plecotus (P.) abeli from Beremend Locs 16-17 and recent Plecotus (P.) auritus from Europe, Korea, Mongolia and recent Plecotus (P.) austriacus from Europe on the other hand.

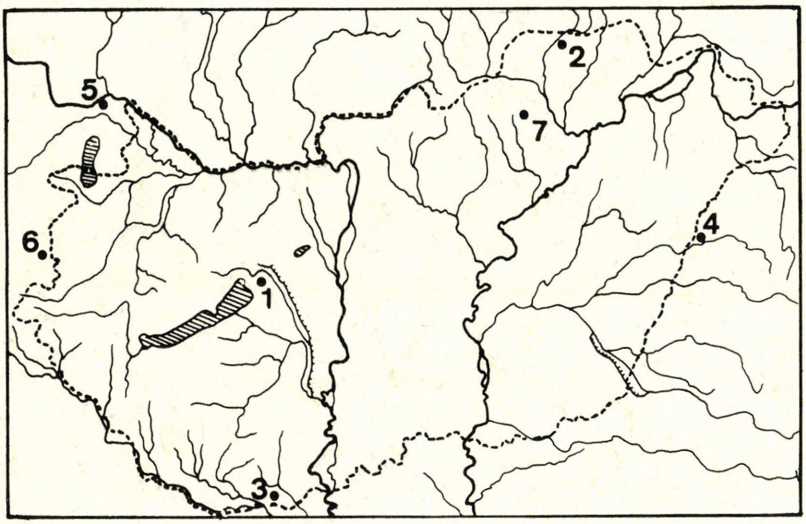
HANDLEY (1959) discussed the evolution and faunal history of plecotine bats in his comprehensive work. The evolution of these bats has also been studied by WILLIAMS et al. (1970) and FEDYK and FEDYK (1971). Since the publication of HANDLEY's work the existence of two Plecotus (Plecotus) species in Eurasia has been proved and later generally accepted by BAUER (1957), TOPÁL (1958), HANÁK (1966), STEBBINGS (1967) and others. Regarding the European fossil big-eared bats KORMOS (1930), KOWALSKI (1956, 1962) and RABEDER (1974) published important data. While HANDLEY (op. cit.) ranked the American genus Corynorhinus as a subgenus of Plecotus, RABEDER (op. cit.) erected the new subgenus Paraplecotus to include Plecotus crassidens Kormos.

Amongst the numerous fossil bat remains found during the recent decades in Hungary, plecotines have always been relatively rare. Still, these furnished important data on the Miocene, Pliocene and Pleistocene history of the Corynorhinus-like (Paraplecotus) bats and that of Plecotus (Plecotus) in the Pliocene and Lower Pleistocene of Hungary. Two new species were described by TOPÁL (1988).

LOCALITIES, MATERIAL AND METHOD

Polgárdi Locality 4 (both lower and upper localities). - A very rich and in many respects relatively intact vertebrate material aged Upper Miocene (MN 13) (about six million years old) was collected here in 1984-1985 for the Hungarian Geological Institute by Dr. L. KORDOS. There are some publications on the mammalian remains by KORDOS (1985, 1987, FREUDENTHAL and KORDOS (1987). Amongst the numerous - unpublished yet - insectivores, rodents, etc., the bats seemed but additional elements. Still, a good number of Rhinolophus cf. lissiensis Mein, Rh. delphinensis Gailard and Miniopterus cf. fossilis Zapfe, and less numerous Myotis spp. 1, 2, 3, 4 and plecotines used in this study, were received for investigation by the courtesy of Dr. L. KORDOS.

Osztramos Locality 9 aged Lower Pliocene. - Small mammals, mostly bats were collected here by Dr. JÁNOSSY and myself for the Palaeontological Department of the Hungarian Natural History Museum during the early 1970es. (JÁNOSSY 1974, JÁNOSSY and KORDOS 1977). The material collected was somewhat younger than the excellent fauna from Podlesice (Poland) (KOWALSKI 1956, 1962). The assemblage of very rich fossil bat material is still mostly unpublished, however, there are publications on some bats (TOPÁL 1975, 1979, 1983, 1985).



Map 1. Localities: 1= Polgárdi, 2= Osztramos, 3= Beremend, 4= Betfia, 5= Deutsch Altenburg, 6= Kohfidisch, 7= Répáshuta

Beremend Localities 16 and 17 Lower Pleistocene aged. - The series of individual localities at the classical locality of Beremend, South Hungary (KRETZOI 1956, JÁNOSSY 1986) has recently been increased by the intensified limestone quarrying operations. During the last weeks of 1984 a well extended cave system was discovered by local miners (TAKÁCS-BOLNER 1985). First collectings of palaeontological samples were made by the staff of the Speleological Institute of the National Authority for Nature Conservation and Environmental Protection and the members of the Hungarian Speleological Society. The cave system at Beremend was named the Crystal Cave and as has been labelled palaeontological site No. 16. Dr. D. JÁNOSSY and I participated in the field work first in January, 1985. During 1986 two field trips were organized to the area of the cave. All fossils found outside the cave - certainly in destroyed former parts of the same cave system - have been labelled as No.17. A very rich vertebrate fauna - mostly mammals - revealed the age of the fossil asemblage. It evidently belongs to the upper portion of the Lower Pleistocene, that is, to the Betfian substage. TAKÁCS-BOLNER (op. cit.) also reviewed the palaeontological data of its time. To the rich fossil bat fauna found inside the cave was added an extremely rich assemblage gathered outside. A few almost complete skulls, intact mandibles and extremity bones, thousands of fragmentary pieces came from two species of Rhinolophus, 8-9 species of Myotis, Eptesicus, Miniopterus and two species of Plecotus (s.l.). The latter comprises less than a few percent of the total bat material.

Of the other faunas a few should be mentioned here because of their close age and/or composition. In Kohfidisch (BACHMAYER and WILSON 1970) besides Rh. delphinensis there is mentioned and also figured in a photo a specimen of a "Chiropterid genus indet". In my opinion it is almost certainly a closely related species or one identical with the Plecotus (Corynorhinus) of Polgárdi Loc. 4. The rich Podlesice fauna - somewhat older than that of Osztramos Loc. 9 - (KOWALSKI, op. cit.) furnished some fine pieces of a Plecotus (Corynorhinus) (= "crassidens"of KOWALSKI) that actually differs from the true crassidens (RABEDER, op. cit.). At Gundersheim (HELLER 1936) there were repòrted (by HORÁČEK, in litt.) the species "crassidens". According to a detailed comparison (11 items), however, these are certainly Plecotus (Plecotus) and not crassidens. The same is true for Plecotus found at Kövesvárad, a Lower Pleistocene locality (TOPÁL 1963). As it has already been pointed out (RABEDER, op. cit.) the Locality Deutsch Altenburg 2 is of Lower Pleistocene age (zone Biharian) thus close to that of the classical type locality of Plecotus crassidens Kormos at Püspökfürdő (=Betfia) (KORMOS, op. cit.).

Plecotus (Corynorhinus) crassidens Kormos, 1930

Holotype, Reg. No. 4727 in the Palaeovertebrate Collection, Hungarian Geological Institute, Budapest from Püspökfürdő (= Betfia). One rostrum, three mandibles and mandibular fragments in the collection of the Palaeontological Department of the Hungarian Natural History Museum, Budapest from Beremend Loc. 17 (see detailed list under the species, below).

Plecotus (Corynorhinus) atavus Topál, 1988

Five maxillary fragments, four mandibles and mandibular fragments from Polgárdi Loc. 4, in the Palaeovertebrate Collection of the Hungarian Geological Institute, Budapest (see detailed list under the species, below).

Plecotus (Corynorhinus) sp.

Four maxillary fragments, five mandibular fragments from Osztramos Loc. 9, in the collection of the Palaeontological Department of the Hungarian Natural History Museum, Budapest (see detailed list below).

Plecotus (Corynorhinus) townsendii pallescens Miller, 1897

Five specimens in the collection of the Zoological Department of the Hungarian Natural History Museum, as follows: Reg. No. 58.74.1. female, Marehew Cave, Woods Co., Oklahoma, 2 mls west, 6 mls south Aetna, Kansas, April 11, 1949, coll. LOOMS; Reg. No. 58. 74.2. female, Marehew Cave, Woods Co., Oklahoma, October 7, 1951, coll. KNOX JONES; Reg. No. 60.234.1. female, 2 mls west, 1 ml south of Reed, Greer Co., Oklahoma, April 2, 1955, coll. CUTTER; Reg. No. 60.234.2. female, 1 ml south 2 mls west of Reed, Greer Co., Oklahoma, May 2, 1955, coll. CUTTER; Reg. No. 62.8.1. female, Bat's Cave, SE Camp, Kiesel, South fork of Ogden River, Weber Co., Utah, May 15, 1950, coll. PORTER.

Plecotus (Plecotus) abeli Wettstein, 1923

Three rostra, nine maxillary fragments (six right, three left) 29 mandibles (10 right, 19 left) and mandibular fragments from Beremend Localities 17 and 16 in the collection of the Palaeontological Department, Hungarian Natural History Museum (see detailed list under the species, below).

Plecotus (Plecotus) cf. abeli Wettstein, 1923

Sixteen maxillary fragments (eight right, eight left) 18 mandibles and mandibular fragments (15 right, three left) from Osztramos Loc. 9, in the collection of the Palaeontological Department, Hungarian Natural History Museum (see detailed list below, under the species).

Plecotus (Plecotus) pliocaenicus Topál, 1988

One rostrum, 13 (six right, seven left) maxillary fragments, 10 (seven right, three left) mandibles and mandibular fragments, all from Osztramos Loc. 9 in the collection of the Palaeontological Department, Hungarian Natural History Museum (see detailed list below, under the species).

Plecotus (Plecotus) auritus (Linnaeus, 1758)

Five specimens from Hungary and Czechoslovakia and one each from Korea and Mongolia in the collection of the Zoological Department, Hungarian Natural History Museum, as follows: Reg. No. 57.244.1. female, Abaliget Cave, Mecsek Mts, November 29, 1955. coll. TOPÁL and VISÓVÖLGYI; Reg. No. 71.16.1. female, Leány Cave, Pilis Mts., March 15, 1964, coll. TOPÁL; Reg. No. 71.19.1. female, Királyrét, old mine, Börzsöny Mts., December 26, 1965, coll. BÉCSY; Reg. No. 71.21.1. sex? , Kőlik Cave, Mánfa, Mecsek Mts., February 1, 1967, coll. MÉSZÁROS; Reg. No. 58.46.1. female, Ice Cave, Dobsina, Czechoslovakia, February 14, 1958, coll. TOPÁL and VACHOLD; Reg. No. 10176 female, old mines 2 km west of Dong Re Dong, foot of Kumgangsan Mts., Democratic People's Republic of Korea, November 18, 1986, coll. DEMETER and party; Reg. No. 74.18.1. male, Szuhe Baator, NW of Barun-urt, Mongolia, 112° 38' 47°25', 1090 m a.s.l., August 11, 1972, coll. MÉSZÁROS.

Plecotus (Plecotus) austriacus (Fischer, 1829)

Six specimens from Hungary and Czechoslovakia in the collection of the Zoological Department, Hungarian Natural History Museum, as follows: Reg. No. 57.31.1. female, Miskolc, January 19, 1955, coll. BORZSÁK; Reg. No. 57.38.1. male, Budapest II, April 6, coll. SZÍJJ; Reg. No. 57.241.1. female, Gyömrő, September 29, 1957, coll. MÉHÉSZ; Reg. No. 57.247.1. female, Kecskelyuk Cave, Bükk Mts., March 24, 1956, coll. TOPÁL; Reg. No. 70.14.1. male, Budapest, Óbuda, June 13, 1970, coll. HAÁS; Reg. No. 68.536.1. female, Dry Cave, Demãnova, Czechoslovakia, March 7, 1964, coll. TOPÁL.

Besides the usual dry-wash-sift-select method, remains of fossil bats were generally singled out before washing in order to keep the teeth in place which otherwise become loose. After individual cleaning and drying again, the fragments were treated with bensolic solution of polystyrol.

The measurements were taken with help of a dial caliper or chiefly with an ocular micrometer in a stereo microscope to the nearest 0.01 mm.

According to MILLER (1907) and the majority of the authors, e.g. MENU (1985), the dental formula of both subgenera Plecotus and Corynorhinus is

$$\frac{-\ 2\ 3.\ 1.\ -\ 2\ -\ 4\ 5\ 6\ 7}{1\ 2\ 3.\ 1\ -\ 2\ 3\ 4\ 5\ 6\ 7} = 36$$

I chose not to follow HANDLEY (1959) and RABEDER (1974) in their numbering of the upper and lower premolars.

The abbreviations used in this work for respective measurements (explanations if necessary are given in parentheses) are as follows.

IOB = interorbital breadth
CCR = width of rostrum at C-C (at outermost borders of crowns)
CCRA = width of rostrum at C-C alveoli (at outermost margins of alveoli)
MMR = M3/-M3/ width (at outermost points of crowns)
MMRA = M3/-M3/ alveolar width (at outermost border of outer alveoli of M3/s)
BIN = greatest breadth of intermaxillary notch
DIN = depth of intermaxillary notch (from connecting line of foremost tips of praemaxillae to hindermost point of intermaxillary notch)
WAPE = greatest width of anterior palatal emargination
DAPE = depth of the interior palatal emargination (from connecting line of foremost tips of praemaxillae to deepest point of anterior palatal emargination)

WRL = width of rostrum at lacrimalia
MHP = maxillary height at P4/ (from dorsal margin of anteorbital foramen to edge of maxilla at anterior root of P4/)
MHM = maxillary height at M2/ (from dorsal edge to alveolar margin of maxilla at M2/)
PL = palatal length (shortest distance from anterior palatal emargination to posterior edge of bony palate)
AB = width of anteorbital bridge (between anterior edge of orbit and posterior margin of anteorbital foramen)
UCM = C-M3/ length
UCMA = C-M3/ alveolar length
UPM = P4/-M3/ length
UPMA = P4/-M3/ alveolar length
UCP = C-P4/ length
UCPA = C-P4/ alveolar length
UMM = M1/-M3/ length
UMMA = M1/-M3/ alveolar length
UCL = upper C basal length (greatest length of basal cross-sectional of crown)
UCLA = upper C alveolar length (antero-posterior length of alveolus)
UCW = upper C width (greatest basal cross-sectional width of crown)
UCWA = upper C alveolar width
UPTL = basal cross-sectional length of P2/
UPTW = basal cross-sectional width of P2/
UPFL = antero-posterior length of P4/
UPFW = width of P4/
UMOL = M1/ length (distance between anteriormost point of parastyl and posteriormost point of metastyl)
UMOW = M1/ mesostylar width (distance between external border of mesostyl and innermost labial border of crown)
UMTL = M2/ length (as for UMOL)
UMTW = M2/ width (as for UMOW)
UTML = M3/ length (distance between anterior border and posteriormost point of crown)
UTMW = M3/ width (distance between labial and lingual edges of crown)
ML = mandibular length (from anteriormost portion of body under I/1 to posterior edge of articular process)
LCM = C-M/3 length
LCMA = C-M/3 alveolar length
LPM = P/4-M/3 length
LCP = C-P/4 length
LCPA = C-P/4 alveolar length
LMM = M/1-M/3 length
LMMA = M/1-M/3 alveolar length
LCL = lower C basal cross-sectional length
LCW = lower C basal cross-sectional width
LPTL = basal cross-sectional length of P/2
LPTW = basal cross-sectional width of P/2
LTPL = basal cross-sectional length of P/3
LTPW = basal cross-sectional width of P/3
LPFL = P/4 length (distance between anteriormost and posteriormost parts of crown)
LPFW = P/4 width (distance between lingualmost and labialmost parts of crown)
LMOL = M/1 length (distance between anteriormost margin of paraconid and posteriormost edge of hypoconid)
LMOW = M/1 talonid width (measured at widest portion in occlusal view)
LMTL = M/2 length (as for LMOL)
LMTW = M/2 talonid width (as for LMOW)
LTML = M/3 length (as for LMOL)
LTMTR = M/3 trigonid width (measured at widest portion in occlusal view)
LTMTA = M/3 talonid width (as for LMOW)
HMUM = height of mandibular body under M/1 (from highest margin between roots of M/1 to ventral edge of ramus)

HMBM = height of mandibular body behind M/3

HCP = height of coronoid process (measured between dorsalmost tip of coronoid process and the closest part of incisura vasorum in labial view).

DESCRIPTIONS AND COMPARISONS

Plecotus (Corynorhinus) crassidens Kormos, 1930

KORMOS (1930) based his species on a single mandible from Betfia, Roumania (Püspökfürdő, Somlyóberg), the type locality for the Betfian substage of the Lower Pleistocene (JÁNOSSY 1986). No figure was given with the original description. In the 1970s it became evident that - compared with the description, the actual specimen lacks P/4. This tooth had probably been broken off and lost later by someone who studied the holotype. The specimen has also been used in this work.

KOWALSKI (1956, 1962) identified the rich plecotine remains from Podlesice, Poland as P. (Corynorhinus) crassidens. He pointed out for the first time the close relationship of North American Corynorhinus to KORMOS' P. crassidens. Later RABEDER (1974), based on new findings including the first maxillary fragments from a Lower Pleistocene locality at Deutsch Altenburg 2, Austria, described in great details its cranial features and based his Paraplecotus g. n. on this very species. RABEDER (op. cit.) already questioned the identity of the Podlesice form with P. crassidens.

Recently a modest material including a rostrum has been found at Beremend Locality 17 and has been studied during this project.

The list of specimens studied is as follows: Holotype, Reg. No. 4727 in the Palaeovertebrate Collection, Hungarian Geological Institute, Budapest, right mandibular fragment with M/1-M/2-M/3 and alveoli of P/2-P/4 (P/4 evidently lost subsequently), damaged ascending ramus (articular process missing). The specimen was collected in the years 1912-1913 by KORMOS. The following specimens are from Beremend Loc. 17 and deposited in the Palaeontological Department, Hungarian Natural History Museum: Register No. V. 86.19, ser. No. 6, damaged rostrum with right P2/, M2/-M3/, left P4/, M1/, damaged M2/, damaged M3/ and full set of alveoli of other teeth; Reg. No. of mandibular pieces V. 86.20.: ser. No. 15 left mandibular fragment with P/2-P/3-P/4-M/1-M/2 and alveoli of I/3, M/3; ser No. 16, right mandibular fragment with alveoli of I/3-M/3; ser. No. 17, left mandible with P/2-P/3-P/4-M/1-M/2-M/3 and alveoli of I/1-C, slightly damaged ascending ramus.

A direct comparison of the probable holotype and the Beremend material showed great similarities, though almost all comparable measurements of the former were slightly greater than those of the latter one. Most of the differences can be explained, however, by considering a larger series from Deutsch Altenburg 2 (see: RABEDER, op. cit.). For the measurements, see Table 2. The recently found mandibles and the holotype of P. crassidens fully agree in the arrangement of the alveoli of the small premolars, that is, the alveolus of P/3 is decidedly smaller (narrower) and set lingually. The other important feature is the buccal basal portion of the angular process (see Plate II, Fig. 3) which is identical in the holotype and the other specimens. The P/4 of the type specimen of P. crassidens certainly had two roots. The Beremend specimens have partly two roots or incipient fusion of roots, especially from buccal view. According to RABEDER (op. cit.) the Deutsch Altenburg 2 specimens have already fused roots of P/4.

There are obvious differences in the shape of the rostrum. The lacrimal area is equally smooth in P. crassidens and in P. townsendii. A dorsomedian rostral depression is deep and extended in P. crassidens as compared to that of P. townsendii, where the foremost part of the rostrum is flat or even convex dorsally. The anteorbital foramen of P. crassidens is great, greater than that of P. townsendii, and placed above the P4/ area, not above M1/ as in P. townsendii (see Plate I, Figs 3, 6). Thus, the distance between the posterior margin of the anteorbital foramen and the foremost tip of the praemaxilla is much shorter (the general size of the skull is somewhat greater) in P. crassidens than in P. townsendii. Though the anteorbital foramen is large, the breadth of the anteorbital bridge is also much greater in P. crassidens (see Table 1). The rostrum of P. crassidens is strikingly broader in every respect than that of P. townsendii. The interorbital width is quite larger in P. crassidens. The rostral width at the outer alveolar border of the canines, and at the crowns (and at alveoli) of M3/-s is greater in P. crassidens than in P. townsendii. The same is true for the lacrimal width and width of the postpalate. The width of the narial notch and that of the anterior palatal emargination, as well as the depth of palatal emargination well exceed those of P. townsendii, whilst the depth of the intermaxillary notch equals the two compared species. Maxillary height at P4/ anterior root equal in the fossil and recent species, the maxillary height above M2/, however, is evidently lower in P. crassidens than that of P. townsendii. Thus almost all rostral width measurements show a decidedly wider rostrum of the fossil species (see Plate I, Figs 1, 4; Table 1).

Table 1 Measurements - minimum and maximum values (number of cases; mean in parentheses) - of rostra, maxillary pieces and upper dentition of fossil and recent Plecotus (Corynorhinus) from Hungary and North America, respectively

Species / Character	P. (C.) atavus Polgárdi	P. (C.) sp. Osztramos	P. (C.) crassidens Beremend	P. (C.) townsendii N. America
IOB			4.30	3.88-3.92(5; 3.905)
CCR				4.06-4.35(5; 4.218)
CCRA			4.42	3.86-4.28(5; 4.022)
MMR			6.68	6.04-6.49(5; 6.326)
MMRA			6.42	5.97-6.33(5; 6.230)
BIN			2.72	2.18-2.31(4; 2.247)
DIN			2.41	2.36-2.45(4; 2.417)
WAPE			2.27	1.95-2.00(4; 1.962)
DAPE	1.81-1.90(2; 1.855)		1.81	1.13-1.54(4; 1.347)
WRL			5.92	5.22-5.26(4; 5.250)
MHP	1.36-1.50(3; 1.436)	1.31	1.95	1.63-1.95(5; 1.838)
MHM	1.00-1.36(4; 1.177)	1.31	0.95	1.13-1.27(5; 1.168)
PL			5.26	5.96-6.42(4; 6.195)
AB	0.55-0.68(3; 0.626)	0.68	0.63	0.31-0.36(5; 0.340)
UCM				5.35-5.58(5; 5.422)
UCMA	5.08-5.35(2; 5.215)		5.38	5.10-5.34(5; 5.230)
UPM	4.19-4.23(2; 4.210)		4.23	4.07-4.27(5; 4.172)
UPMA	3.95-4.23(4; 4.092)		3.99	3.95-4.19(5; 4.054)
UCP		2.41		1.90-2.03(5; 1.986)
UCPA	2.03-2.31(2; 2.170)	2.03	1.95	2.00-2.13(5; 2.108)
UMM	3.46		3.66	3.40-3.64(5; 3.496)
UMMA	3.08-3.44(4; 3.240)		3.32	3.22-3.52(5; 3.304)
UCL		1.00-1.02(2; 1.001)		0.81-0.90(5; 0.882)
UCLA	0.68-0.72(2; 0.700)		0.77	
UCW		0.97-1.00(2; 0.985)		0.81-0.86(5; 0.830)
UCWA	0.63-0.72(2; 0.675)		0.70	
UPTL	0.50	0.45	0.45	0.30-0.36(5; 0.348)
UPTW	0.55	0.45	0.45	0.43-0.55(5; 0.476)
UPFL	1.18-1.29(4; 1.245)	1.00-1.13(2; 1.065)	0.97	1.04-1.13(5; 1.058)
UPFW	1.18-1.36(4; 1.272)	1.27-1.29(2; 1.280)	1.22	1.13-1.22(5; 1.158)
UMOL	1.40-1.45(3; 1.433)	1.40	1.45	1.31-1.45(5; 1.402)
UMOW	1.65-1.77(3; 1.713)	1.77	1.72	1.63-1.90(5; 1.730)
UMTL	1.29-1.45(4; 1.365)	1.31-1.40(2; 1.355)	1.45	1.31-1.40(5; 1.356)
UMTW	1.65-1.79(4; 1.737)	1.68-1.74(2; 1.710)	1.81	1.63-1.81(5; 1.712)
UTML	0.81-0.81(2; 0.810)		0.86	0.72-0.86(5; 0.776)
UTMW	1.68-1.72(2; 1.700)		1.72	1.54-1.86(5; 1.708)

Among the available tooth-row lengths, the C-M3/ alveolar length is slightly greater than in P. townsendii, while the C-P4/ alveolar length is smaller than that of the recent animal. Other measurable tooth-row lengths overlap extensively in the two species (see Table 1). As regards the individual upper teeth, P2/ basal length is clearly greater than in P. townsendii, though the width of this tooth is equal in both species. On the contrary, the P4/ basal length of P. crassidens is appreciably smaller than even that of the smallest P. townsendii studied. Otherwise, all measurements but the length of M2/ seems to exceed those of P. townsendii.

In mandibular morphology the most important difference between P. crassidens and P. townsendii lies in the shape of the basal portion of the angular process on the buccal side. It has a convexity and a sharp ridge in P. crassidens (anatomically corresponds to the linea masseterica in the dog), while in P. townsendii the angular process is more intensively concavely bent outwards in occlusal view, and without a ridge (see Plate I, Figs 3, 5). The height of the mandibular body under M/1 exceeds that of P. townsendii, otherwise the mandible does not seem to differ in the two species. As regards the available lower tooth-row length measurements, these overlap to various extent in the two species. Basal length and especially basal width, thus the crown area of P/2 is clearly greater than in P. townsendii, contrarily, the basal width of P/3 is much smaller in P. crassidens (while its basal length is equal) so this premolar is definitely narrowed, that is, specialized in the species P. crassidens (see Plate II, Figs 3, 5). See also RABEDER (op. cit. Table VI, Fig. 53). The basal length and width of P/4 do not differ in the two species and there are no differences in other tooth measurements, except in M/1 talonid width which is smaller in P. crassidens, and in M/3 talonid width which is wider in P. crassidens than in the recent species.

The tooth measurements of the holotype of P. crassidens (as shown above) are greater than those of the extant species. It has also longer M/3 with wider trigonid and talonid. The species P. crassidens is a more evolved, over specialized form of a more or less separate lineage within the subgenus Corynorhinus.

Plecotus (Corynorhinus) atavus Topál, 1988

At present, this is one of the earliest known plecotine in the Holarctic. It comes from the Upper Miocene (MN 13 zone), Polgárdi Locality 4. A rather primitive plecotine (Corynorhinus) bat with clearly two-rooted P/4 and partly ancestral, partly intermediate characters as compared to Plecotus (Corynorhinus) crassidens Kormos, 1930 and Plecotus (Corynorhinus) townsendii pallescens Miller, 1897.

Holotype: Right maxillary fragment (Plate I, Figs 7, 8) with P4/-M1/-M2/ and alveoli of I1/-I2/, C, M3/. Register No. V. 15228 (VT. 138). Deposited in the Palaeovertebrate Collection, Hungarian Geological Institute, Budapest. Measurements of the holotype: DAPE 1.90, MHP 1.50, MHM 1.22, AB 0.55, UCMA 5.35, UPM 4.23, UCPA 2.31, UMMA 3.44, UCLA 0.72, UCWA 0.72, UPFL 1.29, UPFW 1.33, UMOL 1.45, UMOW 1.72, UMTL 1.36, UMTW 1.74.

Other material and a selected paratype: V. 15230 right maxillary fragment with P2/-damaged P4/-M1/-M2/-damaged M3/; Reg. No. V. 15231 right maxillary fragment with P4/, M2/-M3/ and alveolus of M1/; Reg. No. V. 15232 right detached M1/; Reg. No. V. 15234 right maxillary fragment with P4/, M2/ and alveoli of I1/-P2/, M1/, M3/; Reg. No. V. 15235 slightly fragmentary (with missing angular process) right mandible with alveoli of I/1-M/3; Reg. No. V. 15233 right mandibular fragment with C-P/2-P/3-P/4-M/1-M/2 and alveoli of I/1-I/3; selected paratype Reg. No. 5. 15229 (Plate II, Figs 1, 2) left mandible with P/4 and alveoli of I/1-P/3, M/1-M/3. All in the Palaeovertebrate Collection, Hungarian Geological Institute, Budapest. Measurements of the selected paratype: ML 11.50, LCMA 6.07, LCPA 2.25, LLMA 3.79, HMUM 1.68, HNBM 1.50, HCP 3.56.

Measurements: (including those of holotype and selected paratype) minimum and maximum (sample size and mean in parentheses). DAPE 1.81-1.90 (2; 1.855); MHP 1.36-1.50 (3; 1.436); MHM 1.00-1.36 (4; 1.177); AB 0.5-0.68 (3; 0.626); UCMA 5.08-5.35 (2; 5.215); UPM 4.19-4.23 (2; 4.210); UPMA 3.95-4.23 (4; 4.092); UCPA 2.03-2.31 (2; 2.170);

UMM 3.46; UMMA 3.08-3.44 (4; 3.240); UCLA 0.68-0.72 (2; 0.70); UCWA 0.63-0.72 (2; 0.675); UPTL 0.50; UPTW 0.55; UPFL 1.18-1.29 (4; 1.245); UPFW 1.18-1.36 (4; 1.275); UMOL 1.40-1.45 (3; 1.433); UMOW 1.65-1.77 (3; 1.713); UMTL 1.29-1.45 (4; 1.365); UMTW 1.65-1.79 (4; 1.737); UTML 0.81-0.81 (2; 0.81); UTMW 1.68-1.72 (2; 1.70); ML 10.65-11.50 (2; 11.075); LCMA 5.85-6.07 (2; 5.955); LPM 2.18; LCPA 1.95-2.25 (3; 2.10); LMMA 3.66-3.79 (2; 3.725); LCL 0.50; LCW 0.86; LPTL 0.45; LPTW 0.50; LPFL 0.68-0.77 (2; 0.725); LPFW 0.65-0.72 (2; 0.685); LMOL 1.36; LMOW 0.95; LMTL 1.365; LMTW 0.95; HMUM 1.45-1.68 (3; 1.556); HMBM 1.31-1.50 (2; 1.405); HCP 3.45-3.56 (2; 3.450).

Description and comparisons: No doubts there may be differences in the morphology of the rostrum of P. atavus and the already known P. crassidens and P. townsendii used for comparison in this study. It must be admitted that a number of characters are not properly seen in P. atavus because of its rather fragmentary state. The lacrimal area is smooth as in the other species studied. Regarding the dorso-median rostral depression the species is most probably closer to P. crassidens than to P. townsendii. P. atavus has a medium-sized anteorbital foramen as compared to the other species. It is placed mostly above the P4/ and partly above the M1/ area. The distance from the posterior margin of anteorbital foramen to the foremost tip of the premaxilla is intermediate between that of P. crassidens and P. townsendii. The anterior palatal emargination was probably greater, first of all deeper than even that of P. crassidens. It extends back to the connecting line between P2/-P2/ alveolar centers, while in Beremend P. crassidens it is somewhat less deep. The maxillary height above the anterior root of P4/ is much lower in P. atavus than in P. crassidens and in P. townsendii (see Table 1). P. atavus and P. townsendii are virtually identical in the maxillary height above M2/ or even some Miocene specimens have greater values than P. townsendii has, so these are greater than in P. crassidens.

Regarding the mean values of the upper tooth-row lengths (C-M3/ alveolar length and M1/-M3/ length) the Miocene species is identical with P. townsendii, thus both are smaller than P. crassidens. On the contrary, however, in C-P4/ alveolar length and P4/-M3/ length P. atavus and P. townsendii are equally greater than P. crassidens. Though the upper incisors are missing, one can infer from the alveoli that P. crassidens had definitely greater I1/ as compared with I2/ than P. atavus. The difference between the two incisors is much less pronounced in P. townsendii. The length of the alveole of the upper canine in P. crassidens proved to be greater with no overlap with the new species. One can infer a laterally relatively more pressed, antero-posteriorly more elongated root of canine than that of P. atavus. Unfortunately, until now, the upper canine of P. crassidens, nor that of P. atavus has been found. The bulk of the P2/ of P. atavus is comparatively great and steadily decreasing in basal length from the Miocene P. atavus through the Pleistocene P. crassidens to the recent species. P2/ basal width, however, seems to differ in the two fossil species (one specimen for each). In P. townsendii the range includes all fossil values (see Table 1). The available material of P4/ basal lengths does not overlap between P. atavus and P. townsendii, and at the same time both have greater values of this character than P. crassidens does. Besides, all three species show overlap in P4/ widths. These indicate a pronounced antero-posterior shortening of P4/ in P. crassidens, while P. atavus is less specialized in this respect. There is a characteristic difference in the morphology of the crown of P4/ between the species studied. The anterior edge of the crown has an outer anterior lobe and a deep incision for keeping the posterior portion of the small premolar in P. atavus. These are missing in P. crassidens where the anterior border of P4/ is very slightly pressed by P2/, so it is almost straight without an undulation shown by the former species (see also RABEDER op. cit. Plate II, Fig. 8a). In P. townsendii the anterior border is straight or with a slight lagune. The lingual portion of M1/ and M2/ is bulky in P. crassidens but slender in P. atavus. M3/ is less specialized (less shortened) in P. crassidens, intermediate in P. atavus and variable but generally most specialized (shortened) in the available specimens of P. townsendii. The talon is more or less distinct from the trigon by a narrowing neck in the fossil species, there is no such narrowness in P. crassidens.

The length of the mandible shows overlap in the compared three species, the smallest specimens being found in P. townsendii and the greatest in P. atavus. The foramen mentale is situated under the portion between C and P/2, not under the two small premolars as in Plecotus s. str. (See Plate II, Figs 2, 4, 6, 10). The measurements of the mandibular body and ascending ramus are with considerable overlap in the three compared species, except the height of mandibular body under M/1. In this character P. townsendii is smaller than either P. atavus or P. crassidens. The coronoid and angular processes offer detectable differences. The coronoid process of the Miocene species if higher and pointing less forward than that of the Pleistocene animal. Its posterior descending margin is more oblique and the distance between its anterior margin and the incision between the articular and angular processes is relatively shorter than in P. crassidens (see Plate II, Figs 2, 4). The buccal basal portion of the angular process is concave and without a ridge, not as in P. crassidens (see above and Plate II, Figs 1, 3, 5). The angular process itself is strongly bent outwards, like in P. townsendii.

Table 2. Measurements - minimum and maximum values (number of cases; mean in parentheses) - of mandibular pieces and lower dentition of fossil and recent Plecotus (Corynorhinus) from Hungary and North America, respectively

Species / Character	P. (C.) atavus Polgárdi	P. (C.) sp. Osztramos	P. (C.) crassidens holotype	P. (C.) crassidens Beremend	P. (C.) townsendii N. America
ML	10.65-11.50 (2; 11.075)			10.98	10.58-10.80 (4; 10.692)
LCM					5.62-6.01 (5; 5.850)
LCMA	5.84-6.07 (2; 5.955)			5.75-5.79 (3; 5.763)	5.45-5.99 (5; 5.698)
LPM				4.50	4.27-4.63 (5; 4.458)
LCP	2.18				1.90-2.00 (5; 1.954)
LCPA	1.95-2.25 (3; 2.100)	2.10-2.27 (3; 2.190)		1.90-2.03 (3; 1.983)	1.72-1.90 (5; 1.848)
LMM			4.05	3.91	3.60-3.91 (5; 3.746)
LMMA	3.66-3.79 (2; 3.725)		3.77	3.68-3.86 (3; 3.756)	3.60-3.91 (5; 3.746)
LCL	0.50				0.68-0.72 (5; 0.688)
LCW	0.86				0.68-0.81 (5; 0.754)
LPTL	0.45			0.47-0.47 (2; 0.470)	0.36-0.45 (5; 0.432)
LPTW	0.52			0.57-0.59 (2; 0.580)	0.50-0.55 (5; 0.540)
LTPL	0.36	0.40		0.30-0.36 (2; 0.330)	0.23-0.36 (5; 0.288)
LTPW	0.50	0.52		0.35-0.40 (2; 0.375)	0.45-0.55 (5; 0.494)

Table 2. (continued)

Species / Character	P. (C.) atavus Polgárdi	P. (C.) sp. Osztramos	P. (C.) crassidens holotype	P. (C.) crassidens Beremend	P. (C.) townsendii N. America
LPFL	0.68-0.77 (2; 0.725)	0.72-0.81 (2; 0.765)		0.63	0.55-0.63 (5; 0.594)
LPFW	0.65-0.72 (2; 0.685)	0.68-0.72 (2; 0.700)		0.68	0.63-0.72 (5; 0.652)
LMOL	1.36	1.45-1.50 (2; 1.470)	1.50	1.36-1.45 (2; 1.405)	1.36-1.50 (5; 1.462)
LMOW	0.95	0.86-1.02 (2; 0.940)	1.00	0.86-0.90 (2; 0.880)	0.95-1.00 (5; 0.980)
LMTL	1.36	1.36	1.40	1.36-1.36 (2; 1.360)	1.36-1.45 (5; 1.398)
LMTW	0.95	0.88	1.00	0.90-0.92 (2; 0.910)	0.90-0.95 (5; 0.934)
LTML			1.33	1.22	1.13-1.27 (5; 1.208)
LTMTR			0.90	0.77	0.77-0.81 (5; 0.786)
LTMTA			0.88	0.72	0.68-0.68 (5; 0.680)
HMUM	1.45-1.68 (3; 1.556)	1.50-1.63 (3; 1.580)	1.72	1.54-1.68 (2; 1.603)	1.36-1.50 (5; 1.432)
HMBM	1.31-1.50 (2; 1.405)	1.45-1.59 (2; 1.520)	1.54	1.31-1.45 (2; 1.387)	1.18-1.40 (5; 1.322)
HCP	3.34-3.56 (2; 3.450)	3.10	3.60	3.22-3.48 (2; 3.350)	3.22-3.44 (4; 3.330)

There is a decrease in C-M/3 alveolar length and C-P/4 alveolar length from the Miocene and Pleistocene species to the recent animal, though the M/1-M/3 alveolar lengths considerably overlap in the three species (see Table 2). The basal length of P/2 of the study material greatly coincides in the Miocene and recent species, but it has greater values in P. crassidens. The same is true for the basal width of P/2. The basal length of P/3 fully overlaps in all the study material. Its basal width, however, is the smallest - without overlap - in P. crassidens and is equal P. atavus and P. townsendii. P/4 basal length is clearly the greatest in P. atavus sp. n., intermediate in P. crassidens and smallest in P. townsendii. The widths of P/4s completely overlap in all the three species. Two roots are present in the ancestral species, incipient fusion of roots is sometimes detectable in P. crassidens, and the roots of P/4 are completely fused in P. townsendii. Here in the lower dentition also the antero-posterior chortening of the premolar row and that of P/4 are the most characteristic changes from the old ancestral forms to younger species. In many respects one can conclude from the above comparisons of features the primitiveness of P. atavus and the progressiveness of P. crassidens. Actually the species P. townsendii has retained numerous primitive features. The available material of lower molars of P. atavus is still far from sufficient for reasonable comparisons.

Plecotus (Corynorhinus) sp.

The investigation of the rich bat material excavated in Osztramos Loc. 9 furnished besides two species of Plecotus (Plecotus) a P. (Corynorhinus) sp. The small number and fragmentary state of the latter, however, did not permit an exact identification of the species and a direct comparison with the specimens from Podlesice, the population of the closest geological age, was not performed in the course of this study. List of specimens deposited in the collection of the Palaeontological Department, Hungarian Natural History Museum, Budapest. Reg. No. of the maxillary pieces: V. 86. 10., ser. No. 44, right maxillary fragment with M2/ and alveole of M3/; ser. No. 47, right maxillary fragment with C and alveoli of I1/-I2/, P2/; ser.No. 46., right maxillary fragment with P4/-M1/-M2/ and alveole of P2/; ser. No. 45, left maxillary fragment with C-P2/-P4/; Reg. No. of mandibular pieces V. 86. 11. : ser. No. 52, rigth mandibular fragment with I/2-I/3, P/3-P/4-M/1-trigonid of M/2 and alveoli of I/1, C-P/2; ser. No. 50, left mandibular fragment with M/1-M/2 and alveoli of I/1-P/4; ser. No. 51, left mandibular fragment with ascending ramus (damaged coronoid process); ser. No. 48, left mandibular ascending ramus; ser. No. 96, left mandibular fragment with alveoli of P/2-P/4; ser. No. 94, left mandibular fragment with alveoli of I/1-P/4. For measurements, see Tables 1, 2.

Comparisons with the other fossil specimens revealed a few characters of this animal. As one can infer from the measurements of the available pieces that this animal had a lower rostrum at the anterior root of the P4/ than even P. atavus had, that is, the upper edge of its anteorbital foramen is closer to the edge of the maxilla than either in P. atavus or in P. crassidens. Its anteorbital foramen is greater than those of the other two fossil species. The width of the anteorbital bridge equals that of the greatest P. atavus. C-P4/ alveolar length equals that of P. atavus. Alveoli of I1/ and I2/ do not show such a great size difference as in P. crassidens. Both basal length and basal width of the upper C are definitely greater than those of P. townsendii and probably close to those of P. atavus. The crown of the only available P2/ is identical to that of P. crassidens and not to that of P. atavus. Its alveole seems to differ from that of P. crassidens where it is antero-posteriorly shortened and also seems to be somewhat greater than that of P. crassidens. Basal length of P4/ is smaller than that of P. atavus and approaches that of P. crassidens with no overlap, that is, coincides with that of P. townsendii. Approximately the same is true for the width of P4/, however, there is a considerable overlap with P. atavus. The talon of P4/ in the Osztramos animal is especially wide and extends both anteriorly and posteriorly. It is directed anteriorly and the labial portion of P4/ is drawn back from the canine further away than in P. crassidens, where the talon is nearly perpendicular to the main axis of the skull. It is very interesting that also in the morphology of the P4/ the present sample is closer to the Miocene species with a deep incision on its anterior border. There is a sharp difference between the Osztramos animal on the one hand, and P. crassidens as well as P. atavus on the other hand in the thickness of talon of M1/ and M2/. The lingual portion of the molars is bulky in P. crassidens and slender in the Osztramos form. The measurements of the upper M1/ and M2/overlap, still the means are closer to those of P. townsendii than to those of P. atavus (see Table 1).

Curiously enough the height of the coronoid process is lower than either that of P. atavus or that of P. crassidens. One cannot attach importance to this difference yet, because of the paucity of the available remains. The only comparable lower tooth-row length, the C-P/4 alveolar length equals that of P. atavus, thus it is greater than in P. crassidens. The only P/3 is longer basally than in any specimens of the two other fossil species compared in this study. Its width is slightly greater even than in the only existing P. atavus and falls into the range of this measurement in P. townsendii. The basal length of P/4 equal to that of P. atavus, that is, definitely greater than in P. crassidens. Thus in many respects the Osztramos Loc. 9 species is rather close to the new species from Polgárdi, in a few aspects, however, it is reminescent of P. crassidens.

Plecotus (Plecotus) abeli Wettstein, 1923

The specimens listed and discussed below originate from Beremend Loc. 17 and Beremend Loc. 16, both of the Betfian substage of the Lower Pleistocene. As it was stated before,

Table 3. Measurements - minimum and maximum values (number of cases; mean in parentheses) - of rostra, maxillary pieces and upper dentition of fossil Plecotus (P.) cf. abeli and Plecotus (P.) abeli from Hungary, and Plecotus (P.) auritus from Europe

Species / Character	P. (P.) cf. abeli Osztramos	P. (P.) abeli Beremend	P. (P.) auritus Europe
IOB		3.40-3.80 (3;3.556)	3.42-3.78 (5;3.626)
CCR			3.86
CCRA		3.61-3.78 (3;3.670))	3.84-4.15 (5;3.916)
MMR		6.13	6.18-6.69 (5;6.338)
MMRA		5.98-6.50 (2;6.240)	6.22-6.69 (5;6.364)
BIN		1.77-1.81 (3;1.783)	1.72-1.90 (5;1.802)
DIN		1.81-2.27 (3;2.086)	2.08-2.45 (5;2.276)
WAPE		1.36-1.45 (4;1.415)	1.31-1.36 (5;1.340)
DAPE		1.36	1.13-1.45 (5;1.304)
WRL		4.92-5.09 (3;5.033)	4.68-5.49 (5;4.990)
MHP	1.81-1.95 (8;1.850)	1.63-1.95 (11;1.874)	1.77-2.00 (5;1.878)
MHM	1.13-1.31 (5;1.214)	1.00-1.18 (8;1.155)	1.00-1.13 (5;1.068)
AB	0.16-0.28 (5;0.240)	0.12-0.26 (9;0.216)	0.16-0.36 (5;0.280)
UCM			5.37-5.62 (5;5.508)
UCMA	5.26-5.35 (2;5.305)	5.17-5.44 (4;5.250)	4.59-5.49 (5;5.082)
UPM	4.14-4.19 (3;4.163)	4.23	3.95-4.16 (5;4.074)
UPMA	3.95-4.14 (3;4.026)	3.86-4.31 (5;4.080)	3.82-3.95 (4;3.885)
UCP	2.45-2.55 (2;2.500)	2.59	2.36-2.61 (5;2.484)
UCPA	2.31-2.45 (8;2.371)	2.36-2.45 (9;2.385)	2.13-2.43 (5;2.190)
UMM	3.36-3.48 (3;3.420)	3.46	3.22-3.36 (5;3.300)
UMMA	2.95-3.22 (4;3.040)	2.86-3.36 (5;3.084)	2.90-3.14 (4;3.055)
UCL	1.00-1.00 (2;1.000)	1.00	0.86-1.00 (5;0.952)
UCLA	0.74-0.86 (5;0.806)	0.68-0.81 (8;0.776)	
UCW	0.81-0.90 (2;0.855)	0.81	0.77-0.83 (5;0.806)
UCWA	0.55-0.63 (5;0.594)	0.57-0.63 (8;0.585)	
UPTL	0.36-0.50 (4;0.427)	0.40-0.55 (2;0.475)	0.40-0.45 (5;0.420)
UPTW	0.45-0.59 (4;0.520)	0.52-0.55 (2;0.535)	0.50-0.57 (5;0.534)
UPFL	1.04-1.22 (10;1.187)	1.18-1.40 (10;1.263)	1.09-1.22 (5;1.160)
UPFW	0.86-1.04 (10;0.986)	0.88-1.00 (10;0.950)	0.81-0.95 (5;0.894)
UMOL	1.36-1.50 (7;1.411)	1.36-1.50 (8;1.387)	1.27-1.36 (5;1.332)
UMOW	1.54-1.70 (7;1.635)	1.50-1.72 (8;1.627)	1.59-1.65 (5;1.618)
UMTL	1.31-1.45 (7;1.370)	1.33-1.54 (7;1.398)	1.22-1.36 (5;1.322)
UMTW	1.54-1.81 (9;1.802)	1.61-1.90 (7;1.757)	1.72-1.81 (5;1.768)
UTML	0.68-0.68 (8;0.680)	0.77	0.61-0.72 (5;0.674)
UTMW	1.68-1.77 (3;1.730)	1.63	1.65-1.86 (5;1.754)

the age of this localities was close to, or identical with that of Deutsch Altenburg 2 (RABEDER 1974) where evidently the species composition of plecotines completely equalled.

List of specimens as follows: (marked with + when the specimen is from Beremend Loc. 16 and not - as the majority - from Beremend Loc. 17). The specimens are deposited in the collection of the Palaeontological Department, Hungarian Natural History Museum, Reg. No. of rostra V. 86. 21.: ser. No. 23, fragmentary rostrum in each side with P2/-P4/-M1/-M2/-M3/ and alveoli of I1/-C with attached left mandibular fragment; ser. No. 24, damaged rostrum with full set of alveoli (except of I1/, I1/ and M3/, M3/); ser. No. 26, rostrum with right and left alveoli of I2/-M2/; Reg. No. of the maxillary pieces V. 86. 22: ser. No. 18, left maxillary fragment with P4 and alveole of P2/; ser. No. 19, right maxillary fragment with P4/-M1/-M2/ and alveoli of I1/-P2/; ser. No. 20, right maxillary fragment with P4/-M1/ and alveoli of C-P2/; ser. No. 21, right maxillary fragment with P4/-M1/-M2/ and alveoli of C-P2/, M3/; ser. No. 22, right maxillary fragment with P4/-M1/-M2/ and alveole of P2/; ser. No. 25, right maxillary fragment with I2/, P2/-P4/-M1/-M2/ and alveoli of I1/, C, M3/; ser. No. 27, right maxillary fragment with P4/-M1/-M2/ and alveoli of C, P2/, M3/; ser. No. 28, left maxillary fragment with I1/-I2/-C, P4/-M1/-M2/ and alveole of P2/; ser. No. 134, left maxillary fragment with P4/ and alveoli of I1/-P2/; Reg. No. V. 86. 21., ser. No. 23, left mandibular fragment with full dentition and with attached rostrum; Reg. No. of other mandibular pieces V. 86. 23.: ser. No. 29, left mandibular fragment with P/4-M/1-M/2-M/3 and alveoli of I/1-P/3; ser. No. 30, left mandibular fragment with P/3-P/4-M/1-M/2-M/3 and alveole of P/2; ser. No. 31, left mandibular fragment with I/1, P/4, M/2-M/3 and alveoli of I/3-P/3, M/1; ser. No. 32, left mandible with ascending ramus and M/1-M/2-M/3 and alveoli of I/1-P/4; ser. No. 33, right mandibular fragment with C-P/2-P/3-P/4-M/1; ser. No. 34, right mandibular fragment (ascending ramus) with alveole of M/3; ser. No. 35, left mandibular fragment with I/2, P/4 and alveoli of I/1, I/3-P/3, M/1-M/3; ser. No. 36, left mandibular fragment with ascending ramus and alveoli of M/2-M/3; ser. No. 37, right mandible with P/4 (missing angular process) and alveoli of I/1-P/3, M/1-M/3; ser. No. 38, left mandibular fragment with M/2-M/3; ser. No. 39, right fragmentary mandible with I/2-I/3-C, P/4-M/1-M/2-fragmentary M/3 and alveoli of I/1, P/2-P/3; ser. No. 40, right mandibular fragment with I/1-I/2-I/3-C-P/2-P/3-P/4-M/1-M/2-M/3; ser. No. 41, right mandibular fragment with P/4-M/1-M/2-M/3 and alveoli of I/1-P/3; ser. No. 42, right mandibular fragment with M/1 and alveoli of I/1-P/4, M/2-M/3; ser. No. 43, left mandibular fragment with P/4-M/1-M/2-M/3 and alveoli of I/1-P/3; ser. No. 123, left mandibular fragment with I/2, M/1, M/3 and alveoli of I/1, I/3-P/4, M/2; ser. No. 124, left mandibular fragment with P/3-P/4, M/2-M/3 and alveoli of P/2, M/2; ser. No. 125, left mandibular fragment with I/1-I/2-I/3, P/2-P/3-P/4, M/2 and alveoli of C, M/1; ser. No. 126, left mandibular fragment with M/1-M/2-M/3; ser. No. 127, left mandibular fragment with M/1 and alveoli of I/1-P/4; ser. No. 128, left mandibular fragment with damaged M/1 and alveoli of P/2-P/4; ser. No. 129, left mandibular fragment with alveoli of I/1-P/4; ser. No. 130, left mandibular fragment with alveoli of I/1-P/4; ser. No. 131, right mandibular fragment with P/4, M/2 and alveoli of I/1-P/3, M/1, M/3; ser. No. 132, right mandibular fragment with M/2 and alveole of M/1; ser. No. 133, right mandibular fragment (ascending ramus); Reg. No. of the next two mandibles V. 86. 24. ser. No. 135+, left mandibular fragment with P/4-M/1 and alveole of P/3; ser. No. 136+, left mandible with P/4, M/2-M/3 and alveoli of I/1-P/3, M/1.

Comparisons and remarks. Though the material is rather fragmentary, all teeth are represented in it. Regarding the available measurements (see Tables 3, 5) the sample - without any overlap - is smaller in three characters than in the recent *P. auritus* females from Hungary and Czechoslovakia as: width of rostrum at C-C alveoli, width of rostrum at M3/-M3/, and M3/ width. In other three features the smaller measurements of the Beremend *P. abeli* showed some overlap with the recent *P. auritus*, as in M3/-M3/ alveolar width of rostrum, depth of intermaxillary notch, and basal length of P/3. The available measurements of the Beremend sample were definitely greater than or just slightly overlapping with *P. auritus* in six characters: width of anterior palatal emargination, P4/-M3/ length, M1/-M3/ length, basal length of P4/, length of M1/, length of M3/. The values were greater in *P. abeli* but overlapping in ten features: length of M2/, length of mandible, P/4-M/3 length, M/1-M/3 length, M/1-M/3 alveolar length, P/2 basal length, P/2 basal width, M/2 length, height of mandibular body under M/1, height of mandibular body behind M/3. Because of extensive overlap, the Beremend *P. abeli* and recent *P. auritus* of Europe could be regarded

Table 4. Measurements - minimum and maximum values (number of cases; mean in parentheses) - of mandibular pieces and lower dentition of fossil Plecotus (P.) cf. abeli and Plecotus (P.) abeli from Hungary, and Plecotus (P.) auritus from Europe

Species / Character	P. (P.) cf. abeli Osztramos	P. (P.) abeli Beremend	P. (P.) auritus Europe
ML		10.31-10.98 (6;10.620)	10.25-10.45 (5;10.400)
LCM		5.98-6.03 (2;6.005)	5.75-6.01 (5;5.862)
LCMA	5.49-5.75 (4;5.627)	5.57-6.11 (12;5.765)	5.44-5.89 (5;5.608)
LPM	4.40-4.50 (2;4.441)	4.27-4.72 (9;4.462)	4.14-4.36 (5;4.280)
LCP	2.10	2.27-2.31 (4;2.280)	2.13-2.31 (5;2.196)
LCPA	2.00-2.23 (8;2.104)	2.03-2.27 (18;2.145)	1.90-2.23 (5;2.074)
LMM	3.70-3.84 (4;3.772)	3.56-4.09 (10;3.849)	3.56-3.77 (5;3.660)
LMMA	3.14-3.52 (4;3.405)	3.40-3.91 (16;3.595)	3.28-3.48 (4;3.430)
LCL		0.77-0.81 (4;0.790)	0.72-0.81 (5;0.772)
LCW	0.72	0.72-0.81 (4;0.787)	0.72-0.86 (5;0.762)
LPTL		0.52-0.59 (3;0.553)	0.40-0.55 (5;0.500)
LPTW		0.57-0.77 (3;0.626)	0.55-0.65 (5;0.578)
LTPL	0.34-0.36 (2;0.350)	0.32-0.36 (5;0.352)	0.36-0.36 (5;0.360)
LTPW	0.45-0.57 (2;0.510)	0.43-0.50 (5;0.466)	0.45-0.55 (5;0.500)
LPFL	0.68-0.77 (9;0.737)	0.63-0.79 (16;0.718)	0.68-0.77 (5;0.706)
LPFW	0.59-0.72 (9;0.671)	0.57-0.72 (15;0.658)	0.59-0.70 (5;0.652)
LMOL	1.36-1.45 (10;1.421)	1.31-1.52 (14;1.446)	1.27-1.40 (5;1.316)
LMOW	0.86-1.02 (10;0.982)	0.86-1.00 (14;0.941)	0.86-1.02 (5;0.936)
LMTL	1.27-1.40 (12;1.347)	1.22-1.45 (16;0.376)	1.21-1.33 (5;1.268)
LMTW	0.90-1.04 (11;0.978)	0.86-1.04 (15;0.948)	0.90-1.06 (5;0.966)
LTML	1.09-1.22 (8;1.153)	1.11-1.22 (12;1.186)	1.13-1.18 (5;1.160)
LTMTR	0.81-0.90 (8;0.867)	0.72-0.90 (13;0.810)	0.72-0.90 (5;0.794)
LTMTA	0.61-0.68 (8;0.663)	0.59-0.70 (12;0.631)	0.59-0.74 (5;0.640)
HMUM	1.40-1.63 (13;1.493)	1.36-1.68 (24;1.513)	1.31-1.45 (4;1.392)
HMBM	1.20-1.45 (10;1.362)	1.22-1.59 (19;1.317)	1.27-1.40 (4;1.325)
HCP	2.95-3.04 (2;2.995)	2.77-3.10 (2;2.924)	2.72-2.95 (5;2.850)

as identical in all the other 35 measured and comparable features (see Tables 3, 5). As compared with the Asian specimens, the Beremend P. abeli was smaller in about 24 characters and the most numerous deviations were seen in comparison with the Mongolian animal (see Tables 3, 4, 5, 6). It was interesting to observe that in three features Beremend P. abeli was greater than the Korean P. auritus: in width of intermaxillary notch, width of anterior palatal emargination, M3/ length and greater than the Mongolian P. auritus in two characters such as depth of anterior palatal emargination and M3/ length. As compared with RABEDER's data C-C alveolar width of rostrum was exactly the same in the Mixnitz Cave population aged of Upper Pleistocene and the only available width at M3/-M3/ falls into the range of those of the specimens from Mixnitz. M3/ length an M3/ width measurements are also equal to the longest and the widest values from the Mixnitz Cave. P4/ length is considerably greater than that of P. auritus and the range of its values highly coincides with the values from the Mixnitz Cave. Mean values of M1/ length and M2/ length very close in the Beremend and the Mixnitz Cave materials, being greater than in the recent P. auritus.

All in all, P. abeli seems to have narrower rostrum (C-C alveolar width and M3/-M3/ width consistently smaller) than any of the recent P. auritus including the Asian specimens studied. Its M3/ is probably longer and narrower, and P4/-M3/ alveolar length greater be-

Table 5. Measurements - minimum and maximum values (number of cases; mean in parentheses) - of rostra, maxillary pieces and upper dentition of fossil Plecotus (P.) pliocaenicus, recent Plecotus (P.) austriacus from Europe and recent Plecotus (P.) auritus from Asia

Species / Character	P. (P.) pliocaenicus Osztramos	P. (P.) austriacus Europe	P. (P.) auritus Korea	P. (P.) auritus Mongolia
IOB	4.18	3.49-3.77 (6; 3.558)	3.60	3.79
CCR		4.33	4.20	
CCRA	3.99	4.11-4.33 (6; 4.193)	3.99	4.10
MMR		6.59-6.80 (6; 6.698)	6.60	6.45
MMRA		6.50-6.72 (6; 6.606)	6.56	6.27
BIN	2.03	1.86-2.13 (6; 1.970)	1.72	1.83
DIN	2.00	2.31-2.72 (6; 2.458)	2.41	2.23
WAPE	1.54	1.40-1.65 (6; 1.481)	1.31	1.36
DAPE	1.22	1.27-1.54 (6; 1.343)	1.50	1.27
WRL	5.45	4.85-5.30 (6; 5.108)	5.26	5.26
MHP	1.59-2.03 (8; 1.874)	1.81-2.03 (6; 1.885)	1.90	2.03
MHM	1.13-1.50 (7; 1.277)	1.04-1.13 (5; 1.068)	1.04	1.27
AB	0.16-0.32 (4; 0.270)	0.23-0.36 (6; 0.291)	0.23	0.34
UCM	5.91	6.08-6.47 (6; 6.248)	5.80	5.91
UCMA	5.35-5.66 (3; 5.500)	5.70-6.07 (6; 5.855)	5.49	5.61
UPM	4.50	4.40-4.72 (6; 4.565)	4.31	4.31
UPMA	4.36-4.36 (3; 4.360)	4.23-4.63 (6; 4.420)	4.14	4.19
UCP	2.68-2.86 (3; 2.753)	2.72-3.00 (6; 2.886)	2.77	2.77
UCPA	2.45-2.59 (6; 2.543)	2.45-2.68 (6; 2.565)	2.41	2.41
UMM	3.64	2.48-3.73 (6; 3.616)	3.44	3.44
UMMA	3.18-3.32 (3; 3.240)	3.28-3.56 (6; 3.406)	3.08	3.14
UCL	1.04-1.09 (3; 1.073)	1.09-1.27 (6; 1.186)	1.04	1.04
UCLA	0.81-0.90 (3; 0.856)			
UCW	0.95-1.00 (3; 0.966)	0.95-1.13 (6; 1.013)	0.92	0.92
UCWA	0.59-0.68 (3; 0.650)			
UPTL	0.50-0.55 (2; 0.525)	0.36-0.52 (6; 0.446)	0.50	0.45
UPTW	0.61-0.68 (2; 0.645)	0.52-0.61 (6; 0.568)	0.59	0.55
UPFL	1.22-1.50 (7; 1.342)	1.27-1.36 (6; 1.345)	1.31	1.36
UPFW	0.92-1.04 (7; 1.021)	1.00-1.09 (6; 1.035)	1.00	1.04
UMOL	1.31-1.54 (12; 1.427)	1.40-1.54 (6; 1.465)	1.45	1.45
UMOW	1.59-1.81 (12; 1.702)	1.68-1.77 (6; 1.723)	1.72	1.72
UMTL	1.42-1.54 (7; 1.481)	1.45-1.59 (6; 1.501)	1.42	1.36
UMTW	1.72-1.95 (7; 1.865)	1.81-1.95 (6; 1.856)	1.86	1.81
UTML	0.63-0.68 (2; 0.650)	0.63-0.72 (6; 0.681)	0.63	0.59
UTMW	1.72-1.97 (2; 1.845)	1.72-1.95 (6; 1.850)	1.90	1.72

Table 6. Measurements - minimum and maximum values (number of cases; mean in parentheses) - of mandibular pieces and lower dentition of fossil Plecotus (P.) pliocaenicus, recent Plecotus (P.) austriacus from Europe and recent Plecotus (P.) auritus from Asia

Species / Character	P. (P.) pliocaenicus Osztramos	P. (P.) austriacus Europe	P. (P.) auritus Korea	P. (P.) auritus Mongolia
ML		11.10-11.78 (6; 11.486)	11.04	11.04
LCM		6.30-6.96 (6; 6.645)	6.23	6.31
LCMA	6.11	6.11-6.53 (6; 6.303)	6.15	5.93
LPM	4.68	4.63-5.13 (6; 4.823)	4.56	4.59
LCP	2.56	2.41-2.72 (6; 2.536)	2.47	2.41
LCPA	2.08-2.45 (8; 2.276)	2.27-2.64 (6; 2.413)	2.27	2.13
LMM	3.93	3.91-4.27 (6; 4.083)	3.91	3.86
LMMA	3.77	3.73-4.05 (6; 3.873)	3.68	3.64
LCL	0.83	0.81-0.97 (6; 0.876)	0.86	0.86
LCW	0.92	0.90-1.04 (6; 0.956)	0.90	0.90
LPTL	0.59-0.59 (2; 0.590)	0.55-0.63 (6; 0.586)	0.55	0.59
LPTW	0.72-0.77 (2; 0.745)	0.63-0.72 (6; 0.673)	0.70	0.63
LTPL	0.45-0.47 (2; 0.458)	0.34-0.45 (6; 0.368)	0.36	0.34
LTPW	0.63-0.65 (2; 0.640)	0.50-0.59 (6; 0.538)	0.61	0.52
LPFL	0.72-0.90 (7; 0.818)	0.72-0.86 (6; 0.803)	0.77	0.81
LPFW	0.72-0.81 (7; 0.774)	0.70-0.77 (6; 0.725)	0.72	0.72
LMOL	1.45-1.54 (5; 1.514)	1.47-1.59 (6; 1.531)	1.54	1.50
LMOW	1.04-1.13 (5; 1.092)	1.00-1.09 (6; 1.041)	1.04	1.09
LMTL	1.54	1.45-1.54 (6; 1.496)	1.42	1.47
LMTW	1.15	1.00-1.09 (6; 1.041)	1.06	1.09
LTML	1.09	1.20-1.27 (6; 1.231)	1.20	1.18
LTMTR	0.95	0.77-0.90 (6; 0.856)	0.90	0.86
LTMTA	0.72	0.59-0.72 (6; 0.648)	0.63	0.59
HMUM	1.40-1.59 (6; 1.520)	1.45-1.68 (6; 1.520)	1.45	1.63
HMBM	1.45	1.31-1.59 (6; 1.473)	1.36	1.50
HCP	3.18	3.32-3.48 (6; 3.433)	3.04	3.40

cause of the greater length of P4/, at least compared with the European P. auritus. M1/ and M2/ are antero-posteriorly also longer than in the European P. auritus. Regarding the lower premolars, P/2 basally longer and wider, that is somewhat greater than in European P. auritus, but with considerable overlap. P/3, however, is shorter basally. There are smaller values in this character than in the Asiatic specimens. The mean width of P/3 is smaller as compared to the European specimens, and absolutely narrower than the tooth of specimens from Korea and Mongolia.

Plecotus (Plecotus) cf. abeli Wettstein, 1923

WETTSTEIN's species was reported from the type locality Mixnitz Cave (Upper Pleistocene) and also from the Lower Pleistocene of Deutsch Altenburg 2 by RABEDER (1974). I attribute the same name to this population of a smaller-sized Plecotus (Plecotus) collected along with a greater animal (see below in this paper) from Osztramos Loc. 9, Lower Pliocene. With this population, the abeli-like species must have appeared a few million years earlier than it had been thought before.

List of specimens studied in this work, from Osztramos Loc. 9, deposited in the collection of the Palaeontological Department, Hungarian Natural History Museum: Reg. No. of maxillary pieces V. 86. 12.: ser. No. 85, left maxillary fragment with P4/ and alveoli of I1/-P2/; ser. No. 114, left maxillary fragment with P4/, M2/-M3/ and alveoli of C-P2/, M1/; ser. No. 115, right maxillary fragment with P2/-P4/-M1/-M2/-M3/ and alveoli of I1/-C; ser. No. 77, right maxillary fragment with P4/-M1/-M2/-M3/; ser. No. 78, left maxillary fragment with M1/-M2/ and fragmentary M3/; ser. No. 104, left maxillary fragment with damaged M2/ and alveole of M1/; ser. No. 53, left maxillary fragment with I1/-I2/-C-P2/-P4/; ser. No. 54, left maxillary fragment with damaged M1/-M2/; ser. No. 55, left maxillary fragment with P4/ and alveole of M1/; ser. No. 56, right maxillary fragment with C-P2/-P4/; ser. No. 57, right maxillary fragment with P2/-P4/ and alveoli of I2/-C; ser. No. 59, right maxillary fragment with P4/, M2/ and alveoli of C-P2/, M1/; ser. No. 60, right maxillary fragment with P4/-M1/ and alveoli of C-P2/; ser. No. 61, right maxillary fragment with M1/-M2/; ser. No. 62, right maxillary fragment with M1/; ser. No. 63, left maxillary fragment with M2/; Reg. No. of mandibular pieces V. 86. 13.: ser. No. 79, right mandibular fragment with M/2-M/3, almost intact ascending ramus and alveoli of I/2-M/1; ser. No. 80, right mandibular fragment with M/1-M/2-M/3 and alveole of P/4; ser. No. 81, right mandibular fragment with P/4 and alveoli of I/3-P/3, M/1-M/2; ser. No. 82, right mandibular fragment with P/4 and alveoli of P/3, M/1; ser. No. 83, right mandibular fragment with M/3; ser. No. 49, left mandibular fragment with M/1-M/2-M/3; ser. No. 108, left mandibular fragment with P/3-P/4-M/1 and alveoli of I/1-P/2, M/2; ser. No. 109, left mandibular fragment with P/4-M/1-M/2 and alveoli of P/2-2/3; ser. No. 64, left mandibular fragment with M/1-M/2, fragmentary M/3 and alveoli of I/1-P/4; ser. No. 66, right mandibular fragment with C, P/3-P/4-M/1-M/2 and alveoli of P/2, M/3; ser. No. 67, right mandibular fragment with P/4-M/1-M/2-M/3 and alveole of P/3; ser. No. 68, right mandibular fragment with P/4-M/1-M/2-M/3 and alveoli of P/2-P/3; ser. No. 69, right mandibular fragment with P/4-M/1-M/2-fragment of M/3 and alveole of P/3; ser. No. 70, right mandibular fragment with P/4-M/1-M/2 and alveoli of I/1-P/3; ser. No. 71, right mandibular fragment with M/2-M/3 and damaged ascending ramus; ser. No. 72, right mandibular fragment with M/2-M/3; ser. No. 74, right mandibular fragment with alveoli of I/1-M/3; ser. No. 76, right fragmentary ascending ramus; ser. No. 101, right mandibular fragment with alveoli of I/1-P/4. For measurements of the material see Tables 3, 5.

Comparisons and remarks. Almost all teeth are represented in the extremely fragmentary material (except the lower incisivi), however, some are in very small number. Considering the comparable measurements of characters in P. cf. abeli from Osztramos Loc. 9 (one specimen), it was smaller than P. auritus from Europe in its C-P/4 length. In other two characters, M/1 antero-posterior length and P/4-M/3 length, P. cf. abeli was greater than P. auritus (with no overlap). In four characters there was just a transition of greater measurements of P. cf. abeli, thus, a slight overlap as in maxillary height at M2/, P4/-M3/ length and height of coronoid process. There was more overlap between P. cf. abeli and European P. auritus in the following nine measurements, where of course the former had greater values: P4/-M3/ length, upper C basal width, P2/ basal length, P4/ width, M2/ antero-posterior length, M/1-M/3 length, M/1 antero-posterior length, M/2 antero-posterior length and height of mandibular body under M/1. In all the other 29 comparable features P. cf. abeli and European P. auritus showed extensive overlap. The population of P. cf. abeli was generally smaller than the recent P. auritus from Korea and Mongolia in 21 and 22 characters, respectively, among these 15 were common to both Asiatic specimens. The fossil animal was clearly greater, however, than the Korean specimen in M3/ length and greater than the Mongolian one in M3/ length and M/3 talonid width (see Tables 3, 5, 6). It is worth to be noted that both P. abeli from Beremend and P. cf. abeli from Osztramos in the following eight characters had greater values (with overlap of various degree) than those of the European P. auritus: P4/-M3/ length, M1/-M3/ length, M1/ antero-posterior length, M2/ antero-posterior length, P/4-M/3 length, M/1-M/3 length, M/2 antero-posterior length and height of mandibular body under M/1. As far as one can consider the available measurements, P.abeli and P. cf. abeli had generally similar characters and equal measurements except in maxillary height at M2/, upper C alveolar length, and M3/ width, where the Pliocene population had greater values, and in P4/-M3/ length, C-P4/ length, P4/ antero-posterior length, M3/ length, C-P/4 length and M/1-M/3 length were the Pliocene population had smaller values.

Plecotus (Plecotus) pliocaenicus Topál, 1988

This is one of the earliest Plecotus (Plecotus) species in Hungary. It was found in the Estramontian horizon of the Lower Pliocene of the Osztramos Locality 9. Being a great-sized Plecotus, in some respects related to Plecotus (Plecotus) austriacus (Fischer, 1829), and it has greater measurements than those of Plecotus (Plecotus) abeli Wettstein, 1923.

Holotype: A right mandibular fragment (see Plate II, Figs 9, 10) with I/1-I/2-I/3-C-P/2-P/3-P/4-M/1 Reg. No. V.86.14, deposited in the collection of the Palaeontological Department, Hungarian Natural History Museum, Budapest. Ser. No.111. Measurements of the Holotype: LCP 2.56, LCPA 2.41, LCL 0.83, LCW 0.92, LPTL 0.59, LPTW 0.77, LTPL 0.47, LTPW 0.65, LPFL 0.77, LPFW 0.72, LMOL 1.50, LMOW 1.09, HMUM 1.54.

Other material and selected paratype: Reg. No. V.86.16., ser. No.86, damaged rostrum with damaged right P4/, intact M1/-M2/ and alveoli of I1/-P2/, M3/ and alveoli of left I1/-P2/; Reg. No. of maxillary pieces V.86.17: ser. No.87, right maxillary fragment with P4/-M1/; ser. No.88, right maxillary fragment with M2/-M3/; ser. No.89, right maxillary fragment with M1/; ser. No.91, left maxillary fragment with C-P2/-P4/-M1/ and alveoli of I1/-I2/; ser. No.92, left maxillary fragment with M1/-M2/ and alveole of M3/; ser. No.102, left maxillary fragment with C, P4/-M1/-M2/ and alveoli of I1/-I2/, P2/; ser. No.103, left maxillary fragment with P4/-M1/ and alveoli of I1/-P2/; ser. No. 105, right maxillary fragment with P4/-M1/ and alveoli of I1/-P2/, M2/; ser. No.106, right maxillary fragment with M1/-M2/; ser. No.107, right maxillary fragment with M2/; ser. No.116, left maxillary fragment with P4/-M1/; ser. No.117, left M1/; Reg. No. of mandibular pieces V.86.18.: ser. No.93, left mandibular fragment with P/4-M/1; ser. No.95, left mandibular fragment with alveoli of I/1-P/4; ser. No.97, right mandibular fragment with P/2-P/3-P/4-M/1-M/2 trigonid; ser. No.98, right mandibular fragment with P/4 and alveoli of I/1-P/3; ser. No.100, right mandibular fragment with P/4 and alveoli of C-P/3; ser. No. 110, right mandible with missing articular process, with P/4-M/1, damaged M/2-M/3 and alveoli of I/1-P/3; ser. No.112, right mandibular fragment with P/4-M/1-M/2 and alveoli of I/2-P/3; ser. No.65, left mandibular fragment with no teeth but alveoli of C-M/1; ser. No.75, right mandibular fragment with alveoli of C-M/2; a selected paratype (see Plate II, Fig. 11), Reg. No. V.86.15., ser. No.90, left maxillary fragment with C-P2/-P4/-M1/-M2/-M3/. Measurements of the selected paratype: MHP 1.86, MHM 1.28, AB 0.32, UCM 5.91, UCMA 5.66, UPM 4.50, UPMA 4.36, UCP 2.72, UCPA 2.45, UMM 3.64, UMMA 3.18, UCL 1.09, UCW 0.95, UPTL 0.50, UPTW 0.68, UPFL 1.36, UPFW 0.92, UMOL 1.54, UMOW 1.77, UMTL 1.54, UMTW 1.95, UTML 0.68, UTMW 1.72.

Measurements: including those of holotype and selected paratype, minimum and maximum values (number of cases: mean in parentheses). IOB 4.18, CCRA 3.99, BIN 2.03, DIN 2.00, WAPE 1.54, DAPE 1.22, WRL 5.45, MHP 1.59-2.03 (8:1.874), MHM 1.13-1.50 (7:1.277), AB 0.16-0.32 (4:0.270), UCM 5.91, UCMA 5.35-5.66 (3:5.500), UPM 5.40, UPMA 4.36-4.36 (3:4.360), UCP 2.68-2.86 (3:2.753), UCPA 2.45-2.59 (6:2.343), UMM 3.64, UMMA 3.18-3.32 (3:3.240), UCL 1.04-1.09 (3:1.073), UCLA 0.81-0.90 (3:0.856), UCW 0.95-1.00 (3:0.966), UCWA 0.59-0.68 (3:0.650), UPTL 0.50-0.55 (2:0.525), UPTW 0.61-0.68 (2:0.654), UPFL 1.22-1.50 (7: 1.342), UPFW 0.92-1.04 (7:1.021), UMOL 1.31-1.54 (12:1.427), UMOW 1.59-1.81 (12:1.702), UMTL 1.42-1.54 (7:1.481), UMTW 1.72-1.95 (7:1.865), UTML 0.63-0.68 (2:0.650), UTMW 1.72-1.97 (2:1.845), LCMA 6.11, LPM 4.68, LCP 2.56, LCPA 2.08-2.45 (8:2.276), LMM 3.93, LMMA 3.77, LCL 0.83, LCW 0.92, LPTL 0.59-0.59 (2:0.590), LPTW 0.72-0.77 (2:0.745), LTPL 0.45-0.47 (2:0.458), LTPW 0.63-0.65 (2:0.640), LPFL 0.72-0.90 (7:0.818), LPFW 0.72-0.81 (7:0.774), LMOL 1.45-1.54 (5:1.514), LMOW 1.04-1.13 (5:1.092), LMTL 1.54, LMTW 1.15, LTML 1.09, LTMTR 0.95, LTMTA 0.72, HMUM 1.40-1.59 (6:1.520), HMBM 1.45, HCP 3.18.

Comparisons and remarks. P. pliocaenicus from Osztramos Loc. 9 furnished a rather fragmentary material with almost all teeth (except I1/ and I2/) represented but not in a complete upper or lower row. It seems to combine the size and some features of P. austriacus and some characters of P. auritus. The interorbital breadth (a single specimen) is exceedingly great, greater than that of any specimens used in this study. On the other hand, the C-C alveolar width of the rostrum of the species is smaller than that of P. austriacus, as well as most of P. auritus (except some small specimens). Width of intermaxillary notch of the rostrum exceeds that of recent P. auritus including ones from Asia, but equals that of P. austriacus. The depth of intermaxillary notch is shorter than even that of the smallest value of P. auritus, thus, the whole study material of recent specimens. The width of the anterior palatal emargination agrees well with that of P. austriacus, being greater than that of any auritus. Its depth, however, coincides with that of the smallest P. auritus. The length of the lacrimal crista is equal in P. pliocaenicus and in P. austriacus, however, its surface is not so sharp as in P. austriacus. Amongst the upper tooth-row and tooth measurements, the only available C-M3/ length in P. pliocaenicus falls between the ranges of P. auritus and P. austriacus, but equals that of the Mongolian P. auritus (see Tables 3, 4). P4/-M3/ length, P4/-M3/ alveolar length and M1/-M3/ length partly agree with those of (probably male) P. austriacus, being greater, without overlap, than that of any P. auritus studied. C-P4/ lengths coincide with those of P. austriacus, do not overlap with the European P. auritus, but do so with the Korean and Mongolian specimens. Upper C basal length without overlap falls between the recent P. auritus and P. austriacus, somewhat closer to the latter. The upper C basal width is equal to the smaller values of P. austriacus. The basal width of P2/ of the two available specimens is appreciably greater than that of any P. auritus and there is marginal overlap but with the maximum value of P. austriacus, the other specimen being greater than those in the P. austriacus studied. Basal lengths of P4/ of the seven studied specimens partly exceed the maximum values in P. austriacus, but the range includes the values of the Korean and Mongolian specimens of P. auritus. The width of P4/ is intermediate between that of P. auritus and P. austriacus, but to some extent the range overlaps both. This is also true for M1/ length, M1/ width and M2/ width. M2/ length, however, fits well into the range of P. austriacus and is thus greater than that of P. auritus.

As concerning the lower dentition, the only measurement of C-M/3 alveolar length of Plecotus pliocaenicus agrees with the smallest specimen of P. austriacus and practically with that of the Korean P. auritus. P/4-M/3 length, C-P/4 length, M/1-M/3 length and M/1-M/3 alveolar length of P. pliocaenicus all fall into the range of the same measurement in P. austriacus, thus it is greater than in P. auritus and even in the Asiatic P. auritus (see Tables 5, 6). The lower C basal length agrees with that of P. austriacus and evidently with that of the Asiatic P. auritus. The basal length of P/2 equals that of P. austriacus and P. auritus from Mongolia. The basal width of P/2 overlaps but with the maximum value of P. austriacus and it is even greater. A very similar case is with P/3 basal width. So these small premolars are as bulky as those of P. austriacus, thus greater than in P. auritus. Moreover, these fossil teeth are antero-posteriorly somewhat longer than in the evidently more advanced P. austriacus (see Plate II, Figs 7, 8, 9). This is especially true for P/3 basal length, also in Asiatic specimens of P. auritus. P/2 has a well-developed antero-internal cingulum-cusp both in P. pliocaenicus and in P. austriacus. Such a cusp is missing in P. auritus. There is no actual difference in the dimensions of P/4, however, the basal cross-sectional outline is angular in P. pliocaenicus and antero-posteriorly more elongated than in P. austriacus and its outer anterior margin is not obliquely cut as in P. auritus. The M/1 length and the width of P. pliocaenicus equal those of P. austriacus and Korean and Mongolian P. auritus. M/2 lengths equal to and its width exceeds, however, (one case for each) the maximum values of P. austriacus. The trigonid width of M/3 of P. pliocaenicus seems to be greatest in the present study material. Finally, the heigth of the coronoid process of the new animal exceeds those of the European and Korean P. auritus, though it is lower than that of P. austriacus and Mongolian P. auritus.

A comparison of P. pliocaenicus on the one hand and P. abeli and P. cf. abeli on the other is as follows: value of depth of intermaxillary notch of P. pliocaenicus being smaller than in any recent specimens falls into the observed range of P. abeli from

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PLATE I: Figs 1-8 dorsal, occlusal and lateral views of rostra and maxillae of Plecotus (Corynorhinus) species. Figs 1-3 rostrum of No. 58.74.1. P. (C.) townsendii pallescens: 1= dorsal view, 2= occlusal view, 3= left lateral view. Figs 4-6 No. V.86.19 rostrum of P. (C.) crassidens: 4= dorsal view, 5= occlusal view, 6= left lateral view. Figs 7-8 No. V. 15228 (VT. 138) maxilla, holotype of P. C.) atavus: 7= occlusal view, 8= right lateral view

PLATE I

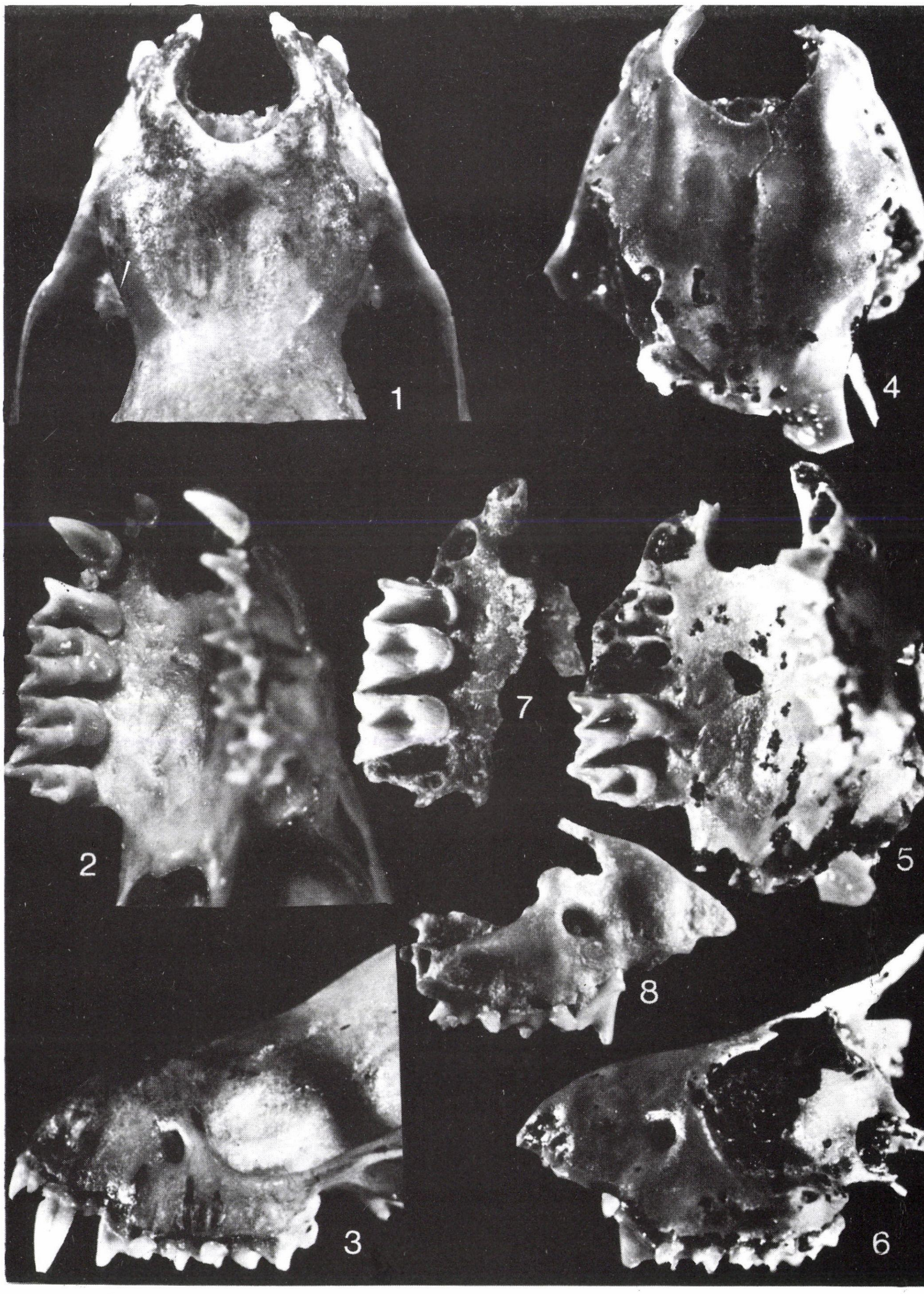
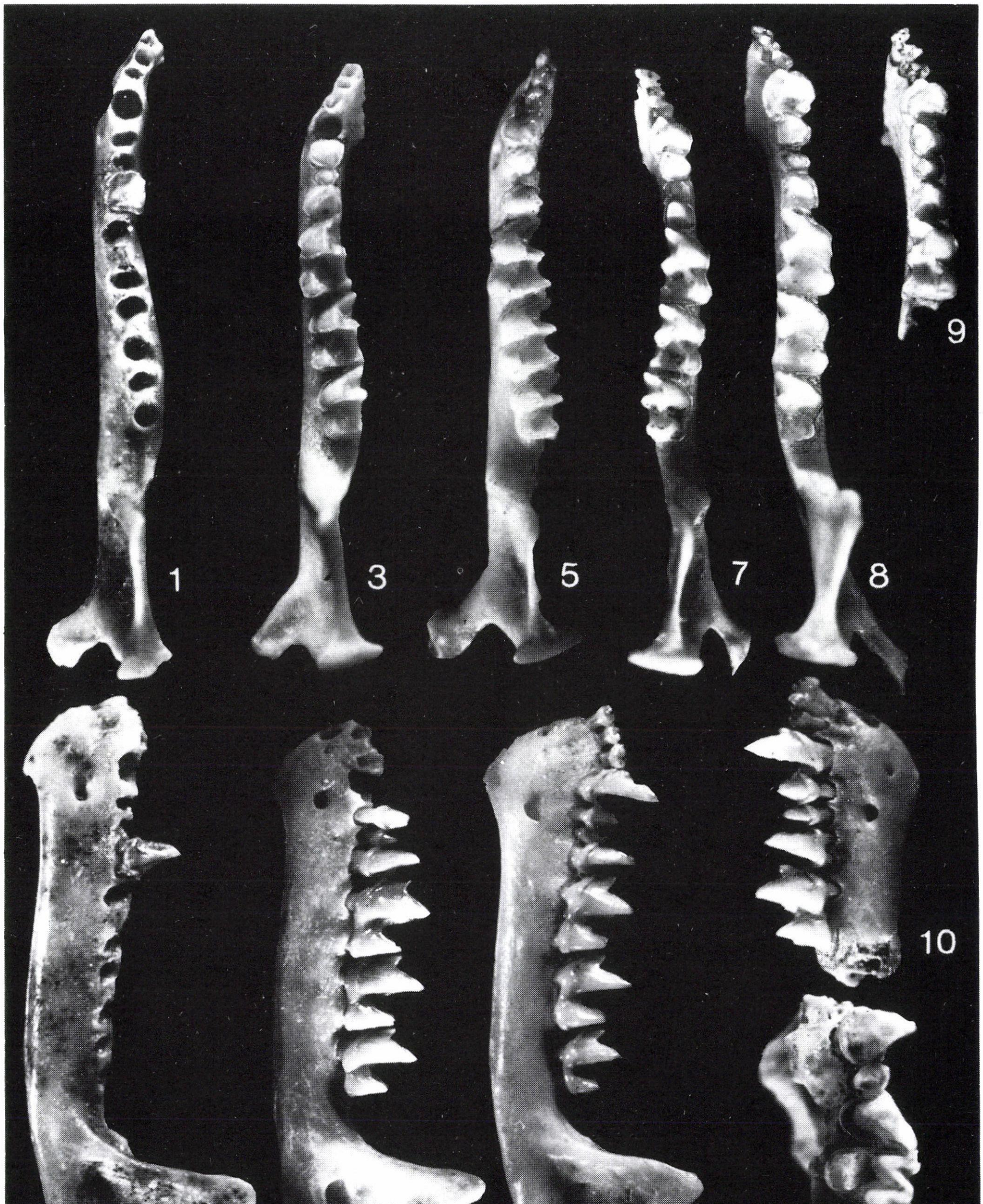


PLATE II



Beremend. There is a fourth, posterior cusp (smaller than in I/2) in I/1 of the new animal, however, it is missing in P. abeli. P. pliocaenicus has greater values than both P. abeli and P. cf. abeli in 19 characters (see Tables 3, 4, 5, 6): P4/-M3/ length, P4/-M3/ alveolar length, C-P4/ length, C-P4/ alveolar length, M1-M3/ length, upper C basal length, upper C basal width, P2/ width, C-P/4 length, lower C basal length, lower C basal width, P/3 basal length, P/3 basal width, P/4 width, M/2 length, M/2 width, M/3 trigonid width, M/3 talonid width, height of coronoid process. Both P/2 and P/3 are basally longer and wider in P. pliocaenicus thus, the species is probably more primitive. The basal cross-sectional outline of P/4 is angular in the new species and not obliquely cut on the anterior buccal margin as in Beremend P. abeli. The posterior outer portion of P/4 in P. abeli seems to be anteriorly drawn or pressed forward, not as in P. pliocaenicus. As compared to P. cf. abeli, P. pliocaenicus was greater (without overlap) in 21 characters (see Tables 3, 4, 5, 6), showed marginal overlap in 7 measurements, and extensive overlap in all the other 15 measurements.

CONCLUSIONS

The most recent findings of Plecotus (Corynorhinus) from the Upper Miocene of Polgárdi prove the presence of this, nowadays Nearctic, plecotine group as early as about six million years ago in Eurasia. One of the oldest known plecotine in the Holarctic. This animal proved to be new for science and was named Plecotus (Corynorhinus) atavus by the author in 1988. The next younger findings of Corynorhinus-like bat came from Podlesice, Poland and Osztramos Loc. 9, Hungary, aged Lower Pliocene. The present study could not show wheter this animal belonged to a new species or how close it was to Plecotus (Corynorhinus) atavus, because of the fragmentary state of the material used in this work. In any case, it was not P. (C.) crassidens as presumed in earlier studies. Corynorhinus-like plecotines disappeared from Europe during the Betfian substage of the Lower Pleistocene. Its most recent record (with the discovery of a well preserved rostrum) means the third known locality of this animal, Plecotus (Corynorhinus=Paraplecotus) crassidens Kormos, 1930 in the Carpathian Basin. A detailed comparison of the fossil remains and the recent Plecotus (C.) townsendii pallescens revealed that Plecotus (C.) atavus sp. n. showed some characters which could be considered as primitive features, though in some respects it was already on the way towards P. (C.) crassidens of the Lower Pleistocene. The latter was most probably on the top of a side-branch somewhat remote from the main stock. However, until such time as other populations and further specimens are discovered and a detailed study of the Pliocene animal, first of all the material from Podlesice is made, retaining Paraplecotus as a subgenus besides Corynorhinus seems to be unnecessary.

Based on rather uncertain evidence, and at present just on negative proof, it seems that Plecotus (Plecotus) species appeared in Europe later than Plecotus (Corynorhinus). Anyhow, their absence at Polgárdi during the Upper Miocene should be considered cautiously. The first known appearance happened during the Lower Pliocene in Europe. Osztramos Loc.9 of this age furnished two species of them. A smaller one, P. cf. abeli is related to P. abeli. At present the rather incomplete and fragmentary material does not allow a separation from P. abeli collected at Beremend Localities 16 and 17, Lower Pleistocene. On the other hand, both P. cf. abeli and P. abeli listed in the present work are evidently related to P. auritus

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PLATE II: Figs 1-6 occlusal and buccal views of left mandibles of Plecotus (Corynorhinus) species: Figs 1-2 No. V. 15229 left mandible, selected paratype of P. (C.) atavus: 1= occlusal view, 2= buccal view. Figs 3-4 No. V. 86. 20. left mandible of P. (C.) crassidens: 3= occlusal view, 4= buccal view. Figs 5-6 left mandible of No. 58. 74. 1. P. (C.) townsendii pallescens: 5= occlusal view, 6= buccal view. Fig. 7 occlusal view of right mandible of No. 71. 20. 1. Plecotus (Plecotus) auritus. Fig. 8 occlusal view of right mandible of No. 70. 14. 1. Plecotus (Plecotus) austriacus. Figs 9-10 No. V. 86. 14. right mandibular fragment, holotype of Plecotus (Plecotus) pliocaenicus: 9 = occlusal view, 10 = buccal view. Fig. 11 occlusal view of No. V. 86. 15. left maxillary fragment, selected paratype of P. (P.) pliocaenicus.

of Europe and in many respects to Asiatic P. auritus. With these findings the existence of abeli-like animals is greatly extended in time-span, down to the Lower Pliocene. Another Plecotus, a greater one from Osztramos Loc. 9 discussed in this paper, Plecotus (P.) pliocaenicus was found to be related to both P. austriacus and P. auritus. It could be considered as a common ancestor of these species, or at least a close relative of the hypothetical common ancestor.

The present material of plecotines studied in this work is still far from giving sufficient clues either of the place (places?) of origin of these bats, or of the time of emergence (evidently, it must have happened much earlier) and even the direction of probable migration routes. All these questions will have to be addressed in future studies of this group.

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