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PLIOCENE AND PLEISTOCENE BATS OF POLAND

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The fossil remains of Pliocene and Pleistocene bats from central and southern Poland have been examined, belonging to three families: Rhinolophidae, Miniopteridae and Vespertilionidae. In the material examined, 15 species of bats have been found, six of which being new: ***Rhinolophus kowalskii*** **Topal**, ***R. wenzensis*** sp. n., *R.* cf. *macrorhinus* Topal, *R. hanaki* sp. n. *R.* cf., *variabilis* Topal, *R. neglectus* Heller, ***Rhinolophus sp.*** **(*mehelyi?*) (Rhinolophidae)**; ***Miniopterus approximatus*** sp. n. (Miniopteridae); *Eptesicus kowalskii* sp. n., *E. mossoczyi* sp. n., *E.* cf. *serotinus* **(Schreber), *E. nilssoni* (Keyserling et Blasius), *Barbastella* cf. *schadleri*** Wettstein-Westersheim, *Plecotus rabederi* sp. n., *P.* cf. *abeli* Wettstein-Westersheim (Vespertilionidae). The material comes from then localities. The Pliocene faunas showed a high share of thermophilous species of the families Rhinolophidae and Miniopteridae. The deterioration of the climate towards the close of the Pliocene brought about a decline in thermophilous forms. The faunas of the middle Pleistocene show a complete absence of thermophilous species, while the share of forest and boreal species increases. It has been shown that from the early Pliocene onwards, changes which appear to be evolutionary trends have continued to take place in skull structure. Some of these trends were analysed, and they were found to consist mainly in the reduction of the splanchnocranium: shortening of the palate and of the premolar toothrows (both in the maxilla and the mandible). Postdental part of the mandible becomes shorter.

Key words: Chiroptera, Mammalia, taxonomy, Pliocene, Pleistocene, evolutionary trends, southern Poland.

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INTRODUCTION

We owe the oldest references to fossil bats in Poland to Roemer (1883) who listed a number of species, identified on the basis of remains found in caves in the region of Ojców. Roemer, however, did not give the stratigraphy, and the fauna he described is probably post-glacial. More recently, the fossil and subfossil bats of Poland were investigated by Kowalski (1956, 1958*a*, 1959, 1962*a*, 1964, 1970, 1971, 1972*a*, *b*, 1973, 1974*a* and others), and later by Wołoszyn (1961, 1963, 1964, 1969, 1970, 1976, 1982).

The fossil remains on which the work presented here was based come from various localities in central and southern Poland, dated at the early Pliocene to the middle Pleistocene. Except for Podlesice, where the remains were abundant and quite complete (skulls, rostral parts of skulls, mandibles, long bones etc.), the material is relatively scarce and rather incomplete. The whole material consists of several thousand specimens, from among which the remains belonging to the taxa investigated were selected.

The species of bats which are the object of study belong to three families: Rhinolophidae, Miniopteridae and Vespertilionidae; they represent about 60% of the fossil species known (or probably occurring) in Tertiary and early Quaternary deposits in Poland.

The genus *Myotis* of the family Vespertilionidae considered in the present paper will be dealt with later. However, the Polish species of this genus are briefly reviewed on pp. 228—230.

The systematics here accepted are mainly after Simpson (1945), with alternations concerning the family Miniopteridae (Mein and Tupinier 1977).

Most of the above-mentioned specimens are housed in the collection of the Department of Systematical and Experimental Zoology of the Polish Academy of Sciences in Kraków (ZZSiD). Materials borrowed from the Department of Paleozoology of the University of Wrocław (ZPALWr) were also used. Moreover, for comparative purposes, some specimens from the collections of the National Museum in Budapest (NMMB), and from the collections of the Institute of Zoology of the Charles University in Prague (ISZ, CU) were considered.

In describing the bone material, the following abbreviations were used: ros — rostrum, mx — maxilla, md — mandible, d — right, s — left, FM — mental foramen (foramen mentale), C/P2/P3/P4 — position of foramen mentale under C_1, P_2, P_3, P_4, Ar — articular process (processus articularis), Co — coronoid process (processus coronoideus), An — angular process (processus angularis).

A bracket in the description indicates that only the alveolus of the tooth in question has been preserved, while a bracket in conjunction with the result of the measurement means that the measurement was taken from the outer margins of the alveolus.

In the description the teeth are numbered according to the convention adopted by Miller (1907). The system of skull measurement used in the present paper is the same as used by Wołoszyn (1970). The method of taking measurements is illustrated in figure 1, while Tables 1A and B give the names of the measurements with their corresponding letter abbreviations.

In descriptions of dentition, the terms used are those given in the papers by Baudelot (1972), DeBlase and Martin (1974), Handley (1959), and others.

Acknowledgements. — I would like to thank Prof. dr. K. Kowalski who encouraged me to undertake this study, made his collection and reprints available, and offered much helpful advice. I would also like to express my gratitude to Prof. dr. Z. Kielan-Jaworowska and Prof. dr. H. Szarski for careful reading through the manuscript, and many constructive suggestions.

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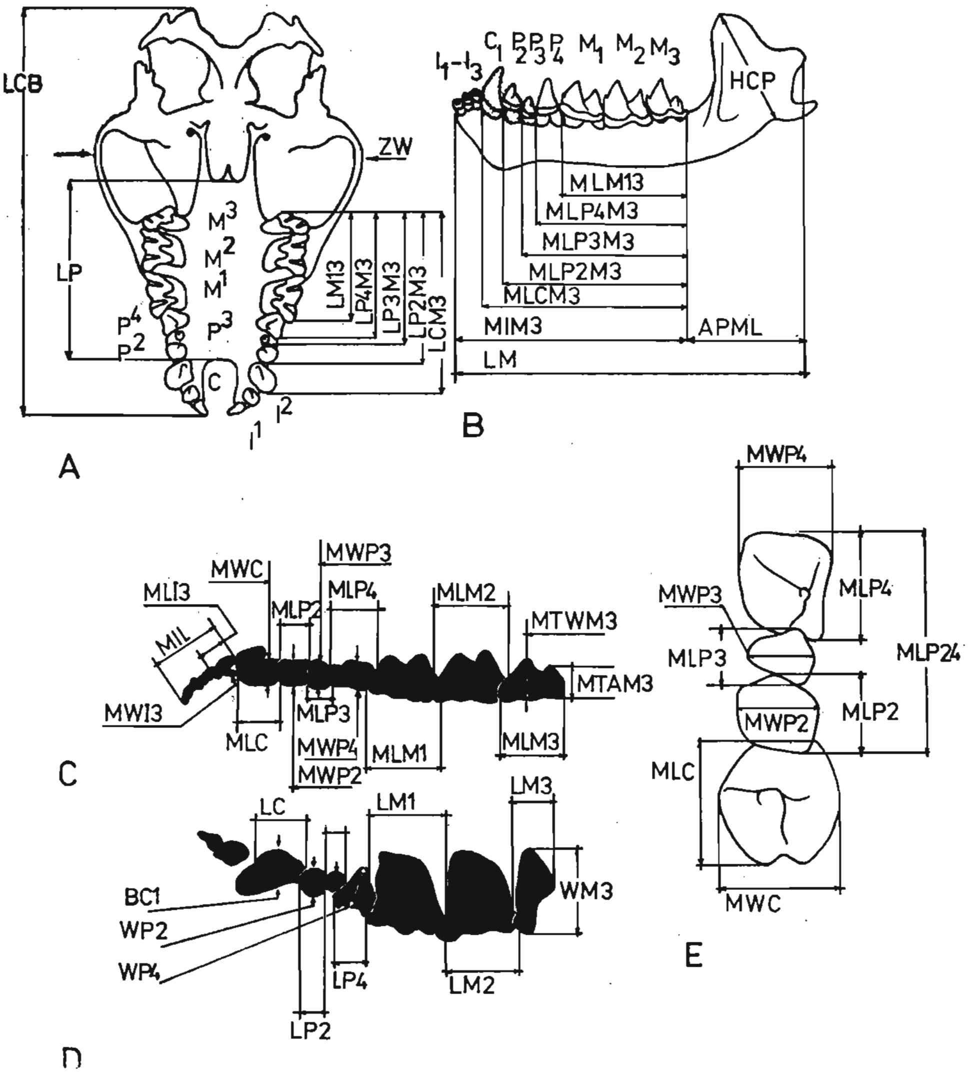

Fig. 1. System of measurements used in the paper. *A* skull measurements, *B* mandible measurements, *C* measurements of lower toothrow (I_1—M_3), *D* measurements of upper toothrow (I^1—M^3), *E* measurements of toothrow C_1—P_4.

DESCRIPTION OF LOCALITIES

The present work covers material of fossil bats of 10 localities from central and southern Poland, dated at the Pliocene, Plio-Pleistocene, also early and mid-Pleistocene. Localities are given in order of their geological age. The description contains the name of the locality, a letter of abbreviation by which it is referred to in the text and in illustrations. Next is given the geographical location, followed by paleoecological remarks with the list of bat species found at the locality.

Table 1. System of measurements used in the paper
A. Skull measurements; B. Mandibular measurements.

A. Skull measurements	Abbreviation	B. Mandibular measurements	Abbreviation
Condylobasal length	LCB	Length of mandible	LM
Width of braincase	WB	Articular process - M_3 length	APML
Zygomatic width	ZW	Height of coronoid process	HCP
Interorbital construction	IC	Incissors length	MIL
Length of palatum	LP	Length of C_1- M_3	MLCM3
Length of C^1- M^3	LCM3	Length of C_1- P_4	MLCP4
Length of P^2- M^3	LP1M3	Length of P_2- P_4	MLP24
Length of P^4- M^3	LP4M3	Length of P_2- M_3	MLP2M3
Length of M^1- M^3	LM13	Length of P_4- M_3	MLP4M3
Length of C^1- P^4	LCP4	Length of M_1- M_3	MLM13
Length of C^1	LC	Length of I_3	MIL3
Width of C^1	BC	Width of I_3	MIW3
Length of P^2	LP2	Length of C_1	MLC
Width of P^2	WP2	Width of C_1	MWC
Length of P^4	LP4	Length of P_2	MLP2
Width of P^4	WP4	Width of P_2	MWP2
Length of M^1	LM1	Length of P_3	MLP3
Width of M^1	WM1	Width of P_3	MWP3
Length of M^2	LM2	Length of P_4	MLP4
Width of M^2	WM2	Width of P_4	MWP4
Length of M^3	LM3	Length of M_1	MLM1
Width of M^3	WM3	Talonid width of M_1	MTWM1
Length of 1st commissure of M^3	K1	Length of M_2	MLM2
Length of 2nd commissure of M^3	K2	Talonid width of M_2	MTWM2
Length of 3rd commissure of M^3	K3	Length of M_3	MLM3
Length of 4th commissure of M^3	K4	Trigonid width of M_3	MTWM3
		Talonid width of M_3	MTAM3

The literature cited consists both of publications where fossil bats are either mentioned or fully discussed, and some other papers relevant to the paleoecology of the fauna of the locality investigated.

Detailed descriptions of localities have been given in numerous publications describing other groups of vertebrates found there; recently, Szyndlar (1984) compiled the descriptions of all the localities (fig. 2).

Podlesice (PO)

Geographical location: cave no. 431 (Kowalski 1951*a*) in Podlesice near Kroczyce (50° 34′N, 19°32′E), central part of the Kraków—Wieluń Upland, Poland.

Age of fauna: Early Pliocene, early Ruscinian (Kowalski 1974*b*; Szyndlar 1984).

Paleoecology: most probably the bat remains accumulated in the cave when the winter colony died out (Kowalski 1956), this being evidenced by the absence of young specimens in the thanatocoenosis.

The following species of bats were found: *Rhinolophus kowalskii* Topal, *Rhinolophus hanaki* sp. n., *Rhinolophus* sp., *Miniopterus approximatus* sp. n., *Myotis* cf. *aemulus* Heller, *Myotis dasycneme subtilis* Kowalski, *Myotis podlesicensis* Kowalski, *Myotis danutae* Kowalski, *Myotis helleri* Kowalski, *Plecotus rabederi* sp. n., *Eptesicus kowalskii* sp. n., *Eptesicus mossoczyi* sp. n. During the formation of breccia a warm climate of the Mediterranean type prevailed, though with fairly distinct seasons (Kowalski 1974 *b*).

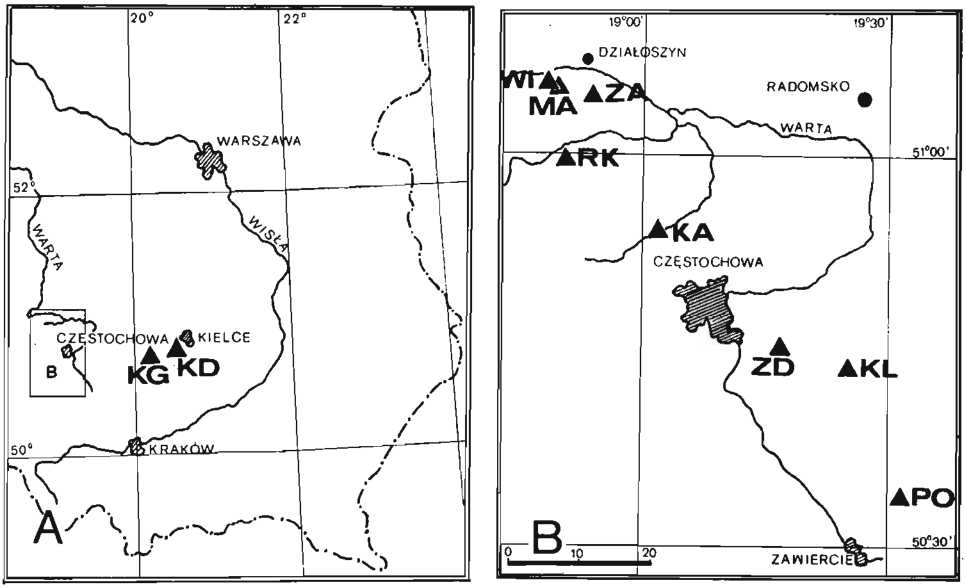

Fig. 2. *A* map of the localities of fossil fauna in the southern Poland, *B* enlarged fragment of map *A*, with localities of fossil bat fauna on the Kraków—Wieluń Upland. Symbols of localities: *PO* Podlesice, *MA* Mała Cave, *WI* Węże I, *RK* Rębielice Królewskie, *ZA* Zalesiaki, *KD* Kadzielnia, *KA* Kamyk, *KL* Kielniki, *KG* Kozi Grzbiet, *ZD* Zamkowa Dolna.

Mała Cave (MA)

Geographical location: Zelce Hill near Działoszyn (51°07′N, 18°49′E) northern part of the Kraków—Wieluń Upland, Poland.

Age of fauna: mid-Pliocene (Sulimski *et al.*, 1979).

Paleoecology: the chiropteran remains probably come from owl pellets, as indicated by their poor state of preservation. The species composition from older strata (4+5) would suggest a climate warmer than at present, close to Mediterranean.

At this locality the following species of bats were found: *Rhinolophus neglectus* Heller, *Rhinolophus hanaki* sp. n., *Rhinolophus kowalskii* Topal, *Myotis podlesicensis* Kowalski, *Myotis bechsteini* (Kuhl), *Myotis nattereri* (Kuhl).

Węże I (WE 1)

Geographical location: cave full of sediment, lying on Zelce Hill near Działoszyn (51°07′N, 18°49′E) northern part of the Kraków—Wieluń Upland, Poland.

Age of fauna: Kowalski (1964, and others) assumed the fossils to come from the Upper Pliocene (upper Ast). This point of view is widely accepted by paleontologists, and the fauna from Węże has been treated as an independent biozone in stratigraphical works (Fejfar and Heinrich 1983). Nevertheless, some authors (Głazek *et al.* 1976; Szyndlar 1984) suggest that deposits at the Węże locality are of a mixed nature, and they give three different sequences, corresponding to different periods of sedimentation of the remains: 1) late Lower Pliocene (Ruscinian), 2) Upper Pliocene (lower Villafranchian, 3) mid-Pleistocene (Cromerian). However, the chiropteran remains, mainly Rhinolophidae, would seem to suggest an older period of sedimentation, i.e. late Lower Pliocene.

Paleoecology: animal remains accumulated in a "sinkhole" type of cave, with a hole in the roof which was a trap for land animals. The remains of bats in the fauna from Węże are few and most probably come from owl pellets, this being supported by the considerable damage to skulls and the preponderance of mandibles over other parts of the skeleton. In the period in which the remains accumulated a warm climate of the Mediterranean type prevailed. The dominant type of vegetation was steppe with scrub and riparian forests (Kowalski 1959, 1962*a*, 1964).

To date, the following species of bats have been found: *Rhinolophus wenzensis* sp. n., *Rhinolophus* cf. *variabilis* Topal, *Myotis podlesicensis* Kowalski, *Myotis* cf. *aemulus* Heller, *Myotis* cf. *exilis* Heller, *Myotis helleri* Kowalski (Kowalski 1962*a*), *Plecotus rabederi* sp. n.

Rębielice Królewskie II (RK 2)

Geographical location: the locality lies in a quarry on a small hill, 258.6 m. alt., called "Góra" (51°00N, 18°51′E), rising near the village of Rębielice Królewskie, in the northern part of the Kraków—Wieluń Upland, Poland.

Age of fauna: Late Pliocene (late Villafranchian: Kowalski 1960 *a*, Villafranchian: Fejfar and Heinrich 1983).

Paleoecology: the source of the bat remains is difficult to determine.

Most probably they come from owl pellets. In the period during which the remains were deposited, a warm climate of the Mediterranean type prevailed, maybe only slightly cooler than at the Węże I locality. The vertebrate fauna comprises many aquatic forms (Kowalski 1960*a*).

In the material from this locality, the following species of bats were found: *Rhinolophus kowalskii* Topal, *Rhinolophus neglectus* Heller, *Myotis* sp.

Zamkowa Dolna (ZD)

Geographical location: cave no. 459 (Kowalski 1951*a*: 439—440, lying on the Castle Hill (Góra Zamkowa) in Olsztyn near Częstochowa 50°45′N, 19°18′E), central part of the Kraków—Wieluń Upland.

Age of fauna: the fauna is of a heterogeneous nature. Part of the remains have been dated at the Late Pleistocene (Würm): late Pleniglacial (Nadachowski 1982; Szyndlar 1984). However, some of the remains are without doubt older and are dated back to the early or middle Villafranchian (Kowalski 1977).

Paleoecology: beneath sediments from the last glaciation (in a wall--pocket) were found some red clays with rich bone material. These were mostly mammalian remains.

The composition of the fauna indicates that this locality is slightly younger than Rębielice Królewskie II. In the fauna there appear boreal and continental elements (Black and Kowalski 1974). The following species of bats were recorded here: *Plecotus* cf. *abeli* Wett., *Myotis* cf. *dasycneme* (Boie), *Myotis* sp.

Zalesiaki (ZA)

Geographical location: this locality lies several km east of the Węże I locality near Działoszyn (51°05′N, 18°54′E), northern part of the Kraków—Wieluń Upland, Poland.

Age of fauna: it is impossible to determine the stratigraphy since the locality was destroyed by a quarry. There are 15 samples of which nos. 1, 2, 5, 7, 8, 9, 10 and 13 contain fauna referred to as Cromerian (this part of the material is referred to in the literature as Zalesiaki A: Kowalski 1979; Szyndlar 1984). Samples nos. 3, 6, 11, 12, 14 and 15 contain also an admixture of Pliocene fauna alongside the Cromerian element, and are described as Zalesiaki B (Lit. op. cit.).

Probable age: Early Pleistocene (Szyndlar 1984).

Paleoecology: remains of bats from this locality are highly fragmentary. It is difficult to say why they have accumulated here; maybe they come from owl pellets.

The species of bats found here are: *Rhinolophus kowalskii* Topal, *Rhinolophus* sp. (*variabilis*?), *Myotis* sp.

Kadzielnia 1 (KD 1)

Geographical location: upper parts of "Skałka Geologów", immediately below the southern entrance to the Górna Cave at Kadzielnia lying within the Kadzielnia reserve, within the city bounds of Kielce (50°52′N, 20°39′E), Świętokrzyskie Mts.

Age of fauna: Early Pleistocene (Tiglian interglacial): Kowalski 1973; late Villanyian: Rabeder 1981; Fejfar and Heinrich 1983.

Paleoecology: climate cooler than during the formation of deposits in Węże I or Rębielice Królewskie II, but warmer than that prevailing in the region at the time. The fauna contains many forms associated with open areas (Kowalski 1958*a*, 1959). Remains of bats are infrequent, the state of their preservation indicating that they come from owl pellets.

The following species of bats were recorded here: *Rhinolophus* cf. *macrorhinus* Topal, *Myotis* cf. *exilis* Heller, *Myotis sp.*

Kamyk (KA)

Geographical location: this station lies in a small quarry, on a hill, close to the village of Kamyk (50°54′N, 19°01′E), northwest of Częstochowa.

Age of fauna: Early Pleistocene (early Biharian): Fejfar and Heinrich 1983.

Paleoecology: the composition of the fauna of small mammals suggests a steppe environment and a climate much cooler than at Kadzielnia 1 (Kowalski 1960*b*, 1964), yet the herpetological material indicates a much warmer climate (Szyndlar 1984).

The presence of a large *Rhinolophus* horseshoe bat of the "*ferrumequinum*" group in the material inclines us to accept the second possibility. The chiropteran fauna from this locality is rather fragmentary. The thanatocoenosis probably came into being due to the accumulation of owl pellets.

The following species of bats were found here: *Rhinolophus* cf. *macrorhinus* Topal, *Myotis* sp.

Kielniki 1 (KI 1)

Geographical location: this locality lies within the Kielniki quarry, several kilometres northeast of Olsztyn near Częstochowa (50°44′N, 19°24′E) central part of the Kraków—Wieluń Upland.

Age of fauna: no precise details of the stratigraphy are at present available for this site. Młynarski (1977) estimates the age of this fauna at the Günz glaciation; Stworzewicz (1975) at the Early Pleistocene.

Paleoecology: Stworzewicz (1981) reported that the malacofauna of the locality described has a basically woodland character. The climate, however, was warmer than at present, this also being suggested by the presence of remains of a large horseshoe bat.

Rhinolophus cf. *macrorhinus* Topal was found here.

Kozi Grzbiet (KG)

Geographical location: in the northern face of the discused quarry in Kozi Grzbiet (50°51′N, 20°27′E) near Miedzianka in the Świętokrzyskie Mts.

Age of fauna: mid-Pleistocene (Głazek *et al.* 1976).

Paleoecology: this is a fragment of a cave filled with deposits containing numerous bone remains. Both the malaco- and herpetofauna indicate that during formation of sediments the climate was fairly warm (Młynarski 1977; Stworzewicz 1981; Szyndlar 1984), which would be consistent with the conclusions of Głazek *et al.* (1977) that layer 2 represents a warm phase preceding the Mindel II glaciation, sample 2b corresponding to the climatic optimum of this phase.

On the basis of the mammalian fauna, Kowalski (1975) suggested that during the period in which deposits were formed the dominating environment was dry steppe. The composition of the chiropteran fauna would rather point to a temperate climate, close to contemporary, this being evidenced by the considerable share of *Plecotus* and the absence of representatives of the Rhinolophidae.

Abundant though very incomplete remains of bats probably accumulated from a winter colony while it died out. The considerable degree of damage to bones may be accounted for by their displacement within the cave; one cannot, however, altogether rule out the possibility that predators participated in the formation of the thanatocoenosis.

The following species were recorded here: *Myotis* cf. *bechsteini* (Kuhl), *Myotis* cf. *blythi* (Tomes), *Myotis* cf. *brandti* (Eversmann), *Myotis dasycneme* (Boie), *Myotis mystacinus* (Kuhl), *Myotis nattereri* (Kuhl), *Eptesicus* cf. *serotinus* (Schreber), *Eptesicus* cf. *nilssoni* (Keyserling et Blasius), *Barbastella* cf. *schadleri* Wett., *Plecotus* cf. *abeli*, Wett.

FORMATION OF THE MODERN BATS' FAUNA IN POLAND

The contemporary pattern of the bat fauna of Central Europe came into being as a result of a very long process, lasting millions of years. Two factors had a decisive effect on its course, namely, migrations from the South in periods when a more favourable climate prevailed, and the extinction or widthdrawal of local populations in periods when the climate was less favourable. These processes existed already in the Pliocene, becoming, however, more intensive in the Pleistocene.

In the Early Pliocene on the northern shores of the Mediterranean

Basin, a damp climate prevailed with a distinct rain season in the summer period. Forest vegetation dominated yet the composition of the flora was varied, hygrophilous in the coastal zone and drier further inland (Suc 1984). The chiropteran fauna of this region showed a considerable proportion of thermophilous elements (Rhinolophidae) and tropical ones (Hipposideridae and Megadermatidae) (Sigé and Legendré 1983). During this period, Megadermatidae reached the Carpathian Basin (*Megaderma janossyi* Topal) this being the northern limit of their distribution (Topal 1974).

Greater climatic changes began roughly in the middle Pliocene (about 3 million years ago). In the initial stages of the evolution of the Mediterranean climate the most characteristic feature was a fluctuation in moisture, particularly the rhythmicity of the rain season. The coastal zone of moist forest disappeared, its place being taken by more xerothermic vegetation, which was replaced by true xerophilous vegetation as the climate gradually continued to become drier. These climatic changes undoubtedly had a fundamental effect on the chiropteran fauna. It was probably at this time that the tropical species began to disappear, the proportion of thermophilous species increased, and also of those adapted to survive long, unfavourable periods of drought. Climatic changes initiated in the mid-Pliocene continued, the climate slowly deteriorated and was at its worst in the Pleistocene.

In the early and middle Pliocene there were no particular obstacles, other than some relatively small climatic differences, to hamper the contact of faunas of central and southern Europe, though even then the gradual drying of the climate in the Pliocene could have prevented the migration of tropical elements into the basin of the Carpathians.

Following a marked deterioration of the climate towards the close of the Pliocene (Suc 1984), the Carpathian barrier began to play a considerable role in the distribution of bats. *Miniopterus* colonized the region north of the Carpathians only once, in the Pliocene (Podlesice, Węże I?), existing later solely in areas lying south of the Carpathians.

In cooler periods of the Pleistocene, the present region of southern Poland was not inhabited by bats of the Rhinolophidae, and also probably of Vespertilionidae. In periods of harsh climate the range of the bats could have been even more restricted, solely to refugial areas lying in the basin of the Mediterranean.

In warmer periods the bats migrated north, colonizing in turn the basin of the Carpathians, and in climatic optima crossing the barrier of the Carpathians and colonizing regions lying north of the mountains. It would be difficult to assess on the basis of such fragmentary material how often these migrations took place. According to Topal (1979), horseshoe bats of the "*ferrumequinum*" group migrated into the basin of the Carpathians at least twice in the Pliocene and at least once in the Pleistocene. In the latter epoch migrations of Rhinolophidae further north were rare, or maybe did not occur at all outside the Cromerian period.

Vespertilionidae, the only group of bats well-adapted to coping with a cooler climate, migrated practically every time it became warmer.

In the postglacial the Carpathian barrier was crossed by many species of the Vespertilionidae, and with moderate success by one species of horseshoe bat, *Rhinolophus hipposideros*. The second modern species of the Rhinolophidae, i.e. *R. ferrumequinum*, was recorded only once on the basis of a single specimen captured in the Nietoperzowa Cave.

There is however a certain obstacle to giving a complete sequence of the changes taking place in the bat fauna from the Pliocene up to modern times. The early Pliocene locality in Podlesice is the oldest, as well as the richest in bat remains. The other sites at which such remains were found, both dated at the Pliocene and later, Pleistocene ones, contain a fairly poor material both in the number of specimens and the taxa represented. This gap is particularly pronounced in the case of the middle and late Pleistocene. This period was very important in the formation of the modern fauna of bats in Poland, particularly for the *Myotis*. The rather scant data derived to date seem to indicate that some fossil species of *Myotis* could have survived even to the close of the Pleistocene. However, owing to the poverty of fossil faunas it is not at present possible to give a full sequence of this process.

The situation of the genera *Plecotus* and *Eptesicus* is rather different, as is that for the already mentioned *Rhinolophus* and *Miniopterus*. For most of these, the late Pliocene and early Pleistocene was a more important period of evolution. It was then that species from the older Pliocene were rapidly dying out and more modern forms were appearing in southern refugial zones. These, in successive waves of migration, colonized the areas lying further north.

At this point it should be added that most of the thanatocoenoses known to date contain only the remains of cave-dwelling bats, using caves as a place of residence, or, periodically, for hibernation. These species comprise 70—75% of Poland's, chiropterofauna. In the thanatocoenoses studied the absence of representatives of the genera *Pipistrellus*, *Vespertilio* and *Nyctalus* is particularly striking: being connected with the forest environment, they left no remains in caves, yet they undoubtedly colonized the area which is now southern Poland.

OCCURRENCE AND RELATIONSHIPS OF FOSSIL BATS IN POLAND

Here will be considered in brief some information relating to the occurrence of bats in the fossil fauna of Poland, their phylogenetic relationships, and distribution in time. The data contained in this chapter are based both on the investigations of the present author, and also gathered from already published papers. The data concerning *Myotis* are a critical compilation from the paleontological literature.

A. Pliocene faunas

The locality at Podlesice, which is the most abundant in bone remains and also the oldest, dated at the Early Pliocene (Biozone MN 14) represents a relatively "modern" bat fauna, lacking tropical elements. In this fauna are represented some extant genera and families, yet recent species are lacking. In the ecological aspect Poland's bat fauna of this period resembles the modern bat fauna of the northern part of the Mediterranean Basin (Table 2). A share of thermophilous species of the families Rhinolophidae and Miniopteridae was characteristic, both were represented by archaic forms (Table 3).

Table 2. The share of particular groups of bats in the modern fauna in the regions of Europe compared

Regions of Europe :	A		B		C		D	
Categories :	N	%	N	%	N	%	N	%
Families	4	100	3	75	2	50	1	25
Genus	10	100	9	90	8	80	7	70
Species	28	100	25	90	22	79	13	46

Explanations of abbreviations:
A — Balkan Peninsula and northern shores of the Mediterranean; B — Pannonian Lowland; C — Southern Poland; D — Southern part of Scandinavian Peninsula.

The family Vespertilionidae was represented by several genera. The genus *Myotis* was represented chiefly by species of medium size, of the subgenera *M.* (*Paramyotis*), *M.* (*Selysius*) and *M.* (*Leucone*). Forms of the subgenus *Plecotus* (*Paraplecotus*) related to the American *P.* (*Corynorhinus*) also occurred (Kowalski 1956, Handley 1959, Rabeder 1974). *Eptesicus* was represented by a form close to the Middle Eastern *E. bottae*, i.e. *E. mossoczyi* sp. n., and large forms of *E. kowalskii* sp. n.

The absence of species connected with forested areas is striking. This was caused chiefly by the type of thanatocoenosis with which we are dealing at the fossil sites examined. Yet on the other hand, the poverty of these forms could reflect the initial stages of a drying out of the climate and a decline in forest area. The fauna of layer 4—5 in the Mała Cave represents a similar thanatocoenosis to that of Podlesice (Sulimski *et al.* 1979).

Table 3. Bats of the Pliocene and Early Pleistocene from Poland

Locality :	PO	ZA1B	MA	ZDB	WE1	MO1	WO	RK2	KD1	KA	JŻ	ZDC	KI1	KG
Epoch	Pliocene								Pleistocene					
Biozone MM	14	14/15	14/15	15	15	15	?	16	$17/Q_1$	Q_1	Q_1	Q_2	Q_1/Q_2	Q_2
Species :	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Rhinolophus cf. ferrumequinum (Schreber)	-	-	-	-	-	-	●	-	-	-	-	-	-	-
R. kowalskii Topal	●	●	-	-	-	●	-	●	-	-	-	-	-	-
R.wenzensis sp.n.	-	-	-	-	●	-	-	-	-	-	-	-	-	-
R. cf. macrorhinus Topal	-	-	-	-	-	-	-	-	●	●	-	-	●	-
R. neglectus Heller	-	-	●	-	-	-	-	●	-	-	-	-	-	-
R. sp. (mehelyi ?)	●	-	-	-	-	-	-	-	-	-	-	-	-	-
R. hanaki sp.n.	●	-	●	-	-	-	-	-	-	-	-	-	-	-
R. cf. variabilis Topal	-	●?	-	-	●	●	-	-	-	-	-	-	-	-
Miniopterus approximatus sp.n.	●	-	-	-	-	-	-	-	-	-	-	-	-	-
Myotis sp.	-	●	-	●	-	●	-	●	●	●	●	●	-	●
M. cf. bechsteini (Kuhl)	-	-	●	-	-	-	-	-	-	-	-	-	-	●
M. cf. blythi (Tomes)	-	-	-	-	-	-	-	-	-	-	-	-	-	●

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
M. cf. brandti (Eversmann)	-	-	-	-	-	-	-	-	-	-	-	-	-	●
M. danutae Kowalski	●	-	●	-	●	-	-	-	-	-	-	-	-	-
M. dasycneme (Boie)	-	-	-	-	-	-	●	-	-	-	-	●	-	●
M. delicatus Heller	●	-	-	-	-	-	-	-	-	-	-	-	-	-
M. cf. exilis Heller	●	-	-	-	●	●	-	-	●	-	-	-	-	-
M. gundersheimensis Heller	●	-	-	-	●	-	-	-	-	-	-	-	-	-
M. helleri Kowalski	-	-	-	-	●	-	-	-	-	-	-	-	-	-
M. mystacinus (Kuhl)	-	-	-	-	-	-	-	-	-	-	-	-	-	●
M. cf. nattereri (Kuhl)	-	-	●	-	-	-	-	-	-	-	●	-	-	●
M. podlesicensis Kowalski	●	-	●	-	●	-	-	-	-	-	-	-	-	-
Eptesicus kowalskii sp.n.	●	-	-	-	-	-	-	-	-	-	-	-	-	-
E. mossoczyi sp.n.	●	-	-	-	-	-	-	-	-	-	-	-	-	-
E. cf. serotinus (Schreber)	-	-	-	-	-	-	-	-	-	-	-	-	-	●
E. nilssoni (Keyserling et Blasius)	-	-	-	-	-	-	-	-	-	-	-	-	-	●
Barbastella cf. schadleri Wett.	-	-	-	-	-	-	-	-	-	-	-	-	-	●
Plecotus rabederi sp.n.	●	-	-	-	●	-	-	-	-	-	-	-	-	-
P. cf. abeli Wett.	-	-	-	-	-	-	-	-	-	-	-	●	●	●

Explanations of abbreviations:
PO — Podlesice; ZA1B — Zalesiaki 1 B, MA — Mała Cave (layer 4+5); ZDB — Zamkowa Dolna Cave (layer B), WE1 — Węże I; MO1 — Mokra Cave (Bednarczyk 1978); WO — Wojcieszów (Zotz 1939); RK2 — Rębielice Królewskie 2; KD1 — Kadzielnia 1; KA — Kamyk; JŻ — Żabia Cave (Bošak *et al.* 1982), ZDC — Zamkowa Dolna, (layer C); KI1 — Kielniki 1; KG — Kozi Grzbiet. Division into biozones according to Mein (1975) — Pliocene, and Horaček (1979) — Pleistocene.

The fauna from the Węże I locality (Biozone MN 15, late Ruscinian, so-called Csarnota — Węże phase, also of Early Pliocene age (Fejfar and Heindrich 1983), is slightly younger than the previously mentioned ones. It is, however, rather different in its species composition. Particularly interesting is the presence of a large horseshoe bat, *R. wenzensis* sp. n., most likely representing a side line of the "*ferrumequinum*" group.

In the middle and late Pliocene, the bat fauna became poorer still, this probably being due to climatic changes. *Miniopterus* disappeared, the share of *Rhinolophus* also declined. *Plecotus* was still represented by the subgenus *P.* (*Paraplecotus*) and the genus *Myotis* by species of the subgenera *M.* (*Selysius*), *M.* (*Leucone*) and *M.* (*Paramyotis*) (Horaček 1976). The faunas of this period, however, containing very little chiropteran material are insufficient for broader paleoecological analysis.

B. Pleistocene faunas

In the early Pleistocene, further changes took place in the fauna. Archaic species of the "*ferrumequinum*" group were replaced by the more "modern" *R. macrorhinus* (Kadzielnia, Kamyk). *P.* (*Paraplecotus*) was on the decline, its place in Central Europe being taken by the more "modern" *P.* (*Plecotus*) *abeli*. Within the genus *Myotis*, species of *M.* (*Paramyotis*) became more common. *M.* (*Myotis*) appeared in Southern Europe.

In the mid- (Kozi Grzbiet) and late Pleistocene (localities in the Kraków Upland: Madeyska 1981) the bat fauna began to assume an increasingly modern aspect. Species known at present dominated: *M.* (*Paramyotis*) cf. *bechsteini*, *M. nattereri*. In a brief warmer episode, *M.* (*Myotis*) cf. *blythi* appeared. The genus *Barbastella* is represented by a fossil species, *B.* cf. *schadleri*, and *Plecotus* still by *P.* (*Plecotus*) cf. *abeli*.

Boreal species began to appear, e.g. *Eptesicus nilssoni*.

C. Holocene faunas

Holocene remains are fairly abundant but they come mostly from the climatic optimum. In the fauna of this period bats are represented exclusively by recent species though the percentages of particular forms depart considerably from the modern ones (Wołoszyn 1970). A dominating element, especially in the climatic optimum of the Holocene, were the species *Myotis bechsteini*, *M. nattereri*, *Plecotus* (*Plecotus*) *auritus*. In southern Poland, *Myotis* (*Myotis*) *myotis* began to appear.

Beginning from the Subatlantic period, the climate gradually deteriorated. The proportion of *M. bechsteini* in the fauna fell dramatically, this doubtless being due to the declining proportion of deciduous trees in forest associations (Table 4).

In the historical period the influence of man on the composition on the bat fauna began to increase. At first it was positive, especially for those species which preferred open areas, and for synanthropic ones. *Rhinolophus hipposideros*, *Myotis emarginatus*, *Plecotus austriacus* appear-

Table 4. Bats of the Late Pleistocene and Holocene of Poland

Species :	A	B	C	D	E	F	G	H	Recent
Rhinolophus hipposideros (Bechstein)	–	●	–	–	●	–	–	●	●
Myotis myotis (Borkhausen)	●	●	●	●	–	●	–	●	●
M. bechsteini (Kuhl)	●	●	●	●	●	●	●	●	●
M. bechsteini robustus Topal	●	–	–	●	–	●	–	●	–
M. nattereri (Kuhl)	●	●	●	●	●	●	●	●	●
M. emarginatus (Geoffroy)	–	–	–	–	–	–	–	–	●
M. mystacinus (Kuhl)	–	–	●	●	●	●	●	●	●
M. brandtii (Eversmann)	●	–	●	●	–	●	–	●	●
M. dasycneme (Boie)	●	●	●	●	●	●	●	●	●
M. daubentoni (Kuhl)	●	●	●	●	●	●	–	●	●
Vespertilio murinus L.	–	–	–	–	●	–	–	–	●
Pipistrellus pipistrellus (Schreber)	●	●	–	–	●	–	–	–	●
P. nathusii (Keyserling et Blasius)	–	–	–	–	–	–	–	–	●
Eptesicus nilssoni (Keyserling et Blasius)	●	–	–	●	●	–	–	●	●
E. serotinus (Schreber)	–	●	–	–	●	–	–	–	●
Nyctalus noctula (Schreber)	–	–	–	–	●	–	–	–	●
Plecotus auritus L.	●	●	●	●	●	●	●	● + P.abeli	●
P. austriacus (Fischer)	–	–	●?	–	–	–	–	●	●
Barbastella barbastellus (Gray)	●	●	●	●	●	●	–	–	●

Explanations of symbols: A — Sediments of the Late Pleistocene caves of the Kraków Upland; B — Holocene cave sediments from the southern part of the Kraków—Wieluń Upland; C — Holocene cave sediments from the northern part of the Kraków—Wieluń Upland; D — Holocene cave sediments from the Tatra Mts; E — Holocene cave sediments from the Pieniny Mts (cave in the Sobczański Gorge); F — Holocene cave sediments from the Świętokrzyskie Mts; G — Holocene remains from Józefów, Roztocze; H — Holocene cave sediments from the Sudety Mts.

ed. The development of civilisation allowed these thermophilous species to migrate quite a long way north.

In recent times, the negative aspects of man's pressure have begun to dominate. Industrialization and the common use of various chemicals in agriculture have contributed to the increasing degradation of the natural environment and this has proved disastrous for the bats. In Poland the modern bat fauna of the second half of the 20th century is poorer in species, representing in numbers about 1% of what it was 40 years ago (Wołoszyn 1976, 1981).

COMPOSITION OF THE FAUNA

In the fossil fauna of Poland, bats are represented by several dozen taxa both extinct and extant, belonging to three families: Rhinolophidae, Miniopteridae and Vespertilionidae (fig. 3).

1. Family Rhinolophidae

A. "*ferrumequinum*" *group*

In this group, Topal (1979) distinguished two phyletic lines. He derived the first line from the Miocene species *R. delphinensis* Gaillard. This line was probably not represented in the fossil fauna of Poland. Bats of the second line, which Topal derived from the species *R. lemanensis* Revillod (known from the Miocene of Europe), inhabited the region of southern Poland in the Pliocene. A typical representative of this line is *Rhinolophus kowalskii* Topal, described from Podlesice, found also in other Pliocene localities: Mała Cave, Rębielice Królewskie II, Zalesiaki B. In regions north of the Carpathians *R. kowalskii* disappeared towards the close of the Pliocene, though it may have survived till the early Pleistocene in the Pannonian Lowland.

Topal (1979) was of the opinion that the recent *R. ferrumequinum* may also have evolved within this line.

The large horseshoe bat *Rhinolophus wenzensis* sp. n. found at the Węże I locality occupies a distinct place. It has many primitive features, but also some progressive ones. It is probable that the morphotype of the species arose owing to endemic evolution in an isolated population.

Pliocene species of the "*ferrumequinum*" group were replaced in the late Pliocene or in the early Pleistocene at the very latest by a more progressive species, first described from Hungary — *Rhinolophus macrorhinus* Topal. The remains of large horseshoe bat, which can probably be assigned to the last species, were reported from Kadzielnia and Kielniki.

The systematic status of a large horseshoe bat, whose remains were described by Heller (1936), is still unclear; it was determined as *R.* cf.

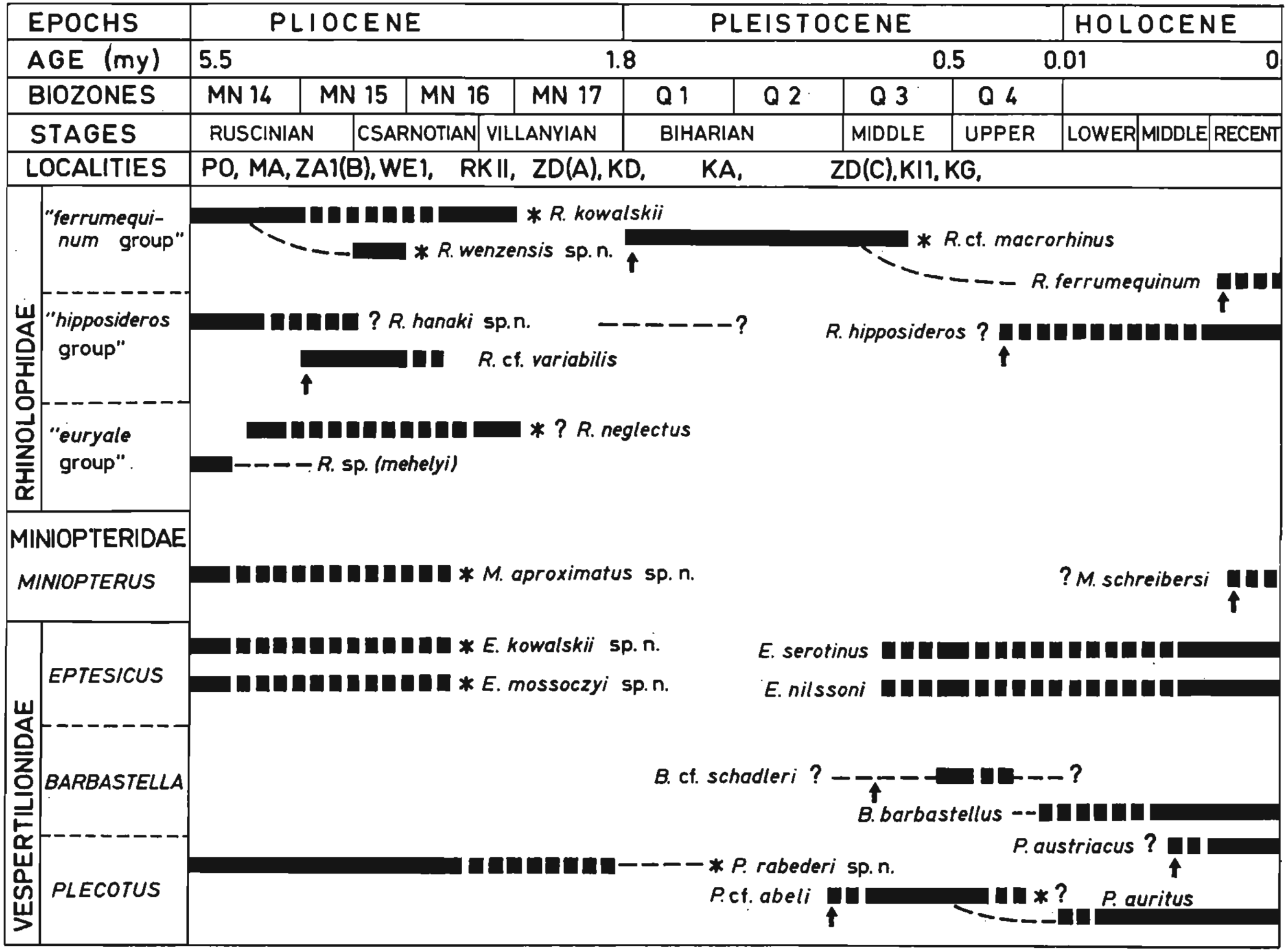

Fig. 3. Stratigraphical table of the bat taxa investigated. Symbols: an asterisk denotes the probable time of extinction of the taxon. An arrow — the probable time of migration from the refugial zone (from the south).

ferrumequinum (Schreber), from the Południowa Cave in Wojcieszów, from strata of Pliocene age.

Beginning with the lower Pleistocene, no remains of large horseshoe bats are found in the fossil material. The recent species *R. ferrumequinum* is not a permanent element of Polish modern fauna, though an occasional vagrant may be found.

B. *"euryale" group*

The remains of a medium-sized horseshoe bat belonging to this group were found at several localities: Mała Cave (4+5), and Rębielice Królewskie II. The remains from the above-mentioned localities were classified as *R. neglectus* Heller, close to the modern species *R. mehelyi* Matschie.

It is most likely that bats of the *"euryale"* group inhabited Central Europe north of the Carpathians in the Pliocene, but were never numerous.

C. *"hipposideros" group*

The phylogenetic relationships within this group are not clear. Most probably its oldest known species is *Rhinolophus grivensis* (Depéret) described from the Miocene from la Grive Saint-Alban in France.

According to Topal ((1974, 1975) the phyletic line evolving from *R. grivensis* split into two, leading on the one hand to *R. lissiensis* Mein, described from the late Miocene locality of Lissieu in France and reported later from the early Pliocene locality Osztramos 10 in Hungary (Topal 1974), and from a locality of similar age, Nova Propast u Ustheho Koné in Czechoslovakia (Horaček 1982). According to Topal, *R. lissiensis* is an ancestor of the recent *R. euryale* Blasius.

According to the same author, the second branch of this line leads to the fossil species *R. variabilis* Topal, described also from the Osztramos 10 locality. Topal (1975) thinks it likely that the recent *R. hipposideros* (Bechstein) may also have evolved from *R. variabilis*. It would be difficult to agree with this, since *R. variabilis* has relatively very small P_3 and P^3, smaller than in *R. hipposideros*. Yet in all the known cases in Rhinolophidae (and also in most other Palearctic bats), exactly the opposite is true, i.e. phylogenetically older species have more massive and more loosely spaced premolars than do their modern counterparts. Hence, it would be prudent to exclude the possibility that *R. variabilis* is a direct ancestor of *R. hipposideros*, since in this case we would be faced with the reversal of a trend which is commonly observed. It should rather be assumed that *R. variabilis*, known also from Węże I, as well as the morphologically close *Rhinolophus hanaki* sp. n. described from Podlesice, represent a phyletic line (or lines) which died out in the Pliocene. In turn, the recent *R. hipposideros* developed independently in the refugial zone in the south (no paleontological evidence of its presence in the Pliocene in available), colonizing Europe much later.

Horseshoe bats of the "*hipposideros*" group are not represented in fossil material from the Pleistocene with the exception of two localities in the Sudety Mts, i.e. in the Wschodnia (Eastern) Cave in Połom — in deposits dated at the last glaciation, and in the Radochowska Cave near Kłodzko, in the layer with "*Ursus spelaeus*". Remains from the mentioned localities have been determined as *Rhinolophus* cf. *hipposideros* (Zotz 1939). The stratigraphy of both localities is however uncertain (Kowalski 1954), and a lack of accessible material makes revision impossible.

According to the present author (Wołoszyn 1981), the expansion of *R. hipposideros* into the Kraków—Wieluń Upland took place relatively recently, probably in historical times, and could have been connected with the development of medieval architecture (castles, dungeons), making it possible for this species to come from Moravia over to the northern side of the Carpathians, through a region which usually lacked any natural shelter.

The absence of this species in subfossil material in southern Poland, but a high frequency in similar material from the Karst region of Moravia (Horaček 1976, and the present author's investigations) could be proof of such a late migration.

A lesser horseshoe bat (*R. hipposideros*) has been found in Poland at only four Holocene sites. Three of these, namely the U Źródła, Na Tomaszówkach Górnych and Nietoperzowa Caves (all three lying in the southern part of the Kraków—Wieluń Upland) contain quite new material, probably subrecent. However, the remains of a lesser horseshoe bat from caves in the Sobczański Gorge in the Pieniny Mts. (Alexandrowicz *et al.* 1985) probably represent a pioneer population occupying this region in the early Holocene.

2. Family Miniopteridae

The oldest remains classified as *Miniopterus* were found in Podlesice (Kowalski 1956), and are described in the present work as *Miniopterus approximatus* sp. n. This is a species close to the modern *M. schreibersi*, and most likely represents the same phyletic line.

There can be no doubt that the expansion of *Miniopterus* north of the Carpathians took place only once, in the early Pliocene (Podlesice). In material from other localities this genus is not represented, though it cannot be ruled out that it could have colonized regions to the north of the Carpathians also later, in the period when the thanatocoenosis from Węże I was formed (Kokurewicz — pers. comm.). It is likely that in the middle Pliocene the *Miniopterus* genus was very rare, and finally became extinct towards the end of this epoch.

3. Family Vespertilionidae

Genus *Myotis* Kaup. — In fossil material from Poland this genus is represented by over a dozen species (of several subgenera) most of which are forms now extinct.

Most of the finds were determined only at the generic level, as *Myotis* sp. Since the subgeneric status of some species is not altogether clear and many of the determinations require revision, the species given by the author have been characterized below in alphabetical order, without mentioning the subgeneric name.

Myotis bechsteini (Kuhl). — Fossil remains determined as *M. bechsteini*, *M.* cf. *bechsteini* or *Myotis* sp. ex. gr. *bechsteini* are known from many localities of fossil and subfossil faunas in Poland. The oldest come from Pliocene deposits (Layer 4+5) from the Mała Cave (Sulimski *et al.* 1979). This species was also reported from Pleistocene deposits from caves of the Kraków—Wieluń Upland (Bošak *et al.* 1982; Madeyska 1981; Nadachowski 1976). It was also found at Kozi Grzbiet (this paper).

Remains undoubtedly belonging to *M. bechsteini* were found in many late Pleistocene localities in the southern part of the Kraków—Wieluń Upland (Madeyska 1981). In material dated at the Holocene it is frequently the dominating species (Wołoszyn 1970).

Myotis cf. *blythi* (Tomes). — In fossil materials *M.* cf. *blythi* was found only in Pleistocene strata from Kozi Grzbiet. It is likely that this species will also be found in Holocene materials (Tatra Mts?).

Myotis danutae Kowalski. — This is a fossil species of *Myotis* first described from Pliocene breccia in Podlesice and reported later from Węże I (Kowalski 1962*a*, 1964) and in layers 4+5 in Mała Cave (Sulimski *et al.* 1979). Both Kowalski (1956) and Topal (1985) emphasized the close affinity of this species to *M. emarginatus* (Geoffroy). Horaček and Hanak (1983—1984) however are inclined to include *M. danutae* in the group of forms close to *M. nattereri.*

Myotis dasycneme Boie. — Remains almost identical with the modern species are known from the middle Pleistocene from the Kozi Grzbiet locality, and also from the Wschodnia Cave in Wojcieszów, from fauna described by Zotz (1939) as "Cromerian" (Kowalski 1954, 1959). Madeyska (1981) lists *M. dasycneme* from some late Pleistocene deposits from the Bramka Cave in the Ojców region.

In Holocene material, *M. dasycneme* is known from fairly numerous localities, though always represented by a small number of specimens. It was recorded in caves of the Tatras (Wołoszyn 1961, 1964, 1967, 1969, 1970), it was also reported from Roztocze in Holocene materials brought up from karst fissures (Kowalski *et al.* 1963), and from the Raj Cave in the Świętokrzyskie Mts (Kowalski 1872*a*, 1974*b*).

Myotis delicatus Heller. — According to Topal (1985) the remains described from Podlesice as *M. dasycneme subtilis* Kowalski should be identified with the fossil species *M. delicatus*. This is a form close to *M. dasycneme*, though probably representing a distinct phyletic line, which became extinct in the Pliocene.

Myotis cf. *exilis* Heller. — The fossil species *M. exilis*, is known from many fossil sites in Europe. In Poland it is known from three localities: Podlesice (Kowalski 1956, 1959; Topal 1985; Rabeder 1972), Węże I (Kowalski 1962*a*, 1964) and Kadzielnia (Kowalski 1958*a*, 1959, 1964). Most likely it also occurs in materials of the Urwista Cave (Horaček, pers. comm.). Further studies will probably confirm the occurrence of this species at other Pliocene and maybe also Pleistocene localities.

Myotis gundersheimensis Heller. — According to Topal (1985) this species is abundant in Podlesice. The mistaken determination of this species by Kowalski (1956) who thought it to be *M.* cf. *aemulus* was due to the erroneous dimensions of the holotype, given by Heller. *M. gundersheimensis* is probably represented in the fauna of Węże I, also at other Pliocene localities, this however remains to be confirmed.

Myotis helleri Kowalski. — This species has not hitherto been found in the materials from the Węże I locality. It probably occurs in Podlesice, maybe also at other Pliocene localities.

According to Horaček (pers. comm.) this is a small *Myotis* species of the "*siligorensis*" group, in its skull anatomy resembling *M. daubentoni* somewhat.

Myotis myotis Borkhausen. — At present this is one of the abundantly represented species in Central Europe. It probably colonized this region in the Pleistocene, yet in fossil material of this period it is always very rare. From Poland it has been reported only from two localities: the Nietoperzowa Cave, in layers 14 and 15 of mid-Pleistocene age (Kowalski 1961; Madeyska 1981) and from the Bramka Cave, in deposits of the younger Pleistocene (Madeyska 1982).

Remains of *M. myotis* are much more numerous in Holocene material. From the Tatras this species was reported by Wołoszyn (1967, 1970) and Rybař (1980). It has also been reported from late Holocene remains from The Duża Sowa Cave near Kraków (Bocheński *et al.* 1983). The remains of a large *Myotis* were also found in the Raj Cave, and the Świętokrzyskie Mts (Wołoszyn 1966). This species has also been reported from the Niedźwiedzia Cave (Wiszniowska 1970; Wołoszyn 1968).

Myotis nattereri Kuhl. — This species was reported from the early Pliocene locality in the Mała Cave (Layer 4+5) (Sulimski *et al.* 1979), this determination however requires revision. Bat remains of the "*nattereri*" group have been listed from the Żabia Cave (Bošak *et al.* 1982), *Myotis nattereri* was also found in deposis dated at the middle and late Pleistocene from caves of the Kraków—Wieluń Upland (Kowalski 1967;

Madeyska 1981; Nadachowski 1976). This species has also been found in materials from Kozi Grzbiet.

The remains of *M. nattereri* are also frequent in Holocene remains. They were found in caves of the Tatras (Wołoszyn 1970), of the Kraków—Wieluń Upland and of the Świętokrzyskie Mts. (Kowalski 1964, 1972*b*). It has also been reported from Roztocze (Kowalski *et al.* 1963) and from the Sudety (Bošak and Horaček 1982; Wołoszyn 1968).

Myotis podlesicensis Kowalski. — Bat remains of this species are at present known from early Pliocene deposits at two localities: Podlesice (Kowalski 1956, 1959, 1964) and from layer 4+5 in the Mała Cave (Sulimski *et al.* 1979).

This is a large representative of the genus *Myotis*, close to the fossil species *M. kormosi* Heller, and *M. aemulus* Heller.

Beside the above-mentioned other species also occur in Holocene materials: *M. brandti*, *M. mystacinus*, *M. daubentoni* (Wołoszyn 1970).

Genus *Pipistrellus* Kaup. — *Pipistrellus pipistrellus* (Schreber). This is a species of bat connected with the forest biotope, very rarely found in cave thanatocoenoses. Remains determined as *P. pipistrellus* are found in small amounts in late Pleistocene and Holocene deposits. Kowalski (1967) mentioned this species from the caves in Puchacza Skała and Żytnia Skała in the southern part of Kraków—Wieluń Upland, Madeyska (1981) from caves in the region of Ojców. From Holocene localities, *P. pipistrellus* was mentioned by: Nadachowski (1976) from the Mamutowa Cave near Kraków, and Alexandrowicz *et al.* (1985) from the Sobczański Gorge in the Pieniny Mts. Moreover, the present author has found *P. pipistrellus* in an unexamined breccia in the Wierzchowska Górna Cave near Kraków.

Genus *Nyctalus* Bowdich. — In the recent bat fauna of Poland, this genus is represented by 2 species, namely *N. noctula* (Schreber) and *N. leisleri* (Kuhl) and a sporadically visiting third one, *N. lasiopterus* (Schreber) (Pucek and Raczyński 1983).

These are typically forest bats which do not take refuge in caves.

Nyctalus noctula. — This species can be found in small numbers in thanatoceoenoses formed from owl pellets. One Holocene locality of *N. noctula* is known from the cave in the Sobczański Gorge in the Pieniny (Alexandrowicz *et al.* 1985).

Genus *Eptesicus* Rafinesque. — In the recent fauna this genus is represented by two species: *E. serotinus*, preferring the forest biotope and *E. nilssoni*, a boreal species, also inhabiting mountain regions and occasionally overwintering in caves. The remains of bats of this genus are a rare find in fossil material. Historically, they first appeared in Pliocene material in Podlesice.

Eptesicus kowalskii sp. n. — This species described from Podlesice is close in size to the recent *E. serotinus*. It probably represents a separate phyletic line which died out in the Pliocene.

Eptesicus mossoczyi sp. n. — The second species of *Eptesicus* described from Podlesice was a medium-sized form close in size to *E. nilssoni*, but similar in certain aspects of its build to the Middle-East species *E. bottae*. To date, both of the *Eptesicus* species mentioned here are known only from lower Pliocene deposits at Podlesice.

Eptesicus nilssoni (Keyserling et Blasius). — In the material from Kozi Grzbiet (samples 2b, 2c, 2a+b+c) from the middle Pleistocene, there were found some remains of northern bats which did not differ from the recent *E. nilssoni*. This species was also mentioned by Madeyska (1981) from several caves near Kraków, from the late Pleistocene deposits. *E. nilssoni* was also listed at Holocene localities from the Niedźwiedzia Cave near Mt. Śnieżnik (Bošak and Horaček 1982), from caves in the Tatras (Wołoszyn (1967, 1970), recently also from caves in the Sobczański Gorge in the Pieniny (Alexandrowicz *et al.* 1985).

Eptesicus serotinus (Schreber). — Bone remains which can be classified as *E.* cf. *serotinus* were found in layer 2a in Kozi Grzbiet. This species was recorded by Zotz (1939), after him by Kowalski (1959) from the Cisowe Cave in Wojcieszów, from deposits dated at the Pleistocene or Holocene. This species was also reported from a late Holocene breccia from the Duża Sowa Cave in the Kraków area (Bocheński *et al.* 1983).

Genus *Barbastella* Gray. — *Barbastella* cf. *schadleri* Wettstein-Westersheim. The fossil remains of bats of this genus are reported from numerous Pleistocene localities in Europe. Several fossil species have been described, these however are probably synonymous with *B. schadleri* (Rabeder 1974). In the Pleistocene material from Poland, *B.* cf. *schadleri* was found only at Kozi Grzbiet. *B.* cf. *schadleri* probably occured in Poland throughout the Pleistocene; yet to date there is no paleontological evidence.

Barbastella barbastellus (Schreber). — The remains of *Barbastella*, which could be assigned to the recent species *B. barbastellus*, were found in late Pleistocene and Holocene deposits.

Late Pleistocene sites are Koziarnia Cave in Sąspowska Valley (Chmielewski *et al.* 1967; Madeyska 1981), Sąspowska Zachodnia Cave and a cave above the Niedostępna one (Madeyska 1981).

Sites of this species are more numerous from Holocene deposits. From the Duża Sowa Cave it was reported by Bocheński *et al.* (1983), and in the Pod Sokolą Górą Cave near Częstochowa it was found by Wołoszyn (unpublished data), in Holocene strata in the Raj Cave in the Świętokrzyskie Mts, it was found by Kowalski (1972*b*, 1974*a*), and also by Madeyska (1981), in the same cave. From caves of the Tatras it was reported by Wołoszyn (1964, 1969, 1970), and from the Pieniny Mts by Alexandrowicz *et al.* (1985) from a cave in Sobczański Gorge. At all the localities, the remains of this species are not very numerous.

Genus Plecotus Geoffroy. — In fossil materials from Poland the genus is represented by at least two phyletic lines. One (the older) includes species classified within *P.* (*Paraplecotus*) Rabeder, the other (younger) species of *P.* (*Plecotus*).

Plecotus (*Paraplecotus*) *rabederi* sp. n. — In the fossil fauna of Poland the remains of *P.* (*P.*) *rabederi* sp. n. are known from two localities: Podlesice and Węże I. It was relatively primitive form, related to the American species of *P.* (*Corynorhinus*). This line became extinct towards the close of the Pliocene or in the late Pleistocene at the latest.

Plecotus (*Plecotus*) cf. *abeli* Wettstein-Westersheim. — This form was reported in materials from Kozi Grzbiet from Zamkowa Dolna, from Zalesiaki A and from Kielniki I.

In Europe *P.* (*P.*) *abeli* appeared in the early Pleistocene and probably disappeared towards the end of this period. Morphologically however it is very close to the recent *P.* (*P.*) *auritus* and according to Rabeder (1974) it is an ancestral form with respect to the recent species.

Plecotus (*Plecotus*) *auritus* (L.). — This species colonized areas lying north of the Carpathians, most likely during the late Pleistocene. It is reported from numerous sites from Poland, dated both at the late Pleistocene and the Holocene.

P. (*P.*) *auritus* has been reported from numerous late Pleistocene localities in the Kraków—Wieluń Upland (Kowalski 1967, Madeyska 1981), from the Raj Cave in the Świętokrzyskie Mts (Kowalski 1972*b*, 1974*a*; Madeyska 1981).

P. (*P.*) *auritus* was reported from caves in the Tatras by Wołoszyn (1961, 1963, 1969, 1970), from Roztocze by Kowalski *et al.* (1963), moreover the present author found this species in deposits of Holocene age from the Zbójecka Cave in the Świętokrzyskie Mts. This species has also been reported from several Holocene localities from the Kraków—Wieluń Upland: the Duża Sowa Cave (Bocheński *et al.* 1983), the Pod Sokolą Górą Cave near Częstochowa (Skalski and Wójcik 1968), the Studnisko Cave (Wołoszyn 1976), moreover from the Niedźwiedzia Cave near Mt. Śnieżnik, Sudetes (Wołoszyn 1968; Wiszniowska 1970).

Plecotus (*Plecotus*) *austriacus* (Fischer). — The second recent representative the *P.* (*P.*) *austriacus*, is reported from only one Holocene locality, namely from the cave in the Sobczański Gorge, in the Pieniny Mts (Alexandrowicz *et al.* 1985).

The history of the migration of both modern species of *P.* (*Plecotus*) to areas north of the Carpathians might have been as follows: in cool periods of the Pleistocene, *P.* (*P.*) *auritus* inhabited a refugial area in the basin of the Mediterranean. In this period *P.* (*P.*) *austriacus* inhabited regions lying even further south (the Middle East?). In periods of climatic optima towards the close of the Pleistocene and definitely in the postglacial, *P.* (*P.*) *auritus* migrated north of the Carpathians, and in the basin of the Mediterranean its range was restricted to a few relict stands in mountain regions, while lowland areas were inhabited by *P.* (*P.*) *austriacus* which penetrated this area from the south.

The migration of *P.* (*P.*) *austriacus* to areas lying north of the Carpathians probably took place relatively recently, maybe in the historical period, and could have been connected with the urbanization of this part of Europe. To support this contention, we have two facts:

1. To date, subfossil remains of *P.* (*P.*) *austriacus* have not been found in southern Poland, except for the site in the Pieniny Mts.

2. *P.* (*P.*) *austriacus* is clearly synanthropic, i.e. both the summer and most of the winter shelters stands are situated in manmade structures. The synanthropism observed in *P.* (*P.*) *austriacus* could be a significant factor facilitating the migration of this species further north.

At present, both species of *P.* (*Plecotus*) occur sympatrically in Europe, in a wide belt of 800—1000 km which covers France, a greater part of Germany, Switzerland, north and central Italy, Austria, Czechoslovakia, Hungary, central and southern Poland, Romania, Bulgaria and the southern Ukraine.

In varied landscape they may appear together but *P.* (*P.*) *auritus* prefers forest and mountain regions, whereas *P.* (*P.*) *austriacus* is clearly attached to open areas and steppes, and predominates in lowland arable land (Wołoszyn 1963; Hanak 1969; Horaček 1975). Hence, despite an overlap in distribution these species are hypsometrically and ecologically isolated to a certain extent.

SYSTEMATIC PART

Family **Rhinolophidae** Bell, 1836

Genus *Rhinolophus* Lecépede, 1799

Rhinolophus kowalskii Topal, 1979

(pl. 11: 1; figs. 4—6; tab. 5—11)

1956. *Rhinolophus* cf. *ferrumequinum* (Schreber); Kowalski: 356, pl. 2: 5, 6.
1958*a*. *Rhinolophus* cf. *ferrumequinum* (Schreber); Kowalski: 15 (partly).
1959. *Rhinolophus* cf. *ferrumequinum* (Schreber); Kowalski: 49.
1979. *Rhinolophus* cf. *delphinensis* Gaillard; Sulimski *et al.*: 390.
1979. *Rhinolophus kowalskii* Topal: 74, pl. 2: 1—7, pl. 7: 8—14, pl. 8: 1—3.

Emended diagnosis (partly after Topal 1979). — A large representative of the genus, close to the contemporary species *R. ferrumequinum*, but differing from it in its generally massive structure, greater (about 25%) length of the lower premolar row P_2—P_4, the permanent presence of P_3 and a massive and straight-tipped coronoid process; the massive P^2 set in the toothrow, C^1 and P^4 are not contiguous. Posterior margin of the maxilla reaches the protocone of M^3. Last upper molar (M^3) has 4 comissures.

Material. — Podlesice: holotype (MF/1687/1); 1 almost complete skull (MF/1695/80); 51 maxillae and their fragments (MF/1687/2—53); about 250 mandibles and their fragments (MF/1687/54—300); over 300 isolated teeth or other skeletal parts; 44 fragments of humeri, about 150 cochleae. All ZZSiD collection.

Mała Cave (l. 4+5): 13 fragments of mandibles, 12 fragments of maxillae and isolated teeth M-675/7/1—25. All ZPAL Wr collection.

Rębielice Królewskie II: 1 fragment of maxilla with M^{2-3} (MF/1688/80), 4 isolated teeth, one cochlea. All ZZSiD collection.

Zalesiaki: 2 fragments of maxillae (MF/1689/1—2), 9 fragments of mandibles (MF/1689/3—12), 17 isolated teeth, 1 fragment of cochlea. All ZZSiD collection.

Measurements see tables 5—11.

Description. — Shape of the rostral part of the skull in *R. kowalskii* close to modern specimens of *R. ferrumequinum* (Schreber) though more massive. Upper canine slightly longer and more oval in outline of crown than in the modern species.

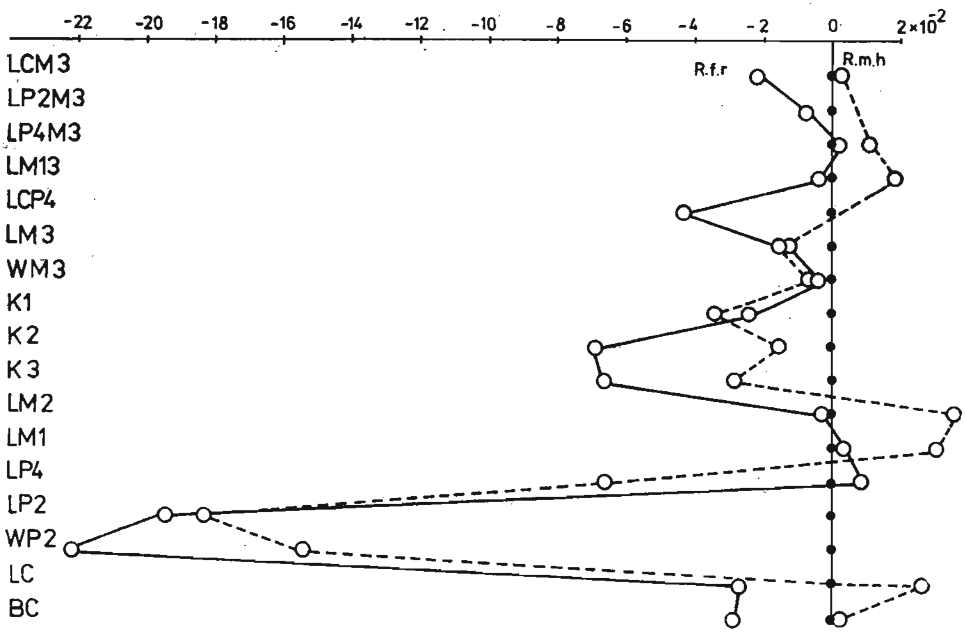

Fig. 4. Simpson's diagram for *Rhinolophus kowalskii* Topal (as a standard). R.m.h. — *R. macrorhinus* Topal (holotype) and R.f.r. — *R. ferrumequinum*, Recent.

P^2 — large, transversely oval, is permanent and lies in toothrow, hence the crowns of C^1 and P^1 are never contiguous. This is an important difference with respect to the modern *R. ferrumequinum* and the early Pleistocene *R. macrorhinus* Topal.

P^4 — has a higher and slightly more elongated hypocone than in the modern species. Paracone moderately high, ridge joining this cusp with the mesostyle falls in a gentle depression, in contrast to a clearly saddle-like one in the modern species. Molars generally like those of *R. ferrumequinum*, but both talons (on M^1 and M^2) are distinctly smaller than in the modern form, and in *R. macrorhinus*. Occipital part of skull higher, sagittal crest less pronounced.

Mandible is massive, coronoid process almost straight, occasionally on its anterior margin with a saddle-like depression, which in the modern species is very well pronounced. In the fossil species, the ascending ramus of the mandible rises higher upward. The symphysis of the mandible is slightly narrower (*R. kowalskii*: 1.32, *R. ferrumequinum*: 1.40).

I_1 is trilobate, broad. On the internal side of the tooth there is a developed broad cingulum. I_2 — also trilobate, very wide, especially in the medio-labial part. On the lingual side the strongly developed cingulum forms a distinct heel, surrounded labially by semicircularly arranged cusps.

C_1 — slightly smaller than in the modern form. Triangular crown with rounded corners and with a strongly developed surface on the labial side. Well-developed talon in posterior part of tooth.

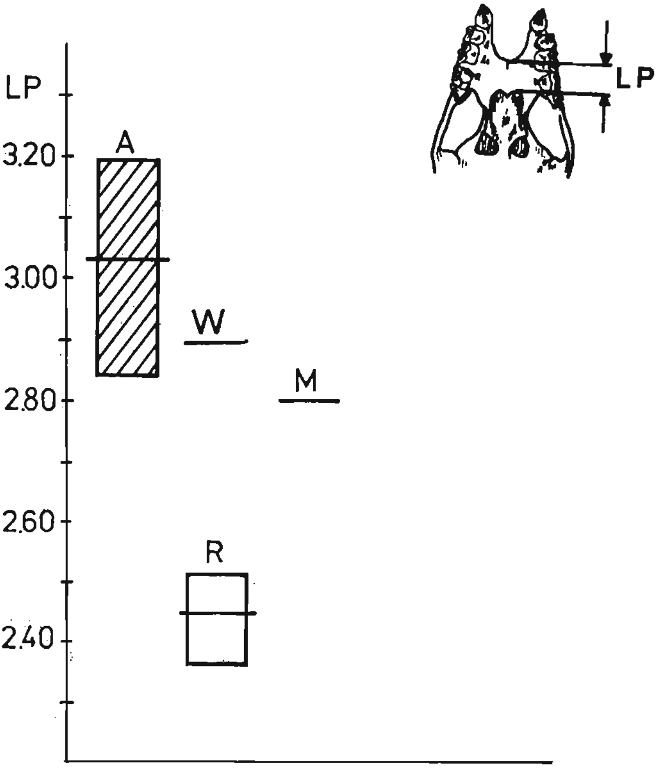

Fig. 5. Palatal length in several species of horseshoe bat of the "*ferrumequinum*" group. A — *Rhinolophus kowalskii* Topal from Podlesice, M — *R.* cf. *macrorhinus* Topal from Kadzielnia, R — *R. ferrumequinum*, Recent, W — *R. wenzensis* sp. n. from Węże I.

P_2 — massive, irregularly oval, its long axis lies transversely to toothrow, similar in outline of its crown to this tooth in the modern species, but much more massive. P_3 — relatively large, almost always present (in 99% of specimens investigated) and wedged deep between neighbouring P_2 and P_4. Outline of crown transversely oval. P_4 — in the outline of the crown it is an irregular trapezium, with its apex pointing labiad. Metacone of tooth strongly developed. Distinct talon in anterior part of tooth.

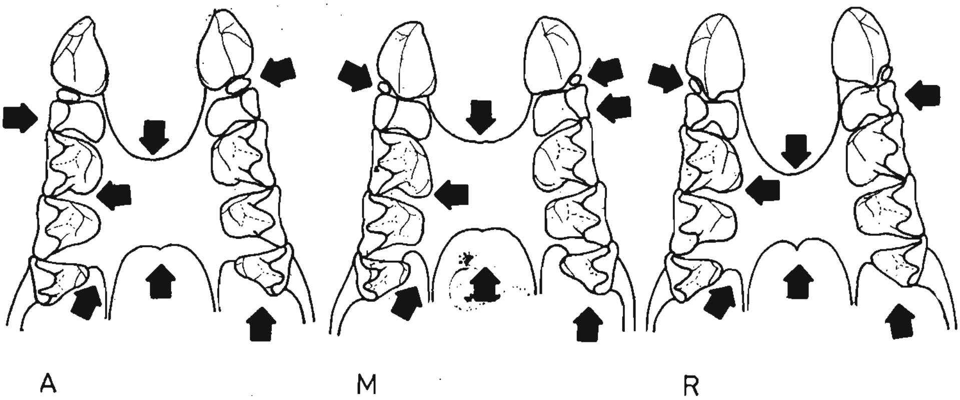

Fig. 6. Comparison of palatal length in three species, of *Rhinolophus*. A — *Rhinolophus kowalskii* Topal from Podlesice, M — *R. macrorhinus* Topal (holotype), R — *R. ferrumequinum*, Recent. Black arrows indicate the cranial regions in which changes resulting from microevolutionary trends are most distinct.

M_1—M_2 — molars similar to the modern species, though slightly smaller.

Comparisons and remarks. — The systematical position of *R. kowalskii* and the relationships of this species to other Miocene and Pliocene groups of the "*ferrumequinum*" group are discussed in the paper of Topal (1979).

Structure of the skull in *R. kowalskii* and *R. macrorhinus* is fairly close, though differing in proportions and dimensions (figs. 4—7). The more important differences are as follows: the length of the toothrow is slightly greater in *R. macrorhinus*, while the P^2 is almost twice as large in the form from Podlesice and it lies in the toothrow, positioned in such a way between C^1 and P^4 that the crowns of these teeth are not contiguous (Topal 1963*b*). The anterior margin of the palate in the form from Podlesice lies further posteriad than in *R. macrorhinus*, attaining the line connecting the mesostyles of M^1, while the anterior margin of the palate reaches the line of the parastyles of M^3 (fig. 6).

The talons on M^1 and M^2 in *R. macrorhinus* are strongly developed and not only do they exceed in dimensions the same from the species in Podlesice, but even those of the modern *R. ferrumequinum*.

Further differences can to be observed in the structure of the M^3. These concern the lengths of particular comissures (fig. 7). In *R. kowalskii* all the comissures are longer than in the specimen from Hungary, moreover comissure IV in both *R. macrorhinus* and in the modern *R. ferrumequinum* reaches such a degree of reduction that measurement is practically impossible.

As compared with *R. delphinensis* Gaillard (specimen from La Grive, ZZSiD MF/720/65) the mandible of *R. kowalskii* is larger in all dimensions and more massive. The front teeth (I_1—P_3) of the specimen from la Grive have not been preserved. Judging by the shape of the alveolus it can be said that I_1 and I_2 in *R. delphinensis* are almost two times smaller in diameter and are positioned more obliquely to the toothrow, as compared with the species from Podlesice. The alveolus of the canine has a similar shape, hence it may be assumed that the canine of *R. delphinensis* was proportionately more massive. The alveolus of P_2 is slightly larger and almost round in *R. delphinensis*. In this species P_3 was much more massive, this being evidenced not only by the much larger alveolus of this tooth, but also a small depression on the mesio-external margin of the cingulum of P_4, absent in the species from Podlesice. P_4 in *R. delphinensis* is smaller and almost square.

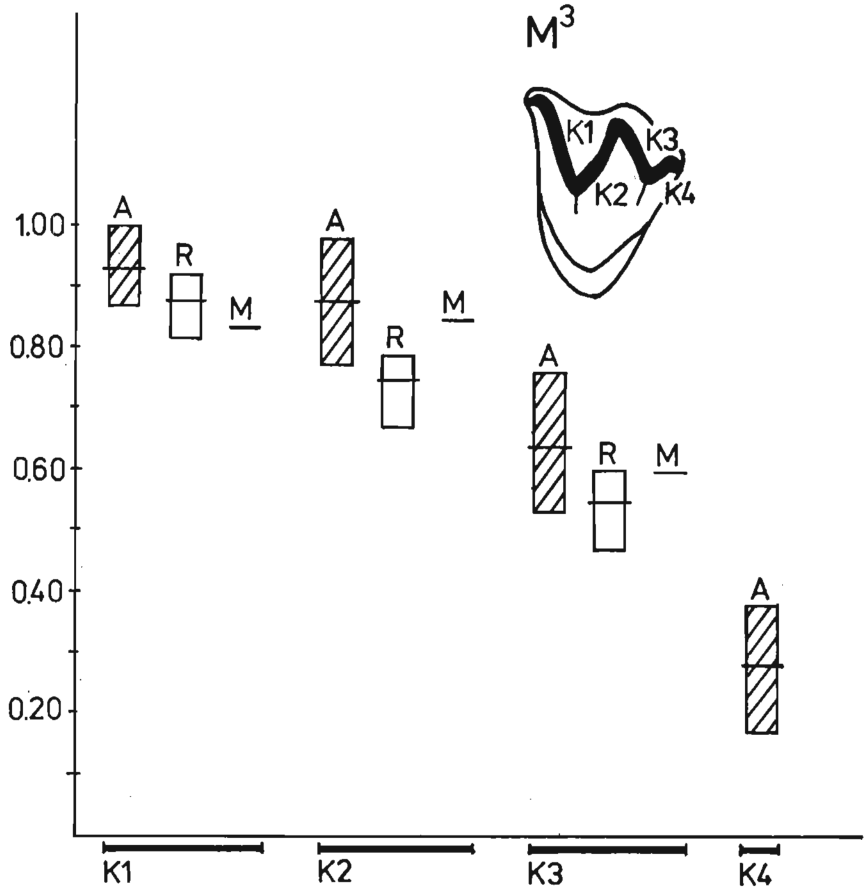

Fig. 7. Comparison of lengths of commissures on M^3 in several species of *Rhinolophus*. K1, K2, K3, K4 — successive commissures of M^3, A — *R. kowalskii* Topal from Podlesice, R — *R. ferrumequinum*, Recent, M — *R. macrorhinus* Topal (holotype).

The two molars preserved (M_1 and M_2) are smaller in the specimen of *R. delphinensis* than in the species from Podlesice. The ascending ramus of the mandible is roughly similar in dimensions, while the articular surface on the articular process in *R. kowalskii* is much larger.

The above-mentioned differences substantiate Topal's hypothesis (1979) that *R. delphinensis* represents a different phyletic line which probably became extinct in the early Pleistocene.

The differences between specimens of *R. kowalskii* from Podlesice and Mała Cave are relatively small, e.g. a smaller C^1 occurs in the population from Podlesice, while a smaller P^4 in the population from the Mała Cave (tables 7—9).

Teeth in specimens from Rębielice Królewskie II are on the whole smaller, especially M^3. The canine lies very close to P^4, consequently P^2 projects somewhat from the toothrow. In size, P^2 comes to the modern species than do specimens from other sites, though it is much more massive.

Certain differences may be observed between the populations from Podlesice and Zalesiaki. The form from Zalesiaki can be considered as slightly more progressive owing to a greater reduction in the premolars, especially in the shortened P_{2-4}.

Table 5. Mandibular measurements of some more complete specimens of *Rhinolophus kowalskii* Topal from Podlesice (Specimen MF/1687/1 — holotype)

Specimen MF/1687/ : Measurements :	1	54	55	56	57	58	59	60	61	63
Length of mandible	-	16.64	16.60	16.82	17.20	16.55	-	-	-	16.94
APML	-	6.52	-	6.41	6.53	6.40	-	-	6.28	6.56
Height of coronoid process	-	4.10	-	4.43	4.40	3.88	-	4.10	3.94	4.03
Length of $C_1 - M_3$	9.68	9.60	-	-	-	-	-	9.94	-	-
Length of $P_2 - P_4$	2.53	2.45	2.57	-	2.86	2.56	-	2.55	-	-
Length of $P_4 - M_3$	7.62	7.50	-	7.73	7.68	7.43	7.67	7.65	7.55	7.65
Length of $M_1 - M_3$	6.33	6.21	-	6.40	6.30	6.08	6.30	6.32	6.16	6.35
Length of P_2	1.20	1.08	1.17	-	1.11	1.12	-	1.10	-	-
Width of P_2	1.31	1.13	1.20	-	1.27	1.21	-	1.22	-	-
Length of P_3	0.37	-	0.40	-	-	-	0.34	0.42	-	-
Width of P_3	0.48	-	0.48	-	-	-	0.50	0.51	-	-
Length of P_4	1.39	1.40	1.38	1.46	1.34	1.40	1.47	1.35	1.48	1.42
Width of P_4	1.36	1.20	1.32	1.35	1.34	1.18	1.37	1.25	1.36	1.37
Length of M_1	2.38	2.33	-	2.28	2.20	2.22	2.31	2.34	2.22	2.25
Length of M_2	2.32	2.11	-	2.23	2.22	2.08	2.21	2.27	2.13	2.20
Length of M_3	2.17	2.01	-	2.07	2.10	1.92	2.03	2.00	1.88	2.10
Talonid width of M_3	1.28	1.16	-	1.28	1.36	1.11	1.26	1.18	-	1.37

Table 6. Descriptive statistics of mandibular measurements of *Rhinolophus kowalskii* Topal from Podlesice

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Length of mandible	12	16.46	17.20	16.74	0.2536	1.5
APML	13	6.19	6.72	6.45	0.1683	2.6
Height of coronoid process	11	3.88	4.56	4.19	0.2208	5.3
Length of $I_1 - I_3$	10	0.85	1.20	1.03	0.1080	10.5
Length of $C_1 - M_3$	9	9.34	10.13	9.70	0.2500	2.6
Length of $C_1 - P_4$	10	3.46	3.94	3.68	0.1352	3.7
Length of $P_2 - P_4$	21	2.45	2.76	2.58	0.1171	4.5
Length of $P_2 - M_3$	9	8.39	9.05	8.64	0.2235	2.6
Length of $P_4 - M_3$	29	7.12	7.75	7.54	0.1731	2.3
Length of $M_1 - M_3$	31	5.94	6.45	6.22	0.1658	2.7
Length of C_1	24	1.12	1.47	1.28	0.1071	8.3
Width of C_1	24	1.41	1.84	1.57	0.0949	6.1
Length of P_2	23	1.05	1.22	1.13	0.0453	4.0
Width of P_2	22	1.08	1.30	1.22	0.0593	4.9
Length of P_3	14	0.33	0.52	0.40	0.0522	13.0
Width of P_3	14	0.48	0.69	0.58	0.0695	11.9
Length of P_4	49	1.28	1.57	1.43	0.0601	4.2
Width of P_4	48	1.18	1.47	1.30	0.0714	5.5
Length of M_1	45	2.10	2.36	2.26	0.0654	2.9
Length of M_2	39	2.06	2.27	2.18	0.1186	5.4
Length of M_3	33	1.83	2.17	2.01	0.0721	3.6
Talonid width of M_3	32	1.07	1.37	1.22	0.0821	6.7

Table 7. Skull measurements of some more complete specimens of *R. kowalskii* Topal from Podlesice

Measurements. Specimen MF/1687/ :	2	3	5	7	10	11	12	14	15	16
Length of palatum	-	-	-	-	-	-	-	-	2.84	3.01
Interorbital construction	-	-	-	-	-	-	-	-	3.02	3.00
Length of $C^1 - M^3$	9.14	9.49	9.37	-	9.10	8.80	-	-	-	-
Length of $C^1 - P^4$	4.00	3.88	3.93	-	3.84	3.80	-	-	-	-
Length of $P^4 - M^3$	6.58	7.05	6.86	6.67	6.80	6.57	-	6.88	6.66	6.68
Length of $M^1 - M^3$	5.34	5.64	5.55	5.49	5.53	5.30	5.44	5.58	5.28	5.40
Length of C^1	2.26	2.21	2.48	-	2.32	2.15	-	-	-	-
Width of C^1	-	1.88	1.75	-	-	1.80	-	-	-	-
Length of P^2	0.63	0.65	-	0.49	0.48	0.52	-	0.50	-	-
Width of P^2	0.75	0.83	-	0.74	0.66	0.75	-	0.63	-	-
Length of P^4	1.32	1.49	1.40	1.31	1.35	1.30	1.22	1.44	1.58	1.47
Length of M^1	2.12	2.17	2.17	2.15	2.14	2.00	2.10	2.29	2.02	-
Length of M^2	1.93	2.13	2.15	2.02	2.15	1.94	2.15	2.05	1.97	-
Length of M^3	1.47	1.64	1.61	1.57	1.55	1.48	1.50	1.50	1.48	1.51
Width of M^3	2.15	2.05	2.21	2.03	-	2.02	2.24	2.10	1.96	2.04

Table 8. Descriptive statistics for the measurements of the skull of *R. kowalskii* Topal from Podlesice

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Length of palatum	2	2.84	3.01	2.92	0.1202	4.1
Interorbital contruction	2	3.00	3.02	3.01	0.0141	0.5
Length of C^1- M^3	6	8.80	9.45	9.17	0.2408	2.6
Length of C^1- P^4	14	3.75	4.40	4.06	0.2151	5.3
Length of P^2- M^3	10	6.86	7.50	7.15	0.1660	2.3
Length of P^4- M^3	23	6.55	7.05	6.73	0.1574	2.3
Length of M^1- M^3	24	5.23	5.75	5.46	0.1365	2.5
Length of C^1	20	2.08	2.50	2.28	0.1059	4.6
Width of C^1	19	1.72	2.06	1.85	0.1009	5.5
Length of P^2	14	0.48	0.78	0.58	0.0917	15.7
Width of P^2	14	0.63	0.95	0.80	0.1018	12.7
Length of P^4	36	1.21	1.66	1.42	0.1056	7.4
Width of P^4	18	1.80	2.22	2.01	0.1352	6.7
Length of M^1	20	2.00	2.29	2.14	0.0761	3.6
Length of M^2	18	1.93	2.18	2.07	0.0877	4.2
Length of M^3	25	1.35	1.64	1.50	0.0661	4.4
Width of M^3	23	1.87	2.24	2.08	0.1104	5.3
Length of 1st commissure of M^3	16	0.87	1.00	0.93	0.0415	4.4
Length of 2nd commissure of M^3	16	0.78	0.98	0.88	0.0572	6.5
Length of 3rd commissure of M^3	16	0.54	0.76	0.64	0.0705	11.0
Length of 4th commissure of M^3	12	0.18	0.38	0.28	0.0529	18.9

Table 9. Descriptive statistics for the measurements of *Rhinolophus kowalskii* Topal from the Mała Cave (layer 4+5)

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
A. Lower teeth						
Length of C_1	3	1.28	1.50	1.37	0.1024	7.5
Width of C_1	3	1.44	1.51	1.47	0.0311	2.1
Length of P_4	3	1.40	1.49	1.45	0.0451	3.1
Width of P_4	3	1.25	1.52	1.35	0.1504	11.2
B. Upper teeth						
Length of C^1	3	2.02	2.25	2.11	0.1229	5.8
Width of C^1	3	1.52	1.72	1.67	0.1361	8.1
Length of M^3	3	1.40	1.47	1.44	0.0361	2.5
Width of M^3	3	1.98	2.10	2.05	0.0624	3.0
Length of 1st commisure of M^3	3	0.72	0.82	0.77	0.0503	6.5
Length of 2nd commisure of M^3	3	0.78	0.90	0.82	0.0693	8.4
Length of 3rd commisure of M^3	3	0.56	0.63	0.59	0.0361	6.1

A. Measurements of lower teeth; B. Measurements of upper teeth

Table 10. Descriptive statistics for the measurements of maxilla of *Rhinolophus kowalskii* Topal from Zalesiaki

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Length of C^1	6	2.13	2.25	2.19	0.0468	2.1
Width of C^1	6	1.55	1.90	1.70	0.1372	8.1
Length of M^3	2	1.51	1.57	1.54	0.0424	2.7
Width of M^3	2	2.10	2.14	2.12	0.0283	1.3

Finally it should be mentioned that *R. kowalskii* from Podlesice comes close in size to the remains of *Rhinolophus* described by Zapfe (1945) from Miocene deposits, determined by this author as *R. delphinensis*. The diagram of the maxilla (Zapfe 1954: fig. 1) presents the alveolus of P^2 placed in the toothrow. Hence it cannot be ruled out that "*R. delphinensis*" from Neudorf could be close to the species from Podlesice.

Occurrence. — The remains of *R. kowalskii* are known from Pliocene deposits from Poland (localities: Podlesice, Mała Cave, Rębielice Królewskie II and Zalesiaki B).

Rhinolophus wenzensis sp. n.

(pl. 11: 2; tables 12—15)

1962*a*. *Rhinolophus delphinensis* Gaillard; Kowalski: 42.

Holotypus: left mandible with preserved teeth P_4—M_3 and a damaged articular process. ZZSiD: MF/551/1 (pl. 11: 2).

Locus typicus: Węże I, northern part of the Kraków—Wieluń Upland, Poland.

Stratum typicum: Late Pliocene (Csarnota — Węże phase) cave sediments.

Derivatio nominis: *wenzensis* — after the name of locality Węże.

Diagnosis. — A large representative of *Rhinolophus*, close in dimensions to *R. kowalskii* Topal, differing from this species in its massive teeth, a robust P_4, whose crown is almost square in outline, a massive talonid on M_3 and a more strongly reduced P_2.

Measurements of holotype see table 12.

Material examined. — Węże I: holotype, md.s.(FM—P2)(I_1—P_3)P_4—M_3AnCo; 1 nearly complete skull (MF/551/12) without zygomatic arcs, occipital part damaged, incisors, canine and small premolars (P^2) absent, M^3 damaged; 4 fragments of rostrum (MF/551/8—11; 16 mandibles or their fragments (MF/551/2—7, 17—24, 26—27); also 6 isolated C^1 and 1 isolated C_1. All ZZSiD collection.

The skull has a structure typical of large species of the „*ferrumequinum*" group; it is, however, slightly smaller than in *R. kowalskii* from Podlesice. Palate short. P^4 has an almost rectangular crown, elongated transversely with respect to the

Table 11. Descriptive statistics for the measurements of the mandible of *Rhinolophus kowalskii* Topal from Zalesiaki

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Length of P_2- P_4	2	2.22	2.28	2.25	0.0424	1.9
Length of C_1	4	1.27	1.51	1.41	0.1036	7.3
Width of C_1	4	1.54	1.60	1.57	0.03	1.9
Length of P_2	2	0.87	1.00	0.93	0.0919	9.8
Length of P_4	2	1.38	1.42	1.40	0.0283	2.0
Width of P_4	2	1.30	1.37	1.33	0.0495	3.7
Length of M_1	4	2.30	2.40	2.34	0.0490	2.1

toothrow. This is a massive tooth, with the linguo-distal part of its talon extensively developed. The anterior margin of the tooth is almost straight, with a slight depression in the medial part, while in the species from Podlesice a distinct "step" is formed at this point (fig. 8). M^{1-3} are massive, of a form typical of *Rhinolophus*. Talon strongly developed, especially on M^1, close in its form to the modern *R. ferrumequinum*.

Mandible is massive with short and oval symphysis (L/W: 2.52/1.46). Mandibular foramen lunate, while in *R. kowalskii* and *R. ferrumequinum* it is round and lies at the bottom of a furrow-like depression. I_1 has been preserved in one specimen only (MF/551/18), and its crown is strongly worn. It is, however, possible to determine that it was trilobate, with poorly separated lobes. Crown oval in outline (L/W: 0.69/0.50).

I_2 fairly massive. Crown in outline resembling a triangle with rounded angles, its apex pointing labiad (L/W: 0.92/0.71). Crown distinctly tricuspid, cingulum on the lingual side robust, less so however than in *R. kowalskii.*

C_1 is massive, strongly elongated transversely. Cingulum well developed, only in the mesial part at the point of contact with I_2 it has a distinct sinus. Talon in distal part of tooth moderately developed.

P_2 similar in outline of crown to P_2 in *R. kowalskii*, but relatively shorter and broader. P_3 — oval in outline of crown, wedged between P_2 and P_4. It is however smaller and projects further labiad from the toothrow than the same tooth in the species from Podlesice. For this reason both neighbouring premolars are spaced much more tightly in their crowns (smallest distance of P_2—P_4 in *R. wenzensis* is 0.06 mm, while in *R. kowalskii* it reaches 0.10 mm). P_4 in outline of its crown resembling a trapezium with rounded conrners, its bas facing linguad. The interior surface of the crown projects slightly obliquely from the toothrow, this giving the impression that it is slightly twisted linguad. Cingulum well developed, forming a large surface anteriorly. Margin of cingulum slightly upturned, without depressions. The rear surface of crown has a distinct depression, the cingulum forming here a kind of smallish talon with a small troughlike depression running vertically to the toothrow (in *R. ferrumequinum* the above-mentioned sulcus on the cingulum runs obliquely).

M_1 and M_2 are massive, of a form typical of large horseshoe bats. M_3 — is particularly massive, its talonid is canted labiad more than in *R. kowalskii*. The trough-like depression between the hypoconid and the hypoconulid (extant only in nyctalodontic teeth) distinct and wide, wider than this depression both in the species from Podlesice and in the modern form. Crista obliqua with a distinct notch in the

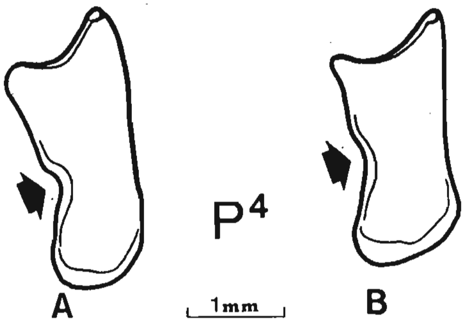

Fig. 8. Comparison of the shape of the crowns of P^4 in *Rhinolophus wenzensis* sp. n. and *R. kowalskii* Topal from Podlesice. Arrows indicate the saddle-like depression on the distal margin of the tooth. A — *R. wenzensis* sp. n. MF/551/8, B — *R. kowalskii* Topal MF/1687/3.

Table 12. Measurements of the mandible of *Rhinolophus wenzensis* sp. n. from Węże I locality (Specimen MF/551/1 — holotype)

Measurements. Specimen MF/551/ :	1	2	3	4	5	17	18	19	20	23
APML	-	6.25	-	-	-	-	-	-	-	-
Height of coronoid process	4.31	-	4.00	-	-	-	-	-	-	-
Length of C_1- P_4	-	-	-	-	-	-	3.50	-	3.53	-
Length of P_2- P_4	-	-	-	-	-	-	2.52	-	2.42	-
Length of P_4- M_3	7.96	8.08	7.83	-	-	-	-	-	-	-
Length of M_1- M_3	6.56	6.69	6.50	-	-	-	-	-	-	-
Length of C_1	-	-	-	-	-	-	1.37	-	1.23	-
Width of C_1	-	-	-	-	-	-	1.75	-	1.50	-
Length of P_2	-	-	-	-	-	-	1.07	-	1.06	-
Width of P_2	-	-	-	-	-	-	1.22	-	1.13	-
Length of P_3	-	-	-	-	-	-	0.33	-	0.32	-
Width of P_3	-	-	-	-	-	-	0.44	-	0.41	-
Length of P_4	1.56	1.60	1.56	1.62	1.51	1.51	1.44	1.55	1.56	1.50
Width of P_4	1.44	1.40	1.53	1.53	1.56	1.46	1.42	1.41	1.37	1.55
Length of M_1	2.39	2.45	2.34	2.41	-	-	-	-	-	-
Length of M_2	2.30	2.32	2.18	-	-	-	-	-	-	-
Length of M_3	2.10	2.20	2.12	-	-	-	-	-	-	-
Talonid width of M_3	1.49	1.38	1.21	-	-	-	-	-	-	-

Table 13. Descriptive statistics for the measurements of the mandible of *Rhinolophus wenzensis* sp. n. from Węże I locality

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Height of coronoid process	2	4.00	4.31	4.15	0.2192	5.3
Length of C_1 - P_4	3	3.50	3.72	3.58	0.1193	3.3
Length of P_2 - P_4	3	2.41	2.52	2.45	0.0608	2.5
Length of P_4 - M_3	3	7.88	8.08	7.97	0.1007	1.3
Length of M_1 - M_3	3	6.50	6.69	6.58	0.0985	1.5
Length of C_1	3	1.23	1.37	1.32	0.0781	5.9
Width of C_1	3	1.50	1.75	1.62	0.1258	7.8
Length of P_2	4	1.00	1.07	1.05	0.0337	3.2
Width of P_2	4	1.10	1.23	1.17	0.7141	6.1
Length of P_3	3	0.32	0.40	0.35	0.0436	12.4
Width of P_3	3	0.41	0.60	0.48	0.1021	21.1
Length of P_4	14	1.36	1.62	1.51	0.0710	4.7
Width of P_4	14	1.27	1.56	1.44	0.0835	5.8
Length of M_1	4	2.34	2.45	2.40	0.0457	1.9
Talonid width of M_1	3	1.46	1.60	1.55	0.0757	4.9
Length of M_2	3	2.18	2.32	2.27	0.0757	3.3
Talonid width of M_2	3	1.48	1.71	1.61	0.1178	7.3
Length of M_3	3	2.10	2.20	2.14	0.0529	2.5
Trigonid width of M_3	3	1.36	1.52	1.46	0.0872	6.0
Talonid width of M_3	3	1.21	1.49	1.36	0.1411	10.4

medial part, while in *R. kowalskii* it is undulate. Coronoid process more pointed and not as massive as in *R. kowalskii*. Angular process massive, strongly canted to the outside. Articular surface of articular process long and sausage-shaped, much as in *R. ferrumequinum*.

Remarks. — Dental formula (2.1.2.3./2.1.3.3.); molars of the nyctalodontic type and the general structure leave no room for doubt that the specimens examined repre-

Table 14. Measurements of the skull of *Rhinolophus wenzensis* sp. n. from the Węże I locality

Specimen MF/551/ : Measurements :	8	9	10	11	12
Total skull length	-	-	-	-	20.46
Interorbital construction	-	-	-	-	3.25
Length of palatum	-	-	-	-	2.85
Length of $C^1 - P^4$	4.16	-	-	4.10	-
Min. distance $C^1 - P^4$	0.35	-	-	0.31	-
Length of $P^2 - M^3$	-	7.28	-	-	-
Length of $P^4 - M^3$	-	6.86	-	-	6.55
Length of $M^1 - M^3$	-	5.63	-	-	5.35
Length of C^1	2.30	-	-	2.30	-
Width of C^1	1.86	-	-	1.88	-
Length of P^2	-	0.51	0.48	0.51	-
Width of P^2	-	0.74	0.68	-	-
Length of P^4	1.70	1.51	1.54	1.57	1.47
Width of P^4	1.91	2.04	2.24	1.97	2.15
Length of M^1	2.04	2.20	2.02	1.98	2.21
Width of M^1	1.97	2.33	2.24	2.17	2.15
Length of M^2	1.99	2.15	1.95	-	1.95
Width of M^2	1.96	2.31	2.15	-	2.00
Length of M^3	-	1.54	-	-	-
Width of M^3	-	2.12	-	-	-
Length of 1st commissure of M^3	-	0.92	-	-	-
Length of 2nd commissure of M^3	-	0.90	-	-	-
Length of 3rd commissure of M^3	-	0.64	-	-	-

sents a species of *Rhinolophus*. In earlier publications all specimens of a large *Rhinolophus* were determined as *R. delphinensis* Gaillard (i.e. Kowalski 1956, 1962*a*), Szynkiewicz *et al.* (1979). Later, Topal (1979) showed that *Rhinolophus delphinensis* represents a different phyletic line (see also the present paper). The above described new species of large horseshoe bat from the site at Węże I differs from the species *R. kowalskii* and also from other known Central European fossil species of the "*ferrumequinum*" group in its more massive dentition. With respect to the structure of its premolars *R. wenzensis* is more progressive than other Miocene and Pliocene species of that group.

Occurrence. — Known so far only from the type horizon and locality.

Rhinolophus cf. *macrorhinus* Topal, 1963

(pl. 11: 3; figs. 5, 9, 10; tables 16—20)

1958*a*. *Rhinolophus* cf. *ferrumequinum* (Schreber); Kowalski: 1, 2, 15, 44, 47.
1959. *Rhinolophus* cf. *ferrumequinum* (Schreber); Kowalski: 15, 50, 89.

Material. — Kadzielnia: 9 fragments of maxillae (MF/33/16—24); 15 fragments of mandibles (MF/33/1—15); 14 isolated teeth. All ZZSiD collection.

Kamyk: 1 fragment of maxilla (MF/1690/1); 2 mandibular fragments, 3 isolated canines (2×C^1 and 1×C_1). All ZZSiD collection.

Kielniki: 1 isolated C^1 with damaged crown (MF/1691/1). All ZZSiD collection.

Measurements of specimens from Kadzielnia see tables 16—20.

Table 15. Descriptive statistics for the measurements of the skull of *Rhinolophus wenzensis* sp. n. from Węże I locality

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Length of C^1 - P^4	2	4.10	4.16	4.13	0.0424	1.0
Length of P^4 - M^3	2	6.55	6.86	6.70	0.2192	3.3
Length of M^1 - M^3	2	5.35	5.63	5.49	0.1980	3.6
Length of C^1	6	2.16	2.31	2.23	0.0786	3.5
Width of C^1	6	1.86	1.98	1.91	0.0492	2.6
Length of P^2	3	0.48	0.51	0.50	0.0173	3.5
Width of P^2	2	0.68	0.74	0.71	0.0424	6.0
Length of P^4	5	1.47	1.70	1.56	0.0876	5.6
Width of P^4	5	1.91	2.24	2.06	0.1337	6.5
Length of M^1	5	1.98	2.21	2.09	0.1072	5.1
Width of M^1	5	1.97	2.33	2.17	0.1331	6.1
Length of M^2	4	1.95	2.15	2.01	0.0952	4.7
Width of M^2	4	1.96	2.31	2.10	0.1593	7.6

Dimensions of remaining specimens:

Kielniki: C^1 L/W — 2.26/1.70, Kamyk: C^1 L/W — 2.31/1.98 and 2.32/1.85, P^4: L/W — 1.50/2.01, M^1: length — 2.10, C_1: L/W — 1.37/1.70, M_3 — length 1.90, width of talonid 1.06.

Description. — The fragments of maxillae preserved are very incomplete. On the basis of one specimen (MF/33/16) it can be seen that the posterior margin of the jaw reached the parastyle of M_3 in the specimen from Kadzielnia, much as is the case in the modern *R. ferrumequinum*. In turn in the fossil species *R. kowalskii* and *R. wenzensis* the posterior margin of the maxilla is slightly shifted caudad and runs at the level of the paracone of M_3. The incisors have not been preserved in the material examined.

C^1 — is fairly massive, crown oval in outline, elongated mesio-caudally, apex strongly curved distally. Crown in outline resembles an irregular rhombus with its corners rounded, with depression on the postero-lingual margin of the cingulum.

Distance between C^1 and P^4 fairly small, under 0.1 mm.

P^2 rather small, projecting from toothrow, though slightly less so than in the holotype of *R. macrorhinus*. P^4 — in outline of crown almost rectangular with gently rounded corners. Mesial margin of tooth has two smallish convexities, one in the anterior part on the labial side, the other half way down the length of the margin. Distal margin of cingulum slightly undulate in outline, sometimes with a small lobe.

M^1 and M^2 similar to the holotype of *R. macrorhinus*. Talon well developed, especially on M^1. M^3 fairly short, but well developed. The first three commissures long, the fourth very short.

Mandible massive, with short and oval symphysis. Position of mental foramen variable: under C_1, C/P_2 or P_2.

C_1 — not very massive, wider than long. Cingulum well-developed both on the labial and lingual side. On anterior margin of cingulum at the point of contact with I_2 there is a distinct sinus.

On the caudal side a well developed talon, which at the point of contact with P_2 has a distinct sinus and a trough-like depression running transversely to the toothrow. P_2 fairly massive with a low, asymmetric crown, developed labially much as in the species *R. ferrumequinum*. This tooth, however, is more massive than in the modern species. P_3 small, projecting outward from toothrow, compressed between the cingulum of the adjacent teeth (P_2 and P_4). P_4 — in outline of crown resembles a square positioned slightly obliquely with respect to toothrow. Cingulum fairly strongly developed except for the lingual margin, where it is altogether absent. Distal margin of cingulum slightly curled upward, thus forming a shallow groove. At the point of contact with M_1 there is a shallow sinus on the cingulum.

Premolars are of the nyctalodontic type, massive, of a structure typical of Rhinolophidae, less massive however than in *R. kowalskii*, similar in size to those of *R. ferrumequinum*.

The isolated canine C^1 from Kamyk, possibly conspecific with Kadzielnia specimens has a characteristic depression on the postero-lingual margin of the cingulum. This depression can be observed both in *R. macrorhinus* and in the modern *R. ferrumequinum*, but in the latter it is deeper. In the fragment of maxilla (MF/1690/1) the alveolus of the canine with an incomplete root is so close to P_4 that these two are certain to have been contiguous at the margins of the cingulum; hence this was a proportion typical both of *R. macrorhinus* and *R. ferrumequinum*. Talon on M^1 well developed.

The isolated canine from Kielniki on the postero-lingual side of the cingulum of this tooth lies the above-mentioned depression, which made it possible to classify the fragment preserved as conspecific with Kadzielnia (fig. 10) and Kamyk specimens.

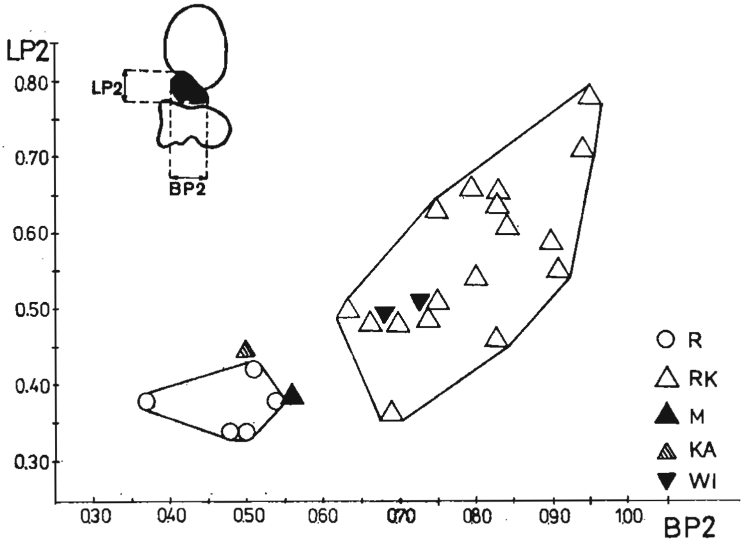

Fig. 9. Comparison of the size of P^2 in several species of **Rhinolophus**. R — *R. ferrumequinum*, Recent, RK — *R. kowalskii* Topal from Podlesice, M — *R. macrorhinus* Topal (holotype), KA — *R.* cf. *macrorhinus* Topal, WI — *R. wenzensis* sp. n. from Węże I.

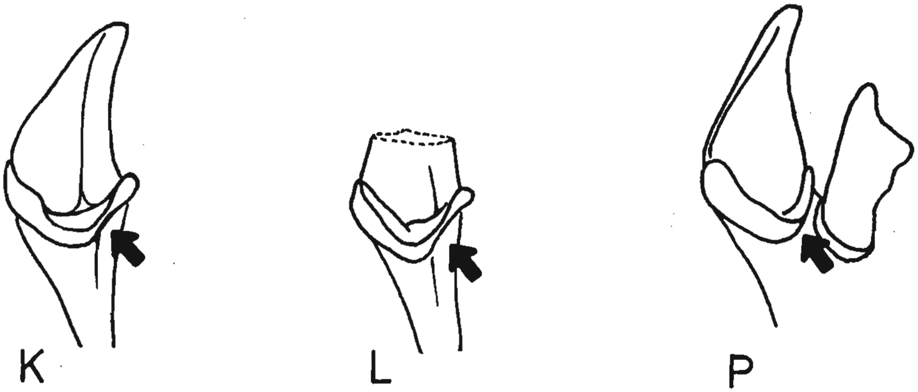

Fig. 10. Comparison of upper canine (C^1) in *Rhinolophus* cf. *macrorhinus* Topal from Kamyk (K) and Kielniki (L) with the specimen of *R. kowalskii* Topal from Podlesice (P). The arrow indicates the location of the depression on the cingulum characteristic of *R. macrorhinus*, which is missing in the specimen from Podlesice.

The remains above described are slightly more massive than the contemporary species *R. ferrumequinum*. In size they come close to the species *R. macrorhinus* described by Topal (table 20). Beside size, this would also be evidenced by the strong development of the talon on M^1, and the close proximity of C^1 and C_4.

Despite the incompleteness of specimens making more detailed analysis impossible, it seems reasonable to classify the remains described here as *R.* cf. *macrorhinus* Topal.

Table 16. Mandibular measurements of *Rhinolophus* cf. *macrorhinus* Topal from the Kadzielnia 1 locality

Measurements. Specimen MF/33/ :	1	3	4	5	7	8	13	14
Length of $C_1 - P_4$	-	3.36	-	-	-	3.38	-	-
Length of $P_2 - P_4$	-	2.36	-	-	-	-	-	-
Length of $P_4 - M_3$	-	-	-	-	-	-	-	7.40
Length of $M_1 - M_3$	-	-	-	-	-	-	6.20	6.04
Length of C_1	-	1.30	-	-	-	1.30	-	-
Width of C_1	-	1.52	-	-	-	1.67	-	-
Length of P_2	-	1.07	-	-	-	-	-	-
Width of P_2	-	1.17	-	-	-	-	-	-
Length of P_3	-	0.25	-	-	-	-	-	-
Width of P_3	-	0.34	-	-	-	-	-	-
Length of P_4	1.43	1.36	1.38	1.40	-	1.38	-	1.42
Width of P_4	1.38	1.26	1.21	1.31	-	1.49	-	1.38
Length of M_1	2.20	-	2.07	2.19	-	-	2.21	2.17
Length of M_2	2.10	-	-	-	2.08	-	2.08	2.08
Length of M_3	-	-	-	-	1.93	-	2.00	1.96
Talonid width of M_3	-	-	-	-	1.16	-	1.14	-

Table 17. Descriptive statistics for the mandibular measurements of *Rhinolophus* cf. *macrorhinus* Topal from the Kadzielnia 1 locality

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Length of C_1 - P_4	2	3.36	3.38	3.37	0.0141	0.4
Length of M_1 - M_3	2	6.04	6.20	6.12	0.1131	1.8
Length of C_1	2	-	-	1.30	-	-
Length of P_4	6	1.36	1.43	1.39	0.0266	1.9
Width of P_4	6	1.21	1.49	1.34	0.0999	7.4
Length of M_1	5	2.07	2.21	2.17	0.0567	2.6
Talonid width of M_1	5	1.38	1.58	1.50	0.0826	5.5
Length of M_2	4	2.08	2.10	2.09	0.01	0.5
Talonid width of M_2	4	1.41	1.64	1.52	0.0974	6.4
Length of M_3	3	1.93	2.00	1.96	0.0351	1.8
Trigonid width of M_3	3	1.29	1.41	1.36	0.0624	4.6
Talonid width of M_3	2	1.14	1.16	1.15	0.0141	1.2

Rhinolophus hanaki sp. n.

(pl. 11: 4, figs. 11—12, tables 21—25)

1962*a*. *Rhinolophus grivensis* (Depéret); Kowalski: 44 (partly).
1975. *Rhinolophus variabilis* sp. n.; Topal: 13 (partly).
1979. *Rhinolophus cf. variabilis*; Sulimski *et al.*: 390.

Holotypus: md. s. (FM—P2) (I_1—P_3) P_4—M_3 ArCo. ZZSiD, MF/1692/1 (pl. 11: 4).

Locus typicus: cave 431 in Podlesice near Kroczyce, central part of the Kraków—Wieluń Upland.

Stratum typicum: cave deposits of the lower Pliocene (Lower Ruscinian).

Derivatio nominis: *hanaki* — in honour of Dr. Vladimir Hanak the distinguished Czech chiropterologist and my friend.

Diagnosis. — A small representative of *Rhinolophus*, close to *R. hipposideros* and to *R. variabilis* Topal. It differs from both in its larger size, especially in its elongated P_4, its broad, massive skull and much smaller talons on M^1 and M^2, also in its relatively short palate.

Measurements see Tables 21—25.

Material. — Podlesice: holotype, 7 fragments of maxillae, (MF/1692/56—61) and 56 mandibles or their fragments (MF/1692/2—54, 62—63). All ZZSiD collection.

Mała Cave: 2 fragments of maxillae, 2 mandibles and several isolated teeth (P^4, M^1, M^2, M^3, C_1, P_3, P_4, M_1, M_2, M_3) from layers 2, 4+5 and 6 of Mała Cave. ZPALWr collection.

Table 18. Skull measurements of *Rhinolophus* cf. *macrorhinus* Topal from the Kadzielnia 1 locality

Specimen MF/33/ : Measurements :	16	17	19	21	22
Length of $C^1 - P^4$	-	-	-	3.83	-
Length of $P^4 - M^3$	6.39	-	-	-	-
Length of $M^1 - M^3$	5.25	-	-	-	-
Length of C^1	-	-	-	2.31	-
Width of C^1	-	-	-	1.78	-
Length of P^2	-	0.44	-	-	-
Width of P^2	-	0.51	-	-	-
Length of P^4	1.25	1.55	1.54	1.67	1.60
Width of P^4	1.88	1.92	1.98	1.80	2.00
Length of M^1	2.22	-	-	-	-
Width of M^1	2.06	-	-	-	-
Length of M^2	2.02	-	-	-	-
Width of M^2	2.08	-	-	-	-
Length of M^3	1.40	-	-	-	-
Width of M^3	1.96	-	-	-	-
Length of 1st commissure of M^3	0.95	-	-	-	-
Length of 2nd commissure of M^3	0.97	-	-	-	-
Length of 3rd commissure of M^3	0.72	-	-	-	-
Length of 4th commissure of M^3	0.15	-	-	-	-

Description. — Only some fragments of maxillae have been preserved. The anterior margin of the palate reaches the distal end of the talon of P^4, the posterior margin reaching the paracone of M^3. Lacrimal foramen large (0.51 mm), while in *R. variabilis* Topal it measures 0.36 mm.

C^1 — not preserved. Alveolus of tooth oriented mesially and obliquely.

P^2 — not preserved. Alveolus of tooth large, oval, elongated oro-caudally, in toothrow. P^4 in shape of its crown resembles an elongated trapezium. Cingulum poorly developed, more pronounced only on the anterior labial side. On the cingulum, at the point of its contact with P^2, there is a small depression. Labial margin of cingulum almost straight. Talon fairly large. Distal margin of tooth has in its medial part a shallow sinus.

Table 19. Descriptive statistics for measurements of the upper teeth of *Rhinolophus* cf. *macrorhinus* Topal from the Kadzielnia 1 locality

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Length of C^1	11	1.78	2.39	2.12	0.2057	9.7
Width of C^1	11	1.70	2.26	1.95	0.1898	9.7
Length of P^4	5	1.25	1.67	1.52	0.1605	10.5
Width of P^4	5	1.88	2.00	1.92	0.0805	4.2

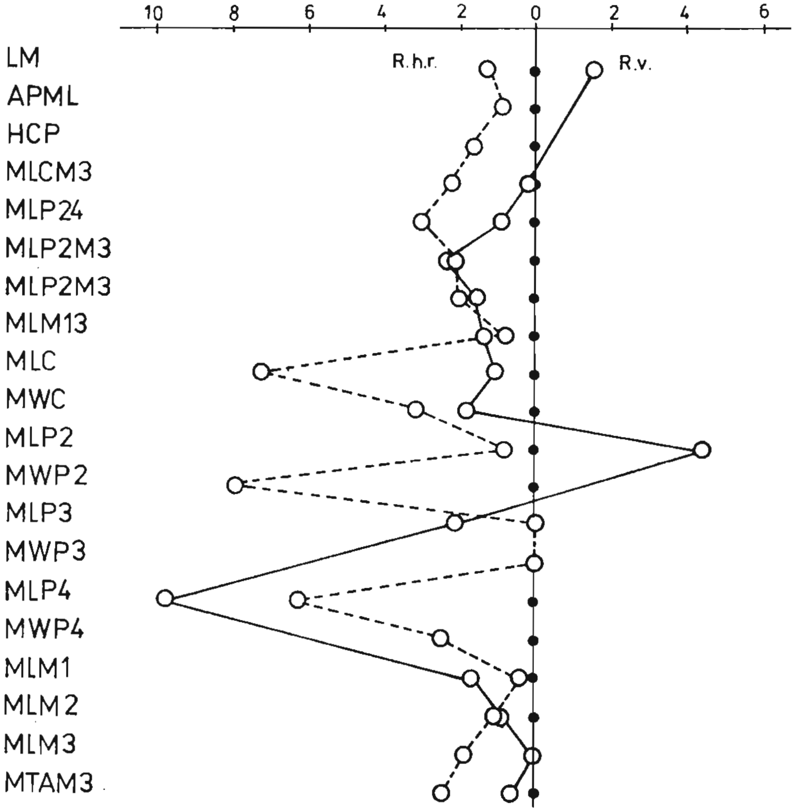

Fig. 11. Simpson's diagram for several species of *Rhinolophus*. *R. hanaki* sp. n. from Podlesice (standard), R.v. — *R. variabilis* Topal (holotype), R.h.r. — *R. hipposideros*, Recent.

Table 20. Comparison of some maxillar dimensions in several fossil species of *Rhinolophus* and the recent *R. ferrumequinum*

Species : Measurements :	R. kowalskii Podlesice	R. wenzensis Węże I	R. macrorhinus holotype	R.cf.macrorhinus Kadzielnia 1	R. ferrumequinum recent
Length of palatum	2.92	2.85	2.80	-	2.45
Length of $C^1 - P^4$	4.06	4.13	3.83	-	3.63
Length of P^2	0.58	0.50	0.38	0.44	0.37
Length of M^1	2.14	2.09	2.24	2.06	2.16
Length of M^3	1.50	1.54	1.45	1.40	1.46
Length of 1st commissure of M^3	0.93	0.92	0.84	0.95	0.88
Length of 2nd commissure of M^3	0.88	0.90	0.85	0.97	0.75
Length of 3rd commissure of M^3	0.64	0.64	0.60	0.72	0.55
Length of 4th commissure of M^3	0.28	absent	absent	0.15	absent

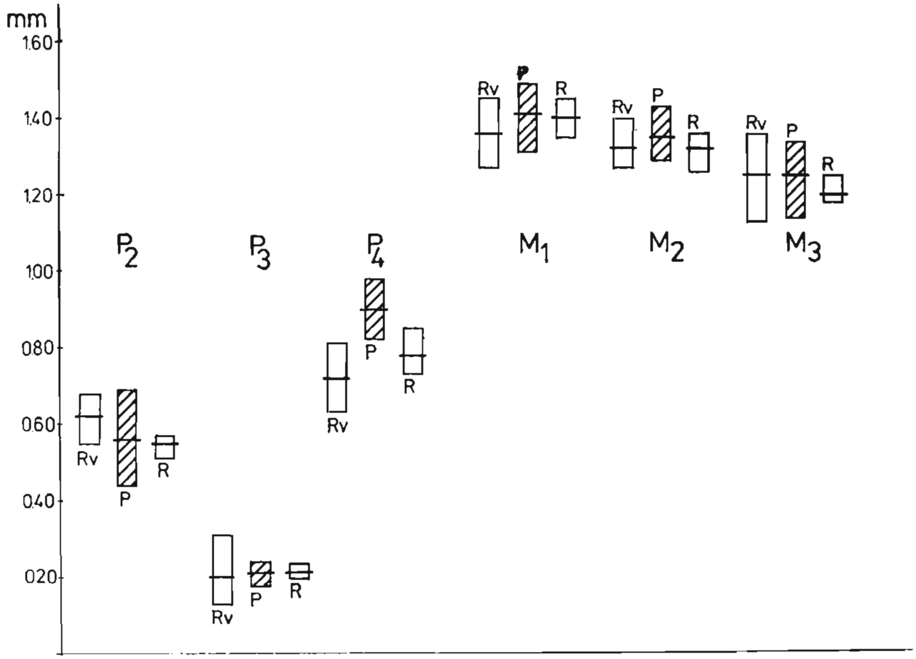

Fig. 12. Comparison of the lengths of the upper teeth in several species of *Rhinolophus*: Rv — *R. variabilis* Topal, P — *R. hanaki* sp. n. from Podlesice, R — *R. hipposideros*, Recent.

M^1 — typical of horseshoe bats of the "*hipposideros*" group. Its talon is however very poorly developed and much smaller than in *R. variabilis* and *R. hipposideros* (Bechstein). M^2 — relatively short, with talon poorly developed. M^3 — is long and massive, commissure IVth very short and sometimes altogether absent.

Mandible is slightly longer and altogether more massive than in the recent *R. hipposideros*, coronoid process high; symphysis of mandible narrow.

I_1 — trilobate, with poorly developed cingulum. Internal cusp present (absent in *R. hipposideros*). I_2 — not preserved, but judging by the alveolus, incisors were massive and loosely spaced teeth.

C_1 — massive, exceeding greatly in size the canine in *R. hipposideros* and *R. variabilis*. Upper surface of tooth distinctly canted linguad, while in *R. hipposideros* it is almost straight. P_2 — quite large, projecting from toothrow, oval in outline of crown, less massive however than in *R. variabilis*.

P_3 — slightly more massive than in *R. hipposideros*, projecting from toothrow. P_4 — massive, exceeding its counterpart in size both in *R. hipposideros* and *R. variabilis*. Its crown resembles a low triangle. Cingulum is poorly developed and only in the anterior part on the lingual side does it form a distinct lobe oriented orally.

M_1 and M_2 similar to those of *R. hipposideros*, but somewhat more massive. M_3 — longer and more massive (especially the talonid) than in *R. hipposideros*.

Comparisons. — Topal (1975) included all the small horseshoe bats of Podlesice and Węże I in *R. variabilis*. However, it turned out that the material from Podlesice is a different taxon, described in the present work as *Rhinolophus hanaki* sp. n. The new species differs from *R. variabilis* Topal in its greater skull size and a larger lobe on the mesio-lingual side of the cingulum of P_4. The latter feature distinguishes it also from the modern *P. hipposideros*. From *R. grivensis* (Depéret) the new species

Table 21. Mandibular measurements of the more complete specimens of *Rhinolophus hanaki* sp. n. from the Podlesice locality

Specimen MF/1692/ : Measurements :	1	2	3	4	5	6	7	8	9	10
Length of mandible	10.52	0.08	10.35	-	10.46	10.44	10.82	10.40	10.46	10.71
APML	3.94	3.81	4.06	-	3.78	4.30	4.25	3.92	3.98	4.13
Height of coronoid process	2.34	2.15	2.16	2.36	2.30	2.21	2.33	2.28	2.31	-
Length of C_1 - M_3 $^{a.}$	5.92	5.70	5.75	5.95	6.07	5.90	5.86	5.94	5.96	5.98
Length of P_4 - M_3	4.62	4.47	4.57	-	-	-	4.62	4.71	-	4.71
Length of M_1 - M_3	3.85	3.70	3.83	3.91	4.01	3.85	3.86	3.89	3.95	3.92
Length of P_2	-	-	-	-	-	-	-	-	-	0.44
Width of P_2	-	-	-	-	-	-	-	-	-	0.33
Length of P_3	-	-	-	-	-	-	-	-	-	0.18
Width of P_3	-	-	-	-	-	-	-	-	-	0.16
Length of P_4	0.86	0.86	0.86	-	-	-	0.84	0.98	-	0.87
Width of P_4	0.72	0.74	0.70	-	-	-	0.84	0.72	-	0.70
Length of M_1	1.37	1.31	1.40	1.37	1.40	1.38	1.40	1.40	1.40	1.45
Length of M_2	1.32	1.30	1.31	1.35	1.41	1.43	1.33	1.37	1.33	1.36
Length of M_3	1.27	1.23	1.20	1.25	1.29	1.27	1.18	1.27	1.28	1.24
Talonid width of M_3	0.70	0.81	0.72	0.78	0.77	0.77	0.78	0.77	0.74	0.79

(a. alveolar length). MF/1692/1 — holotype.

Table 22. Descriptive statistics for the mandibular measurements of *Rhinolophus hanaki* sp. n. from the Podlesice locality

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Length of mandible	10	10.08	10.82	10.44	0.2163	2.1
APML	10	3.78	4.30	4.01	0.1743	4.3
Height of coronoid process	14	2.15	2.36	2.26	0.0713	3.2
Length of I_1- I_3[a.]	14	0.54	0.87	0.72	0.0785	10.9
Length of C_1- M_3[a.]	14	5.70	6.11	5.91	0.1181	2.0
Length of P_2- M_3[a.]	15	5.10	5.45	5.30	0.1078	2.0
Length of P_4- M_3	13	4.47	4.78	4.65	0.0992	2.1
Length of M_1- M_3	20	3.70	4.01	3.88	0.0865	2.2
Length of C_1	2	0.77	0.79	0.78	0.0141	1.8
Width of C_1	2	0.71	0.75	0.73	0.0283	3.9
Length of P_2	2	0.44	0.69	0.56	0.1768	31.3
Width of P_2	2	0.33	0.58	0.45	0.1768	38.8
Length of P_3	4	0.18	0.24	0.21	0.0275	13.0
Width of P_3	4	0.16	0.26	0.22	0.043	19.6
Length of P_4	20	0.83	0.98	0.90	0.0489	5.4
Width of P_4	20	0.70	0.84	0.75	0.041	5.5
Length of M_1	26	1.31	1.49	1.41	0.0383	2.7
Length of M_2	23	1.30	1.43	1.35	0.0364	2.7
Length of M_3	20	1.18	1.34	1.25	0.0483	3.8
Trigonid width of M_3	20	0.75	0.83	0.79	0.0281	3.6
Talonid width of M_3	20	0.68	0.83	0.75	0.0426	5.7

(a. alveolar length)

Table 23. Skull measurements of *Rhinolophus hanaki* sp. n. from the Podlesice locality

Specimen MF/1692/ : Measurements :	55	56	57	59	60	61
Length of P^4- M^3	4.32	4.32	4.21	-	-	-
Length fo M^1- M^3	3.61	3.62	3.40	-	-	-
Length of P^4	0.95	0.87	0.93	0.90	0.98	-
Width of P^4	1.48	1.56	1.47	-	1.27	-
Length of M^1	1.46	1.34	1.34	-	-	-
Width of M^1	1.35	1.27	-	-	-	-
Length fo M^2	1.40	1.36	1.30	-	-	-
Width of M^2	1.52	1.38	-	-	-	-
Length of M^3	0.98	1.04	0.94	1.13	-	1.08
Width of M^3	1.33	1.41	1.29	1.36	-	1.42
Length of 1st commissure of M^3	0.61	0.56	0.57	0.54	-	0.58
Length of 2nd commissure of M^3	0.64	0.61	0.65	0.68	-	0.67
Length of 3rd commissure of M^3	0.51	0.50	0.46	0.46	-	0.51
Length of 4th commissure of M^3	0.35	0.34	0.37	0.43	-	0.40

differs in the less developed talon on the upper molars, in the presence of a residual IVth commissure on M^3 and a massive angular process on the maxilla, inclined orally, while in *R. grivensis* this process is delicate and vertical (Mein 1964; Topal 1974, 1975; Zapfe 1950, 1952).

Occurrence. — The species is known from Pliocene deposits from Poland (Podlesice and Mała Cave).

Rhinolophus cf. *variabilis* Topal, 1975

(fig. 12, Table 25, 26)

1962*a*. *Rhinolophus grivensis* (Depéret); Kowalski: 44 (partly).

Material. — Węże I: 2 fragments of mandibles: md.d. (FM—C/P2 (I_1—P_3) P_4—M_1 (MF/1693/1, specimen no. 2 of Kowalski 1962a); md.s. FM—C(P2) (I_2) C_1(P_2—P_3) P_4—M_1 (MF/1693/2, specimen no. 4 of Kowalski 1962*a*). Moreover, 4 incomplete cochleae have been preserved. All ZZSiD collection.

Description. — The preserved fragments of mandibles are delicate, clearly lower than those in the specimens of *R. hanaki* sp. n.

Table 24. Descriptive statistics for the skull measurements of *Rhinolophus hanaki* sp. n. from the Podlesice locality

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Length of P^4- M^3	3	4.21	4.32	4.28	0.0635	1.5
Length of M^1- M^3	3	3.40	3.62	3.54	0.1242	3.5
Length of P^4	5	0.87	0.98	0.93	0.0428	4.6
Width of P^4	4	1.27	1.56	1.46	0.1234	8.5
Length of M^1	3	1.34	1.46	1.38	0.0693	5.0
Width of M^1	2	1.27	1.35	1.31	0.0566	4.3
Length of M^2	3	1.30	1.40	1.35	0.0503	3.7
Width of M^2	2	1.38	1.52	1.45	0.0990	6.8
Length of M^3	5	0.94	1.13	1.03	0.0760	7.3
Width of M^3	5	1.29	1.42	1.36	0.0545	4.0
Length of 1st commissure of M^3	5	0.54	0.61	0.57	0.0259	4.5
Length of 2nd commissure of M^3	5	0.61	0.68	0.65	0.0274	4.2
Length of 3rd commissure of M^3	5	0.46	0.51	0.49	0.0259	5.3
Length of 4th commissure of M^3	5	0.34	0.43	0.38	0.0370	9.8

Table 25. Comparison of P_4 length of *Rhinolophus* cf. *variabilis* Topal from the Węże I locality with other fossil and recent species of "*hipposideros*" group

Species : Measurement :	R.cf. variabilis Węże I	R. variabilis Hungary	R. hanaki sp.n. Podlesice	R. hipposideros recent
Length of P_4	0.83	0.72	0.90	0.71

Table 26. Skull measurements of *Rhinolophus* cf. *variabilis* Topal from the Węże I locality

Specimen MF/1693/ Measurements :	1	2
Length of C_1 - P_4	-	2.25
Length of C_1	-	0.77
Width of C_1	-	0.75
Length of P_4	0.84	0.82
Width of P_4	0.73	0.79
Length of M_1	1.50	1.54
Talonid width of M_1	0.92	1.00

Symphysis of mandible long and narrow, clearly smaller, however, than in the species from Podlesice. L/W of mandibular symphysis in MF/1693/1 1.50/0.36, in holotype of *R. hanaki*: 1.75/0.56.

Alveoli of incisors large and oval.

C_1 fine with poorly developed cingulum. Crown ellipsoidal on the labial side and almost straight on the lingual side. In the specimen examined, antero-labial part of crown damaged. Crown of tooth high, its tip curved linguad. A small talon in the anterior part of the tooth.

Alveolus of P_2 large and oval, that of P_3 relatively large, projecting labiad from the toothrow by 1/2 its diameter. Judging by the alveolus, P_3 was a fairly massive tooth.

P_4 — in the outline of its crown resembles a triangle with rounded corners. Cingulum well developed, especially on the anterior and lingual side of the crown, forming a small surface here. Crown of this tooth not particularly high, slightly lower than the protoconid of M_1. M_1 — massive, nyctalodontic. Its talonid is particularly massive, yet not departing in shape from the molars of *Rhinolophus* of the "*hipposideros*" group, with which it is compared.

Remarks. — In 1975 Topal described a new species *Rhinolophus variabilis* from the Osztramos 9 locality in Hungary (Middle Pliocene/Estramontian). It was of the "*hipposideros*" group, exceeding the recent species in size, with a long toothrow C—P_4 and M_3 little reduced. It proved difficult to assess the systematical status of the specimens from Węże I. The material from this site, described by Kowalski (1962*a*) was highly incomplete. Some of the specimens in fact represented different species, so in the series described by him only two fragments of the mandibles (MF/1693/1—2) and 4 cochleae could be considered as belonging to *Rhinolophus.* Comparison of material from Węże I and Podlesice showed that P_4 is smaller and more delicate in the *Rhinolophus* specimens from Węże I. In the shape of its crown it resembles one of the specimens of *R. variabilis* from Hungary (table 25).

The mentioned convergences in structure, combined with a similar age of the locality of Węże I and Osztramos 9 made it possible to assign, with a some reservations, the specimens examined from Węże I to *R.* cf. *variabilis.*

Occurrence. — *R.* cf. *variabilis* is known so far only from early Pliocene deposits from Podlesice.

Rhinolophus neglectus Heller, 1936

(pl. 11: 5; fig. 13, tables 27—32)

1936. *Rhinolophus neglectus*; Heller: 110.

1979. *Rhinolophus* cf. *neglectus* Heller; Sulimski *et al.*: 390.

1979. *Rhinolophus* sp. ("*euryale*" group): Sulimski *et al.*: 390.

Material. — Mała Cave (l. 4+5): 5 fragments of maxillae (M-675/8/1—5), 19 fragments of mandibles (M-675/8/6—16, M-675/9/1—8), 22 isolated teeth without numbers. All ZPALWr collection.

Rębielice Królewskie II: 14 fragments of mandible (MF/1694/1—14), 3 isolated teeth without numbers: 1×C_1, 2×C^1. All ZZSiD collection.

Measurements and basic statistics see Tables 26—30, the isolated teeth have the following dimensions. L/W: C^1 (d) 1.39/1.19, C^1 (s) 1.40/1.27, C_1 (s) 0.98/1.06.

Of the skull, only small fragments of jaws have been preserved in the material examined.

C^1 — massive, crown almost oval in outline, longer axis parallel to toothrow. Large talon on lingual side. Distally-labial margin of cingulum oval, without a depression, this pointing to the absence of pressure from P^2. Anterior margin of crown strongly backcurved, so the tip of the tooth points caudad. In most specimens, the posterior margin of the crown has a saddle-like depression at 2/3 of its height, differing in this respect from the three medium-sized recent species of horseshoe bat, in which the posterior margin of this tooth is a gently curving arc.

P^2 — not preserved in the material examined, but the position of the alveolus indicates that it lay in the toothrow, hence the crowns of C^1 and P^4 were not contiguous. P^4 in outline of its crown resembles this tooth in the modern *R. mehelyi*, but is longer than in every one of the three modern species of horseshoe bat of the "*euryale*" group.

M^{1-2} — outline of crown similar to *R. mehelyi* Matschie, but the talon on M^1 is much more strongly developed. M^3 — long, massive, and has a well-developed IVth commissure. Posterior margin of palate much as in the recent species *R. euryale* Blasius and *R. blasii* Peters and only reaches the anterior margin of M^3.

In the mandible, incisors, canines, and first premolars are not preserved. Judging by the alveolus, P_2 must have been fairly massive.

P_3 — also massive, projecting labiad from toothrow. The position of the alveoli of P_2 and P_4 indicates that the crowns of these teeth were not contiguous, as is the case in all modern *Rhinolophus* of the "*euryale*" group. P_4 — also massive, in outline of its crown it is irregularly trapezium-shaped, with the shorter base oriented labiad. Cingulum well developed, forming a small surface in the antero-lingual part.

M_{1-3} — molars do not differ much from those in *R. mehelyi*, they are however less massive, especially their talonids.

Remarks. — Description of *R. neglectus* given by Heller (1936) is very concise.

Both from the original description and from measurements it is apparent that *R. neglectus* Heller is larger than the modern horseshoe bat *R. euryale*. Unfortunately, Heller did not compare the fossil form with the two remaining species of medium-sized *Rhinolophus*, i.e. with *R. blasii* and *R mehelyi*. Both these species are similar in size to *R. neglectus* which is now usually thought to be related to *R. mehelyi*. The present author was able to compare the *R. neglectus* holotype with specimens from Mała Cave. Both in the holotype and in the specimens examined, the positions of P_3 and dimensions are alike, allowing the remains from Mała Cave to be included in the species *R. neglectus* Heller. The specimens from this cave have robust teeth, especially canines (C^1) whose lingual side is strongly developed. P_4 is much longer than in any recent species of horseshoe bat of the "*euryale*" group. Specimens examined from the point of view of the morphology of P_3 look most like *R. blasii*, while in dimensions they come closest to the modern *R. mehelyi*. The specimens from

Table 27. Mandibular measurements of *Rhinolophus neglectus* Heller from the Mała Cave (layer 4+5) locality

Specimen M - 675/8/ : Measurements :	6	7	8	9	10	11	12	13	14	15
Height of coronoid process	-	-	-	3.04	-	-	-	-	-	-
Length of P_2- P_4[a.]	-	-	1.90	-	1.88	-	-	-	-	-
Length of P_4- M_3	5.70	-	-	-	-	-	-	-	-	-
Length of M_1- M_3	4.78	-	-	-	-	-	-	-	-	-
Length of C_1	-	-	-	-	-	-	-	-	0.94	0.98
Width of C_1	-	-	-	-	-	-	-	-	1.15	1.07
Length of P_3	-	-	-	-	-	0.26	-	0.30	-	-
Width of P_3	-	-	-	-	-	0.38	-	0.35	-	-
Length of P_4	1.09	1.12	1.05	1.10	1.05	1.13	1.10	1.06	1.07	-
Width of P_4	0.81	0.90	0.86	0.84	0.86	0.88	0.88	0.94	0.86	-
Length of M_1	1.74	1.80	1.70	-	-	-	1.81	-	-	-
Length of M_2	1.61	1.71	-	-	-	-	-	-	-	-
Length of M_3	1.52	-	-	1.59	-	-	-	-	-	-
Talonid width of M_3	0.83	-	-	-	-	-	-	-	-	-

(a. alveolar length)

Table 28. Descriptive statistics for the mandibular measurements of *Rhinolophus neglectus* Heller from the Mała Cave (l. 4+5) locality (the table also gives the holotype dimensions)

measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.	R.neglectus holotype
Alveolar length of							
P_2- P_4	2	1.88	1.90	1.89	0.0141	0.7	-
Length of P_4- M_3	1	-	-	5.70	-	-	5.76
Length of M_1- M_3	1	-	-	4.78	-	-	4.78
Length of C_1	2	0.94	0.98	0.96	0.0283	2.9	-
Width of C_1	2	1.07	1.15	1.11	0.0566	5.1	-
Length of P_3	2	0.26	0.30	0.28	0.0283	10.1	0.26
Width of P_3	2	0.35	0.38	0.36	0.0212	5.8	0.30
Length of P_4	9	1.05	1.13	1.09	0.0296	2.7	1.08
Width of P_4	9	0.81	0.94	0.87	0.0367	4.2	0.85
Length of M_1	4	1.70	1.81	1.76	0.0519	2.9	1.85
Length of M_2	2	1.61	1.71	1.66	0.0707	4.3	1.70
Length of M_3	2	1.50	1.59	1.55	0.0495	3.2	1.50
Talonid width of M_3	1	-	-	0.83	-	-	0.82

Mała Cave are also much larger than the fossil species *R. lissinensis* Mein and *R. grivensis* (Depéret) (table 32).

There are some slight differences between the specimens of *R. neglectus* from Mała Cave (l. 4+5) and Rębielice II. Those from Mała Cave have, on average, longer teeth, while the width of P_4 is slightly greater in the specimens from Rębielice, the same applying to the talonid on M_3. These differences may equally well result from the different stratigraphic age of sites and from individual variation.

Occurrence. — *R. neglectus* known so far from Pliocene deposits from Europe (West Germany), Poland — Mała Cave and Rębielice Królewskie II.

Rhinolophus sp. (mehelyi?)

Material. — Podlesice: fragment of left mandible md. s. P_2—M_2 (ZZSiD MF/1696/1). Measurements:

	P_2—P_4	P_2	P_3	P_4	M_1	M_1 talonid	M_2	M_2 talonid
length	1.81	0.87	0.24	1.04	1.69	0.64	1.45	0.64
width	—	0.87	0.33	1.01	—	1.11	—	1.23

Description and comparisons. — The specimen examined is a fragment of mandible with the teeth P_2—M_2, partly broken. It belonged to a horseshoe bat of medium size, close to *Rhinolophus mehelyi*; it differs considerably, however, from this species in its much more massive P_2 and P_3 and shorter talonids on the molars.

Table 29. Cranial measurements of *Rhinolophus neglectus* Heller from the Mała Cave (l. 4+5) locality

Specimen ZPAL.Wr. M-675/8/ : Measurements :	1	5
Length of palatum	-	3.82
Length of M^1- M^3	-	4.11
Length of C^1	1.60	-
Width of C^1	1.18	-
Length of P^2	0.52	-
Width of P^2	0.60	-
Length of P^4	1.01	1.17
Length of M^2	1.53	1.58
Length of M^3	-	1.16
Width of M^3	-	1.50

Table 30. Mandibular measurements of *Rhinolophus neglectus* Heller from the Rębielice Królewskie II locality

Specimen MF/1694/ : Measurements :	1	2	3	4	5	11
Length of P_2- P_4 a.	1.85	-	1.76	1.77	-	-
Length of P_4- M_3	5.31	-	-	-	-	-
Length of M_1- M_3	4.43	-	-	-	-	-
Length of P_4	1.03	1.07	-	-	1.05	1.06
Width of P_4	0.86	0.92	-	-	0.90	0.88
Length of M_1	1.72	1.69	1.69	1.67	1.68	1.62
Length of M_2	1.60	1.58	1.57	1.60	1.59	-
Length of M_3	1.44	-	-	-	-	-
Talonid width of M_3	0.85	-	-	-	-	-

(a. alveolar length)

Table 31. Descriptive statistics for the mandibular measurements of *Rhinolophus neglectus* Heller from the Rębielice Królewskie II locality

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Alveolar length of P_2- P_4	5	1.66	1.85	1.77	0.0726	4.1
Length of P_4	4	1.03	1.07	1.05	0.0171	1.6
Width of P_4	4	0.86	0.92	0.89	0.0258	2.9
Length of M_1	9	1.62	1.72	1.67	0.0331	2.0
Length of M_2	7	1.57	1.61	1.59	0.0138	0.9
Length of M_3	2	1.44	1.54	1.49	0.0707	4.7
Talonid width of M_3	2	0.85	0.93	0.89	0.0566	6.4

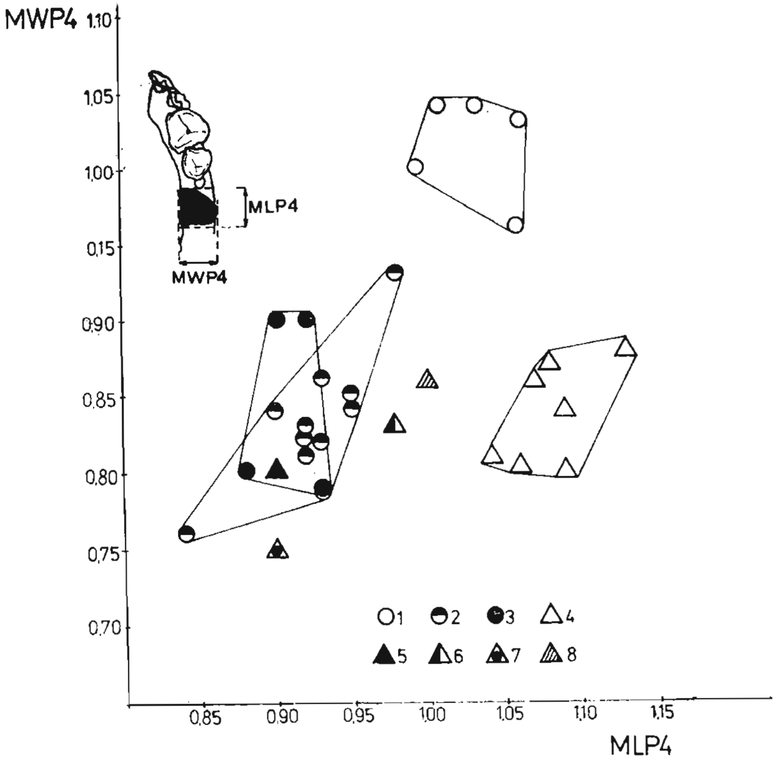

Fig. 13. Comparison of the dimensions of P_4 in several fossil and modern species of *Rhinolophus*: 1 — *R. mehelyi*, Recent, 2 — *R. euryale*, Recent, 3 — *R. blasii*, Recent, 4 — *R. neglectus* from Mała Cave, 5 — *R. lissiensis*, 6 — *R. lissensis* (according to Topal 1975), 7 — *R. grivensis*, 8 — *R. euryale praeglacialis* Kormos, (holotype).

Table 32. Comparison of the dimensions of several fossil and recent species of *Rhinolophus*

Species	Locality	Length of P_4-M_3	Length of M_1-M_3
R. neglectus Heller holotype	Gundersheim	5.6	4.7
R. e. praeglacialis Kormos holotype	Beremend	5.7	4.8
R.neglectus Heller	Mała Cave	5.7	4.7
R. grivensis /Deperet/	La Grive	4.6 - 4.9	4.0
R. lissiensis Mein holotype	Lissieu	5.0	4.2
R. lissiensis Mein	Osztramos	5.2	4.3
R. euryale Blasius	recent	5.2 - 5.5	4.4 - 4.6
R. blasii Peters	recent	5.4 - 5.8	4.5 - 5.0
R. mehelyi Matschie	recent	5.8 - 5.9	4.9 - 5.0

P_2 — massive, clearly asymmetric in the shape of its crown, whose lateral, labial face is strongly elongted. P_3 — also massive, transversely oval, slightly askew in toothrow and projecting outward (labiad) a little, so that in contrast to the modern *R. mehelyi*, the crowns of P_2 and P_4 are not contiguous. P_4 — a massive tooth, in outline of crown resembling a trapezium with its base facing linguad. Cingulum very poorly developed. This is a distinct difference with respect to modern forms, in which the cingulum is usually well developed.

M_1 and M_2 are relatively short, nyctalodontic, characteristic of *Rhinolophus*. Talonids of teeth massive and short.

The jaw fragment examined cannot be identified with other fossil horseshoe bats of medium size known from Central Europe owing either to considerable differences in size (eg. *R. neglectus*), or to the very different shapes of the crowns of P_2 and P_4. It appears to be closest to *R. lissiensis*, but owing to a lack of sufficient material it is at present impossible to determine these relationships.

Since to the features in which the specimen examined differs from the modern *R. mehelyi* are of a less specialised nature, it can be assumed that it has evolved from a form close to the ancestor of the recent species.

Family **Miniopteridae** Mein et Tupinier, 1977

Genus *Miniopterus* Bonaparte, 1837

Miniopterus approximatus sp. n.

(pl. 12: 1; fig. 14—16; tables 33—37)

1956. *Miniopterus schreibersi* (Kuhl); Kowalski: 358, pl. 2: fig. 4.
1959. *Miniopterus schreibersi* (Kuhl); Kowalski: 16 and 92.
1964. *Miniopterus schreibersi* (Kuhl); Kowalski: 84, tab. 1.

Holotypus: left mandible with preserved processes and teeth md. s. (FM—C/P2) (I_1—I_3) C_1—M_3, An, Ar, Co. ZZSiD MF/12/4 (pl. 12: 1).

Locus typicus: Cave 431 in Podlesice near Kroczyce, central part of the Kraków—Wieluń Upland.

Stratum typicum: Cave deposits, lower Pliocene (Lower Ruscinian).

Derivatio nominis: *approximatus* — referring to the probable phylogenetic links with the recent *M. schreibersi*.

Diagnosis. — A medium-sized representative of *Miniopterus*, close to the recent species *Miniopterus schreibersi* but with a more delicately built skull. Teeth less massive and narrower. Molars short. Small premolars loosely spaced, so that they barely touch at the margins of the cingulum.

Material. — Podlesice: holotype, 10 mandibles (MF/12/5—14), 12 fragments of maxillae (MF/12/1—3, 26—34), over 50 mandible fragments, 10 cranial fragments, 4 fragments of humeri. All ZZSiD collection.

Measurements see tables 33—36.

Description. — Rostrum in general outline much more delicate and lower but longer than in *M. schreibersi*. Posterior margin of nasal opening triangularly notched, while it is a squarish-oval in *M. schreibersi*.

Incisors not preserved.

C^1 — delicate with a poorly developed cingulum on lingual side.

P^2 — not preserved, but judging by the size of the alveolus it was somewhat more massive than in the modern form. The presence of this tooth in *Miniopterus* was first found by Mein and Tupinier (1977).

P^3 — surface of crown roughly 1/3 smaller than in the modern species. Depressions on lingual side of cingulum shallow and over twice as small in diameter as in *M. schreibersi*. P^4 — triangular in outline of crown, less massive than in the modern form. Lobe in antero-lingual part rather small, or absent.

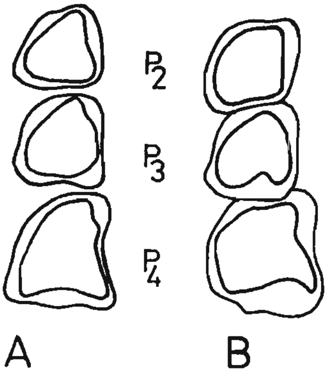

Fig. 14. Comparison of the position of the premolars (P_2—P_4) in *Miniopterus*: A — *M. approximatus* sp. n. (holotype), Podlesice, B — *M. schreibersi*, Recent.

Table 33. Measurement of the more complete specimens of *Miniopterus approximatus* sp. n. from the Podlesice locality (Specimen MF/12/4 — holotype)

Specimen MF/12/ : Measurements :	4	5	6	7	8	9	10	11	12	13
Length of mandible	10.66	10.60	10.88	11.14	10.65	11.03	10.67	10.97	11.10	10.64
APML	3.59	3.67	3.65	3.83	3.51	3.70	3.75	3.86	3.75	3.67
Height of coronoid process	2.70	2.62	2.54	2.70	2.57	2.74	2.76	2.64	2.70	2.63
Length of C_1- M_3	6.15	-	-	-	-	-	-	-	-	-
Length of P_2- P_4	2.00	-	-	-	-	-	-	-	-	-
Length of P_4- M_3	4.30	4.58	4.61	4.55	4.53	-	-	4.43	-	4.40
Length of M_1- M_3	3.60	3.90	3.86	3.95	3.75	3.92	3.75	3.80	3.77	3.72
Length of C_1	0.67	-	-	-	-	-	-	-	-	-
Length of P_2	0.52	-	-	-	-	-	-	-	-	-
Length of P_3	0.57	-	0.60	0.62	-	0.63	-	0.59	0.63	-
Length of P_4	0.83	0.91	0.85	0.90	0.81	-	-	0.81	-	0.72
Width of P_4	0.72	0.74	0.77	0.76	0.75	-	-	0.73	-	0.86
Length of M_1	1.30	1.39	1.36	1.43	1.34	1.41	1.37	1.39	1.41	1.35
Length of M_2	1.24	1.28	1.32	1.28	1.28	1.33	1.33	1.29	1.27	1.25
Length of M_3	1.14	1.27	1.20	1.19	1.16	1.24	1.18	1.19	1.20	1.15
Talonid width of M_3	0.70	0.72	0.66	0.70	0.63	0.71	0.66	0.66	0.70	0.68

Table 34. Descriptive statistics for the mandibular measurements of *Miniopterus approximatus* sp. n. from the Podlesice locality

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Length of mandible	14	10.59	11.14	10.83	0.2031	1.9
APML	12	3.51	3.86	3.70	0.1011	2.7
Height of coronoid process	20	2.54	2.92	2.68	0.0980	3.7
Length of C_1- M_3	5	6.10	6.34	6.20	0.1059	1.7
Length of P_2- P_4	17	1.85	2.11	2.00	0.0661	3.3
Length of P_2- M_3	4	5.51	5.65	5.60	0.0618	1.1
Length of P_3- M_3	10	4.90	5.15	5.04	0.0751	1.5
Length of P_4- M_3	27	4.30	4.63	4.47	0.0911	2.0
Length of M_1- M_3	35	3.65	3.95	3.78	0.0853	2.3
Length of C_1	16	0.65	0.79	0.72	0.0469	6.5
Width of C_1	16	0.65	0.80	0.74	0.0431	5.8
Length of P_2	17	0.52	0.65	0.58	0.0371	6.4
Width of P_2	17	0.53	0.67	0.61	0.0354	5.8
Length of P_3	27	0.57	0.74	0.63	0.0362	5.7
Width of P_3	26	0.56	0.66	0.61	0.0266	4.4
Length of P_4	43	0.72	0.95	0.86	0.0481	5.6
Width of P_4	43	0.70	0.86	0.77	0.0399	5.2
Length of M_1	43	1.31	1.50	1.39	0.0421	3.0
Length of M_2	39	1.23	1.39	1.32	0.0391	3.0
Length of M_3	36	1.14	1.32	1.21	0.0441	3.6
Talonid width of M_3	32	0.62	0.74	0.70	0.0369	5.3

M^1 and M^2 — differ from the modern form in the smaller and more narrow talons. M^3 — more narrow than in the modern species. Ist commissure short (table 34), palatal margin extends beyond the margin of crown of M^3.

Mandible is more delicate, the anterior part elongated, the teeth delicate, loosely spaced, coronoid process higher than in the modern *M. schreibersi.*

Table 35. Skull measurements of *Miniopterus approximatus* sp. n. from the Podlesice locality

Specimen MF/12/ : Measurements :	1	2	3	26	27	29	30	31	32	34
Length of palatum	5.72	5.62	-	-	-	-	-	-	-	-
Length of P^3- M^3	4.93	4.86	4.95	4.98	4.94	4.99	-	5.01	4.88	5.00
Length of P^3- P^4	2.05	1.87	1.99	2.05	1.94	1.92	-	1.96	2.00	1.98
Length of P^4- M^3	4.29	4.24	4.31	4.29	4.36	4.27	4.32	4.45	4.22	4.32
Length of M^1- M^3	-	3.43	3.37	3.51	3.43	3.46	3.45	3.52	-	3.49
Length of P^3	0.94	0.82	0.83	0.92	0.77	0.86	-	0.83	0.80	0.85
Width of P^3	1.04	0.82	0.95	1.03	0.98	0.89	-	0.93	0.94	0.92
Length of P^4	1.21	1.05	1.17	0.98	1.10	1.01	1.04	1.15	1.19	1.10
Length of M^1	-	1.37	1.31	1.44	1.44	1.42	1.37	1.44	-	1.49
Length of M^2	1.41	1.46	1.38	1.48	1.41	1.44	1.43	1.42	1.41	1.40
Length of M^3	0.84	0.86	0.82	0.90	0.88	0.90	0.87	0.90	0.83	0.89
Width of M^3	1.67	1.42	1.44	1.61	1.58	1.57	1.64	1.64	1.52	1.56
Length of 1st commissure of M^3	0.61	0.65	0.67	0.64	0.65	0.64	0.66	0.63	0.61	0.60
Length of 2nd commissure of M^3	0.58	0.54	0.50	0.53	0.48	0.58	0.54	0.52	0.51	0.52
Length of 3rd commissure of M^3	0.60	0.59	0.63	0.64	0.54	0.60	0.60	0.58	0.59	0.60

Table 36. Descriptive statistics for the skull measurements of *Miniopterus approximatus* sp. n. from the Podlesice locality

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Length of palatum	2	5.62	5.72	5.67	0.0707	1.2
Length of C^1- M^3 a.	5	5.75	5.90	5.84	0.0604	1.0
Length of P^3- M^3	9	4.86	5.01	4.95	0.0525	1.1
Length of P^3- P^4	10	1.87	2.11	1.99	0.0702	3.5
Length of P^4- M^3	11	4.22	4.47	4.32	0.0786	1.8
Length of M^1- M^3	9	3.37	3.55	3.47	0.0554	1.6
Length of P^3	10	0.77	0.94	0.85	0.0517	6.1
Width of P^3	10	0.82	1.04	0.95	0.0709	7.5
Length of P^4	12	0.98	1.23	1.12	0.0818	7.3
Length of M^1	9	1.31	1.50	1.42	0.0608	4.3
Length of M^2	12	1.38	1.50	1.43	0.0349	2.4
Length of M^3	11	0.82	0.90	0.87	0.0288	3.3
Width of M^3	11	1.42	1.67	1.57	0.0836	5.3
Length of 1st commissure of M^3	11	0.60	0.67	0.64	0.0232	3.6
Length of 2nd commissure of M^3	11	0.48	0.58	0.53	0.0316	6.0
Length of 3rd commissure of M^3	11	0.54	0.64	0.60	0.0266	4.4

(a. alveolar length)

I_1 — crown of this tooth is trilobate, with a dominating medial lobe. On interior side of posterior lobe there is a small accessory cusp (table 37).

I_2 has a trilobate crown. Medial and posterior lobes almost equal and both larger than the first one (in *M. schreibersi*). On inner face of medial lobe there is no small commissure, typical of the recent species, connecting this lobe with an accessory, internal cusp. I_3 — massive, with one dominating cusp and a robust cingulum, the later produced into two accessory cusps on the antero-lingual and posterior side of the tooth.

Table 37. Comparison of the size of I_1 in fossil *M. approximatus* sp. n. and recent *Miniopterus schreibersi*

Species : Locality : Measurements :	M. approximatus sp.n. Podlesice	M. schreibersi recent
Length of I_1	0.39	0.48
Width of I_1	0.22	0.30

C_1 — its crown narrower that in *M. schreibersi* with a poorly developed cingulum both on the internal and external sides, forming on the antero-internal margin a slight bulge. In *M. schreibersi* there is a strongly developed cusp at this point. Talon of tooth poorly developed, while in the compared species the talon is strongly developed along the posterior margin of the tooth.

Premolars loosely spaced, longer than wide in outline of crown, margins of cingulum barely touching. P_2 resembling a triangle, with the right angle oriented distally and linguad. It has a poorly developed cingulum which in the antero-lingual face forms a slight bulge (in the modern form there is a small cusp at this point). Crown of this tooth markedly lower than that of P_3, while in *M. schreibersi* they are of equal height. P_3 — two-rooted, similar to P_2, but larger and more massive, with a well developed cingulum on the external and posterior side of the tooth. P_4 — similar to the remaining premolars but much larger. Cingulum well developed, with a small cusp on the labio-distal margin, absent in *M. schreibersi.*

M_1—M_3 — similar to *M. schreibersi*, but their talonids are more delicate.

Remarks. — Kowalski (1956) considered the fossil specimens from Podlesice to be identical with the modern *M. schreibersi*. However, studies carried out by present

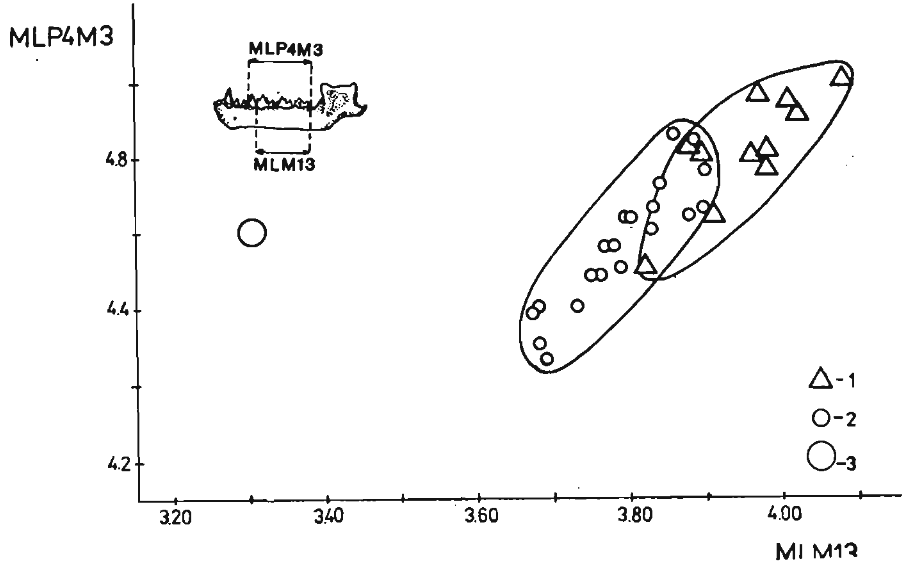

Fig. 15. Correlation between two measurements of the mandible P_4—M_3 and M_1—M_3 in several species of *Miniopterus*: 1 — *M. schreibersi*, Recent, 2 — *M. approximatus* sp. n., Podlesice, 3 — *M. fossilis* Zapfe.

author on much more abundant material, brought to light a number of differences which are marked in the description and warrant establishing of the new species *M. approximatus*.

On fig. 16 all the mandibular dimensions are compared, assuming as the standard the mean mandibular lengths in *M. approximatus. Miniopterus schreibersi* has a smaller distance between M^3 and the posterior surface of the articular process, and a shorter molar row. In all other dimensions it attains a greater size, the increased dental width being particularly striking, most of all in C_1 and P_3.

Fossil remains of *Miniopterus* are not particularly common. It seems that the genus must have inhabited Central Europe until the late Pliocene, and subsequently left these areas as the climate deteriorated. Yet the remains of *Miniopterus* have frequently been discovered at fossil localities south of the Carpathians. The oldest fossil remains probably come from the Miocene locality of Neudorf, where Zapfe (1950) described, on the basis of one incomplete mandible, a new species: *Miniopterus fossilis* Zapfe, 1950. However, Boudelot (1972), also Bachmayer and Wilson (1978) suggested that this mandible should be classified within *Myotis* as there occasionally occurred specimens in which P_3 was double-rooted.

It should be added here that *M. fossilis* is very small, much more so than the other species of the same genus. Moreover the remains described as *Miniopterus*

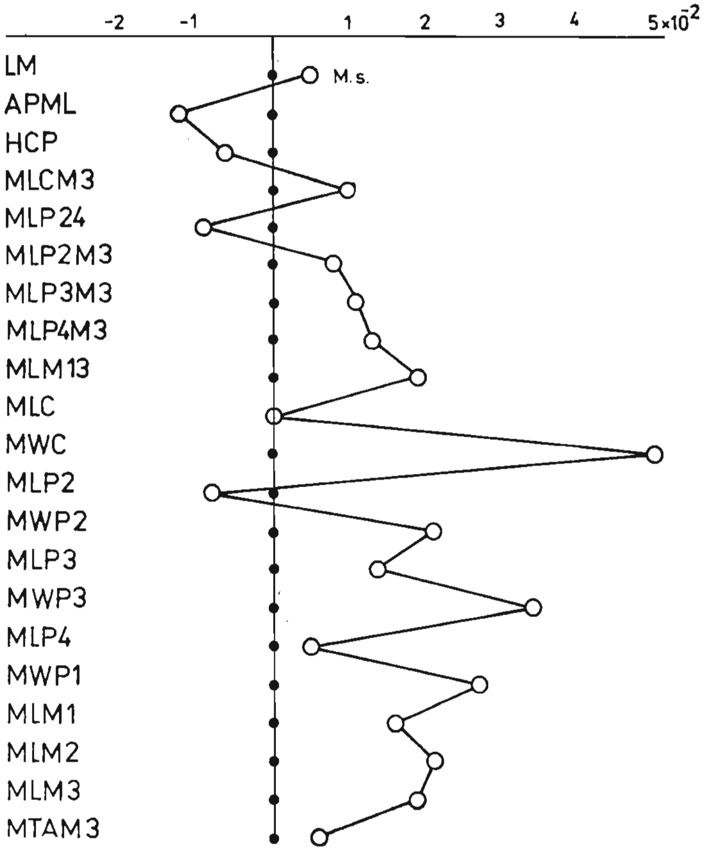

Fig. 16. Simpson's diagram for two species of *Miniopterus*: *Miniopterus approximatus* sp. n. (standard), M.s. — *M. schreibersi*, Recent.

fossilis are mentioned by Guerin and Mein (1971) from two Miocene localities from France, i.e. La Grive St Alban and Vieux-Collonges.

Heller (1930) reported *Miniopterus* from the Moggaster Cave on the basis of determinations by Revilliod, dating the remains at the younger Pliocene and later; he describes (Heller 1936) *Miniopterus* aff. *schreibersi* Kuhl on the basis of two fragments of humerus from Pliocene deposits. Also Kormos (1937) reported *Miniopterus* from Püspüfürdö (= Episkopia).

The Pleistocene finds of *Miniopterus* are somewhat more numerous. Storch (1974) reported *M. schreibersi* from the Ghar Dalam Cave in Malta, Horaček (1976) reported the same species from several localities in Czechoslovakia, dated at the lower Pleistocene. Also Rabeder (1973*a*) mentioned *M. schreibersi* from the Deutsch-Altenburg 2, 3 and 4 localities.

In the mid- and upper Pleistocene *Miniopterus* probably left South Europe. Later in the postglacial climatic optimum *Miniopterus schreibersi* began to reappear again in the Carapathian Basin (Horaček 1976).

Occurrence. — *M. approximatus* known so far only from the type horizon and locality.

Family **Vespertilionidae** Gray, 1821

Genus *Eptesicus* Rafinesque, 1820

Eptesicus kowalskii sp. n.

(pl. 12: 6; fig. 17; tables 38—41)

Holotypus: mandible, partly damaged, md. s. (FM—C/P and P2/4) I_2—C_1 (P_2) P_4—M_1, ZZSiD, MF/1697/1, figured an pl. 12: 6.

Locus typicus: Cave 431 in Podlesice near Kroczyce, central part of Kraków—Wieluń Upland.

Stratum typicum: Cave deposits, Pliocene (Lower Ruscinian).

Derivatio nominis: *kowalskii* — in honour of Kazimierz Kowalski, explorer of fossil fauna in Podlesice, and eminent Polish paleontologist.

Diagnosis. — A large representative of *Eptesicus*. It differs from the recent *E. serotinus* (Schreber) in its smaller size, particularly in the small P_4 and a massive talonid on M_3.

Material. — Holotype, 9 rather incomplete mandibles (MF/1697/2—9, 11), 1 fragment of maxilla (MF/1697/10). All ZZSiD collection.

Measurements and basic statistics see tables 38—41. The dimensions of MF/1697/10: length of P^4 — 1.44, length of M^1 — 2.13, width of M^1 — 1.96.

Description. — Of the skull only a fragment of the left jaw with P^4 and M^1 is known.

P^4 — outline of crown is almost square. On antero-labial side the cingulum forms a distinct projection, similar to *E. serotinus*. Talon of tooth is extensive, with a rounded border and a considerable medial depression. External margin of cingulum with gently rounded but quite deep sinus. Paracone high, much more so than the parastyle of M^1. Margin connecting paracone with mesostyle arched into a saddle shape.

M^1 — in general outline very like this tooth in *E. serotinus*, it is however smaller in all its dimensions, especially in the distal part. Cingulum is poorly developed.

Mandible more delicate and all the teeth in outline of crown are markedly smaller than in recent *E. serotinus*. Mental foramen is often double, position of foramina variable, usually however lying below C/P, P, C/P2, P2 or P2/P4.

Table 38. Mandibular measurements of *Eptesicus kowalskii* sp. n. from the Podlesice locality MF/1697/1 — holotype

Specimen MF/1697/ : Measurements :	1	2	3	4	5	6	7	8	9
Length of $I_1 - I_3$ a.	-	0.92	-	-	-	-	-	-	-
Length of $C_1 - M_3$	7.51	7.70	7.88	-	7.98	-	-	-	-
Length of $C_1 - P_4$	-	-	-	-	-	2.82	-	-	-
Length of $P_2 - P_4$	-	-	-	-	-	2.09	-	-	-
Length of $P_2 - M_3$ a.	6.50	6.84	6.84	-	6.98	-	-	-	-
Length of $P_4 - M_3$ a.	6.03	6.14	6.35	-	6.34	-	-	-	-
Length of $M_1 - M_3$	-	-	5.53	-	-	-	-	-	-
Foramen mentale lying below	C/P2 P2/4	P2/4	P2/4	C and P2	C/P2 P2	P2	P2	P2	P2/4

(a. alveolar length)

Table 39. Measurements of lower teeth of *Eptesicus kowalskii* sp. n. from the Podlesice locality

Specimen MF/1697/ : Measurements :	1	2	3	4	5	6	7	8	9
Length of I_2	0.80	-	-	-	-	-	-	-	-
Width of I_2	0.66	-	-	-	-	-	-	-	-
Length of I_3	0.77	-	-	-	-	-	-	-	-
Width of I_3	0.68	-	-	-	-	-	-	-	-
Length of C_1	1.16	-	-	-	-	-	-	-	-
Width of C_1	1.46	-	-	-	-	-	-	-	-
Length of P_2	0.81	-	-	-	-	-	-	-	-
Width of P_2	0.81	-	-	-	-	-	-	-	-
Length of P_4	1.24	1.15	-	1.19	1.04	1.22	1.24	1.27	1.18
Width of P_4	1.06	1.05	-	1.03	-	1.06	1.10	0.98	1.01
Length of M_1	1.92	1.98	2.00	-	2.02	1.98	1.92	-	1.98
Length of M_2	-	2.00	2.05	1.95	-	1.92	-	-	1.98
Length of M_3	-	-	1.81	-	-	-	-	-	-
Talonid width of M_3	-	-	0.83	-	-	-	-	-	-

Table 40. Descriptive statistics for measurements of the mandible and lower teeth of *Eptesicus kowalskii* sp. n. from the Podlesice locality

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Length of C_1- $M_3$$^{a.}$	4	7.51	7.98	7.77	0.2071	2.7
Length of P_2- $M_3$$^{a.}$	4	6.50	6.98	6.79	0.2043	3.0
Length of P_4- $M_3$$^{a.}$	4	6.03	6.34	6.21	0.1512	2.4
Length of M_1- $M_3$$^{a.}$	3	5.11	5.31	5.18	0.1102	2.1
Length of P_4	8	1.04	1.27	1.19	0.0722	6.1
Width of P_4	7	0.98	1.10	1.04	0.0389	3.7
Length of M_1	7	1.92	2.02	1.97	0.0380	1.9
Talonid width of M_1	6	1.30	1.47	1.38	0.0605	4.4
Length of M_2	5	1.92	2.05	1.98	0.0495	2.5
Talonid width of M_2	5	1.25	1.47	1.34	0.0915	6.8

(a. alveolar length)

I_1 — not preserved in the material examined. I_2 — small, trilobate, its crown set obliquely to toothrow, with small accessory cusp on medial lobe. External lobe well developed, less so however than in the recent species. I_3 — alveolus of this tooth is positioned adjacent to that of I_2. Crown trilobate, set obliquely to toothrow. Cingulum developed on antero-labial side. In posterior part of tooth, between the external and medial lobe there is a small accessory cusp. These accessory cusps (on I_2 and I_3) are both relatively and absolutely smaller than their counterparts presents in *E. serotinus.*

C_1 — crown usually resembling a triangle with rounded corners. Cingulum more robust than in the recent *E. serotinus*. On anterior margin of tooth there is an accessory cusp, which in the recent form is less pronounced or absent. Tip of canine markedly higher than that of P_4. Inner margin of cingulum straight, while in *E. serotinus* it forms a distinct saddle. In posterior part of tooth there is a rather small talon with an accessory cusp in its linguo-distal margin. In *E. serotinus*, this talon is proportionately smaller and has a shallow sinus in its medial part.

P_2 — with single apex, in outline of crown ovally-triangular. Cingulum forms a distinct ridge on labial and distal margins. P_4 — with single apex, paracone roughly equal in height to parastyle on molars. In outline of crown it forms an irregular trapezium. Cingulum developed both on posterior and anterior face of tooth, disappearing medially on the lateral sides. On antero-lingual side the cingulum forms a small convexity, sometimes assuming the form of a small cusp. Posterior part of tooth is extensive, resembling in shape the talon of a canine. Talon separated from paracone by a distinct groove.

M_1—M_3 fairly similar in shape to those teeth in *E. serotinus*, though somewhat smaller. Talonids of M_1 and M_3 are relatively smaller than their counterparts of the modern form, while the talonid on M_3 is more massive, wider and longer than in the modern species.

Remarks. — The shape and size of the fragments preserved combined with the reconstructed dental formula (2).1.1.3./3.1.2.3 and also the fact that the molars of the mandible represent the myotodontic type evidence that the remains represent on *Eptesicus* species.

The features distinguishing the fossil species from the recent one here compared have been pointed out in the description. The species described, *E. kowalskii*, comes close in size to *E. campanensis* Baudelot 1970, known from Miocene sediments from Sansan, France and Pavoa de Santarem Portugal (Sigé and Legendre 1983). Yet *E. campanensis* is larger in almost all its dimensions than *E. kowalskii* except for the width of the talonid on M_3, which is both relatively and absolutely larger in this species. This is an important difference, proving that they belong to distinct phyletic lines, as the talonid of M_3 becomes strongly reduced within *Eptesicus*. In the last premolar (P_4) of *E. campanensis* the margin of the cingulum in undulate. In the specimens of *E. kowalskii* it is almost straight.

Eptesicus praeglacialis Kormos, 1930, described from the early Pleistocene locality of Episkopia, Romania, greatly exceeds in size not only *E. kowalskii*, but also *E. serotinus* (table 41). Rabeder (1972) described from the Hundshein locality remains of bats determined to be *E. serotinus*, which according to him do not differ from the modern species. The same author (Rabeder 1973*a*) mentions *Eptesicus* sp. from the Deutsch-Altenburg locality. Moreover, Kretzoi (1965) listed *E. praeglacialis* from the lower Pleistocene locality Villany III, while Kowalski (1962*c*) described from the lower Pleistocene in Koneprusy (CSSR) a mandible with all its teeth lost as *E.* cf. *serotinus* and also an incomplete mandible, both of Holocene age, from the Stranska Skala I locality (Kowalski 1972*a*).

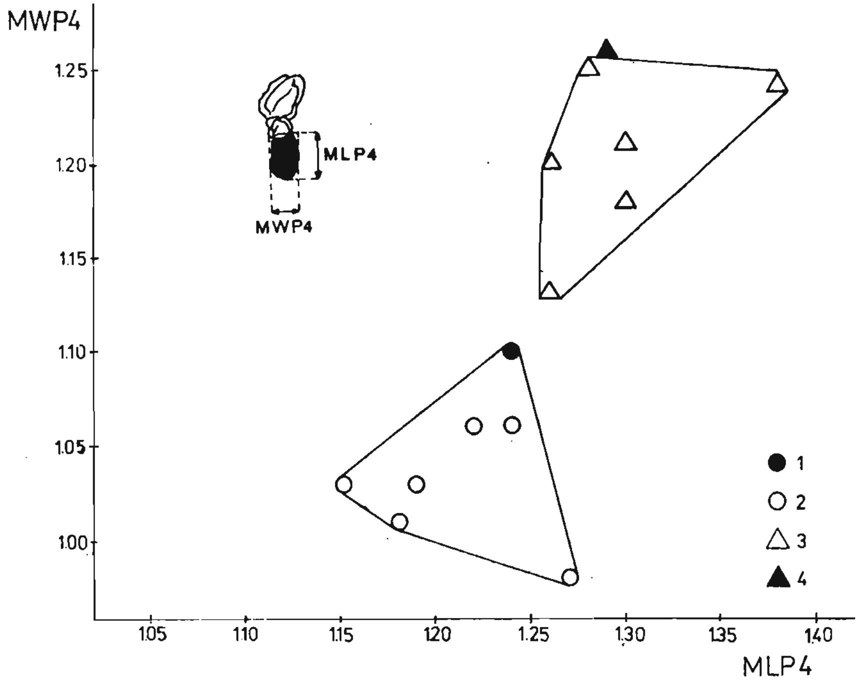

Fig. 17. Comparison of the dimensions of the premolar P_4 in several species of the *Eptesicus* genus: 1 — *E. kowalskii* sp. n. (holotype), 2 — remaining specimens of *E. kowalskii* sp. n. from Podlesice, 3 — *E. serotinus*, recent, 4 — *E. serotinus* specimen from Bacho Kiro Cave, Bulgaria (Wołoszyn 1982).

Table 41. Comparison of the dimensions of the mandible in several fossil and recent species of *Eptesicus*

Species : Measurements :	EK	EP	EC	ESB	ESR
Alveolar length of C_1- M_3	7.73	8.85	-	8.47	8.19
Alveolar length of P_4- M_3	6.17	7.10	-	6.71	6.42
Length of P_2	0.81	-	-	-	1.03
Width of P_2	0.81	-	-	-	1.08
Length of P_4	1.19	1.47	1.27	1.28	1.30
Width of P_4	1.04	1.26	1.13	1.22	1.20

Abbreviations:
EK — *E. kowalskii* sp. n. from the Podlesice locality; EP — *E. praeglacialis* Heller (holotype); EC — *E. campanensis* Baudelot (holotype); ESB — *E.* cf. *serotinus* from the Bacho Kiro locality (Bulgaria); ESB — *E.* cf. *serotinus* (Schreber) — Recent.

Other modern species of *Eptesicus* i.e. *E. nilssoni* (Keyserling et Blasius) from northern and central Europe, *E. bottae* (Peters) from the Middle-East is smaller in size and cannot be identified with the new species described here.

Occurrence. — *E. kowalskii* is known so far only from the type horizon and locality.

Eptesicus mossoczyi sp. n.

(pl. 12: 3; fig. 18; table 42)

Holotypus: right mandible, partly damaged, md. d. (FM—C/P2) (I_1—C_1) P_2—M_3, ZZSiD MF/1698/1 (pl. 12: 3).

Locus typicus: Cave 431 in Podlesice near Kroczyce, central part of Kraków—Wieluń Upland, Poland.

Stratum typicum: Cave deposits, lower Pliocene (Lower Ruscinian).

Derivatio nominis: in honour of Zbigniew Mossoczy, a geologist, explorer of many localities of fossil fauna in Poland.

Diagnosis. — A medium-sized representative of *Eptesicus*, similar in size to the recent species *E. nilssoni* with parallelly arranged alveoli of I_2 and I_3, and a reduced talonid on M_3.

Material. — Podlesice: holotype, fragment of left mandible: md. s. P_4 (M_1) M_2—M_3. (MF/1698/2). All ZZSiD collection.

Measurements: see table 42.

Description. — Mandible similar in size to that of the recent specimens of *E. nilssoni.* Symphysis of mandible elongated, irregularly oval. Mental foramen between C_1 and P_2.

Incisors not preserved. Alveoli of I_1 and I_2 in toothrow and not contiguous. Alveolus of I_3 projects outward from toothrow, and is contiguous with alveolus of the canine. Alveoli form an almost equilateral triangle, hence it may be inferred that the incisors were positioned much as is in *E. serotinus*, i.e. so that the teeth I_2

Table 42. Mandibular measurements of *Eptesicus mossoczyi* sp. n. from the Podlesice locality (the table also gives the dimensions of recent species: *E. nilssoni* and *E. bottae*)

Species : Specimen : Measurements :	E. mossoczyi sp.n. MF/1698/1 holotype	 MF/1698/2 paratype	E.nilssoni M/2557/64 recent	E.bottae M/4960/76 recent
Length of P_2 - P_4	1.30	-	1.52	-
Length of P_2	0.55	-	0.64	0.72
Width of P_2	0.60	-	0.67	0.76
Length of P_4	0.85	0.87	0.90	1.02
Width of P_4	0.77	0.75	0.82	1.02
Length of M_1	1.46	-	1.55	1.74
Trigonid length of M_1	0.80	-	0.74	-
Length of M_2	1.44	1.41	1.42	1.72
Trigonid length of M_2	0.75	-	0.64	-
Length of M_3	1.33	1.28	1.30	1.47
Trigonid length of M_3	0.62	-	0.60	1.01
Talonid width of M_3	0.62	0.68	0.75	0.52

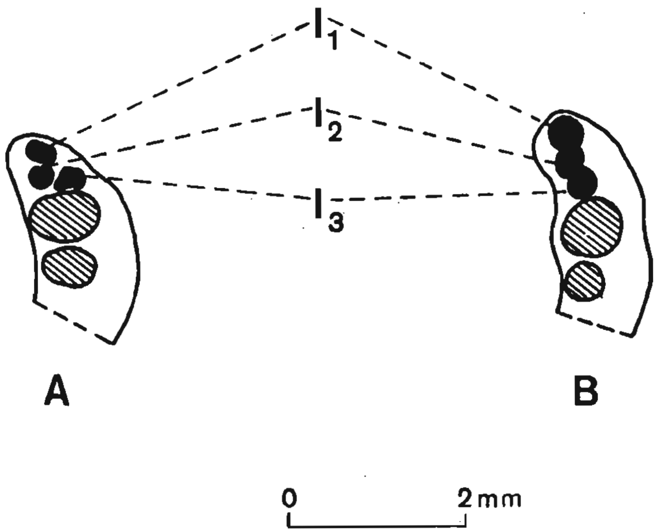

Fig. 18. Comparison of the alveoli of the incisivi in two species of *Eptesicus*. A — holotype of *E. mossoczyi* (no. MF/1698/1), B — Recent *E. nilssoni* (no. M/5531/79).

and I_3 must have been adjacent whereas in the modern *E. nilssoni* the incisors are arranged in a row (fig. 18).

Alveolus of canine is damaged, but judging by the fragments preserved it must have been transversely oval, in contrast to the longitudinally oval one in *E. serotinus* and the almost round one in *E. nilssoni*. From the shape of the alveolus it can be inferred that in *E. mossoczyi* sp. n. the canine must have had a considerable crown width.

P_2 — massive, crown triangular with rounded corners, and robust cingulum. On the internal side both at the anterior and posterior of the cingulum there are some fairly small bulges. P_4 — crown of this tooth almost square in outline. Robust cingulum forms a fairly small cusp in the anterior, labial part of the tooth. In the posterior of the tooth there is a quite extensive talon, with a transverse trough-like depression.

M_1—M_2 myotodontic, smaller than the molars in *E. nilssoni*, but with both relatively and absolutely longer trigonids. M_3 — myotodontic, long, with a massive trigonid, narrow talonid, and a robust cingulum on the anterior margin. The cingulum on the outer and posterior sides of the talonids is very poorly developed. Crista obliqua almost straight.

Remarks. — The species described here, *E. mossoczyi*, differs in its smaller size and more delicate structure of teeth, especially P_2 and M_1—M_3, from recent species of the *Eptesicus* genus. From *E. nilssoni* it differs in the positioning of incisors, which were situated much as in recent *E. serotinus*. The crown of P_4 in the modern *E. nilssoni* is much more elongated and differs from the almost square one in the fossil species described here.

E. bottae from the Middle East differs from *E. mossoczyi* in its greater size, in the considerable degree of reduction of the incisor row and the talonid of M_3.

Neither can *E. mossoczyi* be identified with *E. noctuloides*; described from a Miocene locality in Sansan, France (Baudelot 1972). *E. noctuloides* is smaller in all dimensions, excepting the length of P_2. Also the lower incisors in the species from Sansan were arranged in one row.

P_2 in *E. mossoczyi* is much smaller than this tooth in *E. nilssoni*. Neither can it be maintained that *E. mossoczyi* and the *E. nilssoni* are in ancestor-descendant relation since the fossil species has a number of features which can be seen as progressive, namely a strongly reduced incisor row and a relatively narrow talonid on M_3. It is more likely that *E. mossoczyi* represents a final stage of an extinct phyletic line.

Occurrence. — *E. mossoczyi* known so far only from the type horizon and locality.

Eptesicus cf. *serotinus* (Schreber, 1774)

(tables 43—44)

Material. — A few isolated teeth have been preserved in the samples 2a—c of Kozi Grzbiet (C^1, C_1 P^4). All ZZSiD collection.

C^1 is a massive, high tooth, with its tip curved linguo-distally. Margin of crown on its labial side is almost semicircular, while on the lingual side it is undulate with a distinct convexity at 1/3 of its length. Cingulum robust, though narrow on labial side, and with a fairly small sinus in the labio-distal part. There is a similar sinus on the lingual side in the posterior half of the cingulum.

P^4 — somewhat more massive than in specimens of the recent population. Robust cingulum on mesio-lingual side, though proportionally smaller than in recent specimens.

Table 43. Measurements of teeth of *Eptesicus* cf. *serotinus* from the Kozi Grzbiet locality

Specimen MF/1699/ : Measurements :	1	2	3	4	5
Length of C^1	2.37	2.39	2.31	-	-
Width of C^1	1.76	1.69	1.85	-	-
Length of P^4	-	-	-	1.63	-
Width of P^4	-	-	-	1.70	-
Length of C_1	-	-	-	-	1.51
Width of C_1	-	-	-	-	1.64

Table 44. Comparison of the dimensions of the upper canine of *E.* cf. *serotinus* from the Kozi Grzbiet locality and of the recent *E. serotinus*

Species : Locality : Measurements :		E.cf.serotinus Kozi Grzbiet	E. serotinus recent
Length of C^1	N	3	8
	Min. - Max.	2.31 - 2.39	2.01 - 2.32
	$\bar{x}$	2.36	2.16
Width of C^1	N	3	8
	Min. - Max.	1.69 - 1.85	1.45 - 1.75
	$\bar{x}$	1.75	1.59

C_1 is massive, in crown outline semi-oval. Apex of tooth high, curved linguo-distally. Cingulum robust on antero-labial side, but disappearing on anterior margin of tooth. Smallish talon in distal part of tooth, with a distinct cusp in postero-lingual face.

Remarks. — The teeth preserved are massive, their size indicating that they may belong to *Eptesicus serotinus* but with certain reservations, as the teeth examined, particularly the upper canines, are on average more massive than in the recent specimens compared.

Eptesicus serotinus is a mainly forest species, sometimes hibernating in caves. However, its remains are sometimes relatively frequent in cave sediments formed from accumulating owl-pellets, as it is frequently preyed upon by these birds (Krzanowski 1973).

Occurrence. — The fossil remains determined as *E. serotinus* or *E.* cf. *serotinus* are known from numerous Pleistocene and Holocene localities in Europe (Hungary, Czechoslovakia, Austria, Bulgaria), in Poland — Kozi Grzbiet, some late Pleistocene and Holocene localities in Kraków—Wieluń Upland.

Table 45. Measurements of lower teeth in *Eptesicus nilssoni* (Keys. et Blasius) from the Kozi Grzbiet locality

Specimen MF/1700/ : Measurements :	1	2	3	4	5	6	7	8
Length of I_2	0.60	-	-	-	-	-	-	-
Width of I_2	0.32	-	-	-	-	-	-	-
Length of C_1	-	-	-	-	0.95	-	-	-
Width of C_1	-	-	-	-	0.88	-	-	-
Length of P_2	-	0.62	-	-	-	-	-	-
Width of P_2	-	0.64	-	-	-	-	-	-
Length of P_4	0.86	0.89	0.89	0.88	-	-	-	0.88
Width of P_4	0.74	0.75	0.78	0.78	-	-	-	0.81
Length of $M_1 - M_3$	-	-	-	-	-	-	3.88	-
Length of M_1	1.52	-	-	-	-	-	1.38	-
Length of M_2	-	-	-	-	-	-	1.40	-
Length of M_3	-	-	-	-	-	1.55	1.25	-
Talonid width of M_3	-	-	-	-	-	0.76	0.64	-

Eptesicus nilssoni (Keyserling et Blasius, 1839)

(tables 45—46)

Material. — Kozi Grzbiet: 15 fragments of mandibles found, usually without teeth (MF/1700/1—15) and some isolated teeth. ZZSiD collection.

Measurements see tables 45—46.

Description. — Material from Kozi Grzbiet, though quite abundant, is rather fragmentary. The specimens examined hardly differ from the modern population of *E. nilssoni* from southern Poland.

I_2 — crown of tooth trilobate. In contrast to the recent specimens its internal accessory cusp was much less developed.

I_3 — not preserved. The alveolus has a slight tendency to extend beyond the toothrow. C_1 — the only difference determined is in that the tip of the tooth is straight in fossil specimens, in contrast to a slightly curved one in the recent specimens.

Table 46. Comparison of some measurements of lower teeth of *Eptesicus nilssoni* from the Kozi Grzbiet locality with recent *Eptesicus nilssoni* (Keys. et Blasius)

Species : Locality : Measurements :		E. nilssoni Kozi Grzbiet	E.nilssoni recent
Length of P_4	N	6	6
	Min. - Max.	0.86 - 0.93	0.78 - 0.90
	$\bar{x}$	0.89	0.85
Width of P_4	N	6	6
	Min. - Max.	0.74 - 0.83	0.74 - 0.78
	$\bar{x}$	0.78	0.76
Length of M_3	N	2	6
	Min. - Max.	1.25 - 1.55	1.25 - 1.36
	$\bar{x}$	1.40	1.32
Talonid width of M_3	N	2	6
	Min. - Max.	0.64 - 0.76	0.68 - 0.84
	$\bar{x}$	0.70	0.75

P_2 — on anterior and posterior margin of cingulum there are two slight bulges, assuming the form of distinct cusps in the recent specimens. P_4 — this tooth, though similar in structure is on the average slightly longer and narrower than is the case in recent specimens.

M_1—M_3 — infrequent, the molars preserved do not differ from those in the recent specimens of *E. nilssoni.*

Remarks. — The specimens examined correspond very well to these of the recent species *E. nilssoni.* The slight differences have been covered in the description.

Occurrence. — The bat remains classified as *E. nilssoni* are known in Europe from the Pleistocene onward (Brunner 1954, 1957; Koenigswald 1972; Kowalski 1962c; Rabeder 1973a; Ryberg 1947; Topal 1963*a*; Vereshchagin 1959; Wettstein-Westersheim 1931). In Poland the remains of *E. nilssoni* are found in Kozi Grzbiet and also it was reported from the Tatra Mts in Holocene deposits (Wołoszyn 1967, 1970).

In recent times *E. nilssoni* has inhabited northern regions of the Palearctic. In Central Europe it occurs mainly in the mountains. It overwinters in caves. At presents it occurs throughout Poland, though in small numbers everywhere (Pucek and Raczyński 1983).

Genus *Barbastella* Gray, 1821

Barbastella cf. *schadleri* Wettstein-Westersheim

(pl. 12: 2; table 47)

Material. — Kozi Grzbiet, layer 2b: fragment of mandible: md. s. (FM—C/P2) (I_1—P_4/M_1—M_3) (MF/1701/1). ZZSiD collection.

Description. — Symphysis of mandible in the specimen examined is long and oval, large in cross-section, differing in this respect from that in the recent species, i.e., *Barbastella barbastellus* (Schreber) and *B. leucomelas* (Cretzschmar) (table 47). The mental foramen is large and lies below C/P2.

Table 47. Comparison of some measurements of lower molars and mandibular symphysis in several fossil and recent species of *Barbastella* genus

Species and locality: Measurements :	BSKG	BBR	BSK	BSB	BLR
Lendth of M_1 - M_2	2.88	2.60	2.83	-	2.86
Length of M_1	1.60	1.43	1.54	-	1.56
Talonid width of M_1	0.88	0.78	0.88	-	0.93
Length of M_2	1.47	1.31	1.42	1.34	1.45
Talonid width of M_2	0.83	0.75	0.81	0.77	0.87

Abbreviations:
BSKG — *B.* cf. *schadleri* Wett. from the Kozi Grzbiet locality; BBR — *B. barbastellus* — Recent; BSK — *B. barbastellus* from the Koněprusy locality (Early Pleistocene) Czechoslovakia; BSB — *B.* cf. *schadleri* from the Bacho Kiro locality, Bulgaria; BLR — *B. leucomelas* — Recent.

Alveoli of incisors are round and arranged in a row forming a gentle arc with its concavity facing labiad. Alveolus of canine transversely oval (L/W: 0.50/0.55). Alveolus of P_2 also transversely oval (L/W: 0.32/0.40), its dimensions indicating that this tooth exceeded P_2 in size in both the above-mentioned recent species in which it is relatively small.

P_4 — judging by the root fragments preserved, this was a massive tooth. Molars of the nyctalodontic type. M_1 — is large, with an elongated trigonid, this being typical of the genus *Barbastella*. The talonid of this tooth is wide. Cingulum robust on lingual side, barely marked on the labial side. The hypoconulid is massive, separated by a distinct groove from the ectoconid. Crista obliqua is almost straight, in contrast to the sinusoidal one in *B. leucomelas* and a slightly undulate one in *B. barbastellus*. M_2 — generally similar to M_1, massive. Both molars preserved greatly exceed in size those in the recent *B. barbastellus*.

Remarks. — Material available for study is fragmentary. The dental formula of the mandible which could be reconstructed as 3.1.2.3., the characteristic, long shape of the crowns of the molars and their talonids of the nyctalodontid type allow the fragment of mandible examined to be classified within *Barbastella*. Two modern species are assigned to this genus and also several fossil ones.

The specimen from Kozi Grzbiet comes close in dimensions to *B. leucomelas*, differing however from it in some anatomical details, mentioned in the description.

Topal (1970) included specimens of *Barbastella* from all the early and mid-Pliocene localities from Hungary to *Barbastella rostrata* Topal, 1970. Beside the already mentioned *B. rostrata*, *Barbastella schadleri* Wettstein, described from the locality Drachenhöhle in Mixnitz is also known in the fossil fauna. Rabeder (1974) considers *B. rostrata* Topal to be a younger synonim of *B. schadleri*.

The specimen of *Barbastella* cf. *schadleri* here described exceeds in size the specimens of *B. schadleri* (and *B. rostrata*) from all the localities of central and southern Europe. According to this author the specimen examined may represent an extreme morphotype within the fossil species *Barbastella schadleri*. The distinct trend observed in modern European *Barbastella*, consisting in body size increase in northern populations would also support this view. This trend, which may be linked with Bergman's rule was also demonstrated in some bat species, e.g. in *Myotis daubentoni* (Horaček and Hanak 1983—1984).

Occurrence. — Beside the above described remains from Kozi Grzbiet, bat remains of *Barbastella* cf. *schadleri* have been described from Pleiestocene deposits of Bulgaria (Wołoszyn 1982).

Genus *Plecotus* Geoffroy

Subgenus *Plecotus* (*Paraplecotus*) Rabeder, 1974

Plecotus (*Paraplecotus*) *rabederi* sp. n.

(pl. 12: 4, Tables 48—55)

1956. *Plecotus crassidens* Kormos; Kowalski: 359, pl. 3: 1, 2.
1958*b*. *Plecotus crassidens*; Kowalski: 211.
1959. *Plecotus crassidens*; Kowalski: 91.
1959. *Plecotus crassidens*; Handley: 208.
1962*a*. *Plecotus crassidens*; Kowalski: 45.
1964. *Plecotus crassidens*; Kowalski: 77.
1974. *Plecotus crassidens*; Rabeder: 170, pl. 3: 19, pl. 4: 32, pl. 5: 41, 48, pl. 6: 57.

Holotypus: left mandible, md. s. (FM—C/P2) (I_1—P_3) P_4—M_3. AnArCo. (MF/1702/1). ZZSiD collection (pl. 2: 4).

Derivatio nominis: in honour of G. Rabeder the Austrian zoologist and paleontologist.

Locus typicus: Cave 431, Podlesice near Kroczyce, central part of the Kraków—Wieluń Upland, Poland.

Stratum typicum: Cave sediment, lower Pliocene (Lower Ruscinian).

Diagnosis. — A medium-sized representative of *Plecotus* (*Paraplecotus*) *sensu* Rabeder 1974, with a massive M_3 and also a massive, two-rooted P_4, which has

Table 48. Mandibular measurements of *Plecotus* (*Paraplecotus*) *rabederi* sp. n. from the Podlesice locality

Specimen MF/1702/ : Measurements:	1	2	3	4	6	7	10	18	20	27
Length of mandible	10.38	10.62	10.85	-	-	10.67	10.78	10.70	-	-
APML	3.87	4.11	4.29	-	-	3.99	3.90	4.02	-	-
Height of coronoid process	3.56	3.38	3.43	-	-	3.52	-	-	-	-
Length of $I_1 - I_3$	-	-	-	-	-	-	-	-	-	1.22
Length of $C_1 - M_3$	-	-	-	-	6.11	-	-	-	-	-
Length of $C_1 - P_4$	-	-	-	2.42	-	-	-	-	2.20	2.15
Length of $P_2 - P_4$	-	-	-	1.68	-	-	-	-	-	-
Length of $P_4 - M_3$	4.46	-	4.53	-	4.66	-	4.47	4.51	-	-
Length of $M_1 - M_3$	3.91	-	3.95	-	4.11	-	-	-	-	-

MF/1702/1-holotype.

Table 49. Lower teeth measurements of *Plecotus* (*Paraplecotus*) *rabederi*, sp. n. from the Podlesice locality

Specimen MF/1702/ : Measurements :	1	2	3	4	6	7	10	18	20	27
Length of I_1	-	-	-	-	-	-	-	-	0.55	0.57
Width of I_1	-	-	-	-	-	-	-	-	0.32	0.34
Length of I_2	-	0.53	-	-	-	-	0.58	-	-	-
Width of I_2	-	0.35	-	-	-	-	0.37	-	-	-
Length of I_3	-	-	-	-	-	-	0.60	-	-	0.60
Width of I_3	-	-	-	-	-	-	0.43	-	-	0.44
Length of C_1	-	-	-	0.89	0.84	-	-	-	0.82	0.86
Width of C_1	-	-	-	0.90	0.91	-	-	-	0.92	0.90
Length of P_2	-	-	-	0.63	-	-	-	-	-	-
Width of P_2	-	-	-	0.67	-	-	-	-	-	-
Length of P_3	-	0.41	-	0.45	0.41	-	-	-	0.45	-
Width of P_3	-	0.50	-	0.58	0.51	-	-	-	0.55	-
Length of P_4	0.73	0.72	0.71	0.77	0.83	0.80	0.72	0.77	0.72	0.72
Width of P_4	0.68	0.70	0.72	0.69	0.76	0.75	0.72	0.71	0.71	0.71
Length of M_1	1.49	1.49	1.47	1.50	1.53	-	-	-	1.55	-
Length of M_2	1.38	1.40	1.38	-	1.43	-	-	-	1.45	-
Length of M_3	1.26	-	1.30	-	1.36	-	1.33	1.34	-	-
Talonid width of M_3	0.70	-	0.75	-	0.82	-	0.78	0.74	-	-

Table 50. Descriptive statistics for the mandibular measurements of *Plecotus* (*Paraplecotus*) *rabederi* sp. n. from the Podlesice locality

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Length of mandible	14	10.38	10.90	10.69	0.1551	1.5
APML	8	3.87	4.29	4.02	0.1322	3.3
Height of coronoid process	10	3.26	3.73	3.47	0.1339	3.9
Length of I_1- I_3 a.	26	0.95	1.20	1.08	0.0557	5.1
Length of I_1	2	0.55	0.57	0.56	0.0141	2.5
Length of I_2	3	0.42	0.57	0.51	0.0819	16.0
Length of I_3	2	0.60	0.60	0.60	0.0	0.0
Length of C_1- M_3	2	5.72	6.11	5.91	0.2758	4.7
Length of C_1- P_4	6	2.15	2.42	2.23	0.0991	4.4
Length of P_2- P_4	3	1.52	1.68	1.59	0.0833	5.2
Length of P_4- M_3	13	4.31	4.73	4.53	0.1188	2.6
Length of M_1- M_3	9	3.91	4.16	4.05	0.0783	1.9
Length of C_1	7	0.79	0.91	0.84	0.0450	5.3
Width of C_1	7	0.84	0.92	0.90	0.0263	2.9
Length of P_2	3	0.55	0.63	0.58	0.0436	7.5
Width of P_2	3	0.62	0.67	0.64	0.0265	4.1
Length of P_3	5	0.41	0.45	0.43	0.0205	4.8
Width of P_3	5	0.50	0.58	0.53	0.0327	6.1
Length of P_4	33	0.67	0.88	0.74	0.0468	6.3
Width of P_4	33	0.65	0.78	0.72	0.0339	4.7
Length of M_1	17	1.44	1.60	1.51	0.0395	2.6
Length of M_2	20	1.38	1.48	1.43	0.0409	2.9
Length of M_3	17	1.23	1.38	1.31	0.0390	2.9
Talonid width of M_3	16	0.62	0.82	0.72	0.0474	6.6

(a. alveolar length)

Table 51. Measurements of some more complete fragments of skull of *Plecotus* (*Paraplecotus*) *rabederi* sp. n. from the Podlesice locality

Specimen MF/1702/ : Measurements :	39	40	41	42	43	45	48	49	50	58
Length of palatum	4.33	4.05	4.33	4.70	4.34	4.62	-	-	-	-
Length of P^2– M^3	-	-	-	-	4.56	-	-	-	-	-
Length of P^4– M^3	4.20	4.16	-	4.14	4.20	4.43	4.24	4.21	4.15	4.15
Length of M^1– M^3	3.47	3.44	3.44	3.41	3.50	3.58	3.55	3.43	3.50	3.44
Length of P^2	-	-	-	-	0.46	-	-	-	-	-
Width of P^2	-	-	-	-	0.48	-	-	-	-	-
Length of P^4	0.96	0.84	-	0.90	0.88	0.85	0.93	0.98	0.92	0.98
Width of P^4	1.30	1.23	-	1.28	1.18	1.33	1.24	1.18	1.22	1.17
Talon length of P^4	0.78	0.77	-	0.79	0.74	0.80	0.78	0.80	0.80	0.72
Length of M^1	1.54	1.47	1.50	1.51	1.51	1.53	1.45	1.48	1.50	1.47
Length of M^2	1.32	1.40	1.40	1.36	1.37	1.50	-	1.43	1.42	1.44
Length of M^3	0.92	0.90	0.92	0.92	0.96	0.98	0.91	0.92	0.86	0.94
Width of M^3	1.49	1.45	1.53	1.44	1.55	1.54	1.46	1.42	1.50	1.50
Length of 1st commissure of M^3	0.68	0.68	0.71	0.72	0.76	0.70	0.70	0.68	0.71	0.71
Length of 2nd commissure of M^3	0.60	0.54	0.58	0.61	0.59	0.58	0.59	0.64	0.57	0.60
Length of 3rd commissure of M^3	0.64	0.62	0.61	0.65	0.60	0.61	0.57	0.67	0.58	0.64

Table 52. Descriptive statistics for skull measurements of *Plecotus (Paraplecotus) rabederi* sp. n. from the Podlesice locality

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Length of palatum	9	4.05	4.70	4.43	0.1955	4.4
Length of C^1- P^4	3	2.50	2.58	2.53	0.0436	1.7
Length of P^4- M^3	10	4.14	4.43	4.22	0.0892	2.1
Length of M^1- M^3	11	3.41	3.55	3.47	0.0539	1.6
Length of C^1	5	1.03	1.12	1.08	0.0385	3.6
Width of C^1	5	0.95	1.04	1.00	0.0356	3.6
Length of P^2	6	0.46	0.52	0.50	0.0222	4.4
Width of P^2	6	0.48	0.57	0.52	0.0331	6.3
Length of P^4	14	0.84	1.04	0.95	0.0651	6.9
Width of P^4	14	1.18	1.30	1.23	0.0491	4.0
Length of M^1	13	1.45	1.54	1.49	0.0361	2.4
Width of M^1	13	1.45	1.58	1.51	0.0406	2.7
Length of M^2	11	1.32	1.50	1.40	0.0471	3.4
Width of M^2	10	1.47	1.64	1.58	0.0465	2.9
Length of M^3	12	0.86	0.98	0.93	0.0321	3.5
Width of M^3	12	1.42	1.55	1.48	0.0432	2.9
Length of 1st commissure of M^3	12	0.68	0.76	0.71	0.0231	3.3
Length of 2nd commissure of M^3	12	0.54	0.62	0.59	0.0257	4.3
Length of 3rd commissure of M^3	12	0.57	0.67	0.62	0.0286	4.6

some smallish cusps mesially and distally on the labial side of its cingulum. I_3 has a well developed internal cusp, coronoid process massive and terminated bluntly.

Material. — Podlesice: holotype, 37 mandibles some with dentition (MF/1702/2—38), 21 rostra or maxillae (MF/1702/39—59). There are also about 20 fragments of maxillae damaged to various degrees and about 30 mandibles, mostly lacking teeth, all un-numbered. All ZZSiD collection.

Table 53. Measurements of the mandible of *Plecotus* (*Paraplecotus*) *rabederi* sp. n. from the Węże I locality

Specimen MF/1703/ : Measurements :	1	2
Length of C_1- P_4	2.18	-
Length of P_2- P_4	1.53	-
Length od C_1	0.82	-
Width of C_1	0.80	-
Length of P_2	0.64	-
Width of P_2	0.63	-
Length of P_3	-	0.51
Width of P_3	-	0.56
Length of P_4	-	0.84
Width of P_4	-	0.73
Length of M_1	1.46	1.51
Talonid width of M_1	0.91	0.93
Length of M_2	1.46	-
Talonid width of M_2	0.97	-

Measurements: see tables: 48—53.

Węże I: 2 incomplete mandibles (MF/1703/1, specimen no 1 of Kowalski 1962*a*; MF/1703/2, specimen no 2 of Kowalski 1962*a*). All ZZSiD collection.

Description. — Rostrum relatively long and wide (as compared with species of *Plecotus s.s.*). Nasal opening wide and almost round in outline in contrast to a much narrower, pyriform one in both recent species of *Plecotus s.s.* from Europe. Orbits surrounded anteriorly by a poorly developed bony ridge. Septum between preorbital foramen and eye socket is very wide, the infraorbital foramen shifted far anteriad (table 54).

Alveoli of canines oval and large.

I^1 — massive, oval, with its crown elongated mesio-distally. Cingulum robust on labial side, much less developed on lingual side. On posterior margin there is an accessory cusp, separated from the main apex at 2/3 of its height. I^2 — relatively large, transversely oval, with robust cingulum. Diastema between C^1 and I^2 large.

C^1 — relatively small. Cingulum on internal and postero-internal side, strongly developed. Crown of tooth oval in outline and asymmetrically twisted disto-lingually. In the anterior part of the tooth there is a small bulge on the cingulum, and a sinus, sometimes very shallow at the point of contact with P^2.

P^2 — massive, positioned in toothrow, hence the distance between P^4 and the canine is large. Crown transversely oval in outline. Cingulum well developed. P^4 —

crown subtrapezoidal in outline. Talon extensive with a strongly developed cingulum with a distinct depression in its distal part. On anterior part of tooth a distinct sinus.

M^1 and M^2 — massive, but in their crown shapes do not differ from modern species of *Plecotus.* M_3 — massive, little reduced. Comissures do not differ much in length. IIIrd comissure positioned obliquely with respect to the first one.

Mandible with coronoid process blunt-ended and not very high. Angular process short and blunt-ended. Canalis mandibulae oval and positioned almost immediately below the angular process, while in recent forms of *Plecotus* and *Corynorhinus* it lies further posteriad. Mandibular symphysis wide and oval. Mental foramen usually lies between C_1 and P_2.

Incisors are massive and oval in crown outline.

I_1 — with crown trilobate. Lobes arranged in a gentle arc. First lobe positioned with its long axis transverse to remaining ones; in this respect resembling more the recent *Plecotus* (*Corynorhinus*). On the internal side of the third lobe, on the cingulum, there is a small accessory cusp, which in recent species of *Plecotus s.s.* is barely marked, or altogether absent. I_2 — crown trilobate. Lobes almost equal in size. Cingulum well developed on postero-labial side. On lingual side of the cingulum there is an accessory cusp halfway between the second and third lobe, much as in the recent *Plecotus auritus*; it is smaller, however, in all its dimensions. I_3 — crown is trilobate. Lobes arranged in a horseshoe shape, its concavity facing linguad. At this point on the strongly developed cingulum there is an accessory cusp, much as is the case in *Plecotus abeli* and *Plecotus auritus.*

C_1 — it is relatively high, the crown wider than long in outline. In anterior part of the cingulum there is a smallish accessory cusp. In its rear part this tooth has a smallish talon.

P_2 — fairly massive, conical, similar to this tooth in *P. auritus.* P_3 — much smaller than P_2. Both small premolars are wider than long, set in toothrow. The crowns of these teeth are slightly flattened sagittally, and the alveoli of both teeth are almost round. P_4 — always two-rooted, differing in this respect from the American species of *Plecotus* (*Corynorhinus*), but comes close to European *Plecotus* (*s.s.*). The crown is short and fairly wide, in outline close to a triangle. Cingulum is well developed. On the lingual side the crown has one small cusp orally and second one distally.

M_1—M_3 molars similar to that of recent *Plecotus* but more robust that in *P. auritus.* The talonids of M_1 and M_2 are narrower than the trigonids (in contrast to recent *Plecotus*). The talonid of M_3 is a little narrower than its trigonid but broader and more robust than that in recent *P. auritus.*

Remarks. — In the material examined, skulls and mandibles were anatomically disconnected. Determining the skull fragments presented no greater problem. The dental formula and characteristic shape of the rostrum enabled generic determination of remains. Determining mandibles posed greater problems since some features considered to be typical apply chiefly to the *Plecotus* (*Plecotus*). Those mandibles which had preserved processes and more complete dentition, especially the premolars, could be easily determined specifically. Kowalski (1956) was the first to draw attention to the fact that the remains of *Plecotus* from Podlesice resemble in cranial architecture the American *Plecotus* (*Corynorhinus*). Later, Rabeder (1973*b*, 1974), reexamining the fossil remains of *Plecotus* from Austria proved that the resemblance consisted in the preservation in the American forms of some ancestral features. On the basis of the differences observed, Rabeder (1974) described a new subgenus *Plecotus* (*Paraplecotus*), in which he included the Pliocene and most early Pleistocene species of *Plecotus* from Central Europe. Beside those features listed by Rabeder (1974: table 6) there can also be found others indicative of the dissimilarity of the

American and fossil European subgenera. In specimen MF/1702/56 from Podlesice, I^1 has been preserved, which on the distal margin of its crown has an additional apex, much as is the case in *Plecotus* (*s.s.*). Over 20 specimens of *Plecotus* (*Corynorhinus*) *townsendii australis* and *P.* (*Corynorhinus*) *townsendi pallescens* were compared — in every one of these specimens compared I^1 had a single apex.

Table 54. Position of infraorbital foramen in *Plecotus* (*Pa.*) *rabederi* sp. n. and several recent species of *Plecotus*.

	P. (*Pa.*) *rabederi*	*P.* (*P.*) *auritus*	*P.* (*P.*) *austriacus*	*P.* (*C.*) *townsendii*
Position of infraorbital foramen above:	P^4	P^4/ parastyle of M^1	parastyle/ mesostyle of M^1	

Rabeder (op. cit.) included the specimens he studied in the fossil species *Plecotus crassidens* Kormos.

This author also examined *Plecotus* specimens from Podlesice and found several important differences distinguishing them from the specimens from Austria (Rabeder, 1974).

Table 55. Position of mental foramen in fossil and recent species of *Plecotus* from Europe

Species	N	C_1/P_2	P_2	P_2/P_3	P_3
Plecotus rabederi sp.n.	30	21	2	6	1
Podlesice	%	70	7	20	3
Plecotus cf. abeli	51	1	9	24	17
Kozi Grzbiet	%	2	18	47	33
Plecotus auritus /L./	19	-	3	16	-
recent	%	0	16	84	0
Plecotus austriacus /Fischer/	20	3	16	1	-
recent	%	15	80	5	0

The specimens from Podlesice were compared with the holotype of *P. crassidens* Kormos. The holotype of the species from Hungary proved to be smaller in all its dimensions than the specimens from Podlesice. The specimens from Hungary shows differences in the position of the alveoli of the small premolars. The alveolus of P$_3$ is round and distinctly shifted linguad. The mandible of the holotype of *P. crassidens* is broken off immediately in front of the alveolus of P$_2$ and it was not possible to examine its anterior part. The angular process in the specimen from Hungary has a distinct saddle, in contrast to the sharp-ended one in the species from Podlesice. The fossa mesenterica is more shallow and rounded in its anterior part. The opening of the canalis mandibulae in *P. crassidens* lies somewhat higher than in the form from Podlesice. Taking into account the above-mentioned differences, separating the *Plecotus* (*Paraplecotus*) specimens from Poland into new species seems to be justified.

Occurrence. — *P.* (*Pa.*) *rabederi* known so far only from the type horizon and locality.

Subgenus *Plecotus* (*Plecotus*) Geoffroy, 1813

Plecotus (*Plecotus*) cf. *abeli* Wettstein-Westersheim, 1923

(pl. 12: 5; tables 56—65)

Material. — Kozi Grzbiet: 37 fragments of maxillae (MF/1704/1—13, 30—43, 79—88), 51 fragments of mandibles (MF/1704/14—29, 44—78) from layers 2a, b, c. All ZZSiD collection.

Zamkowa Dolna, layer c: fragment of mandible (MF/1705/1). ZZSiD collection.

Zalesiaki A: 7 fragments of mandibles and one fragment of maxilla (MF/1706/1—8) from layers 1, 2, 5, 8, 9. ZZSiD collection.

Kielniki I: 5 fragments of mandibles (MF/1782/1—5) and 1 isolated P_4 and I^2. ZZSiD collection.

Measurements: see tables 56—65.

Description. — Of skull only fragments of the rostrum have been preserved. In this species the maxilla is longer and more massive as compared with the recent *Plecotus* (*Plecotus*) *auritus*.

I^1 — has an accessory cusp separating off on the distal side of the crown at approximately half its height, much as is the case in the modern *P.* (*P.*) *auritus*. Canines preserved. The alveolus of the canine is oval.

P^2 — in outline of crown it is almost round and loosely placed in relation with the previous teeth. Its crown is more massive than in the recent *P.* (*P.*) *auritus*.

P^4 — in outline of crowns is similar to the same in *P.* (*P.*) *auritus*. The cingulum is developed on the oral and lingual side, proportionally less so, however, than in *P.* (*P.*) *auritus*. The depression in the anterior part of the cingulum is much more shallow than in both recent species, *P.* (*P.*) *auritus* and *Plecotus* (*P.*) *austriacus*.

M^{1-2} do not differ in shape from those teeth in *P.* (*P.*) *auritus*, they are, however, more massive. M^3 — is relatively long. The IIIrd comissure is positioned more obliquely with respect to the first one than is the case in *P.* (*P.*) *auritus* (Rabeder 1974). The sulcus between the meso- and metastyle is deep. Cingulum on lingual side of the tooth poorly developed, more strongly however than in the recent *P.* (*P.*) *auritus*. The mesostyle is well arched, hence it forms a smallish saddle on the posterior margin of the tooth. This arch is even more pronounced in *P.* (*P.*) *auritus*, assuming in the posterior part of the tooth the shape of a small step, while in *P.* (*P.*) *austriacus* the posterior margin of the tooth runs in an almost straight line.

In the fossil species the mandible is somewhat more massive than in *P.* (*P.*) *auritus*, smaller, however, than that of *P.* (*P.*) *austriacus*. The coronoid process is high, terminated with an oblique saddle. The symphysis of the mandible is oval and large, much larger than in *P.* (*P.*) *auritus*.

I_1 — has a trilobate crown. The first lobe is narrow, distinctly separated and higher than the rest. The second and third lobes are wide. I_2 — also trilobate. All the lobes are of equal height, much as in *P.* (*P.*) *auritus*, while in *P.* (*P.*) *austriacus* the first lobe is the highest. On the cingulum, on the internal side of the tooth there is a fourth cusp positioned similarly as in *P.* (*P.*) *auritus*. I_3 — has 4 cusps, hence the

Table 56. Mandibular measurements of *Plecotus* (*P.*) cf. *abeli* Wettstein-Westersheim from the Kozi Grzbiet locality

Specimen MF/1704/ : Measurements :	1	2	3	4	6	8	9	10	**13**	**14**
Length of mandible	-	-	-	-	10.42	-	-	-	-	-
APML	-	-	-	-	4.08	-	-	-	-	-
Height of coronoid process	-	-	-	-	3.05	-	-	-	-	-
Length of $C_1 - M_3$	-	-	6.00	-	6.03	-	-	-	-	-
Length of $P_2 - P_4$	1.58	1.59	1.63	-	1.60	1.57	1.56	-	1.64	1.66
Length of $P_4 - M_3$	-	-	4.45	4.53	4.45	-	-	4.42	-	-
Length of $M_1 - M_3$	-	-	3.85	3.88	3.90	-	-	3.89	-	-
Length of C_1	0.84	0.80	0.97	-	0.85	0.88	0.81	-	-	-
Length of P_2	0.54	0.56	0.63	-	0.52	0.57	0.53	-	0.54	0.59
Width of P_2	0.56	0.51	0.62	-	0.57	0.61	0.61	-	0.57	0.60
Length of P_3	0.35	0.35	0.42	-	0.37	0.41	0.33	0.37	0.38	0.38
Width of P_3	0.48	0.46	0.56	-	0.46	0.50	0.51	0.48	0.54	0.51
Length of P_4	0.82	0.77	0.82	0.78	0.74	0.78	0.76	0.71	0.81	0.79
Width of P_4	0.75	0.72	0.73	0.77	0.70	0.68	0.64	0.62	0.68	0.68
Length of M_1	1.50	1.46	1.39	1.41	1.40	-	1.50	1.39	-	-
Length of M_2	-	-	1.42	1.39	1.41	-	-	1.40	-	-
Length of M_3	-	-	1.23	1.26	1.27	-	-	1.25	-	-
Talonid width of M_3	-	-	0.68	0.64	0.66	-	-	0.66	-	-

Table 57. Descriptive statistics for mandibular measurements of *Plecotus* (*P.*) cf. *abeli* Wett. from the Kozi Grzbiet locality

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Length of mandible	4	10.19	10.73	10.38	0.2533	2.4
APML	5	3.67	4.08	3.87	0.1739	4.5
Height of coronoid process	5	2.92	3.26	3.08	0.1234	4.0
Length of C_1 - M_3	3	6.00	6.34	6.12	0.1882	3.1
Length of P_2 - P_4	14	1.53	1.66	1.60	0.0410	2.6
Length of P_2 - M_3	3	5.24	5.60	5.37	0.1997	3.7
Length of P_4 - M_3	19	4.28	4.73	4.51	0.1149	2.5
Length of M_1 - M_3	14	3.70	4.06	3.90	0.0898	2.3
Length of C_1	15	0.74	0.97	0.84	0.0696	8.3
Width of C_1	15	0.77	0.93	0.84	0.0507	6.1
Length of P_2	16	0.51	0.66	0.57	0.0414	7.3
Width of P_2	16	0.51	0.68	0.60	0.0420	7.0
Length of P_3	29	0.33	0.50	0.40	0.0470	11.8
Width of P_3	29	0.44	0.58	0.51	0.0377	7.5
Length of P_4	65	0.68	0.88	0.79	0.0451	5.7
Width of P_4	65	0.65	0.81	0.73	0.0334	4.6
Length of M_1	53	1.35	1.59	1.43	0.1465	10.2
Length of M_2	42	1.29	1.51	1.41	0.0562	4.0
Length of M_3	22	1.12	1.33	1.25	0.0498	4.0
Talonid width of M_3	22	0.57	0.71	0.66	0.0309	4.7

crown shape resembles a rhombus, more elongated, however, than in *P.* (*P.*) *auritus*. Cingulum strongly developed on external side.

C_1 — the crown is triangular in outline, with rounded corners. The cingulum is less developed than in *P.* (*P.*) *auritus*, forming a cusp on the anterior margin of the tooth. In the posterior part of the tooth there is a developed talon, which on its disto-external margin has an accessory cusp.

P_2 — in outline of crown similar as in *P.* (*P.*) *auritus*. This tooth has a well

Table 58. Maxillar measurements of *Plecotus* (*P.*) cf. *abeli* Wett. from the Kozi Grzbiet locality

Specimen MF/1704/ : Measurements :	1	3	4	6	7	9	10	11	12	15
Length of P^2- M^3	5.05	-	-	-	-	-	-	-	-	-
Length of P^4- M^3	4.65	4.46	-	-	4.40	-	-	-	4.28	-
Length of M^1- M^3	3.65	3.60	3.54	-	3.51	3.58	3.54	3.66	3.43	3.35
Length of P^2	0.55	-	-	0.52	-	-	-	-	-	-
Width of P^2	0.57	-	-	0.59	-	-	-	-	-	-
Length of P^4	1.13	1.08	-	1.17	1.19	-	-	-	1.09	-
Width of P^4	0.88	1.03	-	1.07	1.00	-	-	-	0.99	-
Length of M^1	1.62	1.52	1.43	1.42	1.48	1.54	1.53	1.48	1.51	1.38
Width of M^1	1.40	1.37	1.45	1.39	1.42	1.46	1.37	1.36	1.31	1.38
Length of M^2	1.58	1.55	1.50	-	1.47	1.50	1.45	1.49	1.44	1.39
Width of M^2	1.60	1.56	1.60	-	1.55	1.66	1.52	1.50	1.50	1.50
Length of M^3	0.83	0.81	0.82	-	0.86	-	-	0.80	0.75	0.76
Width of M^3	1.59	1.48	1.59	-	1.47	-	1.50	1.57	1.56	1.53
Length of 1st commissure of M^3	0.80	0.84	0.87	-	0.81	-	0.76	0.82	0.85	0.82
Length of 2nd commissure of M^3	0.52	0.59	0.58	-	0.51	-	0.52	0.59	0.53	0.52
Length of 3rd commissure of M^3	0.44	0.50	0.55	-	0.54	-	0.44	0.60	0.53	0.51

Table 59. Descriptive statistics for maxillar measurements of *Plecotus* (*P.*) cf. *abeli* Wett. from the Kozi Grzbiet locality

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Length of P^4 - M^3	4	4.28	4.65	4.45	0.1543	3.5
Length of M^1 - M^3	9	3.35	3.66	3.54	0.1005	2.8
Length of P^2	3	0.52	0.55	0.53	0.0173	3.3
Width of P^2	3	0.54	0.59	0.57	0.0252	4.4
Length of P^4	16	0.99	1.25	1.15	0.0661	5.8
Width of P^4	16	0.88	1.05	0.99	0.0486	4.9
Length of M^1	21	1.38	1.62	1.48	0.0523	3.5
Width of M^1	21	1.31	1.48	1.40	0.0441	3.1
Length of M^2	23	1.39	1.58	1.47	0.0467	3.2
Width of M^2	23	1.45	1.66	1.53	0.0516	3.4
Length of M^3	12	0.75	0.91	0.82	0.0428	5.2
Width of M^3	13	1.46	1.59	1.52	0.0455	3.0
Length of 1st commissure of M^3	14	0.76	0.87	0.82	0.0294	3.6
Length of 2nd commissure of M^3	14	0.50	0.59	0.55	0.0343	6.3
Length of 3rd commissure of M^3	14	0.44	0.60	0.50	0.0456	9.1

developed cingulum, especially on the labial side. P_3 — similar to *P.* (*P.*) *auritus*, somewhat more massive. P_4 — crown in outline forms a triangle with rounded corners, much a in *P.* (*P.*) *auritus*, the tooth is, however, more massive. The postero-lingual margin of the tooth has at its base, roughly up to 1/3 of its height, an accessory face which is present in *P.* (*P.*) *auritus*, but lacking in *P.* (*P.*) *austriacus*.

M_1—M_2 — similar as in *P.* (*P.*) *auritus*, though somewhat more massive. Crista obliqua forms a smallish depression, readily discernible from a side view; this never occurs in *P.* (*P.*) *auritus*. M_3 — more massive than this tooth in *P.* (*P.*) *auritus*, especially its talonid.

Remarks. — Both the dental formula $\frac{3.1.3.3.}{2.1.2.3.}$ and the morphology of the remains i.e. the characteristic shape of the coronoid process, the position of the mental foramen below the small premolars, the antero-posterior compression of the crowns

Table 60. Measurements of specimens of *Plecotus* (*P.*) cf. *abeli* Wett. from the Kielniki 1 locality

Specimen MF/1782/ : Measurements :	1	2	3	4	5	6	7
Length of C_1- P_4	2.32	-	2.41	-	-	-	-
Length of P_2- P_4	1.59	-	1.69	-	-	-	-
Length of I_1	-	-	-	-	-	-	0.78
Width of I_1	-	-	-	-	-	-	0.48
Length of I_3	0.58	-	-	-	-	-	-
Width of I_3	0.43	-	-	-	-	-	-
Length of C_1	0.89	-	0.88	-	-	-	-
Width of C_1	0.85	-	0.85	-	-	-	-
Length of P_2	0.62	-	0.62	-	-	-	-
Width of P_2	0.68	-	0.66	-	-	-	-
Length of P_3	0.47	-	0.44	-	-	-	-
Width of P_3	0.61	-	0.54	-	-	-	-
Length of P_4	0.80	0.88	0.87	0.84	0.87	0.92	-
Width of P_4	0.84	0.75	0.74	0.72	0.72	0.78	-
Length of M_1	1.53	-	-	1.45	1.57	-	-
Length of M_2	-	1.50	-	1.50	1.52	-	-

Table 61. Descriptive statistics for mandibular measurements of *Plecotus* (*P.*) cf. *abeli* Wett. from the Kielniki 1 locality

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Length of $I_1 - I_3$ a.	2	1.02	1.14	1.08	0.0848	7.9
Length of $C_1 - P_4$	2	2.32	2.41	2.36	0.0636	2.7
Length of $P_2 - P_4$	2	1.59	1.69	1.64	0.0707	4.3
Length of C_1	2	0.88	0.89	0.88	0.0071	0.8
Width of C_1	2	0.85	0.85	0.85	0.0	0.0
Length of P_2	2	0.62	0.62	0.62	0.0	0.0
Width of P_2	2	0.66	0.68	0.67	0.0141	2.1
Length of P_3	2	0.44	0.47	0.45	0.0212	4.7
Width of P_3	2	0.54	0.61	0.57	0.0495	8.6
Length of P_4	6	0.80	0.92	0.86	0.0403	4.7
Width of P_4	6	0.72	0.84	0.76	0.0458	6.0
Length of M_1	3	1.45	1.57	1.52	0.0611	4.0
Talonid width of M_1	3	1.01	1.06	1.04	0.0265	2.5
Length of M_2	3	1.50	1.52	1.51	0.0115	0.8
Talonid width of M_2	3	1.02	1.06	1.04	0.0208	2.0

(a. alveolar length)

of the small premolars, the shapes of the crowns of P^2, P^4 and P_4 (Table 64) allow the remains studied to be classified as *Plecotus* (*s.s.*). The remains examined come close both in size and structure to the fosil species *P.* (*P.*) *abeli* described from the lower Pleistocene deposits of Austria. The original description of the species is very laconic and lacking any kind of illustration (Wettstein-Westersheim 1923). However, Rabeder (1974) revised early Pleistocene species of *Plecotus* from several localities in Austria, proving that they are identical with the species *P.* (*P.*) *abeli* described by Wettstein. On the basis of Rabeder's descriptions and drawings (*op. cit.*) the present author reached the conclusion that the remains studied here can be included though with certain reservations to *P.* (*P.*) *abeli.* The *Plecotus* remains from Kozi Grzbiet differ in some dimensions from *P.* (*P.*) *abeli* described by Rabeder from Mixnitz and Deutsch-Altenburg. The specimens of *P.* (*P.*) *abeli* of the older locality at Deutsch-Altenburg are slightly larger than those from Kozi Grzbiet, while the specimens from the younger locality in Mixnitz are on the whole smaller. This would be consistent with the overall trend observed in the group of these forms. Certain differences in size can also be observed between specimens of *P.* (*P.*) cf. *abeli* taken from four sites examined in Poland, i.e., Kozi Grzbiet, Zamkowa Dolna,

Table 62. Mandibular measurements of *Plecotus* (*P.*) cf. *abeli* Wett. specimens from the Zalesiaki and Zamkowa Dolna localities

Specimen MF/1706/ :	1	2	3	4	5	6	7	MF/1705/1
Locality :	ZA	ZA	ZA	ZA	ZA	ZA	ZA	ZD
Measurements :								
APML	-	-	-	3.85	-	-	-	-
Height of coronoid process	-	-	-	2.88	-	-	-	-
Length of P_4 - M_3	-	-	-	-	4.45	-	-	-
Length of M_1 - M_3	-	-	-	-	3.80	-	-	-
Length of C_1	0.70	-	-	-	-	-	-	-
Width of C_1	0.84	-	-	-	-	-	-	-
Length of P_3	-	-	-	-	-	-	-	0.39
Width of P_3	-	-	-	-	-	-	-	0.54
Length of P_4	0.74	0.81	-	-	0.75	0.78	0.78	0.70
Width of P_4	0.68	0.68	-	-	0.73	0.75	0.67	0.71
Length of M_1	-	-	-	-	1.38	1.40	1.43	-
Length of M_2	-	-	-	-	1.40	-	1.34	-
Length of M_3	-	-	-	-	1.25	-	-	-
Talonid width of M_3	-	-	-	-	0.76	-	-	-

Table 63. Descriptive statistics for mandibular measurements of *Plecotus* (*P.*) cf. *abeli* Wett. from the Zalesiaki locality

Measurements	N	Min.	Max.	$\bar{x}$	S.D.	C.V.
Length of P_4	5	0.74	0.81	0.77	0.0277	3.6
Width of P_4	5	0.67	0.75	0.70	0.0356	5.1
Length of M_1	3	1.38	1.43	1.40	0.0252	1.8
Talonid width of M_1	3	0.97	1.02	1.00	0.0289	2.9
Length of M_2	2	1.34	1.40	1.37	0.0424	3.1
Talonid width of M_2	2	0.93	0.97	0.95	0.0283	3.0

Table 64. Comparison of P^2 dimensions in fossil and recent species of the *Plecotus* (*Plecotus*) genus from Europe

Species : Measurements :	P.cf.abeli	P. auritus	P. austriacus
Length of P^2	0.53	0.46	0.48
N	3	13	11
Width of P^2	0.57	0.51	0.50
N	3	13	11

Table 65. Comparison of the size of lower teeth in the fossil *Plecotus* (*P.*) cf. *abeli* from the Kozi Grzbiet, Zalesiaki and Kielniki I localities and the recent species of *Plecotus auritus* and *P. austriacus*

Species :	Plecotus cf. abeli			P.	P.
Locality :	KG	ZA	KI1	auritus	austriacus
Measurements :				recent	recent
Length of C_1	0.84	0.70	0.88	0.76	0.86
Width of C_1	0.84	0.84	0.85	0.79	0.95
Length of P_2	0.57	-	0.62	0.52	0.60
Width of P_2	0.60	-	0.67	0.57	0.68
Length of P_3	0.40	-	0.45	0.36	0.42
Width of P_3	0.51	-	0.57	0.48	0.51
Length of P_4	0.79	0.77	0.86	0.72	0.83
Width of P_4	0.73	0.70	0.76	0.66	0.76

Kielniki and Zalesiaki (tables 52—59), they are however small and of no greater systematic significance. It is likely that *P.* (*P.*) *abeli* represents an ancestral form, intermediate between *P.* (*P.*) *auritus* and *P.* (*P.*) *austriacus*; however it seems to be closer to *P.* (*P.*) *auritus*.

MICROEVOLUTIONARY TRENDS IN PALEARCTIC BATS

Owing to the delicacy of the skeleton, the fossil remains of bats are fairly infrequent, and their history is relatively poorly documented and full of gaps (Anderson and Jones 1984).

On the basis of the fossil material known to date, it is known that the "model" of bat was already established in the Early Eocene (compare Jepsen 1970).

It would, therefore, seem likely that the group was formed in the Early Paleocene, or even in the Late Cretaceous (Smith 1976). In this period, many groups of insects such as Coleoptera, Diptera and probably Lepidoptera, which are the main food source for insectivorous bats were established in both the evolutionary and in the ecological sense (Leppik 1957). This was also a period in which mammals, both Eutheria and Metatheria flourished, and many land niches were occupied by insectivorous and carnivorous mammals.

The hypothetical ancestor of bats was most likely a small arboreal mammal (Smith 1976) or one living in rocky areas and sheltering in fissures and caves (Jepsen 1970), probably equipped with membranes permitting gliding and hunting in the air for nocturnal insects. This "aerial insectivory" was a very important factor, determining the subsequent course of evolution.

The regime of physical factors which would have to be fulfilled if the adaptations to the aerial environment were to be effective led to the formation of a complex of adaptive traits which were subject to strong selection. This led to the formation of an optimal bat morphotype in a relatively short geological time (Van Valen 1979). As a result of this process, bats as a group show a number of common aromorphoses, such as the capacity for active flight, the evolution of echolocation, active thermoregulation allowing them to go into hibernation, and others.

The "model" of bats, evolved owing to this selection, has proved so ecologically successful that for about 50 millions of years, i.e. at least from the Eocene onward the anatomy of these animals has not undergone any basic changes (Jepsen 1970, Jones and Genoways 1970).

The adaptation of the main evolutionary line of bats to a narrow trophic niche (since we have limited ourselves to insectivorous species), leads to a distinct tendency toward a decline in phenotypic variation, and certain evolutionary trends are repeated in independent phyletic lines (Horaček and Zima 1978).

The skull is the part of the skeleton most frequently present in fossil record, hence most of the studies completed to date have been devoted to it.

Much of the morphometric study of skulls has however concentrated on intraspectific differences, or those between closely related species. So far, less attention has been given to examining skulls from the point of view of microevolutionary changes (Radinsky 1985). A review of the literature on this subject (concerned with various mammal groups) has been given by Raup and Stanley (1978). Bats have not been adequately studied in this aspect.

In comparing the anatomy of the splanchnocranium in populations of fossil bats from various periods and recent species, certain characteristic sequences of changes can be observed, which have the character of microevolutionary trends. The term "microevolution" has been used here in a purely descriptive sense, as a description of small-scale evolutionary processes concerning particular organs (or their parts), and which is probably a reflection of adaptation to the environment by the given species.

A frequently recurring tendency in insectivorous bats is the cephalization of the skull, consisting in the decrease of some elements of the splanchnocranium, i.e. both the maxilla and mandible, with respect to the braincase. This is also reflected in the dental morphology.

Storch (1968) demonstrated that the structure of the jaw apparatus in bats is correlated with the type of diet. In this case, specialization has developed toward modifying the dentition. Two directions of change have been observed:

1. A simplification of the dental formula through a reduction and loss of teeth or their parts.

2. Molarization of premolars, consisting in the complication of the crowns of the teeth by the formation of accessory cusps, a thickening of the cingulum, and other structures. Owing to the satisfactory state of teeth preservation in fossil state, they are the most important elements in morphological studies. Among contemporary bats, about 50 dental formulae are known (Vaughan 1970). Only the canines, premolars and molars occur consistently in all the groups. This variation among bats of the temperate zone is much lower, for example in Europe it is limited to only 6 dental formulae. This is of course a phenomenon which has long been recognized, and the systematics of bats are still based on the dentition to a considerable extent (Miller 1907).

The variation in the proportions of particular groups of teeth has been investigated to a much smaller degree, particularly in the aspects of comparing fossil forms with modern ones.

The examples which will be given in the forthcoming chapter were selected from among species belonging to three families represented in

Table 66

Compilation of unspecialized traits in the build of the splanchnocranium in fossil bats and direction of changes (trends) observed

Specialized trait	Direction of changes observed	Author
1. Rostral part of skull elongated	1′. Shortening of rostral part	Kuzjakin 1950; Sigé 1974; Van Valen 1979; Wołoszyn 1979
2. Long palate	2′. Shortening of palate	Topal 1963, 1979
3. Dental formula: $\frac{2.1.3.3}{3.1.3.3}$	3′. Simplification of dental formula	Handley 1959; Miller 1907; Van Valen 1979, and others
4. Unreduced M^3	4′. Reduction of distal part of M^3	Handley 1959; Rabeder 1974; Topal 1979, and others
5. Elongated mandibular body	5′. Shortening of mandibular body	Sigé 1974 a; Topal 1979; Wołoszyn 1986
6. Frontal position of mental foramen	6′. Distal shifting of mental foramen	see Table 55
7. Elongated molar row	7′. Shortening of premolar row	Kordos 1975; Menu 1985; Topal 1963, 1975, 1979 and others
8. Last premolars P_4 of simple structure	8′. Molarization of P_4	Handley 1959; Kuzjakin 1950; Menu 1985, and others
9. Molars of the “nyctalodonta” type	9′. Appearance of molars of “myotodonta” type	Menu and Sigé 1971
10. Massive talonids on M_3	10′. Reduction of talonid on M_3 and increased robustness of talonids on M_1—M_2	Menu 1985

the fossil material, namely Rhinolophidae, Miniopteridae and Vespertilionidae.

Sigé (1974*a*) in his work on the genus *Stehlinia* from the Paleogene of Europe, and also later Van Valen (1979) in his essay on the evolution of bats, compiled those features thought to be primitive.

Table 66 takes some of these traits relating to the splanchnocranium into account, and the direction of changes with respect to modern species is also marked. Some of the examples mentioned in the table were discussed in the literature quoted in it. The work by Menu (1985) is particularly valuable; he presented various aspects of the evolution of the types of dentition of vespertilionid bats, as well as that by Topal (1979), who worked on changes in the morphology of the maxilla from the point of the phylogenesis of the "*ferrumequinum*" group of *Rhinolophus.*

The aim of the review of microevolutionary trends relating to the splanchnocranium presented in table 66 was to identify such trends which could be of use in determining fossil material, and which could facilitate description of the relative chronology of the fossil faunas examined.

Table 67. Shortening of the palate in bats of the "*ferrumequinum*" group (genus *Rhinolophus*)

Species :	Geological age	Length of palatum		%	Changes in %
R. kowalskii Topal	early Pliocene	$\bar{x}$	3.03	100.0	0
		N	4		
R. wenzensis sp.n.	early Pliocene	$\bar{x}$	2.85	94.1	-5.9
		N	1		
R.cf.macrorhinus Topal	early Pleistocene	$\bar{x}$	2.80	92.4	-1.8
		N	1		
R. ferrumequinum /Schreber/	recent	$\bar{x}$	2.45	80.9	-13.6
		N	5		

From this aspect it is interesting to trace the changes in the palatal length in the Rhinolophidae. As Table 67 and also fig. 6 show, Pliocene species had a much longer palate than do modern bats. A correct evaluation of this phenomenon is of great importance in determining the interrelationships of the species within the group. Topal (1979) gives a characteristic example from the "*ferrumequinum*" group.

Andersen (1975 — *vide* Topal 1979) — traces the *R. ferrumequinum* group back to *R. affinis*, whose dentition has several primitive features. However, the very short palate in *R. affinis*, shorter than that in *R.*

ferrumequinum, is in opposition to the trend observed within the group (Topal 1979) and according to this author, *R. affinis* probably represents a side line. The mean lengths of the palate for several species of *Rhinolophus*, presented in table 67, confirm the existence of the trend observed by Topal.

The fossil species listed in table 67 and the recent *R. ferrumequinum* are close in total cranial length. Over about 6 million years: Pliocene (Podlesice) to recent, the palate has become reduced by aobut 20%, yet the rate of this process fluctuated considerably. During the period: early Pliocene to middle Pliocene (about 3 million years), the palate diminished by about 6% (*R. kowalskii* — *R. wenzensis*), in about two more million years by about 2% (*R. wenzensis* — *R. macrorhinus*), and 14% during the Pleistocene, in roughly a million years (*R. macrorhinus* — *R. ferrumequinum*). The process of shortening the palate was, therefore, relatively rapid in the first half of the Pliocene, slowing down somewhat in the latter half of this period, to accelerate considerably in the Pleistocene.

The calculations presented in table 67 are, however, burdened by a considerable error, for the obvious reason that the comparative material was not sufficiently abundant.

Since in the available material mandibles are more abundantly represented, some more room will be devoted to the analysis of this material.

Fig. 19 depicts the mandible of a bat. Marked are those areas where the process of abbreviation has been particularly intensive. This is foremost the small premolars row (P_2 and P_3), and the postdental part of the mandibular body. The shortening of the row of small molars has been observed and commented by some authors (Menu 1985; Rabeder 1974; Topal 1979), while the diminution of the postdental part of the mandibular body has not yet been studied.

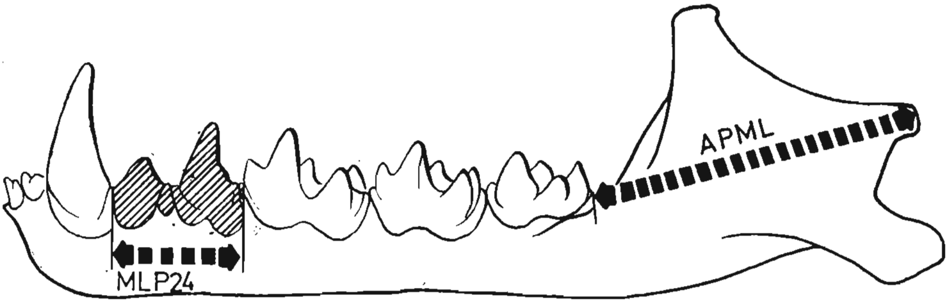

Fig. 19. Mandible of a bat. The dashed line indicates those regions where the process of shortening is taking place. Premolars hatched.

The position of the mental foramen is also an important trait in interpreting fossil material, particularly in determining bat remains of the genus *Plecotus*, where this is one of the criteria used in determining mandibles (especially those with damaged processes).

Table 55 presents the position of the mental foramen in *Plecotus*.

In fossil forms of the *P.* (*Paraplecotus*) the mental foramen lay in the anterior part of the mandible, usually below C_1/P_2.

In the *P.* (*Plecotus*) there is a marked tendency for the mental foramen to shift distally, in extreme cases reaching a position below P_3. It is an interesting fact that the position of the mental foramen in the modern *P.* (*P.*) *austriacus* is rather different, in which it lies more mesially, most often below P_2, in this respect bringing this species closer to species of *P.* (*Paraplecotus*). This fact indicates that *P.* (*P.*) *austriacus* probably represents a different phyletic line than *P.* (*P.*) *auritus*.

The height of the coronoid process is also subject to a considerable fluctuation. In some phyletic lines there is a distinct trend towards decrease in its size, while in others its height remains unchanged, or even increases a little (Friant 1963). Generally however, the coronoid process was relatively higher in older forms.

The gradient of the molarization of teeth departs somewhat from that observed in other mammals, in which, according to Herskovitz (1971) it increases from the canine posteriad. In insectivorous bats, immediately behind the canine there are some small premolars, which show no sign of molarization. The only teeth which undergo strong molarization are the last premolars (P_4) this being so pronounced that Kuzjakin (1950) sets these teeth apart in a separate group, which he calls "premolares prominantes", and considers them to be homologous with the carnassials of carnivores.

The small premolars P_2 and P_3 evidently have a minor role in chewing food. This is evidenced by the considerable degree of their reduction, and a clear tendency to disappear (table 68). A further proof of the low efficiency of these teeth is their high morphological lability. These are teeth in which anomalies most frequently appear (Wołoszyn 1978).

Table 68. Shortening of the premolar toothrow in bats of the "*ferrumequinum*" group

Species	Locality	Length of P_2- P_4	%
R. kowalskii Topal	Podlesice	2.63	100.0
R. wenzensis sp.n.	Węże I	2.46	93.5
R. cf. macrorhinus Topal	Kadzielnia 1	2.36	89.7
R. ferrumequinum Schreber	recent	1.97	74.9

Table 69. Crown of P^2 (in mm^2) in several species of the *Rhinolophus* genus (partly recalculated from data of Topal 1979)

Species and locality	N	Min.	Max.	$\bar{x}$	% of crown area
R. kowalskii Topal Podlesice, early Pliocene	16	0.247	0.582	0.371	100
R. wenzensis sp.n. Węże I, early Pliocene	2	0.260	0.296	0.278	75
R. estramontis Topal Osztramos 1f, mid-Pliocene	2	0.190	0.260	0.220	59
R. cf. macrorhinus Topal Kadzielnia I, early Pleistocene	1	-	-	0.180	48
R. macrorhinus Topal Beremend, early Pleisocene	1	-	-	0.170	46
R. ferrumequinum topali Kretzoi early Pleistocene		-	-	0.122	33
R. f. tarkoensis Topal early Pleisocene, Hungary	-	-	-	0.077	21
R. ferrumequinum /Schreber/ Iraq, recent	-	-	-	0.129	35
R. ferrumequinum /Schreber/ Yugoslavia, recent	-	-	-	0.138	37
R. ferrumequinum Hungary, recent	5	0.110	0.168	0.140	38

The process of the reduction of small premolars takes place in a characteristic sequence. In the first stage they are compressed, the gaps between the teeth disappear, their crowns begin to become contiguous with each other and with the adjacent canines and large premolars (fig. 14). This process is presented on the example of *Miniopterus approximatus* — *M. schreibersi.*

In a further stage of evolution, these teeth began to project lingual from the toothrow, as was the case in the Vespertilionidae, or labial like

Table 70. Relative length of premolars and molars in various bat species (index I PR used in the table)

Species	Locality	Geological age	I_{PR}	% change
Rhinolophus kowalskii Topal	Podlesice	early Pliocene	41.5	100.0
R. wenzensis sp.n.	Węże I	late lower Pliocene	37.2	89.6
R. cf. macrorhinus Topal	Kadzielnia 1	early Pleistocene	38.6	93.0
R. ferrumequinum /Schreber/	recent	recent	33.3	80.2
Miniopterus approximatus sp.n.	Podlesice	early Pliocene	52.9	100.0
M. schreibersi /Kuhl/	recent	recent	49.6	93.8
Plecotus rabederi sp.n.	Podlesice	early Pliocene	39.3	100.0
P. cf. abeli Wett.	Kozi Grzbiet	mid-Pleistocene	41.0	104.3
P. auritus /L./	recent	recent	40.3	102.5
P. austriacus /Fischer/	recent	recent	45.0	114.5
Myotis ex group "bechsteini"	Podlesice	early Pliocene	57.7	100.0
M. bechsteini /Kuhl/	recent	recent	52.8	91.5

in the Rhinolophidae. Later the surface of the crown became smaller and finally disappeared altogether. All the above-mentioned stages of the reduction of the small premolars can be observed in modern forms. It is more interesting, however, to trace this process on the basis of fossil material within the same phyletic lines. Since the process of reduction occurs simultaneously in the mandible and maxilla, observations concerning the evolution of the upper premolars were also used wherever possible (table 69). Examples of the decrease in the size of the small premolars in bats of the "*ferrumequinum*" group are presented in tables 69 and 70, and on figures 20, 21, 22 and 24.

In summary, the shortening of the length of the small molar row takes place by their reduction, compression and sagittal flattening of the crowns (e.g. *Plecotus* and *Miniopterus*: fig. 14, 23), and by projection from the toothrow and a decrease in crown surface (e.g. in Rhinolophidae).

As already mentioned, the second area of the mandible where shortening takes place is the postdental part of the mandibular body. Beginning with the Pliocene, the distance from the posterior margin of the talonid on M_3 to the articular surface of the articular process becomes shorter (table 71) (Wołoszyn 1986).

The biological interpretation of the changes observed may be as follows: the mandible is essentially a second order level. The surface of

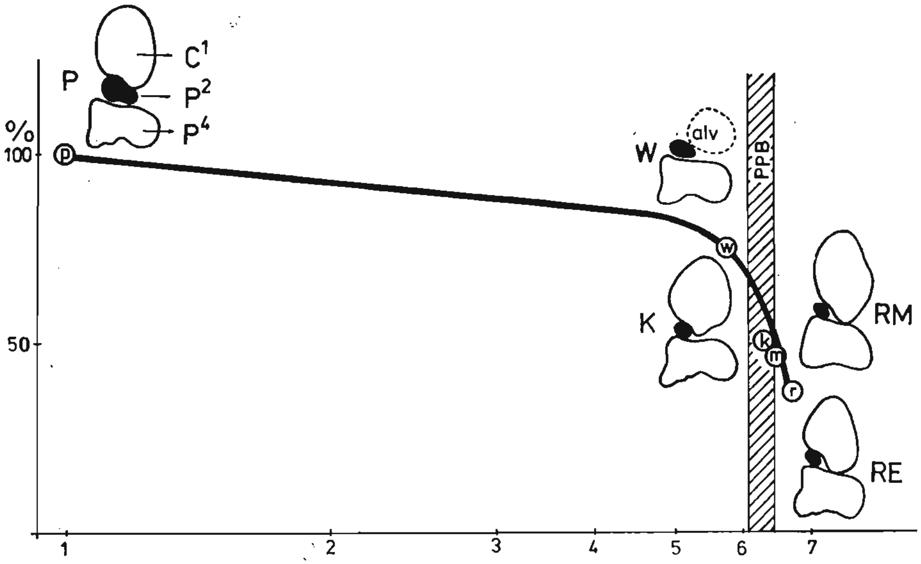

Fig. 20. Decrease in size of the crown of P^2 in horseshoe bats of the "*ferrumequinum*" group. The average surface of the crown of P^2 in *R. kowalskii* from Podlesice was assumed to be 100%. The time is given on the logarithmic abscissa. The age of Podlesice was assumed to be the unit.

Letter symbols: P, p — *R. kowalskii* Topal from Podlesice; W, w — *Rhinolophus wenzensis* sp. n. from Węże I; K, k — *R.* cf. *macrorhinus* Topal from Kadzielnia, RM, m — *R. macrorhinus* Topal (holotype), RE, r — *R. ferrumequinum*, Recent, PPB — Plio-Pleistocene boundary.

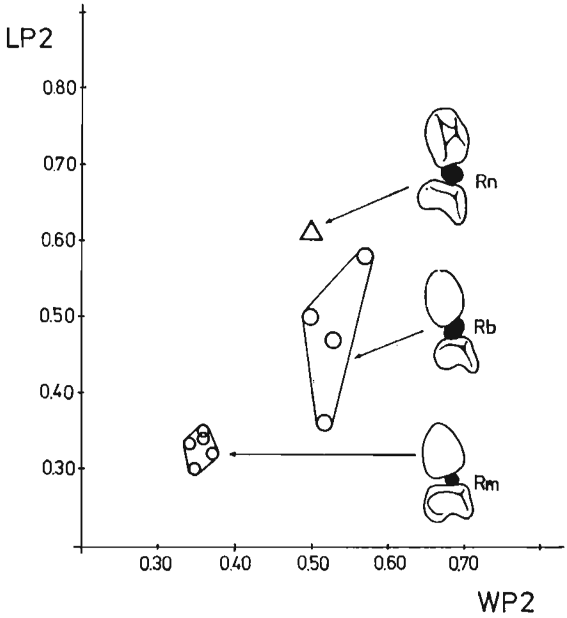

Fig. 21. Comparison of the size of P^2 in several species of *Rhinolophus*: Rn — *R. neglectus* Heller, Rb — *R. blasii*, Recent, Rm — *R. mehelyi*, Recent.

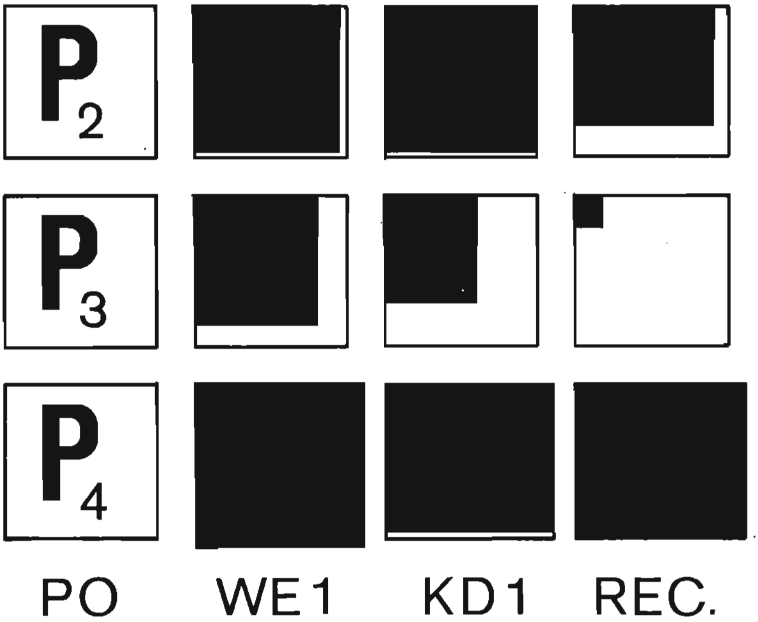

Fig. 22. Comparison of relative lengths of premolars in several fossil species of horseshoe bats of the "*ferrumequinum*" group. The dimensions of teeth in *Rhinolophus kowalskii* Topal from Podlesice are used as a standard (100%). Symbols: PO – *R. kowalskii* from Podlesice, WE1 — *R. wenzensis* sp. n. from Węże I, KD1 — *R.* cf. *macrorhinus* Topal from Kadzielnia 1, REC — Recent *R. ferrumequinum*. Shaded areas represent the size of the crowns of teeth (assumed to be rectangular): length × width (with respect to the standard).

contact of the articular process of the mandible with the mandibular fossa on the skull is the fulcrum. The muscles of the masticatory apparatus (*m. temporalis*, *m. masseter*, *m. mediano-pterygoid*) while contracting raise the mandible upward, causing its teeth to press up on those of the maxilla, this being necessary to break down food.

The pressure of the teeth is proportional to the length of the mandible. Assuming that during the Pliocene bats occupied a similar ecological niche as recently and their diet was similar in its physical properties (hardness of insect exoskeletons, etc.) then the shortening of the mandibular body must have led to a shortening of the postdental part of the mandible, for example through a reduction in the molar row. This process brought about a decline in skull mass, mainly owing to a decrease in the weight of the jaw apparatus, and a simultaneous decrease in body weight, which is desirable in a flying animal.

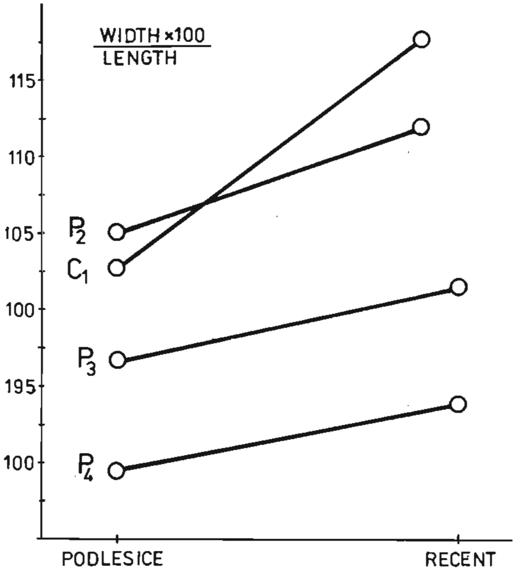

Fig. 23. Graph of changes in the index of tooth width: $\frac{\text{width} \times 100}{\text{length}}$ in *Miniopterus approximatus* sp. n. from Podlesice and *M. schreibersi*, Recent.

In order to make a quantitative assessment of the shortening of the mandibular body, several indices were adopted:

(1) Index of the postdental mandibular length

$$I_{PD} = \frac{(\text{distance of articular process} - M_3) \times 100}{\text{length of } P_4 - M_3}$$

(2) Index of molar compression

$$I_{PC} = \frac{\text{length of } P_2 + \text{length of } P_3 + \text{length of } P_4}{\text{length of } P_2 - P_4}$$

Table 71. Relative length of small premolar row and the postdental part of mandibular body in various groups of bats

Species	Locality	Geological age	I_{PD}	I_{PC}
Rhinolophus kowalskii Topal	Podlesice	early Pliocene	85.5	1.15
R. wenzensis sp.n.	Węże I	late lower Pliocene	78.4	1.18
R. ferrumequinum /Schreber/	recent	recent	78.5	1.24
Miniopterus approximatus sp.n.	Podlesice	early Pliocene	82.8	1.03
M. schreibersi /Kuhl/	recent	recent	78.1	1.10
Myotis ex group "bechsteini"	Podlesice	early Pliocene	88.7	1.05
M. bechsteini	recent	recent	78.1	1.02

(indices 1 and 2 used for assessment)

(3) Index of premolars and molars

$$I_{PR} = \frac{\text{length of premolar row } P_2-P_4}{\text{length of molar row } M_1-M_3}$$

The values of indices thus computed are presented in tables 70, 71.

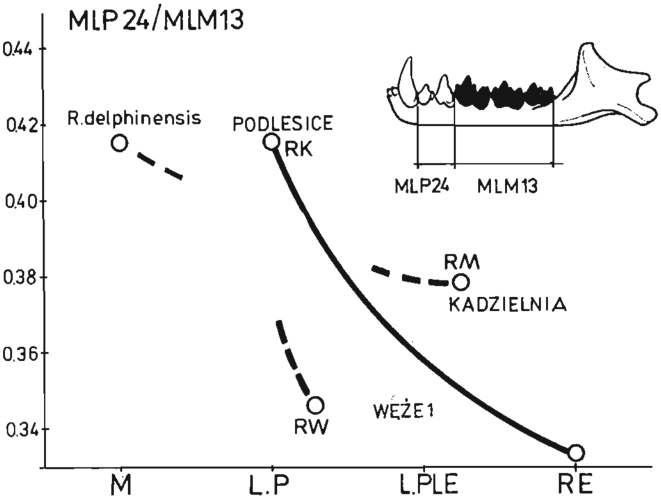

Fig. 24. Graph of changes in proportions of mandibular tooth lengths: MLP24/MLM13, in several species of *Rhinolophus*. Symbols: M — Miocene, L.P. — Lower Pliocene, L.PLE — Lower Pleistocene, RE Recent, RK — *R. kowalskii* Topal from Podlesice, RW — *R. wenzensis* sp. n. from Węże I, RM — *R.* cf. *macrorhinus* Topal from Kadzielnia.

CONCLUSIONS

The examples presented in tables 67—71 and in figures 14, 20, and 23 confirm that among the bats studied in the present paper there exist microevolutionary trends leading to a considerable reduction of the jaw apparatus in a comparatively short geological period. This process involves both the small premolars and the postdental part of the mandible (and probably also of the skull). The course of this process of reduction is slightly different in particular phyletic lines, and changes in the jaw apparatus proceed to different degrees.

Some deviation from the trends described has been observed (e.g. *Plecotus* in table 70); this may result both from the insufficient material, and from other as yet unidentified causes.

Some of the trends described, e.g. the degree of the reduction of the surface of the crown of P^2 in *Rhinolophus*, the size and position of the small premolars, or the length of the postdental part of the mandibular body may be a good indicator of the relative age of faunas in the comparison of fossil materials.

Broadly speaking, the process of the reduction of some elements of the splanchnocranium leads to an improvement of the jaw apparatus.

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BRONISŁAW W. WOŁOSZYN

NIETOPERZE Z PLIOCENU I PLEJSTOCENU POLSKI

Streszczenie

Opracowano kopalne szczątki plioceńskich i pleistoceńskich nietoperzy ze środkowej i południowej Polski. Należą one do trzech rodzin: Rhinolophidae, Miniopteridae i Vespertilionidae. W pracy pominięto rodzaj *Myotis* (Vespertilionidae), który będzie przedmiotem późniejszego opracowania.

W badanym materiale wykazano 15 gatunków nietoperzy, z których 6 opisano jako nowe dla nauki: *Rhinolophus kowalskii* Topal, *R. wenzensis* sp. n., *R. hanaki* sp. n., *R. neglectus* Heller, *R.* cf. *variabilis* Topal, *Rhinolophus* sp. (*mehelyi* ?), *R.* cf. *macrorhinus* Topal (Rhinolophidae); *Miniopterus aproximatus* sp. n., (Miniopteridae); *Eptesicus kowalskii* sp. n., *Eptesicus mossoczyi* sp. n., *Eptesicus* cf. *serotinus* (Schreber), *Eptesicus nilssoni* (Keys. et Blasius), *Barbastella* cf. *schadleri* Wett., *Plecotus* cf. *abeli* Wett., *Plecotus rabederi* sp. n. (Vespertilionidae).

Opisane materiały pochodzą z 10 stanowisk fauny kopalnej: Podlesice, Zalesiaki, Jaskinia Mała (w. 4+5), Węże I, Rębielice Królewskie II (Pliocen); Kadzielnia, Kamyk, Kielniki I, Jaskinia Zamkowa Dolna (dolny plejstocen); Kozi Grzbiet (środkowy plejstocen);

W pracy podano krótki przegląd kopalnej fauny nietoperzy Polski oparty zarówno na badaniach autora jak również na podstawie krytycznego przeglądu literatury. Stwierdzono, że w faunach plioceńskich były reprezentowane współczesne rodziny i rodzaje, brak jednak współczesnych gatunków. Charakterystyczny jest wysoki udział ciepłolubnych gatunków z rodzin Rhinolophidae i Miniopteridae, a w obrębie rodziny Vespertilionidae występuje archaiczny gatunek *Plecotus* (*Paraplecotus*) *rabederi* sp. n. Schyłek pliocenu charakteryzuje się zubożeniem fauny wskutek pogarszającego się klimatu, zmniejsza się udział elementów ciepłolubnych, których całkowity zanik na badanym obszarze nastąpił we wczesnym plejstocenie.

Fauny środkowego plejstocenu (Kozi Grzbiet) charakteryzowały się znacznym udziałem gatunków leśnych i borealnych. W faunach tych reprezentowane są jeszcze kopalne formy (*Plecotus* cf. *abeli* Wett. i *Barbastella* cf. *schadleri* Wett.).

W faunie postglacjalnej reprezentowane są już wyłącznie współczesne gatunki, jednak ich frekwencja odbiega od aktualnej. W okresie optimum klimatycznego holocenu dominują gatunki leśne (*Myotis bechsteini* (Kuhl)).

Wykazano, że niektóre z badanych gatunków t.j.: *Rhinolophus wenzensis* sp. n., *R. hanaki* sp. n., *R.* cf. *variabilis* Topal, *Plecotus* (*Paraplecotus*) *rabederi* sp. n. *Eptesicus kowalskii* sp. n., *E. mossoczyi* sp. n. reprezentują końcowe stadia linii filetycznych wymarłych prawdopodobnie u schyłku pliocenu, natomiast kopalny gatunek *M. approximatus* sp. n. nawiązuje do współczesnego gatunku *M. schreibersi.*

Wykazano, że od wczesnego pliocenu obserwuje się zmiany w budowie czaszki mające charakter trendów ewolucyjnych. Przeanalizowano niektóre z tych trendów i stwierdzono, że polegają one głównie na skracaniu trzewioczaszki i realizują się poprzez skracanie podniebienia oraz skracanie szeregu zębów przedtrzonowych, zarówno w szczęce jak i w żuchwie. Stwierdzono, że w wyniku działania wymienionych trendów ulega skróceniu postdentalna część żuchwy. Wysunięto przypuszczenie, że proces ten powodował obniżenie ciężaru ciała, głównie dzięki obniżeniu ciężaru aparatu szczękowego. Miało to istotne znaczenie dla ekonomiki lotu.

Praca wykonana w ramach problemu MR.II.3 i CPBP.04.06.01.

EXPLANATION OF PLATES 11 AND 12

Plate 11

1. Holotype of *Rhinolophus kowalskii* Topal (MF/1695/1) from the Podlesice locality.
2. Holotype of *Rhinolophus wenzensis* sp. n. (MF/551/1) from the Węże I locality.
3. Mandibular fragment of *Rhinolophus* cf. *macrorhinus* Topal (MF/33/3) from the Kadzielnia 1 locality.
4. Holotype of *Rhinolophus hanaki* sp. n. (MF/1692/1) from the Podlesice locality.

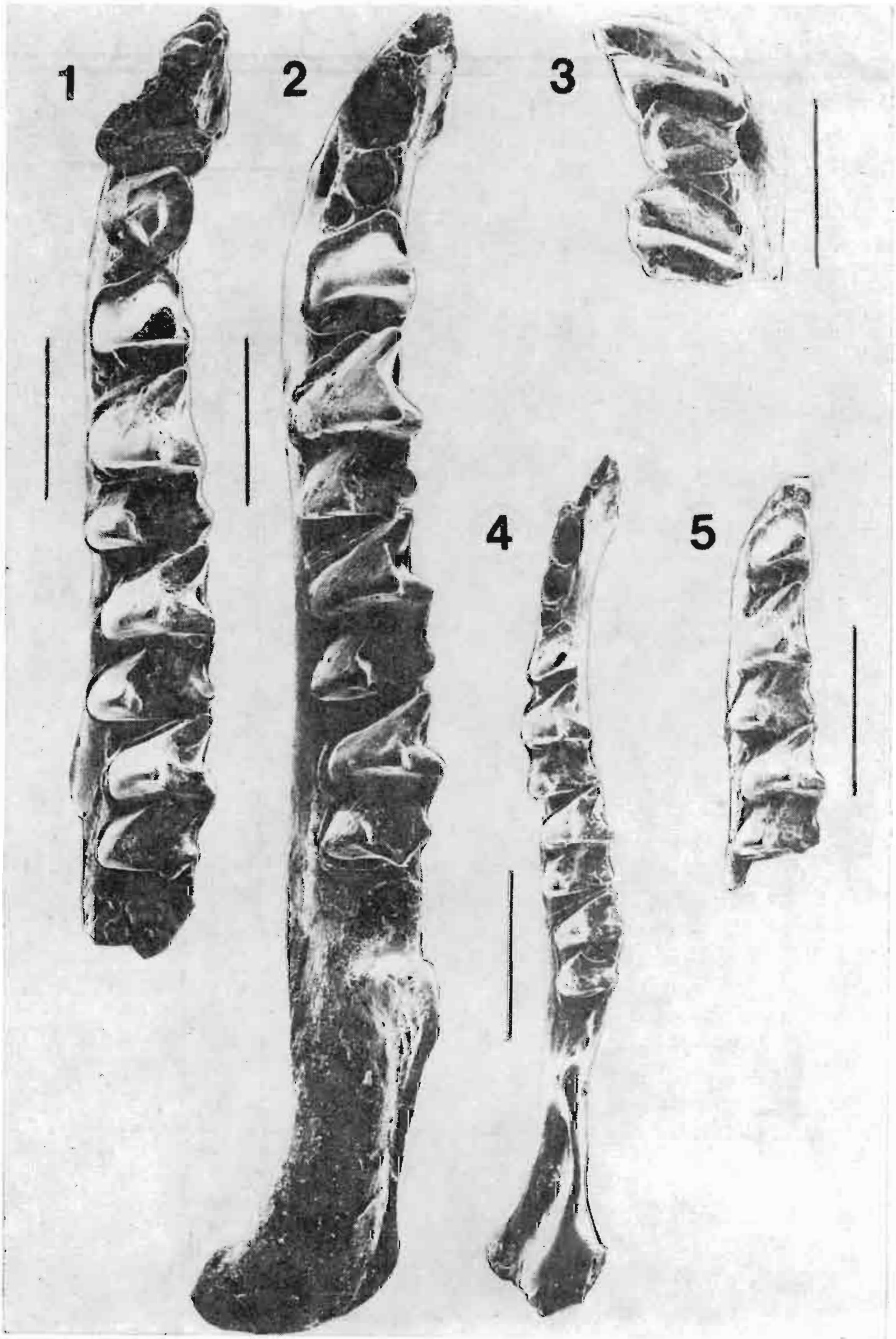
5. Mandibular fragment of *Rhinolophus neglectus* Heller (M-675/8/7) from the Mała Cave (layer 4+5) locality.

Scale bar is 2 mm

Plate 12

1. Holotype of *Miniopterus approximatus* sp. n. (MF/12/4) from the Podlesice locality.
2. Mandibular fragment of *Barbastella* cf. *schadleri* Wett. (MF/1701/1) from the Kozi Grzbiet locality.
3. Holotype of *Eptesicus mossoczyi* sp. n. (MF/1698/1) from the Podlesice locality.
4. Holotype of *Plecotus* (*Paraplecotus*) *rabederi* sp. n. (MF/1702/1) from the Podlesice locality.
5. Right mandible of *Plecotus* (*Plecotus*) cf. *abeli* Wett. (MF/1704/44) from the Kozi Grzbiet locality.
6. Holotype of *Eptesicus kowalskii* sp. n. (MF/1697/1) from the Podlesice locality.

Scale bar is 2 mm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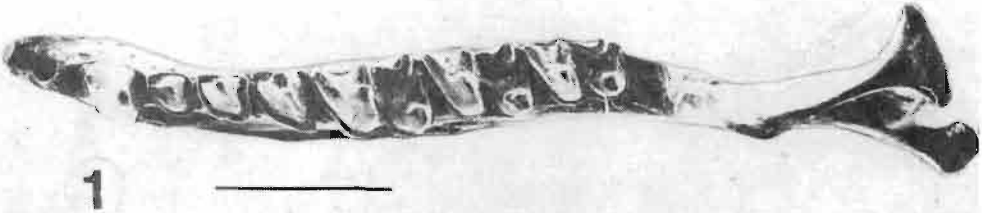

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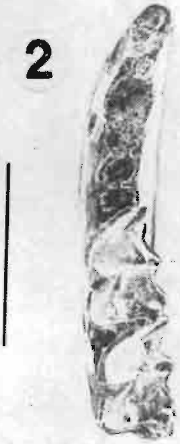

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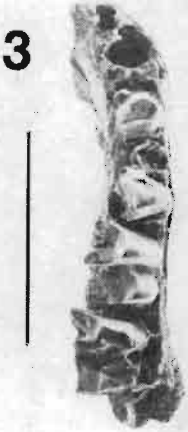

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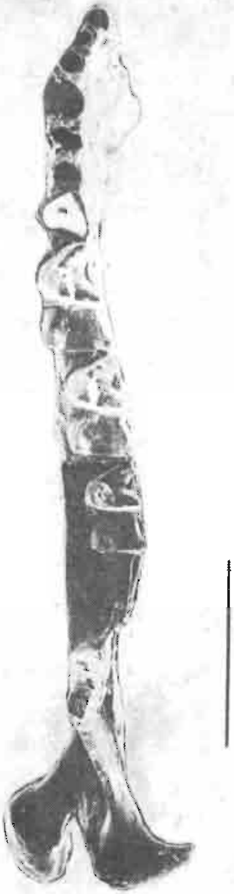

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