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MICROEVOLUTIONARY TRENDS IN WESTERN PALAEARCTIC BATS. CASE STUDY: MICROEVOLUTIONARY TRENDS AMONG BATS OF *RHINOLOPHUS* "*FERRUMEQUINUM*" GROUP (MAMMALIA: CHIROPTERA)

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Abstract. A frecuently recurring tendency in insectivorous bats is the cephalization of he skull. It has been shown that from the early Pliocene onwards, changes which appear to be microevolutionary trends have continued to take place in the skull structure. Some of these trends were analysed, and they were found to consist mainly in the reduction of splanchnocranium: shortening of the palate and of the premolar teethrow (both in the maxilla and the mandible). Postdental part of the mandible becomes shorter.

Résumé. Une tendance fréquemment rencontrée chez les chauve-souris insectivores est la céphalisation du crâne. On a démontré qu'encore à partir du Pliocène précoce, les changements qui paraîssent constituer des tendances microévolutives ont continué à se manifester au niveau du crâne. Quelques-unes de ces tendances ont été analysées et on est arrivé à la conclusion qu'elles apparaîssent par la réduction du splanchnocranium: le raccourcissement du palais et de la rangée de dents prémolaires (tant au niveau du maxillaire qu'à celui de la mandibule). La partie postdentale de la mandibule se raccourcit.

Key words: Chiroptera, "*Rhinolophus ferrumequinum* group", microevolutionary trends, fossil bats, Neogene, Quaternary, Poland.

INTRODUCTION

The regime of physical factors which would have to be fulfilled in the adaptation 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. As a result of this process, bats as a group show a number of common aromorphoses, such a capacity for active flight, the evolution of echolocation, active thermo-regulation allowing them to go into hibernation, and others.

The "model" of bats, evolved owing to this selection, has proved so ecologically succesful 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. 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.

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.

In this respect I consider necessary to mention that microevolution means minor evolutionary events usually viewed over a short period of time, consisting of changes of gene frequencies, chromosome structure or number of small morphological changes within a population over a few generations (A Dictionary of Ecology, Evolution and Systematics, 1982, Cambridge Univ. Press).

Main topic of this publication is focused on morphological changes observed among horseshoe (*Rhinolopus* sp.) bats during Neogene and Quaternary. Some years ago the author studied reach fossil material of bats from ten localities from southern Poland (Wołoszyn, 1987). Present work is an revaluation of some results presented in that publication.

Paleoclimatic background

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 of its course, first was migration from the south in periods when a more favorable climate prevailed, and the extinction or withdrawals of local population in period of deterioration of climate. These processes existed already in the Pliocene, becoming, however, more intensive in the Pleistocene.

In the Early Pliocene (about 6 my) on the northern shores of the Mediterranean Basin, a damp climate prevailed with a distinct rain season in the summer period. The chiropteran fauna of this region showed a considerable proportion of thermophilous elements (Rhinolophidae) and tropical ones (Hipposideridae and Megadermatidae) (Sigé & Legendre, 1983).

During this period Rhinolophidae and Miniopteridae were both represented on the territory of Central Europe (actually Southern Poland).

Greater climatic changes began roughly in the Middle Pliocene (about 3 my). In the initial stages of the evolution of the Mediterranean climate the most characteristic feature was a fluctuation of rhythmicity of the rain season, and vegetation become more xerothermic.

Climatic changes initiated in the mid-Pliocene continued, the climate slowly deteriorated and it worst during the Pleistocene. These climatic changes had a fundamental effect on the chiropteran fauna. 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.

In periods of harsh climate the range of the bats could have been even more restricted, solely to roost areas lying in the basin of the Mediterranean.

In warmer periods the bats migrated northwards, colonizing in turn the Basin of the Carpathians, and in climate optima crossing the barrier of the Carpathians and colonizing in turn of the mountains.

According to Topál (1979), horseshoe bats of the „*ferrumequinum*" group migrated into the Carpathians Basin at least twice in the Pliocene and at least once in the Pleistocene.

MATERIAL AND METHODS

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. The present study is focused on horseshoe bats from "*ferrumequinum*" group.

The fossil remains of bats on which are subject of the present study come from three localities in Central and Southern Poland dated from the Early Pliocene to the Early Pleistocene (Tab. 1).

Table 1

Geological age of the faunas (partly after Wołoszyn, 1987).

Locality	*Rhinolophus* sp.	Geological age	approx. age in my	Biozones
Podlesice	*R. kowalskii* Topál	Early Pliocene	6	MN 14
Węże 1	*R. wenzensis* Wołoszyn	Lower Pliocene	3	MN 15/16
Kadzielnia 1	*R. cf. macrorhinus* Topál	Late Pliocene/Early Pleistoc.	1.8	MN 17/Q 1

The locality at Podlesice (Kraków – Częstochowa Upland) which is the most abundant in bone remains and also the oldest, dated the Early Pliocene (or very late Miocene) – Biozone MN 14 (Tab. 1) represents a relatively "modern" bat fauna lacking tropical elements. In this fauna the same extant families and genera are represented, yet recent species are lacking.

The fauna from Węże 1 locality – Biozone MN 15 (Kraków – Częstochowa Upland) is slightly younger than the previously mentioned one. It is however, rather different in its species composition. Particularly interesting is the presence of a large horseshoe bat, *R. wenzensis* Wołoszyn, most likely representing a side line of the "*ferrumequinum*" group. It has many primitive features but also some progressive ones. It is probable that the morphotype of the species erose owing to endemic evolution in an isolated population (Wołoszyn, 1987).

The locality at Kadzielnia 1 – Biozone MN 17 / Q 1 (Holy Cross Mts.). In the Early Pleistocene, further changes took place in the bat fauna. Archaic species of the "*ferrumequinum*" group were replaced by the more "modern" *R. macrorhinus* Topál.

The fossil material of bats is housed in the collection of the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences in Kraków (Poland). The whole material consists of several thousand specimens, from among which the remains belonging to the taxa investigated were selected. The system of measurements used in this paper is described in the paper "Pliocene and Pleistocene Bats of Poland" (Wołoszyn, 1987).

RESULTS AND DISCUSSIONS

Storch (1974) demonstrated that the structure of the jaw apparatus in bats is correlated with the type of diet. In the studied case, specialization has developed toward modifying the dentition (Wołoszyn, 1987, 2009).

A frecuently recurring tendency in insectivorous bats is the cephalization of the skull. Two directions of change have been observed:

- A simplification of the dental formula through a reduction and loss of teeth or their parts
- Molarization of premolars

This process brought about a decline in skull mass, mainly owing to a decrease in the weight of the jaw apparatus, and a simultaneus decrease in body weight, which is desirable in a flying animal.

Sigé (1974), in his paper 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.

Table 2 takes some of these traits relating to the splanchnocranium into account and the direction of changes with respect to modern species. Some of the examples mentioned in the table were discussed in the literature quoted in it.

Table 2

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

No	Unspecialized traits	Direction of changes observed	Author
1	Rostral part of skull elongated	Shortening of rostral part	Kuzjakin, 1950; Sigé, 1974; Van Valen, 1979; Wołoszyn 1987
2	Long palate	Shortening of palate	Topál, 1963, 1979; Wołoszyn, 1987
3	Dental formula: Maxilla: 2.1.3.3. Mandible: 3.1.3.3.	Simplification of dental formula	Handley, 1959; Miller, 1907; Van Valen, 1979; Wołoszyn, 1987, 2009
4	Unreduced M^3	Reduction of distal part of M^3	Handley, 1959; Rabeder, 1974; Wołoszyn, 1987
5	Elongated mandibular body	Shortening of mandibular body	Sigé, 1974; Topál, 1979; Wołoszyn, 1987
6	Frontal position of mental foramen	Distal shifting of mental foramen	Wołoszyn, 1987
7	Elongated premolar row	Shortening of premolar row	Kordos, 1975; Menu, 1985; Topál, 1963, 1979; Wołoszyn, 1987, 2009
8	Last premolar (P^4) of simple structure	Molarization of P^4	Handley, 1959; Kuzjakin, 1950; Menu, 1985; Wołoszyn, 1987, 2009
9	Molars of the "nyctalo-donta" type	Appearance of molars of "myotodonta" type	Menu & Sigé, 1971
10	Massive talonids of M_3	Reduction of talonid on M_3 and increased robustness of talonids on M_1 - M_2	Menu & Sigé, 1971; Menu 1985

The aim of the review of microevolutionary trends relating to the splanchnocranium presented in the table 2 was to identity such trends which could be of use in identifying fossil material, and which could facilitate description of a relative chronology of the fossil faunas examined.

From this aspect it is interesting to trace the changes in the palatal length in the Rhinolophidae. The fossil species listed in table 3 are close in total cranial length. Over about 6 my i.e. from Podlesice to the recent, the palate has became reduced by about 20%.

Table 3

Shortening of the palate in bats of “*ferrumequium*” group (partly after Wołoszyn, 1987).

Species	Geological age	Length of Palatum in mm (average)	%
R. kowalskii Topál	early Pliocene	3.03	100.0
R. wenzensis Wołoszyn	lower Pliocene	2.85	94.1
R. cf. macrorhinus Topál	early Pleistocene	2.80	92.4
R. ferrumequinum (Schreber)	recent	2.45	80.9

The small premolars P2 and P3 evidently have a minor role in chewing food. This is evident by the considerable degree of their reduction, and a clear tendency to disappear. 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).

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.

In a further stage of evolution, these teeth began to project lingual from the teethrow (Vespertilionidae), or labial like in the Rhinolophidae. Later the surface of the crown became smaller, and finally disappeared altogether.

Examples of the decrease in the size of the small premolars among horseshoe bats of the "*ferrumequinum*" group are presented in table 2 and figures 1 and 2. In summary, the shortening of the length of the small premolar row takes place by their reduction, compression, and by projection from the toothrow and a decrease in crown surface.

Table 4

Shortening of the premolar toothrow in horseshoe bats of the "*ferrumequinum*" group (partly after Wołoszyn, 1987).

Species	Locality	average Length of $P_2 – P_4$ (in mm)	% of change
Rhinolophus kowalskii Topál	Podlesice	2.63	100.00
R. wenzensis Wołoszyn	Węże 1	2.46	93.5
R. cf. macrorhinus Topál	Kadzielnia 1	2.36	89.7
R. ferrumequinum (Schreber)	recent	1.97	74.9

The gradient of the molarization of teeth departs somewhat from that observed in other mammals. 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 and P^4), this being so pronounced that Kuzjakin (1950) sets these teeth apart in a separate group, which he calls "premolars prominantes", and considers them to be a homologous with the carnassials of carnivores.

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 (Tab. 5)

The biological interpretation of the changes observed may be as follow: the mandible is essentially a second order lever. The surface of contact of the articular process of the mandible with the mandibular fosse of the skull is the fulcrum. The muscles of the mastificatory 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.

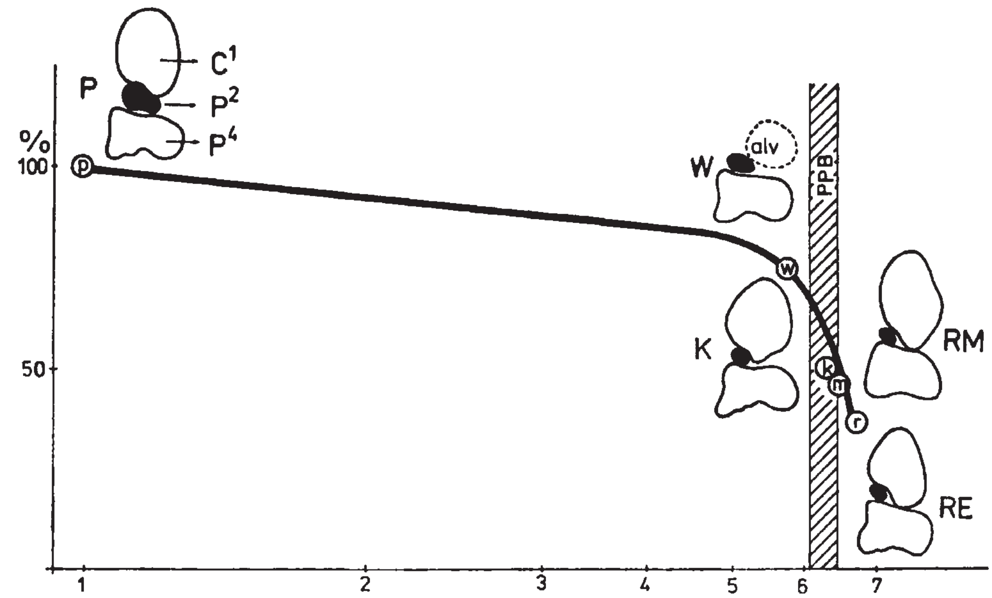

Fig. 1 - Decrease in size of the crown surface of P2 in horseshoe bats of the "*ferrumequinum*" group. The average surface of the crown of P2 in *R. kowalski* from Podlesice was assumed to be 100%. The time is given on the logarithmic abscissa. The age of Podlesice (about 6 my) was assumed to be the unit. Letter symbols: P – *Rhinolophus kowalskii* Topál, from Podlesice; W – *R. wenzensis* Wołoszyn, from Węże 1; K - *R. cf. macrorhinus* Topál, from Kadzielnia 1; RM - *R. macrorhinus* Topál, "modern"; RE – *R. ferrumequinum*, recent; PPB – Plio-Pleistocene boundary.

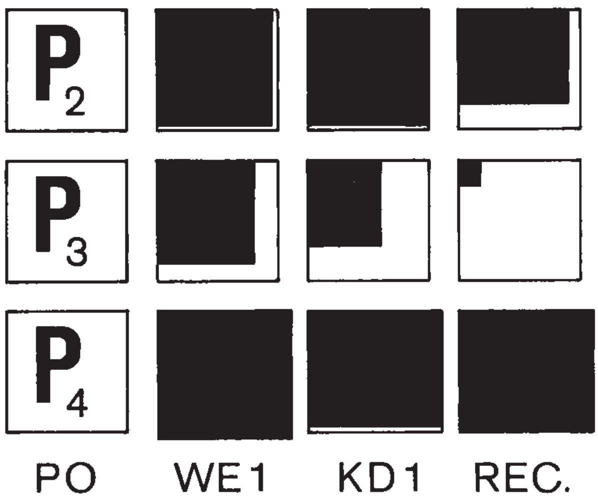

Fig. 2 - Comparison of relative lengths of premolars in several fossil species of horseshoe bats of the "*ferrumequinum*" group. The dimensions of teeth crown in *Rhinolophus kowalskii* Topál, from Podlesice are used as a standard (100%). Symbols: PO – *Rhinolophus kowalskii* Topál, from Podlesice; WE1 – *R. wenzensis* Wołoszyn, from Węże 1; KD1 – *R. cf. macrorhinus* Topál, from Kadzielnia 1; REC – *R. ferrumequinum*, recent. Shaded areas represent the size of the crowns of teeth (assumed to be rectangular): length x width (with respect to the standard).

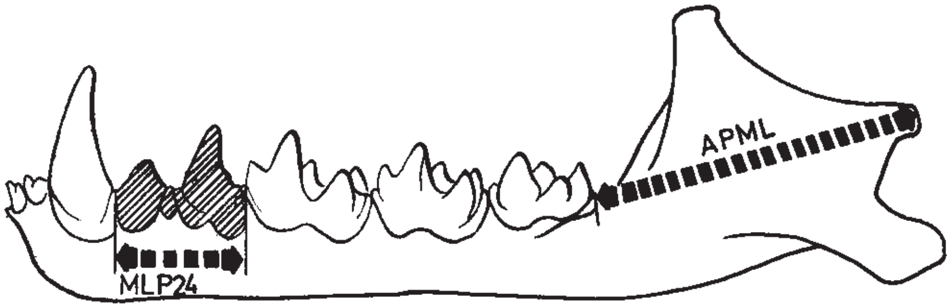

Fig. 3 - Mandible of horseshoe bat. The dashed line indicates those regions where the process of shortening is taking place. Premolars hatched. Symbols: MLP24 – Premolars length ($P_2 – P_4$); APML – Postdental length of mandible (Articular process - M_3 length).

Table 5

Relative length of small premolar row and postdental part of the mandibular body in Rhinolophid bat (partly after Wołoszyn, 1987).

Species	Locality	Geological age	I_{PD}	I_{PC}
Rhinolophus kowalskii Topál	Podlesice	early Pliocene	85.5	1.15
R. wenzezsis Wołoszyn	Węże 1	late lower Pliocene	78.4	1.18
R. ferrumequinum (Schreber)	recent	recent	78.5	1.24

The pressure of the teeth is proportional of the length of the mandible. Assuming that during Neogene 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.

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 whole body weight, which is desiderable in a flying animal.

In order to make a quantitative assessment of the shortening of the mandibular body following indices were adopted (Indices 1 and 2):

(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 premolar compression:

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

Conclusions

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 of its course, first was migration from the south in periods when a more favorable climate prevailed, and the extinction or withdrawals of local population in period of deterioration of climate. These processes existed already in the Pliocene, becoming, however, more intensive in the Pleistocene.

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The fossil remains of bats on which are subject of the present study come from three localities in Central and Southern Poland dated from the Early Pliocene to the Early Pleistocene (Tab. 1).

A frequently recurring tendency in insectivorous bats is the cephalization of the skull. Two directions of change have been observed:

- A simplification of the dental formula through a reduction and loss of teeth or their parts;
- Molarization of premolars;
- Shortening of the postdental part of mandibular body.

This process brought about a decline in skull mass, mainly owing to a decrease in the weight of the jaw apparatus, and a simultaneus decrease in body weight, which is desirable in a flying animal.

The examples presented in the tables 1-5 and in figures 1-3 confirm that among the bats studied there, microevolutionary trends leading to a considerable reduction of the jaw apparatus in a comparatively short geological period exist. This process involves the small premolars (both in mandible and skull) and the postdental part of the mandible.

Some of the trends described, e.g. the degree of reduction of the surface of the crown of premolars P_2 and P^2, also the size and the position of small premolars, and the length of the postdental part of the mandibular body may be a good indicator of a relative age of faunas in the comparison of fossil materials.

TENDINȚE MICROEVOLUTIVE LA LILIECII DIN PALEARCTICUL DE VEST. STUDIU DE CAZ: TENDINȚE MICROEVOLUTIVE LA GRUPUL DE SPECII „*FERRUMEQUINUM*" DIN CADRUL GENULUI *RHINOLOPHUS* (MAMMALIA: CHIROPTERA)

REZUMAT

O tendință frecvent întâlnită la liliecii insectivori este cefalizarea craniului. S-a demonstrat că încă din Pliocenul timpuriu încoace, schimbările care par a fi tendințe microevolutive au continuat să se manifeste la nivelul craniului. Câteva din aceste tendințe au fost analizate și s-a ajuns la concluzia că

ele apar prin reducerea splanchnocraniului: scurtarea palatului şi a şirului de dinţi premolari (atât la nivelul maxilei cât şi al mandibulei). Partea postdentală a mandibulei devine mai scurtă.

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