

***Felidae* and *Hyaenidae* (Carnivora, Mammalia)  
from the Miocene of Przeworno (Lower Silesia, Poland),  
with general remarks on the fauna complex**

Elmar P. J. HEIZMANN and Henryk KUBIAK

Received: 10 Aug. 1992

Accepted for publication: 1 Oct. 1992

HEIZMANN E. P. J., KUBIAK H. 1992. *Felidae* and *Hyaenidae* (Carnivora, Mammalia) from the Miocene of Przeworno (Lower Silesia, Poland), with general remarks on the fauna complex. Acta zool. cracov., 35(2): 241-263.

Abstract. Remains of representatives of three families, i.e. *Felidae*, *Hyaenidae* and *Mustelidae* of the Miocene fauna of Upper Badenian age (MN zone 7) were found in Przeworno, Lower Silesia. The felids represented by *Pseudaelurus* and the hyaenids by *Miohyaena* are described in this paper. The carnivores constitute about 25 per cent of the number of mammalian species known from Przeworno so far. Such percentage of carnivores in the mammalian fauna of Przeworno is similar to that of Steinheim am Albuch (Germany). A revised list of the entire vertebrate fauna is presented. The composition of the fauna indicates one fauna complex contrary to the two faunas of different age reported so far from Przeworno 1 and Przeworno 2. A new reconstruction of the habitat shows a riverplain forest. The climate may be regarded as subtropical.

Key words: fossil mammals, *Carnivora*, *Felidae*, *Hyaenidae*, Middle Miocene, Poland.

Elmar P. J. HEIZMANN, Staatliches Museum für Naturkunde, Rosenstein 1, 7000 Stuttgart, Germany.

Henryk KUBIAK, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków. Poland.

## I. INTRODUCTION

Since the beginning of the 19th century proterozoic marble has been explored in the quarry at Przeworno (17°10'40''E, 50°41'41''N) which is situated on the foreland of the Sudety Mts, about 50 km south of Wrocław and 45 km west of Opole. The first note on the occurrence of fossil karst at Przeworno appeared in 1966 (OBERC 1966). Later on, OBERC (1969) noted the occurrence of bone remains in the clay infilling of a karst passage from the bottom of the quarry (locality Przeworno 1). In June 1970, Dr. J. GŁĄZEK and Dr. S. DYJOR recorded bone remains from a fissure in the western wall of the quarry

(locality Przeworno 2). Thereupon, in the same year bone material could be collected and described. The first preliminary geological and paleontological data were published in 1971 (GŁĄZEK et al. 1971). In the autumn of 1970 further bone remains were collected independently by Prof. K. KOWALSKI and the second co-author. From 1971 (KUBIAK 1978, 1982) until 1979 systematic excavations were carried out by the Institute of Systematics and Evolution of Animals of the Polish Academy of Sciences in Cracow.

The bone material is housed in the collection of the Institute of Systematics and Evolution of Animals of the Polish Academy of Sciences, in Cracow. Pieces on which the inventory numbers follow the letters Z. Pal. and IGUWr belong to the collections of the Institute of Paleobiology, Polish Academy of Sciences, in Warsaw, and, respectively, of the University in Wrocław.

The material preliminarily determined was passed on to specialists of respective groups of animals for detailed examination and description.

The following papers with results hitherto obtained on the remains of vertebrates from Przeworno have been published by (compare the list of the fauna: Table I):

*Amphibia: Discoglossidae* – MŁYNARSKI 1976; SANCHIZ and MŁYNARSKI 1979; *Reptilia: Anguidae, Colubridae* – BACHMAYER and MŁYNARSKI 1977, *Emydidae, Testudinidae* – MŁYNARSKI 1978, *Chelydridae* – MŁYNARSKI 1981; *Aves: Phasianidae* – BOCHENSKI 1987, *Mammalia: Mustelidae, Felidae, Rhinocerotidae, Suidae, Tragulidae, Cervidae* – SULIMSKI in: GŁĄZEK et al. 1971, *Primates* – KOWALSKI and ZAPFE 1974, *Gomphotheriidae* – KUBIAK 1975, *Suidae, Tayassuidae* – KUBIAK 1981a, *Equidae, Rhinocerotidae* – KUBIAK 1981b, *Castoridae* – KUBIAK and WOLSAN 1986, *Chalicotheriidae* – KOROTKIEVICH and SULIMSKI 1990. The mustelids are being studied by M. WOLSAN.

Studies on the geological conditions of the localities at Przeworno and summarizing work on the fauna are presented in papers by OBERC 1966, OBERC & DYJOR 1969, GŁĄZEK et al. 1971, 1972, 1977, GALEWSKI et al. 1973, KUBIAK 1978, 1982, 1987.

All the papers on Przeworno which have appeared so far are listed in this work.

The papers discussed give the up-to-date knowledge of the localities at Przeworno.

The find of remains of insects at the locality Przeworno 3 ought to be mentioned here in brief. From the eastern part of the quarry at that locality of Sarmatian age come several species of insects of the family *Dytiscidae* (*Coleoptera*), studied and published by GALEWSKI and GŁĄZEK (1973, 1977).

It was possible to prepare this paper owing to the cooperation between the Staatliches Museum für Naturkunde Stuttgart (E. P. J. HEIZMANN) and the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow (H. KUBIAK). We are indebted to Mr. P. RIEDERLE for the excellent preparation of the finds. Thanks are also due to Mr. H. LUMPE who prepared the photographs of the material.

A fellowship from the DAAD and a further invitation from Dr. R. WILD and Dr. E. P. J. HEIZMANN gave H. KUBIAK a financial support and the possibility to work on this paper in Stuttgart.

## II. FAUNA ASSEMBLAGE

Hitherto only one preliminary list of the entire vertebrate fauna from Przeworno has been published (KUBIAK 1982). Since our knowledge of all the finds from Przeworno is not yet complete an up-to-date fauna list is presented in this paper (Table I). This list, however, should not be understood as a closed one.

## III. SYSTEMATIC PART

Family *Felidae* FISCHER DE WALDHEIM, 1817

Subfamily *Felinae* FISCHER DE WALDHEIM, 1817

Genus *Pseudaelurus* GERVAIS, 1848-1852

*Pseudaelurus* GERVAIS, 1848-1852

The felids of the genus *Pseudaelurus* known as widely distributed in the Miocene of Europe are represented at Przeworno by two species, one of which occurs in localities Przeworno 1 (*Pseudaelurus* cf. *quadridentatus*), and Przeworno 2 (*Ps.* cf. *lorteti*). Both these species, however, occur together in different European localities (e.g. Sansan, Steinheim, La Grive). Thus, the distribution of the finds in both localities at Przeworno may be rather incidental considering the small number of carnivore remains on the whole.

*Pseudaelurus* (*Schizailurus*) cf. *lorteti* GAILLARD, 1899

**Material and dimensions:** right mandible with root and basal fragment of canine, alveolus of P<sub>2</sub> and fragmentarily preserved P<sub>3</sub>-M<sub>1</sub> (MF/1990/91) (Plate I).

P<sub>3</sub>: ca. 9.3 x -; P<sub>4</sub>: 11.3 x ca. 5.5; M<sub>1</sub>: ca. 13.4 x ca. 5.9

Length of P<sub>3</sub>-M<sub>1</sub>: ca. 34.2

Height of mandible below anterior root of M<sub>1</sub> (labially): 16.0

Entire length (condylus – anterior edge of C): 86.5

Left mandible with root and basal fragment of C, roots of P<sub>3</sub>, P<sub>4</sub> and with M<sub>1</sub> (Z. Pal. M/IV-1)

P<sub>3</sub>: ca. 8.3 x -; P<sub>4</sub>: ca. 11.2 x -; M<sub>1</sub>: 13.7 x 6.0;

C (at the basis): 8.0 x 6.0

P<sub>3</sub>-M<sub>1</sub>: 33.0

Height of mandible below anterior root of M<sub>1</sub> (labially): 17.2.

**Description and comparison:** These two mandibles with only fragmentary dentition are very similar in size and in their general shape. However, on account of the differently worn teeth and the different data concerning the collection of finds they cannot be treated as belonging to the same individual. The root-side end of the lingual file is

Table I

## The vertebrate fauna from Przeworno

Representatives of the fauna from Przeworno		Localities		Publications (cf. References)
		1	2	
Pisces				
	<i>Teleostei</i> : gen. et sp. indet.	-	+	---
Amphibia				
Anura				
	<i>Discoglossidae</i> : <i>Latonia</i> cf. <i>sayfriedi</i> v. MEYER (= <i>Discoglossus giganteus</i> )	+	+	SANCHIZ & MEYNARSKI 1979 MEYNARSKI 1976
Reptilia				
Squamata				
	<i>Anguidae</i> : <i>Ophisaurus fraasi</i> (HILGENDORF)	+	-	BACHMAYER & MEYNARSKI 1977
	<i>Colubridae</i> : <i>Coluber</i> sp. <i>Colubrinae</i> indet.	-	+	BACHMAYER & MEYNARSKI 1977, MEYNARSKI 1981 SZYNDLAR 1984
Testudines				
	<i>Emydidae</i> : <i>Ptychogaster buchelbergense</i> KUSS <i>Geoemyda</i> aff. <i>eurea</i> (WEGNER)	-	+	MEYNARSKI 1978
	<i>Testudinidae</i> : <i>Testudo</i> sp.	-	+	MEYNARSKI 1978
	<i>Chelydridae</i> : <i>Chelydropsis murchisoni</i> (BELL)	+	-	MEYNARSKI 1978
		-	+	MEYNARSKI 1981
Aves				
Galliformes				
	<i>Phasianidae</i> : <i>Miophasianus medius</i> (MILNE EDWARDS)	-	+	BOCHENSKI 1987
Mammalia				
Primates				
	<i>Pongidae</i> : <i>Pliopithecus antiquus</i> (BLAINVILLE)	-	+	KOWALSKI & ZAPFE 1974
Rodentia				
	<i>Castoridae</i> : <i>Chalicomys jaegeri</i> KAUP	+	-	KUBIAK & WOLSAN 1986
	<i>Sciuridae</i> : gen. et sp. indet.	-	+	---
	<i>Cricetidae</i> : gen. et sp. indet.	+	+	---

<i>Proboscidea</i>			
<i>Gomphotheriidae: Gomphotherium angustidens</i> (CUVIER)	-	+	KUBIAK 1975
<i>Perissodactyla</i>			
<i>Equidae: Anchitherium aurelianense</i> (CUVIER)	+	+	KUBIAK 1981b
<i>Rhinocerotidae: Aceratherium (Alicornops) simorrense</i> (LARTET)	+	+	KUBIAK 1981b
(= <i>Aceratherium silesiacum</i> SULIMSKI)			SULIMSKI (in: GŁAZEK et al. 1971)
<i>Brachypotherium brachypus</i> LARTET		+	KUBIAK 1981b
<i>Chalicotheriidae: Chalicotherium grande</i> (BLAINVILLE)	+	+	KOROTKIEVICH & SULIMSKI 1990
<i>Artiodactyla</i>			
<i>Suidae: Conohyus simorrensis</i> (LARTET)	+	+	KUBIAK 1981a
(= <i>Hyootherium simorrense</i> LARTET)			SULIMSKI (in: GŁAZEK et al. 1971)
(= <i>Hyootherium</i> aff. <i>soemmeringi</i> MEYER)			SULIMSKI (in: GŁAZEK et al. 1971)
<i>Tayassuidae: Taucanamo sansaniense</i> (LARTET)	-	+	KUBIAK 1981a
<i>Tragulidae: Dorcatherium</i> cf. <i>crassum</i> (LARTET)	+	+	SULIMSKI (in: GŁAZEK et al. 1971)
<i>Cervidae: Euprox furcatus</i> (HENSEL)	+	+	SULIMSKI (in: GŁAZEK et al. 1971)
? <i>Heteroprox</i> sp.	-	+	---
<i>Palaeomerycidae: ? Palaeomeryx</i> sp.	-	+	---
<i>Lagomerycidae: ? Lagomeryx</i> sp.	-	+	---
<i>Carnivora</i>			
<i>Felidae: Pseudaelurus</i> cf. <i>lorteti</i> GAILLARD	-	+	SULIMSKI (in: GŁAZEK et al. 1971)
<i>Pseudaelurus</i> cf. <i>quadridentatus</i> (BLAINVILLE)	+	-	HEIZMANN & KUBIAK (this paper)
			SULIMSKI (in: GŁAZEK et al. 1971)
<i>Hyaenidae: Miohyaena montadai</i> (VILLALTA & CRUSAFONT PAIRO)	-	+	HEIZMANN & KUBIAK (this paper)
<i>Mustelidae: gen. et sp. indet.</i> (4 taxa)	+	+	HEIZMANN & KUBIAK (this paper)
			SULIMSKI (in: GŁAZEK et al. 1971)

visible in the right part of the mandible, at the canine. As in the type-specimen of *Ps. lorteti* from La Grive (GAILLARD 1899, Pl. 1, Fig. 6) this file is located slightly rostrally to the middle of the crown. The distal part of the crown is lacking.

The alveolus of the one-rooted P<sub>2</sub> is located just before P<sub>3</sub> and unlike to that is shifted lingually. Thus, there is no diasteme between P<sub>2</sub> and P<sub>3</sub> as it is in *Ps. lorteti* from Steinheim, and the alveolus is actually also larger than in that form. The roots and only one part of the posterior portion of the tooth are preserved. The typical caudal widening of the premolars of *Pseudaelurus* is also visible in this tooth.

P<sub>4</sub> with its dominating main cusp, the robust paraconid and the broad talonid-shaped posterior cingulum is in its shape and size very similar to the corresponding tooth of *Ps. lorteti* from Steinheim, but its paraconid is slightly stronger. However, corresponding variants of the paraconid occur e.g. in La Grive. It is still visible that at the posterior file of the main cusp a side tip was present, as in all *Pseudaelurus* species. The small tip beside the lingual end of the posterior cingulum, normally not present in *Ps. lorteti*, may be here an individual feature of no systematic value.

Apart from the tooth base of M<sub>1</sub> only its paraconid is preserved. It corresponds nearly entirely with that in *Ps. lorteti* from Steinheim; only the weak labial cingulum is insignificantly stronger than that from Steinheim.

Except for a ca. 9.5 mm long diasteme between C and P<sub>2</sub> the teeth are close-set in the row.

Mandibular body is short and high as in the type-specimen of *Ps. lorteti*. Both foramina mentalia – one large at the anterior margin and one small in the middle part of P<sub>3</sub> – are similar in proportions as in specimens from Steinheim or Sansan (GINSBURG 1961, Pl. 12, Fig. 7), but in the mandibles from both these localities they lie more rostrally. The deep masseteric cavity reaches rostrally as far as the posterior end of the dental row, and therefore somewhat nearer anteriorly than in the finds from Steinheim, La Grive and Sansan. The dental foramen is in its position comparable with that in *Ps. quadridentatus* from Steinheim (HEIZMANN 1973, Pl. 4, Fig. 1), i.e. it opens relatively deep in the jaw. The chin flaw is even more strongly marked than in *Ps. quadridentatus* from Steinheim; the symphysis is very short as in this last.

The left part of the mandible from Przeworno described by SULIMSKI (in GŁAZEK et al. 1971) is nearly the same size as that described above. The larger height of the mandible is probably connected with the older individual age of the animal, but perhaps also with a pathological change below M<sub>1</sub> in the horizontal ramus.

The mandibular body shows a tumour-like swelling in that place. The dentition is also incomplete in this jaw. Thus, only the proportions of the teeth can be compared, which, judging from the roots of the premolars and the heavily worn M<sub>1</sub>, are very similar to those of the right mandible. No P<sub>2</sub> alveolus is present, which lack is probably connected with the old age of the individual. However, a small cavity located rostralingually to P<sub>3</sub> indicates that there was primarily a tooth, but it was lost by the animal in its life-time, and later the alveolus was closed again. The roots of P<sub>3</sub> and P<sub>4</sub> are similar to those of the right mandible. M<sub>1</sub> is completely worn: paraconid and protoconid are worn down to the base and the talonid is also worn labially, which is shown by the steep grinding surface. The proportions

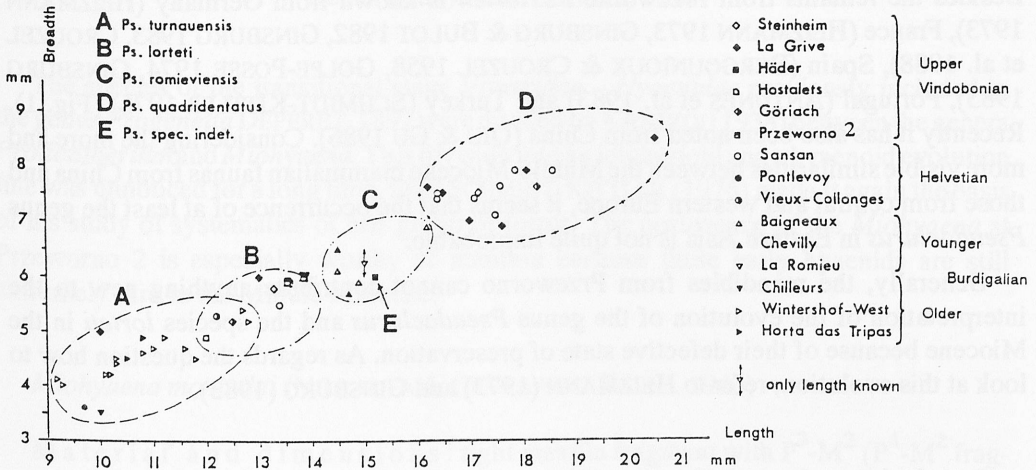


Fig. 1. Length-breadth diagram for M1 inf. of different *Pseudaelurus* species (after HEIZMANN 1973)

of the talonid correspond to those of *Ps. lorteti* from Steinheim. The very small metaconid is, however, deeper located in the posterior part of the protoconid in the mandible from Przeworno than in that from Steinheim. The foramina in both mandibles from Przeworno are in the same position and in both the masseteric dimple reaches only the level of the posterior end of the tooth row. In our opinion, there is no doubt that both mandibles belong to the same species.

**Relationships:** In respect of the size both *Pseudaelurus* mandibles from Przeworno lie in the size range of *Ps. lorteti* (comp. HEIZMANN 1973, Fig. 16; GINSBURG 1983, Fig. 3). Also morphologically – as far as it may be estimated on the basis of the fragmentary dentition – they correspond with the features of this species, as can be seen from the above-given comparison. If however we identify the remains as *Pseudaelurus* cf. *lorteti* – it is so only because of the bad state of preservation of the pieces from Przeworno. The identification of the remains as a small *Ps. romieviensis*, still possible on the basis of their size, cannot be ruled out on account of the structure of the tooth only. Admittedly, the characteristically short and high premolars of this species are unrecognizable in our specimen, and also the very small, low metaconid of M<sub>1</sub> does not agree with the typical one of *Ps. romieviensis*, but this last feature is present in another *Pseudaelurus* mandible described by HEIZMANN (1973: 52) from Häder, which GINSBURG (1983) determined as a more developed form of *Ps. romieviensis*. Since the mandible mentioned is considerably larger than the mandibles from Przeworno, and since it typically lacks P<sub>2</sub>, which in the mandibles from Przeworno does not occur or is only of secondary origin, it seems to us that the identification of these specimens as belonging to *Pseudaelurus* cf. *lorteti* is more reasonable.

SULIMSKI (in GŁĄZEK et al. 1971) has already pointed out that these remains as well as the tooth described below, are so far the only finds of the genus *Pseudaelurus* in Poland. Besides the remains from Przeworno *Ps. lorteti* is known from Germany (HEIZMANN 1973), France (HEIZMANN 1973, GINSBURG & BULOT 1982, GINSBURG 1983, CROUZEL et al. 1988), Spain (BERGOUNIOUX & CROUZEL 1958, GOLPE-POSSE 1974, GINSBURG 1983), Portugal (ANTUNES et al. 1983) and Turkey (SCHMIDT-KITTLER 1976) (Fig. 1). Recently it has also been noted from China (QIU & GU 1986). Considering the more and more visible similarities between the Middle-Miocene mammalian faunas from China and those from central and western Europe, it seems that the occurrence of at least the genus *Pseudaelurus* in Eastern Asia is not quite improbable.

Generally, the mandibles from Przeworno cannot contribute anything new to the interpretation of the evolution of the genus *Pseudaelurus* and the species *lorteti* in the Miocene because of their defective state of preservation. As regards the question how to look at this evolution, refer to HEIZMANN (1973) and GINSBURG (1983).

*Pseudaelurus* cf. *quadridentatus* (BLAINVILLE, 1843)

– P<sup>4</sup> sin. (IGUWr 4) 20.6 × 10.5

Another, larger species of *Pseudaelurus* is represented by one P<sup>4</sup> from Przeworno 1, and already described by SULIMSKI (in GŁĄZEK et al. 1971). From the figure (SULIMSKI, Pl. 5, Fig. 4) it can be seen that this tooth has a slightly marked metacone similar to that of *Ps. quadridentatus* from Sansan (GINSBURG 1961, Pl. 12, Fig. 3). On the contrary, the anterior edge is more robust and the protocone not so strongly directed backwards. It is also striking in the tooth from Przeworno how far the metacone is displaced backwards. Because of these differences we refer this tooth to *Pseudaelurus* cf. *quadridentatus* with reservation, just as SULIMSKI does.

In the dentition of the lower jaw of the larger *Pseudaelurus* from the European Miocene HEIZMANN (1973) managed to show a distinct morphological evolution with a simultaneous increase in size (*Ps. romieviensis* – *Ps. quadridentatus*). There are no corresponding studies on the dentition of the upper jaw so far because of the insufficiency of materials. It may however be noted that the P<sup>4</sup> from Przeworno in its size rather resembles the younger members of *Ps. quadridentatus*). Contrary to the data given by SULIMSKI, this tooth is slightly larger than the only P<sup>4</sup> from Sansan (measurements: No. 616: length 19.3 mm; GINSBURG 1961), and may rather be compared to P<sup>4</sup> from La Grive, for which GAILLARD (1899) gives a length of 21 mm. This tooth provides no confirmation of the Upper-Burdigalian age of Przeworno 1 (GŁĄZEK et al. 1971) as opposed to Przeworno 2.

The species *Ps. quadridentatus*, which is also the type-species of the genus, is, besides Poland, known also from France (MEIN 1958, GINSBURG & TASSY 1977, GINSBURG 1980, 1983), Germany (HEIZMANN 1973, FAHLBUSCH et al. 1974, FRANZEN 1981), Austria (HOFMANN 1893, ZDARSKY 1909), Spain (BERGOUNIOUX & CROUZEL 1958, GOLPE-POSSE 1974, PETTER 1976) and Turkey (SCHMIDT-KITTLER 1976) (Fig. 1). This species occurs mainly in the Middle-Miocene. Whether it really reaches the Turolian, as given by FRANZEN (1981), will be probably known after the study of the finds from Dorn-Dürkheim.

Family *Hyaenidae* GRAY, 1869Genus *Miohyaena* KRETZOI, 1938

The species of the transitional stage *Viverridae* – *Hyaenidae* previously included in the genus *Progenetta* DEPÉRET, 1892 were divided by KRETZOI (1938) between the genera *Protictitherium* and *Miohyaena*. This division into an ictitherioid and a hyaenoid evolution line was unnoticed for a long time, until SCHMIDT-KITTLER (1976) made it again the basis of his study of systematics of this group of forms. The occurrence of the *Miohyaena* at Przeworno 2 is especially worthy of mention because these early hyaenids are still extremely rare in the Middle Miocene.

*Miohyaena montadai* (VILLALTA & CRUSAFONT PAIRO, 1943)

**Material and dimensions:** right maxilla fragment with  $P^3$ - $M^2$  ( $P^4$ - $M^2$  fragmentary), (MF/1991/91) (Plate II).

$P^3$ - $M^2$ : 54.0

$P^3$ : 18.4 x 10.4;  $P^4$ : 26.6 x 15.7;  $M^1$ : ca. 8.5 x ca. 18.2;  $M^2$ : 5.1 x ca. 8.7.

Right mandible with  $P_2$ - $M_1$  and alveoli of  $I_1$ - $I_3$ , C,  $P_1$  and  $M_2$  (MF/1992/91) (Plate III).

Overall length of mandible: 170;  $P_1$ - $M_2$ : 80.7; height of processus coronoideus: 74; height of mandible below anterior root of  $M_1$  (labially): 33.5; C-alveolus: 17.2 x 12.5; diasteme C- $P_1$ : 6.6;  $P_1$ -alveolus: 3.6 x 3.7;  $P_2$ : 13.3 x 7.3;  $P_3$ : 17.7 x 8.6;  $P_4$ : 18.5 x 9.7;  $M_1$ : 20.3 x 10.0;  $M_2$ -alveolus: 6.0 x 2.9.

**Description:** The fragments of the maxilla and the mandible show an excellent occlusion which means that both specimens belong to the same species and perhaps even to the same individual. However, the teeth of the maxilla are partly more heavily damaged, unlike the mandible and its dentition, which are very well preserved.

The fragment of the maxilla has only so much bone preserved that the foramen infraorbitale above the posterior root of  $P^3$  is perceptible. In addition to  $P^3$ - $M^2$ , the alveolus of the posterior root of  $P^2$  is partly present. The palatine part of the bone is depressed between  $P^4$  and  $M^1$ .

$P^3$  makes a typical hyaenoid impression because of its massive tooth-base and the robust, horizontally worn main cusp. A low rounded posterior paracone is above the slightly worn longitudinal crest connected with the main cusp. The crest extends to the rostral-lingual edge of the tooth. There the toothbase is slightly corroded. Therefore, the primary thickness of the enamel cusp in which the crest ends is no longer well seen. Nevertheless, it seems that in any case it was weaker than in the type-specimen of *Miohyaena montadai*. As in that species the rostral-labial edge of the tooth is slightly thickened. A fine, but sharply crested lingual cingulum is present.

In spite of its bad state of preservation  $P^4$  shows that its general proportions come close to those in the type-specimen of *M. montadai*. The protoconus is somewhat more narrowed and therefore it seems to be directed a little more rostral-lingually. The parastyle is robust

and of the same height as the comparatively short metaconus edge. The paraconus is more heavily damaged, but it rises distinctly above the other two cusps. A weak, roller-shaped labial cingulum is marked. Unfortunately, owing to the bad state of preservation nothing can be said about the possible rostral and lingual cingula.

M<sup>1</sup> – in its labial part preserved incomplete – has a contour of an isosceles triangle, with the rostral limitation as the longest side. This last forms, as in *M. montadai*, with the labial side of P<sup>4</sup> at an angle slightly less than 90°. The tooth is strongly cross-expanded. Paraconus and metaconus are damaged. They are separated from the protoconus by a distinctly marked longitudinal groove. The protoconus is connected with the labial cusps by sharp anterior and posterior crests. Two-rooted M<sup>2</sup> is completely corroded; nevertheless, the presence of the three main cusps may be detected.

The nearly complete, robust mandible differs from the type-specimen of *M. montadai*, above all, in a weaker crack of the inferior edge in the range marking of musculus digastricus and in the steeper course of the anterior edge of the processus coronoideus. The foramina dentalia in the mandible from Przeworno are located closer to each other: the anterior below the posterior root of P<sub>2</sub>, the posterior one below the anterior root of P<sub>3</sub>. On the contrary, in *M. montadai* the corresponding foramina appear below the anterior root of P<sub>2</sub> or below the middle of P<sub>3</sub>. Another foramen mentale occurs in the mandible, under description directly at the edge of the symphysis below the incisors. The drop-shaped mark of the insertion of the musculus masseter is on the labial side of the mandible deeply concave. Below it is the nearly flat surface of the attachment of the musculus stenomandibularis which is also well-defined. It is directed rostrally and ends with a small bone swelling. The main part of the processus coronoideus makes the insertion area for the musculus temporalis. The arched margin of the surface against the insertion area of m. masseter is distinctly visible. This surface is rostrally and cranially bounded by bulges. The difference between the upper boundary of the processus coronoideus in our specimen and that in the type-specimen of *M. montadai* (CRUSAFONT PAIRO & PETTER 1969, Pl. 1, Fig. 2) is probably connected with the fact that this part is complete in *M. montadai*. In any case, this upper margin in the mandible from Przeworno is remarkably less rounded.

On the lingual side the surface of the symphysis reaches the position of the anterior border of P<sub>2</sub>. Thus, it is relatively small as for such a robust mandible. The foramen mandibulare is placed at the half height of the mandible ca. 1.5 cm behind M<sub>2</sub>. The processus angularis is in great part broken off. The upper margin of the cylindrical mandibular articulation is at the same height as the mandible margin in the dental part. The mandibular articulation is located steeply to the long axis of the mandible, corresponding to the angle at which both of the mandible branches join. The articulation surface is laterally pointed.

The dentition is represented by P<sub>2</sub>-M<sub>1</sub>. The alveoli of all the remaining teeth are also preserved. The alveoli of the three incisors from mesial to lateral are increased in size. The I<sub>2</sub> alveolus, unlike I<sub>1</sub> and I<sub>3</sub>, is directed backwards. Owing to the more oblique position of the alveolus, the crowns of the incisors form a close row. The canine alveolus is large and slightly twisted outwards. Its labial limitation is more convex than the lingual one. The short diasteme is followed by the round P<sub>1</sub> alveolus. Within the diasteme the upper edge of the mandible forms a weak crest, which labially appears slightly convex.

The main difference between the type-specimen of *M. montadai* and that from Przeworno is visible in P<sub>2</sub>. In the Przeworno specimen it is more assymmetric, i.e. its rostral part is more reduced and in consequence the anterior edge of the main cusp is steeper. At the rostral end of the crest which runs along the whole tooth there is a weak enamel cusp, and so is there a small one in the posterior part of the tooth. The tooth is broader posteriorly and at its posterior end nearly straightly bounded. The posterolingual angle is slightly strenghtened. From it a shallow groove extends toward the main cusp, which shows horizontal traces of wear, as in the remaining premolars.

Seen from above P<sub>3</sub> is rectangular rounded in outline. The anterior and posterior cusps are strenghtened in comparison with P<sub>2</sub>; moreover, a distinct posterior cingulum is visible. This tooth is slightly inclined backwards in relation to the neighbouring premolar.

On P<sub>4</sub> the side cusps are even more strenghtened and worn, as shown by the horizontal wear of their tips. As in *M. montadai* the posterior cingulum of this tooth is thickened at the posterolingual angle of the tooth. A labial cingulum is marked in the rostral part of the tooth.

In comparison with the robust premolars the canine appears delicate. It presents a typical viverrid appearance with its high trigonid and three-top talonid. The paraconid, protoconid and the anterior labial cingulum show steep surfaces of wear. In the part of the incision between the paraconid and protoconid cutting edge the tooth is worn down to its base. Another trace of wear, caused by the paraconus of M<sup>1</sup>, occurs in the incision between the trigonid and talonid. The paraconid cutting edge is unlike that of the protoconid only slightly labially twisted. The pointed metaconid does not quite reach the height of the paraconid cutting edge and is pushed off postero-lingually. A crest runs from its top through the notch to the protoconid top. The posterior margin of the trigonid falls down nearly vertically to the short, low talonid. Three cusps of the talonid are separated from the trigonid by a transverse groove. This transverse groove is a little labial to the middle of the tooth crossed by the anterior crest of the hypoconid. The pointed entoconid is the highest of the talonid cusps. The hypoconid and the aborally directed hypoconulid show horizontal traces of use.

Only the oval alveolus of the one-rooted M<sub>2</sub> is preserved. Like the P<sub>1</sub> alveolus it is slightly lingually displaced, and so the whole tooth row of the mandible, seen from above, forms a curve slightly convex towards the labial side.

**Relationships:** The hyaena material from Przeworno is in its size and morphology comparable with *Miohyaena montadai*. Nevertheless, as can be seen from the description, the conformity with the type-specimen of this species is not complete. However, the differences are not so serious as to justify the systematic separation.

The genus *Miohyaena* is represented by two species from which the type-species *M. certa* (MAJOR 1903) from La Grive is smaller than the *Miohyaena* from Przeworno (comp. VIRET 1951: 83). This species has a complicated history concerning its nomenclature: primarily it was published by DÉPÉRET (1892) as *Progenetta* sp. LARTET, but because it is not identical with *Mustela incerta* LARTET, its name was changed by MAJOR (1903) to *Progenetta certa* and it was described anew. The species is the type-species of the genus *Progenetta* which according to KRETZOI (1938), is not valid (comp. SCHMIDT-KITTLER

1976: 66). Instead of that KRETZOI proposed *Miohyaena* as a new name for the genus. The further development of the nomenclature of this genus will be discussed below.

The species *M. montadai* from the Upper-Astaracian of Can Mata (Hostalets de Pierola) was first reported by VILLALTA & CRUSAFONT PAIRO as an *Ictitherium* species and in 1943 described by them under that generic name. The inclusion in *Miohyaena* – primarily as a subgenus of *Progenetta* – was for the first time mentioned by BEAUMONT (1967). The final verification of the genus *Miohyaena* was given by SCHMIDT-KITTLER (1976).

In course of time two further subspecies were added to the type-subspecies: *M. montadai vallesiensis* (CRUSAFONT 1962) from the uppermost Astaracian of Can Barra and *M. montadai urgellensis* (CRUSAFONT PAIRO & GOLPE-POSSE, 1973). These subspecies hardly differ from the type-subspecies, as it has already been stated by CRUSAFONT PAIRO & PETTER (1969) in their comparison of *M. m. vallesiensis* with the type-subspecies ("Au total ces différences sont assez minimes"). If in fact *M. m. vallesiensis* shows only slightly larger dimensions than *M. m. montadai* (comp. CRUSAFONT PAIRO & GOLPE-POSSE 1973: 107) then in the case of *M. m. urgellensis* we cannot overcome the impression that this subspecies was erected only for stratigraphic purposes. According to the criteria used for the creation of that subspecies, the form from Przeworno could be described without any doubt also as a systematically separate form, but such a purely typological procedure would be, in our opinion, of little importance to the elucidation of the phylogenetic relations of these forms.

In addition to the above-mentioned localities of *M. montadai* this species is now known from other localities in Spain (GOLPE-POSSE 1974), Turkey and Austria (SCHMIDT-KITTLER 1976). In the meantime this species has been also recorded with reservation by RAZA et al. (1983) from the Siwaliks. Out of the remains from those localities, the find from Yeni Eskihsar probably does not belong to this species. The larger dimensions of the teeth, the lack of P<sub>1</sub> and the generally remarkable hyaenid differentiation of the premolar dentition speak against the assignment to this species.

Neither does the material from Przeworno correspond in all details with the type of *M. montadai*. The stronger reduction of P<sup>2</sup> and the more distinct protoconus of P<sup>4</sup> in the form from Poland should especially be mentioned here. Just this last feature occurs also in *Thalassictis* GERVAIS, 1850, a genus which was mainly described as a synonym of *Ictitherium* WAGNER, 1848 and finally redefined by SOLUNIAS (1983). In fact *Miohyaena* was also regarded by KURTÉN (1982) and DE BEAUMONT (1986) as a synonym of *Thalassictis*. SEMENOV (1989) goes even so far that, according to him *Progenetta* (= *Miohyaena*) *certa* MAJOR, 1903 is synonymous with *Thalassictis robustus* GERVAIS, 1850 from the Sarmatian of Kishinev (Moldavia). It is impossible to verify this synonymy in our study. Nevertheless, from the foregoing discussion it may be concluded that in the upper Middle-Miocene several similar but differentiated hyaenid carnivores occurred and were distributed all over Europe.

It is interesting that DE BEAUMONT (1986) records two species of *Thalassictis* from the Lower-Vallesian of Höwenegg: a smaller *T. robusta* GERVAIS and a larger *T. wongii* (ZDANSKY 1924) which is in its dimensions comparable with the material from Przeworno. Of course, it is even according to DE BEAUMONT (1986: 42) improbable that at this

locality two species of one genus similar in size should live side by side, particularly that the possibility of sex dimorphism cannot be excluded (comp. DE BEAUMONT (1986: Fig. 10). Another question arises whether the Höwenegg species may be virtually identified with the species *T. wongii* primarily recorded from China. It is possible that the material from the Siwaliks cited by RAZA et al. (1983) might essentially contribute to the solution of this question. In comparison with Przeworno the Höwenegg species has similarly differentiated premolars with less developed side cusps. But above all the M<sub>1</sub> talonid is in the Höwenegg form longer, higher and less narrowed.

The mosaic of feature combinations, partly contradictory, which occur in particular *Ictitherium* lines of the Middle-Upper-Miocene, is not unusual for an expanding group but it makes the ingenious, phylogenetic point of view considering systematic classification more difficult. Thus, the necessity of a revision of all hyaenids from the Middle and Upper-Miocene pointed out by DE BEAUMONT (1986) ought to be emphasized. Such a revision has been presented recently by SEMENOV (1989) who used in his study mainly – partly very complete – materials from the former Soviet Union. It must be proved that his classification into viverrids differentiated in the direction of hyaenids and, on the other hand, hyaenids of viverrid-type adaptation is virtually right. A study of the material from central and western Europe will be necessary to clear the complicated relations between the early hyaenid carnivores. However, such a research is not included in the scope of our study on the carnivores from Przeworno.

We do not agree with the synonymy of *Miohyaena* with *Thalassictis* but the separation of the younger members of *Thalassictis* from *Miohyaena* seems to be admissible.

The *Miohyaena* finds from Przeworno belong to the earliest records of this genus. They show that in the Upper-Middle-Miocene several hyaenid lines (*M. certa* – *M. montadai*) already existed side by side.

#### IV. CONDITIONS OF SEDIMENTATION AND EMBEDDING OF FOSSILS

Isolated bones, teeth and pieces of jaws, sometimes also complete jaws, more seldom well preserved skulls and shells of turtles or tortoises were found at Przeworno. Complete skeletons or their fairly large parts nearly never occur.

In Przeworno 1 detached teeth and bones were found in fissures several centimeters wide between blocks of rocks. There were fragments of teeth and bones of reptiles and mammals mixed up together. All pieces are very fragile, soft and crumble in fingers, commonly light-yellow coloured, whereas the enamel is perfectly well preserved, hard and blue in colour. The bone fragments become harder when they are dry.

At the main locality, Przeworno 2, there occur better preserved, brown coloured animal remains. The material is here also unsorted and unstratified. The mixed teeth and bones are also present in fissures between blocks of marble. It may be suggested that the blocks come from a collapsed cave.

It was probably a karst fissure which opened in the cave mentioned. This fissure, which connected the "upper" locality Przeworno 2 with a few meters deeper situated Przeworno 1, may have been filled up for a long time with alluvial deposits of vertebrate remains.

On account of the general lack of traces of transportation on the bones, their secondary transport over long distances should be excluded. The high number of fossils in the upper part of the main locality (Przeworno 2) and the considerably decreasing number of finds in the lower parts (as in Przeworno 1) may be explained by the fact that the funnel-shaped cave was a trap for smaller vertebrates which later were carried by water and deposited.

The scarce occurrence of the remains of micro-mammals is perhaps due to the following reasons: 1. the fragile bones may have been destroyed by chemical processes and were not preserved; 2. the scattered small remains could be overlooked in fieldwork. Unfortunately, there was no possibility to use more exact excavation methods – all attempts were unsuccessful.

The rather high number of carnivores at this locality (cf. fauna list) and numerous coprolites pose the question whether here could have been carnivores' feeding place. No observations made so far confirm this supposition. Nevertheless some traces of gnawing could be found on several bones, e.g. at the proximal end of an ulna of a suid (MF/1993/91) as well as at a metatarsus of *Euprox* sp. (MF/1994/91). These traces, however, were caused by gnawing of rodents (Plate I). No traces left by carnivores have as yet been found.

Summarizing, it may be stated that the rich paleontological material from Przeworno comes from vertebrates which simply deceased there, and that the place of death and that of embedding are in this case more or less identical.

## V. AGE OF THE FAUNAS

An opinion has hitherto been held (GŁAZEK et al. 1971, 1977) that two assemblages of vertebrate faunas of different age occur at Przeworno. The results of a fluor-chlorapatite dating as well as collagen dating by WYSOCZAŃSKI-MINKOWICZ (GŁAZEK et al. 1977) indicate an absolute age of 21.0-22.5 million years for Przeworno 1, and 14.5-16.0 million years for Przeworno 2. Thus, the stratigraphical position of Przeworno 1 should be the Karpatian (=Upper Burdigalian) and that of Przeworno 2 – the Younger Badenian (=Upper Vindobonian). This correlation corresponds with the older stratigraphical division (cf. FAHLBUSCH 1981, tab. 1).

The vertebrate assemblages of both infillings show, however, one fauna of more or less similar age. The further discussion is based on this supposition. The mammalian fauna shows nothing which would indicate the occurrence of forms older than Middle-Miocene.

*Conohyus simorreensis* (KUBIAK 1981a) which has been described by SULIMSKI (GŁAZEK et al. 1971) as *Hyotherium simorreense*, occurs in both localities. The information about the occurrence of *Hyotherium soemmeringi* at Przeworno 1 is wrong. This species and its determination are called in question even by SULIMSKI. According to KUBIAK (1981a) this specimen (1 tooth) belongs to *Conohyus simorreensis*.

*Conohyus simorreensis* is, according to CHEN (1984), a younger synonym of *Conohyus steinheimensis* (FRAAS, 1870). In her opinion, the progressive form from Steinheim is represented in Europe from the Astaracian to the Vallesian, which corresponds with the Upper-Miocene – "Tortonian/Sarmatian" in the older stratigraphical division; but acc. to



Plate I. *Pseudaelurus lorteti* GAILLARD, right mandible with C, P<sub>3</sub>-M<sub>1</sub> (MF/1990/91) from Przeworno 2 (natural size): a) buccal view, b) lingual view, c) occlusal view.

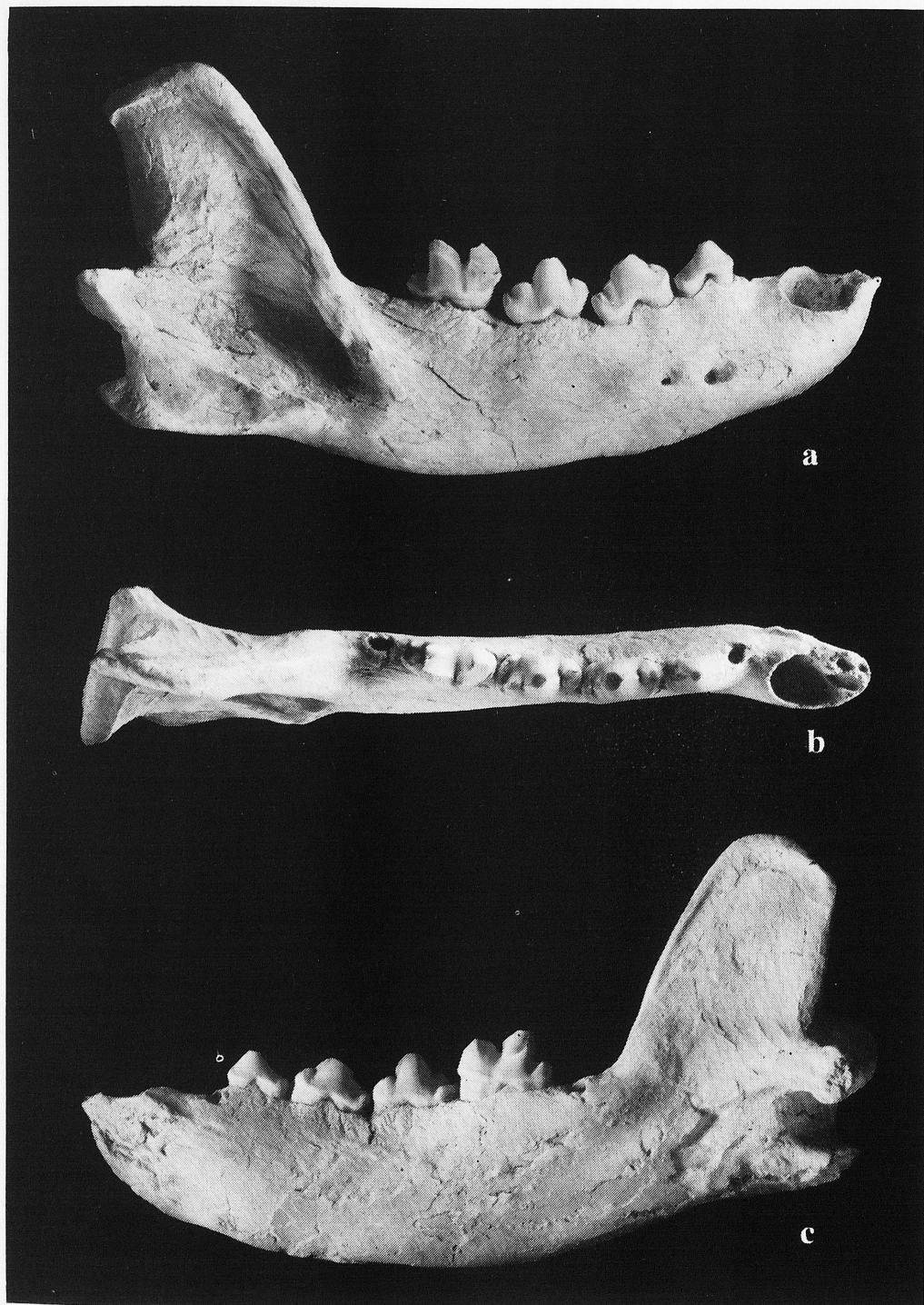


Plate II. *Miohyaena montadai* (VILLALTA & CRUSAFONT PAIRO), right mandible with P<sub>2</sub>-M<sub>1</sub> (MF/1992/91) from Przeworno 2 (ca. 0.7 of natural size): a) buccal view, b) occlusal view, c) lingual view.

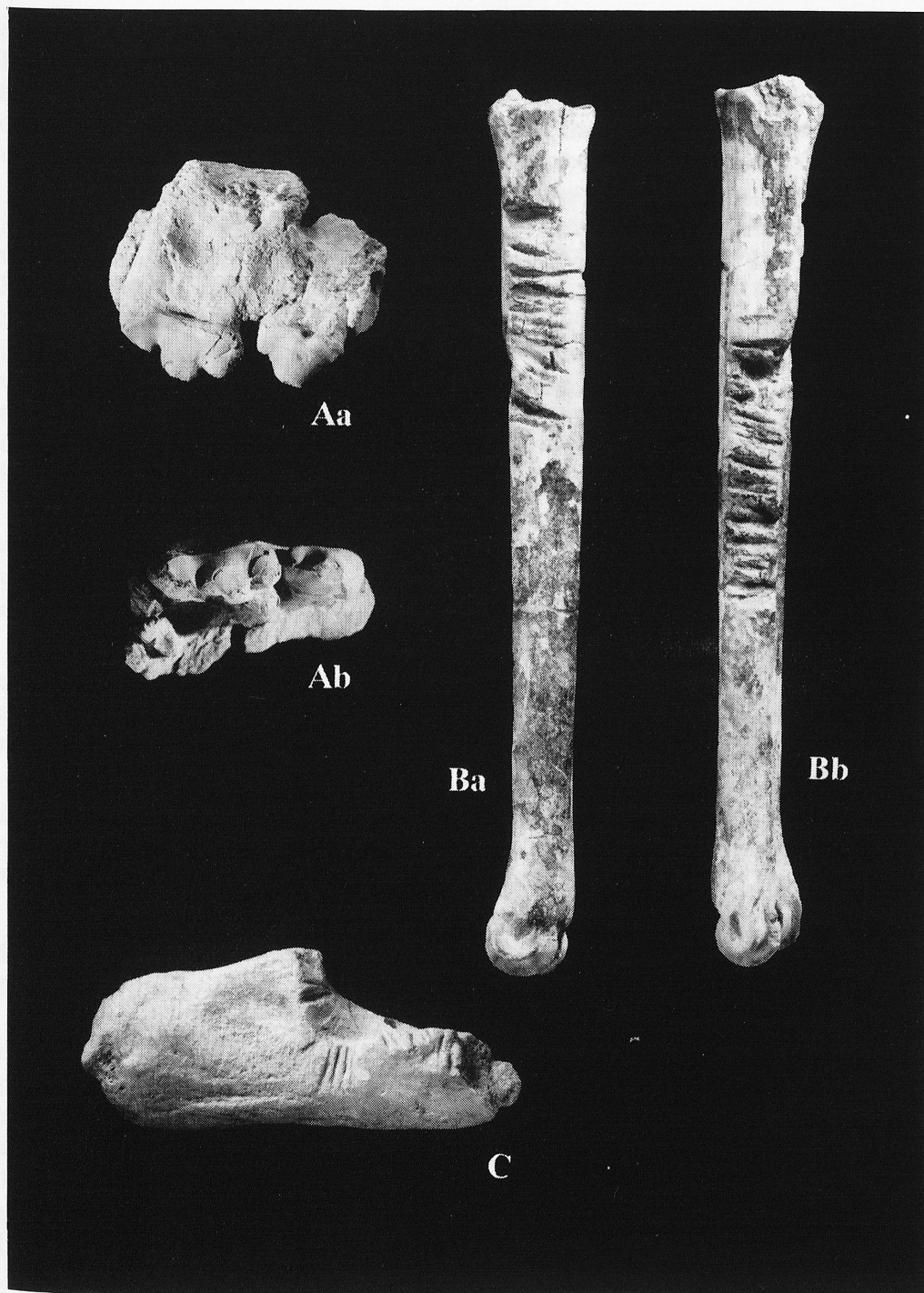


Plate III. A – *Miohyaena montadai* (VILLALTA & CRUSAFONT PAIRO): maxilla fragment with P<sup>4</sup>-M<sup>2</sup> (MF/1991/91): a) buccal view, b) lower view. B – *Euprox* sp.: metatarsus (MF/1994/91) with gnawing marks: a) lateral view, b) mesial view. C – *Suidae*: proximal part of ulna with gnawing marks (MF/1993/91). All specimens come from Przeworno 2 (ca 0.7 of natural size).

the recent stratigraphy it corresponds with the Middle-Miocene and is placed by MEIN (1975) in zone MN 7 in the mammalian zonation (cf. FAHLBUSCH 1981, tab. 1).

The occurrence of *Anchitherium aurelianense*, *Aceratherium simorreense* and *Brachypotherium brachypus* in both localities (KUBIAK 1981b) is noteworthy. The same is true of *Dorcatherium* and *Euprox*. Among the carnivores the mustelids are represented in both localities. Thus, these cannot be two faunas so extremely differentiated in age. According to RABEDER (1978) the occurrence of *Pliopithecus* and the lack of *Dryopithecus* at Przeworno 2 are even symptomatic of an age younger than Middle-Badenian. The remains of *Miophasianus* from Przeworno 2 are, in BOCHENSKI's opinion (1987), similar to those from Sansan and La Grive and therefore lie in zone MN 7. Of the same age are according to SZYNDLAR (1984) the remains of snakes.

The occurrence of *Pseudaelurus lorteti* and *Miohyaena montadai* clearly indicates Upper Vindobonian – Younger Badenian age which also leads to their classification in MN 7.

As there is no connection between the marine Miocene and Przeworno, the direct parallelization of our locality with the marine sediments of the Parathetys is impossible. Thus, the only way to the determination of the age of Przeworno must be based on the mammalian fauna. Unfortunately, no exact data on the artiodactyls (except the *Suidae* and *Tayassuidae* by KUBIAK 1981b) from Przeworno have yet been published. Therefore the possibility of its comparison with other Miocene localities like Sansan, La Grive or Göriach is still limited.

But the determination of the age as Middle-Miocene – Upper-Badenian – MN 7 seems to be right in the light of the data known so far.

It remains to point out that not all of the vertebrate remains from Przeworno need be the same age. It cannot be decided as yet whether or not age differences are also reflected in the evolutionary differences odonto-osteologically measurable in particular species.

## VI. ECOLOGICAL CONCLUSIONS

According to geologists (GŁAZEK et al. 1971, 1977) the older locality Przeworno 1 represents a subtropical swampy wood environment. These authors suggest that such a biotope reached Przeworno at the time when brown-coal sedimentation ("Lausitzer Flöz") took place further northwards.

The younger locality Przeworno 2 (acc. to those authors) had a savanna climate with distinct dry seasons.

MŁYNARSKI (1976, 1978, 1981) is of a different opinion, based on his studies of amphibians and reptiles, namely, that at Przeworno 1 such elements of dry environments as *Testudo* sp. dominated. At Przeworno 2 *Latonia* (*Discoglossidae*) and *Chelydropsis* occupied a swampy forest with larger water bodies.

Members of *Chelydropsis* are always associated with waters. At present those finds are exclusively known from river and lake sediments, e.g. from Steinheim am Albuch, Öhningen (both in Germany), Hajnačka (Czecho-Slovakia), Irimești (Roumania) (MŁY-

NARSKI 1981). According to MŁYNARSKI (1981), the occurrence of this species in Przeworno 2 indicates the presence of a great river which flowed through different biotopes e.g. swampy forests and open terrains. The reptiles found presumably their optimal life conditions in the river-arms. *Chelydropsis* probably lived permanently close to the river banks.

Among the mammals from Przeworno 1 there are also species which had their biotopes in the vicinity of waters. The castorids (KUBIAK & WOLSAN 1986) – analogously to their recent relatives – were apparently especially strongly connected with water reservoirs. Because of the common occurrence of *Conohyus simorrensis* in brown-coal beds, THENIUS (1952) and other authors consider this species also as an inhabitant of a moist region (swampy forest biotope). Therefore THENIUS (1956) distinguished two subspecies within the species *Conohyus simorrensis*, of which *C. simorrensis simorrensis* may be defined as a swampy forest form, while *C. s. steinheimensis* presumably preferred more arid habitats. The occurrence of *Conohyus simorrensis* in both localities (Przeworno 1 and 2) indicates also an arid environment.

In HEIZMANN's (1973) opinion it is true that there are reliable data allowing the assignment of single species to definite biotopes, as was made e.g. by THENIUS, but on the other hand, it should not be overlooked that those species often constitute an insufficient basis for the certain determination of a virtual biotope.

Przeworno 1 with its "mixed fauna" is a good example of that. In addition to the above-mentioned hydrophilous forms of amphibians and reptiles, "forest mammals", such as *Anchitherium* and *Pseudaelurus*, and arid forms like *Testudo* and *Euprox* are also represented.

Przeworno 2 likewise presents a "mixed fauna" where "forms of arid habitats" (e.g. *Euprox*) occur beside "swampy forest forms" (*Latonia*, *Chelydropsis*, *Conohyus*) and "forest forms" (*Pliopithecus*, *Taucanamo*, *Anchitherium*, *Dorcatherium*, *Palaeomeryx*, *Heteroprox*).

Thus, in Przeworno 1 and in Przeworno 2 we are concerned with similar "mixed faunas". The following forms occur in both localities: *Latonia*, *Anchitherium*, *Aceratherium*, *Brachypotherium*, *Conohyus*, *Dorcatherium*, *Euprox*, *Pseudaelurus*, *Mustelidae*.

Presumably in the surroundings of the locality there was a river and probably also a dam lake (river: tortoises; dam lake: castorids/beavers). The river probably ran through a plain forest. For the Miocene plain forest MAI (1981; 566) reports the oligodominance of species belonging to the genera *Liquidambar*, *Planatus*, *Carya*, *Populus*, *Salix*, *Ulmus*, and further *Acer*, *Alnus*, *Celtis* (*Celtis*-stones in the stomach of a tortoise! – cf. MŁYNARSKI 1980), *Forestiera*, *Fraxinus*, *Gleditsia*, *Itea*, *Juglans*, *Pterocarya*, *Quercus*, *Staphylea*, sometimes with *Taxodium* or *Glyptostrobus*, often with a few evergreens such as liana (*Pliopithecus*!) *Menispermum*, *Smilax*, *Parthocissus*, *Vitis*.

Plain forests occurred, according to MAI (1981), as early as in the Upper Cretaceous, in the Middle-Palaeocene and from the Lower-Oligocene to the Lower-Pleistocene. The fossil plain forest is compared to the recent oak-ashtree-hickory plain forest, the elm-silver maple forests of the atlantic Northamerica, oak-hickory forest, elm-ash forest, sycamore forests and liquidambar forests of the plains in the Tierra Templada of Central America,

river-plain forests in south-west Anatolia, *Plantanon orientalis* of the East-Mediterranean, *Fraxineto-Ulmetum* of south-east Europe.

In connection with the foregoing we ought to mention here the locality Przeworno 3, which, acc. to GALEWSKI & GŁAZEK (1973), is presumably of Upper-Miocene – Sarmatian age. Silicified beetles (*Dytiscidae*) (aquatic insects constituting food for a tortoise from the littoral zone (= *Chelydropsis*!) – cf. MŁYNARSKI 1980) occur in a part of the cave. Przeworno 3, unlike Przeworno 1 and 2, provided also remains of plants. On the basis of a pollen analysis (SADOWSKA in GŁAZEK et al. 1971: 484-485) "it may be stated that pollens are of the Tertiary and not older than the Middle Miocene age". The authoress presents some elements of a swampy forest (high percentage of *Taxodiaceae-Cupressaceae*, and pollen of *Salix*, *Alnus* and *Liquidambar* as well as a dry forest (*Quercus*, *Ulmus*, *Fagus*, *Pterocarya*, *Ostrya* and others like e.g. *Celtis*). All of these plants occur in plain forest (cf. MAI 1981). Because of the contemporaneous stratigraphical division, in which the Sarmatian practically belongs to the Middle-Miocene, and the Badenian-Sarmatian-boundary comprehends zone MN 7, it is probably possible to speak here about a relatively narrow temporary connection of both localities, Przeworno 2 and Przeworno 3. The supposed neighbourhood of two so contrasting habitats as forests and open plains is similar to a comparable interpretation for the locality Steinheim, where the adjacent surface of the Alb Mts shows scarcer vegetation than does the Steinheimer-Lake-surrounding forest (HEIZMANN 1973). Against the existence of such a "savanna-landscape" at Przeworno – of course similar to that in Steinheim – speaks the lack of antelopes in the fauna. In the meantime on the basis of his new data concerning the plants from Steinheim GREGOR (1983) finds the vegetation around the lake, i.e. "the dense mesophytic deciduous forest of paleotropical-arctotertiary aspect" to be closer to reality than a savanna.

The surface of the Strzelin highland (Wzgórza Strzelińskie), owing to the inclination of the rocks at Przeworno to change into karst forms, may have been drier than the direct surroundings of the locality. The possible existence of a river and a lake points to a relatively high ground water table, which may have been the basis for richer vegetation in those times. The vegetation around the river and the lake was presumably, owing to higher moisture, very exuberant, because north of Przeworno the density of vegetation and the sedimentation conditions were sufficient to build brown-coal-beds (Lausitzer Flöz).

## REFERENCES

- ANTUNES M. T., GINSBURG L., MEIN P. 1983. Mammifères miocènes de Azambujeira, niveau inférieur (Santarem, Portugal). *Ciencias da Terra*, Lisboa, 7: 161-168.
- BACHMAYER F., MŁYNARSKI M. 1977. Bemerkungen über die fossilen Ophisaurus-Reste (*Reptilia, Anguinae*) von Österreich und Polen. *Sitz.-Ber. Österr. Akad. Wiss., Math.-naturwiss. Kl., Abt. I*, Wien, 186: 285-299.
- DE BEAUMONT G. 1967. Observations sur les *Herpestinae* (*Viverridae, Carnivora*) de l'Oligocène supérieur avec quelques remarques sur des *Hyaenidae* du Néogène. *Arch. Sci. Genève*, 20: 79-108.
- DE BEAUMONT G. 1986. Les carnivores (Mammifères) du Néogène de Höwenegg/Hegau, Baden-Württemberg. *Carolinea*, Karlsruhe, 44: 33-45.
- BERGOUNIOUX F. M., CROUZEL F. 1958. Les mastodontes d'Espagne. *Estud. geol., Madrid*, 14, 40: 223-365.

- BOCHEŃSKI Z. 1987. *Miophasianus medius* (MILNE EDWARDS, 1869) from Przeworno (SW Poland) and some general remarks on the genus *Miophasianus*. Acta zool. cracov., 30: 71-80.
- CHEN G. 1984. *Suidae* and *Tayassuidae* (*Artiodactyla*, *Mammalia*) from the Miocene of Steinheim a. A. (Germany). Palaeontographica A, Stuttgart, 184: 79-93.
- CROUZEL F., DURANTHON F., GINSBURG L. 1988. Découverte d'un riche gisement à petits et grands mammifères d'âge orléanien dans le département du Gers (France). C. R. Acad. Sci. Paris, sér. 2, 307: 101-104.
- CRUSAFONT PAIRO M. 1962. Las especies transientes en la paleomastologia: du importancia en Espana. Notas Comun. Inst. Geol. Min. Espana, Madrid, 65: 49-59.
- CRUSAFONT PAIRO M., GOLPE-POSSE J. M. 1973. Nuevos hallazgos de *Progenetta montadai* en el Mioceno de Cataluna. Bol. Geol. Min. Inst. Geol. Espana, Madrid, 84: 1-9.
- CRUSAFONT PAIRO M., PETTER G. 1969. Contribution à l'étude des *Hyaenidae*. La sous-famille des *Ictitheriinae*. An. Paléont. (Vért.), Paris, 55: 89-127.
- DEPERET CH. 1892. La faune de mammifères miocènes de La Grive-Saint-Alban et quelques autres localités du bassin du Rhône. Arch. Mus. Hist. Nat., Lyon, 5: 1-93.
- FAHLBUSCH V. 1981. Miozän und Pliocän – Was is das? Zur Gliederung des Jungtertiärs in Süddeutschland. Mitt. Bayer. Staatsslg. Paläont. Hist. Geol., München, 21: 121-127.
- FAHLBUSCH V., GALL H., SCHMIDT-KITTLER N. 1974. Die obermiozäne Fossil-Lagerstätte Sandelzhausen. 10. Die Grabungen 1970-73. Beiträge zur Sedimentologie und Fauna. Mitt. Bayer. Staatsslg. Paläont. Hist. Geol., München, 14: 103-128.
- FRANZEN J. L. 1981. Eine turoloische (obermiozäne) Waldfauna aus Rheinhessen. Alzeyer Geschichtsb., Alzey, 16: 192-202.
- GAILLARD C. 1899. Mammifères miocènes nouveaux ou peu connus da La Grive-Saint-Alban (Isère). Arch. Mus. Hist. Nat. Lyon, 7: 1-77.
- GALEWSKI K., GLĄZEK J. 1973. An unusual occurrence of the *Dytiscidae* (*Coleoptera*) in the siliceous flowstone of the Upper Miocene cave at Przeworno, Lower Silesia, Poland. Acta geol. pol., Warszawa, 23: 445-461.
- GALEWSKI K., GLĄZEK J. 1977. Upper Miocene *Dytiscidae* (*Coleoptera*) from Przeworno (Lower Silesia) and the problem of *Dytiscidae* evolution. Bull. Acad. Pol. Sci., Ser. sci. biol., Cl. II, Warszawa, 25: 781-789.
- GALEWSKI K., GLĄZEK J., OBERC J., SULIMSKI A. 1973. Miocene vertebrates and beetles in fossil karst at Przeworno (Lower Silesia, South-Western Poland). VI. Congr. Internat. Spéléologie, Olomouc, Abstr.: 157.
- GINSBURG L. 1961. La faune des carnivores miocènes de Sansan (Gers). Mém. Mus. natn. Hist. nat., N. S. C., Paris, 9: 1-190.
- GINSBURG L. 1980. Paléogéographie et âge de la mer des faluns d'après les Mammifères. Mém. Soc. Et. Sci. Anjou, Angers, 4: 69-77.
- GINSBURG L. 1983. Sur les modalités d'évolution du genre néogène *Pseudaelurus* Gervais (*Felidae*, *Carnivora*, *Mammalia*). Coll. Int. CNRS, Paris, 230: 131-136.
- GINSBURG L., BULOT Ch. 1982. Les carnivores du miocène de Bézian près de la Romieu (Gers, France). Proc. Kon. Ned. Akad. Wet., Amsterdam, B 85: 53-76.
- GINSBURG L., TASSY P. 1977. Les nouveaux gisements à Mastodontes du Vindobonien moyen de Simorre (Gers). C. R. somm. Soc. géol. France, Paris, 1977: 24-26.
- GLĄZEK J., GALEWSKI K., WYSOCZAŃSKI-MINKOWICZ T. 1977. Nowe dane o krasie kopalnym w Przewornie. Kras i Speleologia, Katowice, 1, X: 81-88.
- GLĄZEK J., OBERC J., SULIMSKI A. 1971. Miocene vertebrate faunas from Przeworno (Lower Silesia) and their geological setting. Acta geol. pol., Warszawa, 21: 473-516.
- GLĄZEK J., OBERC J., SULIMSKI A. 1972. Discovery of the Miocene vertebrate faunas at Przeworno, Lower Silesia. Przegl. geol., Warszawa, 20: 65-70.
- GOLPE-POSSE J. M. 1974. Faunas de yacimientos con *Suiformes* en el Terciario espanol. Paleont. Evol., Sabadell, 8: 1-87.

- GREGOR H.-J. 1983. Die miozäne Blatt- und Fruchtfloren von Steinheim am Albuch (Schwäbische Alb). *Documenta naturae*, Stuttgart-München, **10**: 1-45.
- HEIZMANN E. P. J. 1973. Die Carnivoren des Steinheimer Beckens. B. *Ursidae*, *Felidae*, *Viverridae* sowie Ergänzungen und Nachträge zu den *Mustelidae*. *Palaeontographica*, A, Stuttgart, **122**: 1-95.
- HOFMANN A. 1893. Die Fauna von Göriach. Abh. k. k. geol. Reichsanst., Wien, **16**: 1-87.
- KOROTKIEWICH E. L., SULIMSKI A. 1990. A new Chalicotherian finding from the Miocene karst in Poland (*Mammalia*, Badenian). *Acta paleont. pol.*, Warszawa, **35**: 91-96.
- KOWALSKI K., ZAPFE H. 1974. *Pliopithecus antiquus* (BLAINVILLE, 1839) (*Primates*, *Mammalia*) from the Miocene of Przeworno in Silesia (Poland). *Acta zool. cracov.*, **19**: 19-30.
- KRETZOI N. 1938. Die Raubtiere von Gombaszög nebst einer Übersicht der Gesamtf fauna. *Ann. Mus. nat. Hungar.*, Budapest, **31**: 88-137.
- KUBIAK H. 1975. *Gomphotherium angustidens* (CUVIER, 1806) (*Proboscidea*, *Mammalia*) from the Miocene of Przeworno (Silesia, Poland). *Acta zool. cracov.*, **20**: 469-480.
- KUBIAK H. 1978. Upper Miocene mammals of Poland. II. *Congr. Theriol. internat.*, Brno, Abstr.: 123.
- KUBIAK H. 1981a. *Suidae* and *Tayassuidae* (*Artiodactyla*, *Mammalia*) from the Miocene of Przeworno in Lower Silesia. *Acta geol. pol.*, Warszawa, **31**: 59-70.
- KUBIAK H. 1981b. *Equidae* and *Rhinocerotidae* (*Perissodactyla*, *Mammalia*) from the Miocene of Przeworno in Lower Silesia. *Acta geol. pol.*, Warszawa, **31**: 71-79.
- KUBIAK H. 1982. Die miozänen Wirbeltiere von Przeworno (Dolny Śląsk, Polen). *Zr. geol. Wiss.*, Berlin, **10**: 997-1007.
- KUBIAK H. 1987. Przeworno – fauna środkowego miocenu. *Przewodnik Wycieczek*, XI Konfer. Paleontol., Wrocław: 18-21.
- KUBIAK H., WOLSAN M. 1986. *Castoridae* (*Rodentia*, *Mammalia*) from the Miocene of Przeworno in Silesia (Poland). *Investigations on Beavers*, Berne, **5**: 155-160.
- KURTEN B. 1982. Status of the fossil Hyaenids *Ictitherium viverrinum* and *Thalassictis robusta* (*Mammalia*). *Z. geol. Wiss.*, Berlin, **10**: 1009-1018.
- MAI D. H. 1981. Entwicklung und klimatische Differenzierung der Laubwaldflora Mitteleuropas im Tertiär. *Flora*, Berlin, **171**: 525-582.
- MAJOR C. I. F. 1903. New *Carnivora* from the Middle Miocene of La Grive-Saint-Alban, Isère, France. *Geol. Mag.*, London, **10**: 534-538.
- MEIN P. M. 1958. Les mammifères de la faune sidérolithique de Vieux-Collonges. *Nouv. Arch. Mus. Hist. nat. Lyon*, **5**: 1-22.
- MEIN P. M. 1975. Résultats du groupe de travail des Vertébrés. In: Report on Activity of the R. C. M. N. S. Working Group (1971-1975) Bratislava: 78-81.
- MLYNARSKI M. 1976. *Discoglossus giganteus* WETTSTEIN-WESTERHEIM, 1955 (*Discoglossidae*, *Anura*) from the Miocene of Przeworno in Silesia (Poland). *Acta zool. cracov.*, **21**: 1-12.
- MLYNARSKI M. 1978. Tortoises (*Emydidae* and *Testudinidae*) from the Miocene of Przeworno in Silesia (Poland). *Acta zool. cracov.*, **23**: 79-92.
- MLYNARSKI M. 1980. Die tertiären Wirbeltiere des Steinheimer Beckens, II. Die Schildkröten des Steinheimer Beckens. *Palaeontographica*, Stuttgart, Suppl. VIII, II, B: 1-35.
- MLYNARSKI M. 1981. *Chelydrosis murchisoni* (BELL, 1832) (*Testudines*, *Chelydridae*) from the Miocene of Przeworno in Silesia (Poland). *Acta zool. cracov.*, **25**: 219-226.
- OBERC J. 1966. Geologia krystaliniku Wzgórz Strzelińskich. *Studia geol. pol.* Warszawa, **20**: 1-187.
- OBERC J., DYJOR S. 1969. Uskok sudecki brzeżny. *Inst. geol., Biul.*, Warszawa, **236**: 41-142.
- PETTER G. 1976. Etude d'un nouvel ensemble de petits carnivores du Miocène d'Espagne. *Géol. médit.*, Gap, **3**: 135-154.
- QIU Z., GU Y. 1986. The Middle Miocene vertebrate fauna from Xiacaowan, Sihong County, Jiangsu Province. 3. Two species of fossil carnivores: *Semigenetta* and *Pseudaelurus*. *Vert. palasiatica*, Beijing, **24**: 20-31.

- RABEDER G. 1978. Die Säugetiere des Badenien. In: A. PAPP, I. CÍCHA, J. SENES, F. STEININGER: Chronostratigraphie und Neostatotypen, Miozän M<sub>4</sub> Badenian. Veda, Bratislava: 467-480.
- RAZA S., BARRY J. C., PILBEAM D. R., ROSE M. D., SHAH S. M. I., WARD C. S. 1983. New hominoid primates from the Middle Miocene Chinji Formation, Potwar Plateau, Pakistan. *Nature*, London, **306**: 52-54.
- SANCHIZ F. B., MEYNARSKI M. 1979. Remarks on the fossil Anurans from the Polish Neogene. *Acta zool. cracov.* **24**: 153-174.
- SCHMIDT-KITTLER N. 1976. Raubtiere aus dem Jungtertiär Kleinasien. *Palaeontographica*, Abt. A, Stuttgart, **155**: 1-131.
- SEMOV J. A. 1989. Iktiterii i morfologičeski shodnye hyeny neogena SSSR. (Ictitheria and morphologically similar hyaenas from the Neogene of the USSR). *Naukova Dumka*, Kiev, 180 pp.
- SOLUNIAS N. 1983. The Turolian fauna from the Island of Samos, Greece. With special emphasis on the Hyaenids and the Bovids. *Contr. vert. Evol.*, Basel, **6**: I-XVI + 1-232.
- SZYNDLAR Z. 1984. Fossil snakes from Poland. *Acta zool. cracov.* **28**: 3-156.
- THENIUS E. 1952. Die Säugetierfauna aus dem Torton von Neudorf an der March (CSR). *N. Jb. Geol. u. Paläont., Abh.*, Stuttgart, **96**: 27-136.
- THENIUS E. 1956. Die Suiden und Tayassuiden des steirischen Tertiärs. Beiträge zur Kenntnis der Säugetierreste des steirischen Tertiärs VIII. Sitz.-Ber. österr. Akad. Wiss. Math.-naturwiss. Kl., Abt. I, Wien, **165**: 337-382.
- VILLALTA COMELLA J. F., CRUSAFONT PAIRO M. 1943. Los vertebrados del Mioceno continental de la cuenca Vallés-Panadés (Provincia de Barcelona), I. Insectívoros. - II. Carnívoros. *Bol. Inst. Geol. Min. España*, Madrid, **56**: 147-336.
- VIRET J. 1951. Catalogue raisonné de la faune des mammifères de La Grive-Saint-Alban (Isère) I: Chiroptères, Carnivores, Edentés pholidotes. *Nouv. Arch. Mus. Hist. nat. Lyon*, **3**: 1-104.
- ZDARSKY A. 1909. Die miocäne Säugetierfauna von Leoben. *Jb. k. k. geol. Reichsanst., Wien*, **59**: 245-288.

