

## A contribution to the origin of *Allophaiomys* (Arvicolidae, Rodentia) in Central Europe: the relationship between *Mimomys* and *Allophaiomys* from Kamyk (Poland)

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Abstract. The morphology of  $M_1$  and  $M^3$  of *Allophaiomys deucalion* and *Mimomys tornensis* from Kamyk (Poland) was studied using canonical discriminant analysis. The data obtained have confirmed the specific distinctness of these forms. It is doubtful whether the European *M. tornensis* is the direct ancestor of *Allophaiomys*. The appearance of the *Allophaiomys deucalion/pliocaenicus* group in Central Europe is presumably due to immigration, most probably from the Ukraine.

Key words: *Allophaiomys*, Early Pleistocene, taxonomy.

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### I. INTRODUCTION

It is generally assumed that *Allophaiomys* KORMOS, 1933, an arvicolid form without roots and the direct ancestor of *Microtus* SCHRANK, 1798, derived from a small rooted species of *Mimomys* FORSYTH MAJOR, 1902. The place and time of this event is still controversial. This problem became more complicated when new paleontological data confirmed the hypothesis that instead of one widespread species named *Allophaiomys pliocaenicus* KORMOS, 1933, a group of sibling species had existed in the Palaearctic, especially in the Mediterranean region (AGUSTÍ 1991).

All authors are of the opinion that in Central Europe only two species – *Allophaiomys deucalion* KRETZOI, 1969 and *A. pliocaenicus* [sometimes treated as subspecies of *A. pliocaenicus* (cf. FEJFAR & HORÁČEK 1983)] – were present in the Early Pleistocene. Their appearance in this region is a matter of discussion. According to one suggestion, the *Allophaiomys pliocaenicus* group (including *A. deucalion*) is an European species, while an opposing hypothesis indicates its Asiatic origin. The first point of view was already held by KORMOS (1933) who treated *Mimomys pusillus* (MÉHELY, 1914) as the ancestor of *Allophaiomys*. This affinity must be rejected because of the very distinct structure of  $M^2$  and  $M^3$  in the two forms. CHALINE (1972: 88) supposed that the ancestral form of *Allophaiomys* could be found among *Mimomys* from Kamyk, which he named *Mimomys lagurodontoides* SHEVCHENKO, 1965. This, however, appears to be a junior synonym of *Borsodia hungarica* (KORMOS, 1938) (see FEJFAR & HORÁČEK 1983). The latter taxon is very scarce in Kamyk (NADACHOWSKI 1990) and most probably CHALINE had in mind *Mimomys tornensis* (JÁNOSSY & VAN DER MEULEN, 1975), which is the most common species of the genus

in Kamyk. RABEDER (1986) studied material from Schernfeld and came to the conclusion that *Mimomys tornensis* is the most probable ancestor of *Allophaiomys*.

An opposing hypothesis suggesting Asiatic affinities for *Allophaiomys* has been formulated by many authors, but in most cases with reservations (e. g., GROMOV & POLYAKOV 1977; FEJFAR & HORÁČEK 1983).

To resolve these problems, special attention should be paid to localities of Early Pleistocene age where small *Mimomys* species (of the *Mimomys tornensis-blanci* group) occur together with *Allophaiomys*.

The fossil rodent assemblage from Kamyk (Poland) represents such a typical Early Pleistocene association with co-occurrence of *Allophaiomys* and small *Mimomys* species.

A c k n o w l e d g m e n t s. We are much indebted to Dr P. BRUNET-LECOMTE (Dijon) for discussions on the statistical analysis of the data.

## II. MATERIAL

The samples of *Allophaiomys* and *Mimomys tornensis* from Kamyk were compared with each other and, as a control group, with the *Allophaiomys* population from Żabia Cave (Poland). In the analyses,  $M_1$  and  $M^3$  of both forms were used (Table I).

Table I

Measurements of  $M_1$  and  $M^3$  for *Allophaiomys* and *Mimomys tornensis* from Kamyk and Żabia Cave

$M_1$	L (length)			A/L		
	N	Observed range	Mean $\pm$ SD	N	Observed range	Mean $\pm$ SD
<i>Allophaiomys deucalion</i> , Kamyk	87	2.28-3.28	2.74 $\pm$ 0.19	85	32.8-43.7	39.9 $\pm$ 2.0
<i>Mimomys tornensis</i> , Kamyk	51	2.40-3.08	2.69 $\pm$ 0.13	51	26.2-40.4	37.0 $\pm$ 2.8
<i>Allophaiomys deucalion</i> , Żabia Cave	44	2.44-3.02	2.70 $\pm$ 0.14	44	35.8-45.7	41.5 $\pm$ 1.8
$M^3$	L (length)			P/L		
	N	Observed range	Mean $\pm$ SD	N	Observed range	Mean $\pm$ SD
<i>Allophaiomys deucalion</i> , Kamyk	67	1.44-2.04	1.76 $\pm$ 0.13	67	46.5-59.8	52.9 $\pm$ 2.8
<i>Mimomys tornensis</i> , Kamyk	38	1.54-2.08	1.73 $\pm$ 0.11	38	37.2-55.5	49.7 $\pm$ 3.2
<i>Allophaiomys deucalion</i> , Żabia Cave	14	1.68-2.04	1.84 $\pm$ 0.12	14	52.2-60.0	55.1 $\pm$ 2.1

The rodent fauna of Kamyk, described in preliminary fashion by KOWALSKI (1960), consists of 17 species (NADACHOWSKI 1990) with a distinct predominance of *Allophaiomys* and different *Mimomys* species. The proportions (number of  $M_1$ ) of the principal species of rodents are as follows: *Allophaiomys* (87), *Mimomys tornensis* (137), *M. ostramosensis* (JÁNOSSY & VAN DER MEULEN, 1975) (7), *M. pusillus* (36), *M. pitymyoides* (JÁNOSSY & VAN DER MEULEN, 1975) (121) and *M. reidi* HINTON, 1910 (13). The fauna is of lowermost Biharian age (NADACHOWSKI 1990).

The composition of the Żabia Cave fauna, although from several layers (BOSÁK et al. 1982), is rather homogenous and represents a relatively short time span in the lower Biharian. It is slightly younger than the fauna from Kamyk (NADACHOWSKI 1990). The fauna consists of 15-17 rodent taxa, differing slightly between the layers (BOSÁK et al. 1982; NADACHOWSKI 1990). Probably only one species each of *Mimomys* (*M. pusillus*) and *Allophaiomys* are present in this locality, although BOSÁK et al. (1982) also listed *M. cf. savini* HINTON, 1910 from this assemblage.

## III. METHODS

Some 23 parameters are defined on the occlusal surface of  $M_1$  (following BRUNET-LECOMTE 1990), but due to the simple pattern of the tooth only 15 measurements were taken (measurements 1-6, 7, 9, 11, 13, 15, 17, 19, 21, 22). (Fig. 1). For  $M^3$  the original scheme of measurements, corresponding to that used for  $M_1$ , was introduced and the same 15 parameters were used in the analyses (Fig. 1). Samples were analyzed by canonical discriminant analysis (using STATISTICA for Windows) and the results projected on the first two canonical axes. Distances between populations were expressed by Mahalanobis  $d^2$ . Affinities among the samples were also expressed by two parameters following VAN DER MEULEN (1973), the total length of  $M_1$  and  $M^3$  ( $L$  = measure 6) and the relative length of the anteroconid complex in  $M_1$  ( $A/L$  = (measure 6 - measure 3)/measure 6) and posterocone complex in  $M^3$  ( $P/L$ ). The relative enamel thickness (SDQ) was also analyzed according to procedures proposed by HEINRICH (1982, 1990).

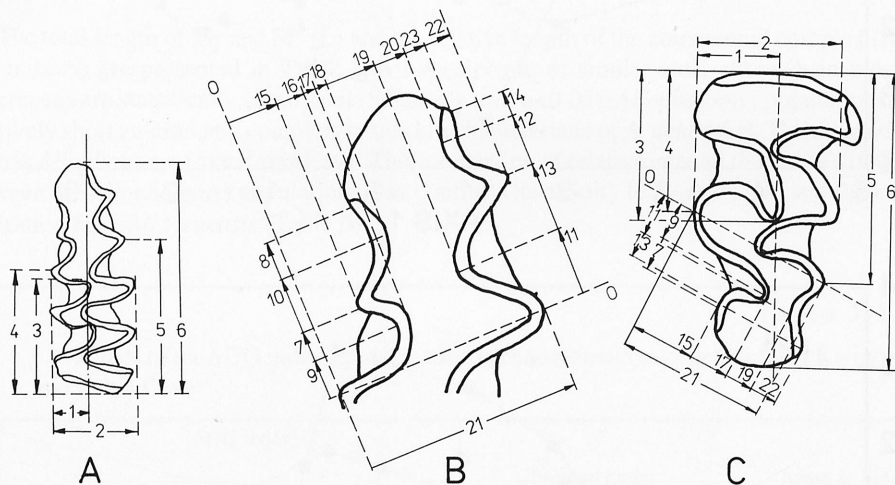


Fig. 1. Measurement methods used for  $M_1$  (A, B) and  $M^3$  (C).

## IV. RESULTS

In the case of  $M_1$ , the first three axes of the discriminant analyses express 32%, 26% and 13% of the interpopulation variance, respectively. Fig. 2 shows the  $M_1$  specimen distribution of two *Allophaiomys* and *M. tornensis* populations in the plane of the first two canonical axes. Axis 1 clearly separates *Allophaiomys* from Žabia Cave from *M. tornensis* from Kamyk. Unrooted specimens from Kamyk treated as *Allophaiomys* occupy an intermediate position; about 30% of the specimens lie on the side of *M. tornensis*. The distribution of specimens along axis 2 does not separate the populations clearly, although the centroids of *Allophaiomys* and *Mimomys* from Kamyk lie in different parts of the plane (Table II).

A similar picture is observed in the distribution pattern of  $M^3$  specimens (Fig. 2). The first three axes express 31 %, 18% and 9% of the interpopulation variance, respectively. Axis 1 separates *Allophaiomys* from Žabia Cave from *M. tornensis* from Kamyk. As in the case of  $M_1$ , about 28% of  $M^3$  *Allophaiomys* specimens from the Kamyk sample lie on the side of *M. tornensis*. However, axis 2 better separates the centroids of *Allophaiomys* and *Mimomys* from Kamyk than was the case with  $M_1$  (Table II).

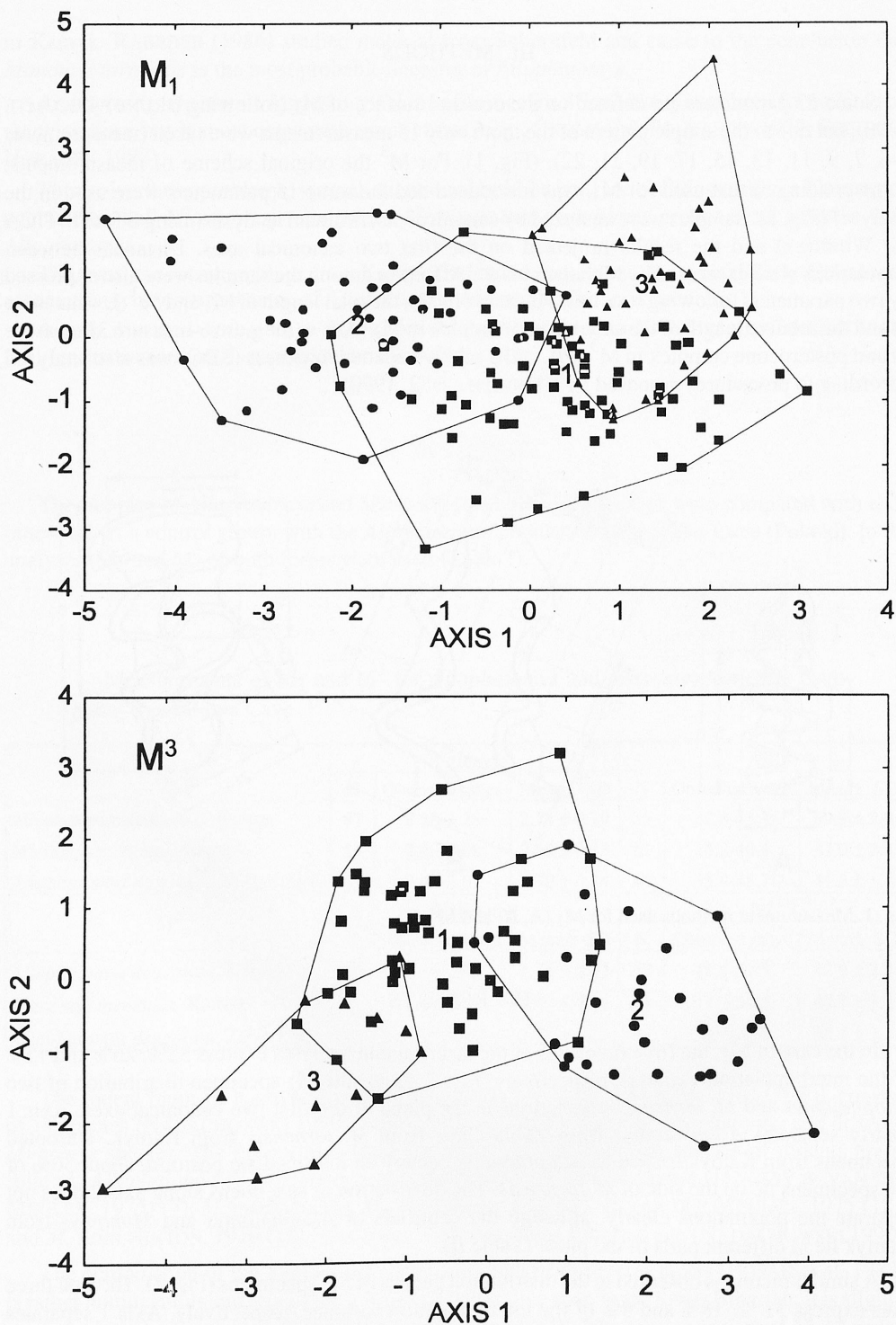


Fig. 2. Projection of  $M_1$  (upper figure) and  $M^3$  (lower figure) specimens of *A. deucalion* from Kamyk (■), *M. tornensis* from Kamyk (●) and *A. deucalion* from Żabia Cave (▲) on the first two canonical axes. Numbers indicate the positions of the centroids.



Table II

Parameters of centroid distributions on the first two canonical axes

Species	M <sub>1</sub>	
	Axis 1	Axis 2
<i>Allophaiomys deucalion</i> , Kamyk	0.413	-0.600
<i>Mimomys tornensis</i> , Kamyk	-1.891	0.287
<i>Allophaiomys deucalion</i> , Žabia Cave	1.337	0.797
Species	M <sup>3</sup>	
	Axis 1	Axis 2
<i>Allophaiomys deucalion</i> , Kamyk	0.598	0.566
<i>Mimomys tornensis</i> , Kamyk	1.906	-0.364
<i>Allophaiomys deucalion</i> , Žabia Cave	-2.153	-1.398

The total length of M<sub>1</sub> and M<sup>3</sup> (L) and the relative length of the anteroconid complex (A/L and P/L indices) are presented in Table I. All species are of similar size, although in most cases differences are statistically significant (Scheffé's test,  $p < 0.05$ ). *Allophaiomys* populations show a relatively short anteroconid complex, which is a characteristic of *A. deucalion*. The most advanced form is *Allophaiomys* from Žabia Cave. The comparison of relative enamel thickness (SDQ index) between the *Allophaiomys* populations also confirms its affinity to *A. deucalion* and their distinct separation from *M. tornensis* (Table III).

Table III

Values of the SDQ index for *Allophaiomys* and *Mimomys tornensis* from Kamyk and Žabia Cave

Species \ SDQ index	N	Observed range	Mean $\pm$ SD
<i>Allophaiomys deucalion</i> , Kamyk	41	81.5-121.4	99.2 $\pm$ 10.5
<i>Mimomys tornensis</i> , Kamyk	35	103.1-179.4	138.6 $\pm$ 21.8
<i>Allophaiomys deucalion</i> , Žabia Cave	26	83.3-123.3	102.0 $\pm$ 12.8

#### IV. DISCUSSION

Around the Pliocene/Pleistocene boundary arvicolids in Eurasia underwent significant evolutionary changes, most importantly in the appearance of evergrowing molars. Among the representatives of the Arvicolini of that time it has been suggested that only *Allophaiomys* shows this innovation. The recent discoveries of rootless *Mimomys* species from Spain bring this opinion into question (AGUSTÍ et al. 1993) and seem to confirm the supposition that perhaps rootlessness appeared independently in different species of *Mimomys*.

Leaving evolution in the Mediterranean region aside, the potential candidate for *Allophaiomys* ancestry in Central Europe is *Mimomys tornensis* (RABEDER 1986). General analysis of the characters of M<sub>1</sub> and M<sup>3</sup> shows that a simple division of the samples based on whether the molar is rooted or rootless is in some cases not sufficient for determination and separation of *M. tornensis* from *Allophaiomys* in the material from Kamyk. A few specimens (ca. 5%) are identical as far as the shape of the grinding surface is concerned and it is difficult to decide if they belong to rootless

*Mimomys* or to *Allophaiomys*. An analysis of enamel thickness confirms that they are simply rootless molars of *M. tornensis*. In spite of some overlap, *M. tornensis* and *A. deucalion* from Kamyk cannot be treated as conspecific.

A similar situation is present in some Central European localities, especially in Koliniany, Mokrá, Včelare 3B/1 (FEJFAR & HORÁČEK 1983), Villány 5 (VAN DER MEULEN 1974) and Schernfeld (RABEDER 1986; CARLS & RABEDER 1988), where both *M. tornensis* and *Allophaiomys* occur. However, their relative abundances differ. In Schernfeld 20% of the specimens are rootless and according to RABEDER (1986) belong to rootless *M. tornensis*. CARLS & RABEDER (1988) argue that the same situation exists in Villány 5, the type locality of *A. deucalion*, and that probably *A. deucalion* is not the valid name due to conspecificity with *M. tornensis*. Our data show that they are distinct species that probably occurred sympatrically in Central Europe during the Early Pleistocene. On the basis of the analyses presented the specific distinctness of the two forms becomes more probable, irrespective of the fact that some rootless specimens belong to *M. tornensis*.

Accordingly, it is suggested that *Allophaiomys deucalion* in Central Europe is an immigrant – most probably from Ukraine. It is interesting to note that in southern Ukraine, *M. tornensis* did not occur at all, while the *A. deucalion/pliocaenicus* group was very common during the Early Pleistocene (REKOVETS 1994; REKOVETS & NADACHOWSKI in press). The nearest eastern localities with forms similar to *M. tornensis* are from Kazakhstan under the name *Mimomys haplodentatus* SAVINOV & TJUTKOVA, 1987 (A. TESAKOV, personal communication).

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