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On the phylogeny of the genus *Acomys* (Mammalia: Rodentia)

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Abstract

Studied the phylogenetic relationships of the genus *Acomys* (represented by *A. minous*) to other rodent genera of the families Muridae and Arvicolidae (represented by *Mus domesticus*, *Rattus norvegicus*, *Apodemus flavicollis*, and *Microtus (Terricola) thomasi*, respectively). A total of 51 adult individuals of both sexes were used to determine the albumin differentiation by means of the microcomplement fixation test (MC'F). The immunological distances of *Acomys* from the murid taxa were found to be greater than that of the *Microtus (T.) thomasi* to the murid species tested. This means that the *Acomys* evolutionary lineage splitted off earlier than the appearance of the common ancestor of murids and arvicolid, at a time of 22–27 million years before present. Consequently, although the morphological and karyological data have suggested so far that the taxonomic position of *Acomys* is within the family Muridae, our immunological results indicate that the systematics of this genus should be reconsidered.

Introduction

The spiny mouse of Crete is a little known rodent of the Greek fauna the taxonomic position of which (at specific and subspecific level) is a matter of controversy since its first description. A review of this controversy is presented by TRICHAS (1988).

Accepting the more recent opinions on the systematics of this taxon (MATTHEY 1963; DIETERLEN 1978) we consider it as a full species, *Acomys minous*, endemic of Crete as it was proposed at first by BATE (1913). Furthermore, the taxonomic status of the genus *Acomys* among the other rodent genera is also unclear. Traditionally, *Acomys* is classified within the family Muridae on the basis of morphological and chromosomal data (ZIMMERMANN 1953; ZAHAVI and WAHRMAN 1956; DIETERLEN 1963, 1978; MATTHEY 1963; MATTHEY and BACCAR 1967; BACCAR 1969) but electrophoretic and immunological data make this very doubtful (BONHOMME et al. 1985; SARICH 1985). Since this problem is not satisfactorily solved so far we have undertaken to study the phylogenetic relationships of *Acomys* not only in comparison with murid rodents but also to rodents of the family Arvicolidae.

The analysis of the phylogenetic relationships among the studied taxa has been carried out by the definition of their albumin differentiation using the microcomplement fixation method (MC'F).

Materials and method

A total of 51 individuals of the species *Mus domesticus*, *Rattus norvegicus*, *Apodemus flavicollis*, of the family Muridae, and the species *Microtus (Terricola) thomasi* of the family Arvicolidae were trapped alive at five localities of the Greek mainland. Also 4 individuals of the *Acomys minous* originating from two localities of Crete were used. Trapping localities and the number of individuals of each species studied are shown in table 1.

The procedure of blood sampling, albumin isolation, antisera preparation and MC'F experiments have been described previously (NIKOLETOPOULOS et al. 1992).

The average immunological distances between the studied taxa resulting from the MC'F experiments were used for the construction of an evolutionary tree according to the FITCH and MARGOLASH (1967) method. PRAGER and WILSON (1978) emphasize that this method is the most reasonable to use for constructing phylogenetic trees on the basis of immunological data.

Table 1. Number of individuals of the studied taxa and trapping localities in Greece

Species	Number of individuals	Trapping locality
<i>Mus domesticus</i>	21	Patra University Campus, Achaia Pref., Peloponnese
<i>Apodemus flavicollis</i>	12	Kastritsi, Achaia Pref., Peloponnese
<i>Rattus norvegicus</i>	4	Patra University Campus, Achaia Pref., Peloponnese
<i>Microtus (Terricola) thomasi</i>	14	Itea, Fokida Pref., Central Greece
<i>Acomys minous</i>	4	Agios Nikolaos and Sitia, Lasithi Pref., Crete

Results and discussion

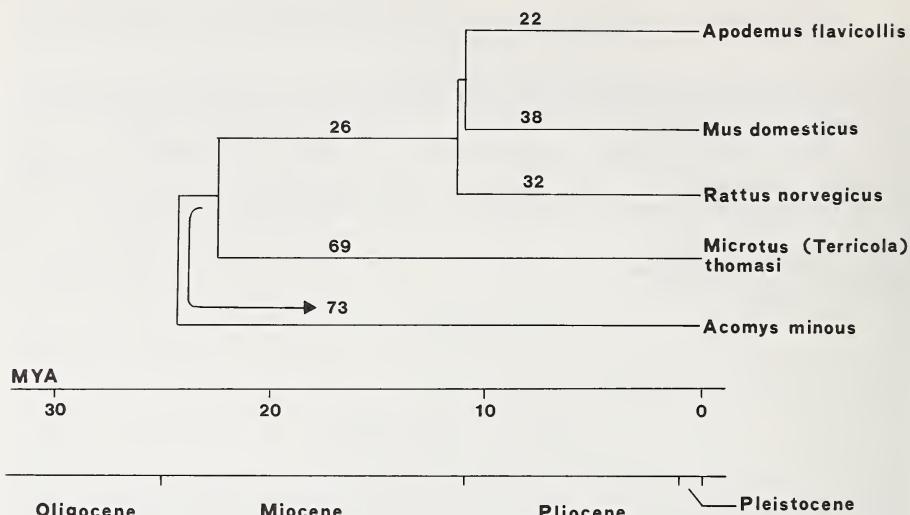
The results of reciprocal MC'F tests concerning the albumin of five species to which antibodies were prepared are given in table 2. The reliability of immunological data for estimating amino acid sequence divergence between proteins is, in part, proportional to the percent standard deviation from reciprocity for two way comparisons (BEVERLEY and WILSON 1982). The standard deviation value derived from our experiments was found to be 7.1; such a value lies within the range reported for similar studies (ELLIS and MAXSON 1980; FULLER et al. 1984; NIKOLETOPOULOS et al. 1992).

Table 2. Matrix of reciprocal immunological distances (I.D. units) of the studied rodent albumins

Species	Immunological distance				
	Antisera against				
	<i>M. d.</i>	<i>A. f.</i>	<i>R. n.</i>	<i>M. (T.) t.</i>	<i>A. m.</i>
<i>Mus domesticus</i> (<i>M. d.</i>)	0	57	61	152	116
<i>Apodemus flavicollis</i> (<i>A. f.</i>)	63	0	61	118	123
<i>Rattus norvegicus</i> (<i>R. n.</i>)	65	61	0	136	166
<i>Microtus (T.) thomasi</i> (<i>M. [T.] t.</i>)	132	102	118	0	136
<i>Acomys minous</i> (<i>A. m.</i>)	140	98	138	147	0

The phylogenetic tree (Figure) was constructed using the average reciprocal values of the albumin immunological distances. The statistical evaluation of the goodness of fit of this tree to the input data is expressed by either the percent standard deviation (s) (FITCH and MARGOLASH 1967) or the percent error (F) (PRAGER and WILSON 1976). In our tree these values are $s = 8.5$ and $F = 6.5$. Comparable values are mentioned in other phylogenetic studies based on the same technique (see NIKOLETOPOULOS et al. 1992).

As is already known (SARICH 1985; NIKOLETOPOULOS et al. 1992) the rate of albumin evolution is faster in rodents than in other mammalian groups. NIKOLETOPOULOS et al. (1992) discussed this subject and proposed a rate equal to 100 amino acid substitutions per 16–20 million years, according to the correlation of the available immunological and paleontological data on rodents. On the basis of this rate the results of the present study indicate that the *Acomys* lineage branched off 22–27 million years ago (MYA), during the late Oligocene – early Miocene period. On the other hand the Muridae-Arvicolidae divergence seems to have taken place 20–25 MYA (early Miocene), as becomes clear from



Phylogenetic tree of the five rodent taxa constructed on the basis of the average albumin immunological distances. The numbers on the branches show the amount of albumin changes estimated to have occurred along each branch

our results. Thus it is apparent that the genus *Acomys* is phylogenetically more distant from the examined taxa of Muridae than that of Arvicolidae, a fact that is also supported by SARICH (1985) who has wondered if *Acomys* is really a murine or even a murid.

Because of the remarkable scarcity of the *Acomys* fossil records, the age of the genus is difficult to determine on the basis of paleontological data. Information on the divergence time of this taxon is given by MATTHEY (1963, 1968), who accepts the existence of *Acomys* in Asian areas during the Miocene period. He also suggests that this genus was therewith distributed to the Near East, Africa, Crete and Cyprus during the upper Pliocene and early Pleistocene period. DENYS (1990) summarizing his own and bibliographic data concludes that the divergence time of *Acomys* is between 11 and 5 MYA; however he cannot give a definitive answer to the question whether *Acomys* is a true murid or not.

To date there is no information about the occurrence of *Acomys* in the Miocene strata. However, JACOBS (1977) suggests that the oldest known murid fossils (*Antemus*) is of a middle Miocene age (15–16 MYA). If our and SARICH's (1985) immunological results are accepted then the phylogenetic position of *Acomys* should not be within the family Muridae, although even some contemporary authors based on morphological and karyological data continue to consider that *Acomys* is a genus of Muridae (NEVO 1985; DIPPENAAR and RAUTENBACH 1986).

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Zusammenfassung

Über die Phylogenie der Gattung Acomys (Mammalia: Rodentia)

Die phylogenetischen Beziehungen der Gattung *Acomys* (vertreten durch *A. minous*) zu anderen Rodentia-Gattungen der Familien Muridae (vertreten durch *Mus domesticus*, *Rattus norvegicus*, *Apodemus flavicollis*) und Arvicolidae (vertreten durch *Microtus (Terricola) thomasi*) werden untersucht. Insgesamt 51 erwachsene Individuen beider Geschlechter wurden untersucht, um die Albumin-

Differenzierung durch den Microcomplement-Fixations-Test (MC'F) klarzustellen. Die immunologischen Abstände von *Acomys* von den Muriden-Taxa erwiesen sich als größer im Vergleich zu den entsprechenden Abständen zwischen *Microtus* (*T.*) *thomasi* und den untersuchten Muriden-Arten. Das bedeutet, daß die Abzweigung der Evolutionslinie zu *Acomys* älter ist als das Auftauchen des gemeinsamen Vorfahren der Muriden und Arvicoliden – etwa vor 22–27 Mio. Jahren. Den immunologischen Ergebnissen zufolge sollte die taxonomische Stellung von *Acomys* innerhalb der Familie Muridae – im Gegensatz zu den bisherigen morphologischen und karyologischen Daten – revidiert werden.

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