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MOLECULAR EVIDENCE CONCERNING THE PHYLOGENETIC INTEGRITY OF THE MURINAE

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ABSTRACT

Amino acid and DNA sequence data are used to infer the phylogenetic position of *Acomys* within or outside the Murinae, as well as to determine the evolutionary relationships of the Murinae with other murid subfamilies. *Acomys* and the non-murine murids *Mesocricetus* and *Cricetulus* possess a single preproinsulin gene, in contrast to *Rattus* and *Mus*, which possess two nonallelic genes. Moreover, both chains A and B of the insulins are identical in their amino acid sequences in *Acomys*, *Mesocricetus*, and *Cricetulus*, and differ from both insulins I and II of *Rattus* and *Mus*. Therefore, *Acomys* does not seem to belong to the Murinae. The genus *Praomys* is most probably paraphyletic, but the various species that have been tested molecularly seem to belong to the Murinae. The murine affiliations of *Stochomys*, *Arvicanthis*, *Apodemus* and *Conilurus* are confirmed, but *Uranomys* and *Lophuromys* may have been misassigned to the Murinae. The closest phylogenetic relatives of the Murinae are the Microtinae, the Cricetinae, and the Dipodinae. Neither the Murinae nor the Muridae is monophyletic.

INTRODUCTION

The Murinae is the largest subfamily within the Muridae, which in turn is the largest family of the largest order of eutherian mammals. The Murinae subfamily is extremely heterogeneous, and on the morphological level is defined solely on the basis of a few dental characteristics (Anderson and Jones, 1984). The phylogenetic validity of this taxon, although undisputed morphologically (e.g., Denys et al., 1992), has been challenged recently on the basis of chromosomal, immunological, and genetic data. In particular, the affiliation of the genus *Acomys* with the Murinae (or even the Muridae) has been questioned (e.g., Pascale et al., 1990,1993; Chevret and Hänni, 1994, this issue). In this note I analyze the available molecular data for members of the Murinae in order to determine the monophyly, and, hence, the validity of this subfamily. I also attempt to determine the position of the Murinae in relationship with other subfamilies within the Muridae. Unfortunately, molecular data from murid genera other than *Rattus* and *Mus* are quite sparse, and in many cases (e.g., Nakata et al., 1992; Howell and Kubacka, 1993) protein and DNA sequences have been determined for only one or two species, thus

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precluding their use in a phylogenetic context. The conclusions must, therefore, be regarded as tentative only.

DATA AND METHODS

Four molecular data banks, GENBANK, EMBL, PIR, and SWISPROT (updated to June 1994), were searched for DNA and protein sequences from genera that are traditionally assigned to the subfamily Murinae. *Rattus* and *Mus* were not included in the search. Homologous sequences were identified by using the appropriate programs of the BLAST package (Altschul et al., 1990). Sequences derived from multigene families (e.g., Wines et al., 1991; Lin et al., 1993) were excluded. DNA sequences were used in preference to amino acid sequences when possible. Alignments and reformatting of the sequences for further analyses were carried out by using the CLUSTAL V package (Higgins et al., 1992). Distances at the DNA and amino acid levels were calculated according to Kimura's (1980) two-parameter model and Kimura's correction for multiple amino acid replacements (Kimura, 1983), respectively. Phylogenetic analyses were carried out by using the neighbor-joining approach (Saitou and Nei, 1987). Internal branches were deemed statistically significant if they appeared in at least 950 out of 1,000 bootstrapping replicates (Felsenstein, 1985). They are marked by asterisks in the figures.

RESULTS AND DISCUSSION

ACOMYS

Only one protein, insulin, has been sequenced in *Acomys*, and no DNA data exists for this genus. The Egyptian spiny mouse, *Acomys cahirinus*, possesses a single preproinsulin gene, in contrast to *Rattus* and *Mus*, which possess two nonallelic genes (Bünzli and Humbel, 1972). The Syrian hamster, *Mesocricetus auratus*, and the long-tailed Chinese hamster, *Cricetulus longicaudatus*, which belong to a different subfamily, Cricetinae, also possess a single preproinsulin gene in their genome (Neelon et al., 1973; Bell and Sanchez-Pescador, 1984). Moreover, both chains A and B of the insulins from *Acomys* are identical in their amino acid sequences to their counterparts in *Mesocricetus* and *Cricetulus*. Chain A from *Acomys* differs from that of insulins I from *Rattus* and *Mus* by one amino acid: at position 3, *Acomys* has an asparagine, whereas *Rattus* and *Mus* have a lysine. Insulin II of *Mus* differs from its counterpart in *Acomys* by an additional amino acid replacement: at position 9, *Acomys* has a serine, whereas *Mus* has a proline. Interestingly, chain A of *Acomys* is identical in sequence to its homologue in the rabbit, *Oryctolagus cuniculus*. A neighbor-joining phylogenetic reconstruction with *Canis* and *Homo* as outgroups is shown in Fig. 1. None of the 6 internal branches is supported in a statistically significant manner by bootstrapping.

A cladistic interpretation of the data indicates that the existence of a single preproinsulin gene and the presence of the amino acid asparagine at position 3 of chain A in *Acomys*, *Mesocricetus*, and *Cricetulus* should be interpreted as primitive characters common to most mammalian taxa, and therefore of limited use in inferring the phylogenetic position

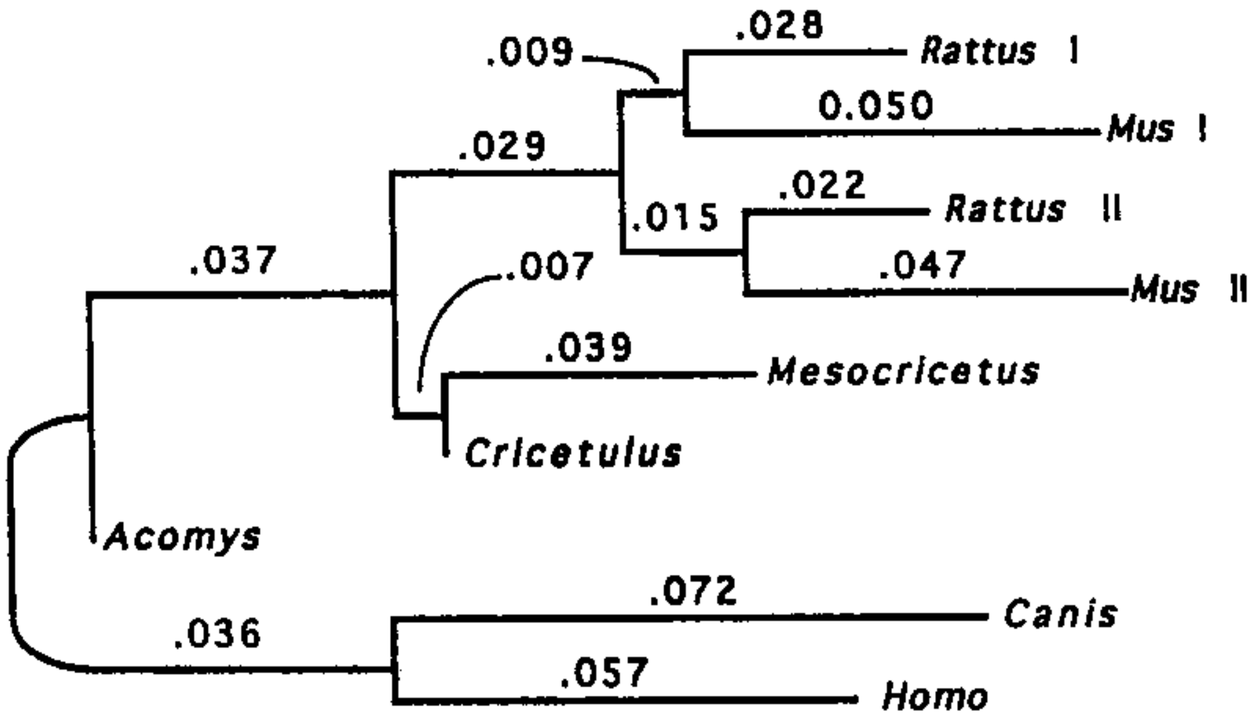

Fig. 1. Neighbor-joining phylogenetic tree based on amino acid sequences of insulin. The branch lengths are given in numbers of amino acid replacements per amino acid site. The lengths of the two branches leading to *Acomys* and *Cricetulus* are 0.

of *Acomys*. Conversely, the existence of two duplicated genes in *Rattus* and *Mus*, and the presence of a lysine at position 3 of chain A should be considered synapomorphic. Nonetheless, the gene numbers and the amino acid sequences add molecular evidence to the one presented by Chevret and Hänni (this issue) for the exclusion of *Acomys* from the subfamily Murinae.

PRAOMYS

Praomys is traditionally divided into 4 subgenera: *Mastomys*, *Myomyscus*, *Praomys*, and *Hylomyscus* (Nowak and Pardiso, 1983). The amino acid sequence of the β nerve growth factor from the South African mutimammate rat, *Praomys* (*Mastomys*) *natalensis*, has been determined by Fahnestock and Bell (1988). A neighbor-joining phylogenetic reconstruction with *Cavia* and *Homo* as outgroups (data from Scott et al., 1983; Ullrich et al., 1983; Schwarz et al., 1989; Borsani et al., 1990; Hallbook et al., 1991) is shown in Fig. 2. The particular arrangement of *Rattus*, *Mus*, and *Praomys* that emerges from this analysis, i.e., ((*Mus*, *Praomys*), *Rattus*), is not deemed statistically significant by bootstrapping, and the trichotomy remains essentially unresolved.

A similar analysis was carried out on about 100 nucleotides at the 5′ end of the 16S ribosomal RNA from the mitochondria of the African soft-furred rat, *Praomys* (*Myomyscus*) *daltoni*, seven *Mus* species and subspecies, and *Rattus*, with *Homo* as an outgroup (data

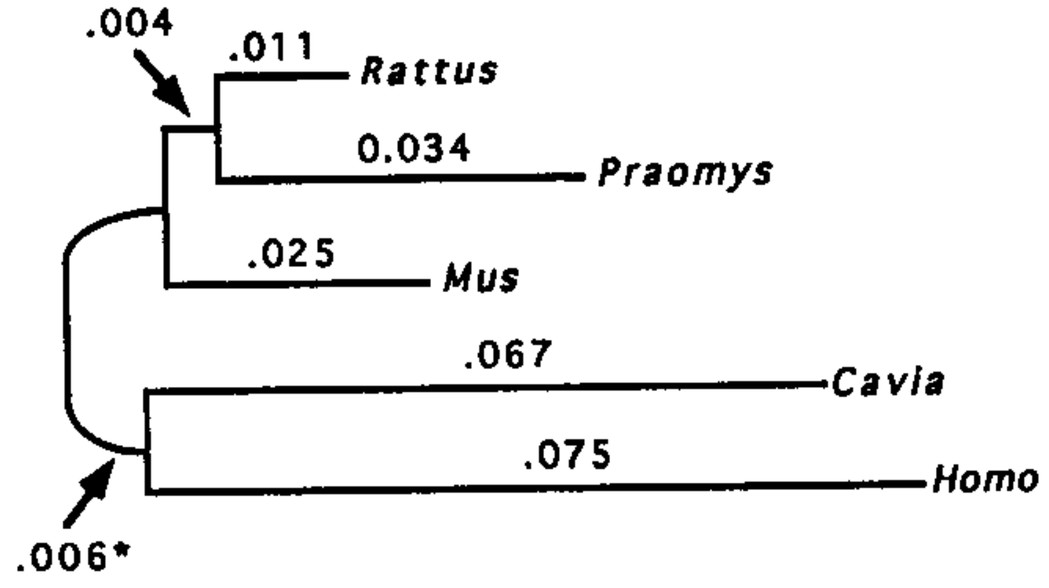

Fig. 2. Neighbor-joining phylogenetic tree based on DNA sequences of the β nerve growth factor gene. The branch lengths are given in numbers of nucleotide substitutions per site.

from Eperon et al., 1980; Saccone et al., 1981; Fort et al., 1984). The phylogenetic arrangement that emerges is ((*Rattus*, *Praomys*), *Mus*). In this case, however, the trichotomy is disentangled in a statistically significant manner (Fig. 3).

In a third analysis, a phylogenetic reconstruction was carried out on the amino acid sequences of the Y-linked sex-determining factor (*SRY*) from 4 murine genera: *Mus* (8 species), *Praomys* (2 species: one from subgenus *Praomys* and one from subgenus *Hylomyscus*), *Rattus exulans*, and *Stochomys longicaudatus*, with *Homo* as an outgroup (data from Bianchi et al. 1993; Clepet et al., 1993; Tucker and Lundrigan, 1993). The resulting phylogenetic tree clusters *Praomys* with *Mus*, followed, in order of relatedness, by *Rattus* and *Stochomys* (Fig. 4).

There are two possible explanations for the differences among the results obtained by using the β nerve growth factor, 16S rRNA, and *SRY*. Either the results reflect a genuine evolutionary difference among the four *Praomys* subgenera, i.e., the genus *Praomys* is paraphyletic, or the difference arose by chance due to the small size of the data. The fact that in all three trees the species belonging to the same genus were never split by the phylogenetic reconstruction implies that the first possibility may be correct.

The genome of two species of the African soft-furred rat, *Praomys daltoni* and *P. erythroleucus*, were shown to possess *Lx* repeats. Since the amplification of this long interspersed family of elements identifies an internal node within the Murinae (Pascale et al., 1990), *Praomys* seems a bona fide murine taxon.

In summary, all species of *Praomys* that have been tested seem to be extremely closely related to both *Rattus* and *Mus*, and, therefore, the affiliation of *Praomys* with the Murinae remains uncontested. The genus, however, may be paraphyletic. The exact relationship of the various *Praomys* species with *Mus* and *Rattus* could be assessed in the future by determining the number of preproinsulin gene copies in their genome (see above).

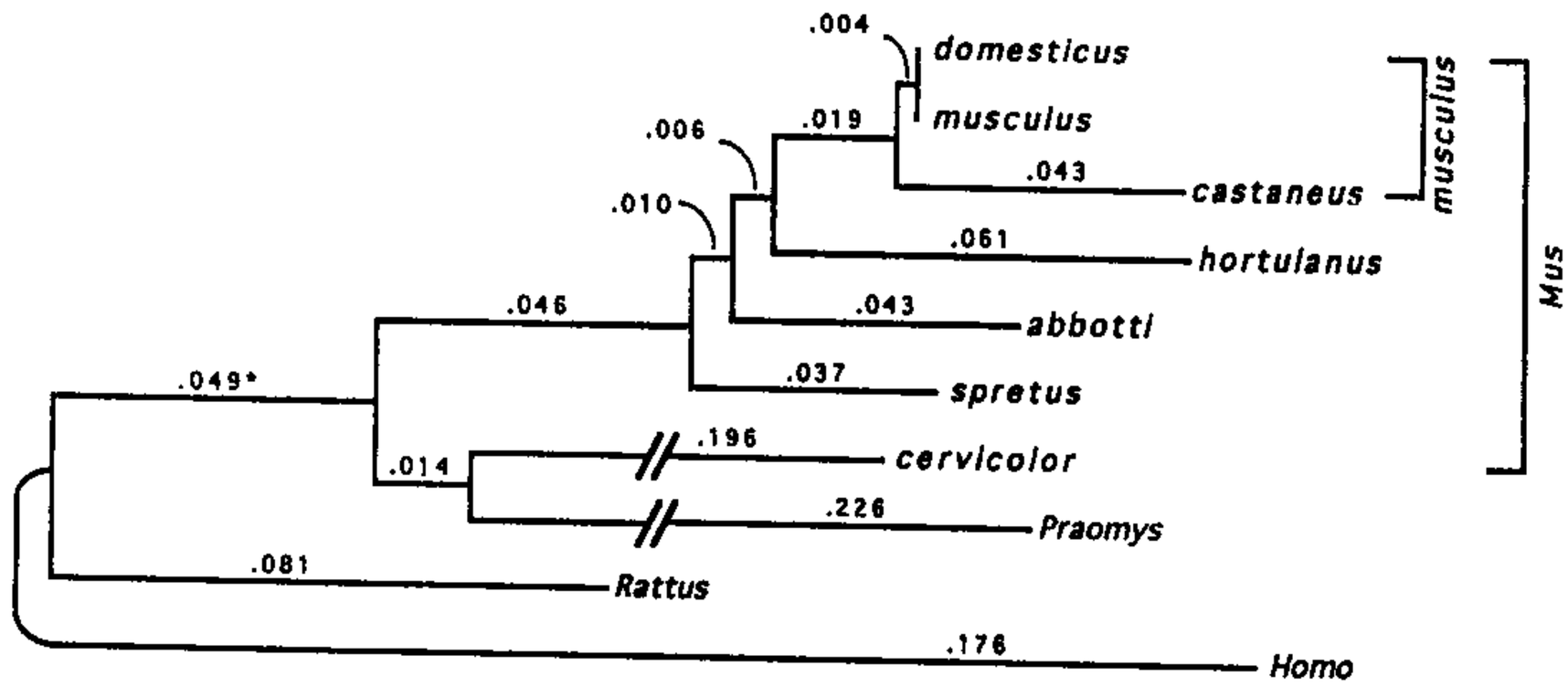

Fig. 3. Neighbor-joining phylogenetic tree based on DNA sequences of the 5′ end of the mitochondrial rRNA gene. The branch lengths are given in numbers of nucleotide substitutions per site. The lengths of the two branches leading to *Mus musculus domesticus* and *Mus musculus musculus* are 0.

STOCHOMYS

DNA data from the *SRY* gene (Tucker and Lundrigan, 1993) indicate that the long-tailed target rat, *Stochomys longicaudatus*, is an outgroup to *Mus*, *Rattus*, and *Praomys* (Fig. 4). However, in the absence of orthologous data from a non-murine murid, the murine affiliation of *Stochomys* cannot be challenged at present.

ARVICANTHIS, APODEMUS, CONILURUS, LOPHUROMYS, AND URANOMYS

Pascale et al. (1990) and Chevret et al. (1993) have shown that the genomes of the kusu rat, *Arvicanthis niloticus*, the field mouse, *Apodemus flavicollis*, and the tree rat, *Conilurus penicillatus*, possess *Lx* repeats. Therefore, they belong unequivocally to the Murinae. In contrast, the brush-furred rat, *Lophuromys sikapusi*, and the white-bellied brush-furred rat, *Uranomys ruddi*, in common with *Acomys cahirinus*, lack this murine-specific element. It is, therefore, possible that in addition to *Acomys*, *Uranomys* and *Lophuromys* may have also been taxonomically misassigned to the Murinae.

THE PHYLOGENETIC POSITION OF THE MURINAE WITHIN THE MURIDAE

In order to elucidate the phylogenetic position of the Murinae within the Muridae, a phylogenetic reconstruction has been attempted for four murid subfamilies. The analysis was first performed on 5 proteins: hemoglobins α and β, myoglobin, crystallin αA, and pancreatic ribonuclease. However, in order to maximize the number of taxa included, the number of proteins was reduced to two: hemoglobins α and β. The Microtinae were represented by the muskrat (*Ondatra zibethica*) and the yellow-cheeked vole (*Microtus*

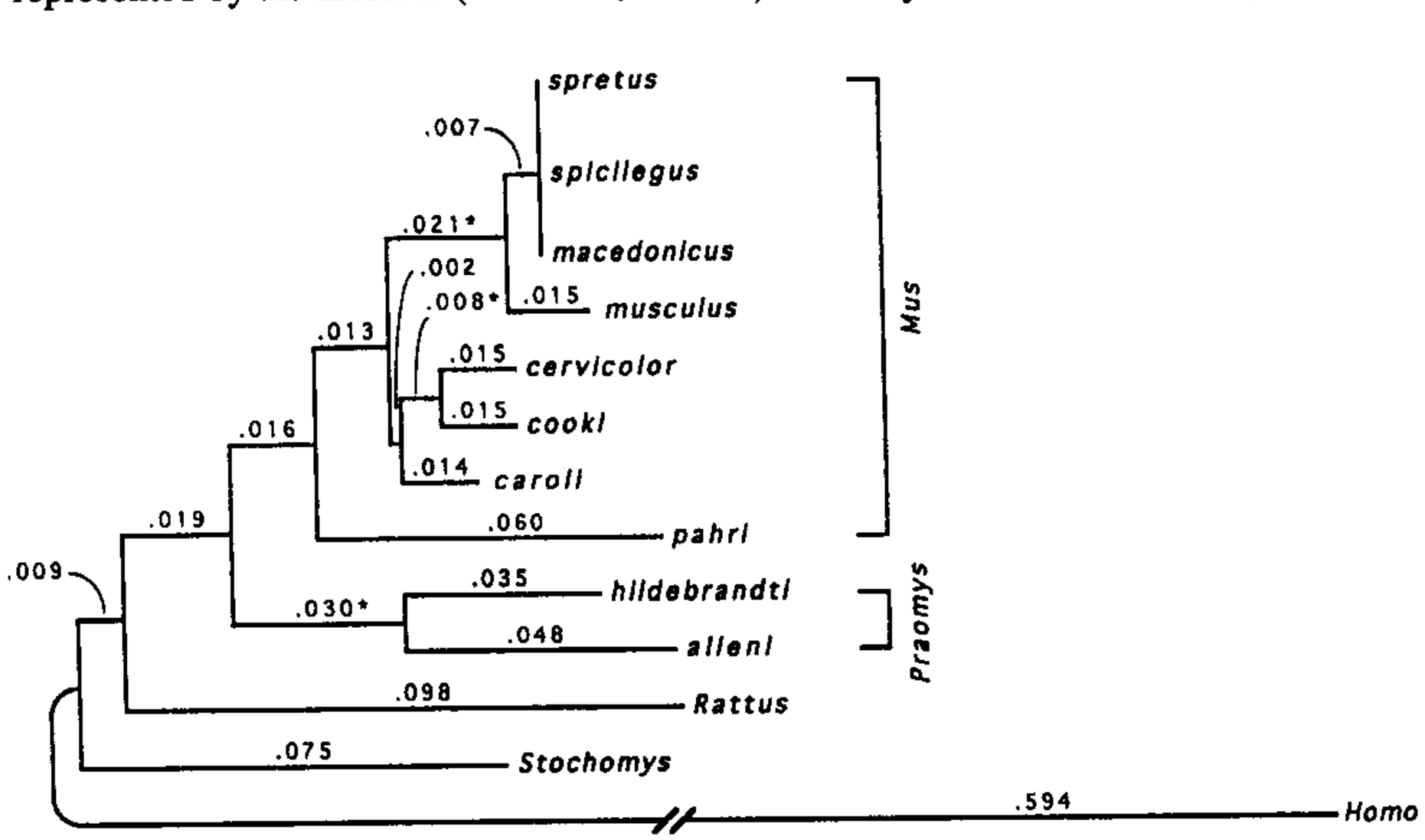

Fig. 4. Neighbor-joining phylogenetic tree based on DNA sequences from the Y-linked sex determining factor (*SRY*) gene. The branch lengths are given in numbers of nucleotide substitutions per site.

xanthognathus), the Cricetinae were represented by the golden hamster (*Mesocricetus auratus*), the Murinae were represented by *Rattus* and *Mus*, and the Spalacinae by the blind mole rat (*Spalax ehrenbergi*). In this case we used two levels of outgroups, a close outgroup consisting of a sciurid, the Alpine marmot (*Marmota marmota marmota*), and a distant outgroup consisting of *Bos* and *Homo* (data from Braunitzer et al., 1961, 1980; Schroeder et al., 1967; Duffy and Genaux, 1977; Lawn et al., 1980; Bieber and Braunitzer, 1983; Kleinschmidt et al., 1984; Sgouros et al., 1986; Satoh et al., 1987; Radosavljevic and Crkvenjakov, 1989; Barkhudaryan et al., 1993). The results indicate that the Microtinae are significantly closer to the Cricetinae to the exclusion of the Murinae and the Spalacinae (Fig. 5). Interestingly, the branch separating the Microtinae and the Cricetinae from the other two murine subfamilies is seven times larger than the branch separating the myomorphs and the sciuromorphs. This indicates that one of the traditional subdivisions of the rodents into three suborders, Myomorpha, Sciuromorpha, and Hystricomorpha, is invalid.

A phylogenetic tree has also been constructed on the basis of mitochondrial cytochrome *b* sequences from two murines (*Mus* and *Rattus*), 11 hesperomine genera (Muridae), and two non-murid sciurognaths (*Pappogeomys* and *Geomys*). The data were taken from Bibb et al. (1981), Gadaleta et al. (1989), DeWalt et al. (1993), Ma et al. (1993), and Smith and Patton (1993). These mitochondrial sequences yield an even more puzzling result (Fig. 6) than that obtained from the hemoglobin analysis. The Geomyidae, which do not belong to the Muridae, seem to be phylogenetically closer to the Hesperomyinae, which do belong, than either of them is to the Murinae. Therefore, the Muridae, as presently defined in the literature, seem to be a paraphiletic, and hence, invalid taxon.

The study of Serdobova and Kramerov (1993) on the *DIP* retroposon confirms the close phylogenetic affinity of the Murinae to the Cricetinae and the Microtinae, and

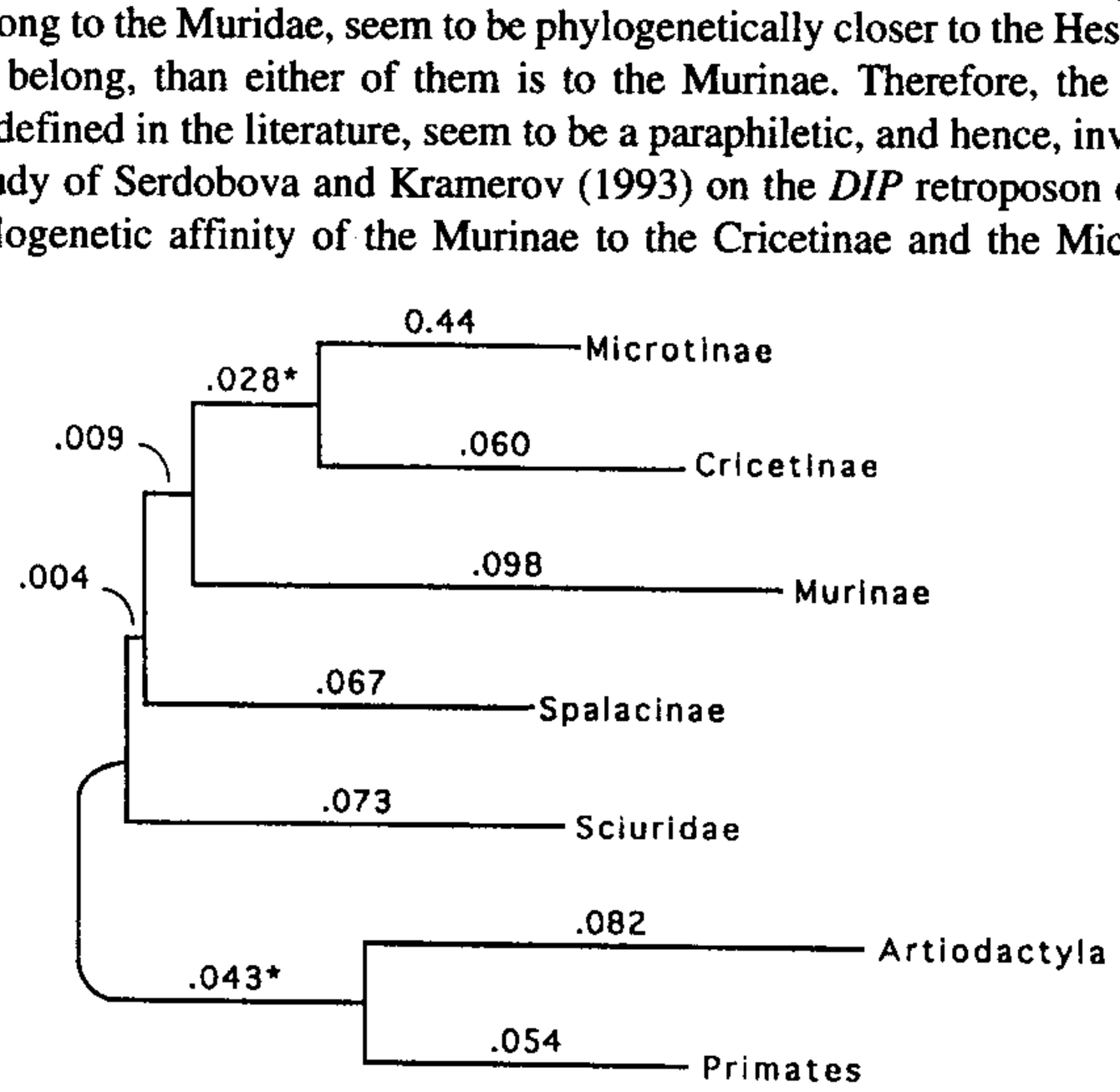

Fig. 5. Neighbor-joining phylogenetic tree based on the amino acid sequences of hemoglobins α and β. The branch lengths are given in numbers of nucleotide substitutions per site.

indicates that the subfamily Dipodinae is also closely related to the Murinae. *DIP* homologues were found in *Mus musculus*, *Rattus norvegicus*, *Apodemus peninsula* (Murinae), *Mesocricetus auratus* (Cricetinae), the mole lemming, *Ellobius tancrei* (Microtinae), the desert jerboas, *Jaculus* (*Eremodipus*) *lichtensteini* and *Allactaga* (*Allactodipus*) *bobrinskii*, and the little earth hare, *Allactagulus pygmaeus* (Dipodinae). No *DIP*-related sequences were found in the forest dormouse, *Dryomys nitedula* (Glirinae), indicating that the Glirinae are quite distant from the Murinae, the Cricetinae, the Microtinae, and the Dipodinae. The absence of DIP homologues was also noted in Berdmore's palm squirrel, *Menetes berdmorei* (Sciuridae), and in the outgroup species *Cavia* and *Homo*.

THE TAXONOMIC "DESTINY" OF RODENTIA

At all taxonomic levels, the order Rodentia seems destined for dismemberment. First, the hystricomorphs were shown to be evolutionarily unrelated to the myomorphs, thereby rendering the bipartite division of Rodentia into Sciurognathi and Hystricognathi meaningless (Graur et al., 1991). Next, a family of rodents that defied taxonomy for years, Ctenodactylidae, was shown tentatively to be unrelated to the Rodentia (Li et al., 1992).

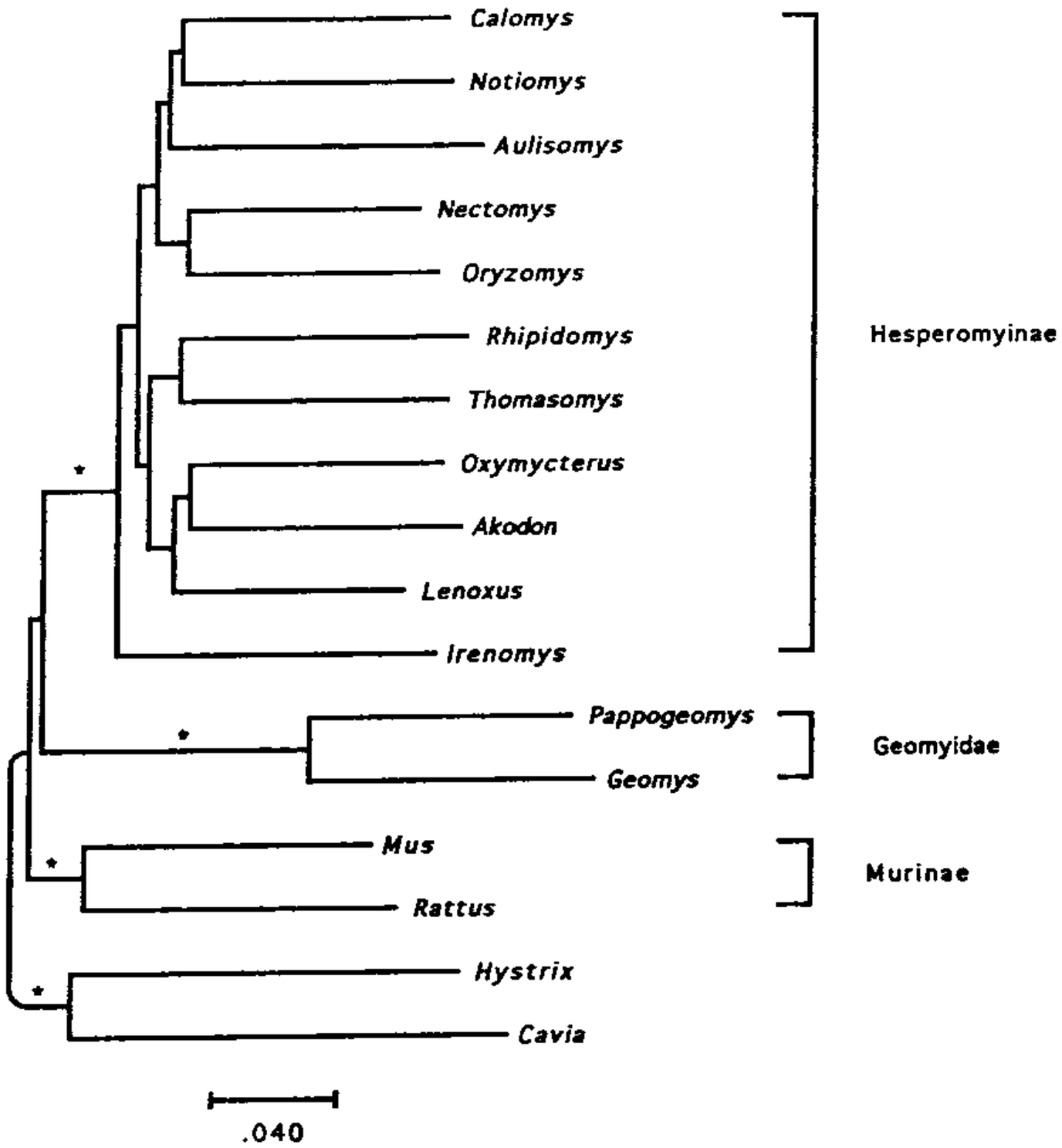

Fig. 6. Neighbor-joining phylogenetic tree based on DNA sequences from the mitochondrially encoded cytochrome *b*. The branches are proportional in length to the scaling bar at the bottom.

In this note, doubts are raised concerning the validity of the division of the Sciurognathi into Sciuromorpha and Myomorpha, and the monophyly of the family Muridae is questioned. Finally, the tentative exclusion of three genera, *Acomys*, *Uranomys*, and *Lophuromys* from the Murinae, places a big question mark on the phylogenetic integrity of the largest subfamily of rodents. Mammalian taxonomy is in a state of upheaval due, in large part, to molecular data (Graur, 1993). The families and subfamilies of rodents will undoubtedly play a major part in this hullabaloo.

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