A mitochondrial cytochrome *b* phylogeny confirms the paraphyly of the Dendromurinae Alston, 1896 (Muridae, Rodentia)

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The subfamily Dendromurinae has occupied various systematic positions in the different classifications of the Muroidea and different genera have been attributed to this taxon (*e.g.* Lindsay 1988, Chaline *et al.* 1977). For example, the genus *Deomys* (Thomas, 1888), originally believed to be a link between the cricetid and murid rodents, has subsequently been attributed to the Dendromurinae Alston, 1896 ; to its own subfamily Deomyinae Ellerman, 1941, before being reallocated to the Dendromurinae by Rosevear (1969) and Meester and Setzer (1971), (*see also* Musser and Carleton 1993).

A recent study using morphological and DNA-DNA hybridisation data concludes that the Dendromurinae are paraphyletic and that the status of this subfamily has to be revised (Denys *et al.* 1995). The present study evaluates this hypothesis by studying a similar set of taxa with another molecular marker. We compare an UPGMA-tree based upon DNA-DNA hybridisation data (Denys *et al.* 1995) with a mitochondrial DNA phylogeny based upon parsimony analyses of a portion of the cytochrome *b* gene (cyt *b*).

DNA was isolated from tissue samples of the collections of the department of biology of the University of Antwerp (RUCA). This study concerns 10 species representing the Murinae Illiger, 1815, Cricetomyinae Roberts, 1951, Dendromurinae Alston, 1896 and Gerbillinae Gray, 1825. We sequenced a portion of the mitochondrial cyt *b* gene of 2 specimens/species of *Arvicanthis nairobae* J.A. Allen, 1909 ; *Cricetomys gambianus* Waterhouse, 1840 ; *Lophuromys flavopunctatus* Thomas, 1888 ; *Deomys ferrugineus* Thomas, 1888 and one specimen/species of *Steatomys krebsii* Peters, 1852 ; *Steatomys pratensis* Peters, 1846 ; *Tatera valida* (Bocage, 1890) ; *Taterillus gracilis* (Thomas, 1892) ; *Hybomys univittatus* (Peters, 1876) and one specimen of an *Hybomys* species to be described yet.

PCR-reactions and DNA sequencing protocols have been described elsewhere (Verheyen *et al.* 1995). The primers used to amplify a 402 bp long cyt *b* gene segment were L13724 (5'-cgaagcttgatatgaaaaaccatcgttg-3') and H14139 (5'-aaactgcagcccctcagaatgatatttgtcctca-3', Kocher *et al.* 1989). The cyt *b* sequences (see annex) as well as information about the origin of the used specimens are available upon request.

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We analysed 357 base pairs (bp) of the mitochondrial cyt *b* fragment. In total 156 sites are variable and 134 sites are parsimony informative (1st codon positions : 28 ; 2nd positions : 9 ; 3rd positions : 97). Pairwise comparisons among the homologous sites of the studied cyt *b* fragment show that the majority of overall transition/transversion (ts/tv) ratios for intersubfamily comparisons approximate one (Verheyen *et al.* in prep.) and suggest that the studied rodents have diverged long ago or have undergone rapid mutation rates in comparison with other mammals (Irwin *et al.* 1991 ; Vrana *et al.* 1994). In agreement with the degenerate nature of the amino acid code, third and first codon positions show most of the observed variation.

The mtDNA sequences were analysed using the parsimony method (Swofford 1993, PAUP 3.1.1). We used the published cyt *b* sequences (Smith and Patton 1991) of *Akodon boliviensis* Meyen, 1833 and *Bolomys amoenus* (Thomas, 1900) – two neotropical murids that belong to the neotropical subfamily Sigmodontinae – as outgroup sequences against the African murids of our dataset. The problem of potentially disinformative mutational changes in first and third codon positions was assessed through analyses using the "transversions only'' settings, by downweighting the mutational changes in first and third codon positions and/or by leaving out transitional changes in first positions of triplets coding for leucine (Meyer 1994).

The tree shown (fig. 1) is the single most parsimonious tree obtained after a heuristic search using conservative changes sensu Irwin *et al.* (1991) *i.e.* considering all substitutions in codon position one – except leucine codons transitions – all substitutions in codon position two, and transversions in codon three positions. PAUP-settings were : acctran, 10 replications, random addition of taxa, weights for 1st, 2nd and 3rd codon positions : 3, 10 and 1 and bootstrap values shown were obtained after 500 replications. Additional heuristic analyses, using different transversion weightings (ts1/tv5 ; ts1/tv10, transversions only) resulted in trees with the same clades than in the phylogeny shown.

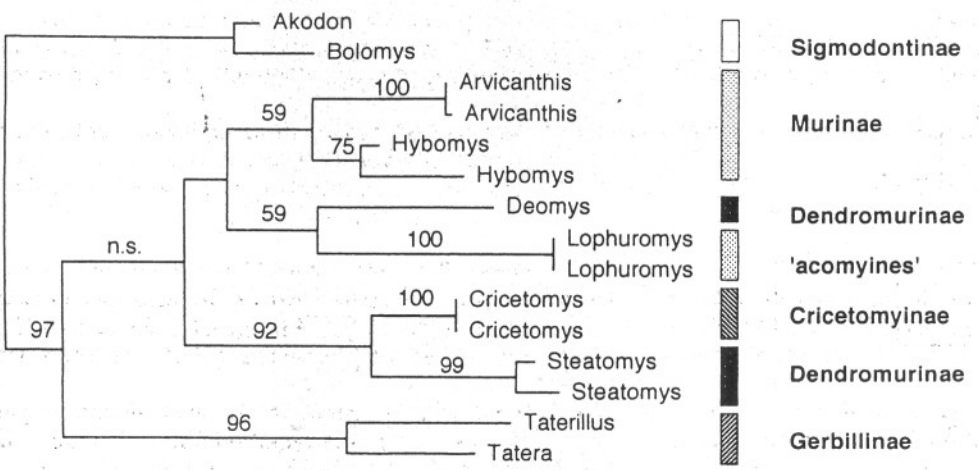

Fig. 1. – With regard to the affilations between the two dendromurine taxa studied here, the shown cytochrome *b* phylogeny is concordant to the tree derived from DNA-DNA hybridisation data (Denys *et al.* 1995). The tree shown is the single most parsimonious tree (CI 0.751, length = 413) obtained after parsimony analyses carried out as described in the text. Numbers above branches are % bootstrap values obtained after 500 replications.

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Akodon_____     CACTCATTCATTGACCTACCAACTCCATCTAACATCTCATCCTGA
Bolomys____     CATTCATTCATTGATCTTCCAACCCCATCTAACATTTCATCATGA
Arvica_7631     CACTCATTCATCGATCTCCCCGCTCCATCTAACATTTCATCATGA
Arvica_6072     CACTCATTCATCGATCTCCCCG?TCCATCTAACATTTCATCATGA
Cricet_7221     CACTCATTCATTGACCTCCCTACCCCATCCAACATCTCATCATGA
Crice_11746     CACTCATTCATTGACCTCCCTACCCCATCCAACATCTCATCATGA
Taterillus_     CACTCATTCATCGACCTACCCACTCCCCCCAATATCTCATCATGA
Deom_R13237     CACTCATTCATTGACCTTCCAACCCCATCCAATATCTCATCATGA
Hybo_R12107     CACTCATTCATTGACCTGCCCGGCCCATCCAACATCTCTTCATGA
Hybo_G10023     CACACATTCATTGACCTGCCTACC?TATCTAACATCCTTTCATGA
Lophur_7253     CACTCATTCATCGACCTTCCTGCCCCCTCCAACATCTCATCCTGA
Lophur_7366     CACTCATTCATCGACCTTCCTGCCCCCTCCAACATCTCATCCTGA
SteaTM40998     ?ACTCATTTATTG?????CCCACCCCATCAAACATCTCATCCTGA
SteaTM41035     GACTCATTCATCGATCTTCCTACCCCATCAAACATTTCATCCTGA
Tater_11734     CACTCATTCATTGATCTTCCCACTCCTCCTAACATTTCATCATGA

Akodon_____     TGAAATTTTGGATCCCTACTAGGCATATGCCTAATAATCCAAATT
Bolomys____     TGAAACTTCGGATCCTTACTAGGCATATGCCTAATAATCCAAATC
Arvica_7631     TGAAACTTTGGCTCCTTACTAGG?ATTTGCCTAATATTACAAATC
Arvica_6072     TGAAACTTTGGATCCTTACTAGGTATTTGCCTAATATTACAAATC
Cricet_7221     TGAAACTTCGGCTCCATTCTAGGCATTTGTTTAATCCTGCAAATC
Crice_11746     TGAAACTTCGGCTCCATCCTAGGCATTTGTTTAATCCTACAAATC
Taterillus_     TGAAACTTTGGATCCCTTCTTGGCATCTGTCTCATTATCCAAATT
Deom_R13237     TGGAACTTTGGCTCCCTACTAGG?ATCTGCCTAATT?TGCAAATC
Hybo_R12107     TGAAACTTTGGCTCTTTACTAGGAATCTGCTTACTAGTACAAATC
Hybo_G10023     TGAAACTTTGGCTCTTTACTAGGAATCTGCTTAATAGTACAAATC
Lophur_7253     TGAAACTTTGGCTCCTTACTAGGCGTCTGCCTCATCCTTCAAATC
Lophur_7366     TGAAACTTTGGCTCCTTACTAGGCGTCTGCCTCATCCTTCAAATC
SteaTM40998     TGGAATTTTGGCTCCCTACTAGGAATTTGCTTAGTAGTCCAAATT
SteaTM41035     TGA?ACTTTGGTTCCCTATTAGGAGTCTGTCTAGTAGTACAAATC
Tater_11734     TGAAATTTTGGGTCACTTCTAGGCCTCTGCCTAATTATCCAAATC

Akodon_____     TTAACAGGCCTATTCCTAGCCATACACTACACATCAGACACAACC
Bolomys____     CTAACAGGCCTATTTCTAGCAATACACTACACATCAGA?ACAACC
Arvica_7631     ATTACAGGCCTATTTCTAGCCATACACTACACATCAGACACAACA
Arvica_6072     ATTACAGGCCTATTTCTAGCCATACACTACACATCAGACACAACA
Cricet_7221     TTAACAGGATTATTTCTAGCTATACATTATACATCAGATACAACA
Crice_11746     TTAACAGGATTATTTCTAGCTATACATTATACATCAGATACAACA
Taterillus_     GCTACAGGATTATTTTTAGCAATACACTACACAGCAGACACAATA
Deom_R13237     ACTACAGGCCTATTCCTAGCTATACACTATACACCAGACACCATA
Hybo_R12107     ATTACAGGCCTATTCCTAGCCATACACTATACATCAGATACAACA
Hybo_G10023     GTTACAGGCCTATTCCTAGCCATACACTATACATCAGATACAACA
Lophur_7253     GCCACAGGCCTTTTCCTAGCTATACATTACACCTCCGACACCGCA
Lophur_7366     GCCACAGGCCTTTTCCTAGCTATACATTACACCTCCGACACCGCA
SteaTM40998     CTCACAGGCCTATTCCTAGCAATACATTATACCTCTGACACTACT
SteaTM41035     CTTACAGGTCTATTTCTAGCAATACATTACACCTCTGATACAACT
Tater_11734     ACAACAGGATTATTTCTAGCAATACACTATACAGCCGATACAACT

Akodon_____     ACAGCATTCTCCTCAGTAGCACATATCTGCCGAGATGTAAACTAC
Bolomys____     ACAGCATTCTCCTCAGTCGCACATATCTGCCGAGACGTGAACTAT
Arvica_7631     ACAGCATTCTCCTCAGTCACTCACATTTGTCGAGATGT?AATTAC
Arvica_6072     ACAGCATTCTCCTCAGTCACTCACATTTGTCGAGATGTCAATTAC
Cricet_7221     ACTGCATTCTCATCAGTCACCCACATCTGCCGAGACGTTAATTAC
Crice_11746     ACTGCATTCTCATCAGTCACCCACATCTGTCGAGACGGTAATTAC
Taterillus_     ACAGCATTTTCATCAGTGTCCCATATCTGTCGAGACGTAAACTAT
Deom_R13237     ACAGCATTCTCATCAGTCACCCATATTTGCCGAGATGTCAACTAT
Hybo_R12107     ACAGCATTCTCATCAGTTACCCACATCTGTCGAGACGTAAACTAC
Hybo_G10023     ACAGCATTTTCATCAGTAACTCACATTTGTCGAGACGTAAACTAC
Lophur_7253     ACAGCATTTACATCAGTCACACACATCTGCCGAGACGTAAATTAC
Lophur_7366     ACAGCATTTACATCAGTCACACACATCTGCCGAGACGTAAATTAC
SteaTM40998     ACCGCATTCTCATCAGTTACTCATATCTGCCGAGACGTAAATTAC
SteaTM41035     ACCGCCTTTTCATCAGTTACCCACATTTGTCCGGGACGTAAACTAC
Tater_11734     ACAGCATTTTCATCCGTATCTCATATCTGCCGAGATGTAAACTAT
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Annex – Mitochondrial cytochrome b sequences used in this paper.

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Akodon_____     GGATGATTAATCCGCTACTTGCACGCTAATGGAGCCTCCATATTC
Bolomys____     GGATGATTAATCCGCTACCTACACGCCAACGGAGCCTCCATATTC
Arvica_7631     GGATGACTAATTCGATACATACATGCAAACGGAGCCTCAATATTC
Arvica_6072     GGATGACTAATTCGATACATACATGCAAACGGGGCCTCAATATTC
Cricet_7221     GGATGACTAATCCGTTATTTACACGCAAACGGAGCCTCAATATTC
Crice_11746     GGATGACTAATCCGTTATTTACACGCAAACGGAGCCTCAATATTC
Taterillus_     GGATGA?TTATTCGATATATACATGCAAACGGAGCTTCAATATTC
Deom_R13237     GGCTGATTAATCCGATATCTCCATGCAAATGGAGCTTCTATATTC
Hybo_R12107     GGATGACTAATCCGATATATACACGCAAATGGAGCCTCAATATTC
Hybo_G10023     GGATGATTAATCCGATATATACACGCAAACGGGGCCTCAATATT?
Lophur_7253     GGCTGACTAATCCGCTATCTCCACGGAAACGGAGCCTCCATATTT
Lophur_7366     GGCTGACTAATCCGCTATCTCCACGGAAACGGAGCCTCCATATTT
SteaTM40998     GG?TGACTAATCCGCTATCTTCACG?CAATGGGGCCTCCATATTT
SteaTM41035     GGATGACTAATCCGTTATCTTCATGCCAACGGAGCTTCCATATT?
Tater_11734     GGATGATTAATTCGATATATACATGCAAACGGAGCTTCCATATTT

Akodon_____     TTTATCTGCCTCTTCATCCACGTAGGCCGAGGTATTTACTATGGT
Bolomys____     TTCATCTGTCTTTTCATCCATGTAGGCCGAGGAATTTACTATGGC
Arvica_7631     TTTATCTGCCTATTCCTACATGTAGGACGAGGCATATACTACGGA
Arvica_6072     TTTATCTGCCTATTCCTACATGTAGGGCGAGGCATATACTACGG?
Cricet_7221     TTCATTTGCCTATTTATCCACGTAGGACGAGGCATCTACTACGGC
Crice_11746     TTCATTTGCCTATTTATCCACGTAGGACGAGGCATCTACTACGGC
Taterillus_     TTCATTTGTCTATTTATTCATATCGGACGGGGAATCTACTATGGA
Deom_R13237     TT?ATTTGCCTAT?TCTACACGTAGGTCGAGGCATTTATTACGGT
Hybo_R12107     TTCATTTGCTTGTTTCTTCATGTAGGACGAGGAATATACTATGGA
Hybo_G10023     TT?ATTTGCCTGTTCCTCCATGTAGGACGAGGGATATACTATGGA
Lophur_7253     TTCATTTGC?TATTCCTACACGTAGGCCGAGGGATTTACTACGGC
Lophur_7366     TTCATTTGC?TATTCCTACACGTAGGCCGAGGGATTTACTACGGC
SteaTM40998     TTCATTTGCCTTTTTATCCATGTAGGCCGAGGAATTTATTATGGA
SteaTM41035     ???ATTTGTCTATTTATTCATGTAGGCCGAGGAATTTACTACGGA
Tater_11734     TTTATTTGCTTATTTATTCACATTGGACGAGGCATTTATTATGGC

Akodon_____     TCCTATACCCTCTCAGAAACCTGAAACATTGGCATCATCTTATTC
Bolomys____     TCCTATGTCCTATCAGAAACCTGAAATATTGGTaTTATCTTATTT
Arvica_7631     TCCTATACATTTCTAGAGACATGAAACATTGGTGTAGCATTACTA
Arvica_6072     TCCTATACATTTCTAGAGACATGAAACATTGGTGTAGCATTACTA
Cricet_7221     TCTTTCACCTCAATAGAAACATGGAACGTAGGCATCATCCTACTA
Crice_11746     TCTTTCACCTCAATAGAAACATGGAACGTAGGCATCATCCTACTA
Taterillus_     TCATATATTTT?ACCGAAACATGAAACATCGGAGTTTTACTACTA
Deom_R13237     TCATATACCTTCATAGAAACCTGAAATATTGGTATTATTCTACTA
Hybo_R12107     TCCTATACATTTCTAGAAACATGAAATATCGGAGTTATCCTACTA
Hybo_G10023     TCCTATACATTTGTAGAAACATGACACATTGGGATTATTCTACTA
Lophur_7253     TCCTACACCATGATTGAAACATGAAACATCGGAATTATCCTACTA
Lophur_7366     TCCTACACCATGATTGAAACATGAAACATCGGAATTATCCTACTA
SteaTM40998     TCATTTACATCAGTAGAAACATGAAACGTTGGCATTATCTTACTG
SteaTM41035     TCATTTACATCAGTAGAAACATGAAATGTTGGCATTATTTTATTG
Tater_11734     TCCTACCTCTACACAGAAACATGAAATATCGGAATCATCTTACTT

Akodon_____     CTCACAACTATAGCAACAGCATTTGTAGGATATGTACTCCCA
Bolomys____     TTTACAACTATAGCAACAGCATTCGTAGGATATGTCCTTCCA
Arvica_7631     TTTGCAGTCATAGCTACAGCATTCATAGGTTATGTACTTCCA
Arvica_6072     TTTGCAGTCATAGCTACAGCATTCATAGGTTATGTACTTCCA
Cricet_7221     TTCACAGTAATAGCAACCGCATTCATAGGCTACGTTCTTCCA
Crice_11746     TTCACAGTAATAGCAACCGCATTCATAGGCTACGTTCTTCCA
Taterillus_     TTTTCCGTTATAGCCACTGCCTTTATAGGGTATGTACTTCCA
Deom_R13237     TTTGCTGTCATAGCCACCGCATTCATAGGATATGTCCTTCCA
Hybo_R12107     TTCACAGTTATAGCTACTGCATTTATAGGCTATGTACTTCCA
Hybo_G10023     TTTACAGTTATAGCCACCGCATTTATAGGATATGTACTTCCA
Lophur_7253     TTCACTGTAATAGCAACTGCATTCATAGGTTATGTACTTCCA
Lophur_7366     TTCACTGT?ATAGCAACTGCATTCATAGG?TATGTACTTCCA
SteaTM40998     TTTACAGTTATAGCAACAGCATTCATAGGTTATGTTCTCCCA
SteaTM41035     TTTACAGTTATAGCCACAGCATTTATAGGTTATGTTCTCCCA
Tater_11734     TTTTCCGTAATAGCTACTGCATTCATAGGTTATGTTCT????
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Annex *(suite)*

Except for the position of the Gerbillinae in our dataset (not supported by significant bootstrap values), our cyt *b* phylogeny agrees with the UPGMA tree derived from DNA-DNA hybridisation data (Denys *et al.* 1995). Also in our cyt *b* phylogeny the dendromurines are paraphyletic, even in parsimony trees obtained using different ts/tv settings and weighting schemes. Whereas in trees obtained without differential weighting for different codon positions the *Steatomys-Cricetomys* clade is absent, the *Deomys-Lophuromys* clade was always present.

We suggest that the clustering of *Deomys* with the *Lophuromys* clade may be less surprising than has been suggested elsewhere (Denys *et al.* 1995). The *Deomys* skull is not only very distinct from that of other dendromurines, but its zygomatic plate and internal organs (stomach) have been reported to resemble the same features in *Lophuromys* (Rosevear 1969, Dieterlen 1976).

It is reassuring to conclude that the presented cyt *b* phylogeny confirms the paraphyly of the Dendromurinae as has been suggested based upon a tree derived from the DNA-DNA hybridisation data (Denys *et al.* 1995). However, in view of the discrepancies between the trees derived from molecular and morphological data from Denys *et al.* (1995), it is clear that additional molecular and morphological data will be required to establish the "true" interrelations among the dendromurines. Finally, as has been suggested earlier, partial cyt *b* sequences are not the most suitable dataset for phylogenetic studies of rodents (*e.g.* Verheyen *et al.* 1995). Early saturation of 3rd position changes and limited variation in 1st and 2nd position changes seem to result in too little phylogenetic information to yield conclusive answers concerning inter(sub) family questions in rodents.

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The effects of additional food on the demography of rodents in a subtropical grassland in Swaziland

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Manipulated increases in food supply have resulted in : 1) extension of the breeding season (Hubert *et al.* 1981, Zubaid and Gorman 1993), 2) increases in population size (Doonan and Slade 1995, Flowerdew 1972), 3) decreases in home range (Taitt 1981), and 4) increases in body weight (Leirs *et al.* 1990, Neal and Alibhai 1991).

The objectives of this study were to experimentally ascertain the effect of addition of supplemental food on a population of rodents in a grassland habitat in Swaziland.

Three permanently marked grids (100 m x 100 m) were established, in May 1995, on an unutilized natural grassland site in the Swaziland middleveld, near Matsapha (26°33'S 31°16'E). One plot served as the control. The experimental plots received 8 kg of food, consisting of equal amounts of rolled oats and rabbit pellets, in opened 340 ml coke cans from July (immediately after the July sampling period) until November. Rodents were trapped monthly on all three plots from June until November. One hundred Elliot and Sherman live-traps were set 10 m apart on each grid on three consecutive nights per month. Each trapped rodent was uniquely toe-clipped, sexed, weighed