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Molecular Phylogenetics and Evolution 37 (2005) 370–388
MOLECULAR PHYLOGENETICS AND EVOLUTION
www.elsevier.com/locate/ympev

Multigene phylogeny of the Old World mice, Murinae, reveals distinct geographic lineages and the declining utility of mitochondrial genes compared to nuclear genes

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Received 30 November 2004; revised 28 March 2005
Available online 21 June 2005

Abstract

Despite its great diversity and biomedical importance, the rodent subfamily Murinae is poorly resolved phylogenetically. We present the first cladistic analysis sampling multiple representatives of most major groups based on DNA sequence for three nuclear (GHR, RAG1, and AP5) and one mitochondrial (COII and parts of COI and ATPase 8) fragments. Analyzed separately, the four partitions agree broadly with each other and the combined analysis. The basal split is between a clade of Philippine Old Endemics and all remaining murines. Within the latter, rapid radiation led to at least seven geographically distinct lineages, including a Southeast Asian *Rattus* clade; a diverse Australo-Papuan and Philippine clade; an African arvicanthine group including the otomyines; an African *Praomys* group; and three independent genera from Africa and Asia, *Mus*, *Apodemus*, and *Malacomys*. The murines appear to have originated in Southeast Asia and then rapidly expanded across all of the Old World. Both nuclear exons provide robust support at all levels. In contrast, the bootstrap proportions from mitochondrial data decline rapidly with increasing depth in the tree, together suggesting that nuclear genes may be more useful even for relatively recent divergences (<10 MYA).

Keywords: Murinae; Gerbillinae; Deomyinae; Biogeography; Mitochondrial; Nuclear; *Mus*; *Rattus*; Africa; Asia

1. Introduction

The Murinae (the Old World mice and rats) are the largest subfamily of mammals, comprising well over 500 species and 113 genera (Musser and Carleton, 1993). They include the most commonly used laboratory species—the mouse *Mus musculus* and the rat *Rattus norvegicus*—as well as many reservoirs for human diseases. The purported fossil record of the transition leading to the *Mus*/*Rattus* split (Jacobs et al., 1990; Jacobs and Downs, 1994) is possibly the most widely applied calibration point for molecular-clock approaches to dating mammalian (and some nonmammalian) divergence dates (e.g., Ducroz et al., 2001; Huchon et al., 2002; Michaux et al., 2001; Salazar-Bravo et al., 2001; She et al., 1990; Smith and Patton, 1999; Steppan et al., 2004a). Nevertheless, we are remarkably ignorant of the phylogeny of the group, particularly the major lineages. No cladistic analyses have been published that sample broadly from among the primary informal groups or across the geographic range (but see Watts and Baverstock, 1995, discussed below). Misonne (1969), author of the most comprehensive systematic treatment to date, resisted making any formal classifications, used divisions and groups, and based them almost entirely on dental characters. Therefore, this most diverse and scientifically important of all mammalian sub-

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doi:10.1016/j.ympev.2005.04.016

families is also the least resolved phylogenetically. In sharp contrast, the second largest mammalian subfamily, the Sigmodontinae (≈325 species, Neotropical mice and rats; sensu Reig, 1986; Steppan, 1995; Steppan et al., 2004a), another muroid rodent group, although also historically problematic, has had several comprehensive treatments (Reig, 1986; Vorontsov, 1959), a generally recognized and fairly stable taxonomy, and morphological (Steppan, 1995) and molecular (D'Elía, 2003; Smith and Patton, 1999; Weksler, 2003) phylogenetic analyses. Resolving the phylogeny of the Murinae will greatly benefit such diverse fields as Old World biogeography, mammalian paleontology, mammalian molecular-clock studies, and even virology, immunology, and related biomedical fields.

Centers of murine diversity are in tropical Africa, Southeast Asia, and Australia/New Guinea (Australo-Papua). Each area seems to have its own characteristic groups (Watts and Baverstock, 1995), which may represent clades. Suggested groups include a suite of tribes (or subfamilies) in the Australasian region: e.g., the Anisomyini, Conilurini, Hydromyini, Rhychomyinae, Phloeomyinae(-idea), and Pseudomyinae. Lee et al. (1981) included the Hydromyini, Conilurini, and Uromyini (but not Anisomyini) in their Hydromyinae. Simpson (1945) elevated the New Guinea water rats to their own subfamily, the Hydromyinae, complementing his Murinae, and considered them an early murid radiation or even a branch of the Cricetidae (Simpson, 1961). A consensus has developed regarding the presence of at least two groups in Africa, the *Praomys* group that includes *Hylomyscus*, *Mastomys*, *Myomys*, and others like *Stenocephalemys* and *Colomys* (LeCompte et al., 2002a,b) and the arvicanthine group that includes *Aethomys*, *Rhabdomys*, and *Grammomys* (Jansa and Weksler, 2004; Steppan et al., 2004a; Watts and Baverstock, 1995). The otomyines, a clade of diurnal chewing specialists that had until recently been placed in their own subfamily, the Otomyinae, have been associated with both the arvicanthine group (Ducroz et al., 2001; Jansa and Weksler, 2004; Pocock, 1976; Senegas and Avery, 1998; Steppan et al., 2004a) and the *Praomys* group (Watts and Baverstock, 1995).

Misonne (1969) proposed four divisions in the Murinae and also recognized the Hydromyinae, although he thought that the latter probably evolved from one of the former. His treatment incorporated fossil taxa as well. His four divisions were: (1) the *Lenothrix–Parapodemus* division, including the likely basal and paraphyletic *Lenothrix* group from Indo-Australia; the *Parapodemus* group spanning Africa and Asia; the Australian *Mesembriones* "series"; and three African series, *Lophuromys–Colomys–Zelotomys*, *Acomys–Uranomys*, and the enigmatic *Malacomys*; (2) the *Arvicanthis* division, largely endemic to Africa but including several Indian forms; (3) the *Rattus* division, including the African *Praomys* group, Southeast Asian *Maxomys* and *Rattus* groups, Asian *Mus* group and the *Uromys* group of Australia, the Philippines, and other islands; (4) the basin-shaped molar division, a hodgepodge of morphologically similar forms thought to be independently derived, including some murines, the Hydromyinae of New Guinea, and the Rhyncomyinae of the Philippines. Some of these groups were hypothesized to be monophyletic and others, especially the *Lenothrix–Parapodemus* division, paraphyletic with respect to other groups.

Watts and Baverstock (1995) provided the best study to date in terms of taxonomic sampling and phylogenetic approach, combining the results of several of their previous studies based on microcomplement fixation of albumin. Although limited by a phenetic approach based on a single protein, they were able to resolve many branches in a large composite tree. The Philippine cloud rat *Phloeomys*, the largest murine at 2 kg, was found to be the sister group to all other sampled murines. *Micromys*, *Vandeleuria*, and *Millardia* also lay outside a diverse radiation, the basal branches of which were not resolved. Among the major clades belonging to this larger radiation was an African clade containing members of the *Praomys* and arvicanthine groups, a New Guinea clade including *Anisomys* and *Pogonomys*, a diverse Australasian clade including taxa sometimes assigned to the Hydromyini and Conilurini, and a Southeast Asian clade including *Rattus*, *Maxomys*, *Niviventer*, and *Sundamys*, among others ("*Rattus sensu lato*," Verneau et al., 1998). Other members of the diverse polytomous radiation not assignable to larger clades include *Mus*, *Apodemus*, and *Dasymys*. Watts and Baverstock concluded that much of the murine radiation took place as a consequence of range expansion across the Old World followed by formation of geographic barriers to gene flow and any subsequent dispersal, leading to local radiations in each of the centers of diversity: Africa, Southeast Asia, Australia, and New Guinea. Their sampling of the diverse Philippine fauna was limited to *Phloeomys*, so the place of that fauna in the radiation could not be assessed.

Two recent cladistic analyses using nuclear genes have provided some complementary insights into murine evolution. These are generally congruent with the microcomplement-fixation studies of Watts and Baverstock (1994a,b, 1995). Combining four genes (GHR, RAG1, BRCA1, and c-myc exon 3), Steppan et al. (2004a) discovered that the Philippine endemic *Batomys* diverged well before the rapid radiation that led to several distinct geographic lineages. The recognition that the basal radiation among murines predated the divergence of the lineages leading to *Mus* and *Rattus* led them to revise the phylogenetic placement of the fossil calibration of the transition of *Antemus* to *Progonomys*. The result was a younger estimate of the *Mus*/*Rattus* split than is normally used for molecular-clock dating. The

lineages resulting from the rapid radiation that occurred 2 MYA after the common ancestor of extant murines included Asian *Rattus*, a Philippine radiation including *Apomys* and the worm specialist *Rhynchomys*, Eurasian *Mus*, and two African clades (a *Praomys* group and an *Arvicanthis* group). The latter also included the diurnal otomyines, confirming previous studies that nested this sometimes-subfamily well within the Murinae. Jansa and Weksler (2004), using IRBP exon 1, also found that a Philippine endemic (*Phloeomys*, confirming the finding of Watts and Baverstock, 1995) diverged before a rapid radiation. They also found the radiation to contain many of the same geographic lineages that Steppan et al. (2004a) and Watts and Baverstock (1995) found: a *Praomys* group that may be closely related to *Mus*, a second African clade that includes the otomyines, a lineage consisting of the Philippine *Rhynchomys*, an expanded *Rattus* clade including other Southeast Asian forms, and also *Micromys*.

1.1. Objectives

Here we (1) identify major clades and outline broad relationships among major geographic groups, (2) identify any biogeographic patterns, and (3) compare the relative information content of four gene regions (three unlinked nuclear genes and one mitochondrial region) using repeatability (bootstrap percentages). We extend the taxon sampling of Steppan et al. (2004a) for growth hormone receptor (GHR) and recombination activating gene 1 (RAG1) to include more representatives of the several geographic regions and add entirely new sequences for acid phosphatase type V intron 2 (AP5) and three contiguous mitochondrial genes, COI, COII, and ATPase 8. In all, we have 4480 base pairs (bp) of nuclear DNA sequence and approximately 1160 bp of mitochondrial DNA.

2. Methods

2.1. Specimens and genes sequenced

We included data from 63 species belonging to 51 genera representing most of the major suspected lineages. Of these taxa, seven additional genera and one additional species from Australo-Papua were sequenced for AP5 only. We tested species identifications by sequencing second individuals for AP5 for 14 species and from unpublished RAG1 data for another 10 species. AP5 sequences for five species of *Mus* and *Rattus* (two of which were also represented in our samples) were downloaded from GenBank (DeBry and Seshadri, 2001). Specimen identification and locality information are listed in Appendix A, GenBank accession numbers in Appendix B. The clade of Deomyinae and Gerbillinae was designated as the sister group to Murinae based upon the results of the broader taxon sampling of Muroidea in Steppan et al. (2004a). Sequences have been submitted to GenBank with accession numbers listed in Appendix B.

Specimens were sequenced for three unlinked nuclear genes (exon 10 of GHR, nearly all of RAG1, and intron 2 and flanking exon regions of AP5) and three mitochondrial genes (COI, COII, and ATPase 8). Intervening tRNA sequences between the mitochondrial genes were excluded from analysis because of difficulty in alignment. Each of the genes included has proven utility for rodent systematics (Adkins et al., 2001a, 2003; DeBry and Sagel, 2001; Steppan et al., 2004a,b). Aligned sequence lengths were 981 bp for GHR, 3053 bp for RAG1, 446 bp for AP5, and 1158 bp, plus 232 bp of excluded tRNAs, for mtDNA, for a total of 5638 bp of aligned and analyzed data.

2.2. DNA extraction and sequencing

Total genomic DNA was extracted from liver or muscle by PCI (phenol/chloroform/isopropanol)/CI (chloroform/isopropanol) "hot" extraction (Sambrook et al., 1989). GHR, RAG1, and AP5 were amplified and sequenced with primers and under reaction conditions described previously (Adkins et al., 2001b; DeBry and Seshadri, 2001; Steppan et al., 2004a,b). All mtDNA amplifications were performed at 45 °C for 30 cycles, because of the high number of substitutions among samples and frequency of primer–template mismatches. Initially, PCR was performed with the primers 6520F (5′-GCWGGMTTYGTNCACTGATTCCC-3′) and 7927R (5′-GAGGMRAAWARATTTTCGTTCAT-3′). If a band was not visible after agarose–ethidium bromide electrophoresis, 3 μL of the initial PCR product was subjected to amplification with every combination of the original PCR primers and primers 6613F (5′-AACATRA CATTYTTYCCWCAACA-3′) and 7766R (5′-GANG AWGTRTCWAGTTGTGGCAT-3′). Successful PCR amplifications were sequenced with the PCR primers and primers 7101F (5′-CAYGAYCAYACNYTWAT AAT-3′) and 7481R (5′-CAKGARTGNARNACRTC TTC-3′). All numbering is based on the revised mtDNA sequence of *M. musculus* C57BL/6J (Bayona-Bafaluy et al., 2003).

Negative (no DNA) controls were included with every reaction to reveal instances of DNA contamination of reagents. PCR products were visualized on an agarose gel with ethidium bromide, and successful amplifications were isolated from a low-melting-point gel with Wizard PCR prep reagents (Promega, USA) or prepared directly by enzymatic digestion with ExoSAP-IT (USP, Cleveland, USA). Both strands of each PCR product were completely sequenced with PCR primers and an arrangement of internal primers that

varied depending on the species by automated DNA sequencing on an ABI 3100 machine using big-dye terminator chemistry (Applied Biosystems).

2.3. Analyses

Results of individual sequencing runs for each species were combined into contiguous sequences with Sequencher (GeneCodes), and regions of ambiguity or disagreement resolved through manual inspection of sequence traces. Initial multiple alignments of sequences across species were performed with Clustal X (Thompson et al., 1997). A range of parameter values were applied (gap opening 5–50, gap extension 0.06–0.60, and DNA transition weight 0.30–0.60); all but the most extreme resulted in alignments identical to that produced by the default values (10, 0.20, and 0.50). Manual refinement consolidated for a small number of noncoding indels and brought coding region indels into the coding frame. Alignment of all protein coding regions was trivial because amino acid indels were rare and unequivocal. Parsimony-informative indels were coded as presence/absence characters regardless of length and appended to the data sets for maximum parsimony analyses. Sequences for the genes were concatenated for each taxon.

Heterogeneity of nucleotide composition among informative sites was determined using PAUP* version 4.0b10 (Swofford, 2002). Phylogenetic analyses were conducted for each gene separately under maximum-parsimony (MP), maximum-likelihood (ML), and Bayesian approaches with the programs PAUP* version 4.0b10 (Swofford, 2002) and MrBayes V3.0 (Huelsenbeck and Ronquist, 2003). All MP analyses used heuristic searches with tree bisection-reconnection (TBR) branch swapping and 100 (AP5), 200 (GHR) or 1000 (all other partitions) random-addition replicates. All transformations were weighted equally, including indels. A sequential optimization approach (Fratti et al., 1997, Swofford et al., 1996) was used to estimate the ML phylogeny. Initial trees were generated under MP. ML parameter values were estimated under a nested array of substitution models for the MP trees as implemented in Modeltest 3.04 (Posada and Crandall, 1998), with parameters for nucleotide substitution rates and among-site rate variation; a portion of the sites was assumed to be invariable (I), and rates among all sites were assumed to vary according to a gamma distribution (Γ: Yang, 1994). Likelihood-ratio tests were used to identify the simplest models of sequence evolution that adequately fit the data and phylogeny (Yang et al., 1995). The following models were selected for each data set: GHR (HKY + I + Γ), RAG1 (SYM + I + Γ), AP5 (HKY + Γ), mtDNA (GTR + I + Γ), and concatenated (GTR + I + Γ). A ML search was then conducted under the preferred model with parameters fixed to the values estimated on the MP tree. Heuristic searches were conducted with 10 (total data) to 30 (individual genes) random-addition replicates and TBR branch swapping. Model parameters were reestimated from the initial ML tree and the process was repeated until the topology remained constant. The optimal phylogeny was always found on the first search.

Nonparametric bootstrapping (Felsenstein, 1985) was performed on all data partitions: 200 replicates for ML and 500 replicates for MP. Bootstrap analyses for MP and ML used 10 random-sequence addition replicates per bootstrap replicate. Likelihood bootstrap analyses were limited to 2–4000 rearrangements for individual nuclear genes (10,000 for AP5) and combined-data set, but 20 random-sequence addition replicates and 40,000 rearrangements (per each sequence-addition replicate) for the mitochondrial data set. The mitochondrial analyses converged on the maximum likelihood much less rapidly than the nuclear genes. Restricting the number of rearrangements reduces the chances that the optimal tree will be found for each replicate but is a conservative procedure more likely to reduce bootstrap values than to inflate them (Steppan et al., 2004b). The ML bootstrapping was performed with PAUP* (Swofford, 2002) on a 200-processor cluster using Condor job management.

Analyses were performed on individual genes and on a concatenation. A partition-homogeneity test (200 replicates) (Farris et al., 1994, 1995) on the set of taxa represented by all four gene regions indicated no significant heterogeneity in phylogenetic signal ($P = 0.87$). Parsimony-informative indels, all corresponding to whole codons in the exonic regions, were excluded from ML and Bayesian analyses.

Bayesian analysis, with MrBayes (Huelsenbeck and Ronquist, 2003), of the total data set used the GTR + I + Γ model with the addition of partitioning by codon position in each genome separately. The result was seven partitions: the three nuclear codon positions, the three mitochondrial codon positions, and the introns/UTR. Parameters were estimated for each partition separately (''unlinked''). Five chains were run for 10 million (nuDNA) to 16 million (mtDNA) generations; trees and parameters were recorded every 500 generations. We ran MCMC parameters ''hot'' to explore parameter space more fully: temp = 0.5, swapfreq = 2. We examined partition frequencies regularly in 200,000-generation bins from one run to verify that partition frequencies were stable. Although stable partition frequencies and overall likelihood were achieved by generation 200,000, we excluded the first 4 million generations as the ''burn-in'' period.

Two sets of analyses were run for AP5: those taxa included in the combined-data analysis and all taxa with available sequences. Trees and alignments for each gene have been submitted to TreeBase under Accession No. S1298 and M2266–2271.

3. Results

3.1. Individual locus phylogenies

The four ML phylogenies estimated from the individual loci are in broad agreement (RAG1, Fig. 1; GHR, Fig. 2; mtDNA, Fig. 3; AP5, Fig. 4). All find a monophyletic Murinae and agree that the Philippine Old Endemics *Batomys* and *Phloeomys* constitute a basal lineage, and three of the four loci (all but AP5) place this pair as the sister group to all other Murinae. AP5 (Fig. 4) groups the Philippine Old Endemic pair with an African clade, but the shared branch is short, and support is weak (48% ML bootstrap, 0.65 posterior probability [pp]). Maximum parsimony trees differed from their respective ML trees at 1–5 nodes, none of which were

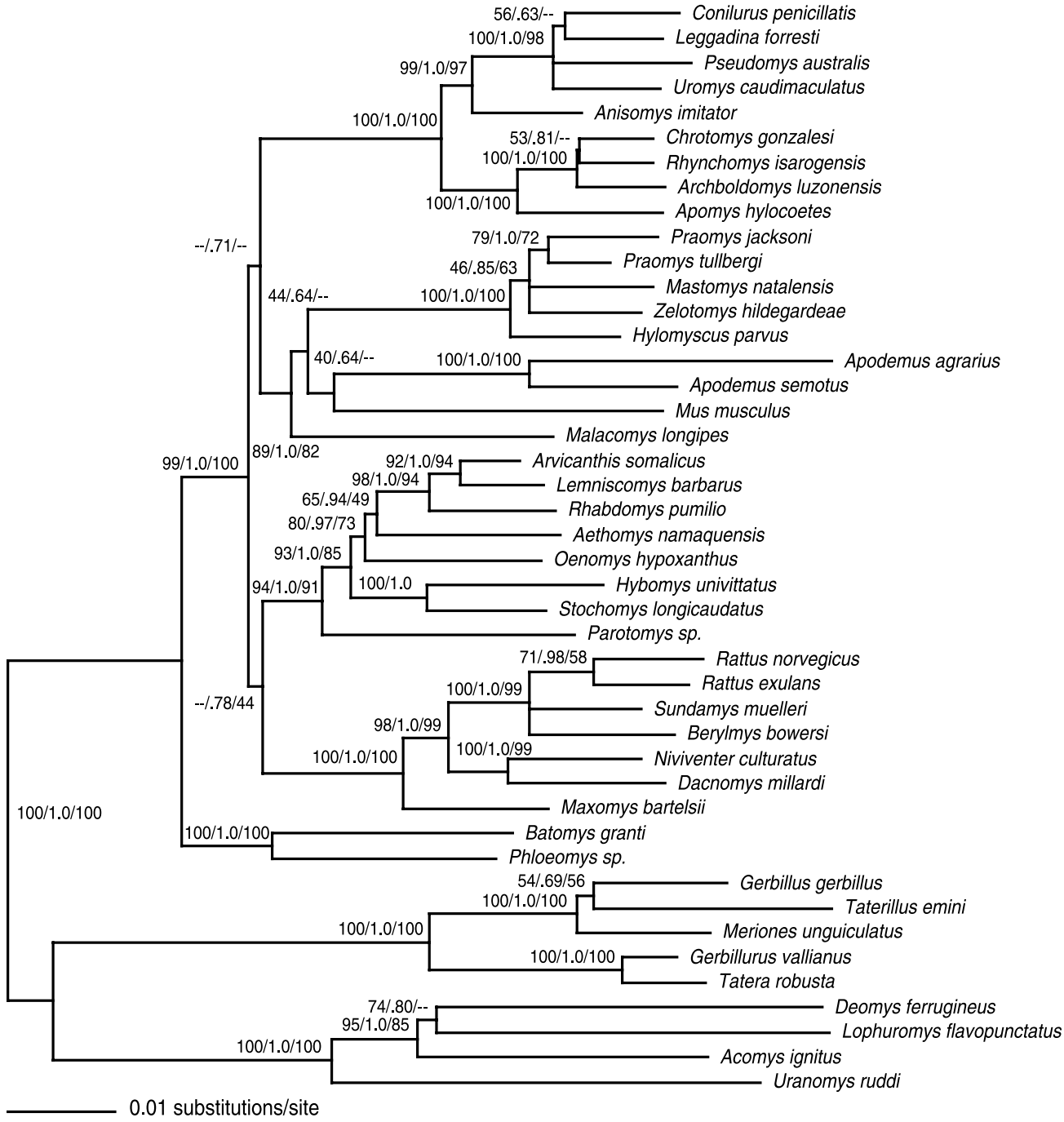

Fig. 1. RAG1 maximum-likelihood phylogram. Numbers above branches are ML bootstrap proportions/Bayesian posterior probabilities/MP bootstrap proportions. Symbol "--" signifies that node was not present in bootstrap consensus tree. Only nodes with either bootstrap or posterior probabilities >50% are labeled.

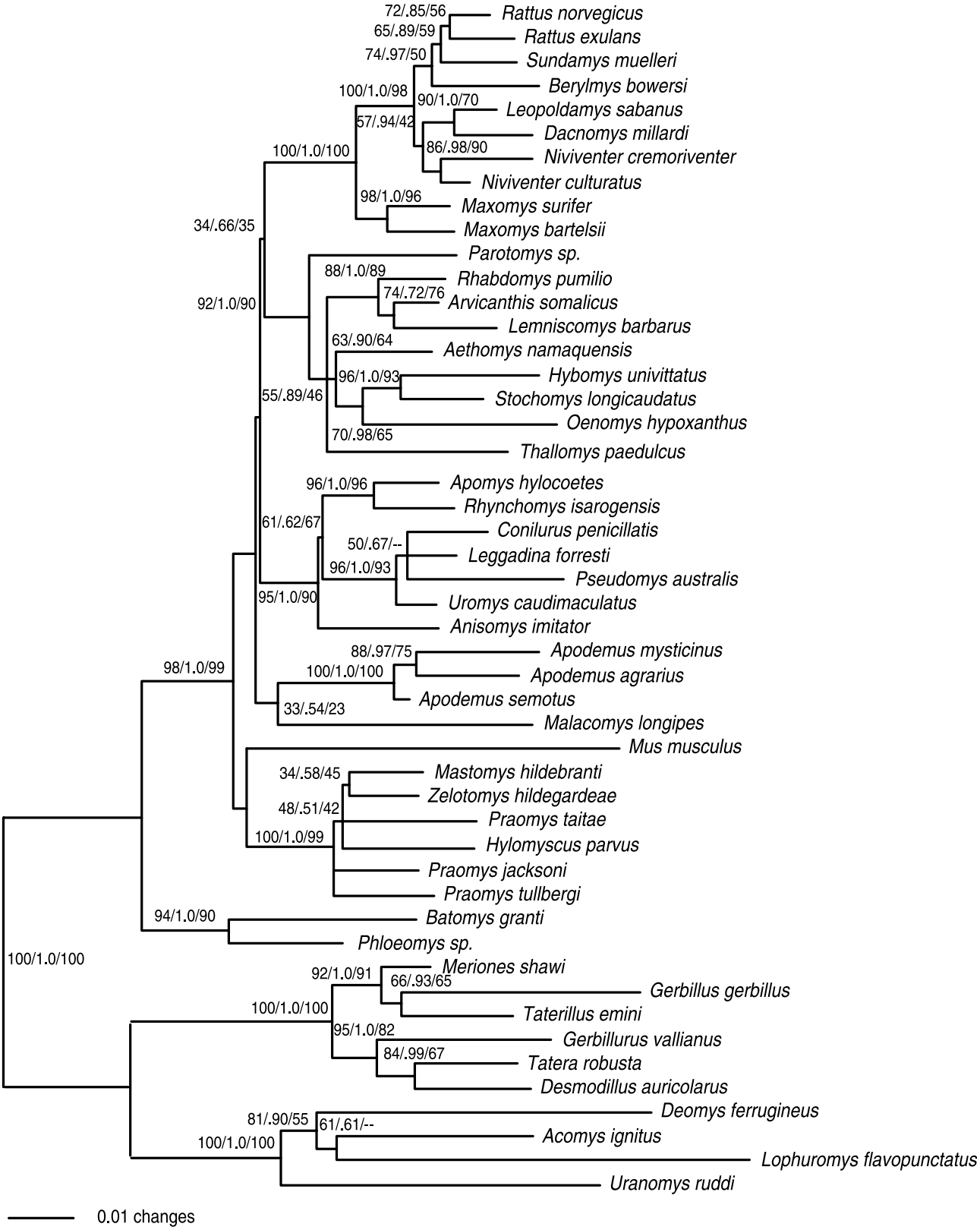

Fig. 2. GHR maximum-likelihood phylogram. Numbers above branches are ML bootstrap proportions/Bayesian posterior probabilities/MP bootstrap proportions. Symbol "--" signifies that node was not present in bootstrap consensus tree. Only nodes with either bootstrap or posterior probabilities >50% are labeled.

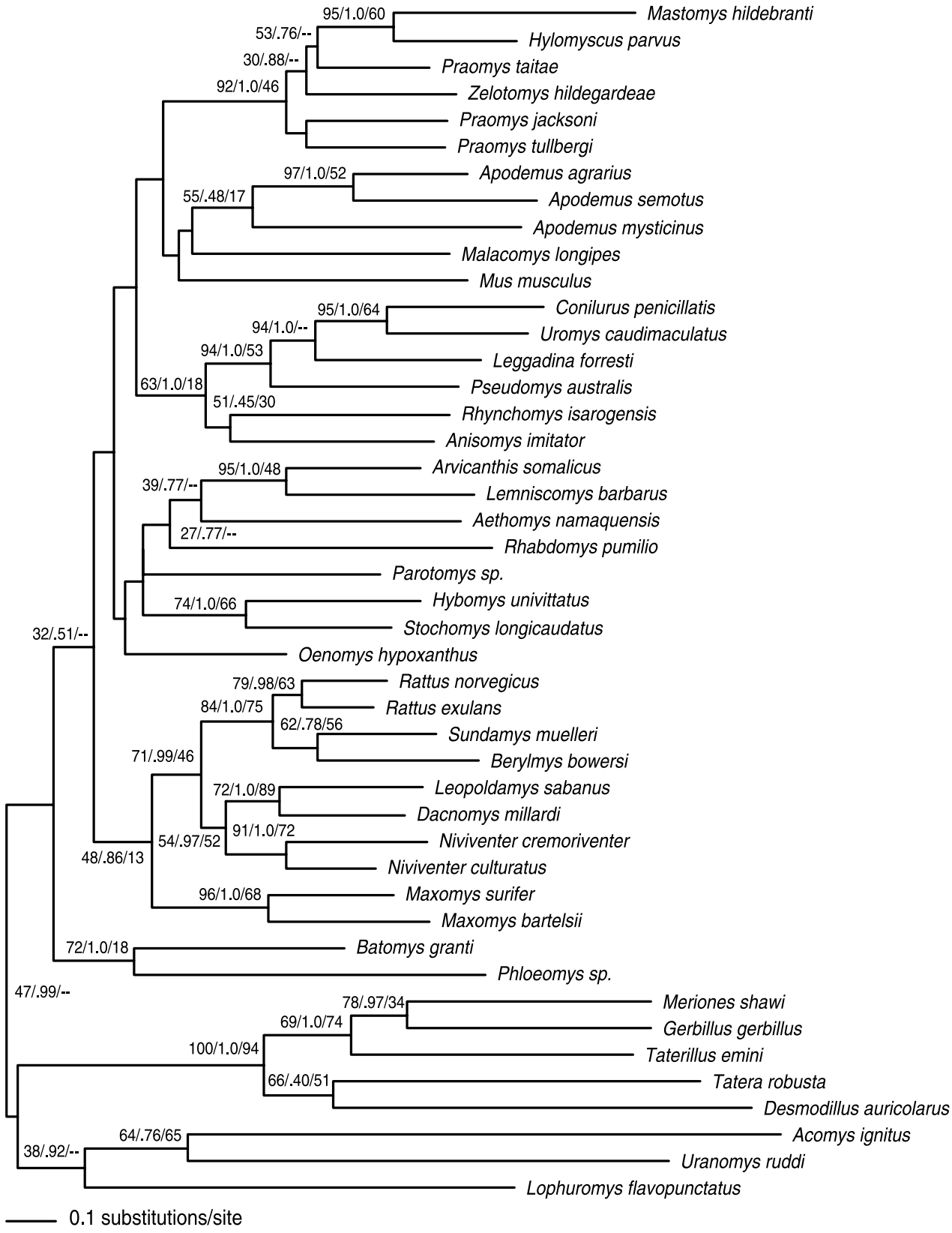

Fig. 3. mtDNA maximum-likelihood phylogram. Numbers above branches are ML bootstrap proportions/Bayesian posterior probabilities/MP bootstrap proportions. Symbol "--" signifies that node was not present in bootstrap consensus tree. Only nodes with either bootstrap or posterior probabilities >50% are labeled.

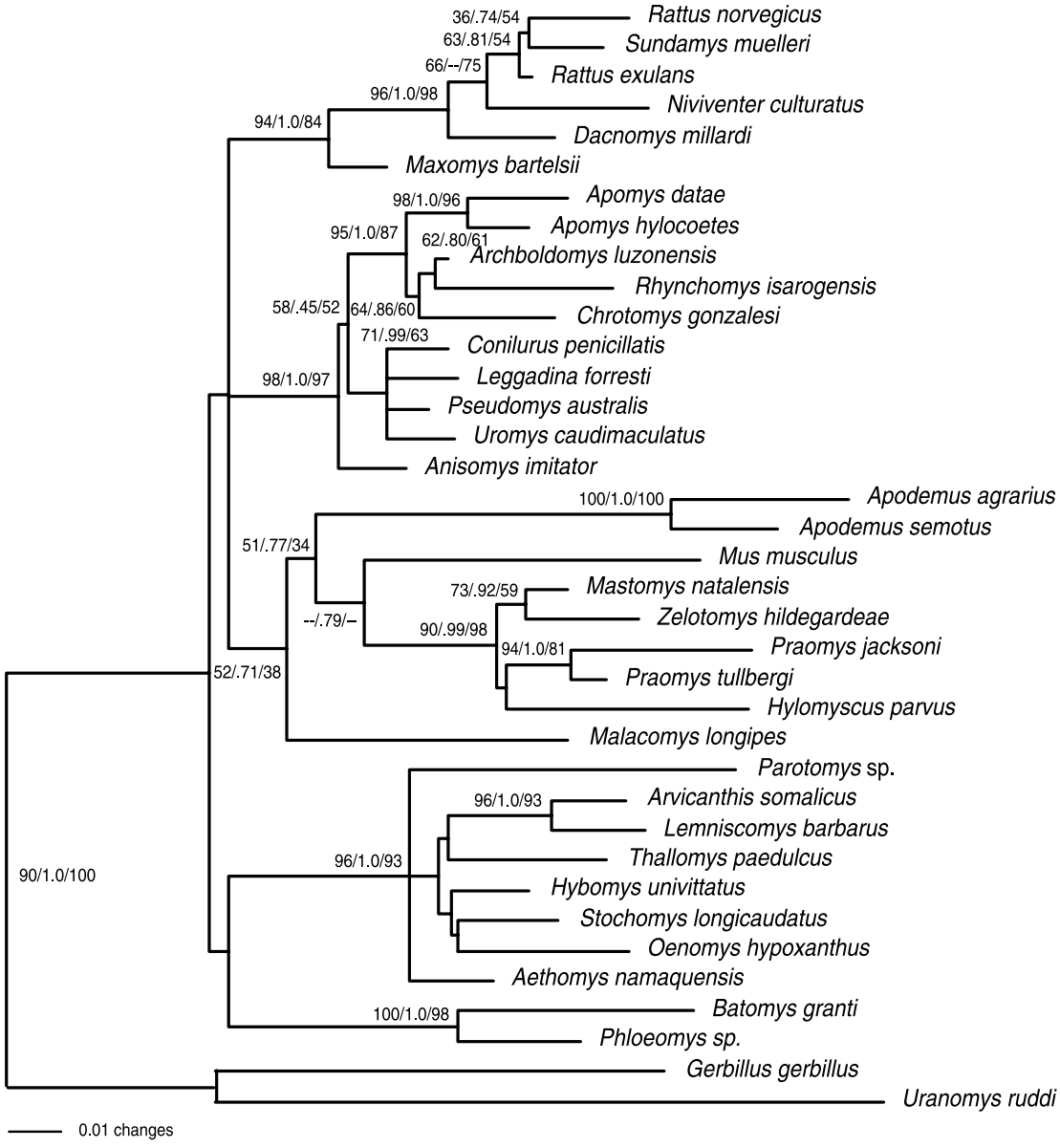

Fig. 4. AP5 maximum-likelihood phylogram. Numbers above branches are ML bootstrap proportions/Bayesian posterior probabilities/MP bootstrap proportions. Symbol "--" signifies that node was not present in bootstrap consensus tree. Only nodes with either bootstrap or posterior probabilities >50% are labeled.

even moderately supported (>50%) in MP bootstrap analyses. Only five nodes conflicting with ML trees had bootstrap values between 40 and 50%—and two of those involved the *Deomys*/*Acomys*/*Lophuromys* trichotomy. Because there is no strong conflict between MP and ML results, unless otherwise noted, reported bootstrap values and topologies are for the ML analyses.

Within the core murines (all murines sister to the *Batomys* and *Phloeomys* clade), all four loci identify seven distinct lineages: (1) a Southeast Asian clade containing *Rattus* sensu lato and *Maxomys*; (2) an African clade consisting of the arvicanthine group sensu lato plus the otomyine *Parotomys*; (3) the African *Malacomys*; (4) Eurasian *Mus*; (5) the Eurasian field mouse *Apodemus*; (6) the African *Praomys* group; (7) an Australasian group including both Philippine and Australo-Papuan clades. Monophyly of each of the five multigeneric lineages is well supported by the three nuclear loci (92–100% bootstrap, 0.99–1.00 pp) but are not as well supported by mtDNA (1–91% bootstrap, 0.35–1.00 pp).

None of the loci provides consistently high support for relationships among these seven lineages nor do they agree on the topology. Among all the results, only one node that unites two or more of these lineages receives greater than 50% bootstrap support, that of the *Malacomys*/*Mus*/*Apodemus*/*Praomys* group for RAG1 (89%, 1.0 pp; Fig. 1) and AP5 (64%, 0.99 pp; Fig. 5). GHR does

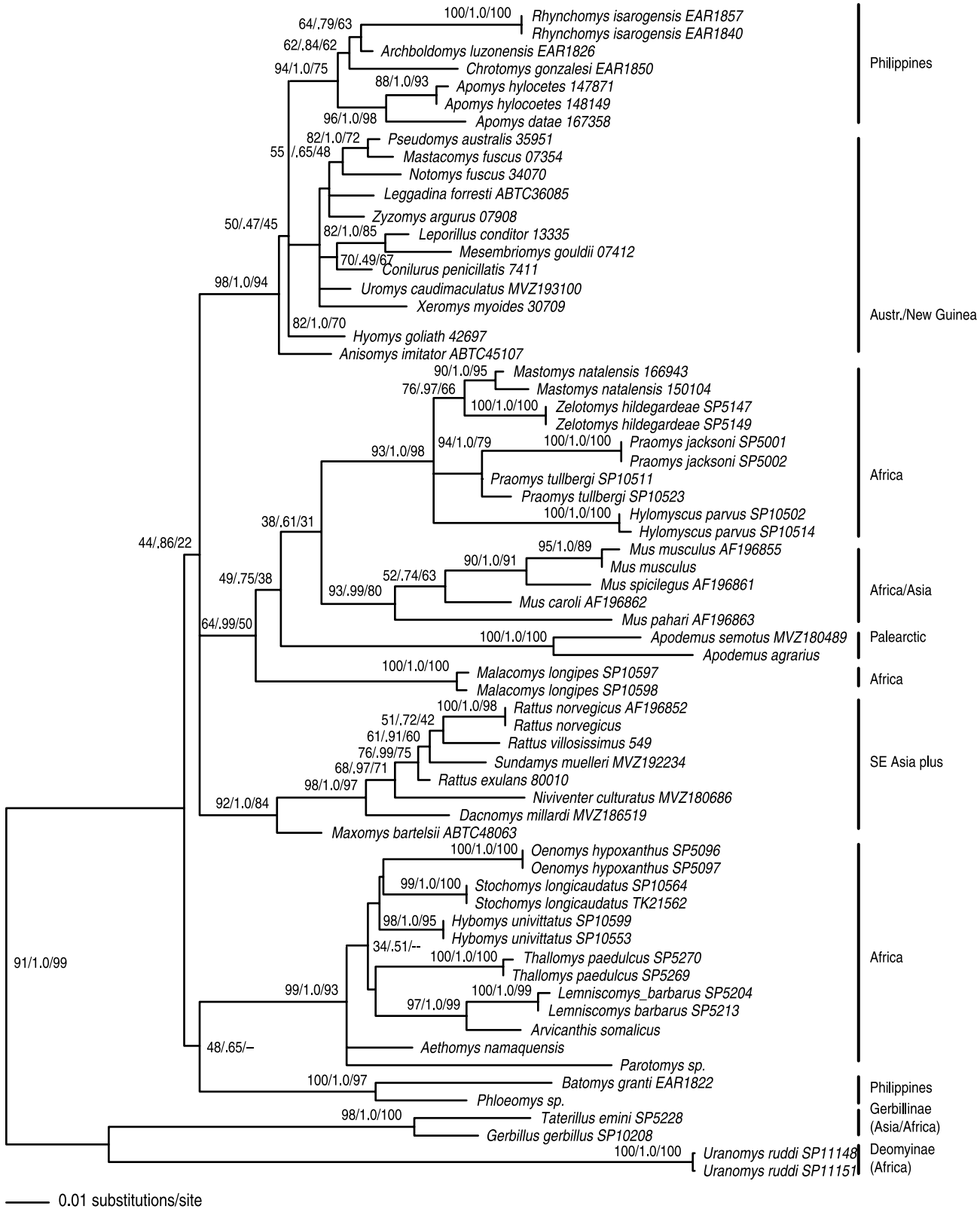

Fig. 5. Maximum-likelihood phylogram for AP5 with expanded taxon sampling. Numbers above branches are ML bootstrap proportions/Bayesian posterior probabilities/MP bootstrap proportions. Symbol "--" signifies that node was not present in bootstrap consensus tree. Only nodes with either bootstrap or posterior probabilities >50% are labeled. Geographic distribution of clades is shown on the right.

not recover this clade, splitting it into two nearby clades, but if the outgroups are removed and the question is viewed as one of rooting with regard to where *Batomys*/*Phloeomys* join the remaining murines, all four genes yield nearly the same unrooted network—the arvicanthine and *Rattus* clades are separated by a short branch from the Australasian and *Malacomys*/*Mus*/*Apodemus*/*Praomys* group clades. The four loci yield four different resolutions within the *Malacomys*/*Mus*/*Apodemus*/*Praomys*-group clade. Thus, with respect to the major lineages, the four loci differ in only two aspects, the rooting of the core murines and the relationships among the *Malacomys*/*Mus*/*Apodemus*/*Praomys* groups.

Within each of the five polytypic lineages, the four loci are generally congruent. For example, all place *Maxomys* as sister to the rest of the *Rattus* clade, identify three Australasian clades (the Papuan *Anisomys*, the Philippine *Apomys*/*Rhynchomys* clade, and the Australian *Conilurus*/*Pseudomys* clade), and place *Arvicanthis* sister to *Lemniscomys*. Much of the rest of the tree is weakly supported by individual loci because of short branches.

Parsimony analysis of the mtDNA yields a poorly supported tree in conflict in many ways with the ML mtDNA tree and all other genes under both criteria. For example, the deomyine *Lophuromys* groups with *Malacomys* (that together break up the Australasian clade), *Batomys* and *Phloeomys* are not sister taxa (the latter grouping with *Apodemus*), the African *Hybomys* and *Stochomys* are placed in the Southeast Asian *Rattus* group rather than the arvicanthine group, and *Parotomys* is sister to *Lemniscomys*. None of these anomalous groupings nor associated intervening nodes are supported by greater than 25% MP bootstrap values and several are not even the most frequent of many alternative resolutions in the bootstrap analysis. In contrast, the ML analysis of the mtDNA is largely congruent with the nuclear genes.

We sequenced additional taxa for AP5 and present Fig. 5 to illustrate a broader view of the Murinae and to test many species assignments by adding second individuals for many species. All species are monophyletic, and the individual pairs are identical or nearly so. The additional species yield several observations: *Rattus villosissimus* is sister to *Rattus norvegicus*; *Mus* is a relatively old genus, whose most recent common ancestor appears to be as old or older than most entire generic groups (e.g., *Praomys* group, arvicanthine group, Southeast Asian group, and the diverse Australasian group); the New Guinea taxa (*Anisomys* and the giant rat *Hyomys*) may be paraphyletic with respect to the rest of the Australasian clade; the Acacia rat *Thallomys* appears to be a basal member of the arvicanthine group (but see caveat in Section 4); *Mastomys* and the hopping mouse *Notomys* may be closely related to *Pseudomys*; and membership of the Australo-Papuan clade is expanded to include the rock rat *Zyzomys*, the stick-nest rat *Leporillus*, *Mesembriones*, and *Xeromys*. Within the Australo-Papuan clade, all 10 Australian genera form a well-supported clade that is sister to the Philippine clade. Relationships among the Australian taxa are poorly resolved except for two small clades; *Pseudomys* and *Mastacomys*, and *Leporillus* and *Mesembriomys*.

3.2. Combined-data phylogeny

The combined data produced a single ML tree (Fig. 6; $L = -46512.76$). All the common features among the individual genes are preserved in the combined-data analysis. Within the core murines (excluding *Phloeomys* and *Batomys*), seven distinct lineages can be recognized (labeled "A" through "G" in Fig. 6), among which the branching order is not decisively estimated as measured by bootstrap values; however, posterior probabilities for several exceed 0.90. Several clades have moderately strong support (e.g., clade D–G, 88% bootstrap, 1.0 pp; clade C–G, 69% bootstrap, 0.92 pp; clade B–G, 64% bootstrap, 0.89 pp). Relationships among clades D, E, F, and G are particularly unstable.

The first clade to diverge from the remaining core murines appears to have been the *Rattus* group (clade A). This is a largely Southeast Asian group; *Maxomys* diverges first, followed by a split between *Rattus sensu lato* (including *Sundamys* and *Berylmys*) and a clade consisting of *Niviventer*, *Dacnomys*, and *Leopoldamys*. Resolution within this group appears to be very robust. The second clade to diverge (clade B) is the Australasian group, including taxa historically assigned to the Rhynchomyidae, Conilurinae, Anisomyinae, and Hydromyinae. Among sampled species, two clades appear to emerge, a Philippine group (*Apomys*, *Archboldomys*, *Chrotomys*, and *Rhynchomys*) and an Australo-Papuan group. Moderate support places *Anisomys* in the Australo-Papuan group, sister to the Australian taxa, although some individual genes place it sister to all members of clade B, as does MP analysis of the concatenated data set. This is the only moderately supported conflict (66% MP versus 81% ML bootstraps) between MP and ML in this study. Despite the large numbers of data, branching within the *Rhynchomys* group appears effectively unresolved. In combination with the more distantly related Philippine Old Endemic pair, three of the four basal lineages are Southeast Asian.

Two of the remaining lineages are African, and we find no support for placing them as sister taxa to form a monophyletic African clade. The earlier of these two to diverge and diversify is the arvicanthine group (clade C), which includes the diurnal whistling-rat *Parotomys*, historically associated with the Otomyinae. Most nodes are well supported within this clade. One subclade in-

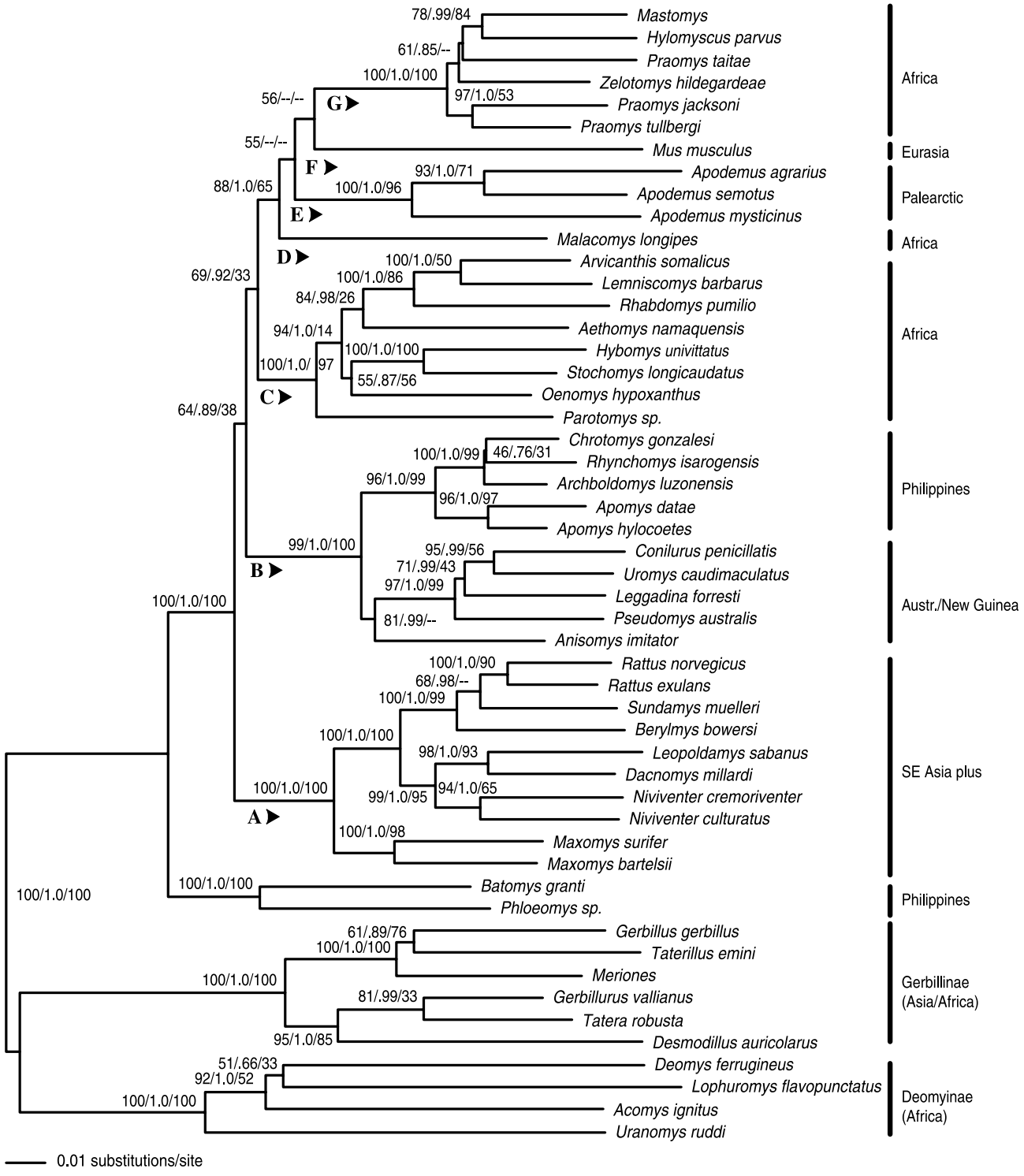

Fig. 6. Combined-data maximum-likelihood phylogram. Numbers above branches are ML bootstrap proportions/Bayesian posterior probabilities/MP bootstrap proportions. Letters identify clades discussed in the text. Symbol "--" signifies that node was not present in Bayesian consensus tree. Geographic distribution of clades is shown on the right.

cludes striped forms (*Rhabdomys* and *Lemniscomys*) and appears sister to the rock mouse *Aethomys*. The second African lineage (clade G) conforms to the *Praomys* group. It appears to have radiated more recently and quite rapidly; resolution among its basal branches is very poor. The multimammate rat *Mastomys* appears most closely related to *Hylomyscus*, a result most likely attributable to the mtDNA data because the nuclear genes yield different results. Although the intervening nodes are poorly supported, *Praomys* appears polyphy-

letic because in none of the individual gene trees is it monophyletic.

The remaining three lineages contain single genera given our sampling: *Malacomys* (clade D), *Apodemus* (clade E), and *Mus* (clade F). *Apodemus*, like *Mus*, is an old genus with internal nodes deeper than several of the diverse radiations already mentioned (e.g., the *Praomys* group, Philippine New Endemics, Australo-Papuan group). Relationships among these three lineages are the most poorly resolved of the seven major lineages of core murines.

Although the Gerbillinae were not the focus of our study, the sampling is sufficient to indicate that the two tribes represented here are not reciprocally monophyletic. *Taterillus* is not in a clade with other "Taterillini" (*Tatera*, *Gerbillurus*) but is instead nested within the Gerbillini.

3.3. Comparison of bootstrap support among loci

In the deeper regions of the tree, bootstrap percentages and posterior probabilities are distinctly lower for the mitochondrial genes than for the nuclear loci, despite many more parsimony-informative characters. Similarly, the deepest branches, particularly among the outgroups, are much shorter than the terminal branches on the mtDNA tree (Fig. 3). We explored these phenomena by comparing bootstrap support for nodes as a function of depth in the tree. Using node depth rather than pairwise distances avoids the problem in which multiple comparisons cause nonindependence of data points and creates a single scale on which the different genes can be directly compared. The basal node (MRCA) of the Murinae was set to a depth of 1.0, and after estimating branch lengths under a molecular-clock assumption, we calculated relative depth for all nodes in the respective phylogenies. RAG1 and GHR show no significant relationship between depth of the nodes and bootstrap percentages, but bootstrap values decrease significantly with increasing depth for mtDNA (Fig. 7).

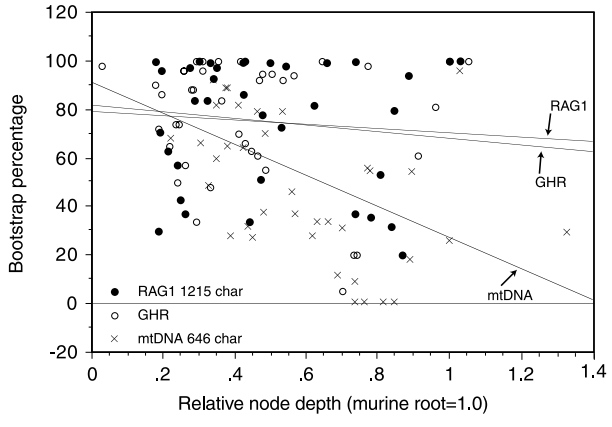

Fig. 7. Bootstrap proportions for three gene regions as a function of node depth. RAG1 and mtDNA regions were subsampled randomly down to the same number of parsimony-informative characters as in GHR. Regression equation are as follows: mtDNA, 646 characters, bp = 79.7–55.2 × mtDNA rel depth, $R^2 = 0.222$; RAG1, 1215 characters, bp = 78.0–5.8 × RAG1 rel depth, $R^2 = 0.003$; GHR, 943 characters, and bp = 81.7–11.5 × GHR rel depth, $R^2 = 0.013$.

4. Discussion

4.1. Murine phylogenetics

Our results confirm and extend the findings of the previous molecular studies that included more than a handful of murines. Watts and Baverstock (1995), using results compiled from microcomplement fixation of albumin (Watts and Baverstock, 1994a,b), identified many of the same groups we did: a Southeast Asian clade (=our clade A), independent *Mus* and *Apodemus* clades (clades E and F), and the early divergence of *Phloeomys*. The albumin data also revealed a rapid radiation of core murines separated by a relatively long branch from the early-diverging groups. Watts and Baverstock (1995) further identified African, Australian, and New Guinean clades, but their results differed somewhat from ours. They recovered a distinct and monophyletic African clade, whereas our data revealed at least two clades, subtended by long intervening branches. Their albumin data separated the Australian taxa from the New Guinea taxa and show the groups diverging at approximately the same time as the Southeast Asian clade, whereas our sequence data unite them into a more recent radiation with the Philippine group. Our data support a monophyletic Australian clade but not a New Guinea clade, suggesting that the *Apomys* group of Philippine endemics might have been derived from the east rather than from Southeast Asia.

We identified or confirmed eight distinct lineages. The oldest of these contains members of the Philippine Old Endemics as defined by Musser and Heaney (1992). Musser and Heaney (1992) suggested several alternative hypotheses regarding Philippine species but seemed to prefer a close association between *Phloeomys* and the *Crateromys* group (including *Batomys* and *Carpomys*). This group is quite distinct from another Philippine radiation that includes *Apomys* and which is closely related to if not part of an Australo-Papuan radiation (clade B). These other Philippine genera constitute most of the remaining lineages from Musser and Heaney's Old Endemics (a group that they cautioned was probably not monophyletic). The early divergence of this *Phloeomys* group was also seen with microcomplement fixation of albumin (Watts and Baverstock, 1995), with IRBP exon 1 (Jansa and Weksler, 2004), and in our broader sampling of muroids including BRCA1 (Step-

pan et al., 2004a). Whether the Philippine Old Endemics represent a relictual distribution from the periphery or the core of the ancestral range of the Murinae cannot be determined. Additional sampling of Philippine (e.g., *Crateromys*, *Crunomys*) and Southeast Asian (e.g., *Bunomys*, *Chiropodomys*, *Melasmothrix*) forms would help resolve this issue provided they do not simply fall into one of the eight existing clades.

Several of the labeled clades were anticipated by other studies. Clade A conforms to the "S-e Asian" clade of Watts and Baverstock (1995) and "*Rattus sensu lato*" of Verneau et al. (1998). We also confirmed and refined the *Praomys* group (sensu LeCompte et al., 2002a,b) and an arvicanthine group (Ducroz et al., 2001). Ducroz et al. (2001) proposed the name Arvicanthini for the sister group to "Otomyini" without defining it formally and restricted the "arvicanthines" to the clade subtended here by *Arvicanthis–Rhabdomys*. We also find evidence of close relationship between *Mus* and the *Praomys* group and moderate support for uniting these with *Apodemus* and *Malacomys* near the base of the rapid radiation of core murines. The short internal branches, low repeatability, and conflict among genes for internal branches within the *Praomys* group are consistent with the findings by LeCompte et al. (2002b) of nonresolution and a rapid radiation.

The Arvicanthine group appears to include the Acacia rat *Thallomys* (Fig. 5), but we hesitate to draw this conclusion because our two *Thallomys* samples were nearly identical to a *Grammomys*. A close association is not surprising (Watts and Baverstock, 1995), but because some sequences were identical, we suspect that the *Grammomys* sample was actually a misidentified *Thallomys*. All three were collected on the same expedition. Until we can examine the vouchers ourselves, we cannot exclude the possibility that the *Thallomys* are actually *Grammomys*.

Perhaps our most surprising finding is the close relationship between a diverse group of Philippine taxa (the forest mouse *Apomys*, the worm specialist *Rhynchomys*, and other shrew-rats *Chrotomys* and *Archboldomys*) and the Australo-Papuan group. The close association of *Apomys* with the shrew-rats was anticipated by Musser and Heaney (1992), although they did not suggest as recent a radiation as our data indicate. The basal divergence of this larger clade (B) appears more recent than that of any of the other major clades except the *Praomys* group (G), even though many of its members have been elevated to subfamily or even family status because many possess highly derived morphologies. Examples include the Hydromyinae (Baverstock et al., 1983; Misonne, 1969; Simpson, 1961; Tate, 1936), Rhynchomyinae (Misonne, 1969), Conilurinae (Simpson, 1961), Anisomyinae, Pseudomyinae (Baverstock et al., 1983; Simpson, 1961), and Uromyini (Lee et al., 1981). Misonne (1969) spread members of this group across five generic groups in three different subfamilies. Carleton and Musser (1984) did suggest that the Philippine shrew-rats and forest mice (e.g., *Rhynchomys*, *Apomys*) should be considered with regard to Baverstock et al.'s (1983) Hydromyinae and that a group of old endemics may include some of these taxa plus others from the Lesser Sundas and Sulawesi.

Despite our success at identifying major murine lineages, we hesitate as yet to formalize a taxonomy. Many more groups must be analyzed, particularly some from Southeast Asia as well as several genera (e.g., *Micromys*, *Vandeleuria*) that other studies indicate may represent basal lineages (Jansa and Weksler, 2004; Watts and Baverstock, 1995). Our ongoing studies are filling in those gaps.

4.2. Gerbillinae and Deomyinae

Molecular data sets, particularly nuclear, have consistently recovered monophyletic Gerbillinae and Deomyinae (Hänni et al., 1995; Jansa and Weksler, 2004; Michaux et al., 2001; Sarich, 1985; Steppan et al., 2004a). Within the Gerbillinae, traditional tribal groups are not recovered, in conflict with the morphological phylogenies of Pavlinov et al. (1990) and Tong (1989). The molecular data strongly support two clades: a *Gerbillus* clade and a *Tatera* clade. The first includes the type genera of both Gerbillinae and Taterillinae (note, both Pavlinov et al. and Tong considered this clade to be a family, the Gerbillidae). The latter clade contains the residuum of Pavlinov et al.'s (1990) Taterillinae, making Taterillinae paraphyletic. Tong (1989), unlike Pavlinov, placed *Desmodillus* in the Gerbillinae, thus making both of his subfamilies paraphyletic on the molecular tree. We lacked tissue samples for the one extant genus that Pavlinov et al. (1990) placed in its own subfamily, *Ammodillus*. As a consequence, these results raise questions about the proper phylogenetic placement of the fossil calibrations used for this group. *Protatera*, dated at about 8 MYA, is the earliest known member of the Gerbillinae, but the two authors disagree strongly regarding its placement; Tong (1989) placed it in the sister group to extant gerbillines, thus making it possibly older than the extant radiation, whereas Pavlinov et al. (1990) nested it well within the Taterillinae. Clearly, these two opinions have profound effects on the dating of basal nodes, and it seems premature to use this fossil as a calibration point for molecular clocks until the conflict between the molecular and two morphological hypotheses is resolved. The morphological definition of this taxon must be reassessed so that the calibration can be refined.

We have now sampled all four genera of Deomyinae (Musser and Carleton, in press; Steppan et al., 2004a). Each gene region resolves the relationships differently. Both nuclear exons place *Uranomys* as sister to the other

three genera with moderately strong support (81–90% bootstrap, 0.90–1.00 pp; Figs. 1 and 2). We had only limited sampling of deomyines for AP5. The mtDNA data place *Lophuromys* as sister to the pair of *Acomys* and *Uranomys* with moderate support (64%, 0.76 pp; Fig. 3), the same topology recovered by microcomplement fixation of albumin (Watts and Baverstock, 1995). We note that mtDNA data, in contrast to data from nuclear genes, provided mixed support for monophyly of the Deomyinae, only 38% bootstrap and 0.92 pp, and in parsimony analysis Deomyinae was polyphyletic. We suspect that mtDNA data have lower informativeness at these depths because of accumulated homoplasy, and the combined-data analysis matches those for the individual nuclear genes (92% bootstrap, 1.00 pp). The remaining three taxa show a virtual polytomy that may reflect an internal branch so short as to allow differential lineage sorting. RAG1 groups *Deomys* with *Lophuromys* (74% bootstrap, 0.80 pp), whereas GHR groups *Acomys* with *Lophuromys* (61% bootstrap, 0.61 pp). The combined analysis agrees with the RAG1 data but with reduced certainty (51% bootstrap, 0.66 pp). Many more loci as well as complete sampling for all genes will probably be needed to resolve this node definitively.

4.3. Biogeography

Three of the four basal branches within the Murinae include taxa almost entirely restricted to Southeast Asia (Philippine Old Endemics and clades A and B). Clades C–G include several African and Palearctic lineages. This biogeographic pattern suggests that the subfamily originated in Southeast Asia and that rapid diversification associated with range expansion led to one or more coincident colonizations of Africa and central and northern Asia, although neither simultaneous vicariance nor dispersal was necessarily the cause of the radiation. For example, the *Praomys* group (G) diversified long after the lineage split from other core murines. Extinction could have pruned early African members, or this clade could represent a more recent dispersal into Africa unassociated with the arvicanthines. Depending on the resolution within the D–G clade and additional taxon sampling, the data support as many as four independent dispersal events into Africa (C, D, G, and some members of *Mus*) or a single colonization followed by at least two dispersals out of Africa (*Apodemus* and some *Mus*). Murines expanding out of Southeast Asia probably passed through western Asia on the way to Africa. The Siwalik Formation in Pakistan, already the best fossil record of the Murinae, may thus record evidence of this early radiation provided the ecosystems at that location harbored the relevant lineages. One problem is our relative undersampling of Eurasian taxa, which limits what we can infer about murine evolution/biogeography in that region. Given the temporal coincidence of the African and Asian periods of rapid diversification, multiple entries into Africa are probably more plausible.

A notable result is the close association of Philippine taxa with Australo-Papuan to the exclusion of the Southeast Asian and insular Indonesian species. It suggests a relatively recent connection or dispersal route between these two areas and at the same time limited dispersal to Indonesia and Indochina.

4.4. Relative phylogenetic utility of mitochondrial and nuclear DNA

Only a few studies have directly compared the utility of mitochondrial and nuclear sequence data for phylogenetic analysis (e.g., Adkins et al., 2001a; Matthee et al., 2001; McCracken and Sorenson, 2005), and most have been for relatively older divergences where the slow rate of nuclear DNA was most informative. Here we compare bootstrap percentages for essentially congruent taxa and find that, even within a recently evolved subfamily, mitochondrial DNA appears to be less informative at deeper nodes (Fig. 7). This result is somewhat surprising because the basal node is only 12 MYA, an age younger than many phylogenetic applications of mtDNA data to mammals (Catzeflis et al., 1995; Honeycutt et al., 1995; Irwin et al., 1991; Jansa et al., 1999; Mercer and Roth, 2003; Naylor and Brown, 1998; Nedbal et al., 1996; Yang and Yoder, 2003). Fig. 7 shows the decline in bootstrap values for deeper nodes in the tree when we compare genes for equal numbers of parsimony-informative characters. The results are qualitatively the same when all available data are used (results not shown). The two nuclear genes exhibit no significant loss of robustness with increasing depth, in contrast to a major decline shown by the mtDNA data. This lower bootstrap support for the deeper mtDNA nodes may be due to the shorter deep branches in the mtDNA tree (Fig. 3). In particular, the branch connecting the ingroup and outgroups and the branches leading to the basal nodes for the Deomyinae, Gerbillinae, *Rattus* group, *Praomys* group, and Australo-Papuan group are much shorter when estimated by mtDNA data than when estimated by the nuclear genes. The specific results will vary with data sets and branch-length distributions, but the impact here is clear; utility of mtDNA data deteriorates measurably for murine nodes older than about 6 MYA. The utility of mtDNA should extend to earlier divergences in nonmuroid groups that exhibit lower rates of evolution (Adkins et al., 1996), but the clear positive conclusion from these results is that, even for relatively recent divergences, within the last 5 MY, slowly evolving nuclear exons provide robust phylogenetic results and thus should be used at these levels more frequently.

Acknowledgments

We thank the many individuals and institutions who graciously loaned tissues or DNA samples: the Texas Cooperative Wildlife Collection (R.L. Honeycutt), the Museum of Vertebrate Zoology (J.L. Patton, C. Cicero), the Field Museum of Natural History (B.D. Patterson, L.R. Heaney, W.S. Stanley, and J. Kerbis-Peterhans), the Carnegie Museum of Natural History (S. McLaren), the South Australian Museum (S. Donnellan), the Smithsonian's Natural History Museum (M.D. Carleton, J. Jacobs), and the Wildlife Conservation Society at the Bronx Zoo (C. Lehn). Fieldwork was supported by grants from the David Klingener Fund of the University of Massachusetts to J. Anderson; the National Geographic Society to W.S. Stanley; the Barbara Brown Fund, and the Marshall Field II Fund, and the John D. and Catherine T. MacArthur Foundation (Chicago) to L.R. Heaney. This research was partially funded by National Science Foundation Grants DEB-0238837 to R.M.A. and S.J.S. and DEB-20013083 to S.J.S. and by startup funds from the University of Massachusetts, University of Tennessee, and Florida State University. M. Stuckey contributed to data collection and coordination of tissues and sequencing. We thank A.B. Thistle and two anonymous reviewers for comments improving the manuscript. J. Wilgenbusch and D.L. Swofford generously provided access to a 200-processor cluster at the FSU School of Computational Science.

Appendix A

List of specimens sequenced. *Abbreviations:* Bronx Zoo (WCS); Carnegie Museum of Natural History (CMNH); Field Museum of Natural History (FMNH); Museum of Vertebrate Zoology, Berkeley (MVZ); Southwestern Australian Museum (ABTC); United States National Museum (USNM). NK is the tissue accession prefix for the Museum of Southwestern Biology (MSB). The collector numbers EAR refer to uncatalogued specimens housed at FMNH and collected by Eric Rickart, and collector numbers H refer to uncatalogued specimens housed in the Texas Cooperative Wildlife Collections and collected by members of the laboratory of Dr. Rodney Honeycutt. RA refers to the collections of Ronald Adkins.

Gerbillinae

Desmodillus auricolarus RA 01. Namibia: Kanabeam, Karasburg District, 375 m. 28°07′17″S, 17°33′32″E.
Gerbillurus vallianus H675. Locality unknown.
Gerbillus gerbillus CMNH 113822. Egypt: Giza Governorate; 50 km SW Giza (by road) on El Faiyum Rd. 29°42′N, 30°58′E.
Meriones shawi H583. Locality unknown.
Tatera robusta FMNH 158105. Tanzania: Arusha Region, Babati District, Tarangire National Park, near Engelhardt Bridge.
Taterillus emini CMNH 102330 SP 5227. Kenya: Eastern Province, Machakos District, Kathekani, 760 m, 02°37′S, 38°09′E.

Deomyinae

Acomys ignitus CMNH 102383. Kenya: Coast Region, Kwale Dist., Shimba Hills Natl. Reserve, 5 km S, 1 km W Kwale. 04°13′S, 39°27′E.
Deomys ferrugineus FMNH 149427. Zaire: Haute Zaire, Ituri, Epulu, 2 km W, Wpulu R, rt bank. *Lophuromys flavopunctatus* FMNH 144777. Uganda: Western, Kasese Dist., Rwenzori Mts, Bujuku R, L bank, John Mate Camp.
Uranomys ruddi CMNH 113723 SP 11148. Ghana: Greater Accra Region, Shai Hills Game Production Reserve Headquarter. 05°53′N, 00°03′E.
Uranomys ruddi CMNH 113726 SP 11151. Ghana: Greater Accra Region, Shai Hills Game Production Reserve Headquarter. 05°53′N, 00°03′E.

Murinae

Aethomys namaquensis RA 12. Namibia: Karasburg District, Kanabeam, 28°07′17″S, 17°33′32″E.
Anisomys imitator ABTC 45107. Papua New Guinea: Bobhole SHP.
Apodemus agrarius MVZ 159220. Yugoslavia: Serbia, Field, 5 km N, 3 km E Sremska Mitrovica.
Apodemus mysticinus. CMNH SP7861. Jordan: Zay Forest.
Apodemus semotus MVZ 180489. Taiwan: Chiayi County, 2 km (by foot) down from Pai-Yun Hostel on trail to Ta-Ta-Jia Saddle, Alishan Township. 23.46667°N, 120.91667°E.
Apomys datae FMNH 167358. Philippines: Luzon I., Kalinga Prov., Balbalan Municipality, Balbalasang, Magdalao.
Apomys hylocoetes FMNH 148149. Philippines: Mindanao I., Bukidnon Prov., Mt. Katanglad Range, 16.5 km S, 4 km E Camp Phillips.
Apomys hylocoetes FMNH 147871. Philippines: Mindanao Is., Bukidnon Prov., Mt. Katanglad Range, 16.5 km S, 4 km E Camp Phillips.
Archboldomys luzonensis EAR 1826. Philippines: Luzon Is., Camarines Sur Prov., Mt. Isarog.
Arvicanthis niloticus ABTC 65696. Locality unknown.
Arvicanthis somalicus H 894. Kenya: Isiolo District, Buffalo Springs National Preserve, 1 km N Buffalo Springs.
Batomys granti EAR 1822. Philippines: Luzon Is., Camarines Sur Prov., Mt. Isarog, 1750 m
Berylmys bowersi MVZ 186482. Vietnam: Vinh Phu Prov., Vinh Yen District, Tam Dao. 21°27′14.2″N, 105°38′31″E.
Chrotomys gonzalesi EAR 1850. Philippines: no locality information given; uncatalogued specimen.
Chrotomys gonzalesi USNM 458952. Philippines: Luzon Is., Camarines Sur Prov., Mt. Isarog, 1350 m.
Conilurus penicillatus ABTC 7411. Australia: Western Australia, Mitchell Plateau.
Dacomys millardi MVZ 186519. Vietnam: Vinh Phu Prov., Vinh Yen District, Tam Dao. 21°27′14.2″N, 105°38′31″E.
Hybomys univittatus CMNH 108039 SP 10553. Cameroon: Southwestern Province, Bake River Bridge, 1 km S, $1\frac{1}{4}$ km W Baro; 05°16′N, 09°13′E.
Hybomys univittatus CMNH 108044 SP 10599. Cameroon: Southwest Province, Korup National Park, Mana River Bridge, $3\frac{1}{2}$ km N, 4 km W Mundemba; 100 m. 05°00′N, 08°52′E.
Hylomyscus parvus CMNH 108105 SP 10502. Cameroon: Southwest Province, Ikenge Research Station, Korup National Park, 160 m. 05°16′N, 09°08′E.
Hylomyscus parvus CMNH 108106 SP 10514. Cameroon: Southwest Province, Ikenge Research Station, Korup National Park, 160 m. 05°16′N, 09°08′E.
Hyomys goliath ABTC 42697. Papua New Guinea: Ofekaman.

Leggadina forresti ABTC 36085. Australia: South Australia, 5.1 km SE Alinga Bore.
Lemniscomys barbarus CMNH 102462 SP 5204. Kenya: Eastern Province, Machakos District, Kathekani, 760 m. 02°37′S, 38°09′E.
Lemniscomys barbarus CMNH 102463 SP 5213. Kenya: Eastern Province, Machakos District, Kathekani, 760 m. 02°37′S, 38°09′E.
Leopoldamys sabanus CMNH 102138. Indonesia: Lalut Birai Reserve Station, East Kalimantan.
Leporillus conditor ABTC 13335. Australia: South Australia, Franklin Island west.
Malacomys longipes CMNH 108117 SP 10597. Cameroon: Southwest Province, Korup National Park, Mana River Bridge, $3\frac{1}{2}$ km N, 4 km W Mundemba, 100 m. 05°00′N, 08°52′E.
Malacomys longipes CMNH 108118 SP 10598. Cameroon: Southwest Province, Korup National Park, Mana River Bridge, $3\frac{1}{2}$ km N, 4 km W Mundemba, 100 m. 05°00′N, 08°52′E.
Mastacomys fuscus ABTC 07354. Australia: New South Wales, Mt. Kosciusko National Park.
Mastomys hildebranti H 783. Locality unkown.
Mastomys natalensis FMNH 166943. Tanzania: Iringa Region, Iringa District, Mulenge Forest.
Mastomys natalensis FMNH 150104. Tanzania: Tanga Region, Muheza District, E. Usambara Mts, 4.5 km ESE Amani, Monga Tea Estate.
Maxomys bartelsii ABTC 48063. Indonesia: Cidodas forest.
Maxomys surifer CMNH 101964. Indonesia: Bukit Soeharto Experimental Forest, East Kalimantan.
Mesembriomys gouldii ABTC 07412. Australia: Western Australia, Mitchell Plateau.
Mus musculus. Lab colony, strain balb/c.
Niviventer culteratus MVZ 180686. Taiwan: Nantou County, Taiwan, 12.8 km (by foot) Ba-Tong-Guan Historic Trail, Xin-Yi Township. 23.51667°N, 120.96667°E.
Notomys fuscus ABTC 34070. Australia: South Australia, Monticollina Bore.
Oenomys hypoxanthus CMNH 102548 SP 5096. Kenya: Western Province, Kakamega District, Ikuywa River Bridge, $6\frac{1}{2}$ km S, 19 km E Kakamega. 00°13′N, 34°55′E.
Oenomys hypoxanthus CMNH 102549 SP 5097. Kenya: Western Province, Kakamega District, Ikuywa River Bridge, $6\frac{1}{2}$ km S, 19 km E Kakamega. 00°13′N, 34°55′E.
Parotomys H 656. Locality unkown.
Phloeomys WCS 931040 2000-298.
Praomys jacksoni CMNH 102583 SP 5001. Kenya: Western Province, Kakamega District, Kakamega Forest Station, $3\frac{1}{2}$ km S, 19 km E Kakamega, 1676 m. 00°14′N, 34°52′E.
Praomys jacksoni CMNH 102584 SP 5002. Kenya: Western Province, Kakamega District, Kakamega Forest Station, $3\frac{1}{2}$ km S, 19 km E Kakamega, 1676 m. 00°14′N, 34°52′E.
Praomys taitae CMNH 102637. Kenya: Taita Dist., Coast Region, Ngangao Forest, Taita Hills. 03°22′S, 38°21′E.
Praomys tullbergi CM 108198 SP 10511. Cameroon: Southwest Province, Ikenge Research Station, Korup National Park, 160 m. 05°16′N, 09°08′E.
Praomys tullbergi CMNH 108199 SP 10523. Cameroon: Southwest Province, Ikenge Research Station, Korup National Park, 160 m. 05°16′N, 09°08′E.
Pseudomys australis ABTC 35951. Australia: South Australia, 5.9 km SSE to Camp Well.
Rattus exulans NK 80010. Indonesia: Sulawesi Prov., Sulawesi Selatan, Regency, Gowa, Kacomatan, Tompo Bulu, Cikoro, Desa, Dusu. Date of death 20 May, 1998.
Rattus norvegicus. Sprague–Dawley laboratory strain.
Rattus villosissimus ABTC 00549 SAMAM 15783. Australia: South Australia, Purni Bore.
Rhabdomys pumilio RA 23. Namibia: Karasburg District, Kanabeam, 28°07′17″S, 17°33′32″E.
Rhynchomys isarogensis EAR 1840. Philippines: Luzon Is., Camarines Sur Prov., Mt. Isarog, 1750 m.
Rhynchomys isarogensis EAR 1857. Philippines: Luzon Is., Camarines Sur Prov., Mt. Isarog.
Stochomys longicaudatus CMNH 108122 SP 10564. Cameroun: Southwest Province, Baro. 05°17′N, 09°13′E.
Stochomys longicaudatus CM 90877 TK 21562. Gabon: Estuaire Province, 1 km SE Cap Esterias.
Sundamys muelleri MVZ 192234. Indonesia: Sumatra, Indonesian Archipelago, Ketambe Research Station. 3.68333°N, 97.65000°E.
Thallomys paedulcus CMNH 102657 SP 5269. Kenya: Eastern Province, Isiolo District, 2 km W Isiolo, 1090 m. 00°22′N, 37°34′E.
Thallomys paedulcus CMNH 102658 SP 5270. Kenya: Eastern Province, Isiolo District, 2 km W Isiolo, 1090 m. 00°22′N, 37°34′E.
Uromys caudimaculatus MVZ 193100. Australia: Queensland, 2 km N of Millaa Millaa, Atherton Tableland.
Xeromys myoides ABTC 30709. Australia: Northern Territory, Ramingining area Arafura Swamp.
Zelotomys hildegardeae CMNH 102659, SP 5147. Kenya: Rift Valley Province, Narok District, Talek Gate, Masai Mara Game Reserve boundary, 1640 m. 01°26′S, 35°13′E.
Zelotomys hildegardeae CMNH 102661, SP 5149. Kenya: Rift Valley Province, Narok District, Talek Gate, Masai Mara Game Reserve boundary, 1640 m. 01°26′S, 35°13′E.
Zyzomys argurus ABTC 07908. Australia: Western Australia, Mitchell Plateau.

Appendix B. Species examined in this study and their GenBank accession numbers

Species	Gene region			
	GHR	RAG1	AP5	mtDNA
Gerbillinae				
Desmodillus auricolarus	DQ019048			DQ019081
Gerbillurus vallianus	AF332022	AY294948		
Gerbillus gerbillus	DQ019049	DQ023452	DQ023416	DQ019082
Meriones shawi		AY294947		DQ019083
Meriones unguiculatus	AF332021			
Tatera robusta	AY294920	AY294949		DQ019084
Taterillus emini CMNH 12330	DQ019050	DQ023453		DQ019085
Taterillus emini CMNH 12331			DQ070370	
Deomyinae				
Acomys ignitus	AY294923	AY294951		DQ019086

(*continued on next page*)

Appendix B (*continued*)

Species	Gene region			
	GHR	RAG1	AP5	mtDNA
Deomys ferrugineus	AY294922	AY241460		
Lophuromys flavopunctatus	AY294921	AY294950		DQ019087
Uranomys ruddi CMNH 113723			DQ070371	
Uranomys ruddi CMNH 113726	DQ019051	DQ023454	DQ023417	DQ019088
Murinae				
Aethomys namaquensis	AY294914	AY294941	DQ023427	DQ019089
Anisomys imitator	DQ019052	DQ023471	DQ023440	DQ019090
Apodemus mysticinus	DQ019053			DQ019091
Apodemus agrarius MVZ 159220	DQ019054	DQ023472	DQ023441	DQ019092
Apodemus semotus	DQ019055	DQ023473	DQ023442	DQ019093
Apomys datae			DQ023431	
Apomys hylocoetes FMNH 147871		AY294942?	DQ070374	
Apomys hylocoetes FMNH 148149	AY294915	DQ023465	DQ023432	
Archboldomys luzonensis		DQ023466	DQ023433	
Arvicanthis somalicus	AY294918	AY294946	DQ023425	DQ019094
Batomys granti	AY294917	AY241461	DQ023450	DQ019095
Berylmys bowersi	DQ019056	DQ023457		DQ019096
Chrotomys gonzalesi EAR 1850			DQ023434	
Chrotomys gonzalesi USNM 458952		AY294943		
Conilurus penicillatus	DQ019057	DQ023467	DQ023436	DQ019097
Dacomys millardi	DQ019058	DQ023459	DQ023422	DQ019098
Hybomys univittatus CMNH 108039			DQ070392	
Hybomys univittatus CMNH 108044	DQ019059	DQ023462	DQ023428	DQ019099
Hylomyscus parvus CMNH 108105			DQ070385	
Hylomyscus parvus CMNH 108106	DQ019060	DQ023479	DQ023449	DQ019100
Hyomys goliath			DQ070375	
Leggadina forresti	DQ019061	DQ023468	DQ023437	DQ019101
Lemniscomys barbarus CMNH 102462	DQ019062	DQ023461	DQ023426	DQ019102
Lemniscomys barbarus CMNH 102463			DQ070394	
Leopoldamys sabanus	DQ019063			DQ019103
Leporillus conditor			DQ070376	
Malacomys longipes CMNH 108117			DQ070383	
Malacomys longipes CMNH 108118	DQ019064	DQ023474	DQ023443	DQ019104
Mastacomys fuscus			DQ070378	
Mastomys hildebranti	AY294916			DQ019105
Mastomys natalensis FMNH 166943		AY294945	DQ070384	
Mastomys natalensis FMNH 150104			DQ023445	
Maxomys bartelsii	DQ019066	DQ023460	DQ023423	DQ019106
Maxomys surifer	DQ019065			DQ019107
Mesembriomys gouldii			DQ070382	
Mus musculus	M33324	AY241462	DQ023444	NC005089
Niviventer culteratus	DQ019068	DQ023458	DQ023421	DQ019108
Niviventer cremoriventer	DQ019067			DQ019109
Notomys fuscus			DQ070379	
Oenomys hypoxanthus CMNH 102548			DQ070389	
Oenomys hypoxanthus CMNH 102549	DQ019069	DQ023464	DQ023430	DQ019110
Parotomys sp.	AY294912	AY294939	DQ023424	DQ019111
Phloeomys sp.	DQ019070	DQ023480	DQ023451	DQ019112
Praomys jacksoni CMNH 102583			DQ070386	
Praomys jacksoni CMNH 102584	DQ019071	DQ023477	DQ023447	DQ019113
Praomys taitae	AY294919			DQ019114
Praomys tullbergi CMNH 108198			DQ070387	
Praomys tullbergi CMNH 108199	DQ019072	DQ023478	DQ023448	DQ019115
Pseudomys australis	DQ019073	DQ023469	DQ023438	DQ019116
Rattus exulans	DQ019074	DQ023455	DQ023419	DQ019117
Rattus norvegicus	X16726	AY294938	DQ023418	J01434
Rattus villosissimus			DQ070372	
Rhabdomys pumilio	AY294913	AY294940		DQ019118
Rhynchomys isarogensis EAR 1840	DQ019075	AY294944	DQ023435	DQ019119
Rhynchomys isarogensis EAR 1857			DQ070373	
Stochomys longicaudatus CMNH 108122	DQ019076	DQ023463	DQ023429	DQ019120
Stochomys longicaudatus CMNH 90877			DQ070393	

Appendix B (*continued*)

Species	Gene region			
	GHR	RAG1	AP5	mtDNA
Sundamys muelleri	DQ019077	DQ023456	DQ023420	DQ019121
Thallomys paedulcus CMNH 102657	DQ019078		DQ070390	
Thallomys paedulcus CMNH 102658			DQ070391	
Uromys caudimaculatus	DQ019079	DQ023470	DQ023439	DQ019122
Xeromys myoides			DQ070380	
Zelotomys hildegardeae CMNH 102659			DQ070388	
Zelotomys hildegardeae CMNH 102661	DQ019080	DQ023476	DQ023446	DQ019123
Zyzomys argurus			DQ070381	

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