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Molecular Phylogeny and Biogeography of the Native Rodents of Madagascar (Muridae: Nesomyinae): A Test of the Single-Origin Hypothesis

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Complete nucleotide sequences from the mitochondrial cytochrome *b* gene (1143 bp) were used to investigate the phylogenetic relationships among the native rodents of Madagascar. Specifically, this study examines whether the nine genera of nesomyines form a monophyletic group relative to other Old World murids. All nine of the nesomyine genera, including multiple individuals from 15 of the 21 described species, were included in the analysis, and their monophyly was assessed relative to the murid subfamilies Mystromyinae, Petromyscinae, Dendromurinae, Cricetomyinae, Murinae, Rhizomyinae, and Calomyscinae. Phylogenetic analysis of the resulting 95 taxa and 540 characters resulted in 502 equally parsimonious cladograms. The strict consensus tree weakly refutes the monophyly of Nesomyinae and suggests that the Malagasy rodents form a clade with dendromurines (as represented by *Steatomys*) and the African rhizomyine *Tachyoryctes*. The cladogram strongly refutes the association of the South African genus *Mystromys* with the Malagasy genera and suggests that *Petromyscus* and *Mystromys* form a monophyletic group. We provide the first explicitly phylogenetic scenario for the biogeographic history of nesomyine rodents. Our phylogenetic hypothesis indicates: (1) rodents invaded Madagascar only once, (2) they came from Asia not from Africa as is commonly assumed, and (3) there was a secondary invasion of rodents from Madagascar into Africa.

INTRODUCTION

The native rodents of Madagascar are a diverse taxonomic assemblage of uncertain phylogenetic affinities. This small assemblage of nine genera includes such diverse forms as the vole-like marsh rat *Brachyuromys*, the scansorial tufted-tail rat *Eliurus*, the semifossorial giant rat *Hypogeomys*, and the saltatorial, gerbil-like *Macrotarsomys*. All 21 species of Malagasy rodents are currently assigned to the subfamily Nesomyinae, part of the large, cosmopolitan family Muridae (Carleton and Musser, 1984; Musser and Carleton, 1993). This classification implies that Madagascar's rodents form a monophyletic group. However, the current classification of nesomyine rodents is based more on their

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shared distribution on Madagascar than on any shared organismal characters, and it has been cautioned that "each of the genera could stand as a separate tribe or subfamily were it not for the centripetal taxonomic influence provided by their common distribution on Madagascar" (Carleton and Musser, 1984:343).

There is little doubt that the nesomyine rodents are part of Muridae, the speciose assemblage of rats, mice, and voles diagnosed by a myomorphous, sciurognathic jaw structure. However, the placement of the nine Malagasy genera relative to other members of Muridae is controversial. Ellerman (1940, 1941) could not find reason to include all nesomyine genera in one subfamily. Under his classification, *Eliurus* became part of Murinae, *Brachytarsomys* was allied with the Holarctic Arvicolinae, *Brachyuromys* and *Tachyoryctes* formed a separate subfamily (Tachyoryctinae), while the remaining genera were either given their own subfamily (Gymnuromyinae) or collected under Cricetinae (Table 1). This classification has not been widely adopted, but it is the most radical formalization of the concept that Madagascar's rodents do not form a natural group. In contrast, Simpson (1945) maintained that nesomyine rodents are monophyletic and included them as a single subfamily of his Cricetidae. Other proponents of nesomyine monophyly (Lavocat, 1978; Chaline *et al.*, 1977) group the Malagasy rodents as part of a overarching family Nesomyidae which includes the Malagasy rodents and a number of fossil and "archaic" African muroids (Table 1).

The controversy surrounding the systematics of nesomyine rodents is inseparable from the interpretation of their origin. The focal questions are whether rodents arrived on Madagascar once and radiated *in situ* or several different times, in which case Nesomyinae, as currently defined, would be polyphyletic. Attempts to infer the origin of nesomyine rodents using fossil data have failed due to the absence of a Tertiary fossil record on Madagascar, and the proposed link between the lower Miocene Kenyan rodent *Protarsomys macinnesi* and nesomyines, particularly *Macrotarsomys* sp. (Lavocat, 1973, 1978; Chaline *et al.*, 1977), has been shown to be poorly founded (Carleton and Goodman, 1996). The extreme morphological diversity encompassed by the nine genera has confounded phylogenetic studies and discouraged identification of comparable cranial,

TABLE 1
Three Prominent Classifications of Nesomyine Genera

Ellerman (1941)	Simpson (1945)	Lavocat (1978)
Family Muridae	Superfamily Muroidea	Superfamily Muroidea
Subfamily Murinae	Family Cricetidae	Family Cricetodontidae
Eliurus	Subfamily Cricetinae	Subfamily Afrocricetodontinae
murines	Subfamily Nesomyinae	Family Nesomyidae
Subfamily Dendromyinae	Subfamily Lophiomyinae	Subfamily Nesomyinae
Petromyscus	Subfamily Microtinae	Subfamily Lophiomyinae
dendromurines	Subfamily Gerbillinae	Subfamily Mystromyinae
Subfamily Cricetinae	Family Spalacidae	Subfamily Tachyoryctinae
Nesomys	Family Rhizomyidae	Subfamily Gerbillinae
Hypogeomys	Family Muridae	Subfamily Otomyinae
Calomyscus	Subfamily Murinae	Family Muridae
Mystromys	Subfamily Dendromurinae	Subfamily Murinae
Old World cricetines	Subfamily Otomyinae	Subfamily Dendromurinae
New World cricetines	Subfamily Phloeomyinae	
Subfamily Gymnuromyinae	Subfamily Rhynchomyinae	
Gymnuromys	Subfamily Hydromyinae	
Subfamily Tachyoryctinae		
Brachyuromys		
Tachyoryctes		
Subfamily Microtinae		
Brachytarsomys		
arvicolines		

dental, or skeletal characters. A recent molecular phylogenetic study of Malagasy rodents used 12S rDNA to conclude that nesomyines are monophyletic with *Cricetomys* as their sister taxon (Dubois *et al.*, 1996). However, this study suffers from incomplete taxon sampling as it included only three nesomyine genera (*Eliurus, Nesomys* and *Macrotarsomys*) and omitted most relevant African and Asian taxa (*Mystromys, Petromyscus, Calomyscus, Tachyoryctes*, and representatives of Dendromurinae).

Our primary goal in this paper is to investigate the monophyly of Nesomyinae. We include a thorough sampling of relevant murid taxa and use complete nucleotide sequence from the cytochrome *b* gene as evidence of relationship. Taxon sampling encompasses all but two of the described species of nesomyines; the probable members of the archaic African murids (Mystromyinae, Petromyscinae, Dendromurinae, Cricetomyinae, and *Tachyoryctes*); both Asian and African representatives of Murinae; and *Calomyscus*, the only genus comprising the archaic Asian Calomyscinae. We use the resulting phylogeny to investigate the relationships among nesomyine genera and to examine their placement in murid evolutionary history. Finally, we present the first phylogenetic scenario for the origin of nesomyines and discuss its implications for murid biogeography.

MATERIALS AND METHODS

The entire cytochrome *b* gene was sequenced for 103 specimens representing 32 species and putative species. This included 18 of the 21 recognized nesomyine species (84 individuals sequenced) and 14 representatives of Asian and African muroid taxa (19 individuals sequenced) (Table 2).

Taxonomic Scope

All but two of the specimens used in this study were wild caught animals; sequences from two species (*Mus musculus* and *Rattus norvegicus*) were taken from GenBank (Table 2, Appendix 1). Work on the alpha-taxonomy of nesomyines during the past decade (Carleton and Schmidt, 1990; Carleton, 1994; Carleton and Goodman, 1996; Goodman and Carleton, 1996; Carleton and Goodman, 1998; Goodman and Carleton, 1998) has increased the number of recognized species from 14 (Musser and Carleton, 1993) to 21 (Carleton and Goodman, 1998). In light of this ongoing revisionary work,

TABLE 2
Muroid Taxa Included in This Study, Their Country of Origin, and Number of Individuals Sequenced (in Parentheses)

Subfamily Nesomyinae	
Brachyuromys betsileoensis (4)	Madagascar
Brachyuromys ramirohitra (1)	Madagascar
Brachytarsomys albicauda (1)	Madagascar
Eliurus grandidieri (2)	Madagascar
Eliurus majori (11)	Madagascar
Eliurus minor (10)	Madagascar
Eliurus myoxinus (10)	Madagascar
Eliurus tanala (9)	Madagascar
Eliurus webbi (8)	Madagascar
Eliurus sp. A (1)*	Madagascar
Eliurus sp. B (3)*	Madagascar
Gymnuromys roberti (4)	Madagascar
Hypogeomys antimena (1)	Madagascar
Macrotarsomys bastardi (1)	Madagascar
Monticolomys koopmani (4)	Madagascar
Nesomys rufus (10)	Madagascar
Nesomys audeberti (2)	Madagascar
Voalavo gymnocaudus (2)	Madagascar
Subfamily Cricetomyinae	
Beamys hindei (2)	Tanzania and Kenya
Cricetomys gambianus (1)	Tanzania
Cricetomys emini (4)	Gabon, Kenya, and Ivory Coast
Subfamily Mystromyinae	
Mystromys albicaudatus (2)	South Africa
Subfamily Dendromurinae	
Steatomys parvus (2)	Kenya
Subfamily Rhizomyinae	
Tachyoryctes splendens (1)	Kenya
Subfamily Murinae	
Apodemus sylvaticus (1)	Pakistan
Nesokia indica (1)	Pakistan
Mastomys hildebrandtii (1)	Kenya
Hylomyscus alleni (1)	Gabon
Mus musculus	Genbank accession V00711
Rattus norvegicus	Genbank accession J01436
Subfamily Petromyscinae	
Petromyscus collinus (2)	Namibia
Subfamily Calomyscinae	
Calomyscus baluchi (1)	Pakistan

* Species indeterminate pending further investigation.

several individuals of each nominate species from different collecting localities were included whenever available to better comprehend species limits and to investigate biogeographic questions within Madagascar. These questions will be discussed in future papers. The present phylogenetic study revealed two potentially new species of *Eliurus*. These are designated *Eliurus* sp. A and *Eliurus* sp. B pending further investigation.

Molecular Methods

Whole genomic DNA was extracted from frozen and buffer-preserved (10% EDTA, 1% NaF) tissues using QIAamp Whole Genomic Isolation kits (Qiagen Inc.). The entire cytochrome *b* gene was PCR amplified using primers MVZ05 5′CGAAGCTTGATATGAAAAACCATCGTTG and UMMZ04 5′TCTTCATTTYWGGTTTACAAGAC. The entire gene was sequenced using these primers and primers UMMZ12 5′RTADGGGTGRAATGGRATTTTWTC and UMMZ13 5′CAYGAAWCAGGVTCAAAYAAYCC. PCR amplifications were done as standard 50- or 100-μL reactions using AmpliTaq DNA Polymerase (Perkin–Elmer) on a Perkin–Elmer 480 Thermal Cycler using the following conditions: denaturation at 95° for 1 min; annealing at 50–55° for 1 min; extension at 72° for 1 min 15 s; 30 cycles. All amplifications were preceded by a 95° soak for 3 min and followed by a 7-min extension at 72°. PCR products were prepared for automated sequencing by separation on a 2% agarose gel (NuSieve GTG, FMC Bioproducts) and subsequent purification using a QIAquick Gel Extraction kit (Qiagen Inc.). The gene was sequenced in two overlapping fragments in both directions using a Perkin Elmer Dye Termination Sequencing kit and an ABI 377 automated sequencer. All sequences were proofed and edited using Sequence Navigator ver. 1.0 (Applied Biosystems). Sequence data from this article have been deposited with GenBank under Accession Nos. AF160514–AF160614.

Alignment and Parsimony Analysis

DNA sequences were aligned using Clustal W (Thompson *et al.*, 1994) and adjusted by eye. A single 3-bp gap, corresponding to a codon deletion at basepairs 1135–1137, was introduced in *Petromyscus* and *Tachyoryctes*. This gap was treated as missing data in the final phylogenetic analysis; however, reanalysis with this gap coded as present or absent produced an identical topology. The resulting complete sequence matrix consisted of 104 taxa and 1143 characters. This matrix was condensed (filtered) using MacClade 3.05 (Maddison and Maddison, 1992), which removed uninformative sites and combined redundant taxa into a single terminal taxon. PAUP considered an additional six characters uninformative; thus, the final matrix consisted of 95 taxa and 540 informative characters.

Aligned sequences were subjected to parsimony analysis using PAUP 3.1 (Swofford, 1993) and PAUP* 4.064 (D. L. Swofford). All nucleotides were treated as unordered and unweighted in all analyses. Heuristic searches were conducted using the following two step search strategy: (1) an initial round of heuristic searching with 100 replicates of random stepwise addition of taxa, followed by tree-bisection-reconnection (TBR) branch-swapping with up to five trees saved from each replicate; (2) a second round of heuristic searching using the trees obtained in the initial search as starting trees, followed by TBR branch-swapping. The first step of this search strategy is designed to maximize the number of starting trees available for branch-swapping. In this case, a set of trees (maximum 500) was constructed with five trees from each of 100 random searches. This allows a more thorough and efficient exploration of available tree space than simply saving all trees resulting from branch-swapping on the results of a single search. The strict consensus of the resulting optimal trees was calculated and *Calomyscus baluchi* was designated as an outgroup (see discussion of rooting below).

Two measures of clade support were calculated. The Bremer Support Index is an unambiguous metric which gives the number of additional steps required to generate a nonminimal length tree in which a given clade does not appear (Bremer, 1988; Kallersjo *et al.*, 1992). Bremer support values were calculated with the aid of TreeRot (Sorenson, 1996) and are expressed in the text as a fraction of the branch length, i.e., Bremer / branch length. Parsimony jackknife values were calculated for 10,000 replicates and a cut point of 50% using JAC (Farris *et al.*, 1996). Parsimony jackknifing randomly removes approximately one-third of the character data, calculates the most parsimonious tree based on this smaller data subset, and repeats this procedure *n* (in this case 10,000) times. Each clade is given a

parsimony jackknife value (PJV), which represents the percentage of replications in which that clade was recovered (Farris *et al.*, 1996).

RESULTS

The initial heuristic search (100 replications of random stepwise addition, saving only 5 trees) resulted in a pool of 95 trees. The subsequent search using these 95 trees as starting trees resulted in 502 trees with length = 4373, CI = 0.22, and RI = 0.72. In a strict consensus of these 502 trees, individuals from each of the nominate species cluster as a monophyletic assemblage (Fig. 1). Because this study is concerned with the more inclusive relationships among murid taxa, individuals were pruned from the complete cladogram to show only the basal structure among the taxa of interest. The resulting simplified cladogram shows phylogenetic structure with species, rather than individual organisms, as terminals (Fig. 2). Bremer support values and branch lengths are given for each node in Fig. 2, and the tree resulting from the parsimony jackknife search is shown in Fig. 3.

Cytochrome *b* has been extensively used in phylogenetic work and has both supporters (Irwin *et al.*, 1991) and detractors (Meyer, 1994; Graybeal, 1993). Those who have reservations about using the gene often advocate differential character weighting as a means of recovering reliable phylogenetic signal from a rapidly evolving gene (Griffiths, 1997; Swofford *et al.*, 1996; Mindell and Thacker, 1996; Knight and Mindell, 1993). It is frequently argued that third position sites have been reduced to noise (i.e., saturated) and therefore provide unreliable (i.e., misleading) phylogenetic signal (Swofford *et al.*, 1996) and should be downweighted or omitted. Others have argued that there is no rational basis for *a priori* differential character weighting or data set partitioning (Allard and Carpenter, 1996; DeSalle and Brower, 1997; Siddall, 1997) and that *a priori* weighting schemes are necessarily arbitrary. We evaluated the implications of treating the current data according to these alternative viewpoints by examining the retention index of the three codon positions on the total evidence tree. Of the 540 informative characters, 129 are first position changes, 48 are second position changes, and 363 are third position changes. As would be expected, second position changes are the most consistent on the total evidence tree (RI = 0.82); however, first and third positions are not markedly less so (RI = 0.73 and 0.71, respectively). Because all three classes of data provide phylogenetic information across the entire tree, we do not differentially weight or exclude that information.

DISCUSSION

The resulting phylogenetic tree encompasses a wide range of hierarchical levels and allows consideration of several problems in nesomyine systematics. The data from cytochrome *b* do not support nesomyine monophyly; however, they consistently reveal certain generic groupings among the nesomyines. Moreover, the resulting phylogeny sheds light on the biogeographic origin of the native Malagasy rodents. Each of these topics is discussed in turn below.

Nesomyinae and Deeper Level Murid Systematics

To assess the monophyly of the nesomyine rodents, it is necessary to determine their placement in Muridae. This is a daunting task as murid rodents are surely one of the most successful mammalian lineages, containing over 1300 extant species or nearly one-third of the 4600 recognized mammalian species. The scope can be narrowed considerably if we use prior classifications for delineating alternative phylogenetic hypotheses. The most explicit scenarios for the evolution of the nesomyine rodents are those of Lavocat (1973, 1978) and Chaline *et al.* (1977). According to these authors, the genera included in Nesomyinae, Dendromurinae, Petromyscinae, Cricetomyinae, and Mystromyinae are considered relicts of a cricetodontine stock present in Africa since the early Miocene. Carleton and Musser (1984) suggested that, with future research, the genera currently included in these subfamilies will be arrayed as tribes of an inclusive subfamily Nesomyinae and that the limits of these tribes will most likely not correspond to the current subfamilial definitions. We provide the first explicitly phylogenetic investigation of this contention.

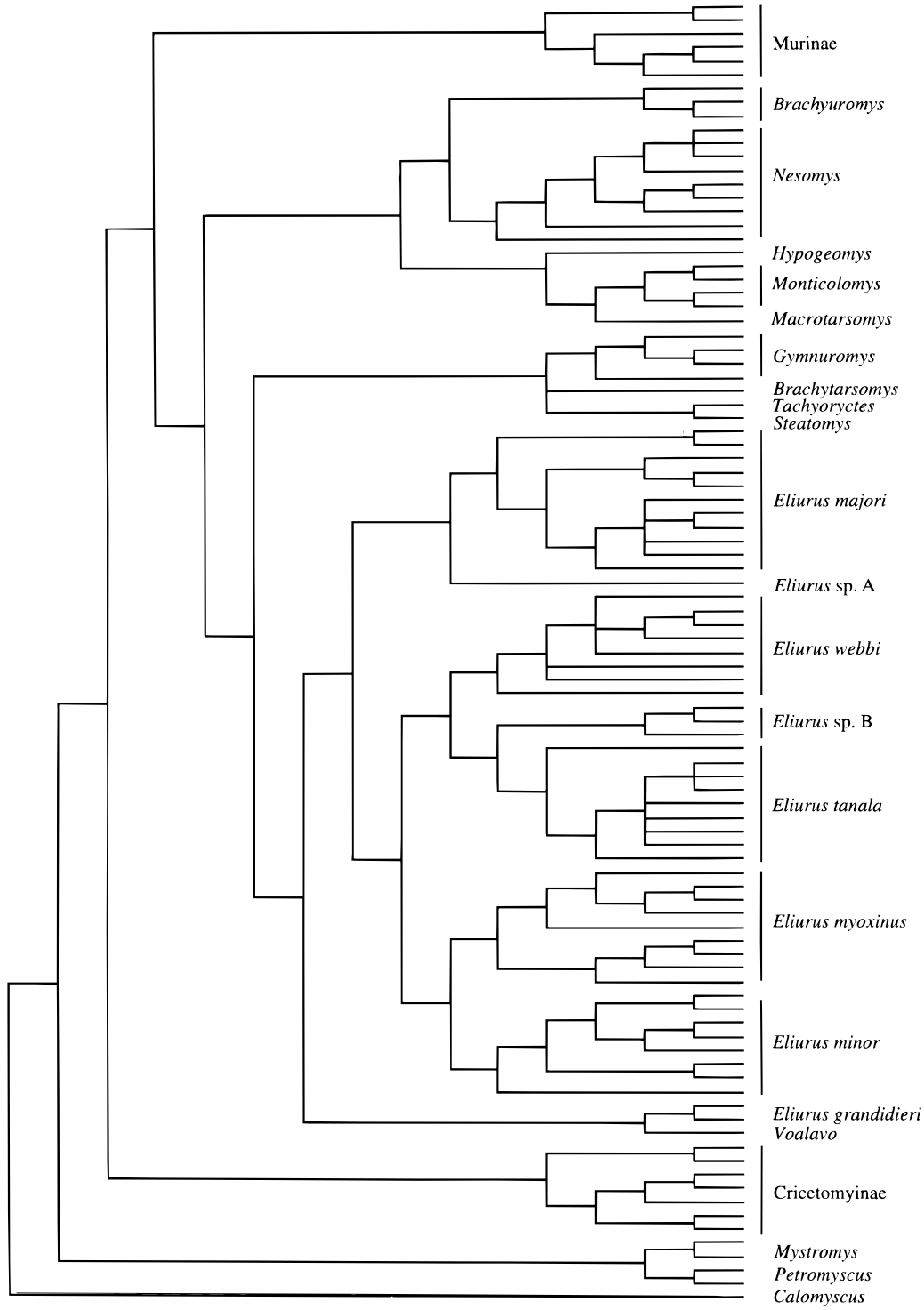

FIG. 1. Strict concensus of 502 most parsimonious cladograms obtained by heuristic search procedures of PAUP. Results are based on complete cytochrome *b* sequence, which yielded 540 informative characters for 95 terminal taxa. Tree length = 4373, CI = 0.22, RI = 0.72.

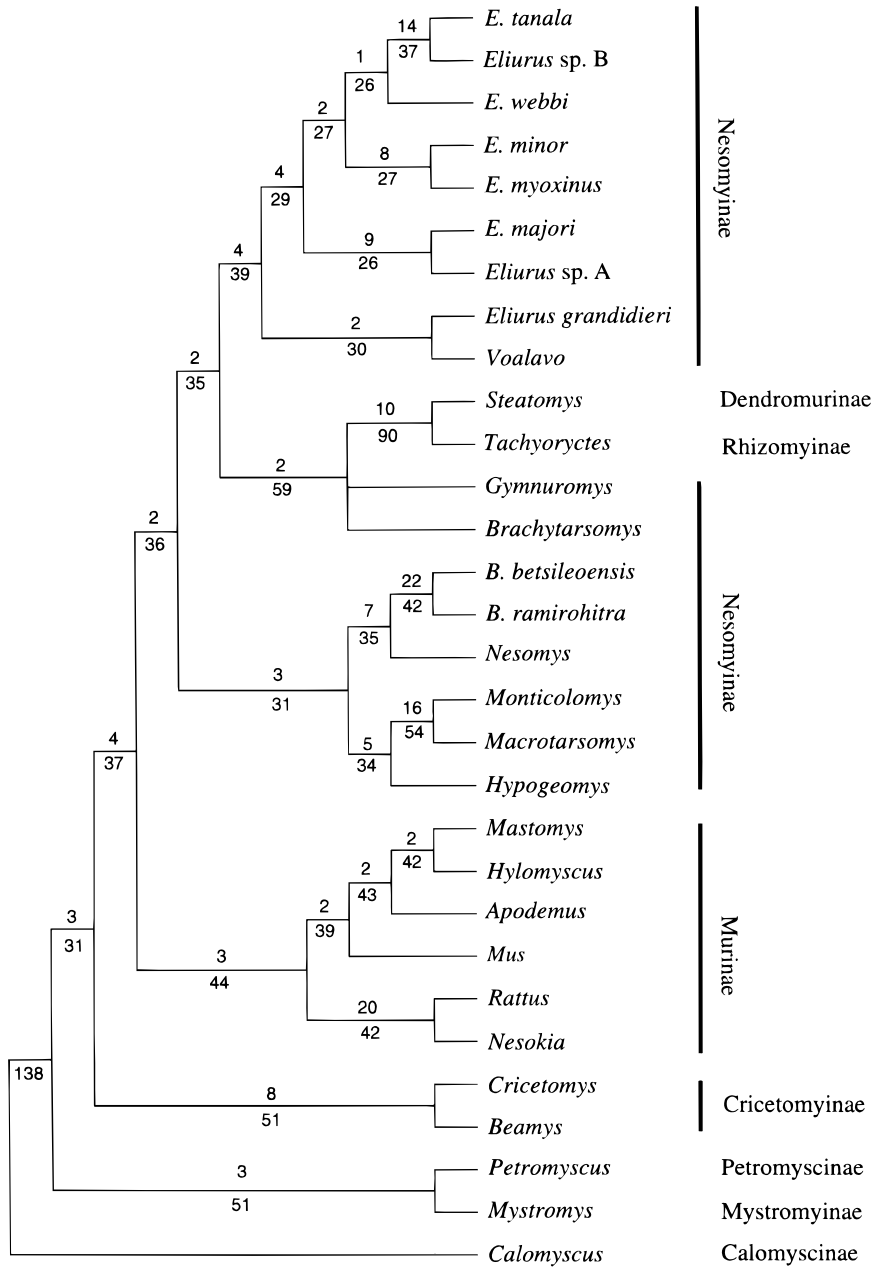

FIG. 2. Cladogram from Fig. 1 simplified to show basal structure among the taxa of interest. Individuals were pruned from the complete cladogram after parsimony analysis. Bremer Support values and branch length shown above and below the branch, respectively.

Interpretations of origin and directionality of murid phylogeny depend on where the network is rooted. We have chosen to root the tree using the Asian genus *Calomyscus*, the sole member of the muroid subfamily Calomyscinae. The phylogenetic position of *Calomyscus* within the muroid rodents is uncertain, but it is probably a primitive member of Muridae. Associations have been suggested with both New World (Pavlinov, 1980) and Old World cricetines (Vorontsov and Potapova, 1979), and more recently, Carleton and Musser (1984) suggested that *Calomyscus* is the sole remaining member of the otherwise extinct Asian

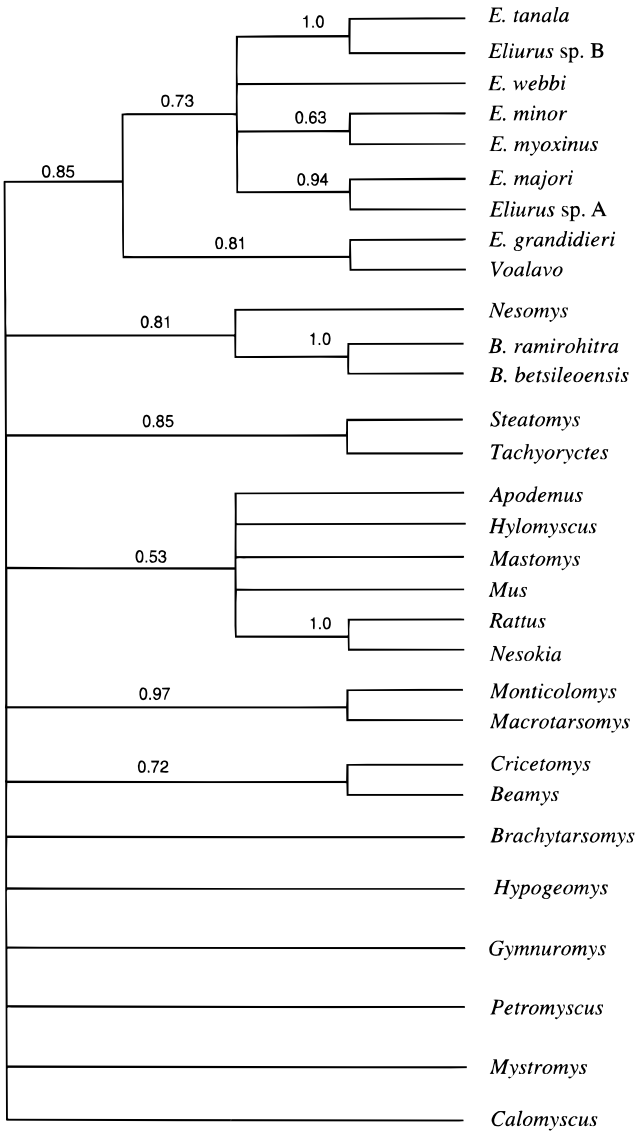

FIG. 3. Cladogram resulting from 10,000 random replications of parsimony jackknifing (JAC, Farris *et al.*, 1996). Numbers indicate the percentage of replications in which the node was recovered; only values >50% are shown.

group Cricetodontinae. Under any of these scenarios, *Calomyscus* provides an appropriate outgroup for the murid rodents included here and suggests that the murid tree is rooted in Asia. This geographic interpretation of murid origin is consistent with the fossil evidence; the earliest murid known to date is from the Eocene of China (Li and Ting, 1983; Vianey-Liaud, 1983).

Nesomyinae, Dendromurinae, and Rhizomyinae

The cytochrome *b* data indicate that the subfamily Nesomyinae, as currently recognized, is not a monophyletic group. The nine nesomyine genera form a paraphyletic assemblage, with Dendromurinae (represented by *Steatomys*) and African Rhizomyinae (*Tachyoryctes*) included as part of the clade. The molecular data strongly support the sister group arrangement of *Steatomys* and *Tachyoryctes* (Bremer / branch length = 10 / 90, PJV = 0.85), suggesting that *Tachyoryctes* is part of the dendromurine assemblage rather than the sole African member of the otherwise Asian Rhizomyinae. However, this study cannot critically address this issue until the Asian rhizomyines *Cannomys* and *Rhizomys* and a broader sampling of dendromurine genera are included. Although the relationships suggested among nesomyines, the African rhizomyine, and dendromurines are intriguing, they are not well-supported by the cytochrome *b* data (Figs. 2 and 3). Only 3 additional steps (out of 4373 total) are required to constrain nesomyines as a monophyletic group excluding *Steatomys* and *Tachyoryctes*.

Mystromyinae and Petromyscinae

The cytochrome *b* phylogeny provides a critical test of the relationship between the enigmatic African genus *Mystromys* and the nesomyine genera. Ellerman (1941:445) professed to be "entirely at a loss to suggest the relationships of this genus, which seems not only isolated from the Palearctic and Neotropical genera, but to have no marked generic characters . . . ." *Mystromys* is considered by some authors to be the sole mainland African member of the subfamily Nesomyinae (Corbet and Hill, 1991). This view arose from the classification of muroid rodents produced by Chaline *et al.* (1977), who considered *Mystromys* and the nesomyines to be direct descendants of Afrocricetodontinae. However, a recent classification of Mammalia admits to the uncertain phyletic placement of *Mystromys* and places the genus as the sole member of the murid subfamily Mystromyinae (Musser and Carleton, 1993). The molecular data clearly refute any close relationship between *Mystromys* and the Malagasy genera, as the clade does not appear in the analysis, and an additional 25 steps (out of 4373) are required to force *Mystromys* to be the sister group of the nesomyines.

In contrast, the molecular data suggest a sister group relationship between *Mystromys* and *Petromyscus*, one of two genera included in Petromyscinae. *Petromyscus* is another enigmatic muroid that has been variably included within Dendromurinae (Simpson, 1945; Ellerman, 1941), within Cricetidae (Petter, 1967, 1972), or within Petromyscinae in Muridae (Musser and Carleton, 1993). Several authors have remarked on the dental similarities between *Mystromys* and *Petromyscus* (Ellerman, 1941; Roberts, 1951; Lavocat, 1956), and Lavocat (1964) considered the petromyscine genera to be intermediate between *Mystromys* and the dendromurines. The molecular data tentatively support a sister group relationship between *Mystromys* and *Petromyscus* (Bremer / branch length = 3 / 51, PJV < 50%); the possible relationship between these two genera should receive further study, particularly relative to additional dendromurine genera and the second petromyscine genus, *Delanymys*.

Cricetomyinae

Cricetomyinae consists of three genera, *Cricetomys*, *Beamys*, and *Saccostomus*, which are diagnosed on the basis of a modified triserial molar pattern and shared internal cheek pouches (Ryan, 1989). The molecular data group *Beamys* and *Cricetomys* as sister taxa (Bremer / branch length = 8 / 51; PJV = 0.72), thus corroborating their association; however, to rigorously assess the monophyly of Cricetomyinae, the third genus in the subfamily should be included. The cricetomyine genera have been shuffled back and forth between Cricetidae and Muridae (*sensu* Simpson, 1945); this uncertainty results from two different interpretations of their molar morphology. The modified triserial pattern seen in the cricetomyine genera has been interpreted either as a simplified murid triserial pattern, in which case the medial cusps on the cricetomyine molars are homologous to similar cusps on the murine molar, or as an independent evolution of the triserial pattern, in which case these cusps are not homologous. In the molecular phylogeny, the cricetomyine rodents are placed as a basal member of the muroid rodents, a position which does not settle the controversy regarding their molar evolution. According to this tree, medial cusps may have evolved once in the ancestor to (Cricetomyinae + Murinae + Rhizomyinae + Dendromurinae) and were subsequently lost or modified in the ancestor to the (Nesomyinae + Dendromurinae + Rhizomyinae); alternatively, these cusps may have evolved independently in both Murinae and Cricetomyinae. Additional taxa and a combined analysis of morphological and molecular characters will provide a more appropriate test of this hypothesis than simply mapping the morphological characters on the present molecular tree (Kluge and Wolf, 1993; Jones *et al.*, 1993; Eernisse and Kluge, 1993).

Murinae

This study was not designed to assess the monophyly of Murinae, a geographically widespread subfamily containing well over 500 species. The murines sampled include the African murine genera *Hylomyscus* and *Mastomys*, the widespread Eastern Hemisphere genera *Mus* and *Apodemus* (probably Asian in origin, Wessels *et al.*, 1982), and the predominantly Asian *Nesokia* and *Rattus*. The present phylogeny clusters all six murine genera as a single monophyletic group and suggests that the African genera are derived relative to the murines of Asian origin. Paleontologists generally believe that murine rodents originated in Asia and spread from there throughout the Eastern Hemisphere; the earliest known murines are from the middle Miocene of Pakistan (Jacobs, 1978; Wessels *et al.*, 1982), and murine fossils do not appear in Europe and Africa until the late Miocene (Jaeger, 1977; Lavocat, 1978). The phylogeny based on cytochrome *b* is consistent with this view of murine biogeography in showing the African taxa *Hylomyscus* and *Mastomys* as derived relative to *Rattus*, *Nesokia*, *Mus*, and *Apodemus*, the murine taxa with presumed Asian origins (Jacobs, 1978; Wessels *et al.*, 1982).

Relationships among Nesomyine Genera

The cytochrome *b* phylogeny suggests that nesomyines form a paraphyletic group, but the basal relationships among nesomyines and other murid taxa are not well supported (Figs. 2 and 3) and deserve to be tested with additional taxa and characters. In contrast, several generic level affinities appear consistently in the cytochrome *b* phylogeny and are well supported. These groupings are discussed below.

Eliurus and Voalavo

A new nesomyine was recently discovered from the northern montane regions of Madagascar; this animal was described as the sole species of the new genus *Voalavo* (Carleton and Goodman, 1998). In their description of the genus, these authors report that *Voalavo gymnocaudus* is the sister taxon to the genus *Eliurus* (Carleton and Goodman, 1998). The molecular data support their contention that *Voalavo* is closely related to *Eliurus*, because the two genera form a clade to the exclusion of all other nesomyine genera. However, the molecular data suggest that *Voalavo* cannot be considered a separate genus without rendering *Eliurus* paraphyletic. According to the cytochrome *b* cladogram, *Voalavo* is the sister taxon to *Eliurus grandidieri* (also described in Carleton and Goodman, 1998). *Eliurus grandidieri* and *Voalavo gymnocaudus* are only known from the northern highlands of Madagascar. The former species occurs in moist montane forest between 1210 and 1550 m and the latter species in montane and sclerophyllous forest from ca. 1300 to 1950 m (Goodman and Carleton, 1998). Monophyly of *Eliurus* and the new genus to the exclusion of all other genera is recovered in 85% of jackknife replications and that of *Eliurus* species excluding *Eliurus grandidieri* and *Voalavo gymnocaudus* is recovered in 73% of the replications. The clade conjoining *Eliurus grandidieri* and *Voalavo* is recovered in 81% of the 10,000 replications.

Meaningful confidence limits cannot be placed on any statistical measure of clade support, including parsimony jackknife values, and the use of resampling techniques as a measure of clade support remains controversial (Carpenter, 1992; Siddall, 1995; but see Hillis and Bull, 1993). The Bremer support value gives the number of extra steps required to lose a clade and, as such, is an unambiguous measure of the amount of corroboration the data give to a particular clade (Kallersjo *et al.*, 1992; Bremer, 1994). The Bremer support values calculated for these taxa reveal a somewhat different picture of support than the parsimony jackknife values. The larger clade containing *Eliurus* and *Voalavo* receives a Bremer/branch length value of 4/39 (PJV = 0.85), and it requires a similar 4 steps of 29 to dissolve the clade containing *Eliurus* species to the exclusion of *E. grandidieri* and *Voalavo* (PJV = 0.73). However, the clade containing *Voalavo* and *E. grandidieri* has a relatively low Bremer/branch length value of 2/30 despite its relatively high recovery rate of 81% in the parsimony jackknife analysis. Furthermore, it requires only three additional steps (out of 4373 total) to constrain the monophyly of *Eliurus* excluding *Voalavo*. These results serve to underscore the need for additional data to address the phylogenetic relationships among *Eliurus* species and *Voalavo*. Further studies would benefit from a combined analysis of the morphological and molecular data and the inclusion of the rare *E. petteri* (tissue samples not available for the present study), which Carleton and Goodman (1998) suggest is closely related to *Eliurus grandidieri*.

Monticolomys, Macrotarsomys, and Hypogeomys

Monticolomys koopmani is the sole species in a newly described genus from the forested high mountain regions of central and southern Madagascar. It ranks after *Voalavo* as the second smallest nesomyine species. The first specimen was collected in 1929, but was not recognized as unusual until the early 1970s by the late Karl Koopman (Carleton and Goodman, 1996). The enigmatic mouse was recently "rediscovered" in the wild in Madagascar by Goodman in 1993 and was formally described as a new genus and species by Carleton and Goodman in 1996. These authors were especially struck by the morphological similarity between *Monticolomys* and *Macrotarsomys* and tentatively suggested (1996:250) a phylogenetic link between the two:

> several cranial and dental characters clearly implicate a sister-group relationship between [*Monticolomys*] and *Macrotarsomys* . . . to be sure, many more resemblences of *Monticolomys* and *Macrotarsomys* involve traits that are plausibly considered as primitive or those whose evolutionary polarity is equivocal . . . at the same time . . . we believe that a hypothesis of cognate affinity warrants attention at this formative stage of phylogenetic understanding among nesomyines.

The *Monticolomys–Macrotarsomys* clade is one of the most stable groupings present in the molecular phylogeny and is the most stable clade conjoining two nesomyine genera (Bremer/branch length = 16/54; PJV = 0.97) (Figs. 2 and 3). The molecular data therefore

strongly corroborate the sister group alliance of *Monticolomys* and *Macrotarsomys* suggested on the basis of morphological comparisons.

The sister group relationship between these two genera is intriguing as they are very different in their geographic distribution, habitat preferences, and ecological specializations. *Macrotarsomys* is restricted to the dry, deciduous forests and spiny forests of western and southern Madagascar. It has been referred to as the "Madagascar gerbil" based on its superficial resemblance to these desert-adapted rodents of Africa and Asia. In contrast, *Monticolomys* is generally murine in overall appearance and is restricted to eastern humid and montane sclerophyllous forest. Despite these ecological differences, both morphological and molecular data suggest the two share an immediate common ancestor.

Hypogeomys is the Malagasy giant jumping rat and is restricted to a small area of western, dry deciduous forests. Like *Macrotarsomys*, it has acquired bipedal, saltatorial locomotion; however, the burrow-dwelling *Hypogeomys* is by far the largest extant Malagasy rodent [although a larger subfossil species *H. australis* is known from Holocene deposits on the Central High Plateau and southeastern Madagascar (Goodman and Rakotondravony, 1996)]. In his taxonomic revision of Rodentia, Ellerman (1941) suggested affinities between *Macrotarsomys* and *Hypogeomys* based on external morphology and molar similarities. Ellerman relied on Milne-Edwards and Grandidier's (1898) comparison of *Macrotarsomys* and *Hypogeomys* as there were no specimens of *Macrotarsomys* in the British Museum at the time. Milne-Edwards and Grandidier's original drawing of *Macrotarsomys* molars are of an older individual with highly worn molars. As Schaub (1925) noted, molars from younger individuals do not resemble *Hypogeomys*, and molar structure provides no obvious basis for suggesting a sister group relationship between the two. Nonetheless, the tree derived from cytochrome *b* data suggests that *Hypogeomys* is the sister taxon to the *Monticolomys-Macrotarsomys* clade. While this clade receives moderate Bremer Support (Bremer/branch length = 5/34), it is not recovered in the parsimony jackknife analysis. Again, combined analysis of molecular and morphological data, and inclusion of the larger species of *Macrotarsomys, M. ingens*, will ultimately provide the strongest test of these phylogenetic hypotheses.

Brachyuromys and Nesomys

The African root-rat *Tachyoryctes* is a fossorial rodent adapted for subterranean habits in having a stocky, short-tailed body and robust skull that are well-suited for burrow excavation. Major (1896, 1897) was the first to propose that the Malagasy vole-like rodent *Brachyuromys* is simply a less-specialized form of *Tachyoryctes*. He based this conclusion on cranial and dental similarities, discounting the possibility that the morphological similarities between these two rodents could be the result of convergence rather than common ancestry. Major (1897:698) argued that by imagining a less-specialized form of *Tachyoryctes*, one could conjure up *Brachyuromys* "if we divest the *Tachyoryctes* skull of its [excessive] fossorial characters and of the consequences of the more hypselodont molars, we obtain a *Brachyuromys* skull . . . there is further a great correspondence in external characters if we disregard the smaller ears and eyes of *Tachyoryctes*." Ellerman (1940) concurred with Major (1897) and formalized his concept by erecting Tachyoryctinae for only these two genera. The molecular data support a sister group relationship between *Brachyuromys* and *Nesomys* (Bremer/branch length = 7/35, PJV = 0.81) (Figs. 2 and 3). Moreover, an additional 58 steps (of a total 4373) are required to constrain a *Tachyoryctes–Brachyuromys* clade, thus clearly refuting this relationship.

The sister group relationship apparent between *Nesomys* and *Brachyuromys* has not been suggested previously. Ellerman (1941) suggested that *Brachyuromys* has affinities with *Hypogeomys* but proposed a more immediate connection between *Hypogeomys* and *Macrotarsomys* (but see above discussion of Ellerman's possible confusion regarding *Macrotarsomys*). Petter (1961) suggested affinities between *Nesomys* and *Hypogeomys* based on similarities in general molar structure. The molecular data provide some resolution of these conflicting classificatory ideas. The present phylogenetic analysis uncovers a single clade containing these four genera (*Hypogeomys, Macrotarsomys, Nesomys*, and *Brachyuromys*) plus *Monticolomys* (described in 1996)

and provides resolution as to the sister group relationships among them (Fig. 2).

Brachytarsomys and Gymnuromys

Brachytarsomys and *Gymnuromys* are two of the more enigmatic nesomyine genera. *Gymnuromys* has a laminate molar morphology unique among murid rodents, an observation which prompted Ellerman (1940) to erect a separate subfamily for this genus. The molars of *Brachytarsomys* are similar superficially to the prismatic molars present in the murid subfamily Arvicolinae (voles and lemmings). Major (1897) and Hinton (1926) proposed that *Brachytarsomys* is the "forerunner" to all voles and lemmings, but both authors stopped short of including *Brachytarsomys* and arvicoline murids in a single subfamily. Ellerman (1941), however, formally included *Brachytarsomys* in Arvicolinae (his Microtinae). Despite these taxonomic conclusions, it seems biogeographically unlikely that *Brachytarsomys* would share an immediate ancestor with the predominantly Holarctic Arvicolinae; therefore, this hypothesis was not addressed in the current study.

The molecular tree is moot with respect to the placement of *Gymnuromys* and *Brachytarsomys*, other than to suggest a relatively poorly supported association with the African rhizomyine *Tachyoryctes* and the dendromurine *Steatomys* (Bremer / branch length = 2 / 59). Further taxonomic sampling, including the Asian rhizomyines and additional members of Dendromurinae, another questionably monophyletic murid subfamily (Verheyen *et al.*, 1996) may aid in resolving the placement of these two genera.

Biogeographic Implications

Madagascar was originally part of the large Gondwanan supercontinent where it was situated between Africa and the Indian subcontinent (Du Toit, 1937; Smith and Hallam, 1970; Dietz and Holden, 1970; Krause *et al.*, 1997). The continental connection between Africa and Madagascar was probably severed in the Middle to Late Jurassic (150–165 MYA) when Madagascar and India drifted south along the coast of Africa (Embleton and McElhinny, 1975; McElhinny and Embleton, 1976; McElhinny *et al.*, 1976; Coffin and Rabinowitz, 1987). Ocean floor spreading data suggest that Madagascar reached its current position relative to Africa in the Early to Middle Cretaceous (124.5–133 MYA) (Martin and Hartanady, 1986; Segoufin and Patriat, 1981; Rabinowitz *et al.*, 1983). The geology and biogeography of India are complicated, but geologists generally believe that India began its northward migration in the mid-Cretaceous (88–90 MYA) (Storey *et al.*, 1995; Storetvedt *et al.*, 1992) and probably contacted Asia during the early Eocene (50–56 MYA) (Patriat and Achache, 1984; Besse and Courtillot, 1988; Klootwijk *et al.*, 1992; Thewissen, 1990; Thewissen and McKenna, 1992; but see Patterson and Owen, 1991, and Jaeger *et al.*, 1989, for evidence that contact occurred at the K / T boundary). Thus, Madagascar has probably been isolated from other major Gondwanan landmasses at least since the Late Cretaceous, and these continents have been in their present position since the early Eocene.

Two main scenarios have been suggested for the origin of the rodent fauna on Madagascar: (1) nesomyine rodents are the result of a single invasion into Madagascar and a subsequent insular radiation; and (2) the endemic species resulted from several independent invasions of the island. The critical test of these propositions lies in identifying the appropriate muroid taxa to include in testing the monophyly of the nesomyines. Simpson (1952) and others have assumed that the ancestor(s) of the nesomyines arrived via waif dispersal from the African mainland. In this case, the likely relatives of the nesomyines should be found among the "archaic" African muroid taxa included in Dendromurinae, Cricetomyinae, Petromyscinae, and African Rhizomyinae. Less commonly considered is a possible Asian origin of the nesomyines. If the nesomyines arrived from Asia, their possible relatives may be found among Calomyscinae, Asian Rhizomyinae, or Murinae. We assessed these competing biogeographic alternatives by including examples of most of these subfamilies.

Superimposing the cladogram (Fig. 2) on a map of the Indo-African region (Fig. 4) supports the following three conclusions. First, given the root of the murid tree in Asia (discussed above), there are two independent invasions of Africa from Asia at the base of the tree, one which gave rise to *Mystromys* and *Petromyscus*, and a second which gave rise to the cricetomyines *Beamys* and *Cricetomys*. However, optimization of the ancestral area for these nodes is ambiguous. Alternately, one could propose an Asian origin for the murids, a single

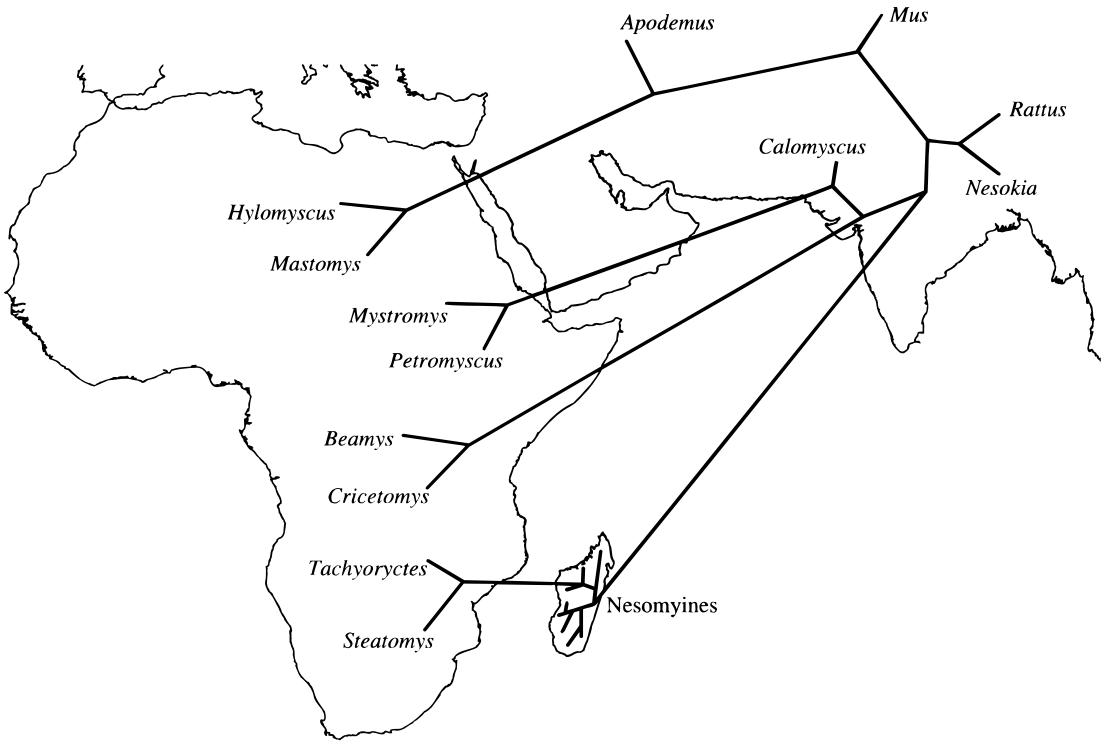

FIG. 4. Biogeographic scenario for the origin of the nesomyines and archaic African muroids. The cladogram from Fig. 2 was superimposed on a map of the Indo-Austrailian region. Assumptions used to generate this scenario and its possible implications for murid biogeography are discussed in the text.

African invasion giving rise to the two basal African clades, and a subsequent reinvasion of Asia to found the ancestor of the murines. Given that the earliest possible ancestor of all murids and of the more derived clade of murines are both found in the Asian fossil record, we consider the first optimization more defensible. Regardless of optimization, however, the molecular phylogenetic hypothesis suggests that the origin of the "archaic" African murids is complex.

Second, rodents arrived on Madagascar only once. The cytochrome *b* phylogeny therefore supports the single origin hypothesis and suggests that the diversity of the nesomyine genera may have resulted from an insular adaptive radiation. Moreover, assuming that the ancestor of both murines and nesomyines arose in Asia, then the Malagasy rodents came from Asia, not from Africa as is commonly assumed (Fig. 4). This conclusion stands in contrast to the suggested origin of Madagascar's other native mammalian taxa. Yoder (1996) found that the Malagasy lemuriform primates form a monophyletic group which dispersed from Africa, the native Malagasy carnivores appear to have African affinities (M. Nedbal, pers. comm.), and insectivores have affinities to African (L. Olson, pers. comm.) or perhaps to New World taxa (Asher, 1997).

Finally, optimization of the ancestral areas unambiguously shows an invasion of the African mainland from Madagascar. This invasion gave rise to a single clade including *Tachyoryctes* (Rhizomyinae) and *Steatomys* (Dendromurinae). This intriguing result suggests that *Tachyoryctes* may not be closely related to the Asian rhizomyines, but rather to the Malagasy rodents and the African dendromurines. Further tests of this hypothesis require the inclusion of the Asian rhizomyines and additional dendromurine genera. Previous hypotheses of murid biogeography have not considered the possibility of dispersal from Madagascar to Africa; however, complex geographic histories have been suggested for other Malagasy organisms. Biogeographic analysis of gekkonid lizards show several dis-

persal events between Madagascar and Africa (Kluge and Nussbaum, 1995), and a similarly complex history may be evident for chamaeleonines (Raxworthy and Nussbaum, pers. comm.).

CONCLUSIONS AND CAVEATS

The present molecular phylogenetic hypothesis of nesomyines contains the most thorough taxonomic sampling to date. The inclusion of all nesomyine genera, representatives from a majority of "archaic" African muroids (*Mystromys, Petromyscus, Steatomys, Tachyoryctes*, and two genera of Cricetomyinae) as well as several Asian taxa including *Calomyscus*, provides a severe test of nesomyine monophyly. The resulting phylogeny, based on complete cytochrome *b* sequence data, indicates that the Malagasy rodents form a paraphyletic assemblage that includes the African genera *Tachyoryctes* (Rhizomyinae) and *Steatomys* (Dendromurinae). Despite this paraphyly, a single dispersal event to Madagascar can still explain the origin of the nesomyines and suggests that their morphological diversity may be the result of an adaptive radiation.

At first glance, the problem of nesomyine origins seems well suited to molecular data—the nesomyine genera are so morphologically diverse that phylogenetic inference based on morphological characters appears difficult. However, no particular "kind" of data is necessarily superior or inferior for addressing the systematics of the nesomyines. While morphological data may prove difficult to code for comparisons among these taxa, clearly molecular data from the cytochrome *b* gene do not strongly corroborate their basal relationships. The systematic and biogeographic conclusions resulting from the present study are intriguing and in some cases novel; however, caution must be exercised before drawing any conclusions because not all parts of the underlying cladogram are strongly supported. The phylogeny presented here, and its attending biogeographic implications, is a hypothesis which is available for further testing with additional taxa and characters.

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APPENDIX 1

List of Specimens Sequenced and Their Vouchers

DNA No.	Species	Voucher specimen[a]
Nesomyinae		
502	*Brachytarsomys albicauda*	USNM 449212
504	*Brachyuromys betsileoensis*	USNM 449216
505	*Brachyuromys betsileoensis*	USNM 449217
591	*Brachyuromys betsileoensis*	FMNH 156227
592	*Brachyuromys betsileoensis*	FMNH 156229
445	*Brachyuromys ramirohitra*	FMNH 151659
650	*Eliurus ellermani*[b]	FMNH 159697
651	*Eliurus grandidieri*	FMNH 159703
655	*Eliurus grandidieri*	FMNH 159699
443	*Eliurus majori*	FMNH 151667
444	*Eliurus majori*	FMNH 151732
556	*Eliurus majori*	FMNH 154610
561	*Eliurus majori*	FMNH 154289
587	*Eliurus majori*	FMNH 156503
614	*Eliurus majori*	FMNH 156616
617	*Eliurus majori*	FMNH 156345
638	*Eliurus majori*	FMNH 151661
639	*Eliurus majori*	FMNH 151662
641	*Eliurus majori*	FMNH 151664
642	*Eliurus majori*	FMNH 151731
447	*Eliurus minor*	FMNH 151673
448	*Eliurus minor*	FMNH 151675
458	*Eliurus minor*	FMNH 151669
464	*Eliurus minor*	FMNH 151672
473	*Eliurus minor*	FMNH 151734
513	*Eliurus minor*	USNM 448978
514	*Eliurus minor*	USNM 449246

List of Specimens Sequenced and Their Vouchers Continued

DNA No.	Species	Voucher specimen[a]
584	*Eliurus minor*	FMNH 156618
613	*Eliurus minor*	FMNH 156211
644	*Eliurus minor*	U. Antananarivo
384	*Eliurus myoxinus*	FMNH 151952
385	*Eliurus myoxinus*	FMNH 151953
453	*Eliurus myoxinus*	FMNH 151954
570	*Eliurus myoxinus*	FMNH 154633
571	*Eliurus myoxinus*	FMNH 154632
590	*Eliurus myoxinus*	FMNH 156630
646	*Eliurus myoxinus*	U. Antananarivo
647	*Eliurus myoxinus*	U. Antananarivo
648	*Eliurus myoxinus*	U. Antananarivo
653	*Eliurus myoxinus*	U. Antananarivo
449	*Eliurus tanala*	FMNH 151689
463	*Eliurus tanala*	FMNH 151687
500	*Eliurus tanala*	FMNH 151744
511	*Eliurus tanala*	USNM 448986
583	*Eliurus tanala*	FMNH 156631
585	*Eliurus tanala*	FMNH 156632
586	*Eliurus tanala*	FMNH 156634
640	*Eliurus tanala*	FMNH 151690
643	*Eliurus tanala*	USNM 448985
573	*Eliurus* undescribed[c]	U. Antananarivo
450	*Eliurus webbi*	FMNH 151742
454	*Eliurus webbi*	FMNH 151680
456	*Eliurus webbi*	FMNH 151739
459	*Eliurus webbi*	FMNH 151682
515	*Eliurus webbi*	USNM 449257
516	*Eliurus webbi*	USNM 449259
582	*Eliurus webbi*	FMNH 156642
652	*Eliurus webbi*	FMNH 159718
558	*Eliurus webbi*?[d]	FMNH 154623
559	*Eliurus webbi*?[d]	FMNH 154625
506	*Gymnuromys roberti*	USNM 449270
441	*Gymnuromys roberti*	FMNH 151693
442	*Gymnuromys roberti*	FMNH 151694
594	*Gymnuromys roberti*	FMNH 156614
555	*Hypogeomys antimena*	FMNH 154636
595	*Macrotarsomys bastardi*	U Antananarivo
618	*Monticolomys koopmani*	FMNH 156212
581	*Monticolomys koopmani*	FMNH 156663
589	*Monticolomys koopmani*	FMNH 156661
649	*Monticolomys koopmani*	FMNH 159494
509	*Nesomys audeberti*	USNM 448893
510	*Nesomys audeberti*	USNM 448948
451	*Nesomys audeberti*?[d]	FMNH 151696
475	*Nesomys rufus*	FMNH 151698
476	*Nesomys rufus*	FMNH 151745
477	*Nesomys rufus*	FMNH 151699
496	*Nesomys rufus*	FMNH 151747
498	*Nesomys rufus*	FMNH 151749
501	*Nesomys rufus*	FMNH 151915
507	*Nesomys rufus*	USNM 448898
508	*Nesomys rufus*	USNM 448899
593	*Nesomys rufus*	FMNH 156645
540	*Voalavo gymnocaudus*	FMNH 154040
560	*Voalavo gymnocaudus*	FMNH 154041

List of Specimens Sequenced and Their Vouchers Continued

DNA No.	Species	Voucher specimen[a]
Mystromyinae		
634	*Mystromys albicaudatus*	DM 3452
635	*Mystromys albicaudatus*	DM 4344
Murinae		
	Mus musculus	GenBank
	Rattus norvegicus	GenBank
580	*Nesokia indica*	FMNH 140571
588	*Apodemus sylvaticus*	FMNH 140541
137	*Mastomys hildebrantii*	
124	*Hylomyscus alleni*	
Petromyscinae		
534	*Petromyscus collinus*	TTU 55216
535	*Petromyscus collinus*	TTU 55218
Dendromurinae		
532	*Steatomys parvus*	CMNH 98494
533	*Steatomys parvus*	CMNH 98495
Rhizomyinae		
536	*Tachyoryctes splendens*	CMNH 98212
Cricetomyinae		
517	*Beamys hindei*	FMNH 151225
529	*Beamys hindei*	CMNH 98246
530	*Cricetomys emini*	CMNH 90808
531	*Cricetomys emini*	CMNH 98248
636	*Cricetomys emini*	ROM 100510
637	*Cricetomys emini*	ROM 100511
518	*Cricetomys gambianus*	FMNH 151227
Calomyscinae		
576	*Calomyscus baluchi*	FMNH 140412

[a] USNM, National Museum of Natural History; FMNH, Field Museum of Natural History; CMNH, Carnegie Museum of Natural History; TTU, The Museum, Texas Tech University; ROM, Royal Ontario Museum; and DM, Durban Museum, South Africa.

[b] Identified as *Eliurus ellermani*, referred to here as *Eliurus* sp. B pending further investigation. *Eliurus webbi* 558 and 559 referred to as *Eliurus* sp. B pending further investigation.

[c] Undescribed *Eliurus* referred to here as *Eliurus* sp. A.

[d] Questionable *N. auderberti*. See discussion of species identification in Carleton and Goodman (1996:273).

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