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Pliocene colonization and adaptive radiations in Australia and New Guinea (Sahul): Multilocus systematics of the old endemic rodents (Muroidea: Murinae)

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Abstract

The old endemic rodents of Australia and New Guinea (Sahul) represent one or more large adaptive radiations including novel morphological adaptations to aquatic, arboreal, hopping, and arid ecologies. Four tribes recognized among the Sahulian old endemics (Hydromini, Conilurini, Anisomyini, and Uromyini) reflect distinct biogeographic and ecomorphological hypotheses about diversification within the Old Endemics. We present the first character-based phylogeny of the Sahulian Old Endemic rodents with broad sampling, nested within a broader phylogeny of the Murinae. We estimated phylogenies from >2500 nucleotides of mtDNA sequence and >9500 nucleotides from six autosomal nuclear loci, for individual genes and for the full concatenated data using parsimony, likelihood, and Bayesian methods. Our results strongly supported monophyly of the group and its sister relationship to the Philippine old endemics of the *Chrotomys* division. Most striking was the rapid diversification after the Late Miocene or Early Pliocene colonization of New Guinea from the west, consistent with a single colonization of the Sahulian continent. That was followed 2–3 My later by a second adaptive radiation resulting from one or more colonizations of Australia. Monophyly was not supported for the Anisomyini or the Conilurini but was for the Uromyini nested within the Conilurini and for the Hydromyini. Conflict among gene phylogenies was weak, and support for the consensus topology increased with more (even conflicting) data.

Keywords: Mammalia; Muridae; Phylogeny; Biogeography; DNA

1. Introduction

Australia, New Guinea, and nearby islands have been exemplary subjects for studies of biogeographic patterns and radiations of endemic flora and fauna throughout much of modern biology (e.g., Wallace, 1860; Mayr, 1944; Simpson 1961, 1977; Raven and Axelrod, 1972). Most of the interest in endemic clades has focused on the relatively ancient groups whose origins date back to the break up of Gondwana (e.g. Ratites, Haddrath and Baker, 2001; and marsupials: Springer et al., 1998) or other clades with Cretaceous or early Tertiary origins (e.g., eucalypts, Ladiges et al., 2003; see also Woodburne and Case, 1996; and Sanmartin and Ronquist, 2004 for review). Other research has focused on the biogeographic consequences of faunal interchange between Oriental and Australasian groups for biodiversity of the Indonesian Archipelago and on such demarcations as Wallace's, Weber's and Lydekker's lines (Fig. 1; Whitten et al., 1987; Moss and Wilson,

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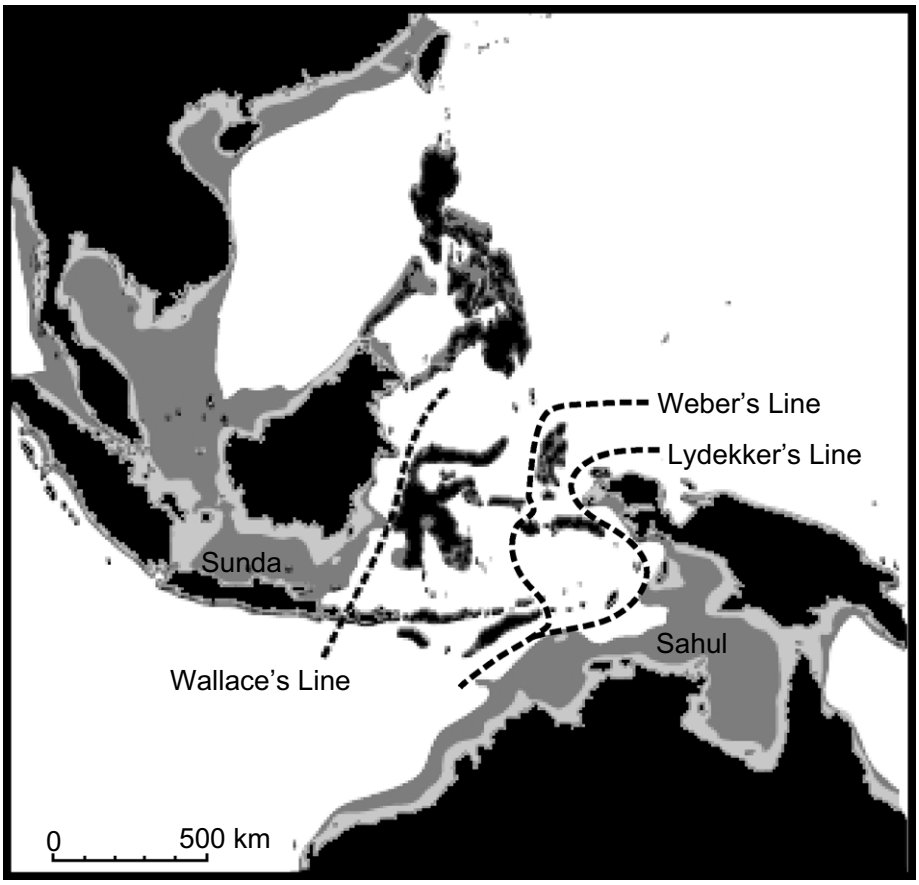

Fig. 1. Map of Australasia (Sunda & Sahul). Light and dark gray areas indicate predicted Pleistocene shoreline at 30 and 120 m below current sea level, respectively. Reproduced from Voris, 2000 with permission from the Field Museum of Natural History©.

1998; Turner et al., 2001; Evans et al., 2003). Comparatively less attention has been paid to the consequences of Australia's relatively recent tectonic approach to southeast Asia for the flora and fauna of Australia (but see Driskell and Christidis, 2004, in birds; Keogh et al., 1998 in snakes; Maekawa et al., 2003, in cockroaches; and Watts and Baverstock, 1995, in rodents). In question are the number and timing of colonizations and whether adaptive radiations either initiated or were the consequence of those dispersal events. We explored the phylogenetics of one of Australia's most diverse endemic faunas, the several tribes of murine rodents, and reconstructed the number of colonizations and tempo of diversification by broadly sampling murine diversity, including insular Southeast Asian groups.

New Guinea and Australia together comprise the continent of Sahul (Fig. 1), which has a geological history independent from Asia that dates back to their separation from Antarctica and the supercontinent of Gondwana 35–50 Mya (Scotese et al., 1988; Woodburne and Case, 1996; Johnson, 2004). Drifting northward, Sahul did not reach its current proximity to the Sunda Shelf of peninsular/insular Southeast Asia and the Philippines until approximately the Late Miocene 10 Mya (Hall, 1998). Much of New Guinea also remained submerged until this time when collision with the Asian plate led to the accretion of most of what is now northern New Guinea (Pigram and Davies, 1987). Despite the relatively small intervening distances among land masses of Sunda, Wallacea, and Sahul since the Late Miocene, they remain isolated by deep ocean channels as delineated by Wallace's, Weber's and Lydekker's lines (Fig. 1; Wallace, 1863; Lydekker, 1896; Weber, 1904; Whitten et al., 1987; Moss and Wilson, 1998). No landbridges have ever connected Sunda to Sahul or the Philippines, and all colonists from Asia have crossed open-ocean from island to island. Colonization of Sahul by terrestrial vertebrates from Asia is therefore expected to have been relatively uncommon.

Muroid rodents (e.g., rats, mice, hamsters, gerbils) are diverse and ubiquitous, comprising nearly one-third of all mammal species. Their taxonomic diversity underlies an extensive ecological and morphological variation. Muroids thrive in virtually every terrestrial environment on earth. Their body size ranges over nearly three orders of magnitude from a few grams (*Baiomys*) to over 2 kg (*Phloeomys*). In addition to the generalized quadrupeds referred to as rats, muroids include bipedal (*Notomys*), semiaquatic (*Ondatra, Hydromys, Icthyomys, Nilopegamys*), arboreal (*Rhipidomys, Phloeomys, Pogonomys, Melomys*), and fossorial (*Spalax, Kunsia*) organisms. Most muroid diets are to some extent generalist but several taxa exhibit varying degrees of specialization for eating grass (*Microtus*, *Masta-*

comys), bamboo (*Hapalomys, Mallomys*), seeds, fruit, insects (*Acomys*), earthworms (*Rhynchomys*), or crustaceans and fish (*Ichthyomys, Hydromys*). This great surfeit of diversity has emerged in a relatively young lineage of mammals, in which most diversity is contained in the clade Eumuroidea, whose origins in North America have been dated by fossil and molecular genetic studies to roughly 25 Mya in the Oligocene (Wood, 1980; Emry, 1981; Steppan et al., 2004a).

Remarkably, the ecomorphological variation within the Muroidea has been recapitulated in several subsequent radiations within the group (Fig. 2). Their expansion into every continent except Antarctica has led to at least four rapid radiations (Steppan et al., 2004a), most notably in the Sigmodontinae in the Neotropics and the Murinae in the eastern hemisphere. The Murinae, comprising over 600 species (Musser and Carleton, 2005), are the largest subfamily of mammals. They have spread throughout the eastern hemisphere from a presumed origin in South/Southeast Asia (Jacobs, 1997; Jacobs et al., 1990; Jacobs and Downs, 1994; Jacobs and Flynn, 2005) and are the only non-volant eutherian mammals native to Sahul. Although the taxonomy of the group remains largely untested phylogenetically, major biogeographic centers of

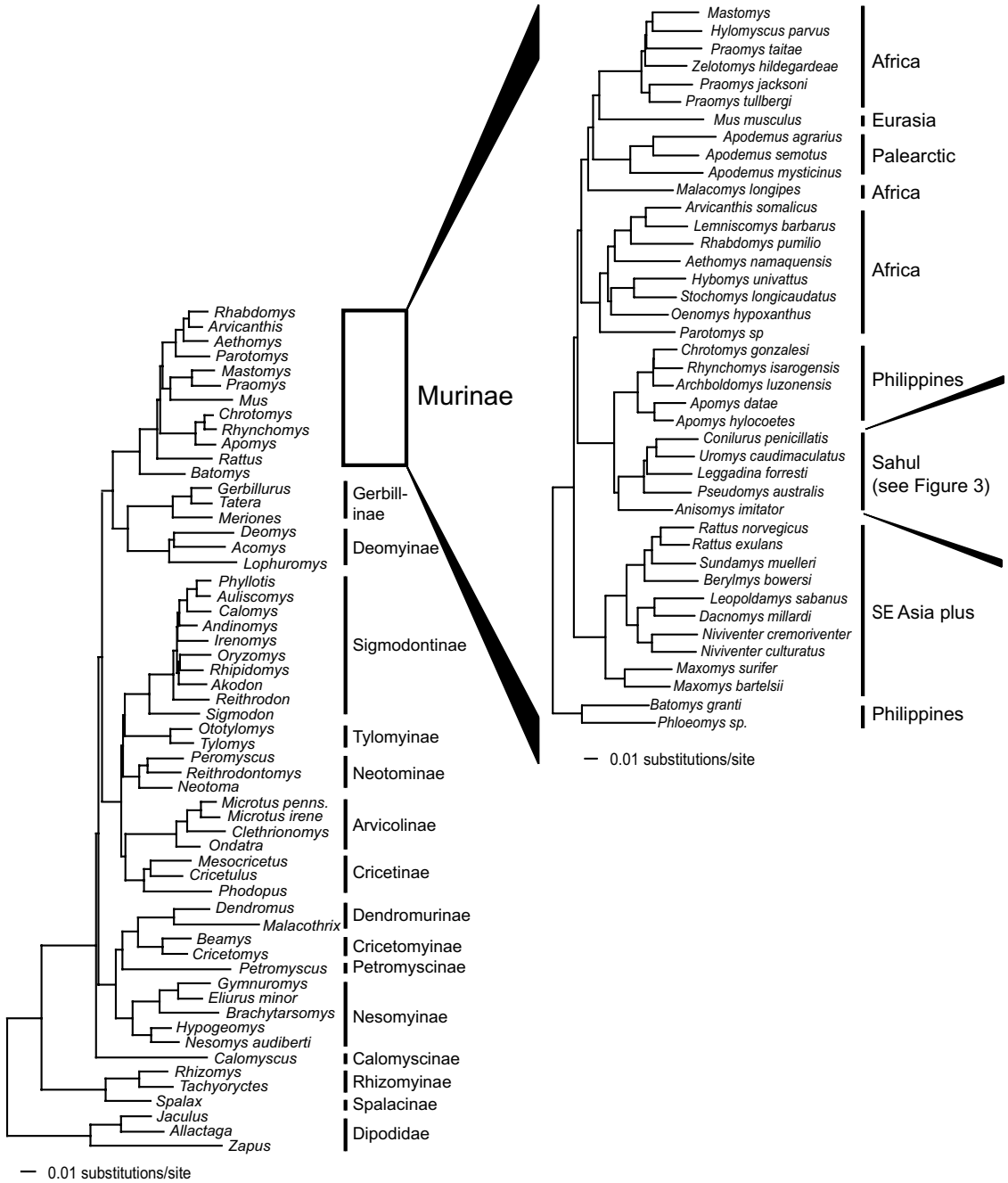

Fig. 2. Maximum-likelihood phylograms for the Muroidea and Murinae demonstrating the nested radiations within Muroidea (recreated from Steppan et al., 2004a, 2005).

diversity reflecting monophyletic lineages are distributed across Southeast Asia, Africa, the Philippines, and Sahul (Steppan et al., 2005). The Sahulian diversity, in particular, represents a terminal expansion of Murinae that exemplifies the great recapitulation of forms that has occurred within nested radiations of Muroidea. The murine colonists of Sahul reflect nearly every ecomorphological form found within the subfamily and within all Muroidea and include nearly 160 species in 37 genera, representing nearly 25% of all Australian mammal species. Roughly 20 species are members of the genus *Rattus* and are not closely related to the remaining taxa with respect to other Murinae. Members of this group have not diverged significantly from their congeners on the Sunda shelf and intervening islands and are similar both morphologically and ecologically. Therefore, Sahulian *Rattus* are thought to be recent colonists with a history independent from that of the remaining Sahulian murines.

The remaining species of Sahulian colonists reflect a taxonomically, ecologically, and morphologically diverse group of "old endemics" (Simpson, 1961) that appeared in the Australian fossil record 4–5 Mya (Lee et al., 1981; Godthelp, 1990, 1997; Rich et al., 1991). They range in size from 10 g (*Lorentzimys*) to over 1000 g (*Hyomys*) and occupy a wide variety of habitats from semiaquatic (*Hydromys*) to desert (*Notomys*) to rainforest canopy (*Pogonomys*). Significant uncertainty remains about the monophyly of the group and the number of Sahulian colonizations that produced their diversity. Tate (1951) and Simpson (1961) both concluded from morphological characters that the Sahulian "old endemics" were not monophyletic and were derived from at least four colonizations. Although later studies of phallic morphology (Lidicker, 1968; Lidicker and Brylski, 1987), sperm morphology (Breed and Sarafis, 1978; Breed, 1984), craniodental morphology (Musser, 1981), and chromosome variation (Baverstock et al., 1977; Donnellan, 1987) supported monophyly of the Sahulian "old endemics" with respect to *Rattus*, those studies did not include representatives from throughout Murinae and could not effectively reject polyphyly and thus multiple colonizations. In contrast, immunological distances among a wide sampling of murines did not support monophyly of the "old endemics" (Watts and Baverstock, 1995), instead separating the Australian and New Guinea taxa into two clades. More recently, a multilocus phylogeny of Murinae including a limited sampling of Sahulian taxa supported monophyly and a sister relationship to some Philippine Old Endemic murines (Steppan et al., 2005). In addition, some authors have argued that, even if the group is monophyletic, its phylogenetic depth indicates a lineage too old to be explained by a single colonization (Ride, 1970; Watts, 1974; Watts and Aslin, 1981; Baverstock et al., 1983; Hand, 1984). Therefore, these earlier studies concluded that the primary diversification of the group occurred outside of Sahul and that multiple colonizations followed once Sahul became accessible to murines of the Sunda shelf or the Philippines roughly 10 Mya.

The diversity of forms among the "old endemics" of Sahul led Tate (1951) and Simpson (1961) to split them among as many as four subfamilies (Hydromyinae, Pseudomyinae, an undefined "old Papuan" group, and Murinae—including a "*Uromys* group"). Although subsequent studies have subsumed all the Sahulian rodents into the Murinae (Musser and Carleton, 2005), the four groups of "old endemics" still survive largely intact as the tribes Anisomyini, Hydromini, Uromyini, and Conilurini (Watts and Aslin, 1981; Lidicker and Brylski, 1987; Watts and Baverstock, 1994a,b). Musser and Carleton (2005) placed the Sahulian taxa in six divisions of uncertain relationship, splitting the Anisomyini into *Pogonomys* and *Lorentzimys* divisions, splitting the Hydromini into *Hydromys* and *Xeromys* divisions, recognizing the Uromyini as a *Uromys* division, and recognizing the Conilurini as a *Pseudomys* division. These tribes and divisions reflect distinct biogeographic and ecomorphological hypotheses about diversification within the Old Endemics.

The Anisomyini (*Pogonomys* and *Lorentzimys* divisions) include twelve extant genera representing the New Guinea old endemics (Lidicker, 1968; Flannery, 1995a,b). Only one species, *Pogonomys mollipilosus,* is found in Australia and only in the extreme northeastern tropics of Cape York, across the Torres Strait from New Guinea (Strahan, 1995). They include a variety of forms from prehensile-tailed canopy dwellers (*Pogonomys*) to large terrestrial rats such as *Hyomys*. Early authors did not support monophyly of anisomyines and allied genera with various other non-Sahulian murines (Ellermann, 1941; Tate, 1951; Misonne, 1969). Misonne, for example, split anisomyine genera into as many as three groups (*Pogonomys, Hyomys, Mallomys*, and *Anisomys* with a diverse *Lenothrix* group; *Pogonomelomys* and *Xenuromys* with a *Uromys* group; *Macruromys* left undefined as an isolated divergent murid). The relationships among genera within Anisomyini remain uncertain, and monophyly of the group is not clearly supported. In particular, the placement of *Lorentzimys* remains enigmatic (Misonne, 1969; Lidicker and Brylski, 1987; Watts and Baverstock, 1994a), so they have been recognized as a separate division (Musser and Carleton, 2005).

The Hydromini include nine genera distributed primarily within New Guinea but also include two species distributed in both New Guinea and Australia (*Hydromys chrysogaster* and *Xeromys myoides*). All species exhibit varying degrees of dental simplification including reduction and loss of molars as well as simplified occlusal patterns (i.e. "basin-shaped" molars). Meristic differences among the Hydromini range from one molar (*Pseudohydromys ellermani*) to the plesiomorphic three (*Leptomys*) per quadrant of the jaw (Misonne, 1969). These dental morphologies are thought to reflect adaptation to diets including largely insects, crustaceans, and fish. Indeed these morphological changes are convergent with similar morphologies in the worm specialist *Rhynchomys* from the Philippines and led early authors to group *Rhynchomys* with the hydromyines (Tate, 1951; Misonne, 1969). Extreme morphologi-

cal adaptation in the hydromyines is exemplified by the adaptation of the "water rats" (*Hydromys* division) to semiaquatic habitat and diets of fish and crustaceans. These adaptations include enlarged, webbed hind feet; elongated and dense vibrissae; broadened muzzles; laterally compressed tails; and basin-shaped molars (Helgen, 2005). The "moss rats" or "shrew mice" (*Xeromys* division) do not exhibit adaptations to aquatic life that are as extreme as those of the water rats but share similar adaptations to a largely insectivorous and carnivorous diet, including the greatest reduction in molar number and complexity of any muroid rodent (*Pseudohydromys ellermani*). As their name suggests, they are convergent with the true shrews (which are notably absent from Sahul) in body plan, pelage, and diet. Despite the wide range of gross morphology, the Hydromyini are thought to be monophyletic, and this view has been supported by phallic and sperm morphology (Lidicker, 1968; Breed and Aplin, 1994). Immunological distances have suggested that the *Hydromys* and *Xeromys* divisions reflect two monophyletic but related lineages (Watts and Baverstock, 1994a; Musser and Carleton, 2005).

The Uromyini (*Uromys* division; mosaic-tailed rats) include five genera widespread throughout Australasia (Sahul and adjacent islands). They are distinguished by nonoverlapping tail scales and transverse rows of cusps on their molars (Flannery, 1995a). They are primarily arboreal species with a generalized *Rattus*-like body plan, and early authors allied them to *Rattus* (Ellermann, 1941; Tate, 1951; Simpson, 1961). Their center of diversity is in New Guinea where twenty species in four genera have been described (Flannery, 1995a; Musser and Carleton, 2005). Outside of New Guinea, ten species in two genera have been described from the Moluccan Islands to the west (Helgen, 2003; Flannery, 1995b), ten species in three genera from the Solomon Islands to the east (Flannery, 1995b), and six species in two genera from Australia to the south (Strahan, 1995; Musser and Carleton, 2005). Despite this broad distribution, the uromyines are thought to reflect a monophyletic lineage with an origin in New Guinea (Menzies and Dennis, 1979; Baverstock, 1984), although some authors have included members of the Anisomyini within the Uromyini, suggesting that they are part of an older Sahulian lineage (Tate, 1951; Flannery, 1995a).

The Conilurini (*Pseudomys* division) include eight genera representing the Australian Old Endemics. Only two of the nearly 50 species, *Conilurus penicillatus* and *Pseudomys delicatulus*, have been reported outside of Australia and then only from a restricted distribution in southern New Guinea (Flannery, 1995a). They represent a great diversity of ecomorphological forms including mouse-like forms (*Pseudomys*), aridity-adapted bipedal hoppers (*Notomys*), stick nest rats (*Leporillus*) that are convergent with *Neotomys* from North America, herbivorous vole-like forms (*Mastacomys*), arboreal tree rats (*Mesembriomys*), and rock rats (*Zyzomys*) convergent with the nonmuroid *Petromys* of southwest Africa. They are nevertheless believed to reflect a single monophyletic radiation within Australia resulting from colonization by an ancestor from New Guinea (Baverstock et al., 1977; Lee et al., 1981), but monophyly has not been clearly established, and studies based on phallic morphology and immunological distances were not able to separate the conilurines from the uromyine genera (Lidicker and Brylski, 1987; Watts et al., 1992). Most recently, a two locus molecular phylogeny of *Pseudomys* that included representatives of all conilurine genera recovered a monophyletic Conilurini (Ford, 2006).

The high taxonomic and morphological diversity of the Sahulian endemic rodent fauna is exceptional among mammals for such a geographically constrained distribution, but phylogenetic analyses of the group are equally notable for their absence. Here we present the results of a multilocus phylogeny of the Sahulian Old Endemics, including 26 of the 34 recognized genera and representing all tribes and divisions, nested within a broader phylogeny of the Murinae, including representatives of 24 of the 27 extant divisions recognized by Musser and Carleton (2005). Our sampling allowed us to test definitively the monophyly or polyphyly of the Sahulians, the number of colonizations of Sahul, and the monophyly of the tribal-level Sahulian taxa. We also reconstructed the biogeographic history of the Murinae in the region. In addition, by adding most of the remaining divisions (sensu Musser and Carleton, 2005) and three nuclear genes to the data of Steppan et al. (2005), we were able to refine our understanding of murine diversification as a whole.

2. Methods

2.1. Specimens and genetic loci sequenced

Our analyses included data from 77 species belonging to 67 genera representing 24 of 27 extant divisions recognized within Murinae plus members of the subfamilies Otomyinae, Deomyinae, and Gerbillinae (taxonomy following Musser and Carleton, 2005). These data included 28 species of Sahulian "old endemics" from 26 genera representing all tribes (Flannery, 1995a; Lee et al., 1981) and divisions (Musser and Carleton, 2005). No data were available for the hydromyine genera *Crossomys, Baiyankamys, Microhydromys,* and *Paraleptomys;* the anisomyine genera *Coccymys, Pogonomelomys,* and *Xenuromys*; or the uromyine genus *Protochromys*. Representatives of all conilurine genera were included in our analyses. All specimen identification and locality information is listed in Supplementary Table 1.

Specimens were sequenced for six unlinked autosomal nuclear loci (exon 10 of GHR, exon 11 of BRCA1, the single large exon of RAG1, intron 3 and flanking regions of BDR, exon 1 of IRBP, and intron 2 and flanking regions of AP5) and four mitochondrial genes (COI, COII, ATPase 8, and cyt *b*, plus the two tRNAs between COI and ATPase 8). Aligned sequence lengths were 945 bp for GHR, 2710 bp for BRCA1, 3074 bp for RAG1, 1122 bp for

BDR, 1316 bp for IRBP, 435 bp for AP5, and 2499 bp for mtDNA, for a total of 12,101 bp of aligned and analyzed data. IRBP sequences for 23 species were obtained from GenBank (Jansa and Weksler, 2004; Lecompte et al., 2005). BDR sequence was obtained for *Rattus norvegicus* by a Blast-N comparison of BDR sequence from *Rattus leucopus* to the *Rattus norvegicus* genome on GenBank. All new sequences were submitted to GenBank with accession numbers listed in Supplementary Table 2. Sequences were not available for all loci for all specimens as identified in Supplementary Table 2. For the concatenated data analyses, the genera *Gerbillurus, Meriones, Phloeomys, Vandeleuria, Millardia, Otomys, Parotomys, Dasymys, Arvicanthis, Aethomys,* and *Apomys* resulted from chimeras of species. In most cases these chimeras were produced by incorporation of IRBP sequences from GenBank. The species *Hydromys chysogaster, Pogonomys loriae, Rattus leucopus* and *Uranomys ruddi* resulted from chimeras of specimens with identical localities and collection dates. The species *Stochomys longicaudatus* and *Tatera robusta* resulted from chimeras of specimens from different localities and collection dates. The identity or near identity of each of these species chimeras was confirmed with at least one locus with overlapping sequence data (data not shown).

2.2. DNA extraction and sequencing

Total genomic DNA was extracted from liver or muscle tissue with PCI (phenol/chloroform/isopropanol)/CI (chloroform/isopropanol) "hot" extractions as described by Sambrook et al. (1989). Amplification of all loci followed similar protocols. All PCR reactions included a negative control (no template DNA), intended to identify any instances of contamination of reagents, and were visualized on agarose gels with ethidium bromide. Successful reactions were prepared directly by enzymatic digestion with Exo-SAP-IT (USP, USA) or isolated from a low-melting-point gel with Wizard PCR prep reagents (Promega, USA). Both strands of each PCR product were completely sequenced with PCR primers and internal primers optimized to specific taxa. Products were sequenced by automated DNA sequencing on an ABI 3100 using big-dye terminator chemistry (Applied Biosystems, USA).

Amplification and sequencing of GHR, BRCA1, RAG1, AP5, COI, COII, IRBP, and ATPase were completed with primers under reaction conditions described previously (Jansa and Voss, 2000; Adkins et al., 2001; DeBry and Seshadri, 2001; Steppan et al., 2004a,b, 2005). Additional primer sequences were used for specific taxa for RAG1 and AP5 (RAG1-S211 (GGGTGMGATCY TTTGAAAA) and S212 (CVGTYCTGTACATCTTRTG RTA); AP5-S223 (CAGCCMGSGAARTDGCSAAYGC)). All BDR amplifications were performed at annealing temperature of 64 °C for 40 cycles using primer sequences S221 (CAGCTYTCRGGARGYTGAAG) and S222 (CARACTTAACAGMAATYCTCCTRCC). Cyt *b* amplifications were performed at annealing temperature of 58 °C for 40 cycles using a combination of the primer sequences S199 (CCTCARAATGATATTTGTCCTCA), P484 (TGAAA AAYCATCGTTGT), and P485 (TYTYCWTYTTNGGT TTACAARAC) depending on specific taxa.

2.3. Phylogenetic analyses

Results of individual sequencing runs for each species were combined into contiguous sequences with Sequencher 4.5 (GeneCodes Corp., Ann Arbor, MI), and regions of ambiguity or disagreement resolved through manual inspection of sequence traces. 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. Sequences for the genes were concatenated for each taxon.

Heterogeneity of nucleotide composition among informative sites was determined with PAUP* version 4.0b10 (Swofford, 2002). Phylogenetic analyses were conducted for each gene separately by maximum-parsimony (MP), maximum-likelihood (ML) and Bayesian methods as implemented in PAUP* 4.0b10 (Swofford, 2002) and MrBayes ver. 3.1.2 (Huelsenbeck and Ronquist, 2005). All MP analyses used heuristic searches with tree bisection-reconnection (TBR) branch swapping and 500 random-addition replicates. All substitutions were weighted equally; gaps were treated as missing data. A sequential optimization approach (Swofford et al., 1996; Fratti et al., 1997; Steppan et al., 2004a) 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). The GTR+I+Γ model was selected by Akaike's Information Criterion for all loci and the concatenated data except BRCA1, for which a GTR+Γ model was selected. An ML search was then conducted under the preferred model with parameters fixed to the values estimated on the MP tree. Model parameters were reestimated from the initial ML tree and the process repeated until the topology remained constant. Heuristic searches were conducted with 20 random-addition replicates and TBR branch swapping. The optimal phylogeny was found on the first search except for AP5, where it was found on the second search.

Nonparametric bootstrapping (Felsenstein, 1985) was performed on all data partitions: 200 replicates for ML, 500 replicates for MP. Bootstrap analyses for MP and ML used 20 random-sequence addition replicates per bootstrap replicate. Likelihood bootstrap analyses were limited to 2000–4000 rearrangements for individual genes and the combined data. 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 repli-

cates) (Farris et al., 1994, 1995) indicated no significant heterogeneity in phylogenetic signal ($P = 0.87$) among the seven loci.

Bayesian analysis of the total data used the GTR+I+Γ model with the addition of partitioning by codon position in each genome separately. The result was eight partitions: the three nuclear codon positions, the three mitochondrial codon positions, intron, and the tRNA regions. Parameters were estimated for each partition separately ('unlinked'). For all data, two independent sets of four chains were run for 2 million (GHR) to 15 million (total) generations; trees and parameters were recorded every 500 generations. Each individual gene was partitioned similarly except that BDR had too few exon sites to subdivide further, so two partitions were used, exon and intron. Convergence was estimated by means of diagnostics from AWTY (Wilgenbusch et al., 2004) as well as by examination of likelihood plots and posterior probabilities of individual clades for subsets of the runs. The data all converged relatively quickly, yielding burn-in periods of 10% or less.

2.4. Divergence-date estimation

We have previously argued (Steppan et al., 2004a) that the age of the transition from *Antemus* to *Progonomys* at 12.1 Mya should be assigned to the divergence of *Phloeomys*/*Batomys* from the remainder of Murinae (the "core" murine taxa), rather than to the younger *Mus*/*Rattus* split to which it is usually assigned, because the transitional fossils described by Jacobs and Downs (1994) document the acquisition of the key synapomorphy (full fusion of lingual cusps with medial and labial) for core murine taxa. Because this date is narrowly constrained by detailed fossil evidence on both sides of the evolutionary transformation (Jacobs and Flynn, 2005) and not merely the earliest appearance of a lineage, we set the date to range from 10 to 14 Mya rather than use a minimum age. Despite the small uncertainty in the timing of the transition (approximately ±0.5 My), we conservatively designated the range to ±2 My to account for the uncertainty regarding the precise phylogenetic placement of the fossil taxa. In addition, we placed a lower limit on the divergence of *Otomys*/*Parotomys* (Otomyinae of Musser and Carleton, 2005) from the *Arvicanthis* clade of 6 Mya in recognition of the earliest appearance of extant taxa clearly assignable to the African *Arvicanthis* lineage (Winkler, 2002).

Divergence-dates were estimated by the method of Thorne and Kishino (2002) with the multidistribute program package (25 September 2003 release). From the Bayesian estimate of relationships derived from the multigene concatenation, the transition/transversion ratio and shape parameter of the gamma distribution of rates among the sites were estimated for each locus by PAUP* (Swofford, 2002). Then, under the F84 model (Felsenstein, 1984), evolutionary parameters for each gene were estimated by the program baseml 3.15 (Yang, 2000). The program paml2modelinf within the multidistribute package was used to prepare input for the program estbranches, which estimated branch lengths for each gene and derived the variance–covariance structure of the branch lengths. Finally, the program multidivtime was used to estimate the divergence-dates from the multilocus data and divergence-date constraints described above. Settings suggested in the documentation for the program were used for multidivtime. To provide a broad, but reasonable, prior estimate of the rate of substitution (Thorne, pers. comm.), we divided the average root-to-tip length of the phylogeny based on the multigene concatenation by the estimated age of the root (12 Mya), and both the point estimate of the rate and its standard deviation were set to this number. Two independent runs of the multidivtime program were performed with different random seeds. The two runs produced divergence-date estimates within a few thousand years of each other, indicating that the Markov chain had been run for a sufficient number of cycles.

2.5. Colonization and diversification

To reconstruct the minimum number of dispersal events into Sahul and between New Guinea and Australia, we coded the geographic distributions (non-Sahulian, New Guinea, Australia, or New Guinea and Australia) of all Sahulian and Philippine Old Endemic taxa in MacClade 4.08 (Maddison and Maddison, 2000). We then mapped these characters onto the phylogeny resulting from the concatenated data. We included in these analyses the unsampled taxa *Pseudomys delicatulus* and *Pogonomys mollipilosus,* as they each extend the distributions of their genera and their placement in the phylogeny is likely to be with other members of their respective genera. The ancestral distributions for all clades were estimated under a parsimony criterion. Dispersal events were identified along branches that indicated a switch from one geographic distribution to another. In addition, we reconstructed the number of dispersal events using an explicit biogeographic model, the dispersal-vicariance approach of Ronquist (1997) using DIVA (Ronquist, 1996). Taxa were coded as to presence in one or more of nine areas (Palearctic, Africa, Mediterranean region/Asian deserts, India, mainland SE Asia, Wallacea, Philippines, New Guinea, Australia). Optimizations were then run in which ancestors were constrained to occupy no more than two, three, or four areas. Because no extant species currently occupy more than two areas, we report results primarily from the three-area restriction as a compromise between conservatism and biological realism. Constraining to fewer areas reduces the number of equally parsimonious solutions.

3. Results

3.1. Phylogenetic analyses: Murinae

The concatenated data produced a highly resolved, robust phylogeny (Fig. 3). The optimized ML tree and

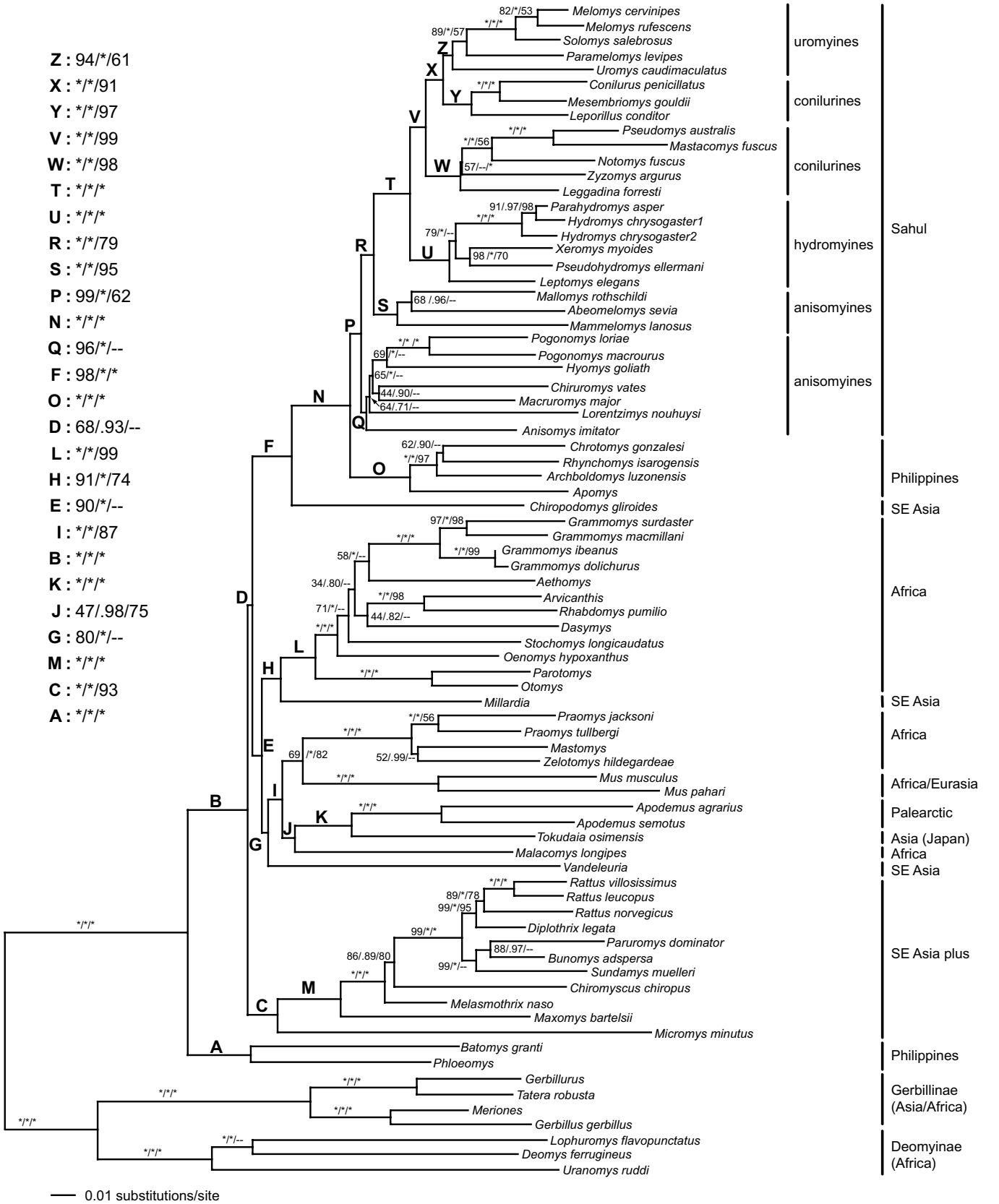

Fig. 3. Maximum-likelihood phylogram resulting from the concatenated data under the GTR+I+Γ model. Nodes discussed in the text are labeled accordingly. Numbers above branches and beside node labels refer to maximum-likelihood bootstrap percentages/Bayesian posterior probabilities/maximum-parsimony bootstrap percentages, respectively. Symbol "*" indicates a bootstrap percentage or Bayesian posterior probability value of 100%. Symbol "–" signifies that the node was not present in the bootstrap consensus tree. Sahulian Old Endemic tribes and geographic distribution of clades are indicated on the right.

the Bayesian tree for the concatenated data agreed at all nodes except that the placements of *Zyzomys* and *Leggadina* were reversed. The strict consensus MP tree agreed with the ML tree at nearly all nodes; only minor differences appeared at some terminal nodes that were not well-supported by bootstrap values. Of the nodes discussed below, only *Vandeleuria* (node G) differed in placement in the MP phylogeny. Unless otherwise stated, therefore, discussions of the concatenated phylogeny are based on strict consensus among the ML, MP, and Bayesian analyses. Optimized ML phylogenies for individual genes were also largely concordant with the phylogenies resulting from the concatenated data, although no individual gene phylogeny agreed with the concatenated data at all nodes (Fig. 4; Supp. Figs. 1–7).

On the basis of the concatenated data, the Philippine old endemics *Phloeomys* and *Batomys* formed a clade (node A) that was sister to all other murines (node B); both clades were supported by 100% bootstrap and posterior probabilities. All individual ML gene phylogenies supported this sister relationship, except the phylogeny resulting from the mitochondrial genes (with weak bootstrap and Bayesian support).

The remaining murines were split by two basal nodes (C and D) into at least four well-supported clades (nodes F, H, G, C). Node B split the clade consisting of a *Rattus* group (node C), including genera from the *Dacnomys*, *Maxomys*, *Melasmothrix,* and *Rattus* divisions plus *Micromys* of the *Micromys* division, from all remaining murines (node D). Node D received weak to moderate support from the concatenated data (68% ML bootstrap support (MLBS), 93% Bayesian posterior probabilities (BPP), and <50% MP bootstrap support (MPBS)) and was recovered by only one individual ML gene phylogeny (BRCA1). Node E was sister to a mostly Sahulian and Philippine clade including *Chiropodomys* of the *Micromys* division (node F) and combined genera from the *Aethomys*, *Arvicanthis*, *Dasymys, Hybomys* divisions and the Otomyinae of Musser and Carleton (2005; node L) plus *Millardia* of southeast Asia (node H), with a widespread African, Eurasian, southeast Asian clade, including genera from the *Apodemus, Colomys, Malacomys, Mus,* and *Stenocephalomys* divisions (node I) plus *Vandeleuria* of the *Micromys* division (node G). Node E received moderate support from the concatenated data (90% MLBS, 100% BPP, and <50% MPBS) and was recovered by three individual ML gene phylogenies with weak to moderate support (BRCA1, RAG1, mitochondrial).

Monophyly of the *Rattus* group plus *Micromys* (node C) was strongly supported by the concatenated data and was recovered by four individual ML gene phylogenies with moderate to strong support (GHR, BRCA1, RAG1, BDR). The IRBP, AP5, and mitochondrial ML phylogenies conflicted with the inclusion of *Micromys* with the *Rattus* group (node M) but received weak support for their placements of *Micromys.* All individual ML gene phylogenies placed *Micromys* close to the base of the core murine radiation and strongly supported monophyly of the *Rattus* group (node M), as did the concatenated data.

A monophyletic African clade (node L) was strongly supported by the concatenated data—all bootstrap and posterior probabilities exceeded 99%—and was strongly supported by six individual ML gene phylogenies. There was weak conflict among individual genes for the placement of *Millardia* sister to this African clade (Fig. 4, Supplemental figures).

Monophyly of the widespread African, Eurasian, southeast Asian clade (node G) was supported by the ML and Bayesian phylogenies for the concatenated data (80% MLBS, 100% BPP) but individually by only two genes, BRCA1 and BDR. The MP phylogeny placed the long-tailed climbing mouse, *Vandeleuria,* as sister to the core Murinae. No gene strongly conflicted. Excluding *Vandeleuria*, the remaining African/Eurasian clade (node I) was strongly supported by all analyses of the concatenated data and by all individual ML gene phylogenies except GHR, (with weak support for the placement of *Vandeleuria* sister to *Malacomys*).

The mostly Sahulian and Philippine clade including *Chiropodomys* (node F) was strongly supported by the concatenated data—all bootstrap and posterior probabilities exceeded 98%. The GHR and mitochondrial ML phylogenies conflicted with the placement of *Chiropodomys* but received weak support for their alternatives.

Five genera new to this set of data branch off early from the core murine radiation: the Asian *Micromys* (sister to the *Rattus* group; node C), *Tokudaia* from the Ryuku Islands of southern Japan (sister to the Asian *Apodemus*; node K), the Indian *Vandeleuria* (sister to the African/Eurasian clade; node G), the Indian *Millardia* (sister to the exclusively African clade; node L), and the Indomalayan *Chiropodomys* (sister to the Sahulian/Philippine clade; node F). Of these five, only *Tokudaia* could be said to be close to any other taxon; all the others represent basal lineages within "core" Murinae.

3.2. Phylogenetic analyses: Sahul

The basal split in the mostly Sahulian/Philippine clade (node F) was between *Chiropodomys* of southeast Asia and Wallacea and a clade (node N) joining the Sahulian old endemics (node P) with the Philippine old endemics of the *Chrotomys* division (node O) Each of these nodes was well-supported in the concatenated data set and with varying degrees of support by individual genes, except for the BRCA1 and AP5 ML phylogenies that conflicted with monophyly of the Sahulian old endemics by nesting the Philippine old endemics within them, but with weak support.

The basal split within the Sahulian clade (node P) created a paraphyletic anisomyines, with the anisomyine genera *Pogonomys, Hyomys, Chiruromys, Macruromys, Lorentzimys,* and *Anisomys* (node Q) sister to the clade node R, consisting of the anisomyine genera *Abeomelomys,*

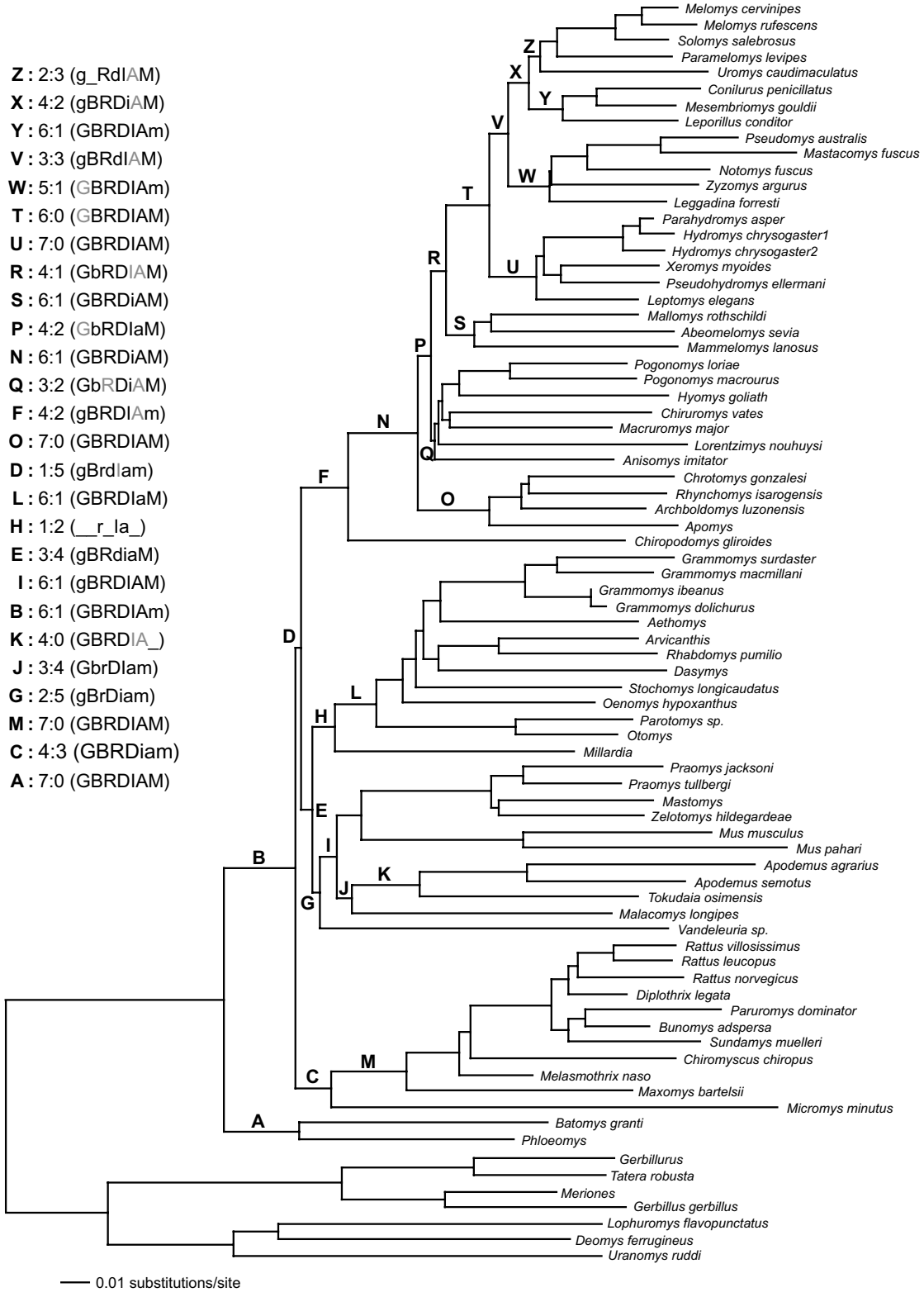

Fig. 4. Agreement of maximum-likelihood phylogenies for individual genes with the maximum-likelihood phylogeny resulting from the concatenated data at nodes discussed in the text. Node labels are the same as those in Fig. 3. Ratios indicate the number of gene phylogenies that support and conflict with the concatenated phylogeny at that node. Individual genes are represented by single letters (G, GHR; B, BRCA1; R, RAG1; D, BDR; I, IRBP; A, AP5; M, mitochondrial loci). Black upper-case letters indicate gene phylogenies that supported monophyly at the node. Black lower-case letters indicate gene phylogenies that conflicted with monophyly at the node. Gray letters indicate gene phylogenies that were equivocal with respect to monophyly at the node. Genes for which monophyly of the node could not be evaluated because sequence data were not available for relevant taxa are not included and are indicated by underscores.

Mammelomys, and *Mallomys* (node S) plus the remaining Sahulian old endemics (node T). Monophyly of each of these nodes was moderately to strongly supported in the concatenated data. Monophyly of node Q was recovered in three individual ML gene phylogenies with weak to moderate support (GHR, BDR, mitochondrial), RAG1 and AP5 yielded a basal polytomy, and IRBP conflicted weakly (<50% MLBS/BPP/MPBS). Monophyly of the remaining Sahulian old endemics (node R) was supported by four individual ML gene phylogenies with moderate to strong support (GHR, RAG1, BDR, mitochondrial), whereas the IRBP and AP5 ML phylogenies were equivocal with respect to this node. The BRCA1 ML phylogeny conflicted with monophyly of node R in placing the Philippine old endemics within the Sahulian Old Endemics.

Within the diverse clade T the hydromyine genera (node U) were sister to all conilurine and uromyine genera (node V). Bootstrap and posterior probabilities for these nodes all exceeded 99% for the concatenated data. All individual ML gene phylogenies strongly supported monophyly of these nodes except AP5 that was equivocal for monophyly of node V, GHR, which allied *Uromys* with the hydromyine genera but with little support, and BDR which joined U and W as sister-groups.

The predominantly Australian clade V contained the conilurine genera *Pseudomys, Mastacomys, Notomys, Zyzomys,* and *Leggadina* (node W) and a clade including all uromyine genera plus the conilurine genera *Conilurus, Mesembriomys*, and *Leporillus* (node X). Monophyly of each of these nodes was strongly supported by the concatenated data. Monophyly of node W was strongly supported by all individual ML gene phylogenies except the GHR phylogeny, which was equivocal, and the mitochondrial phylogeny (weak support). Monophyly of node X was recovered by four individual ML gene phylogenies with moderate to strong support (BRCA1, RAG1, BDR, mitochondrial). The GHR and IRBP ML phylogenies conflicted with monophyly of node X, supporting a monophyletic conilurine clade to the exclusion of the uromyines but with weak support.

Node X joined a clade containing the conilurine genera *Conilurus, Mesembriomys,* and *Leporillus* (node Y) with a clade including all uromyine genera (node Z). Monophyly of nodes Y and Z were strongly supported by the concatenated data, and like many of the other nodes, the few conflicting individual gene phylogenies were not strongly supported.

Within the Sahulian Old Endemics, therefore, the phylogeny resulting from the concatenated data did not support monophyly of either Anisomyini or Conilurini but supported monophyly of both Hydromini and Uromyini. No individual ML gene phylogenies supported a monophyletic Anisomyini. Only the GHR and IRBP ML phylogenies produced limited support for a monophyletic Conilurini. The AP5 phylogeny was equivocal. All individual ML gene phylogenies supported a monophyletic Hydromini. All individual ML gene phylogenies except for GHR, BDR, and AP5 supported a monophyletic Uromyini (the AP5 phylogeny was equivocal, and the conflict from the GHR and BDR phylogenies resulted from the placement of *Uromys*).

3.3. Divergence-date estimation

The results of divergence-date estimation are presented in Table 1. Using the calibrations of the *Batomys*/*Phloeomys*-"core" Murinae split and the *Arvicanthis*-*Otomys* split, we were able to estimate dates for several key phylogenetic events in the diversification of the Sahulian Old Endemic murines. The basal radiation of the "core" Murinae (node B), subtending the split between *Mus* and *Rattus,* was estimated to have occurred 9.7 Mya (credibility interval [CI] 8.7–10.8). The Sahulian and Philippine old endemics were estimated to have split from *Chiropodomys* and the rest of the Murinae (node F) 7.8 Mya (CI 6.8–8.8) and the Sahulian old endemics to have split subsequently from the Philippine old endemics (node N) 5.5 Mya (CI 4.7–6.4). The primary diversification of the Sahulian old endemics (among anisomyine genera and between anisomyines and remaining taxa; nodes P, Q, and R) was estimated to have occurred between 4.7 and 5.1 Mya (CI 3.9–6.0). Secondary diversification of the Sahulian old endemics was estimated to have begun between 3.0 and 3.7 Mya (CI 2.4–4.5), including diversification among the remaining Sahulian "tribes" (Hydromini, Conilurini, and Uromyini; nodes T, V, and X) and among genera within these tribes (nodes U, W, Y, and Z).

3.4. Colonization and biogeography

Our analyses reconstructed a single colonization of Sahul estimated to have occurred between 5.1 and 5.5 Mya (nodes N and P; CI 4.3–6.4). New Guinea was the center of diversification of the Sahulian Old Endemics; all Australian taxa were clustered near the tips of the phylogeny. Using parsimony and geography as a single, multi-

Table 1
Estimated dates of divergence (Mya) for selected nodes in Fig. 3 based on Bayesian approximation from a concatenation of all gene regions

Node	Bayesian estimate of divergence-dates		
	Date	SD	Credibility interval
B	9.7	0.52	8.7–10.8
F	7.8	0.51	6.8–8.8
N	5.5	0.45	4.7–6.4
P	5.1	0.43	4.3–6.0
Q	4.6	0.44	3.9–5.6
R	4.7	0.43	3.9–5.6
T	3.7	0.38	3.0–4.5
U	2.3	0.31	1.8–3.0
V	3.4	0.36	2.7–4.1
W	2.7	0.32	2.1–3.4
X	3.0	0.34	2.4–3.7
Y	2.0	0.27	1.5–2.6
Z	2.8	0.34	2.1–3.5

state character, we reconstructed a minimum of nine dispersal events between New Guinea and Australia (Fig. 5). The DIVA analysis was congruent, although the specific sequence of some events was equivocal because of equally optimal reconstructions. Of these nine, five were reconstructed to be from New Guinea to Australia, two from Australia to New Guinea, and two equivocal. Seven of the dispersal events between New Guinea and Australia were reconstructed as dispersal of single species (Fig. 5: 4 and 10) or expansions of species' ranges (Fig. 5: 5, 6, 7, 8, and 9) and have not led to diversification among the Sahulian Old Endemics. The two equivocal dispersal events could not be resolved by this set of data (Fig. 5: A and B). Under scenario A, a single colonization of Australia from New Guinea estimated to have occurred between 3.4 and 3.7 Mya (nodes T and V; CI 2.7–4.5; Fig. 5: A2) preceded the diversification of the conilurines, and a second dispersal event from Australia to New Guinea estimated to have occurred between 2.4 and 3.4 Mya (CI 1.9–3.7) preceded the diversification of the uromyines (Fig. 5: A3). Under scenario B, conilurine diversity resulted from two independent dispersal events from New Guinea to Australia. A first colonization of Australia estimated to have occurred between 2.7 and 3.4 Mya (nodes V and W; CI 2.1–4.1) preceded the diversification of a first group of conilurines (Fig. 5: B2). A second, between 2.0 and 3.0 Mya (CI 1.5–3.7), preceded the diversification of a second group of conilurines (Fig. 5: B3). Uromyine diversification then occurred within the ancestral distribution in New Guinea.

4. Discussion

4.1. Sahulian biogeography

The monophyly of the Sahulian old endemics is consistent with their diversification within Sahul after a single

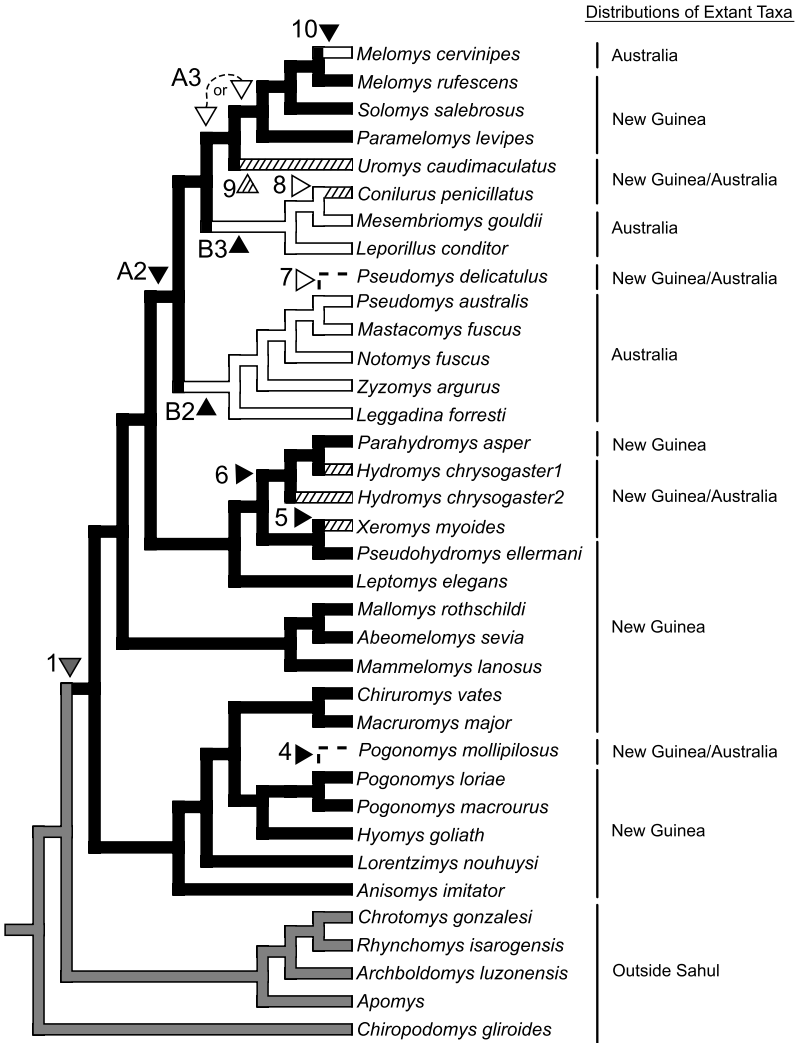

Fig. 5. Parsimony reconstruction of dispersal events. Geographic distributions of extant taxa and reconstructed ancestors are indicated by gray (outside Sahul), black (New Guinea), white (Australia), and hatched (Australia/New Guinea) shading. All reconstructed dispersal events are numbered (1–10) and marked with triangles shaded to indicate the predicted origin of the dispersal. Dispersal events marked with "A" and "B" represent two mutually exclusive and equally parsimonious dispersal scenarios. Taxa for which no sequence data were available are connected to the phylogeny with dashed lines and were included because they are known to represent additional dispersal events between New Guinea and Australia.

colonization of the continent. Molecular dating estimated that diversification of the Sahulian old endemics began no earlier than between 5.1 and 5.5 Mya (CI 4.3–6.4). These dates are consistent with the earliest fossil appearance of murines in Australia 4–5 Mya (Lee et al., 1981; Godthelp, 1990, 1997; Rich et al., 1991) and well within the time since Sahul reached its current proximity to the Philippines and the Sunda shelf. Therefore, contrary to the 15–20 Mya diversification date estimated from albumin variation (Watts and Aslin, 1981), dates estimated from our phylogeny do not imply that diversification of the Sahulian old endemics occurred outside of the Sahulian continent.

Molecular clock studies that sample Rodentia or Mammalia broadly and rely primarily on non-Muroid calibrations tend to give much earlier estimates of divergence-dates within Muroidea. For example, the *Mus*/*Rattus* divergence estimate has ranged from 12 to 43 Mya (Kumar and Hedges, 1998; Cao et al., 2000; Huchon et al., 2000; Adkins et al., 2003; Jansa et al., 2006). In general, older estimates are also associated with simpler models of molecular evolution and strict molecular clocks. We favor using relatively well-constrained internal calibrations over external ones from clades with significantly slower molecular evolution (Wu and Li, 1985; Adkins et al., 2001), but actual divergence-dates could be earlier if the external calibrations are not overestimating dates as much as we suspect.

The sister relationship of the Sahulian old endemics and the Philippine old endemics of the *Chrotomys* division implies two possible biogeographic scenarios: independent colonization of the Philippines and Sahul by two closely related murines from the Sunda shelf and colonization of either the Philippines or Sahul from the other, after one of them was colonized from the Sunda shelf. The first scenario could have produced the sister relationship pattern if (1) we have not yet sampled the closest relatives of the Philippine and Sahulian colonists, (2) these closest relatives are extinct, or (3) the two colonizations occurred within a very short evolutionary interval without diversification among the source populations. The second scenario could have produced reciprocal monophyly of the Philippine and Sahulian old endemics if (1) no diversification occurred on the first landmass before colonization of the second or (2) only one lineage extant at the time of the second colonization has survived to the present. Additional sampling, particularly of genera from the Sunda shelf discussed above, could help resolve these colonization scenarios, but clearly the Philippine old endemics of the *Chrotomys* division and the Sahulian old endemics share a recent evolutionary origin within the Murinae.

Within the Sahulian Old Endemics, monophyly of the Anisomyini (*Pogonomys* and *Lorentzimys* divisions) was not supported. They were paraphyletic; *Mallomys, Abeomelomys*, and *Mammelomys* formed a sister clade to the remaining Sahulian Old Endemics. These results demonstrate that the remaining Sahulian tribes were derived from an anisomyine ancestor and that the New Guinea "old endemics" reflect the earliest colonists of Sahul. Notably, diversification among most anisomyine genera occurred between 4.7 and 5.1 Mya (CI 3.9–6.0), whereas the origin of all other Sahulian tribes occurred later, between 3.0 and 3.7 Mya (CI 2.4–4.5). *Lorentzimys* (sole member of the *Lorentzimys* division) was nested within the basal anisomyine radiation and is no more divergent phyletically from other Sahulian old endemics than are the other basal anisomyines.

The remaining Sahulian Old Endemics, including all hydromyines, uromyines, and conilurines, formed a clade derived from the anisomyines. The Hydromyini were sister to the remaining tribes. The *Xeromys* division was paraphyletic, however; *Xeromys* and *Pseudohydromys* formed a clade with genera of the *Hydromys* division to the exclusion of *Leptomys*. The nested radiation of the *Hydromys* division would imply that the water rats (*Hydromys* division) were derived from a shrew-mouse (*Xeromys* division) progenitor and that carnivorous dietary habits preceded adaptations to semiaquatic habitats, but the relationship is supported by a single node, and broader sampling of the hydromyines would be necessary to confirm it.

All uromyine and conilurine genera formed a clade sister to the Hydromyini. The conilurine genera were paraphyletic; *Conilurus*, *Mesembriomys,* and *Leporillus* formed a clade sister to a uromyine clade. The remaining conilurine genera *Pseudomys, Mastacomys, Notomys, Zyzomys* and *Leggadina* formed a clade sister to the conilurine/uromyine clade. Paraphyly of Conilurini was strongly supported by bootstrapping and Bayesian analyses of the concatenated data and by most individual gene phylogenies. A previous phylogenetic hypothesis based on phallic morphology proposed a paraphyletic Conilurini (Lidicker and Brylski, 1987); however, in that study, the conilurines were split by inclusion of both uromyines and anisomyines. Notably, a recent molecular systematic study of the genus *Pseudomys* (Ford, 2006), that included all conilurine genera, found a monophyletic Conilurini to the exclusion of the uromyines. These results, however, were not supported by bootstrap analyses and were not consistent among methodologies (i.e. distance trees supported parphyly of the Conilurini), suggesting that this data set lacked sufficient characters to adequately test monophyly. Our results, based on considerably more molecular characters and including a much broader sampling of Murinae, were strongly supported by bootstrap and posterior probabilities. In addition, forcing our data to support a monophyletic Conilurini would significantly reduce the log likelihood of the concatenated phylogeny as evaluated by a Shimodaira–Hasegawa test ($-\Delta\ln L = 44.13$, 1000 RELL replicates, $p = 0.001$; Shimodaira and Hasegawa, 1999). Thus, we conclude that our data has sufficient power to reject a monophyletic Conilurini. This conclusion would suggest a more complex biogeographic history than expected, indicating either that conilurine diversity has emerged from two separate colonizations of Australia or that the uromyines are derived from a single conilurine radiation.

Reconstruction of dispersal events between New Guinea and Australia recovered a minimum of nine events. Not surprisingly, such dispersal appears to have been relatively common, but only two dispersal events have preceded major diversifications in rodents. The first was the earliest colonization of Australia by non-volant terrestrial eutherians, which preceded the diversification of a first conilurine clade. The second resulted either in diversification of a second conilurine clade after a second colonization of Australia or in diversification of the uromyine clade after recolonization of New Guinea by a conilurine ancestor. The first scenario would indicate that *Conilurus, Mesembriomys,* and *Leporillus* would be better considered basal members of a uromyine clade that has colonized Australia three times or more (the conilurines, probably *Uromys,* and *Melomys* at least once). The second scenario would indicate that diversification of the conilurines in Australia led to a recolonization of New Guinea and greater Wallacea and diversification of a uromyine clade that would better be considered a derived member of the conilurines. Unless the topology of the phylogeny is changed, more genetic data are unlikely to resolve these two scenarios.

The pattern that emerges from these phylogenies is of rapid and probably adaptive radiations after colonization of landmasses previously unoccupied by muroidlike rodents. Keogh et al. (1998) reached a similar conclusion for elapid snakes—that they underwent a rapid radiation around 5 Mya after colonizing Sahul. Two such geographic radiations seem to have occurred in murines, the first in New Guinea (“anisomyines”) and a second smaller one (but with greater ecological disparity) in Australia (“conilurines”). The same pattern appears to an even greater degree with the colonization of South America by other muroids (Sigmodontinae) at about the same time (6–7 Mya; Steppan et al., 2004b, unpublished data). Together, these very recent radiations account for nearly 10% of all mammalian diversity and therefore the geographic expansions of these groups represent a significant amount of rodent and mammal macroevolution.

Our data support multiple dispersal events between Australia and New Guinea, consistent with expectations given their close proximity and frequent coalescence during the Pleistocene. A sea-level drop of as little as 10 m would expose a land bridge (Voris, 2000). Avian honeyeaters show no evidence of endemic radiations on the two land masses, instead indicating frequent dispersals (Driskell and Christidis, 2004), as did several elapid snake clades (Scanlon and Lee, 2004; Wuster et al., 2005). The initial and sustained diversification on New Guinea that our data reveal, which lasted approximately 1.7 (time between nodes P and V) to 2.5 (N–X) My before the first evidence of a colonization of Australia, is therefore remarkable. The Pliocene time frame of the New Guinea anisomyine radiation predates the large sea-level fluctuations of the Pleistocene, perhaps explaining why most of the reconstructed dispersal events were near the tips of the tree (events 4, 5, 7, 8, 10).

4.2. Murine systematics

Our results confirm and build upon recent molecular phylogenies of Murinae (Steppan et al., 2005; Jansa et al., 2006). Our analyses strongly supported *Phloeomys* and *Batomys* (*Phloeomys* division) as the most divergent members of Murinae. Early diversification of the remaining “core” Murinae produced at least four large, geographically delineated radiations that are strongly supported by our data (nodes I, L, M, and N). As in Steppan et al. (2005), three of the four main radiations were associated with diversification in Africa (node L), Southeast Asia (node M), and the Philippines/Sahul (node N), and the fourth radiation, distributed throughout Africa, Europe, and Asia lacked a clear center of diversification (node I). The relationships among these clades (nodes D and E), although moderately to strongly supported by the concatenated data, were not consistently supported by individual gene phylogenies, consistent with expectations for rapid formation of these lineages during an early murine radiation. Four additional taxa (*Millardia,* node H; *Micromys,* node C; *Chiropodomys,* node F; and *Vandeleuria,* node G) each recovered a sister relationship to one of these basal radiations of the core Murinae. Although these associations were largely supported by bootstrap and Bayesian posterior probabilities based on the concatenated data, individual ML gene phylogenies were inconsistent with these relationships and lacked strong support as evidenced by bootstrap proportions and posterior probabilities. For example, the sister relationship of the Southeast Asian *Millardia* to the African radiation (node L) was only supported by a single gene phylogeny. We interpret these patterns to reflect the rapid diversification at the base of the core Murinae, and disagreement among individual gene phylogenies may stem from a combination of insufficient data within genes and lineage sorting among genes. Therefore, these taxa represent additional basal divergence within the core Murinae, and their exact placement within the Murinae should be considered cautiously. Our robust results for most nodes, however, indicate that we do not lack power and allow us to reject a close relationship with other tribal-level clades.

Our results support monophyly of most divisions of Musser and Carleton (2005), but our results conflict with monophyly of the *Oenomys* and *Micromys* divisions. Members of the former (*Oenomys* and *Grammomys*) did not form a monophyletic group except when genera from the *Aethomys*, *Arvicanthis*, *Dasymys*, and *Hybomys* divisions were included. Together with *Otomys* and *Parotomys*, these divisions form an exclusively African clade that may reflect a single colonization of the continent. As has been reported elsewhere (Chevret et al., 1993; Watts and Baverstock, 1995; Senegas and Avery, 1998; Michaux et al., 2001; Jansa et al., 2006), our data also did not support the elevation of *Otomys* and *Parotomys* to the subfamilial rank (Otomyinae), as they are deeply nested within the core Murinae with close associations with other exclusively African taxa.

Members of the *Micromys* division (*Chiropodomys*, *Micromys*, and *Vandeleuria*) were scattered across the phylogeny and did not form a clade in any of the phylogenies. *Chiropodomys* grouped with the Sahulian and Philippine old endemics (node F), *Micromys* grouped with a largely Southeast Asian "*Rattus*" group (node M, *Dacnomys*, *Maxomys*, *Melasmothrix*, and *Rattus* divisions), and *Vandeleuria* grouped with a largely African/Eurasian group (node I, *Apodemus*, *Colomys*, *Mus*, and *Stenocephalemys* divisions). As discussed above, each of these genera diverged early from the core Murinae. They are therefore unlikely to share many synapomorphies with other lineages within the Murinae, and their grouping by Musser and Carleton (2005) as the *Micromys* division may have resulted from plesiomorphic similarities in morphological and immunological characters (Ellermann, 1941; Misonne, 1969; Watts and Baverstock, 1995).

Our data strongly supported monophyly of the Sahulian old endemics with respect to all other *Murinae* sampled. Although this result supports those of previous studies based on phallic morphology (Lidicker, 1968; Lidicker and Brylski, 1987), sperm morphology (Breed and Sarafis, 1978; Breed, 1984), craniodental morphology (Musser, 1981), and chromosome variation (Baverstock et al., 1977; Donnellan, 1987), our study includes a much broader sampling of murine diversity, providing a more powerful test. Most murine genera not represented in our data are well-supported members of clades/divisions within our data and unlikely to bear on monophyly of the Sahulian Old Endemics, but monophyly of other divisions is not certain. For example, the polyphyletic condition of the *Micromys* division, as evidenced by our data, may bear on monophyly of the Sahulian Old Endemics, as it includes genera from the geographically proximate Sunda shelf. In particular, the placement of *Chiropodomys* as sister to the Philippine/Sahulian Old Endemic clade suggests that further sampling within this group is warranted, including the genera *Haeromys, Hapalomys,* and *Vernaya* and additional species of *Chiropodomys*. Of the three divisions of Murinae not represented in our data, only the *Crunomys* division (*Crunomys* and *Sommeromys*) could be reliably placed within our phylogeny (near *Maxomys)* and should have no bearing on monophyly of the Sahulian old endemics (Jansa et al., 2006). The placement of *Echiothrix* (Sulawesi spiny rat, *Echiothrix* division) and members of the *Pithecheir* division (*Eropleopus*, *Lenomys*, *Lenothrix*, *Margaretamys*, *Pithecheir,* and *Pithecheirops*) within the Murinae remains uncertain. Their distributions on the island of Sulawesi and in greater southeast Asia suggest that they could bear on monophyly of the Sahulian old endemics and should be sampled in further studies, but the Sahulian old endemics are all very closely related, having very short branches among basal lineages, and therefore seem unlikely to be paraphyletic. If they are not monophyletic, then any member outside of Sahul would probably be the result of a back-dispersal event.

4.3. Correction of *Thallomys* sequence

Steppan et al. (2005) included two samples identified as *Thallomys paedulcus* from the Carnegie Museum that fell out within the Arvicanthine group. Those authors noted that these samples were nearly identical to a *Grammomys surdaster* from the same expedition and, given the uncertainty, excluded all three from the combined analyses; they included the two "*Thallomys*" sequences in an expanded sampling of AP5, tentatively concluding that the '*Grammomys*' sample was misidentified. Since that time, cyt *b* sequences for various *Thallomys* and *Grammomys* have become available (*Thallomys paedulcus*, DQ381927; *Thallomys loringi*, DQ381928; *Thallomys nigricauda,* DQ381925; *Grammomys* sp., AF141218**),** and we sequenced three additional species of *Grammomys* from the Field Museum (see Appendices). The three Carnegie samples all fell into a *Grammomys* clade in the concatenated analyses. In addition, separate analysis of our cyt *b* data combined with the published sequences confirmed the result: our "*Thallomys*" samples fell out with all the *Grammomys* and not with the published *Thallomys*. We therefore conclude that the Carnegie *Thallomys* were actually *Grammomys* and that the earlier published AP5 sequences (Steppan et al., 2005) were thus misattributed.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2008.01.001.

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