Repeated evolution of carnivory among Indo-Australian rodents

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Convergent evolution, often observed in island archipelagos, provides compelling evidence for the importance of natural selection as a generator of species and ecological diversity. The Indo-Australian Archipelago (IAA) is the world's largest island system and encompasses distinct biogeographic units, including the Asian (Sunda) and Australian (Sahul) continental shelves, which together bracket the oceanic archipelagos of the Philippines and Wallacea. Each of these biogeographic units houses numerous endemic rodents in the family Muridae. Carnivorous murids, that is those that feed on animals, have evolved independently in Sunda, Sulawesi (part of Wallacea), the Philippines, and Sahul, but the number of origins of carnivory among IAA murids is unknown. We conducted a comprehensive phylogenetic analysis of carnivorous murids of the IAA, combined with estimates of ancestral states for broad diet categories (herbivore, omnivore, and carnivore) and geographic ranges. These analyses demonstrate that carnivory evolved independently four times after overwater colonization, including *in situ* origins on the Philippines, Sulawesi, and Sahul. In each biogeographic unit the origin of carnivory was followed by evolution of more specialized carnivorous ecomorphs such as vermivores, insectivores, and amphibious rats.

KEY WORDS: Biogeography, convergence, diet, Indonesia, Muridae, Philippines, phylogenetics, Sahul, Sulawesi, Sunda.

Biological convergence is a fundamental process in evolution whereby two or more species evolve to be more phenotypically similar to each other than either is to its more closely related species (Stayton 2015). The evolutionary convergence of ecologically relevant traits among species inhabiting geographically isolated, but ecologically similar areas is one of the primary indications that natural selection is the key process in the evolution of life (Endler 1986; Schluter and Nagel 1995; Grundler and Rabosky 2014). Most examples of convergence have been documented in isolated lakes and island archipelagoes, where similar but geographically discrete environments are readily identifiable (e.g., Losos et al. 1998; Rundle et al. 2000; Chiba 2004; Gillespie 2004; Reding et al. 2009; Muschick et al. 2012). In each of these systems, ecologically and phenotypically similar taxa

(i.e., "ecomorphs") evolved repeatedly in similar environmental settings following independent colonization of isolated islands or lakes. Studies defining the characteristics of ecomorph evolution in these systems have fueled understanding of the diversification of species and the assembly of biological communities (e.g., Gillespie 2004, 2013; Mahler et al. 2013).

The Indo-Australian Archipelago (IAA) is the world's largest island system and encompasses the biogeographic units of continental Asian islands (Sunda) and Australia–New Guinea (Sahul) as well as the oceanic archipelagos of the Philippines and Wallacea (Fig. 1; Lohman et al. 2011). Despite the geographic proximity of these four biogeographic units, they have never been connected by dry land (Scotese et al. 1988; Rohling et al. 1998; Voris 2000; Hall 2012). As such, each unit is notable for its high level of endemism. Moreover, the boundaries between these biogeographic units represent some of the most dramatic faunal turnover zones
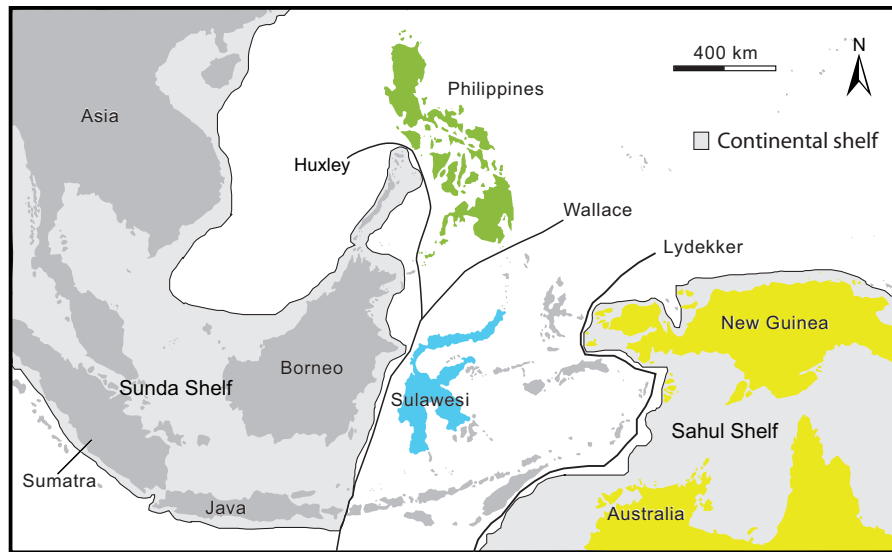
Figure 1. Map of the Indo-Australian Archipelago with major biogeographic units and relevant biogeographic lines indicated. Light gray shading indicates the area of the continental shelves of Sunda and Sahul. During low sea stands for much of the Pleistocene and Pliocene the current islands of each these biogeographic units were connected by dry land (e.g., Borneo, Java, and Sumatra of Sunda and Australia and New Guinea of Sahul).

in the world and are demarcated by Wallace's, Huxley's, and Lydekker's lines (Fig. 1; Huxley 1869; Wallace 1869; Mayr 1944; Simpson 1977; Moss and Wilson 1998; van den Bergh et al. 2001).

Rodents of the family Muridae (778 species) are native to Africa, Eurasia, and Australia (Wilson and Reeder 2005). Although the IAA represents a small portion of the geographic distribution of Muridae, approximately half of murid species (are native to this region. Indeed, murids are the only family of nonvolant, terrestrial mammals that are naturally and broadly distributed across the four biogeographic units of the IAA (Aplin and Helgen 2010; Fabre et al. 2013; Rowe et al. 2014). However, despite the family's broad distribution, every murid species native to the IAA is endemic to only one of the four biogeographic units, and many species are endemic to a single island or portion of an island (e.g., Musser and Durden 2002; Helgen and Helgen 2009; Heaney et al. 2011).

The distribution and diversification of murids in the IAA resulted from multiple dispersal events to landmasses east of the Sunda Shelf (Fig. 1), including multiple independent colonizations of the Philippines, Sulawesi, and Sahul (Musser and Carleton 2005; Jansa et al. 2006; Rowe et al. 2008, 2011). Taxonomic research and detailed natural history data collected by generations of mammalogists (e.g., Flannery 1995; Heaney 2009; Musser 2014; Esselstyn et al. 2015) provide a picture of convergent ecomorphological forms that evolved in each of these colonized units, including arboreal rats (e.g., *Musseromys* [Philippines]; *Margaretamys* [Sulawesi]; and *Lorentzimys* [Sahul]), large terrestrial rats (e.g., *Bullimus* [Philippines], *Paruromys* [Sulawesi], and *Uromys* [Sahul]), amphibious rats (e.g., *Waiomys* [Sulawesi]

and *Hydromys* [Sahul]), and carnivorous species (e.g., *Rhynchomys* [Philippines], *Paucidentomys* [Sulawesi], and *Leptomys* [Sahul]). Indeed, morphological convergence has confused systematic relationships, particularly among carnivorous species that were once lumped into their own subfamily, the Hydromyinae (Tate, 1936).

Specialized diets have evolved in several rodent lineages and each is associated with substantial adaptations in the digestive tract, skull, and dentition (Langer 2002; Samuels 2009). While carnivory (a diet consisting primarily of animals) is not a discrete ecological niche, it is exceptional among rodents, including murids, most of which are omnivores that feed on vegetation, seeds, and invertebrates (Landry 1970). Across mammals, the transition to carnivory has been infrequent, with the diversity of living carnivorous species having emerged primarily through ecological specialization within the few carnivorous clades (Price et al. 2012). Although exceptional, carnivory has evolved independently in multiple rodent families and carnivorous murids are known in each of the four biogeographic units of the IAA (Carleton and Musser 1984; Samuels 2009). Across the IAA, carnivorous murids mostly consume invertebrates, but a few species also consume vertebrates (e.g., *Leptomys* and *Hydromys* of Sahul) and several species are highly specialized and apparently consume only earthworms (Table S1). Although there is undoubtedly considerable variation among murids within the broad categories of herbivory, omnivory, and carnivory, resolving the phylogenetic placement of transitions between these dietary categories is an essential first step to understanding the evolution of more precise dietary and ecological forms.

On the Sunda Shelf, carnivorous murids are represented by four species of "shrew mice" in the genus *Mus*, which together represent an early diverging lineage within the genus (Marshall 1977; Lundrigan et al. 2002; Schenk et al. 2013). East of the Sunda Shelf, carnivorous rodents are represented by nine species in seven genera on Sulawesi, 18 species in five genera in the Philippines, and 31 species in 10 genera on Sahul (Helgen 2005; Musser et al. 2008; Helgen and Helgen 2009; Balete et al. 2012; Esselstyn et al. 2015). Most of the Sahulian diversity is found on New Guinea, but two species also reach Australia (Helgen 2005; Musser et al. 2008; Helgen and Helgen 2009). Among the carnivorous genera, only *Crunomys* is native to more than one biogeographic unit of the IAA. Endemic species of *Crunomys* are found in the Philippines (three species) and Sulawesi (one species). Phylogenetically, *Crunomys* is nested within the genus *Maxomys* (Achmadi et al. 2013), which in general are omnivorous (Table S1; Pimsai et al. 2014). The remaining seven genera of carnivorous rodents of Sulawesi (i.e., excluding *Crunomys*), are represented by eight species of terrestrial "shrew rats" (*Echiothrix* spp., *Hyorhinomys stuempkei*, *Melasmothrix naso*, *Paucidentomys vermidax*, *Sommeromys macrorhinos*, and *Tateomys* spp.) and an amphibious rat (*Waiomys mamasae*). Previous morphological assessments have spread the Sulawesi shrew rats among other noncarnivorous species in at least three divisions (Musser and Carleton 2005), implying that they are distant relatives. These morphological assessments did not include the recently discovered taxa *Hyorhinomys, Paucidentomys*, and *Waiomys* (Esselstyn et al. 2012, 2015; Rowe et al. 2014). Recent phylogenetic analyses incorporating these new species and limited taxon sampling suggest that the shrew rats and water rat of Sulawesi form a clade within Muridae that is not closely related to any other species within the family (Esselstyn et al. 2015). In the Philippines, four genera and 15 species of carnivorous murids (excluding *Crunomys*) form a monophyletic group of terrestrial shrew rats (*Archboldomys, Chrotomys, Rhynchomys*, and *Soricomys*) that are sister to the omnivorous Philippine genus *Apomys* (Heaney et al. 2011, 2014; Balete et al. 2012). The carnivorous rodents of Sahul include five genera each of terrestrial moss mice (*Leptomys, Microhydromys, Mirzamys, Paraleptomys*, and *Pseudohydromys*) and water rats (*Baiyankamys, Crossomys, Hydromys, Parahydromys*, and *Xeromys*) that together form a clade of 31 species nested within an old endemic radiation of Sahulian rodents. The carnivorous Sahulian rodents are sister to a clade formed by members of the Pseudomys and Uromys divisions, in which all species are either omnivorous or herbivorous (Musser and Carleton 2005; Rowe et al. 2008; Van Dyck and Strahan 2008).

Here, we use a well-sampled phylogeny of Muridae to (1) determine the number of independent origins of carnivory among murids of the IAA; (2) identify the geographic origins of carnivorous clades; (3) test whether carnivory evolved after colonization of the biogeographic units east of the Sunda Shelf or rather carnivorous species colonized these landscapes; and (4) estimate the timing of the origins of carnivory among Indo-Australian rodents.

Methods

We compiled sequence data from 137 species in the family Muridae, including 132 species in the subfamily Murinae, three species in the Deomyinae, and two species in the Gerbillinae (Table S2). We obtained sequence data from five unlinked loci including (1) the mitochondrial cytochrome b (CytB); (2) exon 11 of breast cancer 1 (BRCA1); (3) exon 1 of retinol-binding protein 3 (IRBP); (4) exon 1 of recombination activating gene 1 (RAG1); and (5) exon 1 of growth hormone receptor (GHR). We obtained previously published sequences from GenBank for most species in this study, but generated new sequences from the carnivorous genera *Microhydromys, Paraleptomys, Sommeromys*, and *Tateomys* (accession numbers KU375144–KU375184; Table S2). All loci were amplified and sequenced using published primers and procedures (Rowe et al. 2008, 2011). We included representatives of all genera of carnivorous rodents from Sulawesi and the Philippines. From Sahul, we included representatives of eight of the 10 genera of carnivorous rodents. Although *Baiyankamys* and *Mirzamys* were not included this is unlikely to influence our general interpretations because several putative synapomorphies suggest they are closely related to the other water rats and moss mice of Sahul (Helgen 2005; Helgen and Helgen 2009), which are represented in our phylogenetic estimates. We also included one species of "shrew mouse" in the genus *Mus* (subgenus *Coelomys*). However, our analyses focus on the evolution of groups that colonized biogeographic units east of the Sunda Shelf.

We aligned sequences in CodonCode ver. 5.0.1 (CodonCode Corporation, Dedham, MA, USA) and manually inspected alignments in MacClade v.4.08 (Maddison and Maddison 2003). We determined appropriate DNA sequence partitions and substitution models using PartitionFinder ver. 1.1.1 (Lanfear et al. 2012) and estimated phylogenetic relationships using MrBayes ver. 3.2.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003; Ronquist et al. 2012) and RAxML ver. 7.6.3 (Stamatakis 2006). All phylogenetic analyses were run on the CIPRES portal (Miller et al. 2010). In MrBayes we set partitions and models as selected by PartitionFinder, conducted two independent runs of four chains each for 40 million generations, and set additional parameters and priors following Rowe et al. (2011). We assessed convergence and stationarity in our Bayesian analysis using the "sump" command to examine log marginal likelihood plots, average standard deviation of split frequencies among runs, and the potential scale reduction factor for all parameters. We excluded the first 25% of samples as burnin. We conducted RAxML

analyses with 1000 bootstrap pseudoreplicates using the partitions and models selected by PartitionFinder.

To estimate the ages of clades of carnivorous rodents, we used a relaxed molecular clock approach in MrBayes (Bouckaert et al. 2014). We defined data partitions based on the results of PartitionFinder. Among partitions, we unlinked clock and substitution models but linked the trees. We set the priors on substitution models based on the best models obtained from PartitionFinder. A strict molecular clock was rejected for the concatenated data (likelihood ratio test: $P < 0.01$) and therefore we used the uncorrelated lognormal relaxed-clock model for each partition. We applied a Yule speciation prior, set the birthrate prior to exponential with a mean of 10, and left other priors at default settings. We included three fossil calibration priors to provide for estimates of divergence times following recommendations of Kimura et al. (2015). In our phylogeny, these fossil calibrations refer to the shared ancestors of (1) *Mus* and *Arvicanthis* (11.1–12.3 Ma), (2) *Arvicanthis* and *Otomys* (8.7–10.1 Ma), and (3) species of the genus *Mus* (7.3–8.3 Ma). These refined calibrations are similar to but moderately older than previous calibrations used with overlapping datasets (Rowe et al. 2011; Schenk et al. 2013). We used CladeAge within BEAST to set fossil priors using the minimum age and maximum age constraints above and as specified in Kimura et al. (2015). The BEAST analysis was initiated using the topology from MrBayes, but allowed tree space to be fully explored. Preliminary analyses were run to optimize operators, after which we conducted a final MCMC run with 2×10^8 generations, sampling trees and other parameters every 2000 generations. We evaluated convergence and assessed sample adequacy in Tracer v1.5. We used TreeAnnotator to discard the first 20% of trees as burn-in and pool the remaining samples to form the posterior distribution and generate a maximum clade credibility tree.

To reconstruct biogeographic transitions on the phylogeny, we first coded all terminal taxa to one of four biogeographic units: continental, including Africa and Eurasia to the eastern limit of the Sunda Shelf including Palawan (I), Sulawesi (II), Philippines excluding Palawan (III), or Sahul (IV). We then implemented Dispersal-Vicariance Analysis (S-DIVA) in the program RASP v 3.0 (Yu et al. 2010, 2014) and inferred biogeographic states on the ultrametric maximum clade credibility tree from our BEAST analysis. We allowed ranges at ancestral nodes to occupy a maximum of two states because all known extant murid species are endemic to a single biogeographic unit of the IAA, and we assume that the typical sizes of possessive species ranges have remained relatively constant over evolutionary time scales.

We compiled dietary information from the literature for terminal taxa in our phylogeny (Table S1). Dietary information from these sources was derived from direct stomach content examinations and/or feeding trials in the field or laboratory. These data are coarse for many species and additional natural history information is needed to improve resolution beyond the broad diet categories we use here. As such, we coded species into three general categories following Price et al. (2012). These included (1) omnivore (regularly consuming both plant and animal material; $n = 66$), (2) herbivore (consuming almost entirely plant material; $n = 21$), or carnivore (consuming almost entirely animal material; $n = 29$). Taxa for which direct dietary data were not available were coded as "unknown" ($n = 21$). Although these broad diet categories mask ecological differences within bins (e.g., vermivores, insectivores, and consumers of vertebrates within carnivores) their use is analytically tractable and minimizes the extent of missing character data. The carnivorous rodents of the IAA eat primarily invertebrates (details in Table S1). Some eat a wide range of arthropods and other invertebrates (e.g., *Pseudohydromys* and *Crunomys*), whereas other species specialize on earthworms (e.g., *Rhynchomys* and *Paucidentomys*) and still others also consume vertebrates (e.g., *Leptomys* and *Hydromys*). A key question is whether this dietary variety evolved from a common origin, or if vermivores, insectivores, and consumers of vertebrates each evolved independently.

To test the extent to which carnivore origins in rodents of the IAA were derived independently, we estimated ancestral dietary states for internal nodes in our phylogeny using BEAST v.1.8. Following the approach of King and Lee (2015), we used the consensus phylogeny resulting from our MrBayes analysis and fixed the topology and branch lengths by removing relevant operators from the BEAST v.2.1.3 xml input file. We conducted analyses with (1) strict clock and (2) random local clock models for the rate of dietary trait evolution (Drummond and Suchard 2010). Under a strict clock model, the rate of trait evolution does not vary across the tree, but transition rates among dietary states are allowed to differ. However, when the assumption of rate homogeneity is violated (i.e., heterotachy), a strict clock model can result in wildly spurious results (King and Lee 2015), hence our implementation of a random local clock. Transition rate variation is estimated in BEAST v.1.8 using MCMC. Two independent runs of each analysis were performed, each for 10^8 generations, with samples saved every 10^5 generations. We combined the post burn-in samples from the two runs to produce the consensus tree in TreeAnnotator v.2.2.1. We calculated log marginal likelihoods using the stepping stone method for each model and compared the results with a log-transformed Bayes factor calculated as the difference in log marginal likelihoods (Xie et al. 2011; Baele et al. 2012, 2013).

Results

Concatenation of the four exons and one mitochondrial locus resulted in an alignment of 5787 nucleotides. Partitionfinder identified eight optimal partitions of the data. Partitions did

Table 1. Eight partitions of the concatenated sequence data used in phylogenetic analyses.

Partition	Best model	Genes and coding positions
1	HKY+I+Γ	IRBP_pos1, GHR_pos1, RAG1_pos1
2	GTR+I+Γ	IRBP_pos2, GHR_pos2, RAG1_pos2
3	GTR+Γ	IRBP_pos3, RAG1_pos3
4	GTR+Γ	GHR_pos3, BRCA1_pos3
5	GTR+Γ	BRCA1_pos1, BRCA1_pos2
6	GTR+I+Γ	CytB_pos1
7	GTR+I+Γ	CytB_pos2
8	GTR+I+Γ	CytB_pos3

Table 2. Molecular dating estimates of crown and stem ages of carnivorous rodent clades estimated using a fossil calibrated BEAST analysis of concatenated DNA sequences.

Biogeographic unit	Clade	Crown age	Stem age
Philippines	Shrew rats	5.46	6.55
		(4.71–6.28)	(5.71–7.45)
Philippines	Phloeomys Division	10.42	14.00
		(8.94–11.97)	(12.62–15.56)
Philippines	Chrotomys Division	6.55	8.76
		(5.71–7.45)	(7.82–9.76)
Sulawesi	Shrew rats and water rat	5.57	6.86
		(4.85–6.35)	(6.13–7.66)
Sahul	Moss mice and water rats	3.84	6.07
		(3.26–4.43)	(5.39–6.83)
Sahul	First murids	7.85	8.76
		(7.00–8.78)	(7.82–9.76)
Sulawesi	*Maxomys + Crunomys*	4.13	5.07
		(3.50–4.81)	(4.27–5.68)
Philippines and Sulawesi	*Crunomys*	1.59	3.76
		(1.11–2.09)	(3.10–4.28)

Median ages are presented above 95% highest posterior density intervals in parentheses. All units are millions of years before the present.

not correspond to individual gene fragments, but represented multilocus combinations of codon positions with similar substitution rates (Table 1). Partitionfinder estimated that a GTR substitution model was best for seven partitions, whereas HKY was preferred for the remaining partition. Optimal models for all partitions included a Γ-distributed rate heterogeneity parameter, with four models also incorporating a parameter representing the proportion of invariant sites. However, this additional parameter is not recommended for use with RAxML (Stamatakis 2006) and was only used in the Bayesian analyses. For our Bayesian analyses, the average standard deviation of split frequencies among runs was <0.01, the log marginal likelihood plots plateaued, the estimated sample size of all parameters was >100, and the potential scale reduction factor for all parameters approached 1, all of which suggest convergence (Gelman and Rubin 1992).

All phylogenetic analyses (MrBayes, RaxML, BEAST) of the concatenated nuclear and mitochondrial loci supported at least five independent origins of carnivory in murid rodents across the IAA (Fig. 3). These origins included the ancestors of (1) *Mus pahari* of the Sunda Shelf, (2) *Crunomys* of the Philippines and Sulawesi, (3) the shrew rats of the Philippines, (4) the moss mice and water rats of Sahul centered on New Guinea, and (5) the shrew rats and water rat of Sulawesi. Accounting for differences in taxon sampling among loci, phylogenetic analyses of individual gene trees were entirely consistent with these findings (Fig. S1–5). We recovered the carnivorous rats of Sahul, in the Hydromys and Xeromys divisions, including *Crossomys, Hydromys, Leptomys, Microhydromys, Parahydromys, Paraleptomys, Pseudohydromys*, and *Xeromys* as a clade nested within a radiation of "old endemic" rodents from the Sahul region. The shrew rats and water rat of Sulawesi (*Echiothrix centrosa, Hyorhinomys stuempkei, Melasmothrix naso, Paucidentomys vermidax, Sommeromys macrorhinos, Tateomys macrocercus, T. rhinogradoides,* and *Waiomys mamasae*) formed a well-supported clade sister to a clade

comprised of the Dacnomys and Rattus divisions. Previously, the carnivorous rats of Sulawesi were dispersed among three separate divisions of Muridae or unknown to science (Musser and Carleton 2005; Esselstyn et al 2015). For instance, by inclusion of *Sommeromys*, we show that it is not allied with *Crunomys* in the Crunomys Division, but related to the Sulawesi shrew rats and water rat. Our results also supported several previously published conclusions: (1) *Mus pahari* was the earliest diverging lineage in our limited sampling of the genus *Mus*, which were nested within a larger clade of primarily omnivorous species distributed across Africa and Eurasia (Lundrigan et al. 2002; Schenk et al. 2013); (2) the genus *Crunomys*, including species from Sulawesi and the Philippines, was supported as monophyletic, but nested within *Maxomys* and sister to a clade containing the Sulawesi endemics *Maxomys hellwaldii* and *M. dollmani*; and (3) the remaining carnivorous rodents of the Philippines (*Archboldomys, Chrotomys, Rhynchomys*, and *Soricomys*) formed a well-supported clade sister to the omnivorous Philippine genus *Apomys* (Jansa et al. 2006; Balete et al. 2012; Schenk et al. 2013).

Our maximum clade credibility topology from BEAST was identical to our MrBayes and ML analyses with regard to the relationships of the carnivorous murids (Fig. 2). We estimated median crown ages in the late Miocene to middle Pliocene for each of the three clades containing (1) the Philippine shrew rats, (2) the Sulawesi shrew rats and water rat, and (3) the moss mice and water rats of Sahul (Table 2). The median divergences of these
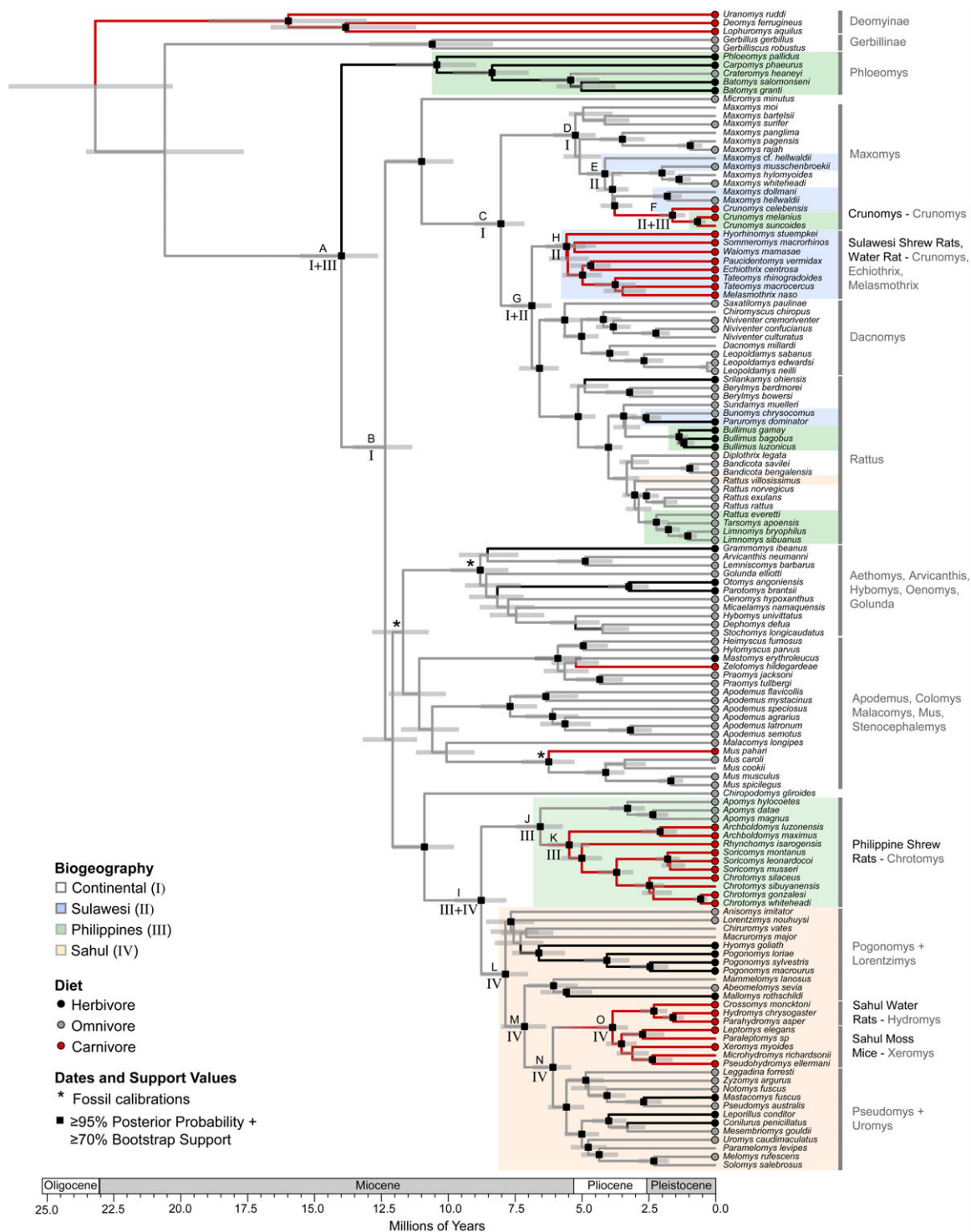
Figure 2. Fossil-calibrated, ultrametric phylogeny estimated in BEAST. Letters above branches indicate nodes discussed in the text. Colors of symbols on terminal branches represent dietary states of species (species with unknown diets lack symbols on terminal branches). Branch color represents the most probable dietary state (posterior probability > 0.8) at internal nodes. Color boxes outline clades from subregions of the IAA. Roman numerals below branches indicate biogeographic distributions inferred for internal nodes using S-DIVA. Terminal branches are grouped into clades by vertical gray bars and labeled to indicate focal carnivores of the IAA (black text) and the taxonomic divisions (gray text; sensu Musser and Carleton 2005) present in each clade (some divisions, e.g., Crunomys, are not monophyletic). The outgroup subfamilies, Deomyinae and Gerbillinae, are also labeled (gray text). Horizontal gray bars spanning nodes represent the 95% highest posterior densities around date estimates. Black squares on nodes represent support values from MrBayes (≥95%) and RaXML (≥70%).

groups from their respective sister clades were no more than 1–2 million years older than their respective crown ages. We recovered a median crown age in the middle Pleistocene for the *Crunomys* clade with a median divergence from *Maxomys* spp. in the middle Pliocene, approximately 1.2 million years earlier (Table 2).

Estimates of the geographic range and dietary state of key nodes in the murine phylogeny suggest four instances of carnivory evolved *in situ* (once in the Philippines, twice in Sulawesi, and once in Sahul) following a biogeographic transition to regions east of Sunda by an omnivorous ancestor, and one dispersal event by a carnivorous lineage from Sulawesi to the Philippines. In our dietary state analysis, the strict clock model (log marginal likelihood = –81.17) and the relaxed local clock model (log marginal likelihood = –88.64) produced identical reconstructions of dietary state. A log-transformed Bayes factor of 7.47 indicates strong support for the simpler strict clock model (Table 3 and Fig. 2). We recovered strong support for an omnivore ancestor at basal nodes of Murinae (nodes A and B, Fig. 2). At node A (Fig. 2), our phylogeny supported a biogeographic split between Philippine and continental distributions with a clear continental distribution for node B, the ancestor of all Murinae except the Philippine cloud rats of the Phloeomys Division (Table 3).

The ancestral nodes of the four well-sampled carnivore clades (*Crunomys* - node F; Sulawesi - node H; Philippines - node K; and Sahul - node O) were recovered as independently derived from omnivore ancestors (nodes D/E, C/G, I/J, and M/N, respectively) after a biogeographic transition from a continental distribution. The three species of *Crunomys* were nested within a clade of *Maxomys*, mostly from Sulawesi. The ancestor of this clade, node E, was reconstructed as an omnivorous ancestor, node D, with a continental distribution. The two sampled species of Philippine *Crunomys* represent a biogeographic transition from Sulawesi, reflecting the sole case of colonization by an already carnivorous lineage. We reconstructed a carnivorous ancestor at node H that represents the common ancestor of the Sulawesi shrew rats and water rat. This Sulawesi clade was sister to a clade containing members of the Dacnomys and Rattus divisions. The common ancestor of these two clades, node G, was reconstructed as most likely an omnivore with an ancestral distribution spanning Sulawesi and our continental region. The Philippine shrew rats split from the Philippine genus *Apomys* (omnivores) at node J, which we reconstructed as most likely an omnivore with a Philippine distribution. The sister of *Apomys* and the Philippine shrew rats was the native rats of Sahul (node I), which we reconstructed as most likely an omnivore. At node I, we recovered an ancestral distribution spanning the Philippines and Sahul with descendant lineages reflecting a split into these two units of the IAA. The carnivorous rats of Sahul (node O) were deeply nested within a clade of Sahul lineages with omnivore ancestors (nodes L, M, N).

Discussion

Murid rodents repeatedly colonized the landmasses east of the Sunda Shelf, providing a natural experiment for examining the diversification of species (Jansa et al. 2006; Rowe et al. 2008; Fabre et al. 2013). Our comprehensive sampling of carnivorous genera from Sulawesi and the Philippines and our sampling of all but two genera from Sahul, demonstrated that the eight species of shrew rats and the water rat from Sulawesi, which include three recently discovered genera (Esselstyn et al. 2012, 2015; Rowe et al. 2014) and have been assigned recently to as many as three separate murine divisions, are members of a single endemic radiation on the island. Thus, our phylogenetic reconstruction inferred four independent origins of carnivory among the murid rodents endemic to the three biogeographic units that lie east of the Sunda Shelf (Jansa et al. 2006; Rowe et al. 2008, 2014). These independent evolutionary events occurred in every biogeographic region, suggesting that the origins of carnivory were facilitated by similar ecological opportunities in different biogeographic regions. Although these events represent a coarse level of evolutionary convergence, we suspect that a detailed morphological study will show striking levels of morphological convergence between members of the different carnivorous clades, especially those with similarly specialized diets and elevational distributions (e.g., *Rhynchomys* and *Paucidentomys*).

Despite the range of dietary niches within carnivorous rodents of the IAA, their reliance on animal material for food is a key ecological trait making them ecologically and phenotypically more similar to each other than to their respective closest relatives. Most of the diversity of insectivores, vermivores, and consumers of vertebrates, endemic to each biogeographic unit of the IAA derive from single, *in situ* origins of carnivory. On both Sulawesi and Sahul one origin of carnivory led to the evolution of both terrestrial and amphibious rats. On Sulawesi, a second *in situ* origin of carnivory produced *Crunomys*, which subsequently colonized the Philippines, where it joined the already diverse Philippine shrew rat clade. These patterns suggest that transitions to a carnivorous diet in IAA murids mostly occurred postcolonization and opened opportunity for specialization within carnivory (e.g., vermivory), as posited for mammals in general by Price et al. (2012).

Several morphological characters that are rare or unknown among herbivorous and omnivorous rodents are shared by most or all of the carnivorous murids of the IAA. These convergent character states highlight the likelihood that selection has shaped their independent evolution. Some of the most striking and consistent character states include (1) unpigmented or pale enamel on the anterior surface of the incisors; (2) reduced complexity of the occlusal surface of molars; and (3) reduced number of molars (Musser 1982; Balete et al. 2012; Esselstyn et al. 2015). These tendencies are especially striking when considering the degree to

Table 3. Relative probability of ancestral dietary states estimated using the strict clock model in BEAST v.1.8 and ancestral geographic distributions inferred using S-DIVA for internal nodes presented in Figure 2.

	Diet			Biogeography									
Node	Omnivore	Herbivore	Carnivore	I	II	III	IV	I+II	I+III	I+IV	II+III	II+IV	III+IV
A	0.85	0.14	0.01	0	0	0	0	0	1.00	0	0	0	0
B	1.00	0	0	1.00	0	0	0	0	0	0	0	0	0
C	1.00	0	0	1.00	0	0	0	0	0	0	0	0	0
D	1.00	0	0	1.00	0	0	0	0	0	0	0	0	0
E	0.99	0.01	0	0	1.00	0	0	0	0	0	0	0	0
F	0.01	0	0.99	0	0	0	0	0	0	0	1.00	0	0
G	0.99	0	0.01	0	0	0	0	1.00	0	0	0	0	0
H	0.01	0	0.99	0	1.00	0	0	0	0	0	0	0	0
I	1.00	0	0	0	0	0	0	0	0	0	0	0	1.00
J	0.88	0	0.12	0	0	1.00	0	0	0	0	0	0	0
K	0.04	0	0.96	0	0	1.00	0	0	0	0	0	0	0
L	1.00	0	0	0	0	0	1.00	0	0	0	0	0	0
M	1.00	0	0	0	0	0	1.00	0	0	0	0	0	0
N	1.00	0	0	0	0	0	1.00	0	0	0	0	0	0
O	0	0	1.00	0	0	0	1.00	0	0	0	0	0	0

which these characters are invariant among other rodents. For instance, rodents are named for their gnawing, chisel-like incisors; these teeth are maintained by continuous growth, with hardened anterior surfaces containing iron-enriched enamel (generally orange due to the high concentration of iron). Although this incisor tissue configuration is not fixed in rodents, it is present in the vast majority of the nearly 2400 species, including all noncarnivorous murids of the IAA, and is considered a key innovation that led to the extraordinary ecological success of rodents (Ungar 2010). Thus, the independent loss of the enamel-hardening, orange pigment at least four times among carnivorous murids of the IAA is an exceptional example of repeated convergence of an ecologically significant trait. The repeated simplification of the occlusal surfaces of molars in these groups is also exceptional among rodents globally and a key character that led to their incorrect grouping as the Hydromyinae (Tate 1936; Simpson 1961). Although extremely rare among murids, reduction in the number of molars evolved independently in each of the three biogeographic units east of the Sunda Shelf, including loss of at least the third upper molar in *Rhynchomys* of the Philippines, loss of all but the first molar in each jaw quadrant in *Pseudohydromys* of Sahul, and loss of all molars in *Paucidentomys* of Sulawesi (Esselstyn et al. 2012). The functional significance of reduced complexity and numbers of molars may reflect a lack of selection to maintain complex occlusal surfaces in species feeding on soft-bodied invertebrates (Esselstyn et al. 2012; Musser and Durden 2014).

Within the different clades of carnivorous IAA murids, qualitatively convergent morphological forms are obvious and appear to correspond to dietary specializations within the broad spectrum of carnivory. These categories include (1) montane, few-toothed and long-snouted vermivores exemplified by *Rhynchomys* spp. from the Philippines and *Paucidentomys vermidax* from Sulawesi; (2) lowland, large vermivores exemplified by *Chrotomys* spp. from the Philippines and *Echiothrix* spp. from Sulawesi; (3) montane, small, soft-furred, grey rats exemplified by *Pseudohydromys ellermanni* from Sahul, *Tateomys macrocercus* from Sulawesi, and *Mus* spp. (subgenus *Coelomys*) from the Sunda shelf; (4) diurnal, dark brown mice with relatively short snouts and legs, exemplified by *Soricomys* spp. from the Philippines and *Melasmothrix naso* from Sulawesi; (5) montane, amphibious rats with reduced pinnae, small eyes, and stiff hairs on the ventral surface of the tail, exemplified by *Crossomys moncktoni* from Sahul and *Waiomys mamasae* from Sulawesi (Musser and Durden 2002, 2014; Rickart et al. 2005; Helgen and Helgen 2009; Balete et al. 2012; Esselstyn et al. 2012; Rowe et al. 2014). Although these ecomorphs are qualitatively obvious (Fig. 3), they warrant further study to quantify the degree of morphological convergence.

The repeated evolution of carnivorous murids of the IAA and subsequent diversification into more specialized carnivores is intriguing because it suggests that independently colonizing groups are evolving in ways that are responsive to similar ecological opportunities, as has been suggested in better known groups such as Caribbean *Anolis* (Losos et al. 1998). However, the timing of carnivorous origins in IAA murids is not consistent with the idea that the ecological opportunity was exploited rapidly after colonization. Carnivory evolved following colonization by an omnivore ancestor in three cases, with only one event of dispersal by a carnivorous lineage (*Crunomys*). However, the *in situ* origins
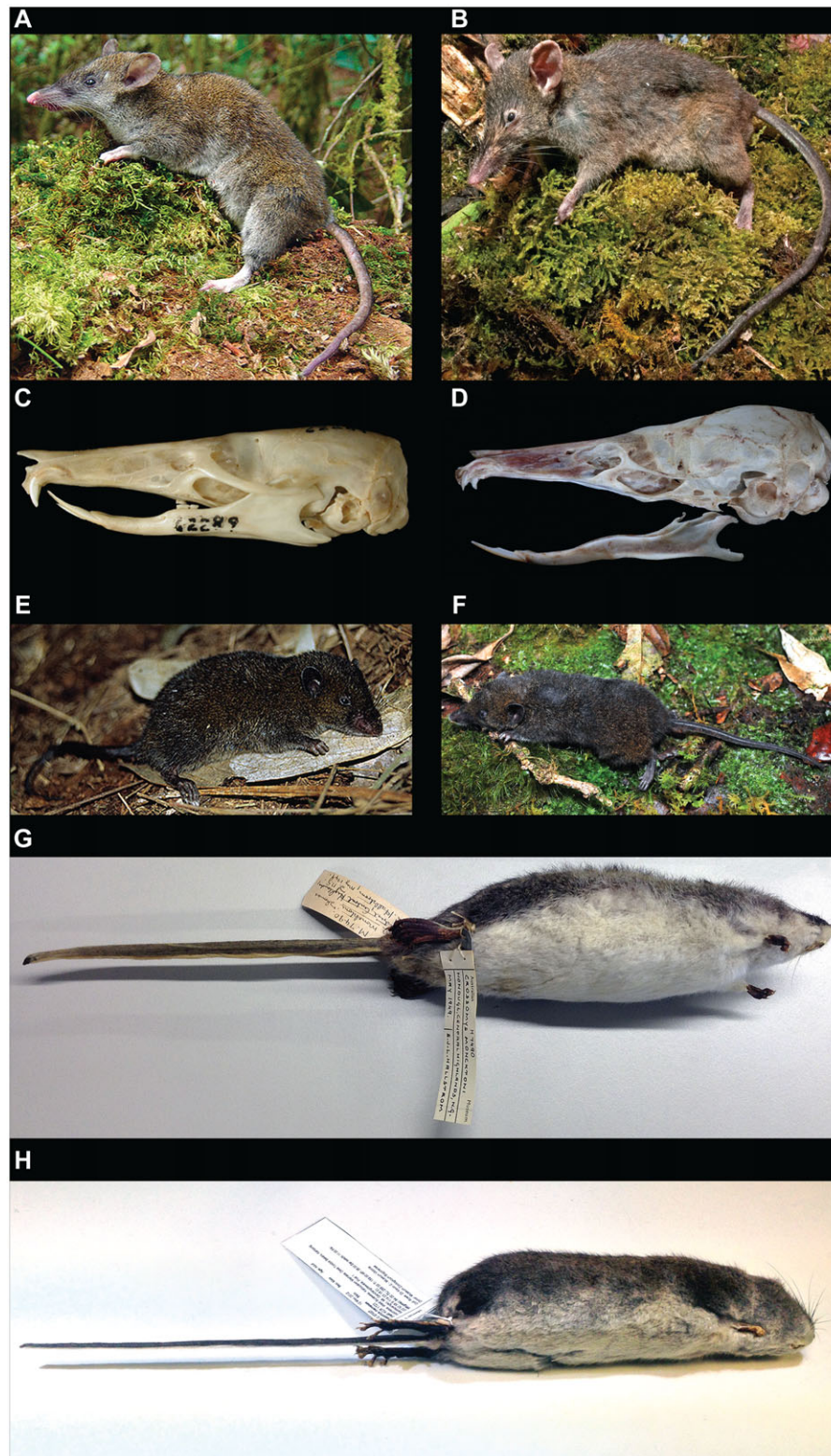
Figure 3. Three examples of convergent ecomorphs among carnivorous rodents of the IAA: montane, few-toothed, and long-snouted vermivores *Rhynchomys soricoides* of the Philippines (A, C) and *Paucidentomys vermidax* of Sulawesi (B, D); diurnal, dark brown mice with relatively short snouts and legs *Soricomys kalinga* of the Philippines (E) and *Melasmothrix naso* of Sulawesi (F); montane, amphibious rats with reduced pinnae, small eyes, and stiff hairs on the ventral surface of the tail *Crossomys moncktoni* of New Guinea (G) and *Waiomys mamasae* of Sulawesi (H). Photographs by (A) E. A. Rickart, Utah Museum of Natural History; (C) R. Banasiak, Field Museum; (D) D. Paul, Museum Victoria; (E) L. R. Heaney, Field Museum; (B, F–H) K. C. Rowe, Museum Victoria.

of carnivory were only once associated with the first arrival of murids in a particular region and did not always occur soon after colonization. From our phylogeny, we can infer that the carnivorous rodents were the first known murids on Sulawesi. The second origin of carnivory on Sulawesi, *Crunomys*, occurred millions of years later and evolved from a lineage of *Maxomys* after a long presence on the island. The carnivorous rodents of Sahul are part of the earliest group of murids to colonize the continent, but they evolved only after a long presence ($\sim$4 MY) and many speciation events that generated a diversity of herbivores and omnivores. In the Philippines, carnivorous rodents were derived from the second lineage to colonize the region; they arrived millions of years after the arboreal species of the Phloeomys Division.

The origins of the Philippine shrew rats (node K) and Sulawesi shrew rats and water rat (node H) are not equivalent relative to the timing of colonization events in their respective areas, but they are nearly simultaneous in absolute time (4.7–6.3 Ma). In contrast, the moss mice and water rats of Sahul, centered on New Guinea, (node O) have a somewhat more recent origin (3.3–4.4 Ma). Perhaps it is only a coincidence, but the age of each of these three clades is temporally associated with the origin of high mountains ($>$1500 m asl) at the end of the Miocene in the Philippines and Sulawesi, and more recently in the early to middle Pliocene in New Guinea (Hall 2002; Hill and Hall 2003; Baldwin et al. 2012). Most of the species in each of the clades are restricted to montane forest and the few lowland species (e.g., *Echiothrix* of Sulawesi, *Chrotomys* of the Philippines, and *Hydromys* of Sahul) are nested phylogenetically among the more diverse montane species, suggesting that the clades originated at high elevation and only later invaded lowland forests. Two possible ecological explanations for the greater diversity of carnivorous murids at montane elevations include (1) greater diversity or abundance of food items and (2) reduced competition with other taxa. In the Philippines, the density of earthworms (a major food source for Philippine shrew rats) is positively correlated with elevation (Rickart et al. 1991). In contrast, the diversity and abundance of ants declines with elevation (the inverse of elevation patterns of murid diversity and abundance), possibly indicating a competitive effect (Samson et al. 1997). Whether these patterns are consistent on Sulawesi and Sahul is uncertain. Nevertheless, the evolution of each of the carnivorous clades that are now nearly exclusive to high elevation habitats was likely dependent on the availability of montane environments. In the Philippines and Sulawesi, species diversity is correlated with elevation, but the importance of these gradients in diversification of species is largely untested (Heaney 2001; Musser and Holden 1991; Brown et al. 2013; but see Justiniano et al. 2015). In New Guinea, recent orogeny has been associated with the diversification of mammals and other taxa (Norman et al. 2007; Macqueen et al. 2011; Unmack et al. 2013; Toussaint et al. 2014) and orogeny represents a plausible,

but untested mechanism that may have promoted convergent evolution among carnivorous murid rodents of the IAA.

In conclusion, our phylogenetic hypothesis indicates five phylogenetically independent origins of carnivory among IAA murids. While an increasing number of systems with replicated radiations are reported, they remain exceptional (Losos et al. 1998; Rundle et al. 2000; Chiba 2004; Gillespie 2004; Reding et al. 2009; Muschick et al. 2012). In murids, the replicated evolution of carnivory following dispersal to islands of the IAA and subsequent divergence into specialized forms such as long-snouted, few-toothed vermivores, hairy-tailed amphibious rats, and diurnal insectivores, suggests, in the words of Darwin (1859, p. 464), that "although only distantly allied [within Muridae, they] have inherited so much ... in their constitution, that they are apt to vary under similar ... causes in a similar manner."

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Supporting Information
Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. Gene tree for cytochrome b estimated using RaXML.
Figure S2. Gene tree for GHR estimated using RaXML.
Figure S3. Gene tree for IRBP estimated using RaXML.
Figure S4. Gene tree for RAG1 estimated using RaXML.
Figure S5. Gene tree for BRCA1 estimated using RaXML.
Table S1. References for Supporting Information Table 2.
Table S2.
Table S3.