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Convergent evolution of aquatic foraging in a new genus and species (Rodentia: Muridae) from Sulawesi Island, Indonesia

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Abstract

The island of Sulawesi, in Indonesia, lies at the crossroads of the Indo-Australian Archipelago and has remained isolated from the Asian (Sunda) and Australian (Sahul) continental shelves for at least the last 10 million years. Of the 50 native species of rodents on Sulawesi, all are endemic and represent the evolution of a variety of ecological and morphological forms within the Muridae and Sciuridae. Carnivorous rodents have evolved, perhaps independently, in Muridae from the Philippines, Sulawesi, and Sahul, but semi-aquatic murids are only known from Sahul. Here we describe a new genus and species of insectivorous water rat from Sulawesi. Phylogenetic analyses demonstrate that it is related to the shrew rats of Sulawesi and represents an origin of aquatic carnivory that is independent from the evolution of water rats on Sahul. Many areas of Sulawesi have not been surveyed systematically and current lists of mammal species are likely to dramatically underestimate actual diversity.

Key words: Indo-Pacific, Mammalia, molecular phylogeny, molecular systematics, Murinae, shrew rats, taxonomy, water rats

Introduction

The Indo-Australian Archipelago is a major area of biogeographic interchange (Lohman *et al.* 2011) and of significant interest to evolutionary biologists because it provides numerous systems for testing the effects of climatic variation, geological evolution, and isolation on the processes of diversification and community assembly (Heaney 1986; Evans *et al.* 2003; Brown *et al.* 2013). The region encompasses the Asian (Sunda) and Australian (Sahul) continental shelves as well as oceanic archipelagos (Philippines, Wallacea) that have never been connected by land to any continent. The island of Sulawesi is the largest landmass between the Sunda and Sahul shelves and was not connected to either during low sea stands of the last 10 million years (Scotese *et al.* 1988; Hall 1998, 2012; Rohling *et al.* 1998; Voris 2000). The combination of a large, topographically complex island that has remained isolated by water barriers, yet is proximally located between two continental landmasses has produced high levels of endemism and a unique mixture of Australian and Asian lineages.

Rodents of the family Muridae comprise over 30% of known mammal species on Sulawesi (Musser & Carleton 2005; Musser *et al.* 2010; Esselstyn *et al.* 2012; Mortelliti *et al.* 2012; Musser 2014). All of the island's murid species are endemic, as are 11 of the 14 murid genera, highlighting the degree to which the rats and mice of Sulawesi represent an endemic radiation. This diversity includes a wide range of eco-morphological forms that have been recapitulated in other, independent radiations of murid rodents (Rowe *et al.* 2008). Examples of this recapitulation include the carnivorous (we use 'carnivorous' to describe animals that primarily eat Metazoans; we consider 'invertebrate-eating' and 'insectivory' to represent nested subcategories of carnivory) rodents of the Philippines (e.g. *Chrotomys*, *Rhynchomys*, *Soricomys*; Musser 1982; Jansa *et al.* 2006) and New Guinea (e.g. *Pseudohydromys*; Jackson & Woolley 1993; Flannery 1995; Helgen & Helgen 2009). On New Guinea, some carnivorous rodents are semi-aquatic, and known commonly as water rats (e.g. *Baiyankamys*, *Crossomys*,

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Hydromys, Parahydromys). All New Guinea water rats share the derived morphological features of a broad muzzle, stiff vibrissae, large, basin-shaped molars, and large, webbed hindfeet (Helgen 2005). High elevation species are found in the genera *Baiyankamys* and *Crossomys*; they are small, have soft grey fur, and small pinnae. Lowland species are found in *Hydromys* and *Parahydromys*; they are large, with brown, glossy fur and large pinnae.

Semi-aquatic mammals are common on most continents and have evolved several times in multiple orders (Veron *et al.* 2008). Among rodents, semi-aquatic species have evolved in at least eight families. However, semi-aquatic carnivory occurs in only a few small-bodied mammals in the orders Soricomorpha (e.g., *Chimarrogale*, *Desmana*, *Galemys*, *Nectogale*, *Neomys, Sorex palustris*), Tenrecomorpha (*Limnogale*, *Micropotamogale*, *Potamogale*), and Rodentia (Voss 1988). In rodents, semi-aquatic carnivory has evolved independently in New Guinea (*Baiyankamys*, *Crossomys*, *Hydromys*, *Parahydromys*; Majnep & Bulmer, 1990; Flannery 1995; Olsen 2008), Africa (*Colomys, Nilopegamys*; Kerbis Peterhans & Patterson, 1995), and South America (Ichthyomyini; Voss 1988; Barnett, 1995). Voss (1988) identified several convergent morphological traits shared among these taxa that appear to be common adaptations to semi-aquatic carnivory. These traits include (1) stiff mystacial vibrissae, (2) reduction of the philtrum, (3) reduced pinnae, (4) fringes of hair on the margins of the hindfeet, (5) webbed hindfeet, (6) increased length and density of hairs on the ventral surface of the tail, (7) elongation of the lateral metatarsals, (8) large infraorbital foramina, and (9) a large foramen magnum.

Here we describe a new genus and species of semi-aquatic, invertebrate-eating rodent from the island of Sulawesi, Indonesia. Our phylogenetic analyses demonstrate that the new species is not a close relative of other semi-aquatic murids and hence represents another independent origin of traits commonly associated with a semi-aquatic, carnivorous lifestyle (e.g. Voss 1988).

Materials and methods

Fieldwork. A single specimen of the new genus and species was caught by hand in a small stream while we were conducting terrestrial mammal surveys in May 2012 around Mount Gandangdewata in the Quarles Range of the western highlands region of Sulawesi Barat, Indonesia (Barat = West; Figure 1, 2).

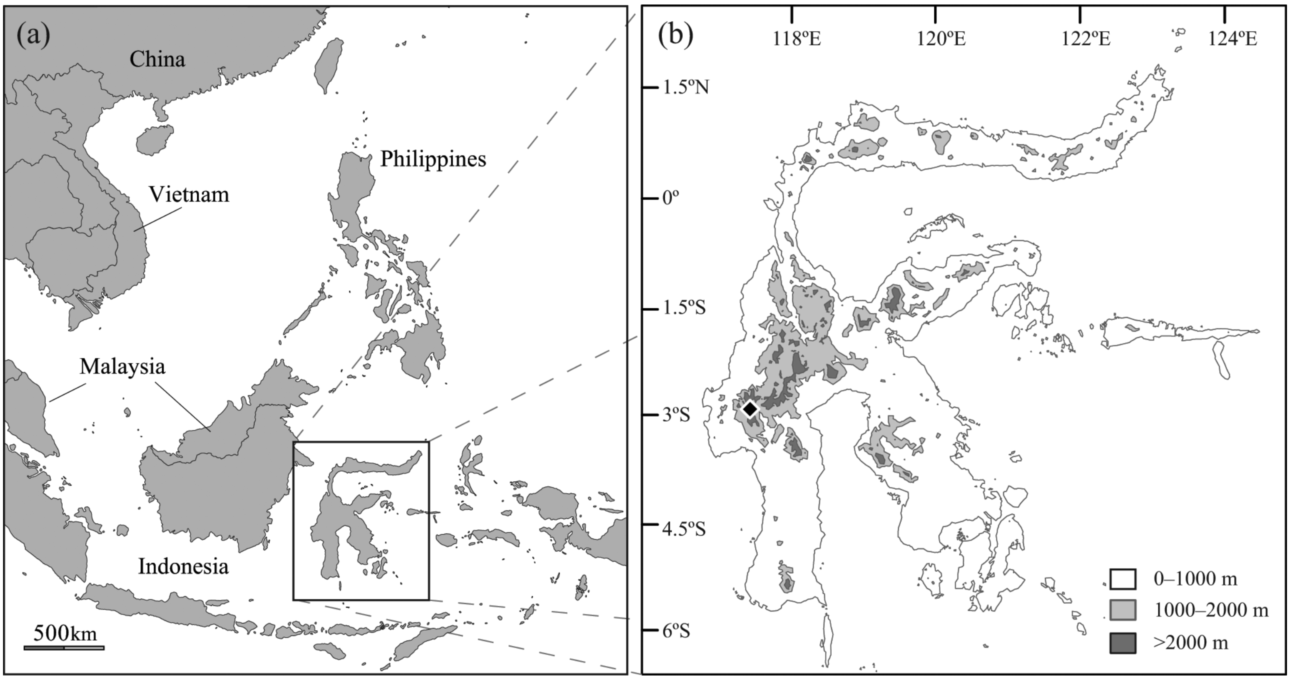

FIGURE 1. Maps of (a) Southeast Asia, showing the position of Sulawesi Island and (b) Sulawesi, showing the type locality of *Waiomys mamasae* (Mt. Gandangdewata [diamond]).

FIGURE 2. Stream on Mount Gandangdewata where type specimen was collected. Specimen was collected within 20 meters where the photo was taken. Shallow riffles shown in photo are consistent with the description of the site by locals who caught the animal. Photograph by Kevin C. Rowe.

Tissue sampling and genetic analysis. Tissue samples were collected in the field and stored in 70% ethanol. We sequenced four unlinked autosomal nuclear exons: (1) exon 11 of breast cancer 1 (BRCA1); (2) exon 1 of retinol binding protein 3 (IRBP); (3) exon 1 of recombination activating gene 1 (RAG1); and (4) exon 1 of growth hormone receptor (GHR). We also sequenced the mitochondrial cytochrome b gene. All loci were amplified and sequenced using published primers following standard procedures described previously (Rowe *et al.* 2008, 2011). We aligned sequences from the new species to those from 109 other species representing most major divisions within the subfamily Murinae (Appendix B). To root the phylogeny we included outgroups from the subfamilies Gerbillinae (2 species) and Deomyinae (3 species). We obtained previously published sequences from GenBank for most species in this study, but generated new sequences for 24 species including the first sequences of the New Guinea earless water rat (*Crossomys moncktoni*) and the few-toothed Sulawesi shrew rat (*Paucidentomys vermidax*). All new DNA sequences were deposited in GenBank (accession numbers KJ607263–KJ607322; Appendix B). We aligned sequences in CodonCode ver. 4.1.1 (CodonCode Corporation, Dedham, MA, USA) and manually inspected alignments in MacClade v.4.08 (Maddison & Maddison 2003). We conducted phylogenetic analyses using MrBayes ver. 3.2.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003; Ronquist *et al.* 2012) and RAxML ver. 7.6.3 (Stamatakis 2006). We implemented all phylogenetic analyses on the CIPRES online portal (Miller *et al.* 2010). We determined appropriate DNA sequence partitions and models using PartitionFinder ver. 1.1.1 (Lanfear *et al.* 2012) and applied these models to both Bayesian and maximum likelihood analyses. We set parameters in MrBayes following Rowe *et al.* (2011) and with two independent runs each with four chains for 40 million generations. We conducted RAxML analyses with 1000 bootstrap replicates using the models selected by PartitionFinder.

Morphometric measurements. Specimens examined in this study are deposited in the collections of the American Museum of Natural History, New York (AMNH), the Australian Museum, Sydney (AM), the Field Museum of Natural History, Chicago (FMNH), Museum Victoria, Melbourne (NMV), and Museum Zoologicum Bogoriense, Bogor (MZB). Registration numbers for all specimens are listed in Appendix A.

Phylogenetic analyses, presented below, supported a closer relationship of the new species with terrestrial, invertebrate-eating rodents (shrew rats) of Sulawesi than to Sahulian water rats and their terrestrial carnivorous relatives, or to Philippine shrew rats. Thus, we made qualitative and quantitative morphological comparisons between the new genus and specimens of all genera of shrew rats of Sulawesi, including the species *Echiothrix leucura* Gray 1867*, Melasmothrix naso* Miller & Hollister 1921*, Paucidentomys vermidax* Esselstyn *et al.* 2012*, Sommeromys macrorhinos* Musser & Durden 2002*, Tateomys macrocercus* Musser 1982*,* and *Tatetomys rhinogradoides* Musser 1969. However, because the new species is eco-morphologically similar to the carnivorous water rats of New Guinea, we also made comparisons to representatives of these species to qualitatively assess the degree of convergence. These species include *Baiyankamys shawmayeri* (Hinton 1943), *Crossomys moncktoni* Thomas, 1907, *Hydromys chrysogaster* E. Geoffroy 1804, *Hydromys hussoni* Musser & Piik 1982, and *Parahydromys asper* (Thomas 1907).

We collected twenty-four cranial and dental measurements from the cleaned skulls of specimens using digital calipers (precise to 0.01 mm): greatest length of skull (GLS), zygomatic breadth (ZB), interorbital breadth (IB), length of the rostrum (LR), breadth of the rostrum (BR), breadth of the zygomatic plate (BZP), breadth of the braincase (BBC), height of the braincase (HBC), length of diastema (LD), post-palatal length (PPL), length of incisive foramina (LIF), breadth of incisive foramina (BIF), length of bony palate (LBP), breadth of mesopterygoid fossa (BMF), length of auditory bulla (LB), length of nasal (LON), crown length of the first maxillary molar (CLMM), breadth of the first maxillary molar (BUM), breadth of the upper incisor (BUI), depth of the upper incisor (DUI), length of the dentary including the incisor (LDII), length of the dentary excluding the incisor (LDEI), crown length of the first mandibular molar (CLMaM), breadth of the first mandibular molar (BLM). We also report standard external measurements collected from freshly caught specimens, including total length (TTL), tail length (Tail), head and body length (HB) hind-foot length including the claws (HF), ear length (Ear), and mass (Mass) in grams. Measurements follow those diagrammed in Musser & Heaney (1992) and Musser & Durden (2002). External measurements were taken from specimen tags and the field notes of collectors.

Results

Phylogenetic analyses. Concatenation of the four exons and one mitochondrial locus resulted in an alignment consisting of 5,787 nucleotides. Partitionfinder analyses identified eight optimal partitions of the data. Partitions did not correspond to individual gene fragments, but represented combinations of codon positions with similar substitution rates across genes (Table 1). Partitionfinder estimated that a GTR substitution model was the best model for six partitions, whereas it selected HKY and SYM substitution models as the best fits for the remaining two partitions. For all partitions the best model included a GAMMA-distributed rate heterogeneity parameter. For four models, partitionfinder also identified that the best model included a proportion of invariable sites parameter. However, this model is not recommended for use with RAxML (Stamatakis 2006) and was only used in the MrBayes analyses.

Both Bayesian and maximum likelihood (ML) analyses strongly supported the phylogenetic placement of the Sulawesi water rat close to our limited sample of the shrew rats of Sulawesi (Figure 3; *Melasmothrix naso* and *Paucidentomys vermidax*). Phylogenetic data were not available for other shrew rats of Sulawesi (i.e. *Echiothrix, Sommeromys,* and *Tateomys*) and their placement within Murinae remains uncertain. Because these species may form a clade of invertebrate-eating specialists on Sulawesi, we compare the morphology of the Sulawesi water rat to all Sulawesi shrew rats in the formal diagnosis (see below). The clade of the Sulawesi water rat*, Melasmothrix,* and *Paucidentomys* was recovered as sister to a clade containing genera of the Dacnomys and Rattus Divisions (Musser & Carleton 2005). This is similar to the placement of *Melasmothrix* in past inferences (Rowe *et al.* 2008). As previously reported, the water rats of New Guinea, in the Hydromys Division, were recovered as part of a radiation of 'old endemic' rodents from the Sahul region (Rowe *et al.* 2008) and sister to the Xeromys Division that includes the terrestrial carnivorous genera *Pseudohydromys* and *Leptomys*. In this analysis we also included a montane water rat from New Guinea, *Crossomys moncktoni,* which was recovered as sister to the lowland water

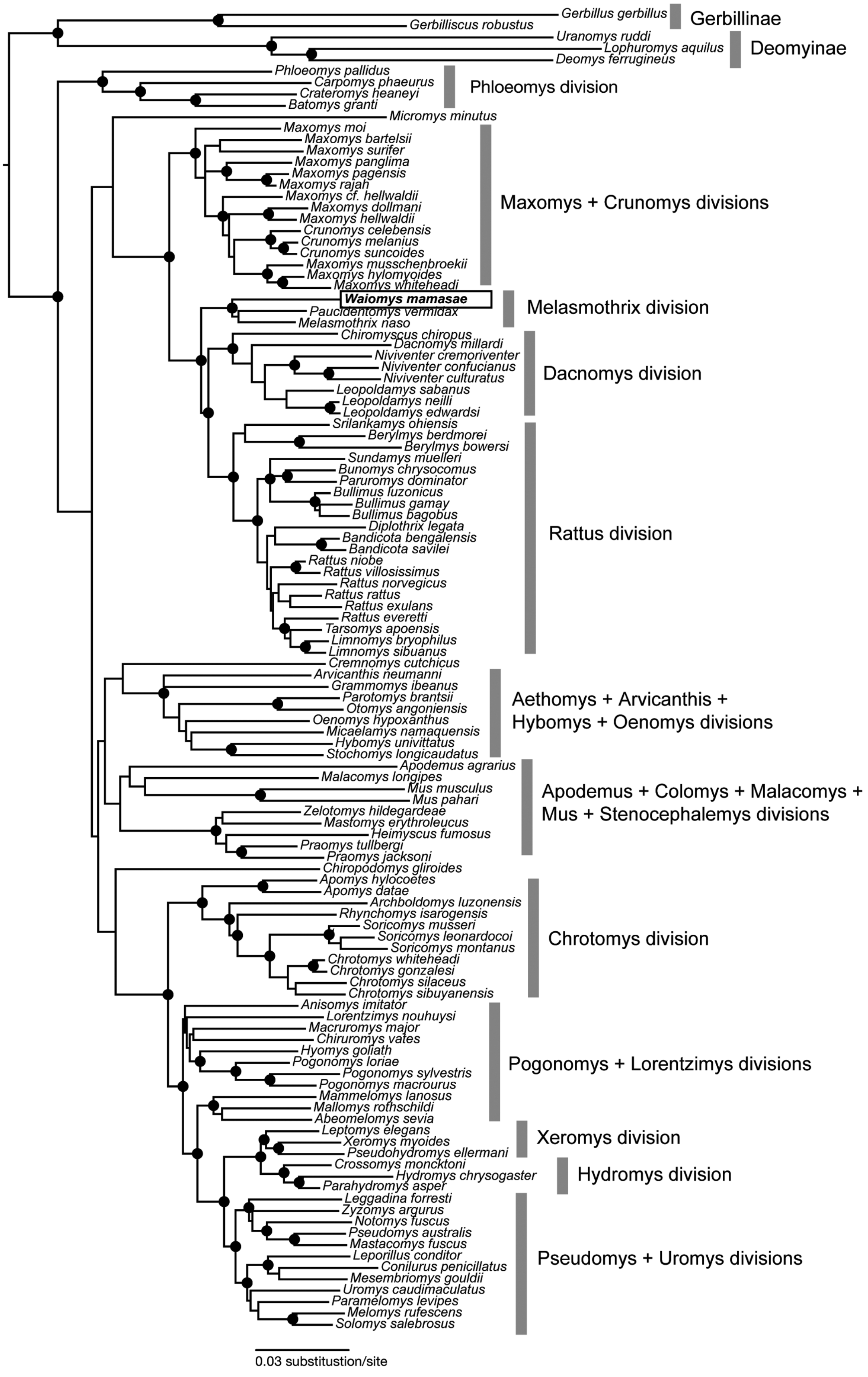

FIGURE 3. Phylogenetic position of *Waiomys mamasae* in Murinae, inferred with Bayesian analysis of a partitioned concatenation of 4 nuclear loci and 1 mitochondrial locus. Nodes supported by >95% Bayesian posterior probability and >90% maximum likelihood bootstrap value are marked with black circles.

rats of New Guinea, *Hydromys* and *Parahydromys.* We did not include any *Baiyankamys* in our analysis, but several putative synapomorphies, in particular, absence of the third lower molar and presence of a masseteric process, along with a suite of external characters (Helgen 2005), suggest that *Baiyankamys* is closely related to the other water rats of the Hydromys Division. Phylogenetically the Sulawesi water rat and the water rats of New Guinea are not closely related within Murinae. Phylogenetic analyses of individual gene trees were topologically consistent with our concatenated analyses. All gene trees thus supported a close relationship of the Sulawesi water rat with our sample of the shrew rats of Sulawesi and a distant relationship with the water rats of New Guinea (data not shown). Our phylogenetic analyses therefore strongly supported an origin of a semi-aquatic, carnivorous rat on Sulawesi that was independent from the evolution of the water rats of New Guinea.

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

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

Systematics

Waiomys new genus

Type species. *Waiomys mamasae*, the new species described below.

Diagnosis. A genus of rodent in the family Muridae, subfamily Murinae that possesses soft, fine, extremely dense grey-brown dorsal fur; similarly textured pale grey ventral fur; small eyes; short ears almost entirely covered dorsally by fur; long tail with white ventral vibrissae; broad, dorso-ventrally flattened muzzle; moderately dense facial vibrissae; long hindfeet that lack webbing or stiff hairs; one white spot ca. 10 mm in diameter on each side of the rump; absence of hypothenar pad on hindfoot; presence of large thenar pad on the lateral margin of the hindfoot; three molars in both maxillary and mandibular tooth rows; narrow incisors with pale orange enamel; absence of a masseteric process; large ovate infraorbital foramen; and large foramen magnum. Phylogenetic analyses place the genus in a clade containing the Sulawesi shrew rats *Melasmothrix* and *Paucidentomys* (Figure 3).

Etymology. The generic name combines the Mamasa Toraja (Gordon 2005) word 'wai' (water; pronounced 'why') with the Greek '*mys*' (mouse) in reference to the semi-aquatic lifestyle of the animal and in recognition of the local Mamasan people who call the animal 'water rat' in their language, Mamasa Toraja.

Description. The same as for the only know species in the genus, which is described below.

Waiomys mamasae sp. nov.

(Figs. 4–6)

Holotype. NMV C37027/MZB 37000, an adult male collected by hand on the night of 12 May 2012 while it was swimming in a shallow, fast flowing mountain stream (Figure 2, 4). The specimen was prepared as a dried skin, cleaned skull and fluid-preserved carcass. The carcass, tongue, and phallus were fixed in 4% formalin solution and later transferred to 70% ethanol for permanent storage. The skull was preserved in 70% ethanol, dried, cleaned by dermestid beetles, and degreased by immersion in 10% ammonia. Molars of the specimen are fully emerged.

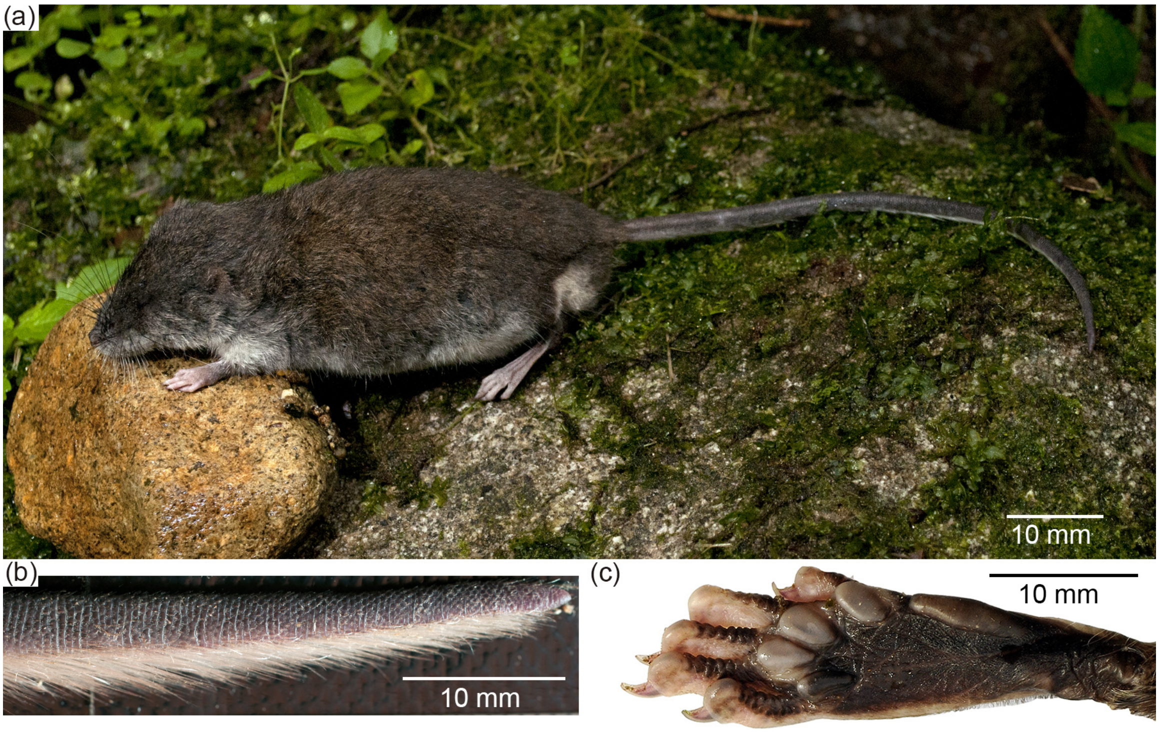

FIGURE 4. Type specimen (NMV C37027/MZB 37000) in the field prior to preparation showing (a) specimen in live pose, (b) distal third of tail, (c) right plantar surface. Photographs by Kevin C. Rowe.

Type locality. Mount Gandangdewata (2.882898º S, 119.386448 º E, 1571 m), Rantepangko, Mamasa, Sulawesi Barat, Indonesia (Figure 1).

Referred material. Only the holotype.

Distribution. *Waiomys* is known only from the type locality in lower montane rainforest of the Quarles Range of the western Sulawesi highlands.

Diagnosis. *mamasae* is the only known species in the genus *Waiomys.* Thus, generic and specific diagnoses are the same.

Etymology. The specific epiphet refers to the type locality, which is near the town of Mamasa. The local people who collected the type specimen and who had existing knowledge of the species, self-identify as Mamasan. Thus, the epithet also recognizes their knowledge and contribution to the scientific discovery of the species.

Description. *Waiomys mamasae* is a small, densely furred rat (Figure 4). The dorsal pelage is grey. The hairs of the underfur are < 10 mm in length and have a grey base and light brown tip (~1–2 mm). The sparse guard hairs are grey on the basal half, dark brown on the distal half, and approximately 10 mm in length, emerging only a few millimeters above the dorsal underfur. The dorsal fur protrudes nearly vertically from the skin and can be brushed naturally in any direction. The ventral fur is as soft and dense as the dorsal underfur and of similar length with fine white guard hairs emerging <5 mm beyond the underfur. The base of the ventral underfur is dark grey whereas the distal quarter is a much paler grey. Both the dorsal and ventral coloration are relatively uniform across the head and body. The margin of the ventral fur is discrete and lies high on the body, extending from above the upper lips, at the midline of the nose, along the side of the body at the base of the limbs. A patch of ventral fur extends 15 mm up each side of the base of the tail and above the hindlimbs forming two conspicuous white spots on the rump. The dorsal fur extends to the fingers of the forefeet and to the ankles of the hindfeet.

The eyes are small (~2 mm diameter) and almost indistinguishable amid the fur of the head. The pinnae are grey in color, short (11 mm), heavily furred on the inner and outer surface, and nearly indistinguishable from the dorsal fur. The mystacial vibrissae are dense and stiff. A minority of the vibrissae approach 40 mm in length and extend beyond the pinnae, while the remaining whiskers are shorter at ~5–25 mm. The base of each vibrissa is black, but the distal quarter lacks pigmentation.

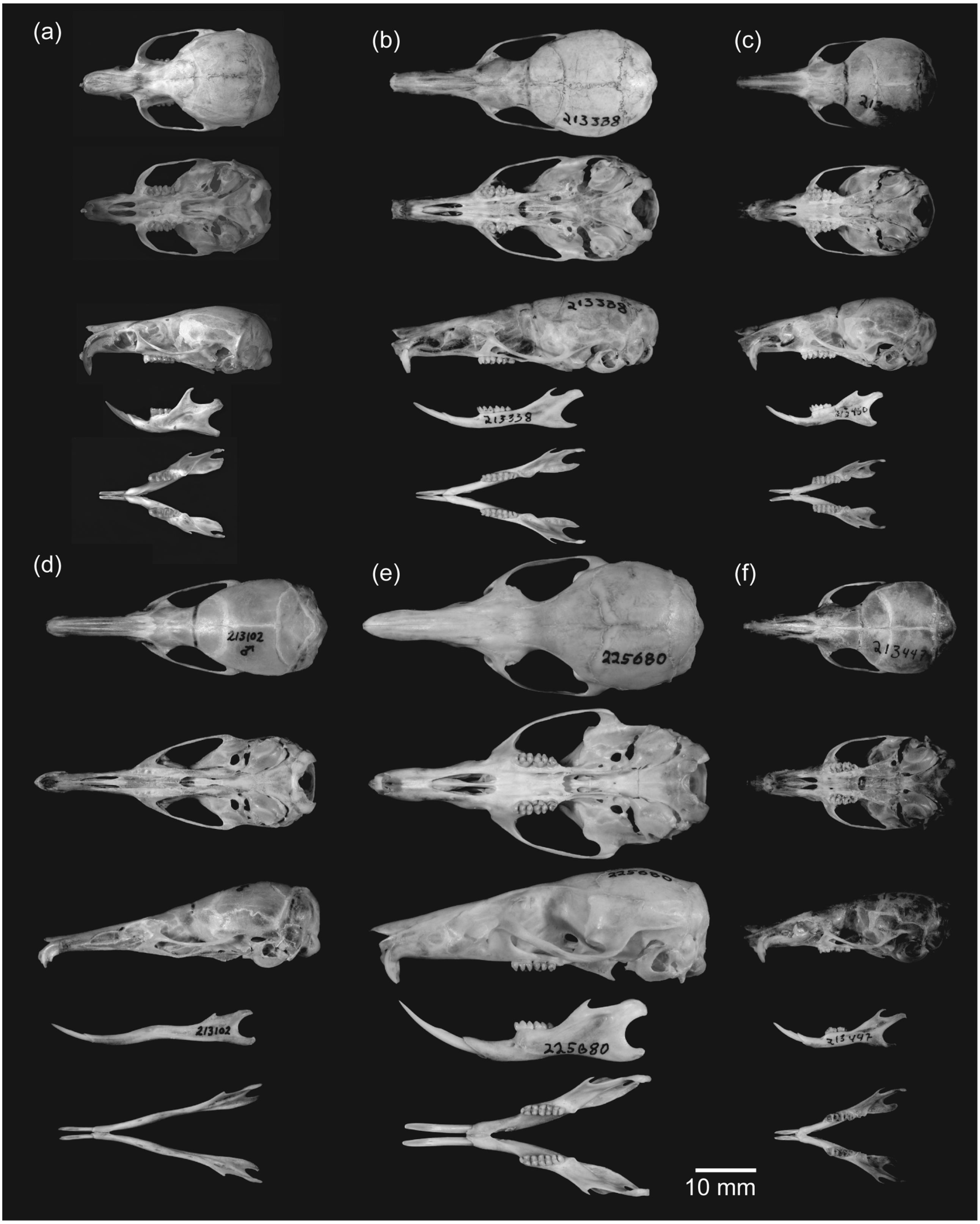

FIGURE 5. Images of the crania and mandibles of (a) *Waiomys mamasae* (NMV C37027/MZB 37000), (b) *Tateomys rhinogradoides* (FMNH 213388), (c) *T. macrocercus* (FMNH 213456), (d) *Paucidentomys vermidax* (FMNH 213102/MZB 35000), (e) *Echiothrix centrosa* (AMNH 225680), and (f) *Melasmothrix naso* (FMNH 213447). Photographs by Kevin C. Rowe and Rebecca Banasiak.

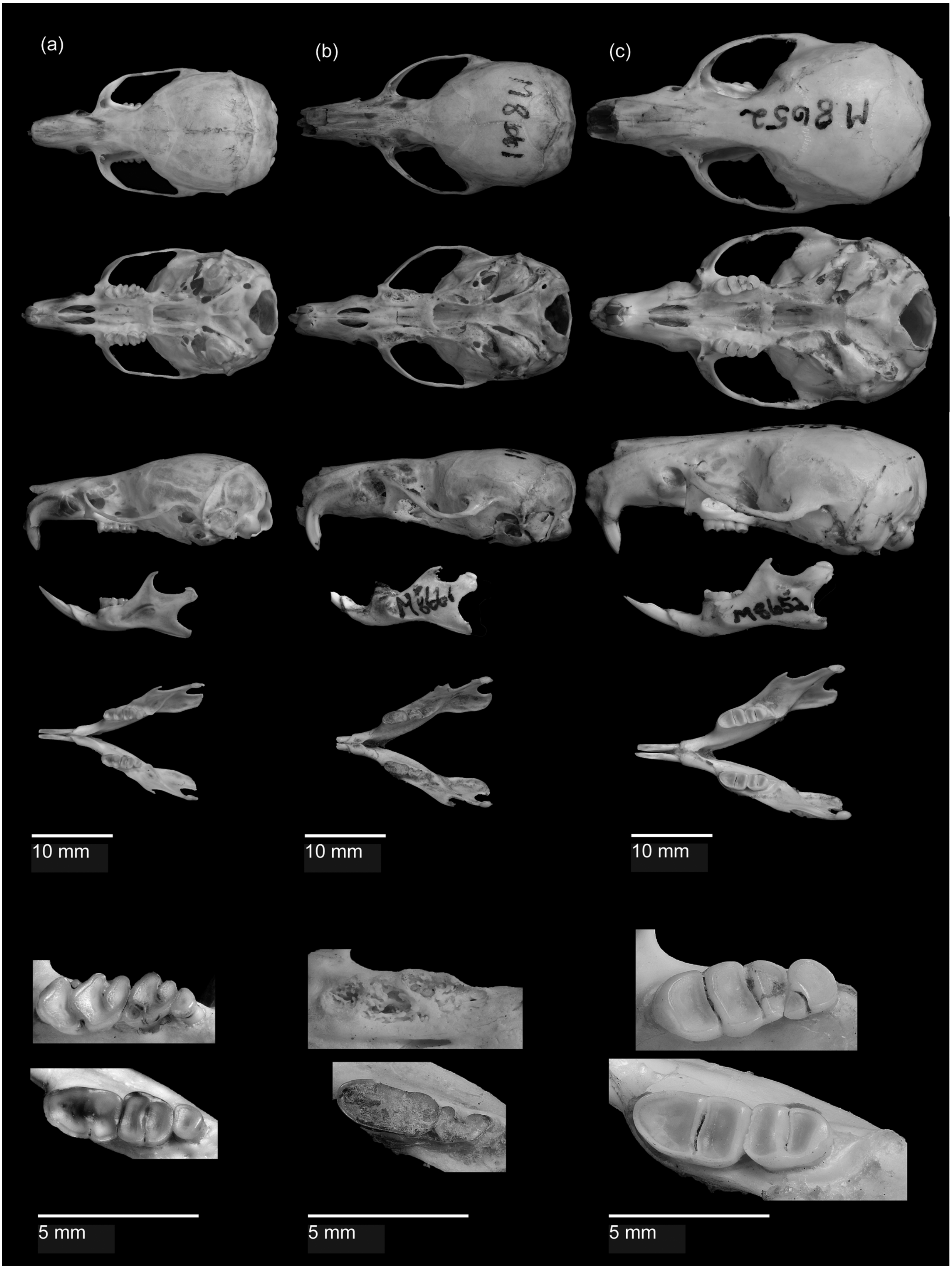

FIGURE 6. Images of the crania, mandibles, left maxillary molar row, and left mandibular molar row of (a) *Waiomys mamasae* (NMV C37027/MZB 37000), (b) *Baiyankamys shawmayeri* (AM-M8661) and (c) *Crossomys moncktoni* (AM-M8652). Maxillary molars for AM-M8661 were present in plate 24 (p. 525) of Flannery (1995) but have since been lost from the specimen. Photographs by Kevin C. Rowe.

The tail is nearly 25% longer than the head and body. The ventral surface of the tail is covered in stiff white vibrissae approximately 5 mm long (Figure 4c). The dorsal surface of the tail is grey-brown and similar to the color of the dorsal pelage. The tail tapers gently from the base to the tip. It is not substantially thickened or flattened and other than the ventral vibrissae, it is typical of murine rodents. The hindfeet are long (27.5% of head and body length) with short, but otherwise typical murine claws. They are light brown on the dorsal surface and dark brown on the plantar surface. The hindfeet lack the hypothenar pad (Figure 4c). On the plantar surface, the first interdigital pad and thenar pad abut each other and are positioned on the lateral margin of the foot. The forefeet are small with short typical murine claws and a nailed pollex fused to the side of the palm. The palmar surface consists of three interdigital pads, a large thenar pad, and a slightly smaller hypothenar.

The skull of *Waiomys mamasae* is delicate with few prominent ridges (Figure 5). However, a distinct occipital ridge and an almost indistinguishable temporal ridge are present. For a murine, the rostrum is moderate in length relative to the basicranial region, comprising approximately one-quarter of the total length of the skull (Table 2). The zygomatic arches are delicate and the large ovate infraorbital foramina make the zygomatic arches appear flared and squared off when viewing the skull from the dorsal or ventral aspect. The incisive foramina also are fairly broad (2.3 mm at their combined maximum breadth). The foramen magnum is large (6.17 mm in width) and equal to 42.6% of the breadth of the braincase. The occipital region is noticeably bulbous and contributes to the globose appearance of the braincase. The auditory bullae are small for a murine of this size (LB = 13% of GLS). The dentary is delicate. The angular process is narrow and elongate but otherwise the dentary is typical of murine rodents.

The upper incisors of *Waiomys mamasae* are narrow (each 0.5 mm wide at the root) and orthodont. The lower incisors are also narrow (0.7 mm at the base). The labial surfaces of the upper and lower incisors are pale orange. Three molars are present in both the maxillary (M1, M2 and M3) and mandibular rows (m1, m2 and m3). The occlusal surfaces of lower and upper molars form little more than basins outlining the basic murine molar cusp pattern (Figure 5) as a result of either tooth wear or an evolutionary trend toward simplification. The first and second upper molars are moderate in size for murine rodents (first upper molar 1.8 mm wide). As is the case for many murine species, the third molars, both upper and lower, are much smaller than the first and second molars.

The contents of the mouth and the nearly distended stomach of the type specimen were examined by R. Marchant (Terrestrial Invertebrates, Museum Victoria) and identified as consisting entirely of stream invertebrate larvae belonging to the families Simulidae (Black flies; genus *Simulium*) and Hydropsychidae (net-spinning caddisflies; genus *Cheumatopsyche*). The larvae of both genera are known to cling to the surface of stones in shallow areas of fast flowing water (Merritt & Cummins 1996), suggesting that *Waiomys* dives and forages for food on the stream bottom. No plant material or terrestrial animal material was identified from the mouth or stomach.

Comparisons. *Waiomys mamasae* is sympatric with several other murine rodents where it was collected on Mount Gandangdewata (Figure 1). These include all but two species of an endemic group of invertebrate-eating rodents on Sulawesi that are referred to as shrew rats: *Melasmothrix naso, Paucidentomys vermidax, Sommeromys macrorhinos, Tateomys macrocercus, Tateomys rhinogradoides,* were all detected during our surveys on Mount Gandangdewata. However, there are no records of either *Echiothrix centrosa* or *Echiothrix leucura* in the Mount Gandangdewata region. The latter species is restricted to the northern peninsula east of Gorontalo, while the former has been documented from several sites in Central and West Sulawesi (Musser & Carleton, 2005). *Crunomys celebensis*, another Sulawesi murine occasionally referred to as a ‘shrew rat,’ was recently shown to be closely related to species of *Maxomys* (Achmadi et al. 2013) and we therefore exclude it from comparisons.

In body size, *Waiomys mamasae* is much smaller than either species of *Echiothrix,* smaller than *Tateomys rhinogradoides* and *Paucidentomys vermidax,* and larger than *Melasmothrix, Sommeromys,* and *Tateomys macrocercus.* The dorsal fur of *Waiomys* has a similarly soft texture as that of *Tateomys*, but that of *Waiomys* is denser and paler in color. The ventral fur of *Waiomys* is also considerably denser and paler in color than any other Sulawesi murines. The two white patches on the rump of *Waiomys* are unique among murines and may represent eyespots.

Waiomys has a considerably broader and blunter rostrum than any of the shrew rats of Sulawesi. The mystacial vibrissae of *Waiomys* are denser and stiffer but not longer than in the shrew rats of Sulawesi. The ears of *Waiomys* are substantially shorter (in relative and absolute terms) and more densely furred than in any other murine on Sulawesi. The eyes of *Waiomys* are similar in size to those of much smaller animals, including *Tateomys macrocercus* and *Sommeromys macrorhinos.* The tail of *Waiomys* is similar in length and thickness to that of *T.*

rhinogradoides, but is more sparsely haired on the dorsal surface. Among all Sulawesi murines, only *Waiomys* possesses ventral vibrissae on the tail. The hindfeet of *Waiomys* are comparable in length to the larger *Tateomys rhinogradoides*, but the forefeet are considerably smaller and similar in size to the feet of the smaller *T. macrocercus* and *S. macrorhinos.* The claws on the forefeet are also much smaller than in *T. rhinogradoides, T. macrocercus,* or *Melasmothrix naso,* and are comparable in size to the claws of *S. macrorhinos.* The position of the thenar pad and first interdigital pad on the lateral margin of the plantar surface of the hindfeet in *Waiomys* is distinct from those of all other murines of Sulawesi. Among Sulawesi murines, only *Waiomys* lacks the hypothenar pad.

TABLE 2. External, cranial and dental measurements of *Waiomys mamasae* compared to the shrew rats of Sulawesi. (Shown are the mean, ± one standard deviation, and the range in parentheses).

Genus	*Waiomys*	*Melasmothrix*	*Sommeromys*	*Tateomys*	*Tateomys*	*Paucidentomys*	*Echiothrix*
Species	*mamasae*	*naso*	*macrorhinos*	*macrocercus*	*rhinogradoides*	*vermidax*	*leucura*
TTL	288	206.67	282.5	278.00	204.50	362.5	460.25
		±7.77	±13.8	±2	±20.51	±7.78	±19.65
		(198–213)	(271–301)	(276–280)	(290–319)	(357–368)	(435–483)
Tail	159	88.33	182.5	166.00	163.00	199	242.4
		±4.73	±8.81	±4.36	±16.97	±1.41	±9.94
		(83–92)	(173–193)	(163–171)	(151–175)	(198–200)	(233–258)
HB	129	118.33	100	112.00	145.50	163.5	213.25
		±3.06	±5.6	±6.24	±5.8	±6.36	±9.14
		(115–121)	(95–108)	(105–117)	(139–153)	(159–168)	(200–221)
HF	36	28	30	30.67	37.25	37.5	51.4
		±0	±0.82	±1.15	±1.89	±0.71	±1.82
		(28–28)	(29–31)	(30–32)	(36–40)	(37–38)	(49–53)
Ear	11	18.33	18.25	19.33	22.00	21.5	33.4
		±0.58	±1.71	±0.58	±1.41	±0.71	±1.14
		(18–19)	(16–20)	(19–20)	(21–24)	(21–22)	(32–35)
Mass	64	47.67	26.83	40.00	86.50	103.5	274.33
		±5.13	±3.06	±1	±7.55	±6.36	±47.82
		(42–52)	(24–30)	(39–41)	(76–92)	(99–108)	(220–310)
GLS	30.73	33.04	31.8	31.65	39.42	43.28	53.39
		±0.65	±0.52	±0.58	±0.68	±0.06	±1.89
		(32.5–32.9)	(31.08–31.93)	(30.99–32.08)	(38.52–40.13)	(43.23–43.32)	(50.33–55.29)
ZB	15.83	14.07	13.09	13.87	15.25	15.24	23.2
		±0.12	±0.24	±0.16	±0.22	±0.4	±1
		(13.98–14.15)	(12.83–13.29)	(13.73–14.04)	(14.96–15.42)	(14.96–15.52)	(21.87–24.51)
LON	9.00	11.64	11.81	11.26	13.30	16.24	22.91
		±0.69	±0.37	±0.5	±0.61	±0.05	±1.37
		(11.07–12.41)	(11.45–12.32)	(10.91–11.84)	(12.76–14.02)	(16.2–16.27)	(20.89–24.52)
LR	7.77	12.52	12.02	11.91	13.83	17.55	21.3
		±0.18	±0.54	±0.78	±0.61	±0	±0.91
		(12.31–12.65)	(11.55–12.72)	(11.06–12.61)	(13.19–14.36)	(17.55–17.55)	(20.06–22.43)
BR	4.30	5.06	4.9	4.18	4.70	4.98	7.43
		±0.32	±0.21	±0.73	±0.25	±0.11	±0.54
		(4.76–5.39)	(4.68–5.16)	(3.52–4.97)	(4.41–5.01)	(4.9–5.05)	(6.77–8.12)

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TABLE 2. (Continued)

Genus	*Waiomys*	*Melasmothrix*	*Sommeromys*	*Tateomys*	*Tateomys*	*Paucidentomys*	*Echiothrix*
Species	*mamasae*	*naso*	*macrorhinos*	*macrocercus*	*rhinogradoides*	*vermidax*	*leucura*
IB	4.89	6.19	5.61	6.10	6.94	5.96	7.12
		±0.08	±0.16	±0.06	±0.12	±0.32	±0.48
		(6.12–6.28)	(5.45–5.80)	(6.03–6.14)	(6.84–7.1)	(5.73–6.18)	(6.7–7.71)
BZP	1.60	1.37	1.43	1.14	1.42	1.27	3.46
		±0.18	±0.03	±0.16	±0.14	±0.12	±0.27
		(1.26–1.64)	(1.39–1.47)	(1.04–1.32)	(1.32–1.63)	(1.18–1.35)	(3.19–3.88)
BBC	14.49	14.22	13.24	14.39	15.82	15.36	18.91
		±0.28	±0.36	±0.25	±0.35	±0.76	±0.55
		(13.85–14.51)	(12.75–13.60)	(14.17–14.66)	(15.46–16.2)	(14.82–15.9)	(18.44–19.83)
HBC	10.57	9.12	10.43	9.89	10.30	11.09	14.15
		±0.7	±0.39	±0.44	±0.49	±0.32	±0.33
		(8.6–10.11)	(10.15–11.00)	(9.41–10.28)	(9.82–10.89)	(10.86–11.31)	(13.6–14.46)
PPL	11.76	12.28	9.58	11.10	16.22	17.85	18.16
		±0.12	±0.37	±0.08	±0.29	±0.5	±0.65
		(12.1–12.33)	(9.10–10.00)	(11.02–11.17)	(15.84–16.55)	(17.49–18.2)	(17.22–18.75)
LD	8.26	6.68	6.76	7.07	9.12	10.28	17.51
		±0.79	±0.43	±0.91	±1.06		±2.51
		(5.74–7.67)	(6.20–7.16)	(6.03–7.7)	(7.99–10.04)		(15.02–20.32)
LBP	7.59	6.22	6.02	6.61	8.10	9.85	10.6
		±0.29	±0.26	±0.12	±0.41	±7.78	±0.97
		(5.9–6.60)	(5.87–6.28)	(6.48–6.7)	(7.62–8.62)	(357–368)	(9.57–12.2)
LIF	4.40	4.78	2.9	3.98	5.46	5.64	9.86
		±0.28	±0.36	±0.28	±0.42	±7.78	±0.67
		(4.4–5.06)	(2.67–3.32)	(3.71–4.27)	(4.97–5.85)	(357–368)	(9.08–10.76)
BIF	2.31	1.83	1.92	1.96	1.97	1.91	3.35
		±0.09	±0.19	±0.09	±0.03	±7.78	±0.15
		(1.73–1.94)	(1.71–2.07)	(1.87–2.05)	(1.95–2.01)	(357–368)	(3.19–3.51)
BMF	2.17	1.81	2.01	1.87	2.26	1.63	2.49
		±0.16	±0.15	±0.09	±0.12	±7.78	±0.18
		(1.68–1.99)	(1.86–2.17)	(1.77–1.95)	(2.13–2.41)	(357–368)	(2.3–2.77)
LB	4.05	5.37	4.28	4.65	5.25	5.65	5.88
		±0.31	±0.22	±0.4	±0.34	±7.78	±0.25
		(5.03–5.73)	(4.07–4.47)	(4.19–4.93)	(4.75–5.51)	(357–368)	(5.58–6.24)
CLMM	4.96	4.78	4.44	4.94	5.43		6.23
			±0.19	±0.34	±0.16		±0.19
			(4.30–4.57)	(4.7–5.18)	(5.32–5.54)		(6.09–6.36)
BUM	1.80	1.79	1.45	1.77	1.92		2.07
			±0.07	±0.07	±0.01		±0.16
			(1.40–1.50)	(1.72–1.82)	(1.91–1.92)		(1.96–2.18)
BUI	0.50	0.97	0.98	0.77	1.10	0.91	1.2
		±0.06	±0.46	±0.13	±0.07		±0.08

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TABLE 2. (Continued)

Genus Species	*Waiomys* *mamasae*	*Melasmothrix* *naso*	*Sommeromys* *macrorhinos*	*Tateomys* *macrocercus*	*Tateomys* *rhinogradoides*	*Paucidentomys* *vermidax*	*Echiothrix* *leucura*
		(0.92–1.06)	(0.65–1.30)	(0.63–0.89)	(1–1.15)		(1.09–1.3)
DUI	1.23	0.97	1.42	1.01	0.99	0.76	1.89
		±0.22		±0.2	±0.38		±0.13
		(0.81–1.29)		(0.78–1.13)	(0.64–1.35)		(1.72–2.04)
LDII	19.74	19.55	15.89	18.79	24.86		37.73
			±0.58	±0.1	±0.35		±0.87
			(19–20)	(18.72–18.86)	(24.61–25.11)		(37.11–38.34)
LDEI	13.74	16.28	12.99	15.32	19.90		26.52
			±0.58	±0.67	±0.44		±0.33
			(19–20)	(14.84–15.79)	(19.59–20.21)		(26.28–26.75)
CLMa	4.89	4.44	4.24	4.60	5.14		6.27
			±0.58	±0.04	±0.21		±0.13
			(19–20)	(4.57–4.63)	(4.99–5.29)		(6.18–6.36)
BLM	1.61	1.2	1.14	1.34	1.29		1.57
			±0.58	±0.06	±0.02		±0.07
			(19–20)	(1.29–1.38)	(1.27–1.3)		(1.52–1.62)

Relative to its body size, the skull of *Waiomys* is shorter than those found in any of the shrew rats of Sulawesi and is comparable to or shorter in absolute length than the skull of the much smaller *Sommeromys* (Table 2). The shortness of the skull is produced primarily by the lack of rostral elongation so prominent in the other species (rostrum is 25% of skull length compared to 35–41% in the shrew rats). However, the braincase of *Waiomys* also is shorter than in most of the shrew rats (Table 2). The length of the post-palatal region in *Waiomys* is comparable to those of the smaller *Tateomys macrocercus* and only slightly larger than in *Sommeromys.* The zygomatic arches and braincase of *Waiomys* are much more square in appearance when viewed from the dorsal surface than in the other species. The infraorbital foramina are more ovate and broad in *Waiomys,* contributing to the flared and squared-off appearance of the zygomatic arches. The length of the auditory bulla in *Waiomys* is both absolutely (LB = 4.05 mm) and proportionately (LB/BBC = 0.28) shorter than in any of the shrew rats on Sulawesi (LB = 4.28-5.88 mm; LB/BBC = 0.31-0.38). Because of the trend toward elongation of the skull in the shrew rats, we used a measure of skull width (BBC) rather than of skull length (e.g. GLS) for proportional comparison. The dental formula of *Waiomys* is shared with all shrew rats on Sulawesi except *Paucidentomys vermidax*, in which the molars are absent. The upper incisors of *Waiomys* are both absolutely (BUI = 0.50 mm) and proportionately (BUI/BBC = 0.035) narrower than in any of the shrew rats (BUI = 0.77-1.2 mm; BUI/BBC = 0.054-0.074). Both upper and lower incisors of *Waiomys* have orange enamel on the labial surface that is typical of most murines, but is absent in the shrew rats of Sulawesi. The upper molars of *Waiomys* are comparable in width to other shrew rats of Sulawesi (excluding *Paucidentomys* which lacks molars), but the lower molars are broader.

Among the water rats of New Guinea, *Waiomys* is similar in size to the smaller species of *Hydromys* (*H. hussoni* and *H. ziegleri*), and to the species of *Baiyankamys* (*B. habbema* and *B. shawmayeri*), but considerably smaller than *Crossomys moncktoni, Hydromys chrysogaster,* and *Parahydromys asper* (Helgen 2005). Like the montane species of water rats from New Guinea (*Baiyankamys* and *Crossomys*), *Waiomys* is distinguishable from the lowland water rats of New Guinea by its soft grey fur and small pinnae. Overall the fur of *Waiomys* is similar to that of *Crossomys.* However, the dorsal guard hairs of *Waiomys* are shorter and less prominent than those of *Crossomys.* The tips of the dorsal underfur in *Waiomys* are a paler brown than in *Crossomys.* The ventral underfur of *Waiomys* is dark grey at the base and light grey at the tip, whereas in *Crossomys* it is a more uniform silvery white. The dorso-ventral margin of the fur in *Waiomys* is similar to that of *Crossomys* both in its distinctiveness and its position high up on the body from the base of the nose and along the body near the base of the limbs. The white rump spots present in *Waiomys* are absent in *Crossomys* and all other New Guinea rodents. The eyes of both

Waiomys and *Crossomys* are greatly reduced. The pinnae of *Waiomys* are similar in size to those of *Baiyankamys* but not as reduced as in *Crossomys,* where the pinnae are all but absent. The tail in *Waiomys, Baiyankamys*, and *Crossomys* is much longer than the head and body. *Waiomys* and *Crossomys* share the presence of stiff, white ventral vibrissae on the tail. In *Waiomys,* the ventral vibrissae form a single line that terminates at the base of the tail whereas in *Crossomys* the vibrissae bifurcate and diverge into two lines at the base of the tail. The tail of *Waiomys* is similar in thickness to those of terrestrial murines, but in *Crossomys* the tail is substantially thicker. The lack of any webbing or hairs on the margins of the plantar surface of *Waiomys* distinguishes it from all water rats of New Guinea. In both *Waiomys* and *Crossomys,* the hypothenar pad is absent from the plantar surface of the hindfeet and the thenar pad is positioned on the lateral margin of the foot. Like *Crossomys* and *Baiyankamys,* the forelimbs of *Waiomys* are small.

The skull of *Waiomys* is similar in size and robustness to those of *Baiyankamys* and *Hydromys hussoni* (Table 3, Figure 6; *H. hussoni* comparison in Helgen 2005)*.* *Waiomys* shares some cranial features with *Baiyankamys* and *Crossomys,* the montane water rats of New Guinea (Helgen 2005), to the exclusion of the lowland water rats of New Guinea. These include (1) slender and delicate zygomata that curve downward from the maxillary roots to the squamosal roots; (2) a tapering rostrum; (3) extremely narrow incisors; (4) a mesopterygoid fossa that is narrower than the width between the lingual margins of the first upper molars. In addition, two morphological characters clearly distinguish *Waiomys* from all water rats of New Guinea: (1) the presence in *Waiomys* of the third mandibular molar and (2) the absence in *Waiomys* of the masseteric process of the zygomatic plate.

TABLE 3. External, cranial and dental measurements of *Waiomys mamasae* compared to water rats of New Guinea (Shown are the mean, ± one standard deviation, and the range in parentheses).

Genus	*Waiomys*	*Baiyankamys*	*Baiyankamys*	*Hydromys*	*Hydromys*	*Hydryomys*	*Crossomys*	*Parahydromys*
Species	*mamasae*	*habbema*	*shawmayeri*	*hussoni*	*hussoni*	*chrysogaster*	*moncktoni*	*asper*
		Voss 1988		Voss 1988				
TTL	288		284		277	592.5 ±26.61 (565–620)	452.33 ±13.58 (438–465)	411.67 ±92.51 (305–470)
Tail	159	172.3 ±12.5 (154–187)	165	126.4 ±13.8 (103–152)	133	304.5 ±55.12 (260–385)	250 ±10.00 (240–260)	248.33 ±17.56 (230–250)
HB	129	148.6 ±8.1 (134–160)		147.9 ±15.4 (122–171)				
HF	36	37 ±1.2 (35–39)	33	29.8 ±2 (17–33)	27	73 ±5.2 (70–79)	48.5 ±6.36 (44–53)	50
Ear	11	8.6 ±0.6 (7–9)	14	12.1 ±0.8 (11–14)	12	20.25 ±8.66 (14–33)		15
Mass	64					782.75 ±96.67 (680–879)		
GLS	30.73	32.7 ±12.5 (154–187)	33.42	30.5 ±13.8 (103–152)	30.88	59.72 ±1.37 (58.4–61.59)	40.8 ±0.85 (39.92–41.	44.57 ±0.15 (44.4–44.66)

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TABLE 3. (Continued)

Genus Species	*Waiomys mamasae*	*Baiyankamys habbema* Voss 1988	*Baiyankamys shawmayeri*	*Hydromys hussoni* Voss 1988	*Hydromys hussoni*	*Hydryomys chrysogaster*	*Crossomys moncktoni*	*Parahydromys asper*
ZB	15.83	17.2 ±12.5 (154–187)	16.67	15.5 ±13.8 (103–152)	15.42	29.88 ±1.28 (29.13–31.8)	22.25 ±0.73 (21.42–23.	25.31 ±0.18 (25.14–25.5)
LON	9.00	11.2 ±12.5 (154–187)	10.35	9.8 ±13.8 (103–152)	10.45	21.14 ±1.38 (20.11–23.11	9.91 ±0.95 (8.75–10.7)	13.1 ±0.23 (12.84–13.27)
LR	7.77		10.17		8.10	19.23 ±1.07 (18.05–20.23	11.6 ±0.74 (10.53–12.	14.11 ±0.48 (13.6–14.54)
BR	4.30		5.44		5.43	12.55 ±0.5 (12.19–13.28	8.05 ±0.63 (7.32–8.68)	11.51 ±0.66 (10.75–11.94)
IB	4.89		5.20		4.98	8.08 ±0.19 (7.85–8.26)	5.64 ±0.34 (5.15–5.93)	8.63 ±0.51 (8.31–9.22)
BZP	1.60	1.5 ±12.5 (154–187)	1.18	1.7 ±13.8 (103–152)	1.63	2.96 ±0.47 (2.35–3.44)	1.98 ±0.04 (1.91–2)	2.18 ±0.27 (1.97–2.48)
BBC	14.49		14.88		13.70	21.89 ±0.72 (21.11–22.7)	19.89 ±0.43 (19.48–20.	22.22 ±0.79 (21.4–22.98)
HBC	10.57		12.10		10.80	16.81 ±1.07 (15.82–18.31	13.37 ±0.22 (13.21–13.	15.5 ±0.98 (14.47–16.41)
PPL	11.76		13.12		12.42	21.82 ±0.52 (21.28–22.43	15.08 ±0.65 (14.59–16.	15.51 ±0.22 (15.3–15.74)
LD	8.26	8.7 ±12.5 (154–187)	8.24	8.5 ±13.8 (103–152)	8.47	16.77 ±0.82 (16.12–17.96	11.13 ±0.48 (10.63–11.6	11.45 ±0.2 (11.23–11.6)
LBP	7.59		7.74		8.15	14.72 ±0.11 (14.62–14.87	10.48 ±0.65 (9.82–11.11	13.86 ±0.21 (13.67–14.08)
LIF	4.40	4 ±12.5 (154–187)	3.41	3 ±13.8 (103–152)	3.07	5.77 ±0.68 (4.79–6.26)	5.12 ±0.27 (4.76–5.4)	4.51 ±0.31 (4.25–4.85)
BIF	2.31	2.1 ±12.5 (154–187)	2.50	2 ±13.8 (103–152)	2.00	3.44 ±0.34 (2.94–3.69)	2.61 ±0.12 (2.52–2.77)	2.71 ±0.25 (2.54–3)

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TABLE 3. (Continued)

Genus	*Waiomys*	*Baiyankamys*	*Baiyankamys*	*Hydromys*	*Hydromys*	*Hydryomys*	*Crossomys*	*Parahydromys*
Species	*mamasae*	*habbema*	*shawmayeri*	*hussoni*	*hussoni*	*chrysogaster*	*moncktoni*	*asper*
		Voss 1988		Voss 1988				
BMF	2.17		2.74		2.54	4.81	3.7	4.4
						±0.15	±0.41	±0.36
						(4.66–5)	(3.26–4.2)	(4.03–4.75)
LB	4.05		3.70		3.84	6.43	4.22	5.15
						±0.18	±0.55	±0.1
						(6.25–6.66)	(3.54–4.7)	(5.04–5.22)
CLMM	4.96	5.1		4.6	4.53	8.41	5.31	8.58
		±12.5		±13.8		±0.31	±0.08	±0.12
		(154–187)		(103–152)		(8.08–8.83)	(5.2–5.39)	(8.45–8.68)
BUM	1.80	1.8		1.6	1.50	3.01	2.22	2.71
		±12.5		±13.8		±0.29	±0.08	±0.28
		(154–187)		(103–152)		(2.7–3.29)	(2.14–2.31)	(2.45–3)
BUI	0.50	1.5	0.98	1.6	0.96	1.79	1.06	1.33
		±12.5		±13.8		±0.13	±0.05	±0.18
		(154–187)		(103–152)		(1.63–1.92)	(1–1.13)	(1.22–1.54)
DUI	1.23		1.47		1.55	3.34	1.69	2.34
						±0.24	±0.11	±0.16
						(3–3.56)	(1.6–1.84)	(2.15–2.44)
LDII	19.74		18.86		19.60	38.6	27.01	30.09
						±1.77	±0.7	±1.04
						(37.1–41.11)	(26.08–27.	(29.17–31.22)
LDEI	13.74		17.62		14.68	31.06	22.35	24.64
						±1.41	±0.42	±0.04
						(29.99–32.99	(21.9–22.9)	(24.59–24.67)
CLMaM	4.89		4.70		4.63	9.34	5.96	9.05
						±0.55	±0.1	±0.49
						(8.54–9.82)	(5.8–6.02)	(8.5–9.45)
BLM	1.61		1.32		1.61	2.88	2.09	2.93
						±0.2	±0.11	±0.28
						(2.67–3.14)	(2.02–2.25)	(2.62–3.18)
						(2.67–3.14)	(2.02–2.25)	(2.62–3.18)

Discussion

Several traits support the conclusion that *Waiomys mamasae* is specialized to a lifestyle of semi-aquatic feeding on invertebrates. The sole specimen was collected while swimming in a stream and the local people of Mamasa indicated to us that, although uncommonly ovserved, it is always found in streams. According to Mamasan legend the aquatic affinities of *Waiomys mamasae* imbue it with powers to protect homes from fire and hence people have a custom of preserving specimens in their homes. The mouth and stomach of the type specimen contained only stream invertebrates, specifically taxa that cling to the surfaces of rock, indicating that the species forages in streams and likely dives while foraging. Although the hindfeet of *Waiomys* lack any webbing or hairs on the lateral margins of the feet, the ventral vibrissae of the tail are characteristic of other semi-aquatic small mammals including *Crossomys* and *Nectogale* (Voss 1988). Compared to its terrestrial invertebrate-eating counterparts on Sulawesi, i.e. shrew rats, *Waiomys* has several features that Voss (1988) identified as characteristic of semi-aquatic, carnivorous small mammals: (1) stiffer and denser mystacial vibrissae; (2) a reduced philtrum; (3) smaller pinnae that are covered in hair; (4) long, stiff hairs on the ventral surface of the tail; (5) metatarsals ordered in size from IV>III>II>V>I (similar to *Hydromys*); (6) large, ovate infraorbital foramina; and (7) a large foramen magnum. The reduced pinnae and soft dense fur are characteristic of the montane semi-aquatic murines of New Guinea, suggesting convergence to this particular ecological condition.

Our phylogenetic analyses demonstrated that *Waiomys mamasae* is related to terrestrial carnivorous rodents of Sulawesi and is not closely related to other semi-aquatic rodents in Murinae. The discovery of a novel origin of a semi-aquatic, invertebrate-eating murine rodent provides another strong example of convergent evolution in the Indo-Australian Archipelago, where previously, semi-aquatic rodents were known only from the continent of Sahul. In both cases, semi-aquatic rodents are allied to an endemic group of invertebrate-eating, terrestrial rodents, suggesting that opportunities for semi-aquatic lifestyles in murines of the Indo-Australian Archipelago are linked to adaptations to carnivory.

Biodiversity of Sulawesi. The alpha-diversity of murine rodents from Sulawesi is vastly underestimated. Since 1969, nine species descriptions have been published. These are largely based on fieldwork from the 1970's and detailed examination of museum specimens, with some descriptions based on a single specimen (Musser 1969; Musser 1981; Musser 1982; Musser 1991; Musser & Durden 2002; Musser 2014). Some of these publications include reference to additional undescribed species (e.g. Musser 1982) and hence more descriptions are expected. In 2012 two species (one a new genus) were described from specimens recently collected from Sulawesi (Esselstyn *et al.* 2012; Mortelliti *et al.* 2012). The description here, of *Waiomys,* brings the number of endemic murine rodent genera to 12. Moreover, the indication by local residents that they collect and preserve *Waiomys* as talismans, to the complete ignorance of the scientific world, is further indication of how limited scientific knowledge of Sulawesi's biodiversity remains. In sum, these circumstances highlight the degree to which both alpha-diversity and eco-morphological diversity of the murine rodents of Sulawesi are underrepresented by current taxonomy.

Both of the recently described Sulawesi endemic murine genera (*Waiomys* and *Paucidentomys*) were collected from highlands of the southern portion of the west-central region of Sulawesi's central core. The west-central region extends west from Lake Poso and south from Palu to Mt. Latimojong (Musser *et al.* 2010). Studies of tarsiers suggest that the west-central region may represent an area of endemism distinct from the east-central region (Merker *et al.* 2009). However, few systematic surveys of small mammals have been conducted in the highlands of the region and the geographic limits of species are unknown. The discovery of *Waiomys* and *Paucidentomys* and their apparent absence from the relatively intensively studied areas around Lore Lindu in the east-central region (reviewed in Musser 2014), lend further support to the biogeographic significance of the west-central highlands of Sulawesi's central core.

Conservation. In the highlands of west-central Sulawesi, the high plateau of Mount Gandangdewata and the Quarles Range north of Mamasa is a prime example of old-growth tropical forest in need of biological inventory. It represents the largest intact area of old growth forest on Sulawesi (Cannon *et al.* 2007) and protects a massive watershed providing water to numerous surrounding communities. During our surveys of small mammals in 2011 and 2012 at localities from 200 – 2600 meters in elevation, we detected at least 22 murine species. We encountered most of this diversity in forests above 1500 m, where we surveyed parts of Mt. Gandangdewata north of the village of Rantepangko. The excellent condition of forests in this area is in no small part a result of the cultural practices of the local people of Mamasa who limit clearing for plantations or other agriculture to areas below 1500 meters. However, the persistence of these forests, despite their remoteness, is uncertain, particularly because of the high mineral value of the region and the expansion of development in the new province of Sulawesi Barat.

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APPENDIX A. Specimens examined.

Baiyankamys shawmayeri: AM M8661
Crossomys moncktoni: AM M14163, AM M15454, AM M8652, AM M9543
Echiothrix leucura: AMNH 101243, AMNH 153013, AMNH 225680, AMNH 225685, MZB 27875
Hydromys hussoni: AM M18627
Hydryomys chrysogaster: NMV C25843, NMV C26872, NMV C32103, NMV C32104
Melasmothrix naso: FMNH 213284, FMNH 213447, FMNH 213448, NMV C37064
Parahydromys asper: AM M14164, AM M15370, AM M9541
Paucidentomys vermidax: FMNH 213102, MZB 35001
Sommeromys macrorhinos: AMNH 226956, MZB 34758, MZB 34903, NMV C37074
Tateomys macrocercus: FMNH 213450, NMV C37080, NMV C37081
Tateomys rhinogradoides: FMNH 213338, FMNH 213434, NMV C37082, NMV C37083

APPENDIX B. GenBank accession numbers for sequences used in this study.

Taxon	Voucher	Voucher Institution	cytb	IRBP	GHR	RAG1	BRCA1
Abeomelomys sevia	KUMNH 161033	University of Kansas Natural History Museum	EU249730	EU349832	EU349793	EU349879	EU349682
Anisomys imitator	ABTC 45107	South Australian Museum	DQ019090	EU349833	DQ019052	DQ023471	na
Apodemus agrarius	MVZ 159220	Museum of Vertebrate Zoology	EU349733	AB096842	DQ019054	DQ023472	EU349658
Apomys datae	FMNH 167243	Field Museum of Natural History	HM371072	EU349836	KJ607288	KC953478	KC953158
Apomys hylocoetes	FMNH 147871/FMNH 148149	Field Museum of Natural History	AY324469	KC953357	AY294915	AY294942	AY295000
Archboldomys luzonensis	EAR 1826	Eric A Rickart	EU349736	EU349956	EU349794	DQ023466	EU349675
Arvicanthis neumanni	H894	na	EU349737	KC953358	AY294918	AY294946	EU349648
Bandicota bengalensis	T065	na	AM408336	AM408331	AM910945	na	na
Bandicota savilei	R1191	na	HM217385	HM217665	na	na	na
Batomys granti	EAR 1822/EAR 2001	Eric A Rickart	EU349738	EU349838	AY294917	AY241461	AY295002
Berylmys berdmorei	R3618	na	HM217432	HM217639	na	na	na
Berylmys bowersi	MVZ 186482/T-861	Museum of Vertebrate Zoology	AM408337	AM407896	DQ019056	DQ023457	KC953160
Bullimus bagobus	USNM 58789/USNM 458785/USNM 458789	United States National Museum	DQ191472	DQ191498	GQ405369	na	na
Bullimus gamay	FMNH 154823/FMNH 154821	Field Museum of Natural History	DQ191473	DQ191499	GQ405370	na	na
Bullimus luzonicus	FMNH 169127/FMNH 167310	Field Museum of Natural History	DQ191474	DQ191500	GQ405371	na	na
Bunomys chrysocomus	ABTC 65755	South Australian Museum	EU349704	EU349839	EU349795	EU349880	EU349667
Carpomys phaeurus	FMNH 175565	Field Museum of Natural History	DQ191475	DQ191501	GQ405373	na	na
Chiromyscus chiropus	ABTC 69097	South Australian Museum	EU349705	EU349840	EU349796	EU349881	EU349665
Chiropodomys gliroides	FMNH 212935	Field Museum of Natural History	KJ607274	KJ607299	KJ607289	na	KJ607263
Chiruromys vates	ABTC 43096	South Australian Museum	KJ607275	KJ607300	KJ607290	na	na
Chrotomys gonzalesi	EAR 1850	Eric A Rickart	EU349742	EU349843	KJ607291	EU349884	na
Chrotomys sibuyanensis	FMNH 145701	Field Museum of Natural History	AY687862	DQ191504	GQ405376	na	na
Chrotomys silaceus	FMNH 169133/FMNH 175725	Field Museum of Natural History	AY687859	DQ191502	GQ405377	na	na
Chrotomys whiteheadi	FMNH 193962	Field Museum of Natural History	AY687864	JQ898074	na	na	na
Conilurus penicillatus	ABTC 7411	South Australian Museum	EU349743	EU349844	DQ019057	DQ023467	EU349694
Crateromys heaneyi	CMC 776/CMNH M628	Carnegie Museum of Natural History	DQ191476	DQ191505	GQ405378	na	na
Crossomys moncktoni	ABTC 46614	South Australian Museum	KJ607276	KJ607301	KJ607292	KJ607310	na
Crunomys celebensis	NMV C37047	Museum Victoria	KC878028	KC878203	KC878172	KJ607311	KJ607264

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APPENDIX B. (Continued)

Taxon	Voucher	Voucher Institution	cytb	IRBP	GHR	RAG1	BRCA1
Crunomys melanius	FMNH 147105	Field Museum of Natural History	DQ191477	DQ191506	GQ405379	na	na
Crunomys suncoides	FMNH 147942	Field Museum of Natural History	DQ191478	DQ191507	na	na	na
Dacnomys millardi	MVZ 186519	Museum of Vertebrate Zoology	KC878029	KC878206	DQ019058	DQ023459	KC953169
Deomys ferrugineus	FMNH 149427/AMNH 269864	Field Museum of Natural History/American Museum of Natural History	EU349745	KC953373	AY294922	AY241460	AY295007
Diplothrix legata	HS 1163	Hitoshi Suzuki	AB033696	AB033706	EU349799	EU349885	EU349670
Gerbilliscus robustus	FMNH 158105/FMNH 151230	Field Museum of Natural History	AJ875235	AY326113	AY294920	AY294949	AY295005
Gerbillus gerbillus	CMNH 113822/CMNH 113823	Carnegie Museum of Natural History	JN652802	EU349846	DQ019049	DQ023452	EU349700
Grammomys ibeanus	FMNH 151235	Field Museum of Natural History	KJ607277	KC953380	EU349801	KC953503	KC953174
Heimyscus fumosus	MNHN 2001-76/MNHN 2001-064	Museum National d'Histoire Naturelle	AF518333	DQ022397	AM910953	na	na
Hybomys univittatus	CMNH 108044/CMNH 108039	Carnegie Museum of Natural History	KJ607278	KC953383	DQ019059	KC953508	KC953181
Hydromys chrysogaster	ABTC 45619/KUMNH 160729/KUMNH 160730	South Australian Museum/Univ. Kansas Museum of Natural History	EU349748	EU349849	EU349804	EU349890	EU349699
Hyomys goliath	ABTC 42697	South Australian Museum	EU349710	KC953384	EU349805	EU349891	EU349679
Leggadina forresti	ABTC 36085	South Australian Museum	EU349751	EU349850	DQ019061	DQ023468	EU349686
Leopoldamys edwardsi	MVZ 186501	Museum of Vertebrate Zoology	KJ607279	HM217687	na	KJ607312	na
Leopoldamys neilli	R4486	na	HM217460	HM217697	na	na	na
Leopoldamys sabanus	CMNH 102138	Carnegie Museum of Natural History	KJ607280	KJ607302	DQ019063	KC953513	KC953186
Leporillus conditor	ABTC 13335	South Australian Museum	EU349711	EU349851	EU349806	EU349892	EU349692
Leptomys elegans	ABTC 45741	South Australian Museum	EU349712	EU349852	EU349807	EU349893	EU349697
Limnomys bryophilus	FMNH 147970	Field Museum of Natural History	DQ191479	DQ191508	GQ405380	na	na
Limnomys sibuanus	FMNH 147947	Field Museum of Natural History	DQ191480	DQ191509	GQ405381	na	na
Lophuromys aquilus	FMNH 144777	Field Museum of Natural History	EU349754	AY326091	AY294921	AY294950	AY295006
Lorentzimys nouhuysi	ABTC 42732/KUMNH 160731	South Australian Museum/University of Kansas Natural History Museum	EU349713	KC953392	EU349808	EU349894	EU349680
Macruromys major	ABTC 43909	South Australian Museum	EU349714	EU349853	EU349809	EU349895	EU349678
Malacomys longipes	CMNH 108118	Carnegie Museum of Natural History	EU349757	DQ022393	DQ019064	DQ023474	EU349656
Mallomys rothschildi	ABTC 47402	South Australian Museum	EU349715	EU349854	EU349810	EU349896	EU349681
Mammelomys lanosus	ABTC 47208	South Australian Museum	EU349716	EU349855	EU349811	EU349897	KC953188
Mastacomys fuscus	ABTC 07354	South Australian Museum	EU349717	EU349856	EU349812	EU349898	EU349687

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APPENDIX B. (Continued)

Taxon	Voucher	Voucher Institution	cytb	IRBP	GHR	RAG1	BRCA1
Mastomys erythroleucus	ABTC 65697	South Australian Museum	EU349718	KJ607303	AM910959	KC953519	KC953189
Maxomys bartelsii	ABTC 48063	South Australian Museum	EU349762	EU349857	DQ019066	DQ023460	EU349666
Maxomys cf. hellwaldii	FMNH 213372	Field Museum of Natural History	KC878039	KC878212	KC878174	KJ607313	na
Maxomys dollmani	MVZ 225725	Museum of Vertebrate Zoology	KC878035	KC878213	KC878175	na	KJ607265
Maxomys hellwaldii	MVZ 225768	Museum of Vertebrate Zoology	KC878044	KC878214	KC878176	KJ607314	KJ607266
Maxomys hylomyoides	FMNH 212980	Field Museum of Natural History	KC878050	KC878218	KC878179	KJ607315	na
Maxomys moi	ROM 111318	Royal Ontario Museum	KC878056	KC878219	KC878180	na	na
Maxomys muschenbroekii	MZB 34728	Museum Zoologicum Bogoriense	KJ607281	KJ607304	KJ607293	KJ607316	KJ607267
Maxomys pagensis	MZB 28335	Museum of Vertebrate Zoology	KC878128	KC878225	KC878186	na	na
Maxomys panglima	KUMNH 165356	University of Kansas Natural History Museum	KC878129	KC878226	KC878187	KJ607317	KJ607268
Maxomys rajah	MVZ 192210	Museum of Vertebrate Zoology	KC878137	KC878227	na	KJ607318	na
Maxomys surifer	ROM 107723	Royal Ontario Museum	KC878157	KC878234	KC878193	na	KJ607269
Maxomys whiteheadi	ROM 113074	Royal Ontario Museum	KJ607282	KJ607305	KJ607294	na	na
Melasmothrix naso	NMV C37064	Museum Victoria	KJ607283	KJ607306	KJ607295	KJ607319	KJ607270
Melomys rufescens	ABTC 43071	South Australian Museum	EU349720	EU349860	EU349816	EU349902	EU349690
Mesembriomys gouldii	ABTC 07412	South Australian Museum	EU349721	EU349861	EU349817	EU349903	EU349693
Micaelamys namaquensis	RA 12	na	DQ019089	AM408330	AY294914	AY294941	EU349649
Micromys minutus	AB 033710	Hitoshi Suzuki	AB201995	HS 1148	EU349818	EU349904	EU349664
Mus musculus	Lab colony, strain balb/c	na	AF520621	EU349863	M33324	AY241462	EU349657
Mus pahari	AMCC 110800	American Museum of Natural History	EU349767	EU349864	KC953280	EU349906	na
Niviventer confucianus	USNM 574365	United States National Museum	JF714942	KC953416	KC953293	KC953540	na
Niviventer cremoriventer	ROM F35796	Royal Ontario Museum	KJ607284	KC953417	DQ019067	KC953541	KC953198
Niviventer culturatus	MVZ 180686	Museum of Vertebrate Zoology	GU479941	KC953418	DQ019068	DQ023458	KC953199
Notomys fuscus	ABTC 34070	South Australian Museum	EU349768	EU360811	KC953295	EU349907	na
Oenomys hypoxanthus	CMNH 102549/CMNH 102548	Carnegie Museum of Natural History	EU349769	KC953425	DQ019069	DQ023464	EU349654
Otomys angoniensis	ABTC 65830	South Australian Museum	EU349722	AM408325	EU349819	EU349909	EU349647
Parahydromys asper	ABTC 45798	South Australian Museum	EU349723	EU349866	EU349820	EU349910	EU349698
Paramelomys levipes	KUMNH 160736	University of Kansas Natural History Museum	EU349772	EU349867	EU349821	EU349911	EU349689
Parotomys brantsii	H656	na	DQ019111	KC953432	AY294912	AY294939	EU349646

……*continued on the next page*

APPENDIX B. (Continued)

Taxon	Voucher	Voucher Institution	cytb	IRBP	GHR	RAG1	BRCA1
Paruromys dominator	NMV C37024	Museum Victoria	KJ607285	KJ607307	KJ607296	KJ607320	KJ607271
Paucidentomys vermidax	FMNH 213102	Field Museum of Natural History	KJ607286	KJ607308	KJ607297	KJ607321	KJ607272
Phloeomys pallidus	WCS 931040	New York Bronx Zoo	EU349775	WCS 931040	DQ019070	DQ023480	EU349644
Pogonomys loriae	KUMNH 160668	University of Kansas Natural History Museum	EU349776	KC953441	EU349823	EU349912	EU349683
Pogonomys macrourus	ABTC 43144	South Australian Museum	EU349727	EU349869	EU349824	EU349913	EU349684
Pogonomys sylvestris	KUMNH 161024	University of Kansas Natural History Museum	na	GQ405365	GQ405389	na	na
Praomys jacksoni	CMNH 102583/CMNH 102584	Carnegie Museum of Natural History	EU349778	KC953443	DQ019071	DQ023477	EU349663
Praomys tullbergi	CMNH 108199	Carnegie Museum of Natural History	EU349779	DQ022413	DQ019072	DQ023478	EU349662
Pseudohydromys ellermani	ABTC 43920	South Australian Museum	EU349763	EU349858	EU349814	EU349900	EU349695
Pseudomys australis	ABTC 35951	South Australian Museum	AM910936	EU349870	DQ019073	DQ023469	EU349688
Rattus everetti	FMNH 142350	Field Museum of Natural History	DQ191485	DQ191513	na	na	na
Rattus exulans	NK 80010	na	NK 80010	KC953446	DQ019074	DQ023455	na
Rattus niobe	ABTC 42489	South Australian Museum	na	HQ334580	na	HQ334648	HQ334394
Rattus norvegicus	Sprague-Dawley laboratory strain	na	EU349782	AB033709	JF412704	AY294938	EU349671
Rattus rattus	T820/T660/CACG A65	Centre for Animal Conservation Genetics	na	HM217606	AM910976	HQ334643	na
Rattus villosissimus	ABTC 00549	South Australian Museum	EU349729	HQ334576	EU349826	EU349915	EU349673
Rhynchomys isarogensis	EAR 1857/EAR 1840	Eric A Rickart	EU349784	KC953453	DQ019075	AY294944	EU349677
Solomys salebrosus	ABTC 64864	South Australian Museum	EU349785	EU349872	EU349827	EU349917	EU349691
Soricomys leonardocoi	FMNH 190982	Field Museum of Natural History	JQ898062	JQ898077	na	na	na
Soricomys montanus	FMNH 193521	Field Museum of Natural History	JQ898066	JQ898076	na	na	na
Soricomys musseri	FMNH 189507	Field Museum of Natural History	JQ898071	JQ898075	na	na	na
Srilankamys ohiensis	na	na	JN009856	JN009857	JN009860	na	na
Stochomys longicaudatus	CMNH 108122/CMNH 90877	Carnegie Museum of Natural History	EU349786	KC953458	DQ019076	KC953585	EU349652
Sundamys muelleri	MVZ 192334	Museum of Vertebrate Zoology	EU349787	AY326111	DQ019077	DQ023456	EU349668
Tarsomys apoensis	FMNH 148178	Field Museum of Natural History	DQ191491	DQ191516	GQ405395	na	na
Uranomys ruddi	CMNH 113723/CMNH 113726	Carnegie Museum of Natural History	HM635858	EU360812	DQ019051	DQ023454	EU349642
Uromys caudimaculatus	MVZ 193100	Museum of Vertebrate Zoology	EU349789	EU349875	DQ019079	DQ023470	na
Waiomys mamasae	MZB 37000 / NMV C37027	Museum Zoologicum Bogoriense	KJ607287	KJ607309	KJ607298	KJ607322	KJ607273
Xeromys myoides	ABTC 30709	South Australian Museum	EU349790	EU349877	EU349830	EU349920	EU349696
Zelotomys hildegardeae	CMNH 102659/CMNH 102661	Carnegie Museum of Natural History	EU349791	DQ022396	DQ019080	DQ023476	EU349661
Zyzomys argurus	ABTC 07908	South Australian Museum	EU349792	EU349878	EU349831	EU349921	EU349685