



A new genus and species of omnivorous rodent (Muridae: Murinae) from Sulawesi, nested within a clade of endemic carnivores

KEVIN C. ROWE,* ANANG S. ACHMADI, AND JACOB A. ESELSTYN

Sciences Department, Museum Victoria, Melbourne, Victoria 3001, Australia (KCR)

Museum Zoologicum Bogoriense, Research Center for Biology, Cibinong, Jawa Barat 16911, Indonesia (ASA)

Museum of Natural Science, 119 Foster Hall, Louisiana State University, Baton Rouge, LA 70803, USA (JAE)

Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA (JAE)

* Correspondent: KRowe@museum.vic.gov.au

We document a new genus and species of rodent (Muridae) from the west-central region of Sulawesi Island, Indonesia. The new taxon is known only from the type locality at around 1,600 m elevation on Mt. Gandangdewata of the Quarles Range, in the district of Mamasa. With phylogenetic analyses of DNA sequences from 5 unlinked loci, we infer that the new taxon is sister to the Sulawesi water rat, *Waiomys mamasae*, and nested within a clade of rodents from Sulawesi that otherwise feed exclusively on invertebrates. The new species is distinguishable from other rodents of Sulawesi by the combination of its small, slender body; soft, gray–brown fur; small, rounded ears; long, sparsely haired tail; long, fine mystacial vibrissae; gracile cranium; short rostrum; pronounced lacrimal bone; prominent, sickle-shaped coronoid process; and pale orange enamel on labial surface of incisors. Unlike its closest relatives, the new species feeds on both plant and animal matter, and may represent a rare evolutionary reversal of traits associated with a carnivorous diet in murids.

Kami mendokumentasikan genus dan spesies hewan pengerat (Muridae) baru dari bagian tengah-barat Pulau Sulawesi, Indonesia. Takson baru ini hanya diketahui dari lokasi spesimen tipe pada ketinggian sekitar 1600 meter di Gunung Gandangdewata yang termasuk dalam rangkaian Pegunungan Quarlesi, Kabupaten Mamasa. Analisa filogenetik pada sekuen DNA dari 5 loci yang tidak terhubung menunjukkan bahwa takson baru ini merupakan kerabat dekat tikus air Sulawesi, *Waiomys mamasae*, dan berada pada kelompok hewan pengerat lainnya dari Sulawesi yang hanya memakan invertebrata. Spesies baru ini dibedakan dari hewan pengerat lainnya dari Sulawesi berdasarkan kombinasi beberapa karakter yaitu: tubuh ramping; rambut lembut abu-abu coklat; telinga kecil dan membulat; ekor panjang dan berambut jarang; kumis panjang dan tipis; tengkorak ramping; tulang hidung pendek; tulang lakrimal jelas; *coronoid process* tampak jelas dan berbentuk bulan sabit; dan enamel berwarna oranye muda pada penampang labial dari gigi seri. Tidak seperti kerabat terdekatnya, species baru ini memakan unsur tumbuhan maupun hewan, dan kemungkinan besar menunjukkan proses evolusi langka yang berbalik dari ciri yang diasosiasi dengan salah satu pemakan daging pada jenis Muridae.

Key words: biodiversity, Indonesia, molecular phylogeny, shrew rat, taxonomy, Wallacea

© 2016 American Society of Mammalogists, www.mammalogy.org

With 778 described species, the Muridae is the most diverse mammalian family and comprises more than 13% of extant mammal species (Musser and Carleton 2005). About one-half of all species in the Muridae are endemic to the Indo-Australian Archipelago (IAA), where diverse communities evolved from independent radiations in continental southeast Asian islands (Sunda), continental Australia (Sahul), the Philippines, and Wallacea (Jansa et al. 2006; Rowe et al. 2008, 2011; Schenk et al. 2013). The island of Sulawesi is the largest landmass in

Wallacea and centrally positioned relative to all other centers of murid diversity and endemism in the IAA.

On Sulawesi, the Muridae is represented by 47 described species in 17 genera, among which all species and 13 genera are endemic (Eselstyn et al. 2015). However, these diversity figures are clear underestimates, as evidenced by recent discoveries of new species and genera on Sulawesi (Musser and Durden 2002; Eselstyn et al. 2012; Mortelliti et al. 2012; Musser 2014; Rowe et al. 2014; Eselstyn et al. 2015; this

paper). Taxonomically, the Muridae of Sulawesi includes representatives of 8 divisions (*Crunomys*, *Dacnomys*, *Echiothrix*, *Maxomys*, *Melasmotherix*, *Micromys*, *Pithecheir*, and *Rattus*), all within the subfamily Murinae (Musser and Carleton 2005; Schenk et al. 2013). However, phylogenetic analyses have shown that only the *Rattus* and *Dacnomys* divisions form a natural grouping (Rowe et al. 2008; Achmadi et al. 2013; Schenk et al. 2013; Rowe et al. 2016). For instance, the 3 genera and 5 species of the *Echiothrix* and *Melasmotherix* divisions are part of an endemic radiation of rodents on Sulawesi that also includes *Sommeromys* Musser and Durden, 2002, a member of the *Crunomys* Division, but not species of the genus *Crunomys* Thomas, 1898. Three recently discovered genera that were not known at the time murid divisions were last formally designated are also members of this Sulawesi radiation, resulting in a total of 9 species in the clade (Musser and Carleton 2005; Esselstyn et al. 2015; Rowe et al. 2016). These species include terrestrial shrew rats and an amphibious water rat, all of which feed primarily on invertebrates (i.e., they are carnivorous), and they represent an example of dietary convergence with independently evolved species from the Philippines and New Guinea (Rowe et al. 2016). All but 2 of the 7 genera in this endemic Sulawesi radiation are currently thought to be monotypic, including the recently discovered *Hyorhinomys* Esselstyn et al., 2015; *Paucidentomys* Esselstyn et al., 2012; and *Waiomys* Rowe et al., 2014. The distinction of these monotypic lineages as genera is supported by the large morphological disparity among taxa without characters suggesting close relationships to previously named genera (Fig. 1; Esselstyn et al. 2015). Furthermore, with few exceptions, phylogenetic analyses of Sulawesi shrew rats have not supported clear relationships among these genera (Rowe et al. 2014; Esselstyn et al. 2015; Rowe et al. 2016), making it difficult to designate natural groupings that contain multiple species.

Here we describe a new genus and species of omnivorous rodent from Sulawesi. Molecular phylogenetic analyses place the new animal within the otherwise carnivorous clade of shrew rats and the water rat, all of which are endemic to Sulawesi.

MATERIALS AND METHODS

Tissue sampling and genetic analysis.—Tissue samples were collected in the field and stored in 70% ethanol. We sequenced fragments of 5 unlinked loci including the mitochondrial cytochrome-*b* gene and 4 autosomal exons, including exon 11 of breast cancer 1 (BRCA1); exon 1 of retinol-binding protein 3 (IRBP); exon 1 of recombination activating gene 1 (RAG1); and exon 1 of growth hormone receptor (GHR). All loci were amplified and sequenced from individuals of the new species using published primers and procedures (Rowe et al. 2008, 2011). We aligned sequences from the holotype of the new species (GenBank accessions KU375185–KU375189) to those from 137 other species from the family Muridae representing the subfamilies Gerbillinae (2 species), Deomyinae (3 species), and most divisions within

the Murinae (132 species). Sequences from these 137 species are the same as reported in a previously published study (Rowe et al. 2016; Supporting Information S1) and available on GenBank. We aligned sequences in CodonCode ver. 5.0.1 (CodonCode Corporation, Dedham, Massachusetts) 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). We conducted phylogenetic analyses 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 implemented on the CIPRES portal (Miller et al. 2010), with parameters set in MrBayes following Rowe et al. (2011) and using partitions and models selected by PartitionFinder. We completed 2 independent runs of 4 chains each for 4×10^7 generations, with samples drawn every 1,000 generations. Likelihood analyses in RAxML were completed with 1,000 bootstrap pseudoreplicates using the models selected by PartitionFinder.

To consider the divergence of the new species from other murid rodents in a time-calibrated phylogeny, we used a relaxed molecular clock approach in BEAST v.2.1.3 (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 3 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 *Arvicantis* (11.1–12.3 Ma), (2) *Arvicantis* 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 data sets (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 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 2,000 generations. We evaluated convergence and assessed sampling adequacy in Tracer v1.5. We used TreeAnnotator to combine trees and discarded the first 20% of trees as burn-in.

Morphological characters.—Specimens examined in this study are deposited in the collections of the Australian Museum, Sydney (AM); the American Museum of Natural History, New York (AMNH); the Field Museum of Natural History, Chicago (FMNH); Museum Victoria, Melbourne (NMV); Louisiana

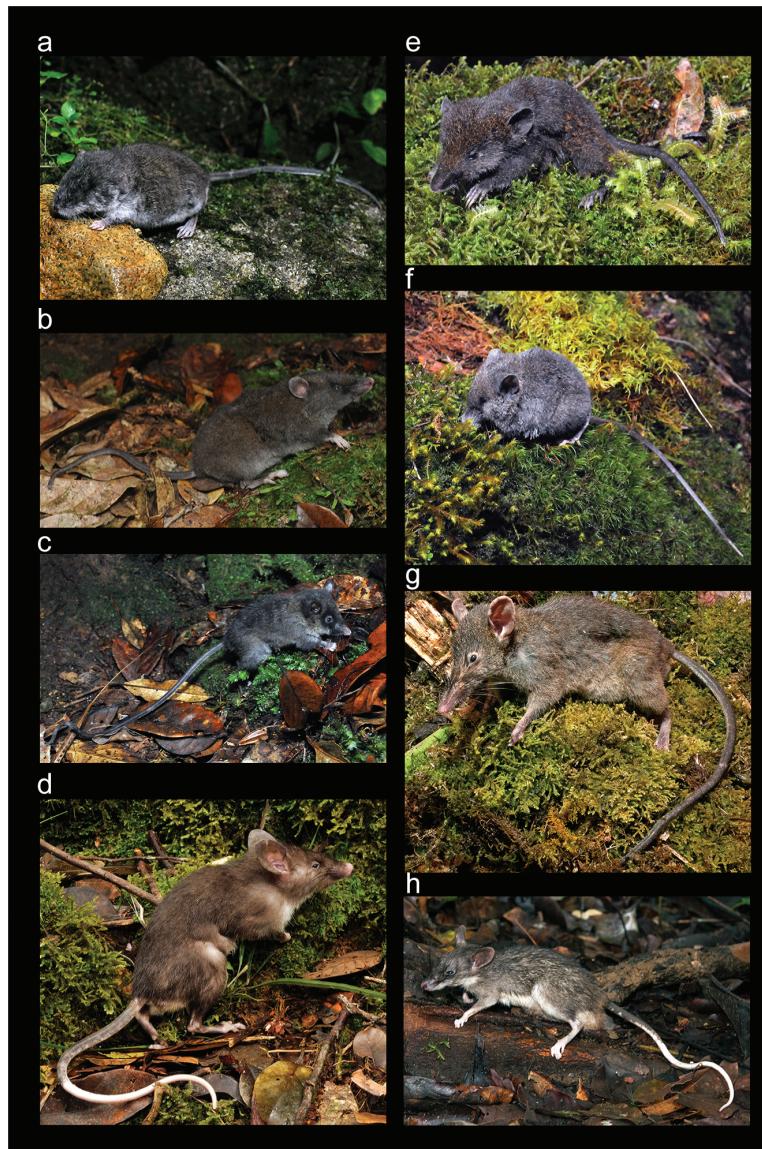


Fig. 1.—Species in the endemic Sulawesi clade of carnivorous rodents: a) *Waiomys mamasae*, b) *Tateomys rhinogradoides*, c) *Sommeromys macrorhinos*, d) *Hyorhinomys stuempkei*, e) *Melasmotherix naso*, f) *Tateomys macrocercus*, g) *Paucidentomys vermidax*, and h) *Echiothrix centrosa* (*E. leucura* not shown). Photo credits: Kevin C. Rowe.

State University Museum of Natural Science, Baton Rouge (LSUMZ); and Museum Zoologicum Bogoriense, Bogor (MZB). Registration numbers for all specimens we examined are listed in Appendix I.

Phylogenetic analyses, presented below, supported a closer relationship of the new species with the shrew rats and water rat of Sulawesi than to any other murine rodents. Thus, we made qualitative and quantitative morphological comparisons between specimens of the new species and those of the water rat and all species of Sulawesi shrew rat. Our comparisons thus included *Echiothrix centrosa* Miller and Hollister, 1921; *Echiothrix leucura* Gray, 1867; *Hyorhinomys stuempkei* Esselstyn et al., 2015; *Melasmotherix naso* Miller and Hollister, 1921; *Paucidentomys vermidax* Esselstyn et al., 2012; *Sommeromys macrorhinos* Musser and Durden, 2002; *Tateomys macrocercus* Musser, 1982; *Tateomys rhinogradoides* Musser, 1969; and *Waiomys mamasae* Rowe et al., 2014.

We collected 24 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), postpalatal 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 1st maxillary molar (CLMM), breadth of the 1st upper 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 1st mandibular molar (CLMaM), and breadth of the 1st mandibular molar (BLM). From freshly caught specimens, we also report standard

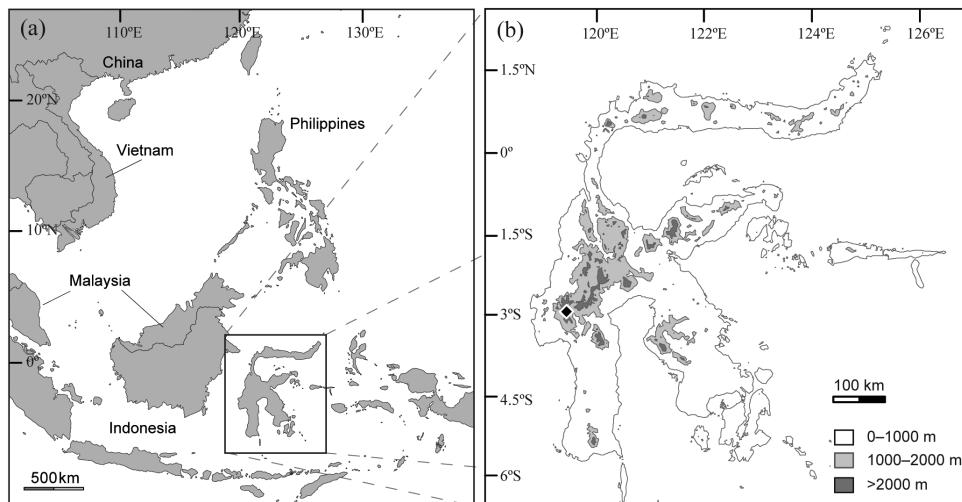


Fig. 2.—Maps of a) Southeast Asia, showing the position of Sulawesi Island and b) Sulawesi, showing the type locality of *Gracilimus radix* (Mount Gandangdewata [diamond]).



Fig. 3.—Habitat on Mount Gandangdewata, where the type series of *Gracilimus radix* was collected. All specimens were collected within 500 m of the photo. Photo credit: Kevin C. Rowe.

external measurements including total length (TTL), tail length (Tail), head and body length (HB), hindfoot length including the claws (HF), ear length (Ear), and mass (Mass) in grams. Skull measurements follow those diagrammed in [Musser and Heaney](#)

(1992) and [Musser and Durden \(2002\)](#). External measurements were taken from specimen tags and the field notes of collectors.

Fieldwork.—Five specimens of the new genus and species were caught in 30-liter pitfall traps during terrestrial mammal surveys conducted in November 2011 and May 2012 around Mount Gandangdewata in the Quarles Range of the western highlands region of Sulawesi Barat (Barat = West), Indonesia (Figs. 2 and 3).

RESULTS

Phylogenetic analyses.—Concatenation of the 4 exons and 1 mitochondrial locus resulted in an alignment of 5,787 nucleotides. PartitionFinder analyses identified 8 optimal partitions of the data. Partitions did not correspond to individual gene fragments, but represented combinations of codon positions with similar substitution rates spread among genes (Table 1). PartitionFinder estimated that a GTR substitution model provided the best fit for 7 partitions, whereas HKY was preferred for the remaining partition. For all partitions, the best-fit model included a Γ -distributed rate heterogeneity parameter. For 4 models, PartitionFinder also determined that the best model included a parameter representing the proportion of invariable sites. However, this parameter is not recommended for use with RAxML ([Stamatakis 2006](#)) and was only used in the Bayesian analyses. For our MrBayes analyses, the average SD of split frequencies among runs was < 0.01 , the marginal likelihood plateaued, the estimated sample size of all parameters was > 100 , and the potential scale reduction factor for all parameters was close to 1, suggesting that independent chains had converged ([Gelman and Rubin 1992](#)).

Phylogenetic analyses of individual gene trees (Supporting Information S2–S6) and those of the concatenated nuclear and mitochondrial loci (Fig. 4) supported a clade that included the Sulawesi shrew rats, Sulawesi water rat, and the new species of rat described below. Thus, this clade included *E. centrosa*, *H. stuempkei*, *M. naso*, *P. vermidax*, *S. macrorhinos*, *T. macrourcuscus*, *Tateomys rhinogradoides*, *W. mamasae*, and the new

species (Fig. 4). *Echiothrix* is the oldest valid genus name in this group (Gray 1867); we therefore suggest the recognition of this natural group as the Echiothrix Division. However, to avoid confusion with the Echiothrix Division as currently recognized, we refer to this group as the Echiothrix Clade in this manuscript. All concatenated phylogenetic analyses supported: (1) the placement of the new species as sister to the Sulawesi water rat, *W. mamasae*; (2) a sister relationship of

Paucidentomys and *Echiothrix*; (3) a clade containing *Tateomys* and *Melasmotherix*; and (4) the grouping of *Echiothrix*, *Melasmotherix*, *Paucidentomys*, and *Tateomys* in a clade. No analysis recovered strong support (posterior probabilities ≥ 0.95 or bootstrap values $\geq 70\%$) for the placement of *Sommeromys*, *Hyorhinomys*, or the *Waiomys* + new genus clade relative to the other members of the Echiothrix Clade.

SYSTEMATICS

Gracilimus, new genus

Type species.—*Gracilimus radix*, the new species described below.

Diagnosis.—A genus of rodent in the family Muridae, subfamily Murinae, that possesses a slender body; short, soft, dark gray–brown dorsal fur flecked with pale brown; short, soft, gray–brown ventral fur; small eyes; small rounded ears; long, sparsely haired tail representing $\sim 130\%$ of head and body length; short, rounded muzzle; fine and long mystacial vibrissae reaching 50 mm and extending well beyond the pinnae (Fig. 5); small, gracile cranium (Fig. 6); smooth

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

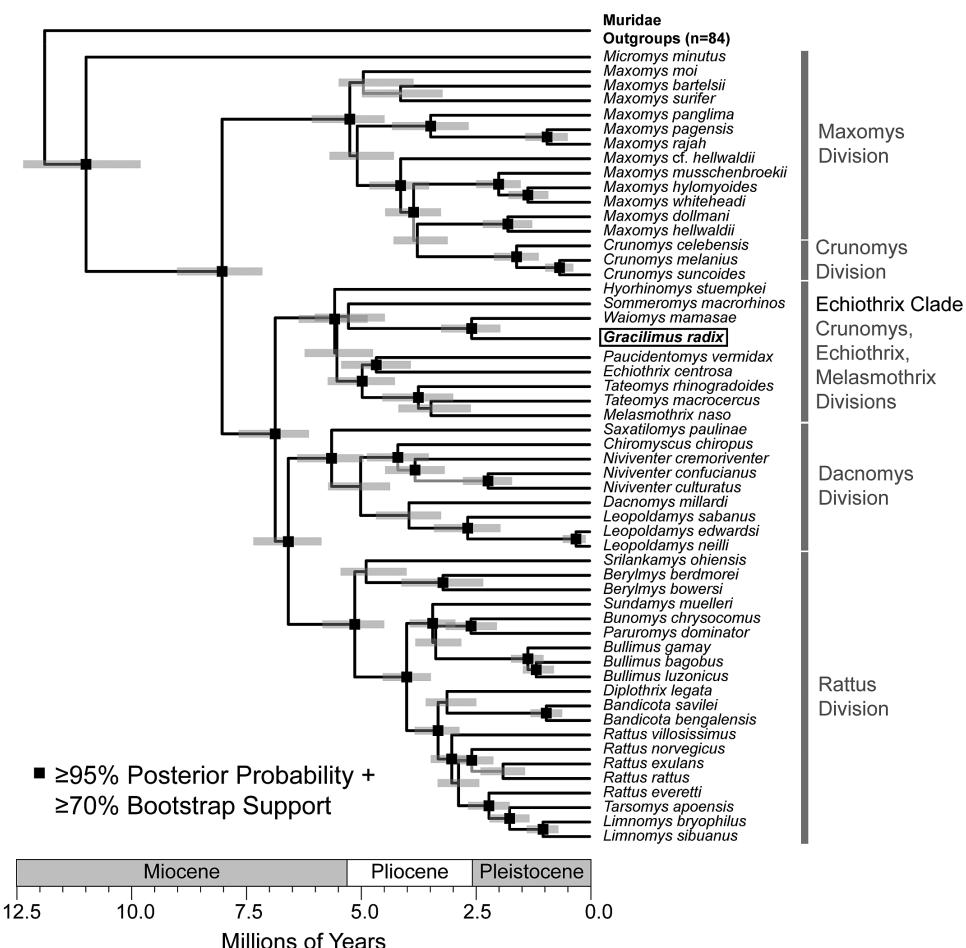


Fig. 4.—Fossil-calibrated, ultrametric phylogeny of the Murinae recovered from BEAST analyses. Calibrated nodes are indicated with an asterisk. The phylogeny was pruned to show the new genus and its closest relatives within Muridae. Outgroups from across Muridae (not shown) are the same as in Rowe et al. 2016. Horizontal gray bars spanning nodes represent the 95% highest posterior densities around date estimates. Black squares on nodes indicate well-supported relationships from MrBayes and RaXML analyses.



Fig. 5.—Holotype of *Gracilimus radix* (MZB 37399) in the field prior to preparation, shown in live pose. Photo credit: Kevin C. Rowe. MZB = Museum Zoologicum Bogoriense, Bogor.

interorbital and postorbital regions without prominent ridges; nasal bones extend ~2 mm beyond the labial margin of the upper incisors; delicate zygomatic arches that flare laterally, just beyond the braincase breadth; pronounced lacrimal bone that projects posteriorly; hamular process of the pterygoid bone that extends beyond the occlusal plane of the molars and bows modestly outward, leaving the mesopterygoid fossa fully visible from a ventral aspect; pterygoid plate present, but not prominent; 3 molars in maxillary and mandibular toothrows; labial surface of upper incisors smooth (i.e., no vertical groove), with pale orange enamel; enamel does not extend to the lateral sides of incisors (i.e., it is barely visible from lateral aspect); cutting edges of upper incisors together form an inverted “V.” Phylogenetic analyses place the genus in a clade containing the Sulawesi rats *Echiothrix*, *Hyorhinomys*, *Melasmotherix*, *Paucidentomys*, *Sommeromys*, *Tateomys*, and *Waiomys* (Fig. 4).

Etymology.—The generic name combines the Latin “*gracilis*” (slender, thin) and “*mus*” (mouse) in reference to the gracile and delicate build of the animal relative to other Sulawesi rodents.

Nomenclatural statement.—A life science identifier (LSID) number was obtained for the new genus and species *G. radix*: urn:lsid:zoobank.org:pub:35235002-24CD-4186-BBAA-1373F185BB4A.

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

Gracilimus radix, new species

Holotype.—NMV C37054/MZB 37399, a female collected in a 30-liter pitfall trap on the morning of 9 November 2011 (Figs. 5–7). The holotype was not lactating and no scars were apparent in the uterine lining, indicating that the specimen was nulliparous. The molars are fully erupted and worn such that their occlusal

surfaces form simple basins, however, the basioccipital-basisphenoid suture is closed but still distinct, suggesting that the specimen was a young adult. The specimen was prepared as a dried skin, cleaned skull, and fluid-preserved carcass. The carcass was fixed in 4% formalin solution and later transferred to 70% ethanol for permanent storage. The skull was initially preserved in 70% ethanol, dried, cleaned by dermestid beetles, and degreased by immersion in 10% ammonia. Separate pieces of liver were preserved in RNALater and archived at NMV (Z21916) and MZB.

Type locality.—Mount Gandangdewata (2.8829°S, 119.3864°E, 1,571 m), Rantepangko, Mamasa, Sulawesi Barat, Indonesia (Figs. 2 and 3).

Paratypes.—Four additional specimens are known (NMV C37053/MZB 37400, NMV C37055/MZB 37401, NMV C36995/MZB 37402, and NMV C36996/MZB 37403). These specimens were collected from within 0.5 km of the type locality on 8 November 2011, 11 November 2011, 4 May 2012, and 5 May 2012, respectively. All 4 paratypes are males. Two were scrotal (NMV C37055 and C36996) and 2 were nonscrotal (NMV C37053 and C36995). In all 4 paratypes, the molars were fully erupted and worn such that their occlusal surfaces form simple basins. In addition, the basioccipital-basisphenoid suture is closed and indistinct in all 4 paratypes, which, together with their molars, suggests that they were all adult. NMV C37053 was prepared as a cleaned skull and fluid-preserved body, whereas the remaining 3 paratypes were each prepared as a skin, skull, and formalin-fixed carcass. For each paratype, separate samples of liver were preserved in RNALater or 70% ethanol and archived at NMV and MZB, respectively.

Distribution.—*Gracilimus radix* is known only from the type locality in lower montane rainforest of the Quarles Range of the western Sulawesi highlands. It has not been collected at other sites in Sulawesi where similar methods (pitfalls) were used, including Mt. Latimojong, Mt. Dako, Mt. Rorekatimbo, Mt. Tompotika,

Mt. Balease, higher elevations on Mt. Gandangdewata, or a nearby low elevation area along the Tiwo River.

Diagnosis.—*radix* is the only species in the genus *Gracilimus*. Thus, generic and specific diagnoses are the same.

Etymology.—The specific epithet uses the Latin “*radix*” (root) to acknowledge the natural history knowledge of the local people of Mamasa, whose name for the animal translates as “root rat.”

Description and comparisons.—We summarize the most distinguishing characters of *G. radix* in Table 2. *G. radix* is a small, slender rodent (Fig. 5; Table 3). It is smaller than its closest known relative, the Sulawesi water rat, *W. mamasae*, which is externally readily distinguishable from *G. radix*, having many adaptations to an amphibious lifestyle (detailed below and in Rowe et al. 2014). *G. radix* is similar in body size to the Sulawesi shrew rats, *M. naso*, *S. macrorhinos*, and

T. macrocercus. It is much smaller than *E. centrosa*, *E. leucura*, *H. stuempkei*, *P. vermidax*, and *T. rhinogradoides*. The body of *G. radix* is noticeably more slender than any of the Sulawesi shrew rats or the Sulawesi water rat.

The upper parts of the pelage of *G. radix* are dark gray–brown and flecked with pale brown. No guard hairs are distinguishable from the underfur, which is similar to the pelage patterns of the soft-furred Sulawesi shrew rats and the water rat. The dorsal hairs are 5–8 mm long, round in cross section, gray at the base, brown in the middle, and pale brown at the tip. The dorsal pelage color of *G. radix* is similar to *S. macrorhinos* and *T. macrocercus*, but more grizzled. The dorsal fur of *G. radix* is soft. It is less dense than the fur of the small Sulawesi shrew rats (*M. naso*, *S. macrorhinos*, and *T. macrocercus*) and the Sulawesi water rat (*W. mamasae*), but denser than the fur of *H. stuempkei*. The ventral hairs of *G. radix* are similar in length



Fig. 6.—Images of the crania and mandibles of the holotype of a) *Gracilimus radix* (MZB 37399) and the holotype of its sister species b) *Waiomys mamasae* (MZB 37000). Photo credits: Kevin C. Rowe. MZB = Museum Zoologicum Bogoriense, Bogor.

Table 2.—Morphological characters of *Gracilimus radix*, and the Echinothrix Clade members with which they are shared.

Character	Shared with
Ear length 10–12% of head and body length	None. <i>Waiomys mamasae</i> < 10%, other species > 13%
Tail length > 125% head and body length	<i>Tateomys macrocercus</i> and <i>Sommeromys macrorhinos</i>
Mystacial vibrissae > 40 mm in length	<i>T. macrocercus</i> and <i>S. macrorhinos</i>
Lacral bone pronounced and projects posteriorly	None. Indistinct in other species
Length of rostrum < 30% of skull length	<i>Waiomys mamasae</i>
Pale orange enamel on labial surface of upper incisors	<i>W. mamasae</i>
Length of the dentary excluding the incisors < 120% of postpalatal length	<i>W. mamasae</i>
Coronoid process prominent and sickle shaped	None. Absent (<i>Hyorhinomys stuempkei</i>), weakly developed (<i>Echinothrix centrosa</i> , <i>E. leucura</i> , <i>Paudentomys vermidax</i>) or not sickle shaped (<i>S. macrorhinos</i> , <i>W. mamasae</i>).

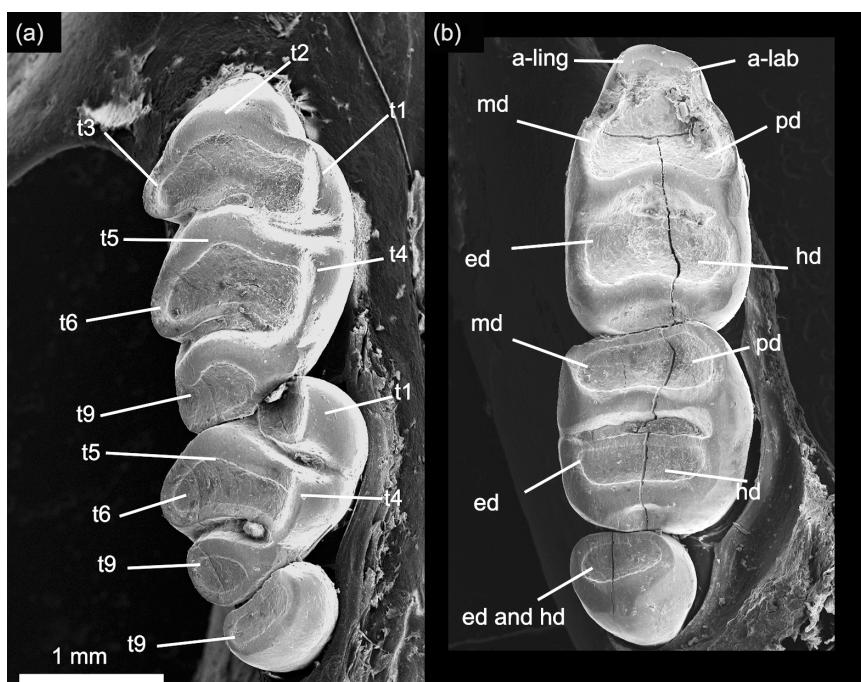


Fig. 7.—Scanning electron micrographs of the a) maxillary (upper) and b) mandibular (lower) right molar rows of the holotype of *Gracilimus radix* (MZB 37399). Anterior is at the top, posterior at the bottom. Cusps are labeled following Musser (1991): a-ling, anterolingual; a-lab, anterolabial; md, metaconid; pd, protoconid; ed, entoconid; and hd, hypoconid. MZB = Museum Zoologicum Bogoriense, Bogor.

to the dorsal hairs, gray at the base, and pale cream or light brown at the tip. Some specimens of *G. radix* contain patches of white hairs on the dorsal or ventral surface. On the limbs, the dorsal pelage coloration of *G. radix* extends nearly to the ankles and wrists, which is similar to the pattern in the small Sulawesi shrew rats.

Commensurate with the body, the limbs of *G. radix* are delicate, similar to the limbs of *S. macrorhinos* and *T. macrocercus*. The hindlimbs of *G. radix* are longer than the forelimbs, but the posture remains that of a general quadrupedal rat. Digits II–V on the forefeet and hindfeet end in a conspicuous fleshy pad bearing a ~2-mm long, sickle-shaped, and laterally compressed claw; the pollex, which is partially fused to the side of the palm, bears a rounded nail. On all digits except the pollex, fine hairs emerge from the base of the claw and extend to nearly the length of the claw (Fig. 8). The claws of *G. radix* are shorter than the claws of *M. naso* and *T. macrocercus* and similar in length to the claws of *S. macrorhinos*. The partial fusion of the

pollex to the side of the palm is shared with the Sulawesi water rat and all Sulawesi shrew rats except *S. macrorhinos*. Three interdigital pads are present on the forefeet, along with distinct thenar and hypothenar pads (Fig. 8a). The thenar is approximately one-half the size of the hypothenar, but similar in size to the 3 interdigital pads. Four interdigital pads are present on the hindfeet, along with a long broad thenar and small hypothenar (Fig. 8b).

The tail of *G. radix* is slender, tapering gently to the tip, and long, on average 30% longer than the head and body length. The relative length of the tail in *G. radix* is shorter than in *S. macrorhinos* and *T. macrocercus*, comparable to that of *T. rhinogradoides*, and longer than in *E. centrosa*, *E. leucura*, *H. stuempkei*, *M. naso*, *P. vermidax*, and *W. mamasae*. The tail of *G. radix* is similar in thickness along its length to that of *T. macrocercus*. The scales of the tail of *G. radix* are nonoverlapping with short unpigmented hairs emerging from between the scales. *G. radix* does not possess the hairless and scaleless tip of the tail noted



Fig. 8.—Photographs of the left a) forefeet and b) hindfeet of *Gracilimus radix*, taken from NMV C37053 after preservation in fluid. Shown are the dorsal (top), lateral (middle), and ventral (lower) aspects. Photo credits: Kevin C. Rowe. NMV = Museum Victoria, Melbourne.

in *S. macrorhinos* (Musser and Durden 2002). The dorsal surface of the tail of *G. radix* is slightly darker than the ventral surface, similar to *S. macrorhinos*, *T. macrocercus*, and *T. rhinogradoides*. The tail of *G. radix* is more uniform in color than the tails of *Echiothrix* and *Hyorhinomys*, which are white on the ventral surface and distal portion.

The mystacial vibrissae of *G. radix* are fine and long, reaching 50 mm and extending 20 mm or more beyond the pinnae. They are similar in both absolute and relative length to the mystacial vibrissae of *S. macrorhinos* and *T. macrocercus*, but are much longer and more delicate than the mystacial vibrissae of *W. mamasae*. The density of the mystacial vibrissae of *G. radix* is less than in *S. macrorhinos*, similar to *W. mamasae*, and greater than in *T. macrocercus*. The bases of the mystacial vibrissae in *G. radix* are dark brown with the distal 3rd unpigmented or light brown, similar to *S. macrorhinos*, *T. macrocercus*, and *W. mamasae*. The eyes of *G. radix* are small and indistinct (~2 mm diameter), similar to *S. macrorhinos*, *T. macrocercus*, and *W. mamasae*. The pinnae of *G. radix* are small (~13 mm notch to top), lightly furred, ovate, and similar in color to the gray–brown dorsal pelage. They are smaller, both absolutely and relatively, than the pinnae of any of the Sulawesi shrew rats, but nevertheless distinct above the dorsal fur, which distinguishes them from the very short, hidden pinnae of *W. mamasae*.

The skull of *G. radix* is small and delicate, with a globose braincase and a short, blunt rostrum (Fig. 6). It is more

delicate than that of *W. mamasae* (Fig. 6) and similar in build to those of *S. macrorhinos*, *T. macrocercus*, and *M. naso* (photographs and illustrations of these taxa and other Sulawesi shrew rats are found in Musser 1990; Musser and Durden 2002; Esselstyn et al. 2012; Achmadi et al. 2014; Musser and Durden 2014; Rowe et al. 2014; Esselstyn et al. 2015). The dorsal surface of the braincase in *G. radix* is smooth, without ridges on the interorbital or postorbital regions, similar to the morphology of *S. macrorhinos*, *T. macrocercus*, and *M. naso*. For a murine, the rostrum (LR) of *G. radix* is moderate in length relative to the basicranial region, comprising 28–29% of the total length of the skull (GLS; Table 3). The relative length of the rostrum in *G. radix* is slightly longer than in *W. mamasae* (LR/GLS ~25%), but much shorter than in the Sulawesi shrew rats, among which the rostrum comprises > 35% of the total length of the skull. The breadth of the foramen magnum of *G. radix* comprises ~40% of the breadth of the braincase, which is slightly less than noted in *W. mamasae* (42.6%). The zygomatic arch of *G. radix* is slender and delicate. It curves inward distinctly from the squamosal before bowing out again as it approaches the lacrimal. The lacrimal bone in *G. radix* is pronounced and projects posteriorly ~1 mm. In the Sulawesi water rat and shrew rats, the lacrimal is nearly indistinguishable and does not project posteriorly. The infraorbital foramina are broader in *G. radix* than in any species of Sulawesi shrew rat, but narrower and shorter in height than in the Sulawesi

Table 3.—External, cranial, and dental measurements of *Gracilimus radix* compared to the small shrew rats and the water rat of Sulawesi (mean, plus or minus 1 SD, and the range are in parentheses). Measurements of the large shrew rats (*Echimys*, *Hyorhinomys*, and *Paucidentomys*) are reported in [Esselstyn et al. 2015](#). TTL = total length; HB = head and body length; HF = hindfoot length; GLS = greatest length of skull; ZB = zygomatic breadth; LON = length of nasal; BBC = breadth of the braincase; HBC = height of the braincase; PPL = postpalatal length; LD = length of diastema; LBP = length of bony palate; LIF = length of incisive foramina; BIF = breadth of incisive foramina; BMF = breadth of mesopterygoid fossa; LB = length of auditory bulla; CLMM = crown length of the 1st maxillary molar; BUM = breadth of the 1st upper molar; BUI = breadth of the upper incisor; DII = depth of the upper incisor; LDII = depth of the dentary including the incisor; CLMaM = crown length of the 1st mandibular molar; BLM = breadth of the 1st mandibular molar.

Genus species	<i>Gracilimus radix</i>	<i>Waionys manasae</i>	<i>Melasmotherix Naso</i>	<i>Somomeromys macrourhinos</i>	<i>Tateomys macrocercus</i>	<i>Tateomys rhinogradoides</i>
TTL	277±8.90 (264–288)	288	206.67±7.77 (198–213)	282.5±13.8 (271–301)	278.00±2 (276–280)	304.50±20.51 (290–319)
Tail	159±5.20 (151–163)	159	88.33±4.73 (83–92)	182.5±8.81 (173–193)	166.00±4.36 (163–171)	163.00±16.97 (151–175)
HB	118±6.28 (108–125)	129	118.33±3.06 (115–121)	100±5.6 (95–108)	112.00±6.24 (105–117)	145.50±5.8 (139–153)
HF	29±0.90 (28–30)	36	28±0 (28)	30±0.82 (29–31)	30.67±1.15 (30–32)	37.25±1.89 (36–40)
Ear	13±0.50 (13–14)	11	18.33±0.58 (18–19)	18.25±1.71 (16–20)	19.33±0.58 (19–20)	22.00±1.41 (21–24)
Mass	41±5.40 (34–45)	64	47.67±5.13 (42–52)	26.83±3.06 (24–30)	40.00±1 (39–41)	86.50±7.55 (76–92)
GLS	29.94±0.71 (29.1–30.95)	30.73	33.04±0.65 (32.5–32.9)	31.8±0.52 (31.08–31.93)	31.65±0.58 (30.99–32.08)	39.42±0.68 (38.52–40.13)
ZB	12.30±0.22 (12.06–12.66)	15.83	14.07±0.12 (13.98–14.15)	13.09±0.24 (12.83–13.29)	13.87±0.16 (13.73–14.04)	15.25±0.22 (14.96–15.42)
LON	10.93±0.53 (10.3–11.7)	9.00	11.64±0.69 (11.07–12.41)	11.81±0.37 (11.45–12.32)	11.26±0.5 (10.91–11.84)	13.30±0.61 (12.76–14.02)
LR	8.22±0.62 (7.31–8.9)	7.77	12.52±0.18 (12.31–12.65)	12.02±0.54 (11.55–12.72)	11.91±0.78 (11.06–12.61)	13.83±0.61 (13.19–14.36)
BR	5.42±0.16 (5.16–5.6)	4.30	5.06±0.32 (4.76–5.39)	4.9±0.21 (4.68–5.16)	4.48±0.22 (3.52–4.97)	4.70±0.25 (4.41–5.01)
IB	5.16±0.16 (4.9–5.31)	4.89	6.19±0.08 (6.12–6.28)	5.61±0.16 (5.45–5.80)	6.10±0.06 (6.03–6.14)	6.94±0.12 (6.84–7.1)
BZP	1.37±0.02 (1.33–1.4)	1.60	1.37±0.18 (1.26–1.64)	1.43±0.03 (1.39–1.47)	1.44±0.16 (1.04–1.32)	1.42±0.14 (1.32–1.63)
BBC	12.23±0.22 (11.95–12.52)	14.49	14.22±0.28 (13.85–14.51)	13.24±0.36 (12.75–13.60)	14.39±0.25 (14.17–14.66)	15.82±0.35 (15.46–16.2)
HBC	9.58±0.27 (9.25–10)	10.57	9.12±0.7 (8.6–10.11)	10.43±0.39 (10.15–11.00)	9.89±0.44 (9.44–10.28)	10.30±0.49 (9.82–10.89)
PPL	11.54±0.35 (11–11.98)	11.76	12.28±0.12 (12.1–12.33)	9.58±0.37 (9.10–10.00)	11.10±0.08 (11.02–11.17)	16.22±0.29 (15.84–16.55)
LD	7.11±0.33 (6.8–7.7)	8.26	6.68±0.79 (5.74–7.67)	6.76±0.43 (6.20–7.16)	7.07±0.91 (6.03–7.7)	9.12±1.06 (7.99–10.04)
LBP	5.77±0.39 (5.23–6.35)	7.59	6.22±0.29 (5.9–6.60)	6.02±0.26 (5.87–6.28)	6.61±0.12 (6.48–6.7)	8.10±0.41 (7.62–8.62)
LIF	3.65±0.24 (3.35–4.04)	4.40	4.78±0.28 (4.4–5.06)	2.9±0.36 (2.67–3.32)	3.98±0.28 (3.71–4.27)	5.46±0.42 (4.97–5.85)
BIF	1.78±0.05 (1.7–1.85)	2.31	1.83±0.09 (1.73–1.94)	1.92±0.19 (1.71–2.07)	1.96±0.09 (1.87–2.05)	1.97±0.03 (1.95–2.01)
BMF	2.05±0.13 (1.9–2.24)	2.17	1.81±0.16 (1.68–1.99)	2.01±0.15 (1.86–2.17)	1.87±0.09 (1.77–1.95)	2.26±0.12 (2.13–2.41)
LB	4.47±0.30 (4.15–4.85)	4.05	5.37±0.31 (5.03–5.73)	4.28±0.22 (4.07–4.47)	4.65±0.4 (4.19–4.93)	5.25±0.34 (4.75–5.51)
CLMM	4.06±0.11 (3.9–4.2)	4.96	4.78	4.44±0.19 (4.30–4.57)	4.94±0.34 (4.7–5.18)	5.43±0.16 (5.32–5.54)
BUM	1.42±0.04 (1.35–1.47)	1.80	1.79	1.45±0.07 (1.40–1.50)	1.77±0.07 (1.72–1.82)	1.92±0.01 (1.91–1.92)
BUI	0.90±0.01 (0.89–0.92)	0.50	0.97±0.06 (0.92–1.06)	0.98±0.46 (0.65–1.30)	0.77±0.13 (0.63–0.89)	1.10±0.07 (1–1.15)
DII	1.60±0.07 (1.51–1.67)	1.23	0.97±0.22 (0.81–1.29)	1.42	1.01±0.2 (0.78–1.13)	0.99±0.38 (0.64–1.35)
LDII	16.81±0.41 (16.2–17.45)	19.74	19.55	15.89±0.58 (19–20)	18.79±0.1 (18.72–18.86)	24.86±0.35 (24.61–25.11)
LDEI	13.48±0.30 (13.1–14)	13.74	16.28	12.99±0.58 (19–20)	15.32±0.67 (14.84–15.79)	19.90±0.44 (19.59–20.21)
CLMaM	4.02±0.08 (3.9–4.14)	4.89	4.44	4.24±0.58 (19–20)	4.60±0.04 (4.57–4.63)	5.14±0.21 (4.99–5.29)
BLM	1.24±0.03 (1.2–1.28)	1.61	1.2	1.14±0.58 (19–20)	1.34±0.06 (1.29–1.38)	1.29±0.02 (1.27–1.3)

water rat; the inner margins of the infraorbital foramina are nearly parallel to the sagittal plane, while the outer margins form the rounded side of an oval. The nasals extend slightly (~2 mm) beyond the vertical plane of the labial margin of the upper incisors; they are much less extended than in *S. macrorhinos*, similar in their degree of extension to the nasals in *M. naso*, *T. macrocercus*, and *T. rhinogradoides*, and more extended than in *Echiothrix* spp., *H. stuempkei*, *P. vermidax*, and *W. mamasae*. The incisive foramina are rounded on the lateral margins and straight on the medial margins. They are narrower anteriorly than posteriorly, where they terminate well before (~1.5 mm) the anterior margin of the molar row. The latter trait is shared with all Sulawesi shrew rat species and *W. mamasae*. The stapedial foramina in *G. radix* are minute but distinct. The middle lacerate foramen is connected to the foramen ovale by a canal, indicating an arterial pathway shared with many murids, including all Sulawesi shrew rats except *Sommeromys* (Musser and Durden 2002; Esselstyn et al. 2015). The hamular process of the pterygoid bone extends beyond the occlusal plane of the molars and bows modestly outward, leaving the mesopterygoid fossa fully visible from a ventral aspect. The pterygoid plate, which is absent in *Echiothrix* spp., *H. stuempkei*, and *P. vermidax* is present, but not prominent in *G. radix*, *M. naso*, *S. macrorhinos*, and *Tateomys* spp.

Like the cranium, the dentary of *G. radix* is delicate, but not particularly long (mean LDEI = 13.5 mm = 117% of PPL). It is shorter in relative length than any of the Sulawesi shrew rats (LDEI = 123–146% of PPL) and comparable in relative length to that of *W. mamasae* (LDEI = 117% of PPL). The coronoid process on the dentary of *G. radix* forms a prominent sickle-shaped hook rising well above, and extending posteriorly to near, the mandibular condyle (Fig. 5). The coronoid process of *G. radix* is much more developed than in any of the Sulawesi shrew rats or water rat, some of which contain a mere spicule (*Echiothrix* spp. and *P. vermidax*) or lack the process altogether (*H. stuempkei*). The angular process is prominent and splay inward forming a small shelf ~2 mm medial to the plane of the coronoid process. Hence, from the condyle to the angular process, the ramus forms a concave arc. Relative to body size, these structures suggest a substantially more muscular mastication system in *G. radix* than is present in the shrew rats. An almost indistinguishable capsular process terminates at the posterior margin of m3, directly below the base of the coronoid process.

Three small molars are present in both the maxillary and mandibular rows of *G. radix* (Fig. 7). In both the upper and lower jaws, M1/m1 is approximately twice as large as M2/m2, which is similarly large relative to M3/m3 (Fig. 4); this pattern is common in murines, including the Sulawesi water rat and shrew rats (excluding *Paucidentomys*, which lacks molars). The upper and lower molars are worn into simple enamel-rimmed, laterally oriented basins in all specimens of *G. radix*, precluding a detailed description of the occlusal cusp patterns. The first 2 upper molars contain 3 longitudinally arranged basins, while the 3rd molar comprised a single small basin. The 2 anterior-most basins of M1 are similar in occlusal area, but

the posterior-most basin is about one-half as large. The middle basin of M2 is approximately twice as large in occlusal area as the anterior and posterior basins. M3 is small, containing a single basin, formed by wear of a single cusp, t9 in the terminology of Musser (1991). In the mandible, m1 and m2 each contain 2 basins that are similar in occlusal area. The lower 3rd molar, m3, is small, containing a single basin. Both the upper and lower incisors of *G. radix* are pale orange on the labial surface, similar to those of *W. mamasae*, but distinct from all species of Sulawesi shrew rat, which lack orange pigment in the enamel. The upper incisors of *G. radix* are orthodont and moderate in breadth (BUI = ~0.9 mm; Table 3). They are comparable to the upper incisors of *M. naso* and broader than the upper incisors of *S. macrorhinos*, *T. macrocercus*, and *W. mamasae*. The lower incisors of *G. radix* are moderately proodont, lying at a similar angle to the lower incisors of *S. macrorhinos* and *W. mamasae*, but at a more acute angle than the extreme proodonty of the remaining Sulawesi shrew rats, *E. centrosa*, *E. leucura*, *H. stuempkei*, *M. naso*, *P. vermidax*, *T. macrocercus*, and *T. rhinogradoides*.

Ecological Notes

The stomach contents of all known specimens of *G. radix* were examined by R. Marchant (Terrestrial Invertebrates, Museum Victoria) for evidence of invertebrate material. Two stomachs were almost empty with 1 (NMV C37055) containing the remains of an adult cockroach (order Blattaria) and the other (C36995) containing trace amounts of plant material. The nearly distended stomachs of NMV C37054 (the holotype), NMV C37053, and NMV C36996 contained only plant material, particularly the fleshy tissue of roots.

DISCUSSION

The diversity of murid rodents from Sulawesi, as we know it, is rapidly increasing. Recent collections of specimens have resulted in several new descriptions, including 7 new species and 4 new genera documented since 2012 (Esselstyn et al. 2012; Mortelliti et al. 2012; Musser 2014; Rowe et al. 2014; Esselstyn et al. 2015; this paper). The 4 recently discovered genera are each monotypic members of an endemic Sulawesi clade, referred to here as the *Echiothrix* Clade, which we define as comprising the shrew rats, water rat, and now *Gracilimus*. Although we inferred a well-supported sister relationship between the terrestrial *Gracilimus* and amphibious *Waiomys*, the extensive morphological and ecological differences between these 2 species warrant their separate generic status (Table 2). Their differences are comparable to those between the terrestrial moss mice (e.g., *Leptomys* and *Pseudohydromys*) and amphibious water rats (e.g., *Crossomys* and *Hydromys*) of New Guinea, each of which comprises multiple genera (Helgen 2005; Helgen and Helgen 2009). We also estimated long terminal phylogenetic branches among the genera in the *Echiothrix* Clade, with limited support for topological relationships, particularly the placement of *Sommeromys*, *Melasmotherix* relative to the 2 species of *Tateomys*, and the recently described

Hyorhinomys. The short internodes among genera at the base of the Echinothrix Clade relative to the long terminal branches suggest rapid diversification of species in the distant past; resolving the true relationships among these genera may prove difficult even with more genetic data (e.g., Giarla and Esselstyn 2015). Given this state of knowledge, the recent descriptions of monotypic genera are justified by both ecomorphological and phylogenetic distinctiveness. Although naming several monotypic genera is unusual, the alternative approach, constrained by making genera natural groupings (i.e., clades), would require placing *Gracilimus*, *Hyorhinomys*, *Melasmotherix*, *Paucidentomys*, *Sommeromys*, *Tateomys*, and *Waiomys* into the genus *Echinothrix*. Doing so would represent a major overhaul to past taxonomic designations. With these circumstances, our preference is to use monotypic genera, which guarantees these genera are monophyletic while maintaining some taxonomic stability. Moreover, recent discoveries suggest that the future discovery of new species in many, if not all, of these genera is distinctly possible.

Three of the recently described murid genera (*Gracilimus*, *Paucidentomys*, and *Waiomys*) and 1 of the new species (*Bunomys torajae*) were collected from the same general locality (Mt. Gandangdewata) in the highlands of the west-central region of Sulawesi's central core and are only known from that general area (Esselstyn et al. 2012; Musser 2014; Rowe et al. 2014). These discoveries lend support to other studies suggesting that the region represents an area of endemism distinct from the east-central region (Merker et al. 2009). More extensive surveys across the 2 regions are needed to understand their biogeographic distinctiveness and the significance of the west-central region as a center of endemism (sensu Evans et al. 2003). The diversity of murid rodents and the number of new genera described from Mt. Gandangdewata highlight the area's potential value for preserving Sulawesi's endemic, and largely undocumented biodiversity.

Our phylogenetic analyses place *Gracilimus*, an omnivorous rodent, within the otherwise carnivorous (i.e., feeding exclusively on invertebrates) Echinothrix Clade of rats from Sulawesi. Cranio-dental characters, which indicate a relatively robust masticatory system, and stomach contents, support the idea that *G. radix* is omnivorous. Of the cranio-dental characters, the presence of a (1) short, broad rostrum; (2) short, well-developed dentaries with large, sickle-shaped coronoid processes; and (3) moderately proodont lower incisors do not indicate a diet specialized to carnivory. Among IAA murids, carnivory evolved at least 4 times in total, twice on Sulawesi (Rowe et al. 2016). The Philippine shrew rats, New Guinea moss mice and water rats, Echinothrix Clade, and *Crunomys* (Sulawesi and Philippines) each represent independent origins of carnivory from an omnivorous ancestor (Rowe et al. 2016). However, *Gracilimus*, the sister to *Waiomys*, is an omnivore phylogenetically nested within its respective clade of otherwise carnivorous species. Thus, the trajectory of dietary evolution among Sulawesi murids is not as simple as 2 origins of carnivory (Echinothrix Clade and *Crunomys*) from omnivorous ancestors (Rowe et al. 2016). If the diet and morphological adaptations

of *Gracilimus* represent retention of a plesiomorphic state, then the water rat, *Waiomys*, would represent a 3rd origin of carnivory within Sulawesi. The cranio-dental morphology of *Waiomys*, including (1) short, broad rostrum; (2) relatively robust dentaries; (3) orange pigmented enamel on the incisors; and (4) moderately proodont lower incisors support the suggestion that their carnivory evolved from a morphology similar to the omnivorous *Gracilimus*. Alternatively, if carnivory evolved once in the Echinothrix Clade then *Gracilimus* would represent the evolution of an omnivore from a carnivorous ancestor, illustrating a reversal not otherwise observed among IAA murines (Rowe et al. 2016).

The Echinothrix Clade of Sulawesian endemic rodents is a remarkable example of ecomorphological evolution in an island radiation (Fig. 1). Compared to comparably aged clades in other Muridae of the IAA (e.g., *Dacnomys*, *Maxomys*, and *Rattus* divisions in Fig. 4), the phenotypic gaps among species of the Echinothrix Clade are vast. Indeed, when murid divisions were last formally designated, the species in the Echinothrix Clade were divided among 3 divisions (Echinothrix, *Melasmotherix*, and *Crunomys*—Musser and Carleton 2005). The recent description of 4 new genera that are also members of this clade has substantially increased their morphological range to include a molarless vermivore (*Paucidentomys*), an amphibious rat (*Waiomys*), a long-limbed, barrel-chested, hog-nosed rat (*Hyorhinomys*), and now a slender omnivore (*Gracilimus*—Esselstyn et al. 2012; Rowe et al. 2014; Esselstyn et al. 2015; this study). These discoveries demonstrate the need for more systematic voucher collection and taxonomic study to provide a foundation for understanding how this spectacular morphological diversity arose among Sulawesi murids.

ACKNOWLEDGMENTS

We are grateful to the local people of Mamasa, especially those from the village of Rantepangko, who were critical to the success of this research. R. Marchant of NMV identified invertebrate remains in the stomachs of *Gracilimus radix*. We are grateful to S. Ingleby of the Australian Museum; R. Voss and E. Westwig of the American Museum of Natural History; and L. Heaney, J. Phelps, and especially the lifetime contributions of the late, eminent W. Stanley of the Field Museum of Natural History for access to comparative specimens. P.-H. Fabre and an anonymous reviewer provided constructive comments on an earlier version of this manuscript. This research was funded by the National Science Foundation (OISE-0965856 and DEB-1343517), National Geographic Society (9025-11), and Australia and Pacific Science Foundation (12-6). K. Riset dan Teknologi and D. Kehutanan Makassar provided research permits.

SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The materials consist of data

provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Specimens used in phylogenetic analyses and GenBank accession numbers for each locus.

Supporting Information S2.—Gene tree for cytochrome *b* estimated using RAxML. Numbers above branches represent bootstrap support values.

Supporting Information S3.—Gene tree for growth hormone receptor (GHR) estimated using RAxML. Numbers above branches represent bootstrap support values.

Supporting Information S4.—Gene tree for retinol-binding protein (IRBP) estimated using RAxML. Numbers above branches represent bootstrap support values.

Supporting Information S5.—Gene tree for recombination activating gene 1 (RAG1) estimated using RAxML. Numbers above branches represent bootstrap support values.

Supporting Information S6.—Gene tree for breast cancer 1 (BRCA1) estimated using RAxML. Numbers above branches represent bootstrap support values.

LITERATURE CITED

- ACHMADI, A. S., J. A. ESSELSTYN, K. C. ROWE, I. MARYANTO, AND M. T. ABDULLAH. 2013. Phylogeny, diversity, and biogeography of Southeast Asian spiny rats (*Maxomys*). *Journal of Mammalogy* 94:1412–1423.
- ACHMADI, A. S., K. C. ROWE, AND J. A. ESSELSTYN. 2014. New records of two rarely encountered, endemic rats (Rodentia: Muridae: Murinae) from Gunung Gandangdewata, West Sulawesi Province. *Treubia* 41:51–60.
- BOUCKAERT, R., ET AL. 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* 10:e1003537.
- ESSELSTYN, J. A., A. S. ACHMADI, H. HANDIKA, AND K. C. ROWE. 2015. A hog-nosed shrew rat (Rodentia: Muridae) from Sulawesi Island, Indonesia. *Journal of Mammalogy* 96:895–907.
- ESSELSTYN, J. A., A. S. ACHMADI, AND K. C. ROWE. 2012. Evolutionary novelty in a rat with no molars. *Biology Letters* 8:990–993.
- EVANS, B. J., J. SUPRIATNA, N. ANDAYANI, M. I. SETIADI, D. C. CANNATELLA, AND D. J. MELNICK. 2003. Monkeys and toads define areas of endemism on Sulawesi. *Evolution* 57:1436–1443.
- GELMAN, A., AND D. B. RUBIN. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7:457–472.
- GIARLA, T. C., AND J. A. ESSELSTYN. 2015. The challenges of resolving a rapid, recent radiation: empirical and simulated phylogenomics of Philippine shrews. *Systematic Biology* 64:727–740.
- GRAY, J. E. 1867. Notes on the variegated or yellow-tailed rats of Australasia. *Proceedings of the Zoological Society of London* 1867:597–600.
- HELGEN, K. M. 2005. The amphibious murines of New Guinea (Rodentia, Muridae): the generic status of *Baiyankamys* and description of a new species of *Hydromys*. *Zootaxa* 913:1–20.
- HELGEN, K. M., AND L. E. HELGEN. 2009. Chapter 8. Biodiversity and biogeography of the moss-mice of New Guinea: a taxonomic revision of *Pseudohydromys* (Muridae: Murinae). Pp. 230–313 in *Systematic mammalogy, contributions in honor of Guy G. Musser*. Bulletin of the American Museum of Natural History (R. S. Voss and M. D. Carleton, eds.). Vol. 331. American Museum of Natural History, New York.
- HUELSENBECK, J. P., AND F. RONQUIST. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17:754–755.
- JANSA, S. A., F. K. BARKER, AND L. R. HEANEY. 2006. The pattern and timing of diversification of Philippine endemic rodents: evidence from mitochondrial and nuclear gene sequences. *Systematic Biology* 55:73–88.
- KIMURA, Y., M. T. HAWKINS, M. M. McDONOUGH, L. L. JACOBS, AND L. J. FLYNN. 2015. Corrected placement of *Mus-Rattus* fossil calibration forces precision in the molecular tree of rodents. *Scientific Reports* 5:14444.
- LANFEAR, R., B. CALCOTT, S. Y. HO, AND S. GUINDON. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 29:1695–1701.
- MADDISON, D. R., AND W. P. MADDISON. 2003. *MacClade*, version 4.06. Sinauer, Sunderland, Massachusetts.
- MERKER, S., C. DRILLER, D. PERWITASARI-FARAJALLAH, J. PAMUNGKAS, AND H. ZISCHLER. 2009. Elucidating geological and biological processes underlying the diversification of Sulawesi tarsiers. *Proceedings of the National Academy of Sciences* 106:8459–8464.
- MILLER, G. S., AND N. HOLLISTER. 1921. Descriptions of sixteen new murine rodents from Celebes. *Proceedings of the Biological Society of Washington* 34:67–76.
- MILLER, M. A., W. PFEIFFER, AND T. SCHWARTZ. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, New Orleans, Louisiana, 1–8.
- MORTELLITI, A., R. CASTIGLIA, G. AMORI, I. MARYANTO, AND G. G. MUSSER. 2012. A new species of *Margaretamys* (Rodentia: Muridae: Murinae: Rattini) from Pegunungan Mekongga, southeastern Sulawesi, Indonesia. *Tropical Zoology* 25:74–107.
- MUSSER, G. G. 1969. Results of the Archbold Expeditions. No. 91. A new genus and species of murid rodent from Celebes, with a discussion of its relationships. *American Museum Novitates* 2384:1–41.
- MUSSER, G. G. 1982. Results of the Archbold expedition. No. 110. *Crunomys* and the small-bodied shrew rats native to the Philippine Islands and Sulawesi (Celebes). *Bulletin of the American Museum of Natural History* 174:1–95.
- MUSSER, G. G. 1990. Sulawesi rodents: species traits and chromosomes of *Haeromys minahassae* and *Echiothrix leucura* (Muridae: Murinae). *American Museum Novitates* 2989:1–18.
- MUSSER, G. G. 1991. Sulawesi rodents: descriptions of new species of *Bunomys* and *Maxomys* (Muridae, Murinae). *American Museum Novitates* 3001:1–41.
- MUSSER, G. G. 2014. A systematic review of Sulawesi *Bunomys* (Muridae, Murinae) with the description of 2 new species. *Bulletin of the American Museum of Natural History* 392:1–313.
- MUSSER, G. G., AND M. D. CARLETON. 2005. Superfamily Muroidea. Pp. 894–1531 in *Mammal species of the world: a taxonomic and geographic reference* (D. E. Wilson and D. M. Reeder, eds.). Johns Hopkins University Press, Baltimore, Maryland.
- MUSSER, G. G., AND L. A. DURDEN. 2002. Sulawesi rodents: description of a new genus and species of Murinae (Muridae, Rodentia) and its parasitic new species of sucking louse (Insecta, Anoplura). *American Museum Novitates* 3368:1–50.
- MUSSER, G. G., AND L. A. DURDEN. 2014. Morphological and geographic definitions of the Sulawesian shrew rats *Echiothrix leucura* and *E. centrosa* (Muridae, Murinae), and description of a new

- species of sucking louse (Phthiraptera: Anoplura). Bulletin of the American Museum of Natural History 871:1–87.
- MUSSER, G. G., AND L. R. HEANEY. 1992. Philippine rodents: definitions of *Tarsomys* and *Limnomys* plus a preliminary assessment of phylogenetic patterns among native Philippine murines (Murinae, Muridae). Bulletin of the American Museum of Natural History 211:1–138.
- RONQUIST, F., AND J. P. HUELSENBECK. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574.
- RONQUIST, F., ET AL. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61:539–542.
- ROWE, K. C., A. S. ACHMADI, AND J. A. ESELSTYN. 2014. Convergent evolution of aquatic foraging in a new genus and species (Rodentia: Muridae) from Sulawesi Island, Indonesia. Zootaxa 3815:541–564.
- ROWE, K. C., A. S. ACHMADI, AND J. A. ESELSTYN. 2016. Repeated evolution of carnivory among Indo-Australian rodents. Evolution.
- ROWE, K. C., K. P. APLIN, P. R. BAVERSTOCK, AND C. MORITZ. 2011. Recent and rapid speciation with limited morphological disparity in the genus *Rattus*. Systematic Biology 60:188–203.
- ROWE, K. C., M. L. RENO, D. M. RICHMOND, R. M. ADKINS, AND S. J. STEPPAN. 2008. Pliocene colonization and adaptive radiations in Australia and New Guinea (Sahul): multilocus systematics of the old endemic rodents (Muroidea: Murinae). Molecular Phylogenetics and Evolution 47:84–101.
- SCHENK, J. J., K. C. ROWE, AND S. J. STEPPAN. 2013. Ecological opportunity and incumbency in the diversification of repeated continental colonizations by muroid rodents. Systematic Biology 62:837–864.
- STAMATAKIS, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22:2688–2690.
- THOMAS, O. 1898. On the mammals collected by Mr. John Whitehead during his recent expedition to the Philippines with field notes by the collector. Transactions of the Zoological Society of London 14:377–414.

Submitted 20 September 2015. Accepted 15 February 2016.

Associate Editor was Ricardo Moratelli.

APPENDIX I

Specimens examined. All *Gracilimus radix* specimens have frozen tissue archived at MZB and NMV

Echiothrix leucura: AMNH 101243

Echiothrix centrosa: AMNH 153013, 225680, 225685; MZB 27875

Gracilimus radix: MZB 37399, 37401, 37402; NMV C37053, C36996

Hyorhinomys stuempkei: MZB 37001; LSUMZ 37059, 37060; NMV C37196, C37198

Melasmotherix naso: FMNH 213284, 213447, 213448; NMV C37064

Paucidentomys vermidax: FMNH 213102; MZB 35001

Sommeromys macrorhinos: AMNH 226956; MZB 34758, 34903; NMV C37074

Tateomys macrocercus: FMNH 213450; NMV C37080, C37081

Tateomys rhinogradoides: FMNH 213338, 213434; NMV C37082, C37083

Waiomys mamasa: MZB 37000