



## A hog-nosed shrew rat (Rodentia: Muridae) from Sulawesi Island, Indonesia

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We document a new genus and species of shrew rat from the north peninsula of Sulawesi Island, Indonesia. The new taxon is known only from the type locality at 1,600 m elevation on Mt. Dako, in the district of Tolitoli. It is distinguished from all other Indonesian murines by its large, flat, pink nose with forward-facing nares. Relative to other Sulawesi murines, the species has extremely large ears (~ 21% of head and body length), very long urogenital hairs, prominent and medially bowing hamular processes on the pterygoid bones, extremely long and procumbent lower incisors, and unusually long articular surfaces on the mandibular condyles. Morphologically, the new taxon is most similar to a group of endemic Sulawesi rats known commonly as “shrew rats.” These are long faced, carnivorous murines, and include the genera *Echiothrix*, *Melasmothrix*, *Paucidentomys*, *Sommeromys*, and *Tateomys*. Our Bayesian and likelihood analyses of DNA sequences concatenated from 5 unlinked loci infer the new shrew rat as sister to a clade consisting of *Melasmothrix*, *Paucidentomys*, and *Echiothrix*, suggesting that Sulawesi shrew rats represent a clade. The Sulawesi water rat, *Waiomys mamasae*, was sister to the shrew rats in our analyses. Discovery of this new genus and species brings known shrew rat diversity on Sulawesi to 6 genera and 8 species. The extent of morphological diversity among these animals is remarkable considering the small number of species currently known.

Kami mendokumentasikan genus dan spesies baru tikus cucurut dari bagian semenanjung utara pulau Sulawesi, Indonesia. Takson baru ini hanya diketahui dari lokasi spesimen tipe pada ketinggian 1,600 mdpl di Gunung Dako, Kabupaten Tolitoli. Ia dibedakan dari spesies tikus Indonesia lainnya berdasarkan ukuran hidung yang besar, datar, berwarna merah muda dengan moncong hidung menghadap ke arah depan. Jika dibandingkan dengan spesies tikus Sulawesi lainnya, spesies ini memiliki telinga yang sangat besar (~ 21% dari panjang kepala dan badan), rambut urogenital yang sangat panjang, prosesus hamular yang jelas dan menonjol pada pertulangan pterygoid, gigi seri bagian bawah yang sangat panjang, dan penampang persendian yang panjang dan tidak biasa pada kondilus mandibula. Secara morfologi, takson ini lebih mirip dengan kelompok tikus endemik Sulawesi yang umumnya dikenal sebagai “tikus cucurut”. Kelompok ini dicirikan dengan mulut yang panjang, pemakan daging, dan termasuk didalamnya adalah genus *Echiothrix*, *Melasmothrix*, *Paucidentomys*, *Sommeromys*, dan *Tateomys*. Analisis Bayesian dan *likelihood* menggunakan sambungan sekuens DNA dari 5 lokus yang tidak terpaut menunjukkan spesies tikus cucurut baru ini berkerabat dekat dengan kelompok yang terdiri dari *Melasmothrix*, *Paucidentomys*, dan *Echiothrix*, memberi kesan tikus cucurut Sulawesi merepresentasikan suatu *clade* atau kelompok tersendiri. Tikus air Sulawesi, *Waiomys mamasae*, diketahui berkerabat dekat dengan tikus cucurut dalam analisis yang dilakukan. Penemuan genus dan spesies baru ini menambah keanekaragaman jenis tikus cucurut di Sulawesi yang telah diketahui menjadi 6 genera dan 8 spesies. Besarnya perbedaan morfologi di antara spesies-spesies tersebut merupakan sesuatu yang luar biasa mengingat sedikitnya jumlah spesies yang telah diketahui saat ini.

Key words: biodiversity, Murinae, new genus, new species, shrew rat, Wallacea

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Murine rodents are a highly successful group representing approximately 10% of mammalian species-level diversity (Musser and Carleton 2005). Most murines are found in Indo–Australia, where distinct radiations comprise diverse communities in the Sunda, Philippine, Sahul, and Wallacean biogeographic regions (Musser and Carleton 2005; Steppan et al. 2005; Jansa et al. 2006; Rowe et al. 2008, 2011; Schenk et al. 2013). With a few notable exceptions (e.g., *Crnomys*, *Haeromys*, *Maxomys*, and *Rattus*—Musser 1982; Musser and Carleton 2005; Achmadi et al. 2013), murine genera are restricted to one of these biogeographic regions. Nevertheless, several distantly related forms occurring in different biogeographic regions have evolved similar morphological traits through convergence, presumably in response to similar ecological conditions and opportunities (e.g., *Paucidentomys* on Sulawesi and *Rhynchomys* on Luzon; *Waiomys* on Sulawesi and some members of the *Hydromys* Division in Sahul—Esselstyn et al. 2012; Rowe et al. 2014).

The murine fauna of Sulawesi, the largest island in Wallacea, includes 46 species in 16 genera, not including the new taxon described below (Musser 2014; Rowe et al. 2014). All of the species and 12 of the genera are endemic to the island. This diversity encapsulates a variety of ecological forms, including large terrestrial rats (*Paruromys* and *Eropeplus*), small arboreal mice (*Haeromys*), amphibious species that feed on aquatic insects (*Waiomys*), and nearly toothless vermivores (*Paucidentomys*—Musser 1987; Esselstyn et al. 2012; Mortelliti et al. 2012; Musser 2014; Rowe et al. 2014). Among these diverse forms, the shrew rats, which include carnivorous species (they feed on earthworms and arthropods—Musser 1982; Musser and Durden 2002; Esselstyn et al. 2012; Musser and Durden 2014) in the genera *Echiothrix*, *Melasmothrix*, *Paucidentomys*, *Sommeromys*, and *Tateomys*, are especially interesting because: 1) they represent one or more independent origins from ecologically similar groups in the Philippines (also known as “shrew rats”) and New Guinea (“moss mice”); 2) despite their low species richness (only 7 species are currently known, 8 including the new species described herein), they encompass a large range of morphological disparity; and 3) their diversity is poorly represented in museum collections, as evidenced by recent species discoveries (Musser and Durden 2002; Esselstyn et al. 2012; this paper) and the near complete absence of Sulawesi shrew rats in molecular phylogenetic estimates of relationships within Murinae (e.g., Jansa et al. 2006; Rowe et al. 2008). As an example of the latter point, Rowe et al. (2014) were the first to incorporate more than 1 species of Sulawesi shrew rat in molecular phylogenetic inference; they found support for a sister relationship between *Paucidentomys vermidax* and *Melasmothrix naso*, providing the first molecular evidence to suggest that the Sulawesi shrew rats form a clade.

Here, we describe another new shrew rat from Sulawesi and estimate its phylogenetic placement among murines, including the Sulawesi shrew rat genera *Echiothrix*, *Melasmothrix*, and *Paucidentomys*.

## MATERIALS AND METHODS

We compared the cranial and external morphology of new specimens of a shrew rat species from Mt. Dako (Fig. 1) with specimens of all other species of shrew rats known from Sulawesi (*Echiothrix centrosa* Miller and Hollister, 1921a; *Echiothrix leucura* Gray, 1867; *Melasmothrix naso* Miller and Hollister, 1921a; *Paucidentomys vermidax* Esselstyn et al., 2012; *Sommeromys macrorhinos* Musser and Durden, 2002; *Tateomys macrocercus* Musser, 1982; and *T. rhinogradoides* Musser, 1969). Because of the somewhat close relationship of the Sulawesi water rat (*Waiomys mamasae* Rowe et al., 2014) to *Melasmothrix* and *Paucidentomys* (Rowe et al. 2014), we also incorporate basic comparisons to this recently described genus and species.

We collected standard external measurements (total length [TTL], tail length [Tail], hind foot length including the claw [HF], ear length [Ear], and mass [Mass]) from fresh specimens or specimen tags. We measured 20 cranio-dental variables on cleaned skulls (see Musser and Heaney 1992) of the new shrew rat using digital calipers precise to 0.01 mm: greatest length of skull (GLS); zygomatic breadth (ZB); interorbital breadth (IB); length of rostrum (LR); breadth of rostrum (BR); breadth of zygomatic plate (BZP); breadth of braincase (BBC); height of 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); breadth of upper incisor (BUI); depth of upper incisor (DUI); length of nasal (LON); crown length of maxillary molar row (CLMMR); alveolar breadth of M1 (BM1). We compiled the same measurements from other species of Sulawesi shrew rats using data from Esselstyn et al. (2012) and Rowe et al. (2014).

We classify the largest individuals of the new shrew rat with fully fused cranial and long bone sutures as adults. Individuals that are similar in size and pelage traits to adults, but which possess open sutures on the cranium and/or long bones and modest molar wear, we classify as subadults. Those individuals that are smaller than adults and subadults, with many open sutures on the skull and long bones, unworn molars, and a dorsal pelage that is slightly greyer than in larger individuals, we consider juveniles.

The specimens we examined are held in the collections of the American Museum of Natural History, New York (AMNH), Field Museum of Natural History, Chicago (FMNH), Louisiana State University Museum of Natural Science, Baton Rouge (LSUMZ), Museum Victoria, Melbourne (NMV), and Museum Zoologicum Bogoriense, Bogor (MZB; see Appendix I for catalog numbers and collection localities).

We sequenced mitochondrial DNA (cytochrome *b*) and fragments of 4 unlinked nuclear protein-coding genes (breast cancer susceptibility 1 [BRCA1], growth hormone receptor [GHR], interphotoreceptor retinoid-binding protein [IRBP], and recombination activating gene 1 [RAG1]) in one specimen each of the new shrew rat and *E. centrosa*. Laboratory protocols followed those of Rowe et al. (2014). All new sequences were deposited in GenBank, under accession numbers KP210084–KP210094. We added these new

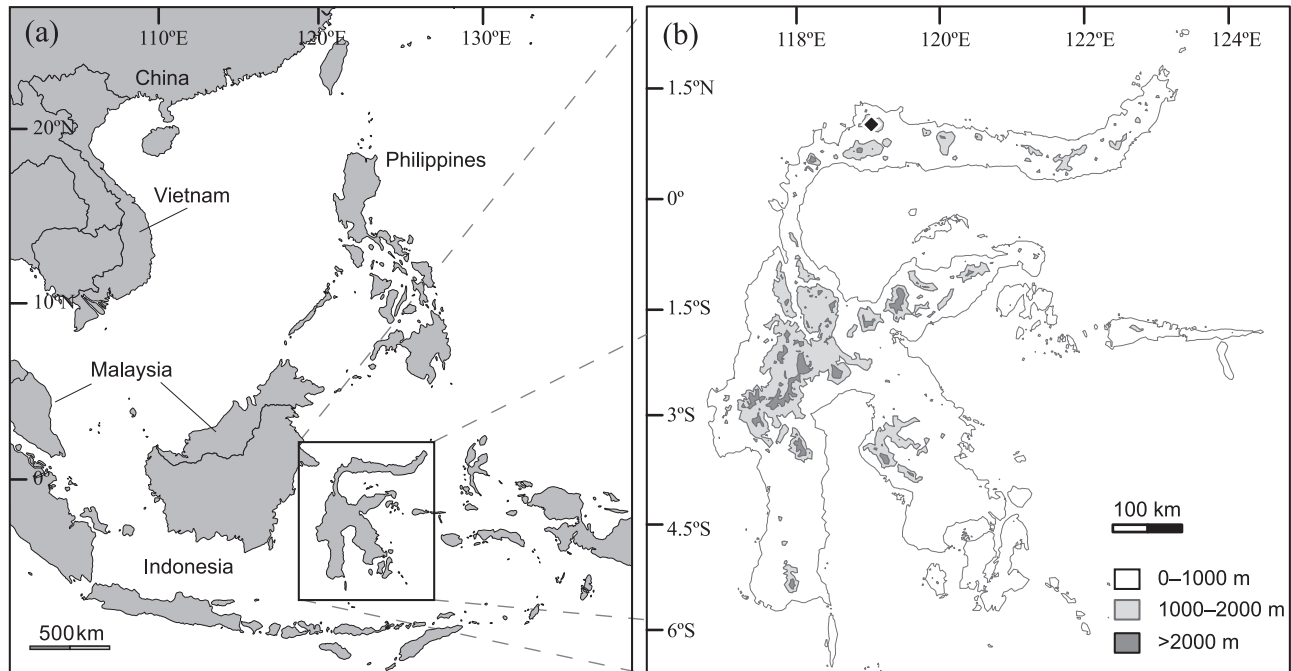


Fig. 1.—Map showing a) the location of Sulawesi in Southeast Asia and b) the type locality of *Hyorhinomys stuempkei* on Mt. Dako (diamond).

sequences to the alignments of Rowe et al. (2014) but removed species that are clearly distant relatives of Sulawesi shrew rats from the previous alignments. Thus, our final alignments contained representatives of the *Echiothrix*, *Melasmothrix*, *Maxomys* + *Crunomys*, *Dacnomys*, and *Rattus* divisions of Murinae (Musser and Carleton 2005; Achmadi et al. 2013; Appendix II). We used *Micromys minutus* as the outgroup because previous, broader-scale phylogenetic analyses recovered this species as sister to the taxa in our alignments (Schenk et al. 2013; Rowe et al. 2014). We estimated phylogenetic relationships using maximum likelihood (ML) and Bayesian inference. Initial analyses of individual genes were unable to resolve relationships among these species and we therefore concatenated all 5 loci into a single alignment. Appropriate models of sequence evolution and character partitions were fit to all sequence data using PartitionFinder 1.1.1 (Lanfear et al. 2012). We estimated ML topology and branch lengths using 1,000 optimizations in the RAxML black box software (Stamatakis 2006; Stamatakis et al. 2008); nodal support was measured by 1,000 bootstrap pseudoreplicates. Bayesian inference incorporated 4 independent runs of 4 Markov chains run for  $10^7$  generations in MrBayes 3.2.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003; Ronquist et al. 2012). Samples were drawn every 500 generations, and convergence was diagnosed by verifying that the average *SD* of split frequencies was  $< 0.01$  and that the likelihood and other parameters achieved stationarity, with adequate effective sample sizes (ESS). Stationarity and ESS for all parameters were examined in Tracer v1.5. We implemented all phylogenetic analyses on the CIPRES online portal (Miller et al. 2010).

## RESULTS

Our examination of morphological characters suggested strongly that the new specimens represent an undocumented lineage of

shrew rat. Our phylogenetic analyses further support this conclusion, with the Mt. Dako species placed as members of a Sulawesi shrew rat clade, but separated from all sampled taxa by relatively long branches (see below). Morphologically, the new specimens share several traits with the Sulawesi shrew rats, including: 1) long rostrum, 2) braincase lacking prominent ridges in the lambdaoidal region, 3) upper and lower incisors with unpigmented (white) enamel on labial surfaces, and 4) procumbent lower incisors. The new specimens, which also possess several morphological characters unique among Indonesian murines, clearly represent a lineage distinct from all known species and show no close morphological affinity with any single described genus of Sulawesi shrew rat. We therefore describe these specimens as representing a new genus and species in the family Muridae, subfamily Murinae.

### *Hyorhinomys*, new genus

*Type species.*—*Hyorhinomys stuempkei*, the new species described below.

*Diagnosis.*—A large shrew rat (Table 1) with forward-facing nares on a large pink nose, a small mouth (relative to head size), large ears measuring  $\sim 21\%$  of head and body length (Table 1), and a soft pelage composed of very fine and somewhat sparse hairs (Fig. 2). The fur is strongly bicolored with a blotchy brown-grey dorsum and white venter. The phallus is covered with long, white, longitudinal hairs in both sexes. The tail is slightly longer than head and body length (Table 1) and bilaterally colored on 2 axes, with a white venter and white distal end representing  $\sim 60\%$  tail length. Digits II–V on the forefeet possess short, broad claws that extend only  $\sim 1$  mm beyond the tip of the phalanges; the pollex bears a nail (Fig. 3a). The tongue has a prominent longitudinal groove along its dorsal surface.

The skull is long and gracile, with only modest lambdaoidal ridges (Fig. 4; Table 1). The hamular process of the pterygoid is very

**Table 1.**—Cranial and external measurements from all known specimens of *Hyorhinomys stuempkei*, and means  $\pm$  1 SD of measurements from specimens of other species of shrew rat from Sulawesi. Abbreviated variables are defined in “MATERIALS AND METHODS.” See [Musser and Heaney \(1992:6, figure 1\)](#) for illustrated definitions of cranio-dental variables. The ages of specimens, as defined in “MATERIALS AND METHODS,” are abbreviated as A (adult), SA (subadult), and J (juvenile). The 2nd row gives the sex of specimens of *H. stuempkei* or the sample size (*n*) of other species. Footnotes specify exceptions to given sample sizes. BBC, breadth of braincase; BIF, breadth of incisive foramina; BMI, alveolar breadth of M1; BMF, breadth of mesopterygoid fossa; BR, breadth of rostrum; BUI, breadth of upper incisor; BZP, breadth of zygomatic plate; CLMMR, crown length of maxillary molar row; DUI, depth of upper incisor; GLS, greatest length of skull; HBC, height of braincase; HF, hind foot length including the claw; IB, interorbital breadth; LB, length of auditory bulla; LBP, length of bony palate; LD, length of diastema; LIF, length of incisive foramina; LON, length of rostrum; PPL, post palatal length; TTL, total length; ZB, zygomatic breadth. LSUMZ, Louisiana State University Museum of Natural Science, Baton Rouge; MZB, Museum Zoologicum Bogoriense, Bogor; NMV, Museum Victoria, Melbourne.

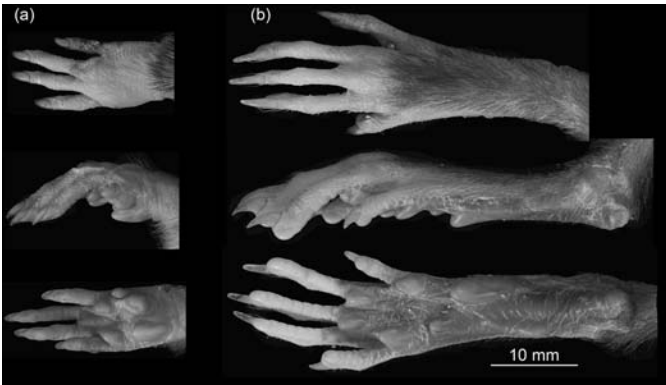
Variable	MZB 37001	LSUMZ 37059	LSUMZ 37060	NMV C37196	NMV C37198	<i>Echiothrix centroxa</i>	<i>Echiothrix leucura</i>	<i>Melasmothrix naso</i>	<i>Paucidentomys vermidax</i>	<i>Sommeromys macrorhinos</i>	<i>Tateomys macrocerus</i>	<i>Tateomys rhinogradoides</i>
Age	A	SA	J	A	SA	A	A	A	A	A	A	A
Sex/ <i>n</i>	M	M	M	F	F	2	2	3	2	4	1	4
GLS	53.47	24.45	48.24	52.26 $\pm$ 2.73	54.75 $\pm$ 2.49	32.68 $\pm$ 0.25 <sup>a</sup>	43.28 $\pm$ 0.06	31.80 $\pm$ 0.52	30.99	39.42 $\pm$ 0.68	30.99	39.42 $\pm$ 0.68
ZB	24.94	8.01	21.63	22.41 $\pm$ 0.76	24.03 $\pm$ 0.30	14.07 $\pm$ 0.12	15.24 $\pm$ 0.40	13.09 $\pm$ 0.24	13.73	15.25 $\pm$ 0.22	13.73	15.25 $\pm$ 0.22
IB	8.20	7.83	7.83	6.78 $\pm$ 0.11	7.37 $\pm$ 0.28	6.19 $\pm$ 0.08	5.96 $\pm$ 0.32	5.61 $\pm$ 0.16	6.14	6.94 $\pm$ 0.12	6.14	6.94 $\pm$ 0.12
LR	19.77	20.72	17.97	21.25 $\pm$ 1.68	22.38 $\pm$ 1.82	12.48 $\pm$ 0.24	17.55 $\pm$ 0.00	12.02 $\pm$ 0.54	12.05	13.83 $\pm$ 0.61	12.05	13.83 $\pm$ 0.61
BR	8.26	7.35	6.36	7.40 $\pm$ 0.49	7.15 $\pm$ 0.53	5.16 $\pm$ 0.31	4.98 $\pm$ 0.11	4.90 $\pm$ 0.21	4.97	4.70 $\pm$ 0.25	4.97	4.70 $\pm$ 0.25
BZP	4.47	4.18	3.69	3.34 $\pm$ 0.21	3.32 $\pm$ 0.79	1.28 $\pm$ 0.03	1.27 $\pm$ 0.12	1.43 $\pm$ 0.03	1.04	1.42 $\pm$ 0.14	1.04	1.42 $\pm$ 0.14
BBC	19.92	13.59	18.64	18.51 $\pm$ 0.10	19.14 $\pm$ 0.51	14.34 $\pm$ 0.16	15.36 $\pm$ 0.76	13.24 $\pm$ 0.36	14.17	15.82 $\pm$ 0.35	14.17	15.82 $\pm$ 0.35
HBC	15.66	14.69	14.69	13.89 $\pm$ 0.41	14.54 $\pm$ 0.24	8.79 $\pm$ 0.28	11.09 $\pm$ 0.32	10.43 $\pm$ 0.39	9.41	10.30 $\pm$ 0.49	9.41	10.30 $\pm$ 0.49
LD	20.68	20.59	17.88	15.80 $\pm$ 1.10	18.15 $\pm$ 3.61	6.34 $\pm$ 0.52	17.85 $\pm$ 0.50	6.76 $\pm$ 0.43	6.03	9.12 $\pm$ 1.06	6.03	9.12 $\pm$ 1.06
PPL	20.01	17.69	17.69	17.99 $\pm$ 1.08	18.67 $\pm$ 0.49	12.26 $\pm$ 0.14	17.85 $\pm$ 0.50	9.58 $\pm$ 0.37	11.02	16.22 $\pm$ 0.29	11.02	16.22 $\pm$ 0.29
LIF	5.78	5.90	5.89	9.92 $\pm$ 1.19	9.69 $\pm$ 0.28	4.75 $\pm$ 0.33	5.64 $\pm$ 0.53	2.90 $\pm$ 0.36	3.71	5.46 $\pm$ 0.42	3.71	5.46 $\pm$ 0.42
BIF	2.97	3.13	2.49	3.33 $\pm$ 0.19	3.89 $\pm$ 0.53	1.84 $\pm$ 0.11	1.91 $\pm$ 0.05	1.92 $\pm$ 0.19	1.95	1.97 $\pm$ 0.03	1.95	1.97 $\pm$ 0.03
LBP	13.71	13.27	11.47	9.93 $\pm$ 0.51	11.48 $\pm$ 1.56	6.09 $\pm$ 0.17	9.85 $\pm$ 0.12	6.02 $\pm$ 0.26	6.48	8.10 $\pm$ 0.41	6.48	8.10 $\pm$ 0.41
BMF	1.61	2.13	2.56	2.64 $\pm$ 0.18	2.36 $\pm$ 0.10	1.81 $\pm$ 0.16	1.63 $\pm$ 0.00	2.01 $\pm$ 0.15	1.89	2.26 $\pm$ 0.12	1.89	2.26 $\pm$ 0.12
LB	8.58	7.21	7.02	5.66 $\pm$ 0.11	6.01 $\pm$ 0.16	5.24 $\pm$ 0.23	5.65 $\pm$ 0.28	4.28 $\pm$ 0.22	4.19	5.25 $\pm$ 0.34	4.19	5.25 $\pm$ 0.34
BUI	1.14	1.13	1.14	1.25 $\pm$ 0.08	1.23 $\pm$ 0.01	0.94 $\pm$ 0.02	0.91 <sup>a</sup>		0.78	1.10 $\pm$ 0.07	0.78	1.10 $\pm$ 0.07
DUI	1.76	1.55	1.25	1.81 $\pm$ 0.13	2.06 $\pm$ 0.03	0.87 $\pm$ 0.05	0.76 <sup>a</sup>		0.78	0.99 $\pm$ 0.38	0.78	0.99 $\pm$ 0.38
LON	21.08	21.61	19.13	22.08 $\pm$ 1.68	23.08 $\pm$ 1.07	11.25 $\pm$ 0.25	16.24 $\pm$ 0.05	11.81 $\pm$ 0.37	11.04	13.30 $\pm$ 0.61	11.04	13.30 $\pm$ 0.61
CLMMR	5.29	5.91	5.72	6.50 <sup>b</sup>	6.48 <sup>b</sup>	4.70 <sup>b</sup>		4.57 <sup>b</sup>	5.11	5.30 $\pm$ 0.25 <sup>c</sup>	5.11	5.30 $\pm$ 0.25 <sup>c</sup>
BMI	1.67	1.89	1.68	2.00 <sup>b</sup>	2.26 <sup>b</sup>	1.79 <sup>b</sup>		1.50 <sup>b</sup>	1.97	1.88 $\pm$ 0.06	1.97	1.88 $\pm$ 0.06
TTL	428	432	368	448.5 $\pm$ 19.09	450.5 $\pm$ 14.85	206.7 $\pm$ 7.77	362.5 $\pm$ 7.78	282.5 $\pm$ 13.80	278	304.5 $\pm$ 20.51 <sup>a</sup>	278	304.5 $\pm$ 20.51 <sup>a</sup>
Tail	220	226	200	238.0 $\pm$ 4.24	232.5 $\pm$ 17.68	88.33 $\pm$ 4.73	199.0 $\pm$ 1.41	182.5 $\pm$ 8.81	164	163.0 $\pm$ 16.97 <sup>a</sup>	164	163.0 $\pm$ 16.97 <sup>a</sup>
HF	54	56	51	52.5 $\pm$ 0.71	50.0 $\pm$ 0.00	28.0 $\pm$ 0.00	37.5 $\pm$ 0.71	30.0 $\pm$ 0.82	30	37.25 $\pm$ 1.89	30	37.25 $\pm$ 1.89
Ear	40	40	37	33.5 $\pm$ 0.71	34.0 $\pm$ 1.41	18.3 $\pm$ 0.58	21.5 $\pm$ 0.71	18.3 $\pm$ 1.71	19	22.0 $\pm$ 1.41	19	22.0 $\pm$ 1.41
Mass	268	242	128	256.5 $\pm$ 51.62	47.7 $\pm$ 5.13	103.5 $\pm$ 6.36	26.8 $\pm$ 3.06	86.5 $\pm$ 7.55	39	86.5 $\pm$ 7.55	39	86.5 $\pm$ 7.55

<sup>a</sup> *n* = 2.  
<sup>b</sup> *n* = 1.  
<sup>c</sup> *n* = 3.





**Fig. 2.**—A paratype of *Hyorhinomys stuempkei* (NMV C37196) in live pose, shortly after capture. Photo credit: Kevin C. Rowe. NMV, Museum Victoria, Melbourne.



**Fig. 3.**—Photographs of the a) forefeet and b) hind feet of *Hyorhinomys stuempkei*, taken from NMV C37198 after preservation in fluid. Shown are the dorsal (top), lateral (middle), and ventral (lower) aspects. NMV, Museum Victoria, Melbourne.

prominent, extending well beyond the horizontal plane of the upper molars. The pterygoid plate and alisphenoid strut are lacking. The foramen ovale opens anteriorly, toward the anterior opening of the alisphenoid canal. The dentary has an unusually long articular surface and lacks a coronoid process (Fig. 4). A deep fossa, laterally encapsulated by thin walls of bone, is present on the dorsal surface of the mandibular body just posterior of m3 and anterior to the mandibular foramen. The lower incisors are extremely long and procumbent, whereas the upper incisors are short and delicate. The jaw houses 3 small molars in each quadrant (Figs. 4 and 5).

**Etymology.**—The new genus is named for its hog-like nose, by combining the Greek “hyo” (hog), “rhino” (nose), and “mys” (mouse).

**Nomenclatural statement.**—A life science identifier (LSID) number was obtained for the new genus and species *Hyorhinomys stuempkei*: urn:lsid:zoobank.org:pub:C96E712B-8D38-444B-83BD-374216B49698.

**Description and comparisons.**—The same as for the only known species, reported below.

*H. stuempkei*, new species

**Holotype.**—An adult male (MZB 37001/LSUMZ 37061) prepared as a dried and stuffed skin, cleaned skull, and fluid-preserved

carcass and tongue. Separate pieces of liver were frozen in liquid nitrogen and fixed in 96% ethanol. The molars are worn such that their occlusal surfaces form simple basins. All cranial sutures are closed. The specimen will be permanently curated at MZB with frozen tissue archived at LSUMZ.

**Paratypes.**—Four additional specimens are known (LSUMZ 37059, 37060; NMV C37196, C37198), all taken within 500 m of the type locality. LSUMZ 37059 is a subadult male with slightly worn molars, prepared as a skin and skeleton, with the stomach and a testis fixed in formalin and subsequently stored in 70% ethanol. The testes were fully descended, but open metaphyses on the femur and tibia indicate the animal was still growing at the time of capture. LSUMZ 37060 is a juvenile male prepared as a skin and skeleton with the stomach preserved in fluid, as above. The molars are fully erupted, but unworn, the basioccipital-basisphenoid suture and long bone metaphyses are open, and the testicles were held in the abdomen. Separate samples of liver from each LSUMZ paratype were frozen in liquid nitrogen and preserved in 96% ethanol. NMV C37196 is a subadult female prepared as a skin and skeleton with the stomach preserved in fluid, as above. The specimen was not lactating and no scars were apparent in the uterine lining, indicating that the specimen was nulliparous. The molars are fully erupted, but the basioccipital-basisphenoid suture is open. NMV C37198 is a juvenile female fixed in formalin and subsequently stored in 70% ethanol. Separate samples of liver from each NMV paratype were preserved in 96% and 70% ethanol.

**Type locality.**—Indonesia, Sulawesi Island, Central Sulawesi, Tolitoli, Galang, Malanga Selatan, Mt. Dako, 1.10607°N 120.93853°E, 1,600 m asl.

**Etymology.**—The species is named in honor of Gerolf Steiner, who used the pseudonym Harald Stümpke, to publish a small book (*Bau und Leben der Rhinogradentia*) commonly known in English as *The Snouters* (Stümpke 1967). *The Snouters* describes a fictional island radiation of mammals with extraordinary nasal and aural adaptations and seemingly anticipates the discovery of *H. stuempkei*, with its large pink nose and long pinnae. We recommend “Sulawesi snouter” as an English common name.

**Distribution.**—Known only from the type locality on Mt. Dako, Tolitoli, located on Sulawesi’s north peninsula. However, no montane sites on the north peninsula have been well surveyed for murines, and the breadth of this species’ geographic distribution remains an open question.

**Diagnosis.**—Because *H. stuempkei* is the only known species of *Hyorhinomys*, the specific diagnosis is the same as reported above for the genus.

**Description and comparisons.**—We summarize the most unusual characters of *H. stuempkei* in Table 2. The new species can be distinguished from all other Indonesian murines by its large, pink nose with forward-facing nares at the end of a long rostrum (Fig. 2). All other Sulawesi shrew rats and the Sulawesi water rat have a much smaller, less conspicuous rhinarium (photographs and illustrations of these taxa are found in Musser 1990; Musser and Durden 2002; Esselstyn et al. 2012; Achmadi et al. 2014; Musser and Durden 2014; and Rowe et al. 2014).



**Fig. 4.**—From top to bottom: dorsal, occlusal, and lateral views of the skull and lateral and occlusal views of the mandible of the holotype of *Hyorhinomys stuempkei* (MZB 37001/LSUMZ 37061). LSUMZ, Louisiana State University Museum of Natural Science, Baton Rouge; MZB, Museum Zoologicum Bogoriense, Bogor.

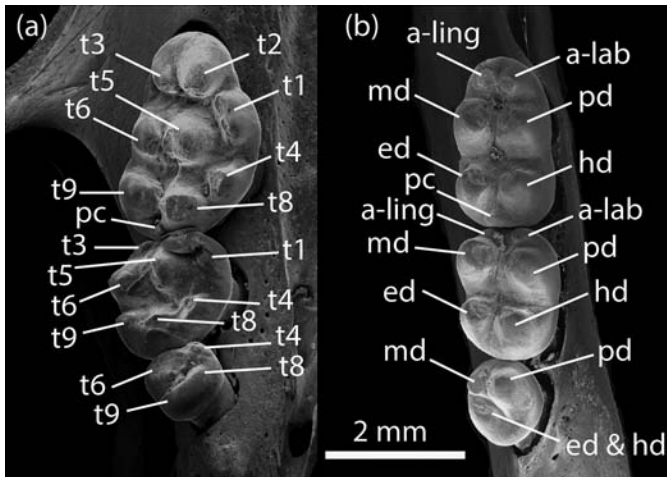
The head and chest are both large relative to body size (Fig. 2), giving *H. stuempkei* a barrel-chested appearance relative to most Sulawesi murines, including the shrew rats and water rat. In overall body size, *Hyorhinomys* is substantially larger than *M. naso*, *S. macrorhinos*, *T. macrocercus*, *W. mamasae*, *P. vermidax*, and *T. rhinogradoides*, but smaller than both species of *Echiothrix* (Table 1). As is typical of Sulawesi shrew rats, the rostrum is long and the eyes and mouth are small. *W. mamasae*, unlike the shrew rats, has a short, broad rostrum along with small eyes and ears, as do many amphibious mammals.

The pelage of *Hyorhinomys* is unlike that of any other murine currently known from Sulawesi, being soft, but relatively short and sparse. All other Sulawesi murines have much denser fur coats. The dorsal hairs are white at the base, pale grey in the middle, and transition to dark brown at the tip. Unlike the other dorsal hairs, guard hairs on the rump terminate with an approximately 2 mm-long white tip. The dorsal pelage has a mild sheen and is slightly darker on the back than on the flanks, giving the animal a blotchy, medium brown appearance (Fig. 2). Some individuals, including one of the juveniles, have a small white spot on top of the head. The longest underfur hairs approach 15 mm at mid-dorsum whereas guard hairs reach ~ 20 mm. The pelage is darkest on parts of the face, where dark patches surround the eyes and mystacial region. The mystacial vibrissae are thin and black at the base, transitioning to pale grey at their termini. The ventral pelage is thin and creamy white. The pale yellow integument can be seen through the ventral fur. The pelage color of the dorsal surface of the arm matches that of the back, until the wrist, where it abruptly changes to white on the hand. Approximately 5 ulnar vibrissae are present with lengths of 6–12 mm. The digits are hairless (Fig. 3a). The hind feet are much darker than the forefeet. Dark brown fur extends from the dorsum to near the base of the toes, which have a sparse coat of short white hairs and a small tuft of longer white hairs originating near the base of each claw (Fig. 3b). The juvenile pelage, as noted from LSUMZ 37060 and NMV C37198, is slightly greyer than the adult pelage on the dorsum, but otherwise resembles that of the adults and subadults in color and texture.

The forefeet of *H. stuempkei* are short and pale, with short, broad, nail-like claws on digits II–V that extend just beyond (ca. 1 mm) the tips of the phalanges (Fig. 3a). The pollex is short and bears a nail (Fig. 3a). *T. rhinogradoides* has similarly broad, nail-like claws on digits II–V, but they are much longer, extending 2–4 mm beyond the tips of the digits. The water rat and all other Sulawesi shrew rats, except *T. rhinogradoides*, have typical (for murines), laterally compressed claws on the forefeet. Three interdigital pads are present on the forefeet, along with distinct thenar and hypothenar pads. The thenar is approximately half as prominent as the hypothenar, but similar in size to the 1st and 3rd interdigital pads. The 2nd interdigital pad is elongate, but indistinct (Fig. 3a). The hind limbs are long and the hind feet have sharp, laterally compressed claws on all 5 digits. The soles are darkly pigmented, but the ventral surfaces of the toes are pale yellow. Four interdigital pads are present, along with a long, broad thenar and small hypothenar (Fig. 3b).

The skull of the new species is large relative to body size (Table 1) for a Sulawesi shrew rat (*Melasmothrix*, *Paucidentomys*, *Sommeromys*, and *Tateomys* are smaller absolutely; the skull of *Echiothrix* is similar in absolute size, despite its larger body) and as compared to *W. mamasae*. The braincase is mostly smooth on the dorsolateral margins but has a modest ridge separating the occiput from the interparietal and parietal bones. The smaller shrew rats all lack ridges on the dorsolateral margins of the braincase, but *Echiothrix* possesses more prominent ridges (comparable images of other Sulawesi shrew rat skulls and *W. mamasae* are found in Musser and Durden 2002;





**Fig. 5.**—Scanning electron micrographs of the a) upper and b) lower right molar row of a juvenile *Hyorhinomys stuempkei* (LSUMZ 37060). 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; hd, hypoconid. LSUMZ, Louisiana State University Museum of Natural Science, Baton Rouge.

**Table 2.**—Morphological characters of *Hyorhinomys stuempkei*, and the Sulawesi shrew rat taxa with which they are shared.

Character	Shared with
Nail-like claws on forefeet	<i>Tateomys rhinogradoides</i>
Large, flat, pink nose	None
Ear length > 20% head and body length	None
Head large relative to body size	None
Hair soft and sparse	None
Very long urogenital hairs	None
Hamular process of pterygoid bone prominent	<i>Echiothrix</i> spp.
Hamular process of pterygoid bone bows medially	None
Anteriorly directed foramen ovale	None
Deep fossa in dentary posterior to m3	Shallow dish in other genera
No pterygoid plate	<i>Echiothrix</i> spp.
Nasal bones terminate above incisors	None
Very long mandibular condyle	None
Large lower incisors rooted to articular condyle on robust dentary	None
No coronoid process on mandible	None
Narrow, slit-like infraorbital foramen	None
Sphenopalatine vacuity adjacent to anterior opening of alisphenoid canal	<i>Tateomys rhinogradoides</i>

Esselstyn et al. 2012; Musser and Durden 2014; and Rowe et al. 2014). The interparietal bone is very small in the new species, at only ~ 1 mm deep along the anteroposterior axis. All other species of Sulawesi shrew rats have interparietal bones that are at least twice as deep. The new species and most other shrew rats have smooth interorbital margins; only *Echiothrix* has prominent ridges on the interorbital margins of the dorsal surface of the skull. The braincase of the new species is squarish relative to the more rounded shapes found in all other Sulawesi shrew rats. The zygomatic arches bow outward modestly beyond the breadth of the braincase before sweeping gradually inward toward their maxillary roots. Zygomatic breadth is also slightly greater than braincase breadth in *Waiomys* and

*Echiothrix*, but less than or equal to braincase breadth in all other Sulawesi shrew rats. The rostrum of *Hyorhinomys* is long, with the nasal bones expanding in width near their distal ends, where they terminate at the vertical plane of the upper incisors; in all other Sulawesi shrew rats, the nasals extend beyond the incisors, greatly so in *Sommeromys*. In contrast, the rostrum of *Waiomys* is short. In the new species, the incisive foramina are short, of moderate width (Table 1), and centered longitudinally on the diastema (Fig. 4). Their posterior margin closes well anterior of the anterior margin of the zygomatic arch; the other Sulawesi shrew rats and the water rat all have longer incisive foramina (relative to skull length) that either overlap with (*Sommeromys*), or approach (*Echiothrix*, *Melasmothrix*, *Paucidentomys*, *Tateomys*, and *Waiomys*) the anterior root of the zygomatic arch. The infraorbital foramina are narrow and slit-like in *Hyorhinomys*; these foramina are broader (relative to their height) in all the other species we examined.

The pterygoid plate, prominent in many species of Murinae, is greatly reduced in *Hyorhinomys* and *Echiothrix* (Musser and Durden 2014:28–29, figures 7 and 8). In this region of the skull, *Hyorhinomys* lacks an alisphenoid strut and the foramen ovale opens anteriorly (it is barely visible from the ventral aspect). The foramen ovale opens ventrally in all other Sulawesi shrew rats. The hamular process of the pterygoid is prominent and bows medially in *Hyorhinomys*, partially obscuring the sphenopalatine vacuity from an occlusal view (Fig. 4). Less prominent hamular processes are found in the Sulawesi water rat and the other shrew rats, excluding *Echiothrix*. In *Echiothrix*, the hamular process is even more prominent but does not bow medially to the extent seen in *Hyorhinomys*. The sphenopalatine vacuity of *Hyorhinomys* is ovate and lies adjacent (along the anteroposterior axis) to the anterior opening of the alisphenoid canal, as it does in *T. rhinogradoides*; in the other species we examined, the vacuity is anterior of the anterior opening in the alisphenoid canal. A stapedial foramen is present at the petromastoid fissure between the bulla and petrotic bone, as is a canal linking the middle lacerate foramen and foramen ovale. This canal is present in LSUMZ 37059, LSUMZ 37060, and NMV C37196, but lacking in LSUMZ 37061. Together, the presence of a stapedial foramen and this canal in all but one specimen indicates that the cephalic circulation pattern of the carotid artery matches that of many other murines (i.e., state 2 of Carleton 1980; Musser and Durden 2014).

In the holotype, the auditory bullae are highly inflated and lack an obvious Eustachian tube. They completely obscure the middle lacerate foramina. In this specimen, the bullae are also comprised of very thin and porous bone, with several foramina piercing their anterior faces. In contrast, the bullae are much less inflated in the other specimens, but one (LSUMZ 37059) also has perforated bullae. These latter specimens possess a typical murine Eustachian tube and the middle lacerate foramina are not obscured by the bullae in occlusal view. The auditory bullae in all other Sulawesi shrew rats are sized similarly (relative to skull size) to those found among the paratypes. The condition of the bullae in the holotype and LSUMZ 37059 may be symptomatic of infection by parasitic nematodes. Miller and Hollister (1921b) noted that in a series of *Maxomys hellwaldii*

from central Sulawesi the "... auditory bullae are abnormally swollen, a condition accompanied by the presence of a nematode parasite within the bullae."

The dentary of the new species is robust and holds extremely long, procumbent lower incisors. It is far more robust than the extremely gracile dentary of *Paucidentomys* and somewhat more robust than in *Echiothrix*. The dentary possesses a slight capsular ridge that extends to the articular condyle. The other Sulawesi shrew rats, excepting *Echiothrix*, lack a capsular ridge or process. In *Echiothrix*, a prominent capsular process is situated between the coronoid and condyloid processes, but nearer the former. *W. mamasae* has a modest capsular process positioned directly below the coronoid process. The mandibular condyle of *Hyorhinomys* is extremely long (Fig. 4), providing a large articular surface, which may facilitate a greater-than-usual fore-and-aft sliding motion of the lower jaw. All other Sulawesi shrew rats and the water rat have a much shorter mandibular condyle, in both absolute and relative terms. The dentary also lacks a coronoid process; all other Sulawesi shrew rats and the water rat have at least a spicule-like coronoid. The angular process of the mandible is prominent and blunt in *H. stuempkei* but does not extend laterally beyond the vertical plane formed by the dentary. A deep pocket is present in the mandibular body just posterior to m3; other Sulawesi shrew rats have a modest depression and *Waiomys* has a shallow shelf in the same position.

Relative to skull size, the molars of the new species are smaller than in the water rat and in all other Sulawesi shrew rats, except *Paucidentomys*, which lacks molars. In both the upper and lower jaws, the 1st molar is approximately twice as large as the 2nd molar, which is similarly large relative to the 3rd molar (Fig. 4); this pattern is common in murines, including all of the Sulawesi shrew rats that possess molars. However, in *Hyorhinomys*, M3 is smaller relative to M2 than in *Echiothrix* or *Melasmothrix*. In the oldest individual (the holotype), the molars are worn into simple basins. We therefore present scanning electron micrographs of the molars of a juvenile (Fig. 5) and describe molar cusp patterns based on the younger animals among the paratype series. We identified each molar cusp (Fig. 5) following Musser (1991). Coronal patterns consist of low but discrete round mounds. The occlusal surface of M1 is dominated by the longitudinal column formed by cusps t2, t5, and t8 (Fig. 5a). On the lingual margin, t1 is approximately twice as prominent as t4, with each cusp forming a small longitudinal ridge. On the buccal side of M1, cusps t3, t6, and t9 are low mounds subtending the more prominent medial cusps (Fig. 5a); the depressions between t3 and t2, t6 and t5, and t9 and t8 are less pronounced than those between t2 and t1, t5 and t4, and t8 and t4. A posterior cingulum is present on M1, but absent from M2 and M3. The occlusal surface of M2 is approximately circular in outline, with a broad t5 dominating the topography and subtended by a sharper t6, while t4, t8, and t9 form an irregular ridge along the posterior margin of the tooth. On the first 2 upper molars, t4 is well posterior of t5 and t6 and forms a continuous ridge with t8 and t9. M3 is small with only a coalesced t8 and t9 forming any prominence. In occlusal outline, m1 approximates a rectangle but is narrower

at the anterior end. Hence, the anterolingual and anterolabial cusps are smaller than the middle and posterior cusps (Fig. 5b). A small posterior cingulum is present on m1, but absent from m2 and m3. The m2 is shorter (along the anteroposterior axis) than m1, mostly due to the very small size of the anterolingual and anterolabial cusps, which together form a small anterocoinid. The m3 is very small but holds a somewhat prominent protoconid (Fig. 5b).

On their labial surfaces, the upper and lower incisors of *Hyorhinomys* have unpigmented enamel with smooth surfaces or a very shallow, barely visible vertical depression. All other Sulawesi shrew rats share this lack of pigment, but some *Echiothrix* have a slight orange tint at the base of their incisors (Musser and Durden 2014). The only known specimen of *W. mamasae* has pale orange enamel on its incisors. On the lateral surfaces of the upper incisors of *Hyorhinomys*, enamel covers approximately three-fourths of the surface, with exposed dentine restricted to the posterior one-fourth; the posterior extension of enamel on the lateral surface of the upper incisors is much less extensive in all other Sulawesi shrew rats except *T. rhinogradoides*. *Echiothrix* is the only Sulawesi shrew rat with vertical grooves on the labial surfaces of the incisors, and there are 2 present on each tooth (Musser and Durden 2014). In *Hyorhinomys*, the upper incisors are very small (Fig. 4) and barely emerge from the gums, which is similar to the pattern in *Melasmothrix* and *Tateomys*. In contrast, *Echiothrix*, *Sommeromys*, and *Waiomys* have much more robust upper incisors, whereas *Paucidentomys* has small, but bifid upper incisors. The lower incisors are extremely long, robust, and procumbent in *Hyorhinomys*; their roots run the entire length of the ramus, extending into the base of the mandibular condyle. They are longer and broader absolutely and relative to skull length than in any of the other species we examined.

*Ecology*.—All 5 individuals of *H. stuempkei* were caught on the ground and at night at 1,600 m elevation. Extensive trapping was conducted simultaneously in mature low elevation forest (400–500 m), but no *H. stuempkei* were taken there. Habitat at the montane site was considered lower montane forest with no indication of human disturbance (Fig. 6). Abundant moss partially covered many surfaces and epiphytes were common in the forest canopy.

*Phylogenetic analyses*.—Concatenation of 4 exons and 1 mitochondrial locus resulted in an alignment consisting of 5,787 nucleotides. PartitionFinder analyses identified 8 optimal partitions of the data, which did not correspond to individual gene fragments, but rather represented combinations of codon positions across genes with similar substitution rates (Table 3). Bayesian analyses of partitioned sequence data appeared to converge within the first million generations, with all parameters having an ESS > 500; we discarded the first 10% of samples as burn-in.

Our phylogenetic results were concordant between Bayesian and likelihood inferences as well as with those of Rowe et al. (2014). *H. stuempkei* was the sister to all other sampled Sulawesi shrew rats (Fig. 7). *Echiothrix* and *Paucidentomys* were highly supported sister lineages,



as posited by Esselstyn et al. (2012), Musser (2014), and Musser and Durden (2014). Together, they were sister to *Melasmothrix*, again with strong support. *Hyorhinomys* was sister to *Echiothrix* + *Paucidentomys* + *Melasmothrix*, but with little support (Fig. 7). The Sulawesi water rat, *W. mamasae*, was sister to the entire clade of Sulawesi shrew rats and this relationship was also strongly supported. Given this topology, with strong support for all nodes discussed above except the one uniting *Hyorhinomys* with *Echiothrix* + *Melasmothrix* + *Paucidentomys*, it may be inferred that *Hyorhinomys* is either sister to all included Sulawesi shrew rats, as depicted (Fig. 7), or perhaps to *Waiomys*. The internal branches characterizing the relationships among these genera are very short (Fig. 7) relative to the terminal branches.

## DISCUSSION

*Hyorhinomys stuempkei* represents another lineage in Sulawesi's small, but morphologically diverse group of shrew rats. The animal shares several morphological features (long rostrum, soft fur, white enamel on incisors, small molars) with other members of this group, but no close morphological affinities for any described genus emerged from our qualitative examination of cranial and external characters. In light of our phylogenetic estimates from DNA sequences, this is not surprising. Using concatenated sequences from 5 genes, we placed *Hyorhinomys* as the sister to *Melasmothrix* + *Paucidentomys* + *Echiothrix*. Terminal branch lengths among these taxa are extremely long, relative to the internode lengths in this clade (Fig. 7). It therefore appears that shrew rats went through a rapid period of diversification a long time ago and the true relationships among these genera will probably prove difficult to estimate. We used concatenated sequences of multiple genes because gene trees estimated from individual loci resolved no relationships among the genera of Sulawesi shrew rats (not shown). However, concatenation assumes concordance among the sorting histories of individual genes and may overestimate confidence in relationships (Kubatko and Degnan 2007). Thus, future species tree estimates using many more loci may alter our current phylogenetic hypothesis.

The Sulawesi snouter's morphology, with its long hind limbs, large chest, and short forelimbs with broad, short claws, suggests it hops around its environment. We captured all 5 individuals at night in traps set on the ground. Therefore, presumably the species is terrestrial (versus arboreal) and nocturnal. The long rostrum and procumbent lower incisors may serve to probe holes in the mossy soil to feed on earthworms and arthropods. Alternatively, the long rostrum may engender a specialized olfactory system adapted to a vermivorous existence (Musser and Durden 2014). Indeed, the stomach contents of 3 individuals (NMV C37196; LSUMZ 37059, 37060) contained the remains of earthworms, beetle larvae, and unidentified insects.



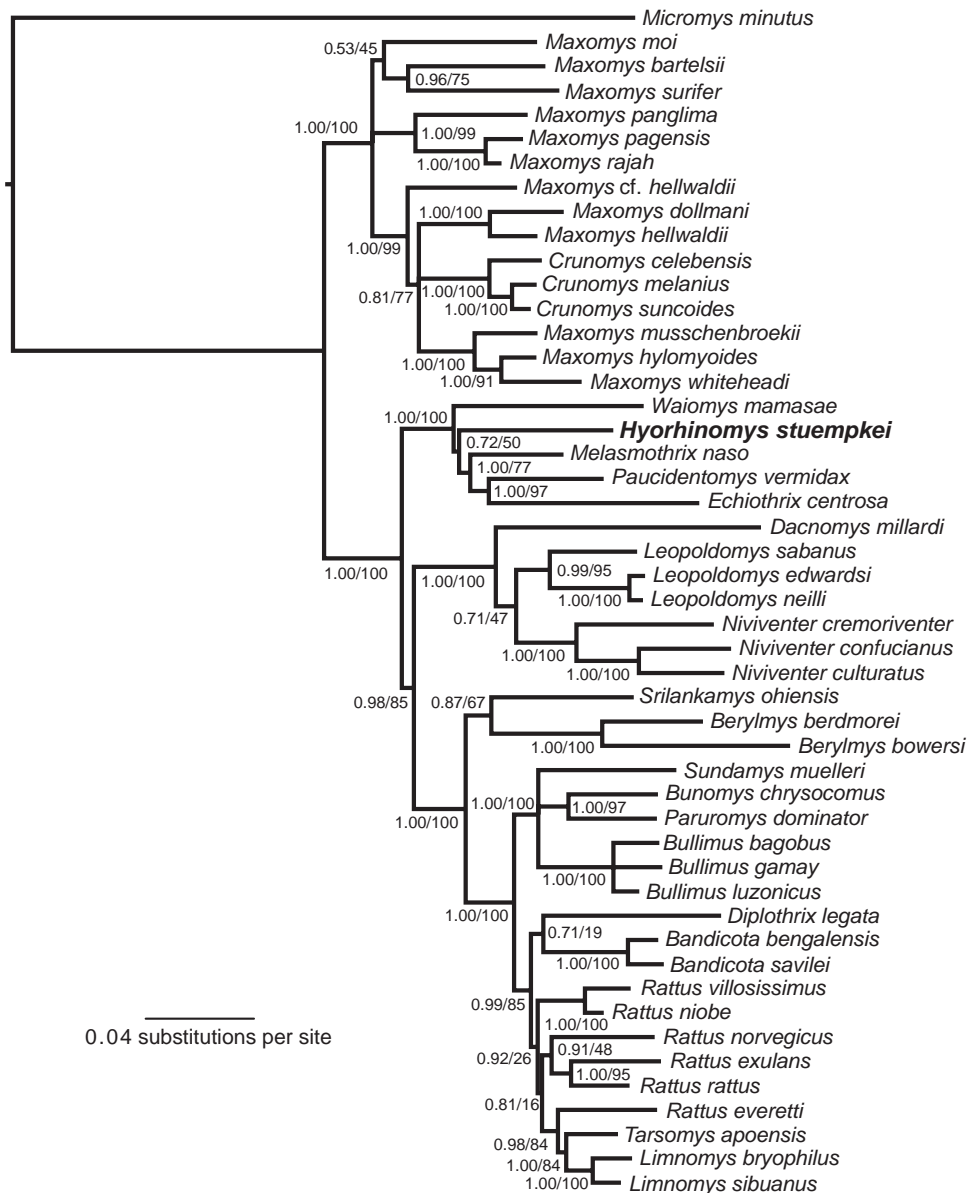
**Fig. 6.**—Lower montane forest at the type locality of *Hyorhinomys stuempkei*. Photo credit: Kevin C. Rowe.

**Table 3.**—Eight partitions of DNA sequence data and their best-fit models of sequence evolution.

Partition	Best model	Genes and codon positions
1	HKY+ $\Gamma$	<i>GHR</i> 1st, <i>IRBP</i> 1st, <i>RAG1</i> 1st
2	HKY+I+ $\Gamma$	<i>Cytb</i> 2nd, <i>IRBP</i> 2nd
3	HKY+ $\Gamma$	<i>GHR</i> 3rd, <i>IRBP</i> 3rd, <i>RAG1</i> 3rd
4	HKY+ $\Gamma$	<i>GHR</i> 2nd, <i>RAG1</i> 2nd
5	HKY+ $\Gamma$	<i>BRCA1</i> 1st, <i>BRCA1</i> 2nd
6	HKY+ $\Gamma$	<i>BRCA1</i> 3rd
7	SYM+I+ $\Gamma$	<i>Cytb</i> 1st
8	GTR+I+ $\Gamma$	<i>Cytb</i> 3rd

The new species was the only shrew rat captured during our survey of the murines of Mt. Dako, suggesting that the shrew rat fauna of the north peninsula of Sulawesi may be depauperate, relative to more central montane regions of the island. In less isolated regions of Sulawesi's central core, we have collected as many as 5 species of shrew rat on the same mountain (e.g., Mt. Gandangewata—Achmadi et al. 2014; Rowe et al. 2014). Thus far, only *H. stuempkei* and the 2 species of *Echiothrix* (*E. centrosa* in Gorontalo and west of the province, and *E. leucura* in the Manado area) have been documented on the north peninsula (Musser and Carleton 2005; Musser 2014; Musser and Durden 2014). Other shrew rats have mostly been recorded from Sulawesi's central core area of endemism (Musser 1982, 1987; Esselstyn et al. 2012; Musser and Durden 2014; Rowe et al. 2014).

On Luzon Island in the Philippines, long-running murine inventories are revealing a fine-scaled pattern of endemism, in which isolated mountain peaks and ranges harbor largely endemic faunas (Balet et al. 2007; Heaney et al. 2011; Balet et al. 2012). A similar, but as yet undocumented, pattern may exist on Sulawesi. If so, the current areas-of-endemism paradigm (Evans et al. 2003) may underestimate the number of unique biogeographic regions on the island, perhaps especially for clades that are most diverse at mid to high elevations, such as murines.



**Fig. 7.**—Bayesian phylogenetic estimate of relationships among Indo-Australian murines, including species of shrew rat from Sulawesi. Numbers at nodes indicate posterior probabilities, followed by percent maximum likelihood bootstrap support.

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**APPENDIX I**

Specimens examined. Asterisks indicate specimens from which cranial and external measurements are reported in [Table 1](#).

*Hyorhinomys stuempkei*—Mt. Dako ( $n=5$ ): MZB 37001/LSUMZ 37061\*; LSUMZ 37059\*, 37060\*; NMV C37196\*, C37198\*.

*Echiothrix centrosa*—Kuala Nuvasu ( $n = 2$ ): AMNH 225680\*, 225685\*; Pinedapa ( $n = 1$ ): FMNH 43409; Mt. Buliohuto ( $n = 1$ ): NMV C37808.

*Echiothrix leucura*—Roeroekan (= Ruruan;  $n = 1$ ): AMNH 101246\*; Bumbulan ( $n = 1$ ): 153013\*.

*Melasmothrix naso*—Mt. Rorekatimbo ( $n = 3$ ): FMNH 213284\*, 213447\*, 213448\*.

*Paucidentomys vermidax*—Mt. Latimojong ( $n = 1$ ): MZB 35000\*; Mt. Gandangdewata ( $n = 1$ ): MZB 35001\*.

*Sommeromys macrorhinos*—Mt. Gandangdewata ( $n = 3$ ): MZB 34758\*, 34759\*, 34903\*. Mt. Tokala ( $n = 1$ ): AMNH 226956\*.

*Tateomys macrocercus*—Mt. Rorekatimbo ( $n = 1$ ): FMNH 213450\*.

*Tateomys rhinogradoides*—Mt. Latimojong ( $n = 1$ ): FMNH 213434\*; Mt. Rorekatimbo ( $n=1$ ): FMNH 213338\*; Mt. Gandangdewata ( $n = 2$ ): NMV C37082\*, C37083\*.

**APPENDIX II**

Museum voucher numbers and GenBank accession numbers associated with DNA sequences used in phylogenetic analyses. na, not available.

Taxon	Voucher (s)	CytB	BRCA1	IRBP	GHR	RAG1
<i>Bandicota bengalensis</i>	T065	AM408336	na	AM408331	AM910945	na
<i>Bandicota savilei</i>	R1191	HM217385	na	HM217665	na	na
<i>Berylmys berdmorei</i>	R3618	HM217432	na	HM217639	na	na
<i>Berylmys bowersi</i>	MVZ 186482/T-861	AM408337	KC953160	AM407896	DQ019056	DQ023457
<i>Bullimus bagobus</i>	USNM 58789/USNM 458785/ USNM 458789	DQ191472	na	DQ191498	GQ405369	na
<i>Bullimus gamay</i>	FMNH 154823/FMNH 154821	DQ191473	na	DQ191499	GQ405370	na
<i>Bullimus luzonicus</i>	FMNH 169127/FMNH 167310	DQ191474	na	DQ191500	GQ405371	na
<i>Bunomys chrysocomus</i>	ABTC 65755	EU349704	EU349667	EU349839	EU349795	EU349880
<i>Crunomys celebensis</i>	NMV C37047	KC878028	KJ607264	KC878203	KC878172	KJ607311
<i>Crunomys melanius</i>	FMNH 147105	DQ191477	na	DQ191506	GQ405379	na
<i>Crunomys suncoides</i>	FMNH 147942	DQ191478	na	DQ191507	na	na
<i>Dacnomys millardi</i>	MVZ 186519	KC878029	KC953169	KC878206	DQ019058	DQ023459
<i>Diplothrix legata</i>	HS 1163	AB033696	EU349670	AB033706	EU349799	EU349885
<i>Echiothrix centrosa</i>	NMV C37808	KP210088	KP210084	KP210092	KP210090	KP210094
<i>Hyorhinomys stuempkei</i>	NMV C37198	KP210087	KP210085	KP210091	KP210089	KP210093
<i>Leopoldamys edwardsi</i>	MVZ 186501	KJ607279	na	HM217687	na	KJ607312
<i>Leopoldamys neilli</i>	R4486	HM217460	na	HM217697	na	na
<i>Leopoldamys sabanus</i>	CMNH 102138	KJ607280	KC953186	KJ607302	DQ019063	KC953513
<i>Limnomys bryophilus</i>	FMNH 147970	DQ191479	na	DQ191508	GQ405380	na
<i>Limnomys sibuanus</i>	FMNH 147947	DQ191480	na	DQ191509	GQ405381	na
<i>Maxomys bartelsii</i>	ABTC 48063	EU349762	EU349666	EU349857	DQ019066	DQ023460
<i>Maxomys cf. hellwaldii</i>	FMNH 213372	KC878039	na	KC878212	KC878174	KJ607313
<i>Maxomys dollmani</i>	MVZ 225725	KC878035	KJ607265	KC878213	KC878175	na
<i>Maxomys hellwaldii</i>	MVZ 225768	KC878044	KJ607266	KC878214	KC878176	KJ607314
<i>Maxomys hylomyoides</i>	FMNH 212980	KC878050	na	KC878218	KC878179	KJ607315
<i>Maxomys moi</i>	ROM 111318	KC878056	na	KC878219	KC878180	na
<i>Maxomys musschenbroekii</i>	MZB 34728	KJ607281	KJ607267	KJ607304	KJ607293	KJ607316
<i>Maxomys pagensis</i>	MZB 28335	KC878128	na	KC878225	KC878186	na
<i>Maxomys panglima</i>	KUMNH 165356	KC878129	KJ607268	KC878226	KC878187	KJ607317
<i>Maxomys rajah</i>	MVZ 192210	KC878137	na	KC878227	na	KJ607318
<i>Maxomys surifer</i>	ROM 107723	KC878157	KJ607269	KC878234	KC878193	na
<i>Maxomys whiteheadi</i>	ROM 113074	KJ607282	na	KJ607305	KJ607294	na
<i>Melasmothrix naso</i>	NMV C37064	KJ607283	KJ607270	KJ607306	KJ607295	KJ607319
<i>Micromys minutus</i>	HS 1148	AB201995	EU349664	AB033710	EU349818	EU349904
<i>Niviventer confucianus</i>	USNM 574365	JF714942	na	KC953416	KC953293	KC953540
<i>Niviventer cremoriventer</i>	F 35796	KJ607284	KC953198	KC953417	DQ019067	KC953541
<i>Niviventer culturatus</i>	MVZ 180686	GU479941	KC953199	KC953418	DQ019068	DQ023458
<i>Paruromys dominator</i>	NMV C37024	KJ607285	KJ607271	KJ607307	KJ607296	KJ607320
<i>Paucidentomys vermidax</i>	FMNH 213102	KJ607286	KJ607272	KJ607308	KJ607297	KJ607321
<i>Rattus everetti</i>	FMNH 142350	DQ191485	na	DQ191513	na	na
<i>Rattus exulans</i>	NK 80010	NK 80010	na	KC953446	DQ019074	DQ023455
<i>Rattus niobe</i>	ABTC 42489	na	HQ334394	HQ334580	na	HQ334648
<i>Rattus norvegicus</i>	Sprague-Dawley lab strain	EU349782	EU349671	AB033709	JF412704	AY294938
<i>Rattus rattus</i>	T820/T660/CACG A65	na	na	HM217606	AM910976	HQ334643
<i>Rattus villosissimus</i>	ABTC 00549	EU349729	EU349673	HQ334576	EU349826	EU349915
<i>Srilankamys ohienis</i>	Unknown	JN009856	na	JN009857	JN009860	na
<i>Sundamys muelleri</i>	MVZ 192334	EU349787	EU349668	AY326111	DQ019077	DQ023456
<i>Tarsomys apoensis</i>	FMNH 148178	DQ191491	na	DQ191516	GQ405395	na
<i>Waiomys mamasae</i>	MZB 37000/NMV C37027	KJ607287	KJ607273	KJ607309	KJ607298	KJ607322