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Authors: Heaney, Lawrence R., Balete, Danilo S., Rickart, Eric A., Veluz, Maria Josefa, and Jansa, Sharon A.

Source: American Museum Novitates, 2014(3802) : 1-27

Published By: American Museum of Natural History

URL: <https://doi.org/10.1206/3802.1>

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Three New Species of *Musseromys* (Muridae, Rodentia), the Endemic Philippine Tree Mouse from Luzon Island

LAWRENCE R. HEANEY,¹ DANILO S. BALETE,¹ ERIC A. RICKART,² MARIA JOSEFA
VELUZ,³ AND SHARON A. JANSA⁴

ABSTRACT

We describe and name three new species of *Musseromys* from the mountains of northern Luzon based on morphological and DNA sequence data. Previously, *Musseromys* was known only from one species from the lowlands of central Luzon. These are the smallest-known members of the cloud rat clade of endemic Philippine murids, weighing only 15–22 g, an order of magnitude smaller than the previously smallest known members of the clade (*Carpomys* spp.), and more than two orders of magnitude smaller than the largest members (*Phloeomys* spp.). These discoveries raise the number of native murids documented on Luzon to 43, 93% of which are endemic, and 88% of which are members of two endemic Philippine clades. *Musseromys* is inferred to have originated in montane habitats, probably in the Central Cordillera of northern Luzon, with movement to two other areas on Luzon, one in montane habitat and one in lowland habitat, associated with the speciation process.

INTRODUCTION

Among the 17 genera of murid rodents that are endemic to the Philippine archipelago (Heaney et al., 2010), the most spectacular are the giant cloud rats. *Phloeomys pallidus* reaches up to 2.7 kg in mass, and *Crateromys schadenbergi* reaches 1.5 kg; both are covered entirely in

¹ Field Museum of Natural History, 1400 S Lake Shore Drive, Chicago, IL 60605.

² Natural History Museum of Utah, 301 Wakara Way, Salt Lake City, UT 84108.

³ National Museum of the Philippines, Padre Burgos St., Ermita, Manila, 1000 Philippines.

⁴ Bell Museum of Natural History, University of Minnesota, Minneapolis, MN 55455.

long fur, either entirely black or very dark brown, or with dramatically contrasting combinations of black, white, and silver-gray. The closely related genera *Carpomys* and *Batomys*, often respectively called dwarf cloud rats and hairy-tailed rats, are smaller, up to 165 g and 225 g, respectively. These four genera, all of which had been described by 1895, have been confirmed as members of an endemic Philippine clade (Fabre et al., 2013; Heaney et al., 2009; Jansa et al., 2006; Musser and Heaney, 1992; Schenk et al., 2013; Thomas, 1895). All species in these genera (13 are currently recognized) are suspected to be entirely herbivorous, and most spend much of their time in the forest canopy; all have long, furry or hairy tails, and all have hind feet that are short, broad, and at least partially grasping (Heaney et al., 2010; Rickart et al., 2011a). Collectively, these species constitute a remarkable example of morphological and ecological radiation of mammals in an oceanic archipelago (Heaney et al., 2009; Heaney and Goodman, 2009; Jansa et al., 2006).

In 2009, we described a fifth genus in this clade, also remarkable for its size: *Musseromys gulantang*, from Mt. Banahaw, Luzon Island (fig. 1), known from a single specimen that weighed only 15.5 g, expanding the documented size range within this endemic Philippine clade by an order of magnitude (Heaney et al., 2009). During our subsequent efforts to document the diversity, biogeography, and evolutionary history of the mammals of Luzon, we recorded the presence of *Musseromys* in three regions in the mountains of northern Luzon Island (fig. 1; Balete et al., 2011; Rickart et al., 2011b), each of which appeared to be morphologically distinctive at the time of discovery. The purpose of this paper is to formally describe these as new species within *Musseromys*, which we rediagnose to encompass the new species.

MATERIALS AND METHODS

FIELD AND PREPARATION PROCEDURES

The specimens examined in this study were all collected by the authors. These specimens are currently deposited at the Field Museum of Natural History (FMNH); half of the specimens, including the holotypes, will be transferred to the National Museum of the Philippines (PNM). The capture and handling of animals in the field followed all relevant laws and regulations of the Philippines.

Tissue samples were taken from the thigh muscle of fresh specimens and preserved in either 95% ethanol or DMSO buffer. Most of the specimens were injected with saturated formalin solution in the field, stored temporarily in 10% formalin, and subsequently transferred to 70% ethanol. Some skulls were then removed, cleaned with dermestid beetles, and briefly soaked in a dilute ammonia solution. Some specimens were preserved as complete skeletons in the field; these were cleaned in the same fashion as the skulls.

Reproductive data were taken in the field from skeletonized specimens or in the laboratory from autopsied specimens stored in 70% ethanol, including, for males: testes descent (scrotal or abdominal), and testes size (length \times width, in mm); for females: number and position of mammae (inguinal, abdominal, axial), size and condition of mammae (small, large, lactating),

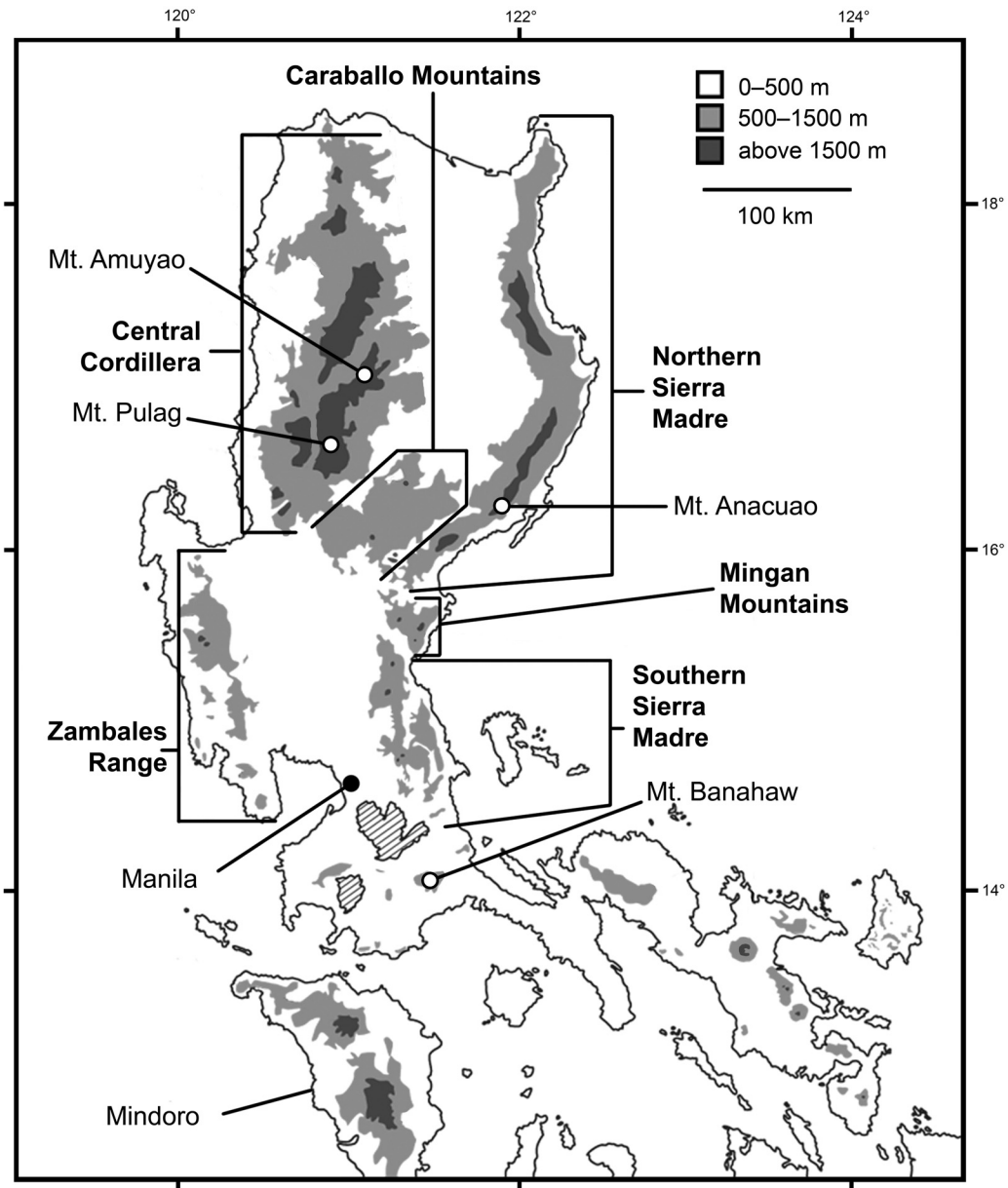


FIG. 1. Map of Luzon Island, Philippines, showing documented distributions of species and geographic features mentioned in the text, including the type localities of the four species of *Musseromys*.

presence or absence of vaginal perforation, number and size (crown to rump length, in mm) of embryos, and number of placental scars in the uterus.

Age determination was done in the field based on relative body size and reproductive condition of freshly caught specimens, and subsequently validated based on molar wear and fusion of cranial sutures, following the age categories defined by Musser and Heaney (1992).

MORPHOLOGICAL METHODS

We followed the terminology of Brown (1971) and Brown and Yalden (1973) for defining the external features of the head and limbs. Terminology for cusps on molar teeth and cranial foramina was adapted from Musser and Heaney (1992: figs. 2, 8).

External measurements (in mm) were taken in the field from fresh specimens, including total length (TOTAL), length of tail (TAIL), length of hind foot including claws (LHF), length of ear from notch (EAR), and weight in grams (WT); field catalogs of the collectors with these measurements and additional notes have been deposited at FMNH. Additional measurements of length of overfur (LOF, measured in the middorsal region) and number of tail scale rings per centimeter (TSR, counted at a point on the tail one-third of its length from the base) were taken from specimens preserved in 70% ethyl alcohol. The length of head and body (HBL) is the length of tail subtracted from total length.

Scanning electron micrographs of crania, mandibles, and teeth were made from uncoated specimens with an AMRAY 1810 scanning electron microscope. Each entire cranium or mandible fit within a single frame.

Eighteen cranial and dental measurements of seven adult specimens were taken by Heaney under a dissecting microscope with digital calipers and recorded to the nearest 0.01 mm, following the terminology and limits of these measurements defined in Heaney et al. (2011; see also Musser and Heaney, 1992): alveolar length of the maxillary molars (M1–M3), basioccipital length (BOL), breadth across upper incisors near their tips (BIT), breadth of first upper molar (BM1), breadth of zygomatic plate (ZP), height of braincase (HBC), inter-orbital breadth (IB), length of diastema (DL), length of incisive foramina (LIF), length of nasal bones (NL), lingual palatal breadth at the upper third molar (LBM3), mastoid breadth (MB), orbito-temporal length (OL), labial palatal breadth at M1 (PBM1), postpalatal length (PPL), rostral depth (RD), rostral length (RL), and zygomatic breadth (ZB). The skull of the holotype of *Musseromys gulantang* was remeasured at the same time as the others to be certain of comparability; some measurements reported and analyzed here differ from those in Heaney et al. (2009). The number of measured adult specimens is less than the total number of specimens because we did not remove and clean skulls from most of the immature individuals or adults with trap-damaged skulls.

We assessed quantitative phenetic variation through principal components analysis (PCA), using the correlation matrix of log₁₀-transformed measurements of adult specimens, using SYSTAT 10 for Windows (SPSS, Inc., 2000). We report and interpret only those axes with eigenvalues greater than 1.5.

MOLECULAR GENETIC METHODS

We used DNA sequences from the mitochondrial cytochrome *b* (CYTB) gene to assess genetic variation among the three putative new *Musseromys* species and *M. gulantang*. For phylogenetic analysis, we also included other members of the cloud rat clade, and we rooted the resulting trees using sequences from *Rattus norvegicus* (Genbank number X14848) and

TABLE 1. Results of principal components analysis of log₁₀-transformed cranial and dental measurements of adult *Musseromys* (see Morphological Methods).

Shown are the character loadings, eigenvalues, and percentage of variance explained on the first three components.

Variable	Principal component		
	1	2	3
BOL	0.955	-0.258	0.059
IB	0.681	0.435	0.423
ZB	0.953	0.026	-0.157
MB	0.873	0.271	-0.049
NL	0.656	0.017	-0.695
LIF	0.666	0.014	0.618
RD	0.685	-0.008	0.720
RL	0.714	-0.599	-0.214
OL	0.539	0.755	0.034
M1–M3	0.657	-0.673	-0.286
PBM1	0.231	0.451	-0.838
DL	0.847	-0.124	0.386
PPL	0.823	-0.473	-0.134
LBM3	0.196	0.831	-0.058
HBC	0.837	0.264	0.148
BM1	0.703	-0.078	-0.659
BIT	0.843	0.372	0.030
ZP	0.124	-0.939	0.192
Eigenvalue	9.0	3.9	3.1
Variance explained	50.2%	21.9%	17.1%

three species of gerbil: *Meriones unguiculatus* (AF119264), *Gerbillus nigeriae* (AJ430555), and *Gerbilliscus guineae* (AJ430562). DNA was extracted from field-collected tissues using a Qiagen DNA Minikit (Qiagen, Inc.). We PCR amplified the complete CYTB gene using primers MVZ05a and UMMZ04 (Jansa et al., 2006). To facilitate sequencing, we modified primers by adding M13 tails to the 5' end of each primer. All PCR amplifications were performed as 25 µL reactions, using GoTaq (Promega Corp.) and recommended reagent concentrations. Reactions were run as a four-stage touchdown protocol as described in Jansa and Weksler (2004). Amplification products were Sanger sequenced in both directions using M13 primers.

DNA sequences were aligned using MUSCLE (Edgar, 2004) with default settings as implemented in Geneious v. 6.1.2 (Drummond et al., 2006). We analyzed the resulting aligned sequences using maximum likelihood inference as implemented in RAxML v. 7.2 (Stamatakis, 2006) running on the CIPRES Science Gateway v. 3.1 (<http://www.phylo.org>). We used the GTRGAMMA model of sequence substitution to infer the best tree and performed 1000 bootstrap replicates to assess nodal support.

TABLE 2. Cranial and dental measurements of adults of four species of *Musseromys*. See Morphological Methods for definitions and abbreviations. Numbers at the heads of columns are FMNH catalog numbers.

Variable	<i>M. gulantang</i>	<i>M. inopinatus</i> , n. sp.		<i>M. beneficus</i> , n. sp.		<i>M. anacuaio</i> , n. sp.	
	178405	193839	193840	198714	198857	209522	209523
	Holotype ♂	Holotype ♂	♀	Holotype ♀	♂	Holotype ♀	♂
BOL	19.93	21.99	21.88	21.91	22.06	19.98	20.65
IB	3.97	4.47	4.49	4.73	4.85	4.45	4.78
ZB	12.52	13.14	13.16	13.85	13.41	12.38	12.51
MB	10.01	10.77	10.86	11.09	10.96	10.16	10.63
NL	7.23	7.10	7.26	7.29	7.46	6.99	7.01
LIF	2.59	3.36	3.53	3.42	3.50	3.47	3.13
RD	5.20	5.76	5.62	5.73	5.59	5.58	5.60
RL	7.82	8.40	8.53	7.95	8.46	7.44	7.75
OL	6.35	6.52	6.18	7.21	7.00	6.64	6.55
M1–M3	3.23	3.37	3.43	3.26	3.35	3.10	3.09
PBM1	4.31	4.03	4.15	4.30	4.30	4.04	4.20
DL	5.59	6.30	6.11	6.38	6.01	5.82	5.91
PPL	8.24	8.89	8.77	8.68	8.67	7.90	8.21
LBM3	2.50	2.47	2.41	2.58	2.70	2.57	2.58
HBC	7.64	7.85	8.13	8.30	8.05	7.83	8.00
BM1	1.06	1.01	1.11	1.12	1.10	0.95	1.00
BIT	1.32	1.41	1.36	1.51	1.48	1.37	1.34
ZP	1.84	2.17	2.12	1.69	1.88	1.83	1.78

To examine the evolution of habitat association for *Musseromys* species, we coded the Philippine taxa in our phylogeny as having distributions in either montane (>1500 m) or lowland (\leq 1500 m) habitats. We reconstructed ancestral habitat types on our phylogeny using parsimony optimization as implemented in Mesquite ver. 2.75 (Maddison and Maddison, 2011).

RESULTS

MORPHOLOGICAL COMPARISONS

In a principal components analysis of 18 cranial and dental measurements from seven adult specimens (one *M. gulantang* and two each of the other three putative species), the first three components each had an eigenvalue greater than 3.0 and together accounted for 89.2% of the total variance (table 1); the fourth and following components had eigenvalues below 1.0, and so are not interpretable. More than half of the variation (50.2%) occurred on the first component, with all but three variables loading positively at 0.5 or higher; this implies that the

first component is an indicator of overall size. Breadth of zygomatic plate, lingual breadth of palate at M3, and palatal breadth at M1 had loadings of lower magnitude on the first component indicating that they did not covary with overall size of the skull. A plot of individual *Musseromys* on this component (fig. 2A) shows the mice from Mt. Pulag as the largest, those from Mt. Amuyao slightly smaller, those from Mt. Anacuaao smaller still, and *M. gulantang* as the smallest of the four samples.

The second and third components, accounting for 21.9% and 17.1% of the variation respectively, reveal proportional (shape) differences among the samples. The second component contrasted individuals from Mt. Pulag and Mt. Anacuaao that have wider palatal breadth at the level of M3, greater orbito-temporal length, narrower zygomatic plates, and shorter molar rows and rostra compared with the single example of *M. gulantang* and the specimens from Mt. Amuyao (fig. 2A). The third component contrasted specimens with long incisive foramina, deep rostra, narrow palatal breadth at M1, short nasals, and narrow M1 with individuals with the converse. Specimens from Mt. Anacuaao scored highly on this axis but overlapped with those from Mt. Amuyao, with the two from Mt. Pulag neutral to slightly negative, and *M. gulantang* scoring strongly negatively (fig 2B).

The bivariate plots of specimen scores on the principal components (fig. 2), together with the measurements in table 2 on which this analysis is based and the cranial images (fig. 6), illustrate the distinctiveness of the four samples of *Musseromys*. *M. gulantang* differs from the other putative species most clearly in being generally small, and having short incisive foramina, a broad palate at M1, moderately long nasals, and fairly broad M1. The *Musseromys* from Mt. Pulag is the largest species overall, with relatively high lingual breadth of palate at M3, narrow zygomatic plates, moderate molar row length, and moderate rostral length. The *Musseromys* from Mt. Amuyao is moderately large, with low lingual breadth of palate at M3, broad zygomatic plates, long molar rows, and long rostra, with long incisive foramina, narrow palatal breadth at M1, and moderately short nasals. The specimens from Mt. Anacuaao are relatively small overall, with fairly high lingual breadth of palate at M3 and narrow zygomatic plates, short molar rows, nasals, and rostra, and relatively long incisive foramina, narrow palatal breadth at M1, and narrow M1.

MOLECULAR PHYLOGENETIC ANALYSIS

CYTB sequences from individual *Musseromys* collected on a single mountain are either identical (i.e., DSB 5325 and DSB 5326 from Mt. Pulag) or differ by no more than four substitutions (fig. 3). Genetic divergence (uncorrected p-distances) among *Musseromys* cytochrome *b* sequences ranges from 7.2% (between specimens from Mt. Anacuaao (*M. anacuaao*, n. sp.) and those from Mt. Pulag (*M. beneficus*, n. sp) to 12.6% (between Mt. Amuyao (*M. inopinatus*, n. sp) and *M. gulantang*). Although a high degree of genetic divergence cannot by itself serve as evidence of species differentiation, we note that these cytochrome *b* divergence values are comparable to or higher than those we recovered among species of *Soricomys* (7.9%–8.9% among four species) and *Archboldomys* (9.2% between *A. luzonensis* and *A. maximus*; Balet

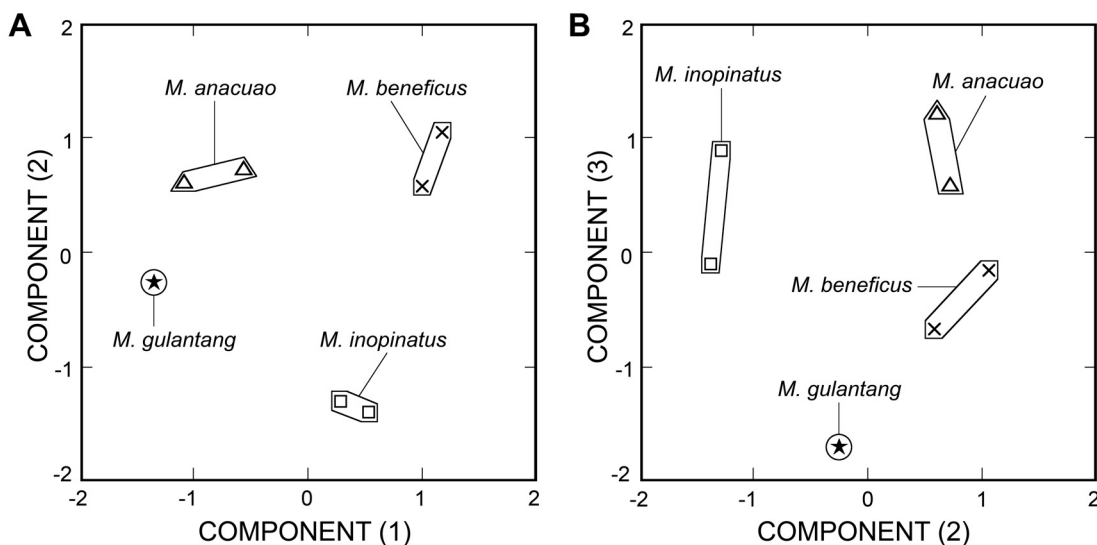


FIG. 2. Projection of specimen scores onto the first two axes (A) and the second and third axes (B) of a principal components analysis (table 1) of 18 craniodental variables (log-10 transformed) from seven specimens representing four putative species of *Musseromys*.

et al., 2012). The maximum-likelihood tree supports the monophyly of *Musseromys* species relative to other members of the cloud rat clade, and strongly supports a sister-taxon relationship between *Musseromys* and *Carpomys* to the exclusion of *Batomys*, *Crateromys*, and *Phloeomys* (fig. 3; see also Fabre et al., 2013; Heaney et al., 2009; Schenk et al., 2013).

TAXONOMY

The foregoing analyses of morphology and molecular genetics support the recognition of three additional species of *Musseromys*, and require a rediagnosis of the genus to encompass the new species.

Musseromys Heaney et al., 2009

TYPE SPECIES: *Musseromys gulantang* Heaney et al., 2009: 216.

INCLUDED SPECIES: The type species, *M. inopinatus* new species, *M. beneficus* new species, and *M. anacuaao* new species.

DISTRIBUTION: Known from four mountainous areas in central and northern Luzon: Mt. Banahaw, the Central Cordillera (Mt. Amuyao and Mt. Pulag), and the northern Sierra Madre (Mt. Anacuaao; fig. 1).

EMENDED DIAGNOSIS: A member of the Muridae, subfamily Murinae, as defined and diagnosed by Carleton and Musser (1984) and Musser and Carleton (2005). *Musseromys* is defined phylogenetically as the most recent common ancestor of *M. gulantang*, *M. inopinatus*, n. sp., *M. beneficus*, n. sp., and *M. anacuaao*, n. sp., and all of its descendants (fig. 3). This emended diagnosis is based primarily on one adult specimen of *M. gulantang* with cleaned skull, and

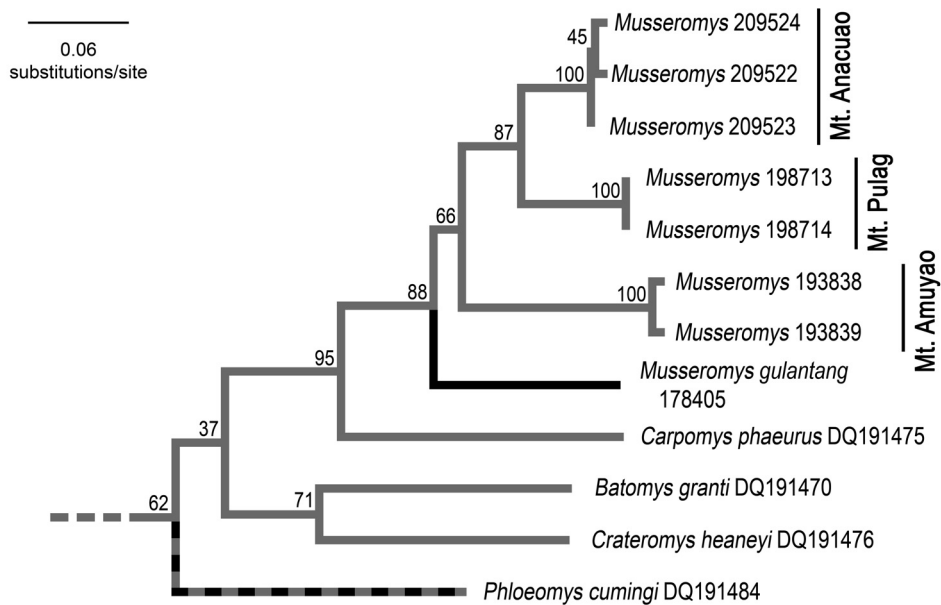


FIG. 3. The tree resulting from a maximum-likelihood analysis of the cytochrome *b* gene from *Phloeomys* Division species under the best-fitting model (GTR+I+ Γ 4). Numbers at nodes indicate maximum-likelihood (above the line) bootstrap support. Terminal taxa are identified by species name and a unique alphanumeric identifier (either FMNH catalog number or Genbank accession number). Trees are rooted with *Rattus norvegicus* (Genbank number X14848) and with three species of gerbil: *Meriones unguiculatus* (AF119264), *Gerbillus nigeriae* (AJ430555), and *Gerbilliscus guineae* (AJ430562) as outgroups (not shown). Black and gray branches indicate elevational range reconstructed using parsimony optimization (see Molecular Genetic Methods), where black and grey indicate lowland and montane distributions, respectively.

two such specimens each of *M. inopinatus*, n. sp., *M. beneficus*, n. sp., and *M. anacuaio*, n. sp. *Musseromys* may be identified by the following combination of morphological traits relative to other murines: size small (15–22 g, head and body length 74–84 mm); dorsal pelage bright orange-russet to dark russet-brown; ventral pelage usually bright ochraceous mixed with off-white; mystacial vibrissae 42–53 mm, ca. 60%–65% length of head and body (fig. 5); postocular patch of bare skin 1.5–3 mm in diameter, with genal vibrissae 5–15 mm long arising from the middle portion; 2–3 ulnar-carpal vibrissae, 4–6 mm long; tail 82–101 mm, ca. 100%–130% length of head and body, with elongated hairs (“pencil”) along the posterior 25%–35%; ears either elongated and bluntly pointed, or large and rounded; all toes with long, sharply pointed claws except pollex, which has a small nail; hind foot with long toes and prominent plantar pads (fig. 4); females with two pairs of inguinal nipples; proodont incisors, about 2.5 times as deep as wide, deeply notched at tip (fig. 6); braincase about as wide as long; basicranial inflection slight; zygomatic arches broader than braincase for most of their length; incisive foramina of moderate length, narrow to moderate in width, ending slightly to substantially anterior to the first molars; palatal bridge of moderate width (slightly less than length of the molar row), ending level with the middle of the third molar to well posterior to the third molars; mesopterygoid fossa moderately narrow; alisphenoid strut absent and accessory foramen ovale and

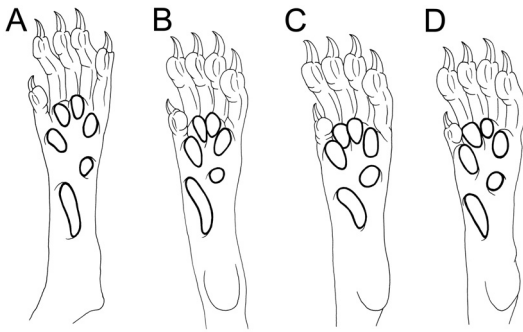


FIG. 4. Ventral surface of the hind feet of **A**, *Musseromys gulantang*; **B**, *M. inopinatus*; **C**, *M. beneficus*; and **D**, *M. anacuaao*, emphasizing the relative size and location of the plantar pads. All drawn to the same scale, ca. $\times 2$.

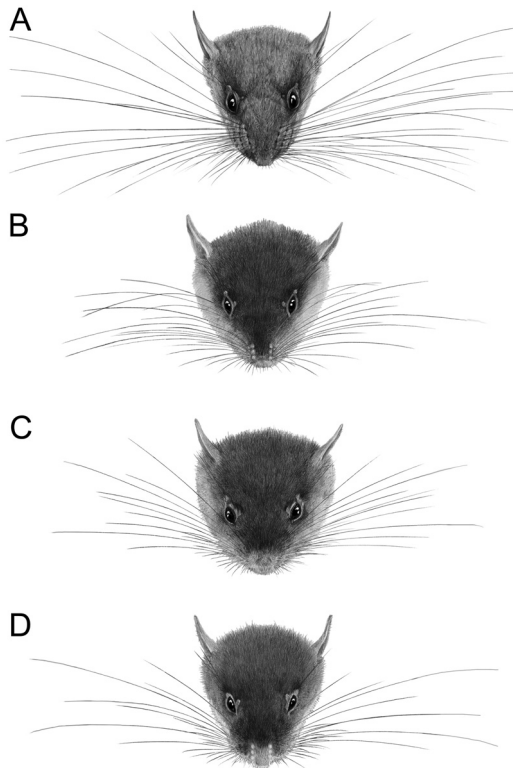


FIG. 5. Drawings of the heads of *Musseromys*: **A**, *M. gulantang*; **B**, *M. inopinatus*; **C**, *M. beneficus*; and **D**, *M. anacuaao*, showing the relative breadth of the head and length of the mystacial and genal vibrissae. All are drawn to the same scale.

foramen ovale coalesced in all four species; sphenopalatine vacuities large; pterygoid ridge weak, tapering posteriorly; middle lacerate foramen large; carotid canal large; stapedial foramen absent; coronoid process of mandible short; molars with thick layers of enamel and prominent cusps; a large, discrete cusp t7 present on each upper molar (fig. 7); cusp t9 relatively small on each upper molar; and a large anteroconid (comprised of anteroconial, anterolabial, and anterolingual cusps) forming the anterior one-third of each lower molar.

DESCRIPTION: All four of the species are small mice, to which the following general description applies (modified from Heaney et al., 2009; see species descriptions for further details). Head and body length ranges from 74–84 mm (table 3). The head is broad and large relative to the size of the torso, and the rostrum short and blunt (fig. 5). The eyes are of moderate size, and the ears are large and moderately to rather tall (15–17 mm), ranging at the tip from rounded to narrow and bluntly pointed. The mystacial vibrissae are long, ranging from 42 to 53 mm among the four species, always more than 60% of HBL. A bare patch of skin posterior to the eye has several genal vibrissae, ranging from 5 to 15 mm long among the species. The pelage is soft and fine, with moderate to high density, and many fine guard hairs project 1–2 mm above the overfur; all species have dorsal fur that ranges from bright rusty orange to dark rusty brown, and ventral fur that is paler and shorter than the dorsal fur, with some individuals having white areas of fur along the midline. The forefeet are slender with moderately long, sharply pointed claws (except the pollex, which has a small nail); the pads range from moderate to large. The hind feet range from moderately long and narrow with plantar pads of moderate size, to shorter and

TABLE 3. External measurements (mm), body mass (g), and measurement ratios (expressed as percentages) of adult *Musseromys*. Numbers at the heads of columns are FMNH catalog numbers.

Variable	<i>M. gulantang</i>	<i>M. inopinatus</i> , n. sp.		<i>M. beneficus</i> , n. sp.			<i>M. anacuaao</i> , n. sp.	
	178405	193839	193840	198713	198714	198857	209522	209523
	Holotype ♂	Holotype ♂	♀	♀	Holotype ♀	♂	Holotype ♀	♂
Total	178	166	163	157	163	172	165	160
HBL	77	78	78	75	81	84	83	74
TAIL	101	88	85	82	82	88	82	86
TAIL/HBL (%)	131	113	109	109	101	105	99	116
HF	20	19	18	18	18	19	18	18
HF/HBL (%)	26	24	24	24	22	22	19	23
EAR	16	17	17	16	16	16	15	16
MASS	15.5	19.5	17	18	22	22	21	17
LOF	6	5	5	6	6	6	6	6
TSR	17/cm	22/cm	22/cm	22/cm	23/cm	23/cm	20/cm	20/cm

broader with large pads (fig. 4). The tail is moderate to long (82–101 mm), 99%–131% of HBL, with hairs visible over the entire length but conspicuously longer over the distal portion (the last 10–25 mm). The tail scales are small, ranging from 17–23/cm.

The cranium is small (basioccipital length 19.9–22.1 mm), but broad with sturdy zygomatic arches (zygomatic breadth 12.4–13.8 mm; table 2; fig. 6). The rostrum is short but broad and deep, with relatively long nasals. There is no zygomatic notch or only a shallow concavity at most. The zygomatic plate is moderately wide; viewed laterally, the anterior edge of the plate is slightly concave, and its posterior edge is dorsal to the middle of the first molar. The infraorbital foramen is large and dorsoventrally elongate, widest at the top. In dorsal view, the orbito-temporal fossa is about as wide as it is long. The interorbital region is broad, and the frontal bones are not inflated. In dorsal view, the braincase is as broad as it is long, and proportionately large compared to most murids. Weak, indistinct temporal ridges are apparent on the braincase of older adults; in lateral view the anterior portion of the braincase is nearly flat, and the posterior portion of the dorsal surface curves smoothly ventrally toward its posterior edge.

In the orbital region, the optic foramen is visible; posterior to that opening can be seen part of the anterior lacerate foramen, and just below it is the anterior extension of the sphenopalatine vacuity (see Heaney et al., 2009: fig. 11; Musser et al., 1985). In all four species, the alisphenoid strut is absent or represented only by a short dorsal projection, so that the accessory foramen ovale is coalesced with the foramen ovale to form a proportionately long and wide opening. The ventral view of the basicranial region (see Heaney et al., 2009: fig. 12) shows a narrow presphenoid and anterior projection of the basisphenoid, with prominent sphenopalatine vacuities lateral to them. The bullae are small and not strongly inflated, and no stapedial foramen is evident. The lateral portion of the middle lacerate foramen is small, but the medial portion is large. The postglenoid foramen is large, and a strut of the squamosal extends

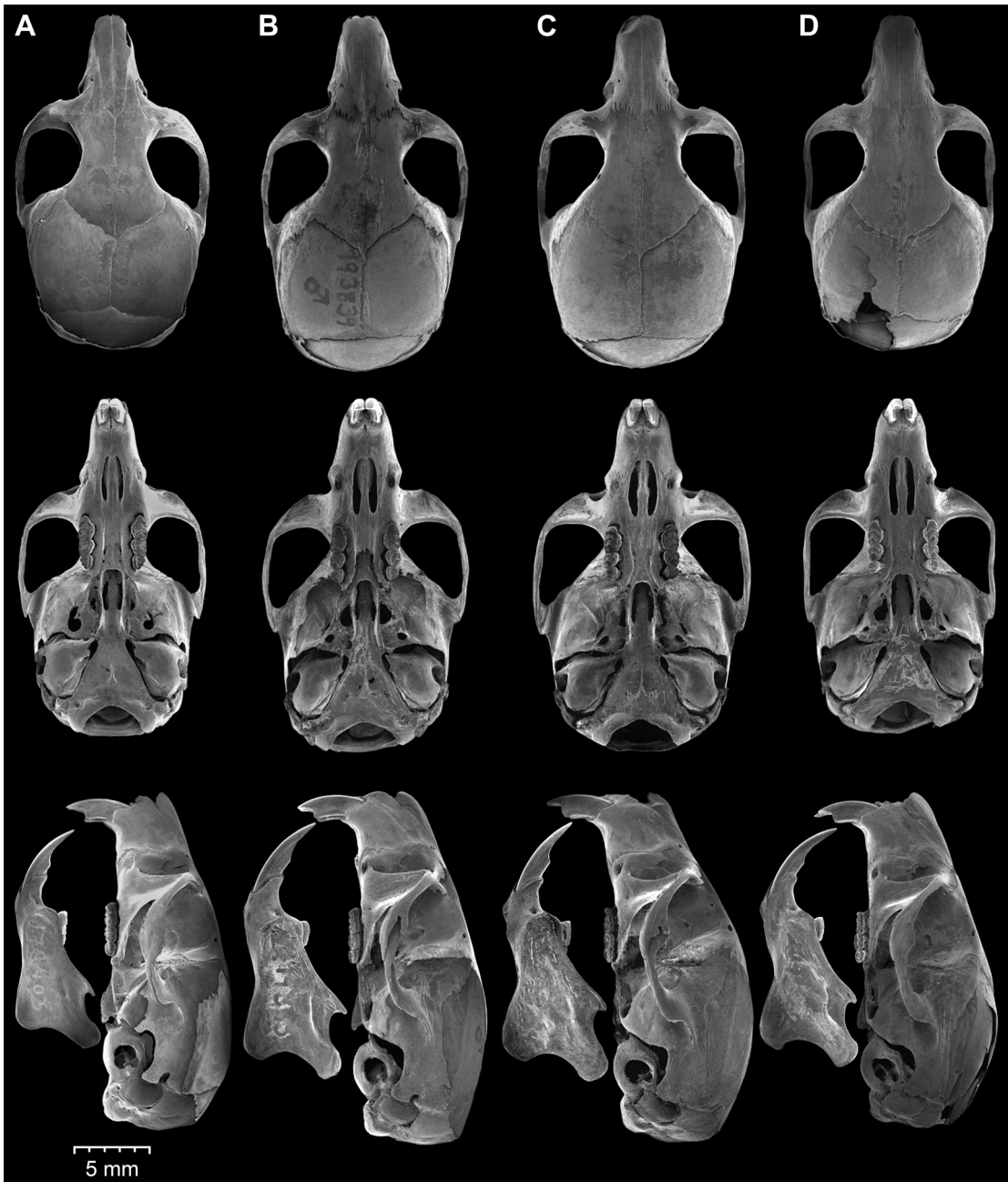


FIG. 6. Cranium (in dorsal, ventral, and lateral views) and mandible of **A**, *Musseromys gulantang*, adult male (FMNH 178405, holotype); **B**, *M. inopinatus*, adult female (FMNH 193839, holotype); **C**, *M. beneficus*, adult female (FMNH 198714, holotype); and **D**, *M. anacuaao*, adult female (FMNH 209522, holotype).

down to contact the mastoid, leaving a small fossa (the squamosal notch) dorsal to the strut in *M. gulantang* and the Mt. Amuyao specimens, but the squamosal strut entirely covers the location of the fossa in the Mt. Pulag and Mt. Anacuaao specimens.

The ventral surface of the bony palate (fig. 6) is slightly concave, with grooves of varying length and depth that extend from about the first molar to at least the level of the last molar (see descriptions, below). The palate is 2 to 2.5 times as wide as the first molar, with a posterior margin that terminates variously from about the middle of the last molar to a distance posterior to the last molar that is about equal to the width of the last molar. The incisive foramina are moderate to narrow in width, and similar to the molar row in length; they terminate variously from the level of the anterior edge of the first molar to a level nearly the length of the first molar anterior to its anterior edge.

The upper incisors are proodont, their anteriormost surface reaching about the anterior edge of the nasals or slightly beyond. They are about 2.5 times as deep as wide, with medium to pale orange enamel layers, smoothly rounded on the anterior surface, and deeply notched at the tip. The molars (as evident in a specimen with lightly worn molars, fig. 7) are tiny but proportionately robust, with thick layers of enamel. On each upper first molar, the anterior lamina is composed of t1, which is distinct, and the coalesced t2 and t3. The second lamina is composed of t4, t5, and t6, again with t4 being distinct. The third lamina is composed of a distinct t7 and what appear to be coalesced t8 and t9. A large posterior cingulum is present (fig. 7A). The cusp pattern of the second upper molar is similar to that of the first except that cusps t2 and t3 are not present—a large cusp t1 is the only remnant of the anterior lamina. Each third upper molar consists of a strong cusp t1, an arcuate lamina formed of merged cusps t4–t6, and a posterior lamina comprised of coalesced cusps t7–t9; a posterior cingulum is not present.

The mandible is robust and large relative to the length of the cranium, and the masseteric fossa is prominent. The coronoid process is variously slightly shorter, equal to, or slightly longer than the condylar process (see descriptions below), is sharply pointed, and is inclined about 45° to the posterior. The margins between the coronoid and condylar processes (sigmoid notch), and between condylar and angular processes, are shallowly concave. The angular process is rounded and does not project as far posteriorly as the condylar

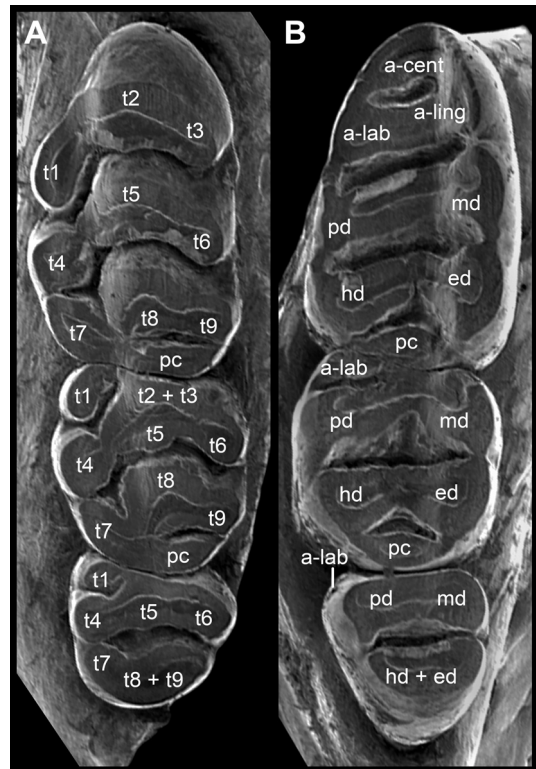


FIG. 7. Upper and lower molar teeth of *M. inopinatus* n. sp. (FMNH 193838), showing terminology used to describe cuspidation. Upper molars (A): cusps are numbered and referred to in the text with the prefix “t”; see Musser and Heaney, 1992. Lower molars (B): a-cent, antero-central cusp; a-lab, antero-labial cusp; a-ling, anterolingual cusp; ed, entocoid; hd, hypoconid; md, metaconid; pc, posterior cingulum; pd, protoconid.

process. The alveolus of the incisor lies directly below the coronoid process, as indicated by a small knob of raised, translucent bone.

The lower molars (in the specimen with slightly worn molars; fig. 7B) are tiny but robust. The first lower molar is about one-third longer than wide. The large anteroconid is made up of distinct anterolabial, anteroconid, and anterolingual cusps. The second and third lamina consist of the coalesced protoconid and metaconid, and coalesced hypoconid and entoconid, respectively. The posterior cingulum is small, elliptical in cross section, and distinct. The second lower molar is similar, but the anterior lamina is much smaller and composed only of the anterolabial cusp, so that the tooth is approximately as wide as long. The third lower molar has at most a tiny anterolabial cusp (and this may be no more than an enamel “blip” on the cingulum), and no posterior cingulum is evident.

Musseromys was originally described to contain a single species, *M. gulantang*. The discovery of three additional species has required that the diagnosis be emended to accommodate the morphological variation represented, but these changes are relatively minor. The primary changes reflect the proportionately shorter tails of the three new species (from 99% to 116% of the length of head and body, rather than 131% in *M. gulantang*); ears that are shorter, more rounded, and not bluntly pointed; and smaller postocular patch of bare skin with shorter genal vibrissae (fig. 5). However, trenchant features remain that clearly distinguish the genus from its nearest relatives, including its tiny size; unusually long mystacial vibrissae; presence of a postocular patch with prominent genal vibrissae; long tail with prominent penciling along more than one-fourth of its length; deep, proodont incisors that are conspicuously notched at their tips; broad, nearly square braincase with poorly developed temporal ridges; and zygomatic arches that are broader than the braincase. Among the many distinctive genera of murids in the Philippines, this combination of features makes it one of the most distinctive. Moreover, the genus adds greatly to the already remarkable morphological diversity known within the cloud rat clade, and the three species add still further to the large number of native murids documented from Luzon (Baleté et al., 2012; Heaney et al., 2009, 2011; Jansa et al., 2006; Musser and Heaney, 1992).

No additional specimens of *Musseromys gulantang* (figs. 4A, 5A, 6A) have been obtained since the original description (Heaney et al., 2009), so no redescription is possible, but comparisons to the new species are included below. Additional information on the ecology of small mammals on Mt. Banahaw, the type locality, is available in Heaney et al. (2013b). Descriptions of the three new species follow.

Musseromys inopinatus, new species

Figures 2, 3, 4B, 5B, 6B, 7, 8; tables 2, 3

HOLOTYPE: FMNH 193839. Adult male collected on 17 March 2007, field number D.S. Baleté 4477. Fresh tissues were removed from the thigh and placed in DMSO buffer solution. The rest of the specimen was initially fixed in formalin, now preserved in ethyl alcohol with skull (fig. 6B) removed and cleaned, complete and in good condition. The

holotype is currently housed at FMNH but will be transferred to PNM.

TYPE LOCALITY: Philippines: Luzon Island: Mountain Province: Barlig Municipality: 1.0 km N, 1.0 km W Mt. Amuyao peak, 2150 m elevation, 17.02213° N, 121.11791° E (fig. 1).

MEASUREMENTS: Tables 2 and 3.

SPECIMENS EXAMINED ($n = 5$): Mountain Province, Barlig Municipality, 0.75 km W Mt. Amuyao peak, 2300 m elevation (FMNH 193838); 1.0 km N, 1.0 km W Mt. Amuyao peak, 2150 m elevation (FMNH 193839 [holotype]); 1.75 km N, 1.5 km W Mt. Amuyao peak, 1950 m elevation (FMNH 193840); 2.15 km N, 1.25 km W Mt. Amuyao peak, 1650 m elevation (FMNH 214332, 214333).

ETYMOLOGY: An adjective from Latin, meaning “unexpected,” which expresses our initial surprise at capturing *Musseromys* in the high mossy forest of the Central Cordillera, the previous species having been captured in the lowland forest of central Luzon.

DIAGNOSIS: A member of the genus *Musseromys* (see Emended Diagnosis and Description, above); relative to other members of the genus, it is of about average size (fig. 8; HBL averaging 78 mm) with a moderately long tail (mean = 86.5 mm, 111% of HBL), relatively long hind foot (mean = 18.5 mm, ca. 23% of HBL), and long ears (mean = 17 mm; table 3). The hind foot (fig. 4B) is moderately wide and long, with plantar pads of moderate size. The palate (fig. 6B) is narrow at M3, extends posteriorly to about the middle of M3, and has deep palatal grooves that extend from the posterior margins of the incisive foramina to the posterior edge of the palate. The zygomatic plates are wide, the molar rows and rostrum long, and nasals moderately short. A small squamosal notch is present; the incisive foramina are long and wide relative to other *Musseromys*; and the anterior surface of the incisors is pale orange.

DESCRIPTION AND COMPARISONS: A small mouse, 17–19.5 g, HBL ca. 78 mm (table 3), similar to its congeners (figs. 5B, 8; see general description above). The dorsal pelage is dense and soft, with the overfur about 5 mm long between the shoulder blades with guard hairs ca. 2 mm longer; ventral pelage is 3–4 mm long, with no apparent guard hairs. Dorsal pelage is dark rusty brown; ventral pelage is buffy reddish brown, paler than dorsum. The head is broad and large relative to the body, and the rostrum is short and blunt. The eyes are small, and the ears are long (17 mm), fairly wide, and broadly rounded at the tips (fig. 5B). The mystacial vibrissae are up to 42 mm long; the postocular patch of skin is small and its genal vibrissae are up to 5 mm long and relatively inconspicuous. The 2–3 ulnar-carpal vibrissae are up to 6 mm long. The tail is short (85–88 mm, 109%–113% of HBL), relatively thick, with conspicuously elongated hairs on about the distal 10 mm; there are ca. 22 scales/cm on the tail. The pads on



FIG. 8. Photograph of a young adult male *Musseromys inopinatus* (FMNH 193838), taken 9 March 2007 by D.S. Balete at 2300 m on Mt. Amuyao.

the forefeet are proportionately large, covering most of its surface; the hind foot is broad and fairly long, and the plantar pads are large (fig. 4B).

The skull (fig. 6B) is large relative to other *Musseromys* (BOL 21.9–22.0 mm), with generic features and species-diagnostic features as described above.

Musseromys inopinatus differs from *M. gulantang* in having darker, less orange fur both dorsally and ventrally, and with darker gray underfur, and slightly longer (ca. 2 mm vs. 1 mm) and more conspicuous guard hairs; mystacial vibrissae (up to 42 vs. 53 mm) and genal vibrissae (5 vs. 15 mm) that are much shorter; ears that are equally long but wider and more rounded at the distal tips (fig. 5); a tail that is substantially shorter (85–88 mm vs. 101 mm) relative to length of head and body (109%–113% vs. 131%), thicker, with elongated hairs on only the last ca. 10 mm (vs. 20 mm), and finer scales (ca. 22/cm vs. 17/cm); and hind feet that are broader, slightly shorter (ca. 18.5 vs. 20 mm), and having plantar pads (especially the interdigital pads) that are larger and less distantly spaced (table 3, fig. 4). *Musseromys inopinatus* has a cranium that is larger overall (BOL 21.9–22.0 vs. 19.9 mm), incisors that are pale orange (rather than medium orange), a substantially broader interorbital region, greater mastoid breadth, longer and broader incisive foramina, longer and deeper rostrum and longer diastema, slightly longer molar rows, narrower labial palatal breadth at M1, longer postpalatal region, greater height of braincase, broader zygomatic plate, smaller squamosal notch, deeper palatal grooves, and coronoid and angular processes on the mandible that are longer and stouter (fig. 6, table 2).

Musseromys inopinatus differs from the Mt. Pulag specimens (*M. beneficus*, n. sp.) in being slightly smaller overall (HBL 78 vs. 75–84 mm, 17–19.2 g vs. 18–22 g); having similar but slightly darker, less reddish, shorter (ca. 5 vs. 6 mm) dorsal fur; shorter mystacial (up to 42 vs. 45 mm) and genal (5 vs. 15 mm) vibrissae; tail slightly longer relative to HBL (109%–113% vs. 101%–109%); long hairs covering a shorter portion of the distal tip of the tail (10 vs. 25 mm); longer ulnar-carpal vibrissae (ca. 6 vs. 4 mm); fore- and hind feet with nearly white hair dorsally (vs. some dark brown hairs reaching from the forearm to the base of the digits); and a hind foot that is slightly longer and narrower (table 3). The skull of *M. inopinatus* is similar to that of the specimens from Mt. Pulag (table 2), but differs in being slightly smaller overall, having a narrower interorbital region, zygomatic breadth, and mastoid breadth. The nasals are slightly shorter, but the rostrum and upper molar row average slightly longer; the zygomatic plate is broader; and the orbito-temporal fossa is shorter. The incisive foramina are similar in length, but in *M. inopinatus* they have straight lateral edges, rather than being bowed outward laterally toward their center. The labial palatal breadth at M1 and lingual palatal breadth at M3 are less, and the palatal grooves are deeper and more conspicuous. The squamosal notch is small on *M. inopinatus*, but absent on specimens from Mt. Pulag.

Musseromys inopinatus differs from specimens from Mt. Anacuao (*M. anacuao* n. sp.) in having slightly less reddish fur dorsally; shorter mystacial (up to 42 vs. 49 mm) and genal (5 vs. 11 mm) vibrissae (fig. 5); ears that are slightly longer (17 vs. 15–16 mm) and wider; hind feet that are longer (19 vs. 16–17 mm); and a tail that is thicker, slightly paler dorsally, with less of the distal tip covered in long hairs (10 vs. 15 mm), and finer scales (22/cm vs. 20/cm; table 3). Compared to specimens from Mt. Anacuao, the skull is larger overall, with greater basioccipital length, zygomatic breadth, mastoid breadth, and nasal length (table 2). The ros-

trum is longer (but not deeper), and the incisive foramina terminate forward of the anterior edge of M1 by an amount about equal to the width of M1, rather than extending nearly to the anterior edge of M1. The molar rows are longer, but lingual palatal breadth at M3 is narrower; the palatal bridge extends only to about the middle of M3 (rather than slightly posterior to the posterior edge of M3), and the palatal grooves are deeper and longer. The coronoid process of the mandible is slightly higher, and the angular process broader.

DISTRIBUTION: Currently known only from 1650 m to 2300 m on Mt. Amuyao (Rickart et al., in prep.), but Mt. Amuyao is the only place in the southern portion of the Central Cordillera where intensive trapping in the canopy has been conducted at these elevations. Additional surveys are needed in mature montane and mossy forest in the Central Cordillera to determine the extent of its distribution.

ECOLOGY: We captured specimens of this mouse in lightly disturbed (1650 m) and mature montane (1950 m and 2150 m) and mossy (2300 m) forest; we did not capture them in mossy forest at 2510 m and 2690 m where we used similar techniques with similar sampling effort (Rickart et al., in prep.). The montane forest at 1650 m was dominated by oaks, laurels, and myrtles in less rocky areas with deeper soil, and with pines (*Pinus kesiya*) and figs (*Ficus* sp.) in rockier and more open areas; we caught *Musseromys inopinatus* only in the former places. Mature montane forest at 1950 m and 2150 m was dominated by oaks, laurels, and myrtles of moderate height (up to 20 m) and small diameter (up to 25–50 cm), with ferns, orchids, and moss growing profusely on the branches. In mossy forest at 2300 m, coniferous trees of the Podocarpaceae were also present, with shorter (15 m or less) and usually thinner (20–40 cm diameter at breast height) trees predominating. All individuals were taken above ground, with one as little as 0.5 m and one as much as 5 m above ground, with two on the horizontal trunks of trees, one on a small branch leaning on the trunk of a tree, and two on hanging vines. All were captured in snap traps baited with slices of fried coconut lightly coated with peanut butter; four were captured overnight, and one in the late afternoon. Other species taken at the same localities included *Crocidura grayi*, *Apomys abrae*, *Apomys datae*, *Archboldomys maximus*, *Bullimus luzonicus*, *Chrotomys silaceus*, *Chrotomys whiteheadi*, *Rhynchomys soricoides*, and *Soricomys montanus* on the ground, *Apomys musculus* in the canopy, and *Batomys granti* and *Rattus everetti* in the canopy and on the ground (Rickart et al., in prep.; see also Balete et al., 2012; Rickart et al., 2011b).

A young adult female (17 g) taken on 24 March 2007 had two pairs of small, inguinal mammae and an imperforate vagina. A subadult male (12 g) taken on 22 April 2011 and a young adult male (15.5 g) taken on 9 March 2007 both had abdominal testes. A young adult male (16.5 g) taken on 26 April 2011 and an adult male (19.5 g) taken on 17 March 2007 both had scrotal testes.

Musseromys beneficus, new species

Figures 2, 3, 4C, 5C, 6C, 9; Tables 2, 3

HOLOTYPE: FMNH 198714. Adult female collected on 19 April 2008, field number D.S. Balete 5326. Fresh tissues were removed from the thigh and placed in DMSO buffer solution. The rest of the specimen was initially fixed in formalin, now preserved in ethyl alcohol with skull (fig. 6C)



FIG. 9. Photograph of an adult male *Musseromys beneficus* (FMNH 198857), taken 21 April 2008 by L.R. Heaney at 2695 m on Mt. Pulag.

75–84 mm) with a moderately long tail (82–88 mm, 101%–109% of HBL), relatively long hind foot (average ca. 18.3 mm, 23% of HBL), and fairly long ears (average 16 mm; table 3). The hind foot (fig. 4C) is broad, with large plantar pads. The interorbital region and zygomatic arches are broad, mastoid breadth is great, and the orbito-temporal fossa is long. The palate (fig. 6C) is broad at M3 relative to other *Musseromys*, extends posteriorly well beyond the posterior edge of M3, and has inconspicuous palatal grooves. The zygomatic plates are narrow, the molar rows and rostrum are of moderate length, and nasals are moderately short (table 2). A small squamosal notch is present; the incisive foramina are long and relatively wide; and the anterior surface of the incisors is pale orange.

DESCRIPTION AND COMPARISONS: A small mouse, 18–22 g, HBL 75–84 mm (table 3), similar to its congeners (see *Musseromys* Emended Diagnosis and Description, above). The dorsal pelage is dense and soft, with the overfur about 6 mm long between the shoulder blades with guard hairs ca. 2 mm longer (figs. 5C, 9); ventral pelage is 3–4 mm long, with no apparent guard hairs. Dorsal pelage is dark rusty brown; ventral pelage is buffy reddish brown, paler than dorsum, usually with white patches along the midline. The head is broad and large relative to the body, and the rostrum is short and blunt. The eyes are moderately small, and the ears are moderately long (16 mm), fairly wide, and broadly rounded at the tips. The mystacial vibrissae are up to 45 mm long; the postocular patch of bare skin is of average size, and its vibrissae are up to 15 mm long and conspicuous. The 2–3 ulnar-carpal vibrissae are up to 4 mm long.

removed and cleaned; all parts are in good condition. The holotype is currently housed at FMNH but will be transferred to PNM.

TYPE LOCALITY: Philippines: Luzon Island: Benguet Province: Mt. Pulag National Park, 1.15 km S, 1.35 km E Mt. Pulag peak, 2695 m elevation, 16.58816° N, 120.90960° E (fig. 1).

MEASUREMENTS: Tables 2 and 3.

SPECIMENS EXAMINED ($n = 3$): Benguet Province, Mt. Pulag National Park, 1.15 km S, 1.35 km E Mt. Pulag peak, 2695 m elevation (FMNH 198713, 198714 [holotype], 198857).

ETYMOLOGY: An adjective from Latin, meaning “beneficial.” We use this term to honor Anton Cornelis Jacobus Burgers, benefactor to D.S. Balete, who generously provided for D.S.B.’s senior high school and college education, and enthusiastically supported his interest in Philippine wildlife.

DIAGNOSIS: A member of the genus *Musseromys* (see Emended Diagnosis and Description, above) of about average size (fig. 9; HBL

The tail is relatively short (82–88 mm, 101%–109% of HBL) and relatively thick, with long hairs on about the distal 25 mm; there are ca. 23 scales/cm on the tail (table 3). The pads on the forefeet are proportionately large, covering most of its surface; the hind foot is broad, and the plantar pads are large (fig. 4C). The skull (fig. 6C) is large (basioccipital length 21.9–22.1 mm), with generic features and species-diagnostic characters as described above.

Musseromys beneficus differs from *M. gulantang* in having darker, less-orange fur both dorsally and ventrally, and with darker gray underfur, and slightly longer (ca. 2 mm vs. 1 mm) and more conspicuous guard hairs; mystacial vibrissae that are shorter (up to 45 vs. 53 mm); ears that are equally long but wider and more rounded at the distal tips; pads on the forefeet and hind feet that are larger, and hind foot that is shorter and broader (fig. 4). The tail is substantially shorter (82–88 mm vs. 101 mm) relative to HBL (101%–109% vs. 131%) and thicker, with more extensive elongated hairs on the distal tip (ca. 25 vs. 20 mm) and finer scales (ca. 23/cm vs. 17/cm; table 3). The skull is larger overall (BOL 21.9–22.1 vs. 19.9 mm), with broader interorbital region, zygomatic arches, and mastoid region; longer nasals and diastema, longer and deeper rostrum, incisive foramina that are longer and broader, longer orbito-temporal fossa and postpalatal region, and higher braincase (table 2). Palatal grooves are shallower and less conspicuous in *M. beneficus*. The incisors are pale orange rather than medium orange, and are broader at the tips.

Musseromys beneficus differs from *M. inopinatus* as described above.

Musseromys beneficus differs from the specimens from Mt. Anacuaao (*M. anacuaao*, n. sp.) in being slightly larger (HBL 75–84 mm vs. 74–83 mm); having pelage that is similar but slightly less cinnamon red; genal vibrissae that are longer (15 vs. 11 mm); ears of similar length but wider and more rounded (vs. slightly pointed at the tip); pads on the forefeet that are larger; hind feet that are longer both absolutely (18–19 vs. 16–17 mm) and relative to HBL (22%–24% vs. 19%–23%), and that have larger plantar pads; a tail that is greater in diameter and having more extensive elongated hairs on the distal tip (ca. 25 vs. 15 mm), and finer scales (22–23/cm vs. 20/cm; tables 2 and 3). The skull is larger overall (BOL 21.9–22.1 vs. 20.0–20.7 mm), with broader zygomatic arches and mastoid region, longer nasals, rostrum, diastema, orbito-temporal fossa, and postpalatal region, and a higher braincase. The upper molar row is longer, the M1 is broader, and the incisors are broader near their tips. The palate has greater labial breadth at M1 and lingual breadth at M3, and the bony palate extends well beyond the posterior edge of M3 rather than ending near the posterior edge of M3. The angular process of the mandible is longer and broader.

DISTRIBUTION: Currently known only from 2695 m elevation on Mt. Pulag, but this is the only place in the Central Cordillera where intensive trapping has been conducted above 2600 m in the canopy of mossy forest. Additional surveys above ca. 2400 m in mature mossy forest using appropriate trapping techniques are needed elsewhere in the Central Cordillera to determine the extent of its distribution and elevational range.

ECOLOGY: We captured three specimens of this species in mature mossy forest at 2695 m. All three were captured in the same Museum Special snap trap, on 18, 19, and 21 April 2008. The branch where they were caught was ca. 3 m above ground, thickly covered with moss, and

with crisscrossed branches of *Vaccinium* a short distance away. The canopy trees, dominated by oaks, laurels, myrtles, and Theaceae, reached ca. 7–10 m in height, with a few emergents reaching to 12 m; diameter at breast height was 20–40 cm. Canopy epiphytes, including mosses, ferns, orchids, and liverworts, were abundant, and canopy vines (*Smilax* sp.) were common. All were captured overnight using slices of fried coconut lightly coated with peanut butter as bait. Other species taken at the same locality were *Apomys datae*, *Bullimus luzonicus*, and *Rhynchomys soricoides* on the ground, and *Apomys musculus* and *Crateromys schadenbergi* in the canopy (field notes in FMNH; see also Balete et al., 2012, Rickart et al., 2011b). We did not capture this species at our localities on Mt. Pulag (with similar canopy sampling effort) in primary mossy forest at 2730 m, or in mossy forest fragments at 2420 m, 2445 m, or 2480 m (field notes at FMNH).

A young adult female (18 g) taken on 18 April 2008 had two pairs of small inguinal mammae and an imperforate vagina, and an adult female (22 g) taken on 19 April 2008 had two pairs of large mammae, a perforate vagina, and one uterine scar. An adult male (22 g) taken on 21 April 2008 had scrotal testes, 11 mm long \times 8 mm wide. All three were taken in the same trap, as noted above.

*Musseromys anacua*o, new species

Figures 2, 3, 4D, 5D, 6D, 10; tables 2, 3

HOLOTYPE: FMNH 209522, adult female collected on 1 May 2010, field number D.S. Balete 7267. Fresh tissues were removed from the thigh and placed in DMSO buffer solution. The rest of the specimen was initially fixed in formalin, now preserved in ethyl alcohol with skull (fig. 6D) removed and cleaned. The dorsoposterior portion of the braincase was damaged by the trap; the specimen is otherwise in good condition. The holotype is currently housed at FMNH but will be transferred to PNM.

TYPE LOCALITY: Philippines: Luzon Island: Aurora Province: Dinalungan Municipality, 0.2 km E Mt. Anacua

o peak, 1725 m elevation, 16.25527° N, 121.88896° E (fig. 1).

MEASUREMENTS: Tables 2 and 3.

SPECIMENS EXAMINED ($n = 3$). Aurora Province: Dinalungan Municipality, 0.2 km E Mt. Anacua

o peak, 1725 m elevation (FMNH 209522 [holotype], 209523, 209524).

ETYMOLOGY: From the name of the mountain where the specimens were obtained, used as a noun in the genitive case.

DIAGNOSIS: A member of the genus *Musseromys* (see Emended Diagnosis and Description, above), of smaller than average size (fig. 10; HBL 74–83 mm) with a moderately long tail (82–86 mm, 99–116% of HBL), hind foot of average length (18 mm) relative to body size (19%–23% of HBL), and moderately short ears (15–16 mm; table 3). The hind foot is broad with proportionately large plantar pads (fig. 4D). The skull (fig. 6D) is small (20.0–20.7 mm), with broad lingual breadth of palate at M3 but narrow labial palatal breadth at M1, narrow zygomatic plates, short molar rows and narrow M1, and short nasals and rostrum. The incisive foramina are long, relatively wide, and terminate posteriorly slightly anterior to the anterior

edge of the first molars. Palatal grooves are evident, principally from a level near the middle of M1 to the posterior edge of M2. There is a very shallow squamosal notch. The anterior surface of the incisors is pale orange.

DESCRIPTION AND COMPARISONS: *Musseromys anacuaeo* differs from *M. gulantang* in having much darker, less orange fur both dorsally and ventrally, with darker gray underfur. The dorsal guard hairs of *M. anacuaeo* are slightly longer, ca. 2 mm vs. 1 mm. Its mystacial vibrissae (fig. 5D) are slightly shorter (up to 49 vs. 53 mm), as are its postocular (genal) vibrissae (up to 11 vs. 15 mm) and ulno-carpal vibrissae (4 vs. 6 mm). Its ears appear slightly shorter (15.5 vs. 16 mm), are slightly broader, and come to a rounded tip rather than being bluntly pointed. Its hind feet are shorter (18 vs. 20 mm) and broader, and the plantar pads are larger (fig. 4). The tail of *M. anacuaeo* is about equally narrow as that of *M. gulantang*, but shorter (82–86 mm vs. 101 mm) relative to HBL (99%–116% vs. 131%), with finer tail scales (20/cm vs. 17/cm) and elongated hairs on ca. 15 mm of the distal tip rather than ca. 20 mm. The skull (table 2) is slightly larger overall with much broader interorbital region, greater mastoid breadth, and longer orbito-temporal fossa. The nasals are longer and the rostrum is longer but less deep. The diastema is slightly shorter, but the incisive foramina are longer and wider and terminate slightly anterior to the anterior edge of the first molar, rather than substantially anterior to the anterior edge of the first molar. The molar row is shorter, width of M1 is less, and labial palatal breadth at M1 is less. The braincase height is greater, but the postpalatal length is shorter, so that the braincase appears shorter and broader overall, especially in ventral view (fig. 6). The anterior surface of the incisors is pale orange rather than medium orange. The angular process of the mandible is longer and broader.

Comparisons with *M. inopinatus* and *M. beneficus* are given above.

DISTRIBUTION: Currently known only from about 1725 m, near the peak of Mt. Anacuaeo (Heaney et al., 2013a), but this is the only place in the northern Sierra Madre where intensive trapping above 1700 m has been conducted in the canopy of mossy forest. Additional surveys in the northern Sierra Madre using appropriate trapping techniques should be conducted above ca. 1500 m elevation to determine the actual extent of the distribution.

ECOLOGY: All three specimens were captured in primary mossy forest at ca. 1760 m, within 0.3 km of the mountain's peak; elaeocarps, myrtles, podocarps, laurels, and oaks were the dominant trees. The canopy reached 7–12 m in height, with some emergents reaching 10–15 m; diameter at breast height ranged from 10–50 cm. Epiphytes (including mosses, ferns, and orchids) and vines (including *Dinochloa*, *Freycinetia*, *Schefflera*, *Smilax*, and *Tetrastigma*) were



FIG. 10. Photograph of an adult male *Musseromys anacuaeo* (FMNH 209523), taken 2 May 2010 by D.S. Balete at 1725 m on Mt. Anacuaeo.

abundant. The three specimens were captured overnight in snap traps baited with slices of fried coconut thinly coated with peanut butter, placed on mossy, leaning tree trunks from 1 to 3 m above ground. Other small mammals captured at the same locality included *Crocidura grayi*, *Apomys sierrae*, *Bullimus luzonicus*, *Chrotomys whiteheadi*, *Rattus everetti*, and *Soricomys musseri* on the ground, and *Apomys microdon* in the canopy. We did not capture this species in our sampling areas (with similar trapping effort) in primary transitional montane-mossy forest at 1500 m, primary montane forest at 1300 m or 1125 m, or transitional lowland-montane forest at 940 m (Heaney et al., 2013a).

A subadult female (12 g) taken on 5 May 2010 had two inguinal pairs of small mammae and an imperforate vagina, and an adult female (21 g) taken on 1 May 2010 had two inguinal pairs of large mammae, a perforate vagina, and one fetus with a crown-rump length of 27 mm. An adult male (17 g) taken on 2 May 2010 had scrotal testes.

DISCUSSION

The discovery of these new species of *Musseromys* has taken place during an intensive study of the evolutionary and ecological biogeography of mammalian diversity on Luzon, using standardized procedures to detect species along the elevational gradients on each of the isolated mountain ranges and individual mountains (e.g., Alviola et al., 2011; Balete et al., 2009, 2011, 2013; Heaney et al., 2013a, 2013b; Rickart et al., 2011a, 2011b, 2013). Targeting arboreal habitats as part of this effort has been crucial in detecting these tree mice.

With the discovery of these three new species, the number of known and fully documented native murids on Luzon Island rises to 43 (Balete et al., 2012; Heaney et al., 2014). *Apomys musculus* and *Chrotomys mindorensis* also occur on Mindoro, and *Rattus everetti* occurs throughout much of the Philippine archipelago; all 40 remaining species (93%) are endemic to Luzon Island or to Luzon plus some smaller islands that are separated from Luzon by shallow water (e.g., Catanduanes and Marinduque). Perhaps more remarkably, 11 species are members of the cloud rat clade, and 27 are members of the earthworm mouse clade; thus, 38 species (88%) of the 43 total species have probably arisen by speciation within the Philippines. Our ongoing studies indicate that additional species in other genera of these two endemic clades remain to be described. Clearly, indigenous speciation has contributed heavily to the present diversity of murids on Luzon.

BIOGEOGRAPHY

The four species of *Musseromys* occur in three distinct geographic regions on Luzon: two (*M. beneficus* and *M. inopinatus*) occur in high montane forest in the southern portion of the Central Cordillera (on Mt. Pulag and Mt. Amuyao, respectively), and one occurs in high montane forest in the northern Sierra Madre (*M. anacuaao*, on Mt. Anacuaao), all in the northern part of Luzon. These three highland species form a clade that is distinct from the one species that occurs in lowland forest in central Luzon (*M. gulantang*, on Mt. Banahaw; fig. 1). Our

analysis of the reconstructed habitat types (fig. 3) suggests that the ancestral state for all *Musseromys* species is montane; *M. gulantang* is the only species of *Musseromys* to have successfully invaded lowland habitats. Only a few species of cloud rats on Luzon occur in lowlands: *M. gulantang* and some *Phloeomys cumingi* and *P. pallidus*, although both of the latter species also occur in montane forest (Balette et al., 2009, 2013; Heaney et al., 2013a, 2013b; Rickart et al., 1991, 2011a, 2011b, in prep.).

We note that with one exception, all of the species of the genera most closely related to *Musseromys* (*Batomys*, *Carpomys*, and *Crateromys*) that occur on Luzon are present in the Central Cordillera; only *B. granti* occurs outside of the Central Cordillera, on Mt. Isarog. We infer that it is most likely that the common ancestor of *Musseromys* occurred in the highlands of the Central Cordillera, with movement to Mt. Banahaw by *M. gulantang* during the diversification of *Musseromys*, and to Mt. Anacuaao by the common ancestor of *M. beneficus* and *M. anacuaao*. Given that the Central Cordillera is the geologically oldest portion of Luzon, with the largest and oldest area of montane habitat (Hall, 1998, 2002), this pattern of movement to geologically younger mountains is not surprising, especially in light of recent evidence of similar processes in mice of the genus *Apomys* (Justiniano et al., in revision).

It is noteworthy that the two species of *Musseromys* in the Central Cordillera occur on mountains that are part of a continuous mountain range (fig. 1), but they are not sister species (fig. 3). Rather, *M. beneficus* from Mt. Pulag is most closely related to the species from Mt. Anacuaao in the northern Sierra Madre, *M. anacuaao*. We know of no other pair of sister species of mammals with this distribution pattern, but we note two potentially related observations. First, one species (*Chrotomys whiteheadi*) occurs in the high elevations of the Central Cordillera, at high elevation in the Caraballos Mountains, and near the peak of Mt. Anacuaao, suggesting that movement between the Central Cordillera and the northern Sierra Madre has occurred in at least one additional species. Second, in the highly speciose forest mice of the subgenus *Megapomys* (genus *Apomys*), of four instances in which two members of the subgenus occur on a single mountain, in three cases the species are not sister species, and only in one are they sister species (Justiniano et al., in revision). Although our studies of phylogenetic relationships and biogeography of Luzon murids are at an early stage, these few observations suggest that periods of geographic isolation and speciation may typically precede development of sympatry in closely related species (e.g., members of a subgenus or species group), which implies a dynamic, long-term history of movement that is associated with both the speciation process and the buildup of diverse murid communities within a single montane region.

Because our surveys have included extensive trapping (using the same type of traps and bait that have captured *Musseromys*) in virtually all highland areas of Luzon, it is possible that we have obtained specimens of all existing species. However, the small number of records of *Musseromys* overall creates some uncertainty regarding the potential for discovering additional species. We recommend that future studies seek them with focused, extensive arboreal trapping in highland regions, especially those with mossy forest, including some areas where we have conducted some surveys: (1) Mossy forest is extensive in the northern Central Cordillera, though we did not detect them in that habitat on Mt. Bali-it, Kalinga Province (Rickart et al.,

2011a); additional surveys are needed. (2) Mossy forest is poorly developed and very limited in extent in the Caraballo Mountains, which lie in a biogeographically crucial area between the Central Cordillera and the northern Sierra Madre. We did not detect them on Mt. Palali, the highest mountain in the Caraballos at 1707 m (Alviola et al., 2011), but further search is warranted. (3) We did not detect them in the Mingan Mountains, but we sampled only to 1785 m, and perhaps they are present nearer the peak, which reaches to 1901 m (Balete et al., 2011). (4) The southern Sierra Madre rise only to about 1500 m, and mossy forest is poorly developed; we did not detect them on Mt. Irid, which is one of the higher peaks but rises only to 1469 m (Balete et al., 2013), but further surveys are needed. It is more difficult to assess the likelihood of capturing *Musseromys* in lowland forest, since our sampling in such habitat has been limited in many areas by the absence of forest below about 800 m elevation. Wherever lowland forest is present throughout Luzon, including other mountains near Mt. Banahaw, such as Mt. Makiling, searching for *Musseromys* might be productive.

ACKNOWLEDGMENTS

During the field portion of this study, we received generous assistance and extensive encouragement from many people in the DENR and NCIP, and at the Provincial, Municipal and Barangay levels. We gratefully received the hospitality, cooperation and assistance of the local community and local government units in the Mountain Province (Governor M. Dalog, Barlig Mayor C. Fiasnilon, Barangay Captains J. Gongon, I. Masong, P. Ongan, W. Panitic, and Barlig MAO C. Oryan), and in Aurora Province (Dinalungan Mayor T. Tubigan). We thank Atty. L. Carante-Gallardo, Atty. B. Masweng, R. Alawas, and A. Olsim of NCIP-CAR, and V. Sal-ly, Atty. W.K. Kalangeg, and J. Falinchao of NCIP-Mountain Province for their patience in initiating and carrying through the complex process of obtaining FPIC. In Barlig, Jeana Away provided unending help in organizing our project, as well as arranging housing and working space for us, and the staff of the SeaWorld Inn and Restaurant, especially Manang Lourdes, showed endless patience and hospitality during our stays. We thank Ranger L. Cayat and F. Aguinse and family for their generous assistance and hospitality in Babadak, Ambangeg Municipality. In Dinalungan, we thank MENRO R. Roberts and her staff for their encouragement and support.

In the DENR-CAR, we thank Regional Executive Director S. Peñafiel, whose steadfast support of biological research has greatly aided the recent increase in our knowledge of this wonderful fauna, and Protected Area Superintendent E. Albas for her enthusiastic support of our project and for her kind hospitality. We thank the Protected Area Management Board of Mt. Pulag, RTD R. Yawan, PENRO P. Osbucan, CENROs L. Apse (Bugias) and M. Pogeyed (Sabangan), J. Behis, and T. Dionisio, all of whom helped us to obtain all of the necessary permits. We further thank the staff of the DENR Protected Areas and Wildlife Bureau for their long-term cooperation and support, especially Director T.M. Lim, Asst. Director for Wildlife A. Manila, Wildlife Chief J. de Leon, and our colleagues C. Custodio, M. Mendoza, and A. Tagtag.

This project could not have been completed without the hard work and expert assistance of J. Sarmiento, R. Buenviaje, R. Plutado, and N. Antoque in the field. We also thank other members of our team who assisted us in our various activities, including T. Atiwag, A. Ayuga, J. Barcelona, C. Finain, S. Liggasi, N. Losaona, and P. Puchana. At the Field Museum, we are thankful to T. Damitz, T. DeCoster, A. Goldman, A. Niedzielski, J. Phelps, and W. Stanley for their help with cataloging and preparing specimens for study. All illustrations and figures were skillfully prepared by A. Niedzielski, who also helped with preparation of the manuscript. Our use of the scanning electron microscope was facilitated by B. Strack. We thank G.G. Musser, R.S. Voss, and an anonymous reviewer for their many helpful comments and suggestions for improving this manuscript.

Our special thanks to the Negaunee Foundation and the Barbara Brown, Ellen Thorne Smith, and Marshall Field Funds of the Field Museum for their long-term support, without which our research and conservation activities in the Philippines would not have been possible.

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