Chapter 7

A New Genus and Species of Small 'Tree-Mouse' (Rodentia, Muridae) Related to the Philippine Giant Cloud Rats

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ABSTRACT

A single specimen of a small mouse from Mt. Banahaw–San Cristobal Natural Park, Quezon Province, Luzon Island, Philippines, is here described as a new genus and species. It is easily distinguished from all other murids by its small size (15 g), rusty orange fur, mystacial vibrissae that are two-thirds the length of head and body, postocular patch of bare skin with long vibrissae arising within it, long tail with elongated hairs only on the posterior quarter, ovate ears, procumbent incisors that are deeply notched at the tip, and other distinctive characters. Both morphological and molecular data (from two nuclear genes) indicate that the new taxon is a member of the endemic Philippine clade of ''giant cloud rats,'' some of which weigh up to 2.6 kg. It is most closely related to the genus *Carpomys*, which includes the smallest previously known member of the clade (ca. 125 g), but differs from it in many features. The discovery of this new taxon reveals an even greater degree of diversification within the giant cloud rat clade than recognized previously, and adds to the 21 previously known genera of mammals endemic to the Philippines. The new mouse was captured in regenerating lowland rain forest located only 80 kilometers from Manila. This discovery highlights the importance of protecting regenerating tropical lowland rain forest, as well as the few remaining tracts of old-growth lowland rain forest on Luzon.

INTRODUCTION

The diversification of lineages within oceanic islands and archipelagoes (often referred to as adaptive radiation) is the source of much of the biodiversity that exists in those isolated areas (e.g., Gillespie, 2004; Roughgarden, 1995; Schluter, 2000; Wagner and Funk, 1995). Familiar examples among mammals include the tenrecs and lemurs of Madagascar (Olson and Goodman, 2003; Yoder et al., 1996). Recent molecular genetic studies (Jansa et al., 2006, 2009) have confirmed evidence from morphological studies (Musser and Heaney, 1992) that the murid rodents of the Philippine Islands are the result of extensive in situ radiation. Most of the 70+ Philippine murids are members of two endemic lineages, one with ca. 15 species and one with at least 36 species; several smaller endemic clades are also present. Both of the large clades show great morphological and ecological diversity (Balete et al., 2006, 2007; Heaney, 1986, 2004; Heaney and Rickart, 1991; Rickart et al., 2003, 2005; Steppan et al., 2003).

In May 2004, as part of an ongoing survey of poorly studied portions of Luzon Island, we conducted a survey of the small mammals of Mt. Banahaw, a dormant volcanic moun-

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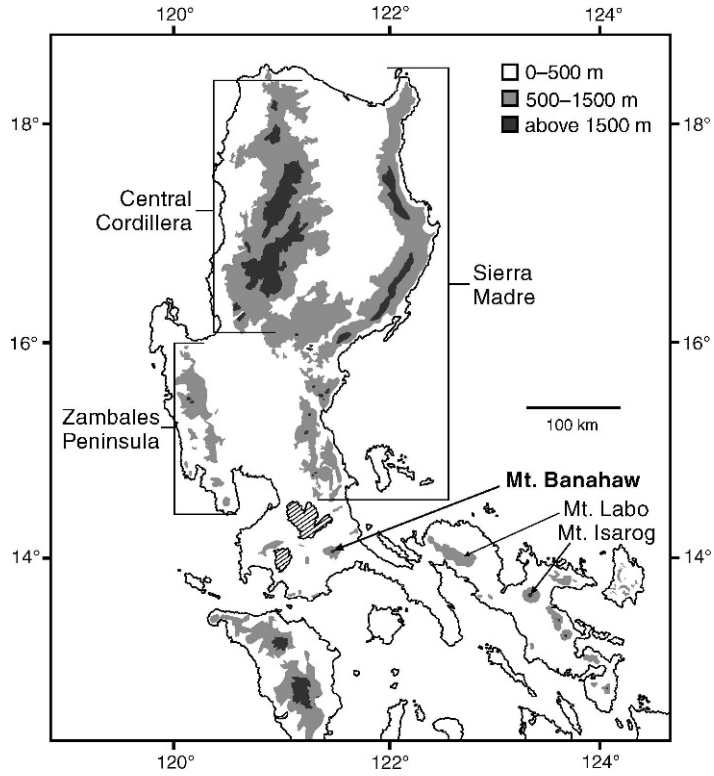

Fig. 1. Map of Luzon Island, Philippines, showing the location of Mt. Banahaw and other places mentioned in the text.

tain with its highest point at 2002 m, that lies about 80 km SE of Manila (fig. 1). In addition to a large number of species endemic to Luzon, we documented the presence of previously unknown species of *Rhynchomys* (Balete et al., 2007), *Apomys* (Heaney et al., in prep.), and a small tree-mouse that superficially resembles tree-mice from continental Asia and New Guinea, but that initially we could not readily assign to a known genus. In this paper, we describe the tree-mouse as a new genus and species, document its phylogenetic relationships, and comment on its implications for mammalian adaptive radiation and conservation in the Philippines.

The Banahaw tree-mouse (fig. 2) is small (15.5 g) with rusty-orange fur dorsally and bright orange fur ventrally, a large head with exceptionally long mystacial vibrissae, a long tail nearly naked near the base but with long hairs near and at the tip, and elongate ears that come to blunt tips. Externally, it resembles the tree-mice of continental Southeast Asia (*Chiropodomys*, *Haeromys*, *Vandeluria*, and *Vernaya*), a generally poorly known set of taxa that may form a monophyletic group, placed as members of the Micromys Division (along with a larger tree-rat, *Hapalomys*; Musser and Carleton, 2005; see photographs and drawings in Lekagul and McNeely, 1977; Nowak, 1999; Payne et al., 1985). The Banahaw mouse also externally resembles the long-footed tree-mouse, *Lorentzimys nouhuysi*, a monotypic genus endemic to New Guinea (Flannery, 1990), which is of unclear phylogenetic position, but probably not closely related to the Southeast Asian tree-mice based on morphological evidence (Musser and Carleton, 2005). There are no other murids in Indo-Australia that are similar in external appearance. We therefore make comparisons to these tree mice, especially to *Chiropodomys*, which includes a species on Palawan Island in the Philippines (which is a continental land-

Fig. 2. The holotype of *Musseromys gulantang* (FMNH 178405), adult male, photographed by L.R. Heaney on 12 May 2004 on Mt. Banahaw, Luzon Island, Philippines.

bridge island, not oceanic; Heaney, 1986, 2004), and to *Lorentzimys* from New Guinea.

The cranium of the Banahaw tree-mouse (fig. 3) is small but robust. In many features discussed below it is remarkably similar to the crania of *Carpomys* and *Crateromys*, especially the former. These genera are members of the ''cloud rat clade,'' a group of at least 15 species (also including *Batomys* and *Phloeomys*) that is endemic to the oceanic islands of the Philippines, recognized as the Phloeomys Division by Musser and Carleton (2005). Most of these are arboreal folivores, though the genus *Batomys* includes species that live on the ground; members of the clade weigh from ca. 125 g to 2.6 kg, with the latter being the largest living members of the subfamily Murinae (Heaney and Rickart, 1990; Jansa et al., 2006; Musser and Heaney, 1992). Many are strikingly colored with white and black or rufus fur, and all have tails that are either hairy or bushy; they are often described as resembling squirrels. These genera share several distinctive cranial synapomorphies, and are easily distinguished from both the *Chiropodomys* clade and *Lorentzimys nouhuysi*. We therefore also make comparisons to the members of the Philippine cloud rat clade.

In order to further clarify the phylogenetic position of the Banahaw mouse, we have analyzed DNA sequences from two nuclear genes, exon 10 of the Growth Hormone Receptor (GHR) gene and exon 1 of the gene for Interphotoreceptor Retinoid-Binding Protein (IRBP), and expanded our existing taxon sample to include several additional murine genera. The resulting analyses provide a robust phylogenetic position for the Banahaw mouse and suggest several novel hypotheses regarding the evolutionary history of murine rodents across Southeast Asia.

MATERIALS AND METHODS

Specimens examined in this study are housed in the Field Museum of Natural History (FMNH), the University of Kansas Natural History Museum (KU), and the American Museum of Natural History (AMNH); most identifications were made or verified by G.G. Musser over a period of many years. Specimens that we collected were obtained in accordance with the animal care and use guidelines of the American Society of Mammalogists (Gannon et al., 2007). Latitude and longitude were determined with a Garmin GPS device. Descriptive terminology for external body features follows Brown (1971) and Brown and Yalden (1973). Terminology for cranial and dental features follows Musser and Heaney (1992). Our use of scientific names and informal higher categories (referred to as ''Divisions'') follows Musser and Carleton (2005). Measurements (in millimeters) of total length, length of hind foot including claws, and length of ear from notch, and weight (in grams) were taken from the field catalogs of the authors, which are on file at FMNH. Head-and-body

Fig. 3. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of the holotype of *Musseromys gulantang* (FMNH 178405).

length was calculated by subtracting tail length from total length. Length of overfur (measured in the middorsal region) and length of vibrissae were measured with a plastic ruler. Cranial and dental measurements were taken by Heaney with dial calipers, as defined by Musser and Heaney (1992) except the following: **Basioccipital Length**: from the portion of the premaxillary that projects between and anterior to the incisors to the posterior edge of the occipital condyles; **Mastoid Breadth**: greatest breadth across the mastoids, including the mastoid processes; **Nasal Length**: greatest length of nasals; **Rostral Depth**: taken from the point where the premaxillary-maxillary suture crosses the ventral portion of the rostrum to the nearest point on the dorsal surface of the rostrum; **Rostral Length**: from the anteriormost point in the orbit to the anterior tips of the nasals; **Orbital Length**: from the anteriormost point to the posteriormost point in the temporal fossa; **Labial Palatal Breadth**: taken across the first upper molars at the outer margins of the alveoli; **Breadth of Incisors**: taken on maxillary incisors near the tip, but not including portions of the incisors that are worn.

Our molecular dataset consisted of 57 taxa, including representatives of all of the endemic Philippine genera except *Abditomys*, *Tryphomys*, and *Anonymomys*. To place these genera within the murine radiation, we included additional taxa to represent the Old Endemic assemblage from Australia and New Guinea (*Uromys*, *Pogonomys*, and *Lorentzimys*); several mainland Southeast Asian genera (*Chiropodomys*, *Maxomys*, *Niviventer*, and *Sundamys*); genera with an African distribution (*Aethomys*, *Otomys*, *Hylomyscus*, *Praomys*, and *Mastomys*); and representatives of the widespread genera *Mus* and *Rattus*. Additionally, to provide a broad phylogenetic context, we included representative taxa from the muroid families Spalacidae, Calomyscidae, Nesomyidae, and Cricetidae, as well as additional members of Muridae. We sequenced exon 1 of IRBP for all taxa except *Uromys* (we were unable to obtain IRBP sequences from either of our two samples of this taxon). We downloaded 23 sequences of GHR exon 10 from Genbank (Adkins et al., 2001; Steppan et al., 2003, 2005). Specimen information, including museum voucher and GenBank accession numbers, is given in table 2.

DNA amplification and sequencing methods are similar to those described in Jansa et al. (2006) with the following modifications. We amplified a portion of IRBP exon 1 from *Chiropodomys*, *Lorentzimys*, *Musseromys*, and *Pogonomys* using primers IRBPA and IRBProd1 (5′CCACTAATGTGTAATAGTCCT), which generated a product that was ca. 350 bp shorter than that generated by Jansa et al. (2006). To generate products of a suitable size for sequencing, this PCR product was used in two subsequent PCR reactions, one using IRBPA paired with IRBProd2 (5′GGYAAGGTCCAGATCTCTGTGG) and one using primers IRBProd3 (5′CATRGRCACCTCCTCCTTGGT) paired with IRBProd1. We amplified a portion of GHR exon 10 using primers GHRF1 (5′GGRAARTTRGAGGAGGRGAACACMATCTT) and GHRendA (5′GATTTTGTTCAGTTGGTCTGTGCTCAC), and reamplified this product using primers GHR750R (5′GTAAGGCTTTCTGTGGTGATRTAA) paired with GHRF1 and GHRF50 (5′TTCTAYARYGATGACTCYTGGGT) paired with GHRend. The resulting PCR products were sequenced in both directions on an ABI 3730, and the resulting chromatograms were edited and compiled using Sequencher ver. 4.1 (GeneCodes, Inc.).

The resulting GHR and IRBP sequences were aligned with reference to their respective amino acid sequence using MacClade ver. 4.03 (Maddison and Maddison, 2001). We analyzed the resulting gene matrices using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) as implemented in PAUP* ver. 4.0b10 (Swofford, 1999) or MrBayes ver. 3.1 (Ronquist and Hulsenbeck, 2003). For the ML and BI analyses, we first determined the best-fit model of nucleotide substitution for each gene alone and the two genes in combination using the Akaike Information Criterion as implemented in ModelTest ver. 3.7 (Posada and Crandall, 1998). For the ML analysis, the parameters describing this best-fit model were used in a heuristic tree search using a neighbor-joining tree as a start point for TBR branch swapping. For the BI analysis, we conducted two runs of Metropolis-Coupled Markov Chain Monte Carlo (with four chains each) on the combined gene dataset. We specified an independent model for each gene (IRBP: GTR + I + Γ; GHR: GTR + Γ) and allowed substitution parameters and overall rates to be estimated for each gene independently. We calculated nodal support under the MP and ML criteria using nonparametric bootstrapping, and we calculated nodal posterior probability values from the post-burnin trees for the BI analysis. For the MP analysis, we performed 1000 bootstrap pseudoreplicates, with heuristic searches of five random taxon additions, TBR branch swapping, and a maximum of 20 trees saved for each replicate. For the ML analysis, we performed 100 bootstrap replicates using genetic algorithm tree searches as implemented in GARLI ver. 0.951 (Zwickl, 2006).

RESULTS

Morphological comparisons

Although the Banahaw mouse is externally similar to *Chiropodomys* (Musser, 1979, 1982), there are three conspicuous differences. The Banahaw mouse has a prominent postocular patch of bare skin from which vibrissae (presumably genal) up to 15 mm long arise (fig. 2); this feature appears to be unique among murids. Second, the Banahaw mouse has ears that are substantially longer than wide, and are ovate in outline. Third, the Banahaw mouse has relatively long, narrow hind feet; those of *Chiropodomys* are relatively short and broad. Other external features, such as the long, penicillated tail may not be considered synapomorphies because they are shared with many murids.

A comparison of cranial characters of the Banahaw mouse fails to show substantial similarities to *Chiropodomys* or other members of the Micromys Division, aside from generalized features, e.g., a short, broad rostrum and a broad braincase. Traits that set apart *Chiropodomys* and its relatives (in comparison to the Banahaw mouse) include orthodont incisors (proodont); prominent supraorbital ridges that extend onto the braincase (braincase smooth, no supraorbital ridges); prominent zygomatic notch (absent); zygomatic arches moderately wide and robust (zygomatic arches very wide and robust); incisive foramina long and broad,

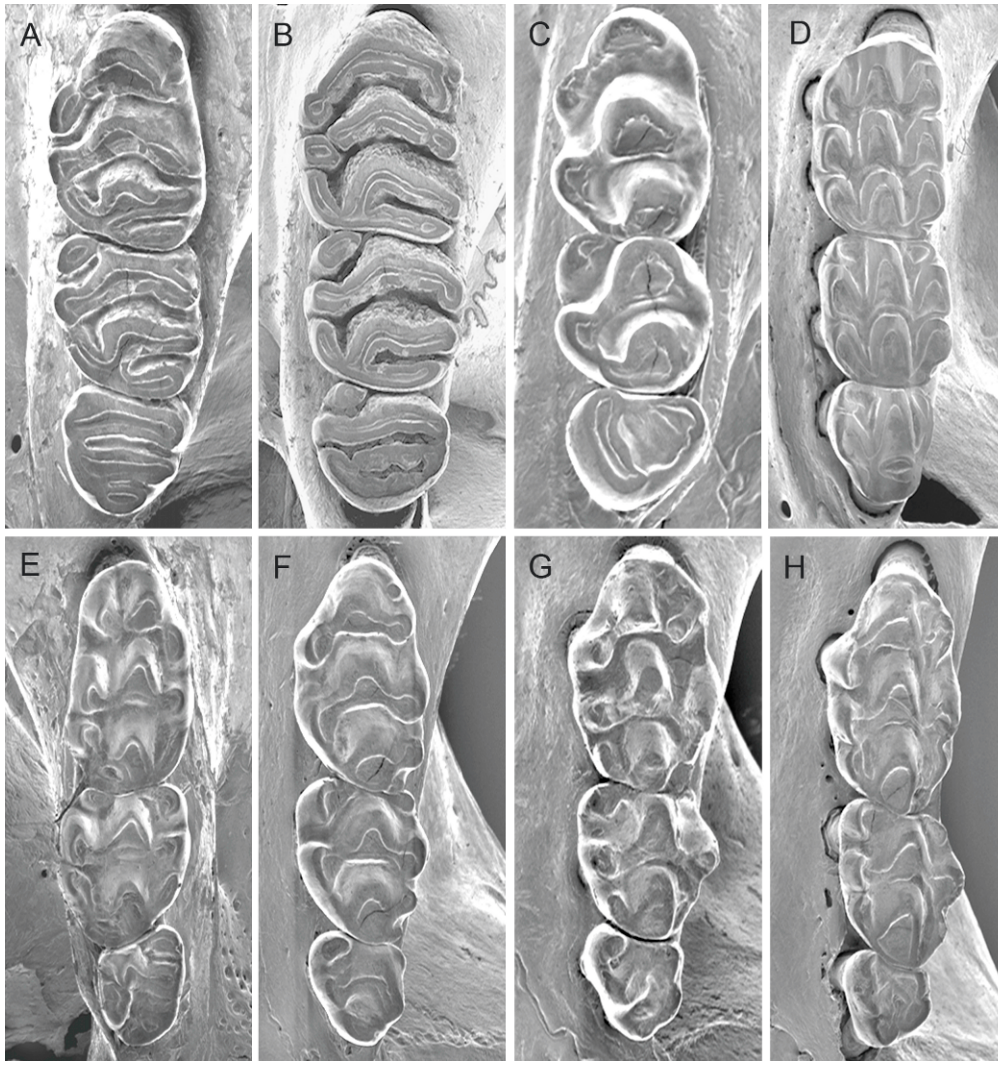

Fig. 4. Left maxillary tooth rows of: **A,** *Musseromys gulantang* (FMNH 178405); **B,** *Carpomys phaeurus* (FMNH 175565); **C,** *Lorentzimys nouhuysi* (KU 161012); **D,** *Hapalomys longicaudatus* (FMNH 32463); **E,** *Chiropodomys gliroides* (FMNH 46725); **F,** *Haeromys pusillus* (FMNH 172885); **G,** *Micromys minutus* (FMNH 129471); and **H,** *Vandeleuria oleracea* (FMNH 99501). All tooth rows standardized to the same size to facilitate comparisons; not to the same scale.

reaching nearly to the level of the first molars (relatively shorter and narrower, ending well anterior to the level of the first molars); palatal bridge broad and extending well beyond the third molar (narrower and ending at the middle of the third molar); mesopterygoid fossa broad (narrower); sphenopalatine vacuities small (large); stapedial foramen in the petromastoid fissure of the bullae large (absent); carotid canal small (large); and coronoid process of the mandible short (moderately long). The morphology of the maxillary molars of *Chiropodomys*, *Haeromys*, *Micromys*, and *Vandeluria* shows little resemblance to the Banahaw mouse in any feature (fig. 4; see Musser, 1979, for descriptions of dental features of the Micromys Division). On the basis of these features, we reject the hypothesis of a close relationship between the Banahaw mouse and members of

the Micromys Division, including *Chiropodomys*.

The Banahaw mouse and *Lorentzimys nouhuysi* are alike externally in one striking feature: both have pinnae that are at least twice as long as wide and that come to a blunt point. They both also have relatively long, narrow hind feet, but this trait is present in many murids. No other external similarities are evident, aside from those shared with nearly all murines. We also note several dissimilarities. The mystacial vibrissae of *Lorentzimys nouhuysi* are typical of murines, and there is no postocular patch of bare skin or vibrissae arising from it. The tail is long, as in the Banahaw mouse, but nearly naked except for a slight amount of pilosity near and at the tip. The pollex of the Banahaw mouse is small and closely appressed to the side of the second digit, but is fairly typical of murines, while the pollex of *Lorentzimys nouhuysi* is even smaller, appearing as a pad that has no separation from the side of the second digit, and has a proportionately smaller nail. These features of the pollex of *Lorentzimys nouhuysi* are apparent on two fluid preserved specimens (AMNH 183805, 197868); on the two dried museum skins available to us (KU 160659, 161012), there is a tiny dried fleshy pad on which no nail is visible.

Similarly, although the cranium of the Banahaw mouse resembles that of *Lorentzimys nouhuysi* in some respects (e.g., both have proodont incisors and short braincases, and neither has a stapedial foramen in the bullae), there are substantial differences. In *L. nouhuysi*, the rostrum is short and tapering anteriorly (slightly longer and less tapering in the Banahaw mouse); zygomatic arches are equal in width to braincase (wider than braincase); braincase is substantially longer than wide (equally wide and long); braincase is globose on dorsal surface (nearly flat); incisive foramina very short (moderately long); palatal bridge extends well beyond the last molar (ending at about the middle of the last molars); the mesopterygoid fossa is very narrow (not as narrow); the carotid canal is tiny, barely evident (large); the cranium is strongly inflected relative to the plane of the basioccipital and basisphenoid (barely inflected); and the coronoid process of the mandible is short (moderately long). In the morphology of the maxillary molars, *L. nouhuysi* shows little resemblance to either the Banahaw mouse or to *Chiropodomys gliroides* (fig. 4), and the teeth are proportionately tiny. We conclude that a hypothesis of a close relationship between the Banahaw mouse and *Lorentzimys nouhuysi* is not supported.

Despite the impressive disparity in size, the cranium of the Banahaw mouse shows great similarity to members of the *Crateromys* and *Phloeomys* groups from the Philippines (the Phloeomys Division of Musser and Carleton, 2005). In particular, the Banahaw mouse possesses the three synapomorphies that define the *Crateromys* group, as defined by Musser and Heaney (1992): (1) a large discrete cusp t7 is present on each upper molar; (2) a large anteroconid forms the anterior one-third of each lower molar; (3) in nearly all of the species (excluding *Batomys russatus*, which has a large stapedial foramen), the internal carotid either gives off a tiny stapedial artery, which passes through a minute stapedial foramen to enter the inner ear from which it does not emerge, or the stapedial artery is entirely absent (Musser and Heaney, 1992: 61). In addition, the Banahaw mouse possesses the following traits that are also present in the Phloeomys Division, as well as some other murids: (4) long and narrow incisive foramina (these are not as long in the Banahaw mouse, but otherwise similar in configuration); (5) the angular process of the mandible is very broad in lateral view and separated from the condyle by a shallow emargination in the caudal margin of the mandible (Musser and Heaney, 1992: 63); (6) cusp t9 is either absent from the labial margin of each upper molar (*Batomys* and *Crateromys*) or reduced in size (*Carpomys* and the Banahaw mouse); (7) most members of the Phloeomys Division have colorful or contrasting fur (rich rufus dorsal and ventral fur in the Banahaw mouse) ; (8) all members of the Phloeomys Division have hairy tails, with caudal hair length varying from short (leaving the scales visible) to very long (and entirely obscuring not only the scales but the tail). All other Philippine murids have tails that appear virtually naked (although three small hairs

are associated with each scale; Musser and Heaney, 1992). On the basis of these characters, an hypothesis of a close relationship between the Banahaw mouse and the Phloeomys Division (as defined by Musser and Carleton, 2005) is supported.

Molecular Phylogenetic Analysis

Parsimony analysis of the 460 informative characters from IRBP resulted in 2160 trees of 1888 steps, and MP analysis of the 353 informative GHR characters resulted in four trees of 1312 steps. The topologies of optimal trees recovered under the MP criterion for each of these datasets are entirely consistent with those recovered under the ML criterion; the trees resulting from ML analysis are shown in figure 5A, B. The topologies inferred from the two genes separately are also remarkably similar to each other and differ only at nodes that receive low ($< 70\%$) bootstrap support in either analysis. We therefore combined the two genes in a single concatenated dataset. Parsimony analysis of these 813 informative characters yielded 24 minimum-length trees of 3208 steps. The strict consensus topology of these trees is identical to the one recovered from mixed-model Bayesian analysis of the concatenated gene dataset (fig. 6). In particular, we recovered the same five, well-supported clades of Philippine endemics that were recovered in a previous analysis of IRBP and mitochondrial cytochrome *b* sequences based on a less extensive sample of murine taxa (Jansa et al., 2006).

Results of all phylogenetic analyses are unequivocal in placing the Banahaw mouse as the sister taxon to *Carpomys*, nested within the Phloeomys Division (clade E, fig. 6). This relationship is strongly supported in independent anlyses of IRBP and GHR using both model-based analyses (ML and BI) and MP inference, as well as by MP and BI analysis of both genes in combination. We found no support for sister-taxon relationships between the Banahaw mouse and either *Chiropodomys* or *Lorentzimys*; in fact, to infer a relationship with either of these genera would require breaking either five (to place with *Chiropodomys*) or seven (with *Lorentzimys*) nodes with posterior probabilities $> 95\%$.

Comparison with *Carpomys phaeurus*

Because both the molecular and morphological data indicate that *Carpomys* is the closest relative of the Banahaw mouse, we note the following points of dissimilarity between these two genera. We use *C. phaeurus* as the point of comparison because it is the smaller of the two known species of *Carpomys*.

The crania of the Banahaw mouse (fig. 3) and *Carpomys phaeurus* (fig. 7) are remarkably similar, although *C. phaeurus* is more than twice the size of the Banahaw mouse in any given dimension (table 1), and weighs nearly an order of magnitude more. They differ in the following ways: (1) The braincase of *C. phaeurus* is slightly more globose and is anteroposteriorly more elongate than that of the Banahaw mouse, though both may be described as broad, short, and not strongly inflated. (2) The zygomatic notch is barely present in *C. phaeurus* and appears to be absent in the Banahaw mouse. (3) The upper incisors of the Banahaw mouse are narrower and more procumbent than those of *C. phaeurus*, and the conspicuous notch at the tip in the Banahaw mouse is absent in *C. phaeurus*. (4) The incisive foramina are proportionately shorter in the Banahaw mouse than in *C. phaeurus*, though in both the foramina are fairly long and narrow. (5) The accessory foramen ovale and foramen ovale in the Banahaw mouse have coalesced into a single foramen, but remain separate in *C. phaeurus*. (6) The middle lacerate foramen in the Banahaw mouse is virtually absent, but is large in *C. phaeurus*. (7) In the Banahaw mouse, a strut of the squamosal extends posterior to contact the mastoid, leaving the squamosal notch dorsal to the strut. This strut is absent in *C. phaeurus*, and so there is no squamosal notch. (8) The lower incisors are more slender in the Banahaw mouse than in *C. phaeurus*. (9) The coronoid process of the mandible is shorter and more sharply pointed in the Banahaw mouse than in *C. phaeurus*, in which it is fairly long and robust. (10) The mystacial vibrissae of *C. phaeurus* are less than 45% of head and body length, whereas those of the Banahaw mouse are 70% of head and body. (11) The postocular patch of bare skin with long vibrissae present on the Banahaw mouse is absent on *C.*

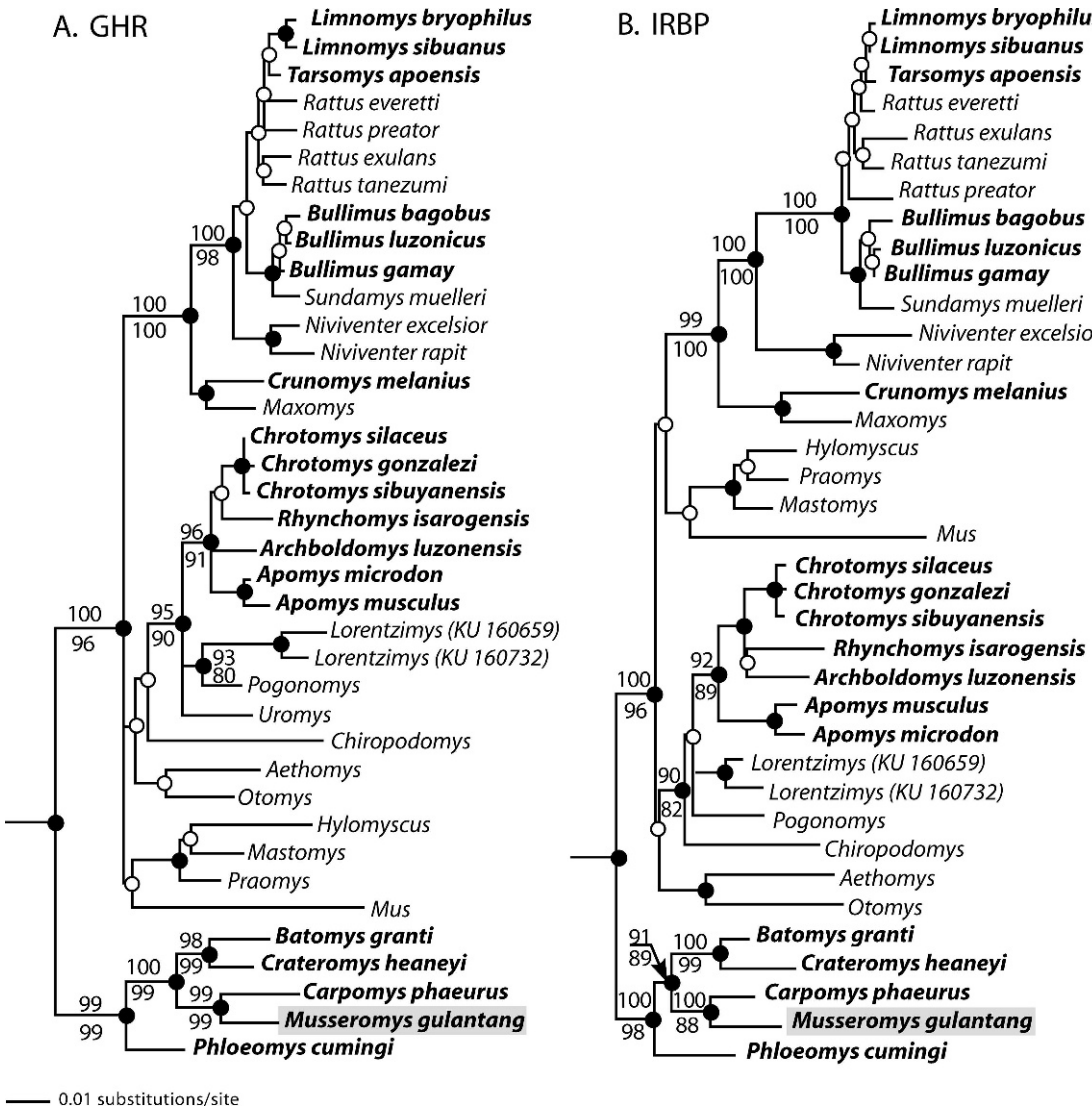

Fig. 5. Trees resulting from maximum-likelihood analysis of the GHR dataset (**A**) and the IRBP dataset (**B**) under their respective best-fit models of nucleotide substitution (GHR: TVM+Γ; IRBP: GTR+I+Γ). Circles at nodes indicate maximum-likelihood bootstrap percentages (BP): Black circles indicate BP $\geq$ 90%; gray circles indicate 70% $<$ BP $<$ 90%; and white circle indicate BP $\leq$ 70%. For selected nodes, bootstrap percentages from both likelihood (top number) and parsimony (bottom number) analysis are given. Taxa that are endemic to the Philippines are shown in bold.

phaeurus. (12) The ears of *C. phaeurus* are short and rounded, unlike the elongated, bluntly pointed ears of the Banahaw mouse. (13) The pollex of the Banahaw mouse has a proportionately small nail; that structure on *C. phaeurus* is longer and broader. (14) The hind feet of *C. phaeurus* are short and broad, while those of the Banahaw mouse are proportionately long and narrow. (15) The hallux of *C. phaeurus* appears to be partially opposable, but that of the Banahaw mouse is not. (16) The tail of *C. phaeurus* has visible brown hairs down its entire length, increasing only slightly in length toward the tip, whereas that of the Banahaw mouse is much more thinly haired at the base, and shows a much

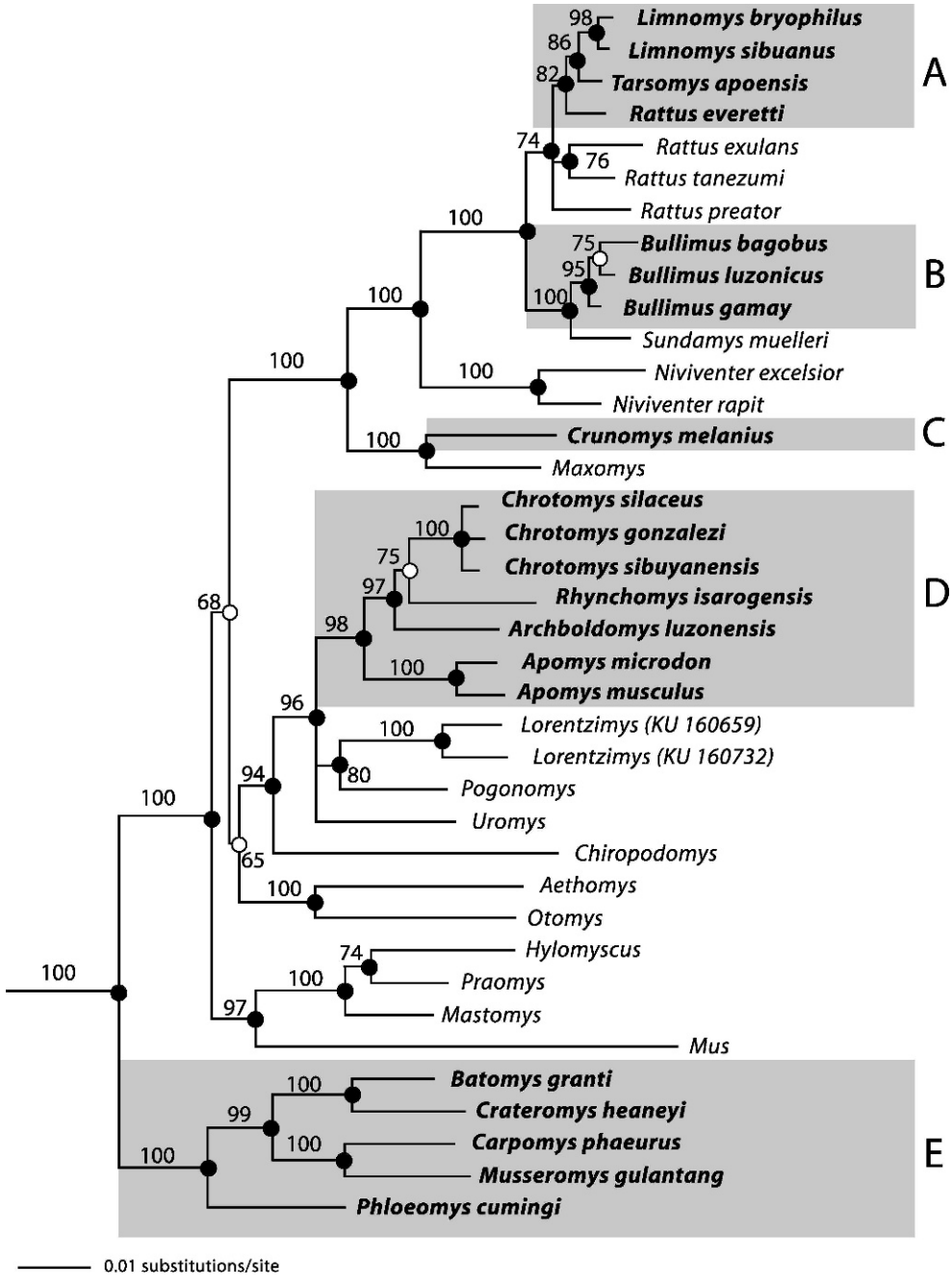

Fig. 6. The majority-rule consensus tree resulting from a mixed-model Bayesian analysis of the combined GHR+IRBP dataset. Circles at nodes indicate Bayesian posterior probability values (BPP): black circles indicate BPP $\geq$ 95%; white circles indicate BPP $<$ 95%. Branch lengths are shown as mean estimates from the Bayesian analysis. Numerals at each node indicate bootstrap percentages resulting from a parsimony analysis of the combined GHR+IRBP dataset. Gray boxes delimit the five clades (A–E) that were recovered in previous analyses of molecular sequence data (Jansa et al., 2006).

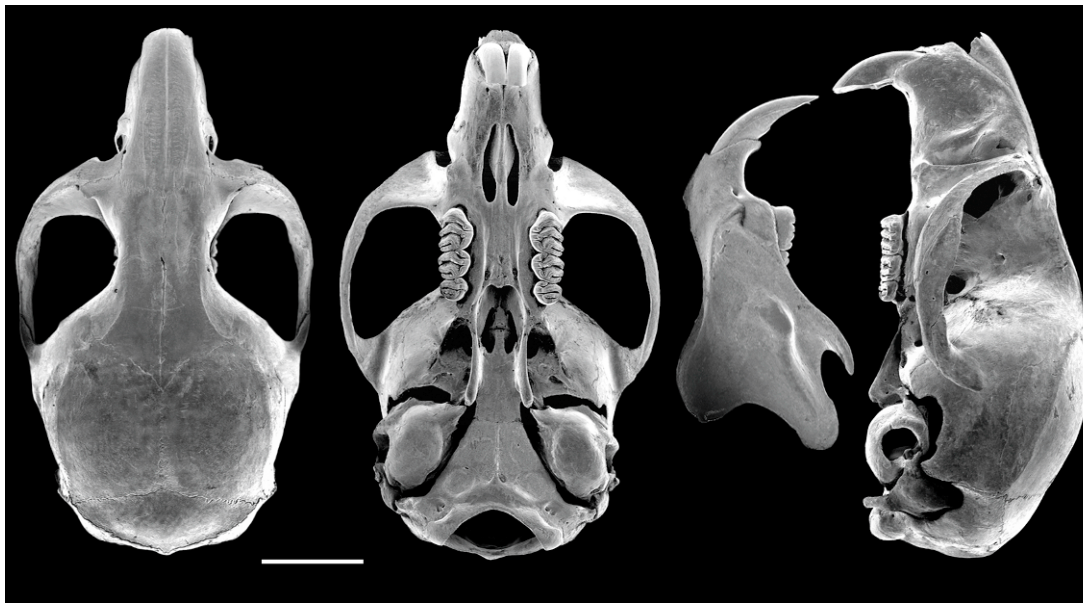

Fig. 7. Dorsal, ventral, and lateral views of the skull and lateral view of the mandible of *Carpomys phaeurus* (FMNH 175565). The scale bar = 10 mm.

greater relative increase in hair length toward the tip.

Although our molecular data strongly suggest that *Carpomys* is the closest relative of the Banahaw mouse, on the basis of these 16 characters, we reject the option of considering them to be members of a single genus.

Given the evidence for the phylogenetic relationship of the Banahaw mouse to the Phloeomys Division, and its evident distinctive features relative to the four currently recognized genera in that clade, we describe it as a new genus and species.

DIAGNOSIS AND DESCRIPTION

Musseromys, new genus

TYPE SPECIES: *Musseromys gulantang*, the new species described below.

ETYMOLOGY: We combine the Greek *mys* (''mouse'') with ''Musser,'' in recognition of the massive and immensely important contributions that Guy Musser has made to studies of the murid rodents of the world, especially those of the Philippines.

DIAGNOSIS AND COMPARISONS: A member of the Muridae, subfamily Murinae, as defined and diagnosed by Carleton and Musser (1984) and Musser and Carleton (2005) that may be identified by the following combination of morphological traits: size small, ca. 15 g, head-and-body length 77 mm (table 1); dorsal pelage orange-russet, ventral pelage bright ochraceous; short, broad muzzle; mystacial vibrissae up to 55 mm, two-thirds the length of head and body; prominent postocular bare patch of skin, ca. 3 mm in diameter, with vibrissae 15 mm in length arising from the middle portion; 2–3 ulnar-carpal vibrissae, up to 6 mm long; tail 101 mm, ca. 130% length of head and body, with elongated hairs (''penciling'') along the posterior 25%; ears elongate and bluntly pointed; except for the pollex, which has a small nail, all toes with long, sharply pointed claws; proodont incisors, about 2.5 times as deep as wide, deeply notched at tip; braincase equally wide as long; braincase smooth, with no supraorbital ridges; basicranial inflection slight; zygomatic arches broader than braincase for most of their length; incisive foramina of moderate length but narrow, ending well anterior to the first molars; palatal bridge of moderate width (less than

TABLE 1
Cranial, Dental, and External Measurements of Adult Tree Mice, Including New Genus and Species from Luzon
Measurements of sample size (*n*) greater than 3 are given as mean ± 1 standard deviation and their ranges. Sample size less than *n* is given in parentheses after the range (see appendix 1).

	Musseromys gulantang	*Carpomys phaeurus*	*Chiropodomys gliroides*	*Lorentzimys nouhuysi*	*Haeromys Pusillus*
	Holotype	*n* = 2	*n* = 7	*n* = 2	*n* = 1
BOL			23.4 ± 0.61		
	20.08	35.41–36.29	22.66–24.01 (6)	19.32–19.97	19.61
IB			4.5 ± 0.15		
	3.97	5.83–5.88	4.28–4.62	4.79–5.23	3.98
ZB			14.2 ± 0.16		
	12.54	21.27–21.52	14.03–14.44 (6)	11.58–11.61	11.29
MB			11.0 ± 0.26		
	9.86	15.17–16.48	10.69–11.28 (5)	10.07–10.10	8.82
NL			7.4 ± 0.26		
	7.03	12.94–14.04	6.99–7.66	5.95–6.73	6.84
LIF			4.2 ± 0.30		
	2.65	6.16–7.20	3.92–4.74	2.11–2.33	2.71
RD			5.3 ± 0.23		
	5.01	8.69–8.99	5.07–5.76	5.45–5.46	4.85
RL			7.8 ± 0.44		
	7.87	13.02–13.71	7.42–8.50	6.98–7.22	7.11
OL			9.0 ± 0.10		
	6.32	12.82–12.85	8.91–9.14	6.08–6.59	8.08
M1–M3			3.8 ± 0.20		
	3.27	6.31–6.43	3.53–4.04	2.66–2.67	3.37
PBM1			5.0 ± 0.12		
	4.30	6.71–6.93	4.74–5.18	4.14–4.20	4.26
DL			6.4 ± 0.15		
	5.47	9.35–10.04	6.16–6.51	5.44–5.46	5.20
PPL			8.8 ± 0.27		
	8.17	15.15–15.41	8.51–9.17 (6)	6.73–6.87	7.31
LBM3			3.5 ± 0.11		
	2.56	4.07–4.26	3.19–3.59 (6)	2.80–2.85	2.63
BH			7.9 ± 0.26		
	7.65	11.59–12.15	7.40–8.22 (5)	7.81–8.44	7.06
BM1			1.1 ± 0.06		
	1.10	2.10–2.13	0.98–1.14	0.79–0.83	0.97
BIT			1.6 ± 0.07		
	1.20	2.35	1.56–1.74	1.00–1.06	1.45
ZP			2.4 ± 0.12		
	1.85	3.35–3.78	2.29–2.72	1.22–1.46	2.18

length of tooth row), ending at the middle of the third molars; mesopterygoid fossa moderately narrow; alisphenoid strut absent; sphenopalatine vacuities large; pterygoid ridge weak, tapering posteriorly; carotid canal large; stapedial foramen in bulla absent; coronoid process of mandible short.

MORPHOLOGICAL DESCRIPTION: The same as for the only known species of the genus, which is described below.

Musseromys gulantang, new species

HOLOTYPE: FMNH 178405, an adult male with scrotal testes, trapped by D.S. Balete (field number 3408) on 12 May 2004. Photographs were taken of the freshly trapped specimen, including figures 2 and 10. A fresh muscle sample for genetic studies was removed from the thigh and placed in 95% ethanol. The specimen was then injected

with saturated formalin and soaked in dilute (10%) formalin solution, and subsequently transferred to 70% ethanol. The skull was removed and cleaned by dermestid beetles, then soaked in a dilute ammonia solution, dried, and numbered. The testes, epididymis, and seminal vesicles were removed for a comparative study (W. Breed, in prep.). External, cranial, mandibular, and dental measurements are listed in table 1. The specimen currently is deposited at FMNH and is to be transferred to the Philippine National Museum.

TYPE LOCALITY: South side of Mt. Banahaw in Barangay Lalo, Tayabas Municipality, Quezon Province, Luzon Island, Philippines, elevation 620 m (14°03′06.5″ N, 121°32′22.5″ E), within the boundaries of Mt. Banahaw–San Cristobal National Park.

REFERRED MATERIAL: Only the holotype is known currently.

ETYMOLOGY: From the Tagalog word *gulantang*, meaning "highly surprising," used as an adjective in apposition. This was the name applied to the mouse by the farmers on Mt. Banahaw when they first saw our specimen. This name also refers to our surprise at finding a tiny relative of the giant cloud rats.

GEOGRAPHIC DISTRIBUTION: Currently known only from regenerating tropical lowland rain forest on the southern lower slopes of Mt. Banahaw, but this type of vegetation is widespread on Luzon, and we predict that the mouse will be found over a broad area on Luzon.

DIAGNOSIS: Because *M. gulantang* is the only known species of *Musseromys*, generic and specific diagnoses are the same.

MORPHOLOGICAL DESCRIPTION: *Musseromys gulantang* is a small mouse with rusty-orange pelage (darker dorsally, paler ventrally); a compact body; a relatively large head with a short, blunt snout; long whiskers arising both from the sides of the snout and from a patch of bare skin posterior to the eye; a long tail with elongated hairs near the tip (i.e., penicillate), and elongate ears (fig. 2).

The snout is broad, short, and blunt. The skin immediately adjacent to the nostrils is hairless, with bare skin adjacent to the medial sulcus down to and adjacent to the mouth. There is a band of skin that grows between the incisors and the opening of the mouth; the mouth is quite small. The mystacial vibrissae extend up to 55 mm long, arising from an area of skin that covers nearly the entire side of the muzzle. The eyes are of moderate size (fig. 2), and each is surrounded by a narrow ring of bare, dark skin. Immediately posterior to the eye, separated by a narrow band of hair, is a patch of bare skin about 3 mm in diameter, slightly elongated dorsoventrally. Six to eight vibrissae (probably genal vibrissae) up to 15 mm long arise within the bare patch. The pinnae are thin and pale brown, with a sparse covering of hair on the basal quarter of the posterior surface, sparse but relatively long brown hairs on the upper three-fourths of the posterior surface, and only tiny, nearly invisible hairs on the interior surface. The pinnae are elongate, about 7 mm wide and 13 mm long, and come to a bluntly pointed tip. The lower anterior and posterior edges of the pinnae are irregular and paler than surrounding skin (fig. 2).

The forefeet are somewhat elongated, each with a very short pollex and four long digits (fig. 8). The pollex is closely appressed to the second digit, with a continuous connection of skin nearly to the distal tip of the pollex. The pollex has a small, slightly convex nail near its tip (fig. 9). Digits 2–5 have short but relatively sturdy, recurved, and sharply pointed claws. The pads on the forefeet are moderately large, covering much of the ventral surface (fig. 8). Two carpal vibrissae are present on each side, one 5–6 mm long and the other about half that length. The hind feet are moderate in length (19 mm) relative to the body, but narrow (ca. 4 mm maximum breadth; fig. 8). The hallux is short and parallel to digit 2, with no evidence of opposability; its claw reaches nearly to the base of the distal phalange on digit 2. Digits 2–4 are equal in length, and digit 5 is only slightly shorter. The claws are similar in shape to those of the forefeet. The ventral surface has no hair. The thenar pad is about 4.0 mm long and 1.2 mm wide. The hypothenar is small and nearly circular, ca. 1.2 mm in diameter. Interdigital pads 1–4 lie in their usual places at the base of the digit; pad 1 is largest, followed by pad 4; pads 2 and 3 are smallest and are equal in size. On both

TABLE 2
List of Genetic Material Used in This Study

	Museum voucher number[a]	Genbank accession (GHR sequences)	Publication (GHR sequences)	Genbank accession (IRBP sequences)	Publication (IRBP sequences)
Allactaga siberica	_	AY294897	Steppan et al., 2004	AY326076	Jansa and Weksler, 2004
Zapus princeps	_	(*hudsonius*) AF332041	Adkins et al., 2001	AF297287	DeBry and Sagel, 2001
Rhizomys pruinosus	_	AY294899	Steppan et al., 2004	AY326107	Jansa and Weksler, 2004
Tachyoryctes splendens	_	AY294900	Steppan et al., 2004	AY326112	Jansa and Weksler, 2004
Acomys spinosissimus	_	(*ignitus*) AY294923	Steppan et al., 2004	AY326074	Jansa and Weksler, 2004
Aethomys chrysophilus	_	(*namaquensis*) AY294914	Steppan et al., 2004	AY326075	Jansa and Weksler, 2004
Akodon azarae	_	(*xanthorhinus*) AF332024	Adkins et al., 2001	AY163578	Weksler, 2003
Apomys microdon	USNM 458907	GQ405366	this study	DQ191493	Jansa et al., 2006
Apomys musculus	USNM 458923	GQ405367	this study	DQ191494	Jansa et al., 2006
Archboldomys luzonensis	USNM 573834	GQ405368	this study	DQ191495	Jansa et al., 2006
Batomys granti	USNM 458914	AY294917	Steppan et al., 2004	DQ191496	Jansa et al., 2006
Bullimus bagobus	USNM 458789	GQ405369	this study	DQ191498	Jansa et al., 2006
Bullimus gamay	FMNH 154821	GQ405370	this study	DQ191499	Jansa et al., 2006
Bullimus luzonicus	FMNH 167310	GQ405371	this study	DQ191500	Jansa et al., 2006
Calomyscus baluchi	FMNH 140412	GQ405372	this study	AY163581	Weksler, 2003
Carpomys phaeurus	FMNH 175565	GQ405373	this study	DQ191501	Jansa et al., 2006
Chiropodomys gliroides	AMNH 272244	GQ405374	this study	GQ405361	this study
Chrotomys gonzalesi	USNM 458952	GQ405375	this study	DQ191503	Jansa et al., 2006
Chrotomys sibuyanensis	FMNH 145701	GQ405376	this study	DQ191504	Jansa et al., 2006
Chrotomys silaceus	FMNH 175725	GQ405377	this study	DQ191502	Jansa et al., 2006
Crateromys heaneyi	CiMNH M628	GQ405378	this study	DQ191505	Jansa et al., 2006
Cricetomys emini	_	(*gambianus*) AY294905	Steppan et al., 2004	AY326081	Jansa and Weksler, 2004
Cricetulus longicaudatus	_	(*migratorius*) AY294926	Steppan et al., 2004	AY326082	Jansa and Weksler, 2004
Crunomys melanius	FMNH 147105	GQ405379	this study	DQ191506	Jansa et al., 2006
Hylomyscus denniae	_	(*parvus*) DQ19060	Steppan et al., 2005	AY326088	Jansa and Weksler, 2004
Limnomys bryophilus	FMNH 147970	GQ405380	this study	DQ191508	Jansa et al., 2006
Limnomys sibuanus	FMNH 147943	GQ405381	this study	DQ191509	Jansa et al., 2006
Lorentzimys cf. nouhuysi	KU 160659	GQ405382	this study	GQ405362	this study
Lorentzimys cf. nouhuysi	KU 160732	GQ405383	this study	GQ405363	this study
Mastomys natalensis	_	(*hildebrandtii*) AY294916	Steppan et al., 2004	AY326093	Jansa and Weksler, 2004
Maxomys whiteheadi	_	(*surifer*) DQ019065	Steppan et al., 2005	DQ191510	Jansa et al., 2006
Meriones unguiculatus	_	(*shawi*) AF332021	Adkins et al., 2001	AY326095	Jansa and Weksler, 2004
Microtus sikimensis	_	(*irene*) AY294924	Steppan et al., 2004	AY163594	Weksler, 2003
Mus musculus	_	NC000081	*Mus* Genome	AF126968	Stanhope et al., 1992
Musseromys gulantang	FMNH 178405	GQ405384	this study	GQ405364	this study

TABLE 2
(Continued)

	Museum voucher number[a]	Genbank accession (GHR sequences)	Publication (GHR sequences)	Genbank accession (IRBP sequences)	Publication (IRBP sequences)
Mystromys albicaudatus	DMB 3452	GQ272600	Jansa et al., 2009	AY163594	Weksler, 2003
Nesomys rufus	FMNH 151915	GQ405385	this study	AY326099	Jansa and Weksler, 2004
Niviventer excelsior	USNM 574372	GQ405386	this study	DQ191511	Jansa et al., 2006
Niviventer rapit	UMMZ 174435	GQ405387	this study	DQ191512	Jansa et al., 2006
Otomys anchietae	FMNH 155623	GQ405388	this study	AY326101	Jansa and Weksler, 2004
Petromyscus collinus	_	(*monticularis*) AY294903	Steppan et al., 2004	DQ191517	Jansa et al., 2006
Phloeomys cumingi	_	DQ019070	Steppan et al., 2005	AY326103	Jansa and Weksler, 2004
Phodopus sungorus	_	AF540640	Adkins et al., 2001	AY163631	Weksler, 2003
Pogonomys sylvestris	KU 161024	GQ405389	this study	GQ405365	this study
Praomys delectorum	_	(*tulbergi*) DQ019072	Steppan et al., 2004	AY326104	Jansa and Weksler, 2004
Rattus everetti	FMNH 142350	GQ405390	this study	DQ191513	Jansa et al., 2006
Rattus exulans	USNM 458836	GQ405391	this study	AY326105	Jansa and Weksler, 2004
Rattus preator	USNM 580077	GQ405392	this study	DQ191514	Jansa et al., 2006
Rattus tanezumi	FMNH 137032	GQ405393	this study	DQ191515	Jansa et al., 2006
Rhynchomys isarogensis	FMNH 573575	GQ405394	this study	AY326108	Jansa and Weksler, 2004
Sigmodon alstoni	_	(*hispidus*) AF540641	Adkins et al., 2001	AY163640	Weksler, 2003
Steatomys parvus	CaMNH 98495	GQ272602	Jansa et al., 2009	AY326110	Jansa and Weksler, 2004
Sundamys muelleri	_	DQ019077	Steppan et al., 2005	AY326111	Jansa and Weksler, 2004
Tarsomys apoensis	FMNH 148178	GQ405395	this study	DQ191516	Jansa et al., 2006
Tatera robusta	_	AY294920	Steppan et al., 2004	AY326113	Jansa and Weksler, 2004
Tylomys nudicaudatus	_	AY294933	Steppan et al., 2004	AY163643	Weksler, 2003
Uromys caudimaculatus	KU 160787	GQ405396	this study	N/A	N/A
Uromys caudimaculatus	KU 160788	GQ405397	this study	N/A	N/A

[a] Museum numbers associated with morphological voucher specimens used in this study. If a voucher number is not listed, that information is available online through the relevant GenBank accession number or is given in the referenced publication. Museum acronyms are defined as follows: CaMNH = Carnegie Museum of Natural History; CiMNH = Cincinnati Museum of Natural History; DMB = Durban Natural Science Museum; FMNH = Field Museum of Natural History; KU = University of Kansas Natural History Museum and Biodiversity Research Center; UMMZ = University of Michigan Museum of Zoology; USNM = United States National Museum of Natural History.

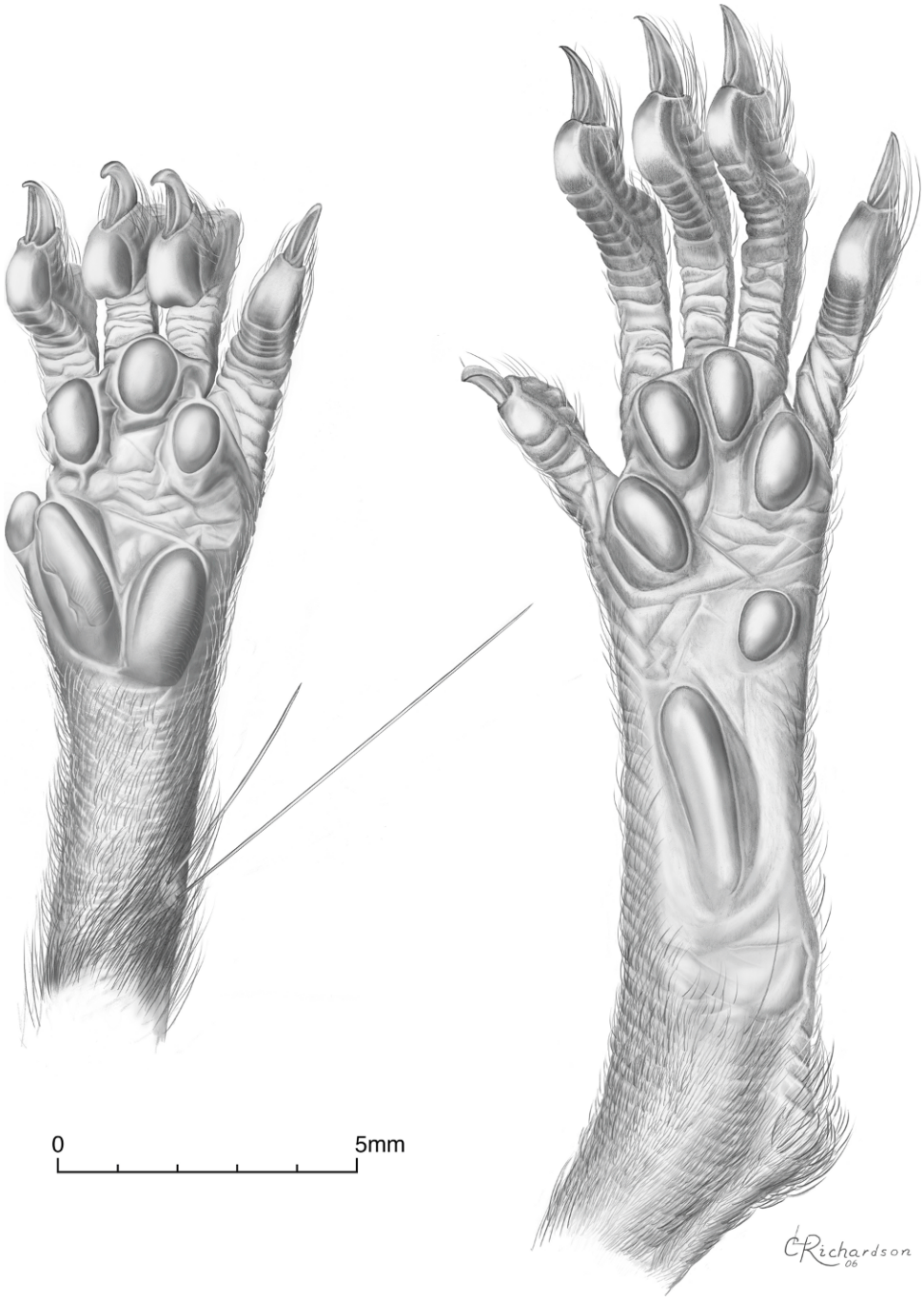

Fig. 8. Ventral surface of the left forefoot (left) and hind foot (right) of the holotype of *Musseromys gulantang* (FMNH 178405).

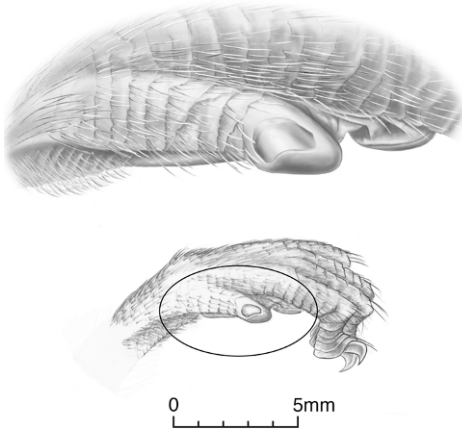

Fig. 9. Lateral view of the left forefoot of the holotype of *Musseromys gulantang* (FMNH 178405), showing the close apposition of the pollex to the second digit (lower), and the appearance of the blunt, slightly convex nail on the pollex (upper).

forefeet and hind feet, the pads are nearly smooth, but in some light, faint striations are visible.

The penis sheath appears bare but is actually covered by tiny white hairs; it is ca. 4 mm wide and 5 mm long. The scrotum is proportionately large and well covered with hair except for the posterodorsal area (posterior to the anus), which is thinly haired. The posterior tip of the scrotum, which has a dark tip of pigmented skin, extends ca. 5 mm posterior to the anus.

The tail is appreciably longer than the length of head and body (130%), and thin, tapering gradually to the tip. Body fur extends a very short distance onto the base, beyond which the tail is visibly scaly (fig. 10). The scales are dark brown and small, forming 16–17 rows per cm as measured near the base of the tail. Each scale is subtended by three fine hairs; those covering the anterior two-thirds of the tail are about 1 mm long. Posterior to this, the hairs become progressively longer and more conspicuous, with hairs near the tip reaching up to 9 mm; the hairs are equally dense dorsally and ventrally.

The dorsal pelage is fine and soft. There are many fine guard hairs that are 1–2 mm longer than the awns; underfur appears to be absent. The awns are about 5–6 mm long in

Fig. 10. Tail of the holotype of *Musseromys gulantang* (FMNH 178405), photographed by L.R. Heaney on the day of capture.

the middorsal region and similar elsewhere dorsally. Over most of the dorsum, the bases of the awns and guard hairs are gray and the tips (ca. 1.5 mm) are a rich rusty orange. The awns are shorter and sparser in the area posterior to the eyes and more of the gray is visible. The muzzle is entirely covered with the same type of hair, though it is shorter, and the vibrissae arise from within this covering of awns. The ventral pelage is composed only of awns and is shorter, ca. 2 mm long, pale gray at the base and bright rusty orange for the ca. two-thirds distal portion. This pelage covers nearly the entire

ventrum of the mouse, from the sides of the mouth to the scrotum. The ventral portion of the forelimbs have sparse hair on the distal half, but the color is the same. On the dorsal surface, the typical dorsal pelage grades into a shorter, darker, grayer pelage beginning at the elbow and terminating at the wrist, except for a small patch of short, dark hairs on the dorsal surface of the forefeet. Typical dorsal pelage ends about 2 mm above the ankle, where it is replaced by short dark brown hairs that cover the dorsal ankle region, and then extend as a scattering of dark brown hairs onto the dorsal surface of the hind foot.

The cranium (fig. 3) is small (basioccipital length = 20.1 mm; table 1) but broad (zygomatic breadth = 12.5 mm). The rostrum is short but deep and sturdy. Each nasal is narrow at its posterior end, expanding laterally and curving down onto the lateral side of the rostrum near the anterior tip, and with the dorsal surface curving ventrally at the tip. The incisors are proodont, the anteriormost point projecting anterior to the anterior tip of the nasals. The incisors are about 2.5 times as deep as wide; they are pale orange and smoothly rounded on the anterior surface. The nasolacrimal capsule is only slightly swollen. The zygomatic notch (fig. 3) is absent. The zygomatic arches are proportionately sturdy. The maxillary root of each zygomatic arch projects laterally at right angles to the skull, then curves smoothly to the squamosal root located moderately high on the side of the braincase (fig. 3). Viewed laterally, the anterior edge of the zygomatic plate is concave. The infraorbital foramen is large but dorsoventrally elongate, widest at the top (about 0.8 mm) and narrowing to its ventral origin about 2.8 mm ventrally. In dorsal view, the orbit is nearly as wide as it is long. The interorbital region is broad and its dorsal surface is slightly concave near its center; the frontal bones are not inflated. The braincase is about as wide as it is long, and is proportionately large compared to larger murids but similar in relative size to species in the Micromys Division and *Lorentzimys*. In ventral view, the zygomatic plate is concave and moderately broad, with its posterior edge dorsal to the middle of the first molar. In lateral view, the anterior portion of the braincase is nearly flat, but the dorsal surface curves smoothly ventrally toward the posterior edge.

In the orbital region (as illustrated by Musser et al., 1985), 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 (fig. 11). The space between the orbital wall and the lateral wall of the braincase is the anterior alar fissure (= sphenoidal fissure) through which cranial vessels and nerves emerge from the braincase to enter the orbit.

The bulk of the alisphenoid strut is absent, and represented only by a short dorsal projection (a1 in fig. 11) and a ventral nubbin (a2 in fig. 11); without the defining strut, the accessory foramen ovale is coalesced with the foramen ovale (figs. 11 and 12) to form a proportionately long and wide opening. The trough formed on the exterior surface of the braincase by the masseteric and buccinator nerves is clearly visible (fig. 11). The opening of the transverse canal is visible medial to the pterygoid plate. The ventral view of the basicranial region (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 (figs. 12 and 13). The lateral portion of the middle lacerate foramen is small, but the medial portion through which the carotid artery passes into the braincase is large. No stapedial foramen is evident (see also fig. 28 in Musser et al., 1998). The postglenoid foramen is large, and a strut of the squamosal extends down to contact the mastoid, leaving a small fossa (the squamosal notch) dorsal to the strut (figs. 3, 13). The hamular processes of the pterygoids are prominent, nearly reaching the anterior processes of the bullae.

The ventral surface of the bony palate (figs. 3 and 12) is slightly concave, with prominent grooves beginning at about the middle of the first molar and terminating in the posterior palatine foramina. The palate, which is about twice as wide as the first molar, terminates at the posterior edge of the third molars. The incisive foramina are narrow and slightly shorter than the length of the molar tooth row; they terminate

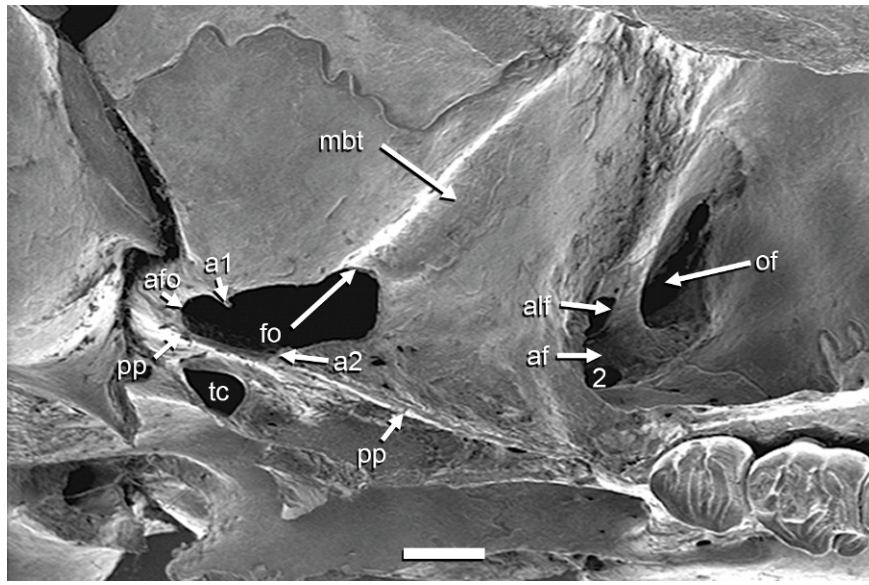

Fig. 11. View of the cranial foramina of *Musseromys gulantang* (holotype, FMNH 178405). The anterior alar fissure (**af**) contains the optical foramen (**of**) and anterior lacerate foramen (**alf**) and an opening that appears to be an extension of the sphenopalatine vacuity (**2**). The accessory foramen ovale (**afo**) is coalesced with the foramen ovale (**fo**), and are bounded medially by the pterygoid plate (**pp**), and give rise anteriorly to the trough formed by the masseteric and buccinator nerves (**mbt**). The transverse canal (**tc**) is clearly visible. Scale bar = 1 mm.

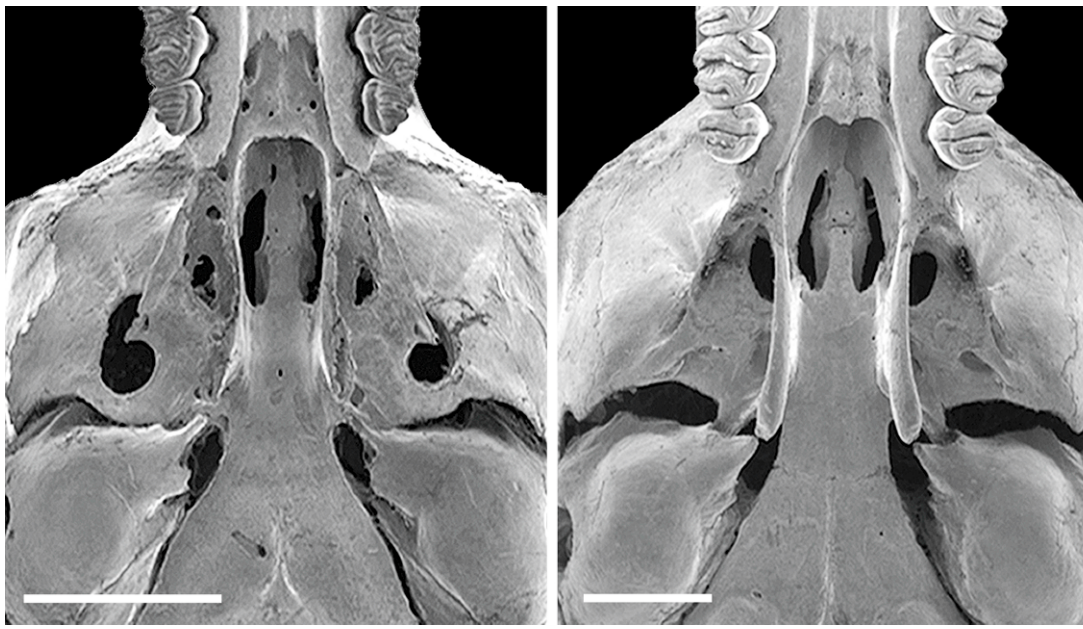

Fig. 12. Basicranial region of (left) *Musseromys gulantang* (holotype, FMNH 178405) and (right) *Carpomys phaeurus* (FMNH 175565). Scale bars = 10 mm left, 5 mm right.

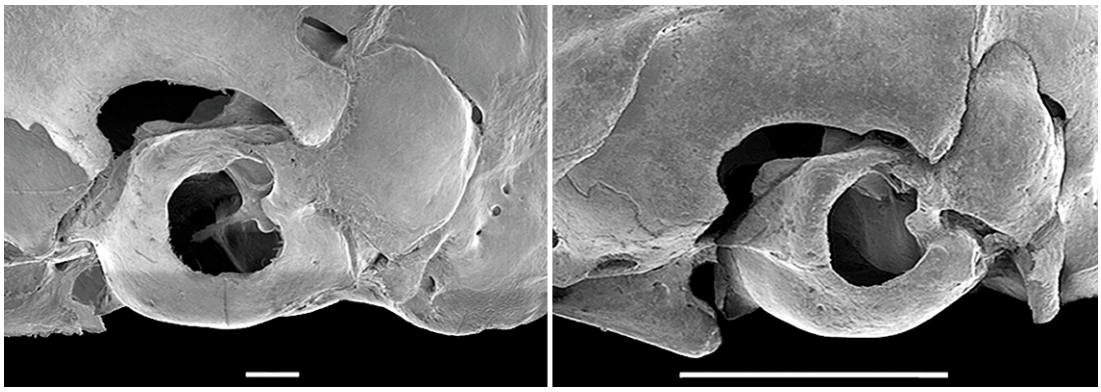

Fig. 13. Lateral view of the bullae of (left) *Musseromys gulantang* (holotype, FMNH 178405) and (right) *Carpomys phaeurus* (FMNH 175565). Scale bars = 1 mm left, 10 mm right.

slightly anterior to the anterior margins of the first molars.

The molars (fig. 4A) are sturdy with proportionately thick layers of enamel surrounding islands of dentin, forming pronounced lamina with configurations very similar to those of *Carpomys phaeurus* (fig. 4B). The teeth are moderately worn, so that details are not clear. On each upper molar, the anterior lamina is composed of t1, which is slightly distinct, and t2 and t3, which are coalesced. The second lamina is composed of t4, t5, and t6, again with t4 slightly distinct. The third lamina consists of t7, which is distinct, and t8; we suspect that t9 is present at the labial margin, but only as a minor component, as in *Carpomys* (Musser and Heaney, 1992); a younger animal would show this more clearly. A bulky and wide posterior cingulum somewhat resembles the configuration of that cusp in both species of *Carpomys*.

Each mandible (fig. 3) is robust, 14.8 mm in length (from anterior tip of incisor to posterior point on the condylar process) and 6.4 mm in height (from the most dorsal point on the condylar process to the most ventral point on the angular process). Both the anterior portion of the mandible (through which the incisors pass) and the main body of the mandible are deep, and the masseteric fossa is prominent. The coronoid process is shorter than the condylar process and is sharply pointed, inclined about 45° to the posterior. The posterior margins of the mandible between the coronoid and condylar processes, and condylar and angular processes, are shallowly concave. The angular process is rounded, and does not project as far posterior as the condylar process.

The lower molars (fig. 14) are similar to those of *Carpomys phaeurus* (see also Musser and Heaney, 1992: fig. 35), but the occlusal surfaces are heavily worn, obscuring some details of the cusps. The first lower molar is

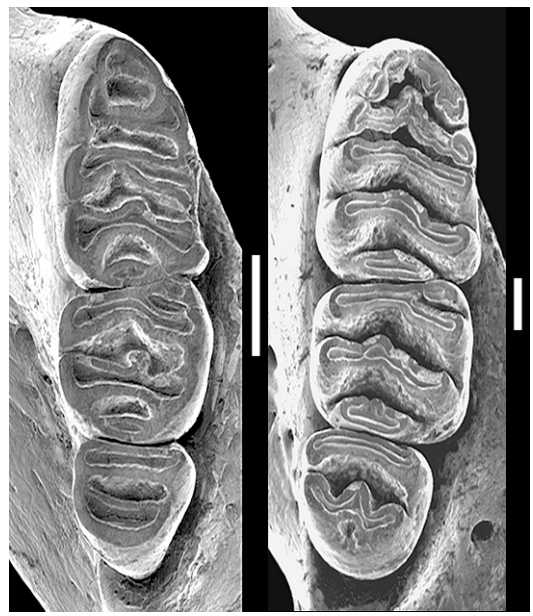

Fig. 14. Lower molars of the holotype of (left) *Musseromys gulantang* (FMNH 178405) and (right) *Carpomys phaeurus* (FMNH 175565). Scale bars = 1 mm.

Fig. 15. The holotype of *Musseromys gulantang* was captured by D.S. Balete in the Museum Special snap trap on the intersecting woody vines in the center of the photo. Note the rather sparse vegetation on the ground that is typical of lowland second-growth forest. Photographed by D.S. Balete on 12 May 2004.

distinctly longer than wide, with four rows of cusps that form three laminae and a posterior cingulum. The first row (the anteroconid) is so worn that the number and placement of cusps cannot be determined, but the outline is similar to that of *Carpomys*. The second and third lamina are similarly worn, but the gently arcing shape is clearly evident. The posterior cingulum is small but clearly present. The second lower molar is similar in configuration but, as in *Carpomys*, the anterior lamina consists only of a small labial cusp, and is slightly broader than long. The third lower molar has only a tiny anterolabial cusp, and no posterior cingulum is evident.

ECOLOGY: Tropical lowland rain forest dominated by trees of the family Dipterocarpaceae (''Philippine mahogany'') originally covered the site where the holotype of *Musseromys gulantang* was captured. The lowland forest had been logged to an elevation of about 900 m; at the site of capture, initial logging may have been done more than a century ago. Some trees continued to be present above ca. 500 m, especially along streams. About 15 years prior to the time of our mammal survey, the park management board and the local farmers' collective designated the area from about 600 m to 900 m as a restoration zone; subsequently, natural vegetation was undisturbed and regenerating well. The area of the capture site was a well-vegetated multiple-use zone, with a combination of coconut groves with heavy undergrowth, some grassy pastures, sweet potato fields, small vegetable gardens, and rice paddies, intermixed with regenerating natural vegetation. Much of the regenerating forest was along a stream that was the water source for farms, homes, and for towns and cities downstream. A set of waterfalls along the stream were accessible by trail, and were being promoted for ecotourism. The holotype of *M. gulantang* was taken in the forested area near the stream, where canopy height averaged 25 m, but some emergents reached 40 m with trunks (above buttresses) of 1 m. The mouse was caught in a Museum Special snap trap set on top of two intersecting lianas that descended from the canopy at the point where they crossed, about 2.5 m above ground level (fig. 15). The trees supporting the lianas had DBH of 25–30 cm. There was no vegetation adjacent to the lianas, and the mouse had probably descended from the canopy on one of them.

Similar lianas were abundant in the canopy. Efforts to capture additional specimens during the one remaining day of the field season were unsuccessful, and the periphery of a typhoon moved through as we departed.

DISCUSSION

Discovery of this remarkable mouse confirms and extends several broad patterns among the mammals of Indo-Australia, particularly the murid rodents that account for much of mammalian diversity in the region. First, it shows that the extent of diversification in Philippine rodents, both phyletic and morphological, is even greater than previously shown: the endemic "cloud rat clade" (= the Phloeomys Division of Musser and Carleton, 2005) contains not four but five genera, ranging from 2.6 kg to 15 g, thus including the largest and the smallest native murids in the Philippines, each with highly distinctive morphology and ecology (Musser and Heaney, 1992; Nowak, 1999). The morphological distinctiveness of *Musseromys gulantang* adds to this already remarkably diverse clade of animals. We speculate, based on the location of capture, and on its exceptionally long vibrissae, long tufted tail, and long hind feet, that it is arboreal and often forages in dense tangles of leaves and vines, almost certainly at night. The powerful masseteric musculature and incisors lead us to speculate that it feeds on hard seeds; we found several seeds of *Elaeocarpus* sp. nearby that had been gnawed open by a rodent with small incisors, perhaps *M. gulantang*.

Second, the new mouse further confirms that the great majority of the diversity of small mammals in the Philippines is the result of in situ speciation from very few ancestral species, not by multiple colonization of Asian mainland species. The dynamics of species richness of small mammals in this fauna has been driven primarily by speciation, not by colonization (Heaney, 1986, 2000, 2004; Heaney and Rickart, 1990).

Third, our studies confirm that the small tree mice of continental Southeast Asia (*Chiropodomys* and relatives), the Philippines (*Musseromys*), and New Guinea (*Lorentzimys*) are not closely related to one another; rather, their superficial similarity is probably convergent. Diversification within each of the three geographic regions has apparently increased species richness through the evolution of morphologically and ecologically similar species.

Although the primary purpose of this study was not to study murid phylogeny overall, our results (fig. 6) have implications that deserve brief comment. First, our results continue to support the position of the Phloeomys Division (labeled "E" in fig. 6) as the most basal of the living murines, as noted by recent molecular phylogenetic studies (Jansa and Weksler, 2004; Jansa et al., 2006, 2009; Steppan et al., 2005). This basal position is also indicated by the morphology of *Batomys russatus*, which alone among murines retains the primitive muroid carotid circulation pattern (Musser et al., 1998).

Second, *Chiropodomys*, a member of the Micromys Division, which has not been included in molecular phylogenies previously, is basal to two large clades: the Australia–New Guinea clade that includes *Anisomys*, *Conilurus*, *Leggadina*, *Lorentzimys*, *Pogonomys*, *Pseudomys*, and *Uromys* (and by implication, the entire Pogonomys, Pseudomys, Uromys, and Xeromys Divisions of Musser and Carleton, 2005) and the Philippine endemic Chrotomys Division of Musser and Carleton (2005, labeled "D" in fig. 6) that includes *Apomys*, *Archboldomys*, *Chrotomys*, and *Rhynchomys*. This ties the origin of these two clades directly to the Sunda Shelf of mainland Southeast Asia, a matter that previously was not apparent.

Third, as indicated above, the phylogenetic position of the enigmatic *Lorentzimys* "whose closest phylogenetic alliance has yet to be uncovered" (Musser and Carleton, 2005: 1352) is partially clarified; support for it as a member of the Australia–New Guinea clade described above is strong, when our results and those of Steppan et al. (2005) are considered together. However, relationships within this large and highly diverse group are largely unresolved at this time.

Fourth, our results continue to support the sister relationship of the Crunomys Division (which includes *Crunomys* [labeled "C" in fig. 6] and *Summeromys*) and the Maxomys Division (which includes only *Maxomys*;

Musser and Carleton, 2005), as we reported previously (Jansa et al., 2006).

Although we know little overall about the ecology of *Musseromys gulantang*, we think that it is associated primarily with lowland rain forest on Luzon Island. This habitat has been decimated by logging, clearing for commercial agriculture, subsistence farming, and urban development (Environmental Science for Social Change, 1999; Heaney et al., 1999; Kummer, 1992; Vitug, 1993), and is clearly the most seriously threatened habitat in the Philippines. However, the new mouse was captured in an area of regenerating second growth. Such habitat, especially in ''foothills'' regions at elevations near 600 m, is scattered widely at the periphery of the Central Cordillera, Sierra Madre, and Zambales mountains, as well as around the isolated peaks in central and southern Luzon (fig. 1), and this species should be sought in all of these areas. Documenting this species in regenerating second growth forest emphasizes the importance of including such habitat in protected areas, especially as the population in the Philippines urbanizes and as emigration increases from the current (2009) ca. 20% of adult citizens, leading to the depopulation of some rural areas. The future of Philippine lowland forest biodiversity may, in the end, hinge primarily on regeneration of natural secondary forest as much as it does on protecting the highly important but increasingly small tracts of remaining old-growth lowland forest.

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APPENDIX 1

Specimens Examined

Batomys granti. Philippines: Luzon Id.: Kalinga Province: Balbalan Municipality, Mt. Bali-it, FMNH 175560, 175561.

Carpomys phaeurus. Philippines: Luzon Id.: Kalinga Province: Balbalan Municipality, Mt. Bali-it, 2150 m. FMNH 175565.

Chiropodomys gliroides. Indonesia: Java: Gunong Slamat, FMNH 47141. Vietnam: Ban Me Thuot, FMNH 46725.

Crateromys schadenbergi. Philippines: Luzon Id.: Mountain Province: Mt. Kapilingan, FMNH 62294, 62295, 62296.

Haeromys pusillus. Philippines: Calauit Id.: Palawan Province: Abangan, FMNH 172885.

Hapalomys longicaudatus. Laos: Phong Saly, FMNH 32463.

Lorentzimys nouhuysi. Papua New Guinea: Eastern Highlands Province: 10.7 km NW of Herowana Village, KU 160659. Papua New Guinea: Morobe Province: 14.2 km at 150 degrees from Tep Tep Airstrip, KU 161012. Papua New Guinea: Western Highlands: Nondugl, AMNH 183805. Papua New Guinea: Eastern Highlands District: Bomai, AMNH 197868.

Micromys minutus. Captive stock, Brookfield Zoo, Chicago, FMNH 129471.

Vandeleuria oleracea. Sri Lanka: Meda-Maha-Nuwara C.P., 3750 ft., FMNH 99501.