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# A new species of *Batomys* (Muridae, Rodentia) from southern Luzon Island, Philippines

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*Abstract.*—We describe a new species of *Batomys* from Mt. Isarog, southern Luzon. Morphological and genetic studies of newly obtained specimens of *Batomys granti* from the type locality on Mt. Data and other high mountains in the Central Cordillera of northern Luzon, and previously referred specimens from Mt. Isarog on the southern peninsula of Luzon, support the separation of the population from Mt. Isarog as a distinct species that is sister to *B. granti* and demonstrate the existence of *B. granti* as a widespread species in the Cordillera. The new species occurs only in montane and mossy forest from 1350 m to 1800 m, and is separated from the nearest known population of *B. granti* by about 450 km. Limited ecological data indicate that it is a nocturnal herbivore. Recognition of this species raises the number of native murid species on Luzon to 44, and the number of species in the endemic Philippine cloud-rat clade to 18. The new species occurs within a national park that is not currently under threat.

Keywords: biodiversity, biogeography, cloud rats, conservation, endemism, mammals, oceanic islands, speciation

Species of *Batomys*, or hairy-tailed rats (fide Heaney et al. 2010) are members of the cloud-rat clade (*Phloeomys* Division sensu Musser & Carleton 2005) that is endemic to the Philippines and, based on current published studies, is consistently shown to be the sister taxon to all other Murinae (Jansa et al. 2006, Lecompte et al. 2008, Rowe et al. 2008, Schenk et al. 2013). *Batomys granti* was described based on specimens obtained by John Whitehead on Mt. Data, Mountain Province, in the Central Cordillera of northern Luzon (Thomas 1895, 1898), and soon thereafter *B. dentatus* was described from a single specimen from Benguet Province, also in the Central Cordillera (Miller 1910). Information on the distribution of *Batomys* on Luzon remained static for more than 75 years until 1988, when we initiated surveys of Mt. Isarog in southeastern Luzon and obtained samples of *Batomys* that we initially identified as *B. granti* (Rickart et al. 1991, Balete & Heaney 1997, Musser et al. 1998, Heaney et al. 1999). Our subsequent surveys, conducted between 2000 and 2012, covered most of the isolated mountains and mountain chains on Luzon, yielded more specimens of *B. granti* from Mt. Data, and extended the range of that species to include additional mountains in the Central Cordillera. However,
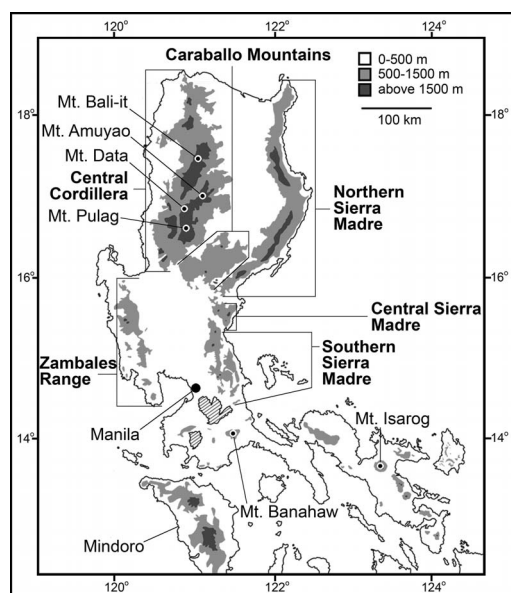
Fig. 1. Luzon Island, Philippines showing mountains and mountain ranges discussed in text.

these surveys did not produce additional records of *Batomys* beyond those from the Central Cordillera and Mt. Isarog (Fig. 1), nor did they lead to rediscovery of Miller's (1910) *B. dentatus* (Balete et al. 2009, 2011, 2013a, 2013b; Alviola et al. 2011, Duya et al. 2011, Rickart et al. 2011a, 2011b, 2013; Heaney et al. 2013a, 2013b).

*Mindanaomys salomonseni*, described by Sanborn (1953) from Mindanao Island, was subsequently considered a species of *Batomys* (Misonne 1969, Musser & Heaney 1992). This species is widespread in the Mindanao faunal region, with records from Biliran, Dinagat, Leyte, and Mindanao islands (Heaney & Rabor 1982, Rickart et al. 1993, Heaney et al. 2006b). Musser et al. (1998) defined the taxonomic and geographic boundaries of the foregoing three species of *Batomys* and also described *B. russatus* from Dinagat Island. Their study highlighted several characters—in particular, length of incisive foramina, tail diameter, and tail pilosity—that consistently differentiate the Luzon *Batomys* from those of the Mindanao faunal region. The discovery of *B. hamiguitan* from the south-eastern-most peninsula of Mindanao (Balete et al. 2008) further confirmed the consistency of these differences. Molecular phylogenetic analyses failed to recover the monophyly of *Batomys*, with *B. granti* appearing as sister to *Crateromys heaneyi* (to date, the only member of that genus for which there are gene sequence data), and *B. salomonseni* as sister to that clade (Jansa et al. 2006, Heaney et al. 2009, Schenk et al. 2013). Further analyses clearly are needed to resolve the generic limits of *Batomys* and *Crateromys*, issues we address only briefly in this paper.

Here, our reference to *Batomys* is limited to Luzon populations. The two recognized species from Luzon, *B. granti* and *B. dentatus*, were described more than a century ago (Thomas 1895, Miller 1910). Musser et al. (1998) rediagnosed *B. dentatus* in detail and reaffirmed its distinctiveness from *B. granti*. They also recognized morphological variation among samples of the nominal *B. granti* from Mt. Data (the type locality in the Central Cordillera), and those from Mt. Isarog, southern Luzon, but the limited material from Mt. Data did not permit a definitive assessment of their level of differentiation. As described here, analysis of new material reveals that specimens from Mt. Data and elsewhere in the Central Cordillera share a similar morphology, whereas animals from Mt. Isarog are morphologically distinct. Morphological examinations and morphometric analyses, together with a molecular phylogenetic analysis, allow us to refine the species boundaries of *B. granti* and to recognize the Mt. Isarog population as a distinct species.

## Materials and Methods

Terminology for external features follows Brown (1972) and Brown & Yalden (1973). Terminology for cranial and dental features follows Musser & Heaney (1992). External measurements (Table 1) in milli-

Table 1.—External measurements (mm), body weight (g), and measurement ratios (expressed as percentages) of adult *Batomys granti* and *B. uragon*. First line of each variable gives the mean ± 1 *SD* for sample size $n \geq 4$, or the average for $n \leq 3$; second line gives the range and sample size (in parentheses) where $< n$. Probabilities are for *t*-tests comparing male and female samples of each species.

| Variable | Batomys granti | | | Batomys uragon | | | |
| | males ($n = 5$)[a] | females ($n = 5$)[b] | P | holotype[c] | males ($n = 5$)[d] | females ($n = 5$)[e] | P |
| --- | --- | --- | --- | --- | --- | --- | --- |
| LHB | 192.0 ± 4.7 | 194.2 ± 5.1 | 0.498 | 206 | 198.3 ± 6.5 | 188.2 ± 9.7 | 0.089 |
| | 185–190 | 188–200 | | | 195–206 | 181–205 | |
| LT | 159.0 ± 8.7 | 157.6 ± 12.7 | 0.844 | 149 | 144.4 ± 4.3 | 141.6 ± 17.4 | 0.765 |
| | 148–180 (4) | 149–170 | | | 140–149 (4) | 128–171 | |
| LHF | 36.6 ± 2.3 | 37.2 ± 1.3 | 0.625 | 38 | 37.4 ± 1.9 | 37.4 ± 2.1 | 0.999 |
| | 33–39 | 35–38 | | | 35–40 | 35–40 | |
| LE | 21.8 ± 0.8 | 22.0 ± 0.7 | 0.685 | 21 | 21.0 ± 0.8 | 20.5 ± 0.6 | 0.356 |
| | 21–23 | 21–23 | | | 20–22 (4) | 20–21 (4) | |
| WT | 184.4 ± 28.7 | 186.8 ± 14.9 | 0.915 | 175 | 178.2 ± 14.4 | 177.0 ± 24.9 | 0.928 |
| | 145–226 | 158–194 | | | 160–200 | 160–220 | |
| LT/LHB (%) | 82.1 ± 5.7 | 81.1 ± 5.7 | 0.801 | 72.3 | 72.8 ± 1.3 | 75.5 ± 11.1 | 0.648 |
| | 75.6–89.5 (4) | 74.4–90.0 | | | 71.8–74.7 (4) | 68.4–92.4 | |
| LHF/LHB (%) | 19.1 ± 0.8 | 19.2 ± 1.0 | 0.866 | 18.4 | 18.9 ± 0.7 | 19.9 ± 0.7 | 0.168 |
| | 17.8–19.8 | 17.6–20.2 | | | 18.2–19.7 | 19.1–21.1 | |

[a] FMNH 169125, 188321, 188323, 193691, 193697; [b] FMNH 169126, 193689, 193693, 193695, 214323; [c] USNM 458949; [d] FMNH 142046, USNM 458941, 458946, 458947, 458949 (holotype); [e] USNM 458939, 458940, 458943, 458945, 458948.

meters (mm) of total length, length of tail vertebrae (LT), length of hind foot (LHF), length of ear from notch (LE), and weight in grams (WT) were taken from fresh specimens in the field; these measurements are found in the field catalogs of the collectors deposited at the Field Museum of Natural History (FMNH) or the National Museum of Natural History, Smithsonian Institution (USNM). The length of head and body (LHB) was determined by subtracting tail length from total length. Tail length measurements for specimens with damaged (shortened) tails were not included in analyses.

Eighteen cranial and dental measurements (Table 2) were made by Heaney using digital calipers graduated to 0.01 mm. Only measurements from adult individuals were included in analyses, and only a subset of measurements was available for individuals with damaged skulls. Measurements included basioccipital length (BOL), interorbital breadth (IB), zygomatic breadth (ZB), mastoid breadth (MB), length of nasal bones (LN), length of incisive foramina (LIF), depth of rostrum (DR), length of rostrum (LR), orbitotemporal length (OL), crown length of maxillary molar toothrow (LM1–3), labial palatal breadth at M1 (PBM1), length of diastema (LD), post-palatal length (PPL), lingual palatal breadth at M3 (PBM3), height of braincase (HBC), breadth of M1 (BM1), breadth of incisors at tip (BIT), and breadth of zygomatic plate (BZP). Descriptive statistics (mean, standard deviation, and range) of external, cranial, and dental measurements were calculated separately for adult males and females. We used Student's *t*-test to assess potential sexual dimorphism. We assessed multivariate variation in cranial morphology through principal component analysis with SYSTAT 10 for Windows (SPSS Inc. 2000) using the correlation matrix of $\log_{10}$-transformed measurements of adult specimens of both sexes for which we had complete measurements. Scanning electron micrographs of crania, mandibles, and teeth were made from uncoated specimens

Table 2.—Cranial and dental measurements (mm) of adult *Batomys granti and B. uragon*. First line of each variable gives the mean $\pm$ 1 *SD* for sample size $n \geq 4$, or the average for $n \leq 3$; second line gives the range and sample size (in parentheses) where $< n$. Probabilities are for *t*-tests comparing male and female samples of *B. granti*.

| Variable | *Batomys granti* | | | *Batomys uragon* | | |
| | males ($n = 7$)[a] | females ($n = 4$)[b] | *P* | holotype[c] | males ($n = 5$)[d] | females ($n = 1$)[e] |
|---|---|---|---|---|---|---|
| BOL | 41.08 $\pm$ 0.67 | 41.07 | | 41.71 | 41.34 | 40.64 |
| | 40.35–41.68 (5) | 40.68–41.29 (3) | | | 40.65–41.71 (3) | |
| IB | 6.09 $\pm$ 0.31 | 5.89 | | 5.77 | 5.59 $\pm$ 0.21 | 5.91 |
| | 5.61–6.34 | 5.51–6.09 (3) | | | 5.25–5.77 | |
| ZB | 22.04 $\pm$ 0.54 | 22.34 | | 21.95 | 22.35 $\pm$ 0.43 | |
| | 21.55–23.11 (6) | 21.75–23.31 (3) | | | 21.95–22.99 | |
| MB | 15.42 $\pm$ 0.32 | 15.44 $\pm$ 0.37 | 0.927 | 15.85 | 15.44 $\pm$ 0.35 | 15.58 |
| | 15.00–15.80 (5) | 15.08–15.93 | | | 15.01–15.84 (4) | |
| LN | 17.97 $\pm$ 0.54 | 17.79 $\pm$ 0.57 | 0.614 | 15.52 | 16.09 $\pm$ 0.58 | |
| | 16.95–18.43 | 16.98–18.24 | | | 15.52–16.76 (4) | |
| LIF | 8.88 $\pm$ 0.49 | 8.82 | | 8.14 | 8.11 $\pm$ 0.36 | 8.46 |
| | 8.34–9.57 | 8.63–8.99 (3) | | | 7.64–8.64 | |
| DR | 9.38 $\pm$ 0.32 | 9.58 | | 10.16 | 9.76 $\pm$ 0.28 | 9.90 |
| | 8.95–9.76 | 9.36–9.85 (3) | | | 9.52–10.16 | |
| LR | 19.02 $\pm$ 0.60 | 18.69 | | 18.79 | 18.14 $\pm$ 0.57 | |
| | 18.20–19.69 | 18.35–19.27 (3) | | | 17.42–18.79 (4) | |
| OL | 13.61 $\pm$ 0.65 | 13.90 $\pm$ 0.51 | 0.465 | 13.79 | 13.89 $\pm$ 0.52 | 13.52 |
| | 12.87–14.79 | 13.39–14.39 | | | 13.41–14.74 | |
| LM1–3 | 7.61 $\pm$ 0.31 | 7.61 $\pm$ 0.23 | 0.999 | 8.37 | 8.26 $\pm$ 0.36 | 8.24 |
| | 7.25–7.97 | 7.30–7.85 | | | 7.80–8.76 | |
| PBM1 | 7.46 $\pm$ 0.37 | 7.53 | | 7.81 | 7.77 $\pm$ 0.31 | 8.09 |
| | 6.77–7.85 | 7.32–7.66 (3) | | | 7.43–8.17 | |
| LD | 12.28 $\pm$ 0.50 | 12.08 | | 12.01 | 11.44 $\pm$ 0.70 | 11.57 |
| | 11.58–13.07 | 11.85–12.22 (3) | | | 10.45–12.21 | |
| PPL | 16.55 $\pm$0.17 | 16.92 $\pm$ 0.57 | 0.205 | 16.3 | 16.74 $\pm$ 0.44 | 16.30 |
| | 16.35–16.81 (5) | 16.21–17.39 | | | 16.30–17.35 (4) | |
| PBM3 | 4.36 $\pm$ 0.27 | 4.53 | | 5.04 | 4.60 $\pm$ 0.36 | 4.26 |
| | 3.90–4.69 | 4.38–4.66 (3) | | | 4.21–5.04 | |
| HBC | 12.06 $\pm$ 0.18 | 11.78 $\pm$ 0.32 | 0.139 | 11.85 | 11.83 $\pm$ 0.13 | 11.86 |
| | 11.87–12.31 (5) | 11.55–12.25 | | | 11.66–11.98 (4) | |
| BM1 | 2.37 $\pm$ 0.18 | 2.30 $\pm$ 0.14 | 0.532 | 2.35 | 2.40 $\pm$ 0.09 | 2.54 |
| | 2.15–2.58 (6) | 2.11–2.45 | | | 2.30–2.51 | |
| BIT | 2.73 $\pm$ 0.13 | 2.46 | | 3.15 | 2.90 $\pm$ 0.18 | 2.80 |
| | 2.58–2.86 (6) | 2.40–2.55 (3) | | | 2.77–3.15 | |
| BZP | 4.36 $\pm$ 0.17 | 3.91 $\pm$ 0.22 | 0.004 | 4.10 | 3.94 $\pm$ 0.18 | 4.18 |
| | 4.18–4.60 | 3.63–4.14 | | | 3.65–4.10 | |

[a] FMNH 62503, 62504, 169125, 188321, 188323, 193691, 193697; [b] FMNH 169126, 193689, 193693, 214323; [c] USNM 458949; [d] FMNH 142046, USNM 458941, 458946, 458947, 458949 (holotype); [e] USNM 458939.

with an AMRAY 1810 scanning electron microscope.

Except for the two specimens of *Batomys granti* from Mt. Data collected by H. H. Hoogstraal et al. in 1946 (Sanborn 1952), all other specimens examined in this study (Appendix) were collected by the authors and their associates (Rickart et al. 1991, 2011a, 2011b; Musser & Heaney 1992, Musser et al. 1998, Heaney et al. 2003). The Hoogstraal specimens from Mt. Data were prepared as skin and skull (FMNH 62503) and as skin, skull, and skeleton (FMNH 62504). The remainder were prepared as either fluid-preserved specimens or skeletons, after tissue sam-

ples were taken from the thigh muscle of fresh specimens and preserved in either ethanol or DMSO buffer. Fluid-preserved specimens were first injected with saturated formalin solution in the field, stored temporarily in 10% formalin, and subsequently transferred to 70% ethanol. For this study, skulls were removed from some fluid-preserved specimens and cleaned with dermestid beetles, as were the skeletons, and briefly soaked in a weak ammonia solution. Age determination of freshly caught specimens was based on relative body size and reproductive condition, and subsequently validated at the museum based on molar tooth wear and fusion of cranial sutures, following the age categories defined by Musser & Heaney (1992) and Musser et al. (1998).

All referred specimens of *Batomys* from Mt. Isarog, with the exception of FMNH 142046 and 152033, are deposited at National Museum of Natural History, Smithsonian Institution (USNM). Specimens from Benguet, Kalinga, and Mountain provinces are deposited at FMNH, half of which will be transferred to the National Museum of the Philippines. The capture and handling of animals in the field followed all relevant laws and regulations of the Philippines.

We used DNA sequences from the mitochondrial cytochrome *b* gene to assess genetic variation among specimens from Luzon previously included within *Batomys granti* (broadly defined). For phylogenetic analysis, we included other members of the cloud-rat clade, and we rooted the resulting trees using sequences from five outgroup species of Muridae, including two deomyines (*Deomys ferrugineus* and *Acomys spinosissimus*) and three gerbilines (*Meriones unguiculatus*, *Gerbillus nigeriae*, and *Gerbilliscus guineae*). DNA was extracted from field-collected tissues using a Qiagen DNA Minikit (Qiagen, Inc.). We PCR amplified the complete cytochrome *b* 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 & 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; last accessed 16 December 2014). We used the GTRGAMMA model of sequence substitution to infer the best tree and performed 1000 bootstrap replicates to assess nodal support.

## Results

*Morphometric analyses.*—There was no significant sexual dimorphism in external measurements of *Batomys* from either the Central Cordillera or Mt. Isarog, although for the sample from Mt. Isarog, males averaged slightly larger than females and the difference in length of head and body approached significance (Table 1). Few cranial measurements involved samples large enough to test for sexual dimorphism, and those only among specimens of *B. granti* from the Central Cordillera; the only significant difference obtained was breadth of the zygomatic plate, which was greater for males (Table 2).

We conducted a principal components analysis of 18 cranial measurements using combined samples of adult male and female individuals of *Batomys* from Mt. Amuyao ($n = 4$), Mt. Data ($n = 2$), Mt. Isarog ($n = 3$), and Kalinga ($n = 2$). The

Table 3.—Character loadings, eigenvalues, and percent variance explained on the first two components of a principal components analysis of $log_{10}$-transformed cranial and dental measurements of adult *Batomys granti* and *B. uragon* (Fig. 2).

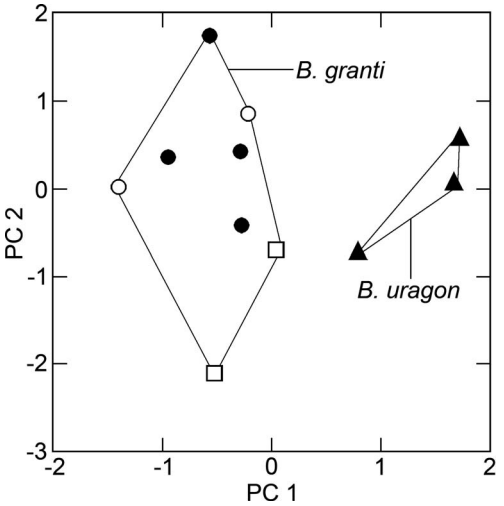| Variable | Principal component | |
|---|---|---|
|  | 1 | 2 |
| Basioccipital length | 0.202 | 0.511 |
| Interorbital breadth | −0.197 | 0.783 |
| Zygomatic breadth | 0.374 | 0.452 |
| Mastoid breadth | 0.108 | 0.774 |
| Length of nasal bones | −0.828 | 0.350 |
| Length of incisive foramen | −0.543 | 0.439 |
| Depth of rostrum | 0.754 | 0.228 |
| Length of rostrum | −0.078 | 0.762 |
| Orbito-temporal length | 0.087 | −0.632 |
| Length of maxillary toothrow | 0.913 | −0.113 |
| Labial palatal breadth at M1 | 0.768 | 0.263 |
| Length of diastema | −0.514 | 0.554 |
| Post-palatal length | 0.335 | 0.379 |
| Lingual palatal breadth at M3 | 0.423 | 0.544 |
| Height of braincase | −0.580 | −0.053 |
| Breadth of M1 | 0.280 | −0.114 |
| Breadth of incisors at tip | 0.770 | 0.052 |
| Breadth of zygomatic plate | −0.377 | −0.157 |
| Eigenvalue | 4.924 | 3.897 |
| Variance explained | 27.4% | 21.7% |



Fig. 2.  Results of principal components analysis of cranial and dental measurements of *Batomys* (see Table 3). Projections of specimen scores on components 1 and 2 for *B. granti* from Mt. Amuyao (closed circles), Mt. Data (open circles), and Mt. Bali-it (open squares), and for *B. uragon* from Mt. Isarog (closed triangles).

first four components accounted for 75% of the total variance. Components 1 and 2 with eigenvalues of 4.9 and 3.9, respectively, together accounted for 49.1% of the total variation (Table 3). Components 3 and 4 together accounted for 25% of the total variation; both had eigenvalues of less than 3 and with few variables having large magnitude loadings. In a bivariate plot of individual specimen scores on components 1 and 2 (Fig. 2), specimens from Mt. Amuyao, Mt. Data, and Mt. Bali-it are clearly separated from those from Mt. Isarog; the latter have longer maxillary toothrows, broader incisors and palates, lower braincases, and shorter nasals, incisive foramina, and diastemas compared to specimens from the Central Cordillera (see the higher positive and negative loadings for these traits in Table 3).

*Molecular analysis.*—The tree derived from the maximum likelihood analysis of the cytochrome *b* data set (Fig. 3) strongly supports (bootstrap = 81%) monophyly of *Batomys granti* specimens from four localities in the Central Cordillera (including Mt. Data, the type locality), monophyly of the specimens from Mt. Isarog (bootstrap = 100%), and the sister-group relationship of these two montane samples (bootstrap = 100%). The Central Cordillera and Mt. Isarog groups are separated by 4.2% net uncorrected *p*-distance. As found in previous genetic analyses, the genus *Batomys*, as currently defined, is paraphyletic because *Crateromys heaneyi,* as generically allocated by Gonzales & Kennedy (1996), is nested within it; however, support for this arrangement is not strong (bootstrap = 67%). As reported previously, the four species of *Musseromys* (Heaney et al. 2014a) form a well-supported clade that is sister to *Carpomys phaeurus*, and *Phloeomys cumingi* is recovered as the basal taxon to all other members of the cloud-rat clade.
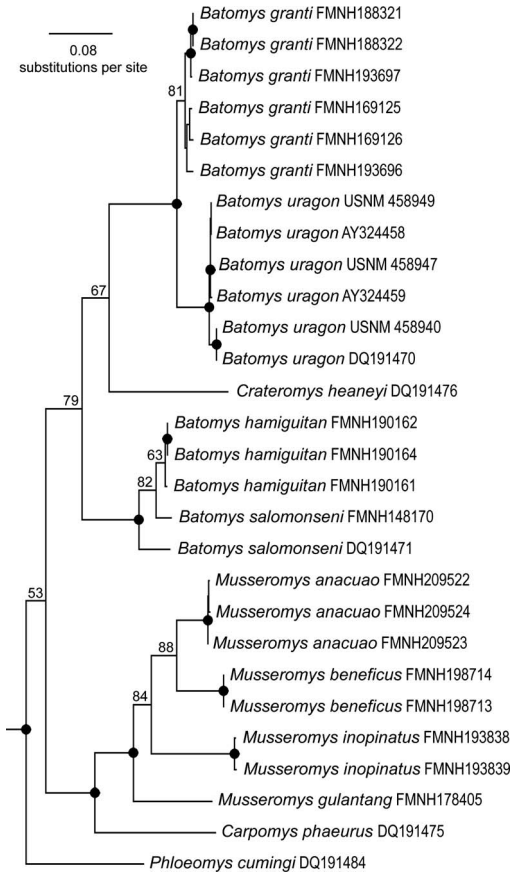
Fig. 3. The maximum-likelihood (lnL = −8305.40) tree resulting from analysis of cytochrome *b* sequences from species of the *Phloeomys* Division under the GTRGAMMA model in RAxML. Solid circles at nodes represent bootstrap values ≥ 90%; numbers at nodes indicate maximum-likelihood bootstrap values < 90%. Terminal taxa are identified by species names and a unique alphanumeric identifier (either museum catalog number or Gen-Bank accession number; Table 4).

Based on these DNA and morphometric results, we restrict *Batomys granti* to include only those populations in the Central Cordillera, and recognize *Batomys* from Mt. Isarog as a new species.

*Batomys uragon*, new species
Figs. 2–6, Tables 1–3

*Batomys granti*: Rickart & Musser, 1993:fig. 2A (part, USNM 458944).—Musser et al., 1998:figs. 5, 6, 16, 17;

Tables 1–2 (part, FMNH 142046, 152033; USNM 458914, 458946, 458947).—Heaney et al., 1999:fig. 17, Table 9 (full series; referred specimens).—Jansa et al., 2006:figs. 1–3 (part, USNM 458914).

*Holotype*.—USNM 458949, old adult male collected on 25 Apr 1988 by Eric A. Rickart (field number: EAR 2004); preserved in ethanol, with skull subsequently removed. The skull (Fig. 5B) is in good condition, except for the broken nasal tips, anterior edge of right premaxilla, and left pterygoid process. A small sample of muscle tissue was removed from the thigh for molecular studies and a section of the femur was taken for karyology (Rickart et al. 1991, Rickart & Musser 1993).

*Type locality*.—Mt. Isarog; 4 km N, 22 km E Naga City, Camarines Sur Province, Luzon Island, Philippines; in primary mossy forest at 1750 m elevation; 13°40′N, 123°22′E (Fig. 1; Site 6 in Heaney et al. 1999).

*Paratypes (n = 14)*.—Aside from the holotype, 14 additional specimens from Mt. Isarog were examined, consisting of five from the type locality (USNM 458914, 458945–458948); six from 4 km N, 21.5 km E Naga City, elev. 1550 m, 13°40′N, 123°22′E (USNM 458939–458944); and one each from the following localities: 4 km N, 21 km E Naga City, elev. 1350 m, 13°40′N, 123°22′E (USNM 458950); 4 km N, 21 km E Naga City, elev. 1650 m, 13°40′N, 123°22′E (FMNH 152033); and 8.9 km N, 0.8 km E Ocampo Municipality, Camarines Sur Province, elev. 1700–1800 m, 13°38′32″N, 123°23′30″E (FMNH 142046).

*Distribution*.—Known only from Mt. Isarog, where it occurs in old-growth montane and mossy forest, elevation 1350–1800 m. The habitat is described in more detail in Heaney et al. (1999, Sites 4–6 and 16–18).

*Etymology*.—From the Bicolano word *uragon* (no direct English word counter-

Fig. 4.   Adult female *Batomys uragon* (USNM 458943, paratype) from Mt. Isarog, 1550 m elevation, Camarines Sur Province, Luzon Island. Photographed by E. A. Rickart, 18 March 1988.

part, but roughly translatable to "*possessing great ability, vitality, or power*"), to highlight its dispersal ability, persistence, and uniqueness to the Bicol Peninsula; adjective in the nominative singular neuter.

*Diagnosis.*—A species of *Batomys*, distinguished from *B. granti*, its nearest phylogenetic relative based on cytochrome *b* sequences (Fig. 3), by the following combination of features: medium body size (combined lengths of head and body 181–206 mm), with absolutely and comparatively shorter tail; moderate body weight, 160–220 g; pale golden-brown pelage dorsally, paler ventrally; skull longer (40.64–41.71 mm) with shallower brain case (11.66–11.98 mm) and narrower interorbital region (5.25–5.91 mm); rostrum deeper (9.52–10.16 mm) but shorter (17.42–18.79 mm) with correspondingly shorter nasals (15.52–16.76 mm) and incisive foramina (7.64–8.64 mm); zygomatic plate narrower (3.65–4.18 mm); palate broader at M1 (7.43–8.17 mm) and at M3 (4.21–5.04 mm); molar toothrow longer (7.80–8.76 mm) and upper incisors broader (2.77–3.15 mm).

*Karyology.*—2n = 52, FN = 52, entirely telocentric chromosomes. The standard karyotype is indistinguishable from those of *Batomys granti* from the Central Cordillera and *B. salomonseni* from Leyte and Mindanao islands (Rickart & Musser 1993, Rickart & Heaney 2002).

*Description and comparisons.*—Among the *Batomys* from Luzon Island, *B. dentatus*, known only from the holotype, is the most distinctive. From both *B. granti* and *B. uragon* it differs in possessing an absolutely and relatively longer tail, which also is
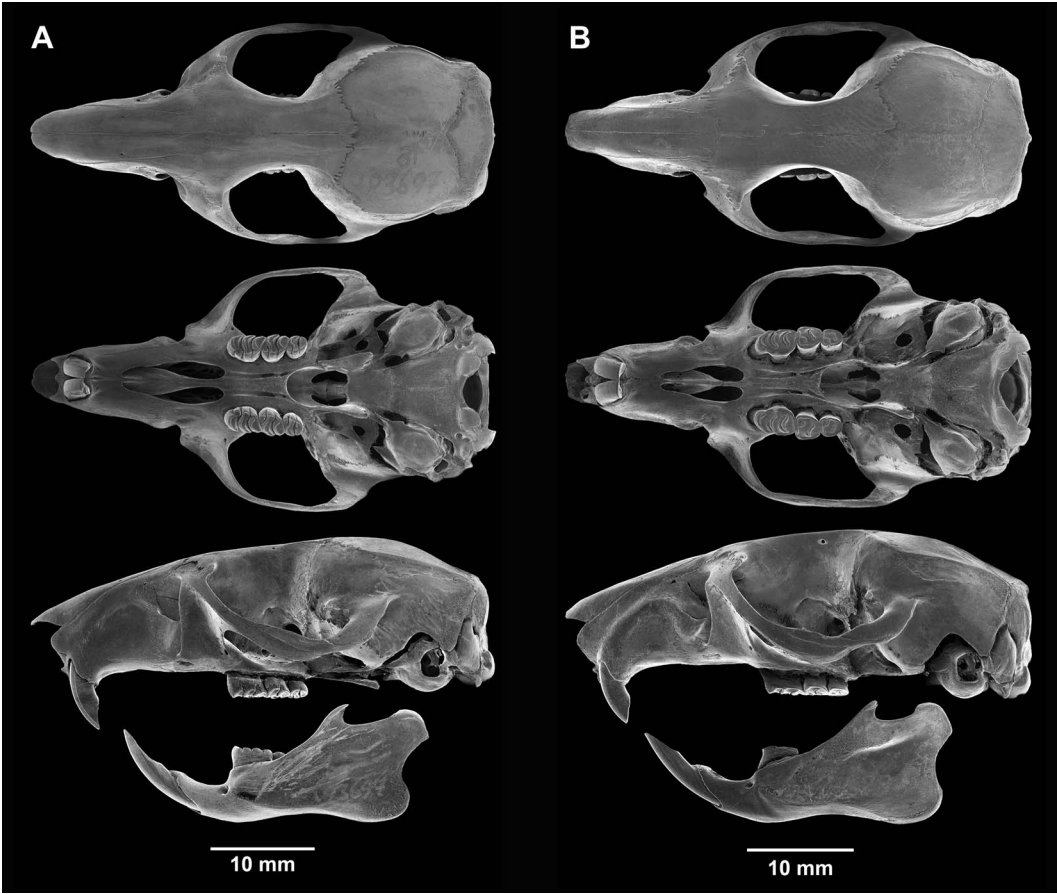
Fig. 5.   Dorsal, ventral, and lateral views of cranium and lateral view of mandible of adult *Batomys* from Luzon Island. A, *B. granti* (FMNH 193697); B, *B. uragon* (USNM 458949, holotype).

distinctive in having the distal third covered in white hairs that form a terminal tuft. Cranially, *B. dentatus* is distinguished from the other two species in having a wider zygomatic plate, shorter incisive foramina relative to the bony palate, and much more robust dentition (see Table 4 and Fig. 20 in Musser et al. 1998). The remainder of this section provides a detailed description of *B. uragon* in comparison to *B. granti*.
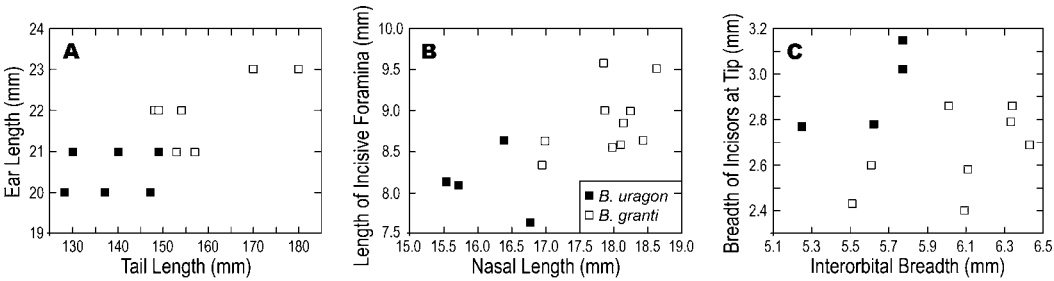


Fig. 6.   Bivariate plots of measurements comparing *Batomys granti* and *B. uragon*. A, tail length vs. ear length; B, nasal length vs. length of incisive foramina; and C, interorbital breadth vs. breadth of incisors at tip.

Table 4.—List of specimens used in genetic analysis.

| Species | Voucher | Collector number | Island | Locality | GenBank accession |
|---|---|---|---|---|---|
| Batomys granti | FMNH 169125 | EAR4560 | Luzon | Kalinga Province, Balbalan Municipality, Barangay Balbalasang, Magdallao | |
| Batomys granti | FMNH 169126 | EAR4577 | Luzon | Kalinga Province, Balbalan Municipality, Barangay Balbalasang, Am-licao | |
| Batomys granti | FMNH 188321 | DSB3799 | Luzon | Mountain Province, Mt. Data, 0.75 km N, 0.6 km E south peak | |
| Batomys granti | FMNH 188322 | DSB3851 | Luzon | Mountain Province, Mt. Data, 0.75 km N, 0.6 km E south peak | |
| Batomys granti | FMNH 193696 | DSB4509 | Luzon | Mountain Province, 1.0 km N, 1.0 km W Mt. Amuyao peak | |
| Batomys granti | FMNH 193697 | DSB4513 | Luzon | Mountain Province, 1.0 km N, 1.0 km W Mt. Amuyao peak | |
| Batomys hamiguitan | FMNH 190161 | RSQ44 | Mindanao | Davao Oriental Province, 2.5 km S, 0.75 km E Mt. Hamiguitan | |
| Batomys hamiguitan | FMNH 190162 | RSQ49 | Mindanao | Davao Oriental Province, 2.5 km S, 0.75 km E Mt. Hamiguitan | |
| Batomys hamiguitan | FMNH 190164 | RSQ55 | Mindanao | Davao Oriental Province, 2.5 km S, 0.75 km E Mt. Hamiguitan | |
| Batomys salomonseni | USNM 458784 | EAR1362 | Leyte | Leyte Province, 10 km N, 4.5 km E Baybay | DQ191471 |
| Batomys salomonseni | FMNH 148170 | LRH5217 | Mindanao | Bukidnon Province, Mt. Katanglad Range, 18.5 km S, 4 km E Camp Phillips | |
| Batomys uragon | USNM 458948 | EAR2001 | Luzon | Camarines Sur Province, Mt. Isarog, 4 km N, 22 km E Naga | AY324459 |
| Batomys uragon | USNM 458943 | EAR1822 | Luzon | Camarines Sur Province, Mt. Isarog, 4 km N, 21.5 km E Naga | AY324458 |
| Batomys uragon | USNM 458914 | EAR1987 | Luzon | Camarines Sur Province, Mt. Isarog, 4 km N, 22 km E Naga | DQ191470 |
| Batomys uragon | USNM 458947 | EAR1993 | Luzon | Camarines Sur Province, Mt. Isarog, 4 km N, 22 km E Naga | |
| Batomys uragon | USNM 458949 | EAR2004 | Luzon | Camarines Sur Province, Mt. Isarog, 4 km N, 22 km E Naga | |
| Batomys uragon | USNM 458940 | LRH4156 | Luzon | Camarines Sur Province, Mt. Isarog, 4 km N, 21.5 km E Naga | |
| Carpomys phaeurus | FMNH 175565 | LRH6866 | Luzon | Kalinga Province, Balbalan Municipality, Barangay Balbalasang, Mt. Bali-it | |
| Crateromys heaneyi | CMC 776 | | Panay | Antique Province, Culasi Municipality, Barangay Osorio, Mt. Madja-as | DQ191476 |
| Musseromys anacuao | FMNH 209522 | DSB7267 | Luzon | Aurora Province, Dinalungan Municipality, 0.2 km E Mt. Anacuao peak | |
| Musseromys anacuao | FMNH 209523 | DSB7287 | Luzon | Aurora Province, Dinalungan Municipality, 0.2 km E Mt. Anacuao peak | |
| Musseromys anacuao | FMNH 209524 | DSB7336 | Luzon | Aurora Province, Dinalungan Municipality, 0.2 km E Mt. Anacuao peak | |
| Musseromys beneficus | FMNH 198713 | DSB5325 | Luzon | Benguet Province, 1.15 km S, 1.35 km E Mt. Pulag peak | |
| Musseromys beneficus | FMNH 198714 | DSB5326 | Luzon | Benguet Province, 1.15 km S, 1.35 km E Mt. Pulag peak | |
| Musseromys gulantang | FMNH 178405 | DSB3408 | Luzon | Quezon Province, Mt. Banahaw, Barangay Lalo | |
| Musseromys inopinatus | FMNH 193838 | DSB4386b | Luzon | Mountain Province, 0.75 km W Mt. Amuyao peak | |
| Musseromys inopinatus | FMNH 193839 | DSB4477 | Luzon | Mountain Province, 1.0 km N, 1.0 km W Mt. Amuyao peak | |
| Phloeomys cumingi | USNM 573332 | EAR1699 | Catanduanes | Catanduanes Province, Barrio Summit | DQ191484 |
| Acomys spinosissimus | | | | | Z96068 |
| Deomys ferrugineus | FMNH 149427 | JCK2443 | | Zaire, Haute Zaire Province, 2 km W Epulu | EU349745 |
| Gerbilliscus guineae | | | | | AJ430562 |
| Gerbillus nigeriae | | | | | AJ430555 |
| Meriones unguiculatus | | | | | AF119264 |

*Batomys uragon* is similar to *B. granti* in external appearance and length of head and body (Figs. 4, 6, Table 1). The dorsal pelage of *B. uragon* is medium to pale golden-brown (Fig. 4); orange-brown to dark brown among congeners. Individual color variation in *B. uragon* was noted in the field; most individuals had golden dorsal fur, but the holotype was paler and was noted in the field by Rickart to have "no red coloration (colored like *Rattus everetti*)." The predominance of the pale golden pelage is particularly evident in FMNH 142046 and 152033. The pelage is woolly and shorter than in *B. granti*; *B. dentatus* has the longest fur overall (Musser et al. 1998). The venter is grayish buff with patches of unpigmented fur in the chin, pectoral, and inguinal regions. One male specimen (FMNH 142046) has a small pale brown patch of fur on the left side of the lower abdomen. The ears are slightly shorter than in *B. granti* (Table 1), and are pale brown covered with short grayish-brown hairs. The eyes are surrounded by pale rings of skin covered with very short grayish-brown and unpigmented hairs, giving the impression of naked eye rings (Fig. 4). The vibrissae are comparable to those of *B. granti* (mystacial up to 65 mm, superciliary 17–36 mm, extending to or slightly beyond the dorsal margin of the ears, and post-ocular vibrissae 24–26 mm). The forefeet are broad, each with a mid-dorsal stripe of short, dark brown fur, bordered with short, pale golden-brown fur on each side (Fig. 4). Claws are opaque, with ungual tufts of unpigmented hairs extending slightly beyond the outer margin of the claws, particularly on digits III and IV. The palmar surface, including pads, is unpigmented. The hind feet are broad and about as long as in *B. granti*, with short, dark brown fur on the dorsal surface, and pale golden-brown fur laterally (Fig. 4). Ungual tufts, composed of unpigmented hairs, extend to the tips of the claws and up to 2 mm beyond them (in

FMNH 152033). Plantar surface and the six large, fleshy plantar pads are unpigmented (Fig. 5 in Musser et al. 1998). Compared to *B. granti*, the tail of *B. uragon* is shorter on average (Fig. 6, Table 1), absolutely and relatively (128–149 mm, or 63–75% of the combined lengths of head and body), except for an adult female (USNM 458939) that has a longer tail (171 mm or 92% of combined lengths of head and body). The tails of *B. uragon* and *B. granti* are uniformly colored, in contrast to the bi-colored tail of *B. dentatus* (basal two-thirds brown, distal third white; Musser et al. 1998). *Batomys uragon* has three hairs arising in association with each caudal scale, but has a less visibly pilose tail than does *B. granti* due to its shorter hairs: 4–9 mm around mid-tail, 7–12 mm at the tip (7–11 mm at mid-tail, 8–30 mm at the tip in *B. granti*).

In Musser et al.'s (1998) redefinition of *B. granti*, the specimens from Mt. Data that were then available had significantly shorter tails than those of specimens from Mt. Isarog (Table 1 in Musser et al. 1998). The tails of specimens in that Mt. Data series have blunt tips and are covered with hairs, suggesting to the authors that their shorter length was natural, rather than caused by damage that occurred during life or during preparation of the specimens. Thomas (1895, 1898), however, suspected that the tail of the holotype of *B. granti* was incomplete. Because of the small number of specimens available from Mt. Data, Musser et al. (1998) refrained from drawing any taxonomic conclusions based on differences in tail length. Three recently obtained specimens of *B. granti* collected on Mt. Data (FMNH 188321–188323) have intact tails that are as long as, or longer than, those of all specimens of *B. uragon*, except USNM 458939 as mentioned above (Table 1). Furthermore, examination of specimens of *B. granti* from Kalinga Province and Mt. Amuyao with blunt tail-tips, which at first appeared natural, revealed that the tips are missing;

in several, one can feel the sharp edges of the broken vertebra that are barely covered with healing skin. Among adult specimens of *B. granti* ($n = 11$), only one specimen from Mt. Amuyao (FMNH 193691) had a distinctly bobbed tail (115 mm or 62% of the combined lengths of head and body). This specimen has a tail that is slightly longer than those of specimens previously available from Mt. Data (75–110 mm; FMNH 62504, BMNH 95.8.2.15 [holotype], BMNH 97.5.2.31; Thomas 1895, 1898; Musser et al. 1998). In summary, we regard the smaller tail length measurements recorded for older specimens of *B. granti* as artifactual; in fact, specimens from the Central Cordillera, including Mt. Data, have significantly longer tails than those of specimens from Mt. Isarog, herein described as *B. uragon* (Table 1).

Cranial features are similar among congeners, as noted earlier by Musser et al. (1998), but distinct and consistent differences in size and proportion are evident among the specimens of *B. granti* and *B. uragon* (Figs. 5, 6, Table 2). *Batomys uragon* has shorter nasals and a narrower interorbital region. The shorter rostrum (associated with short nasals) is nonetheless more robust in terms of rostral depth. Dorsally, the inflated cranium contrasts sharply with its narrow interorbital region, and because the anterior frontal region is narrowly flared relative to its posterior section, the interorbital region has a longer and more slender appearance than in *B. granti*. In contrast to the narrow rostrum of *B. granti*, that of *B. uragon* has a pronounced lateral inflation that is formed by the swollen capsular projection on each side of the upper incisor roots (Fig. 5).

In lateral profile, the dorsal surface of the skull of *B. uragon* traces an evenly convex arc, extending from the tips of the curved nasals, across the arched frontals of the interorbital region, to the gently curved parietals. In contrast, the dorsal surface of the skull in *B. granti* is flatter along the nasals and frontals, and the parietal region is more abruptly convex (Fig. 5). The zygomatic arch of *B. uragon* is similar to *B. granti* in breadth, but it is distinctive in having the central portion, under the jugal, markedly deeper, brought about by broad postero-ventral expansion of the maxillary zygomatic process (Fig. 5). The zygomatic plate is narrower than in *B. granti*. Ventrally, skulls of the two species are generally similar, but *B. uragon* typically has shorter incisive foramina, a broader palate, and smaller auditory bullae that have a moderate to pronounced postero-ventral inflation imparting a rounder appearance (Figs. 5, 6, Table 2).

The dental features of *B. granti* and *B. uragon* are similar, differing mainly in the relative size of incisors and molars, length of the molar toothrow, and orientation of the crown and anterior rooting of the first upper molars (Figs. 5, 6, Table 2). In particular, *B. uragon* has a longer molar toothrow, broader upper incisor tips, and shorter diastema. Its dentition is also distinct in having a pronounced inclination of the first row of cusps of M1, further exaggerated by its similarly inclined anterior molar root. The steep inclination of the anterior root of M1 is present among most specimens of *B. uragon* we examined, except one female (USNM 458939) and one young adult male (USNM 458947), both of which had a more vertical orientation; the latter individual had the posterior edge of the incisive foramina farthest from the anterior root of M1. Compared with *B. granti* (Fig. 5), the posterior portion of the dentary of *B. uragon* is wider due largely to its broadly rounded angular process and more expansive base. The condyloid process is as broad as in *B. granti* but appears shorter due to the shallow sigmoid notch that separates it from the coronoid process. In both species, the coronoid process itself is short and slightly backswept, projecting dorsally to

about the same level as the condyloid process.

*Ecology.*—Specimens of *Batomys uragon* were trapped in montane and mossy forest between 1350 and 1800 m elevation, in habitats with thick leaf litter and humus layers. During the 1988 survey of Mt. Isarog, 11 out of 13 animals (85%) were captured in traps baited with roasted coconut and peanut butter, and two in traps baited with live earthworms. Stomach contents from 3 individuals contained finely chewed vegetable matter only. Two live-trapped animals were presented potential food items. One readily accepted sprouting seeds of an unknown species of dicot, gnawing off and rejecting the sprouts and consuming only the seeds. This animal rejected other plant items that were offered, including a variety of small fruits, bulbs of orchids and other plants, several types of leaves, dried beans, peanuts, and coconut-peanut butter bait. A second animal likewise readily accepted the seeds of the sprouting dicot (again, discarding the sprouts and consuming only the seeds), and also accepted a single type of small fruit as well as coconut-peanut butter bait. Both individuals rejected all animal items including earthworms and various insects. These data suggest that *B. uragon* has a granivorous-frugivorous diet. All specimens were trapped at night on the ground, along runways and among root tangles. We conducted limited arboreal trapping on Mt. Isarog, but some individuals were captured in places where the terrain was very steep, such as on nearly vertical sides of deep ravines, which suggests that the species is a good climber (Rickart et al. 1991, Heaney et al. 1999). During a mark and release trapping study in 1993–1994, one female was caught five times in a three-day period and moved a mean distance of 11 m (range 5–14 m) between captures; another female moved an average of 44 m (range 14–85 m) between eight captures over a period of three months (Balete & Heaney 1997).

There were no signs of reproductive activity among individuals captured in March–May 1988 and December 1993–May 1994 (Rickart et al. 1991, Balete & Heaney 1997, Heaney et al. 1999). Two adult females, both taken in April 1988, had large mammae, perforate vaginas, and old placental scars; there were four scars in USNM 458945 (220 g) and three in USNM 458948 (175 g), but we could not determine the number of litters involved. Further details on reproduction of this species are discussed in Heaney et al. (1999).

Discussion

*Phylogenetic relationships.*—Our phylogenetic analysis using cytochrome *b* produced results (Fig. 3) that are consistent with those of other studies in placing *Phloeomys* in a basal position as the sister taxon to all other cloud rats, *Carpomys* and *Musseromys* as sister genera, species of *Batomys* from Luzon as sister-group to *Crateromys heaneyi*, and species of *Batomys* from Greater Mindanao as sister-group to that clade. Clearly, the phylogenetic relationships within the cloud-rat clade require further study to determine whether species not yet represented in molecular analyses conform to the monophyletic groups currently apparent. Future work should involve additional taxa and sequence data from nuclear genes designed to clarify the relationship of *Batomys* and *Crateromys* from Luzon, the taxonomic status of those species of "*Batomys*" from Mindanao as a separate phylogenetic radiation, and the relationship of the enigmatic Dinagat Island endemics *B. russatus* and *Crateromys australis* to the other cloud rats.

Our phylogenetic analysis (Fig. 3) also provides support for reciprocal monophyly of the Mt. Isarog populations with respect to those from the Central Cordillera. Furthermore, the net uncorrected *p*-dis-

tance of 4.2% between these groups is comparable to that seen between recognized sister species of rodents (Baker & Bradley 2006). This result, coupled with the morphological distinctiveness of the two groups (Fig. 2), provides solid evidence for recognizing the Mt. Isarog population as a species distinct from *B. granti*. This recognition raises the number of native rodent species documented on Luzon to 44, and the number of known members of the endemic Philippine cloudrat clade to 18 species, 12 of which occur on Luzon (Heaney et al. 2014b).

*Biogeography*.—The extant species of *Batomys* on Luzon are narrowly distributed, with two species in the Central Cordillera and one on Mt. Isarog (Fig. 1). Mt. Isarog (1966 m elevation) remains the only location outside of the Central Cordillera where the genus is currently known to exist, in spite of extensive surveys of small mammals on isolated mountains and mountain ranges elsewhere on Luzon with elevations of at least 1500 m and seemingly suitable habitat for *Batomys* (Balete et al. 2009, 2011, 2013a, 2013b; Alviola et al. 2011, Duya et al. 2011, Rickart et al. 2011a, 2011b, 2013; Heaney et al. 2013a, 2013b). The recent discovery of late Pleistocene fossil remains of *Batomys* in a lowland area in the Cagayan Valley between the central Cordillera and Sierra Madre mountain ranges reveals a much wider geographic and elevational distribution in the past, and perhaps a wider habitat association as well (Heaney et al. 2011b). The absence of *Batomys* from other high mountains on Luzon seems enigmatic, yet *Batomys uragon* now joins *Archboldomys luzonensis*, *Chrotomys gonzalesi*, and *Rhynchomys isarogensis* as species that are endemic either entirely to Mt. Isarog or to Mt. Isarog and nearby mountains on the Bicol Peninsula (Musser & Freeman 1981, Rickart & Heaney 1991, Balete et al. 2012, 2013b). We note that the sister species (and only congener) of *Archboldomys luzonensis*

(*A. maximus*) also occurs in the Central Cordillera, whereas the geographically closest congener of *R. isarogensis* (*R. banahao*) is endemic to Mt. Banahaw, which is geographically intermediate between the Central Cordillera and Mt. Isarog (Fig. 1). In contrast to the cognate relationships derived for these montane species, *Chrotomys gonzalesi* is most closely related to *C. mindorensis*, a species that is widespread in the lowlands of central Luzon (Figs. 7, 8 in Balete et al. 2012). Perhaps when additional fossils are found, the current montane distributions of *Batomys*, *Archboldomys*, and *Rhynchomys* will be shown to be relictual patterns derived from more widespread distributions during the Pleistocene. In the meantime, recognition of *Batomys uragon* further reinforces the importance of speciation within Luzon as a primary process generating the island's existing mammalian diversity (e.g., Heaney & Rickart 1990, Heaney et al. 2011a, 2014a, 2014b; Balete et al. 2012, Justiniano et al. 2014).

*Conservation*.—*Batomys uragon* is restricted to primary montane and mossy forest on Mt. Isarog, and appeared to be moderately common during our studies (Rickart et al. 1991, Balete & Heaney 1997, Heaney et al. 1999). These high elevation habitats are within Mount Isarog National Park and populations of *B. uragon* under the present management regime appear to be stable and under no threat, though limited in area. In contrast, *Batomys dentatus* remains to be rediscovered since it was first described by Miller in 1910, and thus is of uncertain status. *Batomys granti* is broadly distributed in the Central Cordillera and was present but relatively uncommon at our study areas on Mts. Amuyao, Bali-it, and Data (Rickart et al. 2011a, 2011b). However, the proliferation of commercial vegetable farming on Mt. Data, the type locality for this species, has reduced the forest cover to a very small (ca. 80 ha) remnant patch of disturbed mossy forest (Heaney et al. 2006a). Fur-

thermore, this species was not encountered during our survey of Mt. Pulag National Park where commercial agriculture also has reduced forest. Although *Batomys granti* is currently widespread and has some tolerance for habitat disturbance (Rickart et al. 2011a), the extensive destruction of mossy forest associated with vegetable farming in some the Cordillera poses a risk to the habitat of the species. The continued survival of *Batomys* and other endemic Philippine rodents will require active protection and careful management of their forest habitats, many of which form crucial watershed areas.

## Acknowledgments

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## Appendix

### Specimens Examined

*Batomys granti* ($n = 25$).—Luzon Island, Kalinga Province, Balbalan Municipality, Barangay Balbalasang, Magdallao, elev. 1600 m (17°27.5′N, 121°04.1′E; FMNH 169125); Am-licao, elev. 1800 m (17°26.5′N, 121°4.25′E; FMNH 169126); Mt. Bali-it, elev. 1950 m (17°25.8′N, 121°00.1′E; FMNH 175560–175561); Mt. Bali-it, elev. 2150 m (17°25.7′N, 121°59.8′E; FMNH 175562–175563); Mountain Province, Mt. Data (FMNH 62503–62504); Bauko Municipality, 0.1 km E south peak Mt. Data, elev. 2290 m (16.85888°N, 120.86078°E; FMNH 188323); 0.75 km N, 0.6 km E south peak Mt. Data, elev. 2241 m (16.86287°N, 120.86108°E; FMNH 188321); Barlig Municipality, 0.5 km N, 0.5 km W Mt. Amuyao peak, elev. 2530 m (17.01717°N, 121.12188°E; FMNH 214322–214323); 0.4 km N, 0.4 km W Mt. Amuyao peak, elev. 2480 m (17.01727°N, 121.12393°E; FMNH 193689); 1 km N, 1 km W Mt. Amuyao peak, elev. 2100–2150 m, (17.02213°N, 121.11791°E; FMNH 193693–193698, 214322); 1.25 km N, 0.5 km W Mt. Amuyao peak, elev. 1990 m (17.026019°N, 121.122761°E; FMNH 193690); 1.75 km N, 0.4 km W Mt. Amuyao peak, elev. 1885 m (17.02929°N, 121.12466°E; FMNH 193691–193692); 2.15 km N, 1.25 km W Mt. Amuyao peak, elev. 1650 m (17.03270°N, 121.11604°E; FMNH 214324); trail to Mt. Amuyao (FMNH 193699).

*Batomys uragon* ($n = 15$).—See "new species" description above.