

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

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*Abstract.*—The Philippine endemic genus *Bullimus* is currently considered to include three species, one each from the Late Pleistocene islands of Greater Mindanao, Greater Luzon, and Camiguin. We describe a fourth species, *Bullimus carletoni*, new species, from the Caramoan Peninsula in southern Luzon based on analyses of molecular and craniodental data. Molecular data suggest that *Bullimus* colonized Luzon from the southern Philippines and began diversifying on Luzon by ca. 232 kya. This species is associated with partially disturbed forest habitat over limestone and ophiolitic soils, where it is active primarily on the ground at night. Recognition of this species raises the number of endemic mammals on the Bicol Peninsula of southern Luzon to six, emphasizing its importance as a center of endemism.

**Keywords:** biodiversity, biogeography, endemism, mammals, oceanic island, speciation

With 78 species of native murid rodents currently named and recognized, nearly all (75, 96%) endemic to the archipelago, including three recently extinct species based on fossils and subfossils, the Philippines has one of the greatest concentrations of murid rodents of any country (Heaney et al. 1998, 2010, 2016a, b; Rickart et al. 2019, Ochoa et al. 2021). Most of these are members of two endemic Philippine radiations, the tribes Phloeomyini (21 species; Ochoa et al. 2021), and Chrotomyini (35 species; Heaney et al. 2010, 2016a; Rowsey et al. 2018, Rickart et al. 2019). The common ancestors of the Phloeomyini and

Chrotomyini are estimated to have arrived in the Philippines ca. 12 and 8 million yr ago (mya), respectively, and as is apparent from their species richness, and supported by recent molecular studies, they have undergone substantial speciation within the oceanic portions of the archipelago (Steppan et al. 2003, Jansa et al. 2006, Justiniano et al. 2015, Heaney et al. 2016a).

The other native murids (22 species) are members of the Rattini, a tribe that occurs widely from Africa through Asia and into Australia and New Guinea (Musser & Carleton 2005, Schenk et al. 2013, Rowe et al. 2016, Rowsey et al. 2018). In contrast to the much older arrival dates of the Phloeomyini and Chrotomyini, the Rattini are estimated to have arrived in the

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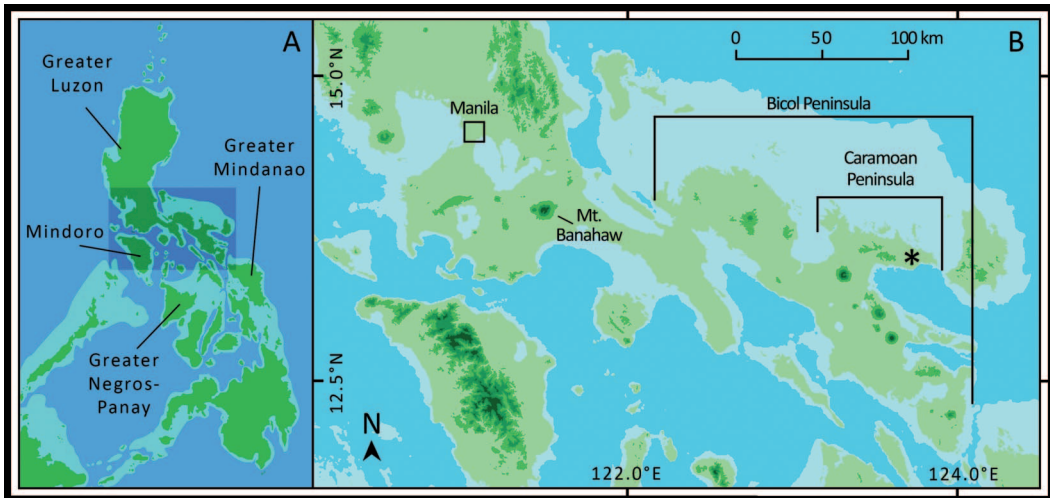


Fig. 1. Maps of (A) the Philippines showing the extent of modern (dark green) and Late Pleistocene (pale blue) islands and areas deeper than 120 m below present sea level (dark blue; from Heaney 1986) and (B) southern Luzon (area shown in box in A), showing mountains and locations referred to in the text. The asterisk indicates the location of samples of *Bullimus carletoni*.

Philippines from about 1 to 4 mya (Rowe et al. 2016, Rowsey et al. 2018). Within the oceanic Philippines (i.e., areas excluding the Palawan region that is biotically part of the continental Sunda Shelf), about nine independent colonizations have taken place, all but two of which produced Philippine endemic genera. The endemic *Tarsomys* clade is currently considered to contain three genera and five species (Musser & Heaney 1992, Rickart et al. 2003). Two genera each have three currently recognized Philippine species: the endemic *Bullimus*, and one genus shared by the Philippines and Sulawesi, *Crunomys* (Rickart et al. 2002, Achmadi et al. 2013). The other Philippine Rattini are monotypic (*Abditomys*, *Anonymomys*, and *Tryphomys*) or are the members of the genus *Rattus*, with three species that probably each colonized the Philippines recently and independently (Musser & Heaney 1985, 1992; Rowe et al. 2016, 2019). Thus, with the exception of the *Tarsomys* clade, recent evidence has indicated little to no speciation by the lineages of Rattini within the Philippines.

As currently defined, the three species of *Bullimus* are present on the Late Pleisto-

cene islands of Greater Mindanao (*B. bagobus*), Camiguin (*B. gamay*), and Greater Luzon (*B. luzonicus*; Musser 1982, Heaney 1986, Rickart et al. 2002, Musser & Carleton 2005, Heaney et al. 2006, 2010; Fig. 1). Initial molecular phylogenetic studies suggested a sister relationship between *Bullimus* and *Sundamys*, a widespread genus from the Sunda Shelf, and estimated a date of colonization into the Philippines of ca. 2–4 mya (Jansa et al. 2006, Schenk et al. 2013). However, subsequent studies with broader phylogenetic representation placed *Bullimus* within a Wallacean clade, including *Bunomys* and *Paruromys*, with *Sundamys* as a close relative of this group (Rowe et al. 2016, 2019). Recent analysis of phylogeographic patterns in *Bullimus* found evidence that *Bullimus* colonized the Philippines initially from the south (from either Borneo or Sulawesi), ca. 1.6–2.6 mya (Kyriazis et al. 2017). Subsequent diversification took place within the Philippines during the last ca. 540 thousand yr, with the oldest diversification events in the southern part of the archipelago, and additional divergence subsequently taking place as *Bulli-*

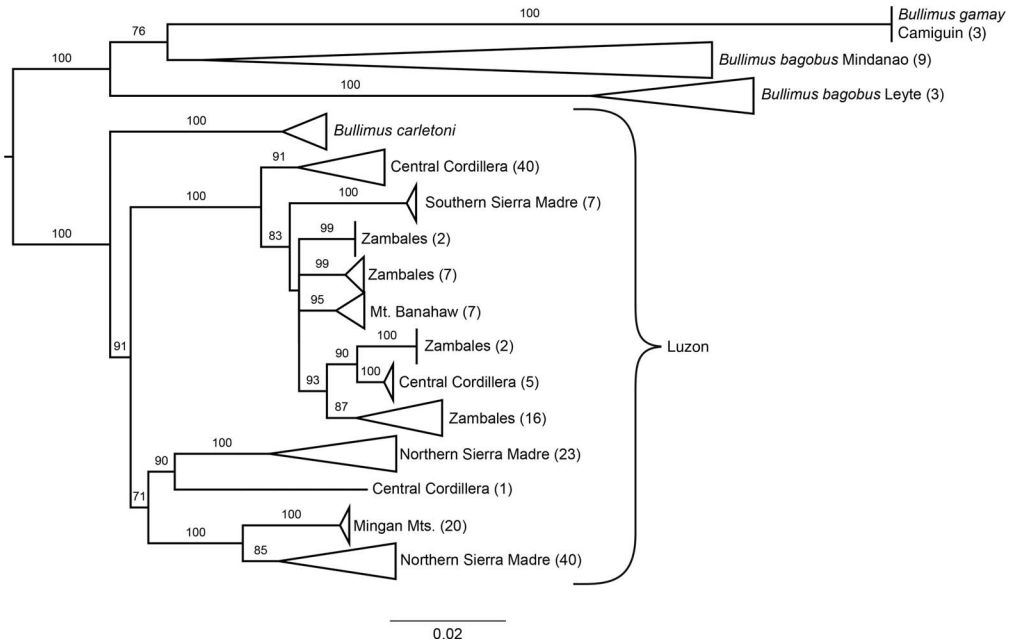


Fig. 2. Phylogenetic relationships of populations of *Bullimus* based on cytochrome *b* (see Methods).

*mus* colonized islands to the north (Kyr-iazis et al. 2017). An analysis using recently obtained specimens from extensive geographic sampling on Luzon found evidence that *Bullimus* began diversifying on Luzon ca. 232 thousand yr ago (kya) (95% = 124–357 kya), with initial colonization of Luzon from Mindanao and associated islands to the south of Luzon. Within Luzon, substantial geographic genetic structure in a mitochondrial gene (cytochrome *b*) indicated incipient speciation in which either on-going gene flow or incomplete lineage sorting was present, with the exception of a population from the Caramoan Peninsula, a small part of the larger Bicol Peninsula of southern Luzon (Fig. 1), which was sister to the other Luzon populations, with a *p*-distance (proportion of sites at which the two populations differ on average) of 3.9% (Fig. 2). Morphometric analysis of craniodental measurements also supported the distinctiveness of the Caramoan Peninsula population, providing strong support for recognition of that population as a previously unrecognized

species. The purpose of this paper is to diagnose that population as a distinct species, using genetic and morphometric analyses and qualitative morphological features.

### 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 millimeters (mm) of length of tail vertebrae (TL), length of hind foot (HFL), length of ear from notch (LE), and weight in grams (WT) were taken from fresh specimens in the field by the authors and close collaborators; these measurements are available in the field catalogs of the collectors deposited at the Field Museum of Natural History (FMNH) or United States National Museum of Natural History (USNM). The length of head and body (HBL) was determined by subtracting tail length from

Table 1.—External measurements of *Bullimus*, given as mean ± standard deviation and range, with sample size. For abbreviations see Methods.

	<i>Bullimus bogobus</i>	<i>Bullimus geoncy</i>	<i>Bullimus luzonicus</i> Female	<i>Bullimus luzonicus</i> Male	<i>Bullimus luzonicus</i> Bantahaw	<i>Bullimus carletoni</i> Caramoan*	<i>Bullimus carletoni</i> Holotype
HBL	273.1 ± 19.5 251–306 (8)	234.5 ± 8.8 223–244 (8)	251.6 ± 13.2 236–283 (14)	251.5 ± 11.2 237–280 (17)	239.0 ± 5.6 233–244 (3)	246.8 ± 12.1 232–262 (9)	260
TL	209.4 ± 16.8 185–229 (8)	177.6 ± 17.7 142–199 (9)	229.6 ± 14.4 207–254 (13)	219.3 ± 14.0 192–256 (17)	202.7 ± 11.0 194–215 (3)	200.2 ± 9.7 187–218 (9)	218
HFL	56.5 ± 2.1 54–60 (8)	51.6 ± 2.4 47–54 (9)	55.8 ± 2.0 52–59 (13)	55.9 ± 2.0 52–59 (17)	52.3 ± 3.8 48–55 (3)	50.9 ± 1.6 49–54 (9)	52
LE	29.3 ± 2.9 25–34 (8)	26.0 ± 1.6 23–26 (9)	30.6 ± 1.9 27–34 (14)	31.3 ± 1.9 30–36 (15)	29.3 ± 0.6 29–30 (3)	30.0 ± 1.4 29–32 (9)	32
WT	556.2 ± 101.1 450–650 (4)	367.8 ± 73.6 290–500 (9)	454.2 ± 68.2 340–600 (14)	453.5 ± 44.0 380–520 (18)	328.3 ± 41.6 295–375 (3)	399.0 ± 35.8 350–445 (9)	415
TL/HBL (%)	77	76	91	87	85	81	84
HFL/HBL (%)	21	22	22	22	22	21	20
LE/HBL (%)	11	12	12	12	12	12	12

\* Includes measurements from the holotype.

total length. Tail and ear measurements of some specimens are not included in analyses due to damage.

Except for specimens from Mindanao taken in 1946–1947 as reported by Sanborn (1952), and four obtained by L. Wilkins in 1983 and deposited in the Florida Museum of Natural History (FLMNH), all specimens examined in this study (see Appendix) were collected by the authors and their associates (Rickart et al. 1991, 2011a, b; Heaney et al. 2011, 2013). The specimens reported by Sanborn (1952) and FLMNH specimens were prepared as skin plus skull. Specimens obtained by the authors and their collaborators were prepared as either fluid-preserved specimens or complete skeletons, after tissue samples were taken from the thigh muscle of fresh specimens. Tissues were preserved in either 95% 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 by dermestid beetles, as were the skeletons, and given final cleaning after briefly being soaked in a weak ammonia solution. Age determination of freshly caught specimens was based on relative body size and reproductive condition, and subsequently validated 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 *Bullimus* collected by the authors and their collaborators since 2000 currently are deposited at FMNH, but one-half will be transferred to the National Museum of the Philippines (PNM) by prior agreement. The capture and handling of animals in the field followed all relevant laws and regulations of the Philippines.

Eighteen cranial and dental measurements (Table 2) were taken by Heaney using digital calipers graduated to 0.01

Table 2.—Craniodental measurements of *Bullimus*, given as mean ± standard deviation and range (and sample size). For abbreviations, see Methods.

	<i>Bullimus bogobus</i>	<i>Bullimus ganoyi</i>	<i>Bullimus luzonicus</i> Female	<i>Bullimus luzonicus</i> Male	<i>Bullimus luzonicus</i> Banahaw	<i>Bullimus carletoni</i> Caramoan*	<i>Bullimus carletoni</i> Holotype
BOL	60.04 ± 2.15 56.68–64.16 (11)		53.79 ± 1.33 51.52–55.65 (12)	53.86 ± 1.18 51.74–55.46 (15)	50.02 ± 0.46 49.75–50.55 (3)	53.66 ± 1.27 52.87–55.13 (3)	55.13
IB	8.25 ± 0.60 7.23–9.20 (11)	7.76 ± 0.47 7.42–8.02 (2)	7.98 ± 0.33 7.28–8.47 (16)	8.13 ± 0.47 7.53–9.08 (17)	7.67 ± 0.43 25.59–26.66 (3)	7.71 ± 0.12	7.08
ZB	30.93 ± 1.54 28.46–34.00 (10)	26.35 (1)	27.84 ± 0.88 26.95–29.72 (11)	27.96 ± 0.72 26.99–29.25 (15)	26.06 ± 0.55 19.81 ± 0.01	27.15 ± 0.41 20.63 ± 0.22	26.68
MB	22.38 ± 0.92 21.18–23.73 (10)	19.52 ± 1.39 18.54–20.5 (2)	20.58 ± 0.64 19.60–21.54 (13)	20.94 ± 0.60 19.63–21.87 (12)	19.80–19.81 (2)	20.48–20.88 (3)	20.53
NL	27.17 ± 1.52 24.85–28.42 (11)	21.57 (1)	23.58 ± 1.04 21.94–25.00 (17)	23.58 ± 0.98 22.03–26.21 (18)	21.62 ± 0.55 9.34 ± 0.22	22.96 ± 0.74 22.33–23.93 (4)	22.44
LIF	10.57 ± 0.64 9.39–11.25 (11)	7.92 (1)	9.47 ± 0.70 8.31–10.63 (17)	9.57 ± 0.62 8.20–10.48 (18)	9.16–9.59 (3)	10.38 ± 0.69 9.48–11.13 (4)	10.34
RD	14.01 ± 0.56 13.12–15.24 (11)	11.67 (1)	12.18 ± 0.49 11.57–13.45 (17)	11.99 ± 0.46 11.21–13.02 (18)	11.36 ± 0.22 11.11–11.51 (3)	12.10 ± 0.36 11.67–12.44 (4)	11.67
OL	21.03 ± 0.78 19.50–22.55 (11)	18.63 ± 0.48 18.29–18.97 (2)	19.44 ± 0.73 18.32–20.71 (14)	19.42 ± 0.67 18.53–20.96 (18)	18.28 ± 0.37 17.90–18.63 (3)	19.21 ± 0.35 18.78–19.52 (4)	19.46
M1–M3	10.10 ± 0.60 9.37–11.08 (11)	8.86 ± 0.39 8.53–9.13 (2)	9.62 ± 0.40 8.94–10.46 (16)	9.68 ± 0.41 9.10–10.71 (18)	9.18 ± 0.21 8.94–9.34 (3)	9.20 ± 0.32 8.93–9.66 (4)	9.17
PBM1	10.07 ± 0.45 9.49–10.91 (11)	9.11 ± 0.53 8.77–9.48 (2)	9.80 ± 0.41 9.06–10.43 (16)	9.66 ± 0.41 9.02–10.66 (17)	9.58 ± 0.23 9.37–9.83 (3)	9.48 ± 0.50 8.83–10.04 (4)	8.83
DL	17.85 ± 0.86 15.44–19.88 (11)	15.12 (1)	15.80 ± 0.90 14.92–18.70 (17)	15.72 ± 0.48 14.34–16.79 (18)	14.89 ± 0.48 14.37–15.32 (3)	16.16 ± 0.60 15.32–16.59 (4)	16.13
PPL	22.79 ± 1.25 20.81–24.91 (11)	20.66 (1)	20.45 ± 0.61 19.42–21.53 (12)	20.19 ± 0.56 19.25–21.16 (15)	18.57 ± 0.47 18.11–19.05 (3)	20.36 ± 1.93 18.48–22.33 (3)	22.33
LBM3	6.23 ± 0.37 5.61–6.83 (11)	6.11 ± 0.31 5.89–6.33 (2)	5.84 ± 0.52 5.01–6.79 (16)	5.98 ± 0.44 5.08–6.57 (18)	5.18 ± 0.50 4.62–5.58 (3)	5.96 ± 0.68 5.48–6.94 (4)	5.52
BH	17.62 ± 1.14 16.15–20.04 (10)	15.97 (1)	15.56 ± 0.57 14.64–16.30 (12)	15.66 ± 0.52 14.51–16.36 (14)	16.05 ± 0.54 15.67–16.43 (2)	15.09 ± 0.91 14.04–15.65 (3)	15.58
BM1	3.09 ± 0.15 2.86–3.37 (11)	2.75 ± 0.18 2.62–2.88 (2)	3.01 ± 0.16 2.69–3.28 (17)	3.00 ± 0.17 2.77–3.43 (18)	2.99 ± 0.01 2.99–3.00 (3)	2.76 ± 0.22 2.56–3.07 (4)	2.65
BIT	3.98 ± 0.31 3.52–4.64 (11)	3.45 (1)	3.51 ± 0.21 3.20–3.78 (17)	3.47 ± 0.20 3.08–3.73 (15)	2.94 ± 0.16 2.83–3.05 (2)	3.33 ± 0.17 3.22–3.52 (3)	3.25
ZP	7.48 ± 0.36 7.05–8.15 (11)	6.50 ± 0.17 6.38–6.62 (2)	6.96 ± 0.48 6.16–7.73 (17)	6.81 ± 0.51 6.20–7.97 (18)	6.47 ± 0.31 6.11–6.65 (3)	6.13 ± 0.66 5.31–6.92 (4)	6.09
BL			8.59 ± 0.45 8.90–9.58 (15)	8.63 ± 0.45 7.79–9.44 (17)	8.69 ± 0.57 8.30–9.35 (3)	9.32 ± 0.35 9.09–9.59 (2)	9.59

\* Includes measurements of the holotype.

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 (NL), length of incisive foramina (LIF), depth of rostrum (RD), orbito-temporal length (OL), alveolar length of maxillary molar toothrow (M1–M3), labial palatal breadth at M1 (PBM1), length of diastema (DL), post-palatal length (PPL), lingual palatal breadth at M3 (LBM3), braincase height (BH), breadth of M1 (BM1), breadth of incisors at tip (BIT), width of zygomatic plate (ZP), and length of bulla (BL), as defined by Musser & Heaney (1992) and Heaney et al. (2011).

Descriptive statistics (mean, standard deviation, and range) of external, cranial, and dental measurements were calculated separately for adult males and females. We assessed multivariate variation in cranio-dental morphology through principal component analysis (PCA) with SYSTAT 10 for Windows (SPSS Inc. 2000), using the correlation matrix of  $\log_{10}$ -transformed measurements of adult specimens of both sexes. For the PCA, because some specimens had damaged skulls, we reduced the number of measurements from 18 to 13 to minimize the number of specimens eliminated. Scanning electron micrographs of teeth were made from uncoated specimens with an AMRAY 1810 scanning electron microscope.

Genetic data were presented in Kyriazis et al. (2017), and detailed sequencing and analysis methods are provided therein. Briefly, our genetic dataset consisted of 192 *Bullimus* specimens, all of which were sequenced for cytochrome *b* (=cyt *b*, below), and fractions of which were sequenced for the nuclear loci OPN (55 specimens), BFIBR (74), and DHFR (57). This dataset included seven *Bullimus* specimens from the Caramoan Peninsula,

which were each sequenced for all four loci. Samples were sequenced using an ABI 3730 DNA analyzer (Life Technologies, Carlsbad, California, U.S.A.) in the Pritzker DNA Lab for Molecular Systematics and Evolution at the Field Museum.

Using these data, we first generated a maximum likelihood cytochrome *b* gene tree using RAXML-HPC 8.2.3 (Stamatakis 2014), which was run on the CIPRES Science Gateway (Miller et al. 2010). We used a GTR+CAT model of nucleotide substitution and assessed clade support using 1000 bootstrap pseudoreplicates. Next, we used our complete genetic dataset to generate a species tree for six *Bullimus* populations/species using \*BEAST (Heled & Drummond 2010). We dated this phylogeny using two sources of prior information. First, we constrained the cyt *b* clock rate using a normally distributed prior on third codon positions with mean 0.1 subs/site/myr and standard deviation of 0.04, reflecting a range of values estimated for rodent cyt *b* (Nabholz et al. 2008). Next, we applied a secondary calibration from a molecular phylogenetic analysis of murid rodent diversification (Schenk et al. 2013) to the split between *Bullimus* and *Sundamys* of 2.20 mya, using a lognormal distribution with a 95% range of (1.67, 4.76 mya).

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## Results

*Distribution.*—Extensive surveys of small mammals across Luzon have shown *Bullimus* to be present from near sea level to 2740 m on this topographically rugged island but to be most common along the middle of the elevational gradient from roughly 1000–1500 m. They are highly tolerant of forest disturbance and are typically more abundant in regenerating

shrub-land and second-growth forest than in mature forest. Limited data suggest that they feed principally on green leafy material, including grasses, but may be somewhat omnivorous (Rickart et al. 2011a, b, 2016, 2021; Heaney et al. 2016a, Balete et al. 2020).

Current records of *Bullimus* show them to be present over most of Luzon (Heaney et al. 2016a). Conspicuous exceptions include the Cagayan River Valley of northern Luzon and the Central Plains to the north of Manila Bay (Kyriazis et al. 2017). These areas have largely been cleared of natural vegetation and have not been the subjects of mammal surveys. The third exception is the Bicol Peninsula of southern Luzon, where mammal surveys on all of the forested mountain peaks have failed to detect *Bullimus*; the only specimens come from below about 300 m on the Caramoan Peninsula, a small projection that forms part of the much larger Bicol Peninsula (Fig. 1; Balete et al. 2013).

*Molecular analyses.*—Analyses of DNA sequences from one mitochondrial and three nuclear genes from 192 specimens of *Bullimus* were presented in detail by Kyriazis et al. (2017), and are summarized here (Fig. 2). Two primary clades are present within *Bullimus*. One of these clades is made up of individuals from Mindanao (which includes the type locality of *B. bagobus*), Leyte, and Camiguin Island (the only known location for *B. gamay*; Rickart et al. 2002). Specimens from Leyte are genetically distinct from those on Mindanao, which indicates the potential presence of a distinct, currently unrecognized species. We note that Johnson (1946) named *B. bagobus barkeri* from southern Samar Island, which is immediately adjacent to Leyte. More extensive study of *Bullimus* from Leyte and Samar, and the adjacent islands of Biliran and Bohol, is needed to determine if a single distinct species is present, and if the species epithet *barkeri* is applicable.

The second major clade within *Bullimus* includes individuals from Luzon Island. Figure 2 includes samples from all areas where they are known to be present. Genetically distinct populations are present on each of the mountain ranges in central and northern Luzon and in the Caramoan Peninsula (Kyriazis et al. 2017 and Fig. 2). The most distinct of these populations is from the Caramoan Peninsula; it is moderately supported as sister to the other clades. Populations from central and northern Luzon also exhibit notable geographic structure, with samples falling into two major clades, one largely consisting of samples from the Northern Sierra Madre and Mangan Mountains, and a second consisting of samples from the Central Cordillera, Zambales Mountains, and Mt. Banahaw (Fig. 2). Within these clades, further geographic structure is present, but the pattern is complex, with individuals from the Central Cordillera appearing in three different parts of the phylogeny, and genetic distances are often short. We note that specimens from Mt. Banahaw, which is geographically closest to the Caramoan Peninsula, are nested deeply within other populations from central and northern Luzon. Species-tree analysis of six distinctive *Bullimus* lineages suggests that diversification within *Bullimus* occurred during the late Pleistocene, and that the divergence between *Bullimus* from the Caramoan Peninsula and *Bullimus luzonicus* from central and northern Luzon occurred at about 232 kya (95% Highest Posterior Density = 124–357 kya; Fig. 3). Overall, these results indicate that within Luzon, only the population from the Caramoan Peninsula is consistently distinct based on the current molecular data (Kyriazis et al. 2017).

*Morphometric analyses.*—We based our analyses of craniodental variation on 11 specimens of *Bullimus bagobus*, 2 specimens of *Bullimus gamay*, 35 *B. luzonicus*, and 4 of the genetically distinctive population from the Caramoan Peninsula of

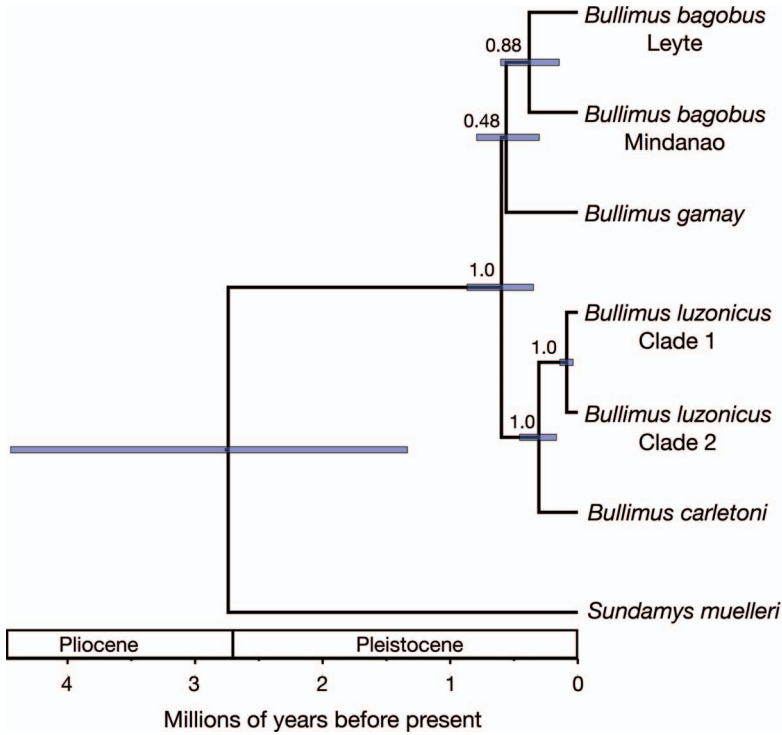


Fig. 3. Time-calibrated species-tree for *Bullimus* based on one mitochondrial and three nuclear loci. Numbers on each node depict posterior probability. Node bars depict 95% HPD for divergence dates labelled on x-axis.

southern Luzon. Because Mt. Banahaw is the locality nearest to the Caramoan Peninsula, we analyzed those specimens as a separate unit so that we can determine if they show greater similarity to the Caramoan specimens or to those from central and northern Luzon. Male and female *B. luzonicus* have similar means and ranges for external and craniodental features (Tables 1, 2), so we pooled the sexes for all analyses.

Inspection of both external (Table 1) and craniodental (Table 2) measurements show *B. bagobus* to be larger than other *Bullimus* in all respects, as noted in previous studies, and *B. gamay* is the smallest (Sanborn 1952, Rickart et al. 2002), based on head and body length. In addition to absolute differences in external measurements, the length of the tail relative to length of head and body varies

substantially between named taxa: tails are proportionately shortest on *Bullimus bagobus* from Mindanao and *Bullimus gamay* from Camiguin Island (77% and 76%, respectively), and relative tail length of *Bullimus bagobus* from Leyte and a nearby small island (Maripipi) averaging 77% and 74% (Rickart et al. 2002). In contrast, *Bullimus luzonicus* females and males have tails that average 91% and 87%, respectively, and tails of specimens from the Caramoan Peninsula average 81%. Relative tail length of a small sample from Mt. Banahaw averages 85%. Thus, *Bullimus* from Mindanao and nearby islands consistently have short tails relative to length of head and body, while those from Luzon have relatively longer tails.

Additionally, we note that *Bullimus gamay* have ears that are smaller than those of other species, but they are largely



Table 3.—Results of principal components analysis (PCA) for specimens of *Bullimus*, based on measurements summarized in Table 2.

Axis	1	2	3
Variable	Principal Component Loadings		
Zygomatic Breadth	0.949	0.036	-0.097
Rostral Length	0.942	0.129	0.139
Rostral Depth	0.936	0.195	-0.021
Nasal Length	0.919	0.221	0.147
Diastema Length	0.843	0.314	0.052
Orbito-temporal Length	0.834	0.235	0.130
Maxillary Tooththrow Length	0.726	-0.457	0.258
Zygomatic Plate Width	0.677	-0.028	-0.309
Incisive Foramen Length	0.652	0.273	0.300
Palatal Breadth at M1	0.624	-0.434	-0.451
Breadth of M1	0.565	-0.698	0.132
Lingual Palatal Breadth at M3	0.547	0.088	-0.675
Interorbital Breadth	0.437	-0.484	0.221
Eigenvalue	7.524	1.460	1.048
Variance Explained	57.9%	11.2%	8.1%

proportional to body size; the ears of *B. bagobus* are proportionately slightly smaller than those of other species. The hind feet of the specimens from Caramoan are absolutely the smallest ( $\bar{X} = 51$  mm), but proportionately equal to those of *B. bagobus* (Table 1).

Our Principal Components Analysis (PCA) yielded three axes of variation that had eigenvalues above 1.0 and, therefore, are interpretable (Table 3), but variation along the third axis showed no discernable geographic or taxonomic pattern, so we say nothing more about it. The first two axes accounted for 57.9% and 11.2% of the total variation, respectively. All variables loaded moderately to heavily on the first axis, with breadth of M1, lingual palatal breadth at M3, and interorbital breadth loading least heavily (less than 0.6; Table 3); we regard this axis as principally showing overall size. The second axis had heaviest loadings, all negatively weighted, from breadth of M1, interorbital breadth, maxillary tooththrow length, and palatal breadth at M1 (loadings from -0.698 to -0.434). This axis reflects a tendency of some individuals to have relatively short

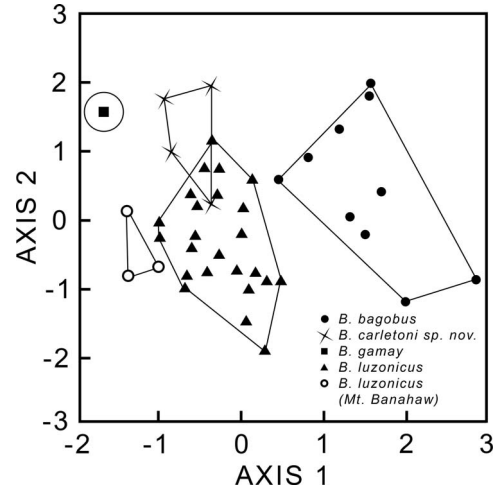


Fig. 4. Plot of factor scores on the first two axes from a Principal Components Analysis (PCA) of 13 selected craniodental measurements (see Methods and Table 3).

tooththrows, narrow upper molars, and a narrow palate, coupled with a narrow interorbital region, compared with individuals that show the converse.

A plot of the scores of each individual specimen on these two axes (Fig. 4) clearly reflects the large size of *B. bagobus*, with high scores on axis 1, and *B. gamay* and the specimens from Mt. Banahaw as the smallest. *Bullimus luzonicus* and the population from Caramoan are intermediate. The second axis shows *B. gamay* and the individuals from Caramoan as scoring highest on average, though with some overlap with some *B. bagobus* and some *B. luzonicus*. Individuals from Mt. Banahaw do not differ in their scores from those of *B. luzonicus* or *B. bagobus*. When the two axes are taken together, it is apparent that *B. luzonicus* and *B. bagobus* differ most clearly in size, and the specimens from Mt. Banahaw differ from *B. luzonicus* only in size, while *B. gamay* and specimens from Caramoan differ from the other populations in having proportionately short tooththrows, and narrow molars, palates, and interorbital regions. One individual from Caramoan overlaps with



Fig. 5. Drawing of lateral view of *Bullimus carletoni* based on FMNH 203244–203246.

*B. luzonicus* when both axes are considered; otherwise, each taxon forms a discrete cloud of points.

On the basis of these genetic and morphological analyses, we conclude that the population of *Bullimus* from the Caramoan Peninsula should be recognized as a distinct species, which we describe here.

***Bullimus carletoni*, new species**

LSID: urn:lsid:zoobank.org:act:C19C1251-0557-473B-A59D-E10F8F4BAA32

Figs. 5–7, Tables 1, 2

*Bullimus luzonicus*: Rickart et al., 1991:466.—Heaney et al., 1999:40 (part).—Rickart et al., 2002:422, Table 1, Figs. 2, 4, Appendix II (part).—Balet et al., 2013, Tables 7–13, Fig 14.—Heaney et al., 2016a:168–170 (part), Fig. 3.6.

*Holotype*.—FMNH 203246. Young adult male collected on 29 May 2008 by Danilo S. Balet (field number DSB 5647).

Currently deposited at FMNH, but will be transferred to the National Museum of the Philippines.

*Type locality*.—Caramoan National Park: 2.5 km N, 2 km E Caramoan poblacion, Camarines Sur Province, Luzon Island, Philippines; taken in heavily disturbed forest over limestone at 50 m elevation; 13.79417°N, 123.87896°E (Fig. 1; Site 16 in Balet et al. 2013).

*Paratypes*.—11 specimens: FMNH 203240, 203241, 203242, 203243 (0.5 km S, 5 km E Port of Guijalo, 50 m elev.); FMNH 203244, 203245 (0.25 km S, 5.25 km E Port of Guijalo, 300 m elev.); FLMNH 30109 (Kasine Mt.); FLMNH 30110, 30111, 30112 (Cabangon Mt., near town of Tina-go), Caramoan Municipality, Camarines Sur Prov.

*Distribution*.—Documented only from the eastern portion of the Caramoan Peninsula (Fig. 1), with a possible report from the base of Saddle Peak (Balet et al. 2013).

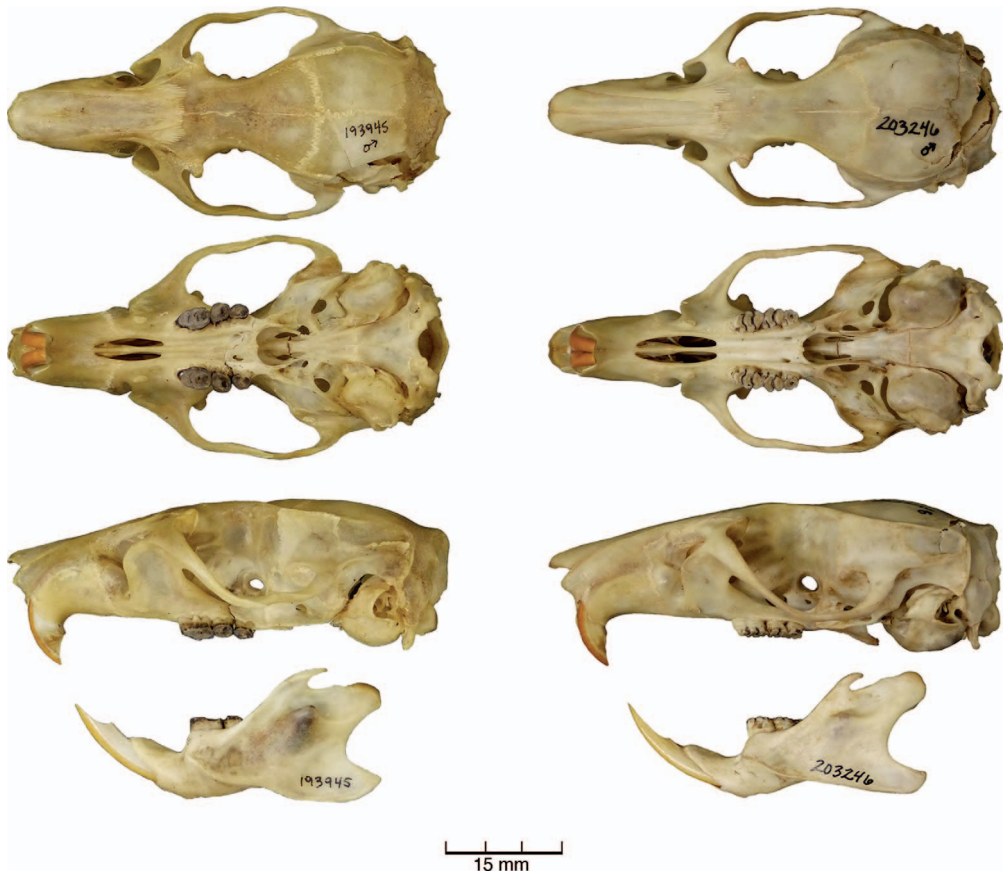


Fig. 6. Photographs of skulls and mandibles of *Bullimus luzonicus* (FMNH 193945, on left) and *B. carletoni* (FMNH 203246, holotype, on right).

*Etymology.*—We take special pleasure in naming this species in honor of our colleague, Michael Dean Carleton, in recognition of his great contributions to scientific knowledge through extensive museum collection-based biodiversity research and decades of patient and exemplary efforts as an Associate Editor of the Proceedings of the Biological Society of Washington.

*Diagnosis.*—A member of the genus *Bullimus* as diagnosed by Musser & Heaney (1992) and Rickart et al. (2002). *Bullimus carletoni* may be recognized by the following combination of characters. Dorsal pelage (Fig. 5) yellow-sandy brown, ventral pelage yellow-white, with an abrupt transition between the two.

Dorsal surface of the fore and hind feet covered by short, yellowish-white hairs. Ventral surface of the fore and hind feet pale brown, skin lightly pigmented, with plantar pads that are often nearly unpigmented but sometimes medium brown. Ears medium brown, fading to nearly white near their base. Mean total length 446 mm, tail 200 mm, head and body 247 mm, hind foot 51 mm, ear 30 mm (Table 1). The cranium (Fig. 6) is nearly flat in lateral profile. The interorbital region and zygomatic plate are relatively narrow, and the incisive foramina and post-palatal region are unusually long. Cranium only slightly arched above zygomatic plate in lateral view. Basioccipital length (means; see Table 2) 53.7 mm, interorbital breadth

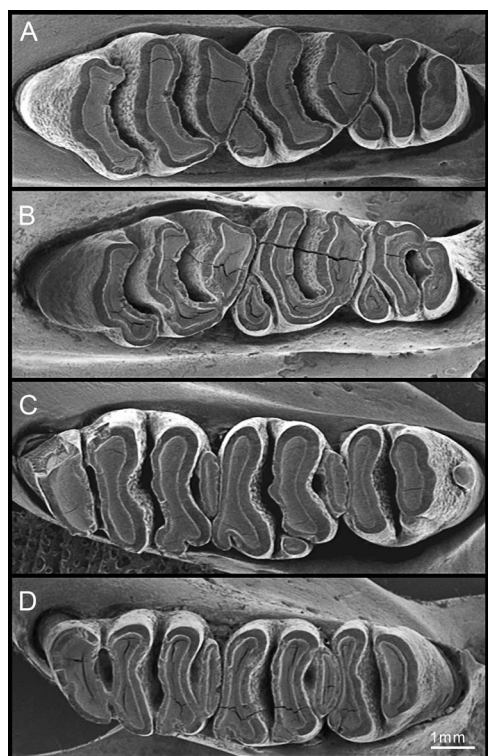


Fig. 7. SEM micrographs of the molar teeth of *Bullimus luzonicus* (FMNH 188451, A and C) and *B. carletoni* (FMNH 203241, B and D). A and B are upper molars, C and D are lower molars.

7.7 mm, maxillary toothrow 9.2 mm, length of incisive foramina 10.4 mm, post-palatal length 20.4 mm.

**Description and comparisons.**—*Bullimus carletoni* is similar in overall size (Tables 1, 2) and general appearance to *B. luzonicus* but differs in many details. The dorsal pelage of *B. carletoni* (Fig. 5) is of moderate length, up to 15 mm at midline, with scattered and inconspicuous black guard hairs up to 25 mm long. The fur is paler than that of conspecifics, medium brown with a yellowish sandy-brown aspect; scattered paler hairs give it a “salt-and-pepper” appearance. Within the dorsal fur are numerous stiff hairs that give the fur a rough, slightly bristly texture. The ventral fur is yellowish-white, ca. 7–8 mm in length along the midline. The transition from the darker dorsal fur

to the paler ventral fur is abrupt. As in all adult *Bullimus*, there is a mid-ventral glandular area that is hairless, ca. 65 mm long, extending from the posterior edge of the sternum to the base of the penile or urinary sheath. In *B. carletoni*, the glandular area is usually about 6 mm wide. The scrotum of adult males is large, with short pale hairs on anterior third and nearly hairless over the posterior two-thirds. Females have two pairs of inguinal and two pairs of abdominal mammae, and some have an additional pair of axial mammae. The darker dorsal fur color extends only a few mm past the wrist onto the top of the forefeet, which then are covered by short hairs of the same pale yellowish-white as the ventral abdomen. The underlying dorsal skin on the forefeet is unpigmented, and scales are not conspicuous. The ventral surface of the forefoot is unpigmented, except that the plantar pads are partially pigmented in some individuals. The plantar pads are proportionately smaller than those of conspecifics, with skin evident between the pads on fluid-preserved specimens. The claws of the forefeet are unpigmented and unremarkable, and the thumb has a nail. The hind foot has short white or yellowish hairs on the dorsal surface; the underlying skin is not pigmented, and the scales are unpigmented and inconspicuous. The ventral skin of the hind feet is lightly pigmented, with pads that are medium brown. The ears of *B. carletoni* are medium brown, except for gradually fading paler to nearly unpigmented at the base; both anterior and posterior surfaces of the ears are virtually hairless. As in all *Bullimus*, the skin around the eye has a thin (less than 1 mm) black rim; beyond this rim, the skin is pale. Mystacial vibrissae are 55–70 mm in length. The tail is darkly pigmented dorsally and is pale ventrally, with an unpigmented tip up to ca. 80 mm long (ca. 40% of the tail length).

Compared to *Bullimus carletoni*, *B. luzonicus* from the Central Cordillera



(including the type locality, Mt. Data), from the northern Sierra Madre (Mts. Cetaceo and Anacua), and from the central Sierra Madre (Mt. Mingan) differ externally in having fur that is softer, often appearing slightly woolly, with more numerous, longer (up to 40 mm), conspicuous black guard hairs. Stiff hairs within the pelage are thinner and less stiff, making them inconspicuous. The dorsal color of *B. luzonicus* is a rich dark brown; that of specimens from Mts. Banahaw and Mingan is especially dark. Most specimens from the northern Sierra Madre have ventral fur that is pale yellowish gray, usually 9–10 mm long along the midline; those from the Central Cordillera have ventral fur that is gray at the base, with pale brown or silver tips; and those from Mt. Mingan have ventral fur that is only slightly paler than that of the dorsum. The midventral glandular area is conspicuous in all populations of *B. luzonicus* but ranges up to 12–13 mm wide in some larger individuals. In all *B. luzonicus*, the darker dorsal pelage color extends down onto the dorsal surface of the forefoot and hindfoot, which have skin and scales that are darkly pigmented. The ventral surface of the fore- and hindfeet has skin and pads that are darkly pigmented, although the pads sometimes have paler areas. All have claws that are lightly pigmented. All have ears that are dark brown, sometimes becoming paler along the distal edges and base; the anterior surface is virtually hairless, but the posterior surface has short but visible dark hairs. All specimens of *B. luzonicus* have a tail that is unpigmented (white) at the distal tip; the white tip averages about 40% of the tail length but varies from as little as 5% to as much as 70%.

Cranial and dental morphology in *B. bagobus* and *B. luzonicus* were described in detail by Musser & Heaney (1992). Compared to *B. luzonicus*, the cranium of *B. carletoni* is flatter (less strongly arched) in lateral profile (Fig. 6). Interorbital breadth

and zygomatic plate width averages less than in all populations of *B. luzonicus* other than that from Mt. Banahaw (Fig. 5, Table 2). The incisive foramina of *B. carletoni* are longer (Table 2) and usually slightly wider (Fig. 6). Post-palatal length of *B. carletoni* is greater (Table 2), and the bullae are longer and slightly more inflated than in *B. luzonicus* (Fig. 6). As in all *Bullimus*, both of these species have bullae that are inflated medially and ventrally and have the auditory meatus directed posteriorly (see Fig. 75 in Musser & Heaney 1992 and Fig. 7A in Rickart et al. 2002).

Incisors (Fig. 6) are similar in *B. carletoni* and *B. luzonicus*, but those of *B. carletoni* are slightly narrower (Table 2). Molars are hypsodont in both, and cuspidation is generally similar in both species; one exception is that *B. luzonicus* rarely has a small posterior cingulum on M3, a feature that is absent on all available specimens of *B. carletoni* (Fig. 7). Molars of *B. carletoni* average slightly shorter and narrower than those of *B. luzonicus*. Upper and lower third molars are smaller relative to second molars in *B. carletoni* than in *B. luzonicus*.

*Bullimus carletoni* is slightly larger than *B. gamay* in most but not all measurements (compare Fig. 6 and Tables 1, 2 with Fig. 6 and Appendix 1 in Rickart et al. 2002). The cranium in lateral profile is similarly flat in both species, but the height of the braincase is greater in *B. gamay*, resulting from its generally more inflated braincase. The interorbital breadth and breadth of braincase are greater in *B. gamay*, as is the length of the bullae. The maxillary tooth-row is slightly shorter but more strongly divergent posteriorly in *B. gamay*. The bony palate of *B. carletoni* extends beyond the posterior edge of M3, rather than ending roughly parallel to the posterior edge.

*Bullimus carletoni* is easily distinguished from *B. bagobus* by its smaller size (Tables 1, 2; see also Figs. 72–74 in Musser & Heaney 1992). In lateral profile, the

cranium of *B. carletoni* is less strongly inflected above the zygomatic plate, the rostrum is less deep, the zygomatic plate is narrower, and the temporal ridges are less prominent. Although the two differ greatly in overall size, the incisive foramina of *B. carletoni* are nearly as long and wide as those of *B. bagobus*. The posterior palatine foramina of *B. carletoni* are located at or slightly posterior to cusp t1 of M3 (Musser & Heaney 1992) rather than lateral to the anterior margin of M3. The maxillary toothrow is shorter and less divergent posteriorly than in *B. bagobus*. The bullae are substantially smaller and less highly inflated than in *B. bagobus*. M3 is notably smaller than M2, rather than nearly equal in size as in *B. bagobus*.

*Ecology*.—All specimens in FMNH reported here were obtained in May 2008; these were captured in disturbed forest, some from karstic limestone and some from ultrabasic soil over ophiolitic rocks, in rugged, hilly terrain. These habitats support plant formations distinct from the more widespread lowland dipterocarp forest (Fernando et al. 2008). Road-building, clearing for small-scale slash-and-burn agriculture (locally referred to as *kaingin*), and cutting of trees for charcoal and timber were conspicuous during 2008, and few commercially valuable trees remained. The tallest trees ranged from 15–30 m, with diameter at breast height (DBH) ranging from 20–90 cm. Common trees included *Ficus* spp., *Dracontomelon dao*, *Pterocarpus indicus*, *Vitex parviflora*, *Syzygium*, and *Sterculia*. Canopy vines were common, including lianas, bamboos (*Dinochloa*), pandans (*Freycinetia*), and *Tetrastigma* sp. Understorey plants included bamboos (*Bambusa* and *Schizostachyum*), fishtail palms (*Caryota*), rattans (*Calamus*), *Leea*, *Spondias*, and *Garcinia*. Ground cover plants were common, including *Alocasia*, *Begonia*, *Zingiber*, and ground orchids. Cultivated plants included coconut (*Cocos nucifera*), bananas (*Musa*), and jackfruit (*Artocarpus*

*heterophyllus*). For further details, see Balete et al. (2013). Specimens in FLMNH were obtained in 1983 in selectively logged lowland forest on uplifted karst (L. Wilkins and K. Auffenberg, pers. comm.); localities are shown and described in Auffenberg (1988).

Our team captured eight specimens of *B. carletoni* in 1800 trap-nights during 2008; all were trapped on the ground, with seven of the eight captured at night and one near dusk. The Philippine native forest rat (*Rattus everetti*) was captured nearly seven times as often as *B. carletoni*; other native species that were less common than *B. carletoni* were *Crocidura grayi* and *Apomys microdon*. Only a single specimen of the exotic pest species *Rattus tanezumi* was captured (Balete et al. 2013).

Two adult females of *B. carletoni* were noted at the time of capture as having two abdominal and two inguinal pairs of mammae, and one had an additional axial pair. Adult males had testes measuring 15 × 9 mm and 18 × 9 mm.

## Discussion

*Biogeography*.—With the recognition of *Bullimus carletoni* as a distinct species, the number of endemic mammal species on the Bicol Peninsula of southern Luzon is raised to six. The other five endemics are high-elevation species (occurring above 1000 m); of these, *Archboldomys luzonensis*, *Batomys uragon*, *Chrotomys gonzalesi*, and *Rhynchomys isarogensis* have been documented only on Mt. Isarog, a volcanic peak that rises to ca. 1966 m near the base of the Caramoan Peninsula (Balete et al. 2012, 2015; Heaney et al. 2016a, b), and *R. labo* is known only from near the top of Mt. Labo (1544 m), also a volcanic peak, near the north end of the Bicol Peninsula (see Fig. 1 in Balete et al. 2013). *B. carletoni* is the only one of these whose ancestor is thought to have arrived in the Bicol Peninsula from Greater Mindanao,

which lies to the south (Fig. 1; Kyriazis et al. 2017); all others are members of clades that have their greatest species richness and most basal members in central and northern Luzon, and appear to have arrived in the Bicol region from the north (Balete et al., 2013, 2015; Heaney et al. 2016a). Clearly, independent colonizations over long periods of time have contributed to the current composition of this fauna, with local endemism developing as a major outcome of these long-term colonizations, contributing greatly to the unusually high level of mammalian endemism on the Bicol Peninsula and Luzon in general (Heaney et al. 2016a, b).

*Conservation.*—Our limited data at this time implies that *Bullimus carletoni* may be restricted to two distinctive forest types—forest over limestone and forest over ultrabasic soils over ophiolite—on the Caramoan Peninsula. The karstic limestone substrate is widespread in Caramoan, covering roughly the northern half of the Caramoan Peninsula (Mines and Geosciences Bureau 2010). The associated caves and craggy limestone formations, with sandy beaches along some shorelines, have made it a popular site for tourists, with attendant degradation of forest, but the terrain's ruggedness has helped to protect some of the forest vegetation (Mallari et al. 2001). Given that all of our specimens came from localities where habitat disturbance was fairly extensive, we conclude that the species is tolerant of a moderate level of disturbance, as is its closest relative, *B. luzonicus* (Rickart et al. 2011a, Heaney et al. 2016a), and the likelihood that it feeds on green vegetation at ground level (see Ecology, above) suggests that, like *B. luzonicus*, it may be more abundant in moderately disturbed areas, where ground-level vegetation is usually dense, than in old-growth forest, where understory vegetation is sparse. Further, we note that part of the species range falls within Caramoan National Park, which affords some level of habitat

protection. We thus do not believe the species requires specific protection, though consistent management and protection of the park and associated watersheds will likely work to the advantage of both the local tourism-based economy and protection of this distinctive endemic species.

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- Bullimus luzonicus* ( $n = 179$ ). Luzon Island:
- Aurora Prov.: Mt. Anacua (209484, 209485, 209487, 209488, 209494, 209496, 209497, 209498, 209502, 209503, 209504, 209507, 209509, 209510, 209511, 209512, 209514, 209515, 209516, 209517, 209589, 209594); Mt. Mingan (FMNH 190983, 190984, 190985, 190986, 190987, 190988, 190989, 190990, 190992, 190993, 190994, 190995, 190996, 190997, 190998, 190999, 191000, 191001, 191002, 191003).
- Bataan Prov.: Mt. Natib (FMNH 183327, 183328, 183329, 183330).
- Benguet Prov.: Mt. Data (FMNH 62298, 62299, 62300, 62301, 62303, 62348, 62349); Mt. Pulag (FMNH 198716, 198717, 198718, 198720, 198721, 198722).
- Cagayan Prov.: Mt. Cagua (FMNH 176588); Mt. Cetaceo (FMNH 180376, 180377, 180378, 180379, 180380, 180383, 185911, 185913, 185914, 185915, 185917, 185918, 185919, 185920, 185922, 185923, 185924, 216482, 216483, 216484, 216485); Mt. Twin Peaks (FMNH 176581, 176582); Penablanca Municipality (216475, 216477, 216479, 216480, 216481).
- Kalinga Prov.: Balbalasang (FMNH 167310, 169127, 169128, 169129, 175564).
- Mountain Prov.: Mt. Data (FMNH 188324, 188325, 188326, 188328, 188329, 188330, 188332, 188333, 188334, 188335, 188336, 188337, 188338, 188339, 188340, 188341, 188450, 188451, 188452, 188453, 188454, 188455, 188488, 188490); Mt. Amuyao (FMNH 193700, 193701, 193703, 191705, 191706, 191707, 193945, 214325, 214327, 214328, 214413, 214414, 214415).
- Pampanga Prov.: Mt. Pinatubo (FMNH 212626, 212628, 212629, 212630, 212631, 212632, 212633, 212634, 212635, 212636, 212638, 212639, 212640, 212641, 212642).
- Quezon Prov.: Mt. Banahaw (178406, 178407, 178408, 178409, 178410, 179520, 179521).
- Quirino Prov.: Mungiao Mountains (180386, 180387, 180388, 180389, 180391, 180394, 180395, 180396, 180397, 180434, 180435, 180436).
- Rizal Prov.: Mt. Irid (FMNH 205482, 205483, 205484, 205485, 205486, 205487, 206337).
- Zambales Prov.: Mt. Tapulao (178253, 178254, 178255, 178256, 178257, 179443, 183547, 183548).
- Full locality data, including latitude, longitude, and elevation, are available upon request.
- Bullimus bagobus* ( $n = 29$ ). Leyte Island: Leyte Prov.: Mt. Pangasugan (USNM 458785, 458786, 458788, 458789, 458890).
- Mindanao Island: Bukidnon Prov.: Mt. Kitan-glad (FMNH 167388, 167389, 167390); Sumilao Munic. (167388).
- Davao de Oro Prov.: Mt. Kampalili (190182, 194792).
- Davao del Sur Prov.: Mt. McKinley (FMNH 56205, 56206, 56207, 56208); Mt. Apo (FMNH 61481, 61482).
- Davao Oriental Prov.: Mt. Hamiguitan (190140, 190141, 190142).
- Misamis Occidental Prov.: Mt. Malindang (FMNH 87483).
- South Cotabato Prov.: Mt. Matutum (FMNH 206271, 206272, 206273, 206274).
- Surigao del Sur Prov.: Mt. Hilonghilog (FMNH 190189, 190192).
- Zamboanga del Norte Prov.: Katipunan Municipality (FMNH 67808, 67809).
- Bullimus carletoni*. See Description.
- Bullimus gamay* ( $n = 14$ ). Camiguin Island: Mt. Tim-poong (FMNH 154821, 154822, 154823, 154877,

## Appendix

### Specimens Examined