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Two new species of Philippine forest mice (*Apomys*, Muridae, Rodentia) from Lubang and Luzon Islands, with a redescription of *Apomys sacobianus* Johnson, 1962

Lawrence R. Heaney*, Danilo S. Balete, Maria Josefa Veluz, Scott J. Steppan, Jacob A. Esselstyn, Andrew W. Pfeiffer, and Eric A. Rickart

(LRH, DSB, and AWP) Field Museum of Natural History, 1400 S. Lake Shore Drive, Chicago, Illinois 60605, U.S.A., e-mail: lheaney@fieldmuseum.org;
(MJV) National Museum of the Philippines, Rizal Park, Ermita, Manila, Philippines;
(SJS) Department of Biological Sciences, Florida State University, Tallahassee, Florida 32306, U.S.A.;
(JAE) Department of Biological Sciences and Museum of Natural Science, Louisiana State University, Baton Rouge, Louisiana 70803, U.S.A.;
(EAR) Natural History Museum of Utah, 301 Wakara Way, Salt Lake City, Utah 84108, U.S.A.

Abstract.—We describe two new species of mice of the endemic Philippine genus *Apomys*, subgenus *Megapomys*. One is from Lubang Island, a small oceanic island off the southwest coast of Luzon, and the other is from Mt. Irid, a peak in the Southern Sierra Madre that lies northeast of Manila on Luzon Island. We also report the first specimens of *Apomys sacobianus* to be seen since the holotype was captured in 1956 at the foot of Mt. Pinatubo; our specimens were obtained subsequent to the eruption of Mt. Pinatubo in 1991, demonstrating the continued existence of this species. Speciation within *Apomys* (*Megapomys*) has contributed substantially to the high level of mammalian diversity and fine-scaled endemism observed on Luzon and adjacent Philippine islands.

Keywords: biodiversity, endemism, mammals, oceanic islands, Philippines, speciation

The genus *Apomys* is the most speciose of the 24 mammalian genera endemic to the Philippine archipelago, with 17 species currently recognized (Steppan et al. 2003, Heaney et al. 2011, Balete et al. 2012). *Apomys* are small mice (ca. 18–110 g) that are members of a clade of five genera endemic to the Philippines (Jansa et al. 2006, Balete et al. 2012). They occur throughout most of the Philippines, being absent only from: 1) the Palawan group, which has a mammalian fauna similar to that of Borneo and the Sunda Shelf, and may have been connected briefly to Borneo during Pleistocene periods of low sea level (Esselstyn et al. 2010, Piper et al. 2011); 2) the Sulu group, a poorly-known area between Mindanao and Borneo (Musser & Heaney 1985); and 3) the small, scattered, isolated islands of the Babuyan and Batan groups that lie between Luzon and Taiwan (Heaney et al. 2010). Speciation within *Apomys* appears to have taken place by a combination of colonization between islands within the Philippines, and colonization or habitat vicariance among isolated areas of high-elevation montane and mossy forest habitats on Luzon Island (Steppan et al. 2003, Heaney et al. 2011, Justiniano et al. 2014).

During our on-going efforts to document the mammalian fauna of the Philip-

* Corresponding author.

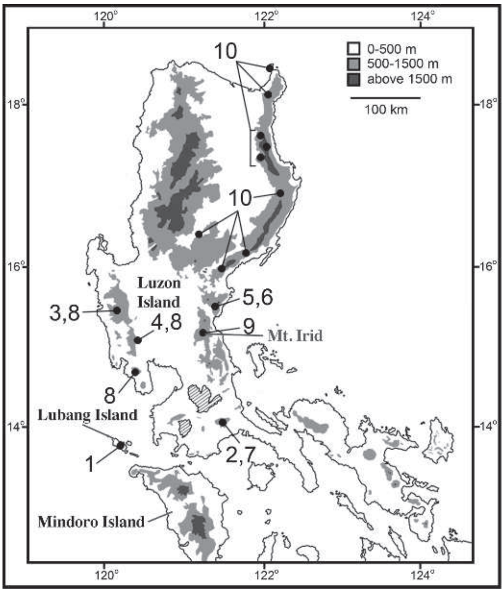

Fig. 1. Map of Luzon Island, Philippines, showing documented distributions of species mentioned in the text. 1 = *Apomys lubangensis*; 2 = *A. banahao*; 3 = *A. brownorum*; 4 = *A. sacobianus*; 5 = *A. aurorae*; 6 = *A. minganensis*; 7 = *A. magnus*; 8 = *A. zambalensis*; 9 = *A. iridensis*; 10 = *A. sierrae*.

pines (e.g., Esselstyn et al. 2008, Balete et al. 2009, 2011, 2013, Heaney et al. 2011, 2013a, 2013b, Rickart et al. 2011a, 2013), we encountered seven previously unknown species of *Apomys*, subgenus *Megapomys* (Heaney et al. 2011). Subsequently, we have discovered two additional populations of *Megapomys* from previously unsurveyed areas. One of these occurs on Mt. Irid in the Southern Sierra Madre northeast of Manila, and the other on Lubang Island, a small (ca. 192 km^2) island that lies off the southwest coast of Luzon and north of Mindoro (Fig. 1); no previous specimens of *Apomys* have been reported from either place.

A genetic analysis of the eleven previously recognized species of *Megapomys* (including a sample from Mt. Pinatubo, the type locality of *Apomys sacobianus*), plus the two newly discovered populations from Mt. Irid and Lubang Island, using one mitochondrial and four nuclear genes, found strong evidence that the Mt. Irid animals are within a clade that includes *A. aurorae*, *A. magnus*, and *A. zambalensis* (Justiniano et al. 2014; Fig. 2). The Lubang animals have their closest relationships within a different part of *Megapomys*; they are sister to *A. sacobianus* (as redefined here), and together those two species are closely related to *A. banahao* and *A. brownorum*. All of these species occur within central Luzon or on the nearby island of Lubang (Fig. 1).

Our investigation of the morphology and taxonomic status of these two new populations, which is the primary purpose of this paper, requires comparison with *Apomys sacobianus*, a species previously known from a single specimen taken in 1956 on Mt. Pinatubo (Johnson 1962) where we recently conducted a mammal survey, as related below.

Materials and Methods

Procedures used in this study were described in detail in Heaney et al. (2011) and are summarized here in brief. Specimens examined are housed in the Field Museum of Natural History, Chicago, Illinois (FMNH), National Museum of the Philippines, Manila (PNM), University of Kansas Museum of Natural History, Lawrence, Kansas (KU), and United States National Museum of Natural History, Washington, D.C. (USNM). Uncoated skulls were imaged using an AMRAY 1810 scanning electron microscope. Because the size of the skulls and mandibles exceeded the photographic frame, we took images of the front, middle and back of each skull in each view, and merged them to produce the images shown here. We took standard external measurements in the field, and Heaney took all cranial and dental measurements with dial calipers graduated to 0.01 mm; only the measurements of individuals considered to have reached adult size and that had adult

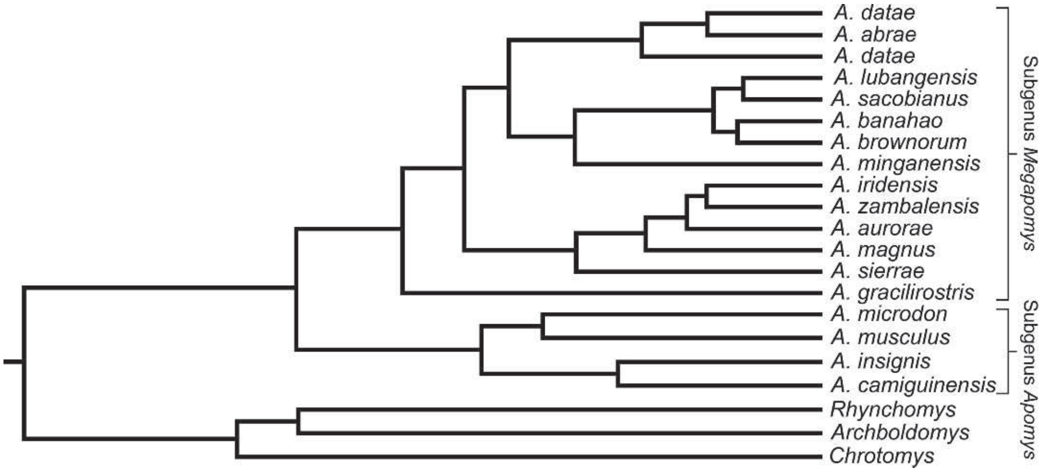

Fig. 2. Phylogenetic relationships of species in the subgenus *Megapomys*, based on analysis of DNA sequence data from one mitochondrial and four nuclear genes (see Methods), including representative species of the subgenus *Apomys* and other genera of the endemic Philippine "earthworm mouse" clade (redrawn from Justiniano et al. 2014).

pelage were included in the tables of measurements and the analyses presented here, with the one exception discussed below. We used Microsoft Excel for Windows (version 2007) to calculate mean, standard deviation, and observed range of sample groups. We assessed multivariate variation in craniodental morphology through Principal Component Analysis with SYSTAT 10 for Windows (SPSS Inc. 2000), using the correlation matrix of log-transformed measurements of adult specimens. Samples included adults of both sexes. We report results only on the first two axes in these analyses because additional axes were not readily interpretable and had eigenvalues less than 1.5.

The genetically-based phylogeny presented here (Fig. 2) is based on DNA sequences from one mitochondrial gene (cytochrome b) and four nuclear genes: the divergent domain of exonic Recombination Activating Gene one (RAG-1), intron two and parts of bounding exons of Acid Phosphatase type V (Acp5), intron three of Benzodiazepine Receptor (BDR), and exon one and part of exon two of Acrosin. We used Beast v. 1.6.1 (Drummond & Rambaut 2007) to estimate an ultrameric tree using the five-gene dataset. Because no fossil calibrations exist for this clade, we set the root to a depth of 1, yielding relative rather than absolute dates. For details, see Justiniano et al. (2014).

Redescription of *Apomys* (*Megapomys*) *sacobianus*

Before assessing the status of the mice from Lubang Island and Mt. Irid, we must investigate the validity of *Apomys sacobianus*, a species that has been known only from the holotype since its discovery (Johnson 1962, Heaney et al. 2011). The holotype was obtained by David H. Johnson in 1956 at the foot of Mt. Pinatubo, which in June 1991 erupted in the second most massive explosive event of the twentieth century (exceeded only by the 1912 eruption of Mt. Novarupta, Alaska; Newhall & Punongbayan 1996). As a little-noted effect at the time, this eruption created doubt as to the continued existence of this enigmatic species (Heaney et al. 2010). In 2011 and 2012, we conducted an extensive survey of the mammals of Mt. Pinatubo, including localities near the type locality, and captured many large-bodied *Apomys* (subgenus *Megapomys*); ecological results will be presented elsewhere. The taxonomic status of the specimens we obtained is documented here.

We obtained 203 specimens of *Megapomys* on Mt. Pinatubo at six localities, including several near the type locality of *Apomys sacobianus* (see Specimens Examined, below). In the field, all appeared similar, with substantial age-related variation but no initially obvious evidence of multiple species. However, subsequent examination of cleaned skulls of the mice immediately showed that eight individuals have a large stapedial foramen in the auditory bulla for the stapedial artery, which denotes the carotid circulatory pattern that typifies *A. datae* (Musser 1982), as well as *A. aurorae*, *A. magnus*, *A. zambalensis*, and the mice from Mt. Irid (Heaney et al. 2011). DNA sequences from individuals from Mt. Pinatubo with this circulatory pattern are nested within samples of *A. zambalensis* from Mt. Tapulao (to the north of Mt. Pinatubo) and from Mt. Natib (to the south; Justiniano et al. 2014). Other features of craniodental anatomy—large size; long, robust rostrum; somewhat elongate braincase and postpalatal region; broad incisive foramina; and maxillary toothrows that slightly diverge posteriorly (Table 1)—also match those of *A. zambalensis*, and we have found no traits by which these Pinatubo mice and *A. zambalensis* differ. We therefore consider those mice to be examples of *A. zambalensis*, as further discussed below.

However, most specimens of *Megapomys* from Mt. Pinatubo lack a stapedial foramen, which denotes a different pattern of carotid circulation that is present in several species of *Megapomys*, including *A. abrae*, *A. banahao*, *A. brownorum*, *A. sacobianus* (as represented by the holotype), and the mice from Lubang Island (see Heaney et al. 2011, this study). With only one known specimen, the holotype, no genetic material has been previously available from *A. sacobianus*. Genetic samples from the Pinatubo mice that lack a stapedial foramen did not match any species of *Megapomys* that has been gene-sequenced, although they were most similar to those of *A. banahao*, *A. brownorum*, and the mice from Lubang (Justiniano et al. 2014; Fig. 2), all of which share the same carotid circulatory pattern. This suggests that these mice from Mt. Pinatubo represent *A. sacobianus*. Testing this hypothesis requires comparison of our indeterminate series from Mt. Pinatubo with the holotype (and only specimen known to date) of *A. sacobianus*.

The holotype of *A. sacobianus* possesses slightly worn molars. Comparison of its external measurements with those of the two species on Mt. Pinatubo (Table 1) shows the holotype to be consistently smaller, though more similar to the indeterminate Pinatubo series than to *A. zambalensis*. Lengths of ear and hind foot fall at or just below the range of the indeterminate Pinatubo adults, but with an 8% smaller head and body than the average adult, and a tail about 20% shorter than on the average adult. The weight is about 25% less than that of the adults. Craniodental measurements that fall within the range of values from our large series of adults (Table 1) include interorbital width, mastoidal breadth, orbito-temporal length, maxillary toothrow length, diastemal length, braincase height, breadth of M^1, and breadth at tip of incisors. Nearly all of these are associated with either the size of the eye or brain, neural features that reach full size before other cranial components, or with the molars, which do not grow after they erupt. Measurements that fall below the range of adult dimensions are basioccipital length, zygomatic breadth, nasal length, incisive foramen length, rostral depth, rostral length, labial palatal breadth at M^1, post-palatal length, lingual breadth of palate at M^3, and width of zygomatic plate. All of these mensural

Table 1.—Cranial, dental, and external measurements (mean + 1 *SD* and range, mm) of the holotype of *Apomys sacobianus*, additional adult specimens referred to that species, and specimens of adult *A. zambalensis* from Mt. Pinatubo, Pampanga Province.

	Apomys sacobianus			*A. zambalensis*
Measurement	M-Holotype USNM 304352	M (n = 12)	F (n = 14)	M & F (n = 5)
Basioccipital length	34.29	35.39 ± 0.45 (11)	35.82 ± 0.49	36.38 ± 0.63
	–	35.01–35.90	35.11–36.36	35.78–37.26
Interorbital breadth	5.75	5.85 ± 0.20	5.71 ± 0.25	6.04 ± 0.15
	–	5.43–6.12	5.38–6.29	5.90–6.23
Zygomatic breadth	17.54	18.57 ± 0.56	18.59 ± 0.41	18.55 ± 0.79
	–	17.63–19.56	17.89–19.39	17.83–19.81
Mastoid breadth	14.01	14.36 ± 0.45	14.43 ± 0.33	14.52 ± 0.28
	–	13.92–15.50	13.92–15.07	14.27–14.80
Nasal length	13.62	14.62 ± 0.36	14.75 ± 0.46	15.12 ± 0.42
	–	14.15–15.14	14.02–15.68	14.73–15.61
Incisive foramen length	4.86	5.47 ± 0.29	5.34 ± 0.27	5.60 ± 0.24
	–	5.14–5.88	4.90–5.92	5.32–5.96
Rostral depth	7.06	7.96 ± 0.27	8.02 ± 0.22	7.89 ± 0.19
	–	7.52–8.41	7.72–8.98	7.66–8.15
Rostral length	14.92	15.73 ± 0.35	15.99 ± 0.31	16.15 ± 0.50
	–	15.95–16.25	15.58–16.55	15.75–16.91
Orbito-temporal length	11.59	12.09 ± 0.45	12.19 ± 0.24	12.36 ± 0.34
	–	11.40–12.73	11.67–12.47	11.89–12.84
Maxillary toothrow length	6.53	7.00 ± 0.22	6.95 ± 0.28	7.24 ± 0.14
	–	6.62–7.42	6.51–7.41	7.03–7.41
Labial palatal breadth at M^1	6.87	7.55 ± 0.24	7.65 ± 0.28	8.00 ± 0.16
	–	7.11–7.90	7.05–8.11	7.79–8.20
Diastemal length	9.44	9.50 ± 0.40	9.77 ± 0.36	10.02 ± 0.25
	–	8.55–10.02	9.18–10.31	9.78–10.45
Post-palatal length	11.66	12.39 ± 0.31	12.39 ± 0.39	12.39 ± 0.18
	–	11.87–12.86	11.91–13.20	12.17–12.60
Lingual palatal breadth at M^3	4.8	5.16 ± 0.37	5.38 ± 0.26	5.64 ± 0.15
	–	4.10–5.49	5.00–5.78	5.39–5.79
Braincase height	11.13	10.71 ± 0.37	10.90 ± 0.32	10.72 ± 0.06
	–	10.11–11.29	10.47–11.49	10.65–10.77
Breadth of M^1	1.76	1.92 ± 0.06	1.86 ± 0.10	1.86 ± 0.06
	–	1.79–1.98	1.72–2.02	1.81–1.95
Breadth of incisors at tip	2.13	2.31 ± 0.09	2.31 ± 0.12	2.28 ± 0.11
	–	2.18–2.46	2.10–2.53	2.10–2.36
Width of zygomatic plate	2.7	3.33 ± 0.23	3.28 ± 0.17	3.74 ± 0.13
	–	2.92–3.64	2.89–3.89	3.53–3.88
Length of head & body	135	147.6 ± 5.2 (10)	145.21 ± 5.1	152.5 ± 5.07
	–	141–158	137–153	148–159
Total length	250	292.8 ± 10.9 (10)	284.6 ± 9.1	298.0 ± 2.8
	–	280–315	277–315	294–300
Length of tail vertebrae	115	146.1 ± 7.3 (11)	139.5 ± 6.0	146.8 ± 7.1
	–	138–159	132–153	135–152
Length of hind foot	34	38.4 ± 0.9 (11)	37.6 ± 1.2	38.6 ± 1.7
	–	37–40	35–39	36–40
Length of ear	21	23.0 ± 0.8 (11)	23.0 ± 1.8	22.4 ± 0.9
	–	22–24	21–25	21–23
Weight (g)	71	97.6 ± 6.0 (10)	91.1 ± 8.4	106.0 ± 13.2
	–	85–105	79–104	95–125

data, coupled with the lightly worn molars, point to the holotype as a young adult (with adult pelage) that has not yet reached full size, reflecting features that increase until cessation of cranial growth, as would be expected in a comparison of a young adult with fully adult mice of the same species.

On the basis of these observations, we accept the hypothesis that our indeterminate series from Mt. Pinatubo (as listed below) represents *A. sacobianus* and present the following redescription of *A. sacobianus*.

Apomys (*Megapomys*) *sacobianus*
Johnson, 1962
Figs. 1–6; Table 1

Apomys sacobianus Johnson, 1962:317–319

Holotype.—USNM 304352. Young adult male, collected 16 Aug 1956. Field number D. H. Johnson 8555. Prepared as stuffed skin plus skull. Measurements are listed in Table 1. The cranium and mandible of the holotype are illustrated in Heaney et al. (2011: Fig. 20).

Type locality.—Philippine Islands: Luzon Island: Pampanga Province: Clark Air Force Base, Sacobia River, in a narrow forested canyon of the Sacobia River "just above the point where it emerges from the foothills of the Zambales Mountains onto the plains of Pampanga" (Johnson 1962:319).

Material examined (*n* = *199*).—Philippine Islands: Luzon Island: Pampanga Province: Mabalacat Municipality: 7.4 km N, 13 km E Mt. Pinatubo peak, 15.20372°N, 120.46206°E, elev. 365 m (FMNH 212553–212587, 212709–212730); 6 km N, 12.7 km E Mt. Pinatubo peak, 15.19177°N, 120.45778°E, elev. 490 m (FMNH 212588–212620, 212731); 3.2 km N, 11.5 km E Mt. Pinatubo peak, 15.17796°N, 120.45014°E, elev. 670 m (FMNH 212621–212624); 1.8 km N, 6.25 km E Mt. Pinatubo peak, 15.15145°N, 120.39784°E, elev. 960 m (FMNH 216225–216247, 216263–216264, 216324–216347); 2 km N, 6.2 km E Mt. Pinatubo peak, 15.15553°N, 120.39856°E, elev. 1080 m (FMNH 216248–216262, 216265–216294, 216348–216371), plus the holotype.

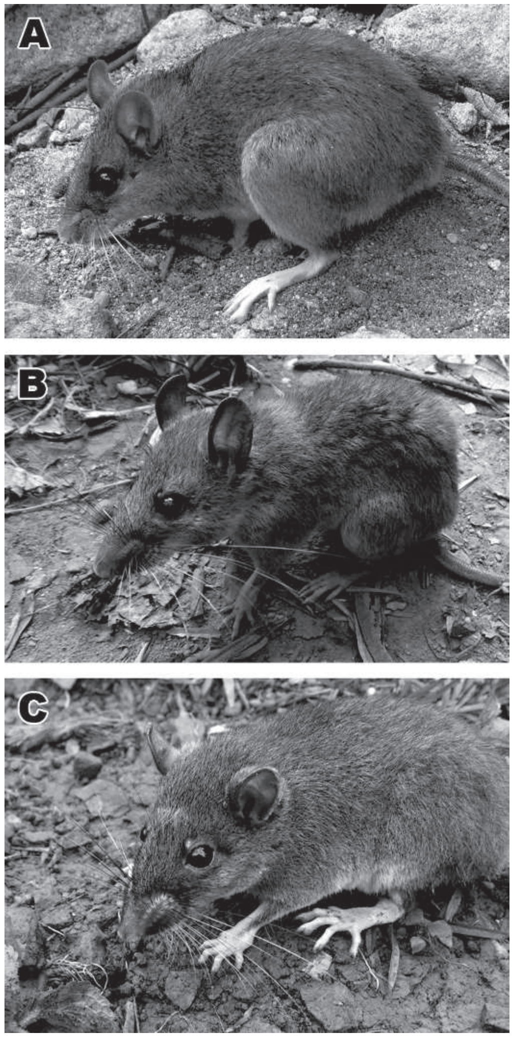

Fig. 3. Photographs of live adult specimens. A, *Apomys sacobianus*, taken 12 March 2012; B, *A. lubangensis*, taken 1 June 2012; C, *A. iridensis*, taken 8 June 2009. All photos by D. S. Balete.

Emended diagnosis.—A large species of *Apomys*, subgenus *Megapomys*, with the following average measurements for males and females (Table 1): head and body length 145–148 mm, tail 140–146 mm, hind foot length 37–38 mm, basioccipital length

Fig. 4. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of a representative adult of *Apomys sacobianus* (FMNH 212562).

35–36 mm, maxillary toothrow length 6.9–7.0 mm, incisive foramina 5.3–5.5 mm, and lingual palatal breadth at M^3 5.1–5.4 mm. There is no stapedial foramen in the auditory bulla. The dorsal pelage is brown with grayish tones, and the ventral pelage appears grayish-white (Fig. 3A). Many individuals have a darkened patch of fur on the dorsal surface of the rostrum. The tail is thicker than that of most *Megapomys* and is pigmented dark grayish-brown dorsally. The hind feet are moderately broad, and the plantar surfaces are heavily pigmented dark gray.

Comparisons.—*Apomys sacobianus* occurs syntopically with *A. zambalensis* on Mt. Pinatubo. The two are similar in

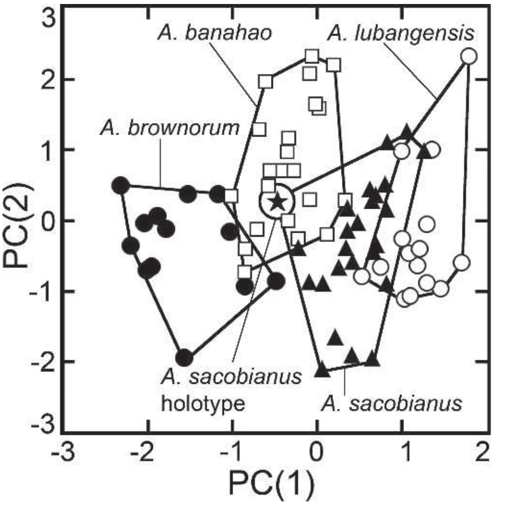

Fig. 5. Results of Principal Components Analysis of craniodental measurements of *Apomys banahao*, *A. brownorum*, *A. sacobianus*, and *A. lubangensis*. For loadings on PC1 and PC2, see Table 3.

external appearance, but show consistent subtle differences. *Apomys sacobianus* is generally smaller than *A. zambalensis*, averaging slightly smaller in all external measurements except length of ear (Table 1). Adult *A. sacobianus* typically weigh less than 100 g, occasionally reaching 105 g, and *A. zambalensis* from Pinatubo weigh 98 g to 110 g (Table 1). The dorsal pelage of *A. sacobianus* appears more variegated, slightly paler, and grayer (less reddish) than that of *A. zambalensis*. The ventral pelage has shorter white tips on the hairs, so that the gray bases show through clearly, and there is usually a slight wash of a cream color on the abdomen; *A. zambalensis* has longer white tips so that the gray bases are less apparent, and the hairs either are pure white or have a wash of pale orange/ochraceous. The transition from dorsal to ventral pelage is more abrupt in *A. zambalensis*, and less so in *A. sacobianus*. The tail of *A. sacobianus* is slightly thicker, with more heavily pigmented scales dorsally, appearing nearly black; that of *A. zambalensis* is more slender and the scales are less heavily

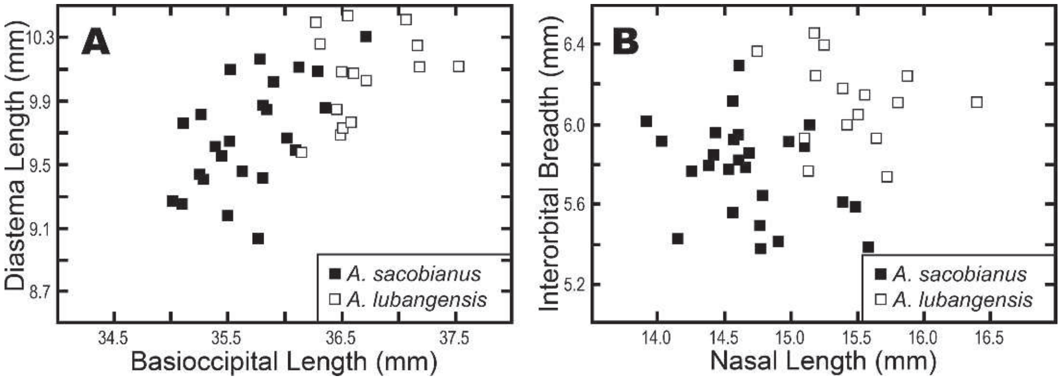

Fig. 6. Bivariate plots of measurements comparing *Apomys sacobianus* and *A. lubangensis*. A = basioccipital length vs. diastema length; B = nasal length vs. interorbital breadth.

pigmented, appearing medium to dark brown. The hind feet of *A. sacobianus* are slightly longer, broader, and less heavily pigmented on the ventral surface. Genetic differences are described in Justiniano et al. (2014).

Cranially, *A. sacobianus* differs from the sympatric *A. zambalensis* in lacking a stapedial foramen in the auditory bulla, a foramen that is present in *A. zambalensis*. The incisive foramina of *A. sacobianus* are narrower posteriorly (vs. broader and more open; compare Fig. 4 with Fig. 46 in Heaney et al. 2011). The maxillary toothrow of *A. sacobianus* rarely exceeds 7.4 mm and averages about 6.9 mm, whereas that of *A. zambalensis* is rarely less than 7.2 mm and averages about 7.6 mm (Table 1; also see Heaney et al. 2011: Table 15). The zygomatic plate of *A. sacobianus* averages narrower than that of *A. zambalensis*, ca. 3.3 mm vs. 3.6 mm (Table 1; also see Heaney et al. 2011: Table 15).

Apomys sacobianus is substantially larger than *A. banahao* and *A. brownorum* in nearly all respects; the latter species have much darker pelage, and both absolutely and proportionately shorter tails (Table 1; also see Heaney et al. 2011: Tables 3 and 9). The cranium of *A. brownorum*, a species that also occurs in the Zambales Mountains, is smaller overall, with a more slender rostrum with shorter nasals, a braincase that is more globose and less squarish, and slightly narrower incisive foramina. As noted in greater detail below, *A. sacobianus* is smaller than the *Apomys* from Lubang Island, with mass less than 105 g (rather than more than 100 g), basioccipital length rarely exceeding 36.5 mm (rather than usually more than 36.3 mm), and the length of the tail as a proportion of the length of the head and body usually 95% to more than 100% (rather than 90% to 95%).

Apomys (*Megapomys*) from Lubang Island

Genetic data show the *Megapomys* from Lubang Island to be closely related to *A. banahao*, *A. brownorum*, and *A. sacobianus* (Fig. 2), all of which also lack a stapedial foramen. To initially explore similarities and differences, we conducted a PCA of 18 craniodental measurements of that clade, using specimen data on which the sample statistics presented in Tables 1 and 2 for *A. sacobianus* and the Lubang population, and in Tables 3 and 9 from Heaney et al. (2011) for *A. banahao* and *A. brownorum,* are based. The first axis explained 56.7% of the variation, with all variables loading positively and most loading heavily; only height of braincase loaded less strongly (Table 3).

Table 2.—Cranial, dental, and external measurements (mean + 1 *SD* and range, mm) of *Apomys lubangensis* from Lubang Island, Mindoro Occidental Province.

	Apomys lubangensis		
	M-Holotype		
Measurement	PNM 4487	M ($n = 9$)	F ($n = 6$)
Basioccipital length	37.06	36.67 ± 0.47	36.66 ± 0.27
	–	36.14–37.52	36.45–37.18
Interorbital breadth	6.11	6.10 ± 0.21	6.13 ± 0.24
	–	5.77–6.40	5.74–6.46
Zygomatic breadth	19.00	19.00 ± 0.42	19.01 ± 0.41
	–	18.26–19.64	18.54–19.78
Mastoid breadth	14.51	14.68 ± 0.29	14.84 ± 0.37
	–	14.26–15.18	14.55–15.56
Nasal length	16.40	15.49 ± 0.50	15.41 ± 0.21
	–	14.75–16.40	15.18–15.72
Incisive foramen length	5.38	5.44 ± 0.25	5.60 ± 0.23
	–	5.09–5.80	5.41–5.94
Rostral depth	8.35	8.21 ± 0.22	8.35 ± 0.16
	–	7.97–8.58	8.11–8.58
Rostral length	16.68	16.13 ± 0.57	15.95 ± 0.27
	–	15.32–16.98	15.51–16.33
Orbito-temporal length	12.66	12.58 ± 0.34	12.60 ± 0.28
	–	12.03–13.13	12.31–13.00
Maxillary toothrow length	7.00	7.12 ± 0.15	7.14 ± 0.16
	–	6.87–7.38	6.86–7.29
Labial palatal breadth at M^1	7.51	7.53 ± 0.18	7.53 ± 0.25
	–	7.25–7.75	7.17–7.93
Diastemal length	10.42	10.06 ± 0.32	10.05 ± 0.24
	–	9.58–10.42	9.77–10.44
Post-palatal length	12.72	12.65 ± 0.33	12.58 ± 0.24
	–	12.33–13.09	12.24–12.90
Lingual palatal breadth at M^3	5.18	5.07 ± 0.13	5.41 ± 0.19
	–	4.81–5.18	5.14–5.68
Braincase height	10.86	10.83 ± 0.16	10.96 ± 0.44
	–	10.62–11.13	10.44–11.66
Breadth of M^1	1.88	1.90 ± 0.05	1.84 ± 0.08
	–	1.85–2.02	1.72–1.96
Breadth of incisors at tip	2.41	2.40 ± 0.09	2.47 ± 0.11
	–	2.28–2.53	2.34–2.66
Width of zygomatic plate	4.02	3.53 ± 0.32	3.59 ± 0.12
	–	3.18–4.02	3.40–3.75
Length of head & body	160	151.0 ± 5.4 (6)	150.3 ± 3.9
	–	143–157	144–155
Total length	300	295.4 ± 9.9 (7)	287.8 ± 7.7
	–	278–310	279–299
Length of tail vertebrae	140	143.2 ± 6.5 (6)	137.5 ± 5.6
	–	135–154	128–144
Length of hind foot	40	40.0 ± 1.5 (7)	39.2 ± 0.8
	–	38–42	38–40
Length of ear	26	24.4 ± 1.5 (7)	24.4 ± 0.9 (5)
	–	22–27	24–26
Weight (g)	–	111.4 ± 10.6 (7)	107.00 ± 6.0
	–	108–128	102–116

Table 3.—Character loadings, eigenvalues, and percent variance explained on the first two components of a Principal Components Analysis of log-transformed craniodental measurements of adult *Apomys aurorae*, *A. brownorum*, *A. lubangensis*, and *A. sacobianus* (see Fig. 5 and Methods).

Variable	Principal component 1	2
Basioccipital length	0.947	−0.245
Interorbital breadth	0.551	0.593
Zygomatic breadth	0.903	0.214
Mastoid breadth	0.703	0.385
Nasal length	0.820	−0.352
Incisive foramen length	0.521	−0.316
Rostral depth	0.935	−0.050
Rostral length	0.778	−0.412
Orbito-temporal length	0.801	−0.068
Maxillary toothrow length	0.730	0.061
Labial palatal breadth at M^1	0.814	0.236
Diastemal length	0.689	−0.347
Post-palatal length	0.897	−0.174
Lingual palatal breadth at M^3	0.643	0.013
Braincase height	0.377	0.583
Breadth of M^1	0.511	0.384
Breadth of incisors at tip	0.802	0.025
Width of zygomatic plate	0.834	0.034
Eigenvalue	10.203	1.704
Variance explained	56.686	9.468

This axis clearly represented overall size. The second axis, which accounted for an additional 9.5% of the total variation, loaded strongly and positively for interorbital breadth and braincase height, positively but moderately strongly for mastoid breadth and breadth of M^1, and moderately strongly but negatively with nasal length, rostral length, and diastemal length (Table 3).

A graph of the scores of individual animals on these two axes (Fig. 5) shows a moderate degree of separation among the species. *Apomys brownorum* is the smallest of the species, loading on the left side of the graph, and load neutrally or negatively on the second axis. *Apomys banahao* is somewhat larger, and have neutral to positive loadings on the second axis (Fig. 5, Table 3). Both of these species show limited overlap with other species. *Apomys sacobianus* are still larger and have neutral to negative loadings on the second axis; they exhibit some overlap in this morphospace with the animals from Lubang Island. Only the holotype of *A. sacobianus* overlaps with *A. banahao*, and that is due to its small size associated with being a young adult, as noted above. The specimens from Lubang are the largest in this clade, and load neutrally to positively on the second axis, with some overlap with *A. sacobianus* (Fig. 5).

Adult *A. sacobianus* (79–105 g) and the Lubang mice (102–128 g) overlap little in weight (compare Tables 1 and 2). Bivariate comparison of some craniodental variables for the Lubang mice with those of *A. sacobianus* also shows limited overlap. A plot of basioccipital length vs. diastemal length (Fig. 6A) shows limited overlap, as does a plot of nasal length vs. interorbital breadth (Fig. 6B). We conclude that these two population samples are similar but usually distinguishable on the basis of these cranial features. A comparison of craniodental and external measurements of the Lubang animals (Table 2) with those of *A. banahao* and *A. brownorum* (Heaney et al. 2011: Tables 3 and 9) shows no overlap on most measurements, as expected from their morphometric separation in the PCA analysis (Fig. 5).

Given that 1) multi-locus sequence data (Justiniano et al. 2014) show the Lubang mice to constitute a well-defined monophyletic unit, with genetic distances from its sister-taxon equivalent to those between other recognized species of *Apomys* (as evident in Fig. 2); 2) PCAs of craniodental measurements of the Lubang mice show them to be equally distinctive as other recognized species within their clade (Fig. 5); and 3) bivariate plots of selected craniodental measurements (Fig. 6) generally distinguish them from their respective sister-taxa, we consider the *Apomys* from Lubang Island to represent a distinct species.

Apomys (*Megapomys*) *lubangensis*, new species
Figs. 1–3, 5–7; Table 2

Holotype.—PNM 4487. Adult male, collected in April 2001 by M. J. Veluz. Field number MJV 27. Prepared as complete body preserved in formalin, then transferred to ethanol. In the museum, the skull (Fig. 7) was removed and cleaned. All parts are in good condition. Measurements appear in Table 2.

Type locality.—Philippine Islands: Lubang Island: Mindoro Occidental Province: Looc Municipality: Barangay Burol: Sitio Bubuyog, 13°48′N, 120°7.8′E.

Paratypes (*n* = *89*).—Philippine Islands: Lubang Island: Mindoro Occidental Province: Lubang Municipality: Barangay Sorville (= Ambulong), ca. 600 m (PNM 4440, 4448); Lubang Municipality: 0.6 km N, 0.8 km W Mt. Ambulong peak, 13.79296°N, 120.14166°E, elev. 300 m (FMNH 218204–218218, 218450–218459, 218473); 0.5 km N, 0.25 km W Mt. Ambulong peak, 13.79226°N, 120.14645°E, elev. 425 m (FMNH 218219–218232, 218460–218472); Lubang Municipality: Barangay Vigo, 13.796°N, 120.159°E, elev. 130 m (KU164194, 164195, 164197, 164200–164202, 164209, 164213).

Etymology.—An adjective based on the name of the island (Lubang) where the species occurs (Fig. 1).

Diagnosis.—A species of the genus *Apomys*, subgenus *Megapomys* (Heaney et al. 2011), of relatively large size, with the following average measurements of males and females (Table 2): total length of adults 288–295 mm, length of head and body about 150 mm, weight range 102–128 g; the tail is somewhat shorter than the length of head and body (138–143 mm). The skull is robust (Fig. 7), with basioccipital length of adults 36–37 mm; braincase height (10.8–11.0 mm), interorbital breadth (about 6.1 mm), and mastoid breadth (13.8 mm) are relatively great; nasal length (15.4–15.5 mm), rostral length (15.9–16.1 mm), diastemal length (10.0 mm) and incisive foramen length (5.4–5.6 mm) are proportionately small for a species of its size (Table 2). The auditory bullae lack a stapedial foramen. The dorsal pelage is brown with grayish tones, and is more highly variegated than any other species of *Megapomys* (Fig. 3B). The tail is nearly black dorsally, with large, prominent scales. The ventral surface of the hind feet is heavily pigmented dark gray, and the plantar pads, which are large, are pale.

Fig. 7. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of *Apomys lubangensis* (holotype, PNM 4487).

Comparisons.—Phylogenetic relationships based on DNA sequences depict *A. lubangensis* and *A. sacobianus* as sister species, in a clade that also includes *A.*

banahao and *A. brownorum* (Fig. 2). *Apomys lubangensis* is larger than *A. sacobianus*, with weight of adults usually greater than 105 g (rather than less than 100 g), basioccipital length usually more than 36.3 mm (rather than rarely exceeding 36.5 mm), and the length of the tail as a proportion of the length of the head and body usually 90% to 95% (rather than 95% to 100%). The dorsal pelage is slightly more reddish in *A. lubangensis*, though both appear brownish-gray; that of *A. lubangensis* is slightly more variegated. The ventral pelage of both species appears grayish-white, though that of *A. sacobianus* usually has a pale creamy wash, and that of *A. lubangensis* is grayer. The tail of *A. lubangensis* is even darker dorsally than that of *A. sacobianus*, and the diameter appears slightly greater. The ventral surface of the hind feet of *A. lubangensis* is more heavily pigmented than in *A. sacobianus*, and the plantar pads are distinctly larger. The scrotum of each adult male *A. lubangensis* has a prominent darkly pigmented posterior tip, ca. 1 cm long; that of *A. sacobianus* is much less heavily pigmented (i.e., it is medium brown rather than nearly black), and the pigmented area covers only ca. 0.5 cm of the posterior tip. The crania are similar, but *A. sacobianus* typically has shorter basioccipital length, diastema, maxillary toothrow, and nasals, along with a narrower interorbital region (Tables 1 and 2).

The other members of the species group defined by DNA sequence data and the absence of the stapedial foramen are *Apomys banahao* and *A. brownorum*. Both species are much smaller than *A. lubangensis*, with darker pelage and absolutely and proportionately shorter tails.

The only species of *Apomys* (*Megapomys*) that is larger than *A. lubangensis* is *A. magnus*, which has a substantially broader interorbital region, longer incisive foramina, longer orbito-temporal region, longer maxillary toothrow, and broader palate (Table 2; also see Heaney et al. 2011: Table 12). Unlike *A. lubangensis*, the auditory bulla of *A. magnus* possesses a stapedial foramen, and DNA sequence data demonstrate that the two species belong to different species groups (Fig. 2). *Apomys zambalensis,* which occurs in west-central Luzon near Lubang Island (Fig. 1), is generally smaller overall, with little overlap in zygomatic breadth, nasal length, and maxillary toothrow length (Table 2; also see Heaney et al. 2011: Table 15). It has a stapedial foramen, which *A. lubangensis* lacks, and DNA sequence data show them to be members of different species groups.

Ecology and distribution.—We conducted brief surveys of the small mammals of Lubang Island in April 2001 and December 2005, and a more extensive survey in May and June 2012. In 2001, M. J. Veluz captured two specimens in mixed second-growth lowland forest and subsistence farm plots at 600 ft (ca. 180 m) elevation, with limited trapping. A third specimen (the holotype) was captured in similar habitat at an unrecorded but similar elevation. From 9 to 15 December 2005, J. A. Esselstyn trapped small mammals at 130 m elevation in secondary lowland forest with a few mature trees on steep terrain; he captured 34 *A. lubangensis*. The soil was shallow and rocky, with limestone outcrops on ridgetops. Leaf litter was sparse, and little humus was present.

In 2012, D. S. Balete sampled at 150 m, 300 m, and 425 m elevation on the slopes of Mt. Ambulong (peak at 510 m). *Rattus exulans* and *R. tanezumi* were captured during brief trapping (92 trap-nights) in a heavily disturbed agricultural area at 150 m; no non-volant native mammals were captured. At 300 m and 425 m, we sampled intensively in disturbed but well-developed, regenerating forest with canopy at 20–25 m and some emergents reaching ca. 30 m; vegetative ground cover was sparse but leaf litter was abundant. In 1480 trap-nights at 300 m, we captured 26 *A. lubangensis*, 10 individuals of a small,

Table 4.—Character loadings, eigenvalues, and percent variance explained on the first two components of a Principal Components Analysis of log-transformed craniodental measurements of adult *Apomys aurorae*, *A. iridensis*, *A. magnus*, and *A. zambalensis* (see Fig. 8 and Methods).

Variable	Principal component 1	Principal component 2
Basioccipital length	0.882	−0.337
Interorbital breadth	0.532	0.468
Zygomatic breadth	0.818	0.093
Mastoid breadth	0.771	0.148
Nasal length	0.795	−0.124
Incisive foramen length	0.581	−0.262
Rostral depth	0.746	−0.207
Rostral length	0.757	−0.146
Orbito-temporal length	0.719	0.144
Maxillary toothrow length	0.652	0.365
Labial palatal breadth at M^1	0.748	0.419
Diastemal length	0.619	−0.637
Post-palatal length	0.551	−0.587
Lingual palatal breadth at M^3	0.580	−0.231
Braincase height	0.424	0.217
Breadth of M^1	0.446	0.774
Breadth of incisors at tip	0.603	0.135
Width of zygomatic plate	0.165	0.308
Eigenvalue	7.718	2.403
Variance explained	42.876	13.352

arboreal species of *Apomys* currently unidentified to species, two *Rattus everetti*, and single individuals of an unidentified *Crocidura* and *R. tanezumi*. At 425 m elevation in 1317 trap-nights, we captured 27 *A. lubangensis*, four of the small, arboreal *Apomys* sp., five *Rattus everetti*, and 10 *R. tanezumi*. All of the *A. lubangensis* were captured on the ground.

Our surveys show that *A. lubangensis* is generally common in both heavily disturbed and regenerating forest on Lubang Island above about 100 m; they should also be sought on the adjacent smaller islands of Ambil and Golo. These three islands lie together on a shallow submarine shelf (ca. 20 m deep), with minimum depths to Luzon of over 200 m, and to Mindoro of over 750 m; since sea level dropped no more than ca. 120 m during the Pleistocene (Piper et al. 2011), these current sea depths establish the Lubang Island group as a distinct set of oceanic islands.

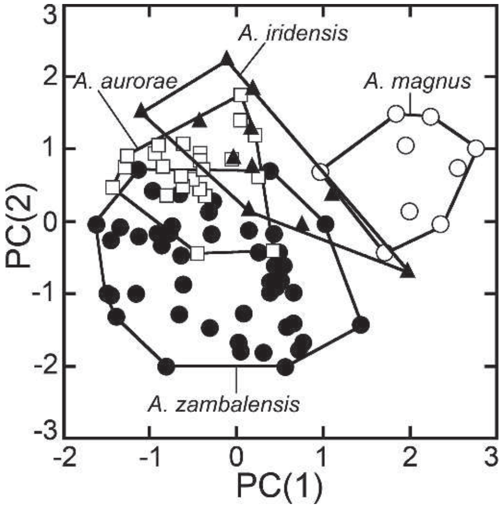

Fig. 8. Results of Principal Components Analysis of craniodental measurements of *Apomys aurorae*, *A. iridensis*, *A. magnus*, and *A. zambalensis*. For loadings on PC1 and PC2, see Table 4.

Apomys (*Megapomys*) from Mount Irid, Rizal Province, Luzon

Analysis of DNA sequence data shows the specimens from Mt. Irid to be the sister group to *A. zambalensis* and closely related to *A. aurorae* and *A. magnus*; the genetic distance of the Irid mice to *A. zambalensis* is similar to that between *A. aurorae* and *A. magnus* (Fig. 2). A PCA of craniodental measurements from those four taxa (Table 4) shows heavy to moderate loadings on the first axis by all variables except zygomatic plate width; this axis explained 42.0% of the variance (eigenvalue = 7.7), and clearly reflects overall size. Breadth of M^1 loads heavily and positively on the second axis, and diastemal length and post-palatal length correlated strongly but negatively on this axis; the second principal component explained 13.4% of the total variance, with an eigenvalue of 2.4 (Table 4).

A plot of PC1 vs. PC2 (Fig. 8) shows *A. magnus* scoring highly on the first axis, in keeping with its large size (see Heaney et al. 2011: Table 12). *Apomys aurorae*, *A. zambalensis*, and the Mt. Irid animals had similar scores on the first axis, but exhibited some differences on the second: the Mt. Irid mice scored highest (reflecting a broad M^1 and relatively short diastema and post-palatal region), and *A. zambalensis* scored lowest, though with considerable variation, reflecting the typically narrow M^1 and long diastema and post-palatal region. *Apomys aurorae* scored near zero, falling between but overlapping broadly with both the Irid animals and *A. zambalensis*. The Mt. Irid animals showed limited overlap with *A. zambalensis*, the most closely related species according to the genetic data.

A comparison of external measurements of the Mt. Irid animals with *A. zambalensis* (Tables 1 and 5; also see Heaney et al. 2011: Table 15) shows little apparent difference, although the Irid animals tend to have a longer tail (average for Mt. Irid mice = 145–147 mm, *A. zambalensis* = 138–141 mm) and shorter ears (Mt. Irid mice average 20.4–20.5 mm, *A. zambalensis* = 21.1–21.9 mm), but there is much overlap. A plot of breadth of M^1 vs. breadth of incisors at their tips shows little overlap, with the Irid animals typically being larger in both respects (Fig. 9). We note also that the Irid animals typically have a greater interorbital breadth but shorter post-palatal length, as anticipated from the PCA (Fig. 8, Table 4). We conclude that the Irid animals and *A. zambalensis*, while being similar to each other, can nearly always be distinguished on the basis of cranial measurements.

Given that 1) the genetic data show monophyly of the specimens from Mt. Irid; 2) genetic distances between the Mt. Irid animals and *A. zambalensis* are equivalent to those between other recognized species of *Apomys* (Fig. 2); 3) PCAs of craniodental measurements of the Irid animals show them to be as distinctive as other recognized species within their clades (Fig. 8); and 4) bivariate plots of selected dental measurements show them to usually be distinguishable from their sister species, we reject the hypothesis that the Mt. Irid samples can be treated as members of any recognized species and instead diagnose them as a distinct species.

***Apomys* (*Megapomys*) *iridensis*,**
new species
Figs. 1–3, 8–10; Table 5

Holotype.—FMNH 205436. Adult female, collected 7 June 2009, field number DS Balete 5958. Prepared as complete body preserved in formalin, then transferred to ethanol. A sample of muscle tissue was removed from the thigh and preserved in ethanol before the body was preserved in formalin. In the museum, the skull (Fig. 10) was removed and cleaned. All parts are in good condition. This specimen will be permanently housed at the PNM. Craniodental and external measurements are shown in Table 5.

Type locality.—Philippine Islands: Luzon Island: Rizal Province: Rodriguez Municipality: 1.25 km S, 0.5 km W Mt. Irid peak, 14.78000°N, 121.32116°E, elev. 920 m.

Paratypes (n = 82).—Philippine Islands: Luzon I.: Rizal Province: Rodriguez Municipality: 1.5 km S, 1 km W Mt. Irid peak, 14.77660°N, 121.31623°E, elev. 700 m (FMNH 205420–205431); 1.25 km S, 0.5 km W Mt. Irid peak, 14.78000°N, 121.32116°E, elev. 920 m (FMNH 205431–205435, 205437–205459; 206318–206336); 0.5 km S, 0.1 km W Mt. Irid peak, 14.78659°N, 121.32460°E, elev. 1110 m (FMNH 205460–205475); 0.25 km S, 0.15 km W Mt. Irid peak, 14.78878°N, 121.32479°E, elev. 1330 m (FMNH 205476–205481).

Etymology.—An adjective based on the name of the mountain (Mt. Irid) where the

Table 5.—Cranial, dental, and external measurements (mean + 1 *SD* and range, mm) of *Apomys iridensis*, from Mt. Irid, Rizal Province.

Measurement	*Apomys iridensis* F-Holotype FMNH 205436	M ($n = 7$)	F ($n = 4$)
Basioccipital length	35.01	35.62 ± 1.19	35.47 ± 0.79
	–	34.54–37.61	34.61–36.25
Interorbital breadth	6.53	6.18 ± 0.15	6.35 ± 0.24
	–	5.94–6.38	6.08–6.57
Zygomatic breadth	18.09	18.44 ± 0.60	18.10 ± 0.13
	–	17.58–19.16	17.93–18.24
Mastoid breadth	14.28	14.57 ± 0.32	14.47 ± 0.36
	–	13.91–15.16	14.06–14.82
Nasal length	14.61	14.82 ± 0.59	14.66 ± 0.50
	–	14.17–15.90	13.97–15.05
Incisive foramen length	5.13	5.74 ± 0.51	5.42 ± 0.40
	–	4.88–6.40	5.02–5.82
Rostral depth	8.15	7.91 ± 0.27	7.94 ± 0.18
	–	7.46–8.35	7.79–8.15
Rostral length	15.40	17.72 ± 0.56	15.67 ± 0.44
	–	15.37–16.85	15.27–16.26
Orbito-temporal length	12.51	12.42 ± 0.59	12.29 ± 0.22
	–	11.39–13.13	12.08–12.51
Maxillary toothrow length	7.22	7.72 ± 0.19	7.51 ± 0.24
	–	7.44–7.93	7.22–7.77
Labial palatal breadth at M^1	7.99	7.96 ± 0.24	7.93 ± 0.07
	–	7.57–8.20	7.86–7.99
Diastemal length	9.41	9.36 ± 0.61	9.44 ± 0.45
	–	8.77–10.43	8.84–9.93
Post-palatal length	11.52	11.79 ± 0.41	11.60 ± 0.21
	–	11.21–12.51	11.38–11.88
Lingual palatal breadth at M^3	5.47	5.50 ± 0.27	5.60 ± 0.25
	–	5.18–5.98	5.39–5.95
Braincase height	11.06	10.65 ± 0.19	10.90 ± 0.44
	–	10.49–10.93	10.58–11.45
Breadth of M^1	1.91	2.01 ± 0.06	1.96 ± 0.06
	–	1.92–2.09	1.90–2.02
Breadth of incisors at tip	2.31	2.38 ± 0.09	2.38 ± 0.05
	–	2.25–2.50	2.31–2.42
Width of zygomatic plate	3.65	3.91 ± 0.26	3.76 ± 0.27
	–	3.56–4.30	3.61–4.16
Length of head & body	144	146.1 ± 6.9	142.0 ± 8.4
	–	136–155	134–153
Total length	285	291.4 ± 14.9	289.2 ± 10.6
	–	274–310	282–305
Length of tail vertebrae	141	145.3 ± 9.7	147.2 ± 4.6
	–	132–157	141–152
Length of hind foot	36	37.3 ± 1.7	36.8 ± 0.50
	–	35–40	36–37
Length of ear	21	20.4 ± 1.0	20.5 ± 0.6
	–	19–21	20–21
Weight (g)	92	89.5 ± 10.0	88.5 ± 2.5
	–	76–104 (6)	88–92

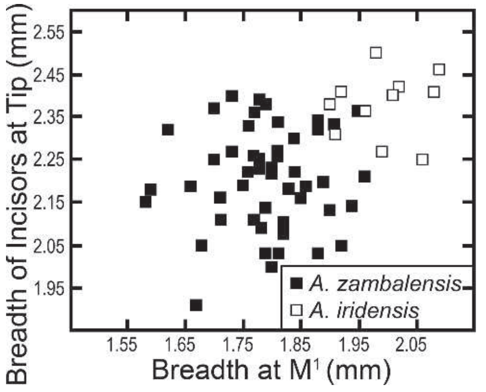

Fig. 9. Bivariate plots of breadth of M^1 vs. breadth of incisors at tip for *Apomys iridensis* and *A. zambalensis*.

species has been documented to occur (Fig. 1).

Diagnosis.—A moderately large species of the genus *Apomys*, subgenus *Megapomys*, basioccipital length of adult males and females averaging 35–36 mm, head and body length 142–146 mm, with a relatively long tail (145–147 mm), broad M^1 (1.9–2.0 mm), short diastema (averaging 9.3–9.5 mm), and short post-palatal region (11.6–11.8 mm; Table 5). The dorsal pelage is dark brown with deep reddish tones, the dorsal surface of the tail is dark brown, and the ventral surface of the hind foot is dark (Fig. 3C). The stapedial foramen is present. Phylogenetic relationships based on DNA sequences are shown in Fig. 2.

Comparisons.—In comparison with *Apomys zambalensis* from the type locality (Mt. Natib), *A. iridensis* has dark brown dorsal pelage rather than golden brown; *A. zambalensis* from Mt. Pinatubo are grayish-brown, as described above. *Apomys iridensis* has ventral pelage that is gray overall, resulting from short white tips on the hairs, with most of the gray base of the hairs clearly evident, and a pale buffy wash barely evident; that of *A. zambalensis* is mostly white with very pale creamy tips. As noted above, *A. iridensis* has, on average, slightly longer tail and shorter ears than *A. zambalensis*, wider M^1 and incisors near their tips, and usually greater interorbital breadth and shorter post-palatal region.

Fig. 10. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of *Apomys iridensis* (holotype, FMNH 205436).

In comparison with *A. aurorae*, a closely-related species that is geographically nearest to *A. iridensis*, the dorsal pelage of *A. iridensis* is very slightly darker, with deep brown tones highlighted with deep red; *A. aurorae* is slightly paler (though still dark brown) with rusty-orange tones. *Apomys iridensis* has more prominently gray ventral pelage due to shorter white tips, allowing the gray bases to be evident; *A. aurorae* is whiter and tends to show more tawny wash. The dorsal surface of the tail and the ventral surface of the hind foot are darker in *A. iridensis*. The dorsal surface of the hind foot of *A. iridensis* is nearly white, with only a few scattered dark hairs; that of *A. aurorae* has many scattered dark hairs, especially in a longitudinal band along the center of the foot. Adult *A. aurorae* are usually 85 g or less, whereas *A. iridensis* are usually 85 g or heavier. *Apomys iridensis* has a slightly longer tail and hind foot than *A. aurorae*. The breadth of incisors near the tip in *A. iridensis* is 2.25 mm or more, whereas that of *A. aurorae* is 2.30 mm or less. The length of nasals of *A. iridensis* is usually 14.3 mm or more, and that of *A. aurorae* is 14.5 mm or less, and the rostral depth of *A. iridensis* is 7.75 mm or more, and that of *A. aurorae* is usually 7.70 mm or less.

Ecology and distribution.—We conducted a survey of the small mammals of Mt. Irid (peak at 1469 m) in June 2009, with intensive sampling centered at 700 m (regenerating lowland forest), 920 m (mature transitional lowland/lower montane forest), 1110 m (mature lower montane forest), and 1330 m (mature montane forest). Detailed results are presented elsewhere (Balete et al. 2013). We captured *Apomys iridensis* at all four localities, with the greatest relative abundance at 920 m, and lowest at 700 m. Overall, *A. iridensis* was the most abundant small mammal on the mountain and occurred syntopically with four other native species of small mammals (*Apomys microdon*, *Bullimus luzonicus*, *Chrotomys mindorensis*, and *Rattus everetti*) and three non-native species (*Suncus murinus*, *Rattus exulans*, and *R. tanezumi*). We captured all specimens of *A. iridensis* but one (of 86) on the ground surface (the other was a short distance above ground on a log), and all but four during the nocturnal/crepuscular portion of the day. They showed no preference between our two baits, fried coconut with peanut butter or live earthworms, suggesting omnivorous feeding habits. We suspect that the species occurs above about 500 m, and most abundantly above 900 m, perhaps throughout the Southern Sierra Madre as represented by the mountainous area (above 500 m) associated with Mt. Irid (Fig. 1). Further surveys are needed to test this hypothesis.

Discussion

The discovery of two previously unknown species of *Apomys* further highlights the unusually high mammalian diversity on Luzon and adjacent islands. The evidence of their membership in a diverse clade endemic to this region lays further groundwork for a comprehensive understanding of the in situ generation of endemic mammals in this exceptionally biodiverse area. For both Lubang Island and Mt. Irid, no locally endemic mammal species had been recorded previously, and these new species thus establish these areas as localized centers of mammalian endemism, emphasizing the small geographic scale by which biodiversity is partitioned in the Luzon region. Mt. Irid and the Southern Sierra Madre are isolated from other mountainous areas on Luzon by lowlands below 200 m elevation, which has previously been shown to form a significant barrier to the presence of these montane mice (Heaney et al. 2011, Justiniano et al. 2014). Lubang Island is still more isolated, since depths to Luzon and Mindoro exceed the levels to which sea level dropped during the Pleistocene, thus establishing Lubang and several smaller, nearby islands as a small but distinct set of oceanic islands.

The presence of *Apomys sacobianus* over a range of elevations on Mt. Pinatubo shows it to be resilient in the presence of massive habitat disturbance. Together with the ability of *A. lubangensis* and *A. iridensis* to persist in regenerating forest as well as mature forest, these data imply a capacity to tolerate a moderate to great level of both natural and anthropogenic forest disturbance, as also shown in recent studies of *Apomys* in the Central Cordillera of northern Luzon (Rickart et al.

2011b). Our species descriptions highlight the need for additional field and museum-based study of the mammals of Luzon and the Philippines, where discovery of previously unknown genera and species continues (e.g., Heaney et al. 2009, 2011, Balete et al. 2012), underscoring the Philippine archipelago as a foremost region for biodiversity research.

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