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ZOOTAXA

A re-assessment of diversity among Philippine gymnures (Mammalia: Erinaceidae: *Podogymnura*), with a new species from eastern Mindanao

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Abstract

Podogymnura, a Philippine endemic genus of gymnures ("soft-furred hedgehogs"), has been known previously only from the highlands of central Mindanao (*P. truei truei* and *P. t. minima*) and from two small islands off the northeast tip of Mindanao (*P. aureospinula*). Based on a combination of mitochondrial genetic and qualitative and quantitative morphological data, we recognize *P. minima*, formerly considered a subspecies of *P. truei*, as a distinct species. We also recognize specimens from two little-studied montane regions of southeastern Mindanao, Mt. Hamiguitan and Mt. Kampalili, as a distinctive new species, *P. intermedia* n. sp. We estimate that dispersal of a common ancestor from Borneo to Mindanao ca. 1.9 to 3.5 Ma gave rise to *Podogymnura*, followed by speciation within Mindanao beginning 0.53 to 0.97 Ma. These results further increase the rich diversity of mammals on Mindanao, and underscore the importance of the eastern Mindanao highlands as a likely important but little-studied center of Philippine mammalian diversity.

Key words: biodiversity, biogeography, ecology, endemism, Hamiguitan, hedgehog, Kampalili, montane forest, phylogeny, speciation

Introduction

Gymnures (Erinaceidae: Galericinae) surely rank highly for their distinctiveness among Southeast Asian mammals. They are the closest living relatives of the spiny hedgehogs (Erinaceinae), but are characterized by pelage that ranges from soft to bristly and a more gracile body form compared to hedgehogs. Extant gymnures range over tropical, subtropical, and southernmost temperate (to 32° N) regions in Southeast Asia, but their fossil record from the early Eocene to Pliocene indicates a much broader global distribution, with records from North America, Europe, and much of Asia (Ostende 2001; Lopatin 2006; Bannikova *et al*. 2014).

Of the five living genera (He *et al*. 2012), *Podogymnura* is found only in the Philippines, where it is confined to Mindanao and two adjacent small islands (Fig. 1; Heaney *et al*. 2010). These Philippine gymnures are most closely allied to the moonrat, *Echinosorex,* of Borneo, Sumatra, and the Malay Peninsula, and this sister relationship is strongly supported by morphological and molecular evidence; this clade, in turn, is sister to a clade containing *Hylomys*, *Neohylomys*, and *Neotetracus* (Frost *et al*. 1991; He *et al*. 2012). A molecular phylogenetic analysis showed gymnures to represent an ancient lineage with recent diversification; the clade composed of *Echinosorex*

and *Podogymnura* showed the most recent divergence within Galericinae, estimated to have begun around the mid-Pliocene, ca. 4 MYA (Bannikova *et al.* 2014).

When we began this study, only two species of *Podogymnura* were recognized. *Podogymnura truei* Mearns, 1905, of relatively small size and with dark pelage, was first found on Mt. Apo in south-central Mindanao Island (Fig. 1). Gymnures from Mt. Kitanglad in central Mindanao were subsequently described as a subspecies, *P. truei minima* Sanborn, 1953, based on their slightly smaller body size. Some subsequent studies questioned this distinction, commenting that morphological differences were subtle (e.g., Heaney & Morgan 1982; Poduschka & Poduschka 1985; Corbet & Hill 1992; Heaney *et al.* 1998, 2006, 2010; Hutterer 2005). A second species, *P. aureospinula* Heaney & Morgan, 1982, known from two islands (Dinagat and Bucas Grande; Fig. 1) that lie off the northeast tip of Mindanao, is substantially larger and generally more robust, with pelage that contains golden semi-spinous hairs, as discussed below.
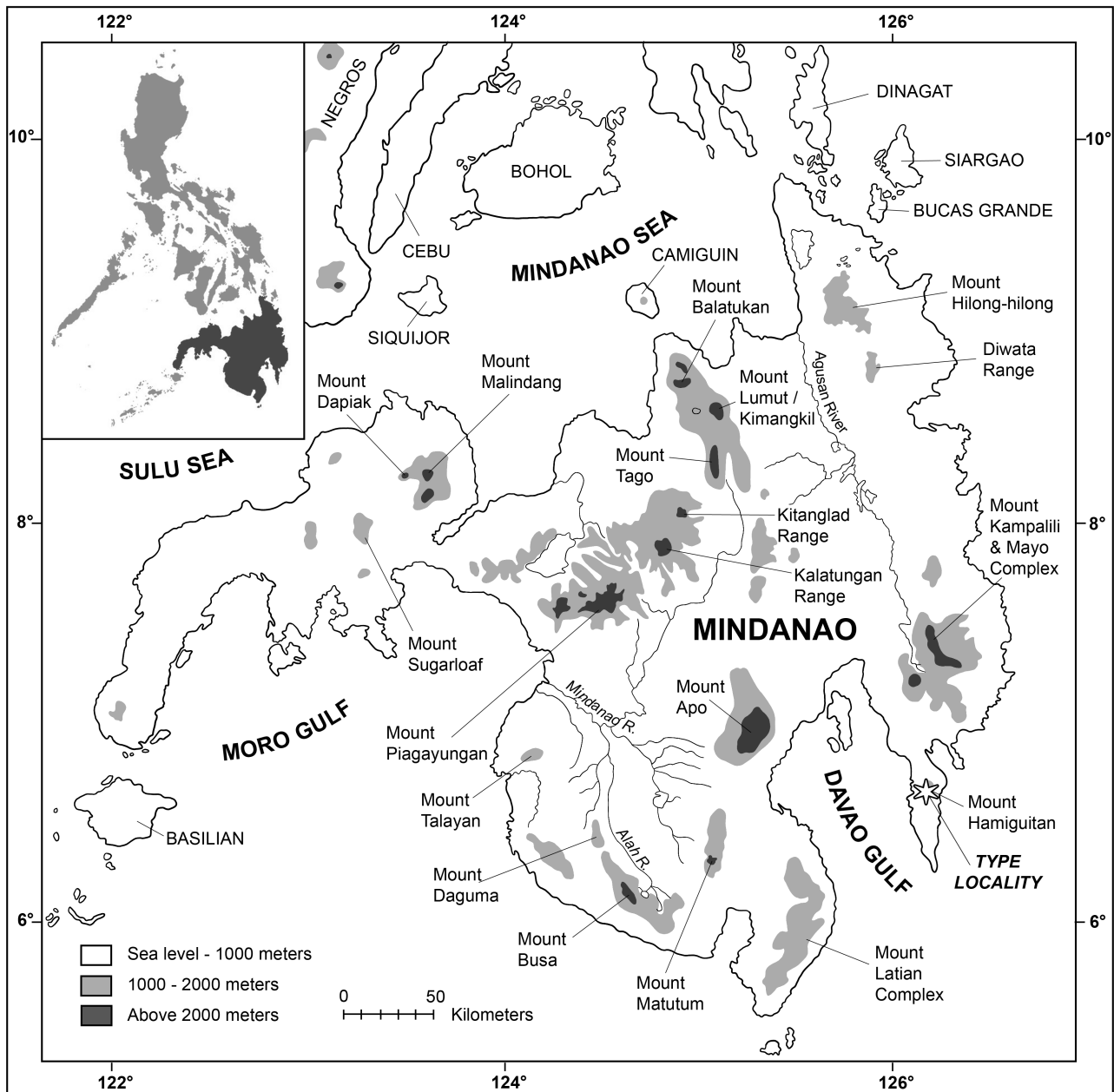
FIGURE 1. Map of Mindanao and adjacent islands showing some major topographic features; mountains where *Podogymnura truei* (Mt. Apo), *P. minima* (Mt. Kitanglad Range), *P. aureospinula* (Bucas Grande and Dinagat Islands), and *P. intermedia* n. sp. (Mt. Hamiguitan and Mt. Kampalili) occur, and other important peaks, are shown.

Following mammal surveys in isolated montane regions on Luzon Island that produced evidence of many previously unknown centers of mammalian endemism with ca. 28 new species of mammals (Heaney *et al*. 2016a, 2016b), we initiated similar field-based surveys in highland regions of Mindanao. During a mammal survey in 2005 on Mt. Hamiguitan, an isolated peak in southeastern Mindanao (Fig. 1), we documented an endemic mammal, *Batomys hamiguitan* (Balete *et al*. 2006, 2008), and also obtained specimens of *Podogymnura* that were intermediate in size between P. *truei* and *P. aureospinula*, with conspicuous gold highlights in the dorsal pelage. Our field surveys in 2007 and 2010 on Mt. Kampalili, a second isolated mountain peak in southeastern Mindanao (Fig. 1), produced similar *Podogymnura*, also with gold highlights in the pelage but smaller and shorter-tailed. These specimens have enabled us to conduct a molecular phylogenetic analysis of *Podogymnura* from multiple localities and to more rigorously assess morphological variation within the genus. Our results demonstrate a small radiation of gymnures in the Philippines, and we discuss here the taxonomic implications of these findings. Our results also have implications for the biogeography of mammalian endemism and the extent of mammalian diversity on Mindanao, a large (ca. 98,000 km^2) oceanic island whose mammalian fauna has been insufficiently studied.

Material and Methods

Specimens of *Podogymnura* examined for this study are listed in Appendix I and in the descriptions of the new species. Except for *P. aureospinula*, all specimens are currently housed at the Field Museum of Natural History, Chicago (FMNH), but half of the specimens of the new species, including the holotype, will be returned to the Philippine National Museum. *P. aureospinula* was represented in morphometric analysis by a specimen from the University of the Philippines at Los Banos (UPLB) and a tissue sample from a specimen housed at the Museum of Natural History, University of Kansas (KU). We also include external measurements from Heaney & Morgan (1982) of the holotype of *P. aureospinula*, housed at the Delaware Museum of Natural History (DMNH). Specimens of *P. aureospinula* and *P. t. truei* were prepared as study skins with cleaned skulls. Specimens of *P. intermedia* n. sp. and *P. t. minima* had muscle tissue sampled from the left thigh of all fresh, intact specimens and preserved in 95% ethanol; most bodies were then fixed in formalin but subsequently transferred to 70% ethanol (some with skulls subsequently removed and cleaned), but several *P. t. minima* were prepared as complete skeletons. We followed all relevant Philippine laws and regulations in the capture and handling of animals in the field.

Molecular analyses

Two mitochondrial DNA markers were sequenced for use in molecular phylogenetic analyses. In general, extraction, PCR amplifications and reamplifications, post-amplification clean-up, sequencing, and sequence-editing protocols for both fresh and historic samples followed those outlined in Roberts *et al*. (2011). Lab work was conducted in either the University of Alaska Museum's (UAM) dedicated ancient DNA extraction facility and associated downstream labs as described in Roberts *et al*. (2011) or the Pritzker Laboratory for Molecular Systematics and Evolution at FMNH. For specimens associated with fresh-frozen or ethanol-preserved tissues, we amplified and sequenced either the complete cytochrome b (CYTB) gene (1,140 bp) or two overlapping fragments thereof. For degraded historic samples, we amplified and sequenced either portions or the entirety of CYTB in up to seven overlapping fragments from toepads of four specimens of *P. t. truei*. In addition to CYTB, we amplified and sequenced a ca. 390-bp region of the 12S rRNA (12S) gene. A list of all primers used and the amplification and sequencing strategies employed for each specimen can be found in Supporting Information File 1. Resulting sequences were aligned using MUSCLE (Edgar 2004), with additional adjustments made by eye for the 12S sequences with reference to the secondary structure model for the mammalian 12S rRNA molecule (Springer & Douzery 1996), resulting in a final alignment of 1140 bp for CYTB and 391 bp for 12S, including inferred insertion-deletion events (indels). The alignment, which consisted of 17 specimens of Philippine *Podogymnura* and one specimen of *Echinosorex gymnura* to root the phylogeny, was then concatenated and seven alignment-ambiguous positions of 12S were excluded from all subsequent analyses. The annotated concatenated alignment of the two markers has been deposited in Zenodo (DOI: 10.5281/zenodo.7335947) and all newly generated sequences have been deposited in GenBank (12S: OP856727-OP856740; CYTB: OP846571-OP846587).

We used PartitionFinder v 1.2.2 (Lanfear *et al*. 2012) to identify the best-fit scheme of nucleotide substitution models and identify differences in substitution rates between the loci. For the Maximum Likelihood workflow,

we specified candidate partitions for every codon position of CYTB, each following a general time-reversible model with gamma-distributed rate heterogeneity (GTR+Γ; Gu *et al.* 1995) according to the model implemented in RAxML (Stamatakis *et al.* 2008). For the Bayesian analysis, we specified candidate partitions according to each locus under the suite of models implemented in BEAST2 (Bouckaert *et al.* 2014). The results of the nucleotide substitution model partitioning analysis can be found in Supporting Information File 2.

The 1531-bp alignment was analyzed using maximum likelihood and Bayesian inference approaches using RAxML v 8.2.12 (Stamatakis *et al.* 2008) and BEAST v 2.6.0 (Bouckaert *et al.* 2014) as implemented on the CIPRES Science Gateway (Miller *et al.* 2010). For the maximum-likelihood analysis, we conducted a tree search using ten random starting trees and assessed nodal support by generating 1000 bootstrap pseudoreplicates. For the Bayesian inference of phylogenetic relationships, we used BEAST v 2.6.0 to estimate the timing of divergence among *Podogymnura* taxa, where both loci were modeled under separate TN93+Γ models parameterizing two transition rates and a single transversion rate (Tamura & Nei 1993). We specified a strict molecular clock for this dataset, an exponential lineage birth rate prior with an initial value of 1.0, and a uniform prior for the node age of the most recent common ancestor of *Podogymnura* and *Echinosorex* between 1.5 and 7.7 Ma, a secondary calibration point based on the age of the node inferred by Bannikova *et al.* (2014). All other priors were assigned default values. We ran the analysis for 1.0×10^8 generations, storing trees every 2.0×10^4 generations. We analyzed convergence of all parameters, defined as an estimated sum of squares (ESS) $\geq$ 200, using Tracer v 1.6 (Rambaut *et al.* 2013). We then generated a maximum clade credibility (MCC) tree from the resulting distribution of 5000 trees using TreeAnnotator v 2.6.0 (Bouckaert *et al.* 2014), discarding 10% of the tree distribution as burn-in and specifying MCC node heights as the median height from the posterior tree distribution. All trees were rooted with *Echinosorex gymnura* (GenBank accession AF348079) as the outgroup.

Morphological analyses.

Specimens were assigned to age categories based on relative closure of basicranial sutures and molar tooth wear. Terminology for external features of the head and limbs follows Brown (1971) and Brown & Yalden (1973). Terminology for cranial and dental features follows Szalay (1969) and Heaney & Morgan (1982). Scanning electron micrographs of teeth were made from uncoated specimens. Measurements (in millimeters) of total length (TOT), length of tail vertebrae (TV), length of hind foot including claws (HF), and length of ear from notch (EAR), and weight in grams (WT) were taken from field catalogs of the authors and collectors in earlier expeditions or from skin labels of voucher specimens at FMNH. The length of head and body (HB) was determined by subtracting length of tail from total length.

Twenty cranial, dental, and mandibular measurements were taken from 30 adult specimens of *Podogymnura*, measured by Heaney over a period of four days and recorded to the nearest 0.01 mm using digital calipers, defined as follows. Condylo-incisive length (CIL), anterior-most point of incisors to posterior edge of occipital condyles; interorbital breadth (IB), least width between orbits; depth of zygomatic plate (DZP), dorso-ventral depth taken from ventral process of plate to nearest point on dorsal surface; breadth of braincase (BBC), taken as greatest width; height of braincase (HBC), from basicranial plane to highest point on midline of braincase; length of rostrum (LR), from posterior termination of orbital canal (inside orbit) to anterior edge of nasal bones at midline; breadth of rostrum (BR), at posterior edge of upper canines; lacrimal breadth (BL), taken in notch at ventral edge of lacrimal bones, just above base of zygomatic arches; mastoid breadth (MB), taken as greatest width; palatal length (PL), from anteriormost point on palate between first upper incisors to posterior edge of palate, not including a palatal spine if present; post-palatal length (PPL), from posterior edge of palate (not including a palatal spine if present) to anteriormost point in foramen magnum; posterior breadth of palate (PB) at posterior palatal ridge; length of upper toothrow (LI^1 – M^3), taken at alveolar margins; length of maxillary molariform toothrow (LP^4–M^3), taken at anterior and posterior alveolar margins; palatal breadth at M3 (PBM^3), taken between lingual edges of molars at alveolus; palatal breadth across the second molars (M^2–M^2), taken at alveoli on labial edges of molars; length of mandible plus lower incisor (LMI), taken from anteriormost margin of lower incisors to line formed by posteriormost points of condyle and angular process; height of coronoid process (HCP), taken from line formed by ventral edges of angular process and main shaft of mandible to anteriormost point on coronoid process; height of mandible (HM), taken from anterior edge of mandible between fourth lower premolar and first lower molar to nearest point on ventral edge of mandible; thickness of mandible (TM), at anterior edge of first lower molar from medial to lateral edge of mandible. We did not measure zygomatic breadth because the zygoma had been broken on many specimens.

Descriptive statistics (mean, standard deviation, and observed range) were calculated for sample groups using spreadsheet software. We used SYSTAT 10 for Windows (SPSS, Inc. 2000) to assess quantitative phenetic variation through principal component analysis (PCA), using the correlation matrix of $\log_{10}$-transformed craniodental measurements of adult specimens. As described below, we conducted three PCA analyses, the first with all specimens from which we obtained a full set of measurements, the second that excluded the specimen of *P. aureospinula* but otherwise included the same specimens, and a third that excluded *P. aureospinula* and included only specimens that had 15 of the 20 craniodental measurements (excluding CIL, BBC, HBC, MB, PPL), which allowed us to include one complete young adult and one damaged full adult from Mt. Hamiguitan.

Ecological data

Descriptions of habitats used by specimens from Mts. Hamiguitan, Kampalili, and Kitanglad were taken from field notes written by the authors at the time of capture of the specimens; these notes are available in the Division of Mammals archive at FMNH. Stomach contents were analysed in the field for specimens prepared as skeletons and in the laboratory for specimens initially fixed in formalin and subsequently preserved in 70% ethanol. Reproduction was assessed in the field for specimens prepared as skeletons or in the laboratory on fluid-preserved specimens. For males, the testes were scored in the field for position (scrotal or abdominal) and size (length x width, in mm). We examined females for the size and condition of teats (small, large, or lactating), and the number and size of embryos and number of placental scars in the uterus, in the field and in the museum using fluid-preserved specimens.

Results

We took a step-wise approach to analyzing patterns of variation and the extent of divergence in *Podogymnura*, proceeding cautiously because of small sample sizes for some of the five geographic samples. We first considered variation in mitochondrial DNA to define phylogenetic relationships of the five samples. We then focused our morphological analyses on patterns of variation and divergence within the clades defined by phylogenetic analyses.

Molecular phylogeny

For the maximum-likelihood nucleotide substitution model selection, we recovered a two-partition model including 12S rRNA and the first codon position of CYTB for the first partition and the second and third positions of CYTB for the second (lnL: -3669; BIC: 7793; *k*: 62). For the Bayesian substitution model selection procedure, the best-fit model partitioned each locus under a separate substitution model, with 12S rRNA best supporting a TrN+I+X model and CYTB best supporting a TRN+Γ+X model (lnL: -3906; BIC: 8172; *k*: 49). Raw (uncorrected) sequence divergences were greater than 5% between all putative species except between *P. aureospinula* and *P. intermedia* n. sp. (Supporting Information File 3).

Our ML and Bayesian analyses of the combined-gene alignment (Fig. 2, Supporting Information File 4) yielded an identical topology, with *Podogymnura* recovered as sister to and deeply divergent from *Echinosorex gymnura*. Within the genus, two major clades were recovered. One clade unites all specimens from Mt. Kitanglad and Mt. Apo with moderate bootstrap support (BS: 79; Fig. 2) and strong posterior probability support (PP: 1.0). Within this clade, we recovered strong support for the reciprocal monophyly of the populations from each mountain (BS: 87%; PP: 1.0%; BS: 98%; PP: 1.0 for *P. t. truei* and *P. t. minima* respectively; Fig. 2). The second major clade includes *P. aureospinula* from Dinagat Island as sister to the populations of *P. intermedia* n. sp. from Mts. Hamiguitan and Kampalili, with strong support from the Bayesian analysis but only weak support from the ML analysis (63% BS, 1.0 PP ; Fig. 2). Specimens from Mt. Hamiguitan and Mt. Kampalili are well supported in the Bayesian analysis as monophyletic and moderately supported in the maximum likelihood analysis (BS: 79%; PP: 1.0; Fig. 2). Interestingly, we do not recover reciprocal monophyly of the populations from Mt. Hamiguitan and Mt. Kampalili, instead recovering one specimen from Mt. Hamiguitan as sister to the remaining specimens but with weak PP support and moderate BS support (BS: 71%; PP: 0.93; Fig. 2). Support within the remaining specimens of *P. intermedia* n. sp. is variable but roughly correspond to mountain provenance.

Node age estimates for the stem and crown ages of *Podogymnura* based on the root calibration derived from Bannikova *et al*. (2014) show age estimates skewed toward the present, with median ages of 2.52 and 0.66 Ma respectively (Fig. 3 and Supporting Information File 4). The distributions of node ages are broad but with long tails:

the range of the stem age estimate spans the entire range of the prior on the root age of the node1 (0.50 to 7.70 Ma), but the 50% highest posterior density (HPD) interval spans 1.95 to 3.56 Ma. Similarly, the crown age estimate for *Podogymnura* spans 0.25 to 2.46 Ma, and the 50% HPD spans 0.50 to 0.92 Ma (Fig. 3 and Supporting Information File 4).
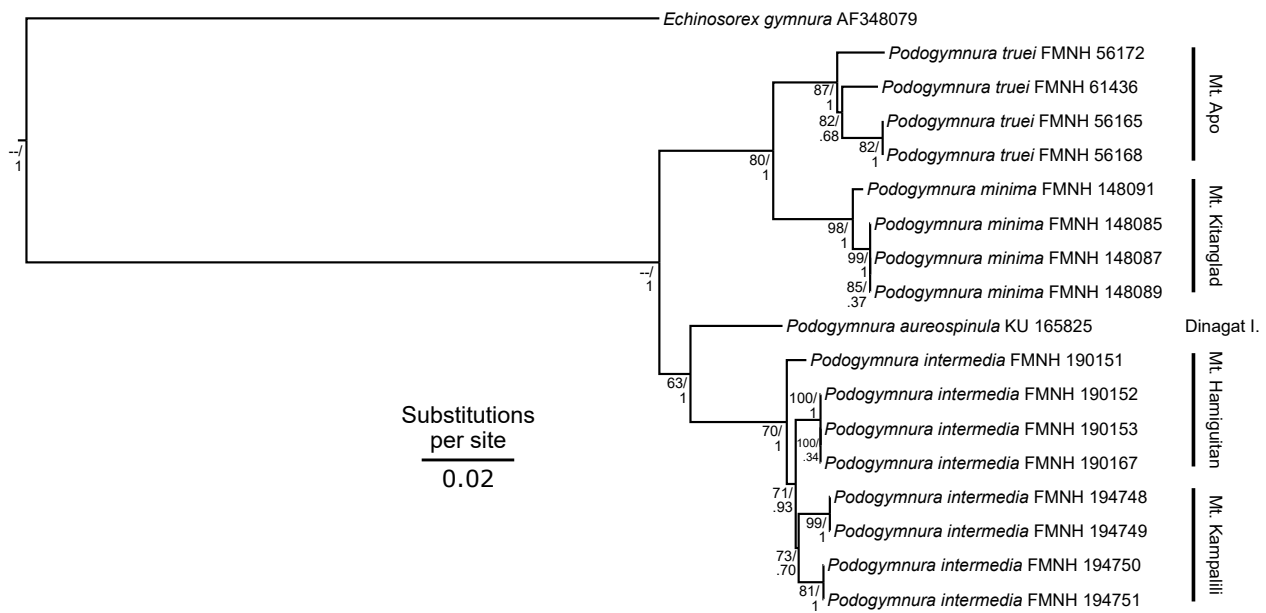

FIGURE 2. Maximum-likelihood topology inferred using RAxML. Branches are scaled in proportion to relative timing of divergence. Numbers at nodes represent bootstrap support and posterior probability (PP) and are given in the form BS/PP. Nodes with dashed BS values reflect manual rooting of the tree in the RAxML analysis.
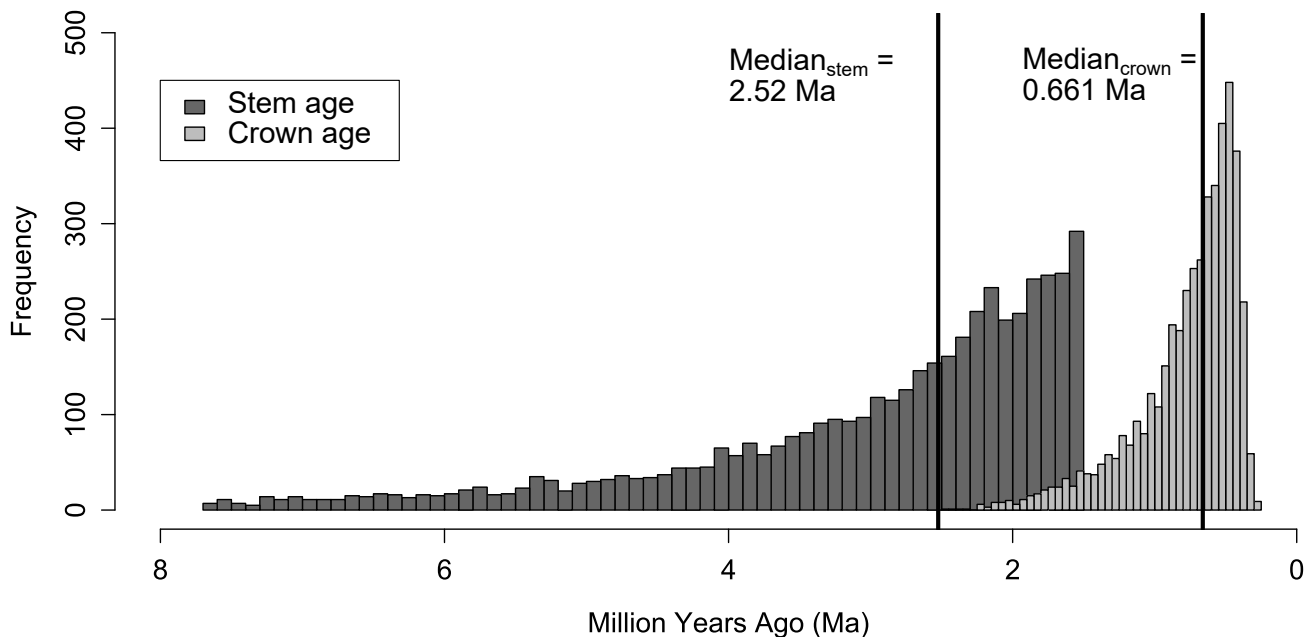
FIGURE 3. Histogram of node age estimates derived from posterior tree distribution of BEAST analysis for the stem (split between *Podogymnura* and *Echinosorex*) and crown (split between *P. truei* + *P. minima* and *P. aureospinula* + *P. intermedia*) nodes of *Podogymnura*. Median node age estimates are given with a solid line.

Overall, this molecular phylogeny shows specimens from Hamiguitan and Kampalili as lacking reciprocal monophyly, and we accept that as evidence that they should be treated as a single species. Based on this, the following qualitative assessments and morphological analyses treat specimens from Hamiguitan and Kampalili as a single species. Given the evidence of reciprocal monophyly of populations from Mt. Apo (*P. t. truei*) and Mt. Kitanglad (*P. t. minima*), we also consider whether they should be recognized as representing one or two species.
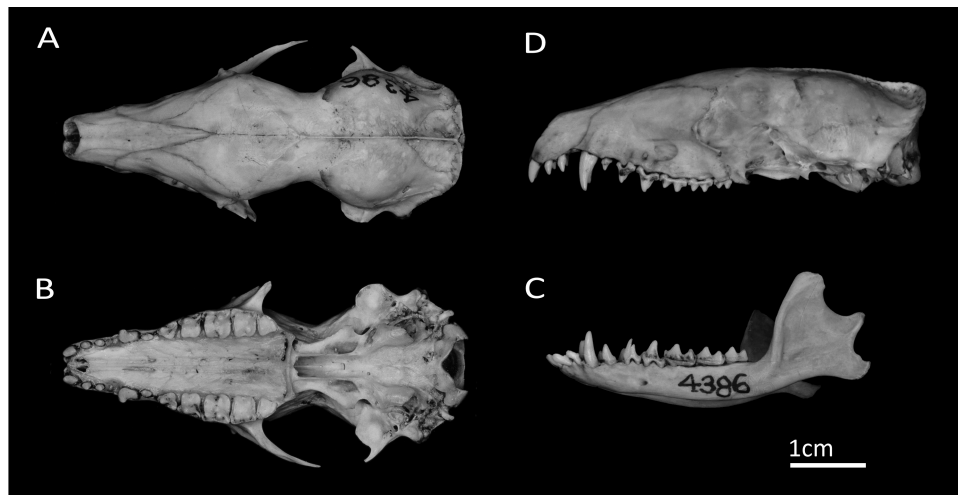
FIGURE 4. Photographs of skull of *Podogymnura aureospinula*, holotype, DMNH 4386, approximately life size. Adapted from Heaney & Morgan 1982.

External characters

Each of the five geographic samples can be distinguished externally from all others; further details are provided in the descriptions that follow. We follow the results of the molecular phylogenetic analyses, above, as providing the framework for morphological comparisons. *Podogymnura aureospinula* differs externally from the other four samples in its large size (HB = 201 mm) and dorsal pelage made up largely of semi-spinous, golden-yellow guard hairs. Specimens from Mts. Hamiguitan and Kampalili share this pelage color to a lesser degree: they have brown dorsal pelage that contains both long black guard hairs and long golden-yellow guard hairs that produce a golden-streaked (Hamiguitan) or golden-speckled (Kampalili) appearance, although the dorsal pelage of specimens from Hamiguitan is coarser and darker than pelage of specimens from Kampalili. Their hind feet and tails are pigmented pale (Kampalili) or dark (Hamiguitan) brown. Specimens from Mt. Hamiguitan are conspicuously larger (HB = 171 mm, weight 96 g; Table 1) than those from Mt. Kampalili (HB = 145 mm, weight 77 g).

Specimens from Mt. Apo (*P. t. truei*) and Mt. Kitanglad (*P. t. minima*) are of similar and overlapping HB length (148 vs. 145 mm), but *P. t. truei* specimens have soft dorsal pelage that is dark brown with small, inconspicuous speckles of golden-brown at the tips, and a tail that is dark brown dorsally and ventrally. *P. t. minima* has reddish-brown dorsal pelage with golden-brown speckles at the tips that are more conspicuous than those of *P. t. truei* but are much darker and smaller than those of specimens from Mts. Hamiguitan or Kampalili, and tail and feet that are pale and unpigmented.

Qualitative cranial comparisons.

Examination of the skulls of *Podogymnura* shows that *P. aureospinula* is the most readily distinguished, characterized by substantially larger size than the others, well-developed cranial crests, broad and inflated frontal region, and relatively narrow interorbital region (Fig. 4). Although there is substantial overlap among the small-bodied populations of *Podogymnura* on many cranio-dental variables (Table 2), many differences are visually apparent. Specimens from Mt. Hamiguitan are largest and most robust in all respects, with broader molars, a broader and deeper rostrum, deeper and more conspicuous anterior palatal grooves, inflated frontal region, wider interorbital region, more expanded and globose braincase (especially evident in the posterior portion of the braincase), and more prominent sagittal and nuchal crests (Fig. 5). Additionally, these specimens have a long post-palatal region. Specimens from Hamiguitan share with *P. aureospinula* and specimens from Kampalili the presence of paired depressions in the basioccipital on either side of a medial ridge between the bullae; these depressions are absent in *P. t. truei* and *P. t. minima*. However, with the exceptions of the longer post-palatal region in the Hamiguitan population and the shared depressions in the basioccipital, all of these traits are less well developed in specimens from Mt. Kampalili compared to specimens from Mt. Hamiguitan. Specimens from Mt. Apo (*P. t. truei*) and Mt. Kitanglad (*P. t. minima*) are progressively even less robustly developed, with narrower molars, narrower rostrum, less inflated frontal region, narrower interorbital region, shallower palatal grooves, less expanded braincase, and lower sagittal and nuchal crests (Fig. 5). These observations imply a possible role for allometry in most or all of these characters.
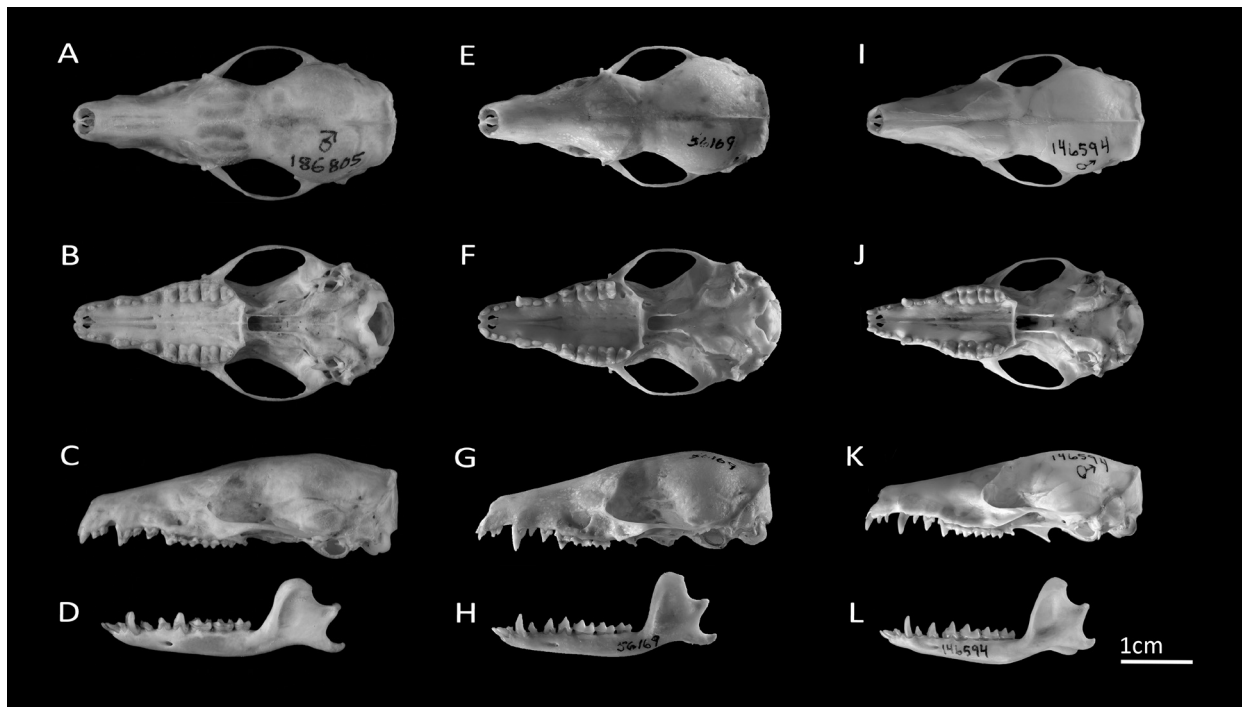
FIGURE 5. Photographs of skulls of *Podogymnura intermedia* (holotype, FMNH 186805, A-D), *P. truei* (FMNH 56169, E-H), and *P. minima* (FMNH 146594; I-L). All skulls approximately life size.

TABLE 1. External measurements (mm), weight (g) and measurement ratios (%) of adult *Podogymnura*, including new species from eastern Mindanao. Measurements of sample size (*n*) greater than 3 are given as mean ± 1 SD and their ranges; as average, for sample size of 3 or less. Sample size less than *n* is indicated in parentheses after the range.

	Podogymnura aureospinula	*Podogymnura intermedia* Mt. Hamiguitan		*Podogymnura intermedia* Mt. Kampalili	*Podogymnura minima*	*Podogymnura truei*
	n = 2[a]	Holotype	*n* = 3[b]	*n* = 8[c]	*n* = 8[d]	*n* = 12[e]
HB	201 190 – 211	157	171 157 – 185	145± 5.6 140 – 149 (7)	145 ± 5.6 137 – 152	148 ± 6.6 138 – 157
TV	66 59 – 73	53	54 53 – 55 (2)	53± 3.4 46 – 54 (7)	54 ± 5.4 49 – 66	56 ± 6.3 47 – 65
HF	41 39 – 42	35	36 35 – 37	34 ± 0.8 33 – 35	34 ± 1.2 33 – 37	34 ± 1.4 33 – 37
EAR	24 22 – 26	20	20 19 – 20	20 ± 0.4 20 – 22	21 ± 0.8 20 – 22	22 ± 1.3 21 – 24
WT	-	96	96 (1)	77± 6.1 70 – 88 (7)	74 ± 6.1 63 – 79	-
TV/HB	33 31 – 35	34	32 30 – 34 (2)	37 35 – 39 (7)	36 33 – 38	38 31 – 42
HF/HB	20 20	22	21 20 – 22	23 23 – 24 (7)	23 22 – 24	23 21 – 24

[a]DMNH 4386, UPLB 3753
[b]FMNH 186805 (holotype), 190152, 190153
[c]FMNH 194750, 194751, 194752, 208699-208702, 208705
[d]FMNH 146591, 146592, 146593, 148071, 148077, 148078, 148081, 148085
[e]FMNH 56165, 56168, 56172, 56190, 56191, 56192, 61436, 61448, 61449, 61453, 61457, 61459

Some of these observable differences are apparent in a plot of condylo-incisive length vs. breadth of braincase (Fig. 6A). The genetically-defined clade from Mts. Hamiguitan and Kampalili shows two groups with no apparent overlap, with four adults from Kampalili having CIL less than 42 mm and the young adult from Mt. Hamiguitan about 43.4 mm; the full adult from Mt. Hamiguitan would likely have had a CIL ≥ 45 mm, and there was no overlap in breadth of braincase. With the exception of one individual each from *P. t. truei* and *P. t. minima,* all individuals of these species occupy different areas of morphospace. Even *P. t. truei* and specimens from Kampalili, which overlap in the PCA plot discussed below (Fig. 6B), do not overlap in Fig. 6A, though they come into close contact for several specimens.
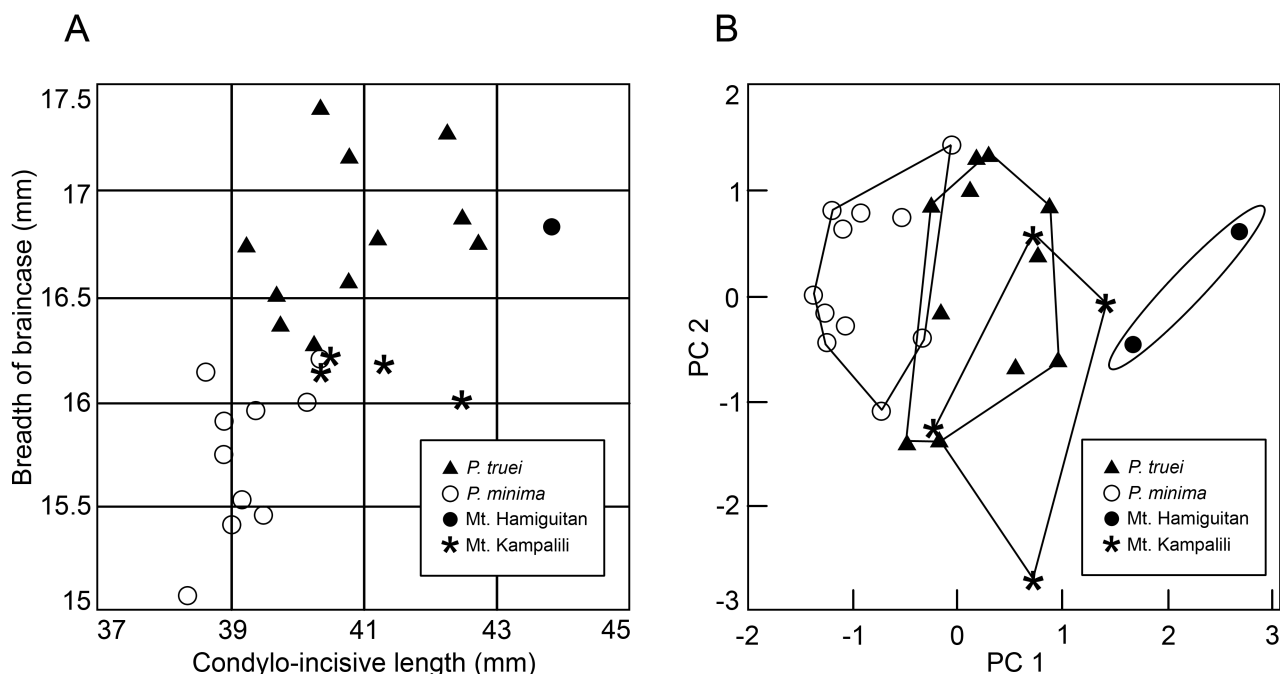
FIGURE 6. A. Bivariate plot of condylo-incisive length (CIL) and breadth of braincase (BBC) measurements comparing *Podogymnura truei*, *P. minima*, and *P. intermedia* n. sp. B. Results from the Principal Component Analysis of four small species of *Podogymnura* (excluding *P. aureospinula*) based on 15 cranial, dental, and mandibular measurements (see text).

We conclude that cranial features of specimens from Mts. Apo and Kitanglad subtly differ from one another, consistent with our molecular results. We also conclude that the crania of populations from Mts. Hamiguitan and Kampalili share some traits with *P. aureospinula*, similarly consistent with our molecular results. However, we found that crania of populations from Mts. Hamiguitan and Kampalili can be distinguished from each other; this finding of a morphological difference is not congruent with our molecular results and clearly indicates the need for further study, as discussed below.

Principal component analyses of craniodental measurements

We further assessed morphological variation in the five geographically defined populations through PCA, using measurements summarized in Table 2. We first conducted an analysis that included individuals from all five populations. The results produced two axes with eigenvalues above 1.0. The first axis accounted for 74.8% of the total variation; all variables loaded heavily (from 0.747 to 0.964), indicating that most of the variation is in overall size. The second axis accounted for only 5.2% additional variation. A plot of the results (not shown) showed *P. aureospinula* at one side of the graph along the first axis, and the four other populations compressed together against the opposite side, clearly resulting from the substantial difference in size between the large *P. aureospinula* and the other four geographic groups, thus producing little informative results beyond emphasizing the distinctiveness of *P. aureospinula*.

TABLE 2. Cranial and dental measurements (mm) of adult *Podogymnura* from Dinagat and Mindanao Islands, including the new species from eastern Mindanao. Measurements of sample size (*n*) greater than 3 are given as mean ± 1 SD and their ranges; as average for sample sizes less than 3. Sample size less than *n* shown in parentheses after the range.

	Podogymnura aureospinula [a]	*Podogymnura intermedia* n. sp.[b] Mt. Hamiguitan		*Podogymnura intermedia* n. sp.[c] Mt. Kampalili	*Podogymnura minima* [d]	*Podogymnura truei* [e]
	n = 1	Holotype	*n* = 2	*n* = 4	*n* = 12	*n* = 11
CIL	51.99	43.35	43.35 (1)	40.6 ± 0.98 39.77 – 41.92	38.6 ± 0.77 37.28 – 39.78	40.3 ± 1.19 38.70 – 42.18
IB	11.16	10.12	10.3 10.12 – 10.47	9.6 ± 0.06 9.60 – 9.74	9.4 ± 0.19 9.02 – 9.62	9.7 ± 0.25 9.26 – 10.03
BZP	4.56	2.89	2.8 2.82 – 2.89	2.7 ± 0.32 2.30 – 3.01	2.6 ± 0.20 2.33 – 2.91	2.8 ± 0.23 2.37 – 3.22
BBC	18.71	16.83	16.83 (1)	16.1 ± 0.10 15.98 – 16.21	15.7 ± 0.39 15.06 – 16.22 (11)	16.8 ± 0.37 16.25 – 17.39
HBC	14.41	11.66	11.66 (1)	11.5 ± 0.30 11.11 – 11.82	11.2 ± 0.33 10.77 – 11.74	11.6 ± 0.53 11.04 – 12.65
LR	21.68	17.87	17.8 17.82 – 17.87	17.2 ± 0.85 16.52 – 18.44	16.5 ± 0.63 15.66 – 17.57	16.8 ± 0.69 16.19 – 18.25
BR	9.27	7.29	7.4 7.29 – 7.50	6.9 ± 0.38 6.39 – 7.29	6.6 ± 0.15 6.24 – 6.74	7.0 ± 0.18 6.65 – 7.19
BL	19.17	13.10	13.4 13.10 – 13.69	12.5 ± 0.80 11.71 – 13.43	12.6 ± 0.46 12.00 – 13.37	13.0 ± 0.46 12.33 – 13.60
MB	20.07	17.03	17.03 (1)	16.0 ± 0.24 15.72 – 16.30	15.2 ± 0.41 14.56 – 15.81	16.2 ± 0.53 15.57 – 17.34
PL	29.22	23.33	23.5 23.33 – 23.76	22.7 ± 0.62 21.99 – 23.48	20.6 ± 0.76 19.45 – 22.03	22.0 ± 0.68 21.39 – 23.03
PPL	18.39	16.47	16.47 (1)	14.7 ± 0.56 14.10 – 15.27	14.8 ± 0.38 13.95 – 15.58	15.1 ± 0.44 14.42 – 15.91
PB	8.28	6.46	7.0 6.46 – 7.55	6.9 ± 0.22 6.69 – 7.20	6.6 ± 0.24 6.13 – 6.95	6.7 ± 0.27 6.37 – 7.17
$LI^1 – M^3$	26.54	21.74	22.2 21.74 – 22.66	21.1 ± 0.62 20.30 – 21.80	19.6 ± 0.66 18.71 – 21.06	20.5 ± 0.68 19.36 – 21.62
$LP^4 – M^3$	12.68	10.35	10.6 10.35 – 10.87	9.6 ± 0.10 9.47 – 9.72	9.0 ± 0.18 8.63 – 9.22	9.4 ± 0.30 8.96 – 9.98
PBM^3	8.06	6.58	6.9 6.58 – 7.29	6.4 ± 0.33 5.99 – 6.79	6.2 ± 0.16 6.00 – 6.53	6.5 ± 0.40 5.83 – 7.12
$M^2 – M^2$	13.97	11.40	11.9 11.44 – 12.43	11.2 ± 0.27 10.77 – 11.38	10.4 ± 0.33 10.00 – 10.93	10.9 ± 0.16 10.66 – 11.25
LMI	40.66	33.25	33.5 33.25 – 33.67	31.6 ± 0.91 30.64 – 32.78	29.6 ± 0.69 28.63 – 30.65	31.0 ± 1.06 29.26 – 32.29
HCP	14.79	10.98	11.3 10.98 – 11.71	10.7 ± 0.26 10.51 – 11.11	10.6 ± 0.48 10.01 – 11.95	10.4 ± 0.44 9.72 – 11.44
HM	4.73	3.60	3.4 3.19 – 3.60	3.4 ± 0.28 3.05 – 3.67	3.0 ± 0.14 2.81 – 3.21	3.3 ± 0.24 2.74 – 3.54
TM	2.60	2.15	2.1 2.09 – 2.15	1.8 ± 0.16 1.55 – 1.92	1.6 ± 0.06 1.52 – 1.72	1.7 ± 0.09 1.53 – 1.81

[a]UPLB 3753
[b]FMNH 186805 (holotype), 190167
[c]FMNH 194750, 194751, 194752, 208705
[d]FMNH 74852, 92780, 92781, 146591, 146592, 146593, 148050, 148077, 148078, 148081, 148085, 148087
[e]FMNH 56165, 56168, 56172, 56178, 56190, 61439, 61448, 61452, 61453, 61459, 61465

Because there is no question as to the morphological distinctiveness of *P. aureospinula*, we twice re-ran the PCA with *P. aureospinula* deleted, to focus on the four populations that are of more similar body size. The first of these PCAs included all individuals with complete sets of 20 craniodental measurements; this included only one specimen from Mt. Hamiguitan, a young adult. The third PCA was based on specimens with a subset of 15 measurements that are available from all adult specimens (i.e., excluding CIL, BBC, HBC, MB, and PPL). The results of these two PCAs were very similar in terms of loadings and scores of individuals on the first and second axes, but this last PCA allowed us to include the second, fully adult specimen from Mt. Hamiguitan, so we describe and show only these results.

As shown in Table 3, the first axis accounted for 54.6% of the variance explained, with an eigenvalue of 8.2. Most variables loaded heavily on this axis, indicating that it depicts a combination of overall size and robustness. Depth of zygomatic plate, lacrimal breadth, and height of the coronoid process loaded least heavily. The second axis accounted for an additional 12.7% of the total variance, with an eigenvalue of 1.9. Of the three variables that loaded least heavily on the first axis, two (lacrimal breadth and depth of zygomatic plate), plus one (palatal breadth at M3) that loaded moderately (0.67) on the first axis, were the variables that loaded most heavily (0.45 to 0.71) on the second axis. The third and fourth axes (Table 3) accounted for 8.0% and 7.2% additional variance, with eigenvalues of 1.2 and 1.1, respectively, making them only marginally interpretable.

TABLE 3. Loadings of 15 log-transformed cranial, dental, and mandibular measurements of four species of *Podogymnura* on four interpretable axes of a principal component analysis. See Methods for definitions and acronyms.

	PC 1	PC 2	PC 3	PC 4
Interorbital Breadth (IB)	0.791	0.134	-0.017	-0.453
Zygomatic Plate Breadth (BZP)	0.434	0.655	-0.212	0.374
Rostral Length (LR)	0.691	-0.419	0.285	0.086
Rostral Breadth (BR)	0.823	0.211	-0.366	-0.132
Lacrimal Breadth (BL)	0.532	0.712	0.058	0.133
Palatal Length (PL)	0.912	-0.232	-0.044	0.092
Posterior Breadth of Palate (PB)	0.561	-0.007	0.479	-0.360
Upper Toothrow (LI^1–M^3)	0.882	-0.288	0.183	0.075
P^4 to M^3 (LP^4–M^3)	0.834	-0.265	0.054	0.138
M^3 to M^3 – Labial (PBM^3)	0.674	0.451	0.018	-0.449
M^2 to M^2 – Lingual (M^2–M^2)	0.890	0.005	0.011	-0.102
Mandible Length (LMI)	0.928	-0.225	0.107	0.164
Coronoid Process Height (HCP)	0.499	0.330	0.456	0.510
Mandible Height (HM)	0.591	-0.394	-0.569	0.169
Mandible Thickness (TM)	0.783	0.008	-0.344	-0.004
Eigenvalue	8.2	1.9	1.2	1.1
Percent of Total Variance	54.6	12.7	7.9	7.2

A plot of the scores of individual specimens on the first two axes (Fig. 6B) shows the four geographic populations as occupying different parts of the morphospace in three out of four cases, principally along the first axis. The one adult specimen from Mt. Hamiguitan had the highest score on the first axis, and the young adult had the second highest score. Specimens from Mt. Kampalili, which our phylogenetic analysis shows to be part of a clade that includes those from Mt. Hamiguitan, on average had the second-highest scores on the first axis, but there was no overlap between specimens from the two mountains, and the Kampalili specimens on average also had lower scores on the second axis. Specimens from Mt. Kitanglad (*P. t. minima*) have the lowest scores on the first axis, in keeping with their prior description as being smaller than those from Mt. Apo (*P. t. truei*), with almost no overlap. The specimens of *P. t. truei* and *P. t. minima* had similar scores on the second axis. The largest amount of overlap in the morphospace defined in this PCA is between specimens from Mt. Apo (*P. t. truei*) and those from Mt. Kampalili, which our molecular phylogenetic analyses recover as members of different clades (Fig. 2).

In summary, the results of our molecular phylogenetic analyses recovered two notably divergent clades represented among the five geographically isolated populations of *Podogymnura* currently known: the first includes *P. t. truei* and *P. t. minima*, which are both genetically and morphologically distinct from each other qualitatively and quantitatively and which we regard as distinct species. The second genetically based clade includes *P. aureospinula*, a species that is much larger and more robust than any of the other four populations, plus a clade containing individuals from Mt. Hamiguitan and Mt. Kampalili. Our morphological analyses also support a close relationship between the populations from Mt. Hamiguitan and Mt. Kampalili, but those same analyses show differences in external appearance, qualitative cranial features, and multivariate morphospace. The incongruity of our genetic and morphological results regarding the two populations from Hamiguitan and Kampalili creates ambiguity about their overall distinctiveness; given that, we treat them as conspecific. These hypotheses of species-level distinctiveness should be tested in the future using additional molecular markers and further morphological studies, preferably with the inclusion of specimens from additional areas in Mindanao, especially from the area between Mts. Hamiguitan and Kampalili.

Taxonomy

Subsequent to the brief generic diagnosis of *Podogymnura* by Mearns (1905) based on *P. truei*, only one additional species was recognized, *P. aureospinula* (Heaney & Morgan 1982). Diagnostic features for the genus noted by Frost *et al.* (1991), together with our additional specimens from eastern Mindanao, require an emendation of the diagnosis to more fully define and encapsulate the morphological diversity of the component species.

Podogymnura Mearns, 1905

Type species: *Podogymnura truei* Mearns, 1905: 436.

Included species: The type species, plus *P. aureospinula*, *P. intermedia* n. sp., and *P. minima* (raised to species rank, below).

   Distribution: Currently known from Bucas Grande Island, Dinagat Island, and the mountains of eastern (Mt. Hamiguitan and Kampalili) and central (Mts. Apo and Kitanglad) Mindanao Island (Fig. 1).

   Emended diagnosis: The genus *Podogymnura* is defined phylogenetically as the most recent common ancestor of *P. aureospinula*, *P. truei*, *P. minima*, and *P. intermedia* n. sp., and all of its descendants, and by the following combination of morphological characters. Small to medium-sized gymnures, HB from ca. 145 mm to 201 mm, CIL from ca. 39 to 52 mm (Tables 1 and 2); dorsal pelage reddish- or grayish-brown to dark brown with variable levels of golden highlights, soft to bristly and variable in length; underfur of woolly hairs fine, soft, and wavy; most guard hairs long, straight, and tapering with golden-yellow or golden-brown tips of varied lengths; black guard hairs long, distally flattened, tapered, and slightly bent. Two to three supragenal vibrissae present. Snout long, slender, and pointed, blunt at tip; nostrils extending slightly laterally, somewhat tubular; ear size moderate, extending far beyond pelage, sparsely covered on both surfaces with short, inconspicuous hairs; tail short relative to head and body, covered with short hairs that emerge posterior to the conspicuous scales that cover the tail; hind feet fairly long and narrow, covered thickly dorsally and thinly ventrally with short hairs. Females with two pairs of small, inconspicuous mammae, one pair inguinal and one pair axial. Adult males with slight swelling in uro-genital area, sometimes with bare skin from base of tail to area around penile sheath; no scrotum is evident. Rostrum elongate and broad, postorbital processes absent, frontals slightly to strongly inflated; interorbital region moderately to strongly constricted; braincase inflated; sagittal crest inconspicuous to prominent, extending no further anterior than anterior tips of interparietals, except extending further anterior then spreading into low temporal crests in *P. aureospinula*; nuchal crest of varying height that originates laterally as low projections from dorsal margin of each mastoid that meet mid-dorsally to form a broadly tapered arch with which the sagittal crest converges; incisive foramina cordate, moderately narrow, and short; anterior palatine foramina small and anterior to the maxilla/palatine suture; infraorbital canal dorsal or posterodorsal to the P4-M1 region; ante-orbital fossa present; posteroventral process of maxillary portion of zygoma present, small to prominent; ophthalmic foramen joined with or closely adjacent to the

ethmoid foramen; lateral fossa absent from palatine anterodorsal to the post-palatal torus. Paired concavities in the basioccipital between the bullae, lateral to a medial ridge present in *P. aureospinula* and *P. intermedia* n. sp., absent in *P. truei* and *P. minima*. Upper molariform teeth with extreme anterior placement relative to orbit and infraorbital foramen; all incisors single-rooted; I2 and I3 similar in size, and both substantially smaller than I1; lower incisors spatulate and procumbent, i1 and i2 longer than i3; upper and lower canines double-rooted, flared laterally, and longest of all teeth. P1 and p1 absent; P2 single-rooted and small compared to other premolars, P3 larger and two- or three-rooted, with lingual lobe small (*P. aureospinula* and *P. intermedia* n. sp.) or absent (all others); P4 large, broad lingually, and nearly square-shaped; M1 and M2 square-shaped, each with a low but discernable metaconule; metacone present on M3; c1 significantly larger than p1; lower molars sometimes with small cusp at base of talonid notch between entoconid and metaconid. Mandible relatively long and thick, with angular process narrow and long, coronoid wide, and condyloid process long and robust, especially in *P. aureospinula*.

Taxonomic Status of *Podogymnura truei minima*

The original description of *P. truei minima* by Sanborn (1953) was brief, highlighting its somewhat smaller size relative to the nominal *P. truei* and its allopatric distribution. Subsequent authors working with larger series from the type locality (Mt. Kitanglad) acknowledged their smaller size on average, but doubted the sufficiency of the size difference for the subspecific designation of *P. t. minima* (Heaney & Morgan 1982; Poduschka & Poduschka 1985; Hutterer 2005; Heaney *et al.* 2006). Our molecular phylogenetic results (Fig. 2) found strong support for a sister-relationship of *minima* with *truei*, and clear evidence of reciprocal monophyly. In our subsequent analyses, we focused on other evidence – especially morphological evidence – of their distinctiveness. As described above, we found features that differ between *P. truei* and *P. minima* in pelage texture and color, body size, appendage proportions, inflation of the braincase, and relative molar size (Tables 1 and 2). A bivariate plot of breadth of braincase against condylo-incisive length showed no overlap (though proximity of several specimens) and substantial differences in means (Fig. 6A, Table 2). PCA of cranial, dental, and mandibular measurements found almost no overlap between the two (Fig. 6B). Based on these results, we conclude the two warrant recognition as distinct species, rather than subspecies of a single species. We therefore provide this emended description.

Podogymnura minima Sanborn, 1953

Podogymnura truei minima Sanborn 1953. Mammals from Mindanao, Philippine Islands collected by the Danish Philippine Expedition, 1951-1952. Videnskabelige Meddelelser Dansk Naturhistorisk Forening 115:283–288.

Podogymnura truei: Heaney & Morgan 1982. Tab. 1-2 (part, DMNH 5949-5953).—Poduschka & Poduschka 1985. Tab. 1C-D, 2B, Abb. 6, 16 (part, FMNH 92777, 92780-81, SMF 31430, 31443, 31755, AMNH 164482; ZMC 1311).—Heaney *et al.* 2006. Tables 2 – 6, Fig. 8 (part, FMNH 74852, 92777, 92778, 92779, 92780, 92781,146592, 146594, 146962, 146963, 146964; 147782, 147783, 147790, 147800, 147801, 147802, 147803, 147804, 147808, 147809, 147810, 147811, 147812, 147813, 147814, 147815, 148003, 148004, 148005, 148006, 148010, 148011, 148012, 148013, 148016, 148017, 148018, 148019, 148050, 148053, 148077, 148078, 148083, 148084, 148085, 148087, 166456, 166457, 166458, 167375, 167376, 167377, 167378).

Holotype. Zoologisk Museum, Copenhagen, catalog number 1311. Adult female collected on 16 December 1951, field number F. Salomonsen K-4. Skin and skull.

    Type locality. Mt. Kitanglad, Bukidnon Province, Mindanao Island, Philippines, 1600 m (Fig. 1).

    Measurements. Tables 1 and 2.

    Specimens examined. Mindanao Island, Bukidnon Province, Kitanglad Range, Mt. Kitanglad, 10.7 km S, 2.9 km W of Sumilao Poblacion, 1,450 m elev., 8°11'10"N, 124°55'10"E (FMNH 166456, 166457, 167375 – 167378); Mt. Kitanglad, 11.5 km S, 2.2 km W of Sumilao Poblacion, 1,500 m elev., 8°11'0"N, 124°55'35"E (FMNH 166458); Mt. Kitanglad, 1,600 m elev. (FMNH 74852); Mt. Imbayao, 15 km S, 7 km E of Baungon, San Vicente Municipality, 1,800 m elev., 8°9'N, 124°45'E (FMNH 146592, 146594, 146962 – 146964); Mt. Nangkabulos, 16.5 km S, 4 km E of Camp Phillips, 1,900 m elev., 8°10.5'N, 124°51'E (FMNH 147782, 147783, 147808, 147809, 147810, 147790, 148077, 148078); Mt. Nangkabulos, 15.5 km S, 4 km E of Camp Phillips, 2,250 m elev., 8°9.5'N, 124°51'E (FMNH 147800 – 147804, 147811, 147812, 147813, 147814, 147815, 148083, 148084, 148085, 148087); Mt. Dulang-

dulang, 15 km S, 11 km W of Dalwangan, Malaybalay City, 2,375 m elev., 8°7.5'N, 124°56'E (FMNH 148003, 148004, 148005, 148006, 148018, 148050); Mt. Dulang-dulang, 15 km S, 11.5 km W of Dalwangan, Malaybalay City, 2,600 m elev., 8°7.5'N, 124°56'E (FMNH 148010, 148011, 148012, 148013); Mt. Dulang-dulang, 15 km S, 12.5 km W of Dalwangan, Malaybalay City, 2,800 m elev., 8°7.5'N, 124°56'E (FMNH 148016, 148017, 148018, 148019, 148053); Mt. Kitanglad, Malaybalay City, 5,000 ft. elev. (ca. 1,524m), (FMNH 92777, 92778, 92779); Mt. Kitanglad, Malaybalay City 6,000 ft. elev. (ca. 1,829 m), FMNH 92780, 92781).

Distribution. Documented from Mt. Kitanglad Range, north-central Mindanao Island, including Mts. Dulang-dulang, Imbayao, and Nangkabulos (Fig. 1).

Emended diagnosis. Overall, the smallest species of the genus (HB = 137 – 152 mm); tail short (49 – 66 mm), about 36% of head and body, pale grayish-brown dorsally and unpigmented ventrally; hindfoot short (HF = 33 – 37 mm, 23% of HB; Table 1) and uniformly pale brown. Dorsal pelage dark reddish-brown, long and soft with conspicuous golden-brown tips; underfur dark gray, dense and wavy, shorter than guard hairs; guard hairs black, with most long, straight, and tapered, but some distally flattened and slightly bent. Ears and feet pale, lightly pigmented. Skull (Fig. 5, Table 2) slender and tapered (CIL = 37.28 – 39.78 mm), sagittal and nuchal crests poorly developed and inconspicuous, rostrum long (LR = 15.00 – 17.57 mm), cranium narrow (BBC = 15.40 – 16.22 mm). Incisive foramina relatively narrow and short. Anterior surface of basioccipital nearly smooth, lacking or barely showing a short ridge running medially parallel to the bullae; paired concavities absent. Tips of tympanic wings of basioccipital short and nearly straight (rather than longer and curved medially). Upper toothrow short (I1 – M3 = 18.71 – 21.06 mm), P3 without lingual lobe; mandible relatively slender (LMI = 28.63 – 30.65 mm), as are its angular, coronoid and condyloid processes. P4 relatively small and triangular. Cusp at base of talonid on m1 and m2 absent.

Comparisons. *Podogymnura minima* and *P. aureospinula*: *P. minima* is the smallest and *P. aureospinula* the largest member of the genus (Tables 1 and 2), and they are easily distinguished on that basis. The long, soft pelage of *P. minima* strongly contrasts with the short and stiff, bristly fur of *P. aureospinula*; in the former species, golden-brown highlights visible only at the tips of black guard hairs, but the latter has conspicuous golden-yellow guard hairs. Paired concavities in basioccipital between bullae that are present in *P. aureospinula* and *P. intermedia* are absent. The lingual lobe of P3 is present in *P. aureospinula* but absent in *P. minima*. P4 relatively small and triangular, vs. large and squarish. Cusp at base of talonid on m$_1$ and m$_2$ absent, vs. present.

Podogymnura minima and *P. intermedia* n. sp: pelage of *P. minima* is soft, similar to that of *P. intermedia* from Mt. Kampalili, and different from the rough and bristly dorsal pelage of *P. intermedia* from Mt Hamiguitan. *P. intermedia* has conspicuous dorsal golden-yellow streaks or speckling, whereas *P. minima* has smaller, less apparent golden-brown speckles. *P. minima* is smaller than *P. intermedia* n. sp. in nearly all respects, especially the large specimens from Mt. Hamiguitan (Tables 1 and 2, Figs. 6A and 6B). It is notable that *P. intermedia* from Mt. Hamiguitan has an especially long and broad rostrum, long post-palatal region, and thick mandible relative to *P. minima* (Table 2). Further comparisons in the new species description below.

Podogymnura minima and *P. truei*: See comments above; external differences include small overall size in *P. minima* (mean HB = 145 mm vs. 148 mm, TV = 54 vs. 56 mm). The skull of *P. minima* is slightly but consistently shorter and more gracile overall, with a narrower rostrum, less inflated braincase, and lower sagittal crest; *P. truei* has slightly shorter condylar process of the mandible (Tables 2, 3, Figs. 5, 6A, 6B).

Karyology. Specimens from the Kitanglad Range have a standard karyotype of 2N = 40, FN = 76 (Rickart 2003).

Ecology. *P. minima* has been recorded in montane and mossy forest, from 1300 m to 2800 m elevation; it was among the most abundant small mammals in middle to high-elevation montane and mossy forest on Mt. Kitanglad (Heaney *et al*. 2006). They are nocturnal, feeding on the surface of the ground. Diet based on stomach contents is composed largely of earthworms, with some arthropods, including hymenopterans and coleopterans. Pregnancy was recorded from March to June; litter size (n = 9) was one, rarely two. Other species of native small mammals documented in the elevational range of *P. minima* were *Crocidura beatus*, *Tupaia everetti*, *Apomys hylocoetes*, *A. insignis*, *Batomys salomonseni*, *Crunomys suncoides*, *Limnomys bryophilus*, *L. sibuanus*, *Rattus everetti*, and *Tarsomys apoensis* (Heaney *et al*., 2006).

Podogymnura intermedia **new species**
Figs. 5, 7, 8, and 9; Tables 1 and 2

Holotype. FMNH 186805, adult male, collected on 28 July 2005 (original number 3769 of D. S. Balete); initially fixed in formalin, now preserved in 70% ethyl alcohol with the skull removed; skull in good condition. A sample of fresh muscle tissue was removed from the left thigh and preserved in 90% ethanol; otherwise the body is in good condition. The holotype has been cataloged and is currently housed at FMNH but will be transferred to the National Museum of the Philippines, Manila.

Type Locality. 3.7 km S, 1.4 km E of Mt. Hamiguitan peak, Mati Municipality, Davao Oriental Province, Mindanao Island, Philippines, 950 m elev., 6°42' 26.2" N, 126°11' 42.8" E (Fig. 1).

Specimens examined. Mt. Hamiguitan: (N = 4) Three additional specimens from the type locality (FMNH 190152, 190153, 190167) and one (FMNH 190151) from 17.5 km S, 4 km E of Mt. Hamiguitan peak, San Isidro Municipality, ca. 1,128 m elevation, 6°43'3" N, 126°11'1.9" E. These include two males and one female, and a specimen of undetermined sex prepared as a skull only (FMNH 190167). The juvenile male (FMNH 190151), adult male (FMNH 190152), and young adult female (FMNH 190153) have had their skulls removed and cleaned. The bodies of the adult male and young-adult female had partially decomposed prior to preservation, but that of the juvenile male is in good condition. The prepared skulls have broken crania, including one with broken coronoid and condyloid processes (FMNH 190152).

Mt. Kampalili: (N = 12) Three males (FMNH 194750, 194751, 194752) from 2 km S, 2 km W of Mt. Kampalili peak, Maragusan Municipality, Compostela Valley Province, Mindanao Island, Philippines, ca. 1,900 m elevation, 7° 17' 11.7" N, 126° 15' 30.9" E; two females (FMNH 194748, 194749) from 2.75 km S, 0.5 km W of Mt. Kampalili peak, ca. 1,500 m elevation, 6°17'39" N, 126°15'38.4" E; two females (FMNH 208700, 208701) and three males (FMNH 208699, 208702, 208705) at 2.25 km S, 3.5 km E of Mt. Kampalili peak, 1,470 m elevation, 7.29112° N, 126.31520° E; and two females (FMNH 208703, 208704) at 1.75 km S, 4.25 km E of Mt. Kampalili peak, 1,640 m elevation, 7.29522° N, 126.31602° E. Three females (FMNH 194748, 208700, 208703) and three males (FMNH 194750, 194752, 208705) have had their skulls removed and cleaned; others preserved intact. Two females (FMNH 194748, 208700) have crushed crania, and one male (FMNH 194752) has a broken left zygomatic arch; and one male (FMNH 208705) has a short crack on the occipital.

Distribution. Currently known from montane forest over ultramafic soil between ca. 950 and 1,128 m on Mount Hamiguitan, and in montane and mossy forest from ca. 1,470 m to 1,900 m on Mount Kampalili (Fig. 1).

Etymology. From the combined Latin *inter* (between) + *medius* (middle), to highlight its intermediate morphology between the two smaller species of *Podogymnura* and the large *P. aureospinula*. We propose eastern Mindanao gymnure as its English common name.

Diagnosis. A member of the genus *Podogymnura* as diagnosed above, of intermediate to small size (Mt. Hamiguitan average HB = 171 mm, weight 96 g; Mt. Kampalili average HB = 145, weight 77 g; Table 1), defined by the following combination of characters. Dorsal pelage generally coarse in Hamiguitan, softer in Kamapalili specimens, with long guard hairs of two types: scattered long, black hairs, and many slightly shorter guard hairs having conspicuous golden-yellow tips that produce an appearance of shiny, golden streaks (Fig. 7). Both types of guard hairs become progressively shorter laterally and anteriorly over the head and snout. Underfur soft, gray, and dense, becoming sparser over head but more conspicuous laterally as guard hairs become sparser laterally and absent ventrally, where silver highlights become apparent. Ventral pelage shorter and paler, lacking golden streaks. Ears short (average = 20 mm), pigmented grayish-brown. Relative to congeners, hindfoot longer in Hamiguitan (average HF = 36 mm), shorter in Kampalili (34 mm) but short relative to HB (21–23 % of HB; Table 1); plantar surface, including plantar pads, darkly pigmented or with mottled grayish-brown areas. Tail pigmented medium to dark grayish brown dorsally, and variable ventrally, usually dark but occasionally mottled with white. Tail relatively short compared to length of head and body (average TV = 53–54 mm; 32–37 % of HB; Table 1). Skull of Hamiguitan specimens (Figs. 5, 8) large (holotype CIL = 43.4 mm, BBC = 16.8 mm), that of Kampalili specimens smaller, (CIL = 40.6 mm, BBC = 16.1 mm). Sagittal and nuchal crests low but readily visible, rostrum long and deep. Incisive foramina relatively long and wide in Hamiguitan specimens, narrower and shorter in Kampalili specimens. Upper toothrow long (average I1– M3 = 21.1 – 22.2 mm). Post-palatal region proportionately long in specimens from Mt. Hamiguitan, average in Kampalili, both samples with paired concavities between the bullae, bisected by a low medial ridge. Mandible long and robust in Hamiguitan (average LMI = 33.5 mm), shorter and more slender in

Kampalili (average LMI = 31.6 mm). Lingual lobe of P3 present in Hamiguitan specimens, absent in Kampalili. P4 proportionately large and square-shaped. A small, inconspicuous cusp present at base of talonid on first and second lower molars (Fig. 8E).

Description and Comparisons. Because specimens from Mt. Hamiguitan (the type locality) differ from those from Mt. Kampalili, we include comparisons of specimens from these two places along with comparison to other species of *Podogymnura*.
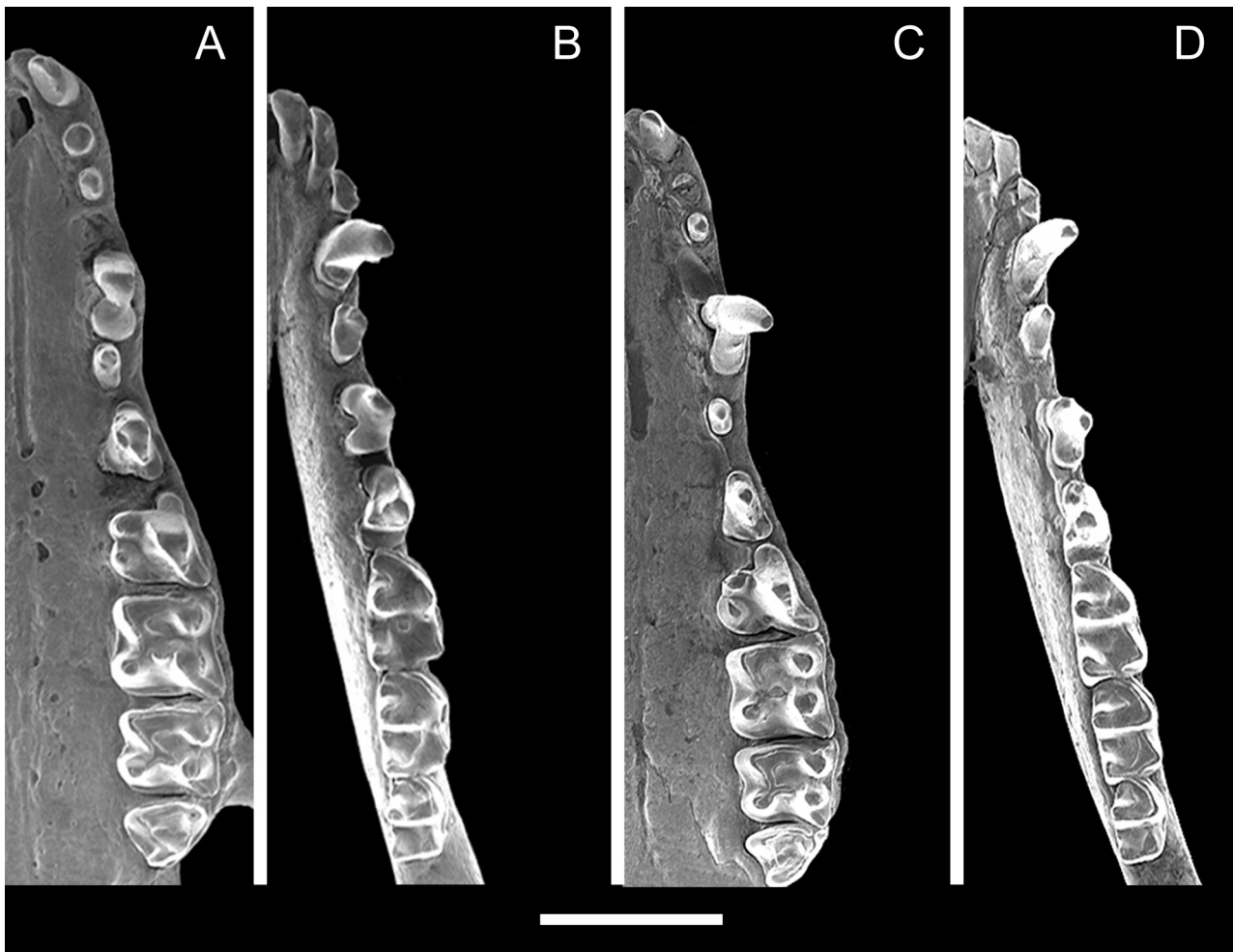

FIGURE 7. *Podogymnura intermedia* (FMNH 186805, holotype), adult male. Photographed 28 July 2005 by D. S. Balete.
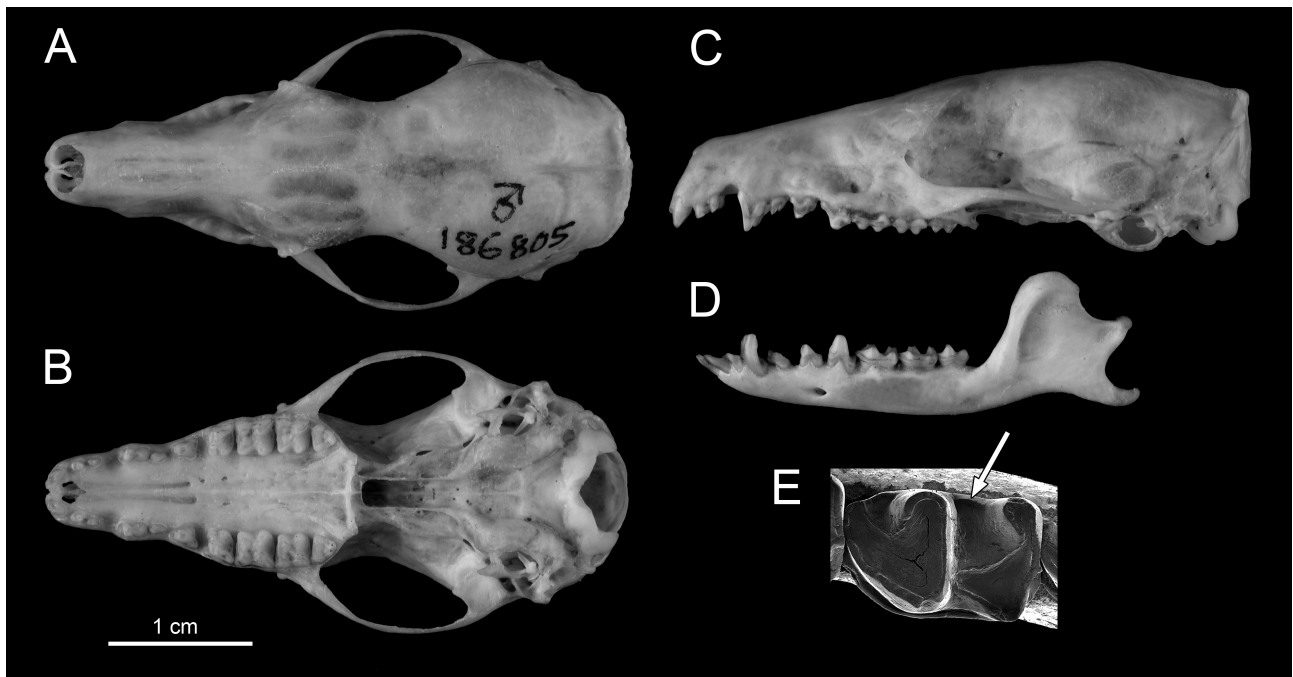
FIGURE 8. Dorsal (A), ventral (B) and lateral (C) views of the skull and lateral view of the mandible (D) of *Podogymnura intermedia* (FMNH 186805, holotype); scale bar refers to these images. E, occlusal view of the second mandibular molar of *Podogymnura intermedia* holotype; arrow points to a small cusp at the base of talonid, between the entoconid and metaconid.

FIGURE 9. Maxillary and mandibular dentition of *Podogymnura intermedia* from Mt. Hamiguitan (A, B; FMNH 186805, holotype); and (C, D; FMNH 194751), from Mt. Kampalili. Scale bar = 5mm.

A medium-sized Philippine gymnure, Hamiguitan specimens larger and more robust than specimens from Mt. Kampalili, *P. minima*, and *P. truei*, but smaller and less robust than *P. aureospinula* (Tables 1 and 2, Figs. 4, 5). Dorsal pelage of *P. intermedia* from Hamiguitan is distinctly darker on head and rostrum, venter slightly paler brownish-gray (Fig. 4); coarse overfur consists of long, stiff guard hairs, ca. 20 mm on mid-dorsum, longer on the rump, ca. 25 mm. The long, coarse, grayish-brown dorsal pelage contains both long black guard hairs and long golden-yellow guard hairs that produce a golden-streaked appearance. Mt. Kampalili specimens have soft, dark brown dorsal pelage with shorter black guard hairs and many short golden-yellow-tipped hairs that produce a golden-speckled appearance. Dorsal pelage of *P. aureospinula* is uniformly paler and golden-brown overall and overfur is shorter and bristly; venter brownish-gray. *P. truei* has soft dorsal pelage that is dark brown with small, inconspicuous speckles of golden-brown at the tips, without conspicuous long and stiff guard hairs. *P. minima* has short, soft, reddish-brown dorsal pelage with golden-brown speckles at the tips that are more conspicuous than those of *P. truei* but are darker and smaller than those of *P. intermedia* from Mt. Hamiguitan or specimens from Mt. Kampalili. Females of all species have two pairs of small, inconspicuous mammae, one pair inguinal and one pair axial; these are well hidden by the fur. Adult males have a swollen area from the base of the tail to the area around the penile sheath; the sheath is small, ca. 1.5 mm wide and long; no scrotum is evident. In specimens from Hamiguitan, the swollen area is covered by typical abdominal fur, but in specimens from Kampalili, the swollen area is bare.

Ears of all *Podogymnura* are short relative to body size, and sparsely covered with short, nearly invisible hairs; ears of specimens from Hamiguitan are pigmented dark gray but from Kampalili are paler. *P. aureospinula* ears are palest of the known species. Ears of *P. truei* and *P. minima* average slightly longer and paler than in *P. intermedia* (Table 1). Length of tail relative to head and body (32%) in *P. intermedia* from Hamiguitan is shortest among all *Podogymnura* (Table 1). Skin of tail of Hamiguitan specimens is uniformly dark gray throughout; on

Kampalili specimens it is ventrally pale brown or mottled with white. Tail of *P. aureospinula* is longer but overlaps in relative length (33% of HB). Tail of *P. truei* is substantially longer both absolutely and proportionately (Table 1). Although *P. minima* is smaller overall, tail is equal in length and proportionately longer. Hind foot of *P. intermedia* is average among *Podogymnura* excepting the larger *P. aureospinula,* but proportionately shorter than all except *P. aureospinula* (Table 1). Hindfoot skin is pigmented medium gray dorsally and ventrally, including digits and plantar pads, paler and often mottled with white in those from Kampalili. Hind feet of *P. aureospinula, P. truei* and *P. minima* are unpigmented, both dorsally and ventrally.

Skull of *P. intermedia* (Fig. 8, Table 2) is smaller than the much larger *P. aureospinula* (Fig. 4), but larger than its congeners in most respects, with Mt. Hamiguitan specimens larger than those from Kampalili (Fig. 5)*.* It is similar to *P. truei* and *P. mimima* in its limited development of the prominent nuchal and sagittal crests that are hallmarks of *P. aureospinula*. Maximum height of sagittal crest is 0.8 mm in *P. intermedia*. The nuchal crest of *P. intermedia* slants slightly posteriad relative to the cranium but does not project beyond occipital margins (Fig. 8), which it does in *P. aureospinula* (Fig. 4).

In lateral view, skull of *P. intermedia* from Hamiguitan (Fig. 8) cuts a nearly straight slanting profile from top of braincase to tip of narrow and tapered rostrum, whereas in specimens from Kampalili the profile is slightly concave. Frontals of *P. aureospinula* are dorsolaterally inflated, making them only about 9% narrower than braincase, and in dorsal view producing a narrow-waisted hour-glass shape in interorbital region (Fig. 4). In lateral view, prominent frontal swellings in *P. aureospinula* produce a convex dorsal profile. All three small-bodied *Podogymnura* share an interorbital region in which there is a relatively broadly-waisted hourglass shape, although lacrimal and interorbital breadths of *P. intermedia* from Hamiguitan are greater than in Kampalili and the other two species (Table 2), and all lack the temporal ridges that in *P. aureospinula* form a low crest converging at the interorbital region. In *P. intermedia* and the two other small-bodied species, the parietals are dorsolaterally inflated from the anterior edge of interparietals, forming a cranium that tapers anteriad to the frontal region and flattens posteriad to the occipital region (Fig. 8). Incisive foramina cordate, similar to those of *P. minima* and *P. truei* in size, in contrast to the wider and longer foramina in *P. aureospinula* and *P. intermedia*. Palatal length, width of the posterior palatal ridge, and lingual palatal breadth at M³ of *P. intermedia* are large (except in comparison to *P. aureospinula*; Table 2). Post-palatal length of *P. intermedia* from Hamiguitan is the greatest among the small *Podogymnura*, with specimens from Kampalili averaging shortest (Table 2).

The basicranium of *P. intermedia* is similar to its congeners, differing mainly in the large size of the basicranial area, auditory bulla, and paraoccipital process (Fig. 8). Aside from overall size, the basicranium of *P. intermedia* is similar to that of *P. aureospinula* (and unlike other *Podogymnura* species) in having paired, shallow concavities traversed medially by a fine, short ridge that runs parallel to the bullae from its base to the tip of the tympanic wing, although in *P. aureospinula* the depressions are more expansive and the mid-ventral ridge longer and larger. The medial ridge is low and poorly defined in *P. truei* and nearly absent in *P. minima*, and the concavities are absent in both.

Mandible of *P. intermedia* (Fig. 8, Table 2) relatively long and thick, except in comparison to *P. aureospinula* (Fig. 5). *P. aureospinula* has larger, wider, and longer angular, coronoid, and condyloid processes than all of its congeners. In *P. intermedia* from Hamiguitan, the angular process is narrower but longer, coronoid wider, and condyloid process longer and more robust than in specimens from Kampalili, *P. minima*, and *P. truei*. Position of mandibular foramina is similar in all species.

Dental features of *P. intermedia* (Figs. 8, 9A, 9B, Table 2) are similar to those of congeners in most respects (see *Podogymnura* Diagnosis), usually differing only in relative sizes. The presence of a discernible lingual lobe in P3 in specimens from Hamiguitan is shared with *P. aureospinula*; this lobe is absent among all other *Podogymnura.* P4 is proportionately larger and more square-shaped in *P. aureospinula* and *P. intermedia* than in *P. truei* or *P. minima*. A small, inconspicuous cusp at base of talonid on m1 and m2 is present in all specimens of *P. intermedia* from Hamiguitan (Fig. 8E) and *P. aureospinula* (Heaney & Morgan 1982); a poorly-developed version is present in a small percentage of *P. truei*, and is absent in other populations, including *P. intermedia* from Kampalili.

Ecology. We recorded *P. intermedia* on Mt. Hamiguitan and Mt. Kampalili in different types of forest formations, and so we present the ecological information separately.

On Mt. Hamiguitan, we captured *P. intermedia* in primary montane forest over ultramafic soil at 950 m to 1,128 m (Balete *et al*. 2006). We did not record it in lowland forest at 525 m in 924 trap-nights. At 950 m, three individuals were caught in 228 trap-nights with earthworm bait (1.3% success) compared to one individual caught in 672

trap-nights with roasted coconut coated with peanut butter (0.15%); none were captured in traps set above ground on vines and trees. On Mt. Kampalili, we recorded this species in upper montane and mossy forest at ca. 1,470 m – 1,900 m elevation; forested habitats below and above these elevations were not surveyed. Seven *P. intermedia* recorded during 2010 were captured in 247 trap-nights with live earthworm bait (2.83 % trap success); none were captured in 506 trap-nights using coconut bait. All were captured on the ground, and none in traps set in trees or on vines, and nearly all were captured at night. On the adjacent peak of Mt. Kangayag (ca. 1,630 m) of the same mountain range, we captured no gymnures in 2,140 trap-nights, of which 250 were baited with live earthworms.

The apparent absence of *P. intermedia* in the lowlands and restriction to montane and mossy forest is similar to *P. minima*, which occurs in secondary and old-growth montane and mossy forest from ca. 1,300 m to 2,800 m (Heaney *et al*. 1998, 2006), and to *P. truei*, which has been recorded from montane and mossy forest at ca. 1,640 m to at least 2,250 m (Hoogstraal 1951, Sanborn 1952). In contrast, *P. aureospinula* occurs in secondary and old-growth lowland forest at low elevations (Heaney & Morgan 1982; Heaney & Rabor 1982; Heaney *et al*. 2010).

Stomach contents of two individuals from Mt. Hamiguitan contained mainly chewed remains of arthropod exoskeletons, including coleopterans and their larvae, as well as an operculum and shell fragments of small land snails. A few pieces that appeared to be partially digested bits of small earthworms were present. Stomach contents of three specimens from Mt. Kampalili contained chewed remains of arthropod exoskeletons, including coleopterans and centipedes, and two contained pieces of earthworms. The presence of land snails in the diet of this species is the first record of this food item among *Podogymnura*. These diet and trapping data indicate that, as with other *Podogymnura*, *P. intermedia* forages on the ground for leaf-litter invertebrates. These feeding habits may differ from those of *P. minima*, which feeds more commonly on earthworms than arthropods (Heaney *et al*. 2006), although this difference may simply reflect differences in prey availability.

An adult male from Mt. Hamiguitan taken in May had testes measuring 11 x 5 mm; an adult female was nulliparous. The presence of a juvenile in May suggests that some breeding occurred earlier in the year. None of the specimens from Mt. Kampalili captured in February and May (five adult males, three adult females, three young adult females and one young adult female) showed signs of reproductive activity.

Three species of murid rodents (*Batomys hamiguitan*, *Bullimus bagobus*, and *Rattus everetti*) were documented as being sympatric with *P. intermedia* on Mt. Hamiguitan along with the Mindanao shrew (*Crocidura beatus*; Balete *et al*. 2006, 2008). In addition to these native species, we recorded the non-native spiny ricefield rat (*Rattus exulans*) at two disturbed sites near the type locality: a narrow patch of non-native cogon grass, *Imperata cylindrica*, surrounding the shoreline and dry lakebed of Tinagong Dagat, a seasonal lake; and in disturbed vegetation along a foot-trail, but not in the nearby forest interior. On Mt. Kampalili this species was associated with *Apomys* sp., *Bullimus bagobus*, *Rattus everetti*, *Baletemys kampalili* (Rowsey *et al*. 2022), an undescribed species of *Tarsomys*, and one squirrel, *Sundasciurus philippinensis* (specimens in FMNH). The commensal house shrew, *Suncus murinus*, was also present. All of the native co-occurring species are endemic to the Philippines, and all but *R. everetti* are restricted to the Mindanao Faunal Region (Heaney 1986; Heaney *et al*. 2006, 2010).

Discussion

The discovery of *Podogymnura intermedia* brings the number of endemic mammals from southeastern Mindanao to three, following an arboreal herbivore (*Batomys hamiguitan*; Balete *et al*. 2008) and a shrew-like forest mouse from Mt. Kampalili (*Baletemys kampalili*; Rowsey *et al*. 2022). These have resulted from the first surveys of montane mammals in this topographically isolated region of eastern Mindanao, and add to the many locally endemic, high-elevation species known from the mountains of central Mindanao (Heaney *et al*. 2006, Rowsey *et al*. 2022). Extensive field surveys and subsequent taxonomic studies on Luzon Island have demonstrated that nearly all isolated mountainous regions on that island are local centers of endemism (Heaney *et al*. 2016a, 2016b). Given the similarities of Mindanao and Luzon in area, climate, topography, and geological history, the existence of additional locally endemic species in this little-known fauna is likely (Rowsey *et al*. 2022).

Although our phylogenetic analysis is based on only two mitochondrial genes, it provides some basis for inferences about the evolutionary history of *Podogymnura*. After dispersing to Mindanao from mainland SE Asia, probably by way of Borneo due to its proximity and the presence there of its sister-genus *Echinosorex*, a disjunction in *Podogymnura* took place between eastern and central Mindanao (Fig. 1). The eastern lineage was subsequently

divided into lineages leading to modern *P. aureospinula* and *P. intermedia.* The central Mindanao lineage also shows subsequent divergence, into *P. truei* (on Mt. Apo) and *P. minima* (on Mt. Kitanglad). Each of the four species of *Podogymnura* recognized here occurs as an allopatric population, with all but *P. aureospinula* occurring in montane forest at elevations above about 1000 m, and subsequently maintaining a level of ecological isolation as "sky-islands" of montane forest surrounded by a "sea" of lowland forest (Fernando *et al.* 2008).

With respect to the timing of dispersal and diversification, our results indicate with reasonable certainty that the *Podogymnura* lineage arrived in the Philippines no sooner than 8 Ma, but probably in the range of 1.9 to 3.5 Ma (see Results and Fig. 3 and Supporting Information File 4). Diversification of the extant lineages likely began not more than 3 Ma, probably within the range of 0.53 to 0.97 Ma (see Results and Fig. 3 and Supporting Information File 4). The discovery and analysis of fossil calibration points would undoubtedly refine the node age estimates we present. This is broadly consistent with the estimated time of the origin of the central Mindanao region ca. 3-4 Ma through volcanic activity, which resulted in the merging of the previously separate islands that today form eastern and southwestern Mindanao, both of which are likely to have much older geological origins (Sajona *et al.* 1997; Hall 1998, 2013; Yumul *et al.* 2008).

Other studies have also documented the likely arrival of non-volant mammals on Mindanao from Borneo, including tree squirrels (*Sundasciurus*; den Tex *et al.* 2010), treeshrews (*Tupaia*; Roberts *et al.* 2011), and several lineages of murid rodents (Rowsey *et al.* 2022), and two (*Crunomys* and *Bullimus*; Rowe *et al.* 2019) from Sulawesi. Several genera also most likely arrived from the northern Philippines, such as shrews (*Crocidura*; Esselstyn *et al.*, 2009), forest mice (*Apomys*; Steppan *et al.*, 2006), and the cloud rats *Batomys* and *Crateromys* (Balete *et al.* 2008, Jansa *et al.* 2006), with diversification taking place during the same rough time-frame. While these few examples of mammalian dispersal to Mindanao imply a complex biogeographic history, they also imply that subsequent diversification within Mindanao may be more closely tied to the complex geological history and mountainous terrain of Mindanao than has been appreciated previously. This clearly points to the need for additional extensive and comprehensive field surveys, followed by morphological and genetic studies to determine the number of species actually present and their history of diversification within the highly species-rich and ecologically diverse mammalian fauna of Mindanao.

Acknowledgments

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Appendix I

Specimens examined. We examined all specimens of *Podogymnura* housed at the Field Museum, Chicago (FMNH, n = 99). These include specimens collected by the authors and their associates, as well as specimens from earlier expeditions (Sanborn 1952; Heaney and Rabor 1982). We examined a single specimen of *P. aureospinula* from the collection of the University of the Philippines at Los Banos (UPLB), and also include external measurements from Heaney and Morgan (1982) of the holotype of *P. aureospinula*, which is housed at the Delaware Museum of Natural History (DMNH). Specimens were prepared as study skins with cleaned skulls, complete skeletons, or fixed in formalin and stored in 70% ethyl alcohol (some with skulls subsequently removed and cleaned).

Podogymnura aureospinula (n = 1). Dinagat Island, Surigao del Norte Province, Loreto Municipality, 17°27.5'N, 122°04.1'E (UPLB 3753).

Podogymnura intermedia (n = 17). see description above.

Podogymnura minima (n = 54). see Emended Description.

Podogymnura truei (n = 32). Mindanao Island, Davao Province, Mt. Apo, east slope, 5,400 ft. elev. (ca. 1,646 m), (FMNH 61449, 61451 – 61453, 61457, 61459); Mt. Apo, east slope, 5,750 ft. elev. (ca. 1,753 m), (FMNH 61445, 61446, 61448); Mt. Apo, north slope, 6,900 ft. elev. (ca. 2,103 m), (FMNH 61435, 61436, 61438, 61439, 61440); Mt. McKinley, east slope, 5,800 ft. elev. (ca. 1,768 m), (FMNH 56165, 56168, 56169, 56172, 56181, 56192, 56193, 56194, 56195); Mt. McKinley, east slope, 6,850 ft. elev. (ca. 2,088 m), (FMNH 56178); Mt. McKinley, east slope, 7,100 ft. elev. (ca. 2,164 m), (FMNH 56179, 56180, 56186, 56188); Mt. McKinley, east slope, 7,400 ft. elev. (ca. 2,256 m), (FMNH 56182, 56189, 56190, 56191).

Supporting Information

Additional Supporting Information may be found in the online version of this article:

File 1 Table of primers used in this study and table illustrating amplification and sequencing strategy for amplification and sequencing work conducted at UAM and FMNH (file type: xlsx)

File 2 Results of PartitionFinder nucleotide substitution model selection analysis (file type: xlsx)

File 3 Raw nucleotide sequence divergences among samples for the 1529 base pair nucleotide alignment (file type: csv)

File 4 Time-calibrated maximum clade credibility (MCC) chronogram inferred using BEAST. Nodal support values indicate posterior probability (PP) and bootstrap support and are given in the form PP/BS. Nodes with dashed BS values reflect manual rooting of the tree in the RAxML analysis; (file type: pdf)