REVIEW OF THE PHILIPPINE GENERA *CHROTOMYS* AND *CELAENOMYS* (MURINAE) AND DESCRIPTION OF A NEW SPECIES

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The murine genera *Celaenomys* and *Chrotomys* comprise a group of semifossorial, vermivorous rodents endemic to the Philippines. Analysis of variation within this group supports the recognition of 4 named species occurring on the large islands of Luzon and Mindoro, as well as our description of a 5th species from Sibuyan, a small island in the central Philippines that has remained isolated from the other islands by deep water channels. Examination of cytochrome-*b* gene sequence data from 4 of the 5 taxa indicates that *Celaenomys silaceus* may be basal and sister to the other taxa but morphological and chromosomal data do not support the recognition of *Celaenomys* as a separate genus. Analysis of the sequence data indicates a relatively early separation of the Sibuyan species and a later split between 2 species of *Chrotomys* on Luzon. Diversification of *Chrotomys* appears to have involved speciation associated with both habitat vicarance on Luzon and overwater dispersal to neighboring islands. Most of the members of this clade are restricted to mid- or high-elevation forests, have limited geographic ranges within the archipelago, and some may be imperiled due to loss of natural habitat.

Key words: biogeography, *Celaenomys*, *Chrotomys*, cytochrome *b*, distribution, morphology, Muridae, new species, Philippines, vermivory

Chrotomys and *Celaenomys* are among the most distinctive members of the spectacular murine rodent fauna indigenous to the Philippine archipelago. Described in the 1890s (Thomas 1895, 1898), the 2 genera form a well-defined clade within the "old endemic" group of Philippine murines (Division I of Musser and Heaney [1992]), and exhibit morphological specializations associated with vermivorous food habits (Musser and Heaney 1992; Rickart and Heaney 1991; Rickart et al. 1991). *Celaenomys* includes 1 species, *C. silaceus*, from northern Luzon. *Chrotomys* includes 3 named species: *C. whiteheadi* from northern Luzon; *C. mindorensis*, which occurs in central Luzon and on Mindoro; and *C. gonzalesi* from Mt. Isarog in southeastern Luzon. In 1992 a specimen of *Chrotomys* was obtained from Sibuyan, a small (ca. 460-km^2) island in the central Philippines (Goodman and Ingle 1993; Fig. 1). Our preliminary examination revealed that this specimen represents a previously undescribed species of *Chrotomys* (Heaney et al. 1998).

Here, we describe the Sibuyan *Chrotomys* and, in doing so, examine morphological variation, phylogenetic relationships, and biogeographic patterns within the entire *Chrotomys–Celaenomys* clade. We also evaluate the generic distinctiveness of *Celaenomys*, which Corbet and Hill (1992) arranged as a junior synonym of *Chrotomys*. In addition, we present information on the ecology and distribution of species derived from recent field surveys.

MATERIALS AND METHODS

Specimens examined in this study (Appendix I) include those obtained during field surveys by the authors and their associates (Goodman and Ingle 1993; Heaney et al. 1999, 2005; Rickart and Heaney 1991) and earlier museum specimens from the Philippine islands of Luzon, Mindoro, and Sibuyan (Fig. 1). Our fieldwork was conducted in accordance with animal care and use guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). Specimens were assigned to 5 age categories (juvenile, juvenile–adult, young adult, adult, and old adult) as defined by Musser and Heaney (1992) based on relative body size, pelage characteristics, and molar tooth wear. Descriptive terminology for external body features follows Brown (1971) and Brown and Yalden (1973). Terminology for cranial and dental features follows Musser and Heaney (1992). Museum acronyms are defined in Appendix I.

Measurements (in millimeters) of total length, length of tail, length of hind foot including claws, and length of ear from notch, and weight
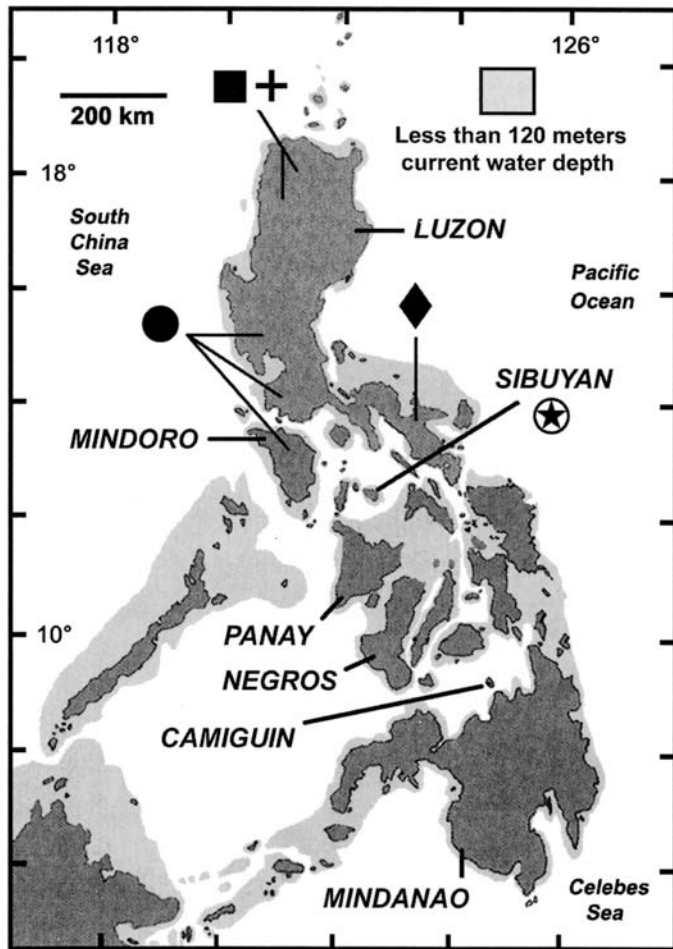

FIG. 1.—Map of the Philippines showing collection localities for specimens of *Celaenomys silaceus* (cross) and *Chrotomys whiteheadi* (closed square) from northern Luzon Island, *Chrotomys gonzalesi* (closed diamond) from southeastern Luzon Island, *Chrotomys mindorensis* (closed circle) from central Luzon Island and Mindoro Island, and a new species of *Chrotomys* (circled star) from Sibuyan Island. Lightly shaded areas show 120-m current water depth, indicating approximate limits of late Pleistocene islands (Heaney 1986).

(in grams) were taken from field catalogs of the authors at the Field Museum of Natural History, Chicago, Illinois (FMNH), and the National Musuem of Natural History, Washington, D.C. (USNM), specimen labels, or from the literature. In some instances, length of hind foot was measured directly from dried skins. The length of head and body was determined by subtracting length of tail from total length. Length of overfur was measured in the middorsal region. The number of tail scale rings per centimeter was counted at a point one-third the distance from the base of the tail.

Twenty-three cranial, mandibular, and dental measurements were taken from adult specimens (young adult, adult, and old adult age categories). Measurements were recorded to the nearest 0.1 mm by using dial calipers (Musser 1979, 1982; Musser and Heaney 1992; Rickart and Heaney 1991). These included condylobasal length, interorbital breadth, zygomatic breadth, breadth of braincase, height of braincase, length of nasal bones, length of rostrum, breadth of rostrum, depth of rostrum, breadth of zygomatic plate, length of diastema, palatal breadth, palatal length, postpalatal length, length of incisive foramina, breadth across incisive foramina, length of auditory bulla,

alveolar length of maxillary molar tooth row, crown length of M1, crown breadth of M1, length of mandible, posterior height of mandible, and depth of mandibular ramus.

For specimens of 3 of the 5 putative taxa (*C. silaceus*, *C. gonzalesi*, and *C. whiteheadi*), karyotypes were prepared from bone marrow cells as reported by Rickart and Musser (1993) and Rickart and Heaney (2002). Microscope slides of chromosome preparations and photomicrograph negatives cross-referenced to voucher specimens cataloged at FMNH and USNM are housed at the Utah Museum of Natural History, University of Utah, Salt Lake City.

Descriptive statistics (mean, standard deviation, and observed range) were calculated for sample groups. Statistical analyses of $\log_{10}$-transformed measurements of adult specimens were performed by using SYSTAT 10 for Windows (SPSS, Inc. 2000). Multivariate analysis of variance was used to assess group differences. Quantitative phenetic variation and group distinctiveness were assessed through principal components analysis (using a correlation matrix) and discriminant function analysis (using backward stepwise estimation and jackknifed classification). A phenogram derived from squared Mahalanobis distances among group centroids was generated with the unweighted pair-group method of arithmetic averages (UPGMA).

Frozen or ethanol-preserved tissue samples (liver, skeletal muscle, or both), were obtained from: *C. gonzalesi* ($n = 2$), *C. whiteheadi* ($n = 3$), the undescribed species of *Chrotomys* from Sibuyan ($n = 1$), and *C. silaceus* ($n = 1$). Tissues were not available for *C. mindorensis*. *Archboldomys luzonensis*, a related Philippine "old endemic" murine (Musser and Heaney 1992; Steppan et al. 2003) was included as the outgroup ($n = 2$). Voucher specimens and their localities are listed in Appendix I.

DNA was extracted from all tissues with a QiaAmp extraction kit (Qiagen Inc., Valencia, California). The entire cytochrome-*b* gene was amplified by using primers MVZ05 and UMMZ04 (Jansa et al. 1999) in 20-µl polymerase chain reactions (PCRs) with AmpliTaq Gold polymerase (Applied Biosystems, Foster City, California) and recommended concentrations of primers, nucleotides, buffer, and $MgCl_2$. Resulting PCR products were purified via electrophoresis through a 2% low melting point agarose gel; the appropriate band was excised from the gel and melted in 300 µl of sterile water. To generate products of a suitable size for sequencing, the resulting purified product was used as a template in 2 subsequent reamplification reactions, 1 with primer MVZ05 paired with UMMZ12 and 1 with UMMZ13 paired with UMMZ04 (Jansa et al. 1999; Smith and Patton 1993). Reamplifications were performed with Taq polymerase (Promega Corp., Madison, Wisconsin) in 30-µl PCR reactions. All reactions were performed on a PerkinElmer 9700 thermal cycler (PerkinElmer, Wellesley, Massachusetts) for 35 cycles with an annealing temperature of 50°C. The resulting products were sequenced in both directions by using amplification primers and dye-terminator chemistry on an ABI 3700 automated sequencer (Applied Biosystems). Sequences were edited and compiled by using Sequencher 4.1 (Gene Codes Corp., Ann Arbor, Michigan). All sequences have been deposited in GenBank, with accession numbers AY687857–AY687865.

The resulting cytochrome-*b* sequences were aligned with reference to the translated amino acid sequences. Aligned sequences were subjected to phylogenetic analysis using maximum parsimony and maximum likelihood as implemented in PAUP* v4.0b10 (Swofford 2002). For the parsimony analysis, all characters were treated as unordered and equally weighted; all parsimony tree searches were exhaustive. The best-fit model for likelihood analysis was determined by evaluating the fit of various substitution models on a neighbor-joining tree and applying sequential likelihood ratio tests as implemented in Modeltest (Posada and Crandall 1998). Once the best-fit

TABLE 1.—External measurements (mm), weight (g), and measurement ratios (expressed as percentages) of adult *Celaenomys* and *Chrotomys*, including a new species from Sibuyan Island. Variables are length of head and body (LHB), length of tail (LT), length of hind foot including claws (LHF), length of ear from notch (LE), weight (WT), length of overfur (LOF), and number of tail scale rings per cm (TSR). First line for each variables gives mean ± 1 SD; 2nd line gives range (with sample size in parentheses).

	Celaenomys silaceus[a]		*Chrotomys gonzalesi*[b]		*Chortomys mindorensis*[c]		*Chrotomys whiteheadi*[d]		*Chrotomys* new species[e]
	Male	Female	Male	Female	Male	Female	Male	Female	Male
LHB	148.9 ± 10.7	148.0 ± 8.6	171.7 ± 14.7	162.5 ± 2.5	173.7 ± 10.2	157.0 ± 2.0	159.6 ± 8.5	160.0 ± 4.9	160
	136−173 (13)	136−158 (4)	145−189 (6)	160−165 (2)	161−186 (3)	155−159 (2)	144−177 (20)	154−166 (7)	
LT	107.9 ± 4.3	105.0 ± 5.8	97.7 ± 7.3	92.0 ± 3.0	114.0 ± 10.7	108.0 ± 8.0	116.4 ± 7.7	109.1 ± 8.3	82
	102−116 (13)	97−111 (4)	87−105 (6)	89−95 (2)	99−123 (3)	100−116 (2)	103−133 (21)	95−118 (7)	
LHF	35.5 ± 1.0	34.3 ± 1.5	36.7 ± 1.7	36	38.8 ± 1.3	36.3 ± 0.5	38.5 ± 1.7	37.6 ± 1.5	34[f]
	34−37 (14)	32−36 (4)	34−39 (6)	36 (2)	37−40 (3)	36−37 (2)	36−42 (24)	35−39 (7)	
LE	20.4 ± 0.9	20.0 ± 0.7	21.7 ± 0.9	21.1 ± 1.0	22.7 ± 0.5	20.3 ± 1.2	24.0 ± 1.1	24.8 ± 1.3	19
	19−22 (12)	19−21 (4)	20−23 (6)	20−22 (2)	22−23 (3)	19−22 (3)	23−26 (20)	23−27 (5)	
WT	90.4 ± 19.1	77.8 ± 6.6	139.3 ± 34.0	105.5 ± 5.5	199	159.0 ± 7.0	117.8 ± 22.8	108.3 ± 14.5	104
	67−130 (11)	71−87 (4)	98−190 (6)	100−111 (2)	(1)	152−166 (2)	73−160 (19)	92−136 (7)	
LOF	10−12 (8)	12 (1)	18 (1)	17 (2)	16 (1)	17 (1)	12−15 (4)	15 (1)	13
TSR	16−19 (18)	17 (1)	20 (1)	18−19 (2)	16 (1)	19 (1)	16−18 (4)	17 (1)	22
LT/LHB	66−79 (13)	67−75 (4)	55−60 (6)	56−58 (2)	57−76 (3)	63−75 (2)	68−79 (20)	58−74 (7)	51
LHF/LHB	22−26 (13)	22−24 (4)	20−23 (6)	22−23 (2)	22−25 (3)	23 (2)	23−26 (19)	22−25 (6)	21

[a] FMNH 62286, 62287, 169132–169134, 170968–170971, 175566–175570, 175723–175726.

[b] USNM 458951, 458952 (holotype), 458953, 458954, 458956–458958; FMNH 147175.

[c] MMNH 12972; USNM 277639, 356290, 536800–536802.

[d] AMNH 185136; USNM 102547, 102552; FMNH 62281, 62282, 167311–167316, 167368–167370, 169135–169137, 169139, 169140, 169142–169144, 170972, 170973, 175571–175576, 175727, 175728.

[e] FMNH 145701 (holotype).

[f] Measured from dried skin.

model was chosen, we used an additional likelihood ratio test to evaluate whether a molecular clock could be enforced. The parameters describing this best-fit model were used in a branch-and-bound tree search as implemented in PAUP*. Bootstrap values (Felsenstein 1985) were calculated under the maximum-likelihood criterion by using 100 pseudoreplicates with heuristic searches employed within each replicate (tree bisection and reconstruction branch swapping on a starting tree obtained via neighbor joining).

Pairwise distance estimates between taxa were corrected for within-species divergence (where applicable) by using the formula $\delta_{xy} = \delta_{xy} - 0.5(\delta_x + \delta_y)$, where δ_x and δ_y are the average pairwise distances within each species and δ_{xy} is the average pairwise distance between species (Nei and Li 1979). Pairwise distances were calculated both as uncorrected percentage difference (p distance) and as corrected maximum-likelihood distances by using the best-fit model.

Our data did not violate the assumption of a molecular clock (see below); therefore, we estimated dates of divergence for particular nodes by using the "calibrate" command in the program r8s (Sanderson 2002). To obtain the standard deviation of divergence time estimates, we constructed 100 bootstrapped data sets by using the seqboot program from PHYLIP 3.5c (Felsenstein 1993), and estimated branch lengths from each bootstrapped data set on our maximum-likelihood topology by using PAUP*. We then performed the dating analysis on each of these data sets and summarized the node statistics by using the "profile" command in r8s.

RESULTS

External, cranial, and dental measurements of *Celaenomys* and *Chrotomys* (Table 1; Appendix II) reveal moderate differences among the 5 putative species in overall size and in hind foot, ear, and tail proportions. There is also a consistent pattern of sexual size dimorphism in which males average slightly larger than females in most measurements. Adult specimens of both sexes were pooled in subsequent multivariate analyses.

A principal components analysis was conducted on 18 cranial and dental measurements from 35 adult specimens including *C. silaceus* ($n = 8$), *C. gonzalesi* ($n = 4$), *C. mindorensis* ($n = 9$), *C. whiteheadi* ($n = 13$), and the Sibuyan *Chrotomys* ($n = 1$). The first 4 components accounted for 90.5% of the total variance (Table 2). Most variables had positive loadings of high magnitude on component 1 (accounting for 73.7% of the total variance), indicating that most of the variation involved size. Component 2 separated individuals mainly on length of incisive foramina and size of the auditory bulla. Component 3 separated individuals based on breadth of the zygomatic plate, length of diastema, and size of molars, whereas component 4 separated specimens based on height of braincase, height of mandible, and interorbital breath (Table 2). A bivariate plot of specimen scores on components 1 and 2 (Fig. 2A) reveals 5 distinct groups representing the 4 named taxa and the specimen from Sibuyan Island. In a plot of components 3 and 4 (Fig. 2B), the 4 named taxa overlap to some extent but the specimen from Sibuyan is separated on component 4. Multivariate analysis of variance revealed highly significant differences between the 5 putative taxa (approximate $F = 5.87$, $d.f. = 72$, 53, $P < 0.001$).

To further assess variation, we conducted a discriminant function analysis of cranial and dental measurement data. Specimens were grouped into 6 population samples representing the 5 putative species. In this analysis, specimens of *C. mindorensis* from Mindoro and Luzon were grouped separately

TABLE 2.—Character loading, eigenvalues, and percentage variance explained on the first 4 components of a principal components analysis of log-transformed cranial and dental measurements of adult *Celaenomys* and *Chrotomys*. Variables are defined in Appendix II.

Variable	Principal component			
	1	2	3	4
IB	0.852	−0.163	0.077	0.292
HBC	0.811	0.006	−0.046	−0.480
LN	0.879	0.118	−0.114	0.075
LR	0.934	0.102	−0.128	−0.068
BR	0.929	−0.024	0.133	−0.018
DR	0.952	−0.060	0.105	0.030
BZP	0.442	−0.183	−0.841	0.181
LD	0.892	0.189	−0.319	0.086
PB	0.926	−0.127	0.233	0.125
PL	0.963	0.109	−0.127	−0.050
LIF	0.091	0.939	0.050	0.278
BIF	0.884	0.197	0.246	−0.102
LB	0.841	−0.281	0.026	0.247
LM1	0.918	−0.101	0.298	0.079
BM1	0.908	−0.210	0.181	0.151
LM	0.972	0.047	0.037	−0.042
HM	0.915	0.105	−0.091	−0.293
DMR	0.867	0.068	−0.135	−0.164
Eigenvalue	13.270	1.225	1.114	0.678
Variance explained (%)	73.723	6.807	6.187	3.765

to assess their distinctiveness. Highly significant differences were detected between sample groups (approximate $F = 9.89$, $d.f. = 50, 94, P < 0.001$). The first 3 canonical variates had eigenvalues of 41.26, 6.50, and 2.37; canonical correlations of 0.99, 0.93, and 0.84; and accounted for 79.1%, 12.5%, and 4.6% of the total variance. The 1st variate was weighted most strongly by length of nasal bones (−1.01), breadth across incisive foramina (0.88), height of braincase (−0.74), and interorbital breadth (0.64). The 2nd variate was weighted by palatal length (2.28), height of braincase (−1.70), interorbital breadth (1.16), depth of rostrum (−1.05), and length of incisive foramina (−0.97). A posteriori jackknifed classification correctly identified 32 of the 35 specimens, including all specimens of *C. silaceus* and *C. gonzalesi*. One specimen of *C. mindorensis* was misclassified as *C. whiteheadi*, 1 *C. whiteheadi* was misclassified as *C. mindorensis*, and the single specimen of *Chrotomys* from Sibuyan Island was identified as *C. whiteheadi*. A plot of the group centroids on the first 2 canonical variates (Fig. 2C) and a UPGMA phenogram (Fig. 2D) reveal close association of the samples of *C. mindorensis* from Mindoro and Luzon; the general proximity of *C. mindorensis*, *C. whiteheadi*, and *C. gonzalesi*; and the distinctiveness of both *Celaenomys* and the Sibuyan *Chrotomys*.

Cytochrome-*b* sequences from specimens representing 4 of the 5 ingroup taxa and 1 outgroup (*A. luzonensis*) yielded 247 informative characters. Parsimony analysis resulted in 2 minimum-length trees with length = 482, consistency index = 0.65, and retention index = 0.70. The topology is consistent with the tree recovered from a likelihood analysis using the best-fit GTR+I+Γ model with a clock enforced (Fig. 3; $\ln\lambda_{\text{clock}} = -4,039.40$; without clock: $\ln\lambda_{\text{no clock}} = -4,035.82$;
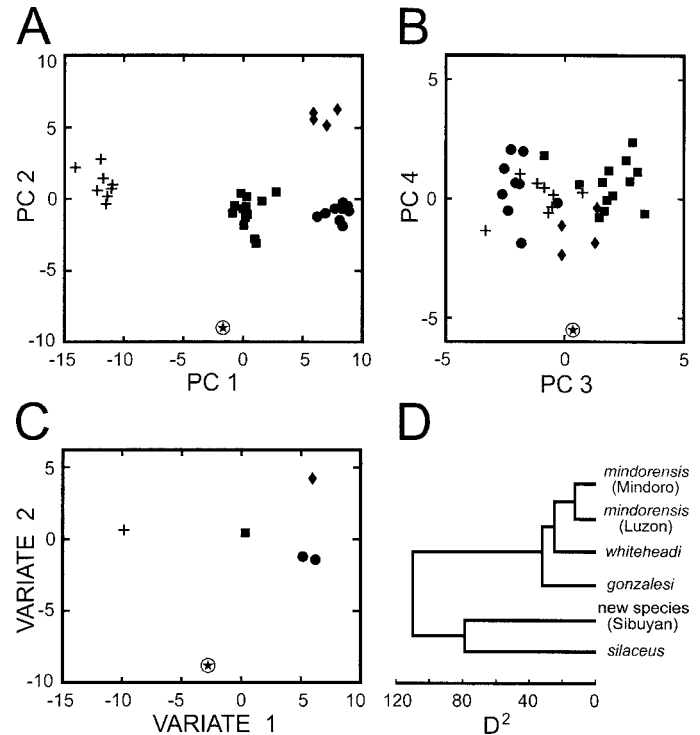

FIG. 2.—Phenetic variation in *Chrotomys* and *Celaenomys*. Results of principal components analysis of cranial measurements of adult specimens: projections of individual specimen scores on A) components 1 and 2, and B) components 3 and 4. Results of discriminant function analysis of cranial measurements: C) plot of 6 sample group centroids on 1st and 2nd canonical variates, D) unweighted pair-group method of arithmetic averages (UPGMA) clustering of samples generated from squared Mahalanobis distances (D^2) among group centroids. Taxa are indicated by crosses (*Celaenomys silaceus*), closed circles (*Chrotomys mindorensis*), closed diamonds (*Chrotomys gonzalesi*), closed squares (*Chrotomys whiteheadi*), and circled star (*Chrotomys*, new species). In the discriminant function analysis, samples of *C. mindorensis* from Mindoro and Luzon were analyzed separately.

$-2\ln\Lambda = 7.15$, $d.f. = 7$, $P = 0.62$). The only difference between trees resulting from the 2 analyses concerns placement of the new species of *Chrotomys*. One of the minimum-length trees places it as the sister taxon to *Celaenomys*; the 2nd tree is topologically identical to the maximum-likelihood tree shown in Fig. 3.

Pairwise sequence divergence within *C. whiteheadi* and *C. gonzalesi* is less than 1% regardless of whether this value was calculated as a raw percentage or was corrected with an explicit model of sequence evolution. These 2 species differ from each other by an average of 5.2%. The Sibuyan *Chrotomys* differs from its congeners by an average of 19.3% and differs from *Celaenomys* by 21.2% (these values are corrected with the best-fit likelihood model; for uncorrected values see Fig. 3).

Using a molecular clock and assuming the often-used *Mus–Rattus* divergence date of 12 million years ago (mya; Jacobs and Downs 1994), we estimate that *Celaenomys* and *Chrotomys* diverged from each other at least 3.9 ± 0.5 mya and that the Sibuyan *Chrotomys* split from its congeners 3.0 ± 0.5 mya.

On the basis of these results and for reasons detailed below, we recognize a single genus (*Chrotomys*) including 5 species as summarized in the following accounts.

SYSTEMATIC ACCOUNTS

Genus *Chrotomys* Thomas, 1895

Chrotomys Thomas, 1895:161.
Celaenomys Thomas, 1898:390.

Type species.—*Chrotomys whiteheadi* Thomas.

Diagnosis.—A genus of Muridae in the subfamily Murinae (Musser and Carleton 1993) distinguished by the following combination of characters: dorsal pelage with a pattern of stripes (pale middorsal stripe flanked by dark lateral stripes) or uniformly silvery gray (sometimes with faint pale middorsal markings on the forehead or between the shoulders); tail much shorter than the combined head and body length; hind foot long and narrow, plantar pads small, hypothenar minute or absent; front feet large with strong digits and large, spatulate claws; nasals truncated anteriorly, external nares, anterior premaxillae and incisors exposed dorsally; skull robust and wedge-shaped, rostrum sharply tapered, supraorbital and temporal surfaces lacking ridges, occipital region inflated; incisive foramina short, posterior palatine foramina positioned opposite the 1st molar or between the 1st and 2nd molars, interpremaxillary foramina very large in most specimens; auditory bulla small with an elongate bony eustachian tube; stapedial foramen large and a groove in the pterygoid plate for the infraorbital branch of the stapedial artery; mandibles elongate, incisor capsule extending into the condyloid process with a prominent capsular process just anterior to the condyle; upper incisors large and procumbent with spatulate wear surfaces, anterior and lateral surfaces rounded in cross section and covered with thick enamel; lower incisors elongate and gently curved, anterior surfaces rounded in cross section, with thick enamel, and wearing to sharp tips; molars small relative to the palatal area, upper and lower 3rd molars reduced or absent; and occlusal surfaces of molars simple, consisting of shallow basins surrounded by enamel rings (Musser and Heaney 1992; Rickart and Heaney 1991).

Content and distribution.—As defined here, *Chrotomys* includes 5 species confined to the islands of Luzon, Mindoro, and Sibuyan within the oceanic portion of the Philippine archipelago.

Chrotomys whiteheadi Thomas, 1895
Luzon Montane Striped Shrew-Rat

Chrotomys whiteheadi Thomas, 1895:161. Type locality "highlands of Northern Luzon," fixed by Thomas (1898) as "Monte Data, Lepanto, N. Luzon, 8000 feet [= 2,440 m]."

Distribution.—Known only from scattered localities in the Central Cordillera of northern Luzon Island (Kalinga, Benguet, and Mountain provinces), between 900 and 2,500 m elevation (Heaney et al. 1998, 2005).

Remarks.—Both this species and the genus were described by Thomas (1895, 1898) based on a small series of specimens
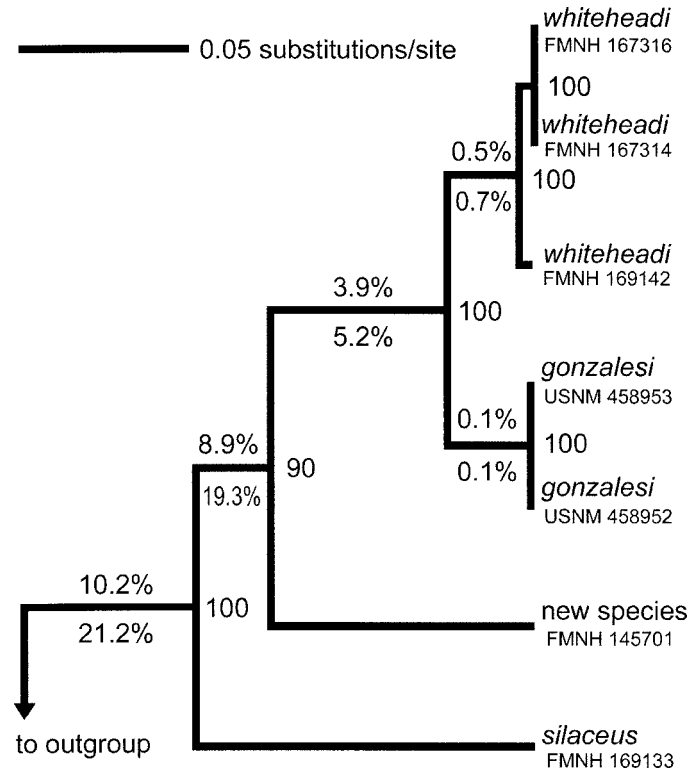

FIG. 3.—Phylogram resulting from analysis of cytochrome-*b* data under the best-fit maximum-likelihood model (GTR+I+Γ with clock enforced). The tree is rooted with *Mus*, *Rattus*, and 2 individuals of *Archboldomys luzonensis* as an outgroup. Average pairwise distances between sister lineages (corrected for intraspecific divergences, where available) are presented above (uncorrected percentage) and below (maximum-likelihood corrected) each corresponding branch. Bootstrap percentages are given beside each node.

from Mt. Data in northern Luzon. Specimens from various highland sites in the Central Cordillera have similar pelage with well-developed dorsal stripe patterns. This species is intermediate in size for the genus (Table 1; Appendix II). A single male specimen yielded a distinctive karyotype of diploid chromosome number (2n) = 38, fundamental number (FN) = 52 (Rickart and Heaney 2002).

Chrotomys mindorensis Kellogg, 1945
Lowland Striped Shrew-Rat

Chrotomys whiteheadi mindorensis Kellogg, 1945:123. Type locality "3 miles south-southeast of San Jose (Central), Mindoro Island, Philippine Islands. Altitude 200 feet [= 60 m]."
Chrotomys mindorensis Musser et al., 1982:514.

Distribution.—Mindoro Island and central portion of Luzon Island (Laguna, Nueva Ecija, Pampanga, and Tarlac provinces) from near sea level to 1,000 m elevation (Heaney et al. 1998; specimen records from the FMNH collection).

Remarks.—*Chrotomys mindorensis* was described by Kellogg (1945) as a subspecies of *C. whiteheadi* based on a single specimen from Mindoro Island. Temme (1974) reported additional specimens from Mindoro and included specimens

from the lowlands of central Luzon within *C. mindorensis*, and Musser et al. (1982) recognized *C. mindorensis* as separate species. This arrangement is corroborated by multivariate analyses of cranial measurements in which specimens of *C. mindorensis* from Mindoro and central Luzon cluster together and are distinct from northern Luzon *C. whiteheadi* (Fig. 2). *C. mindorensis* is larger than other members of the genus in most external and cranial dimensions (Table 1; Appendix II). Available specimens exhibit substantial chromatic variation involving the brightness of the dorsal pelage and distinctiveness of the dorsal stripes. No information is available on the karyotype of this species.

Chromotys gonzalesi Rickart and Heaney, 1991
Isarog Striped Shrew-Rat

Chromotys gonzalesi Rickart and Heaney, 1991:389. Type locality "western slope of Mount Isarog, 4 km N, 21 km E Naga, Camarines Sur Province, Luzon Island, Philippines, 1350 m elevation, 13°40′N, 123°22′E."

Distribution.—Mt. Isarog, Luzon, between 1,350 and 1,800 m elevation (Heaney et al. 1999). This species also may occur on other mountains on the Bicol Peninsula of southeastern Luzon.

Remarks.—In most external and cranial measurements, this species is intermediate in size between *C. whiteheadi* and *C. mindorensis*. The molars are large, and tail and hind foot are comparatively short (Table 1; Appendix II). In multivariate analyses, *C. gonzalesi* is clearly distinguished from congeners (Fig. 2). Pelage is generally darker than in other species, and the development of a pale, middorsal stripe is highly variable among the 9 available specimens. Examination of cytochrome-*b* sequence data indicates a genetic distance of 5.2% between this species and *C. whiteheadi*, the closest association among the 4 taxa that were sequenced (Fig. 3). However, the karyotype of *C. gonzalesi* ($n = 2$ specimens) is 2n = 44, FN = 52. It differs by at least 3 Robertsonian translocations from that of *C. whiteheadi* (2n = 38, FN = 52) but is indistinguishable from the karyotype of *C. silaceus* (Rickart and Heaney 2002; Rickart and Musser 1993).

Chromotys silaceus (Thomas, 1895)
Silver Earth Rat

Xeromys silaceus Thomas, 1895:161. Preliminary diagnosis. Type locality "highlands of Northern Luzon."

Celaenomys silaceus Thomas, 1898:391. Redescription of *Xeromys silaceus*. Type locality fixed as "Monte Data, Lepanto, N. Luzon, 8000 feet [= 2,440 m]."

Chromotys silaceus Corbet and Hill, 1992:383. First use of name combination.

Distribution.—Restricted to the Central Cordillera of northern Luzon Island (Kalinga, Benguet, and Mountain provinces) between 1,900 and 2,500 m elevation (Heaney et al. 1998, 2005).

Remarks.—This species was described by Thomas (1895, 1898) based on 2 specimens obtained from Mt. Data in northern Luzon. Thomas (1895) provisionally referred it to the

Australian hydromyine genus *Xeromys* based on the reduced number of molars, but subsequently placed it in the new genus *Celaenomys* as a close ally of *Chromotys* (Thomas 1898). The loss of the 3rd molar was considered by Thomas (1898) as the principal defining trait of *Celaenomys*. Corbet and Hill (1992) placed this species within *Chromotys* because the absence of the 3rd molar was not a consistent character and therefore was insufficient for generic separation. Guy Musser (pers. comm.) also considers *Celaenomys* to be a synonym of *Chromotys* based on a large number of shared–derived morphological characters that distinguish these taxa from all other Philippine murines (Musser and Heaney 1992). Our results support this arrangement. Although the cytochrome-*b* sequence data place *silaceus* in a basal position relative to the other species (Fig. 3), phenetic analyses show that *silaceus* is no more distinctive than the Sibuyan species (Fig. 2). The morphological features that distinguish *silaceus* from the other species are primarily differences of degree and do not warrant recognition of *Celaenomys* as a separate genus. This species is distinguished from congeners by its smaller body size; pelage that is short, dense, and brownish gray or silvery gray without prominent dorsal stripes (although some specimens have a small pale "blaze" on the forehead or a faint pale line between the shoulders); narrower, more delicate skull; auditory bullae that are separated from, rather than tightly attached to, the squamosal and alisphenoid bones; and greater reduction of the molars including the loss of the 3rd molar in most specimens (Table 1; Appendix II; Musser and Heaney 1992). The standard karyotype (based on 1 specimen) is indistinguishable from that of *C. gonzalesi* (Rickart and Heaney 2002).

Chromotys sibuyanensis, new species

Holotype.—Adult male, FMNH 145701, collected 8 March 1992 (field number 5150 of S. M. Goodman). The specimen consists of a skin, skull, and partial postcranial skeleton (all in excellent condition), and frozen tissue samples (liver and muscle). The specimen currently is deposited at FMNH and is to be transferred to the Philippine National Museum.

Type locality.—Northwest slope of Mt. Guitinguitin, 6.75 km S, 4.5 km E Magdiwang, Romblon Province, Sibuyan Island, Philippines, 1,325 m elevation, 12°26′N, 122°33′E.

Etymology.—The name *sibuyanensis* refers to Sibuyan Island, to which the new species is endemic. "Sibuyan striped earth-rat" is proposed as the English common name.

Diagnosis.—A murine rodent placed in the genus *Chromotys* and distinguished from other Philippine murines by the combination of characters enumerated in the diagnosis of the genus. The following characters distinguish *C. sibuyanensis* from congeners: tail shorter relative to head–body length; hind foot shorter relative to head–body length; cranium smaller (except for *C. silaceus*); interparietal broad and diamond-shaped; occiput flat; zygomatic plate narrow; incisive foramina longer; interpremaxillary foramen absent; and molars smaller relative to palatal area (except for *C. silaceus*). The new species is further distinguished from *C. silaceus* by differences in pelage (general color and presence of a prominent middorsal stripe); larger cranium (in most dimensions); tight attachment of the auditory

bulla to the squamosal and alisphenoid; and larger molars, including upper and lower 3rd molars.

Description and comparisons.—*Chrotomys sibuyanensis* is a medium-sized murine (adult body mass 104 g) with a relatively short tail, strong limbs, and stocky build characteristic of a semifossorial rodent (Fig. 4). Body size is average for the genus, but both the tail and hind foot are absolutely and relatively shorter than in congeners (Table 1).

The new species has dense, soft pelage consisting of a uniform overfur with an average length of 13 mm middorsally. Longer guard hairs are not present. The dorsal overfur is slightly longer than in *C. silaceus*, but shorter than in other species (Table 1). The predominant dorsal coloration from the tip of the snout to the rump is dark blackish brown. Middorsally, a yellowish gray stripe extends from the forehead between the eyes to a point on the rump near the base of the tail. The stripe is continuous but variable in width, and narrower than those of *C. whiteheadi* and most specimens of *C. mindorensis* and *C. gonzalesi*. Individual overfur hairs in dark regions have basal two-thirds dark gray with blackish brown tips. Hairs that constitute the stripe have yellowish tips. Laterally there are scattered hairs with tips that are light brown or gray resulting in a lighter grayish brown color compared to the dark dorsum. The transition from dorsal to lateral color is gradual, rather than abrupt as in most specimens of *C. whiteheadi* and *C. mindorensis*, which appear to have 2 blackish stripes flanking the pale middorsal line. The transition from the sides to the lighter colored venter is abrupt. Ventral coloration is uniform dark yellowish gray with some patches of lighter silvery gray on the throat, wrists, chest, and urogenital region. Individual hairs on the venter are shorter (8 mm on average) and are dark gray basally with tips that are yellowish gray or silvery gray.

With the exception of the middorsal stripe, the dorsal surface of the head is dark blackish brown. Laterally, the cheeks and jowls are brownish gray. The rhinarium is unpigmented with a scattering of very short silvery hairs. The lips and skin near the mouth are slightly pigmented with scattered hairs that are silvery to dark gray. The eyelids are narrowly edged with black but there is no ring of bare skin around the eye. Mystacial vibrissae are numerous, long (extending to the ears), and are brownish gray. The few superciliary vibrissae are of similar color but shorter than the mystacials. Ear pinnae are blackish gray and nearly naked on both surfaces with a scattering of very short silvery gray hairs.

The color of the tail (from color slides taken soon after death) is medium brown, slightly paler on the ventral surface and at the tip. Tail scales are pale to medium brown and substantially smaller than those of congeners (Table 1). Associated with each scale are 3 stiff, brown hairs 1–2 mm long.

Dorsal surfaces of the feet are unpigmented. Fine silvery hairs are scattered on the metapodial surfaces and the digits are nearly naked. As in congeners, the forefeet are large with strong digits. The pollex has a flat, dark-colored nail and the other digits bear dark-colored claws that are long, thick, and only slightly recurved. The palmar surface is naked and unpigmented, with 3 small interdigital pads and a large thenar and hypothenar. The hind feet are long (although smaller

Fig. 4.—A) Dorsal, B) ventral, C) and lateral views of *Chrotomys sibuyanensis* (FMNH 145701, holotype).

relative to body size compared to congeners) with strong digits and large, dark claws. The plantar surface is naked and unpigmented with 4 interdigital pads, a moderate-sized thenar, and a small hypothenar. As in the other species, the plantar pads are small relative to the entire plantar surface.

The skull of *C. sibuyanensis* (Fig. 5) is slightly larger, relatively broader, and more robust than that of *C. silaceus*, but smaller than those of the other species (Fig. 6; Appendix II). From a dorsal perspective (Fig. 5), the rostrum is long and tapered. Anterior surfaces of the procumbent upper incisors project beyond the premaxillae. The nasals terminate posterior to the anterior margins of the premaxillae such that the external nares are exposed dorsally. The zygomatic arches are less strongly backswept and more rounded anteriorly than in congeners. As in the other species, the frontal region is expanded and the interorbit constricted, imparting an hourglass shape to the midcranial region. The braincase is roughly rectangular in outline, and the supraorbital, temporal, and occipital margins are smooth and lack ridges. At the posterior margin of the
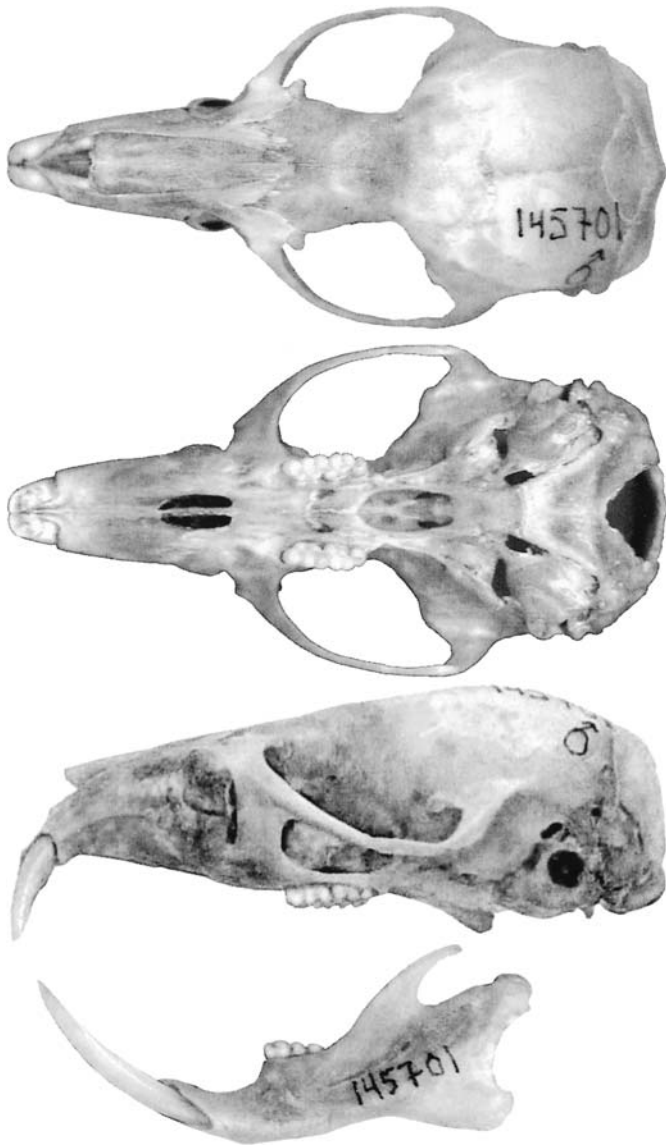
Fig. 5.—Dorsal (top), ventral (2nd row), and left lateral (3rd row) views of cranium, and labial view of left mandible (bottom) of *Chrotomys sibuyanensis* (FMNH 145701, holotype).

Fig. 6.—Ventral views of anterior portion of skulls of A) *Chrotomys silaceus* (FMNH 170968), B) *Chrotomys sibuyanensis* (FMNH 145701, holotype), C) *Chrotomys gonzalesi* (USNM 458956), D) *Chrotomys whiteheadi* (FMNH 169140), and E) *Chrotomys mindorensis* (FMNH 142617).

braincase, the interparietal is wide (anterior–posterior axis), whereas this bone is very narrow in the other species.

In lateral view (Fig. 5), the skull of the new species exhibits features typical for the genus. The highly prognathus upper incisors project well beyond the premaxillae, which themselves are elongated anteriorly. The rostrum is strongly tapered due to the ventral profile of the premaxillae and maxillae, which slope sharply ventrad from the incisor alveoli to the molars. The nasals are rounded laterally, imparting a tubular form to the anterior rostrum. The dorsal profile of the skull is nearly straight, from the nasal tips to the braincase, with only the slightest convexity over the expanded frontals. The braincase has a smoothly rounded profile. There is an abrupt transition to the relatively flat, vertical occiput, although the surface is smooth and there is no medial lambdoidal ridge. In contrast,
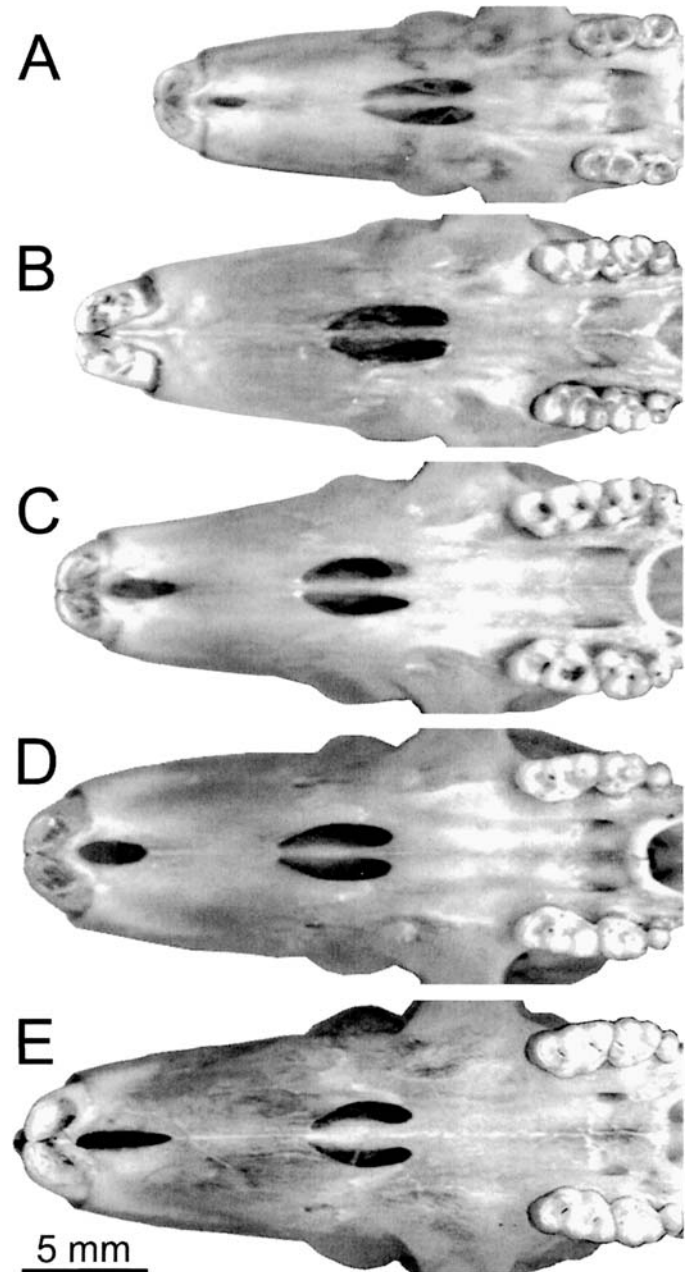
the occipital regions of the other species are more inflated and posterior skull profiles are rounded. In all species of *Chrotomys*, the zygomatic arch is strongly built and relative positions of the anterior and posterior zygomatic roots are similar. The zygomatic plate, although broad in all species, is substantially narrower in *C. sibuyanensis* (Appendix II). The new species has a moderate sqamosal–mastoid foramen. This opening also is found in most specimens of *C. silaceus*, but not in the other species. The mastoid is inflated, and there is a foramen on the dorsal margin near the occipital. The auditory

bulla is small, as in other members of the genus, and is tightly attached to the cranium. As in congeners, a lateral strut of the alisphenoid partially encloses the alisphenoid canal.

A ventral view of the skull of *C. sibuyanensis* (Figs. 5 and 6) reveals some unique features. In the other species of *Chrotomys*, an elongate interpremaxillary foramen is located immediately posterior to incisor alveoli (Fig. 6) and, although variable in size and shape, this is a prominent opening in all specimens that we have examined. In contrast, this opening is not present in the single example of the new species but is replaced by a pair of minute foramina. In all species, the incisive foramina are short and broad in comparison to other murines. However, these openings are relatively longer in *C. sibuyanensis* than in the other taxa (Fig. 6; Appendix II). As in the other species of *Chrotomys* (except for those specimens of *C. silaceus* that lack 3rd molars), the palate is short and does not extend to the end of the molar tooth row. Shallow palatal grooves extend from the posterior margins of the incisive foramina to the posterior end of the palate. The postpalatine foramina are located within the grooves at a position between the 1st and 2nd molars. The mesopterygoid fossa is narrow compared to those of congeners, and the sphenopalatine vacuities in the dorsolateral walls are larger. The lateral pterygoid fossae are narrow and shallow, and each contains a small sphenopterygoid vacuity on the dorsomedial surface. The posterior margin of each pterygoid plate is separated from the auditory bulla by a narrow middle lacerate foramen. As in the other species of *Chrotomys*, there is a large stapedial foramen on the posteromedial margin of the bulla that receives the stapedial artery, and the lateral margin of the pterygoid plate has a groove for the interorbital branch of this artery, which passes from the bulla to the orbit. This is the common (and presumably primitive) pattern of cephalic arterial circulation for murines (Musser and Heaney 1992).

The mandible of *C. sibuyanensis* (Fig. 5) closely resembles those of congeners (Musser and Heaney 1992:84, figure 50). The coronoid process is long and backswept, the angular process is broad, and the posterior margin of the mandible is slightly concave. The root of the elongate incisor extends caudad to a point below the condyle, ending at a prominent capsular process on the labial surface. The ventral surface of the mandibular ramus immediately posterior to the symphysis is flattened and heavily pitted.

As in the other species of *Chrotomys*, the procumbent upper incisors are ungrooved, with rounded anterior faces, thick enamel extending onto the lateral surfaces, and wearing to rounded, spatulate tips. The lower incisors are long and slender with rounded anterior faces, thick enamel, and wearing to sharp, awl-shaped tips (Figs. 5 and 6; Musser and Heaney 1992:79, figure 46). Enamel on both upper and lower incisors is pale ivory colored. The holotype of *C. sibuyanensis* is an adult with relatively unworn molars (Fig. 7). The molar tooth row is substantially shorter than those of congeners with the exception of *C. silaceus* (Fig. 6; Appendix II). In all taxa, the upper and lower 3rd molars are reduced (or absent in most specimens of *C. silaceus*). However, the 3rd molars are relatively larger in *C. sibuyanensis*. Cusp patterns on the upper molars are similar in all taxa, and are simplified through the
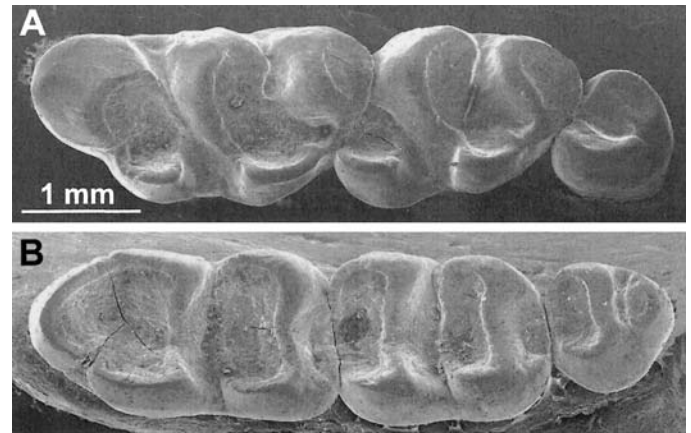

FIG. 7.—Occlusal views of A) maxillary and B) mandibular left molar tooth rows of *Chrotomys sibuyanensis* (FMNH 145701, holotype).

loss or fusion of labial cusps t3, t6, and t9 on the 1st and 2nd molars (Musser and Heaney 1992). Lower molars also have simplified crowns due to the fusion of primary cusps and the loss of secondary labial cusplets. On the 1st lower molar, the anteroconid consists of partially fused anterolabial and anterolingual cusps that are merged (respectively) with the protoconid and metaconid to form a ringed basin comprising the anterior half of the tooth. The posterior portion of the crown consists of a 2nd basinlike lamina formed from the fused hypoconid and entoconid. The crown of the 2nd lower molar includes 2 smaller basinlike laminae (involving the protoconid–metaconid, and the hypoconid–entoconid), whereas the 3rd lower molar includes a small anterior lamina (protoconid–metaconid) and a posterior protuberance (fused hypoconid–entoconid). The 1st lower molar has a posterior cingulum, which, compared to those of the other taxa, is larger and located more medially on the posterior margin of the tooth. The 2nd lower molar also bears a posterior cingulum, a feature that is either absent or much reduced in the other taxa (Fig. 7; Musser et al. 1982:520, figure 4; Musser and Heaney 1992: 80, figure 47).

Ecology.—The holotype, the only known example of *C. sibuyanensis*, was captured at 1,325 m elevation along a steep ridge on the northern slope of Mount Guitinguitin in a transition zone between montane and mossy forest habitat (Goodman et al. 1995). Dominant vegetation at the type locality included climbing bamboo (*Schizostachyum*) and a gymnosperm tree (*Podocarpus*). The understory consisted primarily of creeping pandan (*Freycinetia*). Abundant epiphytes included moss, ferns, orchids, and pitcher plants (*Nepenthes*). Other murines trapped at the type locality included an undescribed species of *Apomys* and an undescribed species allied with *Rattus* or *Tarsomys* (Goodman and Ingle 1993; Heaney et al. 1998; G. Musser, pers. comm.). The holotype of *C. sibuyanensis* was captured in a snap trap placed on the ground in a tunnellike runway formed by bamboo leaves overlaying creeping pandans. The animal was oriented sideways in the trap in a position indicating that it probably was not attracted to the bait, which

consisted of roasted coconut coated with peanut butter. The stomach of the holotype was empty so there is no direct evidence of diet. However, the morphological specializations shared with better-known congeners (stocky build, short tail, strong forelimbs with heavy claws, narrow hind feet with smooth plantar surfaces, sturdy cranium, and strong, prognathus upper incisors) suggest a semifossorial animal with vermivorous habits (Heaney et al. 1999; Rickart et al. 1991). The specimen was fresh when recovered from the trap in late afternoon (about 1600 h), demonstrating diurnal activity, as seen in the other species of *Chrotomys* (Rickart et al. 1991; specimen records from the FMNH collection). The holotype is an adult male that was in reproductive condition with testes measuring 20 × 12 mm, convoluted epididymides, and well-developed seminal vesicles.

DISCUSSION

As with other groups of Philippine murines (Rickart et al. 1998, 2002; Steppan et al. 2003), the diversification of *Chrotomys* (Fig. 3) must be discussed in the context of the complex historical geography of the archipelago (Hall 1996, 1998, 2002). With the exception of the Palawan group, the Philippine islands are oceanic in origin and have never had dry land connections to mainland Asia. *Chrotomys* is represented on Luzon, Mindoro, and Sibuyan. Each of these islands is surrounded by deep water channels, and thus remained isolated from one another during Pleistocene periods of lower sea level; accordingly, any faunal interchange between them has involved overwater dispersal (Heaney 1985, 1986, 2000; Steppan et al. 2003).

Apparently, much of the diversification of *Chrotomys* has occurred on Luzon, the largest and geographically most complex island (Hall 2002). The oldest region is northern Luzon where a large island has existed since at least the middle Miocene (ca. 15 mya). The occurrence of both *C. silaceus* (the basal member of the clade) and *C. whiteheadi* in northern Luzon along with other related "old endemic" murine genera (Musser and Heaney 1992) reflects the probable origin and early diversification of the genus and its nearest relatives within this region (see also Steppan et al. 2003). The Bicol Peninsula of southeastern Luzon had a much more recent origin during the Pliocene (ca. 3.5 mya). The presence of *C. gonzalesi* in the Bicol region may reflect more recent vicariant speciation across montane habitat on Luzon (Rickart and Heaney 1991).

Mindoro also is a relatively old island, with a submarine origin as part of the Asian continental shelf and subsequent uplift during the late Miocene (ca. 8–10 mya). *C. mindorensis* occurs both on Mindoro and in central Luzon. Although we have no genetic or cytogenetic information on this species, the lack of any significant phenetic distinction between island samples along with the similarity between *mindorensis* and both *whiteheadi* and *gonzalesi* (Fig. 2D) suggests a relatively late divergence from the other taxa (either through speciation on Luzon or as a result of dispersal to Mindoro) followed by very recent overwater dispersal between the 2 islands.

The occurrence of *C. mindorensis* on both Luzon and Mindoro reflects a broader pattern. Among approximately 50 species of native murines known from the oceanic portion of the Philippines (i.e., excluding the Palawan region), only 5 (ca. 10%) occur on more than 1 oceanic Pleistocene island (Heaney et al. 1998; Rickart et al. 1998; Steppan et al. 2003). These include *C. mindorensis* and *Apomys musculus* (on Luzon and Mindoro), *Apomys* "sp. A/C" (Negros-Panay and Sibuyan), *Crunomys melanius* (Mindanao and Camiguin), and *Rattus everetti* (Luzon, Mindoro, Mindanao, and some smaller oceanic islands). These islands are separated by water channels that, although deep (> 120 m), are in most instances relatively narrow (Fig. 1). With the possible exception of *A. musculus*, the species involved also are notable in that they are among the few nonvolant small mammals of the Philippines that occur in lowland habitat (Heaney 2001; Heaney et al. 1998). Apparently, occurrence at low elevations has facilitated dispersal across narrow water barriers that persisted during periods of lower sea level associated with Pleistocene glaciation. This pattern is particularly noteworthy given the apparent importance of overwater dispersal and subsequent speciation in the diversification of Philippine murines (Heaney 2000; Heaney and Rickart 1990; Rickart et al. 2002; Steppan et al. 2003).

Examination of the cytochrome-*b* data indicates an origination of *C. sibuyanensis* at least 2–3 mya. Although there are only rough geological dates for the origin of Sibuyan as a dryland island, the origin was sufficiently early to produce a level of endemism that is remarkable for an island of such small size. Of the 6 species of native nonvolant mammals known from Sibuyan, 3 are endemic to the island, including, in addition to *C. sibuyanensis*, an undescribed species of *Apomys* ("sp. B"— Steppan et al. 2003), and an undescribed murine related to *Tarsomys* or *Rattus* (Heaney et al. 1998; G. Musser, pers. comm.). Furthermore, as noted above, a 2nd undescribed species of *Apomys* ("sp. A/C") is endemic to Sibuyan plus the neighboring oceanic island group of Negros–Panay (Steppan et al. 2003). Finally, Sibuyan supports an endemic pteropodid bat in the genus *Haplonycteris*; it is 1 of only 10 species of pteropodids recorded from the island (Goodman and Ingle 1993; Heaney et al. 1998). Camiguin, another small (265-km^2) island that is located just north of Mindanao but isolated by deep water, provides a parallel example; 2 of its 4 species of native rodents are island endemics (Heaney and Tabaranza, in press a, in press b; Rickart et al. 2002).

Although the 5 species of *Chrotomys* exhibit morphological similarities that suggest they share the same basic habits as semifossorial vermivores, they have different elevational distributions and habitat affinities. Both *C. silaceus* and *C. whiteheadi* are endemic to the Central Cordillera of northern Luzon. The former is restricted to montane and mossy forest habitats mainly above 2,000 m elevation, whereas the latter has a broader elevational range and occurs in lower montane forests at midelevations down to 1,000 m (Heaney et al. 2005; Rabor 1955; Sanborn 1952). Although these 2 species occur in local sympatry, differences in external and cranial morphology suggest some behavioral divergence. Furthermore, examination of our field data indicates microhabitat segregation of the 2

species along moisture gradients (specimen records and field notes of the FMNH collection). *C. gonzalesi* is restricted to upper montane and mossy forest habitats from 1,000 m to the peak elevation (1,966 m) on Mt. Isarog (Heaney et al. 1999; Rickart et al. 1991). Likewise, the holotype and sole example of *C. sibuyanensis* also is from high-elevation forest. In contrast, *C. mindorensis* occurs in lowland habitats below 1,000 m elevation (Barbehenn et al. 1973; Temme 1974), and is one of relatively few native Philippine murines with an elevational distribution centered in the lowlands (Heaney et al. 1998).

Chrotomys mindorensis and, to a lesser extent, *C. whiteheadi* are somewhat unusual among native Philippine murines in their tolerance of habitat disturbance. Both occur in 2nd-growth habitat in or near agricultural areas (Barbehenn et al. 1973; Heaney et al. 2005; Temme 1974). This is somewhat surprising given the extreme trophic specialization of these species. However, it may derive from the fact that earthworms, particularly nonnative species, may be especially abundant in disturbed areas (Tsai et al. 2000; S. James, pers. comm.). In contrast, other species of *Chrotomys* are restricted to relatively intact forest habitats, and apparently are uncommon where they do occur (Balete and Heaney 1997; Goodman and Ingle 1993; Heaney et al. 2005; Rickart et al. 1991). In part, apparent rarity may simply reflect dietary specialization that makes these species difficult to trap with conventional baits and techniques (Balete and Heaney 1997; Rickart et al. 1991). However, with the possible exception of *C. mindorensis*, members of this group have restricted geographic and ecological ranges and some populations may be threatened by loss of primary forest habitat.

Discovery of the unusual endemic species *C. sibuyanensis* on Sibuyan reinforces the need for effective protection of the native biota of this small island. A declaration in 1996 established a national park on Sibuyan, in part as a response to the detection of this and other mammal species endemic to the island. Unfortunately, effective measures to limit habitat destruction due to illegal logging have yet to be implemented (Goodman and Ingle 1993; Mallari et al. 2001; Ong et al. 2002).

BUOD

Ang *Celaenomys* at *Chrotomys* ay binubuo ng mga daga na kadalasan ay nakatira sa mga lungga sa lupa at kumakain ng mga bulati. Sila ay makikita lamang sa Pilipinas. Apat na uri ng mga dagang nabanggit ang kinikilala mula sa mga pulo ng Luson at Mindoro. Ang panglimang uri, na siya naming isinalarawan sa lathain na ito, ay makikita naman sa Sibuyan, isang maliit na pulo sa gitnang Pilipinas na nagiisa at nahihiwalay sa mga karatig pulo ng malalalim na karagatan. Ipinapahiwatig ng mga kailangang kabatiran ng cytochrome-*b* ng apat sa limang uri nila na ang *Celaenomys silaceus* ay ang mas nakatatandang angkan at kalipi. Subalit ang kanilang likas na kaanyuhan at chromosomes ay hindi umaayon sa pagkilala ng *Celaenomys* bilang hiwalay na lipi. Batay pa rin sa kanilang cytochrome-*b,* ang *Chrotomys* sa Sibuyan ay ipinapalagay na mas maagang nahiwalay mula sa sinaunang angkan kaysa sa dalawang nasa Luson. Ang pagiba-iba ng uri ng *Chrotomys* ay inaakalang dulot ng pagwatak-watak ng mga saunahing kagubatan sa Luson at ang paglaganap ng mga nabanggit na uri sa mga karatig pulo. Ang mga dagang ito ay karaniwang nabubuhay sa matataas na bahagi ng mga kabundukan at matatagpuan lamang sa iilang bahagi ng Pilipinas. May iba sa kanila na nanganganib nang mawala ng tuluyan sanhi ng pagkawala ng mga tinitirahan nilang kagubatan.

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APPENDIX I

Specimens examined.—The specimens examined in this study are housed at the American Museum of Natural History, New York (AMNH); Field Museum of Natural History, Chicago, Illinois (FMNH); Bell Museum of Natural History, University of Minnesota, Minneapolis (MMNH); and National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and were prepared as museum skins with skulls, skins with skulls and incomplete skeletons, complete skeletons, and formalin-fixed specimens stored in 70% ethyl alcohol (some with skulls subsequently removed and cleaned). Specimens used in molecular analysis are marked with asterisks and their GenBank accession numbers are given in brackets. All locations are in the Philippines.

Archboldomys luzonensis.—LUZON ISLAND: Camarines Sur Province, Mount Isarog, 4 km N, 21.5 km E Naga, 1,350–1,750 m, 13°40′N, 123°22′E (USNM 573834* [AY687858], 573835* [AY687857]).

Chrotomys silaceus.—LUZON ISLAND: Kalinga Province, Balbalan Municipality, Am-licao, 1,800 m, 17°26.5′N, 121°04.25′E (FMNH 169130–169132, 169133* [AY687859], 169134, 170968–170971); Mount Bali-it, 1,950 m, 17°25.8′N, 121°00.1′E (FMNH 175566–175569, 175723), 2,150 m, 17°25.7′N, 121°59.8′E (FMNH 175570, 175724–175726); Mountain Province, Mount Data, 7,000–8,000 feet (FMNH 62286, 62287).

Chrotomys gonzalesi.—LUZON ISLAND: Camarines Sur Province, Mount Isarog, 4 km N, 21.5 km E Naga, 1,350–1,800 m, 13°40′N, 123°22′E (USNM 458951, 458952* [AY687861], 458953* [AY687860], 458954–458958; FMNH 147175).

Chrotomys mindorensis.—LUZON ISLAND: Laguna Province, Los Baños, International Rice Research Institute (USNM 536800–536802); Nueva Ecija Province, San Jose, south of Manikla (USNM 399581); Pampanga Province, Clark Air Base (USNM 356390). MINDORO ISLAND: Mindoro Occidental Province, 3 miles SSE San Jose, Central (USNM 277639); Mount Iglit Station (MMNH 12972); Mindoro Oriental Province, Mount Halcon Range, 725–1,000 m elev. (FMNH 196510, 196627).

Chrotomys whiteheadi.—LUZON ISLAND: Kalinga Province, Balbalan Municipality, Barangay Balbalasang, 925 m, 17°29.1′N, 121°03.3′E (FMNH 175571, 175727, 175734); Mapga, 1,050 m, 17°28.5′N, 121°04.5′E (FMNH 169135–169141, 169142* [AY687864], 169143, 169144, 170972–170975); Magdalao, 1,600 m, 17°27.5′N, 121°04.1′E (FMNH 167311–167313, 167314* [AY687865], 167315, 167316* [AY687863]; 167368–167370); Mount Bali-it, 1,950 m, 17°25.8′N, 121°00.1′E (FMNH 175572–175574, 175728, 175729), 2,150 m, 17°25.7′N, 121°59.8′E (FMNH 175575, 175576); Mountain Province, Mount Data, 7,000–8,200 feet (2,133–2,500 m) elev. (AMNH 185136; FMNH 62281, 62282; USNM 102547, 102548, 102552).

Chrotomys sibuyanensis.—SIBUYAN ISLAND: Romblon Province, northwest slope of Mount Guitinguitin, 6.75 km S, 4.5 km E Magdiwang, 1,325 m, 12°26′N, 122°33′E (FMNH 145701* [AY687862]).

APPENDIX II

Cranial and dental measurements in millimeter (mean, *SD*, range, and sample size) of adult *Celaenomys* and *Chrotomys*, including a new species from Sibuyan Island. Variables are condylobasal length (CBL), interorbital breadth (IB), zygomtic breadth (ZB), breadth of braincase (BBC), height of braincase (HBC), length of nasal bones (LN), length of rostrum (LR), breadth of rostrum (BR), depth of rostrum (DR), breadth of zygomatic plate (BZP), length of diastema (LD), palatal breadth (PB), palatal length (PL), postpalatal length (PPL), length of incisive foramina (LIF), breadth across incisive foramina (BIF), length of auditory bulla (LB), alveolar length of maxillary molar tooth row (ALM), crown length of M1 (LM1), crown breadth of M1 (BM1), length of mandible (LM), posterior height of mandible (HM), and depth of mandibular ramus (DMR).

	Celaenomys silaceus[a]		*Chrotomys gonzalesi*[b]		*Chrotomys mindorensis*[c]		*Chrotomys whiteheadi*[d]		*Chrotomys* new species[e]
	Male	Female	Male	Female	Male	Female	Male	Female	Male
CBL	36.9 ± 1.3	35.1 ± 0.5	41.9	38.7	41.2 ± 1.1	40.9 ± 1.1	39.6 ± 1.3	38.9 ± 0.6	37.4
	34.7−38.7 (5)	34.6−35.5 (2)	(1)	(2)	40.1−43.1 (5)	40.1−42.8 (4)	38.2−42.0 (7)	37.9−40.0 (7)	
IB	6.6 ± 0.1	6.7 ± 0.1	7.8 ± 0.1	7.8	7.5 ± 0.1	7.4 ± 0.3	7.2 ± 0.2	7.1 ± 0.2	6.8
	6.4−6.8 (7)	6.6−6.7 (2)	7.7−7.9 (3)	(2)	7.5−7.7 (5)	6.9−7.7 (4)	7.0−7.5 (7)	6.7−7.3 (7)	
ZB	18.3 ± 0.7	17.1 ± 0.1	22.0 ± 0.4	20.7 ± 0.3	22.0 ± 1.1	21.6 ± 0.6	20.9 ± 0.8	20.4 ± 0.5	19.4
	17.0−19.0 (5)	17.0−17.1 (2)	21.6−22.4 (2)	20.4−21.0 (2)	20.9−24.0 (5)	21.0−22.5 (4)	19.5−22.0 (6)	20.1−21.5 (7)	
BBC	14.7 ± 0.3	14.4 ± 0.1	15.8 ± 0.1	15.9 ± 0.1	16.3 ± 0.4	15.9 ± 0.1	15.7 ± 0.1	15.8 ± 0.3	15.2
	14.2−14.9 (5)	14.3−14.4 (2)	15.7−15.9 (2)	15.8−16.0 (2)	15.9−17.1 (5)	15.8−16.1 (4)	15.5−15.8 (6)	15.5−16.2 (7)	
HBC	11.2 ± 0.4	11.0 ± 0.1	11.5 ± 0.1	11.4 ± 0.1	12.2 ± 0.2	12.3 ± 0.4	11.8 ± 0.2	11.7 ± 0.2	11.7
	10.7−11.8 (6)	10.9−11.0 (2)	11.5−11.6 (2)	11.3−11.4 (2)	12.0−12.5 (5)	11.7−12.6 (4)	11.5−12.1 (6)	11.3−12.0 (7)	
LN	11.3 ± 0.7	10.9 ± 0.9	13.4 ± 0.3	12.6 ± 0.4	13.4 ± 0.1	12.9 ± 0.8	12.3 ± 0.4	11.9 ± 0.6	11.8
	10.5−12.5 (7)	10.0−11.7 (2)	13.1−13.6 (2)	12.2 ± 12.9 (2)	13.2−13.6 (5)	12.1−14.1 (4)	11.7−13.2 (8)	11.0−12.8 (7)	
LR	15.5 ± 0.7	15.1 ± 0.3	18.1 ± 0.1	16.9 ± 0.1	18.0 ± 0.9	17.7 ± 0.6	17.3 ± 0.5	17.1 ± 0.5	16.3
	14.6−16.5 (7)	14.8−15.4 (2)	18.0−18.1 (2)	16.8−16.9 (2)	17.4−19.7 (5)	17.2−18.7 (4)	16.5−18.1 (8)	16.7−17.7 (7)	
BR	6.6 ± 0.3	6.6 ± 0.1	8.6 ± 0.2	8.1	8.7 ± 0.5	8.4 ± 0.2	8.0 ± 0.2	7.9 ± 0.3	8.0
	6.3−7.3 (7)	6.5−6.6 (2)	8.4−8.8 (3)	(2)	8.1−9.6 (5)	8.2−8.8 (4)	7.6−8.3 (8)	7.4−8.3 (7)	
DR	6.2 ± 0.3	6.3 ± 0.3	7.8 ± 0.3	7.4	7.9 ± 0.2	7.7 ± 0.3	7.1 ± 0.1	7.2 ± 0.2	7.3
	5.8−6.6 (7)	6.0−6.5 (2)	7.5−7.8 (2)	(2)	7.5−8.2 (5)	7.4−8.1 (4)	7.0−7.3 (8)	7.0−7.4 (7)	
BZP	2.9 ± 0.1	2.9 ± 0.2	3.1 ± 0.1	3.0 ± 0.1	3.0 ± 0.2	3.1 ± 0.1	3.0 ± 0.2	2.9 ± 0.2	2.6
	2.7−3.1 (7)	2.7−3.0 (2)	3.0−3.3 (2)	2.9−3.0 (2)	2.6−3.2 (5)	2.9−3.2 (4)	2.7−3.3 (8)	2.5−3.2 (7)	
LD	13.4 ± 0.5	12.8 ± 0.3	15.7 ± 0.2	14.1 ± 0.1	15.0 ± 0.6	14.8 ± 0.3	14.4 ± 0.7	14.1 ± 0.6	13.5
	12.7−14.0 (7)	12.5−13.0 (2)	15.5−15.8 (2)	14.0−14.1 (2)	14.3−16.0 (5)	14.5−15.2 (4)	13.5−15.5 (8)	13.5−15.2 (7)	
PB	6.1 ± 0.1	6.1 ± 0.1	8.2 ± 0.2	8.0	7.9 ± 0.3	7.7 ± 0.2	7.2 ± 0.3	7.3 ± 0.2	7.0
	5.9−6.3 (7)	6.0−6.1 (2)	8.1−8.3 (3)	(2)	7.6−8.3 (5)	7.5−8.0 (4)	6.8−7.7 (8)	7.0−7.5 (7)	
PL	19.6 ± 0.7	18.8 ± 0.3	23.0 ± 0.1	21.2 ± 0.2	22.7 ± 0.7	22.5 ± 0.6	21.7 ± 0.8	21.2 ± 0.6	20.1
	18.6−20.7 (7)	18.5−19.0 (2)	22.9−23.1 (2)	21.0−21.4 (2)	22.1−23.8 (5)	21.9−23.5 (4)	20.5−23.2 (8)	20.3−22.4 (7)	
PPL	14.2 ± 0.6	13.6 ± 0.4	15.6 ± 0.4	14.8	15.7 ± 0.4	15.7 ± 0.6	15.2 ± 0.5	14.9 ± 0.3	14.2
	13.2−15.1 (5)	13.2−13.9 (2)	15.2−15.9 (2)	(2)	15.3−16.5 (5)	15.1−16.6 (4)	14.4−15.8 (8)	14.4−15.5 (7)	
LIF	4.1 ± 0.2	3.9 ± 0.2	4.3 ± 0.3	4.0 ± 0.1	4.1 ± 0.2	3.8 ± 0.2	4.3 ± 0.4	4.0 ± 0.4	5.0
	3.7−4.4 (7)	3.7−4.0 (2)	4.0−4.5 (2)	3.9−4.1 (2)	3.9−4.4 (5)	3.5−4.1 (4)	3.7−4.7 (8)	3.5−4.8 (7)	
BIF	1.7 ± 0.2	1.6 ± 0.1	2.2 ± 0.2	2.1 ± 0.1	2.3 ± 0.1	2.2 ± 0.1	2.2 ± 0.1	2.1 ± 0.1	2.2
	1.5−2.0 (7)	1.5−1.6 (2)	2.1−2.3 (2)	2.0−2.1 (2)	2.2−2.4 (5)	2.1−2.3 (4)	2.0−2.3 (8)	1.9−2.2 (7)	
LB	5.1 ± 0.1	5.2 ± 0.2	5.8 ± 0.1	5.8 ± 0.1	6.0 ± 0.1	5.8 ± 0.1	5.4 ± 0.2	5.4 ± 0.2	5.1
	4.9−5.2 (6)	5.0−5.4 (2)	5.6−5.9 (3)	5.7−5.8 (2)	5.8−6.1 (5)	5.7−6.0 (4)	5.2−5.7 (8)	5.0−5.5 (7)	
ALM	3.9 ± 0.4	4.0 ± 0.1	6.2 ± 0.1	6.1 ± 0.1	6.2 ± 0.1	6.1 ± 0.3	5.6 ± 0.2	5.4 ± 0.1	5.0
	3.5−4.5 (7)	3.9−4.0 (2)	6.0−6.4 (3)	6.0−6.2 (3)	5.7−6.6 (5)	5.8−6.5 (4)	5.2−5.8 (7)	5.2−5.6 (9)	
LM1	2.4 ± 0.1	2.5 ± 0.1	3.6 ± 0.1	3.5 ± 0.1	3.7 ± 0.2	3.5 ± 0.1	3.1 ± 0.1	3.1 ± 0.1	3.2
	2.3−2.5 (7)	2.4−2.5 (2)	3.5−3.7 (3)	3.4−3.6 (3)	3.4−4.0 (5)	3.4−3.7 (4)	3.0−3.3 (8)	2.9−3.2 (9)	
BM1	1.3 ± 0.1	1.4 ± 0.1	1.8 ± 0.1	1.9 ± 0.1	1.9 ± 0.1	1.9 ± 0.1	1.6 ± 0.1	1.6 ± 0.1	1.5
	1.2−1.3 (7)	1.3−1.4 (2)	1.7−1.9 (3)	1.8−1.9 (3)	1.8−2.0 (5)	1.8−1.9 (4)	1.5−1.6 (8)	1.5−1.7 (9)	
LM	21.2 ± 0.9	20.4 ± 0.1	25.8 ± 0.4	24.4 ± 0.3	26.1 ± 0.5	25.8 ± 1.0	24.6 ± 0.7	24.3 ± 0.4	23.5
	20.1−22.7 (6)	20.3−20.4 (2)	25.2−26.1 (3)	24.1−24.6 (2)	25.2−26.7 (5)	24.2−26.7 (4)	23.7−26.0 (8)	23.5−24.8 (7)	
HM	10.0 ± 0.5	9.4 ± 0.1	11.3 ± 0.1	10.5 ± 0.1	11.9 ± 0.4	12.0 ± 0.2	11.4 ± 0.4	11.0 ± 0.4	10.7
	9.3−10.7 (6)	9.3−9.5 (2)	11.1−11.4 (3)	10.4−10.5 (2)	11.5−12.4 (5)	11.6−12.2 (4)	10.5−11.8 (8)	10.5−11.6 (7)	
DMR	4.1 ± 0.3	3.9 ± 0.2	5.3 ± 0.1	4.9 ± 0.1	5.5 ± 0.3	5.6 ± 0.1	5.1 ± 0.3	5.0 ± 0.2	4.5
	3.7−4.5 (7)	3.7−4.0 (2)	5.2−5.4 (3)	4.8−5.0 (2)	5.1−6.0 (5)	5.4−5.7 (4)	4.7−5.8 (8)	4.7−5.2 (7)	

[a] FMNH 62286, 62287, 169132, 170968, 170969, 170971, 175723−175725.
[b] USNM 458952 (holotype), 458953, 458955−458958.
[c] FMNH 142616, 142617; MMNH 12972; USNM 277639, 356290, 399581 (holotype), 536800−536802.
[d] AMNH 185136; FMNH 62281, 62282, 167368−167370, 169140, 169142, 170972, 170973, 175727−175729, 175734; USNM 102547, 102548, 102552.
[e] FMNH 145701 (holotype).