DESCRIPTIONS OF TWO NEW SPECIES OF *RHYNCHOMYS* THOMAS (RODENTIA: MURIDAE: MURINAE) FROM LUZON ISLAND, PHILIPPINES

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Rhynchomys belongs to a unique assemblage of Philippine rodents that exhibit a combination of primitive features as well as unique morphological specializations. These nocturnal ''shrew-rats,'' with highly specialized vermivorous and insectivorous food habits, are endemic to Luzon Island. Analyses of external, cranial, and dental features support the recognition of 4 species, 2 of which are described in this paper. All are restricted to high-elevation habitats, about 1,100 m and above, in montane and mossy forest on northern, western, and southeastern Luzon. Habitat vicariance and subsequent divergence in isolation is the probable mode of diversification in *Rhynchomys* as well as in other murid clades whose members are restricted to high-elevation habitats. The discovery of locally endemic species of *Rhynchomys* both confirms the existence of multiple centers of endemism on Luzon and underscores the need to establish and maintain additional protected areas on the island.

Key words: biogeography, conservation, distribution, ecology, morphology, shrew-rats, systematics, vermivory

Rhynchomys constitutes one of the most remarkable components of the extensive adaptive radiation of endemic murids within the Philippine Islands. An extremely elongated rostrum, delicate mandibles, needlelike lower incisors, and tiny molars, all features that reflect the specialized feeding habits of this group, are among the most extreme morphological specializations seen in the Murinae. These morphological features are unique, even in comparison to the other vermivorous and insectivorous ''shrew-rats'' that together with *Rhynchomys* comprise 1 portion (clade D of Jansa et al. 2006) of the ''Old Endemic'' group of Philippine murids (Division I of Musser and Heaney 1992). *Rhynchomys* was established by Oldfield Thomas (1895) with the description of the type species, *R. soricoides*, represented by 5 specimens collected by John Whitehead from the top of Mt. Data, in the Central Cordillera of northern Luzon (Fig. 1).

For more than half a century *Rhynchomys* was not known to occur elsewhere until the discovery of *R. isarogensis* on Mt. Isarog, southeastern Luzon, in the early 1960s (Musser and Freeman 1981). In 1988 and 1992–1994, we obtained addi-

tional specimens of *R. isarogensis*, previously known only from the holotype (Heaney et al. 1999), and in 2000–2003, we collected 17 specimens of *R. soricoides* from localities near Mt. Bali-it, north of Mt. Data in the Central Cordillera. In 2004 and 2005, we collected 2 specimens of *Rhynchomys* from Mt. Banahao (also spelled Banahaw) in south-central Luzon and 3 from Mt. Tapulao in the Zambales Mountains of west-central Luzon (Fig. 1). Specimens from Banahao and Tapulao differ from the 2 currently recognized species in body size, coloration, and cranial and dental features. In this paper, we describe these as new species, make morphological comparisons of both to *R. soricoides* and *R. isarogensis*, and discuss the significance of *Rhynchomys* with respect to both historical biogeography and conservation of the Philippine fauna.

MATERIALS AND METHODS

Specimens examined in this study are listed in Appendix I. They include specimens collected by the authors and their associates (Balete et al., in press; Heaney et al. 1999; Rickart et al. 1991) as well as specimens from earlier expeditions (Musser and Freeman 1981; Sanborn 1952) deposited at the Field Museum (FMNH) and the United States National Museum of Natural History, Smithsonian Institution (USNM). Specimens were assigned to age categories defined by Musser and Heaney (1992), based on relative body size, reproductive condition, and molar tooth wear. Terminology for external features of the
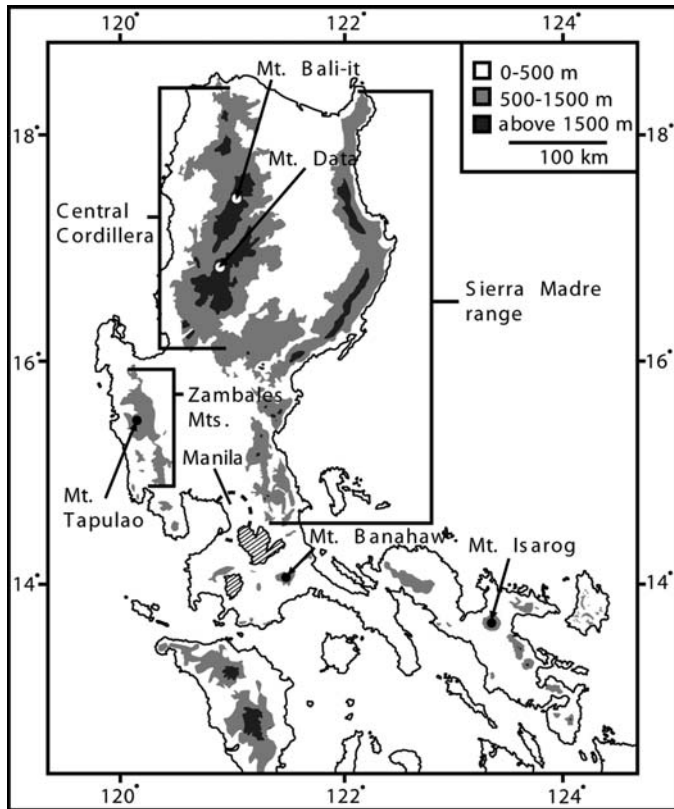

Fig. 1.—Map of Luzon Island, Philippines, showing the location of places mentioned in the text.

head and limbs follows Brown (1971) and Brown and Yalden (1973). Terminology for cranial and dental features follows Musser and Heaney (1992). Scanning electron micrographs of teeth were made from uncoated specimens.

Measurements (in millimeters) of total length, length of tail (LT), length of hind foot including claws (LHF), length of ear from notch (LE), and weight in grams (WT) were taken from field catalogs of the authors located at FMNH and USNM. The length of head and body (LHB) was determined by subtracting length of tail from total length. Length of overfur (LOF) was measured in the middorsal region. The number of tail scale rings per centimeter (TSR) was counted at a point on the tail one-third of the total length from the base.

Twenty-eight cranial and dental measurements were taken from 27 adult specimens of *Rhynchomys*. The following morphological terms and the limits of their measurements are defined and illustrated in Musser and Heaney (1992): greatest length of skull (GLS), interorbital breadth (IB), zygomatic breadth (ZB), breadth of braincase (BBC), height of braincase (HBC), length of nasal bones (LN), length of rostrum (LR), breadth of rostrum (BR), breadth of zygomatic plate (BZP), length of diastema (LD), palatal length (PL), postpalatal length (PPL), length of incisive foramina (LIF), breadth across incisive foramina (BIF), distance from posterior edge of incisive foramina to anterior margin of M1 (IF-M1), length of palatal bridge (LPB), palatal breadth at M1 (PBM1), palatal breadth at M2 (PBM2), breadth of mesopterygoid fossa (BMF), length of auditory bulla (LB), height of auditory bulla (HB), breadth

across incisor tips (BIT), crown length of maxillary molar toothrow (LM1-2), crown length of M1 (LM1), crown breadth of M1 (BM1), length of mandible plus lower incisor (LMI), posterior height of mandible (HM), and crown length of mandibular molar toothrow (Lm1-2). Measurements were taken by DSB and recorded to the nearest 0.1 mm using dial calipers.

We used SYSTAT 10 for Windows (SPSS Inc. 2000) for statistical analysis of measurements. Descriptive statistics (mean, standard deviation, and observed range) were calculated for sample groups. Quantitative phenetic variation was assessed through principal component analysis (using the correlation matrix) of log_{10}-transformed measurements of adult specimens.

Stomach contents were analyzed in the field for specimens prepared as skeletons and in the laboratory for specimens initially fixed in formalin and subsequently preserved in ethyl alcohol. Stomach contents were scored for presence of arthropod exoskeletons, plant matter, and annelid worms. Results are presented as percentage occurrence of each of the 3 categories among the total number of specimens examined of each species.

Reproductive autopsies were performed in the field on specimens prepared as skeletons or in the laboratory on fluid-preserved specimens. For males, the testes were scored for position (scrotal or abdominal), size (length × width, in mm), and relative convolution of the epididymis. For females, data were taken on the size and condition of teats (small, large, or lactating), and the number and size (crown to rump length, in mm) of embryos or number of placental scars in the uterus.

The capture and handling of animals in the field was conducted in accordance with animal care and use guidelines established by the American Society of Mammalogists (Animal Care and Use Committee 1998).

RESULTS

Among the different sample groups, moderate differences are apparent in adult body size and external proportions, as well as cranial and dental measurements (Table 1). Among the 4 groups, only specimens of *R. isarogensis* show sexual size dimorphism in external measurements, with males larger than females (Table 1); because these differences are slight and sample sizes are small, the sexes were pooled in most samples for multivariate analyses of variation among groups.

A principal component analysis was conducted on a subset of 25 external and cranial measurements taken from 12 individuals (adults and young adults with intact crania) including *R. soricoides* ($n = 5$), *R. isarogensis* ($n = 4$), and specimens from Mt. Tapulao ($n = 2$) and Mt. Banahao ($n = 1$). The first 4 components accounted for more than 78% of the total variance (Table 2). Many of the variables had high-magnitude loadings on component 1 (accounting for 47% of the variance), indicating that much of the variation involved size. Component 2 separated individuals with large bodies, broad rostra, large palates, low braincases, small auditory bullae, and small molars from specimens with the opposite features. Component 3 separated specimens with long tails and

hind feet, broad incisive foramina, large bullae, narrow zygomatic plates, narrow posterior palates, low mandibles, and smaller mandibular teeth from those with the opposite configuration. The 4th component distinguished specimens with wide interorbital regions, wide braincases, broad zygomatic plates, and narrow mesopterygoid fossae (Table 2). A bivariate plot of specimen scores on components 1 and 2 (Fig. 2) reveals complete separation of the 4 groups. *R. soricoides* is distinguished from the other taxa by high scores on component 1. On component 2, *R. isarogensis* and the Tapulao specimens have high and low scores, respectively, whereas *R. soricoides* and the Banahao *Rhynchomys* have intermediate scores.

These results support the recognition of 4 species of *Rhynchomys*: *R. soricoides*, *R. isarogensis*, and 2 undescribed species, 1 from Mt. Tapulao in Zambales Province and the other from Mt. Banahao in Quezon Province. The latter 2 are described in the following accounts.

Rhynchomys banahao, new species

Holotype.—Adult male, FMNH 178429, collected 5 May 2004 (original field number 7020 of LRH); initially fixed in formalin, now preserved in ethyl alcohol with the skull removed and cleaned. Muscle tissue from the left femur was removed in the field, otherwise the specimen is in good condition. It is deposited at FMNH but will be transferred to the National Museum of the Philippines, Manila (NMP).

Type locality.—Mt. Banahao, Tayabas Municipality, Quezon Province, Luzon Island, Philippines, in primary montane forest at 1,465 m elevation, 14°03′59.4″N, 121°30′30.9″E (Fig. 1).

Referred specimen.—There is 1 additional specimen from Mt. Banahao, an adult male (FMNH 183590) collected 26 February 2005 in primary montane forest at 1,250 m elevation. The specimen is preserved in ethyl alcohol, with skull removed and cleaned. Muscle tissue was removed from the left femur and the stomach was removed for analysis of contents. The braincase and left mandible are broken, but otherwise the specimen is in good condition.

Distribution.—*Rhynchomys banahao* is known only from Mt. Banahao, Quezon Province, southern Luzon (Fig. 1), where it occurs in primary montane forest at 1,250–1,465 m; apparently absent from localities we surveyed in primary mossy forest (1,750 m), and secondary lowland forest (620–765 m).

Etymology.—The new species is named for Mt. Banahao where the specimens originated. *Banahao*, the traditional name for this mountain in the Tagalog language, is used as a noun in apposition. We propose ''Banahao shrew-rat'' as the English common name.

Diagnosis.—*Rhynchomys banahao* is distinguished from other members of the genus by the following combination of traits (with contrasting characters of congeners in parentheses): pelage dark and dense, without a sharp delineation between the dorsum and venter (pelage less thick, paler and with greater contrast between dorsum and venter); tail uniformly dark (tail variously bicolored); hind feet broader relative to their length and darker dorsally (hind feet relatively narrower and paler); rostrum of skull broader and deeper (rostrum more gracile); wider zygomatic breadth relative to other skull dimensions (relatively narrower zygomatic breadth); broader braincase relative to other skull dimensions (relatively narrower braincase); presence of a mastoid fenestra (fenestra absent); lower 1st molar lacking a posterior cingulum (posterior cingulum well developed), and upper and lower 2nd molars absolutely and relatively larger (molars smaller).

Description and comparisons.—*Rhynchomys banahao* is similar in general body form to *R. isarogensis*, *R. soricoides*, and the Zambales *Rhynchomys*, but exhibits differences in body size, pelage color, and in various external, cranial, and dental features (Tables 1 and 2; Figs. 3–6).

The pelage of *R. banahao* is as short as that of *R. isarogensis* and *R. soricoides* from Kalinga but denser; the Zambales *Rhynchomys* has slightly longer fur. The dark brownish gray dorsum grades into medium gray venter without the sharp delineation seen in the other species. The dorsal fur is tricolored: dark gray in its basal three-fourths, pale golden brown with black tips in its distal one-fourth. The ventral fur is medium gray with white tips, except for white patches on the chest and the lower abdomen of the holotype (absent in the other specimen, FMNH 183590).

The lips and rhinarium of *R. banahao* are unpigmented, as in congeners, and the chin is dark gray (pale gray or white in the other species). The eyelids are finely edged in black and, in the holotype, marked by a narrow pale gray eye-ring. As in other *Rhynchomys*, the mystacial vibrissae are long, the longest extending beyond the ears, but are darker than in the other species. The ears are long and ovate, uniformly darker than in the other species, with a sparse covering of short, black hairs on both outer and inner surfaces.

As in other species of *Rhynchomys*, the front feet of *R. banahao* are short with strong digits. The pollex bears a short nail and the other digits have long, sharp claws that are opaque. The dorsal surface of the foot is dark gray, sparsely covered with short, dark gray hairs that extend to the dorsal surface of the 1st joints of the 3rd and 4th digits (in the other species, the feet are paler and covered with short, sparse white hairs). The distal portions of the digits are pale and sparsely covered with short white hairs. As in the other species, the palmar surface is naked, unpigmented, and bears 2 large metacarpal and 3 smaller interdigital pads.

Hind feet of *R. banahao* are similar in length to those of *R. isarogensis* and the Zambales *Rhynchomys* but slightly shorter than in *R. soricoides* (Table 1). However, the foot of *R. banahao* is relatively broader than those of the other species (Fig. 3). The dorsal surface, including digits, is dark gray and sparsely covered with short, dark gray hairs as in *R. soricoides* from Mt. Data. In all other specimens examined, the dorsal surface of the hind foot is unpigmented and either sparsely covered with white hairs over the entire surface (Zambales *Rhynchomys*) or with white medially and a narrow strip of medium gray (*R. soricoides* from Kalinga) or brownish gray (*R. isarogensis*) hairs along the lateral margin. The plantar surface is naked and dark gray except for the pads, which are paler. In the other species, the plantar surface is paler, and pads either lightly pigmented (*R. soricoides*) or entirely unpigmented (*R. isarogensis* and the Zambales *Rhynchomys*).

Table 1.—External, cranial, and dental measurements ($\bar{X} \pm 1$ *SD* and ranges, in mm; weight in g) of adult *Rhynchomys*. Sample sizes in parentheses. Variables are defined in the "Materials and Methods."

| | *Rhynchomys banahao*[a] | | *Rhynchomys isarogensis*[b] | | *Rhynchomys soricoides* | | | *Rhynchomys tapulao*[e] | | |
| | | | | | Kalinga[c] | | Mt. Data[d] | | | |
	Holotype	Male	Male	Female	Male	Female	Female	Holotype	Male	Female
LHB	190	178	181.2 ± 6.0 173−187 (4)	171.5 170−173 (2)	187.7 ± 3.9 180−192 (9)	187.5 ± 9.8 178−196 (4)	195 (1)	164	175	188 (1)
LT	130	127	115.8 ± 8.1 105−124 (4)	116.0 115−117 (2)	141.0 ± 8.4 136−153 (9)	141 ± 8.4 134−151 (4)	132 (1)	126	128	120 (1)
LHF	40	39	38.5 ± 1.0 37−39 (4)	38.0 38 (2)	41.2 ± 1.0 41−42 (9)	40.8 ± 0.5 40−41 (4)	41 (1)	38	39	40 (1)
LE	25	25	22.0 20−23 (3)	22.0 (2)	24.6 ± 0.5 24−25 (9)	24.8 ± 0.5 24−25 (4)	20 (1)	25	25	24 (1)
WT	155	150	143.3 140−145 (3)	130.0 120−140 (2)	154.4 ± 13.3 135−180 (9)	157.5 ± 2.9 155−160 (4)	—	129	140	156 (1)
LOF	12	13	—	13 (1)	11−12 (8)	11−12 (4)	—	11	11	12 (1)
TSR	19	18	20 (1)	21 (1)	15−18 (8)	17−18 (4)	16 (1)	20	20	20 (1)
LT/LHB	68	71	65−68 (3)	68 (2)	71−80 (9)	68−84 (4)	68 (1)	77	73	64 (1)
LHF/LHB	21	21	21−22 (3)	22 (2)	21−23 (9)	21−23 (4)	21 (1)	23	22	21 (1)
GLS	45.6	45.6	43.9 ± 0.9 42.8−44.6 (4)	44.2 43.9−44.4 (2)	47.1 45.5−47.9 (3)	—	49.2 (1)	45.3	45.4	—
IB	7.1	—	6.8 ± 0.3 6.5−7.1 (4)	6.8 6.7−6.8 (2)	6.6 6.6−6.7 (3)	6.3 (1)	6.4 (1)	6.7	6.8	6.6 (1)
ZB	17.5	—	17.1 ± 0.3 16.8−17.4 (2)	17.1 16.6−17.6 (2)	16.8 16.5−17.2 (2)	17.2 (1)	18.1 (1)	16.7	16.6	17.2 (1)
BBC	16.7	—	16.4 ± 0.4 15.8−16.7 (4)	16.2 16.1−16.2 (2)	16.4 16.0−16.7 (3)	16.4 (1)	16.7 (1)	16.3	16.5	—
HBC	13.4	—	12.5 ± 0.2 12.2−12.8 (4)	12.6 12.5−12.6 (2)	12.8 12.8 (3)	12.6 (1)	12.6 (1)	13.5	13.6	—
LN	18.1	17.8	17.1 ± 0.4 16.8−17.7 (4)	17.6 17.5−17.7 (2)	19.2 18.5−19.9 (3)	19.5 (1)	20.2 (1)	18.3	18.3	18.6 (1)
LR	19.7	20.3	18.3 ± 0.9 17.2−19.0 (4)	18.5 18.4−18.6 (2)	20.8 20.4−21.2 (3)	20.8 (1)	22.0 (1)	20.2	20.3	21.0 (1)
BR	7.9	7.3	7.5 ± 0.2 7.4−7.8 (4)	7.2 7.1−7.3 (2)	6.8 6.7−7.0 (3)	7.0 (1)	7.4 (1)	7.0	7.0	7.5 (1)
BZP	2.7	2.6	2.4 ± 0.1 2.2−2.5 (4)	2.4 2.4 (2)	2.7 2.3−2.9 (3)	2.8 (1)	2.1 (1)	2.7	2.5	2.5 (1)
BIT	1.3	1.2	1.3 ± 0.1 1.2−1.3 (4)	1.3 1.3 (2)	1.3 1.2−1.3 (3)	1.4 (1)	1.4 (1)	1.2	1.4	1.3 (1)
LD	14.2	14.5	13.7 ± 0.3 13.3−14.1 (4)	13.6 13.2−13.9 (2)	15.9 15.3−16.4 (3)	15.5 (1)	16.8 (1)	14.4	14.8	14.5 (1)
PL	23.5	23.9	22.0 ± 0.7 21.0−22.6 (4)	22.3 21.9−22.7 (2)	24.7 24.3−24.9 (3)	24.3 (1)	25.4 (1)	22.7	22.6	23.8 (1)
PPL	15.3	—	14.9 ± 0.2 14.7−15.2 (4)	15.4 15.1−15.6 (2)	16.2 16.1−16.3 (2)	—	17.4 (1)	15.8	16.0	—
LIF	6.3	6.6	6.0 ± 0.1 5.9−6.1 (4)	6.2 5.8−6.5 (2)	7.3 7.0−7.6 (3)	7.1 (1)	7.5 (1)	6.7	6.7	6.9 (1)
BIF	2.0	1.9	2.1 ± 0.1 2.0−2.2 (4)	1.9 1.9 (2)	2.0 2.0−2.1 (3)	1.9 (1)	2.0 (1)	2.1	2.0	2.11 (1)
IF-M1	5.6	6.0	5.8 ± 0.2 5.7−6.0 (4)	5.9 5.8−6.0 (2)	6.3 6.1−6.4 (3)	6.4 (1)	6.6 (1)	5.8	5.9	—
LPB	13.8	13.5	12.8 ± 0.7 11.8−13.3 (4)	12.9 12.7−13.1 (2)	13.6 13.4−13.8 (3)	13.6 (1)	14.6 (1)	12.4	12.2	13.5 (1)
PBM1	5.1	4.9	5.1 ± 0.3 4.8−5.5 (4)	4.6 4.4−4.7 (2)	4.9 4.7−5.1 (3)	5.0 (1)	5.3 (1)	4.7	4.8	4.9 (1)
PBM2	4.8	4.8	4.7 ± 0.1 4.5−4.8 (4)	4.6 4.6 (2)	4.8 4.5−5.0 (3)	5.0 (1)	5.1 (1)	4.6	4.7	4.5 (1)
BMF	2.0	1.9	2.1 ± 0.2 1.9−2.4 (4)	2.1 (1)	1.6 1.5−1.7 (3)	1.8 (1)	2.2 (1)	2.3	2.1	2.2 (1)
LB	5.23	—	5.1 ± 0.3 4.6−5.4 (4)	5.2 5.0−5.3 (2)	5.3 5.2−5.4 (3)	5.3 (1)	5.1 (1)	5.5	5.5	5.3 (1)
HB	4.8	—	4.6 ± 0.3 4.2−4.8 (4)	4.7 4.7−4.8 (2)	4.8 4.6−5.0 (3)	4.8 (1)	5.0 (1)	5.4	5.0	5.0 (1)
LM1-2	2.3	2.3	2.3 ± 0.1 2.2−2.4 (4)	2.4 2.2−2.5 (2)	2.4 2.3−2.4 (3)	2.4 (1)	2.3 (1)	2.6	2.6	3.2 (1)

Table 1.—Continued.

| | *Rhynchomys banahao*[a] | | *Rhynchomys isarogensis*[b] | | *Rhynchomys soricoides* | | | *Rhynchomys tapulao*[e] | | |
| | | | | | Kalinga[c] | | Mt. Data[d] | | | |
	Holotype	Male	Male	Female	Male	Female	Female	Holotype	Male	Female
LM1	1.5	1.6	1.5 ± 0.1 1.4−1.7 (4)	1.4 1.4−1.5 (2)	1.6 1.6−1.8 (3)	1.7 (1)	1.4 (1)	1.6	1.6	1.5 (1)
BM1	1.0	0.9	0.9 ± 0.1 0.8−1.0 (4)	0.9 0.9 (2)	0.8 0.8−0.9 (3)	0.9 (1)	0.8 (1)	1.0	0.8	0.9 (1)
LMI	30.8	31.6	30.6 ± 0.9 29.3−31.5 (4)	30.1 30.5−31.5 (2)	33.7 32.3−34.6 (3)	33.7 (1)	35.2 (1)	31.4	31.4	33.2 (1)
HM	7.6	7.4	7.5 7.4−7.6 (3)	7.5 7.4−7.6 (2)	7.7 7.4−8.1 (3)	8.1 (1)	8.6 (1)	7.7	7.3	7.0 (1)
Lm1-2	2.7	2.7	2.4 ± 0.0 2.4 (4)	2.5 2.3−2.6 (2)	2.7 2.5−2.6 (2)	2.8 (1)	2.6 (1)	2.8	2.8	2.9 (1)

[a] FMNH 178429 (holotype), 183590.
[b] FMNH 95123 (holotype), USNM 573573, 573575, 573579, 573581, 573901.
[c] FMNH 167320, 167321, 167322, 167325, 169170, 169172, 169174, 169175, 170980, 170981, 175617, 175618, 175619.
[d] FMNH 62289, 62290.
[e] FMNH 183553, 183554, 183555 (holotype).

As in the other species, the plantar pads consist of 4 large interdigitals, a smaller hypothenar, and thin, elongate thenar. In all species the pads are small relative to the entire plantar surface but those of *R. banahao* are comparatively larger (Fig. 3).

Table 2.—Character loadings, eigenvalues, and percentage variance explained on the first 4 components of a principal component analysis of log-transformed measurements of adult *Rhynchomys*. Variables are defined in the "Materials and Methods."

| | Principal component | | | |
Variable	1	2	3	4
LHB	0.8	0.438	0.014	0.137
LT	0.84	−0.186	0.325	0.232
LHF	0.839	0.215	0.35	0.01
IB	−0.68	0.048	0.143	0.626
BBC	0.345	0.015	0.082	0.606
HBC	−0.141	−0.823	0.22	0.173
LN	0.935	−0.16	−0.163	0.052
LR	0.922	−0.332	0.065	−0.07
BR	−0.52	0.452	−0.249	0.232
BZP	−0.044	−0.192	−0.36	0.748
LD	0.965	−0.107	0.082	−0.015
PL	0.986	0.02	0.042	0.066
LIF	0.947	−0.264	0.068	0.004
BIF	0.107	0.234	0.768	−0.015
IF-M1	0.857	0.116	−0.134	−0.038
LPB	0.742	0.549	0.019	0.024
PBM1	0.366	0.413	−0.01	−0.124
PBM2	0.798	0.088	−0.492	−0.101
BMF	−0.646	−0.027	−0.191	−0.55
LB	0.083	−0.605	0.57	−0.164
BIT	0.583	0.018	−0.019	−0.27
LM1-2	0.165	−0.748	−0.294	−0.262
LMI	0.968	0.043	0.016	0.006
HM	0.716	0.118	−0.489	−0.005
Lm1-2	0.229	−0.79	−0.336	0.181
Eigenvalue	11.809	3.523	2.191	2.02
Variance explained (%)	47.234	14.092	8.765	8.078

The tail of *R. banahao* is short, about as long as in the Zambales *Rhynchomys*; *R. soricoides* and *R. isarogensis* have, respectively, longer and shorter tails, both absolutely and relatively (Table 1). The tail is robust, uniformly black throughout its length, with a very short unpigmented tip. In contrast, both *R. soricoides* and *R. isarogensis* have tails that are dark dorsally and either lightly pigmented or unpigmented ventrally, whereas the tail of the Zambales *Rhynchomys* is
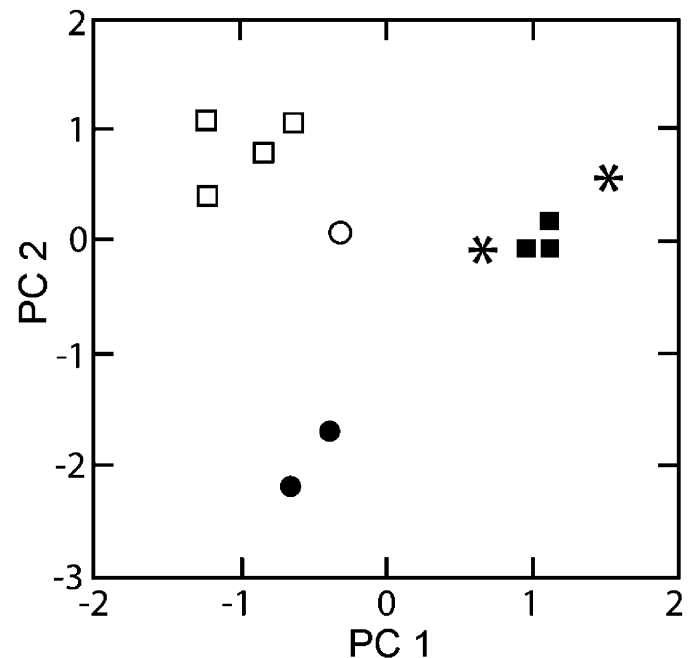
Fig. 2.—Results of principal component analysis of cranial measurements of adult *Rhynchomys*, showing scores of individuals on components 1 and 2. Open squares = *R. isarogensis*; stars = *R. soricoides* from Mt. Data; solid squares = *R. soricoides* from Mt. Bali-it; open circle = Mt. Banahao *Rhynchomys*; and solid circles = Mt. Tapulao *Rhynchomys*.
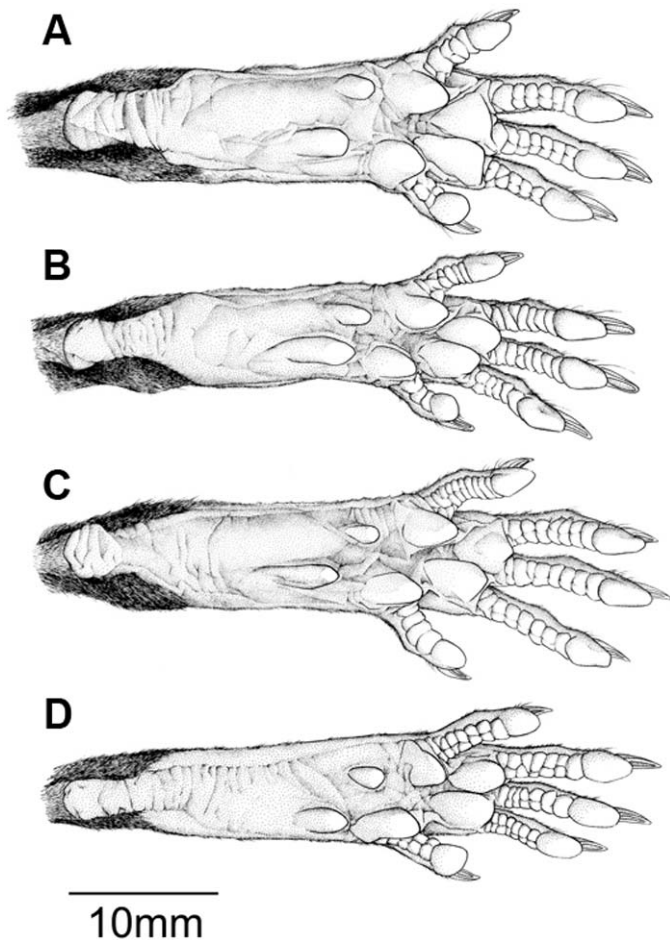
Fig. 3.—Ventral view of right hind feet of A) *Rhynchomys banahao* (FMNH 178429, holotype); B) *R. isarogensis* (FMNH 152038); C) *R. soricoides* (FMNH 167321); and D) *R. tapulao* (FMNH 183555, holotype).

pigmented on the basal two-thirds with the distal one-third unpigmented. *R. banahao* has fewer tail scale rings per centimeter (TSR) than does either *R. isarogensis* or the Zambales *Rhynchomys*, but more than *R. soricoides* (Table 1). In all species there are 3 hairs associated with each tail scale; these are about the same length in *R. banahao* and *R. soricoides*, whereas they are shorter in both *R. isarogensis* and the Zambales *Rhynchomys*.

Rhynchomys banahao is similar to the other 3 species in general cranial morphology (Figs. 4 and 5). Additional cranial illustrations of *R. isarogensis* and *R. soricoides* are shown in Musser and Heaney (1992), Musser and Freeman (1981), Musser (1969), and Thomas (1898). Compared to the other species, the skull is slightly more robust, and is intermediate in overall length between *R. isarogensis* and the Zambales *Rhynchomys* (both with shorter skulls) and *R. soricoides*. The braincase is ovate, wider and rounder at the posterior, and narrower at the anterior. It is about as high as in the Zambales *Rhynchomys* but higher than in *R. isarogensis* and *R. soricoides*. The dorsal surface of the skull is uniformly smooth and free of ridges. The rostrum is elongate and tapered anteriad,

except for the slight capsular projection for the upper incisors toward the tip of the nasals. The base of the rostrum is slightly broader than the interorbit, and exhibits a slight lateral flaring of the nasolacrimal canal that adds little to the broadness of the rostrum. The rostrum and interorbital region are broadest in *R. banahao* (Table 1; Fig. 4). Compared to the other species, the zygomatic arches are more strongly bowed outward; maximum (posterior) zygomatic breadth is greater than the braincase breadth (these dimensions are nearly equal in the other species), and width across the anterior (maxillary) portions is substantially greater (Fig. 4).

As in congeners, dorsal profile of the cranium is narrowly tapered anteriad, brought about by the extreme elongation of the rostrum (Fig. 5). However, the relative depth of the rostrum is greater in *R. banahao* than in the other species. The dorsal surface slopes gradually anteriad from the middle of the parietal to the tips of the relatively flat nasals, giving the skull a nearly straight lateral profile from the top of the braincase to the tip of the rostrum. In contrast, the other species have shallower rostra and nasals that are upturned distally, resulting in dorsal surface profiles that are less linear (Fig. 5). The posterior cranial profile of *R. banahao* slopes slightly downward behind the middle of the parietals to the posterior edge of the interparietal where it meets the inflated supraoccipital and exoccipitals. This imparts a rounder posterior margin, as in *R. isarogensis* and to a lesser degree in the Zambales *Rhynchomys*. In *R. soricoides* the inflation of the supraoccipital and exoccipitals is less pronounced and projects only slightly forward beyond the edge of the interparietal, resulting in a flatter cranial base.

The dorsal maxillary root of the zygomatic arch is positioned above the level of the squamosal root. The zygomatic plate is slanted as in congeners and there is only a minor overlap between the dorsal and ventral maxillary roots. The anterior margin of the zygomatic plate is more strongly convex than in the other species. As in the other species, the ventral maxillary root of the zygomatic plate completely overlaps the maxillary toothrow, with the anterior margin positioned about one-third of its length ahead of the anterior margin of the 1st molar. The posterior margin terminates slightly behind the posterior margin of the 2nd molar, as in the Zambales *Rhynchomys*, in contrast to the relatively wider clearance from the 2nd molar in *R. isarogensis* and *R. soricoides*. The squamosal root of the zygomatic arch is positioned slightly above, and terminating close to, the top of the postglenoid vacuity, as in the other species.

On the ventral surface of the skull there is an interpremaxillary foramen originating close to the anterior incisor alveoli; it is similar to those of the other species but slightly larger (Fig. 4). As in the other species, the incisive foramina of *R. banahao* are long and slender, slightly wider at the posterior end, and at least 3 times as long as they are wide, extending more than one-third of the rostral length. Two shallow palatine grooves run parallel to each other along the maxillae from the posterior margins of the incisive foramina to about the middle of the palate. The grooves sink deeper as they approach the 1st molars and merge with the elongate postpalatine foramina in front of
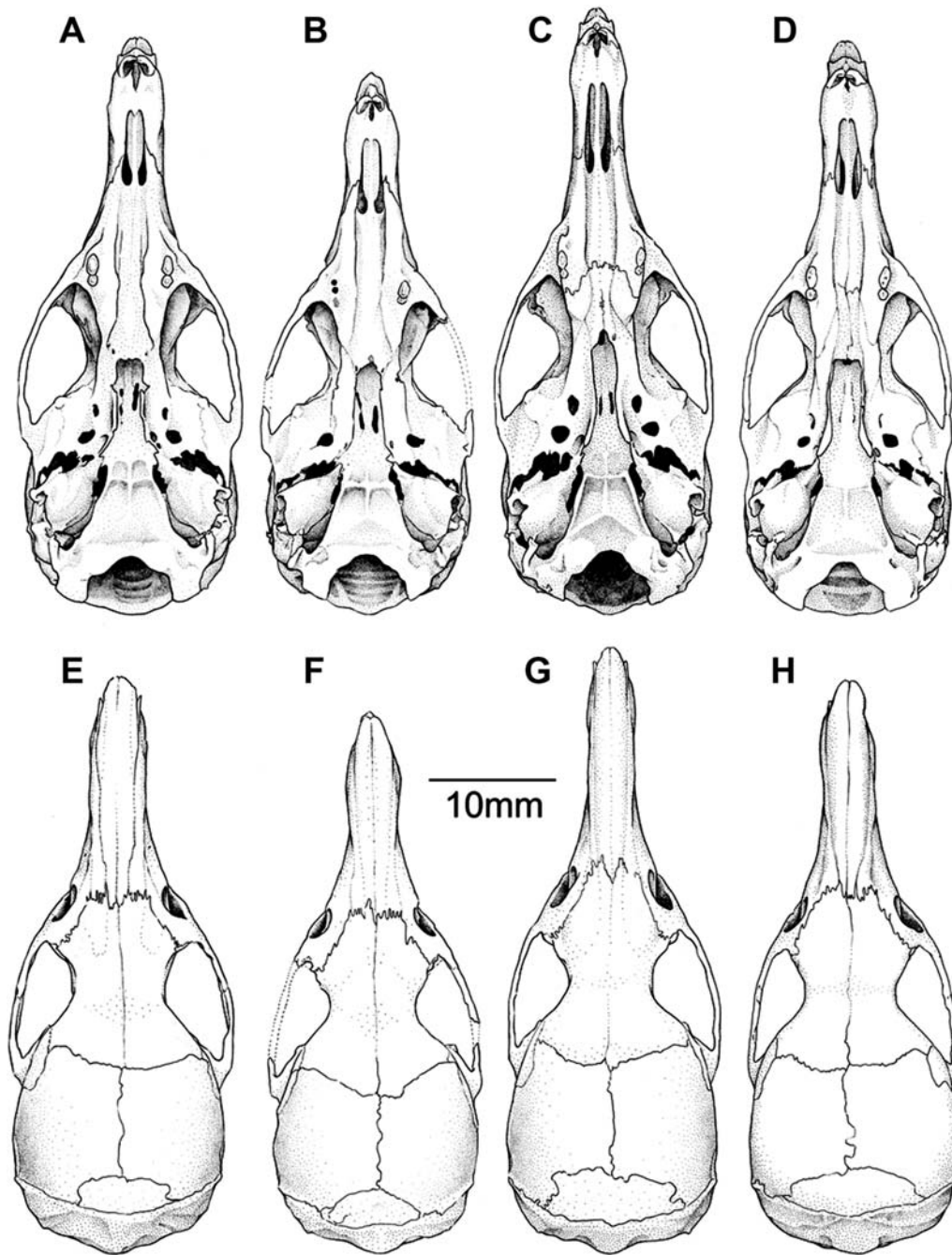
Fig. 4.—A–D) Ventral and E–H) dorsal views of the crania of *Rhynchomys banahao* (A and E, FMNH 178429, holotype); *R. isarogensis* (B and F, FMNH 95123, holotype); *R. soricoides* (C and G, FMNH 170980); and *R. tapulao* (D and H, FMNH 183555, holotype).

the 2nd molars and just above the suture with the palate. The postpalatine foramina are partly hidden under the folded inner edge of the maxillae opposite the 1st molars and anterior halves of the 2nd molars. Behind the posterior edge of the postpalatine foramina, the palatine grooves taper and curve slightly inward, following the suture between the maxilla and palate, becoming less conspicuous as they are reduced to less than one-half of their original width and depth, and disappearing near the middle of the palate. In 1 specimen of *R. banahao* (FMNH 183590), the extension of the palatine grooves behind the postpalatine foramina is inconspicuous as in the case of *R.*

isarogensis, *R. soricoides* from Mt. Data, and the Zambales *Rhynchomys*, but more pronounced in *R. soricoides* from Kalinga.

As in other *Rhynchomys*, the palatine is extremely elongate, extending beyond the 2nd molar by 3 times the length of the maxillary toothrow. The mesopterygoid fossa is narrow and elongate. The auditory bullae are similar in size to those of *R. soricoides* and *R. isarogensis*, but substantially smaller than those of the Zambales *Rhynchomys* (Table 1). The ventral surface of each bulla is inflated uniformly, appearing more rounded than those of the other species, and unlike the anterior
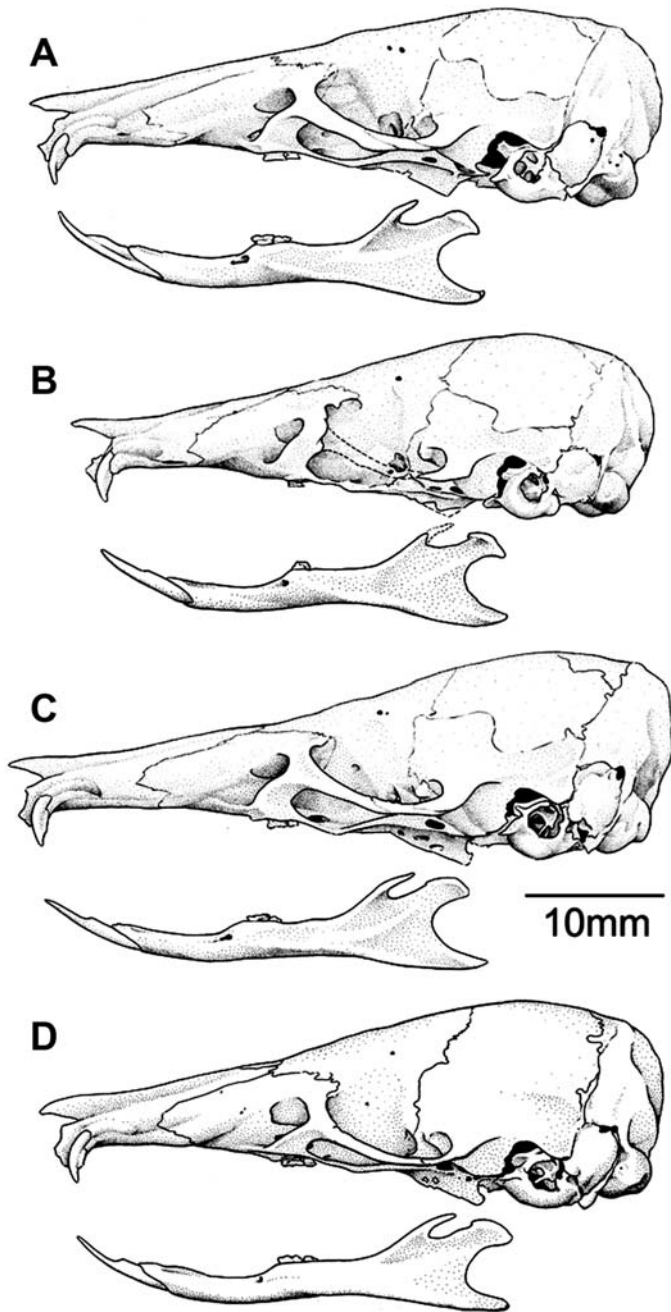
Fig. 5.—Lateral view of crania and left mandible of A) *Rhynchomys banahao* (FMNH 178429, holotype); B) *R. isarogensis* (FMNH 95123, holotype); C) *R. soricoides* (FMNH 170980); and D) *R. tapulao* (FMNH 183555, holotype).

inflation in *R. isarogensis*, *R. soricoides* from Kalinga, and the Zambales *Rhynchomys*, or the slight posterior inflation in *R. soricoides* from Mt. Data. As in the other members of the genus, the bullae are separated from the squamosal and alisphenoid by the postglenoid vacuity and postalar fissure (Figs. 4 and 5; Musser and Heaney 1992:77, figure 44). The latter is more prominent in *R. banahao*, resulting in greater separation of each bulla along its anterior margin; in the other species, the postalar fissure is narrower, allowing contact of the periotic with the squamosal and alisphenoid in some

individuals. A small circular mastoid fenestra is located close to the anterior edge of each mastoid directly below the mastoid foramen. The other species lack a mastoid fenestra. The mastoid foramen of *R. banahao* is slightly wider than in *R. isarogensis* and *R. soricoides* but smaller than in the Zambales *Rhynchomys*.

The mandible of *R. banahao* is very slender as in the other species, with a deeply concave posterior margin (Fig. 5). It is slightly longer than that of *R. isarogensis*, but shorter than those of the other species. The mandibular ramus is thicker and more robust than in the other species. The angular process is similar to those of *R. isarogensis* and *R. soricoides*, but not as long as the latter; the Zambales *Rhynchomys* has a more slender and blunter angular process. The condyloid process is similarly shaped in all species, but is slightly longer and broader in *R. soricoides*. The coronoid process is delicate and backswept, but not as long as in the other species; in both the Zambales *Rhynchomys* and in *R. soricoides* from Kalinga and Mt. Data the process is substantially longer, forming a deeper sigmoid notch between the coronoid and condyloid processes.

As with the other species, the short and narrow upper incisors of *R. banahao* are tiny relative to the size of the cranium and emerge at right angles to the rostrum. The incisors have white enamel, slightly convex anterior faces, and smoothly rounded edges at the tips (in the holotype), that are straight-edged in the relatively younger specimen (FMNH 183590). The incisors are as broad across their tips as those of *R. isarogensis* and *R. soricoides* from Kalinga, but relatively narrower than those of *R. soricoides* from Mt. Data and the Zambales *Rhynchomys*.

The maxillary toothrow is very short and narrow relative to the breadth of the cranium and the expansive bony palate that extends beyond the posterior edge of the last molar by 3 times the length of the toothrow. The toothrow lies completely under the ventral root of the zygomatic plate. Immediately below the anterior edge of the plate, the maxillary bone bears a short, curved, thickened ridge that frames the lateral anterior border of the 1st molars. In *R. soricoides* from Kalinga, this ridge forms a wide bony ledge that extends anteriad by as much as the length of the 1st molar. In *R. isarogensis*, this projection barely extends beyond the anterior edge of the 1st molar or by as much as one-fourth of the molar's length.

In all species of *Rhynchomys*, the 1st upper molar is elongate and tapered at both ends (Figs. 6A–E). In *R. banahao* this tooth is broader relative to its length, with a less-tapered posterior margin compared to those of the other species. The posterior margin slightly overlaps the anterior edge of the 2nd molar. Faint traces of 3 rows of cusps are evident on the occlusal surfaces, mainly as large, shallow basins (Figs. 6A–E; Musser and Heaney 1992:83, figure 49). In *R. banahao*, the lingual cusp t4 is more prominent than in the other species, and contributes to the broadness of the posterior one-third of the 1st molar. In specimen FMNH 183590, the 1st molars are less worn and their coronal surfaces exhibit detectable cusp outlines in 3 groups. The anterocone consists of coalesced cusps t2 and t3. The 2nd group features the coalesced occlusal surfaces of
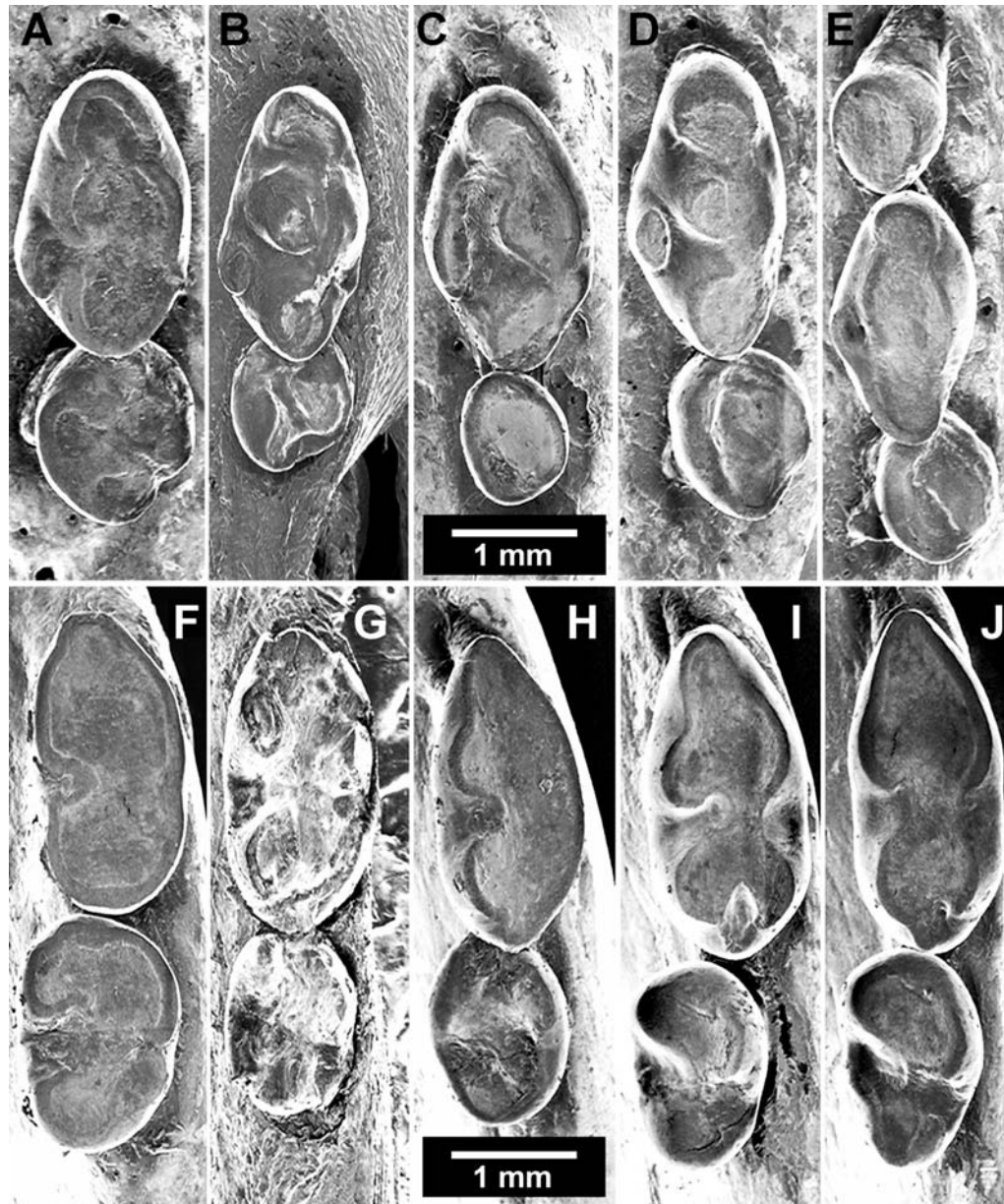
Fig. 6.—Occlusal view of A–E) left maxillary and F–J) right mandibular molar teeth of *Rhynchomys banahao* (A and F, FMNH 178429, holotype); *R. isarogensis* (B and G, FMNH 147182); *R. soricoides* (C and H, FMNH 170980); and *R. tapulao* (D and I, FMNH 183555, holotype; E and J, FMNH 183553). All to the same scale.

central and labial cusps (t5 and t6) and the prominent lingual t4. The posterior group consists of the coalesced cusps t8 and t9.

The 2nd upper molar of *R. banahao* is relatively robust and the largest among all of the species (Figs. 6A–E). It is about as broad as, and more than half as long as, the 1st molar. In the holotype, it is circular in outline and much worn, retaining only a very shallow, but discernible, basin of coalesced cusps. In specimen FMNH 183590, this tooth is lozenge-shaped with rounded edges at the corners. It is only slightly worn, revealing a crown surface composed of 2 groups of cusps: the anterior consisting of a central basin formed by the merger of the cusps t4, t5, and t6, and the posterior formed from the coalesced cusps t8 and t9. As in the other species of *Rhynchomys*, there is

no evidence of a posterior cingulum on either the 1st or 2nd molars.

The lower incisors are long and needlelike with very pale yellow enamel on the anterior surfaces. The other species have pale orange enamel. The lower molars are small, relative to the length of the mandible. The mandibular toothrow is about as long as in *R. soricoides* from Kalinga and the Zambales *Rhynchomys*; *R. soricoides* from Mt. Data has slightly longer and *R. isarogensis* has shorter toothrows (Table 1; Figs. 6F–J). The 2 molars are separated by a narrow gap; in *R. isarogensis* and the Zambales *Rhynchomys* the molars abut, whereas in *R. soricoides* from Kalinga and Mt. Data they overlap.

The 1st lower molar of *R. banahao* is about as long as that of *R. isarogensis* but shorter than those of other species. As in the other species, it has a broadly tapered anterior end, but the posterior margin is rounded rather than tapered (Figs. 6F–J). In the holotype, the crown surface consists of a wide shallow basin that retains only faint traces of the coalesced cusps. In the other specimen of *R. banahao* (FMNH 183590), the right molar retains slightly more-prominent traces of 3 groups of cusps: the anteroconid, formed by the coalesced anterolingual and anterolabial cusps; a 2nd group consisting of the coalesced metaconid and protoconid; and a posterior row formed by the entoconid and hypoconid. In the other species of *Rhynchomys*, there is a prominent posterior cingulum that contributes to the tapered posterior margin of the tooth; this feature is not apparent in either specimen of *R. banahao*, resulting in a rounded, rather than tapered, posterior margin.

The 2nd lower molar of *R. banahao* is substantially larger than those of the other species (Figs. 6F–J). It is slightly broader than, and almost two-thirds the length of, the 1st lower molar. The crown consists of an anterior basin consisting of the coalesced anteroconid, metaconid, and protoconid, and a posterior basin formed by the coalesced hypoconid and entoconid.

Ecology.—*Rhynchomys banahao* was recorded only in the lower montane forest on Mt. Banahao, the holotype at 1,450 m and another specimen at 1,250 m. An earlier record was reported by Rosell (1996) from 1,300 m, on the same side of the mountain as the 1,250-m and 1,450-m sites; the specimen, also a male, is believed to have been lost. Our examples of *R. banahao* were captured in Victor snap traps (Woodstream Corp., Lititz, Pennsylvania) baited with live earthworms. Both were trapped on the ground alongside rotting tree trunks adjacent to river banks in areas that appeared to be well drained given their sloping terrain. The forest canopy at these elevations was about 15 m, with emergents rising to about 25 m at 1,250 m. Dominant trees at both sites included species of *Podocarpus* (Podocarpaceae), *Lithocarpus* (Fagaceae), and *Syzygium* (Myrtaceae). Epiphytic mosses, ferns, *Begonia*, and *Medinilla* were abundant. Understory vegetation included erect palms (*Pinanga*), tree ferns (*Cyathea*), and *Medinilla*. Vines including rattan (*Calamus*) and climbing pandans (*Freycinetia*) were common in the forest. Along river banks, lianas, tree ferns (*Cyathea*), and gingers (Zingiberaceae) were common. Erect pandans (*Pandanus*) were present but uncommon at 1,250 m.

We did not record *R. banahao* elsewhere on the mountain despite moderately extensive trapping using Victor snap traps baited with earthworms. We failed to capture this species in mossy forest at 1,750 m (142 trap-nights) and in lowland forest at 765 m (248 trap-nights) and 620 m (226 trap-nights). The apparent narrow distributional belt for *R. banahao* is in contrast to the wider elevation range of *R. isarogensis* (1,125–1,800 m on Mt. Isarog) and *R. soricoides* (1,600–2,150 m in Kalinga), and both of the latter species are associated with upper montane and mossy forest habitats (Heaney et al. 2005; Rickart et al. 1991). As a further contrast, we recorded the Zambales *Rhynchomys* only in mossy forest at 2,024 m, near the peak of Mt. Tapulao. Trap success for *R. banahao* of 0.5–1.0% (with earthworms as

bait) is comparable to that for *R. isarogensis* (Balete and Heaney 1997; Rickart et al. 1991), indicating that *R. banahao* is not an abundant species. We did not catch any in 1,891 trap-nights using coconut-baited snap traps. The species appears to be nocturnal–crepuscular, as is the case with congeners (Rickart et al. 1991; this paper). The stomach contents of 1 specimen (FMNH 183590) consisted of earthworms and few fragments of wings and exoskeletons of unidentified insects.

The 2 known specimens of *R. banahao* are adult males with scrotal testes. Their capture in February (FMNH 183590) and May (FMNH 178429, holotype) indicate breeding during the 1st half of the year. Although seasonal pattern of breeding is unknown, reproduction during this period is similar to the breeding period observed in *R. isarogensis* on Mt. Isarog, with pregnant females and scrotal males taken from February to April (Heaney et al. 1999). Some other vermivorous taxa have similar reproductive timing around the early part of the year, with pregnancies in March and April among *Archboldomys luzonensis* and *Chrotomys gonzalesi* on Mt. Isarog and a new species of *Archboldomys* from Kalinga (Balete et al. 2006; Heaney et al. 1999). Females of *Rhynchomys* have 2 pairs of inguinal mammae, and the litter size appears to be 1, based on the result of the reproductive autopsies conducted on *R. isarogensis* (Heaney et al. 1999).

At the type locality, the following species of small, nonvolant mammals were recorded: *Apomys* cf. *microdon*, *Apomys* cf. *musculus*, 2 unidentified species of large *Apomys*, *Bullimus* cf. *luzonicus*, and *Rattus everetti*. All of these are endemic to the Philippines, and the 2 large *Apomys* species and *Bullimus* probably are restricted to Luzon. At the 1,250-m site on Mt. Banahao, a similar assemblage was observed with the exception of *A.* cf. *musculus* and *Bullimus*. In addition, we recorded *Crocidura grayi* at this latter site. Both *C. grayi* and a large *Apomys* also were recorded at the site where Rosell (1996) captured *R. banahao*.

Rhynchomys tapulao, *new species*

Holotype.—Young adult male, FMNH 183555, collected on 10 January 2005 (original field number 3505 of DSB); initially fixed in formalin, now preserved in ethyl alcohol with skull removed and cleaned. The specimen is in good condition, except for muscle tissue that was removed from the left femur. It is deposited at FMNH but will be transferred to NMP.

Type locality.—Mt. Tapulao, Palauig Municipality, Zambales Province, Luzon Island, Philippines, in primary mossy forest at 2,024 m elevation, 15°28′54.8″N, 120°07′10.4″E (Fig. 1).

Referred specimens.—Two other specimens of *R. tapulao* are known, both from the type locality. One is a young adult female (FMNH 183553) collected 8 January 2005, and the other is a young adult male (FMNH 183554) collected 9 January 2005. Both are preserved in ethyl alcohol, with skulls removed and cleaned. Stomachs were removed for content analysis and muscle tissue was removed from the left femurs. The braincase and right mandible of FMNH 183553 are broken, but otherwise the specimens are in good condition.

Distribution.—*Rhynchomys tapulao* is known only from the type locality on Mt. Tapulao, Zambales Province (Fig. 1),

where it occurs in primary mossy forest near the peak; it is apparently absent from other localities we surveyed in disturbed montane forest (about 1,200–1,690 m) and secondary lowland forest (about 860–925 m).

Etymology.—This new species is named for the type locality, Mt. Tapulao, the highest peak in the Zambales Mountain range. *Tapulao* is from the Sambal language and is the name used for the local pine (*Pinus merkusii*) found at higher elevations on the mountain. It is used as a noun in apposition. We propose ''Zambales shrew-rat'' as the English common name.

Diagnosis.—A species of *Rhynchomys* distinguished from the other 3 species in the genus by the following combination of characters (with contrasting characters of the other species in parentheses): pelage with a sharp delineation between the brown dorsum and white venter (ventral pelage darker and less contrast between the dorsum and venter); tail bicolored, uniformly dark over basal two-thirds and unpigmented distally (tail unicolored or dorsoventrally bicolored); narrower zygomatic breadth (broader); anterior margin of zygomatic plate straight (anterior margin convex); higher braincase (shallower braincase); larger auditory bullae (shorter and narrower bullae); and longer upper and lower molariform toothrows (shorter toothrows).

Description and comparisons.—*Rhynchomys tapulao* is characterized by a distinctive golden brown dorsum, white venter, and bicolored tail. It is similar to other members of the genus in general form, but differs in size and in various cranial and dental features (Tables 1 and 2; Figs. 3–6).

The pelage of *R. tapulao* is similar to that of other members of the genus in length and texture, but it is not as thick as in *R. banahao*. There is a sharp color delineation between the brown dorsum and the white venter. The dorsal fur is medium golden-brown; individual hairs are tricolored, medium gray on the basal two-thirds, pale brown with black tips on distal one-third. In the holotype and 2nd male specimen (FMNH 183554), the venter is entirely white, as is the back of the forearm; the inner thigh and hind leg are medium gray. The female specimen (FMNH 183553) is similar except for pale gray across the upper abdomen, throat, and inguinal area. In the other species, general ventral color is much darker and there is much less contrast between the dorsum and venter.

As in the other species, the lips and rhinarium of *R. tapulao* are unpigmented. The eyelids are finely edged in black. The mystacial vibrissae are as long as in congeners, with the longest ones extending beyond the ears, but are paler than in *R. banahao*. The ears are similar in length to those of *R. banahao* and *R. soricoides* from Kalinga, whereas *R. isarogensis* and *R. soricoides* from Mt. Data have shorter ears (Table 1). The ears are uniformly medium gray with a sparse covering of short, black hairs on both outer and inner surfaces, as in *R. soricoides* (darker gray in *R. banahao* and paler gray in *R. isarogensis*).

The forefeet are slender with robust digits. The pollex has a short nail; other digits bear long, sharp claws that are opaque. As in *R. isarogensis* and *R. soricoides*, the dorsal surface of the manus, including the digits, is unpigmented and sparsely covered with short, white hairs (in *R. banahao*, the foot is pale gray and covered with black hairs). The palmar surface is similar to those of the other species and the pads are naked and unpigmented.

The hind foot of *R. tapulao* is as long as that of *R. banahao*, but substantially narrower; *R. soricoides* from Kalinga and Mt. Data have the longest feet, and *R. isarogensis* the shortest (Table 1; Fig. 3). The dorsal surface of the foot, including the digits, is sparsely covered with short white hairs, as in *R. isarogensis* and *R. soricoides* from Kalinga, and in contrast to dark gray hairs in *R. banahao* and *R. soricoides* from Mt. Data. The plantar surfaces are naked and gray, as in congeners. The plantar pads are unpigmented, except in the female (FMNH 183553), and consist of 4 large interdigitals, a much smaller medial metatarsal (hypothenar), and thin, elongate metatarsal (thenar). The pads are small relative to the plantar surface, as in the congeners, but are substantially smaller than those of *R. banahao* (Fig. 3).

The tail of *R. tapulao* is slightly shorter than that of *R. banahao*, both of which are relatively and absolutely shorter than in *R. soricoides*; *R. isarogensis* has the shortest tail, both relatively and absolutely (Table 1). The dorsal surface of the tail is medium gray on its basal two-thirds, and sparsely covered with short gray and white hairs, whereas the distal one-third is unpigmented with white hairs. Ventrally, the basal one-fourth of the tail is paler gray, and the remainder unpigmented, except for the faintly pigmented midventral strip that extends to about the basal one-third of the tail (in *R. isarogensis*, the tail is medium gray above and paler below; in *R. soricoides*, it is medium gray above and unpigmented below; in *R. banahao*, the tail is uniformly darker). As in *R. isarogensis*, the tail scales are smaller than in either *R. banahao* or *R. soricoides* (Table 1). In all 4 species, there are 3 hairs associated with each scale; in *R. tapulao* the hairs are as long as in *R. isarogensis* and shorter than those of both *R. banahao* and *R. soricoides*.

The 3 known specimens of *R. tapulao* include a female and 2 males. As in *R. isarogensis* and *R. soricoides*, there are 2 pairs of inguinal mammae. In *R. isarogensis*, females are slightly smaller than males in most external and cranial dimensions (Tables 1 and 2; Heaney et al. 1998). Sexual size dimorphism is not apparent in either *R. tapulao* or *R. soricoides*, for which there are fewer female specimens; *R. banahao* is represented by 2 males only. Aside from minor differences in ventral pelage (noted above), there are no sex-related color differences in any of the species.

General cranial morphology of *R. tapulao* is similar to that of congeners, but differs in size and proportions of certain elements (Table 1; Figs. 4 and 5). The overall skull length is greater than in *R. isarogensis*; *R. banahao* is slightly longer, whereas *R. soricoides* has the longest skull. The braincase *R. tapulao* is inflated dorsally and is substantially higher than in the other species. Breadth of the braincase is similar in all species, but relative to this dimension, zygomatic breadth is less in *R. tapulao* (particularly in comparison to *R. banahao*). The rostrum is about as long as in *R. banahao* (shorter than in *R. soricoides* and longer than in *R. isarogensis*). As in *R. soricoides*, the rostrum is narrowest at its midpoint near the

premaxillary–maxillary suture; it is broader in both *R. banahao* and *R. isarogensis*.

In lateral view (Fig. 5), the braincase is tapered from the inflated cranium to the tip of the rostrum. The dorsal profile is very slightly convex from the midparietal to the anterior margin of the frontals, relatively flat across the posterior portion of the nasals, and again convex along the distal one-fourth of the nasals, where they inflate dorsad and terminate with decurved tips. The profile is most similar to that of *R. isarogensis*; *R. banahao* has a nearly linear lateral profile, whereas that of *R. soricoides* is slightly concave. The posterior cranial profile of *R. tapulao* slopes slightly down caudad from the anterior edge of the interparietal to the inflated supraoccipital. The exoccipitals are less inflated than in *R. banahao*, resulting in a flatter cranial base, as in *R. isarogensis*. The inflation of the supraoccipital and exoccipitals in *R. soricoides* is less pronounced than in the other species and projects only slightly forward beyond the edge of the interparietal.

The zygomatic plate of *R. tapulao* is slanted with only minor overlap between the dorsal and ventral maxillary roots, as in *R. banahao*, *R. isarogensis*, and *R. soricoides* from Mt. Data; the overlap is more substantial in specimens of *R. soricoides* from Kalinga. The anterior edge of the zygomatic plate is nearly straight, in contrast to the relatively convex plate in the other species (Fig. 6). The ventral maxillary root of the zygomatic plate overlaps with the maxillary toothrow, with the anterior margin positioned about one-third of its length ahead of the anterior margin of the 1st molar, as in the other species. The posterior margin terminates slightly behind the posterior margin of the last molar, as in *R. banahao*, in contrast to the relatively wider clearance from the last molar in *R. isarogensis* and *R. soricoides*. As in the other species, the squamosal root of the zygomatic arch is positioned low on the skull at a level just slightly above, and terminating close to, the dorsal margin of the postglenoid vacuity.

As in the other species of *Rhynchomys*, the nasals and premaxillae form a tubelike structure that projects beyond the anterior surfaces of the upper incisors (Figs. 4 and 5). As in congeners, there is a small interpremaxillary foramen located immediately behind the incisor alveoli. The incisive foramina are long and slender, at least 3 times as long as they are wide, and extend for more than one-third of the rostral length. Shallow palatine grooves extend along the maxillae from the posterior margins of the incisive foramina, their outside margins following those of the latter, terminating at the postpalatine foramina. The grooves become deeper as they join the elongate postpalatine foramina, partly hidden under the folded inner edge of the maxillae opposite the posterior half of the 1st molars. Behind the posterior edge of the postpalatine foramina, the palatine grooves become thinner and shallower before terminating at about the middle of the palate.

The palatine of *R. tapulao* is extremely long, extending beyond the 3rd molar by 3 times the length of the maxillary toothrow. The mesopterygoid fossa is comparatively wide. The auditory bullae are larger than those of the other species (Table 1); they are slightly inflated anteriad as in *R. isarogensis* and *R. soricoides* from Kalinga, resulting in a flatter posterior section, unlike the more rounded bullae in *R. banahao* or the slightly inflated posterior section of *R. soricoides* from Mt. Data. As in the other species, the postglenoid fossa is relatively small. The postalar fissure is short and relatively narrow as in *R. isarogensis* and *R. soricoides*. There is no mastoid fenestra. The mastoid foramen of *R. tapulao* is narrow and slitlike, but larger than in the other species.

As in the other species, the mandible of *R. tapulao* is very slender and delicate (Fig. 5). It is longer than in *R. banahao* and *R. isarogensis*, but shorter than in *R. soricoides* (Table 1). The angular process is more slender and has a blunter tip than in the other species. The coronoid process is long, delicate, and backswept, resulting in a deep and narrow sigmoid notch, as in *R. soricoides*.

The short and narrow upper incisors emerge at right angles to the rostrum. The slightly convex anterior surfaces have white enamel, and the tips are straight-edged. Breadth across the tips is slightly wider than in *R. banahao*, *R. isarogensis*, and *R. soricoides* from Kalinga, and narrower than in *R. soricoides* from Mt. Data.

As in congeners, the upper molariform toothrow is very short and narrow, relative to the palate. However, the overall length of the toothrow is greater in *R. tapulao* than in the other species (Table 1, holotype and 2nd male specimen). Below the anterior edge of the ventral zygomatic root, the maxillary bone forms a flat extension that frames the anterior border of the 1st molar. This ridge is more prominent in both *R. soricoides* and *R. banahao*, whereas it is much smaller in *R. isarogensis*.

The 1st upper molar is slender, longer than wide, and overlaps with the anterior margins of the 2nd molar (Fig. 6D). The anterior end is broadly tapered, and the posterior end more narrowly tapered; *R. banahao* has more robust molars that are rounder at both ends. The molars have worn cusps but retain much of the occlusal pattern. As in the other *Rhynchomys*, there are 3 primary cusp groupings, but these form a more linear arrangement along the narrow axis of the tooth. The prominent anterocone is presumably formed from the coalesced central t2 and labial t3. A lingual t1 is not evident in any of the specimens, accounting for the narrow anterior end of the tooth. Behind the anterocone, the main feature is the coalesced labial t5 and central t6 cusp, with a separate lingual t4. The 3rd group includes a prominent central t8 with the fainter labial t9; there is no evidence of a lingual t7. The 2nd molar is roughly circular in outline, about half as long as the 1st molar and slightly narrower. The crown surfaces suggest 2 groups of cusps: an anterior group consisting of the coalesced t4, t5, and t6, and a posterior coalesced t8 and lingual t9.

One of the many specializations of *Rhynchomys* is a reduction in the number of cheek teeth, with the loss of upper and lower 3rd molars resulting in 8 permanent molars (Musser 1969; Musser and Freeman 1981; Musser and Heaney 1992; Thomas 1898). This is the arrangement seen in all but 1 of the 65 known specimens of *Rhynchomys*. This total includes 60 specimens examined by us (Appendix I), and the original series of 5 *R. whiteheadi* examined by Thomas (1895, 1898). The exception is the female specimen of *R. tapulao* (FMNH 183553), which has a 3rd molariform tooth located at the

anterior end of the toothrow (Fig. 6E). The 2 other upper molars of this specimen are of the form typical for M1 and M2 in *Rhynchomys*, although both are smaller than seen in the other specimens of *R. tapulao* (Fig. 6D); the 2 lower molars are similar to those of the other specimens although slightly larger (Fig. 6J). The smaller teeth of this specimen compensate for the presence of an extra tooth such that the upper and lower toothrows occlude correctly. Wear on the crown surface of the supernumerary tooth indicates that it was functional. Although it is not located in the posterior position expected for a 3rd upper molar, the position is correct for a 4th premolar, a tooth that has been lost in all muroid rodents (Carleton and Musser 1984). Supernumerary cheek teeth are relatively uncommon in rodents and the question of their homology is often uncertain (Johnson 1952; Miles and Grigson 1990). As in this instance, supernumerary teeth are generally very small, and often involve compensatory adjustment in the size of the other teeth.

The lower incisors of *R. tapulao* are long and needlelike with very pale orange enamel on the anterior surface, as in the other species except *R. banahao*, which has pale yellow enamel. The mandibular toothrow is longer than in the other species (Table 1; Figs. 6F–J). The 1st lower molar is narrowly tapered anteriad and broadly tapered posteriad, and is most similar to that of *R. soricoides*. The crown surface is similar to those of the other species and includes a posterior cingulum (Figs. 6F–J; Musser and Heaney 1992:83, figure 49). Compared to the other species, the 2nd lower molar is relatively elongated with a tapered posterior margin. As in the others, the coronal surface consists of anterior and posterior basinlike structures.

Ecology.—*Rhynchomys tapulao* was recorded in mossy forest at 2,024 m, near the peak of Mt. Tapulao. We did not find it elsewhere on the mountain despite extensive trapping in lowland and montane forest between 860 m and 1,690 m (approximately 2,200 total trap-nights, half using traps baited with live earthworms). At the type locality, trees were generally small and stunted, with a canopy at about 5–7 m, and emergents up to about 10 m. Dominant trees included several species of *Syzygium* and *Leptospermum* (Myrtaceae), *Lithocarpus* (Fagaceae), and *Podocarpus* (Podocarpaceae). Many trees had gnarled trunks thickly covered with mosses and liverworts. Epiphytic orchids and ferns were common on trunks and branches. Climbing pandans (*Freycinetia*) were abundant, even extending beyond the canopy and crowns of emergent trees. During our survey, the ground surface was relatively dry with a moderate covering of mosses and leaf litter. Humus in the area was thin (Balete et al., in press).

Rhynchomys tapulao appears to be nocturnal–crepuscular. Specimens were caught on the ground in Victor snap traps baited with live earthworms; none were taken in traps baited with coconut (323 trap-nights). Trap success with earthworms was 0.67% (3 individuals out of 445 trap-nights), comparable to success rates for *R. isarogensis* and *R. banahao* (Balete and Heaney 1997; Rickart et al. 1991; this paper) and suggesting that *R. tapulao* may occur at low density. The preference for earthworm bait also was observed in the other species (Rickart et al. 1991; this paper). Stomachs of 2 specimens (FMNH 183553 and FMNH 183554) contained fragments of earth-

worms, centipedes, collembolans, ground beetles (Staphylinidae), and unidentified insect larvae. These invertebrates are associated with leaf litter on the forest floor (see for instance, Balete 1995; Heaney et al. 1999), and their presence in the diet of *R. tapulao* indicates that this species forages over the forest floor, uncovering decaying leaf litter at the soil surface for worms and other, mostly soft-bodied, invertebrates.

At least 7 other species of native, nonvolant small mammals were recorded at or near the type locality, including a shrew (*Crocidura.* cf. *grayi*), an apparently undescribed species of large *Apomys*, 2 small *Apomys* (*A.* cf. *musculus* and *A.* cf. *microdon*), an unidentified *Chrotomys*, and *R. everetti*. With the exception of the last, all of these species are endemic to Luzon.

DISCUSSION

Phylogenetic relationships.—Cladistic analysis of both nuclear and mitochondrial sequence data confirms that *Rhynchomys* belongs to a well-supported clade of endemic Philippine murines that also includes *Archboldomys*, *Chrotomys*, and *Apomys*, with the latter clearly basal but relationships among the other 3 genera unresolved (Jansa et al. 2006:79, figure 2). Although there are many derived morphological features that define *Rhynchomys* (Musser and Heaney 1992), morphology is not particularly useful for assessing relationships within the genus. An analysis, using *Apomys* as the outgroup, suggests that *R. banahao* may be basal but otherwise provides no resolution. A future paper will assess phylogenetic relationships using gene sequence data.

Biogeography.—The mammal fauna of the Philippines displays an exceptionally high level of endemism, exceeding 65% among the roughly 120 native nonvolant mammals (Heaney et al. 1998; Heaney and Rickart 1990). This unique diversity is the product of a long and complex geological history. Most of the islands within the archipelago are oceanic in origin and have never had dry-land connections to continental Asia (Hall 2002; Heaney 1986). Luzon, the oldest and largest island in the archipelago, has remained isolated from all but a few nearby smaller islands that were connected to it during Pleistocene periods of low sea level (Heaney 1986, 2004). Most of the species of nonvolant mammals are the result of extensive adaptive radiation of a few ancestral colonizers from the Asian mainland (Jansa et al. 2006).

Based on current knowledge, Luzon supports at least 34 species of native mammals (other than bats) of which 23 (approximately 68%) are endemic to the island (Balete et al. 2006; Heaney et al. 1998; unpublished FMNH collection data). Although our understanding of species distribution patterns and the full range of mammalian diversity on Luzon is incomplete, examination of current data indicates that most of the species have restricted geographic distributions as local endemics confined to areas of highlands (Heaney 2001, 2004; Heaney and Rickart 1990). The Central Cordillera of north-central Luzon (Fig. 1) is the largest of these, and is the best known on the basis of studies in 2 places: Mt. Data, Benguet Province (Rabor 1955; Sanborn 1952; Thomas 1898), and the vicinity of Balbalasang, Kalinga Province (Balete et al. 2006; Heaney et

al. 2005). At least 9 species are thought to be endemic to the Central Cordillera, including *R. soricoides* (Heaney et al. 1998, 2005). Mt. Isarog, on the southern peninsula of Luzon, is much smaller in area, but supports 3 endemic species including *R. isarogensis* (Heaney et al. 1999). The Sierra Madre range of northeastern Luzon has at least 2 endemic mammals (Balete et al. 2006; Rickart et al. 1998), but it is still quite poorly known with no *Rhynchomys* yet documented (Heaney et al. 2002). With the species of *Rhynchomys* described herein, the Zambales Mountains and Mt. Banahao join the ranks of places on Luzon known to support local endemic species of mammals, as predicted on the basis of their height, area, and relative isolation (Heaney 2004). These 5 highland areas represent islands of montane and mossy forest habitats within the island of Luzon that consistently show localized endemism, as exemplified by the genera *Apomys*, *Archboldomys*, *Chrotomys*, and *Rhynchomys* (Balete et al. 2006; Heaney 2004; Musser and Freeman 1981; Rickart et al. 1998, 2005; Steppan et al. 2003). Both the extent of the localized endemism and the mechanism(s) by which the diversity have been generated deserve much further study.

Conservation.—The discovery of 2 new species of *Rhynchomys* from 2 different and widely separate mountains on Luzon further highlights the richness of small mammal assemblages on isolated mountains on old, oceanic islands of the Philippines. Examination of our current data on the new species suggests that they are not abundant and that they are probably restricted to montane habitats. However, examination of our data does not indicate what the geographic range of either may be. In both cases, the montane habitats are not under substantial threat from logging or agriculture, but plans for mining in Zambales and current levels of use by hikers and religious pilgrims on Mt. Banahao pose some reason for concern (Mallari et al. 2001). Mt. Banahao is currently protected as a national park, but the Zambales Mountains have no designated protected areas. We recommend that a national park or other protected area be designated in Zambales that includes all types of habitats at all elevations, to assure protection of this newly documented center of mammalian endemism, including the highly distinctive *R. tapulao*.

BUOD

Ang *Rhynchomys* as isa sa mga lipi ng dagang sa Pilipinas lang makikita. Sila ay nagtataglay ng kaanyuhan na may pinagsamang mga katangian na nagpapahiwatig ng pagiging sinauna at pambihira. Ang mga dagang ito na tinaguriang "shrew-rats" ay kadalasan mga panggabi at bukod-tangi sa pulo ng Luzon. Pawang mga bulati at insekto lang ang kanilang ikinabubuhay. Sa pagtasa ng kanilang kaanyuhan at mga sukat ng pangatawan, bungo, at ngipin, lumalabas na mayroon silang apat na magkakaibang uri, kasama na ang dalawang ngayon lang isinalarawan at pinangalanan sa lathain na ito. Ang lahat ng *Rhynchomys* ay matatagpuan lamang sa kagubatan ng matataas na bahagi ng mga kabundukan, mula 1,125 m pataas, sa hilaga, kanluran at timog-silangang Luzon. Ang pagkahati-hati ng kagubatan noong sinaunang panahon at ang kasunod na pagkawatak-watak ng mga kawan ng *Rhynchomys* sa mga kagubatang yaon ay ang tinatantiyang paraan na nagbunsod sa pagdami ng kanilang uri. Ang paraang din ito ang malamang na dahilan ng pagdami ng uri ng iba pang lipi ng mga dagang matatagpuan sa matataas na bahagi ng mga kabundukan ng bansa. Ang pagkatuklas ng mga *Rhynchomys* na bukod-tangi sa isa o mangilan-ilang matataas na kabundukan lamang ay karagdagang pagpapatunay ng pagkakaroon ng maraming sentro ng mga katutubong hayop sa Luzon at sa pangangailangang madagdagan pa ang dami nang mga pinangangalagaang pook sa pulong ito.

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APPENDIX I

Specimens examined.—During this project and in the conjunction with earlier studies we examined most of the available specimens of *Rhynchomys*, including all housed at the Field Museum, Chicago, Illinois (FMNH; $n = 28$) and at the Smithsonian Institution, Washington, D.C. (USNM; $n = 32$). 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). All localities are on Luzon Island, Philippines.

Rhynchomys banahao (n = 2).—Quezon Province, Tayabas Municipality, Barangay Lalo, Mt. Banahao, 1,465 m, 14°03′59.4″N, 121°30′39.9″E (FMNH 178429 [holotype]), 1,250 m, 14°03′N, 121°30′E (FMNH 183590).

Rhynchomys isarogensis (n = 36).—Camarines Sur Province, Mt. Isarog, 4 km N, 21.5 km E Naga, 1,350–1,750 m, 13°40′N, 123°22′E (FMNH 152038, USNM 573573–573585, 573900–573918); Mt. Isarog, 8.9 km N, 0.8 km E Ocampo Municipality, 1,700–1,800 m, 13°38′32″N, 123°23′30″E (FMNH 147182, 147183); Mt. Isarog, Pili Municipality, Barangay Curry, 5,500 feet (1,676 m) (FMNH 95123 [holotype]).

Rhynchomys soricoides (n = 19).—Kalinga Province, Balbalan Municipality, Barangay Balbalasang, Magdallao, 1,600 m, 17°27.5′N, 122°04.1′E (FMNH 167320–167325); Amlicao, 1,800 m, 17°26.5′N, 122°04.25′E (FMNH 169170–169175, 170980, 170981); Mt. Bali-it, 1,950 m, 17°25.8′N, 122°00.1′E (FMNH 175617, 175618), 2,150 m, 17°25.7′N, 122°59.8′E (FMNH 175619); Mountain Province, Mt. Data (FMNH 62289, 62290).

Rhynchomys tapulao (n = 3).—Zambales Province, Palauig Municipality, Barangay Dampay-Salaza, Mt. Tapulao, 2,024 m, 15°28′54.8″N, 120°07′10.4″E (FMNH 183553, 183554, 183555 [holotype]).