

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3237, 51 pp., 29 figures, 6 tables August 27, 1998

Philippine Rodents: Redefinitions of Known
Species of *Batomys* (Muridae, Murinae) and
Description of a New Species from Dinagat Island

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ABSTRACT

Batomys russatus, new species, is described and compared with the other species of *Batomys*. The new form is represented by three specimens collected in lowland tropical evergreen rainforests on Dinagat (10°N, 125°45'E), an elongate, mountainous small island off the northwest coast of Mindanao in the Philippine Archipelago. Among diagnostic traits of the new species are its small body size, colorful russet fur, and complete (primitive) cephalic arterial patterns—in this last feature, it is unique among species of extant murines.

Three other species of *Batomys* have been described, all of them larger-bodied animals with somber brown fur and a derived cephalic arterial circulation. All available specimens (N = 162) of these larger-bodied species were studied to reevaluate morphological and distributional species boundaries. Among the three, *B. dentatus* is the most distinct. Represented only by the holotype collected in the highlands of Luzon, it is the only known *Batomys* with a furry brown-and-white tail and exceptionally large molars, both in absolute measurements and relative to cranial size. *Bato-*

mys granti also occurs in the mountains of Luzon, but it is morphologically very similar to *B. salomonseni*, which is now represented by samples from the islands of Mindanao, Leyte, Biliran, and Dinagat. These two species differ in tail diameter and pilosity, hind foot configuration, cranial proportions, and frequency of certain molar cusps.

The new *Batomys* is one of 29 native mammal species currently documented from Dinagat by voucher specimens. It and another rodent, *Crateromys australis*, along with the insectivore *Podogymnura aureospinula*—approximately 10% of the mammalian fauna—have been found only on Dinagat. Other species native to the island either occur on nearby islands that were apparently joined during the late Pleistocene to form a larger land area (Greater Mindanao), or are found throughout the Philippine Archipelago and even in adjacent regions outside the Philippines. Within the Greater Mindanao cluster of islands, only Mindanao, the largest, has a proportion of endemic mammalian species comparable to that on the much smaller Dinagat; the other islands lack endemics altogether. Why this is so is unknown.

INTRODUCTION

The murine *Batomys* contains three species that are found only in the Philippine Archipelago (Musser and Heaney, 1992). Two, *B. granti* and *B. dentatus*, have been recorded from Luzon and a third, *B. salomonseni*, has been listed from Mindanao, Leyte, and Biliran, islands that during the late Pleistocene were part of a single land area described as Greater Mindanao by Heaney (1985; see also fig. 1). These terrestrial rats are of moderate body size with short tails and soft, thick, brown fur. Among Philippine murids, species of *Batomys* are most closely related to species of *Crateromys* and *Carpomys* (Musser and Heaney, 1992).

During 1972 and 1994, survey crews working on the island of Dinagat, off the northwest coast of Mindanao, obtained examples of *B. salomonseni* as well as three specimens of a fourth species of *Batomys*, one that is small in body size with bright russet fur. This form has already been injected into the literature on Philippine mammals as "*Batomys* sp." by Heaney and Rabor (1982), Heaney et al. (1987), Musser et al. (1985), and Musser and Heaney (1992). Our

primary purpose here is to name and describe that Dinagat endemic. To do so we have brought together all samples of *Batomys* that are housed in collections of museums and reevaluated morphological and distributional boundaries of the three species that have already been described. Based on new material comprising larger samples than have ever been available to naturalists, we provide improved definitions of *B. granti*, *B. salomonseni*, and *B. dentatus*, including morphological comparisons among the three as well as ecological information.

MATERIALS AND METHODS

SPECIMENS AND INSTITUTIONS: We examined 165 specimens of *Batomys* (including all holotypes except the type of *Mindanomys salomonseni*) that are stored in collections of the following institutions:

- AMNH American Museum of Natural History, New York City
- BMNH British Museum (Natural History), London [now Natural History Museum, London]
- BRT Field numbers of Blas R. Tabaranza, Jr.,

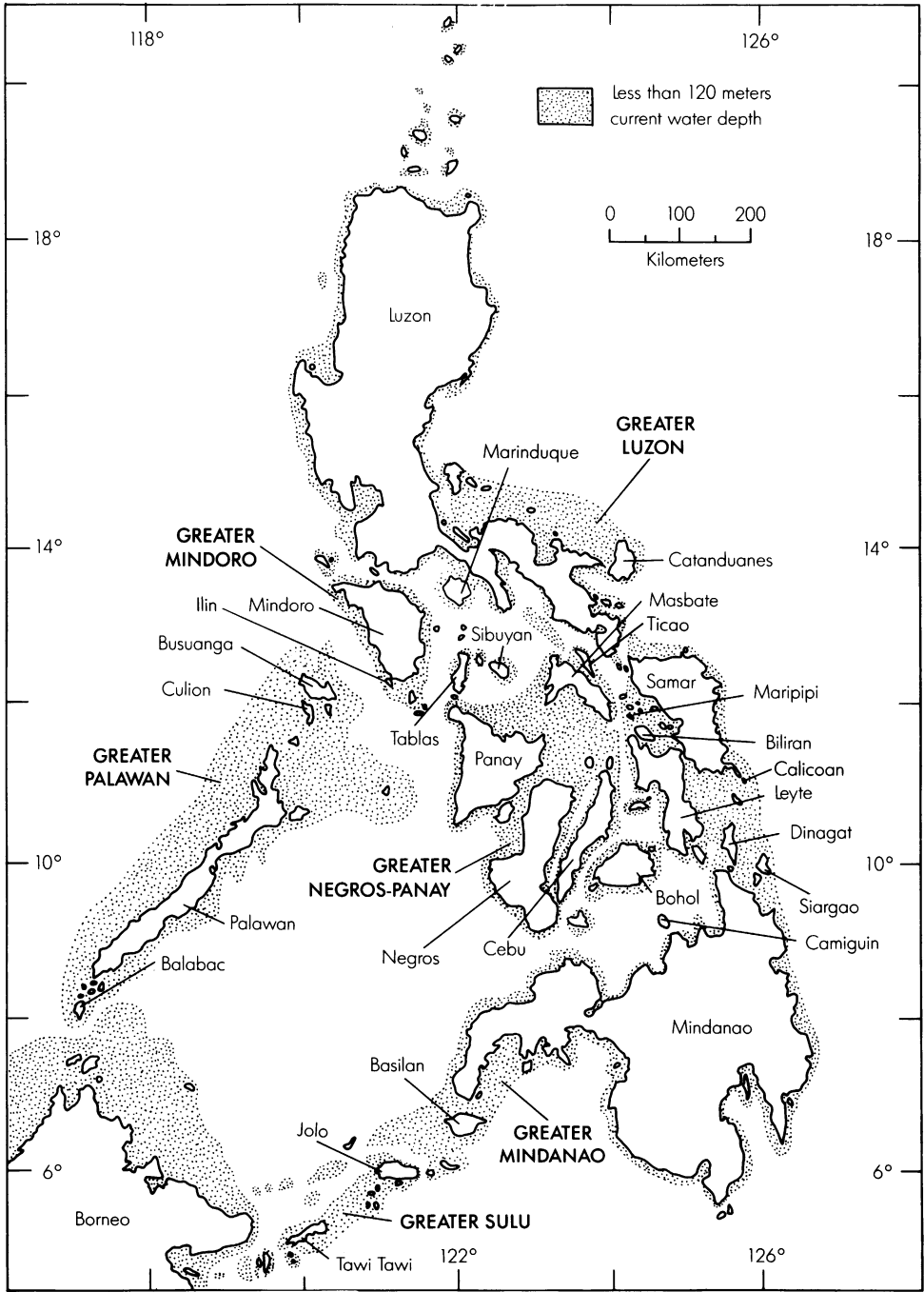


Fig. 1. The Philippine Archipelago. Extent of each late Pleistocene island (Greater Luzon, Greater Mindoro, Greater Palawan, Greater Negros-Panay, Greater Mindanao, and Greater Sulu) is indicated by the contiguously stippled areas. Limits of these Pleistocene land areas are based on the current 120 m bathymetric, which was estimated from hydrographic charts in the 90,000 series generated by the United States Defense Mapping Agency, Washington, D.C. Scale of most charts is 1:100,000; the others vary from 1:20,000 to 1:402,000.

for specimens that will eventually be deposited in the Mindanao State University–Iligan Institute of Technology, Mindanao

DMNH	Delaware Museum of Natural History, Wilmington
FMNH	Field Museum of Natural History, Chicago [now Field Museum, Chicago]
SMF	Senckenberg Museum, Frankfurt am Main
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
UZMC	Universitets Zoologisk Museum, Copenhagen

Specimens we reference by catalog number are preceded by one of these acronyms. Most material consists of standard museum preparations (a stuffed skin and accompanying cranium and mandible), but small series were preserved in formalin in the field and later transferred to 70% ethanol for permanent storage; some skulls were removed from those specimens.

MEASUREMENTS: Values for dimensions (in millimeters) of total, tail, hind foot (including claws), and ear lengths as well as body weight (in grams) were usually taken from either skin labels or field journals; we measured the appendages on a few museum skins (see tables 1 and 4). We estimated pelage thickness on stuffed skins by inserting the end of a short ruler through the dorsal coat to the skin, parting the fur back so it was erect along the base of the ruler, and averaging length of overhairs (excluding the guard hairs). Lengths of vibrissae were taken from dry skins and a few specimens preserved in fluid.

Dial calipers were used to measure (recorded to the nearest 0.1 mm) the following cranial and dental dimensions (listed in the sequence used in the tables):

ONL	occipitonasal length
ZB	greatest zygomatic breadth
IB	interorbital breadth
LR	length of rostrum
BR	breadth of rostrum
BBC	breadth of braincase
HBC	height of braincase
BZP	breadth of zygomatic plate
LD	length of diastema

LBP	length of bony palate
PPL	postpalatal length
LIF	length of incisive foramina
BIF	breadth of incisive foramina
BMF	breadth of mesopterygoid fossa
LB	Length of auditory bulla
CLM1–3	crown length of maxillary toothrow
BM1	breadth of first upper molar

Limits of these measurements are illustrated by Musser and Heaney (1992), and further defined by Musser (1979) and Musser and Newcomb (1983).

AGE AND SEX: Specimens ranging in age from young to old adults (these categories were defined by Musser and Heaney, 1992: 5) were lumped together as “adults” and their measurements used in the multivariate analyses and tables of descriptive statistics.

We grouped males and females together in all analyses. Studies of morphometric differences and similarities between sexes could be investigated with the large samples of *B. salomonseni* available, but samples of the other species are too small.

ANATOMY: Terminology follows Brown (1971) and Brown and Yalden (1973) for particular external features of the head (especially facial vibrissae) and limbs (palmar and plantar pads, for example); Bugge (1970) for the cephalic arteries; Wahlert (1985) for the cranial foramina; and Carleton (1980), Musser and Newcomb (1983), Carleton and Musser (1984), and Musser and Heaney (1992) for cranial morphology. Names of cusps and cusplets of upper and lower molars are noted in figures 12 and 14; sources of this terminology are explained by Musser and Newcomb (1983: 332).

SEM MICROGRAPHS: Illustrations of molar rows in figures 10–15 were generated by a scanning electron microscope from uncoated specimens.

STATISTICS: We calculated standard descriptive statistics (mean, standard deviation, and observed range) for a few samples.

Plottings of cluster analyses provided visual patterns reflecting similarity or contrast in the combination of all cranial and dental dimensions among geographic samples of a single species or between samples of different species. A discriminant function analysis was computed using the combination of cranial and dental measurements indicated in

various tables in the text. All measurement values were transformed to natural logarithms. Canonical variates were extracted from the discriminant function analyses. Cluster analysis employed the squares of Mahalanobis distances to the group centroids. SYSTAT 6.1 for Windows was employed for all analytical procedures.

ACKNOWLEDGMENTS

We are indebted to the curators and support staff at those institutions where we studied samples of *Batomys* and from which we borrowed material.

Illustrations were produced by Eric Brothers (figs. 5, 6, 16–18, 21, 22, 29), Alfred Gardner (fig. 21), Peter Goldberg (figs. 2–4, 7–9, 23–25), Dave Schmidt (fig. 20), Joan Whelan (figs. 10–15), and Patricia Wynne (figs. 1, 26–28).

Eric Rickart, Michael Carleton, and Eric Brothers read the manuscript and provided insightful comments that improved the final product.

We thank the Protected Areas and Wildlife Bureau of the Philippine Department of Environment and Natural Resources, especially W. Pollisco and J. DeLeon, for issuing permits to conduct inventory studies on Dinagat Island in 1994, and in other parts of the Philippines in previous years. Fieldwork on Dinagat was ably assisted by A. Tabaranza, N. A. Mallari, M. Carmona, A. P. Morales, and M. Escobido. The Ellen Thorne Smith Fund and Marshall Field Funds of the Field Museum provided financial support for field and museum studies.

THE DESCRIBED SPECIES OF *BATOMYS*

Three species of *Batomys* have been formally described and are currently recognized in published faunal reports (Musser and Heaney, 1992: 130; Musser and Carleton, 1993: 579): *B. granti* Thomas (1895), *B. dentatus* Miller (1910), and *B. salomonseni* (Sanborn, 1953). Each can be diagnosed by a suite of morphological traits, but those distinguishing characters have never been adequately described or illustrated in a comparative context that would allow unambiguous definition of each species. Providing such a framework

is our purpose in this section and is prerequisite to diagnosing the new species from Dinagat.

We begin by describing morphology of *B. granti*, the type species of the genus, which is known only from Luzon (fig. 1). In its morphology, *B. granti* closely resembles *B. salomonseni*, which is distributed on Mindanao, Dinagat, Letye, and Biliran, islands that coalesced during the late Pleistocene into a larger land area called Greater Mindanao (fig. 1). We identify *B. salomonseni* by elucidating the morphological traits that distinguish it from the Luzon species and by recording its distribution. Finally, samples of these species are contrasted with the only known specimen of *B. dentatus*, another Luzon endemic. Ecological information is summarized for all three.

Batomys granti Thomas, 1895

Thomas's (1895: 162–163) original description of *B. granti* was derived from specimens obtained by John Whitehead on "Plateau of Monte Data" (Thomas, 1898: 406):

General appearance very like that of *Carpomys melanurus*, from which at first sight it only differs by its shorter tail and less hairy ears. Fur of medium length and texture; general colour coarsely grizzled fulvous brown, the longer hairs black, the shorter ones with orange or rufous tips. Face greyer. Ears of medium length, only thinly haired as in ordinary *Mus*. Under surfaces dull slaty buff, not sharply defined; a whitish mesial line sometimes present. Metapodials brown mesially, silvery white laterally; hands apparently unusually elongated; feet rather short, with large solepads. Tail thickly and uniformly clothed (except for its basal half-inch) with dark brown, almost black, hairs some 7 to 9 millim. in length, the scales quite hidden.

Skull long, rounded, the supraorbital edges not ridged; zygomatic plate slightly concave anteriorly; bullae small; third upper molar as long as second [see figs. 2, 3].

Thomas enhanced his description of *Batomys granti* in 1898 and noted that the eyes are "surrounded by a distinct naked, or at least very finely haired, ring, a peculiarity which forms one of the readiest means of distinguishing *Batomys* from *Carpomys* externally."

Our knowledge of *B. granti* is based on the 19 specimens listed below, five (which includes the holotype) from Mount Data and 15 collected on Mount Isarog. Those from

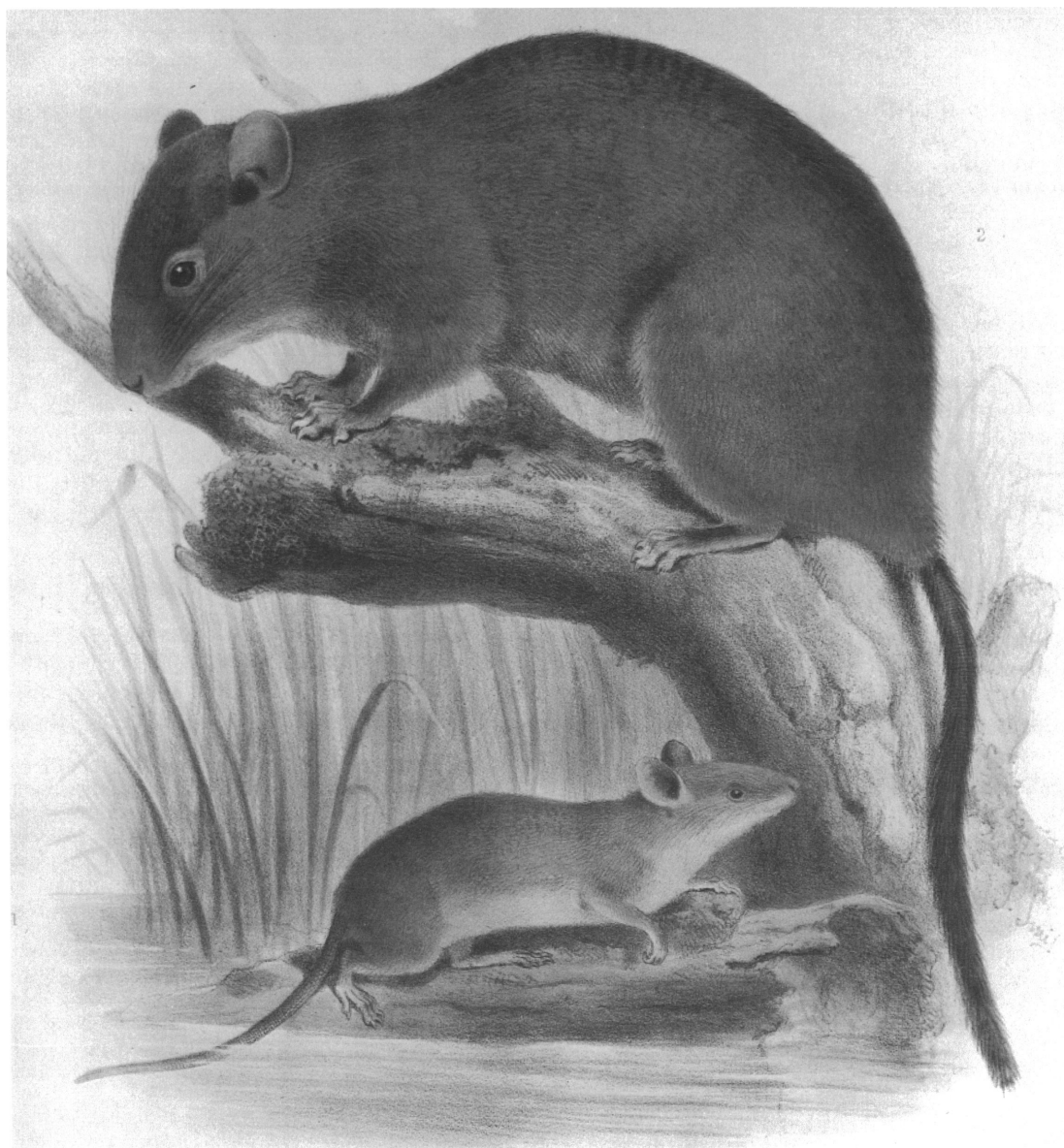


Fig. 2. *Batomys granti* is the large rat, *Crunomys fallax* the smaller one; reproduced from the color plate published in Thomas, 1898. Both species are elements of the unique Luzon rodent fauna.

Mount Data are preserved as stuffed skins and skulls. Fourteen of the other 15 specimens were preserved in formalin from which we extracted six skulls, and one was prepared as a skeleton.

LUZON ISLAND

1. **Mountain Province, Mount Data** (16°51'N/120°52'E; USBGN Philippines, 1989: 428; see

the map in Hoogstraal, 1951: 31) 7000–8000 ft: BMNH 95.8.2.15 (holotype of *Batomys granti*), 97.5.2.31 2500 m, and 97.5.2.32; FMNH 62503 and 62504.

2. **Camarines Sur Province, Mount Isarog** (13°40'N/123°23'E; Rickart et al., 1991: 459), 4 km north and 21.5–22.0 km east of Naga City on western slopes of Mount Isarog, 1350, 1550, and 1750 m (see Goodman and Gonzales [1990] and Heaney et al. [1998] for a map of

the camps at these elevations as well as descriptions of the sites): FMNH 142046, 152033; USNM 458914, 458939–458950.

DIAGNOSIS: A moderately large murine; pelage dense, woolly, and brown with buff and gray overtones on the venter; tail thick in diameter and covered with long brown hairs along its entire length; feet with brown patches on dorsal surfaces; hind feet wide with six large plantar pads; face with darkened masklike pattern; superciliary vibrissae short, not extending beyond pinnae; cranium somewhat elongate with long incisive foramina, alisphenoid struts usually absent; derived carotid circulatory circulation (no squamosal-alisphenoid groove and sphenofrontal foramen, stapedial foramen minute); first upper molar with cusp t1 oriented posterolingually; first and second upper molars lacking a posterior cingulum; first and second lower molars with large posterior cingulum either cordate or oblong in occlusal plane.

DESCRIPTION: Upperparts of head and body of most specimens are dark brown with dark tawny speckling; much darker along middorsal region of dorsum, paler (buffy brown) along sides of body. Some specimens exhibit a slight gray suffusion. The coat is soft and dense, somewhat woolly to the touch, the overhairs 12–15 mm long; guard hairs are only slightly longer (up to 20 mm) and inconspicuous because their tips are unpigmented. Underparts are not sharply demarcated from the dorsal coat and vary in color, ranging from dark grayish buff to bright ochraceous-buff suffused with gray. Expanse of coloration in most specimens is broken by white patches or streaks that vary in expression. Most specimens (FMNH 62504, for example) have a small white chin patch, a pectoral patch, and areas of white in the inguinal region. In others (FMNH 142046, for example), a wide area covered with white hairs extends from the chin, over the throat, and onto most of the chest. Ears are small and dark gray; the outer surfaces appear brown because they are densely covered with long brown and buffy hairs, but inner surfaces appear gray and naked—only a few unpigmented hairs are found there. Vibrissae appear delicate. The genals are short. Each superciliary extends only to the posterior margin of the pinna

when appressed against the head, but many of the mystacials extend 20–25 mm beyond posterior margin of the pinna. Eyelids are dark brown and each eye, as Thomas noted, is surrounded by a nearly naked and unpigmented ring 1–2 mm wide. The fur immediately encircling this eye ring is dark brown as is the fur at the base of the mystacial vibrissae; the combination of these dark patches against the brown face imparts a dark, masklike pattern.

Dorsal surfaces of front and hind feet are patterned. The dark brown fur of the upperparts extends to wrists and ankles and continues onto the dorsal metacarpal and metatarsal regions as a middorsal dark band that covers most of the foot in some specimens (FMNH 62504, for example) or forms a middorsal strip in others (FMNH 152033, for example); in the latter pattern, the strip is bounded by bright buffy hairs. Both front and hind digits are unpigmented and covered with silvery hairs that distally form ungual tufts covering, but not concealing, the short claws and extending beyond them. In the front foot, the two inner digits (III–IV) are the longest and about the same length, the fifth digit is only slightly shorter, and the second digit the shortest, its claw-tip reaching the base of the claw on the third digit. In the hind foot, the first digit (hallux) is the shortest, the next three are long and coequal in length, and the fifth digit is only slightly shorter (fig. 5). Each palmar surface is adorned with five large fleshy pads, three interdigital and two metacarpal. Each plantar surface has six pads: four moderately large interdigitals, an elongate and wide thenar, and a smaller hypothenar (fig. 5).

The robust tail is shorter than length of head and body in all samples and is covered by long (8–13 mm) dark brown hairs (a set of three emerges from beneath each tail scale) that provide the only color to the appendage because the rows of scales forming the epidermal surface are unpigmented.

Females have two pairs of inguinal teats; we detected no variation in number or location of teats among the specimens.

The cranium is robust with smooth dorsal surfaces (figs. 7–9). An overall elongation characterizes dorsal and ventral cranial perspectives, which reflects the visual influence

of the long and gracefully tapered rostrum ending in pointed nasal tips that extend beyond anterior borders of the premaxillaries to appreciably overhang the nasal aperture. The smooth contour of the rostrum is broken by the moderately inflated nasolacrimal capsules, plainly evident just anterior to the zygomatic plates in both dorsal and ventral cranial views. Top and sides of the interorbital and postorbital regions are smooth, unmarked by dorsolateral ridging or bony shelves. Also characterized by absence of prominent ridges, the boxlike braincase has a smooth top and slight dorsolateral elevations that mark origin of temporal muscles. Stout zygomatic arches enhance the robust appearance of the cranium.

From lateral perspective, the premaxillaries and nasals appreciably project beyond incisor faces. The rostrum itself is deep in dorsoventral plane. A moderately wide zygomatic plate has either a straight (the image in fig. 9, which characterizes most specimens) or concave (as in the holotype, fig. 3) anterior margin that barely juts free of the dorsal maxillary zygomatic process. In dorsal view, this slight projection of the zygomatic spine results in a very shallow zygomatic notch; it is imperceptible in some specimens. The ventral maxillary root of the arch originates mostly anterior to the first molar, a widespread configuration among species of murines. A long jugal contributes a significant section of each sturdy zygomatic arch. The squamosal root of each arch is located moderately high on the side of the braincase. Posterior to each squamosal zygomatic root and dorsad of the auditory bulla, the squamosal is intact, unperforated by any sub-squamosal foramen. The occiput is not deep, and its posterior surface is either vertical or slightly convex and does not overhang the occipital condyles in most specimens.

Within the orbit the ethmoid foramen is a narrow slit and the optic foramen is moderately large. Sphenopalatine and dorsal palatine foramina are separate, a pattern similar to the configuration illustrated for *Rattus* (see Musser, 1982: 22).

All but two of the 11 crania we examined do not have a bony alisphenoid strut posterior to the orbit and dorsad of the pterygoid ridge, which is the typical morphology in

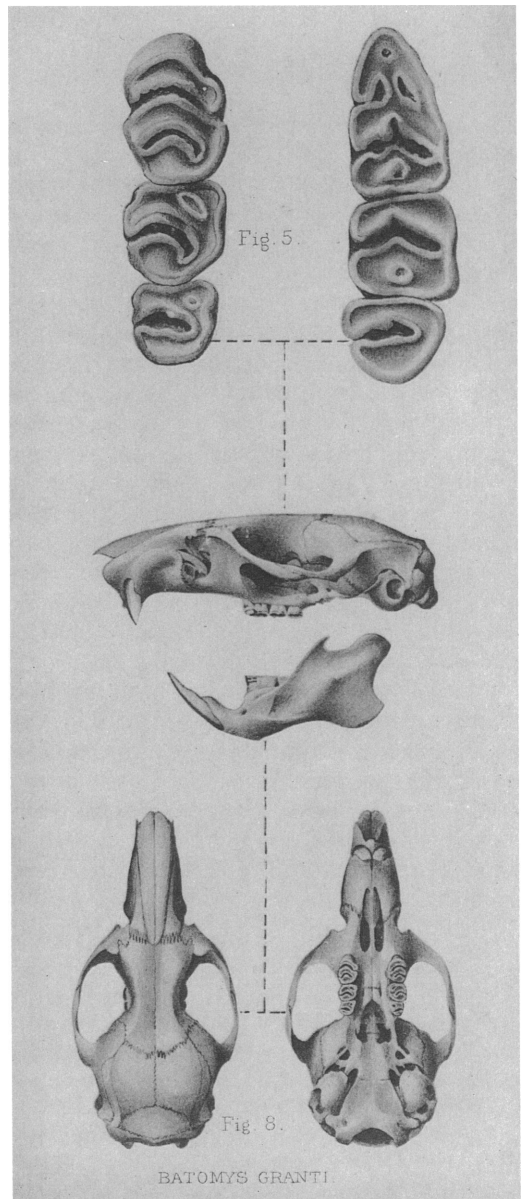


Fig. 3. Reproduction of figures 5 and 8 in plate 33 from Thomas (1898), which depict skull and molar rows of the holotype (BMNH 95.8.2.15, an old adult male) of *Batomys granti*.

species of *Batomys* (figs. 26, 27). A wide strut separating the foramen ovale accessorius from the combined buccinator-masticator foramen occurs on each side of the braincase in one of the six crania from Mount Isarog (USNM 458939), a configuration simi-

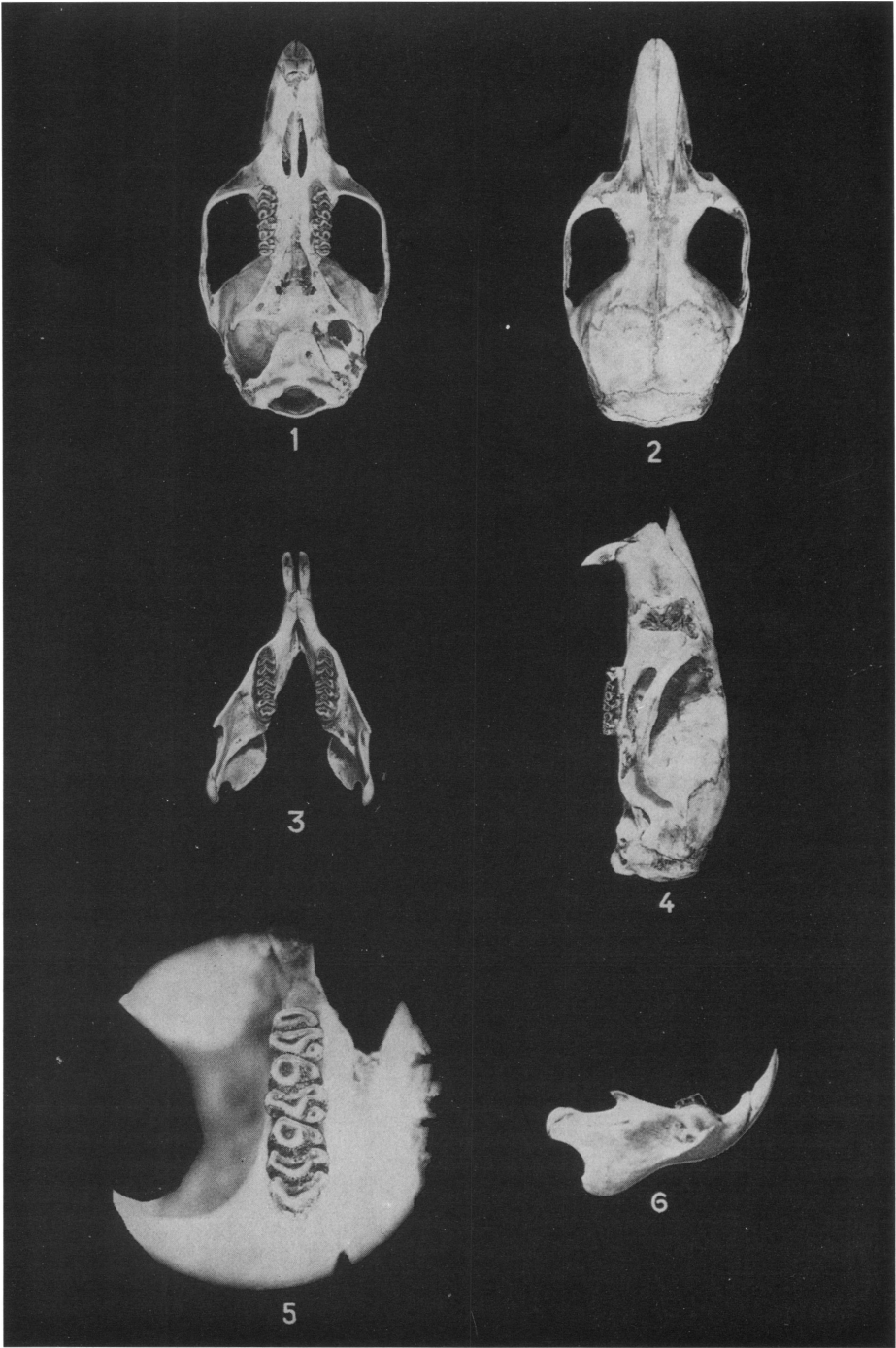


Fig. 4. Reproduction of Plate I from Sanborn (1953): skull and teeth of the holotype (UZMC 11912, an adult male) of *Mindanaomys salomonseni*.

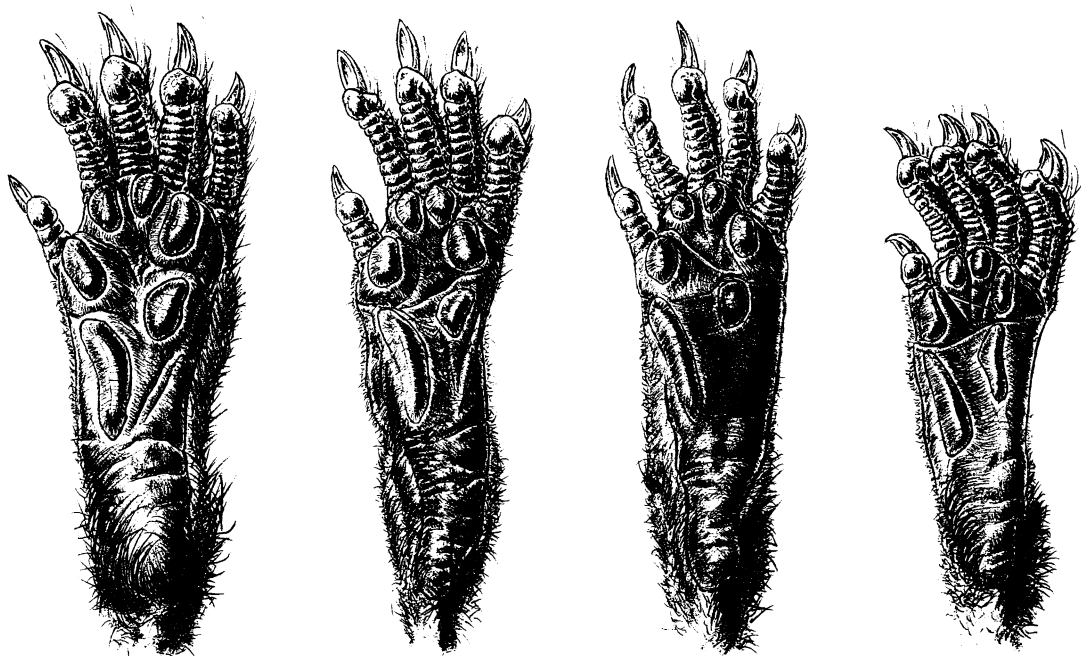


Fig. 5. Plantar views of the left hind foot (from adults) in three species of *Batomys*. From left to right: *B. granti* (Mount Isarog, Luzon; FMNH 142046); *B. salomonseni* (Mindanao; FMNH 147931); *B. salomonseni* (Dinagat; BRT 331); *B. russatus* (Dinagat; BRT 278). *Batomys granti* has a conspicuously broader foot than does *B. salomonseni*, although length of hind foot is not appreciably different between the two species (table 1). The four interdigital pads, elongate thenar, and smaller hypothenar pad are larger and seem thicker relative to total area of the plantar surface in *B. granti* compared with the extent and robustness of the pads in *B. salomonseni*. Note that the fifth digit is nearly as long as the three middle digits in all the species.

lar to that seen in the holotype of *B. dentatus* (fig. 26); there is a slender alisphenoid strut on the left side and a wide strut on the right in one of the five crania studied (BMNH 97.5.2.32) from Mount Data.

The nasal tips extend beyond the incisors in triangular outline, forming just one of several distinctive features seen when the cranium is examined from ventral perspective. A moderately large interpremaxillary foramen is apparent just caudad to the incisors. The incisive foramina are wide and long, their posterior margins located at the level of the anterior faces of the first molars. A bony palate shorter than the molar row is typical of other species of *Batomys*, and *B. granti* is no exception. The palate's emarginate posterior border does not extend past the back of the second molars; its surface is pierced by a pair of elongate posterior palatine foramina in the maxillary-palatine suture, at a

level between the first and second molars in some specimens or opposite the second molars in others. Some specimens have paired nutrient foramina caudad of the posterior palatine openings. Older individuals exhibit a pair of grooves scoring the ventral surface of the palate. In the roof of the wide mesopterygoid fossa is a pair of short but wide sphenopalatine vacuities. Stout hamular processes of the pterygoids separate the mesopterygoid fossa from each adjacent pterygoid plate (also called lateral pterygoid plate, pterygoid fossa, or parapterygoid fossa), which is an elongate triangle with a densely bony surface. Its posterior region is pierced in all specimens by the large ventral opening of the foramen ovale, and its anterior portion is ossified in some specimens but contains a small and irregular opening covered with tissue (sphenopterygoid vacuity) in other individuals.



Fig. 6. Contrast in tail diameter and pilosity between adult examples of *Batomys salomonseni* and *B. granti*. **Left:** *B. salomonseni* (Mindanao; FMNH 147925)—length of tail, 130 mm; greatest width of tail near base, 5 mm; average length of scale hair on proximal third of tail, 1 mm; length of longest hair at tail tip, 3 mm). **Right:** *B. granti* (Mount Isarog, Luzon; FMNH 152033)—length of tail, 132 mm; greatest width of tail near base, 7 mm; average length of hair on proximal third

Short and wide bony eustachian tubes are attached to auditory (ectotympanic) bullae that are small relative to overall size of the cranium, which is typical of the species of Philippine murids that Musser and Heaney (1992) dubbed “Old Endemics.” In this particular configuration, the bullar capsule does not cover the entire surface of the petrosal (= periotic, petromastoid). A wide postero-medial segment of that element is exposed as well as a tapered flange extending between capsule and basioccipital (fig. 28). Only a small portion of the tubular bony eustachian tube touches the basioccipital, and the tube forms the dorsolateral and ventral rim of the carotid canal while the basioccipital forms the canal’s medial edge; in some specimens the passageway for the internal carotid artery is actually less of a canal and more of a large gap between eustachian tube and basioccipital (see also fig. 61 in Musser and Heaney, 1992: 99). The middle lacerate foramen is a large gap between bullar capsule and alisphenoid and squamosal bones (fig. 28).

In the fissure between bullar capsule and periotic is a minute stapedia foramen. The small size of this opening coupled with the lack of a sphenofrontal foramen at the back of the orbit and a squamosal-alisphenoid groove scoring the inside surface of the lateral braincase wall signal a derived cephalic arterial pattern (fig. 28) that among Philippine murids is common to species of *Crateromys*, *Carpomys*, *Crunomys*, and most species of *Batomys* and *Apomys* (Musser and Heaney, 1992: 61–62, 68). Before entering the braincase through the carotid canal, the internal carotid artery gives off a small stapedia artery that passes through the minute stapedia foramen to enter the inner ear from which it does not reemerge. Inside the braincase, the internal carotid artery gives off a

←

of tail, 5 mm; length of longest hair at tail tip, 10 mm). Among specimens we examined, the magnitude of the differences illustrated here distinguishes every adult of *B. salomonseni* (thin tail, short scale hairs), regardless of the island where samples were obtained, from each adult example of *B. granti* (thick tail, long scale hairs) from Luzon.

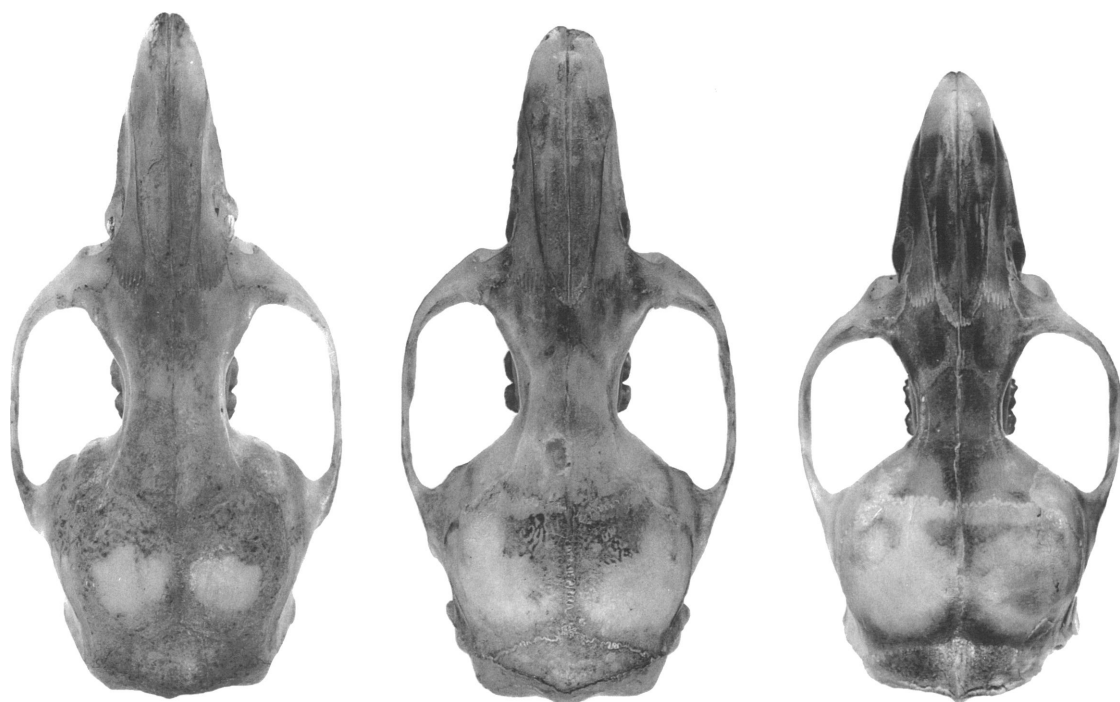


Fig. 7. Dorsal views of adult crania contrasting two species of *Batomys*. **Left:** *B. granti* (Mount Data, Luzon; FMNH 62504). **Middle:** *B. salomonseni* (Leyte; USNM 458776). **Right:** *B. salomonseni* (Dinagat; BRT 261). $\times 2$.

vessel that courses over the dorsal surface of the pterygoid plate and exits the braincase to enter the orbit through the anterior alar fissure. This artery is a secondary connection between the internal carotid and the arterial supply of the orbit and upper jaw. Musser and Heaney (1992) provided additional information, illustrations, and references pertaining to this derived circulatory pattern and the contrasting primitive arrangement in Philippine murids.

Each dentary is robust (fig. 9). A deep sigmoid notch separates the prominent coronoid projection from the condyloid process. The latter projects beyond posterior margins of the angular process, and the posterior margin of the dentary is deeply concave between these two processes. Ascending and ventral masseteric ridges are evident, and the end of the incisor capsule projects slightly from the lateral surface of the ramus at about the level of the coronoid process.

Upper and lower incisors have orange enamel layers; these faces are smooth, with-

out grooves or shallow sulci. In lateral view, the uppers curve slightly caudad after emerging from the premaxillaries, a configuration described as opisthodont (Thomas, 1919; Hershkovitz, 1962: 103). The lowers are moderately long after they exit the mandible.

Alveolar patterns for upper and lower molar roots of *B. granti* (FMNH 62504) are illustrated in figures 10 and 11. Each upper molar is anchored by three large roots; the first tooth has an additional labial holdfast. Two primary roots, some of which are bifid, underlie each lower molar; the first and third teeth have additional anchors. Whether these patterns vary among specimens of *B. granti* is unknown because we were reluctant to remove molars from more than one specimen. The process often results in damage to teeth and bony palate; specimens should not be dissected until variation in root pattern is demonstrated to have special significance in reconstructing phylogenetic relationships among species of *Batomys*.

Moderately high crowns and robust rows

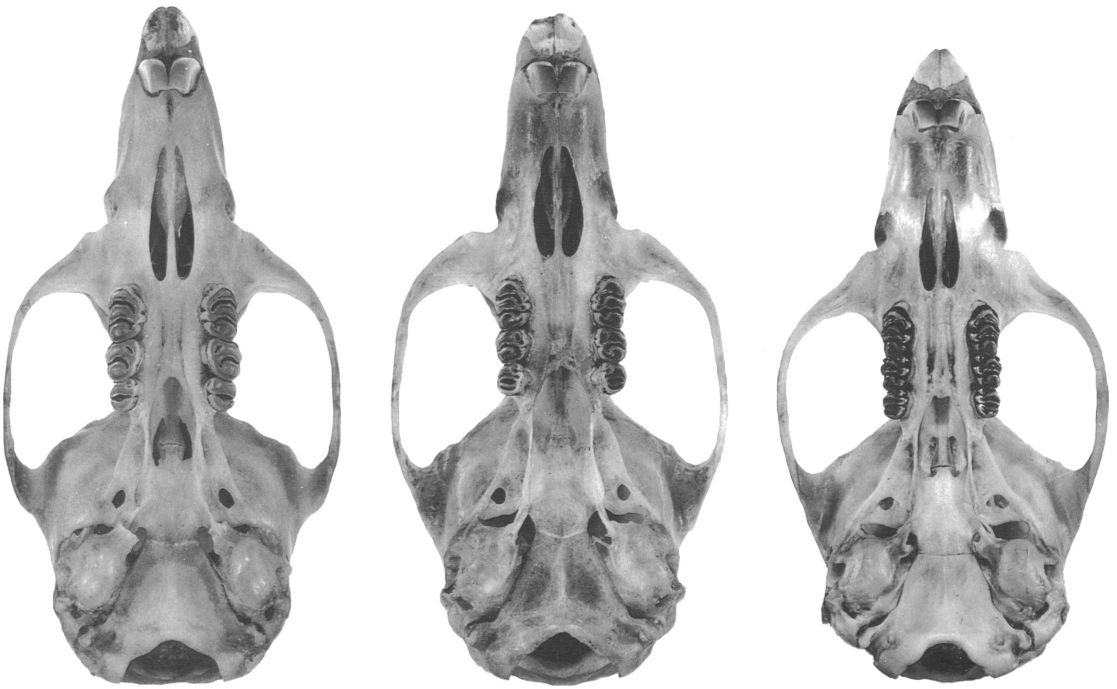


Fig. 8. Ventral views of crania shown in figure 7. **Left:** *B. granti*, Luzon. **Middle:** *B. salomonseni*, Leyte. **Right:** *B. salomonseni*, Dinagat. $\times 2$. Note the very long incisive foramina in *B. granti* compared with the shorter openings in the examples of *B. salomonseni*; the specimen from Dinagat has even shorter foramina than do most of the *B. salomonseni* from Leyte as well as Mindanao (see fig. 18 and table 2). Other contrasts between the two species revealed by discriminant function analysis (fig. 16, table 3) are also apparent: the longer diastema and shorter bony palate of *B. granti*, for example.

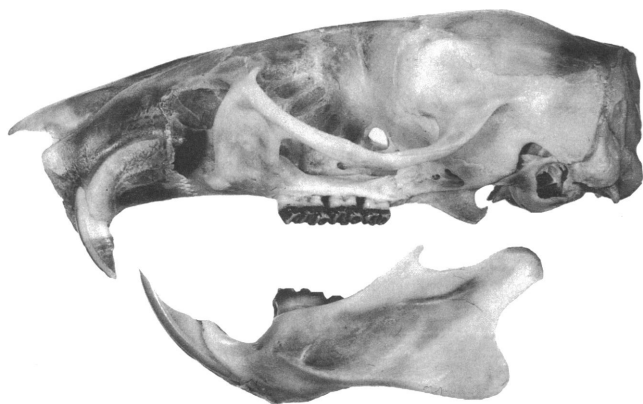
of cusps characterize the blocky molars (figs. 13, 15). The first two rows of cusps of each first upper molar tend to be laminar rather than clearly cuspidate (fig. 13). In the first row, the discrete anterolingual cusp (t1) is orientated posterolingually, the middle cusp (t2) seems stretched, and an anterolabial cusp (t3) has merged with the central cusp to the point that boundaries of both have been obliterated. It is the stretch to the central cusp and fusion with cusp t3 that imparts a laminarlike configuration to the row. All three cusps are evident in the second row, but both outside cusps (t4 and t6) are broadly joined to the stretched central one (t5). A chunky cusp t8 forms most of the chewing surface of the third cusp row. A prominent posterolingual cusp (t7) is pointed anteriorly. No posterolabial cusp (t9) is evident, but there is an enamel ridge on the labial side of the central cusp. No posterior cingulum (a cusp

originating from the posterior margin of cusp t8; see fig. 13) is detectable in any specimen.

A large cusp t1 persists on the second upper molar, but its labial counterpart, cusp t3, is absent or represented only by a cingular ridge. The occlusal conformations of the two complete rows of cusps resemble outlines of the those rows in the first molar. No cusp t9 or posterior cingulum can be identified.

A chunky anterolingual cusp (t1) and two laminae form the occlusal surface of each third upper molar. The anterior lamina is composed of an evident cusp t4 and a large central cusp t5 that has so fully fused with cusp t6 that the lamina appears to consist of only two cusps. An elongate cusp t8 and much smaller cusp t7 form the posterior lamina.

Occlusal surfaces of the lower molars are simple, formed by rows of primary cusps (fig. 15). Second and third rows of the first



molar and the two rows of the second are shaped like a widely spread inverted V, but the two rows of each third lower molar are nearly straight. The large posterior cingulum on each first and second molar is oblong in outline. Labial margins of each tooth are free of anterior and posterior cusplets or any other cingular elaborations. Anterolabial and posterolabial cusps are also absent from the second and third molars. The only significant occlusal complexity is the anteroconid of the first molar. That massive and triangular structure is formed by fused anterolabial, antero-central, and anterolingual cusps, a derived elaboration that is common to species in the *Crateromys* Group, as defined by Musser and Heaney (1992).

Chromosomes have been sampled from the Mount Isarog population of *B. granti*. Rickart and Musser (1993) reported that both diploid and fundamental numbers are 52, a graded series of small to large telocentric chromosomes constitute the karyotype, and those authors could not distinguish the sex chromosomes from the autosomes. The standard karyotype of *B. salomonseni*, derived from animals collected on Leyte, "is indistinguishable from that of *B. granti*" (Rickart and Musser, 1993: 4). Chromosomal data have not been obtained from any other species of *Batomys*.

GEOGRAPHIC VARIATION: Length of tail is conspicuously variable in our geographic samples. Tails of the few specimens from Mount Data are significantly shorter than are those in the series from Mount Isarog (table 1). Tips of the shorter tails are blunt and covered by scale hairs 8–10 mm long; the length seems to be natural and not a result of past damage and subsequent healing or of alteration during skin preparation. Differences in means of certain cranial measurements exist (table 2), but whether they reflect real contrasts between the populations in each highland must be determined by obtaining larger samples from Mount Data.

COMPARISONS: See the accounts of *B. salomonseni*, *B. dentatus*, and the new species from Dinagat for contrasts between each of them and *B. granti*.

ECOLOGY: All specimens of *B. granti* available for study come from mountain forests. Those five collected on Mount Data were taken between 7000 and 8000 ft. Three of these are in the British Museum and were the specimens collected by John Whitehead that formed the basis for Thomas's (1895, 1898) description of the genus and species. Whitehead (*in* Thomas, 1898: 406) recorded that "This interesting new Rat was captured for me by the Igorrotes, with the aid of their small terriers; it seems rare, only three specimens being obtained."

The other two examples of *B. granti* were collected in 1946 by members of an expedition led by Harry Hoogstraal and initially reported in Sanborn's (1952: 119) account of the mammals obtained by the expedition members. During a short visit to the camp on Mount Data, Hoogstraal (1951: 30–32) made the following observations in 1946:

Mount Data, the type locality for Whitehead's astonishing collections of endemic genera of rodents . . . reaches an altitude of about 8,000 feet, almost the highest point in Mountain Province. The peak is unique because of its flat plateau (about three miles long) which supports a well-developed mossy forest. The outer or western slope extends into the lowlands of Lapanto, and is apparently the area worked by Whitehead. . . .

The mossy forest on the summit consists largely of oaks (*Quercus* spp.) and mountain yews (*Taxus wallichiana* Zucc.), together with several other hardwoods and tree ferns. The forest is dark and dense, and most of the trees are dwarfed and shrubby. Ground ferns comprise most of the low vegetation. Bushes and small trees are often heavily entwined by vines and rattan. A heavy growth of moss covers the trees and the ground, together with a considerable variety of ferns, liverworts, lichens, epiphytic orchids, and other herbaceous plants. The soil is rich with wet, woody matter and rotting leaves.

According to Rabor (1955: 201), who was in charge of the camp on Mount Data, both

←

Fig. 9. Lateral views of crania and left dentaries of specimens illustrated in figures 7 and 8. **Top:** *B. granti*, Luzon. **Middle:** *B. salomonseni*, Leyte. **Bottom:** *B. salomonseni*, Dinagat. $\times 2$. Note the wider zygomatic plate of *B. granti*, which is one of the traits in the morphometric suite contrasting the two species as revealed by discriminant function analysis (fig. 16, table 3).

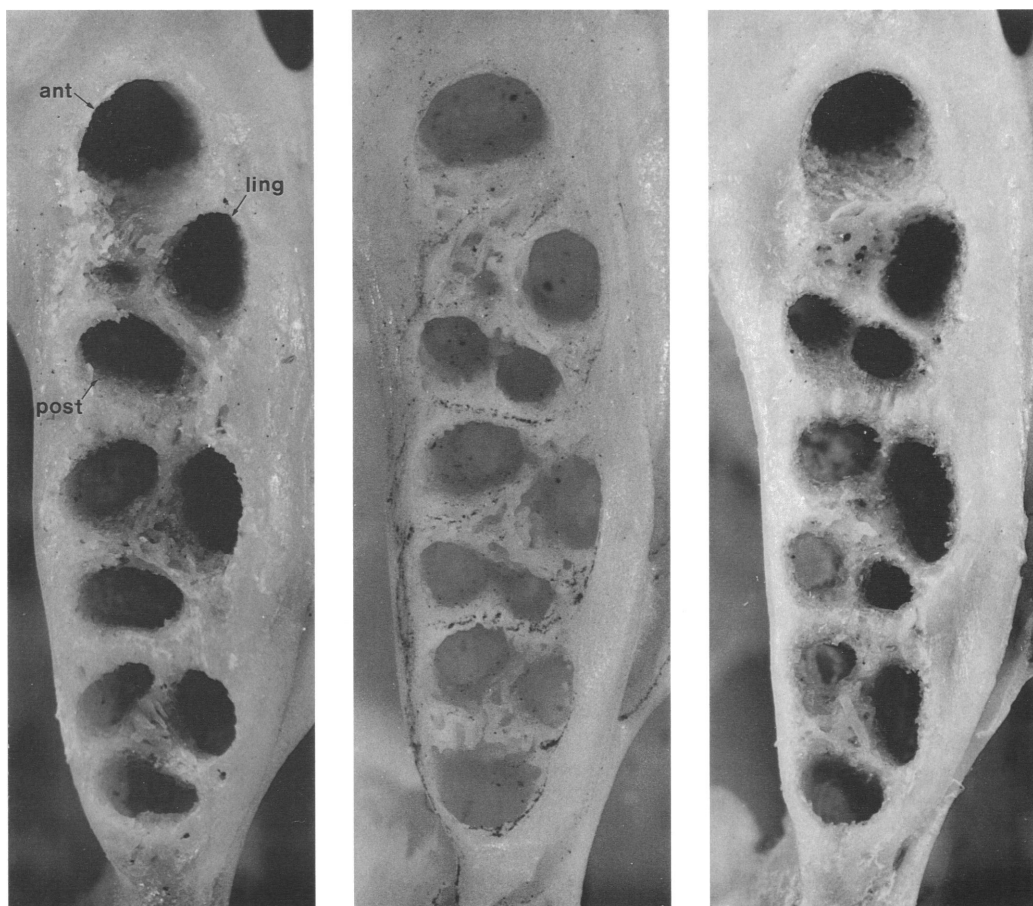


Fig. 10. Examples of alveolar variation of right upper molar roots among three species of *Batomys*. **Left:** *B. granti* (Mount Data, Luzon; FMNH 62504). **Middle:** *B. russatus* (Dinagat; DMNH 4593). **Right:** *B. salomonseni* (Mindanao; FMNH 92824). Except for the small ancillary labial holdfast opposite the lingual root of the first molar, each molar of *B. granti* has only three large roots—anterior (**ant**), lingual (**ling**), and posterior (**post**)—a primitive pattern for muroid rodents (Musser and Heaney, 1992: 100). The posterior root beneath first and second molars is divided in the other two species. See text for additional discussion.

rats “were trapped in very dense growth along the sides of a deep gully, very close to the top of the plateau, at about 2100 meters elevation.”

No other ecological information is associated with any of the three specimens collected by Whitehead or the two obtained by Hoogstraal’s party.

The specimens from Mount Isarog were collected at 1350, 1550, and 1750 m along the western slopes of the volcano. These elevations range through what Rickart et al. (1991) and Goodman and Gonzales (1990) call montane and mossy forests, formations

which are comparable to those often recognized as tropical lower and upper montane rainforests (Whitmore, 1984). Distribution and ecology of the species of small mammals collected along the elevational transect were documented by Rickart et al. (1991), Balete and Heaney (1993), and Heaney et al. (1998); additional descriptions of the forest formations at the different trapping sites supplemented by illustrations can be found in Goodman and Gonzales (1990).

Under the identity of “*Batomys* sp.,” Rickart et al. (1991: 464) reported that the species was “predominantly nocturnal.”

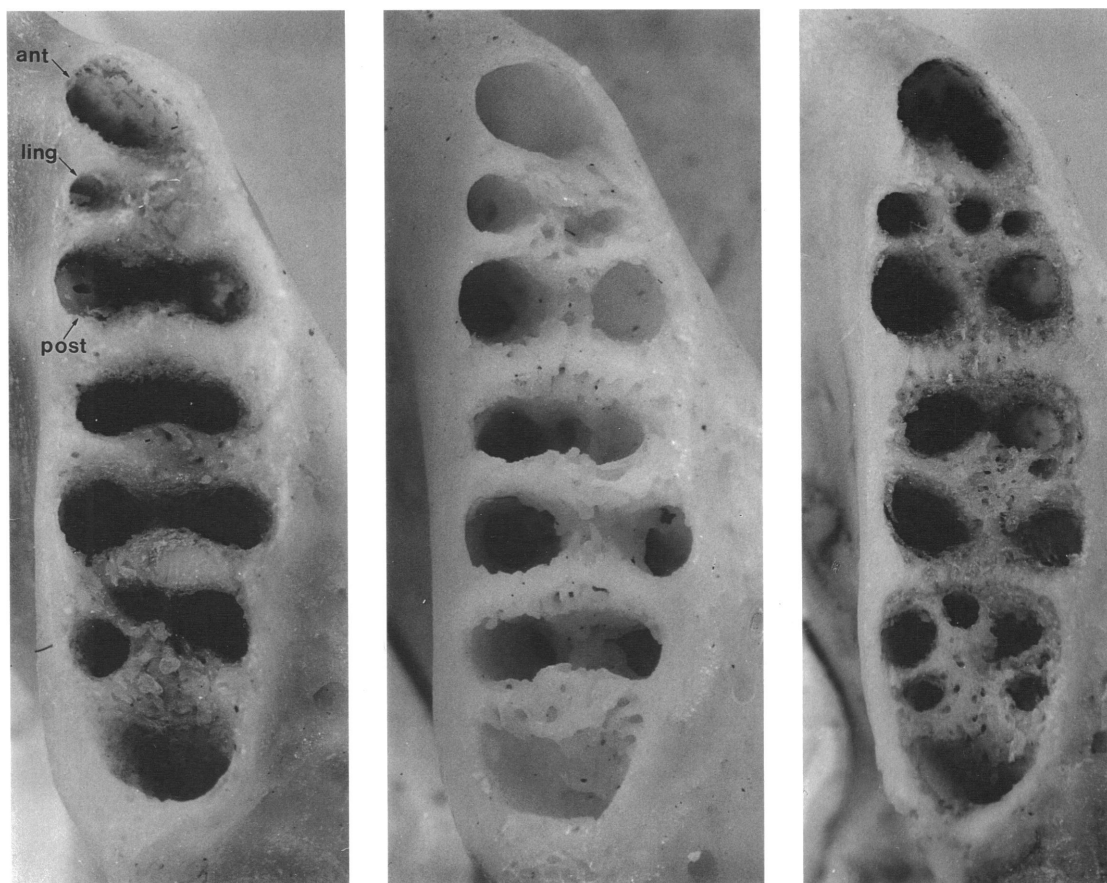


Fig. 11. Examples of the variation in alveolar patterns of right lower molar roots among three species of *Batomys* as reflected in the same specimens shown in figure 10. **Left:** *B. granti*. **Middle:** *B. russatus*. **Right:** *B. salomonseni*. Two roots anchoring each molar is the primitive pattern (Musser and Heaney, 1992: 101), which is modified in different ways in each species. The specimen of *B. granti* has a lingual root (**ling**) between anterior (**ant**) and posterior (**post**) holdfasts beneath each first and third molar, and each posterior root of the first and second molars is bifid. Further elaboration of roots is exhibited by *B. russatus* where there are two, instead of one, posterior roots beneath second and third molars, and divided anterior roots beneath second and third molars. The extreme multi-rooted pattern is seen in the example of *B. salomonseni* where the primary anterior and posterior roots are divided into segments, and there are additional smaller labial, medial, and lingual roots.

Stomach contents of three specimens contained "vegetable matter, including seeds, fruits, and some leaves," and only "seeds were accepted by two captives." All the examples of *Batomys* were trapped on the ground (Heaney, personal obs.)

Batomys salomonseni (Sanborn, 1953)

In 1953, Sanborn described *Mindanaomys salomonseni* as a new genus and species based on three rats collected from Mindanao.

Because the publication in which it appears is not readily available, we reproduce the bulk of the original description:

Type.—No. 11912, Zoologisk Museum, Copenhagen from Mt. Katanglad, 1600 meters, Bukidnon Prov., Mindanao Island, Philippines. Adult male, skin and skull. Collected by Dr. Finn Salomonsen, 19 December 1951. Original number K-7. Skull and teeth of the type are shown in plate I [see fig. 4].

Generic characters.—External form rodent-like, not unusual. The tail is shorter than head and body, the ears of medium size, feet normal, fur soft, thick,

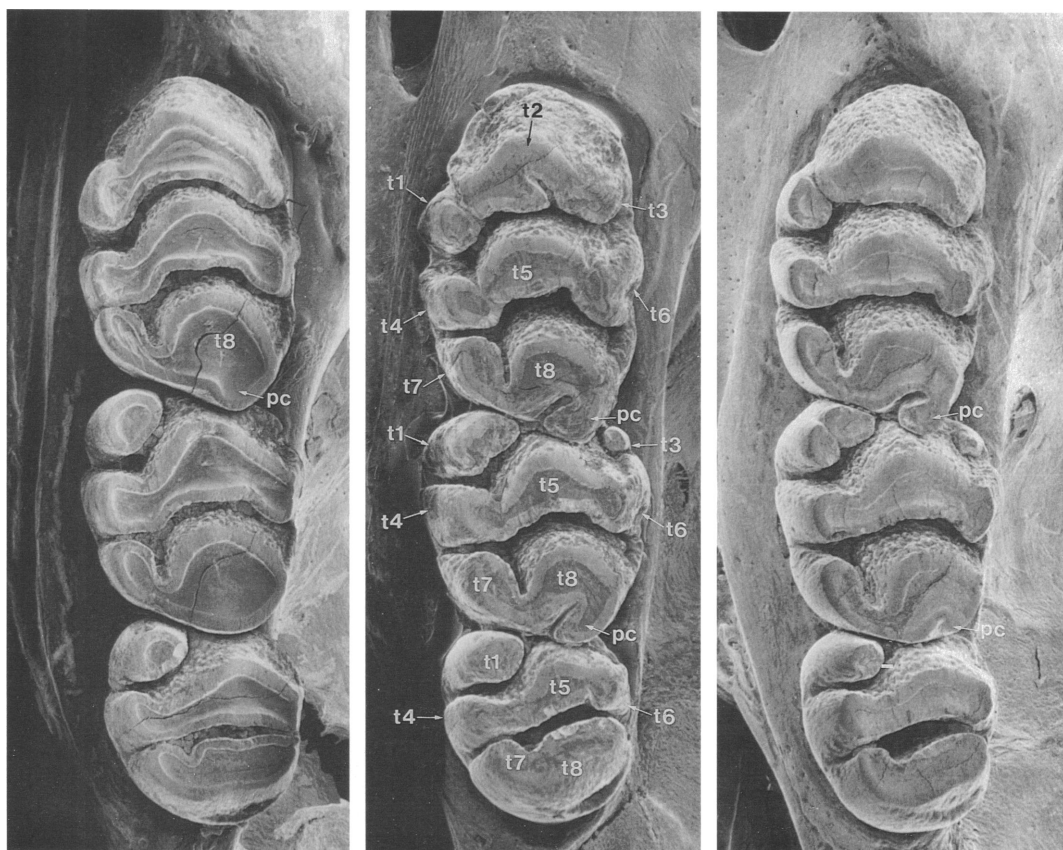


Fig. 12. Occlusal views of upper molar rows (left side) in three specimens of *Batomys salomonseni*. **Left and middle:** FMNH 92826 and 74853, respectively (Mindanao). **Right:** DMNH 6014 (Leyte), $\times 12$. Cusps are numbered according to Miller's (1912) scheme. Note the posterolingual orientation of cusp t1 on the first molar; the large cusp t7 that is directed anterolingually on each of the three molars in the row; the absence of a cusp t9 from all molars; the laminar configuration formed by cusps t4, t5, and t6 in the third molar; and the chunky posterior cingulum (pc) at the back of each first molar. A large posterior cingulum also occurs on the second molar in some specimens (as depicted here in the middle tooththrow), but is small and barely evident in others (exemplified by the second molar in the row on the right). The posterior third or half of each first and second molar in older animals appears to consist of a huge cusp in which the occlusal surface is an oblong basin; whether it is formed only by cusp t8 or the complete fusion of cusp t8 and the posterior cingulum is not always determinable. In the tooththrow on the left, for example, the back border of the posterior cingulum is still evident on the first molar, but no such cusp is evident on the second molar; whether the posterior cingulum was present at an earlier stage of wear or just never existed is indeterminable.

and about 14–16 mm. long on back. The skull has the general shape of that of *Batomys* but with smaller bullae and shorter palatine foramina. The teeth are more like those of *Carpomys* but lack one lamina in each upper molar.

Color.—General color above dark brown, some hairs dark gray at base with reddish brown tips, other pure black to tip; sides lighter, more buffy; hairs on underparts gray basally with long buffy yellow tips. Hind feet with a dark line from wrist half way to toes, remainder of foot and toes white; front feet with same general pattern but one foot wholly white. Tail uni-

color blackish brown above and below, moderately covered with hair.

Skull and teeth.—Skull with full, rounded brain case, long rostrum and nasals, very small bullae, and normally expanded zygomatic arches. The zygomatic plate is broad and straight edged. The teeth are much like those of *Carpomys* but have but three lamina in each upper molar instead of four. . . .

Measurements (from dry skin).—Total length 315.0 mm., tail 140.0, hind foot 37.5, ear 17.5

Skull: greatest length 43.5. mm., condylo-basal length 38.7; palatal length 20.5; length of palatine



Fig. 13. Occlusal views of upper molar rows (left side) in two species of *Batomys*. **Left and middle:** *B. russatus*, DMNH 4593 and 4594 (the holotype), respectively (Dinagat), $\times 17$. **Right:** *B. granti*, BMNH 97.5.2.32 (Mount Data, Luzon), $\times 14$. Occlusal patterns closely resemble those of the three *B. salmonseni* in figure 12 on opposite page, except that each first and second molar of the young example of *B. granti* does not have a posterior cingulum (**pc**). The outline of a posterior cingulum is clear on the second molar of DMNH 4593; the posterolabial margin of each first upper molar of DMNH 4593 and 4594 may represent the border of a posterior cingulum, but we are not certain.

foramina 7.8; interorbital width 6.3; zygomatic width 21.0; width of zygomatic plate 4.3; width of brain case 18.2; bulla 4.0×2.6 ; nasals, length 18.7, width 4.8; upper tooth row 8.0; lower tooth row 8.3; diastema 12.5.

Remarks.—Luzon Island has long been known for its great number of peculiar genera of rodents, some of which are found on other islands. This new genus, which resembles in part two of the Luzon genera, shows that on Mindanao also distinct forms have developed. Besides the type Dr. Salomonsen collected two very young males. The type is sexed as a female but there is no sign of any mammae while what appears to be the os penis is on the skin.

We have not seen the three specimens upon which Sanborn's description is based, but morphology of the holotype, judged by Sanborn's illustration of skull and molars

(fig. 4), is typical of *Batomys*. Misonne (1969: 78) thought so as well, for he wrote that the "genus *Mindanaomys* Sanborn 1953 . . . seems to be a synonym of *Batomys*; its molars are similar to those of that genus. . . ." Characteristics of skulls and dentitions in our large series from the Katanglad Mountain Range are closely similar to the specimen illustrated in Sanborn's original description of *Mindanaomys*. So too are specimens collected on Leyte, Biliran, and Dinagat. In turn, external as well as cranial and dental morphology of these specimens collected from islands in Greater Mindanao (fig. 1) generally resembles that of rats in our samples from Mount Isarog and Mount Data on



Fig. 14. Occlusal views of lower molar rows (left side) in the three specimens of *Batomys salomonseni* depicted in figure 12, $\times 12$. The triangular anteroconid is formed from anterolingual (**ali**), anteroconid (**ac**), and anterolabial (**ala**) cusps. Except for the elaboration of the anteroconid, which is common to species of *Crateromys* and *Carpomys* as well as *Batomys*, the occlusal surface is simple and formed from rows of large primary cusps: protoconid (**pd**), metaconid (**md**), hypoconid (**hd**), entoconid (**ed**), and posterior cingulum (**pc**).

Luzon (see figs. 7–9). The small series from the latter Luzon highland contains the holotype and other specimens that Thomas (1895) described as *Batomys granti*.

Sanborn knew *B. granti*, for he had reported two examples (1952: 119) obtained by members of the Philippine Zoological Expedition during their encampment on Mount Data in 1946 (Hoogstraal, 1951). It has puzzled us why Sanborn did not recognize the characteristics of *Batomys* in the Mindanao rat and why he apparently did not appreciate the close morphological resemblance between specimens of *salomonseni* and *granti*. Their striking similarity spurred our interest in defining just how many species actually exist in this complex of samples. Do the se-

ries of this *Batomys* from Luzon and those from the four islands of Greater Mindanao represent a single species for which the observed morphological variation can be explained by island isolation, or are *granti* and *salomonseni* real biological entities that can be defined by characters?

We can sort the available specimens into two primary groups. One contains the samples from Mount Data and Mount Isarog, which closely resemble one another in most characteristics of body size, pelage, skulls, and teeth. To us, all these specimens represent *Batomys granti*, which we have already described.

The second group consists of 142 specimens collected from the islands of Leyte, Biliran, Dinagat, and Mindanao as listed below.

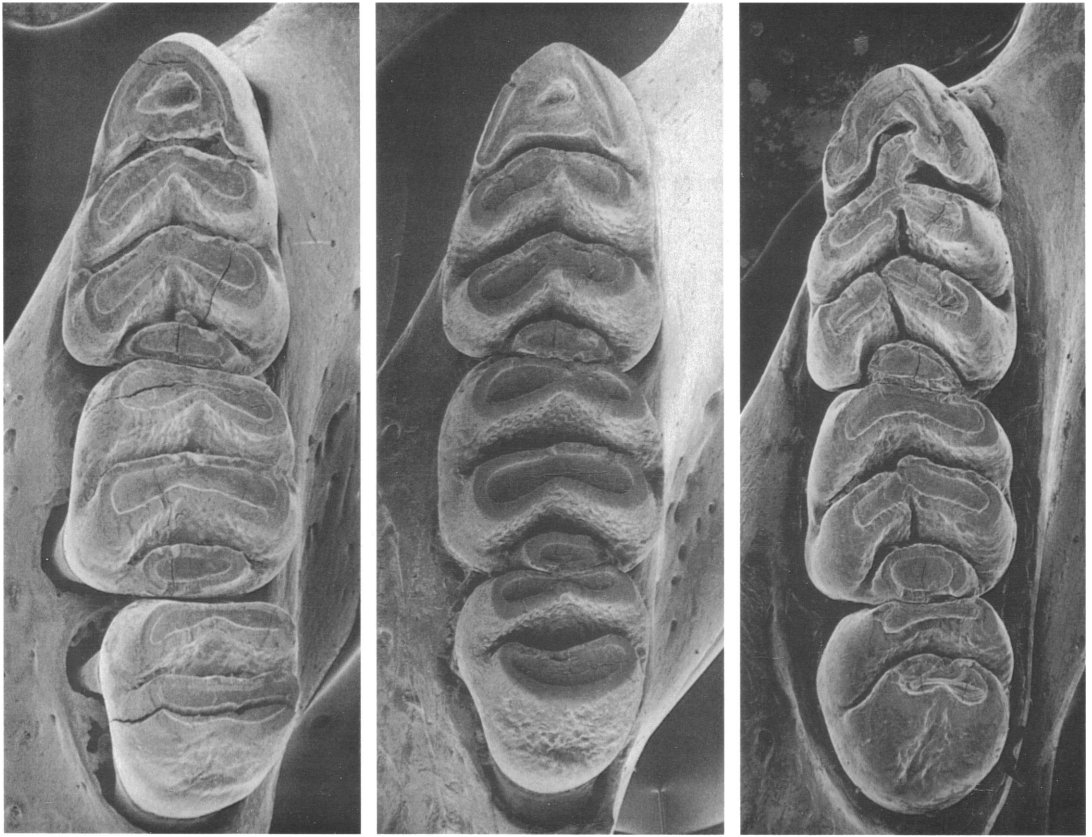


Fig. 15. Occlusal views of lower molar rows (left side) in specimens representing *Batomys russatus* (left and middle views, $\times 17$) and *B. granti* (right view, $\times 14$) depicted in figure 13. The same basic cusp pattern characterizes these three specimens as well as those of *B. salomonseni* shown on the opposite page. Note the elongate elliptical cross-sectional shape of the posterior cingulum at the back of each first and second molar in *B. russatus*. The posterior cingulum in specimens of *B. granti* and *B. salomonseni* is typically cordate or oblong in occlusal outline, and small and round in *B. dentatus* (fig. 21).

Compared with the material from Luzon representing *B. granti*, specimens from the four Greater Mindanao islands are so similar in their morphology and differ in a suite of traits so consistently from the Luzon specimens that we accept the hypothesis that all represent a single species for which *B. salomonseni* is the oldest name.

LEYTE ISLAND

1. Leyte Province, Burauen Municipality, Mount Lobi Range, Barrio Tambis ($11^{\circ}00'N/124^{\circ}50'E$; Rickart et al., 1993: 10 and map on p. 3); DMNH 4111–4114, 6014.
2. Leyte Province, Baybay Municipality, Mount Pangasugan, 8.5–10.5 km north, 2.5–

4.5 km east of Baybay ($10^{\circ}45'30"N/124^{\circ}49'30"E$ – $10^{\circ}47'N/124^{\circ}50'E$; Rickart et al., 1993: 6–8 and map on p. 5), 500–1000 m: USNM 449515, 458766–458778, 458780–458784, 459872–459888.

BILIRAN ISLAND

3. Leyte Province Naval Municipality, Mount Konduko, 5 km north, 10 km east of Naval town ($11^{\circ}36'30"N/124^{\circ}29'E$; Rickart et al., 1993: 13 and map on p. 11), 850 m ($11^{\circ}36'N, 124^{\circ}29'E$): USNM 459871.
4. Leyte Province, Caibiran Municipality, 3.5 km south, 5.5 km west of Caibiran town ($11^{\circ}32'N/124^{\circ}32'E$; Rickart et al., 1993: 13 and map on p. 11), 700 m: UMMZ 160289 and 160431.

TABLE 1
Descriptive Statistics for External Measurements (mm) and Weight (g) of
Batomys granti and *Batomys salomonseni* from the Philippine Islands^a

(Mean, plus or minus one SD, observed range in parentheses, and number of specimens are listed for each measurement. Samples contain both sexes and an age range from young to old adults. Specimens measured are identified in footnotes.)

Species	LHB	LT	LHF	LE	Weight	LT/LHB (%)
<i>Batomys granti</i>						
LUZON						
Holotype ^b	—	110	37	—	—	—
Mount Data ^c	191	93.7 ± 17.62 (75–110) 3	36.7 ± 0.58 (36–37) 3	—	—	50
Mount Isarog ^d	191.6 ± 10.48 (177–203) 5	143.5 ± 10.47 (132–157) 4	37.2 ± 1.64 (36–40) 5	20.8 ± 0.96 (20–22) 4	169.0 ± 24.08 (135–200) 5	75
<i>Batomys salomonseni</i>						
BILIRAN						
UMMZ 160289	189	148	37	22	220	78
UMMZ 160431	166	132	37	22	145	80
LEYTE ^e						
Baybay	173.9 ± 15.31 (138–191) 16	148.6 ± 10.30 (130–167) 16	39.2 ± 1.17 (37–41) 16	22.5 ± 0.82 (21–24) 16	185.2 ± 33.52 (143–255) 16	85
DINAGAT						
BRT 261	186	121	35	20	210	65
BRT 283	190	128	36	20	245	67
BRT 331	170	120	35	19	220	71
MINDANAO ^f						
Katanglad Range	173.6 ± 9.27 (157–191) 30	129.9 ± 7.21 (114–150) 30	36.8 ± 1.63 (33–39) 30	22.3 ± 1.39 (20–27) 30	158.6 ± 25.32 (157–191) 30	75

^a Measurements for the sample from Mount Data were taken from specimen labels; all other measurements were obtained in the field by L. R. Heaney and his colleagues and recorded in various journals.

^b BMNH 95.8.2.15.

^c BMNH 95.8.2.15, 97.5.2.31; FMNH 62504. This third specimen is the only one with a measurement for head and body length (191 mm); 96 mm was recorded for tail length and these two values were used to obtain the 50% ratio for LT/LHB. Judged from the relative tail lengths of the other stuffed skins made from specimens collected on Mount Data, that proportion seems characteristic of the sample.

^d USNM 458914, 458939, 458941, 458946, 458947.

^e USNM 458766, 458768–458771, 458773–458778, 458780–458784.

^f FMNH 146719, 146720, 147103, 147925, 147927–147929, 147931–147933, 147935–147940, 148033 –148035, 148161, 148163–148173.

DINAGAT ISLAND

5. Surigao del Norte Province, Loreto Municipality, Sitio Bilitbiton, Barangay Kambinlio, 6 km NE Loreto: BRT 261 and 283 (10°22'17"N/125°37'05.5"E), 350 m; BRT 331 (10°22'27.5"N/125°37'43"E), 550 m.

MINDANAO ISLAND

6. Bukidnon Province, Katanglad Range (08°27'N/124°21'E; for "Katanglad Mountain

Range," as listed by USBGN Philippines, 1989: 595, and not "Katanglad Mountains" or "Mount Katanglad," which have different coordinates): Malaybalay, 5000–6000 ft, DMNH 5954 and 5955, FMNH 74853 and 92823–92830; 18 km S, 7 km E Baungon, 1800 m, FMNH 146719, 146720, 147103, 147104; 16.5 and 18.5 km S, 4 km E Camp Phillips, 1900 and 2250 m, FMNH 147925–147941, 148161–148173; SMF 30779–30826 (no altitudinal or other location data with specimens).

TABLE 2

Descriptive Statistics for Cranial and Dental Measurements (mm) of *Batomys granti* and *Batomys salomonseni* from the Philippine Islands

(Mean, plus or minus one SD, observed range in parentheses, and number of specimens are listed for each measurement. Samples contain both sexes and an age range from young to old adults. Specimens measured are identified in the footnotes. The specimens from Mount Data, Mount Isarog, Leyte, Mindanao, and BRT 261 from Dinagat constitute the five population samples used for discriminant function and cluster analyses [figs. 16–18; table 3].)

	<i>B. granti</i> LUZON ^b			<i>B. salomonseni</i> GREATER MINDANAO				
	Holotype ^a	Mt. Data	Mt. Isarog	Biliran ^c	Leyte ^d	Dinagat ^e		Mindanao ^f
ONL	45.5	45.5 ± 0.55 (45.0–46.1) 3	43.6 ± 20.6 (41.2–44.9) 3	—	42.3 ± 1.63 (38.9–44.8) 17	42.4	—	42.6 ± 1.18 (40.1–45.3) 51
ZB	22.1	22.2 ± 0.23 (22.1–22.5) 3	21.9 ± 1.28 (20.5–23.0) 3	21.5	21.2 ± 1.09 (19.2–22.8) 17	21.9	—	21.1 ± 0.73 (19.0–23.2) 51
IB	5.8	6.1 ± 0.30 (5.8–6.4) 3	5.5 ± 0.38 (5.1–5.8) 3	6.0	6.0 ± 0.26 (5.6–6.4) 17	5.4	5.8	6.0 ± 0.21 (5.5–6.5) 51
LR	15.8	15.8 ± 0.20 (15.6–16.0) 3	14.2 ± 1.00 (13.1–15.0) 3	15.5	14.6 ± 0.68 (13.3–15.8) 17	15.0	14.9	15.3 ± 0.63 (13.8–16.8) 51
BR	7.9	8.3 ± 0.53 (7.9–8.9) 3	8.1 ± 0.44 (7.6–8.4) 3	8.1	8.0 ± 0.45 (7.1–8.7) 17	8.9	8.0	8.1 ± 0.36 (7.5–9.0) 51
BBC	16.5	16.9 ± 0.61 (16.5–17.6) 3	17.0 ± 0.65 (16.4–17.7) 3	—	16.7 ± 0.44 (15.8–17.4) 17	16.7	—	16.9 ± 0.41 (16.2–17.7) 51
HBC	11.9	12.0 ± 0.12 (11.9–12.1) 3	12.1 ± 0.21 (11.9–12.3) 3	—	11.9 ± 0.59 (10.9–13.1) 17	12.1	—	11.7 ± 0.34 (11.0–12.6) 51
BZP	4.2	4.5 ± 0.25 (4.2–4.7) 3	3.9 ± 0.17 (3.7–4.0) 3	4.5	3.8 ± 0.26 (3.4–4.2) 17	4.4	3.8	4.4 ± 0.33 (3.5–5.0) 51
LD	12.5	12.3 ± 0.29 (12.0–12.5) 3	11.6 ± 1.21 (10.3–12.7) 3	12.0	11.0 ± 0.54 (9.8–12.0) 17	11.0	11.1	11.4 ± 0.52 (10.5–12.6) 51
LBP	6.4	6.6 ± 0.20 (6.4–6.8) 3	6.9 ± 0.72 (6.4–7.7) 3	7.8	7.2 ± 0.38 (6.5–7.9) 17	7.3	7.3	6.8 ± 0.42 (6.0–7.9) 51
PPL	18.2	17.3 ± 0.79 (16.7–18.2) 3	16.3 ± 1.27 (14.9–17.3) 3	—	15.2 ± 1.01 (13.2–17.0) 17	15.7	—	15.4 ± 0.71 (13.9–17.4) 51
LIF	8.7	8.9 ± 0.53 (8.5–9.5) 3	8.2 ± 0.46 (7.8–8.7) 3	7.4	7.0 ± 0.36 (6.6–7.8) 17	6.6	6.4	7.4 ± 0.42 (6.5–8.1) 51
BIF	3.2	3.1 ± 0.17 (2.9–3.2) 3	3.1 ± 0.15 (3.0–3.3) 3	3.6	3.0 ± 0.24 (2.6–3.4) 17	2.6	2.7	2.9 ± 0.22 (2.2–3.5) 51
BMF	3.3	3.3 ± 0.15 (3.1–3.4) 3	3.3 ± 0.25 (3.1–3.6) 3	3.6	3.4 ± 0.24 (3.0–3.8) 17	3.2	3.1	3.1 ± 0.21 (2.5–3.7) 51
LB	5.2	5.3 ± 0.21 (5.1–5.5) 3	5.2 ± 0.21 (5.0–5.4) 3	4.9	5.1 ± 0.21 (4.7–5.5) 17	5.1	5.0	5.3 ± 0.19 (4.7–5.6) 51
CLM1–3	7.8	8.1 ± 0.30 (7.8–8.4) 3	8.1 ± 0.25 (7.8–8.3) 3	8.0	7.9 ± 0.21 (7.6–8.3) 17	7.4	7.4	7.8 ± 0.17 (7.4–8.2) 51
BM1	2.4	2.4 ± 0.15 (2.3–2.6) 3	2.4 ± 0.00 3	2.4	2.5 ± 0.08 (2.3–2.6) 17	2.2	2.3	2.4 ± 0.08 (2.2–2.6) 51

^a BMNH 95.8.2.15 from Luzon.

^b Mount Data: BMNH 97.5.2.31, 95.8.2.15 (holotype); FMNH 62504. Mt Isarog: USNM 458914, 458946, 458947.

^c UMMZ 160289.

^d DMNH 4111, 4112, 4114, 4783, 6014; USNM 458768–458770, 458773–458777, 458780, 458781, 458783, 458784.

^e BRT 261 and 331, respectively.

^f DMNH 5954, 5955; FMNH 92823, 92826–92828; FMNH 146719, 146720, 147931, 148163, 148165–148170; SMF 30779, 30781–30785, 30787–30789, 30791–30797, 30799, 30800, 30802, 30804, 30805, 30808–30814, 30816, 30818–30821, 30823, 30824.

DIAGNOSIS: *Batomys salomonseni* is similar in body size and most morphological traits to *B. granti*, but is distinguished from that species by its slightly brighter fur; narrower hind foot with relatively smaller tubercles; narrower tail that is conspicuously less hairy; lack of facial mask; very long superciliary vibrissae extending well beyond pinnae; conspicuously shorter incisive foramina; shorter (on average) cranium, diastema, postpalatal region, and molar row; narrower zygomatic plate; multiple upper and lower molar roots; posterior cingulum at back of each first upper (and sometimes second) molar in many specimens.

COMPARISONS: Our definition of *B. salomonseni* rests upon the following contrasts between the Greater Mindanao samples and those from Luzon, which represent *B. granti*.

Body Size and Pelage: Overall body size of adults is similar in the two groups of samples (table 1). A subtle difference exists in pelage texture and coloration. In all samples, adult head and body fur is similar in length, but the coat seems shaggy and somewhat woolly on the specimens from Luzon, and slightly sleeker in the series from the Greater Mindanao islands. The coat of *B. granti* also averages darker with dark regions around the eyes and at bases of the mystacial vibrissae. Examples of *B. salomonseni* are, on average, brighter, especially along sides of head and body, which are buffy in many specimens and provide a contrast with the somber brown so typical in *B. granti*. Also, the face of *B. salomonseni* is the same color as the rest of the body and lacks the partial mask pattern that is conspicuous in *B. granti*.

Superciliary Vibrissae: Specimens from Luzon have short superciliary vibrissae; the longest sensory hair originating above each eye extends to the posterior rim of the pinna but not beyond it. All specimens of *B. salomonseni*, however, have very long superciliary vibrissae that extend appreciably past back margins of the pinnae, up to 45 mm in some specimens. This is a conspicuous contrast among our sets of samples.

Hind Feet: There is little difference in length of hind feet among the samples of adult *B. granti* and *B. salomonseni* (table 1), but examples of *B. granti* have a noticeably broader foot with larger and thicker pads rel-

ative to area of plantar surface (fig. 5). A narrower foot with relatively smaller and thinner pads is characteristic of all the specimens from Leyte, Biliran, Dinagat, and Mindanao that we have examined.

Tail: Specimens of *B. granti* from Mount Data have a short tail, about half the length of head and body. In the sample of that species from Mount Isarog and all samples of *B. salomonseni*, the tail is longer, about three-fourths the length of head and body (table 1; range is 65–85%). The diagnostic contrast between the two species is diameter of the tail and length of the scale hairs. Specimens from Luzon have a much thicker tail covered by longer hairs than do any of the specimens from the Greater Mindanao region (fig. 6); the tail appears thick and hairy. By contrast, the tail in all examples of *B. salomonseni* is thinner and scantily covered.

Cranial and Dental Dimensions: Overall conformation and size of the skull and molar rows are surprisingly similar among the samples and do not mirror the striking qualitative contrasts in external traits we described above. Nearly every skull from the Greater Mindanao area is closely similar to skulls in samples from Luzon (figs. 7–9). In our initial observations, we could not find any discrete qualitative characters that could be used to distinguish skulls in the Luzon samples from those in series from the Greater Mindanao islands. To determine similarities and differences in quantitative variables, we subjected the data from cranial and dental measurements to discriminant function analysis. Specimens were pooled into five population samples, two from Luzon (Mount Data, which includes the holotype of *B. granti*, and Mount Isarog), the others from Mindanao (from the Katanglad Range, the general region from which the holotype of *salomonseni* was obtained), Leyte, and Dinagat (size, descriptive statistics, and identity of specimens measured for each sample are listed in table 2); we could not include the specimens from Biliran, the only other island from which we have samples, because the skulls are damaged and only incomplete sets of measurements are available (table 2).

Two nonoverlapping clusters of specimen scores and group centroids are evident in the projection onto the first two canonical vari-

ates extracted: one represents specimens we have identified as *B. granti* from Luzon, the other identifies samples we consider to be *B. salomonseni* from islands in the Greater Mindanao region (fig. 16). The separation of these specimen scores and group centroids results primarily from variation in occipitonasal length, breadth of zygomatic plate, lengths of diastema and bony palate, postpalatal length, and especially length of incisive foramina (fig. 16, table 3). Compared with specimens of *B. salomonseni*, our examples of *B. granti* have a slightly longer cranium, diastema, and molar row; a wider zygomatic plate; appreciably longer postpalatal region; and much longer incisive foramina, which correlates with a shorter bony palate. Differences in means of these variables between the two sets of samples are reflected in the descriptive statistics (table 2), and some of the contrasts can be visually appreciated in figures 7–9. Contrast in length of incisive foramina between *B. granti* and *B. salomonseni* is particularly dramatic both in the statistics (which barely overlap; see observed ranges in table 2) and canonical variate diagram; nearly every cranium of *B. salomonseni* can be separated from samples of *B. granti* by length of incisive foramina alone.

This contrast in length of incisive foramina, as well as other variables between the two species is also reflected in proportional relationships (fig. 22). Relative to occipitonasal length for example, the zygomatic plate is significantly wider in *B. salomonseni* than in *B. granti*, the bony palate is appreciably longer, and the incisive foramina are much shorter, as is postpalatal length. Other proportional differences between the two species can be picked out in the ratio diagram.

The close association between the two samples from Luzon in opposition to the separate cloud of specimen scores for Leyte and Mindanao indicated by discriminant function analysis is also reinforced by the clustering pattern based on Mahalanobis distance (the generalized distance between centroids over all canonical variates derived, which provides more information than can be seen in the scatter of scores on the first two canonical variates). In this diagram (fig. 17) the sample from Dinagat (which consists of a single

specimen) is clearly separate from the two other groups; we elaborate on this pattern in the section on Insular Variation.

Molars: Roots and Occlusal Patterns: Size of each molar relative to others in the tooth-row, height above alveolar surfaces, and most aspects of occlusal patterns are much alike in *B. granti* and *B. salomonseni*. Only two traits may have some discriminating utility. In the few examples where number of roots can be determined, specimens of *B. salomonseni* have a highly derived pattern of multiple roots compared with the fewer roots in the less derived pattern that seems characteristic of *B. granti* (figs. 10, 11). Whether this distinction is real or biased by our meager sample sizes should be verified either by extracting the molars from many more examples or by subjecting them to x-ray analysis. We extracted teeth from the few specimens in which the molars were already very loose.

We could not identify a posterior cingulum at the back of either the first or second upper molars in the few skulls of *B. granti* we examined (fig. 13). When present, this cusp projects caudad from the large cusp t8. A strong posterior cingulum does form a part of the occlusal surface in many examples of *B. salomonseni* (fig. 12). We did not tabulate the frequency of occurrence of this cusp because its potential significance as an interspecific distinguishing trait only became clear late in the study, after we had already returned specimens to the various institutions from which we had borrowed them. An additional problem is that the cusp can be detected only on molars in which the occlusal surface is slightly or moderately worn. It disappears in most older animals, but can sometimes still be detected on the first molar but not the second (fig. 12). So in worn molars, we usually could not determine whether the large cusp at the back of the molar represents only t8 or the fusion of cusp t8 and posterior cingulum.

INSULAR VARIATION: Because of the distribution of *B. salomonseni* on at least four islands in the Greater Mindanao region, one could presume some morphological variation among island populations. We have not noticed any significant variation among the insular samples in such traits as fur coloration,

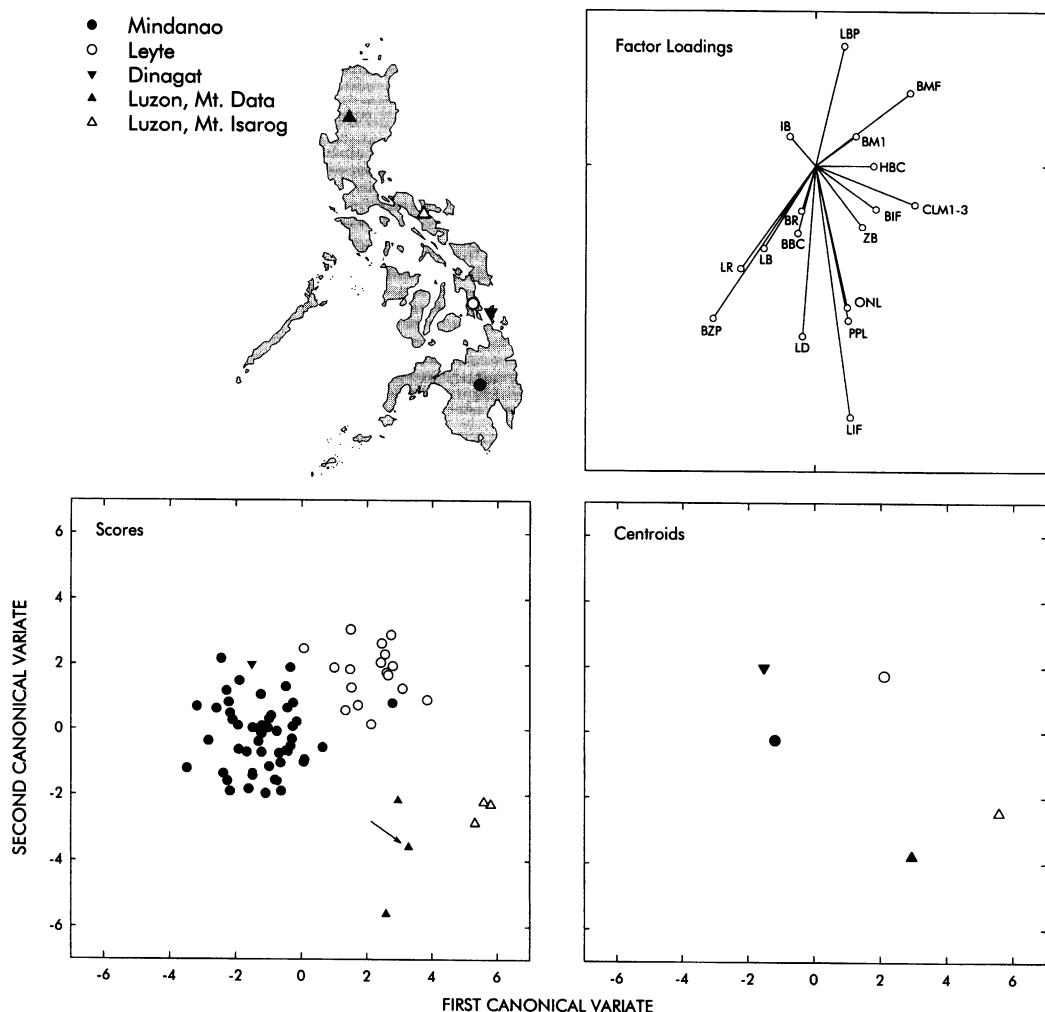


Fig. 16. Results of discriminant function analysis. **Lower left:** Individual specimen scores based on log-transformed values of 15 cranial and 2 dental variables and projected onto the first and second canonical variates extracted from discriminant function analysis of five population samples representing *Batomys granti* (Luzon) and *B. salomonseni* (Mindanao, Leyte, and Dinagat). Arrow identifies score from holotype of *B. granti*. The Mindanao score nestled among those for specimens for Leyte represents DMNH 5955. It differs from most other Mindanao specimens by its narrower zygomatic plate, shorter rostrum, longer bony palate, and wider mesopterygoid fossa, the primary variables separating the Mindanao and Leyte scores. **Lower right:** Plot of group centroids on first two canonical variates derived from discriminant function analysis of the five population samples. **Upper right:** Vectors of 17 cranial and dental variables corresponding to the magnitude and direction of their loadings on first and second canonical variates (also see table 3). Significance of the patterns is discussed in text.

relative lengths of facial vibrissae (especially the superciliary, which extends beyond the ears on specimens in all samples), morphology of plantar surfaces, or tail pilosity and color. There are detectable and sometimes striking differences among samples in cranial

and dental dimensions as revealed by multivariate analysis. In the graph of specimen scores projected onto the first and second canonical variates extracted from discriminant function analysis, the score for the specimen from Dinagat is contained within the cluster

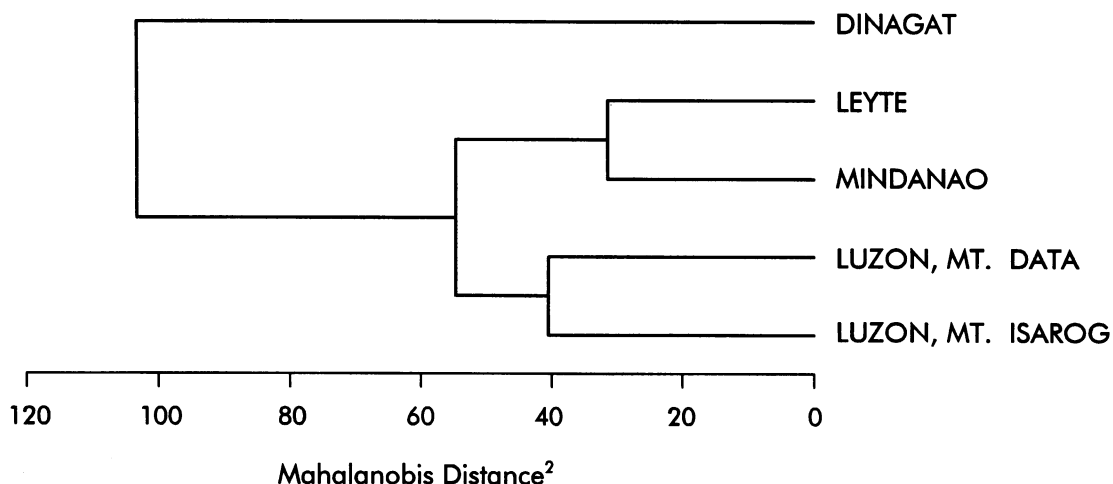


Fig. 17. UPGMA clustering of five population samples representing *Batomys granti* and *B. salomonseni* generated from Mahalanobis distances (D^2) among group centroids. Size of samples, mean values of measurements for variables, and specimens measured are listed in table 2. Significance of the pattern, especially the separation of the Dinagat sample, is discussed in text.

of scores representing specimens from Mindanao (fig. 16). That cloud is adjacent to, but not separate from, scores for the sample from Leyte. Variation in breadth of zygomatic plate, lengths of rostrum and bulla, breadth of mesopterygoid fossa, and length of bony palate most strongly influence this diagonal dispersion of points. Lengths of diastema and incisive foramina and postpalatal length also play a role in the spread. On average, the sample from Leyte has a narrower zygomatic plate compared with the Mindanao specimens; shorter rostrum, bulla, postpalatal region, incisive foramina, and diastema; but a wider mesopterygoid fossa and longer bony palate. These distinctions are also reflected by the differences in sample means listed in table 2.

The close proximity of the Leyte and Mindanao samples depicted in the scatterplot defined by first and second canonical variates is reflected in the clustering pattern based on Mahalanobis distance (D^2), but the apparent tight association between the Dinagat and Mindanao samples indicated on that plot is not (fig. 17). A projection of specimen scores onto the first and third canonical variates provides insight to the basis for this discrepancy. The Dinagat score is far removed from any of the other scores of all other samples along the third canonical variate (fig. 18). This hi-

atus is influenced primarily by variation in breadths of rostrum, interorbit, and first upper molar, and to a lesser extent by length of molar row. Compared with all the other samples of *B. salomonseni* (as well as *B. granti*), the single intact skull from Dinagat (BRT 261) has a wider rostrum, narrower interorbit and first upper molar, and a shorter molar row. These contrasts are also reflected by absolute differences in sample means for these variables (table 2), and can easily be appreciated by visually comparing crania (figs. 7, 8). The values for these four measurements derived from the Dinagat cranium either do not (interorbital breadth) or barely (the rest) overlap the observed range recorded for the samples from Leyte and Mindanao.

Three of these morphometric differences may simply reflect individual variation. The only other Dinagat skull available to us is in pieces (BRT 331), but we could measure the four dimensions. Its interorbit and first upper molar are wider than those same variables on the intact skull (BRT 261), and the rostrum is much narrower; the values are well within the range of variation documented for the samples from Leyte and Mindanao (table 2). Length of molar row, however, is short, which suggests that the Dinagat population may be characterized in part by significantly shorter molar rows compared with the pop-

TABLE 3
Results of Discriminant Function Analyses of
Population Samples of *Batomys granti* (Mount
Data and Mount Isarog, Luzon) and *Batomys
salomonseni* (Leyte, Dinagat, and Mindanao)
(Mean values for measurements in each sample are listed in
table 2; specimens measured are also identified there. See
figs. 16 and 18.)

Variable	Canonical Variates			F (sample)	P
	First	Second	Third		
ONL	0.17	-0.46	0.04	4.189	.004
ZB	0.25	-0.20	-0.13	2.036	.099
IB	-0.14	0.09	0.58	4.923	.001
LR	-0.40	-0.34	0.13	5.660	.001
BR	-0.08	-0.15	-0.28	1.597	.185
BBC	-0.10	-0.22	-0.03	.856	.495
HBC	0.31	-0.00	-0.12	1.852	.129
BZP	-0.55	-0.50	-0.07	12.173	.000
LD	-0.07	-0.56	0.06	4.647	.002
LBP	0.16	0.39	-0.08	2.352	.062
PPL	0.18	-0.51	-0.07	4.853	.002
LIF	0.19	-0.83	0.12	15.506	.000
BIF	0.33	-0.14	0.16	2.208	.077
BMF	0.51	0.24	0.02	5.872	.000
LB	-0.28	-0.27	0.06	2.186	.079
CLM1-3	0.54	-0.13	0.28	6.833	.000
BM1	0.22	0.10	0.41	2.787	.033
Canonical correlation	.89	.79	.73		
Eigenvalue	3.84	1.71	1.14		
% Variance	56.1	24.9	16.7		

ulations on Leyte and Mindanao. Clearly, data from a larger sample from Dinagat needs to be analyzed before we can obtain a realistic estimate of morphometric characteristics of the Dinagat population. (We record a third specimen—see above and table 1—but it is preserved in fluid; the skull is damaged and was not removed.)

Biliran, off the northern coast of Leyte (fig. 1), is the only other island from which examples of *B. salomonseni* have been recorded. The only skull we studied is fragmented, but the measurements we could obtain fall within the range of variation record-

ed for the samples from Leyte and Mindanao (table 2).

COMPARISONS WITH OTHER SPECIES: See the accounts of *Batomys dentatus* and the new species.

INSULAR DISTRIBUTION: *Batomys salomonseni* has been collected from Biliran, Leyte, Dinagat, and Mindanao. Apparently these were once united during the late Pleistocene when sea level was depressed about 120 m below present levels and formed part of a much larger island that Heaney (1985, 1991) has called Greater Mindanao (see fig. 1). Whether *B. salomonseni* occurs on other smaller islands that were once part of Greater Mindanao is unknown because most have not been intensively surveyed for small mammals. The small volcanic island of Maripipi, off the north coast of Leyte, is an exception. Heaney and his colleagues worked there but did not find *B. salomonseni* “despite considerable trapping effort in what appeared to be excellent habitat for the species,” and doubted that it occurred there (Rickart et al., 1993: 47).

ECOLOGY: Collection data associated with examples of *B. salomonseni* indicate that the species has been trapped over an elevational range extending from tropical lowland evergreen rainforest to montane forest formations. Although *B. salomonseni* has been trapped at lower elevations than has *B. granti*, and is not restricted to montane forest as that species apparently is, *B. salomonseni* appears to be more common at higher elevations in mountain forest. Our most extensive information comes from observations recorded for capture sites on Leyte, Biliran, and Dinagat. Rickart et al. (1993: 46, 47) noted that on Mount Pangasugan, Leyte, *B. salomonseni* “was by far the most common species trapped in primary montane and mossy forest at 700 and 950 m . . . whereas it was rare or absent at sites in lowland forest from 50 to 500 m . . . In contrast to the situation on Leyte, *Batomys* was rare on Biliran, where only three animals were trapped, all at sites above 700 m . . .” The specimens “were taken in traps set on the ground, most in dense cover, in subsurface runways, or in root tangles at tree bases.” Samples from Leyte were obtained at elevations from 500 to 1000 m, which includes the range in for-

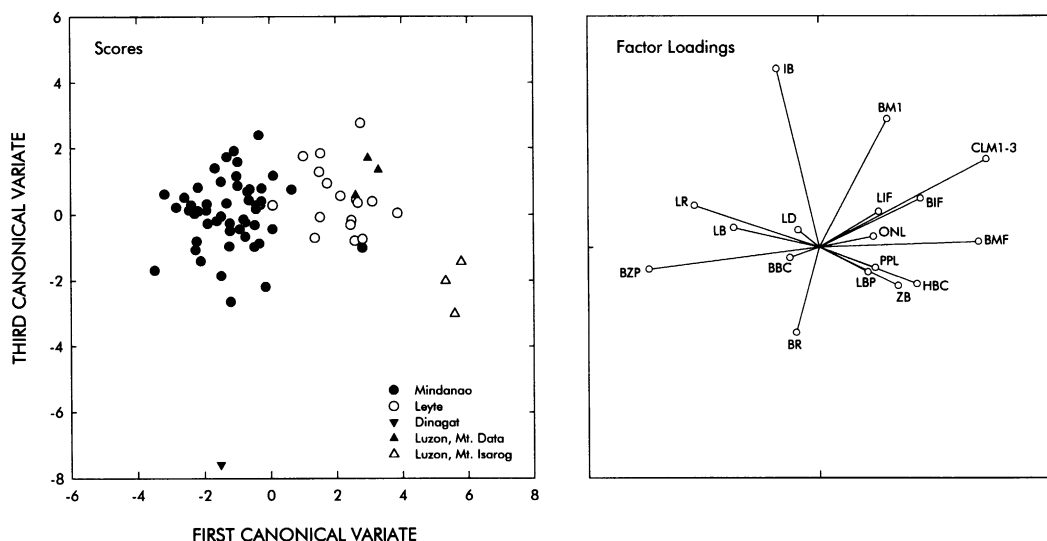


Fig. 18. Results of discriminant function analysis. **Left:** Individual specimen scores based on log-transformed values of 15 cranial and 2 dental variables and projected onto the first and third canonical variates extracted from discriminant function analysis of five population samples representing *Batomys granti* (Luzon) and *B. salomonseni* (Mindanao, Leyte, and Dinagat). **Right:** Vectors of 17 cranial and dental variables corresponding to the magnitude and direction of their loadings on first and third canonical variates (also see table 3). Focus of the scatterplot is the score of the only specimen from Dinagat which is isolated from the other specimen scores distributed along the third canonical variate; a wider rostrum, narrower interorbit, shorter molar row, and narrower first upper molar relative to the other specimens are primarily responsible for its position. Dramatic separation of the Dinagat sample from the other four population samples is also expressed in the cluster diagram in figure 17, but not in the arrangement of specimen scores projected onto first and second canonical variates illustrated in figure 16. See discussion in text.

mations from tropical lowland evergreen rainforest (lowland dipterocarp forest) through lower montane rainforest to upper montane rainforest (mossy forest). On Biliran, *B. salomonseni* were "trapped ... in mixed partially logged and primary lowland forest" at 700 m and "in montane forest" at 850 m. These different habitats on both Leyte and Biliran are described and illustrated by Rickart et al. (1993) based on observations made during mammal surveys in the late 1980s.

Some specimens were collected on Leyte in 1964 in the vicinity of Mount Lobi. Rabor (1973: 12), who led the field teams, described the mosaic of vegetation formations in the area and summarized the habitats surveyed:

As a whole, the interior localities of the Mount Lobi Range where we worked were a mixture of cultivated fields, cleared hills, parang country, secondary forest,

primary dipterocarp forest, and small areas of mixed or transition dipterocarp—mid-mountain forests, the latter found only at the highest elevations on the mountain peaks.

Specimens of *B. salomonseni* from Dinagat were trapped at 350, 550, and 700 m (only three specimens from the two lowland sites are here reported; 11 others were caught at 700 m and are in the collection at MSU-IIT, Mindanao). All examples were collected by members of a survey group led by B. R. Tabaranza, Jr., during November and December 1994. They worked in the mountainous northern tip of the island (see gazetteer) along a transect from 350 to 700 m. To the northeast of the first camp (350 m) could be seen Mount Kambinlio, and Mount Redondo was visible to the south-southwest. Vegetation at this lowland site was originally lowland dipterocarp forest with trees having trunks up to 2 m or more in diameter. How-



Fig. 19. Lowland tropical evergreen rainforest at 550 m on the northern tip of Dinagat (about 6 km NE of Loreto). Photographed November–December 1994, by B. R. Tabaranza, Jr. The cut tree is *Shorea negrosensis*. One *Batomys salomonseni* was trapped at this elevation. Additional specimens of that species and an example of *B. russatus* were captured in similar forest downslope at 350 m.

ever, extensive logging operations beginning in the late 1960s and sustained through the middle 1970s, and subsequent continuous illegal cutting that persisted until 1994, have significantly altered the forest and removed nearly all trees (particularly the dominant *Shorea negrosensis*) with trunks more than 30 cm in diameter. The locally common “Philippine ironwood” (*Diospyros mindanensis*) was left by loggers because of its exceptionally hard wood. In the past, trees were cut by handsaw and chainsaw and the timber extracted using water buffalo. Since 1994, trunks of cut trees have been carved into boat keels. Areas that are relatively flat and easily accessible have been converted to agriculture (including the type locality of *Crateromys australis*). In steeper, more isolated places, such as the first camp at 350 m, the regenerating forest consists of small pole-sized trees. The canopy was open (average height 25–30 m), and ground cover was often dense with dipterocarp seedlings and ferns. Canopy

vines, lianas, screw-pine (species of *Pandanus*), and rattan (various species of *Calamus*) were common. Fig trees were rare. Leaf litter was common but moderately thin. At least two species of pitcher plants were present in the area; moss was thin and scattered. Pieces of fallen trunks (from both logging and typhoon damage) and slash were common. Slopes are moderately steep (30–40°) and drainage systems well-developed.

Tropical lowland evergreen rainforest also characterized the hillside at 550 m, but logging had been less intense and larger standing trees with buttressed bases were present, and the canopy (average 30–40 m) was not as open. Lianas and rattan were moderately common, and palms formed most of the understory. The site was at the end of a trail used by loggers, and illegal cutting was evident. Recently felled red lauán (*Shorea negrosensis*) with a diameter of 2.5 m were common (fig. 19). Species of *Casuarina* and *Podocarpus* were growing close to the trail

along lower ridges. Undisturbed forest prevailed a short distance from the traplines.

At 700 m, traps were set in an area of transition from lowland forest to ridge-top mossy forest (upper montane) with a shorter and denser stand of gnarled trees. No distinct montane (lower montane) vegetation was present. Most trees had some moss on trunks and branches, especially the stunted trees on ridges. The soil was thin and the terrain rocky.

The largest samples of *B. salomonseni* available to us are from Mindanao, and all come from the Katanglad Range between about 1500 and 2250 m. The only reliable habitat information associated with the specimens is that recorded by members of Heaney's survey team who worked in the Katanglad Range during parts of 1992 and 1993. All examples were taken in traps set on the ground in montane forest habitats between 1800 and 2375 m. A full description of the survey area along with specific ecological information dealing with the samples of *B. salomonseni* will be presented in a report on the mammals of the Katanglad area that is now being prepared.

Batomys dentatus Miller, 1910

This distinctive species is still represented only by the holotype (USNM 151506), an adult male collected by E. A. Mearns on July 31, 1907 from "Hights-in-the-Oaks," 7000 ft, in Benguet Province, northern Luzon (Leonard Co, a Philippine botanist, told L. R. Heaney that Hights-in-the-Oaks was a small health resort visited by wayward biologists located near Atok, Sayangan, at Km 52 along the Halsema Road; approximate coordinates are 16°35'N/120°40'E).

Miller named *dentatus* in 1910 (pp. 400–402) and diagnosed it this way: "Size and general appearance as in *Batomys granti* Thomas, but under parts more buffy and terminal half of tail white; no bare area around eye; skull with much deeper brain case than in the related species; crowns of upper molars fully as wide as palate." Based on our comparisons, we provide the following modified diagnosis.

DIAGNOSIS: *Batomys dentatus* is distinguished from all other species in the genus

by the following: long (relative to length of head and body) and bicolored tail (proximal two-thirds brown, distal third white); moderately long superciliary vibrissae (extending a few mm beyond pinnae); very large molars, both absolutely and relative to size of cranium and mandible; cusp t1 oriented horizontally on first upper molar; each first and second lower molar possessing a small and round (in occlusal plane) posterior cingulum.

DESCRIPTION AND COMPARISONS: *Batomys dentatus* is slightly larger in body size than most specimens of either *B. granti* or *B. salomonseni* and is appreciably larger than the Dinagat species (tables 1, 4). Upperparts of head and body are covered by a thick and soft (somewhat woolly texture) dark brown coat costing of woolly underfur, long overhairs (extending up to 20 mm over lower back and rump) and short, inconspicuous guard hairs (25–28 mm long). As Miller (1910: 401) noted, "the entire area finely and inconspicuously varied by the blackish tips to the longer hairs and subterminal annulations on those of under fur." Sides of the body and flanks are suffused with buff, producing a brighter tone over these regions. The ventral pelage is buffy brown; small areas on the throat, chest, and inguinal region are "a pale cream-buff much darkened by the slate-gray under color," in Miller's words. The ventral coat is also thick and soft, but the hairs are not as long as those forming the dorsal pelage (overhairs reach only 10 mm). Miller characterized the holotype as having buffier underparts than *B. granti*, but the range in chromatic variation in that species includes the buffy brown characterizing the only example of *B. dentatus*. Ears are dark brown and densely covered, inside and out, with fine hairs. The face is tinged with gray. An eye ring is present, contrary to Miller's observation.

Lengths of most facial vibrissae relative to body size are similar to the conformation in *B. granti*. Mystacials and genal vibrissae are long relative to head size as they are in *B. granti*. However, when laid against the head, the longest superciliary extends 6–7 mm beyond the posterior margin of the pinnae; in specimens of *B. granti* at hand, the longest superciliary reaches the middle of the pinna or its posterior border, but not beyond. Al-

though they are long in *B. dentatus*, the superciliaries are much shorter when compared to the extraordinarily long superciliary vibrissae of *B. salomonseni* (extending to 45 mm beyond the pinnae in some specimens).

Slightly shorter than combined length of head and body, the tail of *B. dentatus* is thick, conspicuously furred, and strikingly bicolored, a color pattern unique among described species of *Batomys*. The distal 68 mm is covered by white hairs that form a tuft (up to 8 mm long) at the tip of the tail; the remainder of the tail is dark brown; its basal 20 mm is concealed by thick fur similar in color and texture to that of the rump. Relative to body size, tail diameter and degree of pilosity are closely similar to these features seen in our samples of *B. granti* and unlike the relatively thin and sparsely haired tails of *B. salomonseni* and the new species on Dinagat. Length of tail relative to combined lengths of head and body in *B. dentatus* is much greater than the relatively short tails of *B. granti*, *B. salomonseni*, and the new Dinagat species (tables 1, 4).

Dorsal metacarpal and metatarsal surfaces of *B. dentatus* are dark brown; the digits and claws are white. A silvery unguis conceals the base of each claw but does not extend beyond its tip. The hind foot is wide, a configuration similar to that of *B. granti* (fig. 5). Six large pads adorn the plantar surface, which is also typical of *B. granti*, but the thenar, instead of being one elongate tubercle, is partially subdivided into two lobes.

Except for its slightly larger body size and relatively longer tail with its brown and white pattern, the holotype of *B. dentatus* closely resembles specimens in our samples of *B. granti* in coloration and texture of pelage as well as color and conformation of feet. Shapes of crania and mandibles are also much alike (compare figs. 7–9 with fig. 20), and both exhibit a derived cephalic arterial pattern. The primary contrasts are in size and proportions of certain cranial variables. Crania of the two do not differ significantly in length (45.1 mm for *dentatus* versus the range of 45.0–46.1 mm for the three specimens of *granti* from Mount Data, and 41.2–44.9 mm for the Mount Isarog sample), but that of *B. dentatus* has a greater zygomatic breadth; a wider rostrum relative to its

length; a much longer bony palate, both absolutely and relative to any other cranial measurement; shorter incisive foramina relative to lengths of diastema and bony palate; an absolutely narrower mesopterygoid fossa; and a longer auditory bulla, both absolutely and relative to occipitonasal length (see the ratio diagram in fig. 22; compare values listed in tables 2 and 4).

Miller claimed that *B. dentatus* has a deeper braincase than *B. granti*, but that observation is not supported by our absolute measurement values or proportional relationships. Height of the braincase is 12.1 mm in the holotype of *B. dentatus*, which fits within the observed range of values for the samples of *B. granti* from Mount Data (11.9–12.1 mm) and Mount Isarog (11.9–12.3 mm). Furthermore, height of braincase relative to its breadth, or to occipitonasal length, does not differ between *B. dentatus* and *B. granti* (fig. 22).

One qualitative cranial structure separates the holotype of *B. dentatus* from nearly all examples of the other species of *Batomys*. The holotype has a wide and stout alisphenoid strut on each side of the cranium (fig. 26), a structure absent in most specimens representing the other species of *Batomys* (see description of *B. granti*).

Dentaries of *B. dentatus* and *B. granti* are closely similar in shape and relative sizes of coronoid, condyloid, and angular processes. The two species apparently differ only in size, as can be seen by comparing figures 9 and 20 (we did not quantify this contrast).

Dental dimensions provide the most impressive size differences between the two species. *Batomys dentatus* has much longer and wider molars than *B. granti*, or any other described species in the genus (tables 2, 4). Compared with the other species of *Batomys*, molar rows of *B. dentatus* are also appreciably longer and wider relative to most cranial dimensions (fig. 22). By using *dentatus* for the name of this handsome species, Miller highlighted one of its most distinctive and dramatic diagnostic traits.

Molars in the holotype of *B. dentatus*, aside from being absolutely larger (table 2) and larger relative to cranial dimensions (fig. 22), are generally similar to other species in occlusal patterns (compare figs. 12–15 with fig. 21), except for two features. First, the



Fig. 20. Views of cranium and left dentary of holotype of *Batomys dentatus* (USNM 151506), an adult male from Luzon, $\times 2$.

long axis of cusp t1 on each first upper molar of *B. dentatus* is oriented horizontally so that the cusp tip points toward the midline of the cranium. In other species of *Batomys*, the

long axis of cusp t1 points back and toward the sagittal plane—oblique rather than horizontal relative to the other cusps in the front row. Second, the posterior cingulum at the

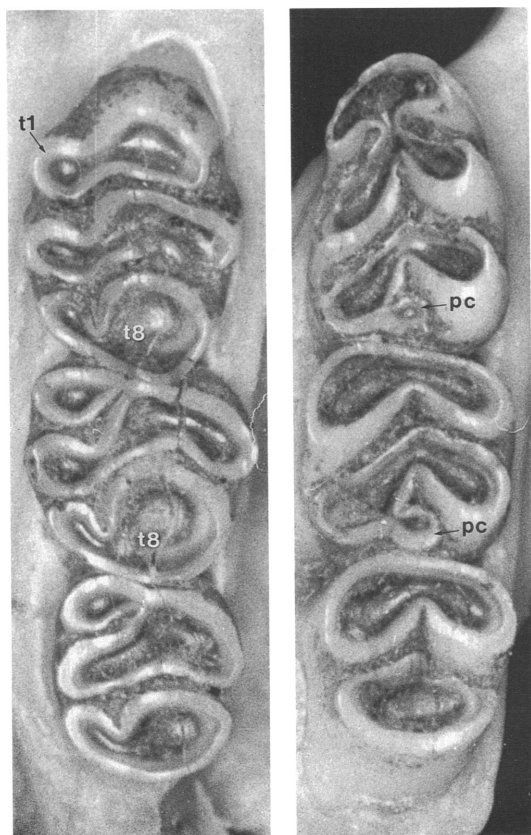


Fig. 21. Occlusal views of left upper (left view) and lower (right view) molar rows of the holotype of *Batomys dentatus*. See measurements in table 4. Notice that the long axis of cusp t1 on the first upper molar is horizontal rather than posterolingual, as is typical in other species of *Batomys* (figs. 12, 13). Also, the posterior cingulum (pc) at the back of each first and second lower molar is small and round in cross section rather than large relative to occlusal surface and either elliptically elongate in outline (*B. russatus*, fig. 15) or cordate (*B. granti* and *B. salomonseni*, figs. 14, 15). Each cusp t8 of first and second molar is worn to a featureless basin; whether a posterior cingulum was or was not associated with each of these cusps cannot be determined.

back of each first and second lower molar is round (in occlusal plane) and small relative to the rest of the molar mass in *B. dentatus*; the contrasting configuration in the other species is a cordate or elliptical posterior cingulum that is much larger relative to the rest of the occlusal surface.

Occurrence of a posterior cingulum on

each first upper and second molar is variable among species of *Batomys* (see the accounts of *B. granti* and *B. salomonseni*). We could not determine if this structure is present or absent in the holotype of *B. dentatus* because the molars are too worn.

ECOLOGY: No habitat data are associated with the holotype of *B. dentatus*. Its collector, E. A. Mearns, referred to the specimen in his field journal as the "chubby rat," but provided no description of the area in which it was caught (for this information we are indebted to Dave Schmidt who read through the appropriate sections of Mearns' journal, which is archived in the Mammal Division, USNM). We presume the species to be a forest inhabitant because areas in Benguet Province at the elevation that the "chubby rat" was caught, 7000 ft, would have been covered to some degree by montane forest.

THE NEW SPECIES OF *BATOMYS*

The three dark-furred and moderately sized species described above stand in stark contrast to the species from Dinagat that we describe below, which is the smallest in body size and possesses the most colorful pelage.

Batomys russatus, new species

HOLOTYPE: DMNH 4594, an adult male collected by members of a field crew from Mindanao State University headed by Roberto Lim (original number, D. S. Rabor 242) from Libjo (= Albor), Plaridel Municipality (10°14'N/125°32'E, for Libjo, according to B. R. Tabaranza, Jr; USBGN Philippines, 1989: 657, lists 16 Libjos, one of which has the coordinates 10°12'N/125°32'E) on the western side of Dinagat Island (Surigao del Norte Province), Republic of the Philippines, on April 18, 1972. A stuffed museum study skin (fig. 23) and skull (fig. 24) form the holotype; its measurements are listed in table 4.

TWO REFERRED SPECIMENS: **DMNH 4593**, an adult female obtained by the same field team and from the same place as the holotype, but on April 17, 1972. The stuffed skin is intact, unfortunately the cranium and mandible were drastically overcleaned with the result that the auditory bullae and several molars are missing. **BRT 278**, a very old adult male (fig. 25) from Dinagat Island, Lo-

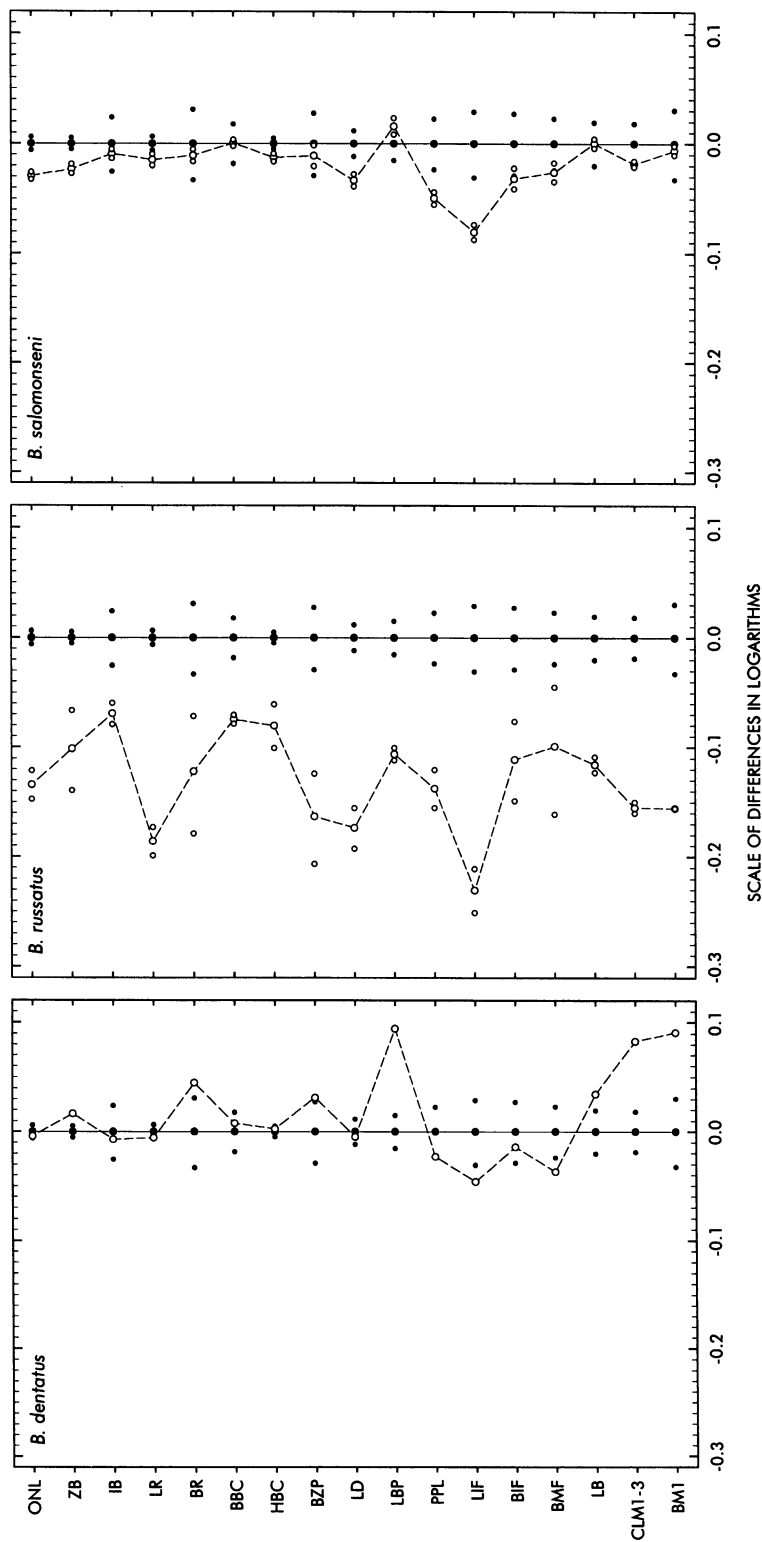


Fig. 22. Ratio diagram illustrating some proportional relationships among samples of adult *Batomys*. The standard (black dots, solid line) is the sample of *B. granti* from Mount Luzon, the sample of *B. russatus* from Dinagat ($N = 3$), and a sample of *B. salomonseni* from Mindanao ($N = 51$). Data are derived from values for mean, standard deviation, and sample size of variates listed in tables 2 and 5, and from values of the single specimen of *B. dentatus* listed in table 4. For each measurement, the absolute value of the mean, and plus or minus two standard errors of the mean, were converted to logarithms. Next, the logarithm of the mean of the standard was subtracted from the logarithms of the mean, and plus or minus two standard errors, of the comparative sample. Measurements larger than the standard are thus represented by positive values, those smaller by negative values. The lines connect sample means, and the bracketing symbols represent ± 2 SE of the mean. A sample having the same proportions as the standard will be represented by mean values on a line parallel to that of the standard regardless of absolute size. Also, if values for the sample being compared with the standard are similar in absolute size, they will be close together on the diagram. If proportions between any of the measured dimensions are similar, the positions of their points relative to each other on the horizontal scale will be similar.

TABLE 4
Sex, Age, External Measurements (mm), and Weight (g) of *Batomys dentatus* and *Batomys russatus*

	<i>B. dentatus</i>		<i>B. russatus</i>	
	Luzon		Dinagat	
	USNM 15106 ^a	BRT 278	DMNH 4593	DMNH 4594 ^a
Sex	Male	Male	Female	Male
Age	Adult	Old adult	Adult	Adult
LHB	195	151	147 (?)	140 (?)
LT	185	—	118 ^b	102 ^b
LHF	36	30	30 ^c	31 ^c
LE	—	18	18	16
W	—	115	—	—
LT/LHB (%)	95	—	80	73
ONL	45.1	34.4	33.2	32.7
ZB	23.1	19.0	17.3	16.5
IB	6.0	5.3	5.2	5.1
LR	15.6	10.5	10.4	10.0
BR	9.2	7.0	6.1	5.7
BBC	17.2	14.3	14.3	14.1
HBC	12.1	10.0	10.4	9.6
BZP	4.8	3.1	3.3	2.8
LD	12.2	8.6	8.0	8.2
LBP	8.2	5.2	5.1	5.2
PPL	16.4	12.8	12.9	12.1
LIF	8.0	5.4	5.0	5.3
BIF	3.0	2.6	2.3	2.3
BMF	3.0	2.9	2.6	2.3
LB	5.7	4.1	—	4.0
CLM1–3	9.8	—	5.6	5.7
BM1	3.0	—	1.7	1.7

^a Holotypes.

^b BRT 278 has only half of a tail. Measurements listed from DMNH 4593 and 4594 were obtained by us from the stuffed skin. Values on the labels are 129 and 117 mm, respectively, which are clearly incorrect. Length of head and body for each DMNH specimen is total length, which was recorded on the skin label, minus our value for tail length.

^c Measured by us on the dry skin.

reto Municipality, Sitio Bilitbiton, Barangay Kambinlio (10°22'17"N/125°37'05.5"E), 350 m, collected on November 26, 1994.

ISLAND DISTRIBUTION: Known only from lowland tropical evergreen rainforest on Dinagat Island, which is about 671 square km in area and located off the tip of northeastern Mindanao (fig. 1). More information about Dinagat is provided by duPont and Rabor (1973), Heaney and Rabor (1982), and King and McKee (1949).

ETYMOLOGY: By combining russet (reddish

brown) with the Latin *atus* (provided with, having the nature of, pertaining to; Brown, 1956), we tie the diagnostic fur color to the scientific name.

DIAGNOSIS: *Batomys russatus* is distinguished from *B. granti*, *B. dentatus*, and *B. salomonseni* by the following combination of traits: much smaller in body size (all the other species of *Batomys* are significantly larger); tail moderately haired (not as hairy as *B. granti* and *B. dentatus*) and monocolored (distal third is white in *B. dentatus*); dorsal



Fig. 23. Holotype of *Batomys russatus* (DMNH 4594), adult male from Dinagat. Measurements are listed in table 4.

TABLE 5
Descriptive Statistics for
Cranial and Dental Measurements (mm) of
Batomys russatus from Dinagat
(Summaries are derived from measurements of the three
specimens listed in table 4.)

	N	M ± SD	Observed range
ONL	3	33.4 ± 0.87	32.7–34.4
ZB	3	17.6 ± 1.28	16.5–19.0
IB	3	5.2 ± 0.10	5.1–5.3
LR	3	10.3 ± 0.27	10.0–10.5
BR	3	6.3 ± 0.67	5.7–7.0
BBC	3	14.2 ± 0.12	14.1–14.3
HBC	3	10.0 ± 0.40	9.6–10.4
BZP	3	3.1 ± 0.25	2.8–3.3
LD	3	8.3 ± 0.31	8.0–8.6
LBP	3	5.2 ± 0.06	5.1–5.2
PPL	3	12.6 ± 0.44	12.1–12.9
LIF	3	5.2 ± 0.21	5.0–5.4
BIF	3	2.4 ± 0.17	2.3–2.6
BMF	3	2.6 ± 0.30	2.3–2.9
LB	2	4.1 ± 0.07	4.0–4.1
CLM1–3	2	5.7 ± 0.07	5.6–5.7
BM1	2	1.7 ± 0.00	–

fur sleek and bright brownish red, ventral coat deep orange-gray, front feet white (all other species have dark brown upperparts and gray or buffy gray underparts and brown patches on dorsal surfaces of the front feet); hypothenar pad large relative to size of the-
nar (relatively smaller in *B. granti* and *B. dentatus*); cephalic arterial pattern complete (the primitive configuration for muroid rodents), as indicated by a sphenofrontal foramen, squamosal-alisphenoid groove, large stapelial foramen, and groove scoring ventral surface of posterolateral pterygoid plate (all the other species possess a derived carotid circulation); posterior cingulum elongate (elliptical in occlusal outline) at the back of each first and second lower molar (either cordate or round in cross section in the other species).

DESCRIPTION AND COMPARISONS: *Batomys russatus* is the smallest in body size of all

the described species in the genus (compare tables 1 and 4) and has the most colorful fur. The dorsal coat is glossy reddish brown from head to rump and sleek and smooth to the touch, not woolly. The fur appears to consist of one thick layer (overhairs are 10–13 mm long) because the slender guard hairs barely extend beyond the overhairs and their tips are unpigmented. Except for dark brown eyelids, the face is colored like the rest of the dorsum and lacks a partial mask, which is the pattern exhibited by specimens of *B. granti*. The ventral coat is short (overhairs up to 5 mm long), bright ochraceous, and slightly infused with the pale gray bases of the hairs; the ochraceous tones extend dorsally onto the cheek and blend with the darker hues of the dorsal coat on the sides of the body—the demarcation between dorsal and ventral coats is not well marked. One specimen (DMNH 4594) has a white patch on the throat, another (DMNH 4593) has small white pectoral and inguinal patches, and the entire throat and chest area is white in a third (BRT 278).

The small ears are dark gray and scantily covered with short russet hairs on both inner and outer surfaces. Facial vibrissae are very long. When laid against the head, the superciliary and mystacial vibrissae extend up to 25 mm beyond posterior margin of the pinna, and many of the mystacial vibrissae extend 30–40 mm past the ear. Genal vibrissae reach the posterior edge of the ears but not beyond. Length of the superciliary vibrissae relative to position of the pinna is similar to the proportions in *B. salomonseni*, but not *B. granti* or *B. dentatus* in which much shorter vibrissae are characteristic.

The monocolored brown tail is shorter than combined lengths of head and body (table 4) and is covered by overlapping rings of brown scales and moderately long brown hairs. Hairs are 3–5 mm long in the proximal portion of the tail and increase to 8–10 mm at the tip where they form a thin tuft. Diameter and pilosity of the tail relative to body size are similar to that in *B. salomonseni* and contrast with the thicker, hairier tails of *B. granti* and *B. dentatus*. Tail length relative to head and body length in *B. russatus* is similar to the sample of *B. granti* from Mount Isarog and most samples of *B. salomonseni* (tables 1, 4).

Lengths of the digits relative to metacarpal and metatarsal regions are similar among all species of *Batomys*. Dorsal metacarpal surface, digits, claws, and palmar area (including tubercles) of *B. russatus* are all unpigmented—because the front feet are white they contrast sharply with the russet body fur. Dorsal metacarpal surfaces are covered with brown hairs that form a patch or streak in the other species of *Batomys*, and although the palmar pads are unpigmented, the intertubercle surfaces are brown. Hind feet are moderately long and wide, each with brownish russet markings on the dorsal metatarsal surfaces and unpigmented digits and claws. The naked plantar region is also unpigmented and supports six tubercles, including a hypothenar that is large relative to size of the thenar; the hypothenar is relatively smaller in all the other species of *Batomys* (fig. 5). At the base of each claw on front and hind feet there is an ungual tuft of short silver hairs that partially sheaths the claw but does not extend beyond the claw tips.

Of the three known specimens of *B. russatus*, one is a female that has two pairs of inguinal teats, the number common to all species in the genus.

Cranium and mandible of *B. russatus* appear to be simply a diminutive version of those observed in other species of *Batomys*, especially *B. granti* and *B. salomonseni* (contrast figs. 7–9 with 24 and 25; tables 2, 4, and 5). There are, however, significant proportional differences and a qualitative character that dramatically set the new species apart. To illustrate the proportional contrasts, we compare means of cranial measurements of the three examples of *B. russatus* with means of three specimens of *B. granti* from Mount Data (the type species of the genus and type locality) in a ratio diagram (fig. 22). Relative to occipitonasal length, the sample of *B. russatus* has a significantly wider interorbit and larger braincase (breadth and height); much shorter rostrum, diastema, and incisive foramina; longer bony palate; and slightly shorter molar rows. Some of these proportional contrasts are also seen in comparisons of *B. dentatus* and *B. salomonseni* with *B. granti*; for example, compared with the type species, samples of the other three all have a longer bony palate and shorter in-

cisive foramina relative to occipitonasal length. *Batomys russatus* differs from *B. dentatus* and *B. salomonseni* by its much shorter rostrum and larger braincase relative to occipitonasal length, two proportions also contrasting the new species with *B. granti*.

One character complex in the cranium distinguishes *B. russatus* from all of the other species of *Batomys*. All three specimens possess a squamosal-alisphenoid groove on the inside wall of the braincase that is clearly visible from the outer surface (fig. 26). The groove leads to a sphenofrontal foramen situated where orbitosphenoid, alisphenoid, and frontal bones meet. This configuration, together with a large stapedial foramen and posterolateral groove on the pterygoid plate (fig. 28), indicates that the cephalic blood supply in *B. russatus* conforms to a pattern that has been postulated as primitive for muroid rodents and is found in cricetines as well as many sigmodontines (Bugge, 1970; Carleton, 1980; Musser, 1982; Musser and Newcomb, 1983; Carleton and Musser, 1989; Musser and Heaney, 1992; Voss, 1988, 1993). As the condition was summarized by Carleton and Musser (1989: 35):

a large stapedial artery enters the optic capsule through the crus of the stapes and tympanic cavity to exit from a stapedial canal deep to the anterior end of the otic capsule. . . . There the stapedial divides into two main branches. One is the supraorbital branch, which passes across the squamosal and alisphenoid bones, scoring the squamosal-alisphenoid groove, and emerges at the sphenofrontal foramen. . . . The second primary stapedial branch is the common trunk of the mandibular and infraorbital arteries: the former supplies the lower jaw; the latter passes along the groove on the pterygoid plate, enters the posterior end of the alisphenoid canal, and emerges into the orbit through the anterior alar (= sphenoidal) fissure

Judged by bony landmarks in the three available crania of *B. russatus* (figs. 26, 28), its cephalic arterial supply has all the components of the primitive pattern (figs. 27, 28), which is similar to that diagrammed for *Microrhynchomys*, a Neotropical sigmodontine, by Carleton and Musser (1989: 39).

Even though this arterial pattern is widespread among subfamily groups of muroid rodents, its presence in *B. russatus* represents a unique occurrence among species of extant Murinae (as the contents of that subfamily

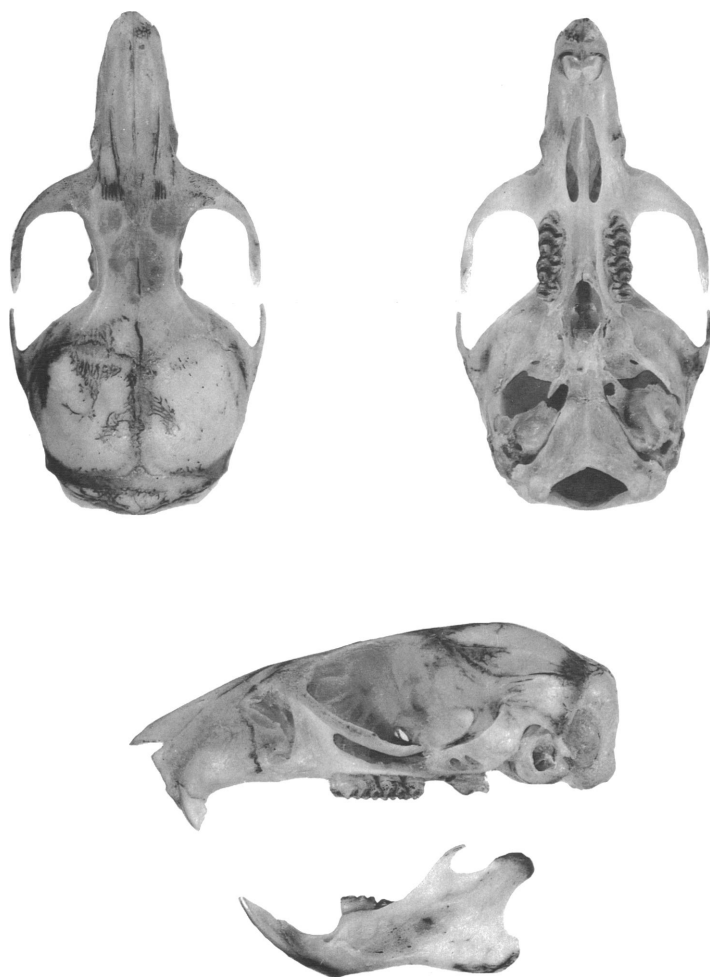


Fig. 24. Views of cranium and left dentary of holotype of *Batomys russatus* (DMNH 4594), adult male from Dinagat, $\times 2$. Measurements are listed in table 4. Age and cranial conformation of DMNH 4593 are similar to the holotype (see table 4).

are delineated by Carleton and Musser [1984] and Musser and Carleton [1993]). Except for *B. russatus*, all extant murines (and those extinct forms represented by fragments in which the carotid pattern can be detected) exhibit a modified arterial pattern like the one described and diagrammed for species of the Neotropical sigmodontine *Oligoryzomys* (Carleton and Musser, 1989) or that common to most Sundaic and Philippine murines (Musser and Newcomb, 1983; Musser and Heaney, 1992): the sphenofrontal foramen, squamosal-alisphenoid groove, and supraor-

bital branch of the stapedia artery are not present.

All the other described species of *Batomys*, as well as *Crateromys*, *Carpomys*, and some species of *Apomys* (Musser, 1982; Musser and Heaney, 1992), have a highly modified cephalic arterial pattern and accompanying osseous components, a configuration interpreted as derived (Bugge, 1970; Carleton, 1980; Musser, 1982; Musser and Newcomb, 1983; Voss, 1988; Carleton and Musser, 1989; Musser and Heaney, 1992; Voss and Carleton, 1993). Specimens with this

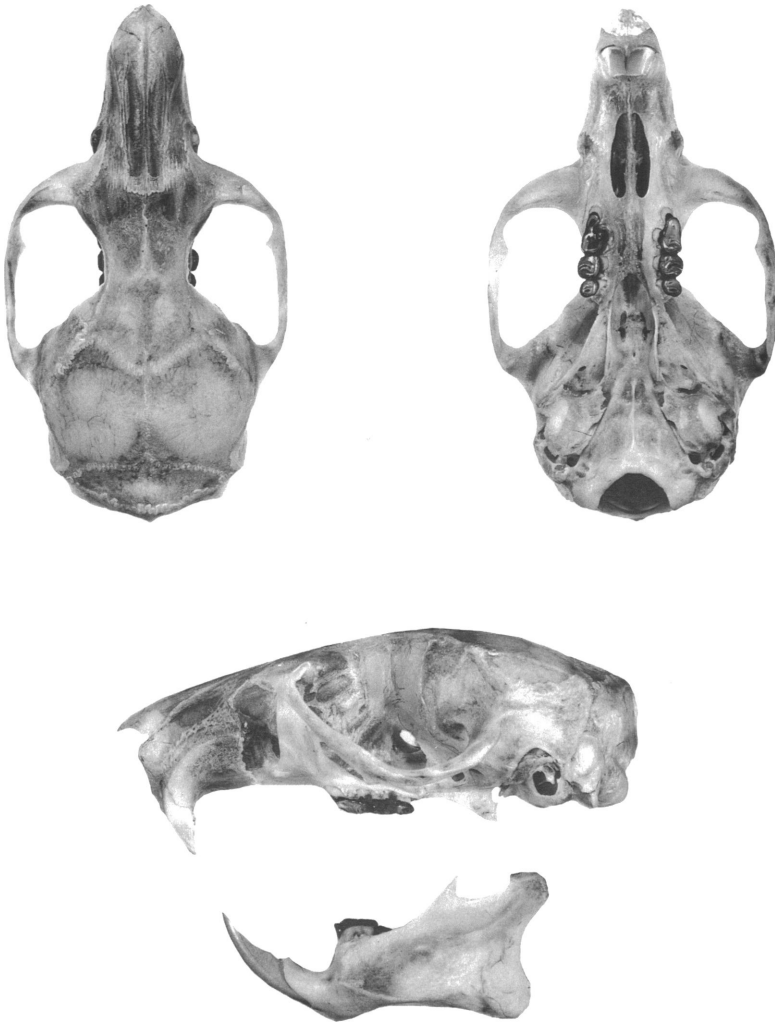


Fig. 25. Views of cranium and left dentary of adult *Batomys russatus* (BRT 278), a very old animal compared with the holotype and other specimen. Measurements are listed in table 4.

pattern lack a sphenofrontal foramen and squamosal-alisphenoid groove and have a minute stapedia foramen in the petrotympanic fissure (between petromastoid and bulbar capsule) (figs. 27, 28). The stapedia artery is small and serves only the otic capsule, having lost its three primary branches. The supply of the orbit and upper jaw, normally served by branches of the stapedia, is taken over by a secondary connection to the facial circulation (ophthalmic and internal maxillary) that branches from the internal carotid artery (instead of the stapedia) after that ves-

sel passes through the carotid canal. This secondary vessel crosses diagonally over the dorsal surface of the pterygoid plate, along the inside wall of the braincase, and exits the braincase through the anterior alar fissure (figs. 27, 28).

Most upper and lower molars are multi-rooted in the three examples of *B. russatus*, a pattern similar to the range of variation we observed in our samples of *B. granti* and *B. salomonseni* (figs. 10, 11). Primary patterns formed by cusps on upper and lower molars in *B. russatus* are also similar to those ex-

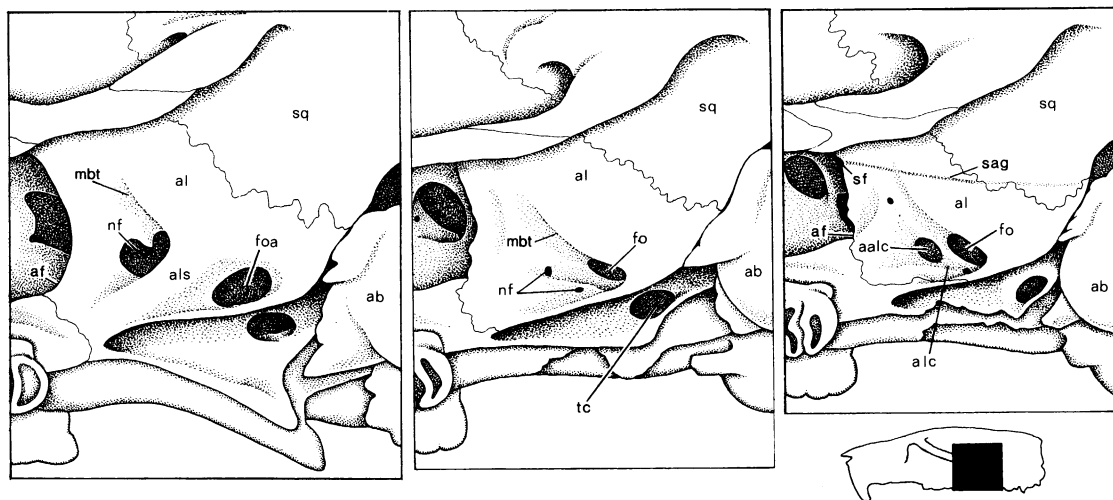


Fig. 26. Views of squamosal-alisphenoid region in species of *Batomys*. **Left:** Holotype of *B. dentatus* (USNM 151506) illustrating stout alisphenoid strut (als). Medial and anterior to the strut is a large vacuity that we interpret as a nutrient foramen (nf). Trough for masticatory and buccinator nerves (mbt) appears to emerge from dorsomedial portion of strut. Posterior margin of strut partially defines foramen ovale accessorius (foa). Foramen ovale (fo) is not visible. **Middle:** *B. salomonseni* (DMNH 5955) in which alisphenoid strut is absent, the configuration in most specimens as well as in *B. granti*. Foramen ovale is visible as is the entire trough for masticatory and buccinator nerves. Anterior to the foramen ovale are small openings in the alisphenoid bone (al) that we identify as nutrient foramina (nf), which vary in size and number. **Right:** Holotype of *B. russatus* (DMNH 4594), which represents the condition in all studied specimens. An alisphenoid strut is absent. A groove (sag) for supraorbital branch of stapedial artery scores the inside of the squamosal (sq) and alisphenoid bones, is visible from outside of the braincase, and ends at the sphenofrontal foramen (sf). In life, infraorbital branch of stapedial artery would course along an open alisphenoid canal (alc) and through the anterior opening of the alisphenoid canal (aalc) to leave the braincase through anterior alar fissure (af). Note the small nutrient foramen below the foramen ovale. Bony landmarks seen in this view—squamosal-alisphenoid groove, sphenofrontal foramen, large vacuity in alisphenoid bone that is the anterior opening of the alisphenoid canal, and a trough that represents the alisphenoid canal—reflect primitive cephalic arterial pattern found in murines (see figs. 27, 28). Other abbreviations: ab, auditory bulla; tc, opening of the transverse canal.

hibited by samples of the other three species of *Batomys* (figs. 12–15 and 21). We identified two dissimilar features among the species. Cusp t1 on the first upper molar is oriented posterolingually in *B. russatus* (as it is in *B. granti* and *B. salomonseni*) but horizontally in *B. dentatus*. The posterior cingulum at the back of each first and second molar is large relative to molar size and has a compressed elliptical shape (in occlusal plane) in the specimens of *B. russatus*; the posterior cingulum is relatively large and cordate in samples of *B. granti* and *B. salomonseni* (oblong in a very few individuals), and relatively much smaller and round in *B. dentatus*.

ECOLOGY: We have little information about habits or habitat. A short tail relative to combined lengths of head and body as well as moderately long hind feet suggest *B. russatus* to be terrestrial. That it is a forest dweller is indicated by place of capture of DMNH 4593 and 4594 near a camp “established in a logged area in rolling country and low hills where there were still many patches of remnant dipterocarp forests in the surrounding localities” (duPont and Rabor, 1973: 4).

BLT 278 was caught (by a Victor snap trap baited with fried coconut coated with peanut butter) in disturbed lowland tropical evergreen rainforest at the 350 m site that has already been described in the account of *B.*

TABLE 6
Non-volant Small Mammals Captured by Members of the 1994 Survey on Dinagat Island

Species	Site, ^a elevation, and duration of trapping		
	1 350 m Nov 22–29	2 550 m Nov 29–Dec 5	3 750 m Dec 4–8
INSECTIVORES			
<i>Podogymnura aureospinula</i>	5	0	4
TREE SHREWS			
<i>Urogale everetti</i>	2	5	1
RATS AND MICE			
<i>Apomys cf. insignis</i>	6	9	2
<i>Apomys cf. musculus</i>	0	0	1 ^b
<i>Batomys salomonseni</i>	2	1	11
<i>Batomys russatus</i>	1	0	0
<i>Bullimus bagobus</i>	7	10	1
<i>Rattus everetti</i>	11	5	4
TOTALS			
Individuals	34	30	24
Species	7	5	7
Trap-nights	782	818	644 ^c
Individuals/100 trap-nights	4.3	3.7	2.2 ^d

^a All three sites are described in the ecological account of *B. salomonseni*.

^b Caught by hand.

^c Protocols for trapping were similar to those described in Rickart et al. (1991, 1993).

^d Total relative abundance of small mammals (measured as the number of animals captured per 100 trap-nights) is similar to that derived from trapping results on small islands of Biliran (498 km²) and Maripipi (22 km²), but about twice that for Leyte (7213 km²) (Rickart et al., 1993); Dinagat is 675 km².

salomonseni. The rat is one of the 34 specimens, and represents one of seven species of small mammals that were captured at the lowland site during the survey of 1994 led by B. R. Tabaranza, Jr.; no examples of *B. russatus* were obtained at the two higher regions (550 and 700 m) surveyed despite focused trapping efforts (table 6).

Among the other specimens captured at 350 m, in addition to the single *B. russatus*, were examples of *Podogymnura aureospinula*, *Urogale everetti*, and *Batomys salomonseni*. Their presence at this low elevation is surprising because on Mindanao the insectivore is known only from above 1250 m, the tree shrew has not been taken below 750 m, and 1500 m is the lowest record for *B. salomonseni*. Neither *Podogymnura* nor *Urogale* have been collected on the islands of

Leyte, Biliran, or Maripipi (Rickart et al., 1993).

CONCLUDING OBSERVATIONS

BATOMYS RUSSATUS AND THE *CRATEROMYS* GROUP

In their compendium on Philippine rodents, Musser and Heaney (1992) pointed out that the species of *Crateromys* (*C. schadenbergi*, *C. paulus*, and *C. australis*), *Carpomys* (*C. melanurus* and *C. phaeus*), and *Batomys* (*B. granti*, *B. dentatus*, and *B. salomonseni*) then known seemed to form a natural group defined by a combination of derived characters. In contrast to the other native species of Philippine murines, all members of the *Crateromys* Group share the following: (1) each upper molar has a large

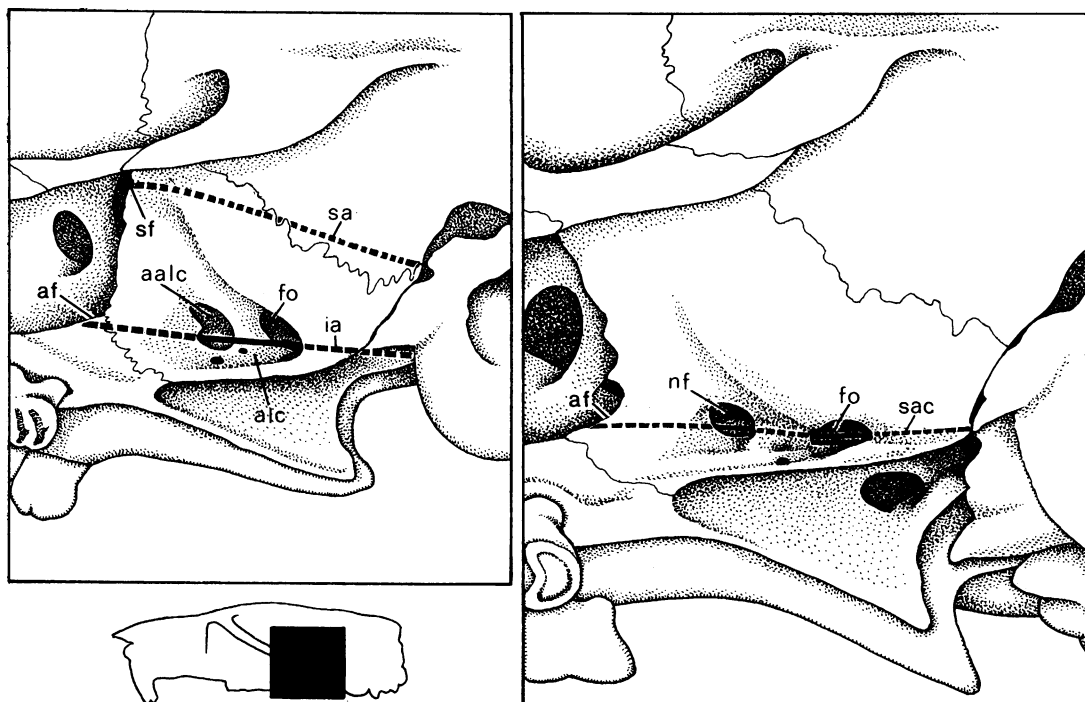


Fig. 27. Portion of cephalic arterial circulation in squamosal-alisphenoid region in two species of *Batomys*. **Left:** *B. russatus* (DMNH 4593), which exhibits the primitive murine arterial pattern. Two branches of stapedial artery (see fig. 28) are depicted in this view. Supraorbital branch (sa) runs in a groove scoring the inner braincase wall along the squamosal and alisphenoid bones (see fig. 26) and enters the orbit through the sphenofrontal foramen (sf). Infraorbital branch (ia) courses along outside the braincase in the open alisphenoid canal (alc), reenters the braincase through anterior opening of alisphenoid canal (aalc), and enters orbit through anterior alar fissure (af). **Right:** *B. granti* (FMNH 62504) possesses derived arterial pattern also common to *B. dentatus* and *B. salomonseni*. Two branches of stapedial artery are absent (see fig. 28), and a secondary arterial connection (sac) courses along inside the braincase to exit into orbit through anterior alar fissure. Other abbreviations: fo, foramen ovale; nf, nutrient foramen.

cuspid t7 in which its long axis is oriented anterolingually relative to the adjacent central cuspid t8; (2) cuspid t9 is either absent from each upper molar or so reduced in size that its definition is ambiguous; (3) a large anteroconid, roughly cordate in occlusal outline, forms the anterior third of each lower molar; (4) the cephalic arterial pattern is derived with its attendant bony landmarks; (5) a very broad angular process (best seen in lateral view) is separated from the condyle by a shallow emargination in the caudal margin of the dentary; (6) molars have some combination of accessory roots. Most species also have long and narrow incisive foramina (*Crateromys paulus* is the exception).

Two other members of the *Crateromys* Group have been described since 1992. The small-bodied *Crateromys heaneyi* (Gonzales and Kennedy, 1996) from Panay Island is a distinctive species that is morphologically most closely related to the larger *C. schadenbergi*. It exhibits all six of the derived traits listed above, as well as long incisive foramina. *Batomys russatus*, described here, possesses all of these diagnostic characters except for the carotid circulatory pattern. Within this context of shared derived features, the complete carotid arterial pattern seen in *B. russatus*, which is the primitive pattern for muroid rodents, may be a new acquisition (reversal of a

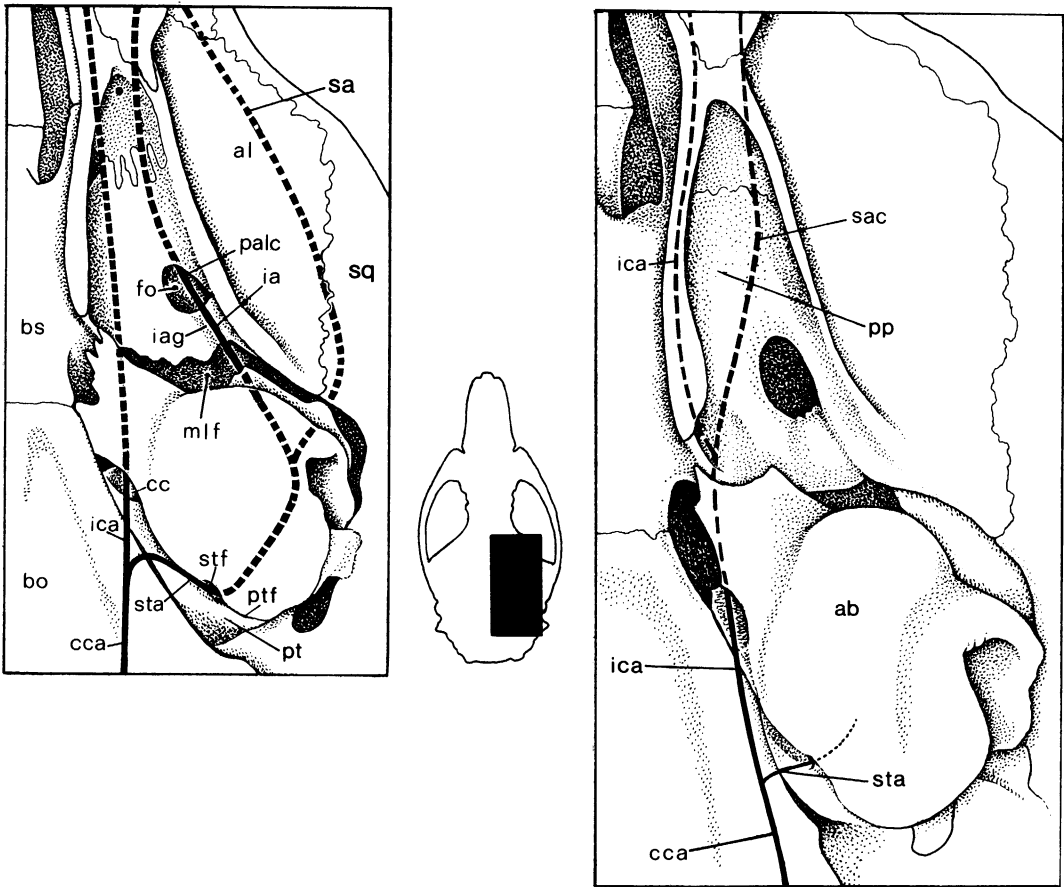


Fig. 28. Portion of cephalic arterial circulation, ventral view in two species of *Batomys*. **Left:** *B. russatus* (constructed from DMNH 4593 and BRT 278), major branches from common carotid artery (cca). After leaving the common carotid artery (cca) and entering large stapedial foramen (stf) in petromastoid fissure (ptf) between periotic (pt) and auditory bulla (ab), stapedial artery (sta) has two primary branches: supraorbital artery (sa) courses along inside squamosal (sq) and alisphenoid (al) bones in a groove (see fig. 26); infraorbital artery (ia) exits the periotic region through middle lacerate foramen (mlf), courses in a groove (iag) on outside of pterygoid plate and disappears through posterior opening of alisphenoid canal (palc), the most anterior portion of the foramen ovale (fo). After giving off the stapedial, the common carotid continues as the internal carotid artery (ica) and enters braincase through carotid canal (cc). These are typical elements of the primitive cephalic arterial circulation in murines. **Right:** *B. granti* (FMNH 62504). Small stapedial artery serves only the periotic region through a minute stapedial foramen. Ophthalmic and internal maxillary circulation (supplied by two large branches of the stapedial in *B. russatus*) is supplied by a secondary arterial circulation (sac) that branches from internal carotid artery and courses obliquely across dorsal surface of pterygoid plate (pp). This is part of the derived carotid circulation found in some murines. Other abbreviations: bo, basioccipital; bs, basisphenoid.

character state) rather than retention of a primitive character. The true polarity of this circulatory complex may be revealed by results of phylogenetic character analyses of all the Philippine murids.

BATOMYS RUSSATUS AND THE OTHER SPECIES OF *BATOMYS*

Judged by their morphologies, *B. granti*, *B. salomonseni*, and *B. dentatus* cluster in

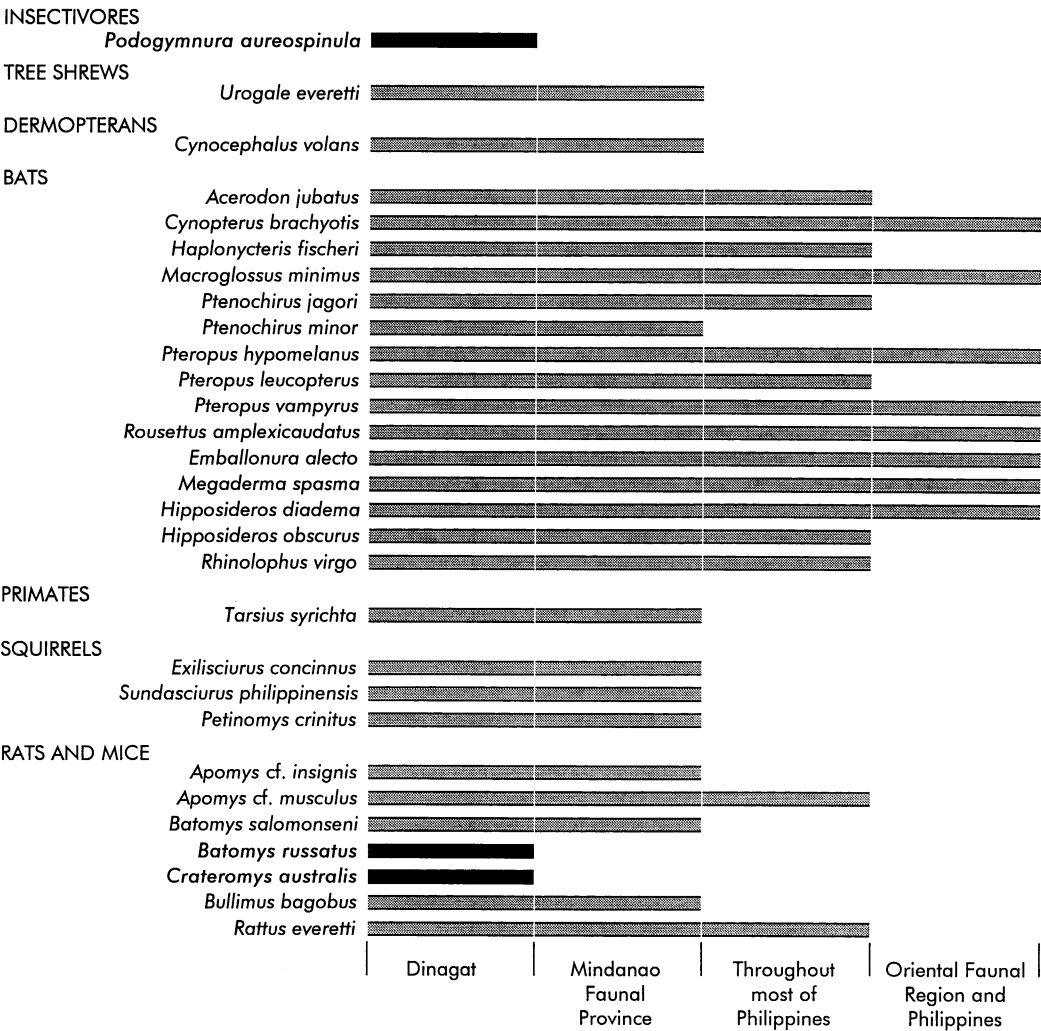


Fig. 29. Native species of mammals documented by voucher specimens from Dinagat Island. Heaney and Rabor (1982), Heaney and Morgan (1982), Musser et al. (1985), and the present report are the primary sources for the list. Reasons for certain changes between the list provided by Musser et al. (1985) and the present compilation require comments.

Rhinolophus virgo and *Apomys* cf. *musculus* are new records for Dinagat and are based on examples collected by B. R. Tabaranza during a survey on Dinagat in 1994; those specimens are in MSU-IIT.

Heaney and Rabor (1982) included *Pteropus vampyrus* as a member of the Dinagat fauna citing Günther's (1879) "List of the mammals, reptiles, and batrachians sent by Mr. Everett from the Philippine Islands." Günther did not list that species, but did list "*Pteropus edulis*." In his "Catalogue of the Chiroptera in the collection of the British Museum," Dobson (1878) recognized *edulis* as "the largest known species of the genus" (p. 50). Included among the specimens Dobson assigned to this species was a juvenile from Dinagat that had been collected by Everett, which was undoubtedly the same one reported by Günther. Anderson (1912) treated *edulis* as a subspecies of *P. vampyrus*, and identified Everett's Dinagat specimen as *P. vampyrus lanensis*. We have not seen the specimen, but have no reason to question Anderson's allocation; *edulis* is still considered to be a synonym of *P. vampyrus* (Corbet and Hill, 1992: 64).

Specimens representing *Sundasciurus philippinensis* were identified as *Sundasciurus mindanensis* by Heaney and Rabor (1982: 17) and Musser et al. (1985: 18). Corbet and Hill (1992: 297) regarded *mindanensis* to be a synonym of *S. philippinensis*, an allocation we accept.

opposition to *B. russatus*. *Batomys granti* and *B. salomonseni* are certainly the most similar in the characters we analyzed. The two species can be distinguished, but the magnitude of the differences is much less than that separating either *B. dentatus* or *B. russatus* from them, and suggests more recent isolation from a common ancestor relative to the other two species. It is tempting to speculate that the ancestral population may have existed during middle Pleistocene times. The large land masses of Greater Luzon and Greater Mindanao (see fig. 1) were separate during late Pleistocene times (16,000 to 18,000 years ago) when sea level had dropped about 120 m below the present level. Earlier, however, during the middle Pleistocene (about 160,000 years ago), sea level may have dropped 160 m below the present level, which (assuming no drastic uplifting or subsidence) would have resulted in a land bridge between Greater Luzon and Greater Mindanao (Heaney, 1985). Such a connection seems unlikely, however, considering the difference of 80% in extant nonvolant mammal species native to each region (Heaney, 1986, 1993). Did the ancestral population occur on a single large land area that split into Greater Luzon and

Greater Mindanao components during subsequent isolation between middle and late Pleistocene time? Or did dispersal take place across the narrow San Bernardino Channel at about the same time? Refined data on the geological history of this channel would be needed to test these hypotheses.

Batomys dentatus is uniquely defined by its relatively long and bicolored tail, massive molars, orientation of cusp t1 on the first upper molar, and round posterior cingulum on each first and second lower molar. In other traits (moderate body size; dense, woolly, somber fur; derived cephalic arterial pattern, for example) it resembles *B. granti* and *B. salomonseni*.

Batomys russatus is clearly the most morphologically divergent species among the four. Small body size, sleek texture and bright coloration of fur, complete cephalic arterial circulation, and elliptical posterior cingulum at the back of each first and second lower molar set the species apart.

BATOMYS RUSSATUS AND THE DINAGAT MAMMAL FAUNA

Twenty-nine species of native mammals have been documented by voucher specimens

←

There are at least two species of *Apomys* documented by specimens that occur on Dinagat, but their identities as listed here are provisional until the taxonomic review of species of *Apomys* from the Greater Mindanao region is completed by Heaney and his colleagues (in prep.). *Apomys musculus* is smallest in body size in the genus and had been recorded only from Luzon and Mindoro. The Dinagat record is based on one specimen and referred to *musculus* because of its small body size and morphological similarity to specimens from Mount Isarog. The other Dinagat *Apomys* was identified as either *A. microdon* (Musser, 1982) or *A. insignis* (Heaney and Rabor, 1982), based on one or two specimens, respectively. Subsequently, Musser et al. (1985) treated this larger-bodied species as *A. microdon*, but Musser and Heaney (1992) listed it as *A. littoralis*, the species that Rickart et al. (1993) claimed occurs also on Leyte and Biliran. During the survey led by Tabaranza in 1994, 17 examples of this larger species were collected; in morphology of skin, skull, and dentition, they resemble samples of *A. insignis* from Mindanao.

In their report on the mammals of Dinagat, Heaney and Rabor (1982) discussed possible records of carnivores, pigs, and deer. Those inclusions were based on Günther's (1879: 74) quotation of Everett's notes: "It is a curious fact in regard to Dinagat that, whilst it is inhabited by Deer, Wild Pigs, Viverridae, *Galeopithecus*, *Sciurus*, and *Tarsius*, it possesses no Monkeys, though these abound in the Surigao peninsula." We exclude these three groups from our present list because no specimens representing them have been documented from Dinagat. Everett may have been referring to either *Paradoxurus hermaphroditus* or *Viverra zangalla* or both; the two species occur throughout the Philippines (Heaney et al., 1987). *Cervus mariannus* is likely the deer on Dinagat (Grubb and Groves, 1983; Heaney et al., 1987), and the pig—if truly wild and not feral *Sus scrofa*—is *Sus philippensis* (Groves, 1997).

We exclude from the list of native mammals the introduced *Rattus exulans* and *R. rattus mindanensis* (= *R. tanezumi*; see Musser and Carleton, 1993) reported by Heaney and Rabor (1982).

from the island of Dinagat (fig. 29; three species new to Dinagat have been added, thus modifying the lists given by Heaney and Rabor [1982] and Musser et al. [1985]). In 1985 (p. 19), Musser et al. wrote that Dinagat

... is typical of small islands that are separated from Mindanao by water less than 120 m deep and thus likely to have been connected to Mindanao during the late Pleistocene. Except for *Crateromys*, all of the genera from Dinagat are also known from Mindanao, and species richness is relatively high, as is typical for land-bridge islands (Heaney, ms [also see Heaney and Rabor, 1982: 28]). Dinagat, however, is unique among these small islands near Mindanao in not only having endemic species, but possessing three of them. We do not know why.

Reasons for this endemism on such a relatively small island still elude us. Nearby islands in the Greater Mindanao cluster, such as Samar and Leyte, for example, are larger but have no mammalian endemics. The very large Mindanao is the only other island in the immediate vicinity (Dinagat is 14 km north of Mindanao and separated from it by water only 64 m deep) that has a proportion of mammalian endemics comparable to that characterizing Dinagat. Relative species-compositions of different mammalian groups are also very similar on Dinagat and Mindanao (Heaney and Rabor, 1982: 28).

What is known about the geological and tectonic history of Dinagat offers no insight, at least at the present time, into the origin of its mammalian endemics. The Philippine Archipelago, as summarized by Hawkins et al. (1985: 460)

represents an evolving microcontinent formed by the amalgamation of many recognizable geologic terranes that include fragments of continental crust; island arc systems; oceanic crust from backarc basins, and, possibly, deep sea floor; and large tracts of depleted mantle peridotite. This tectonic collage has been overprinted by volcanic-plutonic arcs and by successor sedimentary basins. The ... Philippine Islands comprise diverse rock assemblages or terranes, formed at different geographic locations, which have undergone rotation as well as great lateral transport. ...

That basic historical perspective is current a decade later (Hall, 1996).

The geology of Dinagat is no less complex. It consists primarily of rocks derived from oceanic crust and upper mantle, which

are reflected on various geological maps as ultramafic rocks and ophiolite (Hamilton, 1979; Burton, 1986; Hawkins et al., 1985; Hutchison, 1989; Pubellier et al., 1991). Hawkins et al. (1985), who provide the best geological discussion of Dinagat, noted that the northern end of the island "has exposures of upper mantle and lower crustal rocks (gabbro-diabase) that constitute part of a classic ophiolite assemblage" (p. 451), and the southern part "has garnet amphibolite and other metabasites which ... probably were derived largely from cumulate mafic and ultramafic rocks from the basal crustal section of oceanic crust" (p. 451). They concluded "that much of this ophiolite represents disrupted fragments of an island arc terrane" (p. 451).

Interesting comments, but unenlightening from a zoogeographic perspective. Questions relative to understanding the origin of Dinagat's mammalian fauna remain unanswered. What did the island emerge from the sea? How often and at what times has it been isolated from the other islands or joined with them? Such information would help to explain the origin of Dinagat's mammalian endemics.

We close with the observation that two of the three Dinagat endemic species belong to a group that Musser and Heaney (1992) described as "Old Endemics." The old endemics, descendants of the earliest murine migrants to the Philippines, contrast to *Anonymomys*, the sole member of a second group, and to a third group of "New Endemics" (relatively recent arrivals), exemplified by *Rattus* and its allies. Furthermore, compared to the other species of *Crateromys*, the Dinagat *C. australis* retains more primitive traits (Musser et al., 1985). If small body size is primitive among species of *Batomys*, and if the complete cephalic arterial circulation characteristic of the small-bodied *B. russatus* is a retained ancestral complex, then it is the most primitive of any described *Batomys*. The possibility that *C. australis* and *B. russatus* are primitive relicts left on Dinagat deserves serious consideration in the context of attempting to understand the origins of Dinagat's mammalian fauna.

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