PHILIPPINE RODENTS: DEFINITIONS OF *TARSOMYS* AND *LIMNOMYS* PLUS A PRELIMINARY ASSESSMENT OF PHYLOGENETIC PATTERNS AMONG NATIVE PHILIPPINE MURINES (MURINAE, MURIDAE)

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ABSTRACT

Species of *Tarsomys* and *Limnomys* are found only on the island of Mindanao in the Philippine Archipelago. Both genera were named by Mearns in 1905 but never adequately diagnosed or described, a situation we rectify in this report. *Tarsomys* contains the type species, *T. apoensis,* which has been collected only from tropical lower and upper montane rain forest between 5200 and 7500 ft, and a new species, *T. echinatus,* known by a sample from tropical lowland evergreen rain forest between 2700 and 3700 ft. *Limnomys* is monotypic and the species *L. sibuanus* is represented by only five examples obtained from tropical montane rain forest between 6200–7200 and 9000 ft.

Among Philippine murines, the phylogenetic alliances of *Tarsomys* and *Limnomys* are with species of *Tryphomys, Abditomys, Bullimus,* and *Rattus.* These genera form one of three groups which reflect the broad outlines of a pattern of phylogenetic relationships estimated by us from a preliminary survey of primitive and derived character states among samples of native Philippine murine rodents, based primarily on study skins and skulls. Another group contains the species of *Phloeomys, Crateromys, Carpomys, Batomys, Apomys, Crunomys, Archboldomys, Chrotomys, Celaenomys,* and *Rhynchomys.* The final group holds only *Anonymomys mindorensis.* The relationships of *Tarsomys* and *Limnomys* to members within their group are unresolvable within the context of our study.

INTRODUCTION

During June of 1991, Mount Pinatubo, quiescent for at least 600 years, erupted in a vast cloud of swirling ash and molten rock that transformed day into night over the island of Luzon. Modern volcanic cataclysm mirrors past geological convulsions responsible for converting deep sea into vast archipelago, forming a new stage on which the beginnings of a unique evolutionary drama would be played out.

From its origin in the Early to Middle Tertiary (see the geological summaries presented by Heaney, 1986, 1991), the Philippines have grown into an archipelago of more than 7000 islands. Some are very small, others are huge; some are oceanic, others are fragments of islands that were much larger during Pleistocene times; a few had past connections to continental Asia. The interplay of climatological, geological, and evolutionary processes within such an expansive archipelago has resulted in an impressive mammalian fauna. More than 170 species have been recorded from the Archipelago; a few have been introduced, likely through intentional or inadvertent human activities; nearly 100 are endemic; and the rest are native to the Philippines and other nearby regions (Heaney et al., 1987).

The great diversity of species within the mammal fauna on the Philippines has not always been appreciated and we have come to know it only through the continuous efforts of explorers and scholars. Writing nearly a century ago, for example, Oldfield Thomas (1898: 377) explained that the

> Philippine Islands, however rich in birds, have always previously been looked upon as a group very poor in Mammals, especially in comparison with the rich faunas of the other islands of the East Indian Archipelago. This poverty was particularly evident in regard to really peculiar indigenous Mammals; for, with the exception of *Phloeomys cumingi,* scarcely a Mammal was known from the group other than members of widely-distributed genera, of which the Philippine species were either identical with or closely allied to Palawan, Bornean, or Celebean forms.

In that same report, Thomas went on to document the collecting efforts of Mr. John Whitehead, who had worked for much of three years on the island of Luzon. Cynical about expectations at first, Thomas (1898: 377) slipped into enthusiastic explanation:

> Little, therefore, could have been expected from the expedition further than the discovery of a few fresh species of genera known to inhabit the group, and this, so far as regards the islands other than Luzon, is just what has occurred. But in the great northern island of the group Mr. Whitehead has made a most wonderful and unexpected discovery, that of a new and peculiar Mammal-fauna inhabiting the Luzon highlands, and, so far as is yet known, mostly isolated on a small plateau on the top of Monte Data, in the centre of Northern Luzon, at an altitude of from 7000 to 8000 feet.

Out of the 15 species of mammals obtained by Whitehead, 12 were rodents; six of these had never been seen before by western naturalists and were named and described by Thomas in his report of 1898. During the years following Whitehead's discovery, new expeditions and many scholarly and not so scholarly publications revealed the presence of one of the most interesting and spectacular rodent faunas ever found. We now know that murid rodents of the subfamily Murinae (as defined by Carleton and Musser, 1984) make up approximately one-third of the mammal fauna native to the Philippines (excluding the Palawan group of islands) and consist of 18 genera and more than 40 species (table 8).

We continue here in that tradition of discovery and documentation by focusing on the definitions and descriptions of two genera and three species endemic to the island of Mindanao in the southern Philippines. *Tarsomys* and *Limnomys* were originally described by Mearns in 1905 as were the type species, *T. apoensis* and *L. sibuanus.* Because Mearns did not provide illuminating characterizations or illustrations and because members of other expeditions never caught additional material until later in this century, these distinctive rodents remained obscure members of the endemic Mindanao fauna.

Through documentation we transform the opaque view of the two genera into a translucent window on part of the Mindanao fauna in particular, and the Philippine rodents in general. Through discovery we expand our view of Philippine rodent diversity by describing a new species of *Tarsomys* based on a sample collected during the 1960s. Diagnoses, definitions, descriptions, and comparisons form a major segment of our report, but we also try to place the results in zoogeographic and evolutionary context by assessing possible phylogenetic relationships of *Tarsomys* and *Limnomys,* and explaining the significance of their insular and elevational distributions as part of the small flightless mammal fauna on Mindanao.

MATERIALS AND PROCEDURES

INSTITUTIONS AND SPECIMENS: The definitions and contents of *Tarsomys* and *Limnomys* which we document here, and the preliminary phylogenetic views of all the native Philippine murines that we present, are based on our study of specimens housed and cared for in the American Museum of Natural History, New York (AMNH); Delaware Museum of Natural History, Wilmington (DMNH); Field Museum of Natural History, Chicago (FMNH); Florida Museum of Natural History, Gainesville (FSM); University of Minnesota, Bell Museum of Natural History, Minneapolis (MMNH); and National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Specimens we refer to by museum catalog number in the text are preceded by one of these acronyms.

The morphological traits of *Tarsomys* and *Limnomys* we describe and illustrate are associated with standard museum preparations: a stuffed skin and an accompanying cranium and mandible. Only one specimen, the holotype of *Tarsomys apoensis,* is stored in 70% ethanol; the skull has been removed and cleaned.

All the examples of *Tarsomys* and *Limnomys* were collected over a period of 60 years, between 1904 and 1964. They are the only source of information we have about these animals. Neither one of us has seen live examples of the species or trapped them in their native habitats.

COLLECTION DATA: Dates of capture, trapping localities and elevations (whether in meters or feet), and names and field numbers of collectors come from labels attached to specimens. If additional information exists elsewhere—in field journals, for example—we have been unable to locate it. Without such supplemental data, we cannot provide descriptions of the major forest formations or microhabitats in which the animals were encountered. Even our knowledge of the provenances of the specimens is inadequate. Locality data on the skin tags indicate only general designations of region; the name of a mountain is noted, sometimes a secondary locale. Elevations are just as imprecise. For example, most of the specimens in DMNH and FMNH that were collected by Rabor's teams have only an elevational range recorded (5200–7000 ft, for example, for the series of *Tarsomys apoensis* obtained from Mount Malindang) and it is impossible without further information to identify a more precise elevation at which any particular specimen was trapped.

AGE CATEGORIES: We could consistently separate specimens into one of five age groups.

- OA, old adult: body size among the largest in a sample; clothed in full adult pelage; molars worn nearly to tops of roots so cusps are obliterated or nearly so, the crowns featureless and worn into shallow basins in some specimens.
- A, adult: body size among largest in a sample; covered in full adult pelage; molars worn, moderately so in some individuals, excessively in others (fig. 13C, D, for example); occlusal surfaces retain distinct pattern of laminae and major cusps but their enamel margins are worn low so that dentine is broadly exposed and some laminae and cusps have coalesced at labial and lingual margins; labial cusplets have nearly lost their identities.
- YA, young adult: body size usually smaller than adults or older individuals; covered in fresh adult fur; molars slightly worn; enamel borders of laminae and cusps much higher than enclosed dentine, which has a restricted exposure; laminae, cusps, and labial cusplets are discrete, either not coalesced or only slightly so (similar to molar rows in fig. 12A, B).
- J-A, juvenile-adult: all molars erupted and slightly worn; clothed mostly in juvenile fur that conceals replacement hairs of partially proliferated adult coat; older specimens retain juvenile pelage along back and rump but possess fresh adult fur on venter and sides of the body.
- J, juvenile: body size among smallest in a sample; clothed in juvenile fur, which is easily recognizable compared to adult pelage; upper and lower third molars unerupted or if erupted, usually unworn (fig. 13A, B).

These age clusters are unequally represented in our material. Because our samples are small, we combined old adults with adults to obtain summary statistics for particular samples of the two species of *Tarsomys*. In tables 1 and 6 we also list measurements from a "very young adult," which is in full adult pelage, and larger than juveniles but smaller than young adults.

SECONDARY SEXUAL VARIATION: We did not attempt to separate males and females in any analysis comparing means of external, cranial, and dental measurements. Our samples are simply too small. Inquiry into this aspect of morphological variation among each of the species awaits the acquisition of larger series.

MEASUREMENTS: Values for total length, length of tail (LT), length of ear (LE), and body weight (BW) were obtained directly from tags attached to stuffed skins. We subtracted length of tail from total length to get a value for length of head and body (LHB). Musser measured length of hind foot, including claws (LHF) of each specimen as well as ear length (from the notch) of the holotype of *Tarsomys apoensis.* He counted the number of scale rings per centimeter (TSR/cm) on the tail of each rat about one-third the distance from its base. To measure lengths of the overfur (LOF) and guard hairs (LGH) on each individual, he placed a ruler at a right angle to the skin surface and recorded the approximate mark where ends of the bunched hairs rested; the technique is primitive and the results imprecise, but he obtained a descriptive estimate of lengths for those pelage constituents.

Using dial calipers graduated to tenths of millimeters, Musser took the cranial and dental measurements listed below (they are arranged in tables in the sequence listed below).

GLS	greatest length of skull (occipitonasal length)
ZB	zygomatic breadth
IB	interorbital breadth
LR	length of rostrum
BR	breadth of rostrum
BZP	breadth of zygomatic plate
DZN	depth of zygomatic notch
BBC	breadth of braincase
HBC	height of braincase
LD	length of diastema
PPL	postpalatal length
LIF	length of incisive foramina
BIF	breadth across incisive foramina
LBP	length of bony palate
BBPM1	breadth of bony palate at first molar
BMF	breadth of mesopterygoid fossa
LB	length of bulla
CLM1–3	crown length of maxillary molar row
clm1–3	crown length of mandibular molar row
BM1	breadth of first upper molar
BUI	mediolateral breadth of upper incisor
DUI	anteroposterior breadth of upper incisor

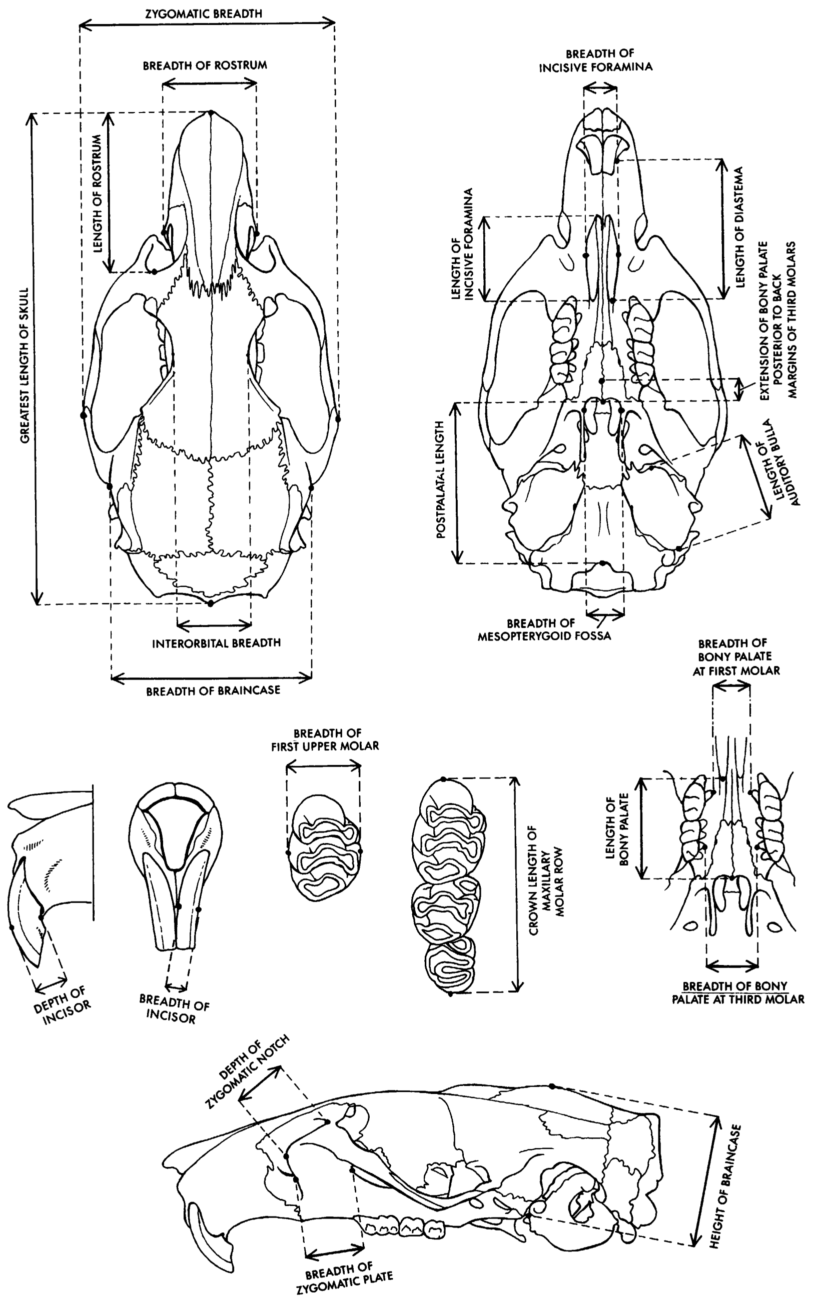

Fig. 1. Schematic views of cranium, molars, and incisors of an adult *Rattus hoffmanni* showing limits of cranial and dental measurements. See the materials and procedures section for abbreviations of the measurements and other information.

Values of these measurements are given in millimeters. Their limits are illustrated in figure 1 and all but the last two are defined by Musser and Newcomb (1983). Musser measured breadth of the left upper incisor from the medial to the lateral surface, and the depth from the anterior face to the posterior margin, as shown in figure 1.

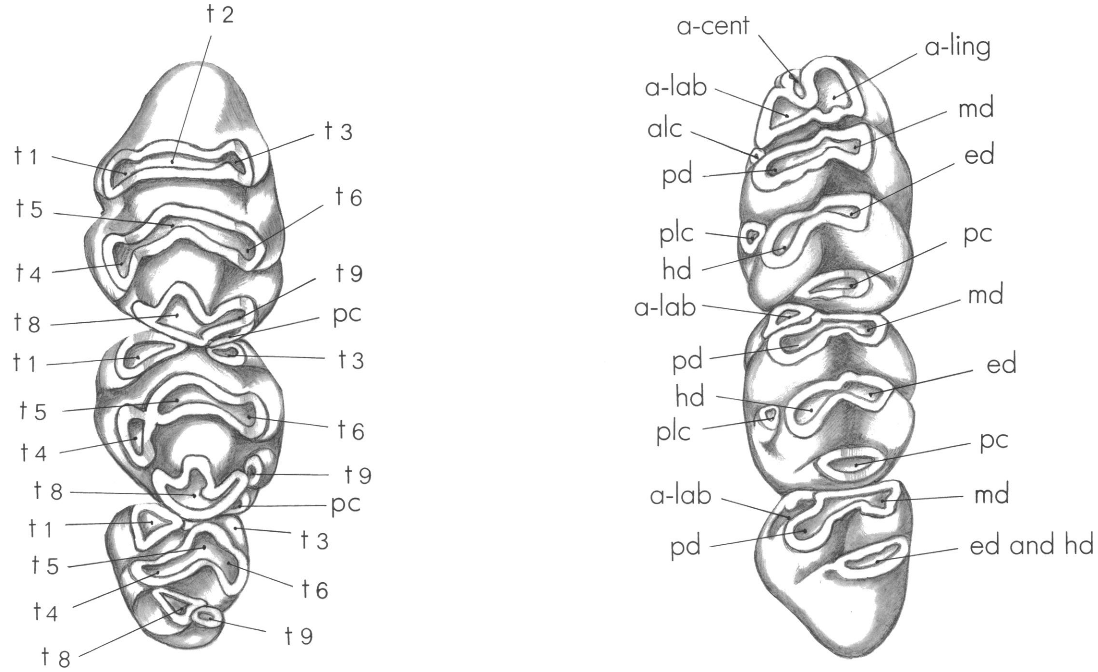

Fig. 2. Diagram of upper (left) and lower (right) molars from left side of *Limnomys sibuanus* illustrating structural terms. Upper molars: cusps are numbered according to Miller's (1912) scheme and referred to in the text with the prefix t; **pc,** posterior cingulum. Cusps t1, t2, and t3 form the anterocone. Lower molars: **a-cent,** anterocentral cusp; **a-lab,** anterolabial cusp; **a-ling,** anterolingual cusp; **hd,** hypoconid; **md,** metaconid; **ed,** entoconid; **pc,** posterior cingulum; **pd,** protoconid; **alc,** anterior labial cusplet; **plc,** posterior labial cusplet. The anterocentral, anterolabial, and anterolingual cusps form the anteroconid.

ANATOMICAL DESCRIPTION AND TERMINOLOGY: Much of our report presents the integument and pelage features, cranial morphology, and dental traits of endemic Philippine murids about which very little is known. We expose these qualities of the species by tabular quantitative data, ratio diagrams, illustrations, and narrative descriptions. The descriptive and illustrative detail is necessary and the documentation important for appreciating not only diagnostic traits of the taxa but for identifying and defining characters which will be used in phylogenetic analyses. In the descriptions, we have tried to employ clearly defined standard terms. For some external features of the head and limbs, we use the terminology defined in Brown (1971) and Brown and Yalden (1973). Wool hairs and awns are terms used by Voss (1988), which we also employ here. Terminology of cephalic arteries derives from Bugge (1970, 1985), of cranial foramina from Wahlert (1974, 1985), and of muroid cranial features from Musser and Newcomb (1983), Carleton and Musser (1984), and Voss (1988). The names we use throughout the text that designate cusps and cusplets of upper and lower molars are presented in figure 2; the sources of this terminology are explained by Musser and Newcomb (1983: 332).

RATIO DIAGRAMS: Proportional relationships among species are illustrated by ratio diagrams (figs. 14, 15). Simpson (1941) described the method for constructing these kinds of figures but ours require additional explanation. For each measurement, the absolute values of the mean and plus or minus two standard errors of the mean were converted to logarithms. For each dimension, the logarithm of the mean of the standard (*Rattus rattus* in each diagram) was subtracted from the logarithm of the mean of each sample to be compared with the standard, and the logarithms of plus or minus two standard errors of the mean of the standard were subtracted from the logarithms of plus or minus two standard errors of the mean of each comparative sample. Measurements larger than the standard are represented on the diagram by positive values, those smaller by negative values. In each sample, the solid or dashed lines connect the means of measurements, the horizontal bars or broken lines represent plus or minus two standard errors of the mean. A sample with 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 (for example, length and breadth of rostrum and breadth of zygomatic plate of *T. echinatus,* n. sp. as compared with the standard, *R. rattus,* in fig. 14). Also, if values for the samples being compared with the standard are similar in absolute size, but differ proportionally, 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.

SEM MICROGRAPHS: Micrographs of molar rows were obtained from specimens uncoated and unaltered before they were placed in the chamber of the scanning electron microscope.

STATISTICS: We calculated the mean, standard deviation, standard error, and recorded the range of measurement values for each sample. We tested the significance of the difference between two sample means by a Student's *t*-test. Wherever we refer to the difference between sample means as being significant, we are rejecting the null hypothesis using the .05 level of significance for the *t*-test.

MAPS: The localities from which specimens were obtained are indicated on the map in figure 4. It is adapted from a map of the Philippine islands (1:1,500,000) prepared under the direction of the chief of engineers, Army Map Service (AM), U.S. Army, Washington, D.C., published in 1944; and Operational Navigation Charts (1:1,000,000) published by the Defense Mapping Agency Aerospace Center, St. Louis. An approximation of the 120-m bathymetric line (stippled area) outlines islands in the Philippine Archipelago in figure 3. That line 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; that of the other maps varies from 1:20,000 to 1:402,000. Figure 3 is modified from figure 16 in Heaney (1985: 54).

Mindanao features mountain ranges and volcanos dissected by valleys. This rugged topography, a background to evolutionary diversity and present distributions of the island's endemic murines, can be visualized from the excellent terrain map featured in King and McKee (1949).

ACKNOWLEDGMENTS

Access to the institutional collections we listed earlier and the ability to borrow specimens, some of which were kept at the American Museum for very long periods, were critical to obtaining the results presented here. We are extremely grateful to the curators and museum staff who allowed us to use the collections under their care and loaned us material.

Sydney Anderson developed a computer program to convert the absolute values from our measurements into logarithms and generate the data in a form that could be plotted in the ratio diagrams. We thank him for this generous contribution to our project. Tim Flannery, Thomas A. Griffiths, Mary Ellen Holden, and Eric Rickart also contributed to the final version of our report by providing critical reviews; we appreciate their interest in our work and their time, which came at the expense of their own research endeavors. Heaney's work in the Philippines has been financed by National Science Foundation Grant BSR-8514223 and the MacArthur Foundation. We are also grateful to Carlo Custodio, Wilbur Dee, Pedro Gonzales, and Ruth Utzurrum for their continuing cooperation and support.

The maps (figs. 3, 4) and diagrams (figs. 14, 15, and 74) were drawn by Ilil Arbel. Patricia Wynne is responsible for the drawings of head skeletons, teeth, and arterial patterns (figs. 1, 2, 36, 46, 49, 50, 55, 56, and 59). All the photographs of skulls and teeth were prepared by Peter Goldberg. The talent,

careful attention to detail, and artistic skills of these illustrators helped us convey results not easily documented or explained by words or lists of measurements.

DEFINITION OF *TARSOMYS*

"Related to *Mus, Apomys,* and *Batomys.* General external appearance similar to *Sigmodon,*" was the introduction to Edgar A. Mearns's (1905: 453) characterization of the new genus *Tarsomys,* "TUBERCULATE-SOLED RATS" which Mearns knew by one animal he had collected from Mount Apo at 6750 ft, July 5, 1904, on Mindanao, the large southern island in the Philippine Archipelago (figs. 3, 4). Mearns continued his description of *Tarsomys* by enumerating its characters:

> Pelage long and rather coarse, but not spiny, with hair of two lengths, the overhair being about twice the length of the ordinary coat. Ear rather prominent, its height from crown nearly one-third the length of head; skin of ear roughened and coated on both surfaces with short, thick hairs. Whiskers long, surpassing the ears. Eyes of medium size. Feet naked below; fore feet 5-tuberculate; hind feet 6-tuberculate, those at base of inner and outer digits 2-lobed, and with several small additional tubercles. Tail hairy. Skull and teeth resembling those of *Batomys* Thomas, but relatively broader, with a more inflated braincase, and large vacuities above the auditory meatus. The lateral teeth are extremely oblique in their position, the upper being rotated outward and the lower correspondingly rotated inward. The anterior upper molar resembles that of *Mus,* differing in that the anterior series comprises but two cusps, a small inner and a large outer one.

Mearns described the single specimen under the name *Tarsomys apoensis,* the sole species in the genus. If the uniqueness of this Mindanao endemic was clear to him he certainly did not convey that impression in his published report. Descriptions of the genus and species are without diagnoses. The characterizations are imprecise and too general for distinguishing either taxon from that of many other genera and species containing dark-furred rats of medium body size. The few comparisons made between *Tarsomys* and either *Mus, Apomys, Batomys,* or *Sigmodon* are largely irrelevant and provide no aid in discriminating the new taxa. This vaporous presentation could have been partially clarified by illustrations but none were provided, leaving readers without a clear image of *Tarsomys apoensis* and no clue to its closest relatives.

References to *Tarsomys apoensis* in the scientific literature published subsequent to Mearns's description have provided no new information about either the genus or the species, and in particular instances have even intensified the opaqueness of an already murky image of its phylogenetic relationships. The early and more recent checklists and faunal surveys of Philippine mammals in which *Tarsomys apoensis* is listed as part of the Mindanao fauna are without diagnostic or new descriptive data about the rat itself (Hollister, 1913; Taylor, 1934; Alcasid, 1970; Musser, 1981b; Carleton and Musser, 1984; Heaney et al., 1987; Corbet and Hill, 1986). Authors of these publications actually looked at specimens of *Tarsomys.* Authors of other checklists or phylogenetic studies which include the species either expressed serious reservations about the distinction of *Tarsomys* relative to the genus *Rattus* (Ellerman, 1941) or listed *apoensis* as a species of *Rattus* (Simpson, 1945; Misonne, 1969). No evidence indicates that any of these researchers examined specimens of *Tarsomys apoensis.*

Between 1904, when the description of the holotype was published, and now, 13 additional specimens have been collected. Study of this material allows us to provide a clear diagnosis and description of *Tarsomys apoensis* and to identify its possible closest relatives, critical information not found in Mearns's original documentation.

Identifying the morphological and geographic characteristics of *Tarsomys apoensis* is important because these features need to be contrasted with those of other species of murines endemic to Mindanao and possibly closely related to *T. apoensis.* One of these is undescribed and shares certain features with *T. apoensis,* traits which we suggest place it in the same genus. In the following text, we diagnose the genus *Tarsomys*; redescribe the species *Tarsomys apoensis*; compare it with relevant species in other genera, particularly *Rattus*; and finally name and describe the new species, comparing its characteristics with those of *T. apoensis.*

TARSOMYS MEARNS

TYPE SPECIES: *Tarsomys apoensis* Mearns (1905: 453).

INCLUDED SPECIES: *Tarsomys apoensis* and *T. echinatus,* new species.

KNOWN DISTRIBUTION: Mountains on the island of Mindanao in the Philippine Archipelago (figs. 3, 4, localities 1–4).

ETYMOLOGY: Mearns combined the Greek *tarsos,* meaning "flat of the foot between toes and heel" (Brown, 1956: 782), with *mys,* the Greek for rat or mouse. He was impressed by the number of accessory plantar tubercles on the holotype.

DIAGNOSIS: A genus of murine rodent characterized by the following combination of traits: (1) body size moderate, tail shorter than head and body, hind feet long and slender with the basic six plantar pads and sometimes small accessory tubercles; (2) claws elongate and robust, those on front feet longest; (3) fur either short and spiny or long and soft, the dorsal coat either brownish gray or rich dark chestnut, the ventral fur either grayish white or dark buffy brown, the appendages either tan, unpigmented, or dark brown, the tail monocolored; (4) six mammae (one postaxillary pair and two inguinal pairs); (5) rostrum moderately long to elongate; (6) hourglass-shaped interorbit with slightly beaded or smooth edges, postorbital and temporal ridges weakly defined; (7) wide zygomatic plate and moderately deep notch; (8) long incisive foramina which project between anterior margins of first molars; long bony palate extending appreciably beyond posterior margins of third molars, and either moderately or very wide; (9) pterygoid fossae shallow to moderately excavated; (10) large sphenopterygoid and sphenopalatine vacuities; (11) groove in pterygoid plate for infraorbital branch of stapedial artery and large stapedial foramen, two traits reflecting the primitive murine cephalic arterial pattern; (12) alisphenoid strut absent; (13) auditory bulla moderately inflated; (14) dentary with delicate coronoid process and deeply concave posterior border; (15) incisors without grooves, uppers either orthodont or opisthodont, slim to wide; (16) molar teeth chunky and either hypsodont or brachyodont, each first upper molar anchored by five roots, each second molar by four, the third by three, each first lower molar with four roots, each second and third molar with three; (17) cuspidate topography of molars in juveniles changing quickly with age into rows of simple arcuate or transverse lamina, cusp t3 on each first molar almost completely merged with cusp t2, cusp t3 on each second and third molar either absent or very small, cusp t7 and posterior cingulum absent from all upper teeth, small anterocentral cusp in some specimens, anterior labial cusplet absent from each first lower molar.

DESCRIPTION: Our elucidation of *Tarsomys* is embodied in the following description and definition of *T. apoensis,* comparisons between it and other taxa, and the diagnosis and description of the new species of *Tarsomys.*

TARSOMYS APOENSIS MEARNS

HOLOTYPE: USNM 125280, an adult male collected by Edgar A. Mearns (original number 5706) from Mount Apo (locality 4 on the map in fig. 4) at 6750 ft, Davao City Province, southern Mindanao on July 5, 1904. The animal was originally preserved in fluid (probably either formalin or ethanol) and is now stored in a 70% solution of ethanol and water. The cranium and mandible were removed (presumably in 1904 because Mearns provided values of various craniodental measurements) and cleaned. The head skeleton is intact and all teeth are present. The body seems to have been well-preserved initially for it is in excellent condition except for a midabdominal slit. Measurements of the holotype are listed in table 1.

REFERRED SPECIMENS AND LOCALITIES: In addition to the holotype, we know of 13 other examples of *T. apoensis* caught on the mountains of Mindanao. They are listed below within each numbered locality; that number corresponds to the numbered symbol on the map in figure 4.

1. Misamis Oriental Province, Summit of Mount Bliss, 5750 ft (a peak in the vicinity

of Mount Malindang whose location is unknown to us): USNM 144616 (adult female) and 144617 (very young adult female). Both examples were caught on May 28, 1906.

2. Misamis Oriental Province, Mount Malindang: Mutia, 5200–d7000 ft (DMNH 5968, adult male; 5969, adult female; 5998, adult male; 5999, adult female; 6000, young adult female; caught January 4–14, 1963); Duminagat, 5200 ft (FMNH 87594, young adult male; caught April 24, 1956); Dapitan Peak, 7450 ft (FMNH 87595, old adult male; caught May 1, 1956); 6100 ft (USNM 144618, old adult female; 144619, old adult female; caught June 2 and 3, 1906).

3. Bukidnon Province, Mount Katanglad, Malaybalay, 6000 ft: FMNH 92802 (old adult female; caught April 21, 1960).

4. Davao City Province, Mount Apo, east slope, 7500 ft: FMNH 61486 (juvenile male; caught November 19, 1946).

DISTRIBUTION: *Tarsomys apoensis* has been collected from four mountains on the island of Mindanao. The known altitudinal range, as represented by museum series, is from 5200 to 7500 ft. These elevations fall within what has been described generally as mountain and mossy forests (Hoogstraal, 1951) or more precisely as tropical lower and upper montane rain forest formations (Whitmore, 1984a).

ETYMOLOGY: Mearns knew *Tarsomys* by the single specimen he had collected from Mount Apo. It was for this mountain that he named the species *apoensis*.

DIAGNOSIS: *Tarsomys apoensis* is distinguished from other species of murine rodents by the following cluster of traits: (1) medium body size; (2) monocolored, short tail that is much shorter than combined lengths of head and body; (3) dark, long, and moderately soft pelage with soft and flexible awns in the overfur; (4) long, curved, and sharp claws on digits of front feet; (5) long and slender rostrum; (6) horizontal or slightly dorsally elevated nasal tips; (7) smooth, unridged dorsolateral interorbital margins, weakly defined postorbital and temporal ridges; (8) wide zygomatic plate with sloping anterior spine; (9) no alisphenoid strut; (10) wide and long incisive foramina; (11) very wide and long bony palate that projects as a shelf far beyond molar rows; (12) shallow pterygoid fossa; (13) spacious sphenopalatine and sphenopterygoid vacuities; (14) small coronoid process on dentary; (15) slim incisors; (16) multirooted, hypsodont molar teeth; (17) molars with simple cusp patterns (cusp t3 frequently absent from each second and third upper molar, posterior cingula not present on uppers, cusp t7 absent from any upper molar, anterior labial cusplet absent from each first lower molar).

DESCRIPTION: *Tarsomys apoensis* adults are dark chestnut, of medium body size, with a moderately long face, short tail, and elongate hind feet (fig. 5). Upperparts of head and body are covered with a brownish chestnut coat; underparts are dark brown washed with buff. Dense, long (up to 18 mm), and soft, the dorsal coat is composed of two layers and three kinds of hairs. Soft, filamentous wool hairs form the underfur. Each hair is dark gray for most of its length and has a subterminal dark brown band and a buff tip. Most hairs of the overfur, awns as Voss (1988) calls them, are longer and stouter versions of the finer wool hairs. Each is dark gray along two-thirds of its length and ends in a wide subterminal dark brown band and buffy tip. The dark brown bands of awns and wool hairs combined with the glistening buffy tips impart the rich lustrous chestnut to the dorsal coat. Scattered among the soft and slender awns are stouter and less flexible awns which provide a slightly harsh resistance when the fur is brushed back. These hairs are thinner, softer and inconspicuous in the fur of some specimens but stronger and more rigid in others. Thick glossy blackish brown guard hairs (some with silver tips) extend 5–10 mm beyond the overfur and contribute their glistening black to the dark cast of the pelage.

The soft and short ventral fur is composed of wool hairs in the underfur and awns in the overfur. Both kinds of hairs are dark gray for most of their lengths; some are tipped with buff, others have a wide subterminal dark brown band and a terminal buff band, and others are tipped with a wide belt of dark brown. The total effect is always a dark coat, but the variation ranges from specimens with dark gray fur washed with buff to coats that are dark brown with buffy highlights and a dark gray suffusion. No sharp demarcation divides tone of the dorsal coat from that of the ventral fur. No trace of any color pattern

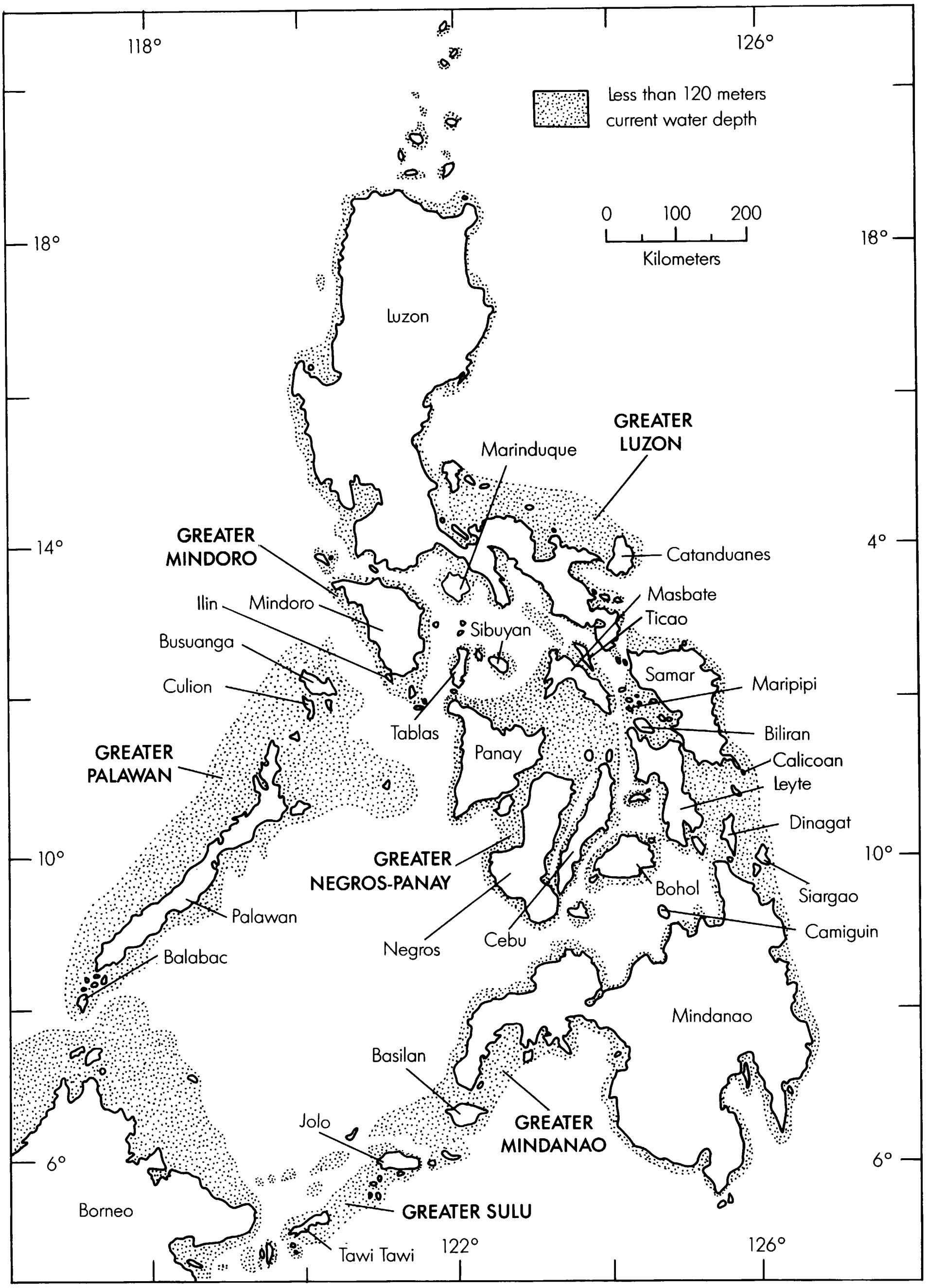

Fig. 3. The Philippine islands. The stippled area shows the extent of each of the late Pleistocene islands (Greater Luzon, Greater Mindoro, Greater Palawan, Greater Negros-Panay, Greater Mindanao, and Greater Sulu); their limits are based on the current 120 m bathymetric.

(facial mask, for example) breaks up the brownish chestnut of the upperparts.

Mystacial, submental, superciliary, genal, and interramal vibrissae project from the fur covering the head. Submental and interramal vibrissae are unpigmented, and so are dis-

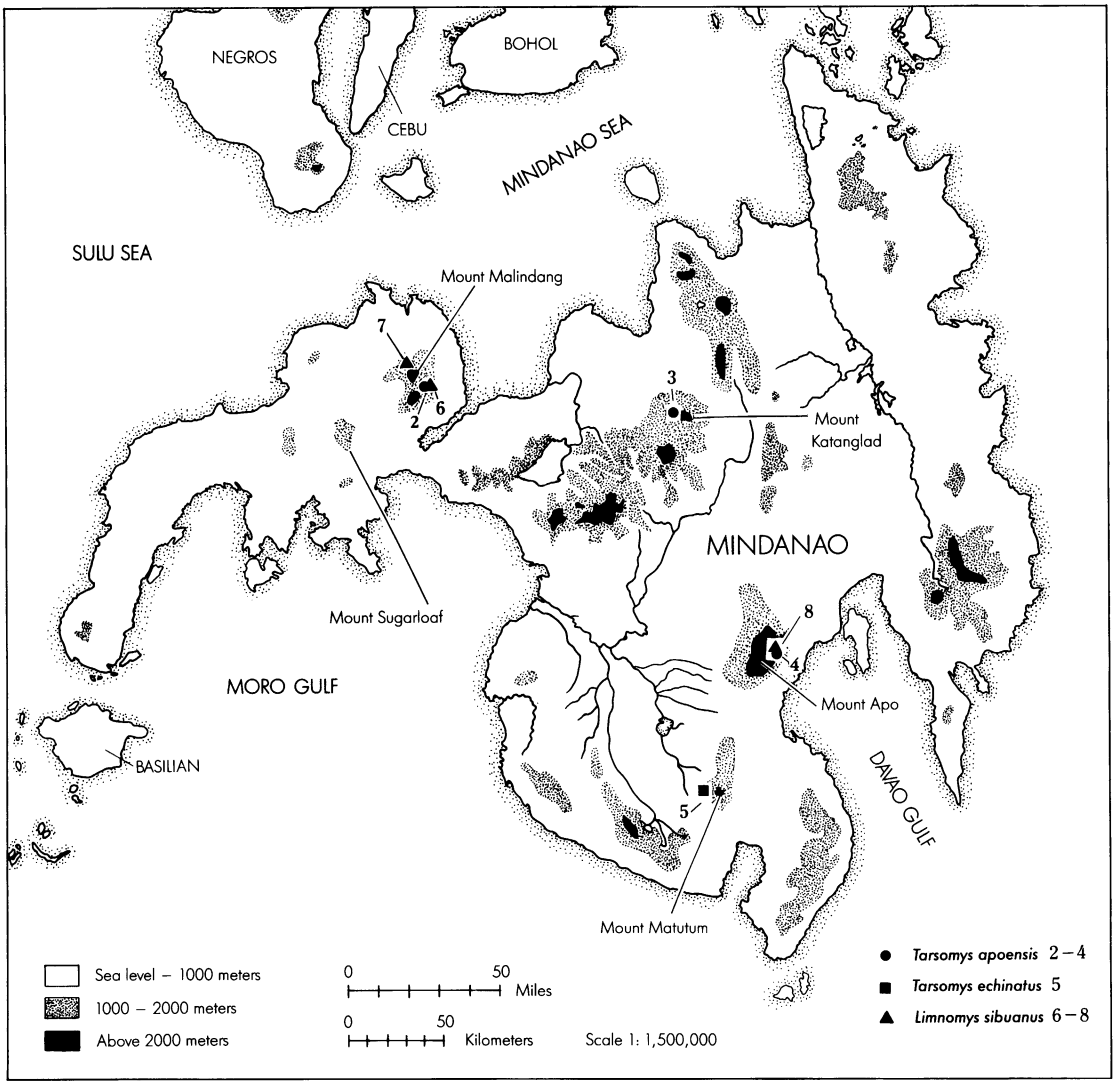

Fig. 4. Geographic and altitudinal distributions of *Tarsomys apoensis, T. echinatus,* and *Limnomys sibuanus* on Mindanao; based on all known samples of the species. Mount Bliss (locality 1 in text), which is in the vicinity of Mount Malindang, but whose actual location is unknown to us, is not indicated on the map.

tinct against the dark brown fur. The other vibrissae are usually a glistening brownish black, although some lack pigment.

The ears are moderate in size relative to dimensions of the head. They are dark brown and both surfaces of the pinnae are densely covered with short dark hairs.

Our knowledge of juvenile pelage is based on FMNH 61486, the only example of the species we have seen with a full juvenile coat. The fur is dense, as it is in the adult coat, but shorter, and much softer. The wool hairs in the underfur form the primary component of the coat and give it a wooly appearance and a silky softness to the touch. The dorsal fur is darker than that of the adult, with flatter tones and more gray in the pelage; the ventral fur is dark gray.

Number of teats is invariate in the small sample of adult females we studied. Each

Fig. 5. An adult female *Tarsomys apoensis* (USNM 144616). Measurements are listed in table 1.

specimen has six teats: one postaxillary pair and two inguinal pairs.

The tail of *T. apoensis* is shorter than combined lengths of head and body (table 1; fig. 5). It is dark brown on all surfaces. Three hairs emerge from the base of each epidermal tail scale, and the scales are small (12–16 overlapping rings of scales per centimeter on adults; table 1). Each hair covers about two scales so their length and distribution impart a short-haired rather than a naked appearance to the tail.

Dorsal epidermal scales and palmar integument of the front feet are brown. Metacarpal surfaces are covered with brown and silver hairs, and silver hairs extend along digits to bases of the claws where they form short tufts. The moundlike pollex supports a wide nail; the other digits end in stout, long, and curved claws. The topography of each palmar surface is formed mostly of three small interdigital mounds and two large metacarpal pads; the conformation is not unlike that illustrated for *Bunomys prolatus* (Musser, 1991: 10, fig. 4).

Hind feet of *T. apoensis* are long and narrow. Their dorsal surfaces, including the epidermal scales, are brown and covered by brown and silver hairs; plantar surfaces are brown, and the pads and heels are blackish. Claws are robust, long, curved, and sharp. The hallux is short and just reaches bases of the three medial digits. The fifth digit is relatively longer, extending to about the level where the second and third phalanges of the fourth digit meet. Relative lengths of the digits resemble the configuration in *Bunomys prolatus* (Musser, 1991: 10, fig. 4).

Each specimen of *T. apoensis* we examined has an array of plantar pads which includes four large interdigital mounds, a large and elongate thenar pad, and a small and oblong hypothenar. Their sizes and shapes resemble, again, the pads of *Bunomys prolatus* illustrated by Musser (1991: 10, fig. 4). Four large interdigital pads, a thenar mound that is either similar in size and shape to the interdigitals (as in the arboreal species of *Margaretamys*, for example, which are illustrated in Musser, 1981a: 279, fig. 27) or much narrower and elongate (as in some terrestrial species such as *Sundamys* and *Berylmys*, as shown in Musser and Newcomb, 1983: 357, fig. 15, or *Maxomys*, figured in Musser, 1991: 27, fig. 13), and a hypothenar that is usually smaller than any of the other mounds is the usual array of plantar pads in most species of murine rodents. Loss of a pad, nearly always the hypothenar (as in some samples of *Maxomys musschenbroekii*; see Musser, 1991: 27, fig. 13) is a specialization that is infrequently encountered among murines.

Multiplication of pads is also a specialization, and it was this feature that so impressed Mearns (1905) he named the genus *Tarsomys* to signal what must have been to him a special configuration ("hind feet 6-tuberculate, those at base of inner and outer digits 2-lobed, and with several small additional tubercles," p. 453). In his characterization of *T. apoensis*, the "APO TUBERCULATE-SOLED RAT," Mearns wrote:

> Hind foot with double-lobed tubercles at the base of the inner and outer digits, small rounded tubercles at the junction of the second and third and third and fourth digits, a small rounded one near the outer margin of the naked sole anteriorly, and an elongated one near the inner margin posteriorly. There are also several additional tubercles of minute size, notably one or two behind the posteroexternal one.

Mearns had described the basic six plantar mounds on which is imposed a pattern of smaller accessory lobes, and the holotype reflects his observations. What Mearns described as a double-lobed tubercle at the base of either the hallux or fifth digit is really an interdigital mound to which is attached a smaller accessory tubercle. Additional small tubercles next to interdigitals are commonly found among southeast Asian murines. Examples are *Niviventer cremoriventer* and *Rattus rattus* (Musser, 1973: 7, fig. 1), *Sundamys muelleri* (Musser and Newcomb, 1983: 357, fig. 15), *Chiropodomys gliroides* (Musser, 1979: 433, fig. 13), *Rattus exulans* (Musser, 1982b: 21, fig. 7), and *Niviventer cameroni* and *Leopoldamys edwardsi* (Medway and Yong, 1976: pls. 3 and 4). Of the 13 dry skins of *T. apoensis* we examined, nine lacked auxiliary tubercles next to the interdigital pads and four specimens had them. Mearns noted other minute tubercles on the holotype. Whether or not such pimple-sized mounds are present on the rest of the specimens is difficult to determine because the feet are dry and any tiny pads would be obscured in the dry folds of skin.

Dorsal, ventral, and lateral cranial views of *T. apoensis* are shown in figure 6; lateral and ventral regions are enlarged in figure 8. General conformations of cranium and dentary are evident from those illustrations; salient details to be pointed out begin with the rostrum, which is moderately long and slender. Margins of premaxillaries forming the anterior extension of the rostrum barely project beyond front faces of upper incisors. The nasals, which form the roof of the rostrum, have an oblanceolate outline and extend beyond the anterior premaxillary borders. Their dorsal surfaces follow the dorsal profile of the cranium to a point about halfway between zygomatic plate and nasal aperture where they depart from the dorsal curvature and become horizontal in some specimens or extend slightly dorsad in others, a configuration best appreciated in lateral view (fig. 6). This deflection of nasal tips from the low convex profile into a horizontal or dorsal projecting plane may result in a wider nasal aperture than would be the case in species where the nasal tips conformed to the dorsal profile, as in *Rattus rattus*, for example (fig. 7). The taper of the rostrum, as seen from dorsal perspective, is interrupted by prominent nasolacrimal capsules. The ventral rostral surface is incised by long and wide foramina. They extend slightly beyond anterior faces of the first molars in all the specimens we have seen (table 2).

In contrast to the slender zygomatic arches, each zygomatic plate appears robust with expansive medial and lateral surfaces, partly a reflection of the zygomatic spine which projects far enough anteriorly from the dorsal zygomatic root to form a moderately deep notch (table 1), as seen in dorsal view. The dorsoanterior margin of the spine forms a convex outline from dorsal to ventral zygomatic roots, a configuration evident in lateral view (fig. 6) and distinct compared to the shape in species such as *Rattus rattus* where the spine is developed into a shoulder and concave front edge (fig. 7).

Behind the zygomatic plates, the interorbital region is shaped like an hourglass and broad (table 1), especially in relation to length of skull (fig. 14). It is distinctive in that its borders are smooth and beveled, not outlined by beading or ridges. Slight beading, however, does delimit frontal margins in the postorbital region, and persists about halfway along dorsolateral borders of the braincase.

TABLE 1

Measurements (mm) and Body Weight (g) of Old Adult (OA), Adult (A), Young Adult (YA), and Very Young Adult (VYA) *Tarsomys apoensis*

(From Mount Apo (6750 ft), Mount Katanglad (6000 ft), Mount Malindang (5200–7450 ft), and Mount Bliss (5750 ft) on the Island of Mindanao.) (The mean plus or minus one standard deviation, number of specimens in parentheses, and range are provided for each measurement.)

	Mt. Apo	Mt. Katanglad	Mt. Malindang			Mt. Bliss	
	Holotype USNM 125280	FMNH 92802	DMNH 5968, 5959 5998, 5999; FMNH 87595; USNM 144618, 144619	DMNH 6000	FMNH 87594	USNM 144616	USNM 144617
Age	A	OA	OA AND A	VYA	YA	A	VYA
LHB	135	–	148.0 ± 8.02 (6) 136–156	112	–	140	116
LT	120	–	128.0 ± 7.77 (6) 116–138	108	–	127	115
TSR/cm	12	12	14.5 ± 1.05 (6) 13–16	15	15	14	15
LHF	30	32	31.6 ± 1.13 (7) 30–33	30	32	31	30
LE	20	–	22.5 ± 0.58 (4) 22–23	18	–	–	–
LOF	18	18	16.2 ± 1.47 (6) 15–18	10	13	14	14
LGH	30	23	25.8 ± 4.92 (6) 20–35	20	18	20	20
BW	–	–	75 (1)	–	–	–	–
GLS	37.3	38.5	39.7 ± 1.01 (5) 38.6–41.1	–	–	39.3	–
ZB	17.5	18.3	19.0 ± 0.38 (4) 18.5–19.3	–	18.5	39.3	16.5
IB	5.6	6.0	6.0 ± 0.17 (6) 5.8–6.3	–	5.8	5.9	5.7
LR	12.5	14.3	13.5 ± 1.00 (6) 12.8–15.4	–	–	14.5	–
BR	6.8	–	6.7 ± 0.21 (5) 6.4–6.9	–	6.3	6.8	–
BZP	3.6	4.3	4.1 ± 0.24 (6) 3.8–4.4	–	3.6	4.3	3.5
DZN	1.8	2.1	2.1 ± 0.31 (6) 1.8–2.5	–	2.1	2.3	–
BBC	15.7	15.8	16.3 ± 0.33 (5) 15.8–16.6	–	16.5	16.0	13.9
HBC	10.6	10.5	10.5 ± 0.39 (5) 10.0–11.1	–	11.1	11.0	8.8
LD	9.7	10.2	11.3 ± 0.33 (6) 10.8–11.7	–	9.9	11.3	–

TABLE 1—(*Continued*)

	Mt. Apo	Mt. Katanglad	Mt. Malindang			Mt. Bliss	
	Holotype USNM 125280	FMNH 92802	DMNH 5968, 5959 5998, 5999; FMNH 87595; USNM 144618, 144619	DMNH 6000	FMNH 87594	USNM 144616	USNM 144617
PPL	11.6	12.4	11.7 ± 0.34 (5) 11.2–12.0	—	11.3	11.5	10.0
LIF	7.0	7.5	8.0 ± 0.34 (6) 7.5–8.5	—	7.4	7.0	—
BIF	2.4	2.5	2.6 ± 0.15 (6) 2.3–2.7	—	2.3	2.5	—
LBP	7.0	7.1	8.1 ± 0.40 (6) 7.7–8.7	—	7.7	8.3	7.5
BBPM1	4.0	4.3	5.2 ± 0.17 (6) 5.0–5.5	—	4.5	5.3	4.0
BMF	2.6	2.9	2.8 ± 0.10 (6) 2.7–3.0	—	2.9	2.7	2.4
LB	6.1	6.1	6.3 ± 0.17 (6) 6.0–6.5	—	6.3	6.4	5.5
CLM1–3	6.1	6.3	6.4 ± 0.18 (9) 6.1–6.7	—	6.5	6.6	6.3
BM1	1.8	1.9	1.9 ± 0.08 (9) 1.8–2.0	2.0	2.0	1.9	2.0

Beyond these points the braincase is smooth. Without prominent and parallel temporal ridges, which in some species (*Rattus rattus*, for example, fig. 7) give the braincase a rectangular appearance, the braincase of *T. apoensis* appears round from dorsal perspective.

The smooth and rounded nature of the braincase is evident from both dorsal and lateral views (fig. 6). The side between squamosal zygomatic root and lambdoidal ridge is also smooth, without any posterior extension of the zygomatic root; in *Rattus rattus*, for example, the zygomatic root continues caudally as a distinct ridge which terminates at the lambdoidal ridge. Low lambdoidal ridges mark the end of the parietals roofing the cranial cavity and the beginning of the deep occiput. The interparietal, which overlies part of the occipital region, is wide and deep (anteroposterior breadth). The occiput itself projects appreciably beyond the occipital condyles.

Several important features of the braincase can be viewed from lateral perspective (figs. 6, 8A). Posterior to each lambdoidal ridge is the intact (without perforations) and slightly inflated mastoid. Anterior to the lambdoidal ridge is the solid squamosal (not perforated by a subsquamosal [squamoso-mastoid] foramen). Dorsal to the auditory bulla, the attachment between squamosal and periotic is interrupted by a moderately wide fissure, the postglenoid foramen. Anterior to the bulla is the alisphenoid region. Here, just above the shelf formed by the margin of the pterygoid plate, is the open alisphenoid canal (fig. 8A). The foramen ovale is the large posterior opening in the alisphenoid bone just above and caudal to the canal, and the anterior opening of the alisphenoid canal is the smaller foramen just anterior to the canal. The infraorbital branch of the stapedial artery passes along the open canal through the anterior opening and into the orbit by way of the anterior alar fissure, as can be seen by the

Fig. 6. Cranium and dentary (×2.5) of an old adult *Tarsomys apoensis* (USNM 144619).

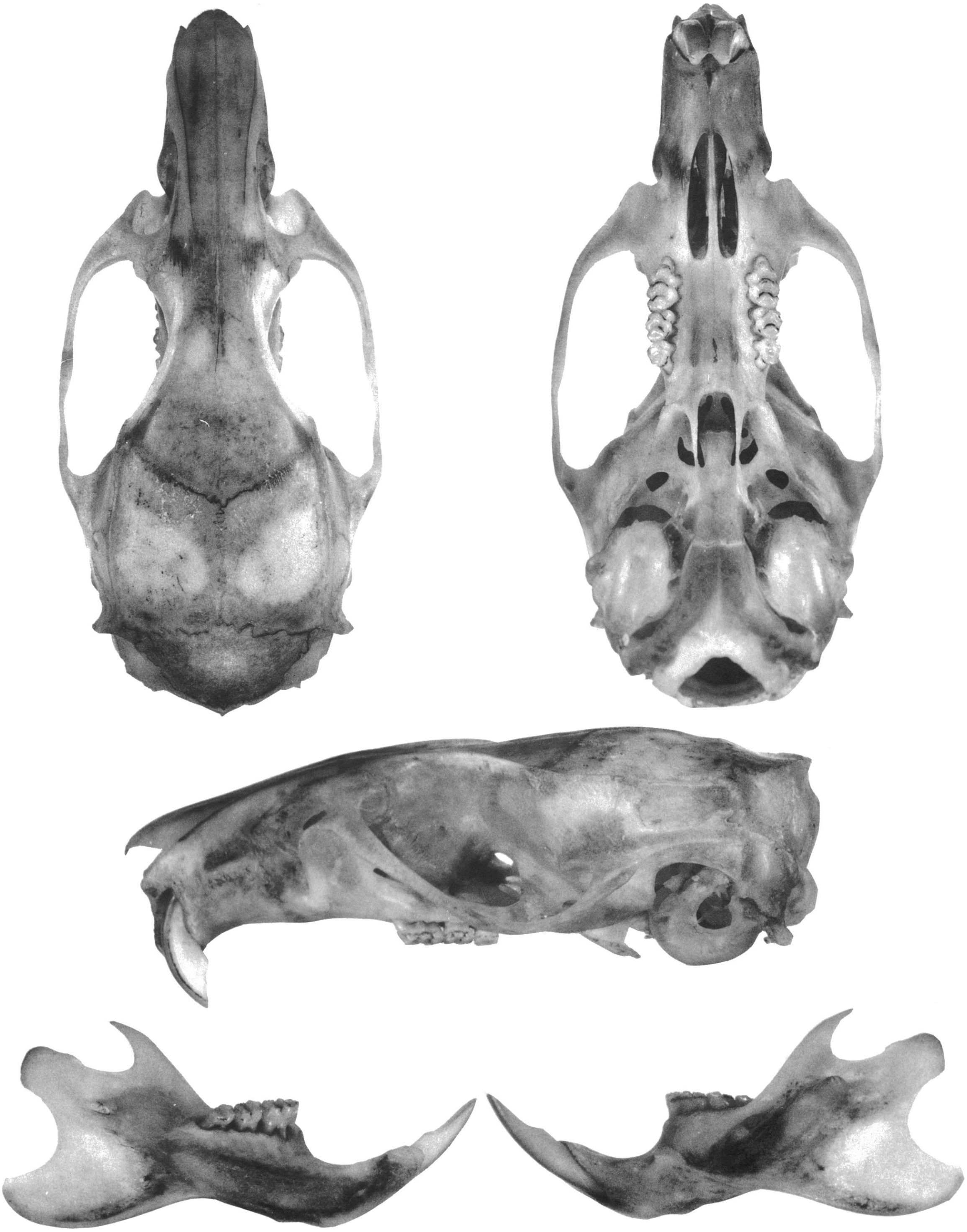

Fig. 7. Cranium and dentary (×2.5) of an adult Sulawesian *Rattus rattus* (AMNH 227767).

TABLE 2

Posterior Margins of Incisive Foramina and Bony Palate Relative to First (M1) and Third (M3) Upper Molars in Adults of *Tarsomys* and *Limnomys*

(Posterior margins of incisive foramina end either anterior to, or posterior to face of M1; margin of bony palate extends past posterior margin of M3. Listed in order are the number of specimens with each trait, the mean extent of foramina or bridge, and the range.)

Species	Incisive foramina at M1		Bony palate at M3	
	Anterior	Posterior	Anterior	Posterior
Tarsomys				
T. apoensis[a]	—	9	—	9
		0.78		1.87
		0.3–1.1		1.4–2.4
T. echinatus[b]	1	7	—	8
	0.25	0.19		1.24
		0.0–0.3		0.9–1.5
Limnomys				
L. sibuanus[c]				
	1	1	—	2
	0.2	0.6	—	0.45
				0.2–0.7

[a] DMNH 5968, 5969, 5998, and 5999; FMNH 87595 and 92802; USNM 125280, 144616, and 144619.

[b] DMNH 5959-5967.

[c] DMNH 5956; USNM 125228.

desiccated artery remaining in some partially cleaned skulls. On one side in all 14 examples of *T. apoensis* and on the other side in 12 specimens, the alisphenoid canal is open laterally and not concealed by a strut of bone, the configuration illustrated in figure 8A. On one side in two specimens is an incomplete and thin strut that covers the anterior portion of the canal. In those specimens where the strut is absent, the foramen ovale accessorius and buccinator-masticatory foramina are united into one large opening. The shallow groove leading dorsad from the top of the foramen ovale reflects the course of buccinator-masticatory nerves. These conformations of bone and foramina, and the cephalic arterial pattern, are common among most species of muroids (see the illustrations in Bugge, 1970, and Carleton and Musser, 1989).

An impression of this arterial pattern can also be seen, from a ventral perspective, on the wide pterygoid plate and at the side of each auditory bulla. The lateral margin of the pterygoid is a flat edge which transforms into a moundlike ridge near the auditory bulla. Medial to this ridge is a shallow groove in which the infraorbital branch of the stapedial artery courses. The place where the infraorbital branch passes to the dorsal surface of the pterygoid plate defines the posterior opening of the alisphenoid canal (fig. 8B). The stapedial artery itself enters the bulla through the large stapedial foramen, located between posteromedial margin of bullar capsule and the petrosal, and is obscured in ventral view by the inflated overhang of the capsule margin.

Other characteristic cranial traits defining *T. apoensis* are evident in ventral view (figs. 6, 8B). The surface of the basioccipital is not deeply excavated. Each pterygoid fossa is shallow and the plate is breached by a large sphenopterygoid opening. Spacious sphenopalatine vacuities outline the presphenoid and part of the basisphenoid in a mesopterygoid fossa which is very wide relative to most other cranial measurements (table 1; fig. 14). The bony palate is also very wide, appreciably wider relative to any other cranial dimension measured (fig. 14); very long, projecting well beyond the molar rows (table 2); and nearly smooth, marked only by nearly indistinguishable palatine grooves. There is a posterior palatine foramen opposite the gap between each second and third upper molar.

Separated from each pterygoid plate by a narrow medial lacerate foramen (fig. 8B), each auditory bulla is moderately large and somewhat inflated. The medial sagittal plane of each bullar capsule is disposed ventromedially so the capsule appears to rest on the basicranium and project toward the midline rather than at a greater angle away from the midline, as in *R. rattus*, for example (fig. 9). At the anteromedial margin of the bullar capsule is the very short but wide bony eustachian tube. The bullar capsule is tightly attached to the cranium in most specimens, without the wide fissure between capsule and squamosal and alisphenoid bones (formed by the confluence of the middle lacerate foramen, postalar fissure, and postglenoid fora-

TABLE 3

Measurements (mm) of Left Upper Incisor from Adults in Samples of *Tarsomys, Limnomys,* and *Rattus*

(The mean plus or minus one standard deviation, number of specimens in parentheses, and range are provided for each measurement.)

Species	Mediolateral breadth	Anteroposterior breadth
Tarsomys		
T. apoensis[a]	0.93 ± 0.08 (11) 0.8–1.1	2.01 ± 0.09 (11) 1.9–2.2
T. echinatus[b]	1.05 ± 0.05 (8) 1.0–1.1	1.93 ± 0.13 (8) 1.8–2.0
Limnomys		
L. sibuanus[c]	0.80 ± 0.00 (2)	1.85 ± 0.21 (2) 1.7–2.0
Rattus		
R. rattus[d]	1.24 ± 0.13 (26) 1.0–1.5	2.32 ± 0.19 (26) 2.0–2.7

[a] DMNH 5968, 5969, 5998, and 5999; FMNH 87594, 87595, and 92808; USNM 125280, 144616, 144618, and 144619.

[b] DMNH 5959–5967.

[c] DMNH 5956; USNM 125228.

[d] AMNH 152994, 152950–152956, 152959, 152960, 152985–152986, 152988, 152989, 152992, and 152995–153004 (from Bumbulan, northern Sulawesi).

men) seen in species like *Rattus rattus,* for example.

The dentary of *T. apoensis* is illustrated in figure 6. It has the basic murine conformation but is somewhat elongate, particularly the body of the ramus between first molar and incisor. Other distinctive traits are the short, delicate coronoid process and the deeply concave caudal margin between the condyloid and angular processes. A capsular process forms a low bulge below the coronoid. On the medial surface of the dentary the mandibular foramen occurs just dorsad to a narrow ridge which extends from the bony molar platform to the condyle.

Tarsomys apoensis has asulcate (no grooves), slim upper incisors in which the enamel is either dense orange or yellow-orange, and their position relative to the rostrum is either orthodont or opisthodont. Narrow incisors are diagnostic. Compared with a species such as *Rattus rattus,* which has a broad incisor relative to its depth, the proportional configuration found among most murines, each upper incisor of *T. apoensis* is significantly narrower relative to its depth (anteroposterior thickness) or relative to greatest length of skull, which is one index of general body size (table 3; fig. 14).

Lower incisors in *T. apoensis* are also slim and without grooves in the enamel. They are long and sharp and their enamel layers are pale orange or pale yellowish orange.

Multiple molar roots are characteristic of *T. apoensis,* reflected by the alveoli as shown in figure 10. Each first upper molar is anchored by five roots: a large anterior, slightly smaller posterior, two medium-sized linguals, and a small labial. Four roots hold down each second upper molar, and three are beneath each third molar. Each first lower molar has four roots: a large anterior, small labial, small lingual, and wide posterior one. Each second and each third molar is anchored by two anterior roots and a large posterior holdfast.

Some gross molar traits of *T. apoensis* are shared with many southeast Asian murines. Rows of cusps, for example, are inclined rather than vertical so within the upper row the first molar slightly overlaps the second and the second inclines against the third; within the lower row, the third molar leans against the second and it in turn slightly overlaps the

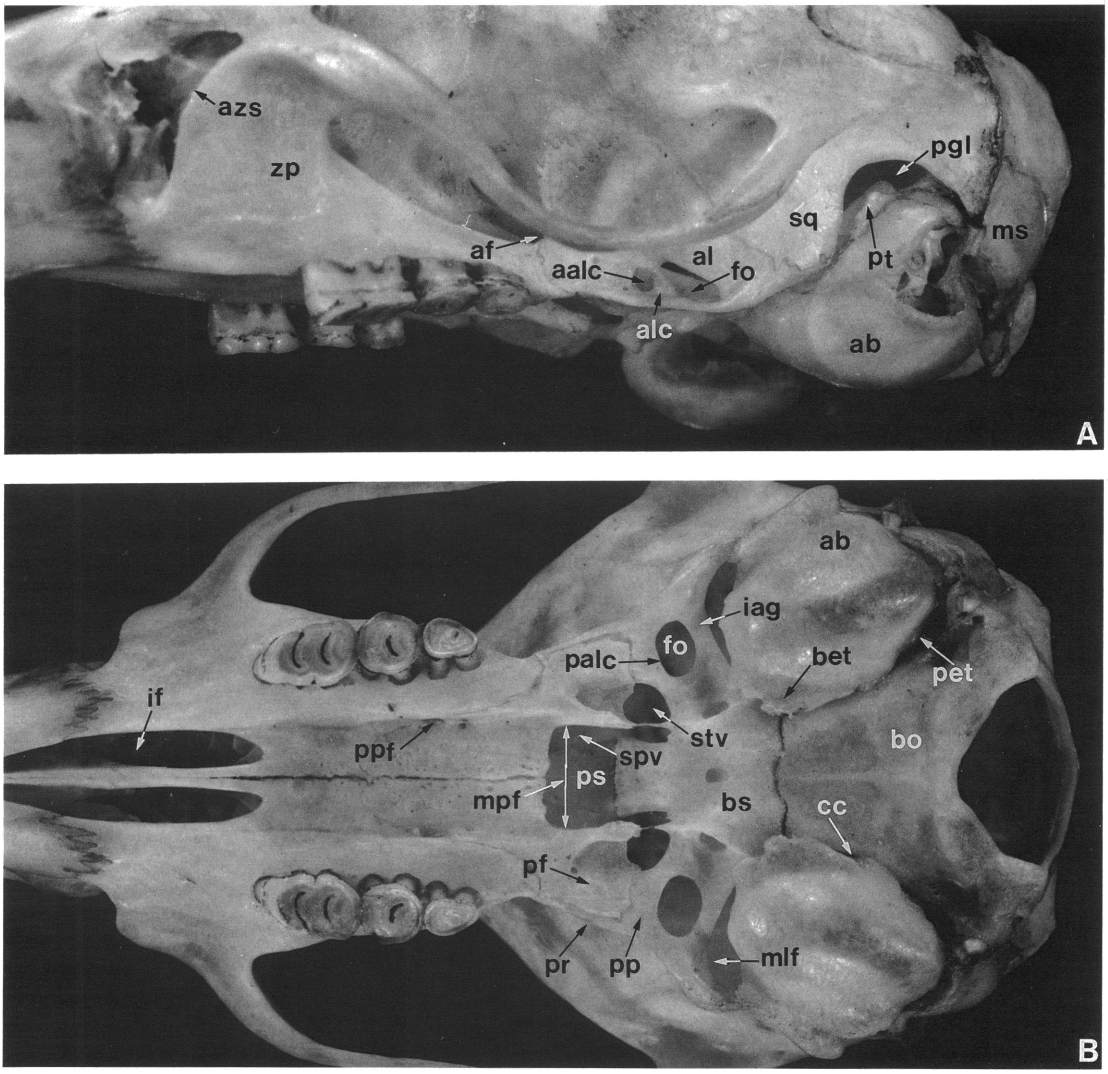

Fig. 8. Lateral (A) and ventral (B) cranial enlargements of *Tarsomys apoensis* (USNM 144619). **aalc,** anterior opening of alisphenoid canal; **ab,** auditory bulla; **af,** anterior alar fissure; **al,** alisphenoid; **alc,** alisphenoid canal; **azs,** anterior spine of zygomatic plate; **bet,** bony eustachian tube; **bo,** basioccipital; **bs,** basisphenoid; **cc,** carotid canal; **fo,** foramen ovale; **iag,** groove for the infraorbital branch of the stapedial artery; **if,** incisive foramen; **mlf,** middle lacerate foramen; **mpf,** mesopterygoid fossa; **ms,** mastoid; **palc,** posterior opening of the alisphenoid canal (arrow points to where the infraorbital branch of the stapedial artery enters the braincase dorsal to the pterygoid plate); **pet,** petrosal; **pf,** pterygoid fossa; **pgf,** postglenoid foramen; **pp,** pterygoid plate; **ppf,** posterior palatine foramen; **ps,** presphenoid; **pt,** periotic; **pr,** pterygoid ridge; **sq,** squamosal; **spv,** sphenopalatine vacuity; **stv,** sphenopterygoid vacuity; **zp,** zygomatic plate.

first. Another general configuration is the decrease in size from the first molar to the third.

One overall feature distinguishes *T. apoensis*. The molars are conspicuously hypsodont, and this vertical elongation involves both crown and cusps. The degree of hypsodonty is best appreciated when high-crowned molars of *T. apoensis* are contrasted with low-crowned (brachyodont) teeth of *R. rattus,* as they are in figure 11.

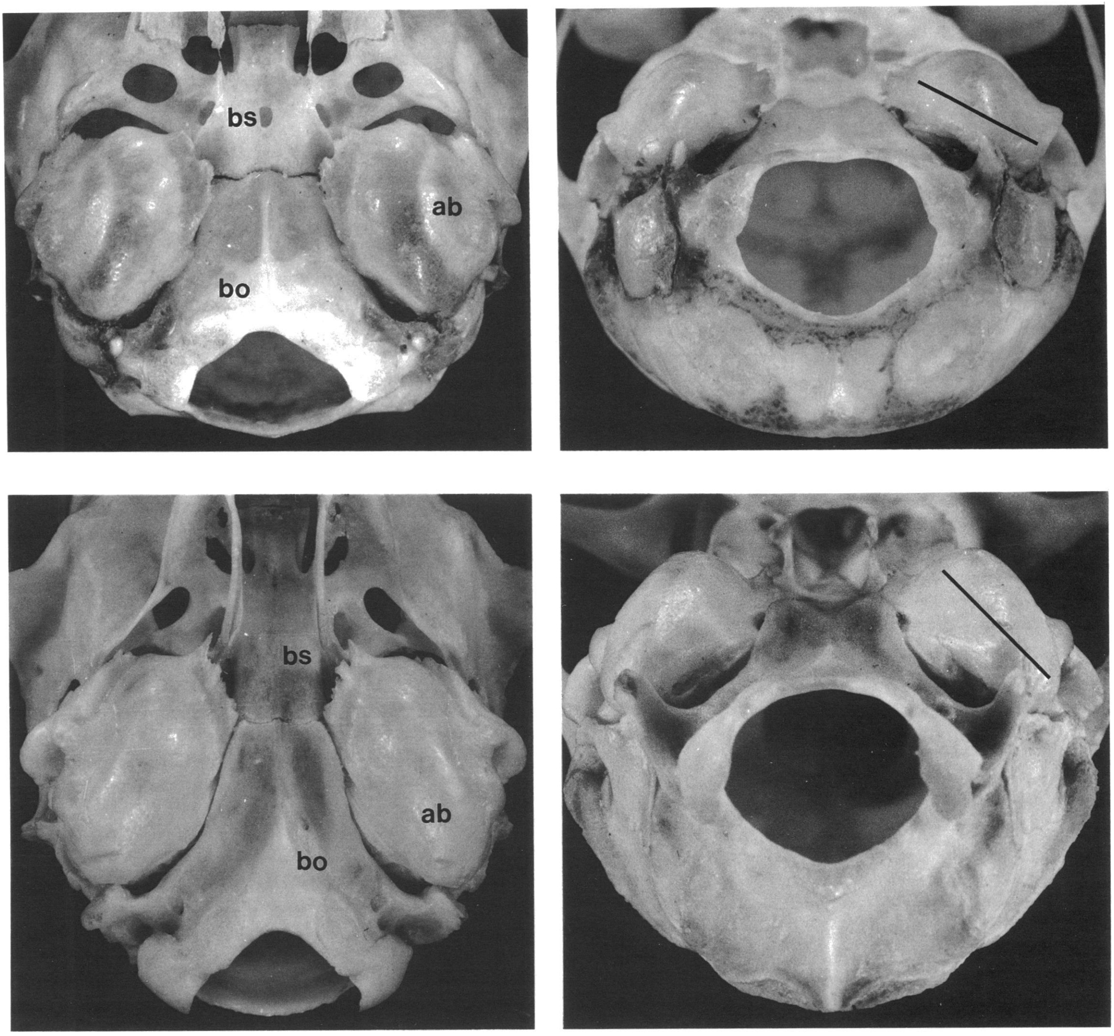

Fig. 9. Contrasts (×4) in auditory bullae between *Tarsomys apoensis* (USNM 144619; **top views**) and Sulawesian *Rattus rattus* (AMNH 152950; **bottom views**). The bullae of *T. apoensis* are shorter and less inflated, and the medial axis (black line in right views) of each otic capsule is closer to the basisphenoid (**bs**) and basioccipital (**bo**).

The molars are relatively wide (fig. 14). This feature, combined with the degree of hypsodonty and the simple occlusal patterns formed by cusp rows, imparts an uncomplicated and chunky appearance to both maxillary and mandibular teeth (fig. 12). Molars are somewhat cuspidate in juveniles (fig. 13) but by a very young adult stage attain the simple occlusal patterns seen in figure 12. These patterns on the upper molars reflect the diminution or absence of certain cusps and cusplets, as listed below.

1. Labial cusp t3 on each first molar, for example, is small and mostly absorbed by the large adjacent cusp (t2), resulting in a lamina composed mostly of a chunky central cusp and a smaller caudally directed lingual cusp t1.
2. The lingual space between cusps t4 and t8 on each tooth lacks a ridge or cusp t7. Such a cusp is present in other Asian murines, *Lenothrix canus*, for example (Musser and Newcomb, 1983: 333).
3. No cusplike caudal extension from la-

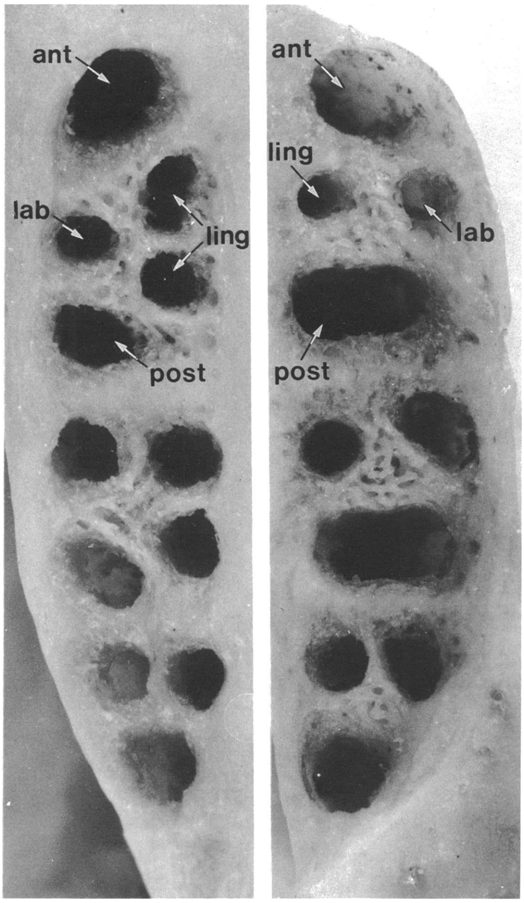

Fig. 10. Alveoli (×15) for right molar roots in *Tarsomys apoensis* (uppers, DMNH 5968; lowers, DMNH 5963). **Left,** ventral view of upper alveoli (number of alveoli per molar is, from top to bottom, 5, 4, and 3, respectively). **Right,** dorsal view of lower alveoli (4, 3, and 3, respectively). **ant,** alveolus for anterior root; **lab,** labial alveolus; **ling,** lingual; **post,** posterior.

bial cusp t6 occurs on any molar. In some specimens, cusp t6 has a short posterior projection but it is more an elongation of the back part of the cusp rather than cusplike. Such a cusplike projection is characteristic of *Lenothrix canus* and some species of *Margaretamys,* for example (Musser, 1981a).

4. The labial cusp t3 on each second molar is present in about two-thirds of the sample (specimens in which the elements of the occlusal pattern have not been obscured because of excessive wear), and on the third molar in about half of the series (table 4). Even when present it is a minute cusp nestled far down from the occlusal surface and against the base of cusp t5 (fig. 12A).

5. No posterior cingulum projects from the back of either the second or third molar. When present in other species, such as *Lenothrix* and *Margaretamys* (Musser, 1981a) as well as *Limnomys sibuanus* (fig. 25), the posterior cingulum is an enamel ridge or definite cusp extending out from the large central cusp t8.

Coronal surfaces of lower molars are also simple, reflecting a configuration developed from rows of chunky lamina with few cingular enamel elaborations (figs. 12, 13). The laminae themselves are thick and without complications. Most are slightly arcuate in occlusal view but the anteroconid and the second lamina on the first molar are nearly transverse, as are the two lamina forming all the chewing surface on the third molar. The posterior cingula forming posterior ramparts of first and second molars are also chunky and high. They are part of the occlusal plane, which is a usual development in hypsodont teeth but unusual at moderate stages of wear in brachyodont molars. The only significant enamel elaboration at the front of the molar row is a small anterocentral cusp on three of the nine specimens examined. Cusplets are absent from lingual margins of molars but present on some labial spots. A posterior labial cusplet is the only one found on each first molar. An anterior labial cusplet frequently occurs in species of other murines (Musser, 1981a; Musser and Newcomb, 1983). An anterolabial cusp is present on the second molar in eight out of nine specimens and on the third molar in seven out of nine animals. A posterior labial cusplet is found on both second and third molars in seven out of the nine specimens. Without these labial cusps, the chewing surface area is reduced and occlusal patterns appear even simpler than they are when cusplets are present.

ECOLOGY: Our lack of any ecological data prevents us from providing significant insights into the natural history of *T. apoensis.* We suspect it is a forest animal. The proportions of tail length to head and body length, its long and slender hind feet, and long face point to terrestrial habits rather than scansorial or arboreal. Its long sharp claws, elongate rostrum, and slim incisors hint of a spe-

Fig. 11. Lingual views of right molar rows contrasting the hypsodont upper molars of *Tarsomys apoensis* (**A**, USNM 114617; CLM1–3 = 6.3 mm) and the brachyodont uppers of Sulawesian *Rattus rattus* (**B**, AMNH 101272; CLM1–3 = 6.5 mm). Note also that the central cusp in each row is less inclined in *Tarsomys* than in *Rattus*, especially cusps t2 and t8.

cial diet, possibly invertebrates. The rich chestnut coat may signify diurnal rather than nocturnal behavior. It is our experience that Asian murines of moderate to small body size that have chestnut fur and live in tropical evergreen rain forests are diurnal; the Sulawesian *Melasmothrix naso* and *Crunomys celebensis* (Musser, 1982c) and Philippine *Archboldomys luzonensis* (Rickart et al., 1991) are examples.

GEOGRAPHIC VARIATION: Our sample of 14 specimens was collected from four mountains. The lowest collecting site was at 5200 ft, the highest was 7500 ft. If these specimens reflect its approximate real altitudinal distributions, then *Tarsomys apoensis* is clearly montane and may consist of insular populations scattered over Mindanao, either completely or partially isolated from one another by lowland forest habitats or other kinds of barriers. Whether or not this possibly insular distribution is reflected in morphology is a question we cannot answer with the samples we have studied. There is clearly variation within and among the series in quantitative traits (table 1) but our samples are simply too small and uneven in age classes to interpret the significance of the variation we have documented.

COMPARISONS: The chromatic and mor-

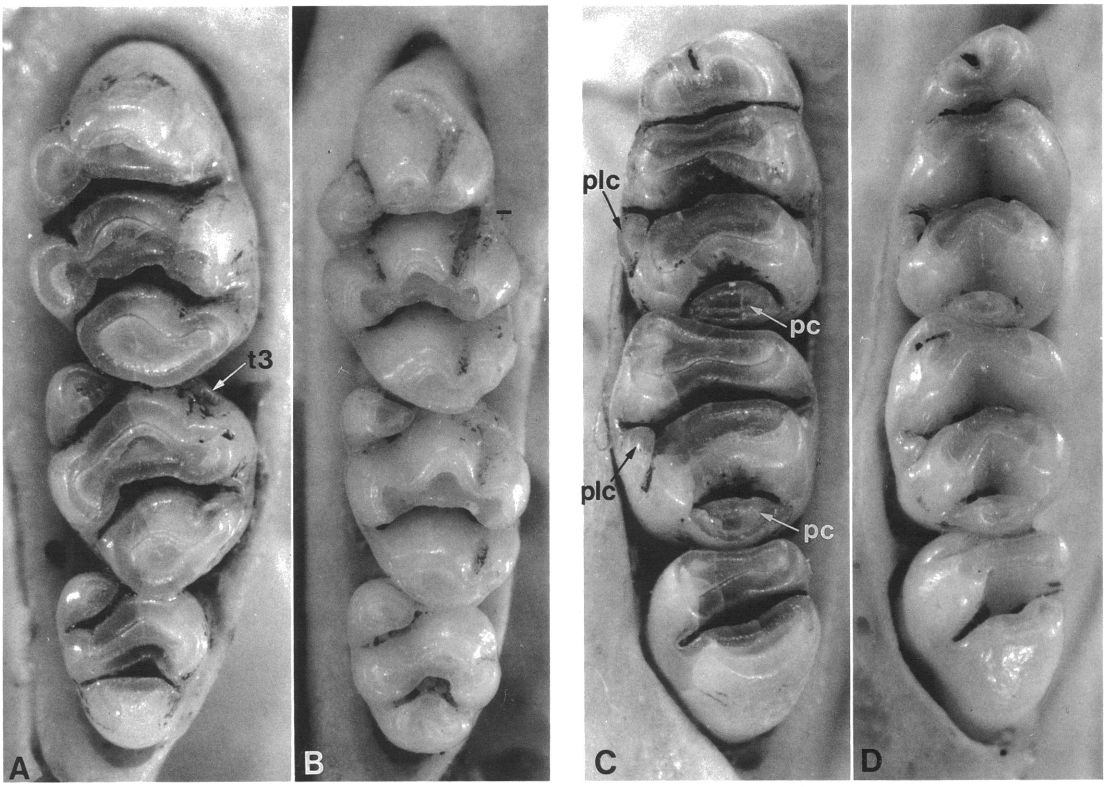

Fig. 12. Occlusal contrasts (×15) between left molar rows of *Tarsomys* and *Rattus*. **A, C,** upper and lower rows of *T. apoensis* (USNM 114617, very young adult). **B, D,** upper and lower rows of Sulawesian *R. rattus* (AMNH 101272, very young adult). The greater inclination of the cusp rows in *Rattus* compared with the more erect rows of *Tarsomys* is also evident in these views (see fig. 11). **pc,** posterior cingulum; **plc,** posterior labial cusplet.

phological traits described in preceding pages define a distinctive species confined to montane habitats in Mindanao and, except for the new species of *Tarsomys* to be described later, without close morphological counterparts elsewhere either in the Philippine Archipelago or in the general Indo-Australian region. Two species, however, from two distinct genera—*Palawanomys* and *Bunomys*—do superficially resemble *T. apoensis,* and the Mindanao endemic also has to be contrasted with species of *Rattus,* comparisons we present below.

Tarsomys apoensis and *Palawanomys furvus*

Palawanomys furvus is known by only four specimens collected from Mount Mantalingajan on Palawan Island (Musser and Newcomb, 1983). In its body size, proportions of external traits, dark pelage, expansive bony palate, shallow pterygoid fossae, and overall cranial conformation, *P. furvus* is at first glance similar to *T. apoensis* (compare figs. 4, 5, and 9 in Musser and Newcomb, 1983, with figs. 5, 6, and 8 here). Close inspection, however, reveals significant differences between the two species. The fur of *P. furvus* is thick, glossy, and brownish black. Except for their unpigmented bases, the hairs are brownish black and unbanded; the hue and texture of the coat, as well as the basically monocolored hairs, are elements associated with melanism. Pelage of *T. apoensis* is brownish chestnut and appears dark but is not melanistic. The Palawan rat has four pairs of mammae, not three as is characteristic of the

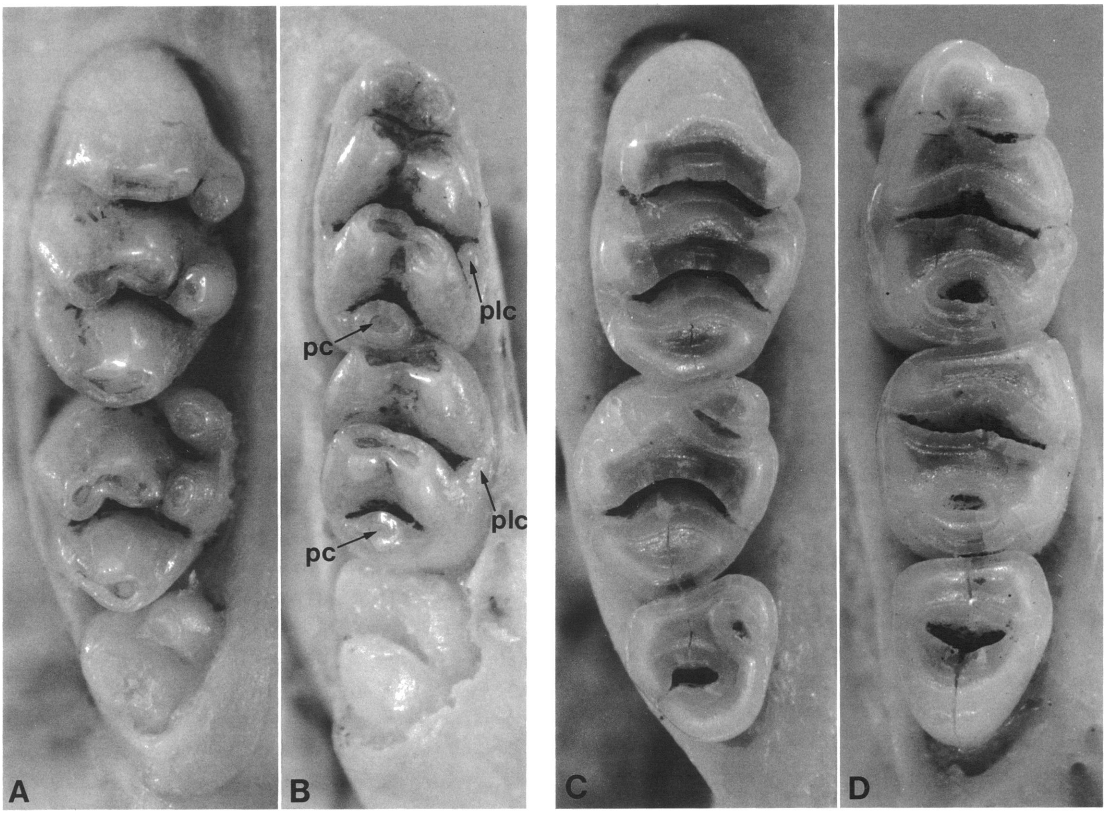

Fig. 13. Occlusal contrasts (×15) between right molar rows of *Tarsomys apoensis* of different ages. **A, B,** upper and lower toothrows of a juvenile (FMNH 61486). **C, D,** upper and lower toothrows of an adult (DMNH 5999). **pc,** posterior cingulum; **plc,** posterior labial cusplet.

Mindanao animal. General features of the cranium appearing similar in both species are primitive (size and shape of auditory bullae, slight beading along dorsolateral margins of interorbital and postorbital regions, round and nearly smooth braincase, pattern of cephalic arterial circulation, for example; Musser and Newcomb, 1983). Conformation of the alisphenoid region is alike in both species, but this derived condition (primarily modifications associated with no bony alisphenoid strut) is so widespread among Indo-Australian murines that its significance for phylogenetic inference is difficult to evaluate unless the trait is part of a concordant character suite. Molars of *P. furvus* are not hypsodont, first upper molars have four roots instead of five, and the coronal patterns formed by cusps and other enamel structures are unlike those found in *T. apoensis* (contrast figs. 12 and 13 in Musser and Newcomb, 1983, with fig. 12 here). The expansive bony palate and shallow pterygoid fossae are possibly important points of resemblance between the two species. These traits are also shared by other murines, however, and may not be phylogenetic but convergent; the significance of this similarity between *P. furvus* and *T. apoensis* seems slight to us in the absence of character analyses of other murines.

Tarsomys apoensis and *Bunomys chrysocomus*

Bunomys chrysocomus lives in the wetter portions of tropical lowland evergreen and tropical lower montane forest formations on Sulawesi. Like the Mindanao endemic, *B. chrysocomus* is medium-sized, short-tailed, and soft and dark-furred (see measurements in Musser, 1991: 8, and photograph of the live animal in Musser et al., 1986: 8). The two species also share cranial and dental traits, among them a moderately long and tapered rostrum, smooth interorbit and braincase, derived alisphenoid configuration, moderately inflated auditory bullae having the same orientation to basicranial region, zygomatic plate with convex anterior spine, elongate dentary, multirooted molars, and simple cusp patterns (compare crania and dentaries of *B. chrysocomus* illustrated in Musser et al., 1986: 9, and Musser, 1991: 13, as well as molar rows in Musser, 1991: 18–19, with figures of skull and teeth of *T. apoensis*).

These character similarities again are mostly superficial or generally reflect either shared primitive traits or shared derived ones that are so widely shared by other murines that their significance is difficult to interpret without further study. The dorsal and ventral coats of *B. chrysocomus,* for example, are not as dark as those of *T. apoensis,* and underparts are always conspicuously paler than upperparts. Tails of the Sulawesi rats are darkly pigmented on dorsal surfaces but usually unpigmented or mottled on the ventral surface, and many specimens have a white tip. *Tarsomys apoensis* has a monocolored dark brown tail. Two pairs of inguinal mammae are usual in *B. chrysocomus.* One pair of postaxillary and two pairs of inguinal teats are diagnostic of *T. apoensis.* The narrower zygomatic plate, shorter incisive foramina, much shorter and narrower bony palate, wider mesopterygoid fossa with short and inconspicuous sphenopalatine vacuities, and deeper pterygoid fossae of *B. chrysocomus* are some of the features providing strong contrast with the cranium of *T. apoensis.* The dissimilarity in molar height between the two species (brachyodont in *B. chrysocomus* and hypsodont in *T. apoensis*) add discordance to any similarity other than a superficial one.

Bunomys chrysocomus is morphologically and phylogenetically closely related to other species found only on Sulawesi (Musser and Newcomb, 1983; Musser, 1991). And although certain morphological similarities exist between it and *T. apoensis,* these are insignificant or at present uninterpretable in the context of phylogenetic alliance, and may even reflect homoplasy. Particular traits (external form, pelage texture and color, elongate rostrum, simple occlusal molar patterns) suggest to us that on Mindanao *T. apoensis* might be the ecological equivalent of *B. chrysocomus* on Sulawesi. While we have information about habitat, diet, breeding, and other aspects of the Sulawesian rat, we lack any primary ecological observations regarding the Mindanao animal and cannot test this idea. But, morphology of skins, skulls, and dentitions in our samples of the two species does not support the notion of a close phylogenetic relationship.

Tarsomys apoensis and *Rattus rattus*

Because an influential checklist (Ellerman, 1941), classification (Simpson, 1945), and systematic revisionary study (Misonne, 1969) either questioned the generic status of *Tarsomys* or treated it as a subgenus of *Rattus,* the features defining the morphological limits of *Tarsomys* require comparison with those characteristic of the group Ellerman (1941) regarded as members of the subgenus *Rattus.* Our example of this group consists of samples from southeast Asia which are currently identified as *R. rattus.* Our representative of *Tarsomys* is the type species, *T. apoensis,* and it contrasts with *Rattus* as outlined below (the expression of the trait in *Rattus* is explained within parentheses). The two species are also compared in figure 14 where proportional contrasts are diagrammed, in figures 6 and 7 where crania and dentaries are illustrated, in figures 11 and 12 where molar teeth are shown, and in table 4 where frequencies of cusps and cusplets are tabulated:

1. The tail is absolutely shorter than combined lengths of head and body, and also much shorter relative to that dimension (tail is as long as head and body or usually much longer).
2. Claws of hind feet are longer, those on front feet are even longer and more robust (short, sharp, recurved claws).
3. There are three pairs of mammae: one postaxillary and two inguinal (five pairs in *R. rattus,* four, five, or six pairs in other related species of *Rattus*).
4. The rostrum is long and tapered, and

significantly much longer relative to its length or to greatest length of skull (relatively shorter and rectangular rostrum).

5. Tips of nasals either horizontal or angled slightly dorsad (nasal tips curve downward following profile of cranium).

6. The interorbital and postorbital region is hourglass-shaped, significantly wider relative to occipitonasal length, and with smooth dorsolateral margins. The braincase is significantly wider relative to cranial length, much lower relative to its breadth, and is outlined by faint postorbital beading. It is smooth and appears circular from dorsal view and has a convex dorsal profile uninterrupted by either temporal ridges or a ridge extending from each squamosal zygomatic root to the lambdoidal ridge as seen from occipital perspective (lyre-shaped interorbit and postorbital region; higher and narrower braincase with prominent ridges outlining dorsolateral margins of cranium from interorbit to lambdoidal ridges; braincase appears rectangular in dorsal view and from an occipital perspective its dorsal outline is punctuated by prominent temporal ridges and ridges extending from squamosal roots to occiput).

7. Margin of zygomatic spine is convex in outline, without a shoulder at its anterodorsal portion (spine projects from dorsal zygomatic root as broad shoulder, not a curved margin).

8. Relative to greatest length of skull, the bony palate is long in both *Tarsomys* and *Rattus* but it is also extremely broad in *Tarsomys,* particularly in relation to its length (much narrower relative to its width).

9. The pterygoid fossae are shallow and ventral surfaces of basioccipital are only slightly concave (pterygoid region deeply excavated, basioccipital surfaces more deeply concave).

10. The postpalatal region is very short relative to length of skull (postpalatal region longer relative to length of skull).

11. Auditory bullae are significantly shorter relative to cranial length and less inflated. In ventral and occipital views (fig. 9), they appear plastered to the basicranial region and the medial sagittal section of each forms a shallow angle—less than 45°—with the surface of the basioccipital (bullae are larger and conspicuously more inflated; they appear to project from the basicranial region and the median sagittal section of each forms an angle of 45° or more with the basioccipital).

TABLE 4

Presence (+) or Absence (−) of Certain Cusps and Cusplets on Maxillary (M) and Mandibular (m) Molars in Species of *Tarsomys, Limnomys,* and *Rattus*

(Number of cusps and cusplets are expressed as percentages; number of specimens are in parentheses.)

	Tarsomys		*Limnomys*	*Rattus*
Cusp/ cusplet	*apoensis*	*echinatus*	*sibuanus*	*rattus*[a]
Cusp t3 on M2				
+	67 (6)	100 (4)	100 (5)	35 (14)
−	33 (3)	−	−	65 (26)
Cusp t3 on M3				
+	56 (5)	−	80 (4)	2 (1)
−	44 (4)	100 (4)	20 (1)	98 (39)
Posterior cingulum on M1				
+	−	−	100 (5)	−
−	100 (9)	100 (4)	−	100 (40)
Posterior cingulum on M2				
+	−	−	100 (5)	−
−	100 (9)	100 (4)	−	100 (40)
Anterocentral cusp on m1				
+	33 (3)	−	100 (5)	−
−	67 (6)	100 (4)	−	100 (4)
Anterior labial cusplet on m1				
+	−	−	60 (3)	5 (2)
−	100 (9)	100 (4)	40 (2)	95 (38)
Posterior labial cusplet on m1				
+	100 (9)	100 (4)	100 (5)	100 (40)
−	−	−	−	−
Anterolabial cusp on m2				
+	89 (8)	100 (4)	100 (5)	100 (40)
−	11 (1)	−	−	−
Posterior labial cusplet on m2				
+	78 (7)	100 (4)	100 (5)	98 (39)
−	22 (2)	−	−	2 (1)
Anterolabial cusp on m3				
+	78 (7)	50 (2)	100 (4)	100 (40)
−	22 (2)	50 (2)	−	−

[a] The sample is from Bumbulan, northern Sulawesi.

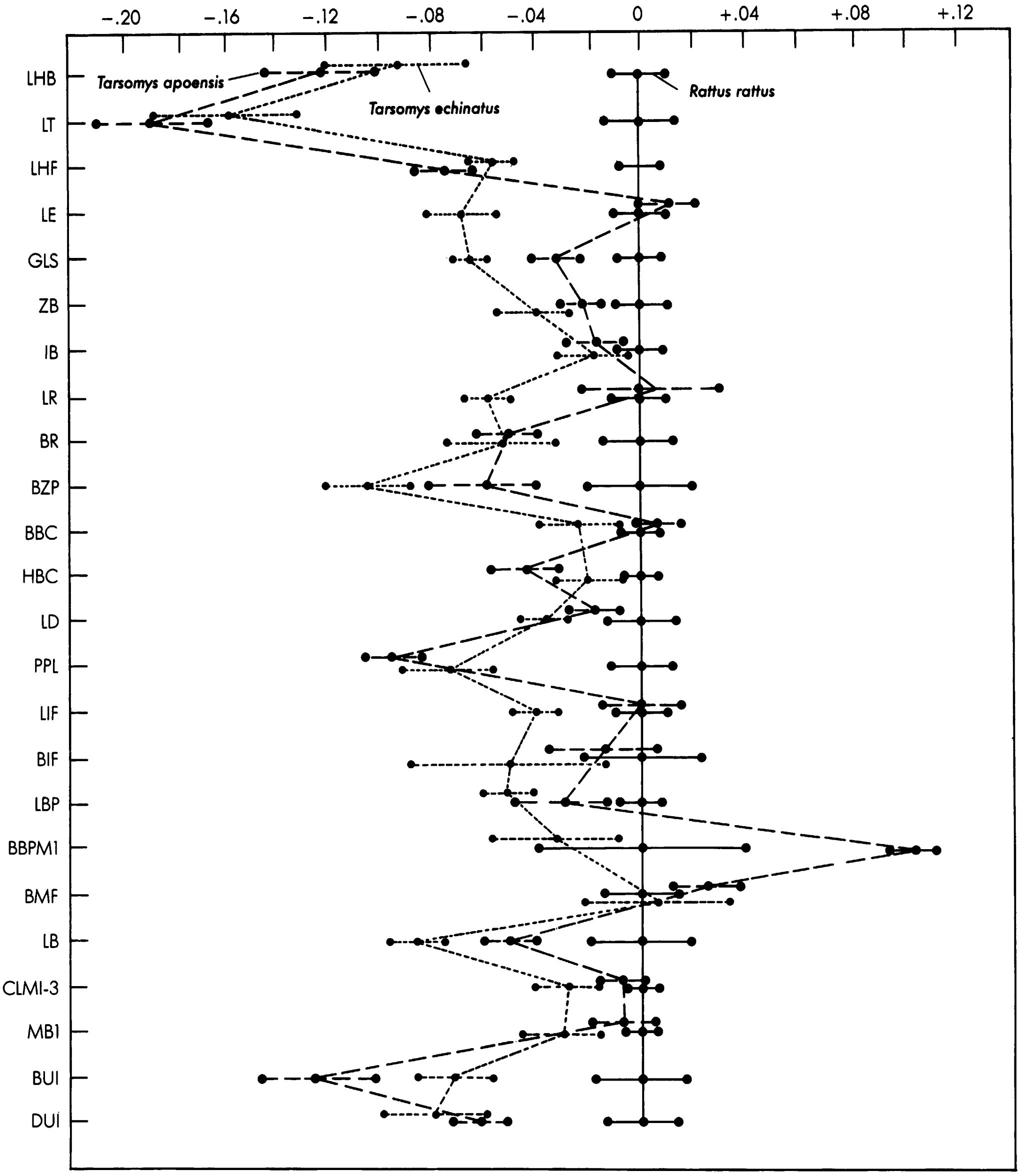

Fig. 14. Ratio diagram. Dimensions are compared among samples of Sulawesian *Rattus rattus* (the standard), *Tarsomys apoensis*, and *T. echinatus*. See Materials and Procedures for an explanation of the diagram.

12. Upper incisors are slim. Furthermore, each incisor is significantly narrower relative to its anteroposterior depth (wider incisors, both absolutely and relative to its depth).

13. Molar teeth are hypsodont and some cusps on first upper molars are nearly erect (brachyodont molars with slanting cusps on first upper molars, fig. 11).

14. Cusp t3 on each first upper molar is small and seems more a slight projection of cusp t2 than a discrete cusp. When present, cusp t3 on each first and second upper molar is very small. Anterolabial cusps and posterior labial cusplets are absent from second and third lower molars of some specimens (cusp t3 on each first upper molar large and

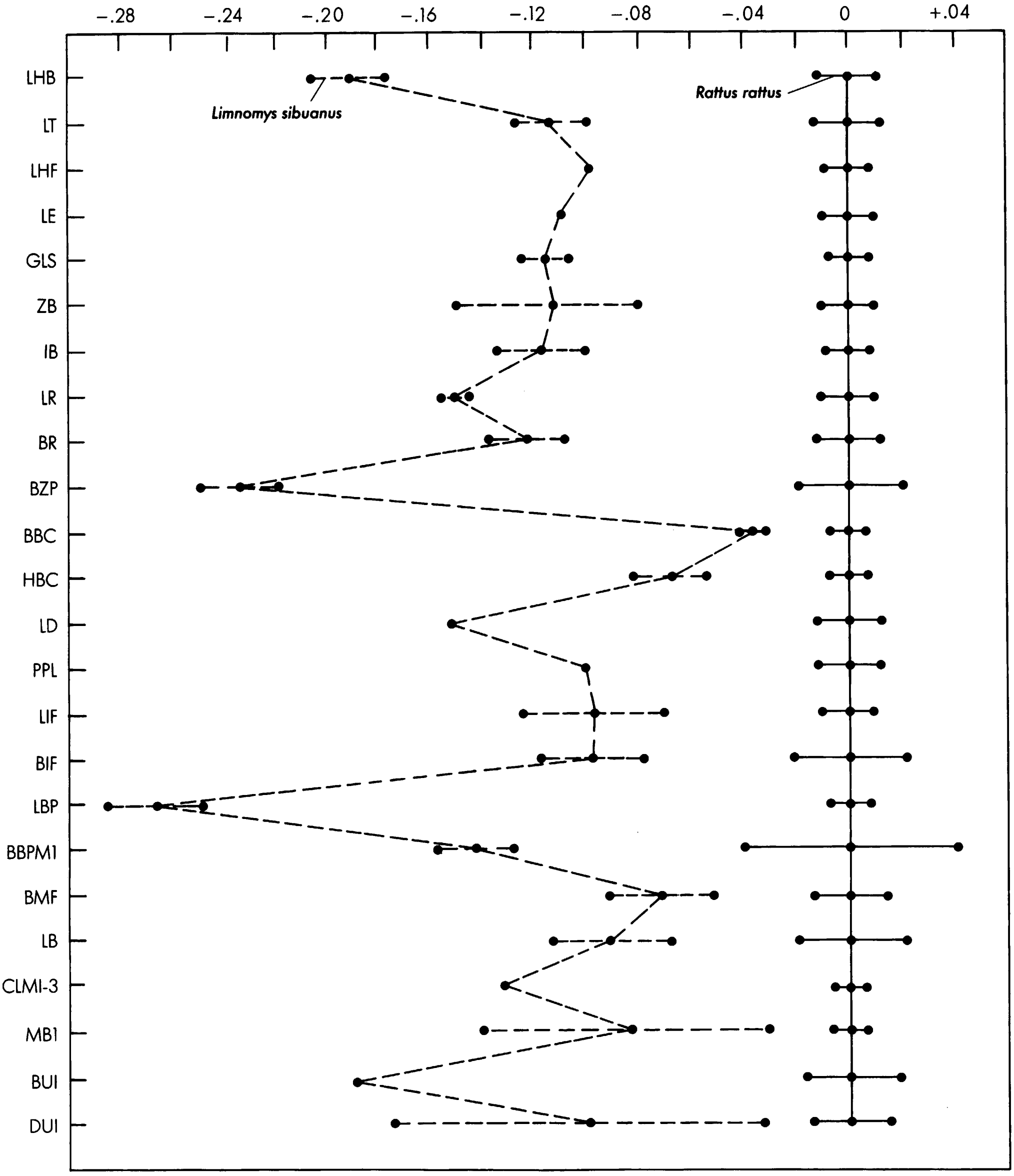

Fig. 15. Ratio diagram. Dimensions are compared among samples of Sulawesian *Rattus rattus* (the standard) and *Limnomys sibuanus*. Note the proportional differences and similarities between *L. sibuanus* and the two species of *Tarsomys* in figure 14.

discrete; when present, cusp t3 is usually large, anterolabial cusps and posterior labial cusplets are found more frequently on second and third lower molars).

Although we have not identified any close relative of *T. apoensis* occurring outside of the Philippines, we have discovered an undescribed species, collected only on Mindanao, whose external form, cranial morphology, and dental patterns, in our view, link it more closely to *T. apoensis* than to any other described murine. We formally give this entity a name and describe it below as a species of *Tarsomys*, which reflects our estimate of its phylogenetic alliance among the Asian murine fauna.

TABLE 5

Measurements (mm) of *Tarsomys echinatus* from Mount Matutum (2700-3700 ft) on the Island of Mindanao

(The mean plus or minus one standard deviation, number of specimens in parentheses, and range are provided for each measurement.)

	Adult holotype	Old adults and adults	Young adults	
	DMNH 5960	DMNH 5960–5965, 5967	DMNH 5966	DMNH 5959
LHB	168	159.0 ± 12.95 (7) 145–179	141	137
LT	158	137.1 ± 11.98 (7) 120–158	129	127
TSR/cm	10	11.4 ± 1.13 (7) 10–13	11	12
LHF	33	33.0 ± 0.82 (7) 32–34	31	31
LE	19	18.7 ± 0.76 (7) 17–19	21	18
LOF	10	12.0 ± 2.00 (7) 10–15	13	10
LGH	14	17.0 ± 2.45 (7) 14–20	15	10
GLS	37.5	36.8 ± 0.57 (4) 36.3–37.5	35.4	36.0
ZB	18.8	18.2 ± 0.72 (5) 17.3–18.9	17.3	19.4
IB	6.1	6.0 ± 0.24 (6) 5.6–6.3	6.4	6.4
LR	12.0	11.6 ± 0.26 (6) 11.3–12.0	10.5	10.4
BR	7.1	6.7 ± 0.41 (6) 6.0–7.1	6.5	6.7
BZP	4.0	3.7 ± 0.18 (6) 3.5–4.0	3.9	3.7
DZN	2.1	1.7 ± 0.30 (6) 1.3–2.1	1.5	1.4
HBC	15.9	15.2 ± 0.63 (5) 14.5–15.9	15.3	15.5
HBC	11.5	11.1 ± 0.39 (4) 10.7–11.5	10.9	11.2
LD	10.5	10.8 ± 0.28 (6) 10.5–11.3	9.9	9.8
PPL	12.4	12.3 ± 0.50 (4) 11.6–12.8	11.6	12.6
LIF	7.1	7.3 ± 0.19 (6) 7.1–7.6	7.1	6.8
BIF	2.2	2.4 ± 0.26 (6) 2.1–2.8	2.3	2.6

TABLE 5—(*Continued*)

	Adult holotype	Old adults and adults	Young adults	
	DMNH 5960	DMNH 5960–5965, 5967	DMNH 5966	DMNH 5959
LBP	7.7	7.7 ± 0.22 (6) 7.4–8.0	7.3	7.1
BBPM1	3.8	3.8 ± 0.26 (6) 3.4–4.1	3.8	4.1
BMF	2.9	2.7 ± 0.19 (5) 2.4–2.9	2.4	2.6
LB	5.7	5.8 ± 0.17 (6) 5.5–6.0	5.9	6.0
CLM1-3	6.2	6.1 ± 0.21 (6) 5.8–6.4	6.3	6.0
BM1	2.0	1.8 ± 0.08 (6) 1.7–2.0	1.9	1.8

***Tarsomys echinatus*, new species**

HOLOTYPE: DMNH 5960, an adult male collected by D. S. Rabor and colleagues (original number 1267) from Balisong, Tupi, Mt. Matutum, South Cotabato Province, southern Mindanao (figs. 3, 4) on January 1, 1964. The interval, 2700–3700 ft, is the elevational range written on the skin tag. The specimen consists of a conventional stuffed museum study skin (similar to the one depicted in fig. 16) accompanied by a skull with intact incisors and molar rows. A patch of skin is missing from the rump. Except for a missing piece of the left zygomatic arch and small portions of the bony palate and mesopterygoid region, the skull is complete. Measurements of the holotype are listed in table 5.

REFERRED SPECIMENS: Eight individuals that were trapped on the slopes of Mt. Matutum (locality 5 in fig. 4) during 1964. One is DMNH 5959, a young adult female from Tucay E-el, 3300 ft, January 25. The other seven come from Balisong and were caught between February 1 and 13: DMNH 5961, adult male, 2700–3700 ft; DMNH 5962, adult male, 2700–3700 ft; DMNH 5963, old adult male, 2700–3300 ft; DMNH 5964, adult male, 2700–3300 ft; DMNH 5965, old adult female, 2700–3300 ft; DMNH 5966, young adult female, 2700–3300 ft; and DMNH 5967, old adult female, 2700–3300 ft. All are represented by stuffed skins and associated crania and mandibles except DMNH 5964, which is only a skin.

DISTRIBUTION: The series comes from between 2700 and 3700 ft on Mt. Matutum but the species likely occurs in highlands at middle elevations elsewhere on Mindanao, and possibly even lower.

ETYMOLOGY: The Latin *echinatus* means spiny or prickly, which calls attention to the harsh and spiny fur of the new *Tarsomys.*

DIAGNOSIS: *Tarsomys echinatus* is distinguished from *T. apoensis* by the following combination of traits: (1) longer head and body, tail, and hind feet; (2) short and spiny fur, brownish gray dorsal coat and grayish ventral fur, pale appendages; (3) fewer rings of scales (per cm) on tail; (4) longer and more robust claws; (5) smaller ears; (6) smaller cranium (and narrower zygomatic plate, shorter diastema, shorter and narrower incisive foramina, shorter and narrower bony palate, and smaller auditory bullae, all probably associated with a smaller cranium); (7) absolutely shorter rostrum and also shorter relative to occipitonasal length, but wider relative to rostral length; (8) narrower braincase but also deeper; (9) much narrower bony palate relative to its length; (10) absolutely shorter molar rows but longer relative to occipitonasal length; (11) lower crowns on molars (brachyodont rather than hypsodont); (12) generally orthodont configuration of upper incisors, each incisor significantly broader and

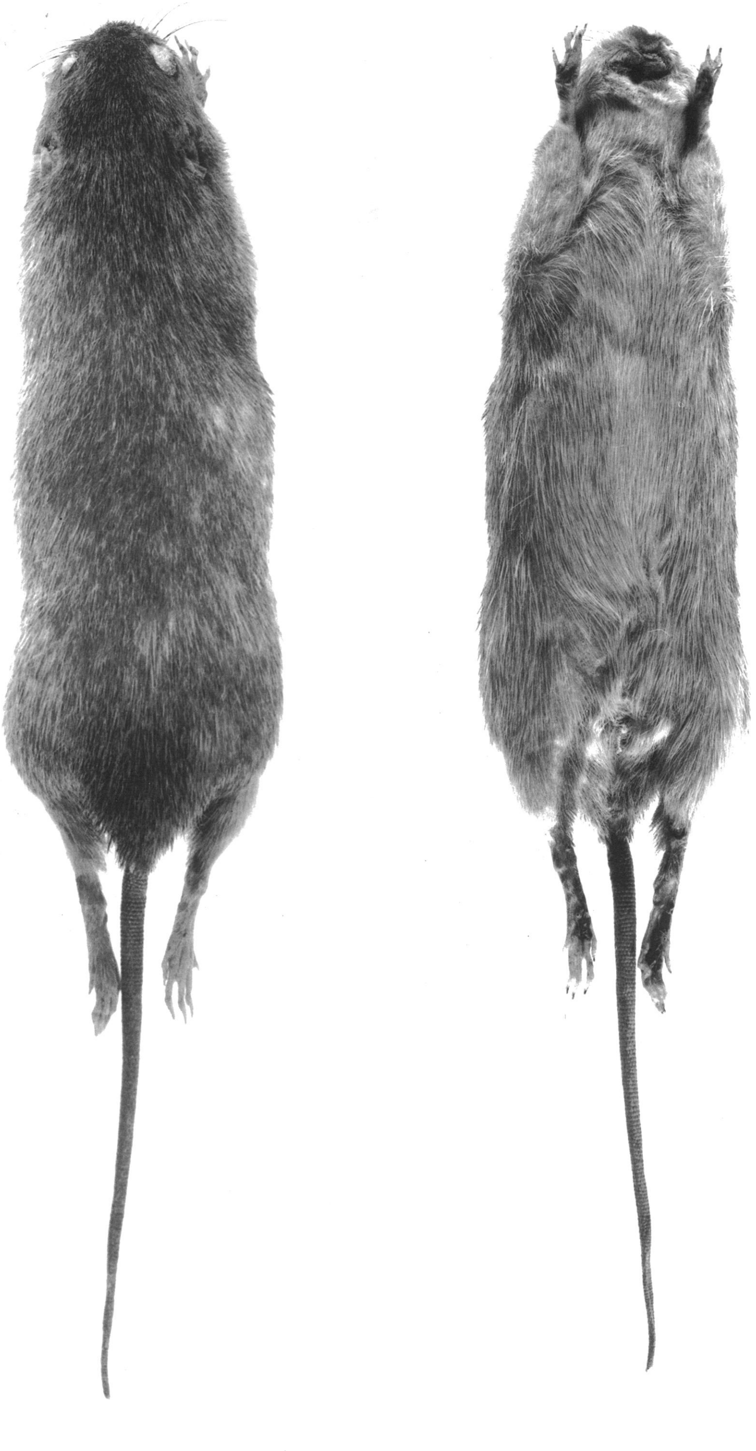

Fig. 16. An adult female *Tarsomys echinatus* (DMNH 5961): LHB, 147 mm; LT, 140 mm; LE, 19 mm; and LHF, 32 mm.

not narrower relative to its depth; (13) smaller mandible with thinner and longer coronoid process.

DESCRIPTION AND COMPARISON: Judged by traits preserved in dry stuffed skins, crania, and mandibles, *Tarsomys echinatus* is unlike any other murine known from either the Philippine Archipelago or from anywhere else in the Indo-Australian region. The species requires comparison only with *Tarsomys apoensis*. Although *T. echinatus* has a significantly longer head and body, tail, and hind foot than does *T. apoensis* (compare tables 1 and 5), the proportions of these dimensions relative to one another are similar when seen quantitatively (fig. 14) and by eye (figs. 5 and 16). Among the external appendages, the ear is an exception; it is smaller in *T. echinatus*. Specimens of *T. apoensis* not only have a larger ear but it is also longer relative to length of head and body (fig. 14). This contrast will have to be substantiated by analyses of measurements made by careful collectors from freshly caught animals. Our values (except for ear length of the holotype of *T. apoensis*) were taken from skin tags and were obtained by different collectors during different decades who may or may not have been measuring the same dimension or applying the same precision. Of all the external measurements usually made on a skin in the field, ear length seems to be most subject to carelessly defined endpoints and imprecision.

Among external traits, the most obvious differences between the two species are thickness, texture, and color of pelage. The dorsal coat of *T. echinatus* is shorter than that of *T. apoensis* (tables 1, 5), and it as well as the ventral coat is spiny, a startling contrast to the thick and soft fur of *T. apoensis*. Overfur containing very wide, flat, and stiff awns defines the dorsal pelage of *T. echinatus*, and the awns are responsible for its spinous texture. The awns are not absolutely rigid but are sufficiently inflexible that they do not bend when brushed forward. The underfur is not identifiable as a definite layer and the filamentous wool hairs that usually provide definition are instead sparsely scattered among the awns. Guard hairs are scattered among the spinelike awns and barely project beyond them (table 5). Wide, flat, and rigid awns mixed with wool hairs comprise the ventral coat. In most examples of *T. apoensis*, abundant wool hairs and thin soft awns combine to form a dense and soft coat. A few specimens have wider and stiffer awns; they resemble those in the coat of *T. echinatus* but are narrower and are scattered through the fur.

The dorsal coat in *T. echinatus* is brownish gray speckled with buff. Wool hairs are pale gray, and the awns unpigmented for most of their lengths, and both terminate in brown and buff bands; this mixture is responsible for the overall hue and tone of the dorsal pelage. The ventral coat is variable in pattern. Three specimens have a grayish white ventral coat; the wide and stiff awns are unpigmented, the filamentous wool hairs are gray with white tips. In six skins, the grayish white is broken by a wide white strip extending from chest to inguinal region; here both awns and wool hairs are white. The contrast between dorsal and ventral coats is always evident, but more sharply defined in some specimens than in others. The rich chestnut upperparts and dark buffy brown underparts of *T. apoensis* are a striking contrast to the tan and gray tones characterizing *T. echinatus*.

Tarsomys echinatus also has pale appendages compared with the dark brown ears, tail, and feet of *T. apoensis*. Ears and tail of the spiny rat are pale brown (tan) on all surfaces. Dorsal surfaces of front and hind feet are unpigmented and covered with white hairs; palmar and plantar surfaces are pale tan.

The two species share similar shapes of front and hind feet, lengths of digits relative to one another, and number of palmar and plantar pads as well as their positions. They differ in size of claws. Those of *Tarsomys apoensis* are long and sharp, particularly the ones on the front feet. *Tarsomys echinatus* has even longer claws. They are also wider and this combination of greater length and width gives each claw the appearance of a more robust element.

Cranial differences between *T. echinatus* and *T. apoensis* can be seen in measurements (tables 1, 2, and 5), proportions as expressed in a ratio diagram (fig. 14), and illustrations of head skeletons (figs. 6, 8, 17, 18, and 19).

The cranium of *T. echinatus* is similar to that of *T. apoensis* in general conformation but not in details. The spiny *Tarsomys* has a

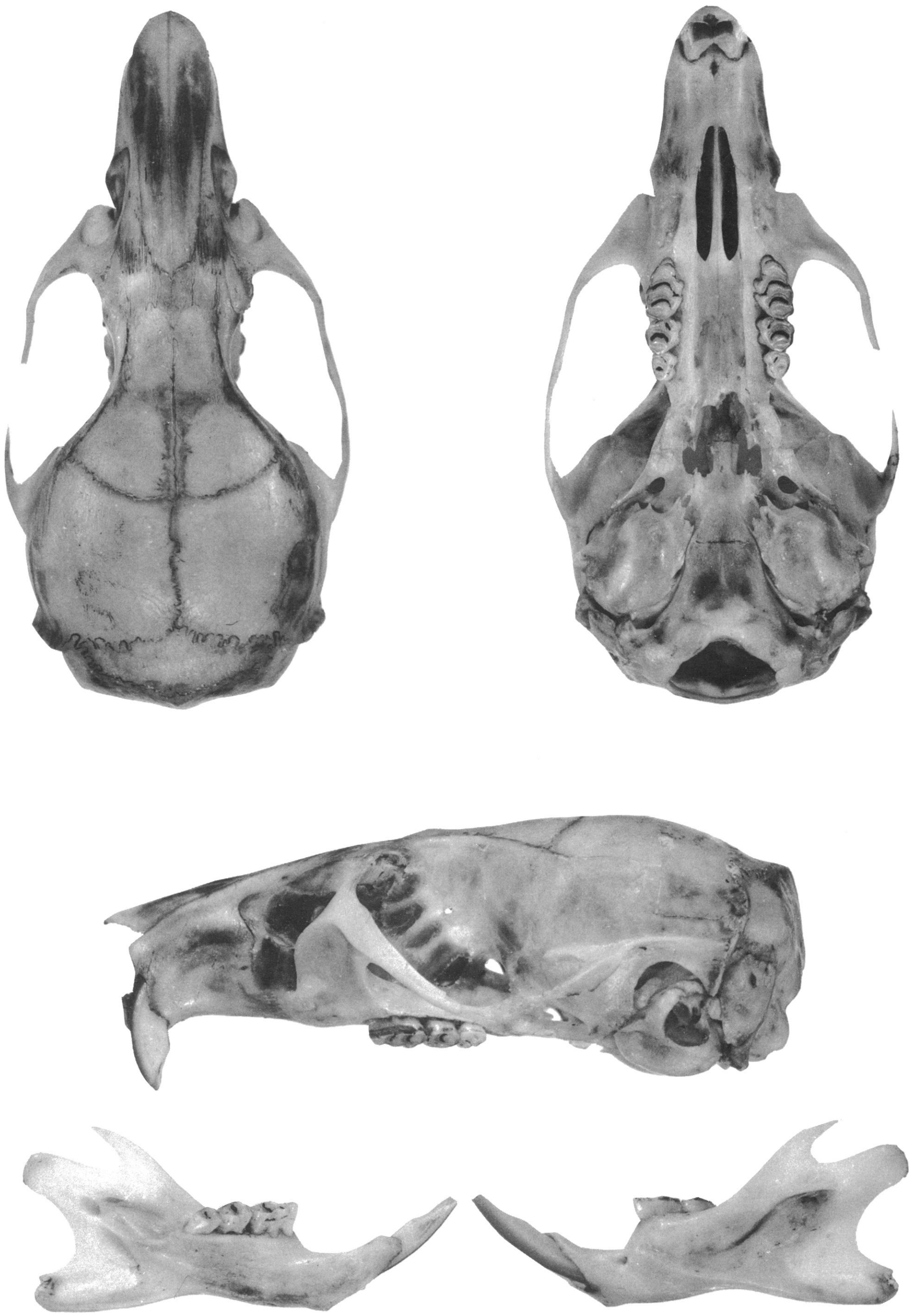

Fig. 17. Cranium and dentary (×2.5) of the holotype of *Tarsomys echinatus* (DMNH 5960), an adult male.

Fig. 18. Cranium and dentary (×2.5) of an old adult *Tarsomys apoensis* (USNM 144619).

significantly smaller cranium; a shorter and deeper rostrum that is significantly wider relative to its length; a significantly wider interorbit relative to occipitonasal length; more prominent beading on dorsolateral margins of braincase and interorbital region; a significantly narrower braincase but one that is also much deeper relative to its breadth; deeper

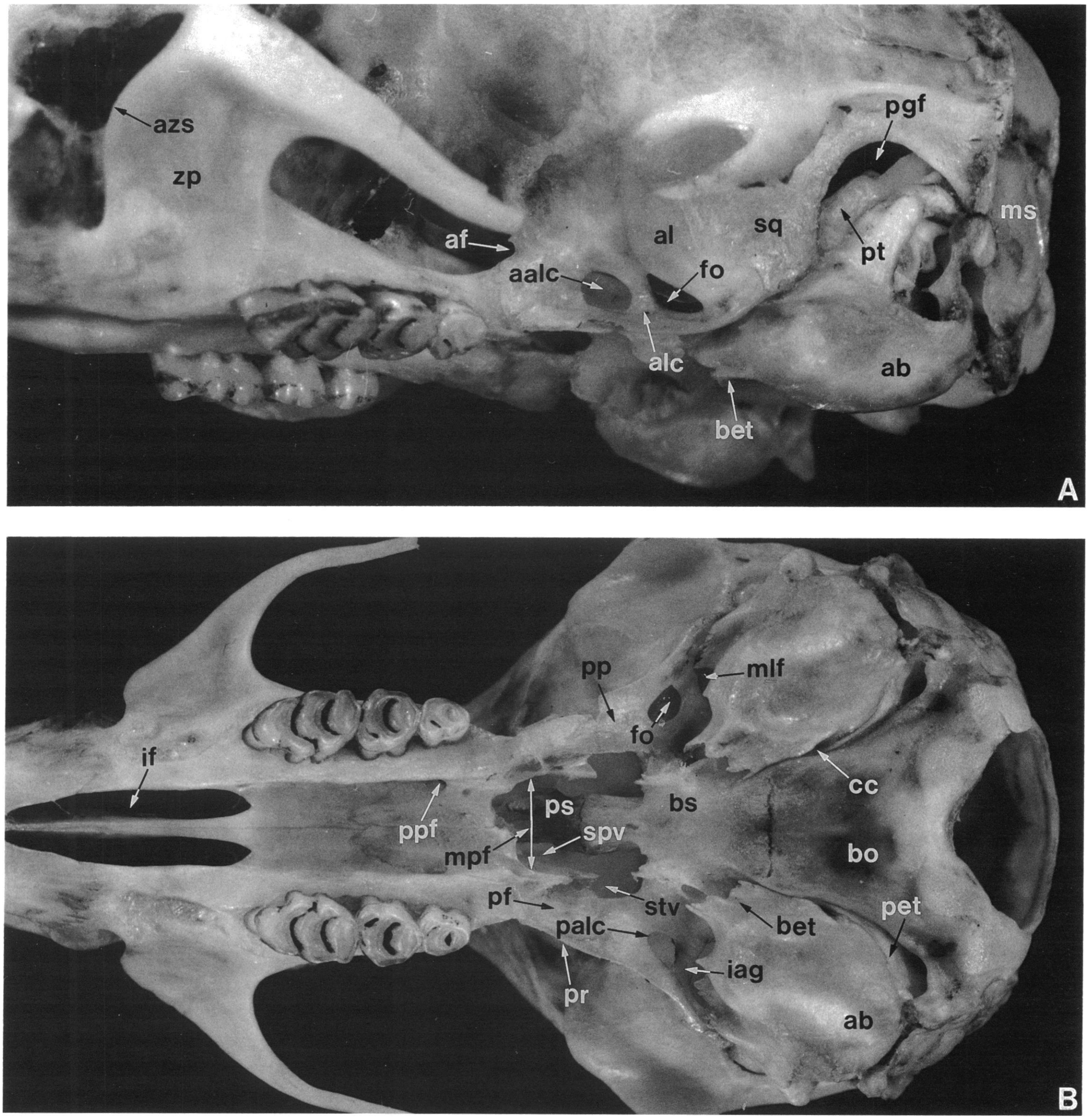

Fig. 19. Lateral (A) and ventral (B) cranial enlargements of *Tarsomys echinatus* (DMNH 5960, holotype). **aalc,** anterior opening of alisphenoid canal; **ab,** auditory bulla; **af,** anterior alar fissure; **al,** alisphenoid; **alc,** alisphenoid canal; **azs,** anterior spine of zygomatic plate; **bet,** bony eustachian tube; **bo,** basioccipital; **bs,** basisphenoid; **cc,** carotid canal; **fo,** foramen ovale; **iag,** groove for the infraorbital branch of the stapedial artery; **if,** incisive foramen; **mlf,** middle lacerate foramen; **mpf,** mesopterygoid fossa; **ms,** mastoid; **palc,** posterior opening of the alisphenoid canal (arrow points to where the infraorbital branch of the stapedial artery enters the braincase dorsal to the pterygoid plate); **pet,** petrosal; **pf,** pterygoid fossa; **pgf,** postglenoid foramen; **pp,** pterygoid plate; **ppf,** posterior palatine foramen; **ps,** presphenoid; **pt,** periotic; **pr,** pterygoid ridge; **sq,** squamosal; **spv,** sphenopalatine vacuity; **stv,** sphenopterygoid vacuity; **zp,** zygomatic plate.

zygomatic notch relative to breadth of zygomatic plate; a less expansive bony palate, being shorter and not only absolutely narrower but significantly narrower relative to its length; slightly more deeply excavated pterygoid fossae; a smaller mesopterygoid

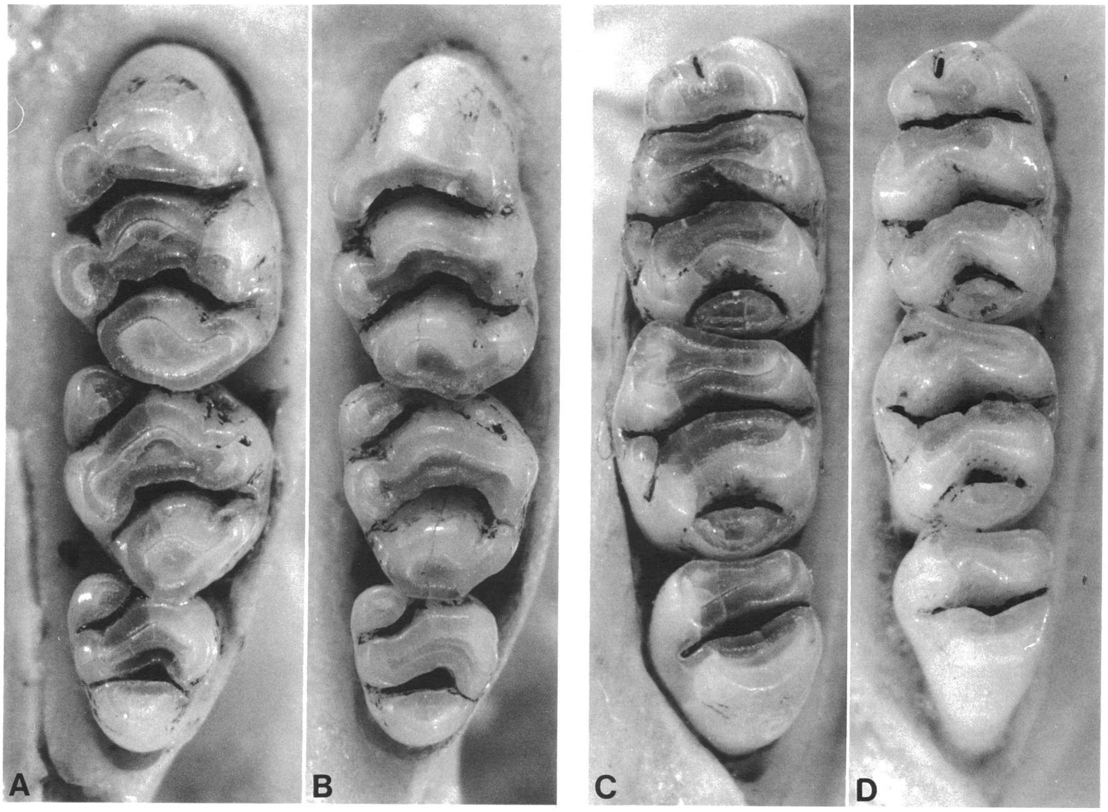

Fig. 20. Occlusal contrasts (×15) between left molar rows of two species of *Tarsomys*. **A, C,** upper and lower toothrows of *T. apoensis* (USNM 114617, very young adult). **B, D,** upper and lower rows of *T. echinatus* (DMNH 5959, young adult).

fossa relative to breadth of bony palate; a significantly longer postpalatal region; and significantly smaller auditory bullae.

Mandibular shape is similar in *T. echinatus* and *T. apoensis* (figs. 17, 18). The spiny *Tarsomys* has a slightly smaller dentary with a longer, more attenuate coronoid process.

Dental contrasts also exist. *Tarsomys echinatus* has upper incisors that are wider relative to their depth (table 3), not the slim elements which characterize *T. apoensis*. They also form an orthodont configuration relative to the rostrum in most specimens; opisthodonty is usual in our sample of the soft-furred *Tarsomys*. Molar rows are shorter in *T. echinatus*, and the teeth are low-crowned rather than hypsodont. Presence of certain cusps and cusplets varies between the two species (table 4) but our sample of *T. echinatus* in which coronal patterns persist is too small for us to properly evaluate the significance of these differences. Overall, coronal patterns of chewing surfaces in the two species are closely similar.

ECOLOGY: The short tail relative to length of head and body, long and slender hind feet, and robust long claws point to terrestrial habits for *T. echinatus*, and food acquisition by digging and scratching through leaf litter or soil. Pale ventral fur is typically associated with rats that are active during the night. Beyond these speculations we are unable to provide insight into ecology of this rat.

The essence in contrast between *Tarsomys apoensis* and *T. echinatus* is reflected in color and texture of pelage, general body and skull size, claw robustness, size and proportions of the rostrum, dimensions and proportions of the bony palate, breadth of upper incisors, and height of molar crowns. These are impressive differences, but we hypothesize that they represent the chromatic, textural, and morphological range of dissimilarity among species within a single monophyletic group, the genus *Tarsomys.* The spectacular distinction between the two species in pelage characteristics does not disallow their membership in the same clade. The Sulawesian *Margaretamys elegans,* for example, has soft and dense fur but its congener *M. beccarii* has a spiny coat, and the species are otherwise very similar in cranial and dental morphology (Musser, 1981a). Outside of pelage, the two *Tarsomys* share many derived features, and closely resemble one another in their external, cranial, and dental traits.

Tarsomys echinatus does not differ from *Rattus rattus* and its close allies in all the same ways as does *T. apoensis,* but none of the traits distinctive to the spiny *Tarsomys* suggest it to be closer to *Rattus* than to *T. apoensis.* Its spiny fur and very long and sturdy claws, for example, are not found among species in the subgenus *Rattus.* It shares many cranial characters with *T. apoensis* and not with *Rattus rattus,* and its molar cusp patterns are like those of the soft-furred *Tarsomys,* not *Rattus.*

DEFINITION OF *LIMNOMYS*

"Resembles *Mus,*" was how Edgar A. Mearns (1905: 451) introduced his characterization of the new genus *Limnomys,* "MARSH-RATS," which was based on a single animal obtained on Mount Apo at 6600 ft, June 30, 1904, on Mindanao. Mearns continued the elaboration of traits:

> Skull relatively broad and high, with flattened audital bullae; supraorbital beading slight, becoming obsolete on front of parietals; teeth of type and only specimen too worn to furnish characters distinguishing them from those of *Mus,* except that the incisors are relatively much narrower. Pelage long and dense, that of underparts resembling *Oryzomys*; tail hairy, especially near the end, where the annuli are concealed; ears moderate in size, coated on edge and outer surface with short hair; feet broad, with underside smooth and naked, with tubercles flattened, the sixth or postero-external one obsolete.

The single specimen was described by Mearns under the name *Limnomys sibuanus,* the "SIBUAN RIVER MARSH-RAT," and that taxon constituted the only species in the genus. *Limnomys sibuanus* and *Tarsomys apoensis* were described in the same report and Mearns's depiction of *Limnomys*'s characteristics resulted in an opaque view of that animal also—similar to the picture he created for *Tarsomys.* Neither generic nor specific diagnoses were provided. Without a specimen in hand, the characterizations were imprecise, rendered only a vague impression of the species, and did not identify traits that would discriminate either genus or species from other murines. Lack of illustrations only added to the frustration of dismayed readers.

Mearns's comparative allusions were to either *Mus* or *Oryzomys.* In 1905, the genus *Mus* was a wastebasket containing a plethora of related and unrelated clades, including groups that were later extracted as true *Mus, Apodemus, Rattus,* and other genera. When Mearns referred to *Mus* he was probably thinking of species that are now placed in *Rattus.* His reference to the Neotropical *Oryzomys* reflected his experience working with North American faunas, the only mammals with which he had any significant experience until his first expedition to the Philippines. Clearly Mearns was impressed with his new discoveries and if they were as distinctive as he claimed, they represented a significant addition to knowledge about mammal diversity and evolution not only on Mindanao but also in the Philippine Archipelago.

Oldfield Thomas, working at the British Museum, needed to assess the validity of Mearns's genera and so in 1906 sent Mr. Malcolm Anderson to the Philippines. According to Thomas (1907: 140),

> [the] chief object of Mr. Anderson's visit to the Philippines was to obtain series of the interesting mammals discovered in Mindanao by Dr. E. A. Mearns, as the mountain fauna of this island was only represented in our National Museum by the duplicates from Dr. Mearns's collection which the authorities of the United States National Museum had been good

> enough to send us. But these of course did not include any of the various new genera and species which had been described by Dr. Mearns on single specimens or on small series, and we therefore hoped that Mr. Anderson might be able to obtain some of them for us.

Mr. Anderson, unfortunately, was "attacked by fever" and could only assemble a small collection until he "was compelled to return to more northern and healthier latitudes." While no examples of either *Limnomys* or *Tarsomys* were caught, Anderson did collect a specimen of *Bullimus bagobus,* a genus and species Mearns had also described in his 1905 report. Thomas (1907: 141) reported the specimen under the combination *Mus bagobus* and also his discontent with Mearns's taxonomic judgments:

> I fail to see any sufficient reason for the creation of a special genus to contain this species. The small supplementary cusps on the lower molars, on which Dr. Mearns mainly founds the genus, are not only present in many Malayan species usually referred to *Mus* [now *Rattus*] but they are even quite well-marked, though small, in his own specimens of *Mus albigularis* Mearns [*Rattus albigularis*], also from Mindanao. None of the other characters mentioned by him appears to me of generic importance.
>
> It is unfortunate that Dr. Mearns had not had experience of the difficulties of Murine dental characters before venturing to describe genera of this group. Had he had such experience I am sure he would not have described *Bullimus,* nor would he have based another genus (*Limnomys*) on a single specimen with teeth 'too worn to furnish characters distinguishing them from *Mus,*' unless the other characters were of a far more striking nature than appears from his account.

This pronouncement on the validity of *Limnomys* was not incorporated into the faunal studies of either Hollister (1913) or Taylor (1934)—both authors recognized *Limnomys* as a valid genus—but was reinforced by Ellerman in 1941 who wrote that "From the original description, this genus has not a single character to distinguish it from *Rattus*" (p. 295). In 1945 the opinions of Thomas and Ellerman, both of whom had never seen any examples of *Limnomys* (or *Tarsomys* for that matter) were transformed into holy writ by Simpson (1945: 89) who included *Limnomys* as part of the genus *Rattus* in his classification of mammals. Misonne's monograph on evolutionary trends in African and Indo-Australian murids, published in 1969, retained *Limnomys* in *Rattus* and without supporting documentation implied it was part of the subgenus *Bullimus* of the genus *Rattus* (p. 141). There *Limnomys* stayed until the 1970s when it regained its generic status in taxonomic reviews and checklists (Alcasid, 1970; Musser, 1977b; Musser, 1981b; Carleton and Musser, 1984; Heaney et al., 1987; Corbet and Hill, 1991).

Between 1905 and the time of this writing, four more specimens have been collected, all from Mindanao. This series plus the holotype of *Limnomys sibuanus* still form a small sample but its composition of adults and juveniles from two mountains allows us to present a diagnosis and description of the genus and species, and discuss its possible relatives. This information contributes to the picture of mammalian evolutionary diversity within the Archipelago.

LIMNOMYS MEARNS

TYPE SPECIES: *Limnomys sibuanus* Mearns (1905: 451).

INCLUDED SPECIES: Only one, *L. sibuanus.* In 1913, Hollister described two other species of *Limnomys*: *L. mearnsi,* documented by three specimens from Mount Malindang on Mindanao, and *L. picinus,* known by a single specimen from Mount Halcon on the island of Mindoro. Musser (1977b) explained that the diagnostic features of *mearnsi* were those of young animals in mostly juvenile pelage, and distinctions between them and the holotype from Mount Apo in body size, fur coloration, and morphology of skin, skull, and teeth were ontogenetic, not phylogenetic (the cranial dissimilarities, for example, between the adult holotype of *sibuanus* and the juvenile-adult holotype of *mearnsi* illustrated in fig. 1 of Musser, 1977b: 5). No evidence supported the hypothesis that the four specimens represented two species, and Musser treated *mearnsi* as a synonym of *L. sibuanus.* The holotype of *picinus* turned out to be a composite specimen: the skin was a juvenile example of *Rattus mindorensis* and the skull was a young *Limnomys* that really belonged to one of the animals from Mount Malindang, so *picinus* disappeared into the synonymy of *Rattus mindorensis.*

KNOWN DISTRIBUTION: Mount Apo and Mount Malindang on the island of Mindanao

TABLE 6
Measurements (mm) and Body Weight (g) of *Limnomys sibuanus* from Mount Apo (6600 ft) and Mount Malindang (6200-7000 ft, 9000 ft) on the Island of Mindanao

	Mount Apo	Mount Malindang			
	USNM 125228[a]	DMNH 5956	USNM 144620	USNM 144621	USNM 144622[b]
Age	adult	adult	very young adult	juvenile–adult	juvenile–adult
LHB	125	129	105	102	87
LT	150	155	136	138	133
TSR/cm	14	14	14	14	15
LHF	30	30	29	29	28
LE	21	21	20	20	19
LOF	13	13	12	10	10
LGH	25	20	15	15	15
BW	—	57	—	—	—
GLS	33.2	32.5	29.8	—	28.5[c]
ZB	16.2	14.9	15.2	—	14.5
IB	4.9	4.7	4.7	4.8	4.5
LR	9.4	9.5	8.9	8.6	8.2[c]
BR	5.8	5.6	5.2	5.3	4.8
BZP	2.7	2.8	2.4	2.2	2.3
DZN	1.1	0.8	1.3	1.3	1.1
BBC	14.8	14.1	14.4	—	14.0
HBC	10.1	9.8	9.9	—	9.7
LD	8.3	8.3	6.8	6.7	6.4
PPL	11.6	11.6	9.8	—	9.3
LIF	6.2	6.6	5.4	5.5	5.4
BIF	2.1	2.2	2.0	2.1	1.9
LBP	4.8	4.6	5.0	4.9	4.5
BBPM1	3.0	2.9	2.7	2.5	2.3
BMF	2.3	2.2	2.0	2.3	2.0
LB	5.6	5.9	5.7	—	5.0
CLM1-3	4.8	4.8	5.2	5.2	5.1
BM1	1.5	1.7	1.8	1.8	1.7

[a] Holotype of *Limnomys sibuanus.*

[b] Holotype of *Limnomys mearnsi.*

[c] These values are estimates; 0.5 mm of the nasal tips are missing.

in the Philippine Archipelago (fig. 4, localities 6–8).

ETYMOLOGY: *Limnomys* results from the combination of the Greek *limne,* for marsh, with *mys,* Greek for mouse or rat. The trapping site on wet vegetation along a small stream influenced Mearns's selection of a name.

DIAGNOSIS: A genus of murine rodent characterized by the following combination of traits: (1) body size small, tail much longer than head and body, hind feet moderately long and slender with six plantar pads including a large hypothenar; (2) claws short, sharp, and recurved; (3) pelage long, soft, and thick, dorsal coat tawny, ventral coat white, tail monocolored brown except for white tip; (4) six mammae (postaxillary pair and two inguinal pairs); (5) rostrum short relative to greatest length of skull; (6) braincase domelike, mostly smooth and rounded, interorbital and postorbital regions framed by weak ridges, foramen magnum directed posteroventrad; (7) narrow zygomatic plate with slight notch; (8) long incisive foramina; (9) bony palate narrow and short, barely projecting beyond posterior margins of third molars; (10) shallow pterygoid fossae with small spenopterygoid vacuities, mesopterygoid fossa breached by spacious sphenopalatine vacuities; (11) groove in posterior section of pterygoid plate for infraorbital branch of stapedial artery, large stapedial foramen (primitive murine cephalic arterial pattern); (12) alisphenoid strut absent; (13) auditory bullae moderately inflated; (14) dentary with delicate coronoid and elongate condylar process; (15) incisors asulcate, uppers slim and orthodont in relation to rostrum, lowers slender and sharp; (16) molar teeth chunky (wide relative to their length) and slightly hypsodont, each first upper molar anchored by five roots, each second by four, the third by three, each first lower molar with four roots, each second and third molar with three; (17) occlusal surfaces of molars formed mostly from wide and thin ridgelike laminae well separated from one another, cusp t3 conspicuous on first upper molar, present and large on second and third molars, cusp t9 coalesced with an elongate flange of cusp t8, cusps t4 and t8 merge forming notched or complete enamel wall along posterolingual margin on each first and second upper molar, cusp t4 and t8 tightly abut on each third molar, cusp t7 absent from all upper molars, posterior cingulum on first and second upper molars, anterocentral cusp present on all specimens, anterior labial cusplets occur on all lowers except first molar in some specimens, posterior labial cusplet found on all lower molars.

LIMNOMYS SIBUANUS MEARNS

HOLOTYPE: USNM 125228, an adult female collected by Edgar A. Mearns (original number 5688) from Mount Apo (locality 8 on the map in fig. 4) at 6600 ft, Davao City Province, southern Mindanao on June 30, 1904. The stuffed museum skin, cranium (illustrated in Musser, 1977b: 5, fig. 1), and mandible compose the holotype; all are preserved in good condition. Measurements of the holotype are listed in table 6.

REFERRED SPECIMENS AND LOCALITIES: In addition to the holotype we are aware of only four other examples of *L. sibuanus*; they are listed below within each numbered locality. That number corresponds to the numbered symbol on the map in figure 4.

6. Misamis Oriental Province, Mount Malindang, 6200–7200 ft: DMNH 5956 (adult female, caught January 6, 1963).

7. Misamis Oriental Province, Mount Malindang, 9000 ft: USNM 144620 (very young adult male), 144621 (juvenile-adult female), and 144622 (juvenile-adult female), all caught on June 6, 1906.

DISTRIBUTION: *Limnomys sibuanus* has been collected from two mountains on the island of Mindanao. The known altitudinal range, as represented by museum specimens, is from 6200–7000 to 9000 ft, elevations falling within tropical upper montane rain forest (Whitmore, 1984a).

ETYMOLOGY: The species name, *sibuanus,* refers to the small stream which becomes the Sibuan River in its lower course. Mearns caught the holotype on a bank of this stream.

DIAGNOSIS: The specific and generic diagnoses are the same.

DESCRIPTION: *Limnomys sibuanus* adults are small-bodied rats with a long tail and elongate hind feet (fig. 21). Upperparts of head and body are clothed in tawny pelage; underparts are white. Dense, moderately long (up to 13 mm), and soft, the dorsal coat consists of two layers and three types of hairs. Soft, filamentous wool hairs form the underfur. Each hair is gray for most of its length and tipped with pale buff. Most hairs that compose the overfur are long, soft, and thin; each is dark gray for about two-thirds of its length and then banded with blackish brown and bright buff. It is the combination of pigmented bands which imparts the rich tawny to the dorsal coat. The back is slightly darker than the sides because here there are more awns with blackish bands. Scattered through the coat are flat and wide awns which are translucent and have a brownish tip. They are less flexible than the other awns and give the coat a silver sparkle and slight resistance when the fur is brushed back. Glossy guard hairs project (up to 12 mm) beyond the overfur layer and form a conspicuous component of the coat.

The soft and short ventral fur is also composed of two layers. Wool hairs form the underfur. Soft and thin as well as flattened semirigid awns define the overfur. All hairs are white from tip to base; only along the sides of the body is there a slight infusion of pale gray in the otherwise white ventral coat. The ventral coat is sharply demarcated from the dorsal fur. Aside from this contrast, no other

Fig. 21. An adult female *Limnomys sibuanus* (DMNH 5956). Measurements are listed in table 6.

color pattern (facial mask, stripes, pectoral or inguinal patches, for example) breaks up either the solid tawny dorsum or white venter.

The usual murine arrays of mystacial, submental, superciliary, genal, and interramal vibrissae are present in *L. sibuanus.* Submental and interramal vibrissae are unpigmented; most of the others are glistening dark brown.

Ears are brown. Both inner and outer surfaces of the pinnae are densely covered with short brown hairs.

Juveniles also have white ventral coats but their dorsal pelage is a dull and dark grayish brown, a striking contrast to the bright tawny buff of the adult. The juvenile coat is shorter than that of adults, much softer, and very thick. It has a wooly appearance. The dark tone was one of the primary features Hollister (1913: 324) used to characterize *L. mearnsi*: "Upperparts an indefinite dull grayish-brown, the pelage long and soft, deep neutral gray, tipped with dull brown." The holotype of *mearnsi* (USNM 144622) is clothed in mostly juvenile pelage; replacement hairs of the adult coat lie beneath the juvenile fur. Juveniles also have paler tails but darker ears than do adults.

Out of the five examples of *L. sibuanus,* four are females and each one has three pairs of mammae: one postaxillary and two inguinal pairs.

The tail of *L. sibuanus* is much longer than combined lengths of head and body (table 6; fig. 21). It is brown on all surfaces except the tip which is white for 7–10 mm in adults. Three hairs emerge from the base of each epidermal tail scale, and the scales are small (14 overlapping rings of scales per centimeter on adults; table 6). Each brown scale hair is long, extending over 3–4 scales, and the tail appears well haired rather than naked.

Dorsal surfaces of front feet are white: the integument is unpigmented and the foot is densely covered by white hairs. These hairs extend along the digits to bases of the claws where they form short tufts. The stubby pollex is covered by a wide and curved nail; the other digits are long and end in short, recurved, and sharp claws, similar to those found in species of *Margaretamys,* for example (Musser, 1981a: 278, fig. 26). The palmar surface is tan and consists of three small interdigital pads and two large metacarpal mounds.

Hind feet of *L. sibuanus* are long and narrow. A wide brown strip covers the dorsal metatarsal surface of each foot; the sides are white as are the digits. Claws are short, recurved, and sharp. The digits are long. The hallux, although short, extends beyond the bases of the three medial digits (hallux just reaches the bases in species of *Tarsomys,* which are probably strictly terrestrial). The fifth digit is relatively long, extending to the base of the claw of the fourth digit. Relative lengths of the digits resemble the proportions characteristic of species of *Margaretamys* (Musser, 1981a: 279, fig. 27). Plantar areas are tan and on the naked surface of each one are four large interdigital pads, a large and elongate thenar, and an oblong hypothenar. Although smaller than the thenar, the hypothenar is a prominent mound. We cannot detect any small accessory tubercles but if present they would be extremely difficult to see on the desiccated and wrinkled skin.

In general form, the cranium of *L. sibuanus* is defined by a short rostrum, moderately constricted interorbit, narrow zygomatic plates, large round braincase, and slender zygomatic arches that do not project very far from the braincase, features evident in the dorsal, ventral, and lateral cranial views shown in figure 22 (cranial measurements are listed in table 6). The short, slightly tapered rostrum is somewhat wider than the interorbit. That area is bounded by low and inconspicuous ridges that continue caudad to outline dorsolateral margins of the postorbital region and extend onto the forward part of the braincase as faint temporal beading. But the tracing is inconspicuous and from dorsal view the braincase is rounded (rather than rectangular or squarish as in *Rattus rattus,* fig. 23, a pattern formed by high and prominent postorbital and temporal shelves and ridges) and the interorbital region is shaped like an hourglass.

In lateral view, the high dome of the braincase marks the highest point of the cranial profile, which sweeps down and back to the occiput and forward in an unbroken line to the nasal tips. The outline reflects the flexion of the cranium, which results in a foramen magnum directed posteroventrad and an oc-

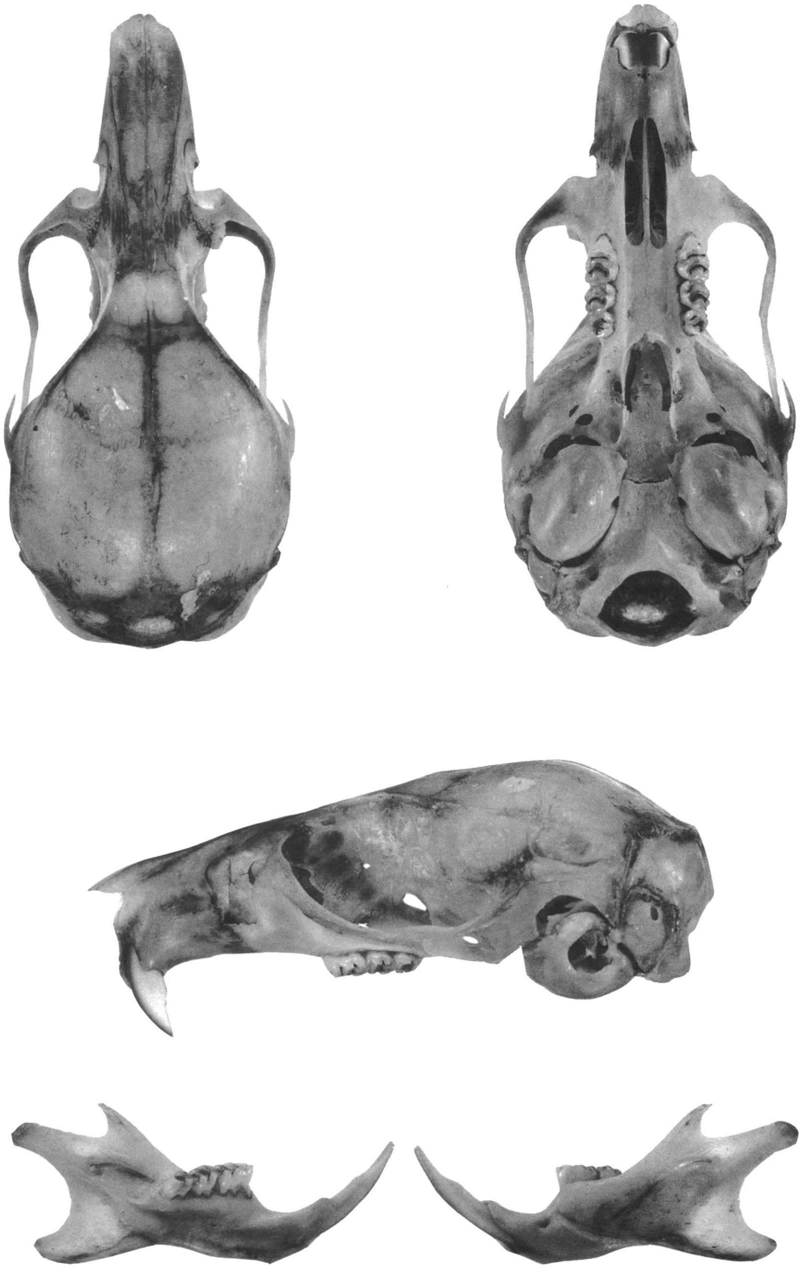

Fig. 22. Cranium and dentary (×2.5) of an adult *Limnomys sibuanus* (DMNH 5956).

ciput that appreciably overhangs the occipital condyles. The occipital region is deep (from front to back) and is roofed by about two-thirds of the interparietal. The squamosal root of each zygomatic arch originates low on the braincase and its posterior shelflike process does not extend all the way to the lambdoidal ridge. The squamosal anterior to the lambdoidal ridge and above the bulla is complete, not perforated by a squamosomastoid fenes-

Fig. 23. Cranium and dentary (×2.5) of an adult Sulawesian *Rattus rattus* (AMNH 227767).

tra, an opening which in *L. sibuanus* is confined to the suture between squamosal and mastoid. The lateral portion of each mastoid segment of the petromastoid complex is large, squarish in outline, and slightly inflated; its lateral surface is smooth, convex, and perforated by a small opening in most specimens. A fissure, the postglenoid foramen, separates the squamosal margin from each auditory bulla. There is also a gap, the middle lacerate foramen, between bullar margin and caudal edge of each pterygoid plate. These gaps are narrow in the holotype and slightly wider in the other adult, DMNH 5956; each bulla is tightly attached to the neurocranium compared with a species like *R. rattus* in which the middle lacerate foramen is usually confluent with the postalar fissure (see Wahlert, 1985: 324) and postglenoid foramen, which separates the bullar capsule from the squamosal and alisphenoid bones.

Each zygomatic plate is narrow with an inconspicuous spine barely projecting anterior to the dorsal zygomatic root. As a result, the zygomatic notch (best seen from dorsal perspective) is a shallow indentation.

The configuration of each alisphenoid region anterior to the bullae and dorsal to the pterygoid plate (fig. 24A) closely resembles the conformation present in *Tarsomys apoensis* that we have already described: the alisphenoid canal is open in most specimens, not concealed by a lateral strut of bone, foramen ovale accessorius has coalesced with buccinator and masticatory foramina, and the small anterior opening of the alisphenoid canal is separate from the larger foramen ovale—both are exposed in side view. An exception is DMNH 5956 in which an alisphenoid strut is absent from the left side but present on the right side as a slim strut enclosing the alisphenoid canal but not obscuring the adjacent foramina.

A ventral view offers a different perspective of the cranium in *L. sibuanus* (figs. 22, 24B). Long incisive foramina project between the molar rows in most specimens (table 2). The bony palate is narrow and short, its posterior margin barely projecting past the caudal edge of each third molar; its surface is scored by a pair of deep palatine grooves. Opposite the gap between each second and third molar is a posterior palatine foramen. Walls of the wide mesopterygoid fossa are fissured by spacious sphenopalatine vacuities. Each pterygoid fossa is excavated but only shallowly, and is complete except for a small sphenopterygoid perforation. The flat edge of each pterygoid plate transforms into a ridge at about the level of the foramen ovale. Medial to the ridge is a deep groove in which the infraorbital branch of the stapedial artery courses. The spot where the artery passes to the dorsal surface of the pterygoid plate defines the posterior opening of the alisphenoid canal (fig. 24B). The opening of the carotid canal is conspicuous between bullar capsule and basioccipital, and there is a large stapedial foramen between bullar capsule and petrosal (obscured by the inflated capsule margin). This configuration of the groove in the pterygoid plate, position of the caudal opening of the alisphenoid canal, and large stapedial foramen reflect the primitive murine cephalic arterial pattern, one that is also shared by both species of *Tarsomys.*

Each bulla is moderately large and inflated. Its medial sagittal plane is oriented relative to the basicranium at an angle similar to that in *Tarsomys apoensis* (fig. 9). Each bony eustachian tube is a wide but very short projection from the capsule.

Each dentary of *L. sibuanus* has a delicate appearance. This effect is probably projected by the small coronoid process, the slim and long condyloid, the deeply concave caudal margin, and the reduced area of the angular process. The capsular process forms a bulge just below the coronoid. On the medial surface of the dentary the mandibular foramen is dorsal to a narrow ridge extending from the bony molar platform to the base of the condylar process.

Limnomys sibuanus has asulcate, slim upper incisors; each is much narrower relative to its depth than in species such as *Rattus rattus,* for example (table 3; fig. 15). The enamel surfaces are orange and the teeth emerge from the rostrum at a right angle (orthodont in conformation). Lower incisors are also narrow, and sharp, but the enamel is paler.

Multiple molar roots are typical in all the specimens of *L. sibuanus* we have studied. The number anchoring each tooth as well as their size and position relative to one another

Fig. 24. Lateral (**A**) and (**B**) cranial enlargements of *Limnomys sibuanus* (DMNH 5956). **aalc,** anterior opening of alisphenoid canal; **ab,** auditory bulla; **af,** anterior alar fissure; **al,** alisphenoid; **alc,** alisphenoid canal; **azs,** anterior spine of zygomatic plate; **bet,** bony eustachian tube; **bo,** basioccipital; **bs,** basisphenoid; **cc,** carotid canal; **fo,** formen ovale; **iag,** groove for the infraorbital branch of the stapedial artery; **if,** incisive foramen; **mlf,** middle lacerate foramen; **mpf,** mesopterygoid fossa; **ms,** mastoid; **palc,** posterior opening of the alisphenoid canal (arrow points to where the infraorbital branch of the stapedial artery enters the braincase dorsal to the pterygoid plate); **pet,** petrosal; **pgf,** postglenoid foramen; **pp,** pterygoid plate; **ppf,** posterior palatine foramen; **ps,** presphenoid; **pt,** periotic; **pf,** pterygoid fossa; **pr,** pterygoid ridge; **sq,** squamosal; **spv,** sphenopalatine vacuity; **stv,** sphenopterygoid vacuity; **zp,** zygomatic plate.

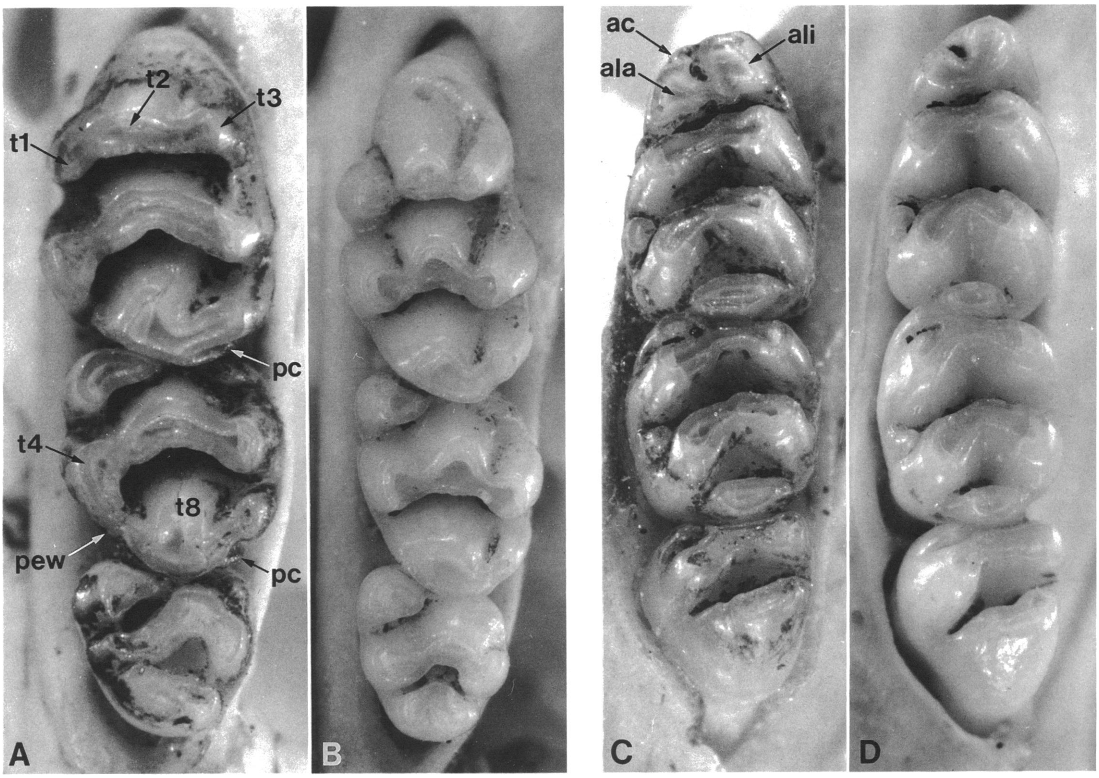

Fig. 25. Occlusal contrasts between left molar rows of *Limnomys* (×18) and *Rattus* (×15). **A, C,** upper and lower toothrows of *L. sibuanus* (USNM 144621, juvenile-adult). **B, D,** upper and lower rows of Sulawesian *R. rattus* (AMNH 101272, very young adult). Note the posterior cingulum (**pc**) at the back of each first and second upper molar of *L. sibuanus* and its absence in *R. rattus*. Each second upper molar of *L. sibuanus* also has a posterolingual enamel wall (**pew**) formed by the posterior extension of cusp t4 and an anterolingual projection from cusp t8; such a structure is absent in *R. rattus*. Other differences between the two species illustrated here are also explained in the text. **ac,** anterocentral cusp; **ala,** anterolabial cusp; **ali,** anterolingual cusp.

mirror the pattern we described for *Tarsomys apoensis,* a pattern illustrated by the alveolar groupings in figure 10.

Other general molar traits common to species of *Tarsomys* are also shared by specimens of *Limnomys*: inclined rows of cusps which result in slight molar overlap, and decrease in molar size within each toothrow.

Molars of *Limnomys* are slightly hypsodont, a configuration shared with *T. echinatus* but not with *T. apoensis,* which has very hypsodont molars. The teeth are also broad. Their coronal exposures express a suite of features distinctive for *L. sibuanus.* Occlusal surfaces of young animals are partly cuspidate and partly in the form of thin arcuate laminae, each separated from the other by a wide gap (fig. 25).

There are three laminae in each first upper molar. A slightly sinuous and nearly transverse lamina forms the anterior margin of the tooth. The width is a function of a stretched central cusp t2 as well as a labial cusp t3 that is nearly in the same plane as the central cusp and a lingual cusp t1 that is small relative to the other cusps and set slightly posterior of cusp t2, a configuration clearly shown in figure 25A. The second lamina is also wide and thin but is bowed, not nearly straight. The lingual part of the bow terminates in a large and angular cusp t4 which abuts against an enamel lingual projection from cusp t8 to form a wall with a shallow notch between cusps t4 and t8 (figs. 25A, 27A), and merges with it in worn molars (fig. 26). The third and posterior lamina consists of a large and somewhat triangular cusp t8 and a long ridge formed from the labial extension of cusp t8 which has completely coalesced with cusp t9. That ridgelike cusp projects anteromedially but does not contact the caudal projecting cusp t6 of the second lamina, even in worn molars. At the back of each molar is a conspicuous posterior cingulum, again ridgelike in form, projecting labially from the back of the central cusp t8. A cusp t7 is not present. In species where that cusp is usual, it is found between cusps t4 and t8; in *Limnomys,* that space is occupied by an enamel and dentine wall representing the coalescence of those cusps along the lingual margin of the molar.

Most of the occlusal surface of the second upper molar is formed of two laminae that in size and shape closely resemble the second and third laminae of the first molar (fig. 25A). The cuspidate framework of the lamina are more apparent in the second molar of young rats, such as that pictured in figure 25A, than in the first tooth. For example, the broadly arcuate anterior lamina on the second molar clearly consists of a round labial cusp t3, a stretched central cusp t5, and a large cusp t4 which tapers caudally and merges with a ridgelike lingual flange of cusp t8 to form a high enamel wall defining posterolingual margin of the tooth (figs. 25A, 27A). That large rounded central cusp forms most of the posterior lamina of the second molar. In addition to its anteromedially projecting lingual flange, it also has a labial process that extends to the round cusp t9 on the labial margin of the tooth. The rest of the chewing surface is formed by a large cusp t1 forming the anterolingual surface, a ridgelike cusp t3 (present in all the specimens studied), and a small posterior cingulum projecting labially from the back of cusp t8. All these structures are visible in figure 25A. Cusp t7 is missing from the coronal pattern on the second molar, although a minute enamel bump on top of the ridge connecting cusps t4 and t8 of some specimens might mistakenly be taken for that cusp.

Chewing surface of each third upper molar is formed from a large cusp t1 similar in shape to the comparable cusp on the second molar; a small but prominent cusp t3 (found in four out of the five specimens, table 4); a comma-shaped thin lamina consisting of cusps t4, t5, and t6 in which the cuspidation is not evident; and a slightly bowed and thick lamina composed of cusps t8 and t9 which forms the posterior margin of the tooth (fig. 25A). The comma-shaped and posterior laminae abut tightly at their lingual margins (involving cusps t4 and t8). Neither cusp t7 nor posterior cingulum is present.

Fig. 26. Occlusal views (×18) of right upper and lower molar rows of an adult *Limnomys sibuanus* (DMNH 5956). Note the differences between this stage of wear and that of the young rat depicted in figure 25.

Lower molars of *L. sibuanus* are also mostly laminar in occlusal topography (fig. 25C). Anterior and posterior labial cusplets are part of the occlusal surface of every tooth in most of the specimens. The anterior labial cusplet

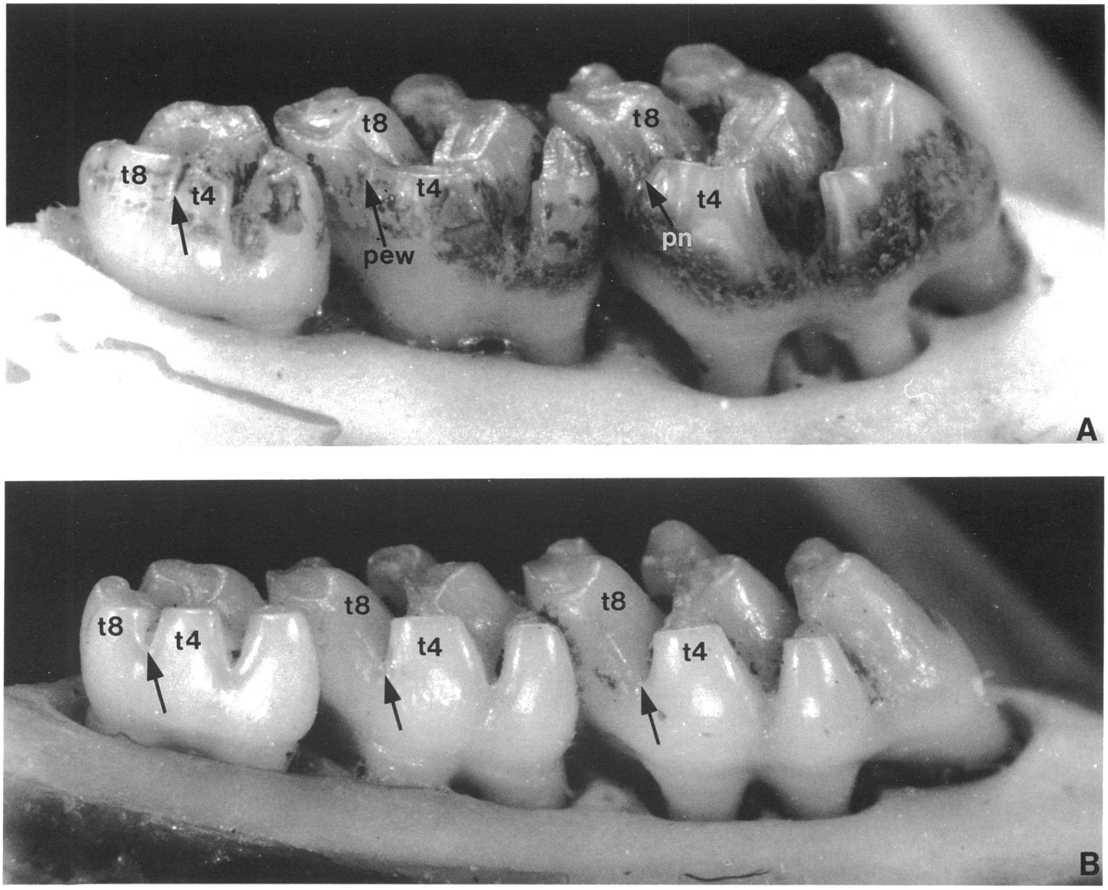

Fig. 27. Lingual contrasts between the right upper molars of *Limnomys sibuanus* (**A**, USNM 144621; CLM1–3 = 5.2) and Sulawesian *Rattus rattus* (**B**, AMNH 101272; CLM1–3 = 6.5). Note the wide and deep valley (indicated by arrow) between cusps t4 and t8 on each molar of *R. rattus.* In the first molar of *L. sibuanus,* cusps t4 and t8 are separated by a shallow posterolingual notch (**pn**), in the second molar the cusps form a posterolingual enamel wall (**pew**), and in the third molar, the cusps are close together (arrow).

on the first molar is the only exception; it is absent from two of the five specimens we examined (table 4). The posterior cingulum forming the back of each first and second molar is in the form of a wide and thick ridge, not a round or oblong cusp.

On the first molar the anteroconid is thick and bulky. It consists of a large squarish (in occlusal view) anterolingual cusp, a slightly smaller anterolabial, and a small anterocentral cusp plastered on the front of the tooth, a feature found in all specimens (table 4). Each second and third of the three laminae forming the occlusal surface of the second molar is wide and slightly chevron-shaped in occlusal plane. A small but prominent anterolabial cusp forms the anterolabial margin of each second lower molar. The two laminae forming most of its surface are gently bowed. An anterolabial cusp, nearly straight anterior lamina, and thick posterior lamina form the coronal surface (crown) of each third lower molar.

ECOLOGY: The holotype of *L. sibuanus,* according to Mearns (1905: 452), "was trapped on a wet, mossy growth of vegetation, on the left bank of a little stream which in its lower course becomes the Sibuan River, flowing from Mount Apo." He lamented that "in spite of persistent efforts we failed to procure other specimens." This note remains the only ecological information ever recorded for *L. sibu-*

anus. Mearns either learned more about the species or was luckier two years later because he trapped three young examples on Mount Malindang. If he recorded information about where he trapped them we have not yet uncovered it. The fifth specimen, caught on the same mountain in the 1960s, is also unaccompanied by habitat description.

The allusion to marsh habitat as implied by the name of the genus is unfortunate, for nothing about the animal, even the trap site of the holotype, suggests it is adapted for that kind of environment. Its external form—long tail relative to length of head and body, long and slender hind feet, short and recurved claws, long digits, prominent palmar and plantar pads—point to a scansorial or possibly arboreal mode of life. If past trapping efforts were focused on terrestrial habitats, *L. sibuanus* may have been infrequently encountered because of its more frequent occurrence on substrates above ground level. New expeditionary efforts involving careful trapping and habitat documentation are clearly needed before we can even begin to understand the ecology of this Mindanao montane forest endemic.

GEOGRAPHIC VARIATION: Available samples of *L. sibuanus* consist of an adult from Mount Apo and an adult and three younger rats from Mount Malindang. The two adults resemble each other closely in body size, color and texture of fur, and cranial and dental morphology as well as cranial and dental measurements (table 6). We detect no evidence from these sources suggesting the small samples were drawn from different populations. Whether or not significant geographic variation exists, and is concordant with a pattern of population isolation in insular montane habitats, can only be answered by study of larger samples gathered from many more locales.

COMPARISONS: *Limnomys sibuanus* requires comparisons with *Anonymomys mindorensis* and species of *Rattus*, which are presented below.

Limnomys and *Anonymomys*

Anonymomys mindorensis is represented by three specimens trapped at 4500 ft from Ilong Peak in the Halcon Range of Mindoro (Musser, 1981a). Of all the species of murines native to the Philippines, only *A. mindorensis* resembles the Mindanao rat in external form and general cranial conformation, resemblances which prompted Musser (1981a: 310) to contrast the two when he described the Mindoro endemic. Both, for example, are about the same body size (see table 10 in Musser, 1981a: 302), both have tawny upperparts, white venters, long brown tails, and long hind feet relative to body length. These, however, are gross similarities. The dorsal pelage of *A. mindorensis* is semispinous and harsh, the tail is much longer relative to length of head and body (see table 10 in Musser, 1981a: 302), and it is more densely haired with a pronounced brush at the end.

The Mindoro and Mindanao animals share a common murine cranial shape and form of incisors and molars. The two species differ significantly, however, in the structural details enumerated by Musser (1981a: 310). Some of these dissimilarities represent the retention of primitive traits in *A. mindorensis,* enumerated below, and its derived expression in *L. sibuanus,* which are given in parentheses. The Mindoro species has a wide and robust alisphenoid strut (absent or threadlike in *L. sibuanus*), narrow sphenopalatine vacuities (spacious), small auditory bullae relative to size of cranium which are also tightly attached to squamosal and alisphenoid bones (larger bullae separated from squamosal and alisphenoid by wide gaps), upper molars with three roots, lower molars with two roots (multirooted molars in *L. sibuanus*), upper molars with a more simple and cuspidate occlusal topography (wide and ridgelike cusp rows, some more laminate than cuspidate), no anterocentral cusp (present), and simple peglike anterolabial and anterolingual cusps (robust and squarish in occlusal plane).

These and other derived features of *L. sibuanus* signify that it is not the morphological and phylogenetic counterpart on Mindanao of *Anonymomys* on Mindoro. *Anonymomys* may have a strong phylogenetic alliance with the Sundaic and Sulawesian *Haeromys,* as speculated by Musser and Newcomb (1983) but that hypothesis is weak and requires testing. It is not in the same phylogenetic group as *Limnomys,* judged by our preliminary character analyses (which we present in the section to follow), and we have to look elsewhere for a close relative of *Limnomys.*

Limnomys and *Rattus*

To some rodent taxonomists, *Rattus* was the nearest relative of *Limnomys,* close enough for them to incorporate the Mindanao endemic into the generic boundaries of *Rattus* (Thomas, 1907; Ellerman, 1941; Misonne, 1969). Other researchers recognized the integrity of *Limnomys* in taxonomic reviews and checklists (Carleton and Musser, 1984; Heaney et al., 1987, for examples) but provided no documentation for their decisions. Clearly, *Limnomys* requires a critical comparison with *Rattus,* which we produce below. As we did in contrasting *Tarsomys* with *Rattus,* we use samples of southeast Asian *R. rattus* as our example of Ellerman's (1941) subgenus *Rattus,* the group at the heart of his definition of the genus. *Limnomys sibuanus* and *Rattus rattus* are also contrasted in figure 15 where proportional relationships are diagrammed, in figures 22 and 23 where crania and dentaries are shown, in figures 25 and 27 where molar teeth are illustrated, and in table 4 where frequencies of cusps and cusplets are tabulated. We present the character in *Limnomys* and the dissimilar expression of it as expressed by *Rattus* in parentheses.

1. The tail is significantly much longer relative to length of head and body and the scale hairs are relatively much longer which produces a more pilose tail.

2. There are three pairs of mammae: one postaxillary and two inguinal (five pairs in *R. rattus,* four, five, or six pairs in other related species of *Rattus*).

3. The rostrum is significantly broader relative to its length, and shorter relative to occipitonasal length.

4. The slightly beaded outline of the interorbital and postorbital regions resembles an hourglass; the braincase is rounded, somewhat globular in appearance, without temporal ridging; the braincase is also significantly broader relative to length of skull or zygomatic breadth and lower relative to its breadth; foramen magnum directed posteroventrad (lyre-shaped interorbit and postorbital region; relatively higher and narrower braincase with prominent ridges outlining dorsolateral margins of cranium from interorbit to lambdoidal ridges; braincase appears rectangular in dorsal view; foramen magnum directed caudad).

5. Each zygomatic plate is significantly narrower relative to any other cranial dimension and the zygomatic notch is shallow (wide plate with a deep notch indicating a significant anterior projection of the zygomatic spine).

6. The bony palate is short, barely projecting past posterior margins of third molars; it is also significantly much shorter relative to any other cranial dimension, and wider relative to its length (long bony palate extending well posterior to the molar rows).

7. The mesopterygoid fossa is significantly wider relative to breadth of bony palate.

8. The auditory bullae are longer relative to length of skull (fig. 15) and their orientation relative to basicranium is more like that of *Tarsomys.*

9. The coronoid process is smaller and delicate relative to the body of the dentary, and the condyloid process is long and slender (larger coronoid, shorter and wider condyloid).

10. The upper incisors are slimmer, each is significantly narrow relative to its anteroposterior depth (incisors wider, more proportional to their depth).

11. The upper molar rows are significantly shorter relative to length of skull but much longer relative to length of bony palate; molar teeth are wider relative to length of molar row (relatively longer toothrows and narrower teeth).

12. Cusp t3 is a part of second upper molar in all specimens and occurs on third upper molar in four out of five individuals (absent from second upper molar in about two-thirds of the sample and from third upper molar in 98% of sample); posterior cingulum on each first and second upper molar (not present on either tooth); anterocentral cusp on all specimens (absent from entire sample); anterior labial cusplet occurring in three out of five specimens (absent from 95% of sample); see table 4.

13. The first and second rows of cusps on each first upper molar and the first complete

row on each second molar are thin arcuate laminae in which the labial and lingual cusps have coalesced with the laterally elongated central cusp to the degree that the usual cuspidate occlusal pattern is obscured and replaced by a pattern of transverse or arcuate ridges (each comparable row clearly consists of a large central cusp, normal in shape, flanked by discrete labial and lingual cusps); cusp t9 on each first and second upper molar is merged with an enamel and dentine projection from the central cusp t8 to form an elongate ridge (cusp t9 a normal cusp flanking cusp t8, the configuration is cuspidate and not laminate).

14. Cusp t4 of each first upper molar abuts against or merges with a short lingual enamel projection from the central cusp t8 to form a notched wall separating cusps t4 and t8; cusp t4 of each second upper molar has a caudal extension which has merged with an anterolingual projection from cusp t8 to form a high and thick enamel wall along the posterolingual margin; cusp t4 and t8 of each third upper molar are tightly pressed against each other (cusp t4 is roundish, no anterolabial ridge projects from cusp t8, there is a wide gap between cusp t4 and the smooth labial margin of cusp t8 on each first, second and third molar; fig. 27).

15. The anterolingual and anterolabial cusps on each first lower molar are chunky, the former squarish in occlusal plane, the latter triangular (each is the usual rounded cusp shape); rows of cusps on all lower molars in the form of thin arcuate ridges in which the cuspidate foundation is obscure (rows thicker and clearly formed from rounded cusps); each posterior cingulum on each first and second lower molar is wide and thick, its reflecting the laterally stretched occlusal surface (narrower).

TARSOMYS AND *LIMNOMYS* IN PHYLOGENETIC CONTEXT

The two species of *Tarsomys* and one of *Limnomys* are a small portion of the more than 40 species of murine rodents known to be endemic to the Philippine Archipelago (excluding Palawan and adjacent islands, which are politically linked to the Philippines but biogeographically allied with the Sunda Shelf; Musser and Newcomb, 1983; Heaney, 1986; table 8). Many questions about this rodent fauna beg answers but among them three seem particularly significant to us. First, how many species are native to the Philippine islands and, within the restrictions of the nature and number of available samples, what are their morphological characteristics, their insular and altitudinal restrictions, and their ecological portraits? During the past decade or more, our efforts have focused on this question, an inquiry which is really directed at determining the constituents, at the taxonomic level of species and genera, of the endemic murine fauna. As part of our results we have identified a set of species which were once regarded as Philippine endemics but turn out to be introduced, most likely through human activities, into the Archipelago (*Rattus rattus mindanensis, R. rattus rattus, R. argentiventer, R. nitidus, R. norvegicus, R. exulans,* and *Mus musculus castaneus*; synonyms applied to Philippine samples of these species are listed by Musser, 1977a). The other part provides discovery and description of the endemic species and genera (Musser, 1977b, 1981a, 1982a, 1982b, 1982c; Musser and Freeman, 1981; Musser and Gordon, 1981; Musser et al., 1982; Musser and Heaney, 1985; Musser et al., 1985; Rickart and Heaney, 1991). This process continues here with our accounts of *Tarsomys* and *Limnomys,* and in the future will provide documentation of other taxa (Musser and Heaney, in prep.).

Second, what are the phylogenetic relationships among the endemic Philippine species? And finally, where does this unique assemblage fit within the evolutionary pattern of the murine faunas native to continents and other archipelagos within the Indo-Australian region? Of these two additional questions holding our attention, research has not yet extended to the third, but we have been working on the second. From our analyses of the variation in selected morphological characters, those features for which we can reasonably determine discrete primitive or derived character states, we are able to formulate hypotheses about phylogenetic alliances. The characters surveyed were taken primarily from study skins, skulls, and dentitions. We have yet to examine the morphological variation in other organ systems (reproductive, alimentary, or postcranial skeleton, for example).

Our basis for establishing polarities comes from studying the distribution of character states throughout muroid rodents (Bugge, 1970, 1985; Carleton, 1980; Musser and Newcomb, 1983; Voss, 1988; Wahlert, 1985, 1991) as well as their expression in some of the earliest Eocene rodents, primarily *Paramys copei* and *Sciuravus* (Wahlert, 1985).

Detailed results will be published in the future (Heaney, in prep.); here we present a preliminary sketch of the phylogenetic patterns to portray the place of *Tarsomys* and *Limnomys* within them. These patterns are founded on our qualitative analyses of character states. Where these traits have already been described and illustrated, we refer to them in the relevant publications; where new illustrations are necessary to convey our qualitative observations to readers, we provide them here.

The Philippine murine fauna consists of three major assemblages, which we label divisions (table 8). *Tarsomys* and *Limnomys* are not closely related to any of the species in either Division I or II; they are members of Division III. To support these assertions, we briefly survey the species in each division and enumerate the combination of traits which define each cluster of species and if possible, each division.

DIVISION I (OLD ENDEMICS)

Here we include the species of *Phloeomys, Crateromys, Batomys, Carpomys, Apomys, Crunomys, Archboldomys, Rhynchomys, Celaenomys,* and *Chrotomys.* These 10 genera have been referred to as Old Endemics (Musser, 1981b; Musser et al., 1985), an assemblage in which the species retain many basic features primitive for rodents yet also exhibit unique combinations of specializations, some of them spectacular. These attributes, the restriction of such distinctive rodents to the Archipelago, and the apparent absence of close living relatives from continental Asia and islands on the Sunda Shelf suggest Division I to be relatively old, the extant members representing highly derived products of divergent evolutionary histories, possibly beginning sometime in the Miocene and early Pliocene, during that time when clusters of land began to appear above sea level to form insular precursors of the present-day Archipelago (see the geological review in Heaney, 1986 and 1991).

Since the time they were discovered by western collectors and described by European naturalists, most of the genera in Division I have been recognized as being restricted insular components of the Philippine mammalian fauna, and highly distinctive among muroid rodents in their unique combination of primitive and derived characteristics (Thomas, 1898). Only one genus, *Apomys,* was perceived as closely related to genera occurring outside of the Philippines. Ellerman (1941), for example, thought it to be closely related to *Rattus,* even treating it as a subgenus of that taxon. During the following decades, that perception was retained by some (Misonne, 1969), rejected by others (Johnson, 1962), and finally completely dispelled (Musser, 1982b); *Apomys* is now looked upon as a cluster of species without any obvious close relatives, another unique component of the Philippine fauna.

By bringing these genera together in one large clump we are not necessarily suggesting that the division represents a monophyletic cluster. On the contrary, the range of morphological expression among the species we list in Division I is so spectacular that we have been able to identify several discrete and highly distinctive groups. The ten genera included in Division I comprise six proposed monophyletic taxa. Each group is defined by a suite of derived (sometimes highly derived) traits, most of which are peculiar to that particular group. Based on the morphological features we have surveyed, each group stands by itself, without compelling indication of relationship either to the other Philippine groups within Division I or to those genera that are endemic to continental regions and other archipelagos. Because of this broad range of morphology, it has been impossible for us to identify traits shared by members of all the groups that would unequivocally define Division I as monophyletic. We are able to set it apart from Divisions II and III only because we can explicitly define each of those clusters by a set of derived traits that are not shared with any of the species in Division I.

Below we provide the contents and definition of each of these six groups of Old Endemics. The characteristics distinguishing members of Divisions II and III from Division I are elaborated upon later in our treatments of those divisions. We also provide a discussion of possible relationships among members of Division I at the end of this section.

1. *PHLOEOMYS* GROUP

Two species of *Phloeomys* have been described, as Thomas (1898: 400) indicated, and both are endemic to Greater Luzon (fig. 3; table 8). The genus retains many primitive traits, particularly in its cranial morphology. Some examples (see figs. 28–30) are the moderately wide zygomatic plates with short anterior spines; shallow occiput, which reflects the slight posterior extension of the fused occipital bones (exoccipital, supraoccipital, and caudal portion of basioccipital) caudad to the posterior margins of the interparietal, parietals, and squamosals; small optic foramen relative to size of cranium; very small auditory bullae; small postglenoid foramen; wide and robust alisphenoid strut, which contains a tubular alisphenoid canal; an accessory foramen ovale; masticatory and buccinator nerves emerging from separate foramina in most specimens; posterior palatine foramina opposite second upper molars; short incisive foramina contained mostly in premaxillaries (the suture between premaxillary and maxillary bones intersects each incisive foramen near its posterior margin); primitive cephalic (carotid) arterial pattern; short and moderately wide sphenopalatine vacuities; and no sphenopterygoid openings.

At the same time, the species of *Phloeomys* possess the following derived features which define it as unique among not only Philippine murines but also within the Murinae in general.

1. Both species are highly arboreal and have specialized hind feet (see the figures in Schauenberg, 1983). Both are characterized by very large body size (Schauenberg, 1978; Heaney et al., 1991), probably the largest of the living members of Murinae.
2. A color pattern is present: in *P. pallidus*, the dorsal fur is white or gray broken up by a brown or black saddle-shaped pattern which extends onto the head in some individuals, and the tail is pale to dark brown (see the superb color plate 12 in Meyer, 1896, and the illustrations in Schauenberg, 1978 and 1983); *P. cumingi* is dark brown all over with a blackish tail.
3. Females in both species have only two teats, which are in the inguinal region.
4. High interorbital ridges sweep back and laterally to form expansive triangular ledges over the postorbital region and extend to the occiput as prominent temporal ridges (figs. 28, 29).
5. The frontal region is inflated just anterior to the interorbit (fig. 29).
6. The squamosal root of each zygomatic arch originates on the braincase, just below the postorbital shelf and temporal ridge, and the squamosal forms most of the braincase wall between the root and the occiput (figs. 29, 30A).
7. The incisive foramina are distinctive in outline: from narrow slits in their anterior one-third, they abruptly widen in the posterior two-thirds (fig. 28).
8. The bony palate is long (partly a reflection of the very short incisive foramina, a primitive trait), and at the caudal margins of the third molars it splits into two shelves which project significantly beyond those teeth (figs. 28, 30B).
9. There is a subsquamosal notch in the caudal margin of each squamosal (fig. 30A).
10. Occlusal surfaces of upper molar teeth are formed by series of thick, wide, and transverse plates, including the anterocone, each without any trace of cuspidation, even in

Fig. 28. Dorsal and ventral cranial views (×1.5) of an adult *Phloeomys pallidus* (USNM 151519) from Luzon.

nestlings in which the molars have not erupted (fig. 34A). A posterior cingulum is absent from each first and second molar. Cusps t1 and t3 are absent from each second and third molar (cusp t1 is a prominent part of the crown on second and third molars in all other species of Philippine endemics). Misonne (1969: 80) speculated that cusp t7 "is probably present, as the last lamina is very wide on the lingual side," and we agree, recognizing that a discrete cusp t7 is impossible to verify in any of the specimens we have checked and we infer its presence only by the great width of the posterior lamina on each molar, which would be unusual without the presence of a cusp t7. We are also unsure just how much of the posterior lamina is formed by cusp t9.

11. Occlusal surfaces of lower molars are also laminar (fig. 35A). The posterior cingulum is a transverse plate on the labial side behind each first and second tooth (among Philippine murines, the posterior cingulum is about in the middle of the tooth, and is on the labial side only in species of *Phloeomys, Chrotomys,* and *Celaenomys*). In worn teeth, the anteroconid is cordate-shaped in occlusal plane, incised along its posterior margin, and

Fig. 29. Lateral views of cranium and dentary (×1.5) of the specimen shown in figure 28.

has a hollow center; in the unworn dentitions of nestlings, it is oblong to cordate in cross-sectional outline with a hollow core and either a posterior incision or gap (fig. 64A). The structure is certainly formed by anterolingual and anterolabial cusps, and we suspect an anterocentral cusp is also involved.

12. The coronoid process is very small relative to area of the dentary, the angular projection is expansive, round, and delimited from the condyle by a shallow concavity in the caudal margin of the dentary (fig. 29).

Other derived traits, used in combination with those listed above, can be used to diagnose *Phloeomys* but they are not exclusive to the genus. The interparietal, for example, is large, narrow, and wedge-shaped, but a similar configuration is found in some species of *Crateromys.* Each first lower molar has four roots, another derivation, and one that is also found in some species of *Batomys*; four roots anchoring each first lower molar is characteristic of *Tarsomys, Limnomys, Bullimus, Abditomys, Tryphomys,* and *Rattus,* all of which we place in Division III.

So unique are the laminated occlusal patterns in *Phloeomys* that they formed the basis for placing the genus in its own subfamily, the Phloeomyinae (see the discussion in Ellerman, 1941: 292). Some researchers (Ellerman, 1941; Misonne, 1969; Carleton and Musser, 1984, for example) have not recognized this rank, but others, who base their judgments on dental patterns, palatine ridges, as well as other characters, would elevate it to family level, the Phloeomyidae (Eisentraut, 1976; Schauenberg, 1978). Jotterand-Bellomo and Schauenberg (1988), who reported the karyotype of *Phloeomys,* noted that (p. 181) "Although chromosome data reveal a close relationship between *Phloeomys* and Muridae, they do not exclude the possible belonging of this species to a separate family, that of Phloeomyidae." Keller (1988) remarked that the hair structure of *Phloeomys* was similar to that found in certain terrestrial murines.

2. *CRATEROMYS* GROUP

The described species of *Crateromys* (Musser et al., 1985), *Carpomys* (Thomas, 1898),

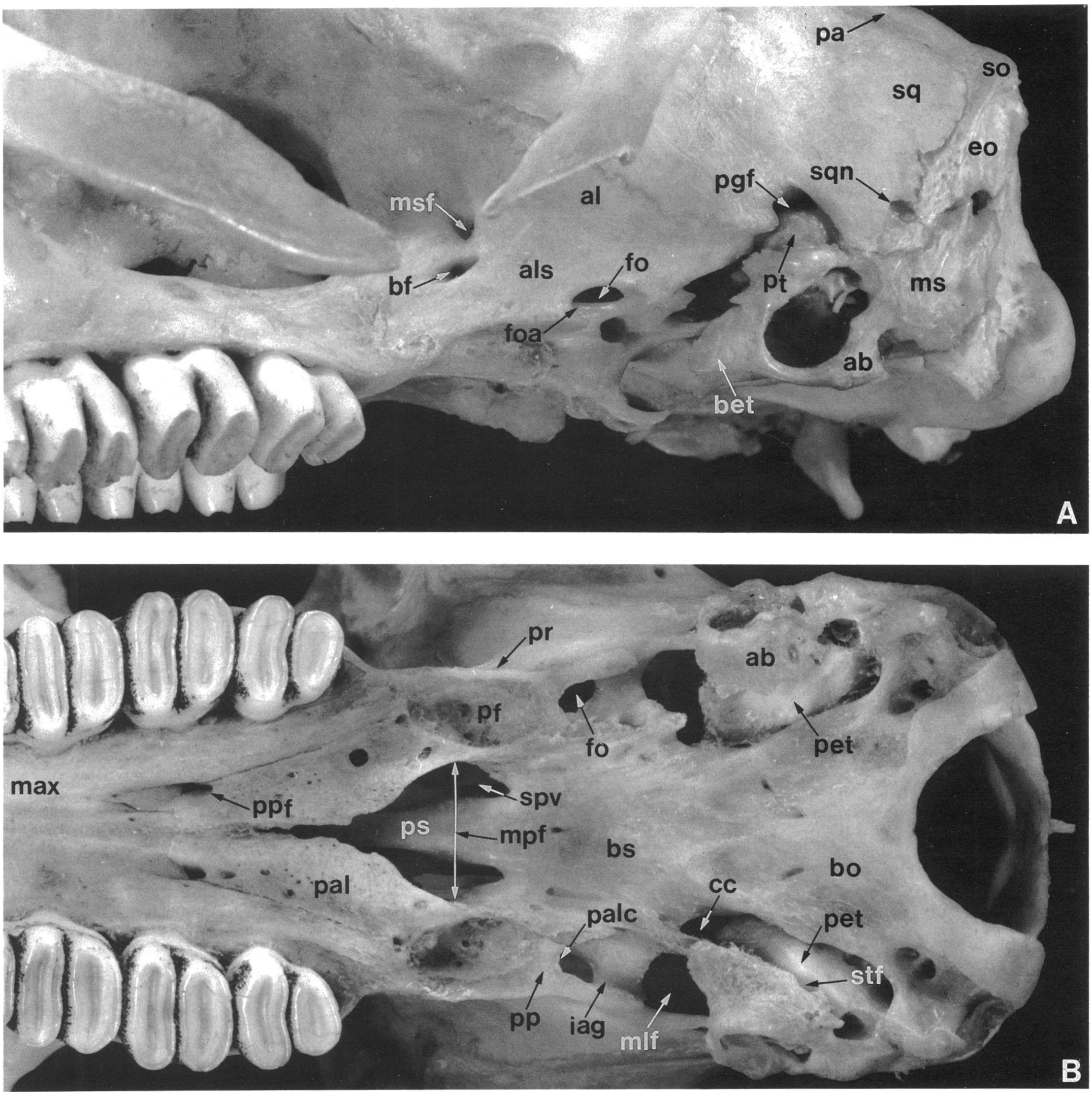

Fig. 30. Lateral (A, AMNH 242103) and ventral (B, USNM 151519) enlargements of *Phloeomys pallidus*. **ab,** auditory bulla; **al,** alisphenoid; **als,** alisphenoid strut (between the foramen ovale accessorius and the masticatory and buccinator foramina; the alisphenoid canal is concealed within the strut); **bet,** bony eustachian tube; **bf,** buccinator foramen; **bo,** basioccipital; **bs,** basisphenoid; **cc,** carotid canal; **eo,** exoccipital; **fo,** foramen ovale; **foa,** foramen ovale accessorius (the ventral segment is missing in A but complete in B); **iag,** groove for the infraorbital branch of the stapedial artery; **max,** maxillary; **mlf,** middle lacerate foramen; **mpf,** mesopterygoid fossa; **ms,** mastoid; **msf,** masticatory foramen; **pa,** parietal; **pal,** palatine; **palc,** posterior opening of the alisphenoid canal (the infraorbital branch of the stapedial artery enters the alisphenoid canal at the arrow, dorsal to the pterygoid plate); **pet,** petrosal; **pf,** pterygoid fossa; **pgf,** postglenoid foramen; **pp,** pterygoid plate; **ppf,** posterior palatine foramen; **ps,** presphenoid; **pt,** periotic; **pr,** pterygoid ridge; **so,** supraoccipital; **sq,** squamosal; **sqn,** squamosal notch; **spv,** sphenopalatine vacuity; **stf,** stapedial foramen.

and *Batomys* (Thomas, 1898; Miller, 1910; Sanborn, 1953) are members of this group. In figures 31–33, we have illustrated crania representing a species of each genus; molar rows are shown in figures 34 and 35. A host of primitive features are shared by species of the three genera. Some examples are a hind foot with the fifth digit only slightly shorter than the others, an hourglass-shaped interorbit and smooth braincase without postorbital or temporal ridging, a shallow zygomatic notch, a short bony palate in which the posterior margin is opposite the union of second and third molars, small otic capsules broadly attached to the squamosal and alisphenoid bones, slitlike sphenopalatine vacuities, an alisphenoid strut and associated accessory foramen ovale in most examples of *Crateromys* and all *Carpomys,* and posterior cingula on upper molars of *Batomys* and *Carpomys.*

The group can be defined by three clearly derived traits shared by all the species to the exclusion of any other Philippine endemic, and by several other specializations shared by most of the species in the *Crateromys* group, but also appearing in some other groups; these are listed below.

1. A large discrete cusp t7, present on each upper molar, has an anterolingual orientation relative to the adjacent central cusp t8, and forms a significant part of the lingual occlusal surface of each tooth (fig. 34B–D).

2. A large anteroconid forms the anterior one-third of each lower molar. In occlusal plane, the structure is roughly cordate in outline. The core is hollow and persists as a deep round, angular, or wide pit lined with enamel until the teeth become excessively worn (fig. 35). Apparently in specimens of *Crateromys* and *Batomys,* this unique anteroconid consists primarily of an arcuate anterocentral cusp fused with sinuous anterolabial and anterolingual cusps (either one or both with medially projecting processes that form the base; fig. 35B, C); in both species of *Carpomys,* the anterocentral component appears to be composed of two cusps (fig. 35D).

Species of *Phloeomys* are the only other Philippine murines with an anteroconid resembling the unique conformation shared by members of the *Crateromys* group (fig. 35A). Components of the structure in adult examples of *Phloeomys* are difficult to detect; there is, however, a hint of at least two and possibly three cusps in adults (fig. 35A, for example), as well as in a nestling with completely unworn molars (fig. 64A). But because the fusion is so complete except along the posterior margin, we will have to survey additional material in order to detect the number of cusps forming the structure and whether or not they are homologous with those in *Crateromys* and its allies. The anteroconid in specimens of *Phloeomys* does differ in that it is much smaller relative to the transverse plate behind it.

3. All the species in the *Crateromys* group which have been described have the derived cephalic arterial pattern and attendant configuration of bone and foramina illustrated in figure 36C. Before entering the braincase through the carotid canal (between the otic capsule and basioccipital), the internal carotid artery gives off a small stapedial artery which passes through a minute stapedial foramen to enter the inner ear which it serves and from which it does not emerge. Once in the braincase, the internal carotid artery gives off a vessel (labeled anastomotic artery A5 in Bugge, 1970: 326, fig. 5G) which courses in a shallow depression diagonally 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.

In the primitive murine pattern (such as that present in *Phloeomys* and *Rattus*), the stapedial artery exits the tympanic cavity and divides into branches. One of these passes through the braincase as the infraorbital branch of the stapedial artery, which courses along a groove on the pterygoid plate, enters the posterior opening of the alisphenoid canal, passes through the canal, and exits into the orbit through the anterior alar fissure to provide the orbitalmaxillary circulation (fig. 36D; also see Bugge, 1970: 325, fig. 5C; Voss, 1988; and Carleton and Musser, 1989, for details).

The pattern in members of the *Crateromys* group is very similar to that illustrated for the Neotropical sigmodontine *Rheomys hartmanni* (Voss, 1988: 296, fig. 18D). It also closely resembles the carotid circulation in the sigmodontine *Oryzomys palustris* (diagrammed in Carleton and Musser, 1989: 38, fig. 21A) except that the deep groove and tunnel which receives the second arterial connection in *O. palustris* is absent from ex-

Fig. 31. Dorsal cranial views (× 1.5) of adult representatives in the *Crateromys* group. **Left,** *Batomys granti* (FMNH 62504) from Luzon; **center,** *Crateromys shadenbergi* (USNM 102546) from Luzon; **right,** *Carpomys melanurus* (USNM 102549) from Luzon.

amples of *Crateromys, Batomys,* and *Carpomys.*

Among other endemic Philippine murines, this derived carotid arterial pattern also occurs in all species of *Apomys* (Division I) except *A. datae,* which retains the infraorbital branch of the stapedial (fig. 36A, B; also Musser, 1982b: 6, fig. 2—there the secondary arterial connection, as well as the infraorbital, were labeled internal maxillary). In addition, the derived arterial pattern is present in all species of *Crunomys* (Division I) (Musser, 1982c: 45, fig. 31; again, the secondary arterial connection is labeled internal maxillary). There is, however, a difference in the osseous expression of the oblique passage of the secondary arterial connection over the pterygoid plate. In most specimens of *Apomys abrae* and *A. sacobianus,* the secondary arterial connection courses in a deep channel scored in the dorsal surface of the pterygoid plate, and along the internal wall of the alisphenoid (fig. 36A). In all the other species of *Apomys,* except *A. datae,* and in all *Crunomys,* the secondary arterial connection passes through a deep diagonal and short groove on the ventral surface of the pterygoid plate and passes into the alisphenoid canal on the dorsal surface through the posterior opening of the canal, which lies anteromedially to the foramen ovale, as seen in ventral view (fig. 36B; Musser, 1982b: 7, fig. 3B; Musser, 1982c: 44, fig. 30B).

4. Long and narrow incisive foramina are found in all members of the *Crateromys* group except *C. paulus,* which has short foramina, the primitive expression of this trait (Musser et al., 1985: 10, fig. 5). Long incisive foramina also characterize most members in Divisions II and III but among the other groups forming Division I, only *Archboldomys* has elongate foramina; in the context of the derived fea-

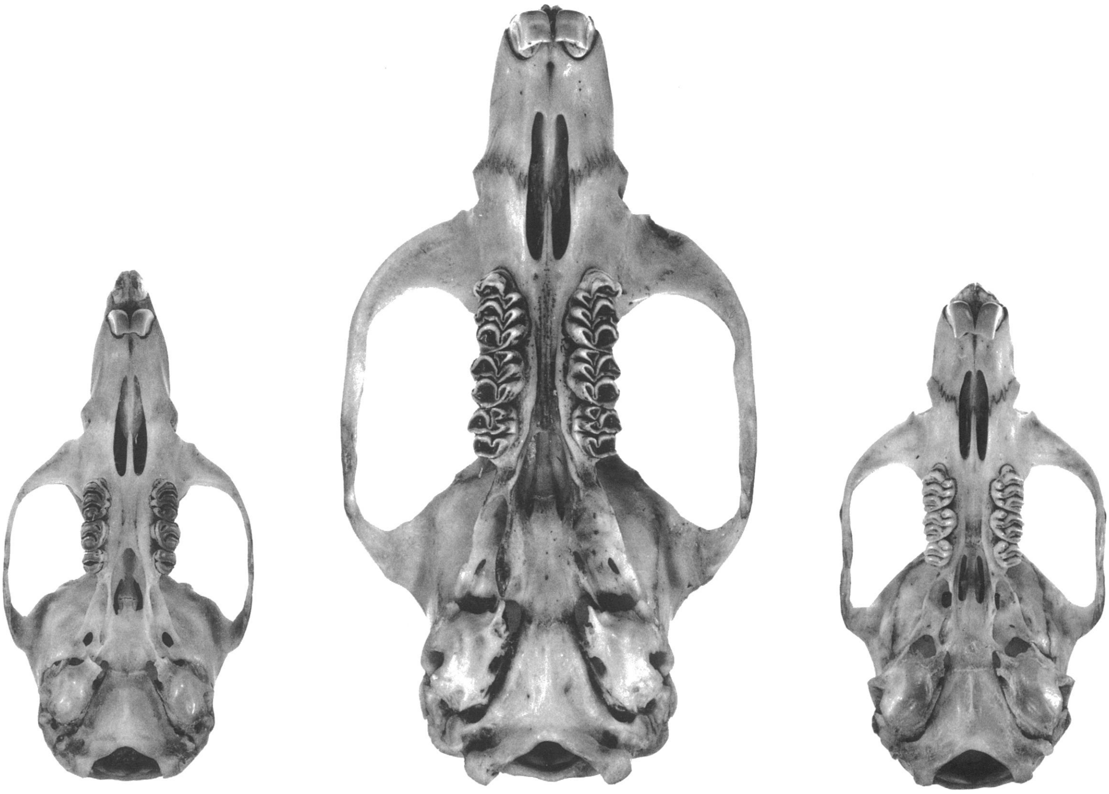

Fig. 32. Ventral cranial views (×1.5) of the specimens shown in figure 31. **Left,** *Batomys granti*; **center,** *Crateromys schadenbergi*; **right,** *Carpomys melanurus.*

tures which define the *Crateromys* group, long incisive foramina represent an independent specialization that expands the combination of derived features identifying the group.

5. The angular process of each dentary is very broad in lateral view and separated from the condyle by a shallow emargination in the caudal margin of the dentary (fig. 33). A similar configuration is found in species of *Phloeomys* but not in any of the other Philippine endemics.

6. The molars have some combination of accessory roots, depending on the species, above the primitive number. We used the first molars to index the number of multiple roots. A large anterior, a single lingual, and a posterior root compose the primitive number and position of roots anchoring each first upper molar; a large anterior and posterior root beneath each first lower molar is primitive (similar to the pattern in *Anonymomys,* figs. 62A and 63A). Species of *Crateromys* and most *Batomys* have four roots beneath each first upper molar: in addition to the anterior and lingual roots there are two posterior roots, which represent a division of the single primitive posterior anchor (fig. 62C). Some specimens of *Batomys granti* and the species of *Carpomys* either retain the primitive number or may have a small labial holdfast (fig. 62B). In all members of the *Crateromys* group, each first lower molar is anchored by a minimum of three roots: a large anterior root, a posterior root of about the same size, and a moderately large lingual root (fig. 63B). Specimens of *Batomys salomonseni* have up to six roots beneath each first lower molar (fig. 63C). *Phloeomys* is the only other Philippine endemic with similar multirooted patterns; each first upper molar has the primitive three, but each first lower has large anterior and posterior roots and a small labial and

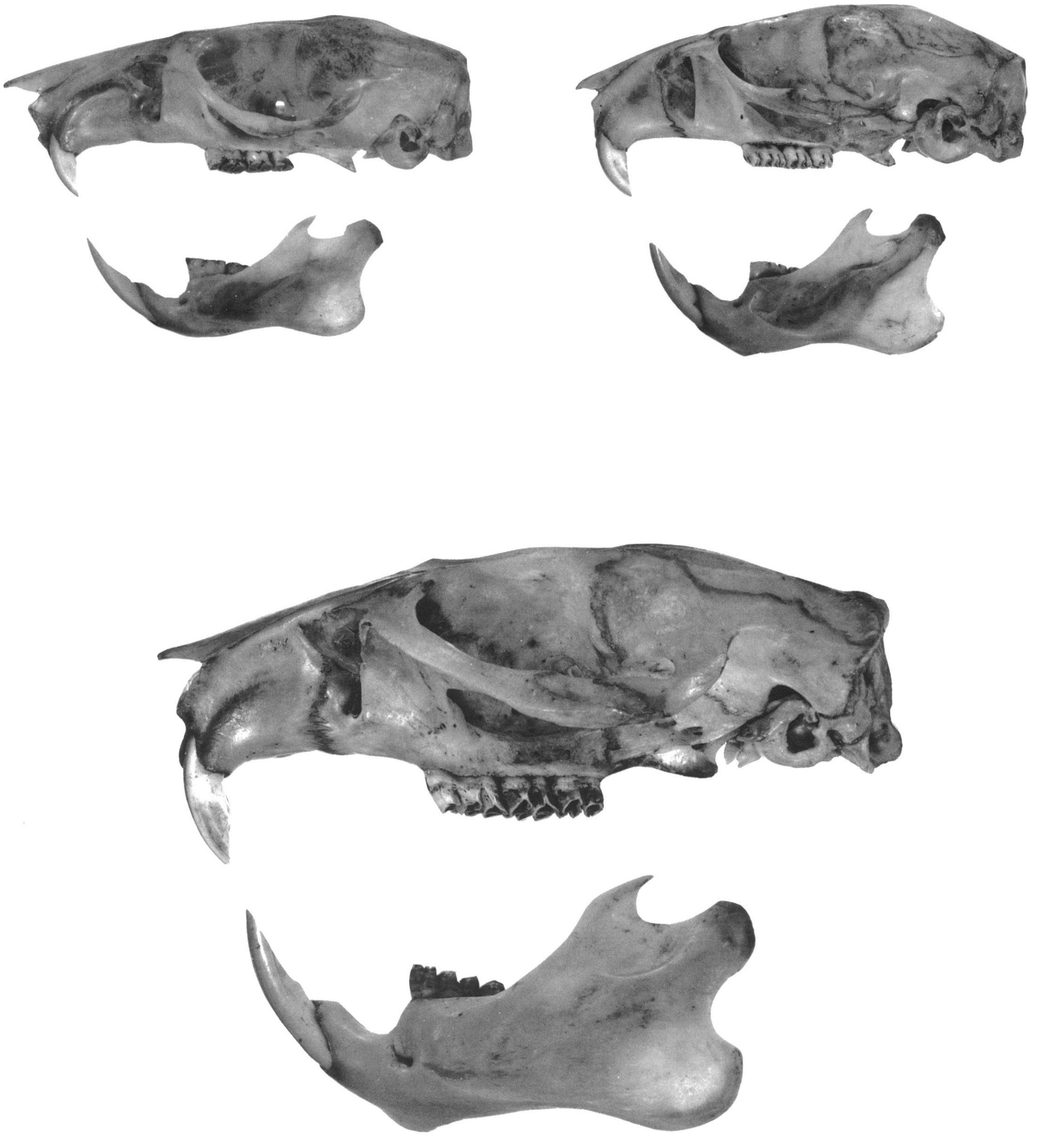

Fig. 33. Lateral cranial and mandibular views (×1.5) of the specimens illustrated in figures 31 and 32. **Left,** *Batomys granti*; **center,** *Crateromys schadenbergi*; **right,** *Carpomys melanurus*.

lingual. All members of Division III also have multirooted molars but the combination of number and position is different from that seen in the *Crateromys* group and in *Phloeomys*.

7. Cusp t9 is apparently absent from the labial margin of each upper molar or reduced in size. It is probably present but only as a minor component of the lamina in *Carpomys* (fig. 34D). If the cusp is present in *Crateromys*, it has so fully merged with the central cusp t8 that it is now represented only by a low enamel ridge on the labial surface of cusp t8 (fig. 34C). Cusp t9 does not occur in *Ba-*

tomys, but it may be represented by a cingular enamel bulge at the labial base of cusp t8 (see the first molar in fig. 34B).

8. Most members of the *Crateromys* group express some kind of chromatic fur pattern (other than the usual dorsal-ventral countershading). They consist of the distinctive saddle and melanistic patterns seen in *Crateromys schadenbergi* (see Musser and Gordon, 1981; Meyer, 1896: pl. 14), the less striking pattern of *C. paulus* (Musser and Gordon, 1981), the bicolored tail (blackish brown over basal half, white to tip) of *C. australis* (Musser et al., 1985) and *Batomys dentatus* (Miller, 1910), and the brownish gray body contrasting with a blackish brown tail in *B. granti* and the two species of *Carpomys* (see the colored plates in Thomas, 1898).

Species of *Phloeomys* are also patterned. The distinctive chromatic patterns of *P. pallidus* are unlike anything in the *Crateromys* group but the dark brown body and blackish tail of *P. cumingi* resemble the patterns in some *Batomys* and *Carpomys.* Among the other Philippine endemics, those in Division II and Division III lack these kinds of pelage features. The only other distinctive body markings are found in the *Chrotomys* group of Division I, and consist of the pattern of pale and dark stripes found in species of *Chrotomys* (Thomas, 1898; Musser et al., 1982; Rickart and Heaney, 1991), and faint forehead blaze and shoulder lines possessed by some examples of *Celaenomys* (Rickart and Heaney, 1991).

3. *APOMYS* GROUP

In the latest review of *Apomys,* Musser (1982b) recognized eight species sorted into the *Apomys datae* group and the *Apomys abrae-hylocetes* group. New information about identities and insular distributions of certain samples in the latter cluster, as well as the descriptions of one and possibly two new species, are being assembled and will be provided by Heaney (in prep.). The species of *Apomys* are defined by the following apomorphies; the first listed are those unique to the genus, followed by others that are noted to help define *Apomys,* but are also shared by some species in other groups.

1. The rostrum is moderately long and narrow, and seen from lateral perspective has a rectangular conformation. This outline is a consequence of the extension of the premaxillaries that project well in front of the incisor faces; the anterodorsal margin of each premaxillary, which has a shoulder and does not follow the curve of the dorsal incisor surface; and the contour of the nasals in which the distal third follows the long and nearly straight cranial profile, thus appearing flat or slightly deflected dorsad. As a result of this combination of features, only a slight notch separates the shoulder of the premaxillary from the nasal roof (fig. 37).

2. The incisive foramina are very broad, especially relative to their length (fig. 37).

3. The bony palate is thin, wide, and long; its ridged caudal margin extends beyond posterior faces of the third molars; and the surface is densely pitted and perforated, particularly over the posterior one-third to one-half (see fig. 14B in Musser, 1982b: 31; also fig. 37 here).

4. Each third upper molar, extremely reduced in size relative to the toothrow, resembles a large round peg with a cusp (t1) at its anterolabial margin (fig. 38A). The peg probably consists primarily of cusp t5; if the lingual cusp t4 and labial cusp t6 are also components they are not identifiable, even in the third molar of young rats. The row containing cusps t8, t9, and sometimes t7 in other genera is absent from the third molar in all species of *Apomys.*

Each third lower molar retains an anterior lamina but the posterior structure is oblong, without sign of the two cusps which form this lamina in other genera (members of the *Crateromys* group, for example, fig. 35), and resembles the posterior cingulum at the back of each first and second molar (fig. 39A).

5. The occlusal surface of each first and second upper molar consists of simple chevron-shaped lamina and a chunky oblong structure, each tightly abutting one another; cuspidation is barely evident, particularly cusp t9 (fig. 38A).

6. The occlusal surface of each first lower molar consists only of a posterior cingulum at the back of the tooth, a chunky chevron-shaped lamina, and a cordate (inverted heart-shape) structure at the front, which forms about one-half of the tooth (fig. 39A). This

Fig. 34. Contrasts in occlusal patterns of right upper molar rows among representative species in the *Phloeomys* and *Crateromys* groups. **A,** *Phloeomys pallidus* (AMNH 242103; CLM1–3 = 18.0 mm); **B,** *Batomys salomonseni* (FMNH 74853; CLM1–3 = 7.9 mm); **C,** *Crateromys schadenbergi* (USNM 102546; CLM1–3 = 16.2); **D,** *Carpomys melanurus* (USNM 102549; CLM1–3 = 8.5 mm). Neither *Phloeomys* nor *Crateromys* shows signs of a posterior cingulum (**pc**) at the back of any molar. Note also that each second and third molar in *Phloeomys* lacks cusps t1 and t3. There is an oblong posterior cingulum on each first and second molar in *Batomys,* and a laminar posterior cingulum on all three molars in *Carpomys.* A large cusp t7 occurs on all molars of *Batomys, Crateromys,* and *Carpomys.* We suspect, but cannot prove, that a cusp t7 forms the lingual portion of the posterior platelike lamina in all three molars of *Phloeomys.*

mass is formed from the fusion of a chevron-shaped anterior lamina (formed from the metaconid and protoconid) with the anteroconid, represented only by the narrow crescent forming the anterior margin of the tooth. A short labial cleft in some specimens remains as a trace of the lamina and anteroconid borders (see fig. 15 in Musser, 1982b: 33). We have been unable to detect which cusp or cusps contribute to what remains of the anteroconid. The structure of the anteroconid in the *Apomys* group is thus very different from the cordate structure shared by *Phloeomys* and members of the *Crateromys* group (fig. 35).

Lower molars also have very simple coronal surfaces (fig. 39A); anterolabial cusps are apparently absent from each second and third molar (and probably the first), as are anterior and posterior labial cusplets.

7. All species of *Apomys,* except *A. datae,* have the derived carotid arterial circulation

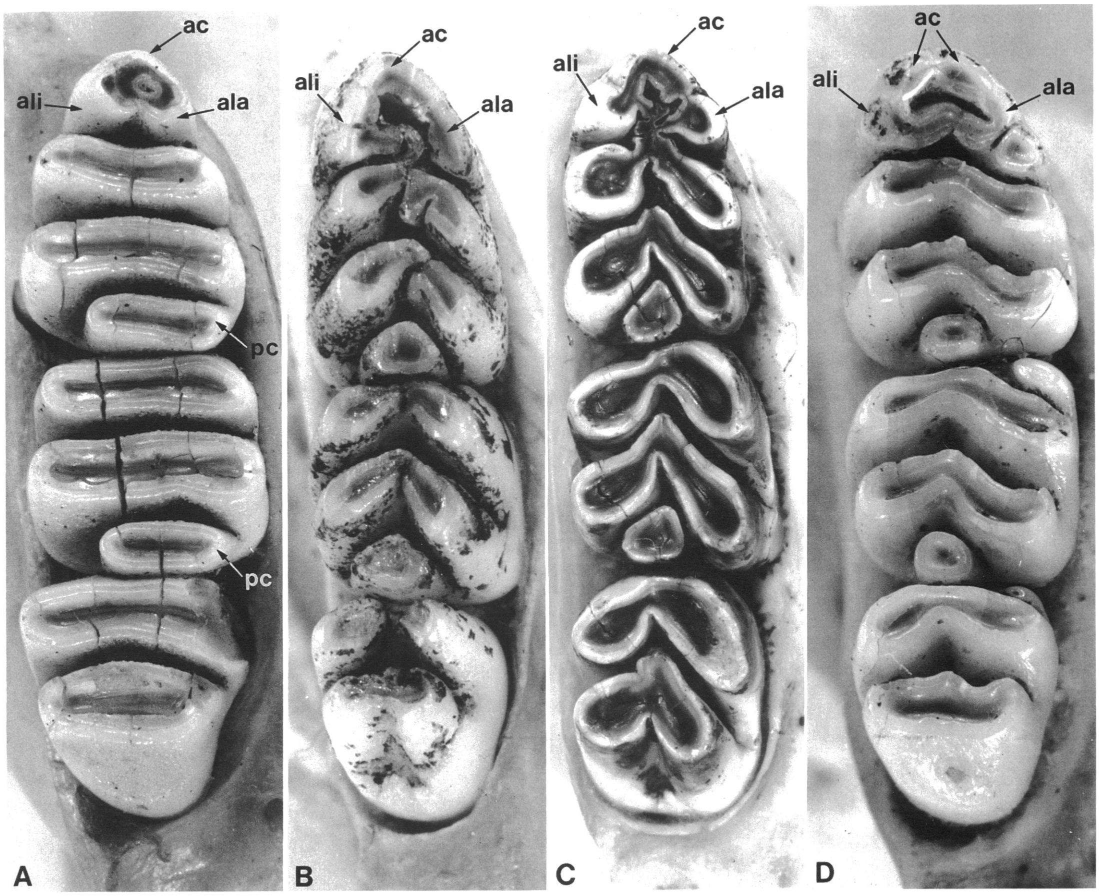

Fig. 35. Contrasts in occlusal patterns of right lower molar rows from the specimens shown in figure 34. **A,** *Phloeomys pallidus* (clm1–3 = 18.8 mm); **B,** *Batomys salomonseni* (clm1–3 = 8.6 mm); **C,** *Crateromys schadenbergi* (clm1–3 = 17.5 mm); **D,** *Carpomys melanurus* (clm1–3 = 9.1 mm). Note the displacement of the posterior cingulum (**pc**) from the middle to the labial side of the toothrow in *Phloemys.* In each genus, the anteroconid has a cordate outline (in occlusal plane); it is formed by anterolingual (**ali**), anterocentral (**ac**), and anterolabial (**ala**) cusps in *Phloeomys, Batomys,* and *Crateromys*; the anterocentral component consists of two cusps in *Carpomys.* Our interpretation is based on these specimens and others that are juveniles and nestlings (see text and fig. 64).

in the basicranial region (fig. 36A, B). This pattern is also common to members of the *Crateromys* group but its osteological imprint is not, as we have already explained. The arterial pattern and its osseous impression in some *Apomys* closely resemble the conformation in species of *Crunomys* (Musser, 1982c), a member of the fourth group in Division I.

8. Each auditory bulla is separated from the squamosal and alisphenoid by a gap, which reflects the coalescence of the postglenoid foramen, the postalar fissure, and the middle lacerate foramen (see figs. 7 and 12 in Musser, 1982c: 7 and 28). This derivation is not unique to *Apomys,* but in the context of the other apomorphies shared only by species in the genus, it is another feature contributing to its definition.

9. Most specimens have a notch or deep concavity in the caudal border of each squamosal dorsal to the auditory bulla. This is the subsquamosal fenestra (also called the squamoso-mastoid foramen by Musser, 1982b: 28). The trait is also found in some other Philippine members of Division I, but taken

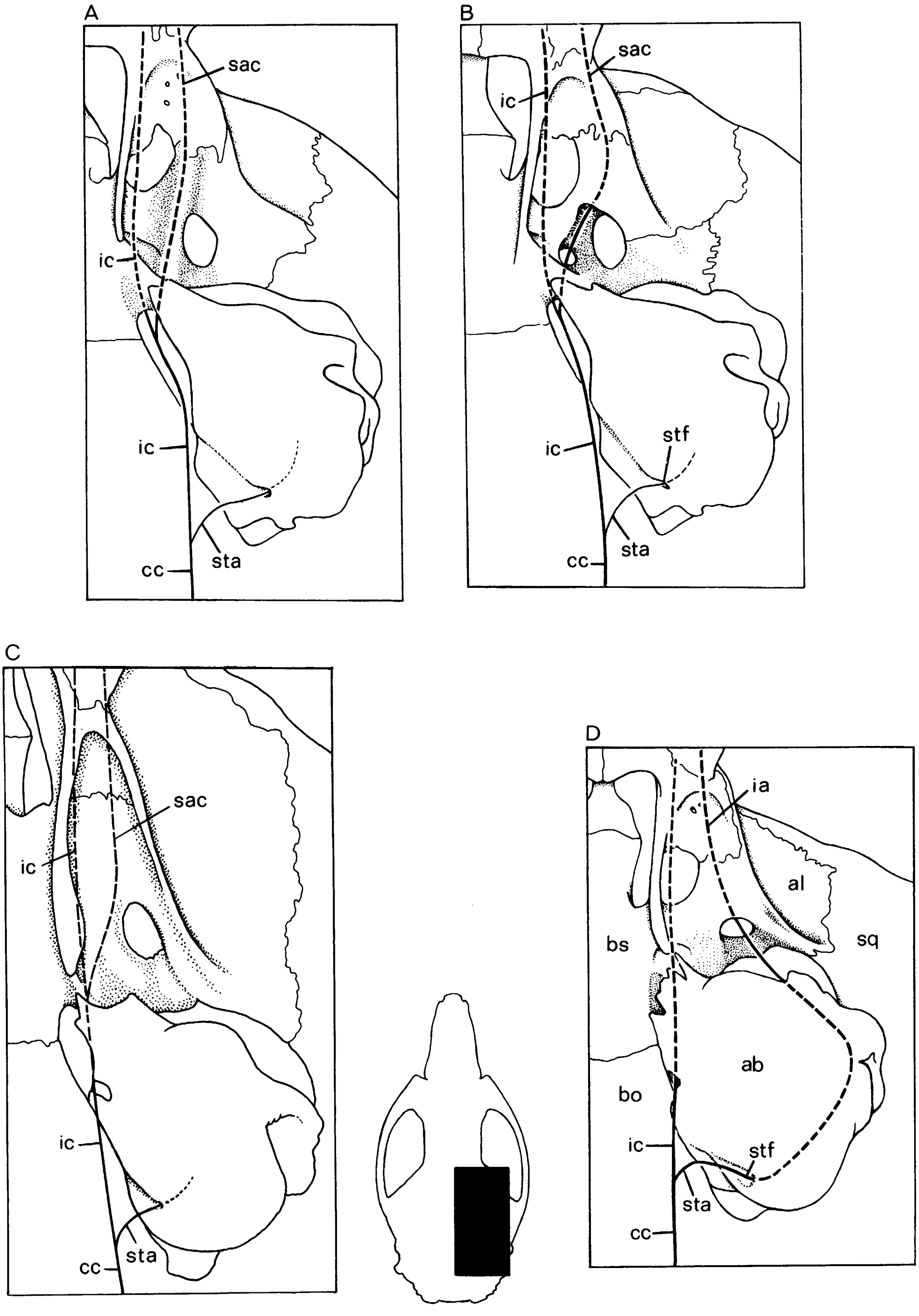

Fig. 36. Diagrams of cephalic arterial patterns in *Apomys, Batomys,* and *Rattus.* **A,** the configuration in *Apomys abrae* and *A. sacobianus.* **B,** the pattern in *Apomys musculus, A. microdon, A. insignis, A. hylocetes,* and *A. littoralis.* **C,** the pattern in *Batomys granti,* which is also found in the other species of *Batomys,* all the species of *Crateromys,* and *Carpomys.* **D,** the primitive pattern occurring in *Apomys datae, Rattus exulans,* and muroid rodents in general. The different patterns and their bony reflections are discussed more fully in the text. **ab,** auditory bulla; **al,** alisphenoid; **bo,** basioccipital; **bs,** basisphenoid; **cc,** common carotid artery; **ia,** infraorbital branch of stapedial artery; **ic,** internal carotid artery; **sac,** secondary arterial connection betwen internal carotid and orbital-maxillary circulation; **sq,** squamosal; **sta,** stapedial artery; **stf,** stapedial foramen.

Fig. 37. Crania and dentaries (×2) of two species of *Apomys.* On the left are dorsal, ventral, and lateral views of *A. datae* (FMNH 62761) from Luzon, the sole member of the *A. datae* group (Musser, 1982b: 8). On the right are views of *A. insignis* (AMNH 227567) from Mindanao, a representative member of the *A. abrae-hylocetes* group (Musser, 1982b: 11).

with the other uniquely derived traits of *Apomys,* helps define the group.

10. The hind feet are long and slender (see fig. 7 in Musser, 1982b: 21), another derived trait not peculiar to *Apomys* but helpful, when used with the synapomorphies, in defining the group.

4. *CRUNOMYS* GROUP

Included within this cluster are the three species of *Crunomys* recorded from the Philippines and *Archboldomys luzonensis* from Mount Isarog in southern Luzon (table 8; Musser, 1982c). The crania and dentaries of

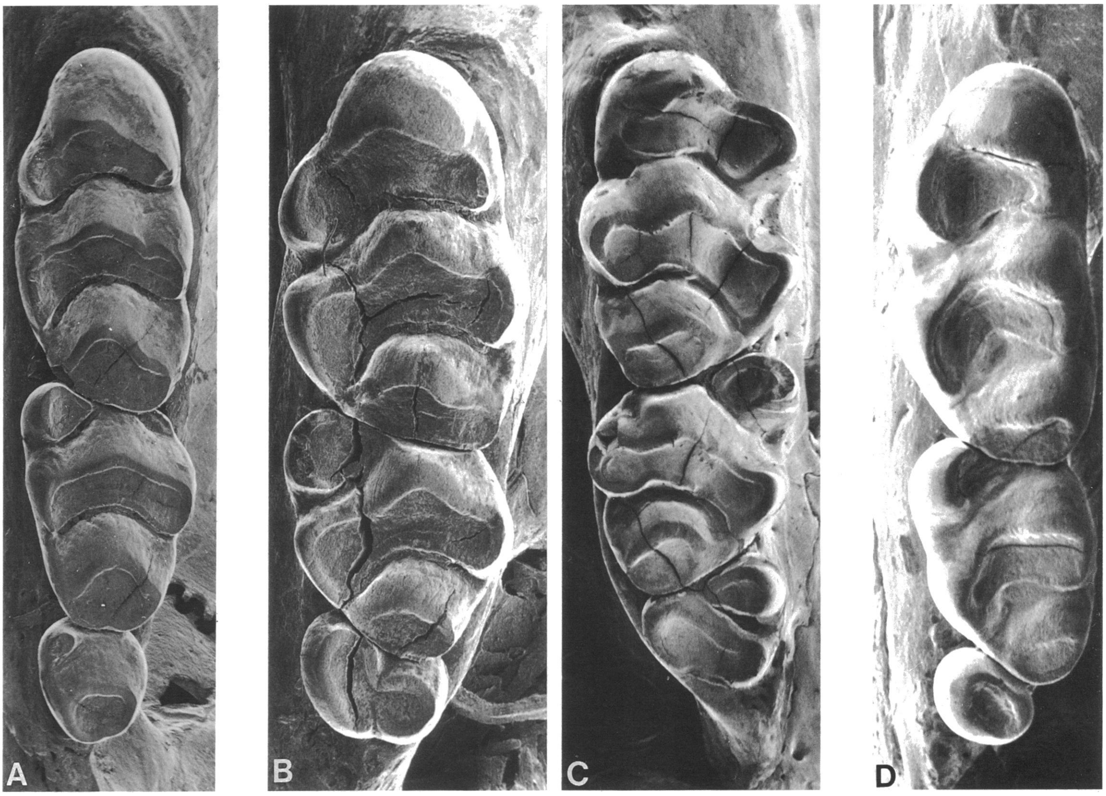

Fig. 38. Occlusal views of maxillary molar rows. **A,** *Apomys musculus* (MMNH 12971, left side, CLM1–3 = 4.6 mm). **B,** *Crunomys melanius* (AMNH 242102, left side, CLM1–3 = 3.9 mm). **C,** *Archboldomys luzonensis* (FMNH 95122, right side, CLM1–3 = 4.7 mm). **D,** *Chrotomys whiteheadi* (FMNH 62279, left side, CLM1–3 = 5.6 mm).

C. melanius and *A. luzonensis* are shown in figure 40. The genera have unique specializations (derived pattern of the cephalic arterial circulation and its bony reflection in *Crunomys*; long and sharp claws, upturned nasal tips, subsqamosal fenestra, elongate incisive foramina, large sphenopterygoid vacuities, slim incisors, and molar crowns exhibiting tubercular hypsodonty in *Archboldomys*), but are joined by the following shared derivations:

1. The tail is much shorter than combined lengths of head and body (see table 1 in Musser, 1982c: 8).
2. The hind feet are elongate with very small plantar pads (see fig. 11 in Musser, 1982c).
3. Cusp t3 is either not present on first upper molar or so reduced in size it is barely evident; cusp t3 is absent from each second molar (for these features and other dental traits, see figs. 38B, C and 39B, C, as well as figs. 6, 7, 32, and 33 in Musser, 1982c).
4. Cusp t9 of first upper molar is nearly obliterated because it has so broadly coalesced with the central cusp t8; cusp t9 appears to be absent from each second upper molar.
5. Each third upper and lower molar is reduced in size compared with the others in the toothrow; each upper is also reduced in number of cusps. Cusps t1 and apparently t4 and t5 form the occlusal surface in species of *Crunomys* (cusps t3, t6, t8, and t9 are missing); cusps t1 and what appears to be distorted cusps t4, t5, and t6 remain in *Archboldomys* (cusps t3, t8, and t9 are not present).
6. The anteroconid, which is a discrete element in young *C. melanius* (see fig. 6 in Musser, 1982c: 13), is composed of broadly

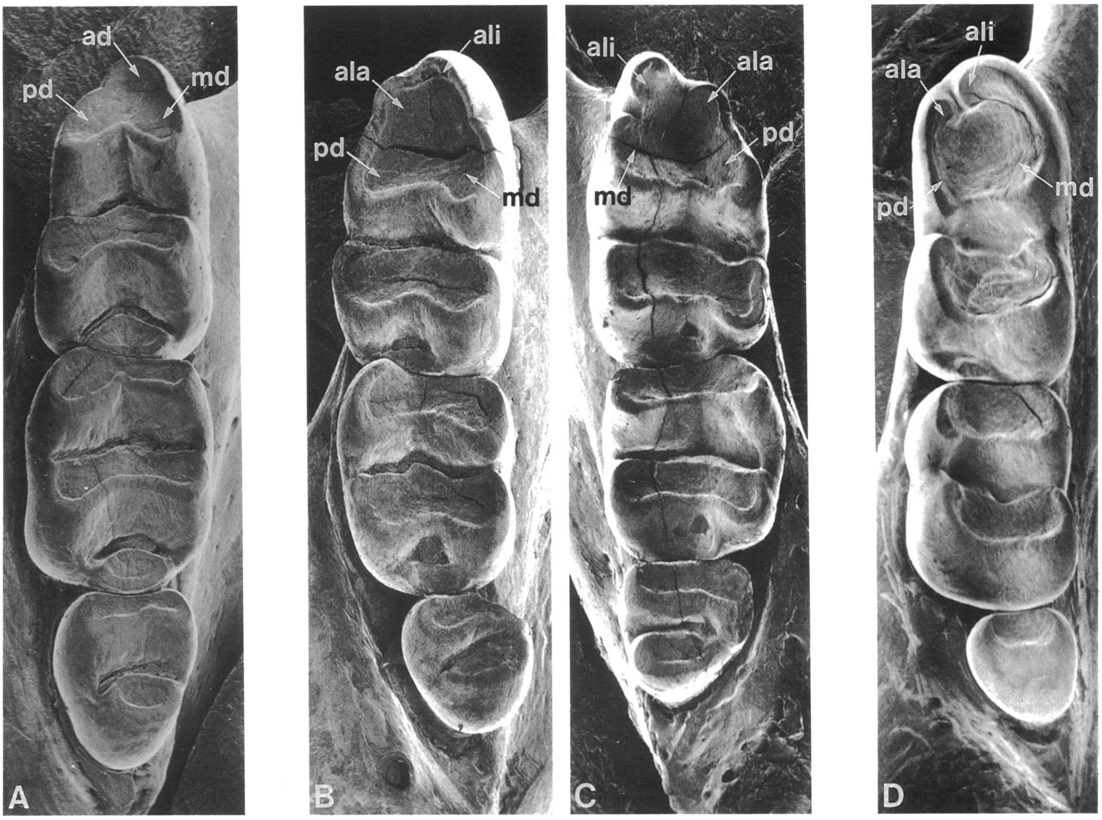

Fig. 39. Occlusal views of mandibular molar rows of the specimens shown in figure 38. **A,** *Apomys musculus* (clm1–3 = 4.3 mm); **B,** *Crunomys melanius* (clm1–3 = 4.1 mm); **C,** *Archboldomys luzonensis* (clm1–3 = 5.0 mm); **D,** *Chrotomys whiteheadi* (clm1–3 = 5.2 mm). In *A. musculus,* the anteroconid (**ad**), protoconid (**pd**), and metaconid (**md**) have completely fused to form the anterior half of the first molar; whether the remnant of the anteroconid consists of the anterolabial cusp (**ala**) or the anterolingual cusp (**ali**) or both is unknown. In the other three species, the metaconid and protoconid have also fused with the anteroconid, which clearly consists of anterolabial and anterolingual cusps. In young *C. melanius,* the anteroconid and first lamina are separate and joined only by a narrow enamel isthmus (see fig. 6 in Musser, 1982c: 13).

coalesced anterolabial and anterolingual cusps which in turn are fused with the anterior lamina (the metaconid and protoconid) to form a chunky basined structure, lobate in outline, occupying half the occlusal surface (fig. 39B, C).

5. *CHROTOMYS* GROUP

Included here are the species of *Chrotomys* (table 8; Thomas, 1898; Musser et al., 1982; Rickart and Heaney, 1991) and *Celaenomys* (table 8; Thomas, 1898; Rickart and Heaney, 1991). Part of the cranial and dental morphology characterizing the group is expressed in primitive traits (see figs. 41–45, 50). Some examples are an alisphenoid strut concealing the alisphenoid canal; masticatory and buccinator foramina that are coalesced in some specimens but separate in others; a foramen ovale accessorius; short incisive foramina; posterior palatine foramina that are either opposite the first molars or the contact between first and second molars; very small sphenopalatine vacuities; no sphenopterygoid vacuities; small auditory bullae with an elongate bony eustachian tube; a large stapedial foramen and a groove in the pterygoid plate for the infraorbital branch of the stapedial artery, which are the foramenal and

Fig. 40. Crania and dentaries (×2.5) of *Crunomys melanius* (AMNH 242102, top row) and *Archboldomys luzonensis* (USNM 573505, bottom row), both of which are members of the *Crunomys* group.

osseous reflections of the primitive cephalic carotid circulation; upper molars with three roots, lowers with two.

The primitive traits listed above are shared with other species in Division I, but there is a suite of derived traits that define the *Chrotomys* group, many of them likely part of a morphology associated with a primarily vermivorous diet (Rickart et al., 1991).

1. There is a prominent dorsal pattern of stripes in *Chrotomys* (a middorsal buffy stripe bordered by black or dark brown ones), and either an inconspicuous blaze on the forehead or pale line over the shoulder in *Celaenomys*.

2. Specimens of both genera have wide spatulate claws on the front feet; those of *Chrotomys* are elongate as well.

3. The hind feet are long and narrow with a hypothenar pad that ranges from being very small to minute.

4. The tail is much shorter than combined lengths of head and body.

5. The nasals are truncated well behind the anterior margins of the premaxillaries leaving the nasal orifice, incisors, and interpremaxillary foramen exposed in dorsal view (fig. 41).

6. The ventral surface of the rostrum is pierced by a very large interpremaxillary opening behind the incisors (fig. 42).

7. The rostrum is slightly tapered in dorsal view but sharply tapered in side view, a configuration resulting from the ventral surfaces of the maxillaries and premaxillaries that slope dorsad from the molar rows toward the incisors coupled with the inclined plane of the incisor profile (figs. 41, 43).

8. The back of the cranium is expansive; from the dorsal edge of the foramen magnum to the occipital-parietal suture, the occiput is rounded (best seen in side view, fig. 43), instead of vertical as is usual in the other Philippine endemics, and its dorsal area has expanded anteriorly resulting in more surface area for muscle attachment and a restriction of the interparietal to a thin band (fig. 41).

9. The procumbent upper incisors are sturdy and wide with spatulate wear surfaces; the lowers are very long, slender, and gracefully curved (figs. 43, 46, and 50). The face and side of each upper incisor is wide and rounded in cross section, and from its medial edge the enamel wraps almost all the way around to the back of the tooth, leaving only a small segment of dentine exposed in side view (fig. 46). Most other species of murine rodents have flat upper incisors in which the dentine is extensive and enamel forms only the face and narrow anterolateral portion of each tooth (fig. 46). The enamel is also thick on each lower incisor, forming nearly half the thickness of the tooth, a striking contrast to the thin enamel rim that is usual in most murines (fig. 46).

10. The molar teeth are reduced in size relative to the expanse of bony palate, and each third upper and lower molar either is reduced to a simple peg or is missing (figs. 38D, 39D, and 47).

11. The upper molars are narrow because the labial row of cusps (t3, t6, and t9 on each first and second molar) is not present (or so fully merged with the respective adjacent cusp as to be undetectable). The occlusal surface of each molar row is simple because it consists of a series of dentine basins outlined by smooth enamel rings (figs. 38D, 47A, B).

12. Anterior and posterior labial cusplets are absent from the lower molars, as is an anterolabial cusp from each second and third molar, and a posterior cingulum from each second molar (figs. 39D, 47C, D).

13. In the first lower molar the anteroconid (which seems to have resulted from the fusion of the anterolabial and anterolingual cusps—see fig. 39D) has completely merged with the lamina behind it (composed of the metaconid and protoconid) to form the round structure depicted in figures 39D and 47C, D, which constitutes at least half of the tooth. The posterior cingulum at the back of each first molar is at the labial side of the tooth rather than in the middle. The occlusal surface of each molar row consists of deep basins bounded by round enamel walls (figs. 39D, 47C, D).

14. In each dentary, the coronoid process is long and slender. The posterior segment of the lower incisor is encased in a wide bony tube that extends in a graceful curve from the ventral margin of the dentary up into the condyloid process to end in a prominent bony bulge, which marks the incisor root, just in front of the articular surface of the condyle. The body of the ramus between molar row and incisor is elongate (figs. 43, 50).

6. *RHYNCHOMYS* GROUP

The shrew rats, *Rhynchomys soricoides* and *R. isarogensis* (Thomas, 1898; Musser, 1969; Musser and Freeman, 1981; table 8; figs. 41–45) are the members of this small cluster. Like members of the *Chrotomys* group, the derived traits defining members of the *Rhynchomys* group appear to be part of a morphology associated with a vermivorous diet (Rickart et al., 1991), but the unique morphological specializations are unlike those

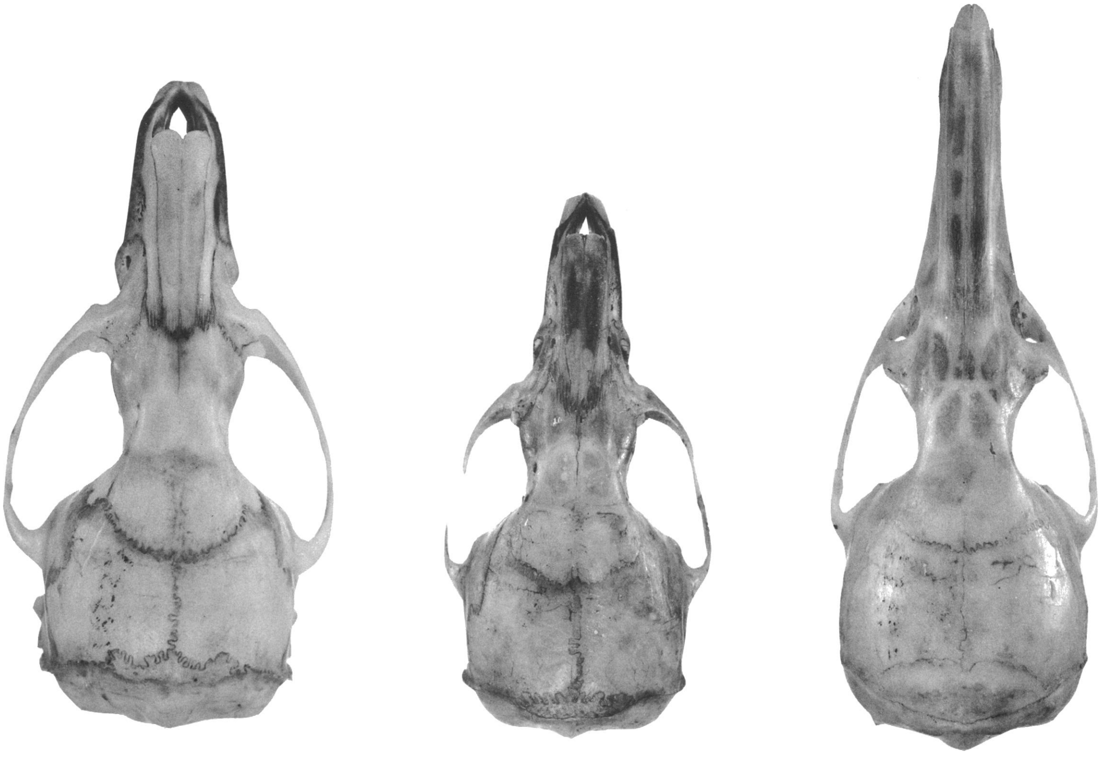

Fig. 41. Dorsal cranial views (×2) of representatives of the *Chrotomys* and *Rhynchomys* groups. **Left,** *Chrotomys whiteheadi* (FMNH 62285) from Luzon; **middle,** *Celaenomys silaceus* (AMNH 185138) from Luzon; **right,** *Rhynchomys soricoides* (FMNH 62289) from Luzon.

characterizing species of *Chrotomys* and *Celaenomys.*

1. The face, from the eyes forward, is extremely protracted ("muzzle enormously elongate," as Thomas, 1898: 396, wrote), an elongation mirrored by the very long, slender, and tapered rostrum and the delicately elongate dentary (figs. 41–43). The cranial region from about the interorbit forward appears stretched compared with the proportions exhibited by *Chrotomys* and its allies (figs. 41–43). The long and slender incisive foramina may also reflect this protraction.

2. The distal portion of the nasals projects dorsad, breaking the sloping dorsal profile of the rostrum (fig. 43).

3. The conformation of each zygomatic plate also likely reflects the cranial elongation, as well as the poorly developed zygomasseteric or chewing musculature. The plate is slender and slanted; its ventral maxillary root is anterior to the dorsal maxillary root, without overlap in *R. soricoides* but with slight overlap in *R. isarogensis* (see fig. 1 in Musser and Freeman, 1981). The form is unique among Philippine murines (figs. 43, 44).

4. The pterygoid plate in the vicinity of each foramen ovale and anterior opening of the alisphenoid canal is not flat (as is usual among species of *Chrotomys* and *Celaenomys*) but instead is inclined and confluent with the slope of the braincase floor, and a pterygoid ridge is absent as is a bony bridge over the foramen ovale; the ridge and bridge define the lateral margins of each pterygoid plate in *Chrotomys* and other Philippine murines, and provide surface area for attachment of the pterygoid musculature (figs. 42, 45).

5. An alisphenoid strut is absent (fig. 44C).

6. The molar teeth are tiny and each toothrow consists only of first and second molars

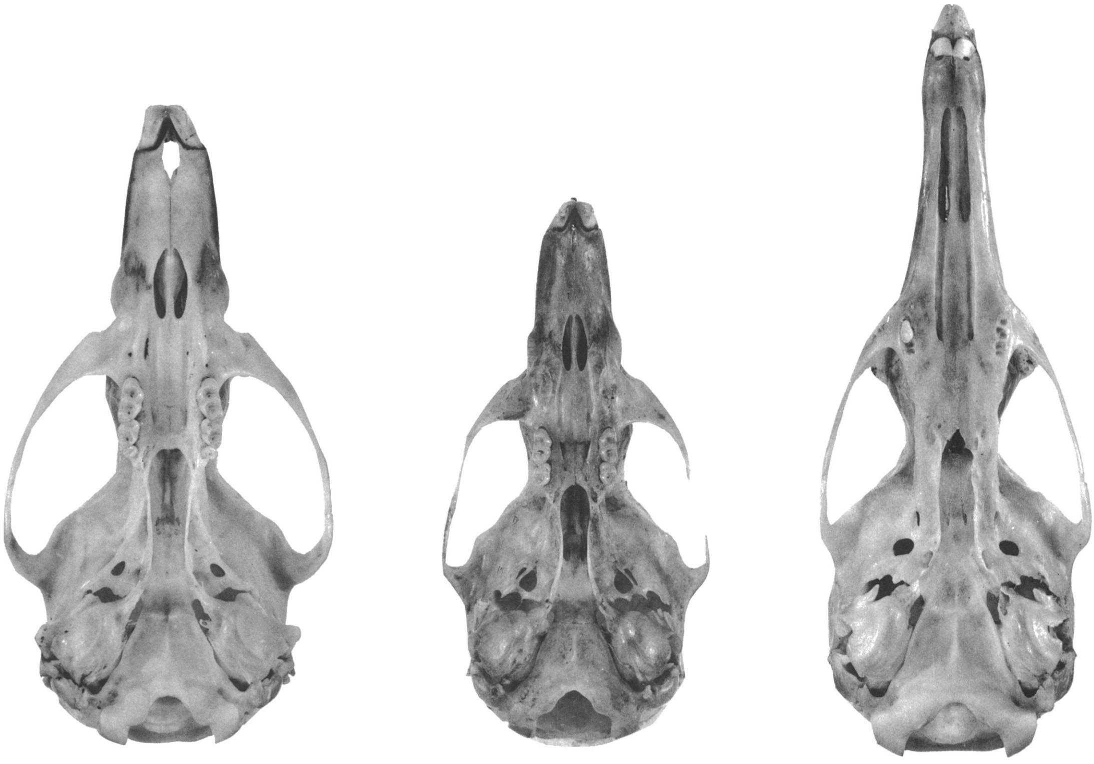

Fig. 42. Ventral cranial views (×2) of the specimens shown in figure 41. **Left,** *Chrotomys whiteheadi*; **middle,** *Celaenomys silaceus*; **right,** *Rhynchomys soricoides.*

(fig. 48). Their cusp patterns are difficult to detect in *R. soricoides* because the occlusal surfaces are worn in the specimens we studied (fig. 49A, E). However, four examples of *R. isarogensis* (USNM 573574, 573576, 573577, and 573580) are young and retain discernable occlusal cusp patterns on their slightly worn molars (fig. 49).

There are clearly three rows of cusps on each first upper molar. The anterocone consists of a large central cusp t2, a lingual cusp t1 that is large in one specimen (fig. 49B) but a low bump on a cingular ridge in others (fig. 49C, D), and what appears to be a remnant of the labial cusp t3.

The second row of cusps is complete. There is a prominent lingual cusp t4 and a round central cusp t5 jammed against a large but compressed cusp t6. Although cusp outlines of the row are distorted, it clearly consists of three large cusps (most clearly seen in fig. 49C), a configuration that contrasts with the first upper molars of *Chrotomys* and *Celaenomys* in which cusp t6 is either absent or undetectable in available specimens.

The third row lacks a lingual cusp t7, which is the usual primitive condition and one common to many of the Philippine endemics. The large round cusp t8 forms most of the occlusal surface of the third row. A much smaller labial cusp t9 is coalesced with cusp t8 but still clearly evident as a round structure on one specimen (fig. 49B); on other individuals, cusp t9 takes the form of a cingular ridge (fig. 49D). We could not identify a posterior cingulum at the back of the first molar, and assume it is absent.

Each second upper molar is oblong or circular in occlusal outline, basined when worn but cuspidate in unworn animals. In specimens with visible cusps (fig. 44), its coronal surface clearly consists of cusps t4, t5, and t6 coalesced into a distorted and nearly featureless row, and a large cusp t8 pressed

Fig. 43. Lateral views (×2) of cranium and dentary of the specimens illustrated in figures 41 and 42. **Upper left,** *Chrotomys whiteheadi*; **upper right,** *Celaenomys silaceus*; **middle,** *Rhynchomys soricoides*.

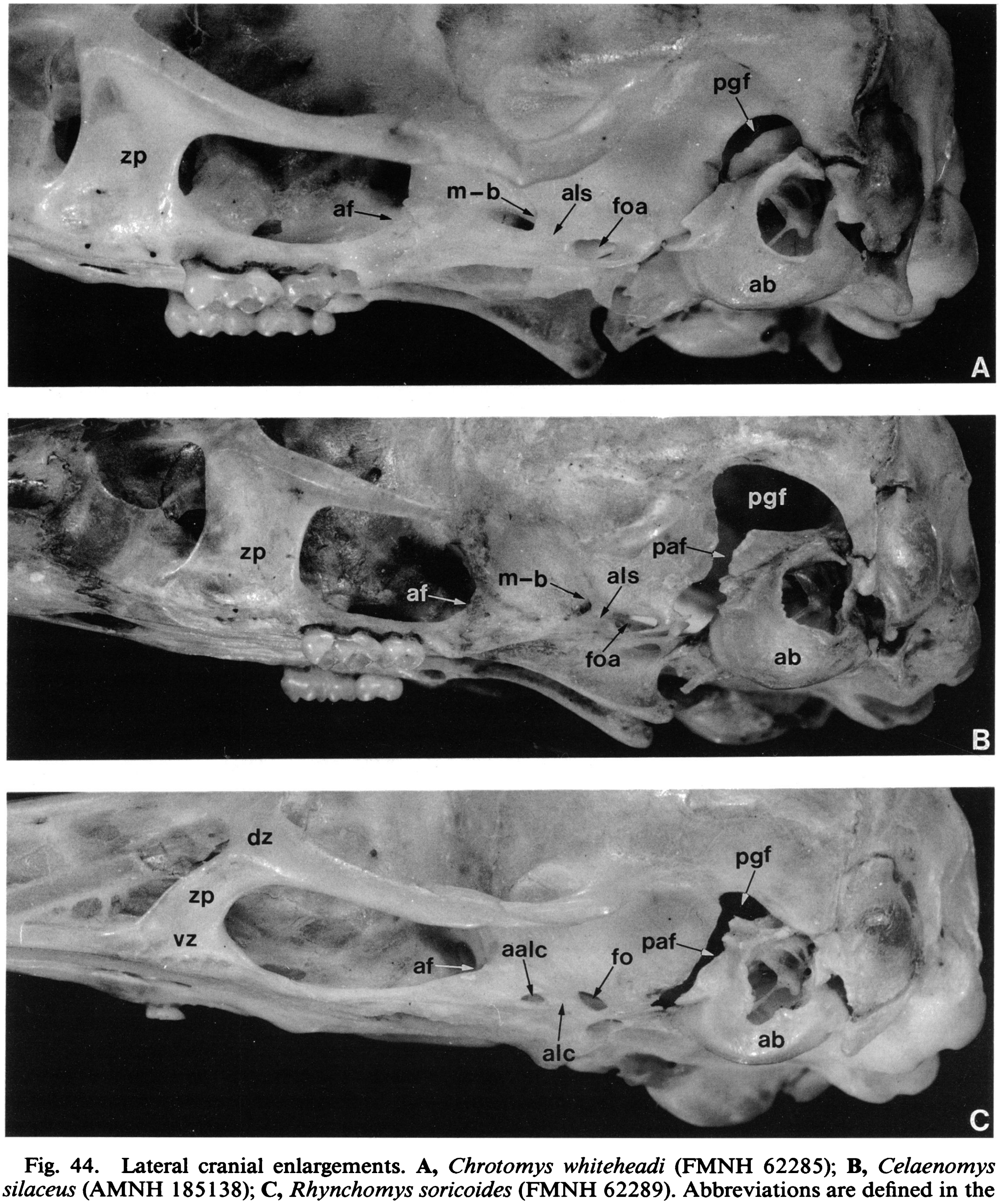

Fig. 44. Lateral cranial enlargements. **A,** *Chrotomys whiteheadi* (FMNH 62285); **B,** *Celaenomys silaceus* (AMNH 185138); **C,** *Rhynchomys soricoides* (FMNH 62289). Abbreviations are defined in the legend of figure 45.

against a remnant of cusp t9. The tooth is so reduced that only some specimens retain this cusp pattern; the cusp outlines are so distorted in other individuals that no consistent pattern is detectable.

Occlusal cusp patterns on the tiny lower molars are also severely reduced but detectable. A row of four basins forms the occlusal surface of each first lower molar in worn dentitions (fig. 49E). These translate into an an-

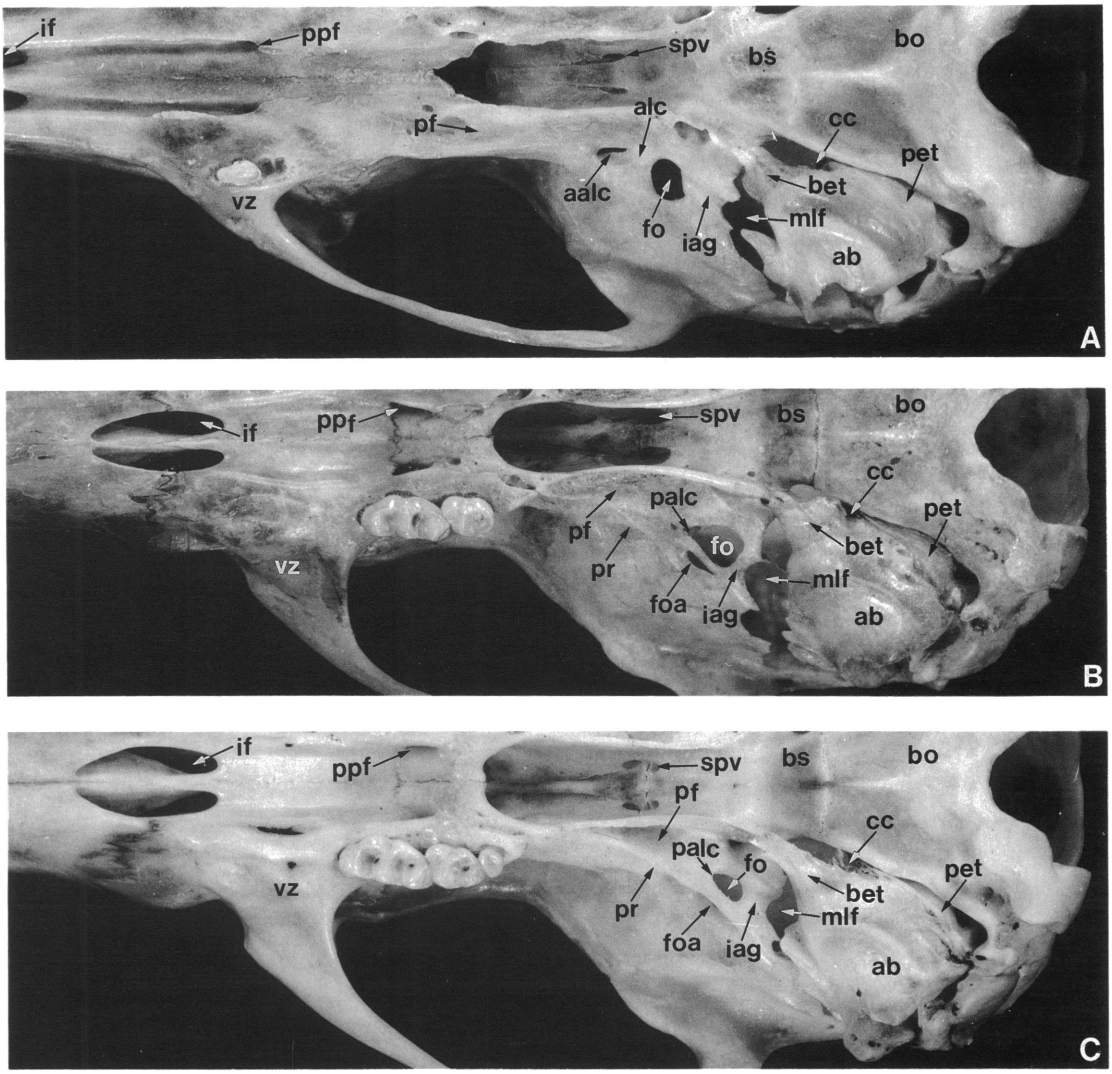

Fig. 45. Ventral cranial enlargements of specimens shown in figure 44. **A**, *Rhynchomys soricoides*; **B**, *Celaenomys silaceus*; **C**, *Chrotomys whiteheadi*. **aalc**, anterior opening of the alisphenoid canal; **ab**, auditory bulla; **af**, anterior alar fissure; **alc**, alisphenoid canal; **als**, alisphenoid strut (which conceals the alisphenoid canal); **bet**, bony eustachian tube; **bo**, basioccipital; **bs**, basisphenoid; **cc**, carotid canal; **dz**, dorsal maxillary root of the zygomatic plate; **fo**, foramen ovale; **foa**, foramen ovale accessorius; **iag**, groove for the infraorbital branch of the stapedial artery; **if**, incisive foramen; **m-b**, masticatory-buccinator foramina; **mlf**, middle lacerate foramen; **paf**, postalar fissure; **palc**, posterior opening of the alisphenoid canal (arrow points to where the infraorbital branch of the stapedial artery enters the braincase dorsal to the pterygoid plate); **pet**, petrosal; **pf**, pterygoid fossa; **pgf**, postglenoid foramen; **ppf**, posterior palatine foramen; **pr**, pterygoid ridge; **spv**, sphenopalatine vacuity (these openings are in the dorsolateral walls of the mesopterygoid fossa); **vz**, ventral maxillary root of the zygomatic plate; **zp**, zygomatic plate.

teroconid, two rows of cusps, and a posterior cingulum in molars that are not as worn (fig. 49F). The anteroconid is small (and probably consists of coalesced anterolabial and anterolingual cusps) and its posterior margin has merged with the metaconid and protoconid. That row is followed by a lamina formed from the entoconid and hypoconid. A prom-

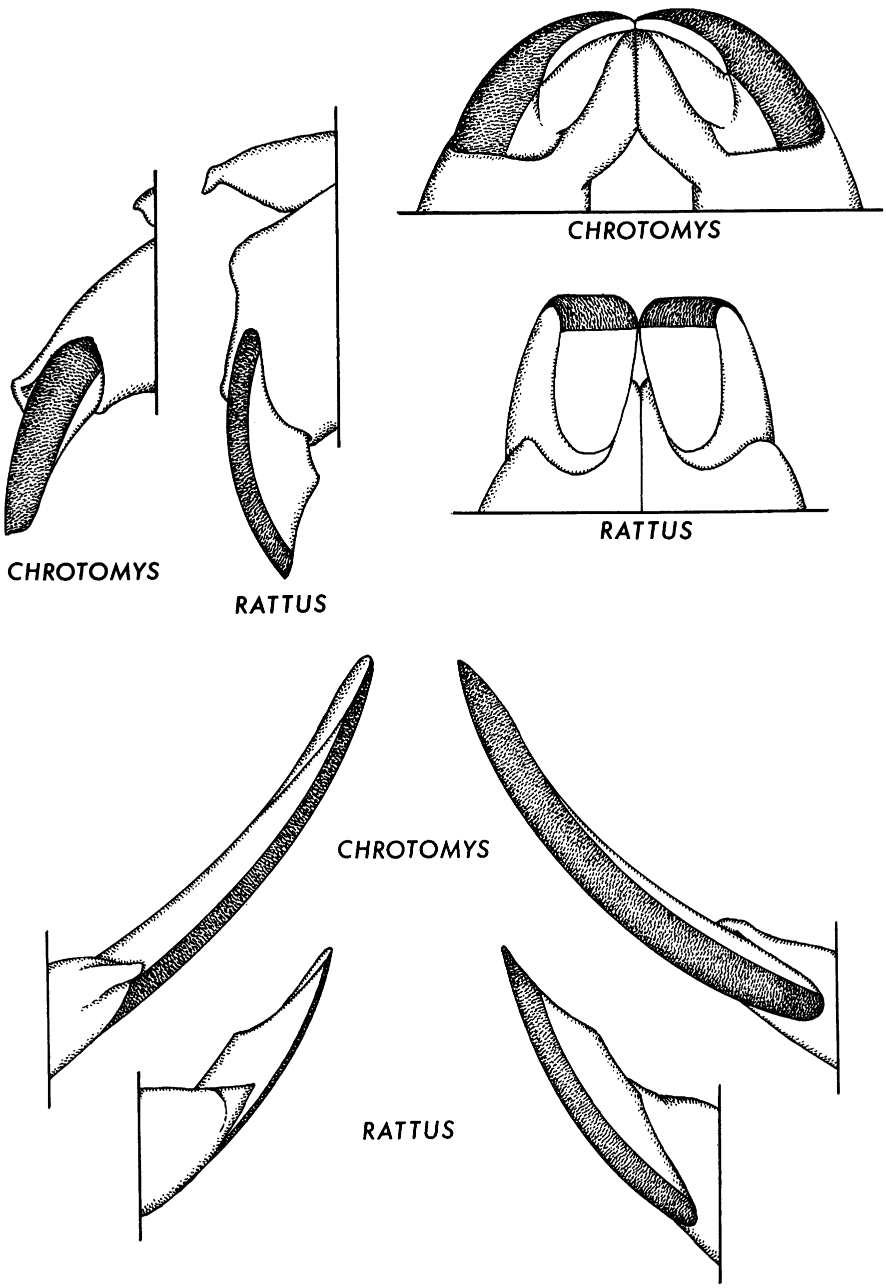

Fig. 46. Contrasts in incisor morphology between the highly derived *Chrotomys* (drawn from *C. whiteheadi*, FMNH 62285) and the generalized configuration represented by *Rattus* (based on *R. rattus*, AMNH 227492). The dense stippling represents enamel. See text for a discussion of the differences illustrated here.

inent posterior cingulum marks the back of the molar.

Each second lower molar is smaller but wider than the first and retains a reduced but similar cusp pattern. The two primary rows of cusps form much of the coronal surface but remnants of the anteroconid as well as the posterior cingulum can be detected.

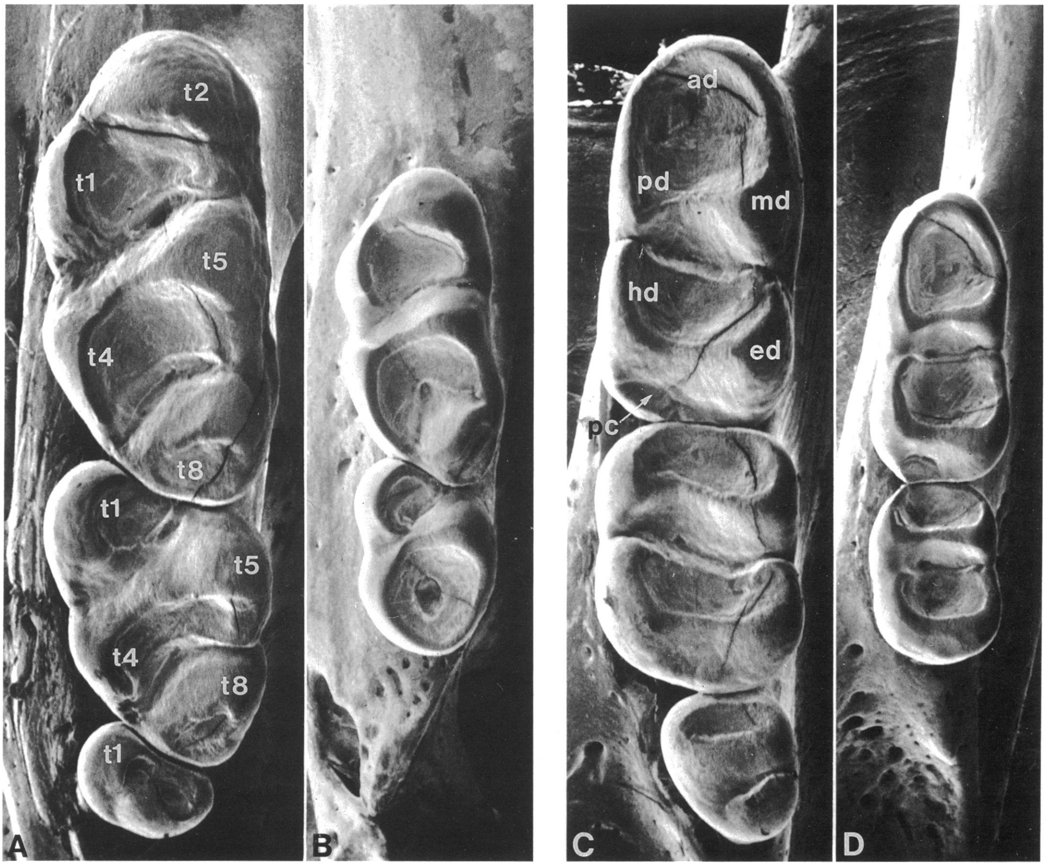

Fig. 47. Occlusal views of left upper (A and B) and lower (C and D) molars in *Chrotomys* and *Celaenomys*. **A, C,** *Chrotomys mindorensis* (MMNH 12972; CLM1–3 = 6.5 mm, clm1–3 = 6.8 mm). **B, D,** *Celaenomys silaceus* (AMNH 185138; CLM1–3 and clm1–3 = 3.6 mm). Cusps t3, t6, and t9, which form the labial components of each cusp row in other species of murines, are absent from all specimens of *Chrotomys* and *Celaenomys*. The third upper molar in *Chrotomys* is so reduced in size that only cusp t1 is identifiable. The example of *Celaenomys* is older than that of *Chrotomys*, and although most of the cusp pattern of the second upper molar is obliterated due to wear, the basined portion is also formed from cusps t4, t5, and t8 (verified by the pattern seen in the unworm molars of a juvenile, USNM 151512).

The anteroconid (**ad**) has fused with the metaconid (**md**) and protoconid (**pd**) to form the anterior portion of each first lower molar, and the posterior segment consists of a lamina representing the coalescence of the entoconid (**ed**) and hypoconid (**hd**), and a small posterior cingulum (**pc**).

Although their reduction is a derived trait, what remains of the occlusal patterns of the first upper and lower molars is unlike the derived patterns characteristic of *Chrotomys* and *Celaenomys*.

7. Each upper molar row is directly beneath the ventral maxillary root of each zygomatic plate (figs. 45A, 48); the molar row is posterior to the plate in other shrew rats and the rest of the Philippine endemic murines. The upper molars of *Rhynchomys* are so small relative to size of the cranium that the bony palate is an expansive flat surface that projects well posterior to the toothrows (figs. 42, 45A). However, the posterior margin of the palate is at the level of the interorbital constriction, which is primitive and the termination point in all other Philippine murines possessing a primitive palate (the species of *Chrotomys* and *Celaenomys*, for

example, and all members of the *Crateromys* group). The palatal extension has been anterior to the interorbit, an elongation process affecting the entire cranium in that region.

8. The upper incisors are very short and small, the lowers are small and needlelike; both pairs are delicate relative to sizes of cranium and mandible (fig. 43). The uppers lack pigment in the enamel, the lowers have very pale orange enamel.

CLUSTERING AMONG GENERA IN DIVISION I

The distribution of certain external, skeletal, and dental derived traits among the species in Division I allows us to define discrete groups of species. We are less satisfied with the results from our attempts to test the relationships among these groups using shared derived traits. Our preliminary analyses have yielded equivocal results, which we discuss below.

Phloeomys and *Crateromys* Groups

Apomorphies defining *Phloeomys* suggest it is distantly related to other Old Endemic groups in Division I and reinforce Thomas's (1898: 378) assertion that "*Phloeomys* is so isolated that I can make no suggestions as to what is its nearest ally." Furthermore, nearly all the other native Philippine murines, including those species in Divisions II and III, show the derived position of the incisive foramen relative to the maxillary-premaxillary suture (the suture intersects at about the middle of each foramen); *Chrotomys* is the exception and retains the primitive pattern (the suture intersects each foramen near its posterior margin so most of the foramina are in the premaxillary). This primitive conformation is also found in *Phloeomys*. Thus, this single trait defines a clade containing all the species (including those of *Chrotomys*, which in this context simply retained the primitive trait) of native Philippine murines except those of *Phloeomys*.

But the position of the incisive foramina is just one trait, and it may not reflect the real phylogenetic pattern. From another perspective, we could assume that (1) the derived cordate structure of the anteroconid of *Phloeomys* is homologous with the anteroconid characterizing members of the *Crateromys* group; (2) cusp t7, which is a derived trait, forms part of the posterior lamina of each upper molar and is homologous with the elongate cusp t7 found in the *Crateromys* group; and (3) the presence of chromatic polymorphism and coat pattern, presumably derived, that is shared between the species of *Phloeomys* and the *Crateromys* group is significant. These traits would then unite the two assemblages to the exclusion of the other genera in Division I, and in this context the primitive position of the incisive foramina in *Phloeomys* would be just another of the many primitive traits retained by that genus. Schauenberg (1978) has already suggested that *Crateromys schadenbergi* may be in the same family (Phloeomyidae) as *Phloeomys*, but offered no data to substantiate this view.

From still another perspective, *Phloeomys* and the *Crateromys* group could be viewed as each being more closely related to a group of genera that included members of an Old Endemic stratum occurring in other archipelagos and continents (the genera listed in table 16 in Musser, 1981b: 167) than to each other or to any other Philippine group in Division I. Thomas (1898: 378), for example, noted that "*Crateromys* seems to have its nearest ally in *Lenomys* from Celebes," and "*Carpomys* and *Batomys* belong to a group of arboreal genera scattered over the oriental part of the East Indian Archipelago." Using data derived from dental patterns, Misonne (1969) included *Phloeomys, Crateromys, Batomys,* and *Carpomys* in a broad *Lenothrix* group that in addition to the Sundaic *Lenothrix* and *Pithecheir,* also contained *Lenomys* and *Eropeplus* from Sulawesi; *Pogonomys, Hyomys, Mallomys,* and *Anisomys* from New Guinea; *Papagomys* and *Spelaeomys* from Flores; *Coryphomys* from Timor; and *Tokudaia* from the Ryukyu Islands. We have examined these genera and none of them possess the suite of synapomorphies that define either the *Phloeomys* or *Crateromys* groups in Division I.

We are able to formulate the following alternative hypotheses that require testing with chromosomal, biochemical, and other kinds of morphological data than that presented here:

1. *Phloeomys* is unique and phylogeneti-

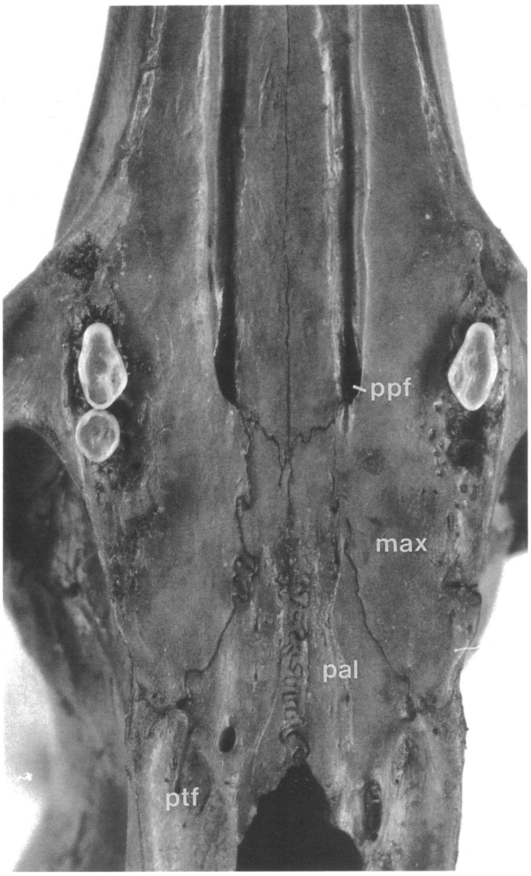

Fig. 48. Palatal view of *Rhynchomys soricoides* (FMNH 62289) to show the minute molar row (CLM1–2 = 2.2 mm) set in an expansive bony palate. We have yet to see a specimen of *Rhynchomys* which has third molars.

cally distant not only from any other Philippine murine, but also from genera in any other regional fauna.

2. The other Philippine groups in Division I are more closely related among themselves than to *Phloeomys.*

3. *Phloeomys* and members of the *Crateromys* group are more closely related to each other than to any other Philippine endemic or to any other genus from the Indo-Australian region, a hypothesis supported by some pelage and dental characters we noted in this report.

4. *Phloeomys* and the *Crateromys* group each has a closer phylogenetic alliance with genera native to island groups and continents outside of the Philippines.

The *Apomys* Group and the Shrew Rats, and the *Apomys* Group and Some Non-Philippine Murines

A host of discrete derived traits defines *Apomys,* and each group of shrew rats (*Crunomys* group, *Chrotomys* group, and *Rhynchomys* group) can also be strongly characterized by morphological specializations. However, within the context of assessing phylogenetic relationships only among Philippine endemics in Division I, we identified four features shared by *Apomys* and shrew rats that may group them but exclude members of the *Phloeomys* and *Crateromys* groups: (1) long and narrow hind feet with moderately or strongly reduced hallux and fifth digit relative to the long middle digits; (2) otic capsule that is separated from the squamosal and alisphenoid by a narrow gap consisting of a large postglenoid foramen combined with the postalar fissure and sometimes the middle lacerate foramen (*Chrotomys* is an exception and retains the primitive condition of the otic capsule being tightly bound to the cranial bones); (3) upper and lower third molars either absent or strongly reduced in size relative to other teeth in the row; and (4) anteroconid, metaconid, and protoconid fused into a bulky structure that forms half or more of the occlusal surface of each first lower molar (except in *Rhynchomys*).

Although these traits appear to provide a tidy definition of an *Apomys* and shrew rat group, we are skeptical about using them because the phylogenetic information they provide is equivocal. Long and narrow hind feet with the accompanying length proportions of outer digits relative to inner digits is a configuration widely distributed among Indo-Australian murines. It is certainly the common form characterizing most of the species in Division III, for example. The trait may be shared among species of *Apomys* and shrew rats because they are phylogenetically related at some level but it could just as well have evolved independently in these groups, all of which are either terrestrial or scansorial, habits associated with an elongate hind foot.

A gap separating the otic capsule from the squamosal and alisphenoid bones is also commonly distributed among Asian murines and is found in members of Division III as

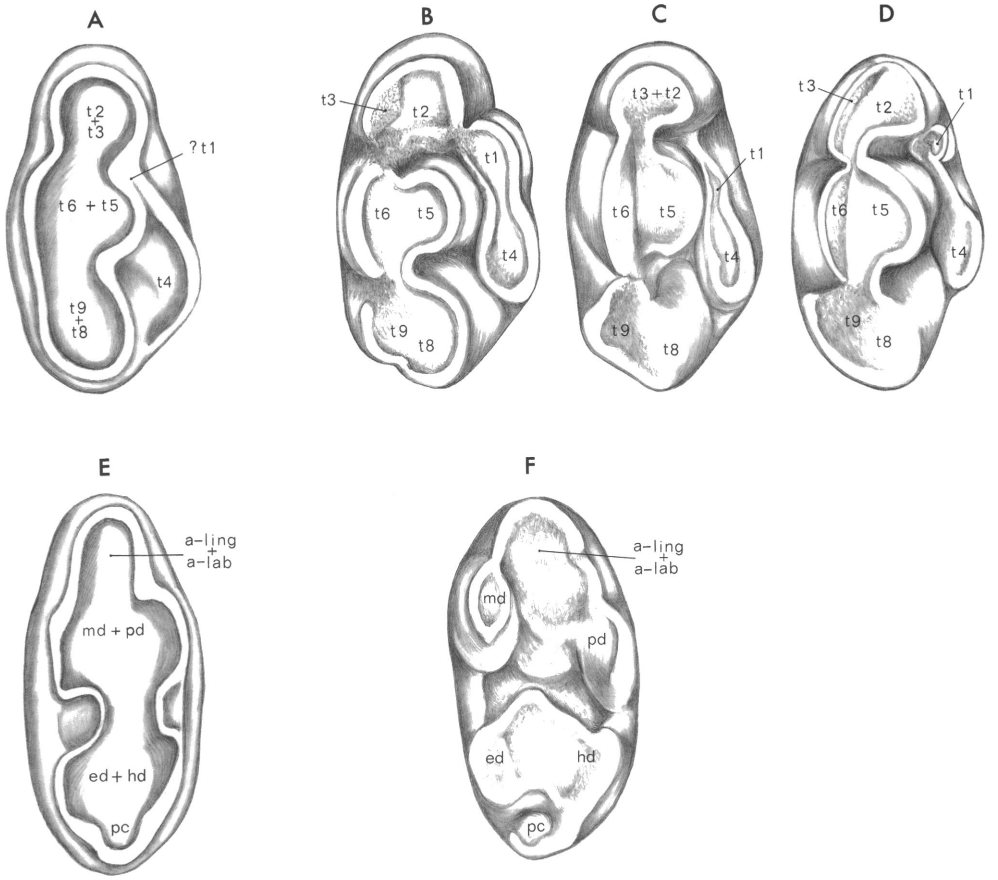

Fig. 49. Enlargements of the first upper (A-D) and lower (E, F) right molars of *Rhynchomys soricoides* (A, E, FMNH 62289) and *R. isarogensis* (B, USNM 573580; C, USNM 573576; D, USNM 573577; F, USNM 573576). The notation represents our best attempt to identify the cusps. In upper molars, the anterocone consists of cusps t1–t3, the second row is formed by cusps t4–t6, and the posterior row by cusps t8 and t9. These are detectable in slightly worn teeth (B–D) but transformed into basins in worn molars (A). In lower molars, the anteroconid is formed from anterolingual (**a-ling**) and anterolabial (**a-lab**) cusps. The anterior row of cusps consists of the metaconid (**md**) and protoconid (**pd**) and the posterior row is formed by the entoconid (**ed**) and hypoconid (**hd**). A prominent posterior cingulum (**pc**) defines the back of the tooth.

We assume that only two cusps from the anteroconid on the lower molar; perhaps it consists of only the anterolingual cusp (this is always the largest cusp), or it could have been formed from the anterolingual, anterolabial, and an anterocentral. What is important is the shape of the anteroconid and its obvious distinction from the first lamina formed by the metaconid and protoconid. The configuration formed by anteroconid and first lamina contrasts with the structure seen in the species of *Chrotomys* and *Celaenomys*. See text for additional discussion.

well. It too seems less reliable as a strong synapomorphy.

Presence of a third molar strongly reduced in size and cuspidation, especially the size and structure of the uppers, and an anteroconid fused with the metaconid and protoconid have to be carefully interpreted in phylogenetic context. A reduced third molar shared among taxa is not by itself diagnostic without examining the change in structure formed by the cusps as well. The upper third molar of *Apomys,* for example, is a simple peg with a very small anterolingual cusp. It does not resemble the molar in either *Cru-*

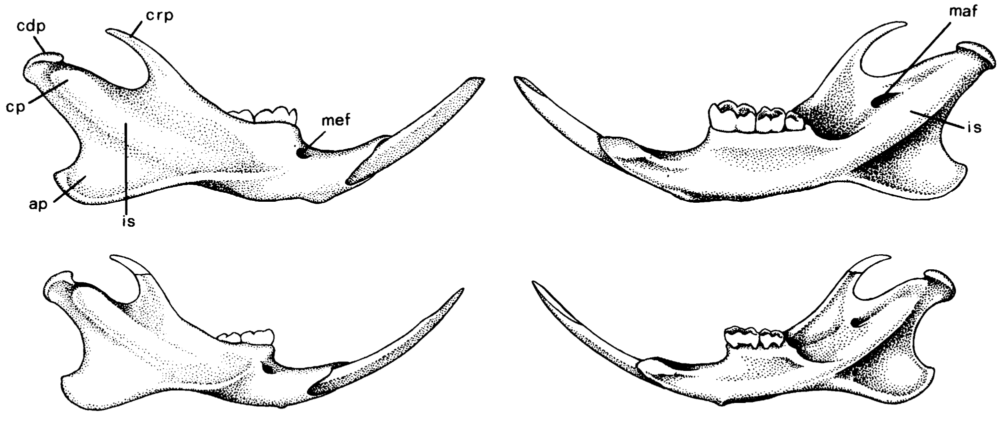

Fig. 50. Lateral (left side of figure) and medial (right side) views of the right dentaries of shrew rats. **Top,** *Chrotomys mindorensis* (MMNH 12972); **bottom,** *Celaenomys silaceus* (AMNH 185138). In both species, the bony sheath enclosing the incisor root (**is**) extends caudad well past the coronoid process (**crp**) to end in a capsular process (**cp**) just beneath the condylar process (**cdp**). The mandibular foramen (**maf**) is always dorsal to the incisor sheath. Other abbreviatons: **ap,** angular process; **mef,** mental foramen. This extension of the incisor root and configuration of the bony sheath is unique to all members of the *Chrotomys* group.

nomys or *Archboldomys* where the third molar is reduced but the cusp structure is still evident and the anterolingual cusp is very large (fig. 38). Even the cuspid structure of the rudimentary third molar in *Chrotomys* is more similar to *Crunomys* and *Archboldomys* than to *Apomys* (compare toothrows in figs. 38 and 47). The shape of the anteroconid in *Apomys* is unique among Philippine endemics. The anterior half of each first lower molar consists primarily of the broadly merged metaconid and protoconid, and this element is fused with a meager remnant of the anteroconid (fig. 39). In members of the *Crunomys* and *Chrotomys* groups, the anterior half of each first lower molar consists of two primary components that are nearly equal in their contribution to occlusal surface area: the coalesced metaconid and protoconid, which is fused with the anterolingual and anterolabial cusps of a large anteroconid (fig. 39). Although the anterior half of each first lower molar consists of one large formation in *Apomys* and most of the shrew rats, the anteroconid is a minor and residual component in *Apomys* but a large and significant structure in species of shrew rats. The trilobed structure in *Apomys* does not appear to be homologous to the bulky formation in the shrew rats.

The occlusal patterns and degree of relative molar reduction seen in *Apomys* are also found in species of *Melomys* (see fig. 18 in Musser, 1982b: 39), a murine indigenous to the Moluccas, and the New Guinea and Australian region. There are differences in details. One of these is a posterior cingulum, a primitive trait, which persists at the back of each first and second upper molar in *Melomys* but is absent from species of *Apomys*. To the west of the Philippines on the Sunda Shelf, a slightly less extreme version of the *Apomys* molar pattern is seen in *Niviventer cremoriventer* (see fig. 107 in Musser and Newcomb, 1983: 567). Because derived cranial and external traits of most species of *Melomys* or *Niviventer* are not shared with *Apomys* (Musser, MS.), and the apomorphic characters of *Apomys* are not shared with either *Melomys* or *Niviventer*, we suspect the similar cusp patterns to have evolved independently.

We can formulate the following alternative hypotheses about phylogenetic relationships of *Apomys*:

1. Species of *Apomys* are more closely related to shrew rats than to members of the *Phloeomys* or *Crateromys* groups in Division I.
2. *Apomys* is no more closely related to shrew rats than to species of the *Phloeomys*

or *Crateromys* groups, and represents an independent colonization from continental Asia.

3. The species of *Apomys* are allied to groups native to other archipelagos and island continents and not to the Philippines.

The Shrew Rats

Although the *Crunomys* group, the *Chrotomys* group, and the *Rhynchomys* group are each defined by a set of very strong synapomorphies, at least two derived traits bring them together into a larger cluster: (1) a tail that is much shorter than length of head and body; and (2) the anterior structure of each first lower molar, which is formed from merger of the anterolabial and anterolingual cusps, the metaconid, and the protoconid. Within this context, three derived traits that we discussed above in assessing the relationship of *Apomys* to shrew rats may be significant in supporting the union of the shrew rat groups into a larger monophyletic assemblage: (1) elongate hind feet with short outer digits relative to the central digits and plantar pads reduced in size relative to area of plantar surface; (2) a gap between the otic capsule and squamosal and alisphenoid bones (except in *Chrotomys*); and (3) reduction in size and cuspidate structure of the third molars (especially the maxillary teeth) in some species and their loss in others.

If these traits define a real assemblage, it is one representing a very early colonization of the Philippine Archipelago with subsequent diversification into three components, one retaining many primitive features (the *Crunomys* group), the other two acquiring highly specialized morphologies (the *Chrotomys* and *Rhynchomys* groups).

We are unable to resolve the degree of phylogenetic alliance among the three groups of shrew rats. An elongate rostrum and enlarged interpremaxillary foramen are the only traits we found that might unite members of the *Chrotomys* and *Rhynchomys* groups. Rostral elongation, however, may have evolved independently in several groups. *Archboldomys*, for example, also has a moderately long and narrow rostrum in relation to cranial size (fig. 40), as do some species of *Apomys*, especially *A. datae* (fig. 37), in which the proportional relationship of rostral to cranial length is about the same at it is in *Celaenomys*. Rostral elongation, by itself, is not a convincing synapomorphy or defining character of a larger assemblage consisting of the *Chrotomys* and *Rhynchomys* groups. That trait coupled with an enlarged interpremaxillary foramen, however, adds strength to the reality of the grouping and at least supports a hypothesis of relationships that can be further tested. In species of the *Crunomys* and *Apomys* groups, the interpremaxillary foramen is minute.

If a short tail and fused occlusal structure of the first lower molar represent homoplastic (independent) derivations in each group of shrew rats, we will eventually have to test the hypothesis that each group may be more closely related to genera native to regions outside of the Philippines than to each other.

Outside the Philippine Archipelago, the *Crunomys* group is represented by *Crunomys celebensis* on Sulawesi (Musser, 1982c) but beyond the murines of that island we cannot tie *Crunomys* and *Archboldomys* to any other faunas. The molar occlusal patterns in *Crunomys* bear a general resemblance to those of some *Mus*, particularly species native to the Sunda Shelf, such as *M. vulcani* (see fig. 109 in Musser and Newcomb, 1983: 569), for example, but *Mus* retains the primitive cephalic arterial circulation and also possesses derivations not found in *Crunomys*.

The species of *Chrotomys* and *Celaenomys* have been considered members of what has been called the Hydromyinae, a group of genera native to the New Guinea and Australian region (Thomas, 1898; Ellerman, 1941; Simpson, 1945; Misonne, 1969). The others in this assemblage are species of *Hydromys, Xeromys, Parahydromys, Crossomys, Microhydromys, Leptomys, Paraleptomys, Pseudohydromys, Neohydromys,* and *Mayermys*. Although in 1945 Simpson listed the Philippine genera as members of the Hydromyinae in his classification of mammals, by 1961 (p. 435) he wrote that "I think it practically certain that *Chrotomys* is convergent toward the Hydromyinae and is of quite different ancestry within the Muridae."

Results of our unpublished surveys of derived character states among *Chrotomys, Celaenomys,* and the hydromyines support

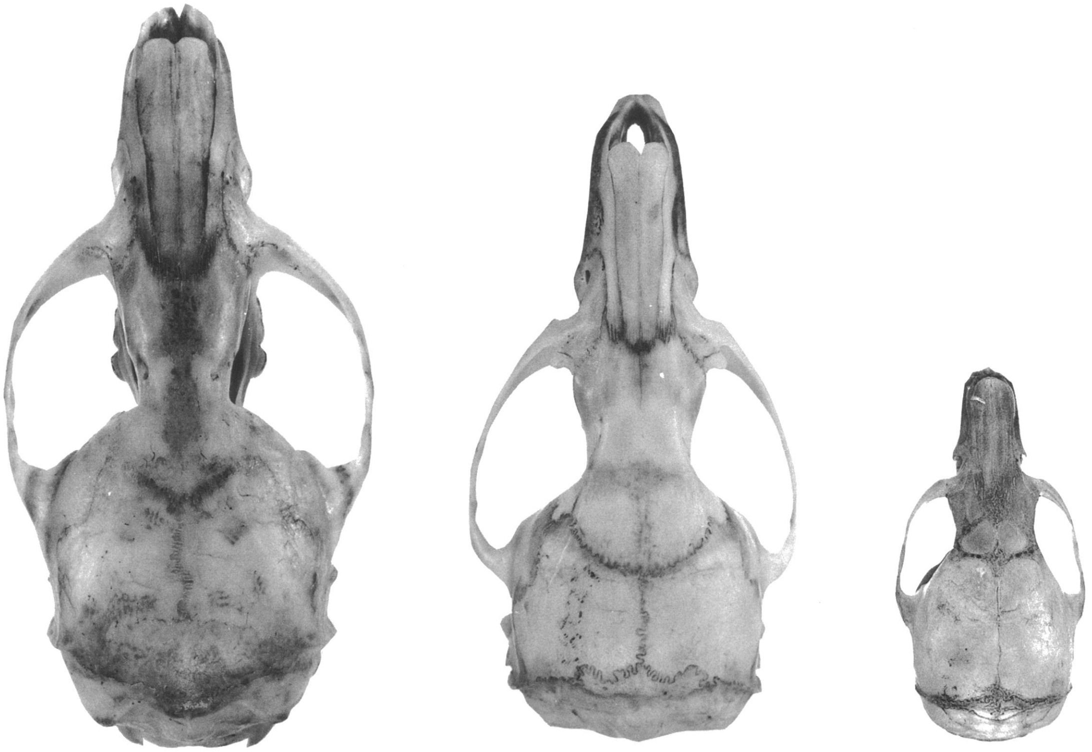

Fig. 51. Dorsal cranial views (× 2). **Left,** *Hydromys chrysogaster* (AMNH 191432); **middle,** *Chrotomys whiteheadi* (FMNH 62285); **right,** *Neohydromys fuscus* (AMNH 191418).

Simpson's view (Musser, MS.). The Philippine group lacks the morphological and trophic diversity seen in the New Guinea and Australian genera. That diversity is bracketed by *Hydromys* at one end, which is a large-bodied amphibious carnivore, and the species of *Pseudohydromys, Neohydromys,* and *Mayermys,* at the other end, which converge toward terrestrial shrews in body size and habits. Because historical and fairly modern views have recorded such strong support for a phylogenetic rather than convergent link between hydromyines and members of the *Chrotomys* group, we record and illustrate here some (only particular examples out of a larger list) of the other significant distinctions we have noted that separate the Philippine and New Guinea–Australian clusters, sets of traits suggesting, at least to us, that the two groups are not very closely related.

1. None of the hydromyines have the derived chromatic patterning characteristic of *Chrotomys* and less so of *Celaenomys.*

2. Among hydromyines, length of tail relative to length of head and body ranges from much longer, to subequal, or slightly shorter (see the measurements listed by Flannery, 1990). None possess the very short tail relative to head and body length that characterizes the Philippine genera.

3. The New Guinea and Australian species have generalized claws and lack the very long and spatulate derived claws that are diagnostic of *Chrotomys* and *Celaenomys.*

4. The nasals are truncated caudad of the anterior margins of the premaxillaries so the nasal orifice is exposed, but not the incisors or the interpremaxillary foramen, in *Hydromys, Parahydromys, Crossomys, Neohydromys,* and *Mayermys.* The interpremaxillary foramen (which pierces the premaxillary suture just behind the incisors) is minute in these genera, as it is in all other species of hydromyines. The incisors are procumbent enough to be seen from dorsal view only in *Neohydromys* and *Mayermys.* The condition

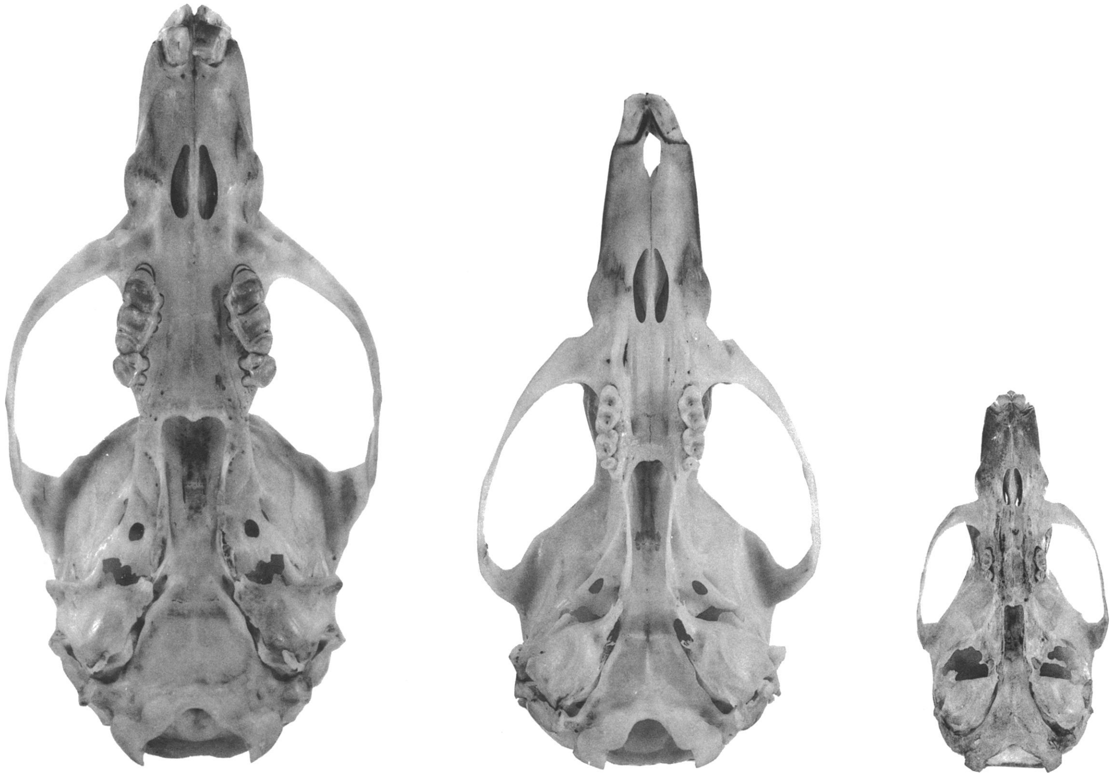

Fig. 52. Ventral cranial views (× 2) of the specimens shown in figure 51. **Left,** *Hydromys chrysogaster*; **middle,** *Chrotomys whiteheadi*; **right,** *Neohydromys fuscus*.

in *Chrotomys* and *Celaenomys* is highly derived compared with the conformation in the hydromyines. In the Philippine genera, the interpremaxillary foramen is a very large opening in the ventral surface of the rostrum behind the incisors, and the upper incisors are far more procumbent (see figs. 51, 52, and 55 for comparison).

5. Of all the hydromyine genera, only *Neohydromys* has a general conformation of the cranium and mandible that resembles the shape and outline in *Chrotomys* and *Celaenomys* (figs. 51–53). There is a significant difference in size, and also in arterial pattern, and even in details of mandibular conformation.

The derived cephalic arterial pattern with its attendant osseous counterpoints (minute stapedial foramen and no groove in the ventral surface of the pterygoid plate for the infraorbital branch of the stapedial artery, for example), a pattern similar to that diagrammed in figure 36C, characterizes *Neohydromys*; the Philippine genera retain the primitive cephalic circulatory pattern. In addition to *Neohydromys*, species of *Mayermys*, *Pseudohydromys*, and *Leptomys* also possess the derived carotid pattern; all the other hydromyines that we have studied (we have not seen *Xeromys*) retain the primitive pattern. Among all the endemic New Guinea murines, we have found the derived cephalic arterial pattern only in *Lorentzimys nouhuysi*, and in *Melomys lanosus* and *M. rattoides*, which in external and cranial traits are also more similar to each other than to any of the other species now placed in *Melomys*.

The dentaries of *Chrotomys* (figs. 43 and 53) and *Celaenomys* (fig. 43) are closely similar in conformation and generally resemble the dentary of *Neohydromys* (see fig. 53 where dentaries of *Chrotomys* and *Neohydromys* are compared). There are slight but significant mandibular differences, however, between the

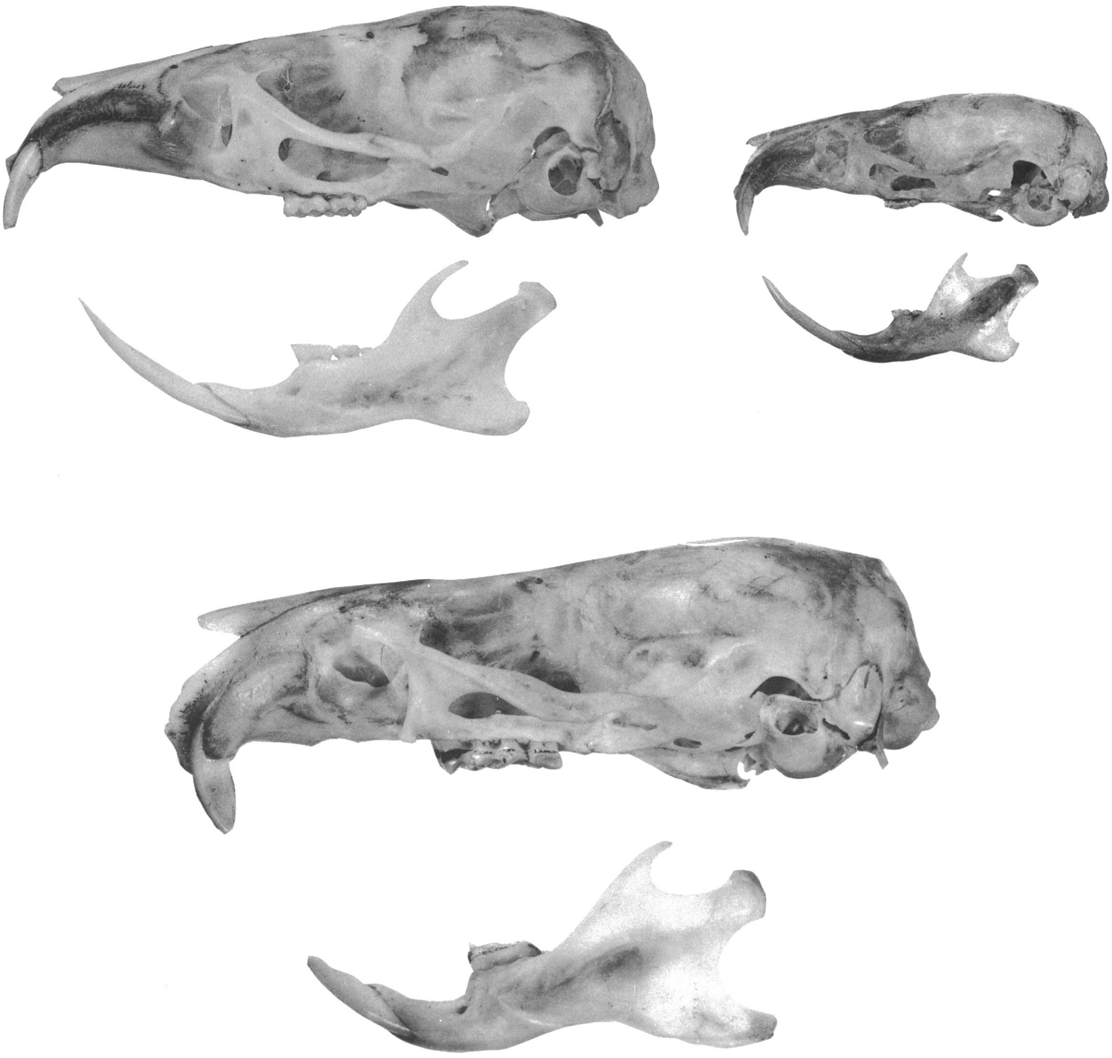

Fig. 53. Lateral views (×2) of crania and dentaries of the specimens illustrated in figure 51. **Upper left,** *Chrotomys whiteheadi*; **upper right,** *Neohydromys fuscus*; **lower middle,** *Hydromys chrysogaster.*

Philippine shrew rats (using *Chrotomys* as the example) and *Neohydromys.* In *Neohydromys,* the ascending ramus is more expansive, its anterior margin ascends at the second molar (rather than the third as in *Chrotomys*), the coronoid process is smaller and the excavation shallower between coronoid and condyloid processes. These differences also contrast dentaries of *Chrotomys* and *Hydromys* (fig. 53); thus, although a general resemblance exists in dentary shape between *Chrotomys* and *Neohydromys,* the differences present indicate closer similarity between *Neohydromys* and *Hydromys.*

6. None of the hydromyines have the specialized and unique shape of the upper incisors that characterizes both *Chrotomys* and *Celaenomys,* not even *Neohydromys* and *Mayermys,* which are the only hydromyines with procumbent upper incisors. Furthermore, none have the derived wide enamel shield of each upper tooth and the thick

enamel layer of each lower incisor that is diagnostic of *Chrotomys* and *Celaenomys* (see fig. 46).

7. Of all the hydromyines, only the species of *Leptomys* have the full complement of molars in each row; of the Philippine shrew rats, only *Chrotomys* consistently retains full molar rows. There are significant differences between them in molar occlusal topography. For example, each first and second upper molar in *Leptomys* has a large cusp t7, a derivation, that is either round and cuspidate or ridgelike; *Chrotomys* lacks cusp t7 (fig. 54). Although somewhat coalesced with the metaconid and protoconid, the anteroconid in *Leptomys* retains its basic structure of a large anterolingual and a smaller anterolabial cusp (fig. 55A). The distinctions between these cusps of the anteroconid and those of the first lamina are obliterated in *Chrotomys* except for a slight anterolabial evagination in some specimens (figs. 39D, 55B). The conformation in *Chrotomys* is more highly derived compared to that in *Leptomys*.

8. In hydromyines, the root of the lower incisor curves all the way up through the articular process to end just anterior to the articular surface only in *Neohydromys* (fig. 53). This derived configuration is typical of both *Chrotomys* and *Celaenomys* (figs. 50, 53).

9. Spermatozoan morphology of the Australian *Hydromys* and *Xeromys* is highly derived (Breed, 1984), but that of *Chrotomys mindorensis* is not and resembles the hypothesized primitive conformation (Breed and Musser, 1991).

In morphology of the front half of the head skeleton and degree of incisor and molar reduction, *Rhynchomys* is highly divergent from the other shrew rats. So impressive are the specializations that the genus was placed in its own subfamily, the Rhynchomyinae (Thomas, 1898; Ellerman, 1941; Simpson, 1945; Misonne, 1969). Separation from the rest of the endemic Philippine murines at this taxonomic level has not been followed in recently published lists (Carleton and Musser, 1984; Heaney et al., 1987).

Thomas (1898) thought *Rhynchomys* might be most closely related to *Echiothrix*, the large-bodied shrew rat of Sulawesi (Musser, 1969, 1990), but Ellerman (1941) and Misonne (1969) disagreed, arguing that the characteristics of *Echiothrix* were more murine than rhynchomyine. We have yet to explore this possible alliance with the Sulawesian murine fauna. None of the character traits we have surveyed for this report suggest phylogenetic affinity between *Rhynchomys* and species either in the Australian and New Guinea region or on southeast Asia and the Sunda Shelf.

Although we are dissatisfied with our lack of sharp phylogenetic resolution among the groups of Philippine shrew rats, the distribution of derived traits we discussed above allows us to formulate the following alternative hypotheses that can be tested with data from other organ systems, chromosomes, and molecules.

1. Members of the *Crunomys, Chrotomys*, and *Rhynchomys* groups are more closely related to one another than they are to any other group of species indigenous to the Indo-Australian region. Some of the traits we surveyed provide weak support for this hypothesis.

2. The phylogenetic affinity of each group of shrew rats is with species native to archipelagos and continents outside the Philippines. *Crunomys* is also part of the Sulawesian fauna, but outside of that connection our set of data would either falsify this hypothesis or provide no information for or against its support.

3. As distinctive as members of the *Chrotomys* and *Rhynchomys* groups are in their morphology, certain derived traits suggest that they form a monophyletic assemblage that excludes all other described Indo-Australian murines, including *Crunomys* and *Archboldomys*.

4. If the third hypothesis cannot be falsified, and the *Chrotomys* and *Rhynchomys* groups form a single monophyletic cluster, the *Crunomys* group may form a sister taxon to the *Chrotomys-Rhynchomys* assemblage.

DIVISION II (*ANONYMOMYS*)

Three specimens (FMNH 87596–87598) obtained at 4500 ft from Ilong Peak in the Halcon Range of Mindoro (fig. 3) during April, 1954, form the only sample of *Anon-*

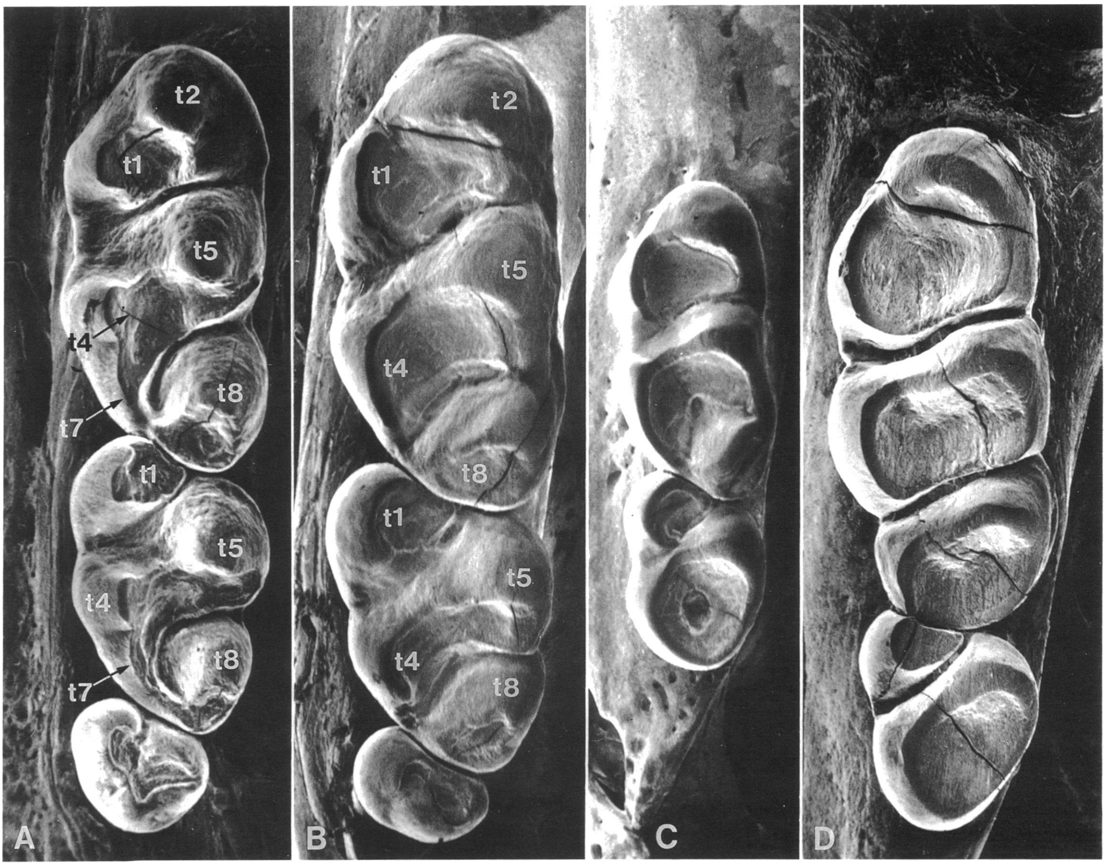

Fig. 54. Occlusal views of left maxillary molar rows. **A,** *Leptomys* sp. (AMNH 105793); **B,** *Chrotomys mindorensis* (MMNH 12972); **C,** *Celaenomys silaceus* (AMNH 185138); **D,** *Hydromys habbema* (AMNH 110057). Note the crescentic cusp t7 on the first and second molars of *Leptomys*. A comparable cusp does not occur on molars of either *Chrotomys* or *Celaenomys*. Whether it has formed part of the third basin of the first molar in *Hydromys* is impossible to detect.

ymomys mindorensis (Musser, 1981a), which is the sole member of Division II. The examples represent a species of small rat with a stocky body, semispinous pelage, short and wide hind feet, and a long brown tail tipped with a short tuft (fig. 56). The upperparts are bright buffy or tawny brown, the underparts are white. The dorsal fur is long (15–20 mm) and dense and contains many flexible spine-like hairs that give the coat a semispinous texture; guard hairs are short, projecting only 4–6 mm beyond the overhairs. The ventral pelage is also dense, up to 10 mm long, and soft. Ears are small, tan, and sparsely haired. The face is the same color as the body, without any dark brown mask. Front and hind feet are short and wide, pale tan, and without distinctive pattern. Claws are short, sharp, and recurved. Large and fleshy palmar and plantar pads are adorned with transverse and semicircular lamellae; a prominent hypothenar pad is present. The tail is much longer than the combined lengths of head and body and is brown on all surfaces. There are 13–15 rings of scales per centimeter; three hairs protrude from beneath each scale. In the basal one-third of the tail these hairs are slightly longer than each scale, those toward the distal

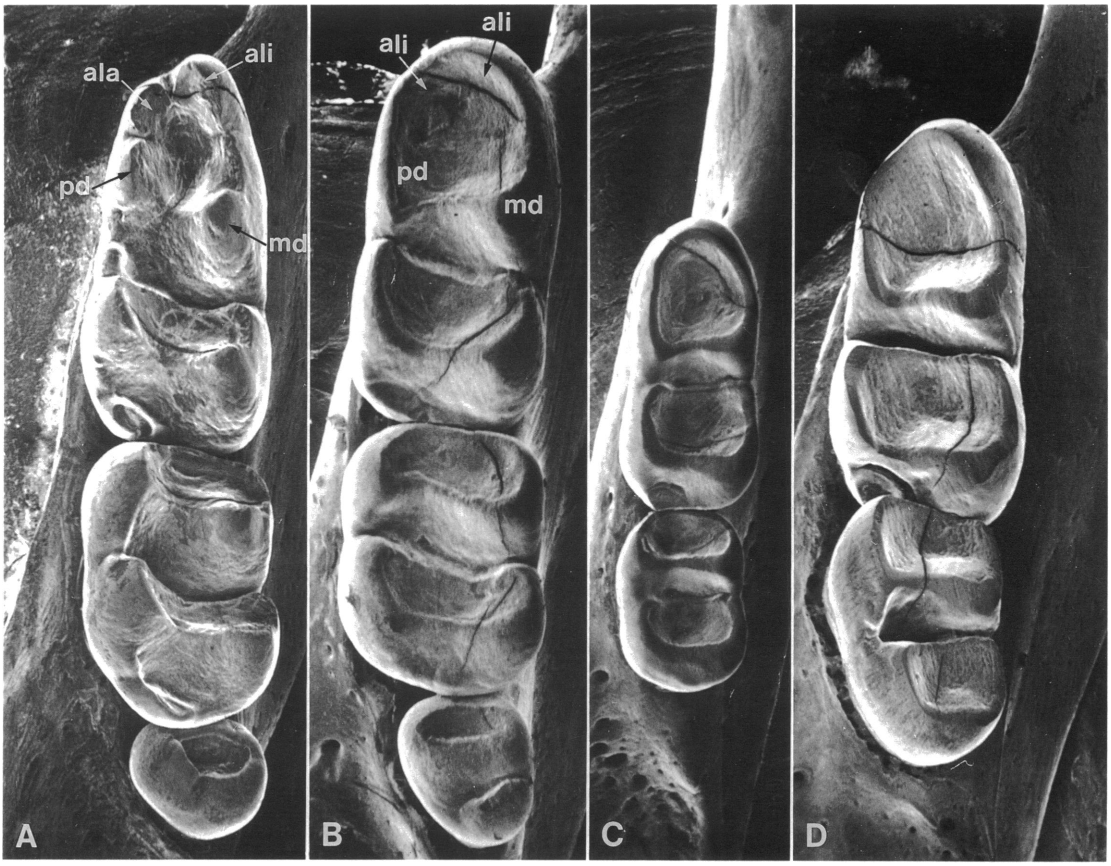

Fig. 55. Occlusal views of mandibular molar rows from the specimens illustrated in figure 53. **A,** *Leptomys* sp.; **B,** *Chrotomys mindorensis*; **C,** *Celaenomys silaceus*; **D,** *Hydromys habbema*. The anterolabial cusp (**ala**), anterolingual cusp (**ali**), metaconid (**md**), and protoconid (**pd**) are still defined in *Leptomys* but their limits are obliterated in the other genera.

end are even longer, culminating in a conspicuous tuft projecting 6–8 mm beyond the tip.

All the specimens of *A. mindorensis* are adult males; the nature of juvenile pelage as well as the number of mammae on females has yet to be discovered.

The cranium of *A. mindorensis* appears stocky with wide interorbital and postorbital regions, and a short and wide rostrum (fig. 57). The braincase is wide and high, domelike when seen from lateral perspective; its dorsolateral margins are defined by low beading. The occiput is deep (from front to back) and roofed by half or two-thirds of the interparietal. Each zygomatic plate is narrow, with only a slight anterior spine, reflected in a very shallow zygomatic notch. Each auditory bulla is small and set tight against the squamosal and alisphenoid bones, resulting in a small postglenoid foramen and narrow middle lacerate foramen (fig. 58). The eustachian tube is short and broad. The squamosal is complete above the bulla, not breached by a subsquamosal fenestra. The configuration of the braincase just above each pterygoid ridge consists of a prominent alisphenoid strut separating an accessory foramen ovale from the coalesced masticatory-buccinator foramina (fig. 58A). The alisphenoid wall medial to the strut is breached by the anterior opening of the alisphenoid canal, and caudal to that the

Fig. 56. *Anonymomys mindorensis* (FMNH 87598, an adult male): LHB = 125 mm; LT = 206 mm; LHF = 31 mm.

foramen ovale. Each mastoid is large and squarish, and its outer surface is smooth and slightly inflated; the mastoid foramen is small. The incisive foramina are wide and long, extending past the front margins of the molar rows by 0.2 to 0.6 mm (three specimens). The bony palate is wide and short, ending 0.1 to 0.4 mm anterior to the back margins of the molar rows. The palate is thick and its ventral surface is scored by two deep palatine grooves. The mesopterygoid fossa is wide and its walls are breached by short and slim sphenopalatine vacuities. Each pterygoid fossa is wide and nearly flat. Anterior to the foramen ovale, the surface is either complete or perforated by a small sphenopterygoid vacuity. Its lateral margin from behind the molar row to the foramen ovale is defined by a prominent pterygoid ridge. The pterygoid ridge posterior to the foramen ovale is thick and rounded. On the ventral surface of the pterygoid plate is a groove for the infraorbital branch of the stapedial artery; this depression along with a large stapedial foramen points to a primitive cephalic arterial pattern, one similar to that found in species of *Rattus* and *Apomys datae* (fig. 36D). The coronoid process is prominent, the condyloid process is long and robust, the angular process is large, and the posterior margin between condyloid and angular processes is deeply concave.

Coronal patterns of the upper and lower molars are illustrated in figure 59. They were described in detail in the original description of *A. mindorensis* (Musser, 1981a: 304–306).

Conformation of the body, tail, feet, and skull of *A. mindorensis* resembles that of *Limnomys sibuanus* from Mindanao, *Margaretamys beccarii* from Sulawesi, and *Niviventer cremoriventer* from islands on the Sunda Shelf. In the original description, the Mindoro rat was contrasted with series of these three species (Musser, 1981a: 300–310). The resemblances probably reflect adaptations to arboreal habits for no close phylogenetic relationship is evident between *A. mindorensis* and any of the other genera.

The Mindoro endemic does not possess any of the spectacular derivations which characterize each of the groups of species in Division I. Furthermore, it does not belong in Division I because beading outlines dorsolateral margins of the postorbital region and braincase (similar in degree of expression to that seen in *Limnomys sibuanus* of Division III), and each anteroconid consists of a round anterolabial cusp and a round and slightly larger anterolingual cusp (figs. 59, 64I). All members of Division I except *phloeomys* have smooth and rounded interorbital, postorbital, and temporal regions. All members of Division I also have a highly derived anteroconid unlike the configuration characteristic of *Anonymomys* (fig. 64I). The shape of each cusp forming the anteroconid is unique to *Anonymomys* but having an anteroconid clearly composed of two cusps that remain unattached to the lamina behind it is a primitive configuration in murine rodents and one shared with all members of Division III.

However, *Anonymomys mindorensis* also retains many primitive features that are not found in the species which we place in Division III. Among these traits are posterior palatine foramina that are opposite the second molars; a broad alisphenoid strut; an accessory foramen ovale; small bullae closely attached to the squamosal and alisphenoid bones; small postglenoid foramina; three-rooted upper molars, and two-rooted lower molars. These traits exclude *A. mindorensis* from Division III, which contains species possessing the derived expression of those characters.

Except to point out that *Anonymomys* appears to have no close morphological tie to members in either Division I or III, we are unable to resolve its phylogenetic alliance without survey of faunas from other regions. We have compared its morphological features with those of each genus in the Old Endemic stratum in the Australia and New Guinea region but are unable to find any derived traits shared exclusively by any of them and *Anonymomys* (Musser, in prep.). In certain derived aspects of its external, cranial, and dental morphology, *Anonymomys* resembles genera native to mainland southeast Asia and islands on the Sunda Shelf rather than faunas in archipelagos east of there. Musser and Newcomb (1983), for example, have suggested a phylogenetic link between *Haeromys* and *Anonymomys*. Clearly, the alternative hypotheses to be tested with other kinds of data sets and broader geographic surveys are the following:

1. *Anonymomys* is more closely related to the native Philippine murines than to species endemic to other regions in the Indo-Australian area. Our analysis of the characters we examined does not support this conclusion.
2. *Anonymomys* has closer phylogenetic ties to murine faunas native to Indochina and islands on the Sunda Shelf. This hypothesis reflects the biogeographic reality that Mindoro supports a mixed mammalian fauna. Some elements (*Chrotomys* and *Apomys*, for example) are entirely Philippine in affinities; others (possibly *Rattus mindorensis* and certainly the dwarf water buffalo, *Bubalus mindorensis*) are either Indochinese or Sundaic.

DIVISION III (NEW ENDEMICS)

The species of *Rattus, Bullimus, Tryphomys, Abditomys, Tarsomys,* and *Limnomys*—sometimes called the New Endemics (Musser, 1981b; Musser et al., 1985)—constitute the members of Division III. *Bullimus, Tryphomys, Tarsomys,* and *Limnomys* have been closely associated with *Rattus,* to the degree that some checklists and revisionary studies have treated them as subgenera of that genus (Ellerman, 1941; Misonne, 1969), despite intentions of the original describers who did not perceive such an alliance. Even the very distinctive *Abditomys latidens,* a Luzon endemic, was originally described as a species of *Rattus* (Sanborn, 1952) but was later transferred to its own genus (Musser, 1982a).

Of these genera, *Abditomys* was diagnosed and defined by Musser (1982a), and we have done the same for *Tarsomys* and *Limnomys* in the present report. *Tryphomys* and *Bullimus,* however, were never adequately characterized or defined, and in this section we stray from the main phylogenetic theme to provide diagnoses for these genera and reasons why they cannot be considered part of the genus *Rattus.* Even *Rattus* has yet to be defined (Musser and Newcomb, 1983), but we shy away from that endeavor here.

The morphological grade containing either

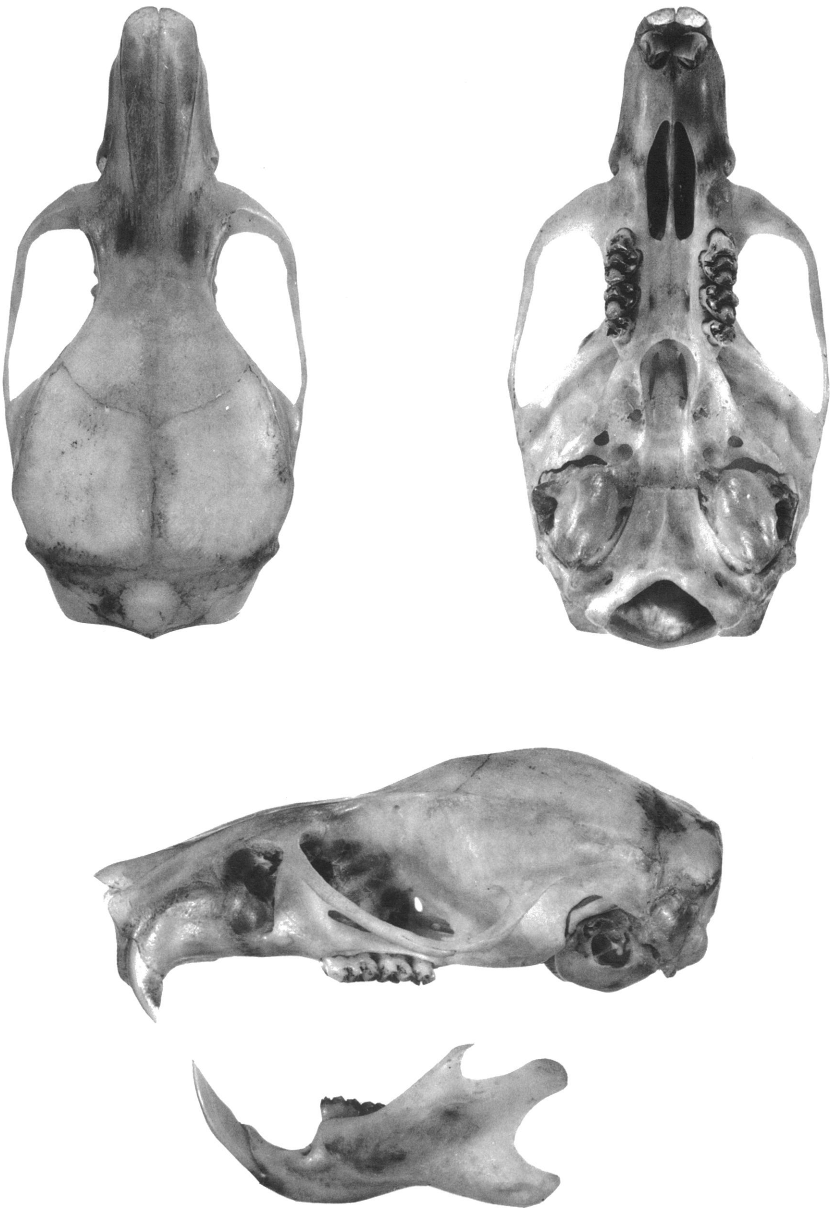

Fig. 57. Crania and dentary (×2.5) of *Anonymomys mindorensis* (FMNH 87598, the holotype, an adult male) from Mindoro. See table 10 in Musser, 1981a: 302, for measurements.

Rattus or *Rattus*-like genera has also been identified as part of the endemic murine fauna of Sulawesi, Flores, Timor, Australia, New Guinea, the Moluccas, and the Sundaic region (Musser, 1981b; Musser and Newcomb, 1983; and listed below on p. 126). Whether the similarity at this morphological level of character-state expression also reflects a stratum of phylogenetic alliance remains to be determined. Compared with the distribution of traits among species in Division I, those in Division III support a hypothesis predicting a later appearance of the ancestors of Division III genera in the Philippine Ar-

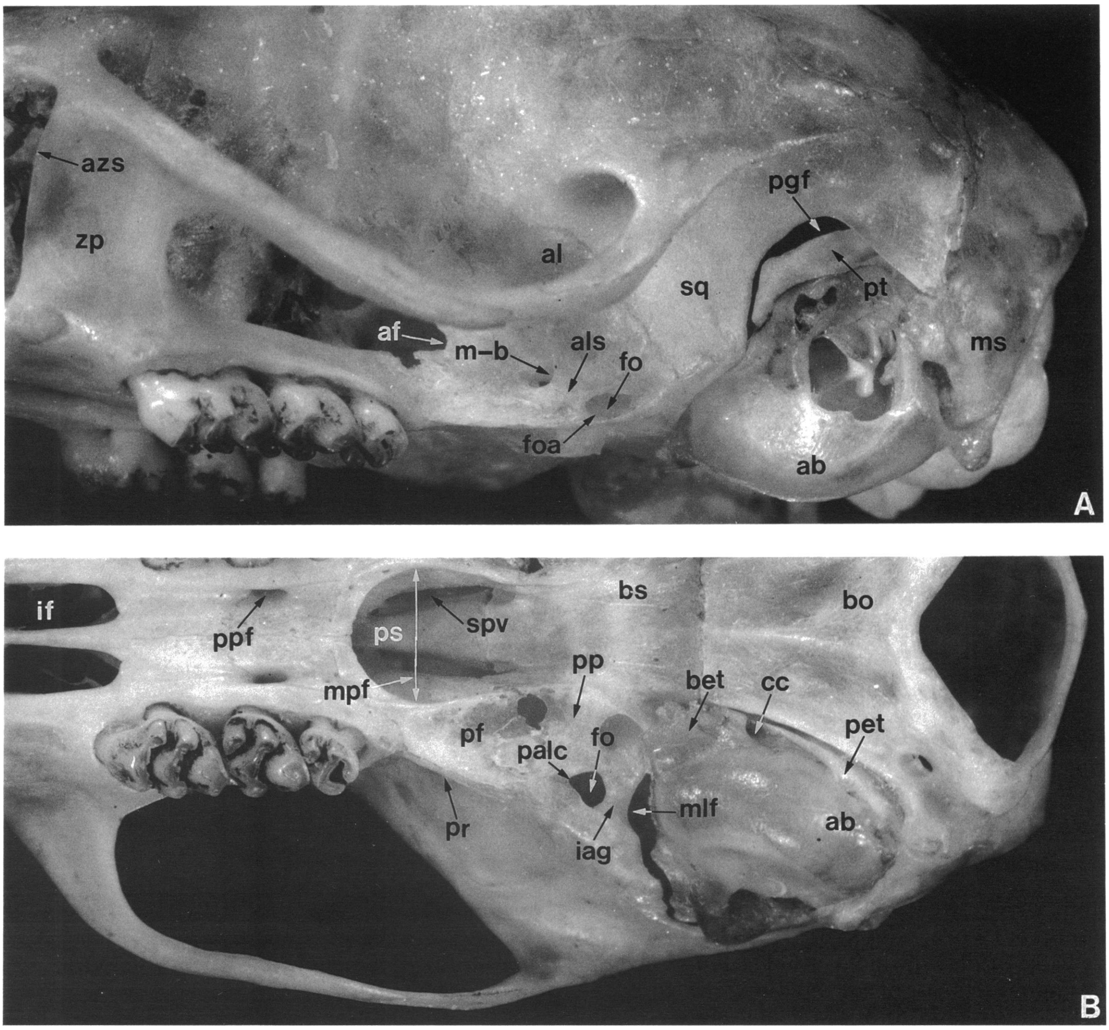

Fig. 58. Lateral (A) and ventral (B) cranial enlargements of *Anonymomys mindorensis* (FMNH 87598). **ab,** auditory bulla; **af,** anterior alar fissure; **al,** alisphenoid; **als,** alisphenoid strut (which conceals the alisphenoid canal and the anterior opening of that passage); **azs,** anterior zygomatic spine; **bet,** bony eustachian tube; **bo,** basioccipital; **bs,** basisphenoid; **cc,** carotid canal; **fo,** foramen ovale; **foa,** foramen ovale accessorius; **iag,** groove for the infraorbital branch of the stapedial artery; **if,** incisive foramen; **mlf,** middle lacerate foramen; **mpf,** mesopterygoid fossa; **ms,** mastoid; **palc,** posterior opening of the alisphenoid canal (arrow points to where the infraorbital branch of the stapedial artery enters the braincase dorsal to the pterygoid plate); **pet,** petrosal; **pf,** pterygoid fossa; **pgf,** postglenoid foramen; **pp,** pterygoid plate; **ppf,** posterior palatine foramen; **pr,** pterygoid ridge; **ps,** presphenoid; **pt,** periotic; **sq,** squamosal; **spv,** sphenopalatine vacuity; **zp,** zygomatic plate.

chipelago, possibly during late Pliocene or early Pleistocene, although this time period is pure speculation based on known sea level lowerings.

Although they retain certain primitive features, a suite of derived traits characterizes the species in Division III. Relative to Division I, Division III is defined by the derived state in the following four traits, and the primitive state in the fifth and sixth.

1. Position of Posterior Palatine Foramina (fig. 60). Outlined as a squarish or rectangular wedge, the palatine bones between the maxillaries form the posterior mar-

Fig. 59. Occlusal views of the left molar rows of *Anonymomys mindorensis* (FMNH 87598, the holotype). **A,** uppers (CLM1–3 = 5.7 mm); **B,** lowers (clm1–3 = 5.7 mm). Note that the anteroconid (**ad**) consists of two distinct and roundish cusps, an anterolingual and slightly smaller anterolabial.

gin of the bony palate and extend anterior to the level of union between first and second upper molars. In all genera of Division I, as well as *Anonymomys* in Division II, each posterior palatine foramen, which "transmits the descending palatine artery and nerve and a small vein" (Wahlert, 1974: 372), is at the anterolateral corner in the suture between maxillary and palatine bones. Each foramen, depending on the species, is either opposite the back third of the first molar or the anterolingual root of the second molar. Among murine rodents, this position of the foramina relative to dorsal margins of the palatines and adjacent molars is primitive.

In the derived state, the posterior palatine openings are set caudad from the anterior border of the palatine bones, and each foramen is opposite the space between second and third molars in some species, or opposite the anterolingual root of the third molar in others (fig. 60). This position of foramina relative to anterior margins of palatines and molars is characteristic of all species in Division III.

2. Supraorbital and Temporal Regions (fig. 60). Most members of Division I have a smooth and rounded braincase; margins of the interorbital and postorbital regions are also smooth and undelimited by ridges or beading (old individuals in the *Crateromys* group develop slightly raised interorbital borders and roughened dorsal margins where the temporal muscle is attached, and some old *Crunomys* develop a slight edge at each postorbital margin). This textural aspect of the cranium is primitive.

Ridges that outline interorbital and postorbital regions and continue caudad onto the braincase characterize all members of Division III. The outlines may be formed by low and inconspicuous beading that passes onto the anterior portion of the braincase where they transform into faint impressions of temporal ridges, the conformation typical of *Tarsomys* and *Limnomys,* or they may be high and sweep back to the occiput, as in *Abditomys* and *Rattus.*

Both species of *Phloeomys* in Division I have high interorbital ridges that form expansive triangular ledges over the postorbital region and extend to the occiput as prominent temporal ridges, but this configuration of ledge and high ridges is unlike, and therefore not homologous with, those found among species in Division III.

3. Auditory Bullae (fig. 61). Among members of Division I, the auditory bullae are small relative to size of cranium. The variation in size ranges from the shape in *Phloeomys* in which each ectotympanic bulla is small and ringlike (figs. 28–30) to the relative size seen in *Apomys* (figs. 37, 61) where each bulla is capsular and slightly inflated. The otic capsule does not cover the entire ventral surface of the petrosal and a wide posteromedial segment of that bone is exposed as well as a tapered flange extending between capsule and basioccipital. The bony

eustachian passage is tubular and only a very small portion of it touches the basioccipital. The eustachian tube forms the dorsal rim of the carotid canal, the basioccipital forms the canal's medial edge, and this passageway for the internal carotid artery is actually less of a canal and more of a large gap between eustachian tube and basioccipital. Small bullae relative to cranial size, particularly the conformation exhibited by species of *Phloeomys*, is primitive.

Large ectotympanic bullae represent a specialization. The otic capsule is inflated and shields the petrosal, leaving only a small posteromedial wedge exposed next to the basioccipital. The stapedial foramen is deeply concealed beneath the inflated posterior capsule margin. The eustachian passage is short, broad, and its entire medial margin contacts the basioccipital and part of the basisphenoid; the passage for the internal carotid artery is a closed canal (or foramen) encircled by otic capsule and basioccipital margin and situated more posteriorly than in the primitive configuration. The degree of ectotympanic inflation among the species in Division III ranges from the conformation typical of *Tarsomys apoensis* (fig. 6) to the highly inflated bullar capsules in species of *Tryphomys* (fig. 67), *Abditomys* (fig. 68), and some *Bullimus* (figs. 72, 74).

4. MOLAR ROOTS (figs. 62, 63). Three robust roots (anterior, lingual, and posterior) anchoring each upper molar (fig. 62A), and two large roots (anterior and posterior) holding each lower molar (fig. 63A) constitute the primitive pattern of molar holdfasts in muroid rodents and is the pattern shared among many species in Division I, as well as *Anonymomys* in Division II. Other species in that cluster have accessory roots. The first molars provide good examples of this multiplication of roots and the pattern they form. In some species of *Crateromys* and *Batomys*, each first upper molar has a small labial rootlet in addition to the three primary roots (fig. 62B). In other species and specimens of those genera, the posterior root is divided into two (fig. 62C). One or several labial rootlets also occur in some specimens. It is significant that the multiplication of roots results either from the addition of a labial holdfast or division of the posterior root, and not the division of the large lingual root. In each lower molar, some species have a small lingual root in addition to the two major roots (fig. 63B), other species have small labial and lingual roots, a divided posterior, and a small central root (fig. 63C).

These multirooted patterns found among members of Division I represent derivations but in different combinations than the derived pattern common to all members of Division III.

All species in Division III have the same derived pattern of molar roots (figs. 62D, 63D). Each first upper molar is anchored by a large anterior root, a moderately large labial, a single posterior, and two lingual roots. Each second upper molar has four roots (resulting from division of the lingual), and each third upper molar has the primitive three. Each first lower molar has a large anterior root, smaller labial and lingual, and a single posterior root. The multirooted pattern in each first and second upper molar results from the division of the primitive single lingual root, not the primitive single posterior root. This derivation is distinct from those multiple root patterns of the upper molars found in some species of Division I. And even though some members of Division I (*Phloeomys* and some *Batomys* and *Crateromys*, for example) have a root pattern of the lowers that resembles that in Division III, the lowers are always associated with a different derived pattern in the uppers.

5. ANTEROCONID. The shape and structure of the anteroconid and its relationship to the first row of cusps (formed from the metaconid and protoconid) are features that separate all members of Division III from those in Division I; however, the configurations found in Division III are primitive, those characteristic of Division I are derived, polarities that are opposite from the four characters discussed above.

In *Tarsomys* (figs. 12C, 13B, D, and 20C, D), *Limnomys* (figs. 25C, 26), *Tryphomys* (fig. 70C), *Abditomys* (fig. 70D), *Bullimus* (fig. 76C, D), and *Rattus* (figs. 12D, 25D, and 78), the anteroconid consists of an anterolingual cusp and a slightly smaller anterolabial cusp, similar to the structure shown in figure 64H, I; some species may also have a small anterocentral cusp (*Limnomys*, for example, fig. 25C). The shape of the anteroconid varies

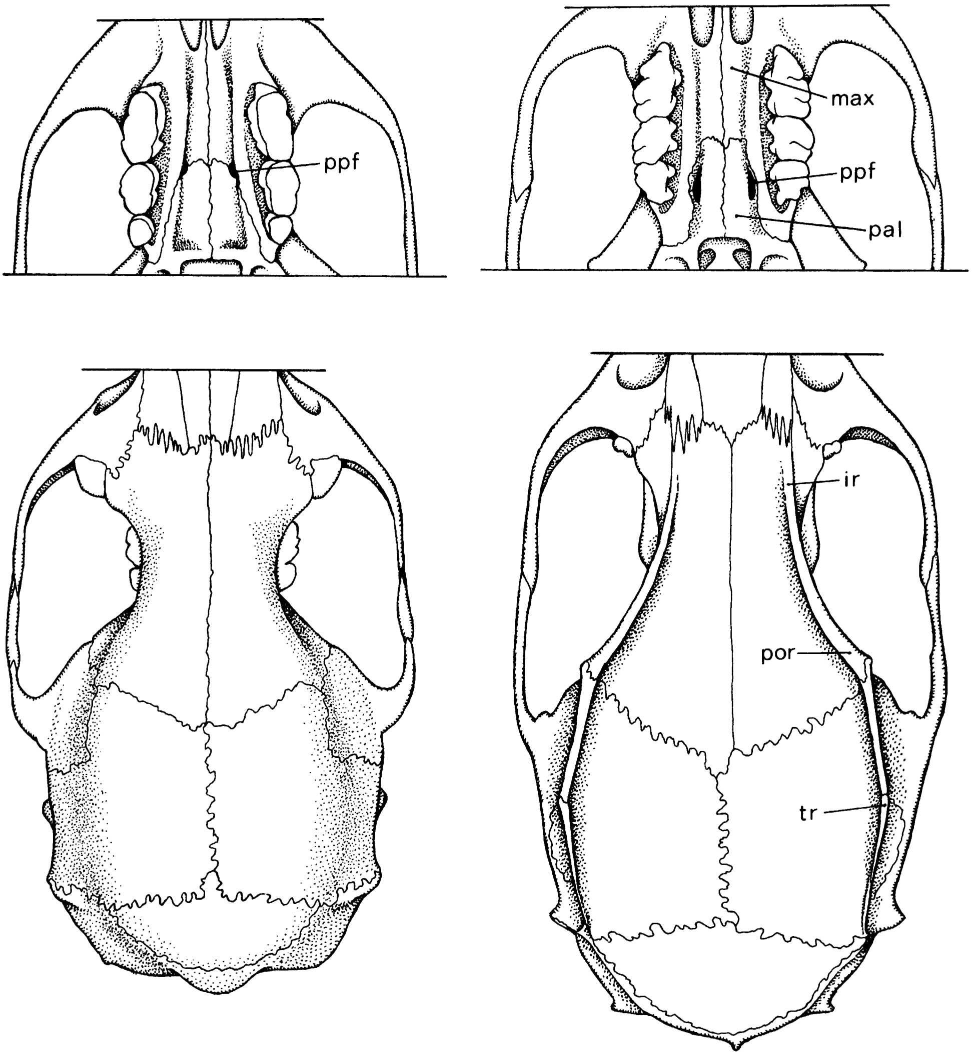

Fig. 60. The bony palate (top two views) and dorsal region of the cranium (bottom two views) in *Apomys datae* (**left**, FMNH 62761) and Sulawesian *Rattus rattus* (**right**, AMNH 227724). The position of each posterior palatine foramen (**ppf**) relative to the suture between maxillary (**max**) and palatine (**pal**) bones as well as each molar in *Apomys* represents the primitive configuration and is characteristic of all the species in Division I, while the conformation in *Rattus* is derived and typical of all the species in Division III. The smooth interorbital, postorbital, and temporal margins seen in *Apomys* are primitive and contrast with the derived interorbital ridges (**ir**), postorbital ridges (**por**), and temporal ridges (**tr**) found in *Rattus*.

among the genera (contrast *Tryphomys* and *Abditomys*, for example), but it always consists of at least two cusps that in occlusal outline are either roundish, oblong, or crescentic, and that stand free of the lamina formed by the metaconid and protoconid (fig. 64H, I); the anteroconid is never cordate in occlusal outline or reduced in size because it has broadly coalesced with the metaconid and protoconid.

By contrast, the anteroconoid is cordate in occlusal outline and is formed from large anterolingual, anterolabial, and anterocentral cusps in all members of the *Crateromys* group

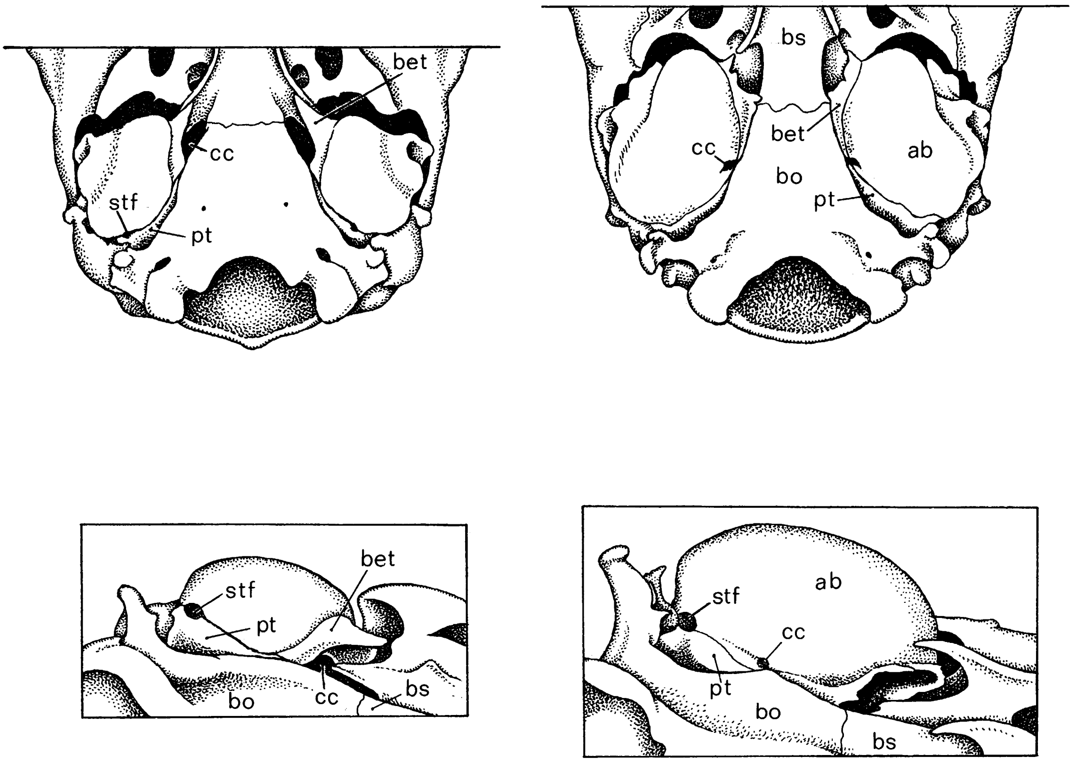

Fig. 61. The otic region in *Apomys datae* (left, FMNH 62761) and Sulawesian *Rattus rattus* (right, AMNH 227724). The size and conformation of the auditory bulla in *Apomys* are primitive and the usual condition found among species in Division I; the bullar region of *Rattus* is derived. **ab,** auditory bulla; **bet,** bony eustachian tube; **bo,** basioccipital; **bs,** basisphenoid; **cc,** carotid canal; **pt,** petrosal; **stf,** stapedial foramen. See text for discussion of the differences between the primitive and derived expressions of the bullar region.

(figs. 35B–D and 64B–D). It is also cordate in adult *Phloeomys* (fig. 35A) and oblong in young animals (fig. 64A). The anteroconid is broadly coalesced with the metaconid and protoconid and this large structure forms half or more of the coronal area of each first lower molar in members of the *Apomys, Crunomys,* and *Chrotomys* groups (figs. 39, 64E–G). In the *Rhynchomys* group, the anteroconid is elongate or round, basined and without cuspidate structure, and fused with the wider lamina formed by the metaconid and protoconid (fig. 49). None of these highly derived conformations of the anteroconid occur among species in Division III.

6. NUMBER OF MAMMARY GLANDS. The species of *Phloeomys* in Division I each have only one pair (two teats) of inguinal mammae. Among the remaining species in Division I, two pairs of inguinal mammae (four teats) are common to all (that is, those represented by females in available samples; *Crateromys australis,* for example, is known only by a male) *Crateromys, Batomys, Carpomys, Apomys, Archboldomys, Chrotomys, Celaenomys,* and *Rhynchomys.* The exception is *Crunomys melanius,* which has four pairs of mammae (eight teats): one pectoral, one postaxillary, and two inguinal (the other Philippine species are known only by males). Possessing only one or two inguinal pairs of mammary glands is a derived condition. Most other rodents within the Murinae and in other groups have more; Avry (1974) concluded that eight was the modal number found in a broad survey of the Rodentia, and Carleton (1980: 71) noted that even though three pairs of mammary glands were usual among neoto-

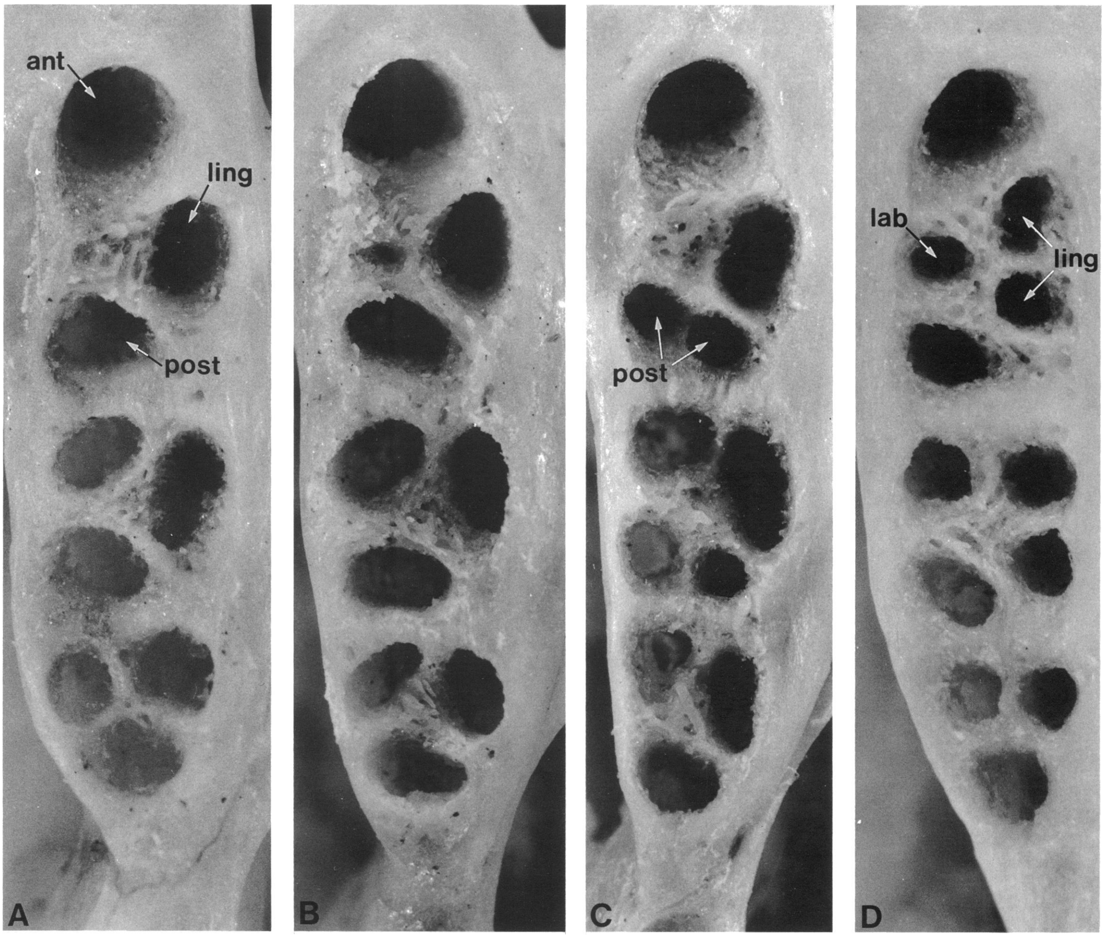

Fig. 62. Variation in number of roots recorded among species of endemic Philippine murines as reflected by alveolar patterns of right upper molars. **A,** *Anonymomys mindorensis* (FMNH 87598), which has the primitive pattern. **B,** *Batomys granti* (FMNH 62504); the basic primitive pattern is present except for the small labial holdfast opposite the lingual root of the first molar. **C,** *Batomys salomonseni* (FMNH 92826); here the primitive pattern is modified by the division of the posterior root beneath each first and second molar into two parts. **D,** *Tarsomys apoensis* (DMNH 5968); here the derived pattern results from the division of the lingual root beneath each first and second molar into two segments, and the addition of a large labial root beneath each first molar.

mine-peromyscines, "a count of eight mammae is more common among my outgroups, and I have recognized that number as ancestral."

All members of Division III have more than two pairs of mammary glands. Three pairs (one postaxillary and two inguinal) characterize the species of *Tarsomys* and *Limnomys*; four pairs (one pectoral, one postaxillary, and two inguinal) occur in *Abditomys latidens* and *Rattus everetti*; four pairs, but in a different combination (one postaxillary, one abdominal, and two inguinal), are found in *Rattus tawitawiensis* and the species of *Bullimus*; and five pairs (one pectoral, one postaxillary, one abdominal, and two inguinal) are usual in *Tryphomys adustus* and *Rattus mindorensis.* This range of mammae numbers is more common among murine rodents and is less specialized than the low counts found in *Phloeomys* and in nearly all members of Division I except *Crunomys,*

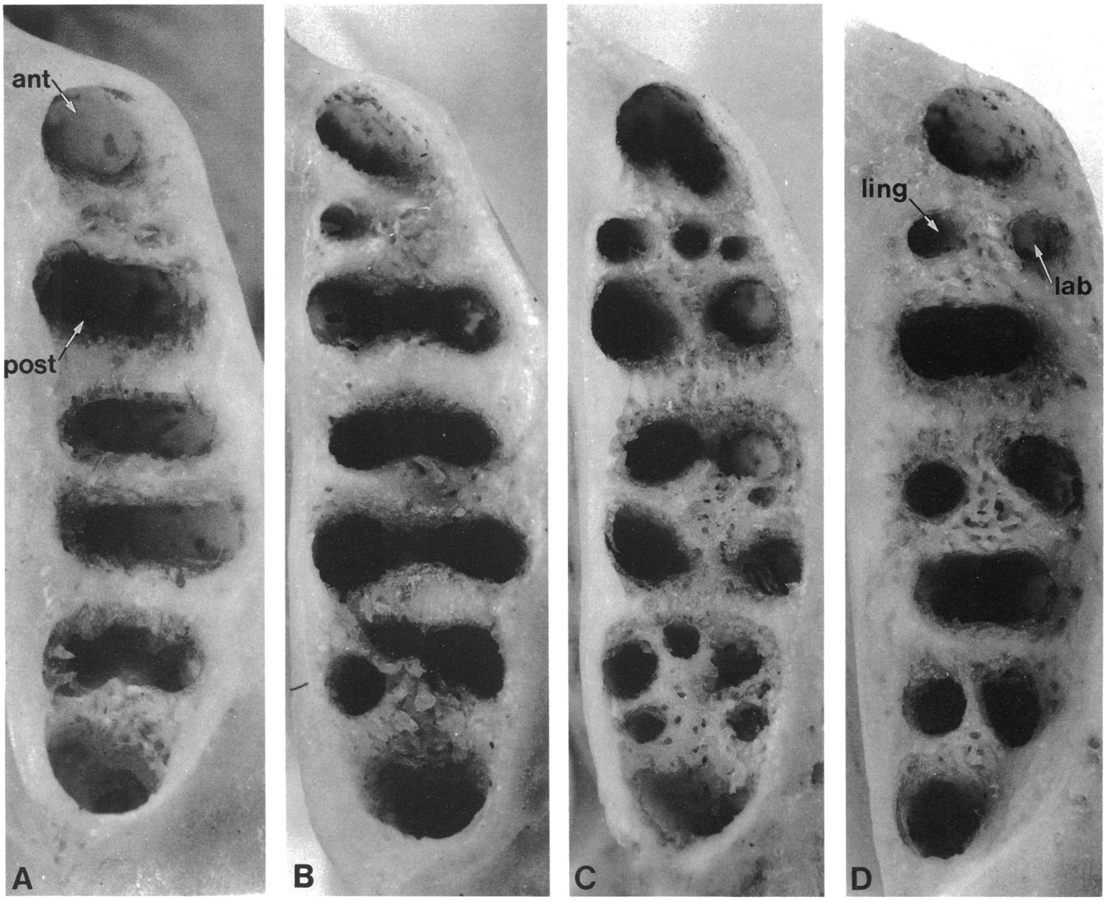

Fig. 63. Variation in number of roots as reflected by alveolar patterns of right lower molars of the specimens depicted in figure 62. **A,** *Anonymomys mindorensis,* which reflects the primitive pattern. **B,** *Batomys granti*; here the primitive pattern is modified by a lingual root beneath each first and third molar, and the bifid conformation of the posterior root beneath each first and second molar. **C,** *Batomys salomonseni*; the pattern is highly derived by the division of the primary anterior and posterior roots into segments, and the addition of labial, lingual, and medial roots. **D,** *Tarsomys apoensis* (DMNH 5963); the pattern common to all members of Division III.

which retains a primitive number of teats, as well as a great many primitive cranial features (Musser, 1982c).

Among the genera in Division III, the only close alliance we have discovered is between the two Luzon endemics, *Tryphomys* and *Abditomys.* We are unable to find traits that will cluster the other genera, and below we discuss the Luzon forms as a group, and the other genera individually.

1. *TRYPHOMYS* AND *ABDITOMYS*

Tryphomys adustus (Miller, 1910; Musser and Newcomb, 1983: 497–500) and *Abditomys latidens* (Sanborn, 1952; Musser, 1982a) are more closely related to each other than to any other species endemic to the Philippines. Samples of each have been obtained only from Luzon (table 8), and these two are the only genera in Division III that are endemic to that large northern island in the Archipelago. The species in each genus have been closely associated with *Rattus.* The species *latidens* was originally described as a *Rattus* by Sanborn (1952: 125) but later placed in the new genus *Abditomys* by Musser (1982a), who provided a diagnosis of the genus, a new description of the species, and the morphological basis for its exclusion from

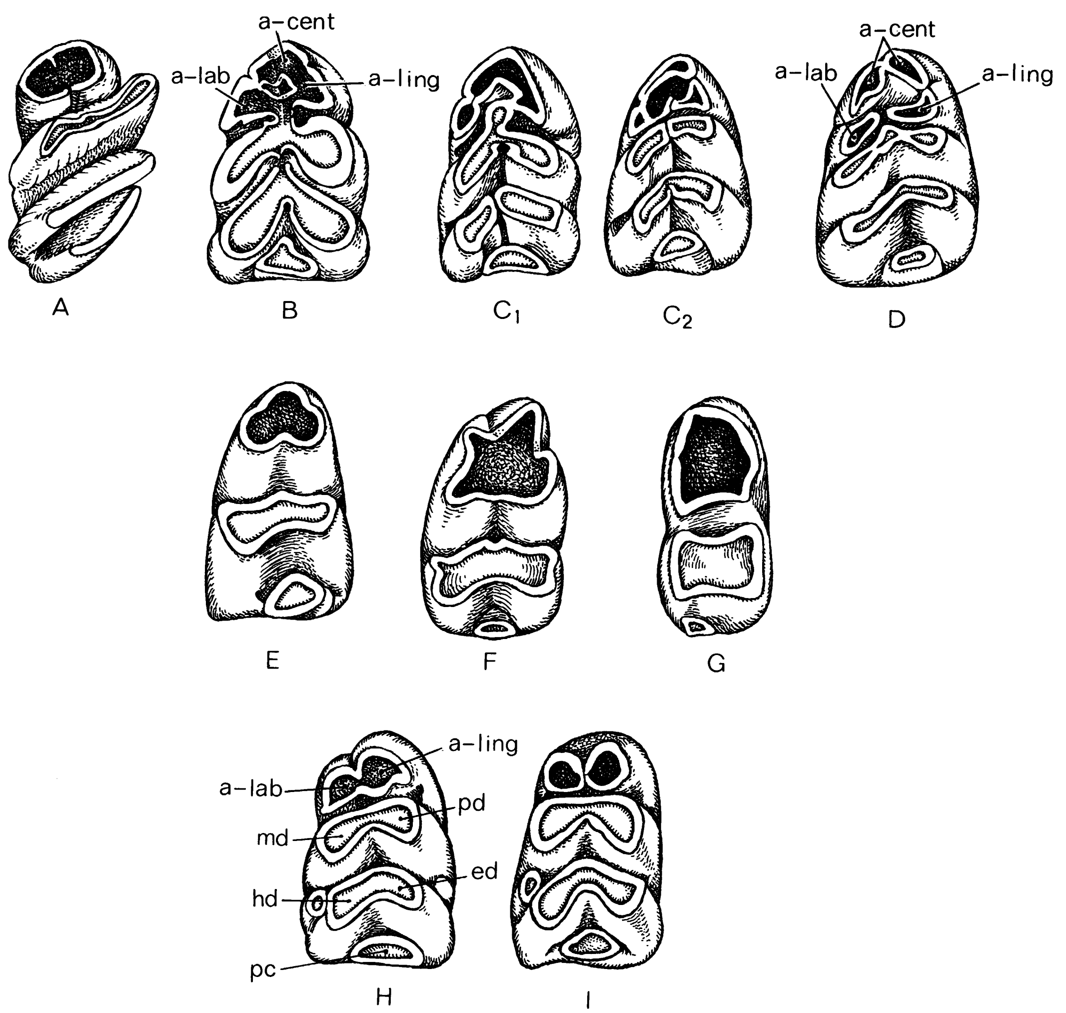

Fig. 64. Variation in shape of the anteroconid and its relationship to the first cusp row among selected species ~~of~~ endemic Philippine murines. **A,** *Phloeomys pallidus* (USNM 299999); **B,** *Crateromys schadenbergi* (USNM 102545); **C_1,** *Batomys granti* (BM 97.5.2.32); **C_2,** *Batomys salomonseni* (FMNH 92829); **D,** *Carpomys melanurus* (USNM 102553); **E,** *Apomys insignis* (FMNH 61483); **F,** *Archboldomys luzonensis* (USNM 573505); **G,** *Celaenomys silaceus* (AMNH 185138); **H,** *Rattus everetti* (AMNH 250038); **I,** *Anonymomys mindorensis* (FMNH 87598).

The anteroconid is formed from anterolabial (**a-lab**), anterocentral (**a-cent**), and anterolingual (**a-ling**) cusps in B through D and is derived in configuration, as is the oblong structure in A. A different derivation is represented by E through G where the anteroconid has completely merged with the metaconid (**md**) and protoconid (**pd**); only the hypoconid (**hd**), entoconid (**ed**), and posterior cingulum (**pc**) remain free. The configuration in H and I represents the primitive expression of the anterolingual and anterolabial cusps that remain separate from the row behind them that is formed by the metaconid and protoconid. See text for a fuller explanation of the variation and its significance.

Rattus. Tryphomys, however, has never been adequately diagnosed, particularly in relation to either *Abditomys* or *Rattus.* At this point in our report we deflect our exposition of the traits defining the groups of species within Division III to discuss the status of *Tryphomys,* provide an emended diagnosis of the genus, and make comparisons between it, *Rattus,* and *Abditomys.*

Named and described as a new genus and

species by Miller in 1910, and based on a single old adult, *Tryphomys adustus* was known only by the holotype until the 1950s when Sanborn (1952: 125) reported seven additional specimens, and the 1970s when Barbehenn et al. (1972–73: 233) documented others. All the samples were obtained from either mountains or lowlands on Luzon.

Miller (1910: 399) thought *Tryphomys* to be a distinctive Philippine murid and characterized it this way:

> External form murine, the tail about as long as body without head; hind foot with outer digits so reduced that neither extends beyond level of base of three median digits; fur of back coarse and harsh, the tips of the shorter hairs tending to curve forward, giving the pelage a peculiar scorched aspect; skull rather short and broad, with widely spreading zygomata and unusually large antorbital foramina; outer alveolar wall swollen into a noticeable protuberance at level of m^1; bony palate terminating in a broad median ridge bounded by lateral vacuities, the resulting form superficially like that of the same region in certain Microtine genera; teeth robust, their structure apparently not differing widely from those of *Epimys.*

From 1910 to 1952, *Tryphomys* was recognized as a genus separate from *Rattus.* Ellerman (1941: 294), in his compendium on the families and genera of living rodents, had not studied the holotype of *Tryphomys,* and noted that the genus was based "apparently on one old specimen; the most noticeable characters from the genus description are that the infraorbital foramen is large, that the outer digits of the hindfoot are much reduced, and the posterior palate said to be slightly abnormal." Despite his obvious skepticism, however, Ellerman listed *Tryphomys* as a separate genus. Simpson (1945: 90) entered *Tryphomys* as a genus in his classification of mammals.

Based on the seven specimens of *adustus* he studied, Sanborn (1952: 125) was not impressed with the generic distinction of *Tryphomys,* and remarked that

> Some of the characters of the genus *Tryphomys* appear to be due to age. The lump opposite the first molar is indicated in some of the skulls in this series. The condition of the palate is certainly due to age. The present skulls agree with that of the type in having the large antorbital foramen, and in size and shape. The skins are a little lighter in color than the type but agree in so many ways that they are considered as representing *adustus.* The teeth have the *Rattus* pattern. *Tryphomys* as a genus should be considered a synonym of *Rattus.*

In the 1960s, Misonne (1969: 143) placed *adustus* in the subgenus *Bullimus* of *Rattus,* and wrote that he had:

> seen only one specimen with missing bullae; there is one abnormal character in M^1; a deep fold between t5 and t6, which however does not seem to be present in M^2; in the skull, the mesopterygoid fossae seem to be very narrow. The hind part of the molars is very broad; there is a trace of SM in M_1; the lower Z is small. The closest species is indeed *R. muelleri,* both of whose upper and lower molars are extremely similar; there is no need to keep *adustus* a distinct genus.

In contrast, Barbehenn et al. (1972–73: 233) thought *adustus* to be distinctive. They pointed out that *Tryphomys* was currently considered a synonym of *Rattus* but noted that "Our recent observations of the palatal mucosa and of the plantar pads suggest that this taxon merits subgeneric status."

By the 1980s, Musser and Newcomb (1983: 497–502) had extracted *Tryphomys* from *Rattus* and contrasted its morphological traits with those of *Sundamys,* the genus which contains *muelleri,* the species Misonne (1969: 143) thought to be most like *adustus.* Musser and Newcomb found no characters indicating close phylogenetic relationship between *Tryphomys* and *Sundamys,* and noted that *Tryphomys* was instead related to the other Luzon endemic, *Abditomys.*

We have carefully studied the holotype of *Tryphomys adustus,* the specimens that Sanborn examined, and the material reported by Barbehenn and his colleagues. Miller had correctly estimated the taxonomic status of *adustus*; it does not share the morphological traits that define *Rattus.* It is true that some of the features Miller thought to be diagnostic are not unique to *Tryphomys*: the outer digits of each hind foot are not quite as short as Miller indicated, but the three inner and longer digits are longer relative to the rest of the foot than is the proportion in most species of *Rattus*; and the swelling at the level of each first upper molar is related to age, as Sanborn noted. Both Miller and Sanborn stated that the dental patterns were like those in *Rattus,* but all their specimens were adults with worn teeth; the cusps in *adustus* wear down quickly so even moderately worn teeth appear to have simple and *Rattus*-like patterns. Details of the cusp configurations on little-worn molars of *adustus,* however, are unlike those char-

TABLE 7

Measurements (mm) of *Tryphomys adustus* and *Abditomys latidens* from the Island of Luzon

(The mean plus or minus one standard deviation, size of sample in parentheses, and range are provided for each measurement.)

	Tryphomys adustus				*Abditomys latidens*	
	USNM 151511[a]	FMNH 62340, 62341, 62343–62345; USNM 348530, 348531	FMNH 356645	USNM 536765	FMNH 62347[a]	USNM 357244
Age	OA	A	YA	YA	A	A
LHB	174	160 (1)	131	151	232	216
LT	150	146.0 ± 12.10 (6) (130–163)	149	164	242	271
LHF	36	39.5 ± 2.35 (6) 36–42	37	35	45	47
LE	16	18.3 ± 1.03 (6) 17–20	21	18	21	24
TSR/cm	9	8.8 ± 0.98 (6) 8–10	10	9	7	9
GLS	39.7	42.2 ± 1.45 (3) 41.3–43.9	36.3	39.1	50.6	49.5
ZB	20.4	21.9 ± 0.69 (4) 21.4–22.9	19.1	19.6	25.9	24.2
IB	5.3	5.1 ± 0.22 (7) 4.7–5.3	5.1	4.6	6.0	5.7
LR	13.5	13.6 ± 0.80 (6) 13.0–14.9	11.1	11.7	16.6	15.3
BR	6.8	7.5 ± 0.45 (7) 7.0–8.0	6.7	7.5	9.6	8.6
BBC	15.8	16.4 ± 0.32 (5) 16.0–16.9	16.1	16.0	18.7	18.0
HBC	12.5	11.9 ± 0.27 (4) 11.6–12.2	11.1	11.2	14.1	13.5
BZP	5.2	5.5 ± 0.24 (7) 5.1–5.7	4.8	4.2	6.0	5.4
DZN	3.1	3.6 ± 0.23 (7) 3.2–3.9	3.0	3.0	3.1	3.1
LD	10.8	10.6 ± 0.82 (7) 9.5–12.1	8.4	9.8	13.4	13.0
PPL	14.4	14.6 ± 0.57 (4) 13.9–15.2	12.5	13.2	19.4	18.3
LIF	8.2	8.4 ± 0.70 (7) 7.9–9.9	7.1	7.6	9.0	9.3
BIF	2.4	2.5 ± 0.18 (7) 2.3–2.8	2.2	2.4	2.9	2.8
LBP	7.2	7.7 ± 0.53 (7) 7.1–8.6	6.3	7.5	9.2	9.1
BBPM1	2.7	2.8 ± 0.20 (7) 2.4–3.0	2.1	2.6	3.4	3.4

TABLE 7—(*Continued*)

	Tryphomys adustus				*Abditomys latidens*	
	USNM 151511[a]	FMNH 62340, 62341, 62343–62345; USNM 348530, 348531	FMNH 356645	USNM 536765	FMNH 62347[a]	USNM 357244
BMF	2.0	2.2 ± 0.15 (7) 2.0–2.3	2.0	2.0	2.7	3.1
LB	6.9	8.0 ± 0.43 (5) 7.6–7.8	7.1	7.6	9.0	9.5
CLM1-3	—	8.2 ± 0.34 (7) 7.7–8.8	8.2	7.6	10.0	9.7
BM1	2.5	2.7 ± 0.10 (7) 2.5–2.8	2.6	2.5	3.4	3.1

[a] Holotypes.

acteristic of *Rattus*. An emended diagnosis and comparisons are provided below.

Tryphomys Miller

Type Species: *Tryphomys adustus* Miller (1910: 399), based on an old adult female (USNM 151511) collected by Dr. Edgar A. Mearns from Haights-in-the-Oaks, Benguet Province, Luzon, on July 26, 1907.

Included Species: *Tryphomys adustus.*

Known Distribution: Highlands and low elevations in northern and central Luzon (Miller, 1910; Sanborn, 1952; Barbehenn et al., 1972–73).

Etymology: Miller combined the Greek *tryphos* with *mys* (mouse or rat) to obtain *Tryphomys.* A lump is one of the meanings of *tryphos* and Miller presumably was referring to the maxillary swelling lateral to the first molar, one of his diagnostic characters.

Emended Diagnosis (see table 7; figs. 65, 67, 69, and 70; and also fig. 78 in Musser and Newcomb, 1983: 501): A terrestrial murine of medium body size characterized by the following combination of features—(1) fur thick, long, and shaggy with long guard hairs; (2) tail brown all over and either shorter than head and body or only slightly longer; (3) hind feet long and narrow, plantar pads small and low relative to plantar area, hypothenar present, outer digits short, three middle digits very long; (4) ten mammae (one pectoral pair, one postaxillary pair, one abdominal pair, and two inguinal pairs); (5) cranium stocky with a broad and short rostrum, constricted interorbit and broad braincase so that from dorsal view the interorbit and top of the oval braincase resemble the neck and bottom of an hourglass, low and indistinct interorbital, postorbital, and temporal ridges; (6) wide zygomatic plates with deep zygomatic notches, the anterior zygomatic spine projecting anteromedially to cover a significant portion of the nasolacrimal capsule and nearly touching it; (7) squamosal intact above each bulla, not divided by a subsquamosal fenestra, no alisphenoid strut, foramen ovale accessorius coalesced with masticatory and buccinator foramina; (8) incisive foramina long and slender, their posterior margins constricted and situated between the first molars; (9) bony palate short, ending before, at, or just behind posterior margins of molar rows, etched by deep palatal grooves; (10) narrow and deep mesopterygoid fossa breached by long and wide sphenopalatine vacuities; (11) pterygoid fossae deeply excavated, small sphenopterygoid vacuities; (12) deep groove in each pterygoid plate for infraorbital branch of stapedial artery, and large stapedial foramen, two traits reflecting the primitive murine cephalic arterial pattern; (13) auditory bullae large and highly inflated, short and inconspicuous bony eustachian tube, each bullar capsule separated from alisphenoid and squamosal bones by wide gap consisting of the coalesced middle lacerate foramen, postalar fissure, and postglenoid foramen; (14) small coronoid process on dentary; (15) in-

Fig. 65. *Tryphomys adustus* (FMNH 62343, adult male) from Luzon.

cisors asulcate, enamel layers orange, uppers opisthodont and very wide relative to rostral breadth; (16) molars large and chunky relative to size of cranium and mandible, somewhat hypsodont, each first upper molar anchored by five roots, each second molar by four, the third by three, each first lower molar with four roots, each second and third molar with three; (17) cusps appreciably slanted, occlusal surfaces of molars cuspidate in young adults with the cusps next to one another forming nearly transverse rows, laminar in adults; (18) posterior cingulum either absent or represented by a slight bulge on each first upper molar, absent from other uppers, no cusp t7, cusp t6 of each first and second upper molar weakly joined to cusp t5 so there is a deep anterior groove between cusps t6 and t5 on each molar, cusp t9 large on first and second upper molars, cusp t3 very small on each second upper molar, usually missing from each third molar, most of each third upper molar consisting of two thick and transverse laminae; (19) each first lower molar with large anterolingual and small anterolabial cusp, no anterocentral cusp, anterolabial cusps on second and third lower molars, anterior labial cusplets absent from first lower molars, posterior labial cusplets present on first and second lowers, most laminae on first and second lower molars formed of weakly connected cusps that retain their discreteness, each third lower molar formed mostly of two thick and transverse laminae, posterior cingulum small and peglike on first and second lower molars but absent from third molars.

DESCRIPTION: The holotype of *Tryphomys adustus* was described by Miller (1910) and a fuller description of the species is provided by Musser and Newcomb (1983).

COMPARISONS: *Tryphomys* possesses the following features that distinguish it from Asian *Rattus rattus* (the expression of the trait in *Rattus* is placed within parentheses); also compare figure 67 (the cranium and mandible of *Tryphomys*) and figure 70 (molar rows of *Tryphomys*) with figures 7 and 12 (skull and teeth, respectively, of *Rattus*).

1. The fifth digit of each hind foot is shorter relative to the other digits, the plantar pads are smaller relative to plantar area (fifth digit

more proportional to other digits, plantar pads larger relative to plantar area).

2. In dorsal view, the narrow interorbit and wide oval braincase are shaped like an hourglass, the dorsolateral margins of interorbit, postorbital region, and braincase are outlined by low and inconspicuous beading (the wider interorbital and postorbital regions are outlined by high ridges that continue caudad to the occiput).

3. Each zygomatic plate is much more expansive, the anterior zygomatic spine projects farther forward and also medially to nearly touch the nasolacrimal capsule and cover one-half to one-third of it (less expansive zygomatic plate, the anterior spine does not conceal part of the nasolacrimal capsule and is not close to it).

4. The incisive foramina are narrow and constricted in their posterior one-third (wide and not constricted).

5. The bony palate is short, ending before, at, or just behind the molar rows (the long bony palate projects well beyond the molar rows to form a long and wide platform).

6. The mesopterygoid fossa is deeper and each pterygoid fossa is more deeply excavated (not as deep and shallower).

7. The auditory bullae are, relative to size of braincase, both much larger and more greatly inflated (bullae relatively smaller, less inflated).

8. The coronoid process of the dentary is smaller and more delicate in appearance (larger and more robust).

9. The upper incisors are wider relative to breadth of the rostrum (incisors narrower relative to rostral breadth).

10. The upper molars appear chunky and are much larger, both in absolute dimensions and relative to area of the short bony palate, and the lower molars are also large, absolutely and relative to size of each dentary (molars are much smaller, appearing delicate relative to the long and expansive bony palate or the dentary).

11. All the rows of cusps on all of the molars are inclined (most cusps are inclined but many are upright; fig. 69B, C).

12. Cusps on the upper molars form nearly transverse rows (most cusps form chevron-shaped rows).

Fig. 66. *Abditomys latidens* (USNM 357244, adult male) from Luzon. Measurements are listed in table 7.

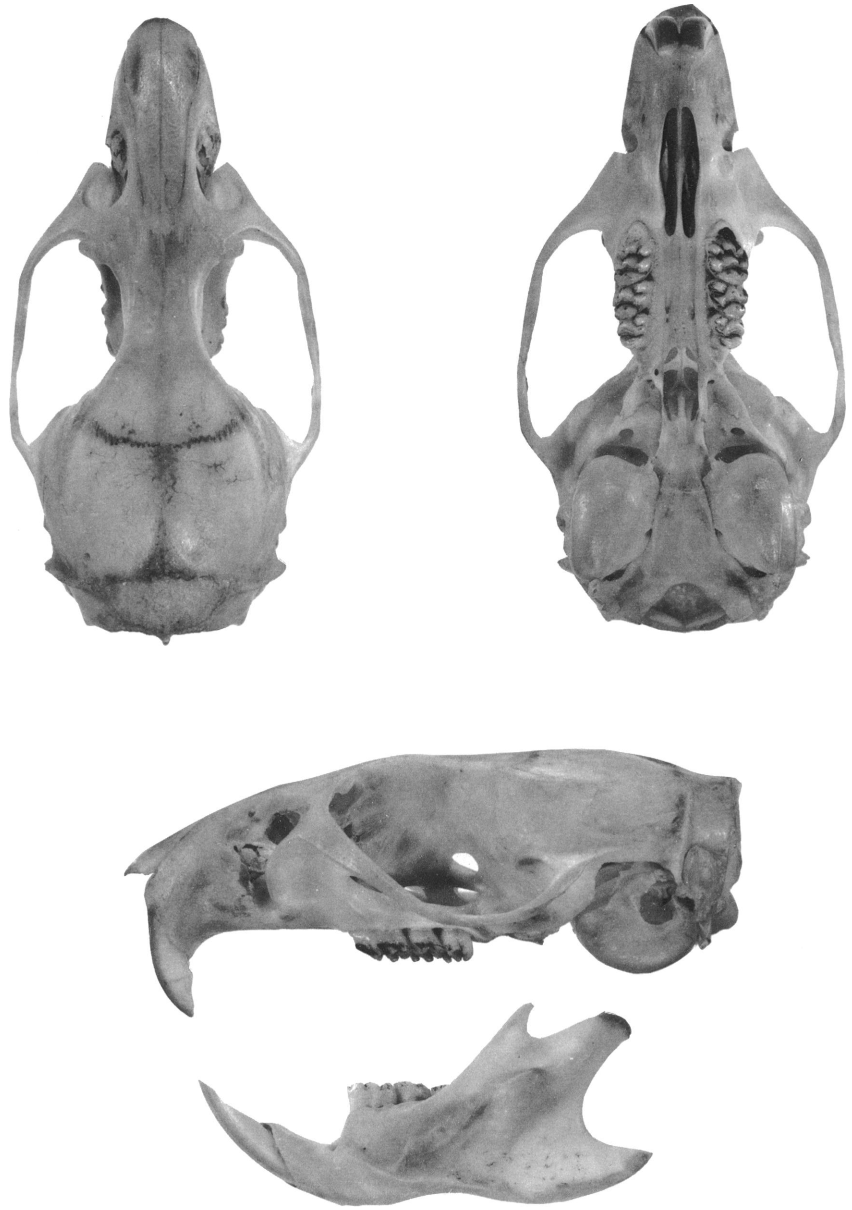

Fig. 67. Cranium and dentary (×2) of an adult *Tryphomys adustus* (USNM 348531) from Luzon.

13. Most of the occlusal surface of each third upper molar consists of two thick and transverse laminae, even in young rats; the laminae are spaced far apart, and their labial and lingual margins do not merge, even when the chewing surfaces are very worn, figure 70A (the anterior lamina on each third upper molar is bent like an inverted comma and clearly cuspidate in young rats, the posterior lamina is also cuspidate and triangular; the labial and lingual margins of each lamina touch or nearly so and merge after wear, fig. 12B).

14. On each first and second upper molar, cusp t6 is narrowly attached to the central cusp t5 and the two are separated by a deep

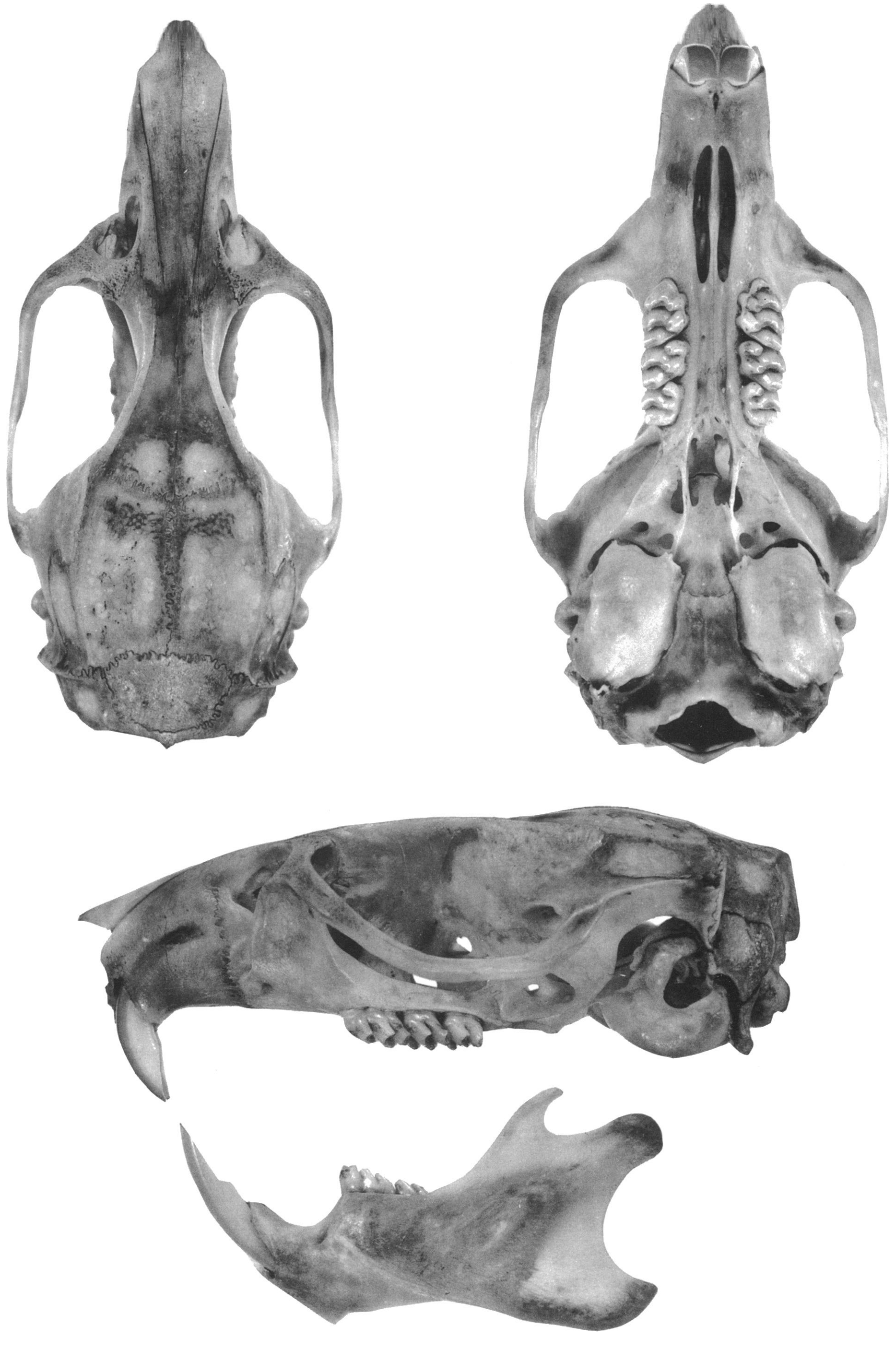

Fig. 68. Cranium and dentary (×2) of an adult *Abditomys latidens* (USNM 357244) from Luzon.

anterolabial groove, even in worn molars, figure 70A (cusp t6 and t5 are more broadly attached, without a deep anterolabial groove separating the cusps, fig. 12B).

15. The anterolingual cusp is crescent-shaped and much larger than the anterolabial cusp on each first lower molar, figure 70C (the anterolingual cusp is simply elliptical in

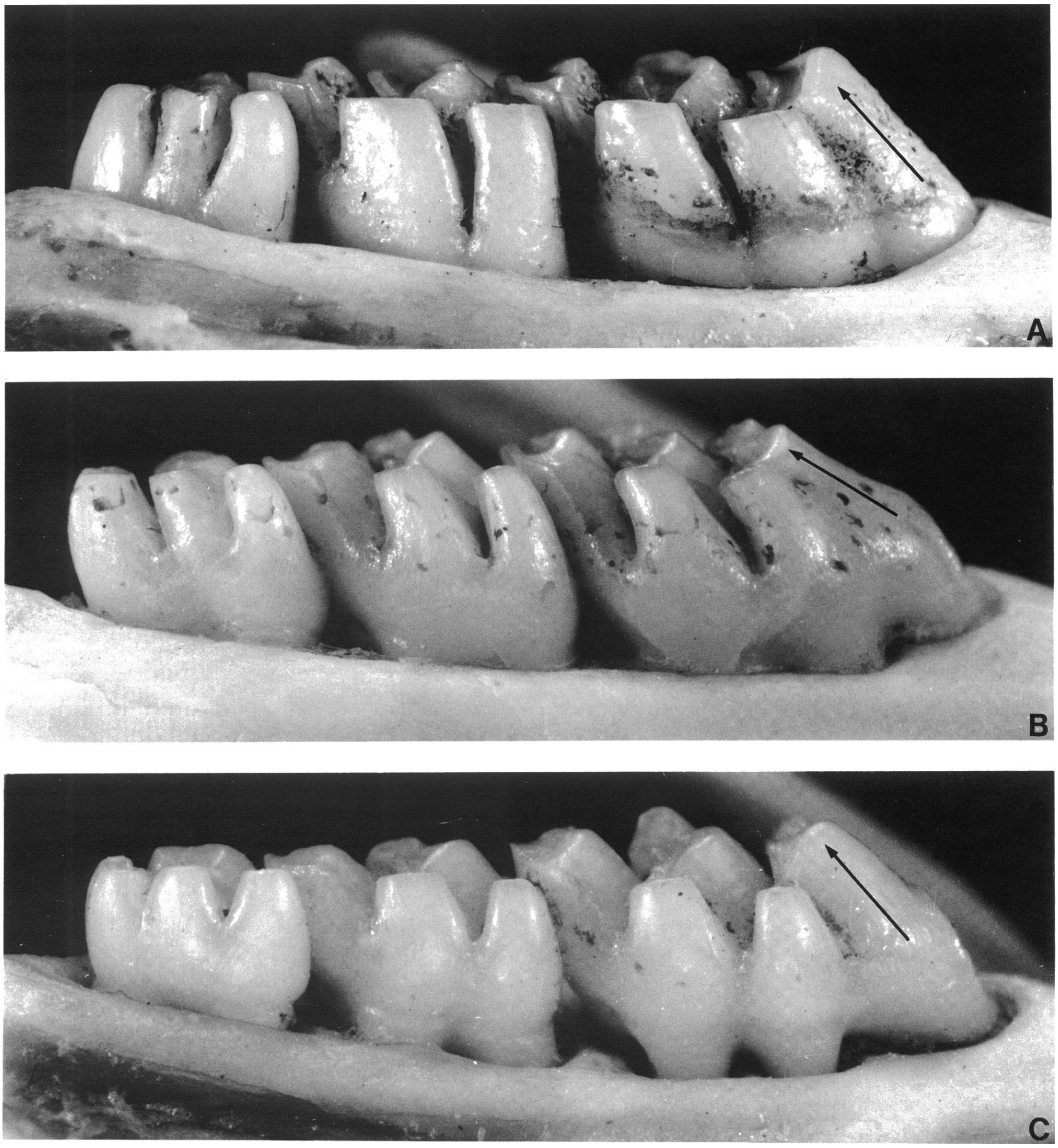

Fig. 69. Lingual contrasts between the right upper molars of *Bullimus bagobus* (**A**, DMNH 4173; CLM1–3 = 9.8 mm), *Tryphomys adustus* (**B**, USNM 536765; CLM1–3 = 7.5 mm), and Sulawesian *Rattus rattus* (**C**, AMNH 101272; CLM1–3 = 6.5 mm). The cusp rows are more steeply inclined (note the inclination of the black arrow) in *Tryphomys* than in either *Bullimus* or *Rattus*.

outline and smaller relative to the opposite anterolabial cusp, fig. 12D).

16. The second and third laminae on each first lower molar, and the posterior lamina on each second lower molar are formed of discrete cusps that are narrowly joined along their anteromedial margins in young rats, figure 70C (the primary cusps forming comparable laminae are broadly joined, and the laminae are without such discrete cuspidation, fig. 12D).

17. Posterior labial cusplets on the first

Fig. 70. Occlusal contrasts (× 12) between right molar rows of *Tryphomys adustus* (USNM 536765; **A,** uppers; **C,** lowers) and *Abditomys latidens* (USNM 357244; **B,** uppers; **D,** lowers). See text for further discussion.

lower molars are usually small and inconspicuous; comparable cusplets are either absent from the second molar or range in size from tiny to small, forming an inconspicuous part of the wear surface of each tooth, figure 70C (the posterior labial cusplets on the first and second lower molars are large and prominent, fig. 12D).

18. The posterior cingulum at the back of each first and second lower molar is a short and thin peg; the one on each first molar has almost merged with the posterior surface of the tooth and is inconspicuous, figure 70C (each posterior cingulum is large, elliptical in cross section, and a prominent part of the occlusal surface, fig. 12D).

Abditomys is the only other genus to which *Tryphomys* needs to be compared. *Abditomys latidens* differs from *Tryphomys adustus* by its possession of the following traits (the expression in *T. adustus* is described within parentheses).

1. Body size is much larger and the tail is appreciably longer than length of head and body, table 7 and figure 66. (Body size smaller, tail subequal to head and body, fig. 65.)

2. The tail appears naked because the scale hairs are short, only slightly longer than the scale itself (the tail appears well-haired, a reflection of the longer scale hairs, most as long as two scales).

3. The hind feet are elongate, as they are in *Tryphomys,* but the digital and plantar pads are huge fleshy mounds deeply textured with

semicircular and transverse striations, and the plantar pads are much larger relative to the plantar surface (low, relatively small, and inconspicuous); the fifth digit is semiopposable and longer relative to the central digits, and the hallus has a nail imbedded in a large fleshy digital pad (see fig. 4 in Musser, 1982a: 6) (fifth digit is not semiopposable, the hallux is clawed, and the digital and plantar pads are small and low); the palmar pads and digital pads of the front feet are also much larger, fleshier, and more deeply scored with striations (palmar and digital pads of forefeet smaller).

4. Females have four pairs of mammae: one pectoral, one postaxillary, and two inguinal (five pairs in *T. adustus*).

5. The only male specimen described has a prominent midventral cutaneous glandular area (apparently absent).

6. Many of these external traits that are diagnostic of *A. latidens* indicate highly arboreal habits (the different expressions seen in *T. adustus* point to terrestrial habits only).

7. High ridges outline the interorbital and postorbital regions and extend back along dorsolateral margins of the braincase to the occiput, figure 68 (inconspicuous beading, fig. 67).

8. Occlusal surfaces of upper molars are very simple, consisting mostly of thin arcuate or transverse laminae (fig. 70B); the labial cusps are coalesced with the central cusps and their boundaries are indefinite; the posterior lamina on each first and second molar is a transverse plate (laminae are cuspidate, labial cusps discrete, the posterior row on first and second molars is cuspidate, fig. 70A).

9. Cusp rows on lower molars are transverse (fig. 70D), the anterolingual cusp is less elaborate and the anteroconid is nearly transverse, the posterior cingulum at the back of each first and second lower molar is large and prominent (most rows of cusps are not transverse, the anteroconid is differently shaped, and the posterior cingula are short and small pegs, fig. 70C).

Tryphomys and *Abditomys* are each sharply defined by a suite of automorphies, but several distinctive derived traits are shared by both, and set *T. adustus* and *A. latidens* apart from any other member of Division III.

1. The upper incisors are wide relative to size of cranium, relatively wider than in any other species in Division III. It was this feature for which *latidens* was named by Sanborn (1952: 126).

2. Each zygomatic plate is very wide, and the zygomatic notch is deep, reflecting the prominent anterior zygomatic spine that projects forward far enough to conceal up to one-third or one-half of the nasolacrimal capsule (figs. 67 and 68; see also fig. 10 in Sanborn, 1952: 126). The anterior zygomatic spine also projects anteromedially to nearly touch the nasolacrimal capsule. In other members of Division III, most of the nasolacrimal capsule is not covered by the zygomatic plate, and the spine projects straight ahead rather than toward the midline of the cranium (*Bullimus* is a good example, fig. 72).

3. The incisive foramina are long enough that they project between the first upper molars, and they are constricted in their posterior one-fourth (figs. 67 and 68). There are other species in Division III with long incisive foramina but they are not posteriorly constricted.

4. Deep palatal grooves extending from the incisive foramina to the posterior palatine foramina score the bony palate (figs. 67 and 68). The bony palate in other species is etched by shallow depressions.

5. The auditory bullae are highly inflated, to the extent that the swollen capsule has incorporated all of the bony eustachian tube except for the short distal portion surrounding the internal auditory meatus (figs. 67 and 68; see also fig. 7B in Musser, 1982a: 8, where the enlarged bullar capsule of *Abditomys* is illustrated; and fig. 78B in Musser and Newcomb, 1983: 501, for a bullar enlargement of *Tryphomys*).

6. Molar rows are relatively larger than in any other genus in Division III.

7. Rows of cusps on upper and lower molars are inclined at a greater angle from the horizontal (slanting backward in the uppers and forward in the lowers) than in any other group of species in Division III (fig. 69).

8. The occlusal surface of each third upper molar is formed predominantly by two transverse or slightly bent laminae, each without indication of any cuspidation (fig. 70A, D).

2. *BULLIMUS*

This genus was described by Mearns (1905: 450) in the same report where he introduced *Limnomys* and *Tarsomys,* and its identity was just as obscurely outlined, leaving readers without definition or diagnosis of what is actually a very distinctive Philippine endemic. Mearns characterized *Bullimus* as being

> Similar to *Mus,* but with three additional subsidiary cusps to the lower molar series of either side, placed externally, one in front of the last series of cusps of the anterior molar, and one in front of each series of the middle molar; lower jaw with a projecting capsule for the accommodation of the base of the lower incisor tooth; audital bullae collapsed and flattened externally so that the audital opening is compressed and directed posteriorly; skull elevated in the anteorbital region; rostrum elongate; fronto-parietal bead slightly marked, bony palate narrow.... Size large; pelage coarse, containing a mixture of ordinarily coarse hair and slender spines on upper surface; whiskers long, reaching the shoulders....

The genus was based on an adult female, which was designated the holotype of *Bullimus bagobus,* and barely made it into the natural history storehouse of western biologists because Mearns (1905: 451) remarked that "the unique specimen was snared by a native, who brought it and a fine specimen of *Mus mindanensis* to me on the trail as I was leaving the Bagobo village of Todaya."

One specimen in the United States was not enough and too far away to study for Oldfield Thomas, who sent Malcolm Anderson to the Philippines to acquire examples of the genera described by Mearns. Anderson caught one specimen of the Bagobo rat, and Thomas (1907: 141) identified it as *Mus bagobus* (*Mus* was used then for species that are now placed in *Rattus*), explaining that

> I fail to see any sufficient reason for the creation of a special genus to contain this species. The small supplementary cusps on the lower molars, on which Dr. Mearns mainly founds the genus, are not only present in many Malayan species usually referred to *Mus,* but they are even quite well-marked, though small, in his own specimens of *Mus albigularis* Mearns, also from Mindanao. None of the other characters mentioned by him appears to me of generic importance.
>
> It is unfortunate that Dr. Mearns had not had experience of the difficulties of Murine dental characters before venturing to describe genera of this group. Had he had such experience I am sure he would not have described *Bullimus*....

Fig. 71. *Bullimus bagobus* (AMNH 203316, adult male) from Luzon.

Fig. 72. Cranium (×2) of a *Bullimus bagobus* adult (AMNH 207557, male) from Mindanao.

Six years after Thomas published his complaint, Hollister (1913), in his "Review of the Philippine Land Mammals in the United States National Museum," recognized *Bullimus,* as did Taylor in 1934 in his monograph on land mammals of the Philippines; whether inertia, nationalism, or critical study influenced their views is unknown. By 1941, Ellerman continued the British view and listed *bagobus* as a species of *Rattus* in his *Rattus xanthurus* group, strongly dissenting from the actions of Hollister and Taylor (Ellerman, 1941: 160), and certainly influencing later investigators. Johnson (1946: 320), for example, in describing a new subspecies of *bagobus,* noted that the species was "a specialized member of the *Rattus xanthurus* group and there are no satisfactorily constant characters by which "*Bullimus*" can be retained."

By 1969, *Bullimus* had become a subgenus of *Rattus* in Misonne's interpretation of the evolutionary trends among African and Indo-Australian murids. Within the subgenus he included *xanthurus, celebensis, adspersus, coelestis,* and *dominator* from Sulawesi; *muelleri* from the Sunda Shelf; *bowersi, manipulus,* and *berdmorei* from southeast Asia; and *everetti* and *adustus* from the Philippines.

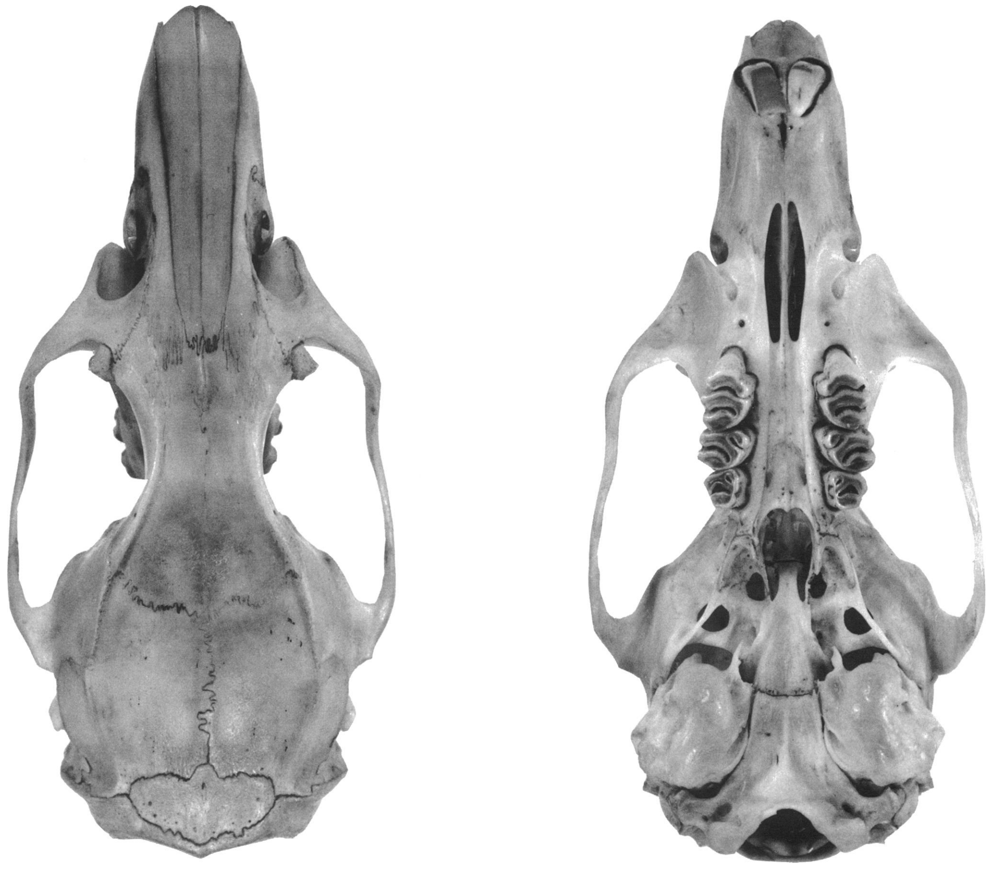

Fig. 73. Cranium (×2) of a *Bullimus luzonicus* adult (USNM 151505) from Luzon.

According to Musser and Newcomb (1983), *xanthurus* is unrelated to *Bullimus*; *celebensis* is a member of the genus *Taeromys*; *adspersus* and *coelestis* are part of *Bunomys*; *dominator* is in the genus *Paruromys*; *muelleri* is one of the species of *Sundamys*, which is endemic to the Malay Peninsula and islands on the Sunda Shelf; *bowersi, manipulus,* and *berdmorei* are members of the distinctive genus *Berylmys*; *adustus* is the only species in *Tryphomys*; and *everetti* is a true member of *Rattus*.

What then is *Bullimus*? Again, it is time to turn from our primary purpose in this section describing possible phylogenetic relationships to provide an emended diagnosis of *Bullimus* and compare its traits with those of *Rattus*. We will then return to the central discussion by enumerating the unique traits of the genus that separate it from all the other members in Division III.

BULLIMUS MEARNS

TYPE SPECIES: *Bullimus bagobus* Mearns (1905: 450), based on an adult female (USNM 125248) obtained by Dr. Edgar A. Mearns from Todaya, village at 4000 ft on Mount Apo, Mindanao, on July 13, 1904.

INCLUDED SPECIES AND KNOWN DISTRIBUTION: *Bullimus luzonicus* from Luzon; and *Bullimus bagobus* from the islands of Samar, Calicoan, Leyte, Dinagat, Siargao, Mindanao, Bohol, and Maripipi (table 8); samples come from both lowlands and highlands.

We do not know how many species of *Bullimus* really exist because, as Musser (1982c: 91) noted, "the genus has never been taxonomically revised and the extent of individual, secondary sexual, geographic, and altitudinal variation in features of skins, skulls, and teeth is unknown." The two species we provisionally recognize here mostly reflect the insular distributions of body size: small-bodied rats occur on Luzon and larger-bodied animals are found on the other islands. Specimens from western Mindanao are the largest in body size and are slightly larger than those from the rest of the island and were named as a separate species, *rabori,* by Sanborn (1952: 130). These size differences can be visualized in figure 57 of Musser's (1982c: 89) report, where crania of samples from Mindanao, Samar, and Luzon are portrayed.

ETYMOLOGY: The Latin *bulla* means bubble (Brown, 1956), and because of its bubblelike shape, morphologists apply the term to the otic capsule of murines and other mammals. When Mearns combined *bulla* with *mus,* the Latin for mouse or rat, he was clearly calling attention to the "audital bullae collapsed and flattened externally so that the audital opening is compressed and directed posteriorly," which turns out to be one of the very distinctive traits defining the genus.

EMENDED DIAGNOSIS (see figs. 71–76; and the cranial enlargements in fig. 86 of Musser and Newcomb, 1983: 512): A terrestrial murine characterized by the following combination of traits—(1) body size large, tail much shorter than combined length of head and body (see the external measurements provided by Thomas, 1898; Mearns, 1905; Johnson, 1946; Sanborn, 1952; and Heaney and Rabor, 1982) and either mottled or bicolored; (2) pelage coarse with short guard hairs; (3) hind feet long and moderately wide, hypothenar pad present but small; (4) adult males with prominent midventral cutaneous glandular area, females with eight mammae (one postaxillary pair, one abdominal pair, and two inguinal pairs); (5) cranium stocky with a long and slender rostrum, narrow interorbit, moderately prominent interorbital, postorbital, and temporal ridges, squarish interparietal; (6) wide zygomatic plates with deep zygomatic notches, the anterior zygomatic spine projecting forward (and not medially) to conceal a small portion of the nasolacrimal capsule, the posterior third of the ventral maxillary root of each arch is above the first molar, and the posterior edge of the plate is about even with the middle of that tooth; (7) squamosal intact above each bulla, not divided by a subsquamosal fenestra, no alisphenoid strut, foramen ovale accessorius coalesced with masticatory and buccinator foramina; (8) incisive foramina moderately long, their posterior margins anterior to or barely projecting beyond anterior margins of first molars; (9) bony palate moderately long, projecting beyond posterior margins of molar rows but not far enough to form a wide shelf, etched by shallow palatal grooves; (10) wide and deep mesopterygoid fossa, its walls breached by medium-sized sphenopalatine vacuities; (11) pterygoid fossae deeply excavated, large sphenopterygoid vacuities; (12) deep groove in ventral surface of each pterygoid plate at its posterolateral margin for infraorbital branch of stapedial artery, and large stapedial foramen, two traits reflecting the primitive murine cephalic arterial pattern; (13) bullar capsule large, inflated medially and ventrally but concave on lower part of lateral surface, dorsal portion of lateral surface in the form of a large shield covering part of the external auditory meatus so that aperture opens caudad instead of laterally, the posterior lamina of the ectotympanic is an expansive osseous flange wide enough to reach the laminar portion of the malleus and conceal most of the incus, the bony eustachian tube is short, narrow, and flattened; (14) postglenoid foramen shall to moderately large; (15) coronoid process large, posterior margin of dentary deeply concave; (16) incisors without grooves, enamel orange, uppers opisthodont; (17) molars large, chunky, and hypsodont, each first upper molar anchored by five roots, each second molar by four, the third by three, each first lower molar with four roots, each second and third molar with three; (18) cusps broadly joined in each row, the cuspidate structure evident in young rats but transformed into arcuate and transverse laminae in older animals; (19) posterior cingulum either absent or represented by low ridge or bulge at back of each first upper molar, no cusp t7, cusp t3 small and inconspicuous on first molar, most specimens without cusp t3 on each second and third upper molar; (20) anteroconid consisting of chunky and distinct anterolabial and anterolingual cusps, no anterocentral cusp, anterolabial cusps on second and third lower molars, anterior labial

Fig. 74. Crania and dentaries (×2) of the specimens shown in figures 72 and 73. **Top,** *Bullimus bagobus*; **bottom,** *Bullimus luzonicus.*

cusplet absent from each first lower molar, posterior labial cusplet on each first and second lower molar.

DESCRIPTION: Brief descriptions have been published for the Luzon *luzonicus* (Thomas, 1898), the holotype of *Bullimus bagobus* (Mearns, 1905), *barkeri* from Calicoan and Samar (Johnson, 1946), and the Mindanao

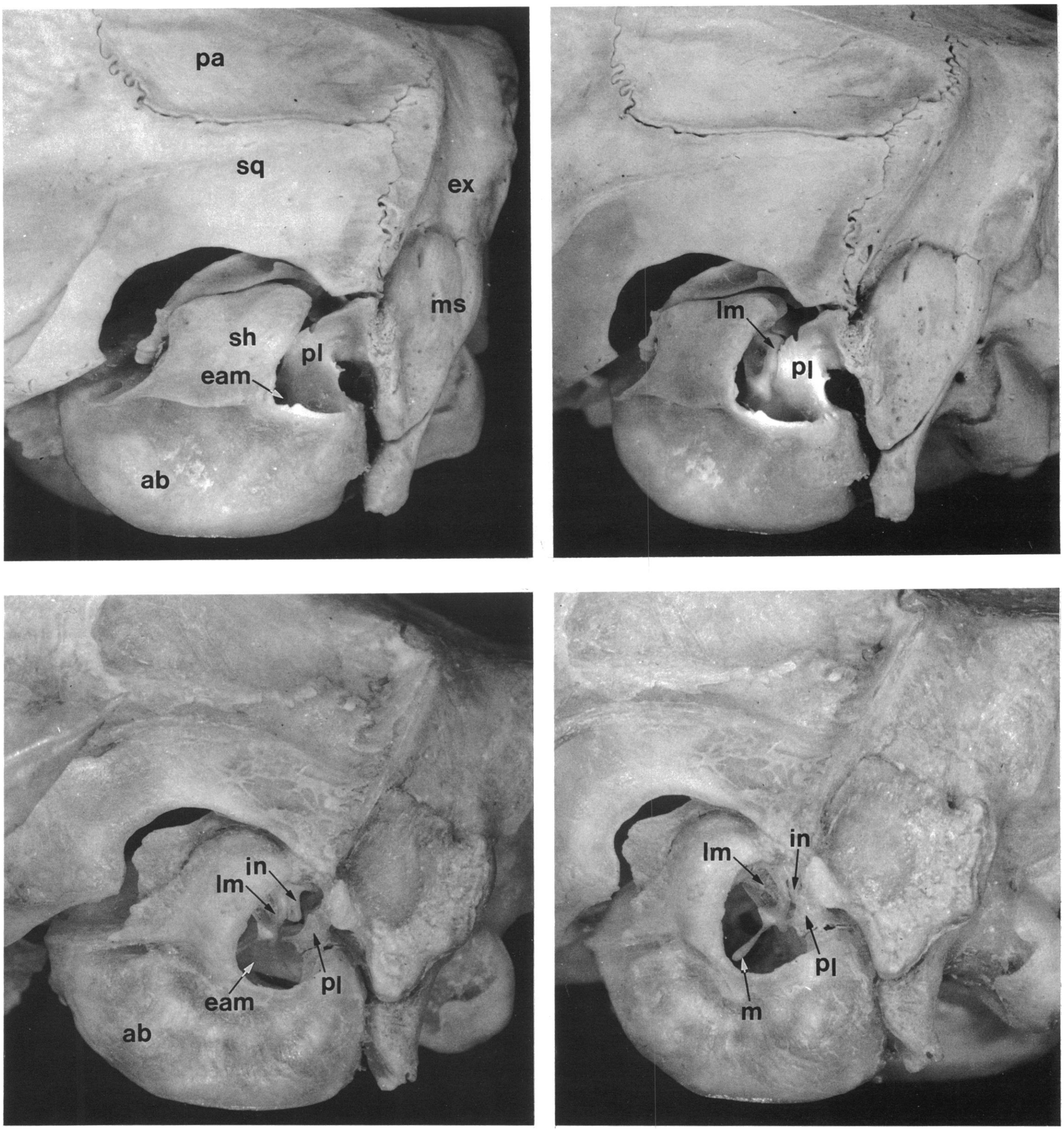

Fig. 75. The otic region in *Bullimus bagobus* (**top views**, DMNH 5850) and *Rattus everetti* (**bottom views**, AMNH 203315). On the left, each auditory bulla (**ab**) is seen directly from the side; on the right, the back of the skull is tilted toward the viewer so more of the inside of the capsule can be seen. In most specimens of *Bullimus*, the posterior lamina (**pl**) of the ectotympanic is an expansive osseous flange wide enough to reach the laminar portion of the malleus (**lm**) and conceal most of the incus (**in**); the small pars flaccida attaches to the anterior margin of this flange. The form of the posterior lamina in *R. everetti* is similar to the shape and size (relative to otic capsule) of this element in all other endemic Philippine murines. It does not cover the incus and the pars flaccida has a greater area. Notice also that in *Bullimus* the external auditory meatus (**eam**) is partially concealed by a bony shield (**sh**) so the aperture is directed caudad, which is derived; the aperture is not shielded in *Rattus* and opens laterally, the general configuration (best seen in the left views). **ex**, exoccipital portion of the occiput; **m**, manubrium; **ms**, mastoid; **pa**, parietal; **sq**, squamosal.

rabori (Sanborn, 1952); Musser and Newcomb (1983) provided additional descriptive information.

COMPARISONS: The following characteristics of *Bullimus* distinguish that genus from Asian *Rattus rattus* (the expression of the trait in *Rattus* is placed within parentheses); also compare the crania, dentaries, and molar patterns of *Bullimus* in figures 72–76 with those of Sulawesian *Rattus rattus* in figures 7, 12, 23, and 27, and *R. everetti* in figure 77 and 78.

1. The tail is much shorter than combined lengths of head and body, figure 71 (equal to or much longer than length of head and body).

2. The hind feet are longer, and the plantar pads are smaller relative to plantar area (hind feet shorter relative to body size, plantar pads relatively larger).

3. The rostrum is longer relative to the cranium, figures 72 and 73 (rostrum is more proportional to the cranium, figs. 7, 23, and 77).

4. Each zygomatic plate is much wider; the anterior zygomatic spine projects forward far enough to conceal part of the nasolacrimal capsule; the posterior margin is even with about the middle of each first molar, and the posterior part of the ventral maxillary root covers that tooth and part of the second in some specimens, figure 74 (the zygomatic plate is narrower, the anterior margin does not project as far forward, and the posterior edge of the plate is about even with the anterior alveolar lip of each first molar, figs. 7, 23, and 77).

5. The interorbital, postorbital, and temporal ridges are not as high or pronounced relative to the size of the cranium, figures 72 and 73 (ridges are high or pronounced relative to cranial size, figs. 7, 23, and 77).

6. The occiput is not deep and the interparietal is squarish in most specimens, figures 72, 73 (the occiput is much deeper, in anterior-posterior direction, and the interparietal is wider relative to its length, figs. 7, 23, 77).

7. The bony palate does not project beyond the molar rows to form a wide shelf, figures 72, 73 (the bony palate is long, a reflection of its significant extension beyond the molar rows to form a wide platform, figs. 7, 23, 77).

8. The sphenopterygoid vacuities are smaller, figures 72, 73 (smaller vacuities, figs. 7, 23, 77).

9. The auditory bullae are about as proportionally inflated as in *R. rattus,* but not as much as in *R. everetti,* but the size of the ectotympanic shield, the posterior orientation of the external auditory meatus, and the expansive posterior lamina of the ectotympanic (fig. 75) are unique to *Bullimus* (usual primitive murine ectotympanic and orientation of the external auditory meatus).

10. The upper and lower molars are large and chunky relative to area of the bony palate and dentary (figs. 72, 73), and conspicuously hypsodont, figures 69A and 74 (molars are smaller, appear delicate relative to the bony palate and mandible [figs. 7, 23, 77], and are brachyodont, figs. 69C, 74).

11. Cusps forming the rows on upper molars are not well defined and with wear the occlusal surfaces consist of arcuate or transverse laminae, cusp t3 on first molar inconspicuous and usually absent from each second and third molar, figure 76A, B (cusps are better defined and after wear they form chevron-shaped rows, cusp t3 relatively larger and distinct on first molar, usually present on each second and third molar, figs. 12B, 78).

12. The anteroconid is formed by large chunky anterolabial and anterolingual cusps, and no anterocentral cusp, figure 76C, D (anterolabial and anterolingual cusps are smaller and different in shape, an anterocentral cusp is common in some species [for example, see the lower toothrow of *R. everetti* shown in fig. 92 in Musser and Newcomb, 1983: 519], figs. 12D, 78).

The combination of traits listed in our emended diagnosis of *Bullimus* serves to define it as a morphologically very distinct group of rats. Some of those features, however, whether primitive or derived, are shared by other members of Division III. One is not: the conformation of the auditory bulla, as illustrated in figure 75. The otic capsule is inflated, primarily ventrally and not so much laterally or medially. The external auditory meatus is directed caudad rather than laterad because a large shieldlike process of the ectotympanic has extended over what would have been the lateral opening. The posterior

Fig. 76. Occlusal contrasts (×10) between right molar rows of a juvenile–very young adult (DMNH 4173; **A**, uppers; **C**, lowers) with an adult (AMNH 207558; **B**, uppers; **D**, lowers) *Bullimus bagobus* from Mindanao.

lamina of the ectotympanic forms a wide and thin bony flange (often destroyed in skulls that were not carefully cleaned) that in most specimens abuts against the malleus and conceals most of the incus (it is not as expansive in a few specimens and does not quite cover the incus, but still remains a wide flange). The structure is not an innovation, but an elaboration derived upon the usual conformation of the ectotympanic bulla that is found in species of *Rattus* and other genera. But among Philippine rodents, this elaboration of shield and posterior lamina is unique to *Bullimus*.

3. *TARSOMYS*

We have defined the genus and the two species of *Tarsomys* in the first section of our report. Each species is distinctive in its morphology. *Tarsomys apoensis* has a very wide zygomatic plate, wide and long bony palate that extends well beyond the molar rows, shallow pterygoid fossae, and narrow incisors, all derived features contrasted with *T. echinatus,* which has the primitive state of these traits. On the other hand, the spiny rat has a spinous coat and longer claws (even though the claws are also long in *T. apoensis*), which are specializations unique to it. Despite these specializations not shared between them, both species appear to be more closely related to each other than to any other endemic Philippine murine; the combination of characteristics given in the emended diagnosis excludes all the other species.

4. *LIMNOMYS*

This genus and its single species, *L. sibuanus,* are also well defined by the combination of features listed in our emended diagnosis. The cusp patterns, resulting from a combination of retained primitive traits and unique specializations, are especially diagnostic and unlike those of any other species in Division III.

5. *RATTUS*

We consider members of the *Rattus everetti* complex, *R. mindorensis,* and *R. tawitawiensis* to represent the endemic representatives of *Rattus* in the Philippine Archipelago (*R. tiomanicus* is the only other native species recorded from within the political boundaries of the Philippines, but it is a Sundaic species that occurs on Palawan [Musser and Califia, 1982], which we exclude from our report because its murine fauna is closely allied with that on the Sunda Shelf and not with the fauna native to the backbone of the Archipelago [Heaney, 1986]).

Specimens usually identified as *R. everetti* have also been described under the names *albigularis, tagulayensis, gala,* and *tyrannus.* All the samples contain large-bodied rats with tails slightly shorter, equal to, or much longer than combined lengths of head and body (see the measurements in Mearns, 1905: 439–441; Sanborn, 1952: 128; and Heaney and Rabor, 1982: 23). The dorsal coat is coarse and shaggy, the overhairs reach 20–25 mm, and the inconspicuous guard hairs project beyond the coat by only 5–10 mm. Upperparts are brown, underparts range from white to buffy white to grayish brown. Ears and tops of the feet are brown. The tail is bicolored: brown over its proximal half and white elsewhere. It appears scantily haired because the scale hairs are very short. The hind feet are long and narrow, the plantar pads are large and fleshy, and the hypothenar is a prominent pad. Adult males have a conspicuous midventral sebaceous gland. Females have eight teats: one pectoral pair, one postaxillary pair, and two inguinal pairs. The cranium and dentary are illustrated in figure 77, occlusal views of the molar rows are shown in figure 78.

Samples come from many islands in the Archipelago (table 8) and exhibit considerable variation in body size and texture of pelage. Animals from Luzon are the smallest and have the softest fur, specimens from Dinagat and Ticao are the largest in body size and have the coarsest pelage. Examples of the variation in size, based on cranial conformation, are illustrated in figure 58 published in Musser (1982c: 90). There it is apparent that the size contrast between the small Luzon animal and the very large *tyrannus* from Ticao Island is striking. Such a difference usually suggests that more than one species is present, and from the time that Miller (1910: 397) described *tyrannus* it has been treated first as a species without certain close relatives, and later as a distinctive species related to *everetti* (Johnson, 1946; Heaney et al., 1987). We do not know if the variation we have seen among the samples available to us represents insular variation within one widespread species or reflects several species, each restricted to an island or group of islands. Heaney and his colleagues (in prep.) are attempting to answer these questions but until a sound systematic revision of the group is available we refer to it simply as the *R. everetti* complex, which reflects our present ignorance.

Rattus mindorensis is known only from Mindoro Island where it is apparently common at high elevations, judged by samples we have studied. The rat is of medium body size with a tail longer than combined lengths of head and body, and dark brown fur that is dense, short, soft, and wooly in appearance. General descriptions of the species are provided by Thomas (1898: 402), Musser (1977b), and Musser and Califia (1982), and the cranium is illustrated in figure 5 in Musser and Califia (1982: 27).

Rattus tawitawiensis was described by Musser and Heaney (1985) from three specimens captured on the island of Tawitawi in the southern end of the Sulu Archipelago ("Greater Sulu" on the map in fig. 3; also see the map in Musser and Heaney, 1985: 2). The species is a large rat with dark brown fur and a tail shorter than the combined lengths of head and body. Detailed morphological description of the species, comparisons between it and other species of *Rattus,* and anything else that is known about the Tawitawi animal is documented in Musser and Heaney (1985).

These three species exhibit a combination of traits that taken together define what we regard as the core of *Rattus,* which includes *R. rattus* and its allies, a group of species whose distributions are primarily tied to India, continental Asia, and the Sunda Shelf. We exclude from this group all the so-called native *Rattus* from Australia, New Guinea, the Moluccas, as well as members of the *R. xanthurus* group on Sulawesi, the native rats of Christmas Island, *R. korinchi* and *R. hoogerwerfi* from Sumatra, *R. annandalei* from the Malay Peninsula, and *R. montanus* from Sri Lanka. Many of the traits are derived, others are primitive; certain traits are also shared by members of *Tryphomys, Abditomys, Tarsomys, Limnomys,* and *Bullimus,* but these genera are characterized by features not found in *Rattus.* No single derived morphological feature can be used by itself to diagnose *Rattus,* and therefore a retinue of characters must be considered to differentiate the genus. This suite of characteristics is briefly outlined below.

1. Body size ranges from small (*R. exulans,* for example) to large (*R. everetti*); pelage from short, soft, and dense to long and harsh.

2. The tail ranges from slightly shorter than length of head and body to much longer. It is monocolored in most of the species, unpigmented or mottled on the ventral surface in a very few; the bicoloration characteristic of *R. everetti* is unique among members of the group.

3. The hind feet are moderately long, and all species have a hypothenar pad. Claws of front and hind feet are not unusual (not elongate as in *Tarsomys,* for example), and the hallux bears a claw in all species (nothing like the naillike claw in *Abditomys*).

4. Number of teats ranges from 8 to 12 in different combinations.

5. Males of some species have a definite midventral cutaneous glandular area.

6. The rostrum is moderately long, but not elongate, and not stubby.

7. Prominent ridges outline the dorsolateral margins of the interorbit, postorbital region, and braincase, usually all the way back to the occiput.

8. The interparietal is wide, deep (anterior-posterior dimension), and forms a roof over most of the occiput. The occiput itself is deep.

9. Each zygomatic plate is wide, and a prominent anterior zygomatic spine (reflected by a well-defined zygomatic notch) projects forward far enough to conceal at least the posterior edge of the nasolacrimal capsule.

10. In the orbit, the sphenopalatine foramen is far anterior to the dorsal palatine foramen (see fig. 8 in Musser and Newcomb, 1983: 344). On the ventral surface of the bony palate, the posterior palatine foramen is either opposite the contact between second and third molars or opposite the third molar.

11. Squamosal roots of the zygomatic arches originate moderately low on sides of the braincase.

12. Each postglenoid foramen is large, and in many species is confluent with the postalar fissure and middle lacerate foramen to form a gap between the auditory bulla and margins of the squamosal and alisphenoid.

13. The squamosal bone dorsal to the bulla is intact, not eroded into a notch or large subsquamosal fenestra.

14. No alisphenoid strut covers the lateral portion of the alisphenoid canal, which is really an open channel. Without the strut, the masticatory-buccinator foramina and the foramen ovale accessorius are united.

15. Long incisive foramina project between anterior faces of the first molars.

16. The bony palate is wide and projects appreciably posterior to the molar rows to form a shelflike expansion.

17. The mesopterygoid fossa is narrow in relation to width of the bony palate. Its walls are breached by spacious sphenopalatine vacuities that extend along each side of the basisphenoid and presphenoid far enough anterior to be seen in the back of the orbit.

18. Each pterygoid plate is wide and slants toward the medial sagittal plane of the cranium, forming a moderately deep fossa. Large sphenopterygoid vacuities perforate the plates, and each plate is margined by a prominent pterygoid ridge.

19. The auditory bullae are globose, large relative to size of the cranium, and moderately (*R. norvegicus,* for example) to greatly inflated (*R. everetti* represents the extreme).

The conformation of the otic capsule relative to the petrosal, basioccipital, basisphenoid, and size of the bony eustachian tube is the derived configuration we described as one of the synapomorphies defining Division III.

20. There is a groove in the ventral surface of each pterygoid plate at its posterolateral region, a large stapedial foramen, and a definite open channel from the posterior opening of the alisphenoid canal to the anterior opening; these are osseous and foraminal reflections of the primitive cephalic carotid circulation.

21. The incisor enamel is orange, the upper incisors are opisthodont relative to the rostrum.

22. Molars have multiple roots, the same patterns described as derived and used by us to define Division III.

23. In each upper toothrow, the first molar broadly overlaps the second and it overlaps the third. In each lower row, there is slight overlap of the third molar on the second, but broader overlap of the second on the first. The rows of cusps are close to one another, separated only by a slight space.

24. Primary cusps are distinct in young rats but broadly connected so that most merge in each row to form weakly cuspidate, chevron-shaped laminae.

25. A posterior cingulum is absent from the back of each upper molar in specimens of most species. If present, it is not fixed, usually occurring in half or less of any sample, and variable in shape, ranging from a slight triangular bulge to a small discrete cusp. Cusp t7 is absent. Cusp t3 occurs on each second and third molar in most species, and is usually small.

26. The anteroconid always consists of a large anterolingual cusp and a smaller anterolabial cusp; an anterocentral cusp occurs at a low to high frequency in some species.

The three species of Philippine *Rattus* may not be especially closely related to one another. *Rattus everetti* is unique among the three in having a bicolored tail, highly inflated bullae, and different distribution of teats (one pectoral pair, one postaxillary pair, and two inguinal pairs). In all the rest of its morphological characteristics, *R. everetti* is a magnified version of *R. rattus*.

External, cranial, and dental features of *R. mindorensis* closely resemble some samples of the Sundaic *R. tiomanicus*, and Musser and Califia (1982: 26) have suggested the hypothesis that the Mindoro rat may be an insular form of the Sundaic species. They also noted that

> It may be significant that Mindoro is the only one of the islands in the backbone of the Philippine archipelago on which a rat with the morphological features of *mindorensis* has been found. Mindoro is close to the northeastern extension of the Sunda Shelf and is separated from the Calamian Islands at the tip of the Shelf by the Mindoro Strait, which is deeper than 100 fathoms. *Rattus tiomanicus* has been found on islands in the Palawan region, including Busuanga in the Calamians.... *Rattus tiomanicus* does occur on some islands beyond the 100 fathom line of the Sunda Shelf (the Maratua Archipelago and P. Enggano), and Mindoro, relative to the northeast segment of the Sunda Shelf, may be just another island off of the Shelf and east of the 100 fathom line that was reached by a population of what is recognized as *R. tiomanicus* on islands of the Shelf.

According to Musser and Heaney (1985: 26), "*R. tawitawiensis* is more closely related to species of *Rattus* native to some islands beyond the Sunda Shelf than to any species living on the islands and peninsula of the Shelf." They also concluded that *R. tawitawiensis* shares some traits with samples of *Rattus* from the Nicobar Islands, Pulau Simalur and nearby islands, the Mentawai Islands, and Pulau Enggano. Other diagnostic features of the Tawitawi species point to a resemblance with *R. hoffmanni* from Sulawesi (Musser and Heaney, 1985; Musser and Holden, 1991). More information is needed to clarify the phylogenetic position of *R. tawitawiensis*, but judging from our study, neither *R. mindorensis* nor *R. everetti* can be identified as a close relative.

PHYLOGENETIC ALLIANCES AMONG THE GENERA IN DIVISION III

We have been able to define the species of *Tryphomys* and *Abditomys* as a cluster that is distinguished from the other genera by a set of derived traits. But we are unable to satisfactorily cluster any of the other genera in Division III using the features surveyed

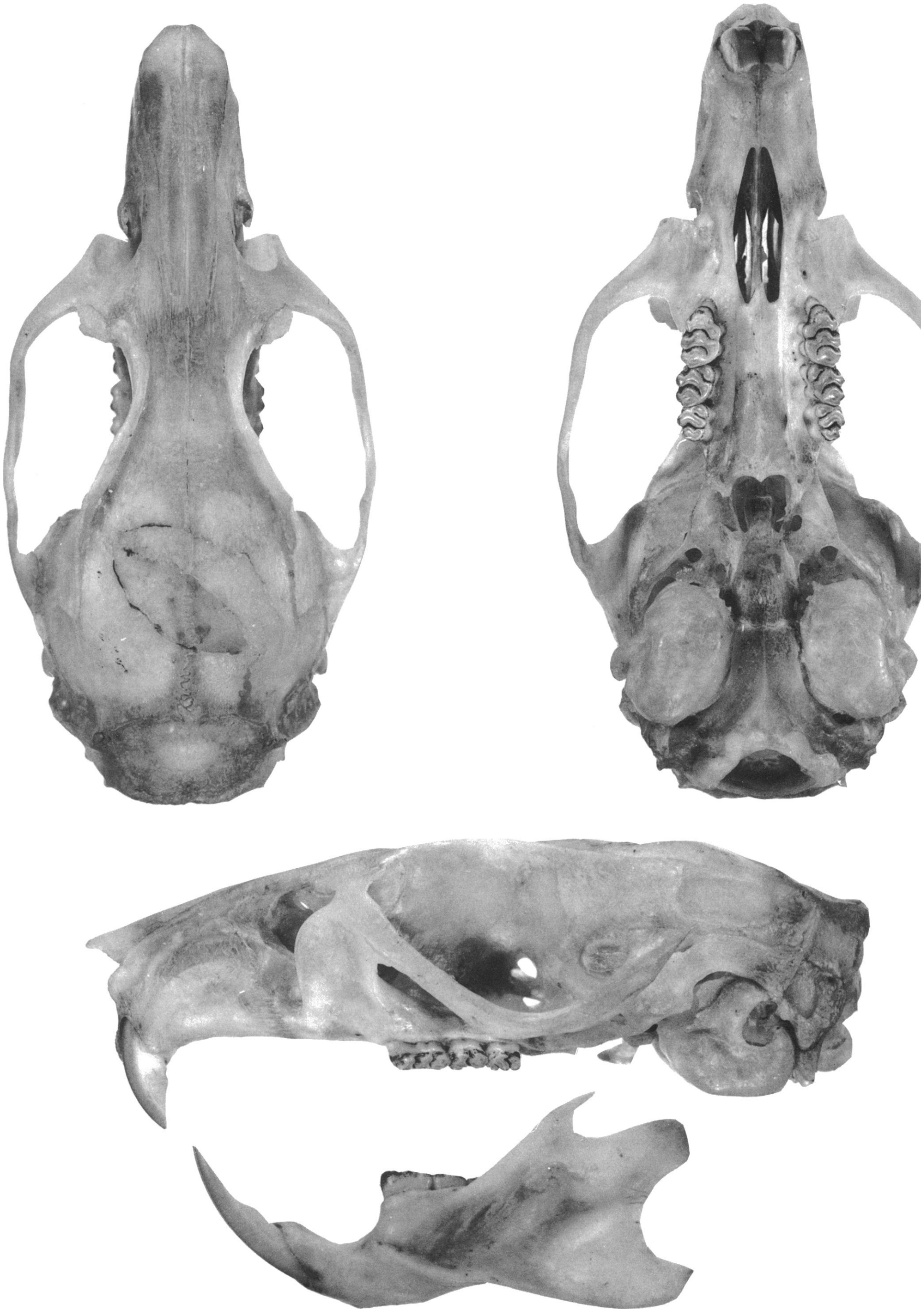

Fig. 77. Cranium and dentary (×2) of a *Rattus everetti* adult (AMNH 203315, female) from Mindanao.

for this report. At an earlier stage in our survey (see Heaney and Rickart, 1990) we identified certain derived traits that seemed to be shared among some genera but after more careful analysis we are skeptical of their use as synapomorphies, and suspect they may be homoplastic.

The potential clustering of *Bullimus* with *Tryphomys-Abditomys* is a good example. All three have wide zygomatic plates in which each anterior zygomatic spine projects so far forward it conceals a significant portion of the nasolacrimal capsule. However, whereas the spine is oriented in an anteroposterior axis in *Bullimus,* in the other two genera it is inflected toward the midline of the cranium. Furthermore, a wide zygomatic plate also characterizes *Tarsomys apoensis.*

Both *Bullimus* and *Tryphomys* have an elongate hind foot, but so do *Tarsomys* and *Limnomys.*

The auditory bulla in all three genera is large and globular, but it is more highly inflated in medial and lateral regions in *Tryphomys* and *Abditomys.* Furthermore, those two genera lack the ectotympanic shield and expansive posterior lamina of *Bullimus.*

No other derived traits of *Bullimus* (short tail that is either mottled or bicolored, elongate rostrum, long bony palate, and hypsodont molars consisting of rows of broadly joined cusps are examples) are shared with either *Tryphomys* or *Abditomys.*

Short tail, hypsodont molars, and derived molar occlusal patterns are shared by *Bullimus* and *Tarsomys,* particularly *T. apoensis,* and may indicate a closer relationship between these genera than between them and any other genus in Division III. This suggestion will have to be tested with additional characters in the context of a wider inquiry.

The species of *Tarsomys* and *Limnomys* share the same derived condition of mammae number and position (one postaxillary pair and two inguinal pairs); all the other species in Division III have eight to ten teats. The two genera also share long incisive foramina and a bony palate that extends past the molar rows, although not very far in *Limnomys.* Long incisive foramina and bony palate, however, are also characteristic of *Bullimus* and *Rattus.* We have been unable to identify any other derived traits which we could combine with the mammary feature to unambiguously define *Limnomys* and *Tarsomys* as a group.

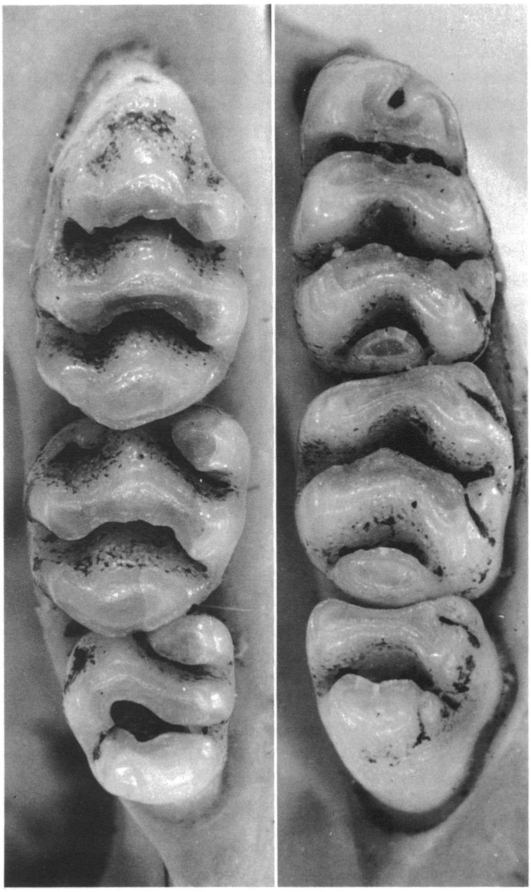

Fig. 78. Occlusal views (×12) of right upper and lower molars of *Rattus everetti* (AMNH 250040) from Luzon.

Rattus, as represented by the three native Philippine species we discussed (and even *R. tiomanicus* from Palawan) does not form a cluster with any of the other genera in Division III, at least in the context of the characters we surveyed in this preliminary assessment of phylogenetic patterns.

Analyses of data from different organ systems as well as molecular approaches may provide better resolution of relationships among the genera in Division III. At the same time a wider regional survey is required. Simply attempting to determine sister-group relationships among species within a regional fauna may generate misleading patterns. Could the species of *Tarsomys*, for example, be more closely related to something in the Moluccas, Sulawesi, or Nusatenggara than to any species occurring in the Philippines? The distributions of derived traits should not only be assessed among the Philippine New Endemics but also among the New Endemics in faunas native to that wide swath of continents and islands from southeast Asia to Australia. Below we provide a list of those species and their general region of occurrence. Many of them are now treated as species of *Rattus* but their diagnostic traits are unlike those characteristic of the core group of that genus; wherever they occur with a group of Old Endemics, their morphological relationship to that older stratum is much like the magnitude of differences seen between members of Divisions I and II and those of Division III on the Philippines. The list was extracted from publications (Taylor and Horner, 1973; Taylor et al., 1982; Watts and Aslin, 1981; Musser, 1981a, 1981b, 1986; Musser and Newcomb, 1983; Musser et al., 1986) and unpublished sources. Those taxa indicated as spp. will be described and documented in coming reports.

Australia
Rattus fuscipes, R. lutreolus, R. tunneyi

New Guinea Region
Rattus niobe, R. richardsoni, R. verecundus, R. vandeuseni (Taylor et al., 1982, treated this as a subspecies of *verecundus*), *R. praetor, R. mordax, R. steini, R. giluwensis, R. novaeguineae,* and *R. jobiensis*

Australia–New Guinea Region
Rattus leucopus and *R. sordidus* (treated as polytypic by Taylor and Horner, 1973, but as consisting of three species by Watts and Aslin, 1981)

Timor
Rattus spp.

Flores and Nearby Islands
Paulamys naso; *Hooijeromys nusatenggara*; *Papagomys armandvillei, P. theodorverhoeveni,* and *P.* spp.; *Komodomys rintjanus*

Sulawesi
Rattus xanthurus complex; *Paruromys dominator* and *P. ursinus*; *Bunomys chrysocomus, B. coelestis, B. andrewsi, B. heinrichi, B. penitus, B. fratrorum, B. prolatus,* and *B.* spp.; *Taeromys celebensis, T. taerae, T. arcuatus, T. hamatus, T. punicans, T. callitrichus,* and *T.* spp.

Moluccas
Rattus ceramicus, R. feliceus, R. morotaiensis, R. elaphinus, and *R.* spp.

Sunda Shelf
Rattus korinchi, R. hoogerwerfi, and *R. annandalei*; *Palawanomys furvus*; *Sundamys muelleri, S. infraluteus,* and *S. maxi*; *Kadarsanomys sodyi*

Christmas Island
Rattus macleari and *R. nativitatis*

Sri Lanka
Rattus montanus

We conclude that the following alternative hypotheses about relationships among the members of Division III require testing:

1. All the species are more closely related among themselves than to members of faunas outside the Philippine Archipelago. Our analyses resolved *Tryphomys* and *Abditomys* as sister groups but did not unequivocally uncover other clusters.
2. The *Tryphomys* group, as well as the other Philippine genera, are more closely related to species native to other regions than they are among themselves. The species of *Rattus* native to the Philippines are an example in that they are, at least in the morphological features we documented, clearly allied to species that comprise the core of *Rattus* and not to any of the other members of Division III on the Philippines.

Recognizing the second hypothesis defines a different perspective from which to view the origin and relationships of the species we assign to Division III. Rather than looking at the Archipelago as an entity, perhaps we should consider it a group of islands, some closer to and others more distant from the continental margins of southeast Asia. Murine species endemic to certain islands close to the continental margin may simply represent the past dispersal of continental ancestral stocks to those islands with or without significant morphological and genetic divergence. *Rattus mindorensis* and *R. tawitawiensis* are good examples. Other islands east of the continental margin may be large enough to have sustained phylogenetic diversification at some taxonomic level. The Luzon endemics *Tryphomys adustus* and *Abditomys latidens* illustrate this pattern. But it does not necessarily follow that members of the *Tryphomys* group should be more closely related to species on other large islands in the Philippine Archipelago, Mindoro or Mindanao, for example. Their phylogenetic diversity may reflect independent radiation from a different ancestral stock originally derived from the Asian mainland.

DISTRIBUTIONS

ALTITUDINAL PATTERNS

The original specimen labels attached to the skins of *Tarsomys echinatus* indicate the series was obtained between elevations of 2700 and 3700 ft; no other ecological information is available. Although our scanty knowledge of the mammals of Mt. Matutum does not permit comments on the community of small mammals in which *T. echinatus* occurs, we are able to provide some context by compiling data on the small mammals of Mindanao as a whole. We have gathered elevational records of insectivores and rodents directly from specimens we studied in the American Museum of Natural History, the British Museum (Nat. Hist.), Delaware Museum of Natural History, Field Museum of Natural History, and the National Museum of Natural History. Some of these records have been published, sometimes under different scientific names (Mearns, 1905; Hollister, 1913; Taylor, 1934; Sanborn, 1952, 1953; Musser 1982b, 1982c) but others have not.

The results (fig. 79) demonstrate a rich and varied small mammal fauna comprising 17 species ranging from sea level to above 2800 m. In four elevational intervals (above 2500 m is too poorly sampled to include), the pattern of species richness follows that described for flightless small mammals on mountains on Leyte (Heaney et al., 1989) and southern Luzon (Heaney and Rickart, 1990; Rickart et al., 1991), with species richness increasing substantially from sea level to the upper reaches of the mountains, and declining only at the highest levels. This is very different from the pattern shown, for example, by birds on tropical mountains (Goodman and Gonzales, 1990; Terborgh, 1977), and by fruit bats on Leyte, Luzon, and Negros (Heaney et al., 1989; Heaney and Rickart, 1990) in which species richness is greatest in the lowlands and declines progressively with increasing elevation.

Generalized altitudinal distributions of forest formations of the tropical Far East, as summarized by Whitmore (1984a: 155), fall into four primary zones: tropical lowland evergreen rain forest extends from lowlands to 1200 m (4000 ft), tropical lower montane rain forest forms a belt between 1200 and 1500 m (5000 ft), tropical upper montane rain forest occurs between 1500 and 3000 m (9900 ft), and tropical subalpine forest generally is found at 3000 m and higher. A simplified picture of the distribution of these formations that remain on Mindanao is provided in a vegetation map compiled by Whitmore (1984b). We have no first-hand experience with the forests on Mindanao and little information exists in the published literature except the general observations made by Hoogstraal (1951) during the Philippine Zoological Expedition of 1946–1947 and the scanty habitat information provided by Rand and Rabor (1960) in their account of the birds collected on Mount Malindang. Hoogstraal's categories of forest through which he and his team walked and in which they camped generally coincide with Whitmore's zones. For example, Hoogstraal noted that on Mount McKinley (a peak north of Mount Apo in the same mountain range), most of the forest had been removed up to about 3000 ft but "dense dipterocarpous" (p. 42) forest occurred near 3300 ft. Dipterocarps are part of the tropical lowland evergreen rain forest formation. Between 3800 and 4800 ft, Hoogstraal and his colleagues passed through "Intermediate Mountain Forest" (p. 44), which lacked dipterocarps, but contained many oaks, moss and lichens, all characteristic of tropical lower montane rain forest. "Mossy Forest" (p. 44) was encountered from 4800 to 8000 ft and here

> to say that it rained almost all the time during our several weeks' stay there is to state the situation quite literally. Not only the density of the moss-covered trees but the continuous clouds and haze make this forest so dark during the day that we often used our flashlights to collect. . . . From 4800 up to 6400 feet the mossy and epiphytic growth becomes increasingly heavier. Beginning at about the 6400-foot camp and extending to 7700 feet, the forest is considerably stunted except in well-protected valleys. One is usually climbing over or crawling under or slipping through a mass of soggy, moss-covered roots and tree trunks. Few of the trunks exceed a foot in diameter at eye level yet their mossy covering makes them appear to be from two to three feet in diameter.

Any field person would recognize this as tropical upper montane rain forest.

Rand and Rabor (1960: 275–276) recognized four primary zones on Mount Malindang. What they called "Lowland forest" originally extended up to 2500 ft but the area had been transformed to second growth and grass. "Three-story dipterocarp" forest still existed between 3000 and 3500 ft. "Transition forest" characterized the zone between 3500 and 5000 ft, which was "transition dipterocarp-mid-mountain forest, where the three-story character of the forest is no longer very distinct." Between 5000 and 6500 ft was "Mid-mountain forest," a "two-storied forest, lacking tall trees . . . Luxuriant epiphytes and mosses begin to grow on the tree trunks and branches . . . the type of forest at about 6200–6500 feet represents a sort of transition mid-mountain-mossy forest type, and the two-story character of the forest is no longer clearly shown." "Mossy forest" occurred from 6500 to near the summit, 7965 ft and was a forest of "low twisted trees, heavily covered with moss."

Apparently the diversity of species of insectivores and rodents is lowest both in lowland rain forest below 500 m and in upper montane forest above 2000 m, and highest in the interval between 500 and 2000 m, a zone encompassing the upper part of tropical lowland evergreen rain forest, all of tropical lower montane rain forest, and the lower portion of tropical upper montane rain forest (fig. 79).

Tarsomys echinatus appears to be a member of the upper section of the tropical lowland forest community. *Crunomys melanius* is the only other Mindanao endemic that has been found only in lowland habitats, and its altitudinal range overlaps that of *Tarsomys echinatus.* Records of *Apomys littoralis* are also primarily from lowland elevations and its known distribution more or less coincides with tropical lowland evergreen rain forest (see Heaney et al., 1989, for elevational data on this species on Leyte). Five other species (*Crocidura beatus, Exilisciurus concinnus, Sundasciurus philippinensis, Bullimus bagobus,* and *Rattus everetti*) range from lowlands up to montane forest formations.

Tarsomys apoensis has been recorded only from tropical lower and upper montane forest formations, and *Limnomys sibuanus* apparently inhabits upper montane forest if present specimens are a reliable index of its distribution (fig. 79). Other species that appear to be strictly montane in distribution are *Podogymnura truei, Crocidura grandis, Apomys hylocetes,* and *Batomys salomonseni.* Most records of *Apomys insignis* also come from montane localities.

Tarsomys echinatus shows no elevational overlap with its relative, *T. apoensis.* Another such pair of nonoverlapping species in the same genus is *Apomys littoralis* and *A. hylocetes,* and perhaps *Crocidura beatus* and *C. grandis.* In the case of the *Apomys,* both overlap to some degree with a third species, *A. insignis.* These two patterns—one genus with two species each occupying a different altitudinal forest formation, and one genus with three or more species in which some are confined to nonoverlapping altitudinal forest belts but do overlap with one or more widespread

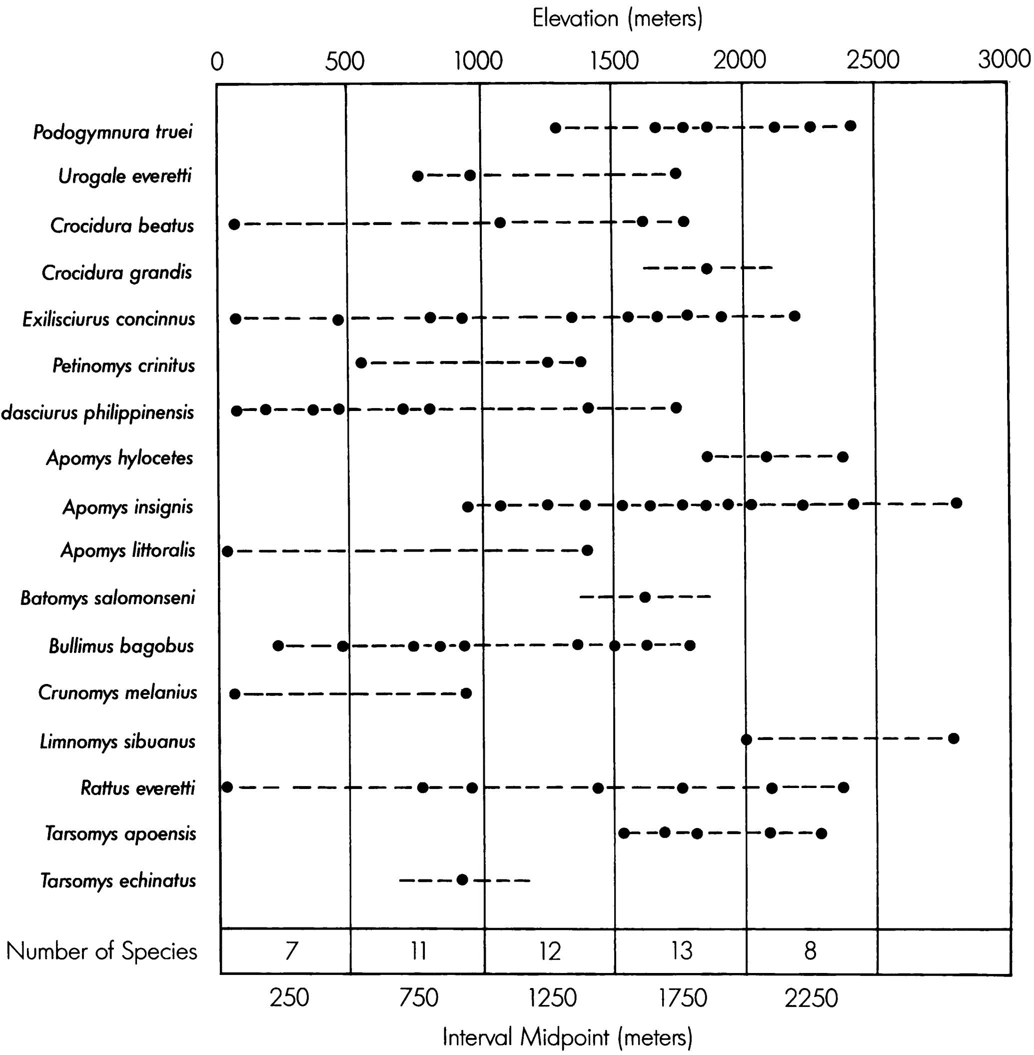

Fig. 79. The elevational distributions of insectivores, squirrels, and murine rodents that are indigenous to Mindanao. Large dots indicate elevations at which specimens were collected. Dashed lines represent hypothesized altitudinal distributions of species.

species—characterize the altitudinal distributions of rodents in other parts of the Far East; Sulawesi is an example (see Musser, 1987; Musser and Dagosto, 1987).

These altitudinal patterns must be viewed with caution. They reflect the acquisition of specimens made by expedition members whose primary task was to collect birds; trapping small mammals was a haphazard endeavor. Furthermore, some of the taxa are represented by very few specimens. *Crunomys melanius* is an example. We know it only by two specimens, one collected near sea level, the other at 3000 ft (Musser, 1982c: 10). It is a small rodent, elusive in habits, probably diurnal, and apparently not easily captured by the trapping techniques used so far. The two examples in museum collections may represent its real altitudinal range on Mindanao, but they may not. Our altitudinal statements about *C. melanius,* as well as the other endemic rodents, and the insectivores,

TABLE 8
Species of Murine Rodents Native to the Philippine Islands[a]

	Greater Luzon			Greater Mindoro			Greater Negros-Panay				Greater Mindanao										Greater Sulu
Genus and species	Marinduque	Luzon	Catanduanes	Mindoro	Ilin	Sibuyan	Tacao	Panay	Negros	Camiguin	Samar	Calicoan	Leyte	Dinagat	Siargao	Mindanao	Basilan	Bohol	Biliran	Maripipi	Tawi Tawi
DIVISION I																					
PHLOEOMYS GROUP																					
Phloeomys pallidus	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phloeomys cumingi	I	I	I	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
CRATEROMYS GROUP																					
Crateromys schadenbergi	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Crateromys paulus	—	—	—	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Crateromys sp.	—	—	—	—	—	—	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—
Crateromys australis	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—	—	—	—
Batomys granti	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Batomys dentatus	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Batomys sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—	—	—	—
Batomys salomonseni	—	—	—	—	—	—	—	—	—	—	—	—	I	—	—	I	—	—	I	—	—
Carpomys melanurus	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Carpomysphaerus	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
APOMYS GROUP[b]																					
Apomys datae	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Apomys abrae	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Apomys sacobianus	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Apomys musculus	—	I	—	I	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Apomys microdon	—	I	I	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Apomys sp. A	—	—	—	—	—	—	—	—	E	—	—	—	—	—	—	—	—	—	—	—	—
Apomys littoralis	—	—	—	—	—	—	—	—	—	—	—	—	I	I	—	I	—	I	I	—	—
Apomys insignis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—	—
Apomys hylocetes	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—	—
Apomys sp. B	—	—	—	—	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 8—(*Continued*)

	Greater Luzon			Greater Mindoro			Greater Negros-Panay				Greater Mindanao										Greater Sulu
Genus and species	Marinduque	Luzon	Catanduanes	Mindoro	Ilin	Sibuyan	Tacao	Panay	Negros	Camiguin	Samar	Calicoan	Leyte	Dinagat	Siargao	Mindanao	Basilan	Bohol	Biliran	Maripipi	Tawi Tawi
CRUNOMYS GROUP																					
Crunomys fallax	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Crunomys rabori	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—	—	—	—	—
Crunomys melanius	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—	—
Archboldomys luzonensis	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
CHROTOMYS GROUP																					
Chrotomys whiteheadi	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chrotomys mindorensis	—	I	—	I	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chrotomys gonzalesi	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Celaenomys silaceus	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
RHYNCHOMYS GROUP																					
Rhynchomys soricoides	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhynchomys isarogensis	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
DIVISION II																					
Anonymomys mindorensis	—	—	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 8—(*Continued*)

	Greater Luzon			Greater Mindoro			Greater Negros-Panay				Greater Mindanao										Greater Sulu
Genus and species	Marinduque	Luzon	Catanduanes	Mindoro	Ilin	Sibuyan	Tacao	Panay	Negros	Camiguin	Samar	Calicoan	Leyte	Dinagat	Siargao	Mindanao	Basilan	Bohol	Biliran	Maripipi	Tawi Tawi
DIVISION III																					
Tryphomys adjustus	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Abditomys latidens	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bullimus luzonicus	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bullimus bagobus	—	—	—	—	—	—	—	—	—	—	I	I	I	I	I	I	—	I	—	I	—
Tarsomys apoensis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—	—
Tarsomys echinatus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—	—
Limnomys sibuanus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—	—
Rattus everetti complex	—	I	I	I	—	—	I	—	—	I	I	I	I	I	I	I	I	I	I	I	—
Rattus mindorensis	—	—	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rattus tawitawiensis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E
New genus and species	—	—	—	—	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

[a] We exclude islands in Greater Palawan (see fig. 3). Records are based mostly on specimens we have examined; some are unpublished, the identity of others are documented in Thomas (1898); Miller (1910); Heaney and Rabor (1982); Musser, 1981a, 1982a, 1982b, 1982c; Musser and Gordon (1981); Musser and Freeman (1981); Musser and Newcomb (1983); Heaney (1984); Musser and Heaney (1985); Musser et al. (1985); Rickart et al. (1991); Heaney et al. (1991). We have not seen specimens of *Phloeomys cumingi* from Marinduque Island mentioned by Thomas (1898) and Steere (1890).

Abbreviations: —, unrecorded, either absent or not yet collected; E, endemic to a particular island; I, indigenous to the Philippine islands excluding those in Greater Palawan.

Rattus rattus mindorensis, R. rattus rattus, R. nitidus, R. norvegicus, R. exulans, and *Mus musculus castaneus* are found on many islands in the Archipelago, but we have omitted them from the list of native Philippine murines because all were most likely introduced by human intervention (Musser, 1977a).

[b] Identification of the *Apomys* from Negros, Leyte, and Dinagat differs from the picture presented by Musser (1982b) and is based on a more recent evaluation of old and newly acquired specimens (Heaney, in prep.).

must be taken as hypotheses, which can be tested only by a rigorous survey in the field.

Our assertion that diversity of species is less in the lowlands should also be received with a degree of skepticism. Through our readings of habitat accounts like those in Hoogstraal (1951) and Rand and Rabor (1960), and looking at Whitmore's (1984b) vegetation map, we have come to realize that virgin lowland forest throughout most of Mindanao has been removed and its place has been taken by cultivated land, secondary forest and scrub, grasslands, and forest plantations. Any rodents and insectivores closely tied to lowland forest habitats may no longer be present or may be living in remnants of lowland forest that have not yet been surveyed. Rigorous field surveys are badly needed.

INSULAR PATTERNS

Mindanao has a fauna of native flightless mammals that is second in the Philippines only to that of Luzon, with 25 on Mindanao and 29 on Luzon (Heaney, 1986, including *Tarsomys echinatus* as "*Rattus* sp. nov."; and one new rodent on Luzon, *Chrotomys gonzalesi,* table 8). Among murine rodents, *Limnomys* and *Tarsomys* are the only two genera endemic to Mindanao, in contrast to Luzon, which has six (*Abditomys, Archboldomys, Carpomys, Celaenomys, Rhynchomys,* and *Tryphomys*). There are nine species of flightless mammals endemic to Mindanao, in contrast to the 22 species that occur only on Luzon (Heaney, 1986). This reckoning makes clear both that Mindanao supports a high level of endemism, and that it lags far behind its neighbor to the north.

In other respects the mammal fauna of Mindanao takes on a more distinctive aspect. If we consider the probable limits of islands during the Pleistocene (fig. 3), it is clear that modern Mindanao is simply the core of a formerly larger island, just as modern Luzon is the core of a larger Pleistocene island. If we consider the mammals from Greater Mindanao and Greater Luzon, we see that 26 of 33 species (79%) of flightless native mammals on Greater Mindanao are endemic, versus 23 of 29 species (79%) on Greater Luzon. Thus, taken in a historical context, the fauna of Greater Mindanao exceeds that of Greater Luzon in diversity of species but has the same level of endemism. Judged by the very few species shared between these two historically defined islands, the faunas of the two are clearly independent of one another, at least in distributions of modern species.

The evidence that *Limnomys* and *Tarsomys* are not closely related to any Luzon endemics that are also members of Division III, namely *Tryphomys* and *Abditomys,* reinforces this pattern of independence since it implies that the two genera and three species have undergone phylogenetic diversification on Mindanao, quite independently of the rodents of Luzon. This pattern of localized diversification is increasingly apparent in the mammalian fauna of the Philippines (Heaney and Rickart, 1990; Heaney, 1991), as well as Sulawesi (Musser, 1982c, 1987, 1991) and should be sought elsewhere in insular southeast Asia.

The species endemic to Mindanao tend to be found at high elevations in tropical montane forest formations, including *Podogymnura truei, Crocidura grandis, Apomys hylocetes, Limnomys sibuanus,* and *Tarsomys apoensis. Tarsomys echinatus* and *Crunomys melanius* appear to be the sole exceptions to this pattern. In general, species of Philippine mammals that occur in lowland forest tend to be widespread, at least within their Pleistocene landbridge group of islands (Heaney, 1986; Heaney and Rickart, 1990). However, the middle elevational range of 2700 to 3700 ft brackets the altitudinal origin of the sample of *T. echinatus* and either this is high enough to serve as an effective ecological barrier to wider distribution at lower elevations, or some unique ecological feature confines them to this, or the species also occurs at lower elevations elsewhere but has not yet been caught there. New field surveys in the lowlands and middle elevations of Mindanao are needed to determine the actual altitudinal range of this spiny *Tarsomys.*

The lowland endemism of *C. melanius* on Mindanao may be an artifact. The sample consists of two young rats. Their morphology is very similar to that of *C. rabori* from Leyte, which is represented only by an old adult; the differences between the two samples could reflect only age and slight differentiation due to insular but not genetic isolation (Musser, 1982c). If that proves to be correct then *C. melanius* would also have a wide distribution within the Greater Mindanao group of islands. This hypothesis deserves testing by field studies.

CONCLUSIONS

The murine rodents of the Philippines (excluding Greater Palawan) represent a spectacular series of species. In body size, the range extends from the mouse-sized *Apomys musculus* to the giant species of *Phloeomys*. Many are strictly terrestrial (the species of *Crunomys* and *Tarsomys*, for example); others are scansorial (some species of *Apomys*); and some, like the giant furry-tailed *Crateromys schadenbergi* that builds stick nests in crowns of oak and pine, are highly arboreal. Some species are diet generalists (*Rattus everetti*), others are primarily folivores (the species of *Phloeomys* and *Crateromys schadenbergi*, for example), and other species are vermivorous (members of *Archboldomys, Chrotomys*, and *Rhynchomys*). Associated with the range of habits among the rodents are definite morphologies: the mouselike *Apomys* and *Crunomys*, for example; the squirrellike *Crateromys* and *Carpomys*; the phalangerlike *Phloeomys*; the shrewlike *Archboldomys, Chrotomys, Celaenomys*, and *Rhynchomys*; and many species that are ratlike. With each discovery of a new species, the diversity becomes more impressive for its richness as well as its morphological and ecological range.

As we have shown here and in our other studies, the endemic portion of this diversity includes all of the species and most of the genera of Philippine murine rodents. Many of the genera occur only on one of the modern islands, and few occur on more than one of the larger Pleistocene islands that define the modern faunal regions within the Archipelago. Thus, the diversity is highly localized, and this emphasizes the uniqueness of the fauna at all geographic levels.

Beyond this local diversity, our present study has shown that within the fauna are groups of genera that almost certainly form monophyletic entities. Although we do not formally recognize them as higher taxonomic units, they nevertheless emphasize that the murine fauna is not formed simply of scattered bits of the Asian or Australasian murine fauna, but rather of a series of taxa that have originated and undergone extensive morphological and ecological diversification in the Philippines. We have also presented a series of hypotheses that examine the possibility that these monophyletic units may unite to form still larger monophyletic groups. Taken in sum, these data suggest that the murine fauna of the Philippines is derived from a small (and perhaps very small) number of successful invaders from adjacent land masses, and that the spectacular array of species we see today is, at any but the most basal level, an entirely local phenomenon. If this is the case, the Philippine murines surely rival the classic cases of local adaptive radiation among terrestrial vertebrates, such as the tenrecs of Madagascar or Darwin's finches in the Galapagos, in richness and diversity. As such, more extensive study of their species richness, phylogenetic relationships, biogeography, ecology, and conservation is clearly warranted. Indeed, these animals suggest that such localized radiations of rodents may characterize the other large islands and archipelagos of the Indo-Australian region, demonstrating the need for increased efforts to understand their evolution in that most geographically diverse portion of the world.

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