

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 2746, pp. 1-43, figs. 1-19, tables 1-8 September 22, 1982

Results of the Archbold Expeditions. No. 108. The Definition of *Apomys*, a Native Rat of the Philippine Islands

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ABSTRACT

Apomys Mearns (1905) contains eight species native to the backbone of islands in the Philippine archipelago. The genus was recognized for more than 40 years after it was described, then merged with *Rattus*, and later reinstated as distinct from *Rattus*. Throughout this period, the morphological

boundaries of the group remained vague, the diagnosis nonexistent, and the contents nebulous. *Apomys* is defined here, the species in it are discussed, and the contrasts between it and *Rattus* are outlined.

INTRODUCTION

Apomys is the name proposed by Edgar A. Mearns in 1905 for a group of species living in forest high on Mount Apo on Mindanao Island in the Philippines. Mearns described three species; additional samples from Mindanao and other Philippine islands were later named and described as species by Miller (1910), Hollister (1913), Sanborn (1952), and Johnson (1962). For more than 40 years mammalogists recognized *Apomys* as a genus but in the late 1940s Ellerman (1947-1948, 1949) reduced it to a subgenus of *Rattus*. This arrangement was followed by Sanborn (1952, 1953) but rejected by Johnson (1962) and Misonne (1969). Such shuffling clouded the identity of *Apomys*. The group was always associated with the Philippine Islands (excluding Palawan and nearby islands, the Calamian group, and the Sulu Archipelago) but whether they formed a distinct assemblage, belonged in *Rattus*, or were more closely al-

lied to other genera either native to the Philippines or from elsewhere was not known.

The problem of identifying *Apomys* really began when Mearns' report was published. So general was his description and undistinguished his characterization that the morphological boundaries of the genus were vague from the start and the diagnostic traits obscure. Subsequent attempts between 1905 and now to either recognize *Apomys* or merge it with *Rattus* were always based on a few characters, primarily those associated with occlusal patterns of the molars. Ellerman (1947-1948) used the molar patterns to unite *Apomys* with *Rattus*; Johnson (1962) and Misonne (1969) used those same traits to disassociate the genus from *Rattus*. What is *Apomys*?

I answer that question by combining description with illustration to outline the morphological boundaries of the genus and dis-

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tinguish it from *Rattus* and certain other genera to which it has been allied. To know what *Apomys* is, and what it is not, is prerequisite to seeking its phylogenetic relationships with the rest of the native Philippine fauna and with faunas from other archipelagos in the Far East. That aspect will be the subject of a later report.

ABBREVIATIONS, MATERIALS, AND METHODS

MATERIALS: Specimens I refer to are in collections of the American Museum of Natural History, New York (AMNH); the British Museum (Nat. Hist.), London (BMNH); the Delaware Museum of Natural History, Delaware (DMNH); the Field Museum of Natural History, Chicago (FMNH); the University of Minnesota Bell Museum of Natural History, Minneapolis (MMNH); Staatliches Museum für Tierkunde, Dresden (SMT); the University of the Philippines at Los Baños, Luzon (UPLB); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Accounts of the species of *Apomys* are based on specimens I examined and cited by museum numbers. Because so many specimens have been misidentified either in museum collections or in the literature, especially those from Luzon, I do not discuss any examples whose identity I could not verify by firsthand study.

Sexes were combined in the samples. Values from measurements of adults only are listed in the tables and were used in the analyses. To obtain adequate sample sizes, I included all specimens ranging from young adults (molars moderately worn, molt completed from juvenile to adult pelage) to old adults (molars well worn, sometimes to their bases). Comparisons of age, individual, and secondary sexual variation among samples of *Apomys* will be the task of future workers who have larger samples from more places and who wish a finer resolution of intra-island and inter-island population variation than I provide.

MEASUREMENTS: Values from measurements are in millimeters, those from body weights in grams. Figures for total length, length of tail (LT), length of hind foot (LHF), length of ear (LE), and body weight (W) are

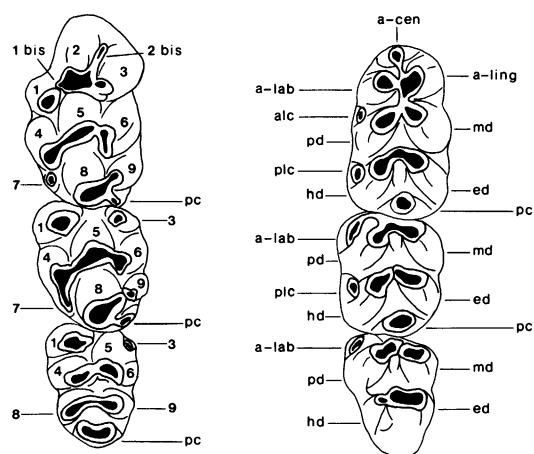


FIG. 1. Terminology of dental structures using right upper and lower molars of *Lenothrix canus*. Upper molars: cusps are numbered according to Miller's (1912) scheme and are referred to in text with the prefix t; pc, posterior cingulum. Lower molars: a-cen, anteroventral cusp; a-lab, anterolabial cusp; a-ling, anterolingual cusp; pd, protoconid; hd, hypoconid; md, metaconid; ed, entoconid; pc, posterior cingulum; alc, anterior labial cusplet; plc, posterior labial cusplet.

those recorded on labels attached to skins. I subtracted length of tail from total length to obtain length of head and body (LHB). Cranial and dental measurements were taken with dial calipers graduated to tenths of millimeters. Limits for greatest length of skull (GLS), zygomatic breadth (ZB), interorbital breadth (IB), breadth of braincase (BBC), height of braincase (HBC), alveolar length of maxillary toothrow (LM^{1-3}), and breadth of first upper molar (BM^1), the measurements used here, are defined in Musser (1970).

TEETH: The terminology I use to describe positions of cusps on upper molars (fig. 1) is a slight modification of the numbering system developed by Miller (1912). The nomenclature for lower molars (fig. 1) is with slight deviations that used by van de Weerd (1976, p. 44). See Musser (1981a) for details.

BONES AND CRANIAL FORAMINA: Descriptions of skins, skulls, and teeth and comparisons of these elements among genera comprise this report. Information from other sources—such as morphology of muscles and gastrointestinal organs, reproductive systems, chromosomes, biochemical and genetic studies, and even postcranial skeletons—are

not used because those kinds of data are unavailable for most specimens of *Apomys*. Nowadays most species of native Philippine rats are known only by a stuffed skin, cranium, mandible, incisors, and molars. But these remnants of the living species if examined carefully, intently, and perceptively in relevant context are a rich source of information which can be used to divine relationships between morphology and environment and test hypotheses of phylogenetic relationships.

Crania and occlusal patterns of molars are especially important. Characteristics of the molars have been used more often than cranial features in assessing relationships between *Apomys* and other genera (see Misonne, 1969, for example). Descriptions of crania and mandibles are available in the literature (Mearns, 1905; Taylor, 1934; Ellerman, 1941; Sanborn, 1952) but the contents reflect superficial examinations. A general outline of size and shape of the skull, along with expositions of a few features the viewer thought important is the substance of most descriptions. Missing are details of the orbit, the alisphenoid area, the pterygoid complex, and the auditory region. These places are significant because the configurations there of foramina and associated bones, due to the nature of their variation among species of *Apomys* in particular and murids in general, are revealing in determining relationships.

Descriptions and illustrations of skulls as well as closeups of the orbit, alisphenoid region, auditory area, pterygoid complex, and palatal region are provided in this report. The bones, foramina, and arterial patterns depicted in those figures are labeled with abbreviations explained in the text. Their identifications are based on my readings of conventional sources such as Greene (1935) and Hill (1935, 1937), and more recent studies by Rinker (1954), Guthrie (1963), Klingener (1968), Bugge (1970), Wahlert (1974, 1978), and Carleton (1980). My own dissections were confined to sporadic probes in fluid-preserved specimens and incompletely cleaned skulls to check details of arterial circulation and foramina position that I could not comprehend from published descriptions or that turned out to be undescribed in the literature.

ACKNOWLEDGMENTS

I am grateful to all curators in charge of the museum collections for allowing me access to specimens and other materials. I especially appreciate the efforts of Dr. Alfred S. Feiler and Konservator Siegfried Eck of Dresden who lent me the holotype of *Mus datae*, and to Dr. Lawrence R. Heaney who provided some of his research materials. Figure 1 was drawn by Ms. Christine Miller, figures 2 and 7 by Ms. Patricia Wynne. Most of the photographs are the excellent work of Mr. Peter Goldberg and Mr. Jim Coxe. Dr. Alfred Gardner photographed the holotype of *A. sacobianus*. Mr. Robert J. Koestler operated the Scanning Electron Microscope; the resulting negatives were developed and printed by Mr. Richard Sheryll. I thank all these talented persons for their fine results. Mrs. Frances A. Hufty of Archbold Expeditions Inc. has continued to support portions of my research.

GENUS *APOMYS* MEARNS (1905)

TYPE SPECIES: *Apomys hylocetes* Mearns (1905, p. 456). The holotype is the skin and skull of an adult female (USNM 125246). The rat was collected by E. A. Mearns at 6000 feet on Mount Apo in the southern part of Mindanao Island, the Philippines, on July 2, 1904. The generic name derives from combining Apo, the name of the mountain, with *mys*, the Greek suffix for mouse.

DISTRIBUTION: Known from the Philippine Islands of Luzon, Catanduanes, Mindoro, Leyte, Dinagat, Mindanao, and Negros. Species of *Apomys* probably occur on other islands in the backbone of the archipelago but not on the Calamian Islands, Palawan and adjacent islands, or the Sulu Archipelago. Members of the genus have been collected at altitudes ranging from coastal plain to mountaintop.

DIAGNOSIS: *Apomys* is distinguished from *Rattus* and all other genera of murid rodents by the following combination of features: habitus terrestrial or scansorial; body size small; tail equal to or much longer than combined lengths of head and body; fur soft and thick; hind feet long and narrow, plantar pads six; mammae four, all inguinal; interorbital

region wide; margins of interorbital and post-orbital areas rounded, without ridges or shelves; braincase smooth and round; interparietal short (front-to-back) and wide (side-to-side), its posterior two-thirds roofing an expanded occiput; anterior spines of zygomatic plates slight or absent; squamosal roots of zygomatic arches originate low on braincase; alisphenoid region usually with lateral strut of alisphenoid bone separating foramen ovale accessorius from coalesced buccinator-masticatory foramina; alisphenoid canal medial to strut not separated from masseteric and buccinator branches of maxillary nerve by a bony roof; incisive foramina short and wide, their posterior edges not extending between molar rows; palatal bridge wide and long, ending slightly behind toothrows, ventral surface densely pitted and fenestrated, posterior margin truncate and ridged; mesopterygoid fossa nearly as wide as palatal bridge, sphenopalatine vacuities short; pterygoid fossa wide and shallow, outlined by ridges, large sphenopterygoid openings in anterior portion; pterygoid platform at level of foramen ovale smooth and rounded, not ridged; stapedial foramen tiny in all but one species, pattern formed by internal carotid, stapedial, and internal maxillary arteries like configurations A and B in figure 2; stapedial foramen large in one species, arterial pattern like configuration C in figure 2; bullae small, loosely attached to braincase, postglenoid vacuity and middle lacerate vacuity very large; eustachian tube long and cylindrical; squamoso-mastoid foramen small to large, separating posterior portion of squamosal into two parts; incisors orange, uppers orthodont; molars brachyodont; first upper molars usually three-rooted; first lower molars two-rooted; third upper and lower molars overlapped by the second, second molars overlapped by the first; first and second upper molars long and narrow, third relatively much smaller and peglike, without cuspidation except for small cusp t1; occlusal surfaces of upper molars simple (cusp t1 on first molar not evident, no cusp t7 or posterior cingulum on any molars, usually no cusp t3 on second or third molars, cusp t9 of first and second molars indistinct); occlusal surfaces of lower molars simple (no anterolabial cusps on second and third molars, no labial cusplets

on any molars); anterior lamina small and fused with second lamina on each first lower molar to form inverted heart-shaped structure (in occlusal outline).

THE SPECIES OF *APOMYS*

I was able to study enough skins and skulls, including those of all holotypes, to define the morphological limits of eight species: *A. datae*, *A. abrae*, *A. sacobianus*, *A. musculus*, *A. hylocetes*, *A. insignis*, *A. microdon*, and *A. littoralis*. They occur on seven Philippine islands where, except for Luzon and Mindanao, there is but one species known from any island (table 1). Where more than one species has been taken from any given place on either Luzon or Mindanao, no more than two have been recorded as sympatric (table 2). All the species dwell in forests. All are either terrestrial or scansorial. All have soft fur, long and narrow hind feet, six plantar pads, and two pairs of inguinal mammae. All are closely similar to one another in dental features and most characteristics of crania and mandibles. So alike are specimens that I used body size as a primary distinguishing feature to separate the species into three groups: large body size, medium, and small. The skulls of *A. datae*, *A. insignis*, and *A. musculus* featured in figure 8 illustrate these categories.

Those three divisions, however, do not reflect phylogenetic relationships. After more careful study of the crania, I discovered that the species could be sorted into two major

TABLE 1
Known Insular Distribution of *Apomys*

Species	Island						
	Luzon	Mindoro	Catanduanes	Leyte	Dinagat	Mindanao	Negros
<i>A. datae</i>	+	-	-	-	-	-	-
<i>A. abrae</i>	+	-	-	-	-	-	-
<i>A. sacobianus</i>	+	-	-	-	-	-	-
<i>A. musculus</i>	+	+	-	-	-	-	-
<i>A. microdon</i>	-	-	+	+	+	-	-
<i>A. insignis</i>	-	-	-	-	-	+	-
<i>A. hylocetes</i>	-	-	-	-	-	+	-
<i>A. littoralis</i>	-	-	-	-	-	+	+

TABLE 2
Known Sympatry between Species of *Apomys*

Species Sympatric	Island	Place	Elevation
<i>A. datae</i> <i>A. abrae</i>	Northern Luzon	Mt. Data Hights-in-the-Oaks	5300–8200 feet 7000 feet
<i>A. abrae</i> <i>A. musculus</i>	Northern Luzon	Baguio, Camp John Hay	5000 feet
<i>A. hylocetes</i> <i>A. insignis</i>	Eastern Mindanao	Mt. Apo	6000 feet

groups based on configurations of the pterygoid and bullar regions, shapes reflecting different patterns of arterial circulation in the basicranium. One, which I refer to as the *datae* pattern, is found only in *Apomys datae*, one of the largest bodied of the species. The other, which I call the *abrae-hylocetes* pattern, occurs in all the other species.

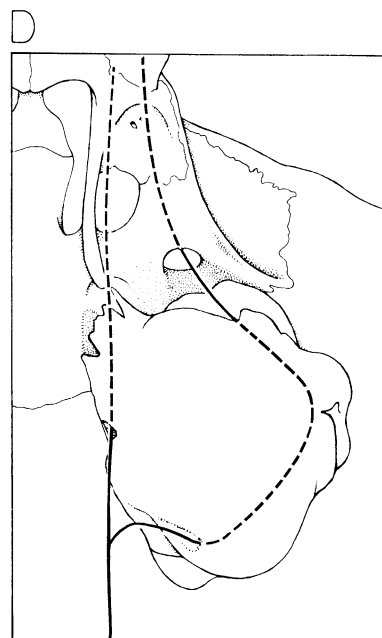
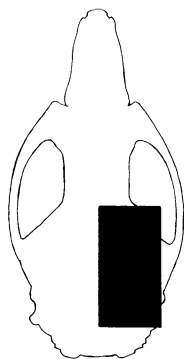
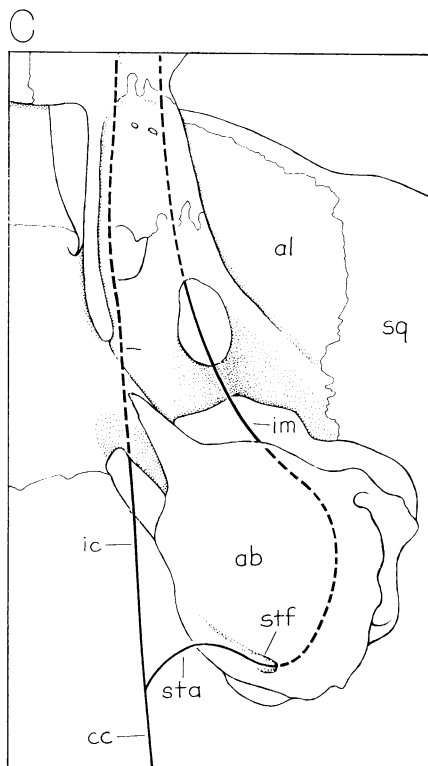
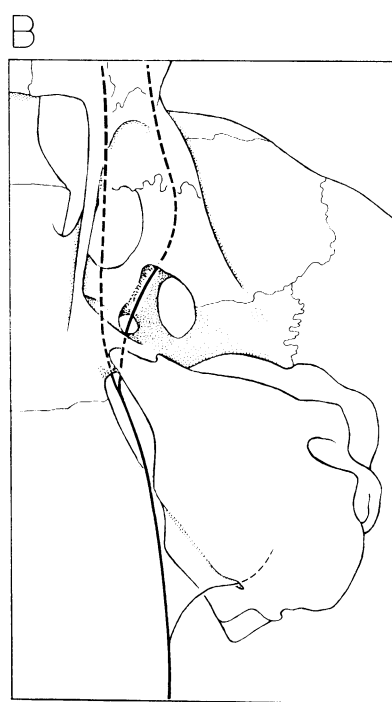
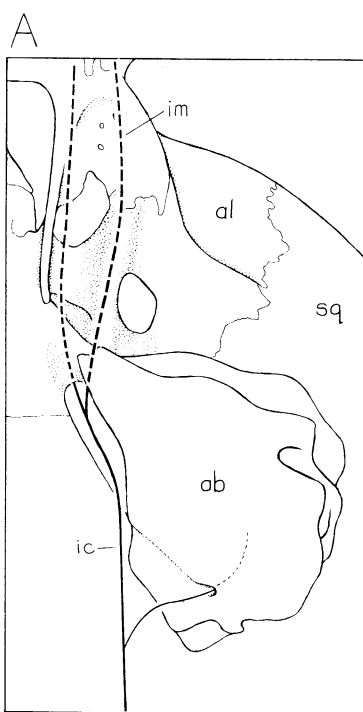
The *datae* pattern is illustrated in figure 2C. As seen from a ventral view, the common carotid artery gives off a large stapedal artery near the posterior margin of each bulla, then extends anteriorly as the internal carotid artery to pass through the carotid canal (fig. 3B) between the anterolateral margin of the basioccipital bone and the bulla and enters the cranial cavity where it passes forward beneath the brain. The stapedal artery enters the bulla through a long channel and wide stapedal foramen (which can be seen without magnification) between the bullar capsule and petrosal portion of the petromastoid bone. The artery courses through the otic region within the bulla to emerge from the spacious middle lacerate foramen (also called the foramen lacerum) as the internal maxillary artery (called the pterygopalatine artery by Greene, 1935, p. 248), which runs onto the pterygoid plate in a wide groove to disappear anteriorly beneath the pterygoid platform above the foramen ovale. The place where the artery disappears beneath the platform is the posterior opening of the alisphenoid canal (fig. 3A). The internal maxillary artery continues anteriorly in the canal and passes through the anterior opening of the alisphenoid canal into the sphenoidal fissure and then the orbit.

In the *datae* configuration, the internal maxillary artery is the continuation of a large stapedal artery, the common pattern in mu-

rids according to Hill (1935); the stapedal foramen is large and conspicuous; and there is a wide groove in the pterygoid plate between the medial lacerate foramen and the foramen ovale, a groove containing the internal maxillary artery. The pattern is similar to that found in *Rattus* (figs. 2D and 3A) and most other species of murids. It is characteristic of every specimen of *A. datae* that I examined. It is also in *A. datae* that the alisphenoid strut, which forms the lateral wall of the alisphenoid canal at the base of the braincase, is absent from half the specimens in the sample; the strut is usually present in nearly all specimens of the other species (table 8).

The *abrae-hylocetes* arterial pattern, illustrated in figure 2A and B, occurs in all the species of *Apomys* except *A. datae*. In this configuration, the common carotid gives off a very small stapedal artery that passes through a tiny and inconspicuous stapedal foramen (seen only with magnification) into the otic region where it ends. The internal maxillary artery is not a continuation of the stapedal and does not emerge from the bulla through the middle lacerate foramen. Instead, the internal maxillary artery branches off the internal carotid just after the latter passes into the cranial cavity through the carotid canal. The internal maxillary, which is large and conspicuous, courses diagonally in a groove or partially enclosed tube within the alisphenoid wing of the pterygoid plate from the posteromedial corner of the plate past the foramen ovale and the alisphenoid strut to the anterior opening of the alisphenoid canal where it passes into the sphenoidal fissure and then the orbit.

The ventral surface of the pterygoid plate is complete in some specimens and in a ventral view of the cranium the groove or canal



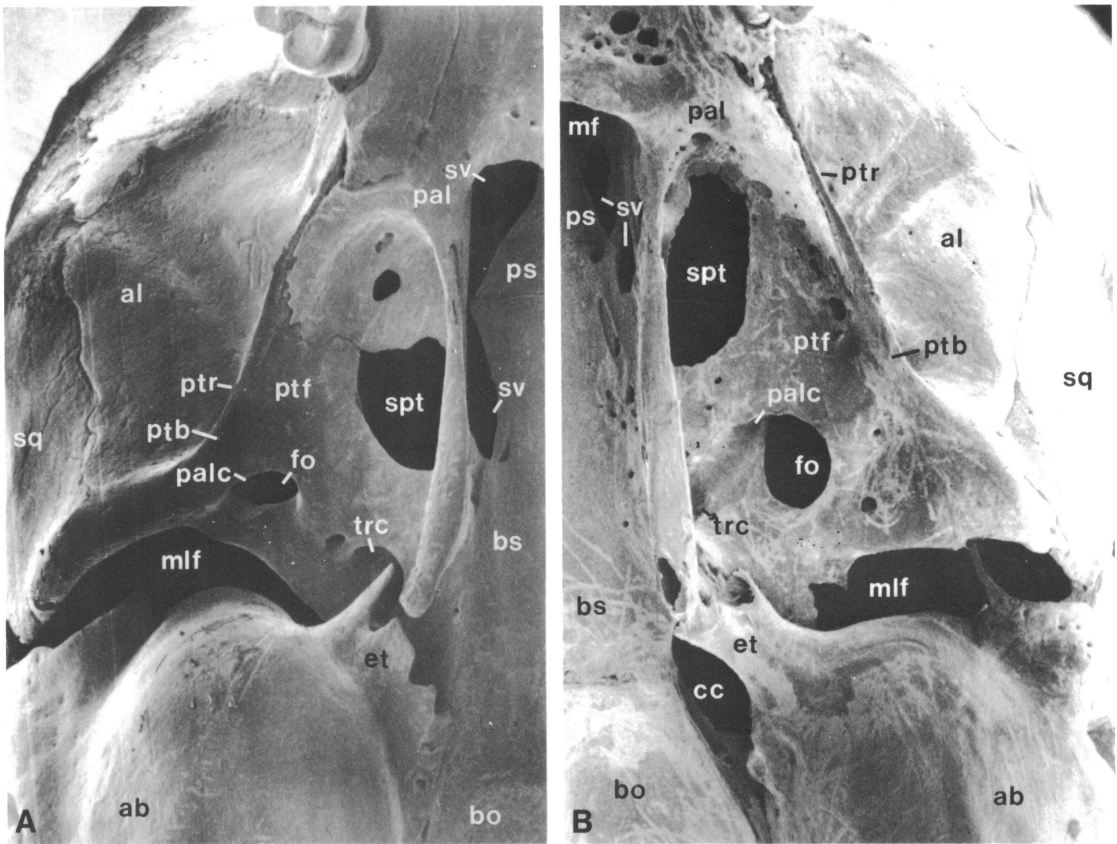


FIG. 3. Views of the pterygoid and mesopterygoid regions in adult *Rattus* and *Apomys*. A, *R. exulans* (AMNH 223141) is contrasted with *A. insignis* (AMNH 207571).

B. Abbreviations: **ab**, auditory bulla; **al**, alisphenoid bone; **bo**, basioccipital bone; **bs**, basisphenoid bone; **cc**, carotid canal; **et**, bony eustachian tube; **fo**, foramen ovale; **mf**, mesopterygoid fossa; **mlf**, middle lacerate foramen; **pal**, palatine bone; **palc**, posterior opening of the alisphenoid canal; **ps**, presphenoid bone; **ptb**, pterygoid bridge; **ptf**, pterygoid fossa; **ptr**, pterygoid ridge; **sq**, squamosal bone; **spt**, sphenopterygoid vacuity; **sv**, sphenopalatine vacuities; **trc**, transverse canal. See text and figure 2 for further comparisons and descriptions, also Hill (1935), Wahlert (1974), and Musser (1981a).

containing the internal maxillary artery is hidden beneath the plate (fig. 2A). The course of the canal is indicated by a slight diagonal ridge (sometimes the dark outline of the ar-

tery can be seen beneath the bone in incompletely cleaned skulls). The posterior opening of the alisphenoid canal is the spot where the groove or canal begins at the posteromedial

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FIG. 2. Diagrams of carotid arterial patterns in *Apomys* and *Rattus*. A: configuration in *A. abrae* and *A. sacobianus*. B: pattern and bony features in *A. musculus*, *A. microdon*, *A. insignis*, *A. hylocetes*, and *A. littoralis*. C: configuration in *A. datae*. D: pattern typical of *Rattus exulans* and muroid rodents in general.

Abbreviations: **ab**, auditory bulla; **al**, alisphenoid bone; **cc**, carotid canal; **ic**, internal carotid artery; **im**, internal maxillary artery; **sq**, squamosal bone; **sta**, stapedial artery; and **stf**, stapedial foramen. Names of other foramina and bones are indicated in figure 3 on facing page. See text for detailed descriptions of different patterns and bony configurations.

TABLE 3
**Presence or Absence of a Complete or Open Canal
 for the Internal Maxillary Artery in the Pterygoid
 Plate of *Apomys***
 (expressed in percentage; number of specimens in
 parentheses)

	Alisphenoid Canal in Pterygoid Plate		
	Complete (fig. 2A)	Open (fig. 2B)	Left Side Complete, Right Side Open
<i>A. abrae</i>	97 (34)	—	3 (1)
<i>A. sacobianus</i>	100 (1)	—	—
<i>A. musculus</i>	—	100 (9)	—
<i>A. insignis</i>	2 (2)	94 (80)	4 (3)
<i>A. hylocetes</i>	—	100 (3)	—
<i>A. microdon</i>	—	100 (31)	—
<i>A. littoralis</i>	—	80 (4)	20 (1)

corner of the plate just after the internal maxillary artery branches from the internal carotid. This variant is typical in most specimens of *A. abrae* and *A. sacobianus* (table 3).

In most specimens of *A. musculus*, *A. hylocetes*, *A. insignis*, *A. microdon*, and *A. littoralis* (table 3) the canal or partial tube is open for part of its length, from the postero-medial corner of the pterygoid plate diagonally to the anterior margin of the foramen ovale, where the internal maxillary artery is exposed (as seen from a ventral view; fig. 2B). The spot where the canal and artery pass beneath the pterygoid plate (medial to and at the anterior margin of the foramen ovale) is the posterior opening of the alisphenoid canal (fig. 3B).

In the *abrae-hylocetes* pattern, the stapedial artery is minute, serving the otic capsule within the bulla; the stapedial foramen is tiny and inconspicuous; no large artery emerges from the middle lacerate foramen onto the posterior part of the pterygoid plate; the plate is smooth and without a wide groove from the middle lacerate foramen to the foramen ovale; and the internal maxillary artery is not a continuation of the stapedial but a branch of the internal carotid artery and passes in a groove or partial tube through the alisphenoid wing of the pterygoid plate. This arterial pattern and the bony configuration associated with it occurs in every specimen examined of *A. abrae*, *A. sacobianus*, *A. mus-*

culus, *A. hylocetes*, *A. insignis*, *A. microdon*, and *A. littoralis* except one *A. insignis* (USNM 125233) which had a configuration like that in *A. datae*. The arterial pattern depicted in figure 2A and B is usually associated with an alisphenoid strut (fig. 13B; table 8).

Below, I discuss the species in each of the two groups. The exposition is a sketch, not a complete taxonomic revision. My outline of morphological species-limits should be taken as a hypothesis to be tested by additional specimens from different places and by larger samples of certain species.

THE *Apomys datae* GROUP

Apomys datae: This species occurs in the western highlands of Mountain Province in northern Luzon. Specimens I examined are from Mount Data, 5300–8300 feet (SMT B.3100; FMNH 62695, 62696, 62699, 62709, 62711, 62712, 62720, 62725, 62727, 62731, 62733–62735, 62741, 62742, and 62744) and Benguet, Hights-in-the-Oaks, 7000 feet (USNM 151513).

One of the largest-bodied species of *Apomys*, *A. datae* is a terrestrial rat with a chunky head and body and a tail as long or slighter longer than the combined lengths of head and body (table 6). The thick and soft fur over the upperparts is rich dark brown with burnished highlights, that on the underparts is dark grayish white. The top of each hind foot is brown over its basal half and white on the rest, including the digits. The tail is brown above and dirty white below from base to tip. The cranium is large, with a squarish braincase (fig. 4b). The configuration of the pterygoid and bullar regions as well as the arterial circulation in those areas is unlike any other species of *Apomys* (fig. 2). An alisphenoid strut is absent from 50 percent of the specimens examined (table 8).

The name *datae* is the earliest available for any species of *Apomys* and specimens of the species were the first to be recorded in the scientific literature, but under a different name. During February of 1895, John Whitehead obtained rats from Lepanto at 8000 feet on Mount Data which Thomas (1898, p. 403) subsequently identified as *Mus chrysocomus*, writing that "This interesting species, which differs from almost every other member of

the genus in the entire absence of sharp supraorbital edges or ridges, has hitherto been recorded only from Celebes. The present specimens, however, seem to agree closely both with Herr Hoffmann's description and figure, and also with the notes which, by the kindness of Dr. Meyer, I was allowed to take on the typical specimen when in Dresden."

Thomas gave a specimen to the Staatliches Museum für Tierkunde at Dresden. There Meyer (1898–1899, p. 25) examined it, wrote that the rat was unlike *Mus chrysocomus* of Celebes, and described it as a new species, *Mus datae*.

Little was known about *Mus datae* and specimens of it were rare in museum collections. In 1913, Hollister identified eight specimens from Luzon as *Epimys datae* (*Epimys* was the name applied to what is now called *Rattus*) but these have since been reidentified as *Rattus nitidus* (Musser, 1977) and have nothing to do with *datae*. Later, in 1934, Taylor listed *Rattus datae* as part of the Philippine fauna and referred to the holotype as well as the specimens that had been identified by Hollister in 1913. Finally, in 1941, Ellerman allocated *datae* to *Apomys* where it belongs.

By the middle 1950s there were still very few specimens of *Apomys datae* but in 1952 Sanborn (pp. 132–133) reported on 54 specimens from Mount Data that he had identified as *A. datae*. Part of that collection is still in the Field Museum of Natural History at Chicago where I was able to study it. Sanborn failed to detect that there were really two species in the large sample that he identified as one. Part of the series, those I listed at the beginning of this account, are large-bodied rats with elongate skulls and squarish braincases. Their external and cranial characteristics are closely similar to the holotype of *A. datae* (SMT B.3100) with which I directly compared them (see fig. 4a and b where the cranium of the holotype is contrasted with that of a specimen from Sanborn's sample).

The rest of Sanborn's sample consists of *A. abrae*, a species he named and described in the same report and one based on two specimens from Abra Province in northern Luzon (Sanborn, 1952, p. 133). Specimens of *A. datae* and *A. abrae* from Mount Data

are superficially similar in external features but they differ in several characters. Compared with adults of *A. datae*, those of *A. abrae* are slightly smaller in body size (table 6); the upperparts are duller brown with more yellowish tones, instead of rich dark brown; the underparts are grayish white as they are in *A. datae*, but most specimens have a buffy wash, which is absent from the examples of *A. datae*; the hind feet are narrower and all the dorsal surfaces are white, instead of brown basally and white distally; the means of the cranial and dental measurements average smaller (table 4); the cranium is less elongate and has a rounded braincase, rather than squarish (fig. 4b and c); and the pterygoid region, stapedia foramen, and arterial circulation involving the stapedia, intermaxillary, common carotid, and internal carotid is like that I described for the *abrae-hylocetes* pattern (fig. 2A). *Apomys abrae* will be discussed further in the accounts to follow.

All but one of the examples of *A. datae* I examined are from Mount Data. One individual is from Hights-in-the-Oaks (USNM 151513) and is the holotype of *A. major*, described by Miller in 1910 (pp. 402–403). "Except for their noticeably greater size the skull and teeth do not differ appreciably from those of *Apomys insignis*" was the contrast Miller noted between *A. major* and the Mindanao *A. insignis*, the species he compared with *A. major*. Miller never compared *A. major* with *Mus datae*. The holotype of *A. major* is an adult; except for being smaller than most individuals in the sample from Mount Apo (table 4), it is closely similar to them in external, cranial, and dental features and represents the same species. Miller also identified three other specimens as *A. major* but they are examples of *A. abrae*.

Apomys datae is probably a rat of the forest floor. Rabor (1955, p. 206) noted that specimens of what Sanborn had identified as *datae* from Mount Data "were trapped in thick cover among the dense vegetations of the gullies on the sides of the plateau, especially along the shallow creeks, at elevations from 2100 to 2300 meters." The sample he referred to consisted of both *A. datae* and *A. abrae*; the two are probably terrestrial but whether they are similar in habits is unknown.

TABLE 4
Cranial and Dental Measurements (in Millimeters) of Adult *Apomys datae*, *Apomys abrae*, *Apomys sacobianus*, and *Apomys musculus* from Luzon

Species and Locality	Catalog Number	GLS	ZB	IB	BBC	HBC	LM ¹⁻³	BM ¹
<i>A. datae</i>								
Mount Data	—	39.2 ± 1.1 (17) 37.0–40.6	17.9 ± .4 (17) 17.0–18.5	6.1 ± .2 (17) 5.7–6.5	15.2 ± .3 (17) 14.5–15.7	11.2 ± .5 (17) 10.5–12.0	7.2 ± .2 (17) 6.9–7.5	1.9 ± .1 (17) 1.7–2.0
Mount Data	SMT B.3100 ^a	39.9	17.9	5.8	14.8	11.1	7.1	1.9
Hights-in-the-Oaks	USNM 151513 ^b	38.4	17.2	5.8	15.0	10.1	6.4	1.7
<i>A. abrae</i>								
Ilocos Norte Prov.	—	35.7 ± .8 (5) 34.7–36.8	—	—	—	—	6.7 ± .3 (13) 6.2–7.0	1.7 ± .1 (13) 1.6–1.8
Abra Prov.	{ FMNH 62750 ^c FMNH 62749	34.7 35.2	15.5 —	5.4 —	14.3 —	10.4 —	6.8 6.8	1.8 1.8
Mount Data	—	35.6 ± .8 (10) 34.3–37.2	16.0 ± .4 (10) 15.3–16.4	5.6 ± .1 (10) 5.4–5.8	14.8 ± .4 (10) 13.8–15.2	10.4 ± .3 (10) 9.7–10.8	6.9 ± .2 (10) 6.4–7.0	1.8 ± .1 (10) 1.7–2.0
Hights-in-the-Oaks	—	34.8 ± 1.5 (3) 33.2–36.3	15.9 ± .6 (3) 15.4–16.6	5.5 ± .2 (4) 5.3–5.8	14.6 ± .4 (3) 14.3–15.1	10.6 ± .5 (3) 10.2–11.2	6.9 ± .1 (4) 6.7–6.9	1.8 ± .1 (4) 1.7–1.8
Baguio	USNM 151510	35.8	16.7	6.0	15.6	10.7	7.1	2.0
Sablan	{ FMNH 92763 FMNH 92764	— —	— —	6.0 —	— —	— —	7.1 7.2	2.0 1.9
<i>A. sacobianus</i>								
Pampanga Prov.	USNM 304352 ^d	38.0	18.0	6.0	15.1	10.2	7.1	2.0
<i>A. musculus</i>								
Luzon Baguio	{ USNM 145770 ^e USNM 145777 USNM 261177	25.7 23.9 —	12.8 12.5 —	3.9 4.0 4.1	12.0 12.1 —	8.0 7.9 —	4.5 4.5 4.4	1.2 1.2 1.2
Luzon, Mt. Isarog	{ FMNH 95124 FMNH 95125 FMNH 95126 FMNH 95127	25.8 — 26.4 26.4	— — — 13.2	4.1 4.5 4.3 4.2	— — 12.5 12.4	— — 8.4 8.6	4.7 4.9 4.9 4.9	1.3 1.2 1.2 1.3
Mindoro	{ FMNH 87566 MMNH 12971	27.4 25.8	13.5 12.3	4.3 4.0	12.1 11.7	8.3 8.2	4.9 4.6	1.2 1.2

^a Holotypes of: *Mus datae* (fig. 3a), ^b *Apomys major*, ^c *Rattus (Apomys) abrae*, ^d *Apomys sacobianus* (fig. 3d), ^e *Apomys musculus*. (Abbreviations: see methods for explanation. The mean plus or minus one standard deviation, size of sample in parentheses, and observed range are listed, in that order, for each measurement.)

Apomys datae may occur over much of Luzon but it is now known only from the western highlands in the northern part of the island. If that is its real geographic range, it may be part of an endemic assemblage that also includes *Crateromys schadenbergi*, *Carpomys phaeus* and *C. melanurus*, *Batomys granti* and *B. dentatus*, *Celaenomys silaceus*, *Chrotomys whiteheadi*, and *Rhynchomys soricoides*.

THE *Apomys abrae-hylocetes* GROUP

Included here are *A. abrae* and *A. sacobianus* from Luzon; *A. musculus* from Luzon and Mindoro; *A. microdon* from Catanduanes, Leyte, and Dinagat; *A. insignis* and *A. hylocetes* from Mindanao; and *A. littoralis* from Mindanao and Negros. I discuss the species in that order.

Apomys abrae: I examined specimens from the following places on Luzon. ILCOS NORTE PROVINCE, Mount Simminublan (Mount Sciapoo on some maps), 4000–4350 feet (DMNH 5973, 59741; FMNH 92752–92762). ABRA PROVINCE, Massisiat, 3500 feet (FMNH 62749, 62750). MOUNTAIN PROVINCE, Mount Data, 5300–8200 feet (FMNH 62700, 62706, 62719, 62723, 62724, 62726, 62728, 62738–62740); Benguet, Hights-in-the-Oaks, 7000 feet (USNM 151507–151509, 151530, 261170); Benguet, Baguio, 3000–4000 feet (USNM 151510, 399573–399580); near Baguio, Mount Santo Tomás (AMNH 242099, 242100); Sablan, 1700–3000 feet (FMNH 92763 and 92764).

Apomys abrae was described in 1952 by Sanborn (pp. 133–134) who based his account on the holotype (FMNH 62750) and another specimen from Abra Province in northwestern Luzon. Sanborn remarked that "The skull is typical *Apomys* with no marked peculiarities. It is intermediate in size between skulls of *datae* and *insignis*. . . . The other *Apomys* known from Luzon are *datae*, which is larger, darker, and from a higher altitude, and *musculus*, which is much smaller and of a different color. *Apomys abrae* is from a lower elevation and a slightly warmer climate north of the other species."

Apomys abrae actually has a wider distribution over Luzon and a greater altitudinal range than Sanborn realized. As I noted in the previous account, Sanborn (1952) thought all the specimens he examined from Mount Data were *A. datae* and failed to recognize that two species were present, one of which was very similar to the specimens he described as *A. abrae*. When I was at the Field Museum, I compared the two examples of *A. abrae* from Abra Province directly with those I separated out of the series from Mount Data. The latter have slightly darker fur; I could not detect any other differences.

Of all the species of *Apomys* on Luzon, *A. abrae* is represented by more specimens from more localities. The species probably occurs throughout northern Luzon and is known from altitudes ranging from 3000 up to 8200 feet.

As might be expected of a species recorded from a large area, there is conspicuous geographic variation in coloration of fur and body size. The specimens from Abra Province have brown upperparts, grayish white underparts, white hind feet, and a bicolored tail that is grayish brown above and white below from base to tip. The examples of *A. abrae* from Mount Data are similar to those from Abra Province in size (table 4) but slightly darker in pelage coloration and many of the specimens have grayish white underparts suffused with buff. Specimens from Hights-in-the-Oaks and Mount Santo Tomás are similar to those from Mount Data.

The series from Mount Simminublan in Ilocos Norte Province are different from the other samples of *A. abrae*. The specimens are similar in body proportions and cranial configuration to those from Abra and Mountain Provinces, but the maxillary molar rows average slightly shorter (table 4) and the pelage is much paler and brighter. All the specimens have bright, tawny buff upperparts and tan ears. The underparts are white suffused with gray in some specimens, pale to dark buff suffused with gray in others.

Sizes of crania and maxillary toothrows are similar among most samples of *A. abrae* (table 4) but there is some variation. The specimen from Baguio (USNM 151510) and the

two from Sablan (FMNH 92763 and 92764) are slightly larger in body size than any of the other specimens of *A. abrae*. They also have paler fur than most *A. abrae*.

The significance of the variation in color and size among available samples is difficult to assess. There are still too few samples and the locality data are so imprecise that no general geographic pattern is evident except that 1) rats from high altitudes have darker fur than those from lower localities and 2) the distinctive series from Ilcos Norte Province may represent a different population. Study of more specimens from other places on Luzon should provide insights into patterns of variation that may have biogeographic significance.

Scanty information exists about habitat or habits of *A. abrae*. Rabor (1955, p. 213) noted that the two specimens obtained from Abra Province were collected at "about 1200 meters elevation, at the sides of a creek heavily grown with climbing bamboos and bushes." There is nothing else.

Apomys abrae has not yet been recorded from either the central or southern parts of Luzon. It is, however, represented by a relative from central Luzon that is discussed in the following account.

Apomys sacobianus: The holotype of *A. sacobianus* (USNM 304352) is from lowlands at Clark Air Base in central Luzon where Johnson (1962, p. 319) trapped it "in the narrow forested canyon of the Sacobia River, just above the point where it emerges from the foothills of the Zambales Mountains onto the Plains of Pampanga." The taxon is represented by the holotype only.

Johnson (1962, p. 318) diagnosed *A. sacobianus* as "A large lowland species of *Apomys*, about the size of the montane *A. major* Miller (?=*datae* Meyer), but shorter-haired, grayer, with lighter feet and underparts, longer hind feet, and a shorter cranial rostrum; larger than *A. abrae* Sanborn and other Philippine species."

The holotype is a large rat in which the tail is just slightly longer than the combined lengths of head and body (table 6). The upperparts are grayish brown, the underparts are whitish gray grading into patches of white along the midline. The tops of the front and hind feet are white. The tail is sharply bicolor,

grayish brown above and white below from base to tip.

Although similar to *A. datae* in body size, the holotype of *A. sacobianus* is simply a larger-bodied, grayer, lowland version of *A. abrae* from central Luzon. The cranium and teeth of *A. sacobianus* are larger than most examples of *A. abrae* (table 4) and the braincase is squarish instead of round but the two species are otherwise closely similar in cranial configuration (fig. 4c and d). Both have the pterygoid configuration and arterial circulation in the basicranium that is typical of the *abrae-hylocetes* pattern and in both the canal or groove containing the internal maxillary artery is complete and not open on the ventral surface of the pterygoid plate (fig. 2A).

The holotype of *A. sacobianus* may represent only a large-bodied lowland subspecies of *A. abrae* but I prefer to retain *sacobianus* as a species until we know more about its real geographic distribution and obtain a better estimate of the range of size and color variation. Possibly the relationship between the northern Luzon and highland *abrae* and the central Luzon and lowland *sacobianus* is similar to that between the samples of *Chrotomys* from Luzon. In that genus, the specimens from the western highlands of northern Luzon represent a different population than those living in the lowlands of central Luzon and Mindoro; the differences have been hypothesized to indicate genetic isolation between two species (Musser, Gordon, and Sommer, in press). Retaining *abrae* separate from *sacobianus* helps point up our ignorance about the two and may prompt workers to obtain more specimens from the right places which can be studied to answer questions about the relationship of one to the other.

Whatever the nature of the genetic link between *abrae* and *sacobianus*, both are more closely related to each other than to any other known species of *Apomys*. Size and proportions of body and skull along with a complete canal for the internal maxillary artery set the two species apart from all others in the *abrae-hylocetes* Group, including *A. musculus*, the other species from Luzon, which is described below.

Apomys musculus: Named and described by Miller in 1910 (pp. 403–404), *A. musculus* is a distinctive species that is represented by

a few specimens from Luzon and Mindoro. The examples from Luzon were collected in the western highlands of northern Luzon at 5000 feet (USNM 145770, 145777, and 261177) at Baguio in Mountain Province and on Mount Isarog at 6500 feet, a volcanic peak in the southeast peninsula of Luzon, Camarines Sur Province (FMNH 95124–95127). Of the two from Mindoro, one was collected at 4500 feet on Ilong Peak, Mount Halcon Range (FMNH 87566), the other from the field station at the Mount Iglit Game Refuge and Bird Sanctuary in southwestern Mindoro (MMNH 12971).

The smallest in body size of the species of *Apomys* (fig. 5e; table 4), *A. musculus* has bright tawny brown upperparts, rich ochraceous buff or buffy gray underparts, buffy white hands and feet, and a tail that is brown above and mottled on its undersurface. The tail is about as long or only slightly longer than the combined lengths of head and body (table 6). The specimen from Ilong Peak is a genetic variant: the fur over the head and body is blond.

I have no information about the habits or habitat of *A. musculus*.

My inclusion of samples from northern Luzon, the Camarines Peninsula, and eastern Mindoro in one species is a temporary arrangement that may be altered after study of larger samples from other areas. There is geographic variation reflected in some cranial and dental measurements from the small series available to me (table 4). Adults from the Baguio region of northern Luzon have smaller skulls and shorter maxillary tooththrows than do adults of comparable age from Mount Isarog in the Camarines Peninsula and eastern Mindoro. The differences between these samples may only reflect sampling procedures and small sample size. If, however, the differences are a good estimate of those actually existing between populations from the three places then they may reflect one or both of the following patterns.

First is the relationship between *A. musculus* from the western highlands of northern Luzon and those from Mount Isarog in the southeastern peninsula of that island. Samples of the shrew rat *Rhynchomys* are also available from the mountains of northern Luzon and Mount Isarog. The morphological

differences between the two sets of specimens led Musser and Freeman (1981) to describe the Mount Isarog rat as a species. Does a comparable morphological distinction between the samples of *A. musculus* from those two highland areas exist?

Second is the possibility that the specimens from the southeast peninsula of Luzon and those from the island of Mindoro may be closely similar and represent a population different from that living in the mountains of northern Luzon. Such a pattern, although dissimilar in details, resembles that for *Chrotomys*, in which *C. whiteheadi* is found in the western mountains of northern Luzon and *C. mindorensis* occurs in central Luzon and on Mindoro (Musser, Gordon, and Sommer, in press). The morphological distinctions between *Apomys abrae* and *A. sacobianus* may also reflect a similar pattern, although the latter has not yet been collected on Mindoro.

Judged by its small size, tawny upperparts, buffy underparts, mottled tail, and pterygoid region in which the canal for the internal maxillary artery is partially open on the ventral surface of the pterygoid plate (fig. 2B; table 3), *A. musculus* may be more closely related to species on islands to the south of Luzon than to either *A. abrae* or *A. sacobianus*; it is certainly not in the same group as *A. datae* of Luzon. Taxonomists who may wish to taxonomically revise *Apomys* at some future time should test the hypothesis that *A. musculus* might be a smaller-bodied and shorter-tailed version of *A. microdon*, which is the subject of the next account.

Apomys microdon: A poorly prepared skin and fragmented skull (USNM 155145) is the holotype of *A. microdon*, which was described by Hollister in 1913 (pp. 327–328). The rat was obtained from Biga on Catanduanes, a small island east of the southeastern peninsula of Luzon. Hollister diagnosed the species as “Of medium size, slightly smaller than the Mindanao forms; thus widely different from either of the two known northern species, from Benguet Province, Luzon. Differs from all other forms of *Apomys* in the relatively small size of teeth.” The tail is very long relative to the combined lengths of head and body, a proportion similar to that of *A. insignis* (table 6). Hollister’s description of fur color is accurate: “Upper-

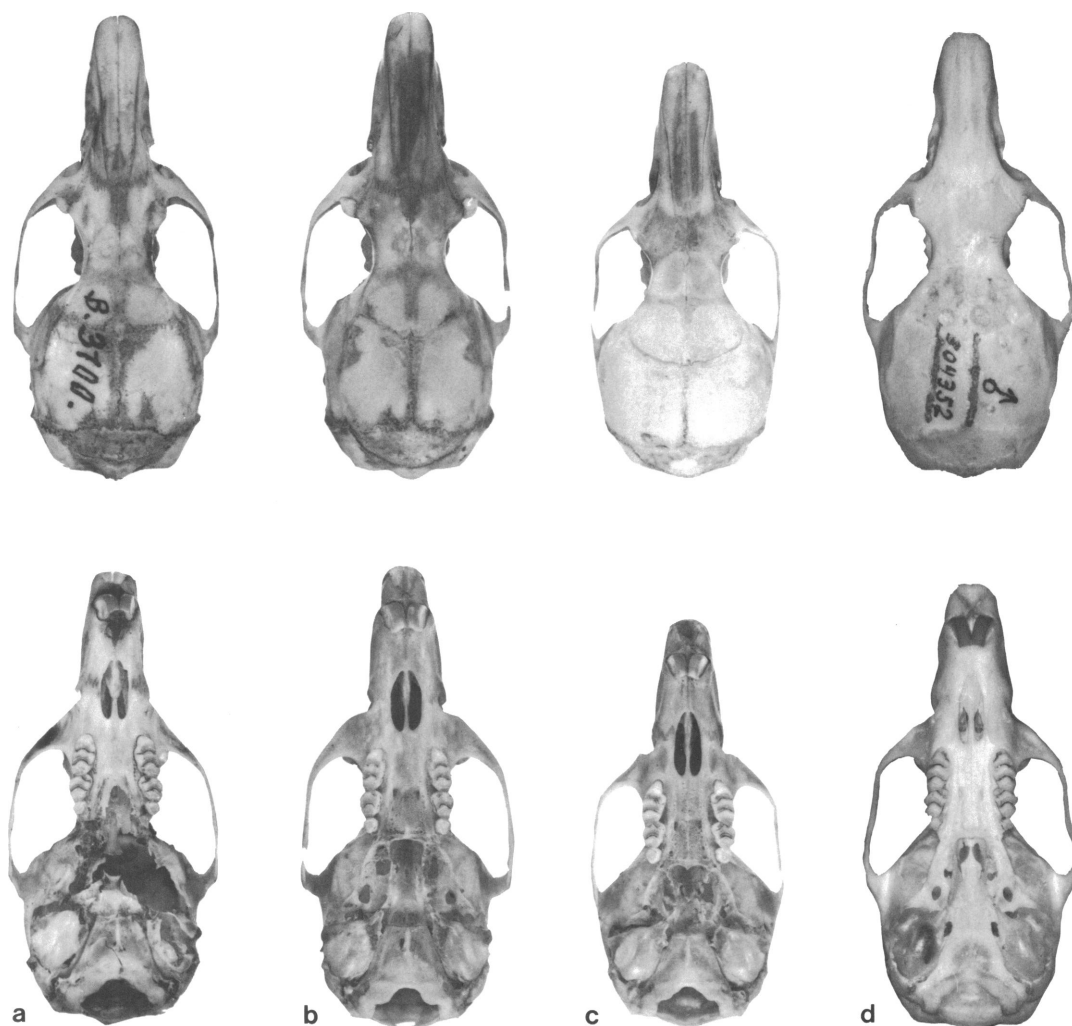


FIG. 4. Dorsal (*top*) and ventral (*bottom*) views of crania of adult *Apomys* from Luzon: a, holotype of *Mus datae* (SMT B.3100); b, *A. datae* (FMNH 62695); c, *A. sacobianus* (FMNH 62728); d, holotype of *A. sacobianus* (USNM 304352). All $\times 1.5$. The first three are from Mount Data.

parts dark cinnamon-brown; sides lighter, almost tawny-olive; underparts buffy-gray, strongly washed with pale cinnamon. Hands, feet, and tail brown, the tail apparently unicolor." Describing the skull and teeth, Hollister wrote that "The skull of the single specimen is broken in the posterior parts, but it is apparently much as in *Apomys insignis* from Mindanao in general shape; the teeth are much less in size, smaller than in any species of *Apomys* except the little *Apomys*

musculus of Luzon." Hollister indicated the holotype to be an adult but it is really a young adult, the molars are only slightly worn. There is no information about the habitat from which the specimen was obtained.

In 1949, Ellerman (p. 76) used *hollisteri* to replace *microdon*. That name had already been proposed by Peters in 1852 for *Mus microdon*, which was later listed by Ellerman (1941, p. 211) as a subspecies of *Rattus coucha*. Because in 1949 Ellerman considered

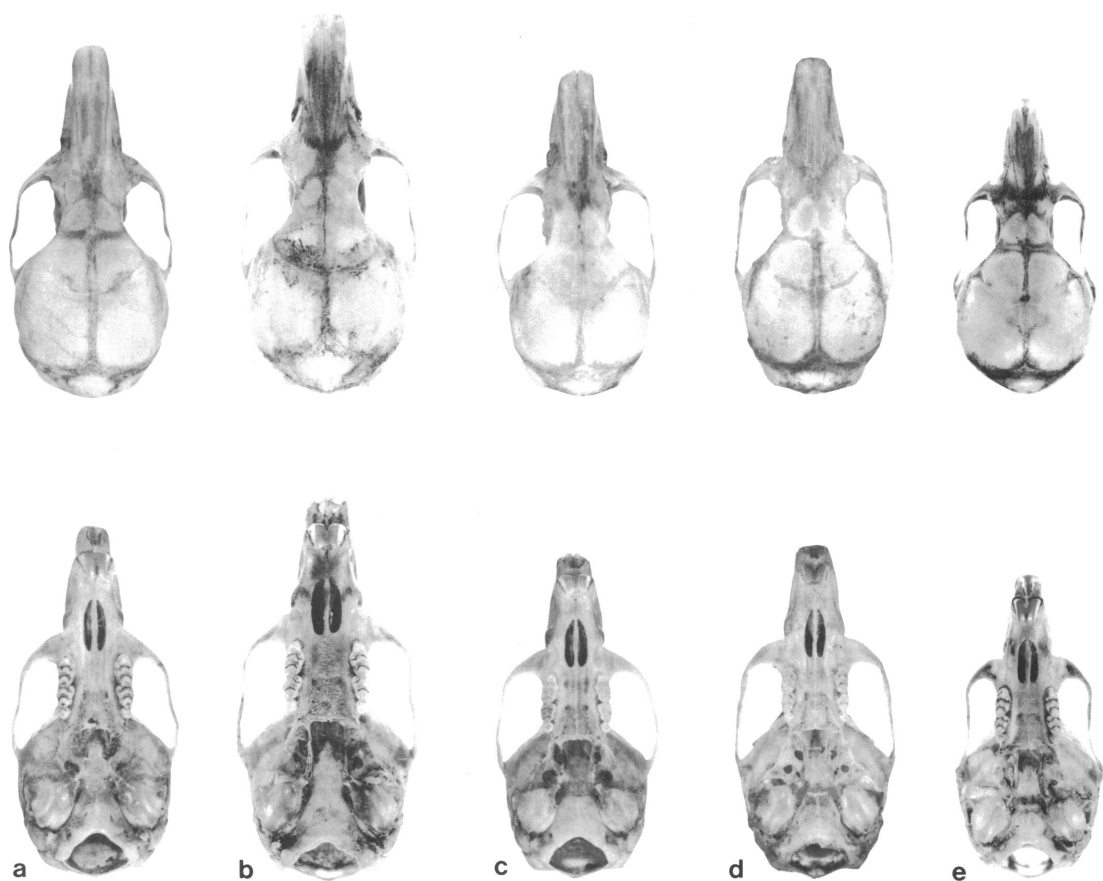


FIG. 5. Dorsal (top) and ventral (bottom) views of crania from adult *Apomys*: a, *A. hylocetes* (USNM 125244), Mindanao; b, *A. insignis* (AMNH 207567), Mindanao; c, *A. microdon* (DMNH 4801), Leyte; d, *A. littoralis* (DMNH 6011), Negros; e, *A. musculus* (MMNH 12971), Mindoro. All $\times 1.5$.

Apomys to be a subgenus of *Rattus*, he regarded Hollister's *microdon* as invalid. I treat *hollisteri* Ellerman (1949) as a synonym of *microdon* Hollister (1913).

Until the 1960s, *A. microdon* was represented by the holotype only. Whether it represented a species endemic to Catanduanes or an island variant of some other species already described was unknown. During 1960 and 1970, Dr. D. S. Rabor and his helpers collected a large series of *Apomys* from the island of Leyte and two from Dinagat Island. Those from Leyte are from altitudes ranging from 800 to 2000 feet and were obtained in the Mount Lobi Range (DMNH 4785, 4786, 4788–4796), at Santa Cruz (DMNH 4797), and on Mount Kabalanti-an

(DMNH 4798–4815, 6013). Of the two from Dinagat Island, I have examined one from Esperanza at Loreto (UPLB 3618).

The series of *Apomys* from Leyte are of medium body size with tails that are much longer than combined lengths of head and body and elongate hind feet (table 6). The upperparts are bright tawny with buffy highlights. Coloration of the underparts varies. In 15 specimens, the venters are rich, solid ochraceous buff; four rats have dark grayish buff underparts; the venters are pale gray slightly suffused with buff in six specimens; and two examples have rich buffy venters broken up by white patches on the chest and midline. The long tails are brown above from base to tip and either the same color on the

ventral surface, mottled, pale brown from base to tip, or whitish. Dorsal surfaces of the front and hind feet are pale brown. The skulls are medium-sized and the tooththrows short (fig. 5c). Skin and skull features of the specimen from Dinagat Island fit within the range of variation seen in the series from Leyte (tables 5 and 6).

To me, the specimens from Leyte and Dinagat represent populations of *A. microdon*. The young adults in the Leyte sample are closely similar to the holotype of *A. microdon* from Catanduanes in body proportions, fur color, skull size and conformation, and tooth-row length. Study of larger series from Catanduanes and Dinagat may reveal significant insular variation but I cannot detect any in the samples I have available.

To what species *A. microdon* may be related in the northern part of the Philippine archipelago is unknown. It may eventually be found on the southeast peninsula of Luzon across from Catanduanes Island. I would look for it there. On the other hand, *A. musculus*, which already occurs on Luzon, may be the smaller-bodied and shorter-tailed northern relative of *A. microdon*. Both possibilities should be tested.

There is no question about what species *A. microdon* is related to in the southern portion of the archipelago. Hollister (1913) noted that the holotype was morphologically similar to *A. insignis* of Mindanao Island. The samples from Catanduanes, Leyte, and Dinagat do represent a smaller-bodied and brighter-colored version of *A. insignis*; the two are closely related as I indicate in the following account.

Apomys insignis: This must be a common species in the highlands of Mindanao if the large series in museum collections reflect its abundance in nature. Named and described by Mearns in 1905 (pp. 459–460), the holotype (USNM 125243) and the rest of the original series were obtained by Mearns from between 4000 and 6000 feet on Mount Apo in Davao Province of southeastern Mindanao (BMNH 5.10.9.6 and 5.10.9.7); USNM 125231, 125233, 125236–125242, and 125247). Additional examples were reported by Sanborn (1952), one of which (AMNH

185142) I have examined. The species also occurs on Mount McKinley, a peak north of Mount Apo in Davao Province (Hoogstraal, 1951; Sanborn, 1952) where specimens were obtained from altitudes between 2950 and 7100 feet (AMNH 185143; BMNH 51.327 and 51.328; FMNH 56266–56278, 56282, 56285, and 56288). A large series (DMNH 6007; FMNH 92806–92822) is also available from between 4200 and 6000 feet on the slopes of Mount Katanglad in Bukidnon Province north of Mount Apo. These three mountains are all in the western portion of Mindanao.

Apomys insignis also occurs in the eastern part of Mindanao. There, large series have been collected at altitudes from 5750 to 9000 feet on various peaks in the Grand Malindang Mountains of Zamboanga del Norte Province (AMNH 207567–207576; DMNH 5975–5997; FMNH 87567–87573; USNM 144579–144586, 144589, 144590–144592, 144826, 144874–144879, and 144911). A small series is also available from 3150 to 5050 feet on Mount Sugar Loaf in Zamboanga del Sur Province (DMNH 5907–5909).

The combination of medium body size, very long tail relative to the combined lengths of head and body (which are only 63–76 percent the length of the tail in my samples), and long, narrow hind feet (figs. 6 and 7) are distinctive for *A. insignis* (table 6). Pelage over the upperparts of the head and body is a dark, rich brown with burnished highlights. The underparts are a rich dark buff suffused with dark gray in some specimens; grayish pale buff in others; and rich buffy gray broken up by white patches on the chest, abdomen, or along the entire midline in many examples. Dorsal surfaces of the front and hind feet range from pale to dark brown. The tail is brown on its dorsal surface from base to tip; the ventral surface is variable in the samples and ranges from being the same color as the dorsum, slightly paler, mottled, grayish brown, or whitish. Tails that are monochrome, mottled below, or only slightly paler below from base to tip are the most frequent variants.

Very little has been recorded about either

TABLE 5
Cranial and Dental Measurements (in Millimeters) of Adult *Apomys microdon* from Catanduanes, Leyte, and Dinagat; *Apomys insignis* and *Apomys hylocetes* from Mindanao; and *Apomys littoralis* from Mindanao and Negros.

Species and Locality	Catalog Number	GLS	ZB	IB	BBC	HBC	LM ¹⁻³	BM ¹
<i>A. microdon</i>								
Catanduanes	USNM 155145 ^a	—	—	5.0	—	—	5.3	1.5
Leyte	—	29.1 ± .9 (26) 27.2–30.8	13.8 ± .6 (20) 12.2–14.4	4.9 ± .2 (29) 4.6–5.2	12.5 ± .3 (27) 11.8–13.1	8.8 ± .3 (27) 8.1–9.6	5.4 ± .2 (29) 5.2–5.7	1.5 ± .1 (28) 1.3–1.6
Dinagat	UPLB 3618	29.9	—	5.1	12.7	8.5	5.7	1.6
<i>A. insignis</i>								
Mount Apo	USNM 125243 ^b	31.6	14.7	5.0	13.5	8.7	6.1	1.6
Mount Katanglad	—	31.6 ± .9 (2) 31.1–32.2	14.4 ± .9 (3) 13.4–15.2	5.1 ± .2 (18) 4.8–5.3	13.2 ± .5 (4) 12.4–13.5	9.5 ± .3 (4) 9.2–9.9	6.0 ± .2 (18) 5.7–6.6	1.6 ± .1 (18) 1.5–1.8
Mount McKinley	—	31.2 ± .6 (13) 30.3–32.4	14.4 ± .4 (12) 13.6–15.1	4.9 ± .2 (13) 4.7–5.3	12.9 ± .4 (13) 12.3–13.6	9.2 ± .4 (13) 8.5–10.0	5.9 ± .1 (13) 5.7–6.1	1.6 ± .1 (13) 1.5–1.8
Mount Apo	—	31.2 ± .8 (5) 30.5–32.4	14.5 ± .3 (6) 14.0–14.7	5.0 ± .1 (7) 4.9–5.2	13.2 ± .2 (5) 13.1–13.5	9.0 ± .3 (5) 8.7–9.3	6.1 ± .1 (7) 5.9–6.3	1.7 ± .1 (7) 1.6–1.7
Mount Bliss	USNM 144582 ^c	32.3	14.3	4.9	13.0	9.5	5.8	1.6
Malindang Moun- tains	—	31.9 ± .8 (30) 30.6–33.3	14.3 ± .4 (26) 13.2–15.2	5.0 ± .2 (38) 4.6–5.4	13.1 ± .3 (30) 12.2–13.7	9.1 ± .4 (30) 8.5–10.1	5.9 ± .2 (43) 5.5–6.2	1.6 ± .1 (43) 1.5–1.7
<i>A. hylocetes</i>								
Mount Apo	{ USNM 125246 ^d USNM 125245 ^e USNM 125244 }	{ 32.0 30.7 30.4 }	{ 14.5 — 14.4 }	{ 5.1 5.1 5.3 }	{ 13.9 13.8 13.7 }	{ 9.9 9.4 9.3 }	{ 5.7 5.7 5.6 }	{ 1.6 1.5 1.6 }
<i>A. littoralis</i>								
Mindanao	{ FMNH 60834 ^f DMNH 6012 }	{ — — }	{ — — }	{ 4.9 5.0 }	{ — — }	{ — — }	{ 5.0 5.2 }	{ 1.3 1.3 }
Negros	{ DMNH 6008 DMNH 6009 DMNH 6010 DMNH 6011 }	{ 28.3 — 28.2 29.6 }	{ 13.6 13.6 14.0 13.9 }	{ 4.9 5.1 4.9 4.9 }	{ 12.8 12.5 12.7 12.5 }	{ 8.9 8.6 8.8 8.8 }	{ 5.0 5.0 5.0 5.2 }	{ 1.3 1.3 1.2 1.3 }

^a Holotypes of: *Apomys microdon*, ^b *Apomys insignis*, ^c *Apomys bardus*, ^d *Apomys hylocetes*, ^e *Apomys petraeus*, ^f *Apomys littoralis*. (Abbreviations: see methods for explanation. The mean plus or minus one standard deviation, and observed range are listed, in that order, for each measurement.)

TABLE 6
External Measurements (in Millimeters) and Body Weight (in Grams) of Adult *Apomys*

Species, Locality, and Catalog Number	LHB	LT	(LHB)/ (LT) (%)	LHF	LE	W
<i>A. datae</i>						
USNM 151513 ^a	143	144	99	34	—	—
<i>A. abrae</i>						
FMNH 62750 ^b	125	130	96	34	18	—
<i>A. sacobianus</i>						
USNM 304352 ^c	141	149	95	40	22	—
<i>A. musculus</i>						
USNM 145770 ^d	86	89	97	20	—	—
USNM 145777	103	82	126	22	—	—
USNM 261177	76	96	79	21	14	—
FMNH 87566	124	133	93	25	15	—
MMNH 12971	95	110	86	22	14	—
<i>A. microdon</i>						
USNM 155145 ^e	106	135	79	26	—	—
Leyte	98.9 ± 5.5 (14) 90–107	134.1 ± 9.0 (14) 125–149	74	29.6 ± 1.2 (14) 27–31	16.9 ± 1.0 (14) 15–19	31.1 ± 2.2 (9) 28.2–34.2
Dinagat	100	128	78	28	18	—
<i>A. insignis</i>						
USNM 125243 ^f	111	176	63	33	—	—
Mount Apo	108.1 ± 6.0 (7) 99–116	152.6 ± 13.1 (7) 140–176	71	32.9 ± 1.3 (7) 31–35	—	—
Malindang Mts.	110.0 ± 9.5 (33) 71–123	145.5 ± 9.2 (33) 115–162	76	31.6 ± 1.4 (33) 30–34	20.6 ± .6 (23) 20–22	41.9 ± 4.3 (22) 32.7–49.5
USNM 144582 ^g	113	162	70	34	—	—
<i>A. hylocetes</i>						
USNM 125246 ^h	115	135	85	29	—	—
USNM 125245 ⁱ	111	120	93	30	—	—
USNM 125244	114	122	93	28	—	—
<i>A. littoralis</i>						
FMNH 60834 ^j	100	122	82	26	16	—
DMNH 6012	103	126	82	27	17	—
DMNH 6008	100	120	83	25	16	20.4
DMNH 6009	95	110	86	24	16	19.3
DMNH 6010	95	118	81	23	16	21.7
DMNH 6011	100	121	83	27	17	25.9

^a Holotypes of: *Mus datae*, ^b*Rattus (Apomys) abrae*, ^c*Apomys sacobianus*, ^d*Apomys musculus*, ^e*Apomys microdon*, ^f*Apomys insignis*, ^g*Apomys bardus*, ^h*Apomys hylocetes*, ⁱ*Apomys petraeus*, ^j*Apomys littoralis*.

(Abbreviations: see methods for explanation. The mean plus or minus one standard deviation, size of sample in parentheses, and observed range are listed, in that order, for each measurement.)

habits or habitat of *A. insignis*. Notes on the skin labels of the specimens caught on Mount McKinley indicate that at 2950 feet a rat was

caught in a “coffee plantation,” and that at altitudes from 3000 to 7100 feet they were trapped in “undergrowth of rattan and



FIG. 6. *Apomys insignis*. Dorsal and ventral views of AMNH 207568, an adult female from Mindanao: length of head and body, 111 mm.; length of tail, 145 mm.; length of hind foot, 31 mm.; length of ear, 20 mm.

ferns," "under mossy log," among "mossy roots and undergrowth of ferns and rattan,"

in a gully "among mossy logs on the ground," on a ridge "in mossy forest," under "bushes and ferns in rain forest," in "woods near fallen log," and in "mossy stunted forest." A specimen from 5750 feet on Mount Apo was caught "among boulders covered by ferns." The species is certainly terrestrial and, judged by its relatively long tail, may be scansorial as well.

Specimens from the summit of Mount Bliss in the Grand Malindang Mountains of eastern Mindanao formed the type series of *A. bardus* (holotype, USNM 144582), described by Miller in 1910 (p. 402). His diagnosis of *bardus* was "Size and general appearance as in the forms inhabiting Mount Apo [*A. insignis*], but skull differing noticeably in the much narrower, less inflated brain case." He noted the color of *bardus* to be "so essentially like that of *Apomys insignis* Mearns as to require no special description. The name, *bardus*, has traditionally been used to designate the samples from eastern Mindanao as a subspecies of *A. insignis* (Hollister, 1913; Taylor, 1934; Ellerman, 1941, 1949).

I consider *bardus* to be a synonym of *insignis* because I could not find marked differences in characteristics of skins and skulls between samples from eastern Mindanao and those from the western part of that island. As Miller noted, there are no appreciable differences between the samples in pelage coloration. I first contrasted the series from Grand Malindang Mountains with that from Mount Apo and found no significant differences between means of most external measurements and all the cranial and dental measurements I took. The rats from Mount Apo do have a significantly longer hind foot ($P = .05-.02$) but the difference could be due to the way the foot was measured, whether from heel to ends of the digits, or to ends of the claws. Then I compared the sample from the Grand Malindang Mountains with that from Mount McKinley and found no differences between them in means of dental measurements and no significant differences between means of all cranial measurements except greatest length of skull. The rats in the sample from the Grand Malindang Mountains have, on the average, significantly longer skulls than those in the Mount McKinley sample (table

TABLE 7
Comparisons between *Apomys microdon* and *Apomys insignis*, and between *insignis* from Eastern Mindanao and *bardus* from Western Mindanao

Measurement	<i>A. microdon</i>		<i>A. insignis</i>		
	Leyte	P ₁	Mt. McKinley (<i>insignis</i>)	P ₂	Malindang Mts. (<i>bardus</i>)
GLS	29.1 ± .9	.001	31.2 ± .6	.01-.001	31.9 ± .9
ZB	13.8 ± .6	.01-.001	14.4 ± .4	.5-.4	14.3 ± .4
IB	4.9 ± .2	—	4.9 ± .2	.2-.1	5.0 ± .2
BBC	12.5 ± .3	.01-.001	12.9 ± .4	.1-.05	13.1 ± .3
HBC	8.8 ± .3	.01-.001	9.2 ± .4	.5-.4	9.1 ± .4
LM ¹⁻³	5.4 ± .2	.001	5.9 ± .1	—	5.9 ± .2
BM ¹	1.5 ± .1	.01-.001	1.6 ± .1	—	1.6 ± .1

(Abbreviations: see methods for explanation. The mean and plus or minus one standard deviation are from table 5. P₁ and P₂ are probabilities that the means of the respective samples were drawn from the same population.)

7). A more refined analysis may demonstrate significant differences not only between samples from eastern and western Mindanao but also among samples from different mountains in the same region; however, I could not detect such geographic variation by my analyses of the samples at hand.

Of all the kinds of *Apomys*, *A. insignis* is morphologically closest to *A. microdon*, the species occurring on the islands north of Mindanao: Dinagat, Leyte, and Catanduanes. The two species are very similar in proportions of tail relative to head and body, in shape of the hind feet, and in conformation of the skulls (fig. 5b and c). They differ in size and color. Specimens of *A. insignis* are significantly larger than those of *A. microdon* as indicated by the highly significant differences between means of all the measurements except interorbital breadth in which there is no difference. In *A. microdon*, the interorbital region is significantly wider relative to length or breadth of the cranium than in *A. insignis* (table 7; fig. 5b and c). The pelage, tail, and feet of *A. insignis* are darker than those elements in the samples of *A. microdon*. *Apomys microdon* is clearly the morphological and probably ecological counterpart of *A. insignis* on the eastern islands of the archipelago north of Mindanao. The differences between the two species are greater than those between *A. insignis* and the sympatric *A. hylocetes* or between *A. insignis* and the smaller-bodied *A. littoralis* from Mindanao.

So far, *A. insignis* has not been found with

another species of *Apomys* anywhere except on Mount Apo where it is sympatric with *A. hylocetes*, the species discussed below.

Apomys hylocetes: This, the type species of the genus, is represented by a small sample collected between 6000 and 7600 feet in forest and beneath rocks above the forest zone on Mount Apo in southern Mindanao (Mearns, 1905). The original series (USNM 125317, 125318, 125243, 125246—the holotype, and 125250–125252) obtained by Mearns remains the only sample of the species. *Apomys hylocetes* is terrestrial, of medium body size, with a tail longer than the combined lengths of head and body (table 6), and short, wide hind feet (fig. 7). Fur over the upperparts of the head and body is dark brown, that on the underparts is deep buffy gray, and the tail is bicolored—brown over the dorsal surface and dark gray beneath—with a white tip.

In his original report, Mearns (1905, pp. 456–457) referred specimens from 6000 and 6750 feet to *A. hylocetes* and described two specimens taken at 7600 feet (USNM 125244 and 125245, the holotype) as a different species, *A. petraeus* (pp. 458–459). These are simply examples of *A. hylocetes* from a higher altitude. Mearns never diagnosed *petraeus* nor did he distinguish it from *hylocetes*. I found no differences in the skins between the two except that the tails of *petraeus* are shorter (but both appear artificially stubby because of missing tips). Skulls of the two series are nearly indistinguishable from each

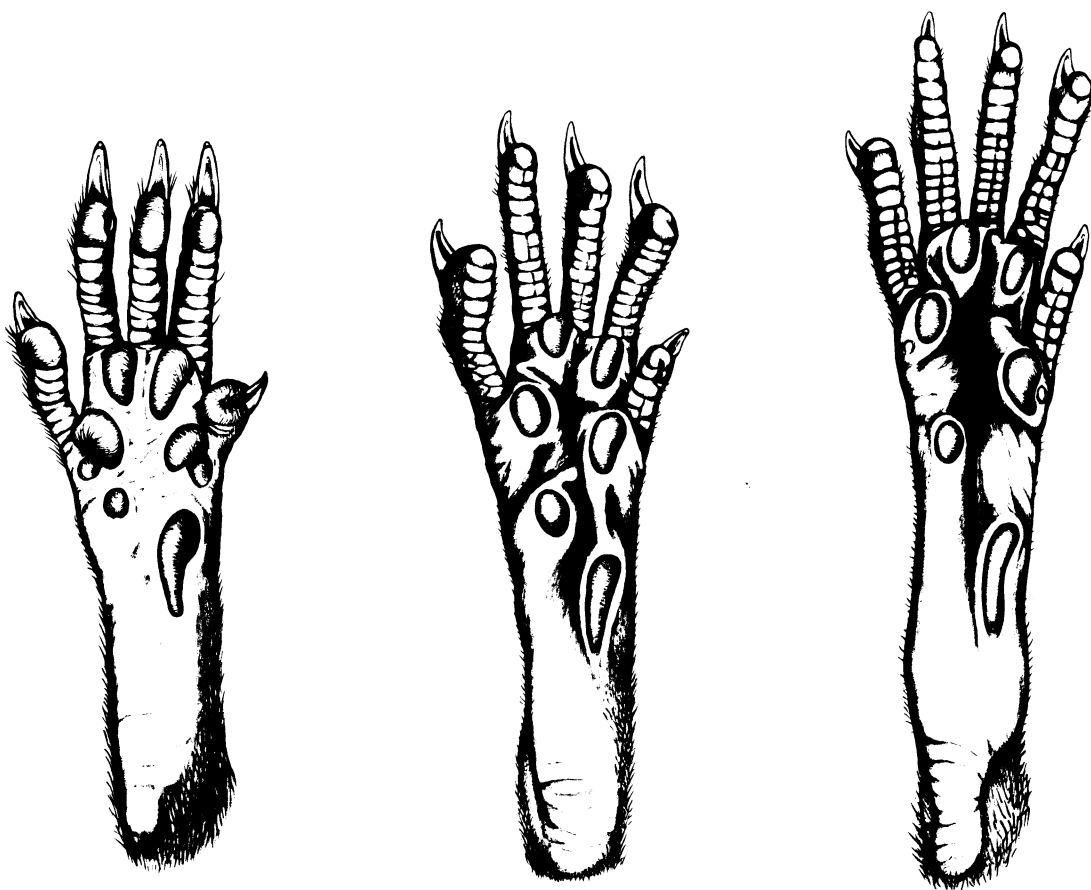


FIG. 7. Plantar views of hind feet. Left: *Rattus exulans* (AMNH 229058; length, 27 mm.), Sulawesi. Center: *Apomys hylocetes* (USNM 125252; length, 30 mm.), Mindanao, Mount Apo. Right: *A. insignis* (USNM 125242; length, 34 mm.), Mindanao, Mount Apo.

other. The rostrum of the holotype of *petraeus* is wider and appears rectangular in dorsal view, while that of the holotype of *hylocetes* is narrower and pointed, a difference reflecting age. The latter is younger than the former; a wide rectangular rostrum is characteristic of older animals.

Mearns collected examples of *A. insignis* and *A. hylocetes* at 6000 feet on Mount Apo. The two species are superficially similar to each other and I studied his original series carefully to test whether all the specimens from Mount Apo represented one or two species. Because specimens of *A. hylocetes* had never been taken on the mountain by later field parties or anywhere else in the highlands of Mindanao there was a possibility the

specimens of *A. hylocetes* were simply shorter-tailed examples of *A. insignis*. Mearns, however, was correct. The two species are closely similar in color of fur but they differ in other characters. The tail is much shorter relative to the length of head and body in *A. hylocetes* than in the longer-tailed *A. insignis* (table 6). *Apomys hylocetes* has shorter and wider hind feet. The plantar tubercles appear relatively larger and take up more of the plantar surface, a feature pointed out by Mearns. The short and wide foot of *A. hylocetes* is contrasted with the long and narrow foot of *A. insignis* in figure 7. *Apomys hylocetes* has a round and inflated braincase (fig. 5a), not squarish and flat as in *A. insignis* (fig. 5b), and slightly shorter maxillary toothrows with narrower

molars (table 5). The laminae of *A. hylocetes* appear thicker from front-to-back than those of *A. insignis*, which are wider and not as thick. Mearns noted that *A. hylocetes* had paler ears and feet than *A. insignis* but I could not detect this difference in the dry study skins.

In addition to *A. hylocetes* and *A. insignis*, there is a third species on Mindanao, which is the subject of the final account below.

Apomys littoralis: Named and described (as a species of *Rattus*) by Sanborn in 1952 (pp. 134–135), *A. littoralis* was known only by the holotype (FMNH 60834), a young adult female trapped at 50 feet from Bugasan on the coastal plain of Mindanao in Cotabato Province (see the map in Hoogstraal, 1951, p. 63). Sanborn described the rat as "Intermediate in size between the small *R. musculus* and the larger *R. hylocetes* and *R. petraeus*; under parts white, in all other known species being buff or darker; upper parts Bister, lightening to near Snuff Brown on sides; all hairs with Dark Neutral Gray bases; hairs of under parts white to the roots; hands and feet light brown, tail uniformly dark; whiskers long, mixed black and white; skull a typical *Apomys* skull, intermediate in size between skulls of *musculus* and the two larger forms." This description is only partially accurate. The tail is dark grayish brown on all surfaces. The underparts are white suffused with gray except for the chest which is white; the venter is not all white as Sanborn implied.

A second specimen (DMNH 6012) was collected by D. S. Rabor in 1970 from Lumba-Bayabao on Piagayungán Mountain between 4000 and 5000 feet in Lanao del Sur Province, which is adjacent to Cotabato Province. The example is a young adult male and like the holotype, it has a monocolored brown tail that is longer than the combined lengths of head and body, short and wide hind feet with tan dorsal surfaces, and tawny brown fur over the upperparts of the head and body. The fur is missing over a third of the venter but that remaining is white suffused with gray. Its external measurements are closely similar to those of the holotype (table 6) as are the dental measurements and the only cranial measurement (table 5) I could obtain from the skulls, which are fragmented with parts, mostly the braincase,

missing. In each specimen, the conformation of the anterior part of the cranium resembles that of *A. insignis*, the interorbital region is about as wide, but the maxillary tooththrows are shorter and the molars narrower (table 5).

Through the courtesy of Dr. Lawrence R. Heaney, I have been able to examine four specimens of a small-bodied *Apomys* from the island of Negros (DMNH 6008–6011). All were taken during March and April of 1964 near San Antonio, Sibulan, between 2800 and 3300 feet in the southern part of the island (Negros Oriental Province). In body size and conformation of hind feet, as well as the proportions of body to tail length, the four specimens are closely similar to the two examples of *A. littoralis* from Mindanao (table 6). Color is the primary external difference between the two series. Fur over the upperparts of the Negros rats is much brighter with a rich ochraceous tone, especially along the sides of the head and body; the underparts are mostly pure white; upper surfaces of the hind feet are whitish buff; the tails are brown over their dorsal surfaces and either mottled pale brown and white beneath or dirty white from base to tip.

The cranium of an adult from Negros is illustrated in figure 5d. The conformation of the interorbital region and anterior portions of the cranium of the four specimens are very much like the two examples of *A. littoralis* from Mindanao. Lengths and breadths of the maxillary tooththrows are practically identical (table 5).

More specimens of this medium-sized rat with small teeth are needed from both Mindanao and Negros before the relationship between the two populations can be resolved. Until that time, I provisionally identify the Negros sample as a brightly colored form of *A. littoralis* with a white belly and partially bicolored tail.

A SPECIES SUMMARY

Characteristics of skins and skulls point to two primary groups of species within *Apomys*. One group consists of *A. datae*, now recorded only from the highlands of northern Luzon. The combination of distinctive features setting this species apart from all the others are large body size (except for *A. sa-*

cobianus, the largest in the genus), brown and white dorsal pattern on upper surfaces of each hind foot, a large and elongate skull with a squarish braincase, and a primitive configuration of the pterygoid plates and stapedial foramina. Those shapes reflect an arterial circulation in which the internal maxillary artery is a continuation of a large stapedial and emerges from the middle lacerate foramen to pass in a shallow groove along the ventral surface of the pterygoid plate and enter the posterior opening of the alisphenoid canal, described previously as the *datae*-pattern. In features associated with the skin and skull, *A. datae* has no close relatives among any of the other species of *Apomys*.

The other primary assemblage contains *A. abrae*, *A. sacobianus*, *A. musculus*, *A. microdon*, *A. insignis*, *A. hylocetes*, and *A. littoralis*. The features uniting these species are those involved in the *datae*-*hylocetes* arterial pattern described in detail previously. In each, the stapedial foramen is tiny and there is a diagonal groove or canal in the alisphenoid portion of each pterygoid plate. The stapedial artery is very small and passes into the bullar capsule only as far as the otic region. Instead of being a continuation of the stapedial artery, the internal maxillary artery branches from the internal carotid after it has entered the cranial cavity through the carotid canal. The internal maxillary artery then courses along in a groove or deep canal diagonally through each pterygoid plate to eventually pass through the anterior opening of the alisphenoid canal, which transmits it into the sphenoidal fissure.

In *A. abrae* and *A. sacobianus*, the alisphenoid portion of each pterygoid plate is complete and the internal maxillary artery courses along the dorsal surface of the plate in a deep groove. This feature, along with large body size (especially in *A. sacobianus*), a sharply bicolored tail (brown above, white below, from base to tip) that is as long or only slightly longer than the combined lengths of head and body, hind feet with white dorsal surfaces, and a geographic distribution encompassing only Luzon (based on available specimens) unite the two species in a subgroup distinct from the other species of *Apomys*.

The remaining species to be considered—*A. musculus*, *A. microdon*, *A. insignis*, *A. hy-*

locetes, and *A. littoralis*—are of small or medium body size in which the canal for the internal maxillary artery is partially open and part of the artery is exposed on the ventral surface of each pterygoid plate. That feature, combined with bright tawny upperparts, buffy underparts, brown or pale buffy feet, and patterning on the tail (usually monocolored or mottled, rarely sharply bicolored) suggest the five species may be more closely related to each other than to any others in *Apomys*.

Apomys musculus is the smallest in body size of any *Apomys* and is known from Luzon and Mindoro. Its morphological characteristics do not tie it closely to *A. datae*, *A. abrae*, or *A. sacobianus*, the other species occurring on Luzon. It may be a shorter-tailed and smaller-bodied version of *A. microdon* but it is also similar to *A. littoralis* in body and skull conformations; the latter resembles a larger-bodied counterpart of *A. musculus*. These suggestions of relationships should be tested with additional specimens and other kinds of data.

Apomys microdon and *A. insignis* are closely related to one another. The former occurs on the islands of Catanduanes, Leyte, and Dinagat and is a smaller-bodied and brighter-colored counterpart of *A. insignis*, which is known only from Mindanao. The combination of medium body size, a very long tail relative to length of head and body, and elongate hind feet set these two species apart from any other *Apomys*.

Apomys hylocetes is still represented only by Mearn's original series collected at the turn of the century from Mount Apo in southern Mindanao. Except that it has been taken between 6000 and 7500 feet; that it is sympatric with *A. insignis*; that it resembles *A. insignis* except for its shorter tail relative to head and body, shorter and wider feet, and more inflated braincase, very little is known about its habits, habitat, or relationships.

Apomys littoralis lives on Mindanao and is the smallest in body size of the three species known from that island. The conformations of its body and skull resemble those of *A. hylocetes* on the one hand and *A. musculus* on the other. Whether *A. littoralis* is the Mindanao counterpart of *A. musculus* or a species of small body size more closely related to *A.*

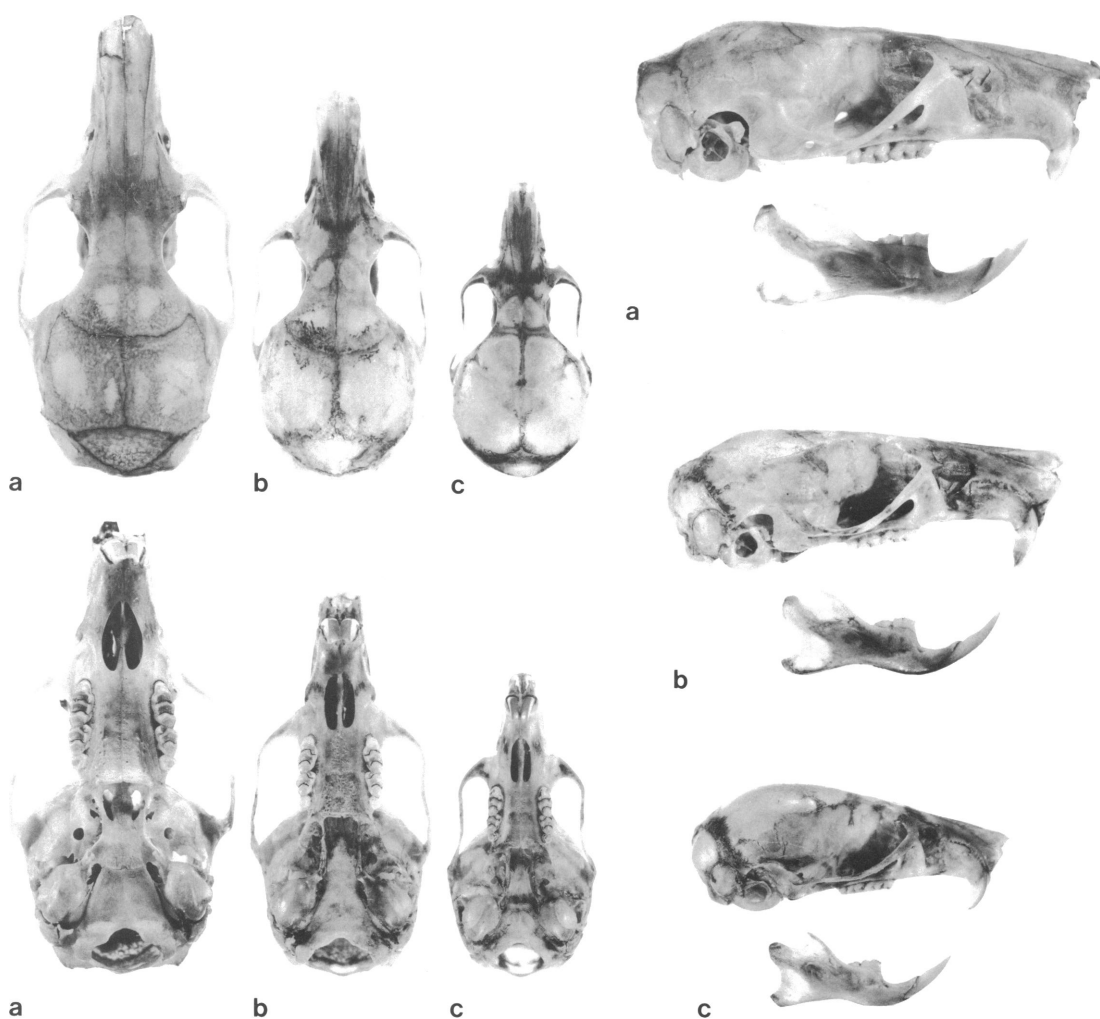


FIG. 8. Views of crania and dentaries from adult *Apomys* of large, medium, and small body sizes: a, *A. datae* (AMNH 252475), Luzon; b, *A. insignis* (AMNH 207567), Mindanao; c, *A. musculus* (MMNH 12971), Mindoro. All $\times 1.5$.

hylocetes remains to be determined. *Apomys littoralis* also occurs on Negros Island if my identification of a small series from there is correct.

APOMYS DESCRIBED AND CONTRASTED

In his monograph on the families and genera of rodents, Ellerman in 1941 initially recognized *Apomys* as a valid genus. Later, however, Ellerman (1947–1948, p. 265) arranged *Apomys* as a subgenus of *Rattus*, explaining

that he would use the name “for the highly specialized rats which have both the palate and palatal foramina shortened and the bullae reduced in size. All these characters are departures from what is found in the typical subgenus *Rattus*, in which the bullae are large, and the palate and palatal foramina are as a rule long.” He included *musschenbroekii*, *hellwaldii*, *alticola*, *rajah*, *surifer*, *baeodon*, *datae*, *niobe*, *insignis*, *hylomyoides*, and *ohiensis* in the subgenus. A year after this arrangement was published, Ellerman (1949) added *sakeratensis*, *hylocetes*, *petraeus*, *ma-*



FIG. 9. *Rattus rattus diardii*. Views of cranium and dentary of an adult (AMNH 250104) from West Java. About $\times 1$. Compare this specimen with those *Apomys* in figure 8.

jor, *musculus*, and *hollisteri* (a replacement name for *microdon*) to the species in subgenus *Apomys*.

In 1951, Ellerman and Morrison-Scott substituted *Lenothrix* for *Apomys*. The subgenus was still based on short palate, short palatal foramina, and small bullae, all primitive traits (Musser, 1981a). Misonne (1969), however, has shown that *Lenothrix* is distinctive in its dental traits and not closely related to either *Rattus* or *Apomys*. His view has been reinforced by subsequent studies of *Lenothrix* based on both cranial and dental features (Medway and Yong, 1976; Musser, 1981a).

Except for the taxa that were associated with *Apomys* by Mearns (1905), Miller (1910), and Hollister (1913), all the other species in subgenus *Lenothrix* have been differently allocated since the publication of Ellerman's lists. The genus *Maxomys* now embraces *musschenbroekii*, *hellwaldii*, *alticola*, *rajah*, *surifer*, *baeodon*, and *hylomy-*

oides (Musser, Marshall, and Boeadi, 1979); *niobe* is a species of New Guinea *Rattus* (Tate, 1951); *ohiensis* belongs in a genus of its own, *Srilankamys* (Musser, 1981a); and *sakeratensis*, originally based on a composite holotype, is used to designate a subspecies of *Rattus losea* (Marshall, 1977).

None of the species discussed above are phylogenetically close to *Apomys*. Below, I present the external, cranial, mandibular, and dental characteristics of *Apomys* that distinguish it first from *Rattus* (exemplified by species in the subgenus *Rattus*), and then from *Maxomys* and the Ceylonese *Srilankamys ohiensis*, the groups to which Ellerman had tied the species of *Apomys*. The points of contrast not only distinguish *Apomys* from *Rattus* and the other groups but add up to a description of the genus as well.

Apomys VERSUS *Rattus*

Apomys possesses the features listed below that distinguish it from *Rattus*.

1. The hind feet of *Apomys*, each with six nearly smooth plantar pads, are long and narrow, especially all the digits. The feet are wider relative to their lengths in *Rattus*, the hallux tends to be shorter and wider, the plantar pads are larger and higher forming a relatively greater part of the plantar surface, and their surfaces are sculptured with semicircular striations (fig. 7).

2. Only two pairs of mammae are present in *Apomys*, both inguinal. There are at least three pairs and usually five or six pairs of mammae in species of *Rattus*.

3. Dorsolateral margins of the interorbital and postorbital areas are smooth, not outlined by beading or ridges. The braincase is also smooth, either without temporal ridges or marked only by weak and indistinct ridging (fig. 8). In *Rattus*, conspicuous strong ridges outline the dorsolateral margins of the interorbital area and sweep back along the braincase to the occiput (fig. 9).

4. In each orbit of *Apomys*, the dorsal palatine foramen is just behind the sphenopalatine foramen (fig. 11B); in some specimens the two have merged to form one long and narrow opening near the bottom of the orbit at a place above the union of the first and second upper molars. In specimens of *Rattus*,

the sphenopalatine foramen is above the place where the first molar overlaps the second but the dorsal palatine foramen is over the third molar and widely separated posteriorly from the sphenopalatine foramen (fig. 11A).

5. Sides of the braincase behind the squamosal roots of the zygomatic arches are smooth because there is no ridgelike extension of the root posterior to the occiput (figs. 8, 10). In *Rattus*, each squamosal root extends as a conspicuous ridge to the occiput (fig. 9).

6. The squamoso-mastoid foramen occurs in most specimens of *Apomys* and is large in many of them, so spacious that it separates the squamosal above the back of each bulla into a dorsal portion and slim ventral part that is called a tympanic hook or hamular process of the squamosal (figs. 10, 12B). Each squamoso-mastoid foramen in *Rattus* is small, confined to the suture between the squamosal and mastoid, and obscured by the lamboidal ridge. The squamosal above the back of the bulla is intact and neither perforated nor notched by the squamoso-mastoid foramen (fig. 12A).

The squamoso-mastoid is the term Wahlert (1974, p. 374) introduced "for the foramen, which is present in many rodents, on the occipital surface between the squamosal and the mastoid. It transmits a vein." The opening is very small and inconspicuous in most species of Philippine murids, as it is in species of *Rattus*. In other species, such as those in *Apomys*, the foramen has enlarged and become a vacuity in the squamosal bone. Hill (1935, p. 127) called this opening the subsquamosal foramen and Wahlert (1974, p. 374) referred to it as one of the temporal foramina. My hypothesis is that this opening in the squamosal, bounded posteriorly by the mastoid and separated by a hook of squamosal bone from the postglenoid cavity and periotic bone just above the back of the bulla, represents an expansion of the squamoso-mastoid foramen. Among some species of murids, the foramen ranges in size from a small notch in the squamosal to a spacious fenestra. The small notch is always a slight enlargement of the squamoso-mastoid foramen where it pierces the squamosal. The increase in size of the vacuity in the squamosal seems to represent further erosion of the squamosal by the foramen. No comparable enlargement occurs in the mastoid. Although the small squamoso-mastoid foramen between the squamosal bone and mastoid transmits a vein, according to Wahlert (1974), the enlarged vacuity in the squamosal, such as that in *Apomys*, does not transmit a vessel and is usually covered by thin tissue.

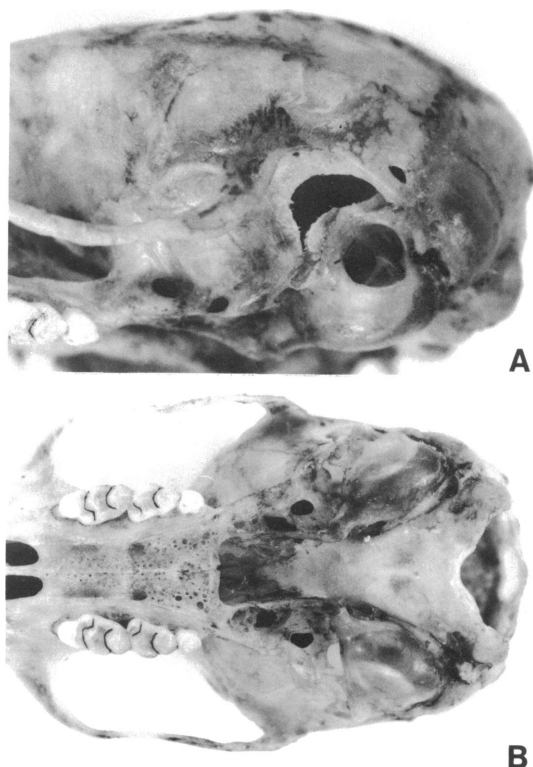


FIG. 10. *Apomys insignis* (AMNH 207567). A, view of alisphenoid region and squamosal above bulla. B, view of palatal area and basicranium.

men where it pierces the squamosal. The increase in size of the vacuity in the squamosal seems to represent further erosion of the squamosal by the foramen. No comparable enlargement occurs in the mastoid. Although the small squamoso-mastoid foramen between the squamosal bone and mastoid transmits a vein, according to Wahlert (1974), the enlarged vacuity in the squamosal, such as that in *Apomys*, does not transmit a vessel and is usually covered by thin tissue.

7. Except for half the sample of *A. datae* and a few specimens of the other species (table 8), a strut of alisphenoid bone forms the lateral surface of the alisphenoid canal and separates a foramen ovale accessorius from the coalesced masticatory-buccinator foramina in *Apomys* (fig. 13B). The alisphenoid

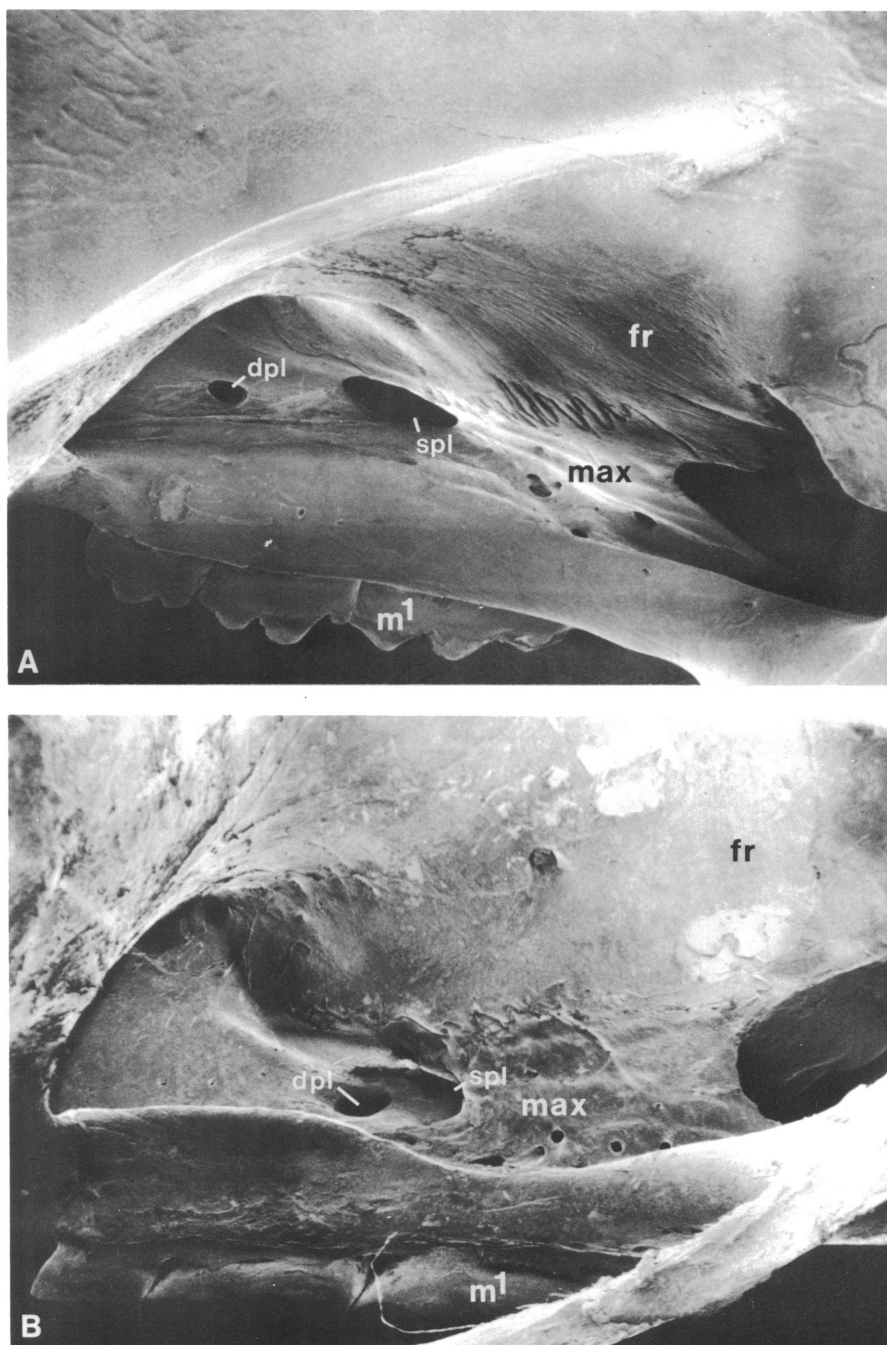


FIG. 11. Orbital views of adult *Rattus* and *Apomys*. Position of sphenopalatine foramen (**spl**) relative to dorsal palatine foramen (**dpl**) in right orbit of *R. exulans* (AMNH 223141) is contrasted with relative positions of these foramina in *A. insignis* (AMNH 207571).

Other abbreviations: **fr**, frontal bone; **max**, maxillary bone; **m¹**, first upper molar. Anterior is to the right.

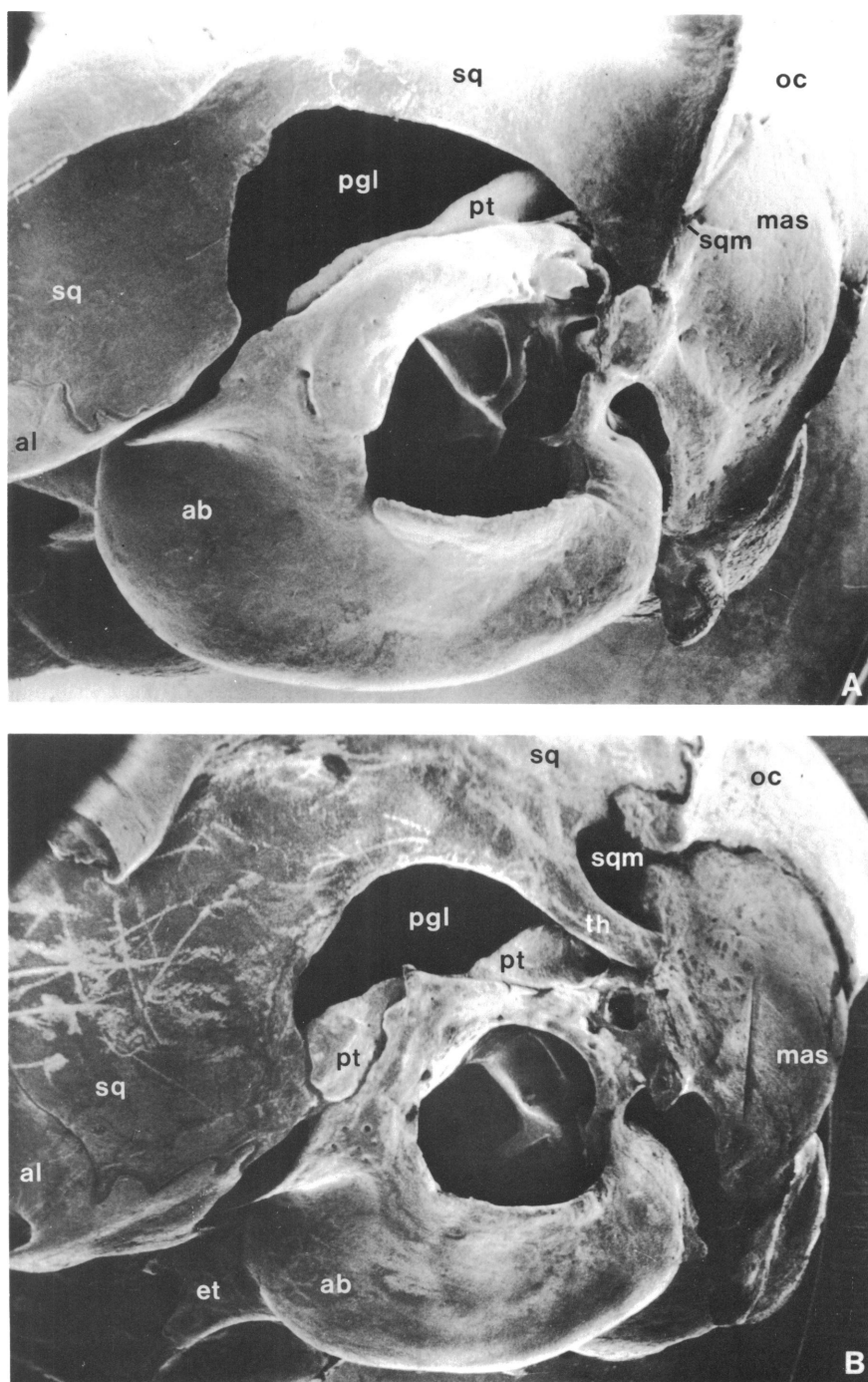


FIG. 12. Views of squamosal and bullar regions in adult *Rattus* and *Apomys*. A, *R. exulans* (AMNH 223141) is compared with *A. insignis* (AMNH 207571).

B. *Abbreviations:* **ab**, auditory bulla; **al**, alisphenoid bone; **et**, bony eustachian tube; **mas**, mastoid portion of the petromastoid complex; **oc**, occipital bone; **pgl**, postglenoid vacuity; **pt**, petrotic portion of the petromastoid; **sq**, squamosal bone; **sqm**, squamoso-mastoid foramen (view A) or fenestra (view B); **th**, tympanic hook of squamosal bone. See text for additional descriptions.

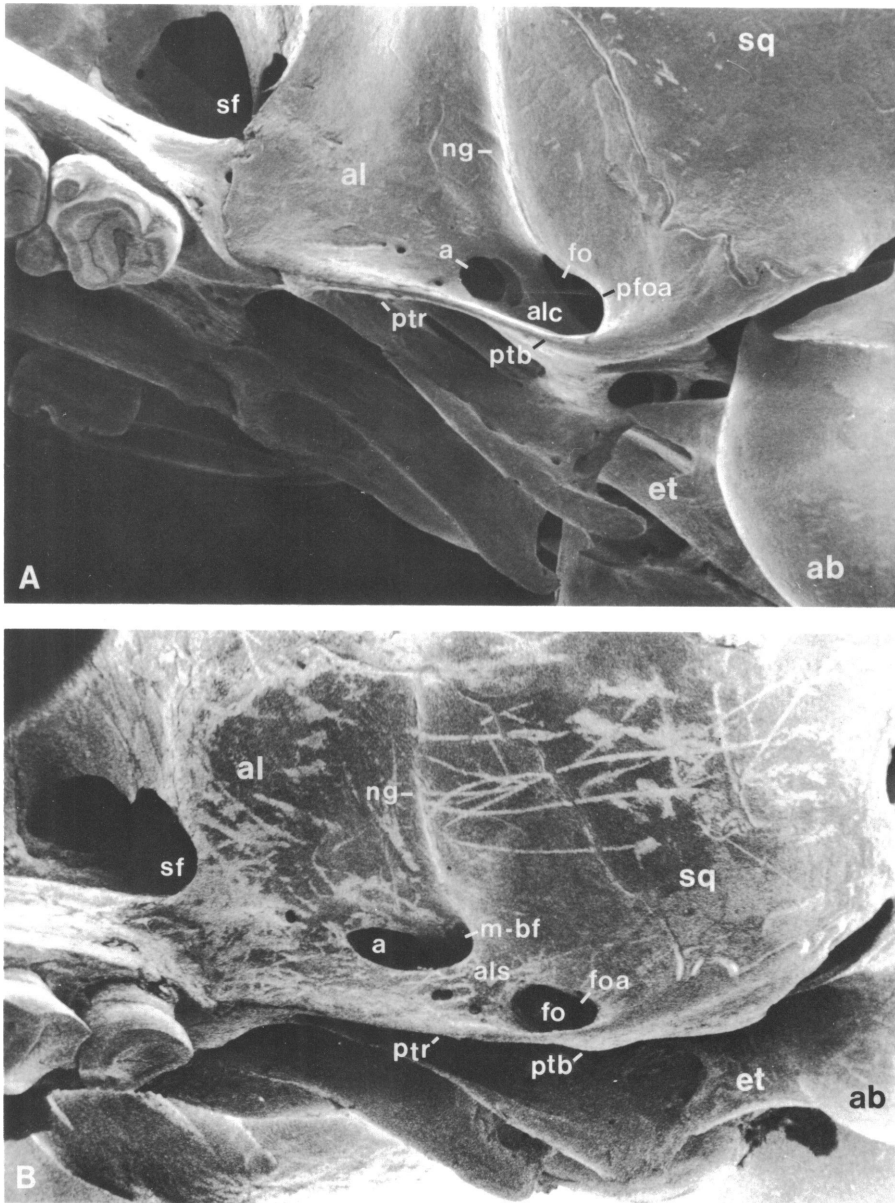


FIG. 13. Views of left alisphenoid regions in adult *Rattus* and *Apomys*. A, *R. exulans* (AMNH 223141), in which alisphenoid canal is an open channel. B, *A. insignis* (AMNH 207571) with a lateral strut of alisphenoid bone concealing alisphenoid canal. See text for additional comparisons and descriptions.

Abbreviations: a, anterior opening of alisphenoid canal; ab, auditory bulla; al, alisphenoid bone; alc, alisphenoid canal; als, lateral strut of alisphenoid bone; et, bony eustachian tube; fo, foramen ovale; foa, foramen ovale accessorius (in view B, foramen ovale is actually medial to foramen ovale accessorius); m-bf, coalesced masticatory–buccinator foramina; ng, channel containing most of masticatory nerve, which emerges directly from foramen ovale in configuration A, or from masticatory–buccinator foramina in configuration B, pfoa, posterior margin of foramen ovale accessorius; ptb, pterygoid bridge; ptr, pterygoid ridge; sf, sphenoidal fissure; sq, squamosal bone. See text, Hill (1935), Wahlert (1974), and Musser (1981a) for additional description.

TABLE 8
**Presence (+) or Absence (–) of Alisphenoid Strut
 in Species of *Apomys***
 (expressed in percentage; number of specimens in
 parentheses)

Species	Alisphenoid Strut	
	+	–
<i>A. datae</i>	50 (9)	50 (9)
<i>A. abrae</i>	88 (28)	12 (4)
<i>A. sacobianus</i>	100 (1)	—
<i>A. musculus</i>	100 (9)	—
<i>A. insignis</i>	89 (77)	11 (10)
<i>A. hylocetes</i>	100 (4)	—
<i>A. microdon</i>	100 (31)	—
<i>A. littoralis</i>	80 (4)	20 (1)

canal is open behind the strut and transmits the internal maxillary artery and masticatory nerve, which pass through the anterior opening of the canal into the sphenoidal fissure. In other groups of rodents, squirrels for example, the internal maxillary vein also courses through the alisphenoid canal (Wahlert, 1974) but not in muroid rodents (Hill, 1935). The masseteric and buccinator branches of the maxillary nerve pass dorsal to the artery and emerge from the masticatory–buccinator foramina. The buccinator nerve runs anteriorly, most of the masticatory courses onto the lateral surface of the alisphenoid bone in a shallow channel or groove. The anterior opening of the alisphenoid canal can be seen anterior to the strut and is separate from the foramen ovale (which is medial to the foramen ovale accessorius), not coalesced with it as is the configuration in some examples of *Crateromys* (Musser and Gordon, 1981).

The foramen ovale accessorius was defined by Wahlert (1974, p. 373). In *Apomys*, the foramen is complete only in those specimens with a strut of alisphenoid bone forming the lateral wall of the alisphenoid canal. The dorsal and anterior margins of the foramen are defined by the posterior edge of the strut. The foramen appears to be absent in species without an alisphenoid strut and I once described it that way (Musser, 1981a). Actually, with-

out the strut the foramen ovale accessorius is incomplete, represented only by posterior and ventral margins that are formed by a rim of alisphenoid bone and the pterygoid bridge. Another way to look at the configuration is to consider the masticatory and buccinator foramina, which would be complete at the anterior margin of the strut if that element were present, to have coalesced with the foramen ovale accessorius.

In *Rattus*, the lateral alisphenoid strut is missing (fig. 13A). The foramen ovale accessorius is merged with the buccinator–masticatory foramina. The anterior opening of the alisphenoid canal, the channel-like canal itself, and the foramen ovale are exposed. The masticatory and buccinator branches of the maxillary nerve emerge directly from the foramen ovale. The internal maxillary artery, but not the internal maxillary vein, passes along the bottom of the open alisphenoid canal and then through the anterior opening of the canal into the sphenoidal fissure. This is the usual pattern in murids (Hill, 1935).

8. The incisive foramina are wide and short, their posterior margins located before the anterior faces of the first upper molars (figs. 8, 14B). The incisive foramina are narrower and long in *Rattus*, their posterior edges situated past the front faces of the molars (figs. 9, 14A).

9. The bony palatal bridge of *Apomys* is wide and long, partly a reflection of the short incisive foramina. The posterior edge of the bridge is nearly straight, set off by a conspicuous ridge, and located just posterior to the back faces of the third molars (figs. 8, 10, 14B). In *Rattus*, the palatal bridge is narrower relative to size of the cranium. The bridge is also long, but that length expresses the posterior extension of the bridge past the molar rows where it forms a long and wide shelf. The posterior edge of the bridge is usually smooth (figs. 8, 14A).

10. The palatal bridge is thin in *Apomys*. Its surface along the middle of the maxillary portion and over the entire palatines is densely pitted and perforated. Some of the openings at the posterolateral margins of the bridge are large and occur in about the same

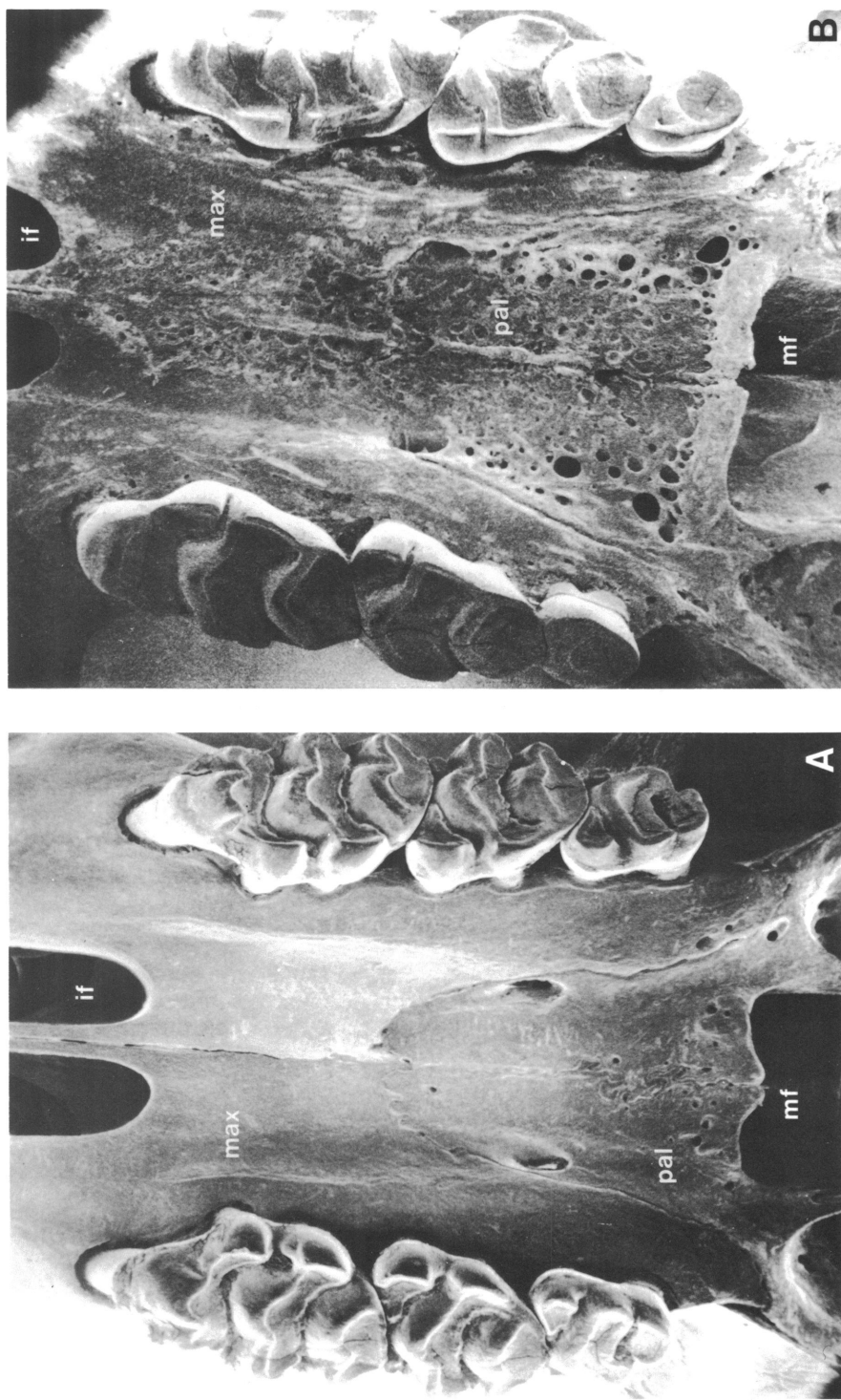


FIG. 14. Palatal views of adult *Rattus* and *Apomys*. A, *R. exulans* (AMNH 223141), in which palatal bridge is smooth over most of its surface. B, *A. insignis* (AMNH 207571), which has a pitted and perforated bony palate. Note also deep penetration of incisive foramina and narrow mesopterygoid fossa in *Rattus* compared with shorter incisive foramina and broader fossa in *Apomys*.

Abbreviations: **if**, incisive foramina; **max**, maxillary bone; **mf**, mesopterygoid fossa; **pal**, palatine bone.

place in many specimens (fig. 8B). The bridge is thicker in *Rattus*; its surface is smooth in most specimens. The surface may be slightly rough in a few examples, and some specimens are pitted and perforated along the midline of the bridge and at the posterior margin of the palatines (fig. 8A).

11. The mesopterygoid fossa is spacious and nearly as wide as the palatal bridge between the first molars. Its walls are breached by short sphenopalatine vacuities (figs. 3B, 8), so short they do not extend into the orbits. The fossa is much narrower than the palatal bridge in *Rattus*. The sphenopalatine vacuities are huge, so spacious in some specimens that the anterior part of the basisphenoid and the back of the presphenoid seem suspended in air (figs. 3A, 9). The vacuities extend into the orbits where their anterior margins can be seen in a side view of the cranium.

The sphenopalatine vacuities in both *Apomys* and *Rattus* are covered by thin tissue and do not appear to transmit either blood vessels or nerves.

12. The posterolateral margin of each pterygoid platform is rounded and the transition from the sides of the braincase to the platform behind the foramen ovale is smooth and level (fig. 3B). In *Rattus*, the posterolateral margin is formed by a high continuation of the pterygoid ridge (fig. 3A).

13. Each pterygoid fossa in *Apomys* is wide and shallow, as seen from a ventral view. The anterior half is breached by a spacious sphenopterygoid vacuity, similar in size to that in *Rattus* (fig. 3A and B). In all the species of *Apomys* except *A. datae*, the configuration of the alisphenoid wing of each pterygoid plate, the size of the stapedia foramen, and the arterial circulation in these regions is as described previously for the *A. abrae-hylocetes* Group (fig. 2A and B).

In *Rattus*, each pterygoid fossa is wide but deeper than that in *Apomys*. The surface of the pterygoid platform between the transverse canal and foramen ovale is smooth (fig. 3A). Each internal maxillary artery emerges from the middle lacerate foramen to run alongside the ridgelike pterygoid bridge and disappear anteriorly beneath the pterygoid platform above the foramen ovale (as seen from a ventral view). The size of the stapedia

foramen, the general configuration of the alisphenoid portion of each pterygoid plate, and the arterial pattern in those places is similar to that previously described for *A. datae*. (fig. 2C and D).

14. Each auditory bulla is small relative to size of the cranium in *Apomys* (in 20 *A. insignis* from the Malindang Mountains of Mindanao, the mean for GLS is 32.0 mm, that for LB is 4.3 mm, and the ratio GLS/LB is 13 percent; the means in 20 *Rattus rattus diardii* from West Java are 40.2 mm (GLS) and 6.5 mm (LB), and the GLS/LB is 16 percent). The dorsal margin of the bulla and the periotic are separated from the squamosal bone by a spacious postglenoid vacuity (fig. 12B). Each bony eustachian tube is a long and slender cylinder (fig. 3B). In *Rattus*, a large postglenoid vacuity also separates the dorsal part of each bulla and the periotic from the squamosal, but the bulla itself is absolutely and relatively much larger. Each eustachian tube is wide and short (fig. 3A).

15. On the lingual surface of each dentary, a shelflike ridge extends from the back of the toothrow to the mandibular foramen but not onto the condylar process so that the lingual surface of that process is smooth. In *Rattus*, the ridge extends beyond the mandibular foramen as a low ridge or mound out to the condyle.

16. Each first upper molar in most specimens of *Apomys* is anchored by three primary roots, an anterior, posterior, and lingual; a small labial rootlet or nubbin occurs in some specimens. Each second upper molar is anchored by three roots. Each third upper molar has two roots in most specimens and three in a few examples. Five roots (anterior, posterior, divided lingual, and large labial) anchor each first upper molar in *Rattus*; four roots occur under each second upper molar; and three roots anchor each third upper molar.

17. Each lower molar in *Apomys* is anchored by two roots, an anterior and posterior. Four roots (large anterior and posterior, small lingual and labial) anchor each first lower molar in *Rattus*; the second and third molars each have three roots.

18. Occlusal patterns of the first and second upper molars in *Apomys* are simple. The chewing surfaces consist of chevron-shaped

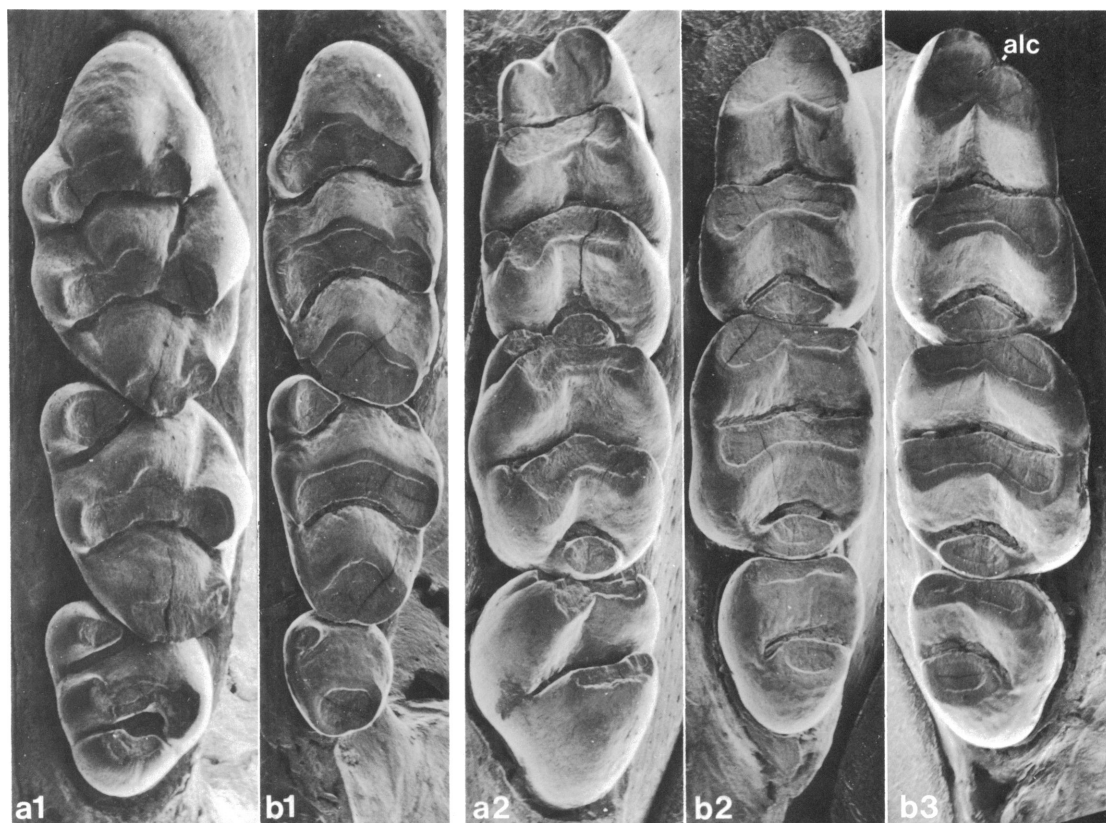


FIG. 15. Occlusal views of maxillary (left two rows) and mandibular (right three rows) molar rows of adult *Rattus rattus* (AMNH 84667) and *Apomys musculus* (MMNH 12971). Maxillary rows: a1, *Rattus* (left side, $LM^{1-3} = 6.6$ mm.); b1, *Apomys* (left side, $LM^{1-3} = 4.6$ mm.). Mandibular rows: a2, *Rattus* (left side, $LM_{1-3} = 6.1$ mm.); b2, *Apomys* (left side, $LM_{1-3} = 4.3$ mm.); b3, *Apomys* (right side, $LM_{1-3} = 4.3$ mm.). Note anterior labial cleft (alc) in b3, which indicates solid heart-shaped anterior half of each M_1 to have been formed from fusion of the two front laminae. See text for further description and comparisons. LM is crown length of either upper or lower molar row.

and oblong laminae, all without cuspidate configuration, even in young rats (figs. 15b1, 16A). The laminae abut tightly against one another. The occlusal surfaces in *Rattus* consist of broadly connected cusps, which form rows that are clearly cuspidate (figs. 15a1, 16B). The rows are farther apart than they are in *Apomys*.

19. Cusp t3 is indistinct in *Apomys*. It is either missing from each first upper molar or united so completely with cusp t2 that its identity is obliterated. Cusp t3 is absent from each second upper molar in most specimens, and from each third upper molar (fig. 15b1). In most species of *Rattus*, cusp t3 is large and discrete on each first molar, and either pres-

ent or absent on each second and third molar (fig. 15a1).

20. Cusp t9 is indistinct on each first and second upper molar. The cusp is merged so tightly with the central cusp t8 that the posterior lamina of each tooth appears oblong in outline and unformed of cusps (fig. 15b1). Cusp t9 on the first and second molar is large and discrete in *Rattus*, even after much wear (fig. 15a1).

21. Each third upper molar in *Apomys* is very small relative to the other molars in the row, shaped like a peg, and mostly without discrete cuspidation except for a small cusp t1 at the anterolingual margin (figs. 15b1, 16A). In *Rattus*, each third molar is much

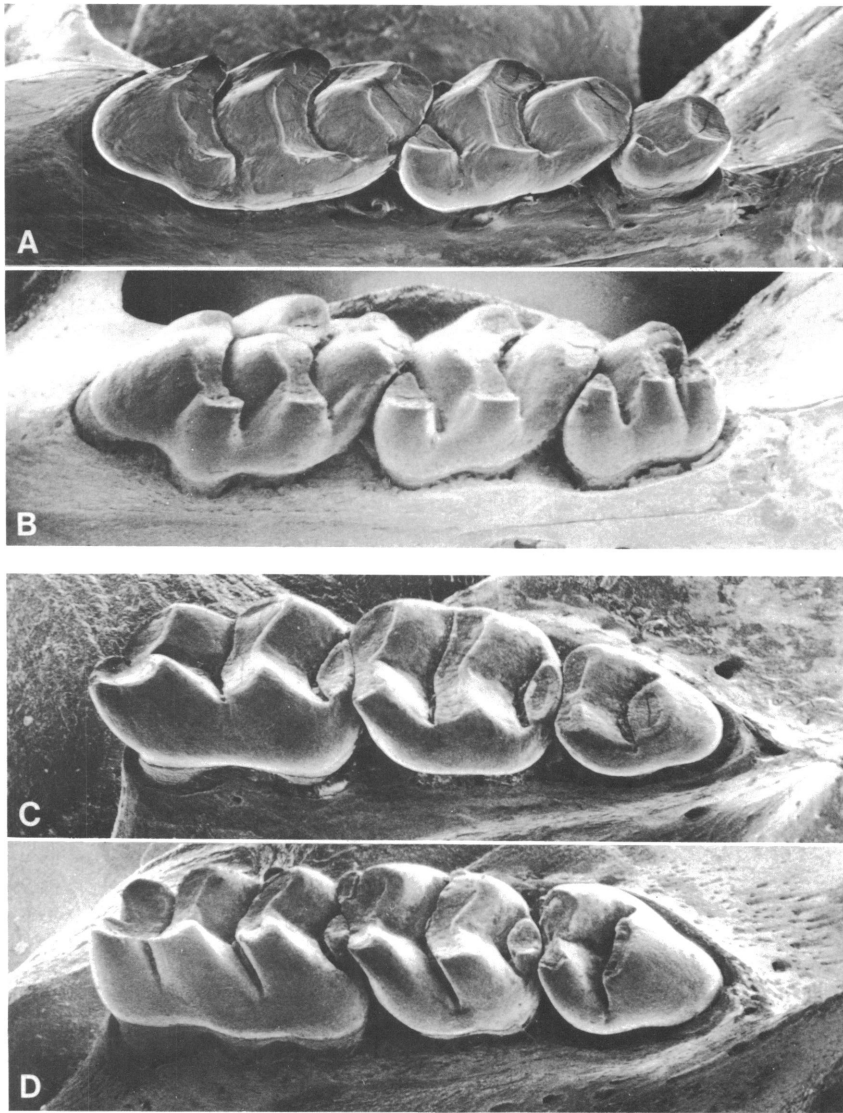


FIG. 16. Oblique views of molar rows comparing wear pattern in *Rattus* with steplike configuration of wear in *Apomys* (using the same specimens illustrated in fig. 11). *Apomys musculus*: A, left maxillary row; C, right mandibular row. *Rattus rattus*: B, left maxillary row; D, right mandibular row.

larger relative to the other molars and squarish or triangular in occlusal outline. It clearly consists of a large cusp t1, usually a small cusp t3, a row formed of cusps t4, t5, and t6, and a posterior lamina formed from cusps t8 and t9 (figs. 15a1, 16B).

22. Occlusal patterns of the lower molars in *Apomys* are simple, consisting of either chevron-shaped or nearly transverse, thick

laminae set closely to one another (figs. 15b2, 16C). Anterior and posterior labial cusplets are absent. No anterolabial cusps occur on the second and third molars. The occlusal patterns are more elaborate in *Rattus*. The laminae are not as close to each other, all are relatively thinner and all clearly consist of broadly connected cusps (figs. 15a2, 16D). Posterior labial cusplets occur on all three

teeth, an anterior labial cusplet is present on each first molar in some specimens, and anterolabial cusps are found on the second and third molars.

23. The occlusal surface of each first lower molar in *Apomys* appears to be formed of three structures rather than four as it is in *Rattus*. The chewing surfaces consist of a wide posterior cingulum, then a posterior lamina, and a solid structure forming the anterior half of each tooth that resembles an inverted heart-shape in occlusal outline (figs. 15b2 and b3, 16C). This uncuspidate mass is apparently formed from the fusion of a chevron-shaped lamina with a smaller and much narrower anterior lamina. The latter probably represents the fused anterolabial and anterolingual cusps. The configuration is present in young and old rats. A short anterolabial cleft is present in some specimens (fig. 15b3), the only indication that the heart-shaped chewing surface has resulted from the fusion of cusps and laminae. In contrast to the shape in *Apomys*, four primary chewing surfaces form the occlusal area of each first lower molar in *Rattus* (figs. 15a2, 16D). The posterior half of each tooth consists of a posterior cingulum and posterior lamina, as it does in *Apomys*. The anterior half of each tooth, however, consists of a cuspidate lamina pressed against, but not merged with an anterior lamina. That latter structure is made up of a large anterolingual cusp set at nearly a right angle to a smaller anterolabial cusp. The front lamina is nearly as wide as those behind it. A small anteroventral cusp sits at the front of the tooth in some specimens.

24. Wear surfaces of the molars are aligned in a steplike configuration in *Apomys* (fig. 16A and C). The effect results from the simple, slanting, closely set, and chunky laminae. The wear surfaces are not as uneven in *Rattus*, the chewing areas being nearly level with each other, especially in the upper molars (fig. 16B and D).

Apomys VERSUS *Srilankamys* AND *Maxomys*

Srilankamys ohienensis is known only from the mountain forest of Ceylon in Uva Province. Its morphological features have been described elsewhere (Musser, 1981a). The

definition and contents of *Maxomys* were outlined by Musser et al. (1979). Most of the 16 species of *Maxomys* occur on the Sunda Shelf; the rest live in Indochina, Sulawesi, and the Mentawai Islands (see the map in Musser, 1981a, p. 318). *Srilankamys ohienensis* and the species of *Maxomys* contrast with those of *Apomys* by possessing the following features (fig. 17).

1. The species of *Maxomys* have either three or four pairs of mammae; *Srilankamys ohienensis* has four pairs. All known species of *Apomys* have only two pairs.

2. In *Maxomys* heavy shelflike ridges extend from the interorbital region along the dorsolateral sides of the postorbital area and braincase to the occiput. The ridging is slight but present in *S. ohienensis*. In contrast, the interorbital and postorbital regions, as well as the braincase, are smooth in *Apomys*.

3. The strut of alisphenoid bone forming the lateral wall of the alisphenoid canal is absent from most specimens of *Maxomys*. The coalesced masticatory-buccinator foramina are merged with the foramen ovale accessorius. The alisphenoid strut is present in *S. ohienensis* and most specimens of *Apomys*. The strut separates the coalesced masticatory-buccinator foramina from the foramen ovale accessorius.

4. The squamoso-mastoid foramen is confined to the suture between the squamosal bone and mastoid in *S. ohienensis* and the species of *Maxomys*. The foramen forms either a notch or large fenestra in the squamosal above the back of each bulla in specimens of *Apomys*.

5. The palatal bridge is shorter and narrower in *Maxomys* and ends well before the posterior margins of the molar rows. The bridge is not pitted or perforated like that in *Apomys*, and lacks a truncate and ridged posterior edge. The palatal bridge is slightly longer in *S. ohienensis*, but otherwise similar in configuration to that in *Maxomys*.

6. In *Maxomys* and *S. ohienensis* the anterior two-thirds of each pterygoid fossa is ossified, not fenestrated by large sphenopterygoid openings, as is the configuration in *Apomys*.

7. In species of *Maxomys* and *Srilankamys* the size of the stapedial foramen, the configuration of the alisphenoid wing of each pterygoid plate, and the arterial circulation in

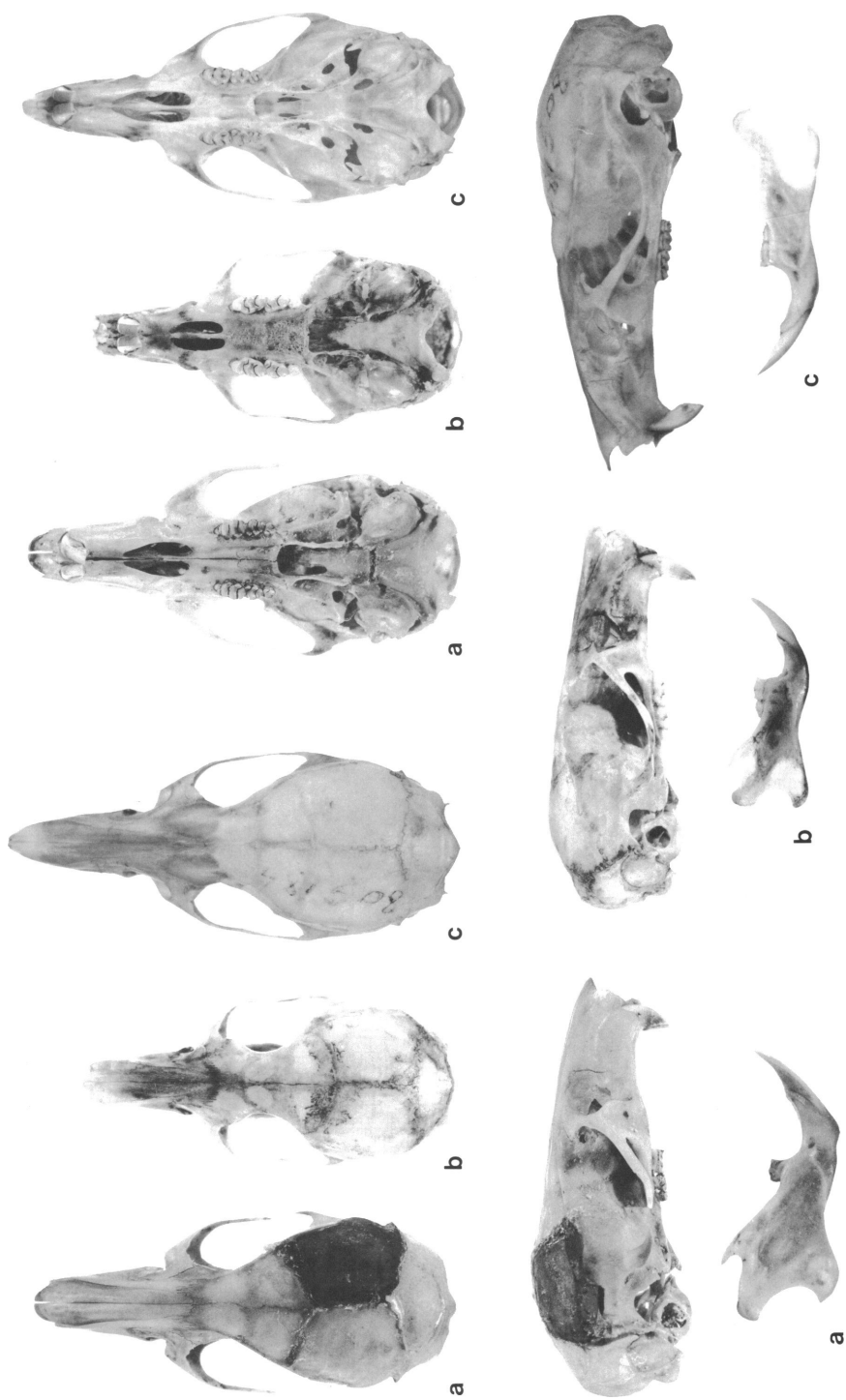


FIG. 17. Views of adult crania and dentaries contrasting *Srilankamys*, *Apomys*, and *Maxomys*; a, *Srilankamys obiensis* from Ceylon (USNM 519589); b, *Apomys insignis* from Mindanao (AMNH 207567); c, *Maxomys bartelsii* from West Java (AMNH 481508). See text and Musser (1981a) for other comparisons and discussion. Approximately $\times 1.5$.

those regions is like that previously described for *Apomys datae* and *Rattus*, and is unlike the *A. abrae-hylocetes* pattern that is characteristic of all the species of *Apomys* except *A. datae*.

8. The incisors (the enamel layers) of *S. ohiensis* are ivory-colored; *Apomys* and *Maxomys* have orange incisors.

9. Upper and lower molars in *S. ohiensis* and *Maxomys* have simple occlusal patterns but the cusps are better defined than in the noncuspidate laminar and oblong configurations in *Apomys*.

10. There is a posterior cingulum at the back of each first upper molar in *S. ohiensis*. Such a cusp is absent from all upper molars in *Apomys* and *Maxomys*.

11. Each third upper molar in *S. ohiensis* and *Maxomys* is small relative to the other teeth in the rows but still relatively larger than that in *Apomys*. Each third molar clearly consists of rows of cusps and is unlike the simple oblong peg with its small cusp t1, which is usual in all species of *Apomys*.

12. Anterolabial cusps are present on the second and third lower molars in *S. ohiensis* and in some species of *Maxomys*, but absent from all species of *Apomys*.

13. The anterolabial and anterolingual cusps on each first lower molar in *S. ohiensis* and *Maxomys* are broadly connected to form a small oblong lamina at the front of the tooth that does not merge with the lamina behind until after the rat is old and the teeth are well worn. In *Apomys*, the anterolingual and anterolabial cusps are fused together and to the lamina behind them to form a single noncuspidate structure that has the occlusal outline of an inverted heart-shape.

14. Wear surfaces of the upper and lower molars are nearly level in *Maxomys* and *S. ohiensis* (resembling that in *Rattus*), not step-like as in *Apomys*.

Apomys is not allied with either *Srilankamys* or *Maxomys*; the last two are affiliated with genera in Southeast Asia and not in the Philippines (Musser, 1981a). The three features used by Ellerman (1947–1948) to unite the species of *Apomys* with *ohiensis* and those

in *Maxomys* were short palate, short incisive foramina, and small bullae. All those traits are widely distributed among muroid rodents and likely primitive features (Musser, 1981a). The specializations found in *Apomys* (pitted and perforated palatal bridge with a truncate margin extending just posterior to the molar rows; large squamoso-mastoid vacuity in the squamosal bone above the back of each bulla; simple occlusal surfaces on the molars that wear in a steplike configuration; very small and peglike third upper molars; and the heart-shaped occlusal area forming the anterior half of each first lower molar) are not shared with species in *Srilankamys* or *Maxomys*.

QUESTIONS

Why did Ellerman unite *Apomys* and *Rattus*? Probably because he thought *Apomys* and *Melomys* were closely allied and *Melomys* was phylogenetically very close to *Rattus*, a view also held by others (Tate, 1951; Misonne, 1969). In his monograph on the families and genera of rodents, Ellerman (1941, p. 54) wrote that "Very doubtfully differentiated from *Rattus* are the mosaic-tailed Rats of North Australia and New Guinea, *Uromys* and *Melomys*, together with *Apomys* from the Philippines, which appears to be essentially like *Melomys*, but with a *Rattus*-tail." Later in that same volume (1941, p. 225) Ellerman noted that the molars of *Apomys* were exactly like those in *Melomys* and wrote of *Apomys* that "The genus connects *Melomys* with *Rattus* so closely that probably both *Apomys* and *Melomys* should be referred to *Rattus*." The tie between *Melomys* and *Rattus* was based upon the simple occlusal surfaces of the molars in *Melomys*, which were thought to be derived from a *Rattus*-like configuration. I cannot find other reasons for Ellerman's action.

Is *Apomys* closely related to *Rattus*? No. *Apomys* has a suite of specializations that are not, either individually or in combination, found in *Rattus*: the tiny stapedial foramen and configuration of the alisphenoid wing of each pterygoid plate, both reflecting the

abrae-hylocetes arterial pattern in the basiocranium (in all but one species); a large squamoso-mastoid vacuity or notch in the squamosal bone; a pitted and perforated wide palate with a truncate margin; the simple occlusal surfaces of the upper and lower molars; absence of labial cusplets on the lower molars and anterolabial cusps on the second and third lower molars; the very small and oblong peg that is the third upper molar; and the small anterior lamina that is fused with the one behind to form the heart-shaped anterior half of each first lower molar. Some of the cranial derivations are shared with other genera. Most of the dental features occur also in species of *Melomys*. The combination of a pitted and perforated bony palate with a truncate margin ending just posterior to the molar rows is unique to *Apomys*. None of the specializations of *Apomys* are shared with *Rattus*.

Rattus, relative to *Apomys*, possesses a set of cranial and dental features that I interpret to be derived (Musser, 1981a): ridges outlining the dorsolateral margins of the cranium from the interorbital region to the occiput; an open alisphenoid canal, and the masticatory-buccinator foramina merged with the foramen ovale accessorius; long incisive foramina that penetrate between the molar rows; a long palatal bridge that forms a wide shelf well posterior to the molar rows; spacious sphenopalatine vacuities that extend anteriorly to the backs of the orbits; a dorsal palatine foramen set far posterior to the sphenopalatine foramen in each orbit; large bullae relative to the size of the cranium; five roots beneath each first upper molar; and four roots beneath each first lower molar. These derivations are shared with many other genera, some of them endemic to the Philippine Islands, but not with *Apomys* (Musser, 1981a, 1981b). No individual or set of external, cranial, or dental features that I surveyed places *Apomys* close to *Rattus*.

What is the relationship between *Apomys* and *Melomys*? Nobody knows but I am trying to find out. An answer may also reveal the phylogenetic position of *Apomys* relative to other members of the murid fauna native to the Philippine Islands, the place of *Melomys* in the native fauna of northeastern Australia and New Guinea, and the nature of the re-

lationship between the native rats of the Philippine archipelago and those of the New Guinea and Australian region.

Ellerman was not the only one who associated *Apomys* closely with *Melomys*. Johnson (1962, p. 319) wrote that "In the simple structure and the steplike manner of wearing of the molar teeth, *Apomys* is closer to the genus *Melomys* than to *Rattus*." Based on his study of dentitions, Misonne (1969) recognized *Apomys* as a genus distinct from *Rattus* and included it within "The *Uromys* group," a cluster composed also of *Uromys*, *Solomys*, *Melomys*, *Pogonomelomys*, and *Xenuromys*. For Misonne (1969, pp. 146-147), "The main character of *Apomys* is the strong reduction of the first lamina of M_1 , a very special character only met with in the *Uromys* group; this character is not to be seen on any *Rattus*; the skull and other molar characters also show that *Apomys* is close to *Melomys*. . . . The dental characters of *Apomys* are closer to those of the *Uromys* group than to the *Rattus* group."

The configurations of the occlusal surfaces in *Apomys* do resemble those in some species of *Melomys*. The simple chewing surfaces, chevron-shaped and oblong noncuspidate laminae that are pressed close to one another, the small size of each third upper molar relative to the others in the row and its peglike shape, the similar shape of the anterior half of each first lower molar, and the steplike configuration of the chewing surfaces are traits common to both *Apomys* and some *Melomys*.

Even the shapes of crania in *Melomys* resemble those in species of *Apomys* (compare figures 8 and 19). But many of the cranial characters responsible for the close resemblances between the two genera are primitive. One that is probably not is associated with the bony palate. In some *Melomys*, that part of the palatal bridge formed by the palatine bones is pitted and perforated; however, the posterior margin of the bridge is unlike that in *Apomys* (fig. 19).

Whether this palatal trait and the diagnostic features of the molars indicate close phylogenetic alliance between *Apomys* and *Melomys* or reflect instead independent derivation requires further inquiry. Such a study must include definitions of the species

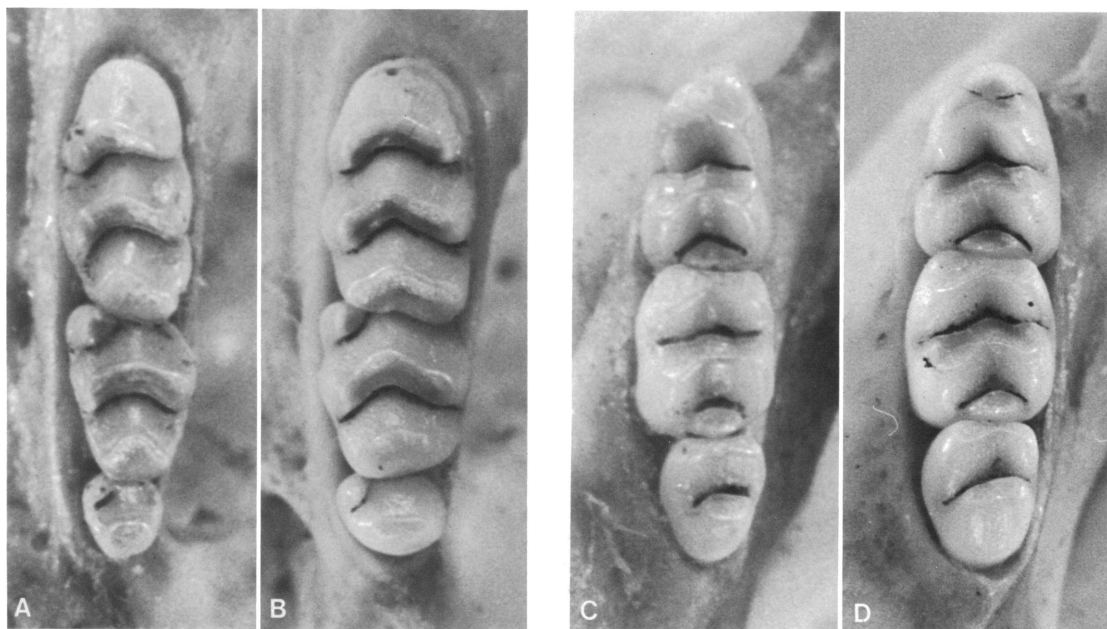


FIG. 18. Occlusal views of maxillary (left two rows) and mandibular (right two rows) molar rows of young adult *Melomys rufescens* (AMNH 104170) and *Apomys musculus* (MMNH 12971). Maxillary rows: A, *Apomys* (crown length, 4.6 mm.); B, *Melomys* (crown length, 6.4 mm.). Mandibular rows: C, *Apomys* (crown length, 4.6 mm.); D, *Melomys* (crown length, 6.4 mm.).

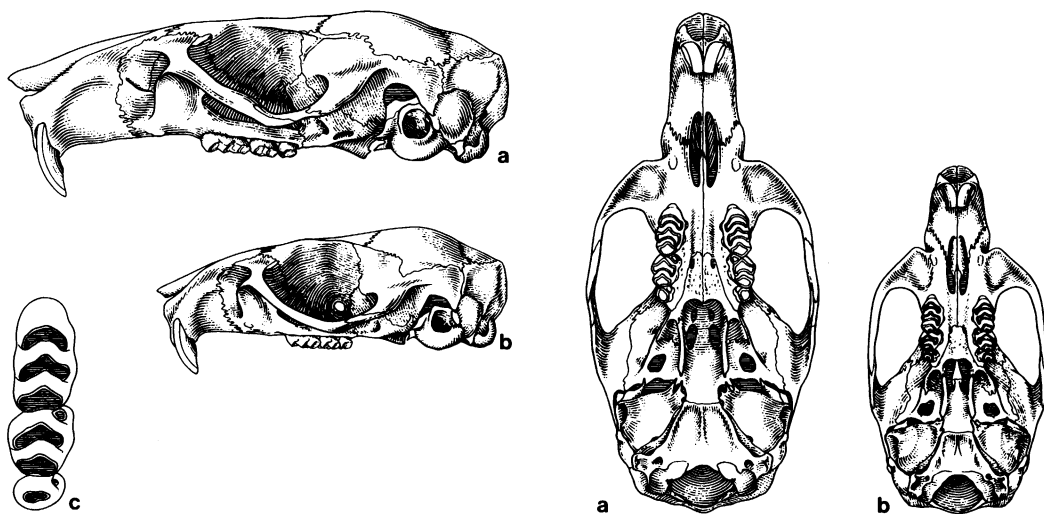


FIG. 19. Views of adult crania and a molar row of *Melomys* from New Guinea: a, *M. levipes* (AMNH 104196; GLS = 41.4 mm.); b, *M. lutillus* (AMNH 104278; GLS = 29.0 mm.); c, left maxillary molar row of *M. rufescens* (AMNH 104170; LM¹⁻³ = 6.4 mm.). Compare these with cranial views of *Apomys* in figure 3 and molar rows in figure 11. Drawings were first published in Tate (1936) but in another context.

native to the Philippines and those native to the region of New Guinea and Australia, as well as comparisons among them.

Melomys, its morphological limits and content still undefined, consists of 15 to 20 species (Rümmler, 1938; Tate, 1951; Laurie and Hill, 1954; Baverstock et al., 1980). Most species are terrestrial, scansorial, or arboreal. Many live in lowland and montane tropical forests, others in savanna or grasslands. Its geographic distribution includes Timor, the northern and northeastern fringes of Australia, New Guinea, the Solomon Islands, the Bismarck Archipelago, Ceram, and the Obi and Talaud islands. The genus was once closely tied to *Rattus*, a phylogenetic view summarized by Tate (1951, p. 216) when he wrote that "*Melomys* and its relatives must originally have branched off the stem leading to *Rattus*."

New information disassociates *Melomys* from *Rattus*. Results from study of chromosomal characteristics (Baverstock et al., 1977), spermatozoal morphology (Breed and Sarafis, 1979), and isozyme electrophoresis (Baverstock et al., 1981) of Australian *Melomys*, and morphology of the glandes penis of New Guinea representatives (Lidicker, 1968) indicate that *Melomys* is not closely related to New Guinea and Australian native *Rattus* but to the old genera endemic to those places. My study of cranial features supports this different affiliation of *Melomys* (Musser, 1981b).

New Guinea *Melomys* is a component of a very large fauna of rats and mice that includes, among others, giant rats (*Mallomys*, *Hyomys*), tree rats (*Chiruromys*), scansorial mice (*Lorentzimys*), shrew mice (*Mayermys*, *Microhydromys*, *Neohydromys*, *Pseudohydromys*), and amphibious rats (*Crossomys*, *Hydromys*, *Parahydromys*). Philippine *Apomys* is one segment of a native fauna that also encompasses giant rats (*Crateromys*, *Phloeomys*), tree rats (*Carpomys*, *Anonymomys*), shrew rats (*Celaenomys*, *Chrotomys*, *Rhynchomys*), and other forms. The highly specialized shrew rats from the Philippines and the shrew mice and amphibious rats of the New Guinea and Australian region (collectively referred to as hydromyines) have already been the subject of study and disagreement. Their molar specializations are very

similar. Simpson (1961) thought the two groups to be sharply distinct from one another and claimed their similarities in dental morphology and habitus to represent convergence rather than close phylogenetic affinity. Other students, however, view the New Guinea and Australian species as being closely related to the Philippine shrew rats. Misonne (1969, p. 157) would place all of them in one group: "There is not the least reason to separate the Philippine Hydromyinae from their New Guinean representatives. . . . The true Hydromyinae, including *Rhynchomys*, make evidently a closely related whole, which owing to its unique and entirely divergent characters of the molars, may be justified as a distinct subfamily."

On New Guinea, the terrestrial and scansorial species of *Melomys* are the morphological and ecological counterparts of *Apomys* in the Philippines. The questions of relationships between them parallel those between the Philippine shrew rats on one hand and the shrew mice and amphibious rats of New Guinea and Australia on the other. Are the groups from each place more closely related to each other than to any other murids? Or do they represent convergence, the result of very distinctive and specialized features independently derived? Answers are important because with them we may begin to understand the phylogenetic relationships among species in those large scattered faunas east of the Sunda Shelf, and something about their historical origins.

I noted elsewhere (Musser, 1981b, p. 169) that "Because so few places east of the Sunda Shelf have been sampled for fossils and because most of the fossils that are available come from young deposits, it is difficult now to discern past species-relationships and patterns of either dispersal or vicariant events that may help to explain present distributions of the Recent murids. And trying to unravel past histories of the rodents within the framework of tectonics that shaped the Indo-Australian region into its present configuration is exasperating. The area is geologically and tectonically extremely complex. It is difficult to reconstruct palaeogeography during the Tertiary and Quaternary from the data presented either in classical studies . . . or that derived from modern inquiries set in the con-

text of plate tectonics. . . . At the present time, the best approach to understanding murid zoogeography in that vast region east of Borneo and Bali is to analyze the phylogenetic relationships among living and extinct species as carefully as possible and let the patterns that emerge from those studies provide clues to the palaeogeography and past tectonic events."

That is why we fuss over the generic definition of *Apomys*. As long as it was a part of *Rattus*, the group was lost in what many considered to be a monophyletic assemblage distantly related to the old endemic genera of the Philippines and those in the New Guinea-Australian region. But the species in *Apomys* have a suite of primitive features, none of the derivations that characterize true *Rattus*, some traits peculiar to themselves, and a set of specializations shared with species of *Melomys*. This information leads to questions about the interrelationships among species of murids on the Philippine Islands, among those native to the New Guinea and Australian region, and between the faunas of those areas. Answers will help us understand the phylogenetic relationships and possibly the evolutionary history of the rats and mice from the islands and continent east of the Sunda Shelf.

LITERATURE CITED

- Baverstock, P. R., C. H. S. Watts, and J. T. Hogarth
1977. Chromosome evolution in Australian rodents. I. The Pseudomyine, the Hydromyine and the *Uromys/Melomys* group. *Chromosoma*, vol. 61, pp. 95-125, figs. 1-31.
- Baverstock, P. R., C. H. S. Watts, M. Adams, and M. Gelder
1980. Chromosomal and electrophoretic studies of Australian *Melomys* (Rodentia: Muridae). *Aust. Jour. Zool.*, vol. 28, pp. 553-574, figs. 1-11.
- Baverstock, P. R., C. H. S. Watts, M. Adams, and S. R. Cole
1981. Genetical relationships among Australian rodents (Muridae). *Ibid.*, vol. 29, pp. 289-303, figs. 1-2.
- Breed, W. G., and V. Sarafis
1979. On the phylogenetic significance of spermatozoal morphology and male reproductive tract anatomy in Australian rodents. *Trans. Roy. Soc. S. Australia*, vol. 103, no. 5, pp. 127-135, figs. 1-3.
- Bugge, Jorgen
1970. The contribution of the stapedia artery to the cephalic arterial supply in murid rodents. *Acta. Anat.*, vol. 76, no. 3, pp. 313-336, figs. 1-8.
- Carleton, Michael Dean
1980. Phylogenetic relationships in Neotomine-Peromyscine rodents (Muroidea) and a reappraisal of the dichotomy within New World Cricetinae. *Misc. Publ. Mus. Zool., Univ. Mich.*, no. 157, pp. i-vii + 1-146, figs. 1-44.
- Ellerman, J. R.
1941. The families and genera of living rodents. London, British Museum (Nat. Hist.), vol. 2, Family Muridae, pp. i-xii, 1-690, figs. 1-50.
1947-1948. Notes on some Asiatic rodents in the British Museum. *Proc. Zool. Soc. London*, vol. 117, pp. 259-271.
1949. The families and genera of living rodents. *Ibid.*, vol. 3, pt. 1, pp. i-v, 1-210.
- Ellerman, J. R., and T. C. S. Morrison-Scott
1951. Checklist of Palearctic and Indian mammals, 1759 to 1946. London, British Museum (Nat. Hist.), pp. 1-810, 1 map.
- Greene, E. C.
1935. Anatomy of the rat. *Trans. Amer. Phil. Soc., N. S.*, vol. 27, pp. i-xi, 1-370, figs. 1-339.
- Guthrie, Daniel A.
1963. The carotid circulation in the Rodentia. *Bull. Mus. Comp. Zool., Harvard Univ.*, vol. 128, no. 10, pp. 455-481, figs. 1-5.
- Hill, J. E.
1935. The cranial foramina in rodents. *Jour. Mammal.*, vol. 16, pp. 121-129, figs. 1-3.
1937. Morphology of the pocket gopher mammalian genus *Thomomys*. *Univ. Calif. Publ. Zool.*, vol. 42, no. 2, pp. 81-172, figs. 1-26.
- Hollister, N.
1913. A review of the Philippine land mammals in the United States National Museum. *Proc. U.S. Natl. Mus.*, vol. 46, pp. 299-341, pls. 27-29.
- Hoogstraal, Harry
1951. Philippine Zoological Expedition 1946-1947. Narrative and Itinerary. *Fieldiana: Zoology*, vol. 33, no. 1, pp. 1-86, figs. 1-7, pls. 1-7.
- Johnson, David H.
1962. Two new murine rodents. *Proc. Biol. Soc. Wash.*, vol. 75, pp. 317-319.

- Klingener, David
1968. Anatomy: pp. 127–147, figs. 1–3. In J. A. King (ed.), *Biology of Peromyscus* (Rodentia). Amer. Soc. Mammal., Spec. Publ. 2.
- Laurie, E. M. O., and J. E. Hill
1954. List of land mammals of New Guinea, Celebes and adjacent islands, 1758–1952. London, British Museum (Nat. Hist.), pp. 1–175, pls. 1–2, 1 map.
- Lidicker, W. Z., Jr.
1968. A phylogeny of New Guinea rodent genera based on phallic morphology. *Jour. Mammal.*, vol. 49, pp. 609–643, figs. 1–7.
- Marshall, Joe T., Jr.
1977. Family Muridae: rats and mice. Pp. 396–487. Reprinted in *Mammals of Thailand* (Boonsong Lekagul and J. A. McNeely). Assoc. Conserv. of Wildlife, Bangkok, Thailand.
- Mearns, E. A.
1905. Descriptions of new genera and species of mammals from the Philippine Islands. *Proc. U.S. Natl. Mus.*, vol. 28, pp. 425–460.
- Medway, Lord, and Yong Hoi-Sen
1976. Problems in the systematics of the rats (Muridae) of Peninsular Malaysia. *Malaysian J. Sci.*, vol. 4 (A), pp. 43–53, pls. 1–4.
- Meyer, A. B.
1898–1899. Säugethiere vom Célebes—und Philippinen-Archipel II. Abhan. u. Ber. d. K. Zool. u. Anthrop.-Ethnog. Mus. Dresden, vol. 7, no. 7, pp. i–viii, 1–55, pls. 1–11.
- Miller, Gerrit S., Jr.
1910. Descriptions of two new genera and sixteen new species of mammals from the Philippine Islands. *Proc. U.S. Natl. Mus.*, vol. 38, pp. 391–404, pls. 18–20.
1912. Catalogue of the mammals of Western Europe (Europe exclusive of Russia) in the collection of the British Museum. London, British Museum (Nat. Hist.), pp. i–xv, 1–1019, figs. 1–213.
- Misonne, Xavier
1969. African and Indo-Australian Muridae. Evolutionary trends. *Mus. Roy. l'Afrique Cent.*, Tervuren, Zool., no. 172, pp. 1–219, figs. A–K, pls. 1–27.
- Musser, Guy G.
1970. Species-limits of *Rattus brahma*, a murid rodent of northeastern India and northern Burma. *Amer. Mus. Novitates*, no. 2406, pp. 1–27, figs. 1–6.
1977. *Epimys benguetensis*, a composite, and one zoogeographic view of rat and mouse faunas in the Philippines and Celebes. *Ibid.*, no. 2624, pp. 1–15, figs. 1–4.
- 1981a. Results of the Archbold Expeditions. No. 105. Notes on systematics of Indo-Malayan murid rodents, and descriptions of new genera and species from Ceylon, Sulawesi, and the Philippines. *Ibid.*, vol. 168, art. 3, pp. 225–334, figs. 1–51.
- 1981b. The giant rat of Flores and its relatives east of Borneo and Bali. *Ibid.*, vol. 169, art. 2, pp. 67–176, figs. 1–40.
- Musser, Guy G., and Patricia W. Freeman
1981. A new species of *Rhynchomys* (Muridae) from the Philippines. *Jour. Mammal.*, vol. 62, no. 1, pp. 154–159, figs. 1–2.
- Musser, Guy G., and Linda K. Gordon
1981. A new species of *Crateromys* (Muridae) from the Philippines. *Ibid.*, vol. 62, no. 3, pp. 513–525, figs. 1–6.
- Musser, Guy G., J. T. Marshall, Jr., and Boeadi
1979. Definition and contents of the Sundaic genus *Maxomys* (Rodentia, Muridae). *Jour. Mammal.*, vol. 60, pp. 594–606, fig. 1.
- Musser, Guy G., Linda K. Gordon, and Helmut Sommer
[In press] Species-limits in the Philippine murid, *Chrotomys*. *Jour. Mammal.*
- Rabor, D. S.
1955. Notes on mammals and birds of the central northern Luzon highlands, Philippines. Part I: notes on mammals. *Silliman Journal*, vol. 2, no. 3, pp. 193–218.
- Rinker, George C.
1954. The comparative Myology of the mammalian genera (*Sigmodon*, *Oryzomys*, *Neotoma*, and *Peromyscus* (Cricetinae), with remarks on their intergeneric relationships. *Misc. Publ. Mus. Zool., Univ. Mich.*, no. 83, pp. 1–124, figs. 1–18.
- Rümmler, H.
1938. Die systematik und verbreitung der Muriden Neuguineas. *Mitteil. Zool. Mus., Berlin*, vol. 23, pp. 1–297, pls. 1–9.
- Sanborn, Colin Campbell
1952. Philippine Zoological Expedition 1946–1947. *Fieldiana: Zoology*, vol. 33, no. 2, pp. 89–158, figs. 8–22.
1953. Mammals from Mindanao, Philippine Islands collected by the Danish Philippine Expedition 1951–1952. *Vidensk. Medd. fra Dansk Naturh. For.*, bd. 115, pp. 283–289, 1 plate.

Simpson, G. G.

1961. Historical zoogeography of Australian mammals. *Evolution*, vol. 15, pp. 431-446, 1 fig.

Tate, G. H. H.

1936. Results of the Archbold Expeditions. No. 13. Some Muridae of the Indo-Australian region. *Bull. Amer. Mus. Nat. Hist.*, vol. 72, pp. 501-728.
1951. Results of the Archbold Expeditions. No. 65. The rodents of Australia and New Guinea. *Ibid.*, vol. 97, pp. 183-430, figs. 1-4.

Taylor, Edward H.

1934. Philippine land mammals. Monograph Bur. Sci. (Manila), no. 30, pp. 1-548, figs. 1-12, pls. 1-25.

Thomas, Oldfield

1898. VIII. On the mammals obtained by Mr. John Whitehead during his recent ex-

pedition to the Philippines. *Trans. Zool. Soc. London*, vol. 14, part 6, no. 1, pp. 377-414, pls. 30-36.

Wahlert, John A.

1974. The cranial foramina of protrogomorphous rodents; an anatomical and phylogenetic study. *Bull. Mus. Comp. Zool.*, vol. 146, pp. 363-410, figs. 1-13.
1978. Cranial foramina and relationships of the Eomyoidea (Rodentia, Geomorphia). Skull and upper teeth of *Kansasimys*. *Amer. Mus. Novitates*, no. 2645, pp. 1-16, figs. 1-8.

Weerd, A. van de

1976. Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alhambra region, Spain. *Utrecht Micropaleo. Bull. Spec. Publ.* 2, pp. 1-218, pls. 1-16, figs. 1-30.

