

RESULTS OF THE ARCHBOLD
EXPEDITIONS. NO. 110.
CRUNOMYS AND THE SMALL-BODIED
SHREW RATS NATIVE TO THE
PHILIPPINE ISLANDS AND
SULAWESI (CELEBES)

GUY G. MUSSER

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CONTENTS

Abstract	3
Introduction	3
Abbreviations and Methods	4
Acknowledgments	5
The Philippine <i>Crunomys</i>	5
<i>Crunomys fallax</i>	5
<i>Crunomys melanius</i>	10
<i>Crunomys rabori</i> , New Species	14
The Sulawesi <i>Crunomys</i>	16
<i>Crunomys celebensis</i> , New Species	16
The Mount Isarog Shrew Rat	30
<i>Archboldomys</i> , New Genus	30
<i>Archboldomys luzonensis</i> , New Species	30
The Sulawesi Shrew Rats	47
<i>Melasmothrix naso</i>	48
<i>Tateomys rhinogradoides</i>	57
<i>Tateomys macrocerus</i> , New Species	64
Habitat and Habits	71
Relationships Among the Shrew Rats	81
Contrasts Among the Philippine Rats	82
<i>Melasmothrix</i> and <i>Archboldomys</i>	82
<i>Archboldomys</i> and <i>Crunomys</i>	86
The Species of <i>Crunomys</i>	86
Literature Cited	94

ABSTRACT

Crunomys contains four species native to the Philippine Islands and Sulawesi (Celebes). *Crunomys fallax* is from Luzon; *C. rabori*, new species, occurs on Leyte; *C. melanius* lives on Mindanao; and *C. celebensis*, new species, is native to middle altitudes in mountainous Central Sulawesi. The species are described and contrasted with one another. *Crunomys* is related to *Archboldomys luzonensis*, new genus and species, a small-bodied

shrew rat from southeastern Luzon. That rat is described, compared with the species of *Crunomys*, then contrasted with the three species of small-bodied shrew rats endemic to Central Sulawesi: *Melasmothrix naso*, *Tateomys rhinogradoides*, and *T. macrocerus*, new species. Relationships among the four genera are discussed. Insular and altitudinal distributions are also presented as well as some data on habitats and habits.

INTRODUCTION

The present report concerns *Crunomys* and small-bodied shrew rats from the Philippine Islands and Sulawesi. *Crunomys* is a terrestrial rat of small body size, short tail, and dark fur that was considered an endemic of the Philippine Islands. The genus and the type species, *C. fallax*, were named and described by Oldfield Thomas in 1898 when he monographed the mammals that had been collected by Mr. John Whitehead from the Philippine Islands. *Crunomys fallax* is known only from the island of Luzon, *C. melanius* lives on Mindanao Island (Thomas, 1907b; Taylor, 1934), and there is a specimen from Leyte Island. *Crunomys* also occurs on Sulawesi, a record based upon three specimens collected at middle altitudes in the mountainous central part of the island.

The species of *Crunomys* are related to a species of small-bodied shrew rats known only from Mount Isarog in the southeastern peninsula of Luzon Island. There is but one specimen of the Isarog rat and it superficially resembles *C. melanius* in body size and conformation, pelage coloration, and molar occlusal patterns. Other characters, however, indicate that the example from Mount Isarog represents an undescribed species in a genus other than *Crunomys*. The specimen was obtained by Dr. D. S. Rabor in 1961 and has been in the collection of the Field Museum of Natural History for more than 15 years under the identification of *C. melanius*. The cranial, mandibular, and dental features of the new genus reflect specializations for eating soft-bodied invertebrates, such as dipteran larvae and earthworms. Some of its adaptations recall those of the Sulawesian

shrew rat, *Melasmothrix naso*, and possibly one is the ecological counterpart of the other.

Melasmothrix naso, *Tateomys rhinogradoides*, and another species of *Tateomys* are the small-bodied shrew rats living in forests on Sulawesi. From 1921, when the first rat was described by Miller and Hollister, until the early 1970s, specimens were rare in collections of museums and consisted only of the holotypes of *M. naso* and *T. rhinogradoides* (Musser, 1969). There are more specimens now, representing three species from four high-altitude localities in Central Sulawesi.

I discuss the specimens of *Crunomys* from the Philippines, which includes the description of a new species based on the example from Leyte Island, then name and describe the Sulawesian species and contrast its external, cranial, and dental features with those in the Philippines. Next, the new genus and species from Mount Isarog is named, described, and compared with the examples of *Crunomys* from both the Philippines and Sulawesi. Characteristics of the Sulawesian shrew rats are presented, a new species of *Tateomys* is named and described, and the three are compared with one another. I also compare the shrew rat from Mount Isarog with the Sulawesian *Melasmothrix naso* to determine if the features similar to both indicate phylogenetic relationship or independent adaptations to similar habitat and mode of living.

The habitat and habits of the *Crunomys* and shrew rats on Sulawesi are included in brief accounts, meant only to introduce the kinds of places these small-bodied rats were

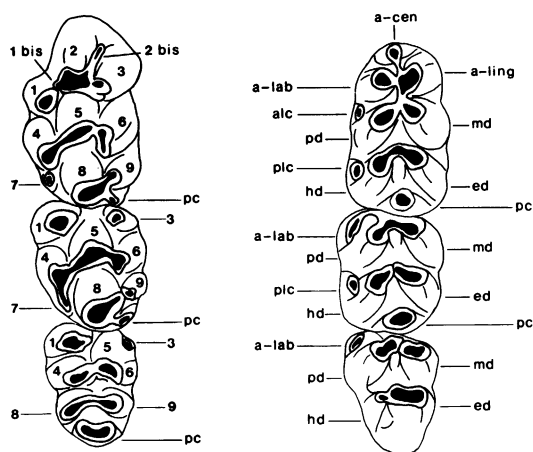


FIG. 1. Terminology of dental structures using right upper and lower molars of *Lenothrix canus*. Upper molars: cusps are numbered according to Miller's (1912) scheme and are referred to in text with prefix t; pc, posterior cingulum. Lower molars: a-cen, anterocentral cusp; a-lab, anterolabial cusp; a-ling, anterolingual cusp; pd, protoconid; hd, hypoconid; md, metaconid; ed, entoconid; pc, posterior cingulum; alc, anterior labial cusplet; plc, posterior labial cusplet (after van de Weerd, 1976, p. 44).

caught. The descriptions are distillations of a fuller report about natural history of rats and forests on Sulawesi to be published later.

The results of my studies reported here pertain only to *Crunomys* and the small-bodied shrew rats on Luzon Island and Sulawesi. There are other kinds of shrew rats from these places. Two species of *Chrotomys* from Luzon and Mindanao, one kind of *Celaenomys* from Luzon, and two species of *Rhynchomys* from northern and southeastern Luzon are shrew rats of large body size. *Echiothrix leucura* is the large-bodied shrew rat on Sulawesi. These species will be introduced and described in a manuscript now being prepared. That paper and the present report are intended to describe morphological characteristics of species native to the Philippine Islands and Sulawesi, clarify their taxonomy, and provide information about insular and altitudinal distributions, habitats, and habits. These studies are part of a broader attempt to determine phylogenetic relationships of rats and mice native to the archipelagos and continent east of continental Asia and the Sunda Shelf.

ABBREVIATIONS AND METHODS

MATERIAL: Specimens I discuss and illustrate are in the 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 Museum Zoologicum Bogoriense, Bogor (MZB); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

MEASUREMENTS: Skins, skulls, and teeth are measured in millimeters; weights are in grams. Some values for lengths of head and body, tail, hind foot, and ear are those recorded by collectors on labels attached to skins. I measured and weighed all specimens of the Sulawesi *Crunomys*, *Melasmothrix*, and *Tateomys* shortly after they were caught. Scale rows were counted along a 1 cm. strip one-third the tail length measured from its base.

Either Anderson's craniometer attached to a Wild M5 Stereomicroscope or dial calipers graduated to tenths of millimeters were used to obtain values for cranial and dental measurements. Limits of most of those measurements are illustrated and defined in Musser (1970, 1979). Those that were not are **length of dentary and incisor** (taken from the posterior edge of the condyloid process to the tip of incisor), **length of dentary** (from the posterior edge of the condyloid process to the anterior margin of the mandibular symphysis), **height of dentary** (from the top of the coronoid process to the bottom of the ramus at the angular process), and **length of M₁₋₃** (from the anterior face of the first molar to the back of the third molar). Also, I excluded the bony eustachian tube when I measured length of bulla in all the specimens.

TEETH: The terminology for positions of cusps and cusplets on upper and lower molars is illustrated in figure 1. See Musser (1981a) for details.

BONES AND CRANIAL FORAMINA: Descriptions and illustrations of skulls, including close-ups of the orbit, alisphenoid region, auditory area, pterygoid complex, and palatal region are provided here. The bones, foramina, and arterial patterns depicted in the figures are labeled with abbreviations that are

defined and explained in figure legends and text. Their identifications are based on my readings of Greene (1935), Hill (1935, 1937), Rinker (1954), Guthrie (1963), Klingener (1968), Bugge (1970), Wahlert (1974, 1978), and Carleton (1980), as well as partial dissection of fluid-preserved specimens and incompletely cleaned skulls to check details of arterial circulation and foraminal position that I could not comprehend from published descriptions.

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Some parts of this report could not have been completed were it not for the Lembaga Ilmu Pengetahuan Indonesia and the Museum Zoologicum Bogoriense, the Indonesian institutions that sponsored my work in Java and Sulawesi. I was financially supported by the anonymous benefactor of the Celebes Fund at the American Museum of Natural History and the late Mr. Richard Archbold of Archbold Expeditions Inc. Dr. P. J. D. Van Peenen, who at the time was Officer-in-Charge of U.S. Navy Medical Research Unit No. 2 in Jakarta, provided me with access to a wide

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THE PHILIPPINE *CRUNOMYS*

Crunomys is known by only four specimens from the Philippine Islands. Each is incomplete or imperfect in some way but still provides information about morphological variation within the genus and about its distribution among the islands. The smallest-bodied and palest of the four is the holotype of *C. fallax* from Luzon. The holotype of *C. melanius* from Mindanao, which is a very young adult barely molted from juvenile to adult pelage, represents the youngest of the four and a form that is darker and larger than the Luzon animal. Another specimen from Mindanao is an adult referable to *C. melanius*, older than the holotype but not an old adult. The fourth is an old adult from Leyte, the oldest and largest in body size of the specimens.

The four can be sorted into three groups: the specimen from Luzon, the two from Mindanao, and the one from Leyte. It is my hypothesis that each group is a sample of a

species. Large series from single localities and more specimens from several islands may alter this interpretation. I am aware that some differences among the groups may be due to individual variation, secondary sexual variation, that of age, or a combination of all three. The primary differences may not be those of species but may instead reflect a pattern of insular variation among genetically compatible populations that are morphologically different because they have been isolated from one another on islands that once formed continuous land surfaces. It is in such a context that I discuss the four specimens and describe the sample from Leyte as a species.

Crunomys fallax

The holotype of *C. fallax* (BMNH 97.4.8.4) consists of a skin and skull obtained by Mr. John Whitehead from Isabella Province in the central part of northern Luzon (fig. 2)

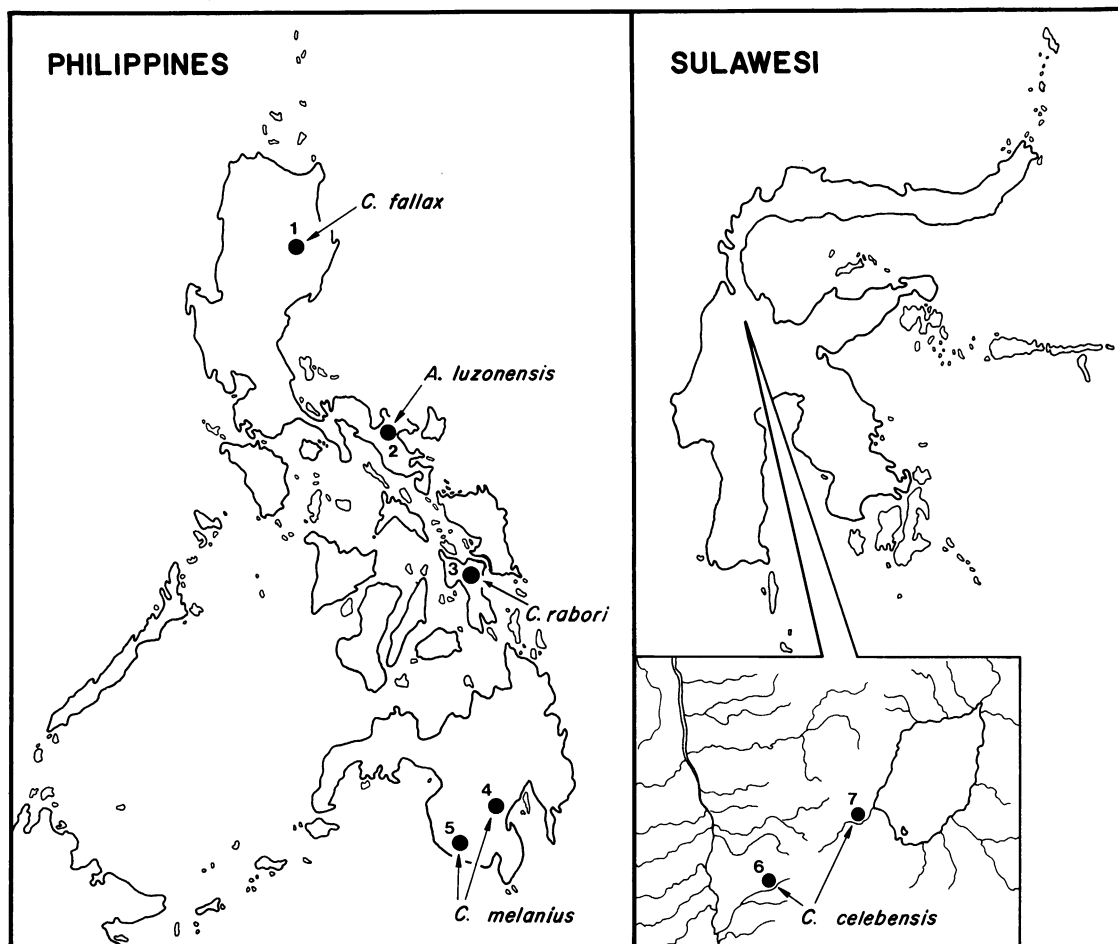


FIG. 2. Map showing where specimens of *Crunomys* and *Archboldomys* were obtained. Localities: 1, Mt. Isabella Province, Luzon; 2, Mount Isarog, Luzon; 3, Mount Lobi Range, Leyte; 4, Mount Apo, Mindanao; 5, Saub, Mindanao; 6, Sungai Sadaunta; and 7, near Tomado. See text for additional information.

sometime during May 1894, at an altitude of 1000 feet. The skin is complete. The skull is damaged: the occipital region and the bullae are missing. The incomplete cranium and a dentary are illustrated in Thomas's (1898) Plate 35, which is reproduced in figure 59. The molars are worn but not to the degree where their occlusal patterns are obliterated (fig. 59). The specimen represents a small adult rat, probably a male (neither Thomas nor Whitehead had sexed it; I could not locate teats, which would have been present on a rat of this age, and what remained of the genital area suggested a male). The holotype remains the only sample of the taxon.

Crunomys fallax is a small-bodied rat with a short tail, much shorter than the combined length of head and body, small ears, and spinous fur (table 1; fig. 3). The pelage over the upperparts of the head and body is very short and dense; flattened spines thickly scattered throughout give the coat a spinous texture unyielding to the touch. The upperparts are grayish brown tinted with buff that darkens to dark brown along the top of the head and body and pales to buffy gray along the sides of the body. The underparts are pale gray from chin to anus; the demarcation between the dark upperparts and pale underparts is not sharply defined. The ears are brown. The



FIG. 3. *Crunomys fallax*. From color plate 33 published in Thomas, 1898.

front and hind feet are grayish brown over most of their upper surfaces and pale to white over the digits. Six small plantar pads adorn the naked surface of each hind foot. The tail is dark brown on its dorsal surface and sides, and pale brown over the ventral surface—a definite bicoloration. The tail hairs are short and stiff; there are three to each scale.

Remains of the cranium and dentaries of *C. fallax* are closely similar in conformation to those elements from the adult *C. melanius*. The two specimens are also alike in occlusal patterns of upper and lower molars. Read the account of *C. melanius* for descriptions of the skull and teeth.

What is known about the natural history of *C. fallax* is contained in Thomas's (1898, p. 396) quote of Whitehead's notes about its capture:

In one of my wanderings through the parched-up forests of Isabella (in North-Central Luzon) I

noticed a small red kingfisher (*Ceyx melanura*) fly into the scrub near a small stream. Having only a large gun with me, I sent my servant back to the village for a small collecting-gun. While seated beside the stream, a small mouse was observed among some large stones on the opposite side, busily searching after food. I opened one of my 16-bore cartridges and picked out all the shot (no. 6) but four or five pellets, and luckily killed the small animal without much damage being done. Being sure, from its peculiar habits, that it must be something interesting, I carefully skinned it and sent it home, and am now rewarded by the addition of another new generic form to this already interesting collection.

From Whitehead's account, Thomas associated the specimen with an aquatic habitat, thus the derivation of the generic name from the Greek *krounos* for spring, and probably the reason the mouse was illustrated in a setting alongside water (fig. 3). The link between rat and aquatic habitats has been reinforced

TABLE 1
Measurements (in Millimeters), Weight (in Grams), and Other Data from Specimens of *Crunomys fallax* (Luzon), *Crunomys melanius* (Mindanao), *Crunomys rabori* (Leyte), *Crunomys celebensis* (Sulawesi), and *Archboldomys* (Luzon)

	Crunomys										Archboldomys				
	C. fallax			C. melanius			C. rabori		C. celebensis			A. luzonensis			
	BMNH	adult	young ad.	BMNH	adult	AMNH	adult	DMNH	adult	AMNH	adult	AMNH	adult	FMNH	young ad.
Age, sex, and measurement ^a	97.4.8.4 ^b	M	M	7.2.2.14 ^b	M	242102	F	4222 ^b	M	240490	F	225042	224316 ^b	95122 ^b	M
Length of head and body	105	98	122	127	115	82	70 ^c	28	28.2	13.7	5.4	11.9	9.0	10.1	125
Length of tail	79	68	79	84	80	25	28	16	13.7	5.4	11.9	9.0	10.1	125	70 ^c
Length of hind foot	23	25	26	27	26	14	14	14	13.7	5.4	11.9	9.0	10.1	125	28
Length of ear	10	13	14	—	—	35	55	55	14	14	14	14	14	16	16
Weight	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Thickness of pelage	4-5	4-6	5-6	5-6	5-6	5-6	5-6	5-6	5-6	5-6	5-6	5-6	5-6	5-6	9-11
Rows of scales on tail (per cm.)	—	18	18	18	14	20	20	20	20	20	20	20	20	20	16
Greatest length of skull	—	28.2	30.0	30.2	32.1	30.2	30.2	30.2	30.2	30.2	30.2	30.2	30.2	30.2	28.2
Zygomatic breadth	—	13.4	13.3	—	—	—	—	—	—	—	—	—	—	—	13.7
Interorbital breadth	4.6	5.7	5.5	5.6	6.0	5.6	5.6	5.6	5.6	5.6	5.6	5.6	5.6	5.6	5.4
Breadth of braincase	10.7	12.1	12.5	12.5	12.7	11.5	11.5	11.5	11.5	11.5	11.5	11.5	11.5	11.5	11.9
Height of braincase	—	8.3	8.5	8.5	9.5	8.5	8.5	8.5	8.5	8.5	8.5	8.5	8.5	8.5	9.0
Length of nasals	9.3	9.8	11.2	13.1	13.1	13.0	13.0	13.0	13.0	13.0	13.0	13.0	13.0	13.0	10.1
Length of rostrum	6.8	7.6	8.5	—	—	9.0	9.0	9.0	9.0	9.0	9.0	9.0	9.0	9.0	9.1
Breadth of rostrum	4.3	5.4	5.1	5.6	5.6	—	—	—	—	—	—	—	—	—	5.2
Breadth of zygomatic plate	1.5	1.5	1.8	2.0	2.0	1.9	1.9	1.9	1.9	1.9	1.9	1.9	1.9	1.9	2.1
Breadth across incisor tips	1.4	1.5	1.7	1.8	1.8	—	—	—	—	—	—	—	—	—	—
Length of diastema	6.8	6.8	7.4	8.6	8.6	8.3	8.3	8.3	8.3	8.3	8.3	8.3	8.3	8.3	6.8
Palatal length	12.7	12.7	12.9	14.6	14.6	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	12.9
Palatilar length	10.7	10.9	11.2	12.7	12.7	12.5	12.5	12.5	12.5	12.5	12.5	12.5	12.5	12.5	11.5
Postpalatal length	—	10.8	12.0	13.3	13.3	—	—	—	—	—	—	—	—	—	9.9
Length of incisive foramina	3.6	3.8	4.1	4.5	4.5	—	—	—	—	—	—	—	—	—	4.4
Breadth of incisive foramina	1.6	2.1	2.1	2.3	2.3	—	—	—	—	—	—	—	—	—	2.0
Incisive foramina to M ¹	—	—	1.4	1.6	1.6	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	0.5
Length of palatal bridge	4.9	5.1	5.1	5.7	5.7	5.1	5.1	5.1	5.1	5.1	5.1	5.1	5.1	5.1	5.3
Breadth of palatal bridge at M ¹	2.4	2.6	2.9	3.0	3.0	—	—	—	—	—	—	—	—	—	2.8
Breadth of palatal bridge at M ³	2.7	3.2	3.3	3.4	3.4	—	—	—	—	—	—	—	—	—	3.3
Breadth of mesopterygoid fossa	1.8	1.6	2.2	2.7	2.7	—	—	—	—	—	—	—	—	—	2.1
Length of bulla	—	—	4.3	4.8	4.8	4.6	4.6	4.6	4.6	4.6	4.6	4.6	4.6	4.6	4.7

TABLE 1—(Continued)

	Crunomys							Archboldomys	
	<i>C. fallax</i>		<i>C. melanius</i>		<i>C. rabori</i>		<i>C. celebensis</i>		<i>A. luzonensis</i> FMNH 95122 ^b
	BMNH		BMNH	AMNH	DMNH	AMNH	AMNH	AMNH	
Age, sex, and measurement ^a	97.4.8.4 ^b	7.2.2.14 ^b	—	2.9	3.2	2.9	2.9	2.9	
Height of bulla	—	—	—	4.1	4.0	3.9	3.8	3.7	2.9
Alveolar length of M ¹⁻³	3.7	4.2	4.2	2.4	2.0	2.1	2.0	1.9	4.8
Length of M ¹	2.1	2.3	2.3	1.6	1.4	1.3	1.3	1.2	2.6
Breadth of M ¹	1.2	1.4	1.4	18.2	19.3	20.4	19.6	18.8	1.7
Length of dentary and incisor	16.3	17.2	17.2	16.2	16.5	17.0	16.6	15.5	18.5
Length of dentary	12.4	13.9	13.9	7.3	8.5	8.9	8.9	8.4	15.6
Height of dentary	6.1	7.0	7.0	4.2	4.1	4.0	3.9	3.8	8.0
Length of M ¹⁻³	3.8	4.3	4.3	—	—	—	—	—	5.1

^a Lengths of head and body, tail, hind foot, and ear of BMNH 97.4.8.4 and 7.2.2.14 were taken from labels attached to the skins. I measured the skin, which had been relaxed and softened, of FMNH 95122, and the tail and hind foot of DMNH 4222. Lengths of head and body and tail for AMNH 242102 were taken by Taylor (1934, p. 410); I measured the hind foot and ear. I measured the three specimens from Sulawesi in the field. I measured thicknesses of pelages and rows of tail scales of all the specimens.

^b Holotypes.

^c This value is from an incomplete tail; the tip is missing.

and broadened by referring to the species in *Crunomys* as "Philippine Swamp Rats" as Walker (1964, p. 926) did. The body form of *C. fallax*, however, is not that typical of an aquatic or amphibious rat, a point Thomas (1898, p. 394) recognized; there are simply no data supporting the assumption that *C. fallax* is tied to either aquatic or semiaquatic environments. We know only that Whitehead was sitting on one side of a small stream, saw the mouse poking among rocks on the other bank, and blasted it with his gun. Many kinds of terrestrial nonaquatic rats and mice search for food along stream banks. The significant aspect of Whitehead's observation is that *C. fallax* may be diurnal.

Crunomys melanius

Crunomys melanius was first named and preliminarily diagnosed by Thomas in 1907 and described more fully later that year (Thomas, 1907a and 1907b). The holotype (BMNH 7.2.2.14) was obtained on February 29, 1906, by Malcom Anderson from the island of Mindanao in the Philippines. According to Thomas (1907b, p. 140),

The chief object of Mr. Anderson's visit to the Philippines was to obtain series of the interesting mammals discovered in Mindanao by Dr. E. A. Mearns, as the mountain fauna of this island was only represented in our National Museum by the duplicates from Dr. Mearns' collection which the authorities of the United States National Museum had been good enough to send us. But these of course did not include any of the various new genera and species which had been described by Dr. Mearns on single specimens or on small series, and we therefore hoped that Mr. Anderson might be able to obtain some of them for us.

The holotype was collected at 3000 feet in "North Central Mindanao," as given by Thomas (1907b, p. 141), but Ellerman (1941, p. 259) and Taylor (1934, p. 410) indicated that the type locality was on Mount Apo in the Davao Province of Mindanao; I have assumed that the specimen came from there. A notation on the label attached to the skin indicates the native name for the animal is "*Talacogun*," which means an animal that lives in the *cogun*, a high and coarse grass. Whether the holotype actually came from *cogun* or from some other habitat is unknown.

The holotype is a very young adult male in full fresh pelage. The molars are slightly worn (fig. 6).

The only other known specimen of *C. melanius* (AMNH 242102) is an adult female collected by E. H. Taylor on April 22, 1923, in forest at sea level near Saub, Cotabato Province, southern Mindanao (Taylor, 1934). Saub (lat. 6°02' N, long. 124°30' E) is on the coastal plain between Kalaong and Pāngi (fig. 2). The skin is in alcohol, the cranium and dentaries were extracted and cleaned.

Crunomys melanius is much larger than *C. fallax* in dimensions of the body, cranium, dentaries, and teeth (table 1), and conspicuously darker in coloration. The upperparts of *C. melanius* are dark chestnut (blackish brown for Thomas, 1907b) over the entire head and body, the underparts are blackish gray, without the chestnut highlights of the dorsum; there is no clear demarcation between back and belly (grayish brown upperparts and pale gray underparts in *C. fallax*). The pelage of the holotype is soft and only slightly stiff to the touch because the spines are fine and soft; however, the adult from Saub has spinous pelage similar in texture to that covering the holotype of *C. fallax*. The tail of *C. melanius* is blackish brown and slightly paler on the ventral surface but not bicolored as in *C. fallax* (which is dark brown above, pale brown below). The ears are blackish brown. The hind feet are blackish brown over both the dorsal and plantar surfaces, and the front feet are blackish brown above but unpigmented on the palms. The female from Saub has eight mammae: one pectoral pair, one postaxillary pair, and two inguinal pairs.

The cranium, dentaries, and occlusal patterns of the molars in the adult *C. melanius* are similar in conformation to those features in the holotype of *C. fallax*; size is the primary difference between the two specimens (table 1). The cranium of the adult *C. melanius* from Saub is incomplete (fig. 4b), most of the nasal bones and pieces of the zygomatic arches are missing. Below, I provide a short and general description of the cranium and mandibles. A fuller description of structural details in particular cranial regions will be presented for the *Crunomys* from Sulawesi. The skull of one specimen from that sample is complete and its configuration in general

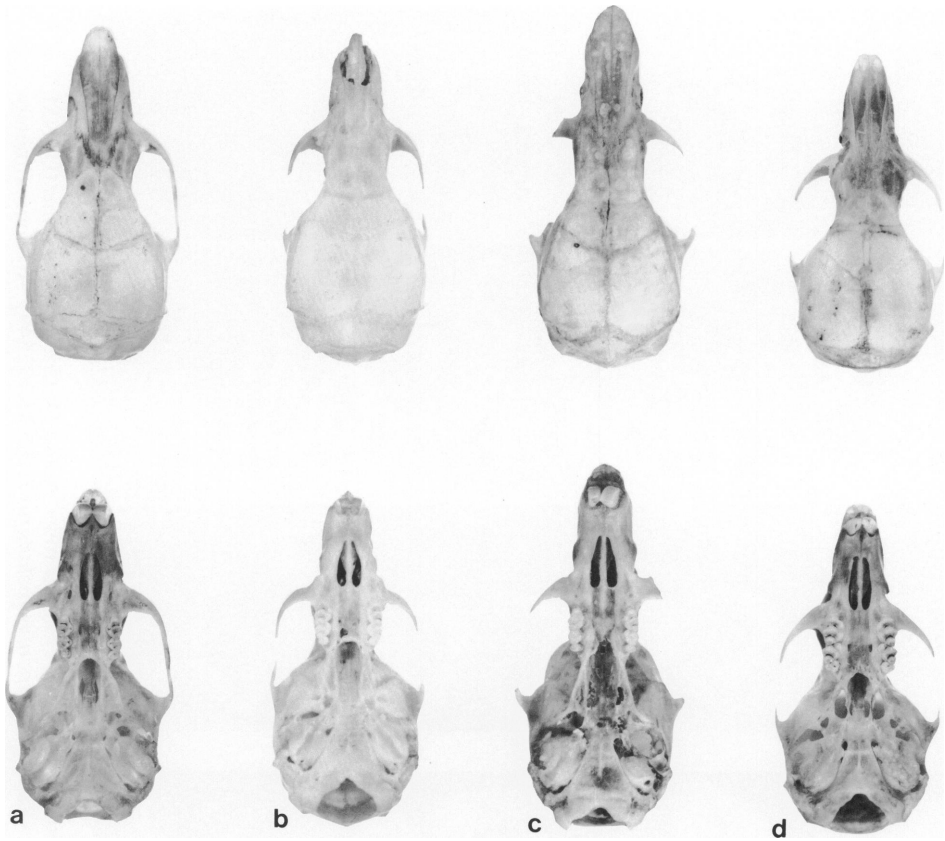


FIG. 4. Dorsal (top) and ventral (bottom) views of adult crania. *Crunomys*: a, *C. celebensis* (AMNH 224316, holotype); b, *C. melanius* (AMNH 242102); c, *C. rabori* (DMNH 4222, holotype). *Archboldomys*: d, *A. luzonensis* (FMNH 95122, holotype). All approximately $\times 1.5$.

and in certain details is like that of *C. melanius*. How the two differ will be enumerated in the diagnosis of the Sulawesi taxon. Skulls of both *C. melanius* and the Sulawesi rat will be further contrasted when I compare them with the specimen from Mount Isarog in the account which follows that of the Sulawesi form.

A small, short, narrow, and deep cranium along with short dentaries characterizes the skull of *C. melanius* in particular and *Crunomys* in general. As viewed from above and the side, the rostrum is short and wide, the interorbital region is wide, and the braincase is elongate and deep. The dorsolateral margins of the interorbital and postorbital regions as well as the braincase are nearly smooth, either without ridging or a trace only. The zygomatic plates are narrow, their anterior

edges concave and not projecting forward of the dorsal maxillary roots of the arches; the posterior margins are set anterior to the molar rows.

Viewed from below, the incisive foramina are short, narrow anteriorly, and wider posteriorly and are shaped like an inverted heart. They lie well anterior to the front margins of the first molars. The palatal bridge is wide and ends slightly anterior to the back margins of the third molars. Posterior to the palatal bridge, the cranium is elongate. The mesopterygoid fossa is long and narrow, nearly as wide as the palatal bridge, and breached by short and slitlike sphenopalatine openings. Each pterygoid fossa is long and narrow, consisting of intact bony surfaces in their anterior two-thirds that are not perforated by sphenopterygoid vacuities. The auditory bullae are

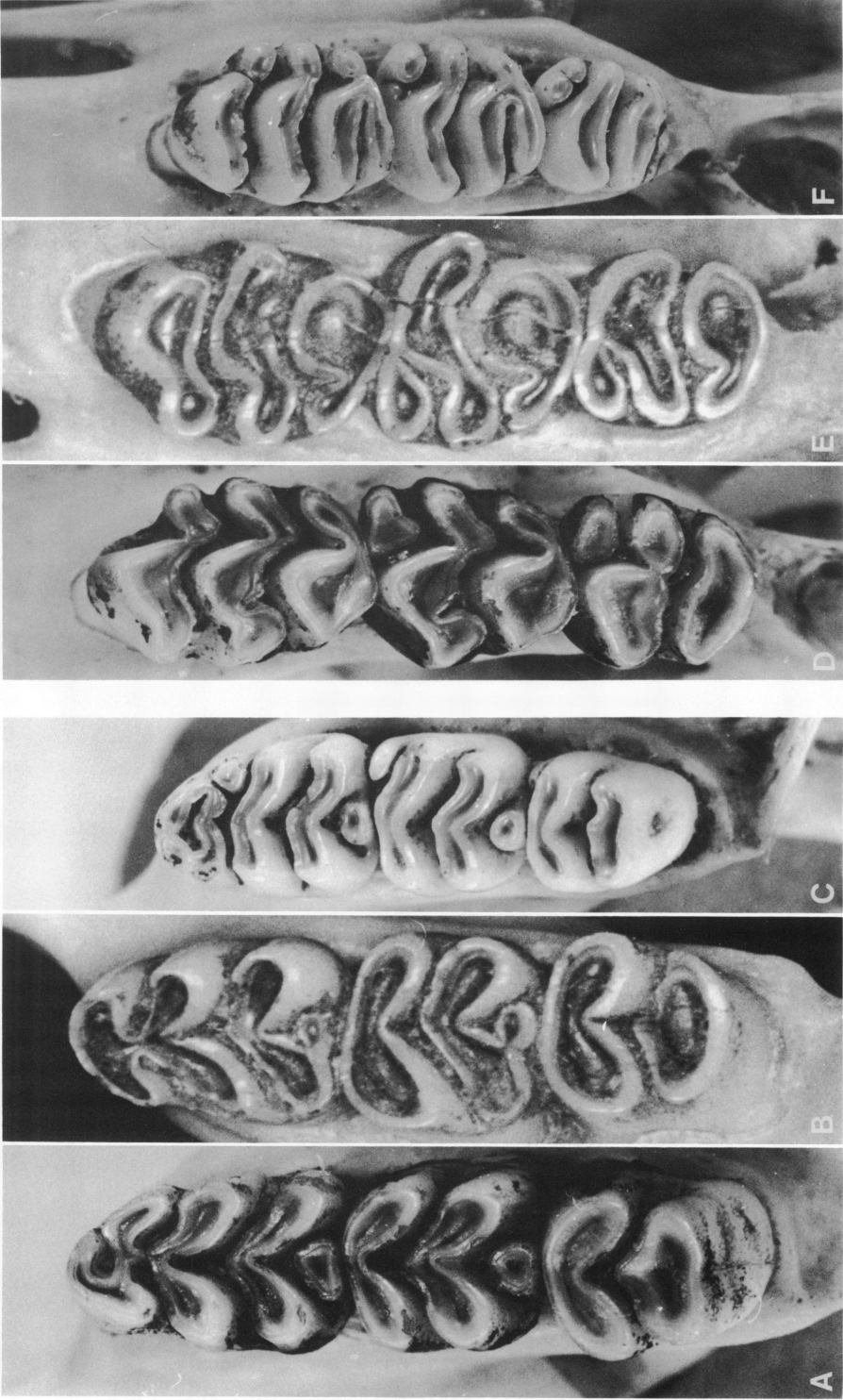


FIG. 5. Occlusal views of right mandibular (A-C) and maxillary (D-F) molar rows. A and D: *Crateromys paulus* (USNM 522023). B and E: *Batomys dentatus* (USNM 151506). C and F: *Carpomys melanurus* (USNM 102549). All approximately X8.

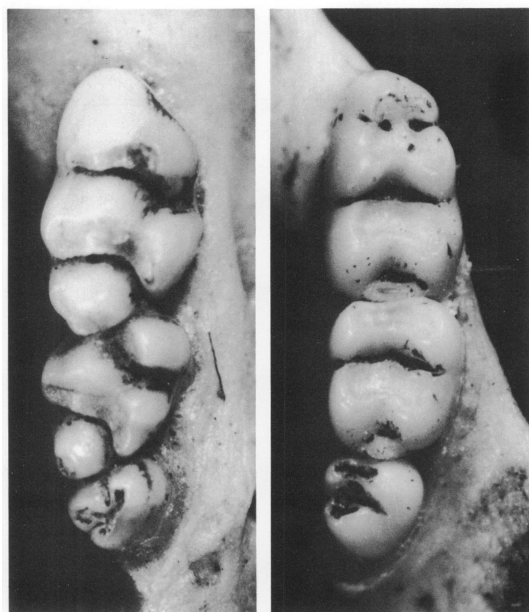


FIG. 6. *Crunomys melanius*. Occlusal views of right maxillary (left side) and mandibular (right side) molar rows of BMNH 7.2.2.14, the holotype. See table 1.



FIG. 7. *Crunomys melanius*. Occlusal views of left maxillary (left side) and mandibular (right side) molar rows of AMNH 242102. Measurements are listed in table 1.

small, both actually and relative to size of the cranium. The bony eustachian tubes are moderately long.

The dentaries of *C. melanius* are similar in configuration to those of the Sulawesi specimens, which will be described later.

The upper and lower incisors are wide and appear robust. Their enamel layers are pale orange. The uppers emerge from the rostrum at nearly a right angle.

Small upper molars set in an expansive bony palate and small lower molars anchored in robust dentaries are the relative dental configurations in *C. melanius*, and in *Crunomys* in general. The molars overlap one another, particularly the uppers. Each first and second upper molar is anchored by three roots: an anterior, lingual, and posterior. It is likely that each third molar also has three roots but each one is so firmly anchored in the bone that I would have to damage the specimens to expose and count the roots. Each lower molar has two roots only, an anterior and posterior. In both upper and lower tooth-

rows, but particularly the uppers, the first molar is very large, the second smaller, and the third very small relative to the other teeth in each row (figs. 6 and 7).

The molars of *C. melanius* are slightly cuspidate in young animals (fig. 6) but in older rats they become basined, a configuration similar to the wear stage shown in figure 7. In contrast to the occlusal patterns in other native Philippine murids such as *Crateromys*, *Batomys*, and *Carpomys* (fig. 5), those in *Crunomys* are simple. Neither a cusp t7 nor posterior cingulum occurs on any of the upper molars. Cusp t3 is present on each first upper molar but it is small and hardly distinguishable. Cusp t3 is absent from each second and third upper molar in all the specimens of *C. melanius* (and the Sulawesi rats)

TABLE 2
Percentages Expressing Proportions of Certain Cranial and Dental Measurements in Samples of
Crunomys and *Archboldomys*

	BR LR	HBR BBR	LIF LD	LM ¹⁻³ LPB	LM ¹⁻³ GLS	LM ₁₋₃ LDY	LB GLS
<i>Crunomys fallax</i>							
BMNH 97.4.8.4	63	—	53	78	—	31	—
<i>Crunomys melanius</i>							
BMNH 7.2.2.14	71	69	56	84	15	31	—
AMNH 242102	60	68	55	82	14	26	14
<i>Crunomys rabori</i>							
DMNH 4222	—	75	52	70	13	25	15
<i>Crunomys celebensis</i>							
AMNH 240490	—	74	—	78	13	24	15
AMNH 225042	70	—	54	70	—	23	—
AMNH 224316	69	75	54	69	13	25	15
<i>Archboldomys luzonensis</i>							
FMNH 95122	57	76	65	96	18	33	17

Abbreviations: BBR, breadth of braincase; BR, breadth of rostrum; GLS, greatest length of skull; HBR, height of braincase; LB, length of bulla; LD, length of diastema; LDY, length of dentary and incisor; LIF, length of incisive foramina; LM¹⁻³, length of M¹⁻³; LM₁₋₃, length of M₁₋₃; LPB, length of palatal bridge; LR, length of rostrum.

but apparently present in the holotype of *C. fallax*, where it is clearly illustrated in Thomas's plate 35 (fig. 59). Cusp t9 on each first molar is large and broadly joined to cusp t8 but absent from each second molar, even in young rats (fig. 6). Each small third upper molar is not only reduced in size relative to the others in the row but in number of cusps as well. In young rats, the occlusal surface is formed by a large anterolingual cusp t1, a small lingual cusp t4, and a large cusp t5 (fig. 6); after wear, these cusps on the third molar merge into the bilobed configuration shown in figure 7.

Each first lower molar of young rats consists of two thick laminae and a third smaller one at the front of the tooth. The latter is formed from the anterolabial and the anterolingual cusps and connected to the lamina behind it by a narrow isthmus; there is no anterocentral cusp (fig. 6). After wear, the two anterior laminae coalesce and form one large basined structure shaped like that illustrated in figure 7. A wide and low posterior cingulum is pressed against the back of the tooth, about in the middle. Two thick laminae and a low posterior cingulum form the surface of each second molar. Each third molar consists

of two simple laminae. An anterolabial cusp is absent from each second and third molar, there are no cusplets along the labial margins of any of the teeth, and a posterior cingulum is absent from each third molar.

The fourth known specimen of *Crunomys* from the Philippine Islands, the individual from Leyte, apparently represents a new species, which is named and diagnosed below.

***Crunomys rabori*, new species**

HOLOTYPE AND LOCALITY: An adult male (DMNH 4222) collected on May 29, 1964, by Dr. D. S. Rabor (original field number, 902) from Barrio Buri, Municipality of Burauen, Mount Lobi Range in Leyte Province on the island of Leyte, the Philippines. The specimen consists of a stuffed skin (fig. 8), a cranium (fig. 4c), and dentaries. The molars are worn and their original cusp patterns are no longer evident. Although overstuffed, the skin is in good condition. The skull is damaged: most of the zygomatic arches are missing, including the dorsal attachments of the zygomatic plates; the posterior rim of the palatal bridge is damaged; the left bullar capsule is missing as well as small pieces of the otic

region. Each dentary is intact. Most of the damage to the cranium resulted from careless cleaning.

REFERRED SPECIMENS: None. The holotype is the only known specimen.

MEASUREMENTS: See table 1.

KNOWN DISTRIBUTION: The Mount Lobi Range in north-central Leyte. I have no information about the habitat or exact place where the holotype was captured. Dr. Rabor (in Parkes, 1973) provided general descriptions of the collecting localities in the Mount Lobi region and summarized his efforts this way (p. 12): "As a whole, the interior localities of the Mount Lobi Range where we worked were a mixture of cultivated fields, cleared hills, parang country, secondary forest, primary dipterocarp forest, and small areas of mixed or transition dipterocarp—mid-mountain forests, the latter found only at the highest elevations on the mountain peaks."

ETYMOLOGY: For more than 30 years, Dr. Discoro S. Rabor and his field crews have been collecting mammals in the Philippine Islands. Those collections have largely formed the basis of our current knowledge about the diversity and distribution of native species of rats and mice in the archipelago and their phylogenetic relationships since that time the first reports about the native Philippine fauna were published just before and after the turn of the Century (Thomas, 1898; Meyer, 1898–1899; Mearns, 1905; and Miller, 1910). To Dr. Rabor goes my respect and appreciation for his interest in Philippine natural history and expeditionary efforts through the years.

DIAGNOSIS: Judged from skins and skulls, *C. rabori* is larger than *C. fallax* from Luzon and *C. melanius* from Mindanao, especially in cranial and mandibular dimensions (table 1). It is darker than *C. fallax* and lacks a bicolored tail but is paler than *C. melanius*, especially on the underparts. Its molars are smaller relative to size of the cranium and mandible than are those in the other species from the Philippines, the braincase is wider relative to its height, and the incisive foramina shorter relative to length of the diastema (table 2).

DESCRIPTION AND COMPARISONS: The holotype of *C. rabori* represents a rat of small body size in which the tail is shorter than the

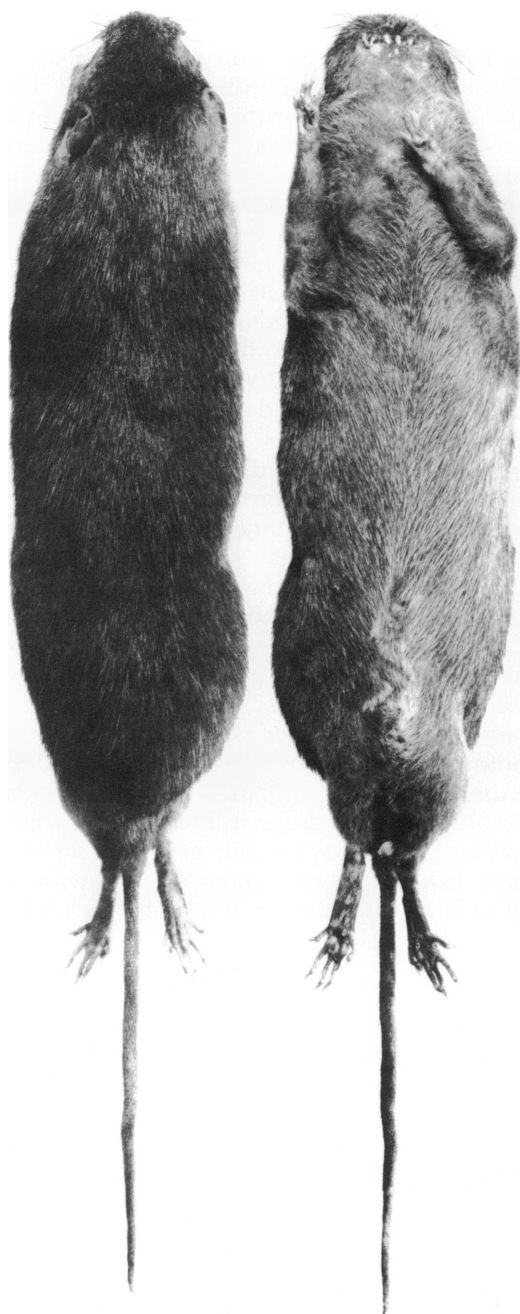


FIG. 8. *Crunomys rabori*. Dorsal (left) and ventral (right) views of the holotype (DMNH 4222) from Mount Lobi Range, Leyte Island, the Philippines. See table 1 for measurements.

combined lengths of head and body and the hind feet are short and slender. The body proportions are those of a terrestrial animal.

The fur over the upperparts consists mostly of flattened spinelike hairs so the pelage is densely spinous and stiff to the touch. The spines are softer over the underparts but the fur is still stiff. The upperparts are very dark brown with a flat tone; the sides of the body and thighs are paler. The underparts are pale brownish gray. The demarcation between dorsum and venter is not sharp but it is apparent, as distinct as that in the holotype of *C. fallax*. The ears are small, round, and blackish brown. The dorsal surfaces of the front feet are covered with brown hairs, the digits are unpigmented as are the palmar surfaces. Upper surfaces of the hind feet are brown, including the digits, and the plantar surfaces are blackish brown. Like all the other specimens of *Crunomys*, there are six low pads on each plantar surface. The tail is blackish brown from base to tip over its dorsal surface and mottled underneath.

Comparisons between the skin of *C. rabori* and the other three specimens of *Crunomys* yield different results. The Leyte specimen is larger and has darker pelage than does the holotype of *C. fallax* from Luzon and lacks a distinctly bicolored tail. It is paler than the holotype of *C. melanius* from Mindanao (dark brown upperparts instead of dark chestnut, pale brownish gray underparts instead of blackish gray). How it might contrast with

adult *C. melanius* of near comparable age is unknown because the skin of the specimen from Saub has been in alcohol since 1923 and its original coloration is now altered to dark straw brown, a hue typical of specimens kept a long time in alcohol.

Although partially damaged, there is enough of the cranium of *C. rabori* to indicate it is larger and appears more robust than that of the *C. melanius* from Saub in both general shape and structural details of particular regions (fig. 4). I could not find any outstanding difference between the two except absolute size and certain proportions already mentioned in the diagnosis (table 2). The dentaries are also large versions of those in *C. melanius*.

Shapes of the incisors of *C. rabori* resemble those in *C. melanius* but the enamel layers are paler. The molars are small, and smaller relative to size of the cranium and mandible than the two examples of *C. melanius* (table 2). Their occlusal surfaces are too worn to determine whether the cuspidation may differ from that characterizing either *C. fallax* or *C. melanius*. The degree of overlapping among the molars of *C. rabori*, their size relative to one another in each row, and the number of roots anchoring each tooth is like that in the three other specimens of Philippine *Crunomys*.

THE SULAWESI *CRUNOMYS*

Always thought to be an endemic of the Philippine Islands, *Crunomys* also occurs on Sulawesi and is the only one of the many murid genera indigenous to either the Philippines or Sulawesi that is common to both places (Musser, 1981b). The features associated with the skins, skulls, and teeth of the three Sulawesi specimens are similar to those characterizing the two examples of *C. melanius* from Mindanao, the closest of the large Philippine islands to Sulawesi. The three are distinguished from *C. melanius* by characters that I hypothesize reflect a population reproductively isolated from the one on Mindanao. The species is named and described below.

Crunomys celebensis, new species

HOLOTYPE AND LOCALITY: An adult male collected on May 20, 1974, by members of the Archbold Sulawesi Expedition (original field number, ASE 1626) from an altitude of 3500 feet in forest near the village of Tomado (lat. 1°19' S, long. 120°5' E) in the mountain valley of Danau (which means Lake) Lindu, Province Sulawesi Tengah, Central Sulawesi, Indonesia (fig. 2).

The specimen consists of a stuffed skin (fig. 10), a cranium and dentaries (figs. 4a and 13), and a carcass that was originally fixed in formalin and is now preserved in alcohol. The molars are worn (fig. 14). Except that three



FIG. 9. *Crunomys celebensis*.

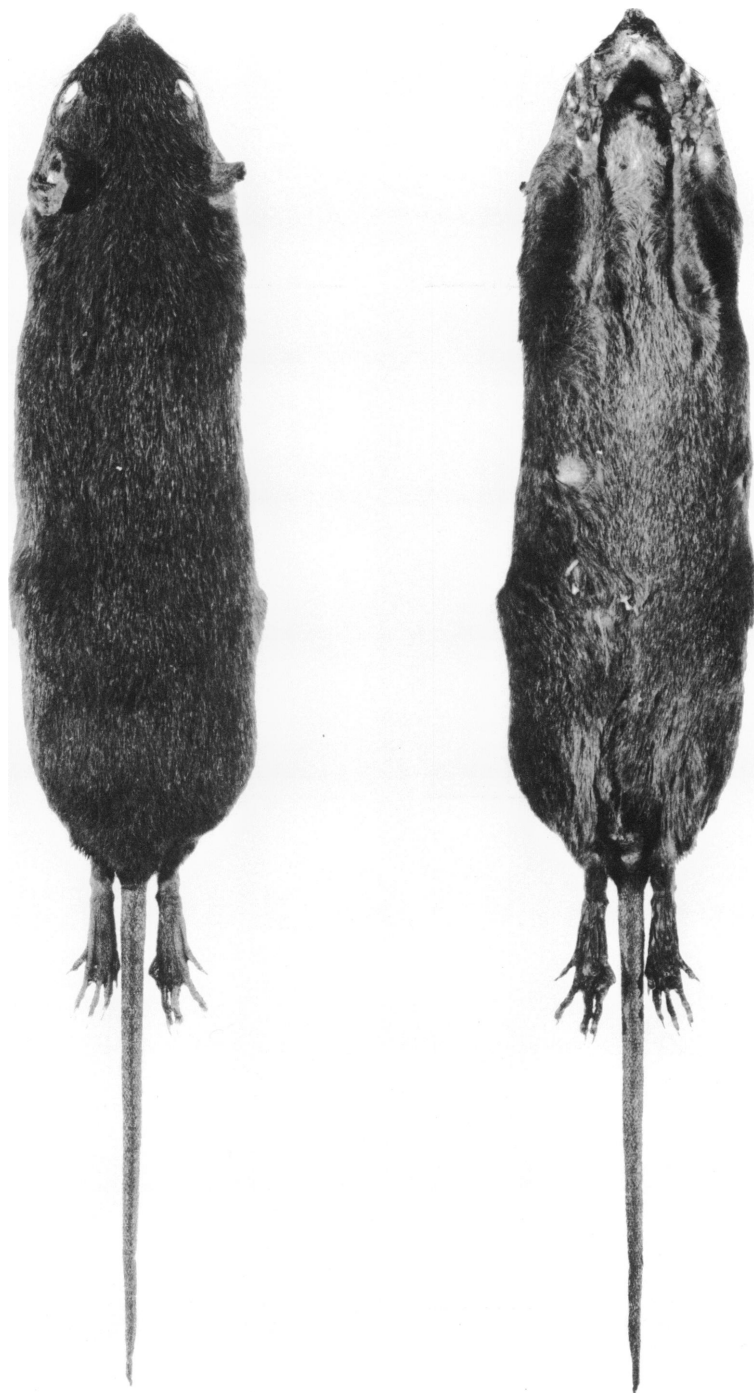


FIG. 10. *Crnomys celebensis*. Dorsal (left) and ventral (right) views of the holotype (AMNH 224316) from Lindu Valley, Central Sulawesi. See table 1 for measurements.

small patches of fur are gone from the skin, all elements are in good condition. The holo-

type was originally placed in the collection of the American Museum of Natural History

and cataloged as AMNH 224316, but it will eventually be transferred to the Museum Zoologicum Bogoriense at Bogor, Indonesia, where it will bear the number MZB 12153.

REFERRED SPECIMENS: Two others, in addition to the holotype. One is an adult female (AMNH 240490) collected January 23, 1972 from forest behind Tomado at about 3500 feet; the animal was fixed in formalin and is now preserved in alcohol, the skull has been extracted and cleaned. The other specimen is an adult female (AMNH 225042) obtained on October 31, 1974, from an altitude of 2700 feet in forest along the Sungai (stream) Sadaunta, a place about 5 airline miles southwest of Tomado (fig. 2). A stuffed skin, cranium and dentaries, and carcass fixed in formalin, now preserved in alcohol, comprise the specimen.

MEASUREMENTS: See table 1.

KNOWN DISTRIBUTION: Central Sulawesi, in tropical evergreen forest at middle altitudes (2700 to 3500 feet) in the mountain valley of Danau Lindu and the upper drainage of Sungai Miu in the Kulawi region.

ETYMOLOGY: Derived from Celebes, the other name for the island of Sulawesi, to denote the Celebesian (or Sulawesian) species of *Crunomys* in contrast to the three Philippine species.

DIAGNOSIS: *Crunomys celebensis* is much larger and darker than *C. fallax* of Luzon, with only slight demarcation in color between upperparts and underparts of body and tail (rather than conspicuously bicolored as in *C. fallax*). It is most like *C. melanius* of Mindanao in body and size, coloration, skull, and teeth but differs from it by having 1) soft pelage (not spinous as in *C. melanius*); 2) a narrower braincase; 3) longer nasals; 4) a wider and stockier rostrum; 5) a longer palatal region; 6) a bullar capsule with a swollen posterior half where the tip encloses an opening or depression (not swollen in *C. melanius*); 7) a tiny stapedial foramen (absent in *C. melanius*); 8) an oblong opening in the outer mastoid wall just below the mastoid foramen (this portion of the mastoid is ossified in *C. melanius*); 9) a smaller mastoid, both absolutely and relative to size of cranium, that is slightly inflated (larger and not as inflated in *C. melanius*); 10) a small and elongate vacuity in the maxilla adjacent to



FIG. 11. *Crunomys celebensis*. Plantar views of left hind foot (left side) and palmar view of left front foot (right side). Drawn from AMNH 240490. See text for descriptions.

the posterior third of each incisive foramen and just below the end of the incisor capsule (absent in *C. melanius*; the maxillary surface is ossified); 11) wider and more robust upper and lower incisors; 12) shorter toothrows and smaller molars; 13) and 14) longer and higher dentaries. See tables 1 and 2.

DESCRIPTION: *Crunomys celebensis* is a terrestrial forest rat with a short and broad head, a stocky body, small ears, short legs, narrow hind feet, and short tail; the impression is of a chunky, little short-tailed rat built close to the ground (fig. 9). The dark chestnut fur clothing the upperparts of the head and body is short, thick, and soft. The throat is grayish brown. The chest is paler than the upperparts because it is slightly suffused with gray. The abdomen and inguinal regions are about the same color as the back and thighs, only slightly paler. The transition in color from dorsum to venter is indistinguishable. The lips are unpigmented. Two concentric rings encircle each eye, an inner thin black one, and an outer wide unpigmented ring. The rostral vibrissae are short, only reaching back to the ears. The ears are small, round, scantily haired, and blackish brown, slightly contrasting in color with the chestnut upperparts.

The body is patterned. The sides of the



FIG. 12. *Crunomys celebensis*. Side views of front (top) and hind (bottom) feet. Drawn from AMNH 240490. See text for other information.

muzzle, as well as the outside and top of each upper and lower arm are blackish brown and this tone extends onto the tops of the front feet out over the digits to the bases of the claws. The sides and tops of the thighs and hind legs are also blackish brown as are all surfaces of the hind feet, the rump, and around the base of the tail and anus. These dark areas contrast with the rest of the body and form a subtle pattern on the upperparts, a pattern more evident on AMNH 224316 than on the other specimens.

The tail is shorter than the combined lengths of head and body. The dorsal surface and sides are blackish brown, the ventral surface is slightly paler. Fine scales (table 1) and stiff hairs (three to a scale) form the surface.

The conformation of the front and hind feet (figs. 11 and 12) reflects a ground-dwelling habitus. The feet are long and narrow as are the digits. The claws are moderately long and not sharply recurved. The palmar and plantar surfaces are naked and adorned with small and fleshy pads (or tubercles). On each palmar surface there are three interdigital pads and two palmar pads, a large and prominent inner one and a smaller outer one. The three interdigital and the outer palmar pads are fleshy, round pimples that range in diameter from 0.5 to 1.0 mm. The large inner palmar pad is oblong, 2–3 mm. wide, hard, and projects prominently above the surface of the palm. The other pads are lower. There are

four interdigital pads and two plantar pads beneath each hind foot. The interdigital pads are small (0.5–1.0 mm. in diameter) and lower than those on the front feet, and not as prominent. Of the two plantar pads, the inner one is elliptical and 2 mm. long. The outer one is tiny and resembles the interdigital pads in configuration and size. The six pads of each hind foot are small and occupy relatively little of the plantar area.

The interdigital, palmar, and plantar pads are nearly smooth. At most their surfaces are scored by shallow striations. There are no prominent transverse or semicircular lamellae like those found on pads of *Rattus rattus* or *R. exulans*, for example, species that are terrestrial but also good climbers, or on arboreal rats such as the species of *Hapalomys*, *Chiropodomys*, or *Margaretamys* (Musser, 1972, 1979, 1981a). Arboreal rats have large interdigital and plantar pads on their hind feet that project prominently and take up much of the surface. The pads are deeply sculptured with transverse and semicircular striae. The larger pads may be used for grasping twigs and the striated surfaces may provide adhesion. In species that are primarily ground-dwellers, the pads are small relative to extent of the plantar areas, they do not project as high above the surfaces, and they are either smooth or only shallowly scored.

The female specimen of *C. celebensis* has eight mammae: one pectoral pair, one post-axillary pair, and two inguinal pairs.

The chunky head and body of *C. celebensis* is reflected in its stocky and compact cranium. The conformation results from the combination of a short and thick rostrum, wide interorbital area, large and compact braincase, and robust zygomatic arches (fig. 13). From a dorsal view, the outline of the cranium is nearly rectangular. The nasals are oblongate in outline and provide a rounded anterior margin to the slightly sloping sides of the rostrum. The dorsolateral margins of the orbit are formed by large diamond-shaped lacrimals. The frontal bones between the orbits are inflated. The dorsolateral margins of the interorbital and postorbital areas, as well as the braincase, are nearly smooth, with at most only traces of ridging. The braincase is rounded. The interparietal is wide (from side-to-side) and short (front-to-back), and

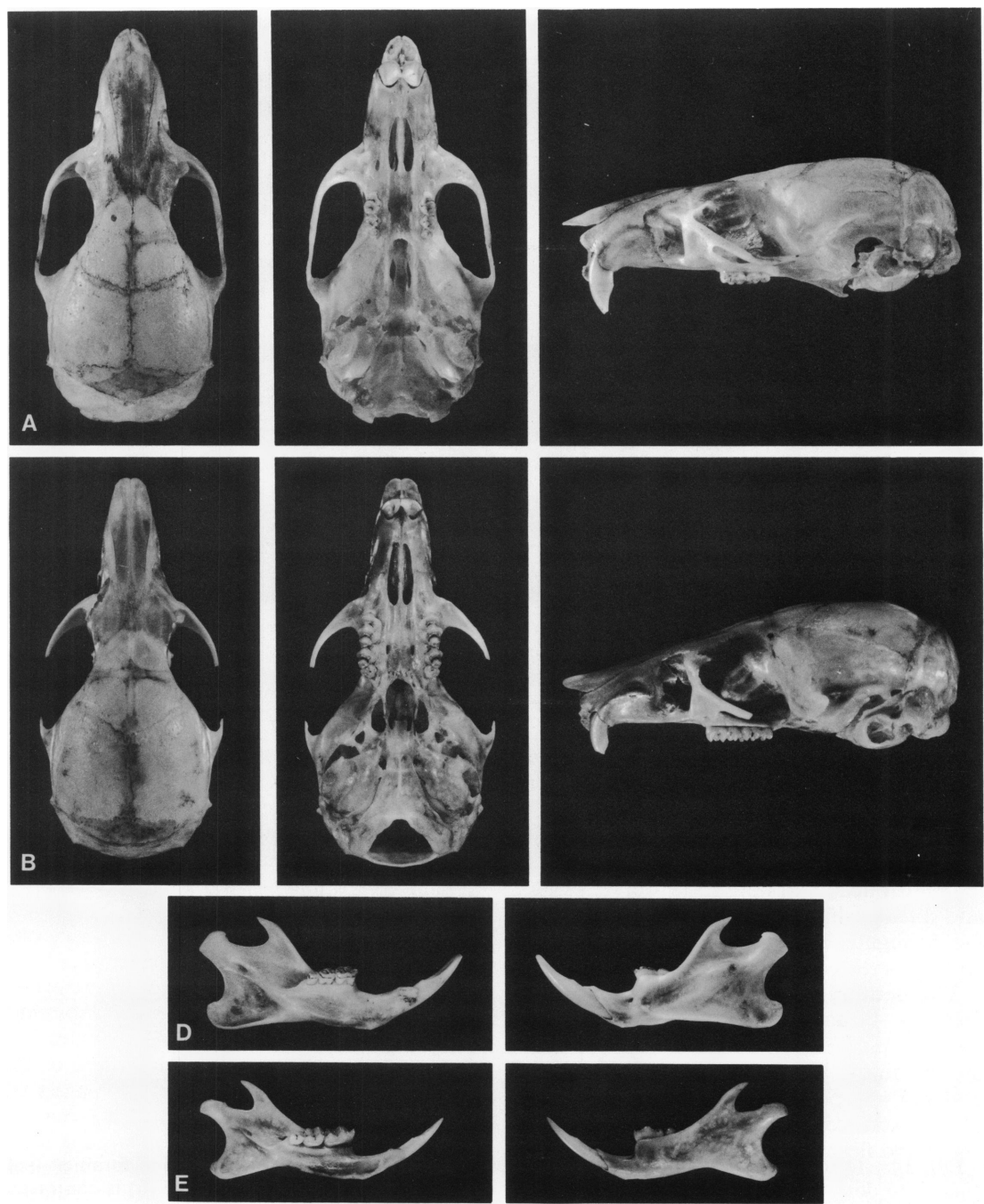


FIG. 13. Views of crania and dentaries from adults. A and D: *Crunomys celebensis* (AMNH 224316, holotype). B and E: *Archboldomys luzonensis* (FMNH 95122, holotype). All approximately $\times 2$. Measurements and other data are listed in table 1.

most of it roofs the deep (front-to-back) occiput rather than being confined between the

parietals. The occipital condyles project slightly beyond the back of the braincase.

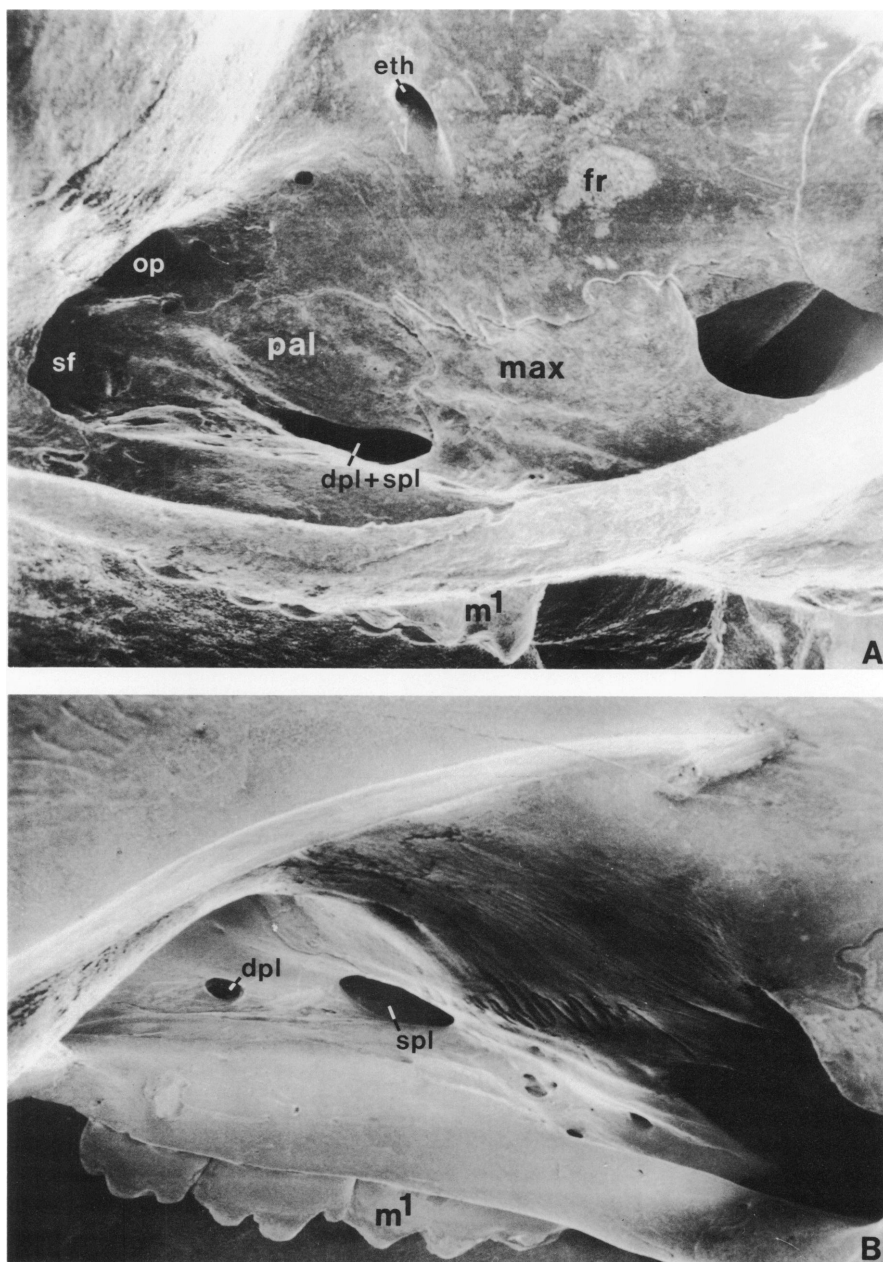


FIG. 14. Orbital views of adult *Crunomys* and *Rattus*. Position of sphenopalatine foramen (**spl**) relative to dorsal palatine foramen (**dpl**) in right orbit of *C. celebensis* (AMNH 224316) is contrasted with relative positions of these foramina in *R. exulans* (AMNH 223141).

Other abbreviations: **eth**, ethmoid foramina; **fr**, frontal bone; **max**, maxillary bone; **pal**, palatine bone; **op**, optic foramina; **sf**, sphenoidal fissure; **m¹**, first upper molar. Anterior is to the right.

From a side view, the dorsal profile of the cranium slopes evenly from the top of the braincase down to the tips of the nasals. The

anterior parts of the nasals appreciably overhang the front end of the rostrum and the upper incisors, and their tips are not hori-

zontal or turned up. Each zygomatic plate is narrow; its anterior margin is without a projecting spine and is either straight (fig. 13) or slightly concave (similar to that in *C. fallax*, fig. 59) in the three specimens. The ventral maxillary roots of the zygomatic plates originate anterior to the first molar so the posterior margin of each plate is anterior to each toothrow.

Two features of each orbit (fig. 14) are important. The first is the single ethmoid foramen, which is large and conspicuous (the diameter ranges from 0.4 to 0.5 mm. among the three specimens). The foramen transmits the ethmoid artery and vein into the cranial cavity, and a branch of the ophthalmic nerve, which is called the anterior ethmoid nerve by Hill (1935, p. 123) or the nasociliary branch of the ophthalmic by Wahler (1974, p. 372). The nerve extends to the nasal cavity through the cribriform plate. The second is the long and narrow sphenopalatine foramen above the first and second molars. The foramen is, as Hill (1935, p. 124) wrote, "situated between the orbital process of the maxillary and the orbital process of the palatine bone, in the ventral medial wall of the orbit. . . . This foramen transmits the sphenopalatine nerve, a branch of the maxillary, and the sphenopalatine blood vessels." Incorporated within the sphenopalatine foramen is the dorsal palatine foramen. This configuration, in which the dorsal palatine and sphenopalatine foramina are united, contrasts with the condition in species of *Rattus*, where the dorsal palatine foramen is in the floor of the orbit separate from the sphenopalatine foramen and well posterior to it. Each dorsal palatine foramina leads into the palatine canal, which courses ventrad from the orbit through the maxillary-palatine suture and into the posterior palatine foramen. The dorsal palatine foramen transmits the descending palatine artery and nerve.

The squamosal roots of the zygomatic arches originate low on sides of the braincase. The posterior margins of the roots do not extend as low ridges back to the occipitals, so the outer braincase walls are smooth behind the roots.

The outer wall of each mastoid is small. Its dorsoposterior surface bulges out from the side of the occiput and is perforated by a large oblong or squarish fenestra just ventral to the

mastoid foramen (fig. 25). I do not know the function of this opening. A groove on the anterior portion of the mastoid leads anteroventrally into the very small squamoso-mastoid foramen in the suture between the squamosal and the mastoid. Because the squamoso-mastoid foramen is small, the squamosal above each bulla is complete (fig. 24) and not separated into a dorsal portion and a hooklike ventral part by a large fenestra formed by the expansion of the squamoso-mastoid foramen as is the case in the Isarog rat (fig. 24), for example.

On the side of each braincase posterior to the orbit and above the pterygoid ridge, the alisphenoid region is without a lateral strut of alisphenoid bone. The alisphenoid canal is an open channel in this area, its entry into the sphenoidal fissure can be seen and the foramen ovale is conspicuous in side view. The alisphenoid canal transmits the internal maxillary artery and masticatory nerve, which pass along the bottom of the channel and through the anterior opening of the canal into the sphenoidal fissure and then the orbit. Without the strut of alisphenoid bone, the buccinator-masticatory foramina are functionally absent and the foramen ovale accessorius lacks an anterior boundary (fig. 23). The masticatory and buccinator branches of the maxillary nerve emerge directly from the foramen ovale. The buccinator nerve runs anteriorly, most of the masticatory courses onto the lateral surface of the alisphenoid bone in a shallow channel. The foramen ovale accessorius was defined by Wahler (1974, p. 373). The foramen is complete only in rats 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. Without the strut, the foramen ovale accessorius is incomplete, represented only by posterior and ventral margins formed by a rim of alisphenoid bone and the pterygoid bridge. The foramen has functionally coalesced with the masticatory-buccinator foramina. The configuration resembles that in *Rattus*, for example, rather than *Apomys* and some other genera in which a strut of bone is present (Musser, 1981a, 1982), including the Isarog rat (fig. 23).

The auditory bullae are small relative to

size of the cranium (fig. 13). Each is attached to the posterolateral margin of the alisphenoid by a slim and fragile extension of the periotic portion of the petromastoid bone. There is a spacious postglenoid vacuity between the periotic and squamosal and a large medial lacerate space (also called the foramen lacerum) separates the anterior margin of each bulla from the pterygoid plate (figs. 24 and 30). The postglenoid vacuity "transmits a large vein which drains most of the cranial cavity, including the brain," wrote Hill (1935, p. 127). The eustachian tube at the front of each bulla is long, wide, and prominent. The posterior half of each bullar capsule is slightly swollen and the postero-medial tip encloses a hole or deep depression. The stapedia artery is minute and passes into the otic region through a tiny foramen between the tympanic and the periotic (figs. 27 and 28). The artery passes over the posterior part of the petrosal in a shallow, barely evident groove. Apparently only the otic region is served by the stapedia artery because it does not emerge from the bulla. No portion of the hyoid remains on the posteromedial part of the bullar capsule.

In a ventral view of the cranium, the incisive foramina are narrow and short, ending far in front of the first molars. In the maxilla lateral to each incisive foramina there is an elongate fenestra (fig. 29) that represents an unossified portion of the maxilla just medial to the tip of the incisor capsule, which touches the inner surface of the maxilla and can be seen through the fenestra. Behind the incisive foramina, the palatal bridge is wide and long, its posterior margin is just anterior to the backs of the toothrows. The surface of the bony palate is mostly smooth with only slight pitting toward the posterior margin, a condition similar to that in *Rattus* and not in *Apomys* in which the bony palate is densely pitted and perforated (Musser, 1982). Posterior to the palate, the mesopterygoid fossa is deep and wide but slightly narrower than the breadth of the palatal bridge. Its walls are breached by short and narrow sphenopalatine vacuities (figs. 13 and 30). Lateral to the mesopterygoid fossa, the anterior two-thirds of each pterygoid fossa is a narrow, flat, and completely ossified platform that is not breached by a sphenopterygoid vacuity. As

seen from a ventral perspective, that plate forms a roof over the alisphenoid canal and part of the foramen ovale. There is a transverse groove in the alisphenoid wing of the pterygoid plate that extends from the outer corner of the eustachian tube across the plate and under the platform. The place where the groove passes beneath the edge of the platform is the posterior opening of the alisphenoid canal (fig. 30). This configuration, along with a minute stapedia foramen, reflects a distinctive carotid circulation in that region, a pattern that is diagrammed in figure 31 and that is described in the account of the Isarog rat.

A sharp pterygoid ridge defines the lateral edge of each fossa. It extends from behind the molar row to the foramen ovale. The posterolateral margin of the pterygoid plate between the foramen ovale and bulla is a smooth moundlike bridge (fig. 30).

The dentaries are thick and sturdy (fig. 13). On each, the coronoid and angular processes are large, the posterior margin is deeply concave, and the incisor root does not extend up into the condyle. The capsular projection is conspicuous on the lateral side of each dentary and forms a prominent bulge between the coronoid and condyloid processes. The medial surface of each condylar process posterior to the mandibular foramen is nearly flat, not ridged.

The upper and lower incisors are wide and appear sturdy. The enamel layers are either pale or intense orange. The uppers emerge from the rostrum at a right angle (fig. 13); their tips form a straight edge. Inside the rostrum the curve of each incisor extends all the way back and down to the floor of the maxilla where the alveolar capsule touches the inside surface of that bone. Within each dentary, the wide lower incisor sweeps back and up to form a prominent and wide rounded margin and partial ridge along the ventral edge of the dentary and behind the molar row.

The molars of the holotype of *C. celebensis* (fig. 15) and those of the other two specimens have occlusal surfaces so worn their cusp patterns are nearly obliterated. The patterns that are present appear to be worn versions of the occlusal surfaces in the adult (fig. 7) and young adult (fig. 6) *C. melanius*. In the specimens of *C. celebensis*, the proportions of the molars

relative to the palatal area and mandibular surface are like those in *C. melanius*. So, too, is the size of each tooth relative to one another in each row, the degree of overlap among the molars, and the number of roots anchoring each tooth.

COMPARISONS: *Crunomys celebensis* requires close comparison with *C. melanius*. Because the holotype of *C. celebensis* has a complete skull, I described that example in detail. Contrasts between it and *C. melanius* were pointed out in the diagnosis of *C. celebensis*. Additional comparisons between the two species will be noted when they are contrasted with the specimen from Mount Isarog, which will be discussed following the next section.

HABITAT AND HABITS: The three specimens of *Crunomys celebensis* came from 2700 and 3500 feet in tropical lowland evergreen rain forest similar to that depicted in figure 16. That formation is rich in species of trees, shrubs, woody vines, palms, and ferns. The still air is warm, damp, and humid beneath the canopy. The understory and ground is a patchwork of bright light and shadow, mosaic patterns formed by sunlight filtering through the high leafy canopy. Whitmore (1975) and Richards (1976) define and discuss this type of forest.

All three rats were caught near or on forested terraces next to wet ravines or small streams, situations similar to the scene in figure 17. The specimen from 2700 feet (AMNH 225042) was trapped on a tree trunk laying from one terrace to the other across a small stream in the valley of the Sungei Sadaunta (fig. 2); the habitat resembles that in figure 18. The terraces on either side of the stream are rocky and muddy. Chunks of rotting tree trunks and tangles of limbs are scattered about. Decayed trunks and long fronds of vanga palms (*Pigafetta filaris*) clutter the ground. Dense broadleaf shrubbery, tall ferns and gingers, rosettes of rattan, understory trees, low woody vines looping through tall shrubs, and an occasional banana tree combine to form a characteristic streamside plant cover. Higher terraces support tall trees that canopy parts of the stream. Pieces of rotten trunks and limbs, part of an old tree-fall, bridge it. Usually wet and slightly mossy, small mammals use the bridge to cross from



FIG. 15. *Crunomys celebensis*. Occlusal views of right maxillary (left side) and mandibular (right side) molar rows of the holotype, AMNH 224316.

one terrace to the other. *Crunomys celebensis*, *Taeromys celebensis*, *Rattus hoffmanni*, and the gray rat (*Bunomys* sp.) were caught within 10 feet of one another on top of the trunk and limbs. *Maxomys hellwaldii*, *Paruromys dominator*, *Rattus marmosurus*, and *Bunomys chrysocomus* were trapped on nearby terraces and hillsides.

During the period, September 16 to November 2, 1974, I obtained maximum and minimum air temperatures every 24 hours at a station on a stream terrace in forest 200 feet down-canyon from where the *Crunomys* was caught. Rainfall and relative humidity were also recorded during those 48 days. All measurements were taken beneath the forest canopy; the thermometer was placed on the ground. Rain, light showers to tropical drenchings, occurred during 34 of the days and nights. Relative humidity ranged from 94 to 100 percent (mean, 96.5%) at daybreak, 65 to 97 percent (mean, 82.4%) at midday, and 91 to 100 percent (mean, 95.7%) after dark. Minimum air temperatures, which occurred during the night, ranged from 62° to 69° F. (mean, 66.3° F.); maximum air temperatures fluctuated from 71° to 81° F. (mean, 74.5° F.).



FIG. 16. Lowland tropical evergreen forest at 3500 feet near village of Tomado in the Lindu Valley, Central Sulawesi. Holotype of *Crunomys celebensis* was trapped nearby. Photographed the latter part of May 1974.

The other two specimens of *C. celebensis* were caught at the base of the first ridge behind the village of Tomado in the valley of Danau (Lake) Lindu (fig. 2). Long waves of steep forested ridges encircle the lake. Those near villages are covered with secondary forest or

a mixture of primary and secondary growth. Ridges and mountains farther from villages are clothed with primary evergreen forest. The first ridge west of Tomado has a mixture of secondary and primary growth. The primary forest was selectively thinned by cutting and



FIG. 17. Primary forest along Sungai Pormina, a tributary of Sungai Sadaunta. Elevation is about 2300 feet, Central Sulawesi. Habitat is typical of that along sections of Sungai Sadaunta where a specimen of *Crunomys celebensis* was caught. Photographed the latter part of April 1974, by Margareta Becker.

removing some large canopy trees. Those remaining, many of them emergent species of strangler fig, form a high and broken canopy (fig. 16). Ferns, broadleaf shrubs, clusters of young rattans and palms, saplings, tree ferns, and mature short trees form a dense

understory. Near the bottom of the ridge next to a small stream, the forest is cool and wet. Mosses, ferns, and herbaceous and woody vines adorn the trees. The forest floor is carpeted with a thick mat of decaying leaves and tangles of rotting tree trunks and limbs.



FIG. 18. Forest near village of Tomado where holotype of *Crunomys celebensis* was trapped. Dense streamside vegetation is typical of these places. The trunk across the stream is used by small mammals, including *Crunomys*, to cross from one stream terrace to the other. Photographed the latter part of May 1974.

It was under such a pile that one specimen of *C. celebensis* (AMNH 240490) was taken.

The place was cool and damp, the ground cover lush. Moss, decaying leaves, ferns, small



FIG. 19. Lowland tropical evergreen forest near village of Tomado, 3500 feet, Central Sulawesi. Holotype of *Crunomys celebensis* was trapped on damp ground (white arrow) beneath trunk. Photographed the latter part of May 1974.

shrubs, leafy vines, and rattan rosettes encased the limbs in a verdant, viny and leafy mantle. The *Crunomys* was trapped in a damp run-way under one of the larger limbs. Examples of *Bunomys chrysocomus* and *Rattus hoffmanni* were caught under the same pile.

The other specimen of *C. celebensis* (AMNH 224316) from near Tomado came from a terrace in similar forest. It was trapped

on damp ground beneath a rotten limb that is part of an old tree-fall. The place and surrounding vegetation is shown in figure 19.

Judged from places the three *C. celebensis* were caught, the species inhabits wet and humid streamside forest at middle elevations in the central part of Sulawesi. I am uncertain, however, if these examples reflect the real altitudinal distribution of the species. The

rat was hard to catch; it did not enter live-traps, did not come to baited kill-traps, and was caught only as it ran across the treadle of a Victor rat-trap or into treadles of Coni-bear traps. On the other hand, I spent a long time (up to three months) at camps in low-lands and mountains below and above the *Crunomys* localities where other species equally difficult to trap were caught.

I learned little about habits of *C. celebensis* during my stay in the forests of Sulawesi. The

species is probably diurnal. Two of them were caught at 9 o'clock in the morning and were not in the traps when we checked the line earlier. In my experience, a terrestrial habit, small body, short tail, and dark chestnut coloration are characteristics of diurnal murids that live in Far Eastern forests. What *C. celebensis* eats is unknown. Two of the specimens had empty stomachs, the third stomach contained a finely ground white plant part.

THE MOUNT ISAROG SHREW RAT

From Mount Isarog in the southeastern peninsula of Luzon Island comes a specimen that superficially resembles *Crunomys melanius* and *C. celebensis* in body size and conformation, pelage color, and molar patterns. Based upon other characters, however, the rat clearly represents an undescribed species in a genus other than *Crunomys*. It is a Philippine shrew rat of small body size, another specialized murid known only from Luzon, a species named and characterized below.

ARCHBOLDOMYS, NEW GENUS

TYPE SPECIES: *Archboldomys luzonensis*, new species.

KNOWN DISTRIBUTION: The type species only.

DIAGNOSIS: A genus of small-bodied terrestrial murid that is more similar to *Crunomys* than any other rat but distinguished from it by the following combination of characters: 1) long and thick fur; 2) elongate claws on the front feet; 3) a slender tapered rostrum; 4) dorsal profile of cranium sloping from top of high and squarish braincase down steeply to nasal tips, which are turned up; 5) ventral maxillary roots of zygomatic plates partly originating over anterior portion of first upper molars; 6) alisphenoid region with narrow alisphenoid strut separating buccinator-masticatory foramina from foramen ovale accessorius; 7) a spacious squamoso-mastoid vacuity dividing squamosal bone into two parts; 8) inflated bullae that are longer relative to length of skull; 9) long incisive foramina; 10) configuration of pterygoid fossa and

alisphenoid wing of pterygoid plate as in figure 30A; 11) carotid arterial circulatory pattern as in figure 31; 12) slender dentaries; 13) molars large, both absolutely and relative to cranium and mandible, their surfaces gleaming white; 14) cusps, especially on upper molars, with high conical margins; 15) no cusps t3, t7, or t9 on upper molars, no posterior cingulum on any uppers; 16) a posterior labial cusplet on each first lower molar.

ETYMOLOGY: The generic name is formed by combining *mys*, from the Greek for mouse, with the surname of Mr. Richard Archbold (see fig. 20).

Archboldomys luzonensis, new species

HOLOTYPE AND LOCALITY: A young adult male (in scrotal condition) collected on April 24, 1961, by D. S. Rabor (original field number, 1449) from an altitude of 6560 feet on Mount Isarog. The specimen (FMNH 95122) consists of a stuffed skin, cranium, and dentaries. The skin is in good condition (fig. 22). The cranium is mostly intact (fig. 13) but the middle of each zygomatic arch is missing, many of the vacuities have been enlarged and some delicate bony processes destroyed by overcleaning, and the incisor tips are gone. The left dentary is intact (fig. 13), the right lacks most of the angular process. Measurements are listed in table 1.

REFERRED MATERIAL: The holotype only.

DISTRIBUTION: Known only from Mount Isarog, a volcanic peak on the southeastern peninsula of Luzon Island, Camarines Sur Province, the Philippines (fig. 21; also, see the map in King and McKee, 1949). The

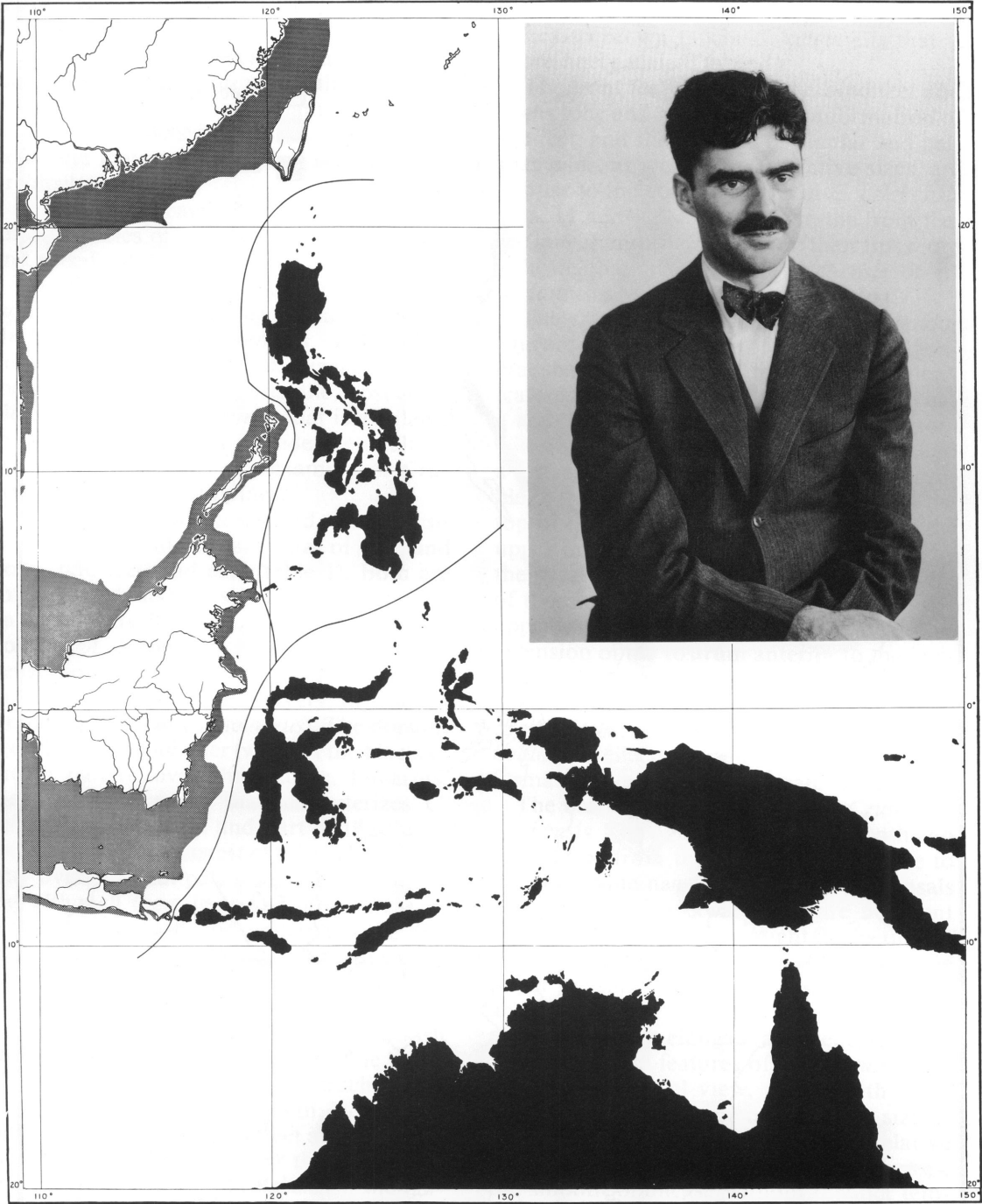


FIG. 20. The late Mr. Richard Archbold. His interest in adventure and natural history stimulated him to share his resources for expeditions to the Far East and research in museums. Usually associated with the New Guinea area, Richard Archbold, through the auspices of Archbold Expeditions, never imposed geographic limits or a particular focus on his associates. Naming a Philippine endemic after him points up the past breadth of his patronage and commitment to indifferent inquiry of whatever and wherever.

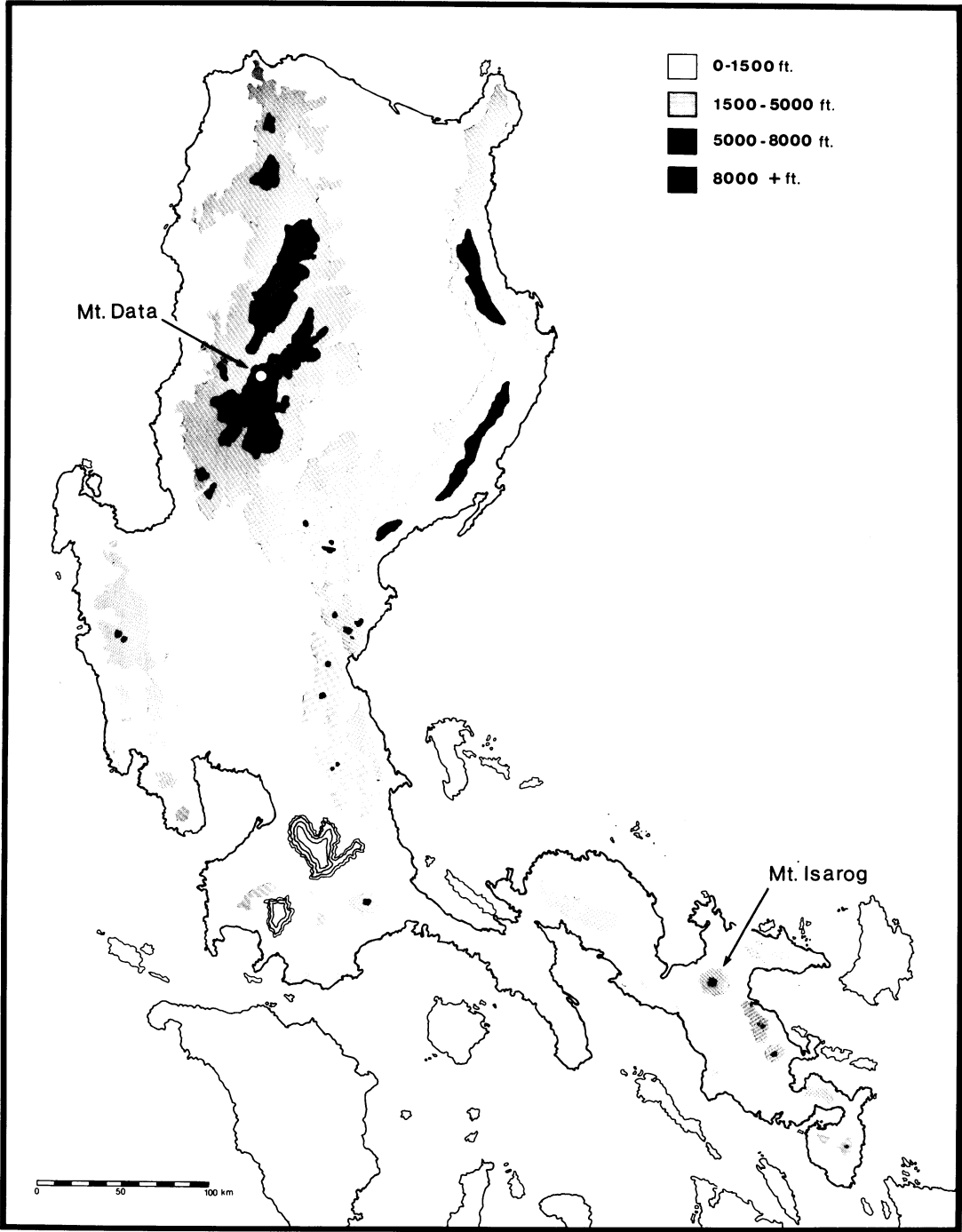


FIG. 21. Map of Luzon Island in the Philippines. Holotype of *Archboldomys luzonensis* was caught on Mount Isarog.

species should be looked for on other islands. *Crateromys*, *Batomys*, *Chrotomys*, and *Cru-*

nomys were once thought to be endemic to Luzon but are now recorded from other Phil-

ippine islands (Misonne, 1969; Temme, 1974; Musser and Gordon, 1981).

ETYMOLOGY: The specific name points out Luzon as the island on which the species is now found, with the attendant implication that distinguishable populations of *Archboldomys* may occur on other islands in the archipelago.

DIAGNOSIS: Because *luzonensis* is the only known species of *Archboldomys*, the generic and specific diagnoses are the same.

DESCRIPTION AND COMPARISONS: Comparisons in the following section are between *Archboldomys* and *Crunomys*, and mostly between the holotype of *A. luzonensis* and the holotype of *C. celebensis*, the most complete example of *Crunomys* that is available to me. Some contrasts include the adult *C. melanius* from Saub, my example of *Crunomys* from the Philippines.

Archboldomys luzonensis and *C. celebensis* are terrestrial and similar in size of head and body, tail, feet, and ears (table 1). Both are small-bodied rats with short tails, narrow feet, and small ears. The pelage over the head and body of *A. luzonensis* is long (9–11 mm.), dense, soft, and slightly woolly (shorter, 5–6 mm., in *C. celebensis*, velvety instead of woolly, spinous in *C. melanius*). The dorsum is dark chestnut all over (without the blackish brown pattern over the muzzle, forearms, hind legs, and rump that characterizes *C. celebensis*). The chin and part of the throat are unpigmented, the rest of the venter is dark gray overlaid with pale buff and silver flecking; although there is no sharp demarcation between upperparts and underparts the two surfaces are conspicuously distinguishable (instead of indistinguishably grading from dorsum to venter, as in *C. celebensis*). The ears are small, dark chestnut (not blackish brown), and densely covered with fine hairs. The rostral vibrissae are short, reaching the ears but not extending past them. Dorsal surfaces of the front and hind feet are brown all the way out to the bases of the claws (not blackish brown as in *C. celebensis*); the palmar surfaces are pale brown, the plantar surfaces are dark brown.

The tail of *A. luzonensis* is shorter than the combined lengths of head and body, brown on its dorsal and lateral surfaces, and slightly paler along its ventral surface. The scales are

large and from each emerge three hairs (blackish brown tail in *C. celebensis* that is more finely scaled; table 1).

The front feet are small, the hind feet and digits long and narrow. The conformation of the feet, and the number of plantar and palmar pads, as well as their relative sizes, are similar to the configurations in *C. celebensis* (figs. 11 and 12). The claws on the front feet are longer, more recurved and their tips more delicate than those of *C. celebensis* or *C. melanius*.

The cranium and dentaries of *Archboldomys* are similar to those of *Crunomys* in general shape but the two genera differ in many features (fig. 13). *Archboldomys luzonensis* has a high boxlike braincase with a domed top, wide interorbital and postorbital regions, and a delicate and slim rostrum. The dorsal profile of the cranium is a steep incline from the top of the high braincase to the level of the upper incisors where the slope is broken by the nasal tips, which turn upward. The sides of the premaxillaries project in front of the upper incisors forming a short bony tube. This extension of the rostrum anterior to the incisors combined with the upturned nasal tips resembles the configuration in the Sulawesi *Melasmothrix* (fig. 37). The cranium in *Archboldomys* reflects a long-nosed shrewlike conformation, and appears delicate in build.

The braincase is not domed in *Crunomys celebensis*. The dorsal profile is a smooth and low incline from the top of the braincase to the end of the nasals. The tips of the nasals curve slightly downward and are not bent upward. There is only a slight projection of the rostrum anterior to the front faces of the upper incisors. The rostrum is broad, deep, and stocky. The cranium appears compact and chunky, not elongate and delicate.

Other cranial features of *A. luzonensis*, as seen from a dorsal view, resemble those in *C. celebensis*: the shape and relative size of the lacrimals; the conformation and relative width of the interorbital and postorbital areas; the smooth braincase without distinct temporal ridging; the shape and relative size of the interparietal, as well as occipital depth (front-to-back) of the braincase.

There are other similarities and differences between the two genera when the crania are viewed from the side. The difference in the

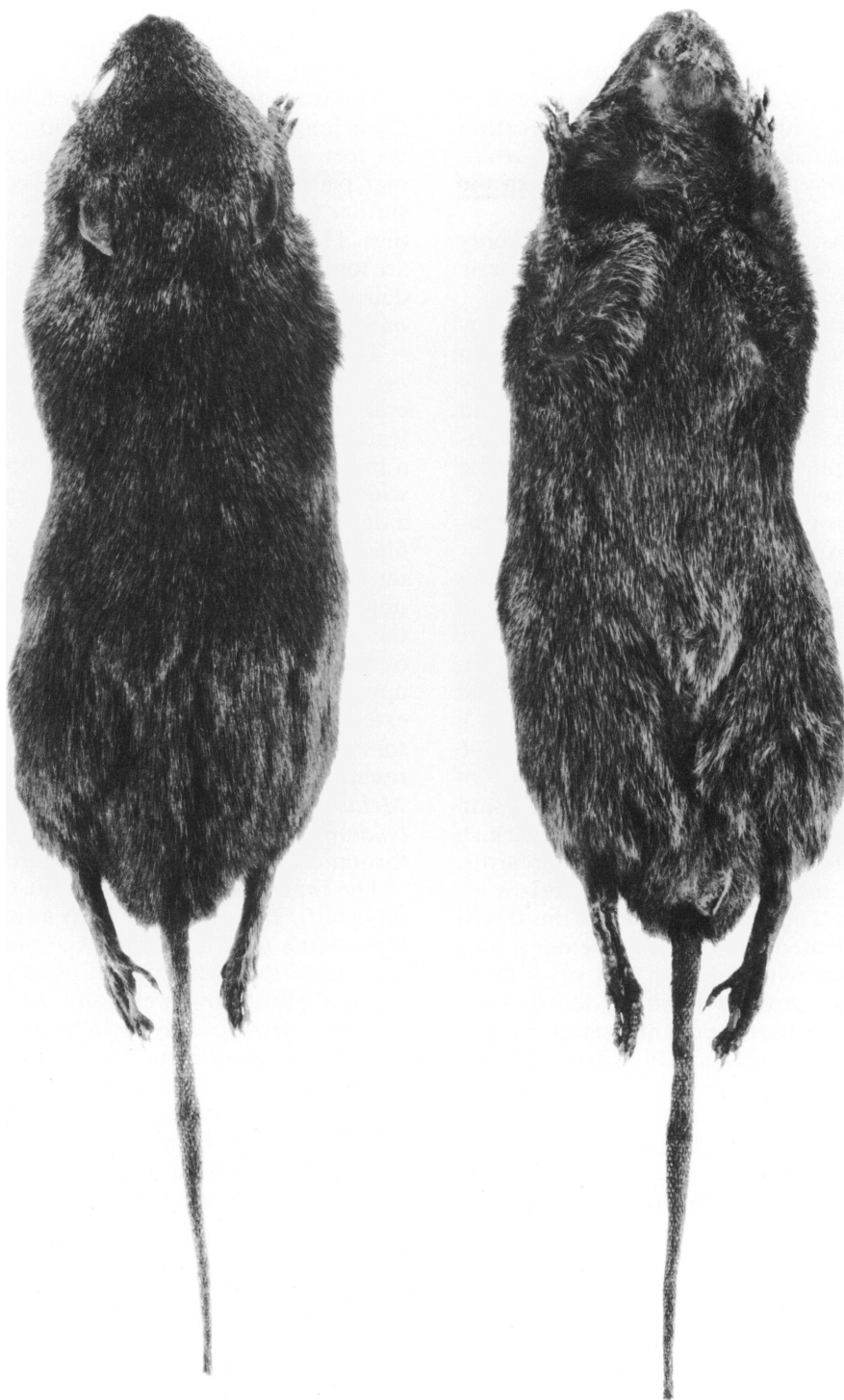


FIG. 22. *Archboldomys luzonensis*. Dorsal (left) and ventral (right) views of holotype (FMNH 95122). Measurements and other data are listed in table 1.

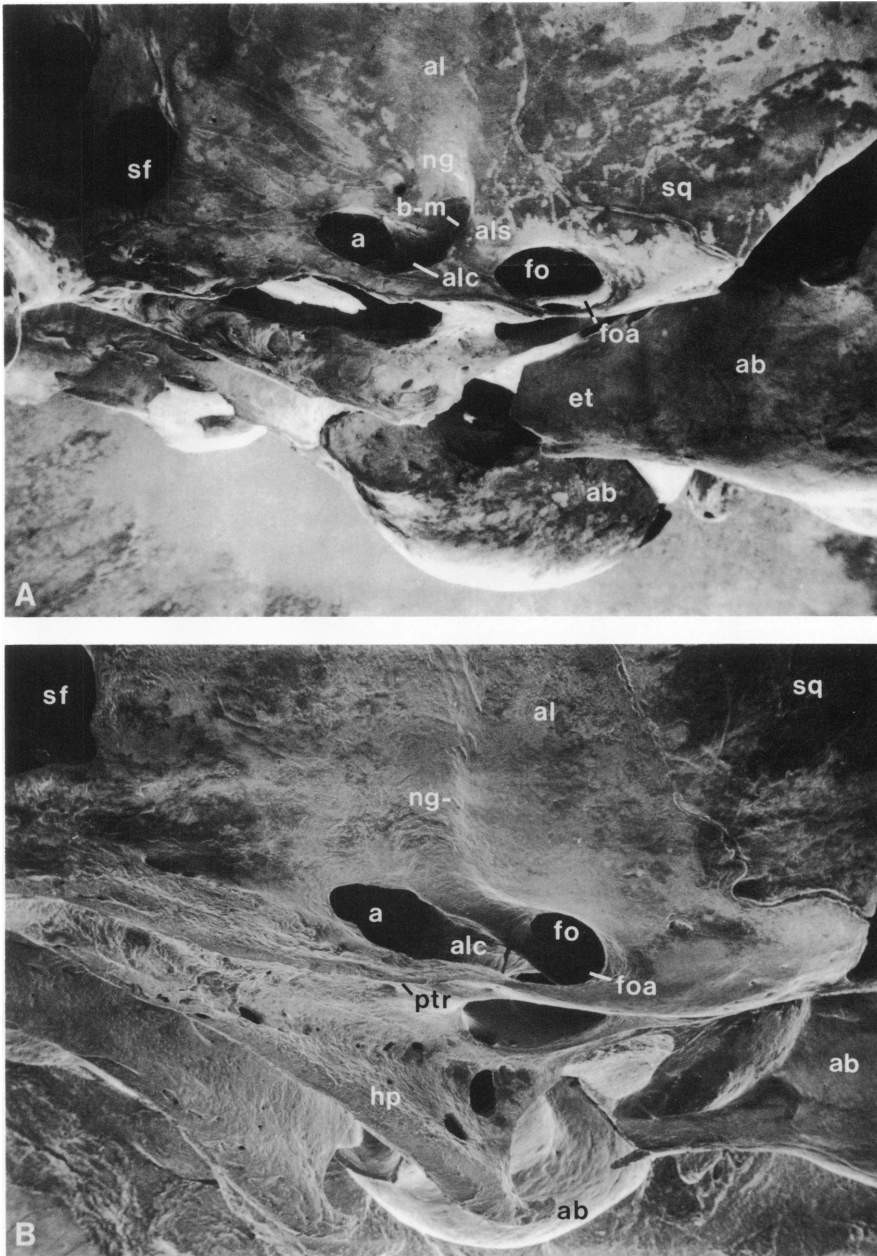


FIG. 23. Views of left alisphenoid regions in adult *Archboldomys* and *Crunomys*. A, *A. luzonensis* (FMNH 95122), in which a lateral strut of alisphenoid bone (als) conceals part of the alisphenoid canal (alc). B, *C. celebensis* (AMNH 224316) in which the alisphenoid strut is absent. See text for additional comparisons and descriptions.

Other abbreviations: a, anterior opening of the alisphenoid canal; ab, auditory bulla; al, alisphenoid bone; b-m, coalesced masticatory-buccinator foramina; et, bony eustachian tube; fo, foramen ovale; foa, foramen ovale accessorius (in view A, the foramen ovale is medial to the foramen ovale accessorius); hp, hamular process; ng, channel containing most of the masticatory nerve, which emerges directly from the foramen ovale in configuration B, or from the masticatory-buccinator foramina in configuration A; ptr, pterygoid ridge; sf, sphenoidal fissure; sq, squamosal bone.

outline of the rostrum noted above is especially striking. The shape and size of the zygomatic plates are similar in the two genera. They differ in slope and position relative to the molar rows. In *A. luzonensis*, each plate slants backward; in *C. celebensis* and the other species of *Crunomys*, the plates are vertical. The zygomatic plates in *A. luzonensis* sit above the anterior half of the first upper molars. The posterior margin of each plate extends 1.0 mm. behind the anterior alveolar edge of each molar to about the middle of the tooth. In the three specimens of *C. celebensis*, the posterior margin of each plate is 0.5–0.8 mm. in front of the anterior alveolar margins of the first molars, 0.3 mm. in front of the molar rows in the adult of *C. melanius*, and 0.5 mm. in the holotype of *C. rabori*. The squamosal roots of the zygomatic arches originate low on the sides of the braincase in the holotype of *A. luzonensis*, close to the top of each postglenoid vacuity. The squamosal roots originate higher on the braincase in *C. celebensis*, a feature clearly shown in figure 13.

The relative positions, sizes, and shapes of most orbital foramina are similar in the two genera. The position of the sphenopalatine foramen in relation to the dorsal palatine foramen within each orbit of *A. luzonensis* resembles the configuration in *C. celebensis* (fig. 14). The ethmoid foramen is smaller, both actually and relative to length of orbit, in *A. luzonensis* than in either *C. celebensis* or *C. melanius*. The diameter of that foramen is 0.2 mm. in the holotype of *A. luzonensis*, ranges from 0.4 to 0.5 mm. in the three specimens of *C. celebensis*, and is 0.4 mm. in the adult *C. melanius*. The diameter of the foramen relative to the length of the orbit in the three species, is, respectively, 4 percent, 8–10 percent, and 7 percent.

Each alisphenoid region near the base of the braincase is different in the two genera. In the holotype of *A. luzonensis* there is a narrow strut of alisphenoid bone, intact on the left side of the braincase but broken on the right, forming the slender outer wall of the alisphenoid canal and separating the foramen ovale accessorius from the coalesced buccinator-masticatory foramina (fig. 23A). The space behind the strut is not partitioned

by bone into a ventral alisphenoid canal and a dorsal canal through which the masseteric and buccinator branches of the maxillary nerve pass. The anterior opening of the alisphenoid canal (into the sphenoidal fissure) is separate from the foramen ovale. In *C. celebensis* and specimens of all the other *Crunomys*, the strut of alisphenoid bone is missing. The masticatory and buccinator foramina are merged with the foramen ovale accessorius and only the dorsal, posterior, and ventral margins of the latter are present. The former masticatory-buccinator foramina are now indicated by the groove in which the masseteric and buccinator branches of the maxillary nerve pass dorsally up the lateral surface of the alisphenoid (fig. 23B).

Archboldomys and *Crunomys* are unlike in the conformation of the squamosal bone dorsal to each bulla. In *A. luzonensis*, the squamosal is separated into a dorsal portion and a hooklike ventral part (tympanic hook) by the squamoso-mastoid foramen, which is a spacious vacuity. The tympanic hook is intact on the right side of the holotype but broken on the left (fig. 24A). 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 *C. celebensis* and specimens of the Philippine *Crunomys* and the squamosal bone is complete between the mastoid-squamosal suture and the postglenoid vacuity (fig. 24B). In *Archboldomys*, 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. I hypothesize 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 squa-

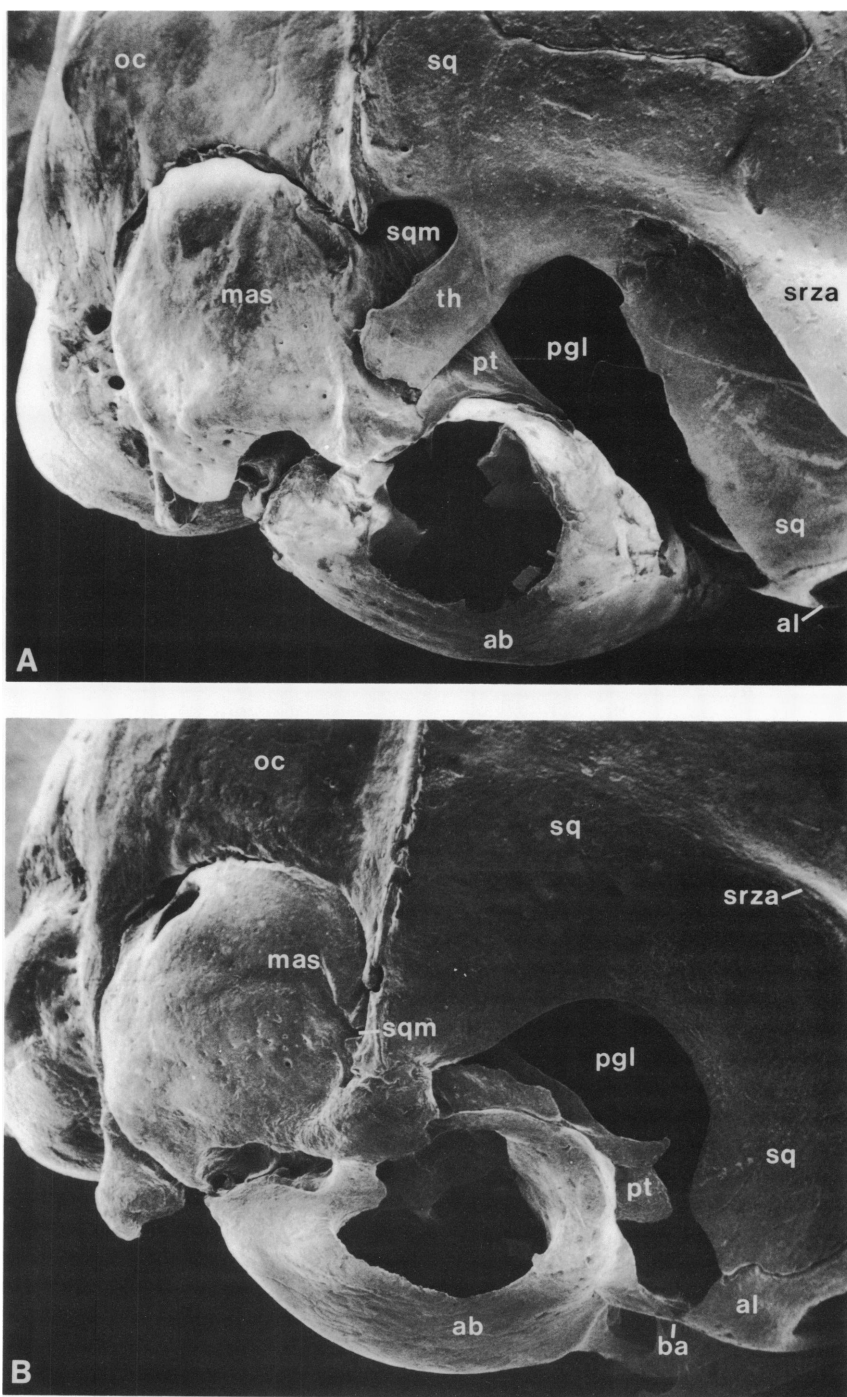


FIG. 24. Views of squamosal and bullar regions in adult *Archboldomys* and *Crunomys*. A, *A. luzonensis* (FMNH 95122) is compared with *C. celebensis* (AMNH 224316), B.

Abbreviations: **ab**, auditory bulla; **al**, alisphenoid bone; **ba**, a point of attachment of bulla to alisphenoid bone; **mas**, mastoid portion of petromastoid complex; **oc**, occipital bone; **pgl**, postglenoid vacuity; **pt**, petrotic part of the petromastoid; **sq**, squamosal bone; **sqm**, squamoso-mastoid foramen (view B) or vacuity (view A); **srza**, squamosal root of zygomatic arch; **th**, tympanic hook of the squamosal bone. See text for additional descriptions.

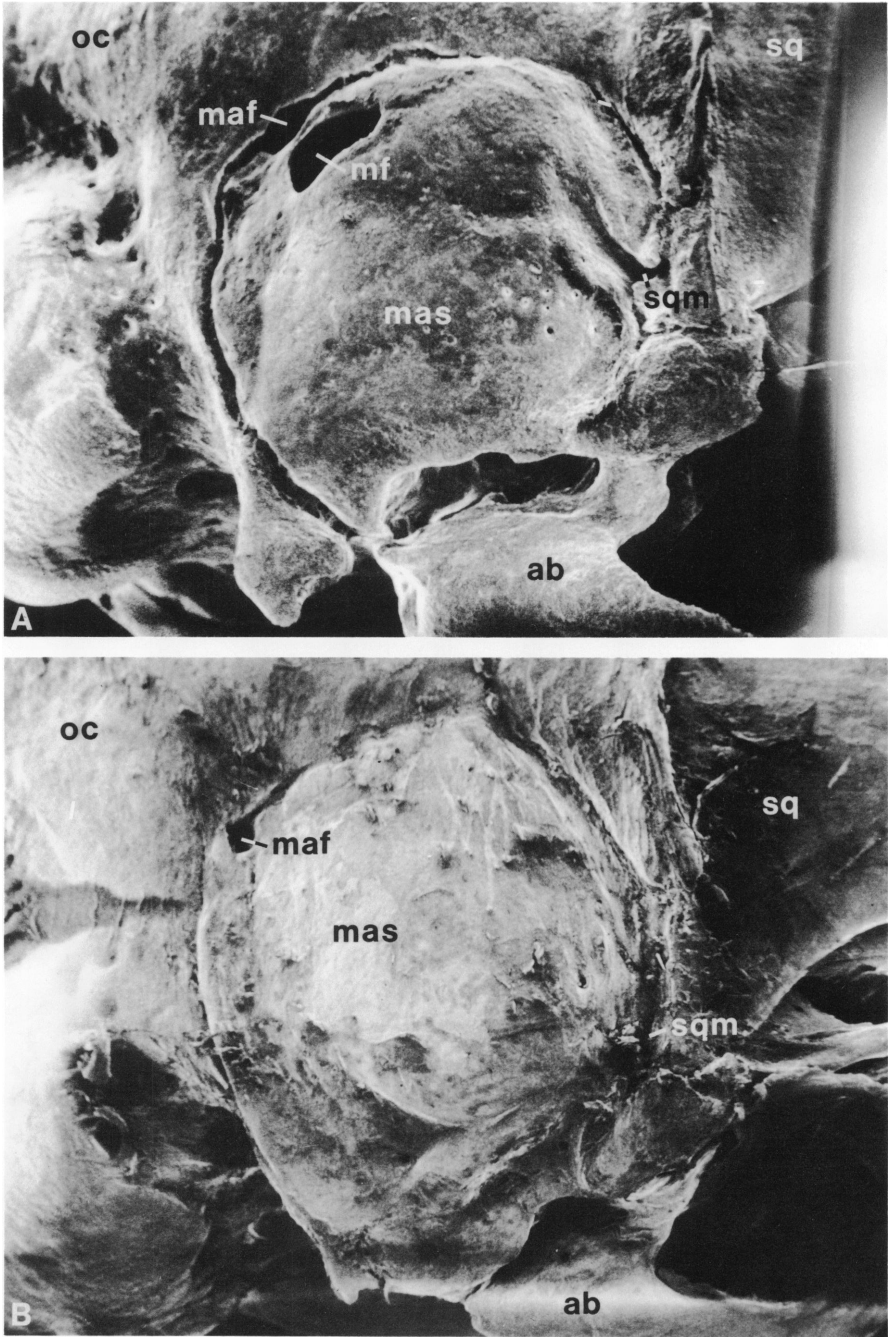


FIG. 25. Views of right mastoids in *Crunomys*. A, *C. celebensis* (AMNH 224316) is contrasted with *C. melanius* (AMNH 242102), B; both should be compared with figure 26.

Abbreviations: **ab**, part of auditory bulla; **maf**, mastoid foramen; **mas**, mastoid portion of the petro-mastoid complex; **mf**, mastoid fenestra; **oc**, occipital bone; **sq**, squamosal bone; **sqm**, squamoso-mastoid foramen. See text for other discussion.

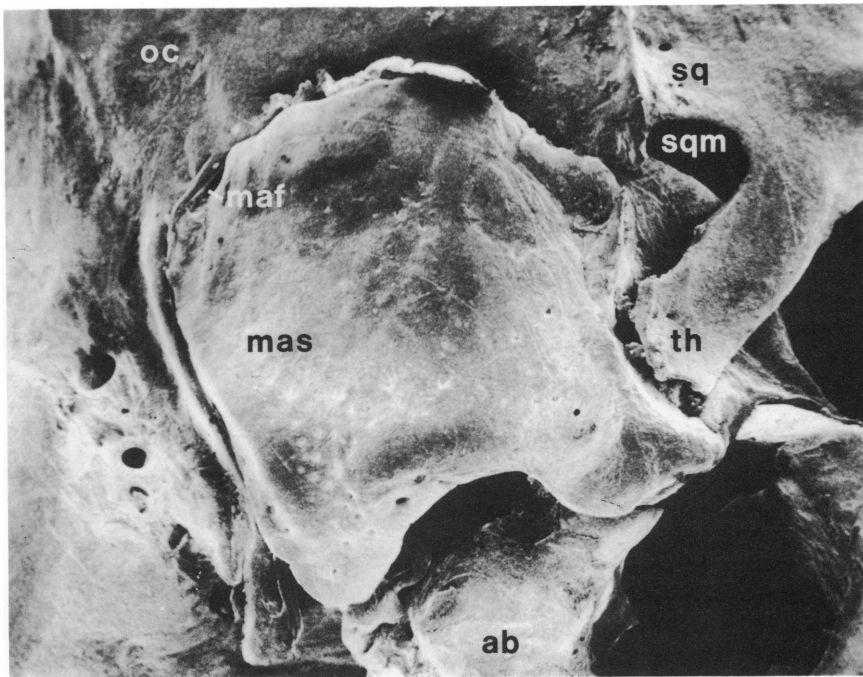


FIG. 26. View of right mastoid (*mas*) in *Archboldomys luzonensis* (FMNH 95122). Compare this view with those of *Crunomys* in figure 25.

Other abbreviations: *ab*, auditory bulla; *maf*, mastoid foramen; *oc*, occipital bone; *sq*, squamosal bone; *sqm*, squamoso-mastoid vacuity; *th*, tympanic hook of squamosal bone. See text for further information.

mosal. 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 Wahler (1974), the enlarged vacuity in the squamosal, such as that in *Archboldomys*, does not transmit a vessel and is usually covered by thin tissue.

There are differences between the two genera in aspects of the mastoid. The rough outline of each mastoid is similar in *A. luzonensis*, *C. celebensis*, and *C. melanius* (figs. 25 and 26). The mastoid is slightly inflated and the mastoid foramen is about the same relative size in *A. luzonensis* and *C. melanius*. The mastoid of *C. celebensis*, however, is conspicuously more inflated, the mastoid foramen is larger relative to the outer mastoidal surface, and there is a spacious fenestra

at the top of the mastoid—such as opening is not present in specimens of either *A. luzonensis*, *C. melanius*, or any other Philippine *Crunomys*.

The size and conformation of the auditory bullae and bony eustachian tubes, as well as the attachment of the bullar capsule to the braincase are similar in the specimens of *Archboldomys* and *Crunomys* (figs. 13, 24, and 27); there are significant differences in details. In specimens of both *Archboldomys* and *Crunomys*, the bullae are small, actually and relative to size of the braincase, but those of *Archboldomys* are inflated and larger relative to cranial size than are the relatively less inflated and smaller bullae of *Crunomys* (fig. 13). The eustachian tubes are moderately long, a spacious postglenoid vacuity separates the pteriotic from the squamosal, and a large middle lacerate foramen is between the anterior portion of each bulla and the pterygoid platform. The other differences,

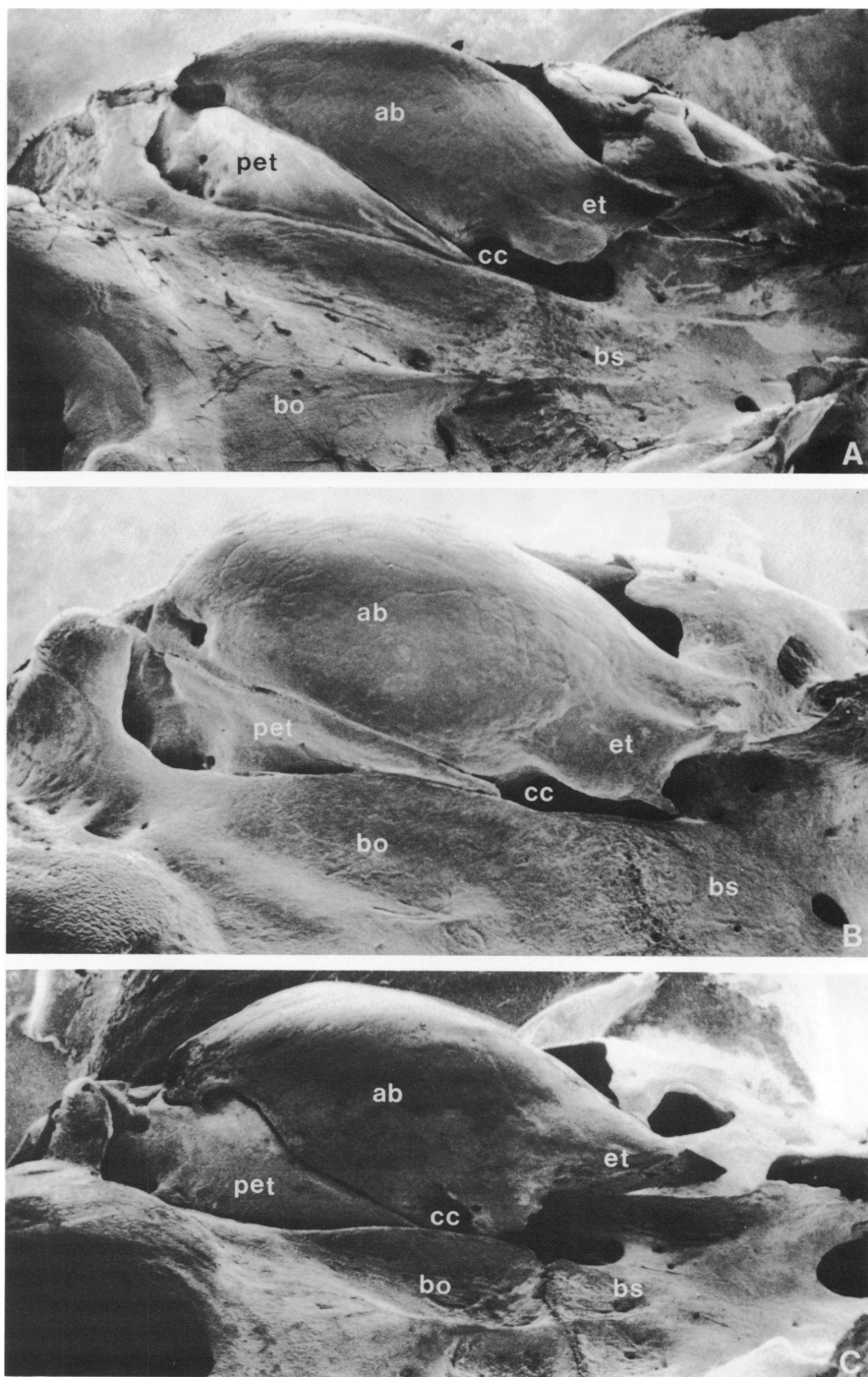


FIG. 27. Views of left bullae of *Crunomys* and *Archboldomys*. A: *C. melanius* (AMNH 242102). B: *C. celebensis* (AMNH 224316). C: *A. luzonensis* (FMNH 95122).

Abbreviations: ab, auditory bulla; bo, basioccipital bone; bs, basisphenoid bone; cc, carotid canal; et, bony eustachian tube; pet, petrosal portion of the petromastoid complex. See figure 28 and text.

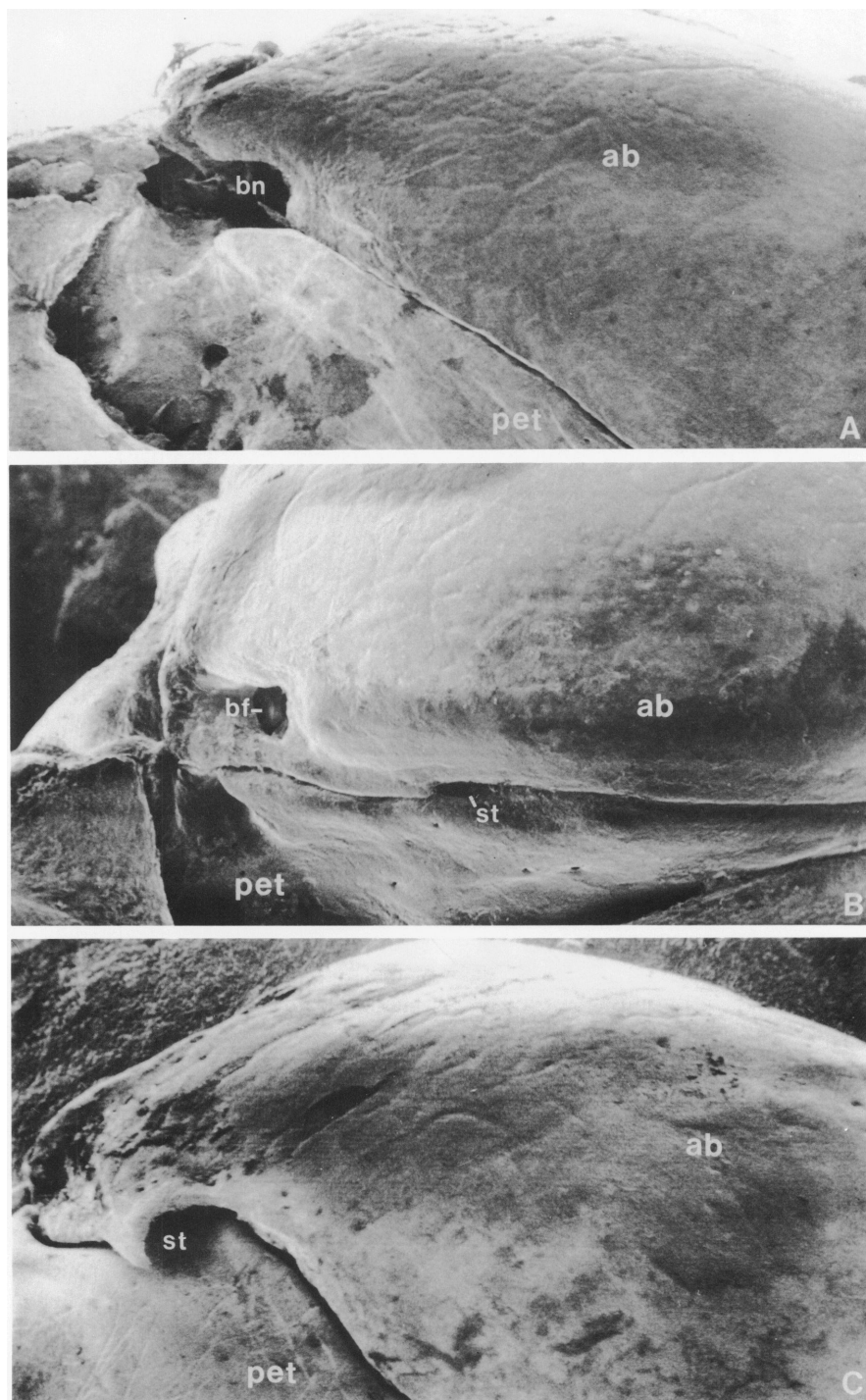


FIG. 28. Close-ups of bullae of same specimens shown in figure 27. A: *Crunomys melanius*. B: *Crunomys celebensis*. C: *Archboldomys luzonensis*.

Abbreviations: **ab**, auditory bulla; **bf**, bullar fenestra; **bn**, bullar notch; **pet**, petrosal portion of the petromastoid complex; **st**, stapedial foramen. See figure 27 and text for additional descriptions and comparisons.

besides degree of inflation and size, in bullar features among the species are in the configuration of the posterior part of the bullar (tympanic) capsule and the nature of the stapedial foramen.

As viewed ventrally and from the medial side, the outline of the bullar capsule is convex in *A. luzonensis* and *C. melanius* (fig. 27A and C). The stapedial foramen is conspicuous and large in the holotype of *A. luzonensis* (the diameter is 0.4 mm.) and located between the capsule and the deeply channeled medial surface of the petrosal portion of the petromastoid bone (figs. 27C and 28C). The deep and wide channel, which holds the large stapedial artery, extends medially across the top and back part of the petrosal within the bullar capsule; it is a prominent landmark.

I cannot locate a stapedial foramen in any specimen of *C. melanius* or in the holotype of *C. rabori*. The tympanic capsule adheres tightly to the petrosal. If there is an opening for a stapedial artery, it is undetectable and the artery itself must be minute. There is no groove across the top and back portion of the petrosal that would have contained an artery. There is a deep convex notch in the margin of the bullar capsule near its posteromedial portion. It is really a partial pit in some specimens but communicates with the space inside the capsule in others (fig. 28A).

The outline of each bulla is like a mound in *C. celebensis* because the posterior portion of the bullar capsule is slightly swollen compared with the conformation in either *A. luzonensis* or *C. melanius* (fig. 27B). The stapedial foramen is tiny (a pinhole), nearly indiscernible between the bullar capsule and the surface of the petrosal (figs. 27B and 28B). A small stapedial artery passes in a narrow but definite groove across the top and back part of each petrosal. A dry remnant of the artery can be seen in the petrosal groove in all three specimens. Near the posteromedial region of each bulla is an oblong or round depression within the capsule that penetrates the capsule in the holotype (and is a fenestra) but is only a deep pit in the other specimens that have intact bullae. The opening was originally filled with what appeared to be muscle

tissue and apparently does not transmit either an artery or nerve. I do not know its function.

The ventral cranial surfaces of *A. luzonensis* and *C. celebensis* are contrasted in figure 13. Both species have a small interpremaxillary foramen. *Archboldomys* has long incisive foramina, relative to length of diastema, that end 0.5 mm. in front of the anterior alveolar margins of the molar rows. The incisive foramina are relatively shorter in *C. celebensis*, their posterior margins are situated 1.3 to 1.4 mm. anterior to the molar rows (in three specimens). The maxilla lateral to each incisive foramina is ossified in the holotype of *A. luzonensis* and the adult *C. melanius* (fig. 29A and C), as well as the holotype of *C. rabori*, but breached by an elongate fenestra in the three examples of *C. celebensis* (fig. 29B).

Archboldomys luzonensis and *C. celebensis* (and the specimens of Philippine *Crunomys*) resemble one another in shape of the bony palatal bridge, the relative positions of the posterior palatine foramina, the position of the back of the bridge relative to the ends of the molar rows, the configuration of the mesopterygoid fossa, and the relative sizes of the sphenopalatine vacuities that breach the fossa walls. The two species contrast in shape of the pterygoid region. The anterior two-thirds of each pterygoid fossa in the holotype of *A. luzonensis* is now mostly a large opening that was probably made when the skull was cleaned; the original surface was either completely ossified or breached by a small or medium sphenopterygoid vacuity. The anterior two-thirds of each fossa and the posterior third form one continuous plate extending from behind the molar row past the foramen ovale to the middle lacerate foramen. As seen from ventral perspective, there is a wide and deep channel in the alisphenoid wing of the pterygoid plate between the middle lacerate foramen and the foramen ovale (fig. 30A). This configuration of the pterygoid plate in *A. luzonensis* and the large stapedial foramen in that species reflect the carotid arterial pattern diagrammed in figure 31. It is a pattern common to most murids (Hill, 1935) but one very different from the configuration found

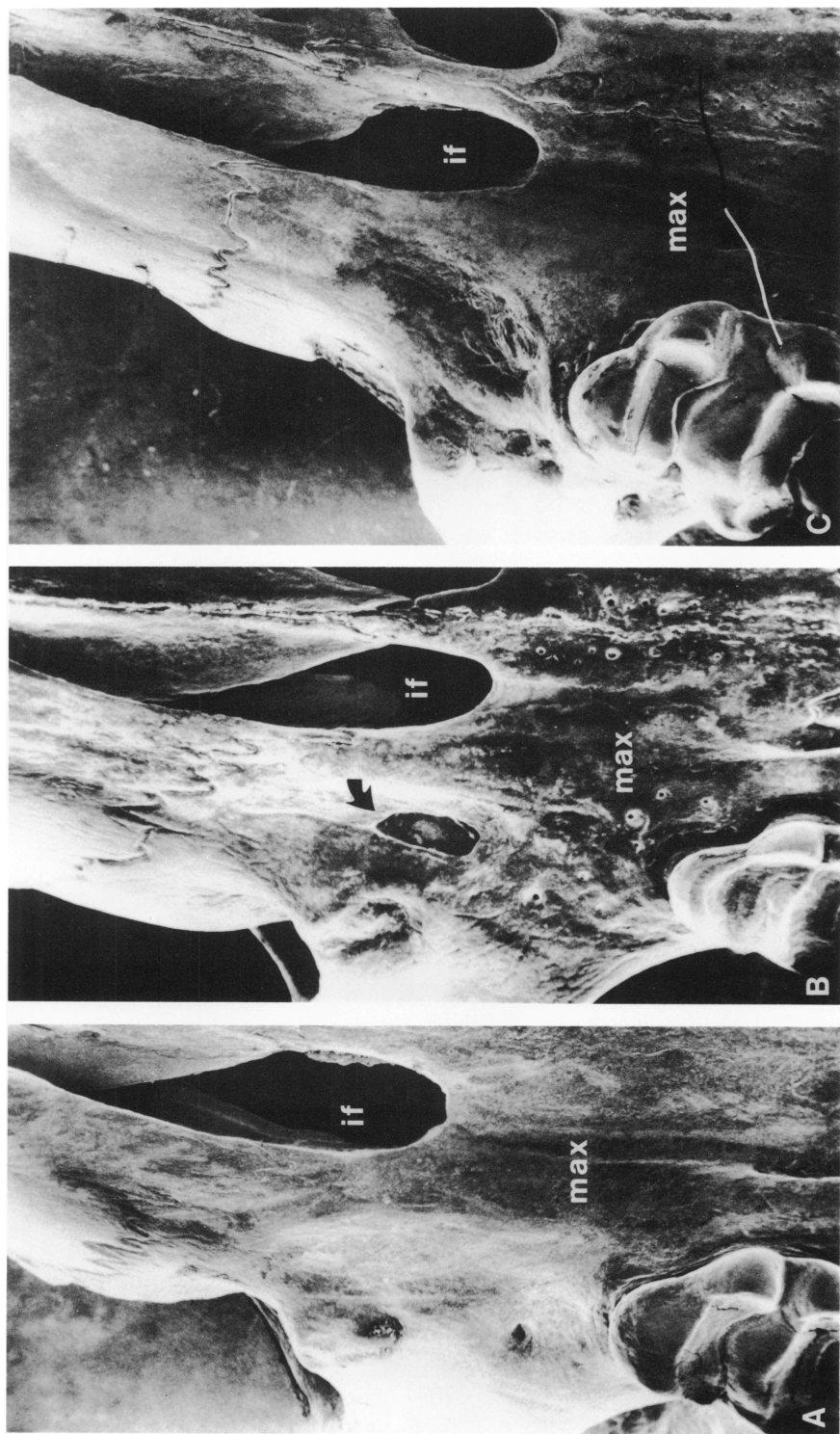


FIG. 29. Ventral views of *Crunomys* and *Archboldomys*. There is a large fenestra in the maxillary bone (**max**) lateral to the incisive foramen (**if**) in *C. celebensis* (AMNH 224316), B, but not in *C. melanius* (AMNH 242102), A, or *A. luzonensis* (FMNH 95122), C. See text for details.

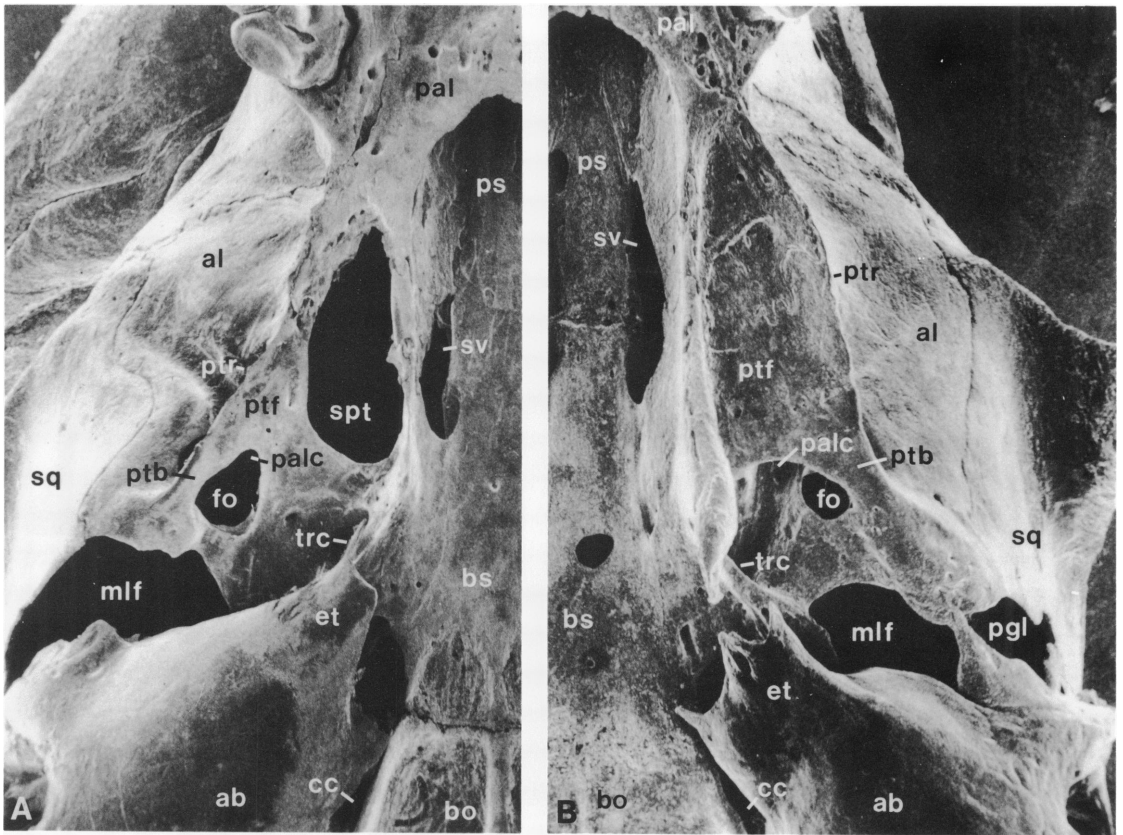


FIG. 30. Views of pterygoid and mesopterygoid regions in adult *Archboldomys* and *Crunomys*. A, *A. luzonensis* (FMNH 95122) is contrasted with *C. celebensis* (AMNH 224316), B.

Abbreviations: ab, auditory bulla; al, alisphenoid bone; bo, basioccipital bone; bs, basisphenoid bone; cc, carotid canal; et, bony eustachian tube; fo, foramen ovale; mlf, middle lacerate foramen; pal, palatine bone; palc, posterior opening of the alisphenoid canal; pgl, postglenoid vacuity; ps, presphenoid bone; ptb, pterygoid bridge; ptf, pterygoid fossa; ptr, pterygoid ridge; sq, squamosal bone; spt, sphenopterygoid vacuity; sv, sphenopalatine vacuity; trc, transverse canal. See text and figure 31 for additional comparisons and descriptions.

in all the Philippine and Sulawesi specimens of *Crunomys*.

In *A. luzonensis*, a large stapedia artery branches off from the common carotid and enters the otic capsule through the stapedia foramen. The stapedia continues through the otic region and emerges from the spacious middle lacerate foramen as the internal maxillary artery. That vessel courses onto the posterior margin of the pterygoid plate in a groove and then passes beneath the plate (as seen in ventral view) into the alisphenoid canal on the side of the braincase where it continues into the orbit via the sphenoidal fissure. Where the internal maxillary artery

passes from beneath the plate into the alisphenoid canal is the posterior opening of the alisphenoid canal (fig. 30A). After giving off the stapedia artery, the common carotid continues anteriorly as the internal carotid artery which enters the cranial cavity through the carotid canal and then passes forward beneath the brain. This combination of bony configuration, large stapedia foramen, and the internal maxillary being a continuation of the stapedia artery is also found in *Apomys datae* of Luzon and species of *Rattus* (Musser, 1982).

In the examples of *C. celebensis* and the specimens of Philippine *Crunomys*, the ante-

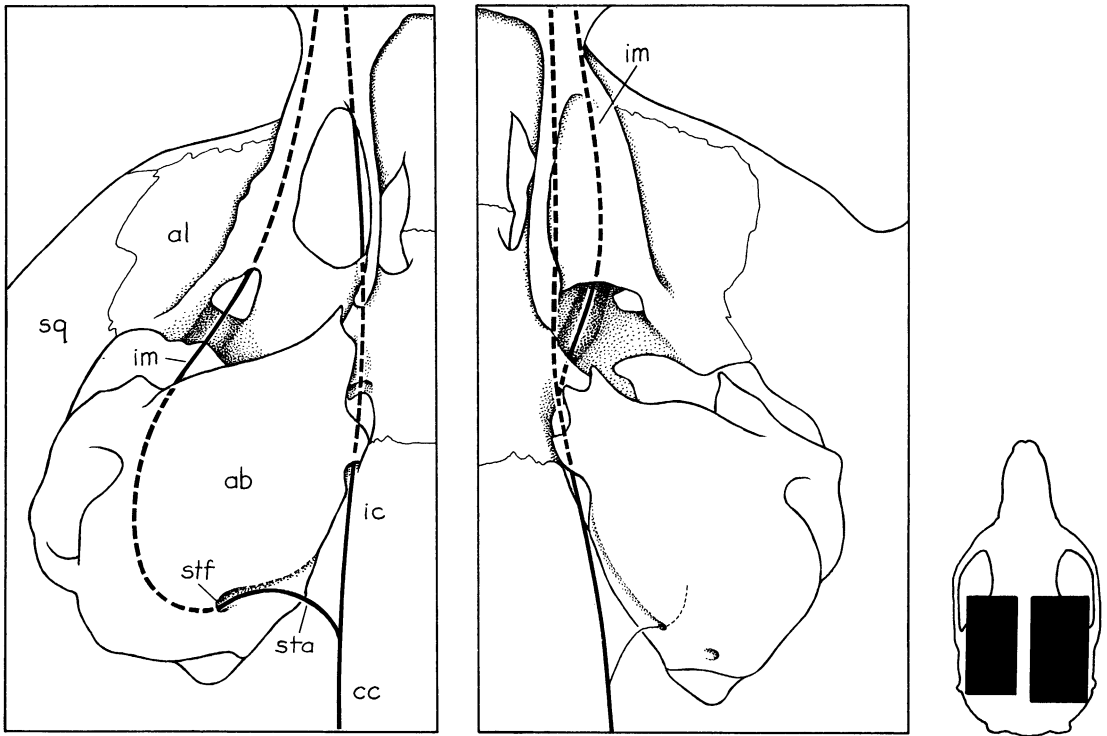


FIG. 31. Diagrams of carotid arterial patterns in *Archboldomys* and *Crunomys*. Left: the configuration in *A. luzonensis*. Right: the pattern and bony features in *C. celebensis*.

Abbreviations: **ab**, auditory bulla; **al**, alisphenoid bone; **cc**, common carotid artery; **ic**, internal carotid artery; **im**, internal maxillary artery; **sq**, squamosal bone; **sta**, stapedial artery; **stf**, stapedial foramen. Names of other foramina and bones are indicated in figure 30 on the facing page. See text for descriptions of the different patterns and bony configurations.

rrior two-thirds of each pterygoid fossa is a narrow, flat, and completely ossified platform (not penetrated by a sphenopterygoid vacuity). As seen from ventral view, the platform forms a roof over the alisphenoid canal and part of the foramen ovale. There is a transverse groove in the alisphenoid wing of the pterygoid plate that extends from the outer corner of the eustachian tube across the plate and under the platform. The place where the groove passes beneath the edge of the platform is the posterior opening of the alisphenoid canal (fig. 30B). This configuration, along with a minute stapedial foramen or no stapedial foramen at all, reflects a carotid circulation that is diagrammed in figure 31. In specimens of *C. celebensis*, the common carotid gives off a small stapedial artery that goes to the otic capsule through a pinhole that is the stapedial foramen. The stapedial serves

the otic capsule only and does not continue out of the bulla. The carotid continues anteriorly as the internal carotid artery to be transmitted through the carotid canal into the cranial cavity. Just after entering the cavity, the artery divides and a branch, the internal maxillary, courses in a diagonal groove across the alisphenoid wing of each pterygoid plate into the alisphenoid canal and then through the anterior opening of the alisphenoid canal into the orbit through the sphenoidal fissure. Instead of being a continuation of the stapedial artery, as is the pattern in *A. luzonensis*, the internal maxillary artery is a large branch of the internal carotid in the specimens of *Crunomys*. This arterial pattern and the bony configuration related to it is also found in all the species of Philippine *Apomys* except *A. datae* (Musser, 1982).

Although similar to the dentaries of *C.*

celebensis in general shape and relative positions of the mental and mandibular foramina, each dentary of *A. luzonensis* is slim, elongate, and gracile compared with the high, thick, stocky, and robust dentaries of *C. celebensis* (fig. 13). The condyloid and angular processes are smaller relative to the body of the dentary than are those in *C. celebensis*. The labial surface of the dentary is nearly smooth and has only a slight bulge marking the end of the incisor capsule, unlike the conspicuous labial bulge between the coronoid and condyloid processes on each dentary of *C. celebensis*.

Narrow and small upper incisors, long and slender lowers are typical of *A. luzonensis*. Enamel surfaces are pale orange in the holotype. The upper incisors are incomplete but enough remains to indicate they are small relative to size of the cranium and emerge from the rostrum at nearly a right angle (orthodont in position). The sharp-tipped lowers are slim, elongate, and small relative to size of the dentaries. Both the upper and lower incisors appear weak in relation to the cranium and mandible as compared with the wide and stout incisors of *C. celebensis*, teeth that appear very large and strong in relation to overall size of the cranium and dentaries (fig. 13).

Slim and delicate as opposed to wide and stocky are the contrasts in incisor conformation between *A. luzonensis* and *C. celebensis*. The molar proportions relative to crania and mandibles are reversed. *Archboldomys* has large chunky molars set in a small gracile cranium and slender dentaries. Specimens of Philippine and Sulawesi *Crunomys* have small molars in a stocky cranium and mandible (tables 1 and 2; fig. 13). Each upper molar of *A. luzonensis* is anchored by three roots, each of the lowers by two. Because the molars in the three specimens of *C. celebensis* are so worn and their occlusal patterns indistinct, I compare the dentition of *A. luzonensis* with that in the adult *C. melanius*, which is about the same age.

The upper and lower molars of *A. luzonensis* and those in species of *Crunomys* are basically similar to one another in shapes and occlusal outlines, size relative to each other in the toothrow, degree that one abuts against the other, and cusp patterns (figs. 32, 33, and

54). There are some striking differences between the two genera. Relative to sizes of cranium and mandible, the molar rows in *A. luzonensis* are much larger and form a greater part of the palatal bridge and dentaries than do those in any species of *Crunomys* (table 2). The cusps in *A. luzonensis* have high margins so that they appear conelike from a side view (fig. 53) and form an occlusal topography similar to the tubercular hypsodonty described by Hershkovitz (1962) and noted in *Onychomys* by Carleton and Eshelman (1979), a configuration associated with insectivory and sometimes carnivory. The cusp relief in *Crunomys* is lower, nearly flat, the occlusal topography is not tubercular. Cusp t3 on each first upper molar in *A. luzonensis* appears to be absent, as I indicated in the diagnosis of *Archboldomys*, but it may be so tightly merged with the central cusp t2 that it is indistinguishable except in very young rats; cusp t3 on each first upper molar in *Crunomys* is also coalesced with cusp t2 but still slightly evident. Cusp t9 on each first and second upper molar in *A. luzonensis* also appears to be absent, at least in the holotype; cusp t9 occurs on each first upper molar in *Crunomys* but not on the second. Each upper and lower third molar in *A. luzonensis* is larger relative to the other molars in the respective rows compared with the relatively smaller third molars in *C. melanius* and the other species of *Crunomys*. Like *Crunomys*, *Archboldomys* lacks anterolabial cusps on the second and third lower molars and anterior and posterior labial cusplets; the holotype of *Archboldomys* does have a posterior labial cusplet on each first lower molar, a structure that does not occur in *Crunomys*.

NATURAL HISTORY: Mount Isarog, a volcanic peak rising to 6500–7000 feet above sea level, is in a region where rains occur throughout the year but with a discrete period of maximum rainfall from November to February. The upper slopes of the mountain are presumably clothed in montane forest that merges with lowland forest at about 2500 feet, the actual transitional elevation determined by seasonal rainfall and other factors (Inger, 1954). The holotype of *A. luzonensis* probably came from montane forest. Unfortunately, no information about habitat or habits is associated with the specimen.

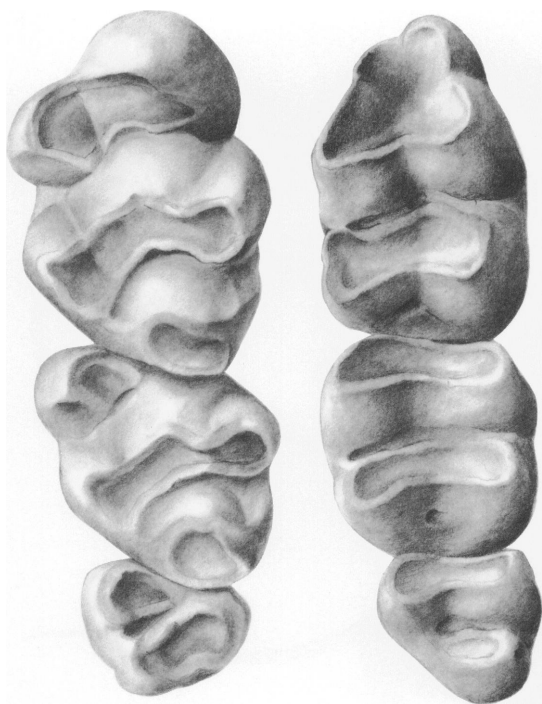


FIG. 32. *Archboldomys luzonensis*. Left maxillary (left side) and mandibular (right side) molar rows of the holotype, FMNH 95122. Measurements are listed in table 1.

Other murids have been collected on Mount Isarog. *Rattus everetti*, large, shaggy-furred, and long-tailed; the large-bodied shrew rat, *Rhynchomys isarogensis*, and the small-bodied *Apomys musculus* are represented by a few specimens obtained from the Peak. Whether they occur in the same habitat as *Archboldomys luzonensis* is unknown. The

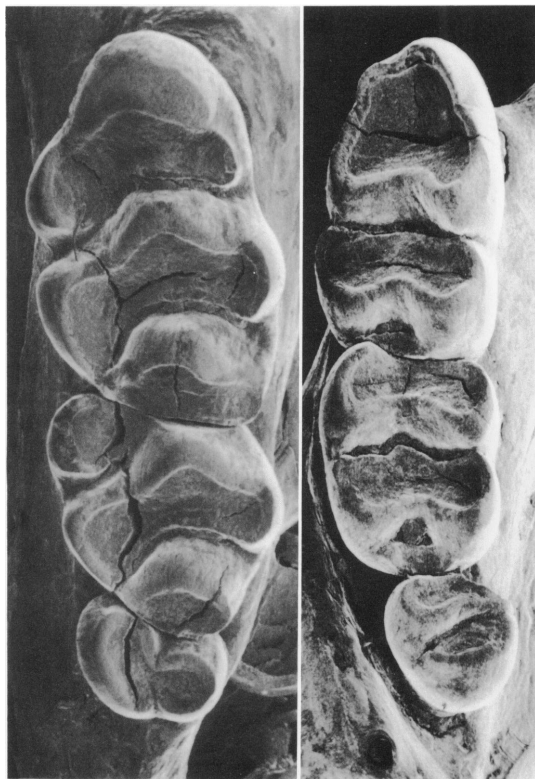


FIG. 33. *Crunomys melanius*. Occlusal views of left maxillary (left side) and mandibular (right side) molar rows of AMNH 242102. See table 1 for measurements. Contrast these rows with those of *Archboldomys luzonensis* in figure 32.

species in *Apomys* and *Rhynchomys* have relatives in the high western mountains of northern Luzon (Musser and Freeman, 1981; Musser, 1982); possibly either *A. luzonensis* or a close relative may also occur there.

THE SULAWESI SHREW RATS

Crunomys is represented by specimens from the Philippine Islands and Sulawesi. It is related to *Archboldomys*, which is a Philippine shrew rat of small body size. Sulawesi, the large island south of the Philippines, has an endemic group of shrew rats. One of these, *Melasmothrix naso*, is similar to *Archboldomys luzonensis* in fur coloration, body conformation, skull configuration, and occurrence in montane habitat. Do the resemblances indicate phylogenetic alliance,

paralleling the relationship between the Philippine and Sulawesi *Crunomys*, or do they reflect morphological specializations for similar habitat and life which have evolved independently within each set of species? Before answering that question, the small-bodied Sulawesi shrew rats have to be introduced and described.

Three small-bodied shrew rats occur on Sulawesi: *Melasmothrix naso*, *Tateomys rhinogradoides*, and another species of



FIG. 34. Sulawesi small-bodied shrew rats. Top right: *Tateomys rhinogradoides*. Left side: *Tateomys macrocerus*. Bottom center: *Melasmothrix naso*.

Tateomys. I discuss *M. naso* first, then *T. rhinogradoides*, name and describe the new species of *Tateomys*, and finally write about habitat and habits of all three.

Melasmothrix naso

Melasmothrix naso was named and described by Miller and Hollister (1921) from an adult male (USNM 219752) collected by H. C. Raven during January 1918, at Rano Rano, 1800 meters, in Central Sulawesi. The holotype (illustrated and described in Musser, 1969) was the only specimen in museum collections until members of the Archbold Sulawesi Expedition obtained samples from the upper slopes of Gunung Nokilalaki (lat. $1^{\circ}13'S$, long. $120^{\circ}08'E$), a highland near the mountainous region where Raven worked

during 1918 (see Riley, 1924, for a short summary of Raven's travels). The 35 new specimens (AMNH 223964, 223965, and 225080–225112) were collected during December 1973, and March and April 1975, at altitudes ranging from 6400 to 7500 feet on the southwest slope and top of the mountain. The mouse is common in the cool and wet moss forest at those montane altitudes.

Melasmothrix naso has an elongate shrew-like head and muzzle, small eyes and ears, chunky body, short tail, wide front feet with large claws, and narrow hind feet (table 3; figs. 34, 35, and 36). The mouse is blackish all over; around the nostrils, anus, and on the teats are about the only unpigmented areas. The upperparts and underparts are a rich, dark chestnut, so dark the animal appears black in most lights. The fur over the head

and body is short (7–9 mm. on the back near the rump), very dense, and velvety. The fleshy lips and nose pad are dark gray, forming a slight contrast with the darker head, and the fur covering sides of the muzzle is black, which stands out against the blackish red of the rest of the head. Each eye is surrounded by a dark gray ring. The ears are small, round, and black. The vibrissae from the muzzle are long enough that if laid back against the head they would reach each ear but would not extend beyond (determined from freshly caught rats). The tail is much shorter than the combined lengths of head and body. Its dorsal surface and sides, from base to tip, are black; the ventral surface is gray and either sparsely speckled with brown or broken by a dark gray or black midventral line. A few specimens have monocolored black tails. The front and hind feet are black over all their surfaces; a few specimens have dark gray palmar areas. The claws are large and all of them are shiny dark gray; those on the front feet are long and stout. The palmar pads are small, especially the three interdigital tubercles. The plantar pads are small, oblong, and nearly smooth. The combination of a wide front foot and large robust claws form a superb structure for digging into soft moist earth. Females have three pairs of mammae: one postaxillary and two inguinal. In some specimens, the postaxillary teats are much smaller than the inguinal. These observations are from my examination of freshly caught specimens.

An elongate rostrum connected by delicate zygomatic arches to a broad rounded braincase is the dorsal cranial conformation of *M. naso* (fig. 37). As seen from above, the nasals roof a long, slender and tapered rostrum; both nasals and rostrum are about the same length (table 3). The zygomatic arches sweep back to sides of the braincase in graceful parallel configurations; they are thin and delicate and do not bow out past the sides of the braincase (zygomatic breadth is about the same as breadth of braincase; table 3). The region between the dorsal maxillary roots of the zygomatic arches and the interorbital area are wide and inflated, their dorsal contours are convex. The frontal sinuses are large and reflected on the dorsal surface by low, bubble-like inflations above each dorsal maxillary root. The orbital process of each lacrimal bone

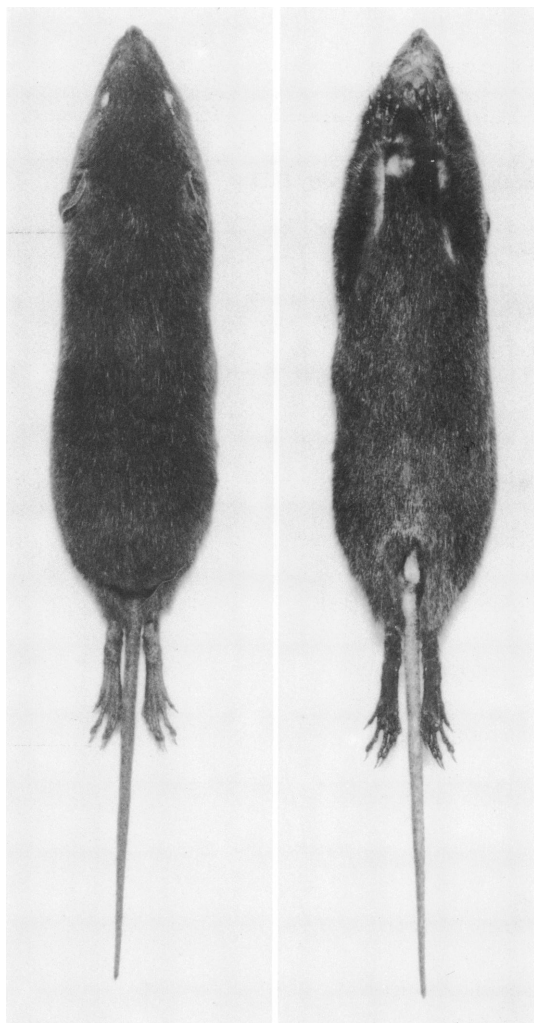


FIG. 35. *Melasmothrix naso*. Dorsal (left) and ventral (right) views of AMNH 225111 from Gunung Nokilalaki, Central Sulawesi. Length of head and body, 120 mm.; length of tail, 85 mm.; length of hind foot, 29 mm.; length of ear, 20 mm.; weight, 48 g.

is large and triangular in dorsal outline. The braincase is circular in outline and rounded over the top. Dorsolateral margins of the interorbital and postorbital regions, as well as the braincase, are rounded and smooth, without shelves or ridges. The interparietal bone is very wide; little of it sits between the parietals, most of the bone roofs the deep (front-to-back) and wide occiput.

TABLE 3
Measurements (in Millimeters), Weight (in Grams), and Other Data of Adult *Melasmothrix naso*
from Gunung Nokilalaki, Central Sulawesi
(The mean plus or minus one standard deviation, number of specimens in parentheses, and observed
ranges are listed in that order for each measurement)

	Males	Females
Length of head and body (LHB)	119.3 ± 4.6 (16) 111–126	112.9 ± 1.9 (8) 111–117
Length of tail (LT)	88.3 ± 2.6 (16) 85–94	85.1 ± 3.8 (8) 81–93
LHB/LT (means; in %)	135	133
Length of hind foot	28.9 ± 0.6 (16) 28–30	28.3 ± 0.7 (8) 27–29
Length of ear	19.3 ± 0.7 (16) 18–20	18.8 ± 0.7 (8) 18–20
Weight	50.8 ± 4.3 (16) 45–58	44.1 ± 4.0 (8) 40–50
Scale rows per centimeter	21.5 ± 1.4 (16) 20–24	21.8 ± 0.9 (8) 20–23
Greatest length of skull	32.7 ± 0.4 (14) 31.6–33.1	32.0 ± 0.5 (7) 31.4–32.9
Zygomatic breadth	14.0 ± 0.3 (15) 13.4–14.3	13.7 ± 0.3 (7) 13.3–14.0
Interorbital breadth	6.4 ± 0.1 (15) 6.1–6.5	6.2 ± 0.1 (7) 6.1–6.5
Breadth of braincase	14.3 ± 0.3 (15) 13.7–14.6	14.1 ± 0.3 (7) 13.6–14.6
Height of braincase	9.0 ± 0.3 (13) 8.1–9.4	9.0 ± 0.3 (7) 8.4–9.3
Length of nasals	12.6 ± 0.3 (15) 12.2–13.2	12.3 ± 0.2 (7) 12.0–12.6
Length of rostrum	12.0 ± 0.3 (15) 11.3–12.5	11.8 ± 0.2 (7) 11.5–12.1
Breadth of rostrum	5.7 ± 0.2 (15) 5.3–6.0	5.6 ± 0.2 (7) 5.3–5.8
Rostrum anterior to incisors	1.9 ± 0.1 (15) 1.7–2.1	1.8 ± 0.1 (8) 1.6–2.1
Breadth of zygomatic plate	1.3 ± 0.1 (16) 1.1–1.4	1.3 ± 0.1 (7) 1.1–1.4
Breadth across incisor tips	1.5 ± 0.1 (15) 1.4–1.7	1.4 ± 0.1 (8) 1.2–1.6
Palatal length	13.9 ± 0.2 (14) 13.6–14.2	13.4 ± 0.3 (7) 12.9–13.8
Postpalatal length	12.4 ± 0.6 (14) 10.6–13.0	12.3 ± 0.2 (7) 11.9–12.4
Length of diastema	7.1 ± 0.2 (15) 6.7–7.4	6.8 ± 0.3 (7) 6.6–7.1

TABLE 3—(Continued)

	Males	Females
Length of incisive foramina (IF)	4.8 ± 0.2 (16) 4.4–5.2	4.7 ± 0.2 (8) 4.4–5.0
Breadth of incisive foramina	1.7 ± 0.1 (15) 1.6–1.9	1.7 ± 0.1 (8) 1.6–1.8
IF to M ¹	0.8 ± 0.2 (16) 0.2–1.0	0.7 ± 0.1 (7) 0.6–0.9
Length of palatal bridge (PB)	6.0 ± 0.1 (16) 5.7–6.1	5.8 ± 0.2 (7) 5.5–6.1
Breadth of PB at M ¹	2.8 ± 0.1 (16) 2.6–3.1	2.8 ± 0.2 (7) 2.5–3.1
Breadth of PB at M ³	3.5 ± 0.1 (16) 3.3–3.8	3.4 ± 0.2 (7) 3.1–3.6
Breadth of mesopterygoid fossa	2.1 ± 0.1 (16) 1.8–2.3	2.0 ± 0.2 (7) 1.8–2.3
Length of bullae	5.9 ± 0.2 (15) 5.7–6.2	5.8 ± 0.2 (8) 5.6–6.1
Length of M ¹⁻³	5.3 ± 0.2 (16) 4.8–5.7	5.2 ± 0.2 (7) 5.0–5.5

In side view, the dorsal cranial outline slopes from the top of the braincase in a graceful long curve to about the middle of the rostrum and then up again (fig. 38). The profile reflects the high inflated braincase and frontal region and the upturned nasal tips. At the anterior end of the cranium, the nasals and sides of the rostrum formed by the premaxillary bones project anterior to the incisors by 1.6 to 2.1 mm. (in 23 specimens) forming a short tube. The opening of the tube, which is the nasal passage, is large because the distal third of the nasals turn dorsad, thus increasing the diameter of the opening into the nasal passage. The sides of the rostrum between the nasolacrimal capsules are inflated and the capsules are conspicuous, wide, and elongate. From their openings, which face posterodorsad, each extends down and forward on the side of the rostrum as a compressed tube running beneath the incisor roots and emptying into the nasal passage just behind the incisors where they emerge from the rostrum.

Posterior to the nasolacrimal capsule is a narrow zygomatic plate. It is slanted back, its anterior margin is flush with the dorsal margin of the maxillary zygomatic root and is

either straight or slightly convex. Each ventral maxillary root sits directly above the first molar. In all the specimens, the anterior edge of the ventral zygomatic root is either even with or just anterior to the front face of the molar. Sweeping back from each zygomatic plate is a thin and delicate arch. The squamosal root of each arch originates low on the side of the braincase, just above the auditory bulla.

The orbital region medial to the slender arch is small. The small optic foramen and sphenoidal fissure, in side view, are concealed by a wall of alisphenoid that projects into the posterior portion of the orbit. Near the base of the orbit, the small sphenopalatine foramen is separated by orbital wall from an even smaller dorsal palatine foramen, which lies posterior to the former; the two are separate in all the specimens examined, not coalesced as are the foramina in *Crunomys* (fig. 14).

Posterior to the orbit, the alisphenoid canal at the base of the braincase is an open channel, not bounded laterally by a strut of alisphenoid bone. Both the anterior opening of the alisphenoid canal and the foramen ovale are visible. Without the strut of alisphenoid bone, the masticatory-buccinator foramen



FIG. 36. *Melasmothrix naso*. An adult caught during the day on the summit of Gunung Nokilalaki, Central Sulawesi.

have coalesced with the foramen ovale accessorius and are functionally absent. The braincase itself is deep and enlarged; the bone appears thin. The occipital portion of the braincase overhangs the occipital condyles. Each mastoid is slightly inflated and breached by an oblong fenestra near its dorsal margin. The squamosal bone above each bulla is complete, not separated by an enlarged squamoso-mastoid foramen into a dorsal portion and a ventral hook; the foramen is small and confined to the suture between the squamosal and mastoid. The dorsal margin of each bulla is separated from the squamosal by a postglenoid vacuity that is continuous with the large middle lacerate vacuity between the alisphenoid bone and anterior margin of the bulla. The periotic flange is low and barely

evident along the dorsal bullar margin. The postglenoid vacuity is so large that it extends up under the posterior margin of each squamosal zygomatic root, which originates low on the braincase (figs. 38 and 45).

The elongate cranial configuration of *M. naso* is apparent in a ventral view of the cranium (fig. 37). The tapered rostrum and tube formed by the nasals and premaxillaries anterior to the incisors are conspicuous. The incisive foramina are elongate. Narrow at their anterior margins, they widen gradually to a broad posterior end. The foramina end 0.2–1.0 mm. (23 specimens) anterior to the front faces of the first molars. The palatal bridge is long, partly reflecting the back margins of the incisive foramina which are well anterior to the molar rows, and wide (table



FIG. 37. Dorsal (top) and ventral (bottom) views of crania: a, *Melasmothrix naso* (AMNH 225091); b, *Tateomys rhinogradoides* (AMNH 225117); c, *Tateomys macrocercus* (AMNH 225077, holotype). All are adults from Gunung Nokilalaki, Central Sulawesi. Approximately $\times 1.5$.

3). Its posterior edge lies 0.1 to 0.4 mm. before the back faces of the third molars in 13 specimens and is even with the backs of the molar rows in ten. The bridge is thin and appears delicate. A pair of long and shallow grooves score its surface; in some specimens there are small openings in the bottom of the grooves. Each posterior palatine foramen is concealed beneath a bony overhang between the second and third molars.

The elongate cranium is reflected in the mesopterygoid and pterygoid fossae, which

are long and narrow. The former is narrower than the back of the palatal bridge (table 3) and its sides and top are nearly completely bony, breached only by a pair of thin inconspicuous sphenopalatine vacuities. The pterygoid fossae are elongate and the pterygoid plates are thin and delicate. In each there is a large sphenopterygoid vacuity. The anterior two-thirds of each plate is outlined by a sharp pterygoid ridge that loses its shape in a bridge connecting the plate with a rounded alisphenoid bone in front of the anterolateral



FIG. 38. Side views of same specimens shown in figure 37: a, *Melasmothrix naso*; b, *Tateomys rhinogradoides*; c, *Tateomys macrocerus*.

margin of the bulla (fig. 42). The anterior one-third of each pterygoid plate is an extension of the palatine bone, as seen in ventral view, and this extension is wide enough that it forms part of the pterygoid ridge; the suture is not on the plate but dorsal to the pterygoid ridge (fig. 42).

The configuration of the posterior one-third of each pterygoid surface (fig. 42) is similar to that in *Archboldomys luzonensis* (fig. 30A) and the carotid arterial pattern that the conformation reflects is like the pattern in *Arch-*

TABLE 4
Number of Specimens with Either White or Pigmented Incisor Enamel in Samples of *Melasmothrix naso*, *Tateomys rhinogradoides*, and *Tateomys macrocerus* from Gunung Nokilalaki, Central Sulawesi

	<i>M. naso</i>	<i>T. rhinogradoides</i>	<i>T. macrocerus</i>
UPPER INCISORS			
Translucent white	—	—	—
Ivory (opaque off-white)	6	5	3
Cream (pale yellow)	10	—	3
Pale yellow-orange	9	—	—
LOWER INCISORS			
Translucent white	19	5	6
Ivory (opaque off-white)	7	—	—
Cream (pale yellow)	—	—	—
Pale yellow-orange	—	—	—

boldomys and unlike that in species of *Crunomys* (fig. 31). In every specimen examined of *M. naso*, there is a longitudinal depression in the ventral surface of the pterygoid plate extending from the anterior margin of the middle lacerate foramen to the posterior edge of the ventral rim of the foramen ovale. The internal maxillary artery emerges from the middle lacerate foramen to pass along this groove and beneath the foramen ovale into the alisphenoid canal on top of the pterygoid plate—that spot in front of the foramen ovale is the posterior opening of the alisphenoid canal.

The large auditory bullae of *M. naso* are evident in a ventral view (fig. 37). The bullar capsules are expanded so the bullae are large and prominent, both actually and relative to size of the cranium. Each bony eustachian tube is evident but very short (more like a low rim), with a longer lateral process. Each stapedia foramen is large and lies between the bullar capsule and petrosal portion of the petromastoid bone. Through it passes a large stapedia artery that courses over the surface of the petrosal in a deep and conspicuous groove. The internal maxillary artery that emerges from the spacious middle lacerate vacuity in front of the bulla is a branch (or continuation) of the stapedia.

Each dentary of *M. naso* is slim, especially the elongate cylindrical portion between the

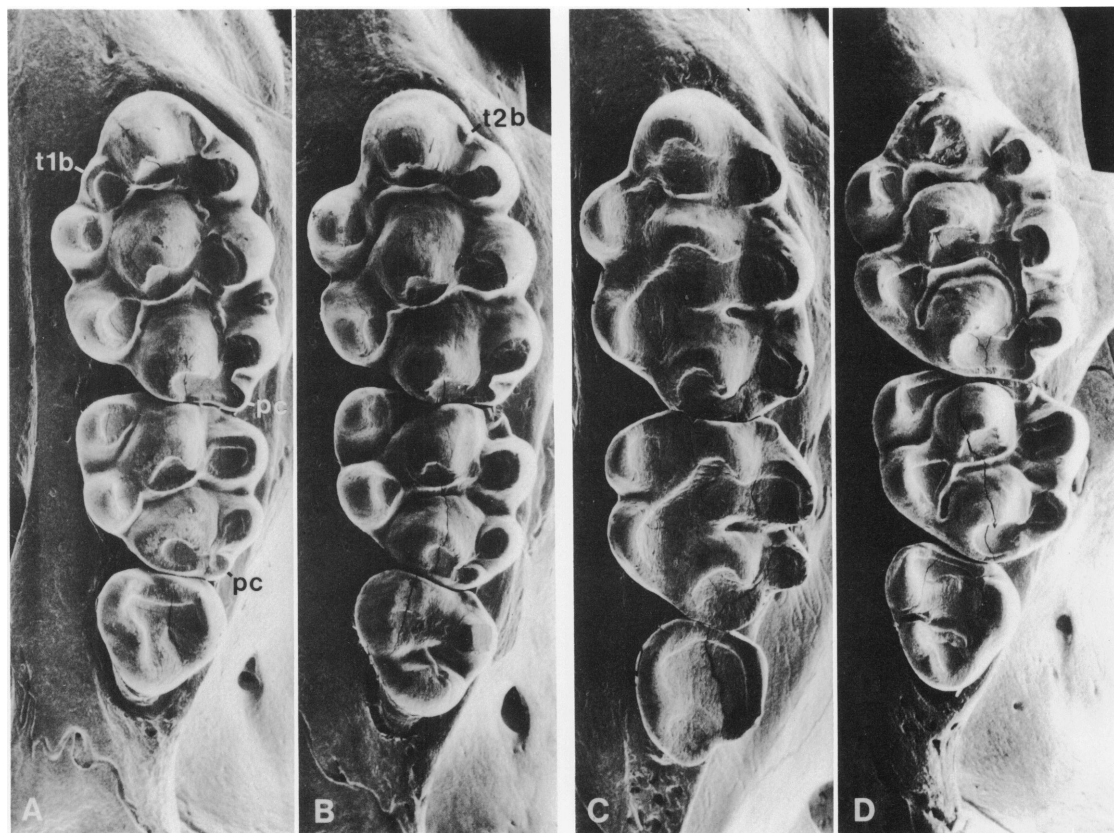


FIG. 39. Occlusal views of left maxillary molar rows. A: *Melasmothrix naso* (AMNH 225081; actual length of M^{1-3} is 4.7 mm.). B: *M. naso* (AMNH 225110; length M^{1-3} , 4.8 mm.). C: *Tateomys rhinogradoides* (AMNH 225115; length M^{1-3} , 5.2 mm.); D: *T. macrocerus* (AMNH 225074; length M^{1-3} , 4.9 mm.).

Abbreviations: pc, posterior cingulum; t1b, cusp t1bis; t2b, cusp t2bis.

first molar and incisor (fig. 37). The body of the dentary is so slender that it appears to function mostly as an anchor for the molars and a slender container for the incisor capsule. There is no swelling, large bulge, or other feature marking the place where the incisor capsule stops within the dentary. The bone itself, however, is translucent enough that the end of the capsule can be seen at a place between the end of the molar row and the mandibular foramen; it does not extend up into the condylar process nor does it project laterally to form a bulge on the outer surface of the dentary as is the configuration in many murids (Musser, 1981b, fig. 22, p. 272). The three posterior mandibular processes are elongate extensions of the dentary body: the

coronoid process is slim and delicate, the condylar process is long and narrow, and the angular process is large and resembles a long hook. The inner surface of each dentary is mostly smooth until just behind the molar row where a wide shelf extends from behind the last molar straight back and then diagonally upward, becoming narrower and finally disappearing at the level of the mandibular foramen. That opening is large relative to area of the dentary.

Melasmothrix naso has distinctive incisors. The uppers emerge from the rostrum at a right angle (orthodont configuration). The incisor capsule containing the end of the incisor itself curves back within the premaxillary portion of the rostrum and ends medial to

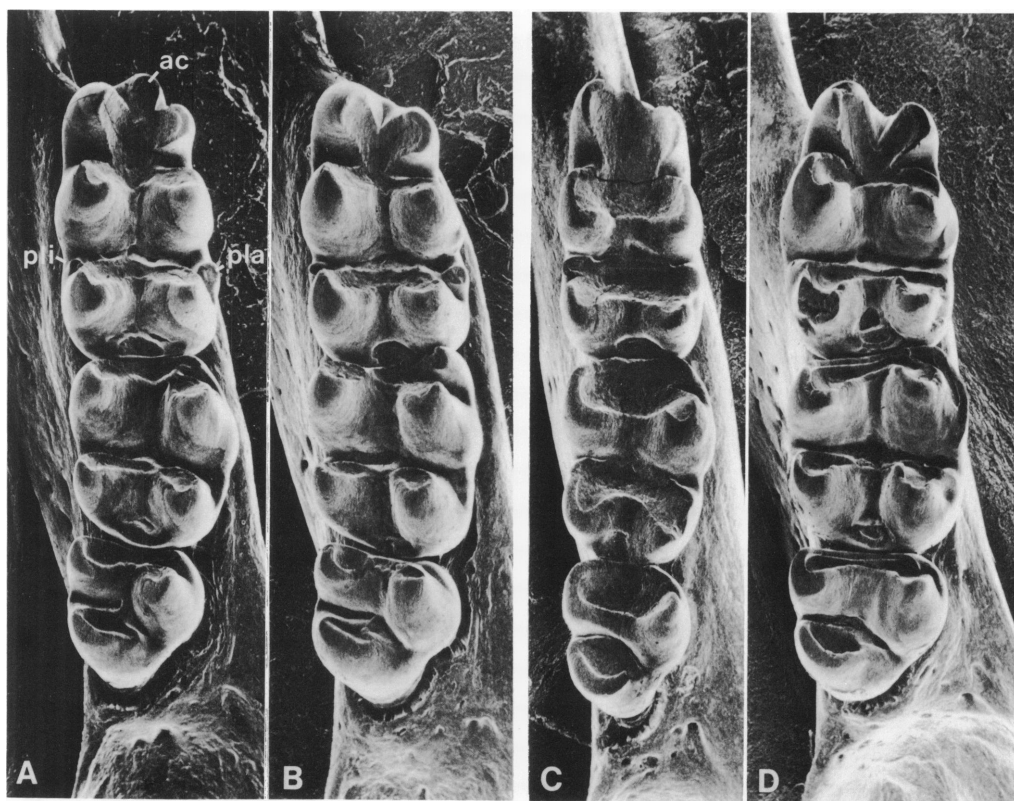


FIG. 40. Occlusal views of right mandibular molar rows of specimens shown in figure 39. A: *Melasmothrix naso* (actual length of M_{1-3} is 4.6 mm.). B: *M. naso* (length M_{1-3} , 4.5 mm.). C: *Tateomys rhinogradoides* (length M_{1-3} , 5.2 mm.). D: *T. macrocercus* (length M_{1-3} , 4.7 mm.).

Abbreviations: **ac**, anterocentral cusp; **pla**, posterior labial cusplet; **pli**, posterior lingual cusplet.

and near the top of the elongate nasolacrimal tube. Each anterior face is slightly convex and the cutting edges meet at an obtuse angle. The enamel is confined to the front face and anterolateral margin of each incisor. Behind the enamel, the dentine is as thick or thicker than the enamel. In the sample at hand, the coloration of the enamel ranges from ivory through cream to pale yellow-orange (table 4). The dentine ends just before the tip of the enamel so that in side view the tip of each incisor is shallowly or deeply notched, a configuration similar to that in species of *Mus* (Marshall, 1977) and one found in all *M. naso* examined in which the incisor tips were not excessively worn (25 out of 26 specimens). The enamel faces are smooth and not grooved.

The lower incisors are slim, round, and awl-shaped; the tips are sharp. They are either

translucent white (seen best in animals just caught) or ivory (table 4).

The molars of *M. naso* are illustrated in figures 39 and 40. Each of the upper molars is anchored by three roots (anterior, posterior, and lingual) and two roots (anterior and posterior) anchor each lower molar (table 6). The teeth abut against one another with little or no overlap, especially those in the maxillary rows. In the latter, the first molar is long and wide, the second about as wide but shorter, and the third very small relative to the others in the row. Similar proportions characterize teeth in the mandibular rows. The distance from tops of the roots to bases of the cusps is low and the cusps are high, at least in slightly worn teeth, but they wear down quickly.

The enamel surfaces are gleaming white.

The occlusal topography consists of rows of discrete, large conelike cusps barely connected to one another in each row. The anterior row of the first molar contains three large cusps: a lingual t1 that is displaced well posteriorly relative to a large central t2 and a prominent t3. Three large cusps (t4, t5, and t6) form the second row. The third row consists of a central cusp t8, a labial cusp t9, and a posterior cingulum that is smaller than the main cusps and present on every specimen examined (fig. 39A and B). There is no lingual cusp t7. On a few specimens (table 5), there is a cusp t1bis (usually large and conspicuous) nestled between cusp t1 and t2 and sometimes a nubbin of a cusp t2bis between cusp t2 and t3 (table 5; fig. 39A and B). In half of the sample, there is a small accessory cusp on the labial margin between cusps t6 and t9 (fig. 39A). On some specimens, there is a low crest extending from cusp t3 to cusp t6 and from cusp t6 to cusp t9; such crests are more evident on worn occlusal surfaces (fig. 39A).

On the second molar, the first row of cusps is represented by a large cusp t1 and a small cusp t3; the latter is inconspicuous but present on all specimens in the sample. The rest of the tooth is a slightly smaller version of the second and third cusp rows in the first molar. The posterior cingulum at the back of the second upper molar is often small and does not occur on every specimen (table 6).

Two rows of indiscrete mounds form the occlusal surface of each third upper molar. The anterolingual margin is a large mound that is apparently the coalesced cusps t1 and t4. Adjacent to it is a small cusp t5. Most of the anterolabial mound of the tooth consists of cusp t6. The boundaries of all these cusps are obscure. Cusp t3 is very small and does not occur in some specimens (table 6). The posterior half of the occlusal surface consists of a bumpy mound that is probably cusps t8 and t9 merged. Neither a cusp t7 nor posterior cingulum is present.

Each first lower molar is long and narrow, rectangular in occlusal outline. Three rows of gleaming white cusps (two in each row) form the topography. The anterolingual and anterocentral cusps forming the front row are about equal in girth and height to one another; the anterolingual is larger in some specimens. In about half the sample, there is a large an-

terocentral cusp (fig. 40A) on the front margin of the molar (table 6). Anterior labial cusplets are usually absent (table 6), as are anterior lingual cusplets. There is a small posterior labial cusplet on each tooth and posterior lingual cusplets occur in three-fourths of the sample (table 5; fig. 40A). The posterior cingulum at the center and back of the molar is small and nestled so tightly between the back faces of the main cusps that it is hardly evident.

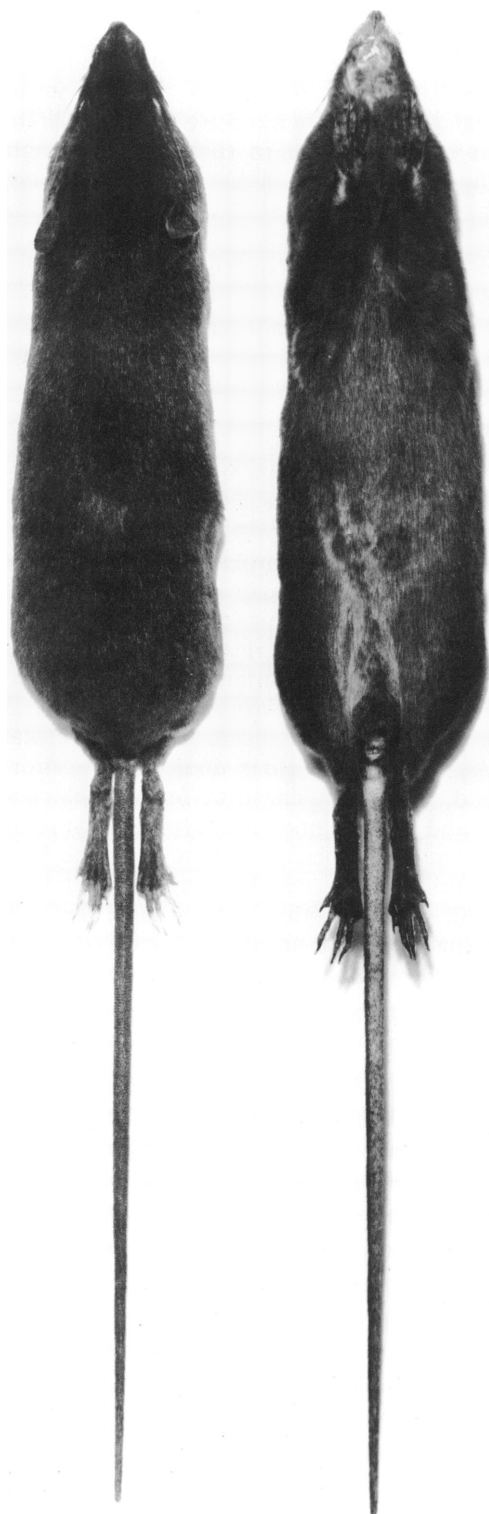
Each second lower molar is about as wide as the first but has only two rows of high cones. The anterolabial cusp is present in each specimen but very small (table 6). A posterior labial cusplet is absent in about half the sample (table 6). The posterior cingulum is even smaller and less evident than that in the first lower molar.

Each third lower molar is very simple. A small anterolabial cusp defines the anterolabial margin in about three-fourths of the sample (table 6). The rest of the occlusal surface is formed by an anterior row of two cusps and a wide posterior lamina. There is no posterior cingulum at the back of the third molar.

Melasmothrix naso is small-bodied, short-tailed, with dark chestnut fur and blackish feet and tail. It stands in sharp contrast to the other named species of shrew mouse from Central Sulawesi, which is large-bodied, long-tailed, with brownish gray pelage, feet, and tail (fig. 34). That animal is discussed below.

Tateomys rhinogradoides

On June 26, 1930, Dr. G. Heinrich collected an adult male shrew mouse from 2200 meters on Gunung Latimodjong (lat. 3°30' S, long. 120°05' E), a high part of the mountains in the northern portion of the southwest peninsula of Sulawesi. The specimen became the holotype of *Tateomys rhinogradoides* (Musser, 1969) and consisted of a stuffed skin and a broken cranium (both are figured in Musser, 1969); the mandible had been lost. The holotype remained the only specimen until the 1970s when an adult female (AMNH 226955) was caught during August 1973 at 2400 meters near the summit of Gunung Tokala (lat. 1°36' S, long. 121°38' E). That mountain is between the Rampi and Seko valleys in the southern section of Central Sulawesi (Province Sula-



wesi Selatan; see the map in Carney et al., 1977, p. 381). Then during December 1973, and March and April 1975, members of the Archbold Sulawesi Expedition obtained seven adults (AMNH 223966–223968, 225115–225118) from the southwestern slope of Gunung Nokilalaki in Central Sulawesi. The animals came from altitudes ranging from 7300 to 7500 feet in cold and wet moss forest near the summit.

Body conformation and coloration of the animals from Gunung Nokilalaki are much like that of the holotype from Gunung Lati-modjong (Musser, 1969). Each of the rats has a large chunky body with a tail that is only slightly longer than combined lengths of head and body (table 5). The elongate head and muzzle, combined with the tiny eyes, appears shrewlike. The thick, short (up to 8 mm. long over the back and rump) and velvety pelage over the upperparts is dark brownish gray with burnished highlights. The dense compact fur without long guard hairs resembles the pelage texture in *Melasmothrix naso*. Fur clothing the underparts is also short and dense. The venter is gray and overlain with a pale buff wash on the pectoral, abdominal, and inguinal regions. The nose is fleshy, similar in shape to the proboscis-like rhinarium of shrews such as *Crociodura*. The tip of the nose, around the nostrils, and the thick fleshy upper and lower lips are unpigmented. The long vibrissae from the muzzle extend at least 5 mm. past the ears when laid back alongside the head (measured on freshly caught specimens). The elongate and small ears are dark brownish gray.

The tail is a thick and sturdy appendage. Its dorsal half, from base to tip, is dark grayish brown. The ventral half, along the full length, is white and finely speckled by dark gray hairs scattered over the surface. Not one of the specimens has a white tail tip.

FIG. 41. *Tateomys rhinogradoides*. Dorsal (left) and ventral (right) views of AMNH 223966 from Gunung Nokilalaki, Central Sulawesi. Length of head and body, 154 mm.; length of tail, 170 mm.; length of hind foot, 38 mm.; length of ear, 24 mm.; weight, 98 g.

TABLE 5
Measurements (in Millimeters), Weight (in Grams), and Other Data from Specimens (in AMNH) of
Adult *Tateomys rhinogradoides* collected on Gunung Latimodjong and Gunung Nokilalaki, Sulawesi

	Gunung Latimod- jong	Gunung Nokilalaki					$\bar{X} \pm SD^b$
	196591 ^a	223966	225116	225118	225117	225115	
Sex		male	female	female	male	female	
Length of head and body (LHB)	137	154	151	156	—	149	152.5 \pm 3.1
Length of tail (LT)	168	170	152	166	—	156	161.0 \pm 8.4
LHB/LT (in %)	82	91	99	94	—	96	—
Length of hind foot	36	38	38	38	—	37	37.8 \pm 0.5
Length of ear	17	24	22	24	—	23	23.3 \pm 1.0
Weight	—	98	88	75	—	70	82.8 \pm 12.7
Scale rows per centimeter	16	16	16	16	—	17	16.3 \pm 0.3
Greatest length of skull	38.1	—	—	39.1	40.1	38.8	39.3 \pm 0.7
Zygomatic breadth	15.3	15.7	15.5	15.2	15.6	15.3	15.5 \pm 0.2
Interorbital breadth	6.5	6.9	—	6.8	7.1	6.9	6.9 \pm 0.1
Breadth of braincase	14.8	16.1	16.5	16.0	16.6	16.3	16.3 \pm 0.3
Height of braincase	9.4	9.8	9.5	9.7	10.0	9.9	9.8 \pm 0.2
Length of nasals	14.4	—	—	13.9	14.7	13.4	14.0 \pm 0.7
Length of rostrum	13.9	—	—	13.7	14.6	13.7	14.0 \pm 0.5
Breadth of rostrum	5.3	—	—	5.4	5.7	5.3	5.5 \pm 0.2
Rostrum anterior to incisors	1.6	—	0.8	1.0	1.5	1.4	1.2 \pm 0.3
Breadth of zygomatic plate	1.3	1.1	—	1.2	1.1	1.2	1.2 \pm 0.1
Breadth across incisor tips	1.6	1.8	1.7	1.7	1.6	1.5	1.7 \pm 0.1
Palatal length	15.3	—	—	17.0	17.4	16.8	17.1 \pm 0.3
Postpalatal length	15.7	16.2	16.1	16.1	16.4	15.8	16.1 \pm 0.2
Length of diastema	10.0	—	—	9.2	9.2	9.2	9.2 \pm 0.0
Length of incisive foramina (IF)	6.1	—	—	5.9	5.8	5.9	5.9 \pm 0.1
Breadth of incisive foramina	1.7	—	—	1.9	1.8	2.0	1.9 \pm 0.1
IF to M ¹	1.8	—	—	1.1	1.8	1.3	1.4 \pm 0.4
Length of palatal bridge (PB)	6.9	—	—	7.5	8.2	7.6	7.8 \pm 0.4
Breadth of PB at M ¹	—	3.0	—	3.0	3.1	2.9	3.0 \pm 0.1
Breadth of PB at M ³	—	3.8	—	3.8	4.0	3.9	3.9 \pm 0.1
Breadth of mesopterygoid fossa	2.0	2.4	2.5	2.2	2.5	2.4	2.4 \pm 0.1
Length of bullae	4.9	5.2	5.3	5.7	5.5	5.3	5.4 \pm 0.2
Length of M ¹⁻³	4.9	5.8	—	6.0	5.9	5.8	5.9 \pm 0.1

^a Holotype.

^b The mean plus or minus one standard deviation.

The front feet (illustrated in fig. 2 in Musser, 1969, p. 7) are broad and stout. The heavy robust claws are long, arcuate, and cylindrical; all are unpigmented. The palmar surfaces, digits, and part of the metacarpal region of each foot is unpigmented; the basal half or third of the metacarpal surface is covered with dark brownish gray fur. In the new specimens, the small interdigital pads and the two large metacarpal pads on each palmar surface resemble my description of the pads on the holotype except that the metacarpal pads are

not bony; they do, however, have a tough covering and are much harder than any of the other pads on either the front or hind feet.

The hind feet (shown in fig. 3 in Musser, 1969, p. 8) are long, narrow, and appear strong. The long slender digits terminate in long unpigmented claws. The plantar pads are small but conspicuous. Most of the plantar surfaces, all the pads, and parts of the undersides of the digits are brownish gray. The entire dorsal surface of the metacarpal

TABLE 6
Molar Features in Samples of *Melasmothrix naso*, *Tateomys rhinogradoides*, and *Tateomys macrocercus* from Gunung Nokilalaki, Central Sulawesi^a

	<i>M. naso</i>	<i>T. rhino- gradoides</i>	<i>T. macro- cercus</i>
Number of roots on M ¹⁻³			
M ¹	3	5	3
M ²	3	4	3
M ³	3	3	3
Number of roots on M ₁₋₃			
M ₁	2	2	2
M ₂	2	2	2
M ₃	2	2	2
Cusp t3 on M ²			
+	100 (17)	100 (3)	100 (6)
—	—	—	—
Cusp t3 on M ³			
+	71 (12)	—	17 (1)
—	29 (5)	100 (3)	83 (5)
Posterior cingulum on M ¹			
+	100 (17)	100 (3) ^b	100 (6)
—	—	—	—
Posterior cingulum on M ²			
+	88 (15)	—	17 (1)
—	12 (2)	100 (3)	83 (5)
ALC between t6 and t9 ^c			
+	50 (13)	—	17 (1)
—	50 (13)	100 (5)	83 (5)
Cusp t1bis on M ¹			
+	18 (3)	—	—
—	82 (14)	100 (3)	100 (6)
Cusp t2bis on M ¹			
+	17 (3)	—	—
—	83 (15)	100 (4)	100 (6)
Anterocentral cusp on M ₁			
+	47 (8)	—	33 (2)
—	53 (9)	100 (3)	67 (4)
Anterior labial cusplet on M ₁			
+	12 (2)	—	—
—	88 (15)	100 (3)	100 (6)
Posterior labial cusplet on M ₁			
+	100 (17)	100 (3)	17 (1)
—	—	—	83 (5)
Posterior lingual cusplet on M ₁			
+	72 (13)	100 (4)	—
—	28 (5)	—	100 (6)
Anterolabial cusp on M ₂			
+	100 (17)	100 (3)	17 (1)
—	—	—	—

TABLE 6—(Continued)

	<i>M. naso</i>	<i>T. rhinogradoides</i>	<i>T. macrocercus</i>
Posterior labial cusplet on M_2			
+	41 (7)	100 (3)	17 (1)
—	59 (10)	—	83 (5)
Posterior lingual cusplet on M_2			
+	17 (3)	100 (4)	—
—	83 (15)	—	100 (6)
Anterolabial cusp on M_3			
+	76 (13)	100 (3)	17 (1)
—	24 (4)	—	83 (5)

^a Number of molar roots (number of specimens examined for root counts: *M. naso*, 26; *T. rhinogradoides*, 5; and *T. macrocercus*, 6); presence (+) or absence (—) of certain cusps (t3, posterior cingulum, accessory labial, t1bis, t2bis, anteroventral, anterolabial), labial cusplets (anterior, posterior), and lingual cusplets (anterior, posterior).

^b The posterior fourth of the occlusal surface on each M^1 is worn in even the youngest *T. rhinogradoides* in my series, but the wear surface appears to be a combination of cusp t8 and the posterior cingulum (fig. 39).

^c Accessory labial cusp between cusps t6 and t9 (figs. 39 and 46).

area is densely covered with brownish gray fur that extends out onto two or three of the outer digits.

Each of the four females has two pairs of inguinal mammae. There are no indications of postaxillary mammae, such as occur in *Melasmothrix naso*, on any of the specimens.

The above descriptions and mammae counts are from notes written in the field with freshly caught rats in hand.

The cranium of *T. rhinogradoides* is much larger than that of *M. naso* (tables 3 and 5) but the overall conformation is similar in the two species (figs. 37 and 38). I (Musser, 1969) previously noted several cranial features that would distinguish the two kinds of rats. Now I see, after examining series of each species, that some of those differences reflect only individual variation. Other differences that were mentioned, however, do distinguish the two different shrew rats. Compared with the cranium of *M. naso*, that of *T. rhinogradoides* has 1) a shorter rostral tube, both actually and relative to length of rostrum, anterior to the upper incisors; 2) an interorbital region that is narrower relative to breadth of the braincase (table 7), and a braincase that is lower relative to its breadth; 3) zygomatic plates that slant backward at a greater angle and are narrower and appear more delicate; 4) incisive foramina that are actually longer but shorter relative to length of the diastema

(table 7); 5) a palatal bridge that is actually longer and longer relative to skull length, its posterior margin ending 0.1–0.6 mm. behind the backs of the third molars (the palatal bridge ends anterior to the molar rows in *M. naso*); 6) each posterior palatine foramen located opposite the anterior half of each second molar (in *M. naso*, each foramen is opposite the junction of the second and third molars); 7) a more elongate mesopterygoid fossa, pterygoid fossae that are much longer and narrower, and sphenopterygoid vacuities that are actually smaller and smaller relative to the area of each pterygoid plate (sphenopterygoid vacuities are spacious in *M. naso*); 8) the extension of palatine bone forming the anterior one-third of each pterygoid plate restricted to the ventral surface and not forming part of the pterygoid ridge (in *M. naso*, the palatine extension is relatively wider, reaching around the lateral margin of the pterygoid plate to form part of the ridge outlining the lateral margin of the plate; fig. 42); 9) the opening of each transverse canal located lateral to the bony eustachian tube, and the basisphenoid bone complete directly anterior to the tube (in *M. naso*, the basisphenoid in front of each eustachian tube is open, which exposes the lateral segment of the transverse canal so that each opening of that canal lies medial to the very short eustachian tube and closer to the midline of the

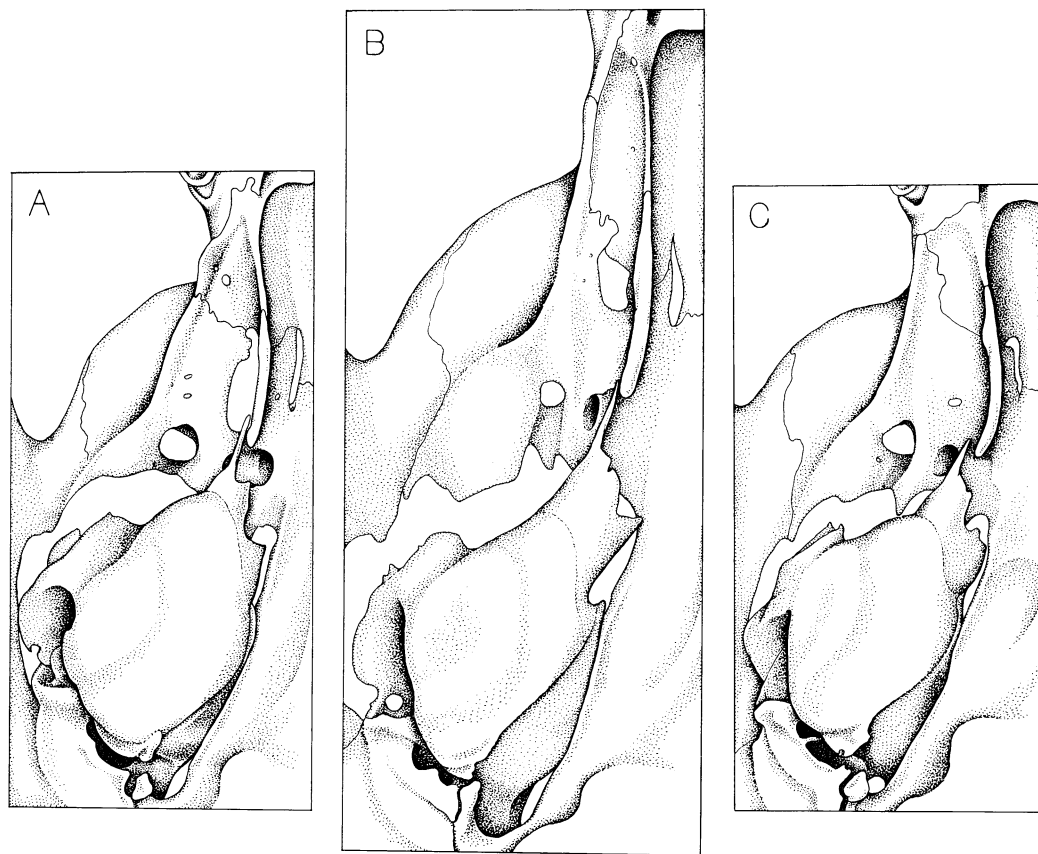


FIG. 42. Views of right pterygoid and mesopterygoid regions and bullae of Sulawesi shrew rats. A: *Melasmothrix naso* (drawn from AMNH 225085). B: *Tateomys rhinogradoides* (based on AMNH 225115). C: *T. macrocercus* (drawn from AMNH 225075). Note configurations of palatine bone forming the anterior one-third of each pterygoid fossa; relative sizes or absence of the sphenopterygoid vacuities; which side of the eustachian tube the opening of the transverse canal is on; the bullar inflation in *M. naso*, elongation in *T. rhinogradoides*, and globular form in *T. macrocercus*; and relative length of each bony eustachian tube. See text for additional comparisons and descriptions.

basicranium; fig. 42); 10) much smaller bullae, both actually and relative to skull length, that are not inflated as they are in *M. naso*, along with slim and long bony eustachian tubes (very short and inconspicuous eustachian tubes in *M. naso*; fig. 42); and 11) a large postglenoid vacuity in which the dorsal rim is below the posterior rim of the squamosal zygomatic root (in *M. naso*, the postglenoid vacuity is larger, so spacious that its dorsal rim is hidden beneath the posterior margin of the squamosal root; fig. 45).

The mandible of *T. rhinogradoides*, which has never been described, is a slimmer elongate version of that in *M. naso* (fig. 38). Other

than its greater length and exaggerated elongation, the structure of each dentary ramus and shapes of the processes in *T. rhinogradoides* resemble those mandibular features of *M. naso*.

The general shapes of the upper and lower incisors are similar in the two species but there are conspicuous differences. The notch at the tip of the incisors is smaller and less noticeable in the few specimens of *T. rhinogradoides* than in the many examples of *M. naso*. All the *T. rhinogradoides* have ivory enamel on the uppers and translucent white enamel on the lower incisors. The enamel on the uppers in the sample of *M. naso* ranges

from ivory to pale yellow-orange, the enamel on the lower incisors is either translucent white or ivory (table 4). Finally, each upper incisor of *T. rhinogradoides* is thinner, the outer surface is more beveled, and most of the anterolateral surface is enamel—very little dentine is exposed on the lateral surface of each incisor (see fig. 8 in Musser, 1969, p. 16).

Although actually longer than those of *M. naso*, molar rows of *T. rhinogradoides* are about the same length relative to length of skull as in *M. naso* (tables 3, 5, and 7). The general conformation of each molar, the way each abuts or slightly overlaps the other, and the size of each molar relative to the others in the row (both maxillary and mandibular) are like the shapes and proportions in *M. naso* (figs. 39 and 40). Except for the first and second upper molars, each tooth is anchored by the same number of roots as are those in *M. naso* (table 6). Each first upper molar of *T. rhinogradoides* is anchored by five roots: an anterior, divided lingual, posterior, and small labial. Four roots anchor each second upper molar, two labial and two lingual. In contrast, *M. naso* has three roots beneath each first and second upper molar.

Even the youngest specimen in my small sample of *T. rhinogradoides* has worn occlusal molar surfaces, but not to the level where the basic resemblance of their cusp patterns to those of *M. naso* is obscured (figs. 39 and 40). The differences (table 6) in occlusal patterns between the two I detected are that in *T. rhinogradoides*; 1) the small cusp t3 on each third upper molar is missing (present in about three-fourths of the sample of *M. naso*); 2) each second upper molar lacks a posterior cingulum (present in 88 percent of the sample of *M. naso*); 3) a small accessory labial cusp between cusps t6 and t9 is absent (occurs in half the sample of *M. naso*); 4) cusps t1bis and t2bis do not occur on the first upper molar (both are present on a few specimens of *M. naso*); 5) each first lower molar lacks an anterocentral cusp (present in about half the sample of *M. naso*); 6) anterior labial cusplets are absent from each specimen (present on a few *M. naso*); 7) posterior lingual cusplets occur on all the specimens (absent in about one-third of the sample of *M. naso*); 8) posterior labial cusplets occur on each specimen (absent

TABLE 7
Percentages Expressing Proportions of Certain Cranial and Dental Measurements in Samples of *Melasmothrix naso*, *Tateomys rhinogradoides*, and *Tateomys macrocercus*

	<i>M. naso</i>	<i>T. rhinogradoides</i>	<i>T. macrocercus</i>
LIF/LD	66	64	58
RAI/LR	16	9	14
IF-M ¹ /LD	11	15	15
IB/BBR	45	42	43
HBR/BBR	63	60	66
LR/GLS	37	36	38
LPB/GLS	18	20	20
LB/GLS	18	14	15
LM ¹⁻² /GLS	16	15	17

Abbreviations: BBR, breadth of braincase; GLS, greatest length of skull; HBR, height of braincase; IB, interorbital breadth; IF-M¹, distance from posterior margins of incisive foramina to anterior faces of first molars; LB, length of bulla; LD, length of diastema; LIF, length of incisive foramina; LM¹⁻², length of maxillary toothrow; LPB, length of palatal bridge; LR, length of rostrum; RAI, length of rostral tube anterior to upper incisors. Values used computed from means listed in tables 3, 5, and 8.

from many *M. naso*); and 10) an anterolabial cusp occurs on each third lower molar (absent in about one-third of the sample of *M. naso*).

There may be geographic variation in *T. rhinogradoides* reflecting the insular nature of its montane distribution. Each specimen from Gunung Nokilalaki is larger than the holotype from Gunung Latimodjong (table 5). The female from Gunung Tokala is in fluid and the skull has not been extracted. Judged by some external measurements (length of tail, 151 mm.; length of hind foot, 35 mm.; and length of ear, 18 mm.), it too is slightly smaller than any specimen from Gunung Nokilalaki. Larger series from the three peaks and samples from different mountaintops will have to be studied to determine if there are montane patterns of morphological variation in this large-bodied shrew rat.

There is a third species of shrew rat. It, like some other endemic species of murids from the high mountains of Central Sulawesi (Musser, 1981a), was unknown to professional biologists, and even local villagers, until the middle 1970s. Coloration of the shrew

rat is similar to color of *T. rhinogradoides* but unlike that large-bodied robust rat with stout feet and large digging claws, the new animal has a small body with a very long tail, slender feet, and small claws. It is named and diagnosed below.

***Tateomys macrocercus*, new species**

HOLOTYPE AND LOCALITY: An adult male collected March 4, 1975, by members of the Archbold Sulawesi Expedition (original number, ASE 2592) from an altitude of 7500 feet in moss forest on the southwestern slope near the summit of Gunung Nokilalaki (lat. 1°13' S, long. 120°08' E), a high peak northeast of Danau Lindu, Province Sulawesi Tengah, Central Sulawesi, Indonesia.

The specimen consists of a stuffed skin (fig. 44), a cranium and dentaries (figs. 37 and 38), and a carcass that was fixed in formalin and is now preserved in alcohol. All parts are complete and in excellent condition. The molars are moderately worn. The holotype is in the American Museum of Natural History and cataloged as AMNH 225077 but it will eventually be transferred to the Museum Zoologicum Bogoriense at Bogor, Java, where it will bear the number MZB 224317.

REFERRED SPECIMENS: In addition to the holotype, there are seven other specimens (AMNH 225072–225076, 225078–225079) collected during March and April 1975, from 6500 to 7500 feet in moss forest on the southwest slope of Gunung Nokilalaki. Two of these were preserved in formalin and later transferred to alcohol, the other five consist of skins, skulls, and carcasses; the latter were fixed in formalin and are now in alcohol.

KNOWN DISTRIBUTION: Between 6500 and 7500 feet in moss forest on Gunung Nokilalaki in the central part of Sulawesi.

ETYMOLOGY: From the Greek *macros* (long) with *kerkos* (tail) (for the most obvious diagnostic characters of the new shrew rat).

DIAGNOSIS: A species of *Tateomys* that is distinguished from *T. rhinogradoides* by its 1) smaller body size and gracile conformation; 2) much longer tail relative to combined lengths of head and body; 3) slender feet with shorter and narrower claws; 4) smaller and less elongate cranium with a round braincase

that is higher relative to its breadth; 5) distal third of nasals swollen rather than turned up; 6) more erect zygomatic plates; 7) shorter incisive foramina, both absolutely and relative to length of diastema; and 8) less elongate dentaries and smaller, nubbin-like, coronoid processes.

DESCRIPTION AND COMPARISONS: A beautiful, small (table 8), grayish brown rat with a long nose, very small eyes, white front feet, and a long tail, *Tateomys macrocercus* seems adapted for a scansorial habit as opposed to *T. rhinogradoides*, which is a terrestrial and heavy-bodied, digging shrew rat, or *Melasmothrix naso*, a compact short-tailed, vole-like form (figs. 34 and 43). The head and body of *T. macrocercus* is clothed in soft and dense pelage, which reaches 7–10 mm. over the back near the rump. The outline of the coat is unbroken by long guard hairs—that evenness combined with the dense and soft texture imparts the velvety quality so characteristic of all three species of shrew rats. The pelage of *T. macrocercus* resembles that of *T. rhinogradoides* in texture, but is longer relative to body size and appears more woolly and less velvety than does the coat of the latter. The upperparts are dark grayish brown, similar to the color of *T. rhinogradoides* but grayer in tone and without burnished highlights. The underparts are dark gray overlain by a pale buffy wash; the overall coloration is similar to but darker than that in *T. rhinogradoides*. The tip of the nose and lips are pale gray. Each small eye is enclosed by a gray ring. The ears are naked and dark gray. The vibrissae from the muzzle are long and extend 5–10 mm. past the ear when laid against the side of the head (measured on freshly caught animals). Such vibrissae are long also in *T. rhinogradoides* but short in *M. naso*, where they reach the ear but no further.

A long tail is distinctive of *T. macrocercus*; it is a third or more longer than the body (table 8). The scales covering the surface are small, 17–19 rows per cm., as they are in the other species of shrew rats; three hairs emerge from each scale. The top and sides of the tail from its base to tip are dark blue-gray. The ventral surface is pale gray from base to tip; some specimens are speckled with dark gray. Seven out of the eight specimens have a white



FIG. 43. *Tateomys macrocerus*. An adult from near the summit of Gunung Nokilalaki, Central Sulawesi.

TABLE 8
Measurements (in Millimeters), Weight (in Grams), and Other Data from Specimens (in AMNH) of
Adult *Tateomys macrocerus* Collected in Gunung Nokilalaki, Central Sulawesi

	225072	225075	225077 ^a	225076	225073	225074	$\bar{X} \pm SD^b$
Sex	female	male	male	male	female	female	
Length of head and body (LHB)	120	120	110	117	110	111	114.7 \pm 4.9
Length of tail (LT)	173	160	175	171	160	165	167.3 \pm 6.6
LHB/LT (in %)	69	75	63	68	69	67	—
Length of hind foot	30	30	31	30	30	31	30.3 \pm 0.5
Length of ear	19	18	18	18	17	19	18.2 \pm 0.8
Weight	55	43	43	45	35	35	42.7 \pm 7.4
Scale rows per centimeter	17	18	18	23	21	20	19.5 \pm 2.3
Greatest length of skull	32.7	31.5	31.8	31.6	30.6	31.0	31.5 \pm 0.7
Zygomatic breadth	14.6	13.9	13.9	13.9	13.3	13.5	13.9 \pm 0.5
Interorbital breadth	6.0	6.0	6.1	6.0	6.1	6.1	6.1 \pm 0.1
Breadth of braincase	14.5	14.3	14.3	14.5	13.6	14.1	14.2 \pm 0.3
Height of braincase	9.0	9.2	9.7	9.2	9.3	9.1	9.3 \pm 0.2
Length of nasals	11.9	11.6	12.1	12.0	11.3	11.0	11.7 \pm 0.4
Length of rostrum	12.7	12.0	12.0	12.1	11.5	11.7	12.0 \pm 0.4
Breadth of rostrum	5.5	5.9	5.5	5.3	5.4	5.3	5.5 \pm 0.2
Rostrum anterior to incisors	1.6	1.7	1.8	1.8	1.7	1.7	1.7 \pm 0.1
Breadth of zygomatic plate	1.2	1.1	0.9	0.9	1.0	1.2	1.1 \pm 0.1
Breadth across incisor tips	1.4	1.4	1.4	1.3	1.2	1.2	1.3 \pm 0.1
Palatal length	14.1	13.5	13.9	13.5	13.3	13.2	13.6 \pm 0.3
Postpalatal length	11.5	11.1	11.7	11.8	11.1	11.3	11.4 \pm 0.3
Length of diastema	7.3	7.0	7.4	7.5	7.1	6.9	7.2 \pm 0.2
Length of incisive foramina (IF)	4.5	4.2	4.3	4.1	4.0	4.1	4.2 \pm 0.2
Breadth of incisive foramina	2.0	2.0	1.7	1.8	1.8	1.8	1.9 \pm 0.1
IF to M ¹	1.0	0.9	1.2	1.5	1.3	0.8	1.1 \pm 0.3
Length of palatal bridge (PB)	6.4	6.1	6.4	6.2	6.2	5.8	6.2 \pm 0.2
Breadth of PB at M ¹	2.9	2.6	2.8	2.7	2.7	2.5	2.7 \pm 0.1
Breadth of PB at M ³	3.5	3.5	3.5	3.3	3.2	3.5	3.4 \pm 0.1
Breadth of mesopterygoid fossa	2.0	2.1	2.0	2.0	1.9	2.3	2.1 \pm 0.1
Length of bullae	4.7	4.9	4.9	4.8	4.8	4.7	4.8 \pm 0.1
Length of M ¹⁻³	5.6	5.3	5.3	5.0	5.2	5.2	5.3 \pm 0.2

^a Holotype.
^b The mean plus or minus one standard deviation.

tail tip that ranges from 1 to 20 mm. The overall coloration and pattern of the tail resembles that in *T. rhinogradoides*; it is, however, much longer relative to combined lengths of head and body than in that shorter-tailed animal (tables 5 and 8).

Tateomys macrocerus has small front feet and long, narrow hind feet; they are gracile and delicate versions of the spatulate, robust front feet and stout hind feet of *T. rhinogradoides*. The front feet are white over their dorsal surfaces from the ankles to the claws and unpigmented on the palmar surfaces. The hind feet are gray dorsally and on the plantar surfaces; the plantar pads are ivory and contrast with the gray background. The pads (or

tubercles) are oblong and large on both front and hind feet, especially the interdigital pads. They are larger relative to the palmar and plantar surface areas than are the tubercles in *T. rhinogradoides*. All the claws are unpigmented, as they are in *T. rhinogradoides* but not *M. naso* (dark gray). Claws on the front feet are long, narrow, and sharp but not as long, broad, or robust as are those of *T. rhinogradoides* and *M. naso*. Claws on the hind feet are long and sharp, similar in shape and proportions (relative to the digits) to the claws of *T. rhinogradoides*.

Two pairs of inguinal mammae were found on each female of *T. macrocerus*. This count is common to *T. rhinogradoides* but not *M.*

naso, which has three pairs of mammae, one postaxillary and two inguinal.

Dorsal, ventral, and lateral cranial views of *T. macrocercus* are shown in figures 37 and 38. A long rostrum and round high braincase characterize the cranial outlines. The cranium is about the same size as that of *M. naso* and smaller than the cranium of *T. rhinogradoides* (tables 3, 5, and 8). The length of the rostrum relative to greatest length of skull is similar to the proportions of rostrum to skull length in *M. naso* and *T. rhinogradoides* (table 7); this feature is responsible for the long-nosed appearance in all three kinds of shrew rats despite their differences in body size and conformation.

The configuration of the rostrum and nasal bones is similar in all three species. Primary differences between them are that the rostrum, as seen in side view (fig. 38), does not taper as much and the distal third of the nasal bones are swollen rather than turned dorsad. The internal nares are higher and wider than those in either *M. naso* or *T. rhinogradoides* because of the deeper rostrum and swollen nasals of *T. macrocercus*. The rostral tube anterior to the upper incisors is longer, actually and relative to length of rostrum, in *T. macrocercus* than in *T. rhinogradoides* (tables 5 and 8). On the ventral surface of the rostrum of *T. macrocercus*, the incisive foramina are absolutely shorter than those in the other two kinds of shrew rats and much shorter relative to length of diastema. In both *T. macrocercus* and *T. rhinogradoides*, the distance from the end of the incisive foramina to the front face of each first molar is greater relative to diastemal length than in *M. naso*, reflecting the relatively longer foramina in the latter (table 7).

Configuration of the interorbital region and braincase of *T. macrocercus* resembles that of *T. rhinogradoides* and *M. naso*. The former has a wider interorbital area relative to breadth of braincase than in *M. naso*, resembling *T. rhinogradoides* in this proportion. The braincase is round and higher relative to its breadth than in the other two species; it appears swollen (figs. 37 and 38).

Each zygomatic plate is narrow and resembles that of the other species in shape. The plates do not slope back as much as do those in *T. rhinogradoides*. The plates of *T. macro-*



FIG. 44. *Tateomys macrocercus*. Dorsal (left) and ventral (right) views of AMNH 225077, the holotype, from Gunung Nokilalaki, Central Sulawesi. Length of head and body, 110 mm.; length of tail, 175 mm.; length of hind foot, 31 mm.; length of ear, 18 mm.; weight, 43 g.

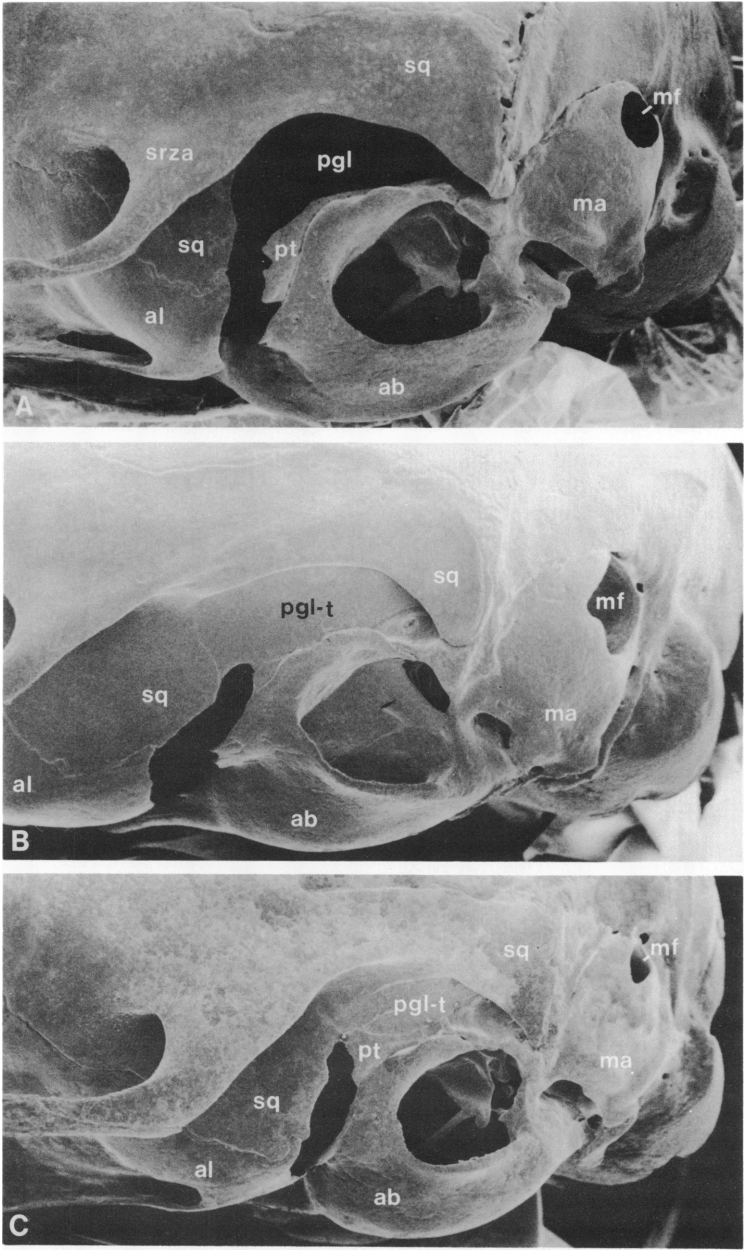


FIG. 45. Views of left bullar regions in Sulawesi shrew rats. A: *Melasmothrix naso* (AMNH 225087). B: *Tateomys rhinogradoides* (AMNH 225118). C: *T. macrocercus* (AMNH 225077).

Abbreviations: **ab**, auditory bulla; **al**, alisphenoid bone; **ma**, mastoid portion of petromastoid complex; **mf**, mastoid fenestra; **pgl**, postglenoid vacuity; **pgl-t**, part of postglenoid vacuity covered by thin tissue; **pt**, petrotic portion of the petromastoid bone; **sq**, squamosal bone; **srza**, squamosal root of zygomatic arch. See text for discussion.

cercus are different from either *M. naso* or *T. rhinogradoides* in that they do not extend out as far from the sides of the cranium, each

plate is higher, and the dorsal maxillary root of the arch medial to the plate is shorter.

The proportion of palatal bridge length to

skull length in *T. macrocercus* is like that in *T. rhinogradoides*, which partly reflects the short incisive foramina in those species as contrasted with the proportions in *M. naso* (table 7). The posterior rim of the palatal bridge ends 0.2–0.3 mm. anterior to the back faces of the molar rows in *T. macrocercus*, a configuration resembling that of *M. naso* and unlike that in *T. rhinogradoides* in which the bridge extends posterior to the molar rows by 0.1 to 0.4 mm. Each posterior palatine foramen is opposite the posterior half of each second upper molar; the foramen is farther forward relative to the molar in *T. rhinogradoides* and relatively farther back in *M. naso*. The foramina are open to the ventral surface and not concealed under shelves of bone as they are in *T. rhinogradoides* and *M. naso*.

Except that the mesopterygoid and pterygoid fossae and basicranium of *T. macrocercus* are not as elongate and narrow as those regions in *T. rhinogradoides*, the general configurations are similar in the two species (figs. 37 and 42). The pterygoid plates are nearly intact, breached by only small or tiny sphenopterygoid foramen, a configuration similar to that in *T. rhinogradoides* and unlike the spacious sphenopterygoid vacuities in *M. naso*. The shape and position of foramina in the posterior one-third of each pterygoid surface is like that in *T. rhinogradoides*: each transverse canal opens lateral to the bony eustachian tube and not medial to it as is the pattern in *M. naso* (fig. 42). The extension of palatine bone that forms the anterior third of the pterygoid fossa in *T. macrocercus* is confined to the ventral surface and does not form part of the lateral pterygoid ridge. The configuration is similar to that in *T. rhinogradoides* and not *M. naso* (fig. 42).

The auditory bullae of *T. macrocercus* are small relative to length of skull and end anteriorly in moderately long bony eustachian tubes. The bullae are rounder and less elongate than those in *T. rhinogradoides*, but otherwise the relative length of eustachian tube to bullar capsule and size of bulla relative to cranium is similar in the two species. On the other hand, the contrast in bullar shape between *T. macrocercus* and *M. naso* is sharp. The latter has large partially inflated bullae and short barely evident eustachian tubes (figs. 42 and 45). Each bulla of *T. macrocercus* is

more closely attached to the squamosal than are the bullae of either *T. rhinogradoides* or *M. naso* (fig. 45). The periotic flange of the petromastoid bone is more extensive than it is in the other two species and the portion of the postglenoid vacuity dorsal to the periotic is smaller. The postglenoid vacuity does not extend up under the posterior rim of the squamosal zygomatic root; the conformation is like that in *T. rhinogradoides* and unlike that in *M. naso* in which the postglenoid space is so large that it extends up under the root of the zygomatic arch.

The occipital region of *T. macrocercus* and its slightly swollen mastoids resemble shapes of these areas in both *T. rhinogradoides* and *M. naso*. A conspicuous fenestra is present in each mastoid of all but one of the specimens of *T. macrocercus* (fig. 45); such an opening is characteristic of all specimens in samples of the other two species.

The dentaries of *T. macrocercus* are not as elongate as those of *T. rhinogradoides* and they are shaped more like the dentaries of *M. naso* (fig. 38). In *T. macrocercus*, the body of the ramus beneath the toothrow is deeper (dorsoventrally) than that in *M. naso* and the coronoid process is smaller, without the long delicate extension characteristic of the process in the other two species.

Shapes of the upper and lower incisors of *T. macrocercus* resemble those teeth in *M. naso* and the tips are narrower than in either *T. rhinogradoides* or *M. naso* (tables 3, 5, and 8). The enamel on the uppers is ivory in color in three specimens and cream in three others; the lower incisors are translucent white in all specimens (table 4). The enamel layers on the upper incisors are beveled to about the same degree as those in *M. naso*; they do not form most of the lateral surface of the teeth as is the configuration in *T. rhinogradoides*. None of the uppers are notched at their tips in my sample of *T. macrocercus*; the tips of the incisors are slightly notched in all examples of *T. rhinogradoides* at hand and either slightly or deeply notched in all the specimens of *M. naso*.

The maxillary molar rows of *T. macrocercus* are shorter than those of *T. rhinogradoides* and about as long as the toothrows in *M. naso*; length of toothrow relative to greatest length of skull is also similar in *T. macro-*

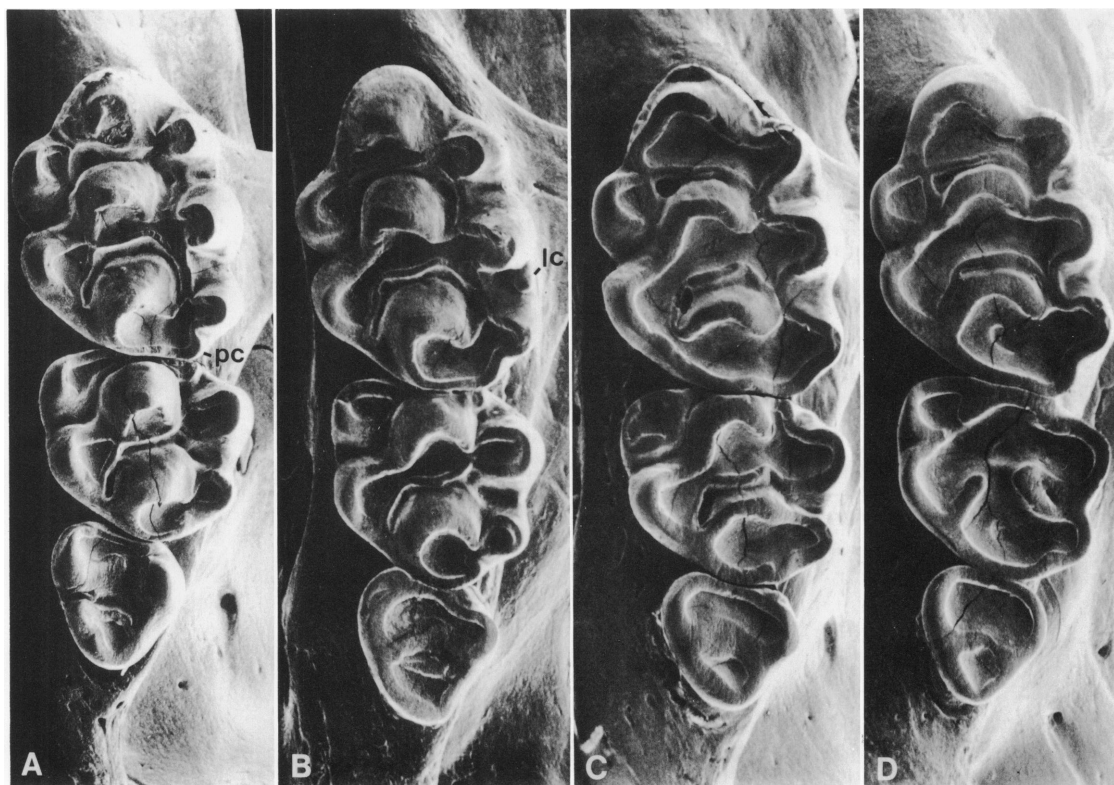


FIG. 46. Occlusal views of left maxillary molar rows in *Tateomys macrocercus* showing different stages of wear. A: AMNH 225074; actual length of M^{1-3} is 4.9 mm. B: AMNH 225077, holotype; length M^{1-3} , 5.0 mm. C: AMNH 225075; length M^{1-3} , 4.9 mm. D: AMNH 225072; length M^{1-3} , 5.3 mm.

Abbreviations: lc, accessory labial cusp; pc, posterior cingulum.

cercus and *M. naso* (tables 3, 5, 7, and 8). Both upper and lower molars of *T. macrocercus* also resemble the molars of *M. naso* in heights of crowns and cusps, number of roots anchoring each tooth (table 6), texture and coloration of the enamel and dentine surfaces, the abutment of one tooth against the next, and the size of each tooth relative to the others in the row (figs. 39 and 40).

Different occlusal patterns reflecting moderate to much wear are illustrated in figures 46 and 47. The basic pattern formed by cusps and cusplets on each molar is similar to that in *T. rhinogradoides* (table 6; figs. 39 and 40). In both species, cusp t3 is usually absent from each third upper molar (present on most specimens of *M. naso*), the posterior cingulum on each first upper molar is indistinct (discrete and distinct in *M. naso*), there is no

posterior cingulum on each second upper molar (occurring on most examples of *M. naso*), an accessory labial cusp between cusps t6 and t9 is usually absent (present in half the sample of *M. naso*), cusps t1bis and t2bis are absent (occur in a few *M. naso*), an antero-central cusp is usually absent or occurs infrequently on each first lower molar (present in about half the sample of *M. naso*), anterior labial cusplets are absent (occur infrequently in *M. naso*), and a posterior labial cusplet is absent or infrequent on each second lower molar (present in about half the sample of *M. naso*). In *T. macrocercus*, there is a posterior lingual cusplet on each first lower molar (occurs in a third of the sample of *M. naso*, absent from all *T. rhinogradoides*) and posterior lingual cusplets are absent from all the

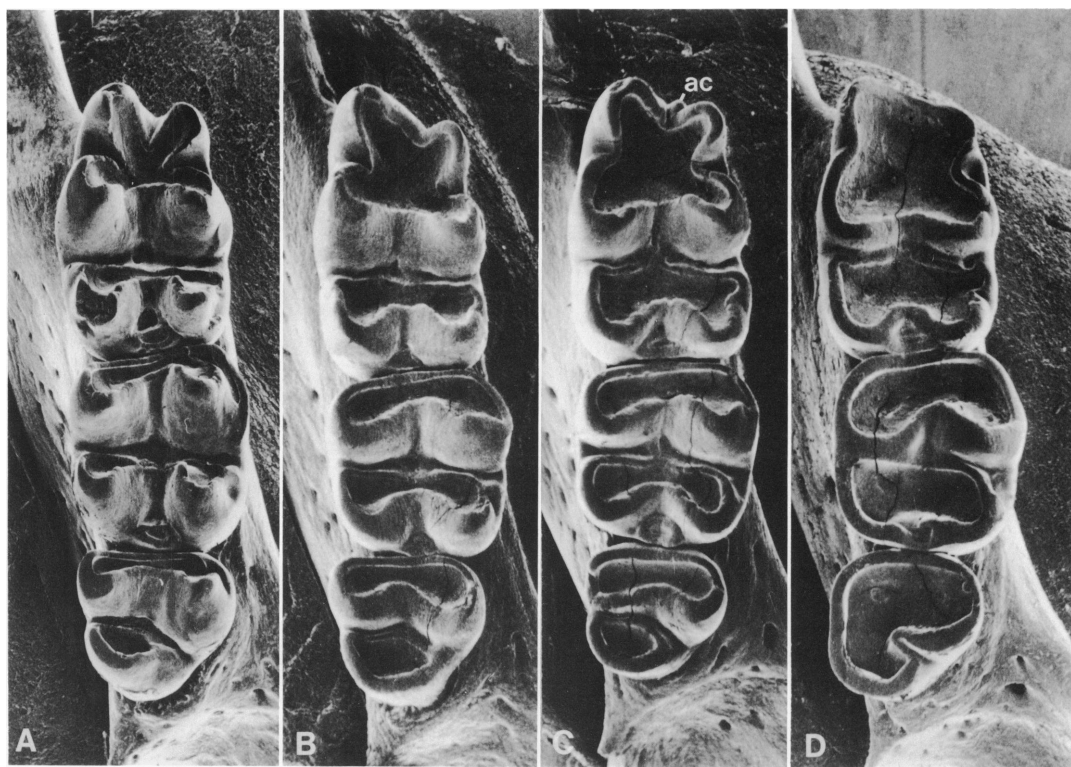


FIG. 47. Occlusal views of right mandibular molar rows of specimens shown in figure 46. A: actual length of M_{1-3} is 4.7 mm. B: length of M_{1-3} , 4.6 mm. C: length of M_{1-3} , 4.6 mm. D: length of M_{1-3} , 4.8 mm.

Abbreviation: ac, anteroventral cusp.

specimens (present in all *T. rhinogradoides* and absent from most examples of *M. naso*).

HABITAT AND HABITS

The highest of all the ridges ringing the mountain valley and deep lake of Lindu, Gunung Nokilalaki looms on the horizon, its summit (at 7520 feet) rising 4500 feet above the lake shore. Tropical upper montane rain forest would be the professional botanist's (Whitmore, 1975) name for the dark green mantle over the upper slopes and top of the mountain but the simple term, moss forest, better labels the image, texture, and mood of these high, wet and dark woods (fig. 48). Here are where the shrew rats live.

A short canopy (40–60 feet high), small trees, and less species diversity are typical of high mountain forest as contrasted with the tall canopy, huge trees, and rich species com-

position of tropical evergreen lowland rain forest. On the summit, the trees grow farther apart and the forest is more open than that at lower altitudes. Trunks are usually without buttresses, leaves are small; oaks, myrtles, laurels, and conifers form a significant part of the flora. Except where tangles of rotting tree-falls and piles of rattan form obstacles, the ground beneath the canopy is open and parklike. Undergrowth consists of scattered gingers, rattan rosettes, small shrubs, saplings, and lacy ferns; sedges cover the ground in some places (fig. 50).

Moss is everywhere in the forest. It encases the exposed roots of trees and covers the trunks, limbs, and branches clear up into the canopy. Everything projecting from the surface of the ground is concealed in round pillow-like layers of thick and wet moss (figs. 49, 51). Where trees grow close together they are intertwined by mossy garlands. Here and

there long, lacy, wet mossy curtains hang from limbs and branches. Where there is no moss, undergrowth, or leaf litter the ground is wet, muddy, and sometimes rocky.

Rain and mist are a daily part of life in the moss forest. The air is humid and cold. I recorded rainfall, air temperatures, and relative humidities in the forest on Gunung Nokilalaki. During 60 days, from March 4 to May 2, 1975, the minimum air temperature during a 24-hour period on the summit ranged from 48° to 54° F. (mean, 51.0° F.), the maximum ranged from 52° to 63° F. (mean, 56.6° F.). At 6800 feet, during the same 60 days, the minimum air temperatures fluctuated from 51° to 58° F. (mean, 54.7° F.) and the maximum temperatures ranged from 54° to 65° F. (mean, 60.4° F.). There was rain during 40 of the 60 days and on many of the rainless days, the forest on the summit and lower slopes was blanketed with mist by late morning or early afternoon. Relative humidity was recorded at 5700 feet where we camped. Values ranged from 86 to 100 percent (mean, 93.8 percent) at daybreak, 68 to 98 percent (mean, 87.4 percent) in early afternoon, and 86 to 100 percent (mean, 94.1 percent) after dark.

Short trees, small leaves, ferns, and moss give the forest a delicate and lacy texture. Dark greens, browns, blacks, and russet, all glistening from dark gray mist, provide somber hues to the surroundings. High relative humidity and cold air make the atmosphere clammy. The forest is quiet except for sounds of wind and rain. Everything is wet.

Examples of *Melasmothrix naso* were caught on the ground in this forest. They come from the summit and downslope to 6400 feet; no shrew rats of any species were seen or trapped below that elevation. Descriptions, summarized from my notes written in the field, of the places where 20 *M. naso* were caught are given below. The kinds of cover and nature of the forest floor where *M. naso* and the two other species of shrew rats were found are similar to the places shown in figures 49, 51, and 52.

AMNH 225101 (7500 feet): Wet runway 3 inches wide under and partly alongside rotten, wet, and moss-covered limb (8–10 inches in diameter) laying across muddy section of narrow terrace on steep slope.

AMNH 225103 (7500 feet): Runway 5 inches wide alongside and some places beneath a long, large, wet, and rotten moss-covered trunk on slope in undergrowth of rattan rosettes and gingers; nearby hillside is muddy and partially mossy.

AMNH 225104 (7500 feet): Mossy ground in wide space beneath a very long, rotten, and moss-covered trunk that had settled into the wet ground; prominent runway extends length of trunk and is partially covered by decaying bark and moss hanging from sides of the trunk.

AMNH 225107 (7500 feet): Mossy runway along moss-covered earth ledge on steep slope; no undercover.

AMNH 225110 (7500 feet): Runway 4 inches wide underneath rotten, moss-covered, slender trunk (6–8 inches in diameter) on washed muddy terrace just below summit; ground is muddy and rotten trunks, limbs, and scattered roots provide the only cover.

AMNH 225111 (7500 feet): Mossy runway 3 inches wide underneath rotten and moss-covered limb that is partially buried in the wet ground.

AMNH 225112 (7500 feet): Runway 4 inches wide underneath very rotten and thickly moss-covered limb on steep muddy slope.

AMNH 223965 (7500 feet): Wet and mossy runway alongside a huge rotting and moss-covered trunk on slope just below summit; clumps of moss, sedges, gingers, rattan rosettes, and scattered shrubs cover the ground; the vegetation partially obscures sides of the trunk and provides good cover for the runway.

AMNH 225090 (7400 feet): Flat tamped ground at base of large canopy tree growing out from side of slope; on downhill side of tree, the trunk and part of larger roots are exposed and extend out over the slope protecting a ledge beneath; no runways but places where rats would run alongside of roots and trunk.

AMNH 225089 (7400 feet): Damp ground beneath part of rotten and moss-covered trunk laying among gingers, ferns, sedges, rattan rosettes, and small shrubs.

AMNH 225091 (7400 feet): Runway 4 inches wide under mass of rotten and moss-



FIG. 48. Profile of moss forest near summit of Gunung Nokilalaki, Central Sulawesi. Long-leaved gingers and lacy ferns in foreground counterpoint dark and somber tone of forest. Photographed December 19, 1973, by Margareta Becker.



FIG. 49. Inside moss forest at 7500 feet near summit of Gunung Nokilalaki. Thick moss covers objects on forest floor, trunks and main limbs of trees, and branches in crowns. Photographed December 19, 1973, by Ms. Margareta Becker.

covered limbs around and over which are growing several understory trees.

AMNH 225092 (7400 feet): Runway 2 to 4 inches wide beneath a rotten and moss-covered limb (8–10 inches in diameter) on steep slope; runway extends along limb and becomes tunnels in several places where the soil is banked against the wood.

AMNH 225093 (7400 feet): Runway 5 inches wide underneath long root of huge canopy oak; large roots (8–10 inches in diameter) radiate in several directions from base of tree (which is about 4 feet in diameter), which is hollow; runways are under each root and lead to pieces of rotten limbs and trunks scattered on ground about the tree; roots and rotten limbs are covered with thick, wet moss.

AMNH 225100 (7400 feet): Trail 6 inches wide alongside long and large (2 feet in diameter), rotten and moss-covered trunk on hillside.

AMNH 225096 (7400 feet): Damp ground beneath rotten section of moss-covered trunk on hillside; no runway, only tamped earth covered by piece of trunk; nearby there are trails into and out of space under piles of rotting wood, roots, and earth.

AMNH 225097 (7400 feet): Runway 3 inches wide beneath a 20-foot section of very rotten, moss-covered trunk (8 inches in diameter) laying across washed hillside; open only a few places along the trunk, the run is mostly enclosed by moss so the open trail narrows into mossy tunnels 2 inches wide and high.

AMNH 225099 (7400 feet): Mossy runway 2 inches wide extending alongside and sometimes under section of very rotten and disintegrating moss-covered trunk (8 inches in diameter) on steep slope.

AMNH 225087 (7200 feet): Muddy runway 3 inches wide alongside moss-covered limb rotting into the earth; sparse undercover; ground muddy and rocky; rotting and moss-covered trunks and limbs scattered over forest floor.

AMNH 225088 (7200 feet): Narrow, muddy trail beneath part of very rotten, moss-covered trunk partially rotted into muddy ground.

AMNH 225086 (7100 feet): Narrow runway, part mossy and part muddy, alongside long and moss-covered root (6–8 inches in

diameter) exposed on muddy slope; runway is mostly exposed along base of root.

AMNH 225083 (6700 feet): Mossy runway leading from holes under roots across an earthen ledge to hillside; one of many small earth ledges, 4–5 feet long, found up and down the steep slope; ledges are uneroded remains of narrow terraces; this particular one covered with moss and supported by roots.

AMNH 225082 (6700 feet): Beneath a huge decaying trunk tilted down the slope and over a narrow terrace; where trunk rests against terrace is runway that extends downslope under rest of trunk.

AMNH 225080 (6400 feet): Narrow mossy runway 3 inches wide along earthen ledge beneath small tree on steep slope; sparse undercover; exposed ledge and earth bank is mossy; this is the lowest altitudinal record for *M. naso*.

More than one *M. naso* was caught in some of the places described above. Examples of both the other shrew rats were taken in some of the same spots as *M. naso*. Occasionally, in a particularly spacious runway, we trapped the ground squirrel, *Hyosciurus heinrichi*, and *Rattus hoffmanni*. A few shrews (*Crocidura*) were caught in some of the same narrow runways that yielded *M. naso*.

Places where some *T. rhinogradoides* were trapped are described below. No specimens were caught lower than 7300 feet.

AMNH 225115 (7300 feet): Wet runway 3–4 inches wide alongside and under very rotten and wet moss-covered section of trunk on steep slope; ground also is covered by moss as are the trees.

AMNH 223968 (7500 feet): Underneath rotten and moss-covered trunk on summit; no runway; ground was wet beneath trunk; muddy hillside covered with gingers, sedges, and scattered shrubs but little other cover.

AMNH 223967 (7500 feet): Wet and mossy runway alongside huge rotting, moss-covered trunk on steep slope just below summit; ground muddy and rocky, partially covered by moss, sedges, clumps of ginger, and shrubs; undergrowth partially obscures sides of trunk and provides good cover over runway.

AMNH 225118 (7400 feet): Mossy runway on earth ledge under moss-covered boulder on very steep hillside; ledge extends under rock for 8–10 inches; runway extends next to



FIG. 50. View of moss forest from a clearing near summit of Gunung Nokilalaki. Because they receive more light, clearings are often covered with a dense carpet of sedges instead of moss (as you see in fig. 49). Photographed April 1975.

rock leading farther back from rock face to passageway with opening 3 inches high and 2 inches wide; several boulders nearby, all covered with wet moss and epiphytes; next to boulders are pieces of rotting, moss-covered trunks, limbs, and small branches; undergrowth of shrubs, many gingers, rosettes of rattan, and coiling stems of mature rattans.

AMNH 225116 (7300 feet): Mossy runway along rocks exposed beneath roots of understory tree growing on nearly vertical slope; many rocks and roots exposed along slope which form ledges and cover for short distances; ground muddy, rocky, and exposed to runoff from daily rains.

AMNH 225117 (7300 feet): Fresh remains of shrew rat found on muddy terrace; animal was partially eaten by predator.

Eight specimens of *T. macrocerus* were caught in the places described below. Most rats were taken between 7500 and 7300 feet, one was caught at 6500 feet, the lowest altitudinal record for the species.

AMNH 225077 (7500 feet): Tunnel-like run alongside rotten, wet, moss-covered trunk; pieces of rotten wood and thick moss provided roof over most of runway; trunk laying on wet ground in an especially mossy part of summit.

AMNH 225076 (7500 feet): Tamped runway 5–8 inches wide resembling well-used trail beneath long, rotten, wet, and moss-covered trunk on slope near summit; runway extends length of trunk (about 30 feet) into tangle of very rotten limbs, then out onto open ground where it disappears.

AMNH 225078 (7500 feet): Wet runway 3 inches wide beneath and sometimes alongside rotten, wet, moss-covered limb across muddy part of a narrow terrace; limb and runway extend down steep slope, across terrace, then farther down the slope.

AMNH 225079 (7400 feet): Mossy runway beneath roots of tree growing on nearly vertical slope; trees are close and their roots form interlacing mat over the slope; beneath larger roots are protected and damp, moss-covered trails and passageways, that probably carry off excess rainwater but are also used by small mammals; rotten limbs, trunks, and roots are scattered over slope protecting the mossy and muddy runways; rocks underlie the shallow soil and outcrop nearby.

AMNH 225074 (7400 feet): Tamped, mossy runway 4 inches wide under decayed wood that is part of an old tree-fall; entire tree now broken and rotting and covered with moss forming good protection for several runs; part of tree-fall forms base for growing understory trees.

AMNH 225075 (7400 feet): Mossy path 8–10 inches wide beneath long strutlike coppice of tall understory tree, the kind with several trunklike struts growing from ground for about 5 feet at a 30-degree angle before shooting up in a twisting trunk; from the strut are roots that descend to ground; often coppicing trunks extend up; entire area is high and encloses a wide space covered by roots, trunks, and wet moss; nearby ground is very wet and mossy except for scattered muddy patches.

AMNH 225073 (7300 feet): Wet runway 3–4 inches wide alongside and under rotten, wet, and moss-covered section of trunk on steep slope; ground and forest here are very mossy.

AMNH 225072 (6500 feet): Runway—partly muddy, partly mossy—about 3 inches wide beneath exposed root on steep slope; sparse undergrowth of shrubs, gingers, and rattan rosettes.

Melasmothrix naso is diurnal. During the day, we often saw them dart out from under moss-covered roots or decaying tree trunks and scoot across small clearings to disappear into mossy passageways beneath other root entanglements. We even caught some specimens with our hands. Many of the shrew rats were trapped between 7 and 10 o'clock in the morning. We could determine this because traps were checked early and then again at 9 or 10 o'clock. A chunky body, tail much shorter than combined lengths of head and body, and dark chestnut coloration are features associated with diurnality in rats living in tropical forests of the Far East. The species of *Crunomys*, for example, may be diurnal and they are similar to *M. naso* in body conformation and coloration.

In contrast to *M. naso*, *Tateomys rhinogradoides* and *T. macrocerus* are nocturnal. They were never seen during the day and all specimens were trapped at night. Rats that have gray or grayish brown fur are usually nocturnal.

Diets of shrew rats were determined by

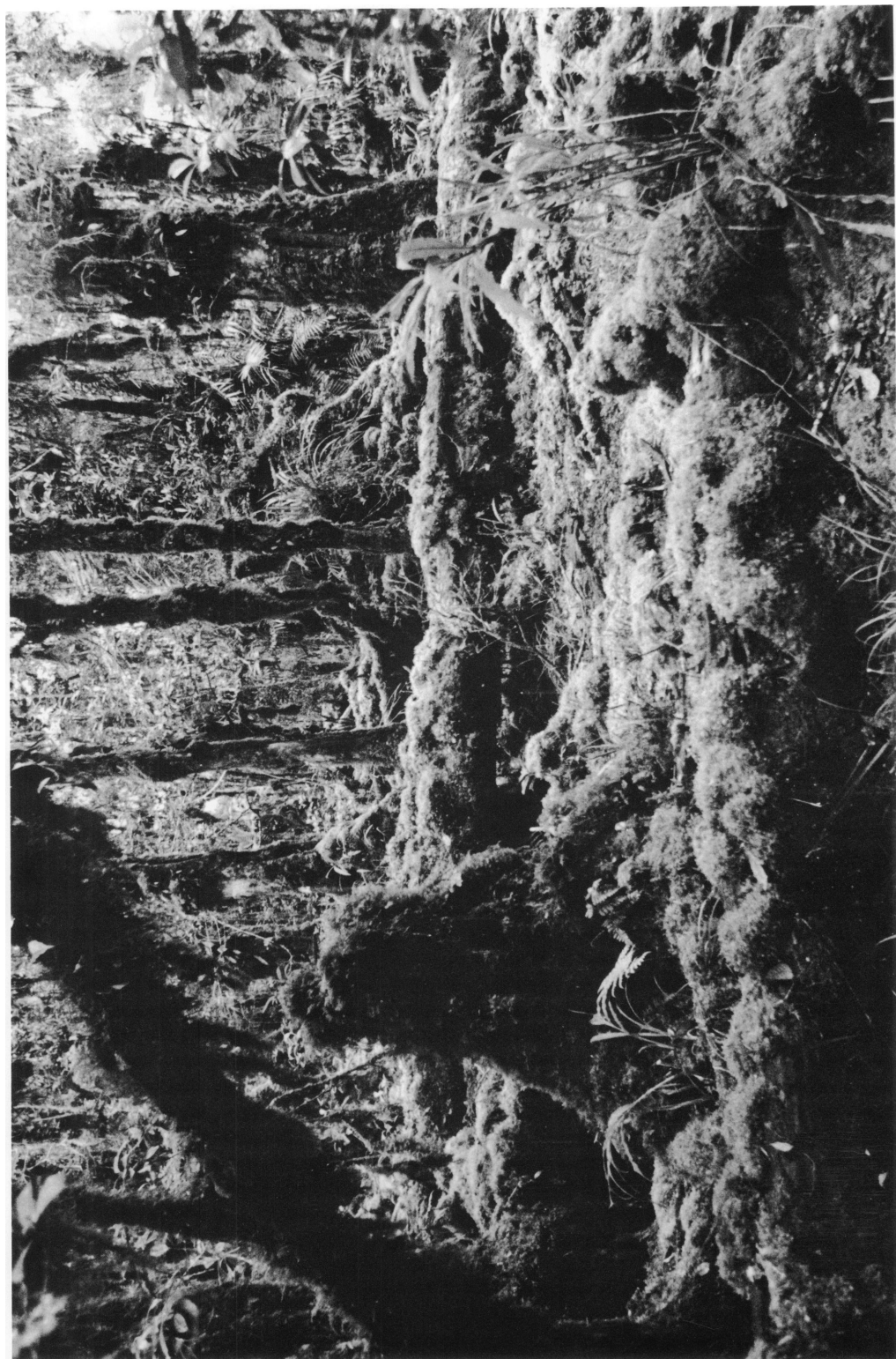


FIG. 51. Inside moss forest at 7500 feet on Gunung Nokilalaki. All three kinds of shrew rats as well as shrews were caught in this habitat. Moss-covered rotting trunks and limbs provide cover for runways. Scattered gingers, rattan rosettes, sedges, and short shrubs constitute the undergrowth. Photographed December 19, 1973, by Ms. Margareta Becker.



FIG. 52. Habitat of shrew rats at 7500 feet on Gunung Nokilalaki. Partially concealed runway beneath large and moss-covered trunk is used by all three species of shrew rats. Spiny plant on left is a young rattan, broadleaf shrubs are gingers, and grasses are sedges. Small ferns add lacy shapes and texture to ground cover. Photographed by Ms. Margareta Becker on December 19, 1973.

TABLE 9
Foods and Habitat of Rats Living with Shrew Rats between 6400 and 7500 Feet on Gunung
Nokilalaki, Central Sulawesi

	Food Categories								Habitat		
	Fruit,		Fruit,		Fruit,		Insects,		Arbo- real ^a	Terres- trial ^b	Ground and Trees ^c
	Fruit	Insects	Leaves, Insects	Fruit, Insects	Snails	Insects, Fungi	Earth- worms	Earth- worms			
<i>Haeromys</i> sp.	+								+		
<i>Paruromys dominator</i>	+										+
<i>Taeromys hamatus</i>	+									+	
<i>Rattus hoffmanni</i>	+									+	
<i>Rattus marmosurus</i>	+									+	+
<i>Eropeplus canus</i>		+								+	
<i>Taeromys callitrichus</i>		+								+	
<i>Margaretamys elegans</i>				+					+		
<i>Margaretamys parvus</i>				+					+		
<i>Maxomys musschenbroekii</i>					+					+	
<i>Bunomys penitus</i>						+				+	
<i>Melasmothrix naso</i>							+			+	
<i>Tateomys macrocercus</i>								+		+	
<i>Tateomys rhinogradoides</i>								+		+	

^a Arboreal rats nest in trees and are sometimes caught on the ground.
^b Includes scansorial: rats that run or climb onto supports above ground but are mainly ground dwellers.
^c Rats that nest in burrows or under roots of large trees and climb about in the crowns of understory and canopy trees for food.

feeding different foods to captive animals and examining contents of stomachs from trapped rats. The two species of *Tateomys* eat only small earthworms. Nothing else was found in stomachs. Other foods (insects, fungi, and snails) were rejected by captive rats that ate only earthworms. *Melasmothrix naso* eats primarily earthworms and the tiny larvae of dark-winged fungus gnats (Sciaridae; Dr. Elmo Hardy kindly identified my samples of dipteran larvae). Some stomachs also contained other kinds of larger larvae and adult Diptera. Captives ate earthworms but ignored adult beetles. Remains of moths, katydids, or cicadas were not found in stomachs of *M. naso*. These are favorite items of other rats living on the summit that include insects in their diets (*Margaretamys elegans* and *M. parvus*, for example).

There is probably little direct competition for foods among the three species of shrew rats. The diurnal activities of *M. naso* and its preference for fungus gnats as well as earthworms allow it to utilize different foods and the same resource (earthworms) at a dif-

ferent time compared to the other shrew rats. The body conformation of *T. rhinogradoides* is that of a rat adapted to working over the forest floor. The wide spatulate-like front feet and large digging claws of this animal suggest that it can dig deep into moss, soil, and rotten wood to extract earthworms. We found worms to be most common deep in moss, under bark of rotting trunks and limbs, and in damp soil protected by leaf litter. *Tateomys macrocercus*, with its small body, very long tail, slender feet and small claws is probably a scansorial rat. It works over the ground but also scampers up onto trunks, boulders, and other surfaces above ground level. Its more delicate claws suggest it may be restricted to hunting for earthworms in moss where they are easier to extract than from rotting wood or damp soil. We found earthworms in moss everywhere we sampled, from the forest floor up to 5 feet aboveground on trunks of trees and boulders.

On Gunung Nokilalaki between 6400 feet and the summit, there are no other small mammals that compete with shrew rats for

food. Of the 14 species of rats living in the same altitudinal range where shrew rats are found, none eat earthworms or larvae of fungus gnats (table 9). At lower elevations, however, in lower montane and lowland tropical evergreen forests, there are several kinds of rats that include earthworms in their diets: *Maxomys hellwaldii*, *Echiothrix leucura*, *Bunomys andrewsi*, and *Bunomys chrysocomus*. And there are no other small mammals living in moss forest along with shrew rats that depend on earthworms. *Hyosciurus heinrichi*, for example, is a long-nosed ground squirrel that is common near the summit. It feeds on acorns (*Lithocarpus* spp.) and large beetle larvae. Four species of shrews, all *Crocidura*, live in the same habitat as the shrew rats: *C. rhoditis*, *C. elongata*, and two undescribed species. One of the undescribed *Crocidura* is short-tailed, has rich dark brown fur, is terrestrial, and may be diurnal; the other undescribed species is arboreal and was taken from passageways in moss growing 8 feet above ground around a tree trunk. *Crocidura rhoditis* and *C. elongata* have blue-gray pelage; the former is terrestrial, the latter scansorial. I have not examined stomachs of all the specimens but those I did contained tiny insects, not earthworms.

RELATIONSHIPS AMONG THE SHREW RATS

Melasmothrix naso, *Tateomys rhinogradoides*, and *T. macrocercus* the three small-bodied shrew rats from Sulawesi, form a tight morphological cluster. Each is more closely related to the other than to any other murid species from the Indo-Malayan and Indo-Australian regions. Morphological characteristics of skins, skulls, and teeth that bind the three into this unique assemblage are specializations involving adaptations to cold, wet, and high moss forest habitat; either diurnal or nocturnal activity cycles; seeking, locating, eating, and processing earthworms and small dipteran larvae. There are other species of murids with similar habitat and habits in the Indo-Australian region but no other rats with the remarkable characters of the Sulawesi animals.

Each species has unique characteristics that separate it from the others. Some features indicate the species can be grouped. *Melas-*

mothrix naso stands apart from the other species in these features: diurnality, diet of earthworms and dipteran larvae, dark coloration, relatively short tail, three pairs of mammae, spacious postglenoid vacuity extending up under the squamosal zygomatic root, large inflated bulla and hardly any eustachian tube, partially open transverse canal and shape of the posterior one-third of each pterygoid plate, configuration of the palatine bone forming the anterior one-third of each pterygoid fossa, position of the posterior palatine foramina relative to the second and third molars, relatively long incisive foramina, incisor enamel more deeply pigmented, discrete and usually large posterior cingulum on each first and second upper molar, cusps t1bis and t2bis on first upper molars, accessory cusps often present on upper molars, cusp t3 present on each third molar, labial cusplets in many specimens, and an anterocentral cusp on first lower molar in half the sample.

Tateomys rhinogradoides and *T. macrocercus* are unlike *M. naso* in several characteristics. Both are nocturnal (instead of diurnal), eat only earthworms, are primarily grayish brown rats with unpigmented claws (instead of dark chestnut with dark gray claws), have tails as long or longer than combined lengths of head and body (instead of shorter than the body), and have only two pairs of mammae (instead of three). The two species share the following cranial and dental features: wide interorbital region, small or large postglenoid vacuity that does not extend up under the squamosal zygomatic root, small bullae with long or moderately long bony eustachian tubes, relatively short incisive foramina, posterior palatine foramina anterior to the junction of the second and third molars, palatine extension forming anterior one-third of each pterygoid fossa does not extend laterally to form ridge, closed transverse canal, similar configuration of the posterior one-third of each pterygoid plate, ivory incisor enamel, posterior cingulum on each first upper molar indistinct, posterior cingulum absent from second upper molar in most specimens, cusp t3 absent from each third upper molar, accessory cusps on upper molars and labial cusplets on lowers absent from most specimens, anterocentral cusp absent from first lower molar in most specimens.

The two species of *Tateomys* have their own special features. A robust body, tail as long or slightly longer than head and body, strong hind feet, spatulate front feet with heavy and long digging claws, extremely elongate head reflected in the long cranium and mandible, configuration of upper incisors, number of roots beneath first upper molars, and extension of bony palate posterior to the molar rows are unique traits of *T. rhinogradoides*. Although spectacular in its body proportions, that rat seems a more robust and stretched version of *T. macrocercus*.

A small body, long tail, small feet, and short claws characterize *T. macrocercus*; the conformation of the feet and claws are less derived than the conditions in either *T. rhinogradoides* or *M. naso*. The proportions of the rostrum and nasals of *T. macrocercus* are similar to those in the other species but the cranium posterior to the interorbital region is less elongate and more like the conformation in rats not so highly specialized as either *T. rhinogradoides* or *M. naso*. The higher braincase, normally proportioned

mesopterygoid and pterygoid regions, and small globular bullae that are tightly attached to the braincase all reflect less derived features than those found in the other shrew rats.

Relationships between the Sulawesi small-bodied shrew rats and other groups of murids are being studied. Neither *Melasmothrix* nor *Tateomys* seems to have any close relative on Sulawesi; neither one is closely related to the large-bodied shrew rat, *Echiothrix leucura*, which lives in tropical lowland evergreen forest throughout Sulawesi (Musser, 1969). To date, I cannot tie *Melasmothrix* and *Tateomys* to any native rats and mice in the Lesser Sunda Islands, Australia, the New Guinea region, or the Moluccas. And no native rats in the Philippine Islands seem closely related to the Sulawesi shrew rats. The only morphological look-alike, *Archboldomys*, may be an ecological counterpart of *Melasmothrix* but not a phylogenetic relative, as I suggest in the following section where relationships between the Philippine shrew rat and species of *Crunomys* are discussed.

CONTRASTS AMONG THE PHILIPPINE RATS

MELASMOTHRIX AND ARCHBOLDOMYS

I had originally intended to report only upon *Archboldomys* and *Crunomys* but ended up by including the shrew rats from Sulawesi because of the resemblance of *Melasmothrix* to *Archboldomys*. By describing the morphological and some ecological characteristics of the Sulawesi animals, I could indicate the close relatives of *Melasmothrix* and then compare that genus with *Archboldomys*.

A shrewlike head and muzzle, small eyes and ears, chunky body, tail much shorter than head and body, long digging claws on the front feet, narrow hind feet, short and velvety fur, and dark chestnut coloration describe *Melasmothrix naso* of Sulawesi. Except that *Archboldomys luzonensis* has paler fur that is more woolly than velvety in texture, and delicate claws on the front feet, the resemblance between the two species in body coloration

and conformation is striking (compare figs. 22 and 35).

Melasmothrix has some cranial and mandibular features that resemble those in *Archboldomys* (fig. 53). Both species have a slender rostrum, upturned nasal tips, a short tube formed by the premaxillary and nasal bones projecting anterior to the incisors, broad and smooth interorbital and postorbital regions, a large and smooth braincase, deep (front-to-back) occiput, sloping zygomatic plates without anterior spines, short incisive foramina, bony palatal bridge ending just anterior to the backs of the molar rows, similar carotid arterial pattern in the basicranium, squamosal roots of zygomatic arches originating low on sides of the braincase, spacious postglenoid and middle lacerate foramina, long and narrow lower incisors, and gracile elongate dentaries. Some of these are primitive features, others are associated with a shrew

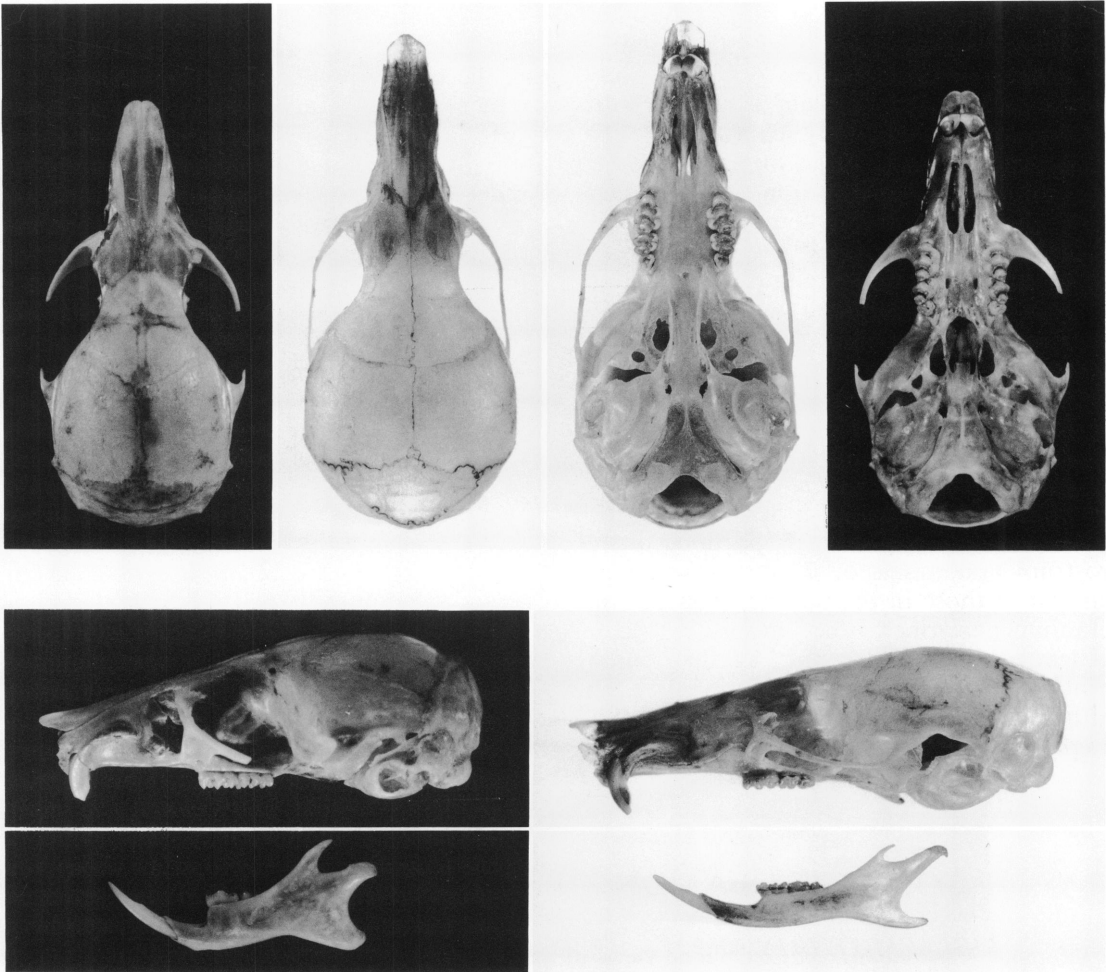


FIG. 53. Views of crania and dentaries. The holotype (FMNH 95122) of *Archboldomys luzonensis* (shown against black background) is contrasted with *Melasmothrix naso* (AMNH 225091). Approximately $\times 2$.

rat habitus: long slender rostrum, upturned nasals, tube anterior to the incisors, shape of the zygomatic plates, and elongate conformation of each dentary.

Other characters point up major differences between the two genera. In essence, the cranium and mandible of *M. naso* are extremely elongate compared with those elements in *A. luzonensis*. Note in figure 53, for example, that the end of the upper incisor capsule is just anterior to the zygomatic plate in *A. luzonensis* but the incisor capsule ends anterior to the premaxillary-maxillary suture, dorsal to the nasolacrimal canal, and well

anterior to the zygomatic plate. The braincase is lower; it and the mesopterygoid and pterygoid fossae are longer in *M. naso*—more stretched out—than are those regions in *A. luzonensis*. Finally, each dentary of *M. naso* is thin and long, an elongate and delicate object compared with each compact and sturdy dentary in *A. luzonensis*.

There are other differences between the two species. In *M. naso*, the ventral maxillary roots of the zygomatic arches originate directly over the first molars rather than mostly anterior to them as they do in *A. luzonensis*. The plates themselves are abso-

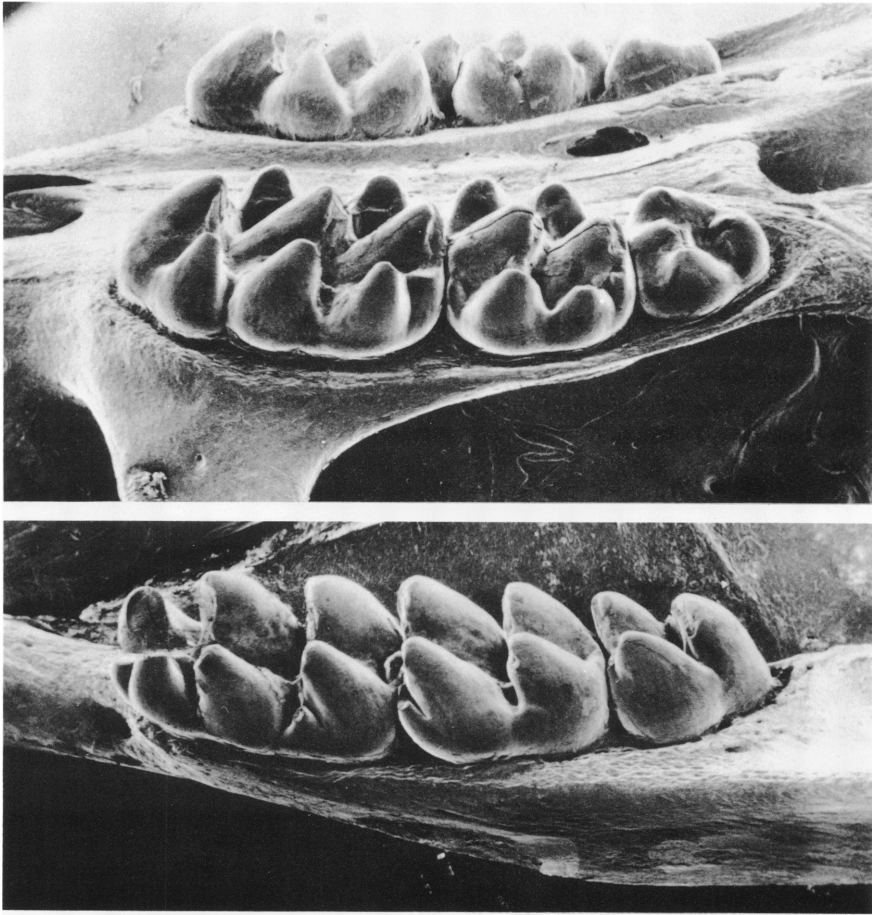


FIG. 54. *Melasmothrix naso*. Oblique views of right maxillary (top) and left mandibular (bottom) molar rows of AMNH 225094. Compare this high cuspidate topography with that of *Archboldomys* in figure 55.

lutely and relatively much narrower and more delicate, as are the entire zygomatic arches. In the alisphenoid region, *M. naso* lacks a lateral alisphenoid strut, with the attendant coalescence of the masticatory-buccinator foramina and the foramen ovale accessorius. The strut and foramina are present in *A. luzonensis* (fig. 23). The squamosal above the back part of each bulla is complete in *M. naso*, not notched or divided by an enlarged squamoso-mastoid foramen as is the configuration in *A. luzonensis* (fig. 24). The mastoid is similar in shape and degree of inflation in the two species but there is a large fenestra in each mastoid of *M. naso* (fig. 45); each mastoid in *A. luzonensis* does not have such

a fenestra. The palatal bridge is relatively thinner in *M. naso*. Its surface anterior to the posterior palatine foramina is perforated by one or two pairs of small vacuities. The posterior palatine foramina are concealed beneath bony shelves opposite the junction of the second and third molars. In *A. luzonensis*, by contrast, the bony palate is thicker, without vacuities, the posterior palatine foramina are not concealed, and they are opposite the anterior portions of the second molars. In the orbit of *M. naso*, each dorsal palatine foramen is separate and posterior to the sphenopalatine foramen; the two are coalesced in *A. luzonensis*, a configuration similar to that in *Crunomys* (fig. 14). The

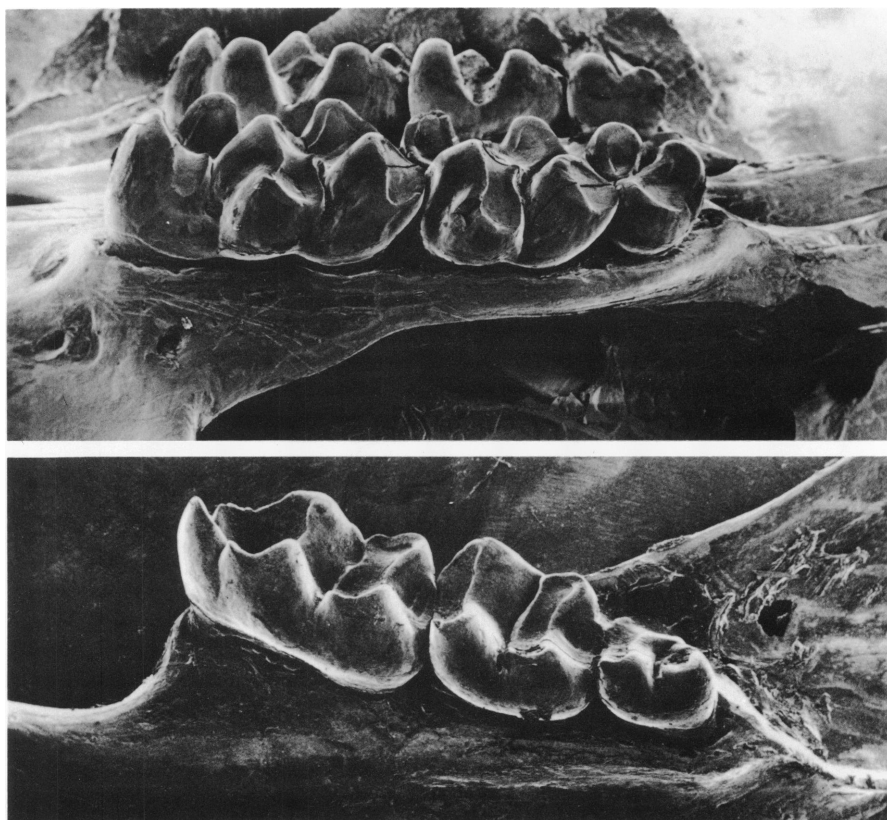


FIG. 55. *Archboldomys luzonensis*. Oblique views of right maxillary (top) and mandibular (bottom) molar rows of the holotype, FMNH 95122. Compare with figure 54. Note high cusp margins, especially those on anterior half of first lower molar.

bullae in *M. naso* are more inflated and larger relative to the cranium than are the bullae in *A. luzonensis*. In addition to being much more slender and delicate, each dentary of *M. naso* differs from that in *A. luzonensis* by having smaller and fragile coronoid and angular processes relative to body of the dentary, and a more elongate condyloid process.

Small incisors relative to size of cranium and mandible and large molars relative to areas of palate and dentaries are typical in *A. luzonensis* and *M. naso*. The upper molars are three-rooted and the lowers two-rooted in both species. Surfaces of all molars are gleaming white, third upper and lower molars are small relative to the other teeth in each row, and the molars abut against each other to about the same degree in both species.

Close dental similarities end with these features. The upper and lower incisors of *M.*

naso are relatively smaller and more delicate compared with those in *A. luzonensis*. The anterolateral surfaces of the uppers are beveled in *M. naso*, not angular as in *A. luzonensis*.

Occlusal surfaces of the molars in *M. naso* are more complex than are those in *A. luzonensis*. The molars of *A. luzonensis* have high cusps that are broadly connected to form a tubercular-like laminar hypsodonty. *Melasmothrix naso* has high cusps also but they are discrete high cones and form a definite tubercular topography because the cusps are barely connected (figs. 54, 55, and 56). Cusps t3 and t9 on each first and second upper molar in *M. naso* are large and a prominent part of the chewing surfaces. Such cusps are absent in *A. luzonensis*. There is a posterior cingulum, prominent and cusplike, at the back of each first and second upper molar in *M. naso*,

a structure that is absent from the molar rows in *A. luzonensis*. Some specimens of *M. naso* have a small cusp t1bis between cusps t1 and t2 and a cusp t2bis between cusps t2 and t3 on each first upper molar. Such accessory cusps are not present in the holotype of *A. luzonensis*. Each third upper molar of *M. naso* has more cusps and a more complex occlusal surface than the simple chewing area of that tooth in *A. luzonensis*.

The cuspidate occlusal surfaces on the upper molars of *M. naso* are reflected in its lower molars, which are a series of high cones down each toothrow. The configuration contrasts with the laminar and basined occlusal patterns in *A. luzonensis* (figs. 54, 55, and 56). The Philippine shrew rat also lacks posterior labial and lingual cusplets, structures that are frequently found in *M. naso*.

Melasmothrix naso has been found only at high altitudes in moss forest. The rat moves about quickly and nervously. It is active during the day, especially in early morning and late afternoon. It eats mostly earthworms and tiny dipteran larvae, all dug out of wet moss, leaf litter, and damp soft soil. *Archboldomys luzonensis* is also known only from a high altitude and it may have habits similar to those of *M. naso*. *Archboldomys* superficially resembles *M. naso* in certain features of the skin, skull, and teeth, characters reflecting adaptations associated with rats living in cool, wet forests and feeding on soft-bodied invertebrates.

The similarities in the two species do not indicate close phylogenetic relationship. The cranium and dentaries of *A. luzonensis* are not as elongate and highly specialized as are those elements in *M. naso*; the molars are strikingly dissimilar. Shapes of molars and their cusp patterns in *Archboldomys* tie that genus to *Crunomys*, molar features in *Melasmothrix* link it with the Sulawesi *Tateomys*. On Luzon Island, *A. luzonensis* may be an ecological counterpart of *M. naso* but not a phylogenetic representative.

ARCHBOLDOMYS AND CRUNOMYS

Archboldomys is distinguished from *Crunomys* by the many features enumerated in

the diagnosis of the former and discussed in the comparisons between *A. luzonensis* and the two *Crunomys*, *C. melanius* and *C. celebensis*. The characters of *A. luzonensis* that indicate adaptations to a montane habitat and shrew-rat diet (long and dense pelage, a tapered rostrum that is long and slender, long incisive foramina, configuration of the zygomatic plates and their position relative to the first upper molars, a short bony tube anterior to upper incisor faces, upturned nasal tips, molars with tubercular-like hypsodonty, slender and gracile dentaries) are one set that separates *Archboldomys* from *Crunomys*. An alisphenoid strut, large squamoso-mastoid vacuity dividing each squamosal bone into two parts, large somewhat inflated bullae, shapes of the pterygoid plates and the carotid arterial pattern they reflect that is shown in figures 30 and 31 form the other set distinguishing the two genera.

Despite this suite of differences, the shapes and occlusal outlines of the molars, their size relative to each other in each row, and their simple and closely similar occlusal patterns clearly indicate close relationship between *Archboldomys* and *Crunomys*. Most of the shared diagnostic dental features are specializations and not primitive traits (see the discussion in Musser, 1981a): relatively very small third molars; cusps broadly joined, not discrete cones; cusp t3 on each first upper molar absent or barely evident, usually absent from each second upper molar; cusp t9 on first upper molar absent or broadly joined to cusp t8, absent from second molar; no posterior cingulum on either the first or second upper molars; only three cusps on each third upper molar; anterior half of each first lower molar a basined structure representing coalescence of anterolabial and anterolingual cusps with first row of cusps behind; no or very few labial cusplets; no anterolabial cusps on second and third molars; posterior cingulum on each first and second molar indistinct and partially merged with back of tooth.

THE SPECIES OF CRUNOMYS

The three specimens of Sulawesi *Crunomys* are distinguished from the Philippine

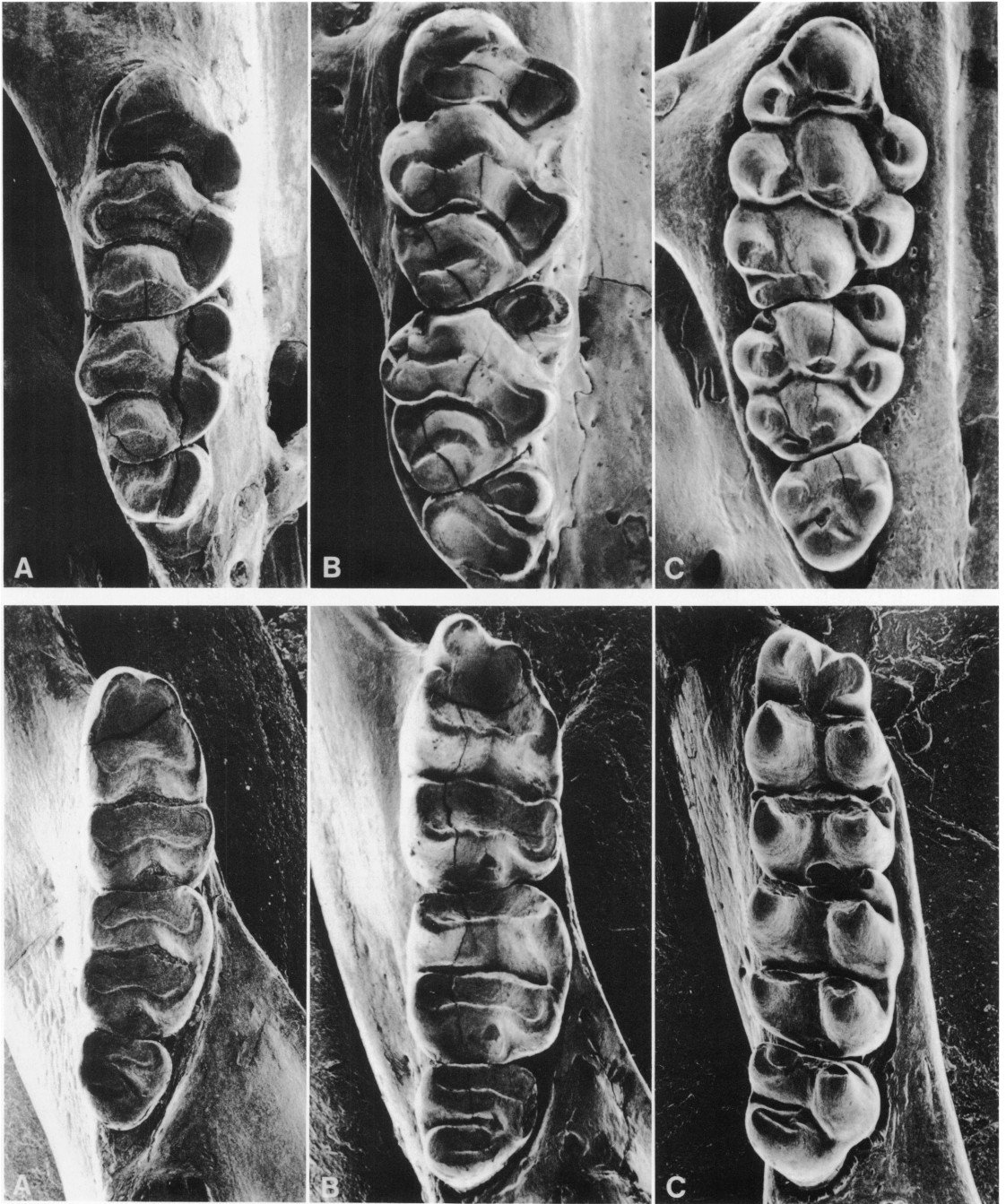


FIG. 56. Occlusal views of right maxillary (top) and mandibular (bottom) molar rows. The simple patterns of *Crunomys melanius* (A; AMNH 242102) and *Archboldomys luzonensis* (B; FMNH 95122) are contrasted with the complex and highly cuspidate patterns in *Melasmothrix naso* (C; AMNH 225110). See text for further information.

samples of that genus by the characters enumerated in the diagnosis of *C. celebensis*. The Sulawesi species is morphologically very distinctive; the magnitude of differences between it and any one of the Philippine forms is greater than that found among the insular samples of *Crunomys* from the Philippines. Early in my study, I examined the specimens carefully to determine if the characters in the Sulawesi sample were only *Crunomys*-like and represented convergent resemblance. But *celebensis* has a body shaped like that of *Crunomys*; the cranium, mandible, incisors, and molars look like those of *Crunomys*. Whether the cusp patterns are closely similar is not known because the teeth of *celebensis* are so worn. The three Sulawesi specimens are clearly morphological counterparts of the Philippine *Crunomys* and are unlike any other genus of known murid, including anything that occurs on Sulawesi.

Many of the traits shared by the Sulawesi and Philippine rats are primitive. These are small size, a moderately long rostrum relative to cranial length, smooth dorsolateral margins of interorbital and postorbital regions, round smooth braincase, very short incisive foramina, zygomatic plates set anterior to the molar rows, bony palate ending anterior to the backs of the molar rows, position of each posterior palatine foramen opposite the back of each first molar or at junction of first and second molars, sphenopalatine foramen coalesced with dorsal palatine foramen in the orbit, slitlike sphenopalatine vacuities in mesopterygoid fossa, pterygoid fossae complete and not breached by sphenopterygoid openings, small round auditory bullae with moderately long bony eustachian tubes, squamoso-mastoid foramen small and confined to suture between squamosal and mastoid, squamosal bone dorsal to each bullae complete and undivided, upper molars each anchored by three roots, and each lower molar with two roots. Although specialized for a certain mode of living, *Crunomys* is structurally a primitive small-bodied rat compared with many of the genera native to the Philippines and Sulawesi.

In addition to the basic shapes of body and skull, there are some derived traits that unite the two sets of species. These are a tail much shorter than length of head and body, dark

coloration, possibly (the Philippine species) and apparently (*C. celebensis*) diurnal, an open alisphenoid canal not bounded by part of the alisphenoid bone and the attendant coalescence of adjacent foramina, a distinctive configuration of each pterygoid plate and the carotid arterial pattern that shape indicates (see figs. 30 and 31), the shapes and occlusal outlines of the molars, the size of each molar relative to one another in each row, and the basic cusp patterns.

A few of the shared derived traits also occur in the native Sulawesi murids (relatively short tail, dark coloration, diurnality, open alisphenoid canals, and relative molar sizes). The conformation of the pterygoid plates in their posterior one-third, nature of the stapedial foramina, and the basicranial arterial pattern (stapedial foramen absent or tiny, minute stapedial artery serving only the otic region, intermaxillary artery branching from internal carotid after the latter enters the cranial cavity; see fig. 30 and the diagram in fig. 31) in *C. celebensis* is unlike that in any native murid known from Sulawesi. All of those species have pterygoid plates, stapedial foramina, and arterial patterns resembling the configuration in *Archboldomys* (stapedial foramen large, large stapedial artery emerging from middle lacerate foramen as internal maxillary artery; figs. 30 and 31). The pterygoid and arterial pattern in *Crunomys* does occur in native Philippine species. All but one of the species of *Apomys*, for example, has the configuration (Musser, 1982) and the larger-bodied species of *Crateromys*, *Batomys*, and *Carpomys* have a variety of the pattern (unpublished ms.).

The Sulawesi *Crunomys* is clearly set apart from the Philippine samples of that genus by many distinctive characters. Such clear and sharp distinctions do not occur among the Philippine forms of *Crunomys*. There are only four specimens: one from Luzon, one from Leyte, and two from Mindanao. The specimen from Luzon is the palest in coloration and the smallest in body size; the examples from Mindanao are the darkest and intermediate in body size between the Luzon and Leyte specimens; the Leyte example is the largest of the group and is pigmented like the specimens from Mindanao. The primary cranial, mandibular, and dental

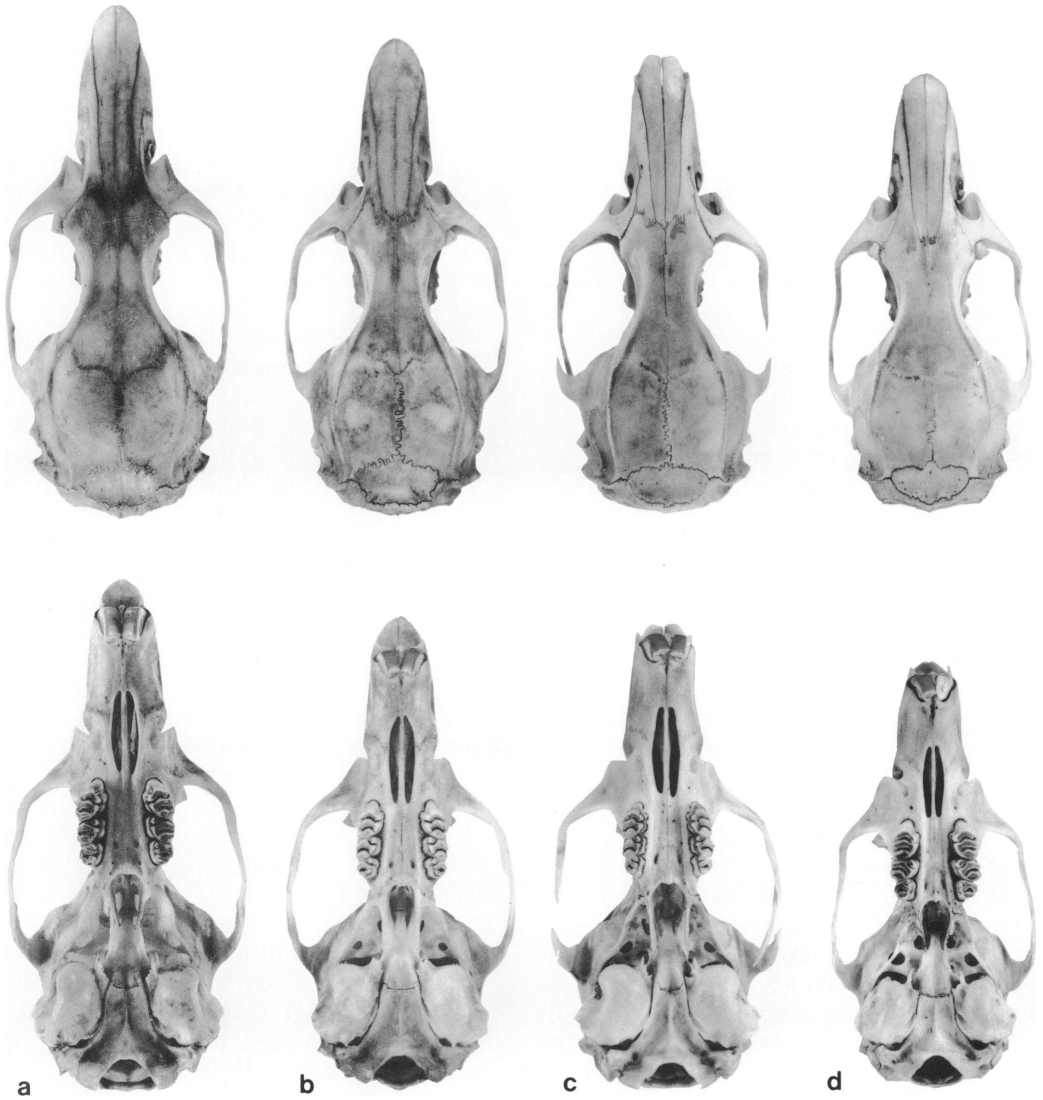


FIG. 57. Dorsal (top) and ventral (bottom) views of crania from adult *Bullimus*: a, *rabori* (AMNH 207557) from western Mindanao Island; b, *bagobus* (AMNH 203316) from eastern Mindanao; c, *barkeri* (USNM 282149) from Samar Island; d, *luzonicus* (USNM 151505) from Luzon Island. Approximately natural size.

differences among the specimens involve size: the Luzon specimen has the smallest skull, the example from Leyte the largest, and those from Mindanao fall between the extremes. Because the samples are so small, because each comes from a different island, because each specimen from a particular island can be told apart from the other specimens by features of skins and skulls, I hypothesize that each island sample represents a different

species: *C. fallax* from Luzon, *C. rabori* from Leyte, and *C. melanius* from Mindanao. Among the three, *C. rabori*, and *C. melanius* are morphologically more similar to each other than either is to *C. fallax*.

The tie between the samples from Leyte and Mindanao parallels that in *Apomys insignis* from Mindanao and *A. microdon* from Leyte; those species are morphologically closer to each other than to any other species

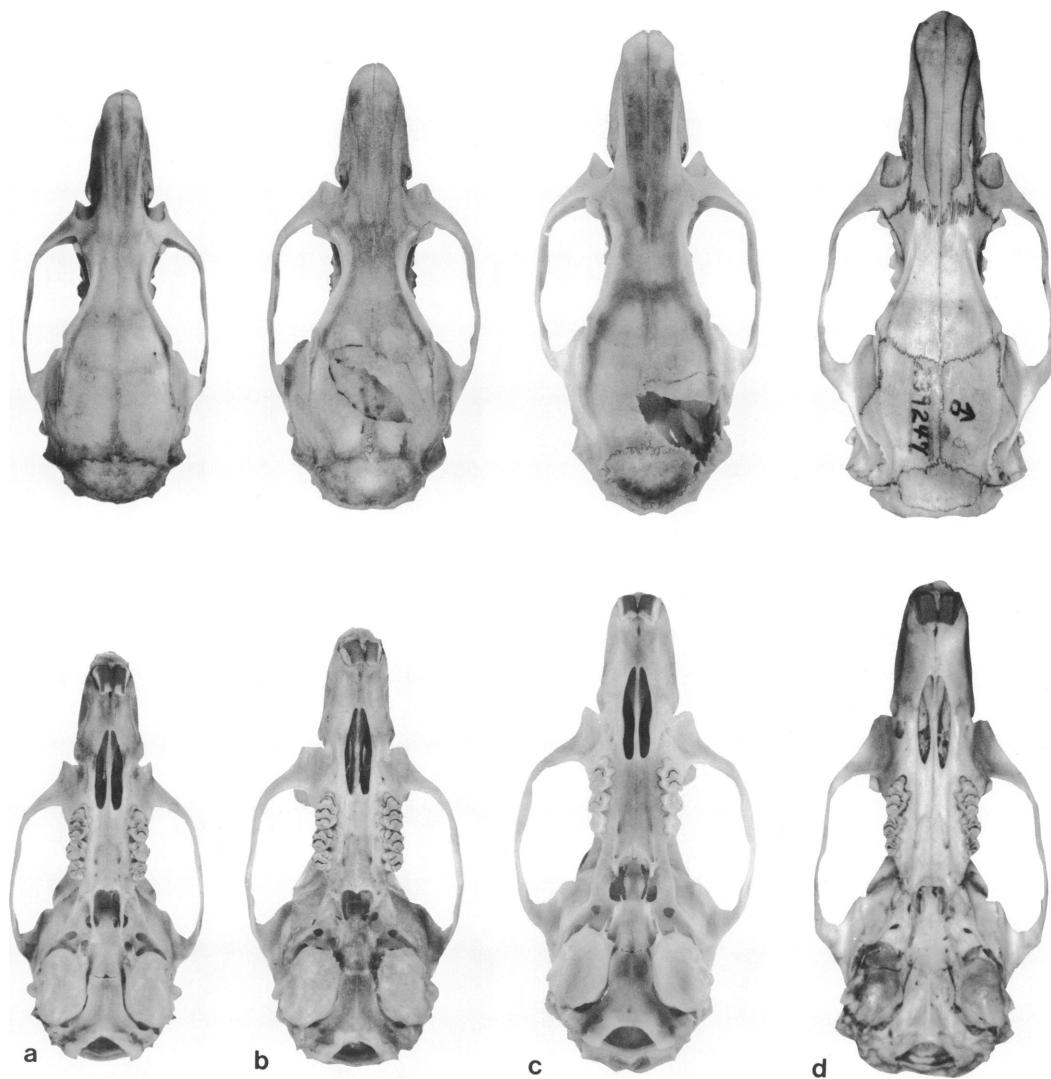


FIG. 58. Dorsal (top) and ventral (bottom) views of crania from adult *Rattus everetti*: a, AMNH 250037 from Luzon Island; b, AMNH 203315 from Mindanao Island; c, USNM 467210 from Dinagat Island; d, USNM 239247 from Ticao Island. Approximately natural size.

of *Apomys* (Musser, 1982). The insular and morphological pattern of *Crunomys* also partly reflects that present in two other murids native to the Philippine Islands: *Bullimus* and *Rattus*.

A long nose, large and bulky body, stubby and short tail, brown upperparts, grayish white or white underparts, long and narrow hind feet, coarse and short pelage, a large conspicuous midventral cutaneous glandular area on males, and four pairs of mammae are

some characteristic features of specimens of *Bullimus* (Mearns, 1905; Sanborn, 1952; Rabor, 1955). Found in both lowlands and mountains, the rats are terrestrial and apparently utilize burrows under thick vegetation (Rabor, 1955). Specimens have been collected from the islands of Luzon, Samar, Calicoan, Leyte, Dinagat, Mindanao, and Bohol (my unpublished records). The scientific names *luzonicus*, *rabori*, *bagobus*, and *barkeri* have been applied to samples from the

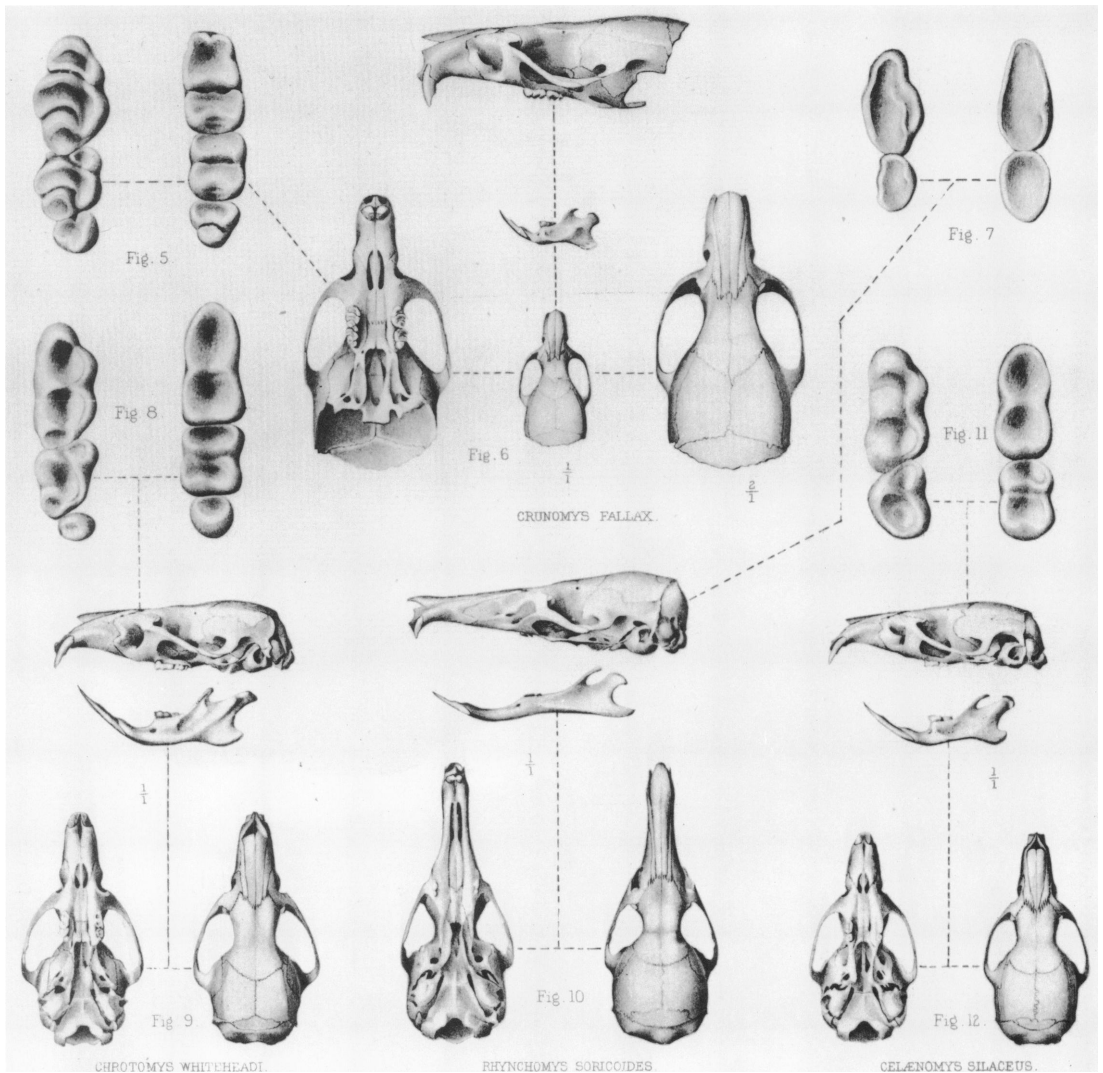


FIG. 59. Reproduction of Plate 35 from Thomas (1898). *Crunomys fallax* from Luzon is contrasted with the large-bodied shrew rats from that island: *Chrotomys whiteheadi*, *Celaenomys silaceus*, and *Rhynchomys soricoides*. See text for discussion.

islands. Three of the names (*luzonicus*, *rabori*, and *bagobus*) are currently used to indicate three species but there is no reliable estimate of how many species actually exist because the genus has never been taxonomically revised and the extent of individual, secondary sexual, geographic, and altitudinal variations in features of skins, skulls, and teeth is unknown.

The most conspicuous variation among samples of *Bullimus* involves body size, which

is reflected by greatest length of skull. The smallest rats are from Luzon (*luzonicus*) and the largest occur in western Mindanao (*rabori*); examples of these size categories are shown in figure 57. Whether variation among the samples represents morphologically distinctive species or that within one species spread throughout the archipelago is difficult to determine with the kinds of data now available for analyses.

A similar distributional pattern and taxo-

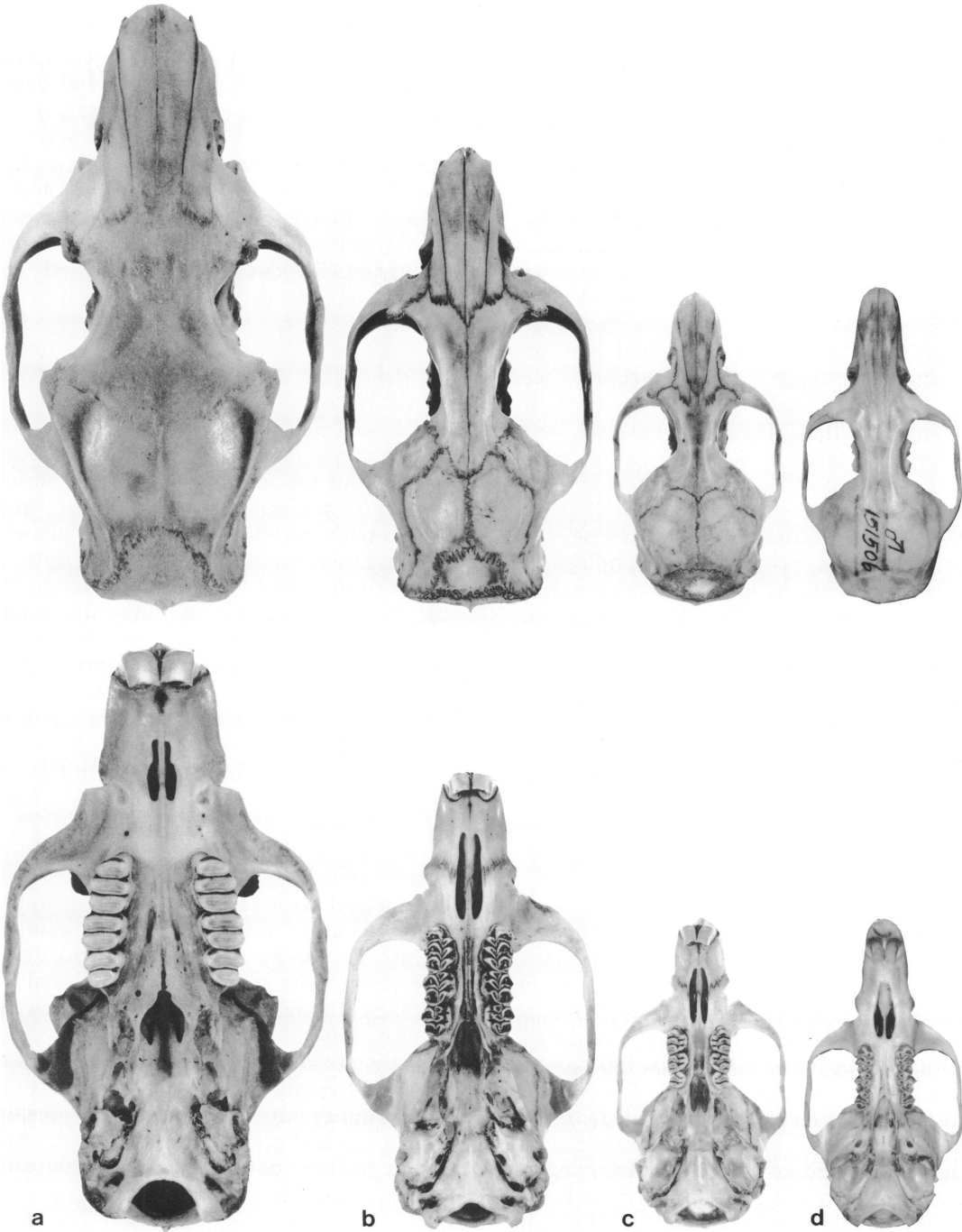


FIG. 60. Dorsal (top) and ventral (bottom) views of adult crania. All species are from Luzon Island: a, *Phloeomys cumingi* (USNM 151519); b, *Crateromys schadenbergi* (USNM 102546); c, *Carpomys melanurus* (USNM 102549); d, *Batomys dentatus* (USNM 151506). Approximately natural size.

nomic problem exists for what is now called *Rattus everetti*. This is a large-bodied rat with long fur and a tail much longer than the combined lengths of head and body. Specimens are from the islands of Luzon, Mindoro, Samar, Calicoan, Leyte, Ticao, Dinagat, Siargao, Camiguin, Mindanao, Bohol, and Basilan (my records based on examination of specimens in museum collections). Four scientific names apply to the samples: *everetti*, *albigularis*, *gala*, and *tyrannus*. Primary variation among the island samples involves body size and texture of pelage. Specimens from Luzon are the smallest and have the softest pelage; those from Dinagat and Ticao are the largest and have the coarsest fur. Examples of the different size classes based on cranial length are shown in figure 58. Do the morphological differences point to different species living on different islands? Do the differences reflect instead variation within one widespread species in which morphologically distinct populations are isolated on various islands throughout the archipelago? There are no answers yet.

Do the specimens of Philippine *Crunomys* really represent three species as I hypothesize or do the samples come from one species in which part of the morphological variation results from past isolation on different islands? To answer these questions we need more specimens from single localities and from many different islands, as well as different kinds of data.

The phylogenetic position of *Crunomys* is obscure. When Thomas described the genus, he noted (1898, pp. 393–394) that “This genus is most interesting from an evolutionary point of view, for it adds another to the links that connect the aberrant *Hydromys* with the true Murinae, and is indeed the last link needed. . . . Like all annectant genera, *Crunomys* is most difficult to place satisfactorily in the system, and it is only with much hesitation that I have included it in the Hydromyinae, a position which will have to be revised when specimens showing the unworn dentition, the

mammary formula, and other characters are available for examination.”

Thomas included the Philippine *Chrotomys* and *Celaenomys* within the Hydromyinae. Those two genera and *Crunomys* do share some features (fig. 59). By 1969, Misonne considered the Hydromyinae to be (p. 159) “a distinct subfamily of the Muridae” and to include “the New Guinea-Australian genera as well as the Philippine *Chrotomys*-*Celaenomys* and *Rhynchomys*.” He excluded *Crunomys* from this group and placed it in the Murinae.

As part of my studies on Indo-Australian murids, I have been gathering data to test several hypotheses of relationships. One is that the old native rodents of the Philippine Islands may represent an adaptive radiation in which all the members are more closely related to each other than to rats and mice on the Asian mainland to the west, Sulawesi and the Lesser Sunda Islands to the south, or the Australian and New Guinea area to the east. In this scheme, *Crunomys* would be part of a group which includes shrew rats of small and large body sizes (*Archboldomys*, *Chrotomys*, *Celaenomys*, and *Rhynchomys*; fig. 59), terrestrial rats (*Batomys* and *Apomys*; fig. 60; Musser, 1982), and arboreal animals (*Crateromys*, *Carpomys*, *Phloeomys*, and *Anonymomys*; fig. 60; Musser, 1981a; Musser and Gordon, 1981).

That the Philippine fauna may be more closely related to the native rats of the New Guinea and Australian regions than to any other group of rats and mice is another hypothesis being tested. Confirming or repeating results from preliminary analyses that the endemic murids of Sulawesi may be more closely related to those on the Sunda Shelf than to any group east of Borneo or Bali is a third hypothesis. This testing is part of a broad inquiry into phylogenetic relationships among rats and mice living in the Indo-Australian regions, one of the most interesting aspects of murid biogeography.

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