

RESULTS OF THE ARCHBOLD
EXPEDITIONS. NO. 105.
NOTES ON SYSTEMATICS OF
INDO-MALAYAN MURID RODENTS,
AND DESCRIPTIONS OF NEW
GENERA AND SPECIES FROM
CEYLON, SULAWESI, AND
THE PHILIPPINES

GUY G. MUSSER

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 168 : ARTICLE 3 NEW YORK : 1981

RESULTS OF THE ARCHBOLD
EXPEDITIONS. NO. 105.
NOTES ON SYSTEMATICS OF
INDO-MALAYAN MURID RODENTS, AND
DESCRIPTIONS OF NEW GENERA AND
SPECIES FROM CEYLON, SULAWESI,
AND THE PHILIPPINES

GUY G. MUSSER
*Archbold Curator, Department of Mammalogy
American Museum of Natural History*

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 168 : ARTICLE 3
NEW YORK : 1981

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 168, article 3, pages 225–334, figures 1–51, tables 1–12

Issued June 19, 1981

Price: \$7.90 a copy

ISSN 0003-0090

CONTENTS

Abstract	229
Introduction	229
Abbreviations and Methods	229
Acknowledgments	231
Introduction to the Groups	231
The <i>niviventer</i> -Group	236
Genus <i>Niviventer</i> Marshall (1976)	236
The <i>sabanus</i> -Group	256
Genus <i>Leopoldamys</i> Ellerman (1947–1948)	256
The Ceylonese <i>ohiensis</i>	267
<i>Srilankamys</i> , New Genus	268
The <i>beccarii</i> -Group	274
<i>Margaretamys</i> , New Genus	275
The Mindoro Rat	300
<i>Anonymomys</i> , New Genus	300
Discussion	310
About <i>Lenothrix</i> , <i>Dacnomys</i> , <i>Chiromyscus</i> , and <i>Maxomys</i>	310
Characters: Primitive and Derived States	318
Notes on Relationships	321
Conclusions	329
Literature Cited	330

ABSTRACT

Four groups of murid rodents that were once included in *Rattus* are taken out of that genus: the *Rattus niviventer*-group from Southeast Asia and the Sunda Shelf, which is placed in the genus *Niviventer*; the *Rattus sabanus*-group, which comprises the genus *Leopoldamys*, also occurring in Southeast Asia, the Sunda Shelf, and the Mentawai Islands; *Rattus ohiensis* from Ceylon, which is placed in *Srilankamys*, new genus; and the *Rattus beccarii*-group of Sulawesi for which the new genus, *Margaretamys*, is proposed not

only for *beccarii* but also for the new species *M. elegans* and *M. parvus*. *Anonymomys mindorensis*, new genus and species, is proposed for an arboreal rat from Mindoro in the Philippines. The genera are diagnosed, described, compared with others, and their contents discussed. Their possible relationships to *Lenothrix*, *Dacnomys*, *Chiromyiscus*, and *Maxomys*, groups that were either once considered to be part of *Rattus* or at least *Rattus*-like, are discussed in the context of their affinities relative to *Rattus*.

INTRODUCTION

I define here the limits of five genera of murid rodents, two from the Sunda Shelf and Southeast Asia, one from Ceylon, one from Sulawesi, and the last from the Philippine Islands; all the groups were once considered to be part of the genus *Rattus*. I had originally intended only to propose new genera and species for arboreal rats on Sulawesi and the Philippines but could not clearly define those genera without reference to groups in Asia west of Wallace's Line, clusters of species that have long been included in *Rattus* but do not belong there. Sorting out these five assemblages from *Rattus* is a small part of a larger inquiry into defining limits of species and genera of Indo-Australian murids with the intent to eventually analyze phylogenetic relationships among them.

The following discussions focus on results from basic alpha-taxonomic study. Possible relationships of the groups will be explored, particularly relative to *Rattus*, but detailed phylogenetic analyses are not presented now. Information about natural history is omitted; that data, especially for the rats on Sulawesi, will be published separately.

ABBREVIATIONS AND METHODS

Material: Specimens that are the basis of this report are in collections of the American Museum of Natural History, New York (AMNH); the British Museum (Natural History), London, (BM); the Field Museum of Natural History, Chicago (FMNH); the Mu-

seum Zoologicum Bogoriense, Bogor (MZB); the Rijksmuseum van Natuurlijke Historie, Leiden; and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), Royal Ontario Museum (ROM).

Measurements: The skin, skull, and teeth are measured in millimeters. Values for total length, length of tail, length of hind foot (including claw), and length of ear are those recorded by collectors on labels attached to the skins. I subtracted length of tail from total length to obtain length of head and body.

Cranial and dental measurements were taken with either Anderson's craniometer attached to a Wild M5 Stereomicroscope or with dial calipers graduated to tenths of millimeters. Limits of the measurements are illustrated and defined elsewhere (Musser, 1970, 1979).

Teeth: Occlusal structures of murid teeth have received various names (Miller, 1912; Misonne, 1969; Michaux, 1971; van de Weerd, 1976; Jacobs, 1978, for example). The nomenclature I use for positions of cusps (also called cones or tubercles) on upper molars is a slight modification of the numbering system developed by Miller (1912) and diagrammed in figure 1. There are 10 primary cusps on the first molar of a species such as *Lenothrix canus*, arranged in three rows, with three cusps to each row, and the tenth cusp by itself at the back of the tooth. The numbering begins with the lingual cusp of the first row and extends across to

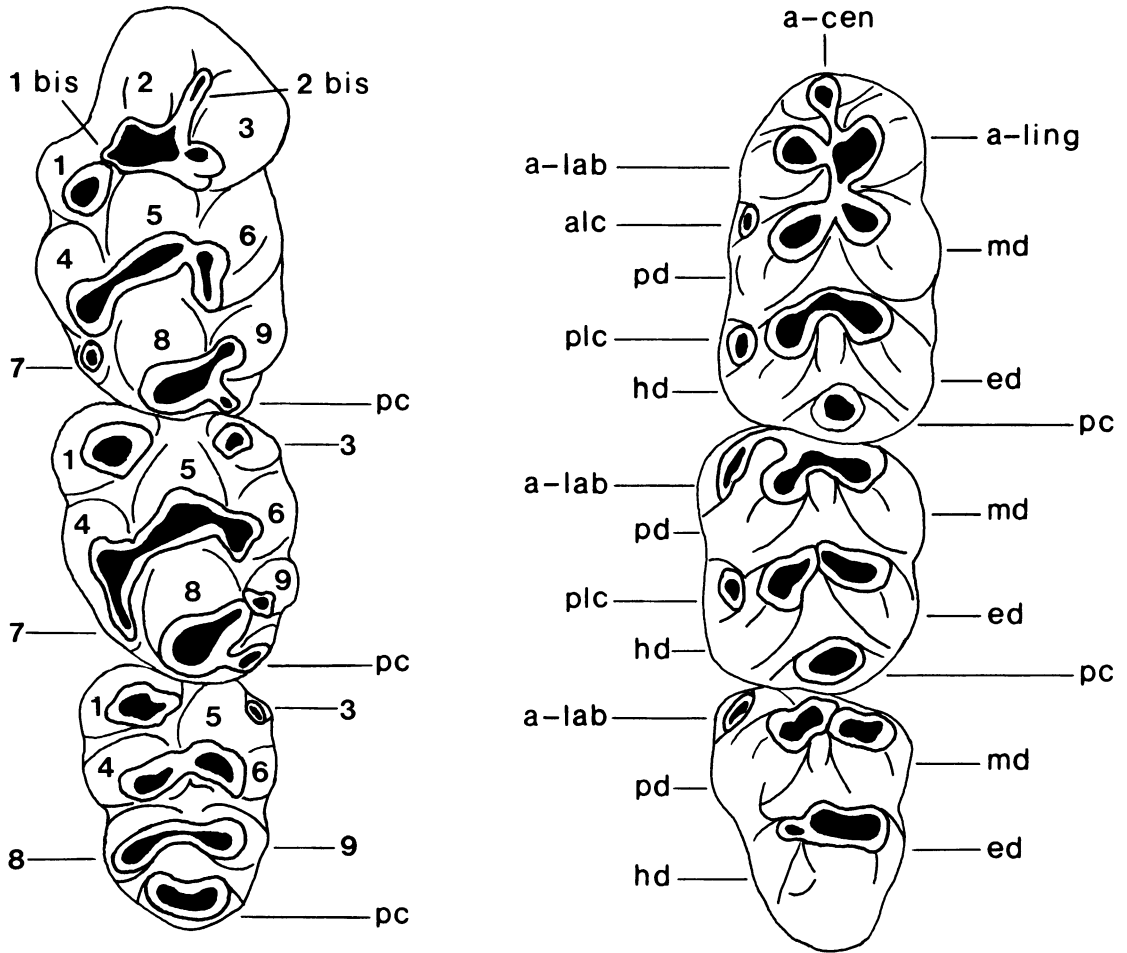


FIG. 1. Nomenclature of dental structures using right upper and lower molars of *Lenothrix canus*. Upper molars: cusps are numbered according to Miller's (1912) scheme and are referred to in the text with the prefix t; pc, posterior cingulum. Lower molars: a-cen, anteroventral cusp; a-lab, anterolabial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

the labial cusp (t1, t2, t3), then continues with the lingual cusp of the second row across to the labial side (t4, t5, t6), and across the third row beginning at the lingual cusp again (t7, t8, t9); the single posterior cusp is the posterior cingulum (which has received several different designations; see Jacobs, 1978). The same numbering sequence is followed for cusps on the second and third molars. In some species, *L. canus*, for example, there is a small cusp between cusps

t1 and t2 (t1bis) and between t2 and t3 (t2bis) on each first molar and a small accessory cusp behind cusp t6 on the first and second molars.

My nomenclature for the lower teeth (fig. 1) is, with slight modifications, that used by van de Weerd (1976, p. 44). Each first lower molar has an occlusal surface formed of three rows of large cusps (cones or tubercles), two in each row, sometimes a small anterior medial cusp at the front of the tooth,

and always a posterior cingulum. Cusplets (conulids) occur along the labial margin and occasionally along the lingual edge. An anterolabial cusp, two rows of cusps, a posterior cingulum, and a cusplet form the surface of the second molar. An anterolabial cusp and two rows of cusps are present on the third molar.

Chromosomes: Some new karyotypes are described. I prepared them in the field from chromosomes of bone marrow, processed by employing colchicine, hypotonic citrate, and flame drying that was outlined by Patton (1967).

I use four terms to describe the shape of each chromosome relative to position of the centromere: **METACENTRIC** (the chromosome is biarmed, one arm being about the same length as the other); **SUBMETACENTRIC** (one arm is shorter than the other, about a third of its length); **SUBTELOCENTRIC** (one arm is very short relative to the long arm on the other side of the centromere); and **TELOCENTRIC** (the centromere is at the tip of the chromosome or near enough that any portion on the other side of the centromere is so short as to be indistinguishable or nearly so). The range of variation of the configurations that I recognized within each category is illustrated in figure 2, which provides a visual guide to my definition of metacentric, submetacentric, subtelocentric, and telocentric, the terms I use throughout the present report.

ACKNOWLEDGMENTS

The curators in charge of collections in the institutions listed previously allowed me to study specimens under their care and to borrow material. The artwork is by Ms. Fran

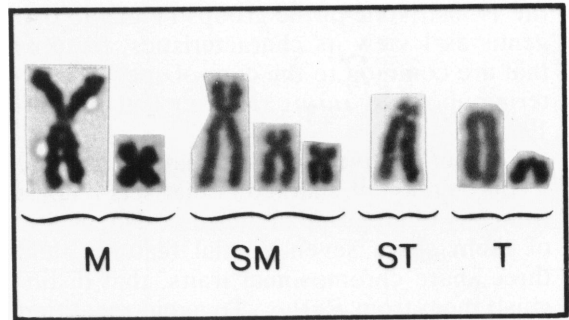


FIG. 2. My visual definition of metacentric (M), submetacentric (SM), subtelocentric (ST), and telocentric (T) chromosomes, based on relative position of the centromere. See text for discussion.

Stiles, Ms. Patricia Wynne, Ms. Christine Miller, and Mr. Helmut Sommer. Photographs were made by either Mr. Robert E. Logan, Mr. Peter Goldberg, or Mr. Arthur Singer. Mr. Robert J. Koestler is responsible for the scanning electron work; Mr. Richard Sheryll developed and printed the micrographs. Dr. Charles J. Cole taught me the techniques required to obtain chromosome spreads in the field, generously allowed me to use equipment and supplies in his laboratory, and guided me through the various interpretations involved with each karyotype; the chromosomal spreads were analyzed and photographed by Ms. Shirley Chiu and prepared for publication by Ms. Soula Priovolos. Mrs. Frances A. Hufty of Archbold Expeditions Inc. has continued her unselfish support of my research. Money for work in Indonesia came from the Celebes Fund of the American Museum of Natural History; I was sponsored in that country by the Lembaga Ilmu Pengetahuan Indonesia and the Museum Zoologicum Bogoriense.

INTRODUCTION TO THE GROUPS

The *niviventer*-group, the *sabanus*-group, the Ceylonese *ohiensis*, the Sulawesian *becarii*-group, and a new species from the island of Mindoro in the Philippines form the

clusters I diagnose and characterize. The first four have long been considered as part of the genus *Rattus*, the last one was hidden in a museum misidentified as *Rattus* since

the 1950s. None of the groups belong in that genus as I view its characteristics, features that are common to the core of species clustering about *R. rattus* (Musser and Boeadi, 1980).

Each of the five groups is characterized by a combination of characters that sets it apart from any other group of murids. Also, all five of them share seven cranial features, and three share chromosomal traits, that distinguish them from *Rattus*. To avoid repetition in the accounts that follow, these characters are described below and contrasted with their counterparts in *Rattus*.

1. The configuration of the lateral walls of the cranium just above each pterygoid fossa is a diagnostic feature. Here the alisphenoid canal (which transmits the internal maxillary arteries and veins as well as the masticatory nerve) passes through the alisphenoid bone that forms the base of the cranium. In four of the murid groups and some individuals of the *beccarii*-cluster, the lateral wall of the canal is formed by either a narrow or wide diagonal strut of alisphenoid bone so the canal itself is hidden (fig. 3A). In front of the strut are the masticatory and buccinator foramina, usually coalesced into a single opening from which the masseteric and buccinator branches of the maxillary nerve emerge to course along the side of the braincase in the bottom of a shallow groove. Just posterior to the bony strut is a large foramen, which Wahlert (1974, p. 373) described this way: "I define as new the foramen ovale accessorius that is lateral to the foramen ovale and transmits the mandibular branch of the trigeminal nerve to the side of the head. It is present in forms having a substantial lateral pterygoid flange that reaches the auditory region."

In *Rattus* and most specimens in the *beccarii*-group, the lateral strutlike wall of the alisphenoid canal is absent. In side view the canal is open between two large, round vacuities: the one at the back is the foramen ovale (which transmits the mandibular branch of the trigeminal nerve); the one in front is the opening where the alisphenoid canal passes through the alisphenoid bone

into the sphenoidal fissure (and labeled the alisphenoid canal by Greene, 1935, p. 14). With the alisphenoid strut gone, there is no longer a foramen ovale accessorius or any masticatory-buccinator foramina; the nerves normally transmitted by the latter emerge directly from the dorsal part of the foramen ovale and pass up along the side of the braincase in the bottom of a shallow groove (fig. 3B).

2. In all five clusters, the squamosal roots of the zygomatic arches originate higher on sides of the braincase (defined here as the region from the temporal margin—marked by prominent ridges or inconspicuous beading—ventrad to the pterygoid ridge at the bottom of the alisphenoid area) and closer to the temporal ridges than they do in *Rattus*, usually because the top of the braincase dips down, instead of being nearly horizontal, or the braincase is flatter than it is in *Rattus* (figs. 4, 6, 18, and 38). The sides of the braincase between the temporal ridges and squamosal roots are reduced in area compared to what they are in *Rattus* of comparable size, which presumably indicates a smaller area for origin of the temporal musculature (fig. 4).

3. In all five groups, the posterior margin of the palatal bridge is situated either well before, at, or slightly beyond the backs of the third upper molars. In *Rattus*, the palatal bridge extends way past the molar rows, forming a long and wide shelf beyond the teeth (figs. 5, 6, 15, 18, 38, and 44).

4. The mesopterygoid fossa is as wide as the palatal bridge between the toothrows, or nearly so, in all five groups. Its walls are perforated by either short slits or short and narrow sphenopalatine vacuities. The mesopterygoid fossa is much narrower than the palatal bridge in *Rattus*, with walls that are breached by huge vacuities, so spacious that the anterior part of the basisphenoid and the presphenoid seem suspended in air (figs. 5, 6, 15, and 18).

5. In all five groups, the pterygoid fossa, which lies anterior to the foramen ovale, appears to be a solid, nearly flat surface that is sometimes pitted, and perforated only by

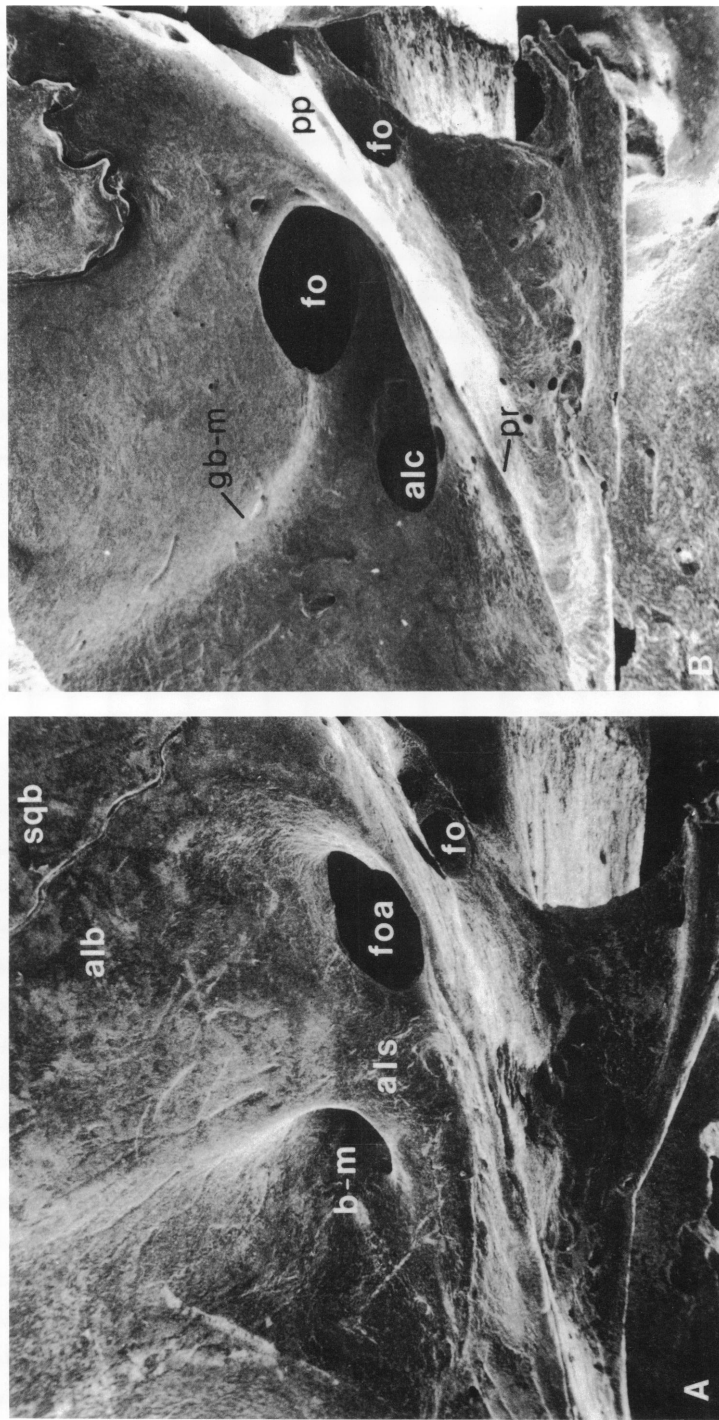


FIG. 3. The primitive (A) and derived (B) configurations of the alisphenoid region at the base of the cranium as represented by *Anonymomys* and *Margaretamys*, respectively. A: the alisphenoid canal (alc) is hidden behind a strut of alisphenoid bone (als) that also separates the buccinator-masticatory foramina (b-m) from the foramen ovale accessory (foa). B: The strut of alisphenoid bone is gone and the alisphenoid canal is exposed, as well as the foramen ovale (fo); the buccinator-masticatory foramina and the foramen ovale accessory are also gone. Other abbreviations: alb, alisphenoid bone; gb-m, the groove in which the masticatory and buccinator branches of the maxillary nerve course up alongside the braincase; pp, pterygoid plate; pr, pterygoid ridge; sqb, squamosal bone. See text for additional explanation.

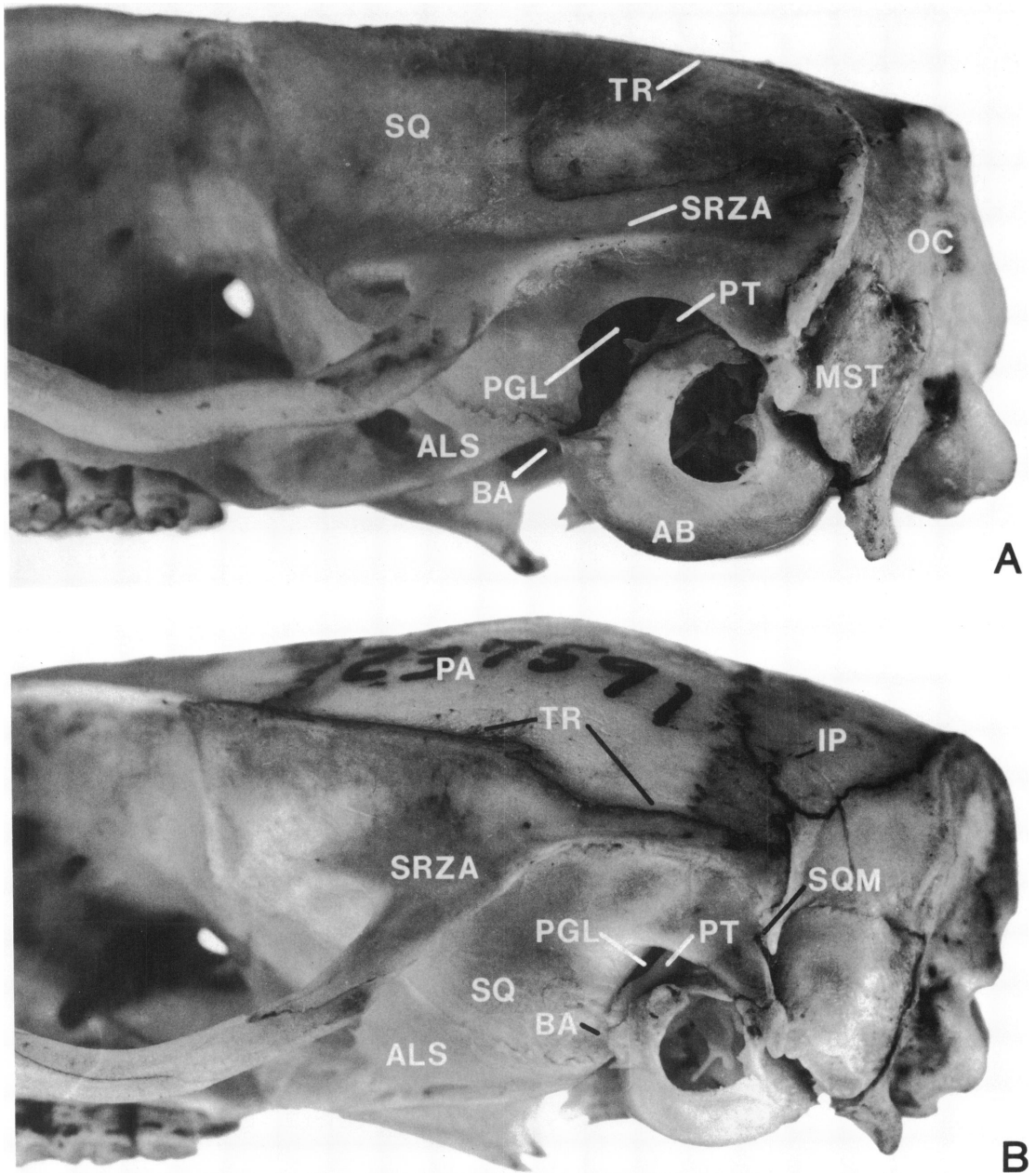


FIG. 4. Lateral views of adult crania ($\times 5$): A, *Rattus norvegicus* (AMNH 207554); B, *Leopoldamys neilli* (AMNH 237591). *Abbreviations:* AB, auditory bulla; ALS, alisphenoid; BA, attachment of bulla to squamosal and alisphenoid; IP, interparietal; MST, mastoid; OC, occipital; PA, parietal; PGL, post-glenoid foramen or vacuity; PT, periotic; SQ, squamosal; SQM, squamoso-mastoid foramen; SRZA, squamosal root of the zygomatic arch; TR, temporal ridge. See text for explanations and Wahlert (1974) for additional information about foramina.

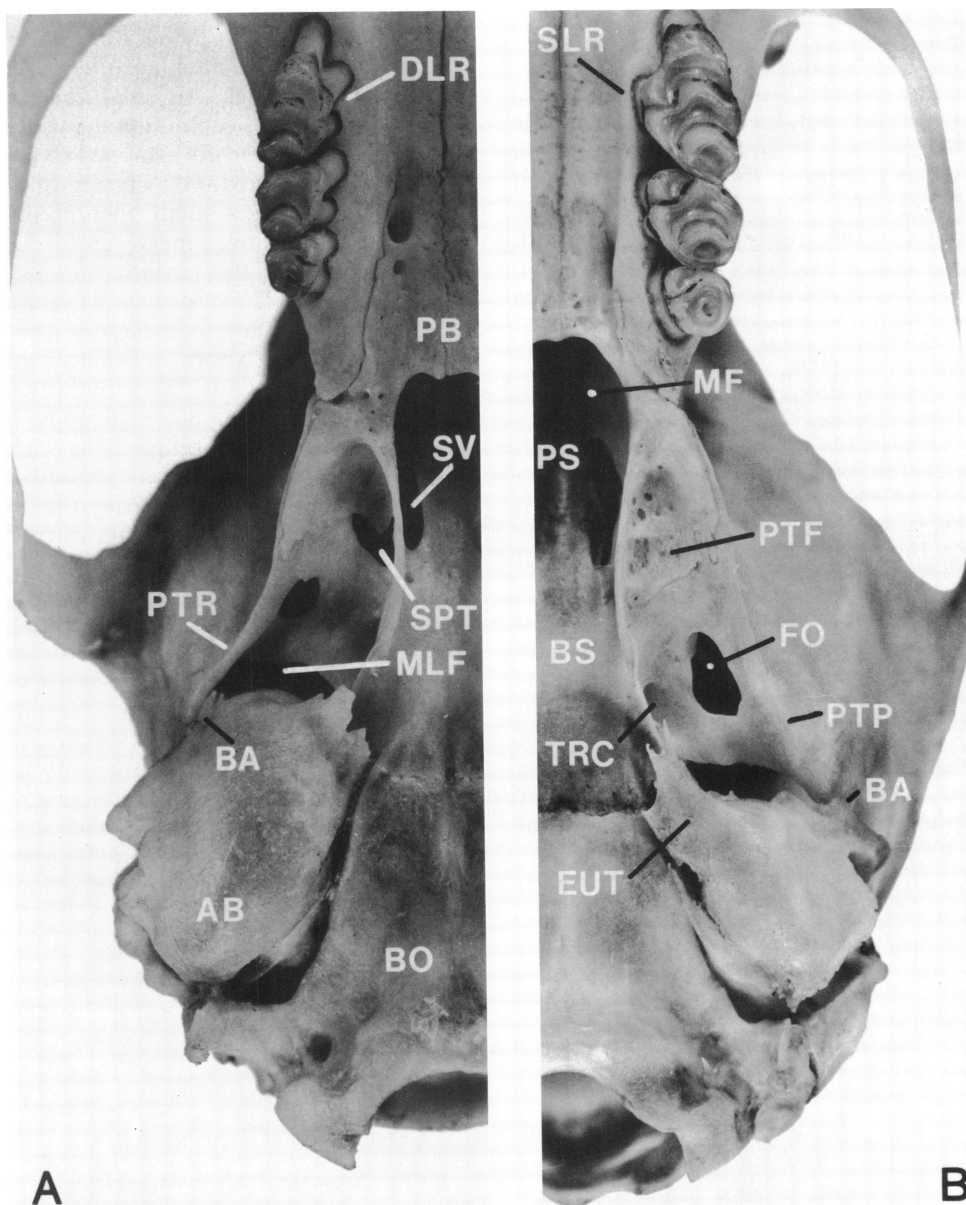


FIG. 5. Ventral views of adult crania ($\times 5$): A, *Rattus norvegicus* (AMNH 207554); B, *Leopoldamys neilli* (AMNH 237591). *Abbreviations:* AB, auditory bulla; BA, attachment of bulla; BO, basioccipital; BS, basisphenoid; DLR, divided lingual root of M^1 ; EUT, eustachian tube; FO, foramen ovale; MF, mesopterygoid fossa; MLF, middle lacerate foramen; PB, palatal bridge; PS, presphenoid; PTF, pterygoid fossa; PTP, pterygoid platform, which is used here to indicate a smooth or moundlike transition from the platform to side of the braincase; PTR, pterygoid ridge, which marks the edge of the platform in *Rattus norvegicus*; SLR, single lingual root of M^1 ; SPT, sphenopterygoid (or interpterygoid) canal or foramen; SV, sphenopalatine vacuity; TRC, transverse (or basisphenoid) canal. See text for explanations and Wahlert (1974) for additional information about foramina.

minute nutrient foramina or tiny spaces along the suture between the palatine and alisphenoid bones (figs. 5 and 18). The pterygoid platform lateral to the transverse canal and between the foramen ovale and middle lacerate foramen is smooth and nearly flat all the way out to the posterolateral margin of the platform in front of the anterolateral edge of the bulla. There the rim is either smooth or formed into a low and wide mound (PTP in fig. 5B). In *Rattus*, each pterygoid fossa is deeper, usually slanted in toward the midline of the cranium, its anterior two-thirds perforated by a large foramen at the palatine-alisphenoid suture. For Greene (1935, p. 16), the opening is the interpterygoid foramen, but it also fits Wahlert's (1974, p. 373) description of the sphenoptyergoid canal, which leads from the pterygoid fossa to the sphenoal fissure and transmits the internal maxillary artery. I have assumed the interpterygoid foramen and the sphenoptyergoid canal to be the same opening and use the terms interchangeably. The pterygoid platform between the foramen ovale and middle lacerate foramen is depressed; a high, thin ridge forms the posterolateral edge of the platform, extending from the posterior part of the pterygoid fossa to the anterolateral margin of the bulla (PTR in fig. 5A).

6. In all five groups, the bullae are small,

both absolutely and relative to size of the cranium, especially those in the *sabanus*-group; the bony eustachian tubes are prominent and long (figs. 4B, 5B, and 18). The anterior portion of each bulla, as well as part of the periotic, is firmly attached to the squamosal and the posterior corner of the alisphenoid; there is a small opening only, the postglenoid foramen, between the anterodorsal margin of the periotic and the squamosal (fig. 4B). The bullae are absolutely and relatively much larger in *Rattus*; the eustachian tubes are short and inconspicuous (figs. 4A, 5A, and 18). Each bulla is loosely attached to the squamosal, usually only at the posteroventral margins of the squamosal and alisphenoid; a wide postglenoid vacuity separates the squamosal from the anterior margin of the bullae and the anterodorsal edge of the periotic (fig. 4A).

7. Chromosomes have been analyzed for some species in the *niviventer*-group, the *sabanus*-group, and the *beccarii*-group. The 2N ranges from 42 to 46, and most clusters are characterized by two or three pairs of metacentrics, generally few submetacentrics or subtelocentrics, and the majority telocentric, including usually the X-chromosome and Y-chromosome. Most species of *Rattus* have a diploid number of 42, which includes seven pairs of small metacentrics (table 4).

THE *NIVIVENTER*-GROUP

The *Rattus niviventer*-group (Ellerman, 1941, 1947–1948, 1949, 1961) is the first to be discussed and formally separated from *Rattus*. Misonne (1969) had already considered that assemblage to be so dentally unlike *Rattus* that he withdrew the species from it and placed them in the genus *Maxomys*. But *Maxomys* is the correct generic name for the *rajah*-group, a cluster that was once also included within *Rattus* (Musser, Marshall, and Boadi, 1979). The *niviventer*-group is characterized below.

GENUS *NIVIVENTER* MARSHALL (1976)¹

TYPE SPECIES: *Mus niviventer* Hodgson (1845, p. 267), based on BM 43.1.12.73, a young adult caught in the Residency House at Katmandu, Nepal.

INCLUDED SPECIES AND DISTRIBUTIONS:

¹ "Subgenus *Niviventer*" was used in Marshall (1976 and 1977, p. 402) to designate the Thai species that were part of the *Rattus niviventer*-group as conceived by Ellerman (1941, 1947–1948, 1949, 1961). Marshall told me

Niviventer contains the following taxa,² which are separated below into two primary clusters, the *N. andersoni*-division and the *N. niviventer*-division. Furthermore, taxa belonging to the *N. niviventer*-division are listed under two headings: (1) species in which the morphological and geographic limits are relatively well defined, and (2) the *niviventer*-complex containing groups that are inadequately known as to species-limits. Within each category the major taxa are grouped according to geography.

Niviventer andersoni-Division

WESTERN CHINA

N. andersoni: Shensi, Szechwan, Yunnan, Tibet

N. excelsior: Szechwan

Niviventer niviventer-Division

Species Outside of the *niviventer*-Complex

SOUTHEASTERN ASIA NORTH OF THE ISTHMUS OF KRA (10° 30' N)

N. brahma: Northern Assam and Burma

N. eha (including *ninus*): Nepal, Sikkim, northern Assam and Burma, and Western China (Yunnan)

N. langbianis (including *indosinicus*, *vienti-anensis*): Assam, Burma, Laos, Vietnam, and Thailand

*N. hinpoona*³: Thailand

that he never intended to use *Niviventer* as a formal subgeneric name. In his manuscript he had discussed the group under the heading "Subgenus of the *niviventer*-Group," but the editor had changed it to "Subgenus *Niviventer*." That explains why Marshall characterized the group but did not designate a type species. But, the species, *niviventer*, becomes the type species by absolute tautonymy under the provision of Article 68d in the International Code of Zoological Nomenclature; *Niviventer*, therefore, is valid for use as a subgeneric or generic name. The name dates from 1976 for the reason given in footnote 3.

² Authors and dates of publication for the scientific names listed here and in the following generic accounts can be found in Chasen (1940), Tien (1966), Sody (1941), Tate (1936), Marshall (1976), Hill (1960), Ellerman (1941, 1949, 1961), and Ghose (1964).

³ Marshall contributed the chapter on the "Family Muridae: Rats and Mice" to the "Mammals of Thai-

SUNDA SHELF, AT AND SOUTH OF THE ISTHMUS OF KRA

N. cremoriventer (including *solus*, *gilbiventer*, *flaviventer*, *sumatrae*, *barussanus*, *mengurus*, *kina*, *spatulatus*, *malawali*, and *creta-ceiventer*): Peninsular Thailand, Malay Peninsula and offshore islands, Mergui Archipelago, Anambas Islands, Sumatra, Nias Island, Billiton and Banka islands, Borneo and offshore islands, Java, and Bali

The *niviventer*-Complex

SOUTHEASTERN ASIA NORTH OF THE ISTHMUS OF KRA

N. niviventer (including *niveiventer*, *lepcha*, and *monticola*): Northeastern Pakistan, Punjab, Nepal, Kumaon District of Uttar Pradesh, Darjeeling District of West Bengal, and Sikkim

N. confucianus (including *mentosus*, *littoreus*, *yaoshanensis*, *sinianus*, *elegans*, *sacer*, *zappayi*, *luticolor*, *canorus*, *chihliensis*, *lotipes*, *culturatus*, *champa*): Northern Burma, northern Thailand, Vietnam, mainland China, Hainan, and Taiwan

N. tenaster: Mountains of Assam, southern Burma, and Vietnam

N. fulvescens (including *caudator*, *octomammis*, *jerdoni*, *lepidus*, *gracilis*, *blythi*, *cinnamomeus*, *wongi*, *ling*, *minor*, *huang*, *flavipilis*, *vulpicolor*, *orbus*, and *mekongis*): Punjab, Nepal, Kumaon District of Uttar Pradesh, Darjeeling District of West Bengal, Sikkim, Assam, Burma, mainland China, Hainan, Vietnam, Laos, Thailand, and Bangladesh

N. coxingi (including *coninga*, *coxinga*): Taiwan, northern Burma

SUNDA SHELF SOUTH OF THE ISTMUS OF KRA

N. rapit (including *cameroni*, *fraternus*, and

land," published in 1977 and edited by Boonsong Lekagul and Jeffrey A. McNeely. In there are the original descriptions of *Rattus hinpoona* and *R. neilli* (*hinpoona* belongs in *Niviventer*, *neilli* in *Leopoldamys*). Those two names, however, date from 1976 where they first appeared in a separate edition of Marshall's chapter on Muridae, as explained by his scrawl across the copy he sent me: "I picked up and paid for 100 copies of this chapter from the Government Printing Office, Bangkok, on 9 December 1976. I got some mailed and handed to colleagues on 10 December 1976 and finished mailing all but one or two in the next few days."

atchinensis): Malay Peninsula, Sumatra, and Borneo

N. lepturus (including *maculipectus* and *fredericae*): Western and Central Java

OCCURRING IN BOTH REGIONS

N. bukit (including *condorensis*, *marinus*, *panlieftincki*, *jacobsoni*, *treubii*, *besuki*, *lepturoides*, *temmincki*, and *baturus*): Southern Burma, southern Thailand and offshore islands, Malay Peninsula, Sumatra, Java, and Bali

EMENDED DIAGNOSIS: Murid rodents characterized by the following combination of features: dense pelage with short, inconspicuous guard hairs; tails of most species with tufts and some type of bicolored pattern; six or eight mammae; long, narrow incisive foramina, narrow zygomatic plates; palatal bridge short and ending either before, at, or just beyond posterior margins of molar rows; walls of mesopterygoid fossa perforated by short, slim sphenopalatine vacuities; pterygoid fossa nearly flat, its anterior two-thirds not perforated by large interpterygoid foramina; small bullae, absolutely and relative to size of cranium; strut of alisphenoid bone present between masticatory-buccinator foramina and foramen ovale accessorius; upper and lower incisors with orange enamel, uppers orthodont or opisthodont; four roots anchoring first upper molars in one species and part of a sample of another, five roots or five with additional rootlets in most specimens of all other species; four roots beneath first lower molars in all species; occlusal patterns of upper molars simple, no cusp t7 or posterior cingulum, cusp t3 of second and third teeth usually absent, cusp t9 of each indistinct; laminae shaped like chevrons on first and second upper molars; third upper molar very small relative to the others; lower molars also simple, anterolabial cusp on second and third usually absent; front lamina on each first lower molar formed of two small cusps, usually joined together into an oblong or triangular lamina much narrower than the one behind it; 2N = 46, composed mostly of telocentrics, with three pairs of metacentrics.

DESCRIPTION: Cursorial (*N. niviventer*

and *N. hinpoon*, for example), scansorial (*N. brahma* is an example), and arboreal (*N. langbianis* and *N. cremoriventer*) habitus types are represented in *Niviventer*, which contains small to medium-sized rats (see the external, cranial, and dental measurements listed for *N. cremoriventer*, *N. langbianis*, and *N. niviventer* in Musser, 1973; for *N. andersoni*, *N. excelsior*, and *N. confucianus* in Musser and Chiu, 1979; for *N. brahma* and *N. eha* in Musser, 1970; and for *N. hinpoon* in Marshall, 1977; Marshall, 1977, has also provided photographs of living *N. confucianus* and *N. hinpoon*). Upperparts of the head and body are grayish brown in some species, reddish brown in a few, and either gray, flat buffy gray, or reddish brown in one. Underparts are white or cream in all but *N. eha* and *N. brahma*, which have dark gray venters, and *N. hinpoon*, which is characterized by dark buffy gray underparts. The pelage is soft and slightly woolly in some species, in others it consists of regular hairs and wide flexible spines, forming a coat that is semi-spinous in texture; both soft and spiny pelages are found within some species, such as *N. confucianus* and *N. fulvescens*. In all species, the pelage over the dorsum is either short or moderately long, with short guard hairs that barely extend beyond the overfur. The tail is about as long as the combined lengths of head and body in *N. hinpoon*, but in all the other species the tail is longer than the head and body, sometimes very much longer (*N. brahma*, *N. rapit*, and *N. lepturus*, for example). The tail is dark above and white below, from the base to the tip in *N. hinpoon*, *N. coxingi*, *N. rapit*, *N. bukit*, and *N. fulvescens*; dark above for the basal two-thirds or three-fourths, then white below and around the distal fourth or third in *N. andersoni* and *N. excelsior* (in any large sample of *N. confucianus*, a few specimens will have short, white tail tips—see Musser and Chiu, 1979; and the distal third of the tail in *N. lepturus* is either paler than the rest of the dorsal surface, mottled, or white); dark brown and monocolored in *N. langbianis* and *N. cremoriventer* (undersides are either mottled or white in a few samples

of the latter); and either brown and monocolored dark above and slightly paler below, or dark above and white below in *N. brahma* and *N. eha*. There are three hairs per scale in all species and the hairs increase in length from base to tip so that the tail-tip is either slightly or prominently tufted. The hind feet of most species are long and slender, but they are short and broad in *N. cremoriventer* and *N. langbianis*, the two that are predominantly arboreal (see the illustrations in Musser, 1973; Medway and Yong, 1976). All species have six plantar pads. Females of *N. eha* and *N. brahma* have three pairs of mammae (a postaxillary pair and two inguinal pairs), four pairs (a pectoral pair in addition to the other three pairs) occur in all the other species.

In all *Niviventer*, the cranium is long, slender, and often flat; the rostrum is moderately long, narrow and nearly parallel-sided, and the anterior margins of the nasals are blunt; the interorbital region is narrow; the zygomatic arches are delicate and graceful; and the braincase is elongate and low (figs. 6, 8–12). Low ridges outline the dorsolateral margins of the interorbital region and extend back along the dorsolateral edges of the braincase to the occiput in most species; such ridges are inconspicuous or absent in *N. andersoni*, *N. excelsior*, and *N. eha*. The squamosal roots of the zygomatic arches originate moderately high on the braincase, and in all species but *N. andersoni* and *N. excelsior*, the sides of the braincase between squamosal roots and the temporal ridges are vertical or nearly so. The sides of the braincase slope outward from the smooth dorsolateral margins to the squamosal roots in *N. andersoni* and *N. excelsior* (shown clearly in fig. 9). The lacrimal bones are small and inconspicuous relative to size of the cranium. The cranium of several species is either nearly straight (*N. niviventer*, for example) or gracefully arched from tip of nasals to occiput (*N. excelsior*), when viewed from the side. The zygomatic plates are narrow, their anterior spines projecting only slightly ahead of the dorsal zygomatic roots. The squamosal roots of the zygomatic arches originate

moderately high on sides of the braincase. The posterior margin of each root continues along the side of the braincase as a low indistinct ridge to the occiput. Each alisphenoid bone forming a side of the braincase is perforated just above each pterygoid ridge by a posterior foramen ovale accessorius and an anterior foramen that is the combined masticatory and buccinator foramina. A strut of alisphenoid wall separates these foramina and conceals the alisphenoid canal. Seen in ventral view, the crania have moderately long and narrow incisive foramina that end just before or at the front faces of the first molars in most species, but extend slightly past them in samples of a few others. The palatal bridge is short but wide, ending either slightly before, at, or just beyond the back margins of the toothrows. The postpalatal distance is long, about half the length of the cranium. The mesopterygoid fossa is about as wide as the palatal bridge and its walls are perforated by short and narrow sphenopalatine vacuities. The pterygoid fossae on either side of the mesopterygoid trough are usually entire in their anterior two-thirds, sometimes perforated by minute nutritive foramina. The bullae are small, not only absolutely but relative to the braincase, a distinctive feature apparent from both ventral and side views.

Each dentary is distinctive (fig. 22). The coronoid process is small. The back margin is shallowly concave between condyloid and angular processes. The capsular projection (containing the end of the incisor) is low, inconspicuous, and mostly contained behind the lateral surface of the dentary; the top of the projection is continuous with a narrow shelf that curves up to the end of the mandibular condyle. On the inner side of each dentary, a ridge extends diagonally from the back of the toothrow to the base of the condyle, disappearing just posterior to the mandibular foramen, so the condyle between the foramen and articular surface is nearly flat and smooth.

The upper and lower incisors are smooth and have orange enamel layers. The uppers emerge from the rostrum at either a right angle (orthodont) or in a slight backward curve

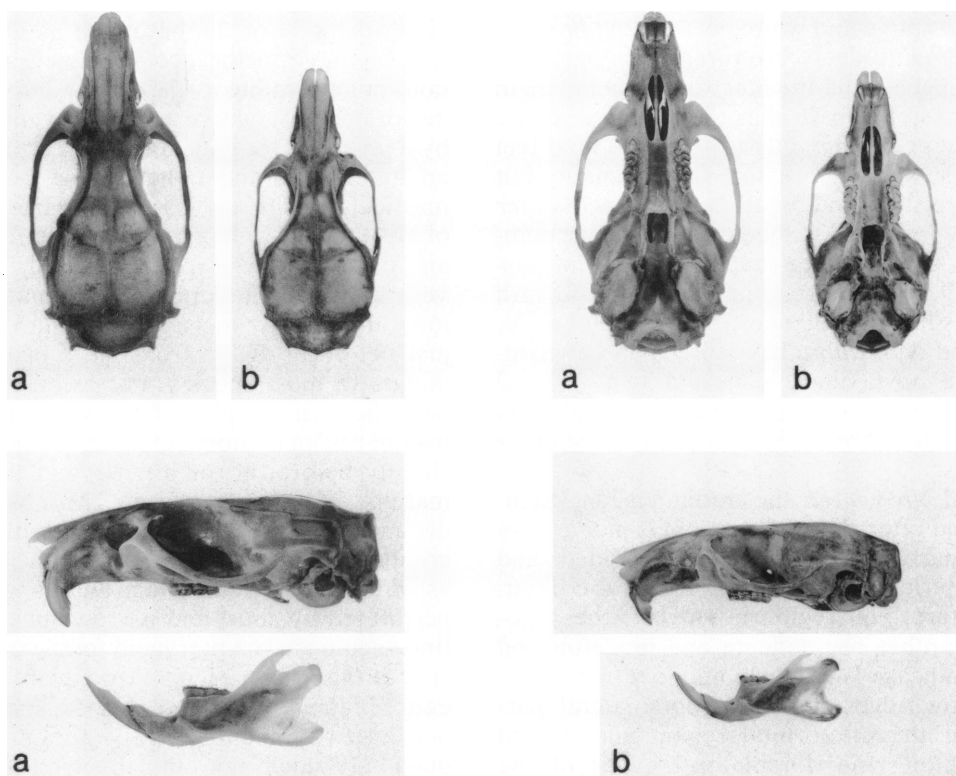


FIG. 6. Views of adult crania and dentaries. *Rattus*, as exemplified by *R. rattus diardii* (AMNH 250104) from Java (a), is contrasted with *Niviventer*, represented by *N. niviventer* (AMNH 56575) from China (b). Natural size.

(opisthodont); either one configuration or the other is characteristic of certain species, and both shapes are found in several—*N. niviventer*, *N. fulvescens*, and *N. bukit*—for example.

The number of roots on each first upper molar varies among the species (table 1). Most specimens of *N. langbianis* and about half the sample of *N. eha* have four roots: large anterior, lingual, and posterior; and a small labial one. Nearly all specimens of the other species have five roots, or, and this is usual among many species, five primary roots and several labial rootlets (the large lingual root is divided into two, and the labial root into several rootlets). The first lower molars are four-rooted (a large anterior and

posterior, small labial and lingual roots) in all the species.

Molars of all species in *Niviventer* are small and have simple occlusal patterns (figs. 7 and 8). In each species, the first and second upper molars are long and slender, each third upper molar is round or oblong and very small relative to the other teeth in the row. None of the upper molars has cusps t1bis or t2bis, a cusp t7, or posterior cingulum, and cusp t3 is usually absent from the second and third molars (table 2). The occlusal surface of each first upper molar consists of two chevron-shaped laminae and a large cusp t8 broadly merged with a small cusp t9; the surface of each second molar consists primarily of a large cusp t1, a chevron-shaped lamina

TABLE 1
Number of Roots on M¹ in Selected Species of *Niviventer*
 (Number of roots in percentage; number of specimens in parentheses.)

Species	Roots ^a			
	3+	4	5	5+
<i>N. andersoni</i>				
Szechwan	—	—	100 (49)	—
<i>N. excelsior</i>				
Szechwan	—	—	92 (12)	8 (1)
<i>N. brahma</i>				
North Burma	—	—	75 (6)	25 (2)
<i>N. eha</i>				
Nepal, Sikkim, Burma	—	50 (16)	47 (15)	3 (1)
<i>N. langbianis</i>				
Indochina	—	100 (21)	—	—
<i>N. cremoriventer</i>				
Sunda Shelf	1 (1)	5 (9)	58 (94)	36 (58)
<i>N. hinpoon</i>				
Thailand	—	—	100 (19)	—
<i>N. confucianus</i>				
China	—	—	6 (4)	94 (125)
North Thailand, Burma	—	—	89 (70)	11 (8)
<i>N. tenaster</i>				
South Burma	—	—	100 (26)	—
Vietnam	—	—	97 (38)	3 (1)
<i>N. coxingi</i>				
Taiwan	—	4 (2)	94 (50)	2 (1)
North Burma	—	5 (1)	95 (20)	—
<i>N. rapit</i>				
Malay Peninsula	—	—	19 (8)	81 (33)
Sumatra	—	—	75 (15)	25 (5)
Borneo	—	—	50 (3)	50 (3)
<i>N. lepturus</i>				
Java	—	—	100 (54)	—

^a Roots on M¹: 3+: large anterior, lingual, posterior, and a labial nubbin. 4: three primary roots and a small, prominent labial root. 5: an anterior, posterior, divided lingual, and prominent labial. 5+: Five roots with one or several additional labial rootlets.

and a large cusp t8 with only a trace of a cusp t9; and each third molar is formed of only a small cusp t1, a small arched lamina and a small cusp at the back of the tooth. Except for cusps t1 on the second and third molars, the other cusps are not discrete and have, even at the stage of wear seen in nestlings and juveniles, merged to form thick, chevron-shaped laminae.

The lower molars are long and slender and their occlusal surfaces are also simple. The surface of each first tooth is formed by a narrow, oblong front lamina, two chunky chevron-shaped laminae behind it, and a large posterior cingulum. The second molar consists of two simple and thick chevron-shaped laminae and a large posterior cingulum. The third molar has only a front and rear lamina.

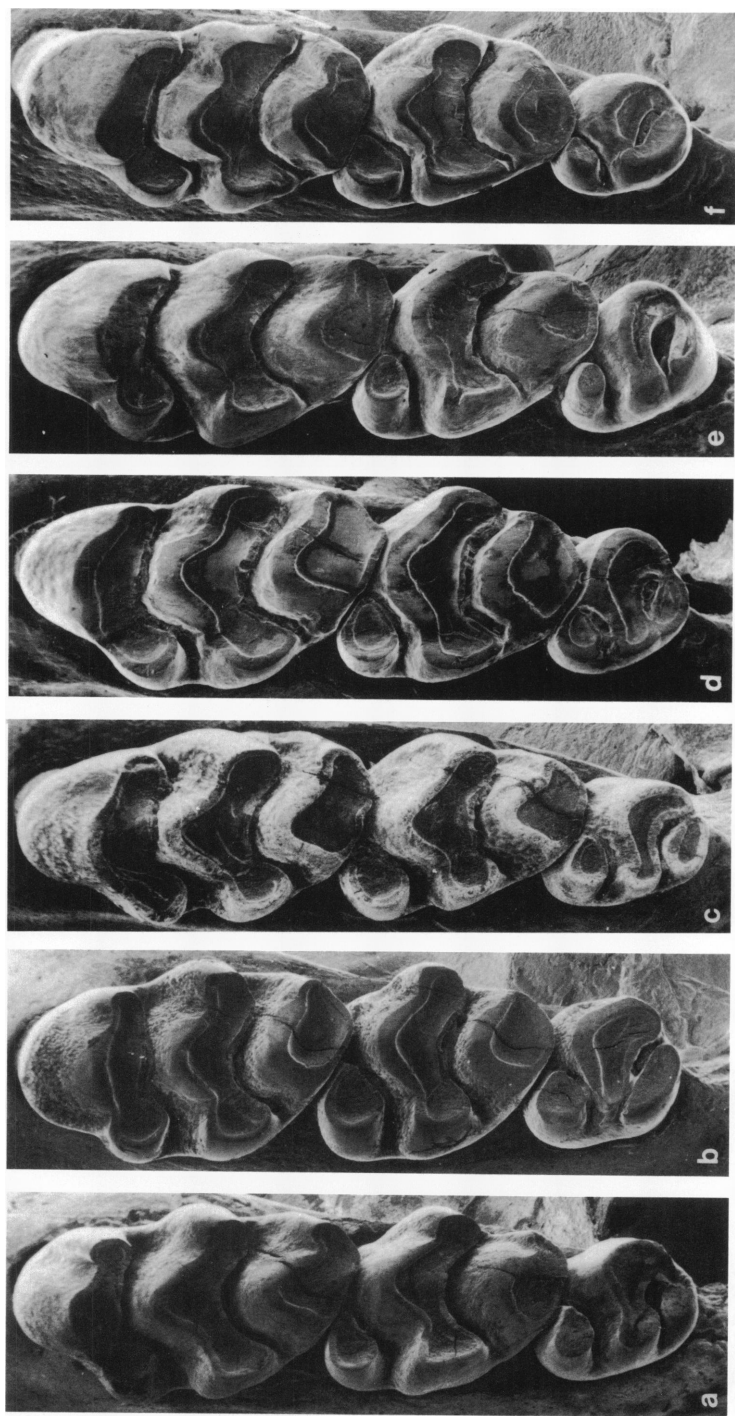


FIG. 7. Occlusal views of left maxillary toothrows in examples of *Niviventer*: a, *N. andersoni* (AMNH 111622; LM¹⁻³, 7.3 mm.); b, *N. excelsior* (AMNH 111666; LM¹⁻³, 6.3 mm.); c, *N. brahma* (FMNH 41021; LM¹⁻³, 6.8 mm.); d, *E. eha* (AMNH 115231; LM¹⁻³, 4.9 mm.); e, *N. confucianus* (AMNH 56644; LM¹⁻³, 5.6 mm.); f, *N. hinpoon* (AMNH 237587; LM¹⁻³, 6.0 mm.).

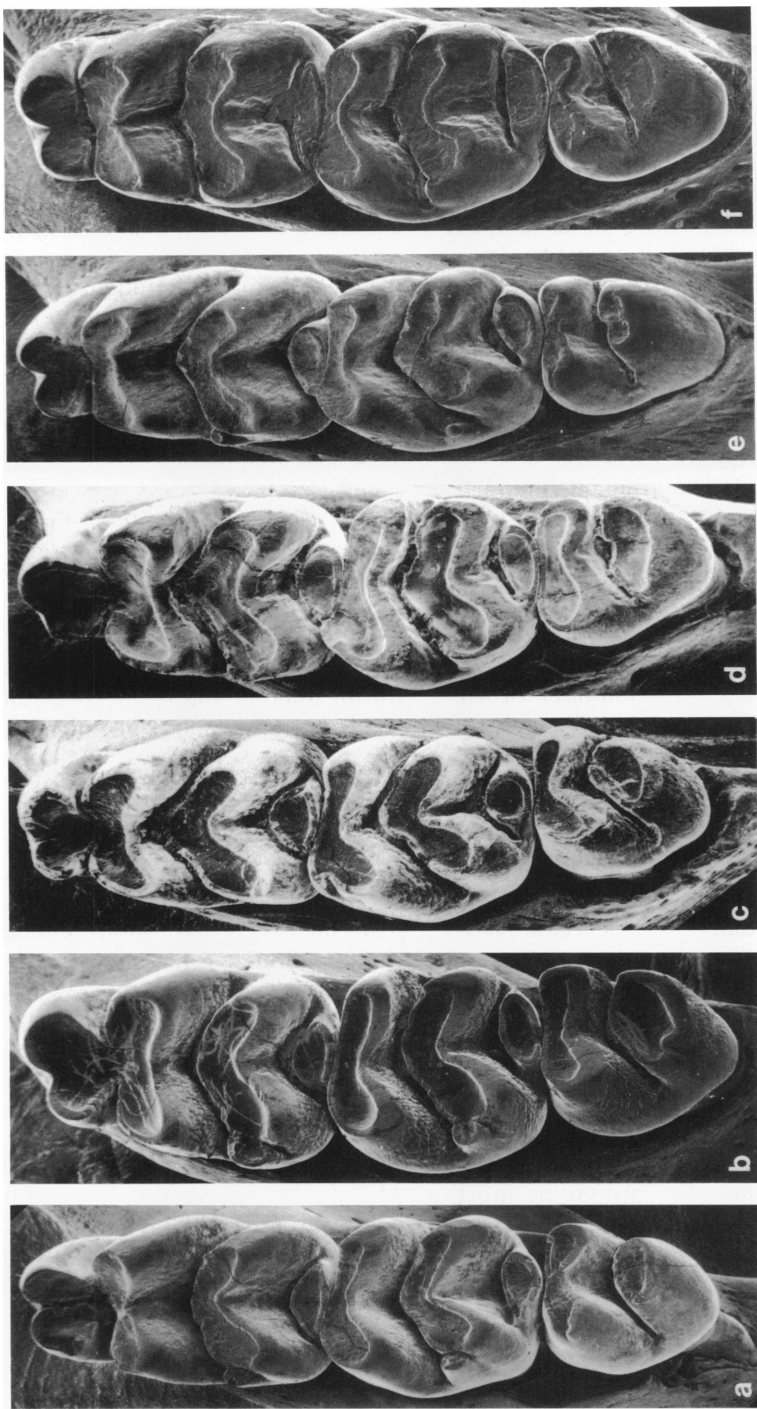


FIG. 8. Occlusal views of left mandibular tooththrows from the same examples of *Niviventer* shown in figure 6: a, *N. andersoni* (LM₁₋₃, 6.7 mm.); b, *N. excelsior* (LM₁₋₃, 6.3 mm.); c, *N. brahma* (LM₁₋₃, 6.7 mm.); d, *N. eha* (LM₁₋₃, 5.0 mm.); e, *N. confucianus* (LM₁₋₃, 5.5 mm.); f, *N. hinpoon* (LM₁₋₃, 5.8 mm.).

All the laminae on the teeth are formed by the coalescence of two large cusps, except the front lamina on the first molar, which is the result of two small, nearly equal-sized cusps merging early in life to form an oblong structure much narrower than the lamina behind. No anterocentral cusp sits on the front margin of the toothrow in any of the species. Cusplets are absent from the labial margins of all the teeth in some species (*N. langbianis*, *N. cremoriventer*, and *N. lepturus*, for example); others have very small cusplets on either the first or second molars but not the third; and anterolabial cusps may or may not be present on the second molars, depending on the species, but usually do not occur on the third molars (table 2).

The species of *Niviventer*, particularly those in the *N. niviventer*-division, are closely similar among themselves in cranial conformation and dental configuration. That morphological uniformity is complimented by the similarities in their chromosomal characteristics (table 4). All the species so far sampled have a diploid number of 46, consisting of three pairs of small metacentrics, one pair or four pairs of submetacentrics or subtelocentrics, and 15, 18, or 19 pairs of telocentrics; the X and Y chromosomes are usually telocentrics.

COMPARISONS: *Niviventer* requires comparisons with *Rattus*, *Maxomys*, and the four groups to be diagnosed beyond. *Niviventer* is compared to each of the four groups in those accounts; here it is contrasted first with *Rattus*, then with *Maxomys*. In addition to the six cranial features and chromosomal characters listed previously, *Rattus* also possesses the following characters that distinguish it from *Niviventer* (see also fig. 6).

1. Tails are monicolor brown in most species of *Rattus*, bicolored patterns are infrequent; tails are rarely tufted at the tips.

2. Zygomatic plates are wider relative to size of cranium, and have prominent anterior spines projecting well forward of the dorsal anterior zygomatic roots.

3. The incisive foramina are longer, extending past the front margins of the molar rows in nearly all species.

4. First upper molars of all *Rattus* have five roots (large anterior and posterior, labial, and divided lingual).

5. First and second upper molars are wider relative to their lengths, third upper molars are larger relative to the others in the toothrows.

6. Cusps that form first and second rows on the first upper molars and front row on second upper molars are discrete, forming arched cuspidate configurations instead of chevron-shaped laminae.

7. Cusp t9 on first and second upper molars is large and not obliterated by union with cusp t8 except after much wear.

8. Cusp t3 on second and third upper molars are usually present, although often small.

9. Front lamina on each first lower molar is nearly as wide as rest of tooth, formed of a large anterolingual cusp and a smaller anterolabial cusp, and sometimes a small anterocentral cusp.

10. Anterolabial cusps are always present on the second and third lower molars.

11. Labial cusplets are always present on the first and second lower molars.

12. The coronoid process is much larger and more prominent relative to size of each dentary; the back margin between condyloid and angular processes is deeply concave; the shelf on the inside of each dentary extends from the end of the toothrow diagonally past the mandibular foramen where it becomes a ridge coursing along the lower part of the condyloid process to the articular surface (fig. 22).

Misonne (1969) associated *bartelsii*, the genotype of *Maxomys*, with the *niviventer*-group and transferred the latter to *Maxomys*. The taxonomy and geographic distribution of *M. bartelsii* have been reviewed by Van Peenen et al. (1974), which includes an illustration of the skull, and the relationship of *bartelsii* to other species brought together into *Maxomys* has been discussed by Musser, Marshall, and Boeadi (1979), along with a definition of the genus, including characteristics of the species in it, and a photograph that contrasts the crania of *Maxomys*, *Rattus*, and *Niviventer*. *Maxomys* in general

TABLE 2

Presence (+) or Absence (-) of Cusp t3 on M² and M³, of the Anterior and Posterior Cusplets on M₁, and of the Anterolabial Cusps on M₂ and M₃ in Selected Species of *Niviventer*
(Number of cusps and cusplets in percentage; number of specimens in parentheses.)

Taxon	Cusp t3 on M ²		Cusp t3 on M ³		Ant. cusp. on M ₁		Post. cusp. on M ₁		Anlab. cusp. on M ₂		Post. cusp. on M ₂		Anlab. cusp. on M ₃	
	+	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>N. andersoni</i>														
Szechwan	8 (4)	92 (45)	100 (49)		100 (49)		100 (49)		100 (49)		98 (48)	2 (1)	100 (49)	
<i>N. excelsior</i>														
Szechwan		100 (13)	100 (13)		100 (13)		54 (7)	46 (6)	100 (13)		62 (8)	38 (5)	100 (13)	
<i>N. brahma</i>														
North Burma		100 (8)	100 (8)		100 (8)			100 (8)	100 (8)			100 (8)	100 (8)	
<i>N. elia</i>														
Nepal, Sikkim, Burma		100 (31)	100 (31)		100 (30)		23 (7)	77 (23)	70 (21)		30 (9)	7 (2)	93 (28)	100 (29)
<i>N. langbianis</i>														
Indochina	30 (3)	70 (7)	100 (10)		100 (9)		22 (2)	78 (7)	100 (9)		33 (3)	67 (6)	100 (9)	
<i>N. cremoriventer</i>														
Sunda Shelf	12 (19)	88 (139)	100 (158)		100 (157)		7 (11)	93 (146)	100 (157)		4 (7)	96 (150)	100 (157)	
<i>N. hinpoon</i>														
Thailand		100 (19)	100 (19)		100 (18)		85 (15)	15 (3)	100 (18)		94 (17)	6 (1)	100 (18)	
<i>N. confucianus</i>														
China	3 (4)	97 (125)	100 (129)		100 (129)		78 (100)	22 (29)	11 (14)		89 (115)	85 (109)	15 (20)	100 (29)
North Thailand, Burma	1 (1)	99 (70)	100 (71)		100 (70)		73 (51)	27 (19)	100 (70)		83 (58)	17 (12)	100 (70)	
<i>N. tenaster</i>														
Vietnam	5 (2)	95 (36)	100 (38)		100 (38)		24 (9)	76 (29)	11 (4)		89 (34)	26 (10)	74 (28)	100 (38)
South Burma	28 (7)	72 (18)	100 (25)		100 (25)		48 (12)	52 (13)	100 (25)		52 (13)	48 (12)	100 (25)	
<i>N. coxingi</i>														
Taiwan		100 (43)	100 (43)	2 (1)	98 (42)		91 (39)	9 (4)	19 (8)		81 (35)	98 (42)	2 (1)	95 (41)
North Burma	12 (2)	88 (14)	100 (15)		100 (16)		75 (12)	25 (14)	100 (16)		82 (13)	18 (3)	100 (16)	
<i>N. rapiti</i>														
Malaya	15 (6)	85 (35)	100 (41)		100 (41)		88 (36)	12 (5)	88 (36)		83 (34)	17 (7)	100 (41)	
Sumatra		100 (20)	100 (20)		100 (19)		63 (12)	37 (7)	100 (19)		63 (12)	37 (7)	100 (19)	
Borneo		100 (6)	100 (6)		100 (6)			100 (6)	100 (6)		17 (1)	83 (5)	100 (6)	
<i>N. lepturus</i>														
Java	7 (4)	93 (50)	100 (54)		100 (54)			100 (54)	100 (54)			100 (54)	100 (54)	

and *M. bartelsii* in particular are distinguished from *Niviventer* by the following external, cranial, dental, and karyotypic features.

1. The pelage, especially that over the upperparts of head and body is dense, short, and velvety or spinous in *Maxomys*.

2. Length of the tail is about as long as the combined lengths of head and body.

3. The rostrum is longer relative to size of the braincase, tapered toward the tip, and the anterior margins of the nasals are triangular.

4. The braincase is broad, inflated, and outlined by much higher, wider and more prominent ridges that begin at the suture between the supraoccipitals and parietals and sweep forward along dorsolateral margins of the braincase to the interorbital region.

5. The lacrimals are large and prominent relative to size of the cranium.

6. The incisive foramina are short and wide, shaped like an inverted heart; they end well in front of the first molars.

7. The palatal bridge ends in front of the back faces of the molar rows.

8. The interorbital region is wider relative to size of the cranium.

9. The configuration of the alisphenoid canal above each pterygoid plate is like that in *Rattus* (no masticatory-buccinator foramina, no strut of alisphenoid bone, and no foramen ovale accessorius).

10. Each first upper molar has three large roots (anterior, lingual, and posterior) or four (a divided lingual)—see table 2 in Musser, Marshall, and Boeadi (1979); each first lower molar is anchored by either two large roots (anterior and posterior) or two roots and a small labial one.

11. The coronoid process of the dentary is a low triangular bump or small tapered structure, much smaller and inconspicuous relative to size of the dentary.

12. The diploid chromosome number ranges from 34 to 52, consisting of four to 10 pairs of metacentrics, one to 10 pairs of submetacentrics and subtelocentrics, and six to 19 pairs of telocentrics (see table 5 in Musser, Marshall, and Boeadi, 1979).

THE SPECIES OF *Niviventer*: The species oc-

cur from eastern Pakistan across the foothills of the Himalayas through northern India and Nepal into northern Burma and much of central and southern China, then southward through Indochina, southern Thailand, and Burma onto the Malay Peninsula and islands on the Sunda Shelf (fig. 13). No member is known from any of the Mentawai Islands, the Nicobars, or the Andamans, and the group does not occur anywhere east of the Sunda Shelf.⁴ Some species are found north of the Isthmus of Kra only (*N. andersoni*, *N. excelsior*, *N. brahma*, *N. eha*, *N. langbianis*, *N. coxingi*, and *N. hinpoon*, for example), a few occur south of the Isthmus on the Sunda Shelf (*N. cremoriventer*, *N. rapit*, and *N. lepturus*, for example), and at least one has been recorded from both regions (*N. bukit*).

Because the configuration of the skull and molars are so similar among species of *Niviventer* and because some groups are so variable, both individually and geographically, in body size and color of pelage, there have been many different opinions regarding taxonomy of the genus and the limits of the species in it. Only recently have the morphological and geographic limits of a few species been defined: *N. brahma* and *N. eha*

⁴ This view is contrary to that presented by Ellerman (1947–1948, p. 265), who placed the Sulawesian *Rattus chrysocomus* (with *fratrorum* as a synonym), along with *niviventer* and its allies in the subgenus *Maxomys*, stating that "This North Celebes species seems to me, on the basis of a considerable number of specimens, to belong with the present group. It is shorter tailed than those above. The nasals are relatively long, and the supraorbital ridges rather weak." Later, Ellerman (1949, p. 70) placed *chrysocomus* in a "*chrysocomus* Group," comparable to his "*niviventer* Group" within the subgenus *Maxomys*. But, in 1936, Tate had allied *chrysocomus* with a group of endemics on Sulawesi, none of which were related to *niviventer*, an arrangement that I also reached after studying specimens from Sulawesi and examples of *niviventer* and its allies (Musser, 1969). Misonne (1969) also excluded *chrysocomus* from close association with *niviventer*. He retained the latter in *Maxomys* and raised that taxon to generic rank but transferred *chrysocomus* to the subgenus *Bullimus* of *Rattus*. Whatever the affinities of *chrysocomus*, it has no close morphological tie to *Niviventer*.

(Musser, 1970), *N. andersoni* and *N. excelsior* (Musser and Chiu, 1979), *N. cremoriventer* and *N. langbianis* (Musser, 1973), and *N. hinpoon* (Marshall, 1976, 1977). These seven are distinctive but at least five of them have been confused with other taxa and their morphological features and geographic distributions obscured because of poor taxonomic studies in the past.

Of the seven, *N. eha* has always been easily recognized and much has been written about its morphological features, geographic distribution, and natural history (Allen, 1940; Anthony, 1941; Ellerman, 1961; Abe, 1971; Weigel, 1969; Neithammer and Martens, 1975; and Musser, 1970). Its close relative, *N. brahma*, however, was for a long time listed as a subspecies of *fulvescens* and some specimens of it had been misidentified as *N. eha* in the literature (Musser, 1970). Both *N. eha* and *N. brahma* are soft-furred rats with reddish brown upperparts, smoky gray underparts, long and tufted tails, three pairs of mammae, and distinctive conformations of the crania (fig. 9); both are confined to high elevations.

Niviventer andersoni and *N. excelsior* (fig. 9) occur in the high mountains of Western China and are part of a mammalian fauna, which includes the giant panda (*Ailuropoda melanoleuca*) and golden monkey (*Rhinopithecus roxellanae*, not including *brelichi*), now known only from that region. The definite geographic distributions and faunal association of the two rodents were elucidated only recently, their identities having been obscured in the past because of poor taxonomy resulting in wrong associations, as Musser and Chiu (1979, p. 583) summarized: "from 1911 until the 1920's and 1940's, *excelsior* and *andersoni* were reported as two distinct species in the literature; by 1926, *zappeyi* was associated with *excelsior* as a subspecies, and, by 1940, both taxa were considered to be synonyms of *confucianus*; *andersoni* was recognized as a good species and in 1940 its definition was expanded to embrace *zappeyi*, and possibly *culturatus*, but, by 1949, *andersoni* was reduced to a subspecies of *coxingi*, in which context it was associated with *moi*."

Niviventer andersoni and *N. excelsior* are more closely related to each other than to any other species of *Niviventer*, and differ from the other species of *Niviventer* in the following features: body size is larger (most, not all, of the other species are smaller); the distal half, two-thirds, or one-fourth of the tails are white and prominently tufted (instead of brown or with a short white tip); dorsolateral margins of the interorbital and postorbital regions are slightly beaded and the edges of the braincase are smooth in *N. excelsior*, the interorbital and postorbital margins of *N. andersoni* are outlined by low ridges with the braincase mostly smooth (ridges along edges of braincase to, or nearly to, occiput in all the other species except *N. eha*); the sides of the braincase slope outward from the dorsolateral margins to the squamosal roots (instead of being vertical or nearly so); molars are larger and tooththrows slightly longer relative to size of cranium and mandible; each third upper molar is slightly larger relative to the others in each tooththrow; the cusps of the upper molars are more angular and slightly better defined, the laminae are not so tightly pressed against each other and not so exaggerated in the form of chevrons. The cranial and dental features distinguishing *N. andersoni* and *N. excelsior* from the rest of the species of *Niviventer* are primitive ones; *N. andersoni* and *N. excelsior* appear to be primitive members of *Niviventer* that are now isolated in the high mountains of Western China.

Niviventer langbianis (fig. 9) is a small-bodied, long-tailed arboreal rat found in the forests of Indochina from Assam in the northeast to peninsular Thailand (north of the Isthmus of Kra) in the south. Its morphological and possibly ecological counterpart, *N. cremoriventer* (fig. 10), occurs on peninsular Thailand south of the Isthmus of Kra, the Malay Peninsula, and islands on the Sunda Shelf (Musser, 1973). Recently, Marshall (1976, 1977) has treated *langbianis* as a subspecies of *N. cremoriventer* but there is no evidence to substantiate that arrangement. The data presented in 1973 and additional information gathered recently by me do not falsify the hypothesis that samples of

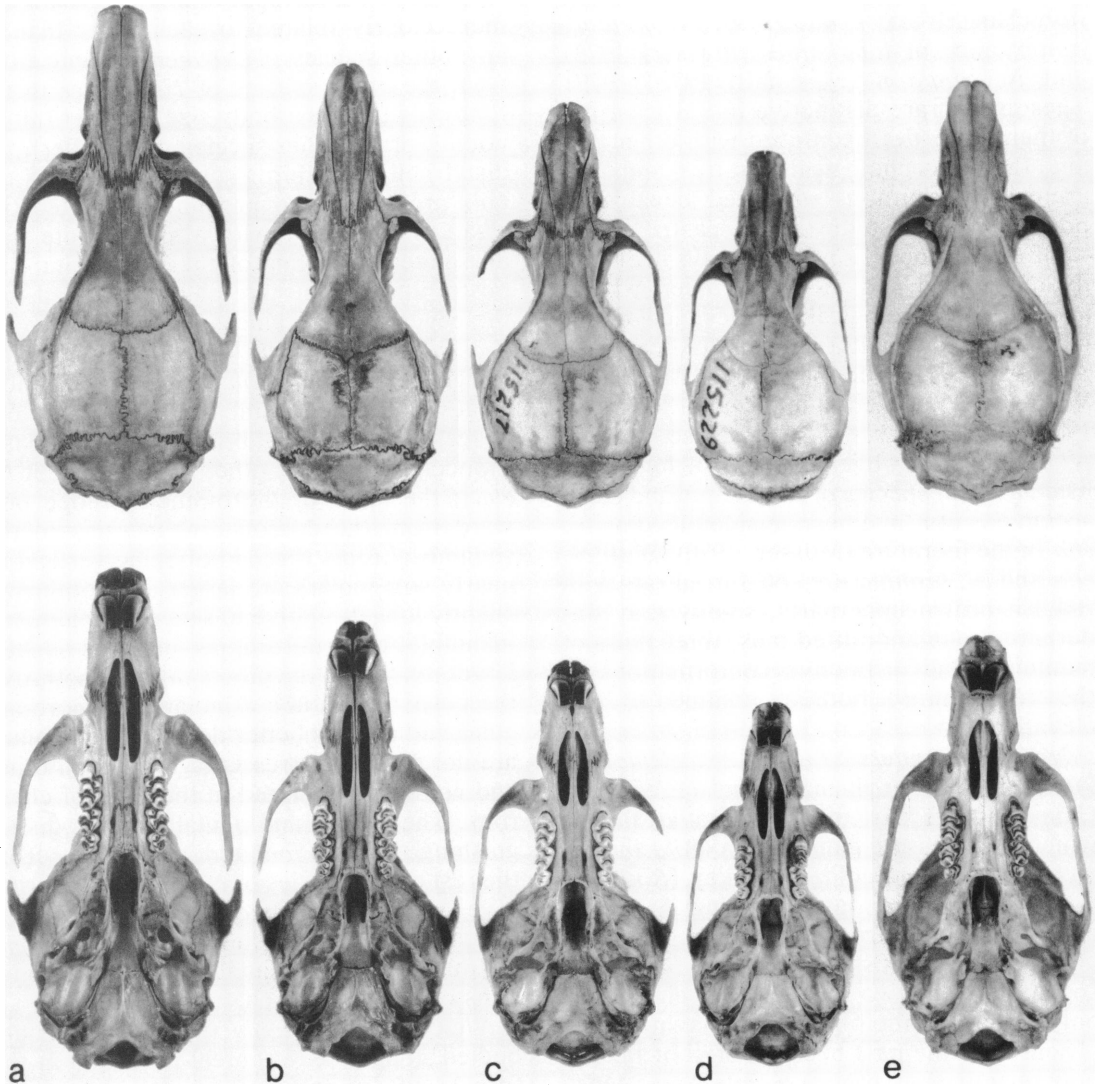


FIG. 9. Dorsal (top) and ventral (bottom) views of adult crania of five species of *Niviventer* from Southeast Asia north of the Isthmus of Kra: a, *N. andersoni* (AMNH 43284), China; b, *N. excelsior* (AMNH 113590), China; c, *N. brahma* (AMNH 115217), northern Burma; d, *N. eha* (AMNH 115229), northern Burma; e, *N. langbianis* (USNM 321435), Vietnam. Approx. $\times 1.5$.

each kind represent different species. The two differ in several qualitative and quantitative features; especially diagnostic are lengths of the incisive foramina and size of the ears and bullae. The incisive foramina in *N. langbianis* extend past the anterior margins of the maxillary toothrows by .5 to 1.0

mm., but in most specimens of *N. cremoriventer* the incisive foramina terminate either well before the toothrows or just at their front edges. The ears are much larger in *N. langbianis* and, as might be expected, the bullae are also much larger, not only absolutely but relative to size of the cranium.

Every specimen of *N. langbianis* can be distinguished from each one of *N. cremoriventer* by size of bullae, no matter where the specimens came from within the respective geographic range of each. There is an additional distinction between the two species: all examples of *N. langbianis* have four roots on each first upper molar (large anterior, lingual, and posterior roots, and a smaller but prominent labial root) and three on each second upper molar (anterior, posterior, and lingual). Most specimens of *N. cremoriventer* have either five roots (a divided lingual root instead of a single large one) or five roots plus rootlets on each first molar (table 1), and four roots (a divided lingual) anchoring each second upper molar. Both *N. langbianis* and *N. cremoriventer* should be compared to other species in *Niviventer* to determine if the two are really closely related, or if *N. langbianis* ties more tightly to species in Indochina, and *N. cremoriventer* to forms on the Sunda Shelf—the resemblances between them (monocolored, slightly penicillate tails and morphologies associated with an arboreal habitus) could be simply shared primitive features.

Discovered only four years ago living in limestone cliffs of southern Thailand, *N. hinpoon* (fig. 11) is an easily recognized species (Marshall, 1976, 1977). Medium body size, a tail that is about as long as the head and body, and dull buffy gray underparts set *N. hinpoon* apart from all other species in *Niviventer*.

How many other species of *Niviventer* exist in addition to the seven previously noted and what their geographic ranges may prove to be will not be known until the large group that I call the *niviventer*-complex is taxonomically revised. At least 59 scientific names have been applied to samples of this assemblage, a reflection of the appreciable, sometimes spectacular color and morphological variation among individuals in a sample, between sexes from one place to another, between samples from different elevations in one area, between different ages, and between samples taken at different times of the year. The variation involves color of the fur (gray to orange and reddish brown), texture

of the pelage (soft and thick to densely spinous and stiff), patterning of the underparts (white or cream venters without patterns to large pectoral patches and collars, as well as midventral streaks of buff or brown), patterning on upper surfaces of the hind feet (white or buffy to pale orange, without a pattern; a dark brown middorsal strip extending part way down the foot or all the way down to the base of the digits), coloration of the tail (brown above and either white below to tip, white below to and around tip, or white below nearly to the tip, which is all brown; or brown above and either brown or mottled below), body size (small to large), length of tail (always longer than head and body, but either moderately longer or very much longer), size of skull and teeth (small to large), and size of bullae (very small relative to cranium or relatively larger).

Throughout the geographic range of the *niviventer*-complex, two species occur together at many places, and three are found at the same locality in a few areas. I shall outline the characteristics of some of these species, beginning with those occurring on the Sunda Shelf where the resolution of species is clearer. Four kinds are found on islands of the Sunda Shelf. One, *N. rapit*, is known by samples from the Cameron Highlands of the Malay Peninsula (Chasen, 1940; Medway, 1969), the highlands of northern Borneo (Medway, 1965), and the mountains of Sumatra (Chasen, 1940; Sody, 1941). All are rats with bright reddish brown and spinous upperparts, white underparts with prominent pectoral patches and sometimes midventral streaks, long bicolored tails in which the dorsal surface is brown and the ventral surface white from the base to the tip, and skulls and teeth that are closely similar in conformation (fig. 10). Body size is the primary difference among rats in the three samples. The specimens from the Malay Peninsula are the largest and have the longest teeth, those from the mountains of Sumatra are similar in body size to the specimens from northern Borneo, but have slightly larger teeth. Rats from the three areas appear to be the same morphological type of animal and the differences between

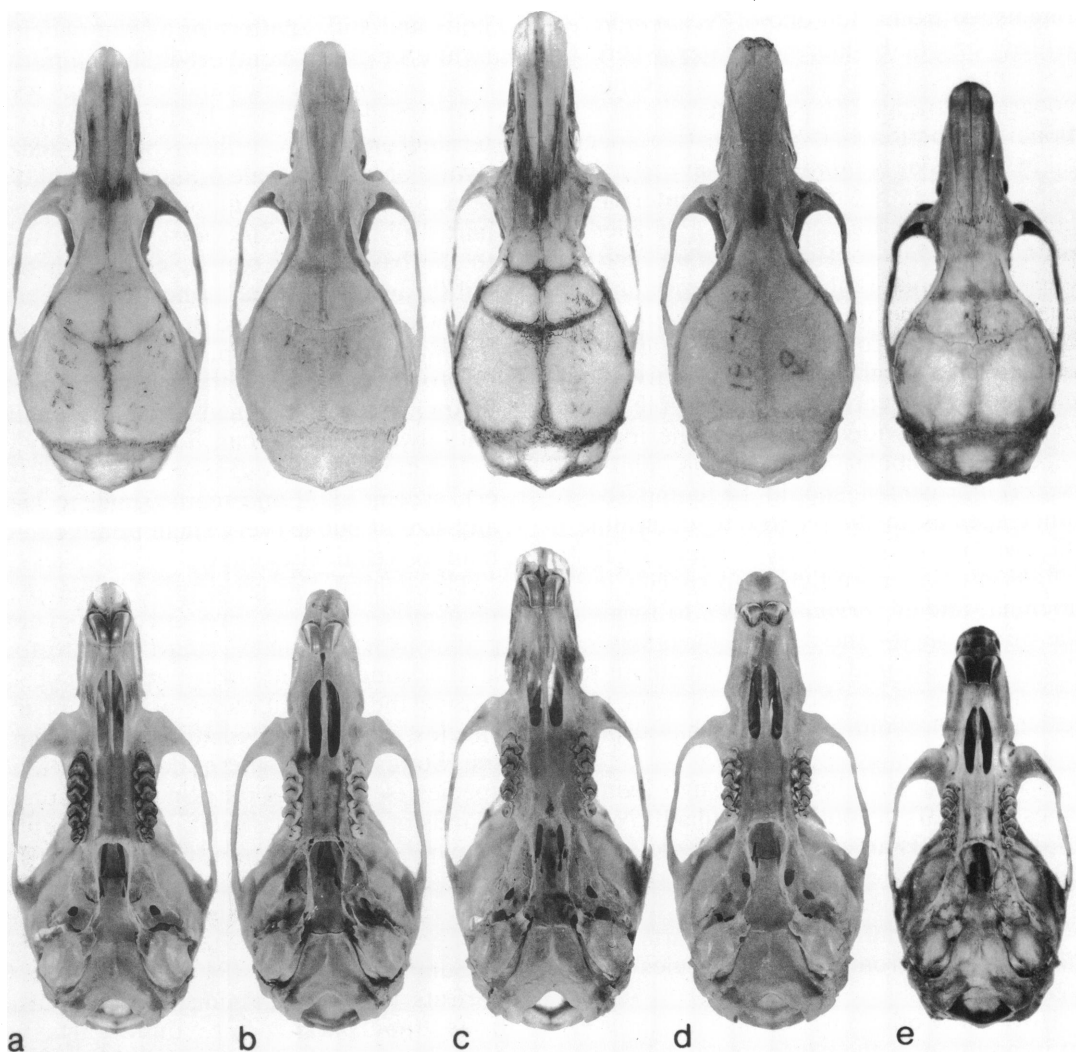


FIG. 10. Dorsal (top) and ventral (bottom) views of adult crania of three species of *Niviventer* from the Sunda Shelf south of the Isthmus of Kra: a, *N. lepturus* (AMNH 250089), West Java; b, *N. rapit fraternus* (AMNH 106349), Sumatra; c, *N. rapit cameroni* (USNM 489018), Malay Peninsula; d, *N. rapit rapit* (USNM 292781), North Borneo; e, *N. cremoriventer* (AMNH 217621), Malay Peninsula. Approx. $\times 1.5$.

them are the kinds found among insular variants of a single species (those distinguishing the subspecies of *N. cremoriventer*, for example; Musser, 1973).

A large, long-tailed rat also lives in the mountain forests of Java. It has been listed as a subspecies of *rapit* (Chasen, 1940; Sody,

1941) but the many specimens I have studied represent a different kind of animal from the *rapit*-form occurring on Sumatra, Borneo, and the Malay Peninsula. *Niviventer lepturus* is the Javan rat; its pelage is soft and dense and the upperparts are dark, with a richer brown tone rather than reddish brown.

The tail is much longer than the combined lengths of head and body, dark above and white below, and in some specimens the entire third or fourth of the tail is mottled or all white. The skull is about the same size as those of *N. rapit* from Sumatra and northern Borneo, but the braincase and rest of the cranium is flatter, the bullae are larger, the incisive foramina are longer, and the teeth are much larger—they appear massive relative to the cranium, as compared with the molars of specimens in samples of *N. rapit* (fig. 10). Labial cusplets are absent from lower molars in *N. lepturus*, but posterior cusplets are usually present on the first and second molars in *N. rapit* (table 2). Finally, both *N. lepturus* and *N. rapit* (as represented by *cameroni* from the Malay Peninsula) have a 2N of 46, but the former has no submetacentric or subtelocentric chromosomes while *N. rapit* has four pairs of subtelocentrics; the chromosomal composition of *N. lepturus* is unique among the chromosomal samples of *Niviventer* that have been analyzed so far (table 4). The sample of *Niviventer* from the mountains of western and central Java seems to be drawn from a different gene pool than those from the highlands of Sumatra, northern Borneo, and the Malay Peninsula.

A rat of smaller body size and shorter tail occurs on Bali, Java, Sumatra, and the Malay Peninsula, but not Borneo. *Niviventer bukit* is the name applied to this smaller animal (Chasen, 1940; Marshall, 1977). It has been found together with *N. lepturus* at some places on Java and with *N. rapit fraternus* at spots on Sumatra (Sody, 1941). It is known from the lowlands and middle elevations of the Malay Peninsula and is both morphologically and biochemically distinct from *N. rapit cameroni* of the Cameron Highlands (Chasen, 1940; Medway, 1969; Chan, Dhalwal, and Young, 1979).

At least three species, possibly more, occur in Southeast Asia north of the Isthmus of Kra, but sorting them out is far more difficult than it is for the *niviventer*-complex on the Sunda Shelf. Three kinds are found in northern Burma, and samples of all have been obtained from some of the same localities. One is a very large rat with a long tail.

It resembles *E. rapit* but is larger in body size than *N. r. cameroni*, the biggest of the three subspecies. It is the large northern Burmese rat that Anthony (1941) misidentified as *andersoni*, a species that had never been recorded from Burma before Anthony's report and is still unknown from that country (Musser and Chiu, 1979). The Burmese specimens are cranially closely similar to specimens of *N. coxingi* from Taiwan (fig. 11) and agree also in proportions of body size and tail length. Animals in the Taiwanese population are reddish brown above and cream or white below, with prominent pectoral patches and sometimes midventral streaks; their pelage is spinous. The Burmese rats are, on the average, softer furred and darker. For the present time, I treat the sample from northern Burma as a mainland counterpart of *N. coxingi*. This large rat has not been taken anywhere else in Southeast Asia outside of northern Burma and Taiwan.

The second species living in northern Burma is a smaller rat with upperparts that are predominantly dark gray, but do range to grayish brown and buffy or reddish brown. *Niviventer confucianus* is the name to apply to this animal for the present time. It occurs throughout much of the central and southern parts of China (Allen, 1940), on Taiwan (described as *culturatus*; Ellerman, 1961), in northern Thailand (Marshall, 1977), and northern Vietnam (Osgood, 1932). It must be a common animal in the highlands of northern Burma and China if the large collections in museums are any indication of its abundance.

The third kind of rat in the *niviventer*-complex from northern Burma is of the same body size as *N. confucianus* but has a relatively longer tail and bright orange-brown or reddish brown upperparts that are spinous in many specimens of any particular sample. *Niviventer fulvescens*, a name based on specimens from Nepal, applies to this colorful, long-tailed rat. It has an extensive geographic distribution, from northeastern India through Nepal to Burma and across southern China. The Chinese samples were once regarded as a different species, *huang*, but are now considered to be the same as the sam-

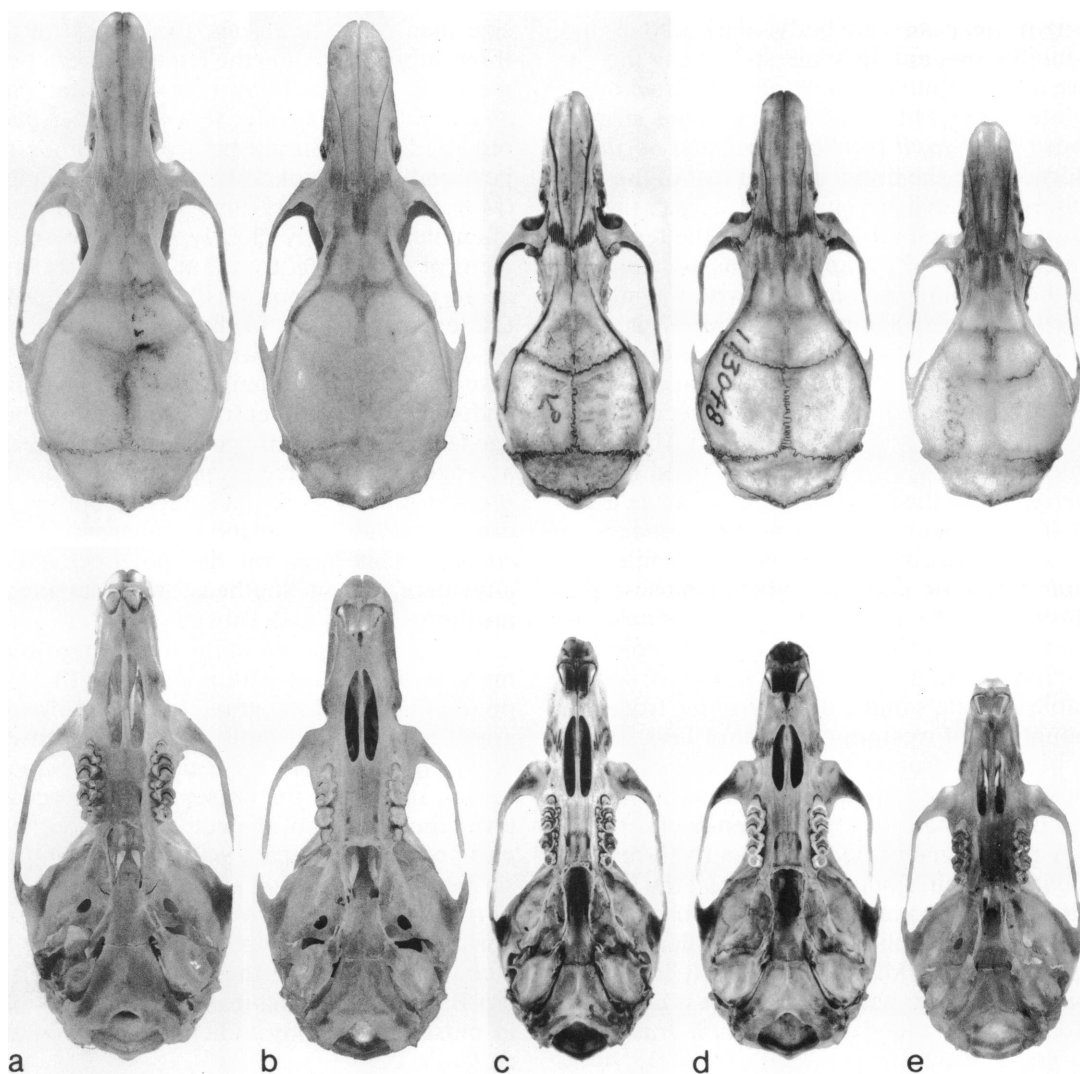


FIG. 11. Dorsal (top) and ventral (bottom) views of adult crania from species of *Niviventer*: a, *N. coxingi* (AMNH 185160), Taiwan; b, *N. coxingi* (AMNH 115253) from northern Burma, which is sympatric with the grayish *N. confucianus* (c) as represented by BM 11.12.1.118 from China and the reddish brown *N. fulvescens* (d), as exemplified by AMNH 113048 from northern Burma; e, *N. hinpoon* (AMNH 237587), Thailand. Approx. $\times 1.5$.

ples from western regions (Osgood, 1932; Allen, 1940). Osgood (1932, p. 305), who pointed out the close similarities between the western *fulvescens* and the eastern *huang*, also noted that "The relationship of *fulvescens* to southern forms is obvious in several

instances, especially in that of *R. f. bukit* which can at most be no more than a subspecies. . . ." Marshall (1977) agreed but used the name *bukit* to refer to this rat—in his view, the species occurred both in Southeast Asia and on the Sunda Shelf. Both *N.*

fulvescens and *N. confucianus* are found together over an extensive part of their respective ranges (Allen, 1940). The two kinds are often difficult to distinguish from one another (fig. 12), a situation so perplexing that Ellerman (1949, p. 81) suggested that the dark gray associated with *confucianus* and the bright reddish hues thought to characterize *fulvescens* and *huang* were possibly only color phases of one species. Osgood (1932, pp. 306–307) recognized the problem but maintained that the two could be distinguished:

Distinction of *R. confucianus* and *R. fulvescens* in overlapping areas, while generally obvious, is often very difficult as to individual specimens. In *confucianus* and its forms, the size is larger, the color darker, the tail is frequently white-tipped and the breast marked with fulvous; the auditory bullae are larger and more globose, the nasals longer and more compressed behind, and the molars are heavier. Apparent contradictions in these characters or in the combination of them crop out in disquieting manner in a number of instances, but they hold in such a large proportion that their significance is scarcely to be doubted.

That view prevails today.

Two other groups can be sorted out within the *niviventer*-complex but the relationships between each of them and the other clusters discussed above are obscure. One is a small rat, probably the smallest in body size of any species in the *niviventer*-complex, with gray upperparts that is found in the mountains from Sikkim westward to northeastern Pakistan (the latter is a new record based on USNM 359793 from 2 miles southwest of Yakh Tangai and 6 miles east of Shangla Swat, 6000 feet). The oldest name in the genus, *niviventer*, applies to samples of this rat. Its specific limits are yet to be defined. Ellerman (1961) recognized *niviventer* as occurring together with *fulvescens* and broadened its definition to include *confucianus*, a view that has prevailed with only a few exceptions (Marshall, 1977; Musser and Chiu, 1979). Niethammer and Martens (1975), however, studied a large sample of the *niviventer*-complex from Nepal, could not distinguish two different kinds, and concluded

that *fulvescens* was simply a bright reddish phase of *niviventer*. But, Abe (1977), who also examined a large series of specimens from Nepal, could clearly distinguish two kinds on the basis of pelage coloration, relative length of tail, configuration of the interorbital area (see fig. 12a–b), and inflation of the braincase. I have not seen the material examined by these people, and my few samples are small, but the specimens in them can be separated into two kinds by using the distinguishing features noted by Abe. Until the *niviventer*-complex is taxonomically revised, I use *niviventer* for the small-bodied gray rat that occurs from northeastern Pakistan to Sikkim, but no farther; there is yet no convincing evidence that the Nepalese populations are the same as those from areas farther east in northern Burma and China.

The other group that is poorly understood consists of specimens from the mountains of Assam, peninsular and southern Burma, and northern and southern Vietnam. All are large-bodied rats with long tails, either soft or spinous bright pelage, large skulls (fig. 12e), and relatively large bullae. They approach the body and skull size of *N. coxingi* from northern Burma, but their teeth are smaller and bullae much more inflated relative to size of the cranium. They are most common at high elevations and occur together at middle elevations with a smaller rat that has been identified as either *bukit* or *fulvescens*. Osgood (1932) referred a large series of this mountain form obtained from Chapa, in northern Vietnam, to *confucianus*, recognizing that the specimens were larger and more brightly colored than typical examples of that species. If the large-bodied mountain rat is a different species, the name *N. tenaster* is available for it.

The *niviventer*-complex clearly requires taxonomic revision to solve the problems that now exist, especially the following examples.

1. Specimens of *N. coxingi* from Taiwan and northern Burma are similar in coloration, and in cranial and dental configurations and proportions to those in samples of *N. rapit* from the Sunda Shelf. Are they closely related? Do they represent relicts of

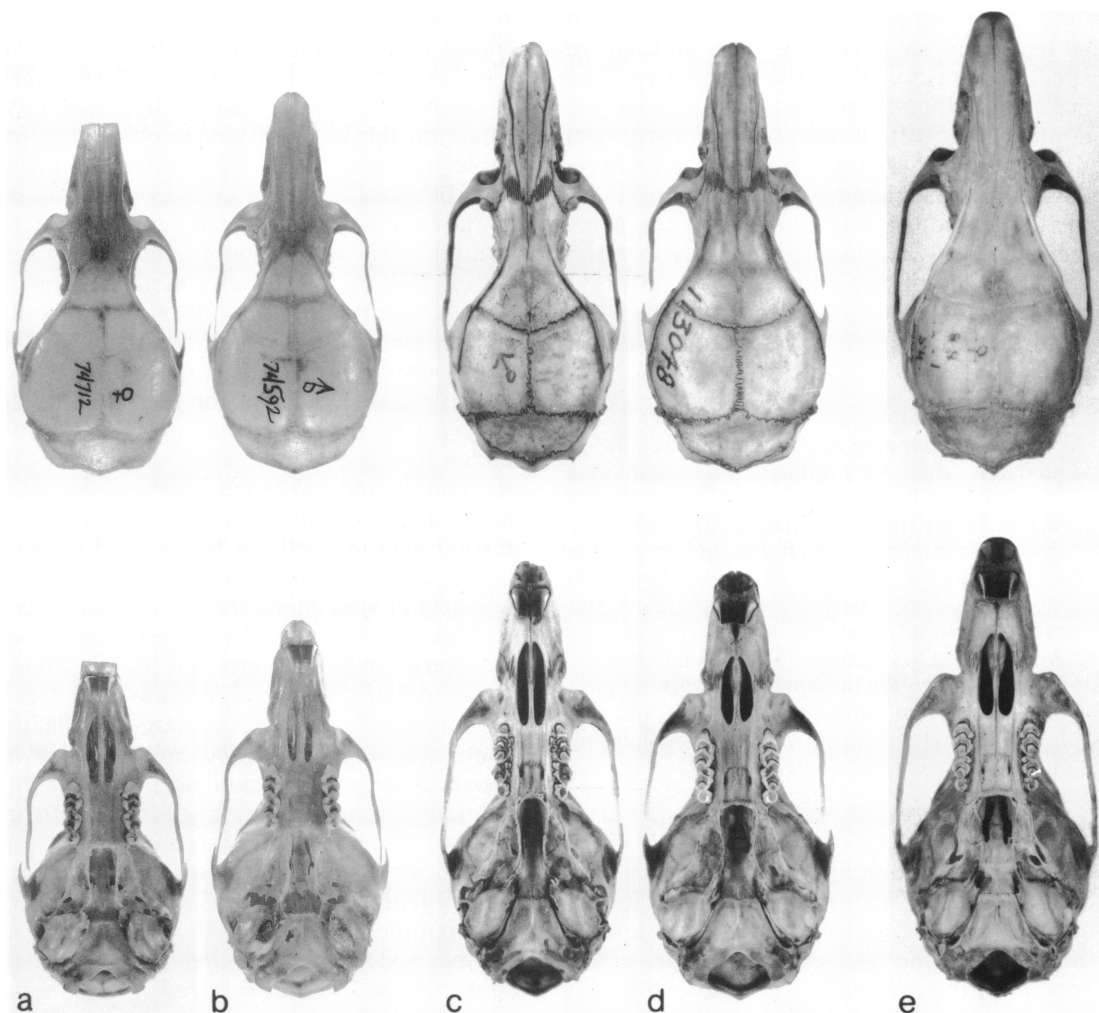


FIG. 12. Dorsal (top) and ventral (bottom) views of adult crania from examples in the *niviventer*-complex of *Niviventer*. Left pair: a, the gray *N. niviventer* (ROM 74712) and b, the reddish brown *N. fulvescens* (ROM 74952), examples of small body size from Nepal. Center pair: c, the grayish *N. confucianus* (BM 11.12.1.118) and d, the reddish brown *N. fulvescens* (AMNH 113048), examples of medium body size found in China, northern Burma, Thailand, Laos, and Vietnam. Far right: e, an example (BM 88.12.1.54) of the large-bodied *Niviventer* that occurs in the mountains of Assam, southern Burma, and Vietnam. Approx. $\times 1.5$.

a species that at one time occurred throughout Southeast Asia and the Sunda Region, or does each represent an independent unit derived from a common ancestor? Is the population in northern Burma really reproductively the same as that on Taiwan?

2. Do the large-bodied rats on mountains in Assam, southern Burma, and Vietnam represent montane outliers of *N. confucianus*, or are they a different but closely related species, *N. tenaster*?

3. Are *N. niviventer* and *N. fulvescens* in

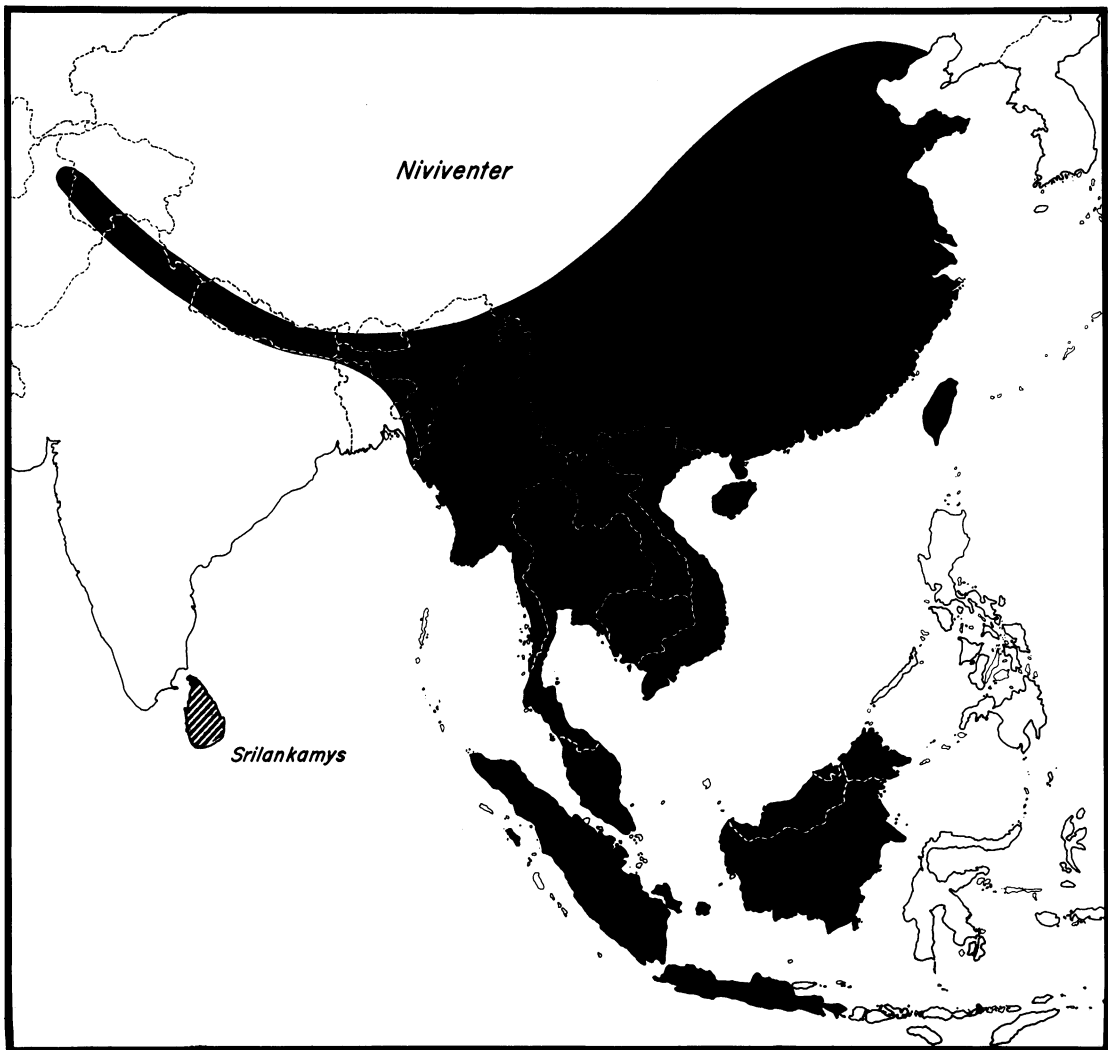


FIG. 13. A summary of the geographic distribution of *Niviventer* and *Srilankamys*.

Nepal two species, or do they represent color phases only of one species? What is the relationship between *N. niviventer* and *N. confucianus*?

4. Marshall (1977) recognized *N. rapit* from Thailand under the banner of *N. rapit orbis*. I have looked at the same material he studied but cannot relate the specimens to anything but samples of *N. fulvescens* from Assam, northern Burma, southern China, and Vietnam. What is the relationship between *orbis*, *fulvescens*, and *huang* on the

one hand and the Sundanese *bukit* on the other?

The identification of subfossil and Pleistocene specimens and the past geographic distributions of the species they represent is another problem in understanding the overall taxonomy and geographic distribution of species in *Niviventer*. *Niviventer* is one of the few genera of living Chinese murids that is represented by subfossil and Pleistocene material. Some of the specimens identified as *Epimys rattus* by Young (1934), Pei

(1936), and Teilhard (1938) are examples of *Niviventer*; particular specimens, including some I have in front of me that are from the collection of the Department of Paleontology at the American Museum of Natural History, are inseparable from what I am calling *N. confucianus*. All the fossils come from the Choukoutien area and are preserved in sediments that may be Pleistocene or younger. Most of the material should be carefully re-examined to determine what species are

present, and if any of them might be *N. andersoni* or *N. excelsior*, species now known only from Western China.

Niviventer contains at least seven well-defined species and possibly as many more that are yet incompletely known. The *sabanus*-group, the next cluster to be formally excluded from *Rattus*, contains far fewer species than does *Niviventer*, but they occur over much of the same geographic region and also require careful taxonomic revision.

THE SABANUS-GROUP

Ellerman (1947–1948, 1949, 1961) recognized the distinctness of *edwardsi* and *sabanus* by placing them together in *Leopoldamys*, which he treated as a subgenus of *Rattus*. Misonne (1969) also noted that the two species were closely related but went further than Ellerman and included them, along with *musschenbroekii*, *whiteheadi*, *rajah*, *hellwaldii*, *baeodon*, *ohiensis*, and *nativitatis*, in *Leopoldamys*—an unlikely cluster in view of the diverse morphological characteristics represented by these nine species. Misonne (1969, p. 138) admitted that “The species which compose this subgenus are not so closely linked to each other as those in the subgenera *Rattus* or *Stenomys*; . . .” Marshall (1976, 1977) used *Leopoldamys* as a subgenus of *Rattus* and included *edwardsi* and *sabanus* in it, as well as *neilli*, a new species he described (Marshall, 1976) based on specimens from Thailand. Taxonomists have consistently underestimated the wide morphological gap between species of *Leopoldamys* and those of *Rattus*; the former is as distinct from the latter, if not more so, as are *Maxomys* and *Niviventer*. *Leopoldamys* is characterized below.

GENUS *LEOPOLDAMYS* ELLERMAN (1947–1948)

TYPE SPECIES: *Mus sabanus* Thomas (1887, p. 269), based on an adult male (BM 95.10.4.27) collected by John Whitehead from the slopes of Gunong Kinabalu at an

altitude of more than 3000 feet in Sabah, North Borneo.

INCLUDED SPECIES AND KNOWN DISTRIBUTIONS: I recognize four species of *Leopoldamys*, as listed below.

SOUTHEASTERN ASIA NORTH OF THE ISTHMUS OF KRA (10° 30' N)

L. neilli: Thailand

SOUTHEASTERN ASIA AND THE SUNDA SHELF

L. edwardsi (including *listeri*, *melli*, *milleti*, *gigas*, *ciliatus*, *garonum*, *setiger*): Darjeeling District of West Bengal, Sikkim, northern Assam, northern Burma, southern China, northern Thailand, Laos, northern Vietnam, mountains of southern Vietnam, mountains of the Malay Peninsula, and the Sumatran highlands

L. sabanus (including *macrourus*⁵, *nasutus*,

⁵ Husson (1963) has shown that the holotype of *Echymys macrourus* Jentink, 1879, a long-tailed spiny rat thought to have come from Suriname, is really an example of what is currently called *Rattus sabanus*, and that the name *macrourus* is older than *sabanus*. Husson (1963, p. 40) explained the nomenclatural implications:

“The fact that *Echymys macrourus* Jentink, 1879, proves to be identical with *Rattus sabanus* (Thomas, 1887), originally described from Mt. Kinabalu, North Borneo, has several nomenclatural implications. Jentink’s name, being the oldest for the species has to replace the name *sabanus*. If Jentink’s type really came from West Sumatra, the name *sabanus* could still be retained for the Bornean subspecies, while either the form now known as *Rattus sabanus tapanulius* Lyon,

luta, *vociferans*, *ululans*, *tapanulius*, *lucas*, *heptneri*, *tersus*, *lancavensis*, *dictatorius*, *salanga*, *stridens*, *fremens*, *strepitans*, *bunguranensis*, *mansalaris*, *tuancus*, *masae*, *balae*, *mayapahit*, *stridulus*, *matthaeus*, *stentor*, *insularum*, *clarae*, *herberti*, *rever-tens*): Vietnam, Cambodia, Laos, Thailand, Bangladesh, Malay Peninsula, Sumatra, Borneo, Java, and smaller islands on the Sunda Shelf

MENTAWAI ISLANDS

L. siporanus (including *soccatus*): North Pagai, South Pagai, Sipora, and Siberut

EMENDED DIAGNOSIS: Large-bodied murids characterized by the following combination: very long tails; short and sleek pelage; four pairs of mammae; a long and narrow cranium, short and oblong incisive foramina; palatal bridge ending before or at backs of maxillary tooththrows; slitlike sphe-nopalatine vacuities; pterygoid fossae not perforated by large foramina; very small bullae pressed tightly against the squamosal bones; squamosal roots of zygomatic arches set very high on sides of braincase; strut of alisphenoid bone between masticatory-buc-cinator foramina and foramen ovale acces-sorius; mandible with small coronoid processes and shallow emargination between condyloid and angular processes; large and

strong incisors with bright orange enamel layers, uppers strongly opisthodont; upper molars large and simple in occlusal patterns, no cusp t7, no posterior cingulum except in *L. siporanus*, cusp t3 usually absent from second molar and always absent from third; first upper and lower molars with four roots (anterior, posterior, lingual, and a small labial); lower molars with simple occlusal patterns, no antero-central cusp, and anterolabial cusp absent from second and third molars; $2N = 42$ or 44 , two or three pairs of small metacentrics, the rest telocentrics or subtelocentrics.

DESCRIPTION: The species of *Leopoldamys* closely resemble one another in features of skins, skulls, teeth, and chromosomes. All are large-bodied rats with tails that greatly exceed the combined lengths of head and body (see the measurements of Thai *L. neilli*, *L. sabanus*, and *L. edwardsi* provided by Marshall, 1977; those of Malayan *L. edwardsi* and *L. sabanus* listed by Yong, 1970; and those of Chinese *L. edwardsi* given by Allen, 1940; Ellerman (1961) also listed measurements of *L. edwardsi* and *L. sabanus* that are in the British Museum; Marshall (1977) has presented photographs of living *L. edwardsi*, *L. sabanus*, and *L. neilli*). All species have short and sleek pelage in which the guard hairs over the back are either as long as the overfur or barely extend beyond it. Color of the upperparts is sharply demarcated from that of the underparts. The head and body are brown above and white below in *L. edwardsi*, rich buffy or ochraceous brown above and either white or cream on the venter in *L. sabanus*, dull grayish brown on top and pure white below in *L. neilli*, and dark to blackish brown on the upperparts and white over the underparts with brown pectoral patches and mid-thoracic strips in *L. siporanus*. The tails of *L. edwardsi* are dark brown above and either white, mottled, or grayish brown below; the basal two-thirds or half are blackish brown and the distal half or third is either white or mostly white with patches of dark brown on tails of *L. siporanus*; and the tails are patterned in brown and white with the distal third either all white

1916 (type locality Tapanuli Bay, North-West Sumatra), or *Rattus sabanus ululans* (Robinson & Kloss, 1916) (type locality Siolak Dara, Korinchi Valley, South-West Sumatra), should then become known as *Rattus macrourus macrourus* (Jentink, 1879), since this is the typical subspecies of Jentink's species. It will be up to a reviser of this group of the genus *Rattus* to decide whether the specific and subspecific identity of *Rattus macrourus* can be ascertained from Jentink's incorrectly labelled and faded type specimens, of which, moreover, the skull is not extant, or whether, in order to prevent confusion, it would be better to have the name *macrourus* suppressed under the Plenary Powers of the International Commission on Zoological Nomenclature."

I use *sabanus* in the present report and leave the nomenclatural problem with whoever eventually revises the taxonomy of all the named forms now associated with *sabanus*. To suppress the name *macrourus* would probably be the most sensible action because the name *sabanus* is entrenched in the literature and tied to a good type specimen taken from a known locality.

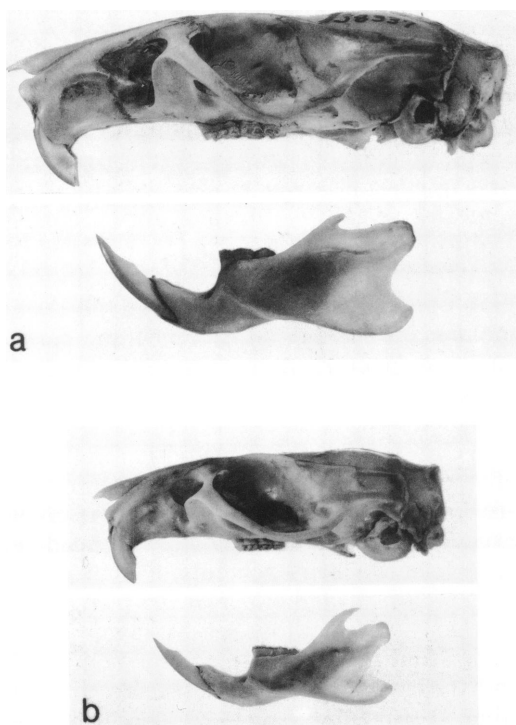


FIG. 14. Side views of adult crania and mandibles: a, *Leopoldamys*, as exemplified by *L. edwardsi* (AMNH 38337) from China is contrasted with *Rattus* (b), represented by *R. rattus diardii* (AMNH 250104) from Java. Natural size.

or all brown above and white below from base to tip in *L. sabanus* and *L. neilli*. There are three hairs emerging from each tail scale. The ears are small, brown, and scantily haired. The hind feet are long and slender, each has six distinct plantar pads (see the photographs in Medway and Yong, 1976). The front and hind feet of *L. edwardsi*, *L. sabanus*, and *L. neilli* have broad brown strips down the dorsal surfaces; the entire upper surfaces of the feet in *L. siporanus* are dark brown. Females of each species have four pairs of mammae: one pectoral pair, one postaxillary pair, and two inguinal pairs.

The conformation of the skulls is similar among the species (fig. 15). Viewed from above, the cranium of each is long and narrow, as are the nasals, which are set in the

top of an elongate rostrum. The zygoma form graceful arches. The interorbital area is wide, as is the braincase. The dorsolateral sides of the braincase are bounded by prominent ridges that sweep forward from the occiput to the dorsolateral margins of the interorbital area. The interparietal bone is large, forming nearly the entire roof of the occipital portion of the cranium.

Viewed from the side (fig. 14) the cranium is low, especially the braincase, and the zygomatic plates are moderately wide, but do not extend appreciably ahead of the dorsal roots of the zygomatic arches. The squamosal root of each zygomatic arch originates high on the braincase and the back margin of the root extends caudad as a low ridge all the way to the occiput. The area between the top of each squamosal root and the temporal ridge is very small relative to size of the braincase, forming a small area for the origin of the temporal musculature. The sides of the braincase beneath the squamosal roots are entire and extend down to the tympanic bullae, embracing them along their tops and front so that the bullae are firmly anchored to the squamosal bones, and the postglenoid vacuity above each bulla is small and inconspicuous. The portion of the alisphenoid bone at the base of the braincase just above each pterygoid ridge is perforated by the foramen ovale accessorius at the back and a large opening set anteriorly that is the combined masticatory and buccinator foramina. Between the latter and the foramen ovale accessorius is a strut of alisphenoid bone that forms the lateral wall of the alisphenoid canal as it passes through this part of the braincase wall.

Viewed from below (fig. 15), the incisive foramina are short, wide, and oblong in outline; they are longer relative to length of the diastema in *L. edwardsi* than in the other species; their posterior margins end well in front of the anterior faces of each toothrow. The palatal bridge is wide, scored by shallow palatine grooves, and terminates before the back edges of the tooththrows in most specimens, at the back faces in a few. The postpalatal distance is great, forming half or more of the total length of the skull. The meso-

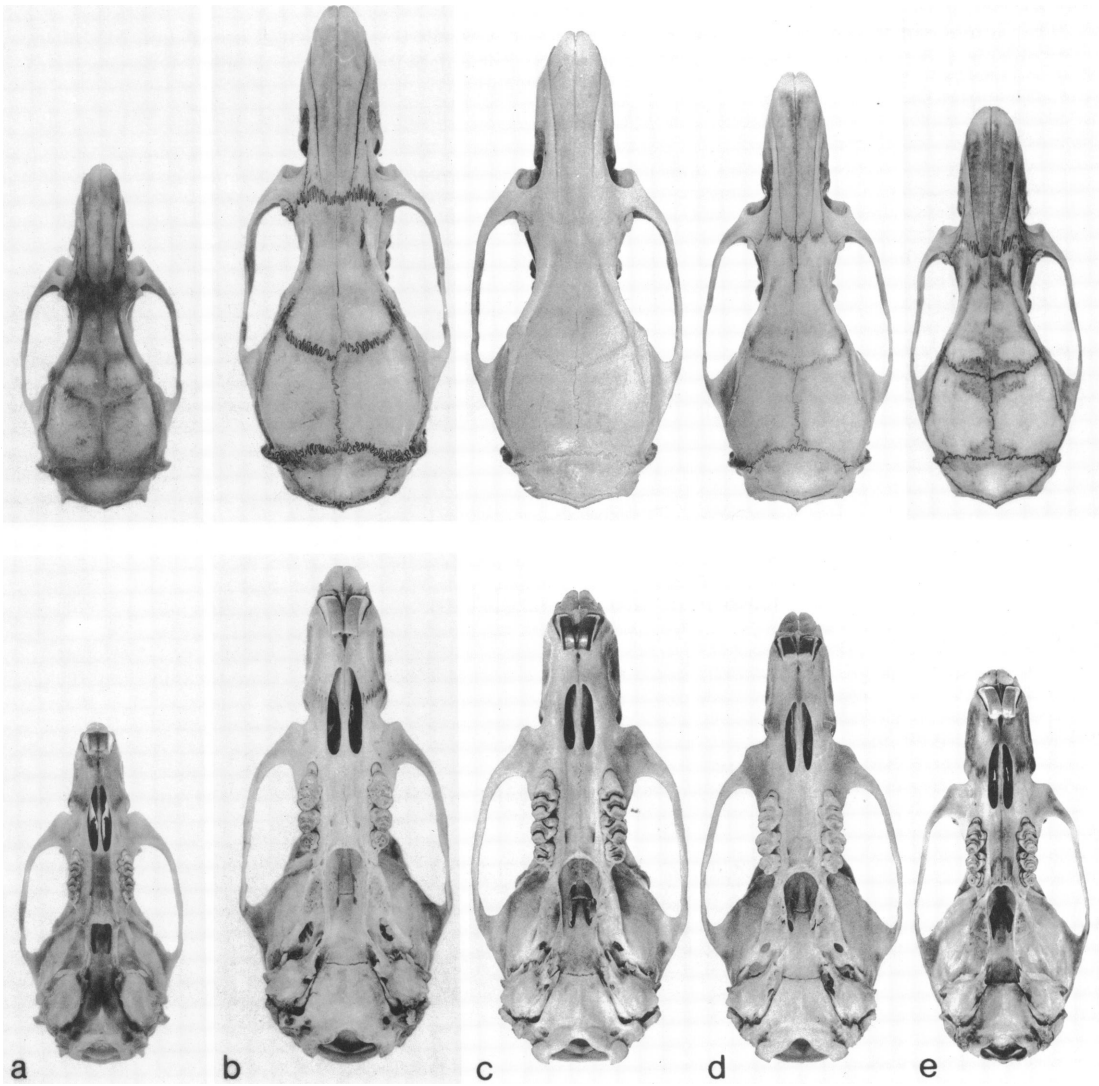


FIG. 15. Dorsal (top) and ventral (bottom) views of adult crania. *Rattus rattus diardii* (a) from Java (AMNH 250104) is contrasted with four species of *Leopoldamys*: b, *L. edwardsi* (AMNH 38337), China; c, *L. siporanus* (AMNH 103052), North Pagai Island; d, *L. sabanus* (AMNH 135025), Malay Peninsula; e, *L. neilli* (AMNH 237591), Thailand. Natural size.

pterygoid fossa is as wide as the palatal bridge, wider in some specimens. Its walls and roof are nearly intact, perforated only by short slits. The pterygoid fossae anterior of the foramen ovale are complete and nearly flat; the anterior half of each is minutely pitted and penetrated by tiny foramina. The

bullae are very small, absolutely and relative to size of the braincase. The long, slim bony eustachian tube in front of each is about two-thirds as long as the bulla itself.

The conformation of each dentary in *Leopoldamys* is closely similar to those in *Niviventer*. The capsular projections are more

TABLE 3
The Number of Roots on M_1^a ; and Presence (+) or Absence (–) of Cusp t3 on M^2 and M^3 , of the Anterior and Posterior Cusplets on M_1 , and of the Anterolabial Cusps on M_2 and M_3 in species of *Leopoldamys*
 (Number of roots, cusps, and cusplets in percentage; number of specimens in parentheses.)

	<i>L. edwardsi</i>		<i>L. siporanus</i>	<i>L. sabanus</i>		<i>L. neilli</i>
	Indochina	Malaya	Mentawai Isls.	Indochina	Malaya	Thailand
Number of roots on M^1						
4	87 (57)	100 (21)	98 (52)	92 (36)	100 (42)	100 (9)
5	13 (8)		2 (1)	8 (3)		
Cusp t3 on M^2						
+	16 (10)	10 (2)	27 (14)	23 (19)	24 (10)	67 (6)
–	84 (52)	90 (18)	73 (37)	77 (30)	76 (31)	33 (3)
Cusp t3 on M^3						
+					15 (6)	
–	100 (62)	100 (20)	100 (51)	100 (39)	85 (35)	100 (9)
Anterior cusplet on M_1						
+						
–	100 (62)	100 (20)	100 (51)	100 (39)	100 (40)	100 (9)
Posterior cusplet on M_1						
+	100 (62)	100 (20)	94 (48)	100 (39)	100 (40)	100 (9)
–			6 (3)			
Anterolabial cusp on M_2						
+	5 (1)					
–	100 (62)	95 (19)	100 (51)	100 (39)	100 (40)	100 (9)
Posterior cusplet on M_2						
+	100 (62)	100 (20)	100 (51)	100 (39)	100 (40)	100 (9)
–						
Anterolateral cusp on M_3						
+		5 (1)	4 (2)			11 (1)
–	100 (62)	95 (19)	96 (49)	100 (39)	100 (40)	89 (8)

^a Roots on M^1 :

4: three primary roots (anterior, posterior, lingual) and a small labial root.

5: a large anterior and posterior, small labial, and divided lingual.

prominent in the latter; otherwise, the mandible is a giant version of that in *Niviventer* (fig. 22).

The upper and lower incisors in each species of *Leopoldamys* are large, appear robust, and have orange enamel surfaces. The uppers curve strongly back as they emerge from the rostrum (opisthodont), a configuration evident when the cranium is viewed from the side.

Each first upper and lower molar in most specimens of all the species (table 3) is an-

chored by three large roots (anterior, lingual, and posterior) and a small labial root between the anterior and posterior roots. A large anterior root, large posterior one, and small labial and lingual roots anchor each first lower molar.

Upper molars in all species are large and have simple occlusal patterns (fig. 16). Their occlusal outlines and surface configurations resemble those in species of *Niviventer*, but the teeth are larger relative to the cranium and mandible and not as narrow, the laminae

on the first and second upper molars are not so strongly chevron-shaped, and each third upper molar is larger relative to the other two teeth in the row. The upper molars in *Leopoldamys* lack cusps t7 and usually cusp t3 on each first and second molar (except for *L. neilli*; table 3). Posterior cingula are absent from all but the first upper molars in some specimens of *L. siporanus*. Cusp t9 on each of the first two molars is small and incorporated into the adjacent and larger cusp t8 to the extent that its outline is nearly lost. Cusp t3 on the front row of the first molar is small and partially merged with cusp t2 so the front lamina appears formed of only small lingual and wide central cusps.

The lower molars are also large and simple in occlusal patterns (fig. 17). The anterolabial and anterolingual cusps on each first molar are pressed together and lean against the second row of cusps; an anterocentral cusp is absent. The posterior cingulum at the back of each first and second molar is wide and prominent. Only two labial cusplets occur on each toothrow, a posterior cusplet on each first and second molar. Anterolabial cusps are absent from the second and third molars.

Chromosome numbers and configurations are available for *L. edwardsi*, *L. sabanus*, and *L. neilli* (table 4). The species are karyologically similar with a 2N of 42 or 44, two or three pairs of small metacentrics, two or four pairs of subtelocentrics, and 13, 14, or 17 pairs of telocentrics. The composition is similar to that found in *Niviventer* and *Lenothrix* and fundamentally different and more primitive than that of *Rattus* (Yosida, 1973).

COMPARISONS: *Leopoldamys* requires comparisons with *Rattus* and *Niviventer*. In addition to the cranial and chromosomal characteristics listed previously, *Rattus* is distinguished from *Leopoldamys* by the following features (see also figs. 4, 5, 14, 16, 18, and 22).

1. Body size is much smaller and the tail is shorter relative to length of the head and body.

2. Tails of most species are brown all over.

3. The pelage is relatively longer, not as sleek, with prominent guard hairs that may be three times the length of the overfur.

4. Most species have gray underparts suf-

fused with brown, black, or buff; underparts of these are not strongly demarcated from the upperparts.

5. The incisive foramina are conspicuously longer, their posterior margins extending between the first molars.

6. The postpalatal distance is much shorter, less than half of the cranial length.

7. Each bulla is separated from the squamosal bone by a spacious postglenoid vacuity.

8. Configuration of the mandible differs from *Leopoldamys* in the same way as it does from *Niviventer*.

9. Incisors are absolutely and relatively smaller, the uppers either opisthodont or orthodont.

10. Five prominent roots (the lingual is divided into two) anchor each first upper molar.

11. Cusp t9 on each first and second upper molar is discrete, conspicuous, and not obliterated by merging with cusp t8 until the toothrow is extremely worn.

12. A large anterolingual cusp and a much smaller anterolabial cusp form the front lamina on each first lower molar; a small anterocentral cusp is present in many species.

13. Anterolabial cusps occur on second and third molars in all species.

The species of *Leopoldamys* superficially resemble greatly enlarged versions of some species of *Niviventer* in certain characters but the former is easily distinguished from *Niviventer* by the following features (compare also figs. 6–12 with 14–17).

1. Body size of all the species is much larger, giants compared to those in *Niviventer*.

2. Squamosal roots of the zygomatic arches originate higher on the braincase, just below the temporal ridges.

3. The incisive foramina are shorter relative to length of the diastema, rarely extending past the front faces of the first molars.

4. The bullae are smaller relative to size of the braincase and set in the squamosal bones more tightly.

5. The incisors are larger relative to the cranium and always opisthodont.

6. The first upper molars have four roots.

7. The third upper molar is larger relative to the others in each toothrow.

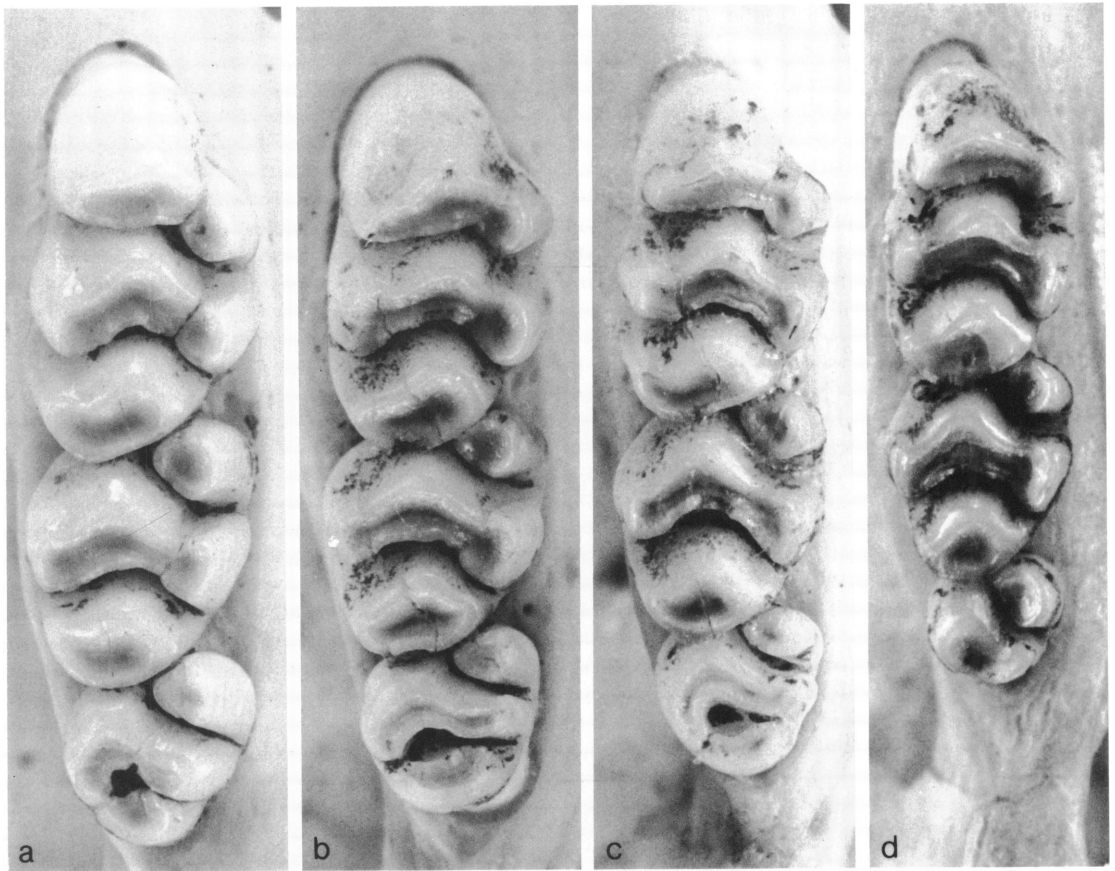


FIG. 16. Occlusal views of right maxillary tooththrows in species of *Leopoldamys*: a, *L. edwardsi* (AMNH 117426), China; b, *L. siporanus* (AMNH 103040), North Pagai Island; c, *L. sabanus* (AMNH 167924), Thailand; d, *L. neilli* (USNM 533481), Thailand. Approx. $\times 10$.

8. A posterior cingulum is present on each first upper molar in some specimens of at least one species.

9. A posterior labial cusplet occurs on the first and second lower molars in nearly all specimens.

10. The diploid number of chromosomes is lower and the number of small metacentrics and subtelocentrics slightly higher (table 4).

THE SPECIES OF *Leopoldamys*: *Leopoldamys* is another group that occurs in Southeast Asia north of the Isthmus of Kra and on the Sunda Shelf; off the Shelf it is found only on the Mentawai Islands (fig. 19).

Of the four species I have listed, only *L. neilli* is well defined. Found in the southern part of Thailand where it lives in limestone crags, *L. neilli* seems a dwarf version of *L. edwardsi*, but is distinguished from it and *L. sabanus* by distinctive external, cranial, dental, and chromosomal characteristics (Marshall, 1976, 1977).

The two groups that I listed as *L. edwardsi* and *L. sabanus* require taxonomic revision; what little bit we know of either species is contained in the results of only a few studies. The morphological and ecological relationships between *L. edwardsi* and *L. sabanus* on the Malay Peninsula was reported by

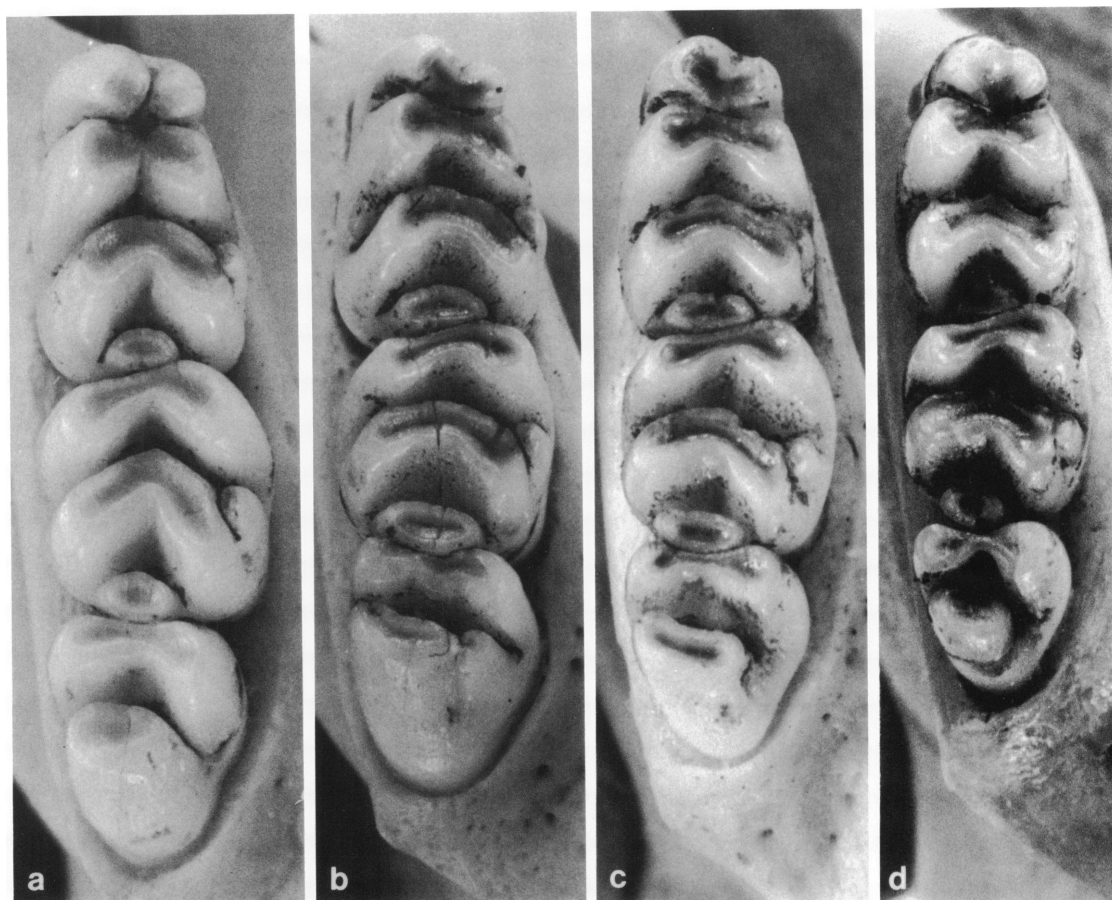


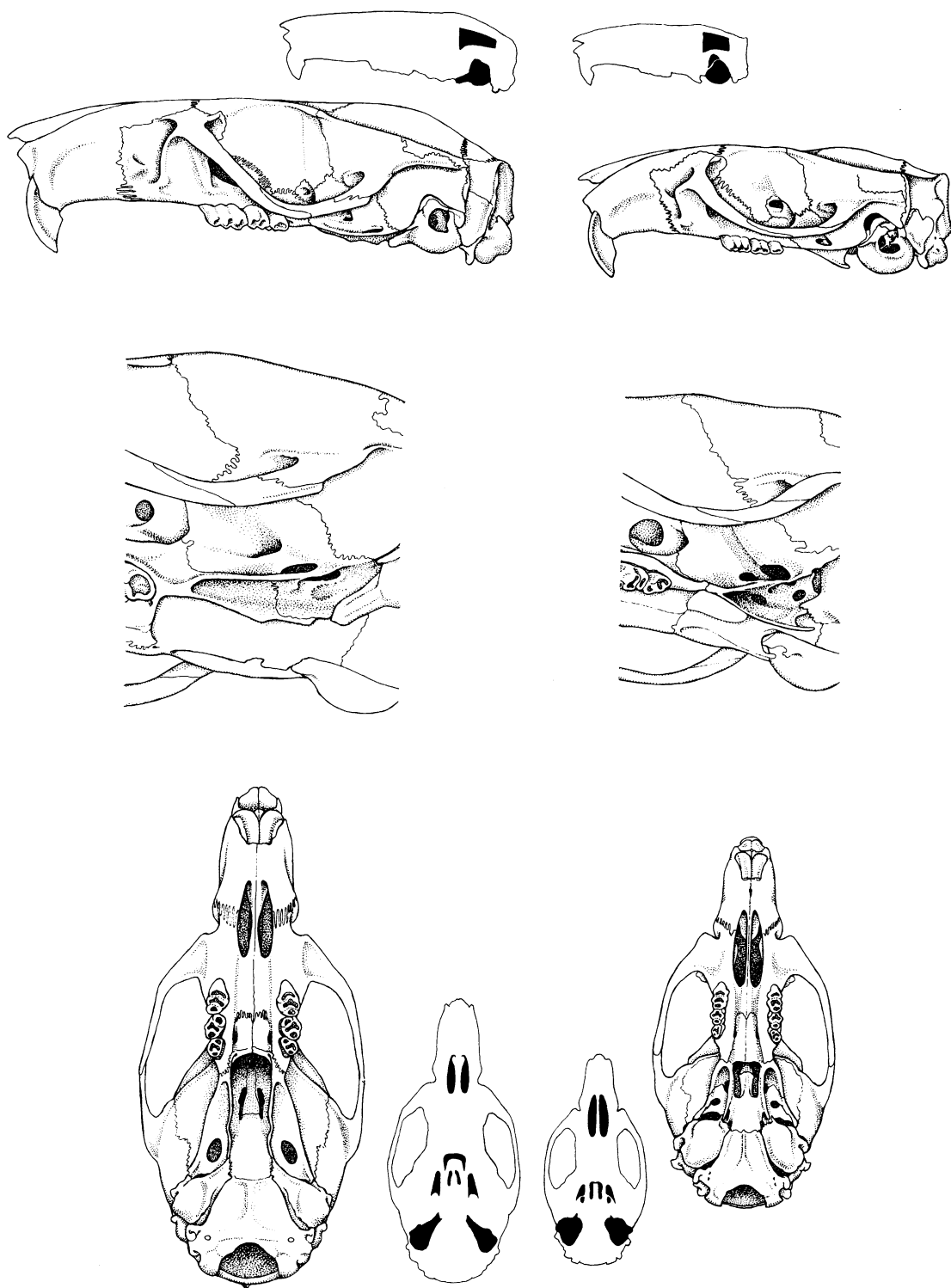
FIG. 17. Occlusal views of right mandibular toothrows in the same specimens of *Leopoldamys* that are shown in figure 16: a, *L. edwardsi*; b, *L. siporanus*; c, *L. sabanus*; d, *L. neilli*. Approx. $\times 10$.

Yong (1970), aspects of their distributions and morphologies in Thailand were given by Marshall (1976, 1977), the geographic distribution and variation of *L. edwardsi* in China was outlined by Allen (1940), the range of *L. sabanus* in southern Vietnam was provided by Van Peenen et al. (1969), their distributions and morphological variation in Indochina were touched on by Osgood (1932), and their characteristics and ranges were discussed by Ellerman (1961).

Whether all the taxa I have associated with *L. edwardsi* actually represent a single species has not been resolved. There may be, for example, two species within what is

now classified as *L. edwardsi*. Samples from the mountains of Sumatra and the Malay Peninsula differ in several cranial and pelage characteristics from those obtained in northern Indochina. There is a large hiatus in the geographic range between populations from northern Indochina and those from Malaya (see the map on p. 482 in Marshall, 1977). If that gap is a real one, the morphological differences may represent distinctions between two species rather than simply distinct geographic variants of one widely distributed species.

It is also uncertain whether one or more species is represented among the named



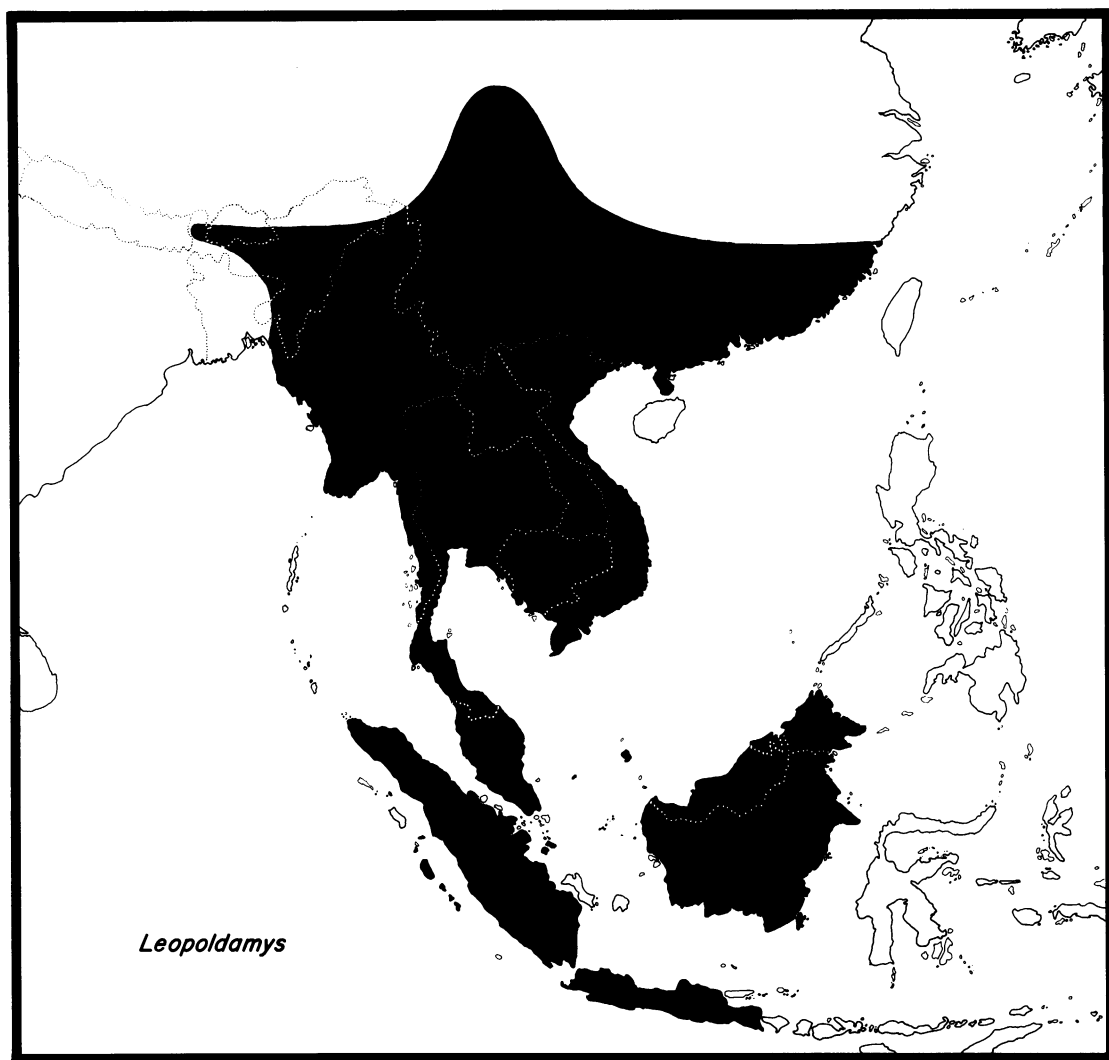


FIG. 19. A summary of the geographic distribution of *Leopoldamys*.

forms I list under *L. sabanus*. Do samples from north of the Isthmus of Kra represent the same species as those on the Sunda Shelf

south of the Isthmus? There is also appreciable morphological variation among insular samples of *L. sabanus* from the Sunda Shelf

←

FIG. 18. Cranial contrasts between *Leopoldamys* (left) and *Rattus* (right). Top pair: side views illustrating differences in position of squamosal root of zygomatic arch, size of bulla, and attachment of bulla to squamosal. Center pair: contrasts between alisphenoid region at base of the cranium. Bottom pair: differences in incisive foramina, back of palatal bridge, mesopterygoid and pterygoid fossae, and bullae. See text for explanations.

TABLE 4
Karyotypes from Samples of *Niviventer*, *Lenothrix*, *Leopoldamys*, *Maxomys*, *Margaretamys*, and *Rattus*

Taxon	Autosomes					Sex		FN	Reference
	2N	M	SM	ST	T	X	Y		
<i>Niviventer</i>									
<i>bukit</i> (Con Son Is., Vietnam)	46	3	0	1	18	T	T	54	Duncan, Van Peenan, and Ryan, 1970
<i>bukit</i> (Thailand)	46	3	0	4	15	T	T	60	Yosida, 1973
<i>bukit</i> (Thailand)	46	3	0	1	18	T	T	54	Markvong, Marshall, and Gropp, 1973
<i>bukit</i> (Malaya)	46	3	0	1	18	T	T	54	Yong, 1969a
<i>bukit</i> (Java)	46	3	0	4	15	T	T	60	Duncan, Irsiana, and Chang, 1974
<i>huang</i> (Hong Kong)	46	3	0	4	15	ST	T	61-♂ 60-♀	Yong, 1969b
<i>cremoriventer</i> (Malaya)	46	3	0	1	18	T	T	54	Yong, 1969a
<i>cremoriventer</i> (Java)	46	3	0	4	15	T	T	60	Duncan, Irsiana, and Chang, 1974
<i>confucianus</i> (North Thailand)	46	3	3	1	15	T	T	60	Markvong, Marshall, and Gropp, 1973
<i>rapit</i> (Malaya)	46	3	0	4	15	T	T	60	Yong, 1969a
<i>lepturus</i> (Java)	46	3	0	0	19	T	T	52	Duncan, Irsiana, and Chang, 1974
<i>hinpoon</i> (Thailand)	46	3	0	1	18	T	T	54	Marshall, 1977
<i>Lenothrix</i>									
<i>canus</i> (Malaya)	46	3	0	5	14	SM	T	63-♂ 62-♀	Yong, 1969a; Yosida, 1973
<i>Leopoldamys</i>									
<i>edwardsi</i> (Malaya)	42	3	0	4	13	T	T	56	Yong, 1969a
<i>sabanus</i> (Malaya)	42	2	0	4	14	T	T	54	Yong, 1969a; Yosida, 1973
<i>sabanus</i> (Thailand)	42	2	0	4	14	T	T	54	Markvong, Marshall, and Gropp, 1973
<i>sabanus</i> (Vietnam)	42	2	0	4	14	T	T	54	Duncan and Van Peenen, 1971
<i>neilli</i> (Thailand)	44	2	0	2	16	T	T	52	Marshall, 1977
<i>Maxomys</i>									
<i>bartelsii</i> (Java)	48	8	0	3	12	T	T	70	Duncan, Irsiana, and Chang, 1974
<i>Margaretamys</i>									
<i>beccarii</i> (Sulawesi)	42	2	0	0	18	?T	?T	46	Present report
<i>elegans</i> (Sulawesi)	42	0	7	0	13	T	SM	57-♂ 56-♀	Present report
<i>Rattus</i>									
<i>norvegicus</i> (Thailand)	42	7	0	4	9	T	T	62	Markvong, Marshall, and Chang, 1973
<i>nitidus</i> (Thailand)	42	7	1	2	10	T	T	60	Markvong, Marshall, and Chang, 1973
<i>losea</i> (Thailand)	42	7	0	2	11	T	T	58	Markvong, Marshall, and Chang, 1973
<i>argentiventer</i> (Thailand)	42	7	0	2	11	T	T	58	Markvong, Marshall, and Chang, 1973
<i>exulans</i> (Thailand)	42	7	0	2	11	T	T	58	Markvong, Marshall, and Chang, 1973
<i>rattus</i> (Thailand)	42	7	0	0	13	T	T	54	Markvong, Marshall, and Chang, 1973

(Abbreviations: 2N, diploid chromosome number; M, metacentric; SM, submetacentric; ST, subtelocentric; T, telocentric; FN, fundamental number.)

and nobody has yet determined whether it reflects insular variation within a single species or the presence of more than one species.

Leopoldamys siporanus must be the most

poorly known of the four kinds. Samples of it have been associated with either *L. sabanus* (Chasen, 1940) or *L. edwardsi* (Ellerman, 1949, 1961). The combination of large body size, dark brown to blackish brown up-

perparts, expansive brown pectoral and mid-ventral areas on the underparts, pattern of bicoloration on the tail, and large skull and teeth distinguish *L. siporanus* from both *L. sabanus* and *L. edwardsi*. Furthermore, there is a posterior cingulum, large and conspicuous on some specimens but small and indistinct on others, on many examples of *L.*

siporanus; this cusp is usually missing from samples of the other three species of *Leopoldamys*. There is every morphological indication that samples from the Mentawai Islands represent a distinct species, an hypothesis that can be tested with results from a careful taxonomic revision of *Leopoldamys*.

THE CEYLONESE *OHIENSIS*

The latest evaluation of the contents of *Leopoldamys*, that of Misonne (1969), included seven other species within it. Five of these (*musschenbroekii*, *whiteheadi*, *rajah*, *hellwaldii*, and *baeodon*) are members of *Maxomys*, not *Leopoldamys* (Musser, Marshall, and Boeadi, 1979). The sixth, *Rattus nativitatis*, known only from Christmas Island, does not belong in *Leopoldamys*. Ellerman (1949) did not think it belonged in the same group as *sabanus* and *edwardsi*, and its cranial features, skin characteristics, and body proportions, as described in Thomas's (1888) original report, are unlike *Leopoldamys*.

The seventh species, *ohiensis*, was allied by Phillips (1929, p. 168), its describer, to "*R. niviventer* (Hodgson)—the white bellied or bicolored rat of the Himalayas. It is curious to note how forms closely allied to Himalayan species crop up in Ceylon while they appear to be absent from the intervening country." Ellerman (1947–1948, p. 267), however, included *ohiensis* within the subgenus *Apomys* of *Rattus*, and for him, "This curiously isolated Ceylonese species agrees in the principal skull characters with the present subgenus. It has an unusually short tooth-row, as in *baeodon*, but differs from that species in the ridges on the skull being weaker, the palate longer in proportion, and the different shape of the palatal foramina." In 1949, Ellerman included *ohiensis* in the "*baeodon* Group" of the subgenus *Apomys*, *baeodon* being the only other species in that group. By 1961, Ellerman had placed *ohiensis* into the subgenus *Lenothrix* of *Rattus* but

the species was still enigmatic to him (Ellerman, 1961, p. 668): "This somewhat extraordinary species is not closely allied to other species referred to subgenus *Lenothrix* and is widely separated from them geographically. Nevertheless, it has the three characters, short palate, short foramina and small bullae, characteristic of that group as here understood. It differs from all others except the Bornean *R. baeodon* in its unusually short toothrow. From *baeodon* it differs in much weaker supraorbital regions, longer palate and the shape of the palatal foramina, which are narrow behind as well as in front. . . . It is curiously isolated in Ceylon and it is difficult to say what is really its nearest ally."

Misonne (1969, p. 140), the latest investigator to comment on the affinities of *ohiensis*, put it in *Leopoldamys*, which he regarded as a subgenus of *Rattus*. For Misonne, "*R. ohiensis* is an isolated species from Ceylon; it may be included in this group with some difficulty. . . . The same difficulties are met if *R. ohiensis* is compared with *Maxomys* [in which Misonne had placed the *niviventer*-group]; the molars characters would perhaps agree rather well, but not the skull characters; the bullae are too small and the incisive foramina too short. The presence of this species in Ceylon is difficult to explain, as there is no real *Rattus* in peninsular India, the genera *Millardia* and *Cremnomys* being no true *Rattus*."

In 1969, I examined the six specimens of *ohiensis* listed by Ellerman (1961, p. 668), including the holotype, that are in the British Museum, and I have before me an additional

example (USNM 519589), an adult female collected on the Horton Plains by George M. McKay on September 8, 1969. It is now clear to me why *ohiensis* has been so difficult to place within a particular subgenus of *Rattus* for the features of its skin, skull, and teeth are unlike any species of *Rattus*—either in the subgenus *Rattus* or in any of the other subgeneric groupings of species recognized by either Ellerman or Misonne—or any other Asian murid that has been named and described. There is nothing else quite like *ohiensis*; it is geographically restricted to mountain forest in Sri Lanka (Ceylon) and morphologically isolated from any other named form of Asian murid. The species belongs in its own genus, which is named and diagnosed below.

SRILANKAMYS, NEW GENUS

TYPE SPECIES: *Rattus ohiensis* Phillips (1929, p. 167), based, according to Phillips on an "Adult male; now in the British Museum [BM 29.1.30.1]. Caught on 1.12.28, at West Haputale Estate, Ohiya, altitude 6,000 ft., in the higher ranges of the central mountain cluster in Ceylon. . . . The Estate where the type specimen was trapped adjoins the forest that surround, on all sides, the highland plateau known as the Horton Plains."

INCLUDED SPECIES: The type species only.

KNOWN DISTRIBUTION: Uva Province of Ceylon (Sri Lanka); figure 13.

ETYMOLOGY: Named for the Republic of Sri Lanka, the political unit embracing the island of Ceylon.

DIAGNOSIS: A genus of medium-sized terrestrial murid with soft, dense, short fur; a bicolored tail longer than the combined lengths of head and body; eight mammae; weak postorbital and temporal beading; short incisive foramina, broad-ovate in outline and ending well before fronts of the molar rows; long palatal bridge ending just behind molar rows; small bullae; strut of alisphenoid bone between foramen ovale accessorius and buccinator-masticatory foramina; short, narrow sphenopalatine vacuities; no interpterygoid foramina perforating pter-

ygoid fossae; dentaries thin and delicate; upper and lower incisors small and narrow relative to size of cranium and mandible, their enamel surfaces ivory in color; maxillary and mandibular tooththrows short and molars very small relative to size of cranium and mandible; each first and second upper molar with anterior, posterior, and divided lingual root; each lower molar two-rooted; occlusal patterns of upper molars simple, cusp t7 absent from all teeth, cusp t3 absent from second and third molars; wide thick, and prominent posterior cingulum at the back of each first upper molar; posterior labial cusplets on first and second lower molars; anterolabial cusps on second and third molars.

MEASUREMENTS: Ellerman (1961, pp. 668–669) listed figures for some external and cranial measurements; the following values (in mm.) are from measurements taken on USNM 519589 (asterisks designate estimates; parts of the cranium were in pieces and had to be restored, as is evident in figure 20): length of head and body, 145; length of tail, 173; length of hind foot (including claw), 31; length of ear, 20; greatest length of skull, 39.0*; basilar length, 30.2*; interorbital breadth, 6.1; length of rostrum, 13.5; breadth of rostrum, 7.0; length of nasals, 15.5; breadth across incisor tips, 1.9; breadth of zygomatic plate, 3.7; depth of zygomatic notch, 1.4; length of diastema, 11.5; palatilar length, 17.3; palatal length, 19.5; postpalatal length, 13.5*; length of incisive foramina, 5.7; breadth of incisive foramina, 2.9; incisive foramina to M¹, 2.1; length of palatal bridge, 7.4; palatal bridge past tooththrows, 0.3; breadth of palatal bridge at M¹ and M³, 3.4 and 3.9, respectively; breadth of mesopterygoid fossa, 2.6; length of bulla, 5.2; alveolar length of M¹⁻³, 5.3; breadth of M¹, 1.5; length of M₁₋₃, 4.9; breadth of M₁, 1.5.

DESCRIPTION: (The following description of the species also applies to the genus.) *Srilankamys ohiensis* is a medium-sized rat. Its upperparts are glossy dark gray, slightly suffused with brown, a coloration extending from the base of the tail to the head, as well as below the cheeks and around the mouth. The underparts are pale cream and sharply demarcated from the dark dorsum. The dor-

sal pelage is soft, fine, dense, and short (12 mm. thick over the back) with guard hairs so short and fine that they barely extend beyond the overfur and are imperceptible, so the coat appears to be of uniform thickness over the sides of the body, back, and rump. The fur over the undersides of the head and body is also soft, fine, dense and short (6 mm. long). The rostral vibrissae are long and fine. The ears are small, scantily haired, and the same color as the dorsal fur. Tops of the front feet are mostly white except for a grayish brown strip extending from the forearm to the wrist. Upper surfaces of the hind feet are white for most of their lengths and brownish gray over the ankles. The hind feet are long and narrow, as are the digits. Each plantar surface is grayish brown, un haired and adorned with six small oblong pads, four interdigital and two plantar. Claws on both front and hind feet are small, short but not recurved. The tail is conspicuously longer than the combined lengths of head and body and finely scaled (12 rows of scales per cm.). It is sharply bicolored: dark grayish brown above, white below for the entire length and all around the last 5 mm. of the tip. The only female specimen I have seen has eight mammae: a pectoral pair, a postaxillary pair, and two inguinal pairs.

In dorsal view, the cranium of *S. ohiensis* is long, narrow, and appears delicate (fig. 20). The rostrum is long and tapered, ending in obtuse margins of the nasals. The interorbital region is wide, the braincase long and narrow. Low, inconspicuous beading outlines the dorsolateral margins of the interorbital and postorbital margins, becomes faint along the front half of the parietals, and disappears farther back on the braincase.

The braincase is deep, as seen in side view. Each zygomatic plate is wide, with a prominent anterior zygomatic spine. The squamosal root of each arch sits high on the side of the braincase. The configuration of the alisphenoid where it forms the braincase wall above each pterygoid fossa is similar to that in *Leopoldamys* and *Niviventer*—a strut of alisphenoid bone is present between the foramen ovale accessorius and the buccinator-masticatory foramina.

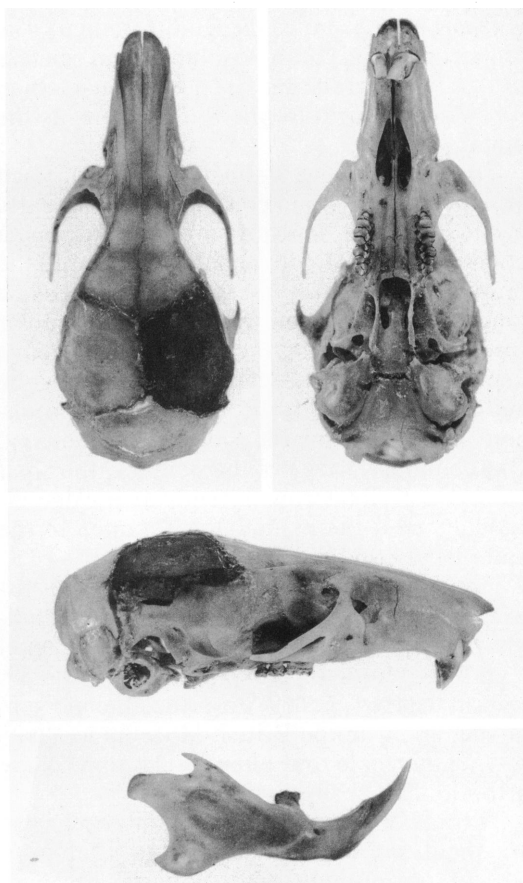


FIG. 20. Cranial and mandibular views of an adult female *Srilankamys ohiensis* (USNM 519589) from Ceylon. Approximately $\times 1.5$.

From a ventral view, the cranium is distinctive in its combination of short incisive foramina, long palatal bridge, small molars, and small bullae. The incisive foramina are short, broad across their basal halves and tapered distally to form a broad-ovate outline; their back margins end at least 2 mm. before the front margins of the maxillary toothrows. The palatal bridge is wide and long, partly because the molars are small and the incisive foramina are short, its back edge extending only slightly beyond the toothrows. The mesopterygoid fossa is wide but narrower than the palatal bridge, its walls perforated by short and narrow sphenopalatine vacuities.

Each pterygoid fossa is nearly flat and solid, without a large interpterygoid foramen. The bullae are small, both absolutely and relative to size of the cranium. Each bony eustachian tube is one-fourth to one-third as long as the bulla behind it.

The dentaries are distinctive (fig. 22). Each is delicate and thin, contains small molars, has a small and delicate coronoid process, a condyle that is directed back well beyond the posterior margin of the angular process, a long portion between the front of the molar row and base of the incisor, and a concave ventral margin. The capsule containing the end of the incisor forms a large and prominent projection on the side of the dentary. On the inner surface of the dentary, the shelf behind the molar row extends as a ridge diagonally past the mandibular foramen to the end of the condyloid process.

Upper and lower incisors are small and narrow relative to size of the cranium and mandible, their surfaces smooth, and their enamel layers the color of ivory in USNM 519589. Ellerman (1961, p. 669) described the incisors of specimens in the British Museum as "narrow, rather pale and plain." The uppers are orthodont in position.

The maxillary and mandibular toothrows are small, not only absolutely but relative to size of the cranium and dentaries, respectively. In USNM 519589, each first and second upper molar is anchored by a large anterior and posterior root, and a lingual root that is solid at its base but distally divided into two so each tooth appears anchored by two primary roots and a divided lingual root. Each third upper molar has three roots. Each lower molar is anchored by two roots only, a large anterior and a large posterior.

The molars of all the specimens I have seen are worn but the occlusal patterns formed by the cusps are still evident (fig. 21). The occlusal surfaces of the upper molars are simple. The first two laminae of the first tooth are wide, horizontal for most of their widths, with the lingual portion of each (cusp t1 and t4, respectively) set well behind the horizontal segments. The large third lamina consists of cusp t8 merged with cusp t9. A

cusp t7 is absent from the posterolingual margin of the tooth. Behind cusp t8 and partly merged with it is a wide and thick posterior cingulum, plainly evident in figure 21.

The second upper molar has an even simpler occlusal pattern than the first. There is a large cusp t1, but no cusp t3 on the labial side, at least in USNM 519589. Misonne (1969, p. 140) claims there is a cusp t3 on the second molar but the cusp he illustrated seems too far in from the labial edge for cusp t3 and might instead be the posterior cingulum at the back of the first molar. The main lamina of the second molar is gently bowed, and the lamina at the back of the tooth consists of cusp t8 merged with cusp t9. Cusps t7 and posterior cingulum are absent.

Each third upper molar is small relative to the other molars. A large cusp t1; a comma-shaped lamina composed of cusps t4, t5, and t6; and an oblong cusp t8 comprise the occlusal surface. Cusps t3, t7, and posterior cingulum are absent.

The lower molars also have simple occlusal surfaces, consisting mostly of gently bowed thick laminae (fig. 21). The front lamina of the first molar is narrower than the second lamina and joins it after wear to form a deep basin that is triangular in occlusal outline. Each posterior cingulum at the back of the first and second molar is wide and thick. Although the teeth of USNM 519589 are worn, there is evidence of posterior labial cusplets on the first and second molars, and anterolabial cusps on the second and third molars.

COMPARISONS: *Srilankamys* requires comparisons with *Rattus*, *Niviventer*, *Leopoldamys*, and *Maxomys*, groups with which it has been associated by other taxonomists. *Srilankamys* differs from *Rattus* not only in the six cranial features already listed that also distinguish *Niviventer* and *Leopoldamys* from the latter but in the following characteristics as well.

1. Short, soft, and fine pelage (coarser, longer, with very long and conspicuous guard hairs in most *Rattus*).

2. A sharply bicolored tail (monocolored in most species).

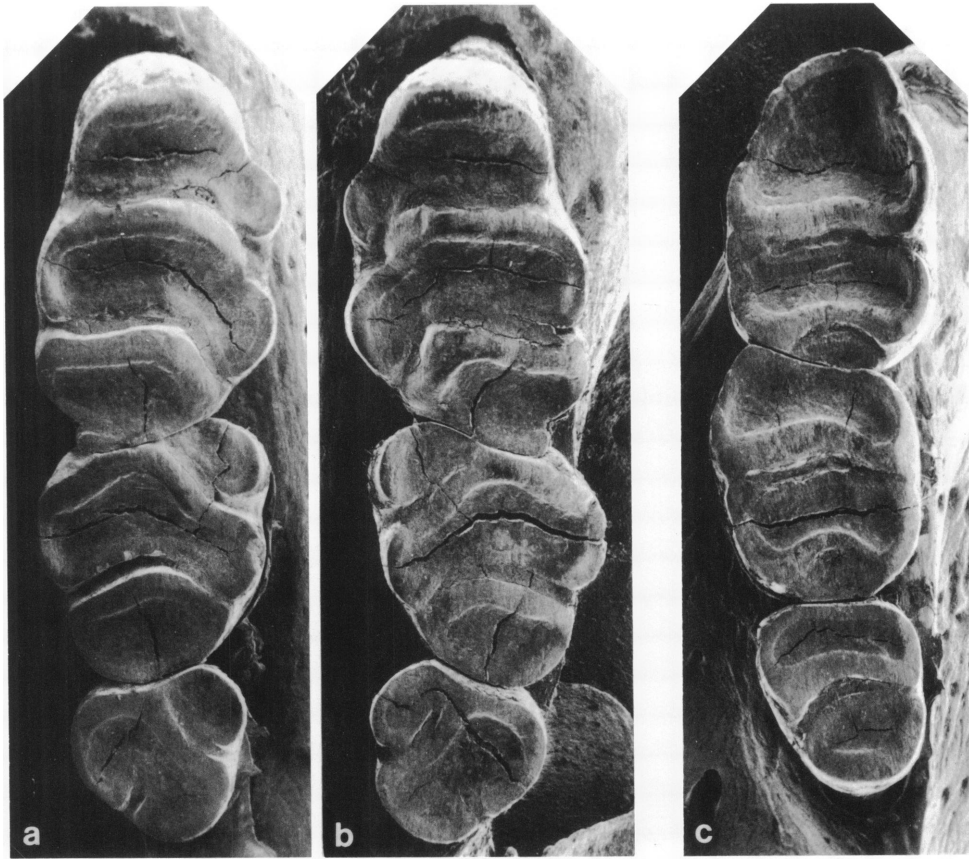


FIG. 21. Occlusal views of tooththrows in the same specimen of *Srilankamys ohiensis* that is depicted in figure 9: a, right maxillary tooththrow (LM^{1-3} , 5.0 mm.); b, left maxillary tooththrow (LM^{1-3} , 5.0 mm.); c, left mandibular tooththrow (LM_{1-3} , 4.9 mm.). Note the large posterior cingulum at the back of each first upper molar.

3. Weak postorbital and temporal beading (high ridges that sometimes are formed into shelves).

4. Very short and wide incisive foramina (long, oblong incisive foramina, terminating between the upper molars).

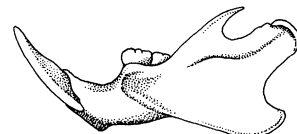
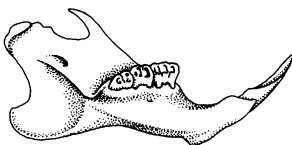
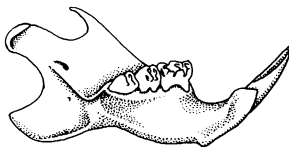
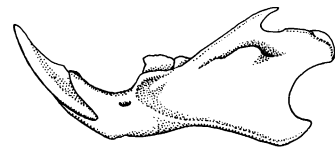
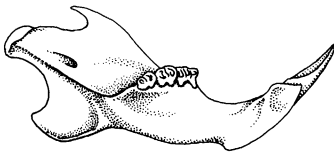
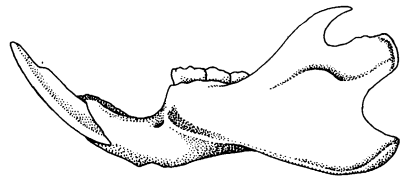
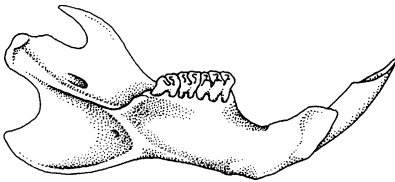
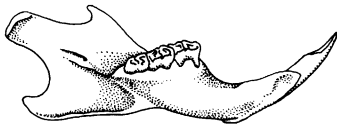
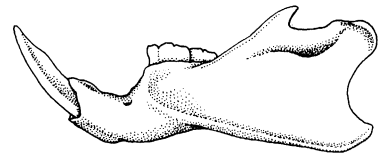
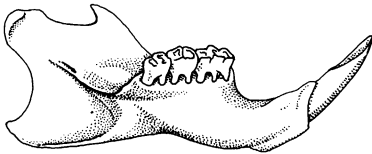
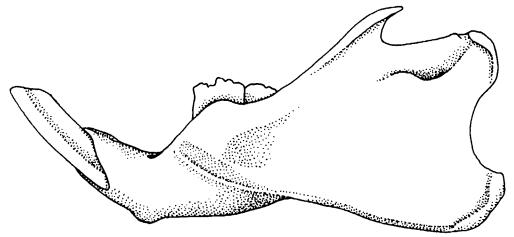
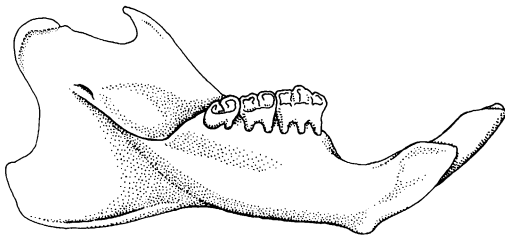
5. Thinner, more delicately built dentaries with smaller coronoid processes, and condyles that project farther posteriorly relative to the back margins of the angular processes (more robust dentaries, larger coronoid processes, posterior edges of condyles and angular processes about even).

6. Ivory-colored incisors (bright orange).

7. Incisors and molars are much smaller and appear more delicate relative to size of cranium and mandible (for example, the alveolar length of M^{1-3} is 14 percent of greatest length of skull in *S. ohiensis*, but an average of 17 percent for 20 specimens of *Rattus rattus diardii*).

8. Two primary roots and a divided lingual root under each first and second upper molar (five prominent roots anchor the first molar, four anchor the second).

9. Two large roots anchor each lower molar (four under each first and second molar, three under the third).



10. A large and conspicuous posterior cingulum at the back of each first upper molar (usually absent in *Rattus*, otherwise, a slight triangular enlargement at the back of cusp t8).

11. Cusp t3 absent from the second and third upper molars (present in most species).

Phillips (1929) thought *ohiensis* was possibly allied to the *niviventer*-group and the former does resemble *niviventer* in body size, pelage, color pattern of the body and tail, and number of mammae, but is unlike *niviventer* or any other species in that group in cranial and dental features. *Srilankamys* is set apart from *Niviventer* by the following.

1. The postorbital and temporal beading is much weaker and less distinct.

2. The incisive foramina are much shorter and broad-ovate in outline (oblong in outline and reaching to or just past the front faces of the upper first molars in *Niviventer*).

3. Each dentary is thinner, the condyloid process projects farther back relative to the angular process (about even), the incisor capsule is large and projects laterally away from the outer surface (smaller and contained in ridge extending from top of capsule to condyle), and there is a ridge running along the inner surface of the condyloid process (ridge fades out just beyond mandibular foramen and condyloid surface is nearly flat).

4. Incisors are ivory-colored (orange in *Niviventer*).

5. Incisors and molars are smaller and appear more delicate relative to size of cranium and mandible (the ratio, alveolar length of M^{1-3} /greatest length of skull, is 14 percent in *S. ohiensis*, 17 percent in a sample of 25 *N. confucianus*).

6. Anterior, posterior, and divided lingual roots anchor each first upper molar (most species with five roots, five and additional rootlets, or four roots in which the lingual

root is single and the fourth root is formed on the labial side between the anterior and posterior roots).

7. First lower molars are two-rooted (four-rooted).

8. A large posterior cingulum sits at the back of each first upper molar (absent in all species of *Niviventer*).

9. Anterolabial cusps are present on second and third lower molars (absent from second molars in some species, absent from third in all).

An association with *Leopoldamys* was proposed for *ohiensis* by Misonne (1969) but there is no evidence linking it to any species in that genus. *Leopoldamys* contains large-bodied, even giant rats; *ohiensis* is a small animal by comparison, more the body size of species in *Niviventer*. *Srilankamys* further contrasts with *Leopoldamys* as follows.

1. *Srilankamys* has very weak postorbital and temporal beading (high, heavy ridging in *Leopoldamys*).

2. The incisive foramina are short, broad-ovate in outline (longer and oblong in outline).

3. The bullae are larger relative to size of the braincase.

4. The dentaries of *Srilankamys* contrast with those in *Leopoldamys* in the same ways they do with dentaries of *Niviventer*.

5. The incisors are relatively small and weak, ivory in color, and the uppers orthodont relative to the rostrum (very large and strong, with bright orange enamel surfaces, and the uppers strongly curving back after they emerge from the rostrum).

6. Molars much smaller relative to size of cranium and mandible.

7. Two main roots and a divided lingual root are under each first upper molar (four roots also, but lingual is complete and labial root present between anterior and posterior roots).

←

FIG. 22. Internal (left) and external (right) views of left dentaries in seven murid genera: a, *Leopoldamys* (*sabanus*); b, *Niviventer* (*andersoni*); c, *Maxomys* (*bartelsii*); d, *Rattus* (*rattus*); e, *Srilankamys* (*ohiensis*); f, *Anonymomys* (*mindorensis*); g, *Margaretamys* (*beccarii*). Approx. $\times 1.7$. See text for explanations.

8. First lower molars are two-rooted (four-rooted in *Leopoldamys*).

9. A large posterior cingulum at the back of each first upper molar (absent from most samples, usually inconspicuous in *L. siporanus*).

10. Anterolabial cusps occur on second and third lower molars (absent from these teeth in *Leopoldamys*).

The Ceylonese rat has also been associated, either by Ellerman (1961) or Misonne (1969), with species that are now included in the genus *Maxomys* (Musser, Marshall, and Boeadi, 1979). Here again, the external features of *S. ohiensis* resemble those in *Maxomys*, except that the fur of *S. ohiensis* is finer and softer to the touch, not as dense and velvety, the texture so characteristic of *Maxomys*. The short and broad-ovate incisive foramina, small bullae, configurations of the mesopterygoid and pterygoid fossae, and high positions of the squamosal roots of the zygomatic arches in *Srilankamys* are also shared by *Maxomys*; but here the resemblances end. *Srilankamys* contrasts with *Maxomys* in the following cranial, mandibular, and dental features.

1. The postorbital and temporal beading is slight (heavy ridges beginning in the interorbital region and sweeping back and around the dorsolateral margins of the braincase, and forming wide shelves back of the orbit as in *Maxomys*; see the figures in Musser, Marshall, and Boeadi, 1979).

2. The braincase is higher and more inflated relative to size of the cranium.

3. The palatal bridge is longer, ending just beyond the back faces of the molar rows (the palatal bridge ends well before the backs of the toothrows, usually at the beginning or middle of each third molar).

4. The postpalatal distance is shorter, the postpalatal length being 69 percent of the pal-

atal length (the postpalatal length is longer in *Maxomys*, nearly the same length as the palate; the values range from 82 to 99 percent among the species; see table 3 in Musser, Marshall, and Boeadi, 1979).

5. A strut of alisphenoid bone is present between the foramen ovale accessorius and the masticatory-buccinator foramina (absent in most species of *Maxomys*—present in some examples of *M. moi*).

6. Each dentary is thinner and more delicate, the coronoid process is larger (a tiny nubbin in *Maxomys*), the condyle extends back past the posterior margin of the angular process (instead of being about even as in *Maxomys*), the incisor capsule protrudes conspicuously from the outer side of the dentary (instead of not projecting outward), and the inner surface of the condyloid process is ridged past the mandibular foramen (instead of smooth).

7. Relatively small incisors that have ivory-colored enamel surfaces (relatively larger and appear stronger, bright or pale orange).

8. Upper and lower molars are smaller, relative to size of cranium and mandible, than in most species of *Maxomys* (the ratio, alveolar length of M^{1-3} /greatest length of skull, is 14 percent in *S. ohiensis*; 14 percent also in *M. baeodon* and *M. moi*; 15 percent in *M. alticola*, *M. bartelsii*, *M. dollmani*, *M. inflatus*, *M. ochraceiventer*, *M. pagensis*, and *M. panglima*; 15 or 16 percent in *M. surifer*; 17 percent in *M. inas*; 18 percent in *M. musschenbroekii* and *M. whiteheadi*; and 19 percent in *M. hylomyoides*).

9. A large posterior cingulum at the back of each first upper molar (absent in all species of *Maxomys*).

10. An anterolabial cusp occurs on each third lower molar (absent in most samples of *Maxomys*; see table 4 in Musser, Marshall, and Boeadi, 1979).

THE *BECCARII*-GROUP

The fourth group discussed here consists of three species from Sulawesi, two of them

new and the third—*beccarii*—known since 1880 but represented by few specimens. Ex-

cept for the original description where it was proposed as a species of *Mus* (Jentink, 1880), *beccarii* has usually been included within the genus *Rattus*. Tate (1936), for example, placed it in his *Rattus cremoriventer*-group, which was part of a larger category, the *Rattus-huang-hellwaldii-sabanus*-division; Ellerman (1949) included *beccarii* in his *niviventer*-group of *Rattus*, noting that he had never examined any examples of the species; Misonne (1969), however, did not think *beccarii* belonged in the *niviventer*-group but expressed no other opinion about its relationship. Several years ago, I examined the type-specimens associated with *beccarii* (Musser, 1971) and later (Musser, 1977) suggested that the species might have morphological ties to *Limnomys*, small-bodied rats from the island of Mindanao in the Philippines. I have now re-examined the few old specimens of *beccarii* in collections of museums and studied series of adults and juveniles recently collected from the forests of Central Sulawesi. There are also two other species living in the primary forests in Sulawesi that are related to *beccarii* and I have examined large samples of each one. The animal that has been called *Rattus beccarii* is not closely related to any species in either *Rattus* or *Limnomys*, nor does it belong in the same genus as *Niviventer cremoriventer*; *beccarii*, along with the other two species from Sulawesi, comprise a new genus, which is named and diagnosed below.

MARGARETAMYS, NEW GENUS

TYPE SPECIES: *Mus beccarii* Jentink (1880, p. 11). The holotype is RMNH 18305 (Musser, 1970), obtained from Menado-Langowah in the Minahassa region of northeastern Sulawesi. Jentink (1879) originally named the species *Mus leucopus* but later changed the name to *beccarii* because *Acanthomys leucopus* had already been proposed by Gray (1867) for a rat from Queensland, which later came to be known as *Rattus leucopus* (Taylor and Horner, 1973). Jentink's *leucopus* is a junior primary homonym because it is antedated by *Musculus leucopus*

Rafinesque (1818), which is the valid specific name for *Peromyscus leucopus*, a North American cricetine (see Osgood, 1909, p. 113).

INCLUDED SPECIES: *Margaretamys beccarii* and two new species, *M. elegans* and *M. parva* (fig. 23).

KNOWN DISTRIBUTION: Northeastern and Central Sulawesi (fig. 43).

ETYMOLOGY: The genus is named for Margaret Becker, who shared the adventure of living and working in the primeval forests of Central Sulawesi.

DIAGNOSIS: A genus of arboreal murids distinguished by the following combination of characteristics: body size small to medium; tail much longer than head and body and conspicuously penicillate; three pairs of mammae; narrow zygomatic plates with either slight or no anterior spines; squamosal roots of zygomatic arches set high on sides of braincase; large lacrimals relative to size of cranium; long, narrow incisive foramina; a short and wide palatal bridge, its posterior margin situated just before backs of the molar rows; wide mesopterygoid fossa breached by slitlike sphenopalatine vacuities; anterior two-thirds of pterygoid fossae usually entire, sometimes perforated by tiny interpterygoid foramina; small bullae; alisphenoid canal open in most specimens, not concealed by strut of alisphenoid bone, foramen ovale accessorius and masticatory-buccinator foramina absent; incisors with bright or pale orange enamel layers; each first upper molar with three large primary roots (anterior, lingual, and posterior) or three primary roots and a labial rootlet or nubbin; second and third upper molars three-rooted; lower molars usually two-rooted, a lingual rootlet on some first molars; molars small, with complex occlusal surfaces; cusp t5 on first and second upper molars with lingual cusplike spur angled towards front of tooth; cusp t4 either separated from cusp t5 or weakly connected to it in all examples of one species, and in juveniles of another; accessory labial cusp behind cusp t6 on each first upper molar; large, prominent posterior cingulum on all upper molars in two species, on first and sec-

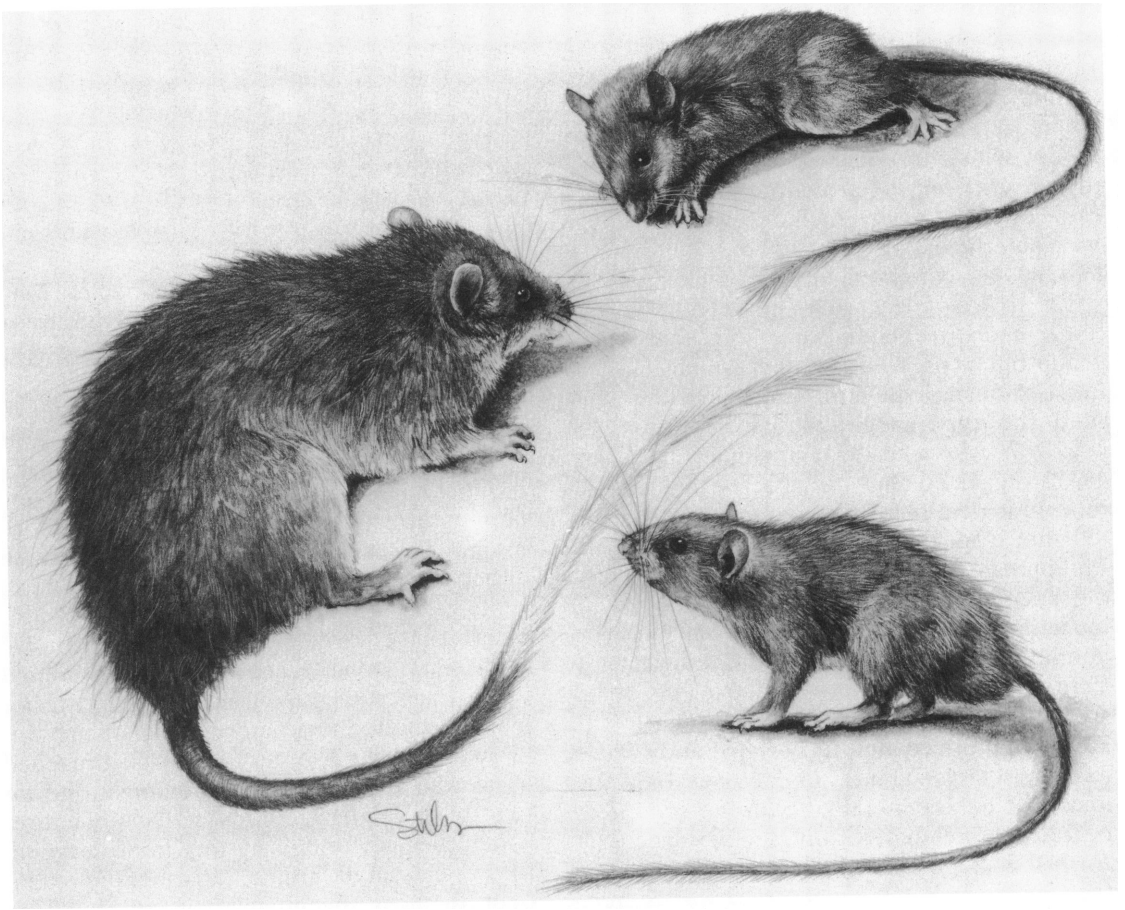


FIG. 23. The three species of *Margaretamys*: left, *M. elegans*; upper right, *M. parvus*; lower right, *M. beccarii*.

ond uppers in a third; no cusp t7 on any teeth; anteroventral cusp usually present on first lower molars; $2N = 42$.

DESCRIPTION: The best way to describe *Margaretamys* is to begin with a description of *M. beccarii*, the type species, and then compare the two new species with it.

Margaretamys beccarii
(Jentink, 1880)

SYNONYMS: *Mus leucopus* Jentink (1879) and *Rattus thysanurus* Sody (1932); see Musser (1971) for details.

DISTRIBUTION: Northeast and Central Su-

lawesi, from near sea level up to limits of tropical evergreen lowland rainforest; not found in montane forests.

LOCALITIES AND REFERRED SPECIMENS: I examined 32 specimens from the following places.

NORTHEASTERN SULAWESI

Toemaratas, Sapoetan Mountains (RMNH 21232, holotype of *thysanurus*)

Menado, Langowan (RMNH 18305, holotype; RMNH 18306)

Rurukan, 800 m. (AMNH 101261)

CENTRAL SULAWESI

Malakosa, Kuala Navusu: 140 ft. (AMNH 225667); 250 ft. (AMNH 225668); 350 ft. (AMNH 225669); 400 ft. (AMNH 225670)

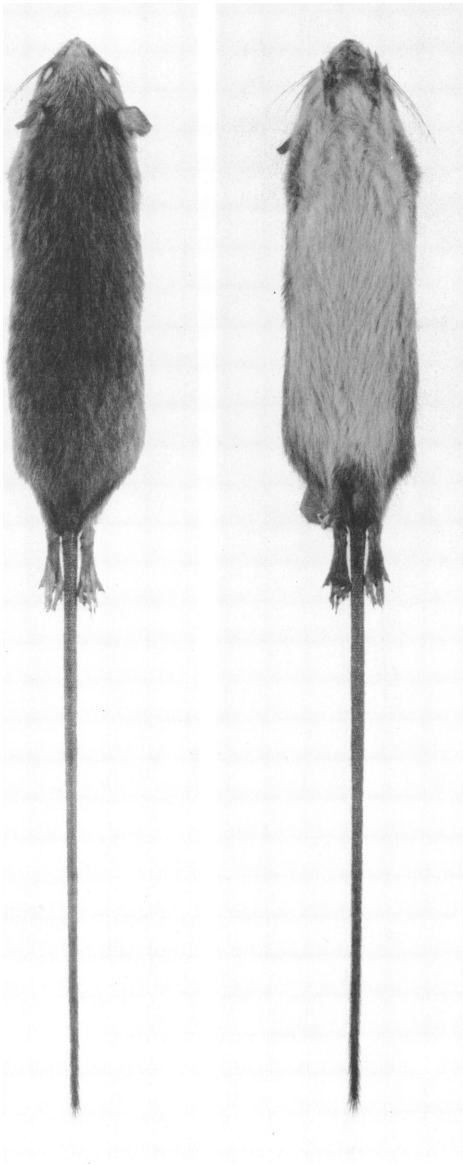


FIG. 24. *Margaretamys beccarii*. Dorsal and ventral views of AMNH 224064, an adult male from Sadaunta, 675 m., Central Sulawesi: length of head and body, 133 mm.; length of tail, 185 mm.; length of hind foot, 28 mm.; length of ear, 19 mm.; weight, 70 g.

Tolai, Sungai Tolewonu: 950 ft. (AMNH 226409); 1100 ft. (AMNH 226410)
Gimpu, 1400 ft. (USNM 219682–219686)

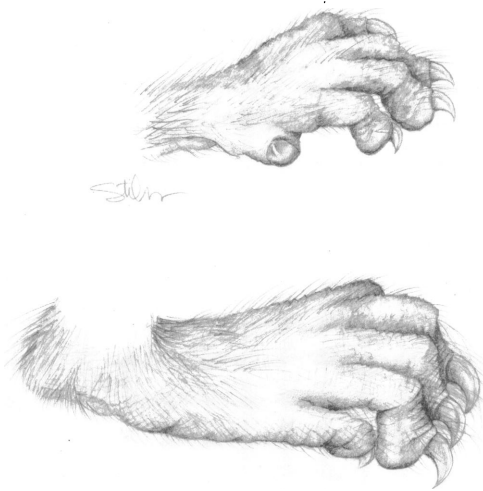


FIG. 25. The left front (top) and hind (bottom) feet of *Margaretamys beccarii* (AMNH 224634).

Sungai Sadaunta: 600 m. (AMNH 224318); 675 m. (AMNH 224058–224068); 2800 ft. (AMNH 224634, 224635); 3050 ft. (AMNH 226818); 3300 ft. (AMNH 224636).

DESCRIPTION: *Margaretamys beccarii* is a small (tables 5, 6) arboreal rat with thick and short pelage, a long tufted tail and short wide feet (fig. 24). The pelage over the upperparts of adults is grayish brown, 10–15 mm. thick, and very dense, composed of thin soft hairs and wide flexible spinelike hairs that together give the fur a dense and semi-spinous texture. Short guard hairs are scattered through the fur, especially over the back and rump and extend 5–10 mm. beyond the overhairs. The ears are pale brown and slightly haired. Wide, dark brown rings around the eyes and dark patches on the rostrum give the appearance of a mask. The vibrissae on the rostrum and above the eyes are very long, some reaching 76 mm. The pelage over the underparts is also semi-spinous and ranges from cream through yellow to a dark ochraceous buff; most examples are pale yellow (these are natural hues, not alterations after preservation). The color of the underparts extends up onto the cheeks and sides of the muzzle.

The front and hind feet are short and wide (figs. 25–27). A broad dark brown strip ex-

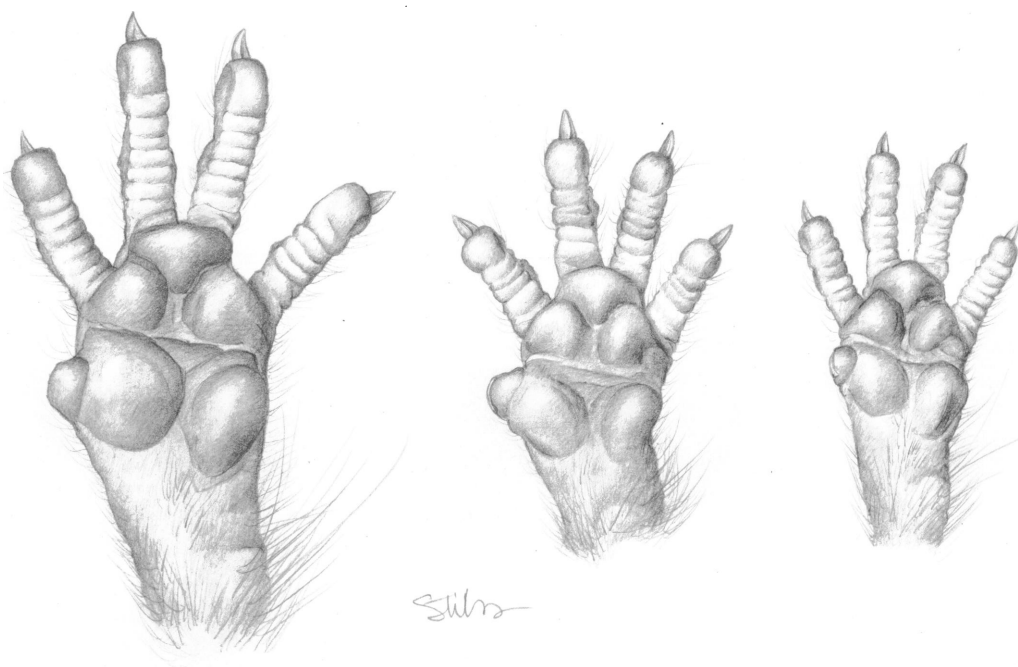


FIG. 26. Palmar views of left front feet in species of *Margaretamys*: left, *M. elegans* (AMNH 225144; length, 20 mm.); center, *M. beccarii* (AMNH 224634; length, 13 mm.); right, *M. parvus* (AMNH 225058; length, 11 mm.).

tends over the dorsal surface of each foot, ending near the bases of the digits; the sides of the feet and digits are white, covered with silvery hairs. The sharp claws are short and recurved. All the hind digits are clawed. The palmar and plantar surfaces are unpigmented and covered with large fleshy pads; those mounds and the pads beneath the claws are textured with circular ridges and grooves.

The tail is much longer than the combined lengths of head and body and covered with hairs that increase in length along the tail so the distal third is penicillate and the end is

tail is brown all over in five out of 20 specimens, brown on top and paler underneath in 14, and white over the distal one-third in one example.

Females have three pairs of mammae: a postaxillary pair and two inguinal pairs.

Gray upperparts and cream underparts characterize juvenile pelage. The fur is dense and soft, without the flexible spines seen in adults. The ears are dark gray, the rest of the animal is colored as in adults.

The cranium of *M. beccarii* is small (table 5), stocky, and rectangular in either dorsal or ventral view. Its distinctive features (figs. 28 and 29) are a short and narrow rostrum; wide interorbital region; wide braincase with nearly vertical sides; wide interparietal in which the anterior third is situated between the parietals and the posterior two-thirds forms the roof of the occiput; weak ridges outlining dorsolateral margins of the interorbital area and sides of the braincase; narrow zygomatic plates that either do not, or barely, extend forward beyond the anterior dorsal roots of the zygomatic arches; large lacrimal bones; long and narrow incisive fo-

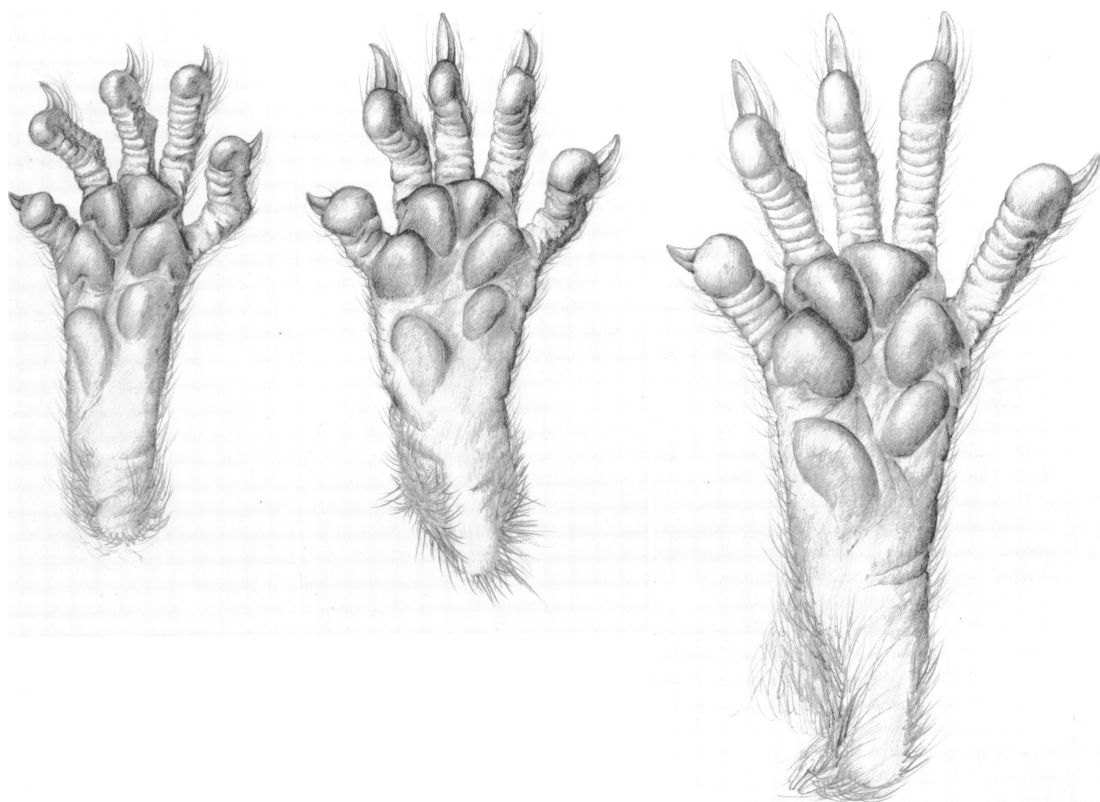


FIG. 27. Plantar views of left hind feet in species of *Margaretamys*: left, *M. parvus* (AMNH 225058; length, 24 mm.); center, *M. beccarii* (AMNH 224634; length, 28 mm.); right, *M. elegans* (AMNH 225144; length, 35 mm.).

ramina that end just before or at the fronts of the first molars; a short and wide palatal bridge, its posterior margin terminating just before backs of the molar rows; a wide mesopterygoid fossa, its walls breached by slit-like sphenopalatine vacuities; pterygoid fossae that are shallowly concave, the anterior two-thirds complete in eight specimens, penetrated by tiny interpterygoid foramina in nine examples; very small bullae, both absolutely and relative to size of the cranium; an open alisphenoid canal, not concealed by a strut of alisphenoid bone, in 13 specimens (fig. 40); a threadlike alisphenoid strut in one specimen, an alisphenoid strut on the left side but not the right in two specimens, and on the right but not the left in one example;

squamosal roots of the zygomatic arches located high on sides of the braincase; back ridge of each squamosal root not extending to the occipital ridge; each bulla firmly attached to the squamosal and alisphenoid bones, and a small postglenoid foramen is present.

The dentary is illustrated in figure 22. On each, the coronoid process is moderately large, the concavity forming the posterior outline between the condyloid and angular processes is shallow, and the bottom of each angular process is widened into a prominent shelf. The incisor capsule forms the anterior part of a broad shelf that extends to the end of the condyloid process. On the inner surface of each dentary, a conspicuous and wide

TABLE 5

Measurements (in Millimeters) of Skins, Skulls, and Teeth in Samples of *Margaretamys beccarii* from Central Sulawesi (Kuala Navusu, 140–400 feet; Sungai Tolewunu, 950 and 1100 feet; Gimpu, 1400 feet; Sungai Sadaunta, 1980–3300 feet) and Northeastern Sulawesi (Tumaratas; Langowan; Rurukan, 2640 Feet).

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

	Central Sulawesi					Northeastern Sulawesi				
	Females		Males			Females		Sex unknown		
	Adults ^a		Adults ^b	Juveniles ^c		Adults		Adults		Adults
Length of head and body	130.4 ± 10.0 (117–152)	14	134.2 ± 9.1 (122–145)	5	105	96	127 ^d	123 ^e	— ^f	— ^g
Length of tail	177.1 ± 11.7 (150–190)	13	195.5 ± 7.1 (185–200)	4	140	141	155	186	162	160
Scale row/cm. on tail	11.4 ± .9 (10–12)	11	11.0 ± 1.0 (10–12)	3	14	14	9	11	13	12
Length of tail brush	7.5 ± 1.9 (5–11)	13	12.0 ± 0.0	2	6	6	5	4	—	—
Length of hind foot	27.7 ± 1.3 (25–29)	14	28.2 ± 2.4 (25–31)	5	27	26	25	25	28	27
Length of ear	20.2 ± .8 (19–21)	11	20.0 ± 1.0 (19–21)	3	18	18	15	20	—	—
Greatest length of skull	33.5 ± .8 (32.3–35.5)	13	33.9 ± .8 (32.9–34.8)	5	28.7	28.2	32.4	33.3	—	—
Basilar length	26.0 ± 1.0 (24.3–27.3)	11	26.4 ± 1.0 (25.4–27.4)	3	21.2	20.9	25.6	—	—	—
Zygomatic breadth	16.5 ± .5 (16.0–17.5)	13	16.3 ± .6 (15.5–17.0)	5	14.5	13.7	15.5	16.3	—	—
Interorbital breadth	5.4 ± .2 (5.1–5.7)	14	5.6 ± .3 (5.3–6.0)	5	5.0	4.8	5.4	5.3	5.4	5.2
Length of rostrum	10.2 ± .4 (9.8–11.0)	14	10.3 ± .3 (10.0–10.6)	5	8.5	8.3	9.8	9.9	9.4	9.2
Breadth of rostrum	6.0 ± .3 (5.4–6.5)	14	6.2 ± .4 (5.7–6.6)	5	4.8	4.7	6.0	5.8	—	5.5
Length of nasals	11.9 ± .6 (10.4–12.9)	14	12.0 ± .5 (11.4–12.7)	5	9.8	8.9	11.6	12.4	12.3	11.4
Breadth of braincase	14.7 ± .4 (14.1–15.5)	13	14.7 ± .4 (14.4–15.2)	5	13.7	13.4	13.7	14.3	—	13.4
Height of braincase	10.3 ± .3 (9.9–10.6)	13	10.0 ± .4 (9.6–10.5)	5	9.6	9.2	9.9	10.0	—	—
Breadth across incisor tips	1.9 ± .1 (1.9–2.1)	14	2.0 ± .1 (1.9–2.1)	5	1.5	1.4	2.0	2.2	2.1	1.9
Breadth of zygomatic plate	2.6 ± .2 (2.3–2.9)	14	2.6 ± .2 (2.4–2.8)	4	1.9	1.7	2.3	2.4	2.4	2.2
Depth of zygomatic notch	.6 ± .2 (2.2–1.0)	13	.6 ± .2 (4–8)	5	.1	.0	.2	.4	.5	.5
Length of diastema	8.6 ± .4 (7.9–9.3)	14	8.8 ± .5 (8.4–9.6)	5	6.9	6.8	9.0	9.0	9.1	8.6
Palatal length	13.7 ± .4 (13.2–14.5)	13	14.0 ± .6 (13.4–14.9)	5	11.8	11.6	13.8	13.6	14.0	13.2
Postpalatal length	15.9 ± .5 (15.2–17.0)	14	15.9 ± .7 (15.4–17.2)	5	13.4	13.3	16.2	15.7	15.7	15.2
Length of incisive foramina	12.4 ± .5 (11.4–13.0)	14	12.3 ± .5 (11.6–12.8)	4	9.6	9.5	12.0	—	—	—
Breadth of incisive foramina	5.9 ± .3 (5.5–6.4)	14	5.7 ± .1 (5.6–5.9)	5	4.9	4.8	5.7	5.8	5.6	5.6
Incisive foramina to M ¹	2.5 ± .2 (2.3–2.8)	13	2.6 ± .2 (2.4–2.9)	5	2.2	2.3	2.5	2.4	2.3	2.2
Length of palatal bridge	.3 ± .2 (even–6)	13	.6 ± .3 (5–9)	5	.2 ^h	.2 ^h	.1	—	—	—
Palatal margin to M ³	5.4 ± .2 (5.1–5.7)	14	5.7 ± .4 (5.3–6.4)	5	4.7	4.7	4.9	5.0	5.4	5.0
Breadth of palatal bridge at M ¹	.1 ± .1 (even–2)	9	.1 ± .1 (even–2)	even	even	even	.6	—	—	—
Breadth of palatal bridge at M ²	3.3 ± .2 (3.0–3.5)	13	3.4 ± .1 (3.3–3.5)	5	2.8	2.9	3.3	3.3	3.2	3.2
Breadth of palatal bridge at M ³	3.7 ± .2 (3.4–3.8)	13	3.8 ± .1 (3.7–3.9)	5	3.5	3.3	3.4	3.9	3.4	3.6

TABLE 5—(Continued)

	Central Sulawesi			Northeastern Sulawesi		
	Females		Males	Females		Sex unknown
	Adults ^a	Adults ^b	Juveniles ^c	Adults	Adults	Adults
Breadth of mesopterygoid fossa	2.5 ± .2 (2.0–2.9) 13	2.5 ± .3 (2.3–2.8) 5	2.1	2.1	2.6	2.0
Length of bulla	4.7 ± .2 (4.3–5.0) 14	4.7 ± .3 (4.4–5.2) 5	4.2	4.4	4.5	—
Height of bulla	3.9 ± .2 (3.7–4.1) 14	3.8 ± .2 (3.6–4.2) 5	3.6	3.7	3.9	—
Alveolar length of M ^{1–3}	5.2 ± .2 (4.9–5.5) 14	5.1 ± .2 (4.8–5.4) 5	4.9	4.9	5.3	4.8
Breadth of M ¹	1.5 ± .1 (1.4–1.6) 14	1.5 ± .1 (1.4–1.6) 5	1.5	1.5	1.5	1.6
Length of M ^{1–3}	5.0 ± .1 (4.8–5.2) 11	5.0 ± .2 (4.8–5.1) 3	4.9	4.9	5.1	—
Breadth of M ₁	1.4 ± .1 (1.3–1.5) 11	1.4 ± .1 (1.3–1.4) 3	1.4	1.3	1.5	—

^a AMNH 224058–224060, 224062, 224063, 224065, 224067, 226818, 226409, 225609; USNM 219684–219686.^b AMNH 224064, 226410, 225667, 225668; USNM 219682, 219683.^c AMNH 224066 and 224061, respectively.^d AMNH 101261.^e RMNH 21235, holotype of *Rattus thysanurus*.^f RMNH 18305, lectotype of *Mus beccarii*.^g RMNH 18306.^h Amount the incisive foramina extend beyond the anterior margins of the first molars.



FIG. 28. Dorsal (top) and ventral (bottom) views of adult crania from species of *Margaretamys*: left, *M. elegans* (AMNH 223693); center, *M. beccarii* (AMNH 224064); right, *M. parvus* (AMNH 225063). Approx. $\times 1.5$.

shelf extends from the back of the molar row diagonally to the end of the mandibular foramen where it disappears; the condyloid process, therefore, is smooth over its inner surface.

The upper and lower incisors are narrow,

their enamel surfaces smooth and pigmented deep or pale orange. The uppers emerge at a right angle from the rostrum (orthodont in position).

Margaretamys beccarii has small, narrow, bunodont molars with distinctive occlusal

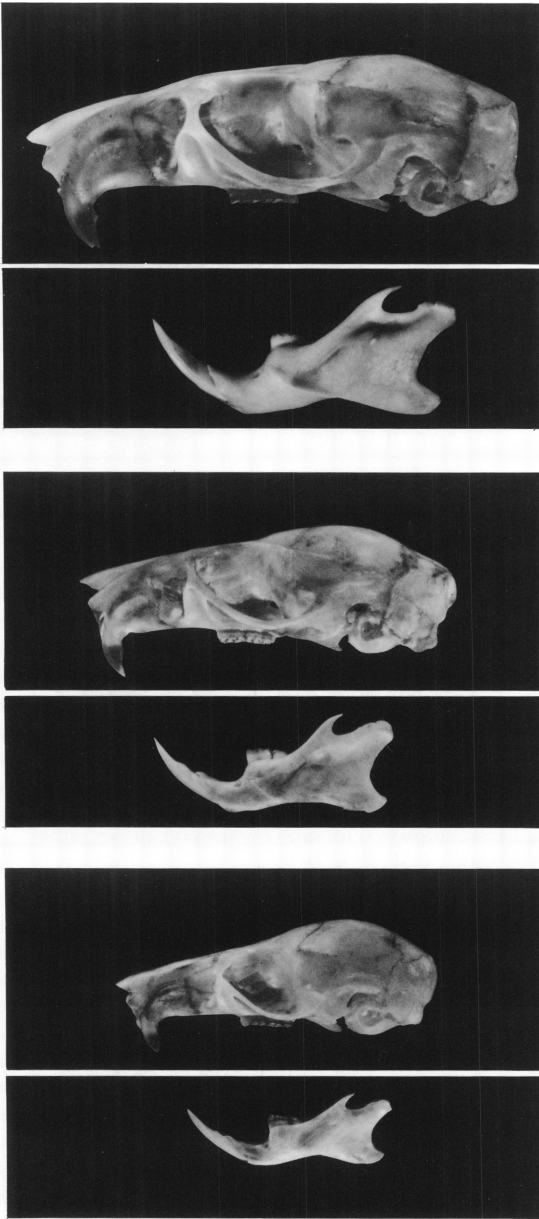


FIG. 29. Lateral views of crania and dentaries from the same specimens of *Margaretamys* that are shown in figure 26: top, *M. elegans*; center, *M. beccarii*; bottom, *M. parvus*. Approx. $\times 1.5$.

patterns (table 5, fig. 30). Each first upper molar is anchored by either three large roots (anterior, posterior, and lingual) or three

roots and a slender labial rootlet (table 7). The second and third upper molars are three-rooted. Two large roots, one at the front of the tooth, another at the back, anchor each of the lower molars; there is a small labial rootlet under the first molar in some specimens. The upper molars abut against each other with some of the first molar overlapping the second, and a small part of the second overlapping the third.

Each first upper molar is long and narrow. The occlusal pattern is formed by three rows of cusps and a wide posterior cingulum. The first row is arcuate with cusp t1 set well posterior of cusps t2 and t3. The second row also forms an arc and consists of a wide cusp t5 bounded by large labial (cusp t6) and lingual (cusp t4) cusps. The second row is distinctive in configuration because in every specimen there is a cusp behind cusp t6 that is separate and discrete in very young rats but usually joined to the back of cusp t6 in older animals so that cusp t6 appears to either have a posterior lobe or to be attached to a crest angled backward. On the lingual side of the second row, the wide central cusp t5 has a lingual cusplike spur angled toward the front of the tooth and this part of the central cusp either abuts against cusp t4 or merges with it. The jutting spur is so large in some specimens that it resembles a cusp that could be identified as cusp t4, which would mean that the large lingual cusp next and slightly below it would be cusp t7; however, the spur is clearly an enlargement of the lingual side of the central cusp t5, and the large cusp next to it is cusp t4. The latter is separated from cusp t5 (as shown in fig. 30) in 13 out of 22 specimens, including the worn teeth of adults; and even when cusps t4 and t5 are attached, the connection is weak. The third row of cusps on the first molar consists of a large arcuate cusp t8 that has a bulge on the lingual side and is attached to a prominent and wide cusp t9 on the labial side. The back of the tooth is formed by a large posterior cingulum, which from its attachment at the back of cusp t8 extends labially, forming a wide laminar wear surface. There is no cusp t7 on either first upper molar.

The second upper molar is also longer than

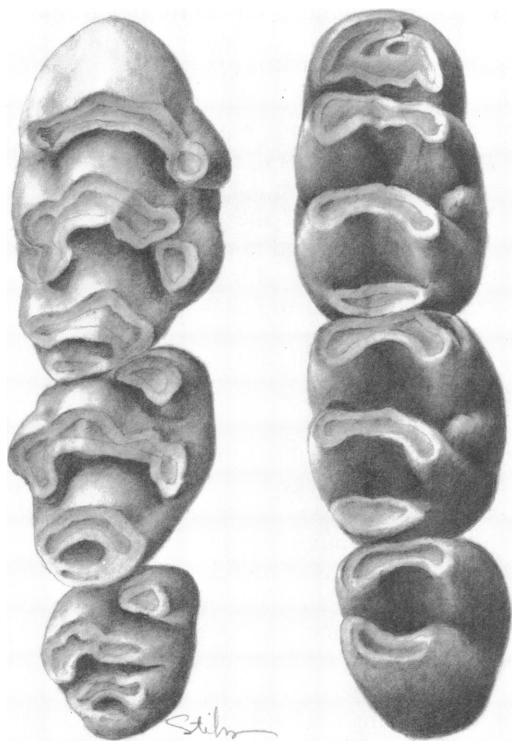


FIG. 30. Occlusal views of right maxillary (left side) and mandibular (right side) tooththrows of *Margaretamys beccarii* (AMNH 224061; LM¹⁻³, 4.8 mm.; LM₁₋₃, 4.8 mm.).

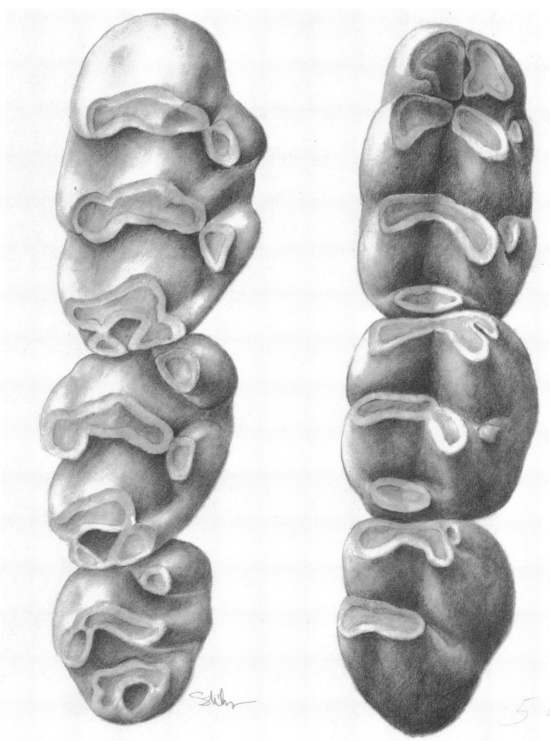


FIG. 31. Occlusal views of right maxillary (left side) and mandibular (right side) tooththrows of *Margaretamys elegans* (AMNH 225143; LM¹⁻³, 6.4 mm.; LM₁₋₃, 6.3).

wide. The central cusp of the first row is missing and that lamina is represented by a large cusp t1 forming the anterolingual corner of the tooth and a small cusp t3, which may be absent in some specimens (table 7). The shape of the second row of cusps resembles the configuration of the second row on the first molar: there is a cusplike spur jutting out from the lingual margin of the central cusp t5 that has merged with cusp t4 in 14 specimens and remained separate in eight. Cusp t6 has a backward extension but it does not represent a cusp, as is the situation on the first molar. The third row is arcuate and formed mostly of the central cusp t8, which has a lingual bulge and a bulge on the labial side representing cusp t9. The posterior cingulum is large, thick, bowed, and its labial end has merged with cusp t9 in most speci-

mens so that the back of the tooth is an oval formed by the arch of cusps t8 and t9 joined with the curved posterior cingulum. There is no cusp t7 on any second upper molar.

The third upper molar is oblong in occlusal outline and small relative to the other teeth. Its wear surface is simple in pattern, formed of a large cusp t1 (the opposite cusp t3 is absent; table 7), an arcuate lamina consisting of cusps t4, t5, and t6, a gently arched second lamina formed mostly of cusp t8 merged with a small cusp t9, and a small but conspicuous posterior cingulum that forms the back of the tooth. Cusp t7 does not occur on any third molar.

The first and second lower molars are long and narrow in occlusal outline, the third oblong. The occlusal surface of the first molar is formed primarily of three rows of cusps

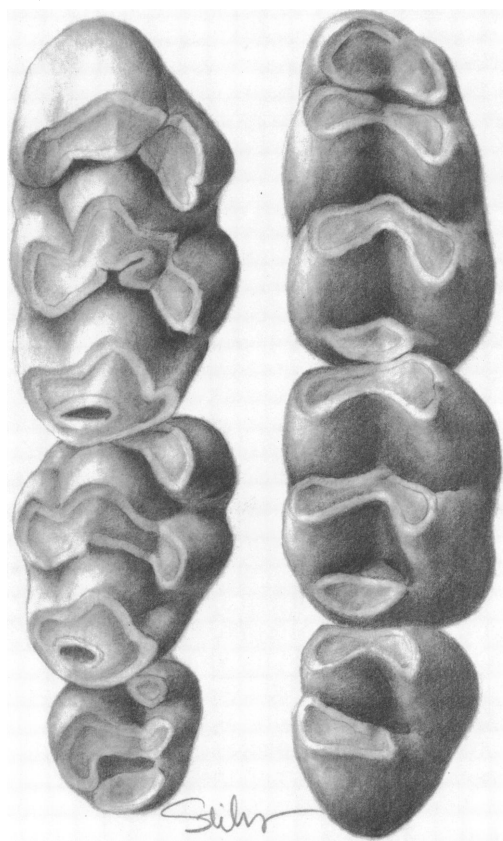


FIG. 32. Occlusal views of right maxillary (left side) and mandibular (right side) tooththrows of *Margaretamys parvus* (AMNH 226068; LM¹⁻³, 4.6 mm.; LM₁₋₃, 4.6 mm.).

and a posterior cingulum. Two large cusps (anterolabial and anterolingual) merged with an elongate antero-central cusp form a peculiarly shaped front lamina (fig. 30). The second and third rows consist of two cusps that have merged, even in juveniles, forming wide gently arcuate laminae. Nearly the entire back margin of the tooth is formed by a thick posterior cingulum. A posterior cusplet sits on the labial margin of every specimen, as well as an anterior labial cusplet, the latter present in half the sample (table 7).

The occlusal surface of each second lower molar consists of two wide and gently ar-

culate laminae, a wide and thick posterior cingulum forming the back of the tooth, a prominent anterolabial cusp, and a large posterior labial cusplet (table 7).

Of the three lower molars, the third has the simplest wear surface, consisting of a gently arched front lamina and a bowed posterior lamina; both an anterolabial cusp and a posterior cingulum are absent (table 7).

Two females (AMNH 224067 and 224636) and three males (AMNH 224635, 225667, and 225670) of *M. beccarii* were analyzed for their chromosomes; 10–20 cells were examined from each individual. Samples of male and female karyotypes are illustrated in figure 33 (see also table 4). All five rats have a diploid number of 42, an FN of 46, 19 pairs of telocentric chromosomes, and two pairs of small metacentrics. The telocentrics in the first pair are the largest chromosomes, and those in the remaining 18 pairs form a series graded in size. The male sex chromosomes appear to be homomorphic; I could not pick them out of the karyotype, even after examining many chromosome spreads from all three males. The presence of homomorphic male sex chromosomes in conventional preparations, such as those obtained from *M. beccarii*, has been found in very few of the many other species of murids already analyzed for their chromosomal characteristics. Gropp et al. (1972) illustrated the karyotype for a male *Vandeleuria oleracea*, a species of long-tailed tree mouse, obtained from Nakhorn Phanom in northeastern Thailand. The X-chromosome was a medium-sized subtelocentric and the Y-chromosome was subtelocentric and about the same size as the X. In other samples of *V. oleracea* from Thailand, the male sex chromosomes were heteromorphic. Baverstock et al. (1977) reported on a sample of *Notomys fuscus*, one of the species of Australian hopping mice, in which the male sex chromosomes appeared to be homomorphic subtelocentrics within a polymorphic system where there were two forms of X-chromosomes and two forms of Y-chromosomes. After C-banding, however, the short arm of the X-chromosome was stained, as was the Y-chromosome for its entire length, clearly revealing differ-

TABLE 6

Body Weights (in Grams) from Samples of *Margaretamys beccarii* (K. Navusu to S. Sadaunta), *M. elegans* (G. Nokilalaki), and *M. parva* (G. Nokilalaki) from Central Sulawesi
(The mean plus or minus one standard deviation, observed range in parentheses, and number of specimens are listed for the larger samples.)

Sex and Age	<i>M. beccarii</i>	<i>M. elegans</i>	<i>M. parvus</i>
Females			
Adults	62.4 ± 12.4 (50–85) 11	116.8 ± 20.4 (97–150) 13	29.6 ± 6.0 (23–35) 7
Young adults		70.0 ± 13.5 (50–80) 4	
Males			
Adults	78.3 ± 7.6 (70–85) 3	125.9 ± 6.6 (110–150) 11	34.6 ± 4.5 (28–40) 7
Young adults		76.8 ± 21.9 (55–110) 6	
Juveniles	70, 35	45	17

ences. Recently, Verheyen and Van der Straeten (1980) reported on the karyotypes of a male and female *Lophuromys nudicaudus* from Cameroon. The 2N is 56, polymorphism is present, and the authors could not identify the sex chromosomes, although they did not indicate why. I could not detect heteromorphism in any specimen of *M. beccarii*. I suspect that banding studies would reveal the sex chromosomes and the nature of the differences between them in the male.

GEOGRAPHIC VARIATION: Because the samples of *M. beccarii* are from either the central part of Sulawesi or the end of the northeastern peninsula, I thought some geographic variation might be evident in skins and skulls. The four specimens from the northeastern peninsula, however, are too few, and some of them too incomplete, to be useful for determining whether any significant geographic variation exists between the areas. Values from measurements of the four fall within the ranges of variation for values obtained from rats in the central portion of the island (table 5). I even compared the four specimens individually with examples from Central Sulawesi that were of comparable age, and each of the four still fit within the range of structural and morphometric variation in the larger sample. The question of whether geographic variation exists within *M. beccarii* is significant because several species of rats show a pattern in which the samples from the northeastern peninsula are

different from those in Central Sulawesi (Laurie and Hill, 1954) and this pattern also extends to other mammals living on Sulawesi, such as macaques (Fooden, 1969). Whether such a pattern exists within *M. beccarii* cannot be determined with the specimens now available for study.

There are two other species in *Margaretamys*; both require scientific names and descriptions. One species consists of animals larger in body size than those of *M. beccarii*, the other of smaller rats. For the larger one I propose the following name.

***Margaretamys elegans*, new species**

HOLOTYPE: AMNH 223693 and MZB 12151 (although now in the collection at the American Museum of Natural History, the holotype of *M. elegans* will be transferred to the Museum Zoologicum Bogoriense), an adult male obtained from Gunung Nokilalaki at an elevation of 6500 feet by members of the Archbold Sulawesi Expedition (original number, ASE 1073) on December 16, 1973. A skin (fig. 35), skull, and carcass preserved in fluid comprise the holotype.

REFERRED SPECIMENS: 38, in addition to the holotype, from the following elevations on Gunung Nokilalaki: 5300 ft. (AMNH 225131); 5380 ft. (AMNH 225132); 5550 ft. (AMNH 225133); 5580 ft. (AMNH 225134); 5700 ft. (AMNH 223677, 223678); 5850 ft. (AMNH 225135); 5950 ft. (AMNH 223136);

6000 ft. (AMNH 223679–223683, 225137, 225138, 225147); 6100 ft. (AMNH 223684–223691); 6150 ft. (AMNH 223692, 223699); 6350 ft. (AMNH 225139, 225140); 6400 ft. (AMNH 223698, 225141, 225142); 7200 ft. (AMNH 223694–223696); 7300 ft. (AMNH 223697, 225144); 7500 ft. (AMNH 225145, 225146).

KNOWN DISTRIBUTION: Central Sulawesi, from 5300 to 7500 feet in montane forest on the steep slopes of Gunung Nokilalaki; unknown from lowland tropical evergreen forest.

ETYMOLOGY: The meanings associated with *elegans*—fine, of uncommon quality, superb—aptly fit this handsome rat.

DIAGNOSIS: An arboreal rat morphologically similar to *M. beccarii* but differing in having a much larger body (table 8); thick, long, very soft fur, with long guard hairs; brown upperparts and whitish gray underparts; a long and bicolored tail, the proximal half or two-thirds brown, the distal half or one-third white; open alisphenoid canals in all specimens; a small but prominent labial root in addition to the three primary roots on each first upper molar (table 7); cusp t3 occurring at a greater frequency on each second and third upper molar (table 7); cusps t4 and t5 on each first and second upper molar merged in adults, separate in juveniles only; an anterolabial cusp on each third lower molar in some specimens (table 7, fig. 31); a karyotype with $2N = 42$, but an FN of 57 in males and 56 in females, seven pairs of submetacentric chromosomes, 13 pairs of telocentrics, and a submetacentric Y-chromosome and telocentric X-chromosome (table 4, fig. 34).

DESCRIPTION AND COMPARISON: *Margaretamys elegans* is a medium-sized rat (tables 6 and 8); its long and soft pelage, brown upperparts that are mixed with tawny along the sides of the body and with black along the top, grayish white underparts, and long bicolored tail contrast with the semi-spinous short pelage of *M. beccarii* and its gray upperparts, cream or yellow underparts, and monocolored tail. The dorsal pelage over the head and body of adult *M. elegans* is 20–30 mm. thick. Conspicuous, long guard hairs

TABLE 7
The Number of Roots on M^1 and M_1^a ; and Presence (+) or Absence (–) of Cusp t3 on M^2 and M^3 , of the Anterior and Posterior Cusplets on M_1 , and of the Anterolabial Cusps on M_2 and M_3 in Species of *Margaretamys*
(Number of roots, cusps, and cusplets in percentage; number of specimens in parentheses.)

	<i>M. beccarii</i>	<i>M. elegans</i>	<i>M. parvus</i>
Number of roots on M^1			
3	45 (10)		27 (4)
3+	55 (12)	11 (4)	67 (10)
4		89 (31)	6 (1)
Number of roots on M_1			
2	55 (12)	71 (25)	67 (10)
2+	45 (10)	29 (10)	33 (5)
Cusp t3 on M^2			
+	85 (17)	94 (32)	93 (14)
–	15 (3)	6 (2)	7 (1)
Cusp t3 on M^3			
+		35 (12)	
–	100 (20)	65 (22)	100 (15)
Anterior cusplet on M_1			
+	50 (9)	100 (34)	36 (5)
–	50 (9)		64 (9)
Posterior cusplet on M_1			
+	100 (19)	100 (34)	86 (12)
–			14 (2)
Anterolabial cusp on M_2			
+	100 (19)	100 (34)	93 (13)
–			7 (1)
Posterior cusplet on M_2			
+	100 (19)	97 (32)	79 (11)
–		3 (2)	21 (3)
Anterolabial cusp on M_3			
+		26 (7)	
–	100 (19)	74 (17)	100 (14)

^a I present the variation in number of roots of first molars only; in all specimens of the three species, each M^2 and M^3 has three roots, each M_2 and M_3 has two.

Upper roots:

3: anterior, lingual, and posterior.

3+: three primary roots and a labial nubbin.

4: three primary roots and a small but prominent labial root.

Lower roots:

2: anterior and posterior.

2+: two primary roots and a small labial nubbin.

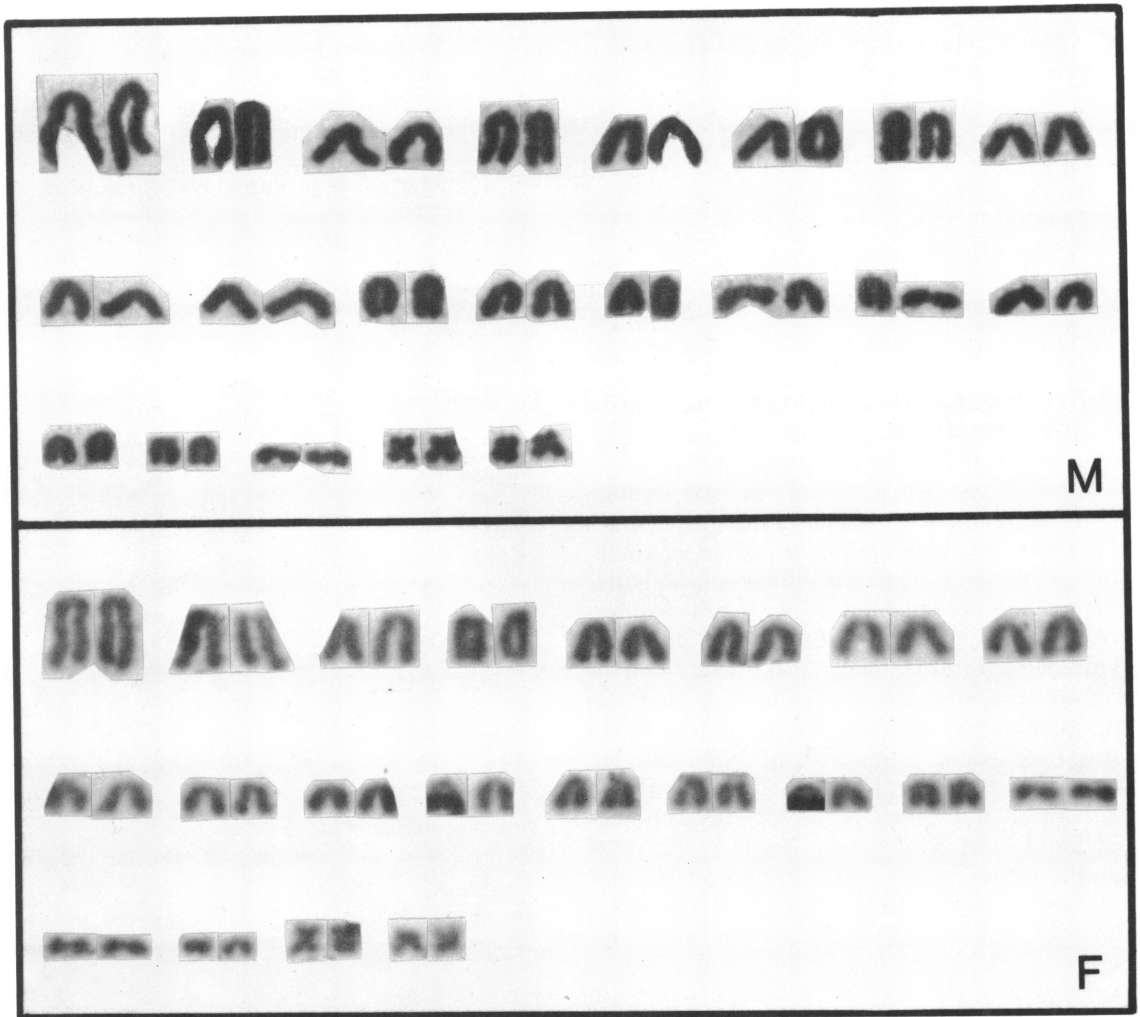


FIG. 33. Karyotypes from a male (AMNH 224635) and female (AMNH 224636) of *Margaretamys beccarii*: $2N = 42$, $FN = 46$. The sex chromosomes could not be identified. See text for discussion.

emerge from the fur over the back and rump, some are up to 52 mm. long. The underparts are covered by soft, dense pelage that is 15–20 mm. thick; the hairs are gray basally and white for most of their lengths so the overall color is grayish white, a tone extending up onto the cheeks and muzzle. Blackish brown encircles the eyes and extends onto sides of the muzzle to form a conspicuous mask. The rostral vibrissae and those above the eyes are very long, some reaching 83 mm. The

ears are small, a translucent pale brown in life, and thinly haired.

Configurations of the front and hind feet, nails, and palmar and plantar pads are similar to shapes of those features in *M. beccarii*, only larger (figs. 26 and 27). The palmar and plantar surfaces are unpigmented, the digits are white and covered with silvery-white hairs, and the tops of the feet are solid dark brown, like the pattern in *N. beccarii*, but more conspicuous.

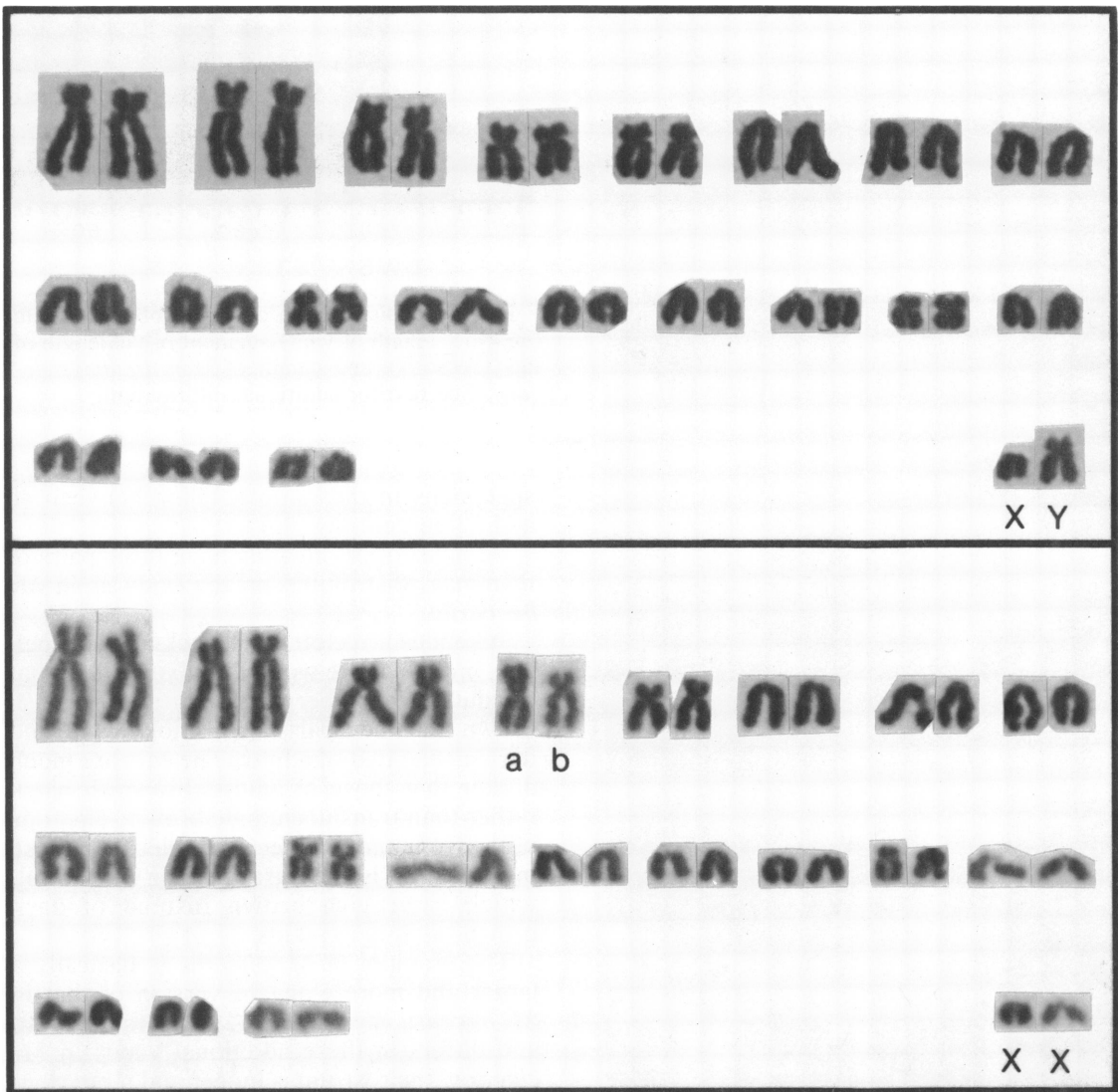


FIG. 34. Karyotypes from a male (AMNH 223677) and female (AMNH 223688) of *Margaretamys elegans*: $2N = 42$; $FN = 57$ in males, 56 in females. The fourth largest pair in the females is dimorphic. In the other two females (AMNH 223679 and 223699), no metacentric (a) is present and the pair consists of two submetacentric chromosomes each similar in shape to b, as in the males. See text for discussion.

The tail of *M. elegans* is much longer than the combined lengths of head and body and covered with hairs that increase along its length until the distal half or third becomes penicillate and the tip tufted (figs. 23 and 35; table 8). The basal portion of each tail is dark

brown, the distal portion white; the tail resembles a long, slender, brown and white feathery plume. Every specimen has a bi-colored tail, but the length of the white portion relative to the total length of the tail varies from 30 to 62 percent with most

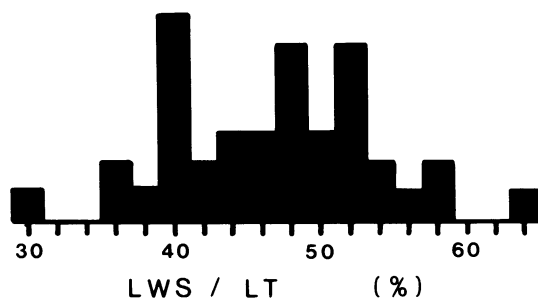
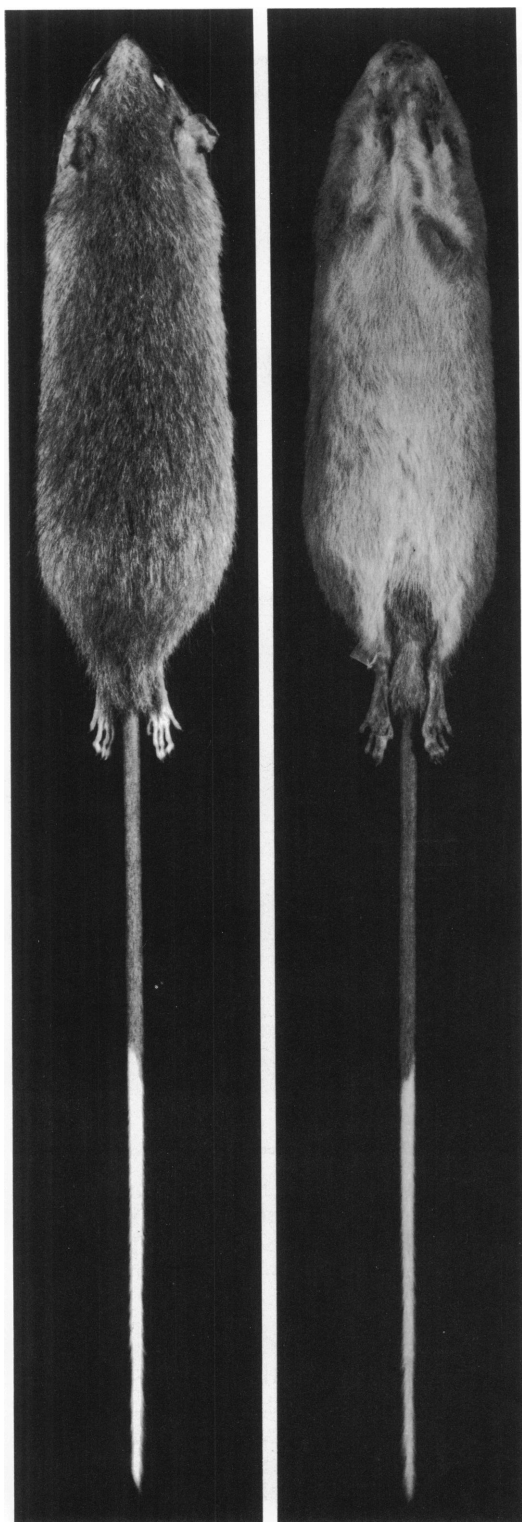


FIG. 36. Distribution of values obtained from the ratio, length of white segment of tail/length of tail (LWS/LT), in a sample of *Margaretamys elegans*. See text for additional information.

specimens in the sample falling between 40 and 52 percent (fig. 36).

Females of *M. elegans* have three pairs of mammae, distributed on the body as in *M. beccarii*.

Juveniles are clothed in thick and soft pelage, but it is more woolly in texture than that of adults. The upperparts are gray to grayish brown, the underparts are a smoky white and darker than that of adults. The ears are much darker than those of adults, brownish black rather than translucent pale brown. The tops of the front and hind feet are paler than those in adults, as is the basal portion of the tail, which is grayish brown instead of dark brown, as it is in adults.

The cranium of *M. elegans* is basically a larger and more elongate version of that in *M. beccarii* (figs. 28 and 29; tables 5 and 8), and differs in these additional ways: in *M. elegans*, the rostrum is longer and more slender, the interorbital area is narrower relative to size of the cranium, the incisive foramina are longer and extend between the front mar-

←

FIG. 35. *Margaretamys elegans*. Dorsal and ventral views of AMNH 223693 (the holotype), an adult male from Gunung Nokilalaki, 6500 ft., Central Sulawesi: length of head and body, 184 mm.; length of tail, 274 mm.; length of hind foot, 38 mm.; length of ear, 23 mm.; weight, 125 g.

TABLE 8
Measurements (in Millimeters) of Skins, Skulls, and Teeth in Samples of *Margaretamys elegans* from Elevations at and between 5300–7500 Feet on Gunung Nokilalaki, Central Sulawesi
(The mean plus or minus one standard deviation, observed range in parentheses, and number of specimens are listed for each measurement.)

Measurement	Males		
	Holotype ^a	Adults ^b	Young adults ^c
Length of head and body	184	188.8 ± 5.2 (183–197) 11	156.5 ± 12.9 (140–174) 6
Length of tail	274	269.1 ± 12.5 (248–286) 11	231.8 ± 8.0 (223–243) 6
Scale rows/cm. on tail	12	11.0 ± .9 (9–12) 11	13.7 ± 1.0 (12–15) 6
Length of tail brush	10	13.3 ± 4.1 (10–20) 11	8.5 ± 3.1 (4–12) 6
Length of hind foot	38	38.4 ± .8 (37–39) 11	36.2 ± .4 (36–37) 6
Length of ear	23	24.5 ± 1.1 (23–27) 11	22.8 ± .4 (22–23) 6
Greatest length of skull	42.9	42.1 ± .6 (40.9–42.9) 11	37.7 ± 1.3 (36.1–39.3) 6
Basilar length	33.9	33.3 ± .8 (31.5–34.7) 11	28.7 ± 1.2 (27.1–30.5) 6
Zygomatic breadth	19.3	19.7 ± .5 (18.9–20.6) 11	17.8 ± .5 (17.2–18.3) 6
Interorbital breadth	5.7	5.6 ± .2 (5.4–5.8) 11	5.4 ± .1 (5.2–5.6) 6
Length of rostrum	14.4	13.9 ± .3 (13.2–14.4) 11	11.9 ± .5 (11.3–12.5) 6
Breadth of rostrum	7.1	7.2 ± .3 (6.8–7.6) 11	6.3 ± .4 (5.8–6.6) 6
Length of nasals	16.3	13.9 ± .3 (13.2–14.4) 11	11.9 ± .5 (11.3–12.5) 6
Breadth of braincase	16.7	16.6 ± .4 (16.1–17.1) 11	16.0 ± .3 (15.6–16.5) 7
Height of braincase	12.0	11.8 ± .3 (11.7–12.5) 11	11.4 ± .4 (11.2–12.1) 6
Breadth across incisor tips	2.5	2.4 ± .1 (2.3–2.6) 11	2.2 ± .2 (2.0–2.4) 6
Breadth of zygomatic plate	3.5	3.4 ± .2 (3.1–3.7) 11	2.8 ± .1 (2.7–2.9) 6
Depth of zygomatic notch	1.2	1.0 ± .2 (.6–1.2) 11	.6 ± .2 (.3–.8) 6
Length of diastema	11.4	11.5 ± .4 (10.8–11.9) 11	10.1 ± .5 (9.4–10.7) 6
Palatilar length	18.0	17.9 ± .3 (17.3–18.2) 11	16.3 ± .5 (15.6–16.8) 6
Palatal length	21.0	20.8 ± .5 (19.7–21.4) 11	18.7 ± .5 (17.9–19.2) 6
Postpalatal length	16.3	16.0 ± .4 (15.4–16.8) 11	13.7 ± .9 (12.5–14.8) 6
Length of incisive foramina	8.3	8.1 ± .4 (7.6–8.9) 11	7.2 ± .1 (6.9–7.2) 6
Breadth of incisive foramina	2.9	2.9 ± .2 (2.7–3.0) 11	2.7 ± .1 (2.6–2.9) 6
Incisive foramina past M ¹	.8	.6 ± .3 (.2–1.0) 11	.6 ± .2 (.3–.9) 6
Length of palatal bridge	5.8	5.9 ± .2 (5.7–6.1) 11	5.6 ± .3 (5.1–5.9) 6
Palatal margin to M ³	.3	.3 ± .2 (even–.5) 11	.3 ± .1 (.1–.5) 6
Breadth of palatal bridge at M ¹	3.6	3.8 ± .1 (3.6–4.0) 11	3.5 ± .1 (3.4–3.6) 6
Breadth of palatal bridge at M ³	4.2	4.2 ± .2 (3.9–4.5) 11	3.9 ± .2 (3.6–4.1) 6
Breadth of mesopterygoid fossa	3.7	3.6 ± .2 (3.0–3.9) 11	3.2 ± .3 (2.7–3.5) 6
Length of bulla	5.5	5.4 ± .2 (5.1–5.6) 11	5.1 ± .2 (4.8–5.2) 6
Height of bulla	4.6	4.6 ± .1 (4.3–4.8) 11	4.4 ± .2 (4.2–4.6) 6
Alveolar length of M ^{1–3}	6.9	6.7 ± .2 (6.3–7.0) 11	6.4 ± .2 (6.2–6.6) 6
Breadth of M ¹	1.8	1.9 ± .1 (1.8–2.0) 11	1.9 ± .4 (1.8–1.9) 6
Length of M _{1–3}	6.6	6.6 ± .2 (6.2–6.8) 11	6.5 ± .1 (6.3–6.6) 6
Breadth of M ₁	1.8	1.8 ± .1 (1.7–1.8) 11	1.8 ± .1 (1.7–1.8) 6

gins of the toothrows, the mesopterygoid fossa is wider relative to width of the palatal bridge, and the alisphenoid canal is exposed above each pterygoid fossa in all specimens.

The dentaries of *M. elegans* are larger versions of those in *M. beccarii*.

In *M. elegans*, the configuration of the in-

cisors, color of their enamel faces, and angle at which the uppers emerge from the rostrum are similar to those in *M. beccarii*.

Although larger (tables 5 and 8), the upper and lower molars in *M. elegans* are basically similar to those of *M. beccarii* in number of roots, shape, and occlusal patterns, with

TABLE 8—(Continued)

Measurement	Females		
	Juvenile ^d	Adults ^e	Young adults ^f
Length of head and body	124	184.4 ± 8.5 (179–197) 13	158.0 ± 10.4 (143–167) 4
Length of tail	176	254.9 ± 17.9 (220–278) 13	236.0 ± 9.0 (224–245) 4
Scale rows/cm. on tail	19	11.4 ± .8 (6.4–7.4) 13	12.8 ± .5 (12–13) 4
Length of tail brush	5	13.4 ± 2.9 (8–19) 13	10.0 ± 1.4 (8–11) 4
Length of hind foot	32	36.8 ± .7 (35–38) 13	35.8 ± 1.3 (34–37) 4
Length of ear	20	24.4 ± .7 (24–25) 13	23.5 ± .6 (23–24) 4
Greatest length of skull	33.6	41.2 ± 1.1 (38.9–42.8) 13	38.5 ± 1.4 (36.7–39.9)
Basilar length	25.6	32.7 ± 1.7 (28.9–34.7) 13	26.8 ± 1.2 (25.6–28.4)
Zygomatic breadth	16.4	19.6 ± .5 (18.7–20.3) 13	18.1 ± .5 (17.3–18.4) 4
Interorbital breadth	5.4	5.5 ± .1 (5.2–5.8) 13	5.4 ± .1 (5.3–5.6) 4
Length of rostrum	9.9	13.4 ± .5 (12.4–14.2) 13	12.1 ± 1.0 (11.2–13.3) 4
Breadth of rostrum	—	7.0 ± .4 (6.4–7.4) 13	6.5 ± .2 (6.3–6.7) 4
Length of nasals	12.1	15.4 ± .7 (14.2–16.7) 13	13.6 ± .9 (12.9–14.9) 4
Breadth of braincase	15.7	16.4 ± .4 (16.1–17.0) 13	16.2 ± .4 (15.6–16.5) 4
Height of braincase	10.7	11.7 ± .3 (11.3–12.1) 13	11.4 ± .6 (10.6–12.0) 4
Breadth across incisor tips	1.6	2.4 ± .1 (2.3–2.7) 13	2.1 ± .2 (2.0–2.4) 4
Breadth of zygomatic plate	2.5	3.4 ± .3 (2.8–3.9) 13	2.9 ± .2 (2.8–3.1) 4
Depth of zygomatic notch	.2	.9 ± .9 (.4–1.5) 13	.6 ± .3 (.3–.9) 4
Length of diastema	8.8	11.3 ± .5 (10.3–11.9) 13	10.2 ± .3 (9.9–10.6) 4
Palatilar length	16.0	17.7 ± .4 (17.1–18.5) 13	16.5 ± .5 (16.0–17.1) 4
Palatal length	16.8	20.5 ± .5 (19.5–21.2) 13	18.9 ± .7 (18.2–19.8) 4
Postpalatal length	11.9	15.6 ± .8 (14.1–16.7) 13	14.0 ± .8 (13.0–14.8) 4
Length of incisive foramina	6.3	7.9 ± .3 (7.4–8.4) 13	7.1 ± .4 (6.6–7.4) 4
Breadth of incisive foramina	2.4	2.9 ± .2 (2.7–3.2) 13	2.8 ± .2 (2.6–2.9) 4
Incisive foramina past M ¹	.7	.6 ± .2 (.2–.9) 12	.5 ± .2 (.3–.8) 4
Length of palatal bridge	6.3	5.9 ± .3 (5.6–6.5) 13	5.8 ± .2 (5.6–6.0) 4
Palatal margin to M ³	.3	.4 ± .3 (even–1.0) 13	.3 ± .1 (.2–.4) 4
Breadth of palatal bridge at M ¹	3.3	3.7 ± .2 (3.5–4.1) 13	3.7 ± .1 (3.5–3.8) 4
Breadth of palatal bridge at M ³	3.7	4.1 ± .2 (3.8–4.3) 13	4.1 ± .1 (3.9–4.1) 4
Breadth of mesopterygoid fossa	3.1	3.7 ± .2 (3.5–4.1) 13	3.5 ± .3 (3.3–3.9) 4
Length of bulla	4.9	5.3 ± .2 (4.8–5.5) 13	5.1 ± .1 (4.9–5.2) 4
Height of bulla	4.0	4.6 ± .2 (4.4–4.8) 13	4.5 ± .2 (4.2–4.6) 4
Alveolar length of M ^{1–3}	6.5	6.7 ± .4 (6.2–7.5) 13	6.5 ± .2 (6.3–6.7) 4
Breadth of M ¹	1.8	1.8 ± .1 (1.8–2.1) 13	1.9 ± .0 4
Length of M _{1–3}	6.4	6.6 ± .3 (6.1–7.0) 13	6.4 ± .1 (6.3–6.6) 4
Breadth of M ₁	1.7	1.8 ± .1 (1.7–1.9) 13	1.7 ± .1 (1.6–1.8) 4

^a AMNH 223693 (MZB 12151).^b AMNH 223677, 223681, 223686, 223691–223693, 223696, 225133, 225135, 225141, 225142.^c AMNH 223678, 223684, 223689, 223690, 223697, 225134.^d AMNH 225143.^e AMNH 223679, 223680, 223685, 223687, 223695, 225131, 225132, 225136–225139, 225145, 225146.^f AMNH 223682, 223683, 223688, 223694.

these differences. Most specimens of *M. elegans* have a labial rootlet in addition to the three large primary roots that anchor each first upper molar (table 7). The second row of cusps on the first upper molar in *M.*

elegans is not as elaborate as in *M. beccarii*; the lingual margin of the central cusp t5 is only slightly expanded, does not resemble a jutting cusp, and is fused to the adjacent cusp t4 in all specimens except the juvenile de-

picted in figure 31; cusp t6 is usually round or may jut backward, but it is a single cusp in 35 specimens and in only five examples is there a discrete accessory labial cusp behind cusp t6 as there is in all examples of *M. beccarii*. The central cusp t8 in the third row tends to have a large, cusplike expansion that is directed back and toward the lingual side so it resembles a separate cusp (fig. 31). This is simply a lingual enlargement of cusp t8 and not a cusp t7. In many specimens, there is a ridge extending anteriorly from this enlargement that merges with cusp t4 in adults. The posterior cingulum is thick and shorter than its counterpart in *M. beccarii*, and when completely merged with the lingual enlargement of cusp t8 it forms a wide, curved lamina. The second row of cusps on the second upper molar differs from its counterpart in *M. beccarii* in the same way as does the second row on the first molar. Cusp t3 occurs slightly more frequently in the sample of *M. elegans* than in *M. beccarii* (table 7). Cusp t3 on the third upper molar of *M. elegans* occurs in about a third of the sample, but is absent from all examples of *M. beccarii* (table 7); the rest of the occlusal pattern resembles that of *M. beccarii*.

In their number of roots, as well as occlusal outlines and patterns, the lower molars of *M. elegans* are also similar to those of *M. beccarii*, with the following differences. More of the sample of *M. elegans* has only two primary roots anchoring each first lower molar instead of two and a labial nubbin (table 7). The two species differ in the frequency of labial cusplets and anterolabial cusps: the anterior cusplet on the first molar is present in all specimens, whereas it is absent in half the sample of *M. beccarii*; there are a few specimens without a posterior cusplet on the second molar; and there is an anterolabial cusp on the third molar in about a fourth of the sample—such a cusp is absent in all specimens of *M. beccarii*.

Three males (AMNH 223677, 223681, and 223684) and three females (AMNH 223679, 223688, and 223699) of *M. elegans* were analyzed for their chromosomal characteristics; 10–20 cells were examined from each individual. Samples of male and female karyo-

types are illustrated in figure 34 (see also table 4). The diploid number is 42, and the FN is 57 in males and 56 in females. In most specimens there are seven pairs of submetacentric chromosomes—two large, one slightly smaller, two medium-sized, and two small pairs—and 13 pairs of telocentric chromosomes that grade in size from medium-sized to small. In addition, in the male, the X-chromosome is the smallest telocentric in the spread; the Y-chromosome, present only in the males, is a medium-sized submetacentric that is slightly smaller than the medium-sized submetacentric autosomes. Fifteen submetacentric chromosomes can be found in complete spreads of each male, as can the small telocentric that I designated the X-chromosome. Neither chromosome can be matched well with any other one in the complement.

The female karyotype resembles that of the male but has only 14 submetacentric chromosomes. If the unpaired fifteenth submetacentric found in the male was an X-chromosome there should have been an eighth pair of medium-sized submetacentrics in the female that would have been the sex chromosomes. Fourteen was the highest count of submetacentrics in the many spreads I examined of each female. For that reason, the medium-sized submetacentric in the male was designated the Y-chromosome and the small telocentric the X-chromosome. It follows that the pair of X-chromosomes in the female consists of the two smallest telocentrics in the complement.

Male sex chromosomes consisting of an X that is smaller than the Y is unusual among species of murid rodents. There are uncommon configurations in the sex chromosomes that involve polymorphism (see Baverstock, Watts, and Hogarth, 1977, and the examples cited therein; Fredga et al., 1976) and unpaired sex chromosomes (Matthey, 1953; Honda, Suzuki, and Itoh, 1977). Of the latter, the Amami spinous country rat, *Tokudaia osimensis osimensis*, has a 2N of 25, and an unpaired medium-sized submetacentric chromosome in both males and females. Polymorphism among sex chromosomes and unpaired sex chromosomes seem to be unusual departures from the configurations

found in most species of rats and mice where the X-chromosome is larger than the Y-chromosome. If the unpaired medium-sized submetacentric in each male of *M. elegans* had been designated as an X-chromosome, then one of the medium-sized pairs of metacentrics in the female—the fifth largest pair, for example—would have to be the sex chromosomes, which would mean that pair five in the female would consist of two medium-sized telocentrics, which would not be consistent with the fifth largest pair of submetacentric counterparts in the male. I suspect that the sex chromosomes in the female can be verified only by banding studies. If my arrangement of the sex chromosomes in the male is correct, then the addition of heterochromatin may account for the Y-chromosome being larger than the X-chromosome, a suggestion that could also be tested by banding studies.

The fourth pair of submetacentric chromosomes is polymorphic in my sample of three females. In one individual, pair four consists of a medium-sized metacentric and a medium-sized submetacentric, a configuration present in all good spreads of the specimen. In the other two females, pair four was homomorphic, composed of two medium-sized submetacentric chromosomes, each similar in size and configuration to those in all three males.

In contrast to *M. beccarii* and *M. elegans*, which are rat-sized, the third species in *Margaretamys* is mouse-sized, for which I propose the following name.

***Margaretamys parvus*, new species**

HOLOTYPE: AMNH 225063 and MZB 12152 (now in the collection at the American Museum of Natural History, the holotype of *M. parvus* will be transferred to the Museum Zoologicum Bogoriense), an adult female collected at 7400 feet on Gunung Nokilalaki by members of the Archbold Sulawesi Expedition (original number, ASE 2715) on March 24, 1975. A skin (fig. 37), skull, and carcass preserved in fluid comprise the specimen.

REFERRED SPECIMENS: 18, in addition to

the holotype, from the following sites on Gunung Nokilalaki: 6000 ft. (AMNH 225068–225071); 6100 ft. (AMNH 225067); 7300 ft. (AMNH 225066); 7350 ft. (AMNH 225065); 7400 ft. (AMNH 225055–225062, 225064); 7500 ft. (AMNH 225053, 225054).

KNOWN DISTRIBUTION: From 6000 to 7500 feet in montane forest on the slopes of Gunung Nokilalaki in Central Sulawesi; not found in lowland tropical evergreen rain-forest.

ETYMOLOGY: The name *parvus* means small and I use it to refer to the size of the animals compared with the larger *M. beccarii* and the even larger *M. elegans*.

DIAGNOSIS: An arboreal rat morphologically like *M. beccarii* and *M. elegans* (fig. 23) but differing by being much smaller in body size (tables 5, 8, and 9); having short, very dense, and soft pelage that is reddish brown over the upperparts and dark gray on the underparts; a very long monocolored tail; a much smaller, more gracile cranium (tables 5, 8, and 9; figs. 28 and 29); a delicate, tapered rostrum; a relatively higher and more inflated braincase; relatively narrower upper and lower molars in which all cusps on the first and second upper molars are pressed together and merged at very early stages of wear to form chevron-shaped laminae; a smaller third upper molar relative to the other teeth in the molar row; and lacking a posterior cingulum on each third upper molar.

DESCRIPTION AND COMPARISONS: Although the three species of *Margaretamys* are similar to one another in conformation of their body, tail, ears, and hind feet, they are dissimilar in body size as well as color and texture of pelage. Where *M. beccarii* is a small rat with semi-spinous pelage, gray upperparts, cream or yellow underparts, and a brown tail, *M. elegans* is a much larger animal with a bicolored tail, dense, soft, and long brown fur over the upperparts, and grayish white underparts. *Margaretamys parva* is the smallest of the three (tables 5, 6, 8, and 9). Its upperparts are a rich reddish brown and there is a conspicuous blackish brown mask on the face. The underparts are dark grayish white in most specimens, dark gray washed with buff in a few. The fur on

the head and body is dense, soft, short (10–13 mm. thick), has a slightly woolly look, and appears compact because the guard hairs are thin, extend only about 5 mm. beyond the overhairs, and inconspicuous—a striking contrast to the long pelage of *M. elegans* with its very long and prominent black guard hairs. The vibrissae above the eyes and on the muzzle of *M. parvus* reach up to 55 mm. The ears are small, dark brown, and slightly haired. The hind feet resemble those of *M. beccarii* and *M. elegans* in basic configuration of claws and palmar and plantar pads, but the feet are smaller, appear more delicate and relatively narrower than those of the other two species (figs. 26 and 27); with their white digits covered with silvery hairs and dark brown strips over the metacarpal and metatarsal areas, the feet are similar to the other two species in color and pattern. The tail of *M. parvus* is much longer than the combined lengths of head and body (table 9), dark brown all over, penicillate in its distal half and distinctly tufted; its color and pilosity are similar to the tails of *M. beccarii* and none of the specimens of *M. parvus* have any indication of either mottling or bicoloration. Finally, the females of *M. parvus* have three pairs of mammae, positioned in the postaxillary and inguinal regions as are their counterparts in *M. beccarii* and *M. elegans*.

One specimen in the series appears to be a juvenile (table 6). Color of its feet and tail are slightly paler than in adults; the upperparts are darker, covered by finer and more woolly hairs; the underparts are dark grayish white, but flat in tone, without the highlights seen in the adults. If this specimen is representative of juvenile pelage, then that coat in *M. parvus* is like the adult fur, a contrast to both *M. beccarii* and *M. elegans* where the juveniles are gray and look very different than the adults.

In contrast to the larger, rectangular, and elongate crania of *M. beccarii* and *M. elegans*, that of *M. parvus* is much smaller (tables 5, 8, and 9), appears more delicate in structure, has a rounded configuration in the back and appears tapered in front (figs. 28 and 29). That effect is due to the braincase and rostrum; the braincase is inflated and rel-

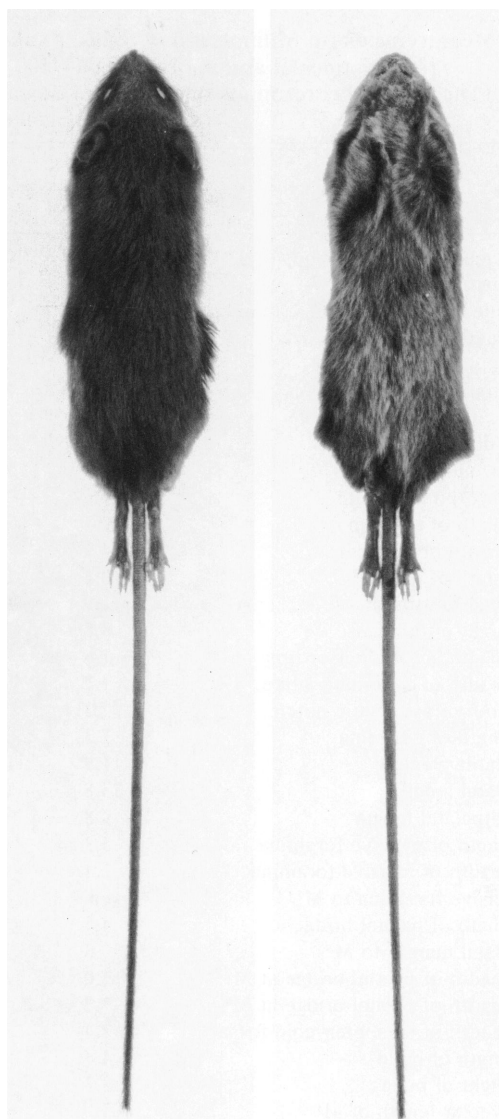


FIG. 37. *Margaretamys parvus*. Dorsal and ventral views of AMNH 225063 (the holotype), an adult female from Gunung Nokilalaki, 7400 ft., Central Sulawesi: length of head and body, 103 mm.; length of tail, 168 mm.; length of hind foot, 25 mm.; length of ear, 20 mm.; weight, 40 g.

atively higher than in the other two species, nearly smooth because of very weak ridges outlining the interorbital and postorbital regions and no temporal ridges, and rounded—

TABLE 9
Measurements (in Millimeters) of Skins, Skulls, and Teeth in Samples of *Margaretamys parvus* from Elevations at and between 6000–7500 Feet on Gunung Nokilalaki, Central Sulawesi
 (The mean plus or minus one standard deviation, observed range in parentheses, and number of specimens is listed for each measurement.)

Measurement	Holotype ^a	Females	Males	
		Adults ^b	Adults ^c	Juvenile ^d
Length of head and body	103	100.4 ± 2.8 (96–103) 7	105.0 ± 5.0 (99–114) 7	86
Length of tail	168	158.3 ± 4.7 (154–168) 7	170.4 ± 6.8 (164–184) 7	130
Scale rows/cm. on tail	16	16.9 ± .7 (16–18) 7	16.1 ± 1.6 (14–18) 7	21
Length of tail brush	8	10.1 ± 2.3 (7–14) 7	10.7 ± 1.8 (8–13) 7	7
Length of hind foot	25	23.9 ± .7 (23–25) 7	25.0 ± .0 (25–25) 7	21
Length of ear	20	19.9 ± .7 (19–20) 7	19.9 ± .7 (19–20) 7	18
Greatest length of skull	28.9	28.4 ± .4 (27.7–28.9) 7	28.9 ± .7 (27.8–29.7) 6	25.4
Basilar length	21.6	21.3 ± .6 (20.1–22.0) 7	21.8 ± .6 (20.8–22.6) 6	18.9
Zygomatic breadth	13.3	13.5 ± .2 (13.2–13.9) 7	13.6 ± .5 (13.1–14.1) 6	12.0
Interorbital breadth	4.6	4.6 ± .2 (4.3–4.7) 7	4.6 ± .2 (4.3–4.8) 7	4.4
Length of rostrum	9.5	9.1 ± .3 (8.5–9.5) 7	9.3 ± .3 (8.8–9.5) 7	7.9
Breadth of rostrum	4.9	4.7 ± .2 (4.3–4.9) 7	4.9 ± .2 (4.7–5.2) 7	3.8
Length of nasals	10.4	10.6 ± .3 (10.1–11.2) 7	10.9 ± .4 (10.0–11.2) 7	9.0
Breadth of braincase	12.9	13.1 ± .1 (12.9–13.3) 7	13.3 ± .4 (12.8–13.7) 6	12.1
Height of braincase	8.8	8.8 ± .3 (8.4–9.2) 7	8.7 ± .3 (8.2–9.1) 6	8.4
Breadth across incisor tips	1.6	1.6 ± .1 (1.5–1.6) 7	1.6 ± .1 (1.5–1.7) 7	1.2
Breadth of zygomatic plate	1.7	1.7 ± .1 (1.6–1.9) 7	1.7 ± .2 (1.7–2.1) 7	1.5
Depth of zygomatic notch	.3	.2 ± .1 (.0–.3) 7	.2 ± .1 (.1–.3) 6	.0
Length of diastema	7.3	7.4 ± .3 (6.8–7.8) 7	7.5 ± .3 (6.8–7.8) 6	6.3
Palatilar length	11.9	11.7 ± .3 (11.1–12.1) 7	12.2 ± .2 (11.8–12.5) 6	10.6
Palatal length	13.8	13.4 ± .4 (12.6–13.8) 7	13.9 ± .2 (13.6–14.2) 6	12.0
Postpalatal length	9.8	9.8 ± .2 (9.3–10.0) 7	9.9 ± .2 (9.6–10.2) 6	8.3
Length of incisive foramina	5.3	5.0 ± .2 (4.6–5.3) 7	5.2 ± .2 (4.9–5.4) 6	4.2
Breadth of incisive foramina	2.1	2.1 ± .2 (2.0–2.4) 7	2.2 ± .2 (2.0–2.5) 6	1.9
Incisive foramina to M ¹	even	.3 ± .1 (even–.4) 7	.3 ± .1 (.2–.5) 5	.2
Length of palatal bridge	4.5	4.6 ± .2 (4.4–4.9) 7	4.9 ± .2 (4.6–5.0) 6	4.5
Palatal margin to M ³	.3	.4 ± .1 (.3–.5) 7	.3 ± .2 (even–.5) 6	.3
Breadth of palatal bridge at M ¹	3.0	3.1 ± .1 (3.0–3.2) 7	3.1 ± .2 (2.9–3.2) 6	2.6
Breadth of palatal bridge at M ³	3.2	3.4 ± .2 (3.1–3.6) 7	3.5 ± .1 (3.4–3.7) 6	3.3
Breadth of mesopterygoid fossa	2.4	2.5 ± .2 (2.2–2.7) 7	2.6 ± .2 (2.3–2.8) 6	2.4
Length of bulla	4.4	4.2 ± .2 (4.0–4.5) 7	4.2 ± .2 (3.8–4.5) 7	4.1
Height of bulla	3.3	3.3 ± .1 (3.1–3.4) 7	3.4 ± .1 (3.3–3.5) 7	3.4
Alveolar length of M ^{1–3}	5.0	4.7 ± .2 (4.5–5.0) 7	4.8 ± .2 (4.6–5.1) 7	4.6
Breadth of M ¹	1.5	1.3 ± .1 (1.2–1.5) 7	1.3 ± .1 (1.3–1.4) 7	1.3
Length of M _{1–3}	4.8	4.7 ± .1 (4.5–4.8) 7	4.7 ± .1 (4.6–4.9) 7	4.7
Breadth of M ₁	1.2	1.2 ± .1 (1.1–1.2) 7	1.2 ± .1 (1.1–1.3) 7	1.2

^a AMNH 225063 (MZB 12152).

^b AMNH 225060–225063, 225069–225071.

^c AMNH 225053–225057, 225066, 225067.

^d AMNH 225068.

a conformation especially evident in dorsal view. The braincase in both *M. beccarii* and *M. elegans* is relatively lower, appears more rectangular in dorsal view, and has promi-

nent shelves and ridges in the interorbital and postorbital areas, and conspicuous low ridges along dorsolateral margins of the braincase. The interorbital region is wide in

M. parvus, as it is in the other two species, and the rostrum is long, but it is tapered and gracile in contrast to the wide rostra of the others. Except for the outline of the rostrum, the configuration of the underside of the cranium is similar to that in *M. beccarii*, especially the incisive foramina, which end either before or at the front of the toothrows and do not penetrate between them as happens in *M. elegans*. The alisphenoid canal is open in 14 examples of *M. parvus* and bounded by a strut of alisphenoid bone in one specimen. The dentaries of *M. parvus* are much smaller and appear more delicate than those in the other two species, but are otherwise similar in shape.

Shapes of the incisors in *M. parvus*, and the orthodont position of the uppers, are like shapes and positions of the incisors in *M. beccarii* and *M. elegans*; the uppers have orange or pale orange enamel layers, the lowers are cream. The molars of *M. parvus* are small (table 9), like the other two species in the number of roots anchoring the upper and lower molars (table 7), and although superficially similar in shape and occlusal patterns to the other species, differ in distinctive details (figs. 30–32).

Both upper and lower molars of *M. parvus* are relatively narrower than those in *M. beccarii* and *M. elegans*, and the third upper molar is smaller relative to the other molars in each tooththrow. The narrower teeth reflect compaction of the cusps, which in turn has produced rows of cusps on the first and second upper molars that are chevron-shaped, not low arches as in *M. beccarii* and *M. elegans*; cusp t4 on each first and second upper molar is closely pressed against and merged with the central cusp t5, which compresses the lingual cusplike spur of cusp t5 into a ridge, in all specimens (instead of separated as cusp t4 is in most *M. beccarii* and in juvenile *M. elegans*); and each first upper molar does not have an additional cusp or ridge behind cusp t6 in any specimen of *M. parvus* (as in most *M. elegans*, but not *M. beccarii* in which the cusp or ridge is always present). A small cusp t3 is usually present on each second upper molar, as it is in samples of *M. beccarii* and *M. elegans*, but cusp t3 is ab-

sent from the third upper molar of all the specimens, as is characteristic of *M. beccarii* (table 7). The cusps on the first and second upper molars are merged even in juveniles, and the posterior cingulum on each tooth is not discrete, already broadly merged with cusps t8 and t9 even in young animals (fig. 32). The occlusal patterns of these two teeth are thus simple compared with those in *M. beccarii* and *M. elegans*; with increasing wear, they become even simpler—cusp t8, cusp t9, and the posterior cingulum on each molar forms one large wear surface broken only by a small enamel-lined cavity in the center.

The relatively smaller size of each third upper molar reflects the absence of a posterior cingulum on that tooth, a structure that is present on the third molars in all specimens of *M. beccarii* and *M. elegans*. The result is that the occlusal pattern on the third molar in *M. parvus* is less elaborate than those in the other two species.

The shapes and occlusal configurations of the lower molars in *M. parvus* (fig. 32) are basically like those in *M. beccarii* and *M. elegans*, with these differences: the rows of cusps, especially those on the first and second molars, are shaped more like chevrons than gentle arcs; the front row on the first molar is simple and usually without an anterocentral cusp at the front of the tooth (present in *M. beccarii* and most *M. elegans*); and the cusplets and anterolabial cusp along the labial margins of the first and second molars are small and already nearly completely merged with the adjacent cusps even in juveniles, and disappear in adults, with the result that the occlusal surfaces are simple. Each third lower molar in *M. parvus* consists of only two laminae, without an anterolabial cusp, like the structure in *M. beccarii*.

Margaretamys COMPARED WITH OTHER GENERA: Comparisons are needed between *Margaretamys* on the one hand, and *Niviventer cremoriventer*, *Limnomys sibuanus*, and *Rattus* on the other. Configurations of the body and tail, nature of the pelage, and general shape of the skull in *Margaretamys beccarii* is similar to that of *Niviventer cre-*

moriventer, and for these reasons the two species have been closely associated. The two, however, are very different from one another in external, cranial, dental, and chromosomal details—there is no morphological evidence supporting close relationship. *Niviventer cremoriventer* contrasts with *M. beccarii* in the following features (figs. 39, 41, and 42).

1. The tail of *N. cremoriventer* is less penicillate than that of *M. beccarii*.

2. There are four pairs of mammae (three pairs in *M. beccarii*).

3. The cranium is flatter.

4. The lacrimals are smaller relative to size of the cranium and oblong in outline (relatively larger and squarish).

5. A strut of alisphenoid bone separates the foramen ovale accessorius from the masticatory-buccinator foramina (such a strut is absent in most specimens of *M. beccarii*, as are the foramen ovale accessorius and the masticatory-buccinator foramina).

6. The bullae are smaller, both absolutely and relative to size of cranium.

7. The coronoid process is much smaller relative to body of the dentary.

8. Each first upper molar has five prominent roots and additional labial rootlets; each first lower molar is anchored by four roots (three-rooted uppers and two-rooted lowers in *M. beccarii*).

9. The upper and lower molar rows are larger, each third upper molar is smaller relative to the other teeth in the row.

10. Occlusal surfaces of the upper molars are much less elaborate (fig. 41): no cusplike lingual spur on cusp t5 of the first molar, no accessory labial cusp behind cusp t6, indistinct cusp t9 on first and second molars, cusp t4 broadly merged with cusp t5, and no posterior cingulum on any of the upper teeth.

11. Occlusal surfaces of the lower molars are also less complex than those in *M. beccarii* (fig. 42): no anterocentral cusp on the first molar, narrow and oblong first lamina on front molar, no posterior labial cusplets on any teeth, no anterolabial cusps on either the second or third molars, and narrower posterior cingula.

12. The karyotype is different: $2N = 46$, with three pairs of small metacentrics, one pair of subtelocentrics, and the rest telocentrics ($2N = 42$ in *M. beccarii*, two pairs of small metacentrics, the rest telocentrics; table 4).

The association of *beccarii* with *Rattus* was through its former inclusion within either the *cremoriventer*-group (Tate, 1936) or the *niviventer*-group (Ellerman, 1949), clusters that I have now separated from *Rattus* and placed in *Niviventer*. *Margaretamys* is not morphologically close to any species of *Niviventer*, nor can it be tied to any in *Rattus* (fig. 38). *Margaretamys* and *M. beccarii* in particular differ from *Rattus* in five of the six cranial features listed previously that also distinguish *Niviventer*, *Leopoldamys*, and *Srilankamys* from *Rattus*, and in the following characters.

1. The tail is prominently penicillate (not so in *Rattus*).

2. There are few roots beneath the upper and lower molars (the first upper molars of *Rattus* have five roots, the second has four, and the third is anchored by three; the first lower molar has four, the second and third molars are anchored by three). Cusp t5 on the first and second upper molars has a lingual, cusplike extension (not found in any *Rattus*).

3. Cusp t4 is separated from cusp t5 or weakly connected (cusps t4 and t5 are broadly connected in all *Rattus*).

4. A prominent accessory labial cusp sits behind cusp t6 on each first upper molar in all specimens of one species, and some of another (no labial cusp behind cusp t6 in any *Rattus*).

5. A wide laminar-like posterior cingulum sits at the back of each upper molar in two species, and at the back of each first and second upper molar in another (absent in most *Rattus*; if present, it consists of a slight triangular projection from the back of cusp t8 on each first molar that represents an inconspicuous remnant).

6. The karyotype is $2N = 42$, with two small pairs of metacentrics and the rest telocentrics (most *Rattus* also have $2n = 42$,

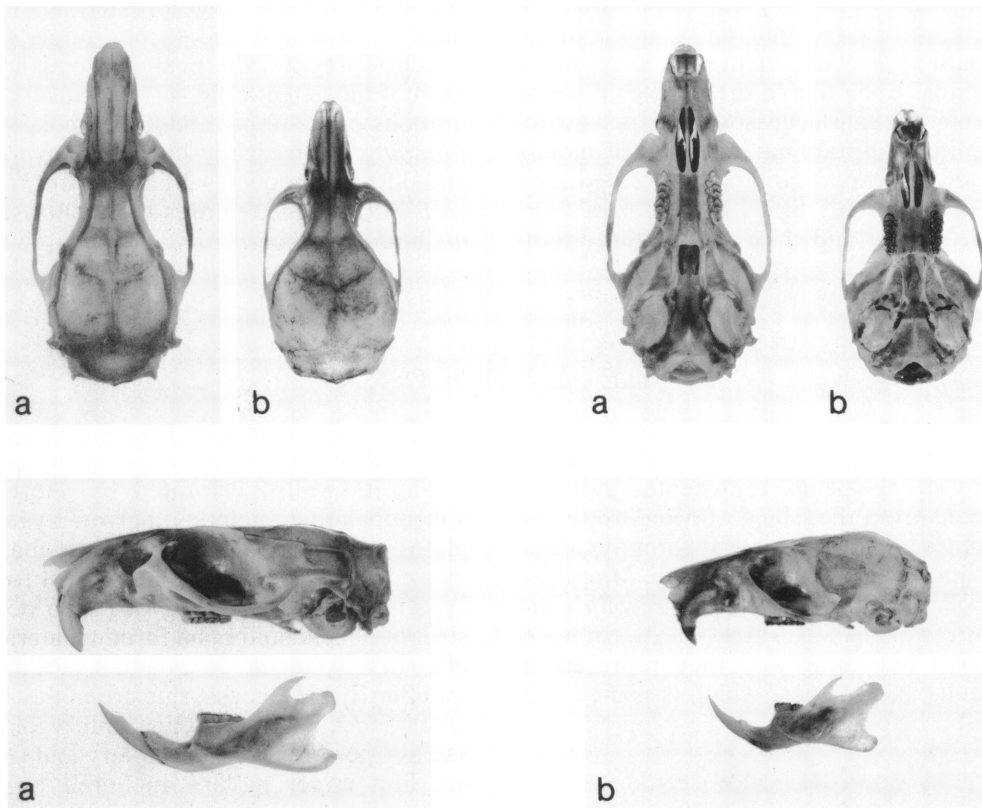


FIG. 38. Views of adult crania and dentaries. *Rattus*, as exemplified by *R. rattus diardii* (AMNH 250104) from Java (a), is contrasted with *Margaretamys*, represented by *M. beccarii* (AMNH 226818) from Central Sulawesi (b). Natural size.

but the karyotype includes seven pairs of small metacentrics, a characteristic feature; Yosida, 1973; Baverstock, Watts, and Hogarth, 1977).

At one time I (Musser, 1977) suggested that *Limnomys sibuanus*, an inhabitant of mountain forest on the island of Mindanao in the Philippines, might be phylogenetically closely related to *beccarii* and its allies on Sulawesi. Although resembling *beccarii* in size, body build, and general cranial configuration, I now realize that the similarities are superficial; *L. sibuanus* is not closely related to any of the species in *Margaretamys*. *Limnomys sibuanus* is about the same body size as *M. beccarii* (tables 5, 10), has tawny brown upperparts, cream underparts, six

mammae, and a long tail; although hairy, the tail is merely tufted at the tip and not penicillate in its distal third as it is in the species of *Margaretamys*.

It is in the characteristics of the skull and teeth, however, where the dissimilarities between *Limnomys* and *Margaretamys* really show up. The cranium and molars of *Limnomys* are like those of *Rattus*, with some of the same derived features: a long palatal bridge extending past the backs of the tooth-rows; narrow mesopterygoid fossae relative to breadth of the palatal bridge; spacious sphenopalatine vacuities; large interpterygoid foramina perforating the pterygoid fossae; moderately large bullae; posterior edges of the squamosal roots of the zygomatic

arches extending as low horizontal ridges to the occiput; each alisphenoid canal open on its lateral side where it passes through the alisphenoid bone above the pterygoid fossa; no foramen ovale accessorius or masticatory-buccinator foramina; first upper molars five-rooted, second molars four-rooted, and third three-rooted; first lower molars four-rooted, second and third molars three-root-

ed; and a narrow ridge pressed against the back of each first and second upper molar, which represents the posterior cingulum on each of those teeth (fig. 41). Occlusal configurations of the upper and lower molars of *L. sibuanus* are basically like those in *Rattus*, and differ from occlusal patterns of *M. beccarii* in the same features that contrast *Rattus* and *M. beccarii*.

THE MINDORO RAT

The fifth group discussed in this section consists of one species represented by three specimens from the island of Mindoro in the Philippines. The rats are apparently arboreal, superficially resemble both *Margaretamys beccarii* and *Niviventer cremoriventer*, but possess a suite of distinctive characters indicating that they represent a new genus and species, which is named and diagnosed below.

ANONYMOMYS, NEW GENUS

TYPE SPECIES: *Anonymomys mindorensis*, new species.

INCLUDED SPECIES: The type species only.

KNOWN DISTRIBUTION: The island of Mindoro in the Philippines (fig. 43).

ETYMOLOGY: Named for the person, who wishes to remain anonymous, whose generous financial contributions to the Celebes Fund at the American Museum of Natural History helped support my work in Indonesia, both in field and museum.

DIAGNOSIS: A genus of small-sized arboreal murid that is superficially similar to *Niviventer cremoriventer*, but is distinguished from *Niviventer*, *Rattus*, and any other known murid by the following combination of cranial and dental features: short, thick rostrum; wide interorbital region; domed braincase; slight ridging only along dorsolateral margins of interorbital and postorbital areas of braincase; wide and long incisive foramina; short palatal bridge terminating be-

fore end of toothrows; wide mesopterygoid fossa, its walls perforated by short, thin sphenopalatine vacuities; narrow zygomatic plates with slight anterior spines; small bullae; posterior margins of squamosal roots of zygoma not extending as ridges to occiput; strut of alisphenoid bone forming lateral wall of each alisphenoid canal and separating the foramen ovale accessorius from the masticatory-buccinator foramina; pterygoid fossae not perforated by interpterygoid foramina; first upper molars anchored by three large primary roots (anterior, lingual, and posterior) and a tiny labial nubbin; second and third upper molars with three roots below each; two large roots (anterior and posterior) beneath each lower molar; occlusal patterns of upper molars simple, no cusp t7 on any tooth, posterior cingulum absent from second and third molars but represented by a thin ridge on first molar; rows of cusps wide and formed by discrete cusps (not chevrons); cusp t9 on first molar large but small on second; cusp t3 present on second molars but absent from third; occlusal configurations of lower molar rows also simple, two large peglike cusps form front row on first molar, no anterocentral cusp at front of that tooth, and no anterolabial cusp on second or third molars.

Anonymomys mindorensis, new species

HOLOTYPE: an adult male (FMNH 87598) collected at 4500 feet from Ilong Peak in the Halcon Range of Mindoro on April 14, 1954

by D. S. Rabor (original number 1285). A skin, cranium, and mandible comprise the holotype; all elements are in good condition.

REFERRED SPECIMENS: Two others, both of them males, in addition to the holotype: FMNH 87596, collected May 10, 1954, and FMNH 87597, obtained on May 11, 1954; both are also from 4500 feet on Ilong Peak.

KNOWN DISTRIBUTION: Recorded only from the type locality. Ilong Peak is part of the Halcon Range, the highland mass that rises above 8500 feet in the northeastern part of Mindoro Island (see the maps and descriptions in King and McKee, 1949; Ripley and Rabor, 1958).

ETYMOLOGY: Named for the island of Mindoro in the northern Philippine Archipelago.

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

DESCRIPTION AND COMPARISONS: (The description of the species applies also for the genus.) About the same body size as *Niviventer cremoriventer* from the Sunda Shelf (compare table 10 with the data tabulated in Musser, 1973) and like it in external appearance, *Anonymomys mindorensis* may be, on Mindoro, the ecological counterpart of the Sundanese species. Both are small rats with stocky bodies, semi-spinous pelage, buffy or reddish brown upperparts and white or cream underparts, short and wide hind feet, and a long tail that is usually monochrome and tipped with a short tuft. The three examples of *A. mindorensis* are paler and not as spiny as most specimens of *N. cremoriventer*. The upperparts of *A. mindorensis* are bright buffy or tawny brown (bright reddish brown in most *N. cremoriventer*), the underparts are cream. Over the top of the head and body, the fur is long (15–20 mm.) and dense, containing numerous flexible spinelike hairs that give the pelage a soft semi-spinous texture; guard hairs are short, extending 4–6 mm. beyond the overhairs (the pelage of *N. cremoriventer* is shorter with stronger spines so the fur feels more rigidly spiny to the touch). Pelage over the underparts is also dense, 8–10 mm. thick, and soft. The ears are small, tan, and sparsely haired. The face is the

same color as the body, without a dark brown mask. The vibrissae above the eyes and on the muzzle are long, reaching up to 55 mm.

The front and hind feet are short and wide, pale tan and without distinctive patterning, and in their shape and size are much like the feet of *N. cremoriventer* (Musser, 1973, fig. 1). Both have short, sharp, and recurved claws, including a claw on each hallux, large and fleshy palmar and plantar pads adorned with transverse and semicircular lamellae, and naked undersurfaces.

The tail is much longer than the combined lengths of head and body (table 10) and is brown on all surfaces. There are 13–15 rows of scales per cm. Three hairs protrude from under each scale. In the basal one-third of the tail these hairs are slightly longer than each scale, those toward the distal end are even longer, culminating in a conspicuous tuft extending 6 to 8 mm. beyond the tail tip; the tuft is white in FMNH 87597. The length of the tail relative to length of head and body, its brown monochrome, and degree of pilosity are similar to specimens of *N. cremoriventer* from places on the Sunda Shelf, except those samples from Borneo and southern Sumatra in which the ventral surfaces of the tails are either unpigmented, paler than the lateral and upper surfaces, or mottled.

Because all the specimens of *A. mindorensis* I have seen are males, I do not know the number of mammae but I suspect that six pairs, possibly eight, will be found when females are collected.

I have not seen any juveniles, so the nature of that pelage remains to be described.

Anonymomys mindorensis also resembles examples of *Margaretamys beccarii* in body size (compare tables 5 and 10) and build, and relative length of tail but the resemblance is superficial. The latter has more rigidly spiny pelage, grayish brown upperparts and yellowish underparts (bright tawny brown and whitish in *A. mindorensis*), a definite dark mask on the face (no mask), brown feet in which the pigment is arranged in a pattern over the upper surfaces (rather than pale tan and unpatterned), and a definitely penicillate

TABLE 10
Measurements (in Millimeters) of Skins, Skulls, and Teeth from Adults of *Anonymomys mindorensis* and *Limnomys sibuanus*

	<i>A. mindorensis</i>			<i>L. sibuanus</i>
	FMNH 87596	FMNH 87597	FMNH 87598	USNM 125228
Length of head and body	—	—	125	125
Length of tail	—	—	206	150
Scale rows/cm. on tail	13	15	13	14
Length of tail brush	7	6	8	—
Length of hind foot	29	28	31	30
Length of ear	19	17	17	21
Greatest length of skull	32.4	32.4	33.8	33.2
Basilar length	24.8	24.9	26.0	—
Zygomatic breadth	16.0	16.9	16.7	16.2
Interorbital breadth	5.7	6.1	5.9	4.9
Length of rostrum	9.3	9.4	10.1	9.4
Breadth of rostrum	6.0	6.5	6.7	5.8
Length of nasals	11.5	11.0	12.5	11.1
Breadth of braincase	14.8	14.8	15.0	14.8
Height of braincase	10.7	10.8	10.8	10.1
Breadth across incisor tips	2.0	2.0	2.1	1.5
Breadth of zygomatic plate	3.0	2.7	3.2	2.7
Depth of zygomatic notch	0.6	0.8	0.7	1.1
Length of diastema	7.9	8.0	8.2	8.3
Palatilar length	13.6	13.1	13.9	13.9
Palatal length	15.5	15.3	16.0	16.3
Postpalatal length	11.3	11.9	12.4	11.6
Length of incisive foramina	6.3	5.7	6.1	6.2
Breadth of incisive foramina	2.4	2.4	2.5	2.1
Incisive foramina past M ₁	0.6	0.2	0.6	0.2
Length of palatal bridge	5.0	5.2	5.1	5.8
Palatal bridge to M ³	0.1	0.4	0.3	^a
Breadth of palatal bridge at M ¹	3.0	3.0	2.9	3.0
Breadth of palatal bridge at M ³	3.6	3.6	3.4	3.7
Breadth of mesopterygoid fossa	2.8	2.7	3.0	2.3
Length of bulla	5.3	5.2	5.4	5.6
Height of bulla	4.0	4.5	4.3	4.6
Alveolar length of M ¹⁻³	5.7	5.7	6.0	5.0
Breadth of M ¹	1.8	1.8	1.9	1.5
Length of M ₁₋₃	5.5	5.6	5.6	4.9
Breadth of M ₁	1.5	1.6	1.6	1.3

^a Palatal bridge extends beyond back margins of toothrows by 0.7 mm.

tail with a long tuft at the tip (not penicillate, only slightly hairier toward the tip than at the base, with a short tuft).

In size and general build, the cranium of *A. mindorensis* resembles those of *N. cremoriventer* and *M. beccarii* (fig. 39; tables 5, 10; table 1 in Musser, 1973), but differs in

distinctive ways. The rostrum is short and broad in *A. mindorensis*, appearing stocky (slender in *N. cremoriventer* and *M. beccarii*). The interorbital region is wide. The braincase is high, domed, and smooth; its dorsolateral margins are defined by low beading, indefinite and nearly indistinguish-

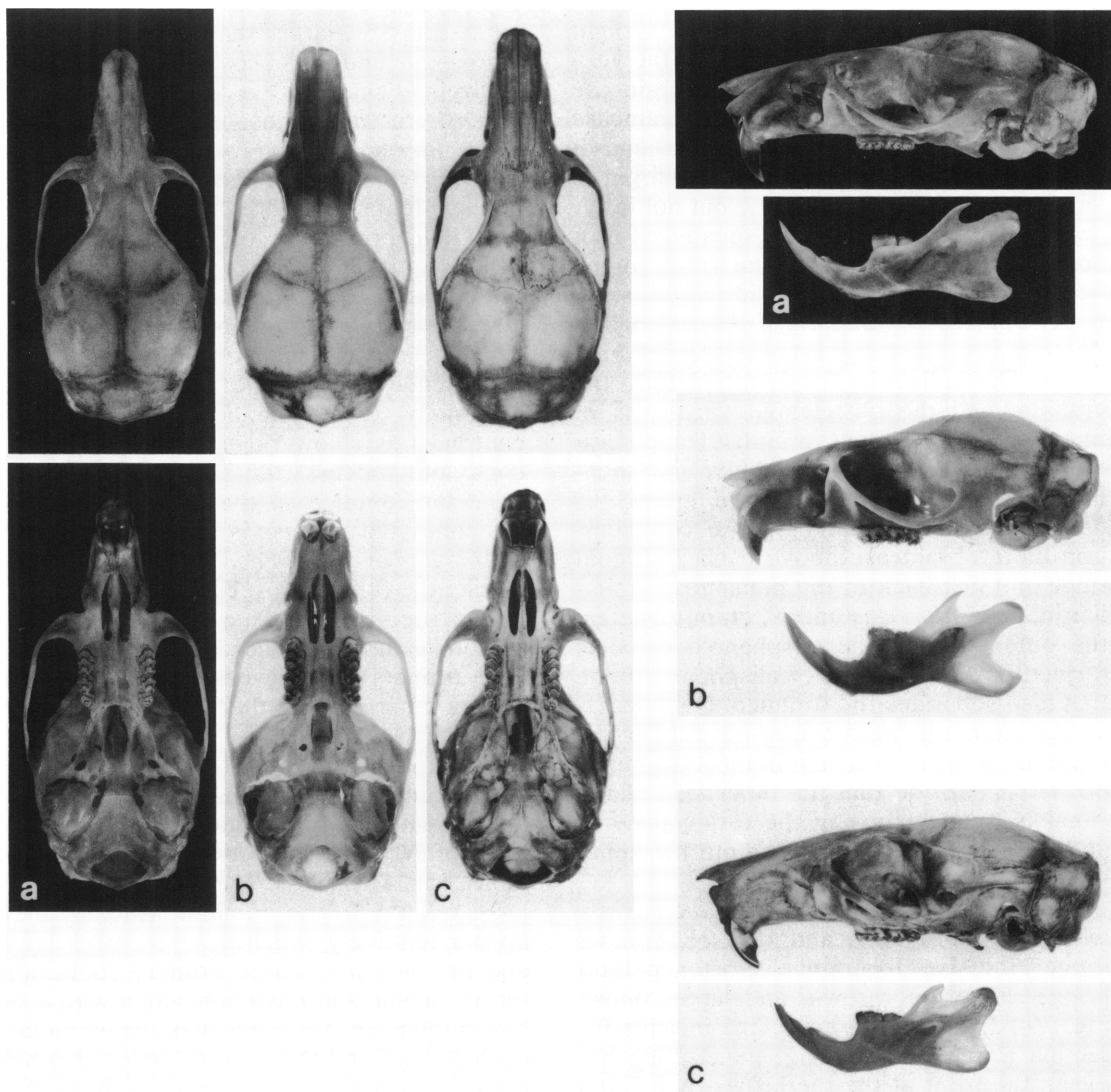


FIG. 39. Views of adult crania contrasting three murid genera: a, *Margaretamys beccarii* (AMNH 224064), Sulawesi; b, *Anonymomys mindorensis* (FMNH 87598), Mindoro Island; c, *Niviventer cremoriventer* (AMNH 217621), Malay Peninsula. Approx. $\times 1.5$.

able from the smooth domed surface (the other two species have low braincases in which the dorsolateral margins are defined by low but conspicuous ridges extending from the frontals nearly to the occiput in *M. beccarii*, and all the way to the occiput in *N. cremoriventer*). That part of each lacrimal bone exposed in the interorbital region

(viewed from above) is oblong, small and inconspicuous (the same configuration in *N. cremoriventer*, but large and squarish in *M. beccarii*). The occiput is deep—front-to-back—and embraces half or two-thirds of the interparietal bone, a configuration like that in *N. cremoriventer* and *M. beccarii*.

In side view, the narrow zygomatic plate

of *A. mindorensis* is evident, with a slight anterior spine only, as indicated by the very shallow zygomatic notch. The high braincase is conspicuous. The sides of the braincase between the back margin of each squamosal zygomatic root and the occipital margin is smooth (as it is in *M. beccarii*, but not in *N. cremoriventer*, in which the squamosal root continues as a low horizontal ridge to the occiput). Apparent also in side view is the larger bulla of *A. mindorensis* (very small in *N. cremoriventer*, slightly smaller in *M. beccarii*). The bullae are firmly attached to the cranium and the postglenoid vacuity is of moderate size (evident in undercleaned crania; the gap between each bulla and squamosal in FMNH 87598 shown in figure 39 is due to excessive cleaning). The configuration of the braincase above each pterygoid ridge and just back of the molar row is similar in *A. mindorensis* and *N. cremoriventer*: the outer wall of the alisphenoid canal is formed by a wide strut of alisphenoid bone that also separates the foramen ovale accessorius from the masticatory-buccinator foramina; this strut is absent in most examples of *M. beccarii* so that the outer side of the canal is open, exposing the foramen ovale and the opening of the canal into the sphenoidal fissure (fig. 40).

In ventral view, *A. mindorensis* contrasts with *N. cremoriventer* and *M. beccarii* in its longer incisive foramina, shorter palatal bridge, larger toothrows, and larger bullae (fig. 39). In *A. mindorensis*, the incisive foramina are wide and long, penetrating between the front of the toothrows by 0.2–0.6 mm. (the foramina are thinner and end in front of the toothrows in *N. cremoriventer* and *M. beccarii*). The palatal bridge is short, ending 0.1 to 0.4 mm. before the back margins of the toothrows. The mesopterygoid fossa is nearly as wide as the palatal bridge and its walls are breached by short, slim sphenopalatine vacuities—the configuration in *N. cremoriventer* and *M. beccarii* as well. The pterygoid fossae are nearly flat, and anterior of the foramen ovale the surface is either complete or perforated by a tiny interpterygoid foramina. The bullae are of

moderate size, larger than those in *N. cremoriventer* and *M. beccarii*.

Size and shape of the dentaries in *A. mindorensis* resemble those elements in *N. cremoriventer* and *M. beccarii* (figs. 22 and 38), differing from them in that the ventral margin of each dentary is more deeply concave; the condyloid process is longer and more slender, as is the angular process; the latter is set off from the condyle by a more deeply concave margin forming the back edge of the dentary; and the shelf on the inner side of each dentary behind the molar row extends diagonally to the mandibular foramen and continues as a low ridge to the end of the condyloid process (the shelf stops just beyond the foramen so the medial surface of the condyloid process is smooth in *N. cremoriventer* and *M. beccarii*).

Like the other two species, the upper and lower incisors in *A. mindorensis* have smooth enamel surfaces that are either orange (uppers) or pale orange (lowers). The uppers emerge from the rostrum at a right angle (orthodont).

The toothrows of *A. mindorensis* are smaller and wider than those in *M. beccarii*, about as long as, but wider than, the toothrows of *N. cremoriventer* (tables 5 and 10; table 1 in Musser, 1973); the teeth appear large relative to the cranium, whereas they appear relatively small in *N. cremoriventer* and *M. beccarii*. Three primary roots (anterior, lingual and posterior) along with a labial nubbin anchor each first upper molar, each second and third upper molar also has three roots (three-rooted upper molars characterize *M. beccarii*, but *N. cremoriventer* has five-rooted first upper molars, four-rooted second molars, and three-rooted third molars). Each of the lower molars is anchored by two large roots, an anterior and posterior (as are the lowers in *M. beccarii*; the second and third lowers of *N. cremoriventer* also have two roots, but the first molar has four—small labial and lingual roots in addition to the anterior and posterior roots). The degree of overlapping among the molars is about the same as that in *N. cremoriventer* and *M. beccarii*, and the interlocking of the

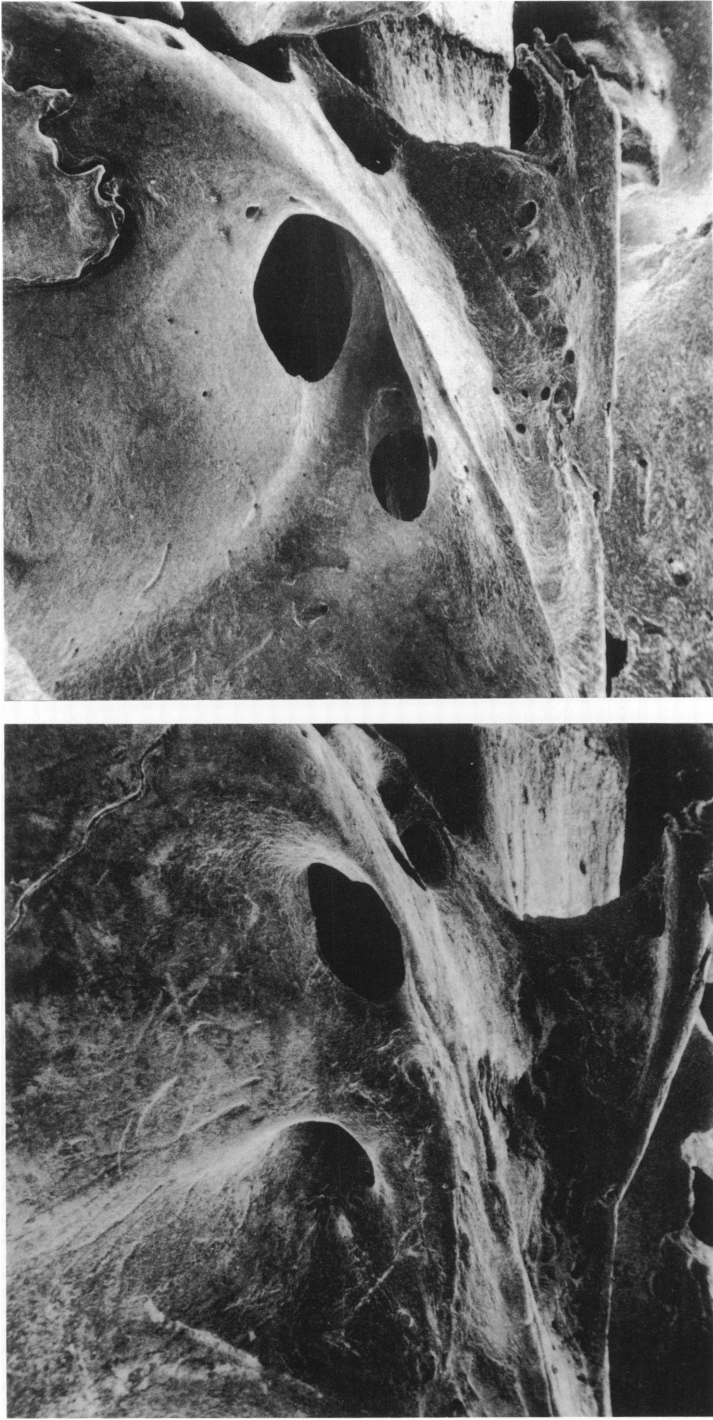


FIG. 40. The alisphenoid region at the base of the cranium in *Anonymomys* and *Margaretamys*. Left: *A. mindorensis* (FMNH 87598) with a strut of alisphenoid bone covering the alisphenoid canal and separating the masticatory-buccinator foramina from the foramen ovale accessorius. Right: *M. beccarii* (AMNH 224064), where the alisphenoid strut is gone and the alisphenoid canal is exposed, as well as the foramen ovale; the masticatory-buccinator foramina and the foramen ovale accessorius are absent. See figure 2 and text for additional information.

molars involves the back of cusp t8 leaning against the anterior faces of cusps t1 and t2 on the tooth behind.

The first and second upper molars are long and wide, the third is wide and short; all have simple occlusal patterns, not as simple as those in *N. cremoriventer* but less elaborate than in *M. beccarii* (fig. 41). Three arcuate rows of cusps form the occlusal surface of each first upper molar. The front row consists of a wide central cusp t2, roughly triangular in cross section; a small round labial cusp t3 situated nearly in line with the central cusp; and a large lingual cusp t1, round to elliptical in cross section, set to the side and back of the row. Large, round lingual and labial cusps along with a wide, roughly triangular central cusp form the second row. The third row consists mostly of a large, roughly diamond-shaped central cusp t8 bounded on the lingual side by a low thick ridge and on the labial margin by a prominent elongate cusp t9. A ridge at the back of the tooth represents the posterior cingulum, a structure that is variable in size, clearly evident in FMNH 87597, but indistinct in the other two specimens. A cusp t7 is absent. In FMNH 87598, there is a small cusp on the labial margin behind each cusp t6, which is likely the counterpart of the cusp that is so large and prominent behind each cusp t6 in *M. beccarii*; the other two specimens of *A. mindorensis* lack such an accessory cusp.

The occlusal surface of the second upper molar is similar to the first except that the central cusp t2 is absent, cusp t1 is large, cusp t3 is small (a low ridge in some specimens), the lingual side of the central cusp t5 is longer than the labial side, cusp t9 is much smaller and appears more like a thick ridge on the labial side of cusp t8 rather than a discrete cusp, and no posterior cingulum sits at the back of each tooth.

The third upper molar is simple in occlusal pattern: a large cusp t1 forms the anterolingual edge of the tooth, a comma-shaped lamina (the merged cusps t4, t5, and t6) forms most of the surface in the central portion, and an elliptical cusp (probably cusps t8 and t9 merged) forms the back margin; cusp t3, cusp t7, and posterior cingulum are absent.

The first lower molars are longer than wide, the second and third molars are about as long as wide, and all have simple occlusal surfaces (fig. 42). Each first molar consists of a front row of two discrete peglike cusps, bulky and either round or oblong in cross section, the lingual slightly larger than the labial; second and third rows of cusps that are arched; and a wide, thick posterior cingulum at the back of the tooth. The only other structure is a posterior cusplet on the labial side of the tooth; an anterior labial cusplet is present only on FMNH 87597; and none of the three specimens has an anterocentral cusp at the front margin of the first molar.

The second lower molar is formed of two wide, bowed laminae, each consisting of two cusps: a wide posterior cingulum and a posterior labial cusplet; there is no anterolabial cusp.

A wide, gently bowed front lamina and narrower, thick back lamina form the occlusal surface of the last lower molar. There is no posterior cingulum or anterolabial cusp.

The molars of *A. mindorensis* require comparison with those of *N. cremoriventer* and *M. beccarii*. *Niviventer cremoriventer* has narrower, more elongate upper and lower molars, third molars that are much smaller relative to the other two in each tooththrow, and less elaborate occlusal patterns (figs. 41 and 42). While the occlusal surfaces of *A. mindorensis* are definitely cuspidate, the cusps have merged in *N. cremoriventer* so that the first and second rows on the first upper molar and the main row on the second tooth resemble thick chevrons. Cusp t8 is large on both the first and second upper molars and cusp t9 is small and merged with the cusp t8 at an early stage of wear. Posterior cingula, as well as cusps t3 on the second and third uppers are absent. The first lower molars are also simple; two thick chevron-shaped rows form most of the surfaces on the first and second teeth; an oblong cusp, sometimes indented in the front surface, comprises the front row on the first lower molar, a configuration that represents the merging of two cusps, even in juveniles; the posterior cingula are thick and prominent;

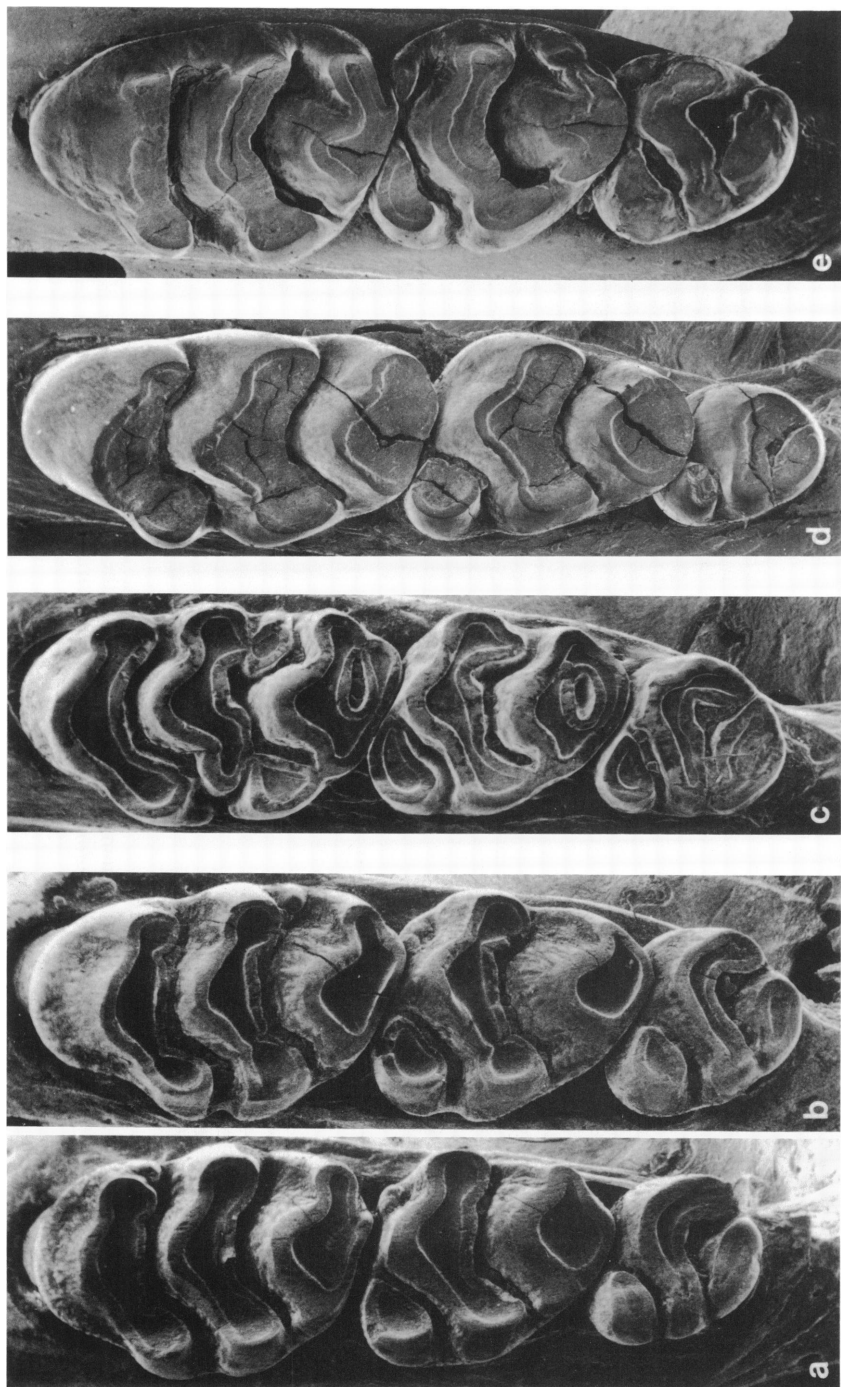


FIG. 41. Occlusal views contrasting left maxillary tooththrows of *Anonymomys*, *Margaretamys*, *Niviventer*, and *Limnomys*: a, *A. mindorensis* (FMNH 87597; LM¹⁻³, 5.7 mm.), note the small posterior cingulum at the back of the first molar; b, *A. mindorensis* (FMNH 87598; LM¹⁻³, 5.9), note the small labial accessory cusp behind cusp t6 on the first molar; c, *M. beccarii* (AMNH 224064; LM¹⁻³, 5.1 mm.), note that cusp t4 is nearly separate from the lingual spur of cusp t5, and the large labial accessory cusp behind cusp t6 on the first molar, as well as the wide posterior cingula on all the teeth; d, *N. cremoriventer* (AMNH 103579; LM¹⁻³, 5.6 mm.), note the simple occlusal patterns; e, *L. sibuanus* (USNM 144621; LM¹⁻³, 5.2 mm.), note the small posterior cingulum on the first tooth and the configurations formed by cusps t8 and t9 on the first and second.

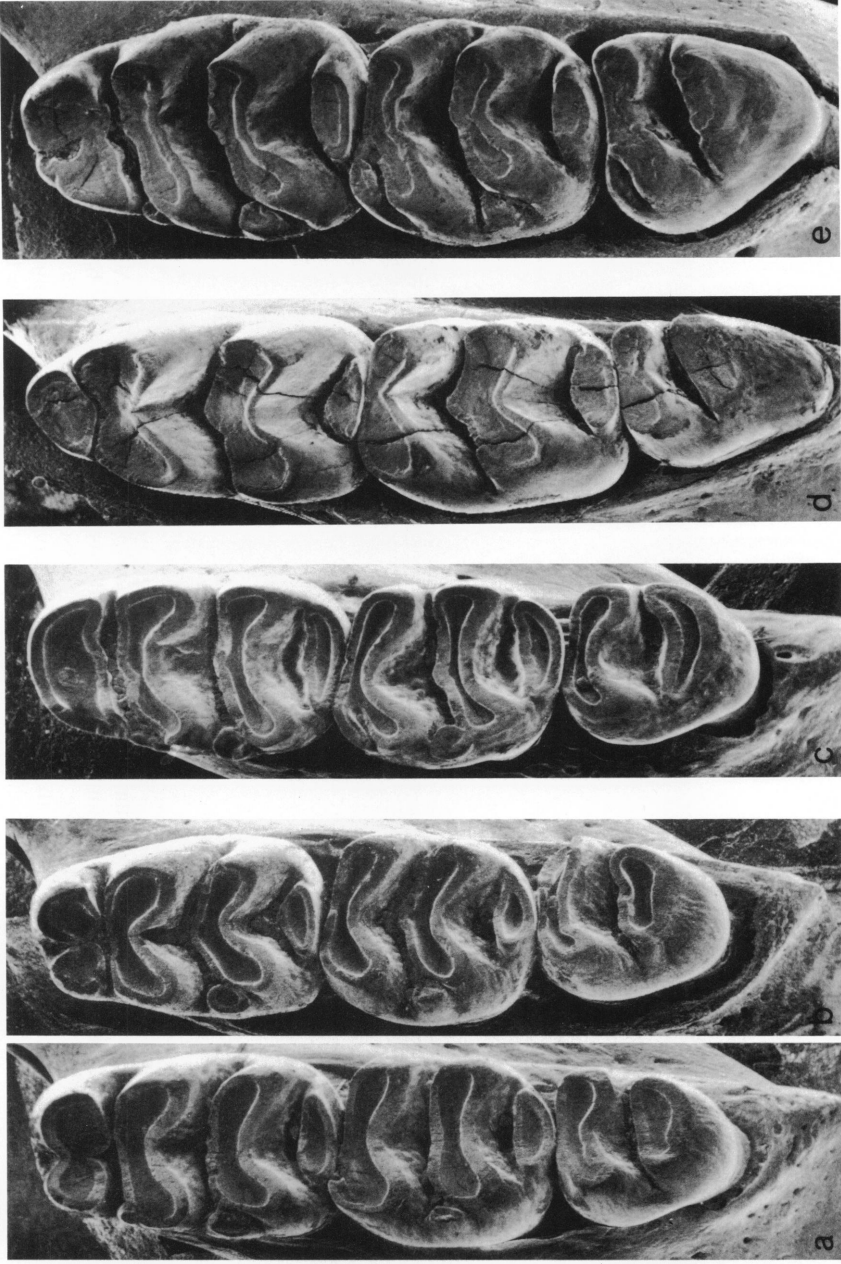


FIG. 42. Occlusal views contrasting left mandibular tooththrows of the same specimens that are shown in figure 40: a, *A. mindorensis* (LM₁₋₃, 5.6 mm.); b, *A. mindorensis* (LM₁₋₃, 5.7 mm.); c, *M. beccarii* (LM₁₋₃, 5.1 mm.); d, *N. cremori-venter* (LM₁₋₃, 5.7 mm.); 3, *L. sibuanus* (LM₁₋₃, 5.2 mm.).

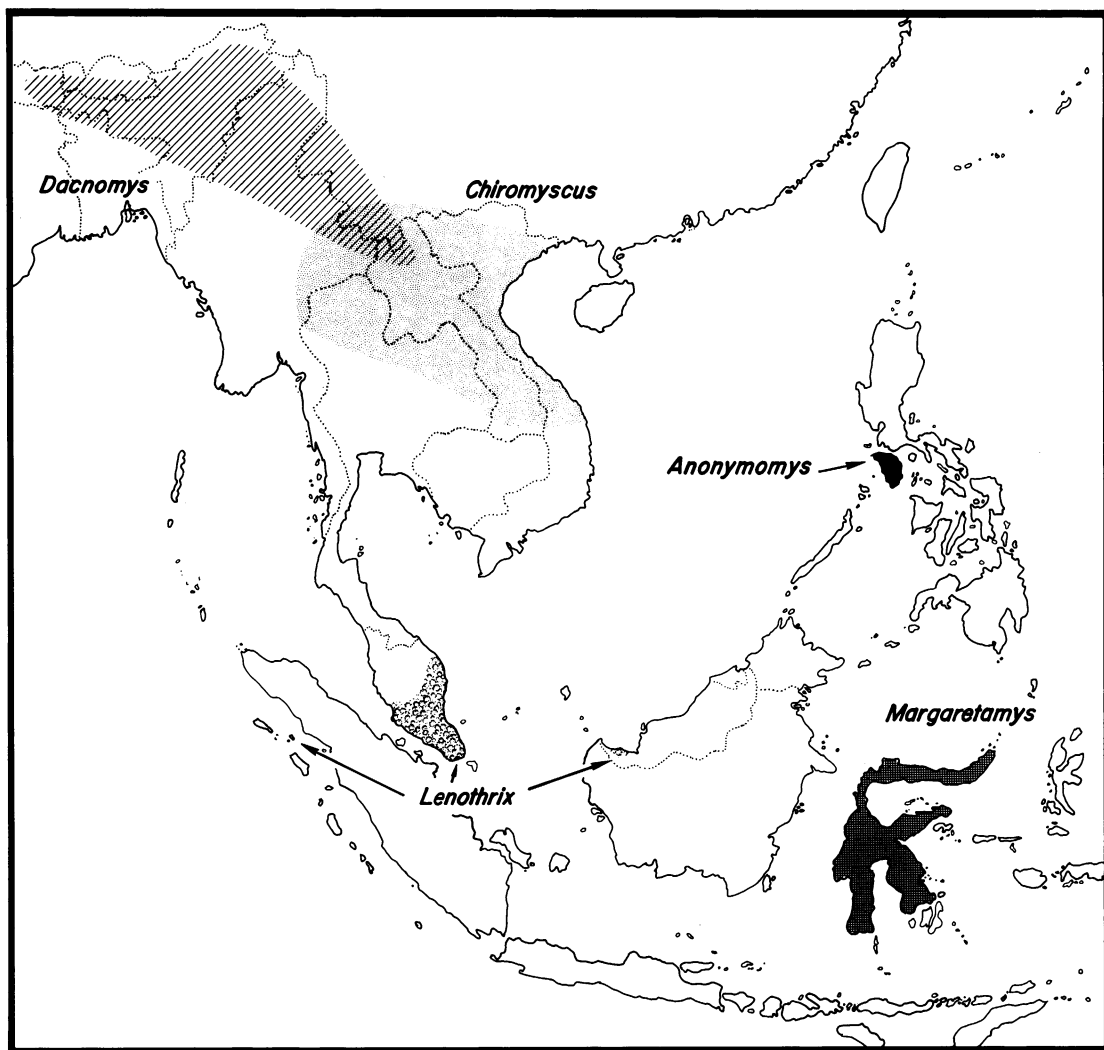


FIG. 43. Summaries of the geographic distributions of *Dacnomys*, *Chiromyscus*, *Lenothrix*, *Anonymomys*, and *Margaretamys*.

and neither labial cusplets nor anterolabial cusps occur in most specimens.

The molars of *Margaretamys beccarii* are shaped like those of *A. mindorensis*, but they have more elaborate occlusal patterns that contrast by having a cusplike spur on the lingual side of cusp t5 on the first molar, cusp t4 usually separated from cusp t5, a large accessory cusp or ridge behind cusp t6, a cusp t8 that has a large lingual bulge resem-

bling a cusp t7, a wide elongate cusp t9, and a thick, wide posterior cingulum on all three upper molars. The lowers are also more elaborate in occlusal pattern. The rows of cusps are gently bowed and wide, the anteroventral cusp at the front of the first molar has merged with the large anterolabial and anterolingual cusps to form a wide lamina that contains no discrete cuspidation, even in young animals; much wider and thicker posterior cingula on

the first and second lower molars; and a definite anterolabial cusp on each second molar.

COMPARISON WITH *Limnomys*: Although *Anonymomys mindorensis* is a rat of about the same body size (table 10) and build as *Limnomys sibuanus* from Mindanao (using USNM 125228, an adult female, for comparison, the only good adult specimen known), and although both have brown upperparts, cream underparts, and a long tufted brown and monocolored tail, the two species are not closely related, as judged from cranial and dental features. The three specimens of *A. mindorensis* contrast with the adult example of *L. sibuanus* (the skull is illustrated in Musser, 1977) in the six cranial features listed previously that also distinguish *A. mindorensis* and the other groups from *Rattus*; in addition, *L. sibuanus* is distinguished from *A. mindorensis* by the following contrasts.

1. *Limnomys sibuanus* has a more slender rostrum.

2. The interorbital area is narrower.

3. The braincase is high but not domed, the postorbital and temporal beading is much more prominent and stronger.

4. Anterior spines on the zygomatic arches are wider.

5. The incisors are narrower.

6. Five, four, and three roots anchor each first, second, and third upper molar, respectively (three-rooted uppers in *A. mindorensis*).

7. Four, three, and three roots are beneath each first, second, and third lower molar, respectively (lowers are two-rooted).

8. Large and prominent cusp t3 on second and third upper molars (tiny on second molar, absent from third).

9. Second upper molar has a larger cusp t4 that extends back to contact prominent lingual ridge of cusp t8; cusp t9 is long, narrow, and directed anteriorly (no such configuration; fig. 41).

10. There is a posterior cingulum on each second upper molar as well as on each of the first molars.

11. The lower molars are wider.

12. A prominent anterocentral cusp at front of the first lower molar joins the large, angular anterolabial and anterolingual cusps to form an extensive surface (no anterocentral cusp in *A. mindorensis*, the other two cusps are peglike and discrete; fig. 42).

13. A large and prominent anterolabial cusp is present on the second and third lower molars (absent; fig. 42).

DISCUSSION

ABOUT *LENOTHRIX*, *DACNOMYS*, *CHIROMYSCUS*, AND *MAXOMYS*

Discussion about relationships of any of the five groups defined in the previous section would be incomplete without including the Indochinese and Sundanese *Lenothrix*, *Dacnomys*, *Chiromyscus*, and *Maxomys*, genera either once included in *Rattus* or considered to be morphologically close to that genus. *Lenothrix* has been pivotal in past attempts by taxonomists to circumscribe the traits that would define *Rattus*; *Dacnomys* and *Chiromyscus* were described as *Rattus*-like (Ellerman, 1941, 1961) but have always been retained as good genera even though

they are no more morphologically distinct from *Rattus* than the *niviventer*-group or the *sabanus*-group, clusters formerly placed in *Rattus*; and *Maxomys* was long part of *Rattus* until its recent exclusion and definition (Musser, Marshall, and Boeadi, 1979). Brief expositions of the four genera follow.

LENOTHRIX

Known from the island of Tuangku (fig. 43), off the northwest coast of Sumatra (Miller, 1903), Sarawak (Medway, 1965), and Malaya (Medway, 1969; Muul and Lim, 1971), *Lenothrix canus* was described by Miller in 1903 and compared with *Lenomys*

meyeri and species of *Mus* (the name then applied to species in what Ellerman defined as *Rattus*). Miller's detailed description—based on the skin, skull, and teeth of an adult—and his cranial and dental illustrations of *canus* indicated an animal very different from any *Rattus* but the distinction was to be obscured by the way other taxonomists handled the relationship of *Lenothrix*.

No other specimens of *Lenothrix* were collected until Kloss, in 1931, reported specimens from Sarawak and Selangor, which he named *malaisia*. Kloss arranged *malaisia* as a subspecies of *canus*, treated the latter as a species of *Rattus*, but gave no reasons for incorporating *canus* into *Rattus*. His action, unfortunately, was accepted by Ellerman and the unique traits of *Lenothrix* were lost in Ellerman's conception of the morphological diversity encompassed by *Rattus*, a view that prevailed from the 1940s to the 1960s. It was not until 1969 that *Lenothrix* was taken out of *Rattus*, when Misonne (1969) reiterated the diagnostic dental features of *Lenothrix* and pointed out that it was not closely related to *Rattus*; in his view, *canus* represented the primitive dental morphology of living murids. Recently, Medway and Yong (1976) have reaffirmed the distinctiveness of *Lenothrix*, and I have also, in the context of contrasting it to *sodyi*, a species with which it had been associated but to which it has no close phylogenetic relationship (Musser, in press).

Lenothrix is an arboreal rat with small ears; gray to grayish brown woolly fur over the upperparts; white, cream, or pale buff underparts; a tail that is brown over the basal two-thirds, white for the distal one-third, and much longer than the combined lengths of head and body; short and wide hind feet; and 10 mammae (a pectoral pair, two postaxillary pairs, and two inguinal pairs). The skull and occlusal patterns of the molars are distinctive (illustrated in Miller, 1903; Misonne, 1969; Medway and Yong, 1976; Musser, in press a; and figs. 44 and 45). The karyotype is similar to those of species in *Niviventer* (table 4).

Lenothrix possesses the following traits

that distinguish it from *Rattus* (see also figs. 44–46).

1. The pelage is woolly (sleek, soft, long, or harsh in *Rattus*, but not woolly).

2. The tail is bicolored (monocolor in most *Rattus*).

3. Each zygomatic plate does not project forward beyond the dorsal zygomatic root (projects well forward to form a prominent anterior spine).

4. Sides of the braincase above squamosal roots of the zygomatic arches slope (vertical or slightly sloping in most species).

5. A strut of alisphenoid bone forms lateral wall of the alisphenoid canal and separates the foramen ovale accessorius from the masticatory-buccinator foramina (the strut is gone in *Rattus*, the foramen ovale accessorius and masticatory-buccinator foramina are absent).

6. Each bulla is small relative to size of the cranium, the bony eustachian tube is prominent, and the bulla is tightly attached to the squamosal so the postglenoid vacuity is small (large bulla, short inconspicuous eustachian tube, and squamosal separated from bulla by wide vacuity).

7. The incisive foramina are very short, their posterior margins ending well in front of the maxillary toothrows (long, penetrating between the first upper molars).

8. The posterior margin of the palatal bridge is situated anterior to the ends of the molar rows (extends to form a wide shelf beyond the toothrows).

9. The mesopterygoid fossa is nearly as wide as the palatal bridge, its walls breached by short and thin sphenopalatine vacuities (the fossa is much narrower than the palatal bridge, the sphenopalatine vacuities are huge).

10. Each pterygoid fossa is nearly flat and its anterior two-thirds is entire, not perforated by an interpterygoid foramen (each fossa is shallowly excavated and perforated by a large interpterygoid foramen).

11. In a sample of 78 specimens, the number of roots anchoring each first upper molar range from three to five: three specimens have large anterior, lingual, and posterior

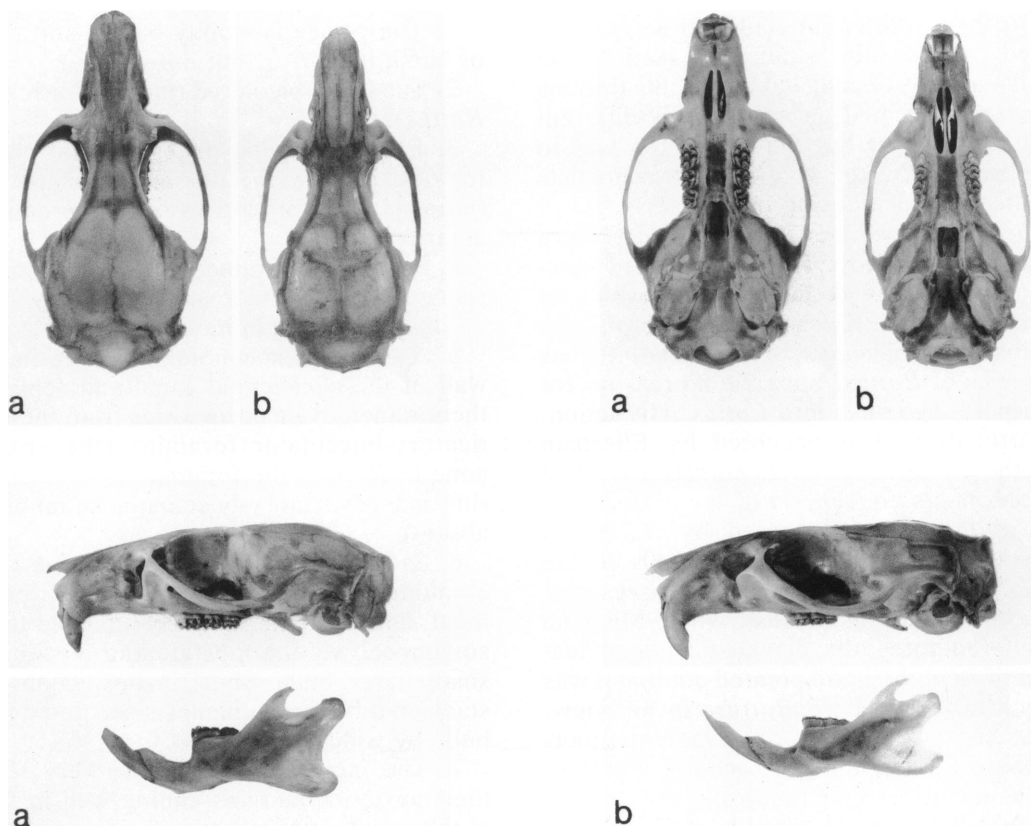


FIG. 44. Views of adult crania and dentaries. *Lenothrix canus* (AMNH 240358) from the Malay Peninsula (a) is contrasted with *Rattus* (b), as represented by *R. rattus diardii* (AMNH 250104) from Java. Natural size.

roots; 48 have three large roots and a thread-like labial rootlet; 21 have the three primary roots and a large labial root; and six have five roots—a large anterior and posterior, prominent labial, and divided lingual (specimens of *Rattus* have five prominent roots).

12. Each first lower molar has three roots: a large anterior and posterior, and prominent lingual (four-rooted first lower molars in *Rattus*: anterior, posterior, lingual, and labial).

13. Cusps on the upper and lower molars are nearly upright; the upper molars abut against each other with slight or no overlapping among the teeth (cusps slanted, first molar strongly overlaps second, and second overlaps third).

14. Each third upper molar is narrower than the second but nearly as long, and much longer than wide (smaller relative to the second, either round or squarish).

15. The main cusps on upper and lower molars are discrete and weakly connected, and many are angular in cross section (cusps tend to be round or oblong in cross section, strongly connected so that most merge together in each row and the occlusal surfaces appear less cuspidate).

16. Rows of cusps on each tooth are set far apart, especially those on lowers; first and second row on each first lower molar are connected by a medial crest (rows of cusps are close together in *Rattus*, first row abuts



FIG. 45. Occlusal views of the left maxillary (left side) and mandibular (right side) toothrows of *Lenothrix canus* (USNM 488914) from the Malay Peninsula. Approx. $\times 10$.

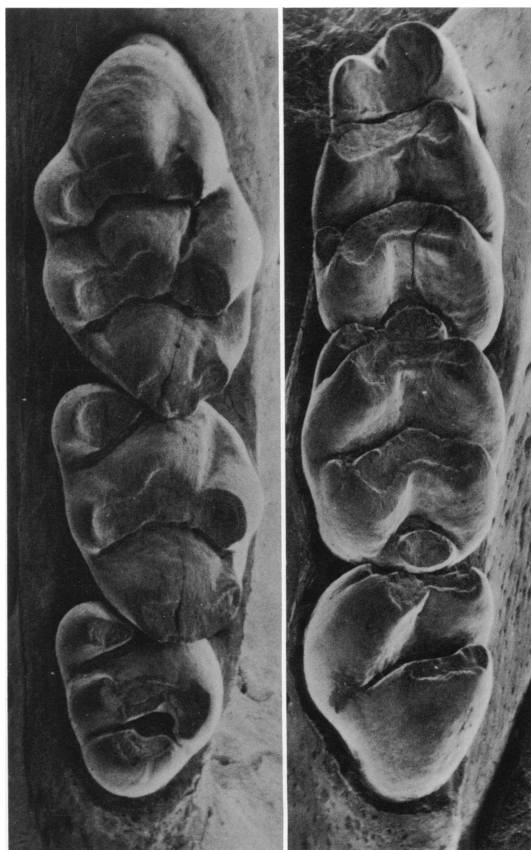


FIG. 46. Occlusal views of the left maxillary (left side) and mandibular (right side) toothrows of *Rattus rattus flavipectus* (AMNH 84667; LM¹⁻³, 6.6 mm.; LM₁₋₃, 6.1 mm.) from Fukien Province, China.

against second with no crest on each first lower molar).

17. There is a prominent posterior cingulum on each upper molar (absent; a slight triangular bulge at the back of each first upper molar on some specimens is the only remnant of one).

18. A cusp t7 is found on the first and second upper molars of most specimens (absent from all upper molars).

19. Cusps t1bis and t2bis are usually present, often prominent, on each first upper molar (absent in *Rattus*).

20. There is an accessory cusp behind cusp t6 on each first upper molar and often the second; and crests behind cusps t1 and t3 of

the first molars (both accessory cusps and crests are absent).

21. There is a prominent anterocentral cusp at the front of each first lower molar, usually separated from the first row of cusps (usually absent; if present, small and mostly merged with the anterolingual cusp).

22. Karyotype of $2N = 46$; three pairs of small metacentrics, five pairs of subtelocentrics, 14 pairs of telocentrics, a submetacentric X, and telocentric Y ($2N = 42$, seven pairs of small metacentrics, the rest mostly telocentrics, and a few subtelocentrics; table 4).

All the features listed above form an im-

pressive list distinguishing *Lenothrix* from *Rattus*. But, even without that combination of traits, some dental features by themselves are diagnostic for *Lenothrix*, as compared with *Rattus*—either slight or no overlapping among the upper molars, for example, and a posterior cingulum at the back of each upper molar, are characters not found in *Rattus*. By placing *canus* in its own genus, Miller (1903) had correctly evaluated the degree of morphological gap between *canus* and *Rattus*, a gap also clearly indicated by more recent study of the dental characteristics of *Lenothrix* (Misonne, 1969).

DACNOMYS

A giant rat about the size of *Leopoldamys sabanus* or *L. edwardsi*, *Dacnomys* is represented by a few specimens from eastern Nepal (Arun Valley), northeastern India (vicinity of Darjeeling, Bengal Presidency; the Khasi and Mishmi Hills of Assam), and northern Laos (Phong Saly); figure 43. Three scientific names—*millardi*, *wroughtoni*, and *ingens*—have been proposed and although there is consensus that only one species exists, *D. millardi* (Osgood, 1932; Ellerman, 1941, 1961), that hypothesis must be tested if large series of different ages and both sexes from several places are ever obtained. The rat lives in highlands but nothing else is known about its natural history.

Measurements and good descriptions of skins, skulls, and teeth are provided by Thomas (1916, 1922), which are supplemented by Osgood (1932) and Ellerman (1941, 1961). I give here only a brief written sketch and illustrations of a skull and tooththrows (figs. 47 and 48). *Dacnomys millardi* is a large brown rat with a very long tail. The fur is thick and short, the upperparts are brown flecked with buff, the underparts range from cream through grayish white to buffy gray, the ears are small and brown, the front and hind feet are brown, there are six plantar pads on each hind foot, the tail is much longer than combined lengths of head and body and brown all over, and females have eight mammae (a pectoral pair, postaxillary pair, and two inguinal pairs).

The cranium is large, long, and narrow, not unlike the species in *Niviventer* in general configuration. The rostrum is long and slim. The lacrimals are triangular and very small relative to size of the cranium. High, wide, prominent ridges bound the dorsolateral sides of the postorbital region and sweep back onto dorsolateral margins of the braincase, gradually becoming indistinct before they reach the occiput. The sides of the braincase slope outward from the temporal ridges to the tops of the squamosal roots of the zygomatic arches. Those roots originate about halfway down on the braincase so there is a large area for insertion of the temporal musculature. The configuration of the alisphenoid above each pterygoid ridge is like that in *Niviventer* and *Leopoldamys*. The bullae are very small, both absolutely and relative to size of the cranium (length of bulla is 10–11 percent of the greatest length of skull in five adults; contrast those values with the average of 16 percent in 20 specimens of *Rattus rattus diardii*); the bony eustachian tubes are prominent and long; and each bulla is set tightly against the squamosal so the postglenoid vacuity is small, much like the configuration in *Leopoldamys*. Each zygomatic plate is narrow, barely projecting forward of the anterior zygomatic root. The incisive foramina are long, reaching past the anterior faces of the first upper molars. The configuration of the palatal bridge, as well as the mesopterygoid and pterygoid fossae, are similar to those in *Niviventer* and *Leopoldamys*; the only exception is that the pterygoid platform between the foramen ovale and bulla is a wide, smooth-topped ridge rather than a flat surface or low mound.

The configuration of each dentary is similar to that in *Niviventer* and *Leopoldamys* with the exception that each coronoid process is larger relative to size of the ramus.

Enamel layers of the upper and lower incisors are dark to pale orange. The uppers emerge from the rostrum at a right angle.

Each upper molar is anchored by a large anterior root, a small labial root, a large posterior root, and a divided lingual root (in which the two parts are close together). Four roots (large anterior and posterior, small la-

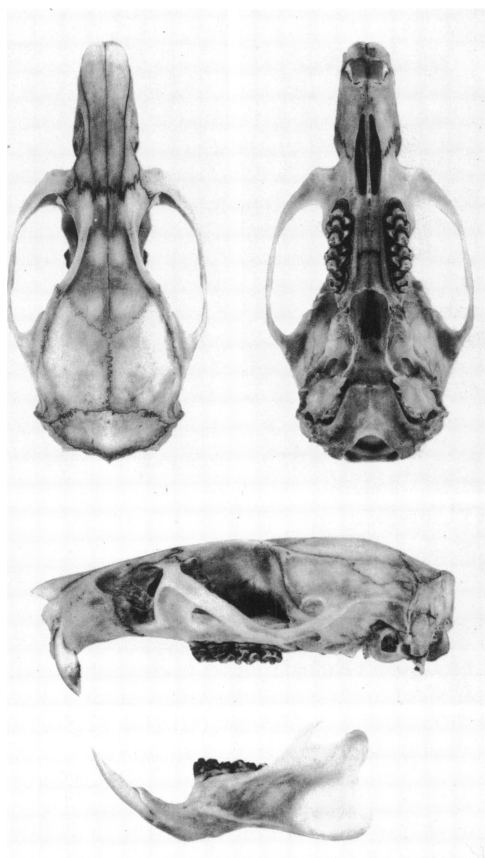


FIG. 47. Views of the cranium and dentary of an adult *Dacnomys millardi* (FMNH 84881) from Assam. Natural size.

bial and lingual) anchor each of the first lower molars.

The molars are wide and chunky, have high crowns, and the toothrows are very long, both actually and relative to sizes of the cranium and mandible, one of the more exceptional features of *Dacnomys* (for example, alveolar length of the maxillary toothrow is 22 percent of the greatest length of skull in five adults; by contrast, the average is 17 percent in a sample of 20 adult *Rattus rattus diardii*). The cusps on the upper molars slant back so the first molar overlaps the second and the second overlaps the third. Each third upper molar is large, but smaller than the second. The primary cusps, espe-



FIG. 48. Occlusal views of the right maxillary (left side) and mandibular (right side) toothrows of *Dacnomys millardi* (FMNH 114175) from eastern Nepal. Approx. $\times 9$.

cially those on the upper first and second molars, are angular in cross section. The occlusal surfaces of the upper molars are simple in configuration because there are no cusps t1bis, t2bis, t7, or posterior cingulum, or accessory cusps behind cusp t6. Short, crestlike extensions at the back of cusps t1, t3, t4, and t6 on the first molar and cusps t1, t4, and t6 on the second provide a degree of complexity and increased angularity to the occlusal configuration. Cusps t9 on the first and second molars are prominent in young rats but nearly merge with cusp t8 and become inconspicuous in older animals. Cusp t3 is absent from the second and third upper molars. There is a small cusplet on the labial margin between cusps t4 and t9 of the second



FIG. 49. Views of the cranium and dentary of an adult *Chiromyscus chiropus* (USNM 321507) from Vietnam. Natural size.

molar in some specimens, clearly seen in figure 48.

The lower molars are simple in their occlusal patterns. An anterocentral cusp is absent. The anterolabial and anterolingual cusps on the first lower molar are small but form a front lamina almost as wide as the lamina behind it. There is no anterior labial cusplet on the first lower molar, but there is a posterior labial cusplet on that tooth and on the second molar. Anterolabial cusps are absent from the second and third molars.

The combination of large and hypsodont molars, and very small bullae were enough for Ellerman (1941, 1961) to retain *Dacnomys* as a genus distinct from *Rattus*.

CHIROMYSCUS

A genus with one species (Thomas, 1891a, 1925), *C. chiropus* is known by a few specimens from the southeastern part of lower Burma (Karin Hills), Thailand (Chiengmai

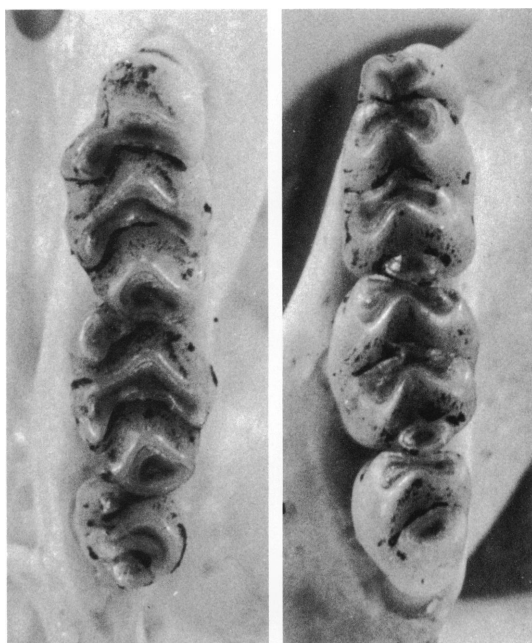


FIG. 50. Occlusal views of the right maxillary (left side) and mandibular (right side) tooththrows of *Chiromyscus chiropus* (USNM 321507) from Vietnam. Approx. $\times 10$.

and Loei Provinces), southern Vietnam (Dakto and Lao Bao), northern Vietnam (Ba Nam Nhung, Chapa, and Bao Ha), and central Laos (Xieng Kuang), figure 43; is probably highly arboreal; and may reside in tropical deciduous forest (Osgood, 1932; Ellerman, 1941, 1961; Van Peenen, Ryan, and Light, 1969; Marshall, 1976, 1977). Measurements and descriptions of the rat are provided by Thomas (1891b), Ellerman (1961), Van Peenen, Ryan, and Light (1969), and Marshall (1977); a skull and tooththrows are illustrated in figures 49 and 50.

Chiromyscus chiropus is morphologically similar to *Niviventer*, particularly *N. cremoriventer* and especially *N. langbianis*. It is separated from those two, and from any other species of *Niviventer* by having a nail on each hallux instead of a claw. *Chiromyscus* differs from *N. langbianis* in other external features: it is larger (see the values and descriptions for *N. langbianis* in Musser, 1973); has orange-brown upperparts with a

buffy orange head, wide dark brown rings around the eyes, and buffy orange legs, feet, and strips along sides of the body; a bi-colored tail, brown above and whitish brown below; and smaller ears relative to size of the head and body.

The cranium of *C. chiropus* is also similar to that of *N. langbianis* in configuration except that it is larger; wide shelves outline the postorbital margins of the braincase, one of the most conspicuous differences between the two species; each pterygoid fossa is perforated by a large interpterygoid foramen; and the bullae are smaller, not only absolutely but relative to size of the cranium.

Each dentary of *C. chiropus* is similar in shape and details to those in species of *Niviventer* especially *N. cremoriventer* and *N. langbianis*.

The teeth of *C. chiropus* closely resemble those of *N. langbianis*. The former also has orange incisors with the uppers leaving the rostrum at about the same angle; the first upper molars are anchored by four roots (large anterior, posterior, lingual, and a small labial) and the first lowers by four (large anterior and posterior, small labial and lingual), as are the first upper and lower molars, respectively, in *N. langbianis*. The occlusal shapes and configurations of the molars and their size relative to one another are also similar in the two species; the primary difference between them is size—the molars are wider and the tooththrows longer relative to size of cranium and mandible in *C. chiropus* than in *N. langbianis*. The occlusal patterns in *C. chiropus* are as simple as those of either *N. langbianis* or *N. cremoriventer*: in all three species, cusp t7 is absent from all the upper molars, as is a posterior cingulum, a cusp t1bis, or any accessory cusps or crests; cusp t3 is missing from the second and third molars; cusp t9 is inconspicuous and mostly merged with cusp t8 on the first and second molars; an anterocentral cusp is absent from each first lower molar, as well as an anterior labial cusplet; and there are no anterolabial cusps on the second and third molars. There is a posterior labial cusplet on each first and second molar in *C. chiropus*; such a cusplet is absent from those teeth in

most specimens of *N. langbianis* and *N. cremoriventer* (table 2).

The combination of halluces with nails instead of claws and wide, shelflike ridges defining the dorsolateral margins of the postorbital region set *Chiromyscus* apart from *Niviventer*, a genus to which it is otherwise morphologically similar.

MAXOMYS

The definitions and contents of *Maxomys* were presented by Musser, Marshall, and Boeadi (1979). The type species is *M. bartelsii*, a common rat in the mountain forests of western and central Java. Observations on its taxonomy, morphology, chromosomes, parasites, natural history, and geographic distribution were provided by Van Peenen, et al. (1974).

Maxomys is basically a Sundaic genus (fig. 51). Ten of its species occur on the Malay Peninsula south of the Isthmus of Kra (10° 30' N) and on islands of the Sunda Shelf: *M. bartelsii* (western and central Java), *M. inas* (Malay Peninsula), *M. inflatus* (Sumatra), *M. hylomyoides* (Sumatra), *M. alticola* (northern Borneo), *M. baeodon* (Borneo), *M. ochraceiventer* (Borneo), *M. panglima* (Balabac, Palawan, Busuanga, and Culion Islands), *M. rajah* (peninsular Thailand, Malay Peninsula, Riau Archipelago, Borneo, and Sumatra), and *M. whiteheadi* (peninsular Thailand, Malay Peninsula, Sumatra, Borneo, and small islands on the Shelf). One species only, *M. surifer*, occurs both on the Sunda Shelf (Malay Peninsula, Borneo, Sumatra, Java, and small islands) and in Indochina (southern Burma, Laos, Cambodia, Vietnam, and Thailand, and offshore islands). A single species, *M. moi*, is endemic to Laos and Vietnam. One species, *M. pagensis*, occurs on the Mentawai Islands (North and South Pagai, Sipora, and Siberut), off the fringe of the Sunda Shelf. Three species are on Sulawesi, the only members of the genus found to the east of Wallace's Line: *M. hellwaldii*, *M. dollmani*, and *M. musschenbroekii*.

The definition of *Maxomys* provided by Musser, Marshall, and Boeadi (1979) was a

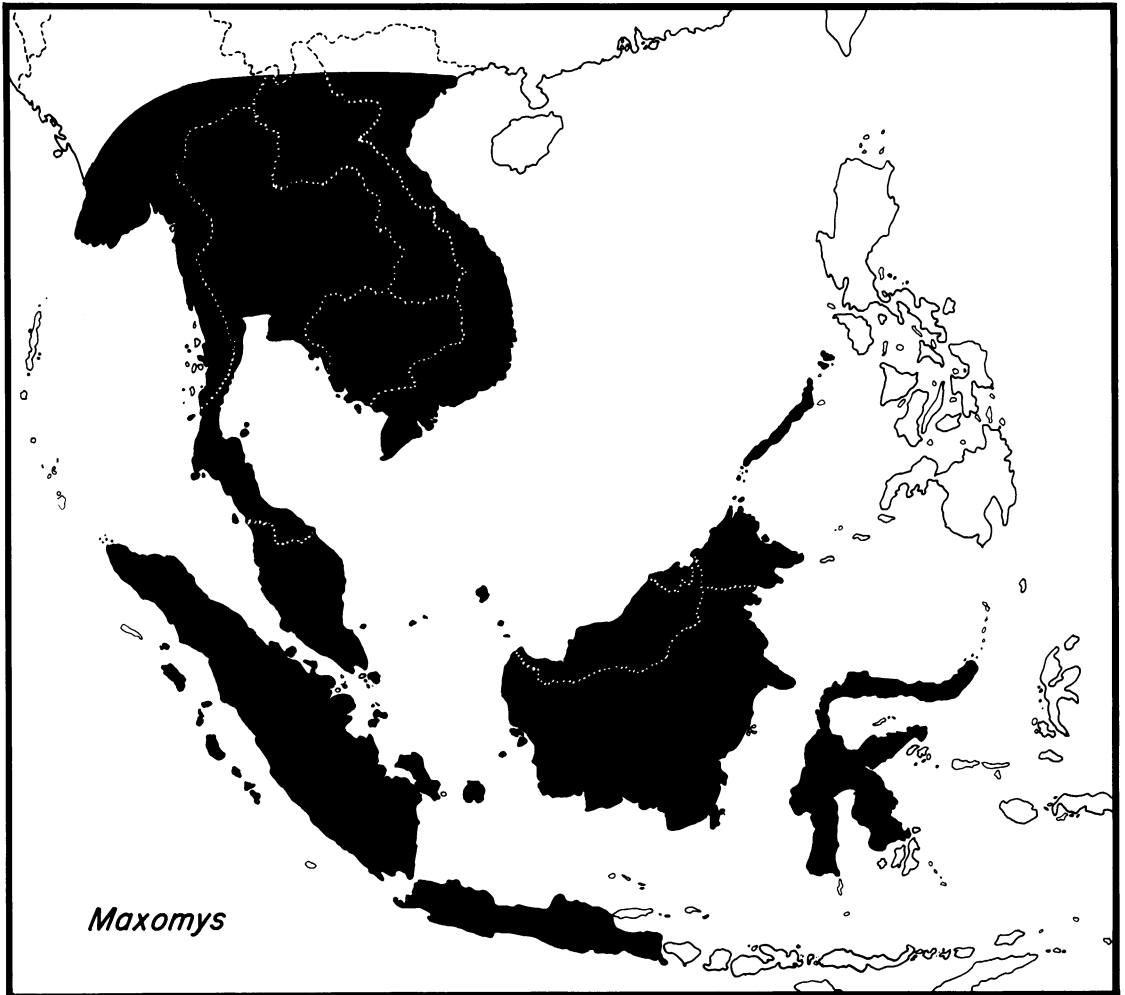


FIG. 51. A summary of the geographic distribution of *Maxomys*.

preliminary statement, intended to associate *M. bartelsii* with a cluster of species that seemed morphologically related to it, and to extract this assemblage from *Rattus*. All the species they placed in *Maxomys* are similar to one another in morphology of skins, skulls, and teeth, but less so in traits associated with chromosomes (Musser, Marshall, and Boeadi, 1979) and erythrocyte proteins (Chan, Dhaliwal, and Yong, 1979). Most species of *Maxomys* require careful taxonomic revision; the phylogenetic relationships among them all need to be determined.

CHARACTERS: PRIMITIVE AND DERIVED STATES

I attempted to determine whether a feature was primitive or derived by noting its occurrence in groups closely related to murines, such as cricetines, and in the Rodentia in general. Many external, cranial, dental, and karyotypic features can be used to distinguish sets of species of genera from one another, but not all the same traits are useful for assessing relationships among the taxa because I do not know whether they represent primitive or derived states. Features associated with the skin

are especially difficult to evaluate, and I am reasonably certain about only one, whether halluces bear claws or nails, claws clearly being primitive because they are widespread in rodents outside of murines and nails occur infrequently within that group. Reasonable hypotheses of polarity—and they are hypotheses—are easier to form for many of the cranial and dental features, although even here there are certain cranial and dental traits that, though useful in discriminating between sets of species or genera, are ambiguous in testing relationships because I cannot determine whether they might be primitive or derived.

The features I used for a preliminary analysis of relationships among taxa discussed in this report are listed below: the primitive condition is described first, followed by the derived state in parentheses. Included are most characters that have traditionally been used to diagnose and define the taxa. Some of the traits may eventually prove to be highly correlated and represent really only one character instead of several, as they are now listed, particularly certain of the dental features. Also, there are other characters for which I have hypothesized polarities but they are common, in either the primitive or derived state, to all the taxa discussed here, therefore provide no information about relationships among them, and are not listed below.

1. Hallux (H): The first digit on each hind foot bears a claw (a nail on each hallux).

2. Dorsolateral margins of braincase (DlmBr): slight beading or prominent ridges may occur along dorsolateral margins of interorbital and postorbital regions, but the braincase proper is either smooth all over or has low beading along the dorsolateral margins of the anterior half and is smooth over the posterior half (medium to high ridges or shelves outline the interorbital area and sweep back along dorsolateral margins of the braincase, all the way to the occiput in some species but fading out before reaching the occiput in others).

3. Sides of braincase (SBr): The sides of the braincase slope outward from the dor-

solateral margins of the cranium to the squamosal roots of the zygomatic arches (the sides are vertical or nearly so).

4. Squamosal roots of zygomatic arches (SrZa): The roots originate high on the upper half of the braincase, often close to the temporal ridges and well above the bullae; there are usually expansive areas of braincase walls between roots and tops of the bullae, and relatively small areas for origin of the temporal musculature between the temporal ridges and tops of the squamosal roots (the roots are set halfway down the braincase or lower, just above the bullae; there are large areas for the origin of the temporal musculature).

5. Alisphenoid complex (Al): In all or more than three-fourths of the samples, a strut of alisphenoid bone covers the lateral part of the alisphenoid canal and separates the foramen ovale accessorius from the masticatory-buccinator foramina (the strut is gone, the alisphenoid canal is open above each pterygoid ridge, and there are no foramen ovale accessorius or masticatory-buccinator foramina).

6. Size of bullae (SB): The bullae are moderately to very small relative to size of the cranium (bullae are large relative to size of the cranium, sometimes highly inflated).

7. Attachment of bullae (AB): Each bulla is tightly attached to the squamosal; the postglenoid vacuity is small and usually confined to the top of the bulla between the periotic and squamosal but may also form a narrow space between the anterodorsal margins of the periotic and squamosal (a wide, spacious vacuity separates the dorsal and anterior margins of the periotic and bulla from the squamosal).

8. Incisive foramina (IF): The incisive foramina are short, their posterior edges terminating well before the maxillary toothrows (long foramina, the back margins ending at the fronts of the first upper molars or beyond them).

9. Palatal bridge (PB): The posterior rim of the palatal bridge is situated before the back margins of the third upper molars, even with them, or only slightly beyond them (the posterior part of the palatal bridge extends

way beyond the third molars to form a wide platform behind the molar rows).

10. Mesopterygoid fossa (MF): The fossa is nearly as wide as the back part of the palatal bridge; its walls are breached by thin, short sphenopalatine vacuities or slits (the fossa is one-third to one-half the width of the palatal bridge; the sphenopalatine vacuities are huge so that the presphenoid and anterior part of the basisphenoid appear suspended in air).

11. Pterygoid fossae (PF): Each fossa is nearly flat or shallowly excavated, its anterior two-thirds entire and not perforated by a large interpterygoid foramina (each fossa is excavated or tilted toward the midline of the skull and perforated by a large interpterygoid foramen).

12. Pterygoid platform (PP): The posterolateral portion of each pterygoid platform behind the foramen ovale is either nearly flat, a low mound, or a wide and smooth low ridge (the edge is thrown up into a definite high and thin ridge).

13. Color of incisors (CI): The enamel layers of both upper and lower incisors range from yellow to deep orange (the incisors are cream or white).

14. Roots of first upper molars (R-M¹): Each first upper molar is three-rooted; anterior, lingual, and posterior; or four-rooted; a labial root in addition to the three primary roots; or an anterior, a posterior, and a divided lingual root (each first upper molar is five-rooted, anterior, posterior, two lingual, and one labial).

15. Roots of first lower molars (R-M₁): each first lower molar is two-rooted; an anterior and posterior root; or three-rooted; either a labial or a lingual rootlet in addition to the two primary roots (each lower molar is four-rooted, anterior, posterior, labial, and lingual).

16. Height of cusps (HC): The molars have low to moderately high cusps, but definitely brachyodont (molars have high cusps, clearly hypsodont).

17. Size of molars (SM): The upper molars gradually decrease in size from the first to the third (each second upper molar is smaller

than the first, but the third is reduced in size and much smaller relative to the second).

18. Overlap of molars (OM): Cusps on the upper molars are only slightly slanted and there is little or no overlap among the three teeth in a toothrow, each essentially abutting against the other (the cusps slant conspicuously back, so that the first molar overlaps the second, and the second overlaps the third).

19. Cusps t1bis and t2bis (t1–t2bis): These cusps do not occur on the first and second upper molars of most specimens (either t1bis, t2bis, or both are present on first upper molars in most specimens, sometimes the second molars).

20. Cusp t7 (t7): No cusp t7 on any of the upper molars (a cusp t7 on the first molars, usually on the second molars, and sometimes on the third).

21. Posterior cingulum (PC): There is a posterior cingulum at the back of each first upper molar, usually the second, and sometimes the third (no posterior cingulum on any of the upper molars, or indicated only by a triangular bump at the back of each first upper molar).

22. Cusp t9 (t9): This cusp is large and discrete on each first and second upper molar (cusp t9 nearly incorporated into the much larger cusp t8 and inconspicuous after wear).

23. Cusp t3 (t3): In all or most of the samples, cusp t3 is present on the second and often on the third upper molars (absent from the second and third molars in all or most specimens).

24. Cusp behind t6 (C-t6): A small accessory labial cusp is not present behind cusp t6 on the first or second upper molars of most specimens (a small accessory cusp sits directly behind cusp t6 on each first upper molar and sometimes on each second molar in most or all specimens; as each tooth wears down, the cusp merges with the back of cusp t6 to form a crest).

25. Cusp t4 and t5 (t4–t5): Cusp t4 is separate from cusp t5 in the first upper molars of juveniles and adults (cusp t4 strongly connected to cusp t5, sometimes weakly connected only in juveniles).

26. Cusp t5 (t5): Cusp t5 is simple in shape; either round, oblong, or triangular in cross section, and without cusplike spurs or extensions (cusp t5 has a lingual, cusplike spur or large extension that either abuts against cusp t4 or merges with it).

27. Union of cusps (UC): Cusps on the upper and lower molars are weakly connected so the occlusal patterns appear strongly cuspidate (all or most cusps are strongly joined, some merged to the point where they nearly lose their identities in several species).

28. Anterolabial and anterolingual cusps (Al-Al): The anterolabial and anterolingual cusps on the first lower molar are large and discrete, forming a lamina nearly as wide as the rest of the tooth (the two cusps are smaller, pressed against each other to form a lamina narrower than the rest of the tooth; in young rats they may be separate but soon merge into an oblong lamina).

29. Anterolabial cusp (ALC): The anterolabial cusp on each second lower molar, and often on each third molar, is present in all or most of the samples (anterolabial cusps are absent from the second and third molars in all or most of the samples).

Finally, a primitive karyotype is most likely one with a high 2N consisting of mostly telocentric chromosomes, with one to three pairs of small metacentrics and a few pairs of subtelocentrics. Species of *Niviventer* and *Lenothrix* have this kind of karyotype (table 4). A lower 2N with many pairs of small metacentrics—at least seven—along with a few telocentrics and submetacentrics, is probably derived, the condition in species of *Rattus* (table 4). I have omitted chromosomal features from my analysis because that kind of data is not available for either *Srilankamys*, *Chiromyscus*, *Dacnomys*, or *Anonymomys*.

NOTES ON RELATIONSHIPS

The distribution of primitive or derived states of the 29 characters among the genera (table 11), and the number of derived features each genus shares with one another (table 12) form a basis for evaluating the pos-

sible phylogenetic affinities of each genus relative to *Rattus*. The broader inquiry of where they may fit within the framework of morphological diversity in murids from the entire Indo-Australian region, or elsewhere, is outside the context of my discussion here.

I include *Apodemus* and *Arvicanthis* in the analysis; both have been traditionally recognized as distinct from *Rattus* (see Misonne, 1969, for example), even by Ellerman (1941); furthermore, Jacobs (1978) placed *Apodemus* in a different section of the murid radiation than either *Arvicanthis* or *Rattus*. *Apodemus*, in his view, is derived from a *Progonomys*-stock, while *Arvicanthis* and *Rattus* are closely related to each other and both descended from a *Karnimata*-stock; *Progonomys* and *Karnimata* have their roots in *Antemus*, which according to Jacobs, represents the oldest (Middle Miocene Siwalik Deposits of Pakistan) and most primitive murid.

The relationship of *Apodemus* and *Arvicanthis* to *Rattus*, as concerns the 29 traits examined here, provide guideposts to how closely the other nine genera may be related to *Rattus*. *Apodemus* is more primitive than either *Arvicanthis* or *Rattus*, sharing only six derived features with those two genera. *Arvicanthis* is one of the least primitive and shares all of its derived features with *Rattus*. None of the other nine genera, six of which contain species once included within *Rattus*, share as many of their derived traits with *Rattus* (nine at the most) as does *Arvicanthis*; and two of them share fewer derived traits with *Rattus* than does *Apodemus*. One of those two is *Lenothrix*, once considered an integral part of *Rattus*.

LENOTHRIX

One of the most primitive of the 12 genera, *Lenothrix* possesses the primitive condition in 24 out of the 29 traits analyzed here. Of the remaining five in which the derived state is present, *Lenothrix* shares four of them with *Apodemus*; a ridge forming posterolateral part of pterygoid plate (trait 12; hereafter, the number in parentheses following

the character refers to the trait in table 11), cusp t7 (20), cusps t1bis and t2bis (19), and cusp t4 connected to cusp t5 (25), and only two with both *Rattus* and *Arvicanthis*—ridged edge of pterygoid plate and cusps t4 and t5 connected—a feature common to all the other genera except *Margaretamys*. No single derived trait or set of them is common to only *Lenothrix* and *Rattus*. Even *Apodemus*, which is regarded by all murid taxonomists to be morphologically and phylogenetically distant from *Rattus*, shares more derived features (still with that genus than does *Lenothrix*).

Lenothrix and *Apodemus* are set apart from all the other genera discussed here because they share the derivations of a cusp t1bis, t2bis, or both (19) on the first upper molars, and a cusp t7 (20) on most of the upper molars. But, because the cusps occur in both genera does not mean that *Lenothrix* is necessarily closely related to *Apodemus*. Cusps t1bis, t2bis, and t7 occur in many other genera (Misonne, 1969) and may have developed independently in several different lineages. A phylogenetic analysis of African, European, Indian, and Indo-Australian murids is required to determine the significance of the occurrence of the cusps in *Lenothrix* and *Apodemus*.

Lenothrix and *Apodemus* fall out from all the other genera when the distribution of the characters are viewed from a different perspective. All the other genera are derived with respect to the degree of overlap among the molars (18) and the connections among the cusps (27). The primitive states of these two characters—molars abut against each other with little or no overlap, the cusps are weakly connected—occur only in *Lenothrix* and *Apodemus*.

Lenothrix shares only one derived feature with *Maxomys*, cusps t4 and t5 connected (25), and the same trait with *Srilankamys*; those two genera contain species that were once placed in the subgenus *Lenothrix* of *Rattus* (Ellerman and Morrison-Scott, 1951; Ellerman, 1961). This derived trait is common to all of the other genera discussed here except *Margaretamys*. "As here understood

based on *Rattus* Rats with short palate, short palatal foramina, and small bullae. . . ." was the diagnosis of the subgenus *Lenothrix* given by Ellerman and Morrison-Scott (1951, p. 596). Those three characters are shared by *Lenothrix canus*, the species in *Maxomys*, and *Srilankamys ohiensis*, but all are primitive and common not to just those three groups of species but to many other murids as well. There is no sound justification, based on cranial and dental characters, for associating *Lenothrix* closely with either *Maxomys* or *Srilankamys*.

Results of karyotypic and biochemical analyses suggest close relationships between *Lenothrix* and *Niviventer*. The karyotype of *L. canus* is similar to that in species of *Niviventer* (table 4), differing only by having five pairs of subtelocentrics (instead of either one or four), a submetacentric X chromosome (either subtelocentric or telocentric), and a FN of 63 (52–60). Chan, Dhaliwal, and Yong (1979, p. 335), who analyzed electrophoretic phenotypes of nine erythrocyte proteins from Malayan murids, reported that the biochemical evidence suggests *canus* should be grouped with *cameroni*, *bukit*, and *cremoriventer*, and that their results "do not support Misonne's (1969) suggestion that *canus* be regarded as a species of a different genus. . . ."

In my analysis, *Lenothrix* shares only a single derived trait with *Niviventer*—cusp t4 and t5 connected (25)—the same feature that is also shared by *Maxomys*, as well as most of the other genera. Similarities in cranial features between *Lenothrix* and *Niviventer*; small bullae, and the primitive configurations of the palatal bridge, mesopterygoid and pterygoid fossae, and alisphenoid region, for example, indicate only that the two genera share some of the same primitive traits. The dentition of *Niviventer* is unlike that of *Lenothrix*, not only in occlusal pattern of the molars, but in number of roots as well (Misonne, 1969; see also previous sections on *Lenothrix* and *Niviventer*, and contrast figures 7, 8, and 45). The karyotypic similarity between *Lenothrix* and *Niviventer* is probably also a primitive feature shared by both,

and possibly the biochemical data is primitive as well, but I cannot evaluate the significance of it.

No convincing evidence indicates *Lenothrix* to be either morphologically or phylogenetically closely related to *Rattus* on the one hand, or *Niviventer*, *Leopoldamys*, *Srilankamys*, *Chiromyscus*, *Dacnomys*, and *Anonymomys* on the other. A small accessory cusp behind cusp t6 is common to only *Lenothrix* and *Margaretamys*, and the possible connection between those two genera will be discussed later on. To Misonne (1969, p. 73), "*Lenothrix* is a very interesting genus and one of the most primitive in many respects; its closest relatives are *Lenomys*, and *Pitecheir* with *Crateromys* as a probable further step." Study of all Indo-Australian murids is necessary before the affinities of *Lenothrix* can be determined.

ANONYMOMYS

Anonymomys too, is primitive compared with most of the other genera listed in table 11; out of the 29 features, the derived states of only six are found in the genus and four of these—vertical sides of the braincase (3), degree of overlapping among the molars (18), strong connection between cusps t4 and t5 (25), and strongly joined cusps on all molars (27)—are shared by most of the other genera. *Anonymomys* shares these same four and a fifth, long incisive foramina (8), with *Rattus*; that feature is also common to many of the other genera. *Anonymomys* does not have a close phylogenetic relationship with *Rattus*.

The external characters of *Anonymomys* closely resemble those in *Niviventer cremoriventer* and *Margaretamys beccarii* but the similarities probably reflect convergence in those features. *Anonymomys* shares only four derived cranial and dental traits with *Margaretamys*; braincase with vertical sides (3), strong overlap among the molars (18), strong connections among most cusps (27), a long incisive foramina (8), and all occur in most of the other genera as well. *Anonymomys* shares those four and two others—cusps t4 and t5 connected (25) and no an-

terolabial cusps on the second and third lower molars (29) with *Niviventer*. Cusps t4 and t5 are strongly connected in all the genera except *Margaretamys*. *Chiromyscus*, *Leopoldamys*, *Maxomys*, and *Dacnomys* also lack anterolabial cusps. If the absence of anterolabial cusps is not independently derived among those genera but instead indicative of relationship, then *Anonymomys* may be distantly related to *Niviventer* and its relatives, perhaps a species with many primitive characters that is part, possibly a remnant, of an early stock from which *Niviventer*, *Chiromyscus*, *Leopoldamys*, *Maxomys*, and *Dacnomys* evolved. This hypothesis, as well as any others about the affinities of *Anonymomys*, must be tested by comparing it with other Indo-Australian genera, particularly those endemics on the other Philippine Islands.

MARGARETAMYS

Margaretamys has many primitive traits compared with most of the other genera discussed in the present report. It is the only genus in which cusp t4 is separate from cusp t5 (the condition, however, occurs in about half the sample of *M. beccarii*, is found in juveniles only of *M. elegans*, and is absent from *M. parva*); and the 21 pairs of chromosomes in *M. beccarii* are mostly telocentric with just two pairs of small metacentrics, which is primitive compared with *Rattus*. Out of the 29 features, the derived condition in eight of them are found in *Margaretamys*; six of these also occur in *Rattus*—postorbital and temporal ridges (2), braincase with vertical sides (3), open alisphenoid canals (5), long incisive foramina (8), appreciable overlap among the molars (18), and most cusps strongly connected (27); the same number as are shared by *Apodemus* and *Rattus*; five of the same features are shared with *Niviventer*; one trait—an accessory cusp behind cusp t6 on the first and second upper molars (24) is found only in *Margaretamys* and *Len-*

TABLE 11
Distribution of Primitive (P) or Derived (+) Expressions of 29 Traits among 13 Groups of Murine Rodents^a

	<i>Chiro-</i> <i>myscus</i>	<i>Nivi-</i> <i>venter</i>	<i>N.</i> <i>ander-</i> <i>soni-</i> division	<i>Dac-</i> <i>nomys</i>	<i>Leo-</i> <i>pold-</i> <i>amys</i>	<i>Maxo-</i> <i>mys</i>	<i>Sri-</i> <i>lank-</i> <i>amys</i>	<i>Anony-</i> <i>momys</i>	<i>Marga-</i> <i>ret-</i> <i>amys</i>	<i>Leno-</i> <i>thrix</i>	<i>Apode-</i> <i>mus</i>	<i>Arvi-</i> <i>can-</i> <i>thus</i>	<i>Rattus</i>
1. H	+	P	P	P	P	P	P	P	P	P	P	P	P
2. DlmBr	+	+	P	+	+	+	P	P	+	P	P	P	+
3. SBr	+	+	P	P	+	+	+	+	+	P	P	P	+
4. SrZa	P	P	P	P	P	P	P	P	P	P	+	+	+
5. Al	P	P	P	P	P	+	P	P	+	P	P	+	+
6. SB	P	P	P	P	P	P	P	P	P	P	P	+	+
7. AB	P	P	P	P	P	P	P	P	P	P	+	+	+
8. IF	+	+	+	+	P	P	P	+	+	P	+	+	+
9. PB	P	P	P	P	P	P	P	P	P	P	P	P	+
10. MF	P	P	P	P	P	P	P	P	P	P	+	+	+
11. PF	+	P	P	P	P	P	P	P	P	P	P	+	+
12. PP	P	P	P	P	P	P	P	P	P	+	+	+	+
13. CI	P	P	P	P	P	P	+	P	P	P	P	P	P
14. R-M ¹	P	+	+	+	P	P	P	P	P	P	P	+	+
15. R-M ₁	+	+	+	+	+	P	P	P	P	P	P	+	+
16. HC	P	P	P	+	P	P	P	P	P	P	P	P	P
17. SM	+	+	+	P	P	+	+	P	P	P	P	P	P
18. OM	+	+	+	+	+	+	+	+	+	P	P	+	+
19. t1-2bis	P	P	P	P	P	P	P	P	P	+	+	P	P
20. t7	P	P	P	P	P	P	P	P	P	+	+	P	P
21. PC	+	+	+	+	+	+	P	P	P	P	P	+	+
22. t9	+	+	+	+	+	+	+	P	P	P	P	P	P
23. t3	+	+	+	+	+	+	+	P	P	P	P	P	P
24. C-t6	P	P	P	P	P	P	P	P	+	+	P	P	P
25. t4-t5	+	+	+	+	+	+	+	+	P	+	+	+	+
26. t5	P	P	P	P	P	P	P	P	+	P	P	P	P
27. UC	+	+	+	+	+	+	+	+	+	P	P	+	+
28. Al-Al	+	+	+	+	+	+	+	P	P	P	P	P	P
29. ALC	+	+	+	+	+	+	P	+	P	P	P	P	P

^a Numbers and abbreviations correspond to numbered descriptions of the traits on pages 318-321, and to the numbers in parentheses following each trait discussed in the section on relationships, pages 321-329.

othrix; and one other feature—cusp t5 with a lingual cusplike spur (26) is unique to *Margaretamys*.

Margaretamys, as represented by *M. beccarii*, has no close phylogenetic relationship with *Rattus*. Four of the traits shared by *Margaretamys* and *Rattus* also occur in most of the other genera; a fifth—long incisive foramina (8) also occurs in *Niviventer*, *Chiromyscus*, *Dacnomys*, *Anonymomys*, *Apodemus*, and *Arvicanthis*; and the sixth—an open alisphenoid canal in which the bony

alisphenoid strut is absent from most specimens, as are the foramen ovale accessorius and the masticatory-buccinator foramina (5) is also shared by *Maxomys*. The primitive condition of the alisphenoid region is present in a few specimens of *Margaretamys*; contrasted with the many primitive traits of *Margaretamys* and the many derived features that are characteristic of *Rattus*, and of *Maxomys* to a lesser extent, the loss of the alisphenoid strut and adjacent foramina in *Margaretamys* is probably convergent

TABLE 12
Number of Derived Traits Shared among 13 Groups

	Chiro- mys- cus	Nivi- venter	N. ander- soni- divi- sion	Dac- nomys	Leo- pold- amys	Maxo- mys	Sri- lank- amys	Anony- momys	Mar- garet- amys	Leno- thrix	Apode- mus	Arvi- can- this	Rattus
<i>Chiromyscus</i>	15	13	11	11	11	11	8	6	5	1	2	7	9
<i>Niviventer</i>	—	14	12	12	11	11	8	6	5	1	2	7	9
<i>N. andersoni</i> - division	—	—	12	11	9	9	7	5	3	1	2	7	7
<i>Dacnomys</i>	—	—	—	13	10	9	6	5	4	1	2	7	8
<i>Leopoldamys</i>	—	—	—	—	11	10	7	5	4	1	1	5	7
<i>Maxomys</i>	—	—	—	—	—	12	8	7	5	1	1	5	7
<i>Srilankamys</i>	—	—	—	—	—	—	9	4	3	1	1	3	4
<i>Anonymomys</i>	—	—	—	—	—	—	—	6	4	1	2	4	5
<i>Margaretamys</i>	—	—	—	—	—	—	—	—	8	1	1	4	6
<i>Lenothrix</i>	—	—	—	—	—	—	—	—	—	5	4	2	2
<i>Apodemus</i>	—	—	—	—	—	—	—	—	—	—	8	6	6
<i>Arvicanthis</i>	—	—	—	—	—	—	—	—	—	—	—	14	14
<i>Rattus</i>	—	—	—	—	—	—	—	—	—	—	—	—	17

and not indicative of close relationship with either *Maxomys* or *Rattus*.

Margaretamys does not have any especially close affinity to *Niviventer*; four of the five derived traits shared by the two are also common to most of the other genera; and the fifth—long incisive foramina (8) is found in *Chiromyscus*, *Niviventer*, *Dacnomys*, *Anonymomys*, and *Rattus*. No single derivation is shared by only *Niviventer* and *Margaretamys*.

The accessory labial cusp behind cusp t6 on each first upper molar, and sometimes each second molar, is a derived trait in *Margaretamys* that is shared by only one other genus—*Lenothrix*. Misonne (1969, p. 73) noted that the primary character of *Lenothrix*'s dentition "is the presence of what may be considered as an extra cusp, set close to t6; such a cusp is rarely met with in the Muridae, and rather clear only in *Lenothrix*, *Rattus xanthurus* and possibly *Pitecheir*. Its interpretation is difficult; it seems very different from the stephanodont crest frequently met with in this group: such crests never develop in that way, as may be clearly seen in *Stephanomys* for instance." In my samples of the taxa mentioned by Misonne, a

discrete accessory cusp behind cusp t6 is present in specimens of *Lenothrix* and *Lenomys* only; such a cusp is best seen in young rats, for with increase in age and attendant wear of the molars the cusp joins the back of cusp t6 to form a crest. A small, discrete accessory cusp sits behind cusp t6 on each first upper molar of one out of the three examples of *Anonymomys mindorensis*; otherwise, *Margaretamys beccarii* and *M. elegans* are the only other species besides *Lenothrix canus* and *Lenomys meyeri* in which I have seen these accessory cusps.

Margaretamys may have closer phylogenetic affinities with either *Lenothrix* or *Lenomys*, or both, than with any of the other genera discussed in this report if the presence of an accessory cusp behind cusp t6 indicates relationship and does not reflect convergence. Possibly the three species of *Margaretamys* represent fragments of an early murid stock of which *Lenothrix* is a more primitive remnant.

SRILANKAMYS

Nine out of the 29 traits are found in their derived states in *Srilankamys ohiensis*. As

with *Lenothrix*, *Anonymomys*, and *Margaretamys*, *Srilankamys* shares few derived traits with *Rattus*—only four: braincase with vertical sides (3), overlap among the molars (18), cusps t4 and t5 connected (25), and the other cusps strongly connected (27); all four also occur in most of the other genera listed in table 11. *Srilankamys* has no close morphological or phylogenetic tie to *Rattus*.

No close phylogenetic relationship is evident between *Srilankamys* and *Lenothrix* either, even though *ohiensis* was once associated with *Lenothrix* when the latter was treated as a subgenus of *Rattus* (Ellerman and Morrison-Scott, 1951; Ellerman, 1961). *Srilankamys* and *Lenothrix* share only one derived trait—cusps t4 and t5 joined—and that feature is common to all the genera except *Margaretamys*.

Srilankamys shares most of its derived traits with *Niviventer* (8), *Leopoldamys* (7), *Maxomys* (8), and *Chiromyscus* (8). Four of these—braincase with vertical sides (3), overlap of molars (18), cusps t4 and t5 joined (25), and all other cusps strongly connected (27) are also shared by most of the other genera. Four others are dental features—small third molars relative to second molars (17), cusp t9 broadly merged with cusp t8 (22), cusp t3 absent (23), and anterolabial and anterolingual cusps that fuse to form a narrow oblong or triangular front lamina (28)—reflecting a decrease in size of the third upper molars relative to the others in the tooththrows and a simplification in the occlusal patterns of the molars, mostly the uppers. The occlusal patterns on the molars in *Srilankamys* are not quite as simple as those in *Niviventer*, *Leopoldamys*, *Maxomys*, and *Chiromyscus* because *Srilankamys* retains a posterior cingulum on each first upper molar and anterolabial cusps on the second and third lower molars; both traits are primitive. As I shall point out farther on, the shared dental derivations may indicate relationship among *Niviventer*, *Leopoldamys* (except the size of each third upper molar, which is relatively larger in *Leopoldamys*), *Maxomys*, and *Chiromyscus*, as well as *Dacnomys*, but I do not know whether the same derivations in *Srilankamys* reflects actual phylogenetic affini-

ty, or instead convergence, without contrasting the latter with other genera from the Indo-Australian region.

Srilankamys is unique in having ivory-colored incisors (13), a feature not found in any of the other genera discussed in the present report. Another possibly unique and derived trait is the small teeth in *Srilankamys*—the molars are narrower and the tooththrows shorter relative to size of the cranium and mandible than in any of the other genera discussed here except for some species of *Maxomys* (see the previous account of *Srilankamys*). I suspect the configuration to be derived but I have not been able to determine the polarity of this character satisfactorily.

Misonne (1969, p. 140), who treated *ohiensis* as a species of *Rattus*, wrote that "The presence of this species in Ceylon is difficult to explain, as there is no real *Rattus* in peninsular India, the genera *Millardia* and *Cremnomys* being no true *Rattus*." Isolating *ohiensis* from true *Rattus* by placing it in *Srilankamys* solves the problem with respect to *Rattus*, but does not illuminate the relationship of *Srilankamys*. *Millardia* and *Cremnomys* were once included as subgenera of *Rattus* by Ellerman (1961), but Misonne (1969) extracted them from that genus on dental evidence; data from chromosomal studies support his treatment (Raman and Sharma, 1977). Neither genus, however, can be tied to *Srilankamys*. Although morphologically and phylogenetically separable from *Rattus*, both *Millardia* and *Cremnomys* possess many derived features and in the analysis presented here would bear about the same relationship to *Rattus* as *Arvicanthis* does. Neither *Millardia* nor *Cremnomys* has anything to do with *Srilankamys*.

Although it resembles *Niviventer* in features of pelage, and in body conformation, and although it has been allied with species that are now placed in either *Niviventer* or *Maxomys* on the basis of cranial or dental features, *Srilankamys* does not appear to be phylogenetically closely related to either *Niviventer* or *Maxomys*. The cranial features common to all three genera are either primitive or derivations that also occur in many of the other genera discussed here.

Considering the derived dental features that *Srilankamys* does share with *Niviventer*, *Chiromyscus*, and *Maxomys*; considering the relatively small molars, the heart-shaped incisive foramina, and the presence of anterolabial cusps on the second lower molars—features that are similar to all or some species in *Maxomys*; and considering the other primitive characteristics of *Srilankamys* that make it less derived than those genera, *Srilankamys* is perhaps a primitive remnant of the stock from which *Maxomys* on the one hand and *Niviventer* and *Chiromyscus* (possibly also *Dacnomys*) on the other evolved. But, whatever its relationships, *Srilankamys* now appears to be a relict, geographically restricted to the highlands of Ceylon and morphologically isolated from other Indian and Indochinese murids. Any future analyses of its phylogenetic relationships will have to involve comparisons between *Srilankamys* and not only living species but also those represented by fossils, especially those from the Miocene and Pliocene sediments of the Siwaliks in northwestern India and northeastern Afghanistan.

NIVIVENTER AND CHIROMYSCUS

Niviventer and *Chiromyscus* have fewer primitive characters than most of the other genera. The derived states in 14 to 15 of the 29 traits are possessed by the two; both share more derived features between themselves (13) than with any of the other genera; and both share nine derived features with *Rattus*, less than the 14 shared by *Rattus* and *Arvicanthis*. Eight of the characters common to *Niviventer*, *Chiromyscus*, and *Rattus*—postorbital and temporal ridges (2), braincase with straight sides (3), long incisive foramina (8), four roots anchoring each first lower molar (15), considerable overlap among the molars (18), no posterior cingulum (21), cusps t4 and t5 connected (25), and the rest of the cusps strongly connected (27)—occur also in most of the other genera discussed here. Five of the derived traits shared by *Niviventer* and *Chiromyscus*, but not *Rattus*, are in the dentition: the third upper molar is small relative to the others in

the toothrow (17), cusp t9 is indistinct and broadly joined to cusp t8 (22), cusp t3 is usually absent from the second and third upper molars (23), the anterolabial and anterolingual cusps are small and usually fuse to form a narrow oblong or triangular lamina at the front of each first lower molar (28), and anterolabial cusps are missing from the second and third lower molars (29).

Chiromyscus and *Niviventer* are closely related. The primary features that distinguish *Chiromyscus* from *Niviventer* reflect the specializations in *Chiromyscus* for a highly arboreal habitus: nails on the halluxes (1) and shelflike postorbital and temporal ridges (2). There are also minor distinguishing features: for example, large pterygoid foramina penetrate the pterygoid fossae (11) in *Chiromyscus*, and the first upper molars are four-rooted (14). Interpterygoid foramina are absent from *Niviventer*, and except for *N. langbianis* and some specimens of *N. eha*, the other species of *Niviventer* have five-rooted (or more) first upper molars. Were it not for the special derivations of nails and wide cranial ridging, there would be no reason for not uniting *Chiromyscus* and *Niviventer* into one genus.

The *N. andersoni*-division (*N. andersoni* and *N. excelsior*) of *Niviventer* has 12 derived traits out of the 29 features; all 12 also occur in *Niviventer*, and if the traits are homologous, then *N. andersoni* and *N. excelsior* are a distinctive group within *Niviventer*. There are several features that distinguish *N. andersoni* and *N. excelsior* from the rest of the species in *Niviventer*, but all of them are primitive: two primary examples are postorbital and temporal ridges either absent or weak, and sides of the braincase slope from the dorsolateral margins outward to the squamosal roots of the zygomatic arches. The derived condition of these two traits occur in *Niviventer*. All the other minor features mentioned earlier in the account of *Niviventer* that help distinguish *N. andersoni* and *N. excelsior* from the rest of the species in the genus are also primitive. The data that is available, all drawn from skulls and teeth, support a hypothesis that *N. andersoni* and *N. excelsior* are a primitive seg-

ment of *Niviventer*. Eventually, study of myology, anatomy of reproductive tracts and other systems, and other kinds of characters such as biochemical and karyological traits, for example, may reveal features that are specialized and unique to the *N. andersoni*-division. Such information may indicate that the phylogenetic relationship between *Niviventer* and the *N. andersoni*-division is better expressed by excluding the latter from *Niviventer* and placing *N. andersoni* and *N. excelsior* in a genus of their own.

DACNOMYS

The derived expression of 13 out of the 29 traits are found in *Dacnomys*; 11 of these also occur in the *N. andersoni*-division. In most of its cranial features and many dental characteristics, *Dacnomys*, at first glance, appears to be a giant version of *Niviventer andersoni*. I carefully compared samples of the two kinds to determine if *andersoni* and *excelsior* were really members of *Dacnomys* rather than *Niviventer*, but *Dacnomys* has derivations that neither *N. andersoni*, *N. excelsior*, nor *Niviventer* have. The primary specialization is the very large and hypsodont molars (16) in *Dacnomys*. The teeth probably partly reflect the overall large size of the animal, but the molars are hypsodont, and the tooththrows are also longer relative to length of cranium than in *N. andersoni*, *N. excelsior*, or other species of *Niviventer*; in five specimens of *Dacnomys*, for example, the ratio, alveolar length of M^{1-3} /greatest length of skull, is 22 percent; this value is 19 percent in 45 *N. andersoni*, 18 percent in 11 *N. excelsior*, and 17 percent in 25 *N. confucianus*. Furthermore, the third upper molars of *Dacnomys* are large relative to others in the tooththrows, a primitive contrast to the derived relatively smaller molars in *N. andersoni*, *N. excelsior*, and the other species of *Niviventer*. Finally, *Dacnomys* has smaller bullae relative to size of the skull than in the other species: the ratio, length of bulla/greatest length of skull, ranges from 10–11 percent in five examples of *Dacnomys*; the value is 13 percent for 36 *N. andersoni*, 13 percent for 11 *N. excelsior*, and 14 percent

for 25 *N. confucianus*. The large, hypsodont molars and tiny bullae exclude *Dacnomys* from union with either *Niviventer* or the *N. andersoni*-division.

Many of the other derived features found in *Dacnomys* also occur in the other genera listed in tables 11 and 12. But there are four dental traits possessed by *Dacnomys* that also occur in *Chiromyscus*, *Niviventer*, *Leopoldamys*, and *Maxomys*: cusp t9 is usually indistinct and broadly joined to cusp t8 (22), cusp t3 is usually absent from the second and third upper molars (23), the anterolabial and anterolingual cusps are small and usually fuse to form a narrow oblong or triangular lamina at the front of each first lower molar (28), and anterolabial cusps are missing from the second and third lower molars (29). These dental features, all derived, support the hypothesis that *Dacnomys* is phylogenetically more closely related to *Chiromyscus*, *Niviventer*, *Leopoldamys*, and *Maxomys* than to *Rattus*. Some of the same derived features do occur in both *Dacnomys* and *Rattus*, but those same traits are found in many of the other genera discussed here as well. Although *Dacnomys* appears to cluster with *Chiromyscus*, *Niviventer*, *Leopoldamys*, and *Maxomys*, I have been unable to resolve with which of those four *Dacnomys* may have its closest affinities.

LEOPOLDAMYS

Leopoldamys shares only seven derived traits with *Rattus*, and all occur in many or several of the other genera as well; there is no derived feature that is unique to both *Leopoldamys* and *Rattus*, and the two genera have no close phylogenetic relationship. On the basis of the derived expressions in cusp t9 (22), cusp t3 (23), size of the anterolabial and anterolingual cusps on the first lower molars (28), and anterolabial cusps on the second and third lower molars (29), *Leopoldamys*, like *Dacnomys* is phylogenetically closer to *Chiromyscus*, *Niviventer*, and *Maxomys* than to *Rattus*. At the present time, however, I cannot resolve to which of the three *Leopoldamys* is most closely related. In many features, the species of *Leopol-*

damys appear to be giant versions of those in *Niviventer*, but as I enumerated in the account of *Leopoldamys* earlier in this report, there is a combination of primitive and derived features that distinguish *Leopoldamys* from *Niviventer*. Most prominent among these are large skull size, squamosal roots of the zygomatic arches set very high on the braincase, higher in relation to the temporal ridges than in any of the other genera discussed here, and very large, strongly opisthodont upper incisors. Although I have not used large size in the analysis here, it is likely a derivation, as are the very high positions of the squamosal roots, and the exaggerated opisthodonty. Most of the other traits that separate *Leopoldamys* from *Niviventer* are primitive ones in the former and derived versions in the latter.

MAXOMYS

Maxomys also shares only seven derived traits with *Rattus*, all of which occur in most or some of the other genera as well. The derived condition of the alisphenoid complex

(5) is found in *Maxomys*, and the same feature occurs in most specimens of *Margaretamys* and in all *Rattus*, but in context of all the other features that distinguish these three genera, the derived state of the alisphenoid complex appears to be convergent in each of them. Because *Maxomys* shares the combination of four derived dental features—cusp t9 indistinct and broadly joined to cusp t8 (22), cusp t3 usually absent from second and third upper molars (23), anterolabial and anterolingual cusps of first lower molars small (28), and no anterolabial cusps on second and third lower molars (29) with *Chiromyscus*, *Niviventer*, *Dacnomys*, and *Leopoldamys*, and one additional dental derivation, small third upper molars relative to size of other teeth (17) with *Chiromyscus* and *Niviventer*—*Maxomys* appears to be phylogenetically more closely related to *Chiromyscus*, *Niviventer*, *Dacnomys*, and *Leopoldamys* than to *Rattus*. On the basis of the characters I have examined here, there are no grounds for considering *Maxomys* to be closely related to *Rattus*.

CONCLUSIONS

The genus *Rattus*, as conceived (but never adequately defined or diagnosed) by Ellerman (1941, 1947–1948, 1949, 1961), was an assemblage of great morphological diversity and geographical spread, so impressive in its scope that Simpson (1945, p. 89) referred to it as “the most varied genus of mammals. . . .” So large and varied was the genus that students of murid taxonomy and zoogeography were hampered and sometimes discouraged from working with the species in it—because of the problems in identifying specimens and of trying to discern relationships among the species—and Ellerman’s view prevailed for a long time. Eventually, certain sets of characters were analyzed in the context of attempting to elucidate phylogenetic relationships among the species of *Rattus*, and a different estimate of

the limits of the genus was produced from study of dentitions by Misonne in 1969, probably the first major attempt to modify Ellerman’s conception. At about the same time, results from chromosomal studies (Yong, 1969a, for example) were being used to assess relationships among the species, and during the last 10 years have attained the unwarranted significance of a touchstone (Raman and Sharma, 1977, for example). Lately, biochemical data has been employed in an attempt to understand the systematics and evolution of *Rattus* (Chan, 1977; Chan, Dhaliwal, and Yong, 1979).

Most species of murid rodents are still represented by specimens consisting of skins and skulls. Crania and mandibles, if examined closely and carefully, are a rich source of data that, added to information gleaned

from study of dentitions, can be used to distinguish species and genera. Those sources of data are important in establishing the primitive and derived polarities in the morphocline of a given character, and thus contain much information for estimating phylogenetic relationships; data from chromosomes and biochemistry tend to be ambiguous more of the time in this context. Still, those data, combined with data from more conventional sources, are being used to reanalyze *Rattus*, and the results indicate that the genus as conceived by Ellerman is really a heterogeneous, possibly polyphyletic, assemblage of morphologically distinctive single species or groups of species. *Niviventer*, *Leopoldamys*, *Srilankamys*, *Margaretamys*, *Lenothrix*, and *Maxomys* are such groups, and there are others that were once hidden in Ellerman's conception of *Rattus* (Misonne, 1969; Musser, in press; Musser and Boeadi, 1980)—and some that are still concealed.

Sorting out these clusters, as well as others, is really an attempt to resolve the monophyly of *Rattus*. In the present report I have tried to demonstrate that *Niviventer*, *Leo-*

poldamys, *Srilankamys*, *Margaretamys*, *Lenothrix*, and *Maxomys* are not part of *Rattus*. *Niviventer*, *Leopoldamys*, and *Maxomys* seem closely related to *Chiromyscus* and *Dacnomys*, all five possibly members of a monophyletic assemblage. *Srilankamys* shares particular dental derivations with this group, but is otherwise more primitive. *Anonymomys* may be a more primitive and remote relative of the *Niviventer*-cluster, based on one derived dental feature, but the connection is still speculative. *Margaretamys* seems isolated, certainly not phylogenetically close to *Rattus*, but not close to the *Niviventer*-cluster either. *Lenothrix* is the most primitive and is clearly unrelated to *Rattus*. There is a suggestion of affinity between *Lenothrix* and *Margaretamys*, but that has to be tested further.

Defining the monophyletic nature of *Rattus* is going to provide a different picture of the generic diversity of African, Indian, and Indo-Australian murids than was available before, and a different context in which to hypothesize phylogenetic affinities.

LITERATURE CITED

- Abe, Hisashi
1971. Small mammals of Central Nepal. Jour. Facul. Agr., Hokkaido Univ., Sapporo, vol. 56, pt. 4, pp. 367–423, 2 pls.
- Allen, Glover M.
1940. The mammals of China and Mongolia. Natural History of Central Asia, vol. 11, pt. 2. New York, The American Museum of Natural History, pp. i–xxvi, 621–1350, pls. 10–20.
- Anthony, Harold E.
1941. Mammals collected by the Vernay-Cutting Burma Expedition. Zool. Ser., Field Mus. Nat. Hist., vol. 27, pp. 37–123, 1 fig., 4 pls.
- Baverstock, P. R., C. H. S. Watts, and Jane T. Hogarth
1977. Polymorphism of the X-chromosome, Y-chromosome and autosomes in the Australian Hopping Mice, *Notomys alexis*, *N. cervinus* and *N. fuscus*. Chromosoma, vol. 61, pp. 243–256, figs. 1–9.
- Baverstock, P. R., C. H. S. Watts, J. T. Hogarth, A. C. Robinson, and J. F. Robinson
1977. Chromosome evolution in Australian rodents. II. The *Rattus* group. Chromosoma, vol. 61, no. 3, pp. 227–241, figs. 1–11.
- Chan, Kean Leong
1977. Enzyme polymorphism in Malayan rats of the subgenus *Rattus*. Biochem. Syst. and Ecol., vol. 5, pp. 161–168, figs. 1–2.
- Chan, K. L., S. S. Dhaliwal, and H. S. Yong
1979. Protein variation and systematics of three subgenera of Malayan rats (Rodentia: Muridae, Genus *Rattus* Fischer). Comp. Biochem. Physiol., vol. 64B, pp. 329–337, figs. 1–3.

Chasen, Frederick Nutter

1940. A handlist of Malaysian mammals (A systematic list of the mammals of the Malay Peninsula, Sumatra, Borneo and Java, including the adjacent small islands). Bull. Raffles Mus., Singapore, Straits Settlement, no. 15, pp. i-xx, 1-209, 1 map.

Corbet, G. B.

1978. The mammals of the Palaearctic Region. A taxonomic review. London, British Museum (Nat. Hist.), and Ithaca, Cornell Univ. Press, pp. 1-314, maps 1-104.

Duncan, J. F., and P. F. D. Van Peenen

1971. Karyotypes of ten rats (Rodentia: Muridae) from Southeast Asia. Caryologia, vol. 24, pp. 331-346, figs. 1-12.

Duncan, J. F., P. F. D. Van Peenen, and P. F. Ryan

1970. Somatic chromosomes of eight mammals from Con Son Island, South Vietnam. Caryologia, vol. 23, pp. 173-181, figs. 1-5.

Duncan, J. F., R. Irsiana, and A. Chang

1974. Karyotypes of five taxa of *Rattus* (Rodentia: Muridae) from Indonesia. Cytologia, vol. 39, pp. 295-302, figs. 1-5.

Ellerman, J. R.

1941. The families and genera of living rodents. London, British Museum (Nat. Hist.), vol. 2, Family Muridae, pp. i-xii, 1-690, figs. 1-50.

- 1947-1948. Notes on some Asiatic rodents in the British Museum. Proc. Zool. Soc. London, vol. 117, pp. 259-271.

1949. The families and genera of living rodents. London, British Museum (Nat. Hist.), vol. 3, pt. 1, pp. i-v, 1-210.

1961. The fauna of India including Pakistan, Burma and Ceylon. Mammalia. Delhi, Manager of Publications, vol. 3, pts. 2, pp. xxxi-xxxv, 483-884, and xxxvii-lil, 1 map, figs. 1-29.

Ellerman, J. R., and T. C. S. Morrison-Scott

1951. Checklist of Palaearctic and Indian mammals, 1759 to 1946. London, British Museum (Nat. Hist.), pp. 1-810, 1 map.

Fooden, Jack

1969. Taxonomy and evolution of the monkeys of Celebes (Primates: Cercopithecidae). Bibliot. Primatologica, no. 10, pp. 1-148, figs. 1-38.

Fredga, Karl, Alfred Gropp, Heinz Winking, and Fritz Frank

1976. Fertile XX- and XY-type females in the

wood lemming *Myopus schisticolor*. Nature, vol. 261, no. 5557, pp. 225-227, figs. 1-3.

Ghose, R. K.

1964. A new rat of the genus *Rattus* Fischer, 1803, (Mammalia: Rodentia), from Darjeeling District, West Bengal, India. Proc. Zool. Soc., Calcutta, vol. 17, pp. 193-197, 1 fig.

Gray, J. E.

1867. Notes on the variegated or yellow-tailed rats of Australasia. Proc. Zool. Soc. London, vol. 2, pp. 299-314, pls. 1-2.

Greene, E. C.

1935. Anatomy of the rat. Trans. Amer. Phil. Soc., N. S., vol. 27, pp. i-xi, 1-370, figs. 1-339.

Gropp, A., A. Markwong, J. Marshall, and Y. J. Kim

1972. Robertsonian chromosomal variation in the longtailed tree mouse (*Vandeleuria*). Sond. Z. f. zool. Syst. u. Evol., bd. 10, h. 3, pp. 210-214, figs. 1-4.

Hill, J. E.

1960. The Robinson collection of Malaysian mammals. Bull. Raffles Mus., Singapore, no. 29, pp. 1-112, figs. 1-4.

Hodgson, B. H.

1845. On the rats, mice, and shrews of the central region of Nepal. Ann. Mag. Nat. Hist., ser. 1, vol. 15, pp. 266-270.

Honda, Takeo, Hiroshi Suzuki, and Masahiro Itoh

1977. An unusual sex chromosome constitution found in the Amami spinous country-rat *Tokudaia osimensis osimensis*. Japan Jour. Genetics, vol. 52, no. 3, pp. 247-249, figs. 1-2.

Husson, A. M.

1963. On *Blarina pyrrhonota* and *Echimys macrourus*: two mammals incorrectly assigned to the Suriname Fauna. Studies on the Fauna of Suriname and other Guyanas, vol. 5, pp. 34-41, pls. 1-2.

Jacobs, L. L.

1978. Fossil rodents (Rhizomyidae & Muridae) from Neogene Siwalik deposits, Pakistan. Mus. North. Arizona Press, Bull. Ser. 52, i-xi, 1-103 pp., 1-37 figs.

Jentink, F. A.

1879. On various species of *Mus*, collected by S. C. I. W. Van Musschenbroek Esq. in Celebes. Notes Roy. Zool. Mus. Netherlands, Leyden, vol. 1, no. 2, pp. 7-13.

1880. A Celebian mouse renamed. Notes

- Leyden Museum, vol. 2, no. 3, pp. 11–12.
- King, P. B., and E. M. McKee
1949. Terrain diagrams of the Philippine Islands. *Bull. Geol. Soc. Amer.*, vol. 60, pp. 1829–1836, 1 fig., pls. 1–5.
- Kloss, C. B.
1931. A new sub-species of Malaysian rat. *Bull. Raffles Mus.*, vol. 5, pp. 105–107.
- Laurie, E. M. O., and J. E. Hill
1954. List of land mammals of New Guinea, Celebes and adjacent islands, 1758–1952. London, British Museum (Nat. Hist.), pp. 1–175, pls. 1–2, 1 map.
- Markvong, A., J. T. Marshall, Jr., and A. Gropp
1973. Chromosomes of rats and mice of Thailand. *Nat. Hist. Bull. Siam Soc.*, vol. 25, pp. 23–40, figs. 1–24.
- Marshall, Joe T., Jr.
1976. Family Muridae: rats and mice. Pp. 396–487. Privately printed by the Government Printing Office, Bangkok.
1977. Family Muridae: rats and mice. Pp. 396–487. Reprinted in *Mammals of Thailand* (Boonsong Lekagul and J. A. McNeely). Assoc. Conserv. of Wildlife, Bangkok, Thailand.
- Matthey, R.
1943. La formule chromosomique et la problème de la détermination sexuelle chez *Ellobius lutescens*. *Arch. Julius Klaus-Stift Vererbungsforsch. Rassenhyg.* 27, pp. 163–166.
- Medway, Lord
1965. *Mammals of Borneo. Field keys and an annotated checklist.* Singapore, Malaysian Branch of the Royal Asiatic Society, Malaysia Printers, pp. i–xiv, 1–193, figs. 1–9, pls. 1–34, 1 map.
1969. *The wild mammals of Malaya and offshore islands including Singapore.* Kuala Lumpur and Singapore, Oxford Univ. Press, xix + 127 pp., figs. 1–11, pls. 1–15.
- Medway, Lord, and H. S. Yong
1976. Problems in the systematics of the rats (Muridae) of peninsular Malaysia. *Malay. Jour. Sci.*, vol. 4, pp. 43–53, pls. 1–4.
- Michaux, J.
1971. Muridae (Rodentia) Neogenes d'Europe sud-occidentale. Evolution et rapports avec les formes actuelles. *Paleobiologie Continentale*, vol. 2, no. 1, pp. 1–67, figs. 1–7, pls. 1–12.
- Miller, G. S.
1903. Mammals collected by Dr. W. L. Abbott on the coast and islands of north-west Sumatra. *Proc. U.S. Natl. Mus.*, vol. 26, pp. 437–484, pls. 16–18.
1912. *Catalogue of the mammals of Western Europe (Europe exclusive of Russia) in the collection of the British Museum.* London, British Museum (Nat. Hist.), pp. i–xv, 1–1019, figs. 1–213.
- Misonne, Xavier
1969. African and Indo-Australian Muridae. Evolutionary trends. *Mus. Roy. l'Afrique Cent., Tervuren, Zool.*, no. 172, pp. 1–219, figs. A–K, pls. 1–27.
- Musser, Guy G.
1969. Results of the Archbold Expeditions. No. 91. A new genus and species of murid rodent from Celebes, with a discussion of its relationships. *Amer. Mus. Novitates*, no. 2384, pp. 1–41, figs. 1–15.
1970. Species-limits of *Rattus brahma*, a murid rodent of northeastern India and northern Burma. *Ibid.*, no. 2406, pp. 1–27, figs. 1–6.
1971. The taxonomic status of *Rattus tondanus* Sody and notes on the holotypes of *R. beccarii* (Jentink) and *R. thysanurus* Sody (Rodentia: Muridae). *Zoologische Mededelingen*, vol. 45, no. 13, pp. 147–157.
1973. Species-limits of *Rattus cremoriventer* and *Rattus langbianis*, murid rodents of Southeast Asia and the Greater Sunda Islands. *Amer. Mus. Novitates*, no. 2525, pp. 1–65, figs. 1–9.
1977. Results of the Archbold Expeditions. No. 100. Notes on the Philippine rat, *Limnomys*, and the identity of *Limnomys picinus*, a composite. *Ibid.*, no. 2636, pp. 1–14, 1 fig.
1979. Results of the Archbold Expeditions. No. 102. The species of *Chiropodomys*, arboreal mice of Indochina and the Malay Archipelago. *Bull. Amer. Mus. Nat. Hist.*, vol. 162, art. 6, pp. 377–445, figs. 1–16.
- [In press.] A new genus of arboreal rat from West Java, Indonesia. *Zoologische Verhandelingen*.
- Musser, Guy G., and Shirley Chiu
1979. Notes on taxonomy of *Rattus andersoni* and *R. excelsior*, murids endemic

- to Western China. Jour. Mammal., vol. 60, no. 3, pp. 581–592, figs. 1–2.
- Musser, Guy G., and Boeadi
1980. A new genus of murid rodent from the Komodo Islands in Nusatenggara, Indonesia. *Ibid.*, vol. 61, no. 3, pp. 395–413, figs. 1–7.
- Musser, Guy G., Joe T. Marshall, Jr., and Boeadi
1979. Definition and contents of the Sundaic genus *Maxomys* (Rodentia, Muridae). *Ibid.*, vol. 60, no. 3, pp. 592–606, 1 fig.
- Muul, Illar, and Lim Boo Liat
1971. New locality records for some mammals of West Malaysia. *Ibid.*, vol. 52, no. 2, pp. 430–437, 1 fig.
- Niethammer, J., and J. Martens
1975. Die gattungen *Rattus* und *Maxomys* in Afghanistan und Nepal. Z. Säugetierk., vol. 40, pp. 325–355, figs. 1–10.
- Osgood, Wilfred H.
1909. Revision of the mice of the American genus *Peromyscus*. North Amer. Fauna, no. 28, pp. 1–285, figs. 1–12, pls. 1–8.
1932. Mammals of the Kelley-Roosevelts and Delacour Asiatic expeditions. Publ. 3.2, Field Mus. Nat. Hist., Zool. Ser., vol. 18, no. 10, pp. 193–339, 1 map, pls. 1–2, 1 fig.
- Patton, James L.
1967. Chromosome studies of certain pocket mice, genus *Perognathus* (Rodentia: Heteromyidae). Jour. Mammal., vol. 48, no. 1, pp. 27–37, figs. 1–7.
- Phillips, W. W. A.
1929. Two new rodents from the highlands of Ceylon. Ceylon Jour. Sci., Sec. B, 15, pp. 165–168.
- Pei, W. C.
1936. On the mammalian remains from Locality 3 at Choukoutien. Palaeontologia Sinica, ser. C, vol. 7, fasc. 5, pp. 1–121, figs. 1–59, pls. 1–4.
- Rafinesque, Constantine Samuel
1818. Further discoveries in natural history, made during a journey through the western region of the United States. Am. Monthly Mag., vol. 3, pp. 445–447.
- Raman, Rajiva, and T. Sharma
1977. Karyotype evolution and speciation in genus *Rattus* Fischer. Jour. Scientific & Indust. Research, vol. 36, no. 8, pp. 385–404, figs. 1–22.
- Ripley, S. Dillon, and D. S. Rabor
1958. Notes on a collection of birds from Mindoro Island, Philippines. Peabody Mus. Nat. Hist., Yale Univ. Bull. 13, pp. i–iv, 1–84, pls. 1–2.
- Simpson, George Gaylord
1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., vol. 85, pp. i–xvi, 1–350.
- Sody, H. J. V.
1932. Six new Indo-Malayan rats. Natuurhist. Maandblad, vol. 21, no. 12, pp. 157–160.
1941. On a collection of rats from the Indo-Malayan and Indo-Australian regions (with descriptions of 43 new genera, species, and subspecies). Treubia, vol. 18, pp. 255–325.
- Tate, G. H. H.
1936. Results of the Archbold Expeditions. No. 13. Some Muridae of the Indo-Australian region. Bull. Amer. Mus. Nat. Hist., vol. 72, pp. 501–728.
- Taylor, J. Mary, and B. Elizabeth Horner
1973. Results of the Archbold Expeditions. No. 98. Systematics of native Australian *Rattus* (Rodentia, Muridae). *Ibid.*, vol. 150, pp. 1–130, figs. 1–44.
- Teilhard, P. de Chardin
1938. The fossils from Locality 12 of Choukoutien. Palaeontologia Sinica, new ser. C, no. 5, whole ser. no. 114, pp. 1–51, figs. 1–36, 1 pl.
- Tien Dao Van
1966. Sur une collection de rongeurs au sud-est de L'Asie. Miss. Zool. Mus. Berlin, Band 42, heft 2, pp. 219–228.
- Thomas, Oldfield
1887. Description of a new rat from North Borneo. Ann. Mag. Nat. Hist., Ser. 5, vol. 20, pp. 269–270.
1888. On the mammals of Christmas Island. Proc. Zool. Soc. London, pp. 532–534.
1891a. Diagnoses of three new mammals collected by Signor L. Fea in the Carin Hills, Burma. Annali Del Museo., Civico di Storia Naturale Di Genova, ser. 2, vol. 10, p. 884.
1891b. On the Mammalia collected by Signor Leonardo Fea in Burma and Tenasserim. *Ibid.*, ser. 2, vol. 10, pp. 913–949, 2 pls.
1916. Scientific results from the mammal survey, No. XIII. On Muridae from Dar-

- jeeling and the Chin Hills. Jour. Bombay Nat. Hist. Soc., vol. 24, pp. 404–407, 1 fig.
1922. Scientific results from the mammal survey, No. XXXII. New and interesting mammals from the Mishmi Hills. *Ibid.*, vol. 28, pp. 428–431.
1925. The mammals obtained by Mr. Herbert Stevens on the Sladen-Godman Expedition to Tonkin. Proc. Zool. Soc. London, pp. 495–506.
- Van Peenen, P. F. D., P. F. Ryan, and R. H. Light
1969. Preliminary identification manual for mammals of South Vietnam. U.S. Natl. Mus., Smithsonian Inst., Washington, D.C., vi + 310 pp., figs. 1–81.
- Van Peenen, P. F. D., R. H. Light, F. J. Duncan, R. See, J. Sulianti Saroso, Boeadi, and W. P. Carney
1974. Observation on *Rattus bartelsii* (Rodentia: Muridae). Treubia, vol. 28, pt. 3, pp. 83–117, figs. 1–22.
- Verheyen, W. N., and E. Van der Straetan
1980. The caryotype of *Lophuromys nudicaudus* Heller 1911 (Mammalia-Muridae). Rev. Zool. afr., vol. 94, no. 2, pp. 311–316, 1 fig.
- Wahlert, J. A.
1974. The cranial foramina of protrogomorphous rodents; an anatomical and phylogenetic study. Bull. Mus. Comp. Zool., 146: 363–410, figs. 1–13.
- Weerd, A. van de
1976. Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alhambra region, Spain. Utrecht Micropaleo. Bull. Spec. Publ., no. 2, pp. 1–218, figs. 1–30, pls. 1–16.
- Weigel, Ingrid
1969. Systematische übersicht über die insektenfresser und nager Nepals nebst bemerkungen zur tiergeographie. Khumbu Himal, Ergebn. Forsch.-Unternehmen Nepal Himalaya, Band 3, lief. 2, pp. 149–312, figs. 1–36.
- Yong, Hoi Sen
1969a. Karyotypes of Malay rats (Rodentia-Muridae, Genus *Rattus* Fischer). Chromosoma, vol. 27, band 3, heft S, pp. 245–267, figs. 1–14.
1969b. Karyotypes of three species of rats from Hong Kong and Thailand (Muridae, genus *Rattus* Fischer). Cytologia, vol. 34, no. 3, pp. 394–398, figs. 1–6.
1970. A Malayan view of *Rattus edwardsi* and *R. sabanus* (Rodentia:Muridae). Zool. Jour. Linn. Soc., vol. 49, no. 4, pp. 359–369, 1 fig., 1 pl.
- Yosida, Toshihide H.
1973. Evolution of karyotypes and differentiation in 13 *Rattus* species. Chromosoma, vol. 40, pp. 285–297, figs. 1–13.
- Young, Chung-Chien
1934. On the Insectivora, Chiroptera, Rodentia and primates other than *Sinanthropus* from Locality 1 at Choukoutien. Palaeontologia Sinica, ser. C, vol. 8, fasc. 3, pp. 1–161, figs. 1–51, pls. 1–10.

