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GUY G. MUSSER AND CAMERON NEWCOMB

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

CAMERON NEWCOMB
Participant, Undergraduate-Graduate Research Program
American Museum of Natural History

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ABSTRACT

We define the morphological boundaries and elucidate the contents of three Indo-Malayan murid genera: *Palawanomys,* new genus, known only from Palawan Island; *Berylmys,* primarily Indochinese in geographic distribution with a representative on the Sunda Shelf; and *Sundamys,* new genus, containing the giant rat of Sumatra and indigenous to the Sunda Shelf. We contrast the characteristics of these three genera with 11 others that have native species on the Sunda Shelf. Five of the Sundanese (or Malaysian) genera are endemic to the Shelf: *Pithecheir, Kadarsanomys, Lenothrix, Palawanomys,* and *Sundamys. Maxomys, Haeromys,* and *Chiropodomys* are basically Sundaic in that most of the species in each genus are endemic to the Shelf. Most of the species in four of the genera (*Berylmys, Niviventer, Mus,* and *Rattus*) occur outside of the Sunda region. *Leopoldamys* and *Hapalomys* are the only two which have an equal number of species in both Indochina and on the Sunda Shelf. We estimate there to be 40 native species of rats and mice on the peninsula and islands of the Sunda Shelf and 10 others whose distributions on the Shelf probably reflect introductions by human agency. Our view of the species and generic diversity of Malaysian murids, in which *Rattus* is a minor part, is contrasted with that of former workers who looked upon *Rattus* as a major component of the Sundaic murid fauna. We analyze the distributions of primitive and derived traits among the 14 native genera and examine possible phylogenetic relationships among them. Patterns formed by these alliances as well as by geographic distributions of the genera are described; questions are posed that will require answers from additional study.

INTRODUCTION

"The giant rat of Sumatra, a story for which the world is not yet prepared," Sherlock Holmes said to Dr. Watson in the beginning of *The Adventure of the Sussex Vampire.* Sir Arthur Conan Doyle never had Holmes recount the tale and the giant rat of Sumatra became part of that fictional bestiary formed in the imagination based on suspicions and faulty facts.

Life reflects art. There is a giant rat on Sumatra. It lives in tropical forests along the mountain backbone of that elongate island. So little was known about the animal it might as well have been an abstraction of the writer's mind. All current data comes from six specimens, the first one found in 1913 and the last two in 1939. The rat is difficult to catch and its habits are unknown. We do know it has a large, chunky body (weighing 500 to 700 grams), a long brown tail, and shaggy brown and buffy fur. In 1942 the animal was described as *Rattus atchinus* (Miller, 1942). Rather than providing identity, that name plunged this large, handsome rat into the obscurity of being just another species in the genus *Rattus,* in which there were already more than 500 named forms. The rat was not heard of again until now.

We retrieve the giant rat of Sumatra from anonymity and explain that the same species also lives in the mountain forests of northern Borneo and was named *infraluteus* by Oldfield Thomas in 1888a. We describe the Sumatran and Bornean populations and show how they are linked to *muelleri* and *maxi,* two species native on the islands and peninsula of the Sunda Shelf. We explain why these three species form a cluster, the *muelleri* group, that should be placed in a genus other than *Rattus.*

Before discussing the *muelleri* group, we define two other clusters: One is a rat endemic to Palawan Island on the Sunda Shelf and is described as a new genus and species, and the other is the genus *Berylmys,* whose species are primarily Asian in distribution with a representative on the Malay Peninsula and northern Sumatra. The thread running through the three groups is that *muelleri* and its relatives, as well as *Berylmys,* have been part of *Rattus* as that genus was defined by Sir John R. Ellerman in 1941 and 1949. Had the Palawan rat been described then, it too would have been named as another species of *Rattus* native to the Sunda Shelf.

There are two primary themes in the present report: One is a continuation of defining the clusters of species once included in *Rattus*

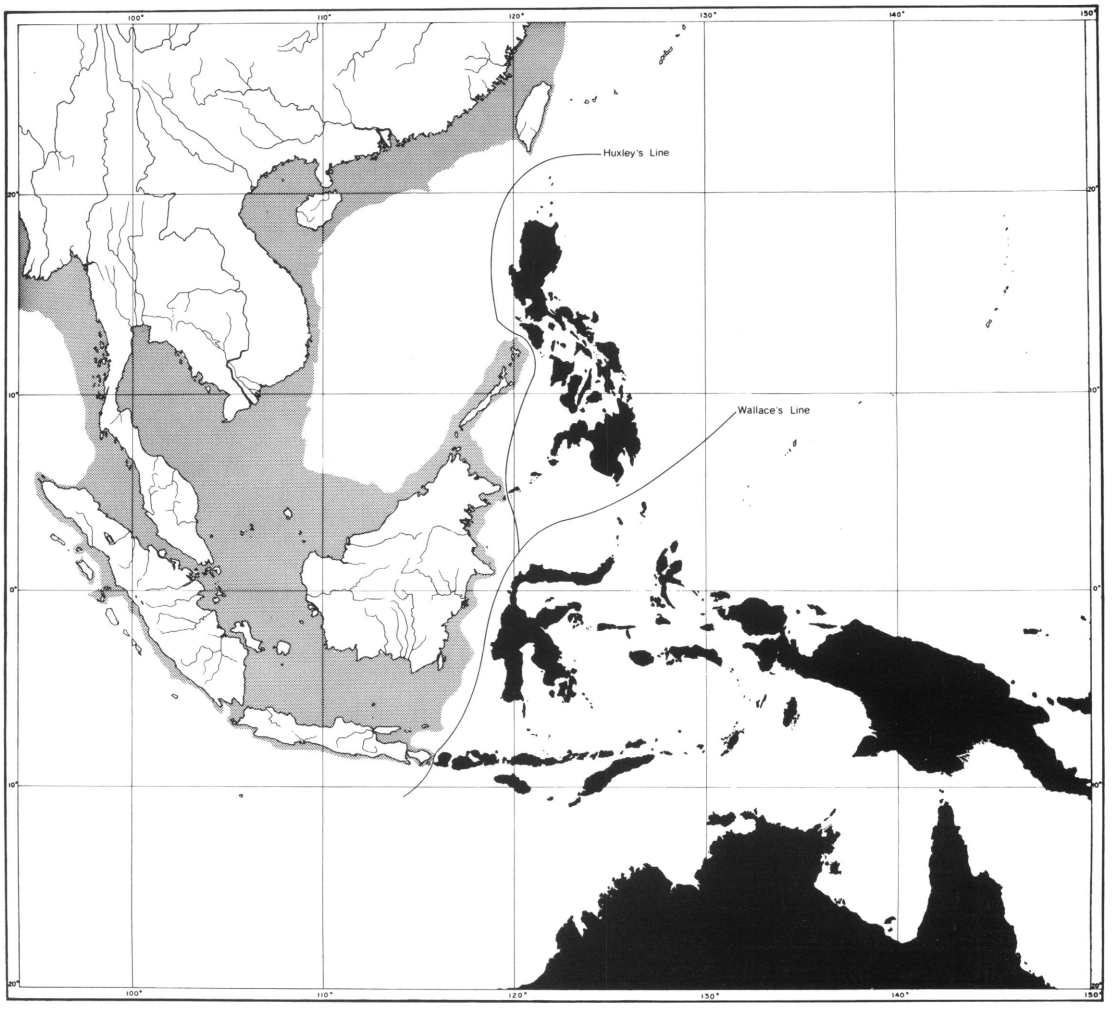

FIG. 1. The Indo-Australian region. The gray area to the west of Wallace's and Huxley's lines denotes approximate margins of the continental shelf; that part of it south of approximately 10°30′ N lat. is the Sunda Shelf.

but really not a part of that genus (Musser, 1981a, 1981b, 1981c, 1982a, 1982b); the other relates these groups to the species of rats and mice native to the islands and peninsula of the Sunda Shelf (fig. 1).

"One of the most extensive shelves in the world," wrote Tjia (1980, p. 406), "lies under the southern part of the South China Sea and under the Java Sea in Southeast Asia." The Sunda Shelf "covers an area of 1,850,000 square kilometres and together with the relatively stable land areas comprising Peninsular Malaysia, Bangka, Belitung (or Billiton) and the western part of Kalimantan (or Borneo) are known as Sunda Land."

To Chasen (1940, p. v), Sunda Land was Malaysia. In his historical and enduring handlist of Malayan mammals, Chasen defined a basic or physiographical Malaysia "as all land standing on the Sunda Shelf below about Lat. 10° N. It is an area in which the sea-depths are less than one-hundred, and usually less than forty fathoms: it leaps to the eye from a bathymetrical map."

The name Sunda, wrote Van Bemmelen (1949, p. 644),

appears for the first time in a stone inscription of West Java of 1030 A.D. The only locality, where Sunda is found as a local geographical name, is the Sunda Mountain, North of Bandung. The name Sunda is etymologically related, according to Prof. Dr. C. C. Berg, with the Sanskrit word 'Cuddha,' which means 'pure,' and is used for 'white' in the Javanese. On the other hand, it is a geological fact that during the eruption phase C of the Tangkuban Prahu [the volcanic peak rising up to more than 2000 meters north of Bandung] the surrounding area was repeatedly covered by white ash-layers, often several feet thick, (in total 30–40 m). Therefore, this volcanic complex was a striking white landmark in the green fertile Preanger or Priangan. It is conceivable that it became customary to indicate the Preanger area by the name of 'Sunda,' meaning 'white.' It is a notable fact that the name Sunda is only found as a local geographical name in this area, viz. one of the summits of the Sunda Caldera. Afterwards, the Portuguese and the Dutch applied the name to the entire western part of Indonesia.

Now the name Sunda denotes a biogeographical and physiographic region (Van Bemmelen, 1949; Haile, 1969; Ben-Avraham and Emery, 1973) where past geological and climatic events combined with evolutionary histories of native rats and mice today form a rich tapestry of species and phylogenetic patterns. The giant rat of Sumatra and Borneo is part of that species diversity. Relating it to other rats on the Sunda Shelf partly describes those patterns of relationships. That is our story. We continue in the pages beyond by first naming and describing the Palawan rat, then defining the genus *Berylmys,* and after that proposing a new genus for the *muelleri* group and defining its geographical and morphological boundaries. We conclude by discussing the 40 species of rats native to the Sunda Shelf, noting some possible relationships among them, and outlining the patterns those relationships form.

ABBREVIATIONS AND PROCEDURES

MATERIALS: Specimens examined and cited here are in collections of the American Museum of Natural History, New York (AMNH); the Philadelphia Academy of Natural Sciences, Philadelphia (ANSP); Applied Scientific Research Corporation of Thailand, Centre for Thai National Reference Collections, Bangkok (ASRCT); the British Museum (Natural History), London (BM); the Delaware Museum of Natural History, Delaware (DMNH); the Field Museum of Natural History, Chicago (FMNH); Museum National d'Histoire Naturelle, Paris (MNHN); the Museum Zoologicum Bogoriense, Bogor (MZB); the Museum of Comparative Zoology at Harvard College, Cambridge (MCZ); Naturhistorisches Museum Basel, Switzerland (NMB); National Museum, Singapore (NMS); the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); the Staatliches Museum für Tierkunde, Dresden (SMT); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

MEASUREMENTS: Values for total length, length of tail, and length of ear are those recorded by collectors on labels attached to skins. We subtracted length of tail from total length to obtain length of head and body. Values for length of hind foot (including claw) were either taken from skin labels or from our measurements of dry skins. Cranial and dental measurements were taken with dial calipers graduated to tenths of millimeters or with Anderson's craniometer attached to a Wild M5 Stereomicroscope. Limits of the measurements are defined below (and illustrated in Musser, 1970a and 1979). Measurements are in millimeters (mm.).

Breadth of braincase: measured from just above the squamosal root of each zygomatic arch.

Breadth of first upper molar: measured across the broadest part of each first upper molar.

Breadth across incisive foramina: the greatest distance across both foramina.

Breadth across incisor tips: the distance across tips of the incisors.

Breadth of palatal bridge at first molars: the least distance between the lingual edge of the alveolus of the first molar and the lingual edge of the alveolus of the opposite tooth.

Breadth of palatal bridge at third molars: the least distance between the lingual edge of the alveolus of the third molar and the lingual edge of the alveolus of the opposite molar.

Breadth of mesopterygoid fossa: the distance from one edge of the mesopterygoid fossa to the other.

Breadth of rostrum: the greatest breadth across the rostrum, including the bony capsules enclosing the nasolacrimal canals.

Breadth of zygomatic plate: the least distance between the anterior and posterior edges of the zygomatic plate.

Depth of zygomatic notch: from the anterior edge of the zygomatic plate to the anterior edge of the dorsal maxillary root of the zygomatic plate, and parallel to the long axis of the skull.

Greatest length of skull: this is the same as occipitonasal length for all material reported in the present paper and is the distance from the tip of the nasals to the posterior margin of the occiput.

Height of braincase: from the top of the braincase to the ventral surface of the basisphenoid bone.

Height of bulla: the distance from the dorsal surface of the bulla to its ventral surface.

Interorbital breadth: the least distance, as viewed dorsally, across the frontal bones between the orbital fossae.

Incisive foramina to first upper molar: the distance from the posterior margins of the incisive foramina to the anterior alveolar margins of the first molars.

Length of bulla: the length of the bulla, excluding the bony eustachian tube.

Length of diastema: the distance from the posterior alveolar margins of the upper incisors to the anterior alveolar margins of the first upper molars.

Length of incisive foramina: the distance from the anterior edge of one of the foramina to its posterior edge. Alveolar length of maxillary toothrow: the distance from the anterior edge of the alveolus of the first molar to the posterior edge of the alveolus of the third molar.

Length of molar row: distance from the anterior edge of the alveolus of the first molar to the posterior edge of the alveolus of the third molar (alveolar length); only crown lengths of molar rows are given in the figures.

Length of nasals: the distance from the anterior lip of the nasal bones to the most posterior suture between the nasal and frontal bones, measured parallel to the surface of the nasals.

Length of palatal bridge: the distance from the posterior edge of the incisive foramina to the posterior margin of the bony palate.

Length of rostrum: from the tip of the nasal bones to the posterior margin of the zygomatic notch (the anterior edge of the dorsal maxillary root of the zygomatic plate).

Third upper molar to posterior rim of palatal bridge: from the edge of the bridge to the posterior alveolar margins of the third upper molars, whether the bridge rim is anterior to the backs of the molars or posterior to them.

Palatal length: the distance from the anterior alveolar margins of the incisors to the posterior edge of the palatal bridge.

Postpalatal length: the distance from the posterior margin of the palatal bridge to the posterior edge of the basioccipital bone—the ventral lip of the foramen magnum.

Zygomatic breadth: the greatest breadth across the zygomatic arches.

TEETH: Many different names have been used to describe occlusal structures of murid teeth (Jacobs, 1978, provides a useful summary of these terms). Our terminology describing positions of cusps on upper molars is a slight modification of the numbering system developed by Miller (1912) and diagrammed in figure 2. There are 10 primary cusps on each first upper molar of a species such as *Lenothrix canus,* arranged in three rows; each row contains three cusps and there is a tenth cusp at the back of the tooth. Beginning with the lingual cusp of the first row and extending across to the labial one, the cusps are denoted t1, t2, and t3. Cusps t4, t5, and t6 designate the second row of cusps, from lingual to labial side. Beginning at the lingual cusp of the third row, the cusps are labeled t7, t8, and t9. The single posterior cusp is the posterior cingulum. A similar numbering sequence applies to cusps, although there are fewer of them, on the second and third molars. In some species, such as *L. canus* in figure 2, there is a small cusp t1bis between cusps t1 and t2 and a cusp t2bis between cusps t2 and t3 on each first molar. There is a small accessory cusp behind cusp t6 on each first and second molar in some specimens.

The nomenclature for occlusal structures on the lower molars (fig. 2) is, with slight deviation, that used by van de Weerd (1976, p. 44). The occlusal surface of each first lower molar consists of three rows of large cusps (also called 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 (often referred to as conulids) occur along the labial margin and occasionally along the lingual edge. An anterolabial cusp, two rows of cusps, a posterior cingulum, and a labial cusplet form the occlusal surface of each second molar. An anterolabial cusp and two rows of cusps provide the chewing surface of each third molar.

CRANIAL BONES AND FORAMINA: We describe the position and sometimes size of various cranial foramina and canals and surrounding bone. Some openings and channels reflect arterial patterns that are significant in distinguishing taxa. The presence or absence of particular foramina and the configuration of specific cranial regions provide information on primitive and derived conditions in a species. The foramina and the vessels or nerves they transmit as well as other kinds of vacuities which we write about have been described by Musser (1982b, 1982c) and based on the careful investigations of Hill (1935) and Wahlert (1974) and his own dissections of material preserved in fluid and partially cleaned skulls.

CHROMOSOMES: We discuss chromosome number and shape. Four terms are used 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. See Musser (1981a) for a visual guide to the range of variation in each of the configurations we refer to.

SEM MICROGRAPHS: Micrographs of teeth and parts of crania are derived from specimens uncoated and unaltered in any way before they were placed in the chamber of the Scanning Electron Microscope.

GEOGRAPHIC NAMES: New and old names of places are used interchangeably throughout the report. The old names of primary regions and their current counterparts follow:

INDOCHINA: Northeastern India (including Assam), Bangladesh, Thailand, Laos, southern China, Vietnam, and Cambodia
CEYLON: Sri Lanka
MALAYA: West Malaysia
SUMATRA: Sumatera
JAVA: Jawa
BORNEO: Sarawak, Sabah, Brunei (East Malaysia); Kalimantan (Indonesian Borneo)
NATUNA ISLANDS: Kepulauan Bunguran
CELEBES: Sulawesi
MOLUCCAS: Maluku
NEW GUINEA: Irian Jaya (Indonesian New Guinea; Papua New Guinea)

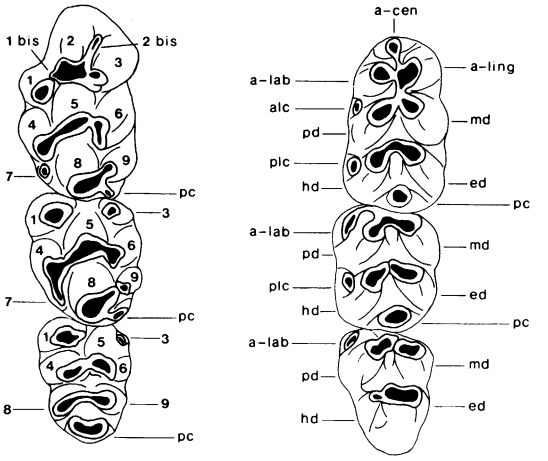

FIG. 2. Nomenclature of dental structures: a diagram of upper and lower molars in *Lenothrix canus*. Upper molars: cusps are numbered according to Miller's (1912) scheme and referred to in the text with the prefix t; **pc**, posterior cingulum. Lower molars: **a-cen**, anterocentral cusp; **a-lab**, anterolabial cusp; **a-ling**, anterolingual cusp; **pd**, protoconid; **hd**, hypoconid; **md**, metaconid; **ed**, entoconid; **pc**, posterior cingulum; **alc**, anterior labial cusplet; **plc**, posterior labial cusplet.

We use Sungai (stream or small river); gunong, the Malay spelling, and gunung, the Indonesian form (mountain), pulau (island), and Kepulauan (archipelago).

Our view of the Philippine Islands is zoogeographic and not political. The islands of Balabac, Palawan, Culion, Busuanga, and nearby smaller islands are politically administered by the Philippine Government but physiographically part of the Sunda Shelf and zoologically tied to the other islands and the peninsula of the Shelf. When we refer to the native fauna of the Philippine Islands we mean the backbone of islands from Luzon to Mindanao that lay east of the Sunda Shelf. In the context of our report, the Palawan region is not part of that backbone but the

northeastern segment of the Sunda Shelf and thus part of the Indo-Malayan region (fig. 1).

Generally, we use Sundanese or Sundaic in referring to the peninsula and islands of the Sunda Shelf south of Lat. 10–12° N. The region approximates that outlined by an unbroken red line on the map in Chasen (1940). Malaysian is used by him and other writers for the same general area, a term we employ in the title and sometimes through the text.

We exclude groups of islands nearby but off the Shelf from our report except in cursory discussion tangential to the main themes. Murid faunas of the Andaman and Nicobar islands, the Mentawai Islands, and several other islands south of Sumatra and Java that are off the Sunda Shelf but populated by native murids related to Sundanese species are subjects of future reports.

ACKNOWLEDGMENTS

Results of our study are based primarily on specimens stored in museum collections. The minute our report is published it becomes a secondary source of information. The specimens are, and remain, the primary source. It is directly from them that we derive information to answer questions about the natural history and evolutionary relationships of the species they represent. Each stuffed skin, each skeleton, each dreary-looking pickled rat is special. The care of this material is the responsibility of museum curators and their supporting staffs. To these persons we are deeply grateful. Not only do they understand the importance of preserving natural history specimens but they also realize that the material must be studied by naturalists like ourselves. They have generously opened their collections to us. Were it not for their gracious cooperation, our study would have been impossible.

We express our appreciation to Ms. Marjorie Shepatin, Ms. Fran Stiles, and Ms. Patricia Wynne who did the drawings, and to Mr. Peter Goldberg and Mr. Jim Coxe who made the photographs. Dr. Alfred Gardner provided photographs of USNM holotypes. Mr. Robert J. Koestler and Ms. Joan Whelan are responsible for the scanning electron work; Mr. Richard Sheryll developed and printed most of the micrographs.

Insights into the problem of systematics of rats and mice of the Sunda Shelf came partly from Musser's work in Indonesia. Financial backing for that trip came from the Celebes Fund of the American Museum of Natural History and Archbold Expeditions Inc. We are grateful to the managers of those funds for their generous past support. Musser was sponsored in Indonesia by the Lembaga Ilmu Pengetahuan Indonesia and the Museum Zoologicum Bogoriense.

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We are grateful to Ms. Debra Califia for her care and competence in transforming the rough copy into the finished manuscript.

This paper is number 111.—Results of the Archbold Expeditions.

THE PALAWAN RAT

Balabac, Palawan, Culion, and Busuanga are the larger islands in the Palawan region. *Rattus tiomanicus, Sundamys muelleri, Maxomys panglima,* and *Chiropodomys calamianensis* are the native species of murids recorded from there (Sanborn, 1952; Musser, 1979, 1981a). Of these, *M. panglima* and *C. calamianensis* are endemic to the Palawan area. *Haeromys* also occurs on Palawan, represented by a species endemic to the island (Musser and Schonewald, MS.). *Rattus tiomanicus* is related to populations of that species on the mainland of northern Borneo (Musser and Califia, 1982), *Sundamys muelleri* from the Palawan area is related to populations of *S. muelleri* on Borneo (present report), and *C. calamianensis* is morphologically closely related to the Bornean *C. major* (Musser, 1979). *Maxomys panglima* may be a relative of *M. rajah* on Borneo but nobody is sure of that (Musser, Marshall, and Boeadi, 1979). The known murid fauna is low in

number of species, which partly reflects the occurrence of less species on small islands than on large islands and the mainland but also indicates incomplete exploration and collection of both large and small islands in the Palawan region.

There are other species of rats and mice yet to be discovered in the Palawan area. The largest series of murids now known from the region were collected by members of the Philippine Zoological Expedition of 1946–1947, which was sponsored by the Field Museum of Natural History (Hoogstraal, 1951; Sanborn, 1952). In the narrative and itinerary of the expedition, the leader, Dr. Harry Hoogstraal (1951, p. 78) reported that when on Palawan the expedition members went to Mount Balabag where they looked for "a very large rat with a white tail, reported many times by the Palawans." No such animal was found.

During an expedition led by Dr. D. S. Rabor in 1962, a new rat was discovered on Mt. Mantalingajan, west of Mt. Balabag. The four specimens collected were not a sample of the large-bodied, white-tailed animal talked about by the Palawans but were small-bodied and dark-tailed. They were sent to the National Museum of Natural History in Washington, D.C. and for many years remained concealed in a cabinet under the identification of *Rattus* sp. The specimens are like *Rattus* in external and some cranial features but are unlike *Rattus* or any other murid in their dental characters. They represent an undescribed genus and species known only from a mountain on Palawan. Description of this new rat and comparisons between it and *Rattus* follow.

PALAWANOMYS, NEW GENUS

TYPE SPECIES: *Palawanomys furvus*, new species.

INCLUDED SPECIES: The type species only.

KNOWN DISTRIBUTION: The island of Palawan politically administered by the Philippines but structurally and faunistically part of the Sunda Shelf.

ETYMOLOGY: Formed by combining the name of the island with *mys*, from the Greek suffix for mouse.

DIAGNOSIS: The following combination of characters set *Palawanomys* apart from *Rattus* and any other known genus of murid: 1) small body size; 2) dark pelage; 3) tail shorter than or equal to combined lengths of head and body; 4) low and weak interorbital, postorbital, and temporal ridges; 5) short incisive foramina ending just before, at, or barely past, front faces of first upper molars; 6) long palatal shelf behind third upper molars; 7) wide, nearly flat pterygoid fossae, the posterolateral margin of each defined by a smooth mound-like pterygoid bridge; 8) each first upper molar with one lingual root instead of two; 9) little overlap among upper molars and among lower molars; 10) cusp t4 on each first upper molar large and either separate from cusps t5 and t6 (which are broadly joined) or barely connected, even in old rats; 11) ridges on anterolateral face of each cusp t5 of first molars and on anterior faces of cusp t9 on first and second molars; 12) small triangular posterior cingulum on each first upper molar; 13) anterocentral cusp on front of each first lower molar; and 14) posterior lingual cusplet on each second lower molar.

Palawanomys furvus, new species

HOLOTYPE AND TYPE LOCALITY: The holotype, USNM 478113, is an adult female collected by Dr. D. S. Rabor (original number, 1438) on April 15, 1962, from 4500 feet on Mount Mantalingajan, Brooke's Point Municipality, Palawan Province, Palawan Island. The specimen consists of a stuffed skin (fig. 4), cranium, and mandible (fig. 5). All elements are in good condition.

REFERRED SPECIMENS: In addition to the holotype, there are three other specimens, all taken during 1962 from Mount Mantalingajan: USNM 478111, a young adult male from 4350 feet (April 16); USNM 478112, an old adult male from 3600–4350 feet (April 13); and USNM 478114, a young adult female from 4350 feet (April 15).

GEOGRAPHIC DISTRIBUTION: Known only from Mount Mantalingajan, which is the highest peak in the Mantalingajan Range in the southeastern portion of Palawan Island (fig. 3). The peak rises to 6839 feet (see the terrain diagram in King and McKee, 1949).

ETYMOLOGY: *Furvus* is the Latin for dark or dusky (also, gloomy, swarthy, and black).

DIAGNOSIS: Because *furvus* is the only

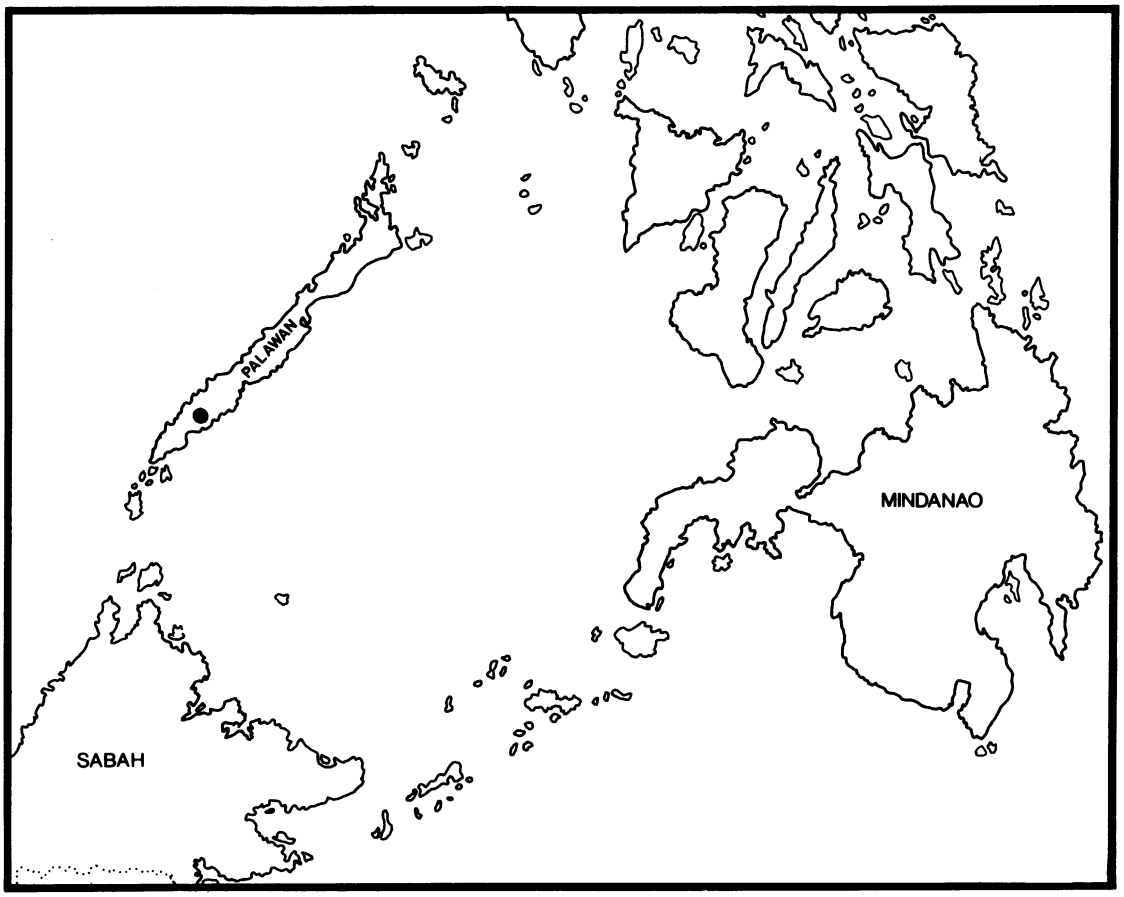

FIG. 3. Northern Borneo (Sabah), Mindanao and the southern backbone of the Philippines, and Palawan Island. Black symbol designates Mount Mantalingajan, the type locality of *Palawanomys furvus*.

known species of *Palawanomys,* the generic and specific diagnoses are the same.

DESCRIPTION: *Palawanomys furvus* is terrestrial, of medium body size, short-tailed, and brownish black. The head and body are covered by long, thick, and glossy fur. Over the back and rump, the overhairs are 10–15 mm. long; the guard hairs are inconspicuous and short, extending past the overfur by 5 mm. Upperparts of head and body are chocolate brown; the hairs are dark brown distally and slate gray basally. Underparts are paler, dark grayish brown. All the specimens have white-tipped hairs on the chest which form conspicuous white patches in two individuals. The demarcation between upper parts and underparts is inconspicuous. The ears are blackish brown and densely covered with short brown hairs.

The tail is either shorter or about as long as combined lengths of head and body (table 1), dark chocolate brown on all surfaces, and covered with short and stiff hairs (three to each scale). There are 10–12 rows of scales per centimeter.

The front and hind feet are brown on their dorsal surfaces, chocolate brown on palmar and plantar surfaces. All claws are unpigmented. Three interdigital and two palmar pads form most of the ventral surface of each front foot. Each hind foot is long and narrow; the plantar surface is naked and adorned by four interdigital and two palmar pads, each conspicuous but not large.

The holotype has four pairs of mammae: a pectoral pair, a postaxillary pair, and two inguinal pairs.

Cranium and dentaries from the holotype of *P. furvus* are shown in figure 5; measurements of the four specimens are listed in table 1. The cranium is small; in shape and proportions of its parts it resembles crania from species of *Rattus* (figs. 6 and 7). From a dorsal view, the rostrum is moderately long and wide. The interorbital region is narrow, the braincase elongate. Dorsolateral margins of the postorbital and interorbital region, as well as the braincase, are outlined by low inconspicuous beading. The parietal is wide and long (anterior-posterior distance); it forms most of the roof over the occipital region. Sides of the braincase between squamosal roots of the zygomatic arches and temporal ridges are not vertical but incline toward the midline of the cranium. The dorsal process of each lacrimal bone is small and oblong in area. The zygomatic arches are long and wider across their squamosal roots than across the maxillary roots.

In side view, the nasals and premaxillary bones barely extend anterior to the front faces of the incisors. Each zygomatic plate is moderately wide; the anterior zygomatic spine is narrow and does not project as far forward relative to the dorsal maxillary zygomatic root as do spines in species of *Rattus,* especially *R. rattus* (figs. 6 and 7). The ventral maxillary roots of the zygoma spring from the cranium well anterior to the molar rows. Squamosal roots of the zygomatic arches are low on sides of the braincase. The auditory bullae are small and globular in outline. The occiput is deep (anterior-to-posterior).

The petrosal and anterior part of each auditory bulla is separated from the squamosal bone by a large postglenoid vacuity (fig. 9). The squamosal dorsal to each bulla is complete, not perforated by a squamoso-mastoid vacuity; that opening is confined to the suture between the squamosal bone and mastoid portion of the petromastoid bone. The lateral surface of each mastoid is squarish in outline; the bone is entire in two specimens and perforated by a small fenestra in two others.

The configurations and relative positions of foramina in each orbit and alisphenoid region are similar to those shapes and positions in species of *Rattus*. In the orbit, the sphenopalatine foramen is large and anterior

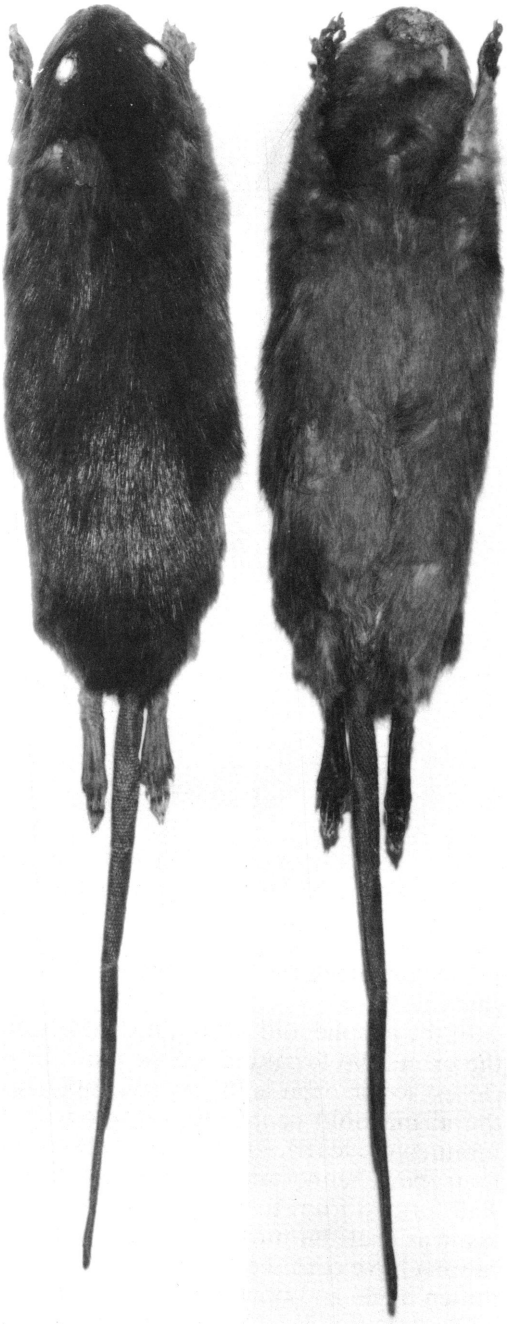

FIG. 4. *Palawanomys furvus*. Dorsal and ventral views of the holotype, USNM 478113. Measurements are listed in table 1.

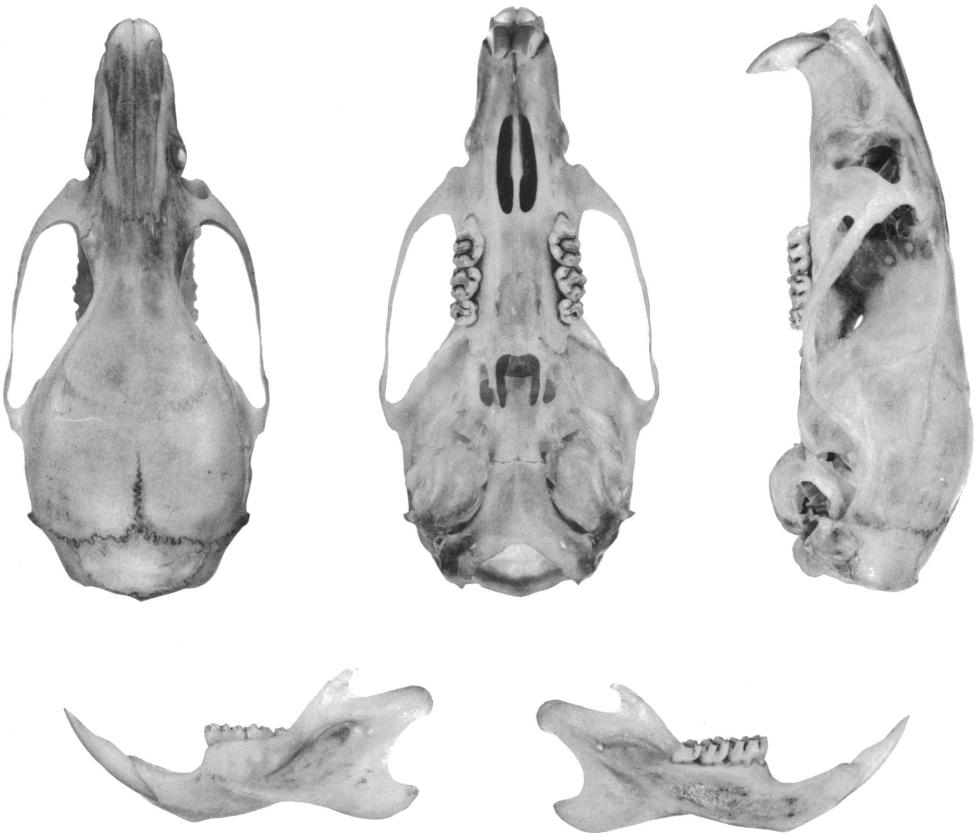

FIG. 5. *Palawanomys furvus.* Views of cranium and left dentary of the holotype, USNM 478113. Approximately ×2. Measurements are listed in table 1.

to the dorsal palatine foramen, which is elongate (fig. 8).

In the alisphenoid region, just posterior to the orbit, two foramina are visible. The one closest to the orbit is the anterior opening of the alisphenoid canal, the other one is the foramen ovale (fig. 9). The alisphenoid canal is an open channel and does not have a lateral wall formed from the alisphenoid bone. The result is that the masticatory-buccinator foramina have coalesced with the accessory foramen ovale and none of these foramina are evident as functional openings. The masseteric and buccinator branches of the maxillary nerve pass directly out of the braincase through the foramen ovale and course up the lateral surface of the alisphenoid in a shallow groove. This configuration is usual in species of *Rattus* and some other genera. The other configuration is one in which a lateral strut of alisphenoid bone forms the outer surface of the alisphenoid canal; the masticatory-buccinator foramina are anterior to the strut and the accessory foramen ovale is posterior to the strut. The two patterns have been contrasted in other reports (Musser, 1981a, 1982b, 1982c).

Short incisive foramina, long and wide bony palate, and globular bullae are distinctive features visible in ventral view. The incisive foramina are wide and short, their posterior margins located either just anterior to the molar rows, even with the front faces of the first molars, or slightly posterior to the molar faces. The bony palate is wide and extends 1.7–2.0 mm. posterior of the molar rows to form a broad shelf. The bridge is thin and relatively smooth; the palatine grooves are

shallow and inconspicuous. Each posterior palatine foramen is opposite the anterior half of each third molar. The auditory bullae are small and globular, each bony eustachian tube is wide and short. The stapedial foramen between the bullar capsule and petrosal is large and conspicuous.

Configurations of the mesopterygoid and pterygoid regions are shown in figures 9 and 11. The mesopterygoid fossa is very wide. The sphenopalatine vacuities in the fossa are wide and so long that their anterior margins are visible in the back of each orbit. Because the vacuities are so spacious the basisphenoid and presphenoid bones seem suspended in air.

Each pterygoid fossa is a large and nearly flat surface that is triangular in outline and perforated by three conspicuous openings (figs. 9 and 11). In the anterior half is a large sphenopterygoid vacuity; in the posterolateral portion is the small posterior opening of the alisphenoid canal, and just in front of the eustachian tube and lateral to the hamular process is an opening to the transverse canal. Instead of being directly beneath the hamular process, the opening to the transverse canal is extended by a short tube past the margins of the basisphenoid, an unusual configuration. The posterolateral corner of the pterygoid plate is swollen and just medial to this mound is a shallow groove extending from the medial lacerate foramen in front of each bulla to the posterior opening of the alisphenoid canal. The internal maxillary artery courses in this groove. The configuration of the posterior third of each pterygoid plate, combined with a large stapedial foramen, reflect an arterial pattern that is common in *Rattus* and many other genera: a large stapedial artery branches off the common carotid to enter the bulla and then emerge through the middle lacerate foramen as the internal maxillary, which courses through the alisphenoid canal into the orbit via the sphenoidal fissure. This pattern is illustrated and more fully described elsewhere (Musser, 1982b, 1982c).

On each dentary, the segment anterior to the molar row is slim, the coronoid process large, and the angular process expansive (fig. 5). The posterior margin between the condyle and angular process is deeply concave. The masseteric ridge is high and prominent. A large bulge containing the posterior end of the incisor forms much of the surface past the molar row. On the lingual surface of each dentary, there is a prominent shelf posterior to the molar row that extends as a shelflike ridge back to the end of the condylar process.

The incisor faces are smooth, not grooved. The uppers have deep orange enamel layers, the enamel on the lowers is pale orange. The uppers emerge from the rostrum at nearly a right angle (orthodont). Each lower incisor ends in a bony capsule protruding from the labial side of the dentary; the posterior margin of the capsule is just beyond the coronoid process (fig. 5).

The molars are large and chunky. Left maxillary molar rows of four specimens are illustrated in figure 12, left mandibular molar rows from two individuals are shown there also. The upper molar rows are not parallel to one another but diverge posteriorly (fig. 5). The teeth in each row are graduated in size: the first is the largest, the second smaller, and the third the smallest of the three. The first molar abuts against the second with only slight overlap; there is a greater overlap between the second and third molars. The lowers overlap each other only slightly. All the molars have low crowns and cusps. Each first upper molar is anchored by four roots: a large anterior and posterior, a single large lingual, and a small labial. Four roots (two small labial and two lingual) are beneath each second upper molar. Three roots anchor each third upper molar: small labial and lingual and a large posterior. Four roots (large anterior and posterior, small labial and lingual) anchor each first lower molar, and three roots (small labial and lingual, large posterior) are beneath each second and third lower molar.

Occlusal patterns formed by cusps on the upper molars of *P. furvus* are distinctive. There are three rows of cusps on each first upper molar. An oblong (in cross-section) cusp t1, large central cusp t2, and smaller but discrete cusp t3 form the front row. In all specimens, there is a conspicuous ridge on the posterolateral margin of cusp t3 (best seen in fig. 12B and C). Nestled between the anterior faces of cusps t2 and t3 is a small mound

TABLE 1

Measurements (in Millimeters) from Samples of Adult *Palawanomys* and *Rattus*[a]

Measurement	*Palawanomys furvus*				*Rattus*		
	478112 ♂	478113[b] ♀	478114 ♀	4781111 ♂	*R. baluensis* Sabah	*R. hoogerwerfi* Sumatra	*R. rattus* Java
Length of head and body	160	160	135	125	168.2 ± 9.0 (30) 150–188	182.7 ± 6.7 (20) 170–196	164.9 ± 10.6 (20) 147–175
Length of tail	145	130	140	126	183.8 ± 13.9 (18) 145–205	236.7 ± 11.7 (20) 210–257	183.5 ± 14.5 (18) 151–201
Length of hind foot	34	34	32	32	32.3 ± 1.5 (30) 29–35	37.4 ± .9 (20) 36–39	35.1 ± 1.9 (20) 32–38
Length of ear	18	20	19	17	21.2 ± 1.1 (29) 19–23	22.5 ± 1.2 (20) 20–25	20.6 ± .1 (20) 18–22
Greatest length of skull	39.5	38.0	36.7	·36.0	40.2 ± 1.9 (28) 36.0–44.1	42.9 ± .8 (16) 41.6–44.2	40.2 ± 1.7 (20) 36.6–44.2
Zygomatic breadth	17.9	17.7	17.4	17.2	18.9 ± .8 (27) 17.0–20.6	20.1 ± .6 (18) 19.2–21.2	18.6 ± 1.0 (20) 17.2–21.3
Interorbital breadth	5.6	5.5	5.6	5.6	6.1 ± .3 (29) 5.2–6.7	6.0 ± .2 (20) 5.7–6.4	5.8 ± .3 (20) 5.2–6.5
Length of nasals	14.0	13.3	13.1	12.5	14.2 ± 1.1 (29) 11.8–16.6	15.7 ± .6 (17) 14.7–16.9	13.9 ± .9 (20) 12.3–15.7
Length of rostrum	11.5	10.8	10.7	10.3	12.5 ± .8 (29) 10.7–14.3	13.8 ± .5 (17) 12.9–14.7	12.4 ± .7 (20) 11.1–13.9
Breadth of rostrum	7.0	6.8	6.7	6.3	7.3 ± .5 (29) 6.2–8.2	7.1 ± .3 (18) 6.6–7.7	6.9 ± .5 (20) 5.9–7.7
Breadth of braincase	15.3	15.0	14.8	15.4	16.5 ± .5 (29) 15.1–17.1	17.5 ± .5 (18) 16.4–18.2	16.0 ± .6 (20) 15.0–17.1
Height of braincase	10.9	10.7	10.5	10.4	11.7 ± .5 (29) 10.2–12.5	12.4 ± .4 (19) 11.4–12.9	11.4 ± .6 (19) 10.5–12.8
Breadth of zygomatic plate	3.2	3.1	3.1	2.9	3.9 ± .3 (29) 3.4–5.1	3.4 ± .3 (20) 3.0–4.0	4.0 ± .3 (20) 3.5–4.5
Depth of zygomatic notch	1.3	1.3	1.2	1.3	1.9 ± .2 (29) 1.4–2.3	1.6 ± .3 (20) 1.1–2.3	2.3 ± .4 (20) 1.7–3.0
Breadth across incisor tips	2.2	2.1	2.1	1.9	2.4 ± .2 (26) 2.0–2.7	2.3 ± .1 (19) 2.2–2.5	2.3 ± .2 (20) 1.9–2.6
Length of diastema	10.3	9.8	9.4	8.9	10.6 ± .7 (29) 9.1–11.9	11.5 ± .5 (20) 10.6–12.4	10.5 ± .8 (20) 9.0–12.0

TABLE 1—(*Continued*)

Measurement	*Palawanomys furvus* 478112 ♂	*Palawanomys furvus* 478113[b] ♀	*Palawanomys furvus* 478114 ♀	*Palawanomys furvus* 4781111 ♂	*Rattus* *R. baluensis* Sabah	*Rattus* *R. hoogerwerfi* Sumatra	*Rattus* *R. rattus* Java
Palatal length	21.5	20.5	19.9	19.0	22.1 ± 1.1 (29) 19.4–24.4	22.6 ± .6 (20) 21.4–24.1	21.5 ± 1.4 (20) 19.4–23.7
Postpalatal length	12.1	11.8	11.3	10.8	12.8 ± .8 (29) 11.1–14.4	14.4 ± .5 (20) 13.7–15.5	13.7 ± .8 (20) 12.0–15.2
Length of palatal bridge	9.2	8.9	8.5	8.3	8.2 ± .4 (29) 7.5–9.1	8.3 ± .4 (20) 7.6–9.1	7.8 ± .6 (20) 6.5–8.5
Palatal bridge past M^3	2.0	1.8	1.8	1.7	1.6 ± .2 (29) 1.0–1.9	0.6 ± .2 (20) 0.4–1.1	1.6 ± .4 (20) 0.9–2.4
Breadth of palatal bridge at M^1	4.1	3.9	4.1	4.0	4.0 ± .3 (29) 3.5–4.6	4.4 ± .2 (20) 4.0–4.9	3.5 ± .4 (20) 2.9–3.8
Breadth of palatal bridge at M^3	5.0	4.8	4.7	4.8	4.8 ± .3 (29) 4.1–5.3	5.3 ± .4 (20) 4.7–5.9	4.4 ± .3 (20) 3.9–4.7
Breadth of mesopterygoid fossa	3.1	2.8	2.7	2.8	2.9 ± .2 (27) 2.7–3.2	3.1 ± .2 (17) 2.7–3.5	2.6 ± .2 (20) 2.2–3.1
Length of incisive foramina	6.4	6.2	6.1	5.8	7.8 ± .5 (29) 6.2–8.5	8.5 ± .4 (20) 7.9–9.5	7.6 ± .4 (20) 7.1–8.4
Breadth of incisive foramina	3.0	2.6	2.6	2.5	2.8 ± .2 (29) 2.4–3.2	3.0 ± .2 (20) 2.7–3.4	2.5 ± .2 (20) 2.2–2.9
Incisive foramina past M^1	—	0.0	0.1	0.1	.7 ± .2 (29) 0.2–1.1	all past	.8 ± .3 (20) 0.1–1.4
Incisive foramina before M^1	0.1	—	—	—	—	—	—
Length of bulla	6.1	5.9	5.8	5.8	6.6 ± .3 (29) 6.1–7.1	6.6 ± .2 (20) 6.3–6.8	6.5 ± .4 (20) 6.0–7.4
Height of bulla	5.4	5.5	5.6	5.2	5.6 ± .3 (29) 4.8–6.1	4.7 ± .3 (20) 4.3–5.3	5.7 ± .4 (20) 5.2–6.4
Alveolar length of M^{1-3}	6.9	7.0	6.8	6.7	7.3 ± .3 (29) 6.4–7.7	8.0 ± .3 (20) 7.5–8.5	6.8 ± .4 (20) 5.9–7.3
Breadth of M^1	1.9	2.0	1.9	1.9	2.1 ± .1 (28) 1.8–2.2	2.2 ± .1 (20) 2.0–2.3	1.8 ± .1 (15) 1.6–2.0

[a] The mean plus or minus one standard deviation, number of specimens in parentheses, and observed range are listed for each measurement in the samples of *Rattus*.

[b] Holotype.

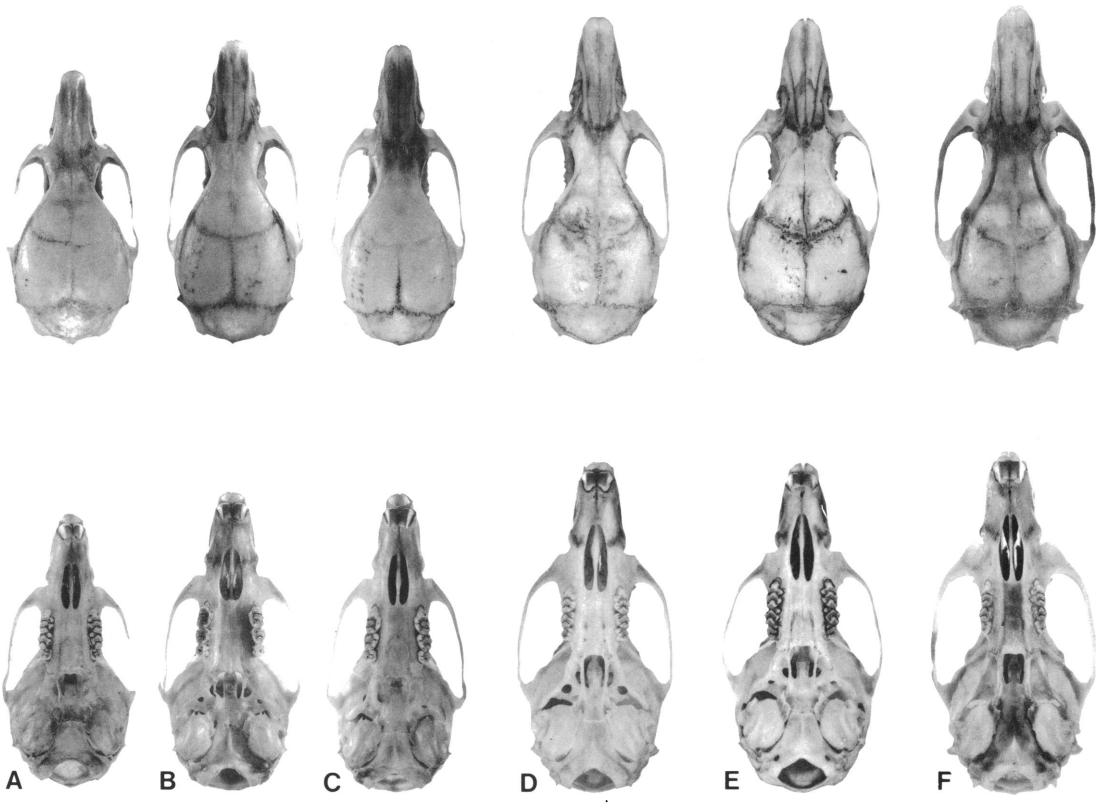

FIG. 6. Views of crania from adult *Palawanomys* (A–C) and *Rattus* (D–F). A–C, *P. furvus* (USNM 478111, 478112, and 478113, respectively). D, *R. baluensis* (USNM 292693), Sabah. E, *R. hoogerwerfi* (USNM 271028), northern Sumatra. F, *R. rattus diardii* (AMNH 250104), Java. Natural size.

or cusplet (cusp t2bis) on each specimen (fig. 12B and C).

The second row of cusps on each first upper molar is unique in its occlusal configuration. The row consists of two parts. One is a large cusp t4 that is either completely separate from the other cusps (fig. 12C) or barely joined to cusp t5. At an early stage of wear, a narrow part of the medial enamel surface of cusp t4 coalesces with a small portion of the lateral enamel wall of cusp t5 (fig. 12A); at later stages of wear, the cusps are united by enamel and a thin portion of dentine (fig. 12B and D). But even in teeth that are heavily worn, cusp t4 is but weakly joined to cusp t5. The other part of the row consists of cusps t5 and t6 broadly joined into one large oblong structure. On every specimen, there is a ridge at the posterolingual margin of cusp t4, a ridge that is either inconspicuous (fig. 12A) or large and prominent (fig. 12B and C) and shaped like a cusplet (fig. 12B and C). In worn teeth, this ridge coalesces with the anterolingual portion of cusp t8 to form an enamel and dentine bridge, the configuration illustrated in figure 12D.

The third row of cusps on each first upper molar is formed of a large cusp t8 broadly coalesced to a large cusp t9. No cusp t7 is present in any of the specimens.

No accessory labial or lingual cusplets occur on any first upper molars but there are ridges, which probably serve to increase surface area as the teeth wear. There is a ridge on the anterolabial face of each cusp t5 (fig. 12C, for example) and a more prominent ridge on the anterior face of each cusp t9 (best seen in fig. 12B and C). In worn teeth, the ridge

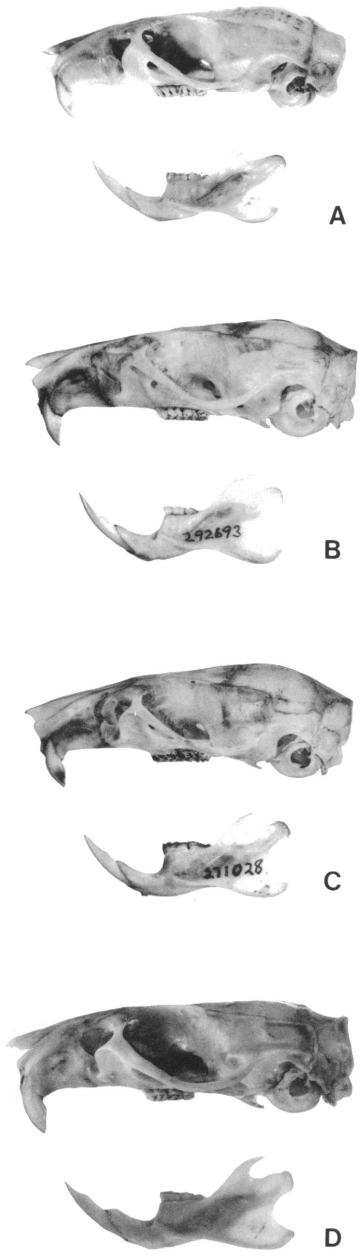

FIG. 7. Views of crania and dentaries from same specimens shown in figure 6. A, *Palawanomys furvus* (USNM 478113); B, *Rattus baluensis*; C, *R. hoogerwerfi*; D, *R. rattus diardii*. Natural size.

on cusp t9 merges with the posterior margin of cusp t6, to form the pattern shown in figure 12D. There is a ridgelike posterior cingulum at the back of each first molar. The ridge is thicker near its base and is more evident in worn teeth (fig. 12D).

Each second upper molar is longer than it is wide. Cusp t1 is very large and forms the anterolingual portion of the tooth. Cusp t3 is smaller than cusp t1 but still conspicuous, oblong in cross-section, and the structure forming the anterolabial wear surface of the tooth. The first complete row of cusps is formed of three broadly joined cusps, t4, t5, and t6. The posterior half of the occlusal surface is formed by a very large and roundish cusp t8 broadly merged with a small but elongate (in cross-section) cusp t9. There is a high and thick ridge along the anterior face of cusp t9, a ridge similar in position but thicker than that on cusp t9 of each first molar (fig. 12A–C). In worn teeth, the occlusal pattern formed by the second and third rows of cusps, which have merged at their lingual and labial borders, is similar to that pattern in the first molar (fig. 12D). Neither a cusp t7 nor a posterior cingulum occurs on second upper molars in any of the specimens.

The third upper molar is the smallest of the three in the row. Its anterolingual margin is formed by a large cusp t1. A small, low but still conspicuous cusp t3 forms the anterolabial edge. The rest of the occlusal surface consists of a thick C-shaped row of cusps (t4, t5, and t6) broadly merged. The posterior margins of this crescent abut against a thick oblong lamina that represents the broad union of cusps t8 and t9 (fig. 12). No ridges, cusp t7, or posterior cingulum exists on any third molar in the sample.

The lower molars are large (fig. 12E and F). Each first molar is rectangular in occlusal outline and the chewing surface is formed mostly by three large laminae. The front one consists of a large anterolingual cusp and a smaller anterolabial cusp. There is a small anterocentral cusp on the front face of the molar in every specimen (best seen in fig. 12E); it has merged with the anterolingual cusp in worn teeth. Posterior to the first row of cusps are two arcuate rows of cusps and at the back of the tooth is a wide posterior cingulum. A conspicuous anterior cusplet and large posterior cusplet occur on the labial margin of the molar. The anterior cusplet is coalesced with the anterolabial cusp in most of the specimens and the posterior cusplet

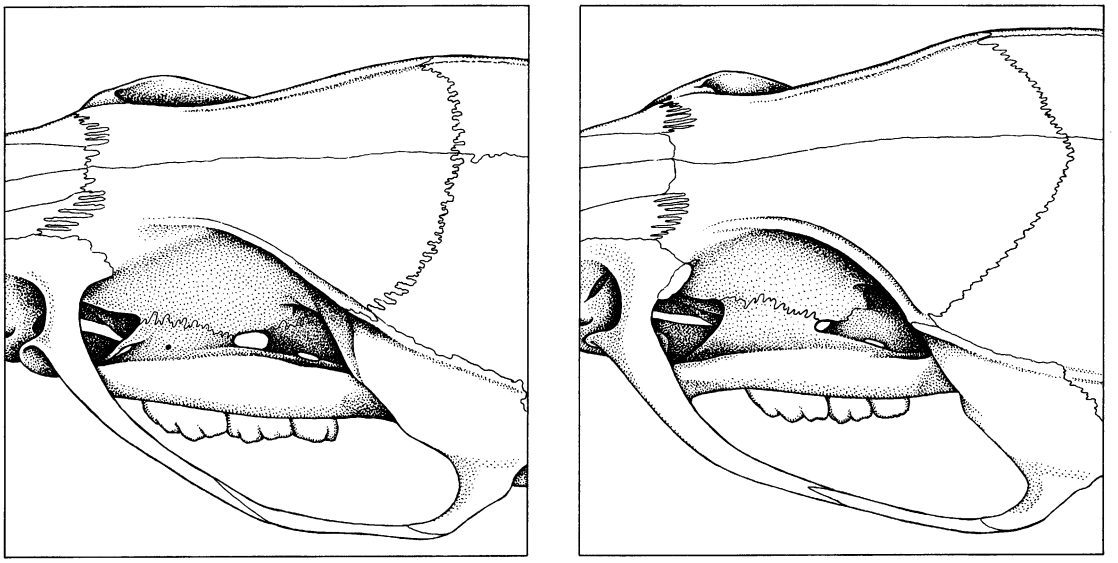

FIG. 8. Orbital regions in *Palawanomys furvus* (left; USNM 478113) and *Rattus rattus diardii* (right; AMNH 229983). In both species the large sphenopalatine foramen (the oblong opening in the orbit above either the second molar or back part of first molar) is well anterior to the smaller and slitlike dorsal palatine foramen.

forms the anterolabial margin of the third lamina.

Each second lower molar is about as long as it is broad. Its wear surface is formed by two arcuate lamina, a broad posterior cingulum, a large anterolabial cusp, and a prominent posterior labial cusplet. Nestled on the lingual cingulum between the two laminae is a cusplet that is slightly smaller than the posterior labial cusplet on the opposite side of the tooth, a cusplet found in each of the four specimens on both right and left molar rows; there is no counterpart of this posterior lingual cusplet on any of the first lower molars.

Each third lower molar is smaller than the second. The occlusal surface consists of two large laminae, as shown in figure 12E and F. The anterolabial margin of the front lamina is formed by a prominent anterolabial cusp, a structure found in each of the specimens. A large posterior labial cusplet forms the labial side of the second lamina. No posterior cingulum is present on any third molar in the four specimens. There is no lingual cusplet between the two laminae on any of the third molars.

The enamel of all molars, especially on the upper, is not smooth as it is in many murids. Instead, the enamel surfaces are rough, imparting a crinkled or pebbly texture to sides of the cusps, best seen in figure 12A and E.

PALAWANOMYS AND *RATTUS* COMPARED

Early in our study, we compared the Palawan rats with specimens of African, Indian, and Indo-Australian murid genera. In characteristics of skins, crania, and mandibles, the four specimens were most like samples of *Rattus,* especially in those traits associated with crania and dentaries. We then contrasted the sample with specimens of *Rattus,* three species in particular: *R. rattus diardii, R. baluensis,* and *R. hoogerwerfi.* We used samples of *R. r. diardii* to examine differences between the Palawan rats and what we regard to be typical *Rattus,* typical in the sense that it is closely related to the type species of the genus. *Rattus rattus diardii* also occurs on the Sunda Shelf, although it has probably been introduced to that region. *Rattus baluensis* and *R. hoogerwerfi* are among the few species of *Rattus* native to the Sunda Shelf (a point we discuss farther on in our report), both have been found only in mountain forests on Bor-

neo and Sumatra, and both have skulls that resemble those of the Palawan animals. We employed samples of *R. baluensis* and *R. hoogerwerfi* to test if they were Sundaic mountain isolates related to the Palawan population, which is also an insular montane species on the Sunda Shelf. Results of our comparisons follow.

Rattus rattus diardii and *Palawanomys*

Rattus rattus diardii is widespread on the Sunda Shelf and on islands off the Shelf. It is common in habitats made and maintained by humans. The name *diardii* has been used by some biologists to designate a species of Asian *Rattus* closely related to the Indian *R. rattus,* by others to indicate a subspecies of *R. rattus* distinguished by morphology, karyotype, and serology. The geographic distribution of *R. r. diardii,* the scientific names proposed over the years which apply to it, and views on either specific or subspecific alliance with Indian *R. rattus* are presented by Musser and Califia (1982). *Rattus rattus diardii* is important to us because characteristics of its skins, crania, mandibles, teeth, and karyotype represent *Rattus* in general. As in many species of rodents, the features associated with *R. r. diardii* are a combination of primitive ones (traits 1–12 listed below), many that are derived (traits 13–31), and a few in which polarity has not yet been determined (traits 32–37), at least by us. We outline these characteristics below.

1. A tail that is moderately longer than combined lengths of head and body.

2. Moderately long hind feet, each with six plantar pads.

3. A claw, not a nail, on each hallux.

4. Dorsal to each bulla, the squamosal bone is complete, not divided by a squamoso-mastoid foramen; the latter is confined to the suture between the mastoid and squamosal (fig. 10A).

5. There is a channel in the pterygoid plate extending from the posterior margin of the plate to the posterior opening of the alisphenoid canal. This configuration, along with a large stapedial foramen, indicates a basicranial arterial pattern in which a large stapedial artery branches off the common carotid, enters the bulla, and emerges through the middle lacerate foramen as the internal maxillary artery to pass along the pterygoid channel into the posterior opening of the alisphenoid canal. From the canal, the artery passes through the anterior opening of the alisphenoid canal into the sphenoidal fissure and then the orbit. After giving off the stapedial artery, the internal carotid passes into the cranial cavity through the carotid canal. The pattern is diagrammed in figure 57.

6. The ventral surface of the palatal bridge is mostly smooth, scored by shallow palatine grooves but not perforated by small holes (as in *Apomys*; Musser, 1982b), and only slightly pitted (fig. 10b).

7. The upper and lower incisors have orange, ungrooved enamel. The upper incisors are either orthodont or opisthodont in position, not proodont (fig. 7).

8. No cusp t7 occurs on any upper molar (fig. 13).

9. Cusps t1bis and t2bis are usually absent from each first upper molar (fig. 13).

10. There is no accessory cusp behind cusp t6 on each first and second upper molar and no crests behind cusps t1 and t3 on any molar (fig. 13).

11. Each second and third lower molar has an anterolabial cusp (fig. 13).

12. On each first lower molar, the anterolingual cusp is larger than the anterolabial; both cusps are large and form a lamina slightly narrower than the laminae posterior to it (fig. 13).

13. Prominent ridges outline the interorbital and postorbital regions, as well as the dorsolateral sides of the braincase (fig. 6).

14. The interparietal bone is wide and deep (anterior-to-posterior) and forms most of the roof over the occipital region (fig. 6).

15. In each orbit, the sphenopalatine foramen is well anterior to the dorsal palatine foramen (fig. 8). On the ventral surface of the palatal bridge, a posterior palatine foramen is opposite the anterior half of each third upper molar (fig. 10B).

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

17. Between the zygomatic roots and temporal ridges, sides of the braincase are vertical or nearly so.

18. Each postglenoid vacuity is spacious (fig. 10A).

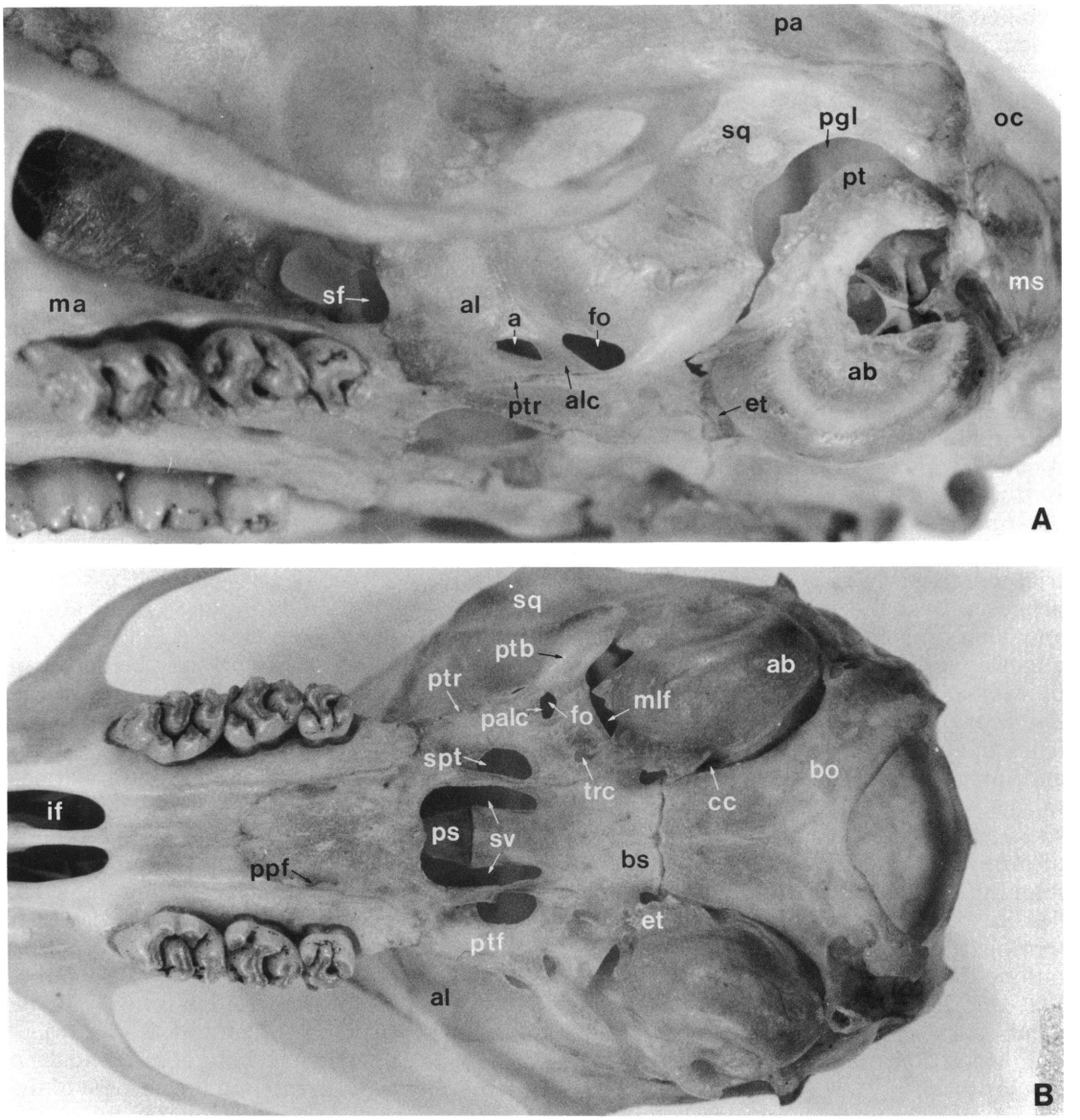

FIG. 9. Lateral (A) and ventral (B) views of the cranium in *Palawanomys furvus* (USNM 478113). *Abbreviations:* **a**, anterior opening of the alisphenoid canal, where it empties into the sphenoidal fissure; **ab**, auditory bulla; **al**, alisphenoid bone; **alc**, alisphenoid canal, which is an open channel; **bo**, basioccipital bone; **bs**, basisphenoid bone; **cc**, carotid canal; **et**, bony eustachian tube; **fo**, foramen ovale; **if**, incisive foramina; **ma**, maxillary bone; **ms**, mastoid portion of the petromastoid; **mlf**, middle lacerate foramen; **oc**, occiput; **pa**, parietal bone; **palc**, posterior opening of the alisphenoid canal; **pgl**, postglenoid vacuity; **ppf**, posterior palatine foramen; **ps**, presphenoid bone; **pt**, periotic portion of the petrosal; **ptb**, pterygoid bridge; **ptf**, pterygoid fossa; **ptr**, pterygoid ridge; **sf**, sphenoidal fissure; **spt**, sphenopterygoid vacuity; **sq**, squamosal bone; **sv**, sphenopalatine vacuity; **trc**, transverse canal.

19. No strut of alisphenoid bone covers the lateral portion of the alisphenoid canal; that canal is really an open channel. Without the strut, the masticatory-buccinator foramina

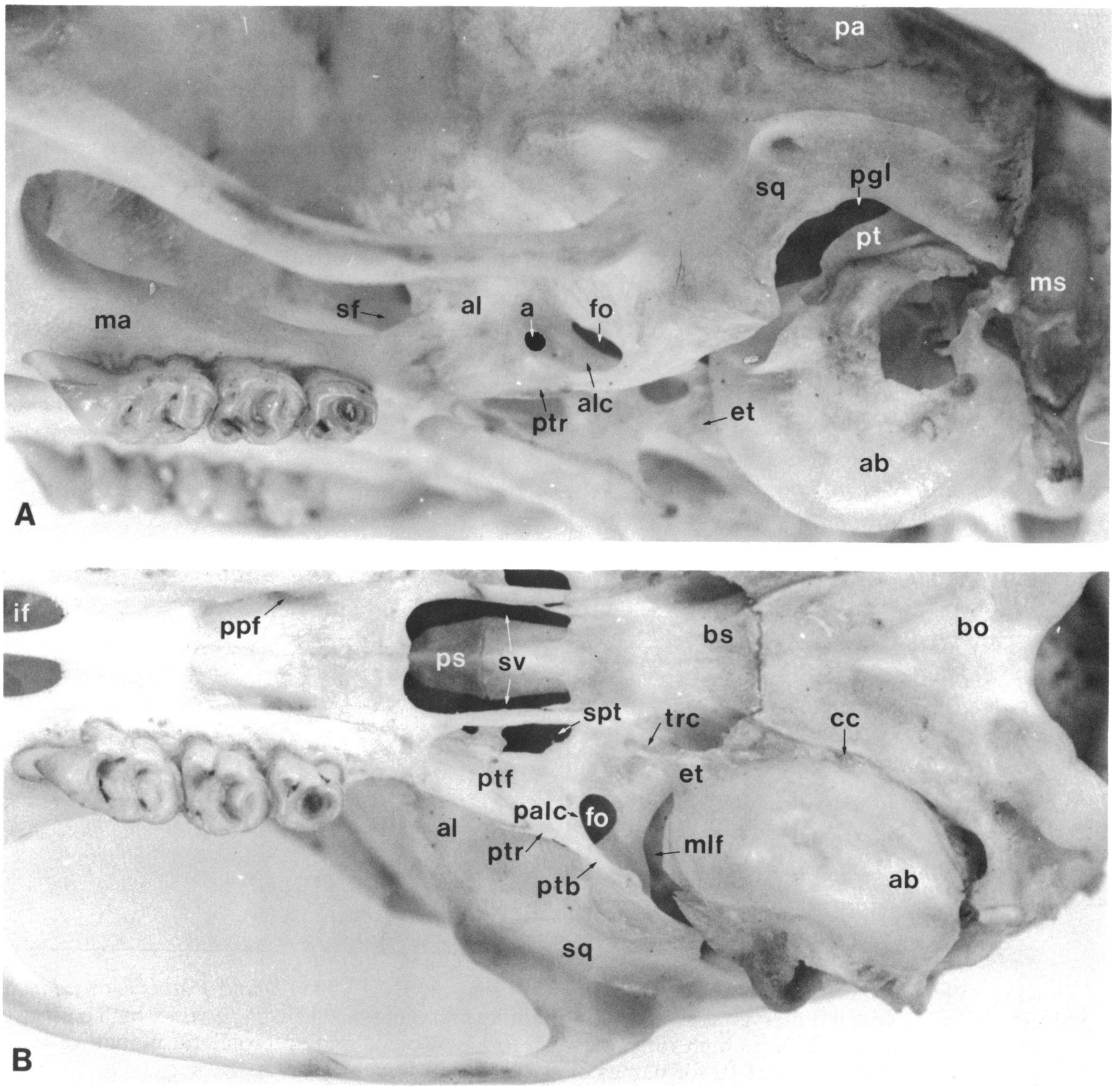

FIG. 10. Lateral (A) and ventral (B) views of cranium in *Rattus rattus diardii* (AMNH 229983). Abbreviations as for figure 9.

are coalesced with the foramen ovale accessorius and all are functionally absent (fig. 10A).

20. The incisive foramina are long, extending well posterior to the anterior faces of the first upper molars (figs. 6 and 10B).

21. The palatal bridge is wide and extends past the molar rows to form a long and wide shelf (figs. 6 and 10B).

22. The mesopterygoid fossa is narrow relative to width of the palatal bridge. Walls of the fossa are perforated by spacious sphenopalatine vacuities, so large that the basisphenoid and presphenoid bones seem suspended in air; the vacuities extend far enough anteriorly that they can be seen, from a side view, in the back part of each orbit (fig. 10B).

23. Each pterygoid fossa is wide and slants toward the midline, forming a deep and sculptured depression. Each fossa is breached

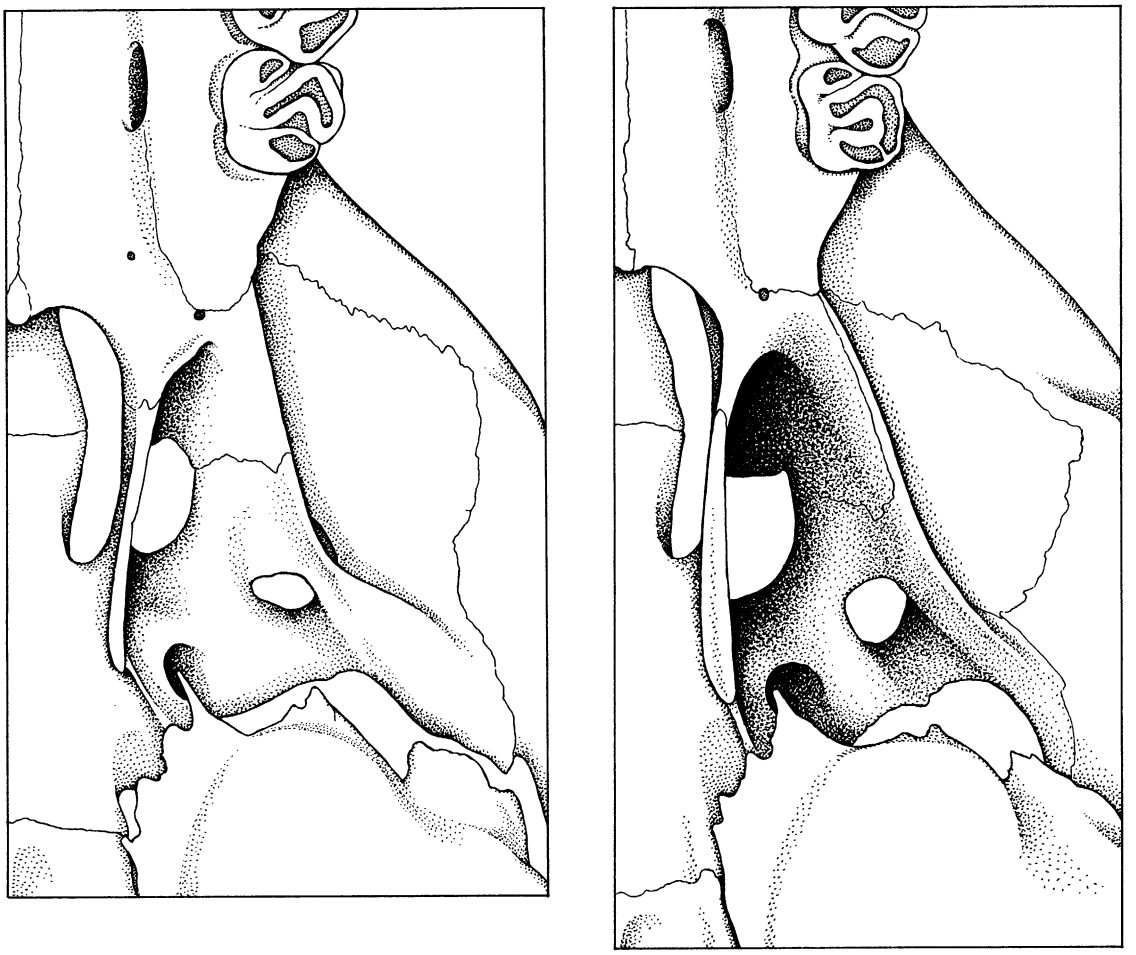

FIG. 11. View of Pterygoid plates in *Palawanomys furvus* (USNM 478113) and *Rattus rattus diardii* (AMNH 229983). Note flat pterygoid fossa and moundlike pterygoid bridge in *P. furvus,* which contrasts with excavated fossa and definite high ridge between foramen ovale and anterolateral margin of bulla in *R. r. diardii.* See figures 9 and 10 for names of structures and openings.

by a large sphenopterygoid vacuity. The pterygoid bridge is a high and narrow ridge, not a low mound (fig. 11).

24. Each auditory bulla is round and large relative to size of the cranium; each eustachian tube is wide and short (fig. 10).

25. The upper and lower molars are brachydont. In each upper molar row, the first molar broadly overlaps the second and the second broadly overlaps the third. In each lower molar row, there is broad overlap of the third molar on the second, and the second on the first (fig. 13). The molars are small relative to area of the palatal bridge and mandible (fig. 6).

26. Each first upper molar is anchored by five roots, each second upper by four roots, and each third upper molar by three. Each first lower molar has four roots, each second and third lower is anchored by three roots.

27. The main cusps are round or oblong (in cross-section) and are strongly connected so that most merge in each row to form a slightly cuspidate lamina. The rows of cusps on each upper and lower molar are close together. On each first lower molar, the first row of cusps abuts tightly against the one behind without a connecting medial crest. The posterior cingulum on each first and second lower molar is nestled against the lamina an-

terior to it; a posterior cingulum is absent from each third lower molar (fig. 13).

28. A posterior cingulum is usually absent from the back of each upper molar; if present in some specimens it is indicated by a slight triangular bulge.

29. On each second and third upper molar, cusp t3 is either absent or very small (fig. 13).

30. An anterocentral cusp is absent from the front of each first lower molar; if a specimen has it, the cusp is tiny and mostly merged with the anterolingual cusp (fig. 13).

31. A diploid number of 42 chromosomes of which there are seven pairs of small metacentric autosomes, few or no submetacentric and subtelocentrics, and the rest telocentric (Yong, 1969a; Yosida, Tsuchiya, and Moriwaki, 1971).

32. The pelage is coarse; guard hairs are conspicuously longer than overhairs; upperparts are brownish, underparts buffy gray.

33. There are five pairs of mammae; one pectoral pair, one postaxillary, one abdominal, and two inguinal.

34. Each zygomatic plate has a moderately wide anterior spine, thus the zygomatic plate is deep (fig. 7).

35. The hamular processes of the pterygoids are large.

36. In each dentary, the coronoid process is large relative to body of the ramus (fig. 7). A prominent ridge extends from behind the molar row along the inner surface of the condyloid process to the condyle (Musser, 1981a, fig. 22).

37. An anterior labial cusplet is usually absent from each first lower molar. Posterior labial cusplets occur on the first and second lower molars (fig. 13).

In characteristics of skins, the four rats from Palawan do not closely resemble *R. rattus diardii*. Small body size, short tail relative to length of head and body, and dark silky pelage separate the Palawan animals from *R. r. diardii* and any other species of *Rattus*.

Palawanomys is basically *Rattus*-like in conformation of cranium and mandible but it differs from *Rattus* by a combination of primitive and derived traits. The following features possessed by *Palawanomys* that distinguish it from *R. r. diardii* and *Rattus* in general are primitive: weak and inconspicuous ridges outlining dorsolateral margins of the interorbital and postorbital regions as well as the braincase; short incisive foramina; each first upper molar with a single lingual root; nearly flat pterygoid fossae and a moundlike pterygoid bridge; little overlap between first and second upper molars in each row; cusp t4 of each first upper molar either separate from the broadly merged cusps t5 and t6 or barely connected, even in old animals; small posterior cingulum on each first upper molar; and an anterocentral cusp at front of each first lower molar. In all these features, *Rattus* is derived relative to *Palawanomys*. The separate cusp t4 is especially distinctive for *Palawanomys*. Cusp t4 is separate from cusp t5 in a few young juvenile *Rattus* and in juveniles of many other murid genera, but fuses with cusp t5 at an early wear stage to form a solid lamina of three broadly coalesced cusps (fig. 13).

Derived features distinguishing *Palawanomys* from *Rattus* are: a palatal bridge forming a wide and deep shelf posterior to the molar rows; prominent enamel ridges on the anterolateral face of each cusp t5 of the first molars and on the anterior faces of cusp t9 on the first and second molars; and a posterior lingual cusplet on each second lower molar.

Rattus baluensis, Rattus hoogerwerfi, and *Palawanomys*

Medium body-size (table 1), long and soft fur, rich tawny brown upperparts, buffy gray underparts, brown feet, and a long (relative to length of head and body) brown tail are the external features of *Rattus baluensis,* which was first described by Thomas in 1894. The species is common on slopes of Mount Kinabalu in Sabah (Medway, 1977) where it occurs from 7000 to 12,500 feet. The holotype (BM 95.10.4.23) was collected by John Whitehead on February 4, 1888. Our knowledge of the species comes from study of the holotype and following specimens: BM 92.9.6.28 and 0.10.8.3; USNM 292694, 292696, 292698, and 292699, 292704–292710, and 301027–301028; FMNH 49267, and 108907–108927.

Rattus baluensis also occurs on Sumatra where it is known by three examples. One is from 7300 feet on Korinchi Peak, a skin and

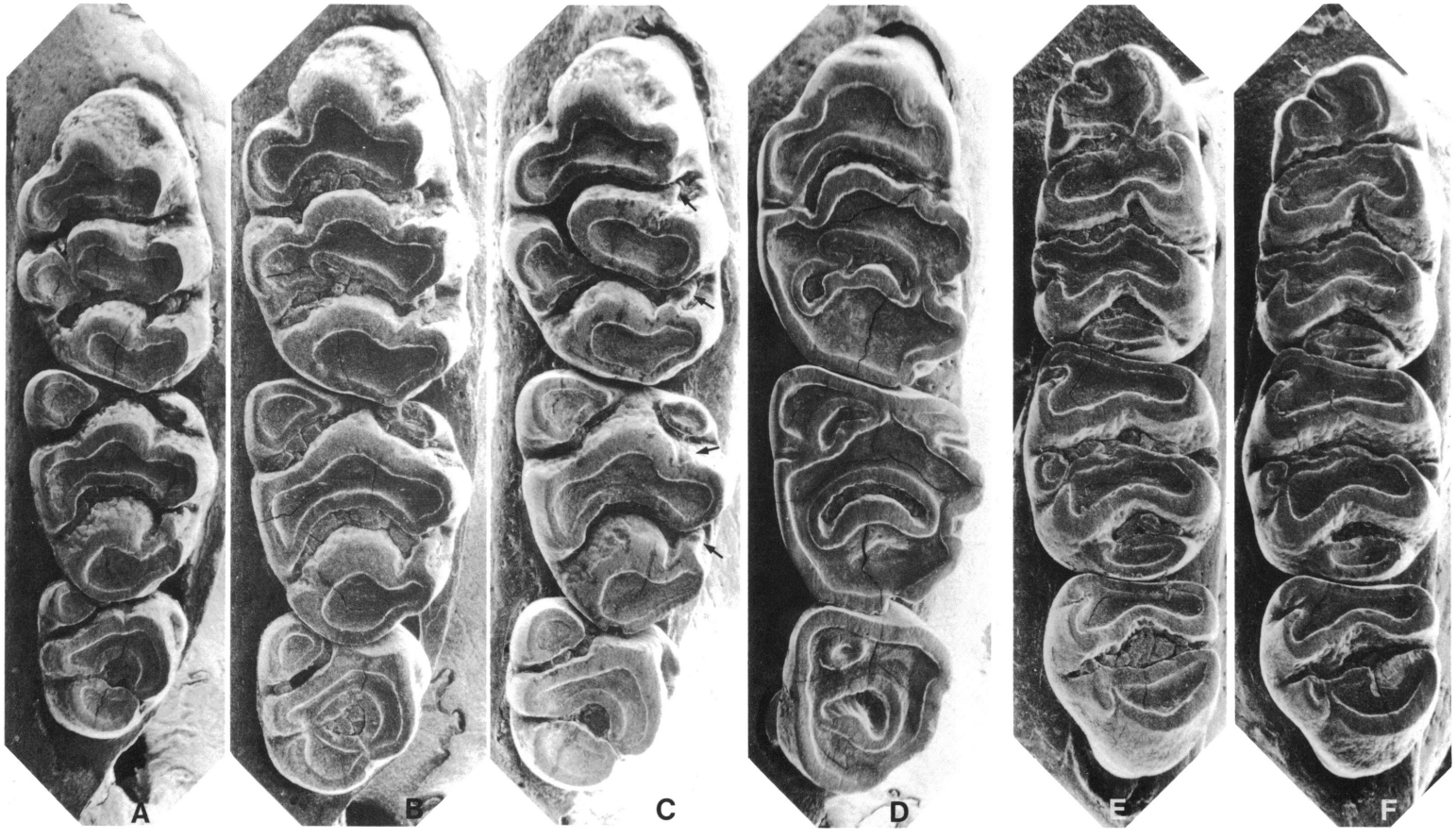

FIG. 12. Occlusal views of left upper (A–D) and lower (E–F) molar rows in *Palawanomys furvus*. A, USNM 478111 (CLM^{1-3}, 6.5 mm.). B, USNM 478114 (CLM^{1-3}, 6.4 mm.). C, USNM 478113 (CLM^{1-3}, 6.7 mm.). D, USNM 478112 (CLM^{1-3}, 6.7 mm.). E, USNM 478114 (CLM_{1-3}, 6.5 mm.). F, USNM 478113 (CLM_{1-3}, 6.6 mm.). Arrows in C point to anterolabial ridges discussed in text, in E and F to anterocentral cusp.

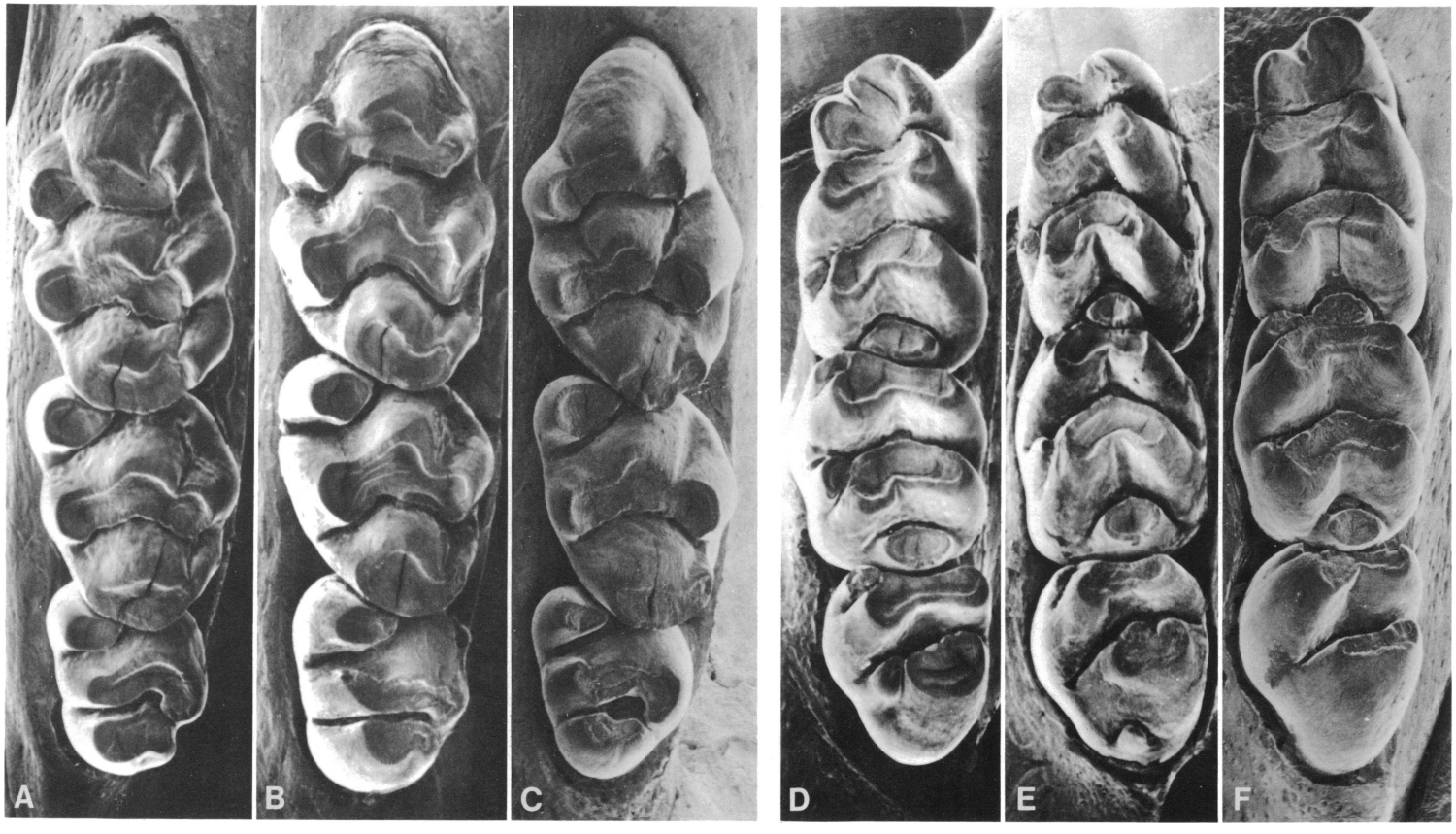

FIG. 13. Occlusal views of left upper (A–C) and lower (D–F) molar rows in three species of *Rattus*. A and D, *R. baluensis,* USNM 292700 (CLM^{1-3}, 6.6 mm.; CLM_{1-3}, 6.6 mm.). B and E, *R. hoogerwerfi,* USNM 271030 (CLM^{1-3}, 7.8 mm.; CLM_{1-3}, 7.9 mm.). C and F, *R. rattus flavipectus,* AMNH 84667 (CLM^{1-3}, 6.6 mm.; CLM_{1-3}, 6.1 mm.).

skull which was designated the holotype (BM 19.11.5.81) of *Epimys korinchi,* named and described by Robinson and Kloss (1916); two others were collected by E. Jacobsen from Gunung Talaman Plateau, Ophir District, 2800 meters (Robinson and Kloss, 1919b, p. 315). Miller (1942, p. 147) identified a specimen (ANSP 20337) from the Aceh area as "*Rattus korinchi*" but that individual is an example of *Niviventer rapit fraternus* (Musser's identification). Robinson and Kloss (1916, p. 275) described *korinchi* as "Like *E. baluensis* (Thomas) with long, soft and spineless fur, beset on the upper surface with numerous longer piles; but with longer tail and paler underparts; nasals broader, but bullae much smaller; teeth considerably larger." The Sumatran form is now regarded as a subspecies of *R. baluensis* (Robinson and Kloss, 1918, p. 53; Chasen, 1940, p. 159).

Rattus hoogerwerfi is known only from the Aceh region of northern Sumatra where specimens have been taken at altitudes from 2600 to 9300 feet. We studied the following examples: ANSP 20296–203309 and 203311–203320; MZB 3148–3150, 4854 (holotype), and 4855–4857; RMNH 5130–5133; USNM 271028–271031. Chasen, who named and described the species, diagnosed it (1939, p. 207) as "A brightly coloured, brown rat of medium size, with long soft pelage. The tail is longer than the head and body, and white for the distal half. The nasals and the interorbital region of the skull are unusually flattened." Miller (1942) examined a much larger series than was available to Chasen and described variation in size, pelage and tail coloration, crania, and teeth.

The relationships of *Rattus hoogerwerfi* are obscure. Chasen remarked that

> This very distinct species of rat seems to require no close comparison with any other Malaysian form. In its parti-coloured tail and in the trough-like frontal region of the skull it bears some resemblance to *Rattus* (*Lenothrix*) *canus,* but this latter form is a grey rat with short, harsh pelage, and the skull seen from below presents many important points of difference when compared with that of *hoogerwerfi* (shorter and differently shaped palatal foramina, larger teeth, narrower palate, smaller and differently shaped bullae; rounded and encroaching interpterygoid space etc.). Perhaps the nearest relative of *R. hoogerwerfi* is *Rattus baluensis korinchi.* If consideration of the tail is excluded, the two forms have some superficial resemblance to each other, and the peculiar characters of the skull of *hoogerwerfi* are to some extent adumbrated in adults of *korinchi.*

In table 1, we contrast measurements from samples of *Palawanomys furvus,* Bornean *Rattus baluensis,* and *R. hoogerwerfi.* Crania and mandibles are compared in figures 6 and 7, upper and lower molar rows in figures 12 and 13. The four specimens of *Palawanomys* are smaller in body size than examples of either *R. baluensis* or *R. hoogerwerfi,* have shorter tails relative to length of head and body, and much darker pelage—chocolate brown as opposed to dark tawny brown. No specimen of *Palawanomys* has a bicolored tail, a diagnostic feature of *R. hoogerwerfi.* Mammae number and position differ among the three species. *Rattus hoogerwerfi* has eight mammae, one postaxillary pair and three inguinal pairs; *R. baluensis* has four pairs in the same places and an additional pectoral pair; *Palawanomys furvus* has two inguinal pairs only, a postaxillary pair, and a pectoral pair. There is nothing in external features suggesting any close tie between the two species of *Rattus* and *Palawanomys.*

Both *Rattus baluensis* and *R. hoogerwerfi* have crania that in their basic conformation are similar to that in *Palawanomys.* Most of the resemblances reflect only the *Rattus*-like traits of *Palawanomys.* In other features of skulls, mandibles, and teeth the specimens of *Palawanomys* differ from those of *R. baluensis* and *R. hoogerwerfi* in the same ways as *Palawanomys* contrasts with *R. rattus diardii.*

In the mountains of Palawan, *Palawanomys furvus* is neither the morphological counterpart of *Rattus baluensis* from the mountains of Sabah and Sumatra nor closely related to *Rattus hoogerwerfi* from the Aceh highlands. Those species, although superficially similar in some cranial features to *Palawanomys,* are still within the morphological limits of *Rattus* as we view the genus; they do not possess the diagnostic characters of the Palawan rat.

The Palawan animals are not examples of *Rattus*; they do not fit with any other known genus of murid, especially any genus now

known to be either native or endemic to the Sunda Shelf. How does *Palawanomys* fit within the framework of relationships among Sundaic murids? To answer that question we discuss the native Sundaic murids and their relationship to the Palawan rat in a later section. First we define the limits and contents of two groups, both formerly placed in *Rattus*. One cluster of species, the *manipulus* group, is primarily Asian in geographic distribution but has a representative in the Sunda region. The other assemblage, the *muelleri* group, is indigenous to the Sunda Shelf.

THE *MANIPULUS* GROUP

Four species comprise this group: *manipulus, berdmorei, bowersii,* and *mackenziei.* In the late 1940s, Ellerman (1947–1948, p. 267) brought together *Rattus manipulus* and *R. berdmorei* into the subgenus *Berylmys*: "This name, which I propose for the *manipulus-berdmorei* rats, is based on the fact that in these rats the incisors are pro-odont, so that the diastema is lengthened more than in other *Rattus* rats of Eurasia and Australia, although the condylobasal length remains shorter than the occipitonasal length. The palate and palatal foramina are both long, and the diastema exceeds 30 per cent. of the occipitonasal length, and may approximate to a third of this length." By 1961, Ellerman (p. 626) wrote that "The difference between this group and *R. bowersi* (of the subgenus *Stenomys* as here understood) is not great; but there is the small difference of elongated diastema between the two present species and the whole of the rest of *Rattus* in Asia and Australia that makes me think it is reasonable to give *manipulus* and *berdmorei* subgeneric rank."

In most of his reports, Ellerman (1947–1948, 1949, 1961) considered *mackenziei* to be a valid subspecies of *Rattus bowersii* and that species a relative of *R. muelleri* and other *Rattus* in the subgenus *Stenomys,* for which the type species is *Rattus verecundus,* a native of New Guinea (Thomas, 1904, 1910; Rümmler, 1938). The diagnostic traits of *Stenomys,* according to Ellerman (1947–1948, p. 261) were a diastema less than 30 percent of the occipitonasal length (which separated it from *Berylmys*); small bullae that, on the average, fell below 15 percent of the occipitonasal length; and a long palate, greater than half of the occipitonasal length. To Ellerman (1947–1948; 1949, pp. 50–51, 68–70), *Stenomys* contained 15 species that could be divided "into four well-marked species groups." The first was the *macleari* group, which contained *R. macleari* and *R. nativitatis,* both known only from Christmas Island. The *callitrichus* group was the second and consisted of *R. muelleri, R. mara, R. enganus, R. rogersi, R. ruber, R. ringens, R. verecundus, R. callitrichus,* and *R. infraluteus.* The third was the *bowersii* group, containing only *R. bowersii.* And the forth was the *dominator* group, to which *R. dominator, R. frosti,* and *R. microbullatus* belonged.

Stenomys is not a monophyletic assemblage. The primary features holding the species together for Ellerman were small bullae relative to occipitonasal length, a primitive character (Musser, 1981a), and a long palate, which reflects the short incisive foramina, also primitive, in many of the species. So artificial was the group that most species in it have either been taken out and placed elsewhere or will be, as we elaborate further on in our discussion of the *muelleri* group. Ellerman (in Laurie and Hill, 1954) later removed some species but even in 1949, he (p. 52) wrote that *R. bowersii* stood "rather apart in relationships from the others in all probability."

That statement has been reinforced by results from later studies. In 1968 Yong, in a report of the karyotypes from four species of Malayan rats, pointed out that the chromosomal characteristics of *R. bowersii* and *R. muelleri* were dissimilar and did not show close affinity because of the different diploid numbers and configurations of the X-chromosomes. In a later paper on karyotypes of Malayan rats, Yong (1969a, p. 265) reported that "The karyotype of *R. muelleri* is more similar to that of subgenus *Rattus,* while the karyotype of *R. bowersii* bears resemblance to that of *Rattus* (*Berylmys*) *berdmorei.* These

two rats are therefore most probably the results of two different lines of evolution." Yosida (1973, p. 294) also noted that *R. bowersii* was remarkable "in that it has one large metacentric pair" of chromosomes.

Misonne, who studied characteristics of molars in African and Indo-Australian murids, transferred *Rattus bowersii* to subgenus *Bullimus* of *Rattus*. In this subgenus he also included *R. manipulus, R. berdmorei, R. xanthurus, R. marmosurus, R. celebensis, R. adspersus, R. coelestis, R. dominator, R. muelleri, R. everetti, R. adustus, R. chrysocomus, R. maculipilis,* and *R. baluensis*. Misonne also noted that (1969, p. 143) "*R. manipulus* and *R. berdmorei* have been separated as a distinct subgenus by Ellerman, who also recognized their relationship with *R. bowersi,* and indeed they seem to be related." Misonne (1969, p. 137) recognized the subgenus *Stenomys* but wrote that it "is geographically restricted to New Guinea, western and southern Australia, Guadalcanal, Bougainville and the smaller islands around New Guinea. Included in it were *R. niobe, R. verecundus, R. leucopus, R. ruber, R. fuscipes,* and *R. richardsoni.*

Musser (MS.) and Marshall (1976), working independently, came to reject the associations of *bowersii* held by either Ellerman or Misonne. During the late 1960s, Musser was assembling materials for a taxonomic revision of *R. bowersii* and its relatives. He concluded that *R. mackenziei* was a species distinct from *R. bowersii*; those two, as well as *R. manipulus* and *R. berdmorei,* formed a monophyletic group that was not part of *Rattus*. At about the same time, Joe T. Marshall, Jr. was trapping rats and mice in Thailand, learning firsthand about their habits and habitats. He also began a taxonomic study of Thai murids and independent of Musser realized that *bowersii, mackenziei,* and *berdmorei* belonged together in *Berlymys*. Publication of Musser's research was delayed but Marshall (1976, 1977) brought together his results in a report on the rats and mice of Thailand. There he (1976, p. 401) assembled *bowersii, mackenziei,* and *berdmorei*—the three species occurring in Thailand—into subgenus *Berylmys* of *Rattus* and provided this diagnosis: "Of medium to giant size, with a white front surface of the upper incisors, these rats have iron-gray dorsal color, pure white ventral color and crisp fur. Their slightly ridged skull, viewed from above, has a characteristic triangular outline that is shared with another white-toothed genus, *Diomys,* and the subgenus *Coelomys*. They are naturally tame. They have 40 chromosomes that typically include 7 metacentric pairs, and they are hosts of the lice *Hoplopleura diaphora* (on *R. bowersi*) and the similar *H. kitti* (on *R. berdmorei*)."

In 1976 Medway and Yong (pp. 46–47), reviewing problems in systematics of rats from the Malay Peninsula, wrote that "The names *Stenomys* (by Ellerman, 1947) and *Bullimus* (by Misonne, 1969) have been used to link rats including the Peninsular Malaysian taxa *validus* and *ferreocanus,* listed by Chasen (1940) as subspecies of *R. muelleri* and *R. bowersii* respectively. . . . Differences in serology and karyotype, however, indicate that these rats are not closely related and cannot be associated in a natural phylogenetic group." They also noted (p. 51) that similarities between *R. muelleri* and *R. bowersii* "appear to be the consequences of convergence."

Three years later, however, Yong and other colleagues (Chan, Dhaliwal, and Yong, 1979) formulated dendrograms of relationships among species of Malayan *Rattus* that were based on biochemical evidence, as well as cranial and external morphological features. Their biochemical data came from analyses of nine erythrocyte proteins, each coded by a separate locus. Their results place *R. bowersii* and *R. muelleri* together in a group, which they relate to Ellerman's subgenus *Stenomys*. Within that subgenus, according to the authors (p. 333), the biochemical data "support morphological and cytological evidence that *R. bowersii* and *R. muelleri* may be regarded as members of separate species groups."

We disagree with the allocation of *bowersii* to either subgenus *Stenomys* as proposed by Ellerman (1947–1948) or to subgenus *Bullimus* as indicated by Misonne (1969) and we do not view *bowersii* to be morphologically close to *Rattus muelleri,* despite the conclusions of Chan, Dhaliwal, and Yong (1969). We agree with Medway and Yong (1976) that any morphological similarities between *R. bowersii* and *R. muelleri* likely reflect con-

vergences rather than phylogenetic alliance. Results of our studies (some of it still in manuscript) indicate that the name *Stenomys* can be used only to embrace *Rattus verecundus* and its allies in the New Guinea area and Australia; it does not include any species of Indochinese or Sundaic murid. We agree with Misonne's restriction of *Stenomys* to the New Guinea area and Australian region, although we would not include some of the species he had placed in the subgenus.

To us *bowersii,* along with the species *manipulus, berdmorei,* and *mackenziei,* should be placed together in the genus *Berylmys.* Our view was anticipated by Osgood in 1932 and even earlier by Bonhote in 1903. In 1932 Osgood recognized the distinctive morphology of *bowersii* and the other forms that were closely related to it. Among the mammals collected by the Kelley-Roosevelts and Delacour Asiatic Expeditions were series of *bowersii* from Tonkin (northern Vietnam) and northern Laos. Reporting their characteristics, Osgood (1932, p. 312) wrote:

> The skull of *R. bowersi* is markedly different from that of *R. edwardsi* and other so-called 'giant rats' of southeastern Asia. The braincase is peculiarly truncate behind, giving an essentially triangular appearance to the whole skull. The interparietal is frequently subtriangular with an anterior apex instead of being elliptical. The orbital ridges are rather weak and mainly confined to the frontals, their continuation over the parietals being faint. The audital bullae are relatively large and the incisors pale. A closely related species is *R. ferreocanus* of the Malay Peninsula, which has smaller audital bullae, but is otherwise so similar to *bowersi* that intergradation between the two is not improbable. Other species of smaller size and well distinguished, but having the same type of skull and similar external appearance, are *manipulus, mackenziei,* and *berdmorei.*

Bonhote (1903) brought together *Mus bowersii, Mus latouchei, Mus ferreocanus,* and *Mus berdmorei* in a cluster he called the "BOWERSI GROUP." The taxa, *latouchei* and *ferreocanus,* are now listed as subspecies of *bowersii* (Osgood, 1932; Chasen, 1940). Bonhote also added to his group specimens from the Hume Collection which had been obtained in Manipur and were originally identified by Thomas as *berdmorei* but later re-identified by him as *manipulus* when he named and described that species (Thomas, 1916, p. 413). So, 79 years ago the phylogenetic relationships of three out of the four species we now include in a monophyletic group had been recognized by someone who studied a handful of specimens from a few widely scattered localities. We characterize *Berylmys* below, recognizing our diagnostic antecedants in the perceptions of Bonhote in 1903 and Osgood in 1932.

GENUS *BERYLMYS*

Berylmys is primarily an Indochinese genus (fig. 14). *Berylmys manipulus, B. berdmorei,* and *B. mackenziei* occur north of the Isthmus of Kra (10°30′ N). All records of them come from the mainland (Osgood, 1932; Allen, 1940; Anthony, 1941; Roonwall, 1949; Ellerman, 1961; Van Peenen, Ryan, and Light, 1969; Marshall, 1977; Tien, 1966a, 1966b, 1978) except for *B. berdmorei,* which was also collected on Con Son Island off the southeastern coast of Vietnam (Duncan, Van Peenen, and Ryan, 1969).

Only one species is found south of the Isthmus of Kra on the Sunda Shelf. There *B. bowersii* is known from the Malay Peninsula (Chasen, 1940; Medway, 1969) and the Medan area of northwestern Sumatra (specimens in the Museum Zoologicum Bogoriense examined by Musser through the courtesy of Mr. Boeadi); it has not been found on any island offshore of either the Malay Peninsula or Sumatra. There are no representatives of *Berylmys* on any of the Mentawai Islands, in the Simalurs, the Nicobars, or the Andamans. No species of the genus occurs in the Philippines, Celebes, or any place east or south of those island groups.

TYPE SPECIES: *Epimys manipulus* Thomas (1916), based on an old adult female (BM 16.3.26.78) from Kabaw Valley, 20 miles west of Kindat, Central Burma, altitude 600 feet. The specimen was obtained by J. M. D. Mackenzie on January 30, 1915, who wrote on the skin label that the rat was dug out of the ground. A skin, cranium, and mandible, all in good condition comprise the holotype.

INCLUDED SPECIES AND KNOWN DISTRIBUTIONS: We recognize the following species of *Berylmys.*

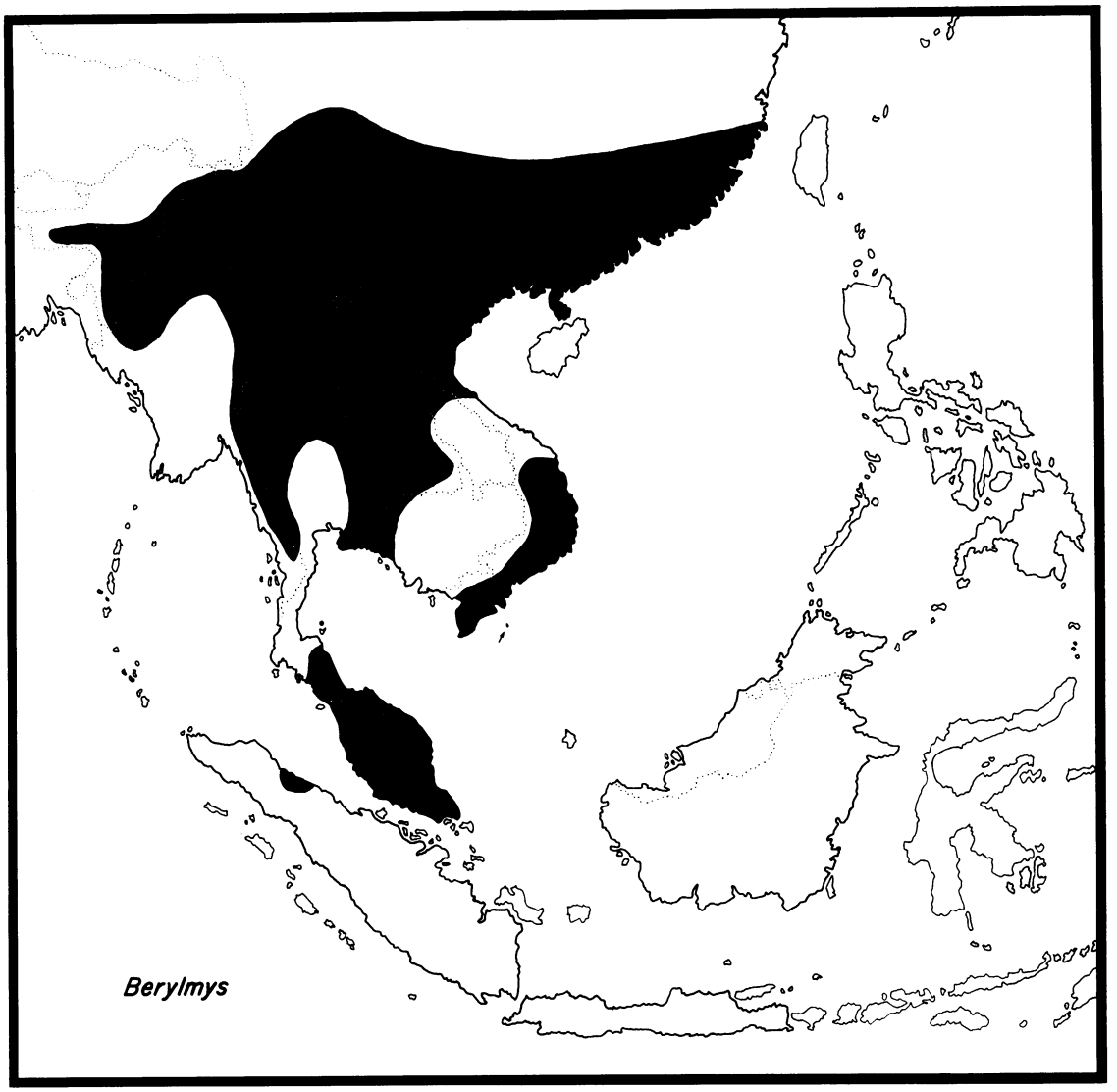

FIG. 14. Geographic distribution of *Berylmys*. Arrow points to Con Son Island, the only offshore island were *Berylmys* (*B. berdmorei*) has been recorded. Distribution of *Berylmys* probably includes blank area in southeastern Indochina but there are no records of specimens from there.

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

B. manipulus (including *kekrimus*): India (Assam) and central and northern Burma

B. mackenziei (including *feae*): India (Assam), central Burma, northern Tenasserim in southern Burma, Szechwan Province of China, and southern Vietnam

B. berdmorei (including *mullulus* and *magnus*): Southern Burma, northern and southeastern Thailand, Cambodia, northern Laos, southern Vietnam, and Con Son Island off the coast of southern Vietnam

SOUTHEASTERN ASIA AND THE SUNDA SHELF

B. bowersii (including *latouchei, lactiventer, kennethi, wellsi, totipes,* and *ferreocanus*): India (Tirap District and Assam), northern and central Burma, southern China, northern Laos, northern Vietnam, northern Thailand, peninsular Thailand and the Malay Peninsula, south of the Isthmus of Kra, and northwestern Sumatra

DIAGNOSIS: Once placed in *Rattus, Berylmys* possesses the following characteristics that distinguish it from that genus: (1) dense and crisp iron gray pelage over upperparts, white fur on underparts, dorsum and venter sharply demarcated; (2) either eight mammae (one pectoral pair, one postaxillary pair, and two inguinal pairs) or 10 mammae (an additional postaxillary pair); (3) braincase triangular in dorsal view, its dorsolateral margins, as well as those of postorbital and interorbital regions, outlined by weak and low ridges; (4) nasolacrimal canals highly inflated; (5) incisive foramina usually end before or at anterior margins of upper molar rows; (6) short palatal bridge, its posterior margin usually either anterior to backs of third upper molars or even with them; (7) pterygoid fossae complete, not breached by sphenopterygoid vacuities; (8) back of occiput expansive and sloping forward, especially in *B. berdmorei* and *B. manipulus*; (9) upper incisors orthodont or slightly proodont, enamel of uppers and lowers range from white to orange (most specimens cream or pale orange); (10) third upper and lower molars small relative to others in row; (11) labial cusps t3, t6, and t9 on first upper molars and cusps t6 and t9 on second uppers so broadly merged with central cusps they are indistinct or appear absent; (12) cusp t3 occurs infrequently on second upper molars of three species and is absent from third upper molars of three out of the four species; (13) small and narrow lamina at front of each first lower molar; (14) anterolabial cusps absent from second lower molars in most specimens of three species, anterolabial cusps absent from third lower molars in all specimens examined of all species; (15) diploid number of 40 chromosomes, which includes seven pairs of small metacentrics and one large metacentric pair.

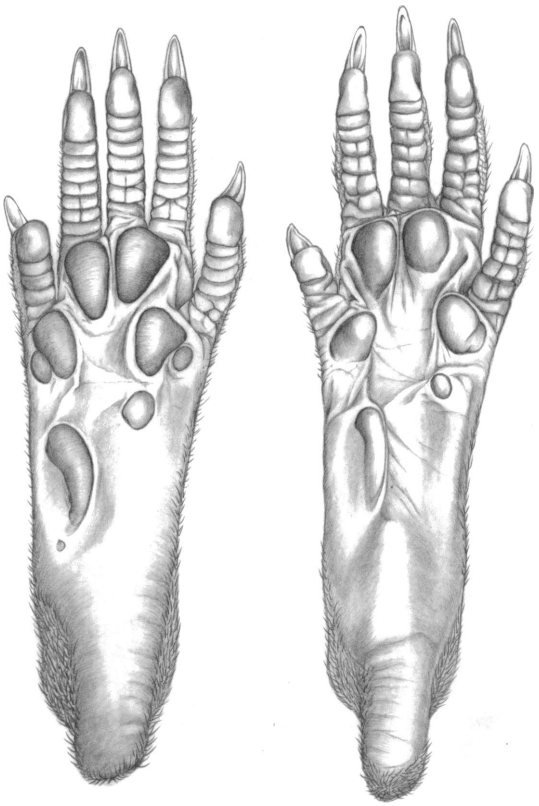

FIG. 15. Plantar views of left hind feet from adult *Sundamys muelleri* (left, AMNH 240377; length, 53 mm.) and *Berlymys bowersii* (right, AMNH 217608; length, 56 mm.).

DESCRIPTION AND COMPARISONS WITH *RATTUS*

There is no other group of species quite like *Berylmys*. All usually live in tropical forests and scrub, sometimes around margins of cultivated fields. The rats are terrestrial and dwell in burrows. Body size is large, as in *B. bowersii,* or medium, as is characteristic of *B. berdmorei* and *B. manipulus* (tables 5–8). Coloration and texture of the fur is distinctive and not shared by species of *Rattus* or by any other species of Indo-Australian murid. The fresh pelage is dense and crisp, iron gray over upperparts of head and body, white on the

underparts; each surface is sharply demarcated from the other. Old pelage, especially that in *B. bowersii,* is tan or dark brown and appears washed out compared to the fresh gray fur. (We know of two exceptions to the normal coloration. Yong and Dhaliwal, 1970, reported an adult female *B. bowersii* from Fraser's Hill in Malaya that had yellow instead of gray pelage and we found a completely melanistic adult *B. mackenziei,* FMNH 76667, from the Khasi Hills of Assam.) The tail is equal to or longer than combined lengths of head and body in all the species except *B. berdmorei,* in which the tail is shorter than the head and body (tables 5–8). The ears are large and dark brown. Upper surfaces of the front and hind feet are white in *B. manipulus,* white or gray in *B. berdmorei.* In *B. bowersii* and *B. mackenziei* the digits and sides of the feet are white, the tops dark brown. All species have long and narrow hind feet and each foot has six plantar pads (fig. 15).

Color of the tail varies. In tails of *B. manipulus,* the distal one-half to one-third is white all around, the basal one-half to two-thirds is dark brown on top and sides and its undersurface is either brown, mottled, or gray. Tails of *B. berdmorei* are dark brown on top and sides from base to tip; the undersurface ranges from solid brown (so the tail is monocolored) to mottled to grayish white speckled with black; none of the specimens we examined had white tips. Specimens of *B. bowersii* from northern Vietnam, northern Laos, and northern Thailand have tails that are brown dorsally from base to tip and either brown below (so the tail is monocolored), slightly paler than the dorsal surface, or mottled; a few rats have short white tips. Tails of most specimens from southern China, Burma, and Assam are white for their distal one-fifth and brown everywhere else; a few specimens are monocolored. In tails of *B. bowersii* from the Malay Peninsula, the distal one-half to one-third of each is white, everywhere else is brown. Specimens of *B. mackenziei* from southern Vietnam have dark brown tails, a short white tip occurs infrequently. In examples of *B. mackenziei* from Szechwan, Assam, and Burma, the basal third to two-thirds of each tail is brown and the rest is white; undersurface of the basal portion is usually white.

There are two sets of mammae numbers among the species. Females of *B. bowersii* have eight mammae: one pectoral pair, one postaxillary pair, and two inguinal pairs. This count is characteristic of all the specimens we examined. All females of *B. mackenziei, B. berdmorei,* and *B. manipulus* we studied have 10 mammae: four pairs in the same positions as in *B. bowersii,* along with an additional postaxillary pair. The number and location of the teats in these three species of *Berylmys* is like that in females of *Lenothrix canus* and unlike the distribution of teats in any species of *Rattus* (Musser, 1981a).

Sexually adult males in all four species of *Berylmys* each have a cutaneous glandular area along the midline of the stomach and inguinal region. The gland is conspicuous and nearby fur is stained by its sebaceous secretions. Rudd (1966b, p. 332) noted similar glands on adult *B. bowersii* from Malaya and wrote that one male "with very large testes had the darkest stained area observed in any species [he examined 12 species of Malayan rats]; the area measured 5 × 67 mm."

Chromosomes have been sampled from *Berylmys bowersii* and *B. berdmorei* (table 2). Both have a diploid number of 40, seven pairs of metacentric autosomes, one pair of submetacentrics, five pairs of subtelocentrics, and six pairs of telocentrics; the X and Y chromosomes are telocentrics; the fundamental number is 66. Compared with those of *Berylmys,* most species of *Rattus* have a 2N of 42, usually no submetacentric autosomes, fewer subtelocentrics, more telocentrics, and lower fundamental numbers (table 2).

Crania of the four species of *Berylmys* are shown in figures 16–18 and contrasted there with the cranium of *Rattus rattus diardii,* which we use as our example of *Rattus.* Cranial measurements are listed in tables 5–8. In each species of *Berylmys,* the cranium is stout and triangular in dorsal outline. A truncate cranium, wide occiput and braincase, wide zygomatic arches that converge on each side toward a rostrum roofed by nasal bones ending in a triangular tip provides the basic triangular conformation of the cranium. The rostrum is long and wide, partly a reflection

TABLE 2
Karyotypes from Samples of *Berylmys*, *Sundamys*, and *Rattus*

Taxon	2N	Autosomes M	SM	ST	T	Sex X	Y	FN	Reference
Berylmys									
bowersii (Malaya)	40	7	1	5	6	T	T	66	Yong, 1968
bowersii (Thailand)	40	7	1	5	6	T	T	66	Yosida, 1973
berdmorei (Thailand)	40	7	1	5	6	T	T	66	Markvong, Marshall, and Gropp, 1973
berdmorei (Vietnam)	40	7	1	5	6	T	T	66	Duncan, Van Peenen, and Ryan, 1970
Sundamys									
muelleri (Malaya)	42	6	0	2	12	SM	T	59-♂ 58-♀	Yong, 1968; Yosida, 1973
Rattus									
norvegicus (Thailand)	42	7	0	4	9	T	T	62	Markvong, Marshall, and Gropp, 1973
nitidus (Thailand)	42	7	1	2	10	T	T	60	
losea (Thailand)	42	7	0	2	11	T	T	58	
argentiventer (Thailand)	42	7	0	2	11	T	T	58	
exulans (Thailand)	42	7	0	2	11	T	T	58	
rattus (Thailand)	42	7	0	0	13	T	T	54	Markvong, Marshall, and Gropp, 1973

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

of the inflated nasolacrimal capsules. The interorbital region is wide. Its dorsolateral margins are outlined by low inconspicuous beading that continues back along dorsolateral margins of the postorbital area onto sides of the braincase. The beading is strongest on skulls of *B. berdmorei* (fig. 17A) where it extends all the way to the occiput. The beading is weakest on skulls of *B. bowersii* (fig. 16) where it is conspicuous over the interorbital and postorbital regions but fades out on the braincase; most specimens of *B. bowersii* have a smooth and round braincase. Sides of the braincase in all species of *Berylmys* are not vertical but slope towards the midline of the cranium. The interparietal is short (anterior-posterior distance) but wide and either triangular or diamond-shaped in dorsal outline. Its anterior half is between the parietals and its posterior half roofs part of the occiput. The occiput is wide but shallow (anterior-posterior), giving a truncate appearance to the back of the cranium, as Osgood (1932) pointed out. The back of the occipital region is expansive and slopes forward; the most sloping occiput is found in *B. berdmorei* (fig. 18B), the species with the largest bullae, the strongest temporal ridges, and the most proodont upper incisors.

Species of *Rattus* do not have a triangular cranium as seen from a dorsal view (fig. 17C). The anterior margins of the nasals are straight or rounded, the zygomatic arches tend to parallel one another, and the occiput is narrower than the braincase, deep, and does not appear truncate. In dorsal outline, the cranium of *Rattus* is rectangular rather than triangular. The most conspicuous features are the high and thick ridges that define dorsolateral margins of the cranium from the interorbital region to the occiput, especially in *R. rattus*. The sides of the braincase are vertical in most species of *Rattus* (*R. norvegicus*, for example, has sloping sides). The interparietal is long (anterior-posterior length) and usually neither triangular nor diamond-shaped in dorsal outline; the shape shown in figure 17C is typical. Its anterior margin abuts against the posterior edges of the parietals and is not located between them; the interparietal forms most of the dorsal surface of the occiput. The back of the cranium is lower, less expansive and does not slope forward in most species (*R. norvegicus*, again, is an exception).

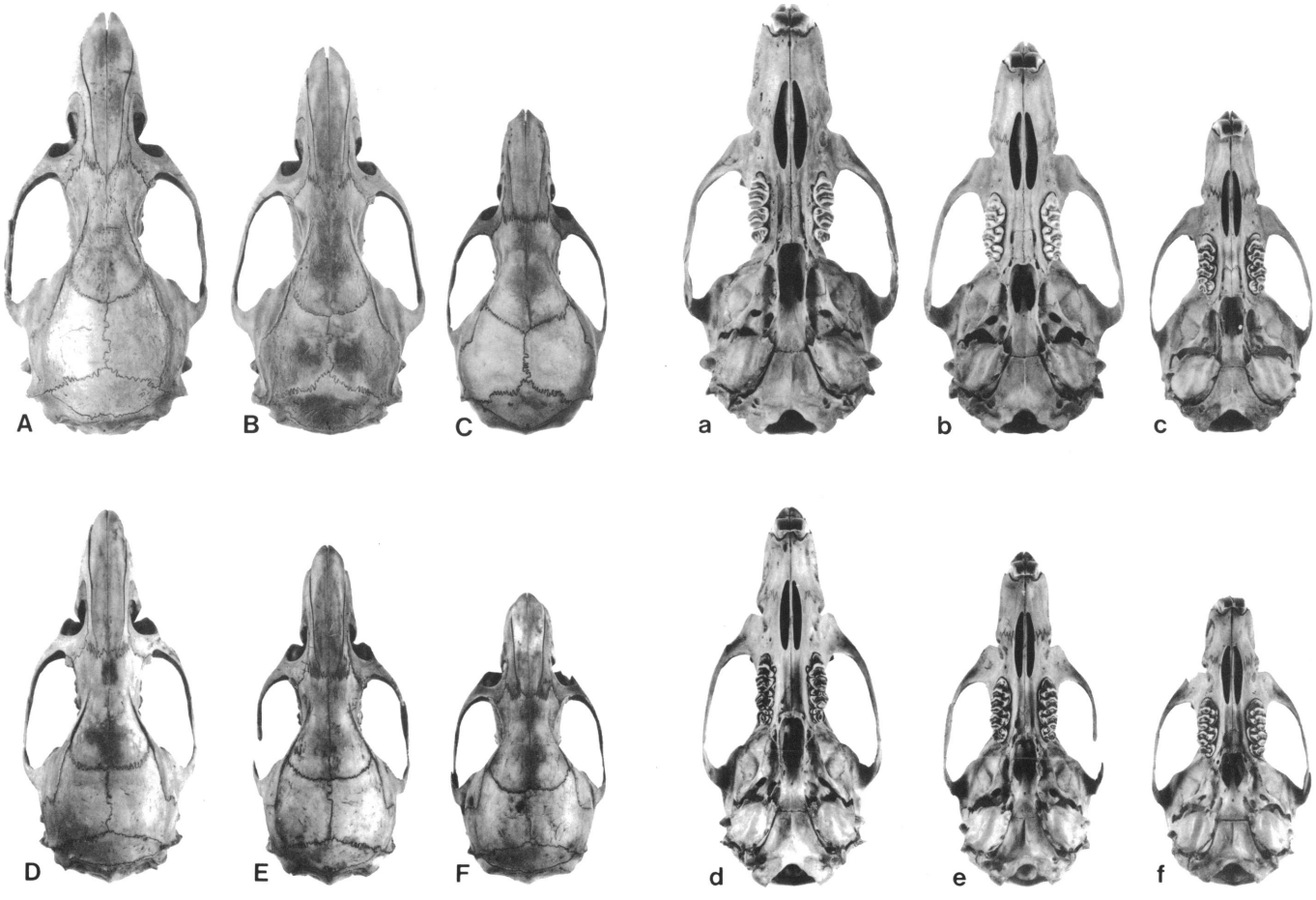

FIG. 16. Views of crania: *Berylmys bowersii* (northern Burma and southern China) is contrasted with *B. mackenziei* (Assam). *Berylmys bowersii*: Aa, adult (AMNH 115238); Bb, young adult (AMNH 115233); Cc, juvenile (AMNH 43303). *Berylmys mackenziei*: Dd, adult (BM 66.3100); Ee, young adult (BM 47.136); Ff, juvenile (BM 47.135). Natural size.

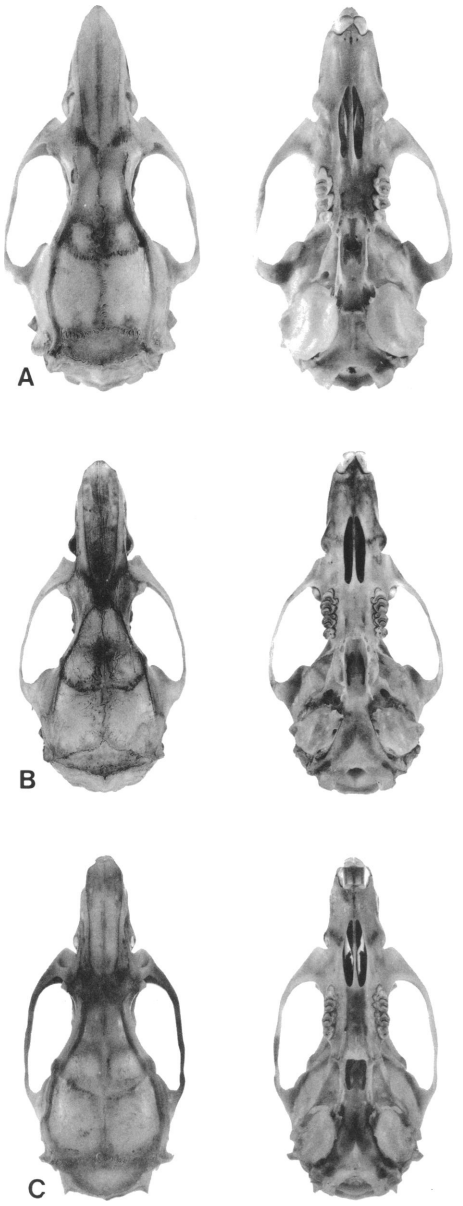

FIG. 17. Views of crania from adults: *Berylmys* (A and B) contrasted with *Rattus* (A). A, *B. berdmorei* (USNM 533371), southeastern Thailand. B, *B. manipulus* (USNM 217420), northern Burma. C, *R. rattus diardii* (AMNH 240104), Java. Natural size.

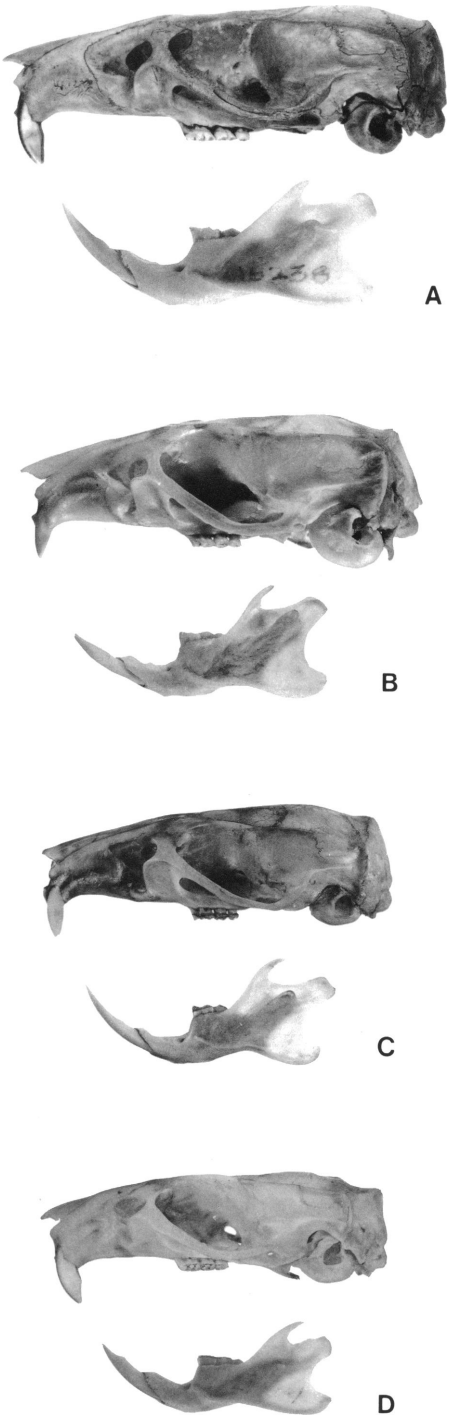

FIG. 18. Views of crania and dentaries from same specimens shown in figures 16 and 17: *Berylmys* (A–C) contrasted with *Rattus* (D). A, *B. bowersii*. B, *B. berdmorei*. C, *B. manipulus*. D, *R. rattus diardii*. Natural size.

Cranial characteristics of *Berylmys* as seen from the side are illustrated in figure 18. The nasals barely extend beyond anterior faces of the upper incisors. Each zygomatic plate is wide and stout. The braincase is deep. Squa-

TABLE 3
Posterior Margins of Incisive Foramina and Palatal Bridge Relative to First and Third Upper Molars in Species of *Berylmys*[a]

Species	Incisive Foramina at M^1			Palatal Bridge at M^3		
	Anterior	Even	Posterior	Anterior	Even	Posterior
B. manipulus	100 (18)	—	—	83 (15)	17 (3)	—
B. berdmorei	88 (15)	6 (1)	6 (1)	88 (15)	12 (2)	—
B. mackenziei	65 (26)	25 (10)	10 (4)	93 (37)	7 (3)	—
B. bowersii	83 (62)	12 (9)	5 (4)	49 (37)	37 (28)	14 (10)

[a] Frequency is expressed as percentage; number of specimens in parentheses. Posterior margins of incisor foramina end either anterior to front faces of first upper molars, even with them, or just posterior (by .1–1.0 mm.); posterior rim of palatal bridge is either anterior to back faces of upper third molars, even with them, or just posterior (by .1–1.0 mm.).

mosal roots of the zygomatic arches are low on sides of the braincase. The squamosal bone above each bulla is complete, not divided by a squamoso-mastoid foramen or vacuity; the squamoso-mastoid foramen is confined to the suture between squamosal bone and mastoid. The high and sloping posterior face of the occiput is especially evident and contrasts sharply with the occipital conformation in *Rattus*. Each mastoid is large and intact; none of the specimens we studied have mastoid fenestrae. The auditory bullae are large relative to the cranium in one species of *Berylmys*; the bullae of the other *Berylmys* are relatively smaller than in species of *Rattus*.

In all the species of *Berylmys*, the relative positions of the sphenopalatine and dorsal palatine foramina in the orbit, and the configuration of each alisphenoid region between bulla and orbit is similar to that in *Palawanomys* and *Rattus*. In each orbit of *Berylmys*, the sphenopalatine foramen is large and separate from the dorsal palatine foramen, which is well posterior to the sphenopalatine. In the alisphenoid region (fig. 19A), a lateral strut of alisphenoid bone is absent, the alisphenoid canal is an open channel, and the buccinator-masticatory foramen is functionally absent, as is the accessory foramen ovale.

The triangular outline of the cranium in *Berylmys* is also evident from a ventral view (figs. 16 and 17). The rostrum is large, the diastema is long, and the incisive foramina are wide and short. In most specimens of all the species, the posterior margins of the incisive foramina are anterior to or even with the front faces of the first upper molars (table 3). The bony palatal bridge is wide and short. Its posterior margin is anterior to or even with the posterior faces of the third upper molars in most specimens of all the species. In a few other specimens, the palatal bridge extends slightly posterior to the backs of the molar rows (table 3). The bridge is scored by moderately deep palatine grooves and each posterior palatine artery is opposite the anterior half or middle of the second upper molar. The mesopterygoid fossa is wide, especially relative to the width of the palatal bridge. Its walls are breached by small or moderately large sphenopalatine vacuities that do not extend anterior beneath the bridge and into the back of each orbit (fig. 19B). The vacuities are slitlike in many specimens. Each pterygoid fossa is wide and flat. Its anterior two-thirds is intact and not perforated by a sphenopterygoid vacuity. The posterior third of each fossa is shaped like that in *Rattus*. Also, as in species of *Rattus*, the lateral margin of each fossa is outlined by a clear ridge from behind each molar row to the anterolateral margin of each bulla (fig. 19B). The middle lacerate foramen between pterygoid fossa and bullar capsule is very large to moderately large in all species except *B. berdmorei* in which it is small and inconspicuous. In *B. berdmorei*, the auditory bullae are large, inflated, and each bony eustachian tube is so short it is hardly evident. The bullae in *B. manipulus*, *B. bowersii*, and *B. mackenziei* are smaller relative to size of the cranium but they still have short and inconspicuous eustachian tubes.

Crania of *Rattus* differ from those of *Be-*

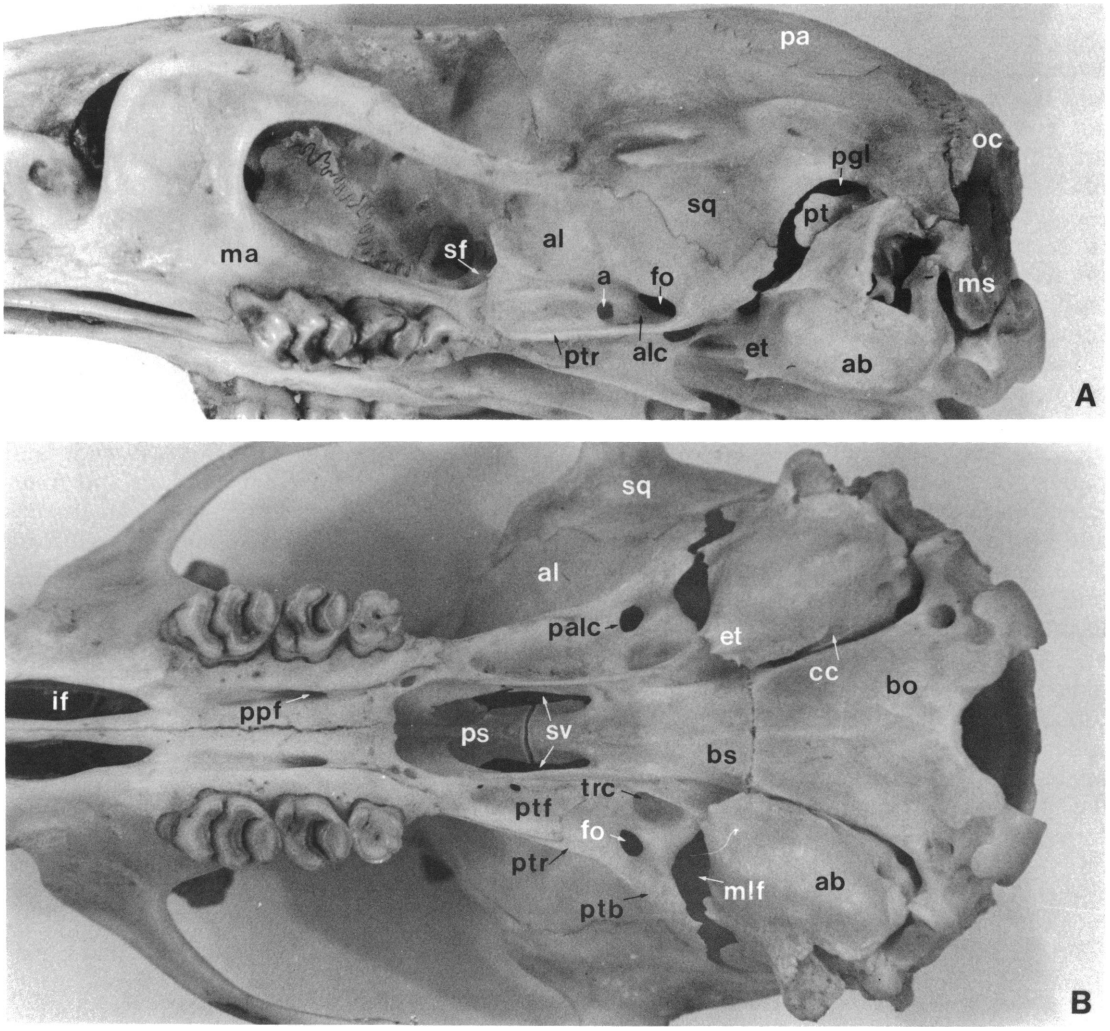

FIG. 19. Lateral (A) and ventral (B) views of cranium in *Berylmys bowersii* (AMNH 115236). *Abbreviations:* **a**, anterior opening of alisphenoid canal, where it empties into sphenoidal fissure; **ab**, auditory bulla; **al**, alisphenoid bone; **alc**, alisphenoid canal, which is an open channel; **bo**, basioccipital bone; **bs**, basiphenoid bone; **cc**, carotid canal; **et**, bony eustachian tube; **fo**, foramen ovale; **if**, incisive foramina; **ma**, maxillary bone; **ms**, mastoid portion of the petromastoid; **mlf**, middle lacerate foramen; **oc**; occiput; **pa**, parietal bone; **palc**, posterior opening of the alisphenoid canal; **pgl**, postglenoid vacuity; **ppf**, posterior palatine foramen; **ps**, presphenoid bone; **pt**, periotic portion of the petrosal; **ptb**, pterygoid bridge; **ptf**, pterygoid fossa; **ptr**, pterygoid ridge; **sf**, sphenoidal fissure; **spt**, sphenopterygoid vacuity; **sq**, squamosal bone; **sv**, sphenopalatine vacuity; **trc**, transverse canal.

rylmys, as seen in ventral view (figs. 10 and 17). In *Rattus,* the rostrum is narrower and not as stout, the incisive foramina are longer and their posterior margins always extend between the anterior margins of the molar rows. The palatal bridge is wider (partly reflecting the relatively smaller molars) in *Rattus,* and longer; it extends posterior to the molar rows to form a wide shelf. Each posterior palatine foramen, instead of being opposite each second upper molar, as in *Berylmys,* is opposite the anterior half of each third upper molar. The mesopterygoid fossa is narrower relative to width of the palatal bridge and its walls

are breached by spacious vacuities that extend anterior into the back of each orbit. So large are the openings that the presphenoid and basisphenoid bones seem suspended in air. The configurations of the pterygoid plates are similar in *Rattus* and *Berylmys,* but those of *Rattus* are perforated by large sphenopterygoid vacuities, openings that are absent in *Berylmys. Rattus* has round and partially inflated bullae that are larger relative to the cranium than in any species of *Berylmys* except *B. berdmorei.*

Judged by the dry arteries in incompletely cleaned skulls, the large stapedial foramina, and the conformation of the posterior third of each pterygoid plate, the carotid arterial pattern in the basicranium in all species of *Berylmys* is similar to that of *Palawanomys* and *Rattus.* The common carotid artery gives off a large stapedial branch that enters the bullar capsule and emerges through the middle lacerate foramen as the internal maxillary artery. That vessel passes over the pterygoid plate in a groove between the middle lacerate foramen and the posterior opening of the alisphenoid canal. Passing through the posterior opening, the internal maxillary courses along the alisphenoid canal to enter the orbit through the sphenoidal fissure. After giving off the stapedial, the common carotid becomes the internal carotid artery and passes into the braincase through the common carotid canal. The pattern is described in more detail and diagrammed elsewhere (Musser, 1982b and 1982c).

The mandibular conformation of three species of *Berylmys* is shown in figure 18A–C. In its shape, relative positions of the mental and mandibular foramina, and sizes of the coronoid, condyloid, and angular processes relative to each other and the ramus, dentaries of *Berylmys* resemble those of *Rattus* (fig. 18D). One evident difference between the two genera is the size and position of the bulge formed by each incisor capsule. In species of *Berylmys,* the incisor capsule forms a huge bulge on the side of the dentary at the base of the condyloid process and sometimes, as in *B. berdmorei,* extends up into that process. In *Rattus* the bulge is smaller, inconspicuous, and well below the base of the condyloid process.

Species of *Berylmys* have wide and stout incisors that appear strong. Upper incisors in *B. bowersii* and *B. mackenziei* emerge from the rostrum at nearly a right angle (orthodont configuration); the uppers of *B. berdmorei* and *B. manipulus* are directed slightly forward (slightly proodont), especially when compared with the other two species of *Berylmys* (fig. 18A–C). On the average, the enamel of upper and lower incisors in all species is cream to tinted with pale orange but the actual range of hues is greater. The enamel surfaces are consistently whitish orange in *B. manipulus,* either cream or pale orange in *B. berdmorei,* and the coloration ranges from cream to solid orange in *B. bowersii* and *B. mackenziei.*

The incisors of *Rattus* are also wide and stout relative to sizes of cranium and mandible. In species of *Rattus,* however, the uppers either curve back as they emerge from the rostrum (opisthodont) or are orthodont; they are never proodont. The enamel layers of upper and lower incisors are always bright solid orange.

Size of upper molar rows relative to palatal bridge are shown in figures 16 and 17, occlusal surfaces of upper and lower molars are illustrated in figures 20 and 21, and dental measurements are listed in tables 5–8. The upper and lower molars are absolutely large and large relative to area of palatal bridge and dorsal dentary surface. Both upper and lower molars are moderately high, brachydont rather than hypsodont. Each first upper and lower molar is long, the second upper and lowers are about as long as they are wide, and the third molars are very small relative to the others in each row. The molars, either uppers or lowers, do not abut against one another as they do in *Lenothrix canus* (Musser, 1981a), for example; instead, the first upper molar broadly overlaps the second, the second upper overlaps the third, the third lower molar overlaps the second and the second lower overlaps the first. In most specimens of all the species, each first upper molar is anchored by five roots (large anterior, posterior, and labial, and two smaller lingual), each second molar has four roots, and each third upper molar ends in three roots. Each first lower molar has four roots (large anterior and posterior, smaller labial and lingual), and each second and third lower molar is anchored by three roots. A few specimens of *B.*

TABLE 4

Number of Roots on M_1 and Presence (+) or Absence (−) of Certain Cusps and Cusplets on Molars in Species of *Berylmys* and *Rattus*[a]

	Berylmys				*Rattus*[b]	
Trait	*B. bowersii*	*B. mackenziei*	*B. berdmorei*	*B. manipulus*	*R. rattus diardii*	*R. norvegicus*
Number of roots on M_1						
4	5 (4)	— —	15 (3)	— —	— —	— —
5	95 (72)	100 (45)	85 (17)	100 (14)	100 (37)	100 (20)
Cusp t3 on M^2						
+	— —	43 (17)	6 (1)	7 (1)	46 (17)	35 (17)
−	100 (73)	57 (23)	94 (16)	92 (12)	54 (20)	65 (13)
Cusp t3 on M^3						
+	— —	23 (9)	— —	— —	5 (2)	— —
−	100 (73)	77 (31)	100 (17)	100 (13)	95 (35)	100 (20)
Anterior labial cusplet on M_1						
+	— —	— —	— —	— —	5 (2)	— —
−	100 (70)	100 (40)	100 (16)	100 (13)	95 (35)	100 (20)
Posterior labial cusplet on M_1						
+	94 (66)	75 (30)	94 (15)	92 (12)	81 (30)	100 (20)
−	6 (4)	25 (10)	6 (1)	8 (1)	19 (7)	— —
Anterolabial cusp on M_2						
+	3 (2)	5 (2)	6 (1)	92 (12)	100 (37)	100 (20)
−	97 (68)	95 (38)	94 (15)	8 (1)	— —	— —
Posterior labial cusplet on M_2						
+	99 (69)	95 (38)	50 (8)	92 (12)	86 (32)	95 (19)
−	1 (1)	5 (2)	50 (8)	8 (1)	14 (5)	5 (1)
Anterolabial cusp on M_3						
+	— —	— —	— —	— —	100 (37)	100 (20)
−	100 (70)	100 (40)	100 (16)	100 (13)	— —	— —

[a] Numbers of roots, cusps, and cusplets are expressed as percentages; number of specimens are in parentheses.
[b] The sample of *R. r. diardii* is from Java, that of *R. norvegicus* is from China.

bowersii and *B. berdmorei* have four roots (one lingual instead of two) beneath each first upper molar (table 4).

In most species of *Rattus,* the upper and lower molars are also brachydont. They also have five roots beneath each first upper molar, four under the second, three beneath the third, four anchoring each first lower molar, and three beneath each second and third lower molar. The molars of *Rattus* also overlap rather than abut against one another. But, *Rattus* has smaller molars relative to areas of palatal bridge and dentary, and each third upper and lower molar is much larger relative to others in each row when contrasted with species of *Berylmys.*

Molar occlusal patterns are simple in all species of *Berylmys.* Many cusps are absent or poorly developed. Most cusps have merged to form featureless laminae, especially when the molar rows are worn (see the worn surfaces in figures 20 and 21). Only in young animals with slightly worn molars are there discrete cusps and these are along lingual margins. The cusps in species of *Rattus* are also not separate and they broadly unite to form rows of laminae, but the cusps retain more of their identities and the occlusal surfaces appear more cuspidate compared to the non-cuspidate patterns in *Berylmys* (contrast figs. 20 and 21 of *Berylmys* with fig. 13 of *Rattus*).

FIG. 20. Occlusal views of right upper molars in *Berylmys* (slightly and very worn in each couplet). Aa, *B. bowersii* (AMNH 115233 and 115238). Bb, *B. mackenziei* (FMNH 75820 and 76488). Cc, *B. berdmorei* (USNM 297163 and 533370). Dd, *B. manipulus* (FMNH 76466 and 82985). ×10.

The simple occlusal surfaces in *Berylmys* result from absence of some cusps and broad merging of others. Cusp t7 and a posterior cingulum does not occur on any upper molar

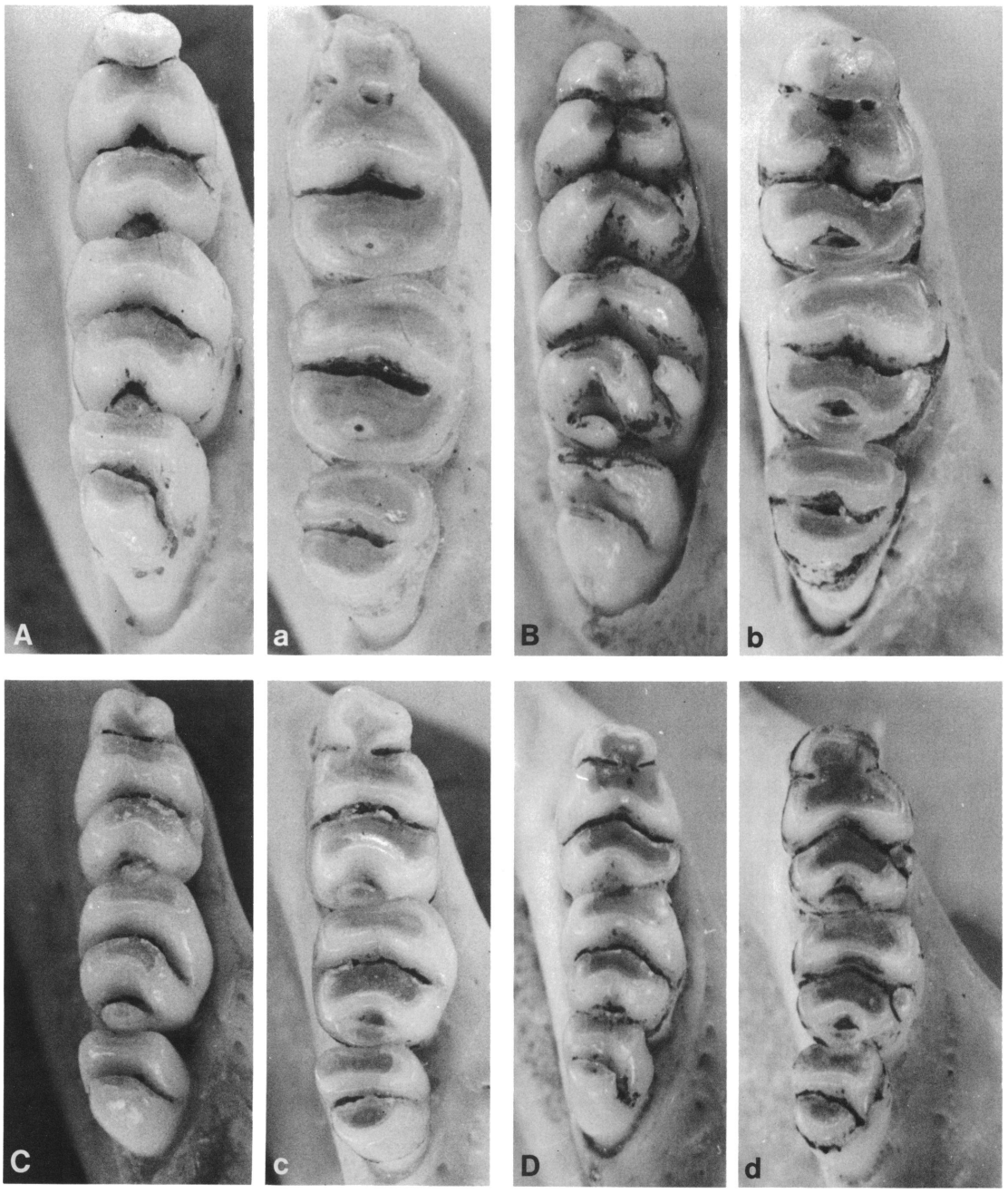

FIG. 21. Occlusal views of right lower molars in *Berylmys* (slightly and very worn in each couplet; same specimens as in fig. 20). Aa, *B. bowersii.* Bb, *B. mackenziei.* Cc, *B. berdmorei.* Dd, *B. manipulus.* ×10.

in any species. Cusp t3 on each second and third upper molar is either absent or occurs at a very low frequency in all species except *B. mackenziei* in which the cusp occurs more frequently (table 4). Even when present, cusp t3 is small and hardly evident. The labial

cusps (t3, t6, and t9) of each second upper molar, cusps t6 and t9 of each second upper, and cusp t6 of each third upper molar are either very small or large but in either case have so broadly united with the central cusp in each row that they are indistinguishable as cusps except in very young rats. The lingual cusps of each upper molar, although separate and discrete in young rats with slightly worn molars, broadly merge with the central cusp of each row as the animals grow older and the teeth wear. The resulting occlusal pattern consists of rows of simple and slightly arcuate laminae.

Each third upper molar has a very simple and relatively small chewing surface in *Berylmys bowersii, B. berdmorei,* and *B. manipulus.* It consists of a large cusp t1, a broad lamina (fused cusps t4, t5, and t6) and an oblong posterior cusp that is featureless and may consist only of cusp t8. The single lamina may be arcuate (fig. 20A) or C-shaped (fig. 20a, C, and c). Each third molar in *B. mackenziei* (fig. 20B and b) has a relatively greater chewing area because the posterior lamina is definitely formed of two cusps, cusps t8 and t9.

Simple occlusal surfaces also characterize the lower molars of *Berylmys.* Laminae on all the molars are thick and arcuate. The front lamina of each first lower molar consists of anterolabial and anterolingual cusps so broadly merged, even in young rats, that they form a single structure which is thick but much narrower than the laminae posterior to it. None of the specimens we examined had an anterocentral cusp at the front of the tooth. Most species of *Rattus* also lack an anterocentral cusp, but the anterolingual cusp is always larger than the anterolabial, the two cusps remain evident except in very worn teeth, and they unite to form a thick and wide lamina, nearly as wide as the laminae posterior to it (fig. 13). An anterior labial cusplet is missing from every specimen in all species of *Berylmys* and most specimens of all the species have a posterior labial cusplet (discrete only in young rats); this frequency of occurrence of labial cusplets on first lower molars is similar to that found in species of *Rattus* (table 4). The posterior cingulum on the first molar and that at the back of each second lower molar is set well to the lingual side of each tooth. The posterior cingula in *Rattus* tend to be in the center of each molar (fig. 13).

Chewing surfaces of the second lower molars have even simpler cusp patterns than do the first. In most specimens, the surface consists of two broad, thick laminae and a small posterior cingulum. An anterolabial cusp is absent from most specimens of *B. bowersii, B. mackenziei,* and *B. berdmorei* but present on most examples of *B. manipulus,* which is the usual condition in *Rattus* (table 4). A small and inconspicuous posterior labial cusplet occurs on most specimens of *B. bowersii, B. mackenziei,* and *B. manipulus,* but in only half the sample of *B. berdmorei*; such a cusplet occurs in most species of *Rattus* (table 4).

Occlusal surfaces of each third lower molar are formed of two simple laminae in all species of *Berylmys.* In none of the specimens of any species did we find an anterolabial cusp; just the opposite condition is found in *Rattus* (table 4).

The Species of *Berylmys*

By using features of skins, skulls, and teeth, we separated all specimens of *Berylmys* we examined into four lots, each of which we regard as a species. It is these four groups that we describe here. Our morphological data supports such assemblages but are inadequate to resolve the nature of geographic variation within each cluster. Studies utilizing larger samples from more places than were available to us are needed to test the significance of the geographic variation we note below. That kind of study will amount to a careful taxonomic revision of the genus, which our report is not. Our accounts are merely introductions to what we hypothesize are species, meant to document the specimens we examined and the localities from which they were collected, provide taxonomic notes, bring together the little information on habits and habitats that is scattered throughout the literature, and formulate questions that can only be answered by further investigation.

Berylmys manipulus

Of the four species of *Berylmys, B. manipulus* has the smallest geographic distribution. It has been recorded only from the As-

sam region of northeastern India and the central and northern parts of Burma. The specimens we studied and the places they were caught are listed below.

INDIA (ASSAM)

1. Manipur: Karong (FMNH 76454, 76458, 76460, 76462, 76463, 76465, 76466, 76468–76470, 76478, 76480, 76481); Bishampur (BM 47.143–47.153); Kopum Thall (BM 85.8.1.316 and 85.8.1.317); Imphal and 5 miles north of there (USNM 279155, 279159–279161); BM 67.151, 67.158, 67.160–67.162)
2. Nagaland (Nata Hills): (BM 47.154 and 47.155)

BURMA

1. Northern Burma: 6 miles north of Myitkyina (USNM 277420)
2. Central Burma: Mansun, Kabaw Valley, Upper Chindwin (BM 15.5.238); Kabaw Valley, 20 miles west of Kindat (BM 16.3.26.78, holotype of *manipulus*; FMNH 82985 and 82986); 6 and 10 miles west of Kindat (BM 16.3.26.69–16.3.26.77); Chin Hills, 50 miles west of Kindat (NMS 290); Mount Victoria (BM 5.5.27.1)

As documented by specimens we studied, the altitudinal range of *B. manipulus* extends from 250 feet (Mansun in the Kabaw Valley) up to 5000 feet (50 miles west of Kindat). Roonwal (1949) reported examples from 5390 feet at Kekrima in the Naga Hills of Assam.

Berylmys manipulus is the smallest in body size of all the species of *Berylmys*. It is easily distinguished from specimens of *B. bowersii* and *B. mackenziei* by its smaller skull, teeth, and skin (tables 5–8; figs. 16–18); by its slightly proodont upper incisors, and by the occurrence of anterolabial cusps on second lower molars in most specimens (table 4). *Berylmys manipulus* has been caught in the same regions of Assam and Burma where examples of *B. bowersii* and *B. mackenziei* were taken but its range does not overlap with that of *B. berdmorei* (table 10), which is similar to it in body size, cranial configuration, incisor proodonty, and possibly natural history.

Specimens of *Berylmys manipulus* from Assam were originally misidentified as *B. berdmorei* until 1916 when Thomas reported on a large series of rats collected by Mackenzie from the Chin Hills of central Burma. He named and described *manipulus* and pointed out the characters that distinguished it from *berdmorei*. Although some specimens of *B. manipulus* and *B. berdmorei* overlap in body size, most *B. manipulus* are smaller, have shorter molar rows, much smaller bullae (both absolutely and relative to size of cranium) that are not inflated as they are in *B. berdmorei*, less proodont upper incisors, tails that are white-tipped and equal to or longer than combined lengths of head and body (instead of lacking white tips and being shorter than head and body as is typical of *B. berdmorei*), and a much higher frequency of anterolabial cusps on the second lower molars (tables 4–6; figs. 17 and 18).

There is appreciable variation in the samples we examined that is due to age; probably variation reflecting secondary sexual features, which we did not investigate; but no geographic variation that appeared significant, at least in features of skins, skulls, and teeth. This was also Ellerman's (1941, 1961) conclusion, but not a view reported by Roonwal, who in 1948 (p. 386) named and described *Rattus manipulus kekrimus* on the basis of four adults caught at Kekrima, about 5390 feet in the Naga Hills of Assam. The holotype, which we have not seen, is in the collections of the Zoological Survey of India (Khajuria, Chaturvedi, and Ghoshal, 1977, p. 37). Roonwal diagnosed *kekrimus* as similar to *manipulus* but with a paler dorsum and, on the average, a longer tail and smaller skull. Other differences between the taxa were expressed as percentages of condylobasal length: the postmolar length is shorter in *kekrimus*, the palatal length greater, the incisive foramina smaller, and the length of upper molar crowns greater.

Ellerman (1961) had examined two specimens from the Naga Hills but made no fuss about any differences between them and specimens from Manipur and Burma. One of us (Musser) also examined those specimens and was not impressed by any morphological distinctions between them and typical *manipulus* from central Burma. External, cranial, and dental measurements of the two specimens from the Naga Hills fall within the range of variation recorded in the samples from Manipur and Burma (table 5). We are not impressed with the distinctions between *kekrimus* and *manipulus* recorded by Roon-

TABLE 5
Measurements (in Millimeters) of Adult *Berylmys manipulus*[a]

Measurement	Holotype BM 16.3.26.78	Assam and Burma
Length of head and body	182	157.8 ± 15.9 (22) 135–185
Length of tail	181	163.6 ± 13.9 (22) 140–187
Length of hind foot	38	36.0 ± 1.5 (22) 33–40
Length of ear	25	24.3 ± 0.7 (22) 23–25
Greatest length of skull	41.5	38.0 ± 1.3 (18) 36.2–40.9
Zygomatic breadth	21.6	19.7 ± 0.8 (18) 18.4–21.4
Interorbital breadth	6.7	6.4 ± 0.2 (20) 6.0–6.6
Length of nasals	18.0	15.3 ± 1.1 (20) 13.2–17.7
Length of rostrum	13.3	11.6 ± 0.8 (20) 9.8–13.6
Breadth of rostrum	8.0	7.0 ± 0.4 (20) 6.4–8.0
Breadth of braincase	16.3	15.4 ± 0.3 (17) 14.7–16.2
Height of braincase	12.0	11.6 ± 0.3 (18) 10.8–12.0
Breadth across incisor tips	—	2.6 ± 0.1 (19) 2.3–2.9
Breadth of zygomatic plate	4.3	4.0 ± 0.3 (20) 3.5–4.5
Length of diastema	14.2	12.6 ± 0.8 (20) 11.2–14.5
Palatal length	22.7	20.5 ± 9.0 (20) 19.0–22.4
Length of incisive foramina	7.8	7.2 ± 0.4 (20) 6.5–7.9
Breadth of incisive foramina	2.7	2.2 ± 0.2 (20) 1.8–2.9
Length of palatal bridge	6.8	6.9 ± 0.3 (20) 6.4–7.5
Breadth of palatal bridge at M^1	4.1	3.4 ± 0.2 (20) 3.0–3.9
Breadth of palatal bridge at M^3	4.3	3.9 ± 0.2 (20) 3.7–4.4
Breadth of mesopterygoid fossa	2.8	2.3 ± 0.2 (20) 2.1–2.8
Length of bulla	5.9	5.7 ± 0.2 (20) 5.2–5.9
Alveolar length of M^{1-3}	6.4	6.4 ± 0.1 (20) 6.2–6.7
Breadth of M^1	2.0	2.0 ± 0.1 (20) 1.8–2.1

[a] Mean plus or minus one standard deviation, number of specimens in parentheses, and observed range are listed for each measurement.

wal. The mean values for cranial measurements that Roonwal (1949a) listed for *kekrimus* do not differ significantly from mean values of our larger series from Burma and Assam listed in table 5. We prefer to treat *kekrimus* as a synonym of *Berylmys manipulus*. There may be significant geographic variation in *B. manipulus* but any patterns are not apparent in the samples we investigated. Study of large series of comparable ages from localities throughout the range of the species are still needed to assess the nature of any significant variation associated with geography.

What little that is known about habitat and habits of *Berylmys manipulus* comes from reports made by Mackenzie, who obtained the original series from central Burma, and the fine observations recorded by Roonwal. *Berylmys manipulus* is strictly terrestrial and a burrower. Mackenzie noted (published in Wroughton, 1916, p. 772) that the rat was "Fairly common in the jungle. I have never obtained it from the fields. The Chins say that, about February–March, 8 or 9 young ones are found with an old female (very rarely an old male) in a single hole; later they break up and pair. Old males are said to live alone except when paired." The best published ecological data associated with *B. manipulus* is that reported by Roonwal (1949b, pp. 101–102) for specimens taken between June and December, 1945, from Manipur between 3500 and 4000 feet. He wrote that the species "is common in various kinds of oak scrub associations (with or without tall grass), and this type of habitat must be regarded as its favourite one. It is not infrequent in ever-

green rain jungle where 5 rats were trapped, including one . . . close to the bank of a hill-stream. The rat was also trapped in riverine meadow, riverine scrub and oak parkland, but never in or near human habitations . . . or in cultivated fields."

Berylmys manipulus feeds on plants, insects, and earthworms. Roonwal (1949b, p. 102) examined the stomach contents of eight specimens caught during late September to October from oak scrub and evergreen jungle. He found that *B. manipulus*

> takes in both vegetable and animal (insects and earthworms) food—sometimes exclusively vegetable (1 case), sometimes exclusively animal (3 cases) and sometimes mixed (4 cases). The vegetable matter taken consisted of leaves and inflorescence of grasses, seeds of Compositae, flowers and leaves of Leguminosae, pieces of unidentified fruit skins, and, finally, liverworts (Bryophyta). The animal matter consisted of earthworms and insects. Earthworms figured prominently and would appear to be a favourite food . . . ; they formed the major portion of the stomach contents in 4 out of a total of 8 specimens examined . . . . Insects occurred in the stomach in 5 cases; in one of these, the entire stomach contents consisted of a single species of winged termites . . . , while in other cases different insects occurred in varying proportions. The following insect orders were represented: Orthoptera (Tettigonidae), Isoptera (winged termites), Hemiptera, Coleoptera (Scarbaeidae) and Diptera (Tipulidae).

Berylmys berdmorei

The geographic range of *Berylmys berdmorei* is east of the range of *B. manipulus*: Southern Burma (Tennasserim), northern Thailand and northern Laos, southeastern Thailand, Cambodia, and southern Vietnam. Although *B. berdmorei* occurs over a much greater region than does *B. manipulus,* the former is known by fewer specimens and they are from widely scattered localities. Specimens we studied (except the holotype of *berdmorei*) and the places they were collected are listed below.

SOUTHERN BURMA
1. Northern Tenasserim, Thagata, Muleyit Range (BM 16.2.16.1, the holotype of *Epimys berdmorei mullulus*)
2. Mergui, southern Tenasserim: holotype of *Mus berdmorei,* in the collections of the Zoological Survey of India (Khajuria, Chaturvedi, and Ghoshal, 1977, p. 37); not examined by us

THAILAND
1. Northern Thailand: Chiengmai Province, Mount Anka (MCZ 35385) and MeMaw (NMS 224)
2. Southeastern Thailand: Provinces of Nakhon Nayok, Rayong, Chanthaburi, Trat, and Nakhon Ratchasima (Khorat) AMNH 240014; USNM 297163, 308219, 355547, 533360–533371, 535205; BM 69.285 and 15.11.4.157, the holotype of *Rattus berdmorei magnus*)

CAMBODIA
1. Region Kampot: (Coll. No. 14 in MNHN)

NORTHERN LAOS
1. Xieng Khoung Region: USNM 355547

SOUTHERN VIETNAM
1. Quang Tri Province: USNM 357706
2. Darlac Province: Buon Mnang (USNM 321226)
3. Tuyen Duc Province: Fyan (USNM 321227)
4. Con Son Island (Poulo Condor): off the southeastern coast of southern Vietnam (USNM 357225)

The known altitudinal range of *Berylmys berdmorei* extends from near sea level in southern Vietnam and southeastern Thailand up to 4300 feet in northern Thailand (Mount Anka).

Berylmys berdmorei is a chunky rat of medium body size. Its upperparts are iron gray, the underparts are white. The tail is shorter than the combined lengths of head and body in all the specimens we examined (table 6). These external features distinguish *B. berdmorei* from the other species of *Berylmys.* Other distinguishing characters of *B. berdmorei* are its stocky cranium, high braincase, large inflated auditory bullae, and slightly proodont upper incisors. The great inflation of the bullae is distinctive and separates *B. berdmorei* from *B. manipulus, B. mackenziei,* and *B. bowersii* (tables 5–8; figs. 16–18).

Until the 1960s and 1970s, *Berylmys berdmorei* was represented by few specimens other than holotypes of the three names associated with the species. The first name, *berdmorei,* was proposed by Blyth in 1851 (p. 173); the holotype was obtained from Mergui, southern Tenasserim. Two other names were published in 1916: *Epimys berdmorei mullulus* was named by Thomas (1916, p. 413) and based on a specimen from north-

TABLE 6
Measurements (in Millimeters) of Adult *Berylmys berdmorei*[a]

Measurement	Holotype of *B. b. mullulus* (Tenaserrim)	Northern Laos	Holotype of *B. b. magnus* (Thailand)	Southeastern Thailand	Southern Vietnam	Con Son Island
Length of head and body	—	191	210	216.6 ± 22.9 (9) 190–255	204.7 ± 4.9 (3) 199–208	197
Length of tail	—	147	182	170.9 ± 13.2 149–192	166.0 ± 8.7 (3) 156–172	189
Length of hind foot	—	38	40	39.8 ± 2.8 (9) 37–46	39.3 ± 1.2 (3) 38–40	41
Length of ear	—	23	20	25.1 ± 2.2 (9) 20–27	27.0 ± 2.8 (2) 25–29	27
Weight	—	—	—	250.6 ± 42.0 (8) 177–300	—	—
Greatest length of skull	39.0	41.5	46.5	44.5 ± 3.4 (9) 38.0–50.3	44.8 ± .7 (2) 44.3–45.3	45.4
Zygomatic breadth	21.3	22.2	23.5	23.6 ± 1.1 (10) 21.8–25.8	22.7 ± .9 (3) 21.7–23.6	23.4
Interorbital breadth	6.7	6.7	6.9	7.0 ± .4 (10) 6.5–7.5	6.9 ± .4 (3) 6.6–7.3	7.1
Length of nasals	—	17.3	19.4	18.7 ± 1.3 (9) 16.4–20.8	18.7 ± .4 (2) 18.4–19.0	18.2
Length of rostrum	—	12.5	15.6	14.9 ± 1.3 (9) 12.9–17.0	15.2 ± .1 (2) 15.1–15.2	15.0
Breadth of rostrum	7.4	7.9	8.2	8.7 ± .7 (10) 7.8–10.0	8.8 ± .6 (3) 8.1–9.3	8.3
Breadth of braincase	15.9	17.4	17.3	17.4 ± .5 (10) 16.6–18.1	17.3 ± .6 (3) 16.9–18.0	16.8
Height of braincase	12.5	12.7	13.4	13.4 ± .5 (10) 12.4–14.3	13.2 ± .9 (3) 12.6–14.3	13.3
Breadth across incisor tips	2.8	3.0	3.5	3.2 ± .2 (10) 2.9–3.4	3.0 ± .2 (3) 2.8–3.2	3.2
Breadth of zygomatic plate	4.0	4.3	4.7	4.7 ± .4 (10) 4.3–5.4	4.6 ± .2 (3) 4.4–4.8	4.4
Length of diastema	12.6	13.4	16.1	14.8 ± 1.0 (10) 13.5–16.8	14.1 ± .2 (3) 13.9–14.2	14.8
Palatal length	21.0	21.9	24.9	23.5 ± 1.2 (10) 22.0–25.5	23.6 ± .8 (3) 22.7–24.2	23.5
Postpalatal length	—	16.4	—	17.1 ± 1.1 (10) 15.6–19.0	16.4 ± .4 (3) 16.1–16.8	17.3
Length of incisive foramina	7.7	7.3	9.5	8.4 ± .7 (10) 7.2–9.7	8.1 ± .1 (3) 8.1–8.2	8.6
Breadth of incisive foramina	2.6	3.1	3.1	3.0 ± .3 (10) 2.5–3.4	2.9 ± .3 (3) 2.6–3.1	3.1
Length of palatal bridge	6.5	7.1	7.4	7.7 ± .4 (10) 7.1–8.5	7.8 ± .4 (3) 7.3–8.1	6.8
Breadth of palatal bridge at M^1	4.1	4.2	4.0	4.3 ± .4 (10) 3.8–5.0	3.7 ± .2 (3) 3.5–3.8	3.6

TABLE 6—(*Continued*)

Measurement	Holotype of *B. b. mullulus* (Tenaserrim)	Northern Laos	Holotype of *B. b. magnus* (Thailand)	Southeastern Thailand	Southern Vietnam	Con Son Island
Breadth of palatal bridge at M^3	4.5	5.0	4.5	4.9 ± .4 (10) 4.5–5.8	4.6 ± .6 (3) 4.0–5.0	4.4
Breadth of mesopterygoid fossa	2.2	2.6	2.8	2.7 ± .2 (10) 2.5–3.0	2.8 ± .3 (3) 2.5–3.1	2.5
Length of bulla	7.1	8.3	8.7	9.0 ± .4 (10) 8.4–9.6	8.1 ± .1 (3) 8.0–8.2	8.7
Alveolar length of M^{1-3}	6.6	6.6	7.2	7.2 ± .3 (10) 6.9–7.8	7.6 ± .4 7.2–8.0	7.4
Breadth of M^1	2.1	2.3	2.2	2.3 ± .1 (10) 2.1–2.5	2.3 ± .1 (3) 2.2–2.4	2.3

[a] Mean plus or minus one standard deviation, number of specimens in parentheses, and observed range are listed for each measurement.

ern Tenasserim at Thagata; *Rattus berdmorei magnus* was proposed by Kloss (1916a, p. 57) for a specimen from southeastern Thailand. The holotypes of *mullulus* and *magnus* consist of skins and complete skulls. That of *berdmorei* is represented by a skin and skull in fluid, according to Khajuria, Chaturvedi, and Ghoshal (1977, p. 37). Kloss (1917, p. 6) examined the specimen and noted that "All that remains of the type of this species . . . is a portion of the skull including the zygomata to their posterior roots and possessing above the greater part of the parietals, but lacking below the bullae and basioccipital, etc."

We do not know whether the three names represent distinctive populations or simply reflect distinctions associated with individual or sexual variation (or both). We find that specimens from southern Burma, northern Thailand, and northern Laos have smaller values for some dimensions, especially length of bulla and alveolar length of maxillary toothrow, than do those rats from southeastern Thailand, southern Vietnam, and Con Son Island (table 6). If that distinction is real and not an artifact of small sample size and too few samples then either *berdmorei* or *mullulus* is the name for those specimens with small bullae and short toothrows. Possibly *mullulus* will prove to be a synonym of *berdmorei*. Kloss's name, *magnus*, is available for the larger rats from southeastern Thailand, southern Vietnam, and Con Son Island. But what the real pattern of geographic variation is in *B. berdmorei* will only be discovered after larger samples are obtained from many more localities. There is now a large series from southeastern Thailand but samples from elsewhere within the known range of the species consist of either one, two or three specimens.

Ecological information for *Berylmys berdmorei* is scanty. The largest sample of the species, that from southeastern Thailand, comes from lowlands at 50 meters (Pantuwatana, Imlarp, and Marshall, 1969). Of these rats, Marshall (1977b, p. 443) wrote: "Although uncommon and spread out in sparse populations, this rat is eventually caught in traplines set in swampy forests and marshy grass, sometimes during the second or third night, after the *R. rattus* have been thinned out. The lesser white-toothed rat is host to the flea, *Xenopsylla vexabilis*." The specimen from Con Son Island was taken in forest at 300 meters (Van Peenen, Cunningham, and Duncan, 1970).

Berylmys mackenziei

Most specimens of *Berylmys mackenziei* come from Assam and Burma. Other records

are from the Szechwan Province of China and southern Vietnam. Between Assam, Burma, and Szechwan on the one hand and southern Vietnam on the other is an extensive region from which the species has not been recorded: southern China, Thailand, Laos, Cambodia, and northern Vietnam. The gap in distribution is probably not real but just where *B. mackenziei* may occur in the area can only be determined by future biological survey. The specimens we examined and localities where they were taken are listed below.

NORTHEASTERN INDIA (ASSAM)

1. Cherrapunji: FMNH 76499–76501
2. Lushai Hills: Sangao (FMNH 76502–76507)
3. Manipur: Bishampur (BM 46.141, 47.142, 66.3110); Khasi Hills (BM 91.10.7.131; Khasi Hills, Mawryngkueng (FMNH 76508–76511); Khasi Hills, Mawphlang (FMNH 75819, 75820, 76479, 76485, 76488, 76489, 76667, 76490–76496, 84852–84866); Karong (FMNH 76456, 76461, 76464, 76467, 76472, 76473, 76482, 76483)
4. Naga Hills (Nagaland): Takubama (BM 47.133–47.140, 66.3100–66.3109; FMNH 76497 and 76498)

CENTRAL BURMA

1. Chin Hills: 50 miles west of Kindat (BM 16.3.26.61–16.3.26.64, 16.3.26.65—holotype of *Epimys mackenziei*—16.3.26.66; NMS 342; FMNH 82974 and 82975); Haingyan (BM 15.5.5.246 and 15.5.5.247)

SOUTHERN BURMA

1. Northern Tenasserim: Thagata, Muleyit Range (BM 88.12.1.47, holotype of *Epimys mackenziei fea*)

CHINA

1. Szechwan Province, Mount Omei (USNM 255354)

SOUTHERN VIETNAM

1. Tuyen Duc Province: 2 miles south of Dalat (USNM 321313 and 321314); Fyan (USNM 321316); Langbian Peak (NMS 3407)
2. Lam Dong Province: 17 miles east of Djiring (USNM 321315)

Altitudinal data is not associated with all specimens of *B. mackenziei* but the information that is available suggests the species to be a highland animal. No elevational records are lower than 3500 feet (Bushampur, Manipur), most of them are around 5000 feet, and the highest is 6000 feet (Szechwan Province of China).

Specimens collected by Mackenzie from 5000 feet in the Chin Hills of central Burma formed the type series of *B. mackenziei,* which was originally described as a species of *Epimys* (the name then used for what is now called *Rattus*) by Thomas in 1916 (p. 411). *Berylmys mackenziei* is large-bodied but most specimens are smaller than most examples of *B. bowersii* and females of *B. mackenziei* invariably have five pairs of mammae as opposed to the four pairs always found in females of *B. bowersii.* Size and number of mammae were the basic features Thomas used to distinguish the two species, and they are still reliable characters to separate most specimens of each from *B. mackenziei* from most *B. bowersii,* especially in places where the two species occur together in Assam and central Burma (table 10).

Thomas's astuteness was not shared by later biologists. Allen, who monographed the mammals of China in 1940, included *mackenziei* within *Rattus bowersii* because he suspected *mackenziei* to probably represent young examples of *bowersii.* Ellerman (1947–1948, 1949, 1961) in his checklists and report on Indian murids, treated *mackenziei* as a subspecies of *R. bowersii.* He (Ellerman, 1961, p. 624) realized that both kinds had been collected at the same place indicating that "*mackenziei* may have to be given specific rank."

Berylmys mackenziei and *B. bowersii* are morphologically more similar to each other than to any other species of *Berylmys.* Where they occur together in central Burma and Assam *B. mackenziei* is distinguished from *B. bowersii* by the following combination of features.

1. The pelage of *B. mackenziei* is thicker and usually softer to the touch than that of *B. bowersii.* Most specimens are dark gray or iron gray and there are few individuals with brownish gray or dark brown pelage, a common phase in *B. bowersii.*

2. More of the tail is white in *B. mackenziei* than in *B. bowersii.* In the former, most specimens have a tail in which the basal half is brown and the distal half is white; in other specimens the white may constitute as much as two-thirds of the tail; in a few examples, the white portion is shorter and takes up one-third of the tail length. Specimens of *B. bow-*

ersii have brown tails in which the distal one-fifth is white.

3. Body size of *B. mackenziei* is smaller than that of *B. bowersii.* This is reflected in the shorter hind foot, skulls, bullae, and maxillary tooth rows of *B. mackenziei* (tables 7 and 8; fig. 16).

4. The zygomatic plates are straighter in *B. mackenziei* and not as sloping as they are in most specimens of *B. bowersii.*

5. In *B. mackenziei,* cusp t3 is present on the second upper molar in nearly half the sample, and occurs on the third upper molar in about one-fourth of the sample; cusp t3 is absent from the second and third molars of all the *B. bowersii* we examined. Also, posterior labial cusplets are absent from the first lower molars in one-fourth of the sample of *B. mackenziei* but the cusplets occur in most specimens of *B. bowersii* (table 4).

6. In dorsal view, dorsolateral outlines of the braincase are usually outlined by low temporal ridges in *B. mackenziei,* beading that extends all the way back to the occiput. The braincase of *B. bowersii* appears rounder and smooth because the temporal ridges usually fade out halfway back on the braincase (fig. 16).

7. In all the material we examined, females of *B. mackenziei* have five pairs of mammae: a pectoral pair, two postaxillary pairs, and two inguinal pairs. *Berylmys bowersii* has four pairs: one pectoral pair, one postaxillary pair, and two inguinal pairs.

Because of geographic variation in both *B. mackenziei* and *B. bowersii,* all the features distinguishing the two in Assam and central Burma may not do so in other parts of their geographic ranges. Length of maxillary toothrow, for example, varies geographically (table 9). Specimens of *B. bowersii* from southern China, northern Thailand and northern Laos are smaller in body size than those from elsewhere in the range of the species (table 8; figs. 24 and 25) and their molar rows are similar in length to those of *B. mackenziei.* In *B. mackenziei,* the specimen from Szechwan, China, and those from southern Vietnam have longer molar rows, on the average, than specimens from Assam and central Burma and there is extensive overlap in this dimension between these *B. mackenziei* and some samples of *B. bowersii.* Tail coloration also varies geographically in *B. mackenziei.* The specimen from Szechwan, the one from northern Tenasserim, and those from southern Vietnam have tails that are either all brown or with a very short white tip, a pattern like that in *B. bowersii.* At none of those places have specimens of *B. bowersii* been taken.

Berylmys mackenziei occurs over an extensive area and there is noticeable geographic variation in some features of the species. We cannot assess the significance of this variation because of the few specimens known from outside Assam and central Burma. Most examples of *B. mackenziei* come from that region; the specimen from Thagata in northern Tenasserim, the example from Szechwan, and the four from southern Vietnam are the only other specimens. Thomas (1916, p. 412) designated the rat from Thagata as holotype of *fea,* a subspecies of *mackenziei*: "Size of body slightly less than in true *mackenziei,* except that there is rather more brown on the feet. Tail with only its extreme tip . . . white, instead of its terminal two-fifths. Skull essentially as in *mackenziei,* but zygomatic plate narrower, palatal foramina less open, bullae rather smaller." One of us (Musser) examined the holotype. It is an adult female with five pairs of mammae and is an example of *B. mackenziei.* But, except for the short white tip of its tail, there is nothing about the specimen that separates it from most examples of *B. mackenziei* from Assam and central Burma.

The specimen from Szechwan marks the northernmost record of *B. mackenziei* and of *Berylmys* in general. It is the largest-bodied of all the specimens we examined and in body size is indistinguishable from most examples of *B. bowersii* (tables 7 and 8). The specimen is an old adult female with five pairs of large teats. The pelage is dark glossy gray and the tail is dark brown with a short white tip. Although large, the configuration of the skull is like that of *B. mackenziei* and not similar to that in *B. bowersii.* If this specimen represents the population of *B. mackenziei* in the mountains of Szechwan, then those rats are larger and much darker than *B. mackenziei* from Assam and central Burma.

The specimens from southern Vietnam

TABLE 7
Measurements (in Millimeters) of Adult *Berylmys mackenziei*[a]

Measurement	Holotype of *mackenziei* BM 16.3.26.65	Assam and Burma	Holotype of *fea* BM 88.12.1.47	Southern Vietnam
Length of head and body	234	195.4 ± 24.4 (23) 155–243	210	231 ± 1.4 (2) 230–232
Length of tail	248	216.2 ± 28.5 (22) 150–254	270	254.5 ± .7 (2) 254–255
Length of hind foot	50	47.8 ± 2.3 (23) 44–51	52	52.0 ± 1.0 (3) 51–53
Length of ear	31	28.2 ± 1.5 (23) 25–31	27	34.0 ± 1.4 (2) 33–35
Greatest length of skull	50.4	46.3 ± 3.5 (22) 40.2–51.5	50.0	53.2 ± .8 (3) 52.3–53.7
Zygomatic breadth	25.4	23.1 ± 1.7 (18) 21.4–25.8	24.5	26.1 ± 1.1 (3) 25.3–27.4
Interorbital breadth	6.9	7.2 ± 0.3 (24) 6.8–8.1	7.7	7.8 ± .4 (3) 7.6–8.3
Length of nasals	20.8	18.7 ± 1.8 (23) 15.3–21.5	20.5	21.5 ± .0 (3) 21.5–21.5
Length of rostrum	16.6	15.1 ± 1.5 (23) 12.6–17.6	16.4	17.9 ± .4 (3) 17.5–18.3
Breadth of rostrum	9.5	8.5 ± 0.7 (20) 7.5–9.8	9.1	9.4 ± .5 (3) 8.9–9.9
Breadth of braincase	18.8	17.9 ± 0.5 (23) 17.0–18.9	19.1	20.0 ± .4 (3) 19.6–20.4
Height of braincase	14.0	13.3 ± 0.7 (23) 12.0–14.6	14.0	14.4 ± .6 (3) 13.8–15.0
Breadth across incisor tips	3.8	3.4 ± 0.2 (23) 3.0–3.8	3.2	3.7 ± .2 (3) 3.5–3.9
Breadth of zygomatic plate	5.5	5.4 ± 0.6 (23) 4.5–6.6	5.6	5.5 ± .1 (3) 5.4–5.6
Length of diastema	16.0	13.5 ± 1.4 (24) 11.2–16.0	15.6	16.2 ± .5 (3) 15.7–16.6
Palatal length	27.1	24.4 ± 1.7 (24) 21.4–27.1	26.5	28.2 ± .7 (3) 27.6–29.0
Postpalatal length	—	—	—	19.3 ± .3 (3) 19.0–19.6
Length of incisive foramina	9.4	8.6 ± 0.6 (24) 7.9–9.6	9.1	9.6 ± .2 (3) 9.5–9.8
Breadth of incisive foramina	3.3	2.8 ± 0.3 (24) 2.4–3.4	3.0	3.2 ± .2 (3) 3.1–3.5
Length of palatal bridge	9.7	8.5 ± 0.7 (24) 6.8–9.7	9.5	10.6 ± .4 (3) 10.1–10.9
Breadth of palatal bridge at M^1	4.6	4.0 ± 0.4 (24) 3.3–4.9	3.9	4.6 ± .1 (3) 4.5–4.7
Breadth of palatal bridge at M^3	5.4	4.6 ± 0.5 (24) 4.0–5.7	4.9	5.4 ± .3 (3) 5.2–5.7
Breadth of mesopterygoid fossa	3.6	3.2 ± 0.2 (24) 2.8–3.6	3.1	3.6 ± .1 (3) 3.5–3.7

TABLE 7—(*Continued*)

Measurement	Holotype of *mackenziei* BM 16.3.26.65	Assam and Burma	Holotype of *fea* BM 88.12.1.47	Southern Vietnam
Length of bulla	6.4	6.3 ± 0.3 (23) 5.8–6.8	7.1	7.1 ± .5 (3) 6.6–7.6
Alveolar length of M^{1-3}	9.2	8.9 ± 0.4 (24) 8.1–9.6	8.7	9.3 ± .4 (3) 9.0–9.8
Breadth of M^1	2.7	2.6 ± 0.1 (24) 2.4–2.8	2.7	2.7 ± .1 (2) 2.6–2.7

[a] Mean plus or minus one standard deviation, number of specimens in parentheses, and observed range are listed for measurements of samples from Assam and Burma and from southern Vietnam.

were originally identified as *Rattus bowersii* (Van Peenen, Ryan, and Light, 1969) but they are examples of *B. mackenziei.* In body size, they are closely similar to samples from Assam and Burma (table 7; fig. 22). They differ in having much darker upperparts and tails that are either all brown or with very short white tips.

We do not know of any specimens from the large region between the disjunct localities where examples of *B. mackenziei* have been taken. Marshall (1977b) recorded the species from northern Thailand but everything he examined are examples of small-bodied *B. bowersii* (table 8; figs. 24 and 25), a point we discuss more fully in the account of *B. bowersii.* To date, we can document only two species of *Berylmys* from Thailand: *B. bowersii* and *B. berdmorei.*

Berylmys mackenziei is terrestrial, probably lives in forests, and is associated with habitats between 3500 and 6000 feet; we can report nothing else about habitat or habits of the species. This is unfortunate because we would like to know the ecological relationships between *B. mackenziei* and *B. bowersii* at the places where they occur together.

Berylmys bowersii

Compared with the other species of *Berylmys, B. bowersii* is the largest in body size, is the only one with four pairs of mammae, occurs over a greater geographic area, and is the only species occurring south of the Isthmus of Kra on the Sunda Shelf. The specimens we examined and the places they were collected are listed below.

NORTHEASTERN INDIA

1. Tirap District: Arunachal Pradesh (USNM 543092)
2. Assam: Manipur, Khasi Hills, Mawphlang (BM 20.11.1.56, holotype of *Rattus wellsi*; FMNH 76486 and 76487); Manipur, Machi (BM 85.8.1.315); Manipur, Karong (FMNH 76455, 76457, 76459, 76471, 76474–76476, 76484); Naga Hills, Mokokchung (BM 20.6.6.19, 20.6.6.20, 20.6.6.25)

BURMA

1. Northern Burma: (BM 20.8.8.7 and 20.8.8.8); Gangfang (AMNH 115232 and 115233); Ngawchaung River (AMNH 115234–115238); Hpawshi (AMNH 115239); Nam Tamai Valley (BM 32.11.1.85, 32.11.1.86, 50.692–50.696; FMNH 41017); Adung Valley (FMNH 41018); Akhe Triangle (BM 50.697); hills east of Nam Tisang (BM 32.11.1.83)
2. Central Burma: Chin Hills, 50 miles west of Kindat (BM 16.3.26.67 and 16.3.26.68); Chin Hills, Kindat (BM 14.7.19.171); Chin Hills, Mount Victoria (AMNH 163693 and 163694)

SOUTHERN CHINA

1. Yunnan Province: Mu Cheng, Salaween Drainage (AMNH 43304 and 43303); Ho Mu Shu Pass (MCZ 23580)
2. Kwangsi Province: Yao Shan (FMNH 41332)
3. Fukien Province: Fuching Hsien (AMNH 84621, 84626, 84659; FMNH 32708; MCZ 24512 and 24513); Yenping (AMNH 60337 and 84643); Northwest Fukien (AMNH 38338); Kuatun (BM 5.6.1.7–5.6.1.9, 5.8.22, 8.8.11.67, 8.8.11.68, 97.6.6.1, 97.6.6.2—ho-

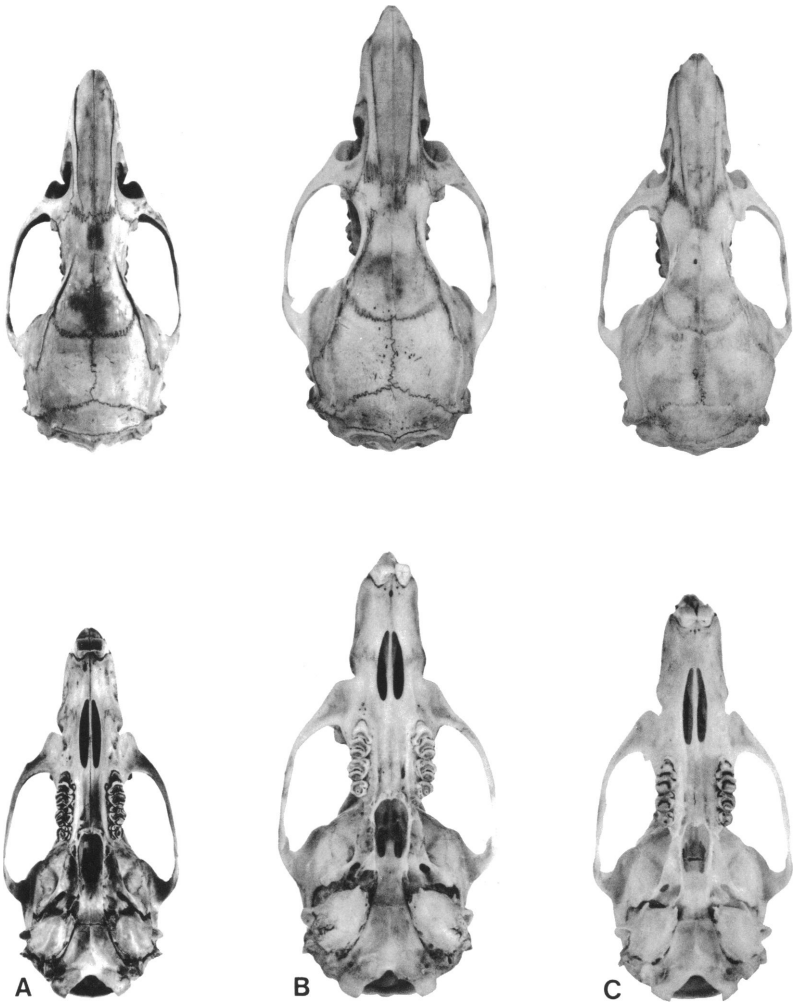

FIG. 22. Views of crania from adult *Berylmys mackenziei*. A, Assam Naga Hills (BM 66.3100). B, China, Szechwan Province, Mt. Omei (USNM 255354). C. southern Vietnam, near Dalat (USNM, 321313). Natural size. See text for discussion of geographic variation in *B. mackenziei*.

lotype of *Mus latouchei*—97.6.63, 13.12.8.31; MNHN 1900-465)

NORTHERN THAILAND

1. Chiengmai Province: AMNH 167928; ASRCT 54-1287; USNM 267248, 533372, 533477
2. Tak Province: Sikawtur, 40 miles northwest of Raheng (BM 47.1461, holotype of *Rattus bowersii lactiventer*; BM 47.1469, holotype of *Rattus kennethi*
3. Kalasin Province: (ASRCT 54-647)

NORTHERN LAOS

1. Phong Saly (FMNH 31985, 31988, 31989, 31991); Ban Theuong, 18 km. northwest of Xieng Khoang (USNM 355544–355546; BM 26.10.4.145; MNHN 1929-291)

NORTHERN VIETNAM

1. Ngai Tio (BM 25.1.1.76–25.1.1.78); Backan (BM 27.12.1.179); Chapa (BM 33.4.1.525–33.4.1.530, 33.4.1.532–33.4.1.535; FMNH 39263–39268, 31984; RMNH 39261; USNM 259497)

SUNDA SHELF

1. Peninsular Thailand south of Isthmus of Kra (10°30′ N): Nakhon Si Thammarat Province (USNM 533373); Trang Province (USNM 84398, 86738, 86739, 86737, holotype of *Mus ferreocanus*); Yala Province (USNM

533374); Narathiwat Province (USNM 533375)
2. Malay Peninsula: Kedah State (BM 55.2928); Perak State (BM 55.2929, 9.4.1.398–9.4.1.400; NMS 1640/08, 701/16, 1643/08, 64/15; Selangor State (AMNH 217611, 239700, 239705, 239706, 239733–239736, 240391–240403; BM 61.1258, 61.1257, 49.218–49.221; USNM 291286, 357890–357892, 357894–357896, 357903–357906, 357909, 357911–357918); Pahang State (BM 61.1259, 61.1260; FMNH 98535–98538; USNM 307591, 307592, 357907; AMNH 217607–217610)
3. Sumatra: Medan region (specimens at MZB examined by Musser)

Most specimens of *Berylmys bowersii* are from elevations between 3000 and 5000 feet. The altitudinal range indicated by data on specimen labels is from 500 feet (Bac-Kan, northern Vietnam) up to 8600 feet (Mount Victoria in the Chin Hills of central Burma).

The earliest name for the species is *Mus bowersii,* proposed by Anderson in 1878 (p. 304). The holotype, which is the basis for Anderson's lovely colored plate reproduced here in figure 23, is an adult female that was collected at Hotha in the Kakhyen Hills of Yunnan, China at 4500 feet. The specimen is in the collections of the Zoological Survey of India at Calcutta (Khajuria, Chaturvedi, and Ghoshal, 1977, p. 36). We did not examine it. Kloss borrowed it and other types and in 1917 reported his observations. Of the holotype of *bowersii,* Kloss (1917, p. 5) wrote that "The body, which is preserved in alcohol, no longer serves to indicate the colour of the animal in life but shows that the pelage is of the same hispid type as in *R. berdmorei* (Blyth) and *R. ferreocanus* (Miller), being composed of long, slender spines or bristles and a much softer under-fur. The skull is in poor condition, as both the zygomata and the whole of the left side of the palate and tooth-row are broken, while the tips of all the incisors are much chipped."

From the time that Anderson's description of *bowersii* was published until now, six scientific names have been applied to samples of the species: *latouchei* (Thomas, 1897), *ferreocanus* (Miller, 1900), *lactiventer* (Kloss, 1918), *wellsi* (Thomas, 1921), and *totipes* (Tien, 1966a). We examined all the holotypes except that of *totipes.*

The name *latouchei* was eventually treated as a subspecies of *B. bowersii,* although not a distinctive one. Writing about specimens of *B. bowersii* from northern Vietnam and northern Laos, Osgood (1932, p. 312) noted that

> Specimens in the British Museum [from northern Vietnam and Laos], all of which are called *bowersi* by Thomas, might better be referred to *latouchei* which is no more than a slight subspecies of *bowersi.* Perhaps *latouchei* may be somewhat paler in color than *bowersi* but otherwise it seems to differ only one slight cranial character. In *bowersi* the nasals are extended posteriorly beyond the premaxillae whereas in *latouchei* the nasals and premaxillae end evenly. In this respect the Tonkin, northern Vietnam and Laos specimens agree with *latouchei* from Kuatun, Fukien, China.

In his monograph on Chinese mammals, Allen (1940) recognized *latouchei* as a valid eastern subspecies of *B. bowersii,* based mainly on paler (gray rather than grayish brown or brown) upperparts. Ellerman (1961, p. 623), however, indicated that *latouchei* "seems almost certainly a synonym of the typical race."

The holotype of *Mus ferreocanus* is an adult female (USNM 86737) collected at 3000 feet in the highlands of Trang in peninsular Thailand south of the Isthmus of Kra. Miller (1900, pp. 140–141) provided a long description of the species (he had two other specimens in addition to the holotype) and characterized it as: "Size large (hind foot about 56; greatest length of skull, 53) tail slightly longer than head and body, dark brown at base, whitish at tip; ear long and narrow, its length greater than distance from eye to nostril; fur composed almost exclusively of fine grooved bristles; general color above bluish iron gray, beneath pure white; skull with slightly developed supraorbital ridges." Miller did not compare *ferreocanus* with *bowersii* and remarked that "This species is not closely related to the other rats of the Malay Peninsula; and I am unable to find any description of an animal at all resembling it among the forms occurring in the East Indian Archipelago." For years, *ferreocanus* was regarded as a species (Thom-

FIG. 23. *Mus bowersii*. A copy of Anderson's original plate 17 published in 1878. Approximately ×⅔ natural size.

as, 1916, for example) but was eventually treated as a subspecies of *Rattus bowersii* (Osgood, 1932; Chasen, 1940; Ellerman, 1961; Medway, 1969).

In a report on "New and Other White-Toothed Rats From SIAM," Kloss in 1918 named and described *Rattus bowersii lactiventer* and *Rattus kennethi.* Each name was based on one specimen and both had been collected at Sikawtur, 40 miles northwest of Raheng in Tak Province of northern Thailand. According to Kloss (pp. 80–82), *R. b. lactiventer* "Differs from *R. b. bowersi* in being white, not yellow beneath, and from *R. b. ferreocanus* in being browner and warmer above and with a good deal of white on the feet; from both in having no pale tip to the tail. . . . Skull like that of *ferreocanus,* the ante-orbital plate with the lower edge vertical; but the nasals not extending so far behind the premaxillaries, posterior edge of frontals more curved, bullae larger, palatal foramina slightly smaller, falling short of the molars by nearly 2 mm., and the tooth-rows markedly diverging posteriorly." For Kloss, *R. kennethi* was "Like *R. b. lactiventer* but smaller and without the warmer colouring on the sides, etc.; feet of more clearly defined dark and white pattern, tail pale below with a distinct pale tip. Skull more rounded and relatively broader, palatal foramina reaching the line of the molars, toothrows diverging rather less posteriorly. . . . Skull with broader ante-orbital foramina than in *R. b. lactiventer,* the front edge of the plate slightly convex and overhanging the base; palatal foramina longer and pointed posteriorly, bullae relatively rather smaller."

The holotype of *lactiventer* has bright tan upperparts and white underparts. The animal is an adult example of *B. bowersii,* the population that occurs in northern Thailand. Marshall (1977), who reported on the rats and mice of Thailand, concluded the same. He, however, regarded the holotype of *kennethi* to represent *B. mackenziei* because he thought the specimen to be an adult; because it was smaller in body size than the holotype of *lactiventer* and because both had been collected at the same place, it was logical to assume that the two specimens represented two species, *B. bowersii* and *B. mackenziei.* We interpret the morphological features of *kennethi* in a different way. To us, the specimen is simply a young *B. bowersii.* The molars of the holotype of *kennethi* are not as worn as those in the holotype of *lactiventer.* Configuration of the skull is similar to that typical of young adult *B. bowersii.* The holotype of *kennethi* also has the same tan upperparts.

The next name to be proposed, *wellsi,* was described by Thomas (1921, pp. 26–27) as a species of *Rattus.* He noted that "This rat is externally very like a small *R. mackenziei,* to which species it is probably most closely allied. But it is readily distinguishable by its smaller skull, its large smooth braincase and small muzzle." The holotype of *wellsi* (BM 20.11.1.56) was collected at Mawphlang in the Khasi Hills of Manipur, Assam, a region where *B. bowersii* and *B. mackenziei* occur together. The holotype is a young adult female. Compared with young examples of *B. mackenziei* of similar age, we found that the holotype is larger, has a large, round, and smooth braincase, sloping zygomatic plates, large molars (alveolar length of M^{1-3} is 9.0 mm.; breadth of M^1 is 2.9 mm.), and large bullae. The cranial proportions are those of young *B. bowersii,* not *B. mackenziei.* Ellerman (1949) first treated *wellsi* as a subspecies of *B. bowersii* but later (Ellerman, 1961) synonymized *wellsi* with *B. mackenziei.* We regard *wellsi* to be an example of *B. bowersii bowersii.*

The most recent scientific name to be proposed for a sample of *B. bowersii* is *totipes* (Tien, 1966a, p. 438), which is based on two specimens from Ha Tinh (105°40′ E, 18°19′ N), 80 meters, in northern Vietnam. Tien distinguished *totipes* from typical *bowersii* by the dirty white underparts of the two specimens from Ha Tinh, and their feet and tail, which are brown all over. We have not examined Tien's specimens but we are not impressed with the diagnostic features of *totipes.* A brown monocolored tail, for example, occurs frequently in samples of *B. bowersii* from southern China, northern Thailand, northern Laos, and northern Vietnam.

Judged by the material we have studied, there is geographic variation in some characters of *B. bowersii* but there are not enough specimens from throughout the range of the

TABLE 8
Measurements (in Millimeters) of Adult *Berylmys bowersii*[a]

Measurement	Northeastern India, Assam, and Northern Burma	Northern Thailand	Northern Laos	Northern Vietnam	Peninsular Thailand and Malaya
Length of head and body	249.7 ± 12.6 (16) 236–285	234.3 ± 1.2 (3) 233–235	245.3 ± 15.4 (4) 228–261	263.6 ± 15.2 (7) 240–285	264.2 ± 18.6 (24) 230–300
Length of tail	269.3 ± 11.4 (16) 249–292	248.3 ± 7.6 (3) 240–255	271.3 ± 14.2 (4) 250–280	284.8 ± 18.0 (6) 260–310	283.3 ± 11.5 (24) 262–300
Length of hind foot	57.0 ± 2.3 (16) 52–61	52.7 ± 1.2 (3) 52–54	54.3 ± 1.5 (4) 53–56	55.6 ± 1.1 (8) 54–57	55.0 ± 1.8 (24) 52–59
Length of ear	33.8 ± 1.1 (11) 32–36	28.0 ± 1.0 (3) 27–29	32.3 ± 1.3 (4) 31–34	34.0 ± 2.3 (7) 30–37	30.5 ± 2.2 (24) 28–36
Weight	—	—	—	—	427.7 ± 103.9 (23) 270–650
Greatest length of skull	56.3 ± 1.9 (14) 52.1–58.5	52.1 ± 1.3 (2) 51.2–53.0	53.3 ± 2.0 (4) 50.9–55.7	55.8 ± .8 (6) 54.7–56.7	57.7 ± 2.5 (27) 52.0–63.1
Zygomatic breadth	27.4 ± .8 (16) 25.4–28.3	26.1 ± .6 (3) 25.4–26.5	25.8 ± 1.1 (4) 24.8–27.0	26.7 ± 1.3 (7) 24.6–28.2	27.0 ± 1.2 (27) 24.4–28.4
Interorbital breadth	8.3 ± .3 (16) 7.9–8.9	7.7 ± .1 (3) 7.6–7.8	7.9 ± .5 (4) 7.4–8.3	8.3 ± .1 (7) 7.8–8.9	8.5 ± .4 (27) 7.9–9.3
Length of nasals	23.4 ± 1.1 (15) 20.7–24.9	21.2 ± 1.1 (3) 20.2–22.3	22.0 ± 1.4 (4) 20.5–23.8	22.4 ± .5 (7) 21.6–23.0	24.9 ± 1.4 (27) 22.0–28.7
Length of rostrum	19.3 ± .8 (15) 17.5–20.7	17.1 ± .8 (3) 16.3–17.8	18.1 ± .3 (4) 17.8–18.5	18.4 ± .6 (7) 17.8–19.2	20.6 ± 1.1 (27) 18.5–22.9
Breadth of rostrum	10.3 ± .6 (16) 9.2–11.5	9.8 ± .4 (3) 9.4–10.2	9.4 ± .4 (4) 8.9–9.9	10.4 ± .6 (7) 9.7–11.7	10.9 ± .7 (27) 9.5–12.0
Breadth of braincase	20.8 ± .6 (16) 19.9–22.5	19.8 ± .6 (3) 19.3–20.4	20.7 ± .9 (4) 19.6–21.5	20.9 ± .3 (7) 20.4–21.2	20.4 ± .5 (27) 19.4–21.2
Height of braincase	15.2 ± .5 (16) 14.5–16.4	14.8 ± 0.0 (2) —	14.8 ± .6 (4) 14.2–15.6	15.8 ± .4 (6) 15.4–16.4	15.2 ± .5 (27) 14.3–16.2
Breadth across incisor tips	4.0 ± .2 (16) 3.6–4.3	3.7 ± .2 (3) 3.5–3.9	3.6 ± .3 (4) 3.2–4.0	4.1 ± .4 (7) 3.7–4.9	4.1 ± .2 (23) 3.5–4.5
Breadth of zygomatic plate	5.8 ± .5 (16) 5.0–6.5	5.2 ± .2 (3) 5.0–5.4	5.4 ± .4 (4) 5.0–5.9	5.6 ± .4 (7) 5.0–6.0	5.5 ± .4 (27) 4.9–6.4
Length of diastema	16.0 ± .9 (16) 15.4–18.2	16.3 ± .6 (3) 15.6–16.7	16.1 ± .9 (4) 15.1–17.2	16.8 ± .7 (7) 16.0–17.8	17.6 ± 1.1 (27) 15.4–19.9

TABLE 8—(*Continued*)

Measurement	Northeastern India, Assam, and Northern Burma	Northern Thailand	Northern Laos	Northern Vietnam	Peninsular Thailand and Malaya
Palatal length	29.6 ± 1.0 (16) 27.3–30.0	28.0 ± .7 (3) 27.3–28.7	28.4 ± 1.1 (4) 27.4–29.8	29.5 ± .7 (7) 28.7–30.5	30.1 ± 1.3 (27) 27.0–33.0
Postpalatal length	21.2 ± .7 (6) 20.0–21.9	19.1 ± .1 (2) 19.0–19.1	19.3 ± .7 (3) 18.7–20.1	22.0 ± 0.0 (1) —	21.2 ± 1.1 (27) 19.2–23.7
Length of incisive foramina	10.9 ± .5 (16) 10.2–11.8	9.5 ± 1.1 (3) 8.5–10.6	9.9 ± .3 (4) 9.5–10.1	10.6 ± .5 (7) 9.7–11.2	10.4 ± ± .5 (27) 9.6–11.3
Breadth of incisive foramina	4.0 ± .3 (16) 3.5–4.5	3.3 ± .2 (3) 3.1–3.5	3.4 ± .2 (4) 3.2–3.6	3.7 ± .3 (7) 3.4–4.2	3.8 ± .3 (27) 3.3–4.4
Length of palatal bridge	9.8 ± .4 (16) 9.3–10.9	9.9 ± .6 (3) 9.6–10.6	10.1 ± .7 (4) 9.3–10.7	10.2 ± .6 (7) 9.5–11.2	11.1 ± .8 (27) 9.6–12.4
Breadth of palatal bridge at M^1	5.0 ± .4 (16) 4.3–5.5	4.9 ± .6 (3) 4.4–5.5	4.5 ± .2 (4) 4.2–4.5	4.8 ± .2 (7) 4.5–5.1	5.1 ± .3 (27) 4.5–5.7
Breadth of palatal bridge at M^3	5.7 ± .3 (16) 4.9–6.3	5.4 ± .7 (3) 4.9–6.2	5.3 ± .4 (4) 4.9–5.9	5.5 ± .3 (7) 5.1–5.9	5.9 ± .4 (27) 5.1–6.6
Breadth of mesopterygoid fossa	3.7 ± .2 (16) 3.4–4.1	3.6 ± .3 (3) 3.2–3.8	3.3 ± .3 (3) 3.0–3.5	3.8 ± .2 (7) 3.5–4.2	3.7 ± .4 (27) 3.0–4.5
Length of bulla	7.8 ± .3 (15) 7.2–8.2	7.1 ± .6 (3) 6.5–7.6	7.6 ± .2 (4) 7.4–7.7	7.5 ± .3 (7) 7.3–8.0	7.0 ± .3 (27) 6.2–7.3
Alveolar length of M^{1-3}	9.9 ± .3 (16) 9.4–10.6	9.0 ± .6 (3) 8.8–9.2	9.6 ± .4 (4) 9.1–10.1	9.8 ± .4 (7) 9.2–10.6	9.8 ± .4 (27) 9.1–10.5
Breadth of M^1	2.8 ± .1 (15) 2.7–3.0	2.6 ± .2 (3) 2.5–2.9	2.8 ± .1 (4) 2.7–3.0	2.8 ± .1 (7) 2.7–2.9	2.7 ± .1 (25) 2.5–3.0

[a] Mean plus or minus one standard deviation, number of specimens in parentheses, and observed range are listed for each measurement.

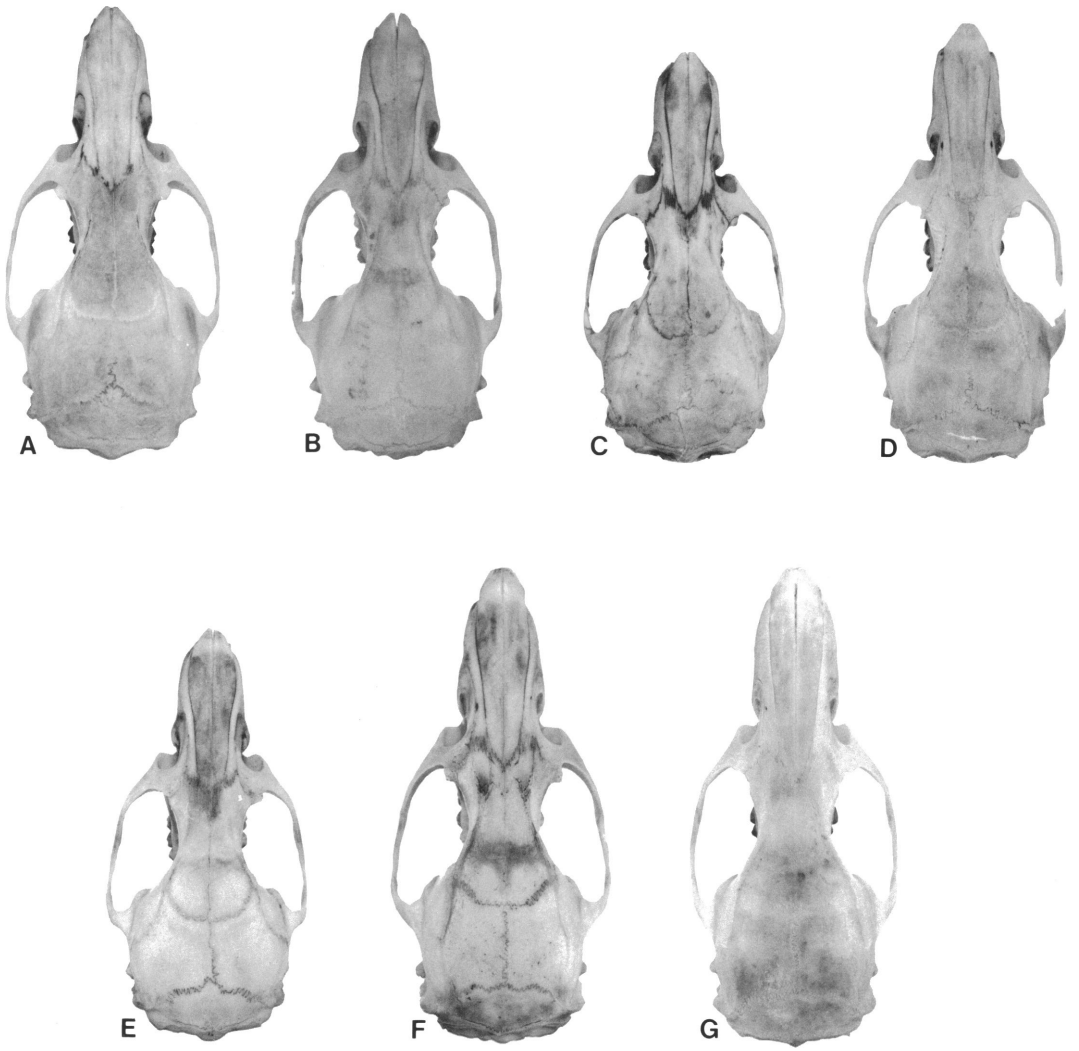

FIG. 24. Dorsal views of crania from adult *Berylmys bowersii*. A, northeastern India, Tirap District (USNM 543092). B, northern Burma (AMNH 115238). C, northern Laos (USNM 355544). D, Chapa, northern Vietnam (USNM 259497). E. Chiengmai Province, northern Thailand (AMNH 167928). F, Narathiwat Province, peninsular Thailand south of the Isthmus of Kra, 10°30′ N (USNM 533375). G, Selangor State, Malaya (USNM 357890). Natural size. Geographic variation is discussed in the text.

species to determine the significance of this variation or whether the scientific names proposed really designate morphologically distinctive segments of the species. We note two features that vary geographically. One is presence or absence of a white tail tip and how extensive the white tip is. Samples of *B. bowersii* from Assam, the Tirap District of northeastern India, and central and northern Burma have white-tipped tails in which the white covers one-fifth of the tail length. Most specimens from southern China, northern Thailand, northern Laos, and northern Vietnam have brown, monocolored tails; white-tipped tails occur infrequently. Specimens from peninsular Thailand and Malaya have extensive white tail tips; one-half or two-thirds of the distal portion is white in these rats.

The other feature that varies geographically is skull size, which reflects body size.

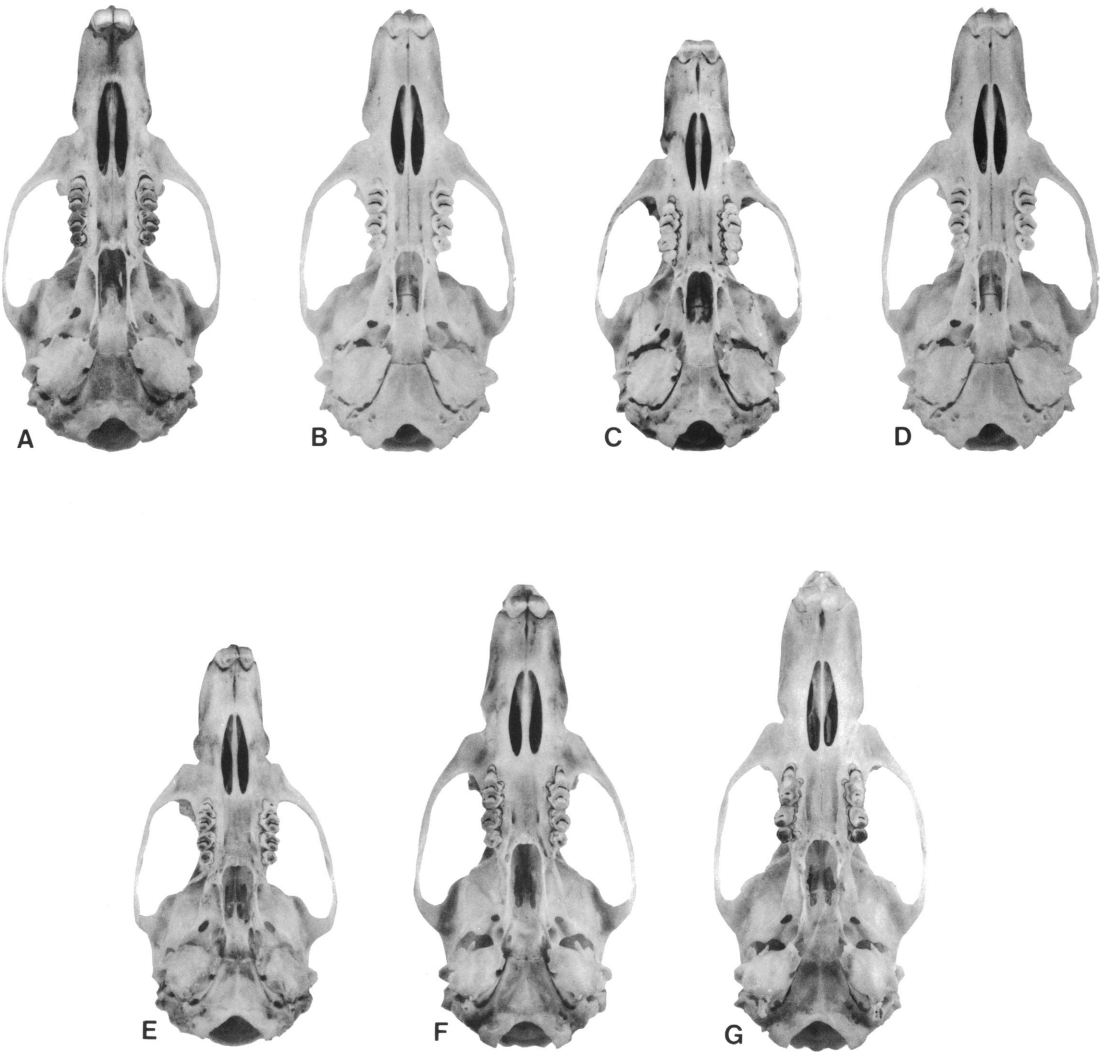

FIG. 25. *Berylmys bowersii:* ventral views of same crania shown in figure 24. Natural size.

Specimens in the small samples from northern Thailand and northern Laos have, on the average, smaller skulls (and other cranial features associated with smaller body size such as smaller bullae and shorter maxillary toothrows) than do those rats in samples from elsewhere within the range of *B. bowersii* (table 8; figs. 24 and 25). The small skulls, short molar rows, and small bullae of some specimens from Thailand led Marshall (1977) to assign them to *B. mackenziei* rather than *B. bowersii.*

The specimens from peninsular Thailand and Malaya differ in two measurements from those in most of the other samples of *B. bowersii.* The palatal bridge is longer, on the average, than any other sample of *B. bowersii* for which we have values and the bullae are shorter than the average in each sample except that one from northern Thailand (table 8; figs. 24 and 25).

What is the relationship between these geographic patterns and the names applied to segments of *B. bowersii*? First, the name *wellsi* is based on a young example of *B. bowersii* from Assam, a specimen whose characteris-

TABLE 9
Geographic Variation in Alveolar Length of Maxillary Toothrow Among Samples of *Berylmys bowersii* and *Berylmys mackenziei*[a]

Geographic Region	*B. bowersii*	*B. mackenziei*
Assam, Central Burma	9.7 ± .44 (30) 8.7–10.6	8.6 ± .4 (67) 7.7–9.6
China, Szechwan	—	9.8
China, Yunnan	8.6 ± .1 (2) 8.5–8.7	—
China, Fukien	9.2 ± .3 (3) 9.0–9.5	—
Thailand	9.0 ± .2 (5) 8.8–9.2	—
Laos	9.4 ± .4 (8) 8.7–10.1	—
Northern Vietnam	9.6 ± .4 (13) 9.1–10.6	—
Southern Vietnam	—	9.3 ± .4 (3) 9.0–9.8
Peninsular Thailand and Malaya	9.8 ± .4 (40) 9.1–10.5	—

[a] Mean plus or minus one standard deviation, number of specimens in parentheses, and observed range are listed for the measurements, which are in millimeters.

tics fall within the range of variation we see in series of *B. b. bowersii* of comparable age. We treat *wellsi* as a synonym of *B. b. bowersii.*

Second, samples from the eastern range of *B. bowersii* that have been referred to *B. b. latouchei* differ from samples in the western segment of the range by having slightly paler upperparts and a higher frequency of brown monocolored tails. The relationship between the end of the nasals and the adjacent premaxillary bones that has been used to separate *B. b. bowersii* from *B. b. latouchei* does not hold up. The nasals are supposed to extend beyond the premaxillae in *B. b. bowersii* and be even with them in *B. b. latouchei.* We found the *latouchei*-configuration to be frequent in samples from Assam and Burma and the *bowersii*-configuration to occur frequently in samples from southeastern China, northern Laos, and northern Vietnam; that feature does not distinguish the two sets of samples. To us, the slight differences between rats from the western and eastern parts of the range are insufficient to separate the two taxonomically and we treat *latouchei* as a synonym of *B. b. bowersii.* We also provisionally add *totipes* to the synonymy of *B. b. bowersii.* There is nothing in the original description which indicates that the two specimens of *totipes* have morphological features different from those in the samples we have examined from northern Vietnam.

Third, specimens in our small samples from northern Thailand are smaller in body size, as estimated by skull length, than those in other samples of *B. bowersii.* If that distinction proves to be real when larger samples from more localities are analyzed, then *B. b. lactiventer* is the name to apply to this segment of the species. We list *kennethi* as a synonym of *B. b. lactiventer.*

Fourth, the rats from peninsular Thailand south of the Isthmus of Kra, Malaya, and the Medan region of northwestern Sumatra should continue to be referred to as *B. b. ferreocanus.* They are distinguished from the northern Thai samples by larger skull size, along with greater values for other cranial and dental measurements (except for length of bullae), and they differ from the other samples of *B. bowersii* by having a longer palatal bridge and smaller bullae. They also differ from all samples north of the Isthmus of Kra by having more extensive white on the tails. Of all the samples of *B. bowersii* that we examined, those from the Sunda Shelf are the most morphologically distinctive.

The real geographic range of *Berylmys bowersii* has yet to be determined but from our study of specimens, we detect a general pattern. Most specimens come from northeastern India, northern and central Burma, southern China, northern Vietnam, northern Laos, and northern Thailand. Even published records based on specimens we have not examined (Tien, 1966b, 1978) are from that region. No specimens have yet been collected from southern Burma (including the Tenasserim region), southern Thailand north of the Isthmus of Kra, southern Laos, Cambodia, and southern Vietnam. We do not know whether *B. bowersii* does not occur in this region or whether it has just not been collected yet. Some areas, Cambodia, for example, have been inadequately surveyed; other places, however, such as southern Burma, southern Thailand, and southern Viet-

TABLE 10
Records of Sympatry Among Species of *Berylmys*

Region	*B. manipulus*	*B. berdmorei*	*B. mackenziei*	*B. bowersii*
NORTHEASTERN INDIA (ASSAM)				
Manipur, Khasi Hills, Mawphlang	–	–	FMNH 76490–76496, 75819, 75820, 76479, 76485, 76488, 76489, 76667, 84852–84866	FMNH 76486, 76487
Manipur, Karong	FMNH 76454, 76458, 76460, 76462, 76463, 76465, 76466, 76468–76470, 76478, 76480, 76481	–	FMNH 76456, 76461, 76464, 76467, 76472, 76473, 76482, 76483	FMNH 76455, 76457, 76459, 76471, 76474–76476, 76484
Manipur, Naga Hills, 5000 feet	BM 47.154, 47.155	–	BM 47.133–47.140, 66.3100–66.3109; FMNH 76497, 76498	BM 20.6.6.19, 20.6.6.20, 20.6.6.25
CENTRAL BURMA				
Chin Hills, 50 miles west of Kindat, 5000 feet	NMS 290	–	BM 16.3.26.61–16.3.26.66; NMS 342; FMNH 82974, 82975	BM 16.3.26.67, 16.3.26.68
SOUTHERN BURMA				
Tenasserim, Thagata, Muleyit Range	–	BM 16.2.16.1	BM 88.12.1.47	–
SOUTHERN VIETNAM				
Fyan, 1200 meters	–	USNM 321227	USNM 321316	–

nam have been the sites of biological surveys sponsored by several countries. The only species of *Berylmys* known to occur throughout that southern tier are *B. berdmorei* (Burma, Thailand, Cambodia, and Vietnam) and *B. mackenziei* (Vietnam).

The only southern population of *B. bowersii* is that occurring on the Sunda Shelf. From Nakhon Si Thammarat Province, the northernmost Province from which *B. b. fereocanus* has been recorded (which is well south of the Isthmus of Kra), there is a gap of 600 to 700 airline miles north to the Provinces of Kalasin and Tak in northern Thailand in which *R. bowersii* is not known to occur. The geographic distribution of another large-bodied Asian rat, *Leopoldamys edwardsi* is similar to that of *Berylmys bowersii*. *Leopoldamys edwardsii* ranges farther east (to Darjeeling District of West Bengal) and farther north (Szechwan Province of China) but is also absent from the southern portions of Burma, Thailand, Laos, Vietnam, and all of Cambodia (see the map in Marshall, 1977b, p. 482; Musser, 1981a). The species also occurs in the mountains on the Malay Peninsula and Sumatra but no specimens have been taken in the extensive region between Malaya and the northern segments of the range. If the gap between the Indochinese and Sundaic populations of *Berylmys bowersii* is real the morphological distinctions between them makes sense in terms of a species once being distributed over the entire area and then being isolated into northern and southern segments. In any future taxonomic revision of the species, biologists should test the hypothesis that the Sundaic population of *B. bowersii* is reproductively isolated from the Indochinese segment.

If specimens in museum collections are any indication of how abundant *Berylmys bowersii* is in its natural habitat, the species is not common anywhere except on the Malay Peninsula. The amount of ecological data reflects that division: data are meager about rats from the north but richer for the population south of the Isthmus of Kra.

The northern *Berylmys bowersii* are terrestrial and some live in burrows. Although primarily a forest rat, it is also found in cultivated fields and scrub as long as these places are near dense forest. The best ecological data available is that associated with the series from northern Burma in the Nam Tamai Valley, the hills east of Nam Tisang, and the Akhe Triangle. All the rats were collected between 2500 and 4000 feet. On labels attached to skins of some specimens are notations that the animals were caught "in jungle, by native in rice field on river bank surrounded by dense jungle," in "dense hill jungle, by native in hole in maize field in dense hill jungle," and "in a hole in thick jungle undergrowth with 3 new-born young."

Writing about the habitat where *Berylmys bowersii* was obtained in northern Burma, Anthony (1941, pp. 109–110) explained that

> All of the specimens of *bowersii* obtained by our expedition were purchased from natives who brought the rats into camp from localities near at hand. One was caught near Gangfang and the native took me to the spot where I examined the burrow and the deadfall set there. The burrow was on a hillside covered with low scrub, so thick that one would have to step almost into the hole to discover it. Although this district was probably forested many years ago, the climax ecology has been destroyed by clearings and fires, and the tangle of low shrubbery, bracken, and herbaceous vegetation which has taken possession of the low hills is radically different from undisturbed regions at the heads of the ravines. If *bowersii* is a forest-dwelling rat, as some authors have described it, the Gangfang capture indicates that it may also occur several miles from large trees.
>
> The rat had dug a large burrow laterally into the hillside and the native had built a little palisade of twigs which compelled the animal to pass under a small log poised as a deadfall by an ingenious system of rattans, levers, and a treadle. The man told me that he had found no other burrows on this particular hillside and he did not catch more than one rat in several nights of trapping.

For samples of *Berylmys bowersii* from Malaya, there is information about abundance and population density (Harrison, 1969; Medway and Wells, 1971), reproduction (Harrison, 1955), survival rates (Harrison, 1956a), body temperatures (Rudd, 1966a), weight and growth (Rudd, 1965), ectoparasites (Traub, 1967), and endoparasitic patterns (Lim, Ow-Yang, and Lie, 1965; Dunn, Lim, and Yap, 1968).

From the research of Harrison (1954a, 1957a, 1957b) and Lim (1970), we learn that Malayan *Berylmys bowersii* is most common in primary forest but also occurs in disturbed primary forest, secondary forest, and scrub. The species is more abundant in the highlands above 2000 feet than in lowland forests. In the lowlands, Harrison (1957a, p. 13) thought *B. bowersii* to be "comparatively rare, and confined to high forest, where, like *R. mülleri,* it is found in the wetter places." But Lim (1970, p. 734) noted that in his survey, "*R. bowersii* was found nearly equally common in both dry and wet parts of the forest floor." Lim also surveyed nest sites and reported (p. 735) that "All of the occupied nests of *R. muelleri* and *R. bowersii* were found on the ground. They were in crevices among rocks, in holes in fallen logs, in holes in the banks of forest pathways, along forest streams, and in holes at the bases of trees in the dry parts of the forest floor."

The diet of Malayan *Berylmys bowersii* consists chiefly of fruit and vegetable matter. Insects and land molluscs are infrequently eaten, and fish scales were found in the stomach of one rat. Lim (1970, p. 739), who studied the distribution, relative abundance, food habits, and parasite patterns of giant Malayan rats (*Leopoldamys edwardsi, L. sabanus, Rattus muelleri,* and *Berylmys bowersii*), summarized his results this way: "*R. bowersii* is least restricted in terms of its habitats. It is commonly found in both low and high elevations and with nearly equal frequency in both wet and dry habitats. It appears to be the least arboreal of the four in its habits. Fruit and other vegetable matter are important components in its diet. Insects and snails are relatively infrequently taken. Correlated

with this is a relatively low incidence of helminth infestation. *R. bowersii* probably is the most vegetarian of the four giant forest rats studied."

This final description of *B. bowersii* by Harrison and Lim (1950, pp. 305–306), who reported that in captivity, the rat

> was a general feeder, accepting anything offered such as bananas, papaya, sweet-potato, tapioca, green vegetables, rice both raw and boiled, rolled oats, groundnuts, and meaty bones. It is remarkable as the tamest rat which we have yet seen. Specimens freshly trapped would allow themselves to be handled with no more than a few protesting squeaks, they would eat out of a hand, and when tickled behind the ear or the angle of the jaw they would roll onto their backs and go to sleep. Being, like *Rattus mülleri,* both lazy and nocturnal, specimens spent most of the day sprawling in one corner of the cage, often indeed on their backs with the feet in the air.

BERYLMYS COMPARED WITH *DIOMYS* AND *BUNOMYS*

Part of defining *Berylmys* is comparing its characteristics with those of *Rattus,* the *muelleri* group, *Diomys,* and *Bunomys.* We have already contrasted *Berylmys* and *Rattus.* We compare *Berylmys* and the *muelleri* group in a following section where we diagnose and define the *muelleri* group. Below, we contrast *Berylmys* first with *Diomys* and then with *Bunomys.* Why these two genera? Because when Musser and Marshall were comparing species of *Berylmys* to those in all the other genera of Indo-Australian murids there were some characters of *Diomys* which suggested it might be morphologically and possibly phylogenetically allied to *Berylmys.* The proodont upper incisors, pale upper and lower incisors, and general conformation of the skull in *Diomys* resembled that of *Berylmys,* features pointed out by Marshall (1977b, p. 401). And, if the single species of *Diomys* did belong in the same monophyletic group containing those of *Berylmys,* the cluster would have to be called *Diomys* because that name is older.

We contrast *Berylmys* with *Bunomys* because Misonne (1969, p. 143) placed *chrysocomus* and *manipulus* in the subgenus *Bullimus* of *Rattus* based on cusp patterns, and noted that "*Rattus chrysocomus* seems to be very similar to *R. manipulus,* though the first lives in Celebes and the second in western Burma. The main difference of structure lies in the absent [posterior cingulum] in M_1; it belongs certainly to this group." *Berylmys* and *Bunomys* do resemble each other in some cranial and dental features and we compared the two genera to determine if *Bunomys* was the Sulawesian counterpart of Asian *Berylmys.*

Diomys and *Berylmys*

Diomys is an Indian genus. There is but one species, *D. crumpi* (Thomas, 1917); most specimens come from either Bihar or Manipur (Ellerman, 1961). The holotype is from Paresnath, Bihar, 4300 feet and consists of only a broken skull (it was, according to Ellerman, mixed with a skin of *Millardia meltada*). The other specimens are from Bishampur, Manipur, 3000–4000 feet in Assam. Ellerman lists 30 specimens from that locality and Musser has examined most of these. There is also an adult female from Namti, 35 miles west of Myitkyina, northern Burma (USNM 279138), taken in 1945 from "tall elephant grass." We list the measurements of this rat in table 11.

Ellerman provides a good description of *Diomys crumpi.* It is a small-bodied rat in which the tail is slightly longer than the combined lengths of head and body in most specimens, shorter in others, and about the same length in a few (Ellerman, 1961, pp. 846–847). Upperparts are brownish gray, underparts are grayish white, ears are grayish brown and large relative to size of head and body. The pelage covering head and body is short (10 mm. thick on the rump), fine and silky to the touch. The tail is brown above and gray below from base to tip; the two surfaces are sharply demarcated. Upper surfaces of the front and hind feet are white, contrasting with coloration of the head and body. Each palmar surface is unpigmented. There are three interdigital pads and two metacarpal pads on the palmar surface. The thumb is very small, resembling a small pad rather than the remnant of a digit. Plantar surfaces are dark brown. There are four small interdigital pads, and a small metatarsal pad. Two metatarsal pads are usual in most species of mu-

rids, a small round or oblong one and an elongate kidney-shaped pad (as in *Berylmys,* fig. 15). A large kidney-shaped pad is absent in *D. crumpi.* All the plantar pads are low and small relative to plantar area. There are three long central digits and two short outer digits; this conformation, along with a long and slender hind foot and small plantar pads points to a terrestrial adaptation.

Most external features of *Diomys crumpi* are unlike those in species of *Berylmys.* Body size of *D. crumpi* is much smaller than the large-bodied species of *Berylmys* (table 11). Coloration of head and body differs from the iron gray upperparts and white underparts, the pattern typical in *Berylmys.* Silky fur is a texture quite different from the crisp pelage in *Berylmys.* A tail that is dark above and gray below is unlike the pattern of bicoloration in *Berylmys.* The absence of a kidney-shaped metatarsal pad is unique to *D. crumpi.* The thumb is smaller relative to the other digits than it is in any species of *Berylmys.* No characters associated with skins indicate that *Diomys* is morphologically closely related to *Berylmys.*

Although *Diomys* and *Berylmys* are dissimilar in external characters, they do resemble each other in certain cranial and dental features, but the similarities are superficial and not indicative of close morphological relationship. Of all the species of *Berylmys,* the cranial configuration of *B. berdmorei* is most like that of *D. crumpi.* These are the two we contrast below. Skulls of each are shown in figure 26. Compare the cranial measurements of *D. crumpi* in table 11 with those of *B. berdmorei* listed in table 6. *Diomys crumpi* has a much smaller skull than that of *B. berdmorei* (or any other species of *Berylmys*) and also differs from it in the following cranial characteristics.

1. The rostrum is shorter and narrower relative to size of the cranium. Its sides are nearly parallel. This aspect from a dorsal view, along with truncate nasal tips, gives the rostrum the shape of a small and thin rectangle. The rostrum of *B. berdmorei* (and other *Berylmys*) is long and wide, tapering from a wide base across the nasolacrimal canals to triangular nasal tips; in dorsal view the rostrum is triangular.

2. *Diomys* has short nasals in which the truncate tips are posterior to the anterior margins of the premaxillaries forming sides of the rostrum, a configuration best seen in figure 26. In *B. berdmorei* and the other species of *Berylmys,* the nasals extend anterior to the front faces of the upper incisors.

3. Sides of the braincase in *D. crumpi* are vertical and the dorsolateral margins are outlined by ridges. The postorbital and temporal ridges in *B. berdmorei* are relatively weaker and sides of the braincase slope toward the midline of the cranium.

4. In *D. crumpi,* the occiput is deeper (anterior-posterior distance) and roofed by a relatively large interparietal bone that is not nestled between the parietal bones but located posterior to them, a configuration similar to that in *Rattus,* not *Berylmys.* The back of the cranium in *D. crumpi* is either vertical or slopes back overhanging the occipital condyles. In *B. berdmorei,* the back of the cranium slopes forward, as it does to a lesser degree in the other species of *Berylmys.*

5. As seen in side view, each zygomatic plate of *D. crumpi* is higher relative to cranial depth than are the plates in *B. berdmorei* or any other species of *Berylmys.*

6. The incisive foramina are very long, slender, and parallel-sided in *D. crumpi.* Their posterior margins extend past the front faces of the first molars by about 1 mm. In most specimens of *B. berdmorei,* the incisive foramina are short, wide, not parallel-sided, and their posterior margins are either anterior to the first molars or even with them (table 3).

7. In *D. crumpi,* the palatal bridge extends posterior to the back faces of the third upper molars by 0.5–1.0 mm. forming a narrow but prominent shelflike extension behind the molar rows. In specimens of *B. berdmorei* the posterior margin of the palatal bridge is either anterior to backs of the third molars, as depicted in figure 26, or even with them (table 3).

8. The mesopterygoid fossa is narrow relative to breadth of the palatal bridge in *D. crumpi* and unlike the relatively much wider fossa in specimens of *B. berdmorei* (and the other species of *Berylmys*).

9. In each dentary of *Diomys crumpi* the coronoid process is delicate and a threadlike

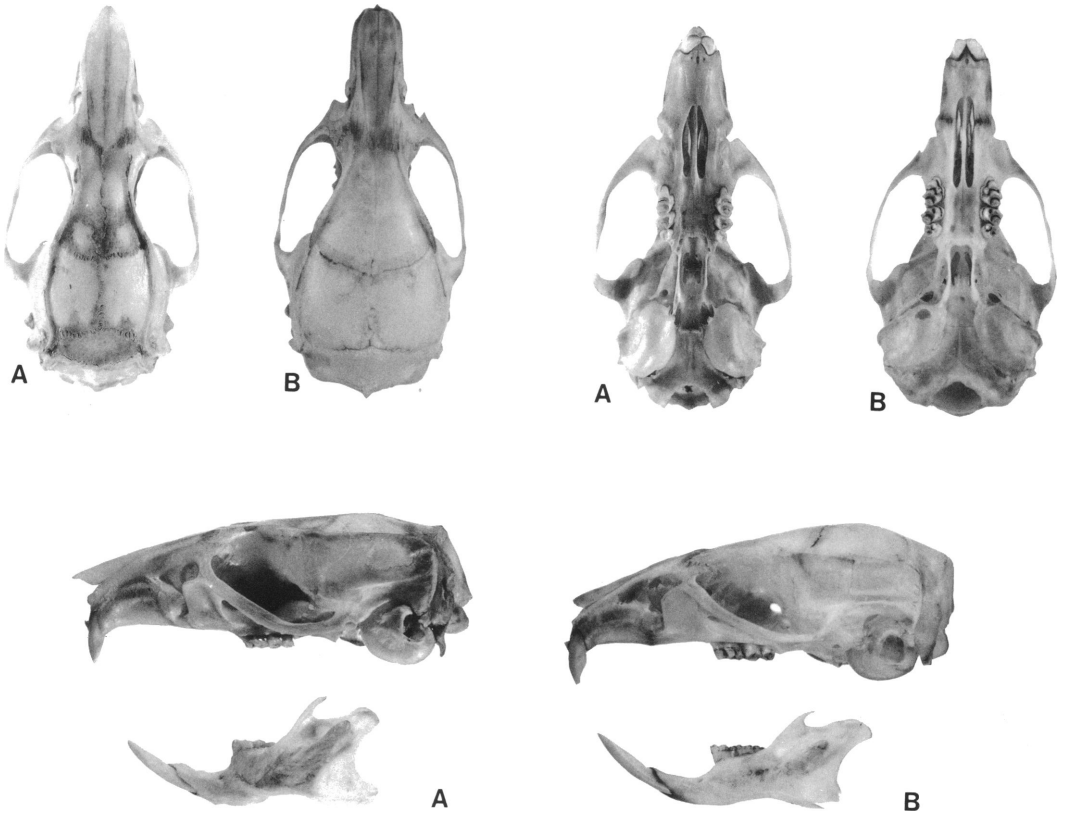

FIG. 26. Views of crania: adult *Berylmys* and *Diomys* compared. A, *B. berdmorei,* southeastern Thailand (USNM 533371); natural size. B, *D. crumpi,* Burma (USNM 279138); ×2.

extension of the ramus; each coronoid process is large and prominent relative to the ramus in *B. berdmorei.* Each condyloid process is directed posteriorly in *D. crumpi* but dorsoposteriorly in *B. berdmorei.* And, each dentary is neither as robust nor as high (distance between coronoid and angular processes) as it is in *B. berdmorei.*

Upper and lower molars of *Diomys crumpi* are contrasted with those of *B. berdmorei* in figure 27. Compare tables 6 and 11 for differences in dental measurements between the two species. The molars of *D. crumpi* are similar to those of *B. berdmorei* in size of one tooth relative to the others in each row, in number of roots, and in degree of overlap among the molars in each row. The occlusal patterns in *D. crumpi* also resemble those of *B. berdmorei,* a reflection of the simple cuspidation in both. But, there are significant differences between the two species that indicate to us the similarities may be independently derived. The upper and lower molars of *D. crumpi* have high crowns with short cusps on top; the molars are conspicuously hypsodont. Molars of *B. berdmorei* and the other species of *Berylmys* are clearly low-crowned (brachydont).

A second important difference is in shapes of the first and second rows of cusps on each first upper molar and the first row on each second upper molar. In *Diomys crumpi* cusp t1 of the first molar is clearly posterior to the other two cusps that form the front lamina and cusp t1 is set at nearly a right angle; the comparable cusp in *B. berdmorei* is also directed posteriorly but not as far relative to the other cusps and it still lies in the arcuate

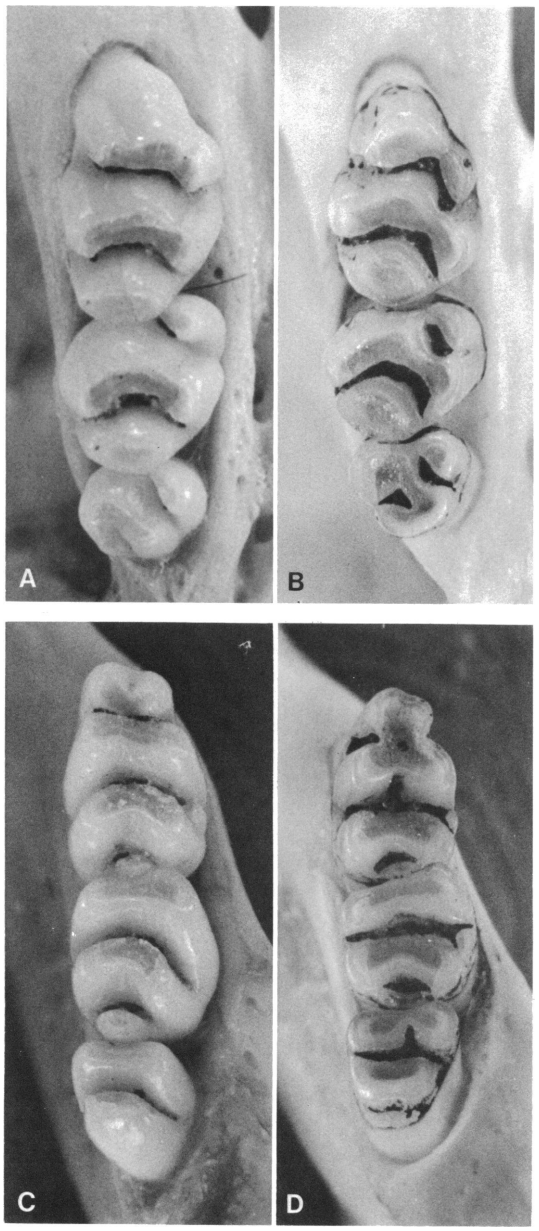

FIG. 27. Occlusal views of left upper (top) and lower (bottom) molar rows in *Berylmys* and *Diomys*. A and C, *B. berdmorei* (USNM 297163). B and D, *D. crumpi* (USNM 279138). ×10.

outline of the lamina. The second lamina on the first molar and its counterpart on the second molar in *D. crumpi* is nearly C-shaped in occlusal outline. The conformation results from the position of cusp t4, which is well posterior to cusps t5 and t6. The shapes are clearly shown in figure 27. By contrast, the comparable laminae in *B. berdmorei* are simple and arcuate, not conspicuously cuspidate and C-shaped.

The third significant difference in cusp patterns of upper molars between *Diomys* and *Berylmys* is in the position of the posterior lamina (the merged cusps t8 and t9) on each first and second molar. In *D. crumpi* the lamina at the back of each first and second molar is not transverse to the longitudinal axis of the cranium, as it is in *B. berdmorei* and the other species of *Berylmys,* but is slanted so the long axis of each lamina is anterolateral to the longitudinal cranial axis. This angle of the posterior lamina also reflects the general trend of the lamina anterior to it, a conformation unlike that in any species of *Berylmys.*

Cusp patterns on lower molars of *Diomys crumpi* and *B. berdmorei* are similar and reflect again the simple cuspidation in both species. Still, there are conspicuous differences. In *D. crumpi* each posterior cingulum is in the middle of the molar rather than on the lingual side as is each posterior cingulum in *B. berdmorei* and the other species of *Berylmys.* The anterior lamina of each third molar in *D. crumpi* is clearly formed of two discrete cusps that retain their identity even when the molars are worn (as is clearly shown in fig. 27); the two cusps forming a comparable lamina in *B. berdmorei* are broadly merged even in young rats and the lamina does not appear cuspidate.

Diomys is a distinctive genus. So is *Berylmys.* We find no characters that indicate the two are closely allied. Misonne (1969) placed *Diomys,* along with *Chiromyscus, Dacnomys,* and *Maxomys* in a cluster he called the *Maxomys* group; the contents of his *Maxomys* were placed in *Niviventer* by Musser (1981a). Simple molar occlusal patterns were the features Misonne used to unite these genera.

Chiromyscus, Dacnomys, and *Niviventer* judged by characteristics of skins, skulls, and teeth, may be phylogenetically closely related (Musser, 1981a). *Dacnomys* and *Chiromyscus* occur in Indochina, *Niviventer* is partly northern Indian but primarily Indochinese and Sundaic in distribution. To us, *Diomys*

does not fit with these genera. Judged by our comparisons, the characters of *Diomys* may tie it to *Millardia* and *Cremnomys,* clusters in which the living species are typically Indian in distribution but with fossil representatives in northern Africa (Sabatier, 1982). Conformation of the cranium in *Diomys,* configurations of its alisphenoid and pterygoid regions, its long and very slender incisive foramina, shape of the auditory bullae, and configurations of laminae on the first and second upper molars closely resemble these features in *Millardia* and *Cremnomys* (compare, for example, molar rows of the three genera illustrated in Misonne, 1969, plates 15 and 16). Furthermore, the silky pelage of *D. crumpi* is also a texture typical in species of *Millardia* and *Cremnomys.* We suggest that any future analysis of phylogenetic relationships among Indian murids tests the hypothesis that *Diomys* is related to the native Indian genera such as *Millardia* and *Cremnomys* and not to Indochinese and Sundaic species, such as those of *Berylmys, Dacnomys, Chiromyscus,* and *Niviventer.*

Bunomys and *Berylmys*

Bunomys was proposed by Thomas (1910) for *Mus coelestis* (Thomas, 1896), a species based on material from Bonthian Peak in the southwestern peninsula of Sulawesi. Except for Tate (1936, p. 580), who recognized *Bunomys* as a distinct genus composed of "offshoots of the *Rattus chrysocomus* group which have become slightly fossorial, as indicated by their lengthened claws," the genus has been treated as a part of *Rattus* (Ellerman, 1941, 1949; Misonne, 1969). *Bunomys* should not be included in *Rattus* (Musser, MS.). It is a morphologically distinctive genus containing at least six species native to Sulawesi and some offshore islands. *Bunomys chrysocomus* is of small body size and occurs throughout Sulawesi at middle and high elevations. The names *nigellus, rallus, brevimolaris, coelestis,* and *koka* apply to the species. *Bunomys fratrorum* is larger-bodied and known only from the northeastern peninsula where it lives in both lowland and mountain forests.

Bunomys andrewsi (*adspersus, inferior,* and *heinrichi* have been applied to samples of this species) is found in lowland forests throughout the island except on the northeastern peninsula. *Bunomys penitus* (*sericatus* is a synonym) occurs in mountain forests in the central part of Sulawesi and in the southwestern peninsula. There are two other species; these are described by Musser in a nearly completed report on the taxonomy of *Bunomys.*

Our comparisons between *Bunomys* and *Berylmys* focus on *Bunomys chrysocomus* and *Berylmys manipulus.* The type species of *Bunomys* is *Mus coelestis,* which is a distinctive subspecies of *B. chrysocomus*; *manipulus* is the type species of *Berylmys.* Furthermore, *B. manipulus* is larger in body size than *B. chrysocomus* but close to the same body size as the other species of *Bunomys,* especially *B. andrewsi, B. fratrorum,* and *B. penitus*; all the other species of *Berylmys* are very large compared with those of *Bunomys.* We contrast the skull and molars of *B. manipulus* with those from four species of *Bunomys* in figures 28–31. Compare also the figures of *Bunomys* skulls and teeth with the cranial and dental views of the species of *Berylmys* in figures 16–18 and 20–21. Listed in table 11 are measurements of the four *Bunomys*; compare these values with those listed for species of *Berylmys* in tables 5–8.

Like species of *Berylmys,* all species of *Bunomys* are terrestrial and live in tropical forest and scrub. Like *B. manipulus,* most species of *Bunomys* include insects, snails, and fruit in their diets, and *B. chrysocomus* also eats earthworms. Beyond these broad similarities, there are no external features that indicate close relationship between the two genera. All the species of *Bunomys* have soft and thick pelage that is either silky or woolly to the touch. Upperparts of head and body range from blue-gray to dark brown among the species. Underparts are either blue-gray, buffy gray, brownish gray, or whitish gray and most underparts do not contrast with coloration of the upperparts. In every species of *Bunomys,* females have only two pairs of mammae, both inguinal. These characteristics contrast sharply with the crisp fur in the species of *Berylmys,* with their iron gray upperparts and sharply demarcated white underparts, and with their greater number of mammae: four pairs in *B. bowersii* and five pairs in the other three species.

Crania of *Bunomys* and *Berylmys* share

TABLE 11
Measurements (in Millimeters) of Adult *Diomys* from Burma and *Bunomys* from Sulawesi[a]

Measurement	*Diomys crumpi* (USNM 279138)	*Bunomys* (females)			
		B. chrysocomus	*B. andrewsi*	*B. penitus*	*B. fratrorum*
Length of head and body	127	161.5 ± 7.9 (17) 147–173	174 ± 9.1 (6) 164–186	178.2 ± 10.1 (20) 158–197	169 ± .1 (16) 157–180
Length of tail	116	134.9 ± 10.8 (17) 102–145	144.5 ± 9.4 (6) 130–154	155.0 ± 10.9 (20) 126–170	167.6 ± 5.9 (16) 160–178
Length of hind foot	27	36.1 ± 2.4 (17) 34–35	39.5 ± 1.2 (6) 38–41	40.8 ± 1.2 (20) 39–42	39.2 ± 1.2 (16) 36–41
Length of ear	22	22.7 ± .8 (17) 22–24	24.0 ± .6 (6) 23–25	25.7 ± 1.0 (20) 24–27	—
Weight	—	83.9 ± 13.0 (17) 60–110	144.3 ± 212 (6) 110–170	124.7 ± 17.8 (20) 90–150	—
Greatest length of skull	32.7[b]	37.7 ± 1.0 (17) 35.8–38.9	40.8 ± .7 (6) 39.8–41.9	41.9 ± 1.6 (20) 39.2–46.0	43.5 ± 1.2 (21) 41.5–45.1
Zygomatic breadth	16.4	17.8 ± .7 (17) 16.8–18.9	20.3 ± .6 (16) 19.6–21.2	19.5 ± .8 (20) 18.0–20.9	20.8 ± .9 (19) 19.5–22.4
Interorbital breadth	5.4	6.5 ± .3 (17) 6.0–6.9	6.6 ± .2 (6) 6.4–6.9	6.8 ± .1 (20) 6.5–7.1	6.2 ± .3 (23) 5.7–6.8
Length of nasals	11.7	15.2 ± .7 (17) 13.8–16.1	17.7 ± .6 (6) 17.2–18.6	16.9 ± 1.0 (20) 15.1–19.1	17.7 ± .7 (22) 16.5–18.9
Length of rostrum	9.4	13.5 ± .4 (17) 12.7–14.3	14.7 ± .3 (6) 14.3–15.0	15.9 ± .9 (20) 14.6–18.5	15.4 ± .6 (21) 14.2–16.6
Breadth of rostrum	5.3	6.6 ± .4 (17) 6.0–7.1	7.1 ± .2 (6) 6.8–7.3	7.5 ± .4 (20) 6.8–8.1	8.1 ± .4 (22) 7.3–8.7
Breadth of braincase	13.2	15.3 ± .4 (17) 14.2–16.0	16.4 ± .2 (6) 16.1–16.6	16.7 ± .3 (20) 16.1–17.1	16.3 ± .3 (23) 15.7–17.0
Height of braincase	10.2	10.8 ± .4 (17) 10.2–11.5	11.5 ± .3 (6) 11.1–11.8	11.9 ± .3 (20) 11.1–12.5	12.2 ± .3 (23) 11.6–12.8
Breadth across incisor tips	2.0	1.9 ± .1 (16) 1.7–2.0	2.1 ± .1 (6) 2.0–2.1	2.2 ± .2 (20) 2.0–2.6	2.8 ± .1 (22) 2.6–3.0
Breadth of zygomatic plate	3.8	3.1 ± .2 (17) 2.9–3.5	4.1 ± .2 (6) 3.9–4.5	3.0 ± .2 (20) 2.7–3.3	3.9 ± .3 (22) 3.5–4.6
Length of diastema	10.3	9.9 ± .5 (17) 9.0–10.9	11.0 ± .5 (6) 10.4–11.6	10.8 ± .5 (20) 10.0–11.8	11.5 ± .5 (22) 10.7–12.2
Palatal length	17.9	18.7 ± .6 (17) 17.7–19.8	20.5 ± 1.0 (6) 19.8–21.3	21.4 ± .9 (6) 20.0–23.6	21.6 ± .6 (22) 20.4–23.0
Postpalatal length	11.6	13.4 ± .6 (17) 12.5–14.4	14.8 ± .4 (6) 14.0–15.2	14.0 ± .6 (20) 12.9–15.1	15.2 ± .5 (21) 14.5–16.0
Length of incisive foramina	8.0	6.0 ± .3 (17) 5.2–6.5	8.2 ± .3 (6) 8.0–8.6	7.9 ± .5 (20) 7.3–9.1	7.1 ± .3 (22) 6.3–7.7
Breadth of incisive foramina	1.7	2.5 ± .2 (17) 2.1–3.1	3.1 ± .2 (6) 2.8–3.1	2.9 ± .2 (20) 2.5–3.3	2.8 ± .2 (22) 2.4–3.2
Length of palatal bridge	5.3	7.5 ± .4 (17) 6.9–8.3	7.6 ± .3 (6) 7.2–8.0	9.0 ± .3 (20) 8.4–9.5	8.2 ± .4 (23) 7.5–9.0
Breadth of palatal bridge at M^1	2.9	3.8 ± .2 (17) 3.3–4.2	3.9 ± .1 (6) 3.7–4.1	3.6 ± .2 (20) 3.3–4.0	3.8 ± .3 (23) 2.3–4.4
Breadth of palatal bridge at M^3	3.2	4.4 ± .3 (17) 3.7–4.8	4.5 ± .2 (6) 4.2–4.7	4.6 ± .3 (20) 4.1–5.0	4.8 ± .3 (23) 4.4–5.5

TABLE 11—(*Continued*)

Measurement	*Diomys crumpi* (USNM 279138)	*Bunomys* (females)			
		B. chrysocomus	*B. andrewsi*	*B. penitus*	*B. fratrorum*
Breadth of mesopterygoid fossa	1.9	3.0 ± .2 (17) 2.7–3.6	3.1 ± .1 (6) 3.0–3.3	3.8 ± .3 (20) 3.3–4.4	3.5 ± .2 (23) 3.0–4.1
Length of bulla	6.3	6.0 ± .2 (17) 5.5–6.4	6.3 ± .2 (6) 5.9–6.5	6.5 ± .3 (20) 5.9–7.0	6.0 ± .2 (23) 5.7–6.4
Alveolar length of M^{1-3}	5.6	6.2 ± .3 (17) 5.7–6.6	7.2 ± .2 (6) 6.9–7.5	7.7 ± .2 (20) 7.4–8.1	7.6 ± .3 (23) 7.1–8.2
Breadth of M^1	1.8	2.1 ± .1 (17) 2.0–2.4	2.3 ± .1 (6) 2.2–2.4	2.5 ± .1 (20) 2.3–2.6	2.3 ± .1 (23) 2.2–2.6

[a] Mean plus or minus one standard deviation, number of specimens in parentheses, and observed range are listed for each measurement.

[b] Taken from back of occiput to end of premaxillary process anterior to upper incisors. Occipitonasal length is 32.1 mm.

some characters. In both groups, 1) the interorbital and postorbital regions, as well as dorsolateral sides of the braincase are outlined by low and inconspicuous ridges, so weak they are barely evident in some species—*B. penitus,* for example; 2) the squamosal root of each zygomatic arch does not extend to the occiput in a low ridge and sides of the braincase between posterior margins of the roots and the occiput are smooth; 3) the squamosal above each bulla is intact, not perforated by a squamoso-mastoid foramen or vacuity, that foramen is confined to the suture between the squamosal and mastoid bones; 4) the outer surface of each mastoid is complete, without a mastoid fenestra; 5) the incisive foramina are either short or long but in both configurations their posterior margins are either anterior to front faces of the first upper molars or even with them in most specimens; 6) posterior margin of the palatal bridge is either anterior to back faces of the third upper molars or even with them in most of the specimens; 7) the mesopterygoid fossa is spacious and wide relative to breadth of palatal bridge; 8) the sphenopalatine vacuities in the sides of the mesopterygoid fossa are short and narrow; 9) the auditory bullae are small relative to size of the cranium; 10) the carotid arterial circulation in the basicranium conforms to the same pattern, as judged by the large stapedial foramina and configurations of each pterygoid plate. All of these are primitive characters. They indicate that *Bunomys* and *Berylmys* share features that are primitive to murids and to rodents in general (Musser, 1981a); they do not reflect close phylogenetic relationship between the two genera.

Crania of *Bunomys* and *Berylmys* differ in important ways. As seen in either dorsal or ventral views, 1) the cranial outline of *Bunomys* is not triangular as it is in *Berylmys*; 2) the nasolacrimal capsules of *Bunomys* are not as large and inflated as they are in *Berylmys,* especially *B. manipulus* and *B. berdmorei,* species with highly inflated capsules; 3) the interparietal bone in *Bunomys* is larger in area relative to braincase area and most of it forms a roof over the occipital region, which is deeper (anterior-posterior length) relative to size of braincase than in *Berylmys* (the interparietal is relatively smaller in *Berylmys* and the anterior half sits between the parietal bones, the posterior half roofs the shallow occiput); 4) in *Bunomys,* the back of the cranium is either vertical or extends backward so it overhangs the occipital condyles instead of inclining forward as in *Berylmys*; 5) in *B. fratrorum* and *B. andrewsi,* each zygomatic plate is wide and nearly vertical, as are the zygomatic plates in all species of *Berylmys,* but the plates in the other species of *Bunomys* are much narrower (actually and relative to size of cranium) and slope backward; 6) in all species of *Bunomys,* each pter-

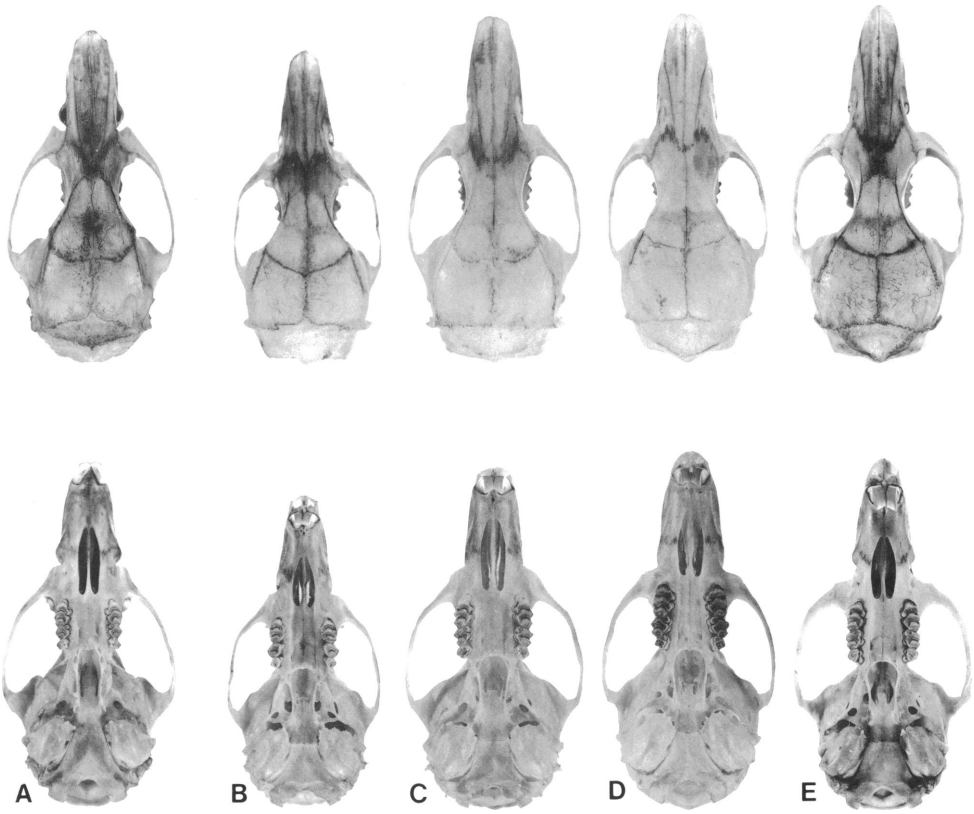

FIG. 28. Views of crania contrasting adult *Berylmys* from Burma (A) and *Bunomys* from Sulawesi (B–E). A, *Berylmys manipulus* (USNM 217420). B, *Bunomys chrysocomus* (AMNH 224698). C, *B. andrewsi* (AMNH 225652). D, *B. penitus* (AMNH 223852). D, *B. fratrorum* (USNM 217650). Natural size.

ygoid plate is perforated by a sphenopterygoid vacuity, such an opening is absent in the species of *Berylmys*.

The differences between *Bunomys* and *Berylmys* in degree of inflation of nasolacrimal capsules and slope of the back of the cranium represent the derived condition in *Berylmys* and the primitive condition in *Bunomys*. In all the other cranial differences noted above, the derived form is found in *Bunomys*.

There are no derived characters shared by the two genera which indicate the two to be closely related, even though they do share two sets of derived features. In each orbit, the sphenopalatine foramen is separate from and anterior to the dorsal palatine foramen and in both genera an alisphenoid strut (which would form the lateral wall of the alisphenoid canal) is not present. These two derivations also occur in many other genera of murid rodents and in the context of the distributions of characters between *Bunomys* and *Berylmys* are ambiguous in their suggestion of relationships.

The two genera also differ slightly in shape of the mandible but we do not know what the significance of these differences mean in a phylogenetic sense. The dentaries are generally similar in configuration in both genera. In species of *Bunomys,* however, each coronoid process is more robust and larger relative to size of the ramus than it is in species of *Berylmys* and the place where the incisors end in *Bunomys* is inconspicuous, not large lateral bulges as in *Berylmys*.

The incisors of *Bunomys* are unlike those of *Berylmys*. In all the species of *Bunomys,* the upper incisors emerge from the rostrum at nearly a right angle (orthodont) as do the

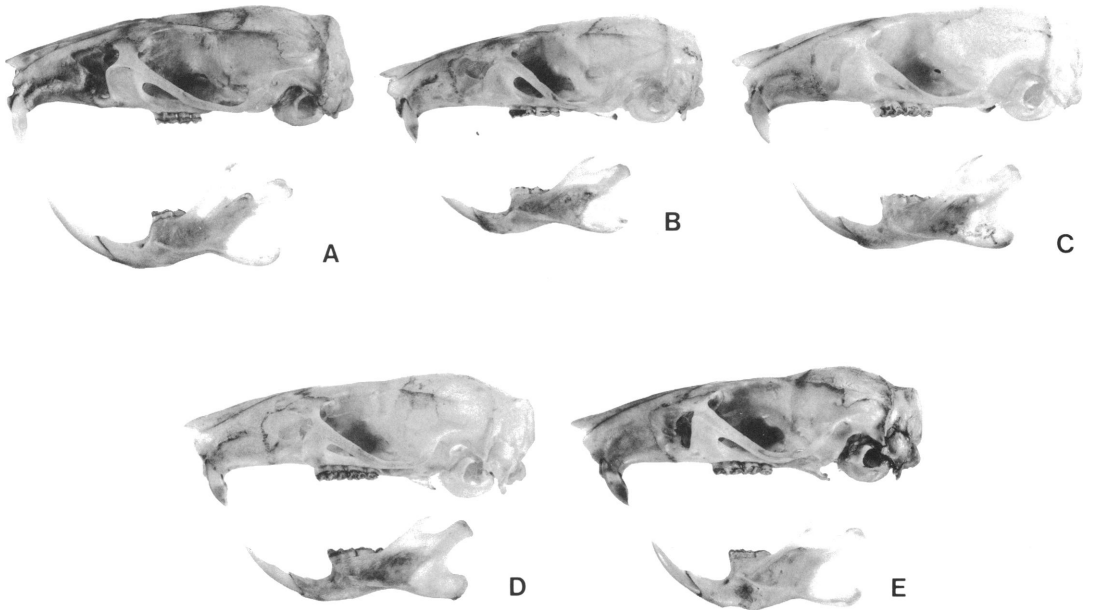

FIG. 29. Lateral views of crania from same specimens shown in figure 28. A, *Berylmys manipulus.* B–E, *Bunomys chrysocomus, B. andrewsi, B. penitus,* and *B. fratrorum,* respectively. Natural size.

TABLE 12

Presence (+) or Absence (−) of Certain Cusps and Cusplets on Molars in Species of *Bunomys* from Sulawesi[a]

Trait	*B. chrysocomus*	*B. andrewsi*	*B. penitus*	*B. fratrorum*
Cusp t3 on M^2				
+	15 (3)	15 (3)	60 (16)	10 (12)
−	75 (17)	75 (17)	30 (4)	90 (8)
Cusp t3 on M^3				
+	10 (2)	— —	10 (2)	30 (6)
−	90 (18)	100 (20)	90 (18)	60 (14)
Anterior labial cusplet on M_1				
+	55 (11)	— —	5 (1)	— —
−	45 (9)	100 (20)	95 (19)	100 (20)
Posterior labial cusplet on M_1				
+	100 (20)	100 (20)	100 (20)	60 (14)
−	— —	— —	— —	30 (6)
Anterolabial cusp on M_2				
+	100 (20)	100 (20)	45 (9)	10 (2)
−	— —	— —	55 (11)	90 (18)
Posterior labial cusplet on M_2				
+	100 (20)	100 (20)	100 (20)	100 (20)
−	— —	— —	— —	— —
Anterolabial cusp on M_3				
+	65 (13)	15 (3)	— —	— —
−	35 (7)	75 (17)	100 (20)	100 (20)

[a] Numbers of cusps and cusplets are expressed as percentages; number of specimens are in parentheses.

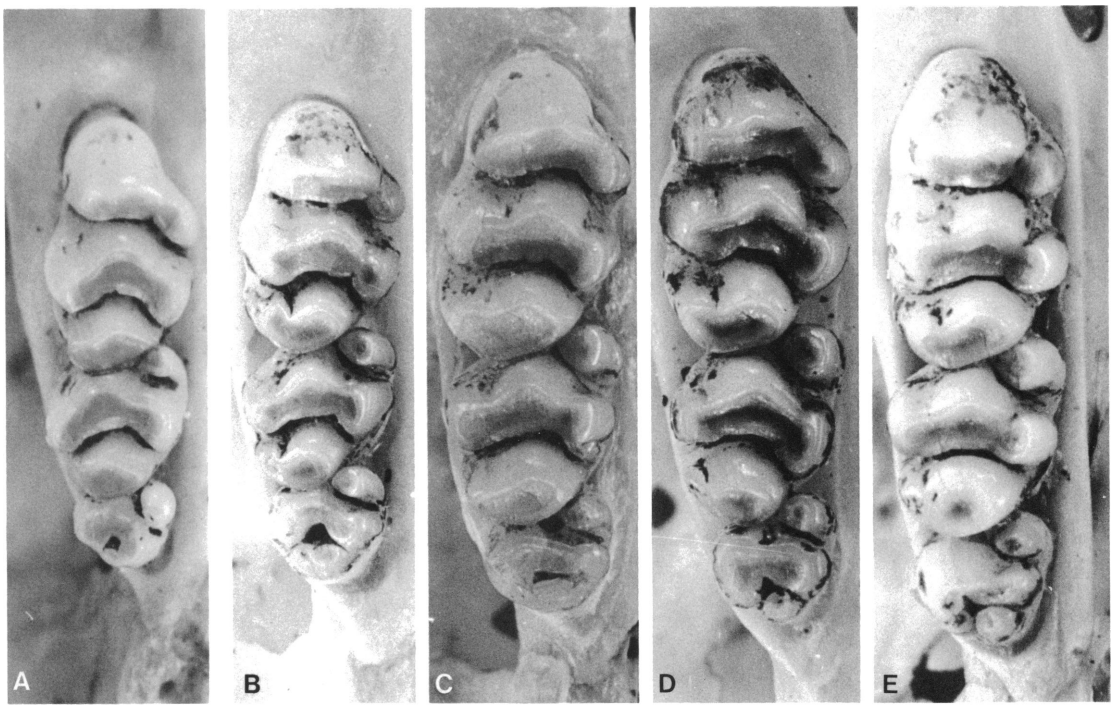

FIG. 30. Occlusal views of right upper molar rows in *Berylmys* (A) and *Bunomys* (B–E). A, *Berylmys manipulus* (FMNH 76463). B, *Bunomys chrysocomus* (AMNH 224760). C, *B. andrewsi* (AMNH 225659). D, *B. penitus* (AMNH 225274). E, *B. fratrorum* (USNM 217644). ×10.

incisors in *Berylmys bowersii* and *B. mackenziei*; no species of *Bunomys* has slightly proodont upper incisors, the configuration in *B. manipulus* and *B. berdmorei*. Both upper and lower incisors have orange enamel in all the species of *Bunomys*; none of them have the cream or whitish orange hues that characterize the incisor enamel in species of *Berylmys*.

Bunomys and *Berylmys* share several molar characteristics: low crowns (brachydont), same number of roots beneath each tooth, degree one molar overlaps the next in each row, and the size of each tooth relative to the others in each row. Low crowns are primitive. The other characters are derived. The molars in all the species of *Bunomys* have simple occlusal patterns that closely resemble the patterns in species of *Berylmys*. It is this feature that led Misonne (1969) to place *Bunomys chrysocomus* and *Berylmys manipulus* in the same group. But, the teeth are slightly more complex in *B. chrysocomus* than in *B. manipulus* because certain cusps and cusplets are present in the former and absent in the latter (compare tables 4 and 12). Cusp t3 on each third upper molar occurs on a few specimens of *B. chrysocomus* but is absent from every example of *B. manipulus*; slightly over half the sample of *B. chrysocomus* has an anterior labial cusplet on each first lower molar, in contrast to *B. manipulus* in which the cusplet is absent; and 65 percent of the sample of *B. chrysocomus* has an anterolabial cusp on each third lower molar, a cusp that is not found on any specimen of *B. manipulus*. Also, each posterior cingulum at the back of each first and second lower molar is in the center of the tooth in all species of *Bunomys* but offset from the center to the lingual side in the species of *Berylmys*.

Other species of *Bunomys* have less complex chewing surfaces than those in *B. chrysocomus*. In *B. andrewsi, B. penitus,* and *B. fratrorum,* for example, an anterior labial cusplet on each first lower molar is usually

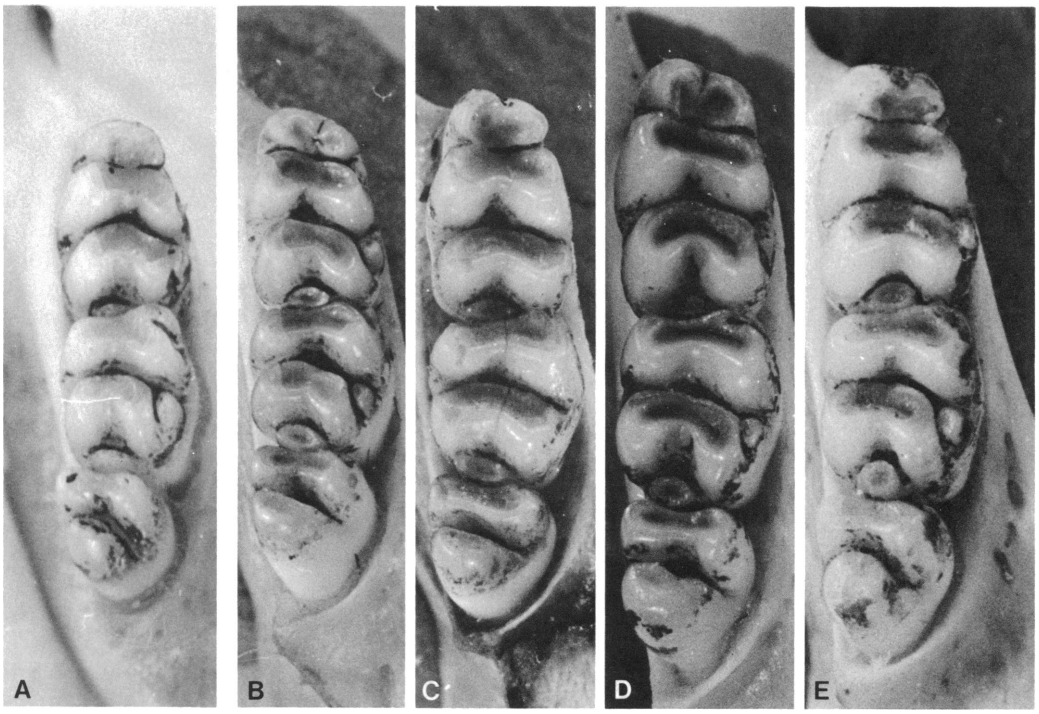

FIG. 31. Occlusal views of right lower molar rows in same specimens of *Berylmys* (A) and *Bunomys* (B–E) shown in figure 30. A, *Berylmys manipulus,* B–E, *Bunomys chrysocomus, B. andrewsi, B. penitus,* and *B. fratrorum,* respectively. ×10.

not present and anterolabial cusps on second and third lower molars are usually missing. The cusp patterns of these species resemble those in the species of *Berylmys.*

Set against the differences between *Bunomys* and *Berylmys* in pelage color and texture, number of mammae, and cranial characters, the similarities in occlusal patterns suggest that simple cusp patterns are independent derivations in each genus. The simple configurations result from loss of cusp t3 on each second and third upper molars, loss of anterolabial cusps from the second and third lower molars, and simple arcuate laminae formed by broadly merged cusps. Such patterns occur in other genera of Asian murids: *Niviventer, Dacnomys, Maxomys, Chiromyscus, Leopoldamys,* and *Anonymomys* are examples. Some of these, *Niviventer* and *Chiromyscus,* are phylogenetically closely allied, others are not (Musser, 1981a). Simple molar occlusal patterns shared by different genera do not always indicate close phylogenetic relationship. It is our hypothesis that they do not point to close affinity between *Bunomys* and *Berylmys.*

Neither *Diomys* of northeastern India and northern Burma nor *Bunomys* of Sulawesi can be closely tied to *Berylmys.* That genus of four species is Indochinese in geographic distribution but has a representative on the Malay Peninsula and northern Sumatra. The species of *Berylmys* have been allied to those in the *muelleri* group, the assemblage we discuss below. In contrast to *Berylmys,* the species in the *muelleri* group are endemic to the peninsula and islands of the Sunda Shelf.

THE *MUELLERI* GROUP AND THE GIANT RAT OF SUMATRA

Trying to discern relationships among Oriental rats, Bonhote in 1903 sorted species into groups based on characters of skins and skulls, the first serious attempt to define monophyletic clusters. His (Bonhote, 1903, p. 37) was the first definition of the "Muelleri Group," which stated that "This group are large dark coloured rats, with long uniformly black tails. They are all grizzled to a greater or less extent with fulvous; the under parts are, in the case of *M. validus,* of a greyish-white, but in *M. muelleri* itself, yellowish-white." In addition to *muelleri,* Bonhote included six other species in the group (table 13).

In 1936 Tate reported on collections of murids from the Indo-Australian region and pointed out Bonhote's pioneering attempts to group the species. Tate (p. 521) also recognized a "*Rattus mulleri* Group" that was delimited by a more expansive definition than that of Bonhote:

> Large, heavy-bodied Malaysian rats with mammary formula 2-2. Colors broadly speaking white-flecked iron-gray above, sometimes with a brownish wash, beneath self-colored (usually) white or buff. Pelage coarse and bristly, with admixture of wool hairs in northern regions; no flat spines. Ears small. Feet terrestrial, tending to be proportionately longer and provided with strong claws. Skull of general *rattus* type, heavily built, well arched, but with rather small bullae (12–14% of occipito-nasal length; about 70% of molar crown length), partly exposing periotic; and quite heavy dentition, incisors being stout and thick, molars large and wide.

For Tate (1936, p. 541), the geographic distribution of the *muelleri* group "seems to be the Malay region, whence the group reaches Java, Borneo, and the Philippines. Northwards it is represented in Siam, and (by a species not yet identified) in Indo China. Its range into Burma and India has not been ascertained." Tate's cluster contained 18 species (table 13).

By 1940, when Chasen's handlist of Malaysian mammals was published, most of the species listed by Tate were arranged as subspecies of *Rattus muelleri* by Chasen. He did not define a *muelleri* group but noted four species from the Malaysian region he thought to be closely allied to *R. muelleri* (table 13).

One year later, in his monumental classification of the genus *Rattus,* Ellerman (1941, p. 159) delimited a *muelleri* group within the subgenus *Rattus* and defined the cluster as "Differing from the *rattus* group as follows: usually larger in size (though the measurements may overlap in large members of *rattus* group); about 180–222 mm. head and body. Mammae 2–2=8. Molars rather heavy. Typically, bullae strongly reduced (about 12–14 per cent of occipitonasal length). However, in *jarak* and *villosus* the bullae are less reduced." For Ellerman, the distribution of this group was "Burma, Malay Peninsula, Sumatra, Java, Borneo." Sixteen species made up Ellerman's *muelleri* group (table 13).

Eight years later, Ellerman (1949) included *Rattus muelleri* and its allies in a *callitrichus* group and brought together that cluster along with three other groups into subgenus *Stenomys* of *Rattus.* Ellerman (1949, p. 38) defined that subgenus as "Rats with *small* bullae, averaging below 15 per cent of occipitonasal length, but with *long* palate, as is usual in the typical subgenus. Usually with long palatal foramina." Fifteen species were in Ellerman's *Stenomys* (table 13) and occurred over an expansive region from New Guinea and Malaysia to southern China and East India.

Based on his study of molar characters, Misonne in 1969 realigned the species in Ellerman's subgenus *Stenomys* and transferred *Rattus muelleri* to the subgenus *Bullimus* of *Rattus* to which he added 13 other species (table 13). For Misonne (1969, p. 140), the species included in subgenus *Bullimus* "are fairly closely related to one another; they are represented by at least five species, or groups of species, from Celebes, by four Bornean and Malayan species, and by at least two Philippine species." Misonne's (p. 141) definition of *Bullimus*:

> members of this subgenus generally show a much enlarged hind part of M^1; when a little worn, t8 extends lingually . . . most of the species have similar palatal foramina, with the exception of *R. dominator*. . . . The opening of the meso-

pterygoid fossae is behind the toothrows; the bullae are of different sizes, and this character is not considered here as of much importance. . . . In most of the species, M^1 is short, M^3 long or moderate; the molars are broad or very broad. . . . The upper Z [posterior cingulum] is clear in M^1 and M^2; M^3 is fairly complete with t1, t3, t4, t5, t6, t8, and t9; t7 may also be present, mainly in M^2; it is joined to t4, not to t8; t9 is broad. A cingular cusplet may be present on the mesio-lingual part of M^1, a rare character in *Rattus*. . . . The lower molars are characteristic: Sm [anterocentral cusp] is large in M_1 and connected with Sl [anterolingual cusp]. . . . The lower Z [posterior cingulum] is rather large and connected to Td [hypoconid] in some specimens; the cingular outer cusplets are not large; Cv2 [anterior labial cusplet] is small and Cv5 [posterior labial cusplet] of medium size. In M_2 and M_3, Sv [anterolabial cusp] is large and strongly connected to the mesial part of the molar.

Authors since Bonhote in 1903 to Misonne in 1969 have recognized that *muelleri* is a distinctive species, whether placed in *Mus* as it was during Bonhote's time or in *Rattus* as it appeared later, but the list of species claimed to be close relatives of *muelleri* has changed in content over the years. In table 13 we list the species associated with *muelleri* by Bonhote (1903), Tate (1936), Chasen (1940), Ellerman (1941, 1949), and Misonne (1969), as well as current estimates of their generic affinities as we understand them, based on both published and unpublished information. We also view *muelleri* as a valid species. For us, it is also the core of a group that is unlike any other murid. But we exclude from that cluster most of the species formerly included by other investigators and bring to it only two other species: *infraluteus* and *maxi*. The three combine to form an assemblage that has morphological definition and geographic distinctiveness. The group does not fit within the boundaries of *Rattus* or any other genus; it is named and diagnosed below.

SUNDAMYS, NEW GENUS

TYPE SPECIES: *Mus mülleri*[1] Jentink (1879). The holotype is RMNH 18347; specimen "*a*" in Jentink (1888, p. 64). It was obtained on Batang Singgalang, a mountain in the Padang Highlands of central Sumatra, and presented to the museum in Leiden by S. Müller. The skin is mounted in a lifelike position as was typical of the specimens in the museum at Leiden during the time that Jentink worked there. The skull was extracted. The cranium and mandibles are present but the back part of the braincase and the bullae are missing. The specimen is a young rat and was molting from juvenile into adult pelage when it was caught. New adult pelage had proliferated along sides of the head and body and the old juvenile fur remains in a strip from head to rump.

INCLUDED SPECIES AND DISTRIBUTIONS: We recognize three species of *Sundamys*, which are listed below. All of them occur on the Sunda Shelf (fig. 32). No species of *Sundamys* is found in the Andaman and Nicobar islands to the west of the Sunda Shelf; no specimens of the genus have been taken from the islands of Simeulue (Simalur), Nias, Siberut, Sipura, Pagai Utara, Pagai Selatan, and Enggano off the southwest coast of Sumatra; and *Sundamys* has never been recorded from east of the Shelf, including the Maratua and Sulu archipelagos.

Sundamys muelleri (including *balabagensis, balmasus, borneanus, campus, chombolis, crassus, credulus, culionensis, domitor, firmus, foederis, integer, otiosus, pinatus, pollens, potens, sebucus, terempa, valens, validus, victor, virtus, waringensis*): Southern peninsular Burma (Tenasserim) and Thailand, Malay Peninsula, Pulau Penang, Anamba islands, Kepulauan Riau, Kepulauan Lingga, Pulau Banka, Sumatra, Banyak islands, Pulau Mansalar, Batu Islands, Natuna islands, Borneo, Pulau Balembangan, Pulau Banggi, Pulau Sebatik, Pulau Miang Besar, Pulau Lamukotan, and the islands of Balabac, Palawan, Busuanga, and Culion in the Palawan area

Sundamys infraluteus (including *atchinus*): Northern Borneo (Sabah) and Sumatra

Sundamys maxi: West Java

ETYMOLOGY: Named for the Sunda region

[1] The original spelling is "*mülleri*" and has been used that way until the 1960s and 1970s when it appeared in most publications as "*muelleri*." Dropping the umlaut and adding *e* behind the *u* is required by Article 32c of the "International Code of Zoological Nomenclature."

TABLE 13
Contents of *muelleri* Groups Proposed Between 1903 and 1969

Taxon	Present Name	Reference
BONHOTE (1903): *muelleri* and *infraluteus* Groups		
Mus muelleri	*Sundamys muelleri*	Present report
Mus validus		
Mus integer		
Mus firmus		
Mus infraluteus	*Sundamys infraluteus*	Present report
Mus palmarum	*Rattus palmarum*	Musser and Califia (1982)
Mus stoicus	*Rattus stoicus*	Musser (MS.)
TATE (1936): *muelleri* Group		
Rattus muelleri (subspecies: *foederis, campus, muelleri, otiosus*)	*Sundamys muelleri*	Present report
Rattus validus (subspecies: *terempa*)		
Rattus victor		
Rattus domitor		
Rattus potens		
Rattus valens		
Rattus pinatus		
Rattus balmasus		
Rattus virtus		
Rattus firmus		
Rattus chombolis		
Rattus integer		
Rattus pollens		
Rattus sebucus		
Rattus borneanus		
Rattus crassus		
Rattus infraluteus	*Sundamys infraluteus*	Present report
Rattus jarak	*Rattus tiomanicus jarak*	Musser and Califia (1982)
CHASEN (1940)		
Rattus muelleri (subspecies: *muelleri*; *campus* with *virtus* as a synonym; *domitor*; *potens*; *valens*; *balmasus*; *pinatus*; *firmus*;*credulus*; *chombolis*; *pollens*;*validus*, with *foederis* and *victor* as synonyms; *borneanus*; *otiosus*; *crassus*; *sebucus*; *integer*)	*Sundamys muelleri*	Present report
Rattus infraluteus	*Sundamys infraluteus*	Present report
Rattus infraluteus maxi	*Sundamys maxi*	Present report
Rattus mara	*Rattus tiomanicus mara*	Musser and Califia (1982)
Rattus enganus	*Rattus enganus*	Present report
Rattus macleari	*Rattus macleari*	Present report
ELLERMAN (1941): *muelleri* Group		
Rattus muelleri (*victor* as a synonym; subspecies: *campus*, with *virtus* as a synonym; *foederis, otiosus, borneanus*)		

TABLE 13—(*Continued*)

Taxon	Present Name	Reference
Rattus validus (subspecies: *terempa*)	*Sundamys muelleri*	Present report
Rattus firmus		
Rattus domitor		
Rattus pollens		
Rattus potens		
Rattus valens		
Rattus balmasus		
Rattus chombolis		
Rattus crassus		
Rattus sebucus		
Rattus integer		
Rattus maxi	*Sundamys maxi*	Present report
Rattus infraluteus	*Sundamys infraluteus*	Present report
Rattus jarak	*Rattus tiomanicus jarak*	Musser and Califia (1982)
Rattus villosus	*Rattus annandalei bullatus*	Chasen (1940)
ELLERMAN (1949): Subgenus *Stenomys*		
macleari Group		
Rattus macleari	*Rattus macleari*	Present report
Rattus nativitatis	*Rattus nativitatis*	Chasen (1940)
callitrichus Group		
Rattus muelleri (subspecies: *campus*; *validus*, with *victor* and *foederis* as synonyms; *otiosus*; *borneanus*; *terempa*; *firmus*; *domitor*; *pollens*; *valens*; *balmasus*; *chombolis*; *crassus*; *integer*; *potens*; *sebucus*)	*Sundamys muelleri*	Present report
Rattus infraluteus	*Sundamys infraluteus*	Present report
Rattus infraluteus maxi	*Sundamys maxi*	Present report
Rattus muelleri remotus	*Rattus sikkimensis*	Musser and Marshall (MS.)
Rattus mara	*Rattus tiomanicus mara*	Musser and Califia (1982)
Rattus enganus	*Rattus enganus*	Present report
Rattus rogersi	*Rattus stoicus*	Present report
Rattus ruber	*Rattus nitidus*	Calaby and Taylor (1982)
Rattus ringens (subspecies: *ratticolor, utakwa, coenorum*)	*Rattus leucopus*	Taylor, Calaby, and Van Deusen (1982)
Rattus ringens mordax	*Rattus mordax*	Taylor, Calaby, and Van Deusen (1982)
Rattus ringens tramitius	*Rattus praetor*	Taylor, Calaby, and Van Deusen (1982)
Rattus ringens steini	*Rattus steini*	Taylor, Calaby, and Van Deusen (1982)
Rattus ringens jobiensis	*Rattus jobiensis*	Taylor, Calaby, and Van Deusen (1982)
Rattus ringens feliceus	*Rattus feliceus*	Musser (MS.)
Rattus ringens praetor	*Rattus praetor*	Taylor, Calaby, and Van Deusen (1982)
Rattus verecundus (subspecies: *mollis, unicolor*)	*Rattus verecundus*	Taylor, Calaby, and Van Deusen (1982)
Rattus verecundus forsteri	*Rattus steini*	Taylor, Calaby, and Van Deusen (1982)
Rattus callitrichus	*Taeromys callitrichus*	Present report
bowersii Group		
Rattus bowersii (subspecies: *latouchei, lactiventer, ferreocanus, wellsi*)	*Berylmys bowersii*	Present report

TABLE 13—(*Continued*)

Taxon	Present Name	Reference
Rattus bowersii mackenziei *Rattus bowersi fea*	*Berylmys mackenziei*	Present report
dominator Group		
Rattus dominator (subspecies: *camarus* *Rattus frosti*	*Paruromys dominator*	Present report
Rattus microbullatus	*Taeromys callitrichus*	Musser (1970)
MISONNE (1969): Subgenus *Bullimus*		
Rattus dominator	*Paruromys dominator*	Present report
Rattus adspersus	*Bunomys andrewsi*	Present report
Rattus chrysocomus	*Bunomys chrysocomus*	Present report
Rattus muelleri	*Sundamys muelleri*	Present report
Rattus adustus	*Tryphomys adustus*	Present report
Rattus bowersii	*Berylmys bowersii*	Present report
Rattus mackenziei	*Berylmys mackenziei*	Present report
Rattus manipulus	*Berylmys manipulus*	Present report
Rattus berdmorei	*Berylmys berdmorei*	Present report
Rattus maculipilis	*Taeromys callitrichus*	Musser (1970)
Rattus celebensis	*Taeromys celebensis*	Present report
Rattus xanthurus	*Rattus xanthurus*	Present report
Rattus everetti	*Rattus everetti*	Musser (1982b)
Rattus baluensis	*Rattus baluensis*	Present report

in which all the species of *Sundamys* are indigenous.

DIAGNOSIS: Once considered part of *Rattus, Sundamys* possesses the following characteristics that taken in combination distinguish it from species in that genus (see figs. 33, 34, 38–40): larger body size (compare tables 1 and 19); slightly swollen rostrum; lateral strut of alisphenoid bone forming the outer surface of the alisphenoid canal in most specimens; auditory bullae relatively very small compared with size of cranium (table 27) and tightly attached to squamosal; incisive foramina relatively shorter compared with skull length, ending before, at, or slightly posterior to faces of first upper molars (table 16); palatal bridge extends slightly posterior to back margins of third upper molars but not far enough to form a wide and deep shelf; sphenopterygoid openings in pterygoid plates either absent or minute in most specimens of *S. muelleri* and *S. infraluteus* but not *S. maxi* (table 15); different basicranial carotid arterial pattern and configuration of pterygoid plate in *S. maxi* (fig. 56); wide mesopterygoid fossa breached by either small or tiny sphenopalatine vacuities, never the spacious vacuities characteristic of *Rattus*; molars large and stocky; third upper and lower molars relatively much larger compared with the other teeth in each row; central cusp in each row on upper molars wide and gently arcuate, not cusplike; laminae on lower molars also wide and arcuate, not as cuspidate as in *Rattus*; posterior cingulum usually present at back of each first upper molar (table 17); cusp t3 on each second and third upper molar usually present and large (table 16); front lamina of each first lower molar a large chunky structure formed by fusion of the anterolingual and anterolabial cusps; 2N of 42, which includes six pairs of metacentric autosomes, 12 pairs of telocentric, and a large submetacentric X chromosome (table 2).

Sundamys muelleri

SPECIMENS AND LOCALITIES: Of the three species in the genus, *Sundamys muelleri* has the widest distribution over the Sunda Shelf. The most northern record is from Thagyet on the Little Tenasserim River, a place less than 2° north of the Isthmus of Kra (10°30′ N). South of Thagyet, *S. muelleri* is recorded

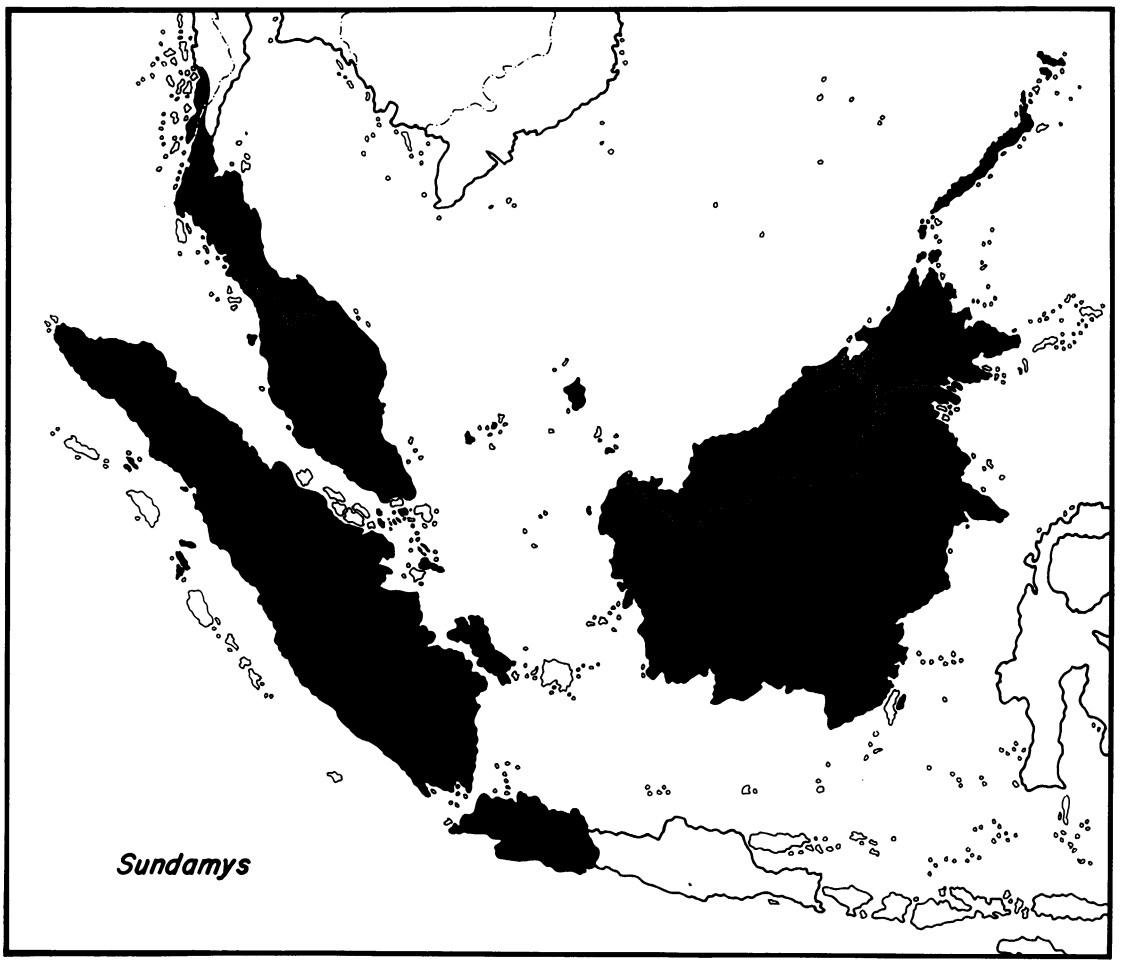

FIG. 32. Geographic distribution of *Sundamys* on the Sunda Shelf.

from peninsular Burma and Thailand, the Malay Peninsula, Sumatra, Borneo, and many smaller islands on the Sunda Shelf, including those in the Palawan region. Fragments from prehistoric sediments at Niah Cave, Sarawak have also been reported (Medway, 1964a, 1979). The specimens we examined and the places they were collected are listed below. The number preceding each locality or group of localities listed below corresponds to the numbered dot in figures 35 and 36. We list the localities under three areas: the Malayan Region, the Sumatran Region, and the Borneo-Palawan Region. We also follow this format in our discussion of geographic variation and subspecies.

MALAYAN REGION

Burma

1. Thagyet, Little Tenasserim River (12°06′ N, 99°07′ E): BM 14.12.8.213.
2. Tenasserim, Maliwum: USNM 104132 and 104133.

Thailand

3. Chumphon, Ban Tha San, 220 feet: BM 55.2910.
4. Ranong: FTM SC-335 and SC-337; RFD SC-336. These three specimens were examined for us by Dr. Joe T. Marshall, who verified their identities.
5. Ban Don, Kao Nong, 1200–1500 feet: BM 55.2912.
6. Takua Thung, Tang Pran: BM 55.2913.
7. Nakhon Si Thammarat: FTM no. 1;

FIG. 33. Views of crania: adult *Sundamys* and *Rattus* compared. A, *S. muelleri* (AMNH 102849), Sumatra. B, *R. rattus diardii* (AMNH 250104), Java. Natural size.

ASRCT SC-82. Both of these rats were examined by Marshall.

8. Trang, Khow Sai Dow: USNM 86740 and 86741 (holotype of *Mus validus*). Lamra: BM 10.10.1.80 and 55.2911.
9. Songkhla; Nga Chang Waterfall, 28 km. by road W Hoad Yai: USNM 533479.
10. Yala, Bannangstar, Tonto Waterfall, 57 km. SW Yala: USNM 533478.
11. Narathiwat: ASRCT (a specimen examined by Marshall).

Malay Peninsula

12. Perak State, Ulu Temengor (also spelled Temengoh), 400 feet: BM 55.2914 and 21.11.8.41 (holotype of *Mus muelleri foederis*).
13. Perak State, Kuala Lognai: USNM 311385.
14. Perak State, Maxwell's Hill, 2500, 2200, 3000, and 3500 feet: BM 9.4.1.395–9.4.1.396, 55.2916.
15. Perak State, Changkat Mentri: BM 55.2915.
16. Perak State, Telom, 3500 feet: BM 55.2917.
17. Trengganu, Bukit Besi (4°46′ N, 103°12′ E): USNM 311386 and 311387.
18. Pahang State, Semangko Pass, 2500–4500 feet: BM 8.7.20.67 and 8.7.20.68.
19. Pahang State, Bentong, Janda Baik, Ulu Cemperoh, 2000 feet: FMNH 98540–98544, 98546, 98547, 98629, and 98636.
20. Pahang State, Rompin River: USNM 115435, 115423, 115424, and 115422 (holotype of *Rattus victor*). Tanjong Panjair, Rompin: BM 55.2918.
21. Selangor State, Ulu Gombak, 1000–3000 feet: USNM 357944, 357945, 489075, 489115–489124, 307584, 290200 and 290198.
22. Selangor State, Bukit Lagong, 1000–3000 feet: USNM 357932, 357934, 357937, 357938–357943, 357946, 357947, 357949, 489080, 489081, 489084, 489086, 489105, 489106, 489107, 489112, 489113, and 489114.
23. Selangor State, Kepong, near Kuala Lumpur: FMNH 65899, 65900; USNM 290205, 290199, and 290204. 3 mi. North Kepong: FMNH 98548–98562; Pahang Road, 16–24 miles north of Kuala Lumpur: USNM 283538, 290191, 290192, 290193, 290195, 290196, 290197, 290206, 290207, 291295, 291300, 291301, 283543, 283558, 283688, 290194, 290201, 290202, 290203, 291299, 291302, 291303, 355401; FMNH 65901–65903.
24. Selangor State, Subang: USNM 489077–489079, 489082, 489083, 489085, 489087, 489088, 489092, 489093, 489101–489104, 489108–489110.
25. Selangor State, Ulu Langat, 0–250 feet: USNM 357920–357931, 291296, 291298, 291297, 489089–489091, and 489094–489100.
26. Johore State, Sembrong River: USNM 112634.
27. Johore State, Tamok: USNM 489076 and 489111.

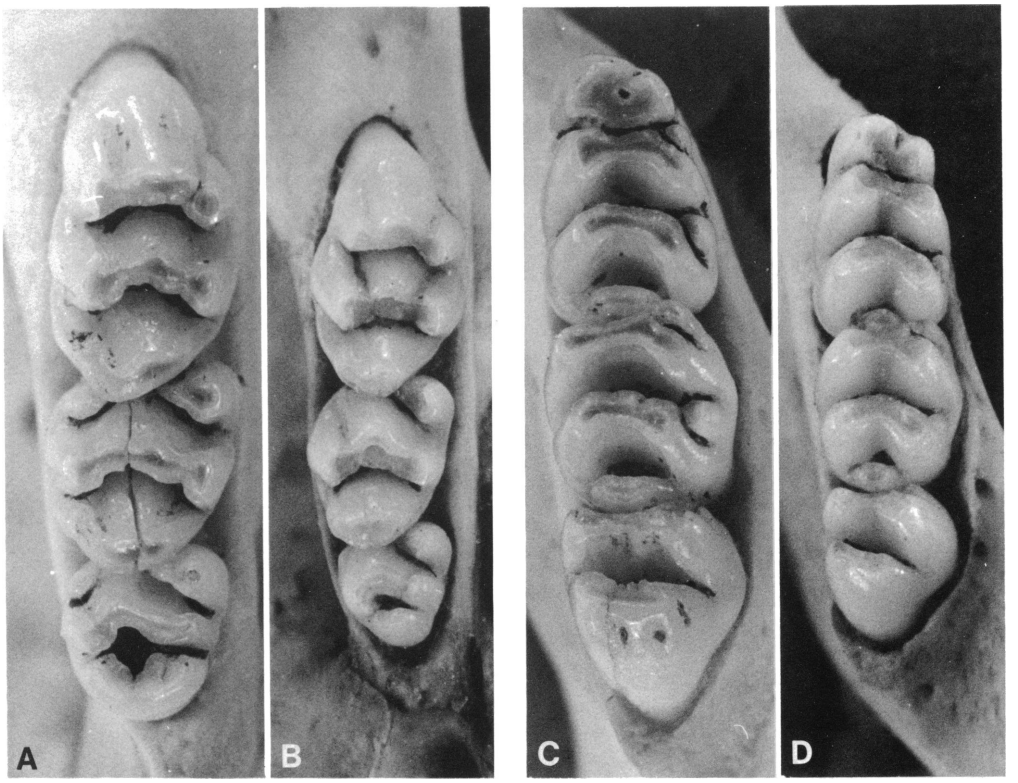

FIG. 34. Occlusal views of upper (left) and lower (right) molar rows in *Sundamys* and *Rattus*. A and C, *S. muelleri* (AMNH 103767), Borneo. B and D, *R. rattus flavipectus* (AMNH 84677), China. ×10.

28. Johore State, Kudong: USNM 357948, 489072–489074.

Kepulauan Anambas

29. Pulau Siantan: MZB 5016; BM 47.1465 (holotype of *Rattus victor terempa*).

SUMATRAN REGION

Islands off East Coast of Sumatra

1. Pulau Karimon Besar: USNM 122820–122822, 122838, and 122839; RMNH 222a and 222b; BM 9.4.1.447 and 9.4.1.448; BM 9.4.1.284, 9.4.1.439, 9.4.1.440, 9.4.1.443–9.4.1.446. Pulau Karimon Kecil: BM 9.4.1.441 and 9.4.1.442.

1a. Pulau Kundur, Bliah: BM 9.4.1.449–9.4.1.452

2. Riau Archipelago, Pulau Moro Besar: USNM 122937 and 122938.

3. Riau Archipelago, Pulau Sugibawa: USNM 115586–115590.

4. Riau Archipelago, Pulau Sugi: USNM 115585, 115591–115596.

5. Riau Archipelago, Pulau Chombol: USNM 144393 (holotype of *Mus chombolis*).

6. Riau Archipelago, Pulau Setoko: USNM 144428 and 144429.

7. Riau Archipelago, Pulau Battam, Senimba Bay: USNM 143237–143239. Pulau Battam, Tanjong Turat: BM 9.4.1.437.

7a. Riau Archipelago, Pulau Sauh: BM 9.4.1.438.

8. Pulau Sebang: USNM 123064 and 123065.

9. Pulau Bakong: USNM 123010, 123011, 123021, 123022, and 123032.

10. Lingga Archipelago, Pulau Lingga: USNM 113035, 113036, 113038 (holotype of *Mus firmus*), 113039, 113041, 113045, and 113052.

11. Pulau Banka, Tanjong Rengsam: USNM 124690, 124691 (holotype of *Epimys pollens*), 124692, and 124885. Pulau Banka: MZB 263, 5017–5019; NMS 1.B.

Mainland Sumatra

12. East Sumatra, Sungai Siak, near mouth

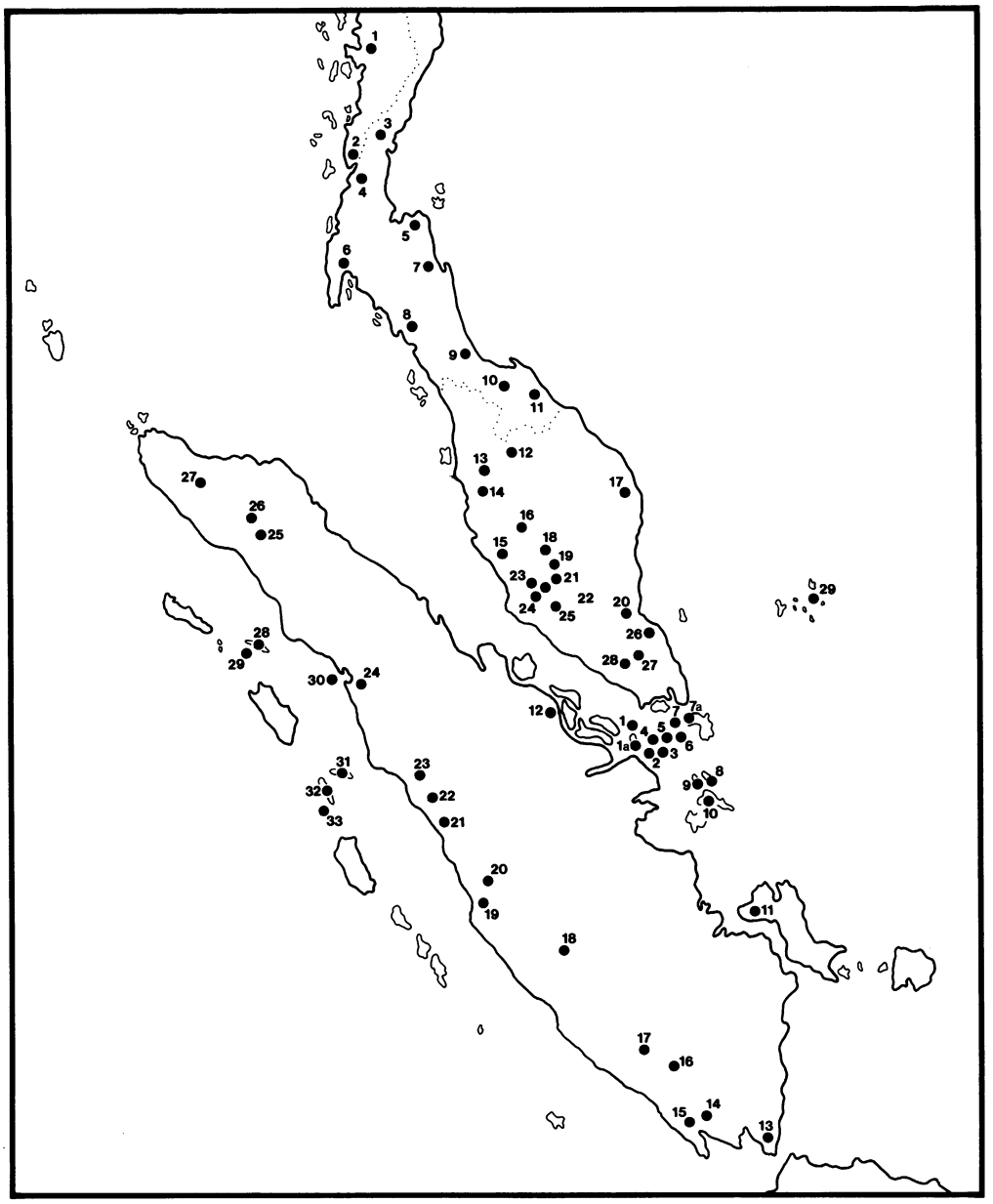

FIG. 35. Geographic distribution of *Sundamys muelleri* in the Malayan and Sumatran regions based on specimens we examined. The number next to a dot keys to numbered localities in the text where we give the name of each place and catalogue numbers of specimens.

of Sungai Gasip: USNM 144223 (holotype of *Rattus virtus*)

13. South Sumatra, Kalianda, 100 meters: AMNH 102804, 102805, 102846–102849, and 102993.
14. South Sumatra, Lampung District, De Giesting, east slopes of Gunung Tanggamoes, 700 and 900 meters: RMNH 13586, 13587, 13639, 13686, 13882, 14093, 14156–14160, 14163, 14164, and 14185; Bartels' Collection (in RMNH) S-31, S-32, S-50, S-65, S-209, and S-291.

15. South Sumatra, Lumpung District, Wai (River) Semangka, about sea level, near Banjarnegeri: RMNH 14161, 14162, and 14165.
16. South Sumatra, Palembang District, Moearadoea, 100 meters: AMNH 102547–102549 (also spelled Macarah Doewa).
17. West Sumatra, Gunung Dempo, 1600 and 1800 meters: AMNH 106400 and 106401; MZB 4998.
18. West Sumatra, Benkoelen District, Suban Ajam (Redjang), 1200 meters, north slope of Bukit Kaba (this locality is discussed in E. Jacobson's itinerary, published in Robinson and Kloss, 1919): RMNH 18352 (E. Jacobson no. 114); SNM-E. Jacobson no. 111. Both specimens were reported by Robinson and Kloss (1919).
19. West Sumatra, Pasir Ganting (2°7′ S): BM 19.11.5.95 (holotype of *Epimys muelleri campus*) and 19.11.5.96; NMS 603/14 and 604/14.
20. West Sumatra, Korinchi, Siolak Daras, 3000 feet: BM 19.11.5.94, SNM 228/14 and 259/14. Both specimens were reported by Robinson and Kloss (1918).
21. West Sumatra, Tarussan Bay: USNM 141060.
22. West Sumatra, Batang Singgalang, Padang Highlands: RMNH 18347 (holotype of *Mus mulleri*).
23. West Sumatra, Ophir District, Sukamenanti, 200 meters: RMNH 18351 (E. Jacobson no. 366). This specimen was reported by Robinson and Kloss (1919).
24. West Sumatra, Tanpanuli Bay: USNM 114450.
25. North Sumatra, Aceh District, Lesten, 700 meters: MZB 4993–4996.
26. North Sumatra, Aceh District, Gunung Ngo Lemboe, Girak I: MZB 4992.
27. North Sumatra, Aceh District, Gunung Geureudong, 1680 meters: MZB 3143–3147; RMNH 5128 and 5129.

Islands off West Coast of Sumatra

28. Banyak Islands, Pulau Tuangku: USNM 114378–114383, 114384 (holotype of *Epimys potens*), and 114291.
29. Banyak Islands, Pulau Bangkaru: USNM 114285 (holotype of *Epimys valens*), 114286–114290.
30. Pulau Mansalar (also spelled Mursala on recent maps): USNM 114614, 114615, 114620, 114621 (holotype of *Mus domitor*), 114622–114626.
31. Batu Islands, Pulau Pinie (also spelled Pini on recent maps): USNM 121775–121777, 121778 (holotype of *Rattus pinatus*), 121779.
32. Batu Islands, Pulau Tanahmasa: USNM 121772–121774.
33. Batu Islands, Pulau Tanahbala: USNM 121763, 121764, 121765 (holotype of *Rattús balmasus*), 121766, 121769, 121770, and 121771.

The following specimens from mainland Sumatra were examined but the localities from which they were collected are not mapped.

1. North Sumatra, Aceh District, Simpang Agoesan, 1000 meters: MZB 4990 and 4991.
2. West Sumatra, Ophir District, Tanangsalu: E. Jacobson specimen A and E. Jacobson no. 4602 in RMNH.
3. West Sumatra, Padang: RMNH 18348, cat. B.
4. West Sumatra, Benkoelen District, Sanggoel, 500 meters: AMNH 106402 and 106403; MZB 4999.
5. South Sumatra, Palembang District, Talang Betoetoe: MZB 214.
6. South Sumatra, Palembang District, Soebandjing: MZB 4997.
7. South Sumatra, Lampoengs District, Wai Lima: MZB 304.

BORNEAN-PALAWAN REGION

Sabah (North Borneo)

1. Pulau Balembangan: BM 47.1460 (holotype of *Rattus muelleri otiosus*; originally SNM 3487); SNM 3473, 3487–3489.
2. Pulau Banggi: SNM 3338, 3355, 3356, 3361, 3362, 3388, 3389, 3400, 3424, 3425, 3440, and 3682.
3. Paitan: BM 94.7.2.18.
4. Tuaran (near Agricultural Research Station), sea level: FMNH 108938, 108939, 108941–108952, 108954, 108955, and 108970.
5. Jesselton; 4 miles northeast of Jesselton; and Menggatel Rubber Estate, 11 miles northeast of Jesselton: BM 71.2895 and 71.2896; USNM 292744–292758.
6. Pulau Labuan: BM 93.6.3.4 and 94.7.2.17.
7. Gunong Kinabalu, Tenompak, 4500 and 5000 feet: USNM 301039; FMNH 108953; Gunong Kinabalu, Kiau, 3100 feet: MCZ 36534. Gunung Kinabalu, Bundu Tuhan: BM 71.2884–71.2890; USNM 292734–292743, and 301038. Bundu Tuhan, Luidan River, 3000 feet: MCZ 36514.
8. Ranau, 1500 and 1800 feet (includes Po-

ring): BM 71.2879–71.2883, 71.2864–71.2870, and 71.2906; USNM 301031–301037, 489046, 489047, and 489049–489071. Kundasong, 4200 feet: BM 71.2859–71.2863, 71.2871–71.2873, 71.2905, 71.2908, and 65.350.

9. Bettotan: SNM 3245, 3229, 3286, 3287, 3295, 3308, 3310, 3318, 3325, 3330, 3333, and 3337.
10. Sandakan District, Sapagaya Forest Reserve: FMNH 76948 and 76949.
11. Gomanton: SNM 3681. Gomanton Cave: BM 92.9.6.14.
12. Kinabatangan District, Sungei Kretam Kecil: FMNH 76942–76947.
13. Tawau, 750 feet: BM 71.2847–71.2858, 71.2903, and 71.2907.
14. Tawau District, Kalabakan, Sungei Tibas: FMNH 85897 and 85898. 12 miles north of Kalabakan, 200 and 600 feet: BM 71.2874–71.2878.
15. Pulau Sebatik: AMNH 31290; USNM 17590.

Kalimantan

16. Telok Karang Tigau (2°26′ N, 118°00′ E): USNM 196749 (holotype of *Epimys borneanus*).
17. Sungei Birang (Berau on recent maps), 2°11′ N, 117°27′ E: USNM 196756, 199013, and 199014.
18. Sungei Segah, 2°12′ N, 117°06′ E: USNM 196757.
19. Long Petak: MZB 1278, 1280, 1281, 1285, and 1288; H. C. Siebers collecting numbers 77, 78, 99, and 110 (in Sody's collection at Leiden). Long Temelen: MZB 1287; H. C. Siebers no. 21 (in Sody's collection at Leiden). There is a map of this area in Chasen and Kloss (1928).
20. Sungei Karangan, 1°19′ N, 117°42′ E: USNM 198168.
21. Pulau Miang Besar: USNM 197322, 197323, and 197638.
22. Sungei Karang Mumus (near Long Bleh, 0°30′ N, 116°10′ E): USNM 198814 and 198815.
23. Sungei Mahakam, Lo Bon Bon (also spelled Loa Bamban), 0°29′ S, 117°02′ E: USNM 196745. For information on this locality as well as localities 9–11, 13, and 15, see Deignan's (1959) account of Raven's itinerary.
24. Kali Tjempaga, Sampit: AMNH 103603, 103604, 103606, 103607, 103760–103774, and 103529; MZB 5006–5014; SMT 11936.
25. Kotawaringin, Riam, 300 meters: AMNH 106168–106178; MZB 5000, 5001, 5003–5005; RMNH 9796 (holotype of *waringensis*; formerly MZB 5002).
26. Perbuah (Landak Region), 900 meters: AMNH 106756, 106887, and 106888.

Sarawak

27. First Division, Gunong Matang: FMNH 85944.
28. First Division, Kuching, Stapok Road (at mile 4 and 5): FMNH 80178–80202.
29. First Division, Sadong: BM 56.9.19.14.
30. Second Division, Paku (Ulu Anyut and Sungei Pelandok): BM 55.936–55.939; SNM 7, 206, 209–211, 219, and 220. Betong: BM 55.943.
31. Third Division, Balingian: BM 11.1.19.5, 11.1.19.6, and 55.940–55.942.
32. Fourth Division, Gunong Dulit, 2000 and 3000 feet: BM 92.9.4.10, 99.12.9.74, and 51.285; SNM 40.
33. Fourth Division, Bario, 3700 feet, Kelabit Plateau: FMNH 88389.
34. Fourth Division, Baram, Sungei Tinjar, 600 feet: BM 55.944, 55.945, and 55.948.
35. Fourth Division, Sungei Baram, Marudi (Claudetown): BM 94.9.29.10.
36. Fifth Division, Lawas: FMNH 88392.

We examined the following specimens from Borneo but did not map the localities from which they came. Kalimantan: Peleben, on the middle Sungei Kayan (AMNH 103924 and 103925); Southern Kalimantan, 13 km. west and 2 km. north of Gunung Besar (USNM 521920); Melawi, Lelang Hara (NMS 1039). Sarawak: Sanarahan, Niova Barne (BM 55.946).

37. Pulau Sebuku, off coast of eastern Kalimantan: USNM 151962, 151963, 151964—holotype of *Epimys sebucus*—151965–151972.
38. Pulau Lamukotan, off west coast of Kalimantan: USNM 145471, holotype of *Epimys crassus,* 145472–145484.

Natuna Islands

39. Pulau Bunguran: BM 47.1459, holotype of *Rattus muelleri credulus.*
40. Pulau Serasan: USNM 104833, 10837, holotype of *Mus integer,* 104838, and 104839.

Palawan Area

41. Balabac Island, Mingas Point, Dalawan Bay: USNM 478127–478145. Balabac: BM 94.2.1.9.
42. Palawan Island, Macaqua, Brook's Point: USNM 478110–478123. South slope Mount Balabag, 3000 feet, Mantalingajan Range: FMNH 63157, holotype of *Rattus muelleri balabagensis.*
43. Culion Island, 6 km. southwest of Culion: USNM 478149. Siuk: FMNH 63154,

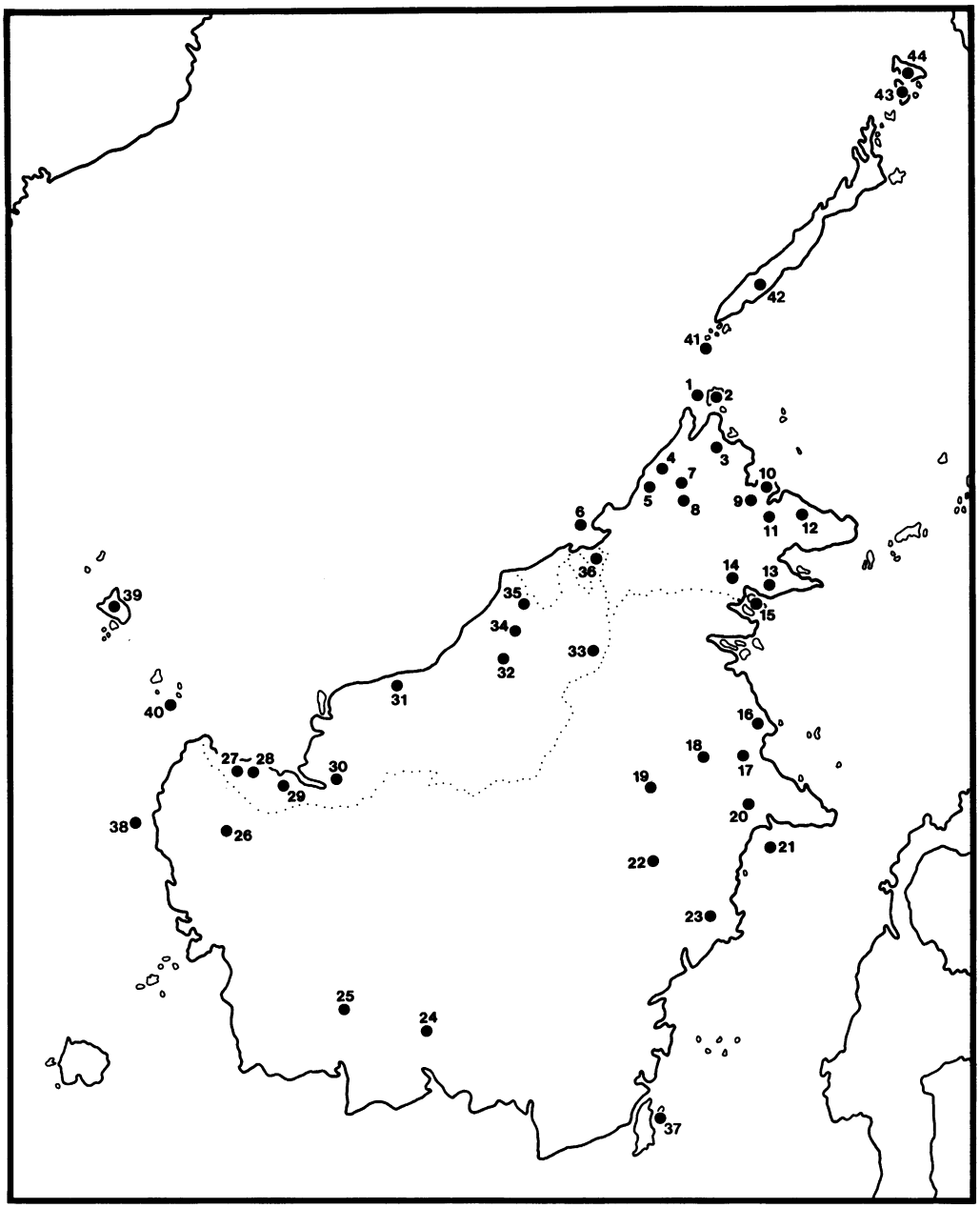

FIG. 36. Geographic distribution of *Sundamys muelleri* in the Bornean and Palawan regions based on specimens we examined. The number next to a dot keys to numbered localities in the text where we give the name of each place and catalogue numbers of specimens.

63155, 63156, holotype of *Rattus culionensis,* 63226–63228.

44. Busuanga Island, 6 km. northeast of San Nicolas: USNM 478146–478148.

DESCRIPTION: This is a large-bodied, chunky rat with a long tail (fig. 37; also, see the photograph in Marshall, 1977, p. 479). *Sundamys muelleri* joins *Berylmys bowersii, Leo-*

FIG. 37. *Sundamys muelleri.*

poldamys edwardsi, and *L. sabanus* in being the largest murids known to occur on the Malay Peninsula, species that Lim (1970) refers to as giant rats. Two sets of body weights illustrate this large size. Rudd (1965) gives the range, 209.4–411.6 grams, for six adult males and 206.1–441.3 grams for six adult females. Lim (1970) records mean body weight for 30 adult males as 335.4 grams and the mean for 30 adult females as 292.4 grams.

Upperparts of adult *Sundamys muelleri* are covered by dark tawny brown fur that is dark-

est along the middle of the back and rump and paler on the sides. The coat is thick and slightly harsh to the touch, but not spinous, and slightly shaggy but not as rough and shaggy as the pelage of *S. infraluteus*. Overhairs on the rump are 12–18 mm. long. Black guard hairs scattered over the back and rump are short, only 8–15 mm. longer than the overhairs. The pelage over head and body is dark in samples from most places on the Sunda Shelf. Rats from the islands of Balabac, Palawan, Culion, and Busuanga in the Palawan region are paler, the fur has pale buffy highlights rather than a dark tawny brown hue.

Underparts are clothed in soft, dense, and short (6–8 mm. long) fur. The venter is usually sharply demarcated from the dorsum and there is individual and geographic variation in coloration of the underparts. We separated specimens into three categories. The first contains those with underparts that are all white, cream, or pale buff from chin to anus. Many rats in this category are slightly suffused with pale gray, either over the belly or along a midventral line from the chest to inguinal area. The second includes rats in which the chin and throat are white, cream, or buffy; the rest of the underparts are whitish gray or buffy gray. The third group has underparts that are whitish gray from chin to anus. The variation ranges from frosted gray venters to dark gray suffused with buffy or rich ochraceous hues. Some specimens are very dark gray and only tinged with white or buff. All three categories are represented in samples from the Malay Peninsula and most islands on the Sunda Shelf (table 14). The exceptions are Pulau Lamukotan, off the west coast of Kalimantan, the islands in the Palawan region; there most of the rats have white or pale buff and gray underparts.

Underparts in the inguinal region of sexually mature males may be stained from a midventral sebaceous gland of unknown function (Rudd, 1966b).

The ears are small, round, and dark brown. The tail is longer than combined lengths of head and body (tables 19–23) and dark brown on all surfaces. We have never seen a specimen with mottling or bicoloration. The tail scales are large, 9 to 12 rows per cm., and three short hairs emerge from beneath each scale. Dorsal and ventral surfaces of the front and hind feet are brown. All the claws are unpigmented. Three large interdigital and two metacarpal pads form most of each plantar surface. There are four large interdigital and two metatarsal pads on each naked plantar area (fig. 15).

TABLE 14
Frequencies of White and Pigmented Underparts in Peninsular and Insular Samples of Adult *Sundamys muelleri*[a]

Origin of Sample	Size of Sample	Categories 0	1	2	Mean
Malay Peninsula	64	18	24	22	1.3
Riau Archipelago	22	2	14	6	1.3
Lingga Archipelago	14	4	6	4	1.3
Pulau Banka	3	—	3	—	1.0
Mainland of Sumatra	11	3	6	2	1.2
Banyak Islands	12	2	9	1	1.1
Pulau Mursala	8	—	2	6	1.7
Batu Islands	11	4	5	2	1.2
South Kalimantan	29	3	22	4	1.2
Sabah	24	5	14	5	1.2
Pulau Lemukutan	12	5	7	—	.6
Pulau Sebuku	9	—	—	9	2.0
Natuna Islands	4	—	3	1	1.3
Balabac and Palawan Islands	25	15	10	—	.4
Busuanga and Culion Islands	7	6	1	—	.1

[a] Definition of categories: 0) Underparts all white, cream, or pale buff from chin to anus. Included are specimens with a slight suffusion of pale gray scattered either over the belly or along a midventral line from chest to inguinal area. 1) Chin and throat white, cream, or buffy; rest of underparts whitish gray or buffy gray. Most specimens are whitish gray or buffy gray from chest to anus, some are pigmented like this only on the belly. 2) Underparts whitish gray or buffy gray from chin to anus. The variation ranges from frosted gray underparts to dark gray suffused with buffy or bright ochraceous hues. Some specimens are dark gray and only tinged with white or buff.

Females have four pairs of mammae: one pectoral, one postaxillary, and two inguinal. We did not find any variation in either number or position of teats among the specimens examined.

Juvenile *Sundamys muelleri* also have brown upperparts and white, gray, or buffy underparts. Juvenile pelage is shorter, softer, less dense, and paler than that of adults. The

texture is most often soft and silky rather than slightly harsh and shaggy. Adult pelage begins to proliferate along sides of the head and body and move toward the mid-dorsal area. Because the juvenile pelage is so different from the adult coat individuals in the molt from juvenile to adult pelages are easy to recognize. Most have the adult pelage along sides of the head and body and juvenile pelage down the middle of the head, back, and rump. This strip becomes narrower as the molt progresses and is eventually obliterated. The strip, either wide or narrow, of juvenile pelage is conspicuous in molting rats and the pattern is characteristic of *S. muelleri.*

The cranium of *Sundamys muelleri* is of medium to large size (tables 19–23), stocky, and appears robust (figs. 33 and 42). In ventral view, the rostrum is moderately long, the zygomatic arches are stout and either parallel to each other or converge anteriorly. The braincase is long, widest between squamosal roots of the zygomatic arches, and decreases in width toward the occiput. The rostrum is wide, appearing almost inflated, wide enough so its sides almost enclose the nasolacrimal capsules; those structures do not form prominent bulges on either side as they do in other genera, *Berylmys* and *Rattus,* for example (figs. 6, 16, and 17). Tips of the nasals slightly overhang sides of the rostrum. The nasals are pointed or rounded at their tips and decrease in width posteriorly so their dorsal outline is often spatulate. Just anterior to the ends of the nasals are broad and deep zygomatic notches formed by prominent anterior extensions of the zygomatic plates. The anteromedial portion of each orbit is occupied by the very small dorsal process of the lacrimal bone. Beginning at the interorbital area, high and wide ridges sweep back to the occiput outlining dorsolateral margins of the interorbital and postorbital regions and the braincase. The sides of the braincase are not vertical but slope medially from tops of squamosal roots of the zygomatic arches to the temporal ridges. The occiput is much narrower than the braincase between the zygomatic roots, it is deep (anterior-posterior), and it is partly roofed by the posterior one-third or one-half of the interparietal bone. The anterior part of that bone is between the parietals. The wide and thick vertical ridges on each side of the cranium that mark the union of braincase and occiput are especially evident from a dorsal perspective.

From a lateral view, the top of the cranium forms a low arc from tip of nasals to occiput (fig. 52). The nasal tips extend slightly anterior to the rostrum and incisor faces. The cranium is high (in dorsal–ventral plane); this, combined with the cranial length and dense bone provide the chunky look to the skull. Each zygomatic plate is stout and broad; its spine extends far enough anterior to the zygomatic arch so that is partially conceals the nasolacrimal capsule and forms a deep zygomatic notch. The squamosal roots of the zygomatic arches originate high on the sides of the braincase relative to the configuration in *Rattus.* A low but prominent shelf extends from the posterior margin of each root to the occiput. The squamosal bone above each auditory bullae is intact and not divided into dorsal and ventral portions by a squamosomastoid foramen; that foramen is confined to the suture between the squamosal bone and mastoid portion of the petromastoid complex. The outer surface of each mastoid is gently curved, smooth, and intact; we did not see a mastoid fenestra in any specimen (fig. 38). The paraoccipital process ventral to the mastoid is prominent and long, extending ventral to the bulla. The auditory bullae are very small relative to size of cranium, a proportion evident in side view. Each bullar capsule is closely joined to the squamosal bone so the periotic bone occupies most of the space between capsule and squamosal, and the postglenoid space is narrow and inconspicuous (fig. 38).

The configuration of the sphenopalatine and dorsal palatine foramina in each orbit of *Sundamys muelleri* resembles that figured for *Palawanomys* and *Rattus* (fig. 8). The sphenopalatine foramen is large and round and separate from the smaller and oblong dorsal palatine foramen, which is well posterior to the other opening.

The configuration of the alisphenoid region beneath the squamosal root of each zygomatic arch is depicted in figure 38A. In 363 out of 377 specimens (97 percent of the sample), there is a prominent and wide strut of alisphenoid bone (codes 3 and 4; fig. 48) forming the lateral side of each alisphenoid

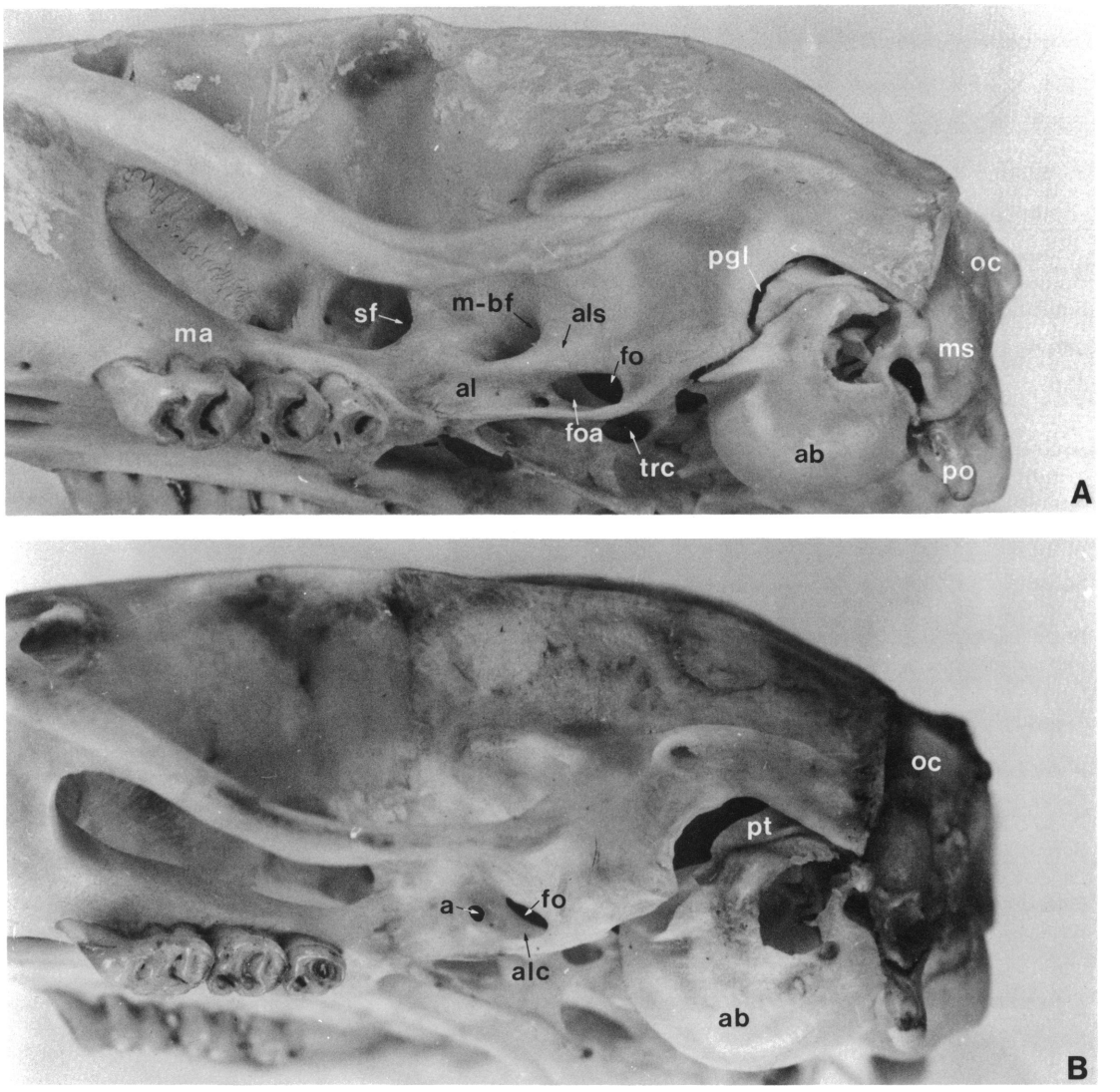

FIG. 38. Posterolateral views of crania focusing on the alisphenoid and bullar regions. A, *Sundamys muelleri* (AMNH 102847). B, *Rattus rattus diardii* (AMNH 229983). *Abbreviations:* **a**, anterior opening of the alisphenoid canal; **ab**, auditory bulla; **al**, alisphenoid bone; **alc**, alisphenoid canal, which is an open channel in *Rattus* but concealed behind a lateral strut of alisphenoid bone (**als**) in *Sundamys*; **fo**, foramen ovale; **foa**, foramen ovale accessorius; **ma**, maxillary bone; **ms**, mastoid portion of the petromastoid; **m-bf**, coalesced masticatory-buccinator foramina; **oc**, occiput; **pgl**, postglenoid vacuity; **po**, paraoccipital process; **pt**, periotic portion of the petrosal; **sf**, sphenoidal fissure; **trc**, transverse canal.

canal; such a strut is absent in only three percent of the sample (table 15). Anterior to the bony strut is the coalesced masticatory-buccinator foramen and posterior to the strut is the accessory foramen ovale. Medial to the strut is the alisphenoid canal. When the strut is wide, the anterior opening of the alisphenoid canal, as well as the foramen ovale, is concealed from lateral view. In specimens with narrower struts, portions of each of those openings are visible (codes 2 and 3; figs. 47 and 48). In the few specimens where the strut is absent (code 0; fig. 47) or represented by small processes (code 1; fig. 47), the ali-

TABLE 15
Distributions of the Different Configurations of the Alisphenoid Strut and Sphenopterygoid Fenestra Among Samples of *Sundamys*
(N refers to the number of specimens in each sample.)

		Alisphenoid Strut[a]						Sphenopterygoid Fenestra[b]			
Species and Locality	N	0	1	2	3	4	N	0	1	2	3
S. infraluteus											
Borneo	19	2	6	3	6	2	19	12	7	—	—
Sumatra	3	—	—	—	1	2	3	—	3	—	—
S. maxi											
Java	18	1	1	1	8	7	17	—	—	4	13
S. muelleri											
Southern Thailand and Burma; Malay Peninsula	127	2	5	—	26	94	128	85	29	13	1
Kepulauan Riau	25	—	—	—	4	21	25	6	5	5	9
Kepulauan Lingga	13	—	—	—	—	13	13	—	5	5	3
Pulau Banka	4	—	1	—	2	1	4	1	1	2	—
Sumatra	17	1	1	—	1	14	17	8	4	1	4
Pulau Mursala	8	—	—	—	1	7	8	3	—	2	3
Pulau Tuangku	7	—	1	—	3	3	7	5	—	1	1
Pulau Bangkaru	7	—	—	—	5	2	7	7	—	—	—
Pulau Pini	5	—	—	—	2	3	5	3	2	—	—
Pulau Tanahmasa and Tanahbala	9	—	—	—	3	6	9	—	2	3	4
Pulau Lemukutan	13	—	—	—	8	5	13	4	5	2	2
Pulau Sebuku	11	—	—	—	2	9	11	4	4	1	2
Pulau Serasan	3	—	—	—	—	3	3	3	—	—	—
Borneo	103	2	—	—	34	67	100	17	29	21	33
Balabac Island	13	—	—	—	—	13	13	2	4	3	4
Palawan Island	8	—	—	—	—	8	8	—	1	2	5
Busuanga Island	4	—	—	—	—	4	4	1	3	—	—
Totals											
S. infraluteus	22	2	6	3	7	4	22	12	10	—	—
percent		(9)	(27)	(14)	(32)	(18)		(55)	(45)	—	—
S. maxi	18	1	1	1	8	7	7	—	—	4	3
percent		(6)	(6)	(6)	(44)	(38)		—	—	(24)	(18)
S. muelleri	377	5	8	—	91	273	375	149	94	61	71
percent		(1)	(2)	—	(24)	(73)		(40)	(25)	(16)	(19)

[a] The lateral strut of alisphenoid bone ranges from being absent (coded 0) to a wide bony structure (coded 4). The five coded configurations are illustrated in figures 47 and 48 and further described in the legend there.

[b] The anterior two-thirds of each pterygoid plate, as seen in ventral view, is either complete or perforated by a fenestra at the suture between the palatine and alisphenoid bones. We qualitatively coded the range of variation in this feature by noting the number of specimens in which it was either absent (0), tiny to small (1), of medium size (2), or a large vacuity (3). If absent, the pterygoid platform is solid, like that in figure 39B; when present, the configuration resembles that shown in figure 39B.

sphenoid canal is open and the masticatory-buccinator foramen is coalesced with the accessory foramen ovale, a configuration like that in all specimens of *Berylmys* (fig. 19A), *Palawanomys* (fig. 9A), and *Rattus* (fig. 38B). Musser (1982b, 1982c) provides details about the architecture of this alisphenoid region and the vessels and nerves passing through the canal and various foramina.

The very wide rostrum and stocky nature of the cranium is also apparent in ventral view (figs. 33 and 42). The incisive foramina

are wide but short relative to length of diastema. They are parallel along most of their lengths and slightly tapered at the anterior and posterior margins. In more than half the specimens in any sample, the posterior margins of the foramina are anterior to the front surfaces of the first upper molars or even with them (see table 16, where values are listed of samples from the Malay Peninsula and Sabah); in the other specimens of each sample, the posterior edges extend past the faces of the first molars by less than a millimeter.

The palatal bridge is long and wide. The posterior edge extends past the back surfaces of the third upper molars in all specimens (table 16; figs. 33, 39B, and 42) but not far enough to form a wide shelf as the bridge does in *Palawanomys* and *Rattus* (figs. 9B and 39A). The surface of the palatal bridge is smooth, the palatine grooves are shallow and inconspicuous, and each posterior palatine foramen is opposite either the place where the second and third molar meet or the anterior portion of the third molar (fig. 39B). The posterior portion of the bridge is solid, its back margin is outlined by ridges, and aside from a few foramina, there is no extensive pitting or fenestration on the surface.

The configuration of the mesopterygoid and pterygoid areas are illustrated in figure 39B. The mesopterygoid fossa is very wide. Its walls are breached by short and wide sphenopalatine vacuities; their anterior margins do not extend forward beneath the back of the palatal bridge and do not show up in the back portion of each orbit. The pterygoid fossa on either side of the mesopterygoid is long and narrow. The floor is nearly flat and only slightly inclined toward the middle of the cranium. The lateral margin of each pterygoid plate is outlined by a prominent ridge extending from the tip of the maxillary behind the molar row to the anterolateral margin of the auditory bulla. The region between the foramen ovale and bullae—the pterygoid bridge—is a thick and high ridge (fig. 39B) that joins the squamosal bone adjacent to the bulla, not a smooth mound, which is the configuration in other Indo-Malayan genera (Musser, 1981a). The anterior two-thirds of each pterygoid fossa is an intact plate in 40 percent (149 out of 375 specimens) of the sample (table 15; fig. 39B). In the remainder of the series, there is a sphenopterygoid vacuity (fenestra) in each plate; the opening ranges from tiny (25 percent of the sample) to medium size (16 percent) to large (19 percent). The posterior one-third of each plate is sculptured and reflects the opening of the transverse canal on the medial side, the bottom of the foramen ovale on the lateral side, and a deep groove extending along the inner side of the pterygoid bridge from the back of the foramen ovale to the middle lacerate foramen, clearly seen in figure 39B. The inter-

TABLE 16
Posterior Margins of Incisive Foramina and Palatal Bridge Relative to First and Third Upper Molars in Species of *Sundamys*[a]

Trait	*S. muelleri*		*S. infraluteus*
	Malay Peninsula	Sabah	Sabah
INCISIVE FORAMINA AT M^1			
Anterior	24 (.3 ± .3; .1–1.0)	7 (.4 ± .1; .3–.4)	14 (1.0 ± .6; .1–2.3
Even	9	6	—
Posterior	21 (.4 ± .2; .1–.7)	8 (.4 ± .2; .1–.7)	—
PALATAL BRIDGE AT M^3			
Anterior	—	—	—
Even	—	—	—
Posterior	54 (.8 ± .3; .1–1.5)	21 (.9 ± .3; .4–1.5)	14 (1.6 ± .3; .9–2.2)

[a] Posterior margins of incisor foramina end either anterior to front faces of first upper molars, even with them, or posterior to them; posterior rim of palatal bridge extends behind back faces of upper third molars. Listed are number of specimens with each trait; in parentheses are extent of foramina or bridge as expressed by mean plus or minus one standard deviation and observed range.

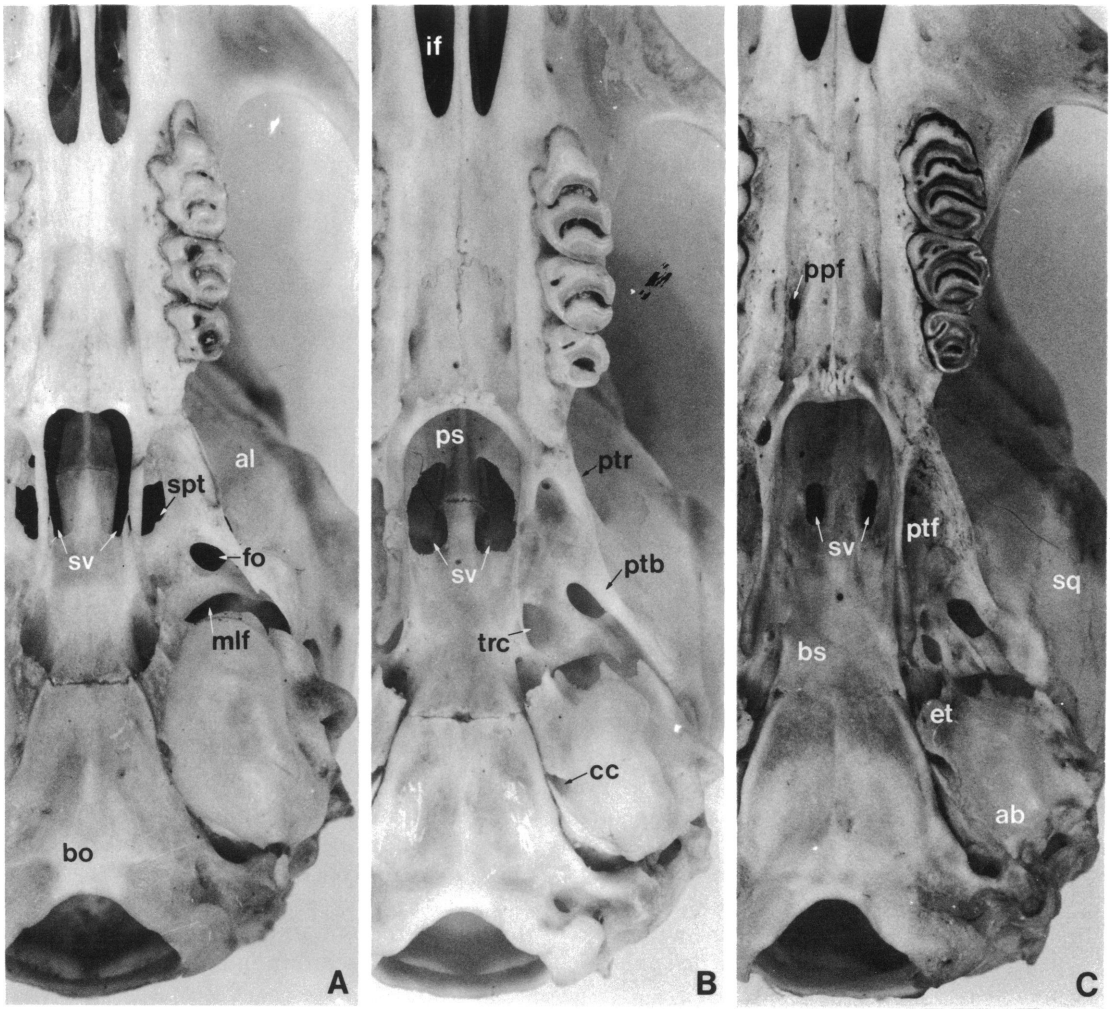

FIG. 39. Ventral views of crania contrasting *Rattus* and *Sundamys*. A, *Rattus rattus diardii* (AMNH 229983). B, *Sundamys muelleri* (AMNH 102847). C, *Sundamys infraluteus* (FMNH 108935). *Abbreviations:* **ab**, auditory bulla; **bo**, basioccipital bone; **bs**, basisphenoid bone; **cc**, carotid canal; **et**, bony eustachian tube; **if**, incisive foramina; **mlf**, middle lacerate foramen; **ppf**, posterior palatine foramen; **ps**, presphenoid bone; **ptf**, pterygoid fossa; **ptr**, pterygoid ridge; **spt**, sphenopterygoid vacuity; **sv**, sphenopalatine vacuity; **trc**, transverse canal.

nal maxillary courses in that groove. The artery exits from the bullar capsule through the middle lacerate foramen, courses in the groove and passes onto the dorsal surface of the pterygoid plate; at that point it passes through the posterior opening of the alisphenoid canal and then extends anterior in the canal to the orbit. The internal maxillary comes from the stapedial artery, which branches from the common carotid and enters the otic region through a large stapedial foramen. After giving off the stapedial, the common carotid extends anteriorly and enters the cranial cavity through the carotid canal. The arterial pattern and bony framework is diagrammed in figure 56 and also depicted in figure 39B. The pattern is typical of most murids, is apparently primitive within the Muridae, and is characteristic of every specimen of *S. muelleri* we examined. See Musser (1982b, 1982c) for additional details.

The auditory bullae are not inflated and

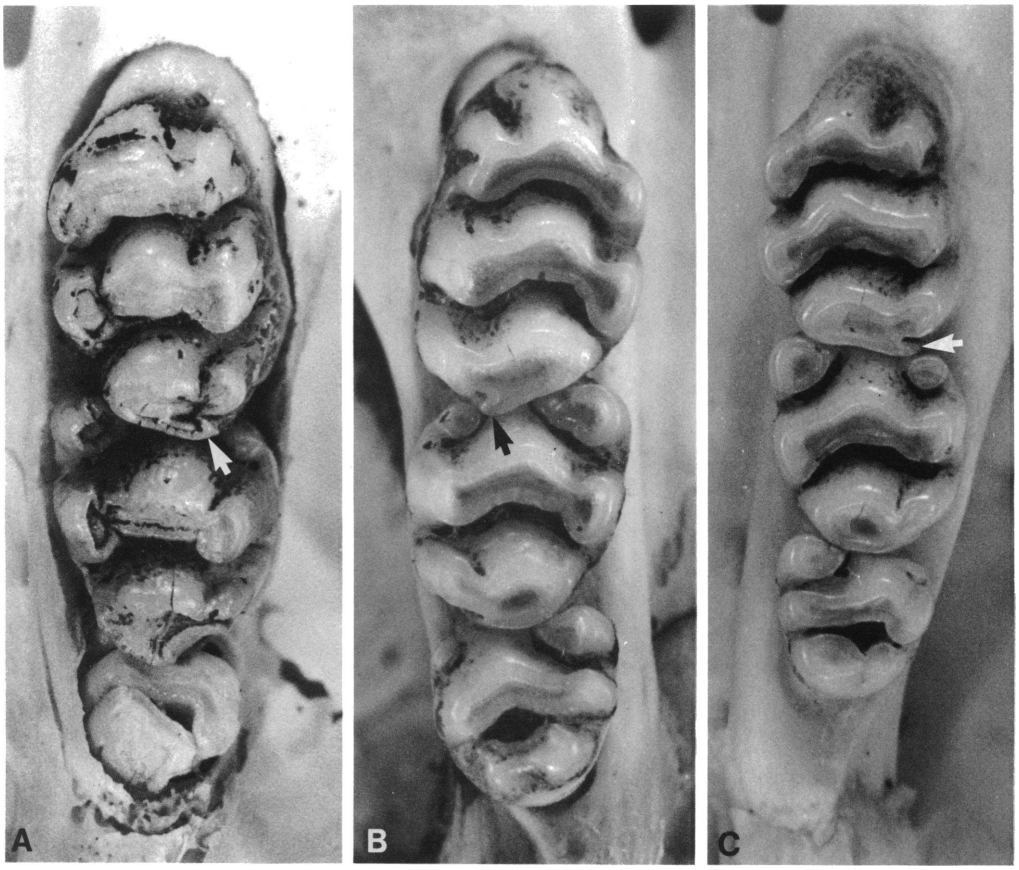

FIG. 40. Occlusal views of molar rows showing the posterior cingulum (arrow) at the back of each first upper molar. A, *Sundamys infraluteus* (USNM 292769), Sabah; ×10. B, *Sundamys muelleri* (USNM 290196), Sabah; ×10. C, *Sundamys maxi* (RMNH 14210), Java, ×8.

are very small relative to size of the cranium (figs. 33, 39B, and 42). Each bony eustachian tube is moderately long.

Each dentary is large and appears sturdy (fig. 52). The coronoid process is prominent. The angular process is expansive but thin and the shelf on the inside ventral margin is narrow. On the lateral surface below the coronoid process is a bulge containing the tip of the incisor capsule. On the lingual surface of the dentary, there is a narrow shelflike ridge extending from behind the molar row to the base of the condyloid process just posterior to the mandibular foramen; the ridge does not extend out to the end of the process.

The incisors are large and sturdy. Enamel surfaces of both uppers and lowers are smooth and deep orange. The uppers emerge from the rostrum and curve slightly back (opisthodont) in most specimens but emerge at right angles (orthodont) in a few.

Upper and lower molars are large and low-crowned (brachydont). Five roots anchor each first upper molar (anterior and posterior, labial, and two lingual) four roots are beneath each second molar, and three roots hold each third molar. In some specimens there is a small fourth root on the lingual side beneath each third molar. Four roots (large anterior and posterior, smaller lingual and labial) anchor each first lower molar, and beneath each second and third lower molar are three roots.

In the upper toothrow, the first molar is long and wide and overlaps the smaller second molar, which overlaps a smaller third molar (fig. 41). Occlusal surface of each first

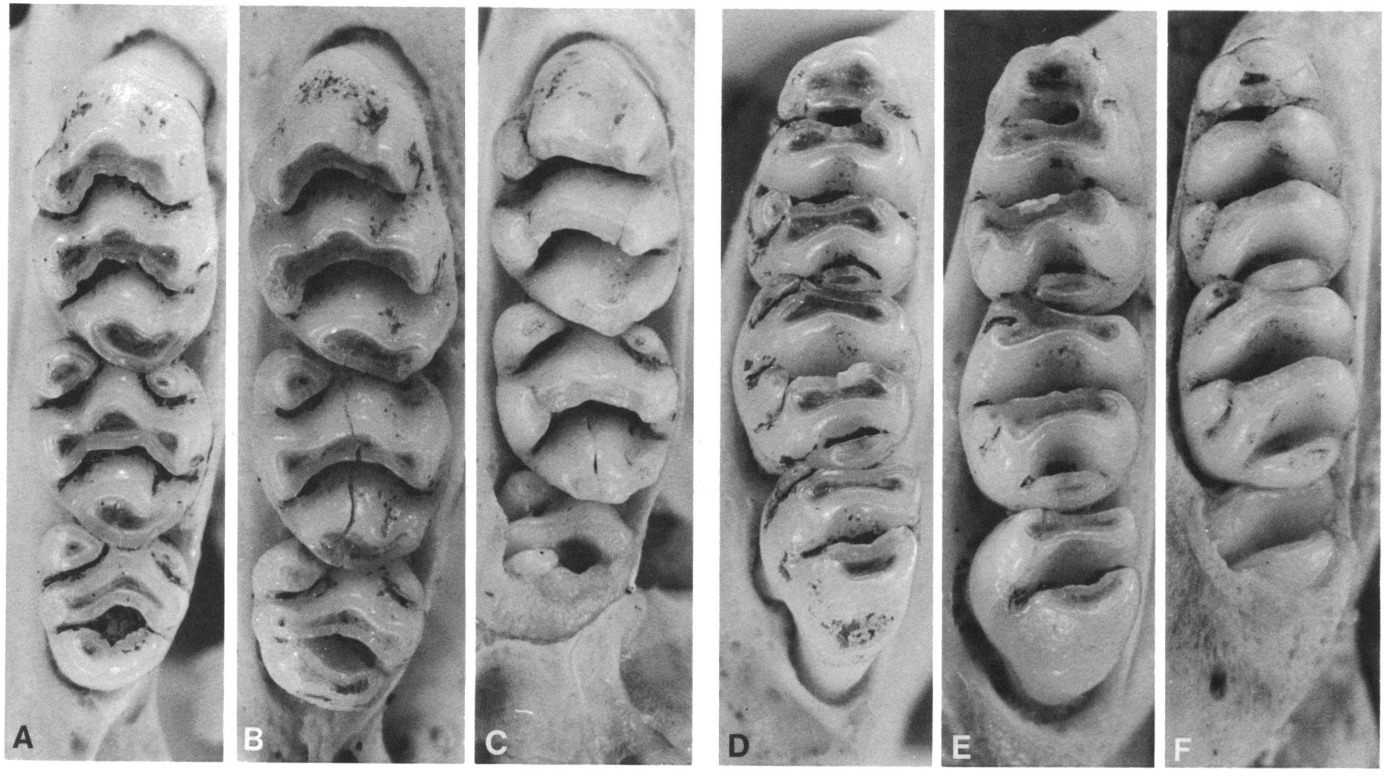

FIG. 41. Occlusal views of left upper (A–C) and lower (D–F) molar rows in *Sundamys muelleri*. A and D, adult (AMNH 106176), Borneo. B and E, young adult (AMNH 102993), Sumatra. C and F, juvenile (AMNH 103924), Borneo. All ×10.

upper molar consists of three chunky, broad, and arcuate laminae. The central cusp in each lamina is thin and wide: there are three smaller labial cusps and two lingual cusps. No cusp t7 occurs on any specimen. The laminae appear slightly cuspidate in young juveniles (fig. 41C) but lose that configuration in older animals because the cusps are so broadly merged in each lamina. There is a wedge-shaped posterior cingulum at the back of each first upper molar in 50 percent of our sample of *S. muelleri* (table 17; fig. 40).

The occlusal surface of each second upper molar consists of a large cusp t1 at the anterolingual margin, a large cusp t3 at the anterolabial corner, and two laminae that are shaped like the second and third laminae of the first molar (fig. 41). Cusp t3 is present and usually large on every specimen of *Sundamys muelleri* we examined (table 17). No cusp t7 occurs on any second upper molar. Most specimens do not have a posterior cingulum at the back of each second upper molar. If present, it is represented by a slight bulge at the back of each tooth.

Each third molar also has a chewing surface composed of two anterior cusps and two laminae (fig. 41). The anterolingual cusp is large and the anterolabial cusp (t3) is small to large in 88 percent of the sample (table 17). The anterior lamina is arcuate or boomerang-shaped in occlusal view and non-cuspidate; it probably consists of cusps t4, t5, and t6 so coalesced that cusp outlines are no longer present. The posterior lamina is broadly U-shaped and its lingual and labial arms abut against the anterior lamina. Two cusps form the lamina, probably t8 and t9. No posterior cingula occur on third molars of any specimen.

Cusp patterns in *Sundamys muelleri,* as well as *S. infraluteus* and *S. maxi,* are not complicated by accessory cusps or crests. There are no lingual or labial cusps (t1bis and t2bis) on the anterior face of the front lamina of each first upper molar. We found no accessory cusp in back of cusp t6 on each first and second upper molars, and no crests joining the laminae. Such accessory cusps and crests are present in some other Sundanese genera, such as *Lenothrix canus* (fig. 1), for example.

TABLE 17
Presence (+) or Absence (−) of Certain Cusps and Cusplets on Upper and Lower Molars in Species of *Sundamys*[a]

Trait	*S. infraluteus*	*S. maxi*	*S. muelleri*
Posterior cingulum on M^1			
+	100 (19)	100 (19)	50 (132)
−	— —	— —	50 (131)
Cusp t3 on M^2			
+	94 (16)	100 (19)	100 (257)
−	6 (1)	— —	—
Cusp t3 on M^3			
+	50 (7)	95 (18)	88 (222)
−	50 (7)	5 (1)	12 (31)
Anterior labial cusplet on M_1			
+	— —	32 (6)	52 (97)
−	100 (14)	68 (13)	48 (90)
Posterior labial cusplet on M_1			
+	100 (14)	100 (19)	99 (220)
−	— —	— —	1 (3)
Anterolabial cusp on M_1			
+	100 (14)	100 (19)	100 (224)
−	— —	— —	— —
Posterior labial cusplet on M_2			
+	100 (14)	100 (19)	99 (222)
−	— —	— —	1 (2)
Anterolabial cusp on M_3			
+	64 (9)	84 (16)	68 (141)
−	36 (5)	16 (3)	32 (68)

[a] Numbers of cusps and cusplets are expressed as percentages; numbers of specimens in parentheses.

Occlusal surfaces of the lower molars consist of broad laminae, posterior cingula, anterolabial cusps, and labial cusplets. The front lamina on each first molar is wide and thick and formed by the coalesced anterolabial and anterolingual cusps. The occlusal shape as shown in figure 41D and E is typical of most specimens, even young rats. We could not detect an anterocentral cusp on any specimen of *S. muelleri.* The second and third laminae are also wide and each is formed of two thinly elongate cusps broadly merged. As the posterior margin of the tooth is a thick and wide posterior cingulum. In half the sample of *S.*

TABLE 18

Scientific Names Associated with *Sundamys muelleri*[a]

Region and Name	Author and Date	Type Locality	Current Status
MALAYAN REGION			
Mus validus	Miller, 1900, p. 141	Peninsular Thailand, Trang	*Sundamys muelleri validus*
Mus mülleri foederis	Robinson and Kloss, 1911, p. 245	Malay Peninsula, Perak State, Ulu Temengor	
Rattus victor	Miller, 1913, p. 16	Malay Peninsula, Pahang State, Sungai Rompin	
Rattus validus terempa	Chasen and Kloss, 1928b, p. 36	Pulau Siantan, Kepulauan Anamba	
SUMATRAN REGION			
Mus mülleri	Jentink, 1879, p. 16	West Sumatra, Padang highlands, Batang Singgalang	*Sundamys muelleri muelleri*
Epimys mülleri campus	Robinson and Kloss, 1916, p. 275	West Sumatra, Pasir Ganting	
Rattus virtus	Lyon, 1916b, p. 210	East Sumatra, Sungai Siak near mouth of Sungai Gasip	
Mus domitor	Miller, 1903a, p. 461	Pulau Mansalar, off west coast of Sumatra	
Epimys potens	Miller, 1913, p. 17	Pulau Tuangku, Kepulauan Banjak, off west coast of Sumatra	
Epimys valens	Miller, 1913, p. 18	Pulau Bankaru, Kepulauan Banjak, off west coast of Sumatra	
Rattus balmasus	Lyon, 1916a, p. 447	Pulau Tanahbala, Kepulauan Batu, off west coast of Sumatra	
Rattus pinatus	Lyon, 1916a, p. 448	Pulau Pini, Kepulauan Batu, off west coast of Sumatra	
Mus firmus	Miller, 1902a, p. 155	Pulau Lingga, Kepulauan Lingga, off southeast coast of Sumatra	
Mus chombolis	Lyon, 1909, p. 484	Pulau Chombol, Kepulauan Riau, off southeast coast of Sumatra	
Epimys pollens	Miller, 1913, p. 17	Pulau Banka, off southeast coast of Sumatra	
BORNEAN AND PALAWAN REGION			
Epimys borneanus	Miller, 1913, p. 15	Southeast Kalimantan, Telok Karang Tiga	
Rattus mülleri waringensis	Sody, 1941, p. 289	Southwest Kalimantan, Riam	
Rattus mülleri otiosus	Chasen, 1934, p. 98	Pulau Balembangan, off north coast of Sabah	
Epimys sebucus	Lyon, 1911, p. 102	Pulau Sebuku, off southeast coast of Kalimantan	
Epimys crassus	Lyon, 1911, p. 103	Pulau Lamukutan, off west coast of Kalimantan	
Rattus mülleri balabagensis	Sanborn, 1952, p. 131	Balabac Island	
Rattus culionensis	Sanborn, 1952, p. 131	Culion Island, Calanian Islands	
Mus integer	Miller, 1901, p. 119	Pulau Serasan, Kepulauan Natuna Selatan	
Rattus mülleri credulus	Chasen, 1940, p. 162	Pulau Bunguran, Kepulauan Natuna Utara	

[a] All holotypes were examined by Musser. Within each region, the names are listed in same order as they are discussed in the text.

muelleri, there is a small anterior labial cusplet on each first molar; a large and conspicuous posterior labial cusp is found in almost every specimen (table 17).

Occlusal surface of each second lower molar consists of a large anterolabial cusp (present in every specimen we examined), two wide laminae shaped like the back two in the first molar, a wide and thick posterior cingulum forming a considerable portion of the back of each tooth, and a large posterior labial cusplet that occurs on each molar in almost all specimens (fig. 41; table 17).

The crown of each third lower molar is formed by two wide laminae in every specimen (fig. 41). Anterolabial cusps are present in 68 percent of the sample. No posterior cingulum was found on any third molar in any specimen.

Chromosomal information is reported by Yong (1968, 1969a), Yosida (1973), Yosida and Sagai (1973), and Markvong, Marshall, and Gropp (1973). The 2N is 42 and consists of six pairs of small metacentric chromosomes, one pair of large subtelocentrics, one pair of small subtelocentrics, 12 pairs of telocentrics, one large submetacentric sex chromosome and a small telocentric sex chromosome (table 2). Yosida (1973) refers to the small subtelocentric as a submetacentric but from Yong's (1968, p. 178) karyogram and the banding patterns shown in Yosida and Sagai (1973, p. 96), the position of the centromere seems too far removed from the center to be anything but a subtelocentric.

Chromosomal data comes only from samples obtained on the Malay Peninsula. There are also some biochemical data associated with samples from that area. Chan, Dhaliwal, and Yong (1979) examined the distribution of nine erythrocyte proteins among species of Malayan murids, including *S. muelleri.* Gutman and Moriwaki (1979) studied the distribution of rat kappa-chain allotype specificities (RI-1a and 1b) detected by RI-1b antisera among *Rattus rattus* and other murids, a survey which included *S. muelleri.*

GEOGRAPHIC VARIATION AND SUBSPECIES: From 1879 when Jentink named and described *Mus muelleri* until now, 24 scientific names have been associated with what came to be called *Rattus muelleri* and is now *Sundamys muelleri* (table 18). Between 1900 and 1920, many of these names were thought to represent valid species in the *muelleri* group, a conclusion reached after reading the papers by Miller and Lyon in which most of the names were proposed. In 1940 Chasen brought together 22 of the names and sorted them into what he regarded as 18 valid subspecies of *Rattus muelleri.* Two other names would not be published until 1952. Eight of the names were given to specimens from peninsular Thailand and Malaya, and the large islands of Sumatra and Borneo. The other 16 were applied to single specimens and larger samples from small islands on the Sunda Shelf.

We are less concerned with the names than with the pattern of insular and peninsular morphological variation that some of them may represent. To discover if patterns exist, we analyzed the morphometric data in several ways. One analysis concerns the hypothesis that variation in body size among the samples may be associated with island area: we wanted to know if body size showed a negative correlation with island area as suggested by Heaney (1978). Results of this study are being prepared and will be published later (Musser and Heaney, MS.). A second method was to summarize the phenetic relationships among the samples of *S. muelleri* by principle component and cluster analyses. That exercise is still in progress and results will be discussed elsewhere (Musser, MS.). Attempting to discern distributional patterns by univariate analysis was the third process and it is the results from this technique that we present here and on which we base our rough and incomplete outline of variation and the allocation of scientific names to that framework.

There are patterns reflecting the morphological variation among samples on the Shelf. The primary pattern that we focus on here concerns body size and pelage color. From a principle components analysis, we discovered that 90 percent of the variation present among the samples was due to size. Based on body size, all specimens can be easily separated into two lots, even without the morphometric data and simply by inspecting the skulls. Those from southern Burma, peninsular Thailand, the Malay Peninsula, and the Anamba islands, which form our Malayan

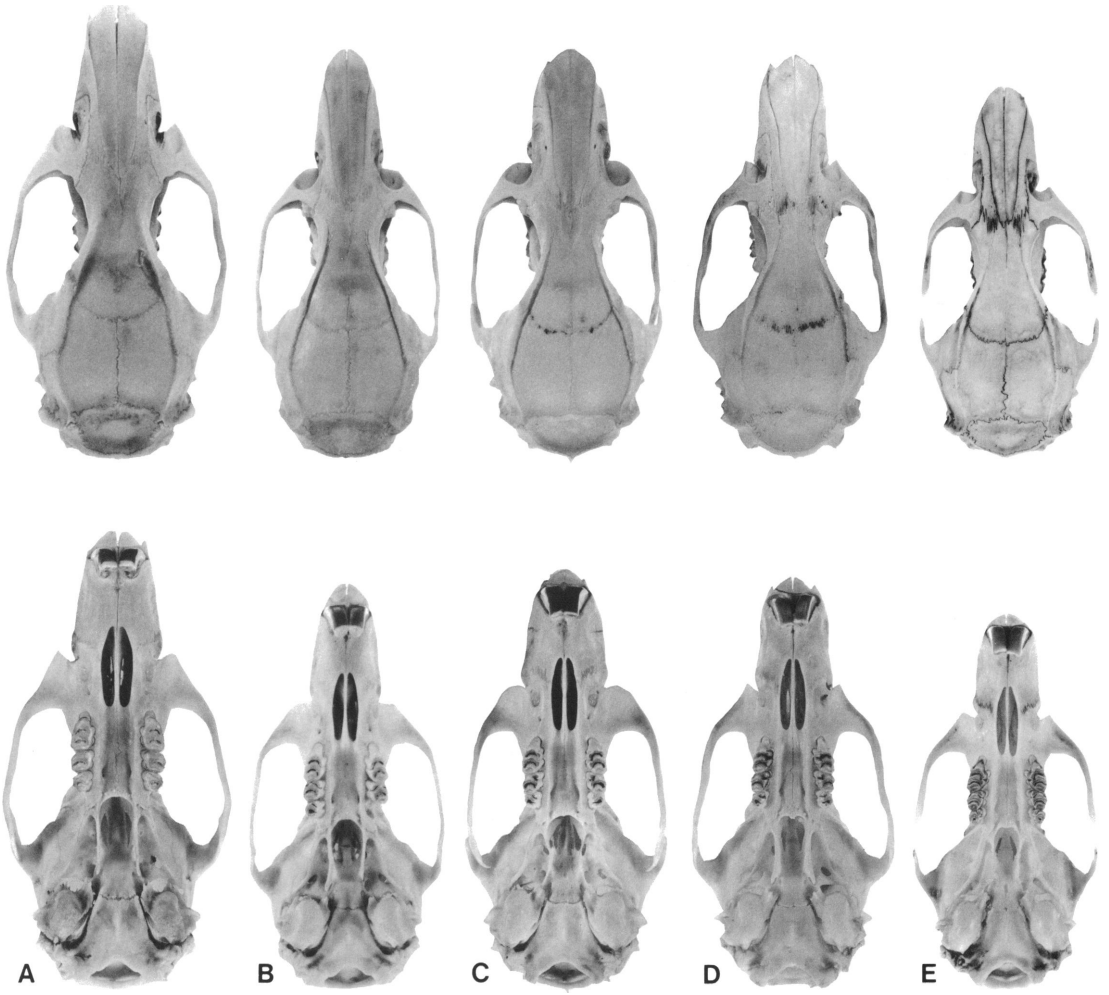

FIG. 42. Views of crania from adults to show geographic variation in *Sundamys muelleri.* A, Malay Peninsula (USNM 290205). B, mainland Sumatra (AMNH 102849). C, mainland Borneo (AMNH 103770). D, Balabac Island (USNM 478127). E, Culion Island (USNM 478147). All natural size.

Region, comprise one bunch. Specimens from Sumatra, Borneo, and the smaller islands on the Sunda Shelf except Java form the other assemblage. The population of *Sundamys muelleri* in the Malayan Region is composed of large-bodied rats. Just how large these animals are compared to members of other populations of *S. muelleri* on the Sunda Shelf can be visualized by viewing the crania in figure 42 where an adult from the Malay Peninsula is contrasted with adults from Sumatra, Borneo, and the Palawan area. The geographic distribution of variation in greatest length of skull and length of maxillary toothrow is illustrated in figure 43; there, the mean value for skull length in the sample from the Malay Peninsula is obviously significantly greater than those values from any other sample of *S. muelleri.* In skull length, the Malayan rats approximate *S. maxi* in size rather than the other samples of *S. muelleri.*

In contrast to the large rats of the Malaysian Region, specimens from elsewhere on the Sunda Shelf are much smaller animals. They are similar to one another in size of most external, cranial, and dental dimensions. Still, there is enough variation in features of skins, skulls, and teeth that define

smaller groupings of samples. In one group we sorted out the samples from mainland Sumatra, the Riau Archipelago, Lingga Archipelago, and Pulau Bangka off the coast of eastern Sumatra; and the Banyak Islands, Pulau Mansalar, and the Batu islands off the west coast of Sumatra. In a second group we place samples from Borneo and some offshore islands, and from the Natuna islands. And a third cluster contains specimens from Balabac, Palawan, Culion, and Busuanga.

We use subspecific names to point out only the basic pattern in morphological variation on the Sunda Shelf. The large-bodied rats from the Malay Region should be *Sundamys muelleri validus*; the animals from the Sumatran, Bornean, and Palawan regions are *Sundamys muelleri muelleri*. The profound difference in skull length between these two major groups justifies using the subspecies. Almost every specimen from the Malayan Region can be separated from every specimen from elsewhere on the Shelf by greatest length of skull, and overall size of skull and teeth (figs. 42 and 43). The population of *S. m. validus* occurs in a discrete region that is isolated from other populations of *S. muelleri* and nearly every specimen is morphologically distinguishable from those of *S. m. muelleri*. That the Malayan population is a subspecies and potentially capable of interbreeding with rats from elsewhere on the Shelf is a hypothesis. They may be reproductively isolated and that possibility must be examined in future studies.

There is morphological variation among insular samples of *Sundamys muelleri*. Some of the variation reflects part of a pattern, most does not. Some of our samples are large, many from the small islands are small. The larger samples come from the mainland of Sumatra and Borneo but they were obtained by pooling smaller samples from only a few places. We do not have enough material to understand what the pattern of geographic variation is on each of those large islands. None of the differences we detect among the samples are as great as that between samples from the Malayan Region and those from the rest of the shelf. We prefer to describe the insular variation within *S. m. muelleri* and point out differences and similarities that may be significant in understanding the effects of past insular isolation and subsequent morphological differentiation. Possibly with more specimens from more islands, with data from other characters, and by a more sophisticated analyses, different patterns of insular morphological variation will be detected. That may be the time to use some of the names we place in synonymy under *S. m. muelleri* if any turn out to apply to really distinctive and discrete morphological units that imply different populations.

In the following section, we discuss the samples from the Malayan Region, then those from the Sumatran Region, and finally the series from the Borneo-Palawan area.

Sundamys muelleri validus

MALAYAN REGION: Specimens are from southern Burma (Tenasserim), peninsular Thailand south of the Isthmus of Kra (10° N), the Malay peninsula, and the Anamba islands (Kepulauan Anambas). We did not study examples that also have been collected on Pulau Penang (Chasen, 1940). Thagyet, on the Little Tenasserim River less than 2° north of the Isthmus of Kra, is the most northern locality from which a specimen has been recorded. The state of Johore, at the southern end of the Malay Peninsula, is as far south as the known distribution extends. There are no records from Singapore.

Throughout the Malayan region, *Sundamys muelleri* is primarily a species of lowland forest; rarely has it been encountered above 3000 feet. Yong's (1969c) account of *S. muelleri* from about 3200 feet at Kedah Peak on the Malay Peninsula is the highest published record. We examined two specimens that were caught at 3500 feet in Perak, one from Maxwell's Hill, the other from Telom.

The largest series of *Sundamys muelleri* from the Malay Peninsula that we studied are from Selangor: Subang (locality 24), Bukit Lagong (locality 25), and from near Kuala Lumpur (locality 23). We pooled these samples to obtain the values listed in table 19. Samples from the northern part of the Peninsula and those from peninsular Thailand and Burma are small and we have not been able to determine if there are any significant patterns of geographic variation in features of skins, skulls, or teeth throughout the pen-

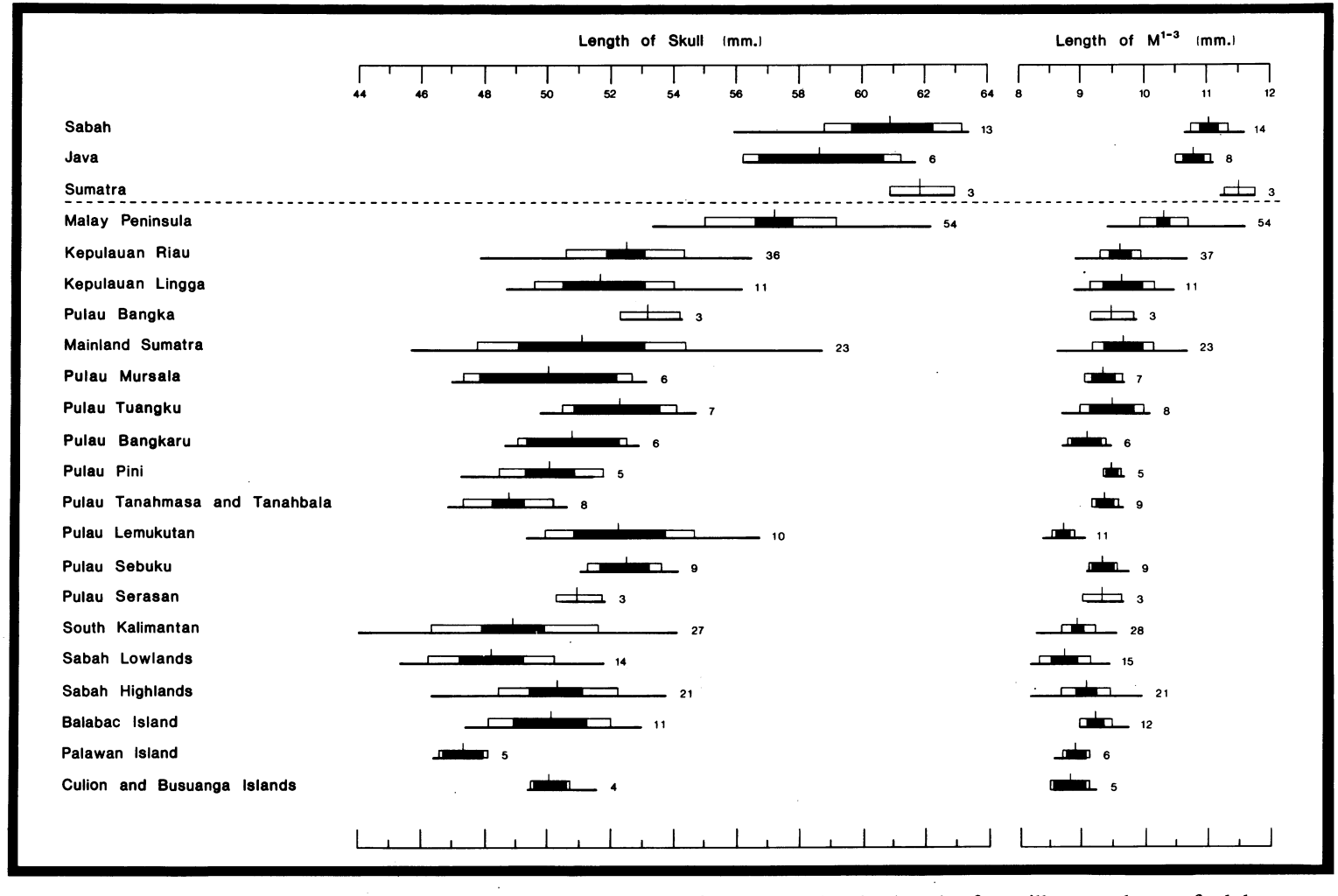

FIG. 43. Insular and peninsular variation in greatest length of skull and alveolar length of maxillary toothrow of adult *Sundamys*. Above the dotted line are samples from *S. maxi* (Java) and *S. infraluteus* (Sabah and Sumatra); below are samples from *S. muelleri*. The mean is a vertical line, hollow rectangles indicate two standard deviations on each side of the mean, black rectangles are two standard errors on either side, the horizontal line represents observed range, and the number adjacent to the line is sample size.

insula. There are also insufficient samples from different elevations for us to assess the magnitude and kind of morphological variation that may be associated with elevation.

The external, cranial, and dental dimensions in specimens of *Sundamys muelleri validus* are much larger than those in any other examples of *S. muelleri* from elsewhere on the Sunda Shelf (tables 19–23; figs. 42 and 43). Compared with rats from the mainland of Sumatra, for example, specimens from the Malay Peninsula have significantly greater mean values for all external and most cranial and dental dimensions; only in breadth of the posterior edge of the palatal bridge, breadth of the mesopterygoid fossa, length of bullae, and breadth of each first upper molar are there no significant differences between rats from the Malay Peninsula and those from the Bornean Region. Compared with specimens from the mainland of Borneo, those from the Peninsula are significantly larger in all dimensions except breadth of the mesopterygoid fossa, in which no significant difference exists between the samples.

So spectacular is the size difference between animals in the Malayan sample and those from elsewhere on the Shelf (fig. 42) that we examined the specimens several times to determine if there were other characters in addition to size that would distinguish them. Possibly the Malayan specimens represented a different species. We detected no other differences in our material, which consists of skins and skulls. For now, we treat the Malayan population as a distinctive subspecies of *S. muelleri.* This arrangement is a hypothesis and must be tested with data from other studies. Results from breeding experiments may help detect the degree of reproductive isolation between the Malayan rats and those from the Sumatran and Bornean regions. There is already information on chromosomal number and morphology as well as variation in erythrocytic proteins for samples from the Malay Peninsula but from nowhere else so the significance of these characters in the context of determining whether species or subspecies are involved is unknown.

Knowing what morphological kind of *muelleri* lives in northeastern Sumatra may also help test the significance of the differences between the Malayan and Sumatran samples. Two murids, *Berylmys bowersii* and the Malayan form of *Niviventer cremoriventer* (Musser, 1973b), and the large flying squirrel *Aeromys tephromelas* (Chasen, 1940) occur on the Malay Peninsula and in northeastern Sumatra. We have not seen specimens of *S. muelleri* from that part of Sumatra. We need to know whether the Malayan or Sumatran *S. muelleri* occurs there. If it is the Malayan kind, the rats may be either allopatric or sympatric with the smaller-bodied Sumatran *S. muelleri* and the morphological integrity of each kind could be assessed. If only the Sumatran *S. muelleri* occurs in the northeast, other kinds of data must be used to estimate the degree of reproductive isolation between the Malayan and Sumatran animals.

Specimens from the Malayan Region were identified and described under four scientific names: *validus, foederis, victor,* and *terempa* (table 18). Miller's (1900, p. 141) *Mus validus* is the oldest name. We use it to designate the Malayan rats as *Sundamys muelleri validus* and we consider the other three names to be synonyms of *validus.* Large body size and occurrence limited to the Malayan Region (as defined here) are the primary diagnostic traits of *S. m. validus.*

Mus validus was named and described by Miller in 1900 and was the second name to be proposed for what was eventually called *Rattus muelleri* (Chasen, 1940). For many years the peninsular form of *S. muelleri* was known as either *Mus validus, Epimys validus,* or *Rattus validus.* In his original description, Miller did not compare the two specimens from Trang with Jentink's (1889) description of *muelleri* nor did he compare them with specimens of *muelleri*-type rats from Sumatra. But he did remark that *validus* was probably related to the "Bornean *Mus infraluteus,*" and so was the first person to suggest affinities between the populations that would later be recognized as *Sundamys muelleri* and *S. infraluteus.*

Chasen (1940) regarded two other names, *foederis* and *victor,* to be synonyms of *validus* and we agree with his assessment. The taxon *foederis* was characterized by Robinson and

TABLE 19

Measurements (in Millimeters) of Adult *Sundamys muelleri* from the Malay Peninsula, Sumatra, and Kepulauan Bunguran[a]

Measurement	Malay Peninsula (localities 21–25; fig. 35)	Sumatra (localities 13–16; fig. 35)	K. Bunguran (Pulau Serasan; fig. 36)
Length of head and body	243.1 ± 17.7 (58) 209–299	207.3 ± 17.1 (23) 185–236	228 ± 0.0 (1)
Length of tail	285.6 ± 19.6 (58) 248–370	260.6 ± 24.6 (22) 214–301	254 ± 0.0 (1)
Tail/head and body (percent)	116	121	111
Length of hind foot	51.5 ± 1.9 (62) 47–55	45.3 ± 2.2 (23) 42–49	45.3 ± 1.5 (3) 44–47
Length of ear	23.2 ± 1.5 (57) 20–27	21.4 ± 0.9 (23) 20–23	— —
Greatest length of skull	57.2 ± 2.1 (54) 53.3–62.2	51.1 ± 3.3 (23) 45.7–58.8	51.0 ± .8 (3) 50.5–51.9
Zygomatic breadth	27.5 ± 1.1 (48) 25.6–30.2	24.8 ± 1.6 (23) 21.7–27.4	24.1 ± .6 (3) 23.7–24.8
Interorbital breadth	8.0 ± .5 (54) 6.9–9.1	7.5 ± .5 (22) 6.5–8.6	7.9 ± 0.0 (3)
Length of nasals	23.1 ± 1.2 (54) 21.0–25.5	20.5 ± 1.8 (23) 17.7–24.0	21.4 ± .4 (3) 21.1–21.8
Length of rostrum	18.5 ± 1.3 (53) 15.7–21.3	16.3 ± 1.3 (23) 14.2–18.8	17.1 ± .1 (3) 17.0–17.2
Breadth of rostrum	10.7 ± .6 (54) 9.5–11.8	9.4 ± .6 (23) 8.0–10.4	9.8 ± .2 (3) 9.7–10.1
Breadth of braincase	19.7 ± .6 (54) 18.2–21.5	18.9 ± .6 (15) 17.9–19.7	18.4 ± .6 (3) 17.9–19.1
Height of braincase	14.5 ± .6 (54) 13.2–16.2	13.5 ± .5 (16) 12.6–14.4	13.7 ± .6 (9) 12.9–13.5
Breadth across incisor tips	4.1 ± .2 (52) 3.4–4.6	3.5 ± .3 (23) 2.8–4.0	3.7 ± .1 (3) 3.6–3.8
Breadth of zygomatic plate	6.7 ± .5 (54) 5.4–8.0	3.4 ± .5 (10) 2.8–4.2	6.6 ± .9 (3) 5.6–7.2
Depth of zygomatic notch	3.8 ± .6 (54) 2.0–5.0	3.4 ± .5 (10) 2.8–4.2	3.6 ± .3 (3) 3.2–3.8
Length of diastema	15.3 ± .8 (54) 13.7–17.1	13.4 ± 1.3 (23) 11.3–15.9	13.7 ± .5 (3) 13.2–14.1
Palatal length	30.2 ± 1.1 (54) 28.2–32.2	27.2 ± 1.7 (23) 24.3–30.8	26.9 ± .5 (3) 26.4–27.3
Postpalatal length	20.0 ± 1.0 (54) 18.3–22.5	17.2 ± 1.2 (10) 15.1–18.9	17.8 ± .9 (3) 17.0–18.7
Length of incisive foramina	9.6 ± .5 (54) 8.6–11.1	8.6 ± .8 (23) 7.3–9.8	8.3 ± .4 (3) 7.9–8.6
Breadth of incisive foramina	3.4 ± .3 (54) 2.8–4.0	3.0 ± .3 (23) 2.7–3.4	3.2 ± .2 (3) 3.0–3.4
Length of palatal bridge	11.1 ± .6 (54) 10.1–12.3	10.2 ± .7 (23) 9.0–11.5	10.0 ± .2 (3) 9.8–10.2
Breadth of palatal bridge at M^1	5.1 ± .4 (54) 4.2–5.7	4.6 ± .4 (23) 3.9–5.2	4.7 ± .2 (3) 4.6–4.9

TABLE 19—(*Continued*)

Measurement	Malay Peninsula (localities 21–25; fig. 35)	Sumatra (localities 13–16; fig. 35)	K. Bunguran (Pulau Serasan; fig. 36)
Breadth of palatal bridge at M^3	5.9 ± .4 (54) 5.0–6.9	5.6 ± .5 (23) 4.7–6.4	5.4 ± .2 (3) 5.3–5.7
Breadth of mesopterygoid fossa	4.1 ± .3 (54) 5.2–7.3	4.0 ± .5 (23) 6.1–7.3	3.5 ± .3 (3) 3.3–3.8
Length of bulla	6.5 ± .3 (54) 5.2–7.3	6.6 ± .2 (23) 6.1–7.3	6.3 ± .2 (3) 6.1–6.5
Height of bulla	6.5 ± .3 (54) 5.5–7.2	5.5 ± .5 (22) 4.2–6.4	6.1 ± .3 (3) 5.9–6.4
Alveolar length of M^{1-3}	10.3 ± .4 (54) 9.4–11.6	9.7 ± .5 (23) 8.6–10.7	9.4 ± .3 (3) 9.1–9.7
Breadth of M^1	2.8 ± .1 (53) 2.5–3.2	2.8 ± .1 (22) 2.5–3.0	2.7 ± .2 (3) 2.5–2.8

[a] Mean plus or minus one standard deviation, size of sample in parentheses, and observed range are listed for each measurement.

Kloss (1911, p. 245) as "A member of the *Muelleri* group agreeing with *Mus validus,* Miller, in its large teeth, shape of the parietals and in the posterior terminations of the nasals but differing in smaller size; with relatively larger feet and slightly more inflated bullae." To those authors, *foederis* "is evidently the peninsular representative of the Sumatran *Mus muelleri,*" and they thought of it as a different species than Miller's *Mus validus.* The holotype of *foederis* was obtained from Ulu Temengoh in Upper Perak and it is an example of *S. muelleri.* The characteristics Robinson and Kloss used to separate it from *validus* are features reflecting individual and age variation. *Mus muelleri foederis* should continue to be considered a synonym of *S. m. validus.*

The name *victor* was applied by Miller (1913, p. 16) to seven specimens obtained by Abbot in 1902 from Pahang and Johore. The holotype was collected near the mouth of the Sungei Rompin in Pahang. Miller diagnosed *Epimys victor* as the "Largest known member of the *firmus*-group, the skull attaining a total length of about 60 mm., as compared with about 55 mm. in *Epimys firmus* and *E. validus*; color as in *E. firmus*; teeth like those of *E. firmus,* therefore relatively smaller than in *E. validus* and with the elements of anterior crescent in m^2 and m^3 less developed." He concluded that "This is a large, south-Peninsular representative of *Epimys firmus.* It is readily distinguishable from *E. validus* of Trong by the relatively smaller teeth with less developed enamel folds. The *Mus muelleri foederis* of Robinson and Kloss, from Selangor, is described as a much smaller animal with greatest length of skull in adult female only 48 mm." The holotype of *victor* and the other specimens that Miller assigned to that taxon are examples of *S. m. validus*; Chasen (1940) had correctly listed *Epimys victor* as a synonym of the latter. The features Miller thought so characteristic of *victor* indicate individual and age variation.

Specimens from the islands of Siantan and Jimaya in the Anamba Islands were described by Chasen and Kloss (1928b, p. 36) under the name, *Rattus validus terempa.* The holotype was obtained in 1925 from Pulau Siantan. The authors characterized *terempa* as "Like *validus* and *firmus* but much darker above than either: differs from *integer* in the possession of an outer anterior tubercle on the posterior upper molar." The sample consists of large rats that closely resemble those from the Malay Peninsula and are unlike samples from either the Sumatran or Bornean Regions. The dimensions (in mm.) of the holotype (greatest length of skull, 56.9; zygomatic breadth, 27.5; interorbital breadth, 8.5; length of nasals, 22.2; palatilar length, 25.7; alveolar length of maxillary toothrow, 9.8; from Chasen and Kloss, 1928b, p. 37) fit within the range of variation of samples

from the Malay Peninsula (table 19); we regard *terempa* to be a synonym of *S. m. validus*.

The geographic range of *Sundamys muelleri validus* approximates the region Chasen (1940, pp. ix–x) designated as the Malayan Province: "The Malay Peninsula; the small islands close to both its coasts; the Anamba and Tambelan Islands in the South China Seas." Chasen explained that

> The northern boundary of this province, and consequently that of the sub-region is here regarded as Lat. 10° N., which is at the narrowest part of the Isthmus of Kra. Any further extension embraces territory within the political limits of British India. The adopted dividing line is, furthermore, not unnatural, for although on the west coast along the region of the heavier rainfall and evergreen forests Malaysian species often extend through Tenasserim to about the latitude of Tavoy, the Pakchan Estuary seems to constitute a real faunal boundary for many birds and mammals, especially on the east coast. A herpetologist would draw the southern line of his Indo-Chinese fauna at about Lat. 12° N. for by raising it from 10° N. about a dozen Malayan species of amphibians and reptiles are excluded. A botanist suggests that the division should be at about the latitude of Singgora in Peninsular Thailand, and that an intermediate area more Indo-Chinese than Malayan lies between Lat. 7° N. and 10° N.

Sundamys muelleri muelleri

SUMATRAN REGION: To this group belong samples from mainland Sumatra; from the Banyak and Batu islands and Pulau Mansalar, all on the Sunda Shelf off the west coast of Sumatra; and from Pulau Banka and islands in the Riau and Lingga archipelagos off the east coast of Sumatra. Specimens from these places are much smaller in body size than rats from the Malayan Region. They are more similar to specimens from mainland Borneo and its offshore islands. Sumatran rats have longer maxillary toothrows than do those from the Bornean area (fig. 43). The difference is average but consistent among the samples. Otherwise, rats from Borneo and Sumatra are closely similar in most external, cranial, and dental features.

Most of the specimens from the Sumatran area are old, collected in the early 1900s and originally examined and reported by taxonomists working during that time—Miller, Lyon, Robinson, and Kloss, for example. Through their efforts, 11 scientific names came to be associated with samples from the Sumatran region (table 18). Our interpretation of data obtained from many of the same specimens studied by these men is different from their results and indicates that the number of names does not reflect the real geographic diversity of *S. muelleri* on Sumatra and the island groups off its west and east coasts. Specimens in all the samples are closely similar to each other in morphology of skins, skulls, and teeth. We discuss the samples below, first those from the mainland, then those from islands off the west coast of Sumatra, and finally the series from islands off the east coast.

MAINLAND: On the mainland of Sumatra, *Sundamys muelleri* lives in forests and has been taken from the coastal lowlands near sea level up to 1800 meters (5940 feet) on Gunung Dempo. Most of the specimens come from lowlands and mountains of western Sumatra; we have seen only one specimen from the eastern coastal lowlands (fig. 35). Many of the samples consist of only one or two specimens, few contain more. By combining certain samples from the lowlands and highlands of southern Sumatra we were able to test the significance of any measured or observed difference between the two altitudinal series. The samples we used to test these differences come from Kalianda (locality 13), Wai Semangka (locality 15), and Moearadoea (locality 16) in the lowlands of South Sumatra, and Gunung Tanggamoes (locality 14) in the highlands of that region. The few specimens from central and northern Sumatra do not differ in any significant morphological way from specimens in the larger samples obtained in southern Sumatra. In our material, specimens from the lowlands differ from those collected at highland localities in only one feature: on the average, lowland rats have a shorter first upper molar; otherwise, we detected no statistically significant difference between mean values in either external, cranial, and other dental measurements, or in color of pelage. For that reason our mainland

series (fig. 43) is formed by pooling all the smaller samples from both highlands and lowlands.

The names, *muelleri, campus,* and *virtus* apply to specimens from mainland Sumatra: *muelleri* to highland series, *campus* and *virtus* to specimens from lowlands (table 18). The oldest name is *muelleri,* proposed by Jentink in 1879 and based on a young rat obtained on Batang Singgalang, a mountain in the Padang Highlands of central Sumatra. Jentink described the taxon under the name "*Mus mülleri,*" and like many of his original descriptions it is imprecise and undiagnostic:

> Fur very soft, slate-colored near the base. The hairs of back, sides of the body, upperparts of head and outside of legs, with brown tips, the underparts of the body with white tips. Bristles long, rather stiff, brown. Ears small, rounded at the tip.
>
> Tail longer than head and body, covered with very scarce, short, bright colored hairs, somewhat harsh to the touch.
>
> Whiskers very short, brown. Hind-foot extraordinarily long and strong. There are five toes on the hind-foot; four well developed fingers on the fore-foot, with a very short thumb, armed with a little claw. The two middle fingers of the fore-foot are nearly of the same length. Claws dirty yellow. Upper and lower molars very large and strong. Distance between incisor and first lower molar extraordinarily large. Upper cutting-teeth orange, lower ones brighter colored.
>
> One specimen.

The identity of Jentink's *Mus mülleri* was a problem for Miller, who had to identify the large collections of rats obtained by Abbott from Sumatra in the early 1900s, and for Robinson and Kloss, who worked in Sumatra trying to study that large and diverse fauna. Jentink's original description of *muelleri* is so poor and so general it could be applied to several different species of rats and taxonomists working then had no opportunity to study the holotype. When Miller (1902a, p. 156) named and described *Mus firmus* in 1902, for example, he had sent specimens to Leiden and wrote that "Two specimens of *Mus firmus* have been compared with the type of *Mus mülleri* by Dr. F. A. Jentink, of the Leyden Museum. They prove to represent a larger animal with more black on the back. and differing also in certain cranial peculiarities, which, however, Dr. Jentink does not specify." In 1919, Robinson and Kloss (1919a) were uncertain whether *muelleri* was the oldest name for a large shaggy rat they had collected in the Ophir District of West Sumatra, or if *muelleri* was the same thing as *bullatus,* a rat from the lowlands of eastern Sumatra described by Lyon (1908). Later, however, Robinson and Kloss (1919b) definitely associated *muelleri* with the large shaggy forest rats and not with *bullatus,* and they were correct in doing so. The holotype of *muelleri* is not a specimen of *Rattus bullatus* (now a subspecies of *R. annandalei*), but a young example of the large Sumatran animal that has been recognized in the more recent mammalogical literature as *Rattus muelleri* (Chasen, 1940; Ellerman, 1941, 1949).

Two other scientific names, *campus* and *virtus,* have been applied to specimens from the mainland of Sumatra. *Epimys mulleri campus* was named and described by Robinson and Kloss in 1916. The original sample consisted of a holotype (BM 19.11.5.95) and two other specimens (NMS 603/14 and 604/14) collected at Pasir Ganting (2°7′ S. Lat.) on the coast of western Sumatra on June 18 and 20, 1914.

The authors of *campus* (Robinson and Kloss, 1916, p. 275) characterized it as, "Like the typical *E. mulleri,* but with the buff element in the upper pelage a little richer in tone: rostrum decidedly broader, zygomatic width greater and the bullae a little larger." In a subsequent report on the mammals obtained from the Korinchi region of western Sumatra, Robinson and Kloss (1918) reported three specimens from Siolak Daras in the Korinchi Valley at 3100 feet which they identified as typical *muelleri.* They also pointed out that *campus* closely resembled the highland sample of *muelleri* but was morphologically different enough to represent a coastal form of the species. Later, Tate (1936) and Ellerman (1941, 1949) recognized *campus* as a subspecies of *Rattus muelleri.* So did Chasen (1940), but he had reservations and in his handlist of Malaysian mammals, wrote that "*R. m. campus,* presumed to be a coastal form, is only doubtfully distinct from *mülleri.*"

We agree with Chasen's evaluation of *cam-*

TABLE 20

Measurements (in Millimeters) of Adult *Sundamys muelleri* from Kepulauan Riau, Kepulauan Lingga, and Pulau Bangka[a]

Measurement	Kepulauan Riau (localities 1, 1a, 3, 4, 6, 7; fig. 35)	Kepulauan Lingga (localities 8–10; fig. 35)	Pulau Bangka (locality 11; fig. 35)
Length of head and body	228.1 ± 16.5 (37) 182–276	230.3 ± 18.7 (9) 211–269	243.0 ± 0.0 (2)
Length of tail	249.2 ± 13.3 (36) 210–276	245.6 ± 20.1 (9) 210–269	270.0 ± 4.2 (2) 267–273
Tail/head and body (percent)	109	107	111
Length of hind foot	46.9 ± 1.8 (35) 40–51	46.8 ± 2.7 (9) 44–52	48.0 ± 1.4 (2) 47–49
Length of ear	23.5 ± 1.2 (15) 22–27	— —	— —
Greatest length of skull	52.5 ± 1.9 (36) 47.9–56.5	51.8 ± 2.2 (11) 48.7–56.2	53.2 ± 1.0 (3) 52.5–54.3
Zygomatic breadth	26.2 ± 1.0 (20) 24.5–29.4	25.8 ± 1.4 (11) 23.8–28.8	25.9 ± .2 (3) 25.7–26.1
Interorbital breadth	7.7 ± .4 (21) 6.9–8.4	7.4 ± .3 (11) 7.0–8.0	7.3 ± .6 (3) 6.8–7.9
Length of nasals	21.6 ± .7 (20) 19.3–29.7	21.0 ± 1.2 (11) 19.0–23.4	21.1 ± .2 (3) 21.0–21.4
Length of rostrum	17.3 ± .9 (20) 16.0–19.0	16.6 ± 1.1 (11) 14.7–18.2	17.2 ± .6 (3) 16.5–17.6
Breadth of rostrum	10.3 ± .5 (21) 9.2–11.3	9.8 ± .5 (11) 9.3–10.8	9.7 ± .1 (3) 9.6–9.7
Breadth of braincase	19.4 ± .4 (20) 18.7–20.4	19.3 ± .5 (11) 18.3–20.0	19.5 ± .2 (3) 19.4–19.7
Height of braincase	13.8 ± .5 (21) 12.4–14.9	13.6 ± .6 (11) 12.7–14.7	13.6 ± .8 (3) 13.1–14.6
Breadth across incisor tips	3.6 ± .2 (20) 3.0–4.2	3.6 ± .4 (11) 3.0–4.2	3.6 ± .2 (3) 3.3–3.7
Breadth of zygomatic plate	6.4 ± .6 (21) 5.4–7.3	6.2 ± .5 (11) 5.5–7.3	6.0 ± .6 (3) 5.5–6.6
Depth of zygomatic notch	3.9 ± .4 (21) 3.1–5.1	3.6 ± .3 (11) 2.9–4.0	2.8 ± .2 (3) 2.5–2.9
Length of diastema	14.6 ± .9 (21) 13.2–15.9	14.3 ± 1.0 (11) 12.9–16.6	14.2 ± 1.0 (3) 13.3–15.3
Palatilar length	24.4 ± .9 (21) 22.9–25.8	24.0 ± 1.4 (11) 22.3–27.2	24.3 ± .5 (3) 24.0–24.9
Palatal length	28.2 ± .9 (21) 26.4–29.7	27.6 ± 1.4 (11) 26.0–30.4	28.1 ± .6 (3) 27.7–28.8
Postpalatal length	18.6 ± .5 (21) 17.0–20.8	17.9 ± 1.2 (11) 15.8–20.3	18.7 ± 1.4 (3) 17.4–20.1
Length of incisive foramina	9.1 ± .5 (21) 7.9–10.0	9.0 ± .5 (11) 8.1–9.9	8.9 ± .4 (3) 8.5–9.1
Breadth of incisive foramina	3.4 ± .2 (21) 2.9–3.7	3.1 ± .3 (11) 2.5–3.6	3.3 ± .2 (3) 3.1–3.4
Length of palatal bridge	10.6 ± .6 (21) 9.7–11.8	10.2 ± .6 (11) 9.2–11.2	10.6 ± .6 (3) 10.1–11.2

TABLE 20—(*Continued*)

Measurement	Kepulauan Riau (localities 1, 1a, 3, 4, 6, 7; fig. 35)	Kepulauan Lingga (localities 8–10; fig. 35)	Pulau Bangka (locality 11; fig. 35)
Breadth of palatal bridge at M^1	4.9 ± .3 (21) 4.3–5.5	4.9 ± .4 (11) 4.2–5.6	5.0 ± .1 (3) 4.9–5.1
Breadth of palatal bridge at M^3	5.9 ± .3 (21) 5.2–6.3	5.9 ± .3 (11) 5.4–6.3	5.6 ± .1 (3) 5.6–5.7
Breadth of mesopterygoid fossa	4.2 ± .2 (21) 3.4–4.9	4.0 ± .3 (11) 3.6–4.5	4.0 ± .3 (3) 3.7–4.3
Length of bulla	6.6 ± .2 (21) 6.1–7.3	6.5 ± .3 (11) 6.1–6.9	6.9 ± .3 (3) 6.7–7.2
Height of bulla	6.3 ± .3 (21) 5.6–6.9	6.3 ± .4 (11) 5.8–6.8	6.5 ± .1 (3) 6.5–6.6
Alveolar length of M^{1-3}	9.6 ± .3 (37) 8.9–10.7	9.7 ± .5 (11) 8.9–10.5	9.5 ± .4 (3) 9.2–9.9
Breadth of M^1	2.7 ± .1 (20) 2.5–2.9	2.7 ± .1 (11) 2.5–2.9	2.6 ± .1 (3) 2.6–2.7

[a] Mean plus or minus one standard deviation, size of sample in parentheses, and observed range are listed for each measurement.

pus. Even Robinson and Kloss admitted that the color differences they recorded were slight, and the differences in the rostrum, zygomatic width and bullae they noted and thought to be distinctive do not hold up in larger series that we examined. Based on features of skins and skulls, *campus* should be treated as a synonym of *Sundamys muelleri muelleri.*

The other form from the Sumatran mainland, *virtus,* was named and described by Lyon (1916b, p. 210) as a species of *Rattus.* The name is based on an adult male (USNM 144223) obtained by W. L. Abbott from the coastal lowlands of eastern Sumatra along the Siak River. Lyon diagnosed *virtus* as, "A member of the *Rattus firmus* group of rats distinguished from *R. firmus* chiefly by its more slender skull, especially pronounced in the rostral and interorbital regions." Chasen (1940) and Ellerman (1941, 1949) listed *virtus* as a synonym of *Rattus muelleri campus* without comment. They were correct. The holotype of *virtus* is simply a lowland example of *S. muelleri* and its morphological features do not differ significantly from those in either the original series of *campus* or the *S. muelleri* from the highlands.

ISLANDS OFF THE COAST OF WESTERN SUMATRA: Samples are available from the Banyak Islands, Pulau Mansalar, and the Batu Islands. *Sundamys muelleri* has never been collected from either Pulau Simeulue (Simalur), Pulau Nias, or any of the Mentawai Islands, or Pulau Enggano. The names *domitor, potens, valens, balmasus,* and *pinatus* have been attached to samples of *S. muelleri* from the western islands. The first proposed is *mus domitor,* named and described by Miller in 1903 and based on seven specimens from Pulau Mansalar (Mursala on recent maps), a small island in the entrance to Tapanuli Bay, Western Sumatra. The holotype (USNM 114621) is an adult female and was obtained by W. L. Abbott on March 4, 1902. In addition to the holotype we studied eight other examples of *domitor,* all in the National Museum of Natural History. When Miller described *domitor,* he had already named and described *Mus firmus* in 1902; although the holotype of that taxon was from Pulau Lingga, Miller applied *firmus* to most samples of large, shaggy forest rats that Abbott had collected from islands off the east coast of Sumatra, the mainland, and some islands off the west coast. So in his descriptions published in the early 1900s Miller compared taxa such as domitor to *firmus,* a species he considered different from Jentink's *muelleri.*

After reading Miller's original description of *domitor* we were not impressed with its distinctness from samples Miller called *firmus,* and our study of skins and skulls substantiated that impression. Miller (1903a, p. 461) characterized *domitor* as "Similar to *Mus firmus* but under parts so little tinged with yellow as to form no marked contrast with color of sides. Mammae 8, as in *Mus firmus* and related species." He also noted that "The external characters, other than color, are so like those of *Mus firmus, Mus integer,* and the previously known members of the group as to need no description." Furthermore, "The skull and teeth so closely resemble those of *Mus firmus* that I can find no tangible characters by which to distinguish them." Yet, at the end of the description Miller remarked that, "The distinctness of this species from the *Mus firmus* of the near-by mainland is unquestionable."

We detect no external, cranial, or dental features that will distinguish the sample of *domitor* from samples obtained on the coast and interior lowlands of the mainland. The only feature that Miller considered to really distinguish the island and mainland samples was the darker underparts of *domitor.* Coloration of the underparts varies individually and a range from whitish gray to dark, buffy gray occur within a sample from one locality nearly everywhere where large samples have been obtained from one place. The range of variation in ventral coloration seen within the sample from Pulau Mansalar is similar to the variation recorded for samples from the mainland of Sumatra and from other areas on the Sunda Shelf (table 14). Color does not set apart the rats from Pulau Mansalar. Miller's *Mus domitor,* in our opinion, is a synonym of *S. m. muelleri.*

When Miller described *Mus domitor* he had in his possession specimens from Pulau Bangkaru and Pulau Tuangku in the Banyak Islands that he identified as *Mus firmus.* Miller compared external measurements between *firmus* from the Banyak Islands and *domitor* from Pulau Mansalar. In 1913, however, Miller named and described the series from Pulau Tuangku as *Epimys potens* and the sample from Pulau Bangkaru as *Epimys valens.* The two islands lay next to each other on the Sunda Shelf and are located between Pulau Simeulu to the north and Pulau Nias to the south. Miller (1913, pp. 17–18) diagnosed *potens* as "Like *Epimys firmus* but tail shorter (about equal to head and body instead of distinctly longer) and cheek teeth smaller," and *valens* as "Like *Epimys potens* of Pulo Tuangku but tail decidedly shorter than head and body, skull with noticeably shortened incisive foramina, and teeth more nearly as large as in *E. firmus.*" By 1913 *Epimys* was the generic name used for species that are now regarded as members of the genus *Rattus. Mus,* an earlier name that embraced species of rats and mice, had been separated out before 1913 and applied to what we now call mice; namely, species of *Mus* and its allies.

We studied eight specimens from Pulau Tuangku and six from Pulau Bangkaru, including the holotypes of *potens* and *valens.* The specimens of *potens* have, on the average, a longer tail and hind foot, longer incisive foramina, deeper bullae and longer toothrows than the sample of *valens.* The differences are barely significant, however, and would probably not be detectable between larger samples. Otherwise, the two sets of specimens are closely similar in color of pelage, other external features, and cranial and dental characteristics. Based on available samples, we see no evidence to consider them as representatives of different populations. Also, they differ in no significant ways from samples collected either on the mainland or Pulau Mansalar, the type locality of *domitor.* We treat *potens* and *valens* as synonyms of *S. m. muelleri.*

Pulau Pini, Pulau Tanahmasa and Pulau Tanah Bala, the largest of the Batu Islands, lay off the west coast of central Sumatra between Pulau Nias and Pulau Siberut, the first large island in the Mentawai group. The Batu islands were visited by Abbott in 1903 and he obtained *muelleri*-type rats from all of them. In 1916 Lyon named and described *Rattus balmasus* from 10 specimens, three from Pulau Tanahmasa and seven from Pulau Tanah Bala; and *Rattus pinatus,* based on five specimens from Pulau Pini. Lyon (1916a, pp. 447–448) diagnosed *balmasus* as "A member of the *Rattus firmus* group distinguished by somewhat small size, short tail more yellowish type of coloration, and skull relatively slender, especially rostral portion."

At the end of the account he remarked that "This species is very closely related to *Rattus pinatus* of Pulo Pinie; the difference between the two being scarcely more than subspecific." *Rattus pinatus* was diagnosed as "A member of the *Rattus firmus* group, distinguished by somewhat small size, rather short tail, more yellowish type of coloration, and skull with a rather heavy rostrum." Lyon remarked that "This species is very closely related to its relative of Masa and Bala Islands, both forms together constituting a group apart from the other members of the *firmus* group."

We examined all the specimens from the Batu Islands that formed the basis of Lyon's descriptions. Rats from the three islands are closely similar to one another. On the average, specimens in the sample of *balmasus* from Pulau Pini differ from those in the other samples in that they have a wider zygomatic breadth and zygomatic plate, deeper bullae, and broader palatal bridge at the posterior margin. These differences are barely significant. When compared sample by sample, we found no significant differences in mean values of external and cranial dimensions between specimens from the Batu Islands and those from the Sumatran mainland. Lyon's names, *balmasus* and *pinatus* are significant only in that they indicate the insular origins of the specimens; they do not appear to represent different populations; *balmasus* and *pinatus* should be listed as synonyms of *S. m. muelleri.*

Islands off the east coast of Sumatra: Samples are from Pulau Banka; Pulau Lingga, Pulau Sebang, and Pulau Bakong in the Lingga Archipelago; Pulau Karimon Besar, Pulau Karimon Kecil, Pulau Kundur, Pulau Sau, and the islands Moro Besar, Sugi, Sugibawa, Setoko, and Battam in the Riau Archipelago. Specimens from Pulau Banka and the Lingga Archipelago are closely similar to those in samples from the mainland of Sumatra. Samples from the Riau Archipelago are not as similar to the mainland samples and are the most distinct of all the specimens from the Sumatran region.

The names *firmus, chombolis,* and *pollens* apply to samples from islands off the east coast of Sumatra (table 18). The oldest name proposed by Miller in 1902 is *Mus firmus.* Miller examined seven specimens from the type locality, Pulau Lingga, and there are two from Pulau Sebang and five from Pulau Bakong. When Miller described *firmus,* he compared it to *Mus integer,* another *muelleri*-type animal from Pulau Sirhassen in the South Natuna Islands. Prior to 1902 only three names had been applied to *muelleri*-type rats: *muelleri* (Jentink, 1879), *validus* (Miller, 1900), and *integer* (Miller, 1901). Miller, on the strength of Jentink's opinion, thought *firmus* to be larger than *muelleri* and a different species. He did not contrast *firmus* with *validus,* a form from the southern part of peninsular Thailand, and he noted a few small differences between *firmus* and *integer.* He never directly compared specimens of *firmus* with specimens from the mainland of Sumatra.

Specimens from the three islands in the Lingga Archipelago have on the average, a longer head and body and wider and deeper bullae than specimens from the mainland of Sumatra. We found no other significant differences. Because of the variation in taking external and bullar measurements, we do not rely on these features to distinguish different populations. In this case the other differences between the samples are average and some only barely significant. Otherwise the specimens from the Lingga Archipelago are like those from the mainland in features of skins, skulls, and teeth. We regard the taxon *firmus* to be another synonym of *Sundamy muelleri muelleri.*

The sample from Pulau Banka was described under the name *Epimys pollens* by Miller in 1913. The holotype (USNM 124691) was obtained by Abbott from Tanjong Rengsam on May 22, 1904. Abbott collected four specimens. We examined these and four others from Banka. In his original description Miller (1913, p. 17) diagnosed pollens as "Like *Epimys firmus* of the Rhio-Linga Archipelago, but tail longer and skull differing from that of all the other known members of the group in the very abruptly constricted interorbital region and weak anterior portion of zygoma." These contrasts do not stand up to critical comparison with other samples. We cannot separate specimens taken on Pulau Banka from rats obtained from either the Lingga Archipelago or mainland Sumatra in any feature of skins, skulls, or teeth. The sam-

TABLE 21

Measurements (in Millimeters) of Adult *Sundamys muelleri* from Islands Off the Coast of West Sumatra[a]

Measurement	Pulau Tuangku (locality 28; fig. 35)	Pulau Bangkaru (locality 29; fig. 35)	Pulau Mursala (locality 30; fig. 35)	Pulau Pini (locality 31; fig. 35)	Pulau Tanahmasa and Tanahbala (localities 32, 33; fig. 35)
Length of head and body	231.7 ± 11.5 (6) 220–249	221.8 ± 18.7 (5) 212–233	219.2 ± 25.6 (6) 185–251	229.8 ± 13.4 (4) 210–239	214.2 ± 14.7 (9) 193–240
Length of tail	230.5 ± 10.3 (6) 213–240	200.6 ± 8.3 (5) 192–210	223.0 ± 24.1 (6) 199–252	191.8 ± 15.7 (4) 175–213	201.7 ± 9.8 (9) 186–219
Tail/head and body (percent)	101	90	102	84	94
Length of hind foot	47.4 ± 1.5 (5) 45–49	44.4 ± .9 (5) 44–46	45.2 ± 2.9 (5) 41–48	44.0 ± 2.0 (3) 42–46	43.5 ± .5 (6) 43–44
Length of ear	— —	— —	— —	— —	— —
Greatest length of skull	52.3 ± 1.8 (7) 49.8–54.8	50.8 ± 1.7 (6) 48.7–53.0	50.1 ± 2.6 (6) 47.0–53.2	50.1 ± 1.7 (5) 47.3–51.5	48.8 ± 1.4 (8) 46.9–50.7
Zygomatic breadth	25.1 ± .6 (5) 24.4–25.7	24.8 ± .9 (6) 23.5–25.8	23.8 ± 1.2 (6) 22.7–25.8	25.5 ± 1.3 (4) 23.6–26.4	23.4 ± 1.4 (7) 20.9–25.3
Interorbital breadth	7.8 ± .2 (7) 7.6–8.1	7.7 ± .4 (6) 7.3–8.2	7.6 ± .4 (7) 7.1–8.1	7.4 ± .5 (5) 6.7–7.9	7.4 ± .4 (9) 6.7–8.1
Length of nasals	21.7 ± 1.0 (8) 20.5–23.6	21.2 ± 1.0 (6) 19.9–22.8	20.2 ± 1.7 (7) 18.1–22.4	19.5 ± 0.9 (5) 18.0–20.3	19.6 ± .1 (9) 18.2–21.0
Length of rostrum	17.0 ± 0.9 (8) 15.7–18.2	16.7 ± .8 (6) 15.7–17.8	15.0 ± 1.6 (7) 14.2–18.8	15.6 ± .8 (5) 14.4–16.5	15.7 ± .7 (9) 14.7–16.7
Breadth of rostrum	9.6 ± .5 (8) 8.9–10.3	9.2 ± .4 (6) 8.7–9.6	9.8 ± .8 (7) 8.8–10.6	9.4 ± .6 (5) 8.4–10.1	9.2 ± .4 (9) 8.6–9.7
Breadth of braincase	18.2 ± .7 (7) 17.7–19.4	18.4 ± .4 (6) 17.9–19.0	18.4 ± .4 (6) 17.9–19.0	19.1 ± .4 (5) 18.5–19.4	18.7 ± .3 (7) 18.2–19.0
Height of braincase	13.7 ± .5 (7) 13.0–14.5	13.2 ± .3 (6) 13.0–13.7	13.2 ± .5 (7) 12.6–13.8	13.4 ± .6 (5) 12.6–14.2	13.2 ± .6 (8) 12.5–14.4
Breadth across incisor tips	3.7 ± .2 (8) 3.4–4.1	3.6 ± .1 (5) 3.5–3.7	3.5 ± .2 (7) 3.2–3.8	3.4 ± .1 (4) 3.3–3.6	3.4 ± .2 (9) 3.0–3.6
Breadth of zygomatic plate	6.3 ± .6 (8) 5.5–7.0	5.9 ± .4 (6) 5.3–6.4	5.7 ± .5 (7) 4.9–6.1	6.3 ± .7 (5) 5.2–6.9	5.3 ± .4 (9) 4.8–6.2

TABLE 21—(*Continued*)

Measurement	Pulau Tuangku (locality 28; fig. 35)	Pulau Bangkaru (locality 29; fig. 35)	Pulau Mursala (locality 30; fig. 35)	Pulau Pini (locality 31; fig. 35)	Pulau Tanahmasa and Tanahbala (localities 32, 33; fig. 35)
Depth of zygomatic notch	3.4 ± .5 (8) 2.9–4.3	2.9 ± .3 (6) 2.5–3.3	2.7 ± .3 (7) 2.2–2.9	3.1 ± .6 (5) 2.3–3.7	2.9 ± .4 (9) 2.3–3.7
Length of diastema	14.1 ± .7 (8) 13.2–15.3	14.2 ± .5 (6) 13.6–14.9	13.6 ± 0.1 (7) 12.1–14.9	13.7 ± 0.9 (5) 12.4–15.0	13.1 ± .6 (9) 12.3–14.2
Palatilar length	24.4 ± 1.1 (8) 22.7–25.9	23.8 ± .7 (6) 23.0–24.6	23.6 ± 1.4 (7) 21.6–25.3	23.6 ± 1.2 (5) 21.8–25.1	22.8 ± .6 (9) 22.0–23.7
Palatal length	27.9 ± 1.2 (8) 25.9–29.6	27.4 ± .8 (6) 26.4–28.5	27.0 ± 1.6 (7) 24.5–28.8	27.0 ± 1.3 (5) 24.9–28.4	25.9 ± .8 (9) 24.9–27.1
Postpalatal length	17.8 ± .8 (7) 16.8–18.9	17.6 ± .6 (6) 16.5–18.2	17.2 ± 1.4 (6) 15.6–18.9	17.4 ± 1.0 (5) 15.7–18.0	16.5 ± .8 (8) 15.6–17.8
Length of incisive foramina	8.8 ± .7 (8) 7.6–9.6	8.1 ± .4 (6) 7.5–8.5	8.3 ± .6 (7) 7.6–9.3	8.4 ± .4 (5) 8.0–8.9	8.1 ± .3 (9) 7.7–8.4
Breadth of incisive foramina	3.2 ± .3 (8) 2.9–3.7	3.1 ± .3 (6) 2.8–3.6	3.1 ± .2 (7) 2.7–3.3	2.9 ± .2 (5) 2.6–3.1	3.1 ± .1 (9) 3.0–3.2
Length of palatal bridge	10.1 ± .5 (8) 9.2–11.0	10.5 ± .5 (6) 9.8–11.2	10.3 ± .6 (7) 9.3–11.0	10.4 ± .6 (5) 9.4–11.1	10.0 ± .5 (9) 9.4–10.8
Breadth of palatal bridge at M^1	4.8 ± .4 (8) 4.3–5.5	4.5 ± .2 (6) 4.3–4.7	4.4 ± .5 (7) 3.9–5.3	4.7 ± .5 (5) 3.9–5.1	4.5 ± .2 (9) 4.3–4.8
Breadth of palatal bridge at M^3	5.7 ± .5 (8) 5.0–6.7	5.7 ± .3 (6) 5.5–6.1	5.4 ± .2 (7) 5.1–5.9	5.8 ± .5 (5) 5.4–6.5	5.5 ± .3 (9) 5.1–6.0
Breadth of mesopterygoid fossa	4.1 ± .4 (8) 3.6–4.6	3.9 ± .1 (6) 3.7–4.0	4.0 ± .2 (6) 3.7–4.2	3.4 ± .2 (5) 3.2–3.6	3.7 ± .2 (9) 3.5–4.2
Length of bulla	6.8 ± .2 (7) 6.5–7.1	6.6 ± .2 (6) 6.2–6.9	6.5 ± .4 (7) 5.9–7.0	6.3 ± .2 (5) 6.1–6.5	6.6 ± .3 (6) 6.2–7.0
Height of bulla	6.3 ± .4 (7) 6.0–6.9	6.0 ± .2 (5) 5.9–6.3	6.0 ± .4 (7) 5.4–6.3	5.6 ± .2 (5) 5.4–5.8	6.2 ± .2 (6) 6.0–6.5
Alveolar length of M^{1-3}	9.5 ± .5 (8) 8.7–10.1	9.1 ± .3 (6) 8.7–9.5	9.4 ± .3 (7) 9.1–9.7	9.5 ± .1 (5) 9.4–9.7	9.4 ± .3 (9) 9.3–9.7
Breadth of M^1	2.7 ± .1 (8) 2.5–2.9	2.7 ± .1 (6) 2.5–2.7	2.8 ± .1 (7) 2.7–2.9	2.7 ± .1 (5) 2.5–2.8	2.7 ± .1 (9) 2.5–2.8

[a] Mean plus or minus one standard deviation, size of sample in parentheses, and observed range are listed for each measurement.

ple from Pulau Banka represents a population of *Sundamys muelleri* that is morphologically closely similar to that of the mainland and to islands in the Lingga Archipelago. *Epimys pollens* is another synonym of *S. m. muelleri.*

We studied 44 specimens from 10 islands in the Riau Archipelago, a sample large enough from which to obtain an estimate of the variation in external, cranial, and dental features of the population on those islands. The small lots from the 10 islands are morphologically closely similar to each other and we estimate they represent the same population. Contrasted with samples of *Sundamys muelleri* from mainland Sumatra and with those from the Lingga Archipelago and Pulau Banka, rats from the Riau Archipelago have a longer head and body, longer hind feet, wider zygomatic breadth, longer nasals, longer and wider rostrum, broader incisive foramina, wider zygomatic plate, greater postpalatal length, wider mesopterygoid fossa, and deeper bullae (tables 19 and 20). The most conspicuous difference between the samples is in the larger rostrum of the specimens from the Riau Archipelago, a size difference reflected in the greater dimensions of nasals, rostrum and incisive foramina enumerated above.

These contrasts are average differences between the samples and some of them are barely significant. Still, they point to rats that seem to be slightly differentiated from the mainland animals. In the larger size of their dimensions the specimens from the Riau Archipelago approach the very large rats from the Malay Peninsula. Those animals, however, are still significantly much larger than *Sundamys muelleri* from the Riau Archipelago in most external and cranial measurements (tables 19 and 20), including length of skull and length of maxillary toothrow (fig. 43). We do not know whether the larger rostrum and certain other greater dimensions of rats from the Riau Archipelago actually represent genetic relationship with the population on the Malay Peninsula, or if those features are peculiar to the population on the islands in the Archipelago.

Because most of the differences that distinguish the specimens from the Riau Archipelago are barely significant, and because in all other features they closely resemble rats from the mainland of Sumatra and from other places in the Sumatran region and are unlike *Sundamys muelleri* from either the Malay Peninsula or the Bornean area, we recognize the samples as members of *S. m. muelleri.* If taxonomists want to separate them sub-specifically, then the name *chombolis* (Lyon, 1909) is available. That taxon is based on a specimen (USNM 144393) obtained by Abbott from Pulau Chombol on March 10, 1907. The rat is a very young adult and is smaller than the adults to which Lyon (1909, p. 484) compared it; thus the reason for his diagnosis: "Similar to *Mus firmus* Miller, but slightly darker in color, smaller in size, and with distinctly smaller skull." Lyon thought the specimen to be adult and distinctive in its small size. It is simply a young animal and in features of skin, skull, and teeth fits with the rest of the specimens from the Riau Archipelago.

Our Sumatran Region corresponds roughly to Chasen's (1940, p. xii–xiii) Sumatran Province: "Sumatra and the shallow water islands off its east coast with which the islands of the Rhio and Lingga Archipelagos are intimately related. The large islands of Banka and Billiton. The chain of islands off the west coast of Sumatra, the most important of which, from north to south are Simalur, the Banjak Islands, Nias, and Batu Islands, the Mentawi Islands (Siberut, Sipora, and the Pagi Islands), and Engano." In the context of the distribution of *S. muelleri,* we exclude the Mentawai Islands and Pulau Enggano. Chasen also noted that "The maze of small islands known as the Rhio-Lingga Archipelago has a mammal fauna poor in species, but extraordinarily rich in subspecies. The species are those common to the south of the Malay Peninsula and the lowlands of Central-East Sumatra, but the Sumatran affinity is the stronger of the two." The statement certainly reflects the affinities of *S. muelleri* from the Riau and Lingga archipelagos.

BORNEAN-PALAWAN REGION: At the turn of the nineteenth century, when Miller and Lyon were working, there were few specimens of *Sundamys muelleri* from the areas of Borneo and Palawan. Unlike the situation with the Sumatran Region, where some of

the largest samples are still those collected by W. L. Abbott in the early 1900s, most of the material from Borneo and islands in the Palawan area has been obtained since the 1930s. From most places the samples are large enough that we could reliably estimate the range of morphological variation and the geographic distribution of *S. muelleri* in those places. Only from the Natuna Islands and the islands of Busuanga and Culion are the samples still very small.

Specimens from Borneo, Palawan, and nearby smaller islands are very much like rats from the Sumatran Region in features of skins, skulls, and teeth. At the same time there is geographic variation among the samples that requires description. We discuss the variation by dividing the samples into four lots. The first is composed of specimens from mainland Borneo and some offshore islands. The second contains samples from Pulau Lemukutan, off the west coast of Kalimantan, and Pulau Sebuku, off the southeastern coast of Kalimantan. The third consists of specimens from the Natuna Islands. Specimens from the Philippine islands of Balabac, Palawan, Culion, and Busuanga comprise the fourth group.

MAINLAND BORNEO AND OFFSHORE ISLANDS: We studied specimens from places scattered throughout the mainland of Sabah, Sarawak, and Kalimantan, and from the offshore islands of Miang, Besar, Sebatik, Labuan, Bangii, and Balembangan (fig. 36).

On the Bornean mainland the largest samples of *S. muelleri* come from Sabah in the north and from Kalimantan in the south. We measured two large series from Sabah: one is from the coastal plain near Jesselton (locality 5, fig. 36), and the other is from the highlands between 1500 and 1800 feet in the vicinity of Ranau in the foothills of Gunong Kinabalu (locality 8, fig. 36). The specimens from Kalimantan come from the lowlands of Sampit and Riam (localities 24 and 25; fig. 36) and we pooled those series to form one large sample. The statistics derived from the lowland and highland samples from Sabah and the lowland sample from southern Kalimantan are listed in table 22.

Sundamys muelleri probably occurs throughout Borneo wherever there is forest habitat. Judged from the data we extracted from specimens the known altitudinal distribution of the species is from swamp forests in the coastal lowlands up to 5000 feet in mountain forest on the slopes of Gunong Kinabalu. Lim and Heyneman (1968) recorded one example of *S. muelleri* from 5400 feet on the slopes of Gunong Kinabalu.

There is altitudinal variation among the three large samples from Mainland Borneo. Rats from the highlands of Sabah average significantly larger (estimated by greatest length of skull and length of maxillary toothrow) than do animals from either the lowlands of Sabah or southern Kalimantan (fig. 43). Whether this difference reflects size of sample, few samples from places many miles apart, or the real pattern of altitudinal variation on the mainland will not be known until larger samples from many localities throughout Borneo are analyzed.

The samples from offshore islands consist of either one or a few specimens. Values of their external, cranial, and dental measurements fall within the range of variation noted in the larger series from the lowlands on mainland Borneo. The exceptions are specimens from Pulau Lemukutan and Pulau Sebuku, series which we discuss later.

Three scientific names have been applied to samples from mainland Borneo and some offshore islands: *borneanus, waringensis,* and *otiosus* (table 18). The name, *borneanus,* is the oldest for rats from mainland Borneo and most offshore islands. *Epimys borneanus* was named and described by Miller in 1913. The holotype (USNM 196749) was obtained by H. C. Raven from Telok Karang Tigau on the coast of eastern Kalimantan on August 12, 1912. Miller (1913, p. 15) diagnosed *borneanus* as "A member of the *firmus*-group resembling *Epimys integer* of the Natuna Islands but color of underparts and cheeks less yellowish (between cream-buff and cartridge-buff instead of chamois), and skull with more slender rostrum." The holotype is an example of *Sundamys muelleri.* The combination, *Rattus muelleri borneanus* has been used for rats from mainland Borneo (Chasen, 1940; Medway, 1965, 1977) but we treat *borneanus* as a synonym of *S. m. muelleri,* recognizing that the Bornean animals have, on the average, significantly shorter molar rows than do those from mainland Sumatra or the

smaller islands in the Sumatran Region (fig. 43), as we noted in the previous account.

The names, *waringensis* and *otiosus,* refer to the same kind of rat as does *borneanus* and we also lump them into synonymy with *S. m. muelleri.* In 1941 Sody named and described *Rattus muelleri waringensis* from six specimens collected at Riam in the Kotawaringin District of southwestern Kalimantan. The holotype is a young adult. The main feature Sody used to distinguish *R. m. waringensis* from *R. m. borneanus* of eastern Kalimantan was length of molar row, which he considered "markedly larger" in the series from Riam. In addition to the six examples from Riam that Sody examined, we also studied 11 in the American Museum of Natural History that are from the same place and are part of the same series that Sody had. Specimens in the Riam sample are closely similar in morphology to rats from eastern Kalimantan and we cannot separate them.

In 1932 Chasen and Kloss wrote about the mammals they obtained from the lowlands of Sabah and the islands off the northern coast. Among the rats collected were 11 specimens of what they identified as *Rattus muelleri* from Pulau Banggi and six from Pulau Balembangan (localities 1 and 2; fig. 36). Chasen and Kloss noted that the animals were similar to those from the mainland but had shorter tails, a difference they thought to be significant and one which indicated a population distinct from that on the mainland. Although they thought the specimens from Banggi and Balembangan represented a good subspecies, Robinson and Kloss did not have comparative material of *Rattus muelleri integer* from the Natuna Islands and so postponed naming the samples from the two islands off the tip of Sabah.

By 1934 Chasen had obtained specimens of *Rattus muelleri* from the Natuna Islands. He pointed out that the series from Banggi and Balembangan were different than *R. muelleri integer* and were also distinct from rats in the mainland samples. Chasen (1934, p. 98) named the island population *R. muelleri otiosus* and characterized it as being "Like *R. m. borneanus* (Miller), on the mainland of Borneo but with a shorter tail." We examined the specimens in Chasen's original series. Morphologically, they are closely similar to rats from the mainland and any difference in length of tail between the samples is average. For example, the mean value for length of tail in the nine specimens that Chasen and Kloss (1932, p. 71) listed in their table of measurements is 252.0 mm. This mean is within the range of variation seen in the large samples of *S. muelleri* from Sabah and in the one from southeastern Kalimantan (table 22). We also cannot detect any other significant differences in features of skins, skulls, and teeth between the samples from Banggi and Balembangan and those from the mainland. We treat *otiosus* as a synonym of *borneanus* and thus include it within the synonymy of *S. m. muelleri.*

Pulau Lemukutan and Pulau Sebuku: Although samples of *Sundamys muelleri* from islands off the northern, eastern, and southeastern coasts of Borneo closely resemble samples from the mainland in features of skins, skulls, and teeth, the series from Pulau Lemukutan (locality 38; fig. 36), off the coast of western Kalimantan, and that from Pulau Sebuku (locality 37; fig. 36), off the southeastern coast of Kalimantan, differ conspicuously from mainland rats in features related to body size.

The rats from Pulau Lemukutan average larger in body size than do those in any sample from the mainland. This is expressed by greatest length of skull: the mean value for the Lemukutan sample is significantly greater than means from any of the mainland samples (fig. 43). Although they have large skulls, the Lemukutan rats, judged by our series, have short molar rows, similar to those in the mainland samples (table 22; fig. 43). The only other notable difference between the island sample and those from the mainland is that the rats from Lemukutan have paler underparts (table 14).

The sample from Pulau Lemukutan formed the basis for Lyon's (1911) *Epimys crassus.* The holotype (145471) and 13 other specimens (USNM 145472–145484) were collected by Abbott in 1907. Lyon (1911, p. 103) diagnosed *crassus* as "A large member of the *Epimys firmus* group, differing from the typical form in larger size, larger and heavier skull, and a rather prominent swelling on the anterior portion of the nasal bones."

In color of pelage, rats from Pulau Sebuku

are within the range of variation present in samples from Kalimantan. In body size, however the Sebuku rats are much larger than those in mainland samples (table 22). Mean values for greatest length of skull and length of maxillary toothrow are significantly greater than means in samples from mainland Kalimantan and Sabah (fig. 43). Lyon (1911) studied the same 11 specimens we examined. The series was collected during January 1908, by Abbott. Lyon (1911, p. 102) described the rats as *Epimys sebucus* and diagnosed the taxon as "A member of the *Epimys firmus* group differing from the typical form in a more reddish brown general coloration." Lyon had compared the specimens from Pulau Sebuku with series from mainland Sumatra and the Lingga and Riau Archipelagos. He had no material from Borneo.

Both *crassus,* based on the sample from Pulau Lemukutan, and *sebucus* were recognized as valid subspecies of *R. muelleri* by Medway (1965, 1977). Specimens from each island certainly average larger than those from the mainland in body size but that distinction is lost when the island samples are compared with those from the Lingga and Riau archipelagos and from mainland Sumatra (fig. 43). Perhaps the populations from Lemukutan and Sebuku are more closely related to those in the Sumatran Region, but possibly they reflect the interaction between body size and island area (Heaney, 1978) and the effects of selection unique to each of those islands.

There is another problem. We have no information about the morphological relationships of populations on mainland Kalimantan adjacent to either Pulau Lemukutan on the western side or Pulau Sebuku on the southeastern side. We would like to know whether rats from those places are small like those from southern Kalimantan or large like those on each offshore island. For now we appreciate the size distinctions between the island and mainland samples and we prefer to describe it as the kinds of insular variation we see in *S. m. muelleri.*

Natuna Islands: There are few specimens of *S. muelleri* from these islands. We studied four from Pulau Serasan (also spelled Sirhassen) that were the basis for Miller's (1901) description of *Mus integer.* In that same report he recorded a specimen from Pulau Lingung, which we could not find in the National Museum of Natural History. The only other specimen from the Natuna Islands we know is the holotype of *Rattus muelleri credulus* from Pulau Bunguran (Chasen, 1940).

The four specimens from Pulau Serasan are similar in features of skins, skulls, and teeth to *S. muelleri* from Sabah and Kalimantan. Compared with those mainland samples, the examples of *integer* have, on the average, a broader interorbital region, longer nasals and rostrum, wider zygomatic plates, and longer molar rows. The wider zygomatic plates and longer toothrows are especially evident. Longer molar rows are more characteristic of *S. muelleri* in the Sumatran Region rather than those in the Bornean Region (fig. 43; tables 19 and 22).

When Miller (1901, p. 119) described *integer* he compared the specimens with samples of *Mus validus* from peninsular Thailand that he had named and described in 1900. Miller had no specimens from mainland Borneo. The morphological differences between specimens of *integer* and those of *validus* are the same kinds of differences that distinguish *S. m. validus* from the Malayan Region from *S. m. muelleri* of the Bornean Region. Miller even remarked of *integer* that "This rat is probably a near relative of the Bornean *Mus mülleri.*"

Pulau Serasan is in the southern cluster of Natuna Islands. The holotype of *R. muelleri credulus* (Chasen, 1940) is from Pulau Bunguran in the group of small islands called North Natuna Islands. Chasen (1940, p. 162) characterized this form as being "Intermediate in characters between *integer* of Sirhassen Island and *firmus* of the Rhio-Lingga Archipelago: colour nearly as in *integer,* but tail and hindfoot longer, and about as in *firmus.*" He amplified this characterization by remarking of *credulus* that "The upper parts are slightly less blackened than in *integer,* and the pale element in the pelage is rather warmer in tone: the flanks especially are brighter in colour. The under parts are as in *integer,* that is to say whiter than in *firmus,* the pale area narrower, and with a thin grey-brown mid-ventral line."

We examined the holotype of *credulus* (BM 47.1459). It is a large adult male: length of head and body, 232 mm.; length of tail, 270

TABLE 22

Measurements (in Millimeters) of Adult *Sundamys muelleri* from the Bornean Region[a]

Measurement	Pulau Lemukutan	Pulau Sebuku	Southern Kalimantan (localities 24, 25; fig. 36)	Sabah Lowlands (locality 5; fig. 36)	Sabah Highlands (locality 8; fig. 36)
Length of head and body	234.8 ± 15.5 (12) 210–259	241.4 ± 12.7 (8) 225–263	213.1 ± 14.6 (28) 189–244	195.5 ± 9.9 (8) 179–213	207.7 ± 11.1 (22) 188–240
Length of tail	254.9 ± 22.9 (12) 219–291	248.4 ± 11.3 (7) 234–267	239.4 ± 21.4 (27) 191–275	226.3 ± 17.5 (8) 201–255	247.4 ± 14.7 (22) 212–271
Tail/head and body (percent)	109	103	113	111	119
Length of hind foot	49.0 ± 1.9 (12) 47–53	47.4 ± 1.9 (9) 46–51	43.2 ± 1.7 (28) 40–47	43.3 ± 1.6 (9) 41–45	40.9 ± 1.9 (22) 37–45
Length of ear	— —	— —	22.2 ± 1.0 (28) 20–24	21.1 ± 0.8 (9) 20–22	21.3 ± 1.0 (22) 19–24
Greatest length of skull	52.3 ± 2.3 (10) 49.4–56.8	52.5 ± 1.2 (9) 51.1–54.2	49.0 ± 2.7 (27) 44.1–54.2	48.3 ± 2.0 (14) 45.4–51.9	50.4 ± 1.9 (21) 46.4–53.9
Zygomatic breadth	25.2 ± 1.4 (11) 23.1–27.7	25.9 ± 1.1 (9) 24.6–27.5	23.2 ± 1.4 (24) 20.5–25.5	24.0 ± .9 (15) 22.2–25.6	24.8 ± .9 (20) 23.2–26.5
Interorbital breadth	7.8 ± .5 (11) 7.2–8.8	7.8 ± .3 (9) 7.4–8.5	7.1 ± .4 (28) 6.3–8.0	6.9 ± .4 (15) 6.0–7.4	7.0 ± .4 (21) 6.3–7.7
Length of nasals	21.8 ± 1.4 (10) 19.6–24.2	21.9 ± .7 (9) 21.0–23.0	19.4 ± 1.3 (28) 16.9–21.9	19.6 ± 1.0 (14) 17.9–21.3	20.0 ± 1.0 (21) 18.0–22.1
Length of rostrum	16.6 ± .9 (10) 14.9–18.3	17.4 ± .5 (9) 16.6–18.2	15.1 ± 1.1 (28) 12.8–17.2	15.3 ± .9 (14) 14.1–16.8	15.9 ± .8 (21) 14.1–17.8
Breadth of rostrum	10.3 ± .7 (11) 9.3–11.7	10.4 ± .6 (9) 9.7–11.6	9.3 ± .6 (28) 8.1–10.9	9.1 ± .6 (15) 8.4–10.5	9.6 ± .5 (21) 8.8–10.6
Breadth of braincase	18.6 ± .6 (11) 17.9–19.6	18.7 ± .3 (9) 18.1–19.1	18.1 ± .7 (26) 16.8–19.3	18.0 ± .5 (15) 17.2–18.8	18.3 ± .5 (21) 17.3–19.2
Height of braincase	13.2 ± .7 (11) 12.3–14.3	13.7 ± .6 (9) 13.2–14.7	12.9 ± .6 (26) 11.8–14.0	12.6 ± .5 (15) 11.5–13.4	13.0 ± .5 (21) 12.3–14.0
Breadth across incisor tips	3.6 ± .3 (11) 2.9–4.0	3.6 ± .2 (7) 3.3–3.9	3.4 ± .3 (26) 2.8–3.9	3.2 ± .2 (13) 2.7–3.5	3.6 ± .2 (21) 3.1–4.1
Breadth of zygomatic plate	6.7 ± .6 (11) 6.0–7.6	6.4 ± .4 (9) 5.8–7.0	5.7 ± .5 (28) 4.8–6.7	5.7 ± .4 (15) 5.1–6.5	5.8 ± .4 (21) 5.1–6.6
Breadth of zygomatic notch	3.1 ± .5 (11) 2.2–3.9	3.2 ± .4 (9) 2.6–3.6	2.9 ± .4 (28) 2.2–3.8	2.9 ± .4 (15) 2.2–3.6	2.8 ± .4 (21) 2.2–3.6

TABLE 22—(*Continued*)

Measurement	Pulau Lemukutan	Pulau Sebuku	Southern Kalimantan (localities 24, 25; fig. 36)	Sabah Lowlands (locality 5; fig. 36)	Sabah Highlands (locality 8; fig. 36)
Length of diastema	15.2 ± 1.3 (11) 13.2–17.5	14.7 ± .7 (9) 13.7–15.5	13.0 ± 1.0 (28) 11.2–14.9	12.9 ± .7 (15) 12.0–14.0	13.5 ± .6 (21) 11.7–14.5
Palatal length	28.3 ± 1.7 (11) 25.8–31.8	28.1 ± .8 (9) 27.0–29.3	26.2 ± 1.4 (28) 23.9–28.8	25.8 ± 1.0 (15) 24.0–27.2	26.7 ± 1.0 (20) 24.6–28.3
Postpalatal length	18.5 ± 1.1 (11) 17.0–20.3	18.6 ± .4 (9) 17.9–19.4	16.8 ± 1.2 (25) 15.1–18.6	16.4 ± .9 (15) 14.5–18.0	17.7 ± 1.0 (19) 15.9–19.6
Length of incisive foramina	8.6 ± .4 (11) 8.1–9.4	8.8 ± .4 (9) 8.3–9.4	7.7 ± .6 (28) 6.6–9.1	7.9 ± .6 (15) 7.1–8.9	8.5 ± .5 (21) 7.7–9.3
Breadth of incisive foramina	3.2 ± .2 (11) 2.8–3.6	3.5 ± .2 (9) 3.1–3.7	3.0 ± .2 (28) 2.7–3.2	2.9 ± .2 (15) 2.6–3.2	3.1 ± .2 (21) 2.8–3.4
Length of palatal bridge	10.5 ± .7 (11) 9.6–12.0	10.4 ± .3 (9) 9.8–10.8	9.9 ± .6 (28) 8.9–10.9	9.9 ± .5 (15) 9.3–10.7	10.0 ± .4 (20) 9.4–10.9
Breadth of palatal bridge at M^1	4.8 ± .3 (11) 4.4–5.4	5.1 ± .4 (9) 4.5–5.8	4.5 ± .3 (28) 3.9–5.3	4.4 ± .3 (15) 4.0–4.8	4.5 ± .3 (21) 4.1–5.5
Breadth of palatal bridge at M^3	5.8 ± .5 (11) 5.1–6.4	5.9 ± .3 (9) 5.5–6.4	5.1 ± .4 (28) 4.5–6.1	5.2 ± .2 (15) 4.9–5.9	5.3 ± .2 (21) 4.9–5.8
Breadth of mesopterygoid fossa	3.8 ± .2 (11) 3.4–4.1	4.1 ± .2 (9) 3.9–4.3	3.6 ± .3 (28) 3.2–4.3	3.8 ± .3 (15) 3.2–4.2	4.0 ± .3 (21) 3.4–4.5
Length of bulla	6.4 ± .2 (11) 6.0–6.7	6.8 ± .3 (9) 6.6–7.2	6.8 ± .4 (27) 6.0–7.4	6.3 ± .2 (15) 5.8–6.7	6.3 ± .3 (21) 5.7–6.7
Height of bulla	6.0 ± .3 (11) 5.5–6.5	6.3 ± .2 (9) 6.1–6.6	6.1 ± .3 (27) 5.4–6.7	5.6 ± .3 (15) 5.3–6.2	5.8 ± .2 (21) 5.4–6.5
Alveolar length of M^{1-3}	8.7 ± .2 (11) 8.4–9.1	9.4 ± .2 (9) 9.1–9.8	9.0 ± .3 (28) 8.3–9.6	8.8 ± .4 (15) 8.2–9.5	9.1 ± .4 (21) 8.2–10.0
Breadth of M^1	2.6 ± .1 (11) 2.4–2.7	— —	2.5 ± .1 (28) 2.3–2.6	2.4 ± .1 (15) 2.4–2.5	2.5 ± .1 (21) 2.3–2.7

[a] Mean plus or minus one standard deviation, size of sample in parentheses, and observed range are listed for each measurement.

mm.; length of hind foot, 50 mm.; and alveolar length of maxillary toothrow, 10.4 mm. These values fit better with samples of *S. muelleri* from the Riau and Lingga archipelagos (table 20) than with specimens from either the southern Natuna Islands or mainland Borneo (tables 19 and 22), which confirms Chasen's (1940) observation.

We treat *credulus* from Pulau Bunguran and *integer* from Pulau Serasan under *Sundamys muelleri muelleri.* We are aware that except for slightly longer molar rows and broader zygomatic plates, the examples of *S. muelleri* from the southern Natuna Islands are very much like those from mainland Sabah and Kalimantan. The specimen from the northern Natuna group resembles samples from the Riau and Lingga archipelagos.

Of the Natuna Islands, Chasen (1940, p. xiv) noted that

> Although closely associated in name the North and South Natuna Islands have little in common faunistically. The southern group is essentially Bornean in its affinities, a relationship primarily indicated by the presence of *Tarsius* and *Tupaia tana* on Sirhassen Island, and emphasised by the facies of the local forms of *Ratufa affinis* and the two *Tragulus.* The northern islands are also linked to Borneo by *Mydaus* which occurs in both places, but in general the subspecies of Bunguran are dissimilar to those inhabiting the nearest Bornean mainland. In a number of cases they bear a strong resemblance to the races on Bintang Island in the Rhio Archipelago.

Our specimens of *Sundamys muelleri* reflect Chasen's statement. However, samples from the north and south Natuna Islands are so small that we are uncertain if they are reliable samples of the morphological characteristics of rats on those islands. Whether their long toothrows and wide zygomatic plates ally them with rats in the Riau and Lingga archipelagos on the one hand and Borneo on the other or are results of local selection and the interplay of body size and island area are unknown. We need more specimens from the Natuna Islands.

Palawan Area: Samples of *Sundamys muelleri* are available from the Philippine islands of Balabac, Palawan, Busuanga, and Culion (fig. 36) and were previously reported by Sanborn (1952) and by Barbehenn, Sumangil, and Libay (1972–1973). The specimens resemble those from mainland Borneo but differ in length of tail, color of pelage, and some cranial dimensions. Specimens from the four islands are not uniform in their morphological features but differ enough that they can be sorted into two groups. One lot contains rats from the islands of Balabac and Palawan, the other consists of specimens from Busuanga and Culion.

The largest sample (20) is from Balabac Island. Most are adults and form a good series with which to compare the samples from Borneo, specifically the two large series from mainland Sabah (localities 5 and 8). The most evident differences between the rats from Sabah and those from Balabac are in pelage color and tail length. Rats from Balabac Island have pale brown to ochraceous brown upperparts, either white or grayish white underparts, and tails that average longer than in any sample from Borneo, both in actual dimension and relative to length of head and body. In contrast, specimens from Sabah have upperparts with more dark brown and blackish hues, underparts that are either grayish white or dark buffy gray (table 14), and shorter tails (table 23).

Size and configurations of skulls and teeth are closely similar in the samples from Balabac Island and Sabah (tables 22 and 23; figs. 42 and 43). Specimens from Balabac have a wider interorbital region, higher braincase, wider zygomatic plates, and longer palatal bridge but the differences are average. The samples from Balabac and mainland Sabah are nearly inseparable in cranial and dental features; the distinguishing characters are clearly those associated with the skins.

There are fewer specimens (eight) from Palawan Island. Most of these are young adults and many of the mean values listed in table 23 average significantly smaller than comparable means in the Balabac sample; the differences reflect age, not insular variation. Young adults of comparable age in samples from each island are nearly indistinguishable in features of skins, skulls, and teeth. Except for pelage color and tail length, *S. muelleri* from Palawan, like those living on Balabac Island, are closely related to populations on mainland Borneo.

In 1952 Sanborn named and described

Rattus muelleri balabagensis from a single specimen collected on Mount Balabag at 3000 feet on the island of Palawan. Sanborn (1952, p. 131) remarked that "The extremely long tail and light color distinguish *balabagensis* from all other members of the *mülleri* group."

In the same report that Sanborn discussed *balabagensis,* he (1952, p. 131) named and described *Rattus culionensis* from two adults obtained at Siuk on Culion Island. Culion, and the larger island of Busuanga are in the Calamian Islands northeast of Palawan. Sanborn compared his specimens with samples from mainland Borneo and remarked that "*R. culionensis* appears to be an offshoot of the *mülleri* group but differing in enough particulars that it can not be considered a subspecies." To Sanborn, the diagnostic features of *R. culionensis* were its reddish brown upperparts, white underparts, large bullae, relatively long palatal foramina, weak supraorbital ridges, and a weakly developed lamboidal crest.

We studied the holotype and nine other examples of *culionensis* from the islands of Culion and Busuanga; only five are adult. Their pelage coloration is closely similar to that in samples from the islands of Palawan and Balabac. The Culion and Busuanga rats have shorter tails (table 23). There are no differences among the island samples in greatest length of skull but the rats from the Calamian group have molar rows that average significantly smaller than those from Balabac but not those in samples from mainland Borneo (tables 22 and 23; figs. 42 and 43). Of all the diagnostic traits listed by Sanborn, only bullar size distinguishes the Calamian rats; adults from Culion and Busuanga have much larger bullae than adults from Palawan and Busuanga (table 23; fig. 42).

In assessing the relationships of rats from the Palawan area we are hampered by the small series from Palawan and the Calamian group that are available for study. In our specimens, the animals from Culion and Busuanga are more like those from Palawan and Balabac than the rats from any other place on the Sunda Shelf. And samples from Palawan and Balabac are morphologically closely related to rats from mainland Borneo, differing only in having paler pelage and longer tails. We include the scientific names, *balabagensis* and *culionensis,* within our concept of *Sundamys muelleri muelleri.*

The Bornean area contains many unique mammals and Chasen (1940, p. xiii) defined a Bornean Province as "Borneo and its coastal islands, the most important of which are Labuan, and Mantanani off the north-west coast; Maratua off the east coast; and Pulau Laut off the south-east corner. The North Bornean Islands of Banguey, Balambangan and Mallewalle; the North and South Natuna Islands, the Karimata Islands." To this we would add the islands of Balabac, Palawan, Culion, and Busuanga. Chasen also noted that "The outstanding feature of the mammal fauna of Borneo is that it is far more specialised than that of any other Malaysian province." *Sundamys muelleri* of the Bornean-Palawan Region is distinguished by its much smaller body size compared with rats of the Malayan Region, as we discussed in a previous section. There are, however, few distinctions between *S. muelleri* from the Sumatran and Bornean regions. Most involve differences in length of toothrow, the paler pelage and longer tails of the Balabac and Palawan animals, and the larger bullae of rats from the Calamian group.

NATURAL HISTORY: Most information about habitat and habits of *S. muelleri* come from samples obtained on the Malay Peninsula and Sabah in North Borneo. The habitat of this rat is tropical evergreen rain forest. Lim (1970, p. 733) notes that *S. muelleri,* "although it is rarely found in lowland primary forests, it is abundant in disturbed lowland primary and secondary forests, and also invades mangrove forests." The rat prefers marshy parts of the forest (Harrison, 1954a, 1957a, 1957b) in low areas, valley bottoms, and along streams. Marshall (1977b, pp. 479 and 480) writes that "A radio tracking study by Glen C. and B. C. Sanderson in Malaya revealed that Müller's rats had elongated home ranges along river banks, and that they frequently swam across the river. The lengthwise spans of radio fixes for four individuals at night were 76, 91, 137, and 183 m. Daytime was spent under logs or in holes, and most individuals maintained permanent territories and dens. One, however, roamed at random and had a different den every two days." Lim and Heyneman (1968, p. 267) reported that 19 specimens from Sabah were

TABLE 23
Measurements (in Millimeters) of Adult *Sundamys muelleri* from Palawan Area[a]

Measurement	Balabac Island (locality 41; fig. 36)	Palawan Island (locality 42; fig. 36)	Culion and Busuanga Islands (localities 43, 44; fig. 36)
Length of head and body	206.6 ± 13.9 (18) 181–230	199.4 ± 16.8 (8) 192–223	210.4 ± 6.1 (5) 202–217
Length of tail	280.7 ± 18.2 (17) 242–307	262.7 ± 13.8 (7) 250–288	271.0 ± 18.0 (5) 247–286
Tail/head and body (percent)	136	132	129
Length of hind foot	44.0 ± 1.2 (18) 42–46	40.6 ± 1.3 (8) 38–42	41.4 ± 1.1 (5) 40–43
Length of ear	23.8 ± 1.6 (17) 21–26	21.7 ± .9 (7) 21–24	24.6 ± 1.1 (5) 23–26
Greatest length of skull	50.2 ± 2.0 (11) 47.5–53.1	47.4 ± .7 (5) 46.5–48.1	50.2 ± .5 (4) 49.6–50.7
Zygomatic breadth	25.0 ± .8 (11) 23.6–26.0	22.9 ± .5 (6) 22.0–23.4	24.9 ± .3 (4) 24.5–25.3
Interorbital breadth	7.3 ± .4 (12) 6.7–8.1	6.8 ± .2 (6) 6.5–7.0	6.9 ± .3 (5) 6.6–7.2
Length of nasals	19.6 ± 1.1 (11) 17.3–21.4	18.4 ± .4 (6) 17.8–19.0	19.7 ± .3 (5) 19.2–20.0
Length of rostrum	16.0 ± .8 (11) 15.1–17.6	14.7 ± .2 (6) 14.6–15.1	15.5 ± .3 (5) 15.1–15.8
Breadth of rostrum	9.5 ± .4 (12) 9.1–10.5	8.4 ± .1 (6) 8.2–8.6	9.3 ± .1 (5) 9.1–9.4
Breadth of braincase	18.5 ± .7 (12) 17.5–19.7	17.8 ± .3 (6) 17.3–18.1	18.0 ± .4 (3) 17.6–18.4
Height of braincase	13.4 ± .6 (12) 12.3–14.2	12.8 ± .4 (6) 12.3–13.3	12.9 ± .3 (4) 12.5–13.2
Breadth across incisor tips	3.6 ± .2 (11) 3.4–3.8	3.1 ± .2 (5) 2.9–3.4	3.6 ± .1 (5) 3.6–3.7
Breadth of zygomatic plate	6.2 ± .3 (12) 5.5–6.5	5.0 ± .2 (6) 4.7–5.3	5.9 ± .3 (5) 5.6–6.4
Breadth of zygomatic notch	2.6 ± .4 (12) 2.0–3.4	2.1 ± .5 (6) 1.5–2.9	2.6 ± .5 (5) 2.2–3.2
Length of diastema	13.1 ± .8 (12) 11.8–13.8	11.9 ± .3 (6) 11.5–12.2	13.6 ± .2 (5) 13.3–13.9
Palatal length	26.9 ± 1.1 (12) 25.0–28.7	25.3 ± .4 (6) 24.7–25.9	26.5 ± .2 (5) 26.4–26.8
Postpalatal length	17.5 ± .8 (12) 16.0–18.6	16.0 ± .6 (6) 15.2–16.7	17.5 ± .2 (4) 17.2–17.7
Length of incisive foramina	8.4 ± .5 (12) 7.6–9.2	8.3 ± .3 (6) 7.7–8.7	8.7 ± .2 (5) 8.5–8.9
Breadth of incisive foramina	2.9 ± .3 (12) 2.5–3.3	2.7 ± .2 (6) 2.4–2.8	2.9 ± .2 (5) 2.8–3.1
Length of palatal bridge	10.6 ± .5 (12) 9.9–11.4	9.8 ± .2 (6) 9.6–10.0	9.9 ± .3 (5) 9.7–10.4
Breadth of palatal bridge at M^1	4.5 ± .3 (12) 4.0–5.0	3.9 ± .3 (6) 3.6–4.3	4.5 ± .2 (5) 4.3–4.8

TABLE 23—(*Continued*)

Measurement	Balabac Island (locality 41; fig. 36)	Palawan Island (locality 42; fig. 36)	Culion and Busuanga Islands (localities 43, 44; fig. 36)
Breadth of palatal bridge at M^3	5.3 ± .4 (12) 4.9–6.3	4.8 ± .2 (6) 4.7–5.1	5.2 ± .4 (5) 4.7–5.5
Breadth of mesopterygoid fossa	3.6 ± .4 (12) 3.0–4.4	3.2 ± .1 (6) 3.1–3.3	3.5 ± .5 (4) 3.1–4.2
Length of bulla	6.8 ± .3 (12) 6.2–7.3	6.6 ± .2 (6) 6.2–6.7	7.2 ± .3 (4) 6.8–7.5
Height of bulla	6.1 ± .3 (12) 5.7–6.5	5.8 ± .2 (6) 5.5–6.1	6.1 ± .3 (3) 5.9–6.3
Alveolar length of M^{1-3}	9.3 ± .3 (12) 9.0–9.8	9.0 ± .2 (6) 8.6–9.1	8.9 ± .3 (5) 8.6–9.3
Breadth of M^1	2.6 ± .1 (12) 2.5–2.7	2.5 ± .1 (6) 2.3–2.7	2.6 ± .1 (3) 2.5–2.6

[a] Mean plus or minus one standard deviation, size of sample in parentheses, and observed range are listed for each measurement.

caught in secondary forests and cultivated fields. They noted it to be common in the lowlands where they worked and considered a serious pest in cultivated crops.

Sundamys muelleri is primarily terrestrial but has been taken on branches of trees; it nests on the ground, usually near streams (Lim, 1970). Food consists of insects, fruit, leaves and shoots, other vegetable matter, crabs, and land snails; a partially digested caecilian was found in the stomach of one rat (Harrison, 1954a; Medway, 1969; Lim, 1966, 1970). Harrison and Lim (1950, p. 305) reported that in captivity, *S. muelleri* "was a general feeder, and drank plenty of water. It seemed rather a lazy rat, and reasonably good natured. It was nocturnal." In a paper on the distribution, relative abundance, food habits, and parasite patterns of giant rats in West Malaysia, Lim (1970, pp. 738–739) summarized his information about *S. muelleri,* stating that the rat is "rather restricted to low elevations (up to 3000 feet), but has the strongest affinity for moist habitats. It is not especially arboreal in its habits. Its diet includes relatively fewer insects. Correlated with this is a relatively low incidence of nematode and cestode infestation. Perhaps correlated with its preference for moist habitats, is a strong preference for crabs and snails as food. The diet also includes a high proportion of leaves and other vegetable matter."

Other natural history information is available for Malayan *Sundamys muelleri*: weight and growth (Rudd, 1965), and analyses of growth and sexual maturation of rats reared in the laboratory (Medway and Ang, 1971); abundance and population density (Harrison, 1969; Medway and Wells, 1971); reproduction (Harrison, 1955); breeding rhythms (Harrison, 1952a); moonlight and its effect on rat breeding and pregnancy (Harrison, 1952b, 1954b); body temperatures (Rudd, 1966a); survival rates (Harrison, 1956a); mark-capture experiments and range of movement (Harrison, 1957c, 1958); and the role of *S. muelleri* as a host of Malaysian parasites (Harrison, 1957b), and its endoparasites (Lim, Ow-Yang, and Lie, 1965; Dunn, Lim, and Yap, 1968; Palmieri, Krishnasamy, and Sullivan, 1979). Much of this data has been summarized by Medway (1969) in his useful book covering the mammals known to occur on the Malay Peninsula.

Sundamys infraluteus

March 22, 1888: "To-day a Dusun brought in a gigantic rat, but in a very decomposed state and full of maggots; but the cold in my head is so bad that my sense of smell has

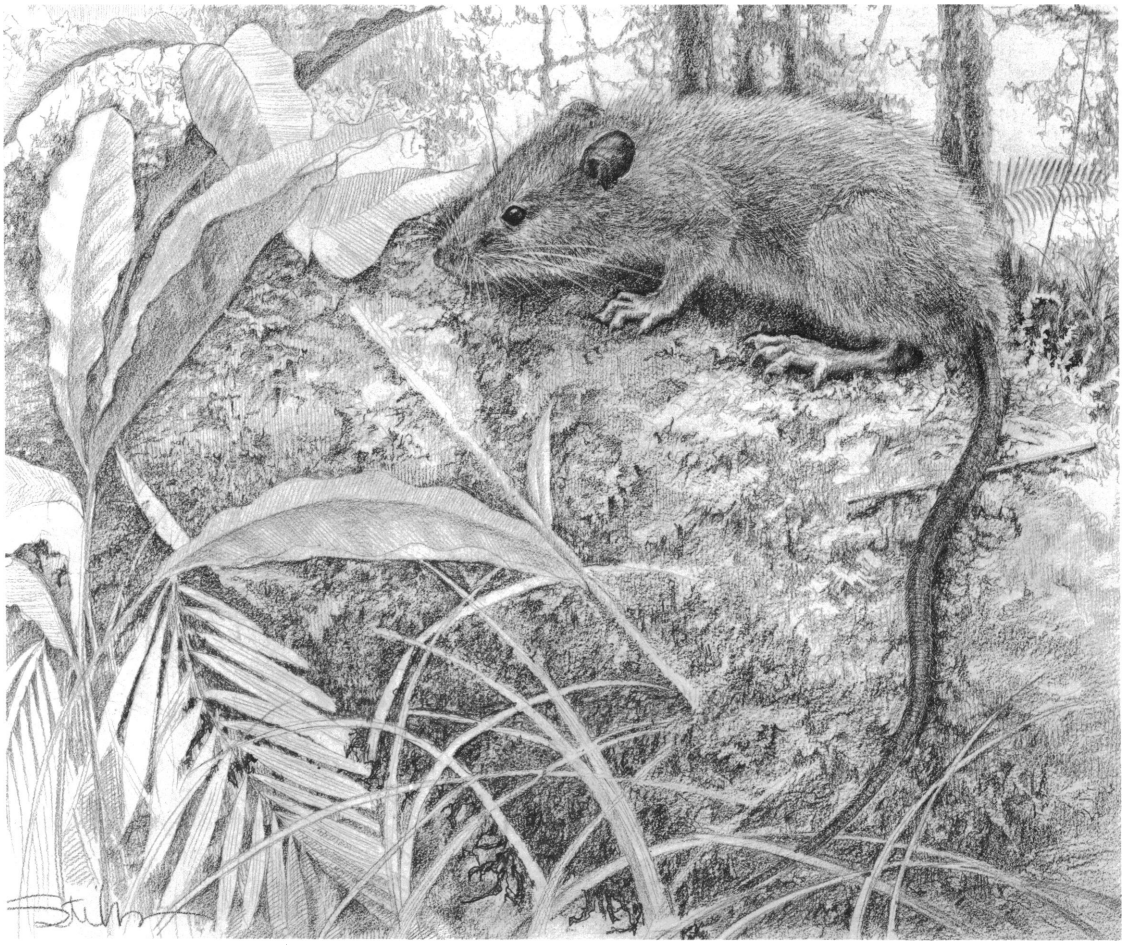

FIG. 44. *Sundamys infraluteus,* the giant rat of Sumatra and Borneo.

completely gone, and to that science may be grateful for the addition of the 'Mankulum' to the genus *Mus.*" So wrote John Whitehead (1893, p. 183) when he was camped in primary forest by the Sungai Kinokok on the slopes of Gunong Kinabalu in Sabah (North Borneo). The large shaggy rat known as *Mankulum* to the Dusan People of North Borneo was introduced to naturalists in the Western World by Oldfield Thomas in 1888. He called the animal *Mus infraluteus* and based this taxon on that decomposed rat brought to John Whitehead in his forest camp. In a short paper where he discussed new mammals from the Malayan Archipelago, Thomas (1888a) diagnosed the new species as, "Size large. Fur coarse and harsh, but not spinous. General colour dark greyish brown, the tips of the shorter hairs with a silvery lustre. The longer straighter hairs numerous, not markedly lengthened on the rump, uniformly black. Under surface a dirty yellowish brown, the tips of the straighter hairs dull orange, their bases and the whole of the underfur slate grey. Hands and feet brown. Tail rather shorter than the head and body, thinly haired, dark brown or black above and below; rings of scales averaging about eight or nine to the centimetre. Skull and teeth large and powerful."

A year later Thomas (1889) elaborated on *Mus infraluteus* in a report about the mammals of Mount Kina Balu, a peak in northern Borneo. The animals described there were

part of a zoological collection made by John Whitehead from Kinabalu during 1887 and 1888. Whitehead, to Thomas, was "a gentleman, who, although primarily an ornithologist, yet wisely collected whatever Mammals he was able to obtain in that most interesting and as yet unknown part of the island." Thomas repeated his earlier published diagnosis of *Mus infraluteus* and in the report wrote that "This fine Rat has a certain similarity to the Indian Bandicoot Rats (*Nesokia*), resembling them both in general external appearance and in the stout and heavy build of the skull and teeth. No species hitherto described can be mistaken for it, as all the Oriental Rats which have external or cranial proportions at all similar are distinguished either by having elongated rump-bristles or parti-coloured white-tipped tails. The single specimen obtained was found lying dead in the forest."

Thomas recognized *infraluteus* as a distinct species but he never discussed its relationships to other kinds of rats. It was not until 15 years later that *infraluteus* was allied with another species of rat from the Indo-Malayan area. In 1903 Bonhote reported on the mammals obtained by Annandale and Robinson from the Malay Peninsula. In that paper he arranged what he called the Oriental rats into groups and among these were the "MUELLERI GROUP" and the "INFRALUTEUS GROUP." Bonhote also appended notes about the features distinguishing some of the species and groups. Here he discussed the "MUELLERI GROUP" and wrote that "*Mus infraluteus* is a fine and distinct species, but allied to the above group [*muelleri*] in size and cranial characters. It is of a uniform very dark brown above, some of the hairs having light, glistening tips. Under parts with dark grey under fur, and long, light, glistening stiff hairs, of a spiny character."

Bonhote recognized not only that *Rattus infraluteus* was a good species, but that it was related to *R. muelleri.* His assessment was based on features of skins and skulls. This association of the two species was retained by Ellerman (1941) in his classic monograph on families and genera of rodents where he listed *infraluteus* as a species of *Rattus* in what he called a "mülleri Group." About the same time Chasen (1940, p. 163) in his handlist of Malaysian mammals recognized *Rattus infraluteus* and termed it "The high level representative of populations of *mulleri,*" a vague statement probably implying that populations of *infraluteus* were only a highland subspecies of *R. muelleri.* Later, Ellerman (1947–1948, p. 263) summarized some alterations and revisions that were to be published in volume 3 of his monograph on families and genera of rodents. Under an account of *Rattus callitrichus,* he wrote: "Possibly the form *infraluteus* is a race, but it is a distinct rat, and should perhaps be given specific rank." By 1949 when volume 3 of Ellerman's monograph was published, consisting mostly of additions and corrections to the two previous volumes, Ellerman had apparently changed his mind about *infraluteus,* for on page 50 he listed that taxon as a subspecies of *Rattus callitrichus,* a species that occurs only on Celebes (Musser, 1970b), and commented that *R. callitrichus infraluteus* was, "A very distinct type, and perhaps it should be given specific rank. It is larger than *callitrichus,* with larger teeth, and a dark tail (*callitrichus* has the tail dark basally, pale terminally)." On page 69 of the same volume, in the section where Ellerman listed the species in *Rattus* that he thought were valid, he entered *infraluteus* as a species of *Rattus* with the comment that "This is very possibly a western race of *callitrichus.*" Similarities between *R. callitrichus* and *R. infraluteus* in characteristics of skins and skulls were also recorded by Laurie and Hill (1954).

Sundamys infraluteus is not related to *Rattus callitrichus.* It is a large, handsome, and distinctive rat as both Thomas and Bonhote recognized. All the specimens of *S. infraluteus* from northern Borneo are from Gunong Kinabalu and Gunong Trus Madi in Sabah. We examined 42 examples from those two mountains, all obtained during the period, 1888 to 1953 and within an altitudinal range of 3000 to 7700 feet.

Sundamys infraluteus also lives in the mountains of Sumatra from Aceh Province in the north to Lampung Province in the south, the length of the Sumatran mainland. The largest-bodied of all the native Sumatran murids, it is really the Giant Rat of Sumatra. Our sample consists of six specimens and we do not know of any others in collections of

museums. All the rats were caught during the period, 1915 to 1937 from altitudes between 2300 and 7900 feet.

Three of the Sumatran specimens are adults, three are juveniles. There are not enough specimens to determine any pattern of morphological variation that may exist along the mountains of western Sumatra. We can only write that in their pale gray underparts tinged with buff, and their long toothrows—both of which are distinctive features of the adult Sumatran sample—the young rats from localities in the central and southern parts of mountainous Sumatra fit with the adults from northern Sumatra and not with adults or juveniles from Sabah.

The first specimen to be obtained from Sumatra is a juvenile collected by E. Jacobsen in 1915 from the Kerinci region of West Java. The record was never published. The specimen remained unidentified in Jacobsen's collection in the Rijksmuseum van Natuurlijke Historie at Leiden until Musser sorted through the material in 1969.

The second specimen was taken 20 years later. In 1937, Bartels reported "On Two New Muridae from Sumatra and Another Rat New to the Sumatran Fauna," the results of his trip to the Lampung area of southern Sumatra in 1935. There he worked in forests on the slopes of Gunung Tanggamoes and in the nearby lowlands. The two new rats Bartels discovered were described as subspecies of *Rattus bukit* and *R. cremoriventer,* and the new record was of *R. infraluteus.* Of the latter, Bartels wrote that

> On my expedition of 1935 I collected on Mt. Tanggamoes, Lampoengs, *ca.* 700 m., a single specimen of a rat which without any doubt must be regarded upon as the Sumatran representative of [*infraluteus*]. Thus, by the capture of this specimen, the occurrence of *infraluteus* in Sumatra, too, was proved for the first time. As the specimen, unfortunately, is a quite young one, it is impossible, for the present, to settle the question whether or not the Sumatran animal differs from the Javan form. It may only be stated that it seems to agree with the latter very well in general appearance.

The specimen Bartels discussed is a juvenile *S. infraluteus.*

Chasen (1939b) provided the third record of *Rattus infraluteus* from Sumatra, an adult obtained by Hoogerwerf at Atang Poetar in the mountains of Leuser and Lemboe, Aceh Province. Chasen identified the specimen as *R. infraluteus maxi. Rattus maxi* had been described by Sody in 1932, who suggested it might be allied to *R. infraluteus.* Chasen considered *maxi* to be a subspecies of *R. infraluteus.* In 1940 in his handlist of Malaysian mammals, Chasen listed *R. i. maxi* as the form on both Sumatra and Java.

In 1942 Miller reported on two adults of *S. infraluteus* from Aceh Province in northern Sumatra, not realizing that they were examples of *infraluteus* and describing them as members of a new species, *Rattus atchinus.* Miller (1942, p. 152) diagnosed *R. atchinus* as "A member of the *Rattus mulleri* group larger than any of the forms hitherto described from Sumatra; fur unusually dense and woolly." He continued by contrasting the two specimens with the named forms of the *mulleri* group from Sumatra and offshore islands, all well represented by specimens in the collection of the National Museum of Natural History. Miller (p. 153) concluded that "Though this large rat is clearly a mountain representative of the *Rattus mulleri* group I think it should be treated as a distinct species until intergradation with some lowland animal shall have been shown to take place. The peculiarities that separate the Atjehan mountain rat from the relatively small *Rattus mulleri* (Jentink) of the Singalang River, Padang, western Sumatra . . . and from the nearest geographical neighbor of both *R. mulleri* and *R. atchinus,* the *R. domitor* (Miller) of Pulo Mansalar, off Tapanuli Bay, seem too great to warrant the assumption of intergradation in the absence of specimens proving that intergradation actually takes place."

By 1942 *Sundamys infraluteus* had been reported from the mountains of northern and southern Sumatra, but the record from Aceh remained as obscure as the name Miller tied to it. Ellerman (1949, 1961) never dealt with *atchinus* in any of his later checklists and reports and the name dropped from sight and was not associated with *S. infraluteus* until now.

SPECIMENS AND LOCALITIES: The specimens of *S. infraluteus* and the places in Sabah and Sumatra where they were caught are listed

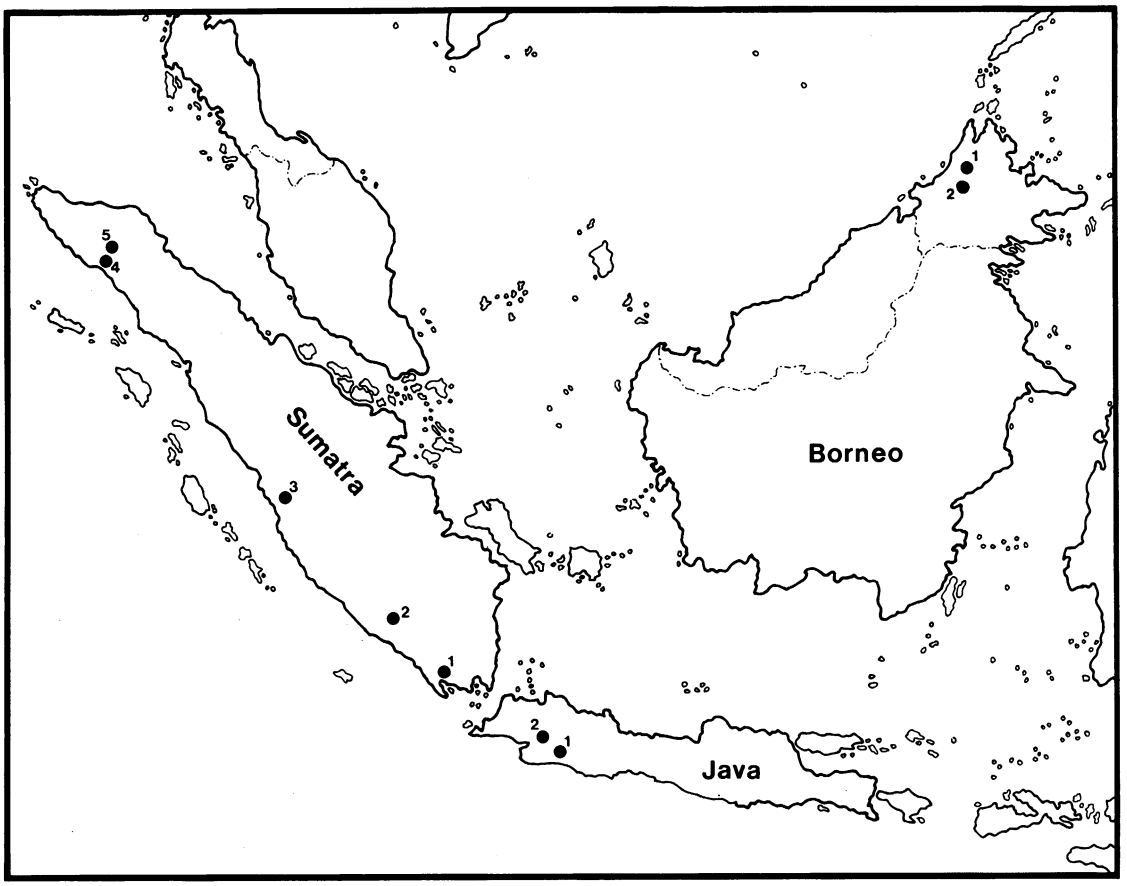

FIG. 45. Geographic distributions of *Sundamys maxi* (Java) and *Sundamys infraluteus* (Borneo and Sumatra) based on specimens examined. Number by each dot keys to numbered localities in text where we give names of places and catalogue numbers of specimens.

below; the localities are shown on the map in figure 45.

SABAH

1. Gunong Kinabalu: BM 93.4.1.13, 94.7.2.15, 94.7.2.16, 95.10.4.22 (holotype of *infraluteus*), and 71.2839–71.2842. Gunong Kinabalu: Kiau, 3000 feet, SNM 3645 and 3654; Kenokok (also spelled Kinokok), 3300 feet, SNM 4152 and 4169; Base camp 35 mi., 5400 feet, FMNH 108932 and 108934; Lumu Lumu, 5500 feet, SNM 4092 and 4061, MCZ 36105 and 36107; Telecommunication Station, 7040 feet, FMNH 108933 and 108935; Kamborangah, 7040 feet, 7200 feet, and 7700 feet, MCZ 36106 and 36108, MZB 9013, USNM 301075; Bundu Tuhan, USNM 292759, 292762–292770, FMNH 108936 and 108937; BM 71.2843–71.2845; Mari Parai, USNM 301076.
2. Gunong Trus Madi, Pampang Camp: USNM 301077, BM 71.2846.

SUMATRA

1. Lampung Province, De Giesting, east slopes of Gunung Tanggamoes, 700 meters: Bartels Coll. No. S-49 (now RMNH 21253). The record was reported by Bartels (1937c).
2. South Sumatra Province, Gunung Dempo, 1800 meters: AMNH 106669.
3. West Sumatra Province, Kerinci (also spelled Kurintji), Sungai Kumbang, 1600 meters: RMNH 21254.
4. Aceh Province, Blangbeke: ANSP 20355 (holotype of *atchinus*). Bivouac 5, 7900 feet: ANSP 20356. These localities have been discussed by de Schauensee and Ripley (1939) and Miller (1942).
5. Aceh Province, Atang Poetar (near Lempelam), 1000 meters: MZB 5084. This specimen was first reported by Chasen (1939–

TABLE 24
Measurements (in Millimeters) of Adult *Sundamys infraluteus* and *Sundamys maxi*[a]

Measurement	*S. infraluteus*		*S. maxi*
	Sabah	North Sumatra	West Java
Length of head and body	258.5 ± 17.5 (10) 229–282	266.0 ± 8.9 (3) 259–276	241.5 ± 16.3 (8) 218–270
Length of tail	315.8 ± 18.4 (10) 289–343	311.7 ± 18.7 (3) 298–333	286.7 ± 16.5 (7) 258–309
Tail/head and body (percent)	122	117	119
Length of hind foot	57.5 ± 1.8 (11) 55–61	58.7 ± 1.5 (3) 57–60	53.1 ± 1.0 (8) 52–55
Length of ear	24.8 ± 1.6 (10) 22–27	25.7 ± 2.9 (3) 24–29	25.4 ± 1.4 (7) 24–28
Greatest length of skull	60.9 ± 2.1 (13) 55.9–63.3	61.9 ± 1.1 (3) 60.9–63.0	58.7 ± 2.5 (6) 56.3–61.7
Zygomatic breadth	30.2 ± 1.5 (14) 28.2–32.8	32.0 ± .4 (3) 31.7–32.4	28.9 ± 1.5 (8) 28.3–30.9
Interorbital breadth	8.4 ± .4 (14) 7.8–9.1	8.5 ± .4 (3) 8.1–8.8	8.1 ± .5 (7) 7.5–8.8
Length of nasals	24.8 ± 1.3 (13) 22.3–26.4	24.9 ± .3 (3) 24.7–25.2	23.3 ± 1.6 (7) 21.4–25.7
Length of rostrum	20.0 ± .9 (13) 18.3–21.2	21.0 ± .5 (3) 20.4–21.3	19.1 ± 1.0 (7) 18.1–21.0
Breadth of rostrum	10.9 ± .6 (14) 10.1–11.7	11.3 ± 1.0 (3) 10.2–12.2	11.1 ± .7 (7) 10.5–12.5
Breadth of braincase	21.4 ± .7 (14) 20.2–22.5	22.5 ± .5 (3) 22.1–23.1	21.0 ± .5 (8) 20.0–21.8
Height of braincase	15.5 ± .8 (14) 14.1–16.7	15.5 ± .7 (3) 14.9–16.2	15.3 ± .6 (7) 14.4–16.3
Breadth across incisor tips	4.5 ± .3 (10) 3.9–4.9	4.8 ± .3 (3) 4.5–5.0	4.5 ± .4 (8) 4.1–5.2
Breadth of zygomatic plate	7.2 ± .5 (14) 6.2–8.2	7.5 ± .3 (3) 7.2–7.7	6.7 ± .5 (8) 6.1–7.4
Depth of zygomatic notch	2.9 ± .4 (14) 2.2–3.7	2.9 ± .1 (2) 2.8–2.9	— —
Length of diastema	16.9 ± 1.1 (14) 14.6–18.7	17.3 ± .3 (3) 16.9–17.5	15.9 ± .7 (7) 15.1–16.9
Palatal length	33.0 ± 1.5 (14) 29.8–35.2	33.7 ± .7 (3) 33.2–34.5	31.3 ± 1.0 (7) 30.0–32.7
Postpalatal length	19.8 ± 1.1 (14) 18.1–21.3	20.6 ± .4 (3) 20.3–21.1	— —
Length of incisive foramina	9.5 ± .4 (14) 8.8–10.1	10.7 ± .3 (3) 10.5–11.0	10.1 ± .4 (7) 9.6–10.8
Breadth of incisive foramina	3.9 ± .2 (14) 3.5–4.3	3.8 ± .1 (3) 3.8–3.9	3.9 ± .4 (7) 3.2–4.3
Length of palatal bridge	13.9 ± .8 (14) 12.1–15.0	13.0 ± .4 (3) 12.6–13.4	12.0 ± .4 (7) 11.4–12.5
Breadth of palatal bridge at M^1	5.1 ± .3 (14) 4.7–5.7	6.5 ± .1 (3) 6.4–6.5	5.2 ± .6 (8) 4.2–5.7
Breadth of palatal bridge at M^3	7.2 ± .5 (14) 6.5–7.7	7.6 ± .4 (3) 7.3–8.0	6.5 ± .5 (8) 5.7–7.2

TABLE 24—(*Continued*)

Measurement	*S. infraluteus*		*S. maxi*
	Sabah	North Sumatra	West Java
Breadth of mesopterygoid fossa	4.7 ± .3 (14) 4.1–5.4	4.7 ± .3 (3) 4.4–4.9	4.7 ± .2 (8) 4.4–5.0
Length of bulla	6.8 ± .4 (14) 6.2–7.7	7.0 ± .4 (3) 6.8–7.5	7.4 ± .4 (8) 6.5–7.9
Height of bulla	5.9 ± .2 (11) 5.7–6.2	5.4 ± .2 (2) 5.2–5.5	5.8 ± .5 (8) 5.1–6.7
Alveolar length of M^{1-3}	11.0 ± .3 (14) 10.6–11.6	11.5 ± .3 (3) 11.2–11.7	10.8 ± .3 (8) 10.5–11.1
Breadth of M^1	3.2 ± .2 (13) 3.0–3.5	3.3 ± .1 (3) 3.2–3.4	3.1 ± .1 (8) 2.9–3.2

[a] Mean plus or minus one standard deviation, size of sample in parentheses, and observed range are listed for each measurement.

1940, p. 497) and later listed by Sody (1941, p. 290). Information about the locality can be found in Chasen and Hoogerwerf (1941).

DESCRIPTION: *Sundamys infraluteus* is a large, long-tailed, dark brown animal with dense, shaggy fur (fig. 44). It is among the largest of the rats known from Borneo and Sumatra. Measurements of head and body, tail, hind feet, and ear of adults from Sabah and Sumatra are listed in table 24. We have weights from only two adults, both taken in Atjeh, northern Sumatra: 643 grams from a male (ANSP 20355) and 521 grams from a female (ANSP 20356).

Upperparts of the head and body of adults are rich, dark brown mingled with buff flecking over the shoulders and back with a strong buffy wash along sides of the body. In certain lights the pelage appears flecked with glistening brass highlights against a deep brown, shaggy background. The fur is thick and long; overhairs extend to 20 mm. and long black guard hairs reach 35 mm.

The chin is dark brown but the rest of the underparts, from throat to inguinal area, is gray and tinged with pale buff in samples from Sumatra, extensively washed with rich, deep, buffy orange in the rats from Borneo. In overall appearance, specimens from Borneo have ochraceous underparts suffused with gray while the Sumatran rats have definite gray underparts that are slightly suffused with pale buffy hues.

The ears are small relative to size of head and body, blackish brown, and inconspicuously haired.

Shapes of the front and hind feet are similar to the feet in *Sundamys muelleri.* Dark brown fur covers the tops out to bases of the digits. The hairless palmar and plantar surfaces are brown and consist mostly of large and fleshy pads; there are four interdigital plantar pads and two metatarsal pads on each hind foot.

The tail is longer than the combined lengths of head and body. It is dark brown all over, covered with short hairs, and has 8 or 9 rows of scales per cm. (counted on tails of adults about one-third the distance from the rump).

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

The ears, feet, and tail of juveniles are pigmented like those of adults. Juvenile fur is very long, thick, and shaggy. Its texture is softer than that of adults and its color is darker. The overall tone is rich, dark brown without the brassy highlights of the adult coat. In the sample of *S. infraluteus* from Sabah, rats with skulls longer than 56 mm. are in full adult pelage. The molt from juvenile to adult coat occurs when head and body length of 200 mm. is attained and skull length of 50–55 mm. is reached. The juvenile cranium is shown in figure 51 and contrasted there with that from an adult, and with the cranium from an animal of intermediate size and age, one that is typical of the time when the molt from juvenile to adult pelage takes place. We do not have data for minimal body sizes of

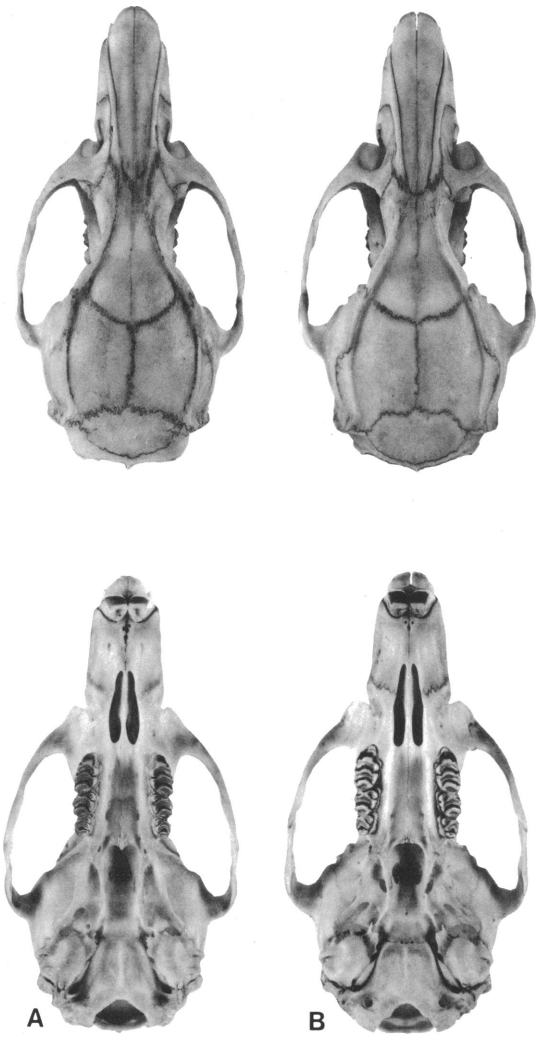

FIG. 46. Views of crania from adult *Sundamys infraluteus*. A, Sabah (USNM 292740). B, Aceh, northern Sumatra (ANSP 20356). Note the larger teeth and longer incisive foramina in the Sumatran example. Both ×10.

adult *S. infraluteus* from Sumatra. Either large adults or rats in full juvenile pelage comprise the sample from that island. We have not seen any young adults in which the molt from juvenile to adult coat had just been completed.

The cranium of adult *Sundamys infraluteus* is large, compact, and stocky. Cranial measurements of specimens from Sabah and northern Sumatra are listed in table 24 and a cranium from each sample is shown in figure 46. As viewed from a dorsal perspective, the rostrum and nasals are long and wide. The nasal tips are round. Each nasolacrimal canal is slightly inflated and its sides do not form a large bulge on the rostrum. The zygomatic arches flare out on either side. The dorsal surface of each lacrimal bone is oblong and small relative to size of the cranium. The braincase is wide and deep. Its dorsolateral margins are sculptured by prominent ridges that extend forward along margins of the frontals to the interorbital area where they are thick and high. The occipital region is deep (anterior-posterior length) and part of its dorsal surface is formed by the posterior two-thirds of the interparietal bone. The anterior portion of that bone is nestled between the parietals. The sides of the braincase between the zygomatic roots and temporal ridges are not vertical but slope toward the midline of the cranium, which is clearly evident in figures 46 and 51.

As seen from a lateral view, the top of the skull is flat over the zygomatic arches and gradually curves down over the occiput and the rostrum (fig. 52). The nasals extend anteriorly beyond the rostrum and front faces of the upper incisors. Each zygomatic plate is wide and its spine projects well forward of the dorsal root of each zygomatic arch, a configuration which forms a deep zygomatic notch as seen in dorsal view (fig. 46). Squamosal roots of the zygomatic arch originate relatively high on sides of the braincase. The squamosal bone above each auditory bulla is complete and not perforated by a squamosomastoid foramen; that foramen is confined to the suture between squamosal bone and mastoid. Shape of the outer surface of each mastoid resembles that in *S. muelleri*. The small size of the auditory bulla relative to braincase (table 52) is clearly seen in side view.

In *Sundamys infraluteus* the configurations of the orbits and alisphenoid areas are similar to those in *S. muelleri*. In the orbit, the sphenopalatine foramen is anterior to and separate from the dorsal palatine foramen. In the alisphenoid regions of most specimens, there is a strut of alisphenoid bone forming the lateral wall of the alisphenoid canal. The wall ranges in size from a slender thread to

a wide strut; the strut is not present in a few specimens (figs. 47 and 48; table 15).

The long rostrum and diastema of *S. infraluteus,* its flaring zygomatic arches, and wide braincase are clearly outlined in ventral view. The incisive foramina are short; their posterior margins are anterior to front faces of the first upper molars (table 16). The palatal bridge is long and wide; its posterior rim extends slightly behind the back surfaces of the third upper molars (table 16) in all specimens we examined. Each posterior palatine foramen is opposite the junction of the second and third molar. The mesopterygoid fossa is broad; its walls are nearly intact, breached only by very small sphenopterygoid vacuities (fig. 39C). The configuration of each pterygoid fossa resembles shapes of the fossae in *S. muelleri* (fig. 39). This conformation, along with a large stapedial foramen, indicates the pattern of carotid circulation in the basicranium of *S. infraluteus* to be like that in *S. muelleri* (fig. 56). The bullae are very small relative to size of the cranium. Each eustachian tube is moderately long.

Each dentary in *Sundamys infraluteus* resembles the dentary of *S. muelleri* in shape and bulk but is much larger (fig. 52). The body of the dentary is thick and appears stocky. The coronoid process is prominent but smaller relative to the ramus than are the processes in *S. muelleri.*

Crania from old and young juveniles are shown in figure 51. Those crania are smaller than those of adults, appear fragile, and the interorbital and temporal ridging are less developed. The stocky molar rows are very large relative to cranial size in these young rats.

The upper and lower incisors of *Sundamys infraluteus* are thick and wide. Their enamel layers are deep orange. The uppers emerge from the rostrum at nearly a right angle (orthodont).

The molars are large and high-crowned. The number of roots anchoring each molar, the size of one relative to the other in each row, and the degree one tooth overlaps the one behind are like the number of roots and configurations in *S. muelleri.* The adult and juvenile patterns formed by cusps and ridges on occlusal surfaces of the molars are simple and closely resemble the occlusal patterns in adult and juvenile *S. muelleri* (figs. 41, 49, and 50). Each first upper molar of *S. infraluteus* has three laminae. Each of the first consists of three broadly merged cusps, the third lamina is composed of a large central cusp t8 and smaller labial cusp t9. No cusp t7 occurs on any specimen. There is a spurlike but prominent posterior cingulum at the back of each first upper molar in all the specimens (fig. 40; table 17).

The anterior labial cusp of each first upper molar (t3) is variable in its prominence. It is small, and the front lamina, especially in worn teeth, appears to consist of but two cusps with the labial one represented by only a slight indentation.

Occlusal surface of each second upper molar consists of two anterior cusps and two laminae similar in configuration and size to the second and third laminae on the first molar. Of the anterior cusps, the lingual one (cusp t1) is always large. The opposite labial cusp (cusp t3) is present in most of the specimens of *S. infraluteus* we studied (table 17); it ranges in size among the specimens from being tiny and inconspicuous to large and prominent.

In each third upper molar, the anterior lingual cusp (t1) is large and conspicuous in all the specimens but the anterior labial cusp (t3) is always small and inconspicuous; it is present in all the specimens from Sumatra but in only about one-half of the samples from Sabah (table 17).

Occlusal patterns of the lower molars also resemble those in *S. muelleri* (figs. 41 and 50). Three wide and thick laminae form most of the chewing surface of each first lower molar; there are two thick laminae on the second molar, and two on the third. The laminae are formed from large cusps broadly merged. Their cuspidate origins are not apparent, even in young rats, so broadly have the cusps joined to each other. Only in very young animals in which all the teeth have not erupted are discrete cusps evident and only on some of the laminae (fig. 50D). At the back of each first and second molar is a very large posterior cingulum, oblong in cross section, and located in the middle of the tooth.

The front lamina on each first lower molar is thick (anterior-posterior length) and nearly as broad as the laminae posterior to it (fig. 50). It is formed of broadly merged anterolabial and anterocentral cusps but the medial

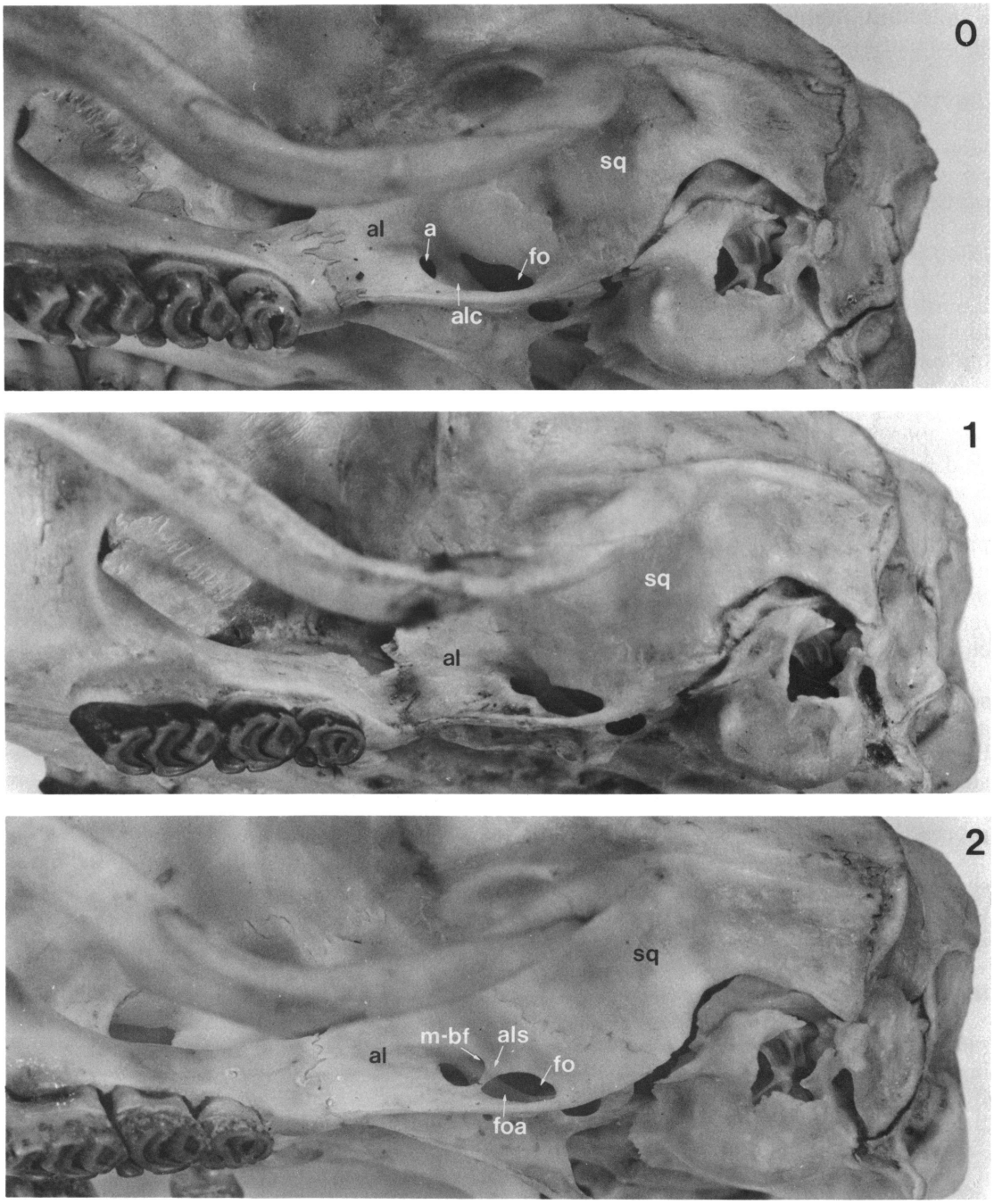

FIG. 47. Views of alisphenoid region in *Sundamys infraluteus*. See figure 48 for explanation.

outlines of these cusps are indistinguishable in most specimens. We could not locate an anterocentral cusp in any specimen. An anterolabial cusp occurs on the second molar in all the specimens but is present on the third molar in only about 60 percent of the sample (table 17).

The cusplets along labial margins of the

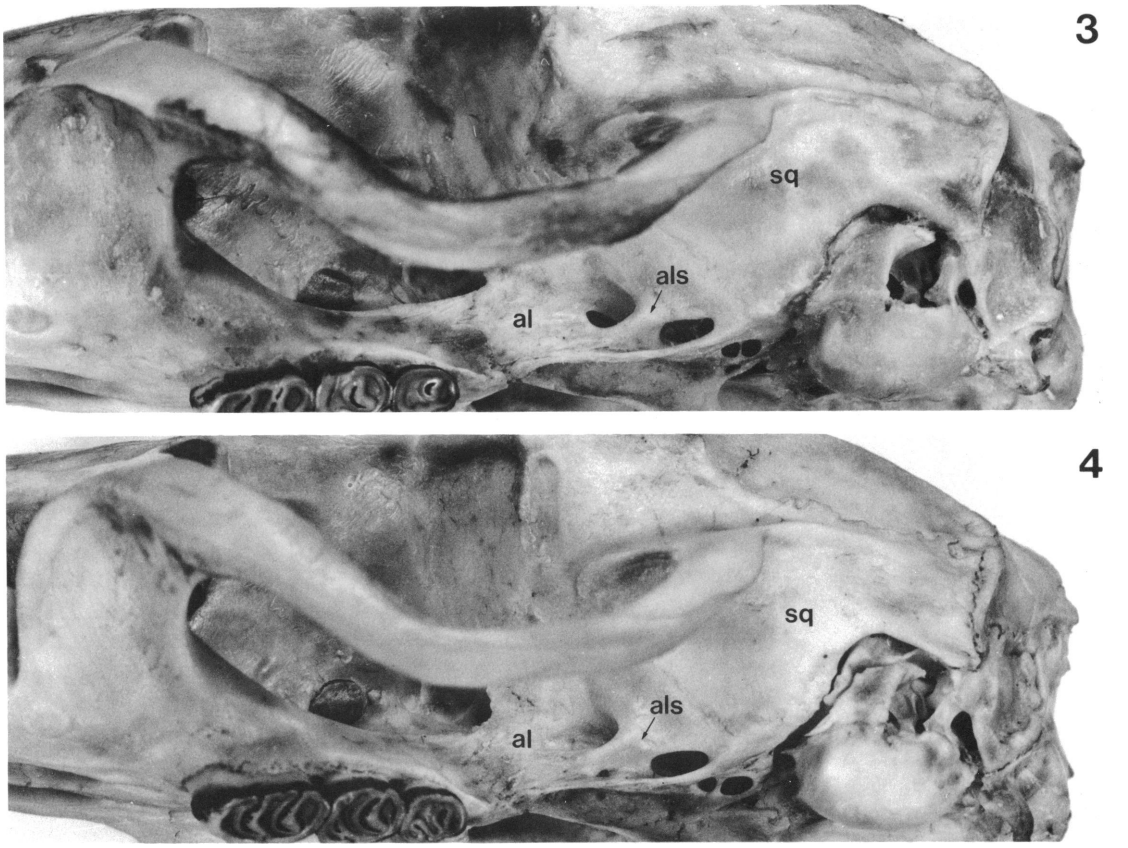

FIG. 48. Views here and in figure 47 illustrate configurations of the alisphenoid region in *Sundamys infraluteus* that were coded 0 to 4, as explained below. **0**, lateral strut of alisphenoid bone (**als**), absent, alisphenoid canal (**alc**) an open channel in the alisphenoid bone (**al**) below the squamosal (**sq**); anterior opening of alisphenoid canal (**a**) and foramen ovale (**fo**) visible (USNM 292764). **1**, alisphenoid strut absent but represented by slight dorsal and ventral extensions from alisphenoid bone (**al**) (FMNH 108932). **2**, lateral wall of alisphenoid canal is a slim strut separating coalesced masticatory-buccinator foramen (**m-bf**) from foramen ovale accessorius (**foa**), which is lateral to the foramen ovale (USNM 292763). **3**, a wide bony strut (**als**) forms lateral wall of alisphenoid canal but strut is not wide enough to conceal anterior opening of the canal (FMNH 108934). **4**, bony alisphenoid strut is so wide it conceals anterior opening of alisphenoid canal (FMNH 108935). Frequencies of these coded states in samples of *S. muelleri, S. infraluteus,* and *S. maxi* are listed in table 15.

molars are large and prominent. An anterior labial cusplet on each first molar is not present but there is a posterior labial cusplet on that tooth in all the specimens. A posterior labial cusplet also occurs on the second lower molar in all the rats (table 17).

NATURAL HISTORY: Very little information is available about habitat or habits of *Sundamys infraluteus.* Lim and Heyneman (1968) reported specimens taken in primary forest at two places: between 4200 and 5400 feet in low montane oak forest and between 7040 and 8900 feet in mossy forest. The two rats from the slopes of Gunung Loeser in Aceh, which Miller (1942) described as *Rattus atchinus,* were taken from moss forest (see descriptions of the camps in de Schauensee and Ripley, 1939).

The little information on diet comes from observations by Lim and Heyneman (1968) and Harrison (1954a) for rats trapped in forest on Gunong Kinabalu and Gunong Trus Madi in Sabah. Lim and Heyneman examined six stomachs of *S. infraluteus*: two were

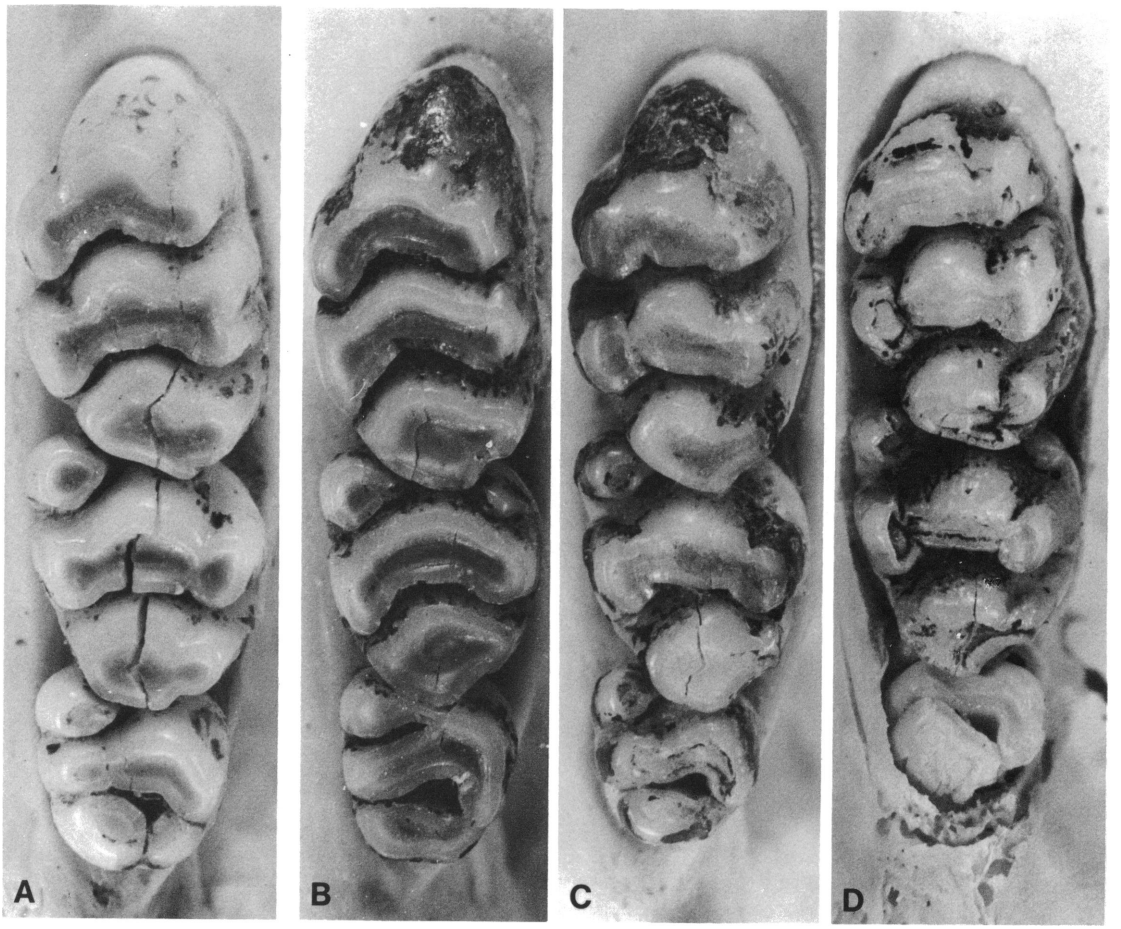

FIG. 49. Occlusal views of left upper molar rows in *Sundamys infraluteus* from Sumatra (A) and Sabah (B–D). A, young adult (AMNH 106669). B, adult (USNM 292764). C, old juvenile (USNM 292769). D, young juvenile (USNM 292762). All ×10.

empty, four had bait, and in one was the partly digested remains of a lizard. Harrison (1954a, p. 160) noted that *S. infraluteus* "replaces *R. mülleri* in the mountains of Borneo. Three specimens examined on Mt. Trus Madi contained nothing but vegetable matter, apparently shoots, twigs and bark."

Much remains to be learned about the ecology of *Sundamys infraluteus* in the forests of northern Borneo and the mountains of Sumatra.

SYMPATRY: In Sabah and Sumatra, *Sundamys infraluteus* lives in mountain forests, *S. muelleri* inhabits forests in the lowlands and the two species overlap in some places. On the slopes of Gunong Kinabalu in Sabah, examples of both species come from Kiau, about 3000 feet, and Bundu Tuhan, about 4200 feet. We have no data indicating whether the two species were caught in the same habitat, or if each was taken from a different habitat at the same locality, or if examples of each kind were actually collected from different places and altitudes but were labeled with the name of the main camp. Our records indicate that *S. infraluteus* occurs between 3000 and 8000 feet on the slopes of Gunong Kinabalu. *Sundamys muelleri,* usually found in lowlands, occurs up to 5400 feet (Lim and Heyneman, 1968). So there is an overlap of 2400 feet between the two species. Just what the differences in habitats and other ecolog-

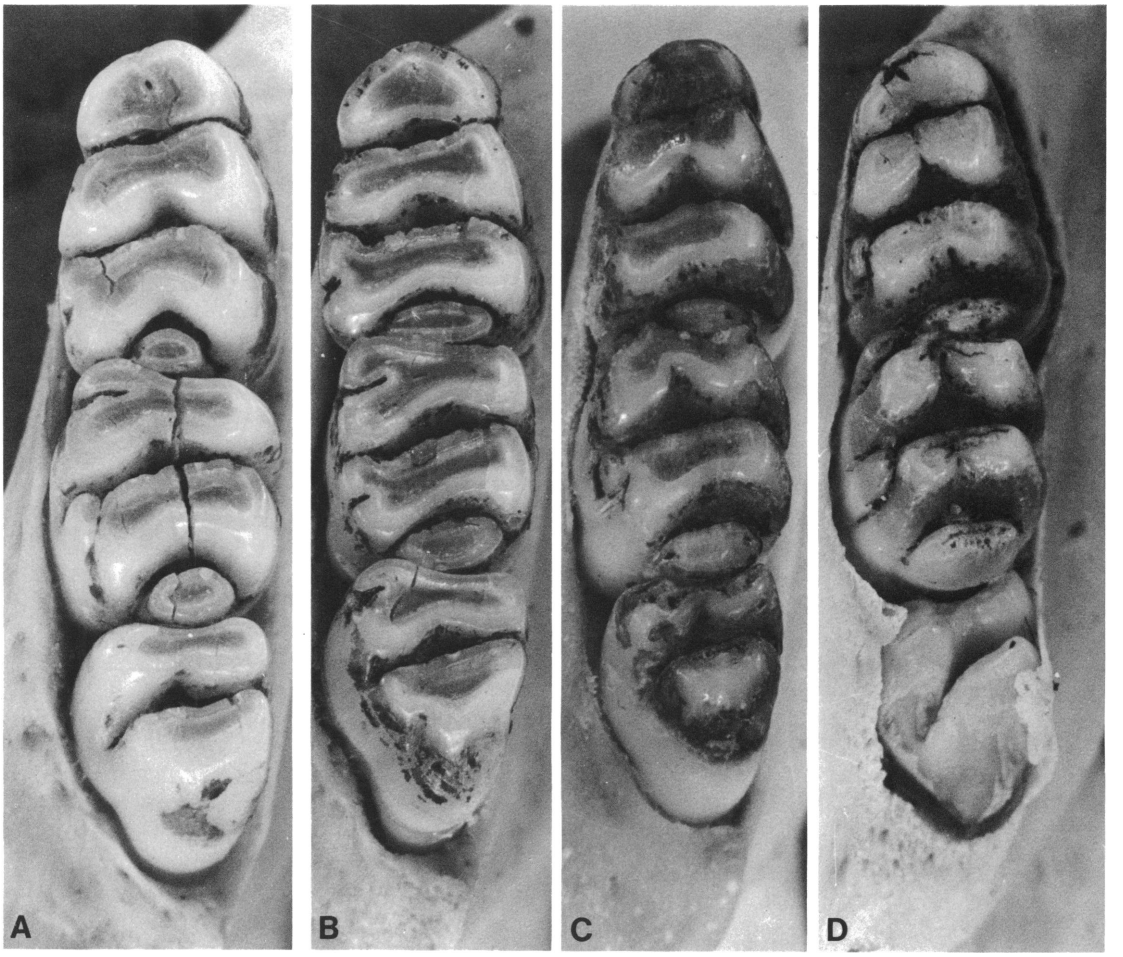

FIG. 50. Occlusal views of left lower molars from same specimens of *Sundamys infraluteus* shown in figure 49. A, Sumatra. B–D, Sabah. All ×10.

ical aspects of the populations of *S. infraluteus* and *S. muelleri* are in this zone is unknown.

In southern Sumatra, *Sundamys infraluteus* and *S. muelleri* were obtained at 700 meters on the east slopes of Gunung Tanggamoes and at 1800 meters on Gunung Dempo. The records from Tanggamoes are scientifically and historically important because the specimens from there were obtained by Max M. Bartels, Jr., a naturalist resident in Java, who spent his life studying birds and mammals of Java and southern Sumatra in their native habitats and who knew the two kinds of rats very well. Bartels (1937c) was the first to document *S. infraluteus* from Sumatra and also recognized, based on his first-hand experience in the forest, that *S. infraluteus* and *S. muelleri* were distinct species. This was new information at the time because the professional naturalist in the region, Chasen, had written to Bartels that *infraluteus* was not a distinct species but merely a montane form of *muelleri,* "the high level representative of *mülleri,*" as Chasen (1940, p. 163) noted in his handlist of Malaysian mammals.

Musser, while working in the Rijksmuseum van Natuurlijke Historie at Leiden in 1969, read the original manuscript of Bartels (1937c) in which the juvenile *S. infraluteus* from Gunung Tanggamoes was recorded. In

that manuscript, Bartels had included a footnote discussing differences between *S. muelleri* and *S. infraluteus* from Tanggamoes. The footnote was not published. We record it here because of its historical significance to study of the Sumatran and Javan faunas, because it points up Bartel's sound contributions to natural history, and because it documents some of the features distinguishing the two species as Bartels understood them from his study of specimens and his experiences in the forests of southern Sumatra.

Bartels first referred to Chasen's opinion, then elaborated these three points:

> 1. Up till now never a rat being *intermediate* between the *mülleri*- and *infraluteus*-groups has been obtained. If the two animals really were only "climatic" forms of one and the same species, as Mr. Chasen supposes them to be, one should expect an intermediate population to occur in the zone where *mülleri* and *infraluteus* meet. This, however, seems not to come true. On Mt. Tanggamoes the one (very "typical") specimen of *infraluteus* was trapped at *exactly the same place* as 17 (likewise quite typical) specimens of *mülleri*. More than this: at an altitude *ca.* 200 m. higher up the same mountain slope we caught two more typical *mülleri*-rats! This shows that the areas of the two forms *overlap* (at least so in Sumatra) without that, apparently, any interbreeding takes place. 2. Whereas true *mülleri*-rats are rather common in Sumatra and Borneo, *no* such animal has as yet been discovered in Java. (If *infraluteus* really were a mountain-subspecies of *mülleri,* then it is not well understood why the latter should not occur, too, in Java.) 3. Besides the differences in the *fur* there exist several other important characters which separate the two groups: a) *infraluteus* has *much larger feet.* The hindfoot of my young Sumatra-specimen with a head-and-body-length of 187.5 mm. measures 51 mm., whereas that of my largest-footed adult specimen of *mülleri* (caught at the same place) with a h.-a.-b.l. of 234 mm. measures only 49 mm. b) in *infraluteus* the feet are *unicolourous,* in *mülleri* they seem always to be more or less lightened on the outer sides. c) *infraluteus* has *larger teeth.* My young specimen (last molar just cutting) has an upper molar row of 10.5 mm., whereas that of the large *mülleri* mentioned above measures only 9.2 mm. d) the upper incisors of my *infraluteus* are *broader,* whereas their *height is less* than in those of my *mülleri.* The lower incisors are broader, too, in *infraluteus,* whilst their *height is about equal* in both species. (As Mr. Chasen informs me (*in litt.*) these differences also come true for the material in the Singapore Museum.) These facts, to my mind, render it rather improbable that we should consider the two groups as conspecific. The more so as on the other hand not one important point in *favour* of Mr. Chasen's view can be brought forward. It may be remembered that none of such large differences do exist in other rats, in which it is beyond doubt that a lowland-form is replaced by a race with longer, softer and denser fur in the mountains.

Our comparisons reflect those noted by Bartels. In Sabah and Sumatra where both *Sundamys infraluteus* and *Rattus muelleri* occur together, the two species can be distinguished by size (tables 19, 22, 24, and 25), color and texture of pelage, number of mammae, and differences in features of skulls and teeth. *Sundamys infraluteus* has a longer body, tail, and ears than does *S. muelleri* of comparable age. The two species are similar in most body proportions with the exception that specimens of *S. infraluteus* from Sabah have tails that are longer relative to head and body than examples of *S. muelleri.* And, although the ears of *S. infraluteus* from both Sabah and Sumatra are absolutely larger than those of *S. muelleri,* they are much smaller relative to body size. (Our statements of comparative proportions derive from ratio diagrams prepared for samples of *S. infraluteus, S. muelleri,* and *S. maxi.* We do not include those diagrams here; they are filed in the Department of Mammalogy at the American Museum of Natural History.)

Adult *Sundamys infraluteus* have darker, thicker, and longer pelage than adult *S. muelleri.* The pelage appears dark and thickly shaggy, whereas the fur of *S. muelleri* is less dense and appears sleek. Underparts of *S. infraluteus* are always gray and suffused with either orange buff in samples from Sabah or pale buff in those from Sumatra. Examples of *S. muelleri* have white, cream, or buffy underparts that may be either plain or suffused with gray over the abdomen and chest. Juvenile *S. infraluteus* have very long, thick, and dark brown pelage that is shaggy like the adults. In contrast, juvenile *S. muelleri* have dark grayish brown fur that is short, dense, and woolly, not shaggy.

Female *Sundamys infraluteus* have three

TABLE 25
Selected Measurements (in Millimeters) Contrasting Adult *Sundamys infraluteus* with *Sundamys muelleri*[a]

Measurement	Sabah		Sumatra	
	S. infraluteus	*S. muelleri*	*S. infraluteus*	*S. muelleri*
Length of head and body	258.5 ± 17.5 229–282 (10)	207.7 ± 11.1 188–240 (22)	266.0 ± 8.9 259–276 (3)	207.3 ± 17.1 185–236 (23)
Length of tail	315.8 ± 18.4 289–343 (10)	247.4 ± 14.7 212–271 (22)	311.7 ± 18.7 298–333 (3)	260.6 ± 24.6 214–301 (22)
Length of hind foot	57.5 ± 1.8 55–61 (11)	40.9 ± 1.9 37–45 (22)	58.7 ± 1.5 57–60 (3)	45.3 ± 2.2 42–49 (23)
Greatest length of skull	60.9 ± 2.1 55.9–63.3 (13)	50.4 ± 1.9 46.4–53.9 (21)	61.9 ± 1.1 60.9–63.0 (3)	51.1 ± 3.3 45.7–58.8 (23)
Breadth across incisor tips	4.5 ± .3 3.9–4.9 (10)	3.6 ± .2 3.1–4.1 (21)	4.8 ± .3 4.5–5.0 (3)	3.5 ± .3 2.8–4.0 (23)
Alveolar length of M^{1-3}	11.0 ± .3 10.6–11.6 (14)	9.1 ± .4 8.2–10.0 (21)	11.5 ± .3 11.2–11.7 (3)	9.7 ± .5 8.6–10.7 (23)

[a] Mean plus or minus one standard deviation, observed range, and number of specimens in parentheses are listed for each measurement. Values are extracted from tables 19, 22, and 24.

pairs of mammae: one postaxillary and two inguinal. Female *S. muelleri* have four pairs: three in the same position as *S. infraluteus* and a pectoral pair. Among the specimens we examined, we did not see any variation in either position of the mammae or number.

Most dimensions of the skull in samples of *S. infraluteus* from Sabah and Sumatra are significantly greater than in samples of *S. muelleri* from the same islands (compare tables 19, 22, 24, and 25). The magnitude of this difference in size can be visualized by looking at figure 51 where we contrast an adult, an old juvenile, and a young juvenile of *S. infraluteus* from Gunong Kinabalu with three *S. muelleri* of about the same ages from the same region. Although the two species differ conspicuously in size where they occur together (table 25), they are proportionally similar with these exceptions: compared with *S. muelleri,* the rostrum of *S. infraluteus* is narrower relative to its length; the braincase is higher relative to its breadth; the incisive foramina are wider relative to their lengths; the bony palate is longer relative to lengths of incisive foramina, diastema, and postpalatal length, and its anterior margin is much narrower relative to the breadth of its posterior margin; the zygomatic notch is shallower relative to breadth of the zygomatic plate, or to any other cranial measurement except those of the bullae; and the bullae are smaller relative to any other cranial dimension.

There are other cranial differences between the two species. In specimens of *Sundamys infraluteus,* posterior margins of the incisive foramina are anterior to front faces of the first upper molars (clearly seen in figs. 39 and 51); in the sample of *S. muelleri* from Sabah, the posterior margins of the foramina may be anterior to the molars, even with them, or extend slightly posterior to them (table 16; figs. 39 and 51). Most specimens of *S. infraluteus* and *S. muelleri* have a lateral strut of alisphenoid bone forming the outer wall of the alisphenoid canal. In the sample of *S. infraluteus,* the width of the strut ranges from a slender threadlike support (code 1; fig. 47) to a wide bony wall concealing the canal and

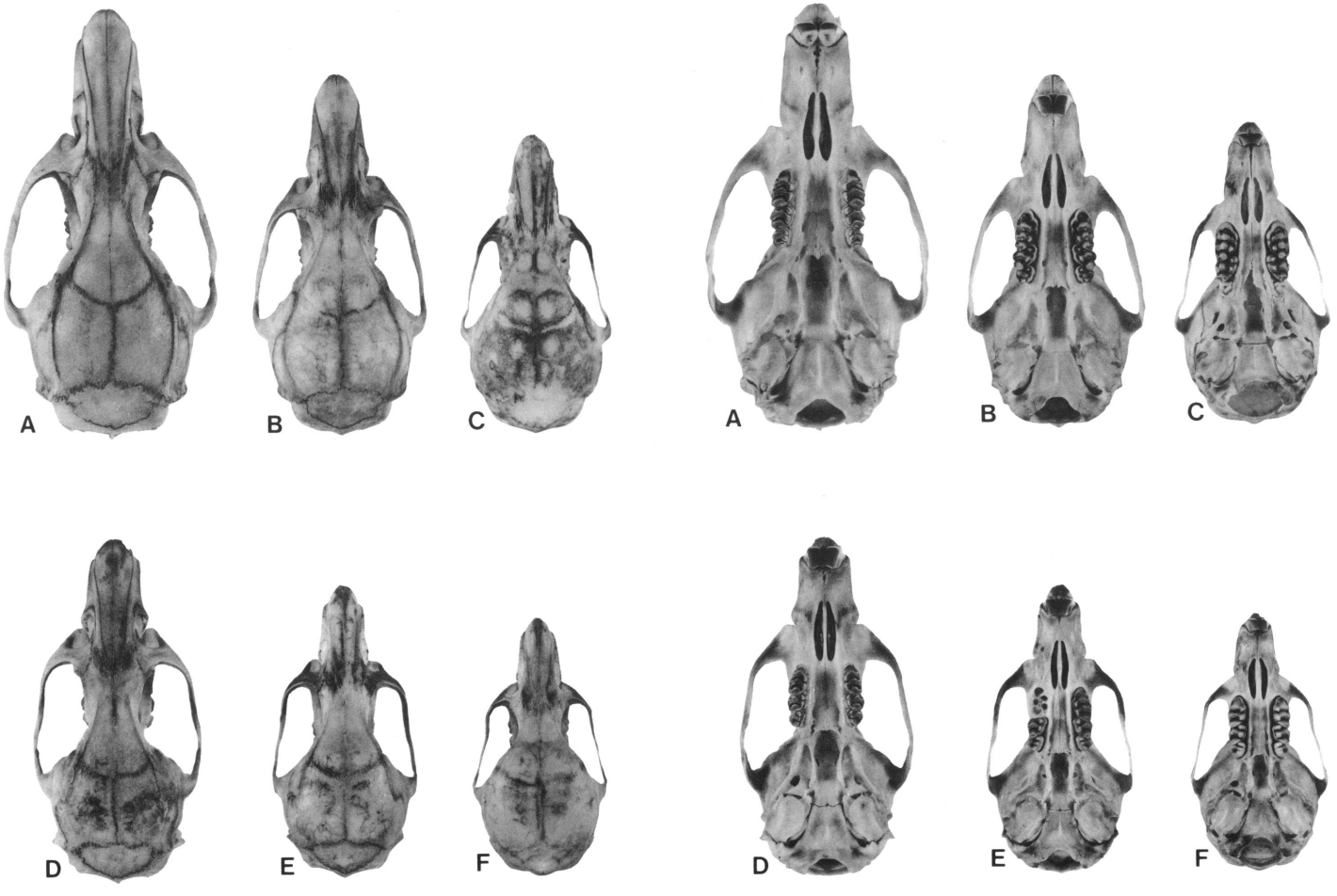

FIG. 51. Views of crania contrasting *Sundamys infraluteus* (top row) with *S. muelleri* (bottom row) from Bundu Tuhan, Mount Kinabalu, Sabah. *S. infraluteus*: A, adult (USNM 292759); B, young adult-juvenile (USNM 292769); C, juvenile (USNM 292762). *S. muelleri*: D, adult (USNM 292740); E, young adult-juvenile (USNM 292742). F, juvenile (USNM 292739). Natural size.

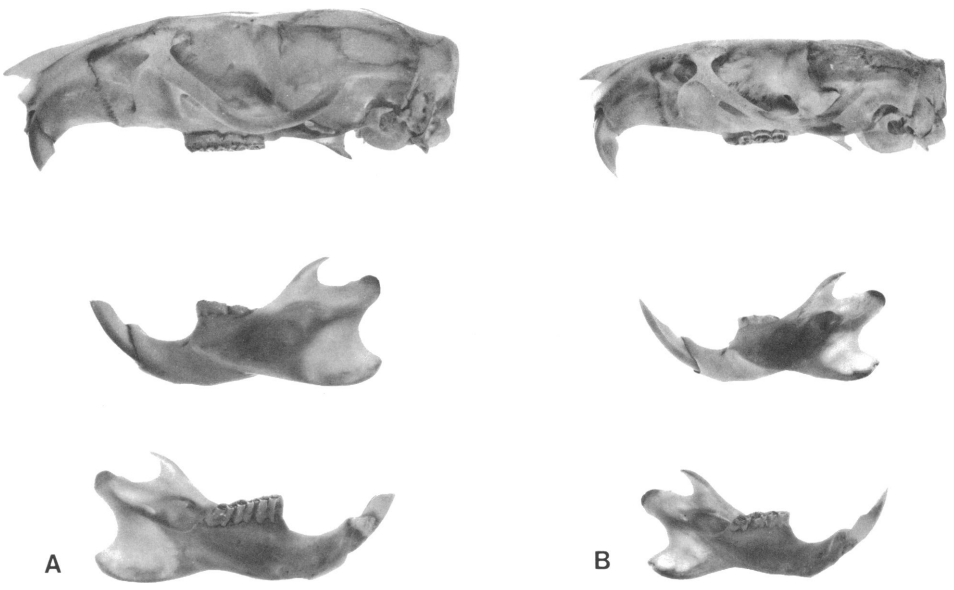

FIG. 52. Views of crania and dentaries contrasting *Sundamys infraluteus* (A, USNM 292759) with *S. muelleri* (B, USNM 292740). Both specimens are from Bundu Tuhan, Mount Kinabalu, Sabah. Natural size.

foramina (code 4; fig. 48); of the four expressions of strut size that we coded, there are about as many specimens for each of them (table 15). In samples of *S. muelleri,* however, most specimens have a wide strut (codes 3 and 4; fig. 48) and very few (2 out of 377) have the threadlike conformation (table 15). The sphenopterygoid vacuity perforating each pterygoid plate is either not present or tiny in all specimens of *S. infraluteus.* In contrast out of 100 examples of *S. muelleri* from all over Borneo only 17 lack the vacuity, and it ranges in size from tiny to large in the rest of the sample (table 15). Finally, the mesopterygoid fossa in each specimen of *S. infraluteus* is breached by very small (both absolutely and relative to cranial size) sphenopalatine vacuities; the vacuities in examples of *S. muelleri* are actually and relatively much larger: the contrasting configurations are clearly evident in figure 39.

The incisors and molars of *S. infraluteus* are larger than those of *S. muelleri*; this difference is conspicuous among samples of all ages (table 25; figs. 39, 48, 49, and 51). Although the molar rows of *S. infraluteus* are absolutely longer than molar rows of *S. muelleri,* they are proportionally similar relative to length of skull but significantly shorter relative to length of bony palate. Each first upper molar of *S. infraluteus* is longer relative to its width than in *S. muelleri.* And the incisors of *S. infraluteus* are wider relative to breadth of the rostrum. Most of these proportional differences can be seen in the crania illustrated in figure 51.

The frequency of occurrence of certain cusps and cusplets differs between the two species (table 17; values listed there are combined from all the insular samples of *S. infraluteus* and all the peninsular and insular samples of *S. muelleri,* but the relative frequencies of occurrence of cusps and cusplets within the sample of each species from Sabah is similar to that in the combined samples). Examples of *S. infraluteus* have a posterior cingulum on each first upper molar; a comparable cusp occurs in only half the sample of *S. muelleri.* Cusp t3 is present on each third upper molar in only half the sample of *S. infraluteus* but occurs in most specimens of *S. muelleri.* Finally, none of the *S. infraluteus* we examined had anterior labial cusplets on the first lower molars but comparable

cusplets are found in about half the sample of *S. muelleri.*

INSULAR VARIATION AND SUBSPECIES: Samples of *Sundamys infraluteus* from Sabah and Sumatra are distinguished from each other by a combination of pelage coloration and absolute and relative size of certain external and cranial dimensions. The differences between the samples are consistent and significant.

Color of pelage varies between island samples of adults. Upperparts of the rats from Sabah are rich brown flecked with buff; the coat is much darker and washed with brighter and richer hues than is the fur on rats from Sumatra. The effect results from bicolored hairs which have dark gray bases and either bright buffy or orange tips. That buffy wash so prominent in Bornean rats is subdued in the Sumatran sample: adults have pale buffy yellow highlights. Specimens from Sumatra have pale underparts: soft pale gray tinged with pale buff, a striking contrast to the rich buffy orange and gray of the animals from Sabah. The hairs have gray bases and pale buff tips.

Absolute sizes of external, cranial, and dental dimensions of the specimens vary between the islands. The sample from Sumatra, however, is small and we do not know if characteristics of the three adults we examined from there are a reliable estimate of the population. If they are, the Sumatran rats are distinctive in that they have wider zygomatic plates, a larger braincase, wider and shorter palatal bridge, shallower bullae, longer incisive foramina, and longer molar rows than do animals from Sabah (table 24).

Rats from Sabah and Sumatra also differ in certain proportions. Compared with the Sabah sample, the Sumatran specimens have rostra that are wider relative to their lengths, incisive foramina that are narrower relative to their lengths and to length of skull, a palatal bridge wider relative to its length, the breadth of skull across zygomatic arches greater relative to length of skull, bullae that are shallower relative to their lengths, and first upper molars shorter relative to their breadths and to lengths of molar rows.

If the Sabah and Sumatran populations should be identified by subspecific names, *Sundamys infraluteus infraluteus* applies to the Sabah rats and *S. i. atchinus* is the name for the Sumatran animals. Among murids native to the Sunda Shelf, the pattern of insular distribution and morphological variation in *S. infraluteus* is found only in *Rattus baluensis,* which occurs on Gunong Kinabalu in Sabah and mountains in the Korinchi region of western Sumatra (see our account of the Palawan rat).

Sundamys muelleri has never been recorded from Java but there is a large-bodied rat native to that island which has always been closely associated with *S. infraluteus* (Sody, 1932; Bartels, 1937c; Chasen, 1940). The sample we examined has pelage characters resembling *S. infraluteus,* some cranial and dental features that are similar to *S. infraluteus* but many that recall *S. muelleri,* and other characters that are unique. The Javan animal is distinctive in morphology and not just an island variant of either *S. muelleri* or *S. infraluteus.* We discuss it below.

Sundamys maxi

Sundamys maxi was named and described by Sody in 1932 under the name, *Rattus maxi.* That taxon was based on three specimens from Tjiboeni, near Bandung in western Java. According to Sody (p. 157), "These specimens were collected by the well known ornithologist, Mr. Max Bartels Jr., who presented them to me, after he himself having at once recognized them as belonging to a species new for Java. Therefore in all respects the honor of having enriched—so shortly after his return from Europe—the Java list of mammals with such an extremely fine and interesting species belongs to the collector." In his diagnosis of *maxi* Sody wrote that

> This large species shows a superficial likeness with the bandicoot-rats and with *Rattus mülleri.* In reality, however, it is so well distinguished from both these forms, that no special distinguishing characters need to be given here. Amongst all the known rats of the Soenda isles and of the Malay Peninsula there appears to be the only one, which seems to approach this new rat rather closely, viz. *Rattus infraluteus* Thos. from Kina Balu, Borneo. Unfortunately our knowledge of this species is not very thorough. Besides the type only one other specimen has been mentioned in the literature, viz. by Gyld-

> enstolpe. Besides the characters in common, however, there are also rather large differences between the two forms. I cannot decide with certainty whether these differences are of specific or of subspecific significance, and therefore, for the present, the Javanese form may be considered as a distinct species.

Bartels (1937c, p. 124) later commented on Sody's new species in a paper where he described new taxa and reported new records from the Lampung District of southern Sumatra:

> In 1932 Sody described, as *R. maxi,* a large dark-coloured rat from the mountains of W. Java, of which he stated that, though the animal bears some (rather superficial!) resemblance to the *mülleri*-group, the only rat with which it could eventually prove to be conspecifically allied was *R. infraluteus* Thos. from Borneo. As, however, Sody could not examine a specimen of this, rare (not easily trapped), species, he judged it better, for the time being, to leave the question there. From Mr. Chasen, Singapore, I lately received a fine specimen (skin and skull) of *infraluteus* and, after careful comparison, feel sure that Mr. Sody was quite right in his supposition. *R. maxi* (of which, besides Mr. Sody's types, I caught 19 more specimens (ad. and juv.) 18 of which are in my collection) certainly is a subspecies of *infraluteus* from which it seems to differ principally in the general colour of the upperparts being more greyish and in the belly being purely greyish without any yellowish tinge. I, therefore, call the Javan rat *R. infraluteus maxi.*

Bartels's allocation of *maxi* was followed by Chasen (1940) who listed *maxi* as a subspecies of *R. infraluteus* in his handlist of Malaysian mammals. At about the same time, Ellerman (1941) entered both *R. infraluteus* and *R. maxi* as species in his checklist; it was not until 1949 that he relegated *maxi* to a subspecies of *R. infraluteus,* an allocation unchanged through the years.

The Javan population is not a subspecies of *S. infraluteus.* It is a distinctive species and part of a unique fauna of murids that are endemic to Java (Musser, 1981c). Below, we describe *S. maxi* in the framework of contrasting it with *S. infraluteus* and *S. muelleri.*

SPECIMENS AND LOCALITIES: Our definition of *Sundamys maxi* is based on 21 specimens from the mountains of western Java. All were obtained by Max Bartels, Jr., from between 900 and 1350 meters during the period, 1932 to 1935. We know of no other examples collected since 1935. Specimens and the places they were caught are listed below and shown on the map in figure 45.

1. Tjiboeni, Bandung, 1350 meters: Sody No. Tjib. 13 (holotype of *maxi*), 56, and 99 (all in the RMNH).
2. Southwest slopes of Gunung Pangrango-Gede: Pasir Datar, 1000 meters, RMNH 13576, 13566, 13535, 13968, 14061, and 14208–14211; Tjiparaj, 900–1000 meters, RMNH 13734, 13746, 14060, 14099, 14125, 14205, and 14207; Sitoe Goenoeng (Situ Gunung), 1200 meters, RMNH 14181; Tjimahi, RMNH 14206.

DESCRIPTION AND COMPARISONS: *Sundamys maxi* is a large brownish gray rat with a tail longer than combined lengths of head and body. Its body proportions are similar to those of *S. infraluteus* and the large-bodied *S. muelleri* from the Malay Peninsula. Judged from most of the external measurements, body size of *S. maxi* is closely similar to the Malayan *S. muelleri* (compare tables 19 and 24). Compared with samples of *S. infraluteus,* the Javan rats are significantly smaller in most dimensions and have a shorter head and body, tail, and hind feet (table 24).

The fur of *Sundamys maxi* is softer than that of *S. infraluteus,* not so coarse and shaggy, a feature also pointed out by Sody (1932, p. 157). The texture is more like the fur of *R. muelleri* than *R. infraluteus.* Sody described the color of *S. maxi* as "dark speckled grey on the dorsal side (darkest on the middle of the back and especially on the head), the belly lighter grey, not sharply defined." Sody only had two specimens, but Bartels (1937c) collected and examined firsthand 20 rats and his description of the fur coloration agrees with that provided by Sody. Bartels noted that the underparts were pure gray without yellowish wash. When we examined the specimens of *S. maxi,* upperparts were speckled brownish gray but the underparts were dark gray washed with pale yellowish buff. We do not know whether that yellowish buff tinge is discoloration or was simply not noticed by Bartels. Overall, *S. maxi* has paler fur than does *S. infraluteus,* especially over the underparts. The ears, front and hind feet, and tail in *S. maxi* are dark brown.

TABLE 26
Features Associated with Age in 18 *Sundamys maxi* from Western Java

RMNH No.	Sex	Pelage	Measurements (mm.)[a] LHB	LT	LHF	LE	GLS	Eruption of M^{3}[b]
14205	M	Adult	270	289	54	28	61.7	Complete
14181	M		238	287	53	25	57.2	
14211	M		229	—	53	—	58.9	
13576	F		230	282	52	25	—	
14206	F		248	258	52	26	56.3	
14210	M	Mostly adult	218	280	53	24	56.4	Complete
13566	F	Mostly juvenile	204	259	50	25	53.1	
14207	F	Mostly juvenile	201	266	51	24	52.1	
13746	F	Juvenile	181	239	48	24	48.1	Complete
14209	F		169	211	46	23	—	
14208	M		180	226	47	24	—	
14099	F		178	230	48	24	—	To ¾ height of M^{1-2}
14061	F		161	205	43	22	45.1	Broken through bone, no higher
13968	M		159	207	45	22	—	
13635	F		154	178	42	22	—	
14125	F		152	192	42	22	—	
14060	M		150	202	44	21	—	
13734	F		144	157	39	22	41.1	Not yet broken through bone

[a] *Abbreviations:* LHB, length of head and body; LT, length of tail; LHF, length of hind foot; GLS, greatest length of skull.

[b] The first and second upper molars had completely erupted in all the juveniles.

Female *Sundamys maxi* have four pairs of mammae, the same number and in similar positions as the mammae in *S. muelleri*. *Sundamys infraluteus* differs from both of these species in having only three pairs of mammae.

The characteristics of *Sundamys maxi* we described and illustrated are those of adults. Some information about juveniles is available, contained in a series from the southwestern slopes of the Pangrango-Gede volcanos in western Java, a sample containing the range of ages from adults to very young juveniles. The 18 animals were collected by Bartels during 1934 and 1935. These specimens are listed in table 26, the oldest at the top and the youngest at the bottom. We arranged them using features of size, pelage, eruption and wear of molars, and cranial configuration. The juvenile skull is shown in figure 53 and contrasted there with the adult cranium and with the cranium from a rat of intermediate size and age, one that represents the size when the molt from juvenile to adult pelage occurs.

Five of the 18 are adults, rats in full adult pelage with skulls longer than 56 mm. Three of the 18 specimens were molting from juvenile to adult pelage when they were caught. The other ten are clothed in juvenile fur. Juvenile pelage resembles that of adults but is finer and feels softer to the touch. The underfur over upperparts of head and body is woolly. The color is darker and duller than in adults, especially on the underparts, which are usually dark gray.

All molars had completely erupted by the time the rats reached a head and body length of 180 mm. and a skull length of more than 45 mm. The rats molt from juvenile to adult pelage when the head and body has reached 200 mm. and the greatest length of the skull is longer than 50 mm.

Crania from an adult *Sundamys maxi* and two juveniles of different ages are shown in figure 53. Views of an adult cranium of *S. maxi* are contrasted with views of adult Sumatran *S. infraluteus* and Malayan *S. muelleri* in figure 54. The cranium of *S. maxi* is large and sturdy. Large size is the primary

feature linking *maxi* to *infraluteus*. Mean values of most cranial and dental measurements in the sample of *S. maxi* are not significantly different from those in the series of *S. infraluteus* from Sumatra and Sabah. Samples of *S. maxi* do differ significantly from samples of the other two by having a shorter skull that is narrower across the zygomatic arches; narrower zygomatic plates; shorter nasals, rostrum, diastema, palate, palatal bridge, and toothrows; but longer bullae.

There are also proportional differences between the species. Compared with samples of *Sundamys infraluteus,* specimens of *S. maxi* have incisive foramina that are wider relative to their lengths, a palatal bridge that is narrower relative to its length, and a zygomatic breadth that is less relative to length of skull. These proportional differences can be seen in figure 54.

The skulls of *Sundamys maxi* are much larger compared with those in all the samples of *S. muelleri* except that from the Malay Peninsula (compare table 24 with tables 19–23). *Sundamys maxi* averages larger than Malayan *S. muelleri* in many cranial measurements. The differences are barely statistically significant and all reflect size: the skulls of *S. maxi* are slightly larger than skulls of Malayan *S. muelleri* but the average differences are present only when samples of each species are compared. Adult *S. maxi* and adult Malayan *S. muelleri* of comparable age are nearly indistinguishable from one another in cranial dimensions. Two features, however, are consistently different no matter whether samples or individuals are compared. *Sundamys maxi* has wider incisors and longer molar rows than does Malayan *S. muelleri.*

The basic configuration of the cranium of *Sundamys maxi* resembles that in both *S. infraluteus* and *S. muelleri* except that its proportions are more like those characteristic of *S. muelleri.* The wide rostrum, narrow interorbital region, narrow cranium and braincase, long incisive foramina, and narrow palatal bridge combine to form a configuration resembling that in skulls of *S. muelleri* more closely than in crania of *S. infraluteus.* The wide incisive foramina of *M. maxi,* each parallel to the other and each similar in shape is characteristic of the configuration in skulls of *S. muelleri* and unlike the incisive foramina in *S. infraluteus,* which are broad in their posterior third and become narrower anteriorly; the two different shapes are evident in figure 54. The sphenopalatine vacuities in each mesopterygoid fossa of *S. maxi* are moderately large and their size relative to the skull resembles the conformation in *S. muelleri,* not the proportions in *S. infraluteus* where the vacuities are very small relative to skull size (compare fig. 39 with 55). Finally, most examples of *S. maxi* have a wide strut of alisphenoid bone forming the lateral wall of each alisphenoid canal, a condition more similar to that in *S. muelleri* than *S. infraluteus* (table 15; compare figs. 38, 47, 48, and 55).

There are two cranial characters that distinguish specimens of *Sundamys maxi* from either *S. infraluteus* or *S. muelleri.* One is the frequency of the sphenopterygoid vacuities that breach the pterygoid plates. All specimens of *S. maxi* we examined have medium- or large-sized vacuities. In most specimens of *S. infraluteus* and *S. muelleri,* the vacuities are either absent or very small (table 15; figs. 39 and 55).

The second character is the pattern of the carotid circulation in the basicranium as reflected by the nature of each stapedial foramen and the shape of the posterior one-third of each pterygoid plate. Every specimen of *S. maxi* has the arterial pattern diagrammed in figure 56. The common carotid artery gives off a very small stapedial artery that passes through a tiny stapedial foramen into the otic region. The stapedial artery ends in the otic area and does not exit from the bullar capsule through the middle lacerate foramen as the internal maxillary artery. Instead, the internal maxillary artery branches from the common carotid after that vessel passes into the cranial cavity through the carotid canal. After it branches from the common carotid, the internal maxillary passes through a foramen, the posterior opening of the alisphenoid canal, into the canal, which is a wide and shallow transverse groove on the ventral surface of each pterygoid plate, and then through the anterior portion of the alisphenoid canal to eventually enter the sphenoidal fissure through the anterior opening of the alisphenoid canal.

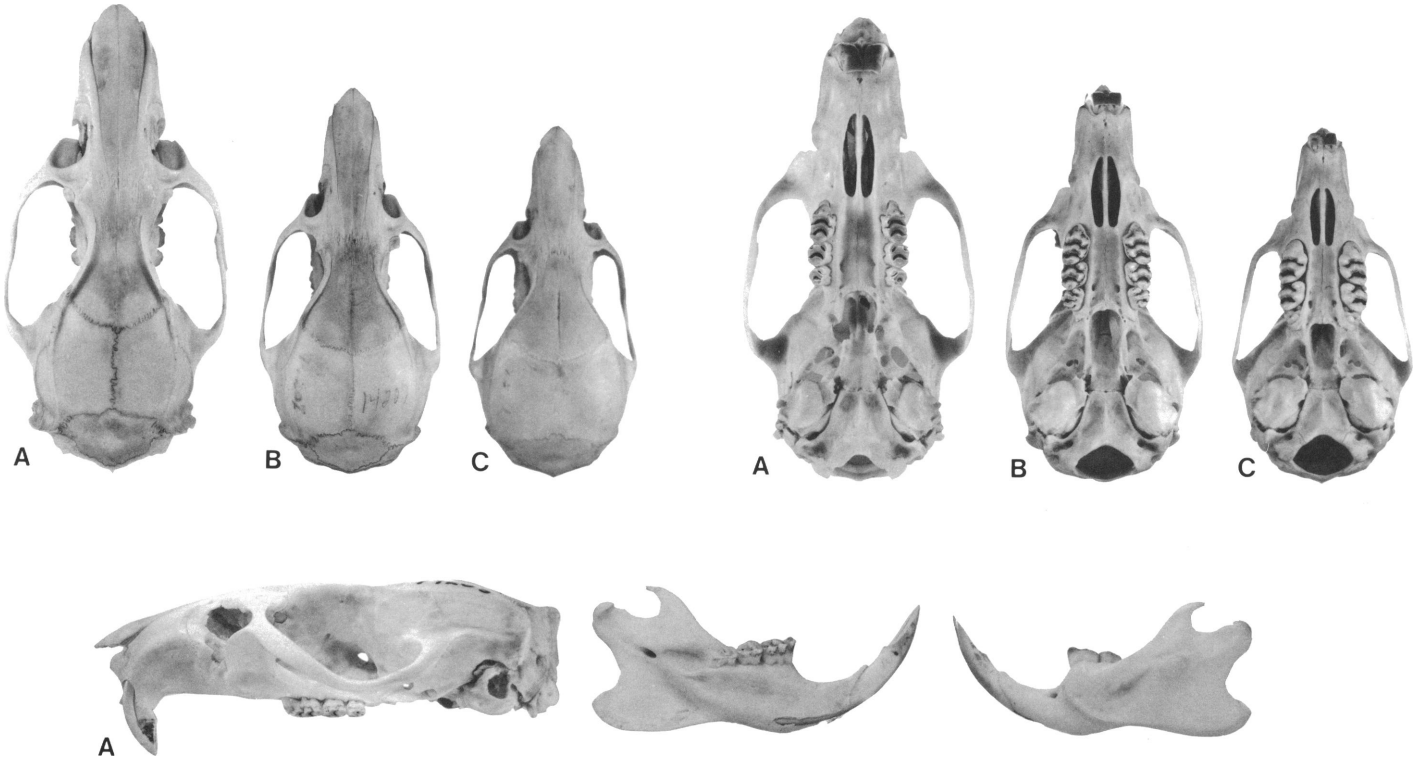

FIG. 53. *Sundamys maxi* from Java: views of crania and dentary. A, adult (RMNH 14205). B, young adult-juvenile (RMNH 14027). C, juvenile (RMNH 14061). Natural size.

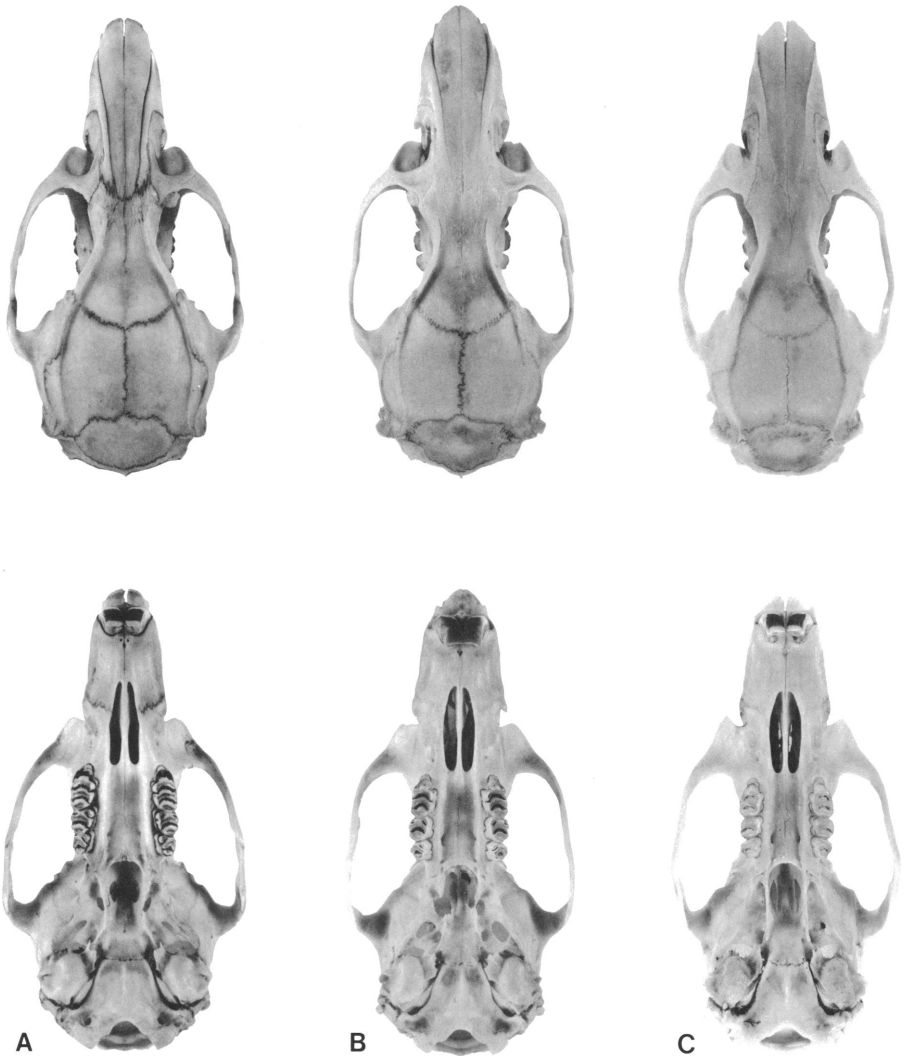

FIG. 54. Views of crania contrasting species of adult *Sundamys*. A, *S. infraluteus,* Sumatra (ANSP 20356). B, *S. maxi,* Java (RMNH 14205). C, *S. muelleri,* Malay Peninsula (USNM 290205). Note the wide rostrum and incisive foramina in *S. maxi* and *S. muelleri* compared with *S. infraluteus*. Natural size.

The bony shape of each pterygoid plate reflecting this arterial pattern is shown in figures 55B and 57A. As seen from a ventral view, there are three large openings in the posterior one-third of each plate: the most medial one is the opening of the transverse canal; lateral to that is the posterior opening of the alisphenoid canal where the internal maxillary artery exits the cranial cavity and courses onto the surface of the plate; the most lateral opening is the ventral portion of the foramen ovale. In some specimens, shape of the pterygoid plate on each side of the cranium is like the configuration in figure 57B where the posterior opening of the alisphenoid canal is posterior to the opening of the transverse canal and nearly concealed by the bony eustachian tube. In a few specimens, one side may have an open channel-like canal so the posterior opening of the canal is ex-

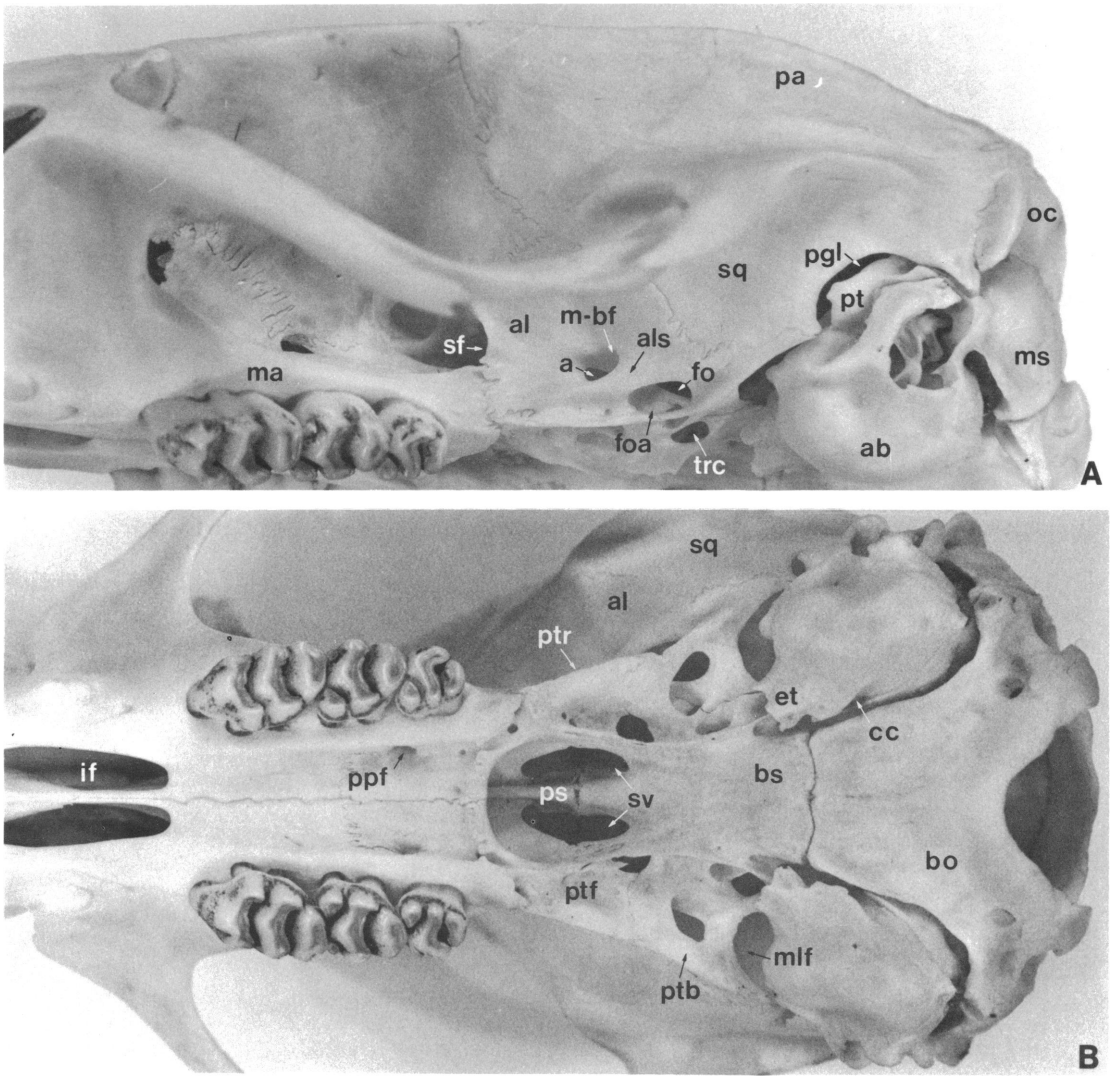

FIG. 55. Lateral (A) and ventral (B) views of the cranium in *Sundamys maxi* (RMNH 14181). *Abbreviations:* **a**, anterior opening of the alisphenoid canal; **ab**, auditory bulla; **al**, alisphenoid bone; **als**, lateral strut of alisphenoid bone; **bo**, basioccipital bone; **bs**, basisphenoid bone; **cc**, carotid canal; **et**, bony eustachian tube; **fo**, foramen ovale; **foa**, foramen ovale accessorius; **if**, incisive foramina; **ma**, maxillary bone; **ms**, mastoid portion of the petromastoid; **mlf**, middle lacerate foramen; **m-bf**, coalesced masticatory-buccinator foramina; **pa**, parietal bone; **pgl**, postglenoid vacuity; **ppf**, posterior palatine foramen; **ps**, presphenoid bone; **pt**, periotic portion of the petrosal; **ptb**, pterygoid bridge; **ptf**, pterygoid fossa; **ptr**, pterygoid ridge; **sf**, sphenoidal fissure; **sq**, squamosal bone; **sv**, sphenopalatine vacuity; **trc**, transverse canal. See figure 57 for names of canal and foramina in the pterygoid regions.

posed and in the other side the canal may be enclosed in bone so only two vacuities are seen in ventral view: the opening of the transverse canal and the foramen ovale.

The carotid arterial pattern in all specimens of *Sundamys muelleri* and *S. infraluteus* that we studied is like that shown in figure 56 (left side) and explained in the accounts of those species. Briefly, the stapedial foramina are large and conspicuous, there is a deep groove along the inner side of each pterygoid ridge in which the internal maxil-

lary artery courses after it exits from the middle lacerate foramen, and the posterior opening of the alisphenoid canal is just above (in ventral view) the foramen ovale (see also fig. 39). This is the most widely distributed pattern in murid rodents and one that is primitive; the pattern in *S. maxi* is uncommon in murids and is derived (Carleton, 1981; Musser, 1982b, 1982c).

The shape of each dentary in *Sundamys maxi* is similar to that in *S. infraluteus* and Malayan *S. muelleri.* The dentaries can be distinguished from those in other samples of *S. muelleri* only by their larger size (compare figs. 52 and 53).

Upper incisors of *Sundamys maxi* are wide and sturdy. Their enamel layers are orange. The uppers leave the rostrum either at nearly right angles (orthodont) or curve slightly back (opisthodont).

Because they are large and appear stocky, the molars of *Sundamys maxi* resemble those in *S. infraluteus* more than the molars in *S. muelleri* but the similarities in bulkiness reflect large size. When examined closely, the molars are large versions of the teeth in *S. muelleri,* particularly the patterns formed by cusps and laminae (the molar rows of worn, moderately worn, and juvenile teeth of *S. maxi* can be contrasted with molar rows of comparable ages in samples of *S. infraluteus* and *S. muelleri* in figs. 41, 49, 50, 58, and 59). The molars of *S. maxi,* like those in *S. muelleri,* appear high-crowned but relative to size of cranium and mandible they are brachydont and not hypsodont. Molars of *S. infraluteus* are relatively higher crowned compared with those in *S. maxi* and *S. muelleri,* and the laminae are thicker and give the occlusal surfaces a more massive appearance.

Not only are the molars of *Sundamys maxi* shaped like those in *S. muelleri,* but they also share similar frequencies of certain cusps and cusplets (table 17). As in all specimens of *S. muelleri* we examined, every specimen of *S. maxi* has a conspicuous and usually large cusp t3 on each second upper molar; comparable cusps are present on the second molars in most specimens of *S. infraluteus.* A cusp t3 also occurs on each third upper molar in most specimens of *S. maxi* and *S. muelleri* but in only half the sample of *S. infraluteus.* All our specimens of S. *infraluteus* lack anterior labial cusplets on the first lower molars but such cusplets are found in a third of the sample of *S. maxi* and about half of the sample of *S. muelleri.*

We note four other dental features of *Sundamys maxi.* All specimens we studied had a posterior cingulum at the back of each first upper molar (fig. 40), a frequency characteristic of *S. infraluteus* but not *S. muelleri* in which only half the sample had posterior cingula (table 17). Anterolabial cusps occur on third lower molars in about 80 percent of the sample of *S. maxi* but in only about two-thirds of the series of *S. infraluteus* and *S. muelleri.* We could not discern an anterocentral cusp at the front of each first lower molar in any specimen of *S. maxi;* a comparable cusp could also not be detected in any example of either *S. infraluteus* or *S. muelleri.* Finally, in our samples of *S. maxi* and *S. muelleri,* the anterior lamina on each first upper molar is composed of three cusps that are tightly merged. The anterolabial cusp (t3) is large and distinct. In samples of *S. infraluteus,* cusp t3 is either small or so coalesced with the central cusp t2 that the front lamina appears to have only two cusps and a slight indentation where the labial cusp should be.

NATURAL HISTORY: We know only that *Sundamys maxi* most likely is terrestrial and lives in tropical evergreen forests in the highlands of West Java. Bartels (1937b) spent much time at Pasir Datar and Situ Gunung observing mammals. He (Bartels, 1937c) noted that *S. maxi* was very difficult to trap. The species was never caught before Bartels made his efforts and has not been taken since. The same is true for *Kadarsanomys sodyi,* another forest rat occurring in the same places as *S. maxi* and known by samples obtained only by Bartels (Musser, 1981c). Forest still exists on some lower slopes of the volcanic peaks and highlands in West Java and possibly both *S. maxi* and *K. sodyi* still live there.

We have no evidence that *Sundamys maxi* once occurred anywhere else on Java except the western portion. Musser has examined samples of subfossils from Sampung Cave, Wadjak Cave, and Goea Djimba Cave in central and eastern Java and found remains of *Kadarsanomys sodyi, Leopoldamys sabanus,* and *Rattus tiomanicus* but not *S. maxi* or any of the other murids native to the island.

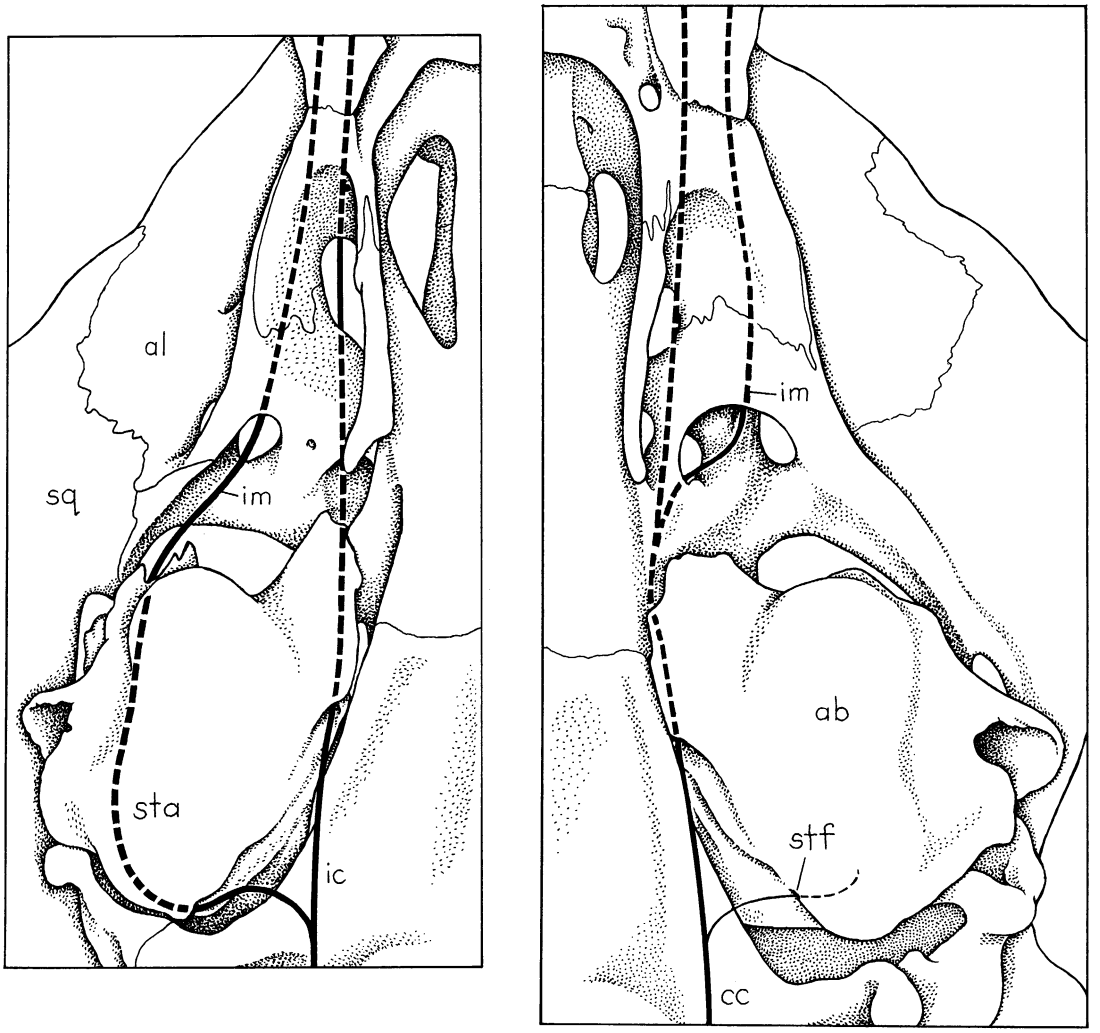

FIG. 56. Diagrams of carotid arterial patterns in *Sundamys muelleri* (left, AMNH 102846) and *S. maxi* (right, RMNH 14211). *Abbreviations:* **ab**, auditory bulla; **al**, alisphenoid bone; common carotid artery; **ic**, internal carotid artery; **im**, internal maxillary artery; **sq**, squamosal bone; **sta**, stapedial artery; **stf**, stapedial foramen. See figures 55 and 57 for names of bones and foramina. The arterial patterns and bony configurations are also described in text.

Bartels collected examples of *L. sabanus, K. sodyi,* and *S. maxi* from the same forest in West Java. If all three species are part of the same tropical evergreen forest community perhaps *S. maxi* was also more widespread in Java at one time as subfossils indicate *L. sabanus* and *K. sodyi* to have been. Collections of subfossil samples made in the future should be carefully examined for remains of this large-bodied rat.

RELATIONSHIPS: *Sundamys maxi* joins five other murids in being native to Java and nowhere else: *Mus vulcani, Niviventer lepturus, Maxomys bartelsii, Kadarsanomys sodyi,* and *Pithecheir melanurus.* These six species comprise 50 percent of the native Javan murid fauna (table 36; Musser, 1981c). Each of the endemic species is morphologically distinctive and all of them live in forests, most at middle and high altitudes. *Sundamys maxi* is no exception.

Among the species of *Sundamys, S. maxi*

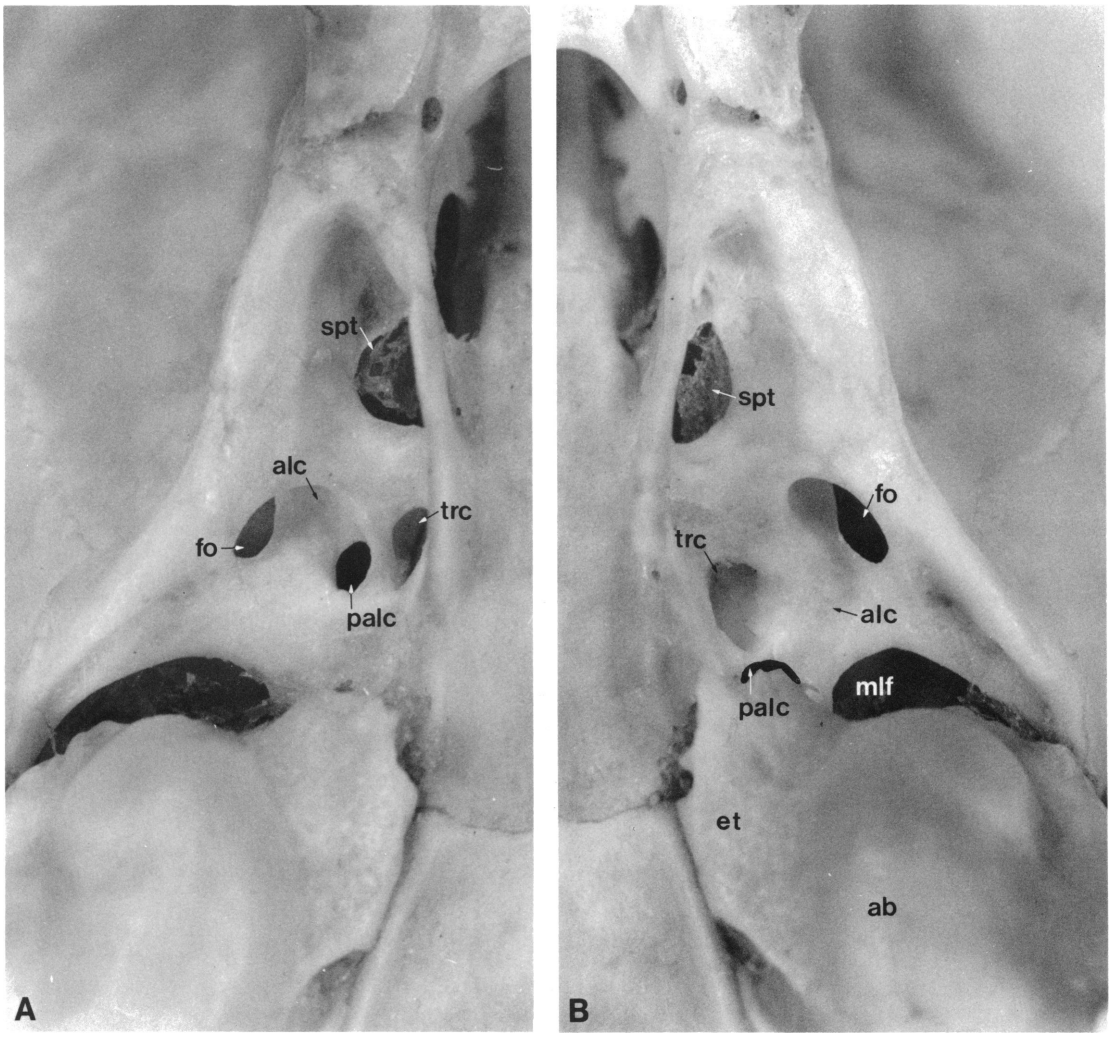

FIG. 57. Ventral views of right (A) and left (B) pterygoid regions in an adult *Sundamys maxi* (RMNH 14211). A: the posterior opening of the alisphenoid canal (**palc**) is dorsal and slightly lateral to the transverse canal (**trc**); the internal maxillary artery (**im** in fig. 56) would exit from the posterior opening and course along the open channel-like alisphenoid canal (**alc**) in the pterygoid plate and disappear above the plate just medial to the foramen ovale (**fo**). B: the configuration is similar to A except that the posterior opening of the alisphenoid canal is posterior to the opening of the transverse canal and nearly hidden by the bony eustachian tube (**et**) of the auditory bulla. In each pterygoid plate, the only other large openings consist of a sphenopterygoid vacuity (**spt**) and middle lacerate foramen (**mlf**). The arterial pattern diagrammed on the left side of figure 56 is superimposed on a bony configuration resembling side A.

is unique in being the only one with the derived carotid arterial pattern and a higher frequency of large sphenopterygoid vacuities in the pterygoid plates, also a derived character. In other characteristics, *S. maxi* combines traits of both *S. infraluteus* and *S. muelleri* but is overall more similar to the latter. Look at cranial and dental features. *Sundamys maxi* has a large, sturdy skull and large molars, as does *S. infraluteus,* but the conformation and proportions of the skull and teeth in *S. maxi* resemble those features

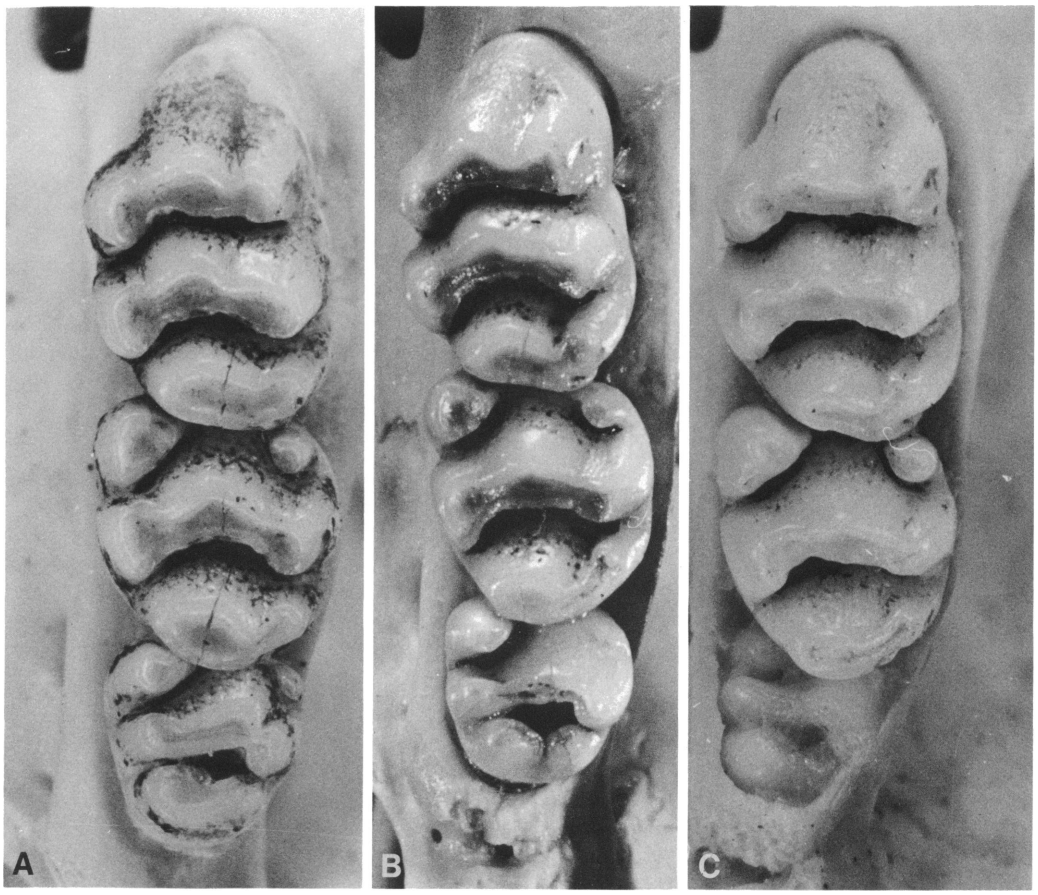

FIG. 58. Occlusal views of left upper molar rows in *Sundamys maxi*. A, adult (RMNH 14207). B, young adult-juvenile (RMNH 13746). C, juvenile (RMNH 13968). All ×10. Note the posterior cingulum at the back of the first molar in each toothrow and the large cusp t3 on each second and third molar.

in skulls of Malayan *S. muelleri* and not *S. infraluteus*. Compared with examples of *S. muelleri* from the Malay Peninsula, specimens of *S. maxi* are very similar except for their slightly larger size, wider incisors, longer molar rows, increased frequency of posterior cingula on first upper molars, different basicranial arterial pattern, and frequency of sphenopterygoid vacuities.

In external features, *Sundamys maxi* combines traits of both *S. infraluteus* and *S. muelleri*. The pelage of *S. maxi* is a paler and softer version than that found in *S. infraluteus*. This and the large body size of *S. maxi* prompted taxonomists to align *maxi* as a subspecies of *infraluteus*. Large body size, however, does not reflect close relationship between the two species. The Malayan *S. muelleri* is also closely similar to *S. maxi* in size. Mean values from all external measurements of *S. maxi* except length of hind foot are not significantly different from mean values in the sample of Malayan *S. muelleri*; *S. maxi* does have, on the average, significantly longer hind feet than *S. muelleri*. Aside from color and texture of pelage, *S. maxi* appears to be a version of *S. muelleri* that is about the same body size as those from the Malay Peninsula but larger-bodied than the other samples of *S. muelleri* rather than a somewhat smaller-bodied counterpart of *S. infraluteus*. The number of mammae, four pairs in *S. maxi* and *S. muelleri* but only three pairs in *S. infraluteus*, reinforce this morphological tie between *S. maxi* and *S. muelleri*.

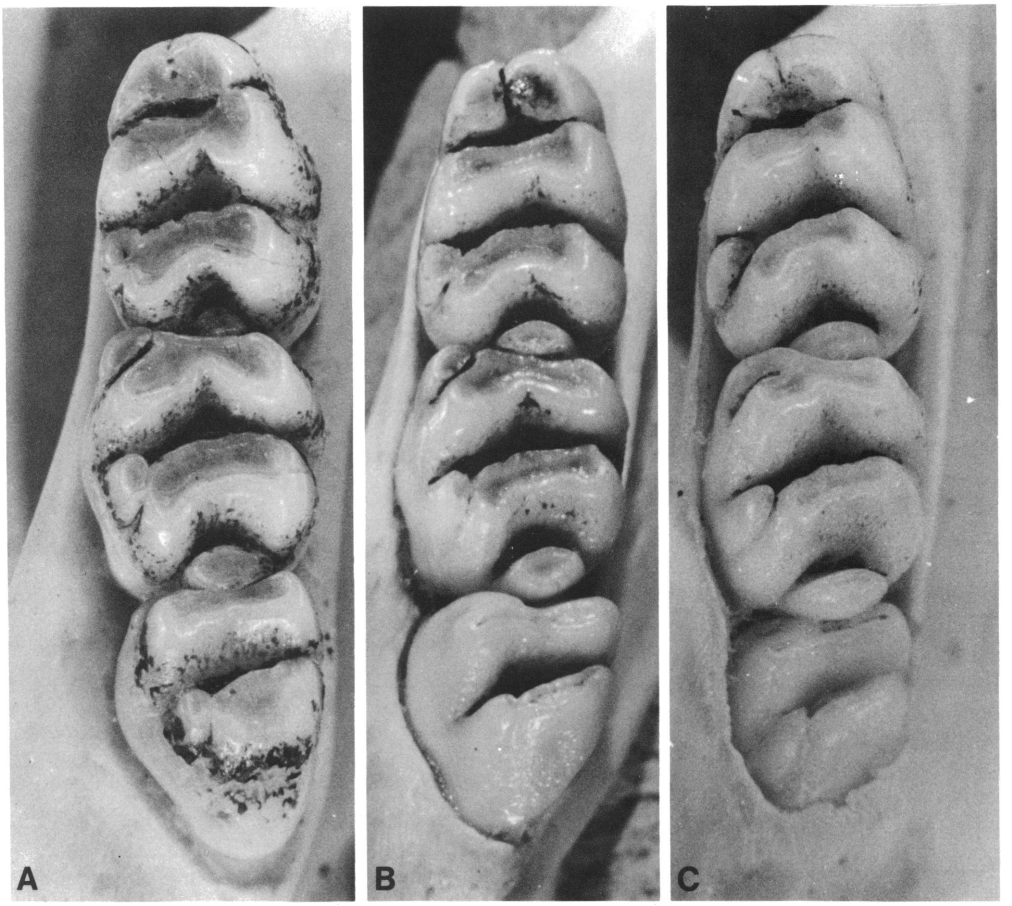

FIG. 59. Occlusal views of left lower molar rows in the same specimens of *Sundamys maxi* shown in figure 59. A, adult; B, young adult-juvenile; C, juvenile. All ×10. Note the chunky lamina at the front of each first molar.

SUNDAMYS COMPARED WITH OTHER GENERA

Disassociating the species of *Sundamys* from those with which they have been allied in the past but to which they bear no close morphological resemblance and are separated by a different evolutionary history is part of defining the genus *Sundamys*. Because the *muelleri* group was long considered to be part of *Rattus*, separating *Sundamys* from *Rattus* is the first important contrast; this we did in our diagnosis of *Sundamys*.

In this section we compare *Sundamys* with the following groups: 1) the species associated with *Stenomys*, which is now considered to be a subgenus of *Rattus*; 2) *Rattus palmarum* of the Nicobar Islands and *Rattus stoicus* on the Andaman Islands because examples of both species were misidentified as *Rattus muelleri* by Ellerman (1961) and are the basis for his inclusion of those island groups within the geographic distribution of *S. muelleri*; 3) *Taeromys callitrichus*, which has been listed as a close relative of *Sundamys infraluteus* (Ellerman, 1949; Laurie and Hill, 1954), and *Taeromys celebensis*, which Misonne (1969) placed in the same subgenus as *muelleri*; 4) the species of *Berylmys*, which have been closely associated with those in *Sundamys*; 5) the Philippine *Tryphomys adustus*, which as *Rattus adustus*, Misonne (1969) associated closely with *Rattus muelleri muelleri*; 6) *Paruromys dominator* because both Ellerman (1949) and Misonne (1969) included the

species in the same subgenus as *muelleri*; 7) *Bullimus bagobus* because that is the type species of the genus *Bullimus,* which Misonne (1969) used as a subgenus of *Rattus* to contain *muelleri* and other species he thought to be dentally similar to it; and 8) some of the other species considered by Ellerman (1941, 1949) and Misonne (1969) to be in the same group or subgenus as *muelleri* and its relatives (table 13).

SUNDAMYS AND *STENOMYS*

Had Ellerman's classification been etched in stone it could not have lasted longer or been more monumental in its overbearing influence on the perception of relationships among species of *Rattus,* particularly those he included within the subgenus *Stenomys.* That *muelleri* was Sundaic in distribution and the type species of *Stenomys* known only from New Guinea did not deter taxonomists from accepting Ellerman's union of these species within the same subgenus and within the same cluster: the *callitrichus* group (Ellerman, 1949). Ellerman's use of *Stenomys* was accepted by Malayan mammalogists as recently as 1979 in reports on *Sundamys muelleri* and *Berylmys bowersii* from the Malay Peninsula (Chan, Dhaliwal, and Yong, 1979, for example) despite Misonne's (1969) contention that the subgenus *Stenomys* contained species confined to the New Guinea and Australian region and *muelleri* belonged in the subgenus *Bullimus* of *Rattus.*

Ellerman's first classification of *Rattus,* published in 1941, delimited a *muelleri* group which, except for two species, is the same as our concept of *Sundamys* (see table 13 and our discussion at the beginning of the *muelleri* group). Several years later, Ellerman (1947–1948) presented modifications of his original classification and placed *muelleri, infraluteus,* and *maxi* in the subgenus *Stenomys.* For Ellerman (p. 261), the key characters defining subgenus *Stenomys* were small bullae ("averaging below 15 per cent of the occipitonasal length") and long palate ("exceeding half the occipitonasal length"). The long palate separated subgenus *Stenomys* from subgenus *Maxomys* and the small bullae distinguished subgenus *Stenomys* from subgenus *Rattus.* By 1949, in the formal revision of his 1941 classification, Ellerman placed *muelleri* and *infraluteus* in the *callitrichus* group, which also contained several species from New Guinea, including *Rattus verecundus,* the type species of *Stenomys.* The *callitrichus* group was one of four species groups that Ellerman brought together under the subgenus *Stenomys* (table 13).

In 1969 Misonne (pp. 136–137), who studied dental features of Indo-Australian murids, took *muelleri* out of *Stenomys* and restricted the subgenus to species that occur in New Guinea, western and southern Autralia, Guadalcanal, Bougainville, and smaller islands in the New Guinea region. In Misonne's view, *Stenomys* contained *Rattus niobe, R. verecundus, R. leucopus, R. ruber, R. assimilis-greyi,* and probably *R. tatei, R. shawmayeri,* and *R. richardsoni.* For Misonne, "the characters of this subgenus are rather clearly defined; the opening of the mesopterygoid fossae is behind the toothrows; the palate is somewhat broad. The cones of the molars are broad, not specially angular, the labial cones being larger than in most other *Rattus.* M^3 is moderately reduced; in M_2, Sv is large and almost always connected to the mesial part of the molar; this character is unusual in other *Rattus.*"

Misonne's concept of *Stenomys* includes species which, based on our studies, do not belong in the subgenus. Three he lists definitely form a distinctive morphological cluster and should be in *Stenomys*: *Rattus verecundus, R. niobe,* and *R. richardsoni. Mus verecundus* was proposed as a new species and described by Thomas in 1904. Six years later, Thomas (1910, p. 507) proposed the genus *Stenomys* with *Mus verecundus* as type species. Thomas compared *Stenomys* with *Epimys* (then the name used for what is now called *Rattus*) and defined the genus this way:

> size medium or small. Tail slender, of medium hairiness, about as in *Epimys* or rather less hairy. Feet slender, the metatarsus somewhat lengthened. Clitoris rather long. Mammae (of type species) 1–2=6. Skull scarcely ridged, low, smooth, with a long narrow muzzle. Interorbital edges square, the beads scarcely perceptible. Interparietal fairly large. Palatal foramina medium or small. Bullae rather small. Incisors rather more flattened in front than in *Epimys.* Molars

as in that genus; m^2 without antero-external cusp (cusp 3).

Thomas gave New Guinea as the range of this genus.

Taylor, Calaby, and Van Deusen (1982) have recently revised the *Rattus* in the New Guinea region. They identify five species that are either old or recent introductions to the area: *R. nitidus, R. rattus, R. norvegicus, R. argentiventer,* and *R. exulans.* None of these are native to New Guinea and nearby islands. Eleven species are native: *R. niobe, R. richardsoni, R. verecundus, R. praetor, R. mordax, R. leucopus, R. steini, R. giluwensis, R. novaeguineae, R. jobiensis,* and *R. sordidus. Rattus leucopus* also occurs on the eastern half of Cape York in Australia. *Rattus sordidus* is an Australian species (Taylor and Horner, 1973) that occurs in New Guinea in the lowlands south of the mountains forming the backbone of the island. The other nine species are native to mainland New Guinea, the Bismarck Archipelago, the Solomon Islands, and other smaller islands in the New Guinea region.

By combining several kinds of analyses, Taylor, Calaby, and Van Deusen (1982, p. 302) "recognize five major groupings: *exulans, sordidus, rattus-nitidus, niobe-richardsoni-verecundus,* and the assemblage of remaining species." Our experience with these species reinforce their conclusions about the cluster containing *R. verecundus, R. niobe,* and *R. richardsoni*; all are closely allied to each other and are members of *Stenomys,* whether that name is used as a subgenus of *Rattus* or as a genus. We do not know if the other native New Guinea species also belong in *Stenomys. Nesoromys ceramicus,* from the island of Ceram is an ally of *R. verecundus* and *R. niobe* and the genus *Nesoromys* is included in *Stenomys* by some authors (Rümmler, 1938; Musser, 1981b) but not by others (Tate, 1936; Laurie and Hill, 1954; Misonne, 1969).

For us, species of *Stenomys* are native to Ceram and the New Guinea area (and Cape York if *R. leucopus* belongs in the subgenus) and are not members of the faunas to the west in either the Philippine Islands, Sulawesi, or the Indo-Malayan region. *Rattus verecundus* and *R. niobe* are our examples of *Stenomys* in the comparisons with *Sundamys muelleri.* Whether *Stenomys* is a genus, as some have used it (Thomas, 1910; Tate, 1936; Rümmler, 1938), or a subgenus of *Rattus,* as it is currently treated (Ellerman, 1941, 1949; Tate, 1951; Misonne, 1969), is not our concern here.

Bullae less than 15 percent of occipitonasal length and palate longer than half of occipitonasal length were the key characters used by Ellerman (1947–1948) to separate the subgenus *Stenomys* from other subgenera of *Rattus.* The relatively long palate separated *Stenomys* and *Rattus* from the subgenus *Maxomys.* The species of *Sundamys* and *Rattus*

TABLE 27
Ratios (expressed as percentage) from Samples of *Berylmys, Sundamys,* and *Rattus*[a]

Genus and Species	Length of Bulla / Skull Length	Palatal Length / Skull Length
BERYLMYS		
B. bowersii	14	53
B. mackenziei	14	53
B. manipulus	15	54
B. berdmorei	20	53
SUNDAMYS		
S. muelleri		
Malay Peninsula	11	53
Sumatra	13	53
Sabah	12	53
S. maxi	13	53
S. infraluteus		
Sabah	11	54
Sumatra	11	54
RATTUS		
R. verecundus	14	53
R. niobe	14	51
R. richardsoni	15	50
R. leucopus	16	53
R. praetor	15	54
R. mordax	15	55
R. steini	15	54
R. jobiensis	13	54
R. rattus diardii	16	54
R. baluensis	14	55
R. hoogerwerfi	15	53

[a] Derived from values in tables 1, 5–8, 19, 22, and 24 except *R. verecundus* to *R. jobiensis,* which are derived from the tables in Taylor, Calaby, and Van Deusen (1982).

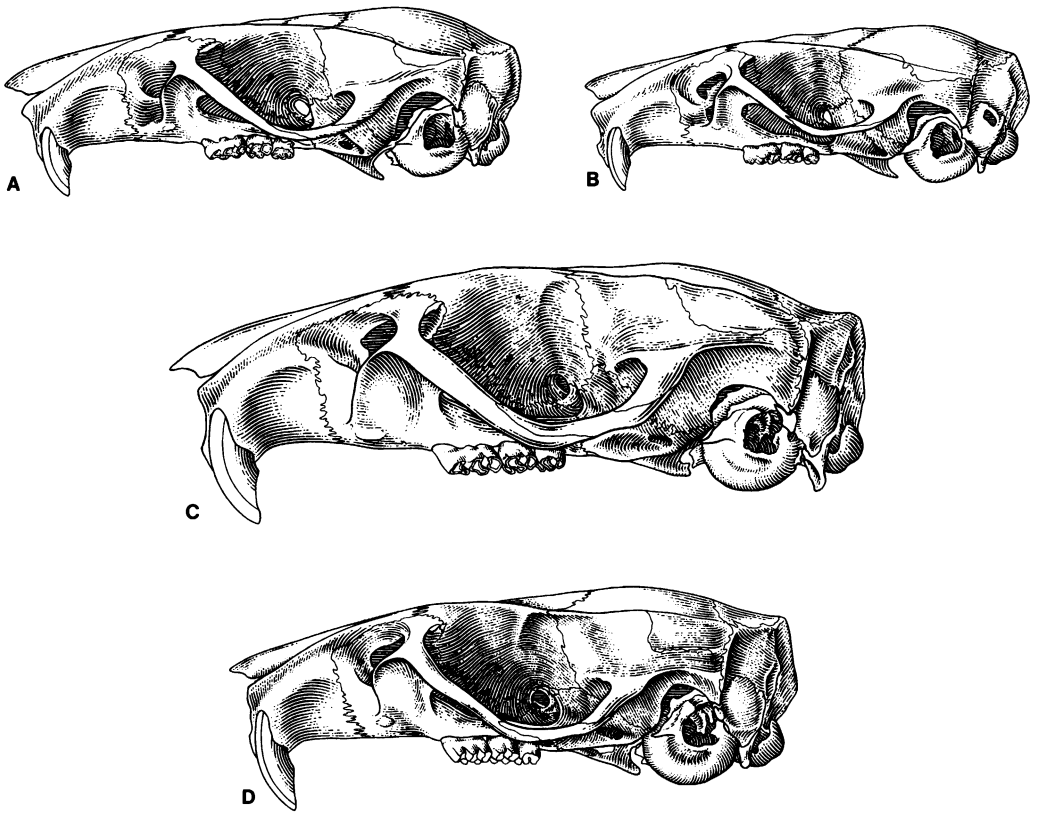

FIG. 60. Lateral views of crania. Adult *Rattus verecundus* (A) and *R. niobe* (B) of subgenus *Stenomys,* and *R. rattus diardii* (D) of subgenus *Rattus* are contrasted with *Sundamys muelleri* (C). Drawn from AMNH 104277 (A), AMNH 104354 (B), AMNH 102845 (C), and AMNH 101845 (D). Originally published in Tate (1936) in a different context. Approximately ×2.

verecundus and its allies do have a relatively long palate (table 27). All of them do not have small bullae. The New Guinea rats, along with *muelleri* and *infraluteus,* were brought into *Stenomys* primarily because they shared relatively small bullae compared with size of the skull. Small bullae is a primitive trait (Musser, 1981a) and is distributed widely among species of muroid rodents. It does not reflect close phylogenetic affinity between many of the species Ellerman listed under either the subgenus *Stenomys* or the *callitrichus* group of that subgenus (Ellerman, 1949). Furthermore, the proportions of the bullae relative to the cranium in *Rattus verecundus* and its relatives are similar to proportions of species in the subgenus *Rattus*: those, for example, listed in table 27. The species of *Sundamys* fit Ellerman's key but *R. verecundus* and other New Guinea rats cannot always be separated from species in the subgenus *Rattus.*

We find no characters indicating a close morphological and phylogenetic link between the species of *Sundamys* and *Rattus verecundus,* our example of *Stenomys.* Of medium body size, (see list of measurements in Taylor, Calaby, and Van Deusen, 1982, p. 207), *R. verecundus* has brown upperparts, gray underparts, and soft, glossy fur. The feet are white. The hind feet are long, very slender, and appear delicate. The tail is as long or longer than the body and is white distally in many specimens. Females have six mammae: one postaxillary pair and two inguinal pairs.

The species of *Sundamys* are large animals, some would even call them giant rats (Lim,

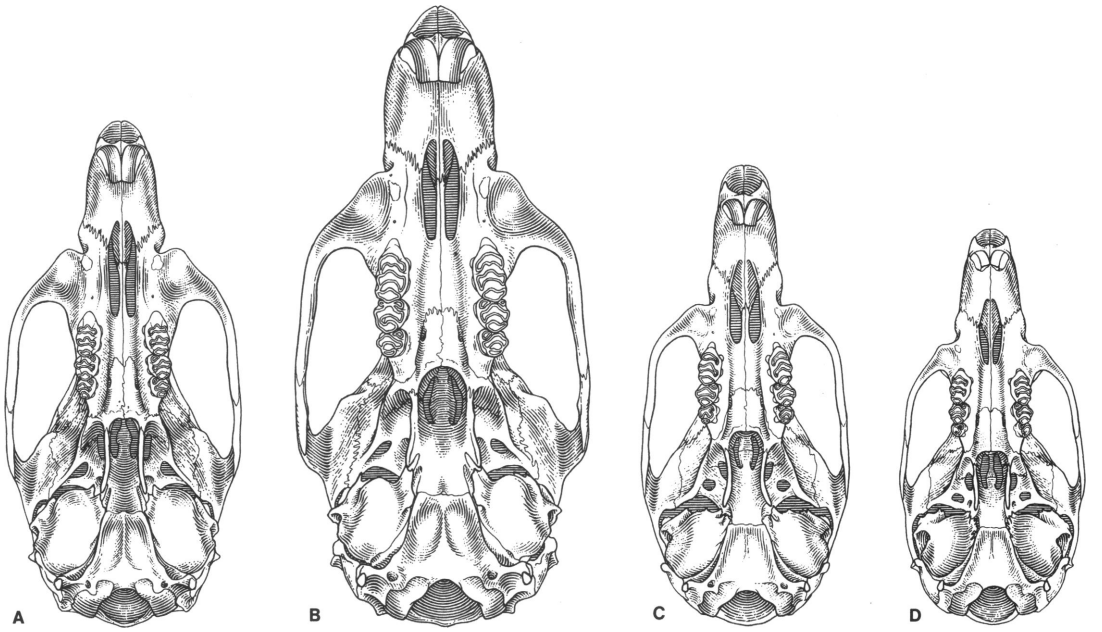

FIG. 61. Ventral views of crania drawn from same specimens shown in figure 60. A, *Rattus rattus diardii*; B, *Sundamys muelleri*; C, *Rattus verecundus*; D, *Rattus niobe*. Approximately ×2.

1970). The fur is rough and shaggy. The tail is always much longer than the body and is dark brown over all surfaces. The feet are brown. The hind feet are large and stocky; they appear robust, not delicate. Only *S. infraluteus* has six mammae, the other species have eight. The delicate and narrow hind feet of *R. verecundus* represent a specialization compared with the feet of *Sundamys*.

The skull of *Rattus verecundus* is small (see list of measurements in Taylor, Calaby, and Van Deusen, 1982, p. 207), its contours are smooth, the braincase is large relative to the rostral area, and the rostrum is long and slender. Supraorbital and temporal ridging is weak and hardly evident. The skull is small, slender, smooth, and delicate compared with the very large skull of *Sundamys muelleri* with its wide stocky rostrum, its deep braincase that is not relatively large compared with the rostral region, and its prominent and thick supraorbital and temporal ridging (figs. 60 and 61).

Many of the other cranial features distinguishing *Sundamys* from *Rattus verecundus* are some of the same characters that separate species of *Rattus* from *Sundamys*; the derived expression occurs in *Rattus* and in *R. verecundus*, the primitive counterpart in *Sundamys*. For example, compared with *Sundamys*, *R. verecundus* has larger bullae relative to skull size (table 27); a small area of squamosal bone is separated from the dorsal rim of the bullar capsule by a spacious postglenoid vacuity, the periotic is narrow and inconspicuous (the periotic fills the space between bulla and squamosal in *Sundamys* and the squamosal is much larger in area between zygomatic root and bullar capsule); the alisphenoid canal dorsal to the pterygoid ridge is an open channel and is not bounded by a lateral strut of alisphenoid bone (a large strut is present in 97 percent of the sample of *S. muelleri* and in most specimens of *S. infraluteus* and *S. maxi*); the sphenopalatine vacuities in the mesopterygoid fossa are relatively longer; and a spacious sphenopterygoid vacuity in each pterygoid plate occurs in every specimen of *R. verecundus* we examined (absent from 40 percent of the sample of *S. muelleri* and usually small in the other species of *Sundamys*). These derived features of *R.*

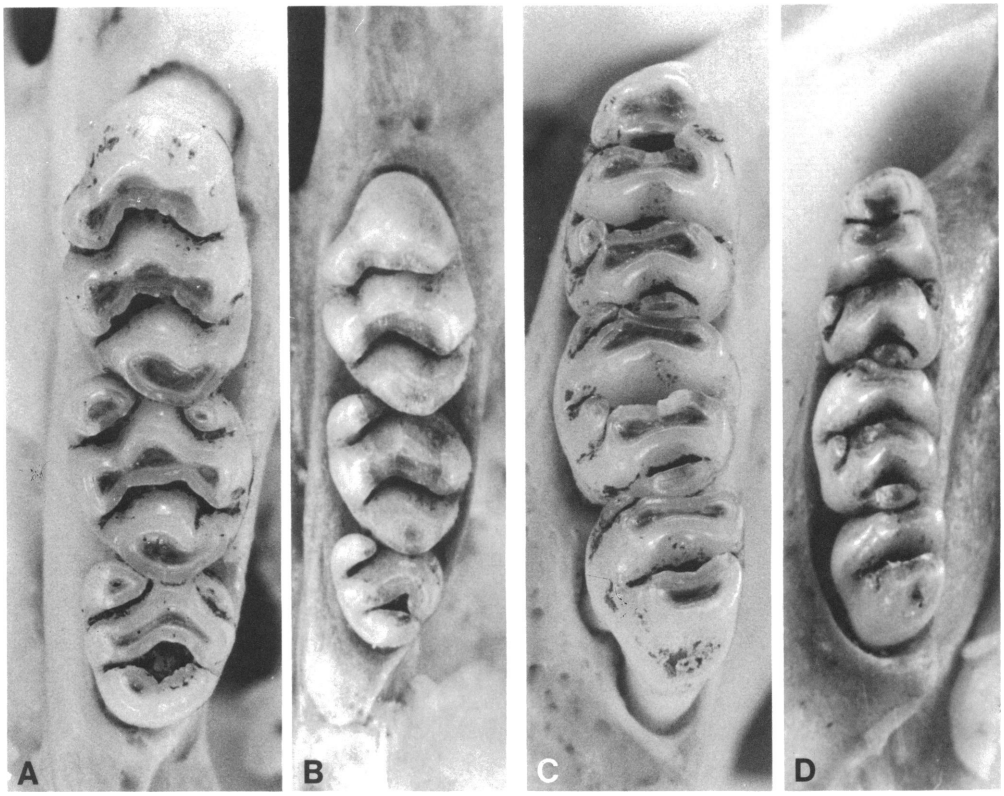

FIG. 62. Occlusal views of left upper (A and B) and lower (C and D) molar rows contrasting *Sundamys* and *Rattus* (subgenus *Stenomys*). A and C, *S. muelleri* (AMNH 106175). B and D, *R. verecundus* (AMNH 157896). All ×10.

verecundus (and *R. niobe* and *R. richardsoni*) link it with species in the genus *Rattus* but not with the species of *Sundamys*.

The molars of *Rattus verecundus* are small and simple compared with those in species of *Sundamys* (fig. 62). Contrasted with *S. muelleri,* upper molars of *R. verecundus* have narrower laminae that are more tightly pressed against each other; smaller third molars relative to the others in the rows; no posterior cingula on the first upper molars (present in 50 percent of the sample of *S. muelleri* and in all the specimens of *S. maxi* and *S. infraluteus*); second and third molars without anterolabial cusps (cusp t3) in most specimens, if present they are tiny (large and conspicuous in most specimens of *S. muelleri*); a tightly C-shaped front lamina on each third molar (elongate and nearly transverse in *S. muelleri*), and a posterior lamina on that tooth consisting of a small oblong mound without evidence of cuspidation (a wide posterior lamina in *S. muelleri* that is obviously formed of two cusps).

Compared with *Sundamys muelleri,* the lower molars of *Rattus verecundus* are relatively narrower with thicker laminae; the laminae are more tightly nestled against one another on each tooth; the posterior cingula are narrower and round in cross-section, not wide and oblong; the anterolabial cusp on each second molar is large and joins the tooth in about the middle of its anterior margin (located farther labially and more a part of the anterolabial corner of the second molar in *S. muelleri*); and the anterolabial cusp is missing from each third molar in some specimens, when present it also springs from near the middle of the anterior margin.

We agree with Misonne (1969) in disassociating *Rattus verecundus* and its allies from what he called *Rattus muelleri* and its rela-

TABLE 28

Species and Subspecies of *Rattus* Native and Introduced to the Andaman and Nicobar Islands[a]

Taxon	Andaman Islands					Nicobar Islands					
	South Andaman	Henry Lawrence	Narcodam	Little Andaman	Barren	Carr Nicobar	Trinkat	Little Nicobar	Great Nicobar	"Nicobars"	Nanhauri
Rattus stoicus (Miller, 1902): including *taciturnus* (Miller, 1902) and *rogersi* (Thomas, 1907)	+	+		+							
Rattus rattus andamanensis (Blyth, 1860): including *flebilis* (Miller, 1902)	+	+	+								
Rattus rattus rattus (Linnaeus, 1758): including *atratus* (Miller, 1902), which equals *atridorsum* (Miller, 1903)					+						
Rattus palmarum (Zelebor, 1869)										+	
Rattus palmarum burrus (Miller, 1902)							+				
Rattus palmarum burrescens (Miller, 1902)								+	+		
Rattus rattus burrulus (Miller, 1902: including *holchu* (Chaturvedi, 1966)						+					
Rattus rattus diardii (Jentink, 1880): including *pulliventer* (Miller, 1902)								+	+		
Rattus rattus rattus (Linnaeus, 1758)											+

[a] Compiled from Musser's records and those reported by Nath and Chaturvedi (1973).

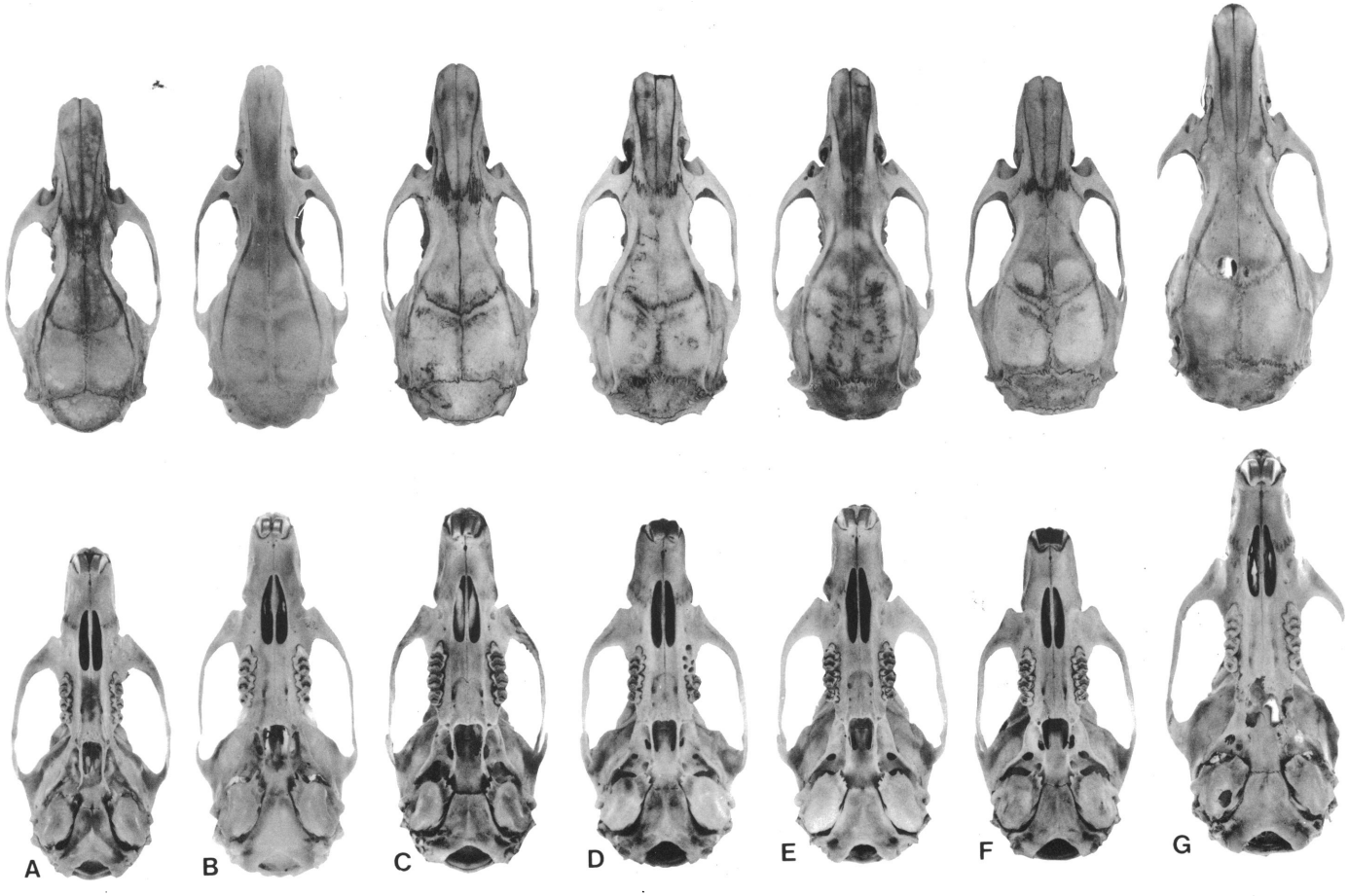

FIG. 63. Views of crania from adult *Rattus*: *R. tiomanicus* (A) and examples of the *R. palmarum* group (B–G). A, *mara* (USNM 197444), Pulau Maratua. B, *lugens* (AMNH 10320), Pulau Pagi Utara. C, *mentawi* (USNM 252469), Pulau Siberut. D, *lasiae* (USNM 114255), Pulau Lasia. E, *simalurensis* (USNM 114221), Pulau Simalur. F, *burrescens* (USNM 111804), Great Nicobar Island. G, *palmarum* (NMW B-27), Nicobar Islands. Natural size. Compare these views with those of *Sundamys muelleri* and *Rattus stoicus* in figure 64.

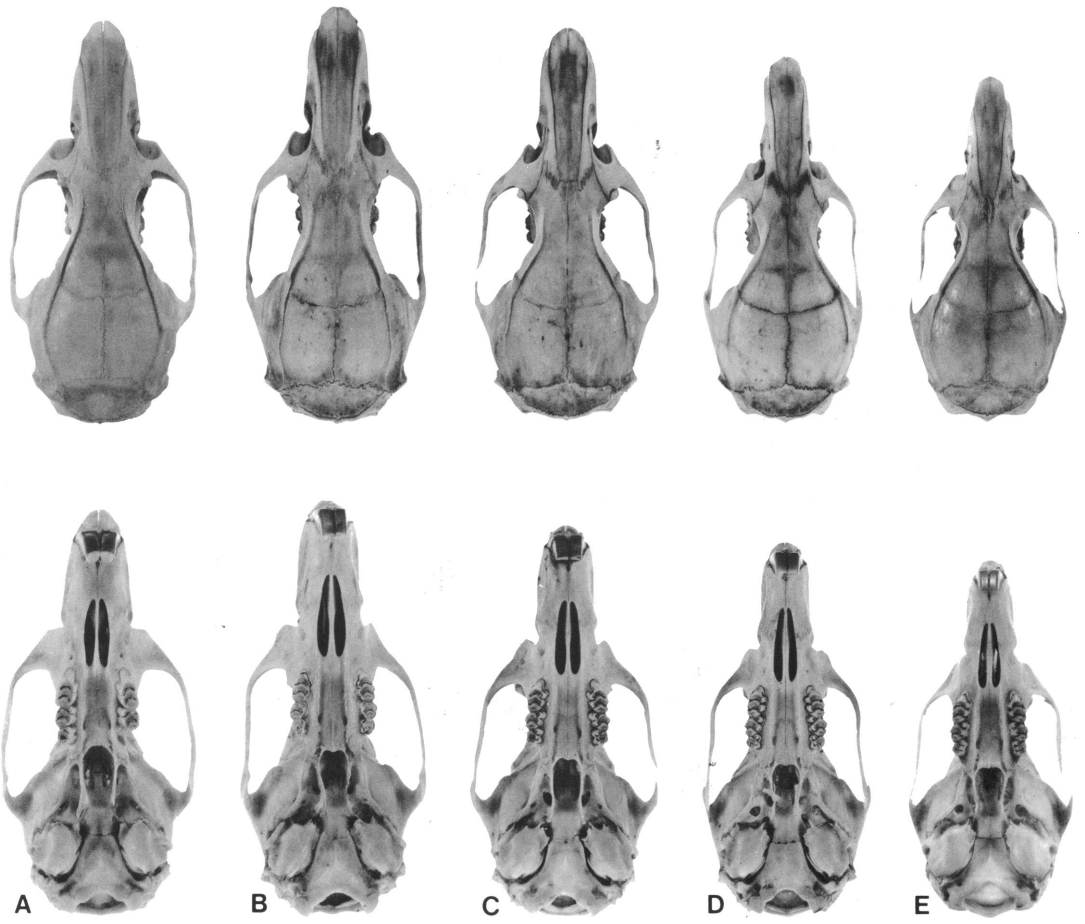

FIG. 64. Views of crania contrasting adult *Sundamys muelleri* from Sumatra (A) with *Rattus stoicus* of different ages from Henry Lawrence Island in the Andamans (B–E). A, AMNH 102849. B, old adult, USNM 111845. C, adult, USNM 111851. D, young adult, USNM 111850. E, young adult-juvenile, USNM 111857. All natural size.

tives. Our assessment of skins, skulls, and dentitions in our samples of *Sundamys* and *Rattus verecundus* (as well as samples of *R. niobe* and *R. richardsoni*) supports the proposition that *Rattus verecundus* and its allies on New Guinea had a different evolutionary history than the species of *Sundamys* on the Sunda Shelf. We disagree with the composition of subgenus *Stenomys* as envisioned by Misonne but when represented by *R. verecundus, R. niobe, R. richardsoni,* and possibly others, we agree with him that *Stenomys* should not be used to embrace species native to the Indo-Malayan region.

RATTUS STOICUS AND *RATTUS PALMARUM*

In his monograph on Indian Murinae, Ellerman (1961, p. 613) wrote about *Rattus muelleri* and included the Andaman Islands and the Nicobar Islands within the geographic distribution of the species. He noted this about one specimen: "There is a skull in our collection from the Andaman Islands which was collected very many years ago and to which there is a skin, which I would also call a form of *mülleri.* Perhaps it represents one of the Andaman forms named by Miller, but

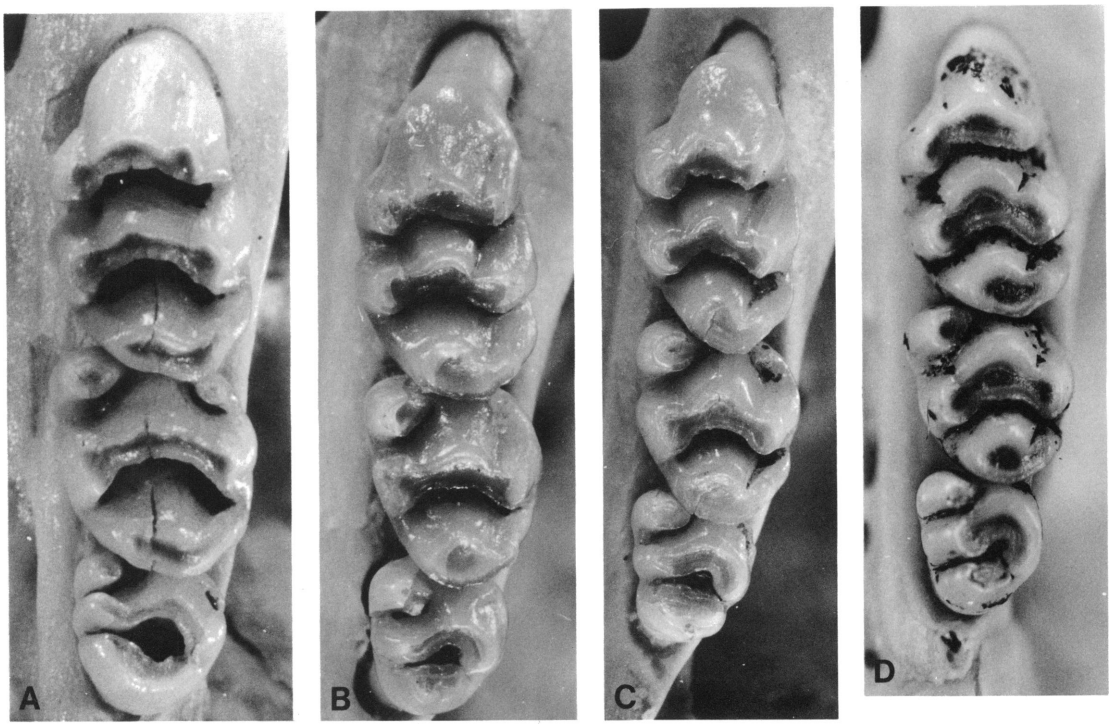

FIG. 65. Occlusal views of left upper molar rows in *Sundamys* (A) and *Rattus* (B–D). A, *S. muelleri* (AMNH 103529). B, *R. palmarum* (NMW B-27). C, *R. lugens* (AMNH 103021). D, *R. stoicus* (USNM 111830). All ×10.

at the moment I have not been able to identify it exactly." And "In 1951 a specimen was sent to London from the Nicobar Islands which I identified as *mülleri,*" was the basis for his Nicobar record.

A taxonomic revision of the rats occurring in the Andaman and Nicobar islands is being prepared by Musser (MS.), who has examined most of the specimens from there, including all holotypes. His results indicate that three kinds occur in the Andaman Islands (table 28): the large-bodied *Rattus stoicus*; the Asian house rat, *Rattus rattus andamanensis*; and the European house or black rat, *Rattus rattus rattus.* The first two species are native, the third was introduced to Barren Island. On the Nicobar Islands, the native rat is *Rattus palmarum*; *Rattus rattus rattus* has been collected on Nanhauri Island; *Rattus rattus diardii,* the Asian house rat that is widespread over the Sunda Shelf, has been introduced to Little Nicobar and Great Nicobar islands (table 28).

Sundamys muelleri does not occur on the Andaman Islands. The specimen from there that Ellerman (1961) identified as *Rattus muelleri* is BM 81.11.10.4, which is a skin and skull of an adult *Rattus stoicus.* Like *S. muelleri, R. stoicus* is large and chunky (table 31). Its upperparts are tawny brown, the underparts are gray. The fur is thick, shaggy, and harsh to the touch; semi-rigid translucent spinelike hairs occur throughout the pelage and provide a densely spinous texture in some specimens (the holotype of *Mus rogersi,* for example). The feet are brown. The tail is shorter than the head and body in most specimens and brown on all surfaces. Females have eight mammae but the arrangement is different than in *S. muelleri*: there is one postaxillary pair, one abdominal pair, and two inguinal pairs. *Sundamys muelleri* has a pectoral pair, a postaxillary pair, and two inguinal pairs.

The skull of *Rattus stoicus* is large and stocky (table 31; fig. 64). It has a relatively

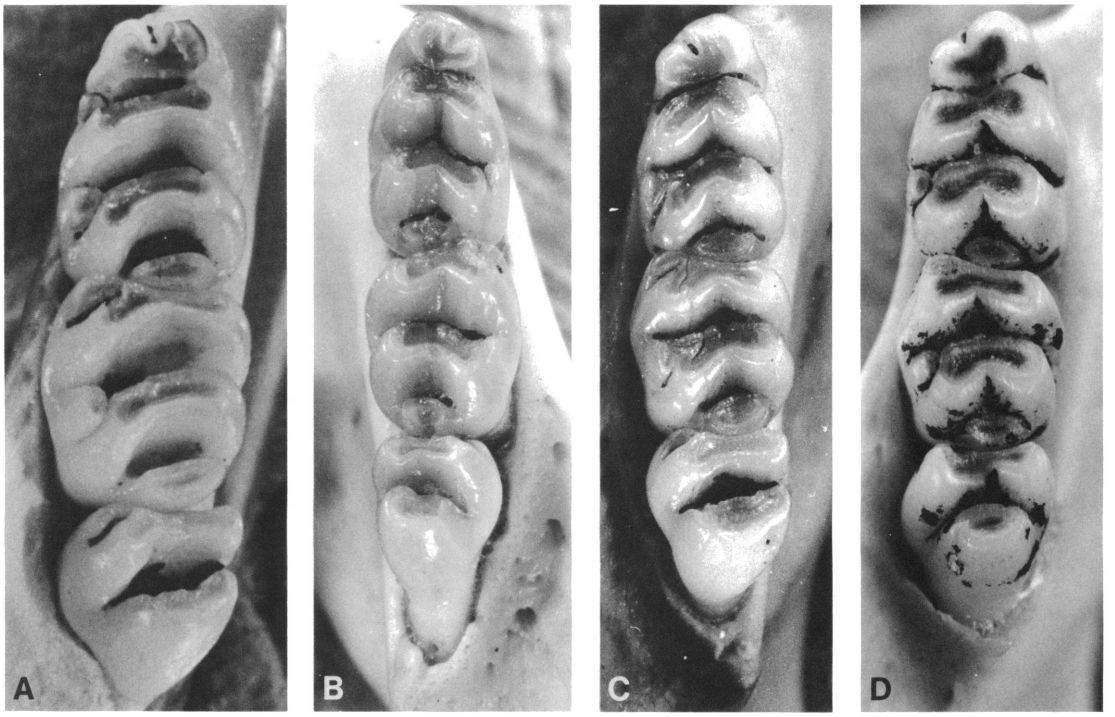

FIG. 66. Occlusal views of left (right in B) lower molar rows from same specimens of *Sundamys* (A) and *Rattus* (B–D) shown in figure 65. A, *S. muelleri*; B, *R. palmarum*; C, *R. lugens*; *R. stoicus*. All ×10.

long rostrum compared with the braincase, long incisive foramina that do not extend past the anterior margins of the first molars in most specimens, small sphenopalatine vacuities in the walls of the mesopterygoid fossa, and small bullae relative to cranial size. In all other features, the skull closely resembles that of *Rattus palmarum* from the Nicobar Islands and the skull of *Rattus lugens* from the Mentawi Islands (figs. 63 and 64). Most of the cranial distinctions between *Sundamys muelleri* and *R. stoicus* are those that set *Sundamys* apart from *Rattus*.

The molar rows are short relative to lengths of palatal bridge and skull in *R. stoicus*, proportions that are characteristic of *Rattus* and not *Sundamys*. All other features of the molars in *R. stoicus*—relative size, number of roots, height of crowns, and cusp patterns—closely resemble those in *Rattus palmarum* and other species of *Rattus* and are unlike the molars of *S. muelleri* (figs. 65 and 66).

We have not seen the specimen from the Nicobar Islands that Ellerman (1961) identified as *Rattus muelleri*. Musser sent an inquiry about it to Ms. Paula Jenkins at the British Museum (Nat. Hist.) and she replied that "It is possible that Ellerman handled and returned the Nicobar Island specimen of *R. muelleri* as a private arrangement, since there is no trace of it in the collection, register or correspondence files." The only large rat known from the Nicobars is *Rattus palmarum*, which in body size is similar to that in many samples of *S. muelleri* (table 31). We suspect it was an example of *R. palmarum* that Ellerman examined.

The name, *palmarum*, is one of nine that has been applied to samples of *Rattus* from the Nicobar Islands and from the islands off the southwestern coast of Sumatra beyond the 100 fathom line (table 29). Musser and Califia (1982) bring these taxa together into a *Rattus palmarum* group. Whether the names represent one or several species is uncertain. All are rats of large body size, tail as long or slightly longer than the body, brown or blackish upperparts, white or gray underparts, and

FIG. 67. *Rattus palmarum* from the Nicobar Islands. A copy of the holotype originally published as Plate 3 in Zelebor (1869).

TABLE 29
Taxa in the *Rattus palmarum* Group

Taxon	Author and Date	Type Locality
palmarum	Zelebor (1869, p. 26)	Nicobar Islands
burrus	Miller (1902, p. 768)	Trinkat Island, Nicobars
burrescens	Miller (1902, p. 771)	Great Nicobar Island
simalurensis	Miller (1903a, p. 458)	Pulau Simalur, off coast of West Sumatra
lugens	Miller (1903b, p. 33)	Pulau Pagi Utara, Mentawai Islands
lasiae	Lyon (1916, p. 446)	Pulau Lasia, off west coast of Sumatra
babi	Lyon (1916, p. 447)	Pulau Babi, off west coast of Sumatra
mentawi	Chasen and Kloss (1927, p. 831)	Pulau Sipora, Mentawai Islands
adustus	Sody (1940, p. 397)	Pulau Enggano, off west coast of Sumatra

10 mammae. Despite their large size, none of the samples represent *Sundamys muelleri.* Features of skins, skulls, and teeth are those characteristic of species in the subgenus *Rattus.* In most of their characters, specimens in the *palmarum* group resemble large-bodied versions of *R. tiomanicus,* which is widespread over the Sunda Shelf and also occurs on several islands off the Shelf (Musser and Califia, 1982). If *Sundamys muelleri* occurs in the Nicobar Islands, or on any of the islands west of Sumatra beyond the 100 fathom line, it is not yet represented by specimens.

TAEROMYS CALLITRICHUS AND *TAEROMYS CELEBENSIS*

We noted in previous sections that *Rattus infraluteus* had been morphologically linked to *Rattus callitrichus* (Ellerman, 1947–1948; Laurie and Hill, 1954) and *Rattus muelleri* to *Rattus celebensis* (Misonne, 1969). Both *callitrichus* and *celebensis* are native to Sulawesi. Twelve years ago Musser (1970b) reviewed the taxonomy of *callitrichus* but little was ever reported about habits, habitats, or phylogenetic relationships of either *callitrichus* or *celebensis.* During the period 1973 to 1976 Musser worked in the forests on Sulawesi and collected specimens of each species. He later found that the species are not members of *Rattus* but of the genus *Taeromys,* proposed by Sody in 1941 (p. 260) with *celebensis* as the type species. A taxonomic revision of *Taeromys* is being prepared by Musser (in MS.) and for our purposes we introduce here the species by summarizing them

TABLE 30
The Species of *Taeromys*

Taxon	Author and Date	Current Status
Mus celebensis	Gray (1867, p. 598)	*Taeromys celebensis*
Mus callitrichus	Jentink (1879, p. 12)	*Taeromys callitrichus*
Rattus microbullatus	Tate and Archbold (1935, p. 8)	
Taeromys tatei	Sody (1941, p. 313)	
Rattus simpsoni	Ellerman (1949, p. 191)	
Rattus maculipilis	Laurie and Hill (1954, p. 115)	
Rattus maculipilis jentinki	Laurie and Hill (1954, p. 115)	
Rattus punicans	Miller and Hollister (1921, p. 98)	*Taeromys punicans*
Rattus hamatus	Miller and Hollister (1921, p. 107)	*Taeromys hamatus*
Rattus taerae	Sody (1932, p. 158)	*Taeromys taerae*
Rattus arcuatus	Tate and Archbold (1935, p. 9)	*Taeromys arcuatus*

[a] Based on Musser's study of holotypes and other specimens.

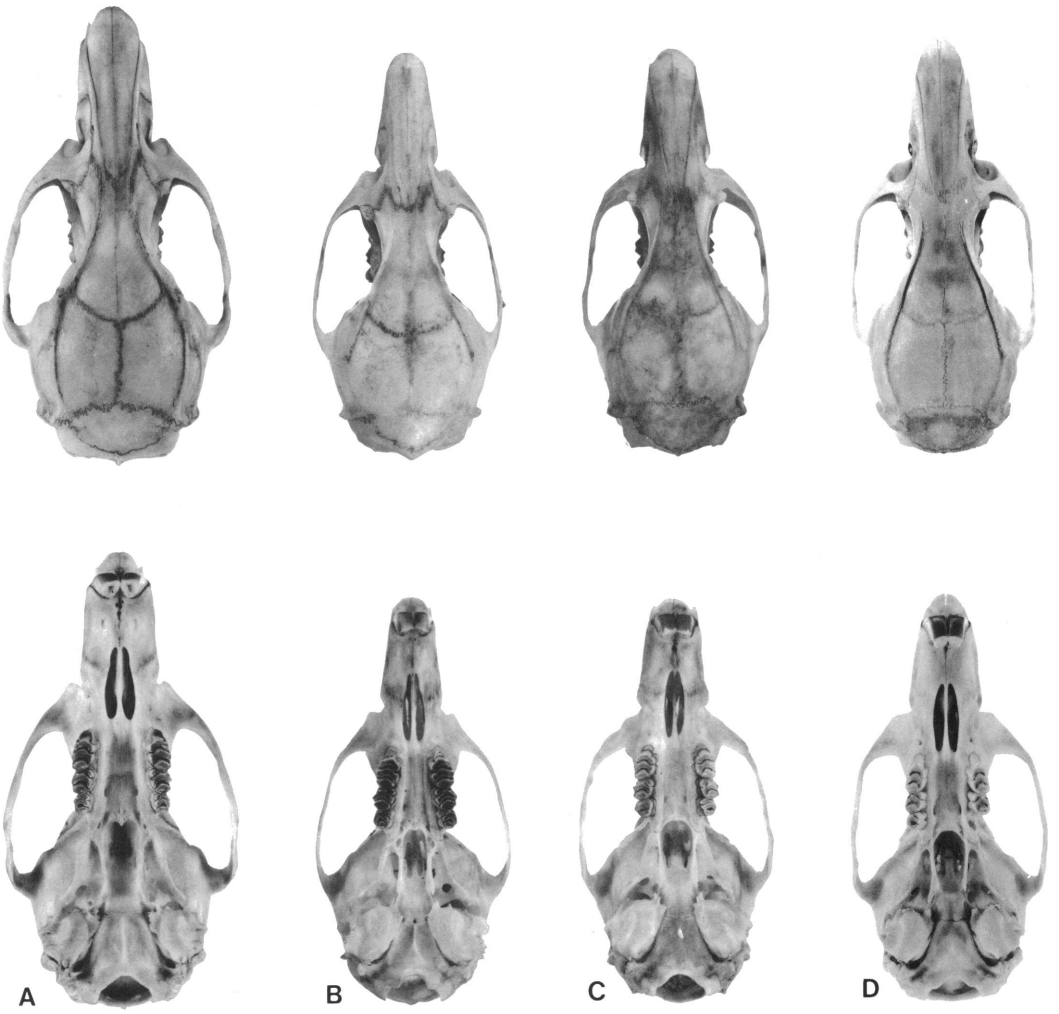

FIG. 68. Views of crania contrasting adult *Sundamys* (A and D) with *Taeromys* (B and C). A, *S. infraluteus,* Sabah (USNM 292759). B, *T. callitrichus,* Central Sulawesi (AMNH 224638). C, *T. celebensis,* Central Sulawesi (AMNH 224643). D, *S. muelleri,* Sumatra (AMNH 102849). All natural size.

and giving the scientific names associated with each in table 30.

The reported alliances between *infraluteus* and *callitrichus* on the one hand and *muelleri* and *celebensis* on the other requires testing for if these two sets of species are really close relatives then the species of *Taeromys* may belong in *Sundamys* and would become one of the several groups native on Sulawesi that could be directly tied to a cluster on the Sunda Shelf. We examine first the relationship between *Sundamys infraluteus* and *Taeromys callitrichus,* then compare *S. muelleri* with *T. celebensis.*

A stout body, tail longer than the head and body, and six mammae are common to *Taeromys callitrichus* and *Sundamys infraluteus.* Color of the pelage is also similar in the two species. Both have dark brown upperparts and buffy gray underparts; specimens of *T. callitrichus* do not have the rich ochraceous wash so common to the *S. infraluteus* from Sabah and are pigmented more like the Sumatran specimens. Both species have dark

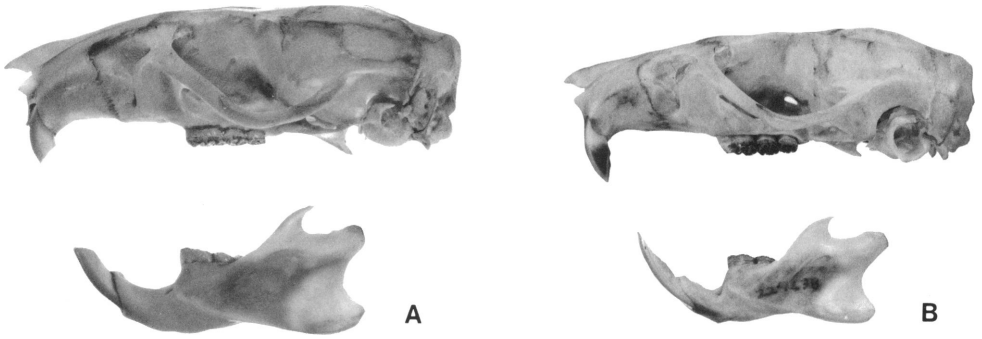

FIG. 69. Views of crania and dentaries of adult *Sundamys infraluteus* (A) and *Taeromys callitrichus* (B). Different views of the same specimens are shown in figure 68.

brown ears and brown feet. Here the resemblance ends. *Taeromys callitrichus* is a smaller rat (compare the values listed in tables 24 and 31). The fur of *T. callitrichus* is very soft and shiny. The hairs are thin, the coat dense, and the guard hairs barely extend beyond the overfur. The appearance and texture contrasts sharply with the harsh and shaggy fur of *S. infraluteus* with its long black guard hairs. The hind feet of *T. callitrichus* are nearly as big as some specimens of *S. infraluteus,* but they are long and slender, not large and stocky, and they are longer relative to length of head and body. Finally, the tail of *T. callitrichus* is blackish brown on its basal half and white over its distal half. The surfaces appear smooth and gleaming—a glistening black and white, especially in live rats. The appearance and texture is due to short hairs (three to each scale) that are no longer than the length of a scale and difficult to see without magnification, and the position of the scales on the tail. Each row consists of squarish scales, and the rows do not overlap one another so each scale is flat against the tail. The configuration resembles the scalation in some species of *Melomys* (see fig. 22 in Tate, 1936, p. 591). The tail in *S. infraluteus* is dark brown all over and the surface is rough and slightly hairy. The tail hairs are thick and long, each extending over two scales. Each row of scales slightly overlaps the row behind it. This texture and position of the scales is typical of most murids.

The skulls of *Taeromys callitrichus* are smaller than those of *S. infraluteus* (tables 24 and 31) and they are dissimilar in other features (figs. 68 and 69). Compared with *S. infraluteus,* the skulls of *T. callitrichus* appear delicate and are relatively smooth; the ridges bounding dorsolateral margins of the interorbital and postorbital regions are low and inconspicuous, the temporal ridging is barely evident (high, thick, and prominent ridges in *S. infraluteus*). The braincase of *T. callitrichus* is relatively large compared with the rostral area (relatively smaller in *S. infraluteus*). The rostrum is moderately long, slender, tapered distally, and delicate in appearance (long, wide, rectangular in dorsal or ventral view, and chunky rather than delicate in *S. infraluteus*). Dorsal processes of each lacrimal are large and conspicuous (relatively very small and inconspicuous in *S. infraluteus*). The zygomatic plates do not partially conceal the nasolacrimal capsules in *T. callitrichus* as do the plates in *S. infraluteus.* The upper molar rows in *T. callitrichus* diverge posteriorly (nearly parallel in *S. infraluteus*). The sphenopalatine vacuities in walls of each mesopterygoid fossa are relatively much wider and longer (very small and inconspicuous in *S. infraluteus*). Each pterygoid fossa is breached by a large sphenopterygoid opening in *T. callitrichus* (either absent or tiny in *S. infraluteus*). The bullae are larger, both actually and especially relative to size of cranium, slightly inflated, and not set as close to the squamosal bones. The outer surface of each mastoid is actually larger and slightly inflated (actually smaller and not inflated in *S. infraluteus*). In the alisphenoid region of *T. callitrichus,* each

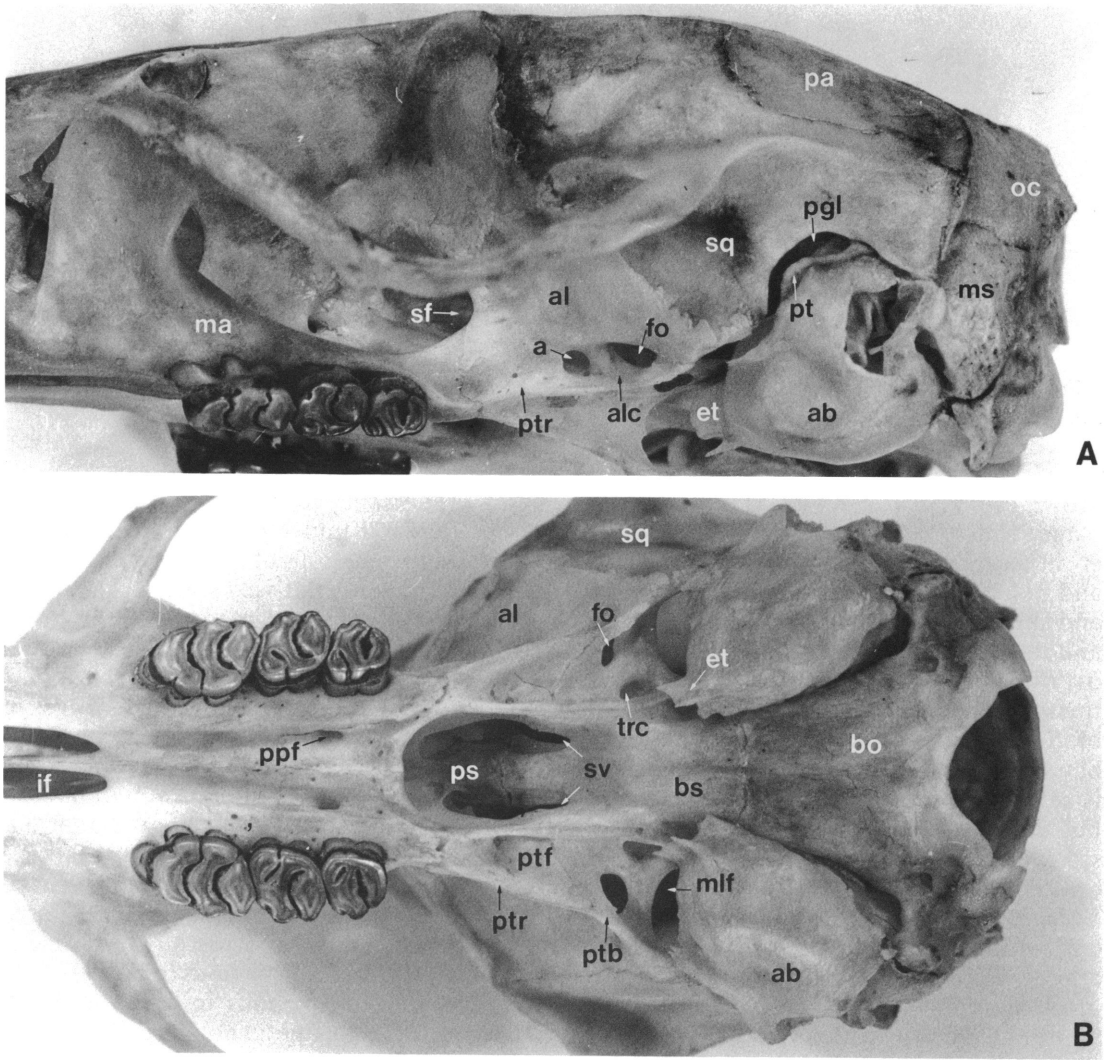

FIG. 70. Lateral (A) and ventral (B) cranial views of *Taeromys celebensis* (AMNH 224643). *Abbreviations:* **a**, anterior opening of the alisphenoid canal; **ab**, auditory bulla; **al**, alisphenoid bone; **alc**, alisphenoid canal, which is an open channel; **bo**, basioccipital bone; **bs**, basisphenoid bone; **et**, bony eustachian tube; **fo**, foramen ovale; **if**, incisive foramina; **ma**, maxillary bone; **ms**, mastoid portion of the petromastoid; **mlf**, middle lacerate foramen; **oc**, occiput; **pa**, parietal bone; **pgl**, postglenoid vacuity; **ppf**, posterior palatine foramen; **ps**, presphenoid bone; **pt**, periotic portion of the petrosal; **ptb**, pterygoid bridge; **ptf**, pterygoid fossa; **ptr**, pterygoid ridge; **sf**, sphenoidal fissure; **spt**, sphenopterygoid vacuity; **sq**, squamosal bone; **sv**, sphenopalatine vacuity; **trc**, transverse canal. See text for additional description.

alisphenoid canal is an open channel and not bounded by a lateral strut of alisphenoid bone (fig. 70A) (such a strut is present in most specimens of *S. infraluteus*).

We detect no derived cranial features shared by *Taeromys callitrichus* and *S. infraluteus* that indicate close phylogenetic affinity. Both species have short incisive foramina, a short palatal bridge (that is, the posterior margin of the palatal bridge barely extends posterior to back margins of the third molars), and, judged by the configuration of the pterygoid

plates and sizes of the stapedial foramina, a similar pattern of carotid arterial circulation in the basicranium. These are primitive features and have a wide distribution within murid rodents.

The molars of *Taeromys callitrichus* are large, especially relative to size of cranium and mandible, slightly hypsodont, and have simple occlusal patterns. In their hypsodonty, the number of roots anchoring each molar, the degree of overlap among molars in each row, and the relative size of molars forming each row, the teeth are closely similar to the relative hypsodonty, proportions, overlap, and number of roots found in *S. infraluteus.* Cusp patterns in the two species also resemble each other (figs. 71 and 72). Broad, thick, and arcuate laminae form the occlusal surfaces. The primary differences between the two species is that the first and second laminae on each first upper molar and the anterior lamina on each second and third molar are straighter in *T. callitrichus* than are the counterparts in *S. infraluteus*; cusp t3 on each first upper molar in *T. callitrichus* is small and inconspicuous compared with the larger central anterolingual cusps; no posterior cingulum occurs on each first upper molar (present in *S. infraluteus*; cusp t3 on each second upper molar is absent or very small in *T. callitrichus* but present and usually large in *S. infraluteus*; and the anterolabial cusp on each second lower molar is small or absent in *T. callitrichus* but large in *S. infraluteus.*

Taeromys callitrichus is terrestrial and lives in forests. *Taeromys celebensis* is found in the same forests. It can be trapped on the ground but is also found above the ground in trees and tangles of woody vines. The species is the semi-arboreal component of *Taeromys,* which contains mostly ground-dwelling rats. *Taeromys celebensis* is smaller than *Sundamys infraluteus* and similar to Sumatran *S. muelleri* in body size (compare tables 19 and 31). It is grayish brown above and either white, cream, or pale yellow on the venter. The general coloration resembles that of most *S. muelleri.* However, *T. celebensis* is a grayer rat and its pelage, like that of *T. callitrichus* is soft and smooth, shiny in appearance and silky in texture. The tail of *T. celebensis* is bicolored and in many specimens the distal white area may take up two-thirds or three-fourths of the length. The texture and position of the tail scales is similar to that in *T. callitrichus.* Although superficially similar in color and body size to *S. muelleri, T. celebensis* differs from that species in some of the same skin and fur features that distinguish *T. callitrichus* and *S. infraluteus.*

The skull of *T. celebensis* is similar in conformation to that in *T. callitrichus* (fig. 68). *Taeromys celebensis* has a wider rostrum that appears more sturdy, zygomatic plates that do not extend as far forward beyond the zygomatic arches, relatively smaller molars compared with skull size, most specimens lack sphenopterygoid vacuities in the pterygoid fossae, and slightly smaller bullae that are more tightly attached to the squamosal bones.

Except for size and sphenopterygoid vacuities, *Taeromys celebensis* is distinguished from *S. muelleri* by the same set of cranial features that contrast *T. callitrichus* and *S. infraluteus.* Although similar in size to *S. muelleri,* we find no special cranial features that suggest the two species are members of the same genus or are phylogenetically closely related.

We understand why Misonne (1969), who analyzed the distribution of dental characters among Indo-Australian murids, placed *celebensis* and *muelleri* in the same group. Their molars are very similar (figs. 71 and 72). They differ from each other in many of the same characters that distinguish *T. callitrichus* from *S. infraluteus.* Compared with *S. muelleri, T. celebensis* has straighter laminae, a relatively small cusp t3 compared with the other cusps on the front lamina of each first upper molar, lacks a posterior cingulum at the back of each first upper molar, lacks cusp t3 on each second molar in most specimens (if present it is small), and a small anterolabial cusp on each second lower molar that is not evident in some specimens.

The differences in cusp patterns between *Taeromys celebensis* and *S. muelleri* and between *T. callitrichus* and *S. infraluteus* reflect the derived condition in species of *Taeromys* and the primitive state in the two *Sundamys.* Some of the contrasts in traits of skulls and skins also represent differences between the

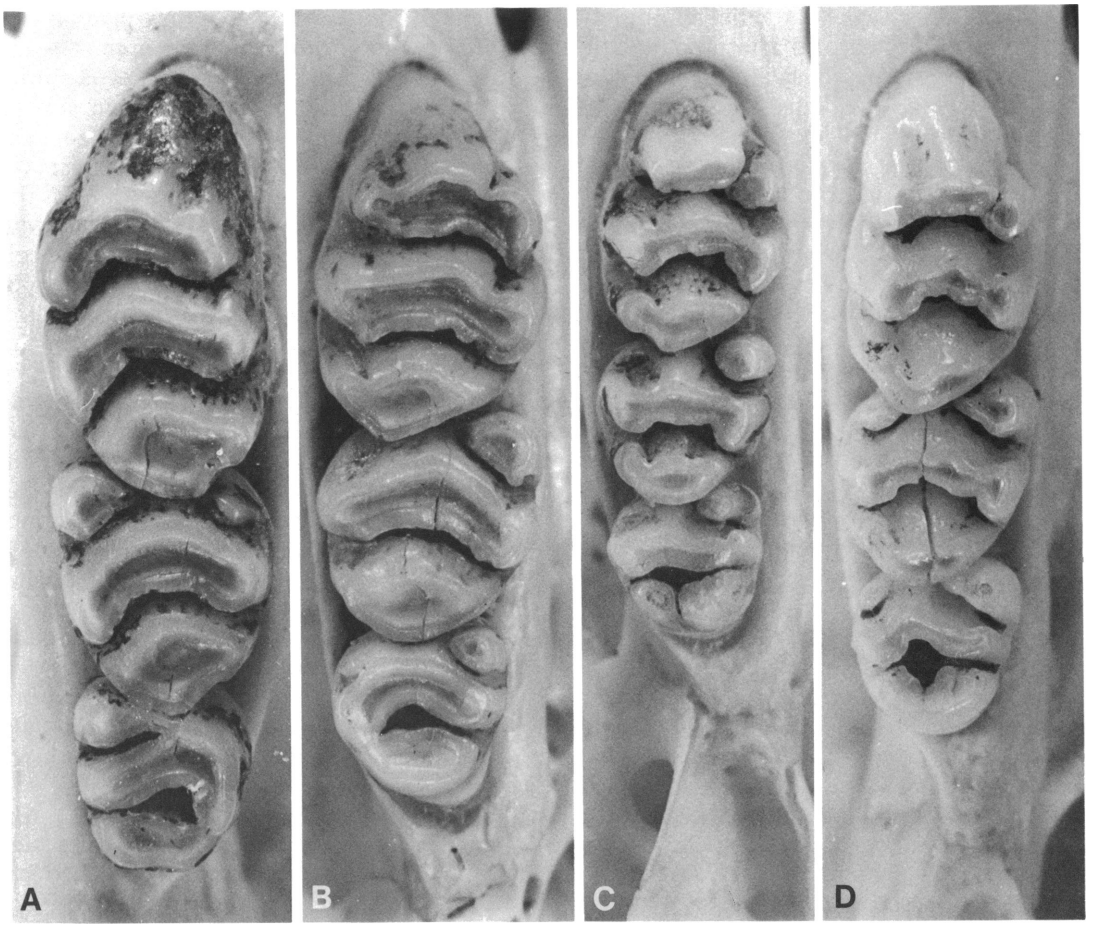

FIG. 71. Occlusal views of upper molar rows in *Sundamys* (A and D) and *Taeromys* (B and C). A, *S. infraluteus,* Sabah (USNM 292764). B, *T. callitrichus,* North Sulawesi (RMNH 21255). C, *T. celebensis,* Central Sulawesi (AMNH 224073). D, *S. muelleri,* Borneo (AMNH 103767). All ×10.

specialized condition in *Taeromys* and the primitive counterpart in *Sundamys.*

SUNDAMYS AND *BERYLMYS*

In a report on the unresolved taxonomic problems associated with Malayan murids, Medway and Yong (1976, pp. 46–47) wrote of *muelleri* and *bowersii* that "The names *Stenomys* (by Ellerman, 1974) and *Bullimus* (by Misonne, 1969) have been used to link rats including the Peninsular Malaysian taxa *validus* and *ferreocanus,* listed by Chasen (1940) as subspecies of *R. muelleri* and *R. bowersii* respectively. Differences in serology and karyotype, however, indicate that these rats are not closely related and cannot be associated in a natural phylogenetic group."

Differences between *muelleri* and *bowersii* in cranial and dental traits reinforce Medway and Yong's assessment. Ellerman (1947–1948) united *Rattus muelleri* and *R. bowersii* in the subgenus *Stenomys* claiming they shared relatively small bullae compared with skull size. That has been the only cranial feature linking *muelleri* and *bowersii.* Misonne (1969) included *muelleri* and *bowersii* in the subgenus *Bullimus* of *Rattus* because they, and other species (table 13), had, to his eye, similar cusp patterns. In the present report, we bring together *bowersii, mackenziei, manipulus,* and *berdmorei* under the genus *Be-*

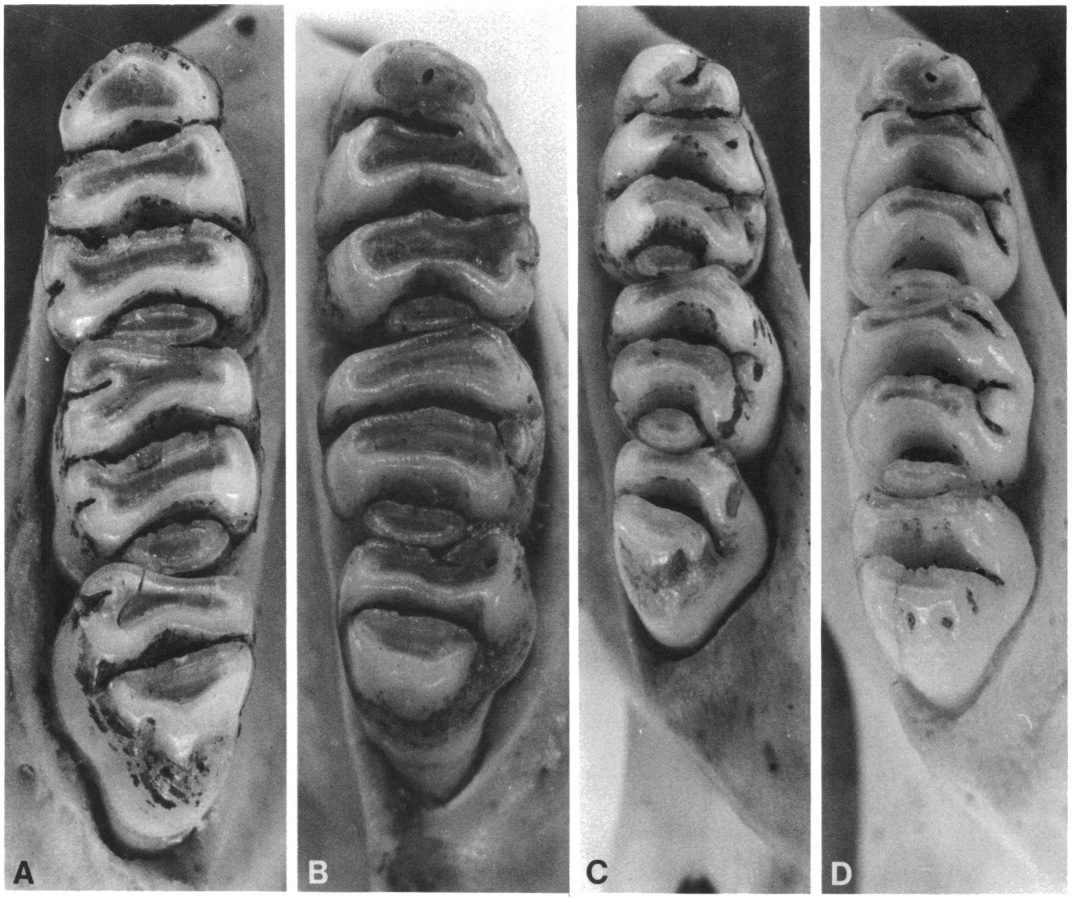

FIG. 72. Occlusal views of lower molar rows from the same specimens of *Sundamys* (A and D) and *Taeromys* (B and C) shown in figure 71. A, *S. infraluteus*; B, *T. callitrichus*; C, *T. celebensis*; D, *S. muelleri*. All ×10.

rylmys, the diagnosis of which excludes all the species, including *muelleri,* that Ellerman placed in *Stenomys* (table 13) and all those Misonne united under *Bullimus.* Based on our study of skins, skulls, and teeth, there is no evidence for uniting *muelleri* and *bowersii* in the same genus or even regarding them as phylogenetically closely related.

Other than being large in body size, the two species are dissimilar in most traits. Crisp iron gray fur over the upperparts and white pelage on the upperparts is a combination of texture and pattern that is unique to *Berylmys* and contrasts with the coarse and shaggy fur of *Sundamys muelleri* and its brown and grayish coloration. Different also is the tail pattern: the tail of *S. muelleri* is dark brown, that of *B. bowersii* and most of the other species of *Berylmys* is patterned with white. The same mammae number and position is shared by *B. bowersii* and *S. muelleri* but the other species of *Berylmys* have ten mammae, not either six or eight as in *Sundamys.*

The conformation of the cranium is not the same in *Berylmys bowersii* and *S. muelleri* (fig. 73; also compare figs. 18 and 52). Compared with the skull of *S. muelleri,* the rostrum of *B. bowersii* is tapered distally and the nasolacrimal capsules form prominent bulges on its side; the rostrum in *S. muelleri* is wide, nearly straight-sided, appears almost swollen, and the nasolacrimal capsules are indistinct swellings. From either a dorsal or ventral view, the cranium of *B. bowersii* and

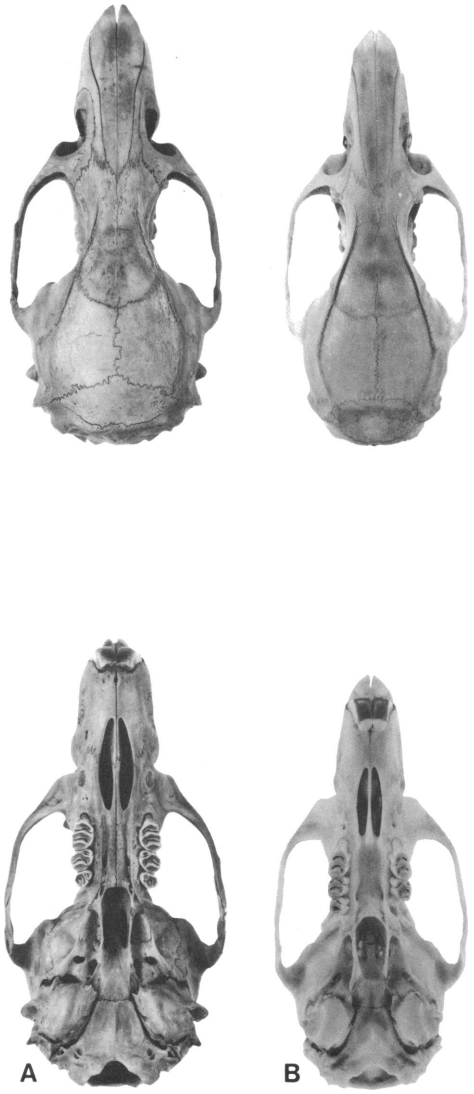

FIG. 73. Views of crania contrasting adult *Berylmys bowersii* (A) with *Sundamys muelleri* (B). A, northern Burma, AMNH 115238. B, Sumatra, AMNH 102849. Natural size.

the other species of *Berylmys* is triangular; the outlines are rectangular in crania of *Sundamys*. Contours of the skull are round and nearly smooth in *B. bowersii,* the supraorbital outlines are marked by low beading that passes onto the anterior half of the braincase to form low and inconspicuous temporal ridges; the thick and high supraorbital and temporal ridges in *S. muelleri* are prominent and define the vase-shaped outline of the interorbital and postorbital regions and braincase. *Berylmys bowersii* and the other species in the genus have a round and wide braincase, and the occiput is nearly as wide; the back of the occiput is expansive in area and not vertical but slants forward. The braincase is narrower in *S. muelleri* and the occiput is much narrower than the braincase at its widest point; the back of the skull is either vertical or slants back so it overhangs the occipital condyles, and the surface area is relatively less compared with the expansive area in *B. bowersii.* The zygomatic plates in *B. bowersii* are relatively narrower compared with skull size and do not extend so far forward that they conceal the nasolacrimal capsules (in side view); in *S. muelleri,* the plates are wide and partially hide the nasolacrimal capsules. In the alisphenoid region of *B. bowersii* and the other species of *Berylmys,* the alisphenoid canal is an open channel, the configuration is much like that in species of *Rattus* (figs. 19 and 38B); a wide strut of alisphenoid bone forms the lateral wall of the canal in most specimens of *S. muelleri* (fig. 38A). *Berylmys bowersii* has relatively larger bullae compared with skull size than does *S. muelleri* and the bullar capsules are not as tightly appressed to the squamosal bones; the postglenoid space is large and the periotic occupies relatively less of it compared to the very small postglenoid in *S. muelleri* with its periotic that takes up most of the space between bullar capsule and squamosal (figs. 19 and 38A). In a ventral view, the posterior margin of the bony palate in *B. bowersii* is either anterior to the back surfaces of the third molars or even with them in most specimens of *B. bowersii* and the other species of *Berylmys* (table 3); the posterior palatine foramina are more anterior relative to the second and third molars. The back of the palatal bridge in *S. muelleri* and the other species of *Sundamys* extends slightly past the third molars in all specimens; the posterior palatine foramina is relatively more posterior (figs. 19 and 39).

The contrast in dental characters between *Berylmys* and *Sundamys* is as great as it is in cranial traits. The difference in color of incisor enamel is especially evident. The species of *Berylmys* are called white-toothed rats (Marshall, 1977b, for example) because

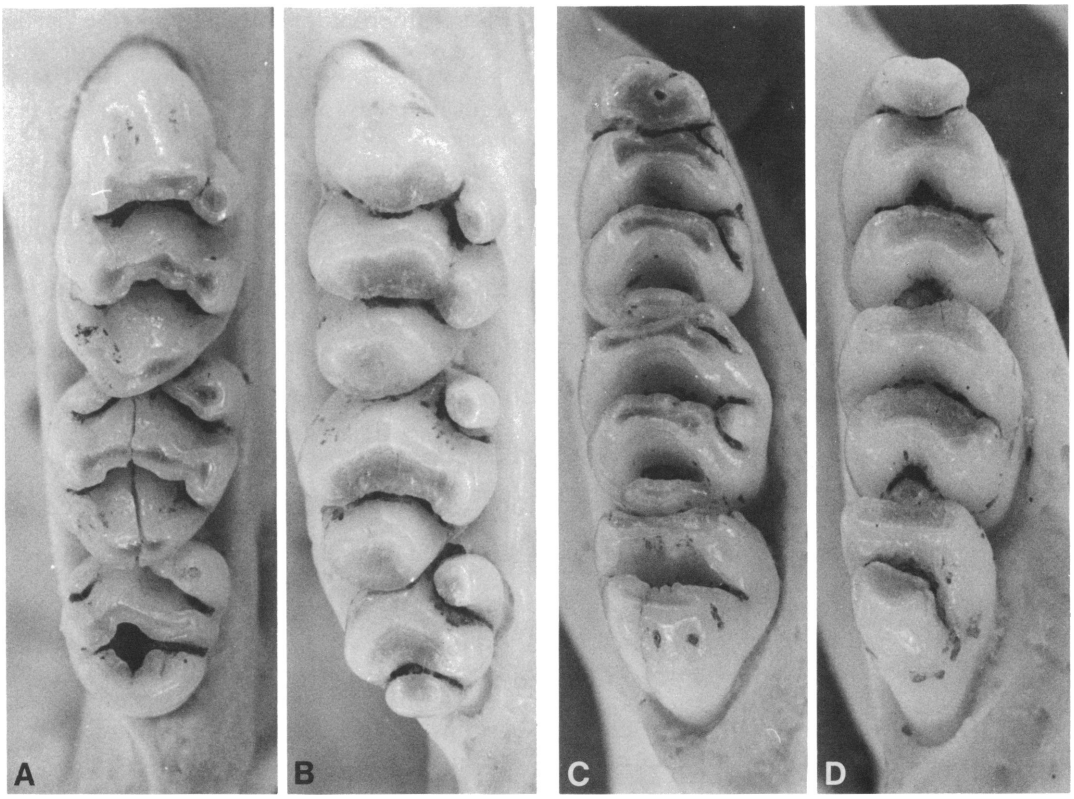

FIG. 74. Occlusal views of right upper (A and B) and lower (C and D) molar rows in *Sundamys* and *Berylmys*. A and C, *S. muelleri*, Borneo (AMNH 103767). B and D, *B. bowersii*, northern Burma (AMNH 115233). All ×10.

most specimens have whitish incisors; the variation ranges from an ivory hue to pale orange. All specimens of *Sundamys* have deep orange incisors. Whitish incisors are uncommon among genera of Indo-Australian murids and probably represent a derived condition (Musser, 1981a).

The molars of *Berylmys* and *Sundamys* are similar in the number of roots beneath each tooth and the degree of overlap among the teeth in each row but are otherwise unlike one another (fig. 74; also compare figs. 20 and 21 with fig. 41). We do not share Misonne's view of close similarity in dental patterns among the species in the two genera. Compared with the molars of *S. muelleri*, those in *B. bowersii* differ in that 1) each third molar is relatively much smaller compared with the others in each row; 2) the cusp patterns are much simpler, the cusps forming each lamina have so coalesced that the laminae appear as non-cuspidate arcuate structures, and the laminae are tightly pressed against each other (laminae are wide and cuspidate in *S. muelleri*, the occlusal surfaces are more complicated, and the laminae are far apart; 3) cusp t3 on each first upper molar is so small that it is quickly worn away and not evident (large and prominent in *S. muelleri*); 4) cusp t9 on each first and second upper molar is merged with the central cusp to the point that it is not evident and that lamina appears to consist of only two broadly merged cusps (although broadly connected to the central cusp, cusp t9 is still large and conspicuous in *S. muelleri*); 5) no posterior cingulum at the back of each first upper molar; 6) cusp t3 on each second and third upper molar is not present in most specimens (occurs in most specimens of *S. muelleri*); 7) each third upper molar is simple, consisting of a large cusp t1, an arcuate lamina, and a small oblong cusp

at the back of the tooth (more complex in *S. muelleri,* with cusps t1 and t3, a wide lamina, and a broad posterior lamina formed of two cusps); and 8) simple occlusal patterns on the lower molars due to a small front lamina on each first lower molar and the lack of anterolabial cusps on the second and third molars and many labial cusplets (a large front lamina on each first lower molar, anterolabial cusps on the second and third lowers, and many labial cusplets form more complicated occlusal surfaces in *S. muelleri*).

In some features (texture of pelage, larger bullae, configuration of the alisphenoid regions, conformation of the braincase and back of the occiput, color of incisors, relatively small third molars, tight packing of laminae, and simple cusp patterns) of *B. bowersii* represent specializations; considering these traits, *S. muelleri* and the other species of *Sundamys* are more primitive rats.

Berylmys bowersii and *S. muelleri* also differ in chromosomal features (table 2). Because of their different diploid number (40 in *B. bowersii,* 42 in *S. muelleri*) and different X-chromosome (telocentric in *B. bowersii,* submetacentric in *S. muelleri*), Yong (1968) did not think the species showed close affinity to one another. Later, Yong (1969a, p. 265) wrote that "They differ in their X-chromosome, their autosome composition, and their diploid number. The karyotype of *R. muelleri* is more similar to that of subgenus *Rattus,* while the karyotype of *R. bowersii* bears resemblance to that of *Rattus* (*Berylmys*) *berdmorei.* These two rats are therefore most probably the results of two different lines of evolution." Results of Yosida's (1973) chromosomal study were similar. He placed *muelleri* in "Group 1. Species with Karyotypes Similar to the Asian Black Rat" and *bowersii* in "Group 2. Species with Lower Chromosome Number than 2n=42 by Robertsonian Fusion." From our point of view, the dissimilarity between *B. bowersii* and *S. muelleri* in chromosomal traits, combined with the differences in characters associated with skins, skulls, and teeth, support the assertions of Yong (1969a) and Medway and Yong (1976) that the species of *Berylmys* have had a different evolutionary history than those of *Sundamys.*

A counterpoint to our interpretation of data from skins, skulls, teeth, and chromosomes are results from analyses of erythrocyte proteins in seven species of Malay rats (*bowersii, muelleri, cremoriventer, cameroni, bukit, sabanus,* and *edwardsi*) reported by Chan, Dhaliwal, and Yong (1979). As the electrophoretic data were interpreted by either a classical or phenetic analysis, the species clustered as follows: *bowersii* and *muelleri*; *cremoriventer, cameroni,* and *bukit*; *sabanus* and *edwardsi.* The second group are part of the genus *Niviventer* as defined by Musser (1981a). The third group belongs in *Leopoldamys* (Musser, 1981a). The first group corresponds to Ellerman's ordering of *bowersii* and *muelleri* as well as Misonne's (1969) but not to ours. Chan, Dhaliwal, and Yong (1979, p. 333) point out that the grouping of *bowersii* and *muelleri* corresponds to Ellerman's subgenus *Stenomys* and their "present result support morphological and cytological evidence that *R. bowersii* and *R. muelleri* may be regarded as members of separate species groups." We also treat them as members of separate groups of species but we place each group in a different genus. We have difficulty interpreting the significance of the electrophoretic data because the results are not presented in the context of what electrophoretic markers may represent primitive versus derived conditions.

Another problem with results from the study by Chan, Dhaliwal, and Yong (1979) is that they analyzed nine loci only. Reporting results based on analysis of allozyme polymorphism at 28 loci in four Indonesian and two French species of *Rattus,* Pasteur et al. (1982, p. 195) point out that analyzing as many loci as possible "increases significantly the probability to have included differentiating loci among the sampled genome." Their pattern of genetic relationships among the species is different from that noted by Chan (1977), who examined some of the same species, but from Malaya, using nine loci. The differences in results, according to Pasteur et al., are "not surprising considering that all available methods of estimating genetic differentiation are based on the assumption that the loci studied are representative of the whole genome." How would the

relationships presented by Chan, Dhaliwal, and Yong (1979) be affected by including more than nine loci in their analysis?

SUNDAMYS AND *TRYPHOMYS*

Native to Luzon Island in the Philippines, *Tryphomys adustus* was never linked closely to *S. muelleri* until 1969 when Misonne (p. 143) wrote: "I have seen only one specimen with missing bullae; there is one abnormal character in M^1: a deep fold between t5 and t6, which however does not seem to be present in M^2; in the skull, the mesopterygoid fossae seem to be very narrow. The hind part of the molars is very broad; there is a trace of Sm in M_1 [anterocentral cusp]; the lower Z [posterior cingulum] is small. The closest species is indeed *R. mülleri,* both of whose upper and lower molars are extremely similar."

The molars of *Sundamys muelleri* are contrasted with those of *Tryphomys adustus* in figures 75 and 76. We see a general resemblance only in number of roots anchoring each molar, degree of overlap among the molars, size of the third molars relative to the other teeth in each row, and cusp patterns but not in details of cusp shapes, their relative positions to one another in each lamina, and the degree to which they have joined within each lamina. The first and second laminae of each first upper molar, and the first lamina on each second upper molar of *T. adustus* consist of discrete cusps that are narrowly joined to one another in each lamina (fig. 75). The configuration is cuspidate rather than noncuspidate as it is in *S. muelleri.* Most of the cusp rows are nearly transverse (arcuate in *S. muelleri.*). All the molars lack posterior cingula (present on first upper molars in 50 percent of the sample of *S. muelleri*), cusp t3 is usually present on each second upper molar but very small and inconspicuous (large and found on every specimen examined of *S. muelleri*), and cusp t3 is usually absent from each third molar (present in most specimens of *S. muelleri*). Cusp t1 on each first upper molar is usually still separate from the central cusp t2 in moderately worn teeth and after more wear joins the central cusp along only a thin part of its medial surface so that cusp t1 remains discrete in most specimens even after much wear (cusp t1 is separate only in young *S. muelleri* and broadly merges with the central cusp in older rats so the anterior lamina appears arcuate and noncuspidate in most specimens). Cusps t3 and t6 on each first upper molar and cusp t6 on each second upper molar are also discrete and they are either oval or elliptical cylinders with the widest plain transverse to the molar row; each is weakly joined to the adjacent and large central cusp t5 (comparable cusps in *S. muelleri* are round and broadly merged with the central cusp). Cusp t6 on each first molar is set off to the labial side of the central cusp t5, connected to it only along a thin segment with most of the cusp remaining separate from the central cusp by a deep groove, which persists in worn teeth as the only groove in an otherwise entire lamina (cusp t6 on each first molar in *S. muelleri* is round in cross-section and broadly merged with the central cusp t5). Cusp t9 on each first and second upper molar is large and set off to the labial side but is broadly joined to the central cusp t8; after wear the two form a broad and nearly transverse lamina (the comparable lamina in *S. muelleri* is bent and never transverse because cusp t9 is angled anterolabially and not labially).

Each third upper molar in *Tryphomys adustus* consists of an elongate and transverse cusp t1 and two broad laminae; the front one is straight and transverse to the main axis of the toothrow in most specimens, gently arcuate in a few others; the second lamina is transverse and noncuspidate (in *S. muelleri,* each third upper molar is formed by a large cusp t1, a smaller cusp t3, a broad and thin curved front lamina, and a bent posterior lamina that is made up of two large cusps).

The three laminae on each first lower molar in *Tryphomys adustus* consists of large, discrete cusps in young adults (fig. 76). The front row is formed from a large anterolingual cusp, roughly crescent-shaped or mushroom-shaped in cross-section, and a much smaller elliptical anterolabial cone. We detect no anterocentral cusp; Misonne (1969), however, noted that the anterocentral cusp, which he referred to as SM, is large in *adustus.* The second and third rows are formed of large

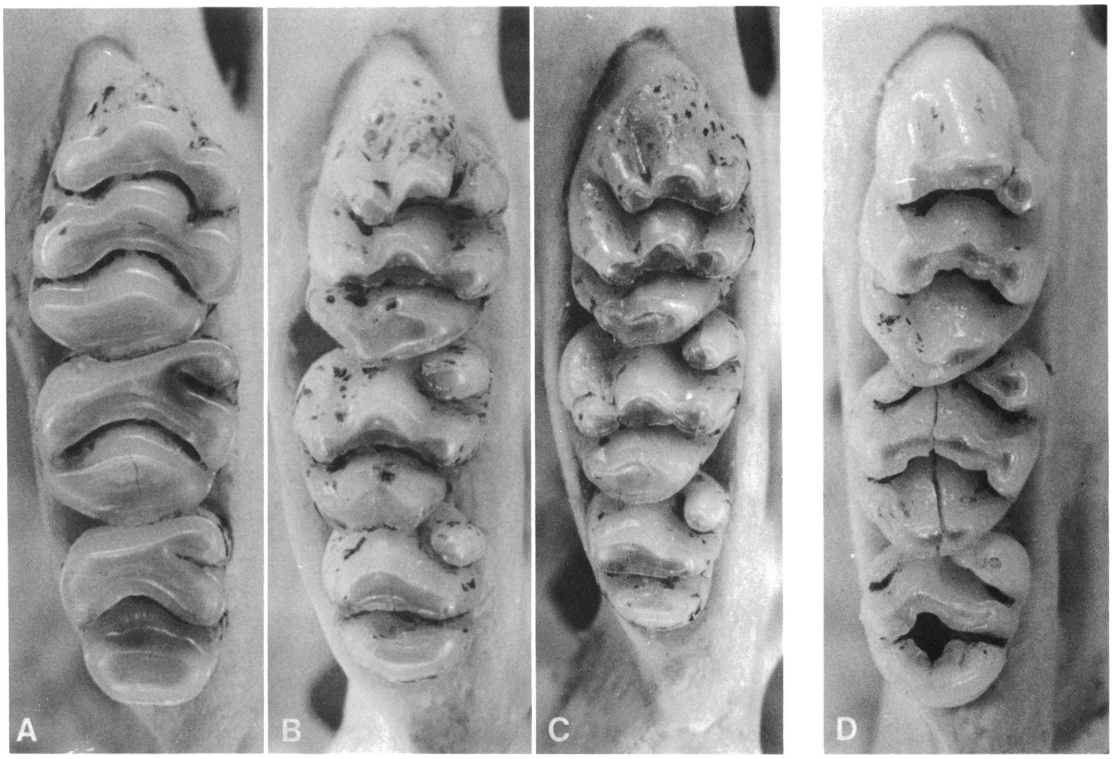

FIG. 75. Occlusal views of right upper molars of *Tryphomys adustus* from Luzon (A–C) and Bornean *Sundamys muelleri* (D). A, old adult (FMNH 62341). B, adult (FMNH 69175). C, young adult (USNM 536765). D, young adult (AMNH 103767). All ×10.

oval cusps that are set at angles and touch along their anteromedial edges in the midline of the tooth so they form laminae with deeply scalloped backs (the three laminae on each first lower molar in *S. muelleri* are non-cuspidate, the second and third lamina are thin, and the anterior lamina is large and bulky and without outlines of the anterolabial and anterolingual cusps that form it). Each second molar consists of a nearly transverse front lamina in which the two cusps have fully merged, and a second row of cusps that are discrete and shaped like the third row of each first molar (the posterior lamina of each second molar in *S. muelleri* is thin and non-cuspidate). Two transverse laminae form the occlusal surface of each third lower molar (the laminae are thinner and not as straight in *S. muelleri*). The posterior cingulum at the back of each first and second molar is a small erect peg (comparable cusps in *S. muelleri* are wide and thick, each forming an additional narrow lamina at the back of the tooth).

To us, the occlusal patterns in *T. adustus* are very different from those characteristics of *S. muelleri*; we do not share Misonne's (1969) opinion about close relationship between the two species based on dental characters.

We detect no cranial features (fig. 77) shared by *Tryphomys adustus* and *Sundamys muelleri* that would indicate close phylogenetic relationship. The rostrum of *T. adustus* is short and wide, relatively shorter compared with the braincase than is the rostrum of *S. muelleri*. The zygomatic plates are very wide and the notch very deep, relatively wider and deeper than in *S. muelleri*. The interorbital region is narrow; from a dorsal view, its sides are concave and widen posteriorly to an oval braincase so the interorbital area and top of the braincase resemble the neck and bottom

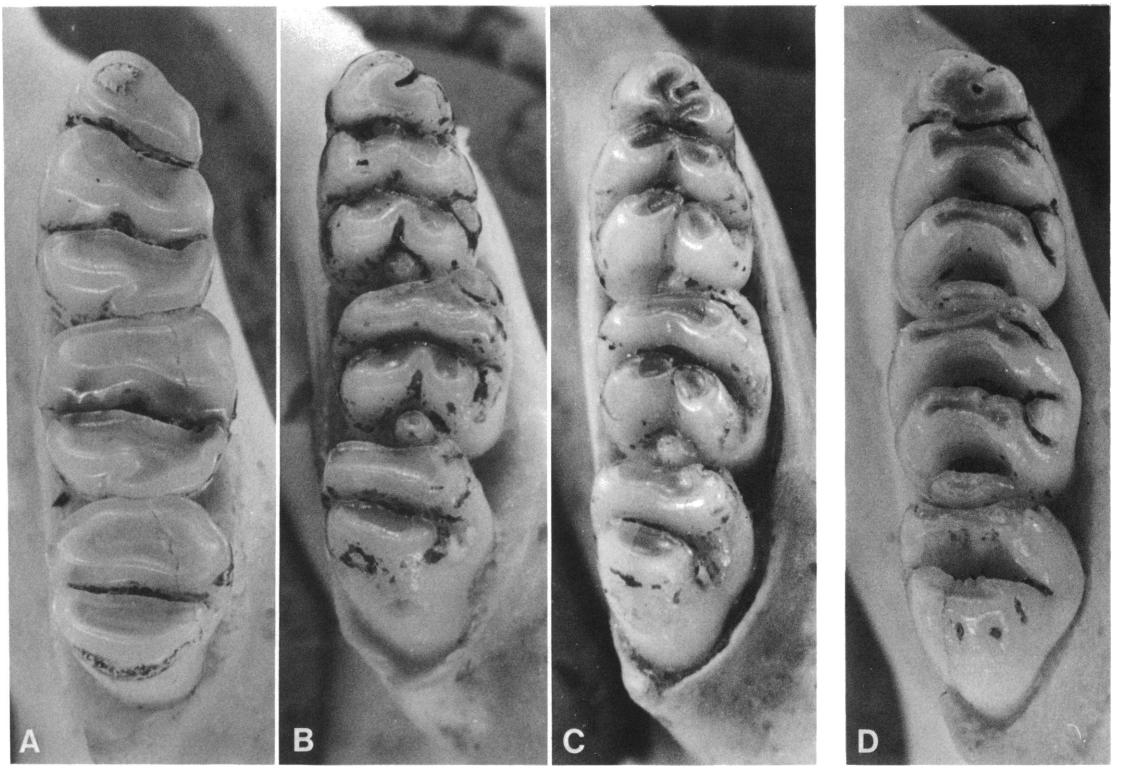

FIG. 76. Occlusal views of right lower molars of the same specimens of *Tryphomys adustus* (A–C) and *Sundamys muelleri* (D) shown in figure 76. All ×10.

of an hourglass (the configuration, as seen in figure 77, is clearly different in *S. muelleri*). There is only slight beading along dorsolateral margins of the interorbital and postorbital regions and the braincase in *T. adustus* (but heavy ridging in *S. muelleri*). The interparietal bone is small, trapezoidal in outline, and forms part of the roof of the occipital area (the interparietal is wider relative to breadth of the occiput in *S. muelleri* and part of it is nestled between the parietals. The configuration of each alisphenoid region (fig. 78) resembles that in *Rattus* (fig. 38B) and not *Sundamys* (fig. 38A): each alisphenoid canal is an open channel and not bounded by a wide lateral strut of alisphenoid bone (as is the condition in most specimens of *S. muelleri*).

Seen from a ventral view (figs. 77 and 78), the incisive foramina of *T. adustus* are long, narrow, and pinched in along their posterior one-fourth; they end 0.7 to 1.6 mm. (10 specimens) posterior to the faces of the first upper molars (incisive foramina of *S. muelleri* are wide, not constricted posteriorly and in half the sample the foramina end either before the molar faces or even with them). The palatal bridge is narrow, deeply grooved, and short; its posterior margin is either 0.4 mm. anterior to the backs of the third molars (one specimen), even with them (three specimens), or 0.1–0.5 mm. posterior to them (six specimens) and does not form a long and broad shelf behind the molar rows (the bridge is relatively longer compared with skull length in *S. muelleri,* relatively wider, and its posterior edge extends posterior to the backs of the molar rows in all specimens). The mesopterygoid fossa is deep and conspicuously narrower than the back of the palatal bridge; its walls are breached by spacious sphenopalatine vacuities, openings so large that the presphenoid and anterior part of the basisphenoid seem suspended in air (fig. 78B), a

FIG. 77. Views of crania. Adult *Sundamys muelleri* from Sumatra is compared with *Tryphomys adustus* from Luzon Island, the Philippines. A, AMNH 102849; B, FMNH 69175. Natural size.

configuration shared by *Rattus* (fig. 39A) but not *Sundamys* (the mesopterygoid fossa is very wide in *S. muelleri* and the sphenopalatine vacuities are very short and do not extend forward past the posterior rim of the palatal bridge; fig. 39B).

Finally, *Tryphomys adustus* has large, inflated auditory bullae that are not only absolutely larger than those in *S. muelleri* but relatively larger compared with skull length (11–12 percent of occipitonasal length in samples of *S. muelleri,* 19 percent in the sample of *T. adustus*; tables 27 and 31). Each bullar capsule is loosely attached to the squamosal bone, the postglenoid vacuity is spacious, and the periotic segment of the petromastoid bone is small and inconspicuous (fig. 78A).

Tryphomys adustus is of medium body size (table 31) with a stocky body, short tail, and shaggy thick fur. Upperparts are flecked with buff, the underparts are either whitish gray or deep buffy gray. The ears are brown. Dorsal surfaces of the front and hind feet are hairy and either whitish gray or whitish brown. The hind feet are long and narrow. The tail in adults is shorter than the body and brown on all surfaces. Females have five pairs of mammae: one pectoral, one postaxillary, one abdominal, and two inguinal. The body and tail conformation is quite different from the long-tailed and stocky *S. muelleri* and *S. maxi* with their four pairs of mammae or the even larger *S. infraluteus* with its three pairs of mammae. The conformation of body, tail, feet, skull, and teeth in *T. adustus* point to a dweller of tropical grassland or savanna; *S. muelleri* lives in forests.

We examined 10 specimens of *Tryphomys adustus* for our comparisons with *Sundamys muelleri.* We find no characters indicating close phylogenetic relationship between *Tryphomys* and *Sundamys. Tryphomys adustus* is known only from lowlands and highlands of Luzon Island in the Philippines. In features of skins, skulls, and teeth, it is morphologically more similar to the arboreal *Abditomys latidens* (Musser, 1982a), another Luzon endemic. The characters of *Tryphomys* and its possible phylogenetic alliances are being examined by Musser (MS.) for publication elsewhere.

SUNDAMYS AND *PARUROMYS*

From the time that Thomas named and described *Rattus dominator* in 1921, the species has been considered a distinctive endemic of Sulawesi but estimates of its relationship to other species of *Rattus* have changed through the years. Tate (1936) thought *R. dominator* to be closely allied with *R. xanthurus* and its relatives and included it within his *Rattus xanthurus* group. Ellerman (1947–1948) placed *R. dominator* in the subgenus *Stenomys,* which also contained *R. muelleri* and its relatives. At that time, El-

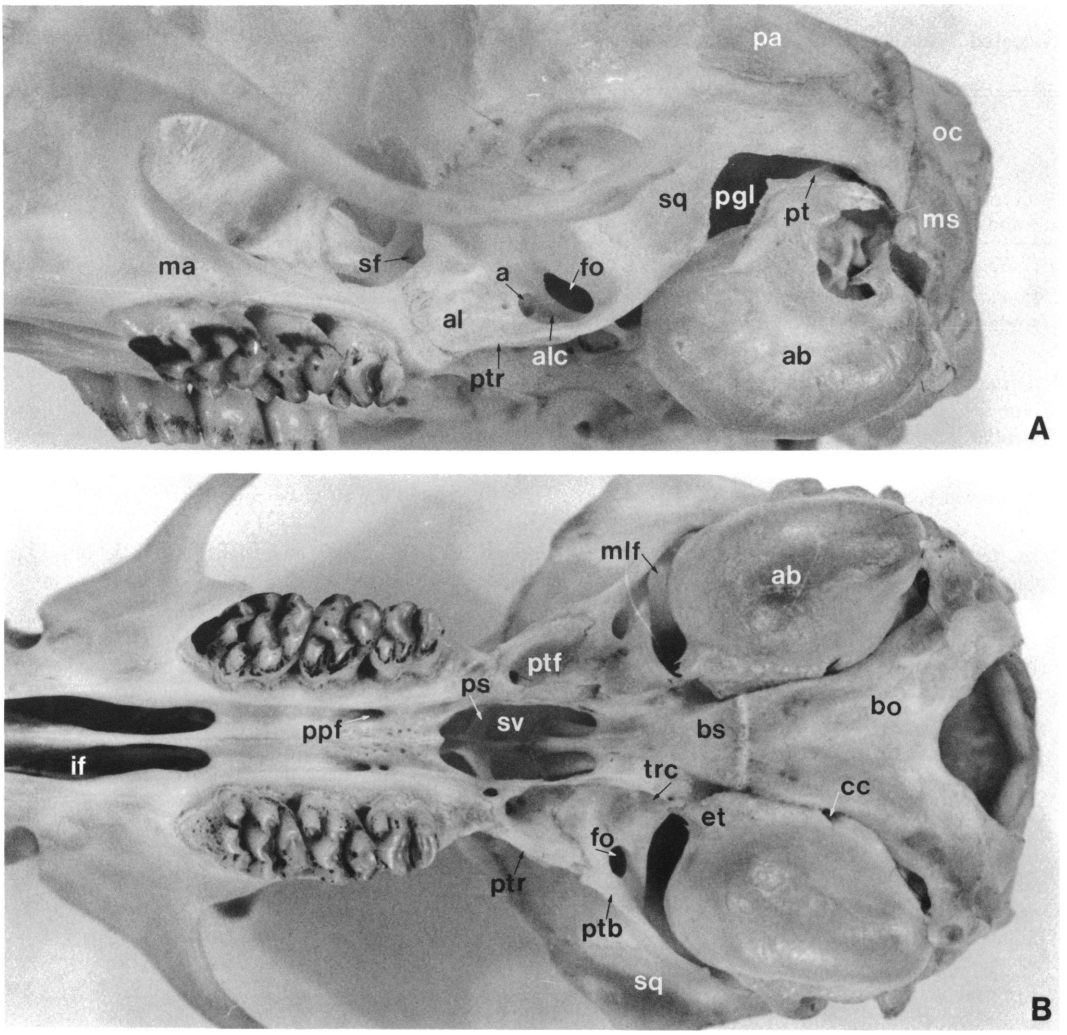

FIG. 78. Lateral (A) and ventral (B) views of the cranium of *Tryphomys adustus* from Luzon (FMNH 69175). *Abbreviations:* **a**, anterior opening of the alisphenoid canal; **ab**, auditory bulla; **al**, alisphenoid bone; **alc**, alisphenoid canal, which is an open channel; **bo**, basioccipital bone; **bs**, basisphenoid bone; **cc**, carotid canal; **et**, bony eustachian tube; **fo**, foramen ovale; **if**, incisive foramina; **ma**, maxillary bone; **ms**, mastoid portion of the petromastoid; **mlf**, middle lacerate foramen; **oc**, occiput; **pa**, parietal bone; **pgl**, postglenoid vacuity; **ppf**, posterior palatine foramen; **ps**, presphenoid bone; **pt**, periotic portion of the petrosal; **ptb**, pterygoid bridge; **ptf**, pterygoid fossa; **ptr**, pterygoid ridge; **sf**, sphenoidal fissure; **spt**, sphenopterygoid vacuity; **trc**, transverse canal.

lerman (1947–1948, p. 265) wrote that *R. dominator* was "Easily distinguished from all the above species by the strongly shortened palatal foramina, and so perhaps should be placed in a separate subgenus." By 1949 Ellerman had formed a *Rattus dominator* group that also contained *R. frosti* and *R. microbullatus*; the group remained in the subgenus *Stenomys*.

In 1954 Ellerman (in Laurie and Hill, 1954; p. 117) recognized that *R. dominator* was at least peripheral to most of the species he had placed in the genus *Rattus* (Ellerman, 1949) when he proposed the subgenus *Paruromys*

TABLE 31
Selected Measurements in Species of *Rattus, Taeromys, Tryphomys,* and *Paruromys* Discussed in Text[a]

Genus and Species	Length of Head and Body	Length of Tail	Length of Hind Foot	Greatest Length of Skull	Length of Bulla	Length of M^{1-3}	Length of Bulla / Length of Skull (%)
RATTUS							
R. stoicus (Andaman Islands)	235.2 ± 14.6 213–260 (13)	197.1 ± 8.9 180–212 (13)	47.1 ± 1.9 44–51 (14)	50.0 ± 2.3 46.4–55.1 (14)	6.8 ± .3 6.4–7.3 (16)	8.3 ± .3 7.6–8.6 (16)	14
R. palmarum (type series from Nicobar Islands)	228.3 ± 2.9 225–230 (3)	226.3 ± 5.7 220–231 (3)	46.7 ± 1.5 45–48 (3)	51.3 ± 2.5 49.0–54.0 (3)	6.7 ± .3 6.5–7.0 (3)	9.0 ± .1 8.9–9.0 (3)	13
R. lugens (Mentawai Islands)	229.0 ± 11.7 212–251 (12)	211.3 ± 11.4 193–231 (12)	41.3 ± 2.6 40–44 (12)	48.9 ± .9 46.6–49.7 (12)	6.7 ± .2 6.4–7.2 (12)	8.1 ± .2 7.7–8.4 (12)	14
R. macleari (Christmas Island)	234.3 ± 15.0 210–260 (7)	255.0 ± 8.7 240–265 (7)	51.9 ± 2.0 49–54 (7)	48.3 ± 4.9 42.5–53.5 (5)	6.6 ± .2 6.2–6.9 (6)	9.6 ± .3 9.3–10.1 (6)	13
R. enganus (Pulau Enggano)	228	257	46	44.6	—	8.6	—
R. xanthurus (Sulawesi)	247.3 ± 11.0 240–260 (3)	311.7 ± 18.5 293–330 (3)	46.7 ± 1.5 45–48 (3)	51.4 ± 3.6 48.8–55.5 (3)	8.6 ± .3 8.3–8.8 (3)	8.4 ± .2 8.2–8.5 (3)	17
R. annandalei (Malay Peninsula)	191.8 ± 12.3 173–220 (24)	240.2 ± 9.9 225–263 (24)	39.5 ± 1.1 37–41 (24)	46.9 ± 1.7 43.8–50.1 (24)	8.0 ± .3 7.5–8.7 (24)	8.2 ± .3 7.7–8.8 (24)	17
TAEROMYS							
T. celebensis (Sulawesi)	226.5 ± 10.7 206–249 (25)	278.4 ± 17.8 253–306 (25)	50.0 ± 1.6 47–53 (26)	50.4 ± 1.4 48.0–53.0 (25)	7.4 ± .4 6.6–8.4 (26)	9.0 ± .4 8.1–9.8 (26)	15
T. callitrichus	225.6 ± 15.8 200–240 (7)	245.1 ± 15.4 220–260 (7)	52.6 ± 1.1 51–54 (5)	50.5 ± 1.7 49.1–52.4 (5)	6.2 ± .5 5.5–6.6 (4)	10.0 ± .3 9.5–10.4 (7)	12
TRYPHOMYS							
T. adustus (Luzon Island)	154.0 ± 18.0 131–174 (4)	149.2 ± 10.3 130–164 (9)	38.3 ± 2.6 35–42 (9)	40.3 ± 2.6 36.3–43.9 (6)	7.7 ± .6 6.9–8.6 (8)	8.5 ± .3 8.0–9.2 (10)	19
PARUROMYS							
P. dominator (Sulawesi)	242.6 ± 10.1 222–257 (19)	290.5 ± 13.5 270–310 (19)	53.1 ± 1.5 50–55 (19)	59.5 ± 1.5 56.7–62.7 (22)	7.2 ± .4 6.4–7.8 (22)	10.3 ± .4 9.6–11.0 (22)	12

[a] Measurements are in millimeters. Mean plus and minus one standard deviation, observed range, and number of specimens in parentheses are listed for each measurement.

to contain it, *R. frosti,* and *R. microbullatus.* Ellerman pointed to the very short incisive foramina in *R. dominator* as the diagnostic feature separating *Paruromys* from the subgenus *Stenomys*: "in its combination of long palate, short palatal foramina and small bullae with large size it is distinctly reminiscent of the genus *Uromys,* which, however, carries

reduction of bullae and lengthening of the palate considerably further, has an extremely naked tail and normally a larger skull. It seems that on account of the reduction of its palatal foramina *Rattus dominator* Thomas, its ally *Rattus frosti* Ellerman and (from descriptions) *Rattus microbullatus* Tate & Archbold (which I have not seen) from Celebes merit subgeneric rank." Musser (1971) pointed out that *R. dominator* is the only species in *Paruromys*; *frosti* was based on very young examples of *R. dominator* and is a synonym of *R. d. camurus* from central Sulawesi; *microbullatus* refers to a subspecies of *Taeromys callitrichus* (Musser, 1970b). Finally, Misonne (1969) treated *Paruromys* as part of the subgenus *Bullimus* and arranged *R. dominator* as one of the many species related to what he knew as *R. muelleri.*

Musser (MS.) has been studying samples of *dominator* collected during the 1970s and older material in collections of museums. In addition to skins, skulls, and teeth there is also data from chromosomes. Musser's results, which are being prepared for publication, indicate that Ellerman was correct in isolating *dominator* from species in the subgenus *Stenomys* but that he did not go far enough. The morphological and phylogenetic relationships between *dominator* on one hand and the species of *Rattus* on the other is more accurately reflected by recognizing *Paruromys* as a genus containing the single species, *P. dominator.* It is another of those species endemic in Sulawesi that was always listed as a *Rattus* but which is neither morphologically or karyotypically part of the genus. There is evidence (Musser, MS.) suggesting that *dominator* may be closely allied with species of *Taeromys,* particularly *T. celebensis,* but just what the relationship is between *Taeromys* and *Paruromys* remains to be worked out; for our comparative purposes here, we use *Paruromys* as a genus. We are interested in contrasting *dominator* with *Sundamys muelleri,* not with species of *Taeromys.* It is no accident that species of *Paruromys* and *Taeromys* have been closely associated with *S. muelleri.* Of all the rats native to Sulawesi, these are the most similar to *S. muelleri* in features of skins, skulls, and teeth. *Paruromys* and *Taeromys* are the two clusters that would most likely be the morphological and possibly the phylogenetic counterparts of *Sundamys* east of the Sunda Shelf. Disassociating *P. dominator* from *S. muelleri* is as important to defining *Sundamys* as was listing the dissimilarities between *Taeromys* and *Sundamys.*

FIG. 79. Views of crania. Adult *Sundamys muelleri* from the Malay Peninsula (A) is contrasted with *Paruromys dominator* from northern Sulawesi (B). A, USNM 290205; B, USNM 217690. Natural size.

Paruromys dominator is appropriately named for it is a very large rat, the largest-bodied of the rats endemic to Sulawesi (table 31). Body weights in the range of 350–500

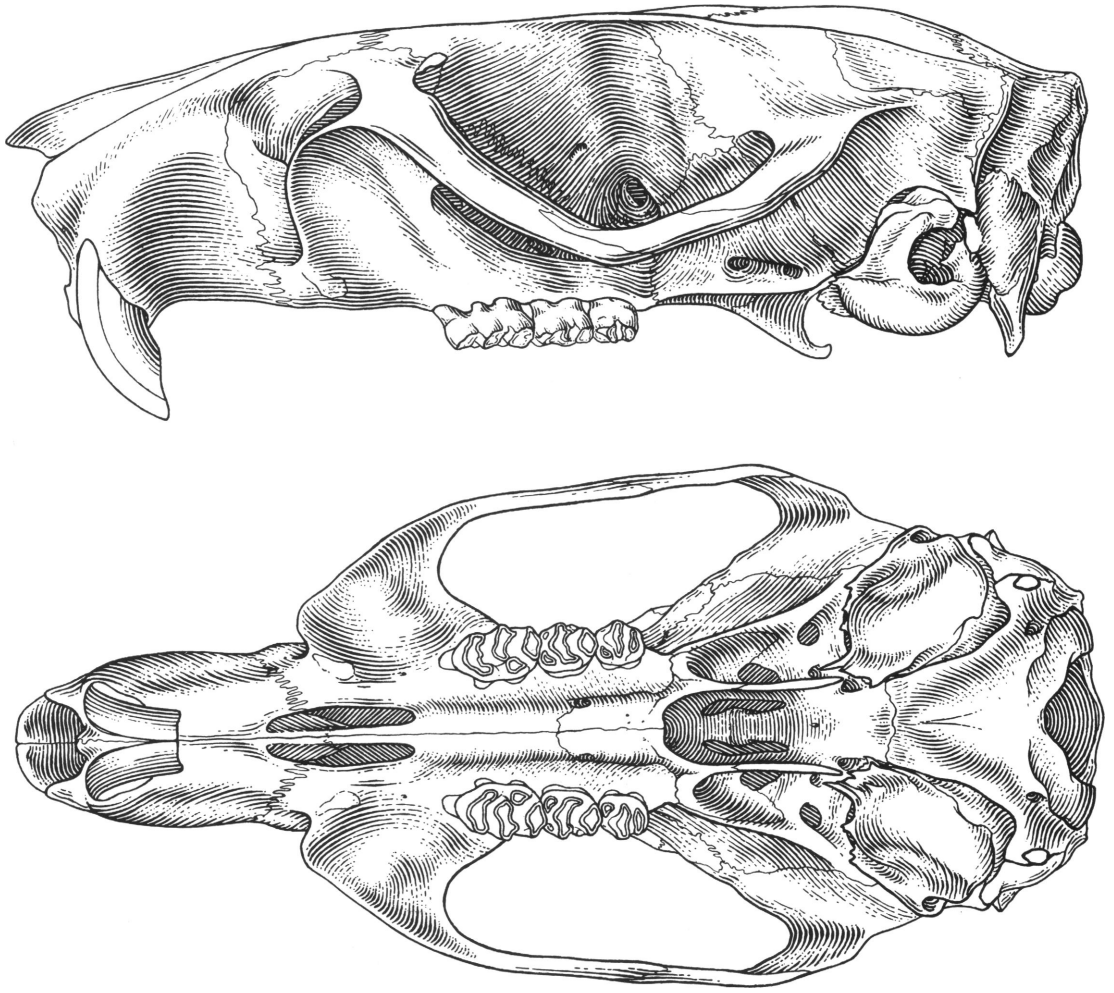

FIG. 80. *Paruromys dominator:* lateral and ventral views of an adult (AMNH 101252). Approximately ×2. Originally published in Tate (1936) in another context.

grams are usual. Adults are larger than adult *S. muelleri* from the Malay Peninsula and many match *S. infraluteus* in size. *Paruromys dominator* occurs throughout Sulawesi wherever there is good forest. It has been taken from the coastal lowlands all the way to tops of mountains, and can be trapped either on the ground or in trees. Fruit is the primary component of its diet.

A large and stocky body, long face, and long bicolored tail are characteristic of *Paruromys dominator.* Upperparts of the head and body are grayish brown, the underparts are either white or cream. The pelage is soft and thick but not long, with short and inconspicuous guard hairs that barely extend beyond the overfur. The coat appears smooth and even, not rough and shaggy as in *S. muelleri*; the appearance and texture of the pelage resembles that in *Taeromys celebensis.* The ears and feet are dark brown. The tail is much longer than the head and body; the basal portion is blackish brown and the distal one-half or two-thirds is white. The pattern is similar to that found in all the species of *Taeromys* and not to the monocolored tails in species of *Sundamys.* The shape of each tail scale and the non-overlapping arrangement of the scale rows is like that in *Taeromys* and unlike the overlapping rows of scales found in *S.*

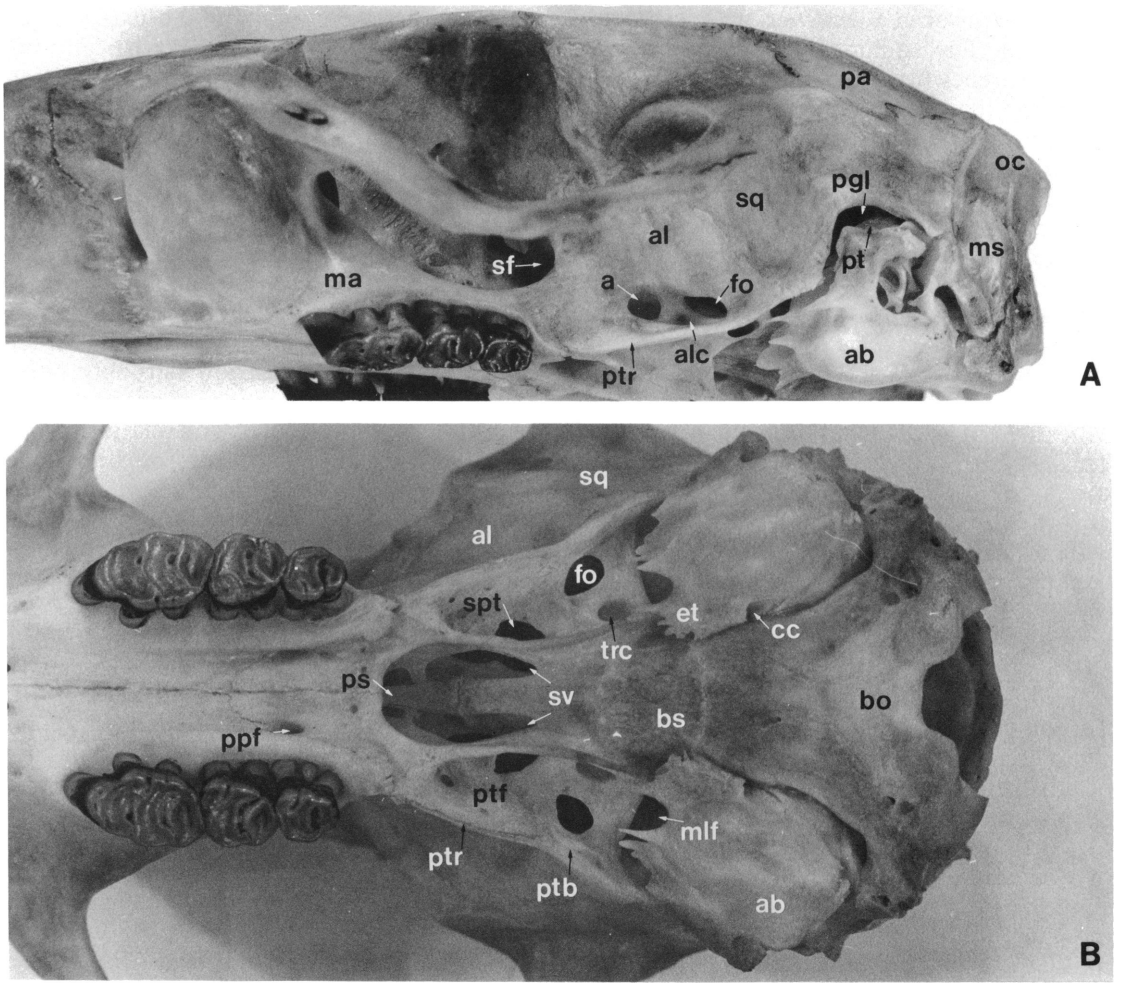

FIG. 81. Lateral (A) and ventral (B) cranial views of *Paruromys dominator* (AMNH 225403) from Central Sulawesi. *Abbreviations:* **a**, anterior opening of the alisphenoid canal; **ab**, auditory bulla; **al**, alisphenoid bone; **alc**, alisphenoid canal, which is an open channel; **bo**, basioccipital bone; **bs**, basisphenoid bone; **cc**, carotid canal; **et**, bony eustachian tube; **fo**, foramen ovale; **ma**, maxillary bone; **ms**, mastoid portion of the petromastoid; **mlf**, middle lacerate foramen; **oc**, occiput; **pa**, parietal bone; **pgl**, postglenoid vacuity; **ppf**, posterior palatine foramen; **ps**, presphenoid bone; **pt**, periotic portion of the petrosal; **ptb**, pterygoid bridge; **ptf**, pterygoid fossa; **ptr**, pterygoid ridge; **sf**, sphenoidal fissure; **spt**, sphenopterygoid vacuity; **trc**, transverse canal.

muelleri. Females have three pairs of mammae: one postaxillary pair and two inguinal pairs. Although similar in its large size, *P. dominator* is unlike *S. muelleri* in appearance and texture of its fur and the color pattern and scale arrangement on the tail.

There is a general similarity between *Paruromys dominator* and *Sundamys muelleri* in skull shape (fig. 79) but not in details of conformation. Compared with the skull of *S. muelleri, P. dominator* has a long and narrow rostrum; the nasolacrimal capsules are close against sides of the rostrum and barely evident (a relatively shorter rostrum compared with size of skull in *S. muelleri,* one that is relatively much wider and appears stocky and slightly swollen instead of elongate; the nasolacrimal capsules are more prominent). The braincase is very wide and has gently sloping sides between zygomatic roots and temporal

ridges (narrower in *S. muelleri* with less sloping sides). The squamosal roots of the zygomatic arches originate high on sides of the braincase (fig. 80), similar to the configuration in species of *Leopoldamys* (Musser, 1981a) but not in *Sundamys* in which the roots are lower. The zygomatic plates are wide and sturdy; their anterior spines project well anterior to the dorsal zygomatic roots, far forward enough that they cover most of the nasolacrimal capsules (figs. 79 and 80). The back part of each plate above the molars is thick and sweeps back to about the middle of the second upper molar (the zygomatic plates are not as wide and massive in *S. muelleri* and their surface areas relative to skull size are more similar to the proportions seen in *Rattus*).

In addition to differences noted in the zygomatic plates, there are other dissimilarities between the two species when the skulls are viewed from the side. In *Paruromys dominator,* the configuration of each alisphenoid region (fig. 81) resembles that in *Rattus* and *Taeromys*: the alisphenoid canal is an open channel and not bounded laterally by a strut of alisphenoid bone (a wide lateral strut of alisphenoid bone occurs in most specimens of *S. muelleri*; fig. 38A). The auditory bullae of *P. dominator* are very small relative to skull size (table 31), as they are in *S. muelleri,* but each bullar capsule is closer to the squamosal bone and separated from it by a narrow postglenoid foramen and small periotic bones (in *S. muelleri,* each capsule is also tightly attached but by a large periotic).

In ventral view (figs. 79 and 80), the short and narrow incisive foramina of *P. dominator* are evident and form a striking contrast to the wider and longer foramina in *S. muelleri.* The ratio, length of incisive foramina/occipitonasal length for 22 specimens of *Paruromys dominator* is 13 percent; in samples of Malayan and Sumatran *S. muelleri, S. infraluteus,* and *S. maxi* (derived from table 24), the values range from 16 to 17 percent. The incisive foramina of *P. dominator* appear as short slits in a long palate. The palatal bridge is narrow and long (partly a reflection of the short incisive foramina), extending past the posterior margins of the molar rows (shorter palatal bridges in *S. muelleri*). Configurations of the mesopterygoid and pterygoid regions are similar in the two species except that *P. dominator* characteristically has conspicuous sphenopterygoid vacuities breaching the pterygoid fossae but *S. muelleri* usually does not and when present they are small.

The upper and lower incisors of *Paruromys dominator* are large and appear sturdy but they are slender relative to size and bulk of the cranium and mandible. The upper incisors are distinctive in that they are thick from front-to-back and curve strongly back after emerging from the rostrum (strongly opisthodont). The combination of anterior-posterior thickness, absolutely and relative to size of the rostral region, and strong opisthodonty are features unlike those in *S. muelleri* in which the incisors are large but not as massive as they are in *P. dominator* and in which they emerge from the rostrum at either a right angle (orthodont) or curve slightly back. The configuration of the upper incisors of *P. dominator* is clearly shown in figure 80.

The maxillary toothrows of *Paruromys dominator* are long and nearly parallel to one another (table 31; figs. 82 and 83). The number of roots beneath each upper and lower molar, height of the crowns, the degree of overlap among the molars in each row, and the relative size of each tooth compared with the others in each row form configurations similar to those seen in *S. muelleri.* Occlusal patterns of the upper molars also resemble the patterns in *S. muelleri* (fig. 82). There are, however, several important differences. First, the laminae of uppers and lower molars in *P. dominator* are thicker and slightly more transverse. Second, cusp t3 on each first upper molar is small and so coalesced with the central cusp t2 that the front lamina appears to consist of only an anterolingual cusp (t1) and a wide central cusp (t2) in most specimens (cusp t3 on each first upper molar in *S. muelleri* is always large and well defined).

The third difference is striking. The anterolingual cusp (t4) on each first and second upper molar is divided in most specimens of *P. dominator,* a configuration clearly shown in figure 82B–D. In some specimens, the two segments fused early in life and appear as one large cusp with a lingual furrow, the only indication that it consisted of two smaller cusps at one time. We examined several hundred

specimens of *P. dominator* and first thought the anterior cusp to be the real cusp t4 and the posterior segment to be cusp t7; this must have been Misonne's (1969) interpretation for he stated that cusp t7 is often present on the first and second upper molars. He may be right, and possibly that is the origin of cusp t7, but in our experience, cusp t7 is also usually closely associated with the central cusp t8 of the posterior lamina and after wear unites with that cusp and with cusp t4. In *P. dominator* the posterior member of the pair of cusps merges with the anterior member, not with cusp t8, to form the configuration seen in figure 82D. Also, cusp t7 is a definite cusp. The configuration of the pair of cusps at the lingual margin of cusp t5 in *P. dominator* appear as divided segments of one cusp, as seen in figure 82B. A divided cusp t4 is also typical of the Sulawesian *Maxomys hellwaldii.* In all specimens of *S. muelleri* we examined, cusp t4 is large and undivided (fig. 82A).

The fourth contrast between the two species is the presence of a large and conspicuous labial ridge behind cusp t6 of each first and second upper molar, as seen in figure 82C and D. Most specimens have this ridge. In most specimens of *S. muelleri,* such a ridge is absent; if present it is very low and inconspicuous.

Fifth, nearly all specimens of *Paruromys dominator* we studied have a posterior cingulum at the back of each first upper molar (present in 50 percent of the sample of *S. muelleri*; table 17). It ranges in size from a low and thin ridge to a thick ridgelike extension, triangular in cross-section, that projects nearly out to the labial margin of the tooth (smaller in most specimens of *S. muelleri*). A posterior cingulum is absent from the second upper molar of some specimens but present in others and then is a thin ridge just below the occlusal surface (absent from second molars in *S. muelleri*).

The karyotype of *P. dominator,* which Musser will publish later, is unlike any species of *Rattus* that has been sampled (those listed in table 2, for example) and unlike that of *S. muelleri.* The 2N is 38 in females and consists of 1 pair of submetacentric autosomes, four pairs of subtelocentrics, and 14 pairs of telocentrics; the X-chromosome is submetacentric and the Y telocentric. There are no small metacentric chromosomes. A submetacentric X and telocentric Y is also characteristic of *S. muelleri* but otherwise that species has 12 pairs of telocentric autosomes, one pair of subtelocentrics, and six pairs of small metacentrics (table 2).

A bicolored tail with non-overlapping scale rows, elongate rostrum, broad and sloping braincase, squamosal roots of the zygomatic arches originating high on sides of the braincase, broad and massive zygomatic plates, alisphenoid canal an open channel, short slitlike incisive foramina, large and strongly opisthodont upper incisors, an inconspicuous cusp t3 on each first upper molar, cusp t4 on each first and second upper molar divided into two large cusps, high and wide labial ridge behind cusp t6 on each first and second upper molar, conspicuous posterior cingulum on each first upper molar and a smaller posterior cingulum usually present on each second molar, broader and thicker laminae, and a very different chromosomal number and composition are the features distinguishing *Paruromys* from *Sundamys.* Although *Paruromys dominator* is large-bodied, long-tailed, and superficially resembles *Sundamys muelleri,* we find no features suggesting close phylogenetic relationship between the two or supporting the notion that *P. dominator* may be the Sulawesian representative of *Sundamys.*

SUNDAMYS AND *BULLIMUS*

We compare these two genera because Misonne (1969) placed *muelleri* in the subgenus *Bullimus* of *Rattus. Bullimus* was named and described by Mearns in 1905 and the type species is *Bullimus bagobus* from the Philippine island of Mindanao. Misonne did not include *bagobus* with the other species he placed in subgenus *Bullimus* because he regarded *bagobus* as a subspecies of *Rattus celebensis,* which he did include in subgenus *Bullimus.* Misonne was following Ellerman (1949, p. 65), who listed *bagobus* and *luzonicus,* a relative on Luzon Island, as subspecies of *Rattus celebensis,* writing that perhaps the two "might be regarded as a full species, but although the palatal foramina are less shortened and the molars rather wider, there is a

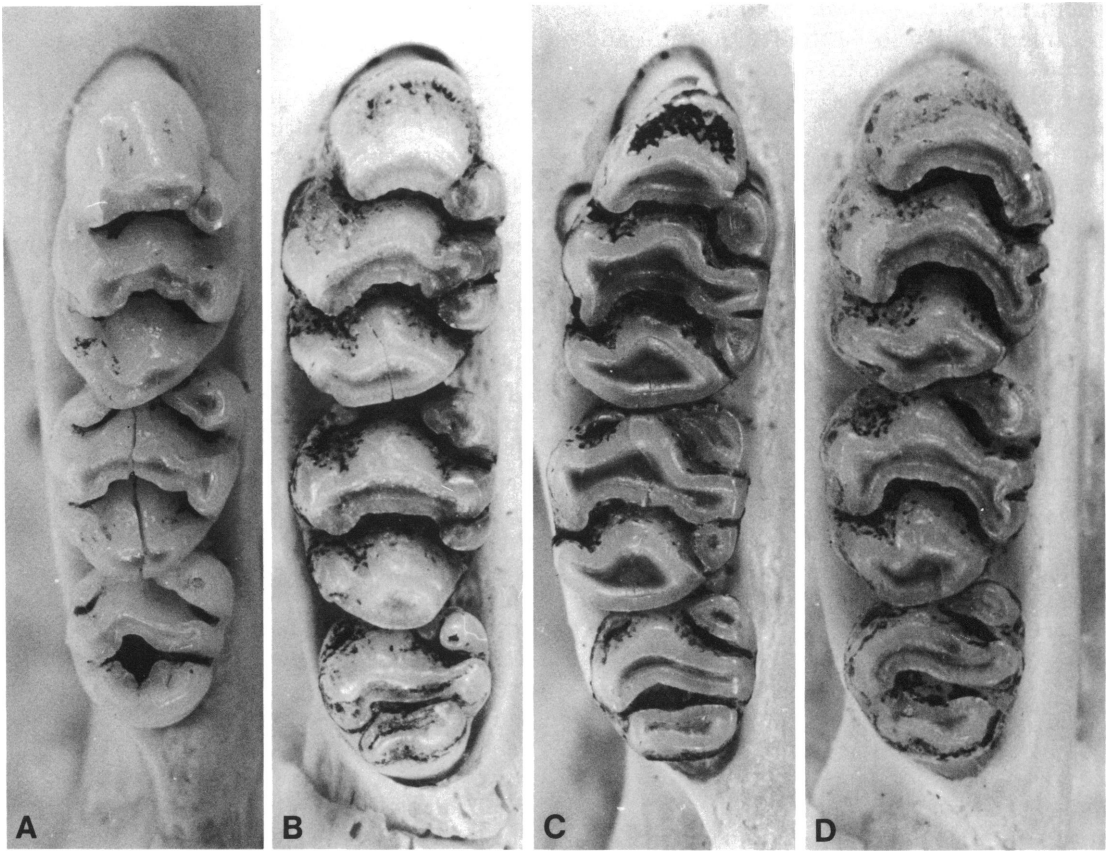

FIG. 82. Occlusal views of right upper molar rows in *Sundamys muelleri* from Borneo (A) and *Paruromys dominator* from Central Sulawesi (B–D). A, young adult (AMNH 103767). B, young adult (AMNH 223585). C, adult (AMNH 225454). D, adult (AMNH 225385). All ×10. Note the configurations of cusp t4 on each first and second molar in both species.

distinct similarity between this and *celebensis.*"

Neither *bagobus* nor *luzonicus* are subspecies of *celebensis.* Both belong in *Bullimus,* which should not be just a subgenus of *Rattus* (Musser, 1982b) and neither one is closely related to *celebensis,* which belongs in the genus *Taeromys,* a group of species endemic to Sulawesi. Apparently Misonne did not examine specimens of either *bagobus* or *luzonicus.* Because *bagobus* is the type species of *Bullimus* and because Misonne used that name as a subgenus for *muelleri* and other species, we felt compelled to compare *Bullimus bagobus* with *Sundamys muelleri* to help define the genus *Sundamys.*

Bullimus is endemic to the Philippine Islands. Specimens are known from the islands of Luzon, Samar, Calicoan, Leyte, Dinagat, Mindanao, and Bohol. Seven scientific names have been tied to samples from the islands (Musser, 1982c). There is, unfortunately, no reliable estimate of how many species actually exist because the genus has never been taxonomically revised and the extent of individual, secondary sexual, insular, and altitudinal variations in features of skins, skulls, and teeth is unknown. The name, *bagobus,* is the oldest for populations from Mindanao Island and we use *Bullimus bagobus* as our example of the genus in the comparisons with *Sundamys muelleri.*

Like the species of *Sundamys,* the samples of *Bullimus* consist of very large rats (Mearns, 1905; Sanborn, 1952; Rabor, 1955; Heaney and Rabor, 1982). The body is large and

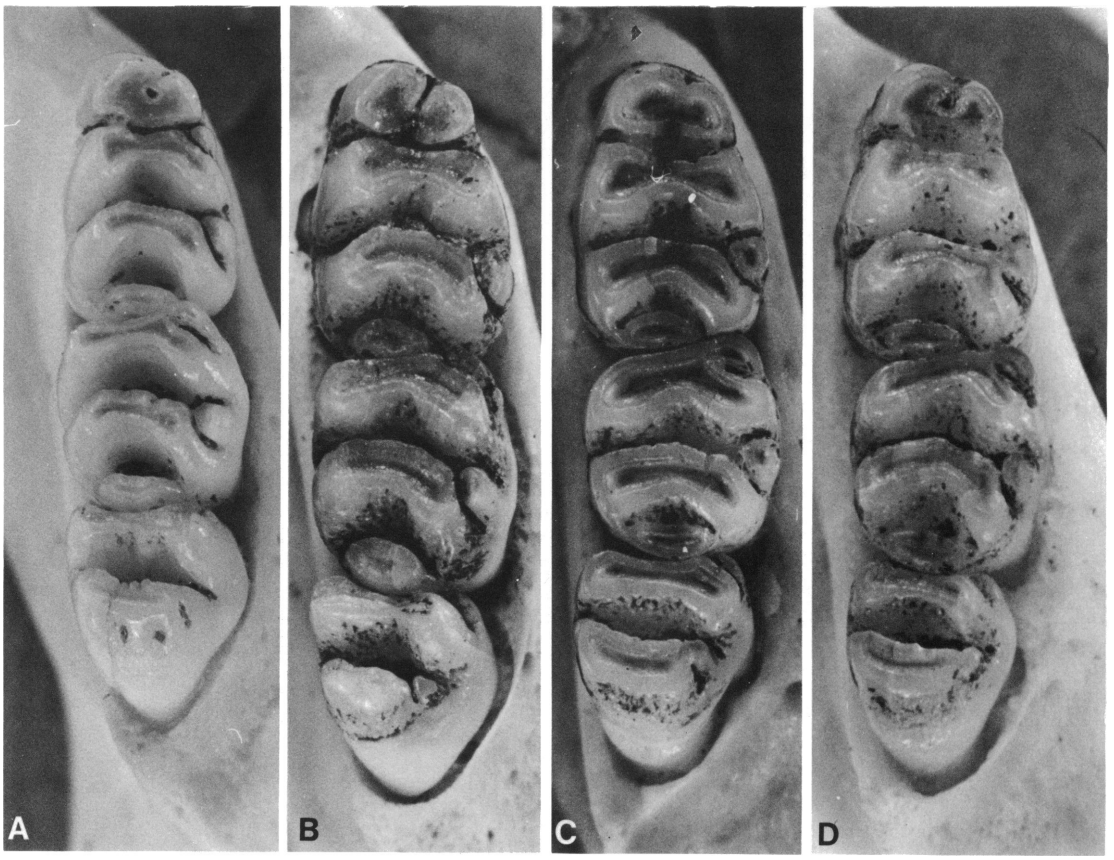

FIG. 83. Occlusal views of right lower molar rows from the same specimens of *Sundamys muelleri* (A) and *Paruromys dominator* (B–D) shown in figure 82. All ×10.

chunky, the face is long, the tail is much shorter than the body and appears stubby; it is brown all over in some specimens, bicolored white and dark brown in others. The upperparts are brown, the underparts are either white or grayish white. The pelage is short and coarse. The ears and feet are brown. The hind feet are very long and narrow, a large and conspicuous midventral cutaneous glandular area is found on males, and females have four pairs of mammae: a pectoral pair, postaxillary pair, and two inguinal pairs. *Bullimus bagobus* has been collected from forests, scrub, and near cultivated fields in lowlands and highlands. The rats are terrestrial and use burrows beneath thick vegetation (Rabor, 1955). Aside from large body size, color of fur, and number and position of mammae, the skins of *B. bullimus* and *S. muelleri* are very different.

The crania of *Sundamys* and *Bullimus* are also dissimilar (figs. 84 and 85). Seen in dorsal view, a long and slender rostrum, constricted interorbital region, and wide braincase form a characteristic conformation to the cranium of *B. bagobus*. The elongate rostrum contrasts with the relatively shorter and wider rostrum in *S. muelleri*. The dorsolateral margins of the interorbital region are outlined by conspicuous ridges that continue back along the braincase as less distinct temporal beading; the outline resembles the shape of a vase rather than the outline in *S. muelleri*. The wide braincase of *B. bullimus* has sloping sides that are not as steep as those in *S. muelleri*. The occipital region is relatively much shallower (anterior-posterior distance) compared to skull length than the relatively deeper occipital area in *S. muelleri*, and the interparietal bone is smaller relative to braincase

roof than the more expansive interparietal of *S. muelleri.*

From side view can be seen six significant features that contrast the crania in *B. bagobus* and species of *Sundamys.* The first is the very deep cranium of *B. bagobus* compared with that in species of *Sundamys* (fig. 85); this deep skull is diagnostic for *Bullimus.* Second is the very broad and high zygomatic plate, much larger than the plates in the species of *Sundamys.* The third is the large optic foramen, absolutely and relative to skull size, in each orbit; the foramen in species of *Sundamys* is small. Fourth is the alisphenoid region (fig. 86A) in which the configuration resembles that of *Tryphomys*: the alisphenoid canal is an open channel not bounded by a lateral strut of alisphenoid bone, a contrast to the configuration in most specimens of *Sundamys* (fig. 38A). The very large and inflated bullae of *B. bagobus* compared with the very small bullae in species of *Sundamys* is the fifth contrasting character. The bullae are not just very deep but elongate as well and the internal auditory meatus is directed to the back of the skull (fig. 86A) rather than laterally as it is in *S. muelleri* and its relatives. This position and the large bullae with its distinctive shape were among the diagnostic features Mearns (1905) used to define *Bullimus* and it does distinguish it from other genera of murids. Finally, the molars are high-crowned in *B. bagobus* but low-crowned in *S. muelleri.*

In ventral view, the incisive foramina in *Bullimus bagobus* are relatively longer compared with skull length than in *S. muelleri.* The pterygoid fossa are deep, not so shallow as they are in species of *Sundamys.* The mesopterygoid fossa is breached by long sphenopalatine vacuities that extend forward far enough to be seen in the back of each orbit; comparable vacuities in species of *Sundamys,* particularly *S. infraluteus,* are short and do not extend forward beneath the palatal bridge.

The dentaries of *Bullimus* and *Sundamys* are dissimilar (fig. 85). Compared with *Sundamys,* each dentary of *B. bagobus* has an elongate condyloid process that is directed posteriorly rather than dorsoposteriorly and a deep concavity between the condyle and angular process, a different configuration than that in species of *Sundamys.*

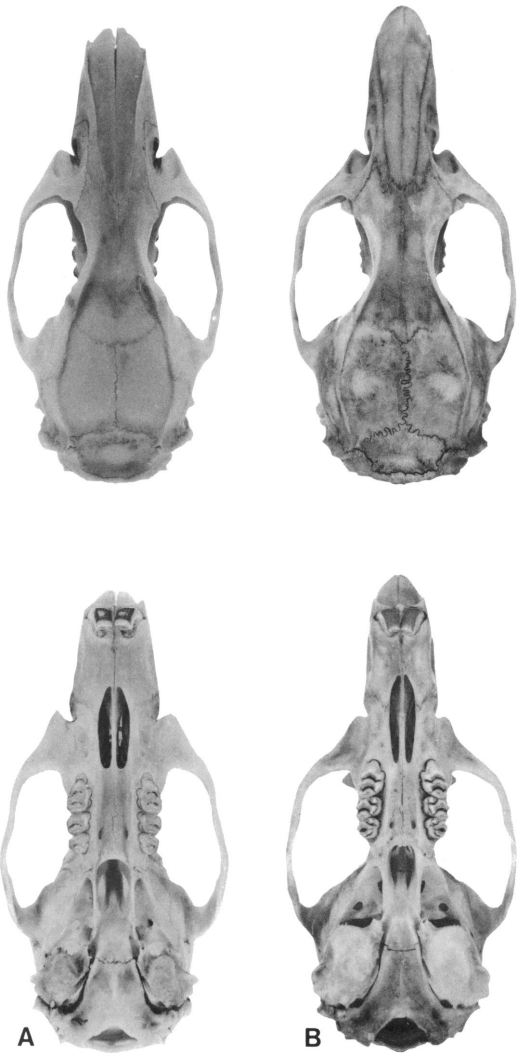

FIG. 84. Views of crania. Adult *Sundamys muelleri* from the Malay Peninsula (A) is contrasted with *Bullimus bagobus* from the Philippine Island of Mindanao (B). A, USNM 290205; B, AMNH 203316. Natural size.

In the features of the skull we examined, we find no characters that link *Bullimus* morphologically with *Sundamys.* There is no evidence that the Philippine *Bullimus* is phylogenetically closely allied to the Malaysian *Sundamys.*

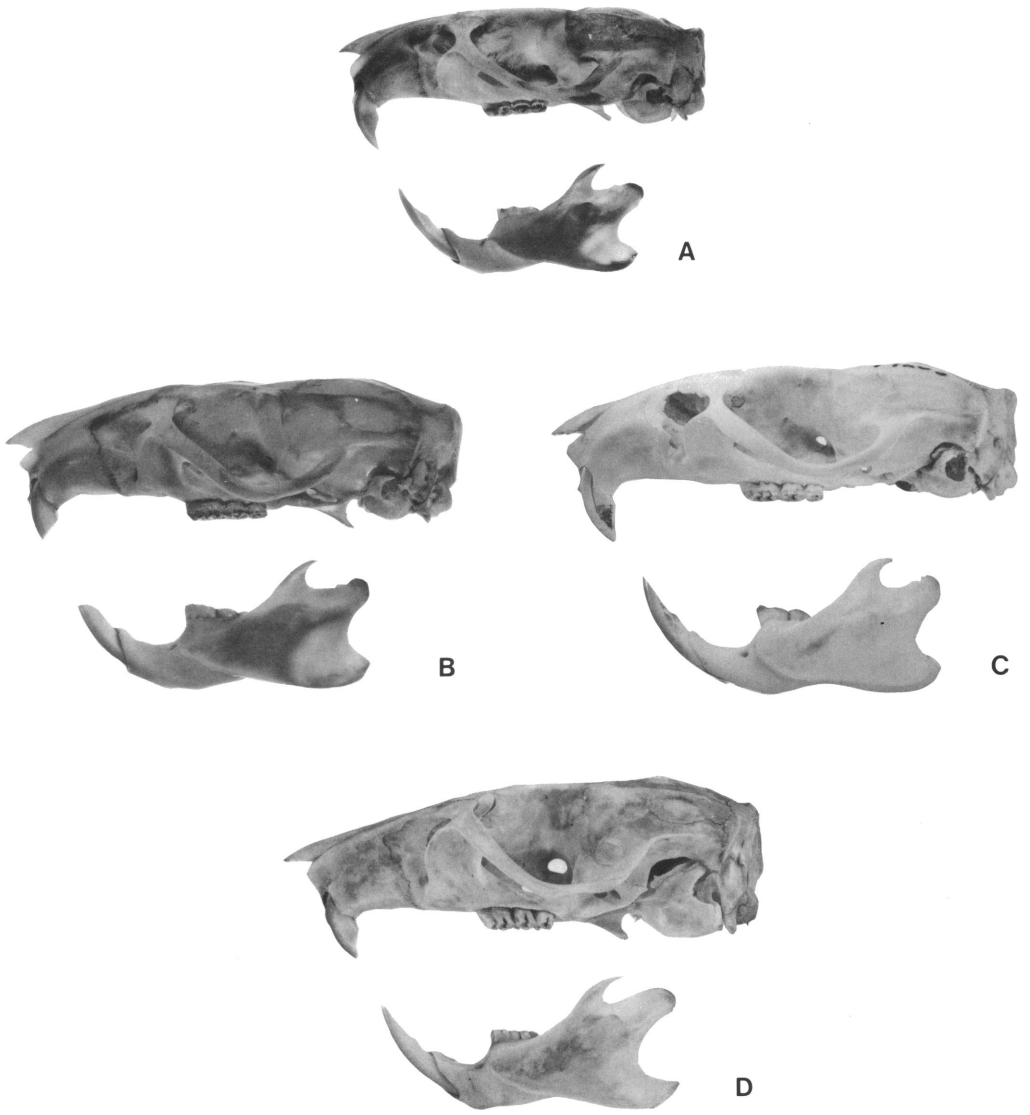

FIG. 85. Lateral views of crania and dentaries. Species of adult *Sundamys* (A–C) are contrasted with that of *Bullimus* (D). A, *S. muelleri,* Sabah (USNM 292740). B, *S. infraluteus,* Sabah (USNM 292759). C, *S. maxi,* Java (RMNH 14205). D, *B. bagobus,* Mindanao (AMNH 203316). Natural size.

We see some resemblances in the molars between *Bullimus* and *Sundamys* (fig. 87) but no characters that would suggest *bagobus* and its allies are close relatives of *S. muelleri, S. infraluteus,* and *S. maxi.* Both genera share the same number of roots beneath each tooth, the extent of overlap among the teeth in each row, and the relative size of the third molars compared with the others. There are significant differences. Compared with the molars of *S. muelleri,* those of *B. bagobus* are chunkier and have higher crowns (they are hypsodont compared with the brachydont molars in *S. muelleri*); the lamina are wider and straighter; some specimens have posterior cingula on the first upper molars but most do

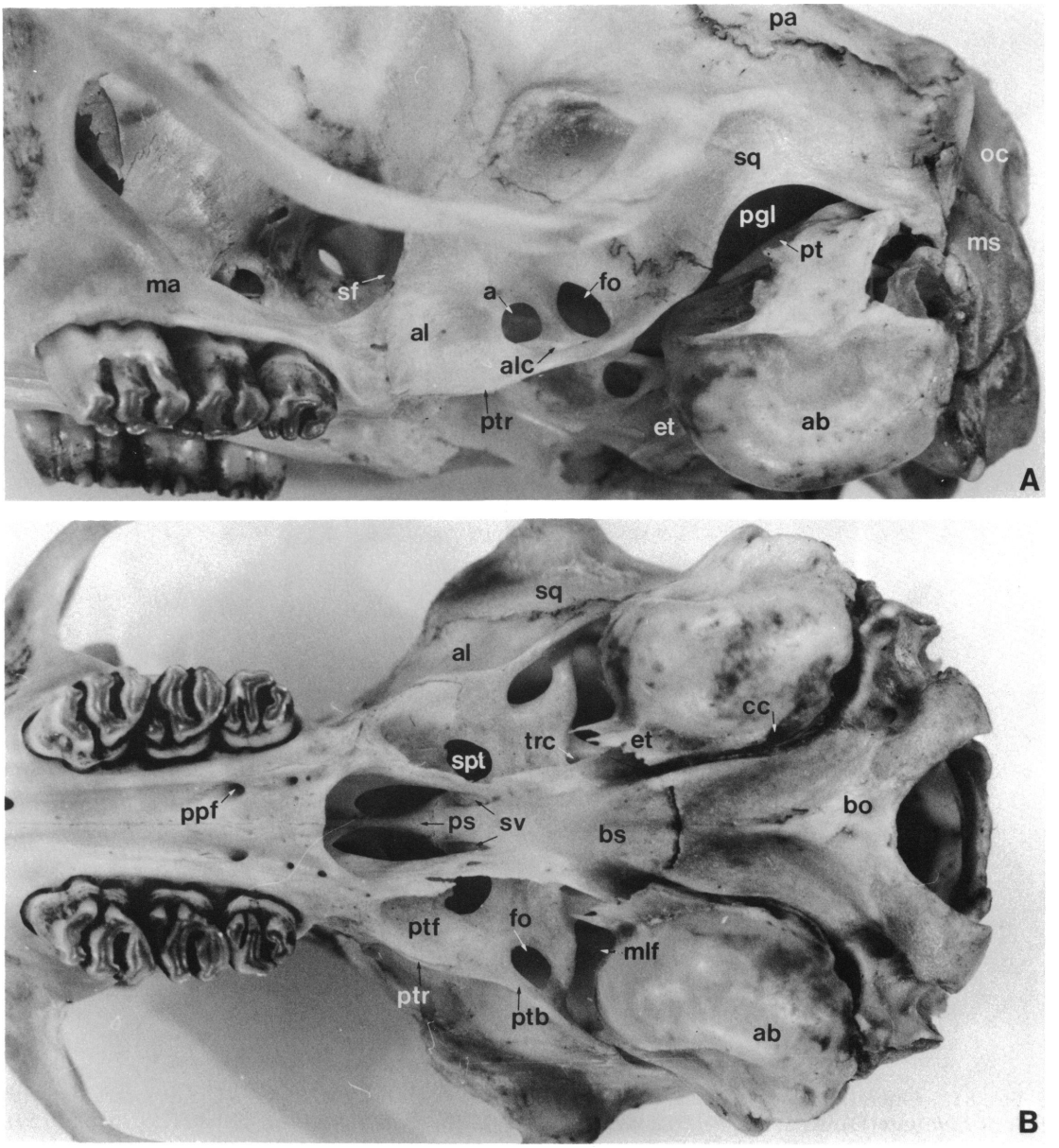

FIG. 86. Lateral (A) and ventral (B) cranial views of *Bullimus bagobus* (AMNH 207572) from Mindanao. *Abbreviations:* **a**, anterior opening of the alisphenoid canal; **ab**, auditory bulla; **al**, alisphenoid bone; **alc**, alisphenoid canal, which is an open channel; **bo**, basioccipital bone; **bs**, basisphenoid bone; **cc**, carotid canal; **et**, bony eustachian tube; **fo**, foramen ovale; **if**, incisive foramina; **ma**, maxillary bone; **ms**, mastoid portion of the petromastoid; **mlf**, middle lacerate foramen; **oc**, occiput; **pa**, parietal bone; **pgl**, postglenoid vacuity; **ppf**, posterior palatine foramen; **ps**, presphenoid bone; **pt**, periotic portion of the petrosal; **ptb**, pterygoid bridge; **ptf**, pterygoid fossa; **ptr**, pterygoid ridge; **sf**, sphenoidal fissure; **spt**, sphenopterygoid vacuity; **trc**, transverse canal.

not (present in half the sample of *S. muelleri* and in all the specimens of *S. infraluteus* and *S. maxi*); and cusp t3 on each second and third upper molar is missing in some specimens and present in others but very small when it is.

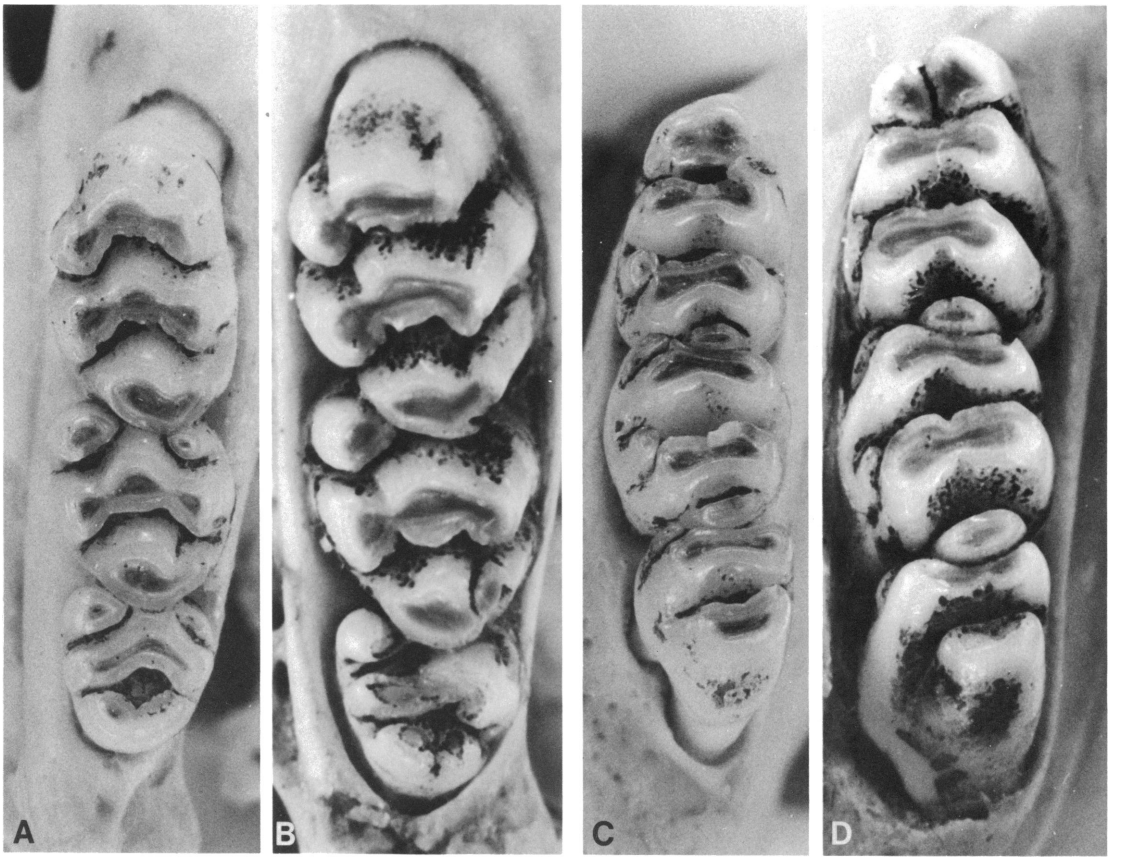

FIG. 87. Occlusal views of left upper (A and B) and lower (C and D) molar rows in *Sundamys* and *Bullimus*. A and C, *S. muelleri*, Borneo (AMNH 106176). B and D, *B. bagobus*, Mindanao (DMNH 4173). All ×10.

Bullimus is another one of those genera in which the molars have been thought to be *Rattus*-like, as they are in *Tryphomys, Taeromys, Paruromys,* and *Sundamys*. But like those genera, *Bullimus* is unlike *Rattus* in details of cusp pattern, cranial features, and some skin characters. And it is in these details of dental patterns, cranial skeleton, and skins that *Bullimus* also differs from *Sundamys*.

SUNDAMYS COMPARED WITH TAXA IN TABLE 13

We round out our definition of *Sundamys* by discussing more than a dozen taxa listed in table 13 that have been associated with *S. muelleri* in either the same group or subgenus. Two of these, *adspersus* and *Chrysocomus,* were placed by Misonne (1969) into subgenus *Bullimus,* which also contained *S. muelleri* and *B. bowersii*. Misonne thought the dental characters of *adspersus* and *chrysocomus* were similar to those of *bowersii*. The name, *andrewsi,* is the oldest for what was called *adspersus* (Musser, MS.); it and *chrysocomus* are members of the genus *Bunomys,* which is not closely related to *Berylmys bowersii* as we already noted and is not related to *Sundamys* either.

The other taxa in table 13 are *jarak, mara, remotus, baluensis, enganus, macleari, annandalei, nativitatus, xanthurus, everetti,* and those which Ellerman listed as *ruber* and subspecies of *ringens*. Both *jarak* and *mara* are subspecies of *Rattus tiomanicus* (Musser and Califia, 1982), which is morphologically and phylogenetically closely related to *R. rattus*. Another close ally is *R. baluensis* (fig. 6),

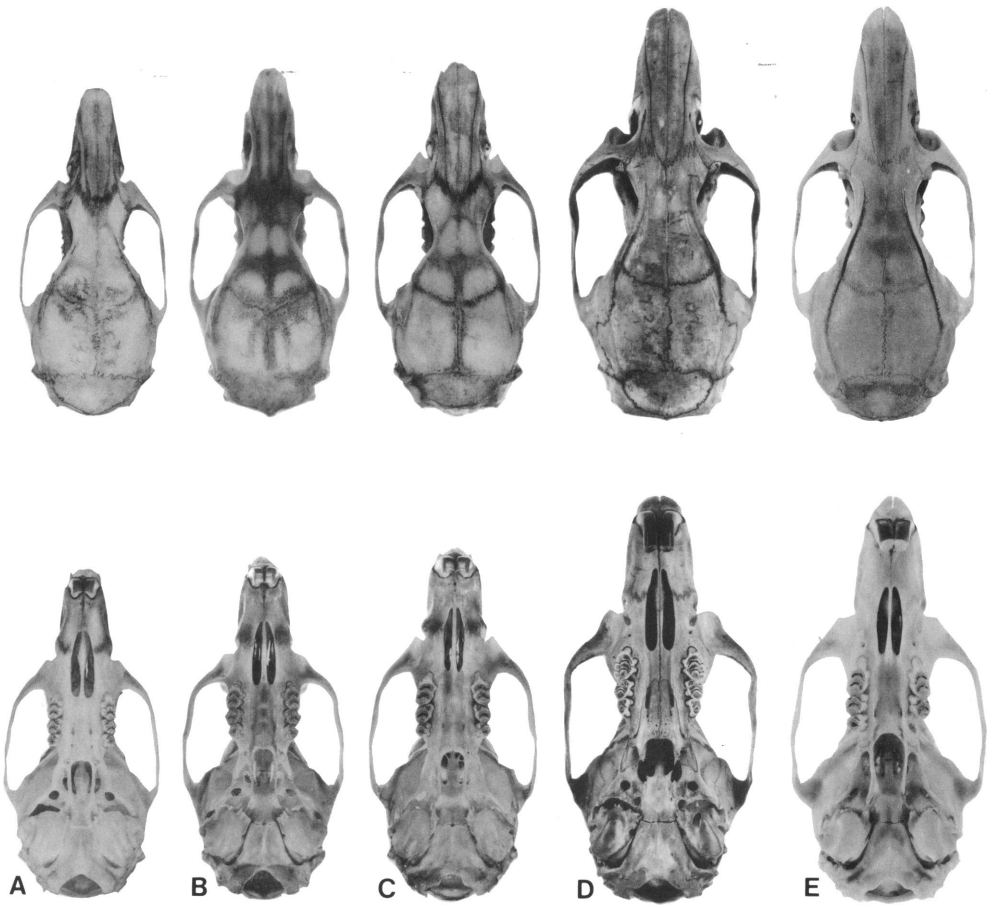

FIG. 88. Views of crania contrasting species of adult *Rattus* (A–D) with that of *Sundamys* (E). A, *R. baluensis,* Sabah (USNM 292693). B, *R. leucopus,* New Guinea (AMNH 157961). C, *R. mordax,* New Guinea (AMNH 158036). D, *R. feliceus,* Ceram (BM 20.7.26.5). E, *S. muelleri,* Sumatra (AMNH 102849). Natural size.

which we discussed in our account of *Palawanomys.* Misonne (1969) thought the molar patterns of *R. baluensis* were similar to those of *S. muelleri* but we see close resemblance only between *R. baluensis* and other species of *Rattus,* such as *R. rattus* and *R. tiomanicus,* which are in the subgenus *Rattus.* Another member of subgenus *Rattus* is *remotus,* which Hill (1960) regarded as a subspecies of *Rattus muelleri.* Marshall (1977b), however, thought *remotus* to be a good species endemic to Koh Samui and nearby islands. It is actually a subspecies of *R. sikkimensis,* which occurs on other islands in the Gulf of Siam and throughout Indochina. Marshall (1977b) knew the species as *R. koratensis* and in the older literature it went under *R. sladeni* (Musser and Marshall, MS.).

Ellerman (table 13) placed *Rattus ringens, R. ruber,* and *R. verecundus* in the *callitrichus* group of the subgenus *Stenomys* and thought those species to be closely allied to *muelleri* and *callitrichus.* We already compared *Sundamys* with *R. verecundus,* the type species of *Stenomys* and discussed our disagreement with Ellerman's grouping. *Stenomys* does not represent *Sundamys* in the New Guinea region and is not closely allied to that Malaysian genus. The same is true for the other native New Guinea and Moluccan species.

The various subspecies of *R. ringens* and *R. ruber* listed by Ellerman actually consist of seven species. *Rattus ruber* was originally described from an example of *R. nitidus,* which is native to Indochina and a commensal on New Guinea (Calaby and Taylor, 1982). *Rattus nitidus* is in the subgenus *Rattus* and a close morphological ally of *R. rattus.*

Rattus ringens was applied by Ellerman to what Taylor, Calaby, and Van Deusen (1982) sort out as *R. leucopus* (fig. 88), *R. mordax* (fig. 88), *R. praetor, R. steini,* and *R. jobiensis* from the New Guinea region. In their elegant analyses, those authors determined that the species clustered and were related to *R. verecundus, R. niobe,* and *R. richardsoni. Rattus feliceus* (fig. 88), formerly *R. ringens feliceus,* is native to Ceram in the Moluccas and related to *R. jobiensis* and *R. praetor* (Musser, MS.).

The remaining six species are medium- to large-bodied rats. Only one, *R. annandalei,* occurs on the Sunda Shelf where it is recorded from the Malay States, Singapore, eastern Sumatra, and the islands of Padang and Rupat off the coast of eastern Sumatra (Chasen, 1940; Hill, 1960; Medway, 1969; and specimens we studied in USNM). *Rattus enganus* is known only by the holotype (USNM 140976) collected on Pulau Enganno, off the coast of southwestern Sumatra and beyond the 100 fathom line (Miller, 1906). *Rattus macleari* and *R. nativitatus* were native to Christmas Island, south of Java and well off the Shelf (Thomas, 1887, 1888). *Rattus xanthurus* is endemic in Sulawesi (Tate, 1936), and *R. everetti* is native to the Philippine Islands, excluding Balabac, Palawan, and the Calamianes (Musser, 1982b; Heaney and Rabor, 1982). *Rattus annandalei* is considered here because Ellerman (1941) listed *R. villosus* under his *muelleri* group and *villosus* is a synonym of *R. annandalei bullatus* (Chasen, 1940). *Rattus macleari* and *R. nativitatis* are included because Ellerman (1949) placed them in a *macleari* group within the subgenus *Stenomys,* which for him also held *muelleri* and its relatives. We studied *R. enganus* because Chasen (1940, p. 164) listed it near *muelleri* and *infraluteus* (noting that it was "perhaps a much altered form of *mülleri*"), Sody (1940, p. 397) supposed "it to be a race of *R. mülleri,*" and Ellerman (1949) placed it, along with *muelleri,* in his *callitrichus* group (table 13). *Rattus xanthurus* and *R. everetti* are discussed because Misonne (1969) brought them, together with *muelleri* and other species, into the subgenus *Bullimus* (table 13).

Views of skulls and dentitions of five of these *Rattus* are shown in figures 89, 91, and 92; some measurements are listed in table 31. In traits of skins, skulls, and teeth each species is distinctive and each is morphologically peripheral to species in the subgenus *Rattus,* that cluster at the core of the genus. *Rattus macleari, R. enganus,* and *R. xanthurus* seem to cluster. A large body, long bicolored tail, reddish brown and thick fur over upperparts, buffy underparts, and long guard hairs characterize *R. macleari. Rattus enganus* has soft fur, long guard hairs, grayish brown upperparts, pale gray underparts, and a long monocolored brown tail. *Rattus xanthurus* is also long-tailed but the tail is bicolored, the head and body are grayish brown, the underparts are cream or grayish buff, and long guard hairs are scattered about in the dorsal pelage.

In overall conformation, the skull of *R. macleari* and *R. enganus* are similar. In both, the bullae are relatively small compared with skull size, maxillary toothrows are nearly parallel, the incisive foramina are long, the shape and height of the braincase is similar, the configuration of the alisphenoid region is the same, and the conformations of the mesopterygoid and pterygoid areas are similar except that *R. macleari* lacks sphenopterygoid vacuities in the pterygoid plates. The occlusal patterns on the molars are similar in the two species. In the upper molars, the cusps are discrete and remain so even after much wear so the laminae are obviously composed of cusps that are only slightly joined.

Most features of the skull and teeth of *Rattus xanthurus* also closely resemble those in *R. macleari* and *R. enganus.* The primary difference is that the bullae are relatively larger compared with skull size, the palatal bridge is relatively shorter, and the sphenopterygoid vacuities breaching the walls of the mesopterygoid fossa are long and spacious.

Rattus macleari, R. enganus, and *R. xanthurus* also share a geographic distribution in which all occur on islands well off the Sunda

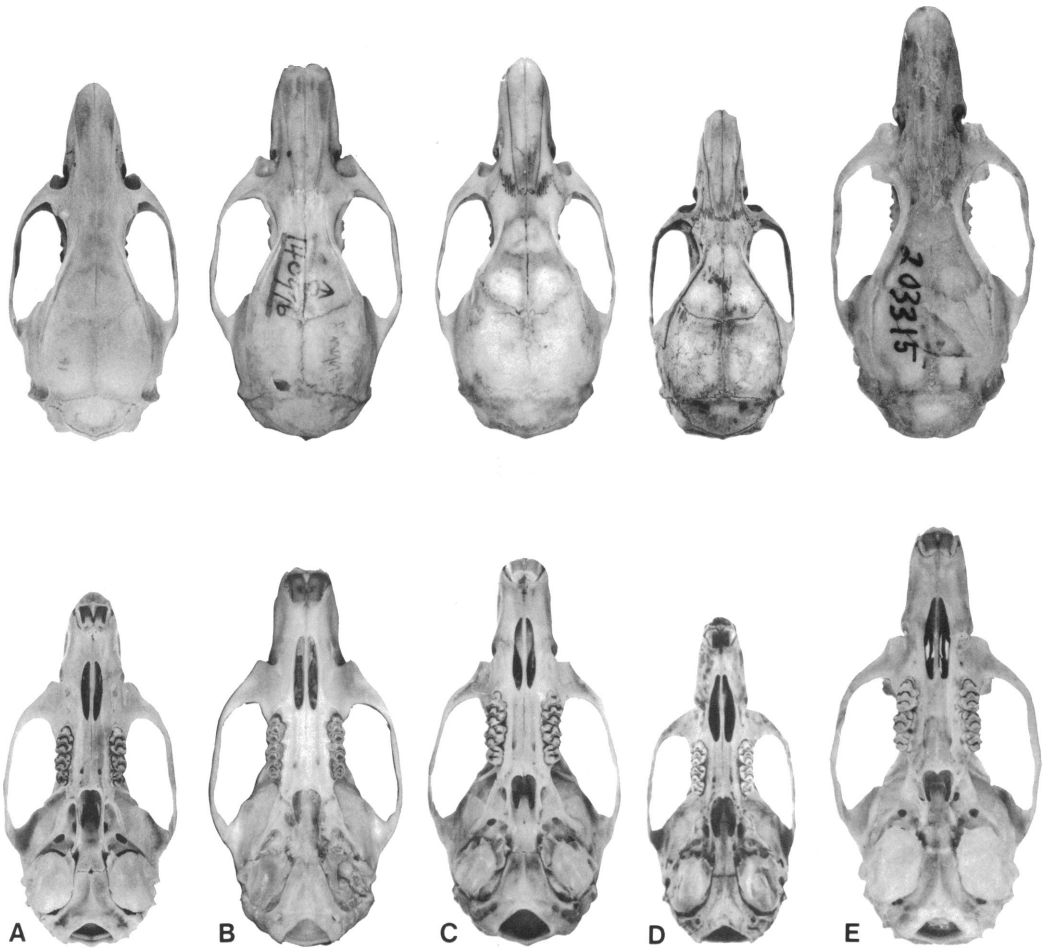

FIG. 89. Views of crania from species of adult *Rattus*. A, *R. annandalei,* Malay Sumatra (AMNH 217951). B, *R. enganus,* Pulau Enggano (USNM 140976). C, *R. macleari,* Christmas Island (USNM 141477). D, *R. marmosurus* (part of the *R. xanthurus* complex), northern Sulawesi (BM 97.1.2.21). E, *R. everetti,* Mindanao Island in the Philippines (AMNH 203315). Natural size.

Shelf. When Thomas (1887) described *Mus macleari,* he considered it part of a group which included *celebensis, xanthurus, everetti, meyeri,* and *muelleri.* But of *muelleri,* Thomas (1887, p. 514) noted that "This last does not properly belong to the present group of species, but is only introduced to complete the list of those of which it is necessary to mention the distinguishing characters when describing *M. macleari* as new." We do not yet know if *R. macleari, R. enganus,* and *R. xanthurus* are more closely related to each other than to any other species of *Rattus*; all three require more intensive study. We do know that Thomas correctly assessed the relationship between *R. macleari* and *R. xanthurus* on one hand and *S. muelleri* on the other. Those two species of *Rattus,* and *R. enganus,* are not island relatives of *Sundamys muelleri.* Most of the same cranial features that distinguish *Rattus* from *Sundamys* also separate the three species from *Sundamys.*

Rattus everetti is large-bodied and has a long and bicolored tail, grayish brown upperparts, and either white or grayish white

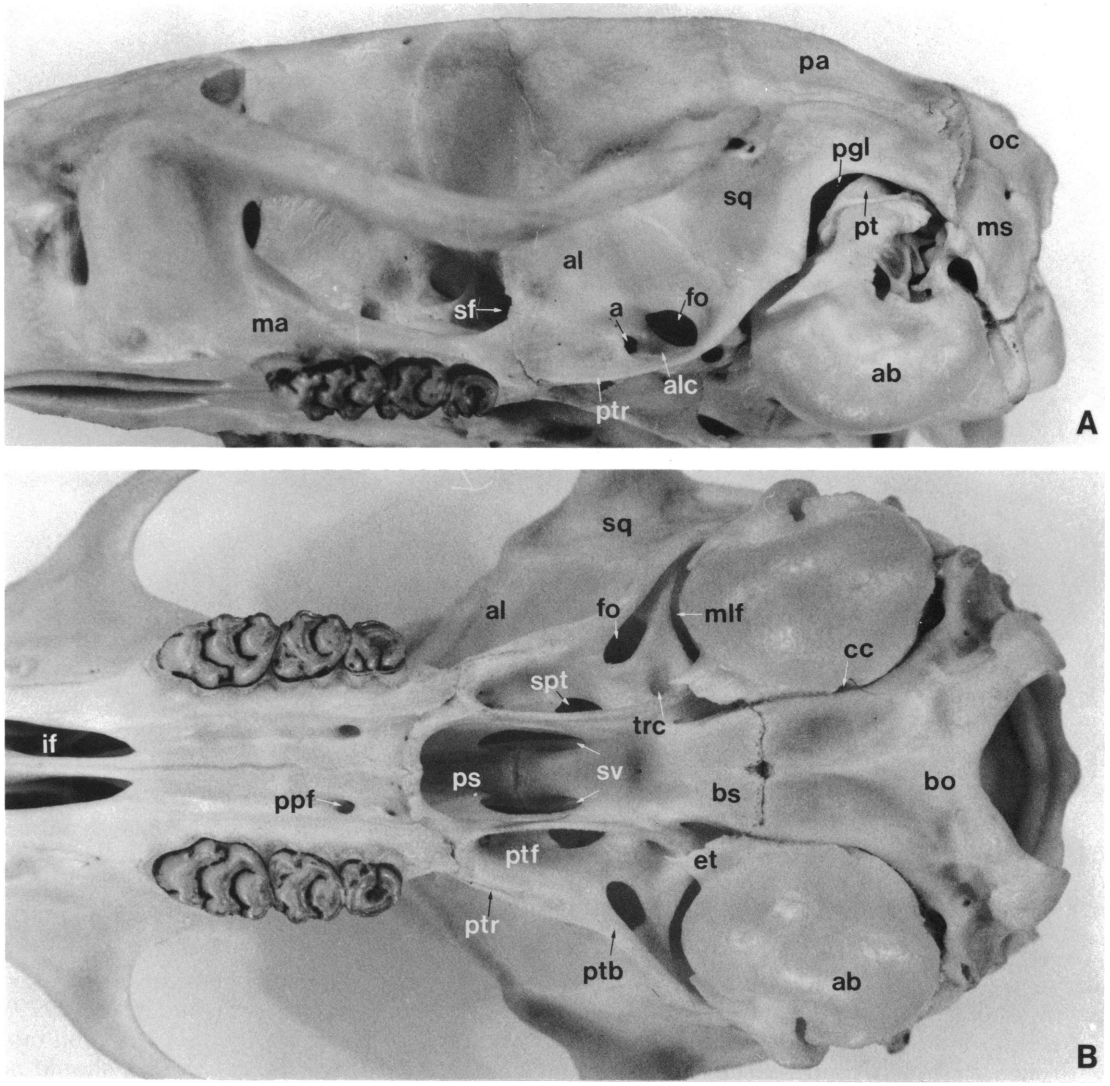

FIG. 90. Lateral (A) and ventral (B) cranial views of *Rattus annandalei* (AMNH 217591) from the Malay Peninsula. *Abbreviations:* **a**, anterior opening of the alisphenoid canal; **ab**, auditory bulla; **al**, alisphenoid bone; **alc**, alisphenoid canal, which is an open channel; **bo**, basioccipital bone; **bs**, basisphenoid bone, **cc**, carotid canal; **et**, bony eustachian tube; **fo**, foramen ovale; **if**, incisive foramina; **ma**, maxillary bone; **ms**, mastoid portion of the petromastoid; **mlf**, middle lacerate foramen; **oc**, occiput; **pa**, parietal bone; **pgl**, postglenoid vacuity; **ppf**, posterior palatine foramen; **ps**, presphenoid bone; **pt**, periotic portion of the petrosal; **ptb**, pterygoid bridge; **ptf**, pterygoid fossa; **ptr**, pterygoid ridge; **sf**, sphenoidal fissure; **spt**, sphenopterygoid vacuity; **trc**, transverse canal.

underparts. Its skull also resembles those of *R. macleari, R. enganus,* and *R. xanthurus* in most features except that it has relatively longer incisive foramina compared with skull size, relatively larger bullae that are also inflated compared with the bullae in the other species, relatively longer bony palate, and long sphenopalatine vacuities. The conformation of the skull in *R. everetti* resembles a very large version of *R. rattus.* Occlusal patterns of upper and lower molars also resemble those in the other three species except that the laminae on the uppers are straighter and usually without the ridges behind cusps t1 and t6 that

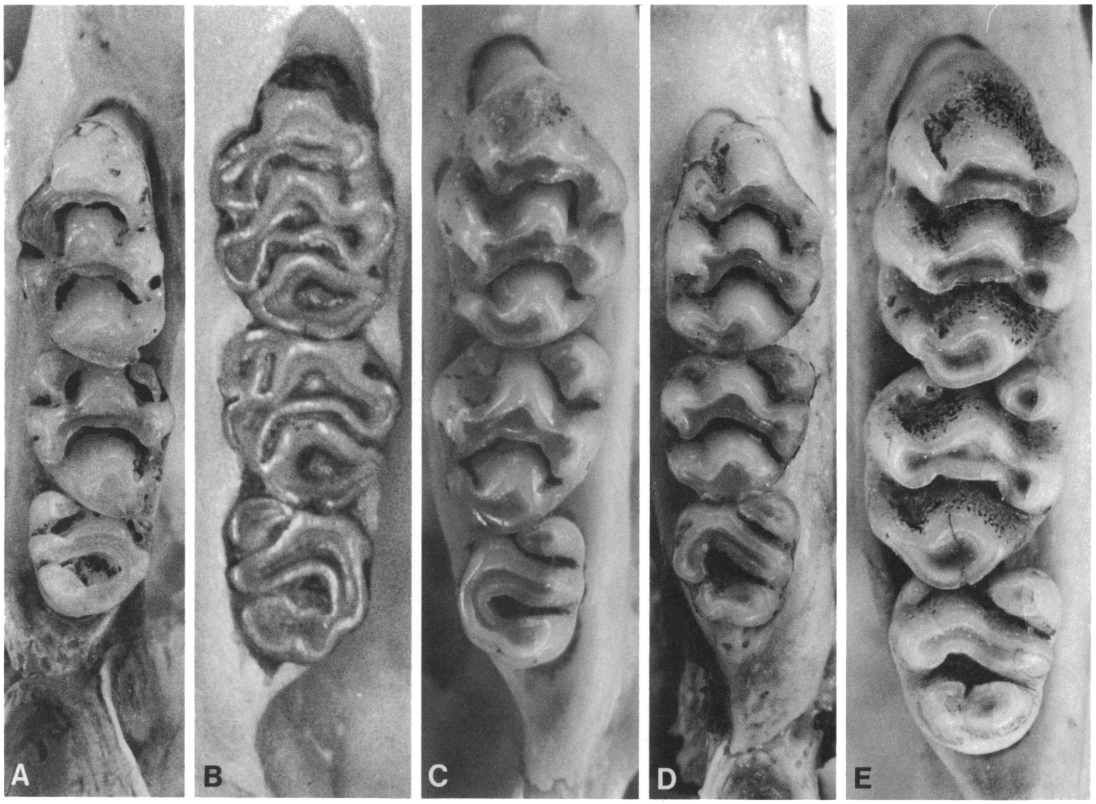

FIG. 91. Occlusal views of upper molar rows in species of *Rattus*. A, *R. annandalei,* Malay Peninsula (USNM 488871). B, *R. enganus,* Pulau Enggano (USNM 140976). C, *R. macleari,* Christmas Island (USNM 141477). D, *R. orientalis* (part of the *R. xanthurus* complex), southeastern Sulawesi (NMB 4768). E, *R. everetti,* Mindanao (AMNH 203317). All ×10.

are so characteristic in *R. macleari, R. enganus,* and *R. xanthurus.*

Rattus annandalei is of medium body size with grayish brown upperparts, underparts that range from white to pale yellow, and a long dark brown tail. The fur is soft and somewhat shaggy. The pelage, coloration, and proportions of *R. annandalei* resemble that in *S. muelleri* (Harrison, 1966); *R. annandalei* even has four pairs of mammae, the same number as *S. muelleri.*

The overall shape of the skull in *Rattus annandalei* is also similar to that in *S. muelleri* (compare figs. 42 and 89). Like many *S. muelleri, R. annandalei* also has short incisive foramina, a palatal bridge that ends just past the posterior margins of the third upper molars, and short sphenopalatine vacuities. The resemblances in skin and some cranial features between *R. annandalei* and *S. muelleri* also extends to biochemical features according to Chan, Dhaliwal, and Yong (1979). Chan (1977) also reported that based on biochemical evidence, *R. annandalei* should be in its own species group rather than that containing *R. rattus* and its allies. This seemed to contradict information from study of chromosomes in which *R. annandalei* was considered very similar to *R. rattus* (Yong, 1969b; Yoshida, 1973).

From our study of skins, skulls, and teeth we would also disassociate *Rattus annandalei* from any close relationship with *R. rattus* and its allies but we would not include it in *Sundamys* either. Many of its characteristics resemble *R. macleari, R. enganus,* and *R. xanthurus* and we look on *R. annandalei* to be, like those species, morphologically peripheral to the core of species in *Rattus.* The proportions of its body, tail, and feet as well

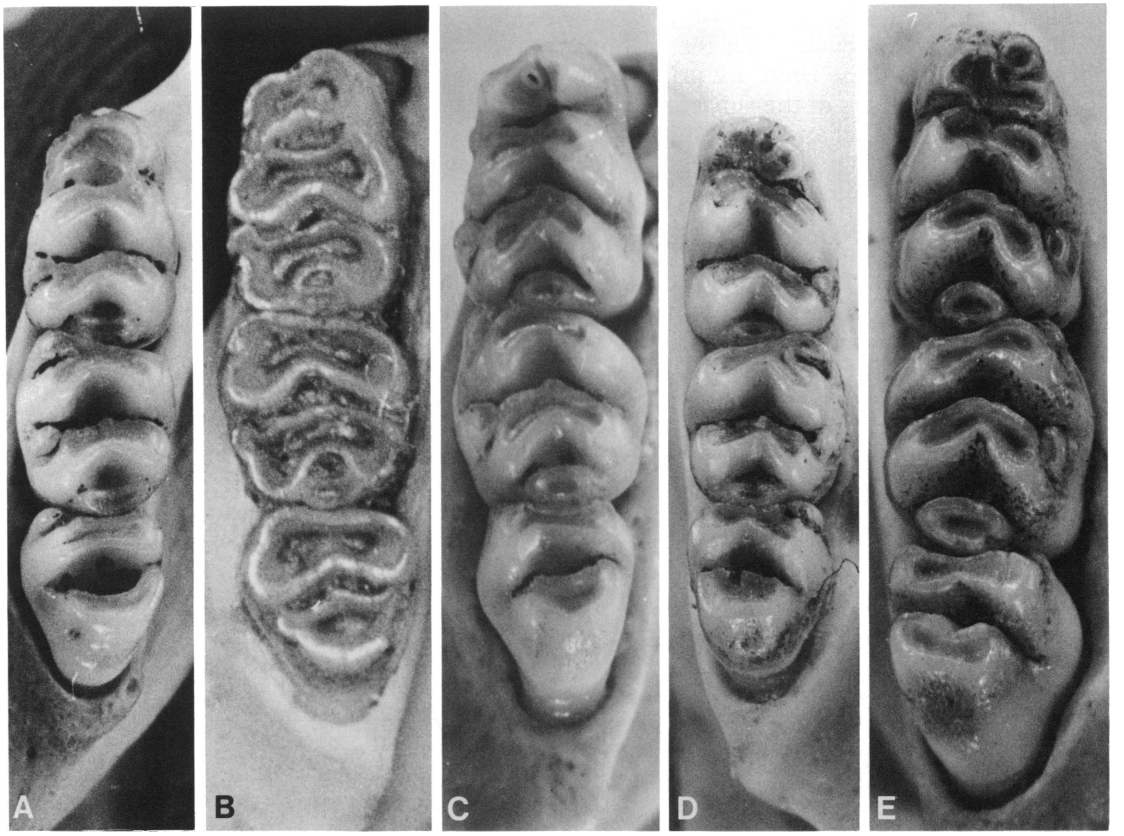

FIG. 92. Occlusal views of lower molar rows from the same specimens of *Rattus* shown in figure 91. A, *R. annandalei*; B, *R. enganus*; C, *R. macleari*; D, *R. orientalis*; E, *R. everetti*. All ×10.

as color and texture of pelage are like that in *R. tiomanicus* and *R. rattus,* and many other murids; the combination seems general and may even be primitive. The short incisive foramina, relatively short palatal bridge compared with skull length, and small sphenopterygoid vacuities in the mesopterygoid fossa are primitive traits (Musser, 1981a) and do not ally *R. annandalei* with *S. muelleri.*

A specialization in *Rattus annandalei* is its relatively large bullae compared with skull size (table 31), bullae that are also inflated. These contrast with the very small bullae in *S. muelleri* and the two other species of *Sundamys.* Furthermore, the bullar capsule is not tightly attached to the squamosal in *R. annandalei* but it is in the species of *Sundamys,* so tight in some species that capsule and squamosal appear fused. In other cranial features, *R. annandalei* differs from *Sundamys* in the same ways that other species of *Rattus* differ. The alisphenoid region in *R. annandalei* is typically *Rattus* in configuration, as are the pterygoid fossa and arrangement of openings in the pterygoid plates (fig. 90).

The number of roots anchoring each molar, the degrees of overlap among the molars in each row, the relative size of the third molars compared with the others, and height of the crowns are similar in *Rattus annandalei* and *Sundamys muelleri.* Low crowns are primitive and the other features are derived and shared by many species of murids, especially those in the Indo-Australian region with a *Rattus*-like cusp pattern. Most specimens of *R. annandalei* have a prominent posterior cingulum at the back of each first upper molar and a large cusp t3 on each second and third molar. Posterior cingula are frequent in the sample of *S. muelleri* and are

characteristic of *S. maxi* and *S. infraluteus*; all three also have a cusp t3 on the second and third molars. These traits are primitive. Compared to members of the subgenus *Rattus, R. annandalei* is set apart in its retention of large posterior cingula and anterolabial cusps on the second and third molars.

The occlusal patterns of *Rattus annandalei* and *S. muelleri* differ in important details (compare figs. 91 and 92 with fig. 41). Cusps forming the laminae of upper molars are discrete and not broadly joined as are their counterparts in *S. muelleri.* The cusps also tend to be triangular in cross-section rather than elongate (the central cusps) or round (the labial and lingual cusps) as they are in most specimens of *S. muelleri.* In *R. annandalei,* cusp t1 on each first upper molar sits more posterior in relation to cusps t2 and t3 than in *S. muelleri* where cusp t1 is about even with the opposite cusp t3. The overall occlusal patterns in *R. annandalei* are more complex. The configuration is due to deep ridges on the posterior margins of cusp t1 and t3 of each first upper molar, cusp t1 of each second upper molar, and sometimes cusp t3. Cusps t4 and t6 on each first and second molar also have posterior extensions and in some specimens cusp t4 on each first and second molar appears to be formed of two cusps, much like the configuration in *Paruromys dominator.* The effect of these ridges and crests is to join the lamina after wear, thus providing more chewing area. Although not as complex, the occlusal patterns in *R. macleari, R. enganus,* and *R. xanthurus* resemble those in *R. annandalei.* Such crests and ridges do not occur in *S. muelleri* or the other species of *Sundamys.*

We cannot tie *Rattus annandalei* to *S. muelleri* by characteristics of skins, skulls, dentition, or chromosomes. Before accepting the biochemical evidence linking *R. annandalei* and *S. muelleri,* we want to see how the two species sort out when compared with biochemical data from the other *Rattus* discussed here, particularly *R. xanthurus* and *R. everetti. Rattus macleari, R. enganus, R. xanthurus,* and others (*R. hoogerwerfi,* for example) are species that require taxonomic revision and detailed comparisons with all the other species in *Rattus.* In any taxonomic study, *R. annandalei* needs to be carefully compared with these to determine if it is more closely related to them than to those now included in the subgenus *Rattus* (Ellerman, 1941, 1949).

Rattus nativitatus is another that should be compared with the other morphological outliers in *Rattus.* It is a large-bodied rat with a short tail and long claws, and is adapted for living on the ground and burrowing. When he named and described *nativitatus,* Thomas (1888b, p. 533) wrote:

> size large; form thick and clumsy, the limbs and tail stout and heavy, but the head peculiarly small, slender and delicate. General colour dark umber-brown all over, the belly not, or scarcely, lighter than the back. . . . Fur of back long, thick, and coarse, but without the extremely long piles so characteristic of *M. macleari.* . . . Hands and feet very thick and heavy; the claws, especially on the fore feet, enormously broad and strong, not compressed, more than twice the size of those of *M. macleari,* and evidently modified for burrowing. . . . Tail shorter than the body without the head, very thick, evenly tapering, nearly or quite naked; its scales triangular, very large, the rings averaging about 7 or 8 to the centimetre; its colour uniform blackish brown throughout, above and below.

The skull is "disproportionally small, light and delicate; compared with that of *M. macleari* it is slightly shorter and very considerably narrower."

For Thomas, "This fine Rat cannot possibly be confounded with any other known species of the genus. Its size, peculiarly small and delicate head, short unicolor tail, large hands and feet, and powerful digging claws, separate it at once from any of its congeners." *Rattus nativitatus* is not a member of *Sundamys.*

With the definitions of *Sundamys, Berylmys,* and *Palawanomys* completed, we now write about all the species of rats and mice known to occur on the Sunda Shelf. We first discuss the species that were certainly introduced to the Shelf by human agency and those likely to have been introduced there by that process. We then review all the native Sundaic species.

SUNDAIC MURIDS: PERSPECTIVE AND PATTERNS

Describing *Palawanomys,* diagnosing *Berylmys,* and identifying the Giant Rat of Sumatra and *Sundamys* form a major part of our report. That taxonomic and distributional information helped outline the context in which we will discuss the generic and specific diversity of murids on the Sunda Shelf, their peninsular and insular distributions, and their possible phylogenetic relationships. The picture of Malaysian murids emerging for us is different than that seen by others. Our viewpoint rests upon analyses of data derived from firsthand study of skins, skulls, teeth, and sometimes fluid-preserved specimens supplemented by information from chromosomal and biochemical studies reported in the literature. From our perspective, relationships among the Malaysian murids form several patterns, some of which were concealed before we began our inquiry. We discuss these patterns in the following pages.

INTRODUCED SPECIES

One pattern is the dichotomy of native species on the one hand and introduced on the other. Among species recorded from the Sunda Shelf, 40 of them are native (table 36) and the distributions of 10 others (table 32) are probably the result of immigration through human activities. This pattern is not one we discovered because *Rattus rattus rattus, R. norvegicus,* and *Mus castaneus* have always been treated as introductions to the peninsula and islands of the Shelf where they occur in commensal relationships with humans. The composition of the group we hypothesize to be introduced to the Shelf is new because we include two additional species of *Rattus,* three species of *Mus,* and two of *Bandicota.* We are concerned primarily with the native rats and mice of the Shelf but some species we think are introductions have always been listed by other taxonomists as part of the native Malaysian fauna. Before writing about the real natives, we must extract the introduced species and explain why we do not treat them as natives.

CERTAIN INTRODUCTIONS

Clearly three have been introduced: the European house rat, *Rattus rattus rattus*; the brown or Norway rat, *Rattus norvegicus*; and the house mouse, *Mus castaneus.* The European house rat, *Rattus rattus rattus* (*frugivorous* and *alexandrinus* are synonyms) is rare on the Sunda Shelf. Chasen (1940, p. 151) wrote of it:

> Rats that can be fairly allocated to *R. r. rattus, R. r. frugivorous* and *R. r. alexandrinus,* and

TABLE 32
Distribution of *Rattus, Bandicota,* and *Mus* Introduced to Islands on the Sunda Shelf

Species	Peninsular Thailand and Malaya	Sumatra	Borneo	Java	Bali	Smaller Islands	Palawan Group
Rattus rattus diardii	+	+	+	+	+	+	–
Rattus rattus mindanensis	–	–	–	–	–	–	+
Rattus rattus rattus	+	?	?	?	?	?	?
Rattus argentiventer	+	+	+	+	+	–	–
Rattus norvegicus	+	+	+	+	+	+	?
Rattus exulans	+	+	+	+	+	+	+
Bandicota bengalensis	+	+	–	+	–	–	–
Bandicota indica	+	–	–	+	–	–	–
Mus castaneus	+	+	+	+	+	+	?
Mus caroli	+	+	–	+	–	–	–
Mus cervicolor	–	+	–	+	–	–	–
Mus dunni	–	+	–	–	–	–	–

> others that are nondescript, occur near the wharves in the port of Singapore, and they certainly infiltrate along the shipping routes to other Malaysian ports for I have seen examples of the first named form (or a nondescript very near to it) from as far afield as Cocos and Christmas Islands, and from a boat trading to these places. But these introduced forms are rare on shore in Singapore, and from the evidence at my disposal they may be even rare, or nonexistent in some other Malaysian ports. For instance, Kopstein (1931), who knew their characters well, recorded their absence from large numbers of house rats examined in the harbour towns of Java. In Singapore, foreign rats seem to have great difficulty in perpetuating their race although occasional long tails among the resident population of *diardi* no doubt indicate the immigrant blood.

Rattus norvegicus is probably endemic in northeastern China (Johnson, 1962). It has spread around the world through human aid. In the tropics, *R. norvegicus* occurs in large port cities. Chasen (1940, p. 182), noted that the species "has spread with shipping and commerce to all countries, but meets with most success as a colonist in temperate lands. In warm regions it is frequently unable to displace *R. rattus.* In Singapore and most other Malayan ports the typical form of *norvegicus* is common and in restricted areas in the towns and their immediate vicinity it is often the dominant species, although the local race of *R. rattus* is always found, commonly, in close proximity." Medway (1969; p. 76) wrote that in Malaya, *R. norvegicus* was "restricted to coastal towns including Kuah, Langkawi, Georgetown, Penang, and Singapore city." According to Medway (1965, p. 123), in Borneo "there are records of *R. norvegicus* from Pontianak and Bandjermasin, and the ports of Sarawak; in Sabah, the brown wild form has been trapped in paddy fields in Kudat district, in the extreme north, and the albino domestic strain—which is widely kept as a pet—appears to exist free in the feral state in one or two towns of the west coast including Telipok." The species is common on Java, especially in large cities such as Jakarta, Cheribon, Semarang, and Surabaya (Sody, 1930, 1941).

Mus castaneus (formerly called *M. musculus castaneus*; see Marshall, 1981; Marshall and Sage, 1981) is the third certain introduction to the Sunda Shelf. According to Marshall and Sage (1981, pp. 20–21), *M. castaneus* is one of man's "closest indoor associates among undomesticated mammals" and has no known feral range. Those authors also claim that "In Asia, *Mus castaneus* is limited to cities and towns mostly along the coast, from Bombay to Fukien and around Taiwan, Indonesia, and the Philippines." Of the Sundanese samples, Chasen (1940, p. 183) wrote that "A house mouse is well established in the ports and certain inland localities in many parts of Malaysia, . . . I know of the species only in association with man. Local adults, even from houses, are washed with ochraceous on the under parts, and I have not yet seen a specimen that could without hesitation be referred to the grey-bellied form found in indoor localities in Europe, although it is certain that such animals must reach eastern ports on ships." In Malaya *Mus castaneus* is confined to towns and lives in houses, outbuildings, and warehouses. Medway (1965, p. 132) noted that the house mouse in Borneo was "commensal with man, and restricted to urban areas. There are records from Jesselton and Kasigui, near Jesselton, and a specimen caught at Kuching 'in a packing case aboard S. S. Rejang shortly after her first arrival from Singapore, 28th July, 1934'."

Probable Introductions

There are two subspecies of *Rattus rattus,* two species of *Rattus,* two *Bandicota,* and three species of *Mus* recorded from the Sunda Shelf (table 33) that we hypothesize are introductions. The house rat, *Rattus rattus diardii,* occurs in croplands, scrub, plantations, houses, villages, towns, and large cities. South of the Isthmus of Kra, the rat is found everywhere on the Sunda Shelf wherever human habitats prevail except the Palawan area (the islands of Palawan, Culion, and Cuyo) where *R. r. mindanensis* occurs, which closely resembles *R. r. diardii* in all morphological features except body size; *mindanensis* is a larger rat, on the average, than *diardii* (Sanborn, 1962). *Rattus rattus diardii* is also found on some islands south and southwest of the Shelf (Pulau Dua, a small island near Pulau Enggano; Pulau Enggano itself; in the Mentawai Islands from Pulau Pagi Utara, Pulau Sipora and Pulau Siberut; the Cocos-Keeling

islands, and Christmas Island), west of the Shelf in the Nicobars (table 28), east of Kalimantan (Kepulauan Maratua), east of Bali (Lombok, Sumbawa, Saleyar, and Komodo), and on Hachijo Island in the Seven Islands of Izu, Japan (Musser and Califia, 1982).

Because *diardii* is closely associated with human habitats, because the rats are similar in body size and coloration over their entire geographic range without the patterns of geographic variation often found in some widespread species of native rats, and because the geographic range reflects the spotty distribution pattern predicted by inadvertent introduction and not that expected of species native to the Sunda Shelf, *Rattus rattus diardii* is thought to have been introduced to the Shelf from someplace outside of that region; from just where is still not known (Harrison, 1961; Medway and Yong, 1976; Musser and Califia, 1982).

On the Sunda Shelf, the ricefield rat, *Rattus argentiventer,* has been recorded from peninsular Thailand and Malaya, Koh Samui, Sumatra, Borneo, Java, Kangean Island, and Bali. North of the Isthmus of Kra, it occurs in Thailand and Vietnam. East of Bali, the rat is found on the islands of Lombok, Sumbawa, Komodo, Rintja, Flores, Sumba, and Timor. *Rattus argentiventer* is also found in Sulawesi, and on the islands of Luzon, Mindoro, and Mindanao in the Philippines. And there is one record from New Guinea (Musser, 1973a, 1981b; Berbehenn, Sumangil, and Libay, 1972–1973; Taylor, Calaby, and Van Deusen, 1982). Superbly adapted to ricefields and grassland, *R. argentiventer* is also found in scrub and plantations. Medway (1969) notes that the ricefield rat is restricted to ricefields, scrub, grassland, and young plantations in Malaya and that it is absent from the forested interior. Ricefield rats are a pest in plantations of young oil palms (Wood, 1969, 1971). In Borneo, according to Medway (1965, p. 122), *R. argentiventer* is "restricted to ricefields and grasslands, and established only in suitable areas near the coast. Rats from this habitat tend to be overlooked or ignored by collectors, and very poorly represented in museum collections. As a result formal records of this rat are scarce and it is not possible to assess its true position in Borneo." The ricefield rat is common throughout Java, considered to be a pest, and has been the object of several studies associated with programs to control its depredations on rice (Van Heurn, 1931).

Specimens of *Rattus argentiventer* from the Sunda Shelf and from islands east of the Shelf are morphologically closely similar to one another. There does not seem to be any significant patterns of peninsular and insular morphological variation in *R. argentiventer* over the Shelf (Musser, 1973a). Distinctive patterns are present in native Sundanese murids, such as *Niviventer cremoriventer* (Musser, 1973b), *Chiropodomys gliroides* (Musser, 1979), and *Sundamys muelleri* (present report), species whose taxonomy and geographic distribution have been analyzed. The absence of distinctive patterns of insular variation in *R. argentiventer* and its spotty distribution on the Shelf where it is so tightly tied to habitats made and then maintained by humans suggests inadvertent introduction to the peninsula and some islands on the Sunda Shelf, possibly associated with rice culture.

On morphological grounds, *Rattus argentiventer* may be a native of Indochina. Characteristics of its skull and teeth indicate the ricefield rat to be related to members of the subgenus *Rattus* that are native to Southeast Asia north of the Isthmus of Kra. Musser and Marshall (MS.) are examining this possible relationship in more detail.

Rattus exulans has a very wide geographic range. North of the Isthmus of Kra it is found in Vietnam, Laos, Cambodia, Thailand, Burma, and Bangladesh. South of the Isthmus it occurs on peninsular Thailand and Malaya and most islands of the Sunda Shelf, as well as Pulau Simalur southeast of the Shelf. It is common in the Philippine Islands, Sulawesi, and the Lesser Sunda Islands (Nusatenggara). The species ranges eastward through the Moluccas to the New Guinea region and the Pacific Islands (Tate, 1935; Chasen, 1940; Sody, 1941; Laurie and Hill, 1954; Berbehenn, Sumangil, and Libay, 1972–1973; Williams, 1973; Poché, 1980; Musser, 1981b; Taylor, Calaby, and Van Deusen, 1982). Wherever *R. exulans* occurs with native rats it seems to be restricted to habitats made and maintained by humans. In any given place the species may be scattered or continuous from coastal plain to mountain top in croplands,

gardens, plantations, scrub, second-growth forest, village and town houses. The rat is one of the most common small rodents in these habitats.

Because samples of *Rattus exulans* are so similar in features of skins, skulls, and teeth from islands east of the Sunda Shelf, its presence on the Philippines, Sulawesi, and islands eastward to the New Guinea region probably reflects immigration by human agency (Musser, 1977, 1981c; Taylor, Calaby, and Van Deusen, 1982). The Sunda Shelf seems to be no exception. Chasen (1940, pp. 159–160) knew the species as *R. concolor* and in his handlist wrote that he could not

> see any difference between specimens from South Tenasserim, many parts of Siam, and the Malay Peninsula and therefore regard them all as *R. c. concolor*. . . . In Malaysia this rat is usually found in, or not far from human settlements. In the Malay Peninsula it is primarily a house rat and although specimens may be trapped in primary forest, such animals are rare, and I have never seen one from a remote, undisturbed collecting ground in old forest. . . . Specimens taken in forest are usually paler and brighter brown on the upper parts and lighter grey on the under parts than those trapped in houses etc. . . . The natural range of the species is now difficult, if not impossible to make out, but judging from the specimens I should say that it is likely that all those examined from the small islands in the South China Sea are importations.

Harrison (1966) indicated that *Rattus exulans* was introduced to Malaya and what is known about its habitat and habits there supports that view. Medway (1969, p. 75) pointed out that in Malaya the species is "widespread and common in settled areas of the mainland, frequenting houses, gardens, paddy fields, grassland, scrub and the forest fringe, from the sea shore up to 4,000 ft in the hill stations." He described its habits as a "ground rat of disturbed or cultivated land, bush and scrub, also freely entering houses. Recorded from tall forest only on the fringes of clearings."

Rattus exulans is also closely tied to human habitats on other islands. In Borneo, for example, the rat is "always associated with man, and common throughout Borneo in houses and among cultivation. Occurs even on high ground (in commensal habits) for instance up to 3,700 ft. in the Kelabit uplands near Bario, and around 3,000 ft. near the villages on the lower slopes of Kinabalu" (Medway, 1965, p. 123). In Java *R. exulans* is one of the most common rats in village houses, fields, croplands, gardens, plantations, and scrub; those habitats characterize much of the island and the rat is widespread there (Sody, 1930). Musser (1982d) has speculated that Java is another place where *R. exulans* was introduced.

On the Sunda Shelf *Rattus exulans* joins *R. norvegicus, R. argentiventer,* and *R. rattus diardii* in being tied to human habitats. And like those species, specimens from all over the Shelf are closely similar to one another in characteristics of skins, skulls, and teeth. *Rattus exulans* living on Borneo look just like those on the Malay Peninsula. In contrast, specimens of *Sundamys muelleri* and *Niviventer cremoriventer* from the Malay Peninsula, for example, are appreciably larger in body and skull size than respective examples from Borneo (Musser, 1973b; present report). The commensal nature of *R. exulans* combined with its relative morphological uniformity compared with the habitats and morphological variation of native rats on the Shelf suggests to us that *R. exulans* is not a Sundanese native.

We echo Chasen's words regarding the natural range of *R. exulans.* We do not know where the rat originally occurred. We speculate that it may be part of the *Rattus* fauna native to Southeast Asia north of the Isthmus of Kra and we invite study to test that suggestion. *Rattus exulans* is one of 10 species of *Rattus* found north of the Isthmus of Kra (table 57). Cranial and dental characters of *R. exulans* fit nicely with this group; possibly it is a small-bodied tropical member of the subgenus *Rattus* from Southeast Asia. It may also be significant that other species in the group have commensal associations with humans and distributions outside of their native range: *R. rattus, R. norvegicus, R. argentiventer,* and *R. nitidus* (Musser, 1973a, 1977; Taylor, Calaby, and Van Deusen, 1982).

Bandicota indica and *B. bengalensis* are Asian rats. The larger-bodied of the two, *B. indica,* occurs on Ceylon, throughout peninsular India north to Nepal and eastward to Burma, southern China (Yunnan and Hong

Kong), Taiwan, Vietnam, Laos, and Thailand (Ellerman, 1961; Marshall, 1977b; Musser, Freeman, and Marshall, MS). On the Malay Peninsula, there are records from the states of Kedah and Perlis in northern Malaya (Harrison, 1956), which for Marshall (1977b, p. 427), represent introductions during 1946. Elsewhere on the Sunda Shelf, *B. indica* is known by specimens with reliable locality data from Java only. There it appears to be common in the right habitat throughout the island (Sody, 1930, 1941). Sumatra is also included within the geographic range of *B. indica* by Chasen (1940), Ellerman (1961), and Marshall (1977b) but Musser (1982d) cannot verify any of the records by either published accounts or specimens and thinks it unlikely that *B. indica* occurs on the island.

Tropical grasslands and their agricultural counterparts are the primary habitats of *B. indica.* In Thailand, for example, the rat is found in ricefields, weed fields, and gardens (Pantuwatana, Imlarp, and Marshall, 1969; Marshall, 1977b). In Java, the rats occur in ricefields and fields of tall grass and low scrub (Sody, 1930; Stafford, Sukeri, and Sutanti, 1976). The rats have also been trapped in grain warehouses in Calcutta, India (Mitchell, 1971). Arjunwadkar and Gadgil (1974, p. 140) report that in Poona, India, *B. indica* forms colonies in extensive burrow systems, and "The colonies are always next to a house or a grain storage godown generally lying at the back of the houses close to a fence or compound wall. The burrows often extend under the floor of the house and occasional burrow openings are produced inside the house especially if it has a mud flooring."

Bandicota bengalensis is primarily Indian in distribution. Its range extends from Ceylon north through India to Pakistan, Kashmir and Nepal, then east to Burma and Bangladesh (Ellerman, 1961; Smiet, Khokhar, and Fulk, 1978). It does not occur in Thailand, Laos, Vietnam, and Cambodia. The *Bandicota* in those countries are *B. indica* and *B. savilei* (Marshall, 1977b; Musser, Freeman, and Marshall, MS.). Outside of the Indian and Burma area, *B. bengalensis* has been recorded from Penang Island off the west coast of Malaya (Chasen, 1936), northern Sumatra, and eastern Java (Kloss, 1921; Sody, 1930, 1941). *Bandicota bengalensis* is another inhabitant of ricefields and other kinds of agricultural areas. It is abundant in irrigated fields in India, as well as villages and towns, and also lives in grain warehouses in large cities such as Calcutta (Barnett and Prakash, 1976).

Specimens of both *Bandicota indica* and *B. bengalensis* from the Sunda Shelf closely resemble those from India, Indochina, and Taiwan. On the Sunda Shelf, both species are absent from primary forest habitats, live in cultivated or fallow fields and scrub, and occur only in agricultural regions that have been densely settled by humans for a very long time. We view their presence in northern Malaya, Penang Island, Sumatra, and Java as resulting from introductions by human agency.

Bandicota bengalensis, if specimens in collections indicate their abundance in the wild, is uncommon in both northern Sumatra and eastern Java. It probably competes in those places with *Rattus argentiventer,* which exists in large populations and lives in the same habitats, especially ricefields, gardens, and scrub. The introduction of *B. bengalensis* to at least Sumatra and Java may have been an inadvertent event associated with the introduction and maintenance of rice culture.

Bandicota indica may also have come to the Sunda Shelf along with rice culture but it is also eaten by people. The rat is a favorite item in the diets of Vietnamese and Thai, for example. It is big; adults weigh more than 500 grams and some reach more than 700 (Pantuwatana, Imlarp, and Marshall, 1969; Marshall, 1977b). Possibly the presence of *B. indica* on Java, and other places around the periphery of its range, resulted originally from being transported for food. Some individuals may have escaped and were able to live in the agricultural habitats maintained by their human captors.

Six species of *Mus* are found on the Sunda Shelf. Two, *M. crociduroides* and *M. vulcani,* are native (table 36); both are in the subgenus *Coelomys* (Marshall, 1977a). The other four are in the subgenus *Mus.* One of these is the house mouse, *M. castaneus,* which has most likely been introduced to the Shelf, as we already noted. Of the three others, *Mus caroli* and *M. cervicolor* are primarily Southeast Asian in distribution, and *M. dunni* is Indian.

According to Marshall (1977b, p. 401), "all species in the subgenus *Mus* are able to live with man; all have been found in a wild habitat as well [except the populations on the Sunda Shelf]."

Mus caroli has been reported from the Ryukyu Islands, Taiwan, southern China (Hainan and Yunnan), Vietnam, and Thailand. On the Sunda Shelf, the species is known from the Malay Peninsula in southern Kedah State (Langham and Ming, 1976), northern Sumatra, central and eastern Java, and the island of Madura. East of the Sunda Shelf, *M. caroli* has been taken on Flores in Nusatenggara (Marshall, 1977a, 1977b). *Mus caroli,* writes Marshall (1977b, p. 434), "inhabits ricefields and other agricultural grassy areas, with or without actual grain, where it evidently can subsist on invertebrates."

The geographic distribution of *Mus cervicolor* covers Nepal, Sikkim, Burma, Thailand, and Vietnam. On the Sunda Shelf, it is known only from northern Sumatra and central and eastern Java (Marshall, 1977a, 1977b). The mouse, according to Marshall (1977b, p. 436), "is a paddy-field mouse, occurring with *caroli* there and in grasses raised for fodder."

The pygmy mouse, *Mus dunni,* was once confused with *M. booduga* but the two are distinguished by chromosomal, cranial, and dental characters. *Mus dunni* has been recorded from the Indian states of Haryana, Uttar Pradesh, Madhya Pradesh, Maharashtra, and Tamil Nadu. There is also a record from the Sunda Shelf. In front of us are five skins and skulls of *M. dunni* (AMNH 244146–244150) prepared by Marshall who trapped the mice in ricefields in the Medan region of northern Sumatra and sent them to us. Characteristics of their skulls and teeth are those Marshall (1977a) used to distinguish *M. dunni* from *M. booduga.*

There may be an earlier record of *Mus dunni.* In their list of mammals known from mainland Sumatra, Robinson and Kloss (1918) recorded *Mus booduga* and noted that "This species is included by Schneider in his list of the Mammals of Sumatra on the strength of a specimen collected in Upper Langkat, N. E. Sumatra, determined by Oldfield Thomas and now in the Basle Museum. Further material is required before the species can be admitted to an unquestioned place in the local list." We have not seen the example and do not know whether it represents either *M. booduga* or *M. dunni.* We are indebted to Dr. Marshall for reminding us of this record.

The spotty distribution of *Mus caroli* and *M. cervicolor* on the Sunda Shelf and to the east of there in Nusatenggara has been interpreted in two ways. Writing about *M. cervicolor,* Marshall (1977a, p. 215) noted that "in Thailand, the small ricefield form has probably extended its range up river valleys into cultivated areas that used to be forest." But, he went on to point out that "the gaps in distribution of *Mus cervicolor* and *M. caroli* covering the entire Malay Peninsula (except Kedah), central and southern Sumatra, and western Java are not vagaries of transport with man. Rather, *Mus cervicolor* and *M. caroli* are excluded from such areas, within the perimeter of their natural range, by an unfavorable, extremely wet climate. I have made substantial efforts to trap these mice in ricefields and short grass at Bogor and Tjibodas, western Java, and concluded that they are indeed absent."

Musser (1981b, p. 136) expressed the opposite view about the Flores population of *Mus caroli,* writing that it "inhabits ricefields and was likely unintentionally introduced on Flores along with rice culture." To us, the occurrence of *M. caroli* and *M. cervicolor* in a few places on the Sunda Shelf is best explained by inadvertent human introductions. Samples from the northern end of the Malay Peninsula, northern Sumatra, and Java are similar to one another in features of skin and skull and do not show the geographic variation seen in native species of murids on the Shelf. Marshall's argument is not convincing. The two species of *Mus* may have been introduced to many places on the Sunda Shelf but were able to survive only in those areas of ricefields and grasslands in which the climate was similar to places where they occur on Southeast Asia north of the Isthmus of Kra. Introduced mice most likely will thrive only in habitats to which they are adapted.

Immigration by human agency may also explain *Mus dunni* in ricefields of northern Sumatra. It is closely related to *M. booduga* and both species are common in ricefields and other irrigated croplands in India (Bar-

nett and Prakash, 1976; Marshall, 1977a, 1981). Although some native Sundanese species of rats are found both on the Sunda Shelf and in Indochina north of the Isthmus of Kra, none of the native rats and mice occur on the Shelf and also in India. The only other rats with geographic distributions similar to that of *M. dunni* are *Bandicota indica* and *B. bengalensis,* species we speculate were introduced to the Sunda Shelf. The occurrence of *M. dunni* in only India and northern Sumatra is difficult to explain in any other context.

That *Rattus rattus rattus, R. norvegicus,* and *Mus castaneus* were introduced to the Sunda Shelf seems clear to us. That two other subspecies of *R. rattus,* two species of *Rattus,* two of *Bandicota,* and three species of *Mus* owe their presence on the Shelf to immigration by human means is our hypothesis. We come to it by comparing the geographic ranges of these eight species with those native on the Sunda Shelf. The Sundanese fauna is really quite special. Of the 40 native species we recognize, 33 (78 percent) are found only on the Shelf; the other seven occur also in Indochina. A few natives, such as *Sundamys muelleri* and *Rattus tiomanicus* are widespread on the islands and peninsula of the Shelf, many others are restricted to but a few islands and some are endemic to either an island or to the peninsula. The native species inhabit primary and disturbed tropical forests, sometimes scrub. A few are occasionally found in ricefields, other croplands, and villages but they do not occur in these habitats off of the Shelf; none have been carried about from place to place by human agency.

None of the commensal species show patterns of morphological variation on the Shelf or patterns of endemism that characterize some native species. For example, specimens of *Sundamys muelleri* from Palawan Island and the Malay Peninsula contain strikingly different rats. Those from Malaya are large and dark, rats from Palawan are pale and small. *Rattus exulans,* a commensal, from the two places cannot be distinguished except by labels on which locality data are recorded.

Java provides a good example of endemism. There are relatively more species of rats and mice endemic in Java compared with the total fauna of native murids (50 percent) there than on any other large island, or on the peninsula, of the Shelf. This relatively high endemism added to what is known about other native species in the present fauna as well as past faunas suggests that Java has been an island or partially isolated peninsula for a long period (Musser, 1982d). Judged from our records, Java is the only place on the Sunda Shelf where *Bandicota indica* has been found. Its presence only there would be consistent with the endemic nature of the fauna if *B. indica* did not occur elsewhere. But it does, and over an expansive area, from India to Vietnam, southern China, and Taiwan. If *B. indica* is a relict left from a distribution that was formerly more extensive over the Shelf, why aren't there populations on the other large Sunda islands and on the southern portion of the Malay Peninsula? And members of a relictual population usually show some morphological differentiation but Javanese *B. indica* look just like those from Southeastern Asia. We also think it significant that the species occurs on a large Sunda island that is the most intensely cultivated and from which the most forest has been removed, and that it has been found elsewhere on the Shelf only in Kedah State in northern Malaya, another region of intensive agriculture.

In the context of distributional and morphological patterns formed by the species native to the Sunda Shelf, those we postulate to be introductions form a discordant picture. Although three genera are involved, all the species share some degree of commensalism with humans, all are found in habitats made and maintained by humans, and all show little morphological variation from place to place.

RELATIONSHIPS AMONG NATIVE RATS AND MICE

We present a different pattern of generic and specific diversity on the Sunda Shelf than that seen by other taxonomists, particularly Chasen (1940). In Chasen's handlist of Malaysian mammals, he recognized 38 species in nine genera: *Chiropodomys, Haeromys, Hapalomys, Mycteromys, Pithecheir, Rattus, Bandicota, Gunomys,* and *Mus* (table 33). Most genera had few species and the majority of the species on the Shelf (23 out of 38) were in *Rattus,* a reflection of the broad morpho-

TABLE 33

Chasen's (1940) List of Genera, Species, and Subspecies of the Sunda Shelf and Their Current Taxonomic Status[a]

Genus and Species	Subspecies and Synonyms[b]	Current Status[c]
Rattus rattus	*rattus*:	*Rattus rattus* (European form)
	diardii (*neglectus, griseiventer, samati, palembang*), *turbidus*:	*Rattus rattus diardii*
	tikos, dentatus, fortunatus, panjius, alangensis, lontaris, kadanus, moheius, pipidonis, pannosus, pannellus, robinsoni:	*Rattus rattus* (Asian form)
	argentiventer (*brevicaudatus, bali*):	*Rattus argentiventer*
	jalorensis, banguei, roquei, viclana, payanus, rumpia, jarak, jemuris, perhentianus, tiomanicus, pemanggis, tingius, roa, batin, kunduris, rhionis, siantanicus, luxuriosus, pauper, mangalumis, tambelanicus, julianus, lamucotanus, ducis, tua, maerens:	*Rattus tiomanicus* (also *sebasianus, lasurius, delirius, generatius, blangorum, pharus, sribuatensis, kabanicus, terutavensis, sabae, ambersoni, piperis, tenggolensis*
Rattus baluensis	*baluensis, korinchi*:	*Rattus baluensis*
Rattus hoogerwerfi		*Rattus hoogerwerfi*
Rattus concolor	*concolor* (*obscurus, pullus, clabatus*), *ephippium* (*schuitemakeri*), *otteni, stragulum, equile*:	*Rattus exulans* (also *meringgit*)
Rattus annandalei	*annandalei, bullatus* (*villosus*):	*Rattus annandalei*
	remotus:	*Rattus sikkimensis*
Rattus muelleri	*muelleri, campus* (*virtus*) *dominator, potens, valens, balmasus, pinatus, firmus, credulus, chombolis, pollens, validus* (*foederis, victor*), *terempa, borneanus, otiosus, crassus, sebucus, integer*:	*Sundamys muelleri* (plus *waringensis, balabagensis, culionensis*)
Rattus mara		*Rattus tiomanicus*
Rattus infraluteus	*infraluteus*:	*Sundamys infraluteus*
	maxi:	*Sundamys maxi*
Rattus sabanus	*sabanus, nasutus, luta, vociferans, ululans, tapanulius, tersus, lancavensis, lucas, dictatorius, salanga, stridens, fremens, strepitans, bunguranensis, mansalaris, tuancus, masae, balae, mayapahit*:	*Leopoldamys sabanus*
Rattus rajah	*rajah, pellax, similis, hidongis*:	*Maxomys rajah*
	verbeeki:	*Maxomys surifer*
Rattus surifer	*surifer, leonis, luteolus, puket, casensis, telibon, muntia, pidonis, butangensis, flavidulus, manicalis, spurcus, flavigrandis, grandis, binominatus, pemangilis, aoris, anambae, ravus, natunae, catellifer, banacus, antucus, pinacus, mabalus, bandahara, saturatus, carimatae, serutus, perflavus, ubecus, solaris*:	*Maxomys surifer*
	lingensis:	*Maxomys rajah*
Rattus inflatus		*Maxomys inflatus*

TABLE 33—(*Continued*)

Genus and Species	Subspecies and Synonyms[b]	Current Status[c]
Rattus cremoriventer	*cremoriventer, flaviventer, kina, barussanus, mengurus, sumatrae, malawali, spatulatus, cretaceiventer*:	*Niviventer cremoriventer* (plus *solus, gilbiventer*)
Rattus rapit	*rapit, fraternus, orbus, cameroni*:	*Niviventer rapit* (plus *atchinensis*)
	solus:	*Niviventer cremoriventer*
	lepturus, maculipectus, fredericae:	*Niviventer lepturus*
Rattus bukit	*bukit, pan, lieftincki, jacobsoni, treubii, besuki, (lepturoides), temmincki, baturus*:	*Niviventer bukit*
Rattus alticola	*alticola, kinabaluensis*:	*Maxomys alticola*
	ochraceiventer:	*Maxomys ochraceiventer*
	inas:	*Maxomys inas*
	hylomyoides:	*Maxomys hylomyoides*
Rattus baeodon	(*trachynotus*):	*Maxomys baeodon*
Rattus bartelsii	*bartelsii* (*tijbuniensis*), *obscuratus*:	*Maxomys bartelsii*
Rattus whiteheadi	*whiteheadi* (*perlutus, melinogaster*), *asper* (*klossi*), *batamanus* (*mandus*), *batus, piratae, subitus*:	*Maxomys whiteheadi* (plus *coritzae, melanurus*)
Rattus edwardsi	*ciliatus, setiger*:	*Leopoldamys edwardsi*
Rattus norvegicus	*norvegicus*:	*Rattus norvegicus* (also *javanus*)
Rattus bowersii	*ferreocanus*:	*Berylmys bowersii*
Rattus canus	*canus, malaisia*:	*Lenothrix canus*
	sodyi:	*Kadarsanomys sodyi*
Mus musculus	*musculus, rama*:	*Mus castaneus*
	ouwensi:	*Mus caroli*
Chiropodomys gliroides	*gliroides, peguensis*:	*Chiropodomys gliroides* (also *penicillatus*)
Chiropodomys niadis		*Chiropodomys gliroides*
Chiropodomys anna		*Chiropodomys gliroides*
Chiropodomys major		*Chiropodomys major*
Chiropodomys legatus		*Chiropodomys major*
Chiropodomys pictor		*Chiropodomys major*
Chiropodomys pusillus		*Chiropodomys gliroides*
Haeromys margarettae		*Haeromys margarettae*
Haeromys pusillus		*Haeromys pusillus*
Hapalomys longicaudatus		*Hapalomys longicaudatus*
Mycteromys crociduroides	*crociduroides*:	*Mus crociduroides*
	vulcani:	*Mus vulcani*
Pithecheir melanurus	*melanurus*:	*Pithecheir melanurus*
	parvus:	*Pithecheir parvus*
Bandicota indica	*setifera*:	*Bandicota indica*
Gunomys bengalensis	*varius, sundavensis*:	*Bandicota bengalensis*

[a] The boundary of the Sunda Shelf is Chasen's (1940) physiographical Malaysia: the peninsula and islands south of 10° to 12° N latitude that are on the continental shelf within the 100 fathom line (we also include the Maratua Archipelago, which is just east of the 100 fathom line). The area is indicated by the unbroken red line on the map at the front of Chasen's handlist of Malaysian mammals.

[b] Names in parentheses are synonyms, according to Chasen (1940), of the name directly preceding the parentheses.

[c] Based on Chasen (1940), Medway (1965, 1969), Muul and Lim (1971), Musser (1972, 1973a, 1973b, 1979, 1981a, 1981c), Musser, Marshall, and Boeadi (1979), Musser and Califia (1982), Marshall (1977a), the present report, and Musser's unpublished data in manuscript.

TABLE 34
Distribution of Murid Genera On and Just Off the Sunda Shelf

	Endemic on Shelf	Shelf and Indochina	Shelf and Andamans	Shelf and Nicobars	Shelf and Mentawais	Shelf and Islands[a]	Shelf and Sulawesi
	Palawanomys	*Rattus*	*Rattus*	*Rattus*	*Rattus*	*Rattus*	*Rattus*
	Kadarsanomys	*Berylmys*					
	Sundamys	*Mus*					
	Pithecheir	*Leopoldamys*			*Leopoldamys*		
	Lenothrix	*Niviventer*					
		Maxomys			*Maxomys*		*Maxomys*
		Chiropodomys			*Chiropodomys*		
		Hapalomys					
							Haeromys
Total	5	8	1	1	4	1	3
Percent	36	57	7	7	29	7	21

[a] Pulau Simalur, Pulau Enggano, Christmas Island, and the Maratua Archipelago.

logical and distributional limits attributed to the genus by taxonomists working in the 1940s. Except for *Mycteromys,* which was eventually placed in *Mus,* and *Gunomys,* which has been combined with *Bandicota,* Chasen's generic composition of Sundanese murids prevailed in the literature up until the late 1960s (Ellerman, 1941, 1949, 1961).

We list 15 genera and 50 species from the Sunda Shelf; one of these genera and 10 species are treated by us as introductions and for that reason we exclude the species Chasen placed in *Mus* (which held species in subgenus *Mus* and not the native *Mus,* which Chasen called *Mycteromys*), *Bandicota,* and *Gunomys.* The natives consist of 14 genera and 40 species (table 36), which includes only six of Chasen's nine genera. The difference between his six and our 14 results partly from the discovery of a new genus in the Palawan region (*Palawanomys*), but mostly from drastic modification of the definition and contents of the genus *Rattus.* The Sundaic species that are now in *Kadarsanomys, Sundamys, Berylmys, Leopoldamys, Niviventer, Maxomys,* and *Lenothrix* were once considered to be part of *Rattus* (Misonne, 1969; Musser, 1981a, 1981c; present report). For Chasen, *Rattus* was a large genus and represented by many species in Malaysia but for us it contains only four native Sundanese species and is a small component of the native Sundaic fauna (40 species). *Rattus* is eclipsed by *Maxomys,* which has more species on the peninsula and islands of the Shelf than do any of the other genera (tables 36 and 37). An attempt to determine the monophyletic nature of *Rattus* has exposed all those species once included in the genus that do not belong there and has illuminated a different picture of generic diversity on the Sunda Shelf.

In that diversity we see distributional patterns formed by the endemic genera and species and by those genera with more extensive geographic ranges. Five of the Sundanese genera are endemic on the Sunda Shelf; eight are known from the Shelf and from north of there in Southeast Asia, China, and India; four are common to the Shelf and to the Mentawai Islands; three are native to the Shelf and Sulawesi; and only one, *Rattus,* occurs on the Shelf and on the Andaman Islands, Nicobar Islands, Pulau Simalur, Pulau Enggano, Christmas Island, and the Maratua Archipelago, all off the Shelf (tables 34 and 35). In eleven out of the 14 genera, all or some of their species are known only from the Sunda Shelf; three—*Hapalomys, Berylmys,* and *Leopoldamys*—do not have species endemic to the Shelf (table 37).

Among the species, 33 out of the 40 occur on the peninsula and islands of the Sunda Shelf and nowhere else. Judged by the peninsular and insular distributions of these species as indicated by samples of them we studied, their evolutionary histories have been intimately associated with the Shelf—they are truly Sundaic. Ten of these 33 occur on the peninsula and several large and small islands, 23 are endemic to either the peninsula, one

TABLE 35
Distribution of *Rattus, Leopoldamys, Maxomys,* and *Chiropodomys* on Islands off the Sunda Shelf

Genus and Species	Pulau Simalur and Pulau Siumat	Pulau Lasia and Pulau Babi	Mentawai Islands	Pulau Enggano	Christmas Island	Kepulauan Maratua
Rattus tiomanicus				+		+
Rattus simalurensis	+	+				
Rattus lugens			+			
Rattus adustus				+		
Rattus enganus				+		
Rattus macleari					+	
Rattus nativitatis					+	
Leopoldamys siporanus			+			
Maxomys pagensis			+			
Chiropodomys karlkoopmani			+			

of the large Sunda islands, or the Palawan region. Seven species occur on the Sunda Shelf and in Indochina. We record *Lenothrix, Pithecheir, Sundamys, Kadarsanomys,* and *Palawanomys* as endemic. All but *Pithecheir* and *Sundamys* are monotypic, two species are in *Pithecheir,* and there are three of *Sundamys.* Judged from samples of living species, the evolutionary histories of these five genera and eight species were tied to the Sunda Shelf.

Maxomys, Chiropodomys, and *Haeromys* are not restricted to the Shelf but most of the species in them (18 out of 28 among them) are found there (table 37). If relative number of species occurring in a particular region compared with the number found outside the area points to where the group evolved, then the evolutionary histories of most species of *Maxomys, Chiropodomys,* and *Haeromys* took place on the Sunda Shelf. These, like the five endemics noted above, are basically Sundanese (or Malaysian) rather than Asian or Indian, with a few species outside of the Sunda region.

In contrast to those eight genera, *Niviventer, Berylmys, Mus,* and *Rattus* have relatively few species on the Shelf (11 out of 12) compared with the number occurring in regions outside the Shelf, from Africa and Europe to Australia and New Guinea (table 37). Most species of *Niviventer* and *Berylmys* are found in Indochina; most of the more than 40 species of *Mus* are native to Africa, Europe, northern Asia, and Indochina; of the approximately 50 species of *Rattus,* only four are native to the Sunda Shelf.

The geographic origin of *Hapalomys* and *Leopoldamys* is uncertain. One species of *Hapalomys* is endemic to Indochina, the other is found both north and south of the Isthmus of Kra (Musser, 1972). Of the four species of *Leopoldamys,* one is known from northern Thailand, one is endemic to the Mentawai Islands, and the other two occur in Indochina and on the Sunda Shelf (Musser, 1981a).

We note possible phylogenetic relationships among the 14 genera found on the Sunda Shelf. First we write about *Lenothrix, Pithecheir, Kadarsanomys, Palawanomys,* and *Sundamys,* the Sundaic endemics. Then we discuss *Maxomys, Chiropodomys,* and *Haeromys,* genera having most of their species on the Sunda Shelf and a few outside that region. Next we review the Sundaic species of *Niviventer, Mus, Berylmys,* and *Rattus,* species in genera that are better represented in geographic regions outside of the Sunda area. We conclude the section with discussions of *Leopoldamys* and *Hapalomys,* the two genera represented by about the same number of species that occur on the Shelf as off of it.

Before discussing each genus, we describe the primitive and derived states in 34 traits and record their distribution among the 14 genera (table 38). Our aim is to determine if there are derived features shared among all the genera or combinations of them which may indicate close phylogenetic alliance.

TABLE 36
Living Murids on Peninsula and Islands of the Sunda Shelf[a]

Genera and Species	Peninsular Thailand and Malaya	Sumatra	Borneo	Java	Bali	Smaller[b] Islands	Palawan Group
Rattus tiomanicus	I	I	I	I	I	I	I
Rattus baluensis	–	I	I	–	–	–	–
Rattus hoogerwerfi	–	E	–	–	–	–	–
Rattus annandalei	I	I	–	–	–	–	–
Palawanomys furvus	–	–	–	–	–	–	E
Kadarsanomys sodyi	–	–	–	E	–	–	–
Sundamys muelleri	I	I	I	–	–	I	I
Sundamys infraluteus	–	I	I	–	–	–	–
Sundamys maxi	–	–	–	E	–	–	–
Berylmys bowersii	O	O	–	–	–	–	–
Mus crociduroides	–	E	–	–	–	–	–
Mus vulcani	–	–	–	E	–	–	–
Leopoldamys sabanus	O	O	O	O	–	O	–
Leopoldamys edwardsi	O	O	–	–	–	–	–
Niviventer bukit	O	O	–	O	O	–	–
Niviventer cremoriventer	I	I	I	I	I	I	–
Niviventer rapit	I	I	I	–	–	–	–
Niviventer lepturus	–	–	–	E	–	–	–
Maxomys surifer	O	O	O	O	–	O	–
Maxomys rajah	I	I	I	–	–	I	–
Maxomys panglima	–	–	–	–	–	–	E
Maxomys whiteheadi	I	I	I	–	–	I	–
Maxomys bartelsii	–	–	–	E	–	–	–
Maxomys inflatus	–	E	–	–	–	–	–
Maxomys hylomyoides	–	E	–	–	–	–	–
Maxomys inas	E	–	–	–	–	–	–
Maxomys alticola	–	–	E	–	–	–	–
Maxomys ochraceiventer	–	–	E	–	–	–	–
Maxomys baeodon	–	–	E	–	–	–	–
Chiropodomys gliroides	O	O	O	O	O	O	–
Chiropodomys muroides	–	–	E	–	–	–	–
Chiropodomys major	–	–	E	–	–	–	–
Chiropodomys calamianus	–	–	–	–	–	–	E
Haeromys margaretae	–	–	E	–	–	–	–
Haeromys pusillus	–	–	E	–	–	–	–
Haeromys sp.	–	–	–	–	–	–	E
Pithecheir melanurus	–	–	–	E	–	–	–
Pithecheir parvus	E	–	–	–	–	–	–
Lenothrix canus	I	I	I	–	–	–	–
Hapalomys longicaudatus	O	–	–	–	–	–	–
Total species	17	20	19	12	4	8	6
Total indigenous	8 (47)[c]	10 (50)	9 (47)	2 (17)	2 (50)	5 (63)	2 (33)
Total also found elsewhere	7 (41)	6 (30)	3 (16)	4 (33)	2 (50)	3 (37)	– –
Total endemic	2 (12)	4 (20)	7 (37)	6 (50)	– –	– –	4 (67)

Abbreviations: –, apparently absent; E, endemic to a particular island; I, indigenous to the Sunda Shelf; O, also found in regions outside the Sunda Shelf.

[a] Defined here, the northern limit of the Sunda Shelf is near the Isthmus of Kra between latitudes 10° and 12° N. South of the Isthmus, the 100 fathom line marks the boundary, as indicated by the unbroken red line on the map at the front of Chasen's handlist of Malaysian mammals and figure 1. Regions outside the Sunda Shelf include Indochina north of the Isthmus of Kra (10°30′ N), the Maratua Archipelago east of Borneo, the Mentawai Islands, and Pulau Enggano.

[b] Includes the Raiu and Lingga archipelagos, the Natuna Islands, Kepulauan Anambas, Pulau Banka, Pulau Billiton, and Pulau Nias.

[c] Percent in parentheses.

TABLE 37
Number of Species in Murid Genera of the Sunda Shelf

Genera	Number of Species				Total on Shelf / Total in Genus (%)
	Restricted to Shelf	Occurring on Shelf and Elsewhere[a]	Total on Shelf	Total in Genus	
ENDEMIC					
Palawanomys	1	0	1	1	100
Lenothrix	1	0	1	1	100
Kadarsanomys	1	0	1	1	100
Pithecheir	2	0	2	2	100
Sundamys	3	0	3	3	100
NOT ENDEMIC					
Rattus	4	0	4	50[b]	8
Mus	2	0	2	43[b]	5
Haeromys	3	0	3	4	75
Niviventer	3	1	4	15	27
Chiropodomys	3	1	4	5	80
Maxomys	10	1	11	19[c]	63
Hapalomys	0	1	1	2	50
Berylmys	0	1	1	4	25
Leopoldamys	0	2	2	4	50
Total species	33	7	40	135	30

[a] Includes Indochina, the Maratua Archipelago, Pulau Enggano, and the Mentawai Islands.
[b] Estimates.
[c] Includes three new but undescribed species from Sulawesi.

Many of the characters we discuss in the present report are useful in distinguishing one species from another or even one genus from another, but not all the traits can be used for assessing relationships among the genera because we do not know if they represent primitive or derived states. The features we describe below are those we can reasonably hypothesize to be primitive or a derivation based on their distributions among species of the Muridae, among the larger group of muroid rodents, and among the Rodentia in general. Our polarities should be taken as hypotheses only. Keep in mind that in future analyses, some traits may prove to be highly correlated and represent but one character rather than several as we now list them. We describe the primitive condition first, then the derivation.

1. Tail (T): The tail in arboreal rats may be relatively long compared with the length of the head and body but it is not prehensile. The distal portion of the tail is prehensile in *Pithecheir* and this is a specialization.

2. Hallux (Ha): The first digit (hallux) on each hind foot bears a claw. Three structural types represent derivations. **SC:** the condition in *Pithecheir* in which each hallux bears a very short claw (as Musser, 1979, called it) or a scalelike claw (in Medway's, 1969, terminology). In some specimens, the structure is short, on top of the digital pad, and resembles a pointed nail with a highly convex surface. In other specimens, the clawlike nail overhangs the pad and looks more like a very small claw. The configuration is not like any of the nails in those genera which have a nail instead of a claw on the hallux; it represents the primitive state in the development of a nail from a claw. **CN:** a short and highly convex nail like that in *Kadarsanomys.* In all specimens of that genus, the nail is relatively very small compared with the very large digital pad and deeply embedded in it. The small nail has a highly convex dorsal surface, and a truncate distal margin (Musser, 1981c). **N:** In specimens of *Chiropodomys* and *Hapalomys,* the nail is small, nearly flat (the dorsal surface is only slightly convex), has either a straight or gently arcuate distal edge, and is

embedded in the top of the digital pad (Medway, 1964; Musser, 1979).

3. Hind feet (HF): Each hind foot is broad and moderately long. The interdigital pads are large, the outer metatarsal pad is conspicuous, and the inner metatarsal pad is elongate, usually kidney-shaped, and always much larger than any interdigital pad. The configuration is characteristic of *Sundamys muelleri* (fig. 15), for example, and species of *Rattus* (Musser, 1973a, 1973b; pl. 3 in Medway and Yong, 1976).

Long, narrow hind feet (**T**) are derived, such as those in *Maxomys inas* and *M. surifer* depicted in plate 3 of Medway and Yong (1976) and species of *Mus* (Marshall, 1977a). The interdigital pads are relatively smaller compared with the plantar surface, the outer metatarsal pad is very small and even absent in some specimens of *Maxomys* (Musser, Marshall, and Boeadi, 1979), and the outer metatarsal pad is usually no larger than the interdigital pads and oblong, not elongate and kidney-shaped. The metatarsal pads are close to the interdigital pads.

A very broad and short hind foot, the kind found in highly arboreal rats, is also specialized (**A**). The digital pads are large, especially those at the end of the hallux, which is swollen compared with those at the end of the other digits. The claws are short, recurved, and sharp. Except for *Lenothrix,* each hallux has a nail or nail-like claw. The two outer digits are semi-opposable and strong. The interdigital and metatarsal pads are large mounds that form most of the plantar. Parts of their surfaces are textured by high ridges and deep grooves. The hind feet of *Hapalomys* are the most specialized (see Medway's, 1964, description of the foot structure and function in *H. longicaudatus*). *Kadarsanomys* and *Lenothrix* are the least specialized of those with arboreal hind feet.

4. Supraorbital ridges (SOR): No or only slight beading along dorsolateral margins of the interorbital and postorbital regions; the braincase is either smooth all over or has low beading along the dorsolateral margins of the anterior half (inconspicuous temporal ridges) and is smooth over the posterior half. The derived condition is medium to high ridges or shelves that outline the interorbital area and the anterior part of the braincase; in some species, the ridges sweep back along dorsolateral margins of the braincase nearly or all the way to the occipital region.

5. Alisphenoid complex (Al): In all or more than three-fourths of a sample, a strut of alisphenoid bone covers the lateral part of the alisphenoid canal and separates the foramen ovale accessorius from the masticatory-buccinator foramina. In the derived state, there is no strut, the alisphenoid canal is an open channel, and the foramina have merged; they appear to be functionally absent.

6. Squamoso-mastoid foramen (Sq-mF): The squamosal bone dorsal to each bulla is intact and not divided into a dorsal portion and a ventral segment (the tympanic hook) by a vacuity. The squamoso-mastoid foramen is confined to the suture between the squamosal bone and mastoid portion of the petromastoid complex. A small or large vacuity or fenestra in the squamosal is derived. This opening usually called the subsquamosal foramen (Klingener, 1968, p. 130), appears to be an enlargement of the squamosomastoid foramen and separates a ventral arm from the dorsal portion of the squamosal.

7. Size of bullae (SB): The auditory bullae are moderately to very small compared with size of the cranium. Relatively large bullae is the derived condition and occurs in two forms among Sundanese murids. **L:** refers to relatively large bullae compared with skull size but not highly inflated ones. **I:** indicates greatly inflated bullae, the kind found in *Pithecheir* and *Hapalomys.*

8. Attachment of bullae (AB): Each bullar capsule is tightly attached to the squamosal bone. The postglenoid vacuity is small and usually confined to the top of the capsule between the periotic and squamosal bones. The derivation is a wide, spacious vacuity that separates the dorsal and anterior margins of the periotic bone and bullar capsule from the squamosal.

9. Incisive foramina (IF): The incisive foramina are either very short (their posterior edges terminating well anterior to the maxillary molar rows) or longer but the posterior margins are still anterior to front faces of first molars in most of a sample. Long incisive foramina are derived. Their posterior edges

end either at the front faces of the upper molars or extend well past them (the usual condition).

10. Palatal bridge (PB): The posterior rim of the palatal bridge is anterior to the back margins of the third upper molars, even with them, or slightly posterior to them. In the derived configuration, the posterior edge of the palatal bridge extends well posterior of the third molars to form a wide platform behind the molar rows.

11. Mesopterygoid fossa (MF): The fossa is nearly as wide as the back part of the palatal bridge. Its walls are either complete or breached by thin and short sphenopalatine vacuities or slits. In the derived state, the fossa is one-third to one-half the width of the palatal bridge. The sphenopalatine vacuities are huge, so spacious that the presphenoid bone and anterior part of the basisphenoid bone appear suspended in air. The anterior portion of each vacuity can be seen in the back half of each orbit.

12. Pterygoid fossae (PF): Each fossa is nearly flat or only shallowly excavated. The opposite configuration is a fossa that is deeply excavated or the fossa floor is tilted down (in ventral view) toward the midline of the cranium.

13. Sphenopterygoid vacuity (SptV): The anterior two-thirds of each pterygoid plate is either complete or perforated by a tiny sphenopterygoid opening. The derivation is a plate in which the sphenopterygoid opening is small to very large.

14. Pterygoid platform (PP): The posterolateral part of each pterygoid platform or plate posterior to the foramen ovale is either nearly flat, a low mound, or a wide and smooth low ridge. The specialized configuration is an edge elevated into a definite high and thin ridge.

15. Color of incisors (CI): The enamel layers of both upper and lower incisors range from deep yellow to orange. Paler incisors—white, cream, pale yellow—are a specialized trait.

16. Tips of incisors (IT): The tips of the upper incisors are not notched (seen in side view), the primitive condition, as seen in species of *Rattus*. The dentine is notched in back of the enamel at the tip of the upper incisors, the typical configuration in species of *Mus* (Marshall, 1977a).

17. Roots of first upper molars (R-M^1): Each first upper molar has either three roots (anterior, lingual, and posterior) or four roots (a labial root in addition to the three primary roots, or a divided lingual root along with only an anterior and posterior root). Five roots (anterior, posterior, two lingual, and one labial) beneath each first upper molar is derived.

18. Roots of first lower molars (R-M_1): Each first lower molar is either two-rooted (an anterior and posterior) or three-rooted (either a labial or a lingual rootlet in addition to the two primary roots). Four roots (anterior, posterior, labial, and lingual) beneath each first lower molar is derived.

19. Size of molars (SM): The upper molars gradually decrease in size from the first to the third. In the derived configuration, each second upper molar is smaller than the first but the third is reduced in size and relatively much smaller compared to the second.

20. 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 the row, each tooth essentially abutting against the other. Conspicuous overlap among the molars is derived. The cusps slant back so that the first molar overlaps the second and the second overlaps the third. Misonne (1969) describes this conformation.

21. Cusps t1bis and 2tbis (t1-t2bis): These cusps do not occur on the first and second upper molars of most specimens in a sample; that is primitive. The opposite condition is that either cusp t1bis, cusp t2bis, or both are present on each first upper molar in most specimens, sometimes also on each second molar.

22. Relative position of cusp t1 on each first upper molar (t1-M^1): On each first upper molar, cusp t1 is well posterior to cusps t2 and t3, the bulk of the cusp usually posterior to the back of cusp t3, a condition Misonne (1969) regards as primitive. The derived state is a cusp t1 relatively farther anterior compared with cusps t2 and t3. Cusp t1 is usually only slightly set back or even with cusp t3.

23. Rows of cusps (RC): On upper and lower molars, especially the uppers, cusps form

TABLE 38

Distribution of Either Primitive (P) or Derived (+) Expressions of 36 Traits Among 14 Genera of Sundanese Murids[a]

	Rattus (subgenus *Rattus*)	*Palawanomys*	*Kadarsanomys*	*Sundamys*	*Berylmys*	*Mus* (subgenus *Coelomys*)	*Leopoldamys*	*Niviventer*	*Maxomys*	*Chiropodomys*	*Haeromys*	*Pithecheir*	*Lenothrix*	*Hapalomys*
1. T	P	P	P	P	P	P	P	P	P	P	P	+	P	P
2. Ha	P	P	+CN	P	P	P	P	P	P	+N	P	+SC	P	+N
3. HF	P	P	+A	P	P	+T	P	P	+T	+A	P	+A	+A	+A
4. SOR	+	P	+	+	P	P	+	+	+	+	P	+	+	+
5. Al	+	+	+	P	+	P	P	P	+	+	P	+	P	+
6. Sq-mf	P	P	P	P	P	+	P	P	P	P	P	+	P	P
7. SB	+L	+L	+I	P	+L	+L	P	P	P	P	P	+I	P	+I
8. AB	+	+	+	P	+	+	P	P	P	+	+	P	P	P
9. IF	+	P	+	P	P	P	P	+	P	P	P	P	P	P
10. PB	+	+	P	P	P	P	P	P	P	P	P	P	P	P
11. MF	+	+	P	P	P	P	P	P	P	P	P	P	P	P
12. PF	+	P	+	+	P	P	P	P	P	P	P	+	P	+
13. SptgV	+	+	+	P	P	P	P	P	P	+	+	P	P	+
14. PP	+	P	+	+	+	P	P	P	P	+	+	+	+	+
15. CI	P	P	P	P	+	P	P	P	P	P	P	P	P	P
16. TI	P	P	P	P	P	+	P	P	P	P	P	P	P	P
17. R-M^1	+	P	+	+	+	P	P	+	P	P	P	P	P	P
18. R-M_1	+	+	+	+	+	P	+	+	P	P	P	P	P	P
19. SM	+	+	P	P	+	+	P	+	+	P	P	P	P	P
20. OM	+	+	+	+	+	+	+	+	+	P	P	+	P	P
21. t1-t2bis	P	+	P	P	P	P	P	P	P	+	+	+	+	+
22. t1-M^1	+	+	+	+	P	P	P	P	P	P	P	P	P	+
23. RC	P	P	P	P	P	P	P	P	P	P	P	P	P	+
24. UC	+	+	P	+	+	+	+	+	+	P	P	P	P	P
25. t4-t5	+	P	–	+	+	+	+	+	+	–	–	–	–	–
26. C-t6	P	P	P	P	P	P	P	P	P	P	P	P	+	P
27. t7	P	P	P	P	P	P	P	P	P	+	P	+	+	+
28. t9	P	P	P	P	+	+	+	+	+	P	P	P	P	P
29. PC	+	P	P	P	+	+	+	+	+	P	P	P	P	+
30. MAC	P	+	P	P	P	P	P	P	P	P	P	P	P	P
31. t3-M^2-M^3	+	P	P	P	+	+	+	+	+	P	P	P	P	P
32. AC	+	P	P	+	+	+	+	+	+	P	P	P	P	P
33. Al-Al	P	P	P	P	+	+	+	+	+	P	P	P	P	P
34. AlC	P	P	P	P	+	+	+	+	+	P	P	P	P	P
Total derived traits	20	13	14	10	17	15	11	14	13	9	4	12	6	13

[a] Numbers and abbreviations correspond to numbered descriptions of traits on pages 533–537.

chevron-shaped or arcuate rows. In the derived conformation, the cusps sit next to each other to form straight rows, the pattern exemplified by *Hapalomys.*

24. Union of cusps (UC): Cusps on the upper and lower molars are weakly connected so the occlusal patterns appear strongly cuspidate. In the derived pattern, all or most cusps are strongly joined, some merged to the degree where they nearly lose their identities.

25. Cusps t4 and t5 (t4-t5): Cusp t4 is either separate from cusp t5 or weakly joined in the first upper molars of juveniles and adults. The rest of the cusps on the upper molars are broadly joined in each row. *Palawanomys furvus* (fig. 12) is the only species that has this primitive configuration. In other genera (*Hapalomys* and *Chiropodomys,* for example), cusps t4 and t5 are either separate or barely joined but so are most of the cusps in each row, which is a primitive configuration for all molars (see trait 24). The derivation of trait 25 is that cusp t4 is strongly connected to cusp t5 (except in some juveniles where the cusps are separate).

26. Cusp behind t6 (C-t6): There is no small or large accessory labial cusp behind cusp t6 on either first or second molar in most specimens of a sample. A specialization, according to Misonne (1969), is an accessory cusp, usually small, behind cusp t6 on each first upper molar and sometimes on each second molar in most or all specimens of a sample (the cusp is prominent in *Lenothrix,* for example). As the tooth wears down, the cusp merges with the back of cusp t6 to form a crest.

27. Cusp t7 (t7): No cusp t7 (also called posterointernal or posterolabial cusp) occurs on any upper molar. A cusp t7 is derived and if present is found on each first molar, usually on the second, and on the third in some species.

28. Cusp t9 (t9): This is a large and discrete cusp on each first and second upper molar. In the derived configuration, cusp t9 is nearly incorporated into the much larger cusp t8 and becomes inconspicuous after wear.

29. Posterior cingulum (PC): There is a cusp, the posterior cingulum, at the back of each first upper molar, often the second, and sometimes the third in most specimens of a sample. The cusp may be discrete, as in *Lenothrix,* or may be a high crest that is elongate or triangular in cross-section, as in *Kadarsanomys* or *Sundamys.* Lack of a posterior cingulum is derived.

30. Molar anterior crests (MC): Anterior faces of cusps on the upper molars lack crests. The derived state is shown by *Palawanomys* (fig. 12). Prominent crests extend anterior from the faces of certain cusps on each first and second upper molar (see the description in the *Palawanomys* account).

31. Cusp t3 on each second and third upper molar (t3-M^2-M^3): In all or most specimens in a sample, cusp t3 is present on the second and usually the third upper molars. The lack of cusp t3 from second and third molars is specialized.

32. Anterocentral cusp (AC): An anterocentral cusp is present at thefront of each first lower molar. The cusp may be large and discrete or small and partially joined to the anterolingual cusp. The absence of an anterocentral cusp is probably derived.

33. 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. In the derived configuration, the two cusps are smaller, pressed against each other to form a lamina narrower than the rest of the tooth. In young rats, the cusps may be separate but soon merge into a narrow and oblong lamina.

34. 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 specimens in a sample. Lack of anterolabial cusps in most or all specimens in a sample is derived.

LENOTHRIX

If low number of derived traits compared with the number of traits examined provides an estimate of how primitive or derived a genus is then the monotypic *Lenothrix* with only six derivations out of the 34 traits studied is one of the most primitive of the Malaysian murids. Originally described as a species of a new genus *Lenothrix* by Miller in 1903, *canus* was relegated to *Rattus* by Kloss in 1931 without reason and subsequently treated as a species of that genus (El-

lerman, 1941, 1949) until the late 1960s. At that time, Misonne (1969), who studied the distribution of molar characters among Indo-Australian Muridae, pointed out that *canus* was not closely related to any species of *Rattus* and reinstated *Lenothrix* as a valid genus, an action supported by Medway and Yong (1976) and Musser (1981a, 1981c), who examined traits of skins, skulls, and chromosomes, as well as teeth.

Specimens of *Lenothrix canus* come from three areas: Pulau Tuangku, off the northwest coast of Sumatra; Sarawak; the Malay Peninsula, and Pulau Penang (Lim, Muul, and Langham, 1971; Musser, 1981a). The species was once thought to be rare but on the Malay Peninsula turned out to be common in lowland secondary forests, kampong rubber plantations, and primary and disturbed primary forests, report Muul and Lim (1971). They collected rats whenever traps were placed in trees.

The arboreal habit of *Lenothrix canus* is reflected in its relatively very long tail compared with length of head and body (table 40) and its short but wide hind foot. Most of the plantar surface of each foot is taken up by large interdigital and metatarsal pads that are textured by high ridges and deep grooves. The pads at the ends of the digits are swollen, especially the hallux pad, which also bears a small claw. It is this type of foot and the arboreal adaptation it reflects that forms one of the six derivations listed in table 39.

Two of the five other derived features are cranial characters, the rest are in the molars. Prominent ridges define dorsolateral margins of the interorbital and postorbital regions and extend onto the anterior portion of the braincase (fig. 94). The back of each pterygoid plate is outlined by a ridge, a shape similar to that in species of *Rattus* (fig. 93). In the molars, *L. canus* has cusps t1bis and t2bis, there is a prominent accessory labial cusp behind cusp t6, and cusp t7 is present (fig. 95). These are three specializations found in molars that are otherwise primitive in most other characters (Misonne, 1969; Musser, 1981a).

The significance of these derivations in *Lenothrix canus* relative to the distributions of primitive and derived traits in genera of Indo-Australian murids that were once part of *Rattus* was discussed by Musser (1981a, p. 323). To him, "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." That disclaimer to close relationship also holds in our comparisons of *Lenothrix* with most of the other Sundanese genera.

Lenothrix does not share any derivations with native Sundanese *Mus* (subgenus *Coelomys*), which has 15 derived traits. Five other genera share only a single trait with *Lenothrix* (table 39). *Palawanomys* (13 derivations) shares the presence of cusps t1bis and t2bis with *Lenothrix.* These cusps occur in other genera of murids, are variable in size and may be either present or absent in any sample of a species. It is our experience that their distribution among murids is discordant with distributions of other derived features and their presence may or may not indicate close relationship. They are the kind of small occlusal structure that develops independently in various lineages. *Palwanomys* shares no other derivations with *Lenothrix* and in this context the presence of the cusps probably reflects independent development.

Berylmys, with 17 derived traits, also shares only one of them with *Lenothrix*: the posterior portion of each pterygoid platform is ridged. This feature is widely distributed among the Muridae of Asia, India, and Africa (but not New Guinea) and is usually associated with species that have other derived characters, especially in the pterygoid and mesopterygoid regions. Because the trait is so common, we do not know whether its presence in *Lenothrix* and *Berylmys* represent close alliance but we suspect it does not because *Berylmys* shares most of its derivations with genera other than *Lenothrix.*

Leopoldamys (with 11 derived traits), *Niviventer* (with 14 derivations), and *Maxomys* (with 13 traits) share only the presence of prominent supraorbital ridges with *Lenothrix.* This trait is also widespread among the the Muridae and is often associated with scansorial or arboreal habits. It is also present in some groups of terrestrial murids. Species that are otherwise dissimilar in details of cranial and dental morphology and distant from

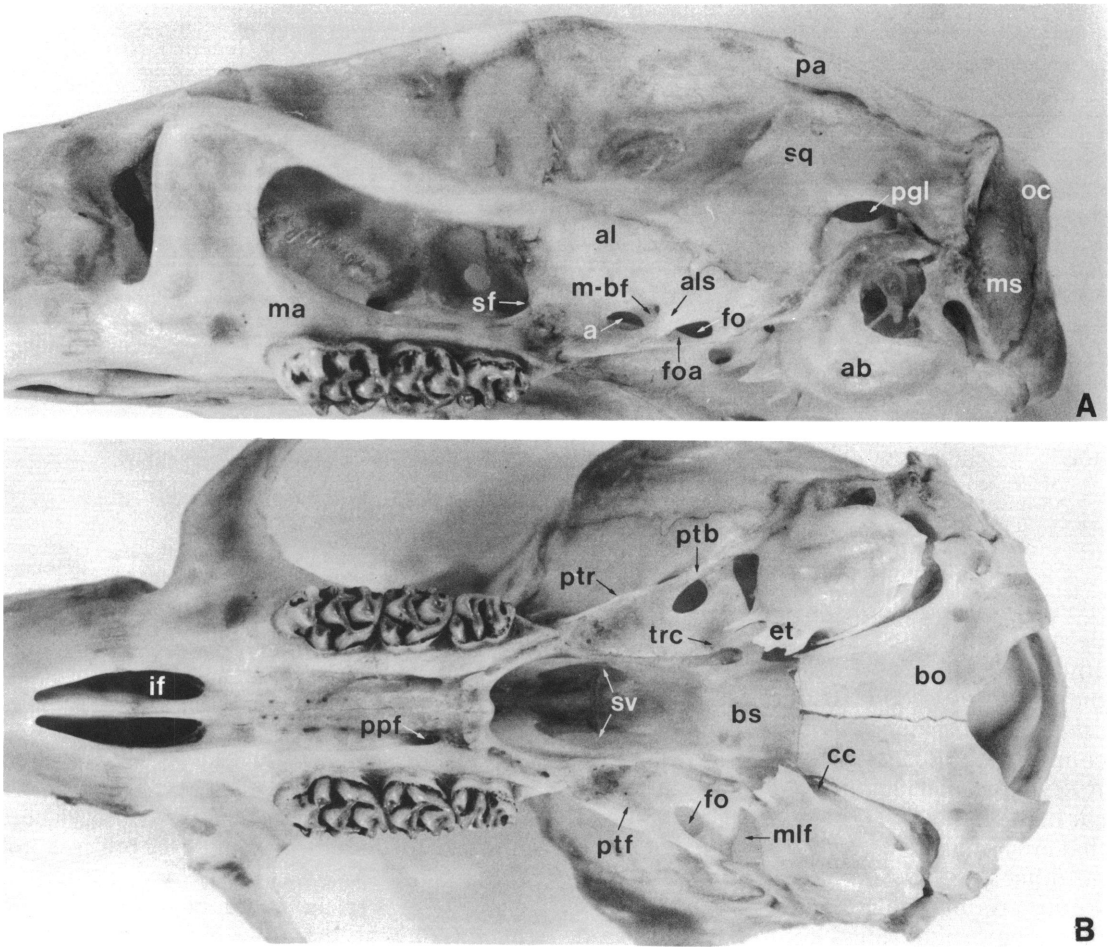

FIG. 93. Lateral (A) and ventral (B) cranial views of *Lenothrix canus* (AMNH 240358) from the Malay Peninsula. *Abbreviations:* **a**, anterior opening of the alisphenoid canal; **ab**, auditory bullae; **al**, alisphenoid bone; **als**, lateral strut of alisphenoid bone forming the outer wall of the alisphenoid canal; **bo**, basioccipital bone; **bs**, basisphenoid bone; **cc**, carotid canal; **et**, bony eustachian tube; **fo**, foramen ovale; **foa**, foramen ovale accessorius; **if**, incisive foramina; **ma**, maxillary bone; **ms**, mastoid portion of the petromastoid; **mlf**, middle lacerate foramen; **m-bf**, coalesced masticatory-buccinator foramina; **oc**, occiput; **pa**, parietal bone; **pgl**, postglenoid vacuity; **ppf**, posterior palatine foramen; **ps**, presphenoid bone; **pt**, periotic portion of the petrosal; **ptb**, pterygoid bridge; **ptr**, pterygoid ridge; **sf**, sphenoidal fissure; **sq**, squamosal bone; **sv**, sphenopalatine vacuity; **trc**, transverse canal.

each other in phylogenetic relationship may resemble one another in the development of the ridges outlining interorbital and postorbital regions. We do not think this shared feature indicates close relationship between *Lenothrix* and either *Leopoldamys, Niviventer* or *Maxomys. Lenothrix* is arboreal; *Niviventer* contains species that are both scansorial and highly arboreal (Musser, 1981a) and the Malaysian species of *Leopoldamys* have been trapped on the ground and in trees where they even nest (Lim, 1970). *Maxomys* contains terrestrial species. Narrow shelves define dorsolateral margins of the interorbital area and the top of the braincase is outlined by low ridges (fig. 99); the configuration is different than that in *Lenothrix.*

Lenothrix shares two derivations—supraorbital ridges and ridged pterygoid platforms—with *Sundamys* (which has 10 de-

TABLE 39
Distribution of Derived Traits in *Lenothrix* Among Sundanese Genera[a]

Genera	HF	SOR	PP	t1-t2bis	C-t6	t7
Pithecheir	+	+	+	+	–	+
Hapalomys	+	+	+	+	–	+
Chiropodomys	+	+	+	+	–	+
Kadarsanomys	+	+	+	–	–	–
Haeromys	–	–	+	+	–	–
Rattus	–	+	+	–	–	–
Sundamys	–	+	+	–	–	–
Niviventer	–	+	–	–	–	–
Leopoldamys	–	+	–	–	–	–
Berylmys	–	–	+	–	–	–
Palawanomys	–	–	–	+	–	–
Maxomys	–	+	–	–	–	–
Mus	–	–	–	–	–	–

[a] All information in this table and tables 41 to 58 is summarized from table 38. Abbreviations in all these tables refer to traits described on pages 533–537.

rived traits) and *Rattus* (with 20 derivations). Because both these features are so widespread among the Muridae, we do not know whether they point to close relationship among *Lenothrix, Rattus,* and *Sundamys.* Both traits are common to *Rattus* and those genera with *Rattus*-like specializations but they also occur in other genera (*Hapalomys,* for example) that are not closely related to *Rattus.* Because no other derived features of *Sundamys* and *Rattus* are shared with *Lenothrix,* we suspect that supraorbital ridges and ridged pterygoid platforms do not indicate close alliance among the three.

Haeromys has only four derived traits out of the 35 we studied. Of these, two are shared with *Lenothrix*; ridged pterygoid platforms and cusps t1bis and t2bis. For the reasons we already expressed, these features may or may not indicate close phylogenetic relationship. *Lenothrix* shares the ridged platforms with six other Sundanese genera and the small cusps with four others (table 39). Perhaps the two traits represent independent derivations in *Lenothrix* and *Haeromys.* But they may also suggest a degree of relationship in the sense that *Lenothrix* and *Haeromys* could be part of a cluster of murids which Misonne (1969, p. 96) brought together into a *Lenothrix-Parapodemus* Division. It contains many genera, most of them old in that they can be tied to species represented by Miocene and Pliocene fossils and that they are parts of old endemic faunas in Africa and the Indo-Australian region. For Misonne, all the genera "are relict forms in one way or another; they are all arboreal to some degree, or live in high mountains, or are isolated on remote islands, or are deep forest dwellers." It is in this large group that cusps t1bis and t2bis are common, as well as cusp t7. That cusp occurs in most specimens of *Lenothrix* but it is not present in *Haeromys,* at least as a discrete cusp. However, in specimens of *Haeromys* from Sulawesi, there is a high ridge between cusps t4 and t8 on each first and second upper molar (fig. 103). Nubbins that resemble cusp t7 are present on the ridges of some specimens and the entire configuration is closely similar to that found in some specimens of *Lenothrix* in which a ridge is present where cusp t7 usually occurs. This trait in *Haeromys* may support the supposition that it belongs in the *Lenothrix-Parapodemus* Division of Misonne. All the other ways that *Lenothrix* and *Haeromys* resemble each other are in primitive features. We cannot link *Lenothrix* any closer to *Haeromys* other than suggesting that both genera are part of a large group, which excludes *Rattus* and its allies.

Lenothrix and *Kadarsanomys* (with 14 derivations) share three derived traits: an arboreal hind foot, supraorbital ridges, and ridged pterygoid platforms. None of these features indicates close phylogenetic relationship. The single species of *Kadarsanomys* was

originally described as a subspecies of *Lenothrix canus* (at the time when *Lenothrix* was included in *Rattus*) but the two have little in common other than being arboreal Sundanese endemics (Musser, 1981c). The platform ridging is ambiguous in assessing alliance here. The supraorbital ridges reflect arboreal adaptation as do the hind feet. But the feet are different in important details. *Lenothrix* has a short and wide hind foot with a claw on the hallux. *Kadarsanomys* has a long and wide foot in which the hallux bears a small and convex nail. In this respect, the hind feet of *Kadarsanomys* are more specialized, as is most of the animal, and neither the more derived feet nor most of the other specializations (some of them reflecting arboreal habit in association with bamboo) are shared with *Lenothrix.*

Lenothrix shares five derived traits with *Hapalomys* (with 13 derivations), *Chiropodomys* (with nine traits), and *Pithecheir* (with 12). The only derivation in *Lenothrix* not shared by the other three genera is an accessory labial cusp behind cusp t6 on each first upper molar (table 39), although there may be a comparable structure in some specimens of *Pithecheir,* which we discuss later. All have an arboreal hind foot but that of *Lenothrix* is primitive compared with the more highly specialized hind feet in the other three genera. *Chiropodomys* lives in trees, palms, and clumps of bamboo. Its hind feet are adapted for climbing in these habitats and among the specializations are good nails on the halluces (Musser, 1979). The halluces of *Hapalomys* also bear nearly flat nails instead of claws and the feet are very specialized, part of a suite of derived traits reflecting high specialization for arboreal habits tied very closely to bamboo, both as a nesting place and food source (Medway, 1964). The hind feet in *Pithecheir* are wide and short and adapted for climbing among slender branches and in palm and fern fronds. They are more specialized than the hind feet in *Lenothrix* but their configuration is more like that of *Lenothrix* than any of the other arboreal murids on the Sunda Shelf. Each hallux in *Pithecheir* even bears a small claw or scalelike claw that in shape resembles the slightly larger claw on each hallux in *Lenothrix.*

All four genera have supraorbital ridges, which may only reflect the arboreal habit of the species in each genus. *Lenothrix* has definite ridges but in *Hapalomys* and *Pithecheir,* the supraorbital structures are wide shelves. Narrow shelves mark the supraorbital margins in *Chiropodomys.* Because supraorbital ridging is widespread throughout murids and the configuration in *Lenothrix* is different from that in *Hapalomys, Chiropodomys,* and *Pithecheir,* we cannot closely ally the four genera using this derivation.

Ridged pterygoid platforms are common to all four genera. The configuration in *Chiropodomys* resembles that in *Lenothrix* but in *Pithecheir* and *Hapalomys* the pterygoid fossa are deeply excavated and abut against greatly inflated auditory bullae (figs. 94 and 102) and the ridges are high partly because of the excavated fossae, a more specialized condition than that in *Lenothrix.* And judged by the wide distribution of ridged pterygoid platforms among murid genera, that feature could be something independently derived in *Lenothrix* and *Chiropodomys.* This feature is ambiguous about indicating close relationship.

All four genera have either cusp t1bis, cusp t2bis, or both on most specimens in each sample. The trait in *Hapalomys* is more specialized than in the other genera. Cusps t1bis and t2bis are large and part of the anterior margin on each first upper molar in *Hapalomys* (fig. 117). In the other genera, the cusps are usually present in most specimens, range in size from nubbins to cusps, and in *Lenothrix* and *Pithecheir* they resemble ridges rather than discrete round cusps, as is their shape in *Hapalomys* and usually in *Chiropodomys.* The presence of these cusps may be significant only in combination with the presence of cusp t7.

All four genera share the presence of cusp t7 but its morphology is different in each. Cusp t7 is part of a complex occlusal pattern and provides more surface to the chewing area and mechanical support to strengthen the molar row (Misonne, 1969, p. 60). In specimens of *Lenothrix,* cusp t7 may be present or absent; when present it ranges in size from a nubbin to a large cusp, and sometimes in its place is a cingular ridge connecting cusps t4 and t8 (fig. 95). In *Hapalomys,* cusp t7 is large and always present on each first and

TABLE 40
Measurements and Ratio from Samples of Adult *Lenothrix* and *Pithecheir*[a]

Measurement and Ratio	*Lenothrix canus*	*Pithecheir melanurus*	*Pithecheir parvus*
Length of head and body	200.2 ± 13.6 161–215 (19)	165.8 ± 6.3 159–176 (6)	165.8 ± 6.5 156–175 (11)
Length of tail	241.2 ± 20.7 190–270 (17)	207.8 ± 4.5 202–213 (6)	186.7 ± 7.0 179–205 (11)
Length of hind foot	35.2 ± 1.4 33–37 (19)	31.2 ± .8 30–32 (6)	27.6 ± 1.2 26–30 (11)
Length of ear	20.6 ± 1.1 19–22 (19)	18.6 ± .7 18–20 (6)	16.6 ± 1.4 15–19 (11)
Greatest length of skull	45.9 ± 1.1 43.8–48.4 (19)	44.6 ± .9 43.2–45.7 (9)	42.3 ± 1.5 39.0–44.0 (11)
Length of bullae	6.0 ± .3 5.5–6.4 (18)	9.1 ± .3 8.4–9.5 (9)	10.6 ± .5 9.6–11.5 (11)
Alveolar length of M^{1-3}	8.8 ± .3 8.4–9.3 (19)	8.8 ± .3 8.3–9.4 (9)	7.9 ± .2 7.5–8.2 (11)
Length bullae/skull length	13	20	25

[a] Measurements are in millimeters; ratio in percentage. Mean plus or minus one standard deviation, observed range, and size of sample in parentheses are listed for each measurement.

second upper molar (fig. 117). It is a prominent member of the back row of cusps of each tooth in all specimens we studied. In examples of *Chiropodomys,* cusp t7 also occurs on each first and second upper molar and is discrete and large, nearly the same size as the other lingual cusps (fig. 104). In *Pithecheir,* cusp t7 on each first and second molar is discrete and larger than the counterpart in *Lenothrix,* but the shape and relative position of each cusp compared to the positions of cusps t8 and t4 resemble the configuration in those examples of *Lenothrix* that have a large cusp t7 (fig. 95).

By themselves, none of the shared derivations indicate close phylogenetic relationship among the four genera. However, the presence of cusps t1bis, and t2bis, as well as cusp t7 may indicate that *Lenothrix, Pithecheir, Hapalomys,* and *Chiropodomys* belong together in a group, a cluster which excludes *Rattus* and its relatives. That group would correspond to Misonne's (1969) *Lenothrix-Parapodemus* Division. Aside from this very rough association, the derived features shared by *Lenothrix, Hapalomys,* and *Chiropodomys* cannot be used to ally the three any closer.

Pithecheir is different. We cannot tie *Lenothrix* closely to *Pithecheir* but it may be more closely related to *Lenothrix* than are either *Hapalomys, Chiropodomys,* or any other Sundanese genus. Misonne (1969, pp. 73–74) believed that the closest relatives of *Lenothrix* are "*Lenomys,* and *Pithecheir* with *Crateromys* as a probable further step," a conclusion based on his study of molar characters. He also noted that "*Lenothrix, Pithecheir,* and *Crateromys* are almost on the same evolutionary line. *Pithecheir* is what may be expected as an offshoot of *Lenothrix,* at least in the dentition."

We understand why Misonne allied *Lenothrix* with *Pithecheir.* Although the species of *Pithecheir* are highly specialized for arboreal living compared with *Lenothrix can-*

us, Pithecheir has the same basic cranial conformation and parts of its molar occlusal patterns resemble those in *Lenothrix,* as Misonne (1969) pointed out. A few specimens of *Pithecheir* even have a ridge connecting cusps t6 and t9 on each first upper molar. If this is comparable to the accessory labial cusp behind cusp t6 found in *Lenothrix,* in which it also forms a ridge in some specimens, then that derivation adds credence to Misonne's close phylogenetic alliance between *Lenothrix* and *Pithecheir.* But if both genera evolved from the same ancestral group, *Lenothrix* has retained many primitive characteristics of that ancestor while *Pithecheir* reflects the development of morphological adaptations associated with highly arboreal habits.

We agree with Misonne's (1969, p. 73) statement that "*Lenothrix* is a very interesting genus and one of the most primitive in many respects." We detect a few cranial and dental derivations, as well as those in the hind feet, that are associated with arboreal life. But in most of its features *Lenothrix* is primitive. The cranium is one of the most generalized and primitive of the Sundanese murids. Even the molars have many primitive characteristics (Misonne, 1969), although Jacobs (1978) does not think they represent a model for the primitive murid dentition.

The presence and size of cusp t7, although a derivation, is consistent with the primitive nature of the teeth. In *Lenothrix,* cusp t7 occurs on some specimens, is absent from others, ranges in size from a regular cusp to a cingular nubbin, and is sometimes represented by a ridge. This kind of variation occurring in an otherwise primitive dental pattern may indicate the cusp was not yet genetically fixed in the species.

For persons seeking living ancestral morphotypes, look to *Lenothrix canus*—it is a good one. Even its arboreal adaptations are interesting in that context. In discussing arboreal specializations in Central and South American cricetines, Hershkovitz (1960, p. 526) speculated that the generalized condition in cricetines is a tail about equal in length to that of the head and body, and a moderately long and wide hind foot. A relatively longer tail compared with length of head and body and a relatively wider foot compared with its length, with the foot becoming "more flexible, the first and fifth digits more powerful and opposable, and the plantar tubercles modified for grasping" are specializations associated with arboreal habitats. Compared with Hershkovitz's view of the generalized configuration, the external features of *Lenothrix* are derived. But if ancestral murids were forest animals and either arboreal or scansorial, as has been hypothesized for New World cricetids by Carleton (1980), then the conformation of the head and body, tail, and hind feet in *Lenothrix* would be primitive. It is from such a configuration in *Lenothrix* that more specialized traits, such as those in *Pithecheir,* could be developed. The tail of *Lenothrix,* for example, is long but not prehensile. The hind feet are broad and the plantar pads large but a definite claw is on the hallux and not some kind of modification that resembles a nail.

Lenothrix deserves more study. Its characters should be compared with those of genera occurring outside the Sunda region, especially those native to the Philippine Islands and Sulawesi. There is evidence suggesting that *Lenothrix* is related to Sulawesian *Lenomys, Eropeplus,* and *Margaretamys* (Musser, 1981a, 1981b) and Misonne (1969) has linked *Lenothrix* with the Philippine *Crateromys.* On the Sunda Shelf, *Lenothrix* may be phylogenetically closer to *Pithecheir* than to any of the other Sundanese genera. *Lenothrix,* and even *Pithecheir,* have the aspects of old endemics, relicts left over from an earlier time in the history of the Sunda region and the early evolution of rats there.

PITHECHEIR

Samples of *Pithecheir* come from the Malay Peninsula and Java. Chasen (1940) records it from Sumatra also but Musser (1982d) explains why that record is likely erroneous. Chasen also listed the Malay rat as a subspecies of the Javan animal. Muul and Lim (1971, p. 436), however, point out that although Kloss (1916) "named and described the only known Malaysian specimen as a subspecies of the Javan species, *P. melanurus,* . . . the Malaysian animals differ from those on Java by their proportionately smaller teeth, shorter toothrows, broader palate, and larger bullae." Animals in the Malayan sample do

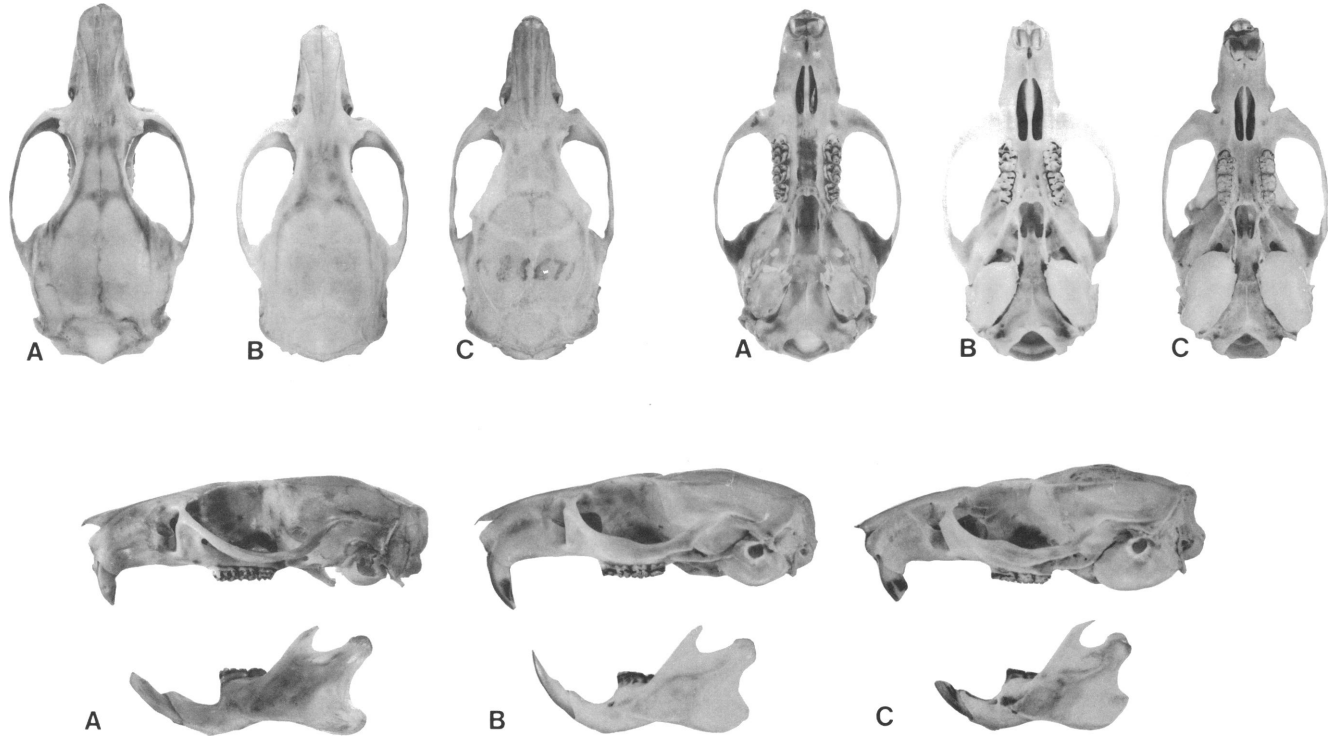

FIG. 94. Views of crania and dentaries from adult *Lenothrix* (A) and *Pithecheir* (B and C). A, *L. canus,* Malay Peninsula (AMNH 240358). B, *P. melanurus,* Java (RMNH 14177). C, *P. parvus,* Malay Peninsula (USNM 488803). Natural size.

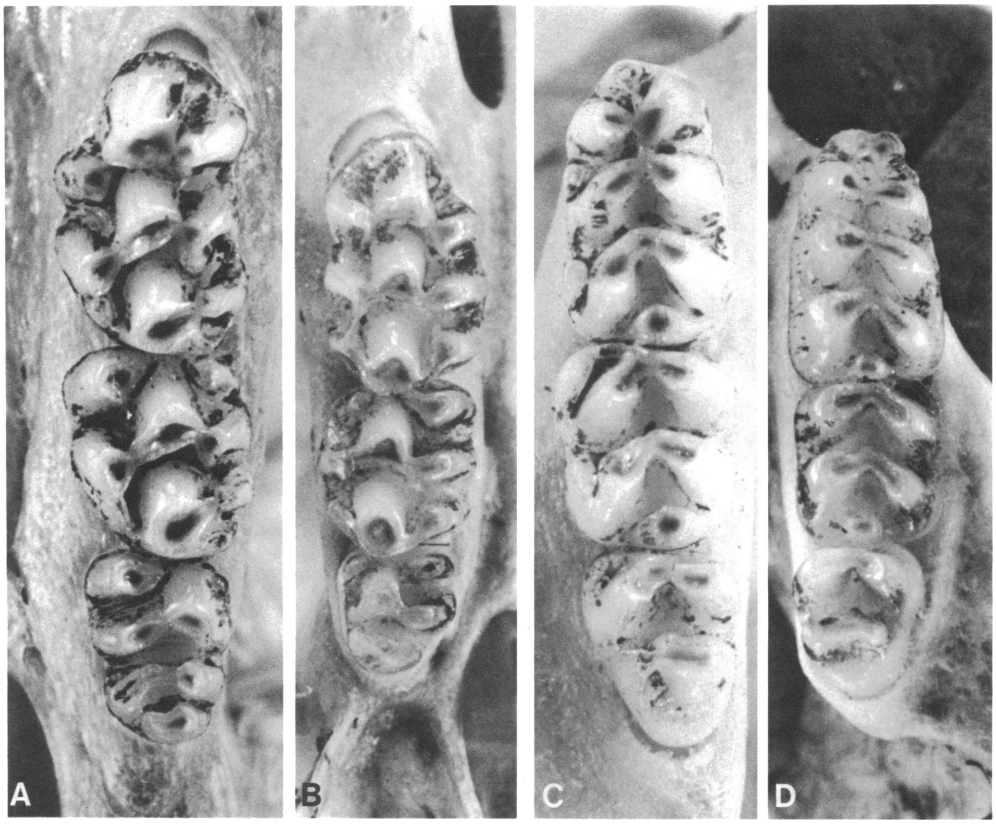

FIG. 95. Occlusal views of upper (A and B) and lower (C and D) molar rows in *Lenothrix* and *Pithecheir*. A and C, *L. canus*, Malay Peninsula (USNM 488914). B and D, *P. parvus*, Malay Peninsula (USNM 488811). All ×10.

have shorter molar rows and larger bullae, both absolutely and relatively compared with size of cranium (table 40), proportions that are illustrated in figure 94. The differences are conspicuous and distinguish each specimen of the Malayan *Pithecheir* from each example of the Javan rat in samples we examined. We agree with Muul and Lim that the Malayan population, *P. parvus*, is a different species than the Javan *P. melanurus*.

Both species of *Pithecheir* are among the most arboreal of the Sundanese murids. The rats have prehensile tails and short but wide hind feet with very large interdigital and metatarsal pads. The feet are adapted for grasping twigs and slim branches, as well as palm and fern fronds. The animals live in the forest understory, climbing about in the short trees, coils of woody vines, and tops of palms and tree ferns; they also build large globular nests (Bartels, 1937b; Lim and Muul, 1975).

Pithecheir has 12 derived traits and these, in different combinations, are shared with all 13 other Sundanese genera (table 41). But the sharing pattern provides little information about phylogenetic relationships between *Pithecheir* and the others. Supraorbital ridges or shelves, absence of an alisphenoid strut, excavated pterygoid fossae, ridges at the posterolateral margins of the pterygoid platforms, and overlap among the molars in each row are derivations occurring in many species of murids throughout the natural range of the family. In this comparison, they contain ambiguous information about phylogenetic alliances. Furthermore, a lateral strut of alisphenoid bone forming the outer wall of the alisphenoid canal is present in some speci-

TABLE 41
Distribution of Derived Traits in *Pithecheir* among Sundanese Genera

Genus	T	Ha	HF	SOR	Al	Sq-mF	SB	PF	PP	OM	t1-t2bis	t7
Hapalomys	–	–	+	+	+	–	+	+	+	–	+	+
Kadarsanomys	–	–	+	+	+	–	+	+	+	+	–	–
Lenothrix	–	–	+	+	–	–	–	–	+	–	+	+
Chiropodomys	–	–	+	+	+	–	–	–	–	–	+	+
Rattus	–	–	–	+	+	–	–	+	+	+	–	–
Sundamys	–	–	–	+	–	–	–	+	+	+	–	–
Palawanomys	–	–	–	–	+	–	–	–	–	+	+	–
Mus	–	–	–	–	–	+	–	–	–	+	–	–
Berylmys	–	–	–	–	+	–	–	–	+	+	–	–
Maxomys	–	–	–	+	+	–	–	–	–	+	–	–
Haeromys	–	–	–	–	–	–	–	–	+	–	+	–
Niviventer	–	–	–	+	–	–	–	–	–	+	–	–
Leopoldamys	–	–	–	+	–	–	–	–	–	+	–	–

mens of *Pithecheir* and in this case is not a reliable character upon which to gauge relationships. For our survey, we examined 19 specimens of *Pithecheir parvus*. Nine had an alisphenoid strut on each side of the cranium ranging in size from a threadlike structure to a wide strut. Nine others lacked the strut. In one specimen, the strut was present on the right side but absent on the left.

Pithecheir and *Mus* share a squamosomastoid foramen that separates the squamosal bone into two parts. In *Mus,* the foramen is a large vacuity and the tympanic hook below it is a slender piece of bone. In *Pithecheir,* the foramen is small, not a vacuity. This feature is found in genera native to New Guinea, the Indian region, and Africa. Because the configuration of the squamosal region above the bullae are similar among some genera the character may indicate close relationship. But it differs in size and shape among other genera and has the aspect of having been developed independently, which it probably was in *Pithecheir* and *Mus*. No other derived features are shared by these two.

Some of the morphological specializations for arboreal habits seen in species of *Pithecheir* also characterize other arboreal species on the Sunda Shelf and it is with these that *Pithecheir* shares most of its derived traits (table 41). Seven are shared with *Kadarsanomys*. But of these, four (no alisphenoid strut, deep pterygoid fossae, ridged pterygoid platforms, and overlapping molars) are ambiguous in their information about relationships. Three other derived features, an arboreal hind foot, supraorbital ridging, and inflated bullae reflect only that both *Kadarsanomys* and *Pithecheir* are arboreal. There are ridges outlining the supraorbital margins in *Kadarsanomys,* not wide shelves as in *Pithecheir*. The hind feet of *Kadarsanomys* are long and wide and each hallux bears a small, convex nail; the hind feet in *Pithecheir* are short and broad and the halluces have very small claws or scalelike claws. *Kadarsanomys* has 14 derived traits and 13 of these are shared with *Rattus*. Both genera have large bullae but those in *Pithecheir* are far more inflated (compare figs. 94 and 96). The only similarities between *Kadarsanomys* and *Pithecheir* are arboreal adaptations, which appear to have been independently derived in each genus.

In the account of *Lenothrix* we discussed most of the features shared by *Pithecheir, Lenothrix, Hapalomys,* and *Chiropodomys*. There is no indication among the shared derivations that *Pithecheir* is any more closely related to *Hapalomys* and *Chiropodomys* than being in the same large group which Misonne (1969) called the *Lenothrix–Parapodemus* Division. *Pithecheir* and *Hapalomys* do share large and highly inflated auditory bullae, and they are the only Sundanese genera with this derivation. The configuration of the pterygoid region is also similar in the two species.

That feature accompanies large inflated bullae. The bullae of *Pithecheir* are relatively much larger compared with size of cranium than they are in *Hapalomys*. The rats in each genus seem highly specialized for different arboreal habitats: bamboo for *Hapalomys*, forest understory and crowns of short palms and tree ferns for *Pithecheir*. We would go along with Misonne and place both genera in the same large diverse group both morphologically and ecologically, but we cannot tie them any closer than that. A distant relative of *Lenothrix*, as we explained in the previous account, is still our best estimate of the phylogenetic alliance of *Pithecheir*.

KADARSANOMYS

Specimens of *Kadarsanomys sodyi* were obtained by Max Bartels, Jr. during the period, 1933 to 1935, from localities on the southwest slopes of Gunung Pangrango-Gede, a high volcanic mountain in western Java (Musser, 1981c). No examples have been collected since 1935. The distribution of *K. sodyi* on Java was once more extensive because it is represented by subfossil fragments collected from Sampung Cave in central Java and Goea Djimba Cave in eastern Java (Musser and Califia, MS.). All examples of the species, whether skins and skulls or subfossils, come from Java and we presume the rat to be endemic there.

A rat of medium body size, with a very long tail (table 43), soft fur, brown upperparts, white underparts, four pairs of mammae, an arboreal hind foot, and a nail instead of a claw on each hallux, *K. sodyi* lives in forest and apparently is closely associated with bamboo, certainly as a nesting site and possibly as a food source (Musser, 1981c). Because this animal was originally described as a subspecies of *Rattus canus*, its distinctive morphology and ecology were unknown for many years. We now realize that *canus* belongs in the genus *Lenothrix*, which is phylogenetically far from *Rattus*, and that *sodyi* is not a species of *Rattus* and has no close phylogenetic link with *Lenothrix*.

Of its 14 derived traits, *Kadarsanomys* shares only three with *Lenothrix* (table 42). Two, an arboreal hind foot and supraorbital ridges, reflect only the arboreal habits of *K. sodyi* and *L. canus*, and the third, ridged pterygoid platforms, is ambiguous in its information about relationships, as we explained in the account of *Lenothrix*. Other than being murids, *Kadarsanomys* and *Lenothrix* have in common only their arboreal adaptations (which in *Kadarsanomys* are specializations for living in bamboo, and in *Lenothrix* for living in the forest aboveground but not in bamboo) and their endemism on the Sunda Shelf.

Kadarsanomys also shares five to eight derived traits with *Pithecheir*, *Chiropodomys*, and *Hapalomys* all containing arboreal species. But some of the derived states are widespread among murids and in the comparisons have no information about relationships, and the other derived traits reflect morphological adaptations for arboreal habit. We have no evidence that *Kadarsanomys* is phylogenetically close to any of these three genera of arboreal rats.

Eleven of 14 derived traits of *Kadarsanomys* are shared with *Rattus*. In both genera, supraorbital ridges are present, an alisphenoid strut is absent, the bullae are not tightly attached to the squamosal bones, the incisive foramina are long and their posterior margins extend beyond front faces of the first upper molars, a large sphenopterygoid vacuity is present in each pterygoid plate, the pterygoid fossae are deep, there is a prominent ridge outlining the back margin of each pterygoid platform, five roots are beneath each first upper molar, four roots anchor each first lower molar, there is conspicuous overlap among the molars in each row, and cusp t1 is nearly in a line with cusps t2 and t3 on each first upper molar (figs. 96–98).

Although *Kadarsanomys* shares most of its derived traits with *Rattus*, it is at the same time both more derived and more primitive overall. *Kadarsanomys* is more specialized than any species of *Rattus* because of its morphological adaptations for arboreal life and its apparent close association with bamboo. The relatively long tail compared with length of head and body; the structure of the hind feet, digits, and claws; long vibrissae; sturdy and stocky skull; short and wide rostrum; prominent supraorbital ridges; narrow zygomatic plates; very large bullae (relatively larger than in *Rattus*); wide incisors; and large,

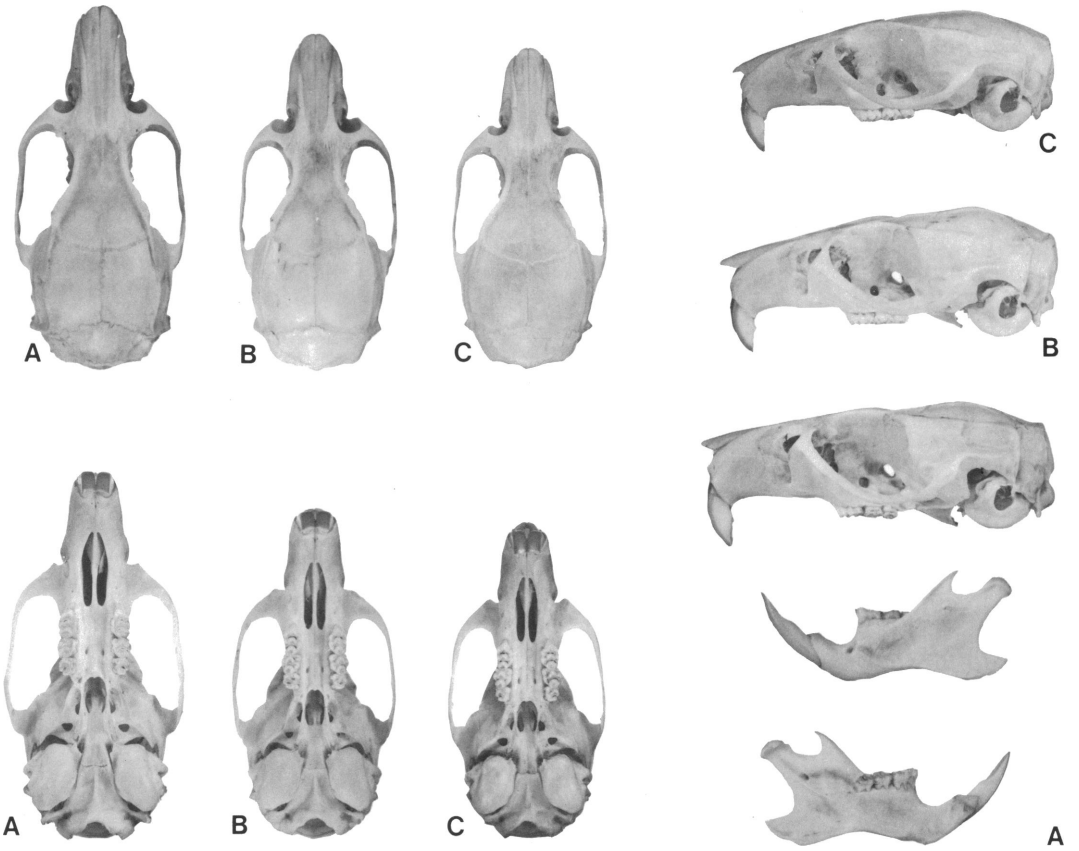

FIG. 96. Views of crania and dentaries from Javan *Kadarsanomys sodyi*. A, old adult (RMNH 14219). B, adult (RMNH 14178). C, young adult (RMNH 14103). Natural size.

gleaming cuspidate molars are all features that Musser (1981c) speculated may be adaptations for arboreal habit in general and living in bamboo in particular.

Kadarsanomys is more primitive than *Rattus* in that it has a short palatal bridge, small sphenopalatine vacuities in the mesopterygoid fossa, relatively large third molars compared with sizes of the other teeth in each row, discrete cusps that are slightly joined in each row, a posterior cingulum at the back of each first and second upper molar, prominent and large cusps t3 on each second and third upper molars, and an anterocentral cusp at the front of each first lower molar (fig. 98). Other distinctions between *Kadarsanomys* and *Rattus* are described by Musser (1981c).

"Set within the context of the present fauna in the Far East, *K. sodyi* must be a relict. It appears to have no close relative and to be one specialized segment of an adaptive radiation that may have had its origin very early in the development of Indochinese and Sundaic murids," was Musser's (1981c, p. 32) comment about the phylogenetic alliance of *Kadarsanomys*. Perhaps the origin of *Kadarsanomys* is not as old as those of *Lenothrix* and *Pithecheir,* but we still see it as a relict without close phylogenetic allies. *Kadarsanomys* is a mixture of primitive and derived traits and most of its derivations are also shared by *Rattus*. It appears to be one of the *Rattus*-like genera, some of which also occur on Sulawesi and the Philippines. *Bunomys, Paruromys,* and *Taeromys,* are examples of the Sulawesian endemics (Musser, 1981b); *Abditomys, Tryphomys, Limnomys,* and *Tarsomys* are Philippine genera with

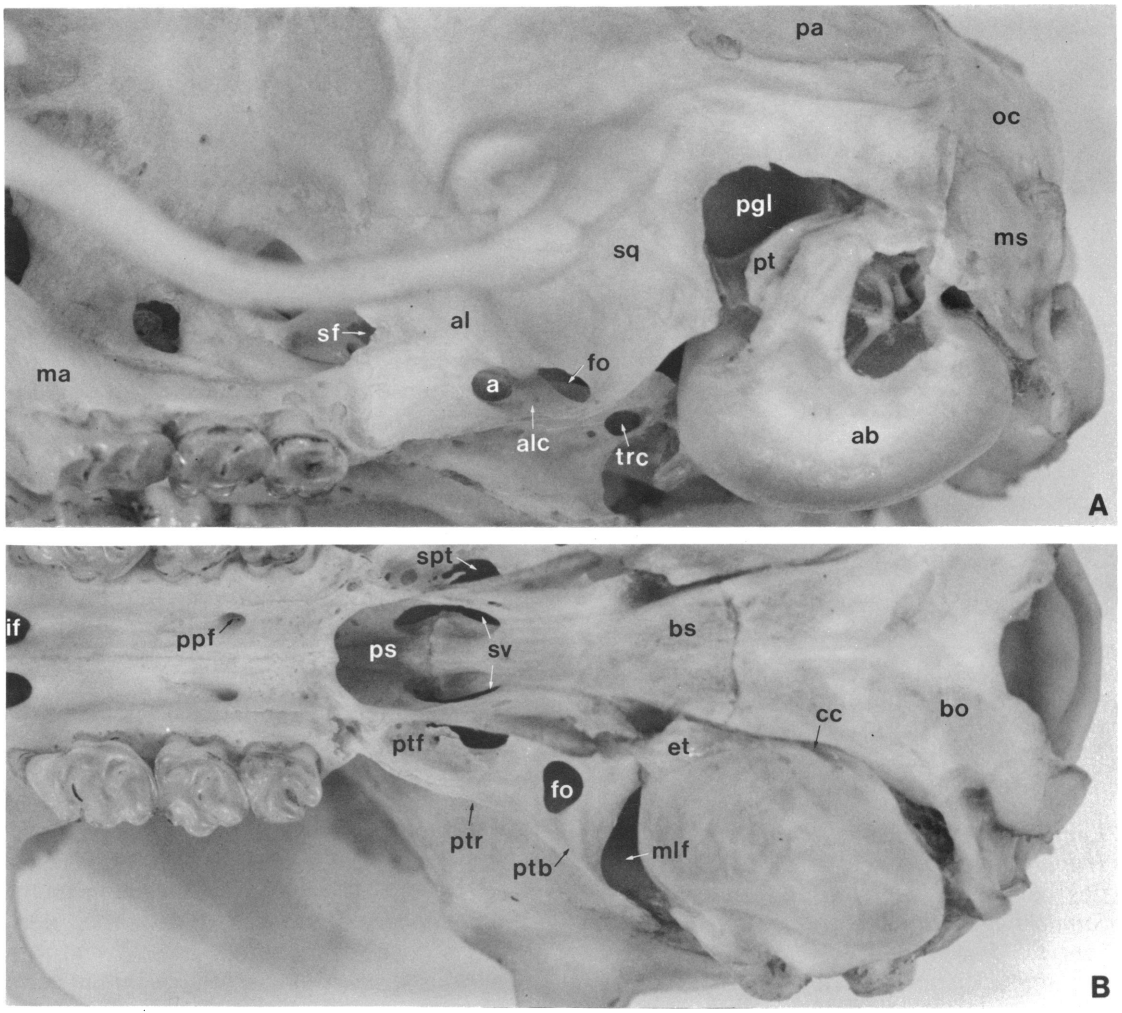

FIG. 97. Lateral (A) and ventral (B) cranial views of *Kadarsanomys sodyi* (RMNH 14219) from eastern Java. *Abbreviations:* **a**, anterior opening of the alisphenoid canal, where it empties into the sphenoidal fissure; **ab**, auditory bulla; **al**, alisphenoid bone; **alc**, alisphenoid canal, which is an open channel; **bo**, basioccipital bone; **bs**, basisphenoid bone; **cc**, carotid canal; **et**, bony eustachian tube; **fo**, foramen ovale; **if**, incisive foramina; **ma**, maxillary bone; **ms**, mastoid portion of the petromastoid; **mlf**, middle lacerate foramen; **oc**, occiput; **pa**, parietal bone; **pgl**, postglenoid vacuity; **ppf**, posterior palatine foramen; **ps**, presphenoid bone; **pt**, periotic portion of the petrosal; **ptb**, pterygoid bridge; **ptf**, pterygoid fossa; **ptr**, pterygoid ridge; **sf**, sphenoidal fissure; **spt**, sphenopterygoid vacuity; **sq**, squamosal bone; **sv**, sphenopalatine vacuity; **trc**, transverse canal.

Rattus-like derivations (Musser, 1981b, 1982b). If *Kadarsanomys* occurred in either Africa or India, Misonne (1969) would have placed it in his *Arvicanthis* Division. Many of the genera in this cluster are characterized by derived traits that are also shared with *Rattus*. Some species of *Arvicanthis* share many of their derived cranial and dental traits with *Rattus* and in this context are more closely related to *Rattus* than are any of the groups, such as *Lenothrix, Leopoldamys, Niviventer,* and *Maxomys,* which once were considered to be part of *Rattus* (Musser, 1981a).

Among Sundaic murids, *Kadarsanomys* does not fit with the other arboreal genera

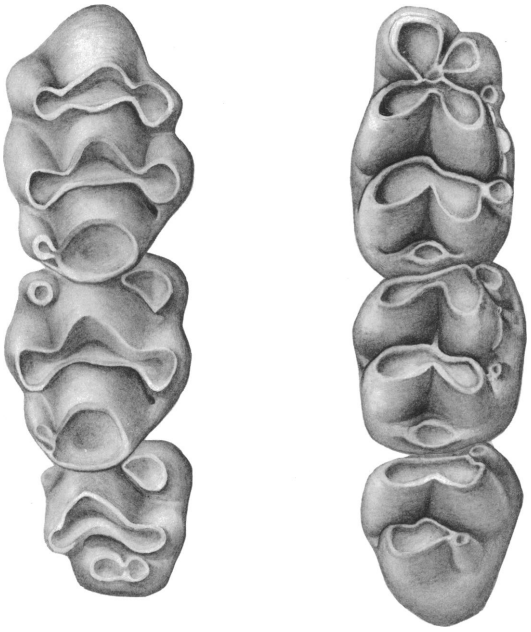

FIG. 98. Occlusal views of right upper (left) and lower (right) molar rows in *Kadarsanomys sodyi* (RMNH 14103; CLM^{1-3}, 7.4 mm.; CLM_{1-3}, 7.5 mm.).

Lenothrix, Pithecheir, Chiropodomys, and *Hapalomys.* We detect no close phylogenetic ties between *Kadarsanomys* and *Berylmys, Sundamys, Palawanomys, Niviventer, Haeromys, Maxomys, Leopoldamys,* and *Mus.* We see a distant relationship with *Rattus.* Finer resolution than this will require comparisons between *Kadarsanomys* and genera on Sulawesi, the Philippines, India, and Africa.

PALAWANOMYS

To date *Palawanomys* is the only murid genus known to be endemic to Palawan Island. Its morphological features combine both primitive and derived traits; it is not as primitive as *Lenothrix* and not as derived as *Rattus. Palawanomys* shares several derived traits with most of the other Sundanese genera but out of its 13 derived features, *Palawanomys* shares 11 with *Rattus* and two of these traits are found only in *Rattus* and *Palawanomys,* at least among the Sundanese species (table 44). We interpret this distribution of derivations to indicate that *Palawanomys,* like *Kadarsanomys,* is not phylogenetically close to *Lenothrix* and others that Misonne placed in the *Lenothrix-Parapodemus* Division but is distantly connected to *Rattus* and possibly other genera with *Rattus*-like cranial and dental derivations.

Palawanomys has cusps t1bis and t2bis, which *Rattus* does not, and *Palawanomys* is unique among Sundaic murids in having prominent crests on the anterior faces of several cusps on the first and second upper molars (see our description of the teeth in the *Palawanomys* account). All its other derivations also characterize *Rattus*: no alisphenoid struts, relatively large bullae compared with cranial size, loose attachment of

TABLE 42
Distribution of Derived Traits in *Kadarsanomys* among Sundanese Genera

Genera	Ha	HF	SOR	Al	SB	AB	IF	PF	SptgV	PP	R-M^1	R-M_1	OM	t1-M^1
Rattus	–	–	+	+	–	+	+	+	+	+	+	+	+	+
Berylmys	–	–	–	+	–	+	–	–	–	+	+	+	+	–
Sundamys	–	–	+	–	–	–	–	+	–	+	+	+	+	+
Palawanomys	–	–	–	+	–	+	–	–	+	–	–	+	+	+
Hapalomys	–	+	+	+	+	–	–	+	+	+	–	–	–	+
Chiropodomys	–	+	+	+	–	+	–	–	+	+	–	–	–	–
Pithecheir	–	+	+	+	+	–	–	–	–	+	–	–	+	–
Niviventer	–	–	+	–	–	–	+	–	–	–	+	+	+	–
Haeromys	–	–	+	–	–	+	–	–	+	+	–	–	–	–
Lenothrix	–	+	+	–	–	–	–	–	–	+	–	–	–	–
Maxomys	–	–	+	+	–	–	–	–	–	–	–	–	+	–
Leopoldamys	–	–	+	–	–	–	–	–	–	–	–	+	+	–
Mus	–	–	–	–	–	+	–	–	–	–	–	–	+	–

TABLE 43
Measurements and Ratio from Samples of Adult *Kadarsanomys, Palawanomys,* and *Sundamys*[a]

Measurement and Ratio	*Kadarsanomys sodyi*	*Palawanomys furvus*	*Sundamys muelleri* (Sumatra)
Length of head and body	187.6 ± 13.0 162–210 (11)	145.0 ± 17.8 125–160 (4)	207.3 ± 17.1 185–236 (23)
Length of tail	275.2 ± 16.3 246–305 (11)	135.3 ± 8.8 126–145 (4)	260.6 ± 24.6 214–301 (22)
Length of hind foot	39.5 ±2.0 37–44 (11)	33.0 ± 1.2 32–34 (4)	45.3 ± 2.2 42–49 (23)
Greatest length of skull	43.6 ± 1.8 40.4–46.5 (10)	37.6 ± 1.5 36.0–39.5 (4)	51.1 ± 3.3 45.7–58.8 (4)
Length of bullae	8.1 ± .3 7.6–8.5 (11)	5.9 ± .1 5.8–6.1 (4)	6.6 ± .2 6.1–7.3 (23)
Alveolar length of M^{1-3}	8.3 ± .3 7.8–8.9 (11)	6.9 ± .1 6.7–7.0 (4)	9.7 ± .5 8.6–10.7 (23)
Length of bullae/skull length	19	16	13

[a] Measurements are in millimeters, ratio in percentages. Mean plus or minus one standard deviation, observed range, and size of sample in parentheses are listed for each measurement.

bullae to squamosal bones, long palatal bridge extending posterior to the molar rows to form a wide shelf, spacious sphenopalatine vacuities, large sphenopterygoid openings in the pterygoid fossae, four roots anchoring each first lower molar, relatively small third upper molars compared with the other teeth in the rows, overlapping molars, cusp t1 not directed far posteriorly compared with cusps t2 and t3 in each anterior lamina on the first upper molars, and most of the cusps broadly joined. Among Sundanese murids, only *Palawanomys* and *Rattus* share the wide palatal shelf posterior to the molar rows and the spacious sphenopalatine vacuities.

Most of the species of *Rattus,* at least those in subgenus *Rattus,* are more highly derived and compared with them *Palawanomys* is a more primitive rat. Compared with *Rattus,* the primitive traits retained by *Palawanomys* are low and inconspicuous supraorbital beading, short incisive foramina, nearly flat pterygoid fossae, the pterygoid bridge between foramen ovale and bulla is moundlike and not outlined by a high ridge, one large lingual root instead of two beneath each first upper molar, cusp t4 either separate from cusp t5 or only narrowly united, posterior cingulum at the back of each first upper molar, a large and prominent cusp t3 on each second and third upper molar, and a conspicuous anterocentral cusp at the front of each first lower molar. The separate cusps t4 and t5 on the first upper molars, especially when the other cusps in each row are broadly joined, is a unique feature among Sundanese species.

Palawanomys shares six of its derived traits with *Kadarsanomys* and eight with *Berylmys.* Most of these traits are also shared by *Palawanomys* and *Rattus. Palawanomys* does not share a single or several traits with only *Kadarsanomys* or with only *Berylmys* and we have no evidence that would link *Palawanomys* phylogenetically close to either of those genera. Nor can we tie *Palawanomys* directly to *Rattus.* We can only estimate, based on such features as the wide palatal shelf behind the molar rows and the spacious sphenopal-

TABLE 44
Distributions of Derived Traits in *Palawanomys* among Sundanese Genera

Genera	Al	SB	AB	PB	MF	SptgV	R-M_1	SM	OM	t1-t2bis	t1-M^1	UC	MAC
Rattus	+	+	+	+	+	+	+	+	+	–	+	+	–
Kadarsanomys	+	–	+	–	–	+	+	–	+	–	+	–	–
Berylmys	+	+	+	–	–	–	+	+	+	–	+	+	–
Mus	+	+	+	–	–	–	–	+	+	–	–	+	–
Sundamys	–	–	–	–	–	–	+	–	+	–	+	+	–
Niviventer	–	–	–	–	–	–	+	+	+	–	–	+	–
Maxomys	+	–	–	–	–	–	–	+	+	–	–	+	–
Chiropodomys	+	–	+	–	–	+	–	–	–	+	–	–	–
Hapalomys	+	–	–	–	–	+	–	–	–	+	+	–	–
Leopoldamys	–	–	–	–	–	–	+	–	+	–	–	+	–
Haeromys	–	–	+	–	–	+	–	–	–	+	–	–	–
Pithecheir	+	–	–	–	–	–	–	–	+	+	–	–	–
Lenothrix	–	–	–	–	–	–	–	–	–	+	–	–	–

atine vacuities, that *Palawanomys* may be phylogenetically closer to *Rattus* than it is to any of the other genera on the Sunda Shelf.

Some genera found outside of the Sunda Shelf are characterized by a few of the same derived traits found in *Rattus*. The Luzon endemics, *Abditomys* and *Tryphomys*, for example, have spacious sphenopalatine vacuities (see Musser, 1982a and our discussion of *Tryphomys* on pages 497–500). The Philippine *Tarsomys* has a long and wide shelf behind the molar rows and very large sphenopalatine vacuities. Even *Apodemus* has spacious sphenopalatine openings (Musser, 1981a). To really determine where *Palawanomys* fits within the framework of phylogenetic relationships among Indo-Australian murids, the genus must be compared with those occurring outside of the Sunda region.

SUNDAMYS

Of the five genera found only on the Sunda Shelf, four have spotty distributions: *Lenothrix* in the Malay Peninsula, Sarawak, and an island off the coast of Sumatra; *Pithecheir* on the Malay Peninsula and Java; *Kadarsanomys* only on Java; and *Palawanomys* from the southern part of Palawan Island. *Sundamys* is different. As a genus it is represented by populations on the peninsula and most of the large and small islands on the Sunda Shelf. The species are more restricted. *Sundamys muelleri* occurs on the peninsula, the large islands of Borneo and Sumatra, and many small islands of the Shelf, including those in the Palawan region (figs. 35 and 36). *Sundamys infraluteus* is known from the mountains in Sabah and the mountainous backbone of Sumatra (fig. 37). *Sundamys maxi* has been recorded from western Java only.

Specimens of *Sundamys*, especially *S. muelleri*, look like primitive and shaggy-furred large rats. Our analysis of the distribution of primitive and derived traits among *Sundamys* and other *Sundaic* genera reinforce that impression. *Sundamys muelleri* and *S. infraluteus* are primitive rats; *S. maxi* is more derived because of a different pterygoid configuration, but it is still primitive compared with *Rattus*. Out of the 34 features we examined in *Sundamys*, 10 are derived. Not one of them is shared exclusively with another genus. All of them also occur in *Rattus* (table 45).

There are three features in *Sundamys* that we did not use in our comparisons of primitive and derived features but that need discussion. One is chromosomal. The X chromosome in *S. muelleri* is a large submetacentric (table 2), which is rare in *Rattus* (Raman and Sharma, 1977, p. 11). Among the Sundanese species examined for chromosomal morphology, *Lenothrix canus* has a large submetacentric X chromosome (Musser, 1981a, p. 266) and in most species of

TABLE 45
Distribution of Derived Traits in *Sundamys* among Sundanese Genera

Genera	SOR	PF	PP	R-M^1	R-M$_1$	OM	t1-M^1	UC	t4-t5	AC
Rattus	+	+	+	+	+	+	+	+	+	+
Berylmys	–	–	+	+	+	+	–	+	+	+
Niviventer	+	–	–	+	+	+	–	+	+	+
Kadarsanomys	+	+	+	+	+	+	+	–	–	–
Leopoldamys	+	–	–	–	+	+	–	+	+	+
Maxomys	+	–	–	–	–	+	–	+	+	+
Pithecheir	+	+	+	–	–	+	–	–	–	–
Palawanomys	–	–	–	–	+	+	+	+	–	–
Hapalomys	+	+	+	–	–	–	+	–	–	–
Lenothrix	+	–	+	–	–	–	–	–	–	–
Chiropodomys	+	–	+	–	–	–	–	–	–	–
Mus	–	–	–	–	–	+	–	+	+	+
Haeromys	–	–	+	–	–	–	–	–	–	–
Maxomys	+	–	–	–	–	+	–	+	+	+

Maxomys the X chromosome is either submetacentric or metacentric (Musser, Marshall, and Boeadi, 1979, p. 602).

The second character is the shapes of the stapedial foramina and posterior third of each pterygoid plate and the basicranial arterial pattern those features reflect (figs. 55 and 56). The carotid arterial pattern in *S. maxi* is uncommon among Indo-Australian murids and represents a derivation compared with the pattern in *S. muelleri* and *S. infraluteus,* one which is widely distributed among murids. We know of no other species on the Sunda Shelf with the basicranial arterial pattern and configuration of the stapedial foramina and pterygoid plates that are found in *S. maxi.* Aside from this pattern, *S. maxi* is morphologically closely allied to *S. muelleri* in features of skulls and teeth.

Third is the size of the molars and shapes of some laminae. Compared with *Rattus, Sundamys* has large molars, even massive in *S. infraluteus.* In the upper molars, the central cusp of each lamina is thin and spread out from side to side so it appears shallowly arcuate in occlusal view. Most laminae on the lowers are elongate, shallowly arcuate, and noncuspidate. These shapes are derived and contrast with the compact central cusp in the upper laminae of *Rattus* and its more cuspidate and chunky lower laminae (fig. 34, for example). The union of cusps in *Rattus* is still derived compared with the condition in *Lenothrix,* but not as specialized as in *Sundamys.*

Sundamys requires careful comparison with genera occurring outside the Sunda Shelf, especially those native to Sulawesi and the Philippine Islands. We point out here only that many of the derivations we see in *Sundamys* are those occurring in *Rattus* and other genera—such as *Berylmys, Kadarsanomys,* and *Niviventer*—that have similar derived cranial and dental features. All 10 traits in table 45 (supraorbital ridges, moderately deep pterygoid fossae, ridge along the posterolateral margins of the pterygoid platforms, five roots anchoring each first upper molar, four roots beneath each first lower molar, cusp t1 not set far posteriorly relative to the positions of cusps t2 and t3, cusps broadly joined, cusps t4 and t5 joined, and no anterolingual cusp at the front of each first lower molar) are widely distributed among African and Indo-Australian murids. We do not know if the shared derivations, especially those shared with *Rattus,* indicate close phylogenetic alliance or whether they reflect independent development. We need to examine cranial and dental features in greater detail and study other sets of characters (such as those associated with the male reproductive tracts) to determine what other derived traits occur in *Sundamys* and how similar traits are distributed among the Muridae. To us, *Sundamys* is not phylogenetically close to Sundanese

TABLE 46
Measurements and Ratio from Samples of Adult Sundanese *Maxomys*[a]

Species	Lengths						Length of Bulla / Skull Length
	Head and Body	Tail	Hind Foot	Skull	Bulla	M^{1-3}	
M. alticola	53.7 ± 9.0 139–176 (23)	161.2 ± 10.5 128–176 (21)	35.6 ± .9 34–37 (23)	39.5 ± 1.2 37.0–4.7 (23)	4.5 ± .2 4.1–4.7 (23)	5.8 ± .2 5.4–6.1 (23)	11
M. bartelsii	145.6 ± 14.5 127–128 (27)	147.7 ± 14.8 117–170 (26)	33.6 ± 1.2 31–36 (27)	37.3 ± 1.5 34.8–40.0 (17)	4.8 ± .2 4.4–5.2 (20)	5.4 ± .2 5.0–5.8 (24)	13
M. baeodon	133.8 ± 5.3 126–140 (6)	124.0 ± 7.8 119–133 (3)	26.8 ± 1.5 25–28 (6)	34.1 ± .7 33.2–35.2 (5)	— — —	4.8 ± .3 4.1–5.0 (6)	—
M. hylomyoides	125.9 ± 6.8 114–132 (8)	119.8 ± 10.4 98–132 (8)	29.4 ± 1.1 28–31 (8)	33.0 ± 1.0 31.3–34.2 (6)	4.6 ± .1 4.5–4.7 (7)	6.2 ± .2 5.9–6.5 (8)	14
M. inas	147.5 ± 11.3 124–162 (10)	149.2 ± 9.5 135–167 (10)	32.0 ± .8 31–33 (10)	37.7 ± 1.6 36.1–40.3 (6)	5.2 ± .1 5.1–5.3 (6)	6.4 ± .2 6.2–6.7 (6)	14
M. inflatus	171.1 ± 7.2 160–193 (35)	165.4 ± 10.4 143–190 (34)	39.8 ± 1.5 37–43 (35)	43.6 ± 1.3 40.8–47.1 (31)	5.0 ± .2 4.8–5.3 (35)	6.7 ± .2 6.3–7.2 (35)	12
M. ochraceiventer	152.8 ± 8.8 140–171 (20)	153.5 ± 14.1 130–175 (18)	32.5 ± 1.5 30–35 (20)	37.9 ± 1.3 35.3–39.6 (13)	3.9 ± .2 3.6–4.3 (13)	5.6 ± .2 5.4–6.0 (13)	10
M. panglima	197.9 ± 12.7 167–222 (22)	201.9 ± 12.2 180–226 (22)	41.5 ± 1.2 40–43 (22)	47.6 ± 1.4 45.5–48.6 (10)	5.4 ± .3 5.0–5.9 (10)	7.3 ± .2 7.1–7.8 (10)	11
M. rajah	192.9 ± 18.4 166–226 (13)	184.1 ± 14.6 162–210 (12)	38.5 ± 2.4 35–43 (13)	45.1 ± 2.6 40.9–48.6 (13)	4.6 ± .3 4.3–5.3 (13)	7.3 ± .3 6.9–8.1 (13)	10
M. surifer	176.8 ± 8.8 160–191 (29)	172.9 ± 12.9 146–148 (27)	37.1 ± 1.6 32–40 (29)	41.9 ± 1.6 39.4–46.1 (28)	4.7 ± .3 4.3–5.3 (29)	6.2 ± .3 5.8–6.8 (29)	11
M. whiteheadi	110.8 ± 8.5 100–126 (22)	96.7 ± 4.5 88–108 (21)	25.8 ± .9 24–28 (22)	31.2 ± 1.3 29.2–33.7 (21)	4.2 ± .2 3.9–4.7 (21)	5.5 ± .3 5.1–6.2 (21)	13

[a] Measurements are in millimeters, ratio in percentages. Mean plus or minus one standard deviation, observed range, and size of sample in parentheses are listed for each measurement.

species of *Lenothrix, Pithecheir, Hapalomys, Chiropodomys,* or *Haeromys.* It may be distantly related to *Rattus* but that connection is tenuous. Except for certain dental features and traits correlated with arboreal specializations, *Sundamys* shares many derived traits with *Kadarsanomys.* In these features (table 45), *Sundamys* bears the same relationship to *Kadarsanomys* as it does to *Rattus*; *Sundamys* is more primitive.

The five genera discussed above are found on the peninsula and islands of the Sunda Shelf and nowhere else. *Maxomys, Haeromys,* and *Chiropodomys,* the next three discussed below have most of their species on the Sunda Shelf; a few occur in the Mentawai Islands, Sulawesi, and Indochina.

MAXOMYS

Maxomys is basically Sundaic and Sulawesian (Musser, Marshall, and Boeadi, 1979; Musser, 1981a). Of the 19 species in

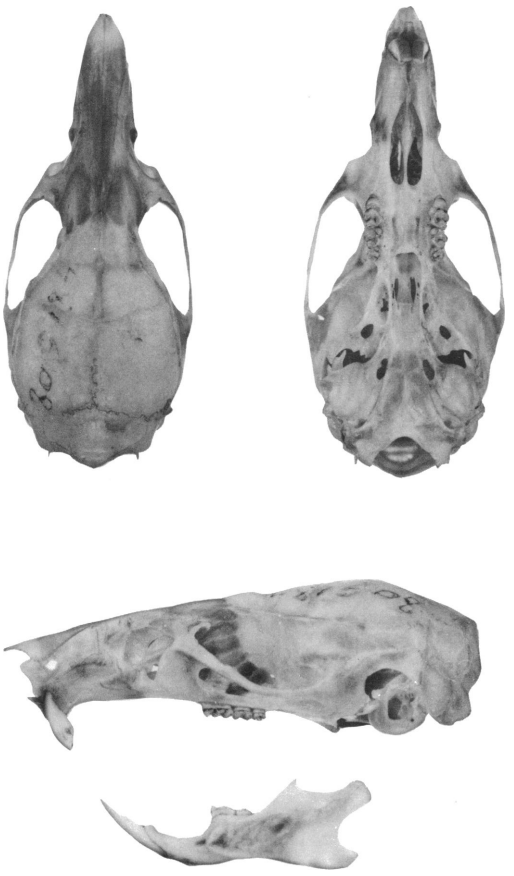

FIG. 99. Views of cranium and dentary of an adult *Maxomys bartelsii* (USNM 481408) from Java. This is the type species of the genus *Maxomys*.

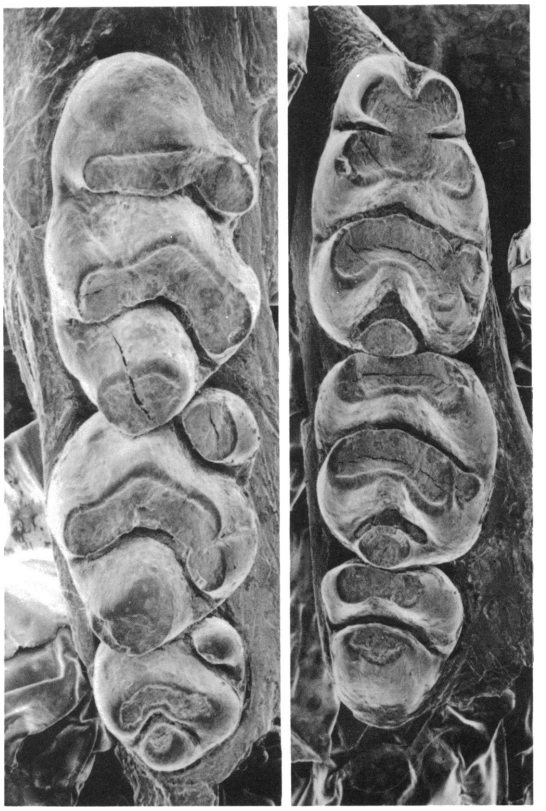

FIG. 100. Occlusal views of right upper (left) and lower (right) molar rows in Javan *Maxomys bartelsii* (AMNH 102650; CLM^{1-3}, 5.3 mm.; CLM_{1-3}, 5.4 mm.).

the genus, six (*M. muschenbroekii, M. hellwaldii, M. dollmani,* and three to be named and described) are found on Sulawesi, east of the Sunda Shelf. One (*M. pagensis*) occurs in the Mentawai Islands, south of the shelf. *Maxomys moi* is the only representative that is endemic to Indochina (southern Vietnam). One (*M. surifer*) is found in Indochina and on the Sunda Shelf. And 10 species (table 36) occur on the Shelf and nowhere else.

Most of the species endemic to the peninsula or a particular island on the Sunda Shelf have been found solely in mountain forests. This is true for the one endemic on the Malay Peninsula (*M. inas*), the two known only from Sumatra (*M. inflatus* and *M. hylomyoides*), the one in Java (*M. bartelsii*), and one (*M. alticola*) of the three endemic in Borneo. Both of the other two known only from Borneo (*M. baeodon* and *M. ochraceiventer*) occur in lowlands and mountains, and the single endemic in the Palawan region (*M. panglima*) inhabits lowlands and foothills. *Maxomys surifer, M. rajah,* and *M. whiteheadi,* the three found on the Malay Peninsula and several Sundaic islands inhabit lowland and foothill forests.

Most of the species of *Maxomys* live on the forest floor, a habit reflected in their body proportions and morphology of their hind feet. The tail is either shorter than the length of the head and body or about as long (table 46). The hind feet are long and slender, the plantar pads are low, smooth, and relatively small compared with the plantar area; one of the metatarsal pads is even absent in all or most specimens of some species (Musser, Marshall, and Boeadi, 1979, p. 598; Medway

TABLE 47
Distribution of Derived Traits in *Maxomys* among Sundanese Genera

Genera	HF	SOR	AL	SM	OM	UC	t4-t5	t9	PC	t3-M^2-M^3	AC	AL-AL	ALC
Niviventer	–	+	–	+	+	+	+	+	+	+	+	+	+
Berylmys	–	–	+	+	+	+	+	+	+	+	+	+	+
Mus	+	–	–	+	+	+	+	+	+	+	+	+	+
Leopoldamys	–	–	–	–	+	+	+	+	+	+	+	+	+
Rattus	–	+	+	+	+	+	+	–	+	+	+	–	–
Sundamys	–	+	–	–	+	+	+	–	–	–	+	–	–
Palawanomys	–	–	+	+	+	+	–	–	–	–	–	–	–
Kadarsanomys	–	+	+	–	+	–	–	–	–	–	–	–	–
Pithecheir	–	+	+	–	+	–	–	–	–	–	–	–	–
Hapalomys	–	+	+	–	–	–	–	–	–	–	–	–	–
Chiropodomys	–	+	+	–	–	–	–	–	–	–	–	–	–
Lenothrix	–	+	–	–	–	–	–	–	–	–	–	–	–
Haeromys	–	–	–	–	–	–	–	–	–	–	–	–	–

and Yong, 1976, pl. 3). The cranium and mandible are distinctive, as exemplified by *M. bartelsii,* the type species of the genus (fig. 99), and the molar occlusal patterns are simple (fig. 100).

Like other Sundanese murids, *Maxomys* is characterized by a combination of primitive and derived traits. Most of its derivations are associated with the elongate hind feet and the simple occlusal patterns on the molars (table 47). These molar features, along with small bullae and short palate were used by Ellerman (1947–1948, 1949) to place many of the species in *Maxomys* into a subgenus of *Rattus.* The small bullae (see table 46) and short palate are primitive traits and uncharacteristic of the derived long palate and large bullae in *Rattus.* The teeth in *Maxomys* have the primitive numbers of roots, not the derived condition found in *Rattus* (Musser, Marshall, and Boeadi, 1979, p. 598), and some of the molar traits shared by *Maxomys* and *Rattus* (relatively small third molars compared with the others in each row, overlapping molars, cusps broadly joined, usually no posterior cingulum, cusp t3 small or absent from the second and third upper molars, and no anterocentral cusp at the front of each first lower molar) also occur in many other murid genera and are likely convergent.

In an earlier analysis comparing *Maxomys* with *Rattus* and other genera once included in *Rattus,* Musser (1981a, p. 329) noted that *Maxomys* "appears to be phylogenetically more closely related to *Chiromyscus, Niviventer, Dacnomys,* and *Leopoldamys* than to *Rattus.*" Judged from the characters he studied, "there are no grounds for considering *Maxomys* to be closely related to *Rattus.*" Our analysis reinforces that view. *Maxomys* is not close to *Rattus.* Among the Sundaic murids, *Maxomys* shares all its dental derivations with *Niviventer, Berylmys,* and *Mus.* These are relatively small third upper molars compared with the others in each row, overlapping molars, cusps broadly merged, cusps t4 and t5 united, cusp t9 indistinct and broadly merged with cusp t8, no posterior cingulum, small or absent cusp t3 on second and third upper molars in most specimens, no anterocentral cusp, narrow anterior lamina on each first lower molar formed of broadly merged anterolabial and anterolingual cusps, and anterolabial cusps absent from second and third lower molars in most specimens.

We do not know whether the dental features shared among *Maxomys, Niviventer, Berylmys,* and *Mus* indicate close phylogenetic relationship or convergence. Supraorbital ridges are the only other feature shared by *Maxomys* and *Niviventer,* and the shapes are different in the two, being more shelflike in *Maxomys.* Species of *Berylmys* and most of *Maxomys* lack an alisphenoid strut; otherwise they share no cranial derivations. *Berylmys* is distinctive in its sloping occiput, a feature not found in *Maxomys.*

Maxomys and *Mus* (subgenus *Coelomys*)

do not share cranial derivations but both have the same kind of specialized hind feet; among Sundanese species, only those in *Maxomys* and *Mus* have this derivation. *Mus* has other derivations that *Maxomys* does not: notched upper incisors and a large squamoso-mastoid vacuity separating the squamosal bone into two parts above each bulla.

Mus does not have supraorbital or temporal ridging and has a wide alisphenoid strut forming the outer wall of each alisphenoid canal. Except for these two features, we note an overall similarity in the skulls, dentaries, and molar occlusal patterns between the two genera, using *Maxomys bartelsii* and *Mus vulcani* (compare figs. 99 and 108, 109 and 100). The molars of *Mus* are more specialized in that the third molars, especially the third upper, is relatively much smaller compared with the other teeth in each row than those in *Maxomys*. The anterolingual cusp is much larger than the small anterolingual cusp in *Mus*; the two cusps are nearly the same size in *Maxomys*. Of course, the two species differ vastly in body size (compare tables 46 and 55). Also, although the incisive foramina of *Mus* are short (relative to those in *Rattus*), they are relatively narrow compared with their lengths when contrasted with the relatively wide (heart-shaped in most species) foramina in *Maxomys*. The primary links between *Maxomys* and *Mus* are the specialized hind feet and simple occlusal patterns of the molars.

Whether the shared derived features reflect close phylogenetic relationship or instead convergence among *Maxomys, Berylmys, Niviventer,* and *Mus* may only be determined after we compare *Maxomys* with other genera occurring outside of the Sunda region. We also need to examine other kinds of characters and look at results of banding studies to make sense of the chromosomal diversity among the species of *Maxomys*.

HAEROMYS

Haeromys is Sundaic and Sulawesian. There are two species on Borneo, one on Palawan, and at least one in Sulawesi. On that large island, samples come from lowlands and highlands and there are distinguishing morphological features associated with altitude; we are uncertain whether the variation represents that found in one or two species.

TABLE 48
Measurements and Ratio from Samples of Adult Sundanese *Haeromys*[a]

Measurement and ratio	*H. pusillus*	*H. margaretae*
Length of head and body	62.3 ± 10.1 56–74 (3)	66
Length of tail	114 ± 7.1 108–122 (3)	145
Length of hind foot	17.4 ± .5 17–18 (5)	20
Greatest length of skull	22.0 ± .8 21.3–22.8 (3)	25.9
Length of bulla	3.1 ± .4 2.5–3.3 (5)	3.1
Alveolar length of M^{1-3}	3.2 ± .2 2.9–3.5 (7)	3.8
Length of bulla/skull length	14	12

[a] Measurements are in millimeters, ratio in percentages. Mean plus or minus one standard deviation, observed range, and size of sample in parentheses are listed for each measurement.

The species of *Haeromys* on the Sunda Shelf are the smallest in body size of all Sundaic species of murids (table 48). If few derived traits compared with many primitive features reflect the overall primitive nature of a species, then species of *Haeromys* are the most primitive on the Sunda Shelf. They do have some specializations which we did not record in table 38. In all the known species, the whiplike tail is slender and relatively very long compared with length of the head and body (Musser, 1977, fig. 1), a configuration that is clearly derived. All species have three pairs of mammae, also a derivation. Of all the other characteristics of skins, skulls, and teeth for which we can determine polarities, we find only four that are derived: a large opening between the bullae and squamosal bones, a sphenopterygoid vacuity in each pterygoid plate, a ridge forming the pterygoid bridge

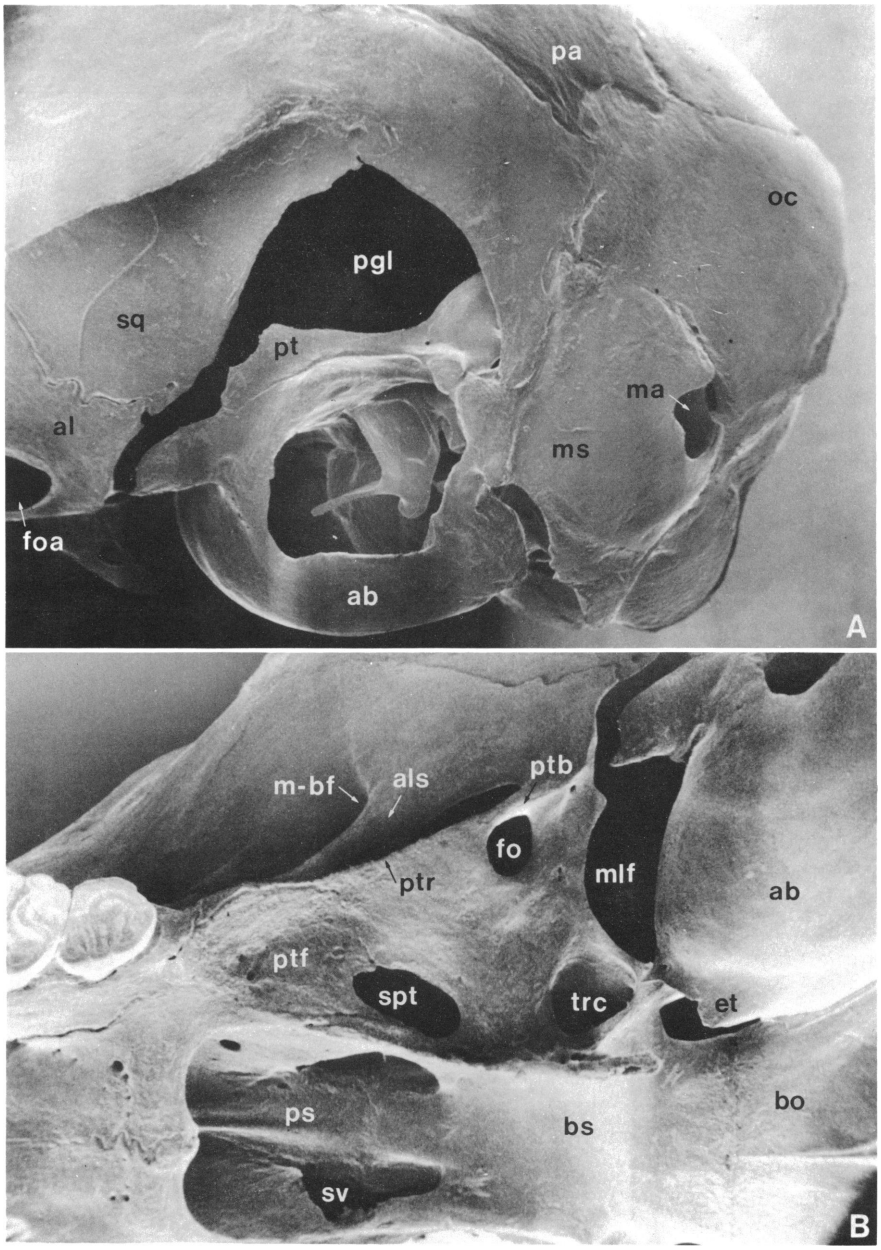

FIG. 101. Views of the auditory region (A) and the alisphenoid (part), pterygoid, and mesopterygoid areas (B) in *Haeromys minahassae* (AMNH 226050) from Central Sulawesi. *Abbreviations:* **ab**, auditory bulla; **al**, alisphenoid bone; **bo**, basioccipital bone; **bs**, basisphenoid bone; **et**, bony eustachian tube; **mf**, mastoid fenestra; **ms**, mastoid portion of the petromastoid; **mlf**, middle lacerate foramen; **oc**, occiput; **pa**, parietal bone; **pgl**, postglenoid vacuity; **ps**, presphenoid bone; **pt**, periotic portion of the petrosal; **ptb**, pterygoid bridge; **ptf**, pterygoid fossa; **ptr**, pterygoid ridge; **spt**, sphenopterygoid vacuity; **sq**, squamosal bone; **sv**, sphenopalatine vacuity; **trc**, opening of the transverse canal. Configurations of the auditory, mesopterygoid, and pterygoid areas resemble those regions in species of *Chiropodomys*.

between foramen ovale and bulla, and cusps t1bis and t2bis on each first upper molar (figs. 101 and 103). *Haeromys* shares these traits, in different combinations, with all Sundaic murids except *Maxomys, Leopoldamys,* and *Niviventer,* genera that share no derivations with *Haeromys* (table 49). All traits except the presence of cusps t1bis and t2bis are widely distributed among murid genera and in the context of our comparisons are ambiguous about indicating close phylogenetic relationship, except perhaps to *Chiropodomys.*

All four derived traits in *Haeromys* are shared with *Chiropodomys.* The overall configuration of the skulls (fig. 102) and molar occlusal patterns (figs. 103 and 104) are similar in the two genera, especially the pterygoid regions and the squamosal areas dorsal to auditory bullae. *Chiropodomys* has more derived traits than *Haeromys* but without the specializations in feet and skull, which reflect adaptations to living in trees, palms, and bamboo, and without cusps t7 on the upper molars, *Chiropodomys* would closely resemble *Haeromys.*

Misonne (1969, p. 104) did not know what to do with *Haeromys.* To him, it was not very closely related to *Chiropodomys.* He reiterated the alliances suggested by Tate (1936), who speculated that *Haeromys* was a derivative of the *Rattus cremoriventer*-group, and Ellerman (1941, 1949), who had originally allied *Haeromys* with *Rattus* but subsequently thought it nearest to *Lorentzimys.* Misonne included *Haeromys* in his *Lenothrix-Parapodemus* Division, which in the context of his study indicated only that *Haeromys* was not a relative of *Rattus* or its allies; that it did not belong with the many Indian and African genera which Misonne brought together into the cluster he called the *Arvicanthis* Division; and that it was one of those genera that are relict in some way, arboreal to some degree, lives in high mountains or are isolated on islands, and dwell in deep forest.

Among the rats and mice known to occur on the Sunda Shelf, the species of *Haeromys* may be more closely related to those of *Chiropodomys* than to any others. This possible

TABLE 49
Distribution of Derived Traits in *Haeromys* Among Sundanese Genera

Genera	AB	SptgV	PP	t1-t2bis
Chiropodomys	+	+	+	+
Hapalomys	–	+	+	+
Kadarsanomys	+	+	+	–
Palawanomys	+	+	–	+
Rattus	+	+	+	–
Pithecheir	–	–	+	+
Lenothrix	–	–	+	+
Berylmys	+	–	+	–
Sundamys	–	–	+	–
Mus	+	–	–	–
Maxomys	–	–	–	–
Leopoldamys	–	–	–	–
Niviventer	–	–	–	–

phylogenetic alliance will have to be tested by studying other sets of characters, and by comparing *Haeromys* and *Chiropodomys* with genera occurring outside of the Sunda region. One of the genera requiring critical comparison with *Haeromys* is *Lorentzimys,* the New Guinea native which Ellerman (1949) allied with *Haeromys.* Another is *Anonymomys,* a native of Mindoro Island in the Philippines (Musser, 1981a). In the context of disassociating certain groups of species from *Rattus,* Musser (1981a) noted that *Anonymomys mindorensis* was a primitive species and because it shared one dental feature with *Niviventer, Leopoldamys, Maxomys,* and others might be tenuously linked to them—a very speculative association. We looked at *A. mindorensis* again to see if it might be related to any of the Sundaic species and found it to be morphologically similar to species of *Haeromys. Anonymomys mindorensis* is a larger rat than any species of *Haeromys* and has a different kind of tail and less complex molar cusp patterns. The occlusal patterns, however, are those that would result from slightly simplifying the patterns in *Haeromys* by omitting posterior cingula on the upper molars (a small one occurs at the back of each first upper molar in one specimen), the anterocentral cusp at the front of each first lower molar, and the anterolabial cusp on each second lower molar. Furthermore, the large,

TABLE 50
Measurements and Ratio from Samples of Adult Sundanese *Chiropodomys*[a]

Measurement and Ratio	*C. gliroides* (Malaya)	*C. muroides* (Borneo)	*C. major* (Borneo)	*C. calamianensis* (Palawan)
Length of head and body	86.2 ± 7.4 69–102 (57)	71.0 ± 7.8 67–80 (3)	105.3 ± 5.5 94–114 (17)	117.0 ± 5.9 109–122 (4)
Length of tail	116.0 ± 10.1 94–143 (57)	88.7 ± 3.2 85–91 (3)	128.4 ± 11.1 109–144 (17)	153.5 ± 15.5 140–171 (4)
Length of hind foot	18.8 ± 1.6 15–22 (57)	16.0 ± 1.0 15–17 (3)	24.1 ± 1.5 21–28 (17)	25.5 ± .1 25–26 (4)
Greatest length of skull	25.4 ± .8 24.0–26.7 (23)	20.8 ± 1.2 19.9–21.6 (2)	29.3 ± .8 27.5–30.2 (17)	28.7 ± .4 28.4–29.2 (3)
Length of bulla	3.4 ± .2 3.1–3.8 (23)	3.1 ± .1 3.0–3.1 (2)	4.0 ± .1 3.8–4.2 (17)	4.2 ± .4 3.9–4.4 (2)
Alveolar length of M^{1-3}	3.8 ± .2 3.3–4.2 (23)	3.0 ± .1 2.9–3.9 (3)	4.7 ± .3 4.2–5.1 (17)	4.4 ± .2 4.2–4.8 (4)
Length of bulla/skull length	13	15	14	14

[a] Measurements are in millimeters, ratio in percentages. Mean plus or minus one standard deviation, observed range, and size of sample in parentheses are listed for each measurement.

nearly equal-sized and peglike anterolabial and anterolingual cusps at the front of each first lower molar are shaped like those in *Haeromys*. *Anonymomys* also has the same cranial derivations seen in *Haeromys*.

The relationship between *Haeromys* and *Anonymomys* will be critically explored in another report. We introduce a brief discussion of their possible relationship here to indicate that although *Haeromys* may be more closely allied to *Chiropodomys* than to any other genus on the Sunda Shelf, the nearest relative of *Haeromys* may not occur on the Shelf.

The phylogenetic alliances of *Haeromys* have been ambiguous to taxonomists partly because the species have so many primitive traits; they resemble many other genera with similar primitive features. Among species on the Sunda Shelf, those of *Haeromys* join *Lenothrix canus* in being the most primitive, at least in the framework of characters we studied. Whether *Haeromys* is as relatively primitive compared with genera outside of the Sunda region, especially those in the Philippines, Sulawesi, Australia, and the New Guinea region, has yet to be determined.

CHIROPODOMYS

This is another genus containing species of small body size (table 50). Judged by specimens of living rats, the species diversity of *Chiropodomys* is south of the Isthmus of Kra on the Sunda Shelf and Mentawai Islands. One, *C. gliroides,* occurs in Indochina and on both the large and small islands of the Shelf; *C. muroides* and *C. major* have been recorded solely from Borneo; one, *C. calamianensis,* is known from the islands of Balabac, Palawan, and Busuanga in the Palawan region; and the fifth, *C. karlkoopmani,* lives in forests on Pulau Pagai Utara and Pulau Siberkut in the Mentawai Islands. Definition of the genus, geographic distributions and taxonomic revisions of the species, and summaries from the literature and other sources of their habitats and habits are presented by Musser (1979) and Jenkins and Hill (1982).

Chiropodomys has been allied to genera

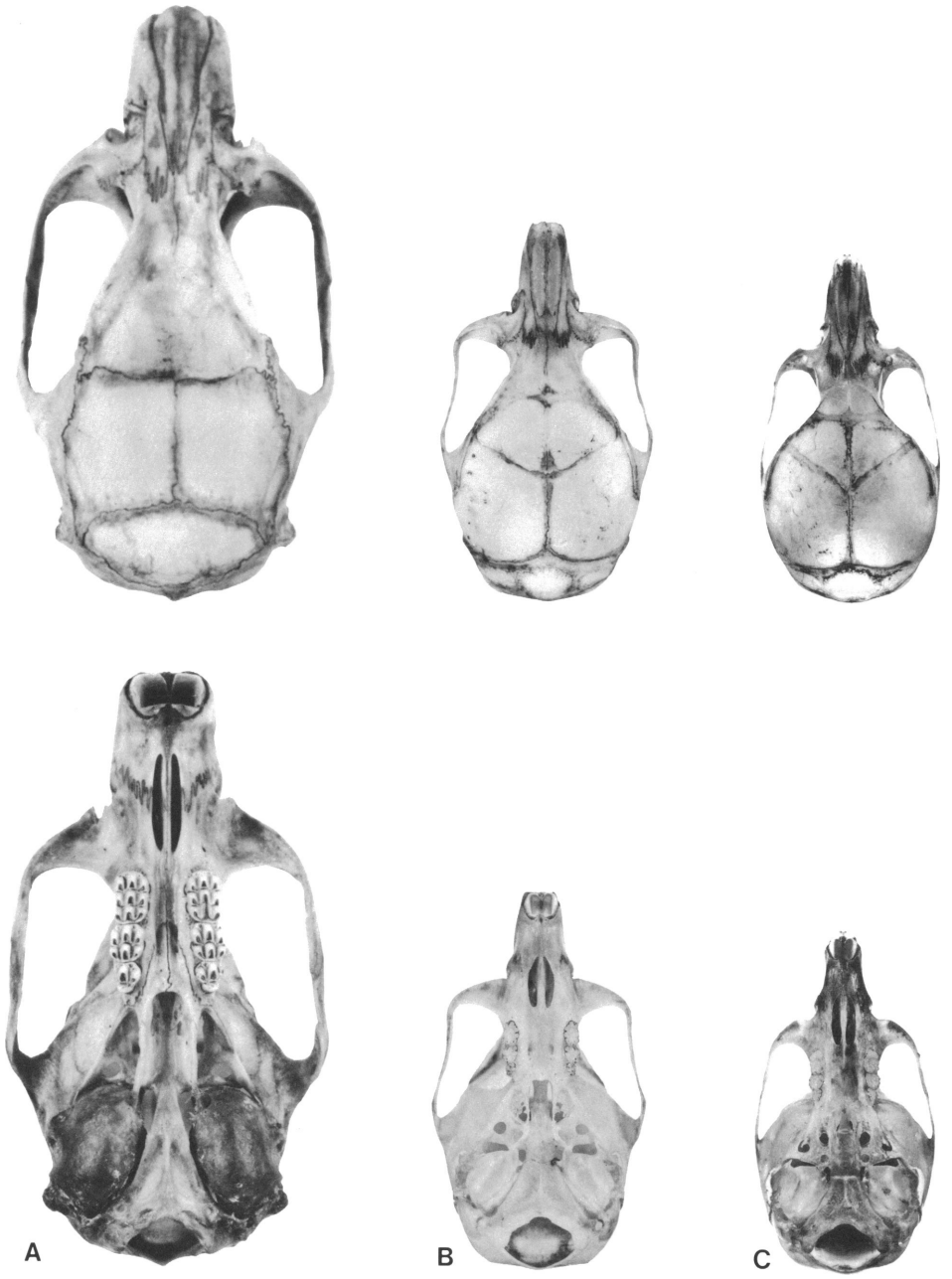

FIG. 102. Views of crania from adult *Hapalomys* (A), *Chiropodomys* (B), and *Haeromys* (C). A, *H. longicaudatus,* Malay Peninsula (BM 63.1160). B, *C. gliroides,* Java (AMNH 198655). C, *H. minahassae,* Central Sulawesi (AMNH 223961). Approximately ×2.

outside of the Sunda region. Ellerman (1941, p. 84), for example, wrote that *Chiropodomys* is "very closely allied to *Vandeleuria,* and appears also to present some relationship towards *Pogonomys.*" Misonne (1969, p. 91) placed *Chiropodomys* in his *Parapodemus* group of the *Lenothrix-Parapodemus* Division. He noted that "*Chiropodomys* is an in-

TABLE 51
Distribution of Derived Traits in *Chiropodomys* Among Sundanese Genera

Genera	Ha	HF	SOR	Al	AB	PP	SptgV	t1-t2bis	t7
Hapalomys	+	+	+	+	–	+	+	+	+
Pithecheir	–	+	+	+	–	+	–	+	+
Kadarsanomys	–	+	+	+	+	+	+	–	–
Lenothrix	–	+	+	–	–	+	–	+	+
Rattus	–	–	+	+	+	+	+	–	–
Haeromys	–	–	–	–	+	+	+	+	–
Palawanomys	–	–	–	+	+	–	+	+	–
Berylmys	–	–	–	+	+	+	–	–	–
Sundamys	–	–	+	–	–	+	–	–	–
Maxomys	–	–	+	+	–	–	–	–	–
Niviventer	–	–	+	–	–	–	–	–	–
Leopoldamys	–	–	+	–	–	–	–	–	–
Mus	–	–	–	–	+	–	–	–	–

teresting genus making the transition between the *Lenothrix* and the *Parapodemus* groups. Aside from its probably direct relationship to *Vernaya, Vandeleuria* and *Micromys,* its dental characters are also related to those of *Apodemus, Lenothrix, Pogonomys,* and others."

In our analysis of derived and primitive traits, *Chiropodomys* possesses nine derived features. It shares eight of these, in different combinations, with all the other Sundanese genera (table 51). We have pointed out in the previous accounts that some of the features, because they are widely distributed among murids, are ambiguous in their information about phylogenetic relationships. This applies to the derivations shared by *Chiropodomys* on one hand and *Mus, Leopoldamys, Niviventer, Maxomys, Sundamys, Berylmys, Palawanomys,* and *Rattus* on the other. Some shared derivations reflect arboreal habit, such as those common to *Chiropodomys* and *Lenothrix, Kadarsanomys, Pithecheir,* and *Hapalomys.* A few of the shared derivations suggest that *Chiropodomys* may be in the same large group as *Lenothrix, Pithecheir, Hapalomys,* and *Haeromys*—a cluster comparable to Misonne's (1969) *Lenothrix-Parapodemus* Division. We cannot point to a very close relationship between *Chiropodomys* and any other Sundanese genus.

There are, however, indications that *Chiropodomys* is more closely allied with some genera than others. *Haeromys* shares all its derived traits with *Chiropodomys* and we suspect those two may be closer than *Chiropodomys* is to either *Lenothrix* or *Pithecheir.* In that combination, *Haeromys* is more primitive in the characteristics of skins, skulls, and teeth that we checked, whereas *Chiropodomys* is more specialized.

Chiropodomys and *Hapalomys* form another couple. Except for attachment of bullae, *Chiropodomys* shares all its derived traits with *Hapalomys,* including the character not shared with any other Sundanese genus, a good nail on each hallux. *Hapalomys* has more derived traits than *Chiropodomys* and many of its external, cranial, and especially dental traits are adaptations for using clumps of bamboo as both nesting site and food resource. *Chiropodomys* also lives in bamboo but it can utilize other arboreal habitats as well and is not as specialized as *Hapalomys.* In this generic combination, *Chiropodomys* is the more primitive and *Hapalomys* is the more specialized.

Taken together, we suspect the shared derivations between *Chiropodomys* and *Hapalomys* may indicate a phylogenetic alliance that is stronger than that between *Chiropodomys* and any of the other Sundanese genera. Even though they appear superficially dissimilar, both genera share the presence of the same derived cusps, both share the same derivations, except for bullar inflation, in the cranium, and both have arboreal hind feet in which the halluces bear small and nearly flat

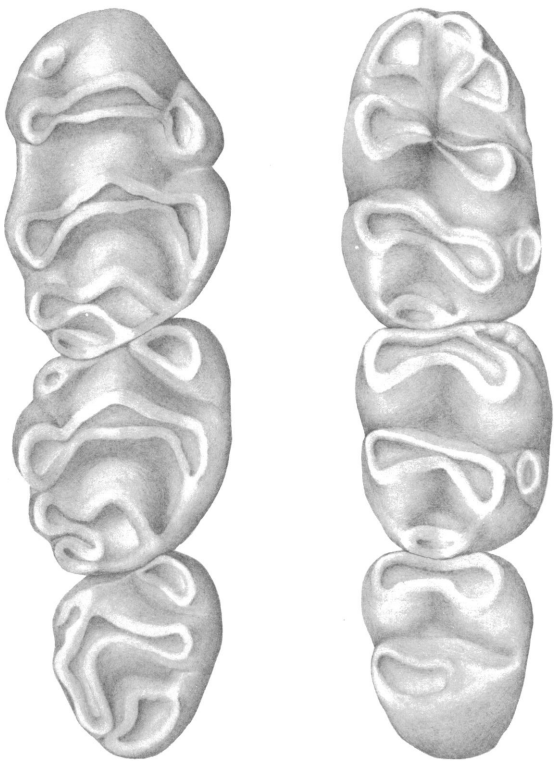

FIG. 103. Occlusal views of right upper (left) and lower (right) molar rows of *Haeromys minahassae* (AMNH 226048; CLM^{1-3}, 3.3 mm.; CLM_{1-3}, 3.4 mm.) from Central Sulawesi.

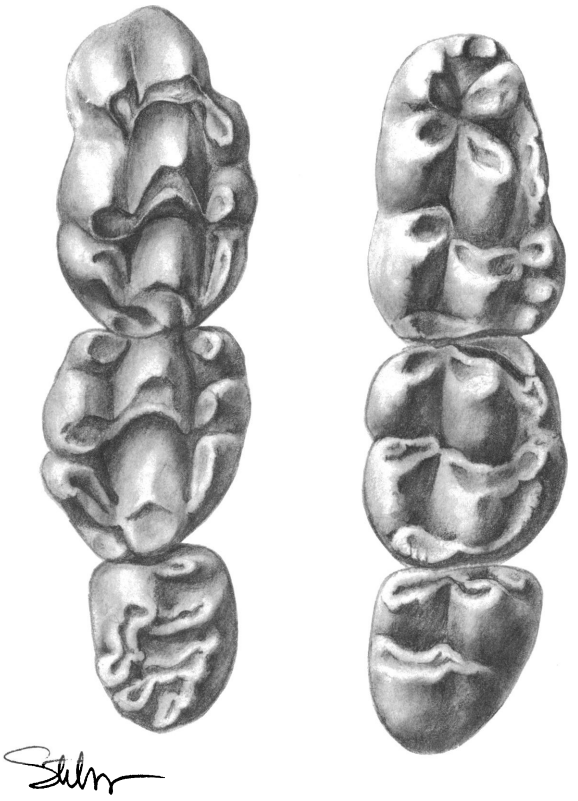

FIG. 104. Occlusal views of right upper (left) and lower (right) molar rows of *Chiropodomys gliroides* (AMNH 113040; $CLM_{1-3}{}^{1-3}$, 3.7 mm.) from northern Burma.

nails. In their general conformation, the crania of the two genera are also similar (fig. 102).

If we had to make groups out of the 14 genera occurring on the Sunda Shelf, we would include *Chiropodomys* and *Hapalomys* in a cluster separate from the other genera. Misonne (1969, p. 92) noted that based on his study of dental characters, the closest relative of *Hapalomys* is probably *Chiropodomys*. Whether *Chiropodomys* has tighter phylogenetic ties to genera outside of the Sunda region, such as *Vandeleuria*, for example, than to *Hapalomys* will have to be determined by future comparisons.

Most of the species of *Maxomys, Haeromys,* and *Chiropodomys* occur south of the Isthmus of Kra and are known only from the Sunda Shelf. The next four genera we discuss, *Niviventer, Berylmys, Mus,* and *Rattus,* have one or several species on the Shelf but most species in each genus occur outside of that region.

NIVIVENTER

There are approximately 15 species of *Niviventer* (Musser, 1981a). Four occur on the Sunda Shelf (table 52). Of these, *N. bukit* is found on Java, Sumatra, and peninsular Thailand and Malaya; the species also occurs north of the Isthmus of Kra in parts of Indochina. The other Sundanese species of *Niviventer* are endemic to the Sunda Shelf: *N. lepturus* has been recorded only from Java; *N. rapit* from the mountains of Sumatra, northern Borneo, and peninsular Thailand and Malaya; *N. cremoriventer* is widespread on the peninsula and both large and small islands of the Shelf south of the Isthmus of Kra. Clearly, the past evolutionary histories

TABLE 52
Measurements and Ratio from Samples of Adult Sundanese *Niviventer*[a]

Measurement and Ratio	*N. cremoriventer* (Malaya)	*N. bukit* (Java)	*N. rapit* (Sumatra)	*N. lepturus* (Java)
Length of head and body	147.5 ± 7.8 137–165 (15)	145.1 ± 13.0 129–174 (9)	147.0 ± 16.5 117–208 (25)	149.1 ± 6.9 141–167 (14)
Length of tail	175.4 ± 17.0 140–200 (14)	187.1 ± 10.7 174–202 (10)	212.7 ± 12.9 187–237 (21)	211.4 ± 15.5 173–227 (13)
Length of hind foot	27.5 ± 1.0 26–29 (15)	28.6 ± .9 27–30 (9)	32.6 ± 1.2 30–35 (24)	29.6 ± .9 28–31 (14)
Greatest length of skull	36.1 ± 1.2 34.1–37.9 (15)	36.4 ± 1.3 34.3–38.4 (11)	38.8 ± 1.4 35.4–41.2 (28)	38.1 ± 1.0 36.3–39.6 (12)
Length of bullae	4.6 ± .2 4.2–4.8 (15)	4.5 ± .2 4.0–4.7 (11)	4.7 ± .2 4.4–5.0 (33)	5.3 ± .2 4.9–5.7 (13)
Alveolar length of M^{1-3}	6.1 ± .3 5.5–6.4 (15)	6.4 ± .1 6.2–6.6 (11)	6.8 ± .2 6.4–7.4 (33)	7.2 ± .2 6.9–7.4 (14)
Length of bulla/skull length	13	12	12	15

[a] Measurements are in millimeters, ratio in percentages. Mean plus or minus one standard deviation, observed range, and size of sample in parentheses are listed for each measurement.

of most species of *Niviventer* are linked to northern India and Southeast Asia north of the Isthmus of Kra. One of those species also occurs south of the Isthmus. How closely the endemic Sundanese species of *Niviventer* are phylogenetically linked to the others in the genus is not known and their affinities will remain obscure until the species in what Musser (1981a, pp. 237–238) called the *niviventer*-complex are revised taxonomically.

The species of *Niviventer* were once part of the genus *Rattus* but have been disassociated from it. In a recent study, the distribution of primitive and derived traits among several Indo-Australian genera thought to be either closely related to *Rattus* or part of the genus indicated that *Niviventer* was not phylogenetically close to *Rattus* but might be more tightly linked with *Dacnomys, Chiromyscus, Leopoldamys,* and *Maxomys* (Musser, 1981a). The closest relative of *Niviventer* is *Chiromyscus chiropus,* an arboreal animal known by few specimens collected from Burma, northern Thailand, Vietnam, and Laos (Musser, 1981a, pp. 316–317). Were it not for the morphological adaptations of the cranium and hind feet (Musser, 1982a) for specialized arboreal habit, there would be no reasons for not uniting *Chiromyscus* and *Niviventer.*

In our analysis of the distributions of primitive and derived traits among Sundanese genera, *Niviventer* shares most of its 14 derived traits with five other genera: *Berylmys,* another genus in which the species are primarily Indochinese in distribution; *Leopoldamys* and *Maxomys,* two genera that clustered close to *Niviventer* in the earlier analysis (Musser, 1981a); *Rattus*; and *Mus* (table 53). The cranial characters *Niviventer* shares with *Rattus,* supraorbital ridges and long incisive foramina, do not help to assess the degree of relationship between the two genera because both traits occur in many other rats, especially supraorbital ridges. Long incisive foramina are not characteristic of most genera found on the Sunda Shelf but their frequency is high in genera from elsewhere in the natural range of the Muridae.

Most of the derived traits shared by *Nivi-*

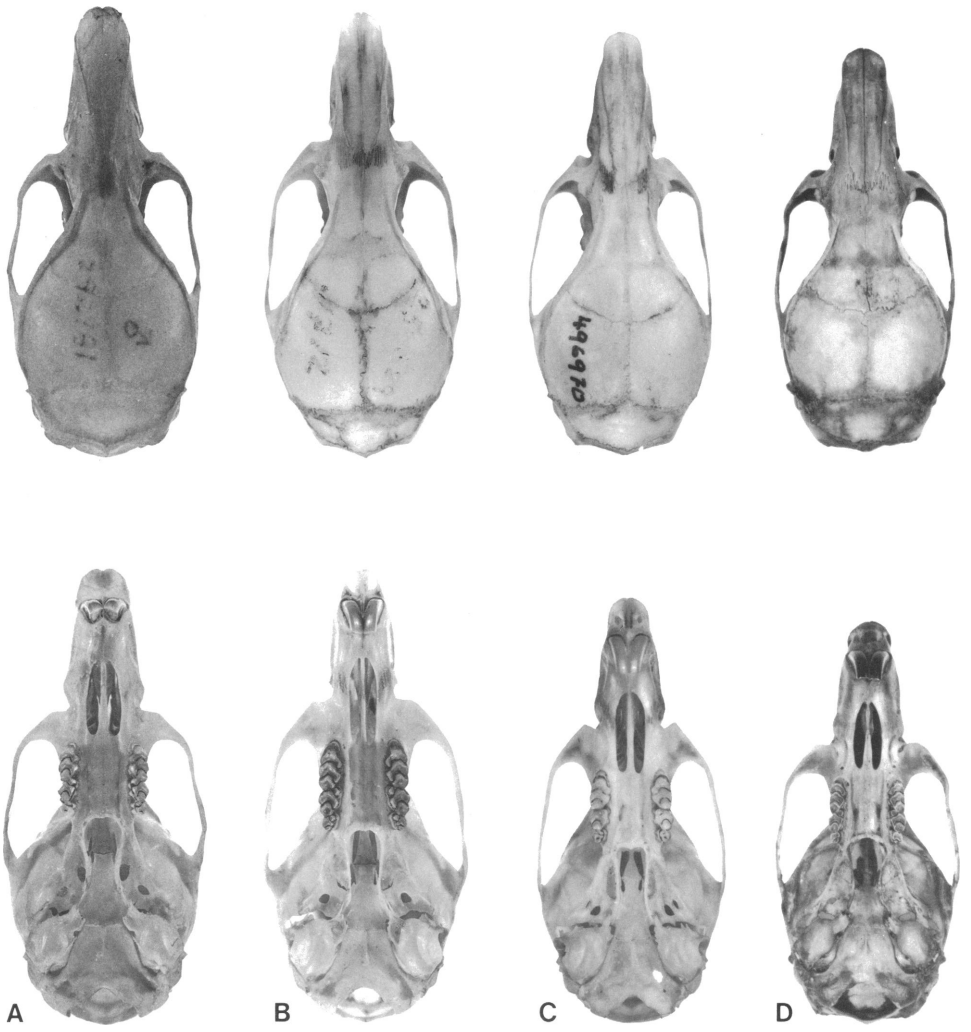

FIG. 105. Cranial views of adult *Niviventer* from the Sunda Shelf. A, *N. rapit,* Sabah (USNM 292781). B, *N. lepturus,* Java (AMNH 250089). C, *N. bukit,* Java (USNM 496970). D, *N. cremoriventer,* Malay Peninsula (AMNH 217621). Natural size.

venter and *Rattus* are those associated with the simple occlusal patterns on the molars. But *Rattus* is not as derived as *Niviventer* because in the former cusp t9 is discrete, the anterior lamina of each first lower molar is broad and the anterolabial and anterolingual cusps are not merged to the degree that their outlines are obliterated, and anterolabial cusps are present on the second and third lower molars (compare figs. 106 and 107 with 112 and 113).

Niviventer shares nearly all its dental derivations with *Berylmys, Leopoldamys, Maxomys,* and *Mus,* derivations reflecting simple molar occlusal patterns (compare figs. 20, 21, 116, 100, 109, 106, and 107), the degree the molars overlap, and the broad union of cusps within each row. Of these genera, *Berylmys* has more derived cranial and incisor features than does *Niviventer. Leopoldamys* and *Maxomys* have the primitive expressions of the incisive foramina (short) and less than five roots beneath each first upper molar. *Maxomys* has less than four roots anchoring each first lower molar, a primitive trait compare with the number found in *Niviventer.*

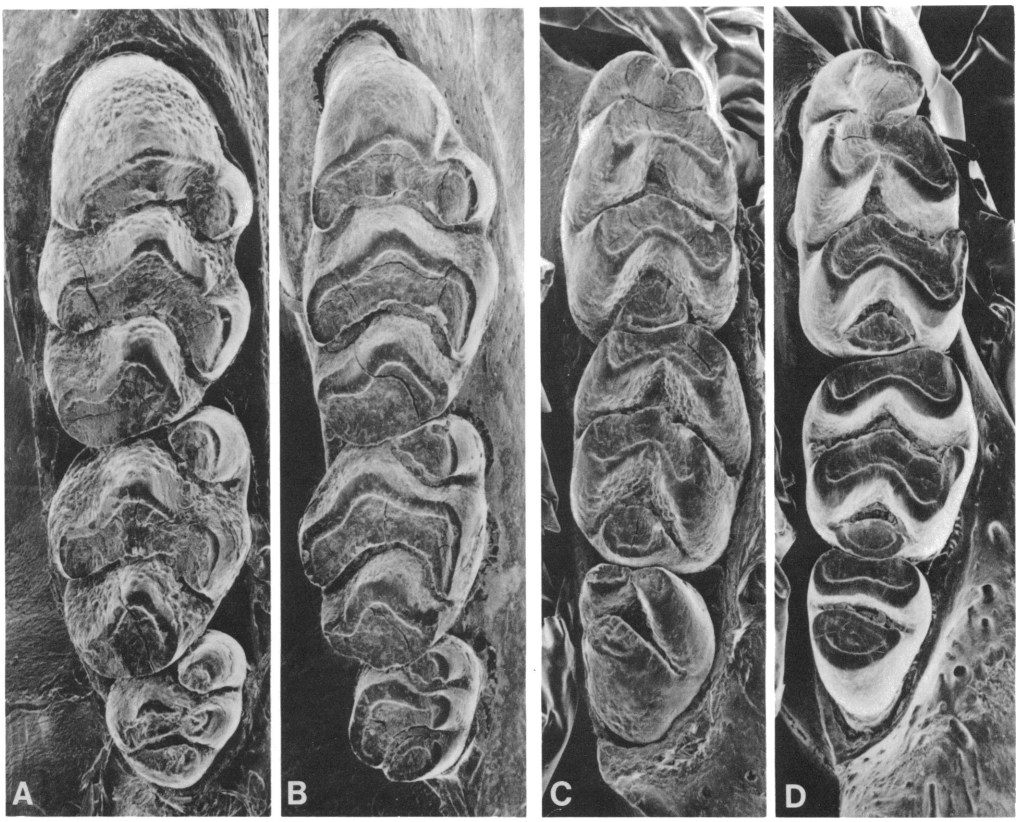

FIG. 106. Occlusal views of right upper (A and C) and lower (B and D) molar rows in species of *Niviventer* from the Sunda Shelf. A and C, *N. lepturus,* Java (AMNH 152497), CLM^{1-3}, 6.8 mm.; CLM_{1-3}, 7.0 mm.). B and D, *N. bukit,* Java (AMNH 103433, CLM^{1-3}, 6.0 mm.; CLM_{1-3}, 6.1 mm.).

Mus has the primitive features of smooth interorbital and temporal regions, short incisive foramina, and few roots; their counterparts are derived in *Niviventer. Mus* also has the derivations of notched incisor tips, long hind feet, and large squamoso-mastoid foramina, traits not shared with *Niviventer.* Although the molar occlusal patterns are similar in the two genera, the third molar of *Mus* is relatively much smaller compared with the other teeth in each row than are the proportions of the molars in *Niviventer* and the shape of the lamina formed by the coalesced anterolabial and anterolingual cusps is different in the two genera. Set against the pattern of other primitive and derived features in each genus, the simple occlusal patterns may reflect convergence.

Niviventer requires comparisons with other murids, especially those in Southeast Asia and the Palearctic Region, before its phylogenetic relationships can be more finely resolved. Musser's (1981a) earlier analysis and our comparisons made here indicate that *Niviventer* shares either few derived or no features at all with *Lenothrix, Haeromys, Chiropodomys, Hapalomys,* and *Pithecheir*; most likely *Niviventer* is not phylogenetically closely related to those genera. If the dental patterns common to *Leopoldamys, Berylmys,* and *Maxomys* point to derivations shared with *Niviventer* through close phylogenetic relationship and not convergence then *Niviventer* may be more closely allied to them than to any other genus found on the Sunda Shelf. North of the Isthmus of Kra, *Niviventer* clearly has closer phylogenetic ties to *Chiromyscus* and possibly *Dacnomys* than to any group of species on the Shelf.

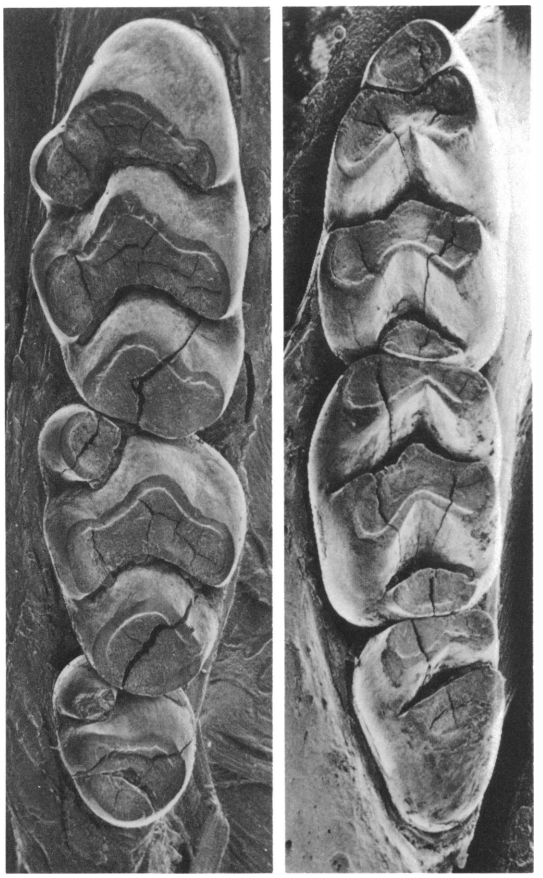

FIG. 107. Occlusal views of left upper (left) and lower (right) molar rows of *Niviventer cremoriventer* (AMNH 103579, CLM^{1-3}, 5.6 mm.; CLM_{1-3}, 5.7 mm.) from Borneo.

BERYLMYS

Usually included in *Rattus* but excluded from that genus by characteristics presented in our report, *Berylmys* has four species (*B. bowersii, B. mackenziei, B. manipulus,* and *B. berdmorei*) that are primarily Indochinese in geographic distribution (fig. 14). One, *B. bowersii,* occurs north of the Isthmus of Kra in northeastern India, southern China, and the northern part of Burma, Thailand, Laos, and Vietnam; there are also populations south of the Isthmus of Kra in peninsular Thailand and Malaya and the Medan region of northern Sumatra (table 55). Assuming that the geographic range of *Berylmys* as we know it from the distribution of living species more or less reflects its natural range and that *Berylmys* has never occurred on other islands of the Sunda Shelf, then *Berylmys,* like *Niviventer,* is one of those genera in which the past evolutionary histories of the species has centered in Indochina. It is really an Asian element on the Shelf rather than Sundaic.

That foreign aspect of *Berylmys* is partially reflected in its relationships to other Sundanese genera. Few of its 17 derived traits are shared with *Kadarsanomys, Palawanomys, Pithecheir, Lenothrix,* and *Sundamys,* genera that are endemic to the peninsula and islands of the Sunda Shelf (table 54). *Sundamys muelleri* and its allies, to which *Berylmys bowersii* was considered closely related, shares six derivations with *Berylmys*: a ridgelike pterygoid bridge, five roots beneath

TABLE 53
Distribution of Derived Traits in *Niviventer* Among Sundanese Genera

Genera	SOR	IF	R-M^1	R-M_1	SM	OM	UC	t4-t5	t9	PC	t3-M^2-M^3	AC	AL-AL	ALC
Berylmys	–	–	+	+	+	+	+	+	+	+	+	+	+	+
Leopoldamys	+	–	–	+	–	+	+	+	+	+	+	+	+	+
Maxomys	+	–	–	–	+	+	+	+	+	+	+	+	+	+
Rattus	+	+	+	+	+	+	+	+	–	+	+	+	–	–
Mus	–	–	–	–	+	+	+	+	+	+	+	+	+	+
Sundamys	+	–	+	+	–	+	+	+	–	–	–	+	–	–
Kadarsanomys	+	+	+	+	–	+	–	–	–	–	–	–	–	–
Palawanomys	–	–	–	+	+	+	+	–	–	–	–	–	–	–
Pithecheir	+	–	–	–	–	+	–	–	–	–	–	–	–	–
Hapalomys	+	–	–	–	–	–	–	–	–	+	–	–	–	–
Chiropodomys	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Lenothrix	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Haeromys	–	–	–	–	–	–	–	–	–	–	–	–	–	–

TABLE 54
Distribution of Derived Traits in *Berylmys* Among Sundanese Genera

Trait	*Nivi-venter*	*Rattus*	*Maxo-mys*	*Leo-pold-amys*	*Mus*	*Sun-damys*	*Kadar-sano-mys*	*Pala-wano-mys*	*Chiro-podo-mys*	*Hapa-lomys*	*Pithe-cheir*	*Hae-romys*	*Leno-thrix*
AL	–	+	+	–	–	–	+	+	+	+	+	–	–
SB	–	+	–	–	+	–	–	+	–	–	–	–	–
AB	–	+	–	–	+	–	+	+	+	–	–	+	–
PP	–	+	–	–	–	+	+	–	+	+	+	+	+
CI	–	–	–	–	–	–	–	–	–	–	–	–	–
R-M^1	+	+	–	–	–	+	+	–	–	–	–	–	–
R-M_1	+	+	–	+	–	+	+	+	–	–	–	–	–
SM	+	+	+	–	+	–	–	+	–	–	–	–	–
OM	+	+	+	+	+	+	+	+	–	–	+	–	–
UC	+	+	+	+	+	+	–	+	–	–	–	–	–
t4-t5	+	+	+	+	+	–	–	–	–	–	–	–	–
t9	+	–	+	+	+	–	–	–	–	–	–	–	–
PC	+	+	+	+	+	–	–	–	–	+	–	–	–
t3-M^2-M^3	+	+	+	+	+	–	–	–	–	–	–	–	–
AC	+	+	+	+	+	+	–	–	–	–	–	–	–
AL-AL	+	–	+	+	+	–	–	–	–	–	–	–	–
ALC	+	–	+	+	+	–	–	–	–	–	–	–	–

each first upper molar, four roots anchoring each first lower molar, overlap among the molars, cusps broadly united, and no anterocentral cusp on each first lower molar. All these features are found in some genera occurring on the Shelf and in many groups of species throughout the range on the Muridae. The shared derivations may indicate that *Berylmys* is phylogenetically closer to *Sundamys* than to primitive rats such as *Lenothrix* and *Haeromys* but the derivations are ambiguous about any closer alliance between *Berylmys* and *Sundamys.*

There is no indication of close relationship between *Berylmys* and either *Chiropodomys* or *Haeromys,* genera containing mostly Sundaic endemics. *Maxomys,* another primarily Sundanese cluster of species, may be the only Sundaic genus to be more closely linked with *Berylmys. Maxomys* shares one derived characteristic of the skull (no alisphenoid struts in all species of *Berylmys* and most of *Maxomys*) and nearly all the traits related to simple cusp patterns on the molars (table 54) with *Berylmys. Maxomys* is more primitive in general cranial configuration and in number of roots anchoring the molars.

Five roots anchoring first upper molars, four below first lower molars, overlapping molars, relatively small third molars compared with the other teeth in each row, and simple molar occlusal patterns are the features shared by *Berylmys* and *Niviventer.* Except for number of roots under first molars and relative size of each third molar, the same dental derivations are also shared by *Berylmys* and *Leopoldamys.* These genera share no cranial derivations with *Berylmys*; both *Niviventer* and *Leopoldamys* have primitive cranial features relative to *Berylmys.*

Berylmys shares some of the same dental traits with *Rattus* (table 54) and four cranial features as well: no alisphenoid struts, relatively moderately large bullae compared with cranial size, loose attachment of bullae to squamosal bones, and ridged pterygoid bridges. These skull features also occur in many other genera and without comparing *Berylmys* with all other murids, we do not know what meaning to attach to these shared cranial features between *Berylmys* and *Rattus.* Other cranial derivations exist in *Rattus* that are not found in *Berylmys* (table 58).

The relative size of the bulla compared with that of the skull, the attachment of the bulla to the squamosal, overlap among the molars, relatively small third molars, broad union of cusps, and simple molar occlusal patterns are

FIG. 108. Cranium and dentary of an adult *Mus vulcani* (AMNH 254561) from West Java.

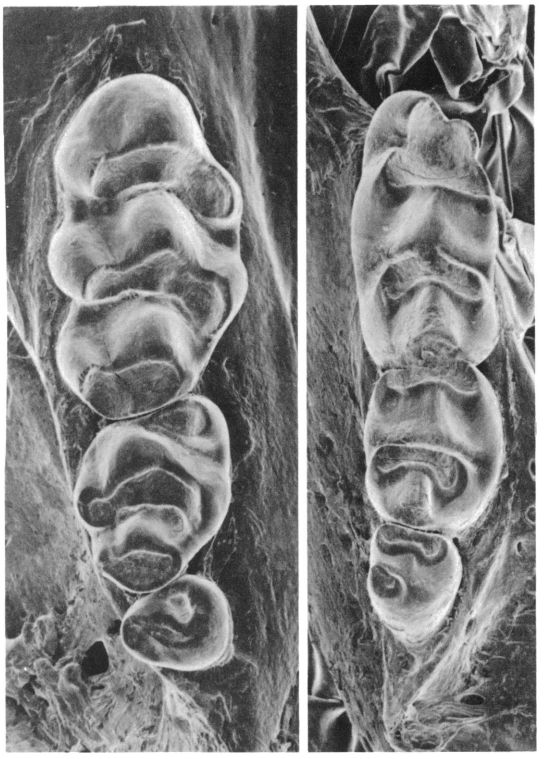

FIG. 109. Occlusal views of right upper (left) and lower (right) molar rows of Javan *Mus vulcani* (MZB 9572, CLM^{1-3}, 3.5 mm.; CLM_{1-3}, 3.4 mm.).

also shared by *Berylmys* and *Mus* (table 54). The relative size of bulla and nature of its attachment are derivations widespread among murids and do not point to close relationship between *Berylmys* and *Mus*. The third molars of *Mus* are relatively much smaller compared with the other teeth in each row than are relative sizes of the molars in *Berylmys*. Except for the bullae, none of the other derivations found in *Mus*, such as notched incisors, large squamoso-mastoid foramina, and specialized elongate hind feet, are shared with *Berylmys*. Most other features of *Mus*, at least the two native Sundaic species in subgenus *Coelomys*, are primitive compared with their counterparts in *Berylmys*. Possibly the simple occlusal patterns are convergent in both.

In context of our comparisons among genera found on the Sunda Shelf, the pattern of shared derived features suggest that *Berylmys* is dentally similar to *Niviventer*, *Maxomys*, and *Leopoldamys* but more like *Rattus* in some derived cranial features. That is the limit of our resolution. *Berylmys* will have to be compared with genera from outside the Sunda region, especially those native to India.

MUS

There are about 43 species of *Mus* recognized in the current literature, a number that will change as groups of species are taxonomically revised. The geographic distribution of native *Mus* takes in Africa, the Palearctic region from Europe to Japan, and the Indo-Malayan area. Six species are recorded from the Peninsula and islands of the Sunda Shelf. We suspect four of these (*M. castaneus*, *M. caroli*, *M. cervicolor*, and *M. dunni*) represent introductions to the Shelf through human means. Two are native: *M. crociduroides* and *M. vulcani*.

According to Marshall (1977a), both Sundanese species are in the subgenus *Coelomys*,

TABLE 55
Measurements and Ratio from Samples of Adult Sundanese *Berylmys* and *Mus* (Subgenus *Coelomys*)[a]

Measurement and Ratio	*Berylmys bowersii* (Peninsular Thailand and Malaya)	*Mus crociduroides* (Sumatra)	*Mus vulcani* (Java)
Length of head and body	264.2 ± 18.6 230–300 (24)	90.6 ± 5.6 77–97 (13)	87.2 ± 5.8 80–92 (5)
Length of tail	283.3± 11.5 262–300 (24)	117.7 ± 5.1 111–129 (12)	86.3 ± 3.0 84–92 (6)
Length of hind foot	55.0 ± 1.8 52–59 (24)	22.0 ± .4 21–23 (12)	21.7 ± 1.0 20–23 (6)
Greatest length of skull	57.7 ± 2.5 52.0–63.1 (27)	24.9 ± .8 23.7–26.3 (13)	25.4 ± .9 23.9–26.5 (7)
Length of bulla	7.0 ± .3 6.2–7.3 (27)	3.8 ± .2 3.5–4.1 (11)	3.8 — (1)
Length of M^{1-3}[b]	9.8 ± .4 9.1–10.5 (27)	3.9 ± .1 3.7–4.1 (13)	3.6 ± .2 3.4–3.8 (7)
Length of bulla/skull length	12	15	15

[a] Measurements are in millimeters, ratio in percentages. Mean plus or minus one standard deviation, observed range, and size of sample in parentheses are listed for each measurement. Data for samples of *Mus* were computed from measurements taken by Dr. Joe T. Marshall, Jr.

[b] Alveolar length for *Berylmys*, crown length for the two species of *Mus*.

a group characterized by a broad interorbital region lacking supraorbital ridges, short and wide incisive foramina, broad mesopterygoid fossa, narrow zygomatic plates that lean backward, velvety or spiny fur, and very small eyes. To Marshall (1977a, p. 189), "the several forms of *Coelomys* are isolated from each other on mountaintops. Their shrew-like propensities, culminating in the long-nosed, small-eyed, velvet-furred species of Indonesian moss forest, suggest they live by poking within soggy leaf litter, ferns, and rotten logs for invertebrates."

There are five species of *Coelomys*. *Mus mayori* is found in moss forest on Ceylon. *Mus pahari* occurs in mountain forests in Sikkim, northeast India, southern China, northern Burma, northern Thailand, Laos, and Vietnam. *Mus famulus* is known only from evergreen forest in the Nilgiri Hills of India. *Mus crociduroides* is endemic to Sumatra and Java is the only place where *M. vulcani* has been found.

Judged by characteristics of skins, skulls, teeth, and chromosomes, species of subgenus *Coelomys* are more primitive than those in the other subgenera of *Mus*. The two Sundaic species are morphologically more similar to one another than to any of the other species in the subgenus. Their elongate crania and shrewlike body conformation are distinctive, so special that Chasen (1940) listed them as members of the genus *Mycteromys*. The Javan animal was regarded as a subspecies of the Sumatran species but the two differ in pelage color, length of tail, length of incisive foramina, length of molar rows (table 55), and other cranial and dental features; there is no evidence supporting the hypothesis that the Javan *vulcani* is a subspecies of the Sumatran *crociduroides*.

To determine the phylogenetic affinities of *Mus*, comparisons are required between it and the many genera occurring outside of the Sunda region, especially *Apodemus*, the Indian *Millardia* and *Cremnomys*, and the Af-

TABLE 56
Distribution of Derived Traits in *Mus* (Subgenus *Coelomys*) Among Sundanese Genera

Genera	HF	Sq-mf	SB	AB	TI	SM	OM	UC	t4-t5	t9	PC	t3-M^2-M^3	AC	ALC
Berylmys	–	–	+	+	–	+	+	+	+	+	+	+	+	+
Maxomys	+	–	–	–	–	+	+	+	+	+	+	+	+	+
Niviventer	–	–	–	–	–	+	+	+	+	+	+	+	+	+
Rattus	–	–	+	+	–	+	+	+	+	–	+	+	+	–
Leopoldamys	–	–	–	–	–	–	+	+	+	+	+	+	+	+
Palawanomys	–	–	+	+	–	+	+	+	–	–	+	+	+	–
Sundamys	–	–	–	–	–	–	+	+	+	–	–	–	+	–
Kadarsanomys	–	–	–	+	–	–	+	–	–	–	–	–	–	–
Pithecheir	–	+	–	–	–	–	+	–	–	–	–	–	–	–
Chiropodomys	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Hapalomys	–	–	–	–	–	–	–	–	–	–	+	–	–	–
Haeromys	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Lenothrix	–	–	–	–	–	–	–	–	–	–	–	–	–	–

rican *Mastomys, Praomys,* and *Hylomyscus.* Specimens of *Mus* also need to be critically contrasted with examples of fossil murids, particularly species of *Progonomys.* Ellerman (1941) thought *Mus* to be closely allied to *Rattus* and this alliance was strengthened by Misonne (1969) who placed *Mus,* as one of four groups of genera, into a *Rattus* Division. Molar cusp patterns formed the primary evidence for these associations.

Mus does share some derived dental features with *Rattus* (table 56) but these are likely convergent for it is our experience that there is little in common between the two genera in cranial and chromosomal characters. The chromosomal number and configurations are primitive in *Mus* but derived in *Rattus* (contrast the karyotypes of species in each genus presented by Marshall, 1977b). *Mus* and *Rattus* share some derived dental features that reflect simple cusp patterns but those simple patterns in *Mus* are built on molars with the primitive number of roots and the primitive position of cusp t1 compared with cusps t2 and t3. The differences in detail of the cusp patterns between *Mus* and *Rattus,* along with the dental morphology of fossil murids found in the Siwalik sediments of Pakistan, led Jacobs (1978) to hypothesize that *Mus* is closely related to the ancestral stock of *Progonomys* and that *Rattus* is in a different lineage, one that also includes the fossil *Karnimata.* To Jacobs, *Rattus* and *Mus* are not phylogenetically close, a relationship also indicated by immunological data and information derived from analyses of amino acid sequences and DNA hybridization experiments (Jacobs and Pilbeam, 1980).

Except for a few dental traits, we detect no close alliance between Sundanese *Mus* and *Rattus.* The endemic Sundaic *Palawanomys* is no closer to *Mus* and neither are *Sundamys, Kadarsanomys, Pithecheir, Chiropodomys, Hapalomys, Haeromys,* nor *Lenothrix. Pithecheir* and *Mus* do share a squamosomastoid foramen that separates the squamosal bone into two parts but the opening is different in each genus, as we explained in the account of *Pithecheir,* and the presence of the vacuity is likely convergent.

Simple molar cusp patterns are shared by *Mus* on one hand and *Berylmys, Maxomys, Niviventer,* and *Leopoldamys* on the other. The cranial features shared by all these genera and *Mus* do not indicate close relationship and we are uncertain whether the simple occlusal patterns do. Except for *Maxomys, Mus* has the primitive number of molar roots and the other genera are derived in this character. The simple cusp patterns and the size of the third molars relative to the others, features that characterize *Berylmys, Maxomys,* and *Niviventer,* possibly indicate that these genera are in the same lineage as *Mus* and developed more than three roots on the first upper molars and more than two on the lowers independently of species in the *Rattus* lineage.

TABLE 57
Species of Native *Rattus*[a]

Geographic Area	Species
Australia	*R. fuscipes, R. lutreolus, R. tunneyi*
New Guinea Region	*R. niobe, R. richardsoni, R. verecundus, R. praetor, R. mordax, R. steini, R. giluwensis, R. novaeguineae, R. jobiensis*
Australia-New Guinea Region	*R. leucopus, R. sordidus*[b]
Moluccas	*R. ceramicus, R. feliceus, R. morotaiensis, R. elaphinus, R.* sp., *R.* sp.
Philippine Islands	*R. everetti, R. mindorensis*
Sulawesi	*R. hoffmanni, R. xanthurus*-complex,[c] *R.* sp.
Small Islands east, south, and west of Sunda Shelf	*R. stoicus, R. palmarum, R. lugens, R. adustus, R. enganno, R. macleari, R. nativitatis, R.* sp.
Sunda Shelf	*R. tiomanicus, R. baluensis, R. hoogerwerfi, R. annandalei*
India and Asia	*R. norvegicus, R. argentiventer,*[d] *R. exulans,*[d] *R. nitidus, R. losea, R. turkestanicus, R. brunneus, R. sikkimensis, R. rattus,*[e] *R.* sp.

[a] Number of species is an estimate. Species for Australian and New Guinea regions are those defined by Taylor and Horner (1973) and Taylor, Calaby, and Van Deusen (1982). The rest come from manuscripts by Musser, Musser and Marshall, and Musser and Newcomb. The *Rattus* sp. listed in this table will be named and described in those reports.

[b] Taylor and Horner (1973) treat Australian *R. sordidus* as polytypic: *R. s. sordidus, R. s. colletti,* and *R. s. villosissimus.* To Watts and Aslin (1981, p. 250), there are three species: *R. sordidus,* the canefield rat; *R. colletti,* the dusky rat; and *R. villosissimus,* the long-haired rat. Those authors note that captive *R. villosissimus* "will cross-breed readily with both the dusky rat and the canefield rat, and one of the hybrids has bred. However, these hybrids are likely to have reduced fertility because of the large differences in chromosome numbers between the species (50 in the long-haired rat, 42 in the dusky rat and 32 in the canefield rat). The cross-breeding of the three species in captivity shows that they are closely related, as suggested by Taylor and Horner who considered all three to be subspecies of the canefield rat." *Rattus sordidus* in New Guinea has recently been defined by Taylor, Calaby, and Van Deusen (1982).

[c] Probably includes several species.

[d] Reflects the hypothesis stated in the present report that these may be native to Indochina despite their present distribution throughout the Indo-Australian region.

[e] Includes both the Asian and Oceanic (or European) forms. Some authors treat these as distinct species; Musser and Califia (1982) discuss the problem.

Our uncertainty will remain until the distributions of primitive and shared derived characters are determined for all the African, Asian, and Indo-Australian murids.

Of all the Sundaic genera, *Maxomys* may be closer to *Mus* in the sense of being in the same lineage because *Maxomys* and *Mus* not only share similar molar derivations but species of both genera have elongate hind feet with relatively small and low plantar pads compared with plantar area. All species of mice that we know of are terrestrial as are most species of *Maxomys.* Whether the shared derivations reflect either phylogenetic alliance or convergence, as we explained in the account of *Maxomys,* is unknown; both *Mus* and *Maxomys* need to be compared with other genera outside of the Sunda region. Aside from this possible link to *Maxomys, Mus* has no close relatives on the Sunda Shelf and is likely more tightly linked to genera in Indochina, India, and possibly Africa.

It may be significant that the only species of *Mus* native to the Sunda Shelf are in subgenus *Coelomys.* This supposes we are correct in assuming *M. caroli, M. cervicolor, M. dunni,* and *M. castaneus,* all in subgenus *Mus,* to be introductions to the peninsula and islands of the Sunda Shelf, coming to the Shelf by inadvertent human means. The statement also accepts Marshall's (1977a) subgeneric grouping of *M. vulcani* and *M. crociduroides* as correct. If those two assumptions are valid, the native Sundaic *Mus* appear to be relicts from an earlier time when species of *Coelomys* were more widespread over the Indo-

Malaysian area; distributions of the other species of *Coelomys,* from Ceylon through Indochina, are also relictual in nature.

RATTUS

Chasen (1940) listed 23 species of *Rattus* from the Sunda Shelf (table 33). We recognize four: *Rattus tiomanicus, R. baluensis, R. hoogerwerfi,* and *R. annandalei.*[2] *Rattus tiomanicus* is widespread on the peninsula and islands of the Sunda Shelf. *Rattus baluensis* is recorded only from the mountains of northern Borneo and the western part of central Sumatra. *Rattus hoogerwerfi* is endemic to highlands of northern Sumatra. *Rattus annandalei* occurs on the Malay Peninsula, Singapore, and the islands of Rupat and Padang, off the coast of eastern Sumatra. These four represent 8 percent of the total number (50) of species we estimate that taxonomists now include in *Rattus* (table 57). The other species are native to Australia and the New Guinea region; the Moluccas; Sulawesi; the Philippine Islands; small islands east, south, and west of the Sunda Shelf; Asia north of the Isthmus of Kra; and India.

The monophyly of *Rattus* has yet to be determined. Some groups of species may eventually be disassociated from *Rattus,* such as the native species in the Australian and New Guinea region. There are, for example, no known members of *Rattus* in the Lesser Sunda Islands, a surprise because that archipelago forms an insular link between the Sunda Shelf to the west and Australia and New Guinea to the east. Instead of trying to tie Australian and New Guinea species to those *Rattus* on continental Asia and the Sunda Shelf, Musser (1981b, p. 169) suggested that biologists should test an alternate idea:

> Possibly the *Rattus*-like features characterizing the species in the New Guinea and Australian region are independently derived from those that define the groups of *Rattus* on the Asian mainland. It is plausible that the species now on New Guinea and Australia evolved from a *Rattus*-like ancestral stock that was characterized by a suite of derived cranial and dental features similar to those found in some of the *Rattus*-like genera on Flores. If this speculation proves to be a better interpretation, then perhaps native species of *Rattus* will not be found in the Lesser Sunda Islands.

Whether the content of *Rattus* remains unaltered or is restricted further, the evolutionary histories of most species are associated with geographic regions outside of the Sunda Shelf. This appears to be the picture on the Asian mainland and Indian subcontinent where *Rattus* is primarily an Indian and Asian genus, not Malaysian. In India and Asia north of the Isthmus of Kra, we estimate there to be 10 species of native *Rattus*: *R. norvegicus, R. argentiventer, R. exulans, R. nitidus, R. losea, R. turkestanicus, R. brunneus, R. sikkimensis, R. rattus,* and a new species we are describing elsewhere (Musser and Newcomb, MS.). All of these, although represented by other combinations of names in some cases, are part of the subgenus *Rattus* as envisioned by Ellerman (1941, 1949) and Misonne (1969). Many of the external, cranial, and dental features that we listed for *R. rattus diardii* (see the account of *Palawanomys*) also characterize this group of species. We do not intend here to define the morphological and distributional limits of the group or explain why we recognize the species we do; those are subjects of reports being prepared (Musser; Musser and Marshall, MSS.). We simply point out that in features of skins, skulls, teeth, and sometimes chromosomes most of the species closely resemble one another (figs. 110 and 111; Yosida, 1973; table 2). Some, such as *R. brunneus, R. sikkimensis,* and *R. argentiventer,* for example, were formerly thought to be, at the most, geographic or ecological variants of *R. rattus.* All the species are more similar to each other than to any of the groups of native species now placed in *Rattus* that occur in regions east of Borneo and Bali.

Three of the Sundaic species of *Rattus*—*R. tiomanicus, R. baluensis,* and *R. hoogerwerfi*—are to us morphologically more similar to the 10 Indochinese species than to any

[2] Chasen (1940) included the Thai islands of Samui and Pennan, just south of the Isthmus of Kra, in his Malaysian region. *Rattus rattus robinsoni* and *R. sikkimensis remotus* occur on the islands (Marshall, 1977b; Musser and Marshall, MS.); they are insular variants of species native to Indochina north of the Isthmus of Kra and we exclude them from our list of species found on the Sunda Shelf.

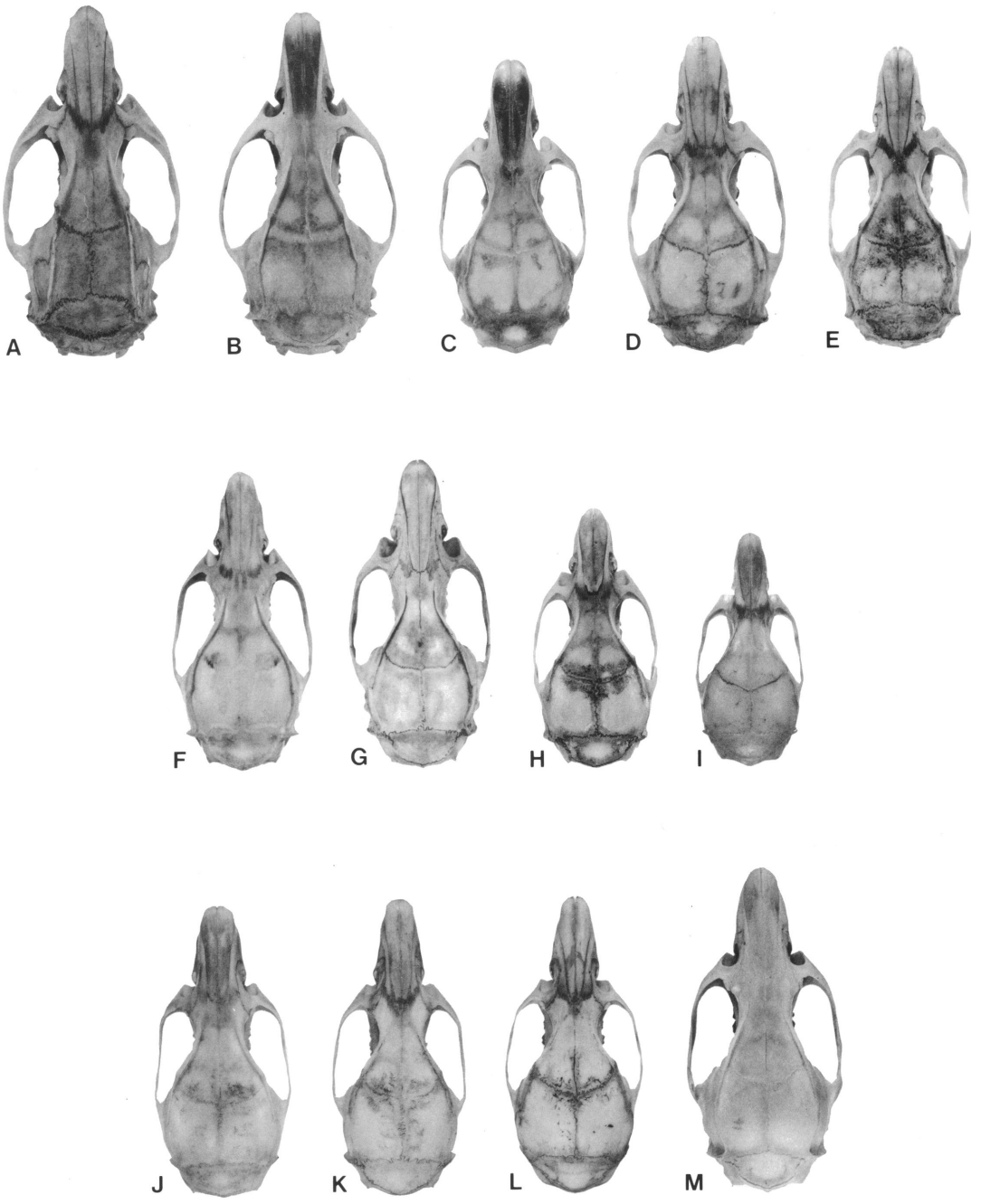

FIG. 110. Dorsal views of crania from adult *Rattus*. A, *R. norvegicus*, Taiwan (AMNH 185196). B, *R. brunneus*, Nepal (AMNH 251647). C, *R. turkestanicus*, Nepal (AMNH 251664). D, *R. sikkimensis*, Thailand (USNM 533456). E, *R. nitidus*, Luzon Island in the Philippines (FMNH 62431). F, *R. rattus*, Thailand (USNM 533641). G, *R. argentiventer*, Bali (AMNH 107543). H, *R. losea*, Hainan Island, southern China (AMNH 59187). I, *R. exulans*, Central Sulawesi (AMNH 215290). J, *R. tiomanicus*, Java (AMNH 250114). K, *R. baluensis*, Sabah (USNM 292693). L, *R. hoogerwerfi*, northern Sumatra (USNM 271028). M, *R. annandalei*, Malay Peninsula (AMNH 217591). Natural size.

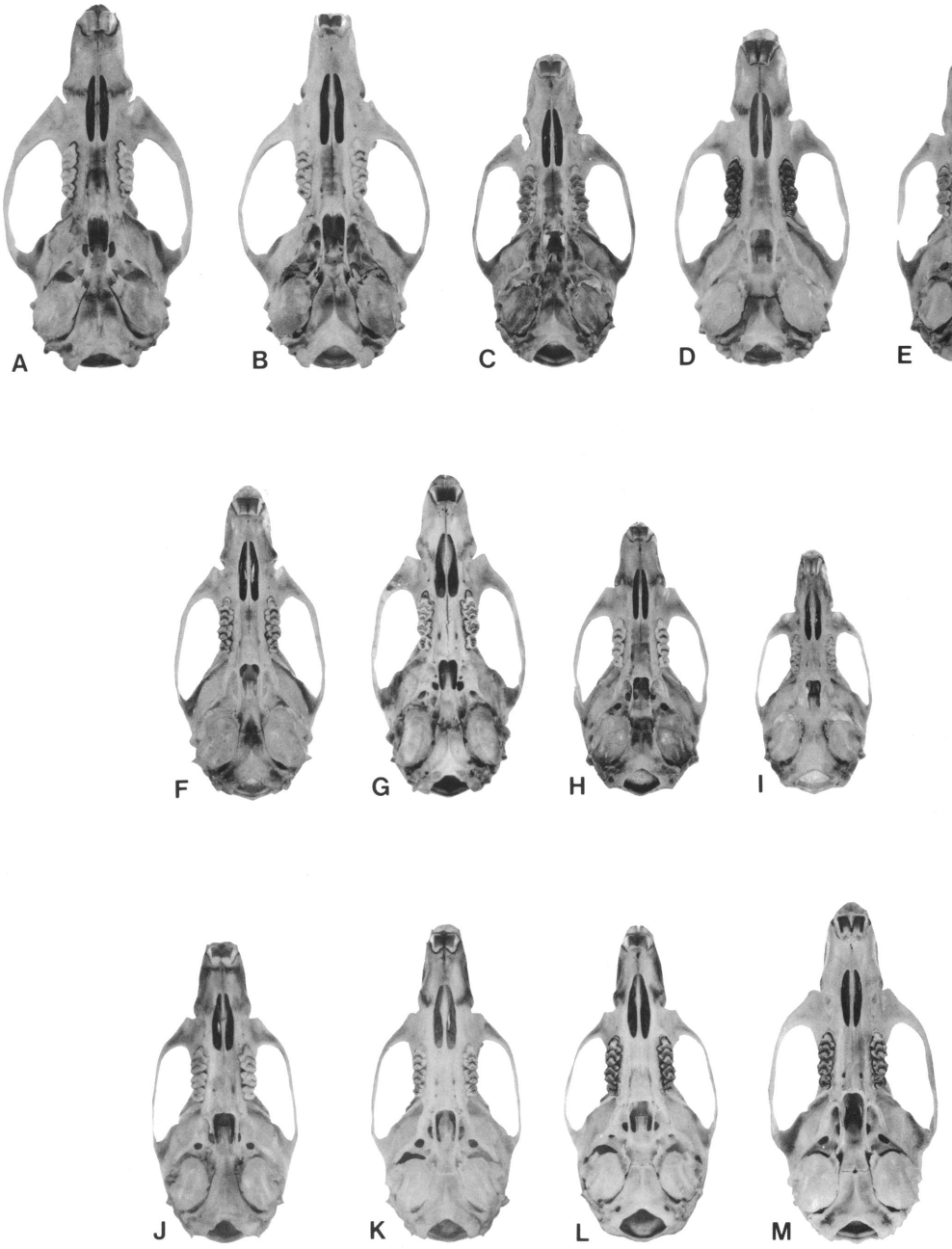

FIG. 111. Ventral views of crania from the same specimens shown in figure 110. A, *R. norvegicus.* B, *R. brunneus.* C, *R. turkestanicus.* D, *R. sikkimensis.* E, *R. nitidus.* F, *R. rattus.* G, *R. argentiventer.* H, *R. losea.* I, *R. exulans.* J, *R. tiomanicus.* K, *R. baluensis.* L, *R. hoogerwerfi.* M, *R. annandalei.* Natural size.

other species of *Rattus* (figs. 110–113; compare these with figs. 13, 88, and 89). *Rattus tiomanicus* is certainly closely related to *R. rattus* and other species in the subgenus *Rattus* (Yong, 1969a; Chan, 1977; Musser and Califia, 1982; Pasteur et al., 1982).

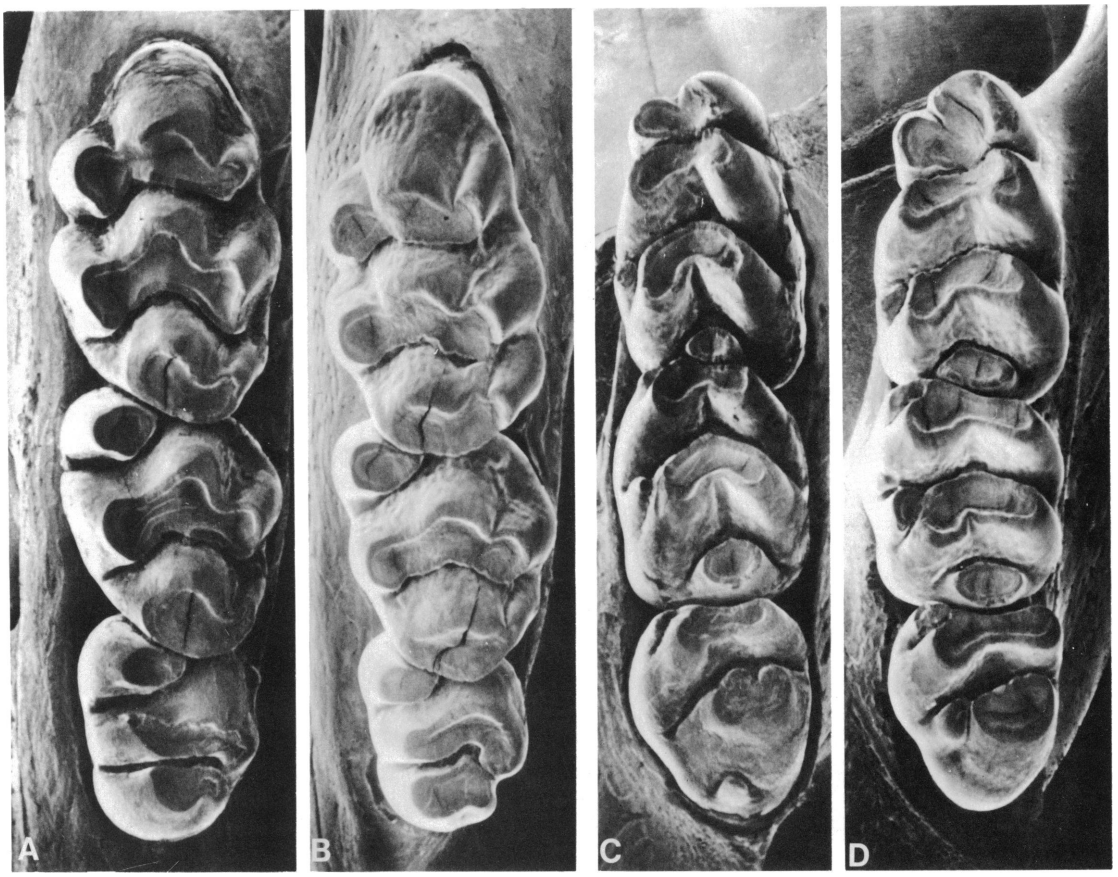

FIG. 112. Occlusal views of left upper (A and B) and lower (C and D) molar rows in Sundanese *Rattus*. A and C, *R. hoogerwerfi* (USNM 271030, CLM^{1-3}, 7.8 mm.; CLM_{1-3}, 7.9 mm.), northern Sumatra. B and D, *R. baluensis* (USNM 292700, $CLM_{1-3}{}^{1-3}$, 6.6 mm.), Sabah.

Rattus baluensis was thought by Misonne (1969) to be close to *R. xanthurus* (p. 136) or *R. muelleri* (p. 143), both of which were placed by him in the subgenus *Bullimus*. He did not regard *R. baluensis* as being part of the subgenus *Rattus*, as he did *R. hoogerwerfi* (p. 136). To us, *R. baluensis* is a morphologically distinctive species but we find no characteristics that would exclude it from close alliance with *R. rattus, R. tiomanicus,* and their allies. And except for its long bicolored tail, different mammae number, and relatively larger molar rows compared with skull length, we see similarity in external, cranial, and dental features between *R. hoogerwerfi* and *R. baluensis*, an alliance earlier suggested by Chasen (1939). We also point out that both live in mountain forests, that *R. hoogerwerfi* has been taken only from northern Sumatra where it appears to be common in the right habitat, and *R. baluensis korinchi* has been found only in the mountains south of the range of *R. hoogerwerfi*. There is a hint here that the two species, through the Sumatran form of *R. baluensis,* may be morphologically and ecologically similar enough that they cannot occur together.

Rattus annandalei is not morphologically close to either *R. tiomanicus, R. baluensis,* and *R. hoogerwerfi* on one hand, or the Indochinese species on the other (figs. 111–114). Large-bodied (table 27) and arboreal (Muul and Lim, 1971), *R. annandalei* is set apart from the species by its relatively large bullae compared with size of skull, bullae that appear inflated, resembling the size and proportions in *Kadarsanomys sodyi* (tables 27, 31, and 42). Several primitive cranial and

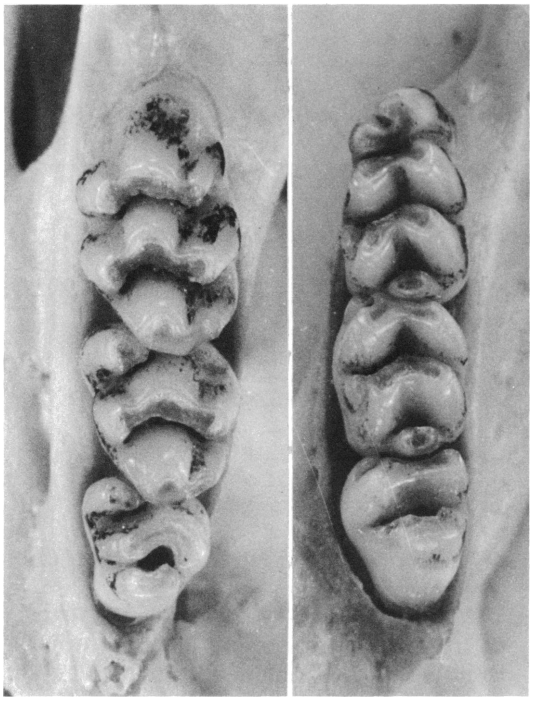

FIG. 113. Occlusal views of left upper (left) and lower (right) molar rows in Javan *Rattus tiomanicus* (AMNH 250124). ×10.

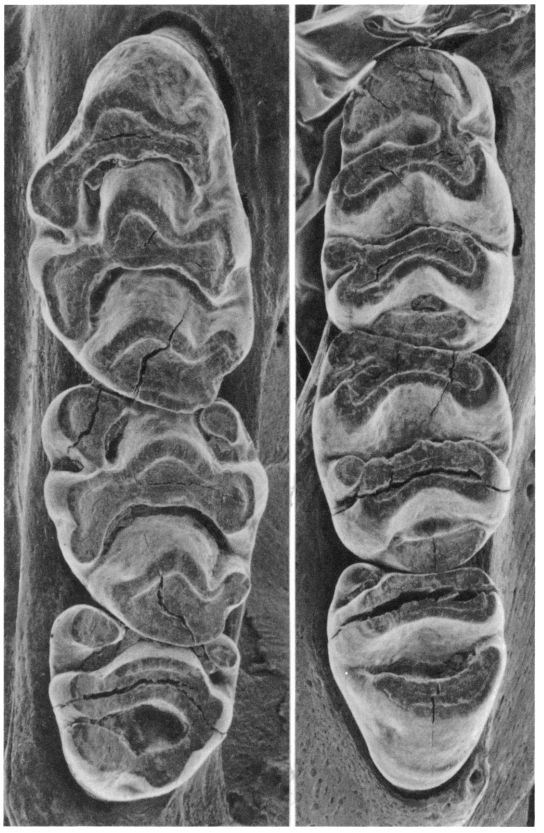

FIG. 114. Occlusal views of left upper (left) and lower (right) molar rows in *Rattus annandalei* (USNM 488871, CLM^{1-3}, 7.4 mm.; CLM_{1-3}, 7.5 mm.), Malay Peninsula.

dental traits, which we already described on pages 518–520, also distinguish *R. annandalei* from the other three Sundaic *Rattus* as well as the Indochinese species. In sum of its features, *R. annandalei* is specialized for living aboveground in secondgrowth forests and similar kinds of habitats (gardens and rubber estates) but is more primitive in some cranial and dental traits than the other Indian, Asian, and Malaysian *Rattus*. Where it fits within the framework of phylogenetic relationships among species of *Rattus* can only be determined after the genus is finally diagnosed and the limits of its species defined.

Out of the 34 traits we examined, the derived condition of 20 are found in *Rattus*, as represented by species in the subgenus *Rattus*, a greater number of derivations than found in any of the other genera known from the Sunda Shelf (table 38). If relative number of derivations compared with number of traits examined reflects the overall primitive or derived nature of rats, then species of *Rattus* are generally more derived than those of other genera. This does not mean that species of *Rattus* are more highly specialized in particular features; for example, none of them have the special adaptations found in such highly specialized arboreal rats as species of *Pithecheir, Hapalomys, Chiropodomys,* and even *Kadarsanomys.*

The distribution of derived traits among *Rattus* on the one hand and the 13 other genera on the other suggest that among them, *Rattus* is phylogenetically closest to *Palawanomys* and *Kadarsanomys,* as we described in previous accounts. *Rattus* shares some derived features with each genus (table 58) but *Palawanomys* is the only one that shares two derivations exclusively with *Rattus*—a long palatal bridge and similar configuration of the mesopterygoid fossa and sphenopalatine vacuities. Other than *Pala-*

TABLE 58
Distribution of Derived Traits in *Rattus* (Subgenus *Rattus*) Among Sundanese Genera

Trait	*Kadar-sano-mys*	*Beryl-mys*	*Pala-wano-mys*	*Nivi-venter*	*Sun-damys*	*Maxo-mys*	*Leo-pol-damys*	*Pithe-cheir*	*Hapa-lomys*	*Mus*	*Chiro-podo-mys*	*Hae-romys*	*Leno-thrix*
SOR	+	–	–	+	+	+	+	+	+	–	+	–	+
Al	+	+	+	–	–	+	–	+	+	–	+	–	–
SB	–	+	+	–	–	–	–	–	–	+	–	–	–
AB	+	+	+	–	–	+	–	–	–	+	+	+	–
IF	+	–	–	+	–	–	–	–	–	–	–	–	–
PB	–	–	+	–	–	–	–	–	–	–	–	–	–
MF	–	–	+	–	–	–	–	–	–	–	–	–	–
PF	+	–	–	–	+	–	–	+	+	–	–	–	–
SptgV	+	–	+	–	–	–	–	–	+	–	+	+	–
PP	+	+	–	–	+	–	–	+	+	–	+	+	+
R-M^1	+	+	–	+	+	–	–	–	–	–	–	–	–
R-M$_1$	+	+	+	+	+	–	+	–	–	–	–	–	–
SM	–	+	+	+	–	+	–	–	–	+	–	–	–
OM	+	+	+	+	+	+	+	+	–	+	–	–	–
t1-M^1	+	–	+	–	+	–	–	–	+	–	–	–	–
UC	–	+	+	+	+	+	+	–	–	+	–	–	–
t4-t5	–	+	–	+	+	+	+	–	–	+	–	–	–
PC	–	+	–	+	–	+	+	–	+	+	–	–	–
t3-M^2-M^3	–	+	–	+	–	+	+	–	–	+	–	–	–
AC	–	+	–	+	+	+	+	–	–	+	–	–	–

wanomys, Rattus has closer affinity to *Kadarsanomys* than with any other genus, but the relationship is distant compared with that between *Rattus* and other genera, such as *Arvicanthis* (Musser, 1981a).

Our present analysis supports the disassociation of *Niviventer, Maxomys,* and *Leopoldamys* from *Rattus* and provides no new information that would alter Musser's (1981a) assessment of the possible phylogenetic relationships between *Rattus* and those three genera. The possible phylogenetic position of *Rattus* relative to *Lenothrix, Pithecheir, Hapalomys, Chiropodomys,* and *Haeromys* reflects that suggested by Misonne's (1969) study of molar cusp patterns: those genera belong in a different group that is not closely related to *Rattus. Berylmys,* although sharing many cranial and some dental derivations with *Rattus,* may be closer to *Niviventer, Leopoldamys,* and *Maxomys,* at least in features of molar occlusal patterns. All 10 of *Sundamys*'s derivations are shared with *Rattus* and relative to that genus *Sundamys* is primitive; it also has cranial and dental derivations not included in the tables that disassociates it from *Rattus.* Finally, *Mus* as exemplified by *M. crociduroides* and *M. vulcani* is phylogenetically far from *Rattus,* a view that clashes with Misonne's (1969) but accords with that of Jacobs (1978) and Jacobs and Pilbeam (1980). Details of these associations or disassociations between *Rattus* and the other genera are presented in other accounts.

Rattus, whatever its ultimate definition, may be closely allied to genera outside of the Sunda region. Those in Africa, such as *Arvicanthis* (Jacobs, 1978; Musser, 1981a), and genera in the Philippine Islands (*Limnomys* and *Tarsomys,* for example), Sulawesi (*Taeromys* and *Paruromys*), and the Lesser Sunda Islands (*Papagomys* and *Komodomys*), have some *Rattus*-like cranial and dental derivations and may prove to be more closely related to *Rattus* than that genus is to any occurring on the Sunda Shelf. Now that the bulk of species of *Rattus* has been taken out of the genus and placed elsewhere, those remaining should be contrasted with other genera of African and Indo-Australian murids to determine their phylogenetic affinities.

Most species of *Niviventer, Berylmys, Mus,* and *Rattus* occur in regions outside of the Sunda Shelf. In *Leopoldamys* and *Hapalomys,* the last to be discussed, there are as many species in Indochina as there are on the Shelf.

LEOPOLDAMYS

These are handsome, large-bodied forest rats with very long tails (table 60). Of the four species, one is endemic to Indochina, one to the Malaysian region, and two are found in both areas (Musser, 1981a). *Leopoldamys neilli* has been recorded from three places in the provinces of Saraburi and Kanchanaburi in southern Thailand well north of the Isthmus of Kra. In two of the localities, the rats were collected from the upper parts of limestone cliffs, at the third place they were found in lowland bamboo forest on a valley floor (Marshall, 1977b; Wiles, 1981). *Leopoldamys siporanus* is known only from south of the Isthmus of Kra on the Mentawai Islands of North Pagai, South Pagai, Sipora, and Siberut. *Leopoldamys edwardsi* and *L. sabanus* occur on the Sunda Shelf and in Indochina.

The genus requires taxonomic review. *Leopoldamys neilli* is morphologically well defined but little is known of either its biology or actual geographic distribution. Morphologically discrete also is *L. siporanus* but whether the phylogenetic relationships of this large-bodied rat are with *L. edwardsi* or *L. sabanus* is unknown. That populations of the large-bodied *L. edwardsi* in Indochina are genetically compatible with those in the mountains of the Malay Peninsula and Sumatra is an assumption, not a conclusion based on hard evidence derived from careful taxonomic study. "There may be two species within what is now classified as *L. edwardsi,*" wrote Musser (1981a, p. 263), who pointed out that samples "from the mountains of Sumatra and the Malay Peninsula differ in several cranial and pelage characteristics from those obtained in northern Indochina [fig. 115]. There is a large hiatus in the geographic range between populations from northern Indochina and those from Malaya [see p. 482 in Marshall, 1977b]. 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." For *L. sabanus,* Musser (1981a, pp. 265–266) asked, "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. 115] and nobody has yet determined whether it reflects insular variation within a single species or the presence of more than one species."

Because of this uncertainty about the actual species diversity of *Leopoldamys,* number of species is no help in determining whether the past evolutionary history of the genus is associated with either the Indochinese or Sudanese regions; evidence at hand suggests *Leopoldamys* has been tied to both areas.

Does the distribution of derived traits among Indo-Malayan murids provide evidence pointing to whether *Leopoldamys* is mainly either Indochinese, Sundaic, or both in its affinities? It is possible. The species of *Leopoldamys* were once regarded as part of *Rattus* until Musser (1981a) pointed out the lack of derived features unique to *Leopoldamys* and *Rattus* and that the two have no close phylogenetic alliance. In Musser's analysis, which was set in the context of evaluating the phylogenetic position of various Indo-Australian genera relative to *Rattus, Leopoldamys* was found to be phylogenetically closer to *Dacnomys, Chiromyscus, Niviventer,* and *Maxomys* than to *Rattus. Dacnomys* and *Chiromyscus* are strictly Indochinese in geographic distribution, *Niviventer* is primarily Indochinese, and *Maxomys* is basically Sundaic.

The close tie to *Niviventer* and *Maxomys* is confirmed in our present analysis of the distribution of derived features among Sundaic genera (table 59). Most of the derived traits shared by these three are associated with simple cusp patterns. *Berylmys* also fits near this group, and among Sundaic murids, *Leopoldamys* is more closely allied to *Niviventer, Maxomys,* and *Berylmys* than to any other genus if the features associated with simple molar occlusal patterns in these genera really indicate close phylogenetic relationship and not patterns independently derived (compare figs. 20, 21, 100, 106, 107, and 116).

Considering all the genera with which *Leo-*

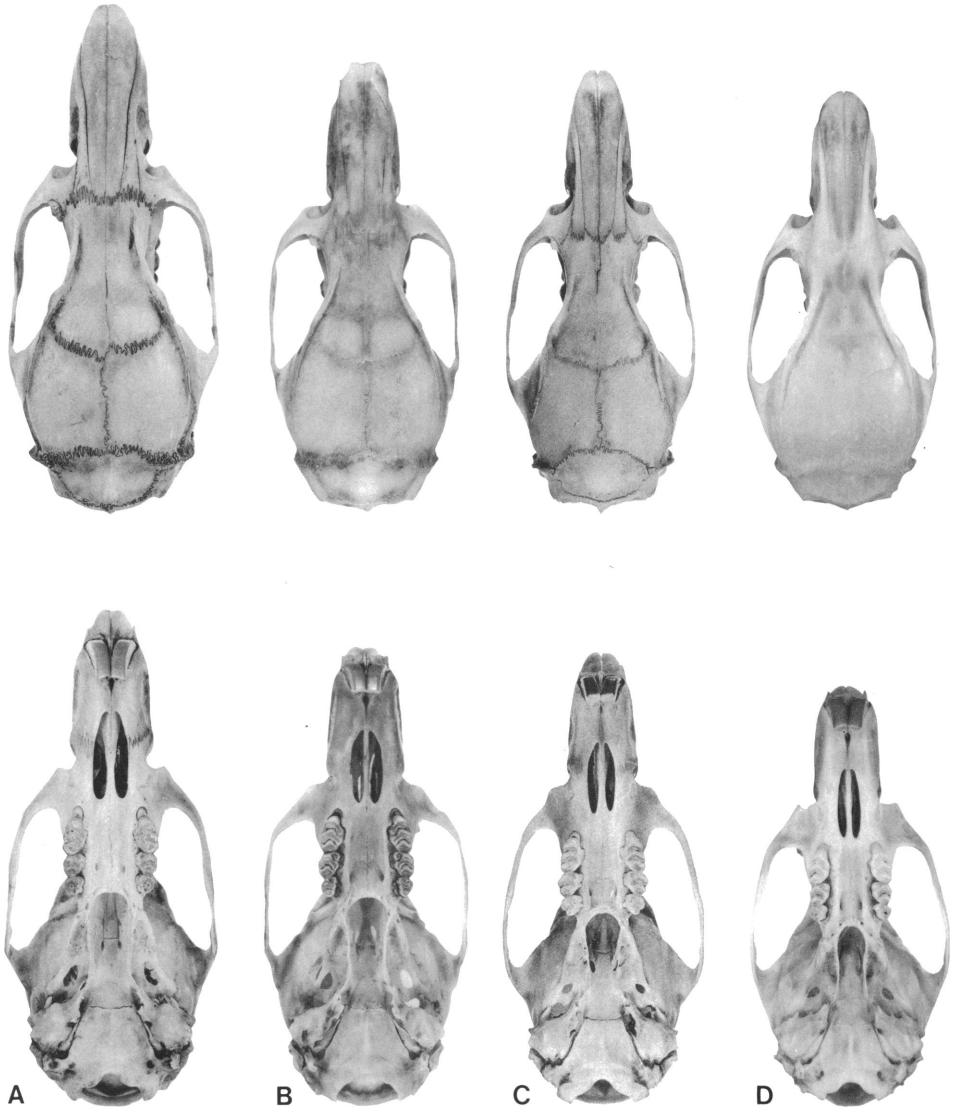

FIG. 115. Crania from adult *Leopoldamys*. A, *L. edwardsi* (AMNH 38337), China. B, *L. edwardsi* (USNM 489004), Malay Peninsula. C, *L. sabanus* (AMNH 135025), Malay Peninsula. D, *L. sabanus* (AMNH 102851), Sumatra. Natural size. Note the difference in size between the Chinese and Malayan specimens of what is now called *L. edwardsi*.

poldamys has been closely tied, four of them (*Dacnomys, Chiromyscus, Niviventer,* and *Berylmys*) are entirely or mostly Indochinese in geographic distribution and probably evolutionary origin; one (*Maxomys*) is primarily Sundaic. Does this mean that *Leopoldamys* too is basically Indochinese? We do not know. We still require more information which a critical taxonomic revision of *Leopoldamys* might provide. We need to compare the characteristics of *Leopoldamys* with other murid genera, and we need to know more about the past geographic distribution and species diversity of the genus as reflected by fossils.

HAPALOMYS

Of medium- to small-size, arboreal habits, and bamboo habitat, *Hapalomys* is Indo-

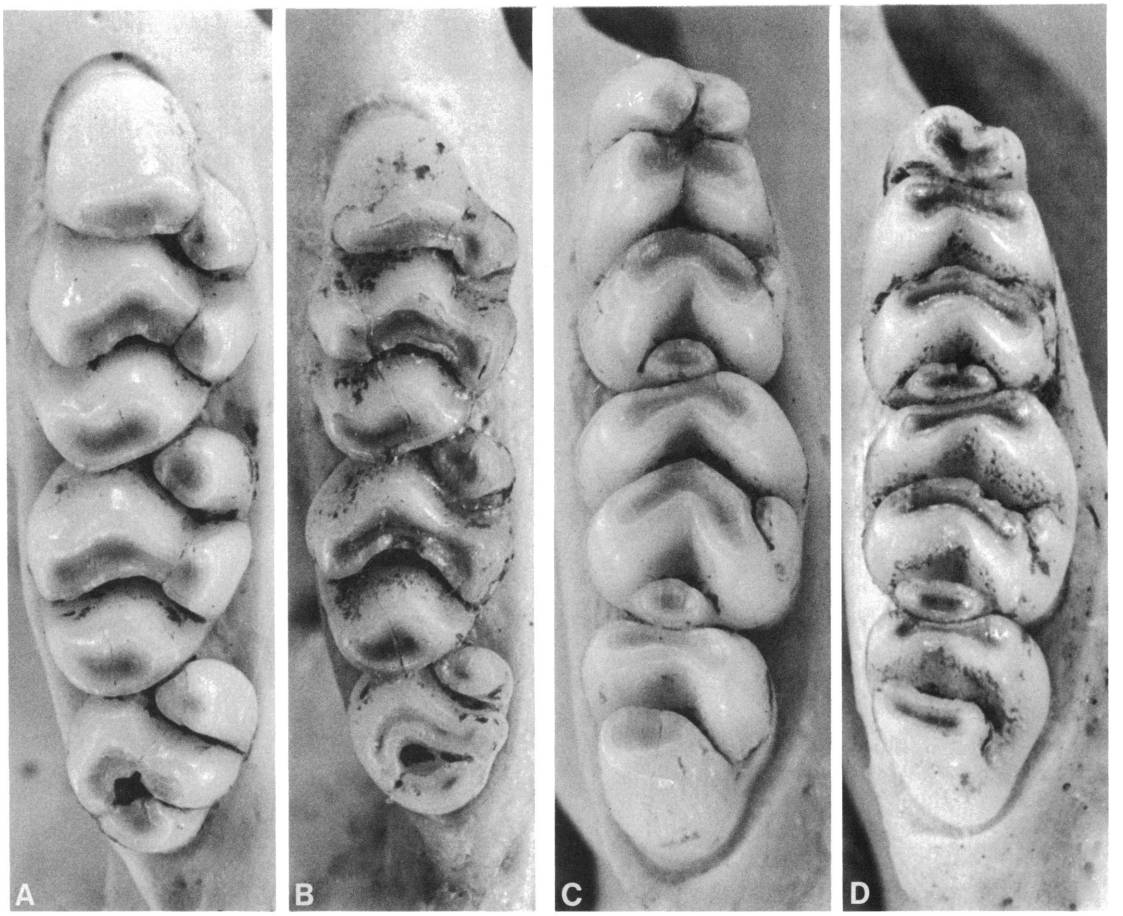

FIG. 116. Occlusal views of right upper (A and B) and lower (C and D) molar rows from *Leopoldamys*. A and C, *L. edwardsi* (AMNH 117426), China. B and D, *L. sabanus* (AMNH 167924), Thailand. All ×10. Compare these with figures 20 and 21 showing molar rows in species of *Berylmys*.

Malayan and contains two species. One, *H. delacouri* is small-bodied and known by a few specimens from Vietnam, northern Laos, and the island of Hainan off the coast of southern China. The other, *H. longicaudatus,* is medium-sized (table 60) and represented by specimens collected in an elongate region from southern Burma south to Selangor State in Malaya (Musser, 1972). On the Sunda Shelf this species has not been recorded from anywhere except peninsular Burma, Thailand, and Malaya. Except for some places in the mountains of the Malay Peninsula where *H. longicaudatus* seems to be common (Medway, 1964; Dr. Illar Muul, personal commun.), it is represented by only a handful of specimens and its actual geographic distribution has yet to be determined. Because there is no species of *Hapalomys* endemic to the Sunda Shelf and because both of the known species occur north of the Isthmus of Kra in Indochina, we are tempted to view the genus as basically Indochinese in its evolutionary history but we do not because we are uncertain whether *H. longicaudatus* is either a Malayan isolate that spread north, or an Indochinese endemic that spread south, or had its entire evolutionary history in the region now represented by specimens (see fig. 12 on p. 23 in Musser, 1972).

The molar cusp patterns of *Hapalomys longicaudatus* (fig. 117) are unique among species native to the Sunda Shelf, as is the nature of its inflated bullae (fig. 102). Many

TABLE 59
Distribution of Derived Traits in Sundaic *Leopoldamys* Among Genera of the Sunda Shelf

Genera	SOR	R-M_1	OM	UC	t4-t5	t9	PC	t3-M^2-M^3	AC	Al-Al	AlC
Niviventer	+	+	+	+	+	+	+	+	+	+	+
Maxomys	+	–	+	+	+	+	+	+	+	+	+
Berylmys	–	+	+	+	+	+	+	+	+	+	+
Rattus	+	+	+	+	+	–	+	+	+	–	–
Sundamys	+	+	+	+	+	–	–	–	+	–	–
Mus	–	–	+	+	+	+	+	+	+	+	+
Kadarsanomys	+	+	+	–	–	–	–	–	–	–	–
Palawanomys	–	+	+	+	–	–	–	–	–	–	–
Hapalomys	+	–	–	–	–	–	+	–	–	–	–
Pithecheir	+	–	+	–	–	–	–	–	–	–	–
Lenothrix	+	–	–	–	–	–	–	–	–	–	–
Chiropodomys	+	–	–	–	–	–	–	–	–	–	–
Haeromys	–	–	–	–	–	–	–	–	–	–	–

of the other derived traits found in *H. longicaudatus* (table 61) are associated with arboreal living in general and probably bamboo in particular (Medway, 1964). Some of these derivations are also shared by *Pithecheir, Chiropodomys, Kadarsanomys,* and *Lenothrix* but as we explained in those accounts particular derivations among them are really not similar and with the possible exception of *Chiropodomys* none of the other genera of

TABLE 60
Measurements and Ratio from Samples of Adult *Hapalomys* and *Leopoldamys* from the Malay Peninsula[a]

Measurement and Ratio	*Hapalomys longicaudatus*	*Leopoldamys sabanus*	*Leopoldamys edwardsi*
Length of head and body	156.6 ± 9.7 140–165 (7)	240.4 ± 1.8 210–260 (50)	251.2 ± 2.8 200–275 (22)
Length of tail	195.3± 9.3 176–203 (7)	369.1 ± 3.1 315–420 (50)	334.6 ± 4.5 310–355 (22)
Length of hind foot	30.0 ± 1.9 28–33 (7)	47.8 ± .3 44–52 (50)	53.2 ± .4 51–56 (22)
Greatest length of skull	39.3 ± 1.5 37.9–41.5 (7)	55.5 ± .6 51.4–60.3 (21)	58.3 ± .6 54.3–62.6 (17)
Length of bulla	8.3 ± .3 7.8–8.6 (7)	5.1 ± .1 4.7–5.6 (21)	5.4 ± .1 5.0–5.6 (17)
Alveolar length of M^{1-3}	7.8 ± .2 7.6–8.0 (9)	9.6 ± .1 8.7–10.3 (21)	10.2 ± .1 9.6–10.7 (17)
Length of bulla/skull length	21	9	9

[a] Measurements are in millimeters, ratio in percentages. Mean plus or minus one standard deviation, observed range, and size of sample in parentheses are listed for each measurement. Values for *Leopoldamys* comes from Yong (1970, p. 362).

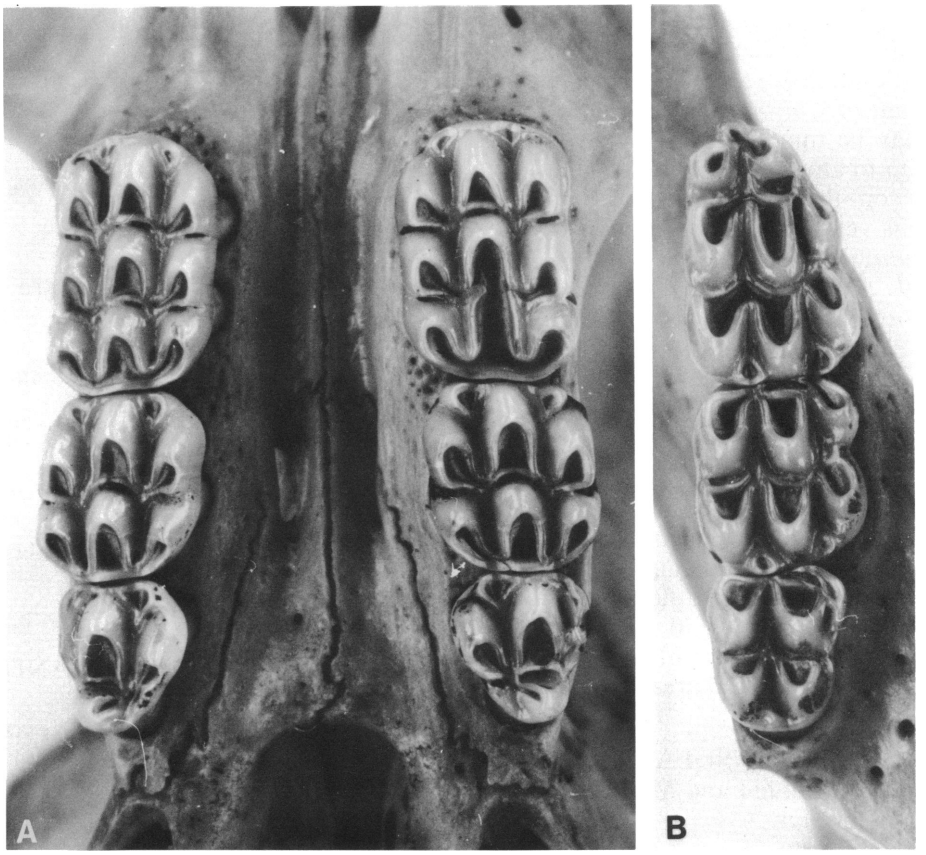

FIG. 117. Occlusal views of both upper (A) and the right lower (B) molar rows of *Hapalomys longicaudatus* (BM 63.1160) from the Malay Peninsula. All ×10.

arboreal rats are closely allied to *Hapalomys*, especially *Kadarsanomys*. Among the arboreal forms, *Chiropodomys* is the only one in which the nail and hallux are similar in con-

TABLE 61

Distribution of Derived Traits in Sundanese *Hapalomys* Among Genera of the Sunda Shelf

Genera	Ha	HF	SOR	Al	SB	PF	SptgV	PP	t1-t2bis	t1-M¹	RC	t7	PC
Pithecheir	–	+	+	+	+	+	–	+	+	–	–	+	–
Chiropodomys	+	+	+	+	–	–	+	+	+	–	–	+	–
Kadarsanomys	–	+	+	+	–	+	+	+	–	+	–	–	–
Rattus	–	–	+	+	–	+	+	+	–	+	–	–	+
Lenothrix	–	+	+	–	–	–	–	+	+	–	–	+	–
Haeromys	–	–	–	–	–	–	+	+	+	–	–	–	–
Palawanomys	–	–	–	+	–	–	+	–	+	+	–	–	–
Berylmys	–	–	–	+	–	–	–	+	–	–	–	–	+
Sundamys	–	–	+	–	–	+	–	+	–	+	–	–	–
Maxomys	–	–	+	+	–	–	–	–	–	–	–	–	+
Niviventer	–	–	+	–	–	–	–	–	–	–	–	–	+
Leopoldamys	–	–	+	–	–	–	–	–	–	–	–	–	+
Mus	–	–	–	–	–	–	–	–	–	–	–	–	+

figuration to that in *Hapalomys*. The two genera also share other derived cranial and dental features (table 60) and, as we indicated in the account of *Chiropodomys*, it and *Hapalomys* may be more closely related to each other than to any of the other genera known to occur on the Sunda Shelf. *Hapalomys* clearly has very little in common with *Mus, Leopoldamys, Niviventer, Maxomys, Sundamys, Berylmys, Palawanomys, Haeromys,* and *Rattus* (table 60).

RELATIONSHIPS AMONG SPECIES, ISLANDS, PENINSULA, AND INDOCHINA

Some of the 40 species from the Sunda Shelf are endemic either to the peninsula or a large island. Others occur in various combinations on the peninsula and islands. Certain species are found in different combinations on the peninsula and islands and in Indochina. These geographic relationships between species and land areas are listed below.

PENINSULAR OR INSULAR ENDEMICS

Peninsula: Thailand and Malaya
- *Maxomys inas*
- *Pithecheir parvus*

Sumatra
- *Rattus hoogerwerfi*
- *Mus crociduroides*
- *Maxomys inflatus*
- *Maxomys hylomyoides*

Borneo
- *Maxomys alticola*
- *Maxomys ochraceiventer*
- *Maxomys baeodon*
- *Chiropodomys muroides*
- *Chiropodomys major*
- *Haeromys margaretae*
- *Haeromys pusillus*

Java
- *Sundamys maxi*
- *Mus vulcani*
- *Niviventer lepturus*
- *Maxomys bartelsii*
- *Pithecheir melanurus*
- *Kadarsanomys sodyi*

Palawan Area
- *Palawanomys furvus*
- *Maxomys panglima*
- *Chiropodomys calamianus*
- *Haeromys* sp.

PENINSULAR AND INSULAR COMBINATIONS

Sumatra and Borneo
- *Rattus baluensis*
- *Sundamys infraluteus*

Peninsula and Sumatra
- *Rattus annandalei*

Peninsula, Borneo, and Sumatra
- *Lenothrix canus*
- *Niviventer rapit*

Peninsula, Borneo, Sumatra, Small Island Groups
- *Maxomys rajah*
- *Maxomys whiteheadi*

Widespread on Shelf except Java and Bali
- *Sundamys muelleri*

Widespread on Shelf except Palawan Area
- *Niviventer cremoriventer*

Widespread on Shelf
- *Rattus tiomanicus*

PENINSULAR, INSULAR, AND INDOCHINESE COMBINATIONS

Widespread on Sunda Shelf (except Palawan Area) and Indochina
- *Leopoldamys sabanus*
- *Maxomys surifer*
- *Chiropodomys gliroides*

Peninsula, Sumatra, Java, Bali and Indochina
- *Niviventer bukit*

Peninsula, Sumatra, and Indochina
- *Berylmys bowersii*
- *Leopoldamys edwardsii*

Peninsula and Indochina
- *Hapalomys longicaudatus*

We made three assumptions in preparing the above list. First, when we refer to the peninsula and one or more of the large Sunda islands, we also include the small offshore islands associated with the larger land area. We assume that populations of a certain species occurring on both the larger land mass and the nearby offshore islands represent the same species. We also assume that if a species has been recorded solely from some offshore islands that it probably will be found on the mainland. *Lenothrix canus* is an example. We record it from mainland Borneo and Malaya and our Sumatran record is from the

Banjak Islands off the western coast of Sumatra.

Second, indicating that a species does not occur on the peninsula or a particular island assumes that the area has been reasonably well explored by biologists and the lack of specimens reflects a real absence of the species. This assumption is valid for some species that are easily obtained wherever they occur but it may be unwarranted for many others that are difficult to trap. *Pithecheir* is an example. There is a species on the Malay Peninsula and one on Java. We record it as absent from Borneo and Sumatra but the rat has been so rarely captured except by persons thoroughly familiar with their habits and habitat that the casual or general collector would miss it and may have missed in on those two large islands, especially on Sumatra. It is our experience that for small mammals, Sumatra remains one of the larger Sunda islands requiring more intensive exploration. We see no reason why future collectors should not find samples of not only *Pithecheir* there but also of *Lenothrix* and species of *Chiropodomys* other than *C. gliroides,* which is the only species currently recorded from the island (Musser, 1979).

A species may have occurred on the peninsula or a particular island at one time but does not now because its habitat was either modified or destroyed. Unless the rat was collected before that kind of change, we would not know it existed unless some other kind of evidence pointed to the species, such as skeletal remains that date to prehistoric or older times. We do not know how large the native murid fauna of Java, for example, really is because so much of the lowland forest was removed from that island before serious collectors began to survey small mammal populations there. On Java subfossil prehistoric fragments will be important to understanding the actual murid fauna there. Even now prehistoric specimens have provided information about the former distribution on Java of one endemic, *Kadarsanomys sodyi.* If it was only known from recent specimens, we would say that it was confined to the volcanoes of western Java, but prehistoric examples from lowland caves in the central and eastern sections of Java indicate that the rat once had a much wider distribution over the island. Our list of species known to occur on the Sunda Shelf includes records based on correctly identified subfossil specimens.

Several species occur in different combinations on the peninsula, islands, and in Indochina. *Leopoldamys edwardsi, L. sabanus, Chiropodomys gliroides,* and *Maxomys surifer* are examples. *Chiropodomys gliroides* has been studied (Musser, 1979) but the others require careful taxonomic revision. Our third assumption is that samples of each of these taxa represent a single species occurring both north and south of the Isthmus of Kra. This, however, may not be so. Specimens of both kinds of *Leopoldamys* and *Maxomys surifer* from Indochina differ from those obtained on the Sunda Shelf in several characters (Musser, Marshall, and Boeadi, 1979; Musser, 1981a). Whether the distinctions reflect reproductive isolation or geographic variation within one species composed of genetically compatible populations is not yet known.

Among species of murids, there is a pattern of endemicity on the Shelf. No species are endemic to the smaller islands and Bali; as far as its murid fauna is concerned, Bali is a small island off the coast of Java containing a depauperate Javan fauna. The lowest endemicity both in actual number of species and percentage of total murid fauna is associated with peninsular Thailand and Malaya, which represents the physical extension of mainland Indochina onto the Shelf. Out of the 17 species known from the peninsula, two are endemic and the rest are nearly equally divided among those indigenous to the Shelf and those found also in Indochina north of the Isthmus of Kra (table 36).

Four out of the 20 species recorded from Sumatra are endemic to that elongate island, 20 percent of the murid fauna. The relative number of endemics compared with the total known to occur on the island is slightly greater than that of the peninsula but much less than the relative figures for Borneo, Java, and the Palawan area (table 36). Of the Sumatran murids 50 percent consists of those species indigenous to the Sunda Shelf: *Rattus tiomanicus, R. baluensis, R. annandalei, Sundamys muelleri, S. infraluteus, Niviventer cremoriventer, N. rapit, Maxomys rajah, M.*

whiteheadi, and *Lenothrix canus.* All but *R. baluensis* and *S. infraluteus* are shared with the Malay peninsula. Six species in the Sumatran fauna also occur in Indochina (*Leopoldamys sabanus, L. edwardsi, Maxomys surifer, Chiropodomys gliroides, Berylmys bowersii,* and *Niviventer bukit*; all of these also occur on the peninsula.

Borneo has more actual murid endemics than any other place (seven out of 19 species). About half of the fauna occurring on that large island consists of species indigenous to the Shelf. The percentage (47) is similar to that of indigenous species recorded from Sumatra and the peninsula. Borneo shares all of its indigenous Shelf species with Sumatra; *Rattus annandalei* occurs on Sumatra but not on Borneo. Borneo and the Malay peninsula share seven indigenous Shelf species: *Lenothrix canus, Niviventer rapit, N. cremoriventer, Maxomys rajah, M. whiteheadi, Sundamys muelleri,* and *Rattus tiomanicus*; present on Borneo but absent from the peninsula are *Rattus baluensis* and *Sundamys infraluteus.* Compared with the total murid fauna native to Borneo, there are relatively few species (three out of 19) that also are found off the Shelf in Indochina: *Leopoldamys sabanus, Maxomys surifer,* and *Chiropodomys gliroides.* All occur on the peninsula and islands on the Shelf except in the Palawan region. *Niviventer bukit, Berylmys bowersii,* and *Leopoldamys edwardsi* occur in Indochina as well as on the peninsula and Sumatra but are absent from Borneo. *Hapalomys longicaudatus* is both Indochinese and peninsular and is not known from Borneo.

Java is much smaller than Borneo and has only 12 species as opposed to 19 but half of these are endemic, a much higher percentage than that characterizing Borneo. Whereas on Borneo, Sumatra, and the peninsula about half of the native fauna consists of species indigenous to the Shelf, indigenous species comprise only 17 percent (two out of 12 species) of the Javan fauna; of the two species, *Rattus tiomanicus* is widespread on the islands and peninsula of the shelf and *Niviventer cremoriventer* occurs on the peninsula and most islands except in the Palawan area. Four out of the 12 Javan species (33 percent), a greater percentage than on Borneo and more similar to the percentages on Sumatra and the peninsula, are also found in Indochina: *Leopoldamys sabanus, Maxomys surifer, Chiropodomys gliroides,* and *Niviventer bukit.* All these species also occur on Sumatra and the peninsula, and all but *N. bukit* are found on Borneo. Basically, half of the Javan fauna is composed of endemics (among them an endemic genus) and the other half of species that are widespread over the Shelf (except for five of the six species in the Palawan area).

Aside from Bali, the Palawan region has the fewest native species but at the same time it has the highest percentage of endemics. Four out of six species in the region are endemic and one is in an endemic genus. One of the other two species, *Rattus tiomanicus,* is widespread over the Shelf and the other, *Sundamys muelleri,* occurs on the peninsula and most of the islands except Java and Bali. To date no native species have been found on Palawan that are also found in Indochina.

The high relative number of endemics compared with the total murid fauna of Java and the Palawan region may indicate long isolation of these areas from the other major Sunda islands and the peninsula. Reinforcing such a view is the absence from both Java and Palawan of species that occur on the peninsula and most islands of the Shelf. *Maxomys rajah* and *M. whiteheadi,* for example, are found on the peninsula, Sumatra, Borneo, and some smaller island groups (among them the Riau and Lingga archipelagos) but have never been collected on Java or any of the islands in the Palawan area. *Sundamys muelleri* occurs on the peninsula, most large Sunda islands, many small ones, and in the Palawan region but not on Java. Widespread over the Shelf are *Niviventer cremoriventer, Leopoldamys sabanus, Maxomys surifer,* and *Chiropodomys gliroides* but not one of these has ever been taken on Palawan or nearby island groups.

The close interrelationship among the Malay peninsula, Sumatra, and Borneo as contrasted with the relative isolation of Java can be looked at from another perspective. Among the indigenous Shelf species, two (*Rattus baluensis* and *Sundamys infraluteus*) are shared by Sumatra and Borneo, one (*Rattus annandalei*) occurs on Sumatra and the peninsula, and two (*Lenothrix canus* and *Niviventer rapit*) are shared by Sumatra, Borneo, and the

peninsula. There is not one species shared by either Sumatra and Java, Borneo and Java, or the peninsula and Java; and no species are common to the peninsula, Borneo, Sumatra, and Java.

One species occurs in Indochina and is common to the peninsula, Sumatra, Java, and Bali but not Borneo: *Niviventer bukit.* Why this widespread rat does not occur on Borneo is a mystery. The other two species of *Niviventer* on that large island are *N. cremoriventer* and *N. rapit*; both also occur on Sumatra and the peninsula along with *N. bukit* so the effects of competition among species of *Niviventer* may not explain the absence of *N. bukit* from Borneo. If the presence of *N. bukit* on the Shelf results from dispersal rather than vicariance, it may not have become established in the Bornean region because suitable habitats were already occupied by another species whose habits and habitat needs were too similar to those of *N. bukit.* The Bornean endemic, *Maxomys ochraceiventer,* is such an animal. It is similar in body size to that of *N. bukit* (see tables 45 and 51) and lives in forests throughout an altitudinal range extending from coastal lowlands to mountains (Medway, 1965). In trying to explain the absence of a species on either the peninsula or an island that is otherwise widespread on the Shelf, the possibility of habitats already occupied by another species with similar resource requirements must be considered.

Other associations between species, peninsula, and islands can be gleaned from our list and table 36, relationships we do not pursue here. We have already pointed out how some species can be used to estimate possible faunal affinities among the peninsula and islands of the Sunda Shelf. Using certain combinations of indigenous species, Borneo, Sumatra, and the peninsula, for example, seem more closely related to each other than any is to Java. But to obtain good estimates of faunal similarities and dissimilarities among the land areas will require analyses of all mammals, not just rats and mice. Possibly in that analytical context, our data will be more illuminating and will help provide finer resolution to the faunal patterns on the Shelf.

REFLECTIONS

Patterns of phylogenetic relationships and geographic distributions of native murids were hidden in the expansive definition and varied content of *Rattus* as that genus was viewed by taxonomists working during the 1940s, 50s, and 60s. Patterns characterizing native rats and mice of the Sunda Shelf were no exception. By careful study of specimens and by looking at distributions of shared derived traits among Indo-Malayan murids we and others (Misonne, 1969; Musser, 1981a, 1981b, 1981c, 1982a, 1982b) have drastically altered the dimensions and content of *Rattus* and uncovered some of the phylogenetic and distributional patterns of species on the Sunda Shelf and outside the region. The alteration has also revealed a greater diversity of genera on the Sunda Shelf than taxonomists ever realized. The unique traits and endemic distributions of *Lenothrix, Sundamys,* and *Kadarsanomys* were once hidden in the definition of *Rattus.* Species of *Niviventer, Leopoldamys, Maxomys,* and *Berylmys* form patterns of relationships and distributions that were not apparent when they were included in various subgenera of *Rattus.*

Along with this new picture of generic diversity comes outlines of patterns unseen before. One is the contrast between primitive and derived genera. *Lenothrix* and *Haeromys* have the fewest derivations among the characters we surveyed and the species in these genera may be among the most primitive on the Sunda Shelf. The primitive nature of *Lenothrix* was earlier recognized by Misonne (1969). *Lenothrix* has a relatively large third molar compared with sizes of the other teeth in each row; for Misonne (1969), this large molar is primitive but for Jacobs (1978), it is a derivation. Contrasted with *Lenothrix,* the third molars in *Haeromys* are relatively smaller compared with sizes of other teeth and the proportion is more similar to what Jacobs (1978) would expect in primitive dentitions. If his is a better estimate than Misonne's, *Haeromys* stands even farther from *Lenothrix* in overall suites of primitive features.

Among Sundanese murids, the species in subgenus *Rattus* have the most derivations of all the characters we surveyed. *Rattus* does not have the unique specializations found in some Sundaic species with fewer derived traits, such as *Kadarsanomys, Chiropodomys, Pithecheir,* and *Hapalomys,* for example; but overall, *Rattus* is more derived than any of the other genera.

Another pattern is formed from phylogenetic alliances among the genera as suggested by distributions of shared derived features. Species of *Lenothrix, Pithecheir, Chiropodomys,* and *Hapalomys* cluster because they share a cusp t7 and either cusp t1bis, t2bis, or both. Cusp t7 is present and large in all specimens of *Pithecheir, Chiropodomys,* and *Hapalomys* we studied but not in every *Lenothrix*; in some specimens of that genus the cusp is represented by a nubbin on a lingual ridge between cusps t4 and t8. We did not score *Haeromys* as having cusp t7 but noted that in many specimens of that genus there are lingual ridges between cusps t4 and t8 supporting nubbins which may be comparable to a cusp t7. If that kind of structure is homologous with cusp t7 then *Haeromys* should also be added to the group for it also has cusps t1bis and t2bis. All these species live in forests. All are arboreal to some degree and some of the most highly specialized traits associated with arboreal habits are found among them (the species of *Pithecheir* and *Hapalomys,* for example). Aside from the derivations associated with arboreal living, all the species have a large suite of primitive features and species in *Lenothrix* and *Haeromys* are the most primitive of all the rats and mice found on the Sunda Shelf. *Lenothrix, Pithecheir, Chiropodomys, Hapalomys,* and *Haeromys* were also brought together by Misonne (1969) who placed them in his *Lenothrix-Parapodemus* Division.

We see patterns of alliances within this cluster of five genera. *Lenothrix* and *Pithecheir,* both endemic to the Shelf, may be more closely allied to each other than to any other genus on the Shelf. Outside the Shelf, the close relatives of *Lenothrix* may be the Sulawesian *Lenomys, Eropeplus,* and *Margaretamys* (Musser, 1981a, 1981b). *Chiropodomys,* which is primarily Sundaic, and *Hapalomys,* with a species on the Shelf and one in Indochina, form another pair. *Haeromys,* Sundaic and Sulawesian in distribution, is isolated from all of them but may be distantly linked to *Chiropodomys* through the derivations shared by both; *Haeromys* may be more closely related to *Anonymomys* on Mindoro Island than to any genus on the Sunda Shelf. Although *Chiropodomys* is nearer *Hapalomys* than any other genus of the Shelf, it may have stronger phylogenetic links to genera outside the Sunda region for both Ellerman (1941) and Misonne (1969) claim it to be closely related to *Vernaya, Vandeleuria,* and *Micromys.*

Niviventer and *Leopoldamys* form another cluster. The species in it are held together primarily by the derived dental traits they share. *Niviventer* has its closest phylogenetic affinities with *Chiromyscus* and *Dacnomys,* genera indigenous to Indochina, not the Sunda Shelf (Musser, 1981a). Like the species in those genera, most species of *Niviventer* are found in Indochina. Of the murids recorded from the Shelf, species of *Leopoldamys* (which has as many species in Indochina as on the Sunda Shelf) may be more tightly linked with those of *Niviventer* than with species in any other genus, an estimate of relationships suggested in an earlier analysis (Musser, 1981a).

Maxomys is primarily Sundaic and Sulawesian in geographic distribution and has no counterpart in Indochina unless it is *Niviventer,* with which it shares overlapping molars and simple molar occlusal patterns. If these features reflect phylogenetic alliance and not convergence, *Maxomys* is nearer *Niviventer* and its allies than *Lenothrix* and the other genera in Misonne's (1969) *Lenothrix-Parapodemus* Division. *Maxomys* has some of the same dental derivations and specializations associated with the hind feet that are found in native Sundaic *Mus,* subgenus *Coelomys.* Again, there is the problem of distinguishing between actual relationship indicated by shared derivations or convergence. Among rats and mice on the Sunda Shelf, the native species of *Mus* are probably more closely related to genera outside of the Sunda region than to any found on the Shelf, including *Maxomys* to which subgenus *Coelomys* may be distantly linked.

Niviventer, Leopoldamys, Maxomys, as well as the Indochinese *Dacnomys* and *Chiro-*

myscus, are not closely related to *Rattus* as Misonne (1969) indicated. Our results reflect those from an earlier analysis of shared derived traits in which *Rattus* was found to be far removed from this group (Musser, 1981a). *Mus,* also placed close to *Rattus* by Misonne (1969), shows no close phylogenetic relationship to that genus in our study, a view according with that seen by Jacobs (1978) and Jacobs and Pilbeam (1980).

We detect no tight phylogenetic link between *Berylmys* and *Sundamys* even though the Malayan *S. muelleri* has been closely associated with Malayan *B. bowersii* (Ellerman, 1961). *Berylmys* is primarily Indochinese in distribution, *Sundamys* is Sundaic. One species of *Sundamys* has a specialized carotid arterial pattern and large sphenopterygoid vacuities but otherwise the species in the genus have few derived traits among those we surveyed and all of them are also found in *Rattus* (except for a few we did not include in our analysis). *Sundamys* has no close phylogenetic counterpart in Indochina. Although it is generically distinct from genera on Sulawesi, *Sundamys* may have links to that fauna, a supposition that will have to be tested. Among genera recorded from the Shelf, *Sundamys* may be closer to *Kadarsanomys* and possibly *Rattus* than to any of the others, being more primitive than either one and still phylogenetically distant. If there is such a cluster as genera that could be called a *Rattus* Division, as Misonne (1969) tried to bring together, *Sundamys* may be a primitive member of it.

Kadarsanomys, endemic to Java, may also fit into such a group. It has many derivations associated with arboreal habit in general and life in bamboo in particular that are not found in *Rattus*; some of its other derivations are also shared by *Rattus* but in other features *Kadarsanomys* is more primitive. Aside from a possible link to *Rattus* on one hand and *Sundamys* on the other, *Kadarsanomys* has no close relative on the Sunda Shelf. It should be compared with genera found off the Shelf, especially those in the Philippine Islands, Sulawesi, and the Lesser Sunda Islands.

Although unique among Sundaic murids in features of its dentition, *Palawanomys,* known only from Palawan Island, may be more closely related to *Rattus* than to any other genus on the Sunda Shelf. It is more primitive than *Rattus* in some of its dental and pterygoid traits but it shares two derivations with *Rattus* that are not found in any other genus on the Shelf: spacious sphenopalatine vacuities and an expansive extension of the palatal bridge posterior to the molar rows. *Palawanomys* is another genus whose traits should be compared with those in genera native to archipelagos east of the Sunda Shelf.

We return to *Rattus.* Defining the Giant Rats of Sumatra and discovering the generic diversity on the Sunda Shelf and the peninsular and insular distributions of species south of the Isthmus of Kra has really been a part of revealing the monophyly of *Rattus.* The genus, at least subgenus *Rattus,* is turning out to be primarily Indian and Indochinese in geographic distribution, not Malaysian. Native species of *Rattus* on the Sunda Shelf comprise a small part of the Sundaic fauna. Distributions of shared derived features suggest *Rattus* may be allied with *Palawanomys,* less closely with *Kadarsanomys,* and distantly with *Sundamys*; *Rattus* has no other phylogenetic allies on the Shelf.

The definition of *Rattus* is still unresolved and relationships of the genus to other genera are still obscure. To really understand where *Rattus* fits within the array of phylogenetic relationships among African and Indo-Australian murids, the genus will have to be compared with those outside of the Sunda region. That kind of study is more feasible now than before because the murids native to Africa and the continents and archipelagos in the vast region from India to Australia and the New Guinea region are better known than they once were, partly because the identities, special characteristics, and endemic distributions of some, once obscured by their inclusion within *Rattus,* have now been revealed. *Rattus* may have closer phylogenetic alliances with some of these genera outside the Sunda region than with those recorded from the Shelf.

The Giant Rat of Sumatra exists. *Rattus* is not the dominant genus of murids on the Sunda Shelf. The Sundaic fauna is more diverse at the level of species and genera than was thought. The majority of Malaysian species are endemic to the peninsula and is-

lands of the Shelf, only a few also occur in Indochina. We have illuminated these aspects of the Sundanese murid fauna. What we have intentionally ignored is inquiry into past climatic and tectonic events that may provide background for understanding distributions and phylogenetic relationships among the murids as we see them today. This should be the subject of another study, one that includes data from biogeography of all the native Sundaic mammals, not just rats and mice. Data should come from groups that are taxonomically revised so there is some estimate of relationships among species on the Sunda islands and the peninsula; now such information is unavailable for many groups of mammals, including murids such as *Maxomys* and *Leopoldamys*.

There is much to learn.

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