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Species-limits of *Rattus cremoriventer* and *Rattus langbianis*, Murid Rodents of Southeast Asia and the Greater Sunda Islands

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ABSTRACT

Morphologic and geographic species-limits of *Rattus cremoriventer* and *R. langbianis* are outlined in the present report. *Rattus cremoriventer* is polytypic (five subspecies) and is recorded from peninsular Thailand and Malaya and some offshore islands, Nias Island, Sumatra, Bangka and Billiton islands, Java, Bali, and Borneo and some of its offshore islands. The species has been collected only in forests and is mostly arboreal and nocturnal. The monotypic *R. langbianis* is morphologically closely related to *R. cremoriventer* and its known geographic distribution extends from eastern India through Burma, Thailand, and Laos to North and South Vietnam. It, too, is a forest animal but little is known of its habits. Thirteen scientific names, including *langbianis*, have been allocated to *R. cremoriventer* by past workers. These names are discussed and properly reallocated in this paper.

Among species of rats native to Celebes is *Rattus beccarii*, a small animal about the size of the Polynesian rat *R. exulans*. It has grayish brown upper parts and white underparts. The pelage is a mixture of spiny and soft hairs. The tail is much longer than the head and body, brown everywhere, and penicillate. The hind feet are short and broad with large plantar pads. Judged from its morphological features, *R. beccarii* is arboreal. The species is known by only a handful of specimens (Musser, 1971) and has been con-

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sidered by some authors (Tate, 1936; Ellerman, 1949) to be the representative on Celebes of *R. cremoriventer*, a rat with about the same body size and configuration and one that lives in forests of Southeast Asia and various islands on the Sunda Shelf.

To test the hypothesis that *Rattus beccarii* is the Celebesan counterpart of *R. cremoriventer*, I have first tried to understand what the morphologic, geographic, and if possible, ecologic limits of *R. cremoriventer* are. This is a prerequisite to a comparative study of *R. beccarii* and *R. cremoriventer*. This step led me to examine specimens of *R. cremoriventer* in collections of museums, and to re-evaluate all taxa that have been associated with that species. Such a firsthand study is necessary because information about species-limits of *R. cremoriventer* is not available in the literature, despite the many published checklists and faunal studies that include *R. cremoriventer* and its allies. The present paper is a report on the morphological and geographic nature of *R. cremoriventer* and its close relative *R. langbianis* and a clarification of their taxonomy.

Abbreviations and Methods

Specimens I studied are in collections of the following institutions:

AMNH, the American Museum of Natural History, New York
ASRCT, Applied Scientific Research Corporation of Thailand (Centre for Thai National Reference Collections), Bangkok
BM, British Museum (Natural History), London
BS, Private Collection of Dr. Boonsong Lekagul, Bangkok
FMNH, Field Museum of Natural History, Chicago
IMC, Indian Museum, Calcutta
IMR, Institute of Medical Research, Kuala Lumpur
MZB, Museum Zoologicum Bogoriense, Bogor, Indonesia
NMS, National Museum (formerly Raffles Museum), Singapore
RMNH, Rijksmuseum van Natuurlijke Historie, Leiden (includes the collections of Max Bartels, Jr., W. A. Collier, and H. J. V. Sody)
SMRL, SEATO Medical Research Laboratory, Bangkok
USNM, National Museum of Natural History, Smithsonian Institution, Washington, D. C.
ZMA, Zoological Museum of the University of Amsterdam, Netherlands

All measurements are in millimeters. Lengths of head and body, tail, and ear are those made by collectors and were taken from labels attached to study skins. I measured lengths of hind feet (including claws) of all specimens from dry skins. Cranial measurements were taken with Anderson's (1968) craniometer attached to a Wild M5 stereomicroscope, or with dial calipers graduated to tenths of millimeters; their limits are defined

elsewhere (Musser, 1970). Greatest length and breadth of each first upper molar were taken with the calipers under a dissecting microscope.

I have combined sexes to increase the sample size, thus to gain a better idea of the range of variation in the dimensions I measured. A more detailed study of morphological variation will probably show significant secondary sexual differences in some dimensions, but such a refinement was not necessary for my present purposes.

THE PROBLEM

Rattus cremoriventer was named and described at the turn of the century (Miller, 1900a). From then to now 14 taxa have been described and listed as subspecies of *R. cremoriventer: barussanus, spatulatus, cretaceiventer, malwali, kina, mengurus, flaviventer, gilbiventer, sumatrae, tenaster, blythi, langbianis, indosinicus,* and *vientianensis* (Chasen, 1940; Ellerman, 1949; Ellerman and Morrison-Scott, 1951). This assemblage is composed of specimens diverse in morphology and from a large geographic region. And that is the problem. Does the range of variation shown by samples of the named forms reflect actual morphologic and geographic limits of the species?

Results of my study indicate the diversity to reflect three situations. First, the taxa represent four species, two of which are not *cremoriventer*-type rats. Second, there is considerable individual and geographic variation within a single species. Third, those taxa that are *cremoriventer*-types can be separated into two distinct morphologic and geographic groups that likely represent two species.

The taxa *tenaster* and *blythi* do not apply to samples of *R. cremoriventer.* Each represents a different species of *Rattus: tenaster* is a form belonging with *R. niviventer,* and *blythi* is a sample of *R. fulvescens.* These two kinds of rats are morphologically similar to *cremoriventer*-type rats and occur in the same geographic regions.

Samples of the other taxa are *cremoriventer*-types and they fall into two lots. One group contains rats with bright orange or reddish brown upper parts, small ears, and small bullae. These animals occur on peninsular Thailand and Malaya and offshore islands, and on various large and small islands of the Sunda Shelf. *Rattus cremoriventer* is the oldest name for this type. The names *barussanus, spatulatus, cretaceiventer, malwali, kina, mengurus, flaviventer, gilbiventer,* and *sumatrae* apply to geographic samples of *R. cremoriventer.* In addition, the taxon *solus,* formerly considered to be a subspecies of *R. fulvescens* (Ellerman, 1949), also represents a sample of *R. cremoriventer.*

The other lot is comprised of rats with dull brown and olive-gray upper parts and larger ears and bullae than *R. cremoriventer.* The geographic range of these rats lies to the north of *R. cremoriventer,* on the mainland of

Southeast Asia from eastern India to North and South Vietnam. *Rattus langbianis* is the oldest name for this morphologic type, and the taxa *indosinicus* and *vientianensis* are associated with it.

Data that support these findings are presented in the following pages. This report is not a thorough taxonomic study; rather, it is a progress report outlining known species-limits of *R. cremoriventer* and *R. langbianis*. Later, detailed studies of individual and geographic variation will fill in gaps and present a more complete picture of the two kinds. The information I provide here was drawn from more specimens than were available to workers in the past, and I now have sufficient data eventually to test the zoogeographic relationships between *cremoriventer*-type rats and samples of *R. beccarii* from Celebes when more specimens of the latter are obtained.

I start the report by describing morphologic characteristics of the southern type, *R. cremoriventer*, as well as its geographic distribution, habitat, and taxonomy and then I contrast the northern type, *R. langbianis*, with *R. cremoriventer*.

RATTUS CREMORIVENTER

External, Cranial, and Dental Features

Rattus cremoriventer is a small (table 1), beautiful rat with reddish brown upper parts, white underparts, and a long, brown, hairy tail. Pelage of upper parts is dense, long, and has a texture both spiny and soft because of a mixture of underfur, overhairs, spines, and guard hairs. Underfur consists of short (5 to 10 mm. long), fine, woolly hairs. These are gray for most of their lengths and tipped with dull orange-brown. Overhairs are longer; some extend up to 20 mm. They are also mostly gray and tipped with bright orange-brown. Numerous flattened and semirigid but flexible spines, about as long as the overhairs, are scattered throughout the pelage over back, rump, and sides of the body. The basal two-thirds of each spine is translucent. Those along the back and rump have black tips, whereas spines on the sides of the body are tipped with pale orange-brown. These spines give the pelage a harsh texture that is counteracted by the softness of the overhairs and underfur. Long guard hairs, which extend 15 to 20 mm. beyond lengths of overhairs and spines, are scattered throughout the pelage over back and rump. Their basal halves either lack pigment or are pale gray and their distal halves are black. Some guard hairs are tipped with white.

Overall color of the upper parts is a bright orange to reddish brown suffused with blackish tones along back and rump due to the black guard hairs and black-tipped spines. Sides of the body between shoulders and

thighs are subdued in tone. Shoulders and thighs are the brightest areas of the body. These regions have more orange tones and less brownish tones than elsewhere. A thin, orange strip—absent from some specimens—provides the demarcation between color of upper parts and underparts. Upper parts are flecked with white in some specimens I have examined, and more extensive partial albinism has been reported for other specimens collected in Malaya (Harrison and Lim, 1951).

The orange to reddish brown coloration of upper parts is characteristic of all samples of *R. cremoriventer* except for one from the island of Bali. Upper parts of those specimens are paler than in other samples of the species. Tips of the underfur and overhairs are orange-yellow. These hairs, combined with the black-tipped spines and guard hairs, produce an overall ochraceous mixed with black, the latter strong over the top of the head and back. The coloration contrasts sharply with the bright orange or reddish brown of upper parts in samples from regions outside Bali.

Rattus cremoriventer has a short face and large ears. Each eye is circled by brownish orange pelage and these areas are conspicuously darker than the sides of the face. Eyelids are blackish brown. Facial vibrissae are blackish brown in their basal portions and paler distally. Some of the shorter, more ventral vibrissae are silvery. When laid back alongside each side of the head the longest vibrissae extend up to 30 mm. beyond the ears. Ears range from pale to dark brown. They appear naked to the unaided eye of the observer, but both inside and outside surfaces are covered with short, fine brown hairs.

Color of the head and body extends onto upper parts of the front and hind legs. Dorsal surfaces of the front and hind feet are brown. Digits and claws are unpigmented. Fine, short, white hairs cover the upper surfaces of front and hind feet, including the digits. These impart a silvery sheen over the brown metacarpal and metatarsal regions and a silvery luster to the digits. There is a conspicuous tuft of white hairs at the base of each claw.

The front feet are short and wide. There are four functional digits on each front foot. The fifth digit is the shortest and is about half the length of the other three. The first digit, or pollex, of each foot is a nubbin consisting of a padlike tubercle covered with a rounded nail. The tip of each other digit terminates in a fleshy pad that supports a small claw. Pads are the same widths as the digits, but they are much deeper (in the dorsoventral plane). Claws are short, narrow, and curved; each is about as long as it is deep. Claws of *Rattus cremoriventer* are conspicuously smaller relative to size of the pads supporting them and more sharply curved than in a species like *R. rattus* in which the claws are about twice as long as they are high and not so curved. The palmar surface of each front foot has three

thick interdigital pads and two fleshy palmar pads near the wrist. The five pads form almost the entire surface of the hand. The two palmar pads are brownish, but the rest of the undersurface of each front foot is unpigmented.

Hind feet are short and broad and each has five functional digits. The three middle digits of each foot are the longest, the outer digit being about one-half to two-thirds as long as the middle ones, and the inner digit, or hallux, the shortest, about one-third the length of the three longest. Each hallux terminates in a large, fleshy pad. This pad is conspicuously wider than the digit and has a flat distal surface. The pad supports a small claw that in size and shape resembles those of the front feet. The other four digits of each foot terminate in a pad that is narrower than the digit but much deeper. Claws are sharply curved, each is about as long as it is high and four to five times as large as those on the front feet. Undersurfaces of the hind feet are naked from heels to tips of the digits. Plantar surfaces range from pale to dark brown and each bears four large, fleshy interdigital pads and two thick plantar pads (fig. 1). A small tubercle is attached to the interdigital pad at the base of each hallux. Transverse and semicircular lamellae (not drawn in figure 1) adorn surfaces of the interdigital and plantar pads, as well as the pads beneath the claws. Pads are used to grasp twigs and vines and lamellae provide adhesion.

Underparts from chin to anus of living animals and freshly prepared specimens are white or cream. The pelage is short (8 to 10 mm.) and consists of soft and fine underhairs, longer overhairs, and flexible, flattened, spinelike hairs. All types of hairs are whitish from tips to bases. Many study skins have yellow underparts, a discoloration of the original white or cream.

The tail is much longer than head and body (table 1) and in samples of most populations it is dark brown on all surfaces. In samples from Borneo and southern Sumatra, however, ventral surfaces of the tails are either unpigmented, paler than the lateral and upper surfaces, or mottled. There are 10 to 15 rows of scales per centimeter (counted on the tail one-third the length from the rump) in adults. Three hairs protrude from under each scale. In the basal one-third of the tail these hairs are slightly longer than each scale. Those toward the distal end are longer, giving the tail a well-haired appearance, and toward the tip they form a conspicuous brush extending 5 to 8 mm. beyond the tip of the tail. Pilosity of the distal one-third of the tail is similar to that illustrated for *Rattus brahma* (Musser, 1970, p. 7).

Females have four pairs of mammae: one pectoral, one postaxillary, and two inguinal. I have not seen any specimens with fewer or more mammae.

The cranium of *Rattus cremoriventer* is small and appears compact. Speci-

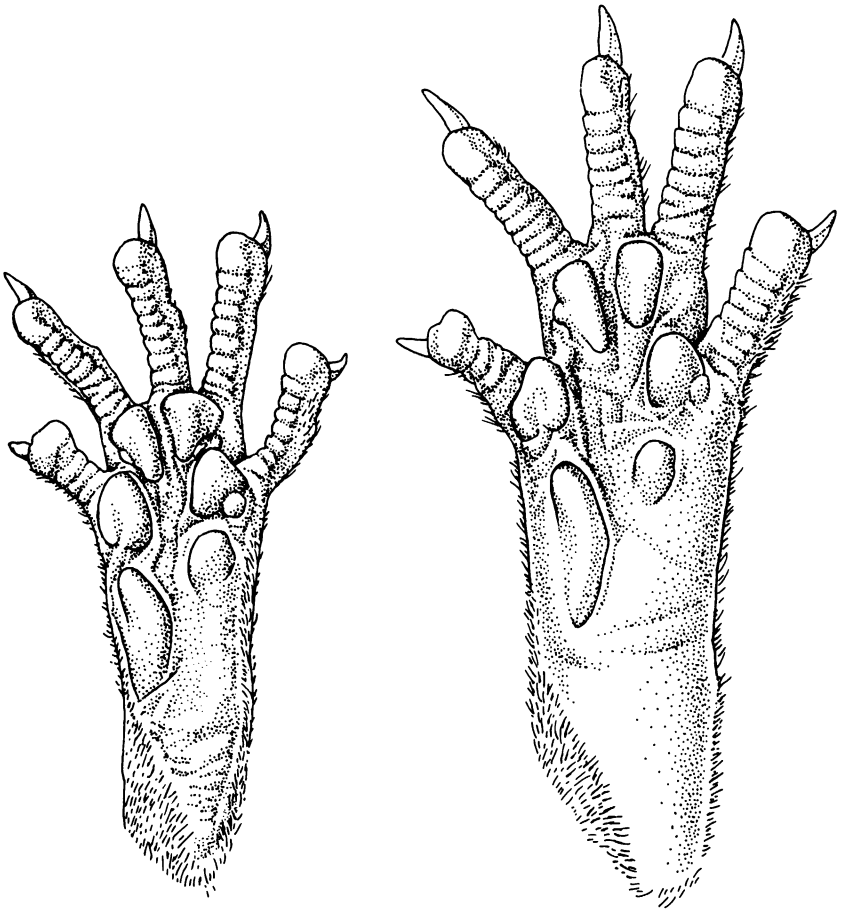

FIG. 1. Plantar views of left hind feet. Left, *Rattus cremoriventer* (AMNH 217621, adult male) from Bukit Mandol, Selangor State, Malaya. To appreciate relative sizes of plantar pads, foot of *R. cremoriventer* is contrasted with foot of *R. rattus diardii*, right (AMNH 217649, adult female), from same locality. Approximately ×3.

mens from Malaya and Bali are illustrated in figures 5, 6, and 7, and measurements of several geographical samples are listed in tables 1 and 2. The rostrum is wide and blunt. Nasals are expanded distally. The interorbital region is inflated and the brain case is wide and low. Supraorbital ridges are well defined; they edge the interorbital area and sweep posteriorly along dorsolateral margins of the brain case to the occiput. Zygo-

matic plates are narrow, their anterior margins barely projecting beyond dorsal roots of the zygomatic arches. Those arches are almost parallel in dorsal view. Anterior incisive foramina are short and broad. Their posterior margins end either about 1 mm. in front of or at the anterior alveolar margins of first molars in almost all specimens I looked at. The incisive foramina end beyond front edges of the first molars in only a few individuals and even then they penetrate less than half a mm. The bony palatal bridge is short and wide. Its posterior margin is shallowly concave and ends in front of posterior alveolar margins of the third molars. The mesopterygoid fossa is broad and generally narrower than the width of each zygomatic plate. Bullae are small and globular. Patterns of cusps of maxillary and mandibular teeth are simple (fig. 2).

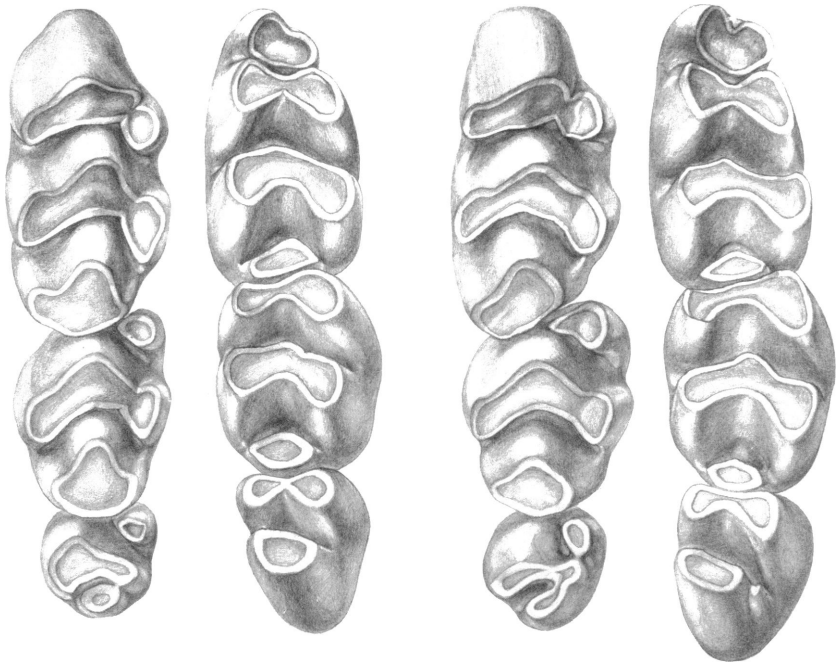

FIG. 2. Views of right toothrows. Left set, maxillary and mandibular toothrows, respectively, of *Rattus cremoriventer kina* (AMNH 103587, young adult female) from Sampit, southwestern Kalimantan. Right set, toothrows of *Rattus langbianis* (AMNH 87485, young adult male) from Plateau des Bolovens, Laos. Approximately ×14. (Occurrence of posterior external cusplet on third lower molar seen in the view of *R. langbianis* is variable. It may be present or absent in samples of both *R. cremoriventer* and *R. langbianis*.)

Habitat and Habits

There is scanty information available about ecology of *Rattus cremoriventer*. What there is in the literature comes from studies by Harrison (1954, 1955, 1957), who worked on populations living in the forests of Malaya. During the past few years, Illar Muul and Lim Boo Liat and their research team at the Institute of Medical Research in Kuala Lumpur have been gathering extensive ecological data on *R. cremoriventer* and other rodents found in the Malayan forests. Their published results will eventually add significantly to knowledge about biology of *R. cremoriventer*. For the present report, I only include a few of my own observations on habitat and review some items on other biological aspects of *R. cremoriventer* that were published by Harrison.

Illar Muul generously allowed me to study both live and preserved specimens of *R. cremoriventer* in the laboratory at the Institute of Medical Research and he arranged for me to spend time in the forest from which the specimens had been obtained. Many examples of *R. cremoriventer* preserved in the collection of the Institute have come from Bukit Lagong Forest Preserve in Selangor State. I visited the particular section of forest from which the animals had been collected and obtained an impression of the habitat. The forest at Bukit Lagong is second-growth mixed with primary elements. Some of the trees forming the canopy are 20 meters or higher, and higher emergents are scattered throughout the forest. The understory is a thick and almost impenetrable tangle of smaller species of trees, saplings, palms, and herbaceous vines. Such a structure is typical of secondary forest. It stands in strong contrast to undisturbed primary forest. There the crowns of trees 30 meters high form a continuous canopy, broken by emergent trees up to 45 meters high. Saplings and smaller species form an incomplete understory and the ground is generally open and parklike (Harrison, 1957).

Illar Muul told me his trapping records indicate *Rattus cremoriventer* to be a common and characteristic part of the rodent fauna in second-growth forests, but to be uncommon or absent in either undisturbed or slightly disturbed primary forest. The species is nocturnal and mostly arboreal; most specimens have been taken in traps set 2 to 4 meters off the ground. Occasionally the rats are taken in traps set on the ground, but that is the exception and not the rule.

Secondary forest provides ideal physical habitat for small arboreal rats like *R. cremoriventer*. The dense understory of small trees, saplings, palms, and herbaceous shrubs, all interconnected by vines, palm fronds, and limbs, provide strata at different levels and angles. The forest structure is

a web of arboreal avenues and paths in which small rodents can scurry through at levels well above the ground.

Little information is available in the literature about food and reproduction of *R. cremoriventer*. Harrison (1954) analyzed contents of stomachs from various species of Malayan rodents to obtain an idea of their foods. He examined three specimens of *R. cremoriventer*. Of the three, "One contained insects and vegetable matter, one vegetable matter only, and the third some translucent glutinous material taken to be fruit pulp."

What little that is known about reproductive biology of *R. cremoriventer* was also reported by Harrison (1955). He found that the species becomes sexually mature at a weight of about 50 grams. Litter size, based on 10 specimens, ranged from two to five, and the mean number of embryos per litter was 3.7.

The karyotype of *Rattus cremoriventer* from Malaya is reported by Yong (1969). Each of the specimens from there has a fundamental number of 54 and a diploid number of 46. This complement consists of one pair of subterminal, 18 pairs of acrocentric, and three pairs of metacentric autosomes, an acrocentric X and acrocentric Y sex-chromosomes.

Geographic Distribution and Taxonomy

I recognize five subspecies of *Rattus cremoriventer: R. c. cremoriventer* (*gilbiventer*, *solus*, and *flaviventer* are synonyms) from Malaya and peninsular Thailand; *R. c. mengurus* from Billiton and Bangka islands and the mainland of southern Sumatra (*sumatrae* is a synonym); *R. c. barussanus* from Nias Island; *R. c. cretaceiventer* from Java and Bali; and *R. c. kina* (*spatulatus* and *malwali* are synonyms) from Borneo. The subspecies are discussed below. In each account I record the distribution, list the specimens I examined and the localities from which they were collected, then discuss the taxonomy. Included in each account are a few remarks on geographic variation of external and cranial features.

Rattus cremoriventer cremoriventer: This subspecies is known to occur on the mainland of peninsular Thailand and Malaya, on certain islands off both the west and east coasts of the peninsula, on one of the Anambas Islands, and on northwestern Sumatra (fig. 3). Sullivan Island (between 10° and 11° N lat.) in the Mergui Archipelago is the northernmost record of occurrence. The northernmost locality on the mainland of peninsular Thailand from which the species has been collected is near Chumphon (10° 28′ N, 98° 55′ E), at the Isthmus of Kra.

Known altitudinal range of *R. c. cremoriventer* extends from near sea level up to approximately 1900 meters.

I have seen 161 specimens from the localities listed below.

BURMA, MERGUI ARCHIPELAGO

Sullivan Island (USNM 104153, holotype of *gilbiventer*).

PENINSULAR THAILAND

Tasan, Chumphon (also spelled Chumporn and pronounced Chumpawn; 10° 28′ N, 98° 55′ E), 67 meters (BM 55.2821).

Tapli (Klong Wan) Pakechan, near Kraburi (the Isthmus of Kra) and about 30 km. north of Ranong (NMS 8408).

Ban Bang Nawn Village, 5 km. north of Ranong (10° 2′ N, 98° 39′ E) (BS 2109).

Kao Luang, Nakonsritammarat (8° 30′ N, 99° 42′ E), 600 meters (BM 55.2836).

Trang, Khow Nok Rann, 900 meters (USNM 86770, holotype of *cremoriventer*; USNM 86771); Muang, Khao Chong (BM 55.2822; NMS 1203/10; USNM 356761, 356762); Ongut (NMS 1280/10).

Pattani, Na Pradu (ASRCT 54-659, 54-660, 54-661).

ISLANDS OFF WEST COAST OF PENINSULAR THAILAND

Butang Islands, Adang Island, 15 miles northwest of Langkawi Island (USNM 104152).

Terutau Island (USNM 123994, holotype of *solus*); Telok Wau (BM 55.2835); S. Udang (BM 9.11.1.149).

PENINSULAR MALAYA

Kedah State, Kedah Peak, 1000 meters (BM 55.2830; IMR 52270, 52271; NMS 912/15).

Perak State: Gunung Kerbau, 1500 meters (BM 55.2824; NMS 1/13); Gunung Ijau, 1500 meters (BM 55.2827–55.2829; NMS 69/15, 70/15, 76/15, 1809/11, 72/15); Gunung Semanggul (BM 55.2826; NMS 1805/11); Tanjong Malim (IMR 79883, 79943); Lenggong (BM 55.2823); Temengoh, 100 meters (NMS 1759/09, 1808/11); Maxwell's Hill, 760 and 1090 meters (BM 55.2825, 9.4.1.423, 9.4.1.424; NMS 1635/08, 1638/08; USNM 311426–311428).

Selangor State: Subang (AMNH 217622); Bukit Mandol (AMNH 217621); Bukit Lagong (IMR 58806, 58807, 60220, 60221, 60225, 60255, 60359, 60426, 65052, 65077, 65078, 65087, 65094, 72247, 72248, 72870, 72871, 72891, 72893, 72956, 72990, 74215, 84513, 85458, 85459, 87816, 88552, 88933, 89239, 89378); Ulu Gombok (IMR 79658); Bukit Lagong Forest Reserve, Kepong (BM 61.1235–61.1238); 27 km. northeast of Kuala Lumpur on the Pahang Road (BM 49.618, 50.105; USNM 283686, 290227); Kepong, near Kuala Lumpur (BM 49.612–49.617, 50.100–50.104; USNM 290222–290226, 290229, 355386); Genting Sempat, 40 km. north of Kuala Lumpur on Pahang Road (USNM 355387).

Pahang State: Lubok Tamang (BM 55.2833); Gunung Sinyom, 500 meters (BM 55.2834; NMS 541/17); Genting, Kuala Lipis (BM 55.2832); Tahan, The Padang (NMS 45); Kuala Tahan, Ulu Tembeling (IMR 4766, 4789, 4812); Gunung Brinchang, Cameron Highlands, 1500 to 1900 meters (BM 62.746; IMR 3579, 3600, 3615, 3745; USNM 283537, 283551).

Trengganu State: Tanjong Dungan (NMS 1438/09; USNM 105057); Kuala Berang (IMR 4610, 4617, 4633, 4648, 4649, 5439); Bukit Besi (USNM 311434, 311435).

ISLANDS OFF WEST COAST OF MALAYA IN THE STRAIT OF MALACCA

Buraw Island, northwest of Langkawi Island (BM 55.2837, 55.2838; NMS 498/17).

TABLE 1

EXTERNAL AND CRANIAL MEASUREMENTS (IN MILLIMETERS) OF ADULTS FROM GEOGRAPHIC SAMPLES OF *Rattus cremoriventer*
(The mean and standard deviation, size of sample after comma, plus and minus two times the standard error of the mean, and the observed range in parentheses are listed, in that order, for each dimension.)

	Thailand	Malaya	Southern Sumatra	Nias Island	Borneo	Java	Bali	Banggi, Balambangan, Malawali Islands
Length of head and body	136.0± 8.5, 4 127.5–144.5 (128–146)	147.5± 7.8, 15 143.5–151.5 (137–165)	131.6± 5.6, 5 126.6–136.6 (124–138)	161.3± 10.8, 4 150.5–172.1 (149–173)	133.5± 9.5, 17 128.9–138.1 (122–155)	134.1± 6.8, 37 131.9–136.5 (123–150)	148.0± 3.7, 4 144.3–151.7 (144–152)	143.6± 8.8, 9 137.7–149.5 (130–155)
Length of tail	171.0± 8.3, 4 162.7–179.3 (160–180)	175.4± 17.0, 14 166.3–184.5 (140–200)	170.0± 13.2, 5 158.1–181.9 (152–185)	180.7± 20.6, 3 157.0–204.4 (157–194)	175.4± 15.0, 17 168.1–182.7 (152–211)	195.7± 9.7, 37 192.5–198.9 (175–229)	184.8± 16.6, 4 168.2–201.4 (168–205)	202.6± 19.6, 7 186.8–218.4 (172–230)
Length of hind foot	24.0± 3.6, 3 19.8–28.2 (20–25)	27.5± 1.0, 15 27.0–28.0 (26–29)	26.2± .8, 5 25.4–27.0 (25–27)	31.8± 1.7, 4 30.1–33.5 (30–34)	26.4± 1.3, 17 25.8–27.0 (24–28)	27.4± 1.1, 37 27.0–27.8 (24–30)	29.5± 1.0, 4 28.5–30.5 (28–30)	28.4± 1.0, 9 27.7–29.1 (27–30)
Length of ear	17.3± 1.9, 4 15.4–19.2 (16–20)	17.9± 1.4, 15 17.2–18.6 (15–21)	16.6± .5, 5 16.1–17.1 (16–17)	16.5± 1.3, 4 15.2–17.8 (15–18)	17.4± .6, 17 17.1–17.7 (16–18)	17.8± 1.0, 35 17.5–18.1 (16–20)	20.3± .5, 4 19.8–20.8 (20–21)	18.3± .8, 8 17.7–18.9 (17–20)
Greatest length of skull	33.70± 6.2, 3 32.98–34.42 (33.2–34.4)	36.10± 1.15, 15 35.51–35.69 (34.1–37.9)	33.98± .91, 5 33.17–34.79 (32.7–35.0)	39.10± .87, 3 38.09–40.11 (38.1–39.7)	33.19± 1.36, 17 32.53–33.85 (31.5–35.4)	35.20± 1.00, 39 34.9–35.5 (33.1–37.5)	36.05± 1.30, 4 34.74–37.36 (34.9–37.7)	35.74± 1.04, 9 35.05–36.43 (34.6–37.6)
Zygomatic breadth	15.65± .64, 2 14.75–16.55 (15.2–16.1)	16.88± .77, 15 16.48–17.28 (15.5–18.2)	15.53± .12, 3 15.40–15.66 (15.4–15.6)	17.60± .30, 3 17.25–17.95 (17.3–17.9)	14.92± .74, 11 14.48–15.36 (14.1–16.3)	16.48± .97, 37 16.29–16.67 (15.3–17.8)	16.70± .26, 3 16.39–17.01 (16.4–16.9)	16.43± .58, 9 16.04–16.82 (15.7–17.5)
Interorbital breadth	5.63± .21, 4 5.43–5.73 (5.4–5.8)	6.10± .29, 15 5.95–6.25 (5.7–6.7)	5.70± .12, 5 5.59–5.81 (5.5–5.8)	6.47± .15, 3 6.29–6.65 (6.3–6.6)	5.63± .23, 17 5.52–5.74 (5.3–6.1)	5.71± .28, 39 5.62–5.80 (5.2–6.3)	5.45± .26, 4 5.19–5.71 (5.1–5.7)	5.89± .23, 9 5.74–6.04 (5.7–6.3)

TABLE 1—(*Continued*)

	Thailand	Malaya	Southern Sumatra	Nias Island	Borneo	Java	Bali	Banggi, Balambangan, Malawali Islands
Length of nasals	11.73± .25, 3 11.45–12.01 (11.5–12.0)	12.77± .51, 15 12.51–13.03 (11.9–13.5)	12.16± .23, 5 12.95–12.37 (11.8–12.4)	13.58± .83, 4 12.75–14.41 (12.5–14.4)	12.29± .77, 17 11.92–12.66 (11.1–13.7)	12.47± .54, 39 12.30–12.64 (11.3–13.8)	13.03± .91, 4 12.12–13.94 (12.1–13.9)	13.72± .65, 9 13.29–14.15 (12.9–15.1)
Length of rostrum	10.30± .26, 3 9.99–10.61 (10.0–10.5)	10.68± .58, 15 10.38–10.98 (9.6–11.5)	10.10± .48, 5 9.67–10.53 (9.6–10.7)	11.83± .82, 4 11.01–12.65 (10.6–12.3)	9.82± .61, 17 9.53–10.11 (8.7–11.0)	10.63± .56, 39 10.45–10.81 (9.8–11.9)	10.63± .85, 4 9.78–11.48 (9.9–11.5)	11.08± .49, 9 10.75–11.41 (10.2–11.9)
Breadth of rostrum	5.90± .36, 3 5.48–6.32 (5.5–6.2)	6.67± .38, 15 6.48–6.86 (6.0–7.2)	6.22± .11, 5 6.10–6.32 (6.1–6.4)	6.60± .54, 4 6.06–7.14 (5.9–7.2)	6.17± .29, 15 6.03–6.31 (5.6–6.7)	6.26± .31, 39 6.16–6.36 (5.5–7.0)	6.48± .28, 4 6.20–6.76 (6.2–6.8)	6.44± .31, 9 6.23–6.65 (6.1–7.2)
Breadth of brain case	13.80± .36, 3 13.38–14.22 (13.4–14.1)	14.56± .46, 15 14.32–14.80 (13.9–15.3)	13.72± .16, 5 13.57–13.87 (13.6–14.0)	15.47± .06, 3 15.40–15.54 (15.4–15.5)	13.59± .27, 17 13.46–13.72 (13.2–14.1)	14.56± .38, 39 14.44–14.68 (13.8–15.3)	14.20± .36, 4 13.84–14.56 (13.7–14.5)	14.11± .30, 9 13.91–14.31 (13.8–14.6)
Height of brain case	9.47± .31, 3 9.12–9.82 (9.2–9.8)	10.16± .41, 15 9.95–10.37 (9.5–11.0)	9.58± .33, 5 9.29–9.87 (9.1–10.0)	10.63± .31, 3 10.28–10.98 (10.3–10.9)	9.71± .31, 17 9.56–9.86 (9.2–10.3)	9.81± .31, 39 9.71–9.91 (8.9–10.3)	9.88± .33, 4 9.55–10.21 (9.5–10.3)	9.82± .31, 9 9.61–10.03 (9.8–10.3)
Breadth of zygomatic plate	2.63± .25, 3 2.34–2.92 (2.4–2.9)	2.78± .17, 15 2.69–2.87 (2.5–3.1)	2.62± .08, 5 2.55–2.69 (2.5–2.7)	3.05± .40, 4 2.65–3.45 (2.5–3.4)	2.84± .37, 17 2.66–3.02 (2.5–3.9)	2.72± .24, 39 2.64–2.80 (2.4–3.4)	3.18± .22, 4 2.96–3.40 (2.9–3.4)	3.01± .27, 9 2.83–3.19 (2.7–3.5)
Depth of zygomatic notch	.80± .00, 3 — —	.89± .24, 15 .76–1.02 (.5–1.4)	1.00± .17, 3 .80–1.20 (.8–1.1)	1.05± .31, 4 .74–1.36 (.6–1.3)	.91± .20, 16 .81–1.01 (.5–1.2)	— — —	.80± .18, 4 .62–.98 (.6–1.0)	— — —
Length of diastema	8.25± .39, 4 7.86–8.64 (7.7–8.6)	9.11± .42, 15 8.89–9.33 (8.3–10.0)	8.40± .24, 5 8.18–8.62 (8.1–8.7)	9.40± .57, 4 8.83–9.97 (8.6–9.8)	8.61± .40, 17 8.42–8.80 (8.0–9.4)	8.99± .35, 39 8.88–9.10 (8.3–9.8)	9.15± .55, 4 8.60–9.70 (8.5–9.7)	8.92± .50, 9 8.59–9.25 (8.3–9.7)

TABLE 1—(*Continued*)

	Thailand	Malaya	Southern Sumatra	Nias Island	Borneo	Java	Bali	Banggi, Balambangan, Malawali Islands
Palatal length	15.88± .38, 4 15.50–16.26 (15.5–16.4)	17.08± .86, 15 16.64–17.52 (15.9–19.4)	16.18± .13, 5 16.06–16.30 (16.0–16.3)	18.30± 1.15, 4 17.15–19.45 (16.8–19.2)	16.35± .60, 17 16.06–16.64 (15.6–17.5)	16.99± .51, 39 16.83–17.15 (16.1–18.4)	17.23± .77, 4 16.46–18.00 (16.4–17.4)	17.10± .63, 9 16.68–17.52 (16.3–17.5)
Length of palatal foramina	5.43± .15, 4 5.28–5.58 (5.3–5.6)	6.05± .28, 15 5.91–6.19 (5.7–6.6)	4.96± .23, 5 4.75–5.17 (4.6–5.2)	6.35± .51, 4 5.84–6.86 (5.7–6.8)	5.51± .36, 17 5.34–5.68 (4.7–6.1)	5.99± .25, 39 5.91–6.07 (5.6–6.6)	6.10± .08, 4 6.02–6.18 (6.0–6.2)	5.56± .29, 9 5.37–5.75 (5.2–6.0)
Breadth of palatal foramina	2.53± .15, 4 2.38–2.68 (2.3–2.6)	2.77± .23, 15 2.65–2.89 (2.4–3.2)	2.50± .14, 5 2.37–2.63 (2.4–2.7)	3.03± .12, 3 2.90–3.16 (2.9–3.1)	2.40± .21, 17 2.30–2.50 (2.0–2.8)	2.68± .15, 39 2.63–2.73 (2.4–3.1)	2.83± .31, 4 2.52–3.14 (2.4–3.1)	2.63± .17, 9 2.51–2.75 (2.3–2.9)
Length of palatal bridge	6.05± .31, 4 5.74–6.36 (5.8–6.5)	6.02± .35, 15 5.84–6.20 (5.5–6.6)	6.50± .14, 5 6.37–6.63 (6.3–6.6)	7.15± .40, 4 6.75–7.55 (6.8–7.5)	6.34± .36, 17 6.16–6.52 (5.8–7.1)	6.13± .31, 39 6.03–6.23 (5.6–6.9)	6.38± .30, 4 6.08–6.68 (6.1–6.8)	6.59± .37, 9 6.35–6.83 (6.0–7.2)
Breadth of palatal bridge at M^1	3.23± .19, 4 3.04–3.42 (3.1–3.5)	— — —	3.20± .10, 5 3.11–3.20 (3.1–3.3)	3.80± .26, 3 3.49–4.11 (3.5–4.0)	3.25± .21, 17 3.15–3.35 (2.9–3.6)	3.35± .19, 39 3.29–2.41 (3.0–3.7)	3.65± .29, 4 3.36–3.94 (3.3–4.0)	3.28± .15, 9 3.18–3.38 (3.1–3.5)
Breadth of palatal bridge at M^3	3.83± .10, 4 3.73–3.93 (3.7–3.9)	— — —	3.98± .21, 5 3.80–4.10 (3.8–4.3)	4.63± .23, 3 4.36–4.90 (4.5–4.9)	3.92± .22, 17 3.81–4.03 (3.6–4.3)	4.16± .27, 39 4.08–4.24 (3.5–4.7)	4.08± .21, 4 3.87–4.29 (3.8–4.3)	3.98± .29, 9 3.79–4.17 (3.5–4.6)
Breadth at mesopterygoid fossa	2.63± .17, 4 2.46–2.80 (2.4–2.8)	2.83± .25, 15 2.70–2.96 (2.4–3.4)	2.64± .13, 5 2.52–2.76 (2.5–2.8)	2.93± .15, 3 2.75–3.11 (2.8–3.1)	2.55± .17, 17 2.47–2.63 (2.2–2.8)	2.79± .21, 39 2.72–2.86 (2.4–3.2)	2.95± .17, 4 2.78–3.12 (2.8–3.2)	2.70± .07, 9 2.56–2.84 (2.5–3.2)
Length of bulla	4.30± .17, 3 4.10–4.50 (4.2–4.5)	4.56± .19, 15 4.46–4.66 (4.2–4.8)	4.42± .19, 5 4.25–4.59 (4.1–4.6)	4.80± .00, 3 — —	4.47± .23, 16 4.36–4.58 (4.1–4.8)	4.58± .16, 38 4.53–4.63 (4.3–5.0)	5.10± .37, 4 4.73–5.47 (4.7–5.6)	4.67± .16, 9 4.56–4.78 (4.4–4.9)

TABLE 1—(*Continued*)

	Thailand	Malaya	Southern Sumatra	Nias Island	Borneo	Java	Bali	Banggi, Balambangan, Malawali Islands
Breadth of bulla	4.40± .17, 3 4.20–4.60 (4.2–4.5)	3.99± .26, 15 3.85–4.13 (3.6–4.4)	3.48± .19, 5 3.31–3.65 (3.2–3.7)	4.47± .58, 3 3.80–5.14 (3.8–4.8)	4.21± .22, 17 4.11–4.31 (3.7–4.5)	3.94± .31, 37 3.84–4.04 (3.2–4.4)	4.20± .22, 4 3.98–4.42 (3.9–4.4)	— — —
Height of bulla	3.87± .12, 3 3.74–4.00 (3.8–4.0)	3.19± .20, 14 3.09–3.29 (3.0–3.6)	2.94± .09, 5 2.86–3.02 (2.8–3.0)	4.17± .06, 3 4.10–4.24 (4.1–4.2)	3.58± .21, 16 3.48–3.68 (3.2–4.0)	3.06± .24, 37 2.98–3.14 (2.7–3.8)	3.48± .15, 4 3.33–3.63 (3.3–3.6)	— — —
Alveolar length of M^{1-3}	6.08± .21, 4 5.87–6.29 (5.8–6.3)	6.09± .27, 15 5.95–6.23 (5.5–6.4)	5.80± .32, 5 2.52–6.08 (5.3–6.1)	6.93± .39, 4 6.54–7.32 (6.7–7.5)	6.01± .27, 17 5.88–6.14 (5.6–6.6)	6.16± .26, 39 6.08–6.24 (5.6–6.7)	6.03± .17, 4 5.86–6.20 (5.8–6.2)	6.20± .32, 9 6.00–6.40 (6.0–6.8)
Length of M^1	2.98± .13, 4 2.85–3.11 (2.8–3.1)	2.92± .13, 15 2.85–2.99 (2.6–3.1)	2.92± .08, 5 2.85–2.99 (2.8–3.0)	3.57± .21, 3 3.33–3.81 (3.4–3.8)	2.99± .14, 17 2.93–3.05 (2.8–3.2)	3.02± .14, 38 2.98–3.06 (2.7–3.2)	3.08± .10, 4 2.99–3.17 (3.0–3.2)	3.16± .05, 9 3.06–3.26 (2.9–3.4)
Breadth of M^1	1.58± .05, 4 1.53–1.63 (1.5–1.6)	1.63± .07, 15 1.59–1.67 (1.5–1.7)	1.50± .07, 5 1.44–1.56 (1.4–1.6)	1.90± .10, 3 1.78–2.02 (1.8–2.0)	1.61± .08, 16 1.58–1.64 (1.5–1.7)	1.71± .07, 38 1.69–1.73 (1.6–1.8)	1.70± .08, 4 1.62–1.78 (1.6–1.8)	1.71± .06, 9 1.67–1.75 (1.6–1.8)

TABLE 2

EXTERNAL, CRANIAL, AND DENTAL MEASUREMENTS (IN MILLIMETERS) OF HOLOTYPES OF TEN TAXA ASSOCIATED WITH *Rattus cremoriventer*

	R. c. cremoriventer (USNM 86770)	*R. c. gilbiventer* (USNM 104153)	*R. c. solus* (USNM 123944)	*R. c. flaviventer* (USNM 101739)	*R. c. sumatrae* (S-180)	*R. c. barussanus* (USNM 141208)	*R. c. mengurus* (USNM 125021)	*R. c. malawali* (BM 47.1463)	*R. c. spatulatus* (USNM 145499)	*R. c. cretaceiventer* (BM 26.10.19.11)
	Thailand	Sullivan Island	Teratou Island	Anambas Islands	Sumatra	Nias Island	Billiton Island	Malawalle Island	Lamukutan Island	Java
	Male	Male	Male	Male	Male	Male	Male	Male	Male	Male
	Young Adult	Adult	Old Adult	Adult	Adult	Adult	Adult	Adult	Adult	Adult
Length of head and body	146	125	160	133	138	173	134	155	158	138
Length of tail	171	185	220	171	185	194	182	225	197	196
Length of hind foot	27	28	29	26	27	34	26	30	31	29
Length of ear	16	16	—	16	17	15	15	19	16	19
Greatest length of skull	33.5	34.7	36.5	34.8	35.0	39.5	33.6	37.6	37.0	35.8
Zygomatic breadth	15.2	15.7	17.0	15.0	15.6	17.9	15.1	17.5	16.2	16.0
Interorbital breadth	5.8	5.8	6.5	5.9	5.5	6.5	5.6	6.3	5.9	5.6
Length of nasals	11.5	12.6	13.2	13.3	12.3	14.4	13.0	15.1	14.6	12.7
Length of rostrum	10.5	10.6	11.7	11.3	10.7	12.2	10.3	11.9	11.6	9.9

TABLE 2—(*Continued*)

	R. c. cremoriventer (USNM 86770)	*R. c. gilbiventer* (USNM 104153)	*R. c. solus* (USNM 123944)	*R. c. flaviventer* (USNM 101739)	*R. c. sumatrae* (S-180)	*R. c. barussanus* (USNM 141208)	*R. c. mengurus* (USNM 125021)	*R. c. malawali* (BM 47.1463)	*R. c. spatulatus* (USNM 145499)	*R. c. cretaceiventer* (BM 26.10.19.11)
	Thailand Male Young Adult	Sullivan Island Male Adult	Teratou Island Male Old Adult	Anambas Islands Male Adult	Sumatra Male Adult	Nias Island Male Adult	Billiton Island Male Adult	Mallawalle Island Male Adult	Lamukutan Island Male Adult	Java Male Adult
Breadth of rostrum	6.0	6.4	6.4	6.3	6.1	7.2	5.8	7.2	6.6	6.6
Breadth of brain case	14.1	14.1	14.4	13.8	13.6	15.5	13.5	14.1	13.8	14.9
Height of brain case	9.8	9.6	10.0	9.7	9.7	10.9	9.7	9.9	9.8	10.0
Breadth of zygomatic plate	2.6	2.6	2.8	2.6	2.7	3.4	2.8	3.3	2.6	2.8
Depth of zygomatic notch	0.8	1.3	0.8	1.1	—	1.1	1.0	0.7	0.5	0.6
Length of diastema	7.7	8.6	8.8	8.7	8.7	9.8	8.4	9.4	9.4	8.9
Palatal length	15.5	16.8	17.4	16.5	16.2	19.2	15.8	18.4	17.6	17.3
Length of palatal foramina	5.3	6.1	6.4	5.5	5.0	6.8	5.6	5.6	6.6	5.8
Breadth of palatal foramina	2.6	2.7	2.8	2.8	2.6	3.1	2.6	2.8	3.1	2.6
Length of palatal bridge	5.9	5.7	6.1	6.4	6.4	7.5	5.9	7.2	6.2	6.6
Breadth of palatal bridge at M^1	3.2	3.6	3.8	3.4	3.1	3.5	3.1	3.2	3.4	3.3

TABLE 2—(*Continued*)

	R. c. cremoriventer (USNM 86770)	*R. c. gilbiventer* (USNM 104153)	*R. c. solus* (USNM 123944)	*R. c. flaviventer* (USNM 101739)	*R. c. sumatrae* (S-180)	*R. c. barussanus* (USNM 141208)	*R. c. mengurus* (USNM 125021)	*R. c. malawali* (BM 47.1463)	*R. c. spatulatus* (USNM 145499)	*R. c. cretaceiventer* (BM 26.10.19.11)
	Thailand	Sullivan Island	Teratou Island	Anambas Islands	Sumatra	Nias Island	Billiton Island	Mallawalle Island	Lamukutan Island	Java
	Male	Male	Male	Male	Male	Male	Male	Male	Male	Male
	Young Adult	Adult	Old Adult	Adult	Adult	Adult	Adult	Adult	Adult	Adult
Breadth of palatal bridge at M^3	3.8	4.0	4.1	4.0	3.8	4.5	3.9	3.8	3.7	3.8
Breadth of mesopterygoid fossa	2.7	2.9	3.4	3.0	2.7	2.8	2.3	2.6	3.1	2.6
Length of bulla	4.5	4.5	4.6	4.6	4.5	4.8	4.4	4.8	4.6	4.8
Breadth of bulla	4.5	4.7	4.6	4.3	3.7	3.8	4.2	4.2	5.0	4.3
Height of bulla	4.0	3.8	3.7	4.0	3.0	4.2	3.8	3.4	4.1	3.2
Alveolar length of M^{1-3}	6.1	6.4	6.7	5.9	6.0	7.5	5.8	6.4	6.0	6.9
Length of M^1	3.0	3.2	3.3	3.0	2.9	3.8	2.9	3.1	3.0	3.1
Breadth of M^1	1.6	1.7	1.7	1.7	1.6	2.0	1.5	1.7	1.7	1.8

Langkawi Island (BM 9.11.1.148, 9.11.1.146; NMS 33/15, 878/09, 1035/09; USNM 104151, 123858, 311430–311433).
Penang Island, Telok Bahang (BM 55.2839, 55.2840, 55.2841; NMS 1795/11, 1796/11, 1523/11, 1804/11, 1806/11, 4142).

ISLANDS OFF EAST COAST OF MALAYA
Tioman Island (IMR 51931).

ANAMBAS ISLANDS
Jimaja (Djemadja) Island (USNM 101739, holotype of *flaviventer*; USNM 101740).

NORTHWESTERN SUMATRA
Medan (ZMA 12.714).

Rattus cremoriventer was named and described in 1900 by Miller (1900a, p. 144). The taxon was based on two specimens obtained from mountains of Trang Province in the southern part of peninsular Thailand by W. L. Abbott. The specimens were collected at an elevation of 900 meters. The holotype (USNM 86770), a young adult male, was taken on January 16, 1899, and the other specimen (USNM 86771), an adult male, was obtained on January 24 of that year.

There are three taxa I consider to be synonyms of *Rattus cremoriventer cremoriventer*: *gilbiventer*, *solus*, and *flaviventer*. The taxon *gilbiventer* is known only from the holotype (USNM 104153), an adult male collected by Abbott from Sullivan Island, Mergui Archipelago on February 2, 1900. Miller (1903, p. 35) described *gilbiventer* as a species of *Mus* and pointed out its similarity to *R. cremoriventer*. Subsequently, Ellerman (1949) listed *gilbiventer* as a subspecies of *R. cremoriventer* with question because he had not examined the holotype and did not know the exact status of the form. Later, however, Ellerman and Morrison-Scott (1951) listed the taxon as an unquestioned subspecies of *R. cremoriventer*.

In his description of *gilbiventer*, Miller (1903) pointed out that color of the holotype resembled that in specimens of *R. cremoriventer*, but there were many more creamy buff spines scattered throughout its pelage than in examples of *R. cremoriventer*. In describing the skull and teeth, Miller remarked that "The skull resembles that of *Mus cremoriventer*, but is slightly larger; the rostrum is deeper, the incisive foramina are longer, and the audital bullae are less globular. Mandible more robust than in the related species, and concavity between condyle and angular process not as deep. Teeth as in *Mus cremoriventer*, but slightly larger throughout."

At the time Miller described *gilbiventer* he had only a handful of examples of typical *cremoriventer* from the mainland of peninsular Thailand. I have compared the holotype of *gilbiventer* with a larger series of *cremoriventer* from the mainland than was available to Miller and find that the features of *gilbiventer* he thought to be distinctive—namely spiny pelage and slightly

larger size—are individually variable in samples from the mainland. The holotype of *gilbiventer* is morphologically like examples of typical *cremoriventer* from Trang and its characteristics fit within the range of variation of external and cranial features shown by those specimens.

The taxon *solus* was described by Miller (1913, p. 22) from a specimen (USNM 123944) collected from Terutau (spelled Terutao on some maps) Island, a small island off the west coast of peninsular Thailand near the Thailand-Malaya border. The specimen, an old adult male, was obtained on November 16, 1903, by Abbott. Miller considered *solus* to represent a species of *Epimys*, but he thought it was related to *cremoriventer* and diagnosed it as "A member of the *Epimys cremoriventer* group agreeing with *E. bukit* from Jalor in large general size, but differing in the longer tail and hind foot; color as in *Epimys gilbiventer* of Sullivan Island, Rhio Archipelago."

Miller's description of *solus* was short and inadequate. He did not provide enough information to identify the taxon and that is probably why most subsequent authors did not associate the name with *R. cremoriventer* but with *R. fulvescens*. For example, Chasen (1940) regarded *solus* as a subspecies of *R. rapit*, a name that would later be associated with *R. fulvescens*, and Ellerman (1949) listed *solus* as a valid subspecies of *R. fulvescens*. Tate (1936) has been the only other author besides Miller to associate *solus* with *R. cremoriventer*. He listed the taxon as a species in the "*Rattus cremoriventer* Group."

In addition to the holotype of *solus* there are two other specimens of *Rattus cremoriventer* from Terutau Island, BM 9.11.1.149 and BM 55.2835. Hill (1960, p. 101) listed BM 55.2835 under *R. c. cremoriventer* and commented that the specimens from there and Langkawi Island "are slightly less bright in dorsal colour than those from the mainland but the difference is very small." I agree. In features of skin and skull the holotype of *solus* and the other two specimens from Terutau Island are like specimens of *R. c. cremoriventer* from the mainland. In fact, differences in cranial morphology between the island and mainland samples are so slight that skulls of each of comparable age are indistinguishable from one another. The difference in color is also slight and not taxonomically significant.

Rattus cremoriventer is now known from several islands off the coasts of peninsular Thailand and Malaya. The species has been taken from Sullivan, Adang, Terutau, Buraw, Langkawi, and Penang islands off the western coast of the mainland, and from Tioman Island off the southeastern shore of Malaya. The samples from each island are small but in morphology of skin and skull, they are closely similar to populations of *R. cremoriventer* on the adjacent mainland. Medway (1966, p. 22), however,

examined four specimens from Tioman Island and thought that, "A longer series would probably warrant subspecific separation." The species will probably be found to occur on other forested islands off the coast of peninsular Thailand and Malaya. A careful study of individual and geographic variation of large samples will probably reveal differences between samples from offshore islands and between samples from the islands and mainland. Morphological differences I found between samples now available from the mainland and from the islands are the kind found between local populations of *R. cremoriventer* on the mainland. In my opinion the differences do not justify nomenclatural recognition of any island population that I looked at.

The third scientific name I regard as a synonym of *Rattus cremoriventer* is *flaviventer*, a taxon originally named and described by Miller (1900b, p. 204) and based on two specimens obtained from Jimaja (also spelled Djemadja) Island in the group of Anambas Islands, situated between the Malay Peninsula and Borneo in the South China Sea. The taxon is known from two specimens. The holotype (USNM 101739) is an adult male and was collected on September 18, 1899; the other specimen (USNM 101740), also an adult male, was collected on September 23. Both were obtained by Abbott.

Miller described *flaviventer* as a species of *Mus* and characterized it as "Similar to *Mus cremoriventer* Miller from Trang, Lower Siam, but slightly larger and with entire pelage much more strongly suffused with yellow." He also pointed out that "The skull closely resembles that of *Mus cremoriventer* differing only in slightly larger size and relatively smaller audital bullae, characters that may prove to be purely individual." In essence, Miller considered *flaviventer* to be "a yellowish, insular form of *M. cremoriventer*. It is not closely related to any of the species thus far recorded from the Natuna Islands." The taxon has invariably been listed in the literature as a subspecies of *R. cremoriventer* (Chasen and Kloss, 1928; Chasen, 1940; Ellerman, 1949).

In their report on a collection of mammals made on the Anambas Islands, Chasen and Kloss (1928) pointed out that faunal affinities of Anambas Islands are with the Malay Peninsula to the west and not with the Natuna Islands to the east. In morphology of skin and skull the two specimens of *flaviventer* are more similar to samples of *Rattus cremoriventer* from Malaya than to samples of the species from the islands to the east or south. In fact, the holotype actually has reddish brown upper parts and is indistinguishable in color from adults taken on the Malayan mainland. The two specimens from Jimaja Island clearly fit within the range of variation of pelage color and cranial features shown by samples from

Malaya and peninsular Thailand. To recognize the sample from Jimaja Island as subspecifically distinct is only to point out its geographic origin; morphologically it fits with *R. c. cremoriventer*, and I regard *flaviventer* as a synonym of that form.

There are a few specimens of *Rattus cremoriventer* from Sumatra and adjacent islands. Two sets of these samples will be discussed later in this report. One set is from Bangka and Billiton islands and the mainland of southern Sumatra and the other is from Nias Island. Each of these two sets represent distinct populations and different subspecies from the form from Malaya and peninsular Thailand. There is one specimen from northwestern Sumatra, however, that is an example of *R. cremoriventer cremoriventer*. Its identity is discussed below.

In addition to the specimens from Bangka and Billiton islands, southern Sumatra, and Nias Island, the only other example of *R. cremoriventer* from Sumatra that I have seen is a specimen (ZMA 12.714) that was obtained from Medan (formerly called Deli), on the northwestern coastal plain of northern Sumatra. It is an adult male and was collected sometime during the period from 1905 to 1917. I asked P. J. H. van Bree of the Zoological Museum if he could supply me with more data about the rat. He wrote that, "The collector, Dr. L. P. Cosquino de Bussy was a Dutch botanist, who worked from 1905 till 1917 at the Hevea Institute at Medan, Sumatra. During that time, he put all mammals he received from the surroundings of Medan (the former residence 'Deli') in large containers with alcohol. When he came back he presented the material to our museum." More precise information about date of capture and locality is not available.

The rat from Medan is preserved in fluid and the cranium and mandibles have been extracted and cleaned. The pelage is discolored, and the cranium is damaged so I could not take all the measurements that I obtained from intact specimens in other samples. Those external and cranial measurements that I could take are, respectively: length of head and body 130, length of tail 185, length of hind foot (including claw) 28, length of ear (from notch) 19, interorbital breadth 6.0, length of nasals 12.4, length of rostrum 10.6, breadth of rostrum 6.5, breadth of zygomatic plate 3.0, depth of zygomatic notch 0.7, breadth of brain case 14.5, height of brain case 10.0, length of palatal bridge 6.1, breadth of palatal bridge at first upper molars 3.2, breadth of palatal bridge at third upper molars 4.4, breadth of mesopterygoid fossa 2.9, alveolar length of maxillary toothrow 6.2, length of first upper molar 3.3, breadth of first upper molar 1.8, length of bulla 4.5, breadth of bulla 4.0, height of bulla 3.9.

In features of skin, skull, and teeth, the specimen from Medan is unlike samples from Nias Island, the mainland of southern Sumatra, or Bangka

and Billiton islands. Its external, cranial, and dental dimensions are smaller than any specimen of comparable age of *R. c. barussanus* from Nias Island and larger than specimens of *R. c. mengurus* from southern Sumatra. Among specimens I have examined, the rat from Medan fits best with samples of *R. c. cremoriventer* from Malaya. Not only do external and cranial dimensions of the animal from Medan fall within the range of variation seen in samples from Malaya (table 1), but in cranial configuration the specimen is indistinguishable from examples of comparable age in the Malayan samples. The teeth of the Medan rat appear slightly more robust than those in the Malayan specimens, but that is the only possibly significant difference I could detect and for the present I am identifying the specimen from Medan as *R. c. cremoriventer*.

Rattus cremoriventer barussanus: This form was named and described by Miller in 1911 (p. 26) and was based on four specimens obtained by W. L. Abbott from the mouth of the Mojeia River, Nias Island, off the west coast of Sumatra. The holotype (USNM 141208), an adult male, was obtained March 10, 1905, and the three other specimens (USNM 141206, 141207, 141209) were collected on March 9, 10, and 17. Miller described the taxon as a full species closely related to *R. cremoriventer*. He diagnosed it as "A member of the *Epimys cremoriventer* group resembling the previously known species in general appearance, but size decidedly greater, and skull with anterior portion of rostrum widened." Although Tate (1936, p. 566) placed *barussanus* in his "*Rattus huang-fulvescens* Group," recent checklists enter the form as a subspecies of *R. cremoriventer* (Chasen, 1940; Ellerman, 1949).

The taxon is still known only from four specimens and these comprise a sample of the most distinctive morphological population of *R. cremoriventer* I have seen and one that is known only from Nias Island (fig. 3). The specimens resemble *R. c. cremoriventer* in coloration, including the monocolor tail, but they are distinguished from samples of that form and from every other geographic sample of *R. cremoriventer* by size. In most external, cranial, and dental measurements (for example, length of head and body, greatest length of skull, and length of maxillary toothrow) examples of *R. c. barussanus* are significantly (at the 0.05 level) larger than specimens of comparable age in any other available sample of *R. cremoriventer* (table 1). When Miller described *barussanus* he noted its large size and also remarked that "Aside from its conspicuously greater size the skull of *Epimys barussanus* differs from that of *E. cremoriventer* in a distinct broadening and deepening of anterior portion of rostrum at once appreciable on comparison of specimens." This feature of the rostrum is a function of the large size of the specimens of *R. c. barussanus*.

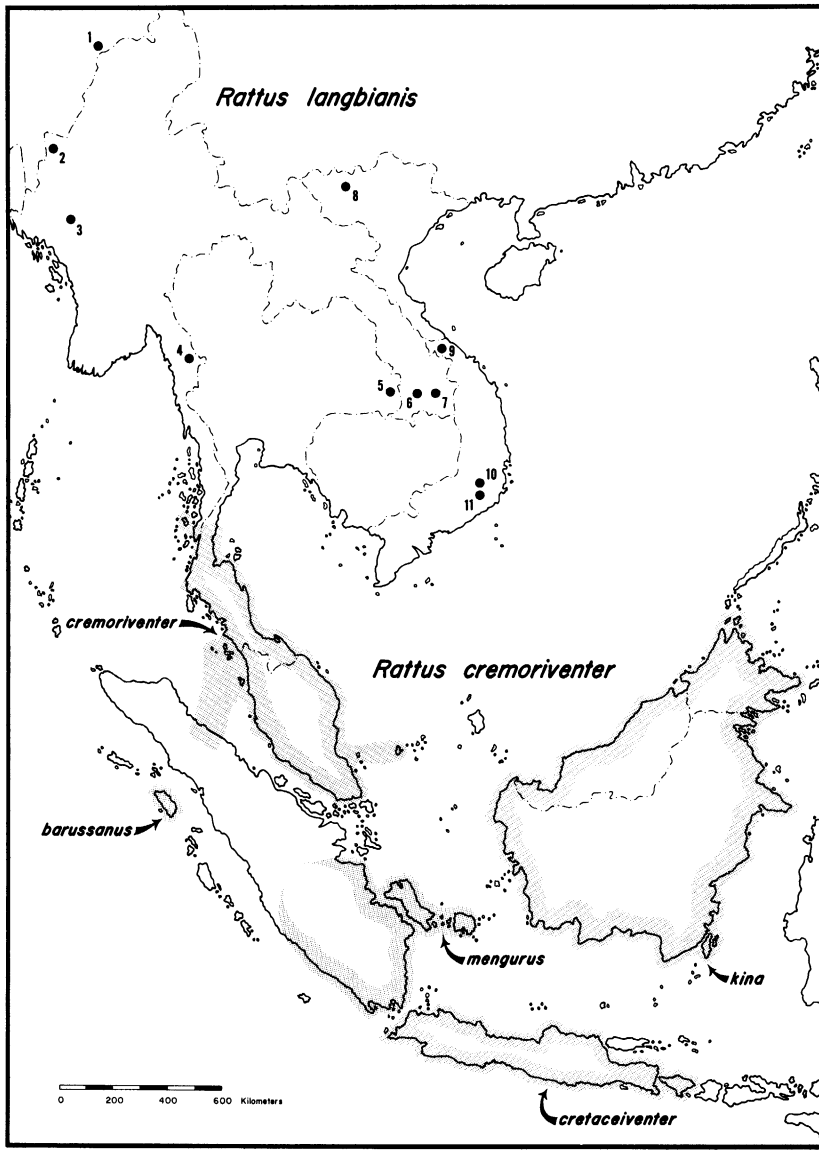

FIG. 3. Geographic distribution of *Rattus langbianis* in Southeast Asia and *R. cremoriventer* on the Malay Peninsula and Greater Sunda Islands, based only on specimens I examined. Localities for *R. langbianis* are represented by numbered dots; numbers correspond to localities listed in text. Geographic ranges of the five subspecies of *R. cremoriventer* that I recognize are outlined in stipple. Localities from which specimens were obtained are listed in text.

Rattus cremoriventer mengurus: This subspecies is known from Billiton and Bangka islands and the adjacent mainland of southern Sumatra. The taxon, named and described by Miller in 1911 (p. 27), was based on an adult male collected by W. L. Abbott on August 14, 1904, from Bukit Menguru, Billiton Island, situated east of Bangka Island off the northeastern coast of southern Sumatra (fig. 3). In addition to the holotype (USNM 125021) from Billiton Island, Miller also referred two specimens from Bangka Island to *mengurus*. These examples (USNM 124887, 124889) were obtained by Abbott on June 24 and 28, 1904, from near Klabat Bay and are represented only by skulls. There is also a fourth specimen (USNM 124695), a young female (skin and skull) from Tanjong Rengsam on Bangka Island.

The specimens from Bukit Menguru and Klabat Bay were first reported by Lyon in 1906 (p. 595) as "*Mus cremoriventer*." Miller (1911), however, thought the specimens represented a distinct species and characterized it "Like *Epimys cremoriventer* but with relatively longer tail, smaller teeth and more slender skull; nasals showing a tendency to widen anteriorly as in *E. barussanus*." The taxon has been regarded as a subspecies of *R. cremoriventer* by Sody (1937), Chasen (1940), and Ellerman (1949), a view with which I agree.

Of the four specimens only the holotype is adult. External, cranial, and dental dimensions of that specimen are smaller than those in most other geographical samples of *R. cremoriventer* (tables 1, 2). In size, the holotype fits only with a sample from the mainland of southern Sumatra. It is also like specimens in that sample in color of head and body and in cranial configuration, but it differs from most of them in coloration of tail. The holotype of *R. c. mengurus* has a tail that is dark brown above and only slightly paler below. In contrast, five of the six specimens from southern Sumatra have tails that are brown above and conspicuously paler below, and the other one has a monocolor tail. The tail of the only other skin from Bangka Island, the female from Tanjon Rengsam, is also brown everywhere.

The taxon *sumatrae* is a synonym of *R. c. mengurus*. The name was proposed by Bartels in 1937 (p. 123) on the basis of two adult males, the holotype (S-180) and paratype (S-161) that are in the collection of Max Bartels, Jr., now housed in the Rijksmuseum van Natuurlijke Historie, Leiden. Both specimens were collected by Bartels and Berkholst from near Bandjarnegri, Wai Semangka, Lampoengs, southeastern Sumatra at about sea level on July 2, 1935. The taxon has invariably been regarded as a subspecies of *R. cremoriventer* (Chasen, 1940). In addition to the two type specimens, I have examined four (AMNH 102666, 102667, 102668,

103303)[1] from Macarah Doewa, Palembang, on the northeastern coastal plain of southern Sumatra, that were taken at an elevation of 100 meters.

In his original description, Bartels diagnosed *R. c. sumatrae* as follows: "Agrees with *R. c. cretaceiventer* Rob. & Kloss from Java, except in having the tail and, apparently, also the ear and the hindfoot *shorter* and all the principal measurements of the skull (except, perhaps, the breadth of the nasals) smaller. The head-and-body-length will probably also prove to be somewhat smaller when a large series is available. Furthermore the tail is distinctly paler beneath than on the upperside, however without being really bicolored, in one of my two specimens; this character occurs in only two (young) specimens (from Wijnkoopsbay, W. Java, and G. Slamet, Central Java) of my large series (75 specimens) of *cretaceiventer*."

External, cranial, and dental measurements of five adults from the mainland of southern Sumatra are listed in table 1. Although I have seen four more specimens than were available to Bartels, I can add little to his description and comparison of *R. c. sumatrae*. The four specimens in the American Museum of Natural History are brightly colored, small-sized rats that are morphologically more like examples of *R. c. mengurus* from Bangka and Billiton islands than any other geographic sample of the species. In fact, the degree of morphological difference between the sample from the mainland of southern Sumatra and those from Billiton and Bangka islands is not so great as that seen between many samples of *R. c. cremoriventer* from Malaya and even between specimens of the latter from one locality.

In my opinion, the slight differences between the sample from the mainland and those from the islands are not taxonomically significant and I regard *sumatrae* as a synonym of *mengurus*. Although small, the samples

[1] The identifications of three of the four specimens from Macarah Doewa, numbers 102666–102668 have a history. These examples, along with three rats (AMNH 102808–102810) from Kalianda, Sumatra were collected by J. J. Menden in 1934. When the specimens were received at the American Museum, they were identified by someone as "*Rattus mengurus*." However, in his report on murid rodents of the Indo-Australian region, Tate (1936, p. 566) discussed the six specimens under the name, "*Rattus* near *hylomyoides*." He also listed measurements of the three from Macarah Doewa under "*Rattus hylomyoides*" in his table (p. 678). The three rats from Macarah Doewa of course are examples of *Rattus cremoriventer*, but the three from Kalianda are examples of *R. bukit* (or *niviventer* in Ellerman's lists) *jacobsoni*. This taxon was named and described by Bartels (1937) in the same paper in which he described *R. cremoriventer sumatrae*. Thus, Tate's sample of "*Rattus* near *hylomyoides*" consisted of two species and it is no wonder that in his account of these specimens he commented that, "Although the animals of the above series are referred now to *hylomyoides* of western Sumatra, they may represent something new."

seem to represent the same population. In their small size, especially in cranial dimensions, and small teeth, the specimens from southern Sumatra and Billiton and Bangka islands are distinctive. The specimens are morphologically unlike both the form from Nias Island, *R. c. barussanus*, and the single example of *R. c. cremoriventer* from Medan in northwestern Sumatra. Judged from the small sample of *R. c. mengurus* available for study, the subspecies is not especially closely allied to any other geographic sample of the species, except possibly the animals from Borneo and its offshore islands. The Bornean rats resemble those from southern Sumatra in that they show some expression of a two-tone tail, but in other external and cranial features the animals from Borneo and southern Sumatra are dissimilar.

Rattus cremoriventer cretaceiventer: This form is known only from Java and Bali (fig. 3). I have examined 113 specimens from the following localities.

WESTERN JAVA

Palaboean, sea level (MZB 5722; RMNH 14054).

Wooded mountainous country near Wijnkoopsbaai on the south coast (RMNH 13749, 13988).

Tjibodas, slopes of Mount Gede, 1200 to 1500 meters (BM 26.10.19.11, holotype of *cretaceiventer*; Collier Coll. 91, 97, 316; Bartels Coll. 211, 215; RMNH 13578, 13656, 13659, 13714, 13771, 13792).

Southwest slopes of Pangrango Gede Mountains: Tjibuni, 1350 meters (Sody Coll. Nos. Tjibouni-80, 143, 144, 164, 165, 193, 194, 195); Pasir Datar, 1000 meters (RMNH 13579, 13633, 13698, 13739, 13761, 13928, 14056, 14085, 15756; Bartels Coll. 266); Situ Gunung, 1200 meters (RMNH 14082); Tjimahi, 900 to 1200 meters (RMNH 13668, 13692); Podjok, 900 to 1200 meters (RMNH 13657, 13660, 13634, 13661, 13696, 13577, 13715, 13716, 13738, 13748, 13740, 13793, 13794, 13779, 13796–13798, 13989, 14109); Tjiparaj, 900 to 1000 meters (Bartels Coll. 181; RMNH 13568, 13569, 13700–13702, 13671, 13717, 13750, 13795, 13842, 13843, 13897, 13898, 13926, 13927, 13943, 13961, 14008, 14009, 14055, 14074, 14075, 14083, 14084, 14108, and 15757).

Pangrango-Gede Mountains, 900–1200 meters (Bartels Coll. 316; RMNH 13643, 13669, 13699, 13762, 13918).

CENTRAL JAVA

Pangandaran, southern coast (RMNH 13552, 13555).

Tjandiroto, 700 meters (Sody Coll. B-87, B-88).

Ngebel (MZB 5568).

Mount Slamet, 800, 1500–2500 meters (Sody Coll. C-145, C-152, C-161, C-162; RMNH 13697).

Mount Lawoe, south slopes, 1500–2000 meters (Bartels Coll. 1933).

EASTERN JAVA

Blawan, Idjen, 950 meters (MZB 681).

Noesa Kambangan (MZB 5724).

Malang (MZB 5727).

BALI

Bratan (AMNH 107974).

Oeboed (AMNH 107535–107539, 107971, 107972; MZB 5725, 5726).

Rattus cremoriventer cretaceiventer was named and described by Robinson and Kloss in 1919 (p. 377) and was based on an adult male (BM 26.10.19. 11) collected by H. C. Robinson from Tjibodas, from the slopes of Mount Gede in western Java, 1367 meters, on February 22, 1916. The describers regarded *cretaceiventer* as a distinctive subspecies of *R. cremoriventer* and characterized it as "A rat of the group represented in the Malay Peninsula by *R. cremoriventer* (Miller) and in Borneo by *R. kina* and *R. rapit* (Bonhote), but pelage longer and less spiny, colour duller, and with the belly almost chalk-white with only a faint tinge of cream. Teeth decidedly heavier and interparietal foramina narrower. Bullae larger and broader." Robinson and Kloss made further distinctions between *R. c. cremoriventer* and *R. c. cretaceiventer* in describing the skull of the latter: "The cranial portion relatively shorter and broader than in *R. c. cremoriventer*, with the parietal ridges less sharply deflected. Orbital constriction more marked and the infra-orbital plate narrower; zygomatic arches decidedly more slender; nasals as in *R. c. cremoriventer*, terminating in a point posteriorly. Beneath, with the palatal foramina narrower, the interpterygoid space almost parallel-sided, not pear-shaped anteriorly; bullae decidedly larger and more globose in an anteroposterior direction. Teeth decidedly larger, the posterior molar much larger."

Judged from geographic samples of *Rattus cremoriventer* that I examined, specimens of *R. c. cretaceiventer* are morphologically similar to *R. c. cremoriventer* from Malaya and peninsular Thailand. I cannot appreciate differences between the two taxa that were pointed out by Robinson and Kloss. In fact, the only consistent difference is length of tail. Samples of *R. c. cretaceiventer* have significantly longer tails than those of *R. c. cremoriventer* (table 1). Samples of *R. cremoriventer* from Borneo (*R. c. kina*), Bangka and Billiton islands and southern Sumatra (*R. c. mengurus*), and Nias Island (*R. c. barussanus*) are far more distinctive compared with samples from Malaya and peninsular Thailand than are samples of *R. c. cretaceiventer* from Java.

Rattus cremoriventer also occurs to the east of Java on the island of Bali. Sody (1941, p. 294) first recorded the species from there and considered specimens he examined to be inseparable from Javanese material. Sody examined two specimens from Bali, and I have seen 10 rats from there. Judged by this small sample, the population of *R. cremoriventer* on Bali is morphologically distinctive. Specimens are larger than those from Java of comparable age and their upper parts are paler—a dull orange-yellow compared with the bright orange or reddish brown of the Javanese

specimens—as I described earlier in this paper. Furthermore, their pelage is more spiny. In color and texture of pelage the sample of *R. cremoriventer* from Bali is one of the most distinctive geographic samples of the species I have seen.

Rattus cremoriventer kina: This subspecies is known from mainland Borneo and some offshore islands (fig. 3). I have studied 126 specimens from the following localities.

SABAH
Mt. Kinabalu (BM 94.7.2.23; 94.7.2.24, holotype of *kina*; 94.7.2.25, 94.7.2.26).
Kian, Mt. Kinabalu, 900 meters (NMS 3619, 3631).
Bundu Tuhan, Mt. Kinabalu (USNM 292782–292788) 5 km. north of Dalas, Mt. Kinabalu (USNM 292789).
Menggatal Rubber Estate, 18 km. northeast of Jesselton (USNM 292790, 292791).
Trus Madi, Pampang Camp (USNM 301090).
Ranau, 450 meters (USNM 301085–301088, 301096).
Rayoh (NMS 3569, 3570, 3585, 3590, 3596).
Bettotan, near Sandakan Harbor (NMS 3211).
SARAWAK
Mt. Dulit (BM 51.290).
Baram, Mt. Dulit, 900 meters (NMS 644/19, 645/19).
Baram District (USNM 141479).
Entawa, Samarahan (BM 55.956; NMS 654/19, 656/19).
Buhar, Samarahan (NMS 652/19, 653/19).
Gunong Sidong, Samarahan, 360 meters (BM 51.954, 51.955; NMS 648/19, 651/19).
Baran, Tinjar River, Sungei Lenin, 150 meters (BM 55.952).
Baran, Tinjar River, Long Lenin (BM 55.953).
Sungei Pelandok, Paku, Sarebas (BM 55.950, 55.957; NMS 298).
Anyut, Paku, Sarebas (BM 55.951).
Ulu Paku, Sarebas (BM 55.949).
Perboewa (Landak), 900 meters (AMNH 106751, 106758).
SOUTHWESTERN KALIMANTAN
Kendawangan River (USNM 153709).
Kotawaringin, Riam, 300 meters (AMNH 106121, 106122, 106208–106222; MZB 5711–5715, 5718–5720).
Sampit on Tjampaga River (AMNH 103571–103589; MZB 5716, 5717, 5721).
NORTHEASTERN KALIMANTAN
Peleben (AMNH 103934).
EASTERN KALIMANTAN
Sungai Pelawan (USNM 198166).
Sungai Karangan (USNM 198162, 198163).
Labuan Klambu (USNM 197356, 197357).
Long Petak (MZB 1293, 1294).
Balik, Papan Bay (USNM 154302–154305).
Gunong Batu (USNM 198164, 198165).

OFFSHORE ISLANDS

Lamukotan Island, western Kalimantan (USNM 145499, holotype of *spatulatus*).
Sebuku Island, southeastern Kalimantan (USNM 151933).
Balambangan Island, off the northernmost coast of Sabah (NMS 3485, 3474).
Banguey Island, off the northernmost coast of Sabah (NMS 3352, 3368, 3386, 3387, 3398, 3439, 3444, 5438).
Malewali Island, off the northernmost coast of Sabah (BM 47.1463, holotype of *malawali*; NMS 3456, 3457).

The taxon *kina* was named and described by Bonhote in 1903 (p. 124) from an adult male (BM 94.7.2.24) collected by A. H. Everett in January, 1894, from Mount Kinabalu, northern Sabah. Bonhote described *kina* as a species of *Mus*, but he compared it with *cremoriventer* and remarked that "Although from the skins there is apparently little difference between this species and *Mus cremoriventer*, the larger size of the skull will enable it to be very easily recognized. Not having any measurements in the flesh, it is difficult to say whether it would be recognizable by its size without reference to the skull." The taxon is currently regarded as a valid subspecies of *Rattus cremoriventer* (Chasen, 1940; Ellerman, 1949; Hill, 1960; Medway, 1965).

Samples of *R. c. kina* are morphologically similar to those of *R. c. cremoriventer* from Malaya and peninsular Thailand; the two kinds differ primarily in size, configuration of nasals, and coloration of tail. My specimens of *R. c. kina* are significantly smaller than those of *R. c. cremoriventer* in all external and cranial measurements except in the length of tail, hind foot, ear, and in breadth of zygomatic plate, depth of zygomatic notch, size of bullae, length of maxillary toothrow, and size of upper first molars. There are no significant differences in these dimensions between available samples of the two forms. However, the sample of *R. c. kina* from which I obtained measurements consists of mostly young adults, whereas the sample of *R. c. cremoriventer* contains a greater proportion of older and larger animals, so the differences recorded here may not be significant when specimens of similar age are compared.

Probably the most distinctive qualitative cranial feature of *R. c. kina* is shape of the nasals. In these specimens ends of the nasals are expanded and wider relative to their lengths than in specimens in geographic samples from outside of Borneo.

Coloration of the tail is variable in samples of *R. c. kina*. One extreme is represented by specimens with tails that are dark brown on all surfaces, like *R. c. cremoriventer*. At the other extreme are specimens with tails that are dark brown above but unpigmented below. In these examples the tails are bicolored. Gradations between these extremes are represented by specimens in which tails are dark brown above and either pale brown or

mottled below. However, approximately 90 percent of the specimens have a completely or partially bicolored tail, and this feature will distinguish most specimens of *R. c. kina* from all other samples of *R. cremoriventer* except for the one from southern Sumatra, a small sample in which the specimens have tails that are dark brown above and pale brown beneath.

I regard the names *spatulatus* and *malawali* to be synonyms of *R. c. kina*. The taxon *spatulatus* was named and described as a species of *Epimys* by Lyon in 1911 (p. 111) and was based on an adult male (USNM 145499) collected by W. L. Abbott from Pulo Lamukotan, a small island off the west coast of Kalimantan on May 10, 1907. To my knowledge the taxon is still known only from the holotype. Lyon described *spatulatus* as a full species and diagnosed it as "A member of the *Epimys cremoriventer* group distinguished by its large size and the widened extremity of the nasals." Tate (1936, p. 566) included *spatulatus* in his "*Rattus huang-fulvescens* Group," but Chasen (1940), Ellerman (1949), and Medway (1965) regarded the taxon as a subspecies of *R. cremoriventer*.

In features of skin and skull the holotype of *spatulatus* is similar to samples of *R. c. kina* from the adjacent mainland. Widened tips of the nasals are a characteristic of *kina*, and like that form, the holotype has a tail that is dark brown above and pale below. The specimen is larger than many examples of *R. c. kina*, but that is the only difference, and some samples of *kina* from the mainland approach or equal the holotype of *spatulatus* in size.

Chasen and Kloss named and described *malawali* in 1931 (p. 32) as a subspecies of *R. cremoriventer*. The taxon was based on 13 specimens from the islands of Balambangan, Banguey, and Malewali. These three islands cluster off the extreme northern coast of Sabah. The rats were obtained by Chasen and Kloss during the first two weeks of September, 1927.

There has been doubt about the taxonomic status of *malawali*. In their checklist of Palearctic and Indian mammals, Ellerman and Morrison-Scott (1951, p. 594) remarked that "(the form named *R. c. malawali* by Chasen and Kloss from Mallewallé Island, North Borneo, the type of which has recently been received in London, is not *cremoriventer* as here understood, and seems more like *R. canus*)." Medway (1965), however, listed *malawali* as a subspecies of *R. cremoriventer* on the strength of the 12 specimens in the National Museum, Singapore; he had not examined the holotype.

The holotype is the oldest and largest of the 13 specimens of *malawali*. It is clearly an old example of *R. cremoriventer*. It and the other 12 specimens are morphologically similar to specimens of *R. c. kina* from the mainland. Like that form, specimens of *malawali* have tails that are dark brown above and either pale brown or unpigmented below. They also have the expanded

nasals so characteristic of *R. c. kina*. Specimens of *malawali* average larger in most external and cranial dimensions than the sample of *R. c. kina* from southwestern Kalimantan that I measured (table 1), but specimens from mainland Sabah are virtually indistinguishable from those of comparable age from Balambangan, Banguey, and Malewali islands.

GENERAL REMARKS ON SUBSPECIES: My arrangement of the subspecies of *R. cremoriventer* is provisional. It is based on study of more than 375 specimens, but those examples are from scattered geographic regions. Some subspecies that I recognize are represented by good samples from several areas, but others are based on only a few specimens, and I cannot report much about their relationships to other populations of *R. cremoriventer*. Detailed studies of individual, sexual, and geographic variation of larger samples from a wider region will alter the pattern of variation I have discussed and may change my taxonomic outline of subspecies.

There are aspects of the subspecies I recognize that should be pointed out. For example, of the samples I studied, *R. c. barussanus* from Nias Island is the largest in body size. If the four specimens from Nias Island are a reliable sample of the morphological features of the population there, then, in size at least, that is one of the most distinctive and best-differentiated populations of the species. The four specimens are so different from the six examples of *R. cremoriventer* from the mainland of southern Sumatra and nearby Bangka and Billiton islands that the two kinds may even be reproductively isolated from each other; at least this possibility should be tested when more specimens are available for study. The population on Nias Island may originally have been derived from the mainland of Sumatra. Unfortunately, the geographic distribution of *R. cremoriventer* on that large island is poorly known. The only specimens have been taken from the southern end of Sumatra and from the region of Medan in northwestern Sumatra. Morphological characteristics of the species from central Sumatra and from the mainland across from Nias Island are unknown.

That three subspecies of *Rattus cremoriventer* are known from Sumatra and offshore islands is of special zoogeographic interest. In addition to the distinctive population of *R. c. barussanus* from Nias Island, the Malayan subspecies *R. c. cremoriventer* is represented on northwestern Sumatra by the specimen from Medan, and the population in the lowlands of southern Sumatra and Billiton and Bangka islands comprise another distinctive morphologic group, *R. c. mengurus*. This is the smallest in body size of any of the subspecies of *R. cremoriventer* and in at least one feature—coloration of tail—it is more like samples from Borneo than samples from any other area on the Sunda Shelf or Malayan Peninsula. A similar general distri-

bution, although not precisely alike in details, has been described by Groves (1971) for the coucang, *Nycticebus coucang*. Populations of this primate from northern Sumatra are allied to those living on the Malayan Peninsula and the population from Bangka Island are like those from Borneo.

The populations of *R. cremoriventer* from Borneo and offshore islands (*R. c. kina*) are of interest because the variation in color of tail exceeds that found in any other sample or group of samples of the species except that of *R. c. mengurus* from southern Sumatra. That sample is small and I do not know if the variation in it is a reliable estimate of the range of variation that occurs in the population. On the other hand, there are more than 100 specimens of *R. cremoriventer* from Borneo and offshore islands that are available for study, enough specimens to indicate that some expression of a bicolored tail is characteristic of the population. Many of the specimens have sharply bicolored tails, the dorsal surface being dark brown and the ventral surface unpigmented. Tails of these specimens resemble those of *R. fulvescens* and *R. niviventer* and not typical *R. cremoriventer*. I do not know what the adaptive advantage of a monocolor dark brown tail is, but apparently on Borneo there is little selection pressure for monocolor tails, whereas in almost every other geographic area outside of Borneo where *R. cremoriventer* has been found, monocolor tails apparently have some adaptive advantage to the species.

The sample from Bali is distinctive and may deserve subspecific recognition. The specimens I have examined combine pale color of pelage with large body size (see figures 5, 6, and 7 where a skull of Malayan *R. cremoriventer* is contrasted with a Balinese specimen). Compared with all other samples of *R. cremoriventer*, the one from Bali is as divergent from typical *R. cremoriventer* in its morphologic features as is the one from Nias Island. I have not named the sample from Bali because I have not seen enough specimens of *R. cremoriventer* from eastern Java where the species might be morphologically like the population on Bali, and consequently I do not know what the morphologic and ecologic relationships are between populations from Java and Bali.

RATTUS LANGBIANIS

Comparisons with *Rattus cremoriventer*

Rattus langbianis is morphologically closely related to *R. cremoriventer* but available samples of the two kinds differ in color of pelage and size and proportions of external, cranial, and dental features.

The most conspicuous external difference between the two species is in color of upper parts. Pelage covering upper parts of *R. langbianis* is brown-

ish gray suffused with pale yellowish orange, with a distinct olive-gray tone. In most specimens a yellow-orange stripe separates color of the upper parts from the whitish underparts. The brownish gray upper parts with pale yellow and olive tones are a striking contrast to the orange or reddish brown upper parts of *R. cremoriventer*. This feature of the pelage will distinguish all specimens of *R. langbianis* from almost all those of *R. cremoriventer*. The sample of *R. cremoriventer* from the island of Bali is the exception. Examples from that island are paler than other samples of *R. cremoriventer*, and in color they approach specimens of *R. langbianis*, differing only in being brighter—the pelage is suffused with more bright yellow-orange tones.

Sides of the body of *R. langbianis* are brighter than the back because more ochraceous-tipped hairs are exposed and there are few black-tipped hairs. Cheeks, sides of the neck, and upper arms are bright orange-yellow in some specimens, a hue that contrasts sharply with the somber brownish gray tones of the rest of the head and body.

Underparts are white or pale cream in living animals, but discolor to sulphur yellow in some study skins.

Most specimens of *R. langbianis* have longer and softer pelage than examples of comparable age of *R. cremoriventer*. In the series of *R. langbianis* I have examined, the individual with the longest and softest pelage is an adult male from Chapa, North Vietnam (FMNH 31992). The over-fur extends up to 15 mm. over the back and rump and there are few of the flexible, flattened spinelike hairs scattered throughout. The pelage is soft and dense to the touch. The opposite extreme is represented by an old adult female from the Taok Plateau in peninsular Thailand (AMNH 54736). Pelage of both upper parts and underparts of that specimen consists mostly of semirigid spines with only scanty soft over-fur and under-fur. Other specimens of *R. langbianis* available for study fall between these extremes in texture of pelage, but most are like the specimen from Chapa.

Differences in proportions of external dimensions between samples of *R. langbianis* and *R. cremoriventer* are illustrated in figure 4. There I have compared five adults of *R. langbianis* from Assam and Burma (BM 20.6.7.34, 16.3.26.58; AMNH 163743-163746) with 15 adults of *R. cremoriventer* from Malaya (BM 49.612–49.618, 50.100–50.103, 50.105, 61.1235–61.1237). The similarities and differences in relative size illustrated by these particular samples provide an idea of the proportional differences between the two species.

The sample of *R. langbianis* from Assam and Burma averages a significantly shorter head and body than the series from Malaya but does not differ significantly in this dimension from other samples of *R. cremoriventer*

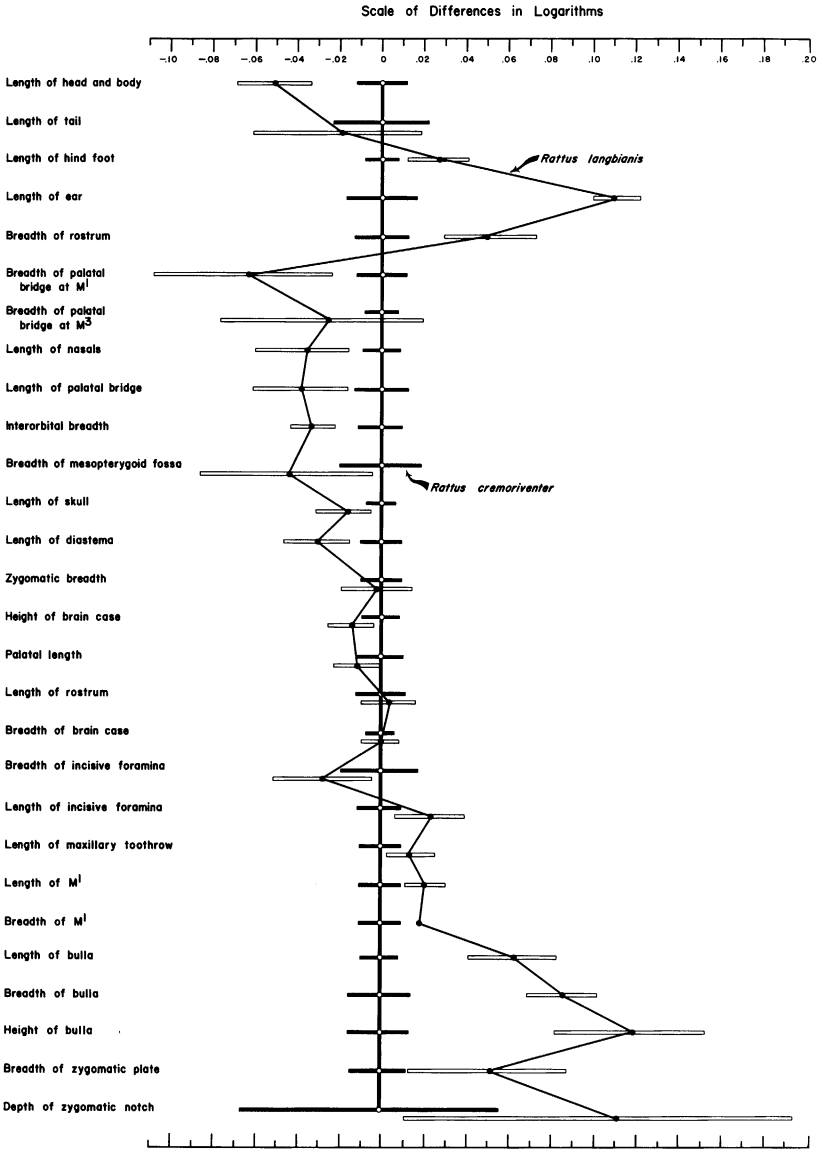

FIG. 4. Ratio diagram. Twenty-eight dimensions are compared in samples of *Rattus cremoriventer* (the standard) and *R. langbianis*. See Simpson (1941) and Musser (1970) for explanations of the ratio diagram.

TABLE 3

EXTERNAL AND CRANIAL MEASUREMENTS (IN MILLIMETERS) FROM SPECIMENS OF *Rattus langbianis*

	Assam	Burma				Tenasserim	Laos	North Vietnam	South Vietnam					
	BM 20.6.7.34	BM 16.3.26.58	AMNH 163746	AMNH 163745	AMNH 163743	AMNH 54736	AMNH 87485	FMNH 31992	USNM 321435	NMS 3430	NMS 3395	NMS 3361	NMS 3573	BM 26.11.17.14[a]
	Adult ♀	Adult ♂	Adult ♀	Adult ♂	Young Adult ♂	Old Adult ♀	Young Adult ♂	Young Adult ♂	Adult ♀	Young Adult ♂	Young Adult ♂	Young Adult ♂	Very Young Adult ♀	Very Young Adult ♂
Length of head and body	139	133	134	125	125	139	136	132	147	133	125	125	113	125
Length of tail	192	177	151	153	166	173	174	192	205	177	183	162	154	175
Length of hind foot	29	28	29	29	31	29	29	31	30	30	28	27	27	27
Length of ear	23	23	24	23	22	25	—	19	19	20	20	21	20	20
Greatest length of skull	35.7	35.5	35.0	34.1	32.9	—	34.6	36.0	37.4	33.9	32.8	32.9	—	—
Zygomatic breadth	16.4	17.7	16.9	17.3	15.8	—	16.4	17.5	18.1	15.7	15.4	15.5	14.8	16.1
Interorbital breadth	5.4	5.7	5.8	5.7	5.7	5.9	5.5	5.7	5.9	5.7	5.6	5.6	5.5	5.8
Length of nasals	12.3	12.0	12.3	11.0	11.0	13.7	12.4	12.6	13.5	11.5	11.8	11.6	—	—
Length of rostrum	10.4	10.8	11.3	10.9	10.5	11.5	10.3	10.6	10.7	9.9	10.4	10.1	—	9.6
Breadth of rostrum	5.8	5.9	6.5	5.9	5.6	6.5	5.6	5.7	6.2	6.2	5.8	5.7	5.1	6.0
Breadth of brain case	14.6	14.9	14.6	14.7	14.0	—	14.1	15.4	14.9	14.5	14.1	14.1	—	14.5
Height of brain case	9.9	9.8	9.4	10.1	10.0	—	9.6	10.1	10.3	10.1	9.1	9.8	—	9.8
Breadth of zygomatic plate	3.4	3.5	3.1	2.9	2.8	3.6	3.4	3.5	3.8	3.1	3.0	3.0	2.6	3.3

TABLE 3—(*Continued*)

	Assam	Burma				Tenasserim	Laos	North Vietnam	South Vietnam					
	BM 20.6.7.34	BM 16.3.26.58	AMNH 163746	AMNH 163745	AMNH 163743	AMNH 54736	AMNH 87485	FMNH 31992	USNM 321435	NMS 3430	NMS 3395	NMS 3361	NMS 3573	BM 26.11.17.14[a]
	Adult ♀	Adult ♂	Adult ♀	Adult ♂	Young Adult ♂	Old Adult ♀	Young Adult ♂	Young Adult ♂	Adult ♀	Young Adult ♂	Young Adult ♂	Young Adult ♂	Very Young Adult ♀	Very Young Adult ♂
Depth of zygomatic notch	1.0	1.5	1.3	.8	1.2	1.9	.7	1.4	1.1	1.4	1.5	1.1	1.3	1.1
Length of diastema	8.4	8.9	8.5	8.7	8.0	9.7	8.7	8.9	9.1	8.6	8.5	8.6	8.0	8.6
Palatal length	17.1	17.0	16.6	16.6	15.9	17.8	16.7	17.5	17.7	16.4	16.5	16.3	—	16.6
Length of palatal foramina	6.4	6.3	6.6	6.7	6.0	7.5	6.4	6.7	6.8	6.0	5.8	5.9	5.4	6.1
Breadth of palatal foramina	2.4	2.5	2.7	2.8	2.6	2.9	2.6	2.6	2.5	2.8	2.5	2.7	2.4	2.5
Length of palatal bridge	6.0	5.7	5.3	5.3	5.3	6.3	5.8	6.2	6.7	5.9	5.8	6.0	5.6	6.0
Breadth of palatal bridge at M^1	2.8	3.4	3.4	3.5	2.8	3.4	3.4	3.0	3.1	2.9	2.9	2.8	2.7	3.0
Breadth of palatal bridge at M^3	3.4	4.4	4.1	4.7	3.8	4.4	4.0	3.8	4.0	3.7	3.7	3.8	3.4	3.5
Breadth of mesopterygoid fossa	—	—	2.5	2.8	2.4	—	2.8	2.7	2.6	2.5	2.6	2.6	2.6	2.2
Length of bulla	4.9	5.5	5.6	5.3	5.1	6.1	5.1	5.4	5.2	5.2	5.2	5.0	—	5.0
Breadth of bulla	4.9	4.9	5.2	4.7	4.7	5.4	4.8	5.1	5.6	—	—	—	—	4.9
Height of bulla	3.7	4.0	4.2	4.7	4.4	4.6	4.5	4.2	4.7	—	—	—	—	4.1
Alveolar length of M^{1-3}	6.5	6.5	6.2	6.1	6.2	6.7	5.8	6.6	7.0	6.4	5.9	6.0	6.0	5.9
Length of M^1	—	—	3.1	3.1	3.0	3.3	3.0	3.3	3.4	3.2	3.0	3.1	3.1	2.9
Breadth of M^1	—	—	1.7	1.7	1.7	2.0	1.5	1.9	1.9	1.9	1.8	1.7	1.8	1.7

[a] Holotype of *R. cremoriventer langbianis*.

FIG. 5. Dorsal views of crania. Top, *Rattus cremoriventer: R. c. cremoriventer* (AMNH 217621, adult male) from Malaya, Selangor State, left; *R. c. cretaceiventer* (AMNH 107972, adult female) from Bali, right. Bottom, *R. langbianis:* adult female from Burma (AMNH 163746), left; adult female from South Vietnam (USNM 321435), right. Approximately ×1.5.

(tables 1 and 3). However, specimens of *R. langbianis* have a significantly longer hind foot—not only actually longer, but also longer relative to length of head and body—than all the samples of *R. cremoriventer* I measured except those from Nias Island and Bali. Specimens from there have longer hind feet than specimens in other samples of *R. cremoriventer.*

The most striking difference in external dimensions between samples of *R. langbianis* and *R. cremoriventer* is in length of the ears, and specimens of each species of comparable age can easily be distinguished by this

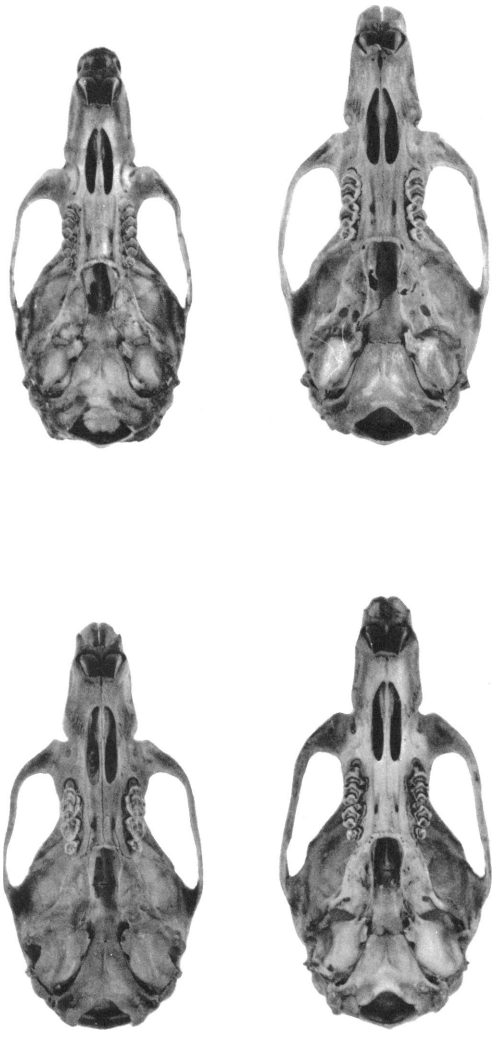

FIG. 6. Ventral views of crania of same specimens as in figure 5. Top, *Rattus cremoriventer*; bottom, *R. langbianis*. Approximately ×1.5.

feature. *Rattus langbianis* has larger ears than those of *R. cremoriventer*, not only in absolute size, but larger relative to lengths of head and body, tail, and hind foot (fig. 4).

Crania of *Rattus langbianis* and *R. cremoriventer* are compared in figures 5, 6, and 7 where two examples of *R. langbianis* are contrasted with two of *R. cremoriventer*. Each set is an example of the kind of geographic variation I found in available samples of the two species. *Rattus langbianis* is illustrated by a specimen from Burma (AMNH 163746) that represents a

FIG. 7. Lateral views of crania of same specimens as in figure 5. Top to bottom: *Rattus c. cremoriventer*, Malaya; *R. c. cretaceiventer*, Bali; *R. langbianis*, Burma; *R. langbianis*, South Vietnam. Approximately ×1.5.

population of small-sized individuals from southwestern Burma, and a specimen from South Vietnam (USNM 321435), which is a good example of the larger individuals in samples from everywhere else in the known geographical range of the species. *Rattus cremoriventer* is exemplified by an individual from Malaya (AMNH 107972), which is an example of the medium-sized geographic variants of *R. cremoriventer*, and a specimen from Bali (AMNH 107972) that indicates size and cranial configuration of the large-sized geographic samples of the species.

Size of skull, as measured by greatest length and zygomatic breadth, will not distinguish some samples of the two species from one another. For example, specimens of *R. langbianis* from Burma are significantly smaller

than specimens of *R. cremoriventer* of comparable age from Bali and Nias islands (tables 1 and 3), but they are closely similar in size of many cranial dimensions to series of *R. cremoriventer* from peninsular Thailand, Malaya, Sumatra, and Borneo.

One cranial feature will distinguish all specimens of each species, regardless of ages or sizes of each that are compared—size of the bullae. Specimens of *R. langbianis* have conspicuously and significantly larger and more inflated bullae than do those of *R. cremoriventer*. Not only are the bullae absolutely larger, but they are longer, deeper, and wider relative to any other cranial and dental dimensions that I measured. These distinctions are clearly shown in the figures of skulls and the ratio diagram.

One other distinguishing cranial feature apparently cuts across variation because of age and geographical locality—length of the anterior incisive foramina. In all specimens of *R. langbianis* that I have seen posterior margins of the incisive foramina lie behind the anterior alveolar margins of the upper first molars. They penetrate at least ½ mm. and generally 1 mm. or more into the palatal bridge. This contrasts with more than 95 percent of the specimens of *R. cremoriventer* in which incisive foramina terminate either well before anterior alveolar margins of the first molars or just at those margins.

There are other distinguishing cranial features that are evident when specimens of *R. langbianis* are compared with those of *R. cremoriventer* of comparable age and size. *Rattus langbianis* has shorter nasals, a shorter and narrower rostrum, a less inflated interorbital region, wider zygomatic plates (but the depth of the zygomatic notch is similar), heavier and higher ridges outlining the interorbital region and dorsolateral margins of the brain case, a wider brain case, a shorter diastema, incisive foramina that are actually longer and longer relative to length of diastema, a conspicuously narrower mesopterygoid fossa, toothrows that are actually longer and longer relative to length of palatal bridge, and longer and wider teeth (as measured by lengths and breadths of first upper molars).

I could not find any significant differences between the two species in dental topography (fig. 2).

Geographic Distribution

Known geographic distribution of *Rattus langbianis* is from eastern India to North and South Vietnam. Known altitudinal range extends from 60 to 2800 meters. I have examined 23 specimens from localities listed below. Most of the localities are mapped in figure 3. The number in front of each locality corresponds to a numbered place on the map.

INDIA

1. Assam, Naga Hills, Margherita, 60 meters (BM 20.6.6.34).

BURMA

2. Chin Hills, 84 km. west of Kindat, 166 meters (BM 16.3.26.58).
3. Mount Victoria, 2200 and 2800 meters (AMNH 163743, 163745, 163746).
4. Tenasserim, Taok Plateau, 970 meters (AMNH 54736).

THAILAND

5. Ubon Province, Pibumangsahan District, village of Chong Mek, near the border of Laos (ASRCT 54-655–54-658; SMRL 4340).

LAOS

6. Plateau des Bolovens (AMNH 87485).
7. Plateau des Bolovens, Ban Ham Say Forest Reserve, 25 km. out of Pakse (USNM 355504).

NORTH VIETNAM

8. Chapa, 1300 to 1400 meters (BM 33.4.1.511; FMNH 31992, paratype of *indosinicus*).

SOUTH VIETNAM

9. 2 km. east of Khe Sanh (USNM 321428, 321434, 321435).
10. Langbian Peaks, 1800 to 2300 meters (BM 26.11.17.14, holotype of *langbianis*; NMS 3430).
11. Dalat, 1360, 1500, and 1515 meters (NMS 3361, 3395, and 3573).

Habitat

Unfortunately, I have very little information on the habitat of *Rattus langbianis*. The specimens from Chong Mek in eastern Thailand were caught on the ground beneath mixed deciduous forest. The species presumably lives in secondary and primary evergreen forests throughout the other parts of its geographic range.

Taxonomy and Geographic Variation

Taxonomy: The taxon *langbianis* was named and described by Robinson and Kloss in 1922 (p. 96). The name is the oldest available for northern *cremoriventer*-type rats. The holotype (BM 26.11.17.14) is a very young adult male collected on Langbian Peak, South Vietnam, on April 28, 1918, by C. Boden Kloss. Robinson and Kloss examined two specimens from the type locality and three others from Dalat. Those authors described *langbianis* as a subspecies of *Rattus cremoriventer*, "Most nearly resembling *R. c. cretaceiventer*, Robinson & Kloss, of Java; but a little duller in colour and the tail more finely ringed."

Two other names applied to samples of *cremoriventer*-type rats in the past are synonyms of *langbianis*: *indosinicus* and *vientianensis*. The taxon *indosinicus* was named and described by Osgood in 1932 (p. 307) on the basis of three specimens obtained from Chapa, North Vietnam. The holotype (FMNH 31933) is an adult male collected on February 15, 1929, by

Harold J. Coolidge, Jr. Another specimen (FMNH 31992), a young adult male, was obtained on February 12, 1929, by the same collector. The third specimen was a younger animal. I have examined only FMNH 31992, but Osgood (1932, p. 308) listed cranial and external measurements for the other two.

Osgood originally described *indosinicus* as a species of *Rattus*, but he remarked, "It is possible that further study will demonstrate a close relationship to *R. cremoriventer*, a dark-tailed species of the upper Malay Peninsula with which actual comparisons have not been made." Tate (1936, p. 566) listed *indosinicus* as a member of his "*Rattus huang-fulvescens* Group," but checklists published subsequent to Tate's paper have listed *indosinicus* as a subspecies of *R. cremoriventer* (Ellerman, 1949, 1961; Ellerman and Morrison-Scott, 1951).

I consider *Rattus indosinicus* Osgood (1932) to be a synonym of *R. langbianis* Robinson and Kloss (1922). I have compared one of the specimens from Osgood's original series (FMNH 31992) of *indosinicus* with specimens of comparable age of *langbianis*—both the original series examined by Robinson and Kloss and more recently collected material—and can find no significant taxonomic difference between the samples; FMNH 31992 is virtually indistinguishable from examples of *langbianis* of comparable age.

There is a record of *indosinicus* from northern Thailand reported in the literature. Allen and Coolidge (1940, p. 163) identified a series of rats taken from Mount Angka in the Chiengmai Province of Thailand as "*Rattus indosinicus*." Through the courtesy of Dr. Barbara Lawrence of the Museum of Comparative Zoology at Harvard College, I was able to study those specimens. None of them are *indosinicus* as that taxon was described by Osgood nor are they examples of *Rattus langbianis*. All the specimens are *Rattus niviventer* and they resemble samples of *R. n. confucianus* in most pelage and cranial features.

The taxon *vientianensis* is apparently another synonym of *Rattus langbianis*, an opinion I reached after reading the type description, not having examined specimens upon which the name was based. The taxon was named and described by Bourret in 1942 (p. 29) from material collected in the Vientiane region of Laos. Bourret regarded *vientianensis* as a subspecies of *indosinicus*, but Ellerman and Morrison-Scott (1951, p. 596) listed it as a subspecies of *R. cremoriventer*. Those authors did not examine any specimens of the taxon.

I was not able to locate a copy of the published description of *vientianensis* in libraries available to me, but Dr. Jean Dorst of the Muséum National d'Histoire Naturelle in Paris kindly sent me a photocopy of

Bourret's paper. Dr. Dorst also wrote me that the report in which the description of *vientianensis* is published is difficult to find for most of the copies were issued during wartime and they have been destroyed. He also mentioned that the type specimen has been lost.

Because the original publication is not generally available, I present here an English translation of Bourret's description of *vientianensis* (pp. 29–30).

"The Bacteriological Laboratory of the Institute Pasteur of Vientian has sent me two collections of rats from the region of Vientian; the first shipment sent in March 1942, comprised, besides a mouse, two species of rats; *Rattus concolor*, and another species represented by two dried specimens, that I had at first assigned to the group *Rattus rattus* without being able to be precise about subspecies or race.

"The second shipment, in May, contained a greater number of specimens preserved in liquid, representing the same species: 3 specimens of *Rattus concolor*, and 3 well preserved examples of another species or variety.

"The assignment I had first made of these rats to the group *R. rattus* must be rectified: the rat of Vientian has 8 mammae (the group *R. rattus* has 12), must be related to the group *Rattus concolor*, but differs slightly from various species and races currently known of that group.

"Diagnosis:

"Tail dark unicolor, a little longer than head and body; size medium; 8 mammae; big toe nail absent; underside white, clearly separated from the color of the sides; hands and feet white.

"This rat differs from *R. concolor* by the noticeably larger size and the color of the underside; it is more closely related to *R. indosinicus* Osgood from Chapa, but has a tail clearly shorter, 99 to 125 per cent the length of the body (average = 111 per cent) instead of 127 to 145 per cent (average = 137 per cent) for the rat of Chapa.

"An adult male has the hair of the back deep grey at the base and ochre at the extremity, a mixture of black hairs and longer white hairs; the pelage is fairly coarse; the underside is uniformly cream white, with hairs the same color throughout their length, paws white with a darker median band, not reaching the extremity.

"A young male has much softer hair, without long black or white hairs; the hair is much darker at birth, and the colored end is shorter and lighter, of the sort that altogether seems to appear to be a grey color washed with red-brown, and not ochre, as that of the preceding; the hair of the underside is very fine, sparse, white, and changes abruptly to grey on the sides of the body."

At the end of the description Bourret listed external measurements of 10 specimens, but he did not indicate from what species they were obtained. Judged from the measurements, two species are listed. Five are the size of *Rattus exulans concolor* and five are much larger and probably correspond to the five specimens of the rat he called *vientianensis*. These latter specimens bear the registration numbers 103, 173, 174, 175, and 176. Bourret's measurements for these specimens are, respectively: length of head and body, 176, 165, 150, 122, and 102; length of tail, 173, 178, 174,

138, and 117; length of hind foot, 30, 30, 30, 27, and 26.5; and length of ear, —, 20, 20, 17, and 18.5. Numbers 175 and 176 are juveniles, the rest are adults.

The combination of a dark unicolor tail that is longer than the head and body, eight mammae, and the description of the adult male agrees well with *Rattus langbianis*, the northern *cremoriventer*-type of rat. Until specimens from Bourret's type series are available for study (he did not designate a holotype), I am considering the name *vientianensis* to be a synonym of *langbianus*.

GEOGRAPHIC VARIATION: There are so few specimens of *R. langbianis* and they are from such widely scattered localities that I have not been able to analyze geographic variation in morphologic features of the species in any detail. All specimens of *R. langbianis* of comparable age are similar in color of head, body, and tail and there does not appear to be any significant geographic variation in pelage coloration. The only geographic variation that may be significant is in texture of pelage and body size.

There is a difference between some of the specimens in texture of pelage. Rats from North Vietnam, for example, have soft, thick fur. The single, old adult female from the Taok Plateau in the Tenasserim region of southeastern Burma has thin and spiny pelage. Specimens from other localities have pelage that is a combination of soft hairs and spines. Still, there are too few individuals from too few localities to determine whether differences in spininess of pelage is because of geographic, altitudinal, ecologic, seasonal, or individual variation.

There is geographic variation in size. The three specimens from Mount Victoria in southwestern Burma have certain smaller external, cranial, and dental dimensions than specimens of comparable ages from elsewhere in Burma, Assam, Thailand, Laos, and North and South Vietnam (table 3; figs. 5, 6, and 7). If those specimens from Mount Victoria actually represent the morphological nature of the population of *R. langbianis* from southwestern Burma, then that population is distinct and merits subspecific recognition. Study of more specimens, however, is needed to test this hypothesis.

TAXA INCORRECTLY ASSOCIATED WITH *RATTUS CREMORIVENTER*

Two taxa, *tenaster* and *blythi*, have been associated with *cremoriventer*-type rats in the literature. Neither, however, belongs with *R. cremoriventer* or *R. langbianis*. The taxon *tenaster* is a form of *R. niviventer* and *blythi* belongs in *R. fulvescens*. Reasons for these allocations follow.

TABLE 4

EXTERNAL AND CRANIAL MEASUREMENTS (IN MILLIMETERS) FROM ADULTS IN SAMPLES OF *Rattus*

	R. fulvescens gracilis Mt. Mooleyit			*R. blythi* Burma	*R. niviventer* Burma					"*Epimys tenaster*" Mt. Mooleyit		*R. langbianis* Burma and Assam				
	USNM 101520[a]	BM 88.12.1.55	BM 88.12.1.56	IMC 366A A.S.B.[b]	AMNH 163709	AMNH 163716	AMNH 163710	AMNH 163727	AMNH 163720	BM 88.12.1.53[c]	BM 88.12.1.54	AMNH 163746	AMNH 163745	AMNH 163743	BM 16.3.26.58	BM 20.6.7.34
	♀	♂	♀	♂	♀	♀	♂	♂	♂	♀	♂	♀	♂	♀	♂	♀
Length of head and body	—	—	—	—	150	155	163	147	144	160	146	134	125	125	133	140
Length of tail	—	—	—	—	210	205	223	194	193	209	211	151	153	166	177	148
Length of hind foot	—	—	—	—	32	32	33	34	32	34	33	26	26	25	28	26
Length of ear	—	—	—	—	24	22	24	22	22	24	23	24	23	22	23	20
Greatest length of skull	36.3	37.6	36.0	38.0	40.2	38.9	40.2	38.3	38.9	41.8	41.5	35.0	34.1	32.9	35.5	35.7
Zygomatic breadth	15.4	16.9	15.9	—	17.3	17.6	18.0	17.2	16.7	18.8	17.8	16.9	17.3	15.8	17.7	16.4
Interorbital breadth	6.0	6.4	5.6	—	6.1	5.8	5.9	5.9	5.6	6.6	6.7	5.8	5.7	5.7	5.7	5.4
Length of nasals	14.0	13.3	14.0	13.6	15.9	14.5	15.5	14.0	14.8	16.6	15.4	12.3	11.0	11.0	12.0	12.3
Length of rostrum	11.6	11.5	11.4	11.3	13.7	13.0	13.2	12.2	12.9	13.4	12.9	11.3	10.9	10.5	10.8	10.4
Breadth of rostrum	5.8	5.8	5.7	6.2	7.5	7.4	6.7	7.3	6.4	7.3	7.2	6.5	5.9	5.6	5.9	5.8
Breadth of brain case	14.6	16.0	14.7	—	15.7	14.9	15.9	15.3	14.9	15.9	15.6	14.6	14.7	14.0	14.9	14.6
Length of diastema	9.1	9.0	8.6	9.3	10.0	10.3	10.3	9.4	10.1	11.0	10.9	8.5	8.7	8.0	8.9	8.4
Palatal length	17.6	17.3	17.4	18.1	19.8	19.2	19.9	18.6	18.9	20.2	19.9	16.6	16.6	15.9	17.0	17.1
Length of palatal foramina	6.6	6.2	6.5	6.4	7.6	7.0	7.2	6.7	6.9	6.9	7.1	6.6	6.7	6.0	6.3	6.4
Length of palatal bridge	6.1	6.1	6.1	6.5	6.8	7.3	7.0	7.3	7.4	7.5	7.1	5.3	5.3	5.3	5.7	6.0
Length of bulla	4.6	4.8	4.5	4.7	5.3	5.2	5.4	5.2	5.2	5.6	5.5	5.6	5.3	5.1	5.5	4.9
Alveolar length of M^{1-3}	6.2	5.8	6.0	6.2	7.1	7.0	6.9	6.6	6.3	6.7	6.4	6.2	6.1	6.2	6.5	6.5

[a]Holotype of *Epimys gracilis*. [b]Holotype. [c]Holotype.

Epimys tenaster

In 1892 Thomas reported on the mammals obtained from Burma and Tenasserim by Signor Leonardo Fea of the Museo Civico in Genoa, during the period from 1885 to 1889. Among the specimens were 27 rats collected on the summit of Mount Mooleyit, 1800 to 1900 meters. Thomas identified these animals as "*Mus jerdoni*" (p. 939).

Following the publication of Thomas's report, some of the specimens of "*Mus jerdoni*" were sent to Gerrit S. Miller, Jr., at the National Museum of Natural History. Miller (1913) named and described these rats as "*Epimys gracilis*"; the holotype, USNM 101520, is an adult female. In 1941, *gracilis* was listed by Ellerman (p. 194) as a species of *Rattus*. Later, however, in 1949 (p. 71) he associated *gracilis* with *R. fulvescens* and regarded it as a valid subspecies, but in most recent checklists *gracilis* is considered a synonym of *R. f. fulvescens* (Ellerman and Morrison-Scott, 1951; Ellerman, 1961).

In 1916 Thomas named and described *Epimys tenaster*, based on two specimens; the holotype (BM 88.12.1.53) and another specimen (BM 88. 12.1.54) from the series collected by Fea. Thomas stated, "This is one of two species put by me under the erroneous heading of *Mus jerdoni*, Blyth, in my account of the Fea collection, the other being a smaller form recently named by Mr. Miller *Epimys gracilis*, and closely allied to *E. bukit*. *E. tenaster* appears to be only nearly related to the Malayan *E. cremoriventer*, from which the dimensions given above will readily distinguish it."

Thomas compared the holotype of *tenaster* with *E. cremoriventer*: "Quite like *E. cremoriventer*, Miller, but much larger. The fur similarly spiny, the colour buffy or ochraceous with sharply defined under surface, and the tail similarly well haired, uniformly brown." Thomas continued and described the skull as "conspicuously larger than that of *cremoriventer*, proportionally perhaps somewhat narrower. Supraorbital ridges well developed, evenly curved, not forming marked postorbital angles as in *E. surifer*."

The name *tenaster* was listed as a valid subspecies of *Rattus cremoriventer* by Ellerman in 1941 and has retained that status in checklists published since then (Ellerman, 1949, 1961; Ellerman and Morrison-Scott, 1951).

In the fall of 1969 I worked at the British Museum (Natural History) and examined the holotype of "*Epimys tenaster*." The holotype (BM 88.12. 1.53), an adult male, and the other specimen on which the name is based (BM 88.12.1.54), an adult female, are preserved in fluid. The skull of each has been extracted and cleaned. The holotype is slightly larger and older than the other specimen (table 4). In each the teeth are well worn. Pattern

of the cusps remains on the first two upper and lower molars, but is almost obliterated on the third upper and lower molars. Pelage of the upper parts of both specimens has many hard, spinelike hairs and is muddy brown. Underparts are straw yellow. These hues are alterations of the original color and are typical of old specimens that have been preserved in fluid for a long time. Dorsal and ventral surfaces of the tails of both specimens are pale, straw yellow; the original color faded long ago. I could not determine if the tails were once brown on both dorsal and ventral surfaces as Thomas claimed in his original description of *tenaster*.

I also compared the two specimens of *tenaster* with examples of *R. niviventer*, *R. fulvescens*, *R. cremoriventer*, and *R. langbianis* in the collection of the British Museum. Subsequently, I borrowed one of the specimens of *tenaster* and compared it directly with series of these four species and allied forms in both the American Museum of Natural History and the National Museum of Natural History, including the holotype of "*Epimys gracilis*," the form named and described by Miller from Mount Mooleyit. The holotype and the other specimen of *tenaster* are not examples of either *R. cremoriventer* or *R. langbianis*. They represent a population of *R. niviventer*, a species that is morphologically similar to *R. cremoriventer*, *R. langbianis*, and *R. fulvescens* and one that occurs together with these species throughout parts of their geographic ranges (Ellerman, 1949, 1961).

Of all the specimens of *Rattus niviventer* that I have examined in museums, the two specimens of *tenaster* are morphologically most similar to 23 specimens (AMNH 163707-163710, 163712-163730) obtained from Mount Victoria in the Chin Hills of southwestern Burma. All the rats were collected by Gerd Heinrich in 1938 at elevations from 2200 to 2800 meters. Most of the series consists of young adults and only five are approximately the same age as the two specimens of *tenaster*, as judged by wear of teeth. These five specimens from Mount Victoria are compared with the two examples of *tenaster* in table 4, and with specimens of *R. fulvescens* and *R. langbianis*. Measurements of nine dimensions of the two skulls of *tenaster* fall within the range of variation seen in the series from Mount Victoria, and in the other eight dimensions, the two specimens of *tenaster* are only slightly larger than comparable dimensions in the sample from Mount Victoria. Cranial configurations and proportions of the two specimens of *tenaster* are also similar to those from Mount Victoria. I could not detect any significant taxonomic differences between the two samples. In my opinion, the two samples represent the same taxon and that taxon should be associated with *R. niviventer*, not with the northern *cremoriventer*-type of rat, *R. langbianis*.

Rattus blythi

The holotype of *Rattus blythi* was originally described by Edward Blyth in 1859 (p. 294) under the name *Mus cinnamomeus*. His description is short and vague: "Like M. FLAVESCENS but smaller, with proportionally longer tail, and softer fur of a fine cinnamon-color (nearly as in M. OLERACEUS), with inconspicuous black tips; the under-parts white, which is abruptly divided from the cinnamon hue above. Length of head and body about 6 in., the tail 7 3/4 in., and hind foot 1 1/4 in."

The taxon was based on two specimens. Both had been collected from Schwe Gyen (also spelled Schwegyin) in the valley of the Sittang River in the Tenasserim region of southeastern Burma by Major Berdmore (Blyth, 1863). The specimens were deposited in the Indian Museum at Calcutta and were registered as numbers 366A A.S.B. and 366B A.S.B.

From 1859 to 1917, *Mus cinnamomeus* Blyth was regarded as a synonym of other species. In his catalogue of the birds and mammals of Burma, Blyth (1875, p. 40) regarded *cinnamomeus* to be a variety of *Mus caudatior*, an allocation followed by Trouessart (1881, p. 120) in his systematic and geographic synopsis of living and fossil rodents. Subsequently, Thomas (1881) listed both *Mus caudatior* and *M. cinnamomeus* as synonyms of *M. fulvescens*. Thomas also indicated that *M. cinnamomeus* Blyth was preoccupied by *M. cinnamomeus* Pictet and Pictet, named and described by those authors 15 years earlier in 1844 (p. 64).

In 1890, Sclater published a report "written during the preparation of the catalogue of the specimens of Rats and Mice in the Indian Museum," (p. 522) based primarily on specimens in the collections of the Indian Museum. There, under the account of *Mus fulvescens*, Sclater wrote (p. 524) that, "Thomas . . . identifies with this species *Mus cinnamomeus* of Blyth, which was procured by Major Berdmore in the Schwegyeen District of Burmah. The type of *Mus cinnamomeus* agrees in every respect with the description given by Thomas of *Mus fulvescens*, so that there is a little doubt of the correctness of his identification . . . The only specimens in the Museum are the two originally sent by Major Berdmore to Mr. Blyth from Burmah, of the skull of which I send figures." The skull that Sclater illustrated in his report (Pl. XLIV, figs. 1a, 1b) was one of the types of *Mus cinnamomeus*.

The identity of *Mus cinnamomeus* was still a question to Blanford in 1891. He (p. 409) listed *M. cinnamomeus* in the synonymy of *M. fulvescens* with question and remarked that, "*Mus cinnamomeus*, Blyth, was united to *Mus caudatior*, which is the same as *Mus fulvescens*, by Mr. Blyth himself. The colour, however, is much paler, the teeth considerably larger, and the

anterior border of the maxillary zygomatic process much more emarginate . . . Further specimens are required to show whether this is the same as *M. fulvescens* or distinct."

In the new edition of his catalogue of living and fossil mammals (1897 [1897-1905], p. 479) and in the supplement of that work (1904 [1897-1905], p. 366), Trouessart followed Thomas and listed *M. cinnamomeus* as a synonym of *M. fulvescens.*

In 1917 Kloss borrowed type specimens of Burmese and Himalayan rats from the Indian Museum at Calcutta and recorded his observations in a paper. He examined both cotypes of *Mus cinnamomeus* and designated one as lectotype. He also briefly described the specimen, pointing out that it was in poor condition and that the tail was missing. Based on its pelage characteristics, Kloss thought the rat was like members of the "*cremoriventer* group," but he could not be certain because the tail was gone. He regarded the skull to be distinctive (p. 8): "The skull, with teeth only slightly worn, closely resembles those of aged examples of *cremoriventer* and appears to differ only in narrower, less spatulate nasals and broader anteorbital plates; the bullae are quite of the 'jerdoni' type—small, flattish and but little dilated.

"The upper incisors are, however, much more curved backwards and both pairs are ivory-white with no tinge of orange on the exposed portion—a character quite unknown in any rats of this section." Because of these features Kloss considered the specimen to be an example of a distinct species and, as the name *cinnamomeus* was preoccupied, he called it *Rattus blythi.*

From the time that Kloss published his observations, the taxon *blythi* has either been regarded as a distinct species or as a subspecies of some other form. Tate (1936), for example, in his report on some Muridae of the Indo-Australian region, listed *blythi* as a species in the "*Rattus cremoriventer* Group." Ellerman too (1941), listed *blythi* as a species and placed it in his "*cremoriventer* Group." By 1949 Ellerman had changed his mind for he then listed *blythi* as a subspecies of *Rattus niviventer.* Then in 1951 (p. 594), Ellerman and Morrison-Scott listed *blythi* as a subspecies of *R. cremoriventer*, but with question: "Status uncertain. Apparently near *cremoriventer* but with white incisors, which is an unusual character. No specimens in London." Finally, in 1961 Ellerman did not discuss *blythi* under the account of *R. cremoriventer.* He wrote about it under "*Rattus blythi*" in a section on species of *Rattus* that were known from the Indian region, but were unrepresented in the collection of the British Museum and thus unavailable to Ellerman (p. 705). His discussion was merely an abridged version of Kloss's description of *blythi.*

I have examined the holotype of *Rattus blythi*. Dr. B. Biswas, Superintending Zoologist, Zoological Survey of India, took the time and effort to lend me the two type specimens of *Mus cinnamomeus*—one of these (IMC 366A A.S.B.) is the holotype of *R. blythi*. It is an adult male (the penis was everted and dried on the skin), stuffed and mounted in a lifelike pose. The right foot and tail are missing. Ears are incomplete; the specimen has the basal parts of each pinnae but their edges are tattered and worn. Otherwise the skin is complete.

Pelage of upper parts is bright orange-brown and composed of both soft and spiny hairs. The spines are either thin, and flexible, or wide and rigid. Pelage of the underparts is yellow-orange, and it also has both soft and spiny hairs.

The skull has been extracted from the skin and cleaned. The mandible is complete but the cranium is broken and parts of the roof and floor of the brain case are missing. The teeth are well worn. The pattern of the cusps remains on the first two upper and lower molars, but is almost obliterated on the third upper and lower molars. Cranial and dental measurements that I could take on the damaged skull are: greatest length of skull 38.0, length of nasals 13.6, length of rostrum 11.3, breadth of rostrum 6.2, breadth of zygomatic plate 3.8, depth of zygomatic notch 1.2, breadth across incisor tips 2.2, length of diastema 9.3, palatal length 18.1, palatilar length 15.2, length of incisive foramina 6.4, length of palatal bridge 6.5, length of bulla 4.7, breadth of bulla 4.6, height of bulla 4.1, alveolar length of maxillary toothrow 6.2, length of first upper molar 3.0, and breadth of first upper molar 1.6. Some of these measurements are listed in table 4 where they are compared with measurements from specimens of *Rattus fulvescens*, *R. niviventer*, and *R. langbianis*.

The holotype of *Rattus blythi*, one of the original type specimens of *Mus cinnamomeus*, is an example of *R. fulvescens*. In 1881 Thomas had correctly allocated the taxon that was originally described by Edward Blyth.

Color and texture of upper parts of *Rattus blythi* are like specimens of *R. fulvescens* from Burma that I have examined. Both have bright orange or reddish brown pelage that is a mixture of soft and spiny hairs. Underparts of the holotype of *R. blythi* are not diagnostic. The pelage is now yellow-orange, but it was still white when Kloss (1917) examined the specimen.

Kloss (1917) attributed special significance to the white incisors of the holotype of *R. blythi* and from reading his account I gained the impression it was this feature that caused him to regard *blythi* as a distinct species. The enamel layers of the lower incisors are cream as are the distal two-thirds of the upper incisors. However, there is orange pigment in the basal

third of each upper incisor and a small patch of orange on the cream-colored portions of the enamel. I suspect the present color to be an alteration and the orange pigment to have been bleached away. I do not think color of the incisors has any taxonomic significance in this case.

The cotype of *Mus cinnamomeus* (IMC 336B A.S.B.) is a young adult. It is preserved in fluid and the skull has been extracted. The specimen is badly decomposed and is dark brown all over. The skull is incomplete; zygomatic arches, back and floor of the brain case, and bullae are missing. In Sclater's (1890) illustration of this skull, the right bulla and part of the left bulla were still intact. The specimen is an example of *R. fulvescens*. In his description of *R. blythi*, Kloss (1917) did not designate this specimen as a paratype of *blythi*, nor did he discuss its identity.

Taxonomic Allocations of *tenaster* and *blythi*

The taxa *tenaster* and *blythi* represent species in what Ellerman (1949) has called the "*niviventer* Group" of *Rattus*. Three species of this group occur in southern and southeastern Burma. They are similar to each other in morphology. Each has either brownish or reddish brown upper parts, whitish underparts, and pelage with a mixture of soft and spiny hairs. In each species the tail is longer than the head and body.

One species is *Rattus langbianis*. This animal has brownish gray upper parts suffused with pale, yellow-orange and its underparts are white or pale cream. The tail is dark brown everywhere, tipped with a short brush of hairs. The hind foot is wide relative to its length and the plantar pads are large and well developed.

The second species is a form of *Rattus niviventer*. Specimens of *R. niviventer* from southern and southeastern Burma are larger than those of *R. langbianis* but the two kinds are similar in color of head and body. Tails of *R. niviventer*, however, are bicolored. The dorsal surface and all around the base of the tail is dark brown; the ventral surface is white to the tip. In some specimens the entire distal fourth of the tail is unpigmented, both above and below, and there is no conspicuous brush at the tip. In addition, *R. niviventer* has feet that are narrower relative to their lengths than those of *R. langbianis*, and the plantar pads are not so large and well developed.

The third species is *Rattus fulvescens*. Morphologically it is most similar to *R. niviventer*. Both kinds have been taken together on the slopes of Mount Victoria and Mount Mooleyit. In southern Burma *R. fulvescens* is smaller in body size than *R. niviventer* and is about the size of *R. langbianis*. Upper parts may be brown or reddish brown. Like *R. niviventer*, the tail of *R. fulvescens* is bicolored and not pencillate. It is dark brown above and white below. Tails of *R. fulvescens* differ from those of *R. niviventer* in that the tip

is dark brown and forms a band up to 10 mm. wide in some specimens. The structure of the foot is more like that in *R. niviventer* than in *R. langbianis*.

Crania of the three kinds are contrasted in figures 8 and 9. The skull of *R. langbianis* is distinctive compared with skulls of *R. niviventer* and those of *R. fulvescens*. The rostrum of *R. langbianis* is shorter relative to length of skull and more rectangular. Ridges bounding dorsolateral edges of the interorbital region and brain case are higher and better developed; from the interorbital area they sweep out and then back over dorsolateral margins of the brain case. In the other two species, the pattern formed by the ridges is more graceful, vase-shaped, without abrupt angles at the junctions of frontals and parietals. *Rattus langbianis* also has a wider brain case and a shallower zygomatic notch. The palatal bridge is shorter relative to length of skull in *R. langbianis*, and bullae of that species are conspicuously larger and more globular than those of *R. fulvescens*, but about the same size and configuration as in *R. niviventer*.

Cranial distinctions between *R. niviventer* and *R. fulvescens* are not so marked and can only be appreciated when specimens of comparable age of each kind are compared. In samples from southern and southeastern Burma, adults of *R. niviventer* have larger and more robust skulls than do specimens of *R. fulvescens* of comparable age. The rostrum is thicker and appears more massive, and the teeth are usually larger. The best distinguishing cranial feature, however, is size of bullae. Specimens of *R. niviventer* have larger bullae than do those of *R. fulvescens*.

The morphological distinctions between *R. langbianis*, *R. niviventer*, and *R. fulvescens* in southern and peninsular Burma are clear to me, but my information about species-limits of the three kinds of rats and what scientific names should be allocated to each in regions outside of southern and peninsular Burma is relatively complete only for *R. langbianis*. Earlier in the present paper, I outlined known morphologic and geographic limits of *R. langbianis* and pointed out that it is most closely related to *R. cremoriventer*. The only scientific names I can associate with *R. langbianis* are *indosinicus* and *vientianensis* and I regard both as synonyms of *langbianis*.

The morphologic and geographic species-limits of *Rattus niviventer* are not clear. The taxa now associated with *R. niviventer* (Ellerman, 1949, 1961) represent samples diverse in geographic origin, morphology, and habitat. As the species is understood by Ellerman (1961) its geographic range extends from Nepal and eastern India eastward across Asia to China, including the islands of Hainan and Taiwan, and southward throughout Southeast Asia, the Malay Peninsula, and some larger islands of the Sunda Shelf. In body size, the taxa now included in *R. niviventer* range from small

FIG. 8. Dorsal (top) and ventral (bottom) views of crania. Left to right: *Rattus langbianis* (USNM 321435, adult female), South Vietnam; "*Epimys tenaster*" (BM 88.12.1.54, adult female), southeastern Burma; *R. fulvescens* (AMNH 113048, adult male), northern Burma. Approximately ×1.5.

rats like *R. n. lepcha* from Sikkim to rats almost twice as large, like those from southern Burma. Geographic variation in color and texture of pelage

FIG. 9. Lateral views of crania of same specimens as in figure 8. Top to bottom: *Rattus langbianis*, South Vietnam; "*Epimys tenaster*," southeastern Burma; *R. fulvescens*, northern Burma. Approximately ×1.5.

is equally great. Color of upper parts, for example, ranges from brownish gray to orange-brown to reddish brown. Some samples have soft and dense pelage, in others it is characteristically spiny and thin. The rats live in forests and have been taken from the lowlands up to mountaintops. Some morphologically distinctive samples are found only in highlands and others only in lowlands.

This morphologic and geographic diversity is reflected in the number of names that have been applied to samples of *R. niviventer*. In his classification of *Rattus* published in 1949, Ellerman associated 29 scientific names with *R. niviventer* and regarded 21 to be valid subspecies. Since then another subspecies of *R. niviventer*, *R. n. monticola*, has been named and described by Ghose in 1964.

All of these names now listed as either synonyms or valid subspecies of *R. niviventer* do not represent samples of one species. For example, the taxon *excelsior* listed by Ellerman (1949, p. 70) as a synonym of *R. niviventer confucianus* is actually a distinct species, which may be more closely related to *R. andersoni* than to *R. niviventer*. This view comes from my own findings, which I am preparing for publication. Two other forms linked by Ellerman to *R. niviventer* apparently do not belong with that species. These are the taxa *bukit*, described from specimens taken on Bukit Besar in the southern tip of peninsular Thailand, and *lepidus*, based on two specimens from

Bokpyin, southern Tenasserim. In his report on the mammals collected by the Kelley-Roosevelts and Delacour Asiatic expeditions, Osgood (1932) discussed specimens he had identified as *R. fulvescens* as well as some of the scientific names he considered to represent subspecies of *R. fulvescens*. One of these was *bukit* and he mentioned that (p. 305) "The relationship of *fulvescens* to southern forms is obvious in several instances, especially in that of *R. f. bukit* which can at most be no more than a subspecies . . . It is somewhat duller in color than *fulvescens* but otherwise agrees closely." My own studies, as well as those of Joe T. Marshall, Jr., who has been working on taxonomy of the species of *Rattus* occurring in Thailand, confirm Osgood's allocation of *bukit* and not Ellerman's. The taxon *bukit* and, in our opinion, *lepidus* represent samples that are geographic variants of *R. fulvescens* and not *R. niviventer*.

Whether other taxa now associated with *R. niviventer* represent valid subspecies, synonyms, or distinct species closely related to true *R. niviventer* is unknown and can only be discovered by a taxonomic revision of *R. niviventer* and its allies, a revision that is not yet available. For my purposes here I can only point out that the name *tenaster* applies to samples of *R. niviventer* of large body size from southern and southeastern Burma. Until the group is taxonomically revised I regard *tenaster* as a subspecies of *R. niviventer*.

Taxonomy of taxa currently associated with *Rattus fulvescens* and its allies (Ellerman, 1949, 1961) is at about the same resolution as that of taxa associated with *R. niviventer*. Some forms once regarded as valid subspecies of *R. fulvescens* have now been differently allocated. The taxon *brahma*, for example, was listed by Ellerman (1961) as a subspecies of *R. fulvescens* but I have shown elsewhere (Musser, 1970) that it represents a distinctive species allied to *R. eha*. Similarly, *solus*, a taxon associated with *R. fulvescens* by Ellerman (1949), is really a representative of *R. cremoriventer* as I discussed earlier in the present report. Most of the other taxa that have been included in *R. fulvescens* represent samples as diverse in geographic origin, morphology, and habitat as those associated with *R. niviventer*. Like that group, *R. fulvescens* and its allies must be taxonomically revised before the relations between taxa now associated with it or considered closely related to it are understood.

I can report that three of the names discussed in this paper—*cinnamomeus*, *blythi*, and *gracilis*—apply to samples of *R. fulvescens* from southeastern Burma. They are morphologically closely similar to samples of *R. fulvescens* from elsewhere in Burma, eastern India, and Nepal that Ellerman (1961) regarded as true *R. fulvescens*. Ellerman even considered *gracilis* to be a synonym of *R. f. fulvescens*. At this time I cannot confirm whether *gracilis*,

cinnamomeus, and *blythi* are synonyms of *R. f. fulvescens*. I can only say that if a taxonomic revision demonstrates the population of *R. fulvescens* from southern Burma and northwestern Thailand to be subspecifically distinct, then *gracilis* is the name available for it. In addition, the names *bukit* and *lepidus* are available for samples of *R. fulvescens* from farther south in peninsular Burma and Thailand.

DISCUSSION

After study of more than 400 specimens, I have been able to outline the morphologic and geographic boundaries of two kinds of *cremoriventer*-type rats, a northern kind that lives in forests in Southeast Asia and is known to occur southward to at least the Tenasserim region of peninsular Burma, and a southern kind known from peninsular Thailand, Malaya, and various of the Greater Sunda Islands, but not recorded from any farther north than Sullivan Island in the Mergui Archipelago and the Isthmus of Kra on the mainland. There is a gap of 650 km. between known localities of the two types. Morphologically, each kind of rat is more similar to the other than to any other species, but the two differ significantly in color, cranial features, and absolute and relative size of some external, cranial, and dental dimensions.

In the preceding pages, I have treated the two kinds as different species, *Rattus langbianis* and *R. cremoriventer*. But, because they are similar in morphology and allopatric in distribution, I have had to consider the possibility that the samples of *langbianis* represent a distinctive population that is genetically linked to *R. cremoriventer*, and that this relationship may best be expressed by regarding *langbianis* as a subspecies of *R. cremoriventer* rather than a separate species. At present I cannot actually test whether populations of *cremoriventer* and *langbianis* are reproductively isolated from each other. To do so requires collection of specimens and ecological data from the gap between known occurrences of the two types in peninsular Burma and Thailand. From the data I have I can estimate the degree of reproductive isolation by the magnitude of morphologic difference between the two. In my opinion, the morphologic and geographic relationships between *cremoriventer* and *langbianis* are best expressed by treating each as a species. The following are my reasons:

First, the two kinds of rats are distinctive in features of skin and skull. Specimens of each can be separated from the others 100 percent of the time, no matter what the geographic origin of the samples. For example, absolute size of the bullae and its size relative to that of the brain case distinguishes all specimens of *R. langbianis* from all those of *R. cremoriventer*, at least in the material I have worked with.

Second, there is significant geographic variation within both the northern and southern types, yet in not one sample of either does that variation indicate any trend of the distinctive characters of one type toward those of the other. Geographic variation in available samples of *Rattus langbianis*, for example, is seen mostly in body size. Specimens in the sample from southwestern Burma are small and all other specimens from Tenassarim, Thailand, Laos, and North and South Vietnam are significantly larger. Size is also one of the features that varies from one place to another in samples of *R. cremoriventer*. The variation ranges from the small individuals living on southern Sumatra and Bangka and Billiton islands (*R. c. mengurus*) to large rats like those on Nias Island (*R. c. barussanus*) and the island of Bali (*R. c. cretaceiventer*). Specimens from Malaya and peninsular Thailand (*R. c. cremoriventer*) fall between these extremes in size. In the last samples there is no morphological evidence indicating intergradation with *R. langbianis*. Furthermore, none of the samples of that northern type provide evidence of intergradation with the southern *R. cremoriventer*. In fact locality 4, the Taok Plateau in the Tenasserim region of southeastern Burma (fig. 3), is the locality of *R. langbianis* closest to any place from which examples of *R. cremoriventer* have been collected and the rat from that place is one of the largest of any of the specimens of *R. langbianis*. In size and in configuration of skull, it is similar to the specimen from South Vietnam illustrated in figures 5, 6, and 7, the individual that I used as an example of the large geographic variant of *R. langbianis*.

Finally, the degree of morphological differences between northern and southern types is of the magnitude found between allied species of *Rattus* in the *niviventer* Group. For example, the morphological differences seen between samples of *R. langbianis* and *R. cremoriventer* are greater than those found between many samples of *R. fulvescens* and *R. niviventer*. Specimens of these two species have been taken at the same localities and samples of each from certain parts of their geographical ranges are difficult to tell apart.

All the data I have seen support the hypothesis that the two kinds of *cremoriventer*-type rats are different species. But this hypothesis will certainly have to be tested by field work in southern and peninsular Burma and Thailand.

Below is a summary of the taxa I associate with *R. cremoriventer* and *R. langbianis*.

Rattus cremoriventer cremoriventer (Miller)

Mus cremoriventer Miller, 1900a, p. 144.
Mus flaviventer Miller, 1900b, p. 204.
Mus gilbiventer Miller, 1903, p. 35.
Epimys solus Miller, 1913, p. 22.

Mainland of peninsular Thailand and Malaya, on some islands off the west and east coasts of the peninsula, on one of the Anambas Islands, and on northwestern Sumatra.

Rattus cremoriventer mengurus (Miller)

Epimys mengurus MILLER, 1911, p. 27.
Rattus cremoriventer sumatrae BARTELS, 1937, p. 123.

Known from Billiton and Bangka islands, and lowlands of southern Sumatra.

Rattus cremoriventer barussanus (Miller)

Epimys barussanus MILLER, 1911, p. 26.

Known from Nias Island.

Rattus cremoriventer cretaceiventer Robinson and Kloss

Rattus cremoriventer cretaceiventer ROBINSON AND KLOSS, 1919, p. 377

Recorded from the islands of Java and Bali.

Rattus cremoriventer kina (Bonhote)

Mus kina BONHOTE, 1903, p. 124.
Epimys spatulatus LYON, 1911, p. 111.
Rattus cremoriventer malawali CHASEN AND KLOSS, 1931, p. 32.

Known from mainland Borneo and some offshore islands.

Rattus langbianis Robinson and Kloss

Rattus cremoriventer langbianis ROBINSON AND KLOSS, 1922, p. 96.
Rattus indosinicus OSGOOD, 1932, p. 307.
Rattus indosinicus vientianensis BOURRET, 1942, p. 29.

Records are from eastern India, Burma, Thailand, Laos, and North and South Vietnam.

Results of my study of *R. langbianis* and *R. cremoriventer* are preliminary but I was still able to derive enough information from available specimens to outline the morphologic and geographic species-limits of these two kinds of rats. The study is an example of the type of taxonomic problem that must be solved before we can understand zoogeographic relationships between the species of murid rodents living in Southeast Asia and the Greater Sunda Islands. The basic problem is one of characterizing the real species that occur there. Many scientific names have been proposed for samples of rats from those regions but these names convey no biological

meaning because no careful taxonomic revisions of the taxa are available—revisions in which scientific names are tied to actual species.

In the present report I have brought together 14 taxa and associated them with two morphologically and geographically distinctive types of rats that are probably species. I believe it is this level at which taxonomy of the rats must be studied. There are probably a few new species to be discovered, named, and described. There are many more, however, whose characteristics can be discovered by studying specimens now available in collections of museums and by resolving the taxonomic identities of the many scientific names now applied to various samples of rats from Asian and Indo-Malayan regions.

Good taxonomy, including knowledge of morphology, geographic distribution, habitat, and other biologic aspects of murid species living in Asia and the Indo-Malayan area is essential to an understanding of zoogeographic relationships between those species and rats living outside of that region. Those animals found to the east on land masses off the Sunda Shelf are of special interest, particularly the rats of Celebes.

There are more than 60 scientific names that have been applied to samples of *Rattus* (as that genus is defined by Ellerman, 1949) from Celebes, but my studies indicate these names to correspond to 29 morphologic units that are probably real species (Musser, 1973). Five of these are native to land masses outside of Celebes and were probably inadvertently brought to Celebes by human transport. The other 24 kinds are native to Celebes and its offshore islands—including the Sula Islands—and do not occur elsewhere.

I am trying to bring into focus the zoogeography of these indigenous rats on Celebes, but the emerging picture is still blurred. Nevertheless, it is a picture portraying a complex set of relationships. Some of the species have closest morphologic affinities with those to the west in the Indo-Malayan region and Southeast Asia, others are more closely related to rats known only from the Philippine Islands to the north, and a few do not seem to have any close living relatives outside of Celebes.

Rattus beccarii of Celebes is one of the kinds that has been morphologically linked to species living in regions to the west on the Sunda Shelf. It has been considered a relative of *R. cremoriventer* (Tate, 1936; Ellerman, 1949), but nobody has ever made detailed comparisons between the two to test this relationship, and there have been good reasons for not doing so. There are few specimens of *R. beccarii*. Nothing is known about the limits of its morphologic variation, the extent of its geographic distribution, or its ecology. And, at the time that Tate and Ellerman were working and writing, the same kinds of information were really unavailable for *R.*

cremoriventer, although many more specimens of it were on hand for study than of *R. beccarii*.

I have had the advantage of studying more specimens than Tate and Ellerman had, or any of the other persons who have reported on taxonomy of rodents from Asia and the Indo-Malayan regions. The resulting report, a documentation of the morphologic and geographic characteristics of *R. langbianis*, the northern *cremoriventer*-type, and *R. cremoriventer*, the southern type, is a more accurate picture of the species complex than was available before. Information presented here forms a structural framework against which samples of *R. beccarii* can eventually be compared.

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