

# AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024  
Number 2862, pp. 1–24, figs. 1–10, tables 1–6  
October 31, 1986

## Sundaic *Rattus*: Definitions of *Rattus baluensis* and *Rattus korinchi*

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### ABSTRACT

Among the 14 genera and 41 species of murid rodents that are native to the peninsula and islands on the Sunda Shelf are five species of *Rattus*. Two of these, *R. baluensis* from Gunung Kinabalu in Sabah and *R. korinchi* from the mountains of central Sumatra, were regarded as isolated mountain populations of one species. Restudy of specimens in museum collections indicates the Bornean pop-

ulation to be a species closely related to the widespread Sundaic *R. tiomanicus*, which is a relative of *R. rattus* and other species native to continental Asia and India. Morphological characteristics of *R. korinchi* are unlike any other species of *Rattus*. These endemic Bornean and Sumatran *Rattus* are contrasted and defined.

### INTRODUCTION

Peninsular Thailand and Malaysia south of about latitude 10°N; the large islands of Sumatra, Borneo, Java, Bali, Palawan; and numerous smaller islands are all part of the great Sunda Shelf, an extensive 1,850,000 square kilometer extension of the Asian continent (Chasen, 1940; Tjia, 1980). In their report on Malaysian murids, Musser and Newcomb (1983) recorded 40 species of rats and mice, representing 14 genera, native to the peninsula and islands of the Sunda Shelf.

Thirty-three of the 40 occur there and nowhere else and their evolutionary histories have probably been closely associated with the Shelf; ten species are found on the peninsula and several large and small islands; and 23 are endemic to either the peninsula, one of the large Sunda islands, or the Palawan region. Seven co-occur on the Shelf and in Indochina. The genera *Lenothrix*, *Pithecheir*, *Sundamys*, *Kadarsanomys*, and *Palawanomys* are endemic to the Shelf; *Maxomys*,

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*Chiropodomys*, and *Haeromys* are not entirely restricted to the Shelf but most of the species in each is found there; and *Niviventer*, *Berylmys*, *Mus*, and *Rattus* have few representatives on the peninsula and islands of the Shelf.

Musser and Newcomb (1983) recognized only 4 of the more than 50 species of *Rattus* as native to the Sunda Shelf: *R. tiomanicus*, *R. annandalei*, *R. hoogerwerfi*, and *R. baluensis*. *Rattus tiomanicus* is widespread on the Shelf and exhibits appreciable insular variation in body size and fur color. *Rattus annandalei* occurs on the Malay Peninsula, Sumatra, and a few small islands. *Rattus hoogerwerfi* is known only from the Aceh region in northern Sumatra. *Rattus baluensis* was thought to consist of a population on Gunung Kinabalu in northern Borneo (*R. R. baluensis*) and a population in the mountains of Sumatra (*R. R. korinchi*).

When Cameron Newcomb and I wrote our report, however, I was impressed by the differences in certain cranial and dental dimensions between samples from Gunung Kinabalu and Sumatra, all of which we had called *R. baluensis*. Our assessment of that geographic variation was based upon my notes and measurements made several years earlier; we did not have the opportunity to reexamine specimens before the paper was finished. Shortly after our report was published, I looked again at the large series of *baluensis* available in museum collections and the few examples of *korinchi* in order to test the hypothesis that the Bornean *baluensis* is more closely related to another Bornean species and that *korinchi* is a derivative of a Sumatran species. At about the same time, I received a stimulating letter from the Earl of Cranbrook, an excellent biologist who has contributed much to our knowledge of Sundaic mammals. He mentioned the great distributional gap between the Bornean and Sumatran *baluensis* and wrote that "it seems to me far more likely that convergent forms, locally derived from *tiomanicus* ancestors, have evolved on high mountain peaks. Characters such as the long fur are likely to be adaptations to the cool climate."

I appreciate the Earl of Cranbrook's independent insight into the problem. He inspired me to carefully study the Sundaic spec-

imens and to also look again at character variation among other species of *Rattus*, a task that seems never to end. The results are redefinitions of *Rattus baluensis* and *Rattus korinchi*. The Bornean species shares many characters with the widespread *R. tiomanicus* and the relationship between these two reflects the picture suggested by the Earl of Cranbrook. *Rattus korinchi*, on the other hand, is not closely allied to *R. baluensis*, *R. tiomanicus*, or any other species of *Rattus*. It is geographically isolated in the mountain forests of Sumatra and appears to be morphologically unique within the present definition of the genus.

#### ABBREVIATIONS AND PROCEDURES

Specimens examined and referred to here are in collections of the American Museum of Natural History, New York (AMNH); the Philadelphia Academy of Natural Sciences, Philadelphia (ANSP); the British Museum (Natural History), London (BM); the Field Museum of Natural History, Chicago (FMNH); the Museum Zoologicum Bogoriense, Bogor (MZB); the Museum of Comparative Zoology at Harvard College, Cambridge (MCZ); the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Values for total length and length of tail are those recorded by collectors on skin labels. I subtracted length of tail from total length to obtain length of head and body. Values for length of hind foot (including claw) were either taken from skin labels or from my measurements of dry skins. Cranial and dental measurements were taken with dial calipers graduated to tenths of millimeters. Their limits are defined in Musser and Newcomb (1983) with the exception that their "length of palatal bridge" is here called length of bony palate.

The nomenclature I use for cusps and cusp-lets of upper and lower molars is presented in figure 1.

See Musser and Newcomb (1983) for explanations of geographic names. Here I use sungai (stream or small river), gunung (mountain), and pulau (island).

## ACKNOWLEDGMENTS

My reliance upon specimens makes me continually appreciate curators and supporting staff of the museums listed above who care for specimens and who have always generously allowed me to study and borrow material. I remain indebted to these responsible persons and grateful for their support.

Mr. Peter Goldberg is responsible for the photographs of crania and teeth, Ms. Patricia Wynne drew figures 9 and 10, and Ms. Lauren Duffy produced the scanning electron micrographs in figure 8. I appreciate the fine efforts of these artists.

The report has been strengthened by reviewer's evaluations, particularly those from Ms. Elizabeth Strasser, Dr. Michael D. Carleton, whose pertinent comments improved my prose without being really obnoxious; also, Dr. Marian Dagosto, Dr. M. Raymond Lee, Mr. Richard L. Green, and the Earl of Cranbrook.

This report forms Results of the Archbold Expeditions Number 117.

# *RATTUS KORINCHI* AND *RATTUS BALUENSIS*

Among the specimens of birds and mammals collected by Herbert C. Robinson and C. Boden Kloss during their expedition to Korinchi Peak in western Sumatra (now known as Gunung Kerinci, which is in Propinsi Jambi on modern Indonesian maps) were two rats obtained at Sungai Kring, on Gunung Kerinci, 7300 ft, in April 1914 (fig. 2). An adult and immature female formed the basis of Robinson and Kloss's (1916, p. 275) description of *Epimys (Rattus) korinchi*, which they briefly characterized as "Like *E. baluensis* (Thomas) with long, soft and spineless fur, beset on the upper surface with numerous longer piles; but with longer tail and paler underparts; nasals broader, but bullae much smaller; teeth considerably larger."

Two years later, Robinson and Kloss (1918, p. 54) reported all of the mammals collected on the expedition to Gunung Kerinci, and listed *korinchi* as a subspecies of *Rattus baluensis*, writing that the rat "is the Sumatran representative of *R. baluensis*." Robinson and

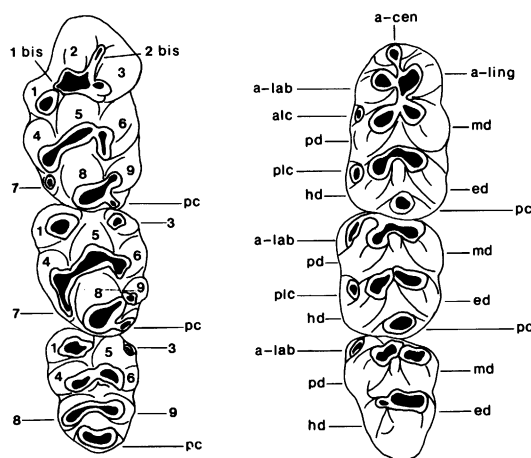


Fig. 1. Nomenclature of dental structures: a diagram of upper and lower molars in *Lenothrix canus*. Upper molars: cusps are numbered according to Miller's (1912) scheme and referred to in the text with the prefix t; pc, posterior cingulum. Lower molars: a-cen, anteroconid; a-lab, anterolabial cusp;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

Kloss knew *Rattus baluensis* by a few specimens collected from the slopes of Gunung Kinabalu in Sabah, where we now know the species to be common at altitudes between 7000 and 12,500 ft (Medway, 1977; Musser and Newcomb, 1983). In their account of *Rattus baluensis korinchi*, Robinson and Kloss provided short descriptions of fur coloration, skull conformation, teeth, and listed some measurements.

During the following year, Robinson and Kloss (1919, p. 315) wrote about the mammals obtained from the Ophir District of western Sumatra (identified as Propinsi Sumatera Barat on modern maps) by E. Jacobson. Among them were two adults of what Robinson and Kloss identified as *Rattus baluensis korinchi* caught near the summit of Gunung Talamau, 9100 ft (known as Mount Ophir in the old literature and as Gunung Talakmau or Talaimu on modern maps), which is northwest of Gunung Kerinci (fig. 2). Both specimens were obtained on June 14, 1917. Robinson and Kloss noted that the "specimens agree closely with the type having

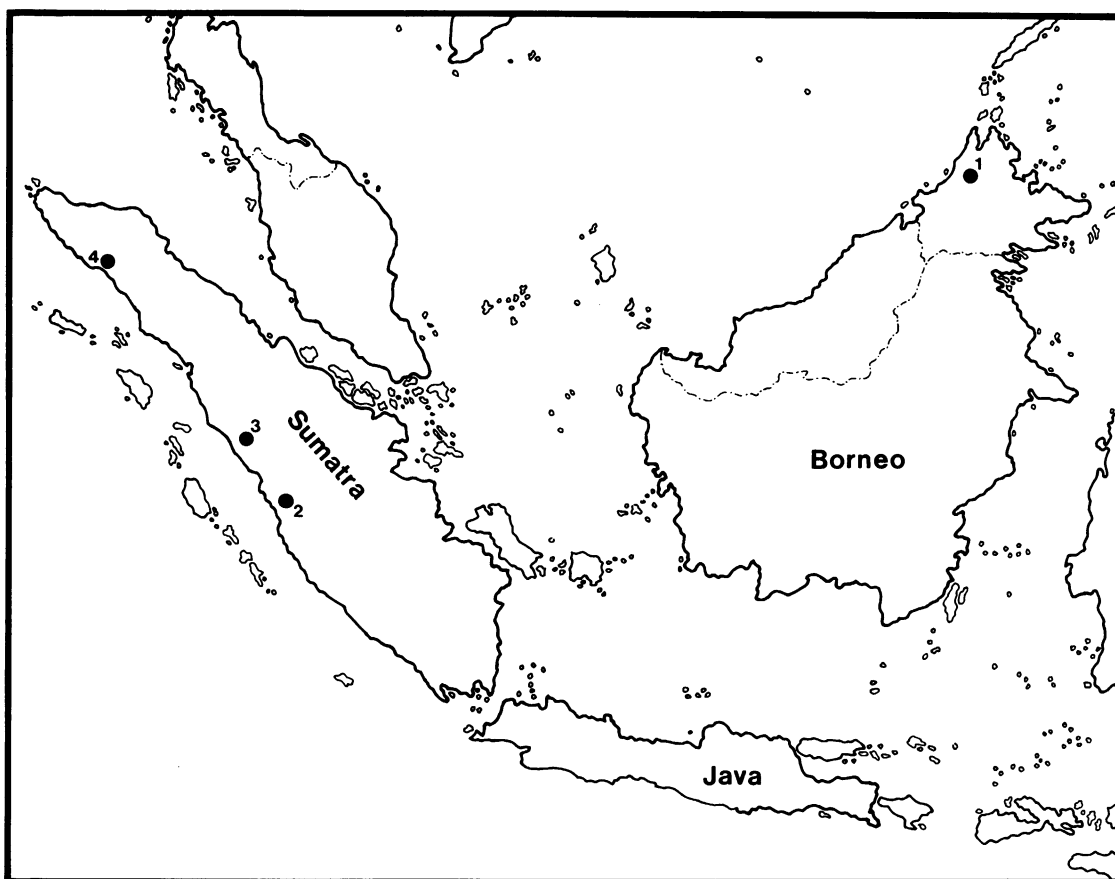


Fig. 2. Geographic distributions of three Sundaic species. *Rattus baluensis*: 1, Gunung Kinabalu, Sabah. *Rattus korinchi*: 2, Gunung Kerinci; 3, Gunung Talakmau. *Rattus hoogerwerfi*: 4, Gunung Leuser.

the same long spineless pelage, with woolly underfur, ochraceous clay above, many of the longer hairs with broad black tips. Beneath greyish, the breast median line whiter, all the pelage grey at the base."

Reference to *Rattus baluensis korinchi* appeared again in the literature with the publication of Robinson and Kloss's Addenda and Corrigenda to the mammals of Korinchi and Sumatra in 1923 where they provided a very good illustration of the skull of the holotype (p. 316, pl. III).

From the early 1900s until now, *korinchi* has been treated as a subspecies of *Rattus baluensis* (Chasen, 1940; Ellerman, 1941; Musser and Newcomb, 1983), an association based upon the early allocation made by Robinson and Kloss and not by critical study

of specimens. The four examples recorded in the reports by Robinson and Kloss are the only specimens ever assigned to *korinchi*. The other published record of *korinchi* proved to be a misidentification (see p. 352 in Musser and Newcomb, 1983). I have been able to locate only two of them: the holotype from Gunung Kerinci, which is in the British Museum (Nat. Hist.) where it is registered as 19.11.5.81; and one of E. Jacobson's specimens (no. 351) from Gunung Talakmau, which is housed in the Rijksmuseum van Natuurlijke Historie and registered as 23151. I know of no new material collected after 1917. Firsthand study of these two adults indicates to me that *korinchi* is a distinct species that is not closely related to *Rattus baluensis*.

The first published reference to what would

later be known as *Rattus baluensis* is by Thomas, who in 1889 recorded four specimens under the name *Mus rattus* that had been collected by John Whitehead during his expedition to Gunung Kinabalu in northern Borneo (fig. 2) in 1888. Two of the specimens came from 8000 ft and two from 3000 ft. Thomas (1889, p. 233) wrote that the "two specimens from an altitude of 8000 feet have their fur long and soft, while in those from 3000 it is short and harsh, so that it seems difficult to believe that both the forms can be referable to the same species." By 1894, when "A Preliminary Revision of the Bornean Species of the Genus *Mus*" appeared, Thomas (1894, p. 454) had examined specimens collected by A. Everett from 7000 to 10,000 ft on the slopes of Gunung Kinabalu in addition to those obtained by Whitehead at 8000 ft and was convinced that all examples represented a new species, *Mus baluensis*, which he characterized as being "Very similar to *M. neglectus* in size, proportions, and colour, but the fur quite long and soft, and the belly of a uniform dirty buff hue."

This *Rattus* of the Kinabalu mountain forest has been recognized as a species by some workers (Sody, 1941; Ellerman, 1941; Misonne, 1969) but not others. Chasen (1940, p. 158), who included *baluensis* in his handlist of Malaysian mammals, wrote that it was "Almost certainly only a high level form of *R. rattus*," which in his view translated to a mountain subspecies of *R. rattus*. Allen and Coolidge (1940, p. 163) did list *baluensis* as a subspecies of *R. rattus* in their report on the mammals collected during the Asiatic Primate Expedition. While Ellerman (1949, p. 61) also placed *baluensis* with *R. rattus*, he noted that it "is an aberrant form, and its former race, *korinchi* is still more aberrant." Medway (1965, pp. 122–123), however, in his annotated checklist of the mammals of Borneo, reaffirmed the morphological and ecological integrity of *Rattus baluensis*, writing that the species "is a very distinct form, separated from other members of the *R. rattus* group by both morphology and habit. It must be considered a good species, and is in fact exceptional in that it is the only species of the group occurring in Borneo which is not in the slightest degree commensal with man."

The distinctive nature of *Rattus baluensis* was also recognized by Musser and Newcomb (1983), and I continue to view it as a species different from *R. rattus*.

My study of *Rattus baluensis* included 78 specimens (BM 0.10.83, 92.9.6.27, 92.9.6.28, 95.10.4.23 (holotype), and 71.2764–71.2788; FMNH 49267, 108907–108922, and 108924–108927; MCZ 36491–36505; USNM 292694, 292696, 292698, 292699, 292704–292710, 301027, and 301028) from an altitudinal range of 7000–12,500 ft on the slopes of Gunung Kinabalu in northern Borneo (now Sabah), where it appears to be endemic.

*Rattus baluensis* must be common if samples in museum collections are reliable indicators of its abundance in the wild. Allen and Coolidge (1940, p. 163), for example, reported that the collector of the series they studied noted *R. baluensis* to occur only "at higher altitudes; very plentiful, from 9 to 11,000 ft. This rat is quite tame, running over your face or eating your food if you sleep out on the ground." Information on tags attached to study skins indicates most specimens to have been caught in "moss" and "heath" forests. Lim and Heyneman (1968, p. 259) collected the rats in a zone between 7040 and 8900 ft, which they termed "mossy forest," and a higher zone between 9800 and 11,200 ft, which they referred to as "sub-summit dwarf forest and scrub." The entire altitudinal zone from which examples of *R. baluensis* have been obtained is montane forest, partially described by Jacobs (1961) and more thoroughly by Corner (1964), who also provided excellent photographs of montane forest on Gunung Kinabalu.

I have no information about habitat or habits of *Rattus korinchi* except that the places where the rats were caught (7300 ft on Gunung Kerinci, 9100 ft on Gunung Talakmau) are in montane or moss forest (see Whitten et al., 1984; Whitmore, 1984).

The two specimens of *korinchi* from Sumatra represent a species of *Rattus* with a moderately large body, a long tail relative to length of head and body, dense and soft fur, large molars, and small auditory bullae (table 1). Fur covering the upperparts of head and body is dark tawny, that on the underparts is grayish white with large white patches on

TABLE 1  
Measurements (in Millimeters) of Adult *Rattus baluensis* from Sabah, *Rattus korinchi* from  
Northwestern Sumatra, and *Rattus hoogerwerfi* from Northern Sumatra<sup>a</sup>

Measurement	<i>R. baluensis</i>	<i>R. korinchi</i>		<i>R. hoogerwerfi</i>
		BM 19.11.5.81 <sup>b</sup>	RMNH 23151	
Length of head and body	170.2 ± 8.4 (158–188) 23	166	169	182.7 ± 6.7 (170–196) 20
Length of tail	188.3 ± 8.7 (175–205) 13	224	209	236.7 ± 11.7 (210–257) 20
Length of hind foot	32.4 ± 1.4 (30–35) 22	34	35	37.4 ± 0.9 (36–39) 20
Greatest length of skull	40.8 ± 1.3 (39.1–44.1) 24	41.0	41.8	42.9 ± 0.8 (41.6–44.2) 16
Zygomatic breadth	19.1 ± 0.6 (18.2–20.6) 25	18.8	19.8	20.1 ± 0.6 (19.2–21.1) 18
Interorbital breadth	6.2 ± 0.2 (5.8–6.7) 25	5.7	6.0	6.0 ± 0.2 (5.7–6.4) 20
Length of rostrum	12.9 ± 0.7 (11.7–14.4) 25	13.1	13.2	13.7 ± 0.5 (12.9–14.7) 17
Breadth of rostrum	7.5 ± 0.3 (7.0–8.2) 25	6.7	7.3	7.1 ± 0.3 (6.6–7.7) 18
Breadth of zygomatic plate	4.0 ± 0.3 (3.5–5.1) 25	3.4	4.1	3.4 ± 0.3 (3.0–4.0) 20
Depth of zygomatic notch	1.9 ± 0.2 (1.4–2.3) 25	1.7	1.1	1.6 ± 0.3 (1.1–2.3) 20
Breadth of braincase	16.6 ± 0.4 (15.9–17.1) 25	16.4	16.3	17.5 ± 0.5 (16.4–18.2) 18
Height of braincase	11.7 ± 0.4 (11.2–12.5) 25	11.4	12.1	12.4 ± 0.4 (11.4–12.9) 19
Length of diastema	10.8 ± 0.6 (10.1–11.9) 25	10.5	11.3	11.5 ± 0.5 (10.6–12.4) 20
Postpalatal length	13.0 ± 0.6 (12.1–14.4) 25	13.0	14.1	14.4 ± 0.5 (13.7–15.5) 20
Length of incisive foramina	7.9 ± 0.3 (7.4–8.5) 25	8.2	8.7	8.5 ± 0.4 (7.9–9.5) 20
Breadth of incisive foramina	2.8 ± 0.2 (2.3–3.2) 25	3.0	3.0	3.0 ± 0.2 (2.7–3.4) 20
Length of bony palate	8.3 ± 0.3 (7.7–9.1) 25	8.3	8.7	8.3 ± 0.4 (7.6–9.1) 20
Breadth of palatal bridge at M <sup>1</sup>	4.1 ± 0.2 (3.6–4.6) 25	3.8	4.0	4.4 ± 0.2 (4.0–4.9) 20
Length of bulla	6.7 ± 0.2 (6.4–7.2) 25	6.3	6.4	6.5 ± 0.2 (6.3–6.8) 20
Crown length of M <sup>1–3</sup>	6.7 ± 0.2 (6.3–6.9) 25	7.7	7.6	7.4 ± 0.2 (7.0–7.7) 20
Breadth of M <sup>1</sup>	2.0 ± 0.1 (2.0–2.2) 25	2.2	2.3	2.2 ± 0.1 (2.0–2.3) 20

<sup>a</sup> Mean plus or minus one standard deviation, observed range in parentheses, and number of specimens are listed. Males and females are combined in the samples of *R. baluensis* and *R. hoogerwerfi*.

<sup>b</sup> Holotype.

the throat, chest, and inguinal region. Sides of the head and body are slightly paler than the back and no sharp demarcation exists between coloration of dorsum and venter. The hairs that make up the dorsal pelage are dark gray for most of their lengths and tipped with ochraceous-tawny. The coat is thick, lax, and long; the hairs of the overfur along the back reaching 20–25 mm in length. Longer and slightly stiffer black guard hairs extend beyond the overfur by 10–15 mm. The ventral coat is also thick and long (10–12 mm) with the hairs being gray and tipped with white. Fur texture and length is typical of species of *Rattus* living in cool and wet tropical mountain forest.

The ears are small, brown, and densely covered with fine, short brown hairs.

Dorsal surfaces of the front and hind feet are brown with a darker brown strip extend-

ing the length of each metacarpal and metatarsal surface onto the bases of the digits. The claws are short, recurved, and sharp. The convex dorsal surface of each claw is covered with a tuft of long silvery hair. Palmar and plantar surfaces are pale brown and naked. Most of the palmar surface is formed of five large fleshy pads (three interdigital and two metacarpal), each adorned with transverse and semicircular lamellae. The hind foot is long and slender, widening distally to the base of the digits. Four large interdigital pads and two metatarsal pads are fleshy and thick and also inscribed with lamellae.

The brown, monocolored tail is much longer than head and body (tables 1 and 2). Circlets of small overlapping scales cover its surface (13–14 rings of scales per cm, counted about a third of the way from the base of the tail). Three dark brown hairs emerge from

the anterior margin of each scale. Near the base of the tail the hairs are twice as long as a scale but distally the scales decrease in size, the tail diameter becomes smaller, the hairs are longer, and the tail more densely covered. Brown and silver hairs extending beyond the tip of the tail to form a brush 3–4 mm long, prompting Robinson and Kloss (1918, p. 53) to write that it was "almost penicillate."

Females have one pectoral and two inguinal pairs of teats.

*Rattus baluensis* resembles *R. korinchi* in size of body and hind feet (table 1); coloration of fur over upperparts; length, density, and texture of the coat; color of ears and feet; as well as configuration of palmar and plantar surfaces and number of pads. In contrast to the Sumatran animal, *R. baluensis* has buffy gray underparts and an absolutely and relatively shorter tail (tables 1 and 2). There are also fewer rings of scales on the tail of *R. baluensis* (10–12 in 25 adults contrasted with 13–14 in *R. korinchi*), and no specimen of *R. baluensis* studied has a tail tuft.

Female *Rattus baluensis* have five pairs of teats, one pectoral, one postaxillary, two abdominal, and one inguinal.

The cranium of *Rattus korinchi* is moderately large with a squarish braincase and a slender rostrum (figs. 3, 4; table 1). Structural details of the orbit, alisphenoid region, palatal bridge, mesopterygoid and pterygoid fossae, and pattern of basicranial arterial circulation resemble those of *R. rattus*, whose features have been described and illustrated by Musser (1981, 1982) and Musser and Newcomb (1983). Aside from these regions, a characteristic of the cranium seen from dorsal view is its slender rostrum, which, except for the slightly protruding nasolacrimal capsules, hardly tapers from back to front. Another feature is the narrow interorbital region and the hourglass outline posterior to the orbits that are bounded by ridges extending back along dorsolateral margins of the braincase to the occiput. Prominent behind the orbits, the ridges decrease to an inconspicuous beading along posterior edges of the braincase. From the union of the frontals and parietals, these temporal ridges are nearly parallel and give the braincase a rectangular conformation. The sides of the braincase are not vertical but have a gentle medial slope from each squamosal root to temporal ridge.

TABLE 2  
Ratios (in Percent) of Some Measurements from Samples of *Rattus baluensis*, *Rattus korinchi*, and *Rattus hoogerwerfi*<sup>a</sup>

Ratio	<i>R. baluensis</i>	<i>R. korinchi</i>	<i>R. hoogerwerfi</i>
$\frac{LT}{LHB}$	111	135, 124	130
$\frac{BR}{LR}$	58	51, 55	52
$\frac{LIF}{LD}$	73	78, 77	74
$\frac{LB}{PPL}$	52	48, 45	44
$\frac{LB}{GLS}$	16	15, 15	15
$\frac{CLM^{1-3}}{LBP}$	81	93, 87	89
$\frac{CLM^{1-3}}{GLS}$	16	19, 18	17

<sup>a</sup> Ratios are derived from data listed in table 1. Abbreviations: BR, breadth of rostrum; CLM<sup>1-3</sup>, crown length of maxillary toothrow; GLS, greatest length of skull; LB, length of bulla; LD, length of diastema; LHB, length of head and body; LIF, length of incisive foramina; LBP, length of bony palate; LR, length of rostrum; LT, length of tail; PPL, postpalatal length.

The zygomatic arches are nearly straight and parallel to one another.

The top of the cranium above the zygomatic plates and orbit is slightly concave, which gives that portion of the cranium anterior to the braincase a flattened configuration, clearly seen in lateral view (fig. 4). The rostrum is high, each zygomatic plate moderately wide, and the bullae small relative to size of the braincase (tables 1 and 2). The incisors are orthodont and the molar rows are relatively long and terminate anteriorly near the level of the posterior edge of the zygomatic plate.

*Rattus korinchi*'s elongate incisive foramina, long maxillary toothrows, and small bullae can be seen in ventral view (fig. 3). Lateral margins of the incisive foramina nearly parallel one another and their posterior margins end less than a millimeter past the anterior alveolar margins of the toothrows. Those molar rows are nearly as long as the bony palate (table 2). The palatal bridge extends



Fig. 3. Crania of adult Sundaic *Rattus* compared. **Left:** *R. baluensis* (FMNH 108918), Gunung Kinabalu, Sabah. **Middle:** *R. korinchi* (RMNH 23151), Gunung Talakmau, Sumatra. **Right:** *R. hoogerwerfi* (USNM 271029), Gunung Leuser, Sumatra.. All  $\times 1.5$ . Measurements are listed in table 1.

posteriorly beyond the rows of teeth in the form of a shelf, a characteristic of most species of *Rattus*. In contrast to most *Rattus*, the auditory bullae are absolutely and relatively smaller (table 2).

Although similar in cranial size, *Rattus baluensis* has a stockier, wider rostrum than that of *R. korinchi* (table 2), and the rostrum is not as deep behind the incisors (figs. 3, 4).

The nasolacrimal capsules of *R. baluensis* are slightly more inflated and each opening is larger. As seen from dorsal view, the ridges bounding the postorbital region sweep back and out resembling the sides of a triangle rather than the bottom half of an hourglass, which is the outline in *R. korinchi*.

The area medial to the dorsal root of each zygomatic arch is swollen in *R. baluensis* but

much less so in *R. korinchi*, which accounts for the generally straight but slightly dished dorsal canial profile between braincase and nasal tips in *R. korinchi* and the slightly convex profile characteristic of *R. baluensis*. The way the upper incisors curve slightly back (opisthodont configuration) in *R. baluensis* contrasts with the orthodont conformation of the teeth in *R. korinchi*, a difference, like the dorsal cranial outlines, that can be seen in side view.

The difference in rostral width between the two species is evident in ventral view. Other contrasts in dimensions and proportions can be appreciated (see also tables 1 and 2). *Rattus baluensis* has, on the average, shorter incisive foramina that are also shorter relative to length of diastema; much shorter toothrows that occupy less of the bony palate and have anterior margins set well behind posterior edges of the zygomatic plates; and larger auditory bullae, not only in actual size but relative to size of braincase. The magnitude of the difference in length of molar row between *R. baluensis* and *R. korinchi* is impressive. The contrast in bullar size is also conspicuous and there is narrow overlap in the range of variation between the two samples; only 3 out of the 25 specimens of *R. baluensis* have a minimum bullar length of 6.4 mm, which is the size of the largest bulla in the two examples of *R. korinchi* (table 1).

The conformation of each dentary of *Rattus korinchi* is similar to that in other species of *Rattus* (Musser, 1981). The bony sheath enclosing the incisor is not elongate, the coronoid process is large and curved back, and the posterior dentary margin is deeply concave (fig. 4). The general shape of each dentary of *R. baluensis* is similar to that of *R. korinchi* but is overall slightly smaller, the coronoid process is shorter and less acute, the region anterior to the molar row is slightly deeper, and the tooththrow is much shorter.

As they are in other species of *Rattus*, the upper and lower incisors of *Rattus korinchi* have smooth surfaces. The enamel layers are pale orange. The incisor enamel of *R. baluensis* is pigmented more intensely—a deep orange.

Many characters in each species, such as the number of roots anchoring each tooth, the degree one tooth overlaps the other, sizes



Fig. 4. Lateral views of crania and mandibles of specimens shown in figure 3. **Top:** *R. baluensis*. **Middle:** *R. korinchi*. **Bottom:** *R. hoogerwerfi*. All  $\times 1.5$ .

of molars relative to one another, height of crowns, general cusp patterns, and no posterior cingula on first and second upper molars, are similar to those found in *Rattus rattus* and many other members of the genus (Musser, 1981, 1982; Musser and Newcomb, 1983). *Rattus korinchi* and *R. baluensis* are

TABLE 3  
Presence (+) or Absence (—) of Certain Cusps and  
Cusplets on Molars in *Rattus baluensis*, *Rattus*  
*korinchi*, and *Rattus hoogerwerfi*<sup>a</sup>

Trait	<i>R.</i> <i>baluensis</i>	<i>R.</i> <i>korinchi</i>	<i>R.</i> <i>hooger-</i> <i>werfi</i>
Cusp t3 on M <sup>2</sup>			
+	60 (34)	50 (1)	70 (14)
—	40 (23)	50 (1)	30 (6)
Cusp t3 on M <sup>3</sup>			
+	—	—	—
—	100 (57)	100 (2)	100 (20)
Anterior labial cusplet on M <sub>1</sub>			
+	—	—	—
—	100 (56)	100 (2)	100 (20)
Posterior labial cusplet on M <sub>1</sub>			
+	96 (54)	100 (2)	95 (19)
—	4 (2)	—	5 (1)
Anterolabial cusp on M <sub>2</sub>			
+	100 (56)	100 (2)	94 (17)
—	—	—	6 (1)
Posterior labial cusplet on M <sub>2</sub>			
+	98 (55)	50 (1)	83 (15)
—	2 (1)	50 (1)	17 (3)
Anterolabial cusp on M <sub>3</sub>			
+	100 (56)	100 (2)	78 (14)
—	—	—	22 (4)
Anterocentral cusp on M <sub>1</sub>			
+	—	100 (2)	—
—	100 (57)	—	100 (20)

<sup>a</sup> Number of cusps and cusplets are expressed as percentages; number of specimens is in parentheses.

also alike in occlusal topography and frequency of occurrence of the cusps and cusplets that are known to vary in both size and number (figs. 5, 6; table 3). For example, in about half the sample of each species, cusp t3 is present on each second upper molar but cusp t3 is absent from the third upper molar of all specimens in both samples. Both species lack an anterior labial cusplet but have a posterior labial cusplet on each first lower molar. The anterolabial cusp is present on each second lower molar in all specimens of each species and the posterior labial cusplet of that tooth occurs in one of the two specimens of *R. korinchi* and in all the examples of *R. baluensis*. The anterolabial cusp is also present on each third lower molar in all speci-

mens of both species and the posterior labial cusplet is part of the third molar in all *R. baluensis* but not the two specimens of *R. korinchi*.

In addition to the impressive differences in toothrow dimensions between *R. korinchi* and *R. baluensis* (table 1), the two species can be distinguished by other dental traits. One complex involves cusps t8 and t9 of the first and second upper molars. On each of these teeth there is a lingual, cusplike ridge (resembling a cusp t7) that extends anterior to touch the back of cusp t4. When cusps are worn to the level seen in RMNH 23151, there is a prominent crescentic ridge connecting the lingual side of cusp t8 with the posterior margin of cusp t4 on each first and second molar (fig. 5). A comparable lingual ridge developed from cusp t8 does not occur in *R. baluensis*. Cusp t9, on the labial side of cusp t8, is large and directed more anteriorly in *R. korinchi* than is cusp t9 on the first and second molars of *R. baluensis*. Furthermore, cusp t9 of the second upper molar in *R. korinchi* is much smaller relative to size of the adjacent cusp t8 than is the relatively larger cusp t9 in *R. baluensis*.

There is another occlusal topographic difference between the two species. In *R. korinchi*, either a mound or cusplet is present on the cingular margin of each first upper molar between cusps t3 and t6. No such structure occurs in *R. baluensis*.

Finally, in both specimens of *R. korinchi* there is a small but prominent anterocentral cusp on the anterior face of each first lower molar (fig. 6). This cusp is discrete in the holotype, which has moderately worn teeth, but indistinct and represented by a slight bulge in the worn molars of the older RMNH 23151. An anterocentral cusp is absent in all the specimens of *R. baluensis* I examined; the front lamina of each first lower molar is composed only of large anterolingual and smaller anterolabial cusps.

In summary, although superficial inspection suggests that *R. baluensis* and *R. korinchi* are alike, careful examination reveals conspicuous morphological differences. Compared with *R. korinchi*, *R. baluensis* has a nonpenicillate tail that is shorter relative to length of head and body, a wider rostrum with more inflated nasolacrimal capsules, a

different dorsal cranial profile, shorter incisive foramina, absolutely and relatively larger tympanic bullae, opisthodont upper incisors, smaller coronoid processes, absolutely and relatively shorter tooththrows, and less cuspidate molars.

#### RELATIONSHIPS TO OTHER *RATTUS* AND ZOOGEOGRAPHIC SIGNIFICANCE

The morphological features of *R. baluensis* are similar to those that characterize species of the *Rattus rattus* group, particularly *R. tiomanicus*. *Rattus tiomanicus* is indigenous to the Sunda Shelf and occurs on Peninsular Thailand and Malaysia, Sumatra, Java, Borneo, and many small islands on the Shelf—except Bali. It has not been recorded from peninsular Burma and Thailand north of the Isthmus of Kra (10°30'N). Off the Shelf, *R. tiomanicus* lives in the Maratua Archipelago, to the east of Borneo, and Pulau Enggano, southwest of Sumatra (Musser and Calafia, 1982). Morphology of skins and skulls indicates that samples of *R. mindorensis* from Mindoro Island in the Philippines, *R. burrus* from the Nicobar islands, and *R. simalurensis* from Pulau Simalulue and nearby islands (table 6) represent insular populations of *R. tiomanicus* found off of the continental shelf (Musser et al., ms).

As might be expected of a species with a discontinuous distribution on a vast number of islands, there is appreciable geographic variation among samples of *R. tiomanicus*, particularly in body size and pelage coloration. In the Bornean region, for example, the mainland populations consist of small animals with brown upperparts and white venters but the rats living on islands in the Maratua Archipelago, off the east coast of Borneo and clear of the continental shelf, are large and richly pigmented (Musser and Calafia, 1982). Yet wherever *R. tiomanicus* is found, there are basic pelage features and a cranial conformation that identify the species. These characteristics are also shared by *R. baluensis*.

The body and tail proportions of *R. baluensis* (tables 1, 4), number of mammae (five pair), configuration of the cranium (as well as the mandible) (fig. 7), size and projection

of incisors, relative size of molars and topography of their occlusal patterns (fig. 8) are more like these features in *R. tiomanicus* than in *R. korinchi*. The Kinabalu rat is larger and has much longer, thicker, and darker fur than *R. tiomanicus* from mainland Borneo living at lower elevations, and the thick dark coat separates *R. baluensis* from most populations of *R. tiomanicus* on the Sunda Shelf. Body size as well as cranial and tooththrow dimensions, however, overlap broadly between the sample of *R. baluensis* and some samples of *R. tiomanicus*; just contrast the values in table 1 with those listed in table 4 for *R. tiomanicus* from Pulau Maratua.

Chasen (1940, p. 158) recognized this morphological link between the Kinabalu animal and *R. tiomanicus* and wrote that *R. baluensis* was "almost certainly only a high level form of *R. rattus*." Chasen was referring to what we now call *R. tiomanicus* because when he compiled his handlist of Malaysian mammals many of the taxa currently associated with *R. tiomanicus* (see Musser and Calafia, 1982, p. 24) were then regarded as subspecies of *R. rattus*. Chasen was not thinking of *R. rattus diardii*, which is the only *R. rattus* that is found on Borneo, because he recognized it as a commensal houserat in his list.

The houserat is not native to Borneo (Medway, 1965) or anyplace on the Sunda Shelf (Musser and Newcomb, 1983). The species is common in lowlands of Sabah wherever there are towns, villages, and gardens (Lim and Heyneman, 1968; Medway, 1965). Specimens of *R. rattus diardii* are similar to those of *R. baluensis* in body size and some proportions (table 4) but contrast with *R. baluensis* in the same ways that they differ from examples of *R. tiomanicus* (Musser and Calafia, 1982, pp. 11–14). The shape of the cranium as viewed dorsally is one of these features (fig. 7). From that viewpoint, the supraorbital ridges flow back on either side of the skull in smooth, vase-shaped curves and disappear near the occiput in *R. baluensis* and *R. tiomanicus*. In *R. rattus diardii*, the supraorbital ridges are high and wide and form a conspicuous angular shelf behind the interorbital area and then sweep back over the sides of the braincase to the occiput, forming, especially in old animals, a square or rectangular configuration.

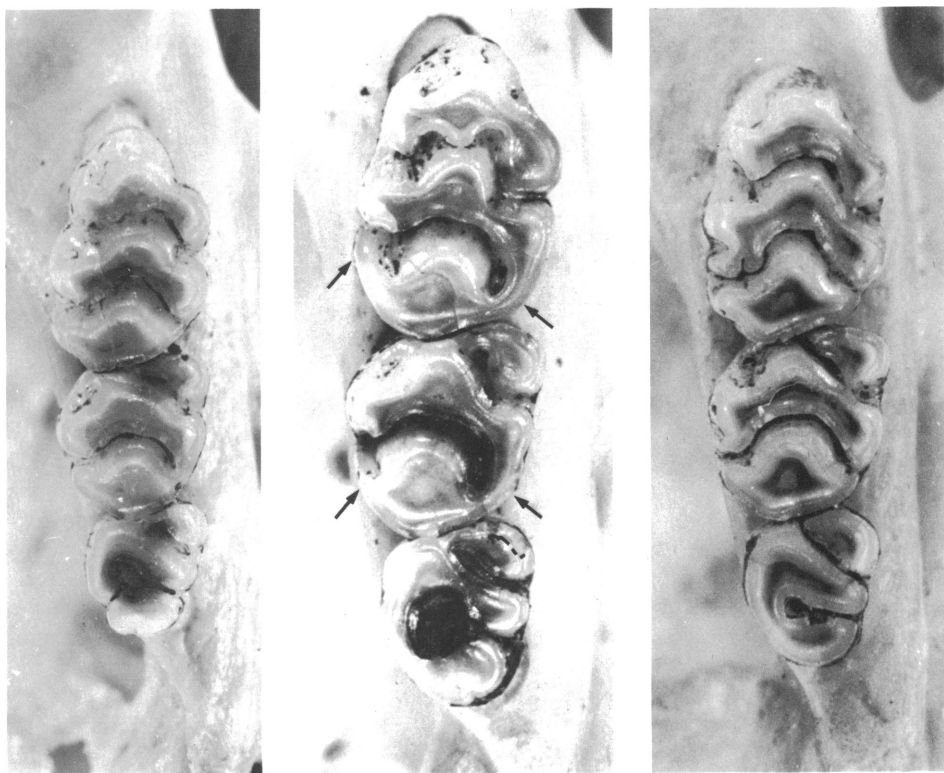


Fig. 5. Upper molar rows of same specimens of *Rattus* shown in figure 3. **Left:** *R. baluensis*. **Middle:** *R. korinchi*. **Right:** *R. hoogerwerfi*. Approximately  $\times 10$ . In middle figure, each arrow on left points to cusp t9, each arrow on right points to crescentic ridge formed by lingual extension of cusp t8 and back of cusp t4.

The character information based upon museum specimens suggests that *R. baluensis*, living in an island of mountain forest on the high slopes of Gunung Kinabalu, is a large-bodied, dark, densely furred morphological counterpart of *R. tiomanicus*, which occurs at middle altitudes on Gunung Kinabalu and in the lowlands of Sabah and regions farther south in Borneo (Medway, 1965; Musser and Califa, 1982). The long, dense fur is certainly an adaptation to low, ambient temperatures; body size may be a similar adaptation, and it may even reflect the association between island area (in this case, the extent of suitable montane habitat) and body size (Heaney, 1978) since mountain forest on Gunung Kinabalu is essentially an island in a vast expanse of lowland tropical evergreen forest—at least where that forest has not been removed. There is no evidence suggesting gene exchange between *R. baluensis* and the smaller-bodied,

brighter *R. tiomanicus sabae*; rather their similarities indicate that they may have shared a common ancestor.

If *Rattus baluensis* is more closely related to *R. tiomanicus* than to *R. korinchi*, then where does that Sumatran species fit in the pattern of phylogenetic relationships among species of *Rattus*? *Rattus korinchi* and *R. baluensis* share many features, as already discussed, that are also shared in common with species of *Rattus*. They also share long, thick, and dark pelage, but that is probably a convergent adaptation to an ambient environment associated with cool and wet mountain forests in the tropics. Excluding these aspects of its morphology, *R. korinchi* differs in the same ways from *R. baluensis* and from *R. tiomanicus*, suggesting that the Sumatran rat is not part of the same species group that embraces *R. baluensis* and *R. tiomanicus*.

*Rattus korinchi* has been linked to another

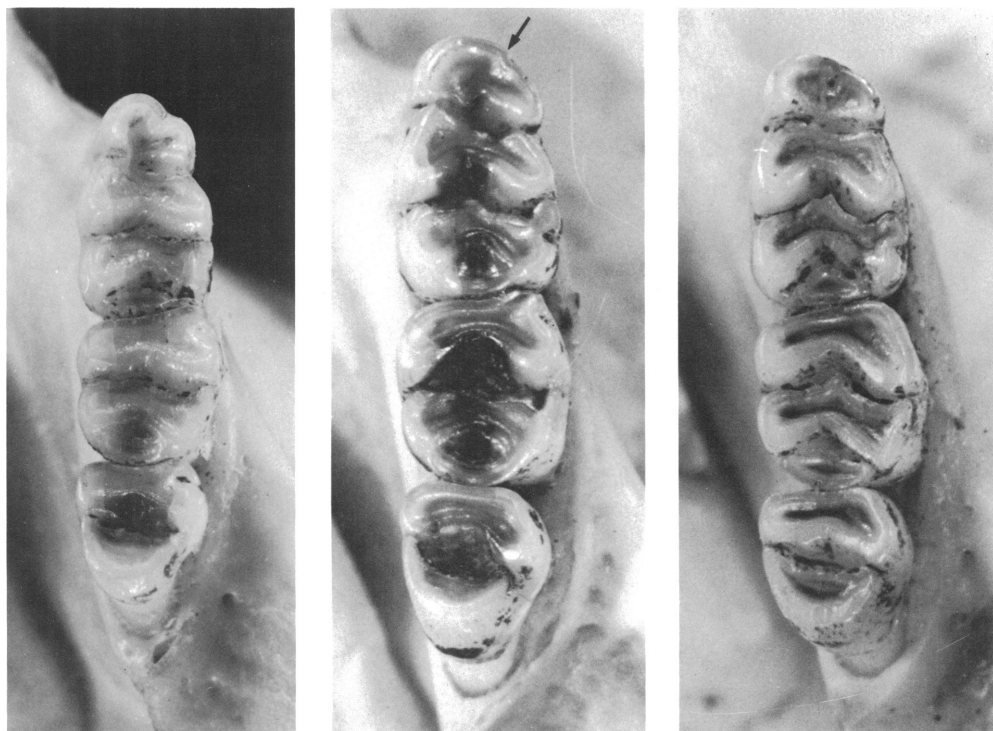


Fig. 6. Lower molar rows of same specimens of *Rattus* shown in figure 3. **Left:** *R. baluensis*. **Middle:** *R. korinchi*. **Right:** *R. hoogerwerfi*. Approximately  $\times 10$ . Arrow at top of middle toothrow points to outline of anteroventral cusp.

Sundaic endemic, *R. hoogerwerfi*, which was described by Chasen in 1939. The species was subsequently characterized in greater detail by Miller (1942), who reported upon a much larger sample. All specimens (ANSP 20296–203309 and 203311–203320; MZB 3148–3150, 4854—holotype, and 4855–4857; RMNH 5130–5133; USNM 271028–271031) come from the Aceh region of northern Sumatra; most were trapped between 2900 and 9300 ft on the forested foothills and upper slopes of Gunung Leuser.

Chasen (1939, p. 208) provided this opinion about the affinities of *R. korinchi*: “perhaps the nearest relative of *R. hoogerwerfi* is *Rattus baluensis korinchi*. If consideration of the tail is excluded, the two forms have some superficial resemblance to each other, and the peculiar characters of the skull of *hoogerwerfi* are to some extent adumbrated in adults of *korinchi*.” Chasen excluded the tail because in *R. hoogerwerfi* it is white for about the distal half, dark brown over the basal half,

and not penicillate; the slightly brushy tail of *R. korinchi* is monocolored dark brown; in both species the tail is very long relative to length of head and body (tables 1, 2).

Features of the tail are not the only external contrasts between the two species. *Rattus hoogerwerfi* is larger in body size than *R. korinchi* (table 1), has eight teats, and has ochraceous brown upperparts and bright buffy to ochraceous gray underparts; the overall coloration of the fur is much richer than the pelage of *R. korinchi*. Morphology and coloration of the ears and feet are similar in the two species, as is density and texture of the fur.

In his diagnosis of *R. hoogerwerfi*, Chasen (1939, p. 207) noted that the “nasals and the interorbital region of the skull is unusually flattened.” This is one of the diagnostic cranial characters that Chasen also thought was typical of *R. korinchi*. However, I cannot see the resemblance; the area above the dorsal root of each zygomatic plate is swollen in *R.*

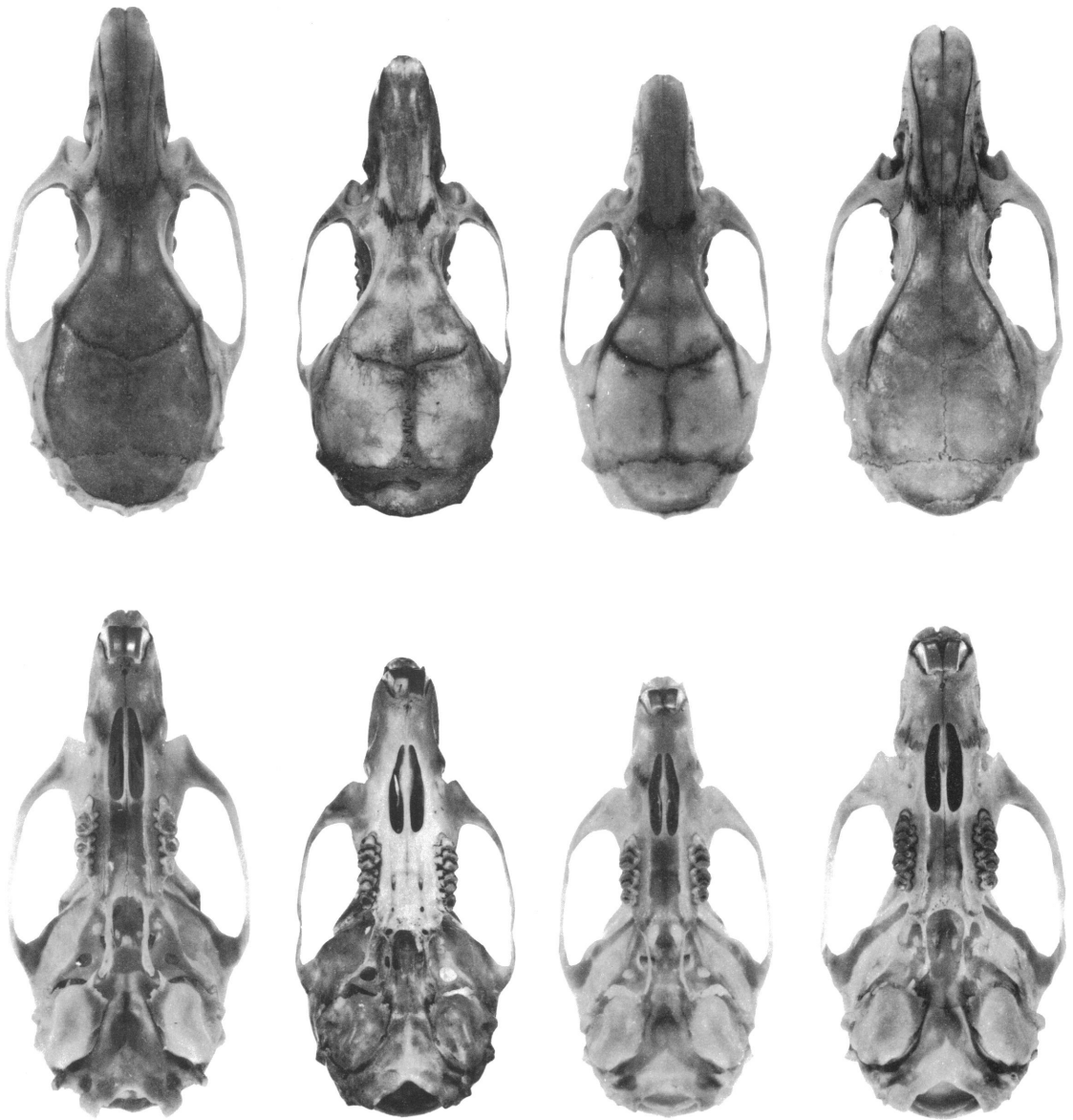


Fig. 7. Crania of adult *Rattus* from the Bornean region. From left to right: *R. rattus diardii* (USNM 292689), Gunung Kinabalu, 4900 ft, Sabah; *R. baluensis* (FMNH 108918), Gunung Kinabalu, 11,200 ft, Sabah; *R. tiomanicus sabae* (USNM 292672), 3300 ft, Sabah; *R. tiomanicus mara* (USNM 197431), Pulau Maratua. All  $\times 1.5$ .

*hoogerwerfi* to the same extent as is seen in specimens of *R. baluensis* (fig. 4). Furthermore, the frontal bones between the orbits are also swollen and unlike the flattened, slightly concave dorsal profile characteristic of *R. korinchi* (fig. 4).

The two species do share cranial and dental characters but some of these are common to

nearly all species of *Rattus* (Musser and Newcomb, 1983) and provide no information about the relationships of *R. korinchi* and *R. hoogerwerfi*. Both have, for example, similar configurations of the orbit, alisphenoid region, palatal bridge, as well as the same pattern of basicranial arterial circulation. Both species share the same number of roots an-



Fig. 8. Upper (two on left) and lower (two on right) molar rows of *Rattus*. Left view of each couplet is *Rattus baluensis* from Gunung Kinabalu (FMNH 250927;  $CLM^{1-3} = 6.8$  mm,  $CLM_{1-3} = 6.6$  mm), right view in each couplet is *Rattus tiomanicus* from Java (AMNH 250124;  $CLM^{1-3} = 7.0$  mm,  $CLM_{1-3} = 7.2$  mm). Note similarity in cusp patterns. A primary but minor difference is the frequency of occurrence of cusp t3 (arrow) on first and second upper molars. Cusp t3 is present on each first molar in 60 percent of the sample of *R. baluensis* and absent from each second molar of all specimens (table 3). In 20 specimens of *R. tiomanicus* from Borneo, cusp t3 occurs on each first molar in 18 (90%) rats and on each second tooth in 9 (45%) specimens. These frequencies are typical for the Javan sample as well as most other samples of *R. tiomanicus*.

choring each molar, the degree one tooth overlaps the other, sizes of molars relative to one another, height of crowns, general cusp patterns; both lack posterior cingula on first and second upper molars.

*Rattus hoogerwerfi* and *R. korinchi* also possess narrow rostra, as well as small bullae and long molar rows relative to size of cranium (tables 1, 2), and orthodont configuration of upper molars (fig. 4). Small auditory bullae are thought to be primitive in murines (Musser and Newcomb, 1983) and do not necessarily reflect a close phylogenetic relationship between the two species. Conformation of the rostrum and incisors and relative molar dimensions may indicate a closer affinity

between *R. hoogerwerfi* and *R. korinchi* than between either of those two species and *R. baluensis*. However, the polarities of these characters are unclear and may not affirm a close link between the two Sumatran species.

The conspicuous differences between *R. hoogerwerfi* and *R. korinchi* are more notable than their few similarities. In addition to the coloration (bicolored versus monocolored) and pilosity (nonpenicillate versus slightly penicillate) of the tail, and the dorsal outline of the cranium (slightly convex from nasal tips to interorbit in *R. hoogerwerfi* but flat to slightly concave in *R. korinchi*; fig. 4), the species contrast in the following features.

1. The nasal bones of *R. hoogerwerfi* have

TABLE 4  
Measurements (in Millimeters) and Ratios (in Percent) of Adult *Rattus rattus diardii* and *Rattus tiomanicus* from Borneo and the Maratua Archipelago<sup>a</sup>

Meas. and Ratio	<i>R. rattus</i> , Sabah	<i>R. tiomanicus</i>		
		Sabah	South Kalimantan	Pulau Maratua
LHB	177.8 ± 16.6 (15) 147–202	157.8 ± 14.6 (5) 133–170	163.1 ± 12.2 (16) 146–188	179.9 ± 31.5 (30) 156–212
LT	184.7 ± 23.8 (15) 142–222	159.0 ± 14.5 (5) 141–174	166.3 ± 10.2 (16) 140–177	203.0 ± 16.7 (30) 170–228
GLS	42.1 ± 1.9 (15) 38.6–44.6	37.7 ± 1.9 (5) 34.6–39.6	38.1 ± 1.4 (16) 35.5–41.2	43.1 ± 2.1 (30) 39.7–47.4
LPB	8.6 ± 0.6 (15) 7.7–9.5	7.8 ± 0.4 (5) 7.3–8.3	8.2 ± 0.4 (16) 7.5–8.8	9.0 ± 0.5 (30) 8.3–10.0
PPL	14.9 ± 1.0 (15) 13.3–16.7	12.9 ± 1.0 (5) 11.4–14.0	12.4 ± 0.7 (16) 11.5–14.2	14.5 ± 0.9 (30) 12.9–16.0
LB	7.0 ± 0.4 (15) 6.4–7.7	6.4 ± 0.2 (5) 6.2–6.7	6.8 ± 0.3 (16) 6.4–7.2	6.9 ± 0.2 (30) 6.4–7.4
CLM <sup>1–3</sup>	6.5 ± 0.2 (15) 5.8–6.7	6.2 ± 0.2 (5) 5.9–6.3	6.4 ± 0.2 (16) 6.1–6.9	6.6 ± 0.2 (30) 6.2–6.9
$\frac{LT}{LHB}$	104	101	102	113
$\frac{LB}{GLS}$	17	17	18	16
$\frac{CLM^{1–3}}{LPB}$	76	79	78	73
$\frac{CLM^{1–3}}{GLS}$	15	16	17	15

<sup>a</sup> Mean plus or minus one standard deviation, number of specimens in parentheses, and observed range are listed. Abbreviations of measurements are explained in table 2.

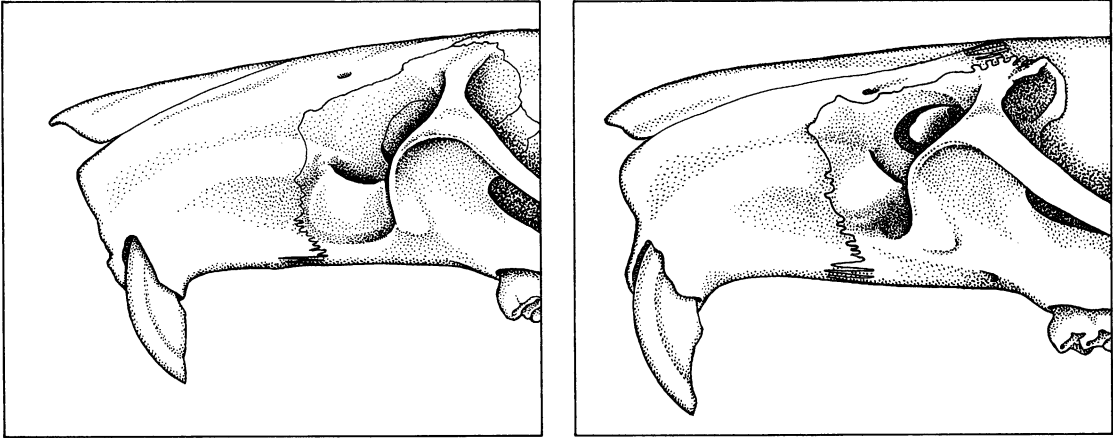


Fig. 9. Nasolacrimal capsules in *Rattus hoogerwerfi* (left) and *Rattus korinchi* (right). Located just anterior to the zygomatic plate, the capsule of *R. hoogerwerfi* has a nearly horizontal opening, while that of *R. korinchi* is aligned at about 45°. Drawings from same specimens shown in figure 4.

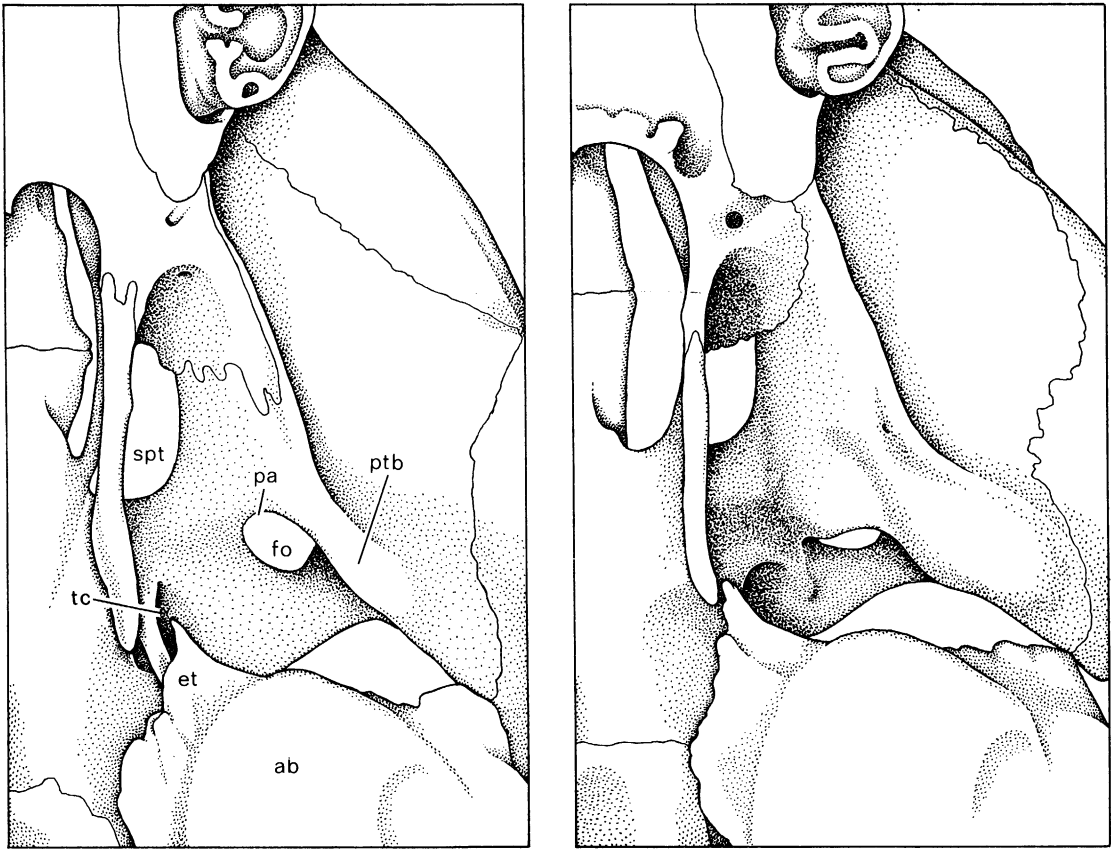


Fig. 10. Pterygoid fossae in *Rattus korinchi* (left) and *Rattus hoogerwerfi* (right). Excavation of the fossa in *R. korinchi* begins at the lateral margin, but the medial half of the fossa is deeply excavated and the lateral half is nearly flat in *R. hoogerwerfi*. Note the different conformation of each pterygoid bridge (ptb), posterior opening of each alisphenoid canal (pa), extent of foramen ovale (fo) exposed, and position of each transverse canal (tc) relative to the bony eustachian tube (et) of the auditory bulla (ab). See text for an expanded discussion of pterygoid contrasts between the species. Spt = sphenopterygoid vacuity; other structures and foramina not labeled can be identified by referring to appropriate illustrations in Musser and Newcomb (1983). Drawn from same specimens shown in figure 3.

an oblongate outline whereas those of *R. korinchi* are linear from dorsal perspective (fig. 3).

2. The rostrum just posterior to the incisors is not as deep in *R. hoogerwerfi* as it is in *R. korinchi* (fig. 4).

3. The nasolacrimal capsules are slightly wider in *R. hoogerwerfi* and each one opens dorsad. Each opening is aligned at about a 45° angle in *R. korinchi* (fig. 9).

4. The braincase of *R. hoogerwerfi* is wider than in *R. korinchi* (table 1) and oval in dorsal outline as contrasted with a more boxlike conformation in *R. korinchi* (fig. 3).

5. The configuration of the pterygoid fos-

sae, which is the site of origin of the internal pterygoid muscles, differs (fig. 10). In *R. hoogerwerfi*, each fossa is only slightly higher than the bony palate and the lateral half of the pterygoid shelf is nearly flat for about three-fourths of the distance from the posterior margin of the palate to the auditory bulla. Anterior to the bulla and at the place where the shelf merges with the pterygoid bridge, the surface turns sharply upward and in that slope are two openings. The lateral one is the posterior opening of the alisphenoid canal, which is vertical, almost like the entrance to a tube. Medial of that but lateral to the bony eustachian tube, is the transverse canal. Anterior to these openings, the pter-

ygoid plate is perforated by a wide sphenopterygoid vacuity. At the level of the posterior opening of the alisphenoid, the lateral margin of each pterygoid plate expands to form a low and broad mound, the pterygoid bridge.

In *R. korinchi*, the pterygoid fossae are excavated beginning at their lateral margins. Each surface is breached by a wide sphenopterygoid vacuity and the lateral half is not nearly flat but slopes upward toward the midline of the cranium. About halfway between margin of the bony palate and tympanic bullae, the pterygoid surface gradually slopes upward. Here there are two openings. The medial one is the entrance to the transverse canal, which is just above the bony eustachian tube (located lateral to the tube in *R. hoogerwerfi*). The spacious, nearly horizontal lateral opening is the posterior opening of the alisphenoid canal. Because the opening is nearly horizontal, from a ventral perspective (fig. 10) you can see into the posterior portion of the foramen ovale, which is located in the side of the braincase above the pterygoid fossa. The edge of the pterygoid surface lateral to the opening into the alisphenoid canal—the pterygoid bridge—is formed by a high and narrow ridge.

The conformation of the pterygoid plates and openings in *R. hoogerwerfi* has been interpreted as primitive in muroid rodents (Carleton, 1980; Musser and Newcomb, 1983). A more fully excavated fossa, nearly horizontal posterior opening to the alisphenoid canal through which the foramen ovale can be seen, and a high ridge forming the pterygoid bridge, as found in *R. korinchi* and most *Rattus* including *R. baluensis*, are specializations (fig. 10; see also Musser, 1981, 1982; Musser and Newcomb, 1983).

6. The shape of the dentary is similar in *R. hoogerwerfi* and *R. korinchi* but the coronoid process is not as large relative to the body of the ramus, the bony sheath enclosing the incisor is not as wide or deep, and in any pair of specimens of approximately the same age, the absolute size of the dentary is smaller in *R. hoogerwerfi*, even though the cranium is larger (fig. 4).

7. Upper incisors of *R. hoogerwerfi* are more deeply pigmented and lowers are smaller in diameter and more gracile than those of *R. korinchi*.

8. Compared to most *Rattus*, *Rattus hoogerwerfi* and *R. korinchi* have large molars and long molar rows, both in absolute dimensions and relative to lengths of bony palate and cranium (tables 1, 2). The two species also share similar cusp patterns of the upper and lower molars (fig. 5; table 3), yet there are differences. The lingual extension of cusp t8 of each first and second upper molar in *R. hoogerwerfi* extends laterally from the cusp and does not merge with the posterior margin of cusp t4; in *R. korinchi*, the lingual process of cusp t8 extends anteriorly and contacts the back of cusp t4 to form a crescentic ridge after some wear. Cusp t9, on the labial surface of the large cusp t8, is also directed laterally in *R. hoogerwerfi*; in *R. korinchi* the comparable cusp extends anteriorly in both first and second upper molars. There are slight differences in occurrence of certain cusps and cusplets on the lower molars (fig. 6; table 3), but the major contrast is the absence of an anterocentral cusp at the anterior end of each first molar in *R. hoogerwerfi*; both examples of *R. korinchi* have such a cusp.

There is no derived character or set of characters suggesting *R. hoogerwerfi* to be a sister species of *R. korinchi*. Their external similarities (long tail relative to head and body, thick and long fur, dark coloration) may be independent adaptations to a scansorial or arboreal life in cool and wet mountain forests. The cranial characters shared by both are either primitive retentions (small bullae relative to cranial dimensions, for example), derived features found in many other species of *Rattus*, or ambiguous in indicating relationships (narrow rostrum, orthodont upper incisors, large molars relative to size of cranium). The combination of bicolored tail, nearly horizontal alignment of the rim of each nasolacrimal capsule, and large oval braincase—all derived characters compared with the nature of these structures in most species of *Rattus* (*R. korinchi* and *R. baluensis*, for example)—and conformation of each pterygoid fossa and associated foramina—which is primitive with respect to other species of *Rattus*—isolate *R. hoogerwerfi* within the genus.

The uniqueness of *R. hoogerwerfi* was appreciated by Sody, who in 1941 (p. 260) proposed that the species be placed in its own

genus, *Cironomys*, at least partly because of the number and distribution of mammae (one pectoral pair, one abdominal pair, and two inguinal pairs). To Miller (1942, p. 150), the "Atjehan mountain rat is a member of the peculiar group (nearly related to *Rattus rattus* and its common Malayan representatives) that includes the Celebean *Rattus xanthurus* (Gray), *R. celebensis* (Gray), *R. marmosurus* (Thomas), and *R. hamatus* (Miller and Hollister), as well, apparently, as the Philippine *R. everetti* (Gunther) and the *R. macleari* (Thomas) of Christmas Island." All these species share medium to large body size, a long bicolored tail, relatively large molars, and distributions on islands; otherwise, there is no set of characters tying *R. hoogerwerfi* any closer to these species than to any other set of species either within or outside of the morphological limits of *Rattus* (Musser, MS).

The morphological isolation of *R. hoogerwerfi* partly illuminates the question about affinities of *R. korinchi*. The two are not closely related, judged from analyses of characters in the stuffed skin, skull, and dentition. Compared with *R. hoogerwerfi*, *R. korinchi* has tail coloration, nasolacrimal capsules, and pterygoid fossae like most species of *Rattus*. However, judged by the morphological differences between *R. korinchi* and *R. baluensis*, the Sumatran rat is not closely allied to species in the *R. rattus* group, and is morphologically isolated compared with most species in the genus. On Borneo, the morphological attributes of *R. baluensis* suggest the hypothesis that it and *R. tiomanicus* shared the same, recent common ancestor. On Sumatra, neither *R. korinchi* nor *R. hoogerwerfi* appears to be derivatives of that ancestral population.

### THE SUNDAIC *RATTUS*

The separation of *R. korinchi* from *R. baluensis* brings to 41 the number of murid species now known to be native to the Sunda Shelf (table 5) and slightly changes the percentage of endemic murids on Borneo and Sumatra (compare table 5 with table 36 in Musser and Newcomb, 1983, p. 532). There are five, not four, species of *Rattus* recognized from the peninsula and islands on the Shelf. Present critical comparisons among

specimens of *R. baluensis*, *R. korinchi*, *R. hoogerwerfi*, and *R. tiomanicus* modify parts of Musser and Newcomb's (1983, pp. 573–577) assertions regarding relationships of these native Sundaic species but support other aspects of their observations.

On Borneo there are 19 species of native murids, of which two (11%) are *Rattus*. One of these, *R. baluensis*, is known to occur only in montane forest on the high slopes of Gunung Kinabalu and in its morphology appears to be closely related to that of *R. tiomanicus*, which is found at lower elevations on Kinabalu and elsewhere throughout Borneo and on nearby islands. *Rattus tiomanicus* is also widespread elsewhere on the Sunda Shelf and has been recorded from beyond the 180-m bathymetric line. Through *R. tiomanicus*, the Kinabalu species appears to be more closely related to *R. rattus*, *R. argentiventer*, *R. nitidus*, and other species in the *R. rattus* group (which occur primarily in India and Indochina) than to any other species of *Rattus* endemic to the Sunda Shelf.

Of the 20 murid species native to Sumatra, four (20%) are *Rattus* (table 5); two of these also occur elsewhere and two are endemic. *Rattus annandalei* has been recorded from the mainland of eastern Sumatra, the islands of Padang and Rupat off the coast of eastern Sumatra, peninsular Malaysia, and Singapore (Musser and Newcomb, 1983). Its range, however, is probably more widespread than is indicated by specimens in museum collections. On peninsular Malaysia, it has usually been regarded as uncommon and local in its distribution (Chasen, 1940; Medway, 1969) but Muul and Lim (1971, p. 435) found it common "in lowland secondary forests . . . and in kampong rubber estates . . . whenever traps were set low on trees." They also noted that some specimens were caught on the ground and that none were encountered in primary forest. There are no specimen records of *R. annandalei* from highlands.

*Rattus tiomanicus* is the other native non-endemic species of the genus occurring on Sumatra. It, like *R. annandalei*, is primarily lowland in distribution but has been recorded from as high as 3600 ft on the slopes of Gunung Leuser (specimens collected there were originally described as a new species, *R. blangorum*, by Miller, 1942).

TABLE 5  
Living Native Murids on Peninsula and Islands of the Sunda Shelf<sup>a</sup>

Genera and Species	Penin- sular Thailand and Malaya	Sumatra	Borneo	Java	Bali	Smaller <sup>b</sup> Islands	Palawan Group
<i>Rattus tiomanicus</i>	I	I	I	I	I	I	I
<i>Rattus baluensis</i>	—	—	E	—	—	—	—
<i>Rattus korinchi</i>	—	E	—	—	—	—	—
<i>Rattus hoogerwerfi</i>	—	E	—	—	—	—	—
<i>Rattus annandalei</i>	I	I	—	—	—	—	—
<i>Palawanomys furvus</i>	—	—	—	—	—	—	E
<i>Kadarsanomys sodyi</i>	—	—	—	E	—	—	—
<i>Sundamys muelleri</i>	I	I	I	—	—	I	I
<i>Sundamys infraluteus</i>	—	I	I	—	—	—	—
<i>Sundamys maxi</i>	—	—	—	E	—	—	—
<i>Berylmys bowersii</i>	O	O	—	—	—	—	—
<i>Mus crociduroides</i>	—	E	—	—	—	—	—
<i>Mus vulcani</i>	—	—	—	E	—	—	—
<i>Leopoldamys sabanus</i>	O	O	O	O	—	O	—
<i>Leopoldamys edwardsi</i>	O	O	—	—	—	—	—
<i>Niviventer bukit</i>	O	O	—	O	O	—	—
<i>Niviventer cremoriventer</i>	I	I	I	I	I	I	—
<i>Niviventer rapit</i>	I	I	I	—	—	—	—
<i>Niviventer lepturus</i>	—	—	—	E	—	—	—
<i>Maxomys surifer</i>	O	O	O	O	—	O	—
<i>Maxomys rajah</i>	I	I	I	—	—	I	—
<i>Maxomys panglima</i>	—	—	—	—	—	—	E
<i>Maxomys whiteheadi</i>	I	I	I	—	—	I	—
<i>Maxomys bartelsii</i>	—	—	—	E	—	—	—
<i>Maxomys inflatus</i>	—	E	—	—	—	—	—
<i>Maxomys hylomyoides</i>	—	E	—	—	—	—	—
<i>Maxomys inas</i>	E	—	—	—	—	—	—
<i>Maxomys alticola</i>	—	—	E	—	—	—	—
<i>Maxomys ochraceiventer</i>	—	—	E	—	—	—	—
<i>Maxomys baeodon</i>	—	—	E	—	—	—	—
<i>Chiropodomys gliroides</i>	O	O	O	O	O	O	—
<i>Chiropodomys muroides</i>	—	—	E	—	—	—	—
<i>Chiropodomys major</i>	—	—	E	—	—	—	—
<i>Chiropodomys calamianus</i>	—	—	—	—	—	—	E
<i>Haeromys margaretae</i>	—	—	E	—	—	—	—
<i>Haeromys pusillus</i>	—	—	E	—	—	—	—
<i>Haeromys</i> sp.	—	—	—	—	—	—	E
<i>Pithecheir melanurus</i>	—	—	—	E	—	—	—
<i>Pithecheir parvus</i>	E	—	—	—	—	—	—
<i>Lenothrix canus</i>	I	I	I	—	—	—	—
<i>Hapalomys longicaudatus</i>	O	—	—	—	—	—	—
Total species	17	20	19	12	4	8	6
Total indigenous	8 (47) <sup>c</sup>	9 (45)	8 (42)	2 (17)	2 (50)	5 (63)	2 (33)
Total also found elsewhere	7 (41)	6 (30)	3 (16)	4 (33)	2 (50)	3 (37)	—
Total endemic	2 (12)	5 (25)	8 (42)	6 (50)	—	—	4 (67)

Abbreviations: —, apparently absent; E, endemic to a particular island; I, indigenous to the Sunda Shelf; O, also found in regions outside the Sunda Shelf.

<sup>a</sup> Defined here, the northern limit of the Sunda Shelf is near the Isthmus of Kra between latitudes 10 and 12°N.

The two Sumatran endemics are *R. hoogerwerfi* and *R. korinchi*. *Rattus baluensis* inhabits a similar ecological situation, living in mountain forests on Gunung Kinabalu in northern Borneo. No such ecologically similar species of *Rattus* is known from any other island on the Sunda Shelf or on peninsular Malaysia. The only native *Rattus* on Java and Bali, where there is dramatic topographic relief, is *R. tiomanicus*. That species and *R. annandalei* represent the genus on peninsular Malaysia and Singapore.

The endemic mountain forest species of *Rattus* on Sumatra likely had a different evolutionary history than did their ecological counterpart on Gunung Kinabalu. On Borneo, the endemic and montane *R. baluensis* is apparently related to the widespread and lowland *R. tiomanicus*. Morphology of the Sumatran *R. hoogerwerfi* and *R. korinchi* does not tie either of these species closely to *R. tiomanicus* and each may represent a separate branching from ancestral *Rattus* at an earlier date than the later divergence of *R. tiomanicus* and *R. baluensis*.

If *R. hoogerwerfi* and *R. korinchi* are not close to *R. tiomanicus* and *R. baluensis* in morphology of characters associated with skins, skulls, and teeth, they are not any more closely related to each other, or to *R. annandalei*, the other Sundaic *Rattus*. That species differs from all other *Rattus* in its retention of many primitive external, cranial, and dental characters combined with highly specialized, large and inflated tympanic bullae. *Rattus annandalei*, like *R. hoogerwerfi* and *R. korinchi*, seems isolated within the present morphological limits of the genus (Musser and Newcomb, 1983).

A phylogenetic study of Sundaic *Rattus* is beyond the scope of the present report. My intention has been to define *R. baluensis* and *R. korinchi* by contrasting their morphology and testing previously suggested relation-

ships of each. Two hypotheses are suggested by this research. First, *R. baluensis* is a sister species of *R. tiomanicus*. Both share many morphological characteristics with *R. rattus* and related species occurring in Indochina and the Indian Region (Musser and Newcomb, 1983). Just how closely all these species are related to one another is unknown at present and any resolution to their phylogenetic alliances awaits critical study, especially of geographic variation within *R. tiomanicus* and an assessment of its affinities to Indochinese *R. rattus* (Musser and Califa, 1982).

The second hypothesis is that *R. korinchi* is not closely related to either *R. baluensis* or *R. hoogerwerfi* as was asserted by Chasen (1940) and Musser and Newcomb (1983). *Rattus korinchi* does share more derived features with *R. tiomanicus* and *R. baluensis* than with *R. hoogerwerfi*, but the Kerinci rat is not part of the *R. tiomanicus*-group radiation. It, like *R. hoogerwerfi*, seems isolated within the morphological framework of *Rattus*.

Perhaps the relatives of *R. korinchi* and *R. hoogerwerfi*, as well as *R. annandalei*, should be looked for in places off of the Sunda Shelf beyond the 180-m bathymetric line. On islands and small archipelagos to the east, south, and west of the Shelf are native *Rattus* that represent either (1) insular populations of *R. tiomanicus*, (2) species that are similar to *R. tiomanicus* in their morphology, or (3) other species characterized by morphologies very different from that typical of *R. tiomanicus* and its relatives (table 6). Most of the islands have only one representative of the three groups. Pulau Enggano is an exception because one member of each group occurs there: *R. tiomanicus vernalis*; *R. adustus*, a relative of *R. tiomanicus*; and *R. enganensis*, which is not closely allied to the *R. tiomanicus* group.

Species listed in the third group in table 6 share the attributes of insular distributions

←

South of the Isthmus, the 100-fathom line marks the boundary, as indicated by the unbroken red line on the map at the front of Chasen's (1940) handlist of Malaysian mammals. Regions outside the Sunda Shelf include Indochina north of the Isthmus of Kra (10°30'N), the Maratua Archipelago east of Borneo, the Mentawai Islands, and Pulau Enggano.

<sup>b</sup> Includes the Raiu and Lingga archipelagos, the Natuna Islands, Kepulauan Anambas, Pulau Banka, Pulau Billiton, and Pulau Nias.

<sup>c</sup> Percent in parentheses.

TABLE 6  
Distribution of Native *Rattus* on Islands Located East, South, and West of the Sunda Shelf  
Beyond the 180-m Bathymetric Line<sup>a</sup>

Taxon	Place
Populations of <i>R. tiomanicus</i>	
<i>R. mindorensis</i>	Mindoro Island, the Philippines
<i>R. tiomanicus mara</i>	Maratua Archipelago, east of Borneo
<i>R. simalurensis</i>	Islands of Babi, Lasia, Siumat, and Simalule
<i>R. burrus</i>	Nicobar islands, northwest of Sumatra
<i>R. tiomanicus vernalus</i>	Pulau Enggano, southwest of Sumatra
Species closed allied with <i>R. tiomanicus</i>	
<i>R. adustus</i>	Pulau Enggano
<i>R. lugens</i>	Mentawai islands, southwest of Sumatra
? <i>R. palmarum</i>	Nicobar islands
Species not closely related to <i>R. tiomanicus</i>	
<i>R. everetti</i>	Philippine islands, from Luzon to Mindanao
<i>R. tawitawiensis</i>	Tawitawi Island, Sulu Archipelago
<i>R. hoffmanni</i>	Sulawesi
<i>R. xanthurus</i>	Sulawesi and Pulau Peleng
<i>R. macleari</i>	Christmas Island, south of Java
<i>R. nativitatis</i>	Christmas Island
<i>R. enganus</i>	Pulau Enggano
<i>R. stoicus</i>	Andaman islands, south of Burma

<sup>a</sup> Distributions, along with maps, and morphological characteristics of the species are discussed by Musser and Calafia (1982), Musser and Newcomb (1983), and Musser and Heaney (1985).

combined with unique morphologies making them unlike most other species of *Rattus* occurring on islands and peninsulas of the Sunda Shelf and on continental Asia and India. All eight, like *R. hoogerwerfi*, *R. korinchi*, and *R. annandalei*, are morphologically and probably phylogenetically peripheral to the main cluster of species in *Rattus* (Musser et al., MS). Some of the species are terrestrial, others are arboreal; all are forest dwellers. Each one is defined by a unique set of characteristics and each retains a greater number of primitive features compared with *Rattus rattus*, *R. tiomanicus*, and allied species. The distributions and morphological characteristics suggest that the species represent island relicts of an ancestral radiation that took place earlier than the one producing *R. tiomanicus* and its relatives. Future critical study of native Sundaic *Rattus* should also include samples from the eight species in table 6.

Such a study should also include *Rattus montanus* from the highlands of Sri Lanka (Phillips, 1981). McKay (1984, p. 422) has speculated that *R. montanus* is "possibly a sample of extremely large *R. rattus kelaarti*

males," but the holotype of *R. montanus* and other specimens I have studied clearly represent a species with very different morphology than is usual for *R. rattus*. In body size and fur color, *R. montanus* closely resembles *R. korinchi*. The two species also share similar conformations of cranium and mandible and both have long tooththrows. *Rattus montanus* has more cuspidate molars with a discrete posterior cingulum at the back of each first upper molar; overall, the molar patterns of *R. montanus* are more primitive than that seen in *R. korinchi*.

The perception that *R. baluensis* and *R. korinchi* are separate species alters our view of the native Sundaic murid fauna. Now, five species are known only from Sumatra: *Rattus korinchi*, *Rattus hoogerwerfi*, *Mus crociduroides*, *Maxomys inflatus*, and *Maxomys hylomyoides*. Eight species are endemic to Borneo: *Rattus baluensis*, *Maxomys alticola*, *Maxomys ochraceiventer*, *Maxomys baeodon*, *Chiropodomys muroides*, *Chiropodomys major*, *Haeromys margaretae*, and *Haeromys pusillus*.

Before *baluensis* was separated from *ko-*

*rinchi*, there were two species common to Borneo and Sumatra only. Now there is but one: *Sundamys infraluteus*, a highland rat that has been collected in the upper part of lowland tropical evergreen forest and higher in montane forest. It has been recorded from five places along the mountain backbone of Sumatra, from two mountains in Sabah, and from one in Sarawak (Anderson et al., 1982; Musser and Newcomb, 1983). Although there are slight differences in coloration and size between samples from the two islands, the samples have the aspect of a species that once consisted of interbreeding populations. Musser and Newcomb (1983) considered them insular populations of one species. Although found mostly in the mountains, specimens from both Sumatra and Borneo come from as low as 2300 and 3000 ft. When the Sunda Shelf was entirely above sea level and drained by great rivers during the Pleistocene, temperatures were cooler, forest formations occurred at lower elevations (Whitten et al., 1984), and populations of *S. infraluteus* were probably continuous in some regions. The morphological differences contrasting the Bornean and Sumatran populations of *Sundamys infraluteus* do not resemble either the magnitude or kinds of differences that distinguish *Rattus baluensis* and *R. korinchi*.

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