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Results of the Archbold Expeditions. No. 106. Identities of Rats from Pulau Maratua and Other Islands off East Borneo

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ABSTRACT

Rats from Pulau Maratua and from off the east coast of Borneo beyond the 100 fathom line were originally identified as *Epimys mara* and *E. tua* (Miller, 1913). Subsequent reports on the original series have allied the taxa with *Rattus muelleri* (Chasen, 1940) and house rats, *R. rattus* (Chasen, 1940; Medway, 1965, 1977; Schwarz and Schwarz, 1967). Actually, two species live on the island, *R. rattus diardii* and *R. tiomanicus mara* (*tua* is a synonym). We explain our identifications in the context of discussion and questions about *R. rattus diardii* and especially *R. tiomanicus* in the Malayan region.

INTRODUCTION

Pulau Maratua lies beyond the 100 fathom line off the east coast of Borneo (Riley, 1930). Rats live on the island. Samples of them have been reported under different identities with the result that their affinities to populations on other islands and the Borneo mainland have remained unclear (Miller, 1913; Chasen, 1940; Medway, 1965, 1977; Schwarz and Schwarz, 1967). Here we identify the species on P. Maratua. That process involved the study of samples from other islands off the east coast of Borneo, from Borneo itself, from the Malay Peninsula, and from large and small islands on and off the Sunda Shelf. The samples from P. Maratua turned out to be a lens through which we could view aspects of the taxonomy and geographic distribution of Sundanese rats and then focus on their identifications. The question of what kind of rats occur on P. Maratua is resolved, but that is only the beginning of inquiries into the identities and phylogenetic relationships of species of *Rattus* in the Malayan region, particularly *Rattus rattus* and *R. tiomanicus*.

Specimens in the National Museum of

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Natural History form the core of our report. We thank curators in the Division of Mammals there for making the collections accessible to us and for lending us material. We are also grateful to curators of the other institutions at which Musser studied for making available to him their collections and other resources. The fine photographs were made by Mr. Arthur Singer, Mr. Peter Goldberg, and Mr. Jim Coxe. Ms. Margot Dembo deserves special mention for her help with figure 1 and the analysis of data; we appreciate her efforts. Musser's research and past visits to museums has been sponsored by Archbold Expeditions, Inc.

ABBREVIATIONS AND METHODS

We studied specimens from many museums but those we refer to by numbers are in the collections at the American Museum of Natural History, New York (AMNH); the Museum Zoologicum Bogoriense, Bogor (MZB); the Naturhistorisches Museum Wien, Wien (NMW); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Values from measurements of greatest length of skull (or occipitonasal length; the distance from the tip of the nasals to the posterior margin of the occiput) and alveolar length of maxillary toothrow (the distance from the anterior edge of the alveolus of the first molar to the posterior edge of the alveolus of the third molar) are in millimeters. Both measurements were taken with dial calipers graduated to tenths of millimeters.

Only adult rats were used in the analyses. These are animals that had completed the molt from juvenile into full adult pelage.

The gradation in underparts from white to dark grayish buff were broken into five categories and given scores from 0 to 4 (tables 4 and 5). Each score represents a tone that we could consistently recognize. The categories were derived from the variation present in the many specimens examined and were not preconceptions as to how finely the range of variation should be divided.

We mostly use older geographic names of places throughout the text; a list of those names and their currently used counterparts follows.

MALAYA: West Malaysia.
SUMATRA: Sumatera.
JAVA: Jawa.
BORNEO: Sarawak, Sabah, Brunei (East Malaysia); Kalimantan (Indonesian Borneo).
CELEBES: Sulawesi.
MOLUCCAS: Maluku.
NEW GUINEA: Irian Jaya (Indonesian New Guinea; Papua New Guinea).

We also use sungei (stream or small river), tanjong (head of land into the sea), gunung (mountain), and pulau (island) to help designate some localities. The letter, P., before a name means Pulau (P. Maratua is Pulau Maratua, which is Maratua Island).

THE PROBLEM

During the period, May 26, 1912 to July 6, 1914, Harry C. Raven worked and traveled on the mainland and islands of then Dutch East Borneo, now East Kalimantan. Raven was collecting specimens of vertebrates, mostly birds and mammals, for the United States National Museum, Smithsonian Institution, working under the direction and support of Dr. W. L. Abbott. A list of Raven's collecting stations during that time was eventually compiled by H. G. Deignan in 1959 from the map used by Raven in Borneo and from his field journal. His journal was incomplete and Deignan (1959, p. 267) lamented that there "are numerous unavoidable hiatuses in the itinerary, upon which no light is cast by the journal. Raven was subjected to attacks of malaria, dysentery, and tropical ulcers throughout his journey, and we may suppose that at times he was able neither to collect nor to write."

However incomplete his journal, we know that for parts of 1912 and 1913 Raven collected samples of rats from places inland and on the coast of the Bornean mainland (Sungei Birang, Sungei Segah, Tanjong Batu, Gunung Talisjan, Tanjong Buaja Buaja, and Sungei Menganne) and on small islands off the coast (table 1). Some of these islands are

on the Sunda Shelf: P. Pandjang, P. Rabu Rabu, P. Derawan, P. Sangka Laki, P. Bilang Bilangan, P. Mataha, P. Eraban, and P. Miang Besar. The larger island of Maratua, along with the smaller islands associated with it that form the Maratua archipelago (P. Alanga, P. Tong Tutup, P. Sangalan, and P. Bakungan), lay off the Sunda Shelf east of the 100 fathom line (fig. 1).

Raven collected more than 240 rats from the mainland and small islands. Of these, 50 were taken on P. Maratua, six during August of 1912, his first visit to the island, and 44 during May 1913. The six specimens obtained during 1912 were among the first of the collections from the islands to be studied by G. S. Miller, Jr., the mammalogist at the Smithsonian Institution. His report begins the first of several inquiries by others into determining the identities of the rats living on P. Maratua, a process that would eventually bring samples not only from the other small East Bornean islands into the study, but from places all over the Sunda Shelf.

Raven (in notes he sent to J. H. Riley and published under that name, 1930, p. 2) described P. Maratua as "a large island 28 nautical miles directly east of Tandjong Batoe, which is the nearest point on the mainland. Maratua is a peculiarly shaped island, in the form of a V with the right arm about twice the length of the left and bent inward, so that it forms a rhomb with one side missing. It is about 11 miles in length on the southwestern arm and five on the northeastern side. Unlike the other islands visited, it is not low and sandy but is composed almost entirely of sharp, cavernous rock of a very dark color. . . . The only place where this rock was not to be found was a narrow strip near the shore on the southwestern part of the island, where the land was flat and sandy and nowhere more than a few feet above the level of the sea. Here at the time of my visit were a few Bandjerese Malays, who were clearing the forest and planting coconuts for one of the Chinamen of Derawan. The rest of the island was covered with heavy forest. . . . In most places in the forest of Maratua no soil was to be seen, nothing but sharp, jagged rock over which the roots of the trees wound as they descended into its holes and crevices. The highest part of the island was about 400 feet."

The six rats obtained by Raven on August 28, 1912, during his first visit to P. Maratua were described as examples of two species by Miller in a report on "Fifty-one new Malayan mammals" published in 1913. Two of the six were segregated as *Epimys mara* (holotype, USNM 196751), diagnosed as a "large member of the *rattus*-group resembling *Epimys pannosus* of the Butang Islands, but color darker, skull larger, and teeth smaller; nasals distinctly spatulate anteriorly" (Miller, 1913, p. 10). The specimens had dark seal brown upperparts and dull vinaceous-buff underparts, without sharp contrast between belly and sides of the body. Miller (1913, p. 11) remarked that the "section of the *Epimys rattus* group containing this species . . . is characterized by large size, coarse fur, and heavy skull, features which cause its members to have a superficial resemblance to the rats allied to *Epimys validus* and *E. firmus*." Those two taxa, *validus* and *firmus*, are associated with the large-bodied Sundanese *Rattus muelleri* (Chasen, 1940). Years after Miller's description was published, Chasen (1940, p. 163), in his checklist of Malaysian mammals, tentatively aligned *mara* with *Rattus muelleri*, writing that "I have not examined an example of this species. According to Miller it occurs together on Maratua with a form compared with *neglectus*. It may therefore be a race of *mülleri*, but the very small teeth seem to preclude this."

Miller (1913, p. 12) gave the name *Epimys tua* (holotype, USNM 196752) to the four other specimens Raven collected on August 28, 1912 on P. Maratua. Miller diagnosed the taxon as being like "*Epimys rattus neglectus* of the Bornean mainland but upperparts blackish brown and underparts slaty." The color "in one adult and one young is essentially like that of *Epimys mara*. In the other two adults it is similar, except that there is less of the isabella on back and sides and of the vinaceous-buff on underparts." The skull and teeth of *E. mara* resembled "that of *Epimys neglectus*. It consequently differs

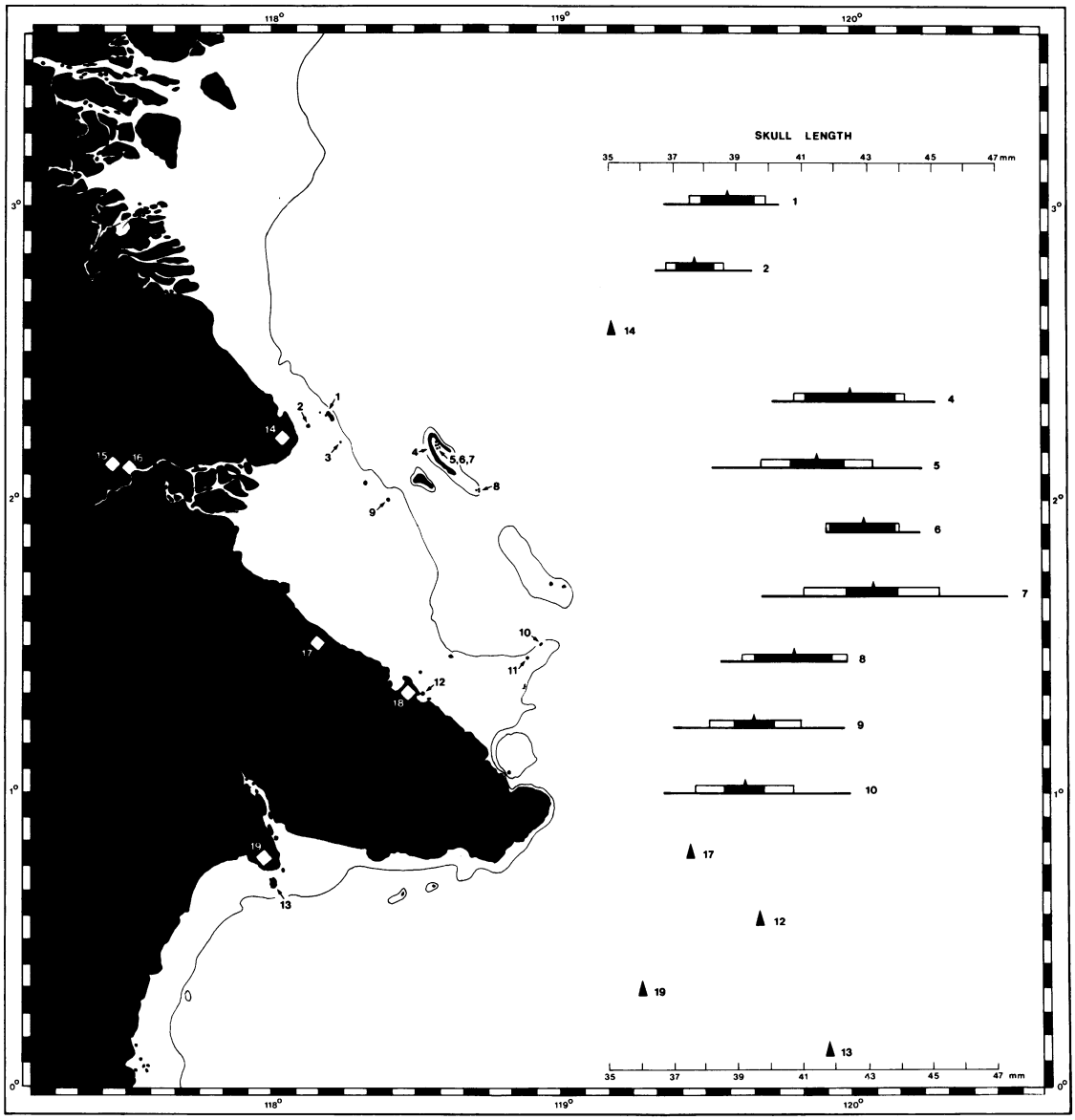

FIG. 1. Map of East Borneo (Kalimantan). Mainland and islands are black. The line east of the coast and surrounding some islands indicates approximately 100 fathoms. Numbers key to the following localities. ISLANDS: 1, P. Pandjang; 2, P. Rabu Rabu; 3, P. Derawan; 4, P. Maratua; 5, P. Alanga; 6, P. Tong Tutup; 7, P. Sangalan; 8, P. Bakungan; 9, P. Sangka Laki; 10, P. Bilang Bilangan; 11, P. Mataha; 12, P. Eraban; 13, P. Miang Besar. MAINLAND: 14, Tanjong Batu; 15, Sungei Birang; 16, Sungei Segah; 17, Gunung Talisjan; 18, Tanjong Buaja Buaja; 19, Sungei Menganne. See table 1. In each sample of skull lengths, the mean is a triangle, black bars outline $\bar{X} \pm 2$ SD, hollow rectangles indicate $\bar{X} \pm 2$ SE, and a horizontal line is the observed range. Number of specimens in each sample is listed in table 3.

from that of *E. mara* in its much smaller size and normally formed nasals. Teeth as in *E. neglectus*." Finally, Miller remarked that the "dark color of the upperparts and the dull, slightly contrasted underparts immediately distinguish the Maratua form from the other local races of the *neglectus*-group represented in Dr. Abbott's and Mr. Raven's Bornean collections."

Chasen (1940) recognized *mara* as a distinct species of *Rattus,* and listed *tua* as a subspecies of *Rattus rattus.*

Chasen's checklist of 1940 was the first alteration of the identification given by Miller to the six rats collected by Raven from P. Maratua. While he was preparing his book on the mammals of Borneo (first published in 1965 and revised in 1977), Lord Medway examined the six specimens and published a slightly different version of their identities. "This rat is not," Medway (1965, p. 117) wrote of *mara,* "a race of *R. muelleri,* but is a well marked melanistic form of *Rattus rattus.* I doubt that it does in fact occur on P. Maratua itself, the purported type locality. . . . On the first occasion apparently only the types of *mara* Miller and *tua* Miller were collected; these are dated 28th August, 1912, and labelled 'Maratua Is.'" Medway went on to note that a "longer series, also preserved in USNM, was collected on the return visit, in May, 1913; these come only from P. Alanga and P. Bakungan in the Maratua archipelago. From P. Maratua itself in 1913 Raven obtained a series of nine typical *R. r. diardii* but no specimens attributable to *mara.*" For Medway, none "of the material collected in 1913 can have been available to Miller at the time that he described *mara* and *tua.* It is legitimate to suppose that on his first visit Raven, young and still relatively inexperienced, did not differentiate as to locality between the various islands of the Maratua archipelago, but used the term 'Maratua Is.' for them all, and that this designation was not challenged by Miller." To Medway, the "longer series now available shows that the types of *mara* and *tua* represent approximately the extremes of variation of the population." He regarded *tua* to be a synonym of *mara* and that name to represent a melanistic subspecies of the house rat: *Rattus rattus mara.* This form he thought to occur on P. Alanga and P. Bakungan, as represented by the six specimens collected in 1912 as well as those obtained in 1913. *Rattus rattus diardii,* not *R. r. mara,* occurred on P. Maratua itself.

Miller did have available to him only the six specimens collected by Raven. He sorted out two kinds of rats in that small sample: two specimens represented a large-bodied and dark-colored species possibly related to other large-bodied species on the Sunda Shelf, and four specimens represented a smaller-bodied animal related to the common house rat, a form he knew as *Epimys neglectus* and one that would come to be called *Rattus rattus diardii.*

Despite Medway's misgivings, there is no evidence that all six specimens came from anywhere but P. Maratua. During May of 1913, Raven did return to the Maratua archipelago and worked on Maratua, Alanga, Tong Tutup, Sangalan, and Bakungan. Alanga, Tong Tutup, and Sangalan are three of five tiny islands in the bay between the two arms of P. Maratua. Pulau Bakungan is, according to Raven's notes (Riley, 1930, p. 2), "6 miles from Maratua, the two being connected by a broad reef. Like Maratua, Bakungan is also made of sharp, dark-colored rock, resembling lava, though whether it is or not I do not know. Part of the shore of Bakungan was covered with white coral sand. The vegetation was scrubby and sparse." Raven obtained specimens from P. Alanga, P. Tong Tutup, P. Sangalan, and P. Bakungan (table 1). All the samples were of one kind of rat and closely resembled the original samples of *mara* and *tua* collected by him from P. Maratua in 1912. But Raven also obtained 44 specimens from P. Maratua in 1913. Eleven were taken on May 22 and 23 and are examples of *R. rattus diardii*; 33 were obtained on May 10, 11, 21, 22, and 23 and represent rats very much like those in

TABLE 1

Past and Present Identifications of Rats obtained by H. C. Raven from the Islands and Mainland of Eastern Borneo

Place[a]	Date	No. of specimens: USNM catalog nos.	Published identification	Source[b]	Our identification
ISLANDS					
1. P. Pandjang	April–May 1913	15: 197393–197406	*R. r. ambersoni*	S + S (1967, p. 130)	*R. t. sabae*
2. P. Rabu Rabu	May 1913	17: 197408, 197409, 197412–197426	*R. r. ambersoni*	S + S (1967, p. 130)	*R. t. sabae*
3. P. Derawan	July 1912	1: 196748	*R. r. diardii*	Me (1965, p. 117)	*R. r. diardii*
	April 1913	2: 197391, 197392			
4. P. Maratua	August 1912	6: 196751–196755, 196767	*E. mara*	Mi (1913, p. 10)	*R. t. mara*
			E. tua	Mi (1913, p. 12)	
			R. mara	C (1940, p. 163)	
			R. r. tua	C (1940, p. 158)	
			R. r. mara	Me (1965, p. 117)	
			R. r. mara	S + S (1967, p. 131)	
	May 1913	33: 197427–197441, 197443–197445, 197451, 197455–197459, 197461–197463, 197465, 197467–197471	*R. r. mara*	S + S (1967, p. 131)	*R. t. mara*
	May 1913	11: 197442–197445, 197447–197450, 197452–197454, 197460, 197464	*R. r. diardii*	Me (1965, p. 117)	*R. r. diardii*
5. P. Alanga	May 1913	7: 197472–197478	*R. r. mara*	Me (1965, p. 117)	*R. t. mara*
			R. r. mara	S + S (1967, p. 131)	
6. P. Tong Tutup	May 1913	13: 197488–197497, 197499–197501	*R. r. mara*	S + S (1967, p. 131)	*R. t. mara*
7. P. Sangalan	May 1913	6: 197482–197487	*R. r. mara*	S + S (1967, p. 131)	*R. t. mara*
8. P. Bakungan	May 1913	10: 197502–197511	*R. r. mara*	Me (1965, p. 117)	*R. t. mara*
			R. r. mara	S + S (1967, p. 131)	
9. P. Sangka Laki	May 1913	29: 197324, 197514–197539, 197544, 199011	*R. r. ambersoni*	S + S (1967, p. 130)	*R. t. sabae*

TABLE 1—(*Continued*)

Place[a]	Date	No. of specimens: USNM catalog nos.	Published identification	Source[b]	Our identification
10. P. Bilang Bilangan	May–June 1913	55: 197546–197599, 199012	*R. t. jalorensis* *R. r. ambersoni*	Me (1965, p. 121) S + S (1967, p. 130)	*R. t. sabae*
	May–June 1913	2: 197545, 199016	*R. r. diardii*	Me (1965, p. 117)	*R. r. diardii*
11. P. Mataha	June 1913	19: 197600–197618	*R. r. diardii*	Me (1965, p. 117)	*R. r. diardii*
12. P. Eraban	June 1913	1: 197620	—	—	*R. t. sabae*
	June 1913	6: 197619, 197621–197625	*R. r. diardii*	Me (1965, p. 117)	*R. r. diardii*
13. P. Miang Besar	September 1913	1: 197639	*R. t. jalorensis*	Me (1965, p. 121)	*R. t. sabae*
MAINLAND					
14. Tanjong Batu	August 1912	1: 196750	—	—	*R. t. sabae*
15. Sungei Birang	June 1913	1: 196774	—	—	*R. r. diardii*
16. Sungei Segah	November 1912	1: 196773	—	—	*R. r. diardii*
17. Gunung Talisjan	February 1913	1: 196758	*R. t. sabae*	Me (1965, p. 121)	*R. t. sabae*
18. Tanjong Buaja Buaja	July 1913	10: 197627–197636	—	—	*R. r. diardii*
19. Sungei Menganne	August 1913	1: 197637	—	—	*R. t. sabae*

[a] Numbers key to numbered localities in figure 1.

[b] Abbreviations for authors: C, Chasen; Me, Medway; Mi, Miller; S + S, Schwarz and Schwarz.
Abbreviations: *E.*, *Epimys*; *R. r.*, *Rattus rattus*; *R. t.*, *Rattus tiomanicus*.

the original series of *mara* and *tua* obtained by him in 1912.

Schwarz and Schwarz (1967) examined this large series from Maratua collected during 1913 and in their monograph on the *Rattus rattus* group, treated *tua* as a synonym of *mara,* and the latter as a subspecies of *Rattus rattus*. Schwarz and Schwarz (1967, p. 131) explained their identification by writing that the "considerable material of this form that we now have before us leaves no doubt that both Miller's names apply to the same animal. The skull characters given are extremes, not restricted to this form and not correlated with coloration. There is a dark mutant on all the islands where this subspecies occurs ('*tua*') with black superposed, probably much in the same way as in the commensal black rat (*R. r. rattus*). On Maratua Island there is also the normal reddish form that has been described as *mara.*" They regarded the samples from the islands of Alanga, Tong Tutup, Sangalan, and Bakungan as also representing *R. rattus mara* (table 1).

Thus, three published identifications have been applied to the samples of rats from P. Maratua. Miller (1913) thought there were two species on the island, *E. mara* and *E. tua*. Medway (1965) indicated that only the commensal house rat, *R. r. diardii,* had been collected on P. Maratua. Schwarz and Schwarz (1967) determined the sample to be a form of house rat, *R. r. mara*. Because samples of both *R. rattus diardii* and a dark-colored rat have been taken from the island (table 1), the published impression is that the population there is conspicuously bimorphic, *diardii* being the normal phase, *mara* the dark one. But instead of a single bimorphic species could there be two species?

That Medway, as well as Schwarz and Schwarz, recognized melanistic populations of *Rattus rattus* in the Malaysian region puzzled us because melanistic examples are uncommon in the hundreds of house rats we examined from the Malay Peninsula, the large and small islands on the Sunda Shelf, and some islands off the Shelf. The occurrence of complete or partial melanism is, in fact, infrequent among samples of Asian house rats from throughout their geographic range. It is among populations of the European or Oceanian house rats that melanism is so common. So after three published reports, the question remained in our minds: what are the identities of the rats living on P. Maratua? To answer it, we returned to Miller's type series of six specimens from P. Maratua and to all the material collected by Raven from East Borneo that is in the National Museum of Natural History. The study provided an answer to the identifications of the rats on P. Maratua and to the identities of related populations on the other small islands off the coast of East Borneo, and on the other large and small islands off the Sunda Shelf.

IDENTIFICATIONS

Rattus rattus diardii

Raven did collect specimens of the house rat, *Rattus rattus diardii,* from P. Maratua. He also obtained examples of that form from Bilang Bilangan, Mataha, and Eraban, and from the mainland at Sungei Birang, Sungei Segah, and Tanjong Buaja Buaja (table 1). During 1912 and 1914, Raven also collected along the Sungei Mahakam, which is on the mainland of East Borneo south of the area mapped in figure 1 (see the outline map provided by Medway, 1965). In that region, Raven obtained specimens of *R. r. diardii* from Samarinda (USNM 196747, 196760, and 196763); Laham (USNM 198816, 198817); Long Iram (USNM 198818–198822); Lo Bon Bon, on the north bank of the Sungei Mahakam (USNM 196759); Tanggarung, on the south bank of the Sungei Mahakam (USNM 196746, which Miller described as *Epimys rattus turbidus,* 1913, p. 12); and Sungei Djambajan (USNM 198823).

All these specimens are good examples of *Rattus rattus diardii*. Among them, the upperparts of the head and body range from brown to dark brown; the fur is coarse and broken up by long black guard hairs over the lower back and rump. The underparts range from pale to bright buff; some specimens are dark grayish buff, others a dark dirty ochraceous brown. The cranium is like that de-

picted in figure 2. This kind of rat occurs over the Sunda Shelf on some large and small islands, as well as on the Malay Peninsula, in habitats characterized by human alteration of the primary forest for agriculture and living space.

Rattus rattus diardii is also found on islands off the Sunda Shelf. In addition to the Maratua archipelago, examples of the subspecies have been taken on the islands south and west of Sumatra from P. Dua, a small island near P. Enggano (USNM 140974, 140975); P. Enggano itself (USNM 141022–141024); and in the Mentawai Islands from P. Pagi Utara (AMNH 103057–103076, 103089, 103285, and 103286; also Sody, 1941), P. Sipora (USNM 252452, 252453; also Chasen and Kloss, 1927; Sody, 1941), and P. Siberut (Chasen and Kloss, 1927; Sody, 1941). To the west of the Shelf, there is a possible record from Great Nicobar Island, the holotype described by Miller (1902) as *pulliventer*. The rats on P. Tikus in the Cocos-Keeling Islands to the southwest of the Sunda Shelf are also *R. r. diardii,* as are the rats on Christmas Island, south of Java. The form occurs to the east of Bali where Sody (1941) recorded it from the islands of Lombok and Sumbawa, as well as from P. Saleyar south of Sulawesi. Musser has seen those specimens and they are typical examples of *R. r. diardii*. He also saw one specimen from Komodo (MZB 7701) that is like the *R. r. diardii* from islands to the west. Komodo may represent the most eastern distribution of *R. r. diardii* in the Lesser Sunda Islands (Nusatenggara) because the house rats from nearby P. Rintja and from Flores are larger-bodied with white to buff underparts and more closely related to *R. r. sumbae* (Musser, 1972). Finally, Imaizumi (1967) claims that *R. r. diardii* occurs on Hachijo Island in the Seven Islands of Izu, Japan.

Other places near the Sunda Shelf where *R. r. diardii* might be found are already occupied by distinctive forms of *Rattus rattus*. For example, there are no records of *R. r. diardii* from west of the Sunda Shelf on any of the Andaman Islands. Probably *R. r. diardii* does not occur in that archipelago because another kind of house rat, *R. rattus anadamensis,* already occupies the habitats that *R. r. diardii* would usually be found in (Musser, MS). *Rattus rattus diardii* has not been taken north of the Isthmus of Kra. The archipelagos east of the Sunda Shelf—Philippines, Moluccas, and the New Guinea region, for example—are occupied by different forms of Asian *R. rattus*. An exception may be northern Sulawesi. There Sody (1941) assigned samples to *R. r. neglectus,* which is a synonym of *R. r. diardii*. House rats from northern Sulawesi are similar in coloration to *R. r. diardii* but they are larger and more often silver-bellied rather than brown-bellied. The relationship between populations from northern Sulawesi and those of *R. r. diardii* from the Sunda Shelf still requires clarification.

Because of the close association between human habitats and populations of *R. r. diardii,* because the rats are similar in body size and coloration over their entire geographic range without the patterns of geographic variation that are often found in some widespread species of native rats, and because the geographic range reflects such a spotty distribution pattern that is discordant with those expected of species native to the Sunda Shelf, *R. r. diardii* is considered to have been introduced to the Sunda Shelf area from someplace outside of that region—from just where is unknown (Harrison, 1961; Medway and Yong, 1976).

Nine scientific names have been applied to this Sundanese house rat (table 2). Jentink's *diardii,* published in 1880 and based on a specimen from West Java, is the oldest. The other names do not reflect insular variation in color, body size, cranial features, or dental characters but rather examples of the range of variation within the subspecies and the describer's ignorance about the nature of variation within a single large sample and between samples from over its geographic range. The reputed diagnostic features associated with each name, usually centered on coloration, can be found within a sample from any given locality virtually anywhere on the Sunda Shelf.

Here we use the combination of *Rattus rattus diardii* knowing that *diardii* may ac-

TABLE 2
Scientific Names Associated with *Rattus rattus diardii*[a]

Name	Author and date	Type locality	Current status
diardii	Jentink 1880, p. 13	West Java	*R. r. diardii*
neglectus	Jentink 1880, p. 14	Bandjermasin, Southeast Borneo	*R. r. diardii*
?pulliventer	Miller 1902, p. 765	Great Nicobar Island	*R. r. diardii*
griseiventer	Bonhote 1903, p. 30	Bidor, South Perak, Malay Peninsula	*R. r. diardii*
turbidus	Miller 1913, p. 12	Tanggarung, south bank of Sungei Mahakam, East Borneo	*R. r. diardii*
samati	Sody 1932, p. 159	Bali	*R. r. diardii*
palembang	Tate and Archbold 1935, p. 1	Morcarah Duwa, Palembang, South Sumatra	*R. r. diardii*
auroreus	Sody 1941, p. 266	Pulau Pagi Utara, Mentawai Islands	*R. r. diardii*
keelingensis	Tate 1950, p. 276	Pulau Tikus, Cocos-Keeling Islands	*R. r. diardii*

[a] Based upon Musser's study of holotypes.

tually be one of the oldest names to apply to Asian house rats in general if their genetic isolation from the European house rats is ever clearly demonstrated in the field. Some workers already accept that separation. The name, *diardii,* applies to populations from places on the Sunda Shelf and elsewhere that are closely related to those of Asian *R. rattus* found north of the Isthmus of Kra and not to true *R. rattus,* referred to as European house rats or Oceanian black rats. The Asian form and European form differ significantly in external features (Johnson, 1962; Jones and Johnson, 1965), karyotypic characteristics (Yosida, Tsuchiya, and Moriwaki, 1971a), giemsa-banding patterns of chromosomes (Yosida and Sagai, 1973), frequencies of chromosome polymorphism in pairs no. 1 and 9 (Yosida, 1977b), variation of C-bands in the chromosomes (Yosida and Sagai, 1975), and serum transferrin patterns (Yosida, Kato, Tsuchiya, and Moriwaki, 1971). F_1 hybrids can easily be obtained from reciprocal crosses between the Asian and European forms kept in the laboratory (Yosida, Tsuchiya, Imai, and Moriwaki, 1969; Yosida, Kato, Tsuchiya, and Moriwaki, 1971; Moriwaki, Tsuchiya, and Yosida, 1973), but according to Yosida (1976, p. 304), "Delivery of F_2 offspring has so far been poor in the laboratory. This suggests that the F_1 hybrids seem to be semisterile."

Hybrids between Asian and Oceanian (European) rats apparently also occur in the wild. Yosida, Kato, Tsuchiya, and Moriwaki (1971) reported that animals obtained from Eniwetok Island in the South Pacific had karyotypes and serum transferrin patterns typical of the F_1 hybrids between the Asian and Oceanian types of rats. When Yosida and his colleagues crossed two of the rats from Eniwetok, one offspring was produced, which had the same karyotype as that of a single F_2 obtained in the laboratory. There is no published indication that such F_2 individuals occur naturally on Eniwetok Island.

Earlier Yong (1969), on the basis of karyological evidence, stated that *diardii* should be treated as a distinct species. Lately, Medway and Yong (1976, p. 48) wrote that the best taxonomic way to reflect the incomplete genetic isolation between the Asian and Oceanian rats would be to recognize each as a species, and so: "Although older names exist—particularly from India—as a provisional expedient we are applying to the house rat the earliest available name from the Sunda region, *diardii* Jentink 1880."

Possibly the two kinds of rats are different species, but the genetic compatibility or in-

compatibility between the Asian and Oceanian rats living in the wild is still unknown. For example, Yosida (1977a, p. 269), in a report on the karyological study of hybrids between Asian and Oceanian types, noted that "The Asian type black rats . . . can be divided into two groups on the basis of electrophoretic transferrin pattern and morphology of chromosome pairs 1 and 9. The Asian type rats distributed in eastern and southeastern Asia showed the R-type transferrin pattern and polymorphic pairs 1 and 9, while those distributed in the northern part of Southwestern Asia (India and Pakistan) invariably showed the C-type transferrin pattern and the subtelocentric pairs 1 and 9, similar to the situation in the Ceylonese and Oceanian type black rats. If the Asian type black rats in northern India or Pakistan can be used for the cross experiment, the hybrids might be fertile."

The genetic relationships between rats in populations from the Indian region and those occurring farther east still require crystallization. That is why we treat *diardii* as a subspecies of *R. rattus,* at least for now.

Rattus tiomanicus

The other specimens of *Rattus* collected by Raven from P. Maratua, both the six in 1912 and the 33 in 1913 are not melanistic examples of *Rattus rattus* but represent a distinctive insular variant of *Rattus tiomanicus*. A similar rat also occurs on the other islands close to P. Maratua: P. Alanga, P. Tong Tutup, P. Sangalan, and P. Bakungan. Raven also collected *R. tiomanicus* from the small islands of P. Pandjang, P. Rabu Rabu, P. Sangka Laki, P. Bilang Bilangan, P. Eraban, and P. Miang Besar on the Sunda Shelf closer to the east coast of Borneo, and at several places on the mainland: Tanjong Batu, Gunung Talisjan, and Sungei Menganne (table 1).

Rattus tiomanicus was once considered to be a form of *R. rattus* and was known by the name, *R. r. jalorensis*. At that time biologists separated what they regarded as subspecies of *R. rattus* from the Indo-Malayan region into three morphological and ecological forms: the house rat, *R. r. diardii,* an animal that lives in and around dwellings of humans; the wood rat, *R. r. jalorensis,* an inhabitant of secondary forest, mixed scrub and grassland, and plantations of rubber trees and oil palms; and the ricefield rat, *R. r. argentiventer,* found mostly in fields of rice and grassland (Chasen, 1933). The taxon *diardii* is now treated as a subspecies of *R. rattus* and the other two, *jalorensis* and *argentiventer,* are actually distinctive species rather than ecological subspecies of *R. rattus* (Harrison, 1961; Medway, 1965; Yong, 1969; Musser, 1973; Medway and Yong, 1976). Sody (1941) had earlier recognized the three groups under the categories of *diardii*-section, *argentiventer*-section, and *tiomanicus*-section. In a study of the wood rat on Pulau Tioman (Medway, 1966), Medway and Lim (1966) noted that *tiomanicus* was the older name for *jalorensis* and discussed the relationship of the sample from P. Tioman relative to samples of *diardii* and *jalorensis* from Selangor. Their report summarizes some ecological aspects of *R. tiomanicus,* both when it is found with *R. r. diardii* and when it occurs by itself, as it does in the areas worked on P. Tioman.

Medway and Lim (1966) compared features of skins and skulls among samples of *diardii, tiomanicus,* and *jalorensis*. They concluded that specimens of *tiomanicus* from P. Tioman and *jalorensis* from Selangor could be distinguished from those of *R. r. diardii* from Selangor and Singapore by the sleek pelage over the upperparts of *tiomanicus* and *jalorensis* (coarser and harsher in *diardii*), their shorter incisive foramina, shorter maxillary toothrows, and weakly developed supraorbital ridges.

In our experience, these features are good ones for distinguishing many samples of *diardii* and *tiomanicus*. We have found additional characters. Most specimens of *R. r. diardii,* in addition to their coarser and harsher pelage, have long black guard hairs that extend well beyond the overhairs and are conspicuous over the lower part of the back and the rump. In most samples of *R. tiomanicus,* the pelage over the upperparts is sleek and the guard hairs are short and

FIG. 2. Crania of adult *Rattus*: a, *R. rattus diardii,* Sabah (USNM 292689, ♂); b, *R. tiomanicus sabae,* Sabah (USNM 292672, ♂); c, *R. t. sabae,* P. Pandjang (USNM 197402, ♀). ×2.

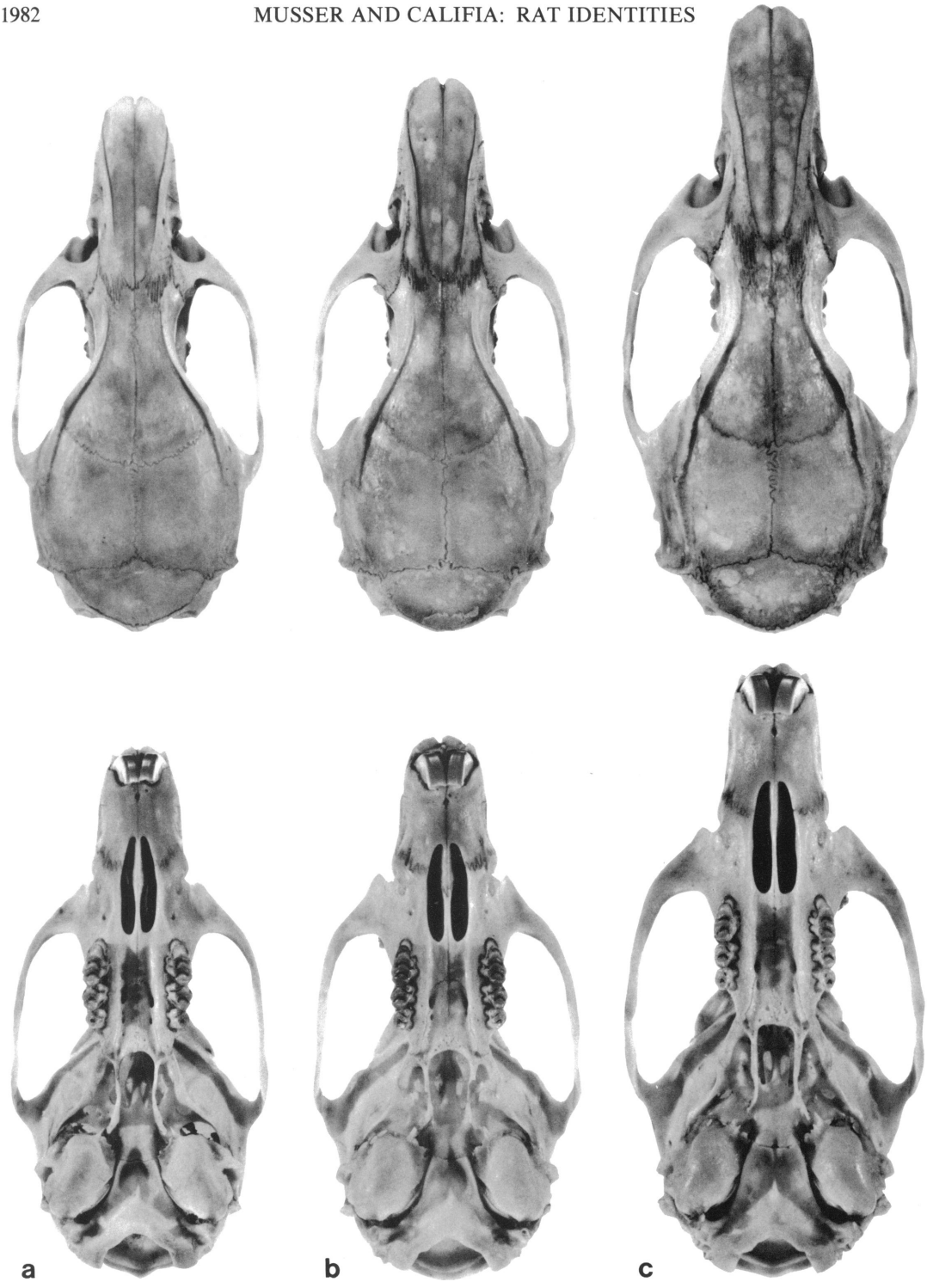

FIG. 3. Crania of adult *Rattus tiomanicus mara* from P. Maratua: a, USNM 197436, ♂; b, USNM 197431, ♀; c, USNM 197444, ♂. ×2.

inconspicuous, barely extending beyond the overhairs. There are exceptions. Some specimens of *R. tiomanicus* from Java, the sample of that species from Pulau Datu (*R. t. ducis*) off the west coast of Borneo, and the rats from the Maratua archipelago have harsher pelage than usually found in *R. tiomanicus* and long conspicuous black guard hairs over the back and rump.

Body and skull lengths can be used to distinguish some populations. The two species are similar in body size in most places where they have been found in the same locality, but in other regions *R. tiomanicus* is a smaller animal. Those from Sabah, for example, are consistently much smaller than individuals of *R. r. diardii* from that area; the two can be separated by skull size alone (fig. 2).

Cranial features, as Medway and Lim (1966) pointed out, are usually best for separating the two species. In addition to the characters they cited, we note that compared with examples of *R. r. diardii,* those of *R. tiomanicus* have a relatively shorter and wider rostrum, sides of the braincase that slope outward from the temporal ridges (usually straight or nearly so in *R. r. diardii*), a wider palatal bridge, and a different shape to the cranium as seen in dorsal view. 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 most specimens, except old individuals where the ridges extend all the way to the occiput. In specimens of *R. r. diardii,* the supraorbital ridges are high and wide and form a conspicuous angular shelf just back of the interorbital area and then sweep back over the sides of the braincase to the occiput. This provides, especially in old animals, a square or rectangular configuration that contrasts with the vaselike outline in *R. tiomanicus* (figs. 2 and 3).

There are other kinds of data that link *jalorensis* and *tiomanicus* and distinguish them from *diardii*. Yong, Dhaliwal, and Teh (1972) have demonstrated chromosomal characters that are shared by specimens of *jalorensis* from the Malay Peninsula and *tiomanicus* from P. Tioman but not by samples of *diardii*. Results from biochemical studies by Chan (1977), who analyzed electrophoretic variation in nine red cell proteins in specimens of Malayan *Rattus,* indicate that samples of *diardii, tiomanicus,* and *jalorensis* are closely related. In contrast to the chromosomal data, the biochemical evidence does not link *jalorensis* and *tiomanicus* to the exclusion of *diardii* but suggests that samples of all three are biochemically equally distinct from one another.

The metrical distinctions between most samples of *tiomanicus* and *diardii* do not apply between the sample of *R. tiomanicus* and that of *R. r. diardii* from P. Maratua because specimens in the former average larger than *R. r. diardii*. The configuration of the cranium, however, is that characteristic of *R. tiomanicus* (figs. 2 and 3). The population of *R. tiomanicus* on P. Maratua consists of large-bodied rats that have chestnut to dark chestnut upperparts and either dark gray or dark buffy gray underparts. Some individuals are darker and seem to be partially melanistic although the hairs are not silky and black as they would be in a truly melanistic phase. The texture of the pelage varies within the sample. Some rats have coarse and harsh fur broken up over the lower back and rump by long black guard hairs; other specimens have smoother pelage that is sleek and more like the usual texture in samples of *R. tiomanicus* from places on the Sunda Shelf. Every specimen of *R. t. mara* from P. Maratua can be separated from those of *R. r. diardii,* which also occurs on the island, by pelage coloration alone.

THE SUBSPECIES OF *RATTUS TIOMANICUS* IN THE EAST BORNEAN REGION

Medway (1965) and Schwarz and Schwarz (1967) were correct in synonymizing *tua* with *mara*. The holotype of *mara* is one of the largest and oldest in the original series of six that was collected in 1912. The holotype of *tua* is smaller and younger, judged by wear of its molars. Rather than representing different species, as Miller (1913) thought, they represent only differences in size and age among adults within a single population, as

TABLE 3

Values (in Millimeters) of Greatest Length of Skull in Samples of Adult *Rattus tiomanicus* from the Mainland of Borneo and Islands off the East Coast

Place	N	$\bar{X} \pm SD$	$\bar{X} \pm 2\ SE$	OR
NORTH BORNEO				
P. Banggi	1	42.3	—	—
Sabah	12	37.4 ± 1.3	36.7–38.2	34.6–39.6
EAST BORNEO				
Tanjong Batu	1	35.0	—	—
P. Pandjang	10	38.6 ± 1.2	37.8–39.4	36.6–40.2
P. Rabu Rabu	8	37.6 ± 0.9	37.0–38.2	36.4–39.4
P. Maratua	30	43.1 ± 2.1	42.3–43.9	39.7–47.4
P. Alanga	7	42.4 ± 1.7	41.0–43.8	40.0–45.0
P. Tong Tutup	18	41.4 ± 1.7	40.6–42.2	38.2–44.6
P. Sangalan	6	42.8 ± 1.1	41.8–43.8	41.7–44.6
P. Bakungan	8	40.7 ± 1.6	39.5–41.9	38.4–42.3
P. Sanga Laki	25	39.5 ± 1.4	38.9–40.1	36.9–42.2
P. Bilang Bilangan	32	39.2 ± 1.5	38.6–39.8	36.6–42.4
P. Eraban	1	39.7	—	—
P. Miang Besar	1	41.8	—	—
Gunung Talisjan	1	37.5	—	—
Sungei Menganne	1	36.0	—	—
SOUTH BORNEO				
Sampit	17	38.1 ± 1.6	37.2–38.9	34.8–41.3

Abbreviations: P., Pulau; N, size of sample; $\bar{X}$, mean; SD, standard deviation; SE, standard error; OR, observed range.

Medway (1965) pointed out. This spectacular range in skull size among adults is graphically illustrated in figure 3.

The samples from P. Alanga, P. Tong Tutup, and P. Sangalan, the small islands in the bay between the two arms of P. Maratua, contain rats that in size, as indicated by greatest length of skull, and color of pelage are very similar to those from P. Maratua (tables 3 and 4). The rats on P. Bakungan, part of the same reef system but south of P. Maratua and the tiny islands it embrances, are also closely similar to those from P. Maratua in pelage coloration and general body size, but the mean skull length is slightly smaller (fig. 1; tables 3 and 4). In our opinion, the rats on the islands of Maratua, Alanga, Tong Tutup, Sangalan, and Bakungan should be called *Rattus tiomanicus mara*.

Large size, coarse pelage, and dark color distinguish the populations of *R. tiomanicus* living on the Maratua archipelago from those on islands to the west that are closer to the mainland and on the Sunda Shelf, and from populations on the mainland of East Borneo. In length of skull and texture of pelage, the samples from P. Pandjang and P. Rabu Rabu in the north, and P. Sangka Laki, P. Bilang Bilangan, P. Eraban, and P. Miang Besar in the south are similar to one another, differing slightly in mean skull length from island to island (fig. 1; table 3). The samples from P. Pandjang, P. Rabu Rabu, P. Sangka Laki, and P. Bilang Bilangan were studied by Schwarz and Schwarz (1967) who considered them to be examples of *Rattus rattus* but sufficiently distinctive in pelage color and cranial features to warrant recognition as a distinct subspecies, *R. r. ambersoni* (table 1); P. Sangka Laki is the type locality. Schwarz and Schwarz compared their samples with those of *mara* and *neglectus* (=*diardii*). The features contrasting *ambersoni* with *neglectus* are those that distinguish *tiomanicus* in

general from *diardii*. And when compared with specimens of *mara*, they noted that examples of *ambersoni* were paler and smaller.

Schwarz and Schwarz (1967, p. 131) concluded that the different rats on the mainland and islands of East Borneo mirrored the color phases found in European house rats: "The conclusion therefore that we have drawn is to distinguish a brown, grey-bellied form (*neglectus*) comparable to *alexandrinus*, a blackened, grey-bellied form (*mara*), comparable to *rattus*, and a white-bellied form (*ambersoni*) comparable to *frugivorus* or *roguei*." They did not recognize *Rattus tiomanicus* in their monograph.

In addition to the slight variation in mean skull length among samples from the small islands on the Sunda Shelf there is a change in color of the underparts from north to south. Rats on P. Pandjang and P. Rabu Rabu in the north have dark bellies, either dark gray or dark grayish buff. Rats south of the Maratua archipelago on P. Sangka Laki, P. Bilang Bilangan, P. Eraban, and P. Miang Besar have paler underparts ranging from white to gray with the average tone being white suffused with gray (table 4).

This north–south change in average color of underparts between the offshore islands parallels the latitudinal variation among samples of *R. tiomanicus* from the mainland of East Borneo. Medway (1965) noted that samples of *R. tiomanicus* from the mainland of North Borneo, particularly Sabah, had darker underparts than those from southern and southwestern Borneo where the rats had either white bellies or white bellies slightly suffused with gray. To Medway (1965, p. 119), the northern form was so distinct that he named it *R. t. sabae* and described it as having upperparts that were "uniform olivaceous brown not or only very slightly darkened towards the mid-dorsal line, black guard hairs being evenly distributed throughout the dorsal pelage. The fur is soft and rather close, without fully developed spines. On the flanks the dorsal colour merges into the ventral without a sharp line of demarcation. The hairs of the belly are soft and close, pale grey basally, distally tipped pale buff." Medway considered *R. t. sabae* to occur throughout Sabah. He also thought it extended along the western part of Borneo down to about Baram District, Sarawak where its features merged with those of the white-bellied form, and down the eastern coast to at least Gunung Talisjan, from where a single specimen was assigned to *R. t. sabae* (table 1).

The samples from the mainland of southern and southwestern Borneo were identified by Medway as *R. t. jalorensis* because they had white bellies. He also noted that white-bellied rats occurred on some of the islands off the coast of southwestern Borneo, and he considered the rats from P. Bilang Bilangan and P. Miang Besar off the coast of East Borneo to be examples of *R. t. jalorensis* because they too had white bellies.

To understand the relationships of Bornean populations of *R. tiomanicus* to those from elsewhere on the Sunda Shelf will require a careful taxonomic revision of the species. Such a broad coverage is not our intent in this report. We only point out that the rats on P. Maratua and nearby islands on the same reef complex are different in features of body size and pelage color and texture from those animals living on islands to the west and from populations on the mainland of East Borneo. We also point to the similarities in size and color between samples from the small islands off the coast on the Shelf and those from the mainland, including the similar trend in dark to pale underparts from north to south on both the islands and mainland. Focusing only on the mainland and eastern islands, we would assign all samples from the mainland, both north and south, and those from the small islands off the east coast, to *R. t. sabae*. The samples we have seen from the mainland and those from the eastern islands are of a small rat, generally smaller-bodied than true *jalorensis* from the Malay Peninsula (compare the measurements of skull length reported by Medway and Lim, 1966, p. 35, with those in table 3, for example). And although belly coloration varies significantly from north to south on the mainland, skull length does not. The mean from our sample of *R. tiomanicus* from Sampit in South Borneo is not signifi-

TABLE 4

Frequencies of White and Pigmented Underparts in Geographic Samples of Adult *Rattus tiomanicus* from the Bornean Area

Origin of sample	Size of sample	Categories[a]					Mean
		0	1	2	3	4	
NORTH BORNEO							
P. Banggi	2	—	—	—	—	2	4.0
Sabah	16	—	—	4	—	12	3.5
Sarawak	16	2	3	3	—	8	2.6
EAST BORNEO							
P. Pandjang	14	—	—	7	6	1	3.1
P. Rabu Rabu	16	—	—	—	2	14	3.9
P. Maratua	39	—	—	—	1	38	3.9
P. Alanga	7	—	—	—	—	7	4.0
P. Tong Tutup	13	—	—	—	—	13	4.0
P. Sangalan	6	—	—	—	—	6	4.0
P. Bakungan	10	—	—	—	2	8	3.8
P. Sanga Laki	27	—	5	20	1	1	1.9
P. Bilang Bilangan	54	13	25	14	2	—	1.1
P. Eraban	1	—	—	1	—	—	2.0
P. Miang Besar	1	—	—	1	—	—	2.0
Tanjong Batu, mainland	1	—	—	—	—	1	4.0
Gunung Talisjan, mainland	4	—	—	—	—	4	4.0
Sungei Menganne, mainland	1	—	1	—	—	—	1.0
SOUTH BORNEO							
Sampit	19	2	9	3	5	—	1.8
P. Bawal	4	1	3	—	—	—	.8
WEST BORNEO							
P. Karimata	7	3	3	1	—	—	.7
P. Pelapis	11	—	10	1	—	—	1.1
P. Penabangan	5	—	2	3	—	—	1.6
Sungei Simpang, mainland	2	—	2	—	—	—	1.0
P. Lamukotau	13	9	3	1	—	—	.4
P. Juanata	5	2	3	—	—	—	.6
P. Datu	11	—	10	1	—	—	1.1

[a] Definition of categories:

0. PURE WHITE: underparts sharply demarcated from sides of body; the hairs white for their entire lengths.
1. WHITE AND WASHED WITH STREAKS OF PALE GRAY: underparts mostly white but with patches of pale gray, either on the chest, inguinal region, or down middle of the abdomen; still sharply demarcated from sides of the body.
2. WHITE SUFFUSED WITH GRAY: some hairs white for their entire lengths but most white distally and pale gray basally; underparts still distinct from sides of body.
3. GRAY TINGED WITH WHITE (FROSTED): hairs solid gray basally and white distally; coloration blends into sides of body; overall appearance is gray or frosted gray.
4. BUFFY GRAY: hairs gray or dark gray basally and buffy or pale ochraceous distally; some specimens brownish gray but most have a buffy hue; no white on belly; underparts not demarcated from sides of body.

cantly different from the mean of the series from Sabah in North Borneo (table 3). The parallel exists among samples from the small islands off the coast of East Borneo. In length of skull the rats from P. Bilang Bilangan, which have predominantly white bellies

TABLE 5

Frequencies of White and Pigmented Underparts in Geographic Samples of Adult *Rattus tiomanicus* from Places on the Sunda Shelf

Origin of sample	Size of sample	Categories[a]					Mean
		0	1	2	3	4	
PALAWAN REGION							
P. Palawan	12	3	3	2	3	1	1.7
P. Arena	6	6	—	—	—	—	0.0
P. Busuanga	2	—	—	1	—	1	3.0
P. Banchoran	2	—	2	—	—	—	1.0
JAVAN REGION							
P. Mata Siri	10	2	4	4	—	—	1.2
West Java	20	19	—	—	1	—	.2
P. Deli	10	10	—	—	—	—	0.0
SUMATRAN REGION							
Kalianda, South Sumatra	4	4	—	—	—	—	0.0
Gunung Dempo, West Sumatra	3	1	2	—	—	—	.7
Mandau and Siak	4	3	1	—	—	—	.3
Atjeh, North Sumatra	2	—	—	—	2	—	3.0
P. Bakong	3	—	—	1	—	2	3.3
P. Nias	24	—	—	—	—	24	4.0
MALAY PENINSULA							
Mainland	18	18	—	—	—	—	0.0
P. Tioman	7	—	—	4	—	3	2.9
P. Langkawi	5	—	2	1	2	—	2.0
P. Terutau	1	1	—	—	—	—	0.0

[a] Categories are defined in the footnote to table 4.

are no different from those dark-bellied animals living on P. Pandjang farther north (table 3).

Dark underparts are discontinuously distributed among samples of *R. tiomanicus* from throughout the Sunda Shelf. In table 5, we list the frequencies of color variants from a few places to illustrate the nature of the variation. Even in samples where white bellies predominate, there are individuals with darker underparts. Those samples from P. Bakong in the Riau archipelago and from P. Nias off the coast of Sumatra have very dark underparts. In color, they are nearly inseparable from our samples of *R. t. sabae* from the mainland of northern Borneo or the northern islands off the coast of East Borneo. Color of underparts, when its geographic distribution in samples of *R. tiomanicus* is fully analyzed, may reflect something other than phylogenetic relationships among insular populations. Medway (1965) and Medway and Lim (1966) have already noted the occurrence of dark-bellied *R. tiomanicus* on the Malay Peninsula and P. Tioman and suggested that the coloration may have something to do with habitat and possibly with the presence or absence of *R. r. diardii* at the same locality.

Medway (1965, p. 118) indicated that at least one author had suggested that the name *banguei* would apply to the field rats from North Borneo. We examined the holotype of that taxon and another adult from P. Banggi, off the north coast of Sabah. Both have very dark buffy bellies (table 4) but the holotype has a much longer skull than any specimen of *R. t. sabae* from Sabah, and falls in with the samples from the Maratua archipelago in skull size (table 3). We have noted that rats

living on large islands off the coast of the Malay Peninsula or large land areas such as Borneo are larger-bodied than those on the nearby mainland. The samples of *R. tiomanicus* from P. Datu (in the USNM), for example, are much larger than those from the adjacent mainland of southwestern Borneo. The difference in size between the specimens of *banguei* and *sabae,* if the holotype truly represents the population on P. Banggi, may reflect this pattern.

Our assignment of the samples from the islands and mainland of East Borneo to *R. t. sabae* is preliminary and may be ephemeral, depending on the results of critical taxonomic study of *R. tiomanicus*. More significant to us is that the rats on the small islands off the coast of East Borneo, islands that are still on the Sunda Shelf, tie to those on the nearby mainland and not to the populations from P. Maratua and the other smaller islands in that archipelago, all of which are beyond the 100 fathom line and off of the Sunda Shelf. The resemblances between samples from the small islands on the Shelf and samples from the mainland include similar skull length, coloration of upperparts, and gradation in underparts from dark gray or dark grayish buff in the north to white in the south.

Perhaps we should expect such a pattern of resemblance. At different times in the geologic past, either the lowering of sea level or the uplift of land or a combination of both, resulted in a much larger Borneo, with its eastern limit extending out to the margin of the Sunda Shelf itself (Batchelor, 1979; Tjia, 1980). What are small islands now would have been parts of continuous land then. We are tempted to speculate that the insular and the mainland latitudinal pattern of skull size and belly coloration reflects the pattern present at the last time Borneo was more expansive and extended eastward to the limits of the Shelf. Certainly it is a hypothesis to test with other kinds of characters from the same specimens and new material taken on more islands and at other places on the mainland.

The population on P. Maratua and nearby islands may represent the dispersal of *R. tiomanicus* from the mainland during that time when Borneo was land surface all the way to the eastern margin of the Shelf. At that time, the archipelago would be much closer to the mainland than it is now. We cannot, however, omit the possibility that passage overwater from island to island was a primary dispersal means from the mainland to the Maratua archipelago.

RATTUS TIOMANICUS MARA COMPARED WITH THE *RATTUS PALMARUM* GROUP

Because rats in the samples of *mara* from the Maratua archipelago are large-bodied and dark-colored, we also compared them with samples of large, dark rats from the islands off the southwestern coast of Sumatra, as well as the Nicobars. Like the islands in the Maratua archipelago, many of the islands southwest of Sumatra are off the Shelf and beyond the 100 fathom line; the Nicobars are separated from the northwestern Sumatran mainland by the Great Channel.

Nine scientific names have been applied to specimens from these islands, specimens that represent populations of large-bodied *Rattus,* not the specimens of smaller-bodied *Rattus* that are samples of *R. rattus, R. tiomanicus,* or *R. exulans*. The names, their authors, the dates of publication, and the type localities are listed below.

palmarum Zelebor (1869, p. 26), Nicobar Islands.
burrus Miller (1902, p. 768), Trinkut Island, Nicobars.
burrescens Miller (1902, p. 771), Great Nicobar Island.
simalurensis Miller (1903a, p. 458), P. Simalur, West Sumatra.
lugens Miller (1903b, p. 33), P. Pagi Utara, Mentawai Islands.
lasiae Lyon (1916, p. 446), P. Lasia, West Sumatra.
babi Lyon (1916, p. 447), P. Babi, West Sumatra.
mentawi Chasen and Kloss (1927, p. 831), P. Sipora, Mentawai Islands.
adustus Sody (1940, p. 397), P. Enggano, West Sumatra.

Rattus enganus, known only by the holotype collected on P. Enggano (Miller, 1906), does not belong to this group. Many of the

TABLE 6

Values (in Millimeters) of Greatest Length of Skull (GLS) and Alveolar Length of Maxillary Toothrow (ALM^{1-3}) in Samples of Adults in the *Rattus palmarum* Group and Two Subspecies of *Rattus tiomanicus*[a]

Taxon	Island	GLS	ALM^{1-3}
R. PALMARUM GROUP			
adustus	P. Enggano	—	8.7
lugens	P. Pagi Utara	48.1 ± 1.7 (23)	8.1 ± .2 (23)
		47.4–48.8	8.0–8.2
		45.5–50.8	7.7–8.5
mentawi	P. Sipora	46.2 ± 1.9 (15)	7.8 ± .3 (12)
		45.1–47.1	7.6–7.9
		43.0–48.9	7.3–8.4
lasiae and *babi*	P. Lasia, P. Babi	46.4 ± 2.0 (12)	7.9 ± .2 (12)
		44.7–48.1	7.7–8.0
		43.1–50.9	7.6–8.3
simalurensis	P. Simalur	44.7 ± 1.4 (11)	7.7 ± .2 (12)
		43.8–45.5	7.6–7.8
		42.8–47.3	7.5–8.0
burrescens	Great Nicobar Island	43.1 ± 1.7 (10)	7.7 ± .1 (12)
		42.1–44.1	7.6–7.8
		41.3–46.7	7.4–7.9
burrus	Trinkut Is., Nicobars	41.6 ± 2.6 (3)	7.6 ± .1 (3)
		38.6–44.6	7.5–7.7
		38.8–43.9	7.6–7.7
palmarum	Nicobar Islands	54.0	9.0
RATTUS TIOMANICUS			
mara	P. Maratua	43.1 ± 2.1 (30)	7.1 ± .2 (27)
		42.3–43.9	7.0–7.2
		39.7–47.4	6.7–7.6
sabae	P. Bilang Bilangan	39.2 ± 1.5 (32)	6.7 ± .2 (33)
		38.6–39.8	6.6–6.8
		36.6–42.4	6.1–7.1
sabae	Sampit, S. Borneo	38.1 ± 1.6 (17)	6.8 ± .2 (19)
		37.2–38.9	6.7–6.9
		34.8–41.3	6.4–7.2
sabae	Sabah, N. Borneo	37.4 ± 1.3 (12)	6.5 ± .2 (14)
		36.7–38.2	6.3–6.6
		34.6–39.6	6.2–6.8

[a] The mean plus or minus one standard deviation, size of sample in parentheses, the mean plus or minus two standard errors, and the observed range are listed in that order for each measurement.

taxa, particularly those representing samples from the Mentawai Islands, have been treated as subspecies of *Rattus rattus* (Chasen, 1940). Their cranial and pelage features actually resemble large versions of *R. tiomanicus* rather than *R. rattus*. None of the island forms, however, represent either one of those species. On P. Enggano, the large and dark *adustus* also occurs with *R. r. diardii* and *R. t. vernalus*. Just how many species are represented by the names in the *palmarum* group and how the species are related to others in *Rattus* is unresolved but the subject of a current taxonomic revision by Musser, who is preparing results for publication.

The names have been tagged to samples of

large-bodied rats. Those from the Nicobars have dark upperparts but usually whitish underparts. Animals from the other islands, especially those in the Mentawai cluster have dark gray or dark buffy gray bellies. Some rats from P. Sipora are melanistic. Most specimens from all the islands have coarse and harsh fur. The resemblance between rats from the Mentawai Islands in particular and those from the Maratua archipelago is striking in pelage color and texture.

Members of the *palmarum* group and examples of *mara* also resemble each other in the general configuration of the skull. With that feature the likeness ends. Lengths of skulls and maxillary toothrows average much smaller in the sample of *mara* than in any sample of the *palmarum* group (table 6), although certain large individuals of *mara* may equal some specimens in the *palmarum* group in skull length. In figure 4, we compare a large individual from P. Maratua with examples of the named forms in the *palmarum* cluster. The toothrows, even in the largest of the specimens from P. Maratua, are shorter and the molars smaller than those from the other islands. Lengths of molar rows in *mara* average only slightly larger than molar rows in samples of *R. tiomanicus* from the smaller islands off the east coast of Borneo, P. Bilang Bilangan, for example, and the mainland (table 6). This feature is also evident in figure 4, where the large skull of *mara* has small teeth compared with the large skulls of the other rats depicted with their long molar rows.

We have no evidence to indicate that the samples of *mara* represent anything other than a morphologically distinctive insular form of *Rattus tiomanicus*. The dark coloration of those rats and the animals on the Mentawai Islands are likely independently derived. Dark coloration of the rats on P. Maratua may be associated with the island substrate, which Raven described as "sharp, cavernous rock of a very dark color."

QUESTIONS ABOUT *RATTUS TIOMANICUS*

What are the species-limits of *Rattus tiomanicus*? We did not try to answer that question. There are many specimens in collections of museums from which data can be derived to obtain a reasonable estimate of at least the morphological and geographic boundaries of the species. We have examined samples from many places on the Sunda Shelf but have not carefully compared them with one another. Musser did study most of the holotypes representing taxa that could be associated with *tiomanicus* (table 7). There are 41 names now applied to what the preliminary results of our analyses indicate is likely one species. That species occurs over the Sunda Shelf on the large islands of Sumatra, Borneo, and Java, on the Malay Peninsula, and on many small islands. The samples are variable in pelage coloration and texture and in body size. Some of the taxonomic names reflect that variation and many do not. They are instead a record of some biologists' opinions that insularity required nomenclatural recognition, a view especially prevalent in the early 1900s and one that resulted in the many names tied to species that are widely distributed over the Sunda Shelf, as a reference to Chasen's (1940) checklist will attest.

What are the morphological and genetic relationships among the populations of *tiomanicus*-like rats on the Sunda islands? Determining the insular distribution of morphological features derived from available museum specimens and the distributions of chromosomal and biochemical characters obtained from fresh material taken over the same area would provide data that might answer this question. When mapped on the Shelf, the variation in some features, color of underparts, for example, might be discontinuously distributed without apparent pattern and indicate independent derivation of similar coloration on widely separated islands rather than close relationship. The insular distribution of variation in other characters may be concordant and reflect the actual phylogenetic alliances among populations on the islands.

Because a population of rats inhabits an island off the coast of the Malay Peninsula or one of the larger islands of Sumatra, Java, or Borneo it does not necessarily mean that the affinities of the island animals will be

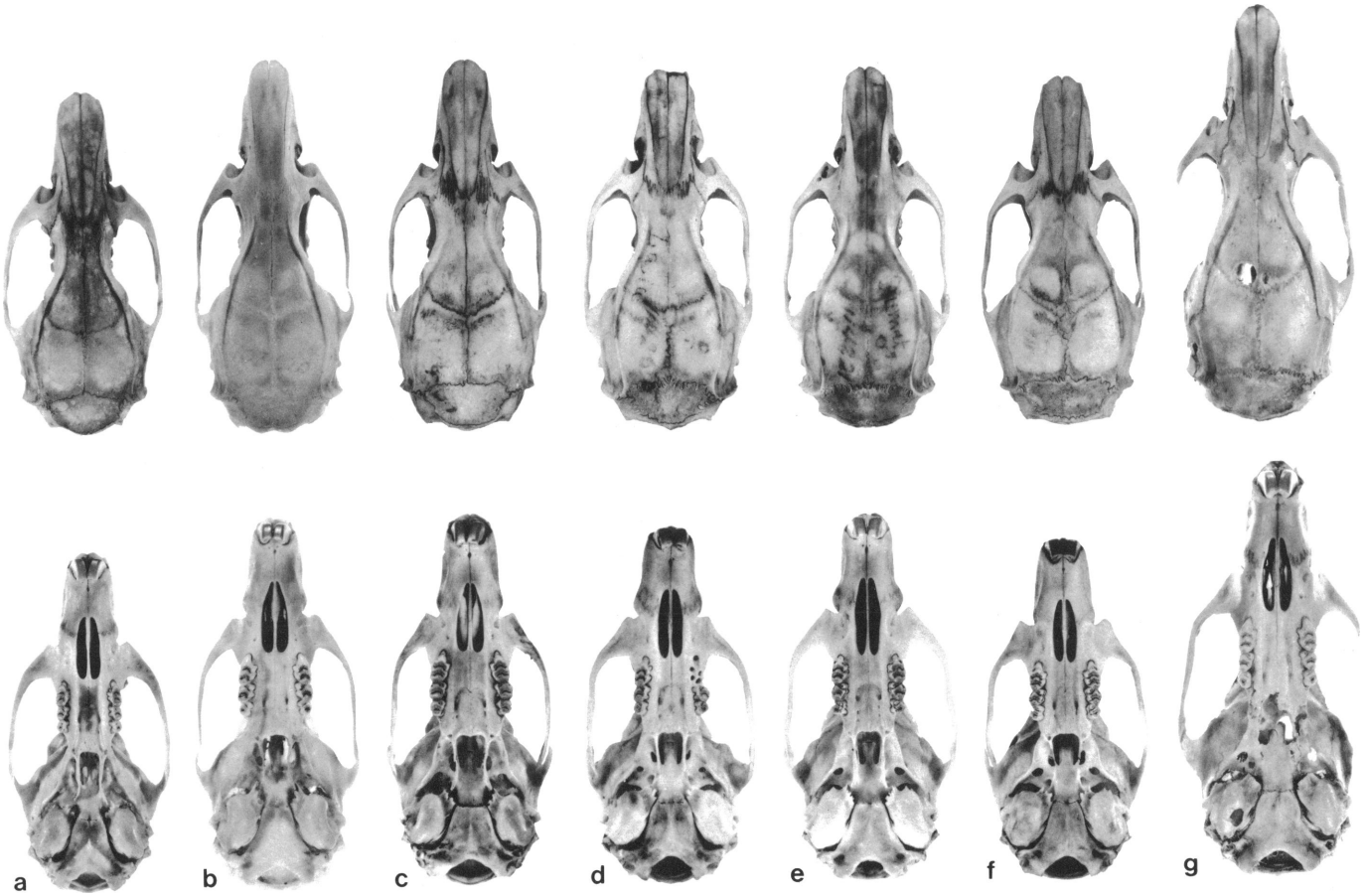

FIG. 4. Crania of adult *Rattus*. *Rattus tiomanicus mara* (USNM 197444) from P. Maratua, a, is compared to examples of the *R. palmarum* group: b, *lugens* (AMNH 103020), P. Pagi Utara; c, *mentawi* (USNM 252469), P. Siberut; d, *lasiae* (USNM 114255), P. Lasia; e, *simalurensis* (USNM 114221), P. Simalur; f, *burrescens* (USNM 111804), Great Nicobar Island; g, *palmarum* (NMW B-27), Nicobar Islands. All views are natural size.

with populations on the adjacent mainland. Populations of rats on some small islands may represent dispersal from the mainland during some past time but populations on many of the small islands are probably relicts, left when most of the Shelf was inundated and extensive land areas shrank to the bits of land that now dot the Sunda Shelf. The populations on those islands may be more closely related to those on other small islands rather than to any on large nearby mainlands. Their morphological and genetic attributes may reflect the geographic pattern of variation present when the island was once part of extensive land surface at times of low sea level. On the other hand, the characteristics of the rats may not fit into any pattern and indicate instead morphological and genetic changes because of adjustment to environmental characteristics of small islands.

Island area may be a significant determinant of some morphological features of *R. tiomanicus*—body size, for example. Heaney (1978) reported on this relationship in the large-bodied *Callosciurus prevosti,* which occurs on the Sunda Shelf. He found that the "body size of tri-colored squirrels is related to the size of the island on which they live; the smallest squirrels occur on the smallest islands and increase in body size on islands up to about 10^4 km^2. On islands larger than this, body size decreases significantly as island area increases." Heaney also developed a model indicating "the major factors which affect the body size of tri-colored squirrels, the situations under which they are most important, and their effects." The model can be applied to other mammals under certain conditions: "equivalent climate on all of the islands, all islands connected to a continental land mass at approximately the same time in the past, little or no gene flow between islands, and no special selective pressure." The model also assumed "that the effects of food limitation are greater on large mammals than on small mammals, that interspecific competition is more important to small mammals than to large mammals, and that predation pressure may have substantial, though different, effects on mammals of any size."

According to Heaney's model, small mammals would be expected to show an increase in body size on small islands compared with the mammals on the larger islands. Results from our limited study of body size in samples of *R. tiomanicus* suggests there is an increase in body size in samples from some small islands off the coasts of the Malay Peninsula (P. Tioman, for example; see Medway and Lim, 1966) and Borneo (P. Banggi and P. Datu, for example). This aspect of insular variation in body size should be thoroughly investigated to see how *R. tiomanicus* fits Heaney's model. The species is ideal for this kind of study because it has been found on so many islands over the entire Sunda Shelf. It may also occur on other islands not yet sampled for their mammalian fauna. *Rattus tiomanicus* also has the advantage of living in secondary forest, scrub, gardens, agricultural fields, and sometimes human dwellings and may still occur on some of the islands where the original forest has been so altered over prehistorical and historical periods that other mammals, which are tied to primary forest, are no longer present.

What is the actual geographic distribution of *R. tiomanicus*? Is it really a Sundanese species or does it tie in to white-bellied rats living in peninsular Thailand and Burma north of the Isthmus of Kra (10°30′N)? Judged from most specimens, *R. tiomanicus* appears to be an indigen of the Sunda Shelf. Medway and Yong (1976) think that the species has been in the region since the Late Pleistocene at least. It has been taken on the Malay Peninsula, the large islands of Sumatra, Java, and Borneo, and many of the small islands on the Shelf except Bali. There are also records from some islands off the Shelf: the Maratua archipelago (*R. t. mara*) to the east and P. Enggano (*R. t. vernalus*) to the southwest. It has not been found in samples from north of the Isthmus of Kra, from the Andaman or Nicobar Islands to the west, or east of the Shelf in the backbone of the Philippines, Sulawesi, or the Lesser Sunda Islands.

The relationship between *R. tiomanicus* and populations of white-bellied rats occurring north of the Sunda Shelf in Southeast

TABLE 7
Scientific Names Associated with *Rattus tiomanicus*[a]

Name	Author and date	Type locality	Current status
tiomanicus	Miller 1900, p. 209	Pulau Tioman, east coast Malay Peninsula	*R. t. tiomanicus*
siantanicus	Miller 1900, p. 210	Pulau Siantan, Anambas Islands	*R. t. siantanicus*
tambelanicus	Miller 1900, p. 212	Pulau Tambelan Besaur, Tambelan Islands	*R. t. tambelanicus*
jalorensis	Bonhote 1903, p. 29	Nong Chik, Pattani, Peninsular Thailand	*R. t. jalorensis*
julianus	Miller 1903b, p. 34	Pulau St. Julian (Kemudi, Tokong), near Tambelan Islands	*R. t. julianus*
jarak	Bonhote 1905, p. 69	Pulau Jarak, Malacca Straits	*R. t. jarak*
rhionis	Thomas & Wroughton 1909, p. 441	Pulau Bintan, Rhio Archipelago	*R. t. rhionis*
ducis	Lyon 1911, p. 99	Pulau Datu, West coast Borneo	*R. t. ducis*
lamucotanus	Lyon 1911, p. 100	Pulau Lamukotan, West coast Borneo	*R. t. lamucotanus*
maerens	Miller 1911, p. 181	Pulau Nias, West Sumatra	*R. t. maerens*
rumpia	Robinson & Kloss 1911, p. 169	Pulau Rembia, Sembilan Islands, West coast Malay Peninsula	*R. t. rumpia*
tingius	Miller 1913, p. 9	Pulau Tinggi, east coast Malay Peninsula	*R. t. tingius*
roa	Miller 1913, p. 10	Pulau Aur, east coast Malay Peninsula	*R. t. roa*
mara	Miller 1913, p. 10	Pulau Maratua, East coast Borneo	*R. t. mara*
tua	Miller 1913, p. 12	Pulau Maratua, east coast Borneo	A synonym of *R. t. mara*
pauper	Miller 1913, p. 13	Pulau Serasan, South Natuna Islands	*R. t. pauper*
viclana	Miller 1913, p. 13	Pulau Lankawi, west coast Malay Peninsula	*R. t. viclana*
batin	Robinson 1916, p. 66	Mentigi, Pulau Mapor, Riau Archipelago	*R. t. tiomanicus*
roquei	Sody 1929, p. 163	West Java	*R. t. roquei*
kunduris	Chasen & Kloss 1931, p. 77	Pulau Kundur, Rhio Archipelago	*R. t. kunduris*
jemuris	Chasen & Kloss 1931, p. 78	Aroa Islands, Straits of Malacca	*R. t. jemuris*
payanus	Chasen & Kloss 1931, p. 79	Pulau Paya, Straits of Malacca	*R. t. payanus*
mangalumis	Kloss 1931, p. 88	Pulau Mangalum, Northwest Borneo	*R. t. mangalumis*

TABLE 7—(*Continued*)

Name	Author and date	Type locality	Current status
banguei	Chasen & Kloss 1932, p. 35	Pulau Banggi, North Borneo	*R. t. banguei*
luxuriosus	Chasen 1935, p. 20	Pulau Bunguran, North Borneo	*R. t. luxuriosus*
perhentianus	Chasen 1940, p. 155	Pulau Perhentian Besar, east coast Malay Peninsula	*R. t. perhentianus*
pemanggis	Chasen 1940, p. 156	Pulau Pemanggil, east coast Malay Peninsula	*R. t. pemanggis*
vernalus	Sody 1940, p. 395	Pulau Enggano	*R. t. vernalus*
sebasianus	Sody 1941, p. 273	Pulau Sebesi, Sunda Strait	*R. t. sebasianus*
lasurius	Sody 1941, p. 274	Pulau Meeuwen, off west coast of Java	A synonym of *R. t. roquei*
delirius	Sody 1941, p. 274	Pulau Deli, off coast of southwest Java	A synonym of *R. t. roquei*
generatius	Sody 1941, p. 274	Nusa Kambangan, southern coast of central Java	A synonym of *R. t. roquei*
blangorum	Miller 1942, p. 145	Atjeh, North Sumatra, near Blangnanga Base Camp	*R. t. blangorum*
pharus	Hill 1960, p. 75	Pulau Pisang, Straits of Malacca	*R. t. pharus*
sribuatensis	Hill 1960, p. 76	Pulau Sribuat, Pahang Archipelago	*R. t. sribuatensis*
kabanicus	Hill 1960, p. 77	Pulau Kaban, Johore Archipelago	*R. t. kabanicus*
terutavensis	Hill 1960, p. 79	Telok Udang, Pulau Terutau, west coast Peninsular Siam	*R. t. terutavensis*
sabae	Medway 1965, p. 119	Near Tenom, Sabah	*R. t. sabae*
ambersoni	Schwarz and Schwarz 1967, p. 130	Pulau Sangka Laki, east coast of Borneo	A synonym of *R. t. sabae*
piperis	Schwarz and Schwarz 1967, p. 132	Pulau Mata Siri, Java Sea south of Borneo	*R. t. piperis*
tenggolensis	Yong 1971, p. 89	Pulau Tenggol, east coast Malay Peninsula	*R. t. tenggolensis*

[a] Based upon Musser's study of all holotypes except that of *tenggolensis*.

Asia and India is unresolved. In his report on the rats and mice of Thailand, Marshall (1977, p. 476) wrote that the coloration of most Thai *Rattus rattus* "is light brown, reddish brown, or buff brown on the back, pure white underneath, often with a little dark streak on the chest." He treated peninsular samples of *jalorensis* as examples of *R. rattus*, realizing there was a clear morphological and ecological separation between *Rattus rattus* and *R. t. jalorensis* farther south on the Malay Peninsula. Marshall did not try to resolve the problem by study of samples from peninsular Thailand, but that is what must be done. Study of samples on a transect from the Malay Peninsula north through peninsular Thailand beyond the Isthmus of Kra into southern Burma and southern Thailand should detect what kind of relationship exists between the northern populations of *R. rattus* and the Sundanese populations of the rats we now call *R. r. diardii* and *R. tiomanicus*.

Are there species of *Rattus* closely related to *Rattus tiomanicus*? Most analyses of biochemical, chromosomal, cranial, and external morphological features in *R. tiomanicus* have been based on samples of *jalorensis* from the Malay Peninsula and *tiomanicus* from P. Tioman. These have been compared with samples of *Rattus* from the Malayan region only. In that context, samples of *jalorensis* and *tiomanicus* fall out together and cluster closer to samples of *R. r. diardii* and *R. argentiventer* (fig. 5) than to any other Malayan rats (Chan, 1977; Chan, Dhaliwal, and Yong, 1979). *Rattus tiomanicus* has never been critically compared with other species in *Rattus* that occur outside of the Malayan region, probably because *R. tiomanicus* itself has not yet been adequately defined and because the genus *Rattus* still lacks diagnosis, definition, and elucidation of the species in it. Until the contents of *Rattus* are taxonomically revised, the relationships between *R. tiomanicus* and other species in the genus will remain unresolved.

We point out, however, two segments of *Rattus* that may be closely allied to *R. tiomanicus,* groups of species that should be considered in any attempts to resolve the identities of close relatives of *R. tiomanicus*. One consists of the *Rattus palmarum* group, which we already introduced. Characteristics of skins and skulls associated with the taxa in that assemblage resemble closely those of *R. tiomanicus*. In overall external and cranial morphology, members of the *R. palmarum* group seem to be large-bodied versions of *R. tiomanicus*. This possible tie between the two is being examined by Musser in connection with a taxonomic review of the *R. palmarum* group.

Rattus mindorensis (Thomas, 1898) is the other segment of *Rattus* that may tie closely to *R. tiomanicus*. The species has been found only in the mountains of Mindoro, an island in the backbone of islands that form the Philippine archipelago. *Rattus mindorensis* is of medium body size and dark brown. The pelage is soft, dense, and short, broken up over the lower back and rump by short black guard hairs. The upperparts of the head and body are dark to blackish brown, highlighted with chestnut hues. The ears, feet, and tail are dark brown. The underparts of the head and body of most specimens are dark gray washed with pale buff, a few have dark slate gray bellies. Females have 10 mammae: a pectoral pair, postaxillary pair, abdominal pair, and two inguinal pairs. Cranial characteristics are shown in figure 5.

External features of this medium-sized, soft-furred, dark-colored rat on Mindoro closely resemble samples of *R. tiomanicus,* especially those from P. Bakong and P. Nias, which also contain dark-colored animals. So do the cranial characters. Based on Musser's (MS) study of the native Philippine murids, *R. mindorensis* is one of the few species of true native *Rattus* in the archipelago and is not closely related to any of the other Philippine murids, including *R. r. mindanensis* and *R. exulans,* species also found on Mindoro, although probably not native to the island (Musser, 1977). Of all the species of *Rattus* on the Sunda Shelf and the Philippines, the cranium of *R. mindorensis* most closely resembles that of *R. tiomanicus*. The resemblance is close enough to suggest that *mindorensis* may be an insular form of *R. tiomanicus*. Whether the morphological features reflect actual close phylogenetic relationship between the two rather than convergence will have to be tested with data obtained from other characters, especially biochemical and chromosomal.

It may be significant that Mindoro is the only one of the islands in the backbone of the Philippine archipelago on which a rat with the morphological features of *mindorensis* has been found. Mindoro is close to the northeastern extension of the Sunda Shelf and is separated from the Calamian Islands at the tip of the Shelf by the Mindoro Strait, which is deeper than 100 fathoms. *Rattus tiomanicus* has been found on islands in the Palawan region, including Busuanga in the Calamians (Barbehenn, Sumangil, and Libay, 1972–1973). *Rattus tiomanicus* does occur on some islands beyond the 100 fathom line of the Sunda Shelf (the Maratua archipelago and P. Enggano), and Mindoro, relative to the northeast segment of the Sun-

FIG. 5. Crania of adult *Rattus*: a, *R. mindorensis* (USNM 144609), Mindoro Island, the Philippines; b, *R. tiomanicus sabae* (USNM 292689), Sabah, North Borneo; c, *R. tiomanicus roquei* (AMNH 250114), Java; d, *R. rattus diardii* (AMNH 250104), Java; e, *R. argentiventer* (AMNH 107543), Bali. All views are natural size.

da Shelf, may be just another island off of the Shelf and east of the 100 fathom line that was reached by a population of what is recognized as *R. tiomanicus* on islands of the Shelf.

Do all the names we associate with *R. tiomanicus* in table 7 tie to samples of that species or do some of them represent samples of populations reproductively isolated from those of *R. tiomanicus*? With this question we return to the fundamental problem: what are the species-limits of *R. tiomanicus*? There are many specimens in museums from many places on the Sunda Shelf and a few places off the Shelf. Some samples contain but a few individuals, most however, consist of large series. The bulk of the material is formed of skins and skulls, some series are preserved in fluid. There are sufficient specimens from enough places from which to derive morphological, geographical, and altitudinal outlines of *R. tiomanicus*. Biochemical and chromosomal data obtained from freshly caught specimens would at least supplement the morphological data and may form a finer resolution of the species-definition. Defining the morphological, ecological, distributional, and genetic boundaries of *R. tiomanicus* is important to understanding the nature of insular variation, distribution, and evolution of rats on the Sunda Shelf, and their phylogenetic relationships to species occurring elsewhere.

LITERATURE CITED

Barbehenn, K. R., J. P. Sumangil, and J. L. Libay
1972–1973. Rodents of the Philippine croplands. The Philippine Agriculturist, vol. LVI, nos. 7 and 8, pp. 217–242, 1 fig.

Batchelor, Brian C.
1979. Discontinuously rising Late Cainozoic eustatic sea-levels, with special reference to Sundaland, Southeast Asia. Geol. Mijnbouw, vol. 58, pp. 1–20, figs. 1–5.

Bonhote, J. L.
1903. On new species of *Mus* from Borneo and the Malay Peninsula. Ann. Mag. Nat. Hist., ser. 7, vol. 11, pp. 123–125.
1905. On a new species of *Mus* from Pulau Jarak. Jour. Fed. Malay States Mus., vol. 1, p. 69.

Chan, Kean Leong
1977. Enzyme polymorphism in Malayan rats of the subgenus *Rattus*. Biochemical Systematics and Ecology, vol. 5, pp. 161–168, figs. 1–2.

Chan, K. L., S. S. Dhaliwal, and H. S. Yong
1979. Protein variation and systematics of three subgenera of Malayan rats (Rodentia: Muridae, genus *Rattus* Fischer). Comp. Biochem. Physiol., vol. 64B, pp. 329–337.

Chasen, F. N.
1933. On the forms of *Rattus rattus* occurring on the mainland of the Malay Peninsula. Bull. Raffles Mus., Singapore, Straits Settlements, no. 8, pp. 5–24.
1935. On a collection of mammals from the Natuna Islands, South China Sea. *Ibid.*, Singapore, Straits Settlements, no. 10, pp. 5–42.
1940. A handlist of Malaysian mammals (A systematic list of the mammals of the Malay Peninsula, Sumatra, Borneo and Java, including the adjacent small islands). *Ibid.*, Singapore, Straits Settlements, no. 15, pp. i–xx, 1–209, 1 map.

Chasen, F. N., and C. Boden Kloss
1927. 41. Spolia Mentawiensia.—Mammals. Proc. Zool. Soc. London, no. LIII, pp. 797–840, pls. I–V, 1 map.
1931. On "rattus" rats of the coasts and islands of Malacca Straits. Bull. Raffles Mus., Singapore, Straits Settlements, no. 5, pp. 76–79.
1932. On a collection of mammals from the lowlands and islands of North Borneo. *Ibid.*, Singapore, Straits Settlements, no. 6, pp. 1–82, 1 pl.

Deignan, H. G.
1959. Harry Cusheir Raven's travels in eastern Borneo. Sarawak Mus. Jour., vol. 9, pp. 267–269.

Harrison, J. L.
1961. Ecology of the forms of *Rattus rattus* in the Malay Peninsula. Proc. Ninth Pacific Sci. Cong., vol. 19, pp. 19–24, 1 fig.

Heaney, Lawrence R.
1978. Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. Evolution, vol. 32, pp. 29–44, figs. 1–5.

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

Imaizumi, Yoshinori
1967. A classification of commensal races of *Rattus rattus*, especially on a subspecies from Hachijo Is., Japan. Jour. Mammal. Soc. Japan, vol. 3, no. 6, pp. 145–151, figs. 1–3.

Jentink, Dr. F. A.
1880. On some hitherto undescribed species of *Mus* in the Leyden Museum. Notes from the Leyden Museum, vol. 2, pp. 13–19.

Johnson, David H.
1962. Two new murine rodents. Proc. Biol. Soc. Wash., vol. 75, pp. 317–319.

Jones, J. Knox, Jr., and David H. Johnson
1965. Synopsis of the lagomorphs and rodents of Korea. Univ. Kansas Publ. Mus. Nat. Hist., vol. 16, no. 2, pp. 357–407.

Kloss, C. B.
1931. A new sub-species of Malaysian rat. Bull. Raffles Mus., vol. 5, pp. 105–107.

Lyon, Marcus Ward, Jr.
1911. Mammals collected by Dr. W. L. Abbott on Borneo and some of the small adjacent islands. Proc. U.S. Natl. Mus., vol. 40, pp. 53–146, pls. 1–7.
1916. Mammals collected by Dr. W. L. Abbott on the chain of islands lying off the western coast of Sumatra, descriptions of twenty-eight new species and subspecies. Proc. U.S. Natl. Mus., vol. 52, pp. 437–462.

Marshall, Joe T., Jr.
1977. Family Muridae: rats and mice. Pp. 396–487. Reprinted in Mammals of

Thailand (Boonsong Lekagul and J. A. McNeely). Assoc. Conserv. of Wildlife, Bangkok, Thailand.

Medway, Lord

1965. Mammals of Borneo. Field keys and an annotated checklist. Singapore, Malaysian Branch of the Royal Asiatic Society, Malaysia Printers, pp. i–xiv, 1–193, figs. 1–9, pls. 1–34, 1 map.

1966. Observations on the fauna of Pulau Tioman and Pulau Tulai. 2. The Mammals. Bull. Natl. Mus., Singapore, no. 34, pp. 9–320.

1977. Mammals of Borneo. Field keys and an annotated checklist. Monographs of the Malaysian Branch of the Royal Asiatic Society, no. 7, Kuala Lumpur, Perchetakan Mas. Sdn. Bhd., pp. xii and 172, figs. 1–11, pls. 1–24.

Medway, Lord, and B. L. Lim

1966. Observations on the fauna of Pulau Tioman and Pulau Tulai. 3. The specific relations of *Rattus tiomanicus* (Miller). Bull. Natl. Mus., Singapore, no. 34, pp. 33–38.

Medway, Lord, and Yong, Hoi Sen

1976. Problems in the systematics of the rats (Muridae) of Peninsular Malaysia. Malaysian Jour. Sci., vol. 4(A), pp. 43–53, pls. 1–4.

Miller, Gerrit S., Jr.

1900. Mammals collected by Dr. W. L. Abbott on islands in the North China Sea. Proc. Washington Acad. Sci., vol. 2, pp. 203–246, figs. 1–16.

1902. The mammals of the Andaman and Nicobar Islands. Proc. U.S. Natl. Mus., vol. 24, pp. 751–795, pls. XLI–XLII.

1903a. Mammals collected by Dr. W. L. Abbott on the coast and islands of northwest Sumatra. Proc. U.S. Natl. Mus., vol. 26, pp. 437–484, pls. 1–2, 1 map.

1903b. Seventy new Malayan mammals. Smithsonian Misc. Coll., vol. 45, pts. 1 and 2, pp. 1–73, pls. 1–19.

1906. The mammals of Enggano Island, West Sumatra. Proc. U.S. Natl. Mus., vol. 30, pp. 819–825.

1911. Descriptions of six new mammals from the Malay Archipelago. Proc. Biol. Soc. Washington, vol. 24, pp. 25–28.

1913. Fifty-one new Malayan mammals. Smithsonian Misc. Coll., vol. 61, no. 21, pp. 1–30.

1942. Zoological results of the George Vanderbilt Sumatran Expedition, 1936–1939. Part V.—Mammals collected by Frederick A. Ulmer, Jr. on Sumatra and Nias. Proc. Acad. Nat. Sci. Philadelphia, vol. xciv, pp. 107–165, pls. 3–6.

Moriwaki, K., K. Tsuchiya, and T. H. Yosida

1973. Breeding and genetics of the black rat, *Rattus rattus*. Exp. Animals, Proc. ICLA Asian Pacific Meeting of Laboratory Animals, Sept. 20–23, Tokyo and Inuyama, vol. 22, pp. 211–220, figs. 1–5.

Musser, Guy G.

1972. Identities of taxa associated with *Rattus rattus* (Rodentia, Muridae) of Sumba Island, Indonesia. Jour. Mammal., vol. 53, no. 4, pp. 861–865.

1973. Zoogeographical significance of the Ricefield Rat, *Rattus argentiventer,* on Celebes and New Guinea and the identity of *Rattus pesticulus*. Amer. Mus. Novitates, no. 2511, pp. 1–30, figs. 1–5.

1977. Results of the Archbold Expeditions. No. 100. Notes on the Philippine rat, *Limnomys,* and the identity of *Limnomys picinus,* a composite. *Ibid.,* no. 2636, pp. 1–14, 1 fig.

Riley, J. H.

1930. Birds from the small islands off the northeast coast of Dutch Borneo. Proc. U.S. Natl. Mus., vol. 77, art. 12, pp. 1–23, 1 pl.

Robinson, Herbert C.

1916. VIII. A collection of mammals and birds from Pulau Panjang or Pulau Mapor, Rhio-Lingga Archipelago. Jour. Fed. Malay States Mus., vol. VII, pt. I, pp. 59–72.

Robinson, Herbert C., and C. Boden Kloss

1911. On six new mammals from the Malay Peninsula and adjacent islands. Jour. Fed. Malay States Mus., vol. IV, nos. 3 and 4, pp. 169–174.

Schwarz, E., and H. K. Schwarz

1967. A monograph of the *Rattus rattus* group. An. Esc. nac. Cienc. biol., Mex., 14, pp. 79–178, figs. 1–7, maps 1–5.

Sody, H. J. V.

1929. Naamlijst van de zoogdieren van Java (met korte beschrijvingen van twee nieuwe subspecies). Natuurk. Tijdschr. Nederl.—Indië, Batavia, vol. 89, pp. 160–166.

1932. Six new Indo-Malayan rats. Overdruk uit het Natuurh. Maand., no. 12, pp. 157–160.

1940. On the mammals of Enggano. Treubia, vol. 17, pp. 391–401, 1 map.

1941. On a collection of rats from the Indo-Malayan and Indo-Australian regions (with descriptions of 43 new genera, species and subspecies). Treubia, vol. 18, pt. 2, pp. 255–325.

Tate, G. H. H.
1950. The Muridae of the Cocos-Keeling Islands. Bull. Raffles Mus., Singapore, no. 22, pp. 271–277.

Tate, G. H. H., and Richard Archbold
1935. Results of the Archbold Expeditions. No. 2. Twelve apparently new forms of *Rattus* from the Indo-Australian region. Amer. Mus. Novitates, no. 802, pp. 1–10.

Thomas, O.
1898. VIII. On the mammals obtained by Mr. John Whitehead during his recent expedition to the Philippines. Trans. Zool. Soc. London, vol. 14, pt. 6, no. 1, pp. 377–414, pls. 30–36.

Thomas, Oldfield, and R. C. Wroughton
1909. LVII.—Diagnoses of new mammals collected by Mr. H. C. Robinson in the Malay Peninsula and Rhio Archipelago. Ann. Mag. Nat. Hist., ser. 8, vol. 3, pp. 439–441.
1911. On mammals from the Rhio Archipelago and Malay Peninsula collected by Messrs. H. C. Robinson, C. Boden Kloss and E. Seimund, and presented to the National Museum by the government of the Federated Malay States. Jour. Fed. Malay States Mus., vol. 4, pp. 99–129.

Tjia, H. D.
1980. The Sunda Shelf, Southeast Asia. Ann. Geomorph., vol. 24, no. 4, pp. 405–427, figs. 1–9.

Yong, Hoi Sen
1969. Karyotypes of Malayan rats (Rodentia-Muridae, genus *Rattus* Fischer). Chromosoma, vol. 27, bd. 3, ht. S, pp. 245–267, figs. 1–14.
1971. Rat from Pulau Tenggol, Trengganu. Malay. Nat. Jour., vol. 24, pp. 87–89, 1 pl.

Yong, Hoi Sen, S. S. Dhaliwal, and Teh Kok-Leng
1972. Chromosomal studies of three Malayan island rats. Cytologia, vol. 37, pp. 507–511, figs. 1–3.

Yosida, T. H.
1976. 83. Karyotypes and meiotic segregation of hybrids between Asian and Oceanian type black rats. Proc. Japan Acad., vol. 52, pp. 304–307, figs. 1–2.
1977a. Karyologic studies on hybrids between Asian, Ceylonese, and Oceanian type black rats, with a note on an XO female occurring in the F_2 generation. Cytogenet. Cell Genet., vol. 19, pp. 262–272, figs. 1–5.
1977b. Frequencies of chromosome polymorphism in pairs no. 1, 9, and 13 in three geographical variants of black rats, *Rattus rattus*. Chromosoma, vol. 60, pp. 391–398, figs. 1–3.

Yosida, T. H., and T. Sagai
1973. Similarity of giensa banding patterns of chromosomes in several species of the genus *Rattus*. Chromosoma, vol. 41, pp. 93–101, figs. 1–2.
1975. Variation of C-bands in the chromosomes of several subspecies of *Rattus rattus*. *Ibid.*, vol. 50, pp. 283–300, figs. 1–11.

Yosida, T. H., H. Kato, K. Tsuchiya, and K. Moriwaki
1971a. Karyotypic differences of black rats, *Rattus rattus*, collected in various localities of East and Southeast Asia and Oceania. Chromosoma, vol. 33, pp. 252–267, figs. 1–4.
1971b. Karyotypes and serum transferrin patterns of hybrids between Asian and Oceanian black rats, *Rattus rattus*. *Ibid.*, vol. 34, pp. 40–50, figs. 1–3.

Yosida, T. H., K. Tsuchiya, H. Imai, and K. Moriwaki
1969. New chromosome types of the black rat, *Rattus rattus*, collected in Oceania and F_1 hybrids between Japanese and Australian rats. Japan Jour. Genet., vol. 44, pp. 89–91, figs. 1–4.

Zelebor, Johann
1869. Reise der österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859. Zoologischer Theil. (Wirbelthiere.) 1. Saugethiere, pp. 1–42, pls. 1–3. Wien.