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Philippine *Rattus*: A New Species from the Sulu Archipelago

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ABSTRACT

A new species, *Rattus tawitawiensis,* is described from Tawitawi Island in the southern Sulu Islands. It is native to the island, whereas *Rattus rattus mindanensis,* which also occurs there is not. The known mammalian fauna of the Sulu Archipelago has characteristics indicating that the islands have had no recent land-bridge connection to either Borneo or Mindanao; this is consistent with geological evidence. The new species has no close relative now living in either the Philippine Islands to the east or on the islands and peninsula of the Sunda Shelf to the west. In morphology, the Tawitawi rat is most similar to species of *Rattus* living on islands rimming the Sunda Shelf beyond the 180 m bathymetric line. These peripheral isolates appear to be most similar to *Rattus tiomanicus* among the extant fauna of the Sunda Shelf.

INTRODUCTION

From September 1971 to January 1972, members of the Delaware Museum of Natural History and Mindanao State University Expedition collected vertebrates in the South Sulu Islands (fig. 1). A report of that expedition has been provided by duPont and Rabor (1973). Birds were the principal quest of the collectors but a small series of mammals was also obtained. Among these were 65 specimens of *Rattus* representing three species. We document the identifications of those species in this report. Two of them, *R. exulans* and *R. rattus mindanensis,* are probably not native to the Sulu Archipelago. The third species, represented by three specimens from Tawitawi Island, is new and endemic to the Sulu Archipelago. Study of that rat provides significant information relevant to understanding the species diversity, insular distributions, possible phylogenetic relationships, and biogeographic histories of *Rattus* in the Malayan region.

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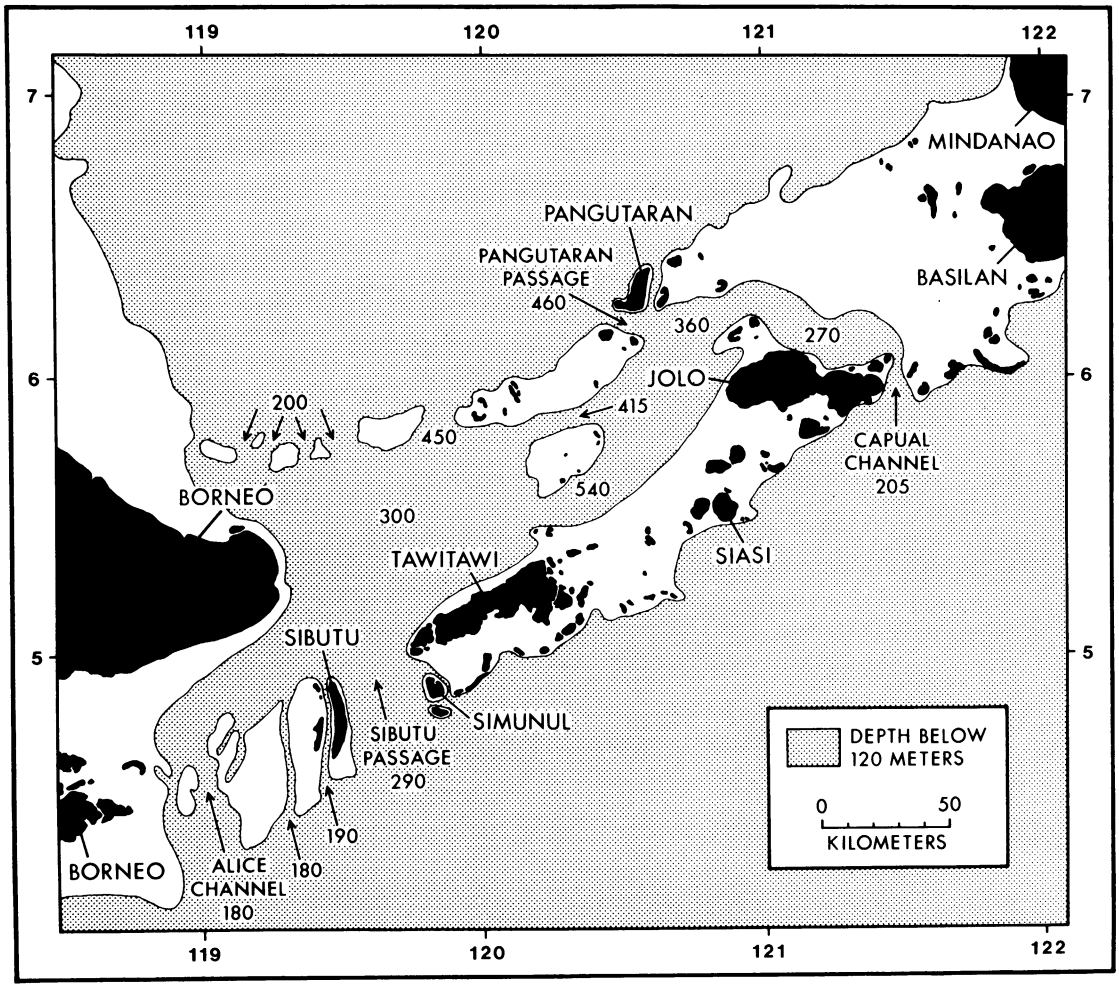

FIG. 1. Sulu Islands. Numbers indicate sea depth in meters. Black denotes present-day land areas. Two islands mentioned in text are not labeled: Sanga Sanga Island is off western tip of Tawitawi and Bangao Island just south of Sanga Sanga. During late Pleistocene when sea level was about 120 m lower than at present and during middle Pleistocene when sea level was probably 160 to 180 m lower than now, Tawitawi, Jolo, and the small islands between them would have been part of one large and elongate island nestled between what would have been the western margin of Sundaland and the eastern edge of a greater Mindanao. Estimates of sea depths and outlines of land areas were made from maps published by the Defense Mapping Center, Washington, D.C., and Operational Navigation Charts published by the Defense Mapping Agency Aerospace Center, St. Louis Air Force Station, Missouri.

ABBREVIATIONS AND PROCEDURES

The specimens we studied and illustrate here are in collections of the American Museum of Natural History, New York (AMNH); the Delaware Museum of Natural History, Delaware (DMNH); the Naturhistorisches Museum, Basel, Switzerland (NMB); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Values for total length, length of tail, length of hind foot, and length of ear are those recorded by collectors on labels attached to skins. We subtracted length of tail from total length to obtain length of head and body. Cranial and dental measurements were taken with dial calipers graduated to tenths of mil-

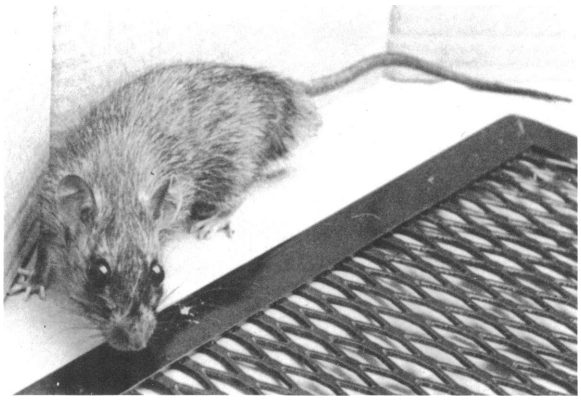

FIG. 2. An adult *Rattus rattus mindanensis* captured on the island of Luzon in the northern Philippines. The photograph was provided by Dr. Kyle R. Barbehenn.

limeters. Limits of those measurements are illustrated and defined in Musser (1970) and Musser and Newcomb (1983).

ACKNOWLEDGMENTS

To the curators and members of their supporting staffs who allowed us to study specimens under their care we are deeply grateful. We especially appreciate the loan of material to Musser—lots of specimens from several institutions. If these specimens had not been available at one place and at the specific time, we could not have completed our report. We have also been helped by Ms. Linda K. Gordon, who measured specimens housed in the National Museum of Natural History; Messrs. Peter Goldberg and Jim Coxe, who are responsible for the photographic prints; and Ms. Patricia Wynne, whose fine craftsmanship is reflected in figure 6. Finally, we thank our colleagues who read the manuscript and provided critical and helpful evaluations.

This paper is number 114—Results of the Archbold Expeditions.

THE INTRODUCED *RATTUS*

Among the series of *Rattus* from the southern Sulu Archipelago are two species that are found where original habitats have been modified or removed: places such as agricultural fields, gardens, and village houses.

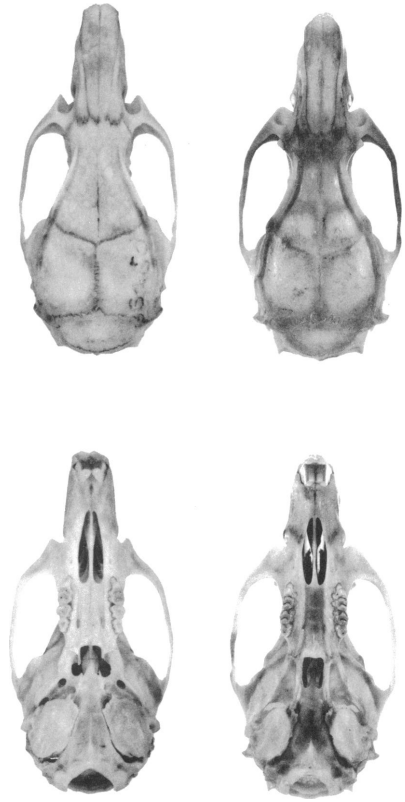

FIG. 3. Crania of adult *Rattus*. Left: *R. rattus mindanensis*, Tawitawi Island (DMNH 3480). Right: *R. rattus diardii*, Java (AMNH 250104). Natural size.

One of these is the small-bodied *R. exulans*, represented by an adult male (DMNH 3531) from Bongao Island, caught in October 1971. Values of external measurements (lengths of head and body, tail, hind foot, and ear are, respectively, 129 mm, 120 mm, 25 mm, and 17 mm), color and texture of fur, shape of skull, and dentition are typical of *R. exulans*, judged by the hundreds of specimens (in the USNM) from other islands in the Philippines that we have examined.

The Asian houserat, *R. rattus* (fig. 2), is the other species from the Sibutu and Tawitawi island groups in the Sulu Archipelago. We studied 61 specimens from the following islands.

1. Sibutu Group, Sibutu Island: DMNH 3474, 3502–3504; all were taken during November 1971.

TABLE 1

Measurements (in Millimeters) of Adults in Samples of *Rattus rattus* from the Sunda Shelf, Southern Sulu Archipelago, and Mindanao

(Mean plus or minus one standard deviation, number of specimens in parentheses, and observed range are listed.)

Subspecies and Island	Lengths	
	Skull	M^{1-3} (alveolar)
R. rattus diardii[a]		
Sumatra	38.6 ± 1.2 (16) 36.8–40.6	6.7 ± 0.2 (16) 6.2–7.1
Java	40.2 ± 1.7 (20) 36.6–44.2	6.8 ± 0.4 (20) 5.9–7.3
Bali	42.1 ± 1.0 (6) 40.6–43.4	6.8 ± 0.4 (6) 6.1–7.0
Borneo	41.4 ± 0.6 (4) 40.5–41.8	6.9 ± 0.2 (8) 6.4–6.9
R. rattus[b]		
Sibutu Island	44.6 ± 2.4 (3) 42.6–47.2	7.5 ± 0.6 (4) 6.8–8.1
Simunul Island	43.3 ± 1.2 (6) 42.0–45.0	7.4 ± 0.2 (7) 7.1–7.7
Bongao Island	42.9 ± 2.3 (5) 38.9–44.9	7.1 ± 0.1 (8) 6.9–7.3
Sanga Sanga Island	44.0 ± 1.7 (21) 40.7–46.9	7.4 ± 0.3 (22) 6.9–7.8
Tawitawi Island	43.2 ± 2.2 (19) 38.0–46.4	7.6 ± 0.3 (20) 7.0–8.2
R. rattus mindanensis[c]		
Mindanao	42.6 ± 2.7 (20) 37.4–46.1	7.7 ± 0.3 (20) 7.1–8.4

[a] Specimens are in the American Museum of Natural History.

[b] Specimens are in the Delaware Museum of Natural History.

[c] Specimens are in the National Museum of Natural History, Smithsonian Institution.

2. Tawitawi Group, Simunul Island: DMNH 3481–3485, 3501, and 3529; collected during October 1971.
3. Tawitawi Group, Bongao Island: DMNH 3486–3488, 3509–3511, 3530, and 3532; collected during October 1971.
4. Tawitawi Group, Sanga Sanga Island: DMNH 3287, 3468–3473, 3505–3508, and 3533–3543; all taken during October 1971.
5. Tawitawi Group, Tawitawi Island, Batu Batu: DMNH 3475–3479, 3512–3523, 3526, and 3527; all collected during December 1971.

The specimens are large for houserats, with tails longer than the combined lengths of head and body (tables 1 and 2; fig. 2). The fur is coarse with long guard hairs over the back and rump. Upperparts range from dark tawny brown through brown to grayish brown; the middle of the back is darker and the sides are paler, usually grayish yellow or buff. Underparts range from pale and dark gray through buffy gray tones to dark brownish buff. Ears and feet are brown. The tail is dark brown throughout its length. Females have 10 mammae: one pectoral pair, a pair in the postaxillary region, an abdominal pair, and two inguinal pairs.

The specimens are large-bodied versions of *R. rattus diardii,* the Asian houserat found on nearly every island on the Sunda Shelf as well as some other places (Musser and Califia, 1982). It is, for example, common in villages, towns, and larger urban areas on Borneo to the west of the Sulu Archipelago (Medway, 1977). In body proportion, texture, and color of pelage, number of mammae, and conformation of skull and teeth, specimens of *R. r. diardii* and *R. rattus* from the southern Sulu Archipelago are quite similar (fig. 3); body size is the primary distinguishing feature. To estimate that parameter, we measured greatest length of skull and alveolar length of maxillary toothrow; values from these measurements are listed in table 1 for samples of *R. r. diardii,* the Sulu houserats, and *R. r. mindanensis,* the houserat found on Mindanao Island in the southern Philippines. Means of skull length and length of molar row are clearly less in the samples of *R. r. diardii* as compared to means from samples of the other groups. Specimens from the Sibutu and Tawitawi island groups resemble those from Mindanao in size, especially in length of molar row.

Larger average body size is the primary difference between samples of the Philippine houserat and those of *R. r. diardii* from the Sunda Shelf. *Rattus rattus mindanensis* is the scientific name applied to populations of Asian houserats on the Philippine Islands (Musser, 1977). We also use this name to

embrace the populations of *R. rattus* living on islands in the Sibutu and Tawitawi groups of the Sulu Archipelago.

It is unlikely that either *R. exulans* or *R. rattus mindanensis* is native to the islands in the Sulu Archipelago. Both live in habitats made and maintained by humans; they are excluded from virgin forests that support a fauna of native rats (Musser, 1977). Their status as commensals and their morphologies contrast sharply with the third species of rat known to occur in the southern Sulus, which is represented by three specimens collected on Tawitawi Island.

THE NATIVE *RATTUS*

The three specimens probably represent a species of *Rattus* native to the Tawitawi Island. No specimen like these has ever been collected from the other Philippine Islands that have been sampled for mammals and they are unlike any species known to occur on islands of the Sunda Shelf. The specimens do share some morphological features with species native to island groups south of the Shelf, such as the Mentawais, but they have their own combination of distinctive features, which supports the hypothesis that the sample represents a biological species native to the southern Sulu Archipelago. We name, diagnose, and describe the species below.

Rattus tawitawiensis, new species

HOLOTYPE: DMNH 3525, the skin (fig. 4) and skull (fig. 5) of an adult female caught at Batu Batu on the southern half of Tawitawi Island, part of the Tawitawi Island Group in the Sulu Archipelago of the Philippines. The rat was collected by Dr. D. S. Rabor (original number 1390) on December 4, 1971. The skin of the holotype is in good condition but the skull is incomplete. The right zygomatic arch is missing as are the hamular processes. All molars are present (fig. 8). The dentaries are entire. Measurements of the holotype are listed in table 2.

REFERRED SPECIMENS: From the same place as the holotype come two other examples of *R. tawitawiensis,* both caught by Dr. Rabor in 1971. DMNH 3528 is a young adult female collected on December 7. Although in full

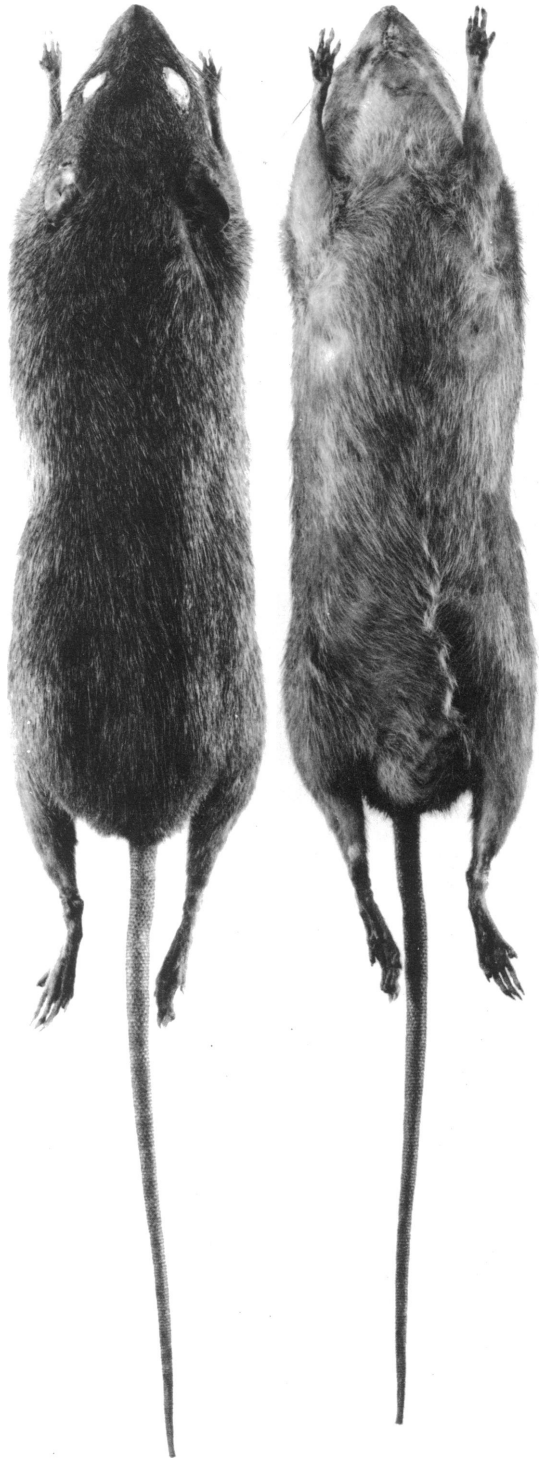

FIG. 4. Stuffed skin of the holotype (DMNH 3525) of *Rattus tawitawiensis.* Measurements are listed in table 2.

adult pelage, the animal was probably not sexually mature because its teats are very small. DMNH 3524, taken on December 4, is a younger female. It is mostly covered with adult fur but there are still large patches of juvenile pelage on top of the head between the ears and on the rump. Skins of both specimens are intact, but the crania are damaged (fig. 7) due to careless cleaning. Molar rows are complete (fig. 8). Measurements are listed in table 2.

KNOWN DISTRIBUTION: Tawitawi Island in the southern part of the Sulu Archipelago (fig. 1).

ETYMOLOGY: Named for the island on which the specimens were collected.

DIAGNOSIS: The following combination of characteristics sets *R. tawitawiensis* apart from any other species of *Rattus*: large body size, tail shorter than combined lengths of head and body, rich, dark brown upperparts, dark gray underparts, dark brown feet, eight mammae (one postaxillary pair, an abdominal pair, and two inguinal pairs), a wide and deep cranium, wide incisive foramina, large teeth, prominent anterolabial cusps on a conspicuous cingular ridge on each second and third upper molar, and small bullae relative to size of cranium.

DESCRIPTION: This is a large rat with dark brown fur and a tail conspicuously shorter than the combined lengths of head and body (fig. 4, table 2). The dorsum is covered in thin, short fur (10 to 15 mm long) over the back. Its overall color is rich, dark brown, and uniformly speckled with buff. The intensity of this deep and dark tone covers the head and body and becomes slightly paler along the sides due to suffusion of gray. Most of the hairs are dark brown or blackish in their distal halves and many are tipped with buff bands; these bands provide the buffy speckling, which when integrated through the brown fur produces a dark agouti pattern. Black guard hairs are short (15 to 20 mm long), barely extend beyond the overhairs, and are inconspicuous in both presence and effect on coloration of the pelage. The fur is soft to the touch and sleek to the eye despite the numerous translucent spines scattered through the coat—spines that are too soft and flexible to produce a coarse texture.

The venter is covered with a soft, thin coat, 3 to 5 mm thick. Most hairs are gray in their basal halves and either unpigmented or buffy in the distal portions; the effect is gray tinged with silver and buff. On the three specimens, there is a pale, rusty patch either on both throat and chest, on chest only, or extending from chin to chest; whether the color results from staining or actual pigment within the hairs cannot be determined.

The appendages are dark. The ears and dorsal surfaces of the front and hind feet are dark brown, as are the plantar surfaces and the tail; the palmar surfaces are pale brown.

The hind feet are long and narrow. The plantar surfaces are naked and adorned with six pads. The shape of each foot and the position and size of the pads relative to plantar surface area resemble the configuration in *Rattus argentiventer* (see fig. 2 in Musser, 1973).

There is nothing special about the tail. It is short relative to length of head and body and dark brown pigment covers all surfaces. There are 8 to 10 rows of scale hairs per centimeter (counted at a spot about one-third the distance from the base of the tail).

All three specimens are females and four pairs of mammae are evident on each animal, although they are small and inconspicuous on DMNH 3524, the youngest of the series. There is a postaxillary pair of teats, an abdominal pair, and two pairs in the inguinal region. Most species of *Rattus* have a pectoral pair, but such mammae do not occur in *R. tawitawiensis*.

The cranium of the adult *R. tawitawiensis* is large, wide, deep, and chunky in general aspect (figs. 5 and 7; table 2). The configuration results from a short and wide rostrum, flaring zygomatic arches (judged by the intact side), and the wide and deep braincase. Seen from above, there are ridges forming an angular outline behind the orbit; the ridges extend to the back of the skull but diminish in size until they are mere traces delimiting the dorsolateral margins of the braincase. From the temporal ridges the sides of the braincase flare outward. An oblong interparietal roofs most of the occipital region. Seen from the side, the zygomatic plates are wide and extend well anterior to the zygoma. The conformation of the alisphenoid region and the back of the braincase above the bulla is not

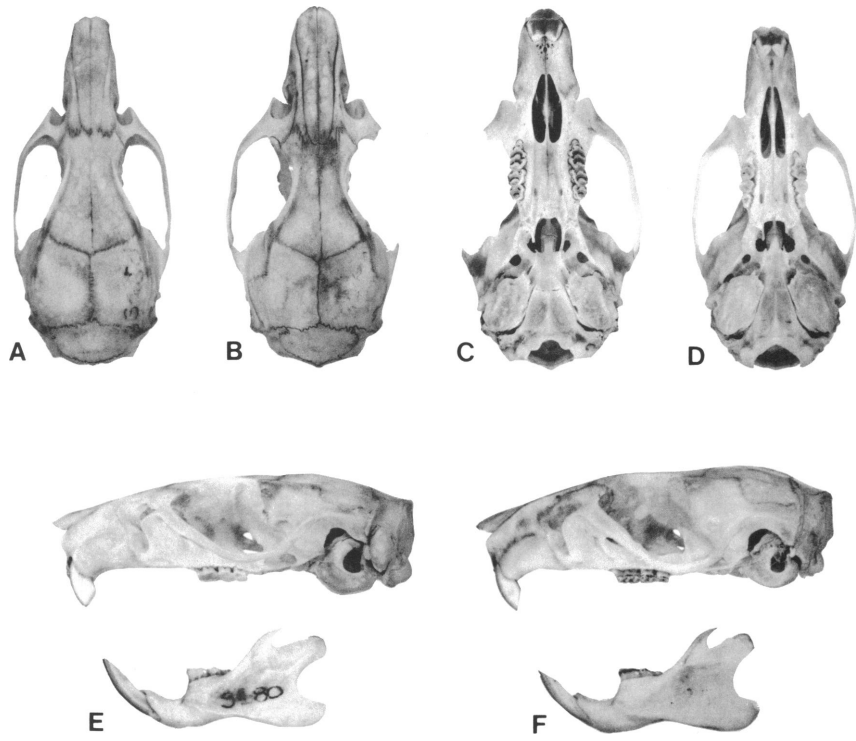

FIG. 5. Crania of adult *Rattus*. A, D, and E: *R. rattus mindanensis,* Tawitawi Island (DMNH 3480). B, C, and F: *R. tawitawiensis,* holotype (DMNH 3525). Natural size. Measurements are listed in table 2.

different from the conditions described for other species of *Rattus* (Musser, 1982a; Musser and Newcomb, 1983).

As viewed from a ventral aspect, the cranium is also similar to other species of *Rattus* in several respects. The incisive foramina, which extend past the anterior margins of the first molars; the long palatal bridge, which projects behind the third molars to form a shelf; the spacious sphenopalatine vacuities; the configuration of the pterygoid fossae and the basicranial region, which reflects a certain carotid circulatory pattern, are basic to species of *Rattus* (Musser, 1982a). The distinctive characteristics of *R. tawitawiensis* are the incisive foramina, which are not just long but very wide, the small bullae (relative to cranial size), and the large, chunky molars.

The general aspect of each dentary is like that in other species of *Rattus* (fig. 5). It is distinctive in its stout appearance, deep ramus, and deep triangular-shaped portion behind the ramus.

The incisors, like those in other species of *Rattus,* appear strong. Enamel surfaces of uppers and lowers are orange.

Occlusal surfaces of upper molars in each of the three specimens of *R. tawitawiensis* are shown in figure 8. The toothrows are long and the molars wide relative to size of the cranium (table 2). The general occlusal patterns, shape of each tooth and its size relative to the others in the toothrow, degree of overlap among molars in a toothrow, and number of roots anchoring each tooth are like those features in many other species of *Rattus* (Musser, 1982a; Musser and Newcomb, 1983).

There are details in the cusp patterns of *R. tawitawiensis* that deserve description. In each first upper molar of DMNH 3525, the second row of cusps is united by an enamel bridge to the third row (clearly seen in fig. 8A). In the two younger rats, the labial cusps of the first and second rows on each first upper molar have a ridge-like posterior extension, a

configuration seen most clearly in figure 8C. Such an extension is present but slight on the labial cusp of the first lamina on each second upper molar. Although the teeth are worn in the oldest specimen, there is still an indication of a posterior cingulum at the back of each first upper molar. A large and conspicuous posterior cingulum also forms the back of not only the first upper molar but also the second in the youngest animal, DMNH 3524 (see fig. 8C); DMNH 3528 lacks posterior cingula on the upper molars. In all three specimens there is a small or large prominent cusp developed from a conspicuous cingular ridge at the anterolabial margin of each second and third upper molar. In each second upper molar, the small labial cusp juts forward so that it nearly touches the back ridge of the cusp forming the labial margin of the first lamina. Finally, the first lamina of each third upper molar is slightly undulate, not bent into the shape of a comma as in *R. rattus.*

The lower molars are also large and chunky (fig. 8) and, in general shape, cusp patterns, and numbers of roots, resemble teeth in other species of *Rattus.* There are small but conspicuous anterior and posterior cusplets on the labial side of each first lower molar. Each second molar bears a posterior labial cusplet. The cusp at the anterolabial margin of each second and third tooth is large and present in all three specimens. It may be significant that the anterolabial and anterolingual cusps forming the front lamina of each first molar are coalesced—even in the youngest rat in which the chewing surfaces are only slightly worn (fig. 8c). Usually in a specimen of *Rattus* of that age the two cusps are discrete and form a bilobed, rather than an oblong, lamina in cross-section (fig. 8f).

HABITATS AND HABITS: Batu Batu, the place where the specimens of *R. tawitawiensis* were caught, is in the southern coastal lowlands on the western third of Tawitawi Island. The northern half of the island is mountainous, the highest elevation about 1800 feet (see the terrain diagram in King and McKee, 1949). According to duPont and Rabor (1973, p. 8), the "largest and most intact areas of dipterocarp forests, many of which have not yet been touched by man, are found in the northern half on Tawitawi Island. Those in the southern half of this island, especially the areas close to the Batu Batu area, have been logged and eventually cleared fully, then planted to various crops." Those authors also note that large areas in the southern half of Tawitawi Island are covered by second-growth forest. Unfortunately, we have no information about the particular habitat where samples of either *R. tawitawiensis* or *R. rattus mindanensis* in the Batu Batu region were obtained. One specimen of *R. rattus* was caught in a house, but there are no data associated with any of the other animals. We suspect that *R. rattus* is common in the fields and villages, whereas *R. tawitawiensis* originally lived in high forest but now occurs in second-growth forest and scrub, at least in the southern half of the island.

We know nothing about the habits of *R. tawitawiensis.* Because of its stout body, tail that is shorter than length of head and body, and long, slender hind feet, we think it to be terrestrial. Its dark coloration suggests habitation in good cover and we suspect that the animal is a rat of the forest floor. Its diet and reproductive characteristics are unknown.

COMPARISONS

The definition of any new species involves not just description but comparisons with related species as well. We present those comparisons here, realizing that because our sample of *R. tawitawiensis* is small, each specimen is of a different age, and only one sex is represented, certain characteristics we now detect as important may lose their significance in larger samples that would better estimate the range of morphological variation within the species.

We will contrast *Rattus tawitawiensis* with several other species of *Rattus.* One comparison involves the Tawitawi animals and our specimens of *R. rattus mindanensis* from the Sulu Archipelago. Then we compare the three specimens of *R. tawitawiensis* with samples of *R. tiomanicus mara* from the Maratua Archipelago off the east coast of Borneo, with *R. hoffmanni* from Sulawesi, with *R. stoicus* from the Andaman Islands west of the Malay Peninsula, and with members of the *R. palmarum* group from Pulau (Island) Enggano, the Mentawai Islands, Pulau Simalur and adjacent islands, and the Ni-

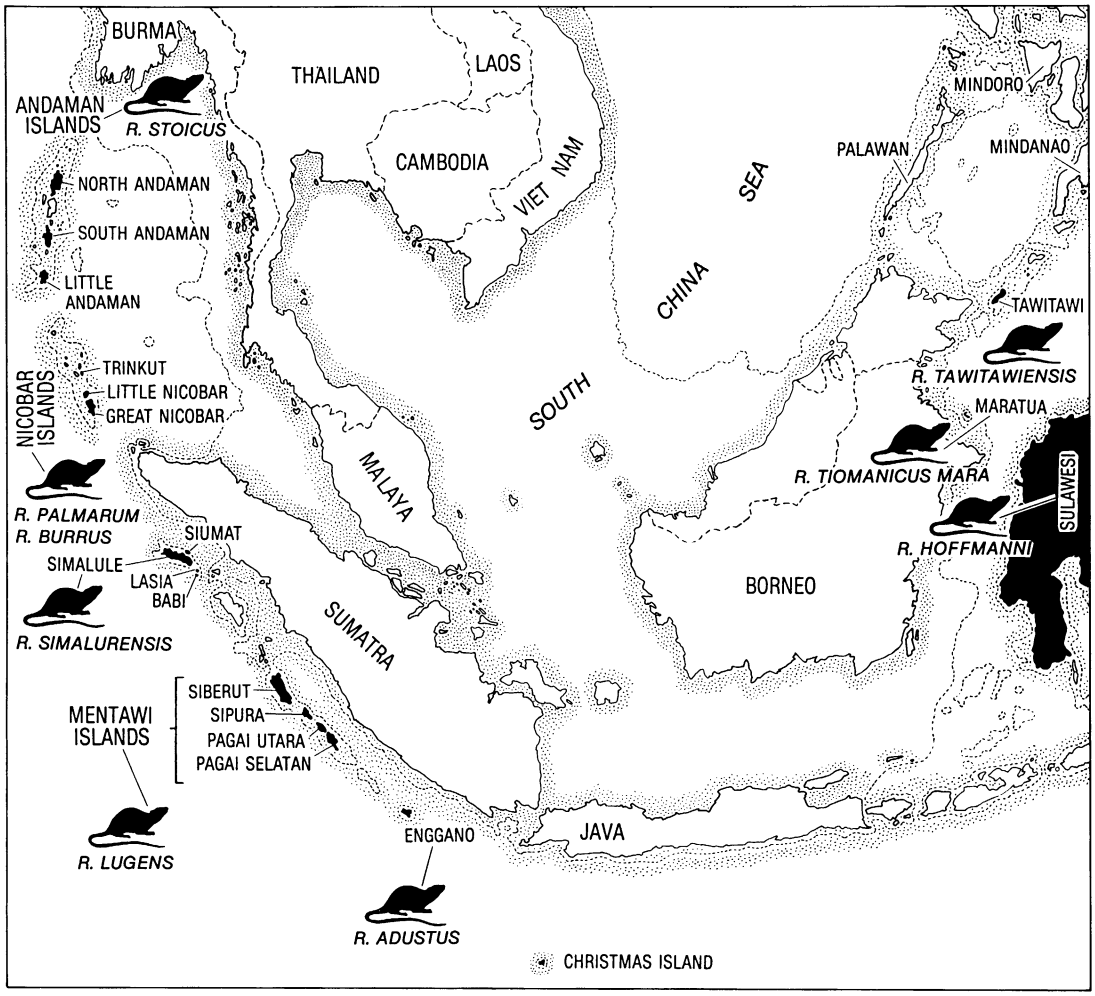

FIG. 6. The Sunda Shelf and offshore islands. The dotted line denotes the 100 fathom (180 m) line. Note that the islands and island groups of Tawitawi, Maratua, Sulawesi, Enggano, Simalur, Nicobar, and Andaman lie beyond the 100 fathom line. Sea level lowered to about 180 m during the Pleistocene would not have been enough to connect most of these islands with the continental margin of Sundaland. The Mentawais were probably an exception, and may have been connected to the mainland by a narrow isthmus.

cobar Islands. The threads connecting these samples of *Rattus* are their morphological similarity to *R. tawitawiensis* and their habitation on islands off of the Sunda Shelf beyond the 180 m (100 fathom) bathymetric line (fig. 6). We have also considered and examined samples of other species, but will not discuss them in detail because the comparions were unnecessary to define *R. tawitawiensis*. Except for *R. tiomanicus* on the Shelf, which we will discuss later, no other species of *Rattus* is as morphologically similar to *R. tawitawiensis* as are certain examples from islands off of the Sunda Shelf.

We begin with the distinctions we see between specimens of *R. tawitawiensis* and those of the houserats taken in the Batu Batu area.

Rattus tawitawiensis and *Rattus rattus mindanensis*

Contrasting these two species is important because species of *Rattus* with a morphology similar to that of *R. tawitawiensis* are often

TABLE 2

Measurements (in Millimeters) Contrasting Specimens of *Rattus tawitawiensis* with Samples of *Rattus rattus mindanensis* from the Southern Sulu Archipelago

(Mean plus or minus one standard deviation, number of specimens in parentheses, and observed range are listed.)

	Species and Age Group							
	Older Adult		Adult	Young Adult		Young Adult-Juvenile		
Measurements	*R.t.*[a]	*R.r.m.*[b]	*R.r.m.*[c]	*R.t.*[d]	*R.r.m.*[e]	*R.t.*[f]	*R.r.m.*[g]	
LHB	**208**	199.2 ± 4.1 (5) 194–205	191.0 ± 10.6 (9) 178–212	**171**	167.8 ± 11.8 (4) 151–178	**160**	175	157
LT	**180**	197.0 ± 10.9 (5) 192–215	189.9 ± 13.0 (9) 170–205	**161**	191.0 ± 10.9 (4) 176–205	**146**	166	158
LHF	**42**	40.6 ± 0.9 (5) 40–42	40.8 ± 1.5 (9) 39–43	**41**	40.5 ± 1.9 (4) 39–43	**39**	36	36
GLS	**46.5**	45.8 ± 0.5 (4) 45.3–46.4	43.9 ± 0.7 (9) 44.9–43.0	**42.1**	41.5 ± 0.9 (4) 40.3–42.4	**41.0**	39.5	38.0
IB	**6.7**	6.6 ±0.3 (5) 6.3 –7.0	6.3 ± 0.2 (9) 6.0–6.5	**6.1**	6.0 ± 0.2 (4) 5.8–6.1	**5.7**	5.8	5.6
LR	**14.5**	14.3 ± 0.2 (5) 14.1–14.5	13.4 ± 0.4 (9) 12.6–14.1	**12.7**	12.5 ± 0.5 (4) 11.9–13.1	**12.5**	11.9	11.6
BR	**8.9**	8.1 ± 0.5 (5) 7.7–8.7	7.6 ± 0.3 (9) 7.0–8.1	**7.7**	7.0 ± 0.1 (4) 6.9–7.1	**6.7**	6.5	6.5
BZP	**5.5**	4.5 ± 0.1 (5) 4.4–4.7	4.5 ± 0.2 (9) 4.2–4.7	**4.6**	4.0 ± 0.2 (4) 3.7–4.2	**4.1**	3.7	4.1
BBC	**18.2**	16.8 ± 0.3 (5) 16.6–17.3	17.0 ± 0.5 (9) 16.4–17.7	**16.6**	16.5 ± 0.3 (4) 16.2–16.9	**16.2**	15.5	15.5
HBC	**12.9**	12.1 ± 0.3 (5) 11.9–12.4	11.9 ± 0.6 (9) 11.2–13.0	**12.6**	11.8 ± 0.1 (4) 11.7–11.9	**11.0**	11.2	10.5
PL	**25.2**	24.8 ± 0.6 (5) 24.1–25.4	23.8 ± 0.3 (7) 23.4–24.2	**22.8**	22.2 ± 0.3 (4) 21.8–22.4	**22.0**	20.1	20.4
LD	**12.1**	12.2 ± 0.5 (5) 11.7–13.0	11.2 ± 0.4 (8) 10.8–11.8	**10.2**	10.7 ± 0.2 (4) 10.5–10.9	**10.2**	9.3	9.7
LIF	**8.6**	8.8 ± 0.5 (5) 8.1–9.2	8.4 ± 0.3 (9) 7.7–8.8	**8.1**	7.9 ± 0.6 (4) 7.1–8.5	**7.7**	6.7	7.0
BIF	**3.9**	3.1 ± 0.1 (5) 2.9–3.2	2.8 ± 0.1 (8) 2.6–3.0	**3.1**	2.5 ± 0.1 (4) 2.3–2.6	**3.0**	2.7	2.5
LPB	**9.6**	9.0 ± 0.5 (5) 8.2–9.5	9.1 ± 0.5 (7) 8.6–9.8	**8.3**	8.3 ± 0.3 (4) 8.1–8.7	**8.4**	8.1	7.9
$BPBM^1$	**5.0**	3.9 ± 0.2 (5) 3.6–4.2	3.9 ± 0.3 (8) 3.5–4.2	**3.9**	3.8 ± 0.1 (4) 3.7–3.9	**3.9**	3.0	3.5
PPL	**15.0**	15.9 ± 0.3 (5) 15.5–16.3	14.9 ± 0.3 (7) 14.3–15.3	**13.3**	14.0 ± 0.2 (4) 13.8–14.2	**13.0**	13.4	12.7
LB	**6.9**	7.7 ± 0.2 (5) 7.3–7.9	7.3 ± 0.3 (8) 7.0–8.0	**6.5**	6.8 ± 0.1 (4) 6.6–6.9	**6.6**	6.7	6.0
ALM^{1-3}	**8.0**	7.6 ± 0.4 (5) 7.3–8.2	7.7 ± 0.2 (8) 7.3–7.9	**7.9**	7.4 ± 0.3 (4) 7.0–7.7	**8.2**	7.6	7.1
CLM^{1-3}	**7.2**	6.7 ± 0.1 (5) 6.6–6.9	6.9 ± 0.2 (9) 6.6–7.2	**7.6**	6.8 ± 0.3 (4) 6.4–7.1	**7.7**	6.8	6.6
BM^1	**2.2**	2.0 ± 0.1 (5) 1.9–2.1	2.0 ± 0.1 (8) 1.9–2.1	**2.2**	2.0 ± 0.0 (4)	**2.3**	2.0	2.0

misidentified as *R. rattus*. Values from measurements are listed in table 2. The older adult specimen of *R. tawitawiensis* can be compared with older adults of *R. r. mindanensis* of about comparable age as well as median-age adults; also, the young adult and young adult-juvenile *R. tawitawiensis* can be contrasted with specimens of *R. r. mindanensis* of comparable age. The age categories are based on degree of molar wear and cranial conformation. We tried to match each specimen of *R. tawitawiensis* with specimens of *R. r. mindanensis* that we judged to be about the same age. Skulls are compared in figures 5 and 7 and occlusal views of molar rows in figure 8. The two kinds of rats are similar in body size but dissimilar in body and tail proportion. In any sample of *R. r. mindanensis,* tails average about as long or longer than average length of head and body; in each specimen of *R. tawitawiensis,* the tail is much shorter than head and body.

The contrast between the two in color of the dorsal coat is striking. *Rattus r. mindanensis* is a paler animal. The ears are medium brown, the brown on tops of the feet tends to be restricted to a mid-dorsal strip extending from the ankle to base of the digits, and the head and body is grayish brown in some specimens and grayish tawny brown in many others. Furthermore, the gray-brown is densely streaked with black over the back and rump, an effect caused by the very long (up to 40 mm) and abundant guard hairs, a feature characteristic of Asian houserats.

Compared with *R. r. mindanensis, R. tawitawiensis* is easily distinguished by its dark brown ears and feet, its dark and rich brown fur uniformly speckled with buff, and absence of black streaking because the guard hairs are very short and inconspicuous. In addition to color, there is a difference between the two species in fur texture: that of *R. r. mindanensis* is harsher to the touch compared with the softer and sleeker coat of *R. tawitawiensis.*

There are distinctions between the two species in color of the ventral coat. Pale gray to grayish buffy brown is the range found in most samples of *R. r. mindanensis*; the three specimens of *R. tawitawiensis* have dark gray venters with silver or very pale buffy highlights.

Female *R. r. mindanensis* have five pairs of mammae; the number and general location of the ten teats are similar in the hundreds of specimens of *R. r. mindanensis* that we have examined from places throughout the Philippine Islands. *Rattus tawitawiensis* has four pair; it lacks pectoral teats, which are present in *R. r. mindanensis.*

Cranial differences are conspicuous. *Rattus tawitawiensis* has a wider and deeper cranium than does *R. r. mindanensis.* When comparable-age specimens of the two species are examined, this difference is reflected in breadth of rostrum, breadth and height of braincase, and breadth of palatal bridge at first upper molars. The two rats differ further in that *R. tawitawiensis* has a broader zygomatic plate, much wider incisive foramina, and smaller bullae. In addition, the postorbital ridging begins farther back on the cranium than in *R. r. mindanensis.*

←

[a] DMNH 3525, holotype of *Rattus tawitawiensis.*

[b] DMNH 3480, 3513, 3517, 3519, and 3522.

[c] DMNH 3475, 3478, 3512, 3514–3516, 3523, 3526, and 3527.

[d] DMNH 3528.

[e] DMNH 3476, 3477, 3479, 3518, and 3521.

[f] DMNH 3524.

[g] DMNH 3518 and 3520, respectively.

Abbreviations: **LHB**, length of head and body; **LT**, length of tail; **LHF**, length of hind foot; **GLS**, greatest length of skull; **IB**, interorbital breadth; **LR**, length of rostrum; **BR**, breadth of rostrum; **BZP**, breadth of zygomatic plate; **BBC**, breadth of braincase; **HBC**, height of braincase; **PL**, palatal length; **LD**, length of diastema; **LIF**, length of incisive foramina; **BIF**, breadth of incisive foramina; **LPB**, length of palatal bridge; **BPBM^1**, breadth of palatal bridge at first upper molar; **PPL**, postpalatal length; **LB**, length of bulla; **ALM$^{1-3}$**, alveolar length of maxillary toothrow; **CLM$^{1-3}$**, crown length of maxillary toothrow; **BM^1**, breadth of first upper molar; ***R.t.***, *Rattus tawitawiensis*; ***R.r.m.***, *Rattus rattus mindanensis.*

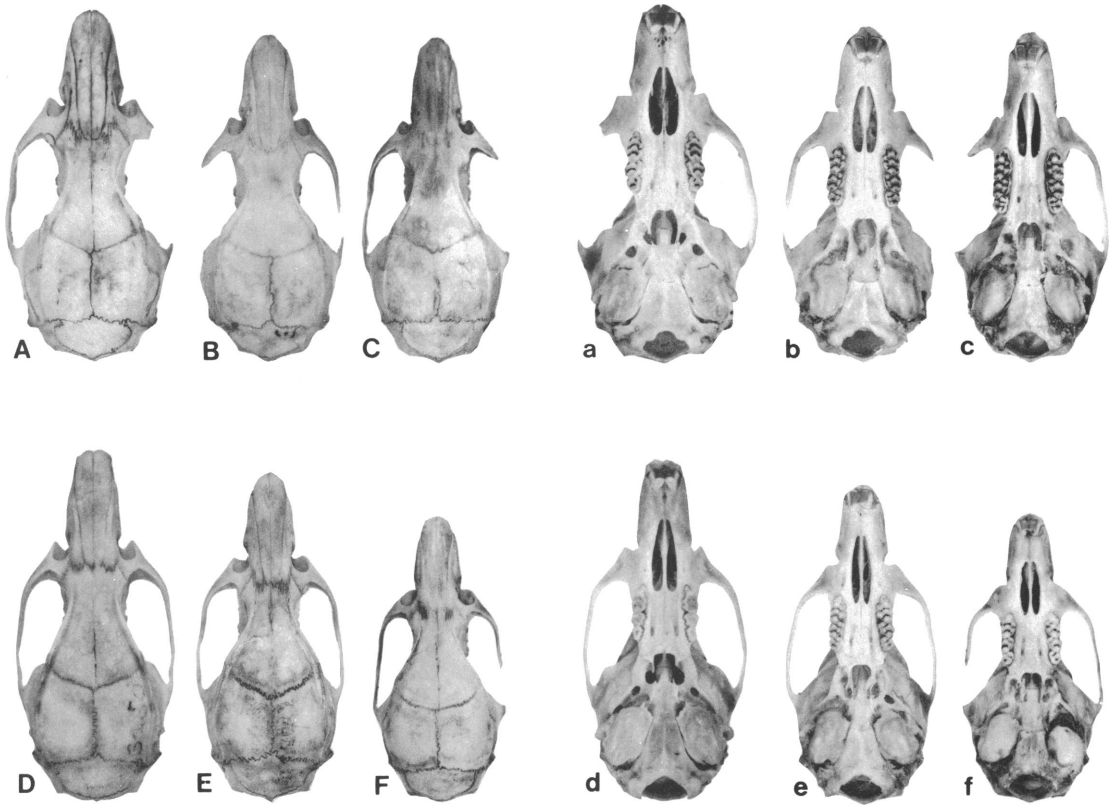

FIG. 7. Crania of *Rattus tawitawiensis* and *R. rattus mindanensis* compared. *Rattus tawitawiensis:* A and a, DMNH 3525; B and b, DMNH 3528; C and c, DMNH 3524. *Rattus rattus mindanensis:* D and d, DMNH 3480; E and e, DMNH 3477; F and f, DMNH 3520. Natural size. An adult, young adult, and very young adult are represented in the three examples of *R. tawitawiensis.* Each specimen of *R. r. mindanensis* is a counterpart of *R. tawitawiensis* in age.

Contrasts between the species in shape of dentaries reflect a cranial distinction. Each dentary of *R. tawitawiensis* is deeper through the ramus and the posterior half than those of *R. r. mindanensis* (fig. 5).

The molar rows are longer in the three examples of *R. tawitawiensis* than in most specimens of *R. r. mindanensis* and the molars wider, using width of each first upper molar as a guide. Occlusal patterns are generally similar in the two species but different in details. *Rattus rattus mindanensis* does not have the posterior ridge-like extensions on labial cusps of first and second upper molars; such ridges are prominent in *R. tawitawiensis.* Out of 19 specimens of *R. r. mindanensis,* 13 have anterolabial cusps on each second upper molar that range in size from a tiny lump to a large cusp, but all are pressed against the front lamina and not part of a singular ridge forming the anterolabial margin of each tooth, as is the configuration in *R. tawitawiensis.* Only five of the 19 examples of *R. r. mindanensis* have either a tiny or small cusp at the anterolabial corner of each third upper molar; such a cusp is large and developed on a cingular ridge in all specimens of *R. tawitawiensis.* Posterior cingula occur on first upper molars in three out of 18 specimens of *R. r. mindanensis.* The frequency is higher in *R. tawitawiensis*; two out of three have the cusps. Finally, the front lamina of each third upper molar is shaped like a comma in the house-rats but is only slightly undulate in *R. tawitawiensis.*

We have compared our sample of *R. tawi-*

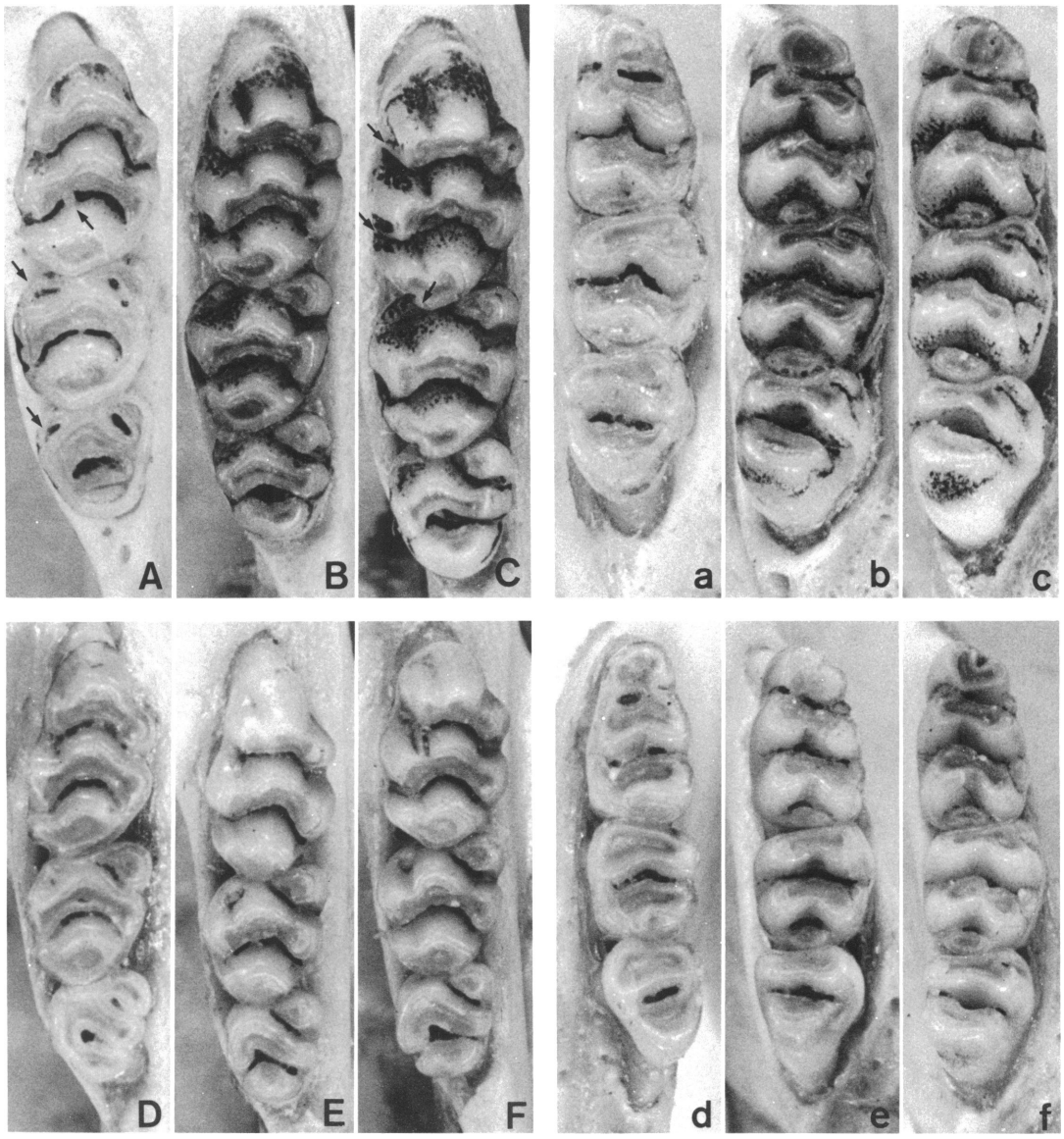

FIG. 8. Upper and lower molar rows of *Rattus tawitawiensis* and *R. rattus mindanensis* compared. Top row, *R. tawitawiensis*: A and a, DMNH 3525; B and b, DMNH 3528; C and c, DMNH 3524. Bottom row, *R. rattus mindanensis*: D and d, DMNH 3519; E and e, DMNH 3477; F and f, DMNH 3521. Approximately ×10. Arrows point to features discussed in text. Each example of *R. rattus mindanensis* is an approximate age counterpart of each *R. tawitawiensis*.

tawiensis with specimens of *R. r. mindanensis*; these are the only two species taken so far on Tawitawi Island. Throughout the Sulu Archipelago, the only other species of *Rattus* known to occur on some islands (Bongao, for example) is *R. exulans*. This is a very small-bodied rat compared with *R. tawitawiensis*, and its fur is pigmented more like that of houserats. It does have four pairs of mammae, but one is pectoral, another is postaxillary, and two pairs are inguinal. These positions in the pectoral and abdominal regions are different from locations of teats in *R. tawitawiensis*. Other species of *Rattus* may be

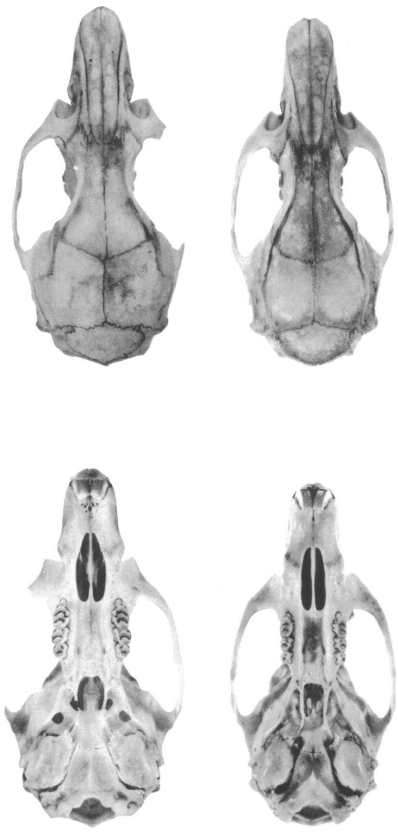

FIG. 9. Crania of adult *Rattus*. Left: *R. tawitawiensis* (DMNH 3525). Right: *R. tiomanicus mara*, Pulau Maratua (USNM 197444). Natural size.

native to Tawitawi Island and other islands in the Sulu Archipelago, but that can be determined only by future mammalogical exploration in the archipelago. We now turn our attention to samples of *Rattus* from outside the Sulu Islands, samples that must be compared with the three specimens of the native Tawitawi rat.

Rattus tawitawiensis and *Rattus tiomanicus mara*

Lying east of the Bornean mainland, beyond the 180 m bathymetric line between 2 and 3°N. lat., Pulau Maratua and the smaller islands of Alanga, Tong Tutup, Sangalan, and Bakungan form a small cluster known as the Maratua Archipelago (Kepulauan Maratua) about 28 nautical miles east of Tanjong Batu, the nearest point on the mainland (see map in Musser and Califia, 1982, p. 4).

The native rat of this small archipelago is *Rattus tiomanicus mara*, an insular morphological variant of a species that occurs on the Malay Peninsula and most large and small islands of the Sunda Shelf. But for a few places, it has not been found on islands off the Shelf—the Maratua Archipelago is one exception. The subspecies is large in body size compared with samples of *R. tiomanicus* from any other place, the upperparts are dark chestnut, and the underparts dark gray to dark buffy gray. Musser and Califia (1982) have documented the taxonomic history associated with samples from the Archipelago, discussed the identity of the animals, compared them with samples of *R. tiomanicus* from other places, and presented a hypothesis about their relationships to samples from populations of *R. tiomanicus* from other islands off the east coast of Borneo and from the mainland.

Because *R. tiomanicus mara* is large in body size compared with all other samples of the species, especially those from mainland Borneo, and because it has dark pelage and comes from islands off the Sunda Shelf, we checked to see if it could be related to *R. tawitawiensis*, another large-bodied and darkly pigmented species from an island east of the Shelf.

We detect no special relationship between *R. tawitawiensis* and *R. tiomanicus mara* other than the fact that they represent insular populations of *Rattus*. Both have dark fur and a similar general aspect of the skulls, but *R. tawitawiensis* is a much larger rat with bigger teeth (table 3). The wider, more spacious (relative to diastemal region) incisive foramina of *R. tawitawiensis* compared to that in *R. t. mara* is striking (fig. 9). The *R. tiomanicus mara* female has five pairs of mammae, as does *R. r. mindanensis*, but not *R. tawitawiensis*. The samples from Kepulauan Maratua represent insular populations of *R. tiomanicus* occurring off the Sunda Shelf; the three specimens of *R. tawitawiensis* are not samples of another dark and large-bodied population of *R. tiomanicus*; they are a different biological species.

The next samples to be compared with specimens of *R. tawitawiensis* come from the

island of Sulawesi and represent a species that also has eight pair of mammae.

Rattus tawitawiensis and *Rattus hoffmanni*

Located south of the Sulu Archipelago and separated from it by the deep Celebes Sea, Sulawesi (Celebes) is a large island directly east of Borneo and beyond the Sunda Shelf. *Rattus hoffmanni* is one of 35 species native to Sulawesi (Musser, 1984). Because it occurs on an island east of the Sunda Shelf, because its general morphology resembles that of *R. tawitawiensis* (and it is the only species of Sulawesian rat that does), and because Sulawesi is the first large island south of the Sulu chain, we compared samples of the two species to determine the extent of their relationship, if any.

Rattus hoffmanni is a common element of the fauna on Sulawesi and lives in forests that extend from coastal lowlands to mountain summits. It has a moderately large body and a tail about as long as combined lengths of head and body. Fur clothing the dorsum is soft, thick, and short. The overall coloration is brown speckled with buff, producing a dark agouti pattern. Top of the back and rump are darker than the grayish sides of the head and body. The ventral coat ranges from dark gray to dark grayish brown. The ears, tops of feet, and tail are brown. Females have four pairs of mammae: one postaxillary pair, an abdominal pair, and two pairs in the inguinal region—there is no pectoral pair, a pattern of teats similar to that in *R. tawitawiensis*. The cranium resembles that of Asian houserats but is more robust; the molars are large.

Seven scientific names have been applied to samples of *R. hoffmanni*. The proliferation reflects the good representation of the species in collections of museums and the fact that through the years different taxonomists described what they considered to be significant geographic variation among the samples. A preliminary study by Musser (1984), however, indicates that most of the names do not designate different populations with distinctive morphological attributes and geographic boundaries. Geographic variation among samples from throughout most of the island is slight; the exception is a small lot of spec-

TABLE 3

Measurements (in Millimeters) from Samples of *Rattus*

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

Species and Island	Lengths	
	Skull	M^{1-3} (Alveolar)
R. tiomanicus sabae, Borneo		
Sampit	38.1 ± 1.6 (17) 34.8–41.3	6.8 ± 0.2 (19) 6.4–7.2
R. tiomanicus mara, Borneo		
Pulau Maratua	43.1 ± 2.1 (30) 39.7–47.4	7.1 ± 0.2 (27) 6.7–7.6
R. tawitawiensis, Sulu Arch.		
DMNH 3525	46.5	8.0
DMNH 3528	42.1	7.9
DMNH 3524	41.0	8.2
R. hoffmanni		
Central Sulawesi	42.3 ± 1.5 (17) 40.2–45.0	7.8 ± 0.1 (20) 7.5–8.3
R. adustus		
Pulau Enggano	—	8.7
R. lugens, Mentawais		
Pulau Pagi Utara	48.1 ± 1.7 (23) 45.5–50.8	8.1 ± 0.2 (23) 7.7–8.5
Pulau Sipora	46.2 ± 1.9 (15) 43.0–48.9	7.8 ± 0.3 (12) 7.3–8.4
R. simalurensis		
Pulau Simalur	44.7 ± 1.4 (11) 42.8–47.3	7.7 ± 0.2 (12) 7.5–8.0
Pulau Lasia and Pulau Babi	46.4 ± 2.0 (12) 43.1–50.9	7.9 ± 0.2 (12) 7.6–8.3
R. burrus, Nicobars		
Great Nicobar Island	41.6 ± 2.6 (3) 38.8–43.9	7.6 ± 0.1 (3) 7.6–7.7
Trinkut Island	43.1 ± 1.7 (10) 41.3–46.7	7.7 ± 0.1 (12) 7.4–7.9
R. palmarum, Nicobars		
NMW B-27	54.0	9.0
NMW 27027	51.0	8.9
NMW B-26	49.0	9.0
R. stoicus, Andamans		
Henry Lawrence Island	50.0 ± 2.3 (14) 46.4–55.1	8.3 ± 0.3 (16) 7.6–8.6
South Andaman Island	50.2 ± 3.0 (7) 46.4–55.1	8.3 ± 0.2 (8) 8.0–8.7

[a] All specimens are adults except for DMNH 3524.

FIG. 10. Crania of adult *Rattus tawitawiensis* compared with examples of named forms of *Rattus hoffmanni*. A, *R. tawitawiensis* (DMNH 3525). B, *R. h. hoffmanni,* northeastern Sulawesi (USNM 216833). C, *R. h. mollicomus,* northeastern Sulawesi (USNM 217758). D, *R. h. linduensis,* central Sulawesi (USNM 219583). E, *R. h. mengkoka,* southeastern Sulawesi (AMNH 101066). F, *R. h. mollicomulus,* southwestern Sulawesi (AMNH 196577). G, *R. h. biformatus,* Togian Islands (AMNH 153352). Natural size.

imens from the southwestern peninsula, which may represent a subspecies different from the population on the rest of Sulawesi.

Rattus tawitawiensis is larger in body size than most specimens of *R. hoffmanni.* An occasional example of the latter, such as AMNH 101258, equals *R. tawitawiensis* in size, but the contrasts between examples of *R. tawitawiensis* and most specimens of *R. hoffmanni* of comparable age resemble those shown in figure 10 where the cranium of the adult *R. tawitawiensis* is compared with crania of adult *R. hoffmanni* from samples representing the geographic series which had received scientific names.

The two species are not so different in coat color. In both, the fur is soft, the upperparts are brown with buffy speckling, and the guard hairs are short and inconspicuous. The tone in *R. tawitawiensis,* however, is darker and richer than in most examples of *R. hoffmanni,* and the intensity extends over the entire dorsum. Most specimens of *R. hoffmanni* have a paler coat and the sides of head and body are definitely grayish and paler than the top of the body; other specimens, however, are as dark or even darker than those of *R. tawitawiensis* and some of these animals are nearly indistinguishable from specimens of the Tawitawi rat. Color of the ventral coat in *R. hoffmanni* resembles that of *R. tawitawiensis,* but most specimens are a more solid and darker gray, and many others have a brownish or dark buffy suffusion—hues which are uncharacteristic of the ventral fur of *R. tawitawiensis.*

Basic configuration of the cranium in the two species is not strikingly dissimilar (fig. 10); the distinctions are of small magnitude as they tend to be among some species of *Rattus.* In addition to the greater size of *R. tawitawiensis* as compared with most examples of *R. hoffmanni* (table 3), the Tawitawi rat differs in having (1) a chunkier skull, largely a result of its relatively wider and shorter rostrum (values from the ratio, breadth of rostrum divided by length of rostrum, are 61 percent in DMNH 3525 and 3528 as opposed to 56 percent, the mean of 20 *R. hoffmanni* from Central Sulawesi); (2) heavier ridges bounding the postorbital margins on top of the cranium (but the ridges begin at about the same level on top of the skull, a place farther back than on specimens of other *Rattus,* such as *R. rattus mindanensis,* for example); (3) a deeper braincase; (4) a narrower and deeper interparietal; (5) conspicuously wider incisive foramina—with few exceptions, the incisive foramina are slitlike in *R. hoffmanni*; (6) and smaller bullae relative to skull size (values from the ratio, length of bulla divided by length of skull is 15 percent in the adult and young adult *R. tawitawiensis* and an average of 17 percent in 20 specimens of *R. hoffmanni*).

Teeth of the two species are similar in length of molar row, width of each first upper molar, and occlusal patterns (fig. 11). A contrast between the two species, although not pronounced, is that most specimens of *R. hoffmanni* lack ridges on the posterior margins of labial cusps on the first and second upper molars, ridges which are conspicuous in the examples of *R. tawitawiensis.*

In pelage features, number of mammae, many aspects of cranial conformation, and dental characteristics, specimens of *R. tawitawiensis* and *R. hoffmanni* are similar. There are differences, however, and these are of the kind and magnitude that we have found to distinguish other species of *Rattus* from one another. There is no evidence from our samples that the series from Tawitawi Island represents an insular subspecies of *R. hoffmanni,* even though the two species share many morphological features, including four pairs of mammae and relatively large molars.

Four pairs of teats are characteristic of another species of *Rattus* that is found on islands well separated from the Sunda Shelf. That animal is the next subject and to set the context for our comparisons we have to jump from Sulawesi, off the eastern edge of the Sunda Shelf, all the way to the Andaman Islands, which lie west of the Shelf margin.

Rattus tawitawiensis and *Rattus stoicus*

Rattus stoicus is native to the Andaman Islands; we have examined specimens from Henry Lawrence Island, South Andaman Island, and Little Andaman Island. The species was named and described by Miller in 1902; *taciturnus* Miller (1902), and *rogersi* Thomas (1907), also apply to the same species. A report now being prepared (Musser and Mi-

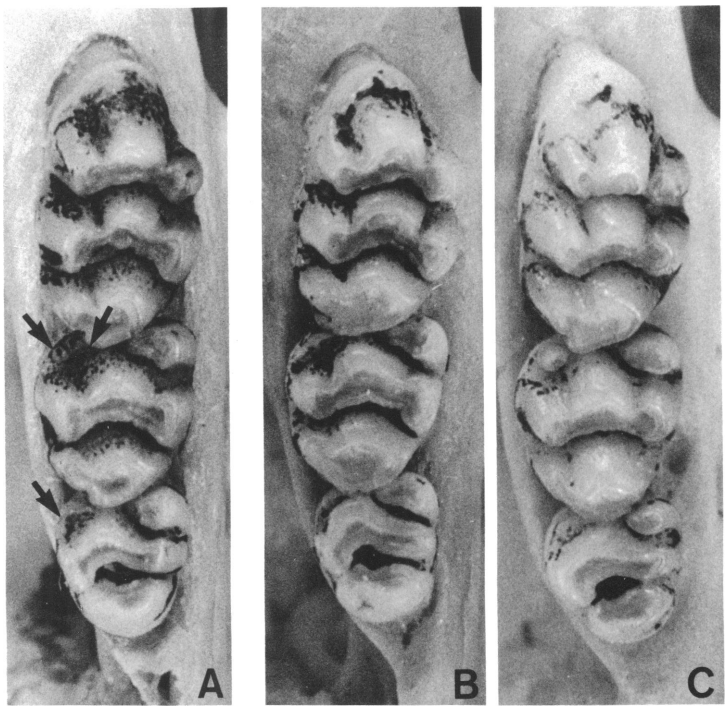

FIG. 11. Upper molar rows of *Rattus tawitawiensis* and *Rattus hoffmanni*. A, *R. tawitawiensis* (DMNH 3524). B (AMNH 224961) and C (AMNH 224252), *R. hoffmanni*, central Sulawesi. Approximately ×10. On all three, note the posterior cingulum at the back of each first molar and the cusp at the anterolabial margin of each second and third molar (indicated by arrows on A).

sonne, MS) will document the taxonomy, natural history, and phylogenetic relationships of the rat.

Rattus stoicus, like *R. tawitawiensis*, is large-bodied, has a tail much shorter than length of head and body, possesses four pairs of mammae, and is found only on islands beyond the Sunda Shelf. With these points, however, any close resemblance ends. Judged by length of skull, specimens of the Andaman rat are larger than those of *R. tawitawiensis* and have longer molar rows (table 3). The dorsal fur of *R. stoicus* is grayish brown, shaggy in appearance, very coarse to the touch because of the many semi-rigid translucent spines scattered throughout the pelage, and topped by long guard hairs (up to 50 mm long) that extend conspicuously beyond the overhair over the back and rump. The fur contrasts sharply with the relatively soft and sleek pelage of *R. tawitawiensis* with its short guard hairs and dark brown agouti pattern. Fur clothing the venter in *R. stoicus* is gray and paler than examples of the Tawitawi rats. The tail of *R. stoicus* is also paler than that in *R. tawitawiensis* and instead of being monocolored, its ventral surface is mottled and much paler than the top. The front feet of the Andaman rat are white with a thin grayish brown strip extending over the top to the base of the digits; the hind feet are unpigmented or very pale grayish brown—very distinctive when compared with the dark brown feet of *R. tawitawiensis*. Aside from relative tail length and number of mammae, no special relationship between the two species is indicated by pelage characteristics.

Our comparisons of skulls and teeth in the two samples also point to a distant morphological relationship between *R. stoicus* and *R. tawitawiensis*. The Andaman animal has an elongate cranium with a very long and slender rostrum; the contrast between the two species is seen in figure 12. The elongate cranial conformation of *R. stoicus* is also evident from a ventral view where two additional

FIG. 12. Crania of adult *Rattus*. Left: *R. tawitawiensis* (DMNH 3525). Right: *R. stoicus*, Henry Lawrence Island in the Andamans (USNM 111845). Natural size.

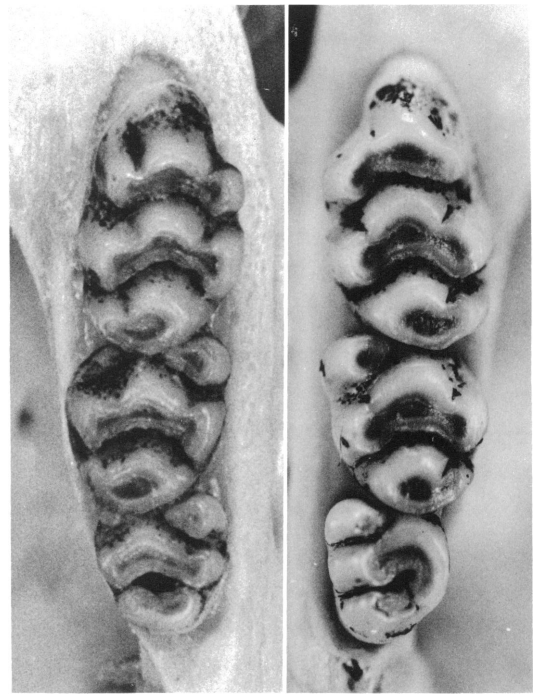

FIG. 13. Upper molar rows. Left: *Rattus tawitawiensis* (DMNH 3528). Right: *Rattus stoicus*, Henry Lawrence Island, the Andamans (USNM 111830). Note the absence of cusps at anterolabial margins of second and third molars of *R. stoicus*, and the C-shaped occlusal pattern of the third molar. Approximately ×10.

distinctions can be seen: (1) the incisive foramina are much longer and narrower in *R. stoicus*, and their posterior margins lie anterior to the molar rows instead of extending between the molars as they do in the Tawitawi rat; and (2) the sphenopalatine vacuities of *R. stoicus* are small, not spacious as they are in *R. tawitawiensis* and most other species of *Rattus* (Musser, 1982a). Distinctions between the two species in molar occlusal patterns (fig. 13) are of the kind and degree seen between specimens of *R. tawitawiensis* and *R. rattus mindanensis*.

So, even though *R. stoicus* is a large-bodied, short-tailed, insular endemic, we detect no morphological evidence linking it closely to *R. tawitawiensis*. This is not the same picture we saw after comparing samples of *Rattus* from islands off the southern margin of the Sunda Shelf with specimens of the Tawitawi rat, as we explain below.

Rattus tawitawiensis and the *Rattus palmarum* Group

We apply the name *palmarum* group, as did Musser and Califia (1982), to samples of *Rattus* from the Nicobar Islands and from the islands off the southwestern coast of Sumatra beyond the 180 m bathymetric line. Scientific names included within the group, their authors and dates of publication, and the island from which each holotype was obtained are listed in table 4. The series contains specimens of large-bodied rats, some with

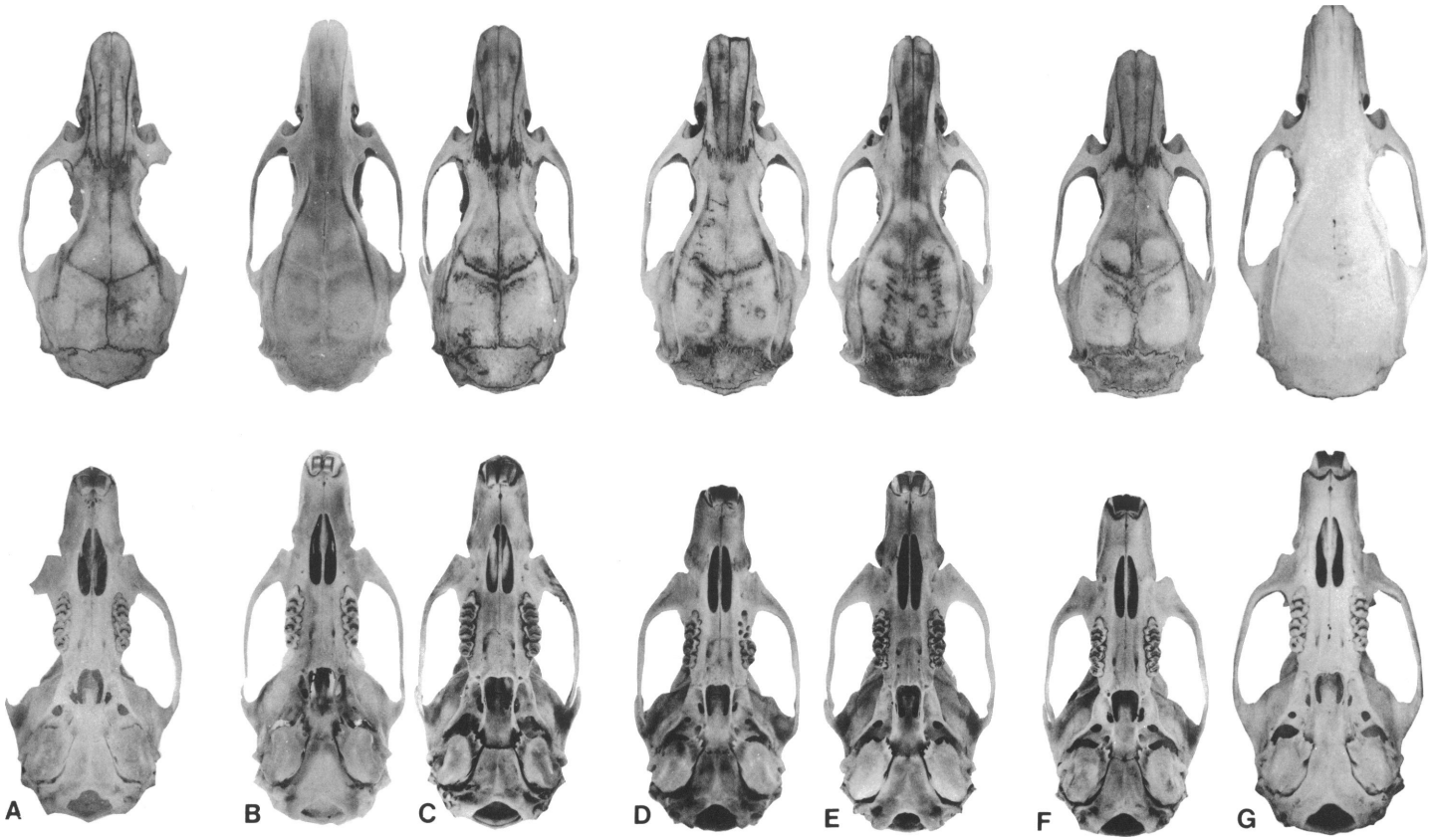

FIG. 14. Comparisons between crania of *Rattus tawitawiensis* and members of the *Rattus palmarum* Group. A, *R. tawitawiensis* (DMNH 3525). B and C, *R. lugens lugens,* Pulau Pagi Utara, Mentawais (AMNH 103020); *R. lugens mentawi,* Pulau Siberut, Mentawais (USNM 252469). D and E, *R. simalurensis lasiae,* Pulau Lasia, Simalur Islands (USNM 114255); *R. simalurensis simalurensis,* Simalur Island (USNM 114221). F, *R. burrus burrus,* Trinkut Island, Nicobars (USNM 111804). G, *R. palmarum,* Nicobars (NMW 27027). Natural size.

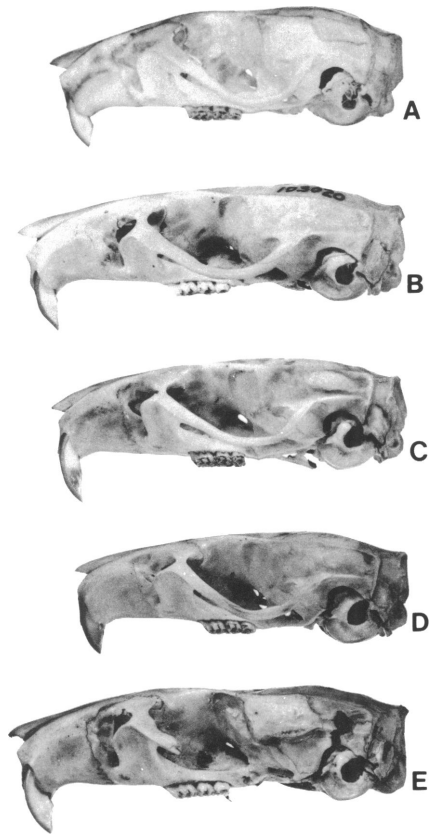

FIG. 15. Crania of adult *Rattus tawitawiensis* contrasted with the *Rattus palmarum* Group. A, *R. tawitawiensis* (DMNH 3525). B, *R. lugens,* Pulau Pagi Utara, Mentawais (AMNH 103020). C, *R. simalurensis,* Pulau Lasia, Simalur Islands (USNM 114255). D, *R. burrus,* Trinkut Island, Nicobars (USNM 111804). E, *R. palmarum,* Nicobar Islands (NMW B-27). Natural size. Note the deeper braincase of *R. tawitawiensis* as compared to the other crania.

dark pelage. Most resemble the specimens from Tawitawi Island in some way, and all have to be contrasted with *R. tawitawiensis* to help define that species.

Whether or not all of the named forms we discuss under the *R. palmarum* group actually belong there will be determined by a future study now being undertaken (Musser, MS). Our analyses so far indicate that the samples can be grouped into the following five clusters.

1. *R. palmarum:* Nicobar Islands; the particular island where the specimens were collected is unknown.
2. *R. burrus burrus:* Trinkut Island in the Nicobars.
   R. burrus burrescens: Great Nicobar Island and Little Nicobar Island.
3. *R. simalurensis simalurensis:* Pulau Simalur and Pulau Siumat, both northwest of Pulau Nias.
   R. simalurensis lasiae (includes *babi*): Pulau Lasia and Pulau Babi, both southeast of Pulau Simalur.
4. *R. lugens lugens:* Pulau Pagai Utara and Pulau Pagai Selattan in the Mentawai Islands.
   R. lugens mentawi: Pulau Sipora and Pulau Siberut in the Mentawais.
5. *R. adustus:* Pulau Enggano, southeast of the Mentawais.

Specimens in all samples are of large body size; the tail is about as long or slightly shorter than length of head and body; upperparts range from brown to dark brown and blackish; underparts are white to dark gray and grayish brown; and five pairs of mammae are positioned as they are in *R. rattus mindanensis.* The skulls are large and tend to be chunky; the molar rows are long and the teeth wide. Values from measurements of skull lengths and toothrow lengths from the samples are contrasted with those of *R. tawitawiensis* in table 3. Crania are compared in figures 14 and 15, and toothrows in figure 16.

We begin our comparisons with samples from the Nicobars, islands that are separated from the tip of Sumatra by a channel more than 700 fathoms deep and from the western margin of the Sunda Shelf by the deep Andaman Sea. Of all the samples provisionally placed in the *R. palmarum* Group, those from the Nicobars representing *R. palmarum* and *R. burrus* are least similar to the three specimens of *R. tawitawiensis* in features of skins and skulls. The three specimens of *R. palmarum* at hand are larger in body size than those of *R. tawitawiensis* and the skulls and molar rows are appreciably longer. Fur clothing the upperparts of *R. palmarum* is brown, very coarse and semispinous to the touch, a texture produced by the numerous semi-rigid translucent spines scattered throughout the coat. The coloration resembles that in *R. rat-*

TABLE 4
Taxa in the *Rattus palmarum* Group

Taxon	Author and Date	Type Locality
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)	Pulau Simalur, off coast of West Sumatra
lugens	Miller (1903b, p. 33)	Pulau Pagi Utara, Mentawai Islands
lasiae	Lyon (1916, p. 446)	Pulau Lasia, off west coast of Sumatra
babi	Lyon (1916, p. 447)	Pulau Babi, off west coast of Sumatra
mentawi	Chasen and Kloss (1927, p. 831)	Pulau Sipora, Mentawai Islands
adustus	Sody (1940, p. 397)	Pulau Enggano, off west coast of Sumatra

tus mindanensis rather than *R. tawitawiensis.* The underparts are whitish gray, paler than those in the Tawitawi rat. Female *R. palmarum* have two pectoral teats in addition to the other four pairs; such a pair is absent from specimens of *R. tawitawiensis.*

In addition to being larger than *R. tawitawiensis,* the cranium of *R. palmarum* is more slender; it appears elongate when compared with the chunky skull of the Tawitawi rat. The rostrum is longer and thinner, the prominent postorbital ridging begins farther forward, the braincase is not as deep, the incisive foramina are not as wide, and the sphenopalatine vacuities are smaller.

There are no dental features that suggest a close relationship between *R. tawitawiensis* and *R. palmarum.* Occlusal patterns of the latter resemble those characteristic of *R. rattus mindanensis* and not *R. tawitawiensis.*

Rattus burrus is smaller-bodied than *R. palmarum* and more like *R. tawitawiensis* in body size, although when compared with specimens of the latter, those of *R. burrus* of comparable age are smaller. Upperparts of *R. burrus* range from brown to a dark brown that tends to be a solid color without the agouti pattern seen in *R. tawitawiensis.* Underparts of most specimens are white or cream; others have gray and buff suffusions. The fur on the dorsum and venter is soft, much different from that in *R. palmarum.* The coloration reminds us of that in most populations of *R. tiomanicus* from places on the Sunda Shelf rather than the color of the rats from Tawitawi Island.

The cranium of *R. burrus* is a smaller and stockier version of that in *R. palmarum,* but with larger sphenopalatine vacuities. The similarity to *R. tiomanicus* suggested by color and texture of fur is reflected in the skull, which is reminiscent of a large and robust cranium of *R. tiomanicus.* The depth of the braincase and narrow incisive foramina seen in skulls of *R. burrus* resemble those features in *R. tiomanicus* and *R. palmarum,* not *R. tawitawiensis.*

The foregoing discussion has pointed out distinctive differences between *R. burrus* and *R. tawitawiensis* in coat color and cranial features. Characteristics of the molars, however, are not so different. On average, the molar rows are shorter in *R. burrus* than in *R. tawitawiensis,* but the occlusal patterns are very similar.

Specimens from Simalur and nearby islands, the Mentawai Islands, and Pulau Enggano, representing (respectively) *R. simalurensis, R. lugens,* and *R. adustus,* bear a greater resemblance to *R. tawitawiensis* than to either *R. palmarum* or *R. burrus.* Among these samples there are two clusters. Series from the Simalur Island Group form one morphological unit, those from the Mentawais and Pulau Enggano the other. The Enggano rat, *R. adustus,* is known only by the holotype, which is a very young adult. Compared with specimens of comparable age from the Mentawais and Simalur islands, it is a much larger animal, as is indicated by length of toothrow (table 3); in all other features of skin and skull, *R. adustus* is most like the series of rats from the Mentawai Islands. Rats in all the other samples are like *R. tawitawiensis* in body size and proportion. All have long toothrows and wide molars that are similar to the dental

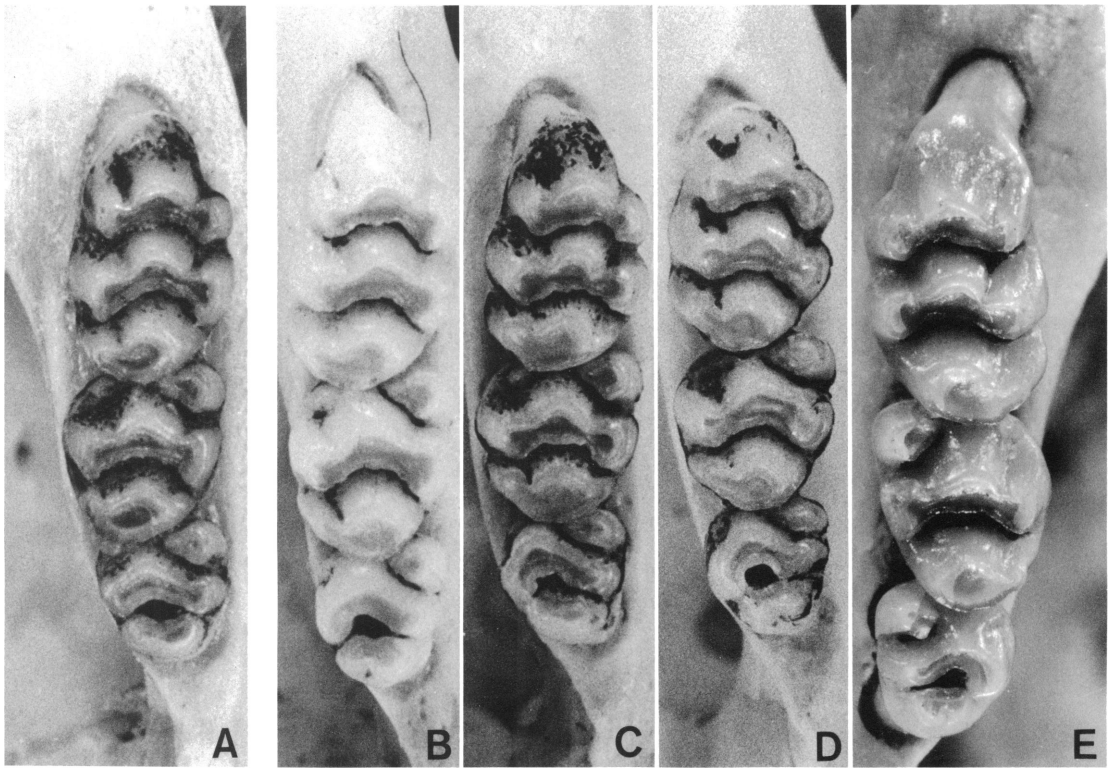

FIG. 16. Upper molar rows of *Rattus tawitawiensis* contrasted with members of the *Rattus palmarum* Group. A, *R. tawitawiensis* (DMNH 3525). B, *R. lugens,* Pulau Pagi Utara, Mentawais (AMNH 103021). C, *R. burrus,* Trinkut Island, Nicobars (USNM 111806). D, *R. simalurensis,* Pulau Simalur (USNM 114224). E, *R. palmarum,* Nicobars (NMW B-26). Approximately ×10.

dimensions of the Tawitawi rat, and there is close resemblance in occlusal patterns.

All samples contain dark animals in which the coat color, agouti pattern, and fur texture are similar to that in *R. tawitawiensis.* The primary difference is tone; the three specimens of *R. tawitawiensis* are not as dark as the examples of *R. simalurensis, R. lugens,* and *R. adustus*; the contrast is prominent in many of the specimens of *R. lugens,* which are brownish black on the dorsum. The ventral fur of *R. tawitawiensis* is paler than in most of the other specimens in which the color ranges from dark gray to dark grayish brown and buff. In contrast to the examples of *R. tawitawiensis,* all females of the three other species have five pairs of mammae, not four.

In general aspect, skulls of *R. tawitawiensis* are similar to those of *R. simalurensis, R. lugens,* and *R. adustus* but there are conspicuous distinctions in details; these differences are similar to those seen between samples of *R. rattus mindanensis* and the Tawitawi animals. Crania of the latter appear more robust and chunky because the rostrum is wider, the zygomatic arches more flaring, and the braincase wider and deeper, as can be seen in figures 14 and 15. Also, the postorbital ridging does not extend as far forward in *R. tawitawiensis.* Aside from the generally wider cranium, the most conspicuous differences among the samples is the wide incisive foramina in *R. tawitawiensis.* That feature in specimens of *R. simalurensis* is narrow; examples of *R. lugens* and *R. adustus* have wider incisive foramina than do those of *R. simalurensis,* but not as wide as those in *R. tawitawiensis.*

Even though *R. tawitawiensis* is more like

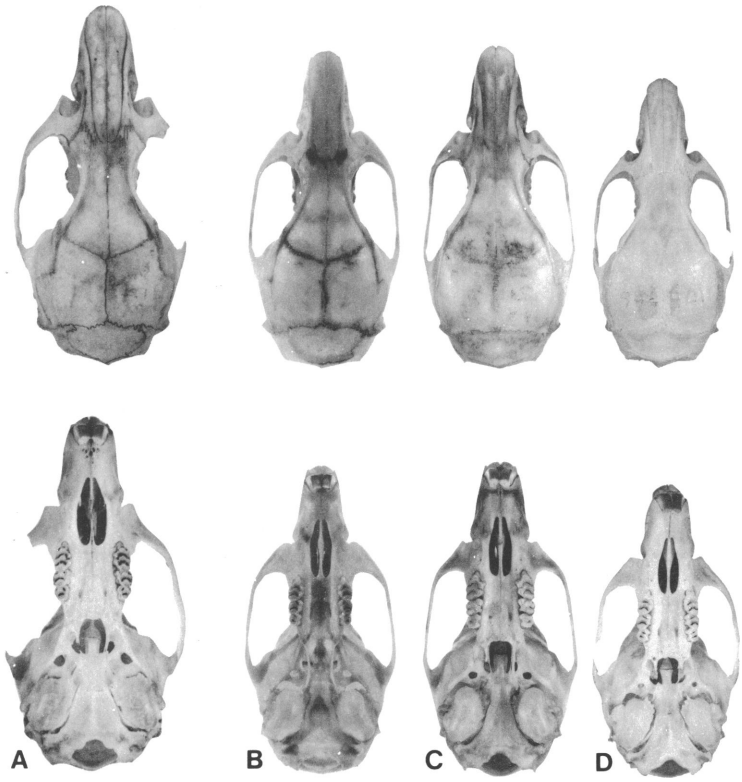

FIG. 17. Crania of adult *Rattus tawitawiensis* compared with *Rattus tiomanicus*. A, *R. tawitawiensis* (DMNH 3525). B, *R. tiomanicus*, Sabah, northern Borneo (USNM 292689). C, *R. tiomanicus*, Java (AMNH 250114). D, *R. tiomanicus*, eastern Sumatra (AMNH 106666). Natural size.

rats from the Mentawai and Simalur islands than those on the Nicobars, it still has a distinctive combination of features which separates it from *R. simalurensis, R. lugens,* and *R. adustus*. We have no evidence suggesting that the specimens from Tawitawi Island represent an insular subspecies of any of the populations on Pulau Enggano, the Mentawais, the Simalur Group, or even the Nicobar Islands.

OTHER COMPARISONS

What other species of *Rattus* did we examine and why didn't we consider them morphologically close enough to the Tawitawi animals for inclusion in this report? Because the sample came from the Sulu Archipelago, that chain of islands forming a broken link between Borneo on the Sunda Shelf and Mindanao in the southern Philippines, we naturally scanned the Philippine murids as well as those native to Borneo and other islands on the Sunda Shelf. No species native to the Philippine Islands bears a close morphological resemblance to *R. tawitawiensis*. Of the two species of *Rattus* from there, *R. everetti* is larger-bodied and has long, shaggy pelage and a long, bicolored tail. Its cranial and dental features (see the illustrations in Musser and Newcomb, 1983) are unlike those characterizing the Tawitawi rat. The other species, *R. mindorensis,* is known to occur only on the island of Mindoro. Its morphology is closely similar to specimens of *R. tiomanicus* from the Sunda Shelf (Musser and Califia, 1982). If there is a species of *Rattus* living on any Philippine island, especially Mindanao, which has a morphology similar to that of *R. tawitawiensis* it has yet to be discovered.

Looking west from the Sulu Archipelago toward the islands and peninsula on the Sunda Shelf, we know of four species of *Rattus*

FIG. 18. Upper molar rows. Left: *Rattus tawitawiensis* (DMNH 3528). Right: *Rattus tiomanicus*, Java (AMNH 250111). Approximately ×10.

native to that region. *Rattus baluensis* occurs in the mountains of Sabah (northern Borneo) and Sumatra. *Rattus hoogerwerfi* is a mountain rat of northern Sumatra. *Rattus annandalei* has been recorded from the Malay Peninsula, Singapore, eastern Sumatra, and the islands of Padang and Rupat off the coast of eastern Sumatra (see Musser and Newcomb, 1983, for illustrations, measurements, and descriptions of these species). *Rattus tiomanicus* occurs on the Malay Peninsula, Borneo, Sumatra, Java, Bali, many smaller islands on the Shelf, and two places off of the Shelf: the Maratua Archipelago and Pulau Enggano (Musser and Califia, 1982).

Morphologies of three of these species are unlike that of *R. tawitawiensis*. *Rattus baluensis* and *R. hoogerwerfi* are smaller-bodied. Both have thick, long fur that is tawny or chocolate brown on the dorsum and buffy gray or deep ochraceous on the venter. Both have tails that are much longer than length of head and body; the distal half in *R. hoogerwerfi* is white. *Rattus baluensis* has five pairs of mammae, *R. hoogerwerfi* has four; it, like *R. tawitawiensis*, lacks the pectoral pair. The skulls of *R. baluensis* and *R. hoogerwerfi* are gracile and flat compared with the chunky, deep cranium of *R. tawitawiensis*; postorbital and temporal ridges are low and inconspicuous in comparison; sides of the braincase are vertical or nearly so, not flaring outward from the temporal ridges as they do in *R. tawitawiensis*; and the incisive foramina are narrow, not expansive. There are no dental features suggesting that either of these species is morphologically close to *R. tawitawiensis*.

Rattus annandalei resembles *R. tawitawiensis* in body size but little else. The tail is much longer than length of head and body, upperparts are grayish brown, underparts range from white to pale yellow, and females have four pairs of mammae, including one pectoral pair. *Rattus annandalei* also has narrower and much shorter incisive foramina; a palatal bridge that ends just past posterior margins of the third molars, instead of forming a shelf behind those teeth as in the Tawitawi rat; very small sphenopalatine vacuities, which are unlike the wide and spacious openings in *R. tawitawiensis*; and large, somewhat inflated auditory bullae. Occlusal patterns of the molars, especially the uppers, are more complex than those of *R. tawitawiensis* (see fig. 91 in Musser and Newcomb, 1983, p. 518). These are just a few of the many features distinguishing the two species. The overall morphology of *R. annandalei* suggests that it is peripheral to the core of species in the genus *Rattus*; it certainly has no close morphological resemblance to *R. tawitawiensis*.

Rattus tiomanicus is the fourth species native to the peninsula and islands on the Sunda Shelf. It is smaller in body size than *R. tawitawiensis*, although more similar than the three other native Sundanese *Rattus*. Upperparts are brown or tawny in most samples of *R. tiomanicus*; underparts range from white to grayish white. Samples from some places, such as Pulau Nias and the Maratua Archipelago, are much darker and represent one extreme in color variation: the dorsum is blackish brown or chestnut and the venter is dark buffy gray (Musser and Califia, 1982). The tail of *R. tiomanicus* is monocolored and averages slightly longer than combined lengths of head and body. The feet are brown.

Pelage is soft and sleek with short guard hairs; its texture is similar to that in *R. tawitawiensis.* Females have five pairs of mammae positioned as they are in *R. rattus.* The darkly pigmented populations of *R. tiomanicus* resemble the three specimens of *R. tawitawiensis,* but the paler samples contrast sharply with the Tawitawi animal. *Rattus tawitawiensis* also differs from *R. tiomanicus* in its shorter tail relative to length of head and body and only four pairs of mammae.

Except for its much smaller size, the skull of *R. tiomanicus* closely resembles that of *R. tawitawiensis* (table 3, fig. 17). The latter is chunkier in overall configuration, has a relatively wider incisive foramina, and has a deeper braincase with outwardly sloping rather than nearly vertical sides. Molar cusp patterns are similar in the two species (fig. 18). Other than size (table 3), there is really no obvious feature that will distinguish them.

We did not confine our investigation to comparing the Tawitawi sample with samples of *Rattus* from the Sunda Shelf and the Philippines only. We also examined groups of *Rattus* from east of the Shelf in Australia, New Guinea, and the Moluccas; those from Pulau Enggano, Christmas Island, and Sulawesi that are not part of the *R. palmarum* Group; and species from continental Southeast Asia north of the Isthmus of Kra (see Musser and Newcomb, 1983, p. 572, for a list of native *Rattus*). We did not neglect subfossil remains of Sundanese *Rattus* or the specimen of *R. trinilensis* from the Middle Pleistocene of Java (Musser, 1982b) in our comparisons. In the end, we could not detect close morphological resemblance between *R. tawitawiensis* and any of the species in these other groups of *Rattus.*

CONCLUSION

Morphological evidence gathered from skins and skulls supports the hypothesis that the three specimens of large-bodied, short-tailed, and dark-colored *Rattus* from Tawitawi Island represent a biological species distinguished from any other species of *Rattus* by the combination of characters presented in the diagnosis of *R. tawitawiensis.*

The evidence is also consistent with the hypothesis that *R. tawitawiensis* is more closely related to species of *Rattus* native to some islands beyond the Sunda Shelf than to any species living on the islands and peninsula of the Shelf. Of these insular populations, the Tawitawi rat bears a general morphological resemblance to *R. tiomanicus mara* from the Maratua Archipelago, but the tie involves coloration and habitation of oceanic islands; beyond these points, *R. tawitawiensis* is no more closely related to the Maratua population than to *R. tiomanicus* from mainland Borneo and other islands on the Sunda Shelf.

The Tawitawi rat shares oceanic insular endemism, large body size, short tail, and four pairs of mammae (with the pectoral pair absent) with *Rattus stoicus,* known only to inhabit the Andaman Islands west of the Sunda Shelf. However, no other features provide a tight link between the species.

Specimens from the Nicobar Islands, Pulau Simalur and nearby islands, the Mentawai Islands, and Pulau Enggano have a closer morphological similarity to *R. tawitawiensis* than does *R. stoicus.* The dark coloration and relatively wide incisive foramina of *R. lugens* from the Mentawai Islands are especially reminiscent of *R. tawitawiensis.* Even more similar to *R. tawitawiensis* is *R. hoffmanni* from Sulawesi. Although smaller in body size and usually paler in color, the Sulawesian rat shares pelage texture and pattern, number of mammae (which includes no pectoral pairs), extent of supraorbital ridging, and general cranial configuration with the Tawitawi animal.

Resolution of relationships beyond this general picture is not posssible at present. The sample of *Rattus tawitawiensis* is too small. Our evidence points to a closer morphological relationship between *R. tawitawiensis* and populations of *R. hoffmanni* from Sulawesi and most of the *R. palmarum* Group than to any other species of *Rattus.* Study of larger series from the Sulu Archipelago will be necessary to refine this outline.

What is significant to us is that the native Tawitawi *Rattus* seems part of a pattern. It and populations of *Rattus* from Sulawesi, Pulau Enggano, the Mentawai and Simalur islands, the Nicobars, and possibly the Andaman Islands appear to be more closely related to one another than to any species known to occur on the islands and peninsula of the Sunda Shelf or on continental South-

east Asia. Furthermore, aside from *R. hoffmanni,* there is no other native Sulawesian *Rattus* and no species from the Philippine Islands that has a morphology consistent with the pattern.

What we know of these insular *Rattus* suggests that each population has its own distinctive morphological features and that each may have been derived from populations that once occurred on the Sunda Shelf but are not present there now. The only species now native to the large and small islands of the Shelf, as well as the Malay Peninsula, that has a morphology similar to those of the rats on islands beyond margins of the Shelf is *Rattus tiomanicus.* Whether that species is more closely related to the insular oceanic species or to Asian *R. rattus* and its allies has yet to be determined. Except for the population of large-bodied, dark rats in the Maratua Archipelago, the morphological evidence supports the hypothesis that *R. tiomanicus* may be genetically isolated from populations of the dark and large-bodied rats from the Sulu Archipelago, Sulawesi, Pulau Enggano, the Mentawai and Simalur islands, the Nicobars, and the Andaman Islands. We know this is true on Pulau Enggano because both *R. tiomanicus* and *R. adustus* inhabit that island. We are analyzing the relationships between *R. tiomanicus* and samples of *Rattus* from the oceanic islands mentioned above and our results will be presented in another report.

The picture of possible relationships between *R. tawitawiensis* and species from other islands is a pattern we frequently encounter in the Malayan region. Populations on islands may be closely related to those on an adjacent mainland. Some insular populations, however, have no close relatives on the nearby mainland; instead they tie to populations on other islands. *Rattus tawitawiensis,* for example, appears to be more closely allied to populations of *Rattus* on islands situated beyond margins of the Sunda Shelf than to any other population of the genus, and it has no close relative on the adjacent Bornean mainland. A similar situation is seen in the distribution of *Rattus sikkimensis* on islands that are a part of the Sunda Shelf. The distribution of that species is shown in figure 19. It is primarily Indochinese, extending from Nepal east through southern China and south to Cambodia and Vietnam. *Rattus sikkimensis* also occurs on four islands in the South China Sea near and south of the Isthmus of Kra. These are numbered 46 to 49 on the map of figure 19 and and are, respectively, Koh Tau, Koh Pangan, Koh Samui, and Koh Kra. The population on Koh Samui was regarded as a distinctive species, *R. remotus,* by Marshall (1977). It wasn't until Musser (MS) plotted the geographic distribution of *R. sikkimensis* and studied the island samples that it became apparent that *remotus* was really an insular population of *R. sikkimensis.* That species has not been recorded from the nearby peninsula. Therefore, populations on the four islands are more closely related to each other than to any species of *Rattus* now known from the adjacent peninsular mainland.

A variant of the pattern is formed by the relationships between populations of rats on island groups next to one another. *Rattus mindorensis* is a good example. This species has always been regarded as part of the Philippine Island fauna. However, it is found nowhere in the Philippines outside of Mindoro and has no close relative on any other Philippine Island. In features of skin, skull, and teeth, it is closely similar to samples of *Rattus tiomanicus* of the Sunda Shelf, and Musser and Califia (1982, pp. 26–27) hypothesized that it represented an insular form of *R. tiomanicus.* The latter has representatives on the oceanic islands of Enggano, the Maratua Archipelago, and, according to Musser and Califia), "Mindoro, relative to the northeast segment of the Sunda 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."

We return to the Tawitawi rat. We know something of its distinctive morphology and we have formulated an hypothesis about its relationship to other species of *Rattus.* There is much we do not know. We are ignorant of its natural history and we do not know the extent of its geographic range. *Rattus tawitawiensis* may have a larger distribution than is indicated by our sample from one island. Tawitawi Island is the southwestern segment of a submerged ridge that extends northeast to form Jolo Island. The sea is less than 45

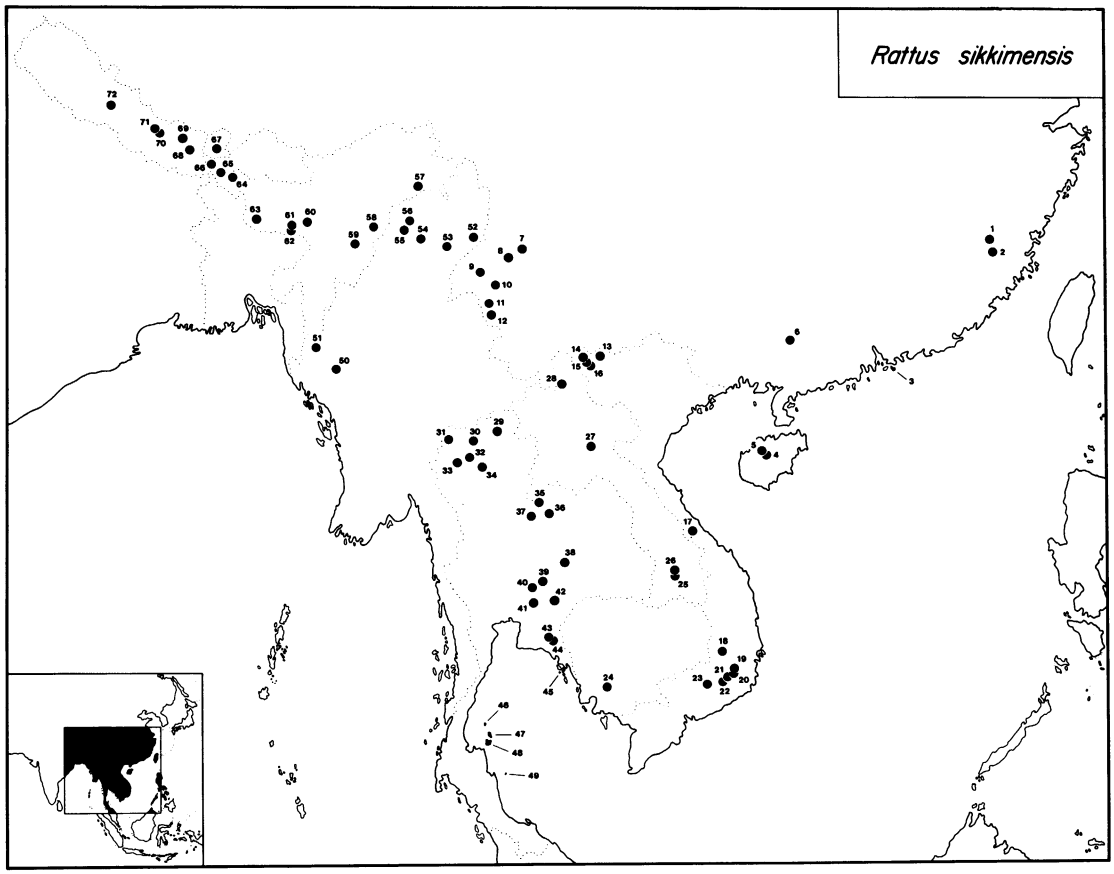

FIG. 19. Geographic distribution of *Rattus sikkimensis*. In addition to the mainland and the offshore islands of Hong Kong (locality 3), Hainan (localities 4 and 5), and Koh Klum (locality 45), the species also occurs on four islands in the South China sea opposite the Malay Peninsula: Koh Tau, Koh Pangan, Koh Samui, and Koh Kra (localities 46 to 49, respectively). See text for further discussion.

m deep over this ridge. During late Pleistocene, when sea level has been estimated to have dropped 100 to 120 m below present level (Chappell and Thom, 1977; Gascoyne, Benjamin, and Schwarcz, 1979; Bloom, 1983), Tawitawi and Jolo would have been part of the much larger island shown in figure 1. During middle Pleistocene, when sea level was probably 160 to 180 m lower than at present (Donn, Farrand, and Ewing, 1962; Gascoyne, Benjamin, and Schwarcz, 1979), the island would have been even larger. Assuming populations of *R. tawitawiensis* were present on Tawitawi during late or middle Pleistocene times, we would expect to find it now on other islands between Tawitawi and Jolo, and certainly on Jolo, provided that suitable habitat is present now and also existed when Jolo was part of the larger land area embracing Tawitawi.

How and when *Rattus tawitawiensis* got to Tawitawi Island are both mysteries. The large Philippine island of Mindanao to the east and Borneo to the west bracket the Tawitawi-Jolo group of islands. Jolo is separated from Mindanao by a deep channel and deep waters isolate Tawitawi from Borneo. During middle or late Pleistocene when sea levels were lower than at present, there is no evidence that the larger land area of Tawitawi-Jolo would have been connected to either Mindanao or Borneo. There is no way that these connections could have occurred without a fair dose of either tectonics or magic. The

TABLE 5
Mammals from the Sulu Archipelago

Genus and Species	Island					
	Sibutu	Simunul	Bongao	Sanga Sanga	Tawitawi	Jolo
Shrews						
Crocidura edwardsiana[a]	–	–	–	–	–	T
Bats						
Acerodon jubatus	X	–	X	X	X	–
Cynopterus brachyotis	X	X	X	X	X	–
Eonycteris spelaea	–	–	–	X	–	–
Ptenochirus jagori	–	–	X	X	–	–
Pteropus hypomelanus	T	–	–	–	–	–
Pteropus pumilus	–	–	X	X	X	–
Pteropus speciosus	X	–	X	X	–	–
Rousettus amplexicaudatus	X	X	X	X	X	–
Rhinolophus virgo	–	–	–	–	–	T
Rhinolophus sp.	X	–	–	–	X	–
Kerivoula pellucida	–	–	–	–	–	T
Miniopterus sp.	–	–	X	–	–	–
Myotis macrotarsus	–	–	–	–	T	–
Primates						
Nycticebus coucang	–	X	G	X	TB	–
Macaca fascicularis	–	–	–	–	–	T
Rodents						
Mus castaneus	–	–	–	X	–	–
Rattus exulans	–	–	X	–	–	T
Rattus rattus mindanensis	X	X	X	X	X	–
Rattus tawitawiensis[a]	–	–	–	–	X	–
Carnivores						
Paradoxurus hermaphroditus	–	–	T	X	–	–
Pigs						
Sus barbatus	–	–	–	–	Gr	–
Deer						
Cervus nippon	–	–	–	–	–	GG

[a] Endemic to the Sulu Archipelago.

Abbreviations: T = Taylor, 1934; TB = Timm and Birney, 1980; G = Groves, 1971; Gr = Groves, 1981; GG = Grubb and Groves, 1983; X = specimens in the Delaware Museum of Natural History.

presence of an endemic species of *Rattus* on Tawitawi likely represents the past dispersal of a founding population from either Mindanao or what is now Borneo, perhaps at a time in the past when sea levels were lower than they are now and land areas closer to one another.

One possible source of information regarding the origin of *R. tawitawiensis* is the zoogeography of the mammalian fauna of the Sulu Archipelago as a whole. Because no one has considered this topic previously, we will do so here briefly.

The available records of mammals from the Sulu Islands are summarized in table 5. Most of these records are from specimens in the Delaware Museum of Natural History. Thirteen of the 23 species are bats. Four of the bats are Philippine endemics; the others are widespread in Southeast Asia, including the Philippines. Of the 10 non-volant species, three are introduced commensals (*Rattus ex-*

ulans, R. rattus mindanensis, and *Mus castaneus*), four are widespread in Southeast Asia (*Macaca fascicularis, Paradoxurus hermaphroditus, Sus barbatus,* and *Cervus nippon*), two are endemic to the Sulus (*Crocidura edwardsiana* and *Rattus tawitawiensis*), and one is otherwise found only on the Sunda Shelf (*Nycticebus coucang*). The depauperate nature of the non-volant fauna is similar to that of oceanic islands in the Philippines (Camiguin Island, for example; Heaney, 1984), except for the presence of the two endemic species. None of the species characteristic of the southern Philippines is known to occur in the Sulus, even though such species (for example, *Cynocephalus volans, Exilisciurus concinnus,* and the *Sundasciurus philippinensis* group) occur on Basilan, and *C. volans* is known from the small islands of the Tonkil Group between Basilan and Jolo, at the edge of the 120 m bathymetric line around Mindanao (Taylor, 1934). *Nycticebus coucang* is the only member of the Bornean fauna that occurs on the Sulus, and it is sufficiently popular as a pet that it may have been introduced.

The bat fauna is similar to that found on many small islands in the southern Philippines, both oceanic and Mindanao landbridge in origin. There is no evidence of a close relationship to Borneo.

We believe that these data (presence of two endemic species of non-volant mammals, absence of characteristic members of the Bornean or Mindanao faunas) are consistent with the geological data in indicating that there were no continuous land-bridge connections to either Borneo or Mindanao during the late Pleistocene. Thus, dispersal of the ancestor of *R. tawitawiensis* over a narrow salt-water channel is indicated.

We look toward Borneo and the Sunda Shelf for that dispersal source. We know of no species of *Rattus* now living on Mindanao that is closely related to *R. tawitawiensis.* On the other hand, of several species of *Rattus* native to the Sunda Shelf (to the west of Tawitawi Island), *R. tiomanicus* is similar to *R. tawitawiensis* in many aspects of its morphology. We have also suggested that *R. tawitawiensis* is closely related to species of *Rattus* inhabiting oceanic islands that rim the margin of the Shelf; likely the Shelf was the source for these insular populations. The occurrence of *Rattus* on the Shelf is not a Recent event because a species of that genus, or a related genus with similar dental and mandibular morphology, was present during middle Pleistocene in what is now the Trinil region of Java (Musser, 1982b). That species, *R. trinilensis,* is not part of the fauna now living in the Sunda region. We wonder what other species of *Rattus* may have been on the Sunda Shelf in the past when Sundaland consisted of islands and peninsula during times of high sea levels and a large continental expanse above water at times of lower sea levels. Perhaps an ancestral species occurred there that is absent from the Recent fauna and now represented by *R. stoicus* in the Andaman Islands, *R. palmarum* and *R. burrus* in the Nicobars, *R. simalurensis* in the Simalur Islands, *R. lugens* in the Mentawais, *R. adustus* on Pulau Enggano, *R. hoffmanni* on Sulawesi, and *R. tawitawiensis* in the Sulu Archipelago.

We close with an alternative notion that should be tested with data from a larger series of *R. tawitawiensis* than is now available. Judged by our three specimens of the Sulu rat, the species has close morphological similarity with *R. hoffmanni* from Sulawesi. Could that large island have been the source of the Tawitawi animal, or does the similarity between the two species represent derivation from an ancestral population that was present on what is now Borneo and dispersal to the Sulu Archipelago and Sulawesi?

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