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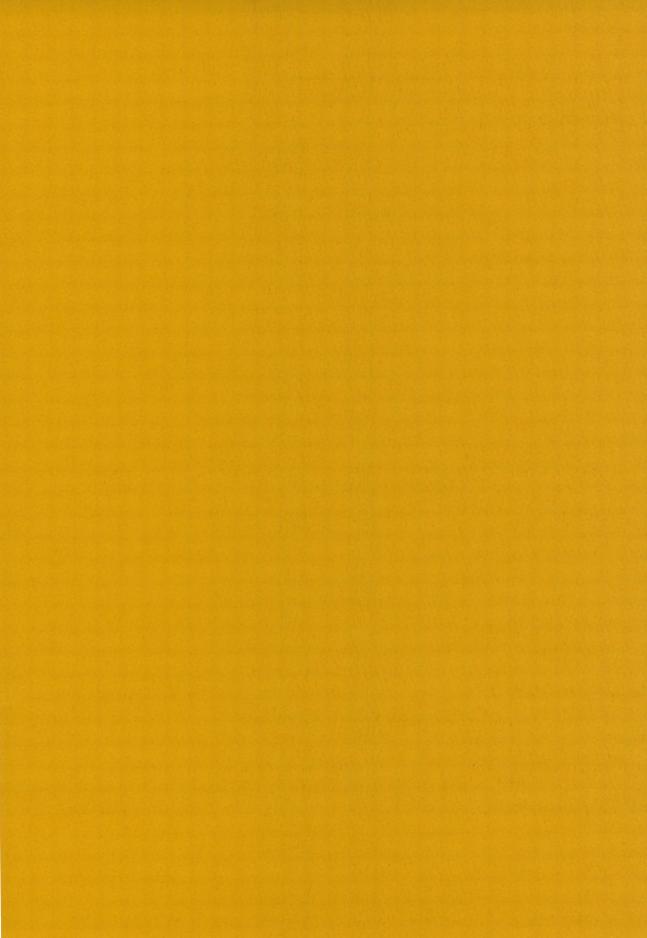
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GUY G. MUSSER1

ABSTRACT

I record here that the name Epimys benguetensis is based on a composite holotype: the skin is an example of Rattus rattus mindanensis and the skull is from R. nitidus. I also discuss a dichotomy between endemic and commensal murid rodents on the Philippine Islands and Celebes. Each area has its unique assemblage of endemic species of rats and mice; these are mostly restricted to primary forest. Each area shares a commensal fauna composed of Rattus rattus, R. exulans, R. argentiventer, R. norvegicus, R. nitidus, and Mus musculus. These animals live in habitats made and maintained by humans. Such a faunal dichotomy occurs wherever there is an endemic fauna and wherever humans have settled throughout the Indonesian Archipelago east of Wallace's Line.

INTRODUCTION

During May 1976, I was camped in tall forest by a clear mountain stream in the highlands of Central Celebes. It was my last camp in Celebes where I had spent most of three years living in undisturbed primary forest from the warm, humid coastal lowlands to the cool mountains. During that time I found and learned something about nearly every endemic species of murid rodent that was known to occur on Celebes as well as several rats and mice that had never been taken there before. All these animals live in primary forest. Six other kinds of rats and mice live on Celebes: Rattus rattus, R. exulans, R. argentiventer, R. nitidus, R. norvegicus and Mus musculus, but I never encountered these in the tall forest.

My experiences in the forests of Celebes gave reality to a picture that I had formed while I was working in museums, sorting specimens and distributional data, and learning about the murid faunas of the Indo-Malayan and Indo-Australian regions. The data had resolved into a picture of two groups of rats and mice on Celebes: one that lived mostly in primary forest and was unknown outside of Celebes and its offshore islands, the other a group that appeared to be closely tied to human habitats and composed of species that occurred from the Asian mainland to New Guinea.

I found a report by Barbehenn, Sumangil, and Libay (1972-1973) on my desk when I returned to the American Museum of Natural History in

¹Archbold Curator, Department of Mammalogy, the American Museum of Natural History.

September 1976. Their paper on the rodents of the Philippine croplands reminded me of the dual nature of the rat and mouse fauna on Celebes and the same picture was brought into focus for the Philippine Islands. My own data, accumulated over the years, dovetailed nicely with that presented by Barbehenn, Sumangil, and Libay, and pointed to two distinct groups on the Philippines, one endemic and one associated with human habitats. I was also reminded of the problems I had encountered earlier as I sorted specimens and tried to define real species by using available data, and then working through the morass of scientific names in the literature, matching them with species. Many of the names that had been proposed for specimens from Celebes, for example, had been associated only with the holotype and little was known about the species it was supposed to represent. One name was based on a type-series that, in fact, consisted of several species. Other names were tied to holotypes that turned out to be composites and not actual biological entities. The real diversity and nature of the rats and mice from the Philippines were also hidden behind a screen of names and incomplete information.

Barbehenn, Sumangil, and Libay (1972-1973) mentioned one of these names, writing that its status was uncertain. The name is Rattus benguetensis and it was originally proposed as Epimys benguetensis by Hollister in 1913 on the basis of a specimen obtained from northern Luzon in the Philippines. For years the name was thought to represent a valid species of Rattus (Taylor, 1934; Ellerman, 1941) but known only by the holotype. Then, in 1952, Sanborn reported on the results of his study of Philippine mammals obtained by the Philippine Zoological Expedition of 1946-1947, sponsored by the Field Museum of Natural History, Chicago. One large series of Rattus gathered by the expedition from Mount Data in northern Luzon was identified by Sanborn as Rattus benguetensis (1952, p. 121). That was the first-and except for Rabor's (1955) published field observations for the same specimens-the only time someone associated the name with specimens other than the holotype. Recently, Barbehenn, Sumangil, and Libay (1972-1973) pointed out that most of Sanborn's specimens of R. benguetensis from Mount Data had been identified by David H. Johnson as Rattus nitidus. I also examined part of the lot of R. benguetensis from Mount Data and found that sample to consist of both R. nitidus and R. rattus mindanensis. So Sanborn brought together specimens of two species under the name R. benguetensis, and that prompts the question, just what is R. benguetensis?

During one of several visits to the National Museum of Natural History, Smithsonian Institution (USNM), I had studied specimens of Rattus from the Philippines and had identified the holotype of *Epimys benguetensis*. It is one of many names associated with the Philippine rodent fauna and I needed to know if the name applied to either Rattus nitidus or R. rattus, species that are closely associated with human habitats and not part of the endemic murid fauna of the Philippines, or if it was actually one of the many endemic rats. Determining the validity of the name is part of separating out the rats and mice likely brought to the Philippine Islands through human agency from those endemic and presumably having evolved in the Philippines.

The identification and allocation of Epimys benguetensis is one of the subjects of the present paper. I point to the resolution of that name and to the published identifications of scientific names applied to specimens from Celebes (see Musser, 1973, and other references listed there) as examples of the basic taxonomic problems that are involved in working with the large rodent fauna from the Philippines and the Indo-Australian area. Now, based on better taxonomy than was available before, the murid faunas of the Philippine Islands, Celebes, and other areas east of Borneo are beginning to form several zoogeographic patterns. One pattern is a dichotomy between the endemic and commensal rat and mouse faunas on the Philippines and Celebes. The pattern I sketch here is based on my research and that of recently published work by others. I have omitted details—they will be eventually published elsewhere-and give only a general pat-

My work in museums and tropical forests was financed by the late Mr. Richard Archbold of the Archbold Expeditions, the American Museum of Natural History; the Council of the Scientific Staff of that institution, and the Celebes Fund of the Museum. I appreciate their unselfish support. The Lembaga Ilmu Pengetahuan Indonesia (Indonesian Institute of Sciences) and Dr. Sampumo Kadarsan, Director of the Museum Zoologicum Bogoriense sponsored my work in Celebes. I am grateful for their assistance and cooperation. My colleagues in the Department of Mammalogy and those elsewhere who concern themselves with the nature of rats and mice have read the manuscript. As is usual with these intelligent persons, their thoughtful questions, criticisms, and suggestions have improved the report.

IDENTIFICATION AND ALLOCATION OF EPIMYS BENGUETENSIS

In 1913, Hollister reviewed the Philippine land mammals in the collections of the United States National Museum (now the National Museum of Natural History, Smithsonian Institution). Among the specimens of rats important to my inquiry were small series from two localities in Benguet Province, Luzon, that were obtained by Dr. E. A. Mearns in 1907. Eight specimens are from Haights-in-the-oaks and Hollister (1913, p. 323) incorrectly identified these as Epimys datae. Epimys was the generic name then applied to species that are now in the genus Rattus. Another specimen, also obtained by Mearns in 1907, but from Camp John Hay, south of Haights-in-the-oaks, was the basis for Hollister's description of Epimys benguetensis (Hollister, 1913, p. 323).

I was able to locate only seven of the eight specimens identified by Hollister as *E. datae*. All were collected in July and August of 1907. Two (USNM 145798 and 145809) are young adults that had just completed their molts from juvenal to adult pelages. Five (USNM 145799, 145801, 145802, 145803, and 145808) are juveniles. In his report Hollister listed measurements for an eighth specimen, USNM 145797, but in May 1936, it had been sent to the Bureau of Science in Manilla and was no longer in the collection of the National Museum of Natural History.

None of these specimens is true *datae*, a conclusion made earlier by Sanborn (1952). That scientific name refers to a taxon described by Meyer (1898-1899) and now considered to be a valid species in the genus *Apomys*, a group found

only in the Philippines. Apomys was proposed by Mearns in 1905 and regarded as a distinct genus until 1949 when Ellerman reduced it to a subgenus of Rattus. Then Johnson (1962) and more recently Misonne (1969) reaffirmed the distinctness of Apomys and pointed out that the genus is unlike Rattus in dental morphology and more like the genera Melomys and Uromys. I have also concluded from my own studies that Apomys should be separated from Rattus but am uncertain of its affinities. The species of Apomys live in forests. They are small animals and apparently terrestrial. All have thick and soft pelage. Their skulls and teeth are distinctive. In each species the interorbital region is smooth and the braincase smooth and globular, without the supraorbital ridges that extend back along the margins of the braincase, a characteristic of most species of Rattus. The bony palatal bridge is long and wide, the incisive foramina are short and wide. Occlusal surfaces of the first and second upper molars are simple, consisting of chevron-shaped laminae. The upper third molar is tiny relative to the size of the first and second upper molars.

Sanborn regarded Hollister's series of datae to be members of Rattus benguetensis, considered them all immature, and remarked that the type of benguetensis was the youngest of the series. He applied the name to 71 specimens taken on Mount Data, Luzon, between 5300 and 6500 feet: "The specimens collected on Mount Data by the Philippine Zoological Expedition are all adult. Direct comparison of this material, unsatisfactory as it is, leads to the conclusion that all these specimens must be referred to benguetensis. This cannot be fully settled until adult topotypes of benguetensis are available." The seven specimens I examined from Haights-in-theoaks that were identified as E. datae by Hollister are simply juveniles and young adults of Rattus nitidus. Of the 71 specimens from Mount Data in collections of the Field Museum of Natural History (FMNH), I have studied 47, not the entire series but enough to know what species are involved. The lot consists of samples of two species, adults and juveniles, as follows.

Rattus nitidus: FMNH 62357, 62363, 62371, 62381, 62383, 62392, 62397, 62398, 62405, 62406, 62408, 62413, 62415, 62431, 62435, 62440, 62447, 62450, 62452, 62454,

62455, 62458, 62480, 62491, 62493, 62680.

Rattus rattus mindanensis: FMNH 62360, 62373, 62377, 62391, 62422, 62430, 62471, 62475, 62506, 62546, 62671, 62672, 62673, 62675, 62677, 62678, 62682, 62683, 62684, 62686, 62687.

These two kinds of rats resemble each other in morphology of skins and skulls and both have been taken in similar habitats. Rattus rattus mindanensis apparently occurs on every major island of the Philippines except Balabac, Busuanga, and probably Palawan, Culion, and Cuyo.1 Most specimens I examined were collected in gardens and fields of rice and the species is common in those habitats (Rabor, 1955; Barbehenn, Sumangil, and Libay, 1972-1973). It also lives in secondary growth and scrub near croplands. The taxon was named and described by Mearns in 1905, has always been considered a prominent part of the rodent fauna of the Philippines and has often been the focus of field studies because of its close association with humans and its depredations on crops.

Rattus nitidus was named and described by Hodgson in 1845 and until recently was never associated with the rodent fauna of the Philippines. Its primary geographic range is in southeastern Asia. I have examined specimens from northern India (Kumaon, Assam, and Sikkim), Burma, northern Thailand, Laos, Vietnam, and China (Fukien, Hunan, Szechwan, Yunnan, Kwangtung, Kansu, and Hainan). East of the Asian mainland the geographic distribution of R. nitidus is spotty. My records of it are from Luzon, Central Celebes, the Palau Islands (Peleliu and Babelthaup, originally identified by David H. Johnson [Barbehenn, 1974]), Ceram, and Irian Java (western New Guinea). Specimens from some of these areas, Luzon and Celebes, for example, have been in museum collections since the early 1900s, but were hidden under other scientific names and have been sorted out and correctly identified as R. nitidus only within the last 20 years.

¹Sanborn (1952) recorded specimens of *R. rattus mindanensis* from Palawan, Culion, and Cuyo. I have not examined these but I suspect they are *R. rattus diardii*. The only specimens of *R. rattus* I have seen from Palawan (in the American Museum of Natural History) are typical diardii.

On the Asian mainland Rattus nitidus inhabits highlands. Allen (1940) suggested that in China it lived both in wild country and in houses. In northern Thailand the rat lives in houses in mountain villages (Marshall, 1972), and in Vietnam it was taken in or near dwellings and bunkers built in forest clearings at elevations of 300 to 500 meters (Van Peenen, Ryan, and Light, 1969). East of the mainland of Asia the species is found only in the mountains of Luzon, Central Celebes, and Irian Jaya; it occurs in both the coastal lowlands and mountains of Ceram, and has been taken at about 100 feet elevation on the Palau Islands (which do not get much higher). From the Philippines to New Guinea the rat lives in close association with humans, either in village houses or gardens, and has not been found in primary forest.

Rattus nitidus and R. rattus mindanensis are similar in external morphology but each can be distinguished by certain features of skins and skulls. Both have been described in the literature. Taylor (1934) and Schwarz and Schwarz (1967) enumerated characteristics of R. rattus mindanensis, and Barbehenn, Sumangil, and Libay (1972-1973) provided a good account. General descriptions of R. nitidus can be found in Ellerman (1961), Schwarz and Schwarz (1967) and Barbehenn, Sumangil, and Libay (1972-1973); but Allen (1940) has the best description of the species. Adults of both kinds of rats are about the same size. The tail of R. nitidus is about as long as the head and body (see measurements in Allen, 1940, p. 1001) and is brown all over, but the tail of R. rattus mindanensis is generally longer than the head and body and very dark brown or black. Pelage over the upper parts of R. nitidus is darker, shorter, and softer than in examples of R. rattus mindanensis. My impression is of dark, subdued tones and slightly woolly texture when contrasted to the bright brown and ochraceous tones and sleek texture that are characteristic of adult R. rattus mindanensis. Underparts of R. nitidus are consistently gray; those of R. rattus mindanensis vary from creamy white, where they are sharply demarcated from the upper parts, to dark gray, and all tones are often suffused with ochraceous or buff washes. A very conspicuous feature of R. nitidus is the upper surfaces of its front and hind feet, which are

pearly white; those of *R. rattus mindanensis* are buff to brown and usually have a darker strip down the middle of each. Female *R. nitidus* have 12 mammae, those of *R. rattus mindanensis* have 10. All these features will also distinguish juvenile and very young adults of each species. And because young *R. nitidus* have shorter, darker, and more woolly pelage than adults the contrast with the longer, brighter, and sleek pelage of young *R. rattus mindanensis* is even greater than between adults.

Skulls of the two species are similar in size and configuration, but *R. nitidus* usually has longer nasals and smaller bullae. The two differ most conspicuously and consistently in configuration of the first upper molars. The anterior labial cusp is minute or absent in *R. nitidus*, so there appear to be only two large cusps in the front row instead of three. This cusp is large and conspicuous in *R. rattus mindanensis* and the front row is composed of three prominent cusps. With this single trait I can distinguish all specimens of all ages of the two species.

If two species have been identified as R. benguetensis, what then is the holotype? The specimen on which the name is based, USNM 145790, consists of a dry study skin and a skull. Information on the label attached to the skin indicates it was taken from Camp John Hay, Baguio, Benguet Province, Luzon, elevation 5000 feet, on May 1, 1907, by Dr. E. A. Mearns. In his original description Hollister thought benguetensis to be closely related to "Epimys datae" except that the animal was smaller and paler with ochraceous buff underparts and a skull closely similar to those of the series he had incorrectly identified as datae. He remarked that (1913, p. 121) "The type of this new species has been compared with a series of eight skins and skulls of Epimys datae collected by Doctor Mearns at Haights-in-theoaks, northern Benguet Province. From color characters the forms seem very different, but the skulls indicate a close relationship."

After I examined the holotype of Epimys benguetensis I realized why nobody has been able to identify it with any certainty and why the name has been applied to two species of Rattus. The skin is that of a young R. rattus mindanensis and the skull is from a specimen of R. nitidus. The skin is from an animal that had nearly completed

the molt from juvenal to adult pelage and that pelage covers all but the back and rump which is still in worn juvenal fur. The upper parts are brown suffused with ochraceous-buff and the underparts are buffy-gray with a conspicuous ochraceous wash. The tops of the feet are brown and the tail is dark brown. Hollister indicated the animal to be female, but I could not sex the skin and there is no notation of sex on the label. Nor are there external measurements recorded on the skin label. My measurement of length of hind foot, the only external dimension that I could accurately measure, is 33 mm. The coloration of the skin is typical of R. rattus mindanensis and unlike R. nitidus or any other rat of comparable body size known to live in the Philippines.

The skull is from a very young adult Rattus nitidus. Some measurements (in millimeters) are: greatest length, 35.4; zygomatic breadth, 15.9; interorbital breadth, 5.3; length of nasals, 13.4; length of rostrum, 10.4; breadth of rostrum, 6.2; breadth of braincase, 15.0; length of diastema, 9.7; length of incisive foramina, 7.0; postpalatal length, 11.9; palatal length, 18.7; alveolar length of upper toothrow, 6.1; length of bulla, 5.8; breadth of bulla, 5.2. The bullae are small relative to size of the braincase and each first upper molar does not have an anterior labial cusp. Hollister was correct when he wrote that the skull "does not differ appreciably from that of Epimys datae," and in fact, the holotype is nearly identical with USNM 145809, one of the specimens of R. nitidus from Haights-in-the-oaks, which Hollister thought was datae.

Somewhere, either in the field or in the museum, the skull of a Rattus nitidus was incorrectly associated with the skin of a R. rattus mindanensis. I was not able to locate a skin of R. nitidus from the Mearns series that was not correctly matched with a skull so I cannot explain how the skull of the holotype came to be associated with a skin of R. rattus mindanensis. I can say something about the skin of the holotype. It was one of five specimens collected by Mearns from Camp John Hay. Of the other four, three are large adults and one is a juvenile R. rattus mindanensis. The adults, USNM 145788 and 145789, were caught on April 29, 1907, and USNM 145793 on May 6 of the same year. The juvenile, USNM 145810, was caught in July

1907. Three of the specimens consist of skins associated with the right skulls. However, the skin of USNM 145789 is matched with two skulls. One of these is from a large adult rat, matches the skin in age, and is an example of R. rattus mindanensis. The other skull is from a young R. rattus mindanensis. Its size, configuration, and wear of teeth indicate a rat of about the same age as the skin of the holotype of benguetensis. Possibly that is the skull that really belongs with the skin of the holotype.

When Mearns was collecting mammals in the Philippines he identified each specimen by tying a small rectangular paper tag to the hind leg. On the tag was Mearns's collecting number. Any information about the specimen was recorded in his field catalogue under that number. When the specimens reached the museum in Washington, D. C., the data from the field catalogue was typed on a regular museum skin label and tied to the hind foot of each skin. In some cases the skull was not properly labeled in the field and later could not be matched with the right skin. Mearns's field catalogues are preserved in the Division of Mammals of the National Museum of Natural History and in the catalogue where he recorded the specimens from Camp John Hay, Baguio, the type-locality of benguetensis, he wrote after the last entry (p. 80): "Ceriaco put foot numbers on several skulls, from Baguio, instead of copying the numbers of tag attached to foot. These can be straightened out when the skins and skulls are brought together." Not all of them were later straightened out.

I designate only the skin of USNM 145790 as the holotype of *Epimys benguetensis*. It bears Mearns's original little paper tag with his field number and a museum label on which data and place of capture are typed; the information matches that recorded in Mearns's field catalogue for that number. The name *Epimys benguetensis* Hollister 1913, becomes a subjective synonym of *Mus mindanensis* Mearns, 1905, a taxon now regarded as a subspecies of *Rattus rattus*. ¹

¹Of the many scientific names that have been applied to samples of *Rattus* from the Philippines, I consider the following five to be synonyms of *R. rattus mindanensis: Mus zamboangae* Mearns (1905, p. 443), holotype USNM 125279, young adult male from Zamboanga, western Mindanao; *Mus kelleri* Mearns (1905, p. 444),

DISCUSSION

We know very little about rats and mice of the Philippines. The species-limits of many have yet to be defined, the natural histories of most are unknown, and their zoogeographic relationships with faunas outside of the Philippines are still unresolved. Reports on taxonomy and zoogeography of the fauna are few and old, and except for the fine paper by Rabor (1955), little has been published about their life histories. So I was pleased to read the recent publication by Barbehenn, Sumangil, and Libay (1972-1973) which adds good information to our knowledge about rats and mice of the Philippines. And, because they focus on species associated with humans, their paper provides a lead to discussing the basic dichotomy of the rat and mouse fauna from there; namely, those species generally linked with humans-often called commensals-on the one hand, and the endemic fauna, usually confined to primary forests, on the other.

Barbehenn, Sumangil, and Libay (1972-1973) reported on 14 species of rats and mice that have been found in croplands of the Philippines. Their account of each species includes comments about taxonomy, how to identify the animal, its distribution in the Philippines, habitats, and economic relationships. Six of the species are part of the endemic fauna and usually inhabit primary forest but are occasionally caught in disturbed forest and scrub near abandoned clearings, gardens, and villages. Of these, Rattus mülleri and R. panglima occur on Palawan, Balabac, Busuanga, and Culion islands and are part of the fauna associated with the Greater Sunda Islands rather than with the main island backbone of the Philippines. Rattus everetti, R. latidens, R. adustus, and Chrotomys

holotype USNM 125278, adult female from Davao, southern Mindanao; Epimys coloratus Hollister (1913, p. 317), holotype USNM 144571, adult female from Basilan Island; Epimys robiginosus Hollister (1913, p. 318), holotype USNM 239246, adult male from Cagayan Island; and Rattus mindanensis tablasi Taylor (1934, p. 439), holotype AMNH 242134 (originally no. 652 in Taylor's collection, but now in the collection of the American Museum of Natural History), young adult from Tablas Island. Schwarz and Schwarz (1967) placed kelleri in synonymy under R. rattus diardii and the other four names as synonyms of mindanensis.

whiteheadi are members of the large murid rodent fauna known from the main group of Philippine Islands and do not occur elsewhere. These animals live in the forest; they are infrequently encountered in habitats associated with or maintained by humans, and none are known or considered to be economically important in their effects on agricultural crops.

The other eight species discussed by Barbehenn, Sumangil, and Libay are found mainly in habitats maintained or altered by humans-cities, towns, villages, gardens, croplands, plantations, and scrub. Rattus rattus, the European house rat, is confined to port cities and Mus musculus castaneus, the house mouse, lives in houses and other buildings. Rattus tiomanicus, the Malaysian wood rat, is known from Palawan and Busuanga (reported by Sanborn, 1952, as R. rattus jalorensis) where it lives in gardens, scrub, and possibly secondary forest. It seems to be of minor economic importance there and is, in fact, a species that is part of the rodent fauna of the Malay Peninsula (south of the Isthmus of Kra), the Greater Sunda Islands, and many smaller islands on the Sunda Shelf and just off of it (Musser, 1972). Rattus argentiventer, the ricefield rat, is common on Mindoro and Mindanao; R. nitidus, the Himalayan rat, has been taken only in the mountains of northern Luzon; but R. norvegicus, the Norway rat, R. exulans, the Polynesian rat, and R. rattus mindanensis, the Philippine house rat, are spread, in varying degrees, throughout the Philippines. All five species are significant competitors with humans for agricultural products.

The assemblage of rats and mice that is composed of Rattus rattus, R. argentiventer, R. exulans, R. nitidus, R. norvegicus, and Mus musculus (fig. 2) is a significant one, not only to inhabitants of towns and villages, farmers, agricultural scientists, and ecologists but also to students of rodent systematics and zoogeography. This group of species is not peculiar to the Philippines but occurs with humans throughout the eastern tropics. On the main islands of the Philippines and in the Indonesian Archipelago east of Wallace's Line these six species, occurring in the same or different combinations, are ecologically and morphologically distinct from the endemic fauna of murid rodents. Wherever they have been

found they have usually been found with humans. All six species also range westward onto the Asian mainland. In contrast, the endemic species generally inhabit primary forest or natural secondary growth and scrub, are peculiar to an island or group of islands, and are not found to the west of Wallace's Line or west of the main island backbone of the Philippines.

The rats and mice of Celebes are a good example of this dichotomy. There, R. rattus palelae lives in cities, towns, villages, and gardens throughout Celebes from sea level up to about 2000 feet elevation (fig. 4). Rattus rattus rattus has been found only in Ujungpandang (Makassar), a large port city in southwestern Celebes, and I would expect to find it in Menado, another large port in northern Celebes. Rattus nitidus has been collected only in the mountains of Central Celebes in the Napu and Besoa regions where it lives in houses and gardens. Rattus exulans is found throughout Celebes in villages, gardens, ricefields, plantations, scrub, secondary forest, and slightly altered primary forest near habitats maintained by humans. Rattus norvegicus seems to be restricted to large port cities like Ujungpandang, Gorontalo, and Menado. Rattus argentiventer lives in fields of rice and scrub near lowland villages and has been collected in southwestern, central, and northern parts of the island. Mus musculus castaneus has been collected only in houses and other buildings. All these species are found to the west on islands of the Sunda Shelf and the Asian mainland, and they are morphologically closely similar to samples of populations from those areas. Opposed to these seven species is a group of more than 30 described and several undescribed endemic rats and mice in the genera Eropeplus, Lenomys, Haeromys (fig. 1), Echiothrix, Crunomys, Melasmothrix, Tateomys, and Rattus that occur only on Celebes and its offshore islands (Laurie and Hill, 1954; Musser, 1973). Most of these animals have been caught only in primary forests (fig. 3). A few can exist in scrub, coffee groves, gardens, and croplands, but only if those habitats are next to forest.

Over the past few years I have been trying to answer questions about taxonomies and natural histories of the rats and mice that live on Celebes. Early in my inquiries I realized that al-





FIG. 1. Lenomys meyeri (top) and Haeromys minahassae (bottom). Two adult representatives of the endemic rats and mice of Central Celebes. Both are from primary evergreen forest. Photographed by Margareta Becker.



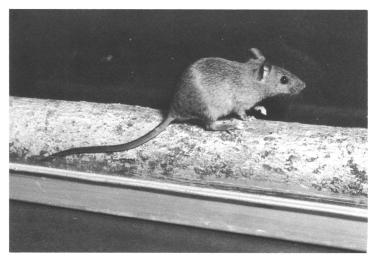


FIG. 2. Rattus nitidus (top) and Mus musculus castaneus (bottom). Both adults were caught in Thailand. These same species are part of the commensal rat and mouse faunas of the Philippine Islands and Celebes. Photographed by Boonsong Lekagul.

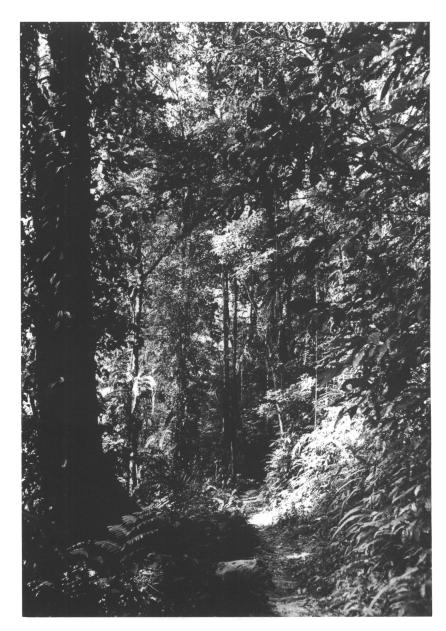


FIG. 3. Primary evergreen forest on hillside at 2600 feet near Sadaunta, Central Celebes. Photographed by Margareta Becker.

though Celebes is geographically isolated—east of Borneo and west of the Spice Islands—I could not answer questions about its rodent fauna without studying that fauna within the context of the great adaptive radiation of murid rodents

throughout Asia, from the mainland through the Philippines and the Indonesian Archipelago to Australia. I began my studies by asking two simple questions. What are the real species on Celebes? What is the correct scientific name to



FIG. 4. Sadaunta, 1950 feet, Central Celebes. *Mus musculus castaneus* lives inside the buildings. *Rattus exulans* lives inside the buildings and outside in nearby gardens, scrub and secondary forest. *Rattus rattus palelae* was caught beneath the dwellings. Photographed by Margareta Becker.

associate with each? To answer the first I went to primary source material: specimens and the distributional data associated with them. Though there is a large literature dealing with murid rodents of Celebes, and though most of that literature is taxonomic, the nature of the murid fauna has been obscured because of the many scientific names that have been applied to specimens and small samples of mice and rats from Celebes. When I began work, these scientific names carried very little information. Specimens were the only reliable sources from which I could obtain data to estimate limits of species. I went through specimens from mainland Asia to Australia and through enough holotypes so that I can now provide answers to the second question and associate names with what appear to be real species. Eventually I traveled to tropical forests where I tested some of the conclusions formed in museums. By this simple sorting I learned about the dual nature of the murid fauna of Celebes—those kinds of rats and mice that are tied to human habitats and those that are endemic—and with further sorting I found a similar pattern throughout the Indonesian Archipelago and in the Philippines.

The Philippine Islands have really been a part of my studies on the fauna of Celebes. The islands east of Palawan and the Calamian Group are occupied by commensals, and by a native group of murid rodents that occurs nowhere else. There are species in the genera Apomys, Carpomys, Batomys, Phloemys, Crateromys, Chrotomys, Celaenomys, Rhynchomys, Cru-

nomys, Limnomys, and Tarsomys, as well as several kinds of endemic Rattus. Two groups of rats, Rattus and Crunomys, and possibly a third, Limnomys, are also found in Celebes, but the species there are different from those in the Philippines. No endemic species are shared by the Philippines and Celebes. The species of rats and mice that are shared by these two areas also occur elsewhere and are those closely associated with humans.

At this point I provide a list of the commensal species of rats and mice from Celebes and the Philippine Islands (excluding Balabac, Palawan, and the Calamian and Cuyo groups). I also include scientific names that I think are synonyms of each of the speces. The list is instructive. It shows how many times different names have been proposed for the same species, such as those entered under Rattus rattus and R. exulans, and you can get a sense of the original overlay of noise generated by these names that concealed identities of the commensal faunas and the endemic-commensal dichotomy I discuss in the present paper. Many of the names I list here as synonyms were thought by their proposers to represent species peculiar to either Celebes or the Philippines and others were originally proposed as subspecies of a known endemic species. These synonyms are only part of the many scientific names that have been applied to rats and mice from Celebes and the Philippines.

CELEBES

Rattus rattus palelae Miller and Hollister, 1921 Rattus lalolis Tate and Archbold, 1935 Rattus rattus makassarius Sody, 1941 Rattus rattus argyraceus Sody, 1941 Rattus rattus barussanoides Sody, 1941 Rattus rattus sapoensis Sody, 1941

Rattus rattus pelengensis Sody, 1941

Rattus rattus rattus (Linnaeus), 1758

Rattus argentiventer (Robinson and Kloss), 1916 Rattus pesticulus Thomas, 1921

Rattus nitidus (Hodgson), 1845 Rattus hoffmanni subditivus Miller and Hollister, 1921

Rattus norvegicus (Berkenhout), 1769 Mus decumanus var. major Hoffmann, 1887 Epimys norvegicus hoffmanni Trouessart, 1904

Mus norvegicus praestans Trouessart, 1904

Rattus exulans (Peale), 1848

Mus aemuli Thomas, 1896

Rattus raveni Miller and Hollister, 1921

Rattus raveni eurous Miller and Hollister, 1921

Rattus concolor malengiensis Sody, 1941

Mus musculus castaneus Waterhouse, 1843 Mus musculus fredericae Sody, 1933

PHILIPPINE ISLANDS

Rattus rattus mindanensis (Mearns), 1905
Mus zamboangae Mearns, 1905
Mus kelleri Mearns, 1905
Epimys coloratus Hollister, 1913
Epimys robiginosus Hollister, 1913
Epimys benguetensis Hollister, 1913
Rattus mindanensis tablasi Taylor, 1934

Rattus rattus rattus (Linnaeus), 1758

Rattus argentiventer (Robinson and Kloss), 1916 Rattus rattus umbriventer Kellogg, 1945

Rattus nitidus (Hodgson), 1845

Rattus norvegicus (Berkenhout), 1769 Mus magnirostris Mearns, 1905

Rattus exulans (Peale), 1848

Mus ephippium negrinus Thomas, 1898

Mus todayensis Mearns, 1905

Mus vulcani Mearns, 1905

Mus vulcani apicis Mearns, 1905

Mus pantarensis Mearns, 1905

Mus luteiventris Allen, 1910

Epimys calcis Hollister, 1911

Epimys querceti Hollister, 1911

Epimys mayonicus Hollister, 1913

Epimys leucophaetus Hollister, 1913

Epimys vigoratus Hollister, 1913

Epimys basilanus Hollister, 1913

Epimys ornatulus Hollister, 1913

Mus musculus castaneus Waterhouse, 1843 Mus commissarius Mearns, 1905

The association of Rattus rattus, R. argentiventer, R. exulans, R. nitidus, R. norvegicus, and Mus musculus with habitats that were originally modified from primary forest by humans, and

with those maintained by humans, is a tight one. I can predict that wherever humans have settled in the Philippine Islands and in areas east of Wallace's Line this group of rats and mice, or at least one or several members of it, will be found. Furthermore, those species of Rattus and Mus will be different from the kinds of endemic murid rodents that live in primary forests and from those few endemic species in a given area that usually live in forest but can exist in modified habitats near forest. Looking at the association from another view, I can say that specimens of the six species in museums that are labeled as to locality and date but not habitat were probably caught in human habitats or close to them. Because the occurrence of some species with humans is so predictable; because these kinds also live on the Sunda Shelf and Asian mainland. and appear to be an intrusive element into the local endemic fauna on the Philippines and islands east of Borneo, the geographic distributions of most, if not all, of these human associates in those places probably have resulted from transport and colonization through human agency. At least this seems the most reasonable working hypothesis at this time.

In themselves the commensal species are of interest. Their taxonomies, life histories, geographic distributions, and nature of interactions with human populations require careful study. But, at the same time they are a component that must be sorted out from the endemic fauna, understood, and then, like a veneer, removed and set aside so we can begin to learn about the natural histories of the endemic rats and mice that live on the Philippine Islands and Indonesian Archipelago east of Wallace's Line.

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