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Definitions of Indochinese *Rattus losea* and a New Species from Vietnam

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ABSTRACT

The morphological characteristics, geographic distribution, habitat, and habits of *Rattus losea* are presented. The species occurs in grass, scrub, and agricultural habitats of Indochina north of the Isthmus of Kra (lat. 10°50'N). Its closest phylogenetic relative is the new species, *Rattus osgoodi*, known from samples obtained from the Langbian Peak region in southern Vietnam. The morphological and geographic features of *R. losea* and its relative are contrasted with those of other Indo-

chinese *Rattus*, namely, *R. rattus*, *R. norvegicus*, *R. exulans*, *R. sikkimensis*, *R. nitidus*, *R. turkestanicus*, *R. argentiventer*, and *R. brunneus*. The ricefield rat, *R. argentiventer*, may be more closely related to *R. losea* and the new species than to any other species of Indochinese *Rattus*, a hypothesis that should be tested with other kinds of data. Results presented here are part of a systematic study of native Asian *Rattus*.

INTRODUCTION

The lesser ricefield rat, *Rattus losea*, has a spotty distribution extending from Taiwan and adjacent islands through the mainland of southern China, onto Hainan, then over to Vietnam, Laos, and into Thailand. The rat is small in body size, terrestrial, and inhabits grass, scrub, and mangrove forest. We provide data to help define the distributional and morphological boundaries of *R. losea*. We also discuss identities of the scientific names associated with that species. Defining *R. losea* allowed us to compare samples of it with

specimens of a much smaller, dark-furred and short-tailed animal from the highlands of southern Vietnam. Those samples represent a new species, which we name, describe, and contrast with *R. losea*, probably its closest relative. There are eight other kinds of *Rattus* native to mainland Indochina and we compare the characteristics of each with those of the lesser ricefield rat and the new species from Vietnam.

Information we present was derived from assembling specimens, studying their mor-

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phological features, identifying them as either *R. losea* or the new species, and mapping localities where they were obtained. Through this endeavor an estimate of the morphological and geographic limits of each species was learned. Sorting out the scientific names that had been associated either directly or tangentially with *R. losea*, and identifying the holotypes upon which they were based were also involved in defining the species and identifying the names to be applied to it.

The process described above is fundamental to a broader study discovering the real species-diversity of *Rattus* in Southeast Asia. We want to know how many species occur in the region and the characteristics of each. We want to determine their geographic distributions, as of now, as they were in the past before natural habitats were altered by human migration, and, as shown by records of their existence and range at earlier times, if we can find and identify fossils. We need to identify the range of altitudinal distribution of each species, the kinds of habitats each occurs in, the nature of any interrelationships among species living in the same place, and learn all about the habits of each. Elucidating phylogenetic relationships among species of Southeast Asian *Rattus* is an important part of the answers to questions about the evolutionary history of the region and of its biota. We also need to know how *Rattus* species are related to *Rattus* faunas in other parts of its native range, from the Sunda Shelf to Australia. We asked many questions about *R. losea* and its relative from Vietnam; the answers we obtained provide a contribution to this larger inquiry.

ACKNOWLEDGMENTS

The core of our study is from specimens made available to us by curators and supporting staffs of several institutions; we are grateful to these persons for their past and continuing assistance. From about the middle 1960s, Musser has been slowly accumulating materials for a systematic study of Indochinese *Rattus*, and has discussed problems and identification of specimens with several persons. Among them were Drs. Joe T. Marshall, Jr. and Dirk Van Peenen, who have also studied many of the same samples of

Rattus losea that we did. Dr. Van Peenen was the first to concern himself with the identity of the series from Langbian Peak. We appreciate the interchange of information with these intelligent and thoughtful men.

Illustrations are very important in communicating results. We have been helped by the fine photographs made by Mr. Peter Goldberg and Mr. Jim Cox of the skins and skulls. Micrographs of molar rows in figure 6 are the careful efforts of Messrs. Robert J. Koestler and Richard Sheryll.

Ms. Cameron Newcomb thanks the Greenwall Foundation for her award (administered by the American Museum of Natural History) from the Undergraduate-Graduate Research Program.

Ms. Linda K. Gordon and Mr. Robert Izor kindly checked certain specimens for us at the National Museum of Natural History and the Field Museum of Natural History.

The present paper is no. 113—Results of the Archbold Expeditions.

INSTITUTIONS AND METHODS

Specimens examined and cited here by number are in collections of the American Museum of Natural History, New York (AMNH); the British Museum of Natural History, London (BM); the Field Museum of Natural History, Chicago (FMNH); the Muséum National d'Histoire Naturelle, Paris (MNHN); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Measurements were made on skins, skulls, and teeth. Values for total length, and tail length, hind foot, and 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. Measurements of the cranium and molar rows were obtained with dial calipers graduated to tenths of millimeters. Limits of the measurements are defined and illustrated by Musser (1970) and Musser and Newcomb (1983).

Micrographs of teeth shown in figure 6 were obtained from specimens uncoated and unaltered in any way before they were placed in the chamber of a Scanning Electron Microscope.

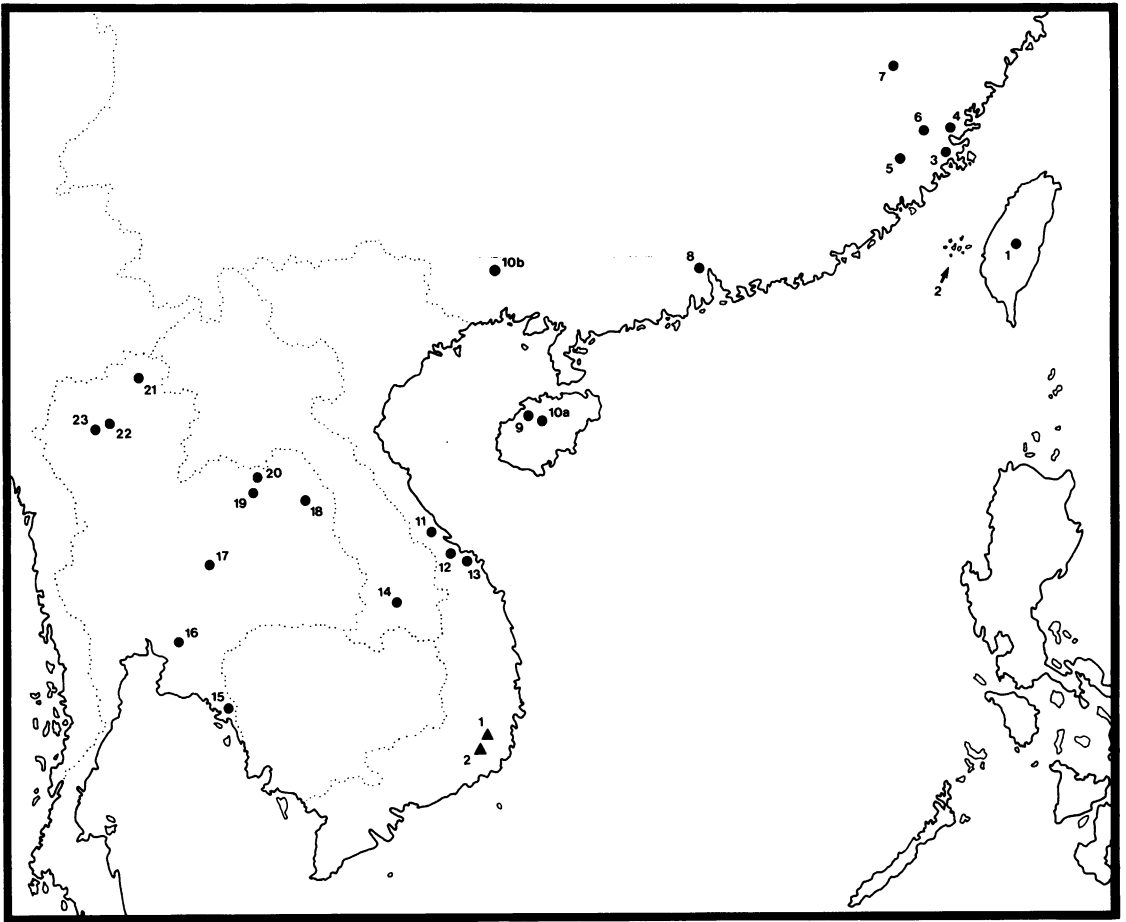


FIG. 1. Geographic distributions of *Rattus losea* (filled circles) and *R. osgoodi* (filled triangles). Numbers key to numbered localities listed in text. The range depicted here is based upon specimens we examined, not literature records. *R. losea* likely occurs in northern Vietnam, northern Laos, Cambodia, and parts of peninsular Thailand; we have not seen specimens from those places.

RATTUS LOSEA

DISTRIBUTION AND SPECIMENS

A native of Southeast Asia, *Rattus losea* is known from Taiwan, the nearby Pescadores, the island of Hainan, the mainland of southern China south of the Chang Jiang (Yangtze) River, Vietnam, Laos, and Thailand. Our understanding of the species comes from study of 595 specimens that were collected from 1921 to 1982. These examples and the places they were obtained are listed below; the number preceding each locality keys to a solid circle on the map in figure 1.

PEOPLE'S REPUBLIC OF CHINA (SOUTHERN HALF)

1. Taiwan Province (Chang Hua, Tai Pei, Ping-tung, Nan Tou, I-Lan, Tai Chung, Kao Hsiung, Mino-Li, Chini, and Hua-lien): USNM 261062–261066, 283744, 283745, 294225–294233, 294235, 294238, 308436, 313687, 330298–330379, 330381–330388, 330390–330409, 330517, 330518, 330522, 330524, 330530, 330534, 330543, 330547, 330548, 330554, 330555, 330557, 330558, 330568, 330569, 330612, 330652, 333080–333111,

- 355847–355850, 358418, 358421, 358422, 358424–358461.
2. Peng-hu Lieh-tao (Pescadores): USNM 294577, 294578, 294580.
 3. Fujian (Fukien) Province, Futsing (Fuching Hsien): AMNH 44622, 44627, 44628, 84656, 84660, 84661, 84669, 84670, 84672, 84674–84693, 84696–84699, 84716, 84743.
 4. Fujian Province, Foochow: USNM 239760 and 239761.
 5. Fujian Province, Yen-ping-fu and 70 miles southwest of there: USNM 238185 (holotype of *exiguus*), 238176–238184, 238186–238189.
 6. Fujian Province, Yenping: AMNH 44736–44739, 44749, 45531, 45532, 45534–45541, 45543, 45544, 45546–45557, 45559, 47924–47928, 47931, 47933, 47936, 47937.
 7. Fujian Province, Chungan Hsien: AMNH 60320 and 60321.
 8. Guangdong (Kwangtung) Province, Canton: USNM 243278 and 243282.
 9. Guangdong Province, Hainan Island, Nodoo: AMNH 58976, 58979, 58982–58984, 58986–58988, 58993–58995, 58999, 59001, 59003–59008, 59011, 59012, 59014–59017, 59021–59025, 59027, 59035, 59043, 59050, 59052, 59056, 59058–59067, 59070, 59073–59077, 59080–59084, 59086–59088, 59090–59095, 59098–59112, 59114, 59117, 59133, 59136, 59137, 59139–59145, 59147–59150, 59153, 59163, 59165–59177, 59179–59183, 59185–59187, 59189, 59190, 59192, 59193, 59254, 59259, 59270, 59273–59283, 59285, 59286, 59288, 59289, 59292, 59294, 59295, 59297, 59298, 59301, 59306, 59307, 59309, 59310; FMNH 32798–32805, 32807, 32809, 32812–32817, 32895.
 - 10a. Guangdong Province, Hainan Island, Nam Fong: AMNH 58916, 59118–59121, 59123–59129, 59132, 59198, 59199, 59200–59212, 59217, 59219–59221, 59226–59229, 59233–59236, 59239–59242, 59245, 59248, 59249, 59251–59253, 59255, 59256, 59258, 59260–59262, 59264, 59266, 59268, 59272; FMNH 32817.
 - 10b. Jiangxi (Kwangsi) Province, Lao Long Dong: AMNH 244955.
- SOUTHERN VIETNAM
11. Quang Tri Province, Quang Tri (Phouc Mon), 10 m: USNM 357691 and FMNH 30988.
 12. Thua Thien Province, Phu Bai Military Area, 10 m: USNM 356893–356898.
 13. Thua Thien Province, 14 km southeast of Hue, 10 m: USNM 356535–556540.
- SOUTHERN LAOS
14. Bolovens Plateau, 16 km south of Thatteng: USNM 355501.
- THAILAND
15. Trat Province, near Trat (also spelled Trad): USNM 356307–356309, 356310–356312, 356363–356368, 533475, 533476.
 16. Prachinburi Province, Sakaew District, Tungha Village: USNM 533474.
 17. Chaiyaphum Province, Pookeio and Ban Non Koon: USNM 294930–294935, 297164.
 18. Udon Thani Province, Ban Nong Bua: USNM 355307.
 19. Sakon Nakhon Province, Ban Sangkho, Khok Phu: USNM 300135 and 300136.
 20. Nong Khai Province: USNM 357880, 533462–533464.
 21. Chiangmai Province, Pan: USNM 533465.
 22. Chiangmai Province, Saraphi District, Ban Nong Pa Sae and Wat Phya Cham-poo: USNM 533467, 533469–533472.
 23. Chiangmai Province, San Patong District: USNM 533466, 533468, 533473.
- We omit places based on published records of specimens we have not examined. Tien (1960, 1961, 1978), for example, wrote about samples of *R. losea* from central and northern Vietnam. Under the name *R. rattoides exiguus*, Wang et al. (1962) recorded *R. losea* from southwestern Kwangsi Province in China, and Shaw et al. (1966) discussed *R. losea* on Hainan. We have not seen these particular Vietnamese and Chinese samples.
- Although we do not have records of *Rattus*

losea from northern Laos and Cambodia, we suspect the species also occurs in those places. Except for the Pescadores, we have not found *R. losea* on any of the small offshore islands in the South China Sea; we do not know whether it is absent or present on some of the islands and not yet collected.

We have not seen any specimens of *R. losea* from places south of the Isthmus of Kra (lat. 10°50'N) but Marshall (1977) indicates the species occurs in the southern part of peninsular Thailand. He told us the record is based upon a specimen from Phattalung Province, 9 km east of Phattalung (lat. 7°37'N, long. 100°5'E) that was caught in a ricefield at a rice experimental station on the margin of a large lake. The rat has blackish pelage, similar to animals in the population from Trat Province in southeastern Thailand. We cannot locate the specimen, nor can Marshall, who once looked at it and took measurements of the skin and skull, nor can Mr. Songsakdi Yenvutra, who studied the rat when it was caught in Phattalung.

DESCRIPTION

Rattus losea is terrestrial, small-bodied, short-tailed, and furry (tables 1 and 2; fig. 4; see also the photograph of a live rat in Marshall, 1977, p. 465; and the lovely color plate 8 in Aoki and Tanaka, 1941). Adult pelage is long and slightly shaggy in most samples, sleek in a few. Narrow, soft, translucent spines occur throughout the dorsal fur. Black guard hairs are inconspicuous because they are short, extending beyond the overfur by no more than 10 mm. The kinds of hairs that make up adult pelage are described in more detail by Tanaka (1939). Coloration of the fur clothing head and body, ears, and feet is geographically variable. Specimens from throughout most of the range of *R. losea*—mainland China, Hainan, Laos, and most of Thailand—have brownish gray upperparts in which the tone is darker along the back and rump and paler on the sides of the body where scattered pale yellow or buffy hairs provide highlights. Most hairs forming the dense coat over underparts of head and body are gray basally and white distally; the overall effect is grayish white except for the inguinal region

and underside of the chin, which are white in most specimens. Ears are pale brown and upper surfaces of front and hind feet of most specimens are covered with whitish gray hairs, the others with grayish brown.

Specimens in two samples differ slightly from the general coloration described above and examples in a third sample are strikingly different. Rats from Taiwan (locality 1, fig. 1) and the Pescadores (locality 2, fig. 1) have slightly darker backs and grayer bellies than those from the Chinese mainland. Examples of *R. losea* from Vietnam (localities 11–13, fig. 1) have brighter upperparts than do those from southern China and most of Thailand; the fur is a bright buffy brown without the grayish tones so characteristic of the Chinese and Thai animals. The difference, however, is slight and the range of variation overlaps among the series. Compared with all the other samples of *Rattus losea*, the most distinctively colored rats are those from the Province of Trat in southeastern Thailand (locality 15, fig. 1). Upperparts of these animals range from solid dark brown to blackish. Underparts are dark gray or gray washed with dark buff. Feet are either gray or dark brown. No other series of *R. losea* is so dark and richly pigmented.

Apparently there is a relationship between different pelage features and seasons in some populations. Tanaka (1939), for example, examined nearly 500 adult *R. losea* from northern Taiwan and concluded that (p. 92) "A summer pelage may be distinguished from a winter one by the fact that, in summer, the skin is found to be generally coarser and looser, consisting of more developed spines and thicker but shorter hairs of the underfur, while in winter the tendency is reversed." The coloration, however, Tanaka noted, "shows no significant seasonal variation, except for some tendency toward a ventral yellowish tinge occurring from August to November." Molting may occur during any month of the year but "appears to occur more infrequently during colder seasons."

Melanism occurs in *R. losea* but is rare. In all the specimens we examined, we found only one completely melanistic individual (USNM 330360) that was trapped on Taiwan.

On the average, the tail is shorter than the

TABLE 1
Measurements (in Millimeters) of Adult *Rattus losea* from China^a

Measurement	Taiwan	Fukien Province	Hainan	Holotype of <i>exiguus</i> ^b
Length of head and body	161.0 ± 14.7 (60) 121–193	143.6 ± 5.9 (9) 137–295	154.0 ± 17.1 (45) 100–185	152
Length of tail	165.5 ± 12.6 (60) 124–189	141.2 ± 9.5 (9) 125–155	142.1 ± 14.6 (46) 100–180	158
Length of hind foot	32.6 ± 2.0 (60) 28–37	28.2 ± 1.2 (9) 26–30	29.6 ± 2.6 (45) 19–31	29
Length of ear	20.9 ± 1.4 (60) 18–24	17.6 ± 1.3 (9) 16–19	18.7 ± 1.6 (43) 16–21	20
Greatest length of skull	38.8 ± 1.8 (60) 35.3–43.5	35.3 ± 1.3 (15) 33.4–38.2	36.2 ± 1.7 (50) 33.0–39.7	36.8
Zygomatic breadth	19.0 ± 0.8 (60) 17.1–21.0	17.2 ± 0.8 (17) 16.2–18.9	17.5 ± 0.8 (50) 16.2–19.5	17.9
Interorbital breadth	57.0 ± 0.3 (60) 5.2–6.3	5.1 ± 0.2 (17) 4.8–5.3	5.2 ± 0.2 (50) 4.7–5.8	4.9
Length of nasals	13.8 ± 0.8 (60) 12.1–16.3	12.3 ± 1.0 (17) 10.7–14.3	12.5 ± 0.9 (49) 10.7–14.3	13.3
Length of rostrum	11.1 ± 0.7 (60) 9.8–13.1	10.7 ± 0.6 (17) 9.9–12.1	10.9 ± 0.8 (49) 9.5–12.3	11.4
Breadth of rostrum	7.4 ± 0.4 (60) 6.5–8.3	6.6 ± 0.4 (17) 6.2–7.3	6.8 ± 0.6 (50) 5.7–7.9	6.8
Breadth of braincase	15.3 ± 0.5 (60) 13.9–16.0	14.5 ± 0.3 (17) 13.9–15.2	14.5 ± 0.5 (50) 13.6–15.6	14.7
Height of braincase	10.5 ± 0.4 (60) 9.4–11.4	10.3 ± 0.3 (17) 9.8–10.7	10.7 ± 0.4 (50) 10.0–11.6	10.3
Breadth of zygomatic plate	4.9 ± 0.4 (60) 4.3–5.8	13.8 ± 0.4 (17) 13.4–14.5	4.1 ± 0.3 (49) 3.7–4.9	4.7
Depth of zygomatic notch	2.8 ± 0.3 (44) 2.1–3.3	—	—	3.0
Length of incisive foramina	7.3 ± 0.5 (60) 6.5–8.6	7.1 ± 0.4 (17) 6.5–8.0	6.7 ± 0.4 (50) 5.7–7.5	7.3
Breadth of incisive foramina	2.3 ± 0.2 (60) 2.0–2.7	2.2 ± 0.3 (17) 1.8–3.1	2.2 ± 0.2 (50) 1.8–2.7	2.4
Length of diastema	10.4 ± 0.7 (60) 9.1–12.2	9.6 ± 0.6 (17) 8.7–11.0	9.4 ± 0.8 (50) 8.1–11.0	10.5
Palatal length	21.6 ± 0.9 (60) 19.5–23.6	19.9 ± 1.1 (17) 18.3–21.9	19.9 ± 1.1 (50) 18.2–22.2	20.2
Postpalatal length	13.2 ± 0.7 (60) 11.5–15.3	11.2 ± 1.6 (16) 7.8–13.3	12.5 ± 0.8 (50) 11.0–14.0	13.3
Length of palatal bridge	8.1 ± 0.4 (60) 7.3–8.9	6.9 ± 0.4 (17) 6.5–7.8	8.0 ± 0.3 (50) 7.2–8.7	7.0
Breadth of palatal bridge at M ¹	3.9 ± 0.3 (60) 3.2–4.6	3.5 ± 0.3 (17) 3.2–4.1	3.6 ± 0.3 (50) 3.0–4.4	3.8
Breadth of palatal bridge at M ³	4.5 ± 0.4 (60) 3.7–5.6	4.3 ± 0.2 (17) 4.0–4.6	4.6 ± 0.4 (50) 3.7–5.7	4.9

TABLE 1—(Continued)

Measurement	Taiwan	Fukien Province	Hainan	Holotype of <i>exiguus</i> ^b
Breadth of mesopterygoid fossa	2.4 ± 0.2 (60) 2.0–2.8	2.2 ± 0.2 (17) 1.9–2.5	2.2 ± 0.2 (47) 1.6–2.7	2.0
Length of bulla	6.6 ± 0.3 (60) 5.9–7.5	6.5 ± 0.3 (17) 6.0–7.1	6.8 ± 0.4 (47) 5.8–7.5	7.0
Height of bulla	5.3 ± 0.2 (60) 4.7–5.6	5.3 ± 0.2 (17) 4.9–5.7	—	5.5
Alveolar length of M ¹⁻³	7.1 ± 0.2 (60) 6.5–7.5	6.3 ± 0.3 (17) 5.9–6.7	6.9 ± 0.3 (50) 6.2–7.5	6.5

^a The mean plus or minus one standard deviation, number of specimens in parentheses, and observed range are listed for each measurement.

^b USNM 238185, an adult female from Fujian Province, 70 miles southwest of Yen-ping-fu, 500 feet.

combined lengths of head and body in all samples studied except the one from Taiwan in which the average length of the tail is slightly greater (tables 1 and 2). All tail surfaces are brown but the intensity of the pigmentation is unequal. In many specimens, the underside of the tail, especially along the basal third, is slightly paler than the dorsal surface; however, the tails are not distinctly bicolored. There are 10 to 12 rows of tail scales per cm (counted at a spot about one-third of the way from the tail base).

The long and narrow hind feet have naked plantar surfaces with four interdigital and two plantar pads. All are small, low, and adorned by shallow striations, a relative size and texture similar to that in such terrestrial rats as *R. argentiventer* (see fig. 2 in Musser, 1973) and unlike the large pads with conspicuous transverse and semicircular lamellae so characteristic of good climbers—*R. rattus*, for example (Marshall, 1977).

In addition to being much smaller, juveniles have darker, softer, and finer pelage than do adults.

Females have five pairs of mammae: one pectoral, one postaxillary, one abdominal, and two inguinal.

The skull of *Rattus losea* is small in size and stocky in appearance (tables 1–3; fig. 2). Its general structural aspect as well as details of the orbit, alisphenoid region, palatal bridge, mesopterygoid and pterygoid fossae, and pattern of basicranial arterial circulation resembles that of *R. rattus* whose features have

been described and illustrated by Musser (1981, 1982) and Musser and Newcomb (1983).

Diagnostic characteristics of *R. losea* are its short and wide rostrum, deep braincase, wide zygomatic plates, narrow and long incisive foramina, and large bullae relative to skull size (the ratio, length of bulla divided by length of skull, ranges from 17 to 19 percent among the seven samples of *R. losea* in tables 1–3). The short rostrum and nasals together with the high and sturdy braincase combine to impart a stubby and chunky aspect to the cranium. The zygomatic plates are wide enough so that their anterior margins cover the lower portions of the nasolacrimal capsules. Dorsolateral margins of the cranium, from the orbit to the parietals, are outlined by ridges that become smaller and inconspicuous as they reach corners of the interparietal. That bone roofs most of the occipital region. Except that it is smaller, the mandible is shaped like that in *R. rattus* (see illustrations in Musser, 1981).

Like other species of *Rattus*, the upper and lower incisors of *R. losea* have smooth surfaces and deep orange enamel layers. The uppers emerge from the rostrum at nearly a right angle (orthodont configuration) in most specimens.

Characteristics of the upper and lower molars (fig. 6)—number of roots anchoring each tooth, the degree one tooth overlaps the other, sizes of molars relative to one another, height of crowns, and occlusal cusp pat-

TABLE 2
Measurements (in Millimeters) of Adult *Rattus losea* from Thailand^a

Measurement	Northeast (Localities 17–20)	Northwest (Localities 21–23)	Southeast (Locality 15)
Length of head and body	147.3 ± 10.1 (7) 128–158	152.4 ± 11.6 (7) 133–165	145.3 ± 10.4 (7) 135–160
Length of tail	132.7 ± 28.4 (7) 75–163	138.3 ± 11.6 (7) 123–160	133.3 ± 4.4 (7) 127–140
Length of hind foot	29.9 ± 1.1 (7) 28–31	30.9 ± 1.5 (7) 29–32	31.1 ± 1.2 (7) 30–33
Length of ear	18.3 ± 2.4 (4) 15–20	17.6 ± 1.0 (7) 16–19	18.0 ± 1.5 (7) 16–20
Greatest length of skull	36.6 ± 2.3 (7) 32.4–38.7	36.4 ± 1.5 (8) 33.5–37.9	35.4 ± 0.9 (7) 34.2–36.9
Zygomatic breadth	18.4 ± 1.0 (5) 17.0–19.4	17.7 ± 0.5 (8) 16.9–18.4	17.1 ± 0.9 (7) 16.1–18.8
Interorbital breadth	5.3 ± 0.3 (8) 5.0–5.7	5.2 ± 0.2 (8) 5.0–5.5	5.4 ± 0.3 (7) 5.1–5.7
Length of nasal	12.8 ± 1.0 (7) 10.9–13.8	13.2 ± 0.7 (8) 11.9–14.0	12.6 ± 0.4 (7) 12.2–13.2
Length of rostrum	10.2 ± 1.0 (7) 8.4–11.6	10.3 ± 0.5 (8) 9.3–10.9	10.0 ± 0.5 (7) 9.2–10.5
Breadth of rostrum	6.8 ± 0.5 (8) 5.7–7.3	6.3 ± 0.2 (8) 6.1–6.5	6.3 ± 0.4 (7) 6.0–6.9
Breadth of braincase	14.5 ± 0.5 (8) 13.8–15.3	14.5 ± 0.3 (8) 14.0–14.9	14.5 ± 0.4 (7) 14.2–15.2
Height of braincase	10.7 ± 0.5 (8) 9.5–11.2	10.5 ± 0.3 (8) 10.0–10.9	10.5 ± 0.5 (7) 9.9–11.1
Breadth of zygomatic plate	4.5 ± 0.5 (8) 3.9–5.0	4.7 ± 0.3 (8) 4.3–5.1	3.9 ± 0.3 (7) 3.6–4.3
Depth of zygomatic notch	2.5 ± 0.3 (8) 2.0–2.8	2.5 ± 0.2 (8) 2.2–2.8	2.0 ± 0.3 (7) 1.7–2.4
Length of incisive foramina	6.9 ± 0.4 (8) 6.0–7.2	6.8 ± 0.5 (8) 6.3–7.5	6.6 ± 0.2 (7) 6.3–6.8
Breadth of incisive foramina	2.2 ± 0.3 (8) 1.3–2.5	2.1 ± 0.1 (8) 2.0–2.3	2.2 ± 0.2 (7) 2.0–2.4
Length of diastema	10.0 ± 0.8 (8) 8.5–10.8	9.5 ± 0.4 (8) 8.7–9.8	9.4 ± 0.4 (7) 8.9–10.0
Palatal length	20.7 ± 1.3 (8) 18.2–22.1	20.3 ± 0.7 (8) 19.2–21.3	19.7 ± 0.6 (7) 19.2–20.7
Postpalatal length	12.6 ± 1.0 (8) 10.6–13.4	12.0 ± 0.6 (8) 11.0–12.7	11.9 ± 0.5 (7) 11.3–12.9
Length of palatal bridge	8.1 ± 0.6 (8) 7.2–8.7	7.9 ± 0.3 (8) 7.5–8.3	7.3 ± 0.2 (7) 7.0–7.5
Breadth of palatal bridge at M ¹	3.5 ± 0.5 (8) 2.8–4.1	3.3 ± 0.2 (8) 3.1–3.5	3.3 ± 0.2 (7) 3.0–3.6
Breadth of palatal bridge at M ³	4.5 ± 0.3 (8) 3.9–4.9	4.5 ± 0.2 (8) 4.3–4.7	4.1 ± 0.2 (7) 3.9–4.6

TABLE 2—(Continued)

Measurement	Northeast (Localities 17–20)	Northwest (Localities 21–23)	Southeast (Locality 15)
Breadth of mesopterygoid fossa	2.3 ± 0.2 (8) 2.0–2.5	2.2 ± 0.1 (8) 2.1–2.4	2.0 ± 0.1 (7) 1.8–2.1
Length of bulla	7.0 ± 0.5 (8) 6.2–7.7	6.8 ± 0.4 (8) 6.3–7.4	6.6 ± 0.2 (7) 6.4–6.8
Height of bulla	5.7 ± 0.3 (8) 5.3–6.1	5.5 ± 0.3 (8) 5.0–5.9	5.7 ± 0.1 (7) 5.5–5.9
Alveolar length of M ¹⁻³	6.7 ± 0.3 (8) 6.4–7.1	6.7 ± 0.3 (8) 6.3–7.1	6.5 ± 0.2 (7) 6.3–6.8

^a Mean plus or minus one standard deviation, number of specimens in parentheses, and observed range are listed for each measurement.

terns—are similar to those found in *R. rattus* (see Musser, 1981, 1982; Musser and Newcomb, 1983). About three-fifths of any sample of *R. losea* has a small triangular bulge representing the posterior cingulum at the back of each first upper molar. A small cusp t3 is present on each second upper molar but absent from the third upper molar on most specimens. No anterocentral cusp occurs at the front of each first lower molar. An anterior labial cusplet is found on the first lower molar in about one-fifth of every sample. Posterior labial cusplets on the first and second lower molars are characteristic of every specimen. Anterolabial cusps on the second and third lower molars occur in nearly all specimens.

Chromosomes have been examined from specimens of *Rattus losea* that were collected in Taiwan, Thailand, and southern Vietnam (Makino, 1943; Duncan and Van Peenen, 1971; Markvong, Marshall, and Gropp, 1973; Yosida, 1979). The diploid number is 42. Among the autosomes, there are seven pairs of small to medium metacentrics, one large pair and one medium-sized pair of subtelocentrics, and 11 pairs of large to small telocentrics. The X and Y chromosomes are telocentrics. The diploid number and chromosomal composition of the karyotype are similar to that in other species embraced by the subgenus *Rattus*.

Other biological aspects of *R. losea* are best known for the population on Taiwan. In 1938, Aoki and Tanaka published results of their study of 784 skins and 614 skulls of *R. losea*

from Taiwan. They discuss external qualitative characters of the species, relative growths in external and skull measurements, characteristics of molar cusps, general consideration of relative growth in the skull, determination of size at which sexual maturity is attained, and individual variation and mean values of adult measurements.

ALTITUDINAL DISTRIBUTION AND HABITATS

A species of the lowlands and middle altitudes, our records of *Rattus losea* indicate it to occur throughout a range from lowlands near sea level up to between 800 and 900 m in highlands of China, Vietnam, Laos, and Thailand. Throughout its geographic range, most specimens have been taken from grass and scrub habitats, agricultural fields and orchards, and around houses; a few records exist from native forests and grasslands. On Hainan, for example, Allen (1940, p. 1009) wrote that one collector noted *R. losea* to be the "common rat about Nodao, Hainan, . . . we found it in numbers in the high grass and bushes bordering the rice fields. We would get a dozen or more of these to one of any other kind in the open country about Nodao, but in the jungles it was much less plentiful. Thirty traps would yield over night eight or nine of these rats." Another trapper, wrote Allen, indicated that *R. losea* "is the common field and house rat in hilly mountainous districts up to 800 meters in the country inland from Canton, Kwangtung," on main-

TABLE 3
Measurements (in Millimeters) of Adult Vietnamese *Rattus losea* and *Rattus osgoodi*^a

Measurement	<i>R. losea</i> (Localities 11–13)	<i>P</i> ^b	<i>R. osgoodi</i> (Localities 1, 2)	Holotype of <i>osgoodi</i> ^c
Length of head and body	152.0 ± 10.7 (10) 136–166	.02–.01	138.8 ± 11.8 (16) 124–171	145
Length of tail	152.7 ± 3.7 (10) 147–161	<.001	119.7 ± 10.1 (14) 102–137	124
Length of hind foot	32.7 ± 1.2 (10) 31–34	<.001	28.1 ± 2.6 (16) 26–37	27
Length of ear	18.8 ± 1.2 (10) 17–20	—	—	—
Greatest length of skull	36.6 ± 1.0 (10) 34.6–37.8	<.001	32.8 ± 1.4 (15) 31.0–36.2	33.7
Zygomatic breadth	17.3 ± 0.8 (7) 16.0–18.2	.2–.1	16.6 ± 0.9 (12) 15.2–17.9	17.2
Interorbital breadth	5.1 ± 0.1 (10) 4.8–5.3	<.9	5.1 ± 0.2 (16) 4.8–5.5	5.2
Length of nasal	13.1 ± 0.6 (10) 12.3–14.1	<.001	11.3 ± 1.2 (16) 9.1–13.7	11.9
Length of rostrum	10.9 ± 0.5 (10) 10.3–11.6	<.001	9.5 ± 0.8 (16) 8.1–11.1	9.7
Breadth of rostrum	6.8 ± 0.3 (10) 6.4–7.2	<.001	6.0 ± 0.4 (16) 5.6–6.7	6.6
Breadth of braincase	14.1 ± 0.3 (10) 13.6–14.6	.2–.1	13.9 ± 0.3 (16) 13.4–14.5	13.8
Height of braincase	10.6 ± 0.3 (10) 10.1–11.1	<.001	9.9 ± 0.2 (15) 9.6–10.4	10.4
Breadth of zygomatic plate	4.2 ± 0.3 (10) 3.6–4.5	<.001	3.4 ± 0.2 (16) 3.1–3.8	3.6
Depth of zygomatic notch	2.5 ± 0.3 (10) 2.0–3.0	.001	1.9 ± 0.2 (15) 1.5–2.2	2.2
Length of incisive foramina	7.0 ± 0.4 (10) 6.4–7.6	.01–.001	6.5 ± 0.4 (16) 5.9–7.2	6.9
Breadth of incisive foramina	2.4 ± 0.2 (10) 2.2–2.8	<.001	2.0 ± 0.2 (16) 1.7–2.5	2.5
Length of diastema	10.2 ± 0.5 (10) 9.3–10.9	<.001	8.8 ± 0.6 (16) 8.0–10.0	9.4
Palatal length	20.5 ± 0.1 (10) 18.9–21.7	<.001	18.2 ± 0.9 (16) 16.9–20.2	19.0
Postpalatal length	12.4 ± 0.4 (10) 11.6–12.8	<.001	10.8 ± 0.6 (15) 10.0–12.0	11.0
Length of palatal bridge	7.5 ± 0.4 (10) 7.0–8.0	<.001	6.5 ± 0.3 (16) 6.0–7.1	6.7
Breadth of palatal bridge at M ¹	3.5 ± 0.3 (10) 3.1–3.9	.05–.02	3.2 ± 0.3 (16) 2.7–3.7	3.6

TABLE 3—(Continued)

Measurement	<i>R. losea</i> (Localities 11–13)	<i>P</i> ^b	<i>R. osgoodi</i> (Localities 1, 2)	Holotype of <i>osgoodi</i> ^c
Breadth of palatal bridge at M ³	4.8 ± 0.4 (10) 4.2–5.4	<.001	4.0 ± 0.4 (16) 3.5–4.6	4.3
Breadth of mesopterygoid fossa	2.3 ± 0.1 (10) 2.2–2.4	<.001	2.0 ± 0.2 (16) 1.7–2.3	2.0
Length of bulla	6.6 ± 0.2 (10) 6.2–7.0	<.001	6.1 ± 0.3 (16) 5.8–6.7	6.0
Height of bulla	5.5 ± 0.2 (10) 5.2–5.8	.1–.05	5.3 ± 0.3 (16) 4.8–6.0	4.8
Alveolar length of M ^{1–3}	6.6 ± 0.3 (10) 6.2–6.7	<.001	5.8 ± 0.2 (16) 5.3–6.0	5.3

^a Mean plus or minus one standard deviation, size of sample in parentheses, and observed range are listed for each measurement.

^b Probability that means from each sample were drawn from the same population.

^c FMNH 47671, an adult female.

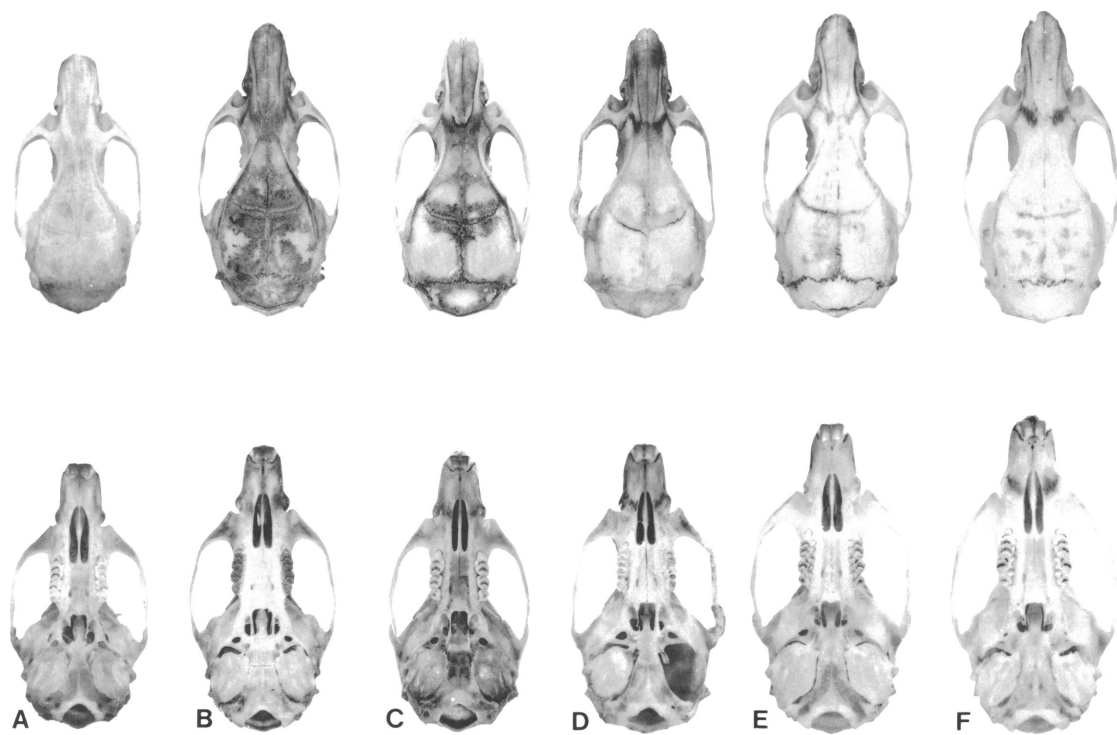


FIG. 2. Dorsal (top) and ventral (bottom) views of adult crania contrasting two species of *Rattus*. A, holotype of *R. osgoodi*, southern Vietnam (FMNH 46761). B–F, *R. losea*: B, central Vietnam (USNM 357691); C, Hainan Island, southern China (AMNH 59187); D, Trad Province, southeastern Thailand (USNM 356307); E, northern Thailand (USNM 294931); F, Taiwan (USNM 330348). Natural size.

land China. Information on skin labels attached to specimens collected on Taiwan indicate the rats came from "houses," around "private dwellings," in "flat agricultural areas," in "agricultural areas around private dwellings," and in "scrub brush and high grass." Aoki and Tanaka (1941, p. 170) noted that on Taiwan, *R. losea* is one "of the most dominant field rats, mainly inhabiting entire lowlands of Formosa, but not ascending higher than 2,000–2,500 ft. in the northern and 4,000–4,500 ft. in the central and southern parts."

Van Peenen, Ryan, and Light (1969, p. 169) report that specimens from Thua Thien Province in southern Vietnam were "trapped in grass and low bushes."

Rattus losea has been taken in both native habitats and agricultural areas in Thailand. Marshall (1977, p. 466) wrote that individuals were trapped "in grass beneath pine forest at 850 m in Chaiyaphum Province" and are common in mangrove forest in Chantaburi Province. Marshall noted that the species was abundant in vegetable gardens on the banks of the Mekong River, along strips between rice paddies and orchards in Chiangmai Province, and in ricefields and gardens in Trat Province. Notes written on skin labels indicate other specimens were taken in a "cluster of bamboo at edge of ricefield," in an "orchard," and in a "cultivated area of sweet potato."

SCIENTIFIC NAMES

Three scientific names can be applied to samples of *Rattus losea*: *Mus losea* Swinhoe (1870, p. 637), *Rattus rattus exiguus* Howell (1927, p. 44), and *Rattus sakeratensis* Gyldestolpe (1917, p. 46). A fourth, *Mus canna* Swinhoe (1870, p. 636), may also belong here. We need to first discuss *Mus canna* and *Mus losea*.

During 1870 Swinhoe authored a "Catalogue of the Mammals of China (south of the River Yangtsze) and of the Island of Formosa." In the catalogue are the descriptions of two new species of *Mus* based upon specimens collected near Tamsuy (now designated Tamsui, Taipei Hsien, lat. 25°10'N, long. 121°26'E) on Taiwan (which was called For-

mosa). *Mus canna*, the "Silken Country-rat," was described on page 636 from a male:

Length 5.5; tail 5.25; ear bare, .6 high, oblong, rounded at tip. Hind foot from tarsal joint 1.4. Hair short, soft, and mouse-like. Front teeth narrow and slender, with orange surface. Upper parts and legs brown, tinged with light chestnut, more conspicuous on the head and along the sides; underparts dingy ochreous; tail light brown, nearly naked, with minute inconspicuous setae. Underfur light slaty. It resembles the immature of *M. indicus*, but has smaller feet, and a soft silky pelage. A Rat affecting villages in the country near Tamsuy, Formosa, and ascending trees.

On page 637, Swinhoe described another male under the title of *Mus losea*, the "Brown Country-rat," and it was:

Length 6 inches, tail 3.75. Teeth broader than in the last, and of the same colour. General colour of upper parts a rich brown, many of the hairs of the head and upper parts tipped with black, giving a dark appearance in some lights; fur soft and moderately long; under-fur dark slate-grey. Underparts dingy whitish; legs brown, with a streak of whitish on each edge of fore foot. Ears moderate, naked. Moustache rather short. Tail brown, with minute black setae scarcely visible. This is also a Country-rat at Tamsuy, Formosa.

Neither of these two names have been tied to holotypes but are still used to designate a series of specimens collected by Swinhoe that are in the British Museum. In 1969, Musser looked at the specimens and decided that most were examples of what Bonhote (1906) and Allen (1940) had identified as *R. losea*. Musser did not locate holotypes; neither of us have studied the material since. We trace our use of the name *losea* back to Musser's examination and back farther to Bonhote (1906) and Allen (1940). In a report on Chinese Murinae, Bonhote (1906, pp. 385, 391) recognized *Mus losea* as part of the fauna. Judged from the short description and values from measurements of skin, skull, and dentition, Bonhote's definition of *losea* is the same as we present in this paper. Bonhote noted that the species was originally described from Formosa but that there was a specimen from Amoy and others from western Fukien, all places on the Chinese mainland.

In 1926, Allen identified specimens of the

common small-bodied *Rattus* of northern China as *Rattus humiliatus*. Then in 1940 (p. 1007), he used the combination *Rattus losea exiguus* for the same species and noted that the

rat that Swinhoe described from Tamsuy, Formosa, as *Mus losea* has been more or less of a puzzle for many years. Having recently, however, had the opportunity of examining a series of ten specimens so labeled in the British Museum, including the one selected as a "type" probably by Thomas, it appears that this is really only a dark insular representative of the common small rat of South China which I had previously supposed from Milne-Edward's figure and description to be his *M. humiliatus*, and which A. B. Howell, correcting this error, later named *R. rattus exiguus*. It is a species quite distinct from *R. rattus*, however, though with a similar superficial appearance, yet the subspecific designation will probably hold for the race of the mainland of southern China and Hainan.

We are uncertain about the identity of *Mus canna*. Bonhote (1906) listed it as a synonym of *Mus flavipectus*, which is now known as *Rattus rattus flavipectus*, the common house rat of southern China. Later authors have treated the name differently. Ellerman (1941, p. 214; 1949, p. 79) listed it as *Rattus canna* and Ellerman and Morrison-Scott (1951, p. 588) suggested that both *losea* and *canna* referred to the same species, which they listed as *Rattus* (?) *rattoides losea*. Finally, in his catalogue of mammal holotypes from Taiwan, Jones (1975, pp. 195–196) listed *canna* under *Rattus* sp.

There is a possibility that *Mus canna* does refer to *Rattus rattus flavipectus*; Swinhoe (1870) indicated that it climbed trees, which *R. r. flavipectus* does and *R. losea* does not. This allocation, however, was a problem for Aoki and Tanaka (1941, p. 130) in their monograph on the rats and mice of Formosa, because they claimed that "*Rattus flavipectus*" did not occur on the island. Aoki and Tanaka (1941, p. 178) did record "*Rattus rattus*" from Taiwan and noted that the "rat is found mainly in houses throughout the island, possibly ascending with man to a considerable height, 7,000 ft. having so far been recorded." For Aoki and Tanaka, this animal was the Formosan equivalent of the European house rat, not the Asian *R. rattus fla-*

vipectus. But Bonhote (1906) was right, the *R. rattus* living on Taiwan are referable to the Asian *R. rattus flavipectus* and not to the European *R. rattus rattus*. We have studied 272 *R. rattus flavipectus* collected on Taiwan, 85 from nearby Orchid Island, and 31 from the Pescadores—all in the collection of the National Museum of Natural History—and all specimens are closely similar in pelage color and body size to samples of *R. r. flavipectus* from mainland China. We have not yet seen specimens of the European *R. rattus rattus* from Taiwan. Our experience reflects that expressed by Jones and Johnson (1965, p. 392) who wrote that the names *rattus* and *alexandrinus* occur frequently in the literature to designate samples of Asian *R. rattus*. But each "of these names was based originally on a different color phase of the house rat or roof rat of western Europe and the Mediterranean region (*Rattus rattus rattus*), a subspecies that seldom is found in eastern Asia except in the holds of ships. It seems never to have become established permanently on the mainland or adjacent islands, probably owing to the presence there of well entrenched populations of *R. r. flavipectus* or other races that resemble *R. r. rattus* in size and have about the same ecological requirements." Jones and Johnson also noted that in "a restricted sense the subspecific name *rattus* has been used most frequently to designate the melanistic color phase of the European house rat, and unfortunately it frequently has been applied by mistake to black individuals of other subspecies and even of another species, *Rattus norvegicus*. We are therefore inclined to view Asian records of '*Rattus rattus rattus*' with considerable skepticism, especially where it appears that identifications were based solely or principally on black color." We have seen blackish *R. rattus* from Taiwan but they are simply melanistic specimens of *R. r. flavipectus*.

We regard *losea* to be the earliest name of the small-bodied *Rattus* living on Taiwan. *Mus canna* may be the same species, but it may also refer to what is now known as Taiwanese *R. r. flavipectus*. We can not be sure of the proper allocation of *canna* until we restudy Swinhoe's series at the British Museum.

The combination, *Rattus losea losea* refers

to samples from Taiwan, as Allen (1940) noted. There are two scientific names available for series of *R. losea* from the mainland of Southeast Asia: *sakeratensis* and *exiguus*. Gyldenstolpe's (1917) *Rattus sakeratensis* was shown by Marshall (1977, p. 446) to consist of a skin of *R. losea* from Thailand mismatched with a skull of *R. whiteheadi* (now known as *Maxomys whiteheadi*) from the Malay Peninsula. Marshall has explained the problem, described how he solved it, and designated the skin from Sakaerat, Thailand, as lectotype of *Rattus losea sakeratensis*, which he regarded as "a valid subspecies pertaining to the plain brown population of northern and central Thailand."

Howell's (1927, p. 43) *Rattus rattus exiguus* is based upon an adult female (USNM 238185) collected in Fujian (Fukien) Province of mainland China. The specimen is closely similar to samples of *R. losea* from Taiwan in characteristics of skin and skull. The holotype is not an example of *R. rattus* as Howell originally thought and continued to treat it (Howell, 1929, p. 59). Allen (1940, p. 1005) was correct in identifying the holotype as an example of *R. losea* and using the combination *R. losea exiguus* for samples from southern mainland China and Hainan. But, as we shall explain further on in this report, we would synonymize *exiguus* with *sakeratensis*, which is the oldest subspecific name available to identify all samples of *R. losea* from the mainland of Southeast Asia.

There are other scientific names which have been applied to samples of what we now refer to as *R. losea*. One of these is *Mus humiliatus*, named and described by Milne-Edwards in 1868 (p. 137). Allen (1926) was the first to use *Rattus humiliatus* to identify what he later called *Rattus losea exiguus* (Allen, 1940). Osgood (1932, pp. 302–303) also used *humiliatus* when he reported a specimen of *exiguus* from southern Vietnam. He wrote that

a "cotype" of *humiliatus* collected by Père David and now labeled "Suenhoafu, Pekin" is in the British Museum. The end of its tail is missing, but otherwise it is in good condition although doubtless originally preserved "in spirit." The color is decidedly rufescent, perhaps partly due to preservative, but another specimen collected more recently (1903) near Nanking is only slightly paler. The feet are white in both spec-

imens and the tail is definitely bicolored. This last character distinguishes it from specimens from Fukien, Hainan, and Annam, all of which have entirely blackish tails.

To Osgood, it "seems evident therefore, that two eastern forms of *humiliatus* may be recognized, one with a bicolored tail ranging from Nanking northward and the other with a blackish unicolored tail extending south to northern Annam. For the southern form, the name *exiguus* is available."

By 1940, Allen had switched from using *humiliatus* for *Rattus losea* to using the name as a subspecies of *R. nitidus*. Ellerman (1941, 1949), however, used the combination, *Rattus humiliatus humiliatus* and brought additional scientific names together as either synonyms or subspecies of *R. humiliatus*. By 1951, Ellerman and Morrison-Scott (p. 589) treated *humiliatus* as a synonym of *Rattus norvegicus caraco*, an allocation based upon the opinion of Schwarz's examination of holotypes, which was later documented in Schwarz and Schwarz (1967, p. 117).

We have examined the holotype of *humiliatus* (MNHN 342) and two other specimens labeled as paratypes (MNHN 342a and 342b), which are housed at the Muséum National d'Histoire Naturelle in Paris. All three specimens are represented by skins and skulls, all three are young, and all three are clearly examples of *Rattus norvegicus*, the conclusion reported by Schwarz and Schwarz (1967). We also studied the cotype of *humiliatus* (BM 82.6.16.3) mentioned by Osgood. It too is simply a young example of *R. norvegicus* and has nothing to do with *R. losea*. The name *humiliatus* has most recently been used to designate a subspecies of *Rattus norvegicus* from the provinces of Hebei, Liaoning, Shandong, and northern Jiangsu (Wu, 1982).

The name *rattoides* is another that has been associated with both *losea* and *exiguus*. In a revised checklist of the genus *Rattus*, Ellerman (1949, p. 62) listed the combinations *Rattus rattoides* (?) *losea* and *Rattus rattoides exiguus*, arrangements that were also used by Ellerman and Morrison-Scott (1951, p. 588). The combination has appeared in the literature up to the 1960s where records of *exiguus* from southwestern Kwangsi Province in China (Wang et al., 1962) and Hainan (Shaw

et al., 1966) were reported under *Rattus rattoides exiguus*.

Mus rattoides was named and described by Hodgson in 1845 (p. 267) from specimens collected in central Nepal. Hodgson's *rattoides*, however, is preoccupied by *Mus rattoides* Pictet and Pictet (1844), and as Schlitter and Thonglongya (1971) explained, the earliest available scientific name for Hodgson's species is *Rattus turkestanicus*, named and described by Satuñin in 1902. The species is distributed to the north and east of *R. losea*. Our records and those in the literature are from southern and eastern Russian Turkistan (Schlitter and Thonglongya, 1971; Corbet, 1978), northeastern Iran (Etemad, 1964), north and eastern Afghanistan (Hassinger, 1973; Niethammer and Martens, 1975), northern Pakistan (Akhtar, 1959; Roberts, 1977), northern India, Sikkim, Kashmir, Nepal (Ellerman and Morrison-Scott, 1951; Abe, 1971; Corbet, 1978), and the Yunnan (the series described by Allen, 1926, as *Rattus humiliatus celsus*) and Guangdong (AMNH 244957) provinces of China.

Rattus turkestanicus is a much larger-bodied animal than *R. losea*, with a gray back, white to grayish white belly, bicolored tail conspicuously longer than combined lengths of head and body, six pairs of mammae, somewhat flattened cranium, widely spreading zygomatic arches, and long toothrows. Other than being in the genus *Rattus*, there are no close morphological resemblances between the two.

Another name formerly associated with *Rattus losea* was *celsus*, given to a series of rats from Yunnan Province in China described by Allen in 1926 (p. 5) under the name *Rattus humiliatus celsus*. All specimens were obtained at elevations ranging from 6000 to 10,000 ft. Allen (1940, p. 1009) later treated *celsus* as a subspecies of *Rattus losea*. Others listed it as *Rattus humiliatus celsus* (Ellerman, 1941, p. 184) or *Rattus rattoides celsus* (Ellerman, 1949, p. 62; Ellerman and Morrison-Scott, 1951, p. 588). All the specimens of *celsus* that we have studied, including the holotype (AMNH 43393) are examples of *Rattus turkestanicus*, a conclusion earlier noted by Marshall (1977, p. 465).

There are five other scientific names that

have been tied to either *Rattus humiliatus* or *R. rattoides* at one time or another and thus tangentially associated with what we refer to as *R. losea*. All five were based upon specimens collected in China and we had to identify the holotypes to be sure none of them were examples of *R. losea*. The first of these is *Mus griseipectus*, described by Milne-Edwards in 1871 (in David, 1871, p. 93) and based upon a specimen from Sichuan (Szechwan) Province in China. Allen (1926) first recognized it as a distinctive species, then later as a synonym of *Rattus nitidus nitidus* (Allen, 1940, p. 999) following Osgood (1932, p. 299). Ellerman (1941, p. 180; 1949, p. 63) also considered *griseipectus* to be the same as *R. nitidus* but Ellerman and Morrison-Scott (1951, p. 589) treated the name under *Rattus norvegicus caraco*, following an identification by Schwarz, which was published later in Schwarz and Schwarz (1967, p. 117). We have examined the holotype, consisting of a mounted skin from which the skull has been extracted, at the Muséum National d'Histoire Naturelle in Paris. The specimen is a young adult *Rattus norvegicus*.

Mus ouangthomae, another species proposed by Milne-Edwards in 1871 (in David, 1871, p. 93), was described from a specimen obtained in Jiangxi (Kiangsi) Province of southern China. The name was synonymized with *Rattus flavipectus flavipectus* by Allen (1940, p. 994) but in that same monograph (p. 1008) Allen wrote that it "is by no means certain that Milne-Edward's *Mus ouangthomae* from Kiangsi is not the mainland race of *M. losea*, for his figure, said to be of natural size, represents a small animal of practically the same size and color as an immature *R. l. exiguus*, with a hind foot measuring only 21 mm. in total length." Still, Allen thought *ouangthomae* really to be a synonym of *flavipectus*. In 1941 (p. 184), Ellerman listed *ouangthomae* as a synonym of *Rattus humiliatus humiliatus* but by 1949 (p. 58) he had transferred it to *Rattus rattus flavipectus*, a combination repeated by Ellerman and Morrison-Scott in 1951 (p. 583). The holotype of *ouangthomae* (MNHN 338) is a mounted skin with skull extracted but lost when we visited Paris. The rat is a young adult. The pelage is faded from its original hues to straw brown over the upperparts, and

TABLE 4
Allocation of Scientific Names Bearing upon the Identity of *Rattus losea*

Original name	Source	Locality	Current allocation
<i>Mus rattoides</i>	Hodgson, 1845, p. 267	Nepal	<i>Rattus turkestanicus</i>
<i>Mus humiliatus</i>	Milne-Edwards, 1868, p. 137	China (Hebei)	<i>Rattus norvegicus</i>
<i>Mus canna</i>	Swinhoe, 1870, p. 636	China (Taiwan)	<i>Rattus</i> sp.
<i>Mus losea</i>	Swinhoe, 1870, p. 637	China (Taiwan)	<i>Rattus losea losea</i>
<i>Mus griseipectus</i>	Milne-Edwards, 1871, p. 93	China (Sichuan)	<i>Rattus norvegicus</i>
<i>Mus flavipectus</i>	Milne-Edwards, 1871, p. 93	China (Sichuan)	<i>Rattus rattus flavipectus</i>
<i>Mus ouangthomae</i>	Milne-Edwards, 1871, p. 93	China (Jiangxi)	<i>Rattus rattus flavipectus</i>
<i>Mus plumbeus</i>	Milne-Edwards, 1874, p. 138	China (Hebei)	<i>Rattus norvegicus</i>
<i>Rattus sakeratensis</i>	Gyldenstolpe, 1917, p. 46	Thailand	<i>Rattus losea sakeratensis</i>
<i>Rattus humiliatus celsus</i>	Allen, 1926, p. 5	China (Yunnan)	<i>Rattus turkestanicus</i>
<i>Rattus rattus exiguus</i>	Howell, 1927, p. 43	China (Fujian)	<i>Rattus losea sakeratensis</i>
<i>Rattus humiliatus insolatus</i>	Howell, 1927, p. 44	China (Shaanxi)	<i>Rattus norvegicus</i>
<i>Rattus humiliatus sowerbyi</i>	Howell, 1928, p. 42	China (Jilin)	<i>Rattus norvegicus</i>

the underparts are whitish washed with grayish brown. It is not an example of *R. losea* but fits best with *R. rattus flavipectus*.

The next name is *Mus plumbeus*, a species also named and described by Milne-Edwards (1874, p. 138) from a specimen caught in Hebei (Chihli) Province of northern China. Allen (1940, p. 1010) regarded the name to be a synonym of *Rattus norvegicus socer*. Ellerman (1941, p. 184) placed it under *Rattus humiliatus humiliatus* but in his revised checklist published in 1949 (p. 66) listed it as a questioned synonym of *R. norvegicus socer*. By 1951 (p. 589), Ellerman and Morrison-Scott treated the name as a synonym of *R. norvegicus caraco*, following the recommendation of Schwarz, which was published and explained in Schwarz and Schwarz (1967, p. 117), although they discussed it under *R. rattus caraco*. We looked at the holotype of *plumbeus* (MNHN 343) in Paris. It is a mounted skin from which the skull had been extracted and is a very young, possibly juvenile, example of *R. norvegicus*.

The other two names out of the five are *Rattus humiliatus insolatus* (Howell, 1927, p. 44) and *Rattus humiliatus sowerbyi* (Howell, 1928, p. 42). The first was described from four specimens collected in Shaanxi (Shensi) Province, China; the latter was described from a young adult collected in Jilin (Manchuria). In his checklist of 1941, Ellerman retained Howell's name combinations but in 1949 (pp. 62–63), Ellerman listed *insolatus* as a subspecies of *Rattus rattoides* and kept *sowerbyi*

as a subspecies of *R. humiliatus*. Ellerman and Morrison-Scott (1951, pp. 588, 599) followed Ellerman's (1949) arrangement for *insolatus* but considered *sowerbyi* to be a synonym of *R. norvegicus caraco*, which was also the conclusion reached by Jones and Johnson (1965, p. 390). Schwarz and Schwarz (1967, p. 117) regarded both *insolatus* and *sowerbyi* to be synonyms of *caraco*, which they listed under *R. rattus*. We have studied the holotype of *insolatus* (USNM 172569) and that of *sowerbyi* (USNM 199620), which consist of well-preserved skins and skulls in the National Museum of Natural History. Both specimens are examples of *R. norvegicus*.

Finally, we should mention that one of the most common species of rats occurring within the geographic range of *R. losea* is now called *R. rattus flavipectus*, the house rat of central and southern China, including the islands of Taiwan and Hainan. To be certain that the holotype upon which the name *flavipectus* is based is not an example of *R. losea*, we examined it carefully in Paris. The holotype (MNHN 340) is a young adult male; the skin is mounted, the skull had been extracted. The specimen, according to Allen (1940, p. 994), was "sent by Père Armand David from Muping, Szechwan, China, to the Muséum d'Histoire Naturelle at Paris" and was described by Milne-Edwards in 1871 (in David, 1871, p. 93) under the name *Mus flavipectus*. We compared the mounted skin and the extracted skull directly with specimens of what we had identified as *R. rattus*

and *R. losea* from southern China. The morphological features of the holotype clearly fit with those characterizing *R. rattus* from China and not *R. losea*.

Information about the scientific names discussed above, and their allocations, are summarized in table 4.

GEOGRAPHIC VARIATION AND SUBSPECIES

We did not thoroughly analyze geographic variation within *Rattus losea*. Except for series from Taiwan and Hainan, our samples are small. To obtain even these we pooled males and females, which cover a range in age from young to old adults. Because of this method, details of any significant patterns of variation that may be present are difficult to detect; more specimens from more localities, and a refined separation of specimens into less heterogeneous groups would be necessary to provide samples from which data could be obtained that might yield better information about geographic variation in the species. With the number of specimens we had and the nature of the samples, we could detect variation from place to place in only a few features, primarily pelage coloration and body size. Color, however, has been used in allocating subspecific names to geographic segments of *R. losea* so from our crude analysis we can better tie names to particular populations.

Judged from our specimens, the population of *R. losea* on Taiwan contains darker, larger-bodied animals than those from other places. Compared with samples from the mainland and Hainan, *R. losea* from Taiwan have darker upperparts with more gray and yellowish tones to the pelage, and denser gray underparts. The Taiwanese rats also average significantly larger than do animals from elsewhere within the geographic range of *R. losea*. The magnitude can be appreciated by looking at the mean differences listed in tables 1–3 in lengths of head and body, tail, skull, and molar rows between the sample from Taiwan and any of those from mainland Southeast Asia and Hainan (see also the crania in fig. 2). These contrasts are distinctive enough that the Taiwanese rats should be referred to as *Rattus losea losea*, a name com-

bination already used by Allen in 1940 (p. 1008).

Osgood (1932) and Allen (1940) placed specimens from mainland China, the island of Hainan, and Vietnam under one subspecies, *exiguus*. We agree with this arrangement of samples but not with the name applied to them. We would add specimens from Thailand and Laos and identify everything from mainland Indochina as *R. losea sakeratensis*. Marshall (1977, p. 465) used the combination *R. l. sakeratensis* strictly for samples from northern and central Thailand because rats from there had plain brown pelage over the upperparts in contrast to the bright brown pelage with yellowish highlights characterizing animals from northeastern Thailand, which he referred to *R. l. exiguus*. Certain specimens from northern Thailand are slightly grayer than those from elsewhere on the Southeast Asian mainland and Hainan but other specimens are inseparable. The differences that do exist between the grayer rats and those with richer brown fur are slight and there is much overlap among the samples. Using pelage coloration alone, we cannot separate samples that are distinct enough to warrant subspecific recognition, at least those samples from northern and central Thailand. For most Thai series we interpret the variation in color among individuals and among samples as being within the range of variation that is characteristic of one subspecies.

The sample from Trat Province in southeastern Thailand is, as we described earlier, composed of very dark brown or blackish rats; they contrast sharply with those in any other sample of *R. losea*. If color is used to define subspecies in *R. losea*, then the population from Trat deserves nomenclatural recognition. We decline such an action and prefer to consider the specimens from southeastern Thailand as representing a richly pigmented population of *R. losea sakeratensis* for there are no features associated with body size, skull, or teeth that will distinguish the specimens available to us from other samples taken from mainland Southeast Asia and Hainan.

Aside from color of pelage, there seems to be little geographic variation among samples taken outside of Taiwan and the Pescadores. Differences in measurements among series

from mainland China, Hainan, Vietnam, and Thailand in external, cranial, and dental features are small and not significant (tables 1–3; fig. 2). Some individuals from northern Thailand are nearly as large as those from Taiwan (see the crania in fig. 2) but these are exceptions. We could not detect any significant patterns of geographic variation in means of external, cranial, and dental measurements, or in qualitative features of skulls and dentitions.

In summary, differences among samples of *R. losea* involving values from measurements reflecting body size, as well as pelage coloration, are the basis for our allocation of samples to subspecies. *Rattus losea losea* refers to the populations on Taiwan and the Pescadores (localities 1–2 in fig. 1). *Rattus losea sakeratensis* (with *exiguus* as a synonym; table 4) should be used for rats from mainland China, Hainan, Laos, Thailand, and Vietnam (localities 3–23 in fig. 1).

The range of variation in pelage color, body size, and qualitative cranial and dental features within and among samples of *R. losea* does not embrace the characteristics associated with the small-bodied and dark-furred rats from the highlands of southern Vietnam that have been associated with the species. And of the many scientific names available for species and subspecies of *Rattus* in Southeast Asia, none apply to the Vietnamese population. Naming and describing this mountain relative of *R. losea* is the subject of the following section.

THE VIETNAMESE RAT

The specimens from Langbian Peak and Gougah in the mountains of southern Vietnam that we refer to a new species were originally identified by other workers as mountain variants of *Rattus losea* (Van Peenen, Ryan, and Light, 1969; Marshall, 1977). But the diagnostic morphological features of the southern Vietnamese animals fall outside the range of variation of external and cranial characteristics seen within samples of *R. losea* from throughout its geographic range. Also, *R. losea* is primarily lowland, the new rat is basically montane. In their pelage color, body size, and other morphological features, examples of the latter from 900 m are similar

to specimens from higher altitudes on the slopes of Langbian Peak and unlike *R. losea* from 800–900 m in nearby countries (Thailand, for example). There is no evidence at hand that characteristics of the new rat in samples from middle altitudes are morphologically convergent towards *R. losea* that live at middle altitudes. And there is no indication in samples of *R. losea* that rats living in lowlands are morphologically different from those in highlands. All of our evidence is consistent with this hypothesis: the samples from Gougah and Langbian Peak represent a morphologically and possibly ecologically distinctive population of *Rattus* that is reproductively isolated from populations of *R. losea*.

Rattus osgoodi, new species

HOLOTYPE: FMNH 46761, the stuffed skin (fig. 4) and skull (fig. 5) of an adult female obtained from Langbian Peak, probably 5000 ft (see explanation below) on February 19, 1937, by W. H. Osgood (field number 6619). Langbian Peak is in Tuyen Duc Province of southern Vietnam and rises slightly higher than 2100 m above sea level. The coronoid process is missing from the left dentary; otherwise, the holotype is intact and well preserved. Measurements of the skin and skull are listed in table 3.

OTHER SPECIMENS: In addition to the holotype, we studied 26 other examples of *R. osgoodi* from the following two localities in Tuyen Duc Province of southern Vietnam (numbers preceding localities key to the places mapped in fig. 1). All FMNH specimens were collected during the period, February 10 to March 2, 1937; the USNM material was obtained on May 27 and 28, 1961.

1. Langbian Peak (also referred to as Mount Lang Bian), lat. 12°03'N, long. 108°26'E: FMNH 46735–46740, 46744–46750, 46752, 46753, 46759, 46760, and 46762–46764; USNM 321523 and 321524. All the FMNH specimens were collected by Osgood. His field catalogue is in the archives of the Department of Mammalogy at the Field Museum of Natural History where Dr. Robert Timm kindly checked some entries for us. Osgood indicated that nine specimens (FMNH 46735–46740 and

46744–46746) were from the southeast base of Langbian Peak, 5000 ft, about 6 miles east of Bankia. There followed an entry recording two specimens of *Manis* from a different locality, then specimens again from simply “Langbian Peak,” which includes the rest of the series we list under *R. osgoodi*. We suspect that Osgood used “Langbian Peak” to refer to the locality at 5000 ft and that all of the rats came from there. Of the two USNM specimens, one was taken at 1500 m, the other at 2000 m.

2. Gougah (Gougah Thac, Gongah, and Chutes de Gongah are other names for the same place), lat. 11°41'N, long. 108°20'E: FMNH 46754 and 46765–46767. Osgood collected these rats and wrote in his field catalogue that they came from “Gougah (Da Nhim River, 25 miles southwest of Dalat), 908 meters.”

DISTRIBUTION: Known only from the highlands of southern Vietnam at altitudes ranging from 3000 to 6600 ft.

ETYMOLOGY: The species is named for the late Dr. Wilfred H. Osgood; see the legend beneath figure 3.

DIAGNOSIS: A species of *Rattus* that in features of skin, skull, and teeth is most like *R. losea* but differs from it by being smaller in most external, cranial, and dental dimensions (table 3); by having a shorter tail relative to head and body length; by its thick, soft, and dark brown fur (fig. 4); by its much smaller skull and molars (fig. 2); by its relatively wider zygomatic arch, interorbital region, and braincase relative to skull length; by its deeper bullae relative to height of braincase; by its lack of anterior labial cusplets on first lower molars of all specimens, and by its occurrence in the mountains of southern Vietnam at altitudes between 3000 and 6600 ft.

DESCRIPTION AND COMPARISON

Small and dark brown, *Rattus osgoodi* is a distinctive species of Indochinese *Rattus*. In features of skin, skull, and dentition, it is most similar to *R. losea* but differs from that species by being smaller in body size, having a shorter tail relative to head and body length, and darker pelage. We compared our specimens of *R. osgoodi* with all available specimens of



FIG. 3. Dr. Wilfred H. Osgood: 1875–1947. Nearly the entire sample of *Rattus osgoodi* was collected by Dr. Osgood on one of the many expeditions in which he participated during his career (see the obituary written by Sanborn, 1948). We are pleased to name the small, dark, thick-furred rat from Langbian Peak in honor of his memory and contributions to mammalian systematics.

R. losea and especially closely with the samples from central Vietnam (localities 11–13, fig. 1). Means of head and body, tail, and hind foot lengths from the series of *R. osgoodi* are significantly smaller than means from Vietnamese samples of *R. losea* (table 3). In addition, the tail is shorter relative to head and

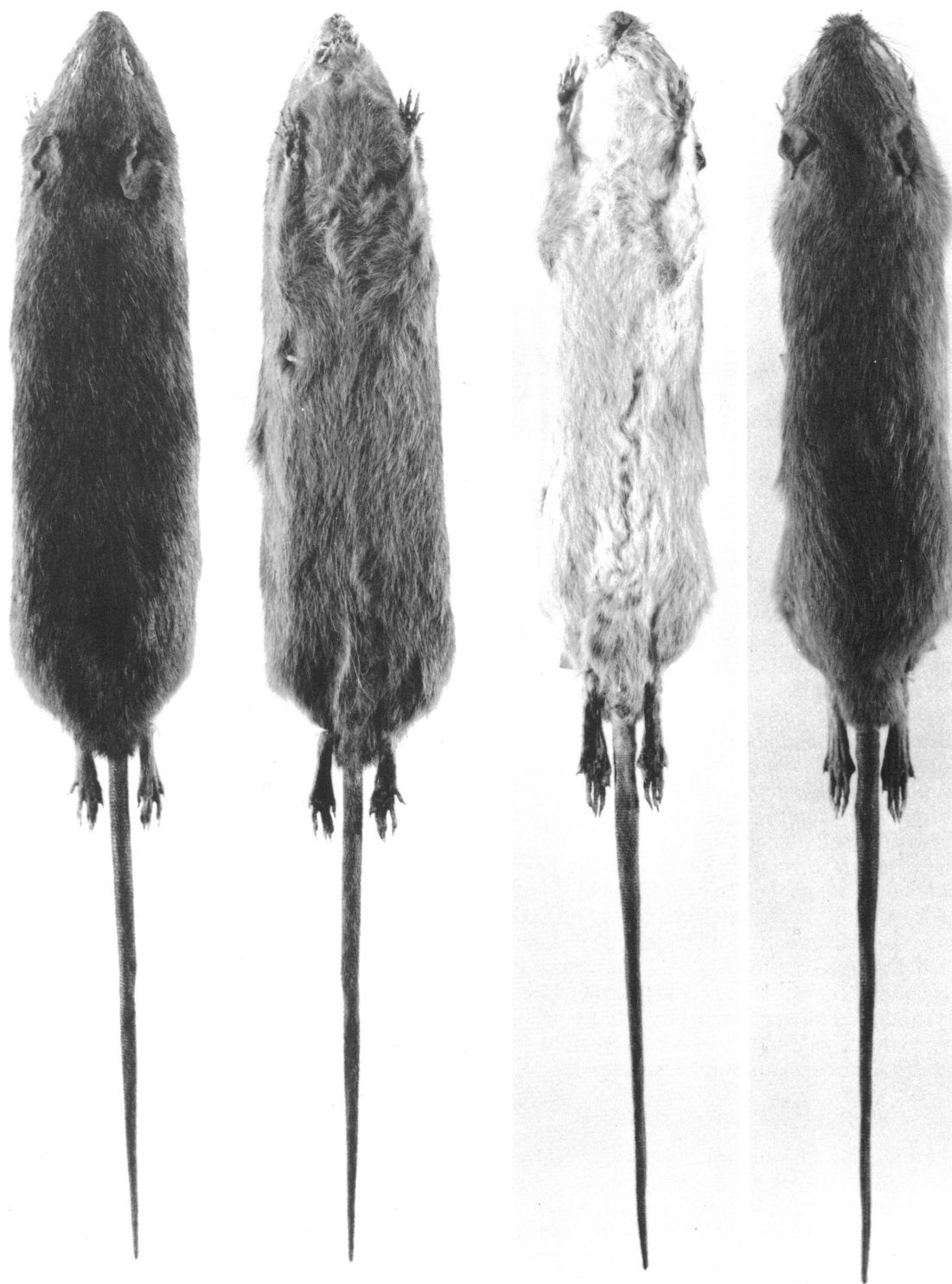


FIG. 4. Dorsal and ventral views of skins. Holotype of *Rattus osgoodi* (FMNH 46761; left) contrasted with adult *R. losea* (FMNH 30988; right) from Quang Tri Province, Vietnam. See table 3 for measurements.

body length in *R. osgoodi* than in any sample of *R. losea*. The ratio, length of tail divided by length of head and body, is 86 percent for *R. osgoodi* and ranges from 90 to 103 percent among the seven samples of *R. losea* whose measurements are listed in tables 1–3.

Pelage of *R. osgoodi* is dense and long, thick and silky to the touch compared with the thin and slightly shaggy fur of *R. losea*. The upperparts of *R. osgoodi* are rich dark brown (instead of brownish gray, as in *R. losea*); the back and rump are darker than the buffy brown sides of the body. The underside of the chin and the inguinal region are dark gray, the rest of the underparts is dark grayish brown washed with buff (contrasted with the grayish white venters of most *R. losea*; fig. 4). The ears and dorsal surfaces of the feet and tail are dark brown (unlike the whitish and buffy gray tones so characteristic of most *R. losea*).

Because the *R. losea* from Trat Province in southeastern Thailand have dark brown or blackish pelage, we compared them closely with *R. osgoodi* to test the notion that the latter might be a dark variant of *R. losea*. It is not. The differences in size and cranial configuration between *R. osgoodi* and specimens in the Trat sample are similar to the differences between *R. osgoodi* and samples of *R. losea* from other places in Thailand and from places outside of that country. In its length and texture, pelage of the Trat rats is like that of *R. losea* and not *R. osgoodi*. Also, the underparts of the latter are darker and more richly pigmented than are those in the sample from Trat Province. The animals from southeastern Thailand are simply dark and richly pigmented versions of *R. losea*.

Juvenile *R. osgoodi* have dark fur but it is duller than that of adults, shorter, and the texture finer. Juvenile *R. osgoodi* are a rich dark brown and contrast strikingly with the brownish gray upperparts of *R. losea* with its suffusion of pale yellow and buff along sides of the body.

Like *R. losea*, female *R. osgoodi* have five pairs of mammae, located in comparable regions of the body.

In its conformation, the skull of *R. osgoodi* is a smaller version of that in *R. losea* (figs. 2 and 5). Mean values of nearly all cranial measurements from our sample of *R. osgoodi* are significantly less than means of the sam-

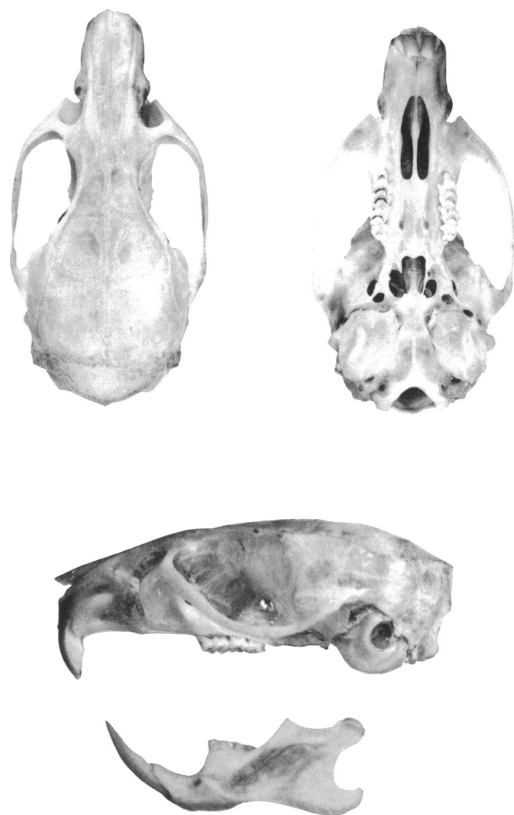


FIG. 5. Holotype of *Rattus osgoodi*. Views of cranium and dentary from FMNH 46571, collected on Langbian Peak, southern Vietnam. Coronoid process is missing from dentary. Approximately $\times 1.5$.

ple from Vietnam (table 3). Similar magnitudes of differences exist between means from *R. osgoodi* and those from samples of *R. losea* collected in China and Thailand (compare table 3 with tables 1 and 2). There are also a few proportional differences between the two species. Compared with *R. losea*, specimens in our sample of *R. osgoodi* have wider zygomatic, interorbital, and braincase breadths relative to length of skull; longer incisive foramina relative to skull length; and deeper bullae relative to depth of braincase.

Morphology of the molars is similar in *R. osgoodi* and *R. losea* (fig. 6); primary differences are size of teeth and frequency of occurrence of anterior labial cusplets on first lower molars. *Rattus osgoodi* has much smaller teeth than *R. losea* (table 3) and each specimen we examined lacked an anterior la-

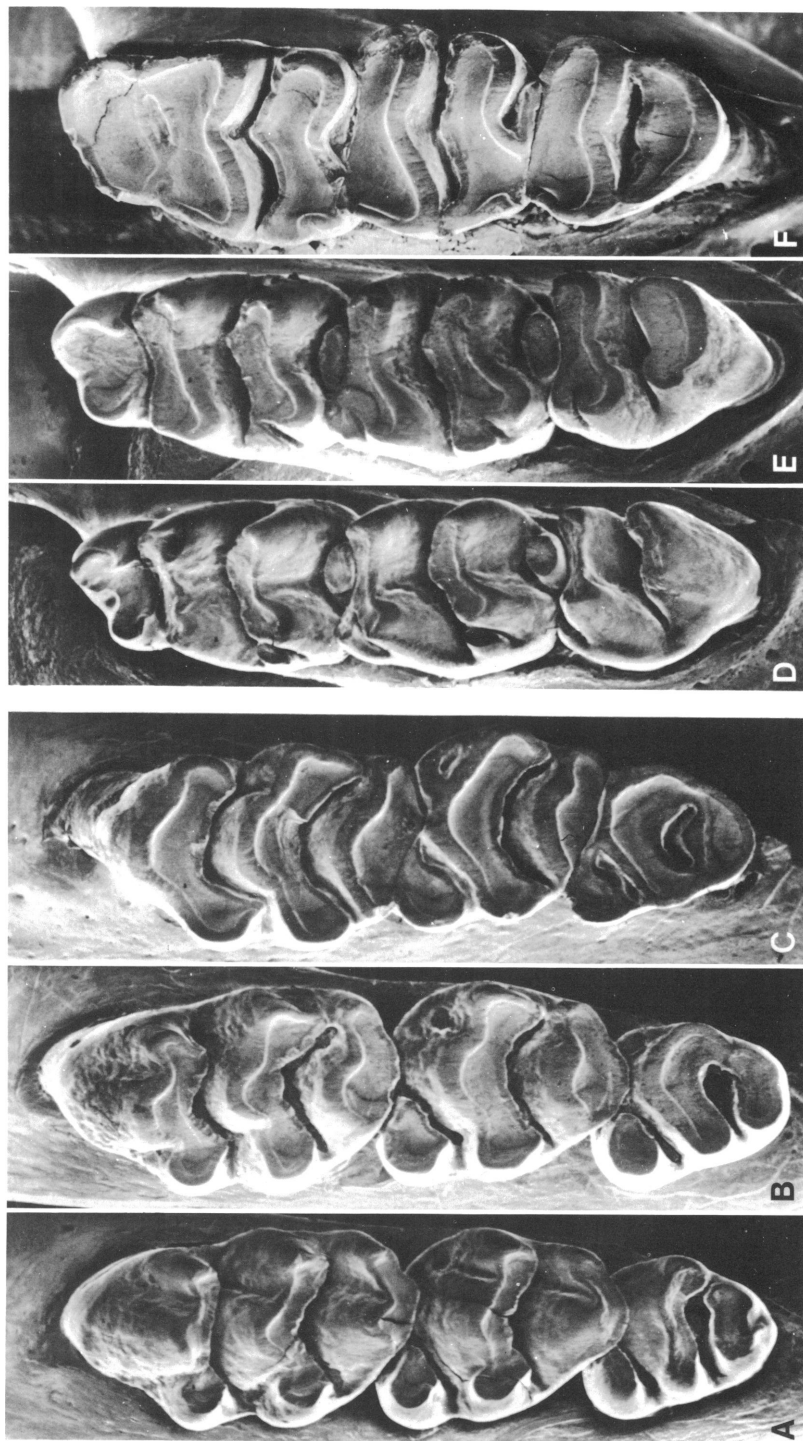


FIG. 6. Occlusal views of left upper (A-C) and lower (D-F) molars of *Rattus osgoodi*. A and D, young adult, FMNH 46745 (CLM₁₋₃, 6.1 mm); B and E, adult, FMNH 46747 (CLM₁₋₃, 6.1 mm); C and F, an older adult and the holotype, FMNH 46571 (CLM₁₋₃, 5.3 mm); CLM₁₋₃, 4.9 mm). Shapes of molars, their sizes relative to each other in a toothrow, and patterns formed by cusps are similar to molar features in *R. losea*.

TABLE 5
Some Measurements (in Millimeters) from Samples of *Rattus* Occurring in Southeast Asia

Species	Lengths			
	Head and body	Tail	Hind foot	Skull
<i>R. losea</i>				
Vietnam	152 (10) ^a	153 (10)	33 (10)	36.6 (10)
Thailand	148 (21)	135 (21)	31 (21)	36.1 (22)
<i>R. osgoodi</i>				
Vietnam	139 (16)	120 (14)	28 (16)	32.8 (15)
<i>R. rattus</i>				
Vietnam	173 (22)	196 (22)	34 (22)	40.9 (22)
Thailand	184 (22)	192 (22)	34 (22)	42.3 (20)
<i>R. nitidus</i>				
Thailand ^b	177 (17)	168 (17)	37 (17)	42.9 (17)
<i>R. sikkimensis</i>				
Thailand	185 (13)	204 (12)	36 (15)	44.8 (14)
<i>R. exulans</i>				
Thailand ^b	115 (32)	128 (32)	23 (32)	28.8 (32)
<i>R. argentiventer</i>				
Thailand ^b	204 (15)	187 (15)	39 (15)	43.7 (15)
<i>R. norvegicus</i>				
Thailand ^b	233 (15)	201 (15)	44 (15)	48.5 (15)
<i>R. turkestanicus</i>				
Pakistan ^c	176 (30)	193 (30)	34 (30)	41.4 (30)

^a Mean; number of specimens in parentheses. Samples contain adults.

^b Values are from Marshall (1977).

^c Our series of *R. turkestanicus celsus*, which is the form occurring closest to the geographic range of *R. losea* and *R. osgoodi* consists of young animals; our best sample of adult *R. turkestanicus* comes from northern Pakistan.

bial cusplet; such a cusp is present on each first lower molar in about one out of every five examples of *R. losea*.

ALTITUDINAL DISTRIBUTION AND HABITAT

In contrast with our records of Vietnamese *R. losea*, which come from regions below 100 m, *R. osgoodi* is montane. All specimens have been trapped in the range from 900 to 2000 m. We have no specific information about either habitat or habits of the species. The combination of small body size, relatively

TABLE 6
Presence (+) or Absence (–) of Anterolabial Cusps (t3) on Second and Third Upper Molars in Samples of *Rattus* (Number of Cusps Expressed as Percentage; Size of Sample in Parentheses)

Species	Second molar		Third molar	
	+	–	+	–
<i>R. losea</i>	89 (39)	11 (5)	5 (2)	95 (42)
<i>R. osgoodi</i>	77 (17)	23 (5)	23 (5)	77 (17)
<i>R. rattus</i>	46 (17)	54 (20)	5 (2)	95 (35)
<i>R. argentiventer</i>	77 (10)	23 (3)	46 (6)	54 (7)
<i>R. nitidus</i>	52 (22)	48 (20)	10 (4)	90 (38)
<i>R. norvegicus</i>	35 (7)	65 (13)	—	100 (20)
<i>R. exulans</i>	100 (44)	—	16 (7)	84 (37)
<i>R. sikkimensis</i>	100 (32)	—	59 (19)	41 (13)
<i>R. turkestanicus</i>	50 (29)	50 (29)	10 (6)	90 (52)

short tail, dark and dense fur, and stubby skull recall the configuration associated with voles (*Microtus*, for example). We suspect *R. osgoodi* to be terrestrial and to live in grass and dense shrubbery providing good cover that may occur either along forest margins or scattered through forest with an open canopy. Thick scrub cover adjacent to agricultural fields may also be good habitat.

CONTRASTS WITH OTHER INDOCHINESE *RATTUS*

Comparing samples of *Rattus losea* with those of *R. osgoodi* is part of the process involved in defining their morphological and distributional limits. Contrasting these two with other species of *Rattus* occurring in the same region is also necessary for their definition. Here we compare the two species with samples of *R. rattus*, *R. nitidus*, *R. sikkimensis*, *R. exulans*, *R. argentiventer*, *R. norvegicus*, and *R. turkestanicus* from Southeast Asia. Values from measurements selected to indicate variation in body size among the nine species are listed in table 5. Frequency of occurrence of certain cusps on upper molars that vary among the species are listed in table 6. Data in these tables are mostly from samples obtained within the range of *R. losea* but a few are from outside that region because

we did not have adequate series from Indochina. Views of crania of the nine species are contrasted in figures 7 to 9. Refer to both tables and figures as you read our comparisons.

Geographic distributions of most of these *Rattus* overlap the ranges of *R. losea* and *R. osgoodi*. Several species have been collected at the same place. We have records of *R. rattus*, *R. argentiventer*, *R. nitidus*, and *R. sikkimensis* from Langbian Peak in southern Vietnam, the type-locality of *R. osgoodi*. Specimens of *R. losea* have been taken at the same localities as *R. rattus*, *R. nitidus*, *R. sikkimensis*, *R. exulans*, and *R. norvegicus*. Specimens caught at the same place may or may not have been taken from the same habitat. We have little data regarding the kind of habitat where each specimen was obtained at any of the localities where either *R. losea* or *R. osgoodi* were taken along with other species of *Rattus*.

Two species have ranges that either overlap slightly or approach those of *Rattus losea* and *R. osgoodi*. *Rattus argentiventer* is known to occur in central and southern Vietnam and southern Thailand (Musser, 1973; Marshall, 1977), near or within the range of *R. losea* and *R. osgoodi*. There are no records of it being collected at the same places as *R. losea* but *R. argentiventer* and *R. osgoodi* have been collected from the same localities. The geographic distribution of *R. turkestanicus celus* approaches that of *R. losea* in southeastern China but the two have yet to be obtained at the same place.

In its small body size, short tail relative to head and body length, thick dark brown upperparts, dark buffy brown underparts, small stocky skull with short rostrum and high cranium, and five pairs of mammae, *R. osgoodi* contrasts sharply with any of the other species of *Rattus*. Only *R. exulans* is smaller, and this species is easily distinguished from *R. osgoodi* by its grayish brown upperparts, pale gray underparts, long tail (conspicuously longer than length of head and body), four pairs of mammae (one pectoral, another in the postaxillary region, and two in the inguinal area), and smaller and more delicate skull with a relatively longer rostrum and lower braincase.

Rattus losea is also smaller in body size than *R. rattus*, *R. argentiventer*, *R. nitidus*,

R. norvegicus, *R. turkestanicus*, and *R. sikkimensis* but is larger than *R. exulans*. Color of pelage is similar in *R. losea* and *R. exulans* but the latter has smaller feet, a tail much longer than head and body, and four pair of mammae, not five as is characteristic of *R. losea*. Cranial differences between *R. exulans* and *R. losea* are similar to those distinguishing *R. osgoodi* and *R. exulans*. Finally, at the anterolabial margin of each second upper molar there is a large cusp (t3) present in all specimens of *R. exulans*; such a cusp is smaller and often absent in *R. losea*.

Specimens of *R. losea* in museum collections are often misidentified as either *R. norvegicus* or *R. rattus*, and, as we explained in the previous section, the scientific names associated with those two species, and with *R. turkestanicus*, have been applied either directly or indirectly to specimens of *R. losea*. Young adult *R. norvegicus* do resemble adult *R. losea*, especially in coloration of fur. They can be distinguished, however, by the thicker and somewhat woolly pelage of *R. norvegicus* as contrasted with the less dense and shaggier pelage of *R. losea*; by the bicolored tail of *R. norvegicus* (dark above, white to gray below for its length), not monocolored brown as in *R. losea*; by the white dorsal surfaces of the feet in *R. norvegicus* as opposed to the grayish white or grayish brown tones of *R. losea*; and the six pairs of mammae so characteristic of *R. norvegicus*, never five pair as in *R. losea* (there is a second postaxillary pair in *R. norvegicus*). The two differ in cranial and dental features as well. Compared with specimens of *R. losea*, those of *R. norvegicus* have larger, chunkier and heavier crania, even young adults; the rostrum is longer relative to skull length; pronounced temporal ridges provide the top of the cranium with a rectangular, not vase-shaped, outline, clearly seen in figure 7; sides of the braincase slope outward from the temporal ridges instead of being vertical; the anterolabial cusp (t3) of each first upper molar is either very small or absent (always large and distinct in *R. losea*), and the comparable cusp on each second upper molar is usually absent in a third of the specimens in any sample (usually present in *R. losea*).

The fur of *R. losea* and native Asian *R. rattus* is much alike in thickness, texture, and color; both species have five pairs of mammae. The two can be distinguished by size

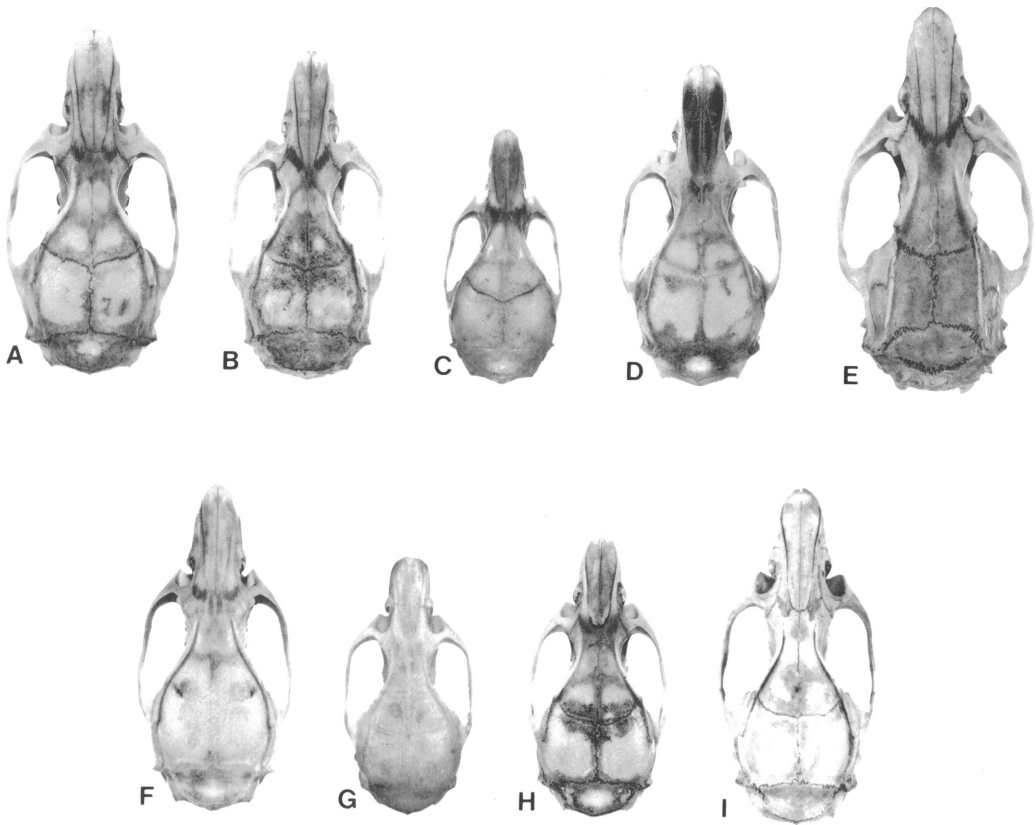


FIG. 7. Dorsal views of crania from adult *Rattus*. A, *R. sikkimensis*, Thailand (USNM 533456). B, *R. nitidus*, Luzon Island in the Philippines (FMNH 62431). C, *R. exulans*, Central Sulawesi (AMNH 215290). D, *R. turkestanicus*, Nepal (AMNH 251664). E, *R. norvegicus*, Taiwan (AMNH 185196). F, *R. rattus*, Thailand (USNM 533641). G, *R. osgoodi*, southern Vietnam (FMNH 46571). H, *R. losea*, Hainan Island, southern China (AMNH 59187). I, *R. argentiventer*, Bali (AMNH 107543). Natural size. Note similarity in dorsal configuration between *R. losea* (H) and *R. argentiventer* (I).

and tail length. Adults of *R. losea* are smaller in body size than those of *R. rattus* and have tails that are as long as the head and body or shorter, as opposed to tails much longer than head and body length, which is typical of *R. rattus*. Configurations of skulls and molars of the two species are basically similar but *R. rattus* does not have such a compact and chunky cranium, its rostrum is relatively longer and narrower, and the anterolabial cusp on each second upper molar is usually missing in half of the specimens in any sample (as opposed to being present on most specimens in any sample of *R. losea*).

Rattus turkestanicus is larger than *R. losea* in body size, its tail is much longer than combined lengths of head and body, and females have six pairs of mammae, not five. Upper-

parts of *R. turkestanicus* are conspicuously grayer than those of *R. losea*; the underparts are usually cottony white and sharply demarcated from sides of the body in most samples, grayish white in others (contrasting with the darker gray and grayish buff tones of *R. losea*); the tail is bicolored in a pattern similar to that of *R. norvegicus* except for samples of *R. t. celsus* in which the tail is dark brown above and pale brown on the undersurface. The cranium of *R. turkestanicus* is much wider, longer, and flatter compared with that of *R. losea*, the rostrum is long and thin, not short and blunt, the incisive foramina are wider, and the bullae smaller relative to size of the cranium. The molars are larger in *R. turkestanicus* and the anterolabial cusp of each second upper molar is not present in about

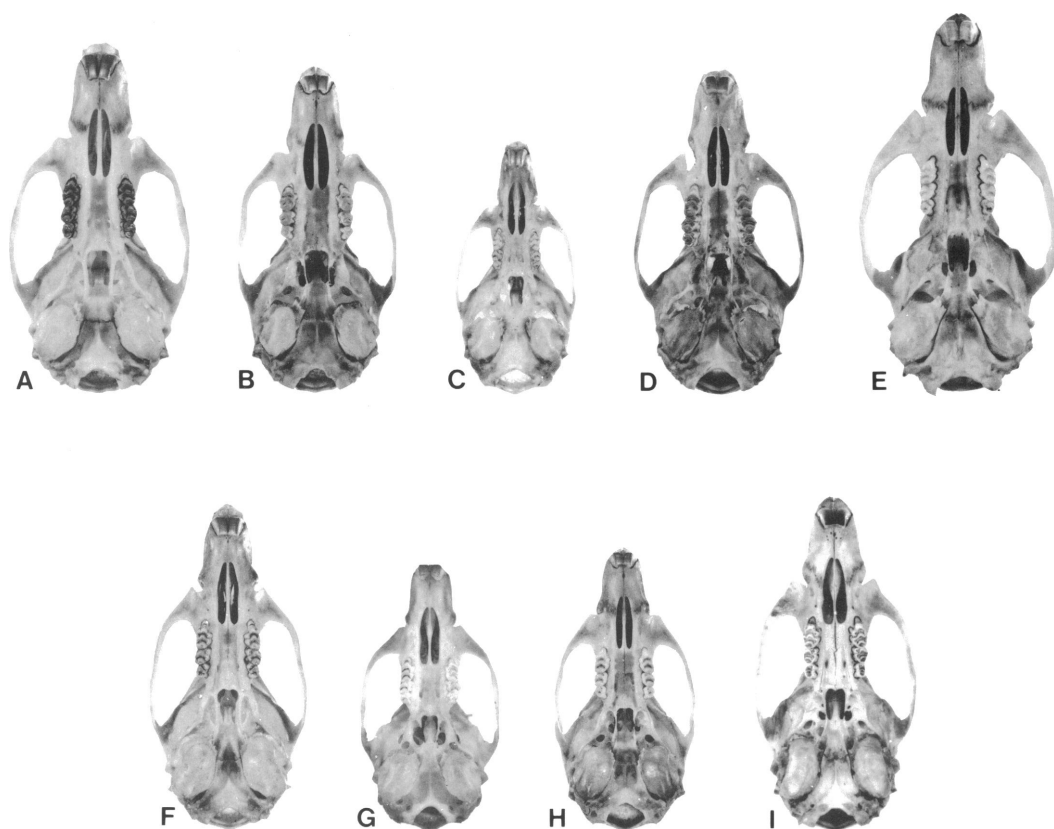


FIG. 8. Ventral views of crania from same specimens shown in figure 7. A, *R. sikkimensis*. B, *R. nitidus*. C, *R. exulans*. D, *R. turkestanicus*. E, *R. norvegicus*. F, *R. rattus*. G, *R. osgoodi*. H, *R. losea*. I, *R. argentiventer*. Natural size.

half of any sample (usually a part of the occlusal surface in *R. losea*).

There are three other species we have not yet contrasted with *R. losea*: *R. sikkimensis*, *R. nitidus*, and *R. argentiventer*. Of these, *R. sikkimensis*, in addition to being much larger than *R. losea*, is distinguished by having long and thick dorsal pelage with long guard hairs down the middle, creamy white underparts, a monocolored tail that is much longer than length of head and body, large, dark brown feet, and six pairs of mammae. The cranium of *R. sikkimensis* is large and appears sturdy, the rostrum relatively longer and narrower than that in *R. losea*, and the sides of the braincase slope outward from the temporal ridges rather than being vertical or nearly so as is typical of *R. losea*. Molars of *R. sikkimensis* are larger and appear chunkier than those in *R. losea*, and are usually rimmed with a hard black coating; such a tarry substance is

absent from the smaller and more delicate teeth of *R. losea*.

Rattus nitidus resembles *R. losea* in color of fur and length of tail relative to head and body length but has a larger body and bigger feet. Tops of the feet are pearly white, not grayish white or brown as they usually are in *R. losea*. Like *R. norvegicus*, *R. turkestanicus*, *R. sikkimensis*, and *R. argentiventer*, female *R. nitidus* have six pairs of mammae. Cranial differences between the two species are evident in figures 7 to 9. In addition to size, *R. nitidus* has wider and more flared zygomatic arches, a relatively longer and more slender rostrum, lower cranium, wider incisive foramina, and smaller bullae relative to size of braincase. Occlusal configurations of the molars are similar in both species but *R. nitidus* has larger teeth, the anterolabial cusp of each first upper molar is either very small or so reduced in size that it is inconspicuous

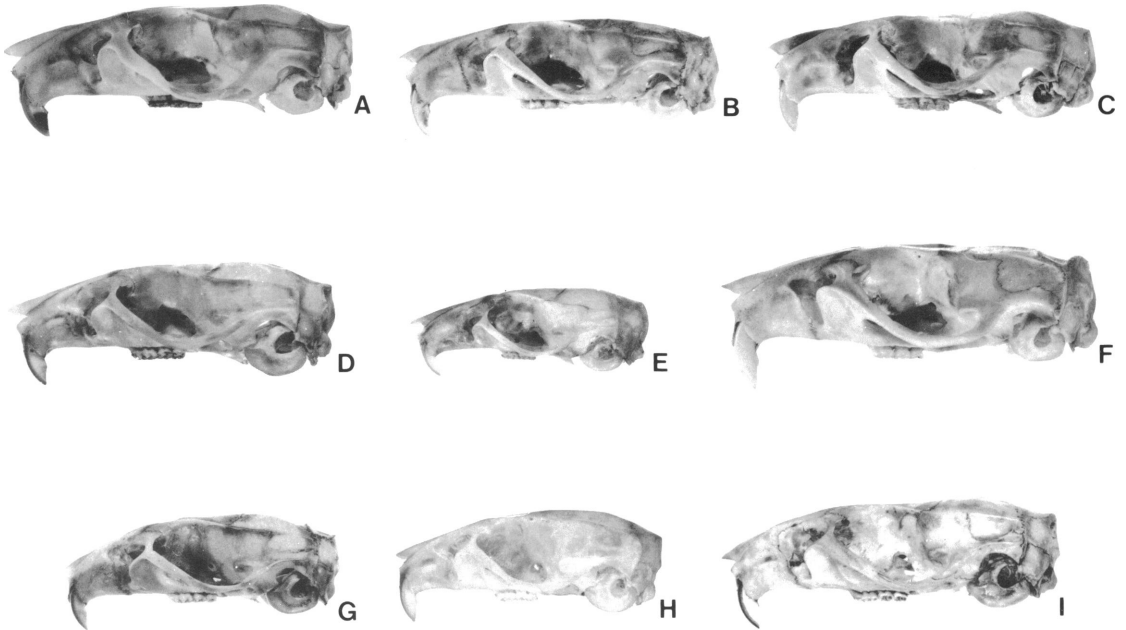


FIG. 9. Lateral views of crania from same specimens shown in figures 7 and 8. A, *R. sikkimensis*. B, *R. turkestanicus*. C, *R. nitidus*. D, *R. rattus*. E, *R. exulans*. F, *R. norvegicus*. G, *R. losea*. H, *R. osgoodi*. I, *R. argentiventer*. Natural size.

(large and evident in *R. losea*), and comparable cusps on second upper molars are usually absent in about half of any sample (usually present in *R. losea*).

The body proportions of *R. argentiventer*, the ricefield rat, are very much like those in *R. losea*, including length of tail relative to that of head and body. *Rattus argentiventer* is a larger animal, however, with upperparts clothed in variegated black and yellowish brown fur, underparts covered by silvery white pelage, and six pairs of mammae. Preauricular orange hair tufts contrast with the top of the head, a pattern absent from specimens of *R. losea*. Configurations of cranium and cusp patterns are much alike in the two species. Both have deep and chunky crania, conspicuous vase-shaped outlines formed by ridges bounding the dorsal margins of the cranium, short and wide rostra, and large bullae relative to skull size (the ratio, length of bulla divided by skull length, ranges from 17 to 19 percent among samples of *R. losea*, 18 percent in that of *R. osgoodi*, 19 percent in *R. argentiventer*, and 15 to 17 percent in species with relatively smaller bullae such as *R. sikkimensis*, *R. rattus*, *R. turkestanicus*,

and *R. nitidus*). Frequency of occurrence of anterolabial cusps on upper molars is similar in the two species except that the cusp on each third upper molar is present in about half of any sample of *R. argentiventer* but absent from most specimens in any sample of *R. losea*.

We also compared our specimens of *R. losea* and *R. osgoodi* with samples of *R. brunneus*, the only other species of *Rattus* from mainland Southeast Asia that we did not discuss above, mainly because it is so different from *R. losea* and its distribution in Nepal is so far removed from those of the other two species. *Rattus brunneus* has a body size about like that of *R. sikkimensis*, body and tail proportions similar to *R. rattus*, dark brown upperparts and either grayish buff or dark buffy brown underparts, and six pairs of mammae. Configurations of skull and molars resemble those seen in *R. rattus* and *R. sikkimensis*.

We did not restrict our comparisons of *R. losea* and *R. osgoodi* only to the species discussed above. We also brought together samples of native *Rattus* found on the Malay Peninsula and islands of the Sunda Shelf to test the possibility that either *R. losea* or *R. os-*

goodi might be Indochinese relatives of species native to the Sunda Shelf: *R. tiomanicus*, *R. annandalei*, *R. baluensis*, and *R. hoogerwerfi*. See Musser and Newcomb (1983) for discussions of these four, and illustrations of skulls and dentitions. None of these rats have any close morphological tie to *R. losea* and *R. osgoodi* unless it is to *R. tiomanicus*, which is the most widespread on the Shelf and the species most closely related to native Asian *R. rattus* (Musser and Califfa, 1982). Morphological contrasts between *R. tiomanicus* and *R. losea* and its mountain relative are of the same kinds and degree as those distinguishing *R. rattus* from *R. losea* and *R. osgoodi*.

UNANSWERED QUESTIONS

As we wrote in the Introduction, ours is not a major taxonomic revision of *Rattus losea*. We brought together specimens in order to obtain an estimate of the morphological and geographic limits of the species so we could determine what relationship the samples from southern Vietnam had with *R. losea*—whether part of that species or sufficiently different to represent a genetically isolated population. To determine whether the montane samples represented a geographical variant of one species or a separate entity with distinct morphological and distributional characteristics implying a separate evolutionary history is important to learning about the present diversity of *Rattus* in Asia.

We learned more about *Rattus losea* than we knew before and we have added another species to the murid fauna of Southeast Asia. We remain ignorant about many aspects of *R. losea* and *R. osgoodi*: their actual geographic and altitudinal distributions, many details of their ecologies, habitat relationships between them and other species of *Rattus* living in the same areas, and where both species fit within the picture of phylogenetic relationships among species of Indochinese *Rattus*.

What are the geographic limits of *Rattus losea*, especially in Laos, Cambodia, and northern Vietnam? Does *R. osgoodi* occur outside the Langbian region? What are the biological and historical reasons for their distributions? Does *R. losea* extend down peninsular Thailand to places south of the Isth-

mus of Kra as Marshall (1977) indicated? *Rattus losea*, according to our data, is found in tropical and subtropical habitats on the Indochinese mainland north of the Isthmus of Kra (lat. 10°50'N) and the islands of Taiwan, the Pescadores, and Hainan. We do not have any records of the species from the many smaller islands off the coast of Indochina in the South China Sea. Whether the rat occurs on those places but has not yet been collected or has been caught but is masquerading under misidentifications in collections of museums we have not visited is unknown.

We have examined sufficient specimens of *Rattus* from the Indo-Australian region to confidently state that *R. losea* does not occur in island archipelagos east of Indochina. Why has not this species extended its geographic distribution onto archipelagos east of mainland Indochina through human agency? Ricefields, scrub, gardens, and other kinds of habitats made and maintained by humans seem to be prime habitat for *R. losea*. Similar situations support populations of *R. argentiventer* and that species has a spotty distribution throughout the Indo-Australian region all the way to New Guinea (Musser, 1973), a range best explained by the hypothesis that it was originally native to Southeast Asia and spread farther east, possibly along with the expansion of wet rice culture.

How are the resources of the habitat utilized wherever either *R. losea* or *R. osgoodi* occur together with another species of *Rattus*? At present, there are few ecological data by which we can assess the interrelationships between these two species and other *Rattus* as to such factors as utilization of food resources, nesting sites, and amount of time a particular species spends on the ground or in trees and shrubs. Wherever *R. losea* and *R. osgoodi* occur together with species such as *R. sikkimensis* and *R. rattus*, for example, we can only suppose that the former two are primarily terrestrial and dependent on resources near the ground, whereas the others are able to utilize resources on and above ground because both are agile climbers. Supposition, however, is not good enough—careful field study is necessary.

Study of skins and skulls supports the hypothesis that *R. losea* and *R. osgoodi* are morphologically and probably phylogenetically closer to one another than to any other

species of *Rattus*. Of the native Indochinese *Rattus*, which are likely the closest relatives of *R. losea* and its mountain relation? We do not have results from extensive quantitative or qualitative analyses that might clearly resolve phylogenetic relationships among the species. Results we did obtain from comparisons among the samples of different *Rattus* utilizing data from skins and skulls suggest a relationship that should be tested with other kinds of data. In Marshall's (1977) lively report on the rats and mice known to occur in Thailand, he referred to *R. argentiventer* as the ricefield rat and *R. losea* as the lesser ricefield rat; the common names reflect results obtained in our study.

In many ways *Rattus losea* is a small version of *R. argentiventer*. They share such features as short muzzle, length of tail relative to length of head and body, configurations of body and feet, relative sizes of palmar and plantar footpads, shape and proportions of the skull and molars, large bullae relative to skull size, as well as chromosomal characteristics (see the karyotypes in Markvong, Marshall, and Gropp, 1973). There are some differences between them, such as coloration of fur and number of mammae, but otherwise, they are much alike. The resemblances may point to a real phylogenetic link between them rather than to convergent evolutionary development of features associated with grassland and scrub habitats.

Both *Rattus losea* and *R. argentiventer* are terrestrial. Prime habitat for each is grass and shrubs, especially where this association borders ricefields and other croplands or fills in abandoned fields. We have no records of the two occurring together. Is this relationship real or does it simply reflect inadequate collecting at the right places? *Rattus losea* has a range that is mostly north of the geographic distribution of *R. argentiventer* (see Marshall's, 1977, distribution maps for the two species). On mainland Indochina, the latter is known only from southern Thailand and southern Vietnam. Joe Marshall told us that he had not found the two species at the same localities in Thailand. Both have been taken in Quang Tri Province in the central part of Vietnam, but at different places; we have not seen specimens from anywhere north of Quang Tri Province and none are noted in the literature; *R. losea*, on the other hand,

has been recorded from northern Vietnam (Tien, 1961, 1978). If specimens actually indicate the entire geographic distributions of *R. losea* and *R. argentiventer*, and if they are as closely related as we suspect them to be, then the two might not be found at the same place.

Rattus losea and *R. argentiventer* may not be sympatric, but *R. argentiventer* and *R. osgoodi* might occur together. Both have been collected on Langbian Peak. Four specimens of *R. argentiventer* (FMNH 46734 and 46741–46743) are from the same place where most of the *R. osgoodi* came from at 5000 ft and two others are from 1700 m (USNM 321268 and 321271). Both species were also obtained at Gougah at 908 m (FMNH 46770–46772 and 46775–46777 are the examples of *R. argentiventer*). We do not know if the two occupy the same habitat and utilize similar resources. Possibly there is a separation; the ricefield rat may prefer grass cover, for example, and *R. osgoodi* may be restricted to dense scrub or even forest where those associations abut against grass and shrubs. This is the kind of ecological information we need. The only data we have comes from the field notes of Bernard Feinstein, who collected the two USNM *R. osgoodi* and the two USNM *R. argentiventer*; one of the former was "taken from primary fagacious cover," and one of the latter was obtained "from grass along bank of stream."

In an attempt to understand relationships between *R. losea* and *R. argentiventer*, especially the possible significance of their ranges as we see them now to biogeographic relationships, we assume that the evolutionary history of each species is associated with the geo-climatic history of Indochina. The contemporary distributions and the morphologies of each suggest that *R. losea* may have evolved in the northern portion of Indochina, *R. argentiventer* in the southern part. We assume here, as we hypothesized before (Musser and Newcomb, 1983), that *R. argentiventer* is native to mainland Indochina north of the Isthmus of Kra. But, as Marshall (1977) has pointed out, the species has never been taken in native habitats in Thailand north of the Isthmus, only in ricefields. Most specimens from Vietnam for which we have data come from ricefields and other agricultural formations. If the expan-

sive range of *R. argentiventer* outside of Indochina came about through inadvertent human transport and introduction to peninsulas and islands, there is no reason why the occurrence of the species in some places in Indochina, Thailand for example, could not likewise have resulted from similar introductions. The original geographic range of *R. argentiventer*, if the rat is really native to the southern portion of mainland Indochina, may have been much smaller than it is at present and originally may not have overlapped that of *R. losea*, as it barely does now in central Vietnam.

And possibly the geographic distribution of *R. losea* was not as large as we see it now. Except for the specimens taken in grass beneath pine forest in Chaiphum Province and those from mangrove forest in Chantaburi Province, the only places Marshall (1977) considered to be native habitats in Thailand for the species, all other examples of *R. losea* for which we have habitat data come from environments associated with humans. We are convinced that *R. losea* is a true native of Indochina but we are not sure that its present distribution is similar to what it was before the natural vegetational formations were transformed to extensive agricultural associations.

Samples of the vole-like *R. osgoodi* come from one small region in southern Vietnam. We lack detailed habitat information for most of the specimens. We speculate that the rats live in habitats similar to those supporting *R. losea* but at higher altitudes; still, we are not sure. Based on morphological evidence, *Rattus osgoodi* is closely related to *R. losea*. Their closest living relative may be *R. argentiventer*. Finally, we do not know if the Langbian area is the only place where *R. osgoodi* occurs. We might expect it to also be found farther north in the highlands scattered between Quang Tri and Langbian Peak and in the nearby mountains of southeastern Laos. Very little collecting of mammals has been done in these hilly regions.

It is of special interest that such a distinctive species as *R. osgoodi* is part of the fauna of southern Vietnam. Another rat, *Maxomys moi*, has a geographic range in the highlands of southern Vietnam and southern Laos (Musser, Marshall, and Boeadi, 1979) and is found nowhere else. Both species may be as-

sociated with subtropical mountain evergreen forest, which is restricted to the mountainous backbone of Laos and Vietnam in that part of Indochina (see fig. 1 in Fooden, 1982). That mountain region deserves more study in the context of understanding biogeographic relationships of Asian mammals. It is, for example, part of what Eudey (1980) calls the Annamitic Cordillera, one of the postulated refugia during the Quaternary which was hypothesized to be important in the evolution of Asian macaques. What part these highlands played in the evolutionary histories of small mammals such as *Rattus osgoodi* and *Maxomys moi* is unknown and should be investigated. There are many questions to be answered.

LITERATURE CITED

- Abe, Hisashi
1971. Small mammals of central Nepal. Jour. Fac. Agricult. Hokkaido Univ., vol. 56, pt. 4, pp. 367-423, figs. 1-11, pls. 1-2.
- Akhtar, S. A.
1959. A new rat from Gilgit (Kashmir). Pakistan Jour. Sci. Res., vol. 2, no. 2, pp. 41-44, p. 53, pls. 1-4.
- Allen, Glover M.
1926. Rats (genus *Rattus*) from the Asiatic Expeditions. Amer. Mus. Novitates, no. 217, pp. 1-16.
1940. The mammals of China and Mongolia. Natural History of Central Asia, vol. 11, pt. 2. New York, The American Museum of Natural History, pp. i-xxvi, 621-1350, pls. 10-20.
- Aoki, Bunichiro, and Ryo Tanaka
1938. Biostatistical research on *Rattus losea* (Swinhoe, 1870), a Formosan wild rat, with special reference to its diagnostic characters for taxonomy. Mem. Fac. Sci. and Agric. Taihoku Imperial Univ., vol. 23, no. 1, pp. 1-74, figs. 1-14.
1941. The rats and mice of Formosa illustrated. Mem. Fac. Sci. and Agric. Taihoku Imperial Univ., vol. 23, no. 4, pp. 121-191, many figs. and pls.
- Bonhote, J. Lewis
1906. The mammalian fauna of China. Part I. Murinae. Proc. Zool. Soc. London, 1905, vol. ii, pp. 384-397.
- Corbet, G. B.
1978. The mammals of the Palearctic Region: a taxonomic review. London, British Museum (Nat. Hist.), pp. 1-314, maps 1-104.

- David, Armand
1871. Journal d'un voyage [géologique] en Mongolie et en Chine fait en 1866-68. *Nouv. Arch. Mus. d'Hist. Nat. Paris*, 1867, 1871, 7 (Bull.), pp. 75-100.
- Duncan, J. F., and P. F. D. Van Peenen
1971. Karyotypes of ten rats (Rodentia: Muridae) from Southeast Asia. *Caryologia*, vol. 24, pp. 331-346, figs. 1-12.
- Ellerman, J. R.
1941. The families and genera of living rodents. London, British Museum (Nat. Hist.), vol. 2, Family Muridae, pp. i-ixii, 1-690, figs. 1-50.
1949. The families and genera of living rodents. London, British Museum (Nat. Hist.), vol. 3, pt. 1, pp. i-v, 1-210.
- Ellerman, J. R., and T. C. S. Morrison-Scott
1951. Checklist of Palearctic and Indian mammals, 1759 to 1946. London, British Museum (Nat. Hist.), pp. 1-810, 1 map.
- Etemad, E.
1964. On three new mammals from Iran (one rat and two bats). *Mammalia*, vol. 28, supp. 1, pp. 652-654, figs. 1-5.
- Eudey, Ardieth A.
1980. Pleistocene glacial phenomena and the evolution of Asian macaques. In, Lindburg, Donald G. (ed.), *The Macaques: studies in ecology, behavior and evolution*. New York, Van Nostrand Reinhold Co., pp. 52-83, 4 figs.
- Fooden, Jack
1982. Taxonomy and evolution of the *sinica* group of macaques: 3. Species and subspecies accounts of *Macaca assamensis*. *Fieldiana, Zool.*, new ser., no. 10, publ. 1329, pp. 1-52, figs. 1-10.
- Gyldenstolpe, Nils
1917. Zoological results of the Swedish Zoological expeditions to Siam, 1911-1912 and 1914-1915. V. Mammals. *Kung, Svenska Vetenskap. Handl.*, vol. 57, no. 2, pp. 1-59, pls. 1-6.
- Hassinger, Jerry D.
1973. A survey of the mammals of Afghanistan resulting from the 1965 Street Expedition (excluding bats). *Fieldiana, Zool.*, vol. 60, pp. i-ix, 1-195, figs. 1-50.
- Hodgson, B. H.
1845. On the rats, mice, and shrews of the central region of Nepal. *Ann. Mag. Nat. Hist.*, ser. 1, vol. 15, pp. 266-270.
- Howell, A. Brazier
1927. Two new Chinese rats. *Proc. Biol. Soc. Wash.*, vol. 40, pp. 43-46.
1928. New Chinese mammals. *Ibid.*, vol. 41, pp. 41-44.
1929. Mammals from China in the collections of the United States National Museum. *Proc. U.S. Natl. Mus.*, vol. 75, art. 1, pp. 1-82, pls. 1-10.
- Jones, Gwilym S.
1975. Catalogue of the type specimens of mammals of Taiwan. *Quart. Jour. Taiwan Mus.*, vol. 28, nos. 1 and 2, pp. 183-217.
- Jones, J. Knox, Jr., and David H. Johnson
1965. Synopsis of the lagomorphs and rodents of Korea. *Univ. Kansas Publ. Mus. Nat. Hist.*, vol. 16, no. 2, pp. 357-407.
- Makino, Sajiro
1943. Studies on the murinae chromosomes III. A comparative study of chromosomes in five species of *Rattus*. *Jour. Fac. Sci. Hokkaido Imperial Univ.*, Series VI, vol. 9, no. 1, pp. 19-60, figs. 1-130.
- Markvong, A., J. T. Marshall, Jr., and A. Gropp
1973. Chromosomes of rats and mice of Thailand. *Nat. Hist. Bull. Siam Soc.*, vol. 25, pp. 23-40, figs. 1-24.
- Marshall, Joe T.
1977. Family Muridae: rats and mice. Pp. 396-487. Reprinted in *Mammals of Thailand* (Boosong, L. and J. A. McNeely, eds.), Assoc., Conserv. of Wildlife, Bangkok, Thailand.
- Milne-Edwards, Alphonse
1864-1874. *Recherches pour servir à l'histoire naturelle des mammifères, comprenant des considérations sur la classification de ces animaux par M. H. Milne-Edwards, des observations sur l'hippopotame de Liberia et des études sur la faune de la Chine et du Tibet oriental.* (With Henri Milne-Edwards.) 4to, Paris, 394, atlas of 105 pls.
- Musser, Guy G.
1970. Species-limits of *Rattus brahma*, a murid rodent of northeastern India and northern Burma. *Amer. Mus. Novitates*, no. 2406, pp. 1-27, figs. 1-6.
1973. Zoogeographical significance of the rice-field rat, *Rattus argentiventer*, on Celebes and New Guinea and the identity of *Rattus pestivulus*. *Ibid.*, no. 2511, pp. 1-30, figs. 1-5.
1981. Results of the Archbold Expeditions. No. 105. Notes on systematics of Indo-Malayan murid rodents, and descriptions of new genera and species from Ceylon, Sulawesi, and the Philippines. *Bull. Amer. Mus. Nat. Hist.*, vol. 168, art. 3, pp. 225-334, figs. 1-51.

1982. Results of the Archbold Expeditions. No. 108. The definition of *Apomys*, a native rat of the Philippine Islands. Amer. Mus. Novitates, no. 2746, pp. 1-43, figs. 1-19.
- Musser, Guy G., and Debra Calafia
1982. Results of the Archbold Expeditions. No. 106. Identities of rats from Pulau Maratua and other islands off East Borneo. Bull. Amer. Mus. Nat. Hist., no. 2726, pp. 1-30, figs. 1-5.
- Musser, Guy G., Joe T. Marshall, Jr., and Boeadi
1979. Definition and contents of the Sundaic genus *Maxomys* (Rodentia, Muridae). Jour. Mammal., vol. 60, pp. 594-606, 1 fig.
- Musser, Guy G., and Cameron Newcomb
1983. Malaysian murids and the giant rat of Sumatra. Bull. Amer. Mus. Nat. Hist., vol. 174, art. 4, pp. 327-598, figs. 1-117.
- Niethammer, J., and J. Martens
1975. Die gattungen *Rattus* und *Maxomys* in Afghanistan und Nepal. Z. Säugetierkunde, vol. 40, pp. 325-355, figs. 1-10.
- Osgood, Wilfred H.
1932. Mammals of the Kelley-Roosevelts and Delacour Asiatic Expeditions, Publ. 312, Field Mus. Nat. Hist., Zool. Ser., vol. 18, no. 10, pp. 193-339, 1 map, pls. 1-2, 1 fig.
- Pictet, Francois-Jules, and Charles Pictet
1844. Notices sur les animaux nouveaux ou peu connus du Musée de Genève. Description des rats envoyés de Bahia au Musée de Genève. Privately printed. Pp. 41-82, pls. 12-23.
- Roberts, T. J.
1977. The mammals of Pakistan. Pp. i-xxv, 1-361, figs. 1-90, species illus. 1-95, maps 1-118, color pls. 1-4. London and Tonbridge, Ernest Benn Limited.
- Sanborn, Colin Campbell
1948. Wilfred Hudson Osgood: 1875-1947. Jour. Mammal., vol. 29, no. 2, pp. 95-112, frontis., pls. 1-2.
- Satuñin, K. A.
1903. Neue Nagetiere aus Centralasien. Annuaire Mus. Zool. Acad. Imp. Sci. St. Pétersbourg, vol. 7, pp. 547-589, 2 figs.
- Schlitler, Duane A., and Kitti Thonglongya
1971. *Rattus turkestanicus* (Satunin, 1903), the valid name for *Rattus rattoides* Hodgson, 1845 (Mammalia: Rodentia). Proc. Biol. Soc. Wash., vol. 84, no. 20, pp. 171-174.
- Schwarz, Ernst, and Henriette K. Schwarz
1967. A monograph of the *Rattus rattus* group. Ann. Esc. Nac. Cien. Biol. Mexico, vol. 14, pp. 79-178, 7 figs, 5 maps.
- Shaw, Tsen-hwang, Wang Sung, Lu Chang-kwun, and Chang Luan-kuang
1966. A survey of the mammals of Hainan Island, China. Acta. Zool. Sinica, vol. 3, no. 3, pp. 260-276.
- Swinhoe, Robert
1870. Catalogue of the mammals of China (south of the River Yangtze) and of the island of Formosa. Proc. Zool. Soc. London, 1870, no. XLII, pp. 615-654.
- Tanaka, Ryô
1939. Seasonal variations in the pelage characters of a Formosan wild rat, *Rattus losea* (Swinhoe). Mem. Fac. Sci. and Agricul. Taihoku Imperial Univ., vol. 23, no. 2, pp. 74-93, figs. 1-4.
- Tien, Dao Van
1960. Recherches zoologiques dans la région de Vinh-Ling (Province de Quảng-tri, Centre Vietnam). Zool. Anzeiger, vol. 164, nos. 1 and 2, pp. 221-239, figs. 1-4.
1961. Notes sur une collection de micromammifères de la région de Hon-Gay. *Ibid.*, vol. 166, nos. 7 and 8, pp. 290-298, figs. 1-2.
1978. Sur une collection de mammifères du Plateau de Moc Chau (Province de Sơn-la, Nord-Vietnam). Mitt. Zool. Mus. Berlin, vol. 54, no. 2, pp. 377-391.
- Van Peenen, P. F. D., P. F. Ryan, and R. H. Light
1969. Preliminary identification manual for mammals of South Vietnam. U.S. Natl. Mus., Smithsonian Inst., Washington, D.C., vi + 310 pp., figs. 1-81.
- Wang, Sung, Lu Chang-kwun, Kao Yueh-ting, Loo Tai-chun
1962. On the mammals from southwestern Kwangsi, China. Acta Zool. Sinica, vol. 14, no. 4, pp. 555-568, 2 pls.
- Wu, Delin
1982. On subspecific differentiation of brown rat (*Rattus norvegicus* Berkenhout) in China. Acta Theriol. Sinica, vol. 2, no. 1, pp. 107-112, figs. 1-2.
- Yosida, Toshihide H.
1979. A comparative study on nucleolus organizer regions (NORs) in *Rattus* species with special emphasis on the organizer differentiation and species evolution. Proc. Japan Acad., vol. 55, ser. B, no. 10, pp. 481-486, figs. 1-7.