RESULTS OF THE ARCHBOLD EXPEDITIONS. NO. 98
SYSTEMATICS OF NATIVE AUSTRALIAN *RATTUS* (RODENTIA, MURIDAE)

J. MARY TAYLOR AND B. ELIZABETH HORNER

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ABSTRACT

THE NATIVE AUSTRALIAN *Rattus* are represented by five species and 14 subspecies. The progenitor of these native *Rattus* appears to be an ancestral form of *R. lutreolus* which gave rise to two major lines. One line represents the forest species, *R. fuscipes* and *R. leucopus*, and of these, *R. fuscipes* appears to have given rise to *R. leucopus* through a *R. f. coracius*-like ancestor. The other major line is composed of the grassland species, *R. sordidus* and *R. tunneyi*. The link between these two is postulated as being through the two subspecies *R. t. culmorum*-*R. s. sordidus*. *Rattus tunneyi tunneyi* is the most distant subspecies from the *R. lutreolus*-type progenitor along this line, and *R. leucopus cooktownensis* is the most remote along the line of forest forms. *Rattus exulans* subspecies, which occurs within the political boundaries of Australia probably as a result of human biochore dispersal, is included in this study chiefly because it has been allied with native *Rattus* on occasion in previous investigations.

We recognize four subspecies of *Rattus fuscipes*: *R. f. fuscipes* (synonyms =*R. f. mondraineus* and *R. f. glauerti*), *R. f. greyii* (synonyms =*R. murrayi*, *R. greyii ravus*, *R. greyii peccatus*, and *R. greyii pelori*), *R. f. assimilis*, and *R. f. coracius* (synonym =*R. manicatus*); two subspecies of *Rattus leucopus*: *R. l. leucopus* (synonym =*R. l. mcilwraithi*) and *R. l. cooktownensis*; three subspecies of *Rattus lutreolus*: *R. l. lutreolus* (synonyms =*R. vellerosus*, *R. l. cambricus*, and *R. l. imbil*), *R. l. velutinus* (synonym = ?*Mus tasmaniensis*), and *R. l. lacus*; three subspecies of *Rattus sordidus*: *R. s. sordidus* (synonyms =*R. conatus* and *R. youngi*), *R. s. villosissimus* (synonym =*R. villosissimus profusus*), and *R. s. colletti*; and two subspecies of *R. tunneyi*: *R. t. tunneyi* (synonyms =*Mus woodwardi*, *R. melvilleus*, and *R. tunneyi dispar*) and *R. t. culmorum* (synonyms =*R. culmorum vallesius*, *R. culmorum austrinus*, and *R. culmorum apex*).

INTRODUCTION

IN TERMS OF DESCRIBED FORMS, *Rattus* is the largest genus of mammals (Ellerman, 1941; Simpson, 1945). Indigenous species occur in Asia, Europe, Africa, Australia, and New Guinea, and introduced species prosper throughout the world in the wake of human settlement.

In Australia, where interest in the native rodents has long been subordinated to that in the more spectacular monotremes and marsupials, *Rattus* is one of about a dozen eutherian genera, all murid rodents, included in the native, flightless terrestrial fauna. These genera of murids are of scientific concern, not only because they are so little known biologically, but because of the zoogeographical questions they pose. With the exception of *Rattus*, all genera are autochthonous to the Australasian region and apparently evolved within that region from ancestors originating on the Asian side of Wallace's Line. *Rattus*, on the other hand, had reached its present generic status before entering Australia from its presumed embarkation region of southeastern Asia and is probably the most recent prehistoric murid immigrant. It therefore occupies an especially favorable position for the study of its natural relationships within the island continent of Australia. Its initial arrival in Australia is recent enough that most of the forms that evolved there may still be extant. It is against this background of evolutionary interest that much of the intellectual impetus of the present study has been derived.

In preparing this systematic assessment of the native *Rattus* of Australia, we have collected in their own habitats representatives of all extant forms of *Rattus* of continental Australia and Tasmania recognized by us and have given much attention to ecological and morphological adaptations. We have examined all Australian *Rattus* specimens known to us in the public museums of Australia, North America, and Europe and have drawn freely upon the published conclusions of others, especially of Ellerman (1949) and Tate (1951).

Our reassessment of the members of the genus *Rattus* in Australia has a twofold purpose: to reevaluate systematic relationships among *Rattus* in Australia in the light of current knowledge of the distribution, ecology, and morphology of its members and to contribute to the interpretation of temporal and geographical patterns of spread on the Australian continent.

With Australian *Rattus*, as with so many other groups, systematic assessments tended to accumulate haphazardly, with collecting localities reflecting in large measure the exploration routes of early colonizers and adventurers. Names were often applied without benefit of carefully prepared and well-documented specimens. Comparative materials and habitat information were usually minimal. Reference specimens were housed far from their native land. It was against such a background that Ellerman (1941, 1949) and Tate (1951) erected their comprehensive interpretative scaffoldings, Tate contributing additionally his expertise as a highly trained field and museum scientist, and Ellerman making detailed assessments of Australian *Rattus* as facets of his worldwide survey of rodents based chiefly on the vast collections of the British Museum (Natural History). To the extent that the present study adds to the understanding of natural relationships among the Australian *Rattus* it pays homage to the pioneer studies of these two men.

The conclusions reached by Ellerman and by Tate differ greatly and are only partially reflected in the fact that Tate (1951) listed 13 species of Australian *Rattus* as opposed to the six listed by Ellerman (1949). Troughton, in the 1967 revision of his popular book on Australian mammals, recognized 15 species, and Ride (1970) included seven.

Our own classification, as here proposed, recognizes six species which, together with their subspecies, are as follows:

Rattus exulans subspecies
Rattus fuscipes fuscipes
Rattus fuscipes greyii
Rattus fuscipes assimilis
Rattus fuscipes coracius
Rattus leucopus leucopus
Rattus leucopus cooktownensis
Rattus lutreolus lutreolus
Rattus lutreolus velutinus
Rattus lutreolus lacus
Rattus sordidus sordidus
Rattus sordidus villosissimus
Rattus sordidus colletti
Rattus tunneyi tunneyi
Rattus tunneyi culmorum

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Mr. J. H. Calaby, Senior Principal Research Scientist of the Division, has been our intellectual counselor and sounding board, sharing generously his wealth of knowledge of Australian mammals and their literature. His sustained critical interest in our work has added immeasurably to our own enrichment as well as to that of the project.

To Mr. Calaby, and to Dr. K. F. Koopman, Dr. G. G. Musser, Mr. H. M. Van Deusen, and Dr. R. G. Van Gelder, of the American Museum of Natural History, we express our gratitude for their readings of the manuscript and helpful suggestions.

Mr. H. M. Van Deusen has graciously welcomed our use of the valuable specimens and records of the Archbold Expeditions, generously volunteered extensive loans of material, removed skulls from mounted and alcoholic specimens, and extracted useful information from the field journals of Dr. G. H. H. Tate. He has contributed also much personal knowledge of Australian habitats and given us permission to use one of his photographs.

Mr. J. E. Hill has offered valuable information regarding the histories and fates of important specimens that have become part of the collections of the British Museum (Natural History), and Mr. B. J. Marlow has responded enthusiastically to our several requests for information regarding early records at the Australian Museum.

Dr. D. P. Snyder, Department of Zoology, University of Massachusetts, has not only made freely available to us his unpublished program for discriminant analysis, but has also guided its modifications for our particular tests. Additional advice on statistical procedures was rendered by Dr. R. M. Kleyle, Department of Statistics, University of Massachusetts.

Mr. J. A. Mahoney, Department of Geology and Geophysics, University of Sydney, has kindly allowed us to incorporate into our paper his conclusions regarding the identity of *Hapalotis personata*. He has also provided us with important information and loans of specimens for which we are most grateful.

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L. S. Hall, Division of Wildlife Research, CSIRO, kindly permitted us to use one of his photographs for figure 34.

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MATERIALS AND METHODS

The field aspect of the present study was carried out by trapping various subspecies of *Rattus* alive in Sherman folding traps. All rats captured in this fashion were prepared fresh in the field as museum study skins and skulls, and tissues for reproductive analysis (Taylor and Horner, MS) were obtained for histological preparation. Bait used was a mixture of rolled oats, sunflower seeds, and peanut butter. Our usual trapping procedure was to set from 100 to 300 live traps in the late afternoon in areas deemed suitable and to retrieve them early next morning. The limited period of time available for field work and the extent of traveling necessary to obtain the various subspecies made it obligatory, except on rare occasions, to trap a given locality for only one night and then move on to the next. At each location a brief analysis of the general habitat and identification of dominant plant species provided a basis on which to generalize in terms of major habitat utilization by each subspecies.

Although most of the anatomical analysis was made from prepared material, the mammary formula was checked on fresh specimens. This is a useful criterion for aid in separating subspecies, and only on fresh material can the teats be counted with some degree of certainty.

Cross-breeding experiments with wild-caught animals established as laboratory stock provided one of the major sources of information in our analysis of the *R. fuscipes* group. This aspect of our systematic study has already been published (Horner and Taylor, 1965).

Specimens of Australian *Rattus* were examined in each of the following museums: the American Museum of Natural History, Archbold Collection and Department of Mammalogy, New York (AMNH); Australian Museum, Sydney (AM); British Museum (Natural History), London (BM); CSIRO Collection of the Division of Wildlife Research, Canberra (CSIRO); Field Museum of Natural History, Chicago (FMNH); Fisheries and Wildlife Department, Melbourne (FWD); Liverpool Museum (LM); Macleay Museum, University of Sydney (MM); Museo Civico di Storia Naturale, Genoa (MCSN); Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ); Museum of Michigan State University, East Lansing (MSU); Museum National D'Histoire Naturelle, Paris (MNHN); Museum of Natural History, Lawrence, Kansas (KU); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); National Museum of Victoria, Melbourne (NMV); Naturhistoriska Riksmuseet, Stockholm (NR); Queen Victoria Museum, Launceston (QVM); Queensland Museum, Brisbane (QM); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); South Australian Museum, Adelaide (SAM); Tasmanian Museum, Hobart (TM); United States National Museum, Smithsonian Institution, Washington, D.C. (USNM); Western Australian Museum, Perth (WAM); Zoologisches Museum, Berlin (ZM); Zoologisk Museum, Oslo (ZMO).

We examined the following material of each subspecies. A full list of specimens and the institutions in which they are housed is given on pages 117–124.

Rattus exulans subspecies. Total 4: 2 adults, skins and skulls; 1 adult or juvenile, skin and skull; 1 juvenile, skin and skull.

Rattus fuscipes fuscipes. Total 226: 105 adults, skins and skulls, or skulls only; 37 juveniles, skins and skulls, or skulls only; 24 adults and juveniles, skins only, or skulls in skins; 51 laboratory specimens, skins and skulls; 9 specimens, no locality data.

Rattus fuscipes greyii. Total 228: 90 adults, skins and skulls, or skulls only; 41 juveniles, skins and skulls, or skulls only; 36 adults and juveniles, skins only, or skulls in skins; 50 laboratory specimens, skins and skulls; 11 specimens, no locality data.

Rattus fuscipes assimilis. Total 687: 303 adults, skins and skulls, or skulls only; 64 juveniles, skins and skulls, or skulls only; 68 adults and juveniles, skins only; 243 laboratory specimens, skins and skulls, or skulls only; 9 specimens, no locality data.

Rattus fuscipes coracius. Total 328: 274 adults, skins and skulls, or skulls only; 25 juveniles, skins and skulls, or skulls only; 23 adults and juveniles, skins only, or skulls in skins; 6 adults, no locality data.

Rattus leucopus leucopus. Total 265: 212 adults, skins and skulls, or skulls only; 39 juveniles, skins and skulls, or skulls only; 11 adults and juveniles, skins only, or skulls in skins; 3 adults and juveniles, no locality data.

Rattus leucopus cooktownensis. Total 215: 154 adults, skins and skulls, or skulls only; 34 adults and juveniles, skulls in skins; 24 juveniles, skins and skulls, or skulls only; 3 adults and juveniles, skins only.

Rattus lutreolus lutreolus. Total 188: 112 adults, skins and skulls, or skulls only; 24 juveniles, skins and skulls, or skulls only; 28 adults, skins only, or skulls in skins; 10 juveniles, skins only, or skulls in skins; 14 adults, no locality data.

Rattus lutreolus velutinus. Total 255: 189 adults, skins and skulls, or skulls only; 45 juveniles, skins and skulls, or skulls only; 21 adults and juveniles, skins only, or skulls in skins.

Rattus lutreolus lacus. Total 5: 3 skins and skulls; 1 skin only; 1 skin with mismatched skull.

Rattus sordidus sordidus. Total 239: 162 adults, skins and skulls, or skulls only; 57 juveniles, skins and skulls, or skulls only; 18 adults and juveniles, skins only, or skulls in skins; 2 specimens, no locality data.

Rattus sordidus villosissimus. Total 240: 153 adults, skins and skulls, or skulls only; 48 juveniles, skins and skulls, or skulls only; 21 adults and juveniles, skins only, or skulls in skins; 18 adults and juveniles, no locality data.

Rattus sordidus colletti. Total 88: 36 adults, skins and skulls, or skulls only; 23 juveniles, skins and skulls, or skulls only; 16 adults, skins only, or skulls in skins; 13 juveniles, skins only, or skulls in skins.

Rattus tunneyi tunneyi. Total 164: 116 adults, skins and skulls, or skulls only; 35 juveniles, skins and skulls, or skulls only; 12 adults and juveniles, skins only, or skulls in skins; 1 adult, no locality data.

Rattus tunneyi culmorum. Total 219: 171 adults, skins and skulls, or skulls only; 16 juveniles, skins and skulls, or skulls only; 29 adults and juveniles, skins only, or skulls in skins; 3 adults and juveniles, no locality data.

The above listing represents a total of 3351 specimens, of which we prepared 704 that were subsequently presented to the Museum of Vertebrate Zoology.

Twenty cranial measurements were taken to the nearest 0.1 mm. with dial calipers graduated in 0.05 units. The basic orientation plane of the skull was determined by the ventralmost point of the upper incisors and the ventralmost points of the basicranium as the skull rested on a horizontal surface.

1. Occipitonasal length: dorsal measurement from anteriormost tip of nasals to posteriormost point of occiput.
2. Condylobasal length: ventral measurement from anteriormost faces of upper incisors to posterior margins of occipital condyles.
3. Basal length: ventral measurement from anteriormost faces of upper incisors to midventral limit of foramen magnum.
4. Zygomatic width: measurement of greatest width across zygomatic arches.
5. Interorbital width: dorsal measurement of least distance across frontals between orbital fossae.
6. Interparietal length: middorsal measurement of interparietal taken from point of contact with sagittal suture of parietals to just anterior to lambdoidal crest.
7. Interparietal width: dorsal measurement across interparietal at its points of junction with parietals and occipital.
8. Braincase width: dorsal measurement taken from one squamosal to the other immediately posterior to termination of zygomatic arch.
9. Mastoid width: dorsal measurement taken across occipital immediately posterior to post-tympanic hook of squamosal and anterodorsal to periotic capsule of each side.
10. Nasal length: dorsal measurement of right nasal taken from tip to posterior suture line in sagittal or parasagittal plane determined by nasal tip. (Paired features were measured on the side indicated except where complete only on the other side.)
11. Nasal width: dorsal measurement across two nasals at anterior points of contact with premaxillae.
12. Palatal length: ventral measurement taken from face of left upper incisor to anteriormost point on posterior margin of left palatine.
13. Incisive foramen length: ventral measurement of left incisive foramen.
14. Incisive foramina width: ventral measurement of greatest width across two incisive foramina.
15. Inside m^{1-1} width: ventral measurement of least width between crowns of first upper molars.
16. Outside m^{1-1} width: ventral measurement of greatest width across crowns of first upper molars.
17. Bulla length: ventral measurement of left tympanic bulla taken from lateral base of bony Eustachian tube to posteriormost point of bulla.
18. Crowns m^{1-3} length: ventral measurement of left upper molar row taken from anteriormost point of crown surface of first molar to posteriormost point of crown surface of third molar.
19. Alveoli m^{1-3} length: ventral measurement of left upper molar alveoli taken from anteriormost edge of first alveolus to posteriormost edge of alveolus of third molar.

20. Crowns m^{1-2} length: ventral measurement of combined lengths of first two left upper molars taken from anteriormost point of crown surface of first molar to posteriormost point of crown surface of second molar.

An additional measurement, m^{1-1} width $\times 2$, was derived secondarily by subtracting measurement 15 from measurement 16, giving a close approximation of the combined maximum widths across the two upper molar rows.

Comparison of pelage color and texture was made from museum specimens no more than three years preserved, except in the cases of *Rattus exulans* and *Rattus lutreolus lacus* for which no recent material is available.

For each subspecies, except *R. exulans* subspecies and *R. l. lacus* for which there is insufficient material, we have established two age categories: juvenile and adult. This is done on the basis of a single parameter, occipitonasal length, a measurement repeatable with minimum error and one that seems to reflect most faithfully various other features useful in distinguishing sexually immature animals from those that have attained adulthood. The measurement value selected to separate the two categories was independently derived for each subspecies and is included in the individual subspecies accounts.

Statistical treatment of all measurements was handled on the basis of adult categories for each subspecies. The discriminant analysis program employed was that of Dana P. Snyder, designed for use with the CDC computer. In the total of 3351 specimens examined, the full complement of the 20 individual measurements used in the computer program was available from 1274 adults.

The distribution maps (figs. 2, 12, 18, 28, and 36) show locality records generalized as dots. The lines circumscribing the geographical extent of each subspecies are visual aids only and do not represent the precise extremities of distribution either in these maps or in figure 44.

RESULTS

Rattus exulans (Peale) subspecies

Mus exulans Peale, 1848, p. 47.

Lectotype: Skin only, sex undetermined, USNM 3730, from the United States Exploring Expedition (1838–1842), catalogued December 20, 1859, taken from Tahiti, and selected as the lectotype by Lyon and Osgood (1909, p. 148).

Distribution in Australia: Adele Island, near Derby in Western Australia, and Mer, Murray Islands, Queensland (fig. 18).

Description of Australian Specimens: This is the smallest and most delicate of the Australian *Rattus*. Although total body length and tail measurements are not available from fresh material, measurements of preserved specimens indicate that the tail is longer than the head and body combined. The pelage is light brown to cinnamon dorsally and is sharply defined from the white ventral surface. The ventral hairs are white to the base. The pelage is very spinous, the flattened spines being translucent and dark-tipped dorsally and fully translucent ventrally. The dorsal surface of the manus is lightly covered with brown hairs, whereas that of the pes is white. All four specimens are, or have been, preserved in alcohol, which has undoubtedly caused considerable fading of the pelage. On one specimen (BM 99.9.10.2) we were able to distinguish teats, the mammary formula being $2+2=8$, which is the formula typical of the *exulans* group (Waite, 1897).

The skull is delicate with fine incisors and narrow molars. The nasals protrude well anterior to the upper incisors. The incisive foramina are strongly bowed laterally, and the palate terminates beyond the posterior face of the third molar. The supraorbital-temporal ridges are narrow but well defined, about 0.2 mm. wide by 0.3 mm. high, from the narrowest width of the frontals back well onto each parietal. The bullae average 21 per cent of the basal skull length and are as long as, or longer than, the alveoli of m^{1-3} (fig. 1).

Mean Measurements (in Mm.): External (from BM 91.10.9.1): head and body 130 (dry skin measurement); tail 135 (dry skin measurement); hind foot (s.u.) 28; ear 19 (presumably from crown). Skull: occipitonasal length 31.4; braincase width 13.6; bulla length 5.7; crowns m^{1-3} length 4.4. (See table 1 for complete list of measurements and statistical presentation for the two adults and the one possible adult.)

Diagnostic Characters: The smallest of all

Rattus occurring in Australia and in most mensural characters we used stands well apart from the remaining subspecies. The ratio of bulla length to basal length of skull in *Rattus exulans* (21.2 per cent) exceeds that of each of the subspecies of *R. fuscipes*, *R. leucopus*, and *R. lutreolus*. In this regard it is most similar to *Rattus sordidus colletti* (21.5 per cent), this same ratio being still larger in the other forms of *R. sordidus* and in *R. tunneyi*. *Rattus exulans* has been confused in Australia only with young *R. fuscipes fuscipes* (synonym =*R. f. glauerti*). *Rattus exulans* has more bowed incisive foramina that reach posteriorly only in line with the anterior face of the alveoli

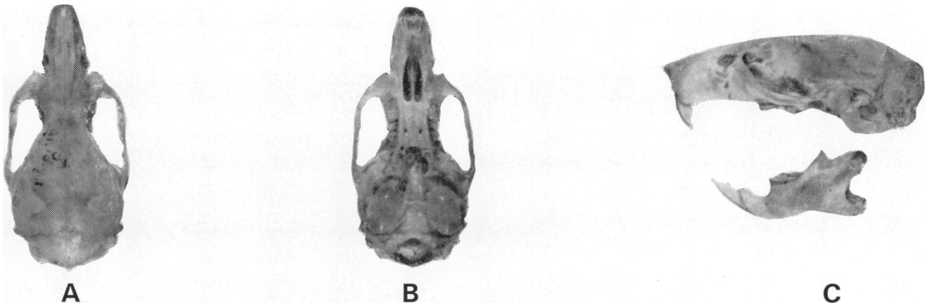

FIG. 1. Dorsal (A), ventral (B), and lateral (C) views of skull of adult *Rattus exulans* subspecies, BM 91.10.9.1. Occipitonasal length 34.9 mm.

TABLE 1
MEASUREMENTS (IN MILLIMETERS) OF *Rattus exulans* SUBSPECIES

Measurement	N	Mean±SE[a]	SD[a]	Range
Head and body length	1	130	—	—
Tail length	1	135	—	—
Hind foot (s.u.) length	1	28	—	—
Ear length (presumably from crown)	1	19	—	—
Occipitonasal length of skull	2	31.45±2.44	3.45	28.0–34.9
Condylobasal length	3	29.43±1.46	2.52	26.0–32.0
Basal length	3	26.90±1.37	2.38	21.7–29.1
Zygomatic width	3	15.07±0.55	0.95	14.0–16.3
Interorbital width	3	4.80±0.20	0.36	4.4– 5.1
Interparietal length	3	4.60±0.29	0.51	3.6– 5.2
Interparietal width	3	9.43±0.20	0.34	9.1– 9.9
Braincase width	3	13.63±0.38	0.65	12.8–14.4
Mastoid width	3	11.50±0.37	0.65	10.9–12.4
Nasal length	2	11.25±1.10	1.55	9.7–12.8
Nasal width	2	3.20±0.28	0.40	2.8– 3.6
Palatal length	3	15.87±0.81	1.40	13.9–17.0
Incisive foramen length	3	5.47±0.32	0.56	4.7– 6.0
Incisive foramina width	3	2.13±0.18	0.31	1.7– 2.4
Inside m^{1-1} width	3	3.00±0.29	0.50	2.3– 3.4
Outside m^{1-1} width	3	6.17±0.27	0.47	5.5– 6.5
Bulla length	3	5.70±0.28	0.49	5.1– 6.3
Crowns m^{1-3} length	3	4.40±0.04	0.08	4.3– 4.5
Alveoli m^{1-3} length	3	4.77±0.07	0.12	4.6– 4.9
Crowns m^{1-2} length	3	3.37±0.11	0.19	3.1– 3.5
M^{1-1} width × 2	3	3.17±0.03	0.04	3.1– 3.2

[a] SE indicates standard error of the mean; SD, standard deviation from the mean.

of m^1, whereas in *R. f. fuscipes* they usually extend more posteriorly. The incisive foramina are wider in *R. exulans* but similar in the two forms in relative length. *Rattus exulans* has well-developed supraorbital-temporal ridges, whereas in *R. f. fuscipes* they may be developed along the parietals but are inconspicuous or lacking along the frontals. The upper molar row is relatively narrower and shorter in *R. exulans* than in *R. f. fuscipes*.

PREVIOUS DESCRIPTIVE ACCOUNTS: The only description of Australian *R. exulans* prior to the account given here was that by Tate (1951). He described two specimens, but only one is *R. exulans*; the other is *R. tunneyi tunneyi* that he misidentified as *R. exulans*. Ride (1970) has listed a few characters of this form.

HABITS AND HABITAT: The three Adele Island specimens were taken in 1891 by J. J. Walker and there are no notes available on the habits or habitat of this rat at the time of collection. Thomas (1926), who was the first to record the occurrence of *R. exulans* in Australia, suggested that the Adele rats obtained access to the island by native canoe, a common mode of dispersal of this rat throughout the Pacific and Indonesian archipelago. The single specimen from Mer, Murray Islands, presented by A. C. Haddon, was incorporated into the collection of the British Museum (Natural History) in 1899. There are no notes of ecological significance regarding this specimen. The date of collection is not recorded, but Haddon probably obtained it in 1888–1889 or 1898, the years of his two visits to Mer (Haddon, 1908, p. xviii). Mer Island is a volcano with no mainland affinity and may be of very recent origin.

The natives of the Torres Strait region traveled frequently by canoe between islands, including, no doubt, the Murray Islands, and also maintained contact with the Fly River area of Papua (J. H. Calaby, personal commun.) where *R. exulans* occurs. There seems little question that the Mer specimen of *R. exulans* is an example of human biochore dispersal by native canoe and that its origin may well have been Papua. The advent of *R. exulans* on Adele Island may, however, not have been by native canoe as Thomas (1926) suggested. Throughout the nineteenth century, and possibly considerably earlier as well, the whole north coastline of Australia from the Kimberleys to the Gulf of Carpentaria was visited annually by Indonesians in quest of bêche-de-mer, and they came in large vessels called praus of 10 to 20 tons or more that were laden with food and equipment (Mulvaney, 1966, 1969). They established temporary camps on the coast and offshore islands. Many of these people came from the port of Macassar in the southern Celebes (Mulvaney, 1966) where *R. exulans* is numerous. *Rattus exulans* may have been a frequent uninvited occupant of their vessels and accompanying supplies during these trips. It is likely, therefore, that the Australian records of *R. exulans* originate from two distinct geographical sources and are not necessarily of the same subspecies.

Rattus exulans is primarily a vegetarian and utilizes the softer tissues of plants for food (Fall, Medina, and Jackson, 1971). It eats fruits of native plants, such as *Pandanus*, as well as those of introduced forms including coconuts, bananas, and breadfruit. Stomach analyses of rats studied on Ponape and Majuro (Strecker and Jackson, 1962) and on Guam (Baker, 1946) indicate that the diet is mainly plant material with up to 20 per cent of invertebrate material. In some areas these rats appear to reject the abundant crustacean and molluscan fauna of the shore (Peale, 1848; Waite, 1897), although in Hawaii they feast on snails (Stone, 1917). They will also take young birds and bird eggs (Arundel, 1890), and in times of food shortage may even feed from living adult albatrosses (Kepler, 1967).

Rattus exulans was reputed to be a dexterous tree climber and to make its nests in trees, root systems, and tussock grass and also to construct burrows (Peale, 1848; Waite, 1897). Baker (1946), however, found no evidence that it climbs trees; furthermore, Jackson (1969) characterized it as a non-burrowing animal that nests under surface materials. The recent study by McCartney (1970) contrasts with those of Baker (1946) and Jackson (1969) by demonstrating conclusively that *R. exulans* exhibits arboreal behavior. In New Guinea it is common in houses made of native materials and in native gardens (J. H. Calaby, personal commun.) and is generally associated with man (Muul, 1970).

There are many parts of north coastal Australia that have *Pandanus*, palms, and other features seemingly favorable to *R. exulans* settlement. It is somewhat surprising, both from an ecological and from a zoogeographical standpoint, that *R. exulans* has never become established on the Australian mainland unless the climate is in large measure too dry.

SYMPATRY: *Rattus exulans* is allopatric with all other subspecies of Australian *Rattus*.

TAXONOMIC HISTORY: The unusual distributional position that *R. exulans* assumes as part of the Australian fauna is unparalleled among the mammals of Australia. This rat, so plentiful among the islands of the South Pacific and the southeast Asian island chain, is known in Australia only from two offshore islands of the northeast and northwest mainland. It was never recorded in the literature as part of the Australian fauna until 1926 and nothing is known about the status or habits of *R. exulans* in Australia.

Rattus exulans was first described by Peale (1848) as *Mus exulans* and was recorded by him from several islands of the South Pacific: Tahiti, Wake's Island, Hull's Island, Dog Island, and Disappointment Island. Although a type specimen was not selected at that time, Lyon and Osgood (1909) later chose the one from Tahiti to represent the type. The original edition of the United States Exploring Expedition, in which Peale's description appeared, was suppressed and 10 years later another similar account of *M. exulans* with long quotes from Peale's account appeared under the authorship of Cassin (1858). Cassin put *Mus penicillatus* Gould and *Mus jacobiae vel decumanoides* Waterhouse into provisional synonymy with *M. exulans*.

Alston (1877) described a new species which he called *Mus browni* from the Duke-of-York Island north of New Britain. Later it came to be recognized as a subspecies of *M. exulans*. At the time of its description, however, and also in a later paper, Alston (1879) expressed an alliance of *M. browni* with the Australian *Mus leucopus* from northern Queensland. Both have strongly bowed incisive foramina and very spinous pelage. Although this recommendation linked *M. exulans* to the Australian fauna, the proposed alliance of this species to *M. leucopus* was in error. Fortunately Alston's assessment received little support.

Thomas (1895) disagreed with Cassin that *M. penicillatus* and *M. jacobiae* were synonyms of *M. exulans*, but did include several other forms, including *M. maorium*, *M. vitiensis*, and *M. novae-zealandiae*. Waite (1897), in his work on the vertebrates of Funafuti Atoll, followed the assessment made by Thomas. Furthermore, Waite was able to correct the error in mammary formula of *M. exulans* from $1+2=6$, as given by Peale (1848), to $2+2=8$.

It is beyond the province of this paper to discuss at length the known history of *R. exulans* as it occurs outside Australia. In fact, a glimpse into the literature on this species soon reveals that it is still a very poorly understood group.

Thomas (1926b), as the first to record the incidence of *R. exulans* in Australia from the Adele Island specimens, allied them to the *concolor-ephippium* group and indicated that they were not related to any *Rattus* of the Australian mainland. Raven (1935) recorded *R. exulans* as part of the Australian fauna but did not appreciate its restricted insular distribution, for he gave the locality simply as "Australia," along with New Guinea where it is actually widely distributed. Tate (1935) was not familiar with the record of *R. exulans* from Adele Island, for he stated, "*browni* of New Guinea and the Solomon Islands appears to be a peripheral species which has failed to enter North Australia" (Tate, 1935, p. 165). Sody (1941) was also unfamiliar with this record. Later, in a paper by Mumford (1942), Tate provided the identification of an immature *Rattus* from Fiji, misidentified it as *R. assimilis*, and thus allied a rat from the South Pacific to one from Australia. This rat was formerly thought to be *R. huegeli* (a synonym of *R. exulans*). This earlier assessment is probably correct.

Ellerman worked extensively with specimens in the British Museum (Natural History) when he was formulating his assessment of the familial and generic relationships of living rodents. It is surprising, therefore, that he never mentioned the four specimens of Australian *R. exulans*, all of which are in the collection of that museum. Although Ellerman (1949) placed *Rattus glauerti* as a distinct species, he noted, with only the type skull before him, that it had a marked size resemblance to *R. exulans*.

Tate (1951) altered considerably his views of *R. exulans* from those expressed in his earlier papers and followed Ellerman in treating a large number of his former species as subspecies of *R. exulans*. He created an *exulans-concolor-browni* division in the Australian and New Guinea region in which he placed three species, *R. exulans*, *R. rennelli*, and *R. glauerti*. Only the first and third are Australian and concern us here.

Tate examined two specimens from northwestern Australia that he called *R. exulans*: one was *R. exulans* from Adele Island, off Collier Bay, and the other, from La Grange Bay, was actually a juvenile *Rattus tunneyi tunneyi* (WAM 620). Although the skull of the latter exists, Tate was unable to locate it at the time of his examination and made his judgment on the basis of the skin alone. He placed both specimens as subspecies of *R. exulans* but neither designated the subspecies to which they belonged nor erected a new one (Tate, 1951). In view of his obvious appreciation of the distributional and systematic problems posed by Australian *R. exulans* and of his expressed awareness (Tate, 1951, p. 323) of the presence in the British Museum (Natural History) of more than a single specimen off Collier Bay, it is surprising that he made no detailed reference to the two additional specimens. He apparently never saw the specimen from Mer.

Tate (1951) was the first to suggest an alliance of *R. glauerti* to the *R. exulans* complex, although Ellerman (1949) had noted a size resemblance. In fact, on the basis of the type specimen of *R. glauerti* alone (he apparently saw no other specimens from East Wallabi Island), Tate suggested that *R. glauerti* was an "*exulans*" rat which in typical *exulans* fashion had gained access to the island by boat. Even so, he retained *R. glauerti* as a full species on the basis of differences that he did not specify.

The type specimen of *R. glauerti* (BM 26.7.12.2) is unfortunately a juvenile. The small skull is delicate, like that of *R. exulans*, and is about the same size as the *R. exulans* specimen Tate used for comparison (BM 91.10.9.1). The cranium is highly inflated in proportion to skull length, as is typical of all juvenile *Rattus*. The incisive foramina, however, do not terminate widely as they do in *R. exulans*, but taper somewhat, as do those of *R. f. fuscipes*. The bullae are conspicuously smaller [19.4 per cent of basal skull length (19.2 per cent for all *R. f. fuscipes*)] than in *R. exulans* (21.2 per cent of basal skull length). The tail of *R. glauerti* (about 90 mm.) is shorter than the head and body length (about 110 mm.).

We remove *R. glauerti* from consideration as an ally of *R. exulans* and place it with *R. f. fuscipes*. Furthermore, we feel that the paucity of specimens of *R. exulans* from Australia makes it unwise to commit subspecific designation to this group which may, as previously stated, be represented by more than one subspecies.

It may be contested that *R. exulans* should not be included in an analysis of the native Australian *Rattus* any more than should *R. rattus* or *R. norvegicus*, all of which appear to have gained access to this region through human biochore dispersal. However, since *R. exulans* has been allied by systematists on at least two occasions with subspecies of *Rattus* that are endemic to Australia, we consider it important to discuss our interpretation of its position in conjunction with the status of native Australian *Rattus*.

Rattus fuscipes (Waterhouse)

DISTRIBUTION: Coastal, subcoastal, and offshore islands of southwestern Australia; south coast from Eyre Peninsula to western Victoria; coastal and subcoastal Victoria from the Otway Peninsula to near Rockhampton, Queensland; coastal Queensland from Townsville to Cooktown (fig. 2).

GENERAL DESCRIPTION: The subspecies of *Rattus fuscipes* range from among the smallest to among the largest of the Australian mainland *Rattus* in combined head and body length and in hind-foot length. The pelage is soft and dense and lacks spines. The body coloration is a warm brownish gray dorsally blending to a light gray to buffy ventrally. The hairs are a translucent gray at their bases and the dorsal and lateral

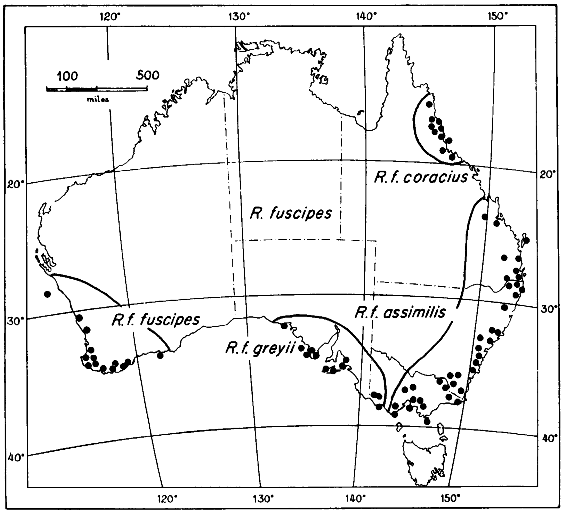

FIG. 2. Distribution map of *Rattus fuscipes*. Locality records for each of the four subspecies are indicated by dots.

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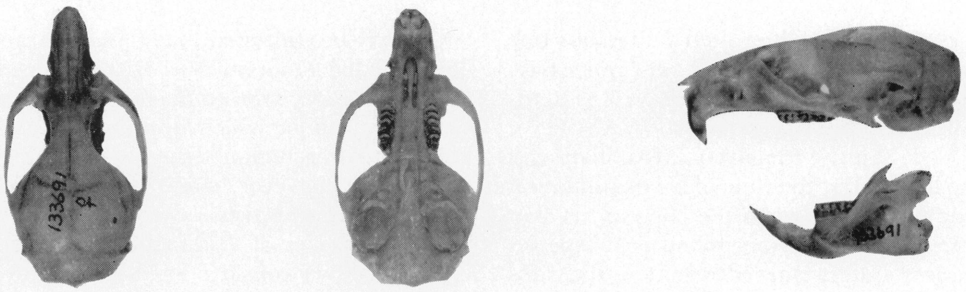

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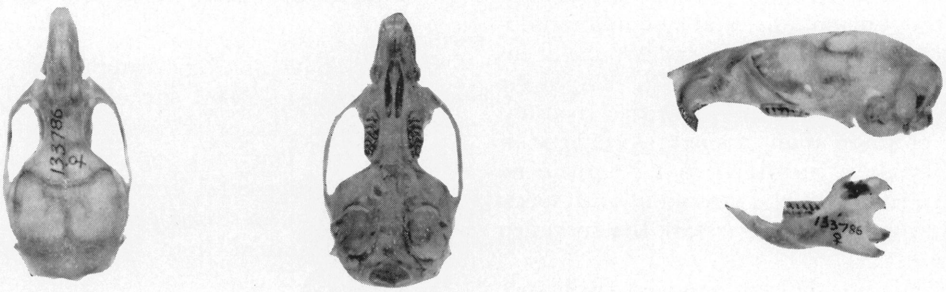

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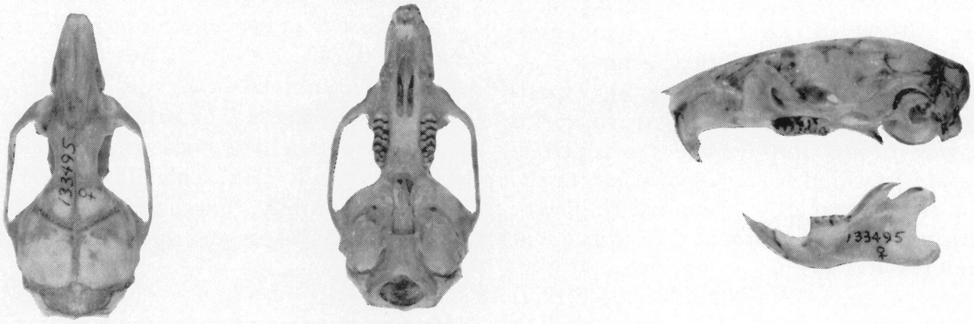

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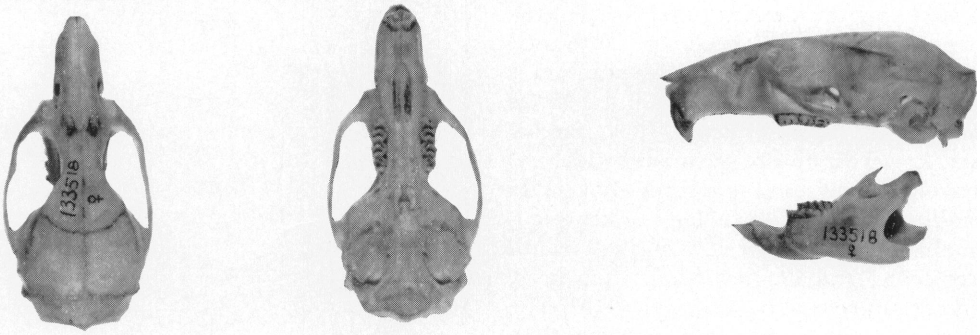

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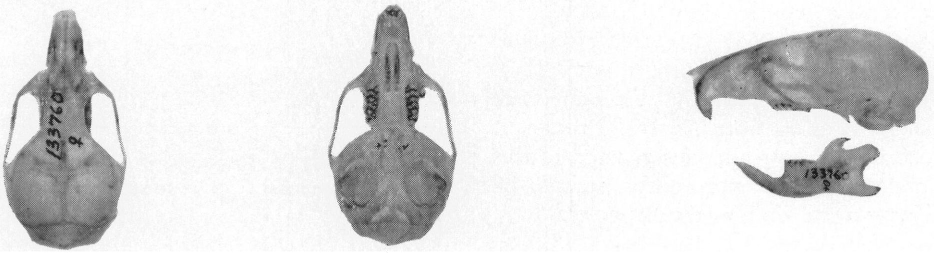

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coloration is enhanced in brightness by distal banding of the hairs, usually with brown or black, and by the presence of coarse, dark guard hairs. The ears are gray or brown and the feet may be whitish, gray, buff, or brown. The tail, in most cases a little shorter than head and body combined, is brown, gray, or blackish. The mammary formula is $2+3=10$ throughout most of the range, shifting to $1+3=8$ in the north.

The skull is elongate, somewhat flattened, and with the supraorbital-temporal ridging inconspicuous or feebly developed, especially as it expands over the parietals. The incisive foramina are elongate, moderately expanded, and generally terminate just posterior to the anterior faces of the molar rows. The rostrum is relatively narrow and the nasals overhang the anterior faces of the incisors and anterior ends of the premaxillae. The bullae average 17.5 to 19.6 per cent of the basal skull length and are about the same length as, or smaller than, the alveoli of m^{1-3} (figs. 3–7).

DIAGNOSTIC CHARACTERS: The most distinguishing feature of this species is the combination of relatively straight-sided incisive foramina and small tympanic bullae.

TAXONOMIC HISTORY: Of all the species of *Rattus* native to Australia, *Rattus fuscipes* has received the most diverse and complicated taxonomic treatment. The original description was given by Waterhouse (1839) as *Mus fuscipes*, the brown-footed mouse. Since then, not only have various workers included a number of different subspecies in this group, or separated them out as distinct species, but there has also been a historical misapplication of the name and a consequent confusion with another species, *Rattus lutreolus*. A full review of this misapplication has been published separately (Taylor and Horner, 1967), so it will be covered only briefly here.

The first Australian *Rattus* was collected at King George's Sound, Western Australia, in March, 1836, during the famous voyage of H.M.S. "Beagle." A single specimen of *Rattus fuscipes* was prepared and subsequently presented to the Museum of the Zoological Society of London. Waterhouse (1839) published a description of this species based on the sole specimen that had been catalogued in the Museum and listed by him (Waterhouse, 1838). At the time, Waterhouse was not sure that *fuscipes* belonged in the genus *Mus* since he had not had the opportunity to examine the cranium and molar teeth. However, in external characters and also incisor teeth, he considered that it fell well within the boundaries of that genus. The genus "*Mus*," however, was much more inclusive then than it is today and the term *Rattus* did not come into general use for the true rats until Thomas (1916) instigated this move. It is not possible to tell from his description whether Waterhouse allied *fuscipes* more closely to the species *Mus rattus* than to other murids, but it is only with *M. rattus* that he made direct comparison. His description of *Mus fuscipes* is informative and agrees well with the rats more recently collected in both the type locality and in the remainder of the range in southwestern Australia.

Following the transfer of a portion of the collection of the Zoological Society to the British Museum (Natural History), the sole specimen of *Mus fuscipes* was lost; and the taxonomic picture was soon complicated by the mistaken inclusion of *Mus lutreola* (=*Rattus lutreolus lutreolus* and/or *R. l. velutinus*) in the *M. fuscipes* group. The confusion of *M. fuscipes* with *M. lutreola* originated when Gray (1843) placed the latter in subjective synonymy with *M. fuscipes*. This error gathered momentum as later workers, hampered by the paucity of specimens and data for both species and lacking a type specimen for *M. fuscipes*, tended to accept uncritically the accounts of their predecessors. It was not until 1967, when a neotype of *R. f. fuscipes* was designated, that the distinction of the two groups became fully clarified (Taylor and Horner, 1967) and that a reference specimen was once more available for the *R. fuscipes* group.

The chaotic interjection of *R. lutreolus* into the

FIGS. 3–7. Dorsal (A), ventral (B), and lateral (C) views of skulls of *Rattus fuscipes*. 3. Adult *R. f. fuscipes*, MVZ 133691. Occipitonasal length 37.5 mm. 4. Adult *R. f. greyii*, MVZ 133786, and MVZ 133789 (ventral view). Occipitonasal length of MVZ 133786 36.5 mm. and of MVZ 133789 36.0 mm. 5. Adult *R. f. assimilis*, MVZ 133495. Occipitonasal length 41.0 mm. 6. Adult *R. f. coracius*, MVZ 133518. Occipitonasal length 42.1 mm. 7. Juvenile *R. f. greyii*, MVZ 133760. Occipitonasal length 32.3 mm.

taxonomic story of *R. fuscipes* is but one of two major sources of confusion. The second arose from the historically casual inclusion and exclusion of a number of other taxonomic entities.

Our evaluation of the *R. fuscipes* group leads to the inclusion of *R. greyii*, *R. assimilis*, *R. manicatus*, *R. mondraineus*, *R. murrayi*, *R. assimilis coracius*, *R. glauerti*, *R. greyii peccatus*, and *R. greyii pelori* as subspecies or population variants of *Rattus fuscipes*. The precise relationship of each of these subgroups to *R. fuscipes* will be discussed later when the morphological and ecological analyses are presented.

In 1841 Gray described another member belonging to the present genus *Rattus* under the name *Mus greyii*. At the time no relationship of *M. greyii* to *M. fuscipes* was recognized, and this situation pertained for over a century until Ellerman (1949) proposed that the two are conspecific. In his 1841 work Gray described another species, *Mus lutreola*, but two years later he synonymized it under *M. fuscipes*. As stated earlier, this was the first misapplication of *R. lutreolus* to *R. fuscipes*, an error that had major consequences in later confusion among Australian *Rattus*. Gray subjected his *M. greyii* to a similar demotion, although the consequences were considerably less in this case. In 1843, in the publication in which he misapplied *M. lutreola*, he also misapplied *M. greyii* by including it under *Mus gouldii*, a murid described by Waterhouse in 1839 and later removed to the genus *Thetomys*. Following Gray, Gould (1855) also placed *M. greyii* in synonymy with *M. gouldii*. Fortunately, later authors did not follow this.

By the year 1858, when two more members of the *Rattus fuscipes* group (as we interpret the species) were proposed, the three previously described forms, *M. fuscipes*, *M. greyii*, and *M. lutreola*, had already been confused in one way or another. The two new forms were described by Gould (1858b, 1858c) as full species, and even in the original descriptions a mix-up occurred. These two new species were *Mus assimilis* and *Mus manicatus*. *Mus assimilis* was described from two specimens taken at the Clarence River, New South Wales, but unfortunately Gould also included specimens from King George's Sound, Western Australia, under this new species. In terms of natural relationships Gould was correct in that the specimens from Western Australia that he examined were actually topotypes of the first rat to be described, *M. fuscipes*, now recognized by us as a conspecific ally of *M. assimilis*. At the time of his description of *M. assimilis*, however, *M. fuscipes* had been confused with *M. lutreola* and hence Gould did not recognize the western material as *M. fuscipes*. He treated this *fuscipes* material as true *M. assimilis* and thus concluded that *M. assimilis* extended along southern continental Australia from east to west. The other rat described by Gould in 1858, *M. manicatus*, presented its own difficulties. It was known then and is still known from only one specimen, and the accuracy of the locality data (Port Essington, Northern Territory) is subject to serious question in our study. At the time of its description no affiliation with *M. fuscipes* or *M. assimilis* was proposed.

Sixty-three years passed before another member of the modern *Rattus fuscipes* group was described. This, and the four that followed, were not generally confused with unrelated groups. Rather, the dispute that ensued after their description was whether or not they were "good" species. The first of these was described by Thomas (1921a) as *Rattus mondraineus*, a rat from Mondrain Island, Western Australia. At the time of its description Thomas indicated that it was closely allied to *R. fuscipes*, although he chose to nominate it as a distinct species owing to differences in cranial details.

In 1923 Thomas described two more rats now relegated to *Rattus fuscipes*. These were *Rattus murrayi* (Thomas, 1923a) and *Rattus assimilis coracius* (Thomas, 1923b). He recognized *R. murrayi* as a close relative of *R. greyii*; like *R. mondraineus*, it is an island form from off the south coast of Australia. He indirectly and unwittingly acknowledged the alliance of *coracius* from north coastal Queensland to the modern *R. fuscipes* group by naming it a subspecies of *R. assimilis*.

Rattus glauerti was the next of this group to be described, again by Thomas (1926b), and again it is another island form, this time from the Houtman's Abrolhos Islands, Western Australia. Thomas recognized it as a species allied to *R. fuscipes* from Western Australia but did not propose conspecificity. The material which he had available for description was unfortunately an immature specimen and the skin was badly discolored.

Next, Brazenor (1936a) described *Rattus* *greyii ravus* from southwestern Victoria. Although the name *ravus* was discovered to be a homonym of *Rattus ravus* (Robinson and Kloss, 1916), Troughton (1937a) supported the integrity of this group by submitting the replacement name of *Rattus greyii peccatus* for it. Three years later Tate (1940) also recognized Brazenor's error and re-named it *Rattus greyii brazenori*, but according to the Law of Priority the name *R. g. peccatus* had to be selected.

The most recent rat of the *Rattus fuscipes* group to be proposed is *Rattus greyii pelori* (Finlayson, 1960), occurring on Greenly Island off the coast of South Australia.

The nine forms of rat discussed above represent their status at the time of their original descriptions. They will now be treated group by group under the headings of our proposed classification.

Rattus fuscipes fuscipes (Waterhouse)

Mus fuscipes WATERHOUSE, 1839, pp. 66–67.
Rattus mondraineus THOMAS, 1921a, p. 428.
Rattus glauerti THOMAS, 1926b, p. 308.

NEOTYPE: Skin and complete skull, adult female, WAM M6634, collected January 4, 1966, by M. H. and W. G. Henderson, 4 miles south of Mt. Melville, Albany, Western Australia. Original type lost; neotype designated by Taylor and Horner (1967, p. 8).

DISTRIBUTION: *Rattus fuscipes fuscipes* is confined to the southwestern portion of Western Australia, from the vicinity of Albany to the vicinity of Perth on the mainland, and is largely coastal in distribution. Lundelius (1960) stated that it occurs as far north as Jurien Bay, 130 miles north of Perth. In insular situations it is found as far north as the Houtman's Abrolhos

TABLE 2

MEASUREMENTS (IN MILLIMETERS) AND WEIGHTS (IN GRAMS) OF ADULT *Rattus fuscipes fuscipes*

Measurement	N	Mean ± SE[a]	SD[a]	Range
Head and body length	72	147.58±1.46	12.39	125–172
Tail length	72	123.89±1.21	10.24	105–159
Hind foot (s.u.) length	72	28.81±0.23	1.95	25–35
Ear length (from notch)	82	20.12±0.15	1.39	15–24
Occipitonasal length of skull	80	37.09±0.16	1.43	35.1–40.2
Condylobasal length	76	34.77±0.18	1.61	32.3–38.3
Basal length	75	32.04±0.18	1.59	29.5–35.3
Zygomatic width	73	18.80±0.11	0.94	16.7–21.2
Interorbital width	103	5.06±0.03	0.27	4.3– 5.9
Interparietal length	85	4.60±0.05	0.45	3.7– 5.5
Interparietal width	83	10.09±0.07	0.63	8.3–11.3
Braincase width	88	16.05±0.05	0.50	14.8–17.3
Mastoid width	82	13.36±0.05	0.49	12.1–14.3
Nasal length	96	13.28±0.08	0.82	11.6–14.9
Nasal width	96	3.77±0.03	0.27	3.3– 4.5
Palatal length	99	19.06±0.10	0.99	16.9–20.8
Incisive foramen length	102	6.70±0.05	0.51	5.7– 8.1
Incisive foramina width	100	1.87±0.02	0.19	1.4– 2.6
Inside m^{1-1} width	102	2.94±0.03	0.35	2.1– 3.9
Outside m^{1-1} width	102	7.51±0.04	0.45	6.5– 8.5
Bulla length	89	6.14±0.03	0.27	5.5– 7.0
Crowns m^{1-3} length	101	6.10±0.05	0.47	4.9– 6.9
Alveoli m^{1-3} length	101	6.61±0.05	0.49	5.5– 7.6
Crowns m^{1-2} length	104	4.83±0.04	0.40	3.5– 5.6
M^{1-1} width × 2	102	4.57±0.04	0.35	3.5– 5.5
Body weight	46	90.10±2.33	15.79	50–118

[a] SE indicates standard error of the mean; SD, standard deviation from the mean.

Islands, which have been separated from the mainland for about 11,500 years, and as far east as some islands of the Recherche Archipelago, isolated about 10,500 years (Main, 1961). It would not be surprising to find evidence of it on the adjacent mainland (fig. 2).

MEAN MEASUREMENTS (IN MM.): External: head and body 148; tail 124; hind foot (s.u.) 28.8; ear (from notch) 20. Skull: occipitonasal length 37.1; braincase width 16.0; bulla length 6.1; crowns m^{1-3} length 6.1. (See table 2 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 35.0 or less.

DESCRIPTION: This is one of the smaller of the *Rattus fuscipes* group, with tail and hind foot shorter relative to head and body length than in other subspecies of *R. fuscipes*. The pelage is soft and dorsally is rust-brown. The middorsal hairs measure about 18 mm., are gray basally and the terminal 3 mm. of rusty hue. Long guard hairs cover the dorsum and are up to 43 mm. long and grayish at the base, dark brown distally. In the rump region the main pelage hairs measure only about 13 mm. long, whereas the guard hairs are more than 40 mm. and here are tipped with rust and very conspicuous. The ears are similar to the dorsum in color and contain sparse silvery hairs. Facial vibrissae measure to 43 mm. The ventral surface is buff-gray, darker than other subspecies of *R. fuscipes* because the basal portion of the ventral hairs is darker gray. The ventrolateral and ventral parts of the head are similar to the body venter in color. The feet are an over-all light brown color and contain a mixture of whitish and brown hairs. The hind feet are narrow as in *R. f. greyii* and have a dusky hue, from which the scientific name of *fuscipes* originates. The tail has 11 scales per cm. It is darker than that of more eastern subspecies and has a fine covering of dark brown hairs. The juvenile pelage lacks the long guard hairs, dorsally, is a dull gray tipped with rust-brown in older specimens, and has a lighter gray venter. The mammary formula is 2+3=10.

In the adult skull the incisive foramina are narrower than in other subspecies of *R. fuscipes*, except in some *R. f. assimilis*, being straight-sided to slightly hourglass-shaped. They extend posteriorly to a point in line with the anterior loph of m^1. The hard palate terminates behind the molar row. The supraorbital-temporal ridges are inconspicuous in the frontal region but continue posteriorly along the parietals for almost their full length. Each ridge is about 1 mm. high and 1 mm. wide. The skull is less elongate in over-all shape than it is in either *R. f. assimilis* or *R. f. coracius* (fig. 3). On juveniles the supraorbital-temporal ridges are even less pronounced. The skull is typical for juvenile *Rattus* in having a very rounded cranial portion, especially in the region of the parietals (fig. 7).

PREVIOUS DESCRIPTIVE ACCOUNTS: Morphological descriptions have been given by Waterhouse (1839), Thomas (1921a, 1926b), Le Souef and Burrell (1926), Troughton (1941 and subsequent editions), Tate (1951), and Storr (1965a). In the original description of *R. f. fuscipes*, Waterhouse (1839) remarked on the black lower incisors of the type specimen. Among the 170 skulls of *R. f. fuscipes* examined by us we have never encountered lower incisors that varied from the usual ivory to orange color. The type examined by Waterhouse, and now lost, must have been subject to an agent that resulted in extensive discoloration of these teeth.

Tate (1951) recorded the mammary formula of *R. f. fuscipes* as 2+3=10, and we have never found exception to this.

Taylor and Horner (1972, MS) have discussed aspects of its breeding biology.

Colored illustrations of *R. f. fuscipes* are presented by Waterhouse (1839, pl. 25) and by Troughton (1941 and subsequent editions, pl. 19, fig. 4), and a drawing is given by Ride (1970, pl. 42).

REMARKS: It is a quirk of collecting that in island situations all the *R. f. fuscipes* (synonym =*R. f. glauerti*) specimens available to us through 1965, of which there are only 20, and all the *R. f. fuscipes* (synonym =*R. f. mondraineus*), of which there are only 17, have been trapped, with but two exceptions, only in the period that is generally off-season for breeding in *R. f. fuscipes*. All materials from the Houtman's Abrolhos Islands have been taken from April through September (except for one animal taken in October and the type specimen taken November 17), and all specimens from the Recherche Archipelago (except for two from Woody Island) have been taken in April. This is the time of year when the populations would be heavily endowed with juveniles and young adults (Taylor and Horner, MS). Hence, it is not surprising that there is a tendency for the measurements of these island forms to be smaller than those of mainland *R. f. fuscipes* (Thomas, 1926b), which have been trapped almost the year round, for the supraorbital-temporal ridges to be less distinct (Thomas, 1926b; Storr, 1965a), and for relative inflation of the cranium to be more pronounced (Tate, 1951; Storr, 1965a). All these features are characteristic of any young *Rattus* and are not valid taxonomic distinctions within this genus. Alexander (1921) also recognized that the *R. f. fuscipes* from the Houtman's Abrolhos Islands was young material and he was not willing to give them distinction at the level of subspecies.

HABITS AND HABITAT: The confusion of *R. f. fuscipes* and *R. l. lutreolus*, which has been reviewed by Taylor and Horner (1967), has taken its toll not only from the standpoint of systematics but also in the description of the habits and habitat of *R. f. fuscipes*. As recently as 1965, Troughton described *R. f. fuscipes* as being "water-loving" and rarely leaving swampy cover of grass and reeds. This is much more characteristic of *R. l. lutreolus* than of *R. f. fuscipes*, and we have shown (Horner and Taylor, 1965) that *R. f. fuscipes* is not confined to a swamp environment, but rather that a major requirement is dense undercover. In southwestern Australia this type of vegetation density can be found either in swamps or in many drier situations. Storr (1965b) reported having trapped *R. f. fuscipes* in beach sandplains. Soil friability is also very important to *R. f. fuscipes* for this rat constructs conspicuous burrows that are interconnected by runways.

Although swamps are numerous in southwestern Australia, the occurrence of dense vegetation in drier environments is not uncommon. In fact, the original description of *R. f. fuscipes* (Waterhouse, 1839) indicates that Darwin actually collected the type specimen "amongst bushes" at King George's Sound and

FIG. 8. Habitat of *Rattus fuscipes fuscipes* in tea-tree (*Leptospermum*) swamp 5 miles west of Denmark, Western Australia. Photographed November 28, 1963.

that he made no reference to a swamp environment.

The population of *R. f. fuscipes* that we sampled in the vicinity of Denmark was taken from two distinct ecological regions. One is a tea-tree (*Leptospermum firmum*) swamp (fig. 8). Its central zone contains free water for most of the year, and the vegetation is composed of tall sedges (mostly Cyperaceae) grading peripherally into sclerophyllous shrubs and a taller story of shrubs consisting mainly of *Agonis linearifolia*. A second, more peripheral zone, composed of a dense sedge region (mostly Restionaceae), perennial herbs, and myrtaceous and leguminous shrubs, is seasonally flooded. Sword sedge (*Lepidosperma gladiatum*), bracken (*Pteridium aquilinum*), and paperbark trees (*Melaleuca parviflora*) are the main components of the damp fringe of the swamp. *Rattus fuscipes fuscipes* was trapped in the outer two zones and it is likely that it navigated freely in the inner zone including the central area of the swamp that is devoid of vegetation. The second major area in which we worked is a drier upland forest habitat supporting low shrub vegetation, acacias, *Banksia*, *Xanthorrhoea*, and trees such as karri (*Eucalyptus diversicolor*), jarrah (*Eucalyptus marginata*), marri (*Eucalyptus calophylla*), peppermint (*Agonis flexuosa*), and bulloak (*Casuarina decussata*). There are no water courses or pools in this habitat.

The distribution of the *R. f. fuscipes* taken is as follows. A total of 879 trap nights in the swamp environment yielded 18 *R. f. fuscipes*, and 755 trap nights in the forest environment yielded 20. This is a 2.05 per cent yield in the swamp environment and a 2.65 per cent yield in the forest area. Although both of these major habitats are in some regions adjacent to cultivated land, *R. f. fuscipes* was never caught in the open expanses of cultivation; but if the crops offered sufficient cover the rat would probably invade them. Open grassland, pure stands of bracken, and a high canopy forest with sparse undergrowth are also unsuitable for *R. f. fuscipes*. On the Wallabi Islands, Storr (1965a) trapped *R. f. fuscipes* (synonym=*R. f. glauerti*) in shell-grit flats supporting saltbush and, more often, in sandy areas well covered with *Spinifex longifolius*. John Kirsch (personal commun.) has also trapped this rat on sandy terrain covered with *Spinifex* clumps, about 4 feet in height. At Waychinicup River *R. f. fuscipes* has been taken in mallee thickets.

Runway and burrow systems constructed by *R. f. fuscipes* in the moister environment offer the rat the opportunity to travel inconspicuously day or night, but our field evidence suggests that it is strictly nocturnal in its use of runways and first becomes active at twilight. Storr (1965a) also described *R. f. fuscipes* as essentially nocturnal. Runways are evident in the drier areas only where ground litter carpets the soil.

Of the four subspecies of *Rattus fuscipes*, *R. f. fuscipes* is the only one which in its entire distribution is nowhere in contact with a subspecies of *Rattus lutreolus*. In the absence of a swamp-dwelling ally *R. f. fuscipes*, unlike its conspecific relatives, has taken advantage of the heavy vegetation of swamps (the primary habitat of mainland *R. lutreolus*) as well as, like its conspecific forms, of the dense cover offered by forests and shrub layers. In Tasmania, on the other hand, *R. l. velutinus* is the only subspecies of *R. lutreolus* that is nowhere sympatric with *R. fuscipes*. Here the reverse situation occurs, and it is *R. l. velutinus* that is opportunistic in habitat exploitation, utilizing the dense cover of rain forests and sedgelands (Green, 1967) in addition to that of the swamps.

SYMPATRY: The only other native *Rattus* with which *R. f. fuscipes* is, or has been, sympatric in historical time is *Rattus tunneyi culmorum* in the northern extremity of the mainland range of *R. f. fuscipes*.

TAXONOMIC HISTORY: The early confusion of *R. f. fuscipes* with *R. l. lutreolus* (Gray, 1843), only four years after the original description of the former (Waterhouse, 1839), resulted in the misapplication of the name *R. f. fuscipes* to specimens of *R. l. lutreolus* and/or *R. l. velutinus* by all subsequent authors until Thomas (1906a) made the first attempt to correct the error. So major was the error that no Western Australian material, and hence no *R. f. fuscipes*, was included under the name *Mus fuscipes* by Gerrard (1862) or Waite (1900). Gould (1851), Krefft (1871), Ogilby (1892), and Trouessart (1897) included true *R. f. fuscipes* under *Mus fuscipes* but also included *R. l. lutreolus* and *R. l. velutinus*. In Jentink's (1888) listing of *Mus fuscipes*, specimen "e" is *R. lutreolus* (Mahoney, 1969). Gerrard (1862), Krefft (1871), and Ogilby (1892), furthermore, followed Gould (1858a) and in effect included true *R. f. fuscipes* under *Mus assimilis*. In 1900 Waite published a detailed description of what he thought was *Mus fuscipes* but what was actually *R. l. lutreolus*.

Although Thomas (1906a) attempted to straighten out the confusion between *R. l. lutreolus* and *R. f. fuscipes* by supporting the full species status of *Mus lutreola* and the integrity of *M. fuscipes* as a discrete Western Australian form, his recommendations were largely ignored. Using the generic names of *Mus* and *Epimys*, respectively, Lucas and Le Souëf (1909) and Longman (1916a, 1916b) included *R. l. lutreolus* and *R. l. velutinus* under true *R. f. fuscipes* and true *R. f. fuscipes* under *R. f. assimilis*. Only Lord (1923) and Lord and Scott (1924) followed the proposal made by Thomas in 1906.

Using Waite's paper of 1900 as a guide, Troughton (1920) published an extended description of *R. f. assimilis* (and *R. f. greyii*) in the name of *Epimys assimilis* confident that his comparisons of *assimilis* with the form Waite described were actually with *Epimys fuscipes* (=*R. f. fuscipes*). Troughton did not realize that Waite's animal was in fact *R. l. lutreolus*. The outcome of this was that Troughton failed to recognize that *R. f. assimilis* and *R. f. fuscipes* are conspecific. Rather, he considered the range of *E. assimilis* to extend to southwestern Australia and hence, like so many of his predecessors, subordinated true *R. f. fuscipes* (and also *R. f. greyii*) under his *E. assimilis*.

When Thomas originally described the insular form *R. mondraineus*, he stated that it was "alone related to *R. fuscipes*" (Thomas, 1921a, p. 429), but, as with *R. murrayi*, he judged that *R. mondraineus* possessed characters which were sufficiently distinct to warrant full species status. The description of *R. mondraineus* by Le Souef and Burrell (1926) is almost a verbatim statement of the original description.

Le Souef and Burrell (1926) unwittingly subordinated true *R. f. fuscipes* under their *R. assimilis* in the same fashion that Troughton did in 1920. They, however, confined their recognition of *R. fuscipes* (=*R. f. fuscipes*) to southwestern Australia, as did Thomas (1921a). The major difference between their assessment and Troughton's (1920) was that they recognized that Waite (1900) had misidentified *R. l. lutreolus* as *R. f. fuscipes* and could thus apply Waite's description to their account of *Rattus lutreola*. They did not realize, however, that their description of *R. fuscipes*, in being but a rewording of the description by Gould (1851), was in fact a description of *R. l. lutreolus*.

Jones (1925) gave *R. f. fuscipes*, on the one hand, and *R. l. lutreolus* and *R. l. velutinus*, on the other, full species rank as *R. fuscipes* and *R. lutreola*, respectively, although he believed they were closely related. Furthermore, his description of *R. fuscipes* (=*R. f. fuscipes*) was taken from Waterhouse (1839) and hence was correct. He erred in describing *R. assimilis* as a full species, for he used the account and geographical range as given by Gould (1858b) and in so doing inadvertently incorporated *R. f. fuscipes* under *R. f. assimilis*.

At the time Thomas (1926b) described *Rattus glauerti*, another insular form, he recognized that it was a close relative of *R. fuscipes* of Western Australia. He commented that *R. glauerti* "appears to correspond to the mainland *R. fuscipes* exactly as *R. murrayi* . . . does to the S. Australian *R. greyi*" (Thomas, 1926b, p. 309), and, like *R. murrayi*, possesses molars that are considerably smaller than those of the mainland counterpart. It is unfortunate that the only specimen he possessed for description was not fully adult. Thomas (1926b) placed *R. glauerti* as a full species although closely related to *R. fuscipes*. Iredale and Troughton (1934) formally recognized the close affinity of the two forms and were the first to place *glauerti* as a subspecies of *R. fuscipes*. They also gave an accurate account of the geographical ranges of what we now recognize as *R. f. fuscipes* and *R. f. assimilis*, as well as of *R. f. glauerti* and *R. f. mondraineus* over which there had been no question.

In ensuing accounts Troughton (1937b, 1941–1967, First through Eighth editions) has continued to refer to *R. fuscipes* (=*R. f. fuscipes*) and *R. lutreolus* as members of a common swamp-rat group, even though he has considered them separate species. "The range of the species [*fuscipes*] was once vastly extended to include the eastern swamp-rat [*lutreolus*], but owing to the break of range in the drier region along the Bight, and well-marked differences, the species are now regarded as distinct, though of similar habits" (Troughton, 1941–1967, Eighth edition, p. 282). In the 1967 edition of his book Troughton altered his view by stating that the semiaquatic habitat of this rat had been exaggerated.

Raven (1935) treated *R. l. velutinus* under *R. fuscipes* but restricted his *R. assimilis* to the eastern portion of Australia. On the other hand, he retained *glauerti* as a full species (and erred in the spelling of the locality name).

Brazenor (1936a) was not convinced of the separation of *R. fuscipes* and *R. lutreolus* into distinct species. In the same year Shortridge (1936) not only stated that both *M. fuscipes* and *M. assimilis* occurred in southwestern Australia, but erroneously named this as the type locality of *M. assimilis*. Furthermore, Shortridge (1936) identified specimens collected during the Balston Expeditions from "Modrain" Island as *M. fuscipes* and *M. greyi* and stated that native rats occurring on the Wallabi Group of the Abrolhos Islands may also be referable to *M. greyi*. He neither mentioned *R. f. glauerti*, nor appeared to possess any specimens from the Abrolhos Islands. Teichert (1946) suggested that the *R. fuscipes* from the Abrolhos were subspecifically distinct but did not mention the name *R. f. glauerti*.

It was not until 1949 that the natural relationships of *fuscipes*, *lutreolus*, and *assimilis* were established when Ellerman proposed that *assimilis* was an eastern Australian subspecies of *R. fuscipes* and recognized *R. lutreolus* as a separate species. Ellerman (1949) was also the first to ally *R. mondraineus* with *R. fuscipes* by placing it as a subspecies of the latter, this differing from his 1941 assessment of it as a full species. He stated in 1949 that *R. f. mondraineus*, like *R. f. murrayi*, is an aberrant island form with a palate that is shorter than usual for members of the *R. fuscipes* group. Although he had earlier (1941) considered *glauerti* a subspecies of *R. fuscipes*, he later (1947, 1949) treated *R. glauerti* as a distinct species on the basis of his examination of the type skull and noted its size resemblance to *R. exulans*.

Two years later Tate (1951) countered the proposal made by Ellerman (1949) and once again linked *R. f. fuscipes* and *R. lutreolus* under one species. This assessment was complicated further by the fact that Tate ignored the Law of Priority and placed *R. f. fuscipes* as a subspecies of *R. lutreolus*. He regarded *R. assimilis* as a separate species. The full explanation of his treatment has been reviewed separately (Taylor and Horner, 1967). He believed that *R. glauerti* so resembled *R. exulans* that it may belong to the latter species, apparently making his judgment solely on the basis of the type specimen. Tate (1951) handled *R. f. mondraineus* in a unique way by placing it as a subspecies of *R. lutreolus*. This move is consistent with his assessment of *R. f. fuscipes* as *R. lutreolus*, but it is surprising that after examining the type of *R. f. mondraineus* and the series at the United States National Museum he did not ally it with his *R. assimilis* or *R. greyii* group rather than with *R. lutreolus*. He was probably strongly influenced by his predecessors who noted the alliance of *mondraineus* with *R. fuscipes*. No one has since followed his treatment of *mondraineus*.

Troughton (1941–1967, Eighth and Ninth editions) followed Ellerman (1949) in his assessment of *R. f. mondraineus* and also retained *R. glauerti* as a full species. He disagreed with Tate's (1951) statement that *R. glauerti* may really be *R. exulans* that had gained access to the Houtman's Abrolhos Islands by boat and thought, rather, that *R. glauerti* should be regarded an indigenous species.

We support the proposal made by Ellerman (1949) that *R. f. fuscipes* is a subspecies confined to southwestern Australia, that *R. lutreolus* is not conspecific with it, and that *R. f. fuscipes* shares no part of its range with *R. f. assimilis*. In an effort to clarify this position further we have designated a neotype for *R. f. fuscipes* (Taylor and Horner, 1967) and have brought additional evidence in support of the assessment made by Ellerman (1949) of the three above-named taxa (Horner and Taylor, 1965). We treat both *mondraineus* (type, BM 7.7.18.3♂ from Mondrain Island) and *glauerti* (type, BM 26.7.12.2♂ from East Wallabi Island) as subspecifically indistinguishable from the mainland *R. f. fuscipes*.

Rattus fuscipes greyii (Gray)

Mus greyii Gray, 1841, p. 410.
Mus murrayi Thomas, 1923a, p. 601.
Rattus greyi ravus Brazenor, 1936a, p. 69.
Rattus greyi peccatus Troughton, 1937a, p. 189.
Rattus greyi pelori Finlayson, 1960, pp. 140–141.

Lectotype: Skin and broken skull lacking occipital and basal portions, juvenile male, BM 41.1266, from the Gould Collection, procured in South Australia in 1839 or 1840. Selected as the lectotype by Thomas (1921a, p. 432).

Distribution: On the mainland *R. f. greyii* extends from the vicinity of Portland, Victoria, westward to Mt. Drummond on Eyre Peninsula, South Australia. Subfossil post-Pleistocene skull fragments of *R. f. greyii* are recorded 40 miles northeast of Portland (Wakefield, 1964a, 1964b). This rat is mainly coastal in distribution and in

TABLE 3

MEASUREMENTS (IN MILLIMETERS) AND WEIGHTS (IN GRAMS) OF ADULT *Rattus fuscipes greyii*

Measurement	N	Mean±SE[a]	SD[a]	Range
Head and body length	60	145.67±1.72	13.30	119–176
Tail length	60	140.80±1.71	13.24	110–167
Hind foot (s.u.) length	60	30.18±0.21	1.62	27– 33
Ear length (from notch)	41	21.31±0.21	1.36	19– 24
Occipitonasal length of skull	75	36.45±0.14	1.22	34.1–39.7
Condylobasal length	79	34.20±0.15	1.31	31.3–37.4
Basal length	76	31.45±0.15	1.34	28.6–34.6
Zygomatic width	67	18.36±0.09	0.73	16.8–20.2
Interorbital width	87	5.06±0.03	0.25	4.5– 5.7
Interparietal length	79	4.32±0.04	0.37	3.3– 5.3
Interparietal width	79	9.73±0.08	0.72	7.9–11.4
Braincase width	79	16.04±0.05	0.42	15.2–17.0
Mastoid width	76	13.52±0.05	0.46	12.5–14.9
Nasal length	84	13.40±0.09	0.79	11.8–15.1
Nasal width	85	3.55±0.03	0.30	2.8– 4.4
Palatal length	89	18.64±0.09	0.83	17.0–21.0
Incisive foramen length	89	6.83±0.05	0.46	5.9– 8.5
Incisive foramina width	89	2.22±0.03	0.29	1.6– 3.2
Inside m^{1-1} width	88	3.24±0.03	0.33	2.5– 4.2
Outside m^{1-1} width	88	7.41±0.05	0.44	6.4– 8.4
Bulla length	85	6.16±0.03	0.27	5.4– 7.4
Crowns m^{1-3} length	88	5.65±0.04	0.39	4.6– 7.0
Alveoli m^{1-3} length	90	6.12±0.05	0.46	4.9– 7.3
Crowns m^{1-2} length	89	4.48±0.04	0.34	3.4– 5.7
M^{1-1} width × 2	88	4.18±0.04	0.34	3.1– 5.2
Body weight	25	77.08±3.88	19.39	40– 110

[a] SE indicates standard error of the mean; SD, standard deviation from the mean.

living form has never been recorded from the Grampians Mountains in Victoria, a seemingly suitable habitat that is a mere 60 miles inland and 40 miles north-northeast of the nearest locality record. Wakefield (1963b), however, discovered subfossil *R. f. greyii* in the Grampians and suggested that the former distribution of this rat was continuous from here to the south coast. *Rattus fuscipes greyii* extends farther west in insular distribution than it does on the mainland, its westernmost limit being Goat Island off Ceduna, South Australia. Although no records are known of *R. f. greyii* west of Mt. Drummond on the mainland, we located habitat suitable for this rat as far west as Elliston where, unfortunately, most of the surrounding area is severely overgrazed and is low grassland or mallee scrub with sparse undercover. As in *R. f. fuscipes*, it would not be surprising to find it on mainland sites adjacent to its insular distribution. There is a large hiatus in the distribution of *R. f. greyii* on the mainland between the Victoria-South Australia border and the Fleurieu Peninsula, which is accountable by the absence of vegetation of sufficient density to support a *R. f. greyii* population today (fig. 2).

MEAN MEASUREMENTS (IN MM.): External: head and body 146; tail 141; hind foot (s.u.) 30.2; ear (from notch) 21. Skull: occipitonasal length 36.4; braincase width 16.0; bulla length 6.2; crowns m^{1-3} length 5.6. (See table 3 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 34.0 or less.

DESCRIPTION: *Rattus fuscipes greyii* joins *R. f. fuscipes* in being one of the small members of the *Rattus fuscipes* group but has a relatively longer tail and hind foot than does the southwestern *R. f. fuscipes*. The pelage is soft and dorsally rust-brown. The dorsal hair is about 17 mm. long and slate-gray basally. The last 3 mm. is rust in color. The guard hairs are about three times longer and in most cases are colored in similar fashion to the dorsal body hairs. Along the rump the guard hairs tend to be tipped in white rather than rust, and over the entire animal some guard hairs are white to the base. The ears are dorsal body color and have a mixture of short silvery and rust hairs. Facial vibrissae measure to 50 mm. Ventrally the rat is silvery buff with hairs basally a slate-gray. The ventral and ventrolateral portions of the head are similarly colored. The feet are covered with silvery hairs and in color resemble the ventral body pelage. As in *R. f. fuscipes* the hind feet are narrow. The tail is finely covered with hairs up to 2 mm. long that are darker on the dorsal side of the tail than on the ventral. The over-all color of the tail is brown, and there are 11 scales per cm. Juvenile *R. f. greyii* are dull gray with a lighter venter and lack the long guard hairs. The mammary formula is $2+3=10$.

In the adult skull the lateral walls of the incisive foramina tend to be very straight or slightly bowed and, as in *R. f. fuscipes* from Western Australia, terminate in line with the first loph of m^1. The palate ends behind the molar row. Supraorbital-temporal ridging is generally very poorly defined except on old adults. It is less than 0.1 mm. wide and is raised about 0.1 mm. from the skull surface. It usually terminates before the posterior border of the parietals (fig. 4). On the juvenile skulls it is usually difficult to define these ridges, and the cranial region is typically more inflated (fig. 7).

PREVIOUS DESCRIPTIVE ACCOUNTS: Morphological accounts of *R. f. greyii* have been made by Gray (1841), Ogilby (1892), Lucas and Le Souëf (1909), Jones (1922, 1925), Thomas (1923a), Le Souef and Burrell (1926), Brazenor (1936a, 1950), Troughton (1941 and subsequent editions), Tate (1951), and Finlayson (1960). Several of these are but minor rewordings of the original description and often include more than *R. f. greyii*. The yellowish tinge along the lateral body region mentioned by Jones (1925) was evident on some of our freshly caught material but it is not a general character of the group. Although several describers (Ogilby, 1892; Lucas and Le Souëf, 1909; Thomas, 1923a; Jones, 1925; Le Souef and Burrell, 1926) emphasize that *R. f. greyii* has a shorter tail than the head and body length, our material from 60 specimens indicates that it is only in the order of 5 mm. on the average. It would be difficult to discern.

Although Jones (1925) reported some thoracic variation in mammary formula, Tate (1951) established that the formula is $2+3=10$. The findings of Finlayson (1960) confirm this number, and we have found little deviation. It is not easy, however, to locate the full complement of teats on juvenile females.

Taylor and Horner (1972, MS) have described aspects of its reproductive biology.

There are no colored illustrations of *R. f. greyii*. Finlayson (1960) provided photographs of the whole animal, and Brazenor (1950) presented a drawing. Jones (1922, 1925), Brazenor (1936a), and Finlayson (1960) illustrated skulls, feet, and tooth patterns. Misonne (1969, fig. 116) has detailed drawings of upper and lower molar rows.

REMARKS: There is minor coat color variation in *R. f. greyii*, some rats tending to have a more grayish hue than others, but usually it is not correlated with geographical distribution, except as follows. There are small isolated colonies of *R. f. greyii* on Eyre Peninsula, on Goat Island, and on the Investigator Group, in which the pelage is distinctive from that of *R. f. greyii* at other localities in being lighter in hue and having more reddish coloration in the dorsal region. The feet are also slightly more buffy. Troughton (1920), using the misnomer *Epimys assimilis*, referred to this feature of reddish coloration of the rats at the Port Lincoln locality on Eyre Peninsula. A second instance occurs at the western end of Kangaroo Island where the population has a slightly dusky foot color that is distinct from the normal silvery hue of other *R. f. greyii*.

The seven adult *R. murrayi* available to us from Pearson Island are subspecifically indistinguishable from *R. f. greyii*. Our measurements of the skull features on which Thomas (1923a) established a new species fall well within the ranges of those for *R. f. greyii*. Bulla size, which Thomas (1923a) cited as distinctive, is 17.5 per cent of the occipitonasal length in *R. murrayi* and 16.9 per cent in *R. f. greyii*. The average skull length of the two is within 0.4 mm. Although the length of crowns m^{1-3} is only 13.7 per cent of the occipitonasal length in *R. murrayi* as compared with 15.6 per cent in *R. f. greyii* and the incisive foramina average 0.17 mm. wider in *R. murrayi*, these two features seem to us insufficient basis for separate subspecific relegation. The paler pelage described for *R. murrayi* is found at other *R. f. greyii* localities, as previously discussed.

The other proposal for an insular form, *Rattus greyii pelori*, is based on dimensional features of about a dozen rats taken from nearby Greenly Island (Finlayson, 1960). This group also falls well within the subspecies *R. f. greyii*. Finlayson (1960) stated that the skull, although slightly larger in *R. g. pelori*, is very similar to that of *R. g. murrayi*. Two of the "distinctive" features he listed, greater bulla size and decidedly reduced molar rows, do not appear to hold when compared to *R. f. greyii* as a whole. On the basis of the four adult specimens from Greenly Island available to us, the bullae are actually relatively smaller, being 16.4 per cent of the occipitonasal length, than in the whole subspecies *R. f. greyii* (or are the same, 17.0 per cent, based on Finlayson's figures for adult males), and the molar row is only slightly smaller, being 14.7 per cent of the occipitonasal length (or is larger, 15.4 per cent, based on Finlayson's adult male measurements). The incisive foramina, however, are wider than in either the whole subspecies *R. f. greyii* (by 0.35 mm.) or "*murrayi*" (by 0.18 mm.). Undoubtedly, demonstrable insular variation occurs for each island population of *R. f. greyii*, but in our estimation none has yet been shown to be of sufficient magnitude to warrant separate subspecific designation.

The proposal of a mainland subspecies, *Rattus greyii ravus*, by Brazenor (1936a) was based on his comparison of a series of 60 rats from Portland, Victoria, with the measurements by Jones (1925) of four *R. f. greyii* of undisclosed locality in South Australia. The four specimens measured by Jones are all young adults, whereas Brazenor had before him a much greater size range. Brazenor (1936a) proposed *R. g. ravus* mainly on the basis of its larger size, apparently not realizing that the specimens measured by Jones were not fully grown.

HABITS AND HABITAT: *Rattus fuscipes greyii* inhabits areas along the south coastal region of Australia that offer a low canopy of dense vegetation or shelter in the form of boulders and fallen logs. The two investigators who have contributed the most information regarding the habitat of *R. f. greyii* are Jones (1924, 1925) and Finlayson (1960). Jones (1925) found that it frequents damp places containing luxuriant undergrowth, stream borders of low-lying country, and sandhill country (on the tip of Eyre Peninsula). It lives by day in the crevices between large rocks and in the recesses provided by fallen timber. On Pearson Island, Jones (1924, 1925) has seen the rats at night on beaches foraging above the high-tide mark. Their runways are numerous on travertine plateaus and they utilize the shelter provided by large boulders. Finlayson (1960) has also trapped *R. f. greyii* in mangrove belts and in the vicinity of human settlements near Adelaide in locations where vegetation cover is still adequate. Slopes of hills covered with bracken and *Xanthorrhoea*, dry laterite ridges in stands of stringybark trees (*Eucalyptus obliqua* and *E. baxteri*), dwarf eucalypt shrubs, and the dense, tangled growth near swampy creek heads also harbor this rat (Finlayson, 1960).

In the vicinity of Portland, Victoria, *R. f. greyii* makes extensive use of fallen timber and decaying logs for refuge. Grasses, acacias, bracken, heath, *Banksia*, and young gums offer dense undercover as do leaf and bark litter. The soil is sandy, friable in some parts and relatively hard in others, and supports, in addition to a dense undercover 3 to 6 feet high, an open stand of second-growth eucalypts ranging from 75 to 100 feet high and 10 to 20 feet apart. In 1964 the typical middle canopy of 15 to 25 feet was lacking in this area, for regular burning had inhibited the re-establishment of a middle canopy in these dry sclerophyll forests. Wherever the vegetation near the ground becomes sparse owing to recent fire, cultivation, or grazing, the rats are generally absent. They appear to be confined to areas where the ground cover is dense, both in the dry sclerophyll forests and in brush areas.

On Kangaroo Island, Troughton (1920) trapped *R. f. greyii* on a rocky hillside and by the banks of a dry watercourse. We found them to be most abundant on Kangaroo Island in the stands of *Melaleuca* growing in seasonally dry swamps (fig. 9). These swamps are dry for most of the year and become wet only for a few weeks at a time after heavy rains. Nothing is known about the movements of *R. f. greyii* in this habitat, but it is likely that the rat occupies the *Melaleuca* stands only when the swamp is dry. *Melaleuca* affords excellent cover for it is 1 to 1½ feet high and closely spaced. Between these bushes and covering the surface of the soil is a small-leafed ground plant. The *Melaleuca* swamps contain hardened light-colored soil and they

FIG. 9. Habitat of *Rattus fuscipes greyii* in *Melaleuca* swamp near Rocky River, Kangaroo Island, South Australia. Photographed March 8, 1964.

border well-timbered eucalypt woodland 15 to 25 feet high. At the junction of these two habitats is a fringe of spiny *Acacia* and *Xanthorrhoea*, both of which offer good cover for the rats. One of the marginal habitats for *R. f. greyii* on Kangaroo Island is mixed *Melaleuca*-mallee country that affords moderate undercover and a canopy of *Acacia* and *Xanthorrhoea.*

A pocket of *R. f. greyii* occurs at the tip of Eyre Peninsula in a very dry situation. The soil is hard and rocky in some areas and sandy in others. Leaf litter is light to moderate and the ground is partly covered by common broad-leafed grass which grows up to 15 inches high. *Melaleuca*, up to 8 feet or more in height, is abundant, as is the velvet plant (*Lasiopetalum*), which provides a dense understory. Occasional *Casuarina* trees are the only tall vegetation. The area is mainly sand dune country and the vegetation just described occurs only in pockets, and, as a consequence of extensive overgrazing by domestic animals, the distribution of this vegetation is probably more limited now than in the past. Although the area is extremely dry in summer with no free water available anywhere, central parts of the vegetation pockets have the appearance of being subjected to flooding by rains for brief periods of the year. The rats seem to be confined to the dense portions of the vegetation and do not occupy the bare sand dunes nearby.

We also trapped *R. f. greyii* near the tip of Eyre Peninsula adjacent to a swamp but north of the sand dune region. This was Big Swamp where, surrounding a swamp of reed vegetation, there was a grassy zone about 30 feet wide and 2 to 2½ feet high. *Rattus fuscipes greyii* occurred in the grass zone and its runways were evident both here and at the edge of the reed vegetation of the swamp itself. There were no shrubs or trees in this area. In the absence of *R. l. lutreolus* in this area, *R. f. greyii*, like *R. f. fuscipes*, appears to be opportunistic in utilizing a habitat that is more typical of mainland *R. lutreolus.*

The Mt. Drummond locality on Eyre Peninsula, where we trapped a small sample of *R. f.*

greyii in 1964, is the westernmost record for *R. f. greyii* on the mainland. Dense stands of *Melaleuca* up to 6 feet high occur in clumps, sedges and grasses grow 2 to 4 feet high, and scattered acacias grow to 6 feet. The soil is very hard and sandy, gravelly or rocky, and leaf litter is sparse although large eucalypts grow in the area. The vegetation types indicate that this area is also subject to seasonal flooding in times of heavy rain.

Jones (1925), Brazenor (1936a), and Finlayson (1960) commented on the absence of runways and other signs of rat activity in *R. f. greyii* habitats on the mainland. Finlayson (1960) stated that *R. f. greyii* digs more burrows in the Portland (Heathmere), Victoria, region than on the Fleurieu Peninsula. However, on island situations considerable evidence of rat activity has been described. Jones (1925) found deeply excavated burrows along creek banks on Kangaroo Island and on travertine plateaus of Pearson Island. Mitchell and Behrndt (1949) remarked on the presence of tunnels of this rat on Greenly Island, but reported a total lack of activity above ground except at night. In our experience, burrows and runways of *R. f. greyii* are poorly defined and to some degree associated with soil texture. All the soils of the areas just described, with the exception of Big Swamp, are hard and the vegetation it supports, although dense, is mostly brushy or hard leafed and would not adapt to becoming molded as part of conspicuous runway systems. At Big Swamp, however, where grass is the only plant type and is dense but pliable, *R. f. greyii* can establish runway systems as well marked as those of the typical swamp dweller, *R. l. lutreolus*. The lack of runways throughout most of the range of *R. f. greyii* is probably not a behavioral feature of the rat that would suggest lack of utilization of specific pathways in the course of its daily wanderings, but rather a feature of its environment where the nature of the soil and vegetation do not reflect the well-used routes.

Little is known of the food habits of *R. f. greyii*. Like other Australian *Rattus*, it is primarily vegetarian, eating seeds, roots, and tubers and selecting insects and small vertebrates as well (Finlayson, 1960). Jones (1925) found *R. f. greyii* eating the ground plant, *Mesembryanthemum* (synonym =*Carpobrotus*), on Pearson Island but never located food caches. Although the rat has been seen foraging at the tide mark (Jones, 1925), there is no information as to what it is selecting from the tide detritus.

Rattus fuscipes greyii is mainly a nocturnal rat. Finlayson (1960) has seen it foraging in the late afternoon on Greenly Island, which is uninhabited by man. The earliest capture record we have is at 7 P.M. in the Portland area during October when it is still twilight.

SYMPATRY: *Rattus fuscipes greyii* is sympatric with only one other native *Rattus*, *R. lutreolus lutreolus*. In historic times *Rattus tunneyi culmorum* (synonym =*R. culmorum austrinus*) may have come in close contact with *R. f. greyii* but there are insufficient data on the locality records of *R. t. culmorum* in South Australia to pinpoint the area. Furthermore, *R. t. culmorum* has not been taken in that state during the present century.

TAXONOMIC HISTORY: In 1843, two years after *R. f. greyii* had been described as *Mus greyii* by Gray, this same author synonymized it with another murid, *Mus gouldii*, a form that is now relegated to the genus *Thetomys* or *Pseudomys*. This was the beginning of errors in the *R. f. greyii* group. The next major reference to *R. f. greyii* came 44 years later when Collett (1887) identified two specimens from Coomooboolaroo, Queensland, as *M. greyii*. Fortunately, these two specimens still exist, but neither one of them is *R. f. greyii*. One (ZMO 99) is *Rattus sordidus sordidus* and the other (ZMO 2121) is *Rattus tunneyi culmorum*. Gould (1855) did not recognize *Mus greyii* as a distinct form. He followed Gray's error by synonymizing it under *Mus gouldii*. Ogilby (1892) pointed out Gould's error, recognized *Mus greyii*, but unfortunately included the specimens that Collett had misidentified. He also erred in citing the description of *Mus gouldii* (Waterhouse, 1839) as a reference to *M. greyii*.

Waite (1896, 1898) complicated the situation further by describing under *Mus greyii* three specimens collected on the Horn Scientific Expedition that are actually *R. t. tunneyi*. This was a rational move to a certain extent because he was relying on skull characters of "*greyii*" as they had been described by Collett (1887). As just discussed, Collett's specimens are actually *R. s. sordidus* and *R. t. culmorum*, both of which have large bullae, relatively short nasals, and conspicuous supraorbital-temporal ridges, characters that are also diagnostic of *R. t. tunneyi* but not of *R. f. greyii*. Since *R. t. tunneyi* and *R. t. culmorum* are conspecific, it is reasonable that under the circumstances Waite would have been misled. He clearly stated that he did not have full confidence in his identification of these three central Australian specimens.

Trouessart (1897) recognized *Mus greyii* as a full species in his *Catalogus Mammalium* and, like Waite, had not recognized Collett's error, so he included Queensland in the distribution of this group. Thomas and Dollman (1908) were the first to recognize that *Mus culmorum* might be confused with *Mus greyii*, although they did not refer specifically to Collett's assessment.

Lucas and Le Souëf (1909) incorporated all previous errors, a fact that is obvious from their claim that *Mus greyii* existed not only in South Australia but also in central Australia and in northeast Queensland. Their description of *M. greyii* is an exact copy of the description made by Ogilby (1892), who in turn had taken his largely from that of Gray (1841) and of Collett (1887), the last reference being a description of *R. s. sordidus* and *R. t. culmorum* rather than of *R. f. greyii*. Thomas (1910) recognized *greyii* as a full species, shifting it to the genus *Epimys*, but he did not indicate in his paper how he was defining this species. Longman (1916a, 1916b) was uncritical in his evaluation of *Epimys greyii* and included all the previous errors that had been made except that he did not include *Mus gouldii*. Troughton (1920) included *R. f. greyii* and several other forms in his range description of *Epimys assimilis*.

Thomas (1921a) was the first to make a careful statement about both *Rattus greyii* and *R. culmorum*. He presented characters by which they could be distinguished and correctly identified and described a new specimen of *R. greyii* that had recently been sent to the British Museum (Natural History). This additional specimen was the first material of this form to be sent to the museum since the acquisition of the original eight specimens sent between 1841 and 1845. Thomas (1921a) designated the lectotype of *R. greyii*, a move that was particularly necessary since he found *R. culmorum* among the cotypes of the original *R. greyii* in the museum. Unfortunately, however, he selected a juvenile.

Following this clarification of *R. greyii* (Thomas, 1921a), Jones (1922) published a careful account of the dental characters of *R. greyii* and from this was able to establish that a rat from Goat Island, off South Australia, was closely related. The alliance of the mainland *R. greyii* to rats of the islands off South Australia was suggested by Thomas (1923a) when he described a form from Pearson Island, Investigator Group. He nominated it as a distinct species but a close relative of *R. greyii* and named it *Rattus murrayi*. He distinguished it largely on the basis of its paler coloration, larger bullae, reduced size of teeth, and shortened tail. The last feature is subject to question since he found the tail to be imperfect on most specimens. Jones (1925) studied *R. murrayi* and even attempted to breed it, but without success. He contributed significantly to the habitat description and to body measurements for this form. He regarded it as an insular form of *R. greyii* but, like Thomas (1923a), did not formalize the move.

Jones (1925) also added considerable information regarding mainland *R. greyii* and made a thorough and accurate redescription of this rat. He pointed out that Ogilby (1892) had applied the description of another rat to his account of *Mus greyii*, but Jones did not detect that part of Ogilby's source was Collett (1887), who was actually describing *R. s. sordidus* and *R. t. culmorum*. Jones (1925) also questioned the identification of the "*greyii*" obtained on the Horn Expedition but made no attempt to assess its taxonomic status.

Le Souef and Burrell (1926) took a backward step in their evaluation of *R. greyii*. They incorporated all the previous mistakes. By citing Gould (1855) they were accepting *Mus gouldii* within the *R. greyii* complex and by designating the distribution as southern, central, and northeastern Australia they were including the *R. s. sordidus* and *R. t. culmorum* misidentified by Collett and the *R. t. tunneyi* misidentified by Waite. Fortunately, however, their description of the features of the animal was essentially a rewording and condensation of the recent careful redescription of true *R. greyii* made by Jones (1925). Their description of *R. murrayi* is a virtual copy of the original description (Thomas, 1923a).

Thomas (1926b) compared *R. murrayi* with another new form, *R. glauerti*, and found that both insular forms have very narrow molars, those of *R. glauerti* being especially reduced. He thought that *R. murrayi* has the same relationship to *R. greyii* of the South Australian mainland that *R. glauerti* has to *R. fuscipes* of mainland

Western Australia. He maintained all four groups, however, as distinct species.

The assessment made by Iredale and Troughton (1934) was critical and a step forward, because they not only had the correct concept of *R. greyii* as strictly a South Australian form (as it was known to occur at that time) but also considered the relationship of *R. murrayi* to be so close to *R. greyii* that they reduced it to a subspecies, *Rattus greyii murrayi*.

Raven (1935), on the other hand, repeated previous errors adding at the same time new ones. His concept of *R. greyii* was unprecedented and was based, it seems, on carelessness rather than simply blind repetition of previous errors. Raven stated that *R. greyii* occurred in Queensland (probable influence of Collett) and also New South Wales, but apparently not South Australia, its type locality. No one had previously recorded it in New South Wales, nor has anyone else to the present day. Raven also retained *R. murrayi* as a full species.

Brazenor (1936a) was the first to make more than mere passing comment [as made by Jones (1925)] that *R. greyii* and *R. assimilis* resemble each other in many features. On the strength of this comparison he judged that a series of 60 rats, taken from western coastal Victoria, belonged to *R. greyii* rather than to *R. assimilis*, and proposed the name *Rattus greyii ravus* for this group. This was the first recognition of *R. greyii* in Victoria. He compared *R. g. ravus* with both *R. assimilis* and *R. greyii* and concluded that *R. g. ravus* was not really intermediate but more closely resembled *R. greyii*.

In the same year, Brazenor (1936b) clarified the identification of the Horn Expedition "*greyii*" by assigning them to the *tunneyi* group as a new subspecies, *Rattus tunneyi dispar*. Shortridge (1936) made an uncritical and grossly inaccurate statement about *M. greyii*. He identified two specimens from "Modrain" (should be Mondrain) Island as *Mus greyii*, claimed it to be an insular species, and furthermore stated that rats from the Abrolhos Islands (previously described by Thomas in 1926) were also possibly *M. greyii*. This was erroneous and was the first time that *M. greyii* had been placed in the fauna of Western Australia.

In 1937 Troughton picked up a nomenclatural error made by Brazenor (1936a) when he named *R. g. ravus*. Troughton pointed out that the name *ravus* was a homonym of another rat, *Rattus ravus*, named by Robinson and Kloss (1916), thus rendering invalid the name proposed by Brazenor. As a replacement name for *ravus* Troughton (1937a) proposed *Rattus greyii peccatus*. In 1940 Tate also recognized Brazenor's, error and proposed *Rattus greyii brazenori* as the replacement name for *ravus*, but the Law of Priority held that the earlier replacement name *R. g. peccatus*, was valid. Later Troughton (1941–1967, First edition) cast some doubt on the validity of *R. g. peccatus* as a distinct subspecies, but gave no substantiating evidence. Brazenor (1950) continued to recognize this subspecies.

Although implications had been made that *R. greyii* had strong resemblance to *R. assimilis* and to the Western Australian *R. fuscipes*, Ellerman (1949) was the first to formalize the close affinities by placing *greyii* and also *murrayi* as subspecies of *R. fuscipes*, along with *assimilis* and others. His recognition of *R. f. greyii* as a subspecific ally of *R. fuscipes* was a major step in the clarification of the natural relationships of these rats and one which we have endorsed with additional evidence (Horner and Taylor, 1965). Ellerman (1949) made no mention of *R. g. peccatus* and he was either unaware of its description or perhaps regarded it within the subspecies *R. f. greyii*.

Tate (1951), on the other hand, recognized *R. greyii* as a full species, but only provisionally so. He realized its close affinity to *R. assimilis* and indicated that it was quite likely only a geographical race of *R. assimilis*. Misonne (1969) also suggested alliance of *R. greyii* with *R. assimilis*. Since Tate's concept of *R. f. fuscipes* was erroneous due to a confusion with *R. l. lutreolus* (Taylor and Horner, 1967), he did not ally either *R. greyii* or *R. assimilis* with *R. fuscipes*. Furthermore, he placed *austrinus* (=*R. t. culmorum*) as a subspecies of *R. greyii*, neglecting to recognize it as a member of the *R. tunneyi* complex. Along with *austrinus* he regarded *R. g. peccatus* and *R. g. murrayi* as possibly only weakly separable as subspecies of *R. greyii*.

The most thoughtful and critical review of the *R. greyii* group is that of Finlayson (1960) who has worked closely with this form for many years and has made a substantial contribution to our knowledge. Unlike most of his predecessors, he worked from a whole series of specimens and on this basis recognized four subspecies of *R. greyii*: *R. g. greyii* from the mainland of South Australia, *R. g. murrayi* from Pearson Island, *R. g. peccatus* from mainland southwestern Victoria, and a new subspecies, *Rattus greyii pelori*, proposed by him and known only from Greenly Island. Geographically, *R. g. pelori* is separated from *R. g. murrayi* by a water barrier of 60 miles. On Gambier Island Finlayson obtained three *R. greyii* that he regarded as intermediate between *R. g. pelori* and *R. g. murrayi*. He suggested that this might be still another subspecies, but with the lack of a good series was unwilling to evaluate it taxonomically. He accepted *R. g. peccatus* as a good subspecies and made a detailed comparison of it with *R. assimilis*.

Unlike both Ellerman and Tate, Finlayson was not sympathetic with the view that *R. assimilis* might be conspecific with *R. greyii*. Neither was Troughton (1941–1967, Eighth edition) who, although neglecting to cite Finlayson (1960), also regarded *R. g. murrayi* and *R. g. peccatus* as subspecies of *R. greyii*. Troughton also was in accord with Tate (1951) in allying "*austrinus*" with *R. greyii*.

We agree with Ellerman (1949) in the placement of *R. f. greyii* as a subspecies of *R. fuscipes*. We find "*murrayi*" (type, BM 23.3.28.6♂, from Pearson Island), "*peccatus*" (type, NMV C688♀, from Portland), and "*pelori*" (type, SAM M6268♂, from Greenly Island) to be indistinguishable from *R. f. greyii* at the subspecific level, and we regard "*austrinus*" to be a *Rattus tunneyi culmorum*.

Rattus fuscipes assimilis (Gould)

Mus assimilis Gould, 1858a, p. 241.

Lectotype: Skin and broken skull lacking much of basicranial region, adult male, BM 58.11.24.10, from the Gould Collection, collected at Clarence River, New South Wales, by F. Strange. Selected as the lectotype by Thomas (1921a, p. 432).

Distribution: *Rattus fuscipes assimilis* is mainly coastal and subcoastal in distribution. The westernmost record of its occurrence as a living form is 12 miles southwest of Terang, Victoria. Gill (1953) has described it from a subfossil locality 8 miles west-southwest of this. Wakefield (1964b), who re-examined Gill's material, did not find *R. f. assimilis*, but instead recorded *R. lutreolus* and two species of *Pseudomys*, neither of which was listed by Gill. *Rattus fuscipes assimilis* extends eastward along the coast of Victoria and north through New South Wales and Queensland to Coomooboolaroo in a band about 1400 miles long. Inland it occurs 150 miles from the coast in the Australian Alps and about 100 miles from the coast in the Bunya Mountains northwest of Brisbane. Except for these and other mountain localities less far inland, *R. f. assimilis* is largely confined to coastal localities. There are very few offshore islands along this portion of the Australian coast, but *R. f. assimilis* is known from two of them: Cribb Island, off Brisbane, and Fraser Island, about 150 miles farther north and the largest island adjacent to the mainland distribution of this rat. *Rattus fuscipes assimilis* is the most geographically widespread of any member of the *R. fuscipes* group (fig. 2).

Mean Measurements (in Mm.): External: head and body 165; tail 158; hind foot (s.u.) 34.9; ear (from notch) 23. Skull: occipitonasal length 40.7; braincase width 16.8; bulla length 6.7; crowns m^{1-3} length 6.7. (See table 4 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 36.9 or less.

Description: This is one of the larger members of the *Rattus fuscipes* group. The hind foot is relatively smaller than it is in the other large subspecies, *R. f. coracius*. There is a subtle, but genuine, array of dorsal pelage color and texture between different populations of *R. f. assimilis*. The differences are evident on freshly prepared specimens before appreciable fading has occurred. The dorsal coat color appears to follow Gloger's Rule in being darker in more humid localities (i.e. Beech Forest, Victoria, and Woodenbong, New South Wales) and lighter in areas of only 20 to 30 inches of rainfall per annum (i.e. Dawes Range, Queensland). The pelage, which is usually very soft and long, is shorter in the specimens from Dawes Range and, in both this and the other northern locality from which we had fresh material, Woodenbong, the guard hairs are more plentiful. Although they are not truly spinous, these hairs seem stiffer than those of southern specimens.

Most *R. f. assimilis* are rusty brown dorsally, and the dorsum is darkened by guard hairs. The main body hairs are dull gray for most of their length of 16–20 mm. and are tipped with warm brown that has a sheen. The gray basal portion usually shows through to some extent, as it does in other *R. f. fuscipes*. The dorsal guard hairs are

TABLE 4

MEASUREMENTS (IN MILLIMETERS) AND WEIGHTS (IN GRAMS) OF ADULT *Rattus fuscipes assimilis*

Measurement	N	Mean±SE[a]	SD[a]	Range
Head and body length	193	164.55±0.93	12.88	111–194
Tail length	193	157.90±1.01	14.06	106–195
Hind foot (s.u.) length	193	34.89±0.15	2.07	29– 40
Ear length (from notch)	141	23.34±0.13	1.60	19– 27
Occipitonasal length of skull	250	40.73±0.12	1.95	37.0–46.2
Condylobasal length	255	38.47±0.12	1.85	33.3–43.6
Basal length	252	35.62±0.12	1.89	30.2–40.9
Zygomatic width	231	20.31±0.07	1.01	17.7–23.2
Interorbital width	298	5.51±0.01	0.16	4.6– 6.6
Interparietal length	269	4.54±0.03	0.47	3.1– 6.2
Interparietal width	266	9.93±0.05	0.80	7.8–11.9
Braincase width	264	16.77±0.04	0.59	15.2–18.5
Mastoid width	247	14.28±0.03	0.51	12.6–15.6
Nasal length	280	15.37±0.09	1.47	12.1–19.0
Nasal width	274	4.22±0.03	0.47	3.3– 5.5
Palatal length	294	21.54±0.07	1.17	18.5–24.5
Incisive foramen length	299	7.40±0.03	0.59	5.9– 9.2
Incisive foramina width	298	2.29±0.02	0.37	1.4– 3.4
Inside m^{1-1} width	294	3.40±0.03	0.54	2.2– 5.0
Outside m^{1-1} width	294	8.31±0.03	0.50	7.0– 9.8
Bulla length	271	6.71±0.03	0.50	5.5– 8.3
Crowns m^{1-3} length	296	6.68±0.02	0.39	5.4– 7.7
Alveoli m^{1-3} length	296	7.25±0.02	0.44	6.0– 8.7
Crowns m^{1-2} length	298	5.33±0.02	0.32	4.1– 6.3
M^{1-1} width × 2	295	4.91±0.02	0.33	3.9– 5.7
Body weight	49	125.19±5.09	35.65	65 – 225

[a] SE indicates standard error of the mean; SD, standard deviation from the mean.

also slate-gray basally for about 16 mm., then shiny black for about 11 mm., and tipped in rust-brown for the last 2 mm. The main body hair is shorter in the rump region, making the guard hairs more conspicuous there. The degree of rust color dorsally is greater on older adult specimens. Guard hairs may be tipped with white on the rump region, some may be white for their length, and some may be all black.

The ears are the color of the dorsal body and are sparsely covered with short reddish brown, grayish, and/or silvery white hairs that increase in density as they extend to the free edge of the pinna. Facial vibrissae may reach 70 mm. in length. The more dorsal vibrissae tend to be black, or black basally with grayish white tips, and the more ventral ones are usually grayish white for their full length. The dorsal muzzle and head is the color of the dorsal body region. The hairs are much shorter, being about 8–9 mm. between the eyes and 14–15 mm. between the pinnae. Laterally, on both head and body, the rust-brown gives way to buff-brown and blends into the grayish white to creamy white of the ventral surface. Guard hairs are sparse on the ventral surface. The ventral fur is slate-gray at the base, like the dorsal fur, for about 7 mm. and terminates in off-white for the last 3–4 mm. The inner sides of the legs are also this color, but the outer sides are rust-brown.

The feet are covered with silvery white or brownish gray hairs. The hind feet are much wider than they are in either *R. f. fuscipes* or *R. f. greyii*. The tail is covered sparsely with hairs, about 1–2 mm. long, that have a brown base and are silvery white at the tip, are all brown, or are all silver. Tail scales are 8–11 per cm. In most populations we examined, the ventral tail is perceptibly lighter than the dorsal tail, which is of similar hue to the dorsal body pelage.

The juveniles of *R. f. assimilis*, like other *R.*

fuscipes, have a much grayer dorsal body hue, with far less brown tipping to the fur. Guard hairs are inconspicuous. The dorsal body fur on young three to four weeks old is 9–11 mm. long, and the last millimeter or less may be tipped in brown. Ventrally the color is more gray-white as distinct from the buffy or creamy white of adults.

The mammary formula is $2+3=10$, or $1+3=8$.

The adult skull of *R. f. assimilis* is more elongate than in *R. f. fuscipes* or *R. f. greyii* (fig. 5). The incisive foramina are long with the lateral sides almost parallel, slightly bowed, or slightly hourglass in shape. The posterior extent of these foramina is in line with the first loph of m^1. The slight bowing of the foramina is more evident on younger adults with little tooth wear and the hourglass appearance generally develops on older specimens, especially those with well-worn molars.

The extent of the supraorbital-temporal ridging is also a function of age, being more pronounced on older adults. In young adults the ridging is distinct interorbitally and continues usually to the posterior end of the parietals. It is up to 0.1 mm. wide. On young adults it is raised 0.1–0.2 mm. from the skull surface, and on older specimens may be raised as much as 0.4 mm. The hard palate terminates about in line with m^3 or within 1 mm. behind it.

In juvenile skulls (fig. 7) the incisive foramina bow slightly on their lateral surfaces and terminate posteriorly more sharply. The supraorbital-temporal ridges are either undeveloped or just discernible. The cranium is typically inflated.

PREVIOUS DESCRIPTIVE ACCOUNTS: Descriptions of *R. f. assimilis* have been given by Gould (1858a, 1858b), Ogilby (1892), Lucas and Le Souëf (1909), Longman (1916b), Troughton (1920, 1941 and subsequent editions), Le Souef and Burrell (1926), Brazenor (1936a, 1950), Tate (1951), and Finlayson (1960). Several are but rewordings of the original description and include more than true *R. f. assimilis*. Troughton (1920), Brazenor (1936a), Tate (1951), and Finlayson (1960) are the four who have made extensive contributions to the description of this subspecies.

Brazenor (1936a) recognized pelage color differences but, contrary to our findings, did not associate them in a geographical sense, whereas Finlayson (1960) suggested that the differences might be localized to some extent.

The mammary formula of $2+3=10$ was first noted by Troughton (1937a) and was later confirmed by Tate (1951) and Taylor (1961). This formula does not, however, hold throughout the whole range of *R. f. assimilis*. It appears to occur in all southern members, but in specimens from northern New South Wales it shifts to $1+3=8$ and continues as this reduced number in the remainder of the northerly distribution of this subspecies. This shift was first brought to our notice when Calaby (1966) reported the reduced formula from *R. f. assimilis* at Woodenbong. Our subsequent trapping there confirmed his finding, and in all populations that we sampled farther north the mammary formula continued to be $1+3=8$.

Colored illustrations of *R. f. assimilis* occur in Gould (1858b, pl. 15) and Troughton (1941 and subsequent editions, pl. 19, fig. 3). Photographs of the whole animal appear in Audas (1950) and Taylor (1961), and Brazenor (1950) gave a drawing. Troughton (1920) and Brazenor (1936a) illustrated skull and dental features and Finlayson (1960) illustrated the hind skull.

REMARKS: Pectoral spotting occurs in *R. f. assimilis*, although not to the degree that it does in *R. f. coracius*. It is usually in the form of a white spot on the pectoral region, ranging from barely evident to a mark of 2 cm. or so in diameter. In this region alone the hairs forming the spot are white to the base. In any given locality only some members of a population bear this pectoral marking. We have recorded it from the following locations: Many Peaks Range and Forest Station on Fraser Island, Queensland; Woodenbong, Bombah Point, Pearl Beach, Mt. Irvine, and Wandandian, New South Wales. It is absent on all material we examined from Victoria and from New South Wales south of Jervis Bay.

The breeding biology and growth features of *R. f. assimilis* have been described in several papers (Horner and Taylor, 1958; Taylor, 1961; Horner and Taylor, 1965; Taylor and Horner, 1971, 1972, MS; Wood, 1971). This subspecies and *Rattus sordidus sordidus* are the only two native Australian *Rattus* for which there is considerable information regarding breeding biology.

Rattus fuscipes assimilis is the only subspecies of native *Rattus* in Australia in which the mammary formula shifts in relation to geographical occurrence of the rat. Although minor variations in teat number of the pectoral region occur in other subspecies, the mammary formula is a generally reliable feature in these other forms.

HABITS AND HABITAT: Brazenor (1936a) was the first to present a detailed account of the habits and habitat of *R. f. assimilis* as it occurs in Victoria. He found that this rat is most commonly trapped in thick scrub and that it makes burrows under the overhang of bushes, at the base of thick clumps of grass, and under logs. He described these burrows as sloping gently down into a chamber that houses a grass nest. The inner portion of the nest contains short, bitten ends of grass and the outer portion is interwoven with long grass stems. At Tidbinbilla we dissected a tunnel of *R. f. assimilis* that opened less than a foot below ground level within the entrance of the burrow of a wombat (*Vombatus hirsutus*). The soil was very friable and gravelly. The rat tunnel was 2½ inches in diameter and less than 2 feet long from end to end. The entrance, from the wombat burrow, led into a horizontal tunnel about 1 foot long to the base of a buried log. Here the tunnel turned upward along the side of the log to emerge on the surface of the ground 10 inches above the turning point. This second entrance was inconspicuous for it was camouflaged by extensive surface leaf litter. There was no nesting material in the tunnel. The surface opening looked unused and may have been an escape route only.

Like *R. f. fuscipes* and *R. f. greyii*, *R. f. assimilis* occurs in a variety of habitats, the main requirement being adequate vegetational cover and soil friability. In the absence of workable soil the rat can rely on refuge in hollow logs and rock crevices.

At its westernmost limit, near Terang, *R. f. assimilis* occurs in large stands of dry sclerophyll forest that are cleared or burned regularly, being found among the small patches of cover that remain relatively undisturbed. These patches contain ample ground litter from leaves and bark and a low dense canopy of vegetation composed largely of heaths and small acacias. The soil is friable.

A fairly similar, but much more extensive, eucalypt area occurs east of Terang on the Otway Peninsula, where one of the main trees, *Eucalyptus regnans*, grows to 100 feet or more. Beneath the trees in regions where light can penetrate a compact understory of shrubs and vines is usually found. The inner recesses of the forest are more open and contain numerous fallen logs in various stages of decay. *Rattus fuscipes assimilis* occurs both at the forest edge (fig. 10) where low dense vegetation is abundant and also in the inner portions of the forest among logs where it burrows in the friable soil. The southern portion of the Otway Peninsula harbors both wet sclerophyll and temperate rain forests and it is in these habitats that *R. f. assimilis* is plentiful.

Rattus fuscipes assimilis occupies the dry and wet sclerophyll forests that extend from eastern Victoria up the coastal portion of New South Wales wherever undercover is abundant. It also utilizes the alpine areas of the Australian Alps along stream courses where vegetation is sufficient to provide good cover. It has been recorded up to an altitude of 5600 feet at White's River, Mt. Kosciusko (CSIRO CM397 and CM398).

Tidbinbilla provides a good example of the wet sclerophyll forests of the Australian Capital Territory. The major tree association where we trapped is brown barrel (*Eucalyptus fastigata*) and narrow-leafed peppermint (*Eucalyptus robertsoni*). Tree ferns occur in gullies along with extensive leaf litter and rocks covered by moss. The drier exposed slopes blend into a dry sclerophyll forest, with acacias and smaller bushes forming the lower canopy. In such a varied environment, *R. f. assimilis* tends to follow the wetter portions along gullies and stream courses where the ground vegetation is especially thick.

A description of the Hawkesbury sandstone region of central coastal New South Wales, where *R. f. assimilis* occurs, has already been given by Taylor (1961). Here the rat is sharply restricted to the sclerophyll forests. An introduced rat, *Rattus rattus*, inhabits cultivated areas nearby but does not penetrate far into the forests. Hence, although the two rats are sympatric, there is little chance of social encounter between them except along a marginal buffer strip (Taylor, 1961).

Rattus fuscipes assimilis is sympatric with *R. l. lutreolus* along portions of its range to the extent that the two rats can be caught 200 to 300 feet apart in the same trapline. This close association occurs when suitable heath cover or dense forest is adjacent to swamp land. At the very edges of

FIG. 10. Habitat of *Rattus fuscipes assimilis* in a dry sclerophyll forest near Beech Forest, Victoria. Photographed March 19, 1964.

the swamps, in an area of floral transition where *R. l. lutreolus* constructs peripheral runways, *R. f. assimilis* may share these runways and come into contact with the swamp rat. The zone of overlap is narrow, however, for *R. f. assimilis* does not penetrate the swamp regions. *Rattus lutreolus lutreolus*, in turn, does not generally leave swamps, stream edges, or wet grasslands and hollows except when attracted by the habitat of forest plantations or well vegetated beach shores.

Subtropical rain forests of northern New South Wales and southern Queensland are also habitats of *R. f. assimilis*. Calaby (1966) has described the habitat in the Upper Richmond and Clarence River area (near the type locality of *R. assimilis*), where this rat occurs in riparian situations, rain forests, and heavily vegetated gullies. We found it also along roadcuts through this rain forest where roadside grass affords a narrow zone of high thick cover.

From about the Dawes Range north to Coomooboolaroo, *R. f. assimilis* occupies patchy areas of tropical rain forest, and on Fraser Island wet sclerophyll forests as well. On Dawes Range the rats occur both in and at the edge of rain forest. Vines and epiphytes hang from the trees but the forest floor lacks plant cover and is dark. The hanging vines impede human progress but would be no hazard to ground predators of rats. The rats take advantage of the ample cover of leaves and bark, rotting logs, and friable soil. However, they appear to frequent to a greater degree the forest edge where low plants abound than they do the heart of the rain forest. They do not utilize the extensive grasslands between stands of rain forest.

Except for occasional burrow entrances evidence of *R. f. assimilis* is difficult to detect. Runway systems, where visible at all, are generally indistinct except in regions of very dense ground cover. Brazenor (1934) found numerous runs in the Otway forest that he attributed to

R. f. assimilis, and Wakefield (1963a) reported trapping a pigmy possum (*Cercartetus nanus*) in a terrestrial runway used by *R. f. assimilis* in a forested region with substantial undergrowth. Only in regions where the rats occur in considerable abundance are their droppings easily found. Like other members of the *Rattus fuscipes* group, *R. f. assimilis* is an inconspicuous rodent and in surface activity appears to be largely nocturnal. After trapping for three 24-hour periods in each season of a year, Wood (1971) concluded that *R. f. assimilis* is continually active throughout the night and is inactive during daylight hours.

In most areas *R. f. assimilis* is not of economic importance, but causes damage to cultivated pine trees. In Victoria the rat invades plantations of *Pinus radiata* where it gnaws the bark of four- to six-year-old trees and eventually girdles them (McNally, 1955). The animals apparently seek the sugars and starches of cambial tissue. They also attack young trees in hoop pine (*Araucaria cunninghamii* Ait.) plantations of southern Queensland (Davis, MS). Although *R. f. assimilis* is primarily a vegetarian, little is known about the food habits of this rat in its native environment. Brazenor (1936a) discovered fibrous material, such as grass stems, in the stomach contents but he made no specific identifications.

Rattus fuscipes assimilis, like the other *R. fuscipes*, is mainly terrestrial. However, about 10 per cent of the damage it does to pines is inflicted 2 to 3 feet above ground when it climbs to lower whorls of branches (McNally, 1955).

SYMPATRY: In the southern portion of its range and northwards to the level of Imbil, *R. f. assimilis* is sympatric with *Rattus lutreolus lutreolus*. In Queensland it is also sympatric with *Rattus tunneyi culmorum* and *Rattus sordidus sordidus*.

TAXONOMIC HISTORY: Although *R. f. assimilis* has never been subject to the confusion that has plagued *R. f. fuscipes* in terms of being linked with *R. lutreolus*, it has been confused with *R. f. fuscipes*. *Rattus fuscipes fuscipes* material from Western Australia was identified erroneously as *R. f. assimilis* even at the time of the original description of *Mus assimilis* (Gould, 1858a), when Gould included specimens from the King George's Sound. In his monumental work on the mammals of Australia, Gould (1858b) repeated his original view and so did many of his successors, including Fraser (1903).

The northern geographical limit of *R. f. assimilis* as we now know it was recorded very early in the history of this subspecies by Collett (1887), who described a specimen (ZMO 98) from Coomooboolaroo. From his description, it is impossible, however, to determine exactly how he was evaluating *Mus assimilis*. His contemporaries, Ogilby (1892) and Lucas and Le Souëf (1909), and later Jones (1925), simply paraphrased Gould's original description, so it is likely that Collett, too, was adherent to the Gouldian view.

Trouessart (1897) recorded New South Wales and Queensland as the localities of *M. assimilis* and, unlike Gould and his followers, did not include southwestern Australia. It is difficult to tell whether this is a judgment or an omission, for neither did he name southwestern Australia as a locality for *M. fuscipes*.

Longman (1916a, 1916b) followed Gould in his assessment of *Epimys assimilis* and gave a brief further description of it including a count of the mammary teats. There is some question as to whether Longman had *R. f. assimilis* alone before him or perhaps also *R. rattus*. The mammary count of 12 that he recorded fits *R. rattus* but not *R. f. assimilis*. Additionally, he claimed that specimens from Brisbane have been regarded as hybrids between the black (*R. rattus*) and the brown (*R. norvegicus*) rats. It is most likely that he was dealing with a mixture of *R. f. assimilis* and *R. rattus*.

In 1920 Troughton gave a careful description of *Epimys assimilis*, and, although he included southwestern Australia in its range, he drew his description from specimens collected in southeastern Australia and had true *R. f. assimilis* and/or *R. f. greyii* before him. Troughton not only gave the first adequate account of this southeastern *R. fuscipes* that was well illustrated, but he also recorded range extensions in New South Wales. He did, however, confuse *R. f. assimilis* with its conspecific ally, *R. f. greyii*, in South Australian material, and with another conspecific ally, *R. f. coracius*, taken at Herberton, Queensland. The last was not formally described until three years later when it was made a subspecies of *R. assimilis*.

Le Souef and Burrell (1926) retained the Gouldian view on *R. assimilis* (and on *R. manicatus*) but made no mention of *R. a. coracius*. In 1934 Iredale and Troughton made some important evaluations in their check list: *R. a.*

assimilis was accorded a southern Queensland, New South Wales, and ?Victoria range; *R. a. coracius* was recognized as the subspecies from North Queensland; and the South Australian form, once called *Epimys assimilis* by Troughton (1920), was now recognized as *R. greyii*. Raven (1935) essentially followed their view of *R. a. assimilis* and *R. a. coracius* but ascribed a different distribution to *R. greyii*. Brazenor (1936a) described specimens of *R. assimilis* from Victoria and stated that it is replaced in the southwestern corner of Victoria by a race of *R. greyii*. Presumably, he did not believe that *R. assimilis* ranged into southwestern Australia and was in accord with Iredale and Troughton (1934) in this regard. Troughton (1941 and subsequent editions) followed the views expressed by Iredale and himself in 1934 and incorporated Brazenor's findings. Shortridge (1936), however, took a backward step, not only by stating that *Mus assimilis* occurs in southwestern Australia, but also by claiming that it is the type locality for this form, an error which no one before or since has made.

Tate (1936) handled *R. assimilis* in an unusual manner and used the name in a broad and poorly defined sense. Under his *Rattus rattus* division he listed nine "groups," one of which was the *Rattus assimilis* group. The only other *Rattus* from Australia that he mentioned is the *Rattus tunneyi* group, and one can only assume from his arrangement that he regarded *R. assimilis* in a very specialized sense. He stated that the *R. assimilis* group is apparently restricted to Australia and Tasmania (so he must have been including *R. lutreolus velutinus* in this group) and reported that the mammary formula is $0+2=4$, a formula that is unknown for any Australian *Rattus*. He also gave a series of skull ratios which rightfully cannot be applied to such a broad category. It appears impossible to bring this treatment of *R. assimilis* in line with prior assessments of this form.

Confusion over the geographical extent of *R. assimilis* was enhanced by the identification of a *Rattus* from Fiji as *R. assimilis*, an identification made by Tate and recorded by Mumford (1942). It was said to be an immature specimen. We suspect that it was *Rattus exulans*, a species that has successfully inhabited many islands of the South Pacific.

Ellerman (1949) was the first to recognize the natural affinity of *R. f. assimilis* to *R. fuscipes* by placing *assimilis* as a subspecies of the latter. We have supplied additional evidence, including results of cross-breeding experiments, which supports his view (Horner and Taylor, 1965).

Tate (1951) published his views on the *R. assimilis* material. Owing to his link of *R. f. fuscipes* with *R. lutreolus*, an error resulting not only from historical misapplication of these names but probably, too, from a series of mismatched skulls before him (Taylor and Horner, 1967), Tate regarded *R. assimilis* as a full species and not closely related to *R. fuscipes*. He synonymized *Mus arboricola*, which is actually *R. rattus*, under *R. a. assimilis*. The *arboricola* material, which had been taken within the city limits of Sydney, had a white throat and abdomen and a tail appreciably longer than head and body. The name and Krefft's description (*in* Gould, 1863) reflect the semiarboreal habits. None of these characters is compatible with those of *R. f. assimilis*. Tate (1951) appears to be the only one who allied *M. arboricola* to *R. f. assimilis*. Thomas (1910) claimed that *Epimys arboricola* was a synonym of *E. rattus*. Ellerman (1949) was in accord with this synonymy under *R. rattus*, and so are we.

By this time, although Ellerman and Tate differed markedly in their treatment of *R. f. assimilis*, it was generally acknowledged that the subspecies *assimilis* ranges on the mainland of eastern Australia from southern Queensland through New South Wales and into Victoria and that it is mainly coastal in distribution. Hence, it comes somewhat as a surprise to find that in 1958 Guiler identified a *Rattus* from Tasmania as, "probably of the *assimilis* group" (Guiler, 1958, p. 49). His evidence was never substantiated and we have cast doubt on his identification (Taylor and Horner, 1967), as also has Green (1967).

Tate, as well as Ellerman, believed *R. f. assimilis* to be a very close relative of *R. f. greyii*. Ellerman treated them as subspecies and Tate treated them as closely allied, but full, species. Misonne (1969) also regarded them as close allies. Finlayson (1960) did not fully sympathize with Ellerman. He considered *R. f. assimilis* and *R. f. greyii* to be more than subspecifically distinct and assumed that they shared a region of sympatry in midwestern Victoria. There is no evidence of sympatry. We focused special attention on the geographic hiatus of distribution between the Portland *R. f. greyii* and the Terang

R. f. assimilis and found no indication of rats. Furthermore, the habitat was inhospitable for any member of the *R. fuscipes* group. Troughton (1941–1967, Ninth edition) has continued to regard *R. f. assimilis* and *R. f. greyii* as separate species.

We concur with the move suggested by Ellerman (1949) to place *R. f. assimilis* as a subspecies of *R. fuscipes* (Horner and Taylor, 1965), and we regard *Mus arboricola* (BM 97.11.23.1, from Sydney) as a synonym of *R. rattus*.

Rattus fuscipes coracius (Thomas)

Rattus assimilis coracius Thomas, 1923b, p. 173.
[*Mus manicatus* Gould, 1858a, p. 242].

Holotype: Skin and complete skull, adult female, BM 22.12.18.28, collected May 5, 1922, by T. V. Sherrin, at Dinner Creek, Ravenshoe, Queensland, 2900 feet.

Distribution: *Rattus fuscipes coracius* has the most restricted geographical distribution of any member of the *R. fuscipes* group. It is known from as far south as the Paluma Range near Townsville and as far north as Mt. Finnegan near Cooktown. Its distribution is roughly coincident with the extensive continuum of rain forest (see Tate, 1952, p. 571, fig. 2) between these points (fig. 2).

Mean Measurements (in Mm.): External: head and body 164; tail 159; hind foot (s.u.) 35.6; ear (from notch) 22. Skull: occipitonasal length 41.9; braincase width 16.5; bulla length 6.3; crowns m^{1-3} length 6.4. (See table 5 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 36.9 or less.

Description: *Rattus fuscipes coracius* is one of the larger members of the *fuscipes* group, being about the same size as *R. f. assimilis*. The soft pelage is rust-brown dorsally. The dorsal body fur at the midline is about 15 mm., most of which is slate-gray basally, darker and shinier than in *R. f. assimilis*, and the distal 1–2 mm. is

TABLE 5
Measurements (in Millimeters) and Weights (in Grams) of Adult *Rattus fuscipes coracius*

Measurement	N	Mean ± SE[a]	SD[a]	Range
Head and body length	205	163.51 ± 0.94	13.48	119–204
Tail length	205	158.52 ± 0.75	10.70	128–180
Hind foot (s.u.) length	205	35.60 ± 0.11	1.54	30–38
Ear length (from notch)	142	22.21 ± 0.16	1.96	17–27
Occipitonasal length of skull	218	41.87 ± 0.13	1.87	37.0–46.9
Condylobasal length	220	39.33 ± 0.14	2.02	33.7–44.8
Basal length	216	36.29 ± 0.13	1.97	30.8–41.4
Zygomatic width	228	19.93 ± 0.06	0.98	16.8–22.2
Interorbital width	262	5.50 ± 0.02	0.32	4.8–6.7
Interparietal length	229	4.51 ± 0.03	0.42	3.3–6.2
Interparietal width	229	10.03 ± 0.04	0.64	7.9–11.7
Braincase width	231	16.50 ± 0.04	0.55	15.0–17.7
Mastoid width	214	14.35 ± 0.02	0.34	12.7–15.9
Nasal length	256	16.06 ± 0.05	0.80	11.8–18.9
Nasal width	257	4.28 ± 0.03	0.44	3.3–5.8
Palatal length	258	22.37 ± 0.07	1.08	18.3–25.4
Incisive foramen length	260	7.68 ± 0.03	0.56	5.8–9.1
Incisive foramina width	258	2.49 ± 0.02	0.33	1.8–3.4
Inside m^{1-1} width	235	3.80 ± 0.03	0.46	2.5–5.0
Outside m^{1-1} width	235	8.48 ± 0.03	0.42	6.9–9.4
Bulla length	248	6.34 ± 0.02	0.32	5.4–7.2
Crowns m^{1-3} length	250	6.43 ± 0.02	0.35	5.6–7.6
Alveoli m^{1-3} length	250	6.85 ± 0.02	0.40	5.8–8.0
Crowns m^{1-2} length	256	5.10 ± 0.02	0.30	4.0–5.9
M^{1-1} width × 2	235	4.68 ± 0.02	0.28	3.8–5.4
Body weight	64	127.97 ± 4.16	33.27	61–198

[a] SE indicates standard error of the mean; SD, standard deviation from the mean.

tipped in yellow-brown to rust. The guard hairs are not conspicuous except at the rump. They are 18–20 mm. long over most of the dorsum and up to 25 mm. at the rump. Although tipped in black or rust over most of the dorsal body surface, the guard hairs may terminate in light buff at the rump. The ears are the same color as the dorsal body pelage and sparsely covered with short, light hairs. Muzzle vibrissae measure up to 62 mm., with the more dorsal ones blackish, the more ventral ones light in color. The dorsal region of the head is the same color as the dorsal body, with hairs about 8 mm. long on the muzzle and about 10 mm. long between the ears. The rust-brown of the dorsum becomes gradually buffier laterally and blends to buffy gray or creamy white ventrally. The ventral fur is gray for the basal 6 mm. or so, and only the terminal 2 mm. are grayish to creamy white. The ventrolateral and ventral parts of the head are similarly colored. The feet are covered by dull white hairs and do not have the silvery cast that the hairs on *R. f. assimilis* feet have. The hind feet are relatively wide, as in *R. f. assimilis*. The tail has 10 scales per cm. Dorsally the tail is the same hue as the dorsal body pelage and ventrally slightly lighter. It is covered sparsely with brown hairs about 1–1.5 mm. long. The juvenile pelage lacks the warm coloration of the adult and is grayer, and the guard hairs are inconspicuous. The mammary formula is $1+3=8$.

The skull is elongate (fig. 6). The incisive foramina are either straight-sided or slightly bowed. They do not assume the hourglass shape that they do in *R. f. assimilis*. They terminate posteriorly just anterior to the level of the anterior loph of m^1. The hard palate extends farther posteriorly from the end of the molar row in *R. f. coracius* than it does in other *R. fuscipes*, in the order of 1.5 mm. behind m^3. The supraorbital portion of the ridging is less conspicuous than it is in *R. f. assimilis* but the ridging is more distinct in its temporal course and terminates in the posterior half of the parietals. The bullae are relatively smaller in *R. f. coracius* than in *R. f. assimilis*. Inflation of the cranium is distinct on juveniles, and the supraorbital and temporal ridging is poorly defined (fig. 7).

PREVIOUS DESCRIPTIVE ACCOUNTS: Morphological accounts have been given by Gould [1858a, 1858c (for *manicatus*)], Ogilby [1892 (for *manicatus*)], Thomas (1923b), Le Souef and Burrell [1926 (for *manicatus*)], Troughton (1941 and subsequent editions), and Tate (1951). All the descriptions are very brief.

Tate (1951) recorded the mammary formula as $1+3=8$. We have found only one deviation from this in adult material: one adult (AMNH 155036) has a mammary formula of $2+3=10$. It is difficult to locate the full complement on juveniles. Some skin labels of *R. f. coracius* record the formula as $1+2=6$. Harrison (1962a) found the count to vary from 6 to 8, but did not indicate whether counts were made on fresh specimens. Our records are all from fresh material.

Aspects of the reproductive biology of *R. f. coracius* have been studied by Taylor and Horner (MS).

The only illustrative material of this rat is the colored plate of *Mus manicatus* by Gould (1858c, pl. 16) and a photograph of the skull (McDougall, 1944, p. 62, pl. 7).

REMARKS: White spotting on the ventral surface of the body is common in *R. f. coracius*. Usually it is situated in the pectoral and/or abdominal regions and ranges from a small spot to one or more patches that may almost cover the ventral surface. The spot is formed by hairs that are white to the base. Thomas (1923b) commented on the occurrence of these spots in his original description of *R. a. coracius*, claiming that about half the specimens he examined had such marking. Tate (1951) also remarked on this character. On the material from which we recorded this spotting, 123 out of 316 were positive, and there were probably more. Our positive records come from the following localities: Spewah, Atherton, Lake Barrine, Mt. Bellenden Ker, Danbulla, Junction Creek, Walter Hill Range, Babinda, Etty Bay, Palmerston, Ravenshoe, Townsville, and Hinchinbrook Island. Some of the rats from Danbulla also have a small white blaze between the ears, a character that we have not seen in any other native Australian *Rattus*.

HABITS AND HABITAT: The paucity of information on the habits and habitat of *R. f. coracius* is almost unrivaled considering the number of persons who have had experience in collecting this rat. Lönnberg and Mjöberg (1916) recorded one specimen from a leaf nest under a fallen tree trunk. Brass (1953) stated that it occurs in the rain forests of the Cairns area to Mt. Finnegan in the north, that it is nocturnal, terrestrial, and common where it occurs. Harrison (1962a)

FIG. 11. Habitat of *Rattus fuscipes coracius* in a tropical rain forest on the Atherton Tableland, 8 miles southeast of Ravenshoe, Queensland. Photographed May 4, 1964.

found that it is generally restricted to the floor of the rain forest and occasionally frequents woodland. He also found its diet to consist of insects as well as plant matter (Harrison, 1962b).

We trapped *R. f. coracius* in three localities on the Atherton Tableland: Millaa Millaa, vicinity of Ravenshoe (fig. 11), and Danbulla. We also took it as far north as Mossman Gorge. All four areas are tropical rain forests, of high humidity the year round, and the vegetation is lush and dense, providing abundant ground cover. Ginger, lawyer vine, and many ferns, including tree ferns, grow profusely in gullies and other moist hollows. Cuts for power lines and roads are quickly invaded by the introduced *Lantana*, which also provides thick cover. The soil is rich and loamy and very friable. The elevations here range from 2200 feet at Millaa Millaa down to 300 feet at Mossman Gorge. In all localities the large trees of the rain forest grow to 100 feet or more in height, have small trunk diameters of about 1 foot or less, and are closely spaced. Leaf litter is very thick in these forests, although the forest floor is usually devoid of green vegetation except where breaks occur in the upper canopy and light can penetrate.

At its northernmost limit of distribution, Mt. Finnegan, *R. f. coracius* has been trapped only at 2600 feet. Brass (1953) described a change in moisture conditions above the 1500-foot level on Mt. Finnegan where the rain forest contains much more dense undergrowth than in the lower reaches. The northernmost low-altitude locality for *R. f. coracius* is Mossman Gorge where at an elevation of 300 feet the swiftly flowing Mossman River, which drains the Great Dividing Range throughout the year, provides a high-moisture environment. The floor of the rain forest here has sparse ground cover except for ample leaf litter, rotting logs, and a discontinuous cover of small ferns. Lawyer vine is plentiful and the gorge itself contains numerous large boulders. *Rattus fuscipes coracius* occurs in the heart of the rain forest only and does not invade the bladey grass of more open areas where another murid rodent, *Melomys*, occurs.

This particular rain forest is the only locality in which we took both *R. f. coracius* and *Rattus leucopus cooktownensis* in the same trapline, but it was impossible to discern any differences in microhabitat preference between them. They have been taken simultaneously in a number of other localities farther south, at both high and low elevations. The greatest elevation at which *R. f. coracius* has been taken is 4000 feet on Mt. Spurgeon, west of Mossman. The lowlands immediately north of Mossman are savanna woodlands.

One feature common to all these localities is the presence of rain forest in conjunction with dense peripheral shrub-vegetation, ground litter, decaying logs, and friable soil. This habitat situation is made possible in all lowland localities on record by the presence of a river or stream course that supports a continuum of dense rain forest from higher elevations.

The insular locality record of *R. f. coracius*, Hinchinbrook Island, is merely an exposed portion of the coastal range and is separated from the mainland by a channel only 2 to 4 miles wide.

The western limit of *R. f. coracius* is determined by the western extent of the Great Dividing Range. The western slope of the range is, for the most part, considerably drier than the eastern slope and in lower altitudes the rain forest gives way to a vast expanse of tropical woodland.

Systematic trapping for *R. f. coracius* south of the Paluma Range was unsuccessful. Between Ayr and Bowen the country is flat grazing land and unsuitable for this rat. In the rain forests near Proserpine the soil is hard and rocky with little ground cover, and the same generally holds for the rain forests of Eungella and Mt. Jukes near Mackay, and for Connor's Range between Mackay and Rockhampton. These drier rain forests south of the Paluma Range apparently cannot fulfill the habitat requirements of this rat.

Rattus fuscipes coracius is a nocturnal, terrestrial rat that is confined to rain forests where ground litter is abundant or where there is a good cover of low-growing vegetation. The rat appears to favor friable soil. In such habitat runways and burrows are almost impossible to locate.

SYMPATRY: *Rattus fuscipes coracius* is sympatric with *Rattus leucopus cooktownensis*, *Rattus sordidus sordidus*, *Rattus lutreolus lacus*, and possibly *Rattus tunneyi culmorum*. The most intimate habitat association of *R. f. coracius* is with *R. l. cooktownensis* where they share a large part of the rain forest from Mt. Finnegan to the vicinity of Ingham. Where open grassland abuts rain forest *R. s. sordidus* can be taken in the same trapline. *Rattus fuscipes coracius* has been trapped at Lake Barrine, the only known locality of *R. l. lacus*. *Rattus tunneyi culmorum* has been taken within 30 miles of *R. f. coracius* in the Ingham area, so it is possible that the two are sympatric.

TAXONOMIC HISTORY: At the same time he described *Mus assimilis*, Gould (1858a) also described the species *Mus manicatus* from a single specimen presented to him by J. B. Turner. The recorded locality of *Mus manicatus* is Port Essington, Cobourg Peninsula, Northern Territory. Between 1838 and 1849, when the settlement of Victoria in Port Essington was inhabited by English soldiers and officials, several naturalists made collections in the area, and it is the type locality of many tropical Australian animals and plants. Although Victoria Settlement was abandoned in 1849 and the Peninsula ceased to be occupied by white settlers in any number, there has in recent years been a renewed attempt to survey the fauna of this area (Johnson, 1964; CSIRO collections). In July, 1965, when we collected on the Cobourg Peninsula, including the Victoria Settlement site, we trapped in all types of vegetation communities for three weeks but found no evidence of "*manicatus*."

All published accounts of *Mus manicatus* are either a rewording of the original description or an attempt to redescribe it from the only specimen ever collected (BM 58.11.24.7). Although *M. manicatus* was originally named as a new species (Gould, 1858a), Krefft (1871) noted its resemblance to *M. assimilis* and called it an "allied species." He did not, however, propose that it should be a subspecies of the latter.

It is difficult to understand how Ogilby (1892, p. 106) came to record *M. manicatus* from, "York Peninsula; Mount Kosciusko?" The former could be either Cape York Peninsula, Queensland, or Yorke Peninsula, South Australia. Not only had *M. manicatus* never been described from any of these localities, but it was still known in the literature from only one specimen. His account is an almost verbatim repeat of that given by Gould (1858a). Ogilby's error was perpetuated by Trouessart (1897), who stated the localities as Port Essington plus those named by Ogilby.

Lucas and Le Souëf (1909) gave the locality of *M. manicatus* as South Australia. At that time the Northern Territory was part of the state of South Australia. It is unfortunate that they were not more specific in designating the locality, for as it stands it can easily be misinterpreted. Thomas (1910) regarded *Epimys manicatus* as a distinct species, as did Longman (1916a, 1916b), the latter recording it from Port Essington only.

In 1923 Thomas described *R. f. coracius* as a subspecies of *R. assimilis*. Le Souef and Burrell (1926) made no mention of it but Iredale and Troughton (1934) recognized this new subspecies. The latter authors recognized *R. manicatus* as a full species from Port Essington and so did Raven (1935).

Although Tate (1940) retained *R. manicatus* as a full species, he stated that the sole specimen, a young female, is "representative" of *R. assimilis* of eastern Australia. Troughton (1941–1967, First edition) also examined the type specimen but did not ally it with any other species and kept it a full species.

Ellerman (1949) was the first to place both *R. manicatus* and *R. a. coracius* as subspecies of *R. fuscipes*. Although Tate (1951) was unwilling to relate *R. fuscipes* to *R. assimilis* and to southern *R. assimilis* allies, he, like Ellerman, regarded *R. manicatus* as a close relative of *R. assimilis* and placed it as a subspecies of the latter along with *R. a. coracius*. Tate was the first to question the locality purported for *R. manicatus* and referred to Port Essington as its "alleged" locality. Tate stated that in the course of personal discussion Troughton, too, had questioned the locality data of *R. manicatus*, and had even suggested that *R. manicatus* may be *R. a. coracius*. Tate made a more extensive description of *R. manicatus*, including skull characters, than had hitherto been published.

Finlayson (1960) regarded *R. a. coracius* and *R. manicatus* as separate subspecies of *assimilis*. Troughton (1941–1967, Eighth and Ninth editions) continued to place *R. a. coracius* as a subspecies of *R. assimilis* but never endorsed his informal view that *R. manicatus* was *R. a. coracius*. He kept *R. manicatus* a distinct species and again (as in all earlier editions) said, "my examination of the type specimen at the British Museum did not indicate its actual identity with any other species..." (Troughton, 1941–1967, Eighth edition, p. 290).

We support Ellerman (1949) in his designation of *R. f. coracius* as a subspecies of *R. fuscipes*. The problematic "*manicatus*" also seems to fit most closely into the *R. f. coracius* subspecies. The skull of "*manicatus*" resembles that of eastern forms of *R. fuscipes*, and the relatively small and narrow bullae suggest closer affinity with *R. f. coracius* than with *R. f. assimilis*. This relationship is further supported by the presence of a white patch of ventral fur, a type of spotting found far more frequently in *R. f. coracius* than in *R. f. assimilis*. We endorse Troughton's view, "that *manicatus* bears an erroneous label and may in reality be a specimen of *coracius*" (Tate, 1951, p. 328). Because "*manicatus*" is of dubious origin and some of the more informative skull characters are damaged, and its identity with *R. f. coracius* therefore depends to some extent on probabilities, we retain *R. f. coracius* as the subspecific name for this whole group and synonymize "*manicatus*" (type, BM 58.11.24.7) in a tentative fashion only.

Rattus leucopus (Gray)

DISTRIBUTION: Eastern half of Cape York Peninsula from the northern tip south to Coen; east coastal and subcoastal portion of Cape York Peninsula from Cooktown to Tully (fig. 12). It is the most geographically restricted species of *Rattus* of the Australian mainland.

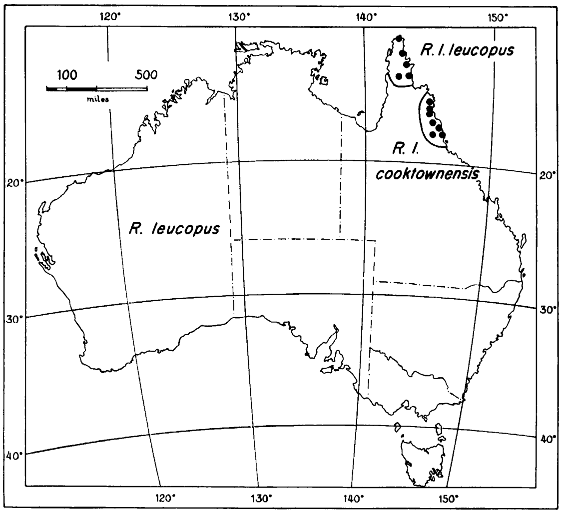
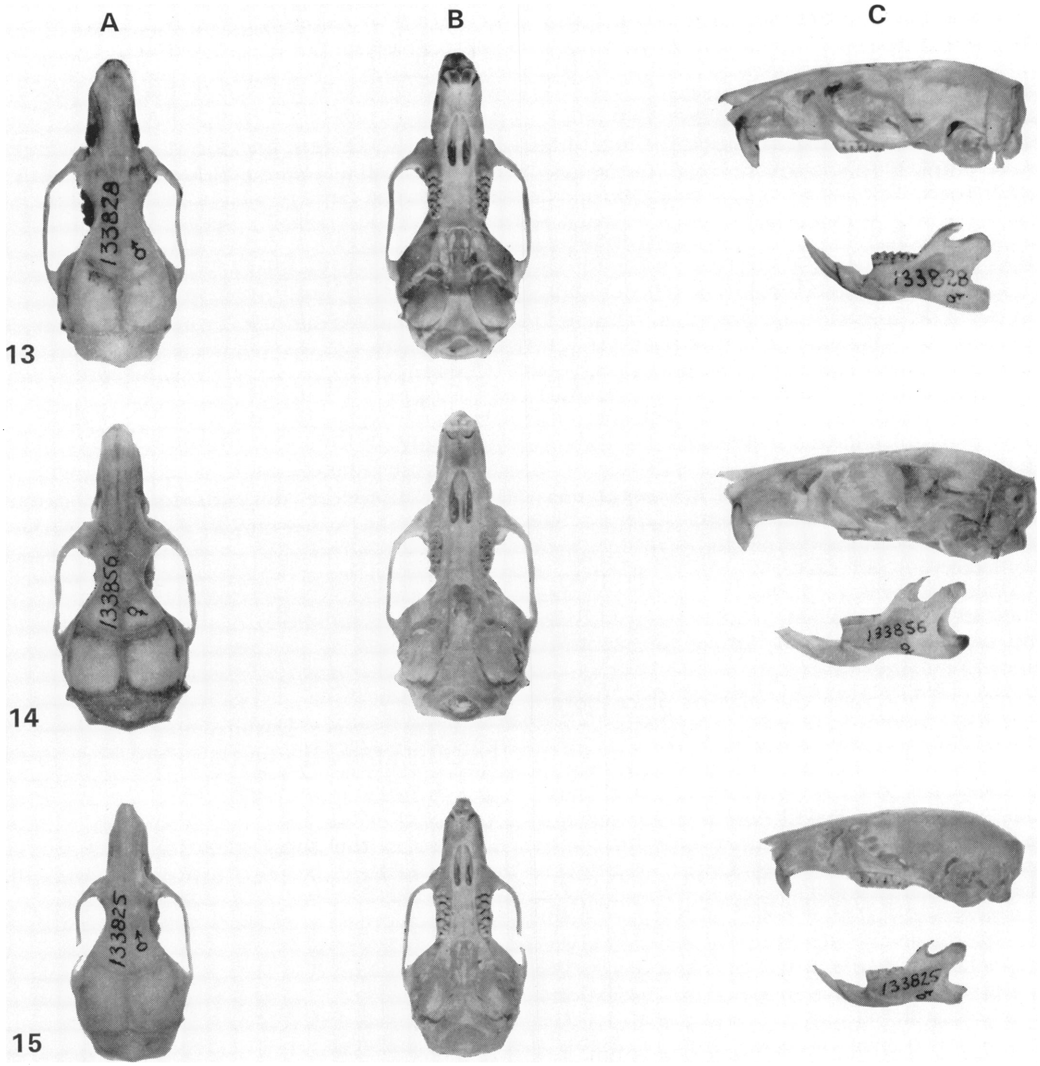


FIG. 12. Distribution map of *Rattus leucopus*. Locality records for each of the two subspecies are indicated by dots.



FIGS. 13–15. Dorsal (A), ventral (B), and lateral (C) views of skulls of *Rattus leucopus*. 13. Adult *R. l. leucopus*, MVZ 133828. Occipitonasal length 41.2 mm. 14. Adult *R. l. cooktownensis*, MVZ 133856. Occipitonasal length 41.6 mm. 15. Juvenile *R. l. leucopus*, MVZ 133825. Occipitonasal length 34.3 mm.

GENERAL DESCRIPTION: These are among the largest native *Rattus* in Australia with both the tail and the hind foot averaging longer than in any other species. The pelage is grizzled blackish brown dorsally, sometimes modified toward reddish or tawny. A greater admixture of buff or orange buff in the more lateral hairs gives the sides a correspondingly brighter appearance. The hairs may be coarsely spinous and include both flattened, channeled spines and long cylindrical guard hairs. The short ventral fur is light, white to the roots or gray with buffy tips. The feet are white or yellowish white; the hind feet are stout and long. The tail is about the length of the head and body combined, drab brownish or blackish, and may be white distally or mottled with patches of soiled white. The ears are large, dark brown, and sparsely covered with short buff to reddish brown hairs. The mammary formula is 1+2=6.

The skull is long and narrow. The rostrum is elongate, and the nasals conspicuously overhang the anterior surfaces of both the incisors and the premaxillaries. The incisive formina are strongly bowed laterally and terminate just anterior to, or in line with, the anterior face of m^1. The supraorbital-temporal ridging usually extends to the posterior aspect of the parietals. The interorbital aspect of the frontals is "waisted," or hourglass-shaped, in dorsal view. The molars are small and there is a broad intervening palatal region. The bullae average 18 per cent of the basal skull length and are about the same length as the crowns of m^{1-3}. The palate usually terminates 1 mm. or more behind the posterior end of the molar row (figs. 13–15).

Certain characters of *R. leucopus* show a north-south clinal trend. Spinousness of the pelage is most marked in the northernmost animals, less so among those near Coen, and sparse to absent in this species from Cooktown southward. Tail mottling decreases southward. Molar size shows a reduction from north to south. These trends are subtle north of Coen and in our assessment are of insufficient magnitude to warrant recognition of the race *R. l. mcilwraithi* proposed by Tate (1951).

Diagnostic Characters: The strongly bowed incisive foramina, small bullae, and large skull size are features that together separate *R. leucopus* from all other native Australian *Rattus*. The mammary formula of $1+2=6$ is also unique among Australian *Rattus*.

Taxonomic History: In 1867 Gray described a new species of rat from Cape York which he named *Acanthomys leucopus* in recognition of its spinous pelage and white feet. The light irregular rings on the dark tail, a feature that is unique to this species of *Rattus* in Australia, led Gray to call it the variegated or yellow-tailed rat.

Simultaneously Krefft (1867) also described a new species from Cape York under the name *Hapalotis personata*. Krefft's species has been largely ignored since its description. Ogilby (1892) placed it in the genus *Conilurus*, and Troughton (1923) who examined the original specimens concluded that they were examples of *R. rattus*. Mahoney (1972) has reexamined the syntypical series and shown that *H. personata* is identical with *R. leucopus*. Although the name *personata* has page priority, Mahoney has designated *leucopus* as senior synonym to preserve current usage.

Alston (1877), noting the apparent similarity of *Acanthomys leucopus* to an island form from the New Guinea region, *Mus browni* (now *Rattus exulans*), concluded that *leucopus* is a true *Mus* rather than *Acanthomys*. The name *Mus leucopus*, however, was preoccupied, he stated, by a North American form *Mus leucopus* Rafinesque, a situation requiring that the Australian *M. leucopus* be renamed.

Jentink (1879) supported Alston in considering *leucopus* a true *Mus*, and at the same time complicated the picture briefly by including in this species a form from the Celebes. On the grounds that the North American *M. leucopus* had been reassigned to the genus *Hesperomys*, he held that *Mus leucopus* was now a valid name for the Australian rat.

Alston (1879) finding that Jentink (1879) had, like himself, rejected the name *Acanthomys* for the Australian *M. leucopus*, but had then erred in not acknowledging preoccupation of the name *Mus leucopus*, proposed *Mus terrae-reginae* as a new species name for the Cape York *M. leucopus*. In the same paper Alston pointed out that the Celebes rat, regarded by Jentink as *M. leucopus*, was indeed a separate species. Jentink renamed the Celebes rat as *Mus beccarii* in 1880 and a lectotype has recently been designated (Musser, 1971).

Jentink (1887, 1888) followed Alston's new nomenclatural proposal but erred once more in synonymizing the Cape York species with one from the Aru Islands. Ogilby (1892) accepted Alston's nomenclature as well as his designation of Cape York as the only known locality for the rat. His description is but a slight rewording of Alston's extended account. Trouessart (1897) also followed Alston, as did Lucas and Le Souëf (1909), who copied Ogilby's rewording of the description. Thomas (1910), in transferring this rat from *Mus* to *Epimys*, retained Alston's new species name, as did Longman (1916a, 1916b).

In 1920 Thomas proposed that, as *terrae-reginae* was now in the genus *Rattus* rather than *Mus* and the North American form in *Peromyscus* rather than *Mus*, Gray's original name, *leucopus*, should be reinstated. At the same time Thomas (1920, 1921a) selected a lectotype for this Queensland rat. Jones (1922) reverted to the name *R. terrae-reginae* for this rat in his discussion of dental characters, and the last published acceptance of Alston's (1879) term *terrae-reginae* for this species is in the listing of Indo-Australian mammals by Raven (1935).

Le Souef and Burrell (1926) followed the proposal made by Thomas (1920) and their description of *R. leucopus* is almost identical to the redescription made by Alston (1879). Iredale and Troughton (1934), using the same nomenclature, stated incorrectly that *R. leucopus* was named by Gould rather than by Gray and then cited the proper reference. Troughton (1941 and subsequent editions) followed the name and author as presented by Iredale and Troughton (1934).

Rümmler (1935) described three new subspecies from New Guinea which he placed in *R. leucopus*, later shifting these, several New Guinea and other non-Australian forms, and the Cape York rat to the genus *Stenomys* (Rümmler, 1938). Ellerman (1941) designated as *R. leucopus* the 12 subspecies assigned by Rümmler (1938) to *Stenomys leucopus* but later (Ellerman, 1949) separated out the non-Australian forms as *R. ringens* and restricted the species *R. leucopus* to the Cape York rat.

Tate (1951) was the first to break down Australian *R. leucopus* into subspecies and this he did in large measure on the basis of the extensive collection of *R. leucopus* recently obtained by him and H. M. Van Deusen during the 1948 Archbold Cape York Expedition. At the time, it was the largest single collection of any species of Australian *Rattus*. Tate recognized three subspecies in Australia: the typical one, from the tip of Cape York south to Iron Range; *R. l. mcilwraithi*, from the McIlwraith Range; and the still more southern form, *R. l. cooktownensis*, from the vicinity of Cooktown to near Cairns. In interpreting *R. leucopus* to include additional New Guinea forms, he was more in sympathy with the judgment of Rümmler (1935, 1938) than that of Ellerman (1949). Like Iredale and Troughton (1934), Tate (1951) attributed authorship of the name *Mus leucopus* to Gould rather than to Gray, and he cited the wrong page reference as well. Troughton (1941–1967, Fifth through Ninth editions) made no reference to the three subspecies of Australian *R. leucopus* proposed by Tate (1951). The ambiguity shrouding the specific epithet *leucopus* was confused still further when Troughton (1941 and subsequent editions) misconstrued taxonomic preoccupation as applying to *terraereginae* rather than to *leucopus*.

An attempt to stabilize the nomenclature of this Cape York rat was made by Calaby, Horner, and Taylor (1966), who asked the International Commission on Zoological Nomenclature to conserve the currently used named *Rattus leucopus* in favor of what they believed was the technically valid name *R. terraereginae*, even though the latter name was not a *nomen oblitum*. No action has been taken so far on this request. Several years have elapsed since the application was made and the Commission has now repealed Article 23(b), the *nomen oblitum* rule, of the International Code of Zoological Nomenclature and replaced it by a new one [Declaration 43. Bull. Zool. Nomenclature, vol. 27, p. 135 (1970)]. In the sense of the new wording of Article 23(b), the names *personatus* and *terraereginae* have not been used for 50 years and the name *leucopus* satisfies the criteria for being considered in general current use for the past 50 years. In our view this strengthens the case for conservation of the name *leucopus*, and in the interests of stability and universality of nomenclature we continue to use the name *leucopus*, even though a ruling under the plenary powers by the Commission is needed to validate it.

We recognize two subspecies of *R. leucopus* in Australia. Their taxonomic affinities with New Guinea forms are not discussed.

Rattus leucopus leucopus (Gray)

Acanthomys leucopus Gray, 1867, p. 598.
Hapalotis personata Krefft, 1867, p. 318.
Mus leucopus Jentink, 1879, p. 8.
Mus terra-reginae Alston, 1879, p. 646.
Stenomys leucopus leucopus Rümmler, 1938, pp. 182–183.
Rattus leucopus leucopus Tate, 1951, p. 335.
Rattus leucopus mcilwraithi Tate, 1951, pp. 335–336.
Rattus personatus Mahoney, 1972, pp. 14–19.

Lectotype: Skin in alcohol and complete skull, adult female, BM 67.5.6.4, collected by R. Damon, Cape York, Queensland, and purchased from Higgins. Selected as lectotype by Thomas (1920, p. 424).

Distribution: *Rattus leucopus leucopus* occurs from the tip of Cape York south to Massy Creek and Lankelly Scrub, east of Coen, a span of about 120 miles. It has been recorded only in the eastern half of Cape York (fig. 12).

Mean Measurements (in Mm.): External: head and body 164; tail 168; hind foot (s.u.) 36.8; ear (from notch) 22. Skull: occipitonasal length 42.0; braincase width 16.5; bulla length 6.5; crowns m^{1-3} length 6.5. (See table 6 for complete list of measurements and statistical

TABLE 6

MEASUREMENTS (IN MILLIMETERS) AND WEIGHTS (IN GRAMS) OF ADULT *Rattus leucopus leucopus*

Measurement	N	Mean±SE[a]	SD[a]	Range
Head and body length	190	164.01±1.06	14.55	133–197
Tail length	190	167.52±0.90	12.36	138–202
Hind foot (s.u.) length	190	36.85±0.11	1.50	33–42
Ear length (from notch)	22	22.43±0.22	1.04	20.7–24.0
Occipitonasal length of skull	164	41.98±0.17	2.14	38.3–46.9
Condylobasal length	164	39.00±0.17	2.15	35.2–44.0
Basal length	164	35.98±0.17	2.13	32.2–41.0
Zygomatic width	151	19.79±0.09	1.06	17.9–22.0
Interorbital width	200	5.84±0.03	0.38	4.8– 6.9
Interparietal length	178	4.70±0.04	0.60	3.3– 5.9
Interparietal width	178	10.39±0.09	1.14	8.0–12.5
Braincase width	181	16.46±0.04	0.61	15.1–18.3
Mastoid width	166	14.20±0.05	0.59	12.4–16.3
Nasal length	204	15.99±0.08	1.08	13.2–18.6
Nasal width	206	4.20±0.03	0.37	3.3– 5.3
Palatal length	203	22.03±0.09	1.33	19.5–25.0
Incisive foramen length	206	6.83±0.04	0.56	5.7– 8.8
Incisive foramina width	205	2.88±0.02	0.32	2.1– 4.0
Inside m^{1-1} width	191	3.80±0.03	0.43	2.5– 5.0
Outside m^{1-1} width	191	8.41±0.03	0.39	7.0– 9.9
Bulla length	191	6.49±0.03	0.36	5.7– 7.4
Crowns m^{1-3} length	196	6.50±0.02	0.30	5.7– 7.3
Alveoli m^{1-3} length	196	6.81±0.02	0.32	6.1– 7.8
Crowns m^{1-2} length	199	5.14±0.03	0.45	4.4– 5.9
M^{1-1} width × 2	191	4.62±0.02	0.28	3.8– 5.5
Body weight	112	134.25±2.90	30.67	72–212.6

[a] SE indicates standard error of the mean; SD, standard deviation from the mean.

presentation.) Juveniles: occipitonasal length 38.0 or less.

DESCRIPTION: The tail is either equal to, or slightly longer than, the head and body length. The pelage is very coarse and hispid, more spinous than that of any other subspecies of *Rattus* on the Australian mainland. The dorsal pelage is reddish brown mixed with gray-brown. It is lighter than in any subspecies of the *R. fuscipes* or *R. lutreolus* groups, lighter also than in *R. s. sordidus* or *R. s. colletti*, and more reddish than in *R. s. villosissimus*. A very fine, dull gray underfur about 9 mm. long covers the dorsal body but does not readily show on the surface. A second type of hair, not so fine and about 17 mm. long, is basally gray for 13 mm. and reddish buff brown for the last 4 mm. The second type, along with the spines, gives the main color to the dorsum. The spines are about 20 mm. long. Their basal portion is translucent for the first 11 mm. and then blends into brown. The last 2.5 mm. may or may not be tipped with reddish buff. The spines are extremely dense, to within a distance of 0.5 mm. of one another as they emerge from the surface of the skin. The density and the stiffness of the spines diminish in the vicinity of the ears and are further reduced in the facial region. Spines are absent just posterior to the pinnae, where the soft, short fur is either gray or reddish buff. Near the base the dorsal spines are about 0.3 mm. wide in the northern *R. l. leucopus* and about 0.1 mm. wide in rats from more southern localities near Coen. The southern type of pelage is less harsh to the touch but is still very bristly. The guard hairs are gray in the basal half and brown in the terminal half. In the middorsum they are about 27 mm. long but are more conspicuous in the rump region where they stand out about 12 mm. from the rest of the pelage.

Between the ears the pelage is about 9.5 mm. and between the eyes is only about 7 mm. The dorsal facial region is like the dorsum in color. The vibrissae on the muzzle measure to 65 mm. and are mostly black or dark brown in the more dorsal positions and light to white ventrally. The ears are broad and conspicuous and a medium brown-gray, although much of the sparse hair cover is white.

The ventrolateral facial region is a light yellowish buff blending to white ventrally. The body pelage changes fairly sharply from the dorsal color to white or cream below. Two types of ventral hairs are conspicuous: fine white hairs of about 6 mm. in length and white spines about 9 mm. long. The ventral fur is not quite so harsh for, although the spines are very dense, they are narrower and hence not so stiff. In some individuals the ventral hair is tipped with yellowish buff instead of white, and in some southern rats the ventral fur is light gray instead of white at the base. This character varies within a given population.

The feet are clothed in silvery white hairs. The brown scaly tail is usually mottled with a variable amount of white and commonly terminates in white. The tail hairs, about 1.5 mm. in length, match the local coloring, and there are about eight rows of tail scales to the cm.

The juvenile pelage is darker and much softer than that of the adult and dorsally somewhat resembles the adult pelage of *R. fuscipes*. Spines are absent. The basal portion of the dorsal hairs is medium to dark gray and for the last 1 mm. they are tipped in rust. The venter is white and sharply delineated from the dorsum, as in adults. Often the basal portions of the ventral hairs are gray at the base instead of white. The cheeks are grayish. The feet are clothed in white hairs, and tail mottling is evident. The juvenile pelage is retained until the young rat reaches a total length of 270 to 300 mm.

The mammary formula is $1+2=6$.

The adult skull is elongate (fig. 13). The supraorbital-temporal ridging is not strongly developed but it is distinct from the interorbital region to the posterior end of the parietals. The ridging is about 0.2 mm. wide and is raised 0.2 mm. from the surface at the posterior part of the supraorbital area. The upper incisors are more strongly recurved than in any other native Australian *Rattus*. The bulla length is about equal to the m^{1-3} crown length.

The juvenile skull is also elongate and the "waisting" of the interorbital region is evident (fig. 15). The supraorbital-temporal ridges are discernible only in the anterior region of the parietals. The palate tends to be relatively shorter and terminates about in line with the posterior face of m^3.

PREVIOUS DESCRIPTIVE ACCOUNTS: Morphological accounts of *R. l. leucopus* have been made by Gray (1867), Krefft (1867) (as *Hapalotis personata*), Alston (1879), Ogilby (1892), Lucas and Le Souëf (1909), Le Souef and Burrell (1926), Rümmler (1938), Troughton (1941 and subsequent editions), Ellerman (1949), Tate (1951), and Mahoney (1972). As only one form of *R. leucopus* was recognized in Australia until 1951, and more importantly, as all *R. l. cooktownensis* specimens prior to that date were either in North American museums or misidentified as other species of *Rattus* in Australian museums, it is safe to assume that the above accounts all refer to *R. l. leucopus*.

The mammary formula of $1+2=6$ was recorded by Gray (1867), and we have found no exceptions.

Alston (1879) misrepresented *R. l. leucopus* in the statement that the tail is "considerably shorter" than the head and body, for it is typically either about equal to, or somewhat longer than, the head and body. The yellowish tinge on the underparts is evident on the live animal and is not necessarily due, as he suggested, to preservative. Ogilby (1892) and Lucas and Le Souëf (1909) copied the account given by Alston (1879) and made the same error regarding tail length.

Rümmler (1938), who examined the two specimens in Berlin as well as two in London, provided the first measurements of the skull and the hairs but, from the body measurements included, appears to have accepted uncritically those presented by Alston (1879) as indicating an appreciably shorter tail than head plus body. Troughton (1941–1967, First edition) gave a brief account distinguishing this form from sympatric ones; but it was Tate (1951) who described this subspecies most fully, his measurements (Tate, 1951, p. 402) of the type specimen being the first to indicate that the tail is longer, rather than shorter, than head and body combined. He remarked on the opisthodont incisors but also included this character for *R. l. cooktownensis* when he stated, "other characters as in *leucopus*" (Tate, 1951, p. 336) in describing the latter form. He did not recognize the uniqueness of this feature of *R. l. leucopus* among Australian *Rattus*.

Some aspects of the reproductive biology of this form have been described (Taylor and Horner, MS).

Misonne (1969, fig. 117) has illustrated the upper and lower molars, and Mahoney (1972) has published photographs of skulls and teeth.

REMARKS: To a certain degree, at least, spinosity is a function of age. It is acquired as the animal changes from juvenile to adult pelage and within the adult category is less pronounced in young adults than in those showing considerable tooth wear. It is unfortunate that *R. l. leucopus* has never been collected in the summer months, from November through February, for possibly the degree of spinousness may also vary seasonally. Some older adults contain red laterite soil in the channels of the spines (Tate, 1951; Brass, 1953). Our description of the adult pelage is from specimens with moderate to heavy tooth wear and we attempt to represent the fully adult stage rather than the transitional young adult phase.

Erection of a new subspecies, *R. l. mcilwraithi*, proposed by Tate (1951), is not supported in our reassessment. The overlap in cranial measurements between the more northern *R. l. leucopus* and "*mcilwraithi*" is extensive (see section on Computer Analysis), and in nonmensural characters also there is insufficient separation to warrant subspecific designation. The most distinctive feature of this more southern representation is the reduction of the density and width of the spines. This, however, appears to be a clinal feature of the entire species *R. leucopus*.

HABITS AND HABITAT: *Rattus leucopus leucopus* occupies the northern segment of Cape York wherever there is a substantial patch of rain forest. These forests generally occur in areas where the annual rainfall is 50 to 80 inches. They may be seasonally dry and harbor woody undergrowth (fig. 16). According to Tate (1952,

FIG. 16. Habitat of *Rattus leucopus leucopus* at the edge of a rain forest at Massy Creek, Queensland. Photographed July 16, 1964.

p. 571, fig. 2), there is an almost continuous stretch of rain forest from the tip of Cape York to the McIlwraith Range. This must refer to the central ridge of the Cape, for in areas accessible to us from the track, rain forest occurred in pockets and was often associated with drainage systems. The rain forests of higher-rainfall areas are generally devoid of ground vegetation, but the forest floor is covered with ample leaf litter and fallen branches. The trees reach to 50 feet or so and are entwined by large vines. Grasslands or mixed coastal woodland with a transitional zone of bushes border these rain forests. *Rattus leucopus leucopus* appears to remain confined to the forests. At Lockerbie, Tate (1951) trapped *R. l. leucopus* commonly among tumbled heaps of ochraceous ironstone and at Iron Range in flood forests by rivers or on the hillside slopes of rain forest.

Signs of rat activity are negligible in these rain forests. We were unable to locate runways or burrows. The rat appears to be strictly nocturnal.

SYMPATRY: *Rattus leucopus leucopus* is sympatric with *Rattus sordidus sordidus* and *Rattus tunneyi culmorum* in habitats where rain forest abuts a ground cover of grass. Although *Rattus exulans* has never been taken on the Australian mainland it has been recorded only about 110 miles northeast of the tip of Cape York in the Torres Strait.

TAXONOMIC HISTORY: This is discussed under *Rattus leucopus*. We regard "*mcilwraithi*" (type, AMNH 153968♂, from upper Nesbit River) as indistinct from *R. l. leucopus*.

Rattus leucopus cooktownensis Tate

Rattus leucopus cooktownensis TATE, 1951, pp. 336–337.

HOLOTYPE: Skin and complete skull, adult male, AMNH 153986, collected September 5, 1948, by G. H. H. Tate and H. M. Van Deusen, Shipton's Flat, 30 miles south of Cooktown, Cape York Peninsula, Queensland, 900 feet.

TABLE 7

MEASUREMENTS (IN MILLIMETERS) AND WEIGHTS (IN GRAMS) OF ADULT *Rattus leucopus cooktownensis*

Measurement	N	Mean±SE[a]	SD[a]	Range
Head and body length	106	159.55±0.94	9.64	140–193
Tail length	106	162.57±0.89	9.17	141–183
Hind foot (s.u.) length	106	35.65±0.14	1.39	32–39
Ear length (from notch)	11	22.43±0.24	0.81	21.5–24.2
Occipitonasal length of skull	117	41.26±0.13	1.45	38.3–44.6
Condylobasal length	117	38.36±0.14	1.49	35.3–42.2
Basal length	115	35.51±0.14	1.54	32.3–39.5
Zygomatic width	106	18.97±0.08	0.86	17.2–20.9
Interorbital width	133	5.88±0.03	0.31	5.3– 6.6
Interparietal length	120	5.13±0.04	0.45	4.0– 6.7
Interparietal width	120	10.70±0.07	0.74	8.3–12.6
Braincase width	118	16.20±0.04	0.48	15.1–17.6
Mastoid width	116	14.27±0.04	0.43	12.8–15.5
Nasal length	130	15.76±0.08	0.97	12.6–18.0
Nasal width	128	4.24±0.03	0.32	3.4– 5.4
Palatal length	134	21.49±0.08	0.94	19.6–24.3
Incisive foramen length	134	6.75±0.05	0.58	5.7– 8.8
Incisive foramina width	134	2.80±0.02	0.28	1.9– 3.7
Inside m^{1-1} width	130	3.80±0.04	0.46	2.8– 5.6
Outside m^{1-1} width	129	8.20±0.01	0.11	7.2– 9.6
Bulla length	123	6.50±0.03	0.33	5.4– 7.5
Crowns m^{1-3} length	131	6.18±0.03	0.33	5.3– 7.1
Alveoli m^{1-3} length	131	6.52±0.03	0.35	5.7– 7.3
Crowns m^{1-2} length	133	4.82±0.03	0.33	4.1– 5.8
M^{1-1} width × 2	129	4.39±0.03	0.31	3.5– 5.3
Body weight	56	115.15±3.30	24.71	78–155.9

[a] SE indicates standard error of the mean; SD, standard deviation from the mean.

Distribution: *Rattus leucopus cooktownensis* occurs at high and low altitudes from the vicinity of Cooktown south along the eastern coastal and subcoastal area, including the Atherton Tableland, to Clump Point, near Tully, a distance of about 180 miles. There are no records west of the Great Dividing Range (fig. 12).

Mean Measurements (in Mm.): External: head and body 160; tail 163; hind foot (s.u.) 35.6; ear (from notch) 22.4. Skull: occipitonasal length 41.3; braincase width 16.2; bulla length 6.5; crowns m^{1-3} length 6.2. (See table 7 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 38.0 or less.

Description: The tail is usually about equal in length to that of the head and body. In some rats the tail may be slightly longer, but this is less common in *R. l. cooktownensis* than in *R. l. leucopus*. The pelage of *R. l. cooktownensis* is far less coarse than that of *R. l. leucopus* and in some adults is totally devoid of spines. If spines are present they are usually less than 0.1 mm. wide and less densely distributed than in *R. l. leucopus*. They are translucent basally and are tipped with brown. The over-all color of the dorsal pelage is darker than in *R. l. leucopus* and has a less rusty hue. The fur is medium to dark gray and is tipped with warm brown. The guard hairs are generally more conspicuous in *R. l. cooktownensis*, probably because of the reduction in spines. The guard hairs are generally tipped in black or brown or may be all dark and lack a gray basal portion. The ventral pelage is darker than in *R. l. leucopus* and not so sharply demarcated from the dorsal pelage. The hairs of the venter have a gray base and are tipped with buffy white. The mammary formula is $1+2=6$.

The ears are the same color as the dorsal pelage and the white feet are clothed in silvery or buffy hairs. The mottling of the tail is more extensive in the more northerly animals than in those farther south where, in many cases, it may even be absent.

The juvenile pelage is very similar to that described for *R. l. leucopus* except that the transition from dorsal to ventral pelage is more gradual.

The most distinctive features of the adult skull, in comparison with *R. l. leucopus*, are that the molar row at the crown level is generally shorter than the bulla and the upper incisors are less opisthodont. In other cranial features they are very similar (fig. 14).

We found it virtually impossible to distinguish the juvenile skull from that of *R. l. leucopus* (fig. 15).

Previous Descriptive Accounts: There is no evidence that any of the descriptions applied to *R. l. leucopus* include the form *R. l. cooktownensis* (see this section under *R. l. leucopus*). The only account of *R. l. cooktownensis* is that given by Tate (1951) in the course of nominating it as a new subspecies. He stated that the tail scales are 11 per cm. Although it is generally true that *R. l. cooktownensis* has finer scalation on the tail than does *R. l. leucopus*, the scale rows are somewhat variable in both subspecies. His account is very brief and he makes no attempt to separate the two subspecies on the basis of skull differences.

We found only one exception to the mammary formula of $1+2=6$ described by Tate (1951). One specimen (MVZ 133859) has a formula of $1+3=8$.

Aspects of its reproductive biology are discussed by Taylor and Horner (ms).

Remarks: *Rattus leucopus cooktownensis* and *Rattus fuscipes coracius* are sibling species and overlap in distribution and in general habitat. Their appearance is so similar that the two are often confused. They tend toward parallel development in features such as general pelage coloration and texture. Even in certain skull features the two are remarkably close. In *R. l. cooktownensis* the interorbital region is broader, however, and its "waisting" is distinctive to the trained eye; the incisive foramina are shorter and more bowed, and the rami of the lower jaw are also more delicate. However, these are all subtle differences and the strong similarities tempt contemplation of hybridization. In our opinion, the two subspecies stand sufficiently well apart morphologically to make this unlikely; nonetheless, the possibility should be tested by attempts at crossbreeding.

Although Tate (1951) stated that *R. l. cooktownensis* extends southward to just north of Cairns in the northern part of the Atherton Tableland, the rat actually ranges considerably farther south than he realized. In fact, a member of his own expedition collected two specimens at Junction Creek (AMNH 153732 and AMNH 153733) but Tate misidentified them as *R. f.*

coracius. Since then several specimens have been taken in the southern portion of the Atherton Tableland (AM M8141, M8142, M8162, M8271, and M8289); and, as early as 1921, 15 specimens (in the American Museum of Natural History) were taken at Babinda Creek. At some unrecorded time two (AM M8334 and NMV C2633) were trapped at Clump Point, the southernmost locality. Most of these specimens have been unidentified until now, and a few were labeled *R. f. coracius*.

HABITS AND HABITAT: *Rattus leucopus cooktownensis* is a rain-forest rat and throughout most of its range shares this habitat with *R. f. coracius*. The rain forest it occupies generally receives 80 or more inches of rain per year and contains numerous vines and a dense upper canopy (fig. 17). Whereas *R. f. coracius* is confined to very humid rain forests, *R. l. cooktownensis* appears to have more tolerance for the drier rain forests as well. This is particularly evident at the northern and southern extremities of the ranges of these two rats.

In the north on Mt. Finnegan, near Cooktown, *R. f. coracius* has been trapped only at 2600 feet where, according to Brass (1953), a shift to higher moisture conditions has occurred and the rain forest contains denser undergrowth. On the other hand, *R. l. cooktownensis* occurs not only at the same altitude on Mt. Finnegan but also on the low terrain of that area, such as Shipton's Flat at 900 feet above sea level, where the rain forest is drier and the undergrowth sparser. Our own trapping at Shipton's Flat suggests that the rat is confined to the rain forest and does not utilize the more luxuriant fringe. In this particular rain forest the ground is devoid of vegetation although leaf litter and fallen logs are abundant. The vine-laden trees are closely spaced and the soil is

FIG. 17. Habitat of *Rattus leucopus cooktownensis* in a rain forest at Shipton's Flat, Queensland. Photographed July 13, 1964.

friable. Brass (1953) has given a floral description of this area.

At the southern extremity of its distribution, *R. f. coracius* is known again only at high elevations, between 2000 and 2900 feet, on Mt. Spec, in the Paluma Range. [Although Tate (1951, p. 328) gave the elevation on his specimens from this collecting locality as 1200 feet, this seems to be an erroneous transcription of his original data.] There are no records of its occurrence in the lowlands south of the Atherton Tableland drainage systems. On the other hand, the southernmost extent of *R. l. cooktownensis* is at a lowland coast locality, Clump Point. Apparently, it has not spread farther south into the rain forests of Proserpine and the Mackay area, which are seemingly suitable habitats. Our limited trapping results suggest that *R. l. cooktownensis* is ecologically excluded from the most humid portions of the rain forest on the Atherton Tableland where *R. f. coracius* is well established.

We found no evidence of burrows or runways associated with this nocturnal rat.

SYMPATRY: *Rattus leucopus cooktownensis* is sympatric with *Rattus fuscipes coracius*, *Rattus sordidus sordidus*, *Rattus lutreolus lacus*, and *Rattus tunneyi culmorum*. It is most intimately and extensively associated with *R. f. coracius*. It meets *R. l. lacus* at the lake edge of rain forest, and *R. s. sordidus* and *R. t. culmorum* are associates where rain forest borders onto grassland.

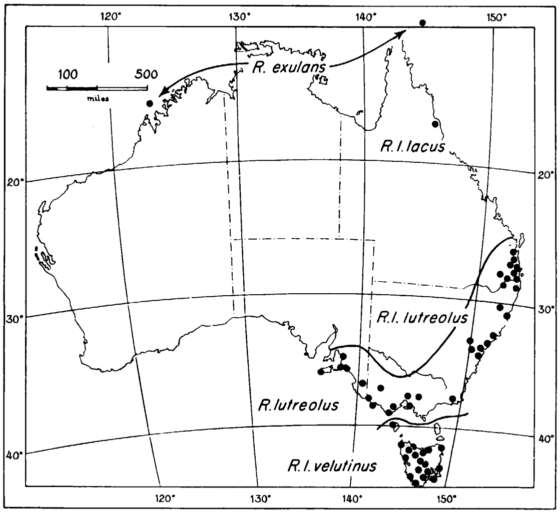


FIG. 18. Distribution map of *Rattus exulans* subspecies and of *Rattus lutreolus*. Locality records for *R. exulans* subspecies and for the three subspecies of *R. lutreolus* are indicated by dots.

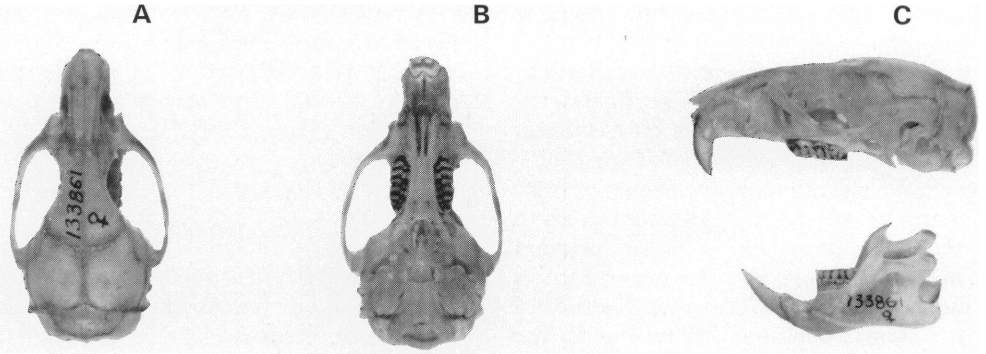
TAXONOMIC HISTORY: The only previous account of *R. l. cooktownensis* is the original description (Tate, 1951).

Rattus lutreolus (Gray)

DISTRIBUTION: Tasmania; coastal and subcoastal southeastern Australia from the vicinity of Adelaide eastward and northward through Victoria, New South Wales, and southeastern Queensland to Imbil; Lake Barrine, Atherton Tableland, Queensland (fig. 18).

GENERAL DESCRIPTION: This rat is robust in body form, and both the tail and hind feet are short. The pelage is predominantly dark grayish, reddish brown, or blackish above and less dark below, the hairs having gray translucent bases. The dorsal hairs may be tipped or terminally banded with bronze, yellow, or rust. The fur is soft and loose and generally longer in the more southern and in the higher, cooler parts of the range. The ears are short, finely haired, and largely concealed by surrounding body hairs. The hind feet are very dark, with the length averaging less than 20 per cent of the combined head and body length, and the forefeet are dark gray-brown. The mammary formula is either $2+2=8$ or $2+3=10$. The tail is about three-quarters the length of the head and body and uniformly dark brown or blackish.

The skull is slightly convex above and sturdy with heavy incisors and molars. The rostrum is stout, the base being embraced closely on either side by the broad zygomatic plate of the maxillary bone. The nasals terminate almost directly above the anterior faces of the upper incisors. The supraorbital-temporal ridges are distinct and wider than in *R. fuscipes*, and they either terminate about midway along the length of each parietal or continue the full length. The narrow, elongate incisive foramina are slitlike posteriorly and end just anterior to, or in line with, the first loph of m^1. The upper molar rows are relatively long as compared with the basal length of skull, the molars are broad, and the intermolar width is correspondingly narrow. The palate terminates in line with the posterior limit of the molar rows. The bullae average 18 to 20 per cent of the basal length and are rarely as long as the alveoli of m^{1-3} (figs. 19–23).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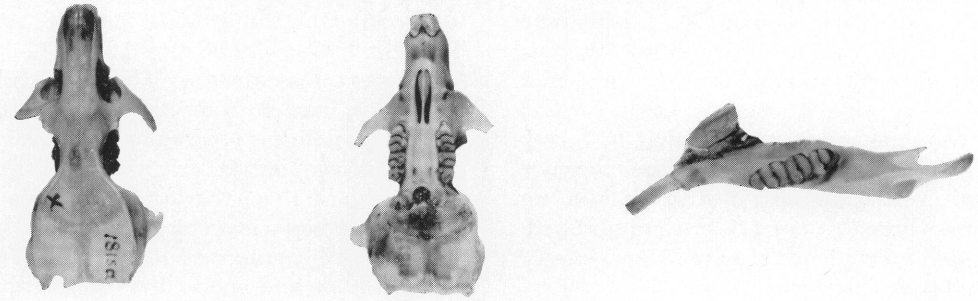
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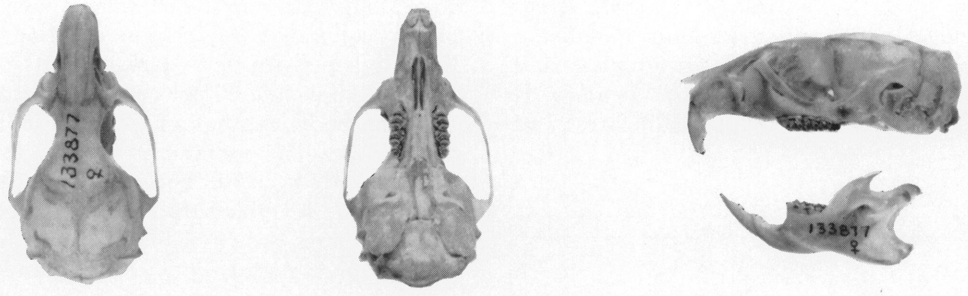
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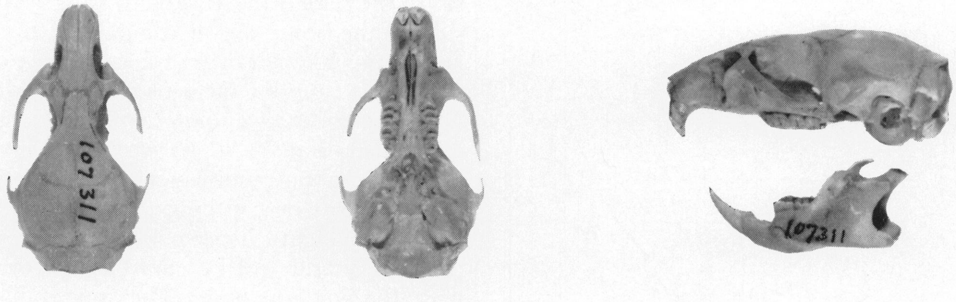
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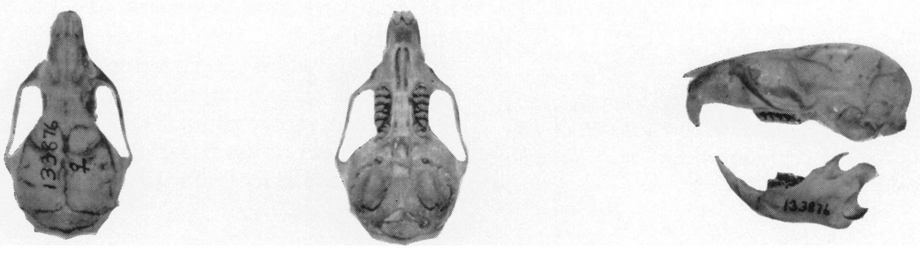
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DIAGNOSTIC CHARACTERS: The tail is shorter and the hind feet are darker than in any other species of Australian *Rattus*. *Rattus lutreolus* also has the narrowest incisive foramina and the broadest molars and incisors. The palate reaches its greatest length in this form when compared with the occipitonasal length, and m^3 contributes relatively less to the length of the molar row than in other species.

TAXONOMIC HISTORY: In 1841 Gray described as *Mus lutreola* a rat that had been termed the "water-rat" by the early colonists of South Australia. He had before him six specimens which are regarded as the syntypes of his original description. They are from varied localities ranging from South Australia to northern New South Wales and including Tasmania as well. All but one of the syntypes are still present in the British Museum (Natural History). The missing one is 163a (BM 41.1256), and it seems likely that this is now present in the American Museum of Natural History (AMNH 668). According to J. E. Hill (personal commun.) Gray probably gave this specimen to Peters at the Zoologisches Museum in Berlin in 1858, the year that exchange specimens from Berlin were registered in the British Museum (Natural History), and from there it is likely that it came into the collection of Maximilian. The specimen at the American Museum of Natural History is registered as having come from the Maximilian Collection. If the above is so, "specimen *a*." (as it was then termed) came from the River Torrens, South Australia.

Gray (1843) included *M. lutreola* under *M. fuscipes*, which had been described by Waterhouse in 1839, and this represents the first misapplication of *M. fuscipes*, one that resulted in a chaotic mix-up with *M. lutreola*. Gray (1843) listed the specimens of "*fuscipes*" then present in the collection of the British Museum (Natural History), identifying them by letters from *a.* to *f.* None of these is true *R. fuscipes*; they are all *R. lutreolus*. These syntypes are undoubtedly those identified by the following registration numbers: *a.*=163a (BM 41.1256 or AMNH 668), *b.*=163b (BM 41.1257), *c.*=163c (BM 41.1255), *d.*=163d (BM 41.1258), *e.*=163e (BM 41.1254), and *f.*=163f (BM 41.1259). The last one is subject to question because according to Gray (1843) it comes from Van Diemen's Land (Tasmania) but according to the museum label it was taken at the Macdonald River, New South Wales. The latter locality is the more likely as its mammary formula is $2+3=10$, the formula that is typical for *R. lutreolus* from the Australian mainland and too high for the Tasmanian *R. lutreolus*. In either case, however, the specimen is marked as having come from the Gould Collection.

The second member of the *R. lutreolus* group to be named was *Mus vellerosus*, a rat known originally from the plains between the Glenelg and Murray rivers in southern Australia. Gray (1847) described this as a new species on the basis of specimens sent to him by Captain Grey. Two specimens exist today [BM 47.3.1.1 (skin only) and BM 47.3.1.2].

By describing *M. lutreola* under the name *M. fuscipes*, Gould (1851) in effect synonymized the two species. His description of *M. fuscipes* is actually of *M. lutreola*. He gave the distribution of *M. fuscipes* as occurring throughout the entire portion of southern Australia. Through the error made by Gould, *Mus fuscipes* came to be known as a water-rat, and subsequent statements based on Gould's description continued to refer to the "water-loving" nature of *M. fuscipes*.

Krefft (1868) in his annotated listing of the fauna of Tasmania referred to a new species of land-rat, taken by George Masters on the banks of the Ouse River, and called it *Mus tasmaniensis*. His description, unfortunately, is inadequate, and it is possible that he was examining either *R. lutreolus* or a similar-looking rodent, *Mastacomys fuscus*. His statement that *Mus tasmaniensis* was not known from Victoria or New South Wales suggests that it was more likely *Mastacomys*, which had not yet been recorded from southeastern Australia as part of the living fauna (Calaby and Wimbush, 1964). We believe, however, that Krefft's *Mus tasmaniensis*

FIGS. 19–23. Dorsal (A), ventral (B), and lateral (C) views of skulls of *Rattus lutreolus*. 19. Adult *R. l. lutreolus*, MVZ 133861. Occipitonasal length 38.7 mm. 20. Skull (life size) and left ramus of lower jaw (C) (× 1½) of "*R. vellerosus*," BM 47.3.1.2. 21. Adult *R. l. velutinus*, MVZ 133877. Occipitonasal length 36.8 mm. 22. Adult *R. l. lacus*, AMNH 107311. Occipitonasal length 35.3 mm. 23. Juvenile *R. l. lutreolus*, MVZ 133876. Occipitonasal length 30.9 mm.

may be AM 22, which is from the Ouse River and which appears from the museum register to have been collected in 1866 by Masters, who was then Assistant Curator and Collector for the Australian Museum. It is the only specimen registered from the Ouse River in the name of Masters (Basil Marlow, personal commun.). The specimen, a young adult female, has a good skull and is clearly *R. lutreolus velutinus*. Its mammary formula is $2+2=8$.

Allport (1868) suspected that Krefft's *M. tasmaniensis* was identical with *M. lutreolus* (under the misnomer *M. fuscipes*). Krefft (1871) made no mention of *M. tasmaniensis* and seems simply to have followed Gould in synonymizing *M. lutreola* with the "water-loving" *M. fuscipes*.

In 1882 Thomas described a species of rat from Tasmania that he called *Mus velutinus* and included the skin and skull measurements from the three specimens he had before him. The lectotype is present in the British Museum (Natural History) (BM 77.7.3.1) and from the measurements it could be specimen *a* recorded by Thomas. In the same paper Thomas commented on the importance of cranial characters in distinguishing *Mus velutinus* and two other Tasmanian rats, *Mus fuscipes* and *Mus lineolatus*. The *M. fuscipes* that Thomas was examining was probably one of the five syntypes of *M. lutreola* and the *M. lineolatus*, a *Pseudomys*. It is somewhat surprising that Thomas did not regard the relationship of *M. velutinus* with "*fuscipes*" as being closer, for *M. velutinus* was later allied to *M. lutreola* as a subspecies. Thomas (1882) referred also to Krefft's inadequately documented *Mus tasmaniensis*, suggesting that it was undoubtedly one of the following: *Mastacomys fuscus*, *Mus velutinus*, *Mus fuscipes*, or *Mus lineolatus*.

At this point in history two of the three major forms of *Rattus lutreolus* had been described, the nominate form, *R. l. lutreolus*, of the southeastern

TABLE 8

MEASUREMENTS (IN MILLIMETERS) AND WEIGHTS (IN GRAMS) OF ADULT *Rattus lutreolus lutreolus*

Measurement	N	Mean ± SE[a]	SD[a]	Range
Head and body length	43	164.40 ± 4.22	15.21	134–197
Tail length	43	113.09 ± 3.38	12.18	82–147
Hind foot (s.u.) length	43	31.70 ± 0.53	1.92	29–37
Ear length (from notch)	41	19.16 ± 0.24	1.55	12–21
Occipitonasal length of skull	85	38.34 ± 0.17	1.57	35.2–43.3
Condylobasal length	87	37.33 ± 0.17	1.60	34.1–42.1
Basal length	87	34.64 ± 0.17	1.62	31.1–39.5
Zygomatic width	79	20.95 ± 0.10	0.86	19.0–22.7
Interorbital width	97	5.08 ± 0.03	0.28	4.3–5.9
Interparietal length	89	3.94 ± 0.04	0.40	2.9–4.9
Interparietal width	89	9.62 ± 0.07	0.67	7.5–10.9
Braincase width	86	16.34 ± 0.06	0.58	15.3–18.0
Mastoid width	82	13.90 ± 0.06	0.52	12.8–15.0
Nasal length	91	13.65 ± 0.09	0.90	11.9–16.5
Nasal width	92	4.07 ± 0.04	0.37	3.3–5.2
Palatal length	94	20.95 ± 0.10	1.01	18.7–24.0
Incisive foramen length	96	6.72 ± 0.05	0.52	5.5–7.9
Incisive foramina width	96	1.75 ± 0.02	0.23	1.2–2.3
Inside m^{1-1} width	95	2.74 ± 0.04	0.41	1.8–3.5
Outside m^{1-1} width	95	8.29 ± 0.05	0.48	7.0–9.2
Bulla length	87	6.53 ± 0.04	0.35	5.7–7.5
Crowns m^{1-3} length	98	7.11 ± 0.04	0.42	6.0–8.2
Alveoli m^{1-3} length	98	7.73 ± 0.04	0.43	6.8–9.0
Crowns m^{1-2} length	98	5.69 ± 0.03	0.33	4.9–6.4
M^{1-1} width × 2	95	5.55 ± 0.04	0.35	4.6–6.7
Body weight	14	122.20 ± 4.30	16.08	91.7–155.8

[a] SE indicates standard error of the mean; SD, standard deviation from the mean.

mainland, and *R. l. velutinus*, of Tasmania. The third, *R. l. lacus*, was not described until 1951 when Tate erected it as a full species. We regard all three forms as subspecies of *R. lutreolus*.

Rattus lutreolus lutreolus (Gray)

Mus lutreola Gray, 1841, p. 409.
Mus vellerosus Gray, 1847, pp. 5–6.
Rattus lutreolus cambricus Troughton, 1937b, p. 283.
Rattus lutreolus imbil Troughton, 1937b, p. 283.

Lectotype: Skin and incomplete skull consisting of the anterior half only, adult male, BM 41.1258, from the Gould Collection, taken September 1839, at Mosquito Island, Hunter River, New South Wales, and selected as the lectotype by Thomas (1921a, p. 432).

Distribution: *Rattus lutreolus lutreolus* is coastal and subcoastal in distribution, from the Gympie area of southern Queensland through New South Wales and Victoria and into South Australia as far west as the Fleurieu Peninsula on the mainland. It occurs even farther west in its insular distribution on Kangaroo Island. It has not been recorded west of the Great Dividing Range except in the Darling Downs, and its presence at higher altitudes is known only from the vicinity of Ebor (5200 feet), the Blue Mountains (3000 feet), and the Grampians Mountains (2000 feet) (fig. 18).

Mean Measurements (in Mm.): External: head and body 164; tail 113; hind foot (s.u.) 31.7; ear (from notch) 19. Skull: occipitonasal length 38.3; braincase width 16.3; bulla length 6.5; crowns m^{1-3} length 7.1. (See table 8 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 35.0 or less.

Description: This is the largest of the three subspecies of *R. lutreolus*. The pelage is soft. The dorsum is dark brown with a tinge of rust to yellowish. The hairs of the middorsum and rump are up to 16 mm. long, with the dark gray basal portion blending to blackish immediately preceding a reddish buff to yellowish tip of 2 mm. The middorsal guard hairs are up to 20 mm. long, gray at the base, and black for the last 6 mm. The rump guard hairs are up to 42 mm. long, blackish, and a few have light tips. These guard hairs are particularly conspicuous. The lateral hairs are more slatey gray basally. The ventral body is gray with a cast of rust to yellow. Midventral hairs measure to 10 mm. and are slatey gray tipped with lighter grayish to buff or rust. The rust cast to the venter is more pronounced in *R. l. lutreolus* than in the other two subspecies. Facial coloring is similar to that of the dorsum, with the fur length to 9 mm. between the ears and to 6 mm. between the eyes. Muzzle vibrissae measure to 37 mm. long and are dark in more dorsal positions, blending to light in more ventral areas. The ears are covered with short reddish buff hairs. The hairs and skin of the hind feet are an over-all dusky brown. The tail is uniformly very dark, with the scales measuring 10 per cm., and clothed with dark hairs about 1–1.5 mm. in length.

The juvenile pelage is similar to that of the adult but is much shorter and lacks guard hairs. The tipping of the dorsal hair is reddish and lacks the yellowish hue. Adult pelage is acquired when the animal reaches about 220 mm. in total length.

The mammary formula is $2+3=10$.

The skull is compact and stocky (fig. 19). The attributes of a stout rostrum, broad braincase, and zygomatic spread together with broad molars give it this appearance. The molars are appreciably wider in *R. l. lutreolus* than in the other two subspecies, and the posterior cusp, or teloloph (Misonne, 1969, p. 37), is lacking on m_1 and m_2 (fig. 24). The bullae are consistently shorter than alveoli m^{1-3}. The supraorbital-temporal ridges are conspicuous and usually extend posteriorly as far as the midparietal region or, in some, continue the full length of the parietal. In the posterior supraorbital region they are about 0.4 mm. wide and raised 0.3 mm. from the skull surface.

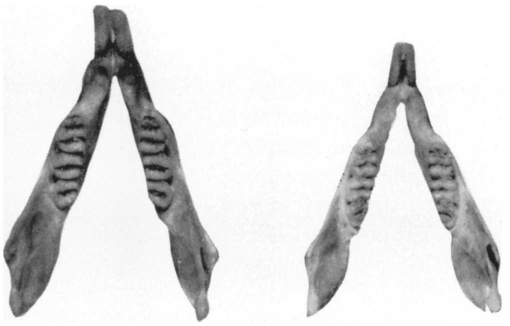


Fig. 24. Dorsal view of lower jaws of *Rattus lutreolus lutreolus* MVZ 133874 (left) and *Rattus sordidus villosissimus* MVZ 133930 (right). × 1⅜.

The juvenile skull is similar to the adult except for the more expanded cranium and the weak supraorbital-temporal ridging. The slit-like termination of the incisive foramina is not as pronounced (fig. 23).

Previous Descriptive Accounts: Various aspects of the morphology of *R. l. lutreolus* have been treated by Gray [1841, 1847 (*M. vellerosus*)], Gould [1859 (*M. vellerosus*)], Ogilby [1892 (*M. vellerosus*)], Waite (1900) under the misnomer *M. fuscipes*, Jones (1925), Le Souef and Burrell (1926), Finlayson (1935), Brazenor (1936a, 1950), Troughton (1937b, 1941 and subsequent editions), Ellerman (1949), and Tate (1951). Of all these, the description by Waite (1900) is the most extensive.

Finlayson (1935) and Troughton (1937b) made particular note of coat color variability. Finlayson (1935, pp. 224–225) described two types of dorsal coloration: a "rufous brown of varying richness" and a predominantly blackish coloration that is more grizzled. He correlated these body colorations with differences in altitude.

The suggestion by Finlayson (1935) that *R. l. lutreolus* reaches a larger size in New South Wales than it does farther south is not fully supported by our computations. Measurements for 31 adult New South Wales specimens average 165.3 mm. ±2.9 for head and body length and 32.5 mm. ±0.4 for length of hind foot (s.u.). Comparable measurements for nine animals from Victoria are 169.9 mm. ±3.1 and 31.1 mm. ±0.4. For neither measurement is the difference in means statistically significant. The external dimensions presented by Brazenor (1936a, p. 70) for specimens from Victoria support Finlayson's suggestion, however. We suspect, although we cannot be certain, that both authors have included juveniles in making their assessments. Our own state-by-state averages, based on adults alone, reveal no significant differences (5 per cent confidence level) in either external or cranial measurements.

The beaded appearance of the supraorbital-temporal ridges was noted originally by Waite (1900). Although it is a variable feature, even in specimens with well-worn teeth, it is usually present in adult skulls.

The mammary formula of 2+3=10 was provided by Waite (1900), and we have never found an exception.

Taylor and Horner (ms) have discussed some aspects of the reproductive biology of this subspecies.

Colored figures of this rat have been presented by Gould [1851, pl. 11 (under the name *Mus fuscipes*); 1859, pl. 12 (under the name *vellerosus*)], and Troughton (1941 and subsequent editions, pl. 19, fig. 5); and a drawing of the whole animal is given by Brazenor (1950). The following cranial figures have been published: dorsal and ventral views of the skull, lateral view of the skull and lower jaw, occlusal view of the upper molar row (Waite, 1900); occlusal view of the upper and lower molar rows, the former after Waite, and both under the name *Epimys fuscipes* (Troughton, 1920); dorsal, ventral, and lateral views of the skull, plantar surface of the hind foot, occlusal view of the upper molar row (Brazenor, 1936a); ventral view of the anterior region of the skull (Brazenor, 1950, fig. 7B); and occlusal view of the upper and lower molar rows (Misonne, 1969, fig. 129).

Remarks: Although there is characteristically some black in the dorsal pelage, either in the guard hairs or in the tipping or banding of the fur hairs, even this feature is not universal. In BM 72.11.8.5, a young adult male from Port Stephens, New South Wales, the dorsal pelage is grizzled in tones of deep rich brown, showing no black hairs; the ventral coloration is cinnamon brown; and the fur hairs have gray bases. Again, although the dorsal coloration commonly shows various tones of yellowish or reddish, we have noted one specimen (BM 45.11.3.14), an adult, listed simply as from "South Australia," in which the hairs are tipped with silvery white.

White marking occurs in three specimens trapped by us at North Avoca Beach, New South Wales. Two have white sternal streaks and the third has small patches of white hairs in the shoulder and rump regions.

The proposals of two subspecies, *Rattus lutreolus cambricus* and *Rattus lutreolus imbil*, by Troughton (1937b) have not been perpetuated, even by Troughton (1941–1967, Eighth and Ninth editions). He withdrew *R. l. cambricus* when he found the type locality of *R. l. lutreolus* to be very close to that of *R. l. cambricus* (Troughton, 1941–1967, Eighth and Ninth editions) and withdrew *R. l. imbil* on the basis that it was perhaps the "lost" *sordidus*. We fail to recognize *R. l. imbil* on the grounds that it is inseparable morphologically from *R. l. lutreolus*. The features cited as distinct by Troughton (1937b) do not hold when the two adult topotypes available are compared with other *R. l. lutreolus.* Troughton (1937b) stated that the cranium of *R. l. imbil* is relatively broader [it is broader in *R. l. lutreolus* (42.6 per cent of occipitonasal length) than in "*imbil*" (41.6 per cent)], the anterior nasal width is narrower [it is narrower in *R. l. lutreolus* (4.1 mm.) than in "*imbil*" (4.7 mm.)], the incisive foramina are relatively shorter [they are shorter in *R. l. lutreolus* (17.5 per cent of skull length) than in "*imbil*" (18.6 per cent)] and narrower (4.7 per cent of skull length in both), the bullae are shorter [shorter in *R. l. lutreolus* (6.5 mm.) than in "*imbil*" (6.6 mm.)], and the upper molar row is wider (2.9 mm. in "*imbil*" and 2.8 mm. in *R. l. lutreolus*). The last skull character given by Troughton (1937b) is the only one to hold up to this comparison and does so by a mere 0.1 mm.

Attempts to determine the relationship of *R. vellerosus* to other species of *Rattus* have usually led to the conclusion that it is close to *R. lutreolus* (Gould, 1859; Troughton, 1941 and subsequent editions; Tate, 1951), although the suggestion has also been made that it might be a hybrid (Troughton, 1941 and subsequent editions). Two skins and the anterior portion of one skull, including both rami of the lower jaw, exist today (BM 47.3.1.1 and BM 47.3.1.2) (fig. 20). The skins bear very long hair, longer than is generally recorded for *R. l. lutreolus*, and the guard hairs measure to about 60 mm. in length. The pelage has been subjected to wet preservation and the specimen has been mounted in the past and has gathered dust. The hairs are now very faded, being darker in the basal half and buff distally. The pelage is very thick and somewhat coarse and, although there is no evidence of spines, is very different from the soft pliable pelage of either a fresh or an old clean skin of *R. l. lutreolus*, in which the hairs can be stroked easily in either direction. It is likely that the present coarseness of the fur of *R. vellerosus* is due in large measure to dust. When Gray (1847) characterized *M. vellerosus*, soon after it was collected, he described the fur as being longer and paler than that of *M. fuscipes* (by which he probably meant *M. lutreolus*). A few years later, Gould (1859) gave it the popular name of tawny rat, a most unlikely appellation for *R. l. lutreolus*, one of the darkest of the native Australian *Rattus.* The skin is indeed bizarre when compared with any species of Australian *Rattus* and tends to resemble somewhat that of "*profusus*" (=*R. sordidus villosissimus*). The texture of the pelage in the latter form is very similar to that of "*vellerosus*," and the guard hairs measure to 62 mm. The hind feet of "*vellerosus*" are, however, covered by dark hair and in this respect the type specimen resembles *R. l. lutreolus* strongly, and to a lesser extent, "*profusus*." In characters of the anterior region of the skull, "*vellerosus*" bears considerable resemblance to *R. s. villosissimus* as well as to *R. l. lutreolus* (cf. figs. 19, 20, and 30). Because the ventral part of the cranium is entirely missing, diagnostic features such as bulla length, which would readily separate the two species, are not available. The only description made of the skull in the previous century is that by Gray (1847) and he confined his discussion largely to molar patterning. His description could apply to any one of the native Australian *Rattus* in this regard. In measurements of interorbital width (5.4 mm.), incisive foramen length (7.3 mm.), molar width ×2 (5.7 mm.), crowns m^{1-3} length (7.3 mm.), alveoli m^{1-3} length (8.1 mm.), and crowns m^{1-2} length (5.9 mm.), the "*vellerosus*" skull is closer to *R. l. lutreolus* (cf. table 8). In occipitonasal length [44 mm., as measured by Gray (1847)], nasal length (15.2 mm.), palatal length (23.1 mm.), and inside m^{1-1} (3.1 mm.), "*vellerosus*" resembles *R. s. villosissimus* more closely (cf. table 12). However, when viewed together, the measurements available favor the identity of "*vellerosus*" with *R. l. lutreolus.* Furthermore, "*vellerosus*" shares with *R. l. lutreolus* the distinctive feature of absence of a teloloph on m_1 and m_2 (cf. figs. 20C and 24).

The alleged type locality of "*vellerosus*" is a plains area between the Murray and Glenelg rivers. The donor of the "*vellerosus*" material was Captain George Grey. On his one trip to this area Grey was accompanied by George French Angas, who has described part of the region between the Murray and Glenelg rivers as swampy with much evidence of rat burrows (Angas, 1850). This type of habitat would be compatible only with that of *R. l. lutreolus.*

Since in morphology and presumably in ecology "*vellerosus*" resembles more closely *R. l. lutreolus* than any other Australian *Rattus*, we regard it a synonym of the latter form.

HABITS AND HABITAT: More has been published on the habits and habitat of *R. l. lutreolus* than on any other Australian *Rattus.* Although for many years after its original description, confusion existed between *R. f. fuscipes* of Western Australia and *R. l. lutreolus* of the eastern segment of the continent, it has long been appreciated that *R. l. lutreolus* (under this name or the misnomer of *R. f. fuscipes*) is associated with a moist grass or reed type of environment. Gould (1851) was the first to describe it (under *M. fuscipes*) as being aquatic, swimming with ease and inhabiting moist areas of long grass by lagoons and the banks of watercourses.

Waite (1900, p. 190) extended our knowledge of the habits of *R. l. lutreolus* (also under the misnomer *M. fuscipes*). Referring to a population in the Blue Mountains, he stated (from notes made by the collector, E. G. W. Palmer) that the rats inhabit peaty ridges, where they burrow to great depths and also make conspicuous surface runways. They feed on grasses, fruit, and herbage, he remarked; they gnaw roots and dead timber during burrow construction; and they "swim freely." Noting that in mid-August of 1899, they rarely emerged from their nests, he suggested that they might be hibernating, but such a suggestion has never been pursued. We found *R. l. lutreolus* active in the Blue Mountains in late June, which is also a cold winter month. There are museum records of them from this area for both June and July but none for August. They have been taken in August at about 5000 feet above sea level farther to the north, near Armidale, and we have trapped them in August in lowland localities. This does not, of course, preclude the possibility that this rat may at times become torpid at higher elevations such as the Blue Mountains and the New England Range; and such a possibility is actually of potential interest when one attempts to explain the apparent absence of *R. l. lutreolus* from the Australian Alps, where still lower temperatures occur. (The literature reports of *R. l. lutreolus* in the Australian Alps represent misidentifications of *Mastacomys fuscus*).

Le Souef and Burrell (1926) purported to describe in some detail the breeding burrows and nests of *R. l. lutreolus*, but their comments are suspect as they have undoubtedly confused this rat with *Mastacomys fuscus*. They stated, for example, that the young are haired at birth, which is true for *Mastacomys* (Calaby and Wimbush, 1964) but not for *R. l. lutreolus*, as we have seen. Furthermore, although there are no museum records of *R. l. lutreolus* from the Australian Alps, Le Souef and Burrell (1926) claimed that it occurs at an elevation of over 5000 feet on Mount Kosciusko. Even though Le Souef is now known to have collected *Mastacomys* on Mount Kosciusko in 1923 (Calaby and Wimbush, 1964), the genus was not recognized among the living fauna of New South Wales until trapped there in 1946 by Troughton (Calaby and Wimbush, 1964). Surprisingly, Troughton, even in the 1967 edition of his book, still stated that *R. l. lutreolus* occurs on Mt. Kosciusko.

Brazenor (1936a) found *R. l. lutreolus* in the marshes of Cape Otway, Victoria, and in coastal sand dunes. In the swamp situations, where the water fluctuates seasonally, the rats move to higher ground when their original burrows are flooded out. He also stated that their nests are never above ground. Brazenor considered them destructive in pine plantations in Victoria, noting that they eat the outer bark of the roots of young trees; and their damage to the hoop pine plantations of southeastern Queensland has been noted by Troughton (1937b) and Davis (MS). McNally (1955) believed that they do relatively little damage to the pine plantations in Victoria.

In northeastern New South Wales Calaby (1966) trapped *R. l. lutreolus* in long grass, such as *Poa*, along creeks, in wet hollows of woodlands, and on wet shelves of hillsides. Their runways ramified through the vegetation and under logs. He found one *R. l. lutreolus* sharing with a spiny anteater (*Tachyglossus aculeatus*) the cover provided by a fallen staghorn fern.

On the basis of our own trapping we have acquired a still greater appreciation of the diversity of habitats which *R. l. lutreolus* can occupy. It is most commonly associated with a swamp environment and indeed probably occurs most densely in this situation (fig. 25). It is restricted here to the swamp itself and does not usually invade adjacent scrub or forest. Only in the peripheral portions of a swamp is it in contact with forest dwellers such as *R. f. assimilis*. In these swamps, whether lowland, as in the Gosford area, or upland, as in the Blue Mountains, a dense cover of tall reeds, sedges, or grasses appeared to us prerequisite to the occurrence of *R. l. lutreolus*. Wherever the vegetation thinned there would be no evidence of this rat. The extent of ground water in which *R. l. lutreolus* is active is much greater than is the case with *R. f. fuscipes* in the swamps of Western Australia.

FIG. 25. Habitat of *Rattus lutreolus lutreolus* in a swamp near Clarence, New South Wales. Photographed June 23, 1964.

Rattus lutreolus lutreolus maneuvers readily through soil that is sodden or even overlain by shallow water. Fresh runways and the animals themselves have been seen under these conditions. Although we never saw them swimming in deeper water, it is evident that they must navigate freely into the water from the runways. Runways typically became less numerous toward the periphery of the swamp.

Keith and Calaby (1968) have provided a detailed description and photograph of a swamp near Port Stephens, New South Wales, where they trapped *R. l. lutreolus* along with *Pseudomys novaehollandiae* and *Mus musculus*. At the edge of the swamp, which contained no free water except after heavy rain, the dense sedgy vegetation was primarily *Restio tetraphyllus meiostachyus*, and the shrub *Banksia aspleniifolia* was common. At our North Avoca Beach locality, also in New South Wales, the swamp surrounded standing water and was characterized by a compact cover of a cyperaceous sedge, *Machaerina juncea* (R. Br.) T. Koyama (synonym =*Cladium junceum* R. Br.), averaging about 2 feet high and relieved by a scattering of paperbark trees (*Melaleuca*). The *R. l. lutreolus* runways were completely concealed from above. At Clarence, in the Blue Mountains, a stream ran the length of the swamp where we trapped *R. l. lutreolus*, and the soil surface was damp in some places, submerged in others, usually in less than 1 inch of water. In addition to *Leptospermum juniperinum* and *L. lanigerum* (Myrtaceae), there was dense cover of *Restio australis* (Restionaceae) and *Lepidosperma limicola* (Cyperaceae). Numerous patches of *Drosera* were noted, and both *Melaleuca* and *Rosa* were common along the edge. Runways and holes of *R. l. lutreolus* were plentiful.

A second major habitat in which *R. l. lutreolus* occurs is along a watercourse which may or may not be associated with a nearby swamp. The first record of *R. l. lutreolus* on Kangaroo Island (Horner and Taylor, 1965) was obtained in such a situation at the bank of Rocky River where thick grass lines the river. The adjacent *Melaleuca* swamp which was dry at that time (March 8, 1964) yielded *R. f. greyii* but not *R. l. lutreolus*. It may be that when the swamp is seasonally wet *R. l. lutreolus* moves in and replaces *R. f. greyii*, which cannot tolerate so much moisture. In the absence of a swamp, *R. l. lutreolus* is restricted to the thick grassy edges of stream courses. In the Grampians we trapped it by a stream course with major brush cover of *Caustis* species and *Gahnia radula* (Cyperaceae), *Acacia verticillata* (Leguminosae), *Leptospermum juniperinum*, and *L. myrsinoides* (Myrtaceae).

A third type of situation in which *R. l. lutreolus* occurs is a coastal environment where low beach vegetation forms extensive cover above the high-tide level. Brazenor (1936a) found this habitat to be a haunt of *R. l. lutreolus* in southwestern Victoria; we trapped it in a similar situation on Bribie Island on which there was neither a swamp nor a stream course nearby. The rat occurred on a coastal dune which was characterized by dense undercover of heavy grass and bracken that provided a 2-foot layer of vegetation. Higher vegetation consisted of a few large eucalypts and numerous banksias in the landward portion of the strip. The rat inhabited the low ground vegetation and presumably formed its burrow systems in the root network that held the sand firm. No well-marked runways were detected. This is the one natural environmental situation where *R. l. lutreolus* occupies a habitat that lacks a permanent or temporary freshwater source, although, as mentioned earlier, it also invades pine plantations of *Araucaria cunninghamii* in the northern portion of its range and of *Pinus radiata* in the southern, both of which are devoid of streams or swamps.

SYMPATRY: The range of *R. l. lutreolus* extensively overlaps that of *Rattus fuscipes assimilis* in Queensland, New South Wales, and Victoria west through the Otway Peninsula. In western Victoria and South Australia it is sympatric with *Rattus fuscipes greyii*. In Queensland *R. l. lutreolus* is sympatric with *Rattus tunneyi culmorum* and *Rattus sordidus sordidus*.

TAXONOMIC HISTORY: Gould (1859) expressed the view that *M. vellerosus* might be an abnormal *Mus fuscipes* (=*M. lutreola*), describing it as a freak (or *lusus*). He thought it had no relationship to *M. longipilis*. Next Krefft (1871) stated that it was probably an ally of *Mus longipilis* (=*R. s. villosissimus*). Since then, Jones (1925) gave a brief description of *R. vellerosus* and was dubious about its status, and Le Souef and Burrell (1926), Iredale and Troughton (1934), Raven (1935), and Troughton (1941 and subsequent editions) all treated *R. vellerosus* as a separate species. However, Troughton regarded it as possibly either an abnormal *R. lutreolus* or a hybrid between that and another species. Ellerman (1949) treated it tentatively as a subspecies of *R. fuscipes*, and Tate (1951) formalized earlier views by making it a subspecies of *R. lutreolus*, a move that Troughton (1941–1967, Eighth and Ninth editions) followed.

The confusion of *R. f. fuscipes* and *R. l. lutreolus* was perpetuated for decades. Jentink (1888) listed two specimens (*d* and *e* of the Rijksmuseum van Natuurlijke Historie) under *fuscipes*. We have found *e* to be *R. lutreolus*, as did Mahoney (1969). The description of *M. fuscipes* by Ogilby (1892) is but a slight rewording of the description first made by Waterhouse (1839), and Ogilby included *M. lutreola* under *M. fuscipes* by following Gould in both habitat notes and geographical distribution. Trouessart (1897) also synonymized *M. fuscipes* and *M. lutreola*.

The first extensive description of *M. lutreola* was made by Waite (1900). He, too, synonymized *M. fuscipes* and *M. lutreola*. Although his description is nominally of *M. fuscipes*, every character described is of *M. lutreola* from New South Wales; nothing is included of *M. fuscipes* from Western Australia.

Thomas was the first to try to rectify the mix-up between *M. fuscipes* and *M. lutreola*. Following study of new *M. fuscipes* material from southwestern Australia, which had been collected by the Balston Expedition, Thomas (1906a, p. 473) wrote, "These specimens are clearly Waterhouse's *M. fuscipes*, of which they are practically topotypes, while the aquatic Rat figured and described by Gould as *M. fuscipes* in the Mammals of Australia should bear Gray's name of *M. lutreola*."

Lucas and Le Souëf (1909), like most of their predecessors, regarded *M. lutreola* as a synonym of *M. fuscipes*. Although Thomas (1906a, 1910) had attempted to clarify the *fuscipes-lutreolus* confusion, he was largely ignored in this respect by his contemporaries. Longman (1916a, 1916b) made it very clear that he was including *Epimys lutreolus* with *E. fuscipes*.

In 1920 Troughton made an extended description of *Epimys assimilis* and, as he modeled his paper after the "*fuscipes*" paper by Waite (1900), he made extensive comparisons with Waite's rat. Troughton did not realize at the time that, owing to Waite's error, he was actually comparing *R. f. assimilis* with *R. l. lutreolus* and not with *R. f. fuscipes*. Meanwhile Thomas (1921a) made a further attempt to rectify the confusion by selecting lectotypes of both *R. lutreola* and *R. velutinus* and by pointing out that *R. fuscipes* is confined to Western Australia. Lord (1923), who was the first to follow Thomas in his extrication of *R. fuscipes* from *R. lutreolus*, regarded *R. lutreola* as occurring with *R. velutinus* in Tasmania (although it is not possible to tell whether Thomas did as well).

Jones (1925) considered *R. fuscipes* and *R. lutreola* to be closely related but chose to regard them as distinct species. He thought, too, that South Australia might possibly be the meeting place of the two forms and hence gave a description of both forms. At the time he wrote he knew of only one locality in which *R. lutreola* could be taken and his description was apparently made from a single specimen. The remainder of the description was taken directly from Waite (1900).

Le Souef and Burrell (1926) also followed Thomas (1921a) in considering *R. lutreola* a species distinct from *R. fuscipes*. Their morphological description of *R. lutreola* is from Waite (1900) but they added considerable information concerning habits and habitat. They, too, regarded *R. lutreola* as extending into Tasmania as a form distinct from *R. velutinus*, describing the latter in terms of Thomas's original description of 1882. Iredale and Troughton (1934) treated *R. lutreolus* and *R. velutinus* exactly the same way.

By this time a growing trend was evolving to distinguish *R. fuscipes* from *R. lutreolus* at the species level. It is thus unfortunate that as late as 1935 Raven, using Trouessart (1897) as his guide, took the earlier view of including *lutreolus* as an *R. fuscipes*.

Finlayson (1935) was struck by the large degree of variability in the pelage color of *R. lutreolus* and suggested that the richer tones were characteristic of specimens taken from higher altitudes. He believed that color variability within the species exceeds that exhibited when individuals of *R. lutreolus* are compared with *R. fuscipes*.

Brazenor (1936a) expressed some doubt as to whether *R. lutreolus* and *R. fuscipes* should be distinguished at the species level but chose to do so himself. He was of the opinion that, although *R. lutreolus* had at one time been widely distributed throughout the state of Victoria, it was now confined to the southwestern portion. He erred in this assumption because it has since been taken in several localities in both southeastern and south-central Victoria.

Troughton (1937b) made a substantial contribution to the understanding of the species *R. lutreolus* by being the first to recognize that *R. lutreolus* from Tasmania and *R. velutinus* were, in fact, but one extremely variable form, and under the name *R. l. velutinus* he separated out all specimens from Tasmania as a subspecies of *R. lutreolus*. Troughton thought that *R. lutreolus* of the mainland could be divided into two further subspecies. One he designated as a form occurring in the southeastern portion of Queensland and the other in the coastal regions of New South Wales. The Queensland form he called *Rattus lutreolus imbil*, and the New South Wales one, *Rattus lutreolus cambricus*. These he regarded as distinguishable at the subspecific level from the more southern member, *R. l. lutreolus*, the type of which was at that time considered to be a specimen from South Australia. Troughton added a few comments about *R. l. velutinus* to indicate that it is a highly variable form in Tasmania, not only in its pelage coloration but also in portions of skull morphology. One is led to suspect that, although Troughton was willing to accept such variability in the subspecies from Tasmania, he reversed his stand with regard to the mainland *R. lutreolus* and on the same grounds felt rather that they must be separated out into three discrete units or subspecies. His same views on the taxonomic structure of the species *R. lutreolus* were also expressed in his book (Troughton, 1941–1967, First to Fifth editions).

Considering the clarification made by Troughton (1937b) of the *R. l. velutinus* from Tasmania, Ellerman (1949) had a somewhat unusual way of handling the whole *R. lutreolus* complex. He made it clear from the start, however, that *R. lutreolus* is quite distinct from *R. fuscipes*. He followed Troughton in regarding *R. l. velutinus* as a subspecies of *R. lutreolus*. Where Ellerman differed was in regarding *R. l. lutreolus* as both a mainland form and one that occurs along with

R. l. velutinus in Tasmania. Unfortunately, he did not indicate how he distinguished the two forms in Tasmania. He did not recognize the two new subspecies proposed by Troughton (1937b).

Tate (1951) handled the *R. lutreolus* group under partial influence from his predecessors and partly in a unique way. He recognized six subspecies, accepting *R. l. velutinus* as the only Tasmanian form. He did not acknowledge Troughton's *R. l. cambricus* as a distinct subspecies but placed it in synonymy under *R. l. lutreolus*. He did, however, recognize *R. l. imbil*. Tate went back to the earlier view that *R. lutreolus* and *R. fuscipes* are related at the species level. He ignored the Law of Priority and placed *R. f. fuscipes* as a subspecies of *R. lutreolus*. He also placed "*mondraineus*" as a subspecies of *R. lutreolus*. His apparent reasoning behind this was in part due to a mix-up of skins and skulls, the details of which have been given elsewhere (Taylor and Horner, 1967). As mentioned earlier, Tate (1951) also formally recognized "*vellerosus*" as a distinct subspecies of *R. lutreolus*.

In the later editions of his book on Australian mammals Troughton (1941–1967, Eighth and Ninth editions) modified his views somewhat about *R. lutreolus*. First he acknowledged Thomas's lectotype of the typical subspecies, a specimen from coastal New South Wales, and in so doing he withdrew his subspecies *R. l. cambricus*. Troughton included *Rattus lacus* as a likely subspecies of *R. lutreolus*, providing no evidence to support his suggestion. As for *R. l. imbil*, which he had described some years earlier, Troughton now suspected that it might be a synonym of *Rattus sordidus*, even though earlier (1937b) he described certain features by which the two forms could be distinguished.

Taylor and Horner (1967) provided evidence for the close affiliation of *R. lutreolus* and *R. lacus* and proposed that they be considered conspecific although subspecifically distinct. We cannot agree with Troughton's assessment of *R. sordidus* (Taylor and Horner, 1967, p. 11). We regard "*cambricus*" (type, AM M3192♂, from Booloombayt), "*imbil*" (type, AM M6228♂, from Imbil), and also "*vellerosus*" (cotypes, BM 47.3.1.1 and BM 47.3.1.2♂, from plains between the Murray and Glenelg rivers) as synonyms of *R. l. lutreolus* and "*mondraineus*" as a synonym of *R. f. fuscipes*.

Rattus lutreolus velutinus (Thomas)

Mus velutinus THOMAS, 1882, p. 415.
?*Mus tasmaniensis* KREFFT [*nomen nudum*], 1868, p. 93.
Rattus lutreolus velutinus TROUGHTON, 1937b, p. 284.

LECTOTYPE: Skin and broken skull lacking occipital region and left bulla, young adult female, BM 77.7.3.1, from Tasmania, presented to the British Museum (Natural History) by A. Simson, and selected as the lectotype by Thomas (1921a, p. 432).

DISTRIBUTION: *Rattus lutreolus velutinus* is confined to Tasmania and to adjacent small offshore islands, including some in Bass Strait. Records of this rat are more abundant in the western half of Tasmania, the portion that is less altered by human settlement, than in remaining areas (Green, 1967). Both our analysis of museum materials and the extensive trapping done by Green (1967) demonstrate this trend. We have records of *R. l. velutinus* in southeastern Tasmania and in the Tasman Peninsula and Maria Island regions that are lacking in the map by Green (1967, p. 4, fig. 1), whereas he has a record from Flinders Island, Bass Strait, that we have not seen. Both Green's data and ours suggest that *R. l. velutinus* is scarce or absent in central eastern Tasmania which, like central Tasmania, is highly developed grazing land. The extent of its distribution on the islands of Bass Strait toward the mainland is so poorly known that it is impossible to determine its precise geographical relationship with *R. l. lutreolus*. The insular distribution of the latter in Victoria is known only from a record on French Island (fig. 18).

MEAN MEASUREMENTS (IN MM.): External: head and body 153; tail 114; hind foot (s.u.) 29.7; ear (from notch) 21. Skull: occipitonasal length 37.4; braincase width 16.3; bulla length 6.2; crowns m^{1-3} length 6.8. (See table 9 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 34.9 or less.

DESCRIPTION: The soft, dense pelage of this rat inspired Thomas (1882) to give it the common name velvet-furred rat. Actually, *R. l. velutinus* is very similar to *R. l. lutreolus* in this regard and in the range of color variability. The middorsal fur is variably long, measuring about 16 mm. in specimens from northeastern Tasmania. The dark gray basal portion of the fur blends to a rust or yellowish tip of about 2 mm.

TABLE 9

MEASUREMENTS (IN MILLIMETERS) AND WEIGHTS (IN GRAMS) OF ADULT *Rattus lutreolus velutinus*

Measurement	N	Mean±SE[a]	SD[a]	Range
Head and body length	146	152.53±0.89	10.81	122–179
Tail length	146	114.02±0.82	9.90	86–140
Hind foot (s.u.) length	146	29.73±0.13	1.62	26–34
Ear length (from notch)	127	20.57±0.12	1.38	16–25
Occipitonasal length of skull	124	37.42±0.14	1.52	35.0–41.4
Condylobasal length	124	36.30±0.14	1.62	33.3–40.6
Basal length	123	33.61±0.14	1.56	30.4–37.9
Zygomatic width	136	19.88±0.07	0.78	18.2–22.1
Interorbital width	182	5.47±0.02	0.30	4.5– 6.6
Interparietal length	134	3.81±0.04	0.49	2.5– 5.1
Interparietal width	131	9.40±0.07	0.84	6.5–11.8
Braincase width	140	16.30±0.04	0.51	14.5–17.7
Mastoid width	126	14.09±0.04	0.51	12.5–15.4
Nasal length	174	13.54±0.06	0.83	11.6–16.0
Nasal width	174	3.82±0.02	0.33	3.0– 4.6
Palatal length	166	20.36±0.08	0.98	18.4–22.9
Incisive foramen length	170	6.70±0.03	0.43	5.6– 7.7
Incisive foramina width	171	1.68±0.01	0.18	1.3– 2.2
Inside m^{1-1} width	173	2.80±0.03	0.45	2.1– 3.8
Outside m^{1-1} width	173	7.92±0.03	0.38	7.0– 8.9
Bulla length	138	6.16±0.03	0.34	5.6– 7.6
Crowns m^{1-3} length	172	6.76±0.02	0.32	5.8– 7.7
Alveoli m^{1-3} length	172	7.29±0.03	0.36	6.3– 8.2
Crowns m^{1-2} length	175	5.40±0.02	0.28	4.7– 6.0
M^{1-1} width×2	173	5.10±0.02	0.28	4.2– 5.8
Body weight	117	101.07±0.64	6.97	56–167

[a] SE indicates standard error of the mean; SD, standard deviation from the mean.

Guard hairs are about 20 mm. in the middorsum and are either a translucent gray at the basal 15 mm. and tipped in black or buff or are totally black. Like *R. l. lutreolus*, *R. l. velutinus* is blackish rust to blackish yellow in dorsal coloring. The ears, with short rust-colored hairs, are largely hidden by the pile of the dorsal pelage, as is true in *R. l. lutreolus*. The head is similar in color to the body dorsum and the longest muzzle vibrissae are about 37 mm. Ventrally the fur is dark-based and tipped in gray or buff, becoming very gray in the throat region. The rust cast of the venter, so characteristic of *R. l. lutreolus*, is not pronounced on *R. l. velutinus*. The skin of the hind feet is darkly pigmented, as it is in *R. l. lutreolus*, and the feet are clothed in brown hairs. The tail is uniformly dark and finely covered with dark hairs of 1–1.5 mm. in length.

The juvenile pelage appears identical with that of the subspecies *R. l. lutreolus*.

The mammary formula is 2+2=8.

The adult skull is very similar to that of the mainland *R. l. lutreolus* (fig. 21). There is a variable amount of development in the supraorbital-temporal ridging. It may be less than 0.1 mm. wide and barely raised from the skull surface, or developed to a width of 0.4 mm. and a height of 0.3 mm. The ridges usually extend at least to the midparietal and in some cases to the full length of the parietal. The bullae are smaller in *R. l. velutinus* than in *R. l. lutreolus* and each molar row is shorter and narrower.

The juvenile skull appears indistinguishable from the juvenile skull of *R. l. lutreolus* except in the possession of posterior cusps on m_1 and m_2 (fig. 23).

PREVIOUS DESCRIPTIVE ACCOUNTS: *Rattus lutreolus velutinus* has been described by Thomas (1882), Le Souef and Burrell (1926), Troughton (1937b, 1941 and subsequent editions), Tate (1951), and Green (1967). The most extensive of these is the one offered by Green (1967), who has personally obtained a far larger series than have any of his predecessors.

In describing *R. l. velutinus* as a new species, Thomas (1882, p. 415) based his account on "two skins and a skeleton . . . presented to the Museum in 1877 by Mr. A. Simson," and published measurements for skins *a* and *b* and for skull *b* plus the skull "of the skeleton." At the present time there are four *R. l. velutinus* specimens in the British Museum (Natural History) donated by Simson (BM 77.7.3.1, BM 77.7.3.2, BM 77.7.3.4, and BM 77.7.3.6). Of these, BM 77.7.3.1, a young adult female with skin and badly broken skull, appears to be Thomas's specimen *a*, for which skull measurements were not given; and BM 77.7.3.2, a smaller unsexed specimen with skin and good subadult skull, appears to be his specimen *b*. His slightly smaller skull "of the skeleton" is very likely the slightly smaller subadult skull, without skin, numbered BM 77.7.3.6. The fourth *R. l. velutinus*, BM 77.7.3.4, also represented by skull only, is the largest and is clearly adult. The omission of this skull from his description suggests that he may have regarded it a different Tasmanian form.

Thomas (1882) applied the name *R. l. velutinus* in recognition of the soft, velvety quality of the fur, a character that has been consistently repeated in subsequent descriptions (Lord and Scott, 1924; Le Souef and Burrell, 1926; Troughton, 1937b; Tate, 1951; and Green, 1967). Thomas (1882) found the dorsal hairs to be almost an inch long with still longer black hairs mixed among them, whereas Green (1967), basing his detailed pelage description on examination of 207 skins, noted that guard hairs on the rump may be as long as 50 mm. The extensive variability in color has been discussed by Finlayson (1935), Troughton (1937b), and Green (1967).

The original description of the skull of *R. l. velutinus* as "rather light and slender" (Thomas, 1882, p. 415), is justifiable in the intended context of comparing these young specimens with the generally heavier skull of *Mastacomys fuscus* described in the same paper. On the other hand, Thomas's stress of the diagnostic value of the anterior curvature of the zygomatic plate of *R. l. velutinus* has been questioned by Troughton (1937b) who, working with considerably more material than was available to Thomas, found this character too variable for taxonomic use.

No exceptions to the mammary formula of 2+2=8 (Green, 1967) are known to us.

Some aspects of the reproductive biology of this subspecies have been described by Green (1967) and by Taylor and Horner (MS).

There is one small colored figure of *R. l. velutinus* (Troughton, 1941 and subsequent editions, pl. 19, fig. 5a), and the following photographs are published in Green (1967, pls. 3–7): full length external view; lateral, dorsal, and ventral aspects of skull and dorsal view of mandible; occlusal surface of upper molar row showing three progressive stages of tooth wear; and side views of one-day and 12-day young. Thomas (1882, p. 414, fig. 4) drew the anterior plate of the zygomatic arch in lateral aspect; Finlayson (1933, pl. VI, figs. B, G, and H, labeled *Rattus lutreola*) illustrated the dorsal view of the skull and the ventral surfaces of the manus and pes; and Green (1967, p. 6, fig. 2) showed the mammary pattern.

REMARKS: Troughton (1920) referred to a tooth character in *R. l. lutreolus* (under the misnomer *R. fuscipes*) that gave some promise to distinguishing *R. l. lutreolus* from other species of *Rattus*. The character is the absence of a posterior cusp, the teloloph, on m_1 and m_2 that he found to be present on the lower molars of *R. f. assimilis*. We have checked this feature and find that the absence of these cusps is a reliable feature in both *R. l. lutreolus* and *R. l. lacus* (fig. 24) and that *R. l. velutinus* stands apart from the two mainland subspecies in possessing these cusps. Furthermore, all other subspecies of native *Rattus* have these cusps. It is a character that is useful on all dentition except that which is well worn. This point of distinction may prove of considerable value in the identification of Pleistocene and Recent fossil fragments of this genus in Australia.

HABITS AND HABITAT: Until recently there has been little published information on the habitat of *R. l. velutinus* and it has been generally assumed that this rat shares the "water-loving" ways of the mainland *R. l. lutreolus* (i.e. Troughton, 1941–1967, Ninth edition, p. 263). This assumption, explained partly by a long confusion of *R. l. lutreolus* with *R. f. fuscipes* and partly by a dearth of information, was based primarily on the field experience of a single collector. Finlayson (1933), who trapped *R. l. velutinus* (and at the time regarded it as a distinct species) in a mountainous area, noted that the grassy habitat

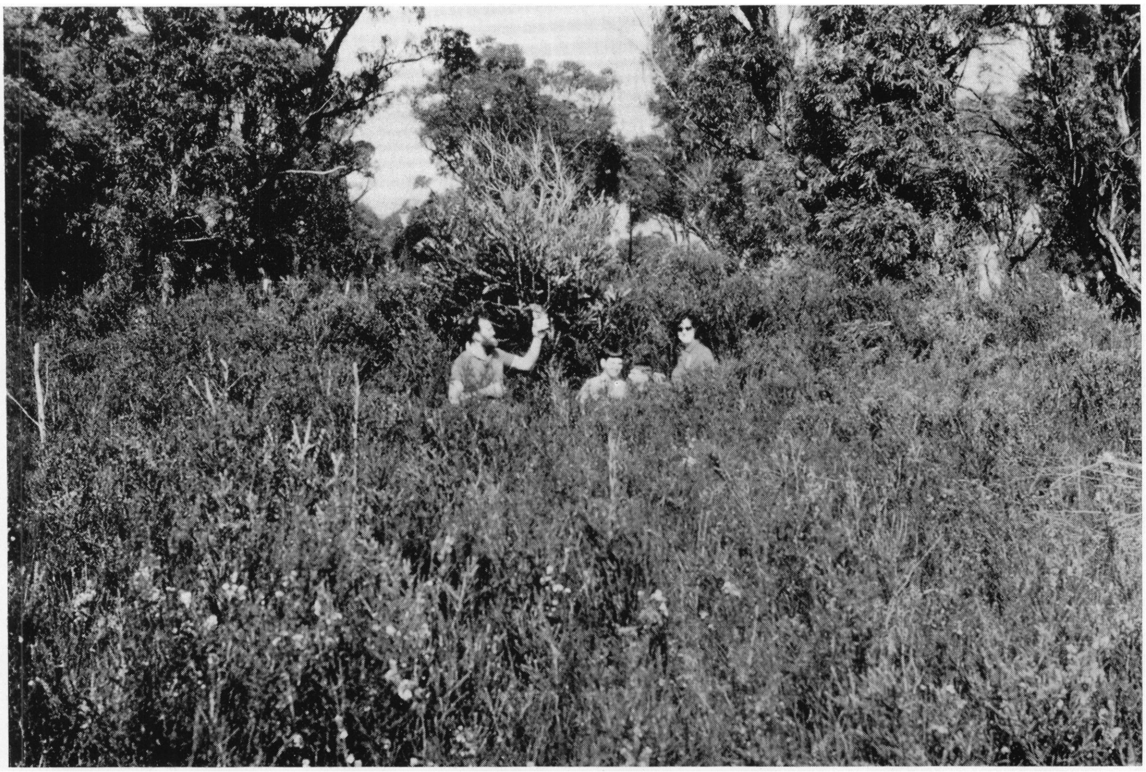


FIG. 26. Habitat of *Rattus lutreolus velutinus* in a *Melaleuca* swamp at Green's Beach, Tasmania. Photographed April 3, 1964.

was covered by snow in winter and in summer was "always sodden and frequently awash" (Finlayson, 1933, p. 126).

Green (1967) has now expanded greatly our understanding of *R. l. velutinus*, and his findings refute any implication that it is associated only with swampy or riparian surroundings. Describing the wide range of habitats occupied by this rat, he summarized them as falling into three major categories: myrtle (*Nothofagus*)-predominant temperate rain forest, button-grass sedgelands, and coastal swamp lands (fig. 26). Mollison (1960) also commented on its abundance in rain forest. Green (1967) found that it shows a preference for well-drained habitats and is often associated with free water only in rainy periods, evacuating living areas that become inundated by water in favor of higher ground. He noted instances in which *R. l. velutinus* utilized runways made through the dense tops of partially submerged vegetation. "It prefers," he reported (1967, p.10), "to keep its body fur dry and avoids swimming when possible."

We trapped *R. l. velutinus* in two of the three major habitats, temperate rain forest and coastal swamp land, the latter with the considerable help of Green. We can contribute nothing to his excellent account of habitat structure and utilization except to add to his extensive list the following plants collected in the productive swamp habitat at Green's Beach: *Leucopogon collinus* (Epacridaceae), *Lepidosperma gladiatum* (Cyperaceae), and *Lepidosperma tenax* and *Restio complanatus* (Restionaceae).

Comparison of what is now known of the habits and habitats of *R. l. velutinus* and *R. l. lutreolus* suggests subtle distinctions in habitat exploitation. Although *R. l. lutreolus* has been recorded at altitudes up to 5000 feet, it seems never to have been taken in subalpine situations as defined by Costin (1959). This is not the case, however, with *R. l. velutinus*. Where it occurs in the higher elevations of rain forest and sedgelands it occupies a habitat that is well covered with snow for several weeks during the winter (Finlayson, 1933; Green, 1967). The apparently greater tolerance of *R. l. velutinus* to withstand severe subalpine winter conditions may reflect different physiological and behavioral adaptations in the two subspecies.

In *R. l. lutreolus* habitats the dense vegetation usually affords ample cover in which the rat can form runway systems that are completely concealed from above. Sedges and other compact vegetation contribute to the continuous canopy and the rat seems to favor such situations. Except in the coastal sand-dune environment, where *R. l. lutreolus* is forced to navigate across the substrate without benefit of continuous cover (but where burrowing into the loose sand may be compensatorily rapid in fulfilling temporary cover requirements), utilization of concealed runways seems more characteristic of *R. l. lutreolus* than of *R. l. velutinus*. *Rattus lutreolus velutinus* frequently traverses more open areas, exposing itself for several yards as it runs along essentially bare ground (Green, 1967; Mollison, personal commun.). In this respect *R. l. velutinus* is more like the mainland form, *R. fuscipes*, and it may be that *R. l. velutinus* has been able to exploit this more open habitat in the absence of competition from members of the *R. fuscipes* group in Tasmania.

Another apparent difference between *R. l. lutreolus* and *R. l. velutinus* is the closer association of the former with a permanent freshwater source, although the association is not obligatory for either form. We suspect that this difference, as documented earlier, is an actual one; and, again, it is tempting to speculate that *R. l. velutinus* may be under less rigorous competitive pressure for widespread habitat exploitation than is *R. l. lutreolus*. It must be recognized, however, that even *R. l. velutinus* utilizes wet runways and will "take to water if circumstances necessitate" (Green, 1967, p. 10), and that, indeed, any *Rattus* would be likely to swim if no other recourse were available. Definitive ecological and behavioral studies are needed to explore further the "water-loving" tendencies of both of these subspecies. Two of the problems besetting even the keenest of field observers, the unnatural behavioral situation and the identification difficulty, are alluded to by Green (1967, p. 10): "On two occasions . . . [*velutinus*] (or possibly the broad-toothed rat, *Mastacomys fuscus*) have been flushed from creekside growth and have jumped into the stream, swum on the surface to the other side and disappeared on another runway." A less critical naturalist might easily have interpreted this as "water-loving."

Much additional information has been provided by Green (1967) on the habits of *R. l. velutinus* and is abstracted here. Well-defined runways in dense vegetation are about 1½ inches wide and are formed and maintained by the gnawing activities of the rats. In the swamps and sedgelands much of the material cleared away by the rats contributes to their primarily vegetarian diet of succulent roots, stems, and leaves. They readily eat moss sporangia (Mollison, 1960). Green (1967) found that in rain forest, where runways are likely to be superficial where discernible at all, the rats include seeds and insects in their diet of vegetation, and a few rat stomachs were found to be filled almost entirely with insect larvae. Subsurface burrows, usually shallow and often extensively branched, are excavated in sandy soils of the coastal swamp lands and are largely confined here to the drier sites. In the rain forest greater use is made of natural hollows beneath roots and in rotting logs. Excavated soil heaps in the swamp areas are conspicuous, but well-concealed openings, free of adjacent soil heaps, are usually present also. Dried vegetation carried into the tunnels serves as nesting material. In the sedgelands, subsurface burrows, which would usually be swamped by seepage, are rare and are replaced by tunnels through the base of the vegetation; and somewhat elevated nests of dry vegetation are situated in grassy tussocks. These rats are active in the day as well as at night.

SYMPATRY: *Rattus lutreolus velutinus* is geographically isolated from all other native Australian *Rattus*.

TAXONOMIC HISTORY: A year after Thomas described *Mus velutinus*, Higgins and Petterd (1883) described a new Tasmanian species called *Mus castaneus*. It is clear from their drawings of the mandible and the upper and lower tooth rows (Higgins and Petterd, 1883, figs. 2, 2a, and 2b), however, that their so-called new species is the previously described *Mastacomys fuscus* (Thomas, 1882). Although Lord (1923) stated that *M. castaneus* is a synonym for *R. l. velutinus*, *M. castaneus* must be relegated to synonymy with *Mastacomys fuscus* instead.

Ogilby (1892), who recognized *M. velutinus* as a separate species, took his description directly from the original description (Thomas, 1882). Trouessart (1897) also regarded *M. velutinus* as a full species as did Lucas and Le Souëf (1909), Longman (1916a, 1916b), and Raven (1935). These last five authors also regarded *M. fuscipes* (in their confusion of it with *M. lutreola*) to occur in Tasmania along with *M. velutinus*. Thomas (1921a) selected lectotypes of both *R. velutinus* from Tasmania and *R. lutreola* from New South Wales in an attempt to clarify the species distinction of *R. fuscipes* from the latter. Lord (1923) was the first to follow Thomas's suggestion of the distinctness of *R. fuscipes* and *R. lutreola* at the species level but still considered the latter to be a co-inhabitant of Tasmania along with *R. velutinus*. Le Souef and Burrell (1926) expressed the same views as Lord and their description of *R. velutinus* is only a slight rewording of Thomas's (1882) original description. Iredale and Troughton (1934) not only adhered to this, but also agreed with Lord (1923) in including *M. castaneus* as a synonym of *R. velutinus*.

There appears to have been some historical confusion of *R. l. velutinus* with *Mastacomys*. With the first recognition of living *Mastacomys* on mainland Australia, Brazenor (1934) specified certain characters whereby *Mastacomys* could be distinguished from *R. lutreolus*.

Troughton (1937b) was the first to appreciate the natural relationships of *R. velutinus* with *R. lutreolus*. He recognized that all the Tasmanian specimens hitherto variously identified as *R. velutinus*, *R. lutreolus*, or *R. fuscipes* were in fact one variable subspecies, *R. l. velutinus*. Unfortunately, Ellerman (1949) supported only a portion of Troughton's proposal. He concurred that *R. l. velutinus* is a subspecies of *R. lutreolus*, but he simultaneously adhered to the earlier view that *R. l. lutreolus* occurs not only on the mainland but in Tasmania as well. He made no attempt to distinguish the two subspecies he recognized in Tasmania.

Tate (1951) followed both Troughton (1937b, 1941 and subsequent editions) and Ellerman (1949) in regarding *R. l. velutinus* as a subspecies but, unlike Ellerman, restricted the nominate subspecies, *R. l. lutreolus*, to the Australian mainland.

Although it is not primarily a taxonomic study, by far the most extensive examination ever made of *R. l. velutinus* is the recent study of Green (1967), who utilized more than 200 freshly collected specimens from various localities in Tasmania. From this material he has been able to derive information on the gamut of variability of external dimensions and skull measurements.

We regard *R. l. velutinus* a subspecies of *R. lutreolus* and the only one to occur in Tasmania. We reject *M. castaneus* as a synonym of *R. l. velutinus* and place it in synonymy with *Mastacomys fuscus*.

Rattus lutreolus lacus Tate

Rattus lacus TATE, 1951, pp. 347–348.
Rattus lutreolus lacus TAYLOR AND HORNER, 1967, p. 11.

HOLOTYPE: Skin and complete skull, young adult male, AMNH 107312, collected October 21, 1937, by Gabriele Neuhäuser, at Lake Barrine, Atherton Tableland, northern Queensland.

DISTRIBUTION: *Rattus lutreolus lacus* is known only from Lake Barrine (fig. 18).

MEAN MEASUREMENTS (IN MM.): External: head and body 147; tail 98; hind foot (s.u.) 28.6; ear (from notch) 20. Skull: occipitonasal length 36.0; braincase width 16.5; bulla length 6.6; crowns m^{1-3} length 7.1. (See table 10 for complete list of measurements and statistical presentation.) Juveniles: unknown.

DESCRIPTION: The five specimens known to science all appear to be young adults; thus the description of features of the skin and skull may not be entirely representative of the adult condition. The pelage is lighter in color, with more brown than black, than in the other two subspecies of *R. lutreolus*. The "velvet" quality of the two southern subspecies is lacking in this northern form. The dorsal pelage is predominantly bronzy brown. Middorsal hairs of the trunk and rump measure up to 17 mm., have gray bases, and are variously tipped and banded in shades of yellowish, reddish, and bronzy brown. Rump guard hairs are up to 27 mm., with their visible portions deep bronzy brown. Lateral body hairs have a greater preponderance of yellowish brown in their terminal portions. Fine midventral hairs, light gray at their bases and tipped with buff, are overlain with soft buffy hairs measuring up to 12 mm. long. Facial coloration is like that of the dorsum, with the hair length 10 mm. between the ears

TABLE 10

MEASUREMENTS (IN MILLIMETERS) OF ADULT *Rattus lutreolus lacus*

Measurement	N	Mean±SE[a]	SD[a]	Range
Head and body length	5	146.80±3.79	8.47	134–154
Tail length	5	98.40±2.24	5.00	92–106
Hind foot (s.u.) length	5	28.60±0.22	0.49	28–29
Ear length (from notch)[b]	5	19.60±0.83	1.86	16–21
Occipitonasal length of skull	2	35.95±0.46	0.65	35.3–36.6
Condylobasal length	2	34.95±0.46	0.65	34.3–35.6
Basal length	2	32.40±0.35	0.50	31.9–32.9
Zygomatic width	2	19.15±0.18	0.25	18.9–19.4
Interorbital width	3	5.00±0.04	0.08	4.9–5.1
Interparietal length	2	3.85±0.03	0.05	3.8–3.9
Interparietal width	2	10.20±0.07	0.10	10.1–10.3
Braincase width	2	16.50±0.07	0.10	16.4–16.6
Mastoid width	2	13.35±0.18	0.25	13.1–13.6
Nasal length	2	12.95±0.32	0.45	12.5–13.4
Nasal width	2	4.40±0.00	0.00	4.4–4.4
Palatal length	3	19.77±0.21	0.37	19.3–20.2
Incisive foramen length	3	7.03±0.05	0.09	6.9–7.1
Incisive foramina width	3	1.77±0.02	0.04	1.7–1.8
Inside m^{1-1} width	3	2.60±0.08	0.14	2.5–2.8
Outside m^{1-1} width	3	7.77±0.02	0.05	7.7–7.8
Bulla length	2	6.60±0.07	0.10	6.5–6.7
Crowns m^{1-3} length	3	7.07±0.07	0.12	6.9–7.2
Alveoli m^{1-3} length	3	7.83±0.10	0.19	7.7–8.1
Crowns m^{1-2} length	3	5.93±0.05	0.09	5.8–6.0
M^{1-1} width × 2	3	5.17±0.07	0.12	5.0–5.3

[a] SE indicates standard error of the mean; SD, standard deviation from the mean.

[b] "apparently from notch" (Tate, 1951, p. 348).

and 6.5 mm. between the eyes. Muzzle vibrissae are dark brown, some tipped in white, and measure to 33 mm. long. The ears are sparsely clothed with short buff and reddish buff hairs. The hair and skin clothing the feet are dusky brown. The bristle-like dark brown tail hairs vary in length from 1.5 mm. near the tail base to 2 mm. near the tip and to 5 mm. terminally. Dusky brown tail scales, visible through the hairs, are about 12.5 per cm. The five known skins of *R. l. lacus* have relatively shorter tails than have *R. l. lutreolus* or *R. l. velutinus*.

The mammary formula can be determined only to the extent that there are two pairs of pectoral teats on AMNH 107311.

The skull is more like that of *R. l. lutreolus* than of *R. l. velutinus* in its general proportions and it averages a little larger than that of *R. l. lutreolus* in both nasal width and braincase width (fig. 22). The incisive foramina terminate in line with the first loph of m^1. Supraorbital-temporal ridging is present and distinct to the midparietal region and continues posteriorly to the posterior limit of the parietal as a much finer line. In the posterior supraorbital region it measures 0.3 mm. wide and 0.2 mm. above the skull surface. In the small sample available the bullae average larger than in the other two subspecies. The posterior subsidiary cusp is lacking on m_1 and m_2. *Rattus lutreolus lacus* is like *R. l. lutreolus* in this regard.

PREVIOUS DESCRIPTIVE ACCOUNTS: Tate (1951), who first described *R. l. lacus*, gave the only account available for this subspecies. He commented on the similarity of dark coloring of *R. l. lacus* and *R. l. lutreolus*, but did not ally the two formally. He was unable to determine the mammary formula on the two female specimens. Our cranial measurements agree closely with those of Tate, and his published value of 17.2 mm., rather than 7.2 mm., for incisive foramen length is clearly a transcription error. There have been no published illustrations of *R. l. lacus*.

REMARKS: The five specimens are not all complete. Two (AMNH 107311 and AMNH 107312) have complete skins and skulls. One (AMNH 107313) is a skin only, another (AMNH 107314) has both skin and skull but the hind skull is broken and repaired, and the last (AMNH 107315) has a skin and a mismatched skull. This skull, which Tate (1951) recognized as mismatched, is fragmented, the incisive foramina are still intact, and are wide and do not taper posteriorly as do those of all subspecies of *R. lutreolus*. It is probably the skull of a young *R. f. coracius* or *R. l. cooktownensis*, both of which are known from Lake Barrine.

HABITS AND HABITAT: The only habitat note that accompanies the series of five *R. l. lacus* trapped at Lake Barrine states that they were taken in bladey grass. Lake Barrine is one of two large deep lakes on the Atherton Tableland formed from volcanic action. In 1964 we visited Lake Barrine to examine the area more closely, but unfortunately had not sought in advance the required permit to trap there. The lake is situated at an altitude of 2400 feet in the middle of undisturbed luxuriant rain forest that comes almost to the water (fig. 27). Immediately bordering the lake is a substantial growth of bladey grass and other grasslike vegetation,

FIG. 27. Presumed habitat of *Rattus lutreolus lacus* at Lake Barrine, Queensland. The lake is an old volcanic cone surrounded by grass and rain forest. Photographed by Hobart M. Van Deusen March 8, 1948.

occurring in irregular patches and providing a dense cover for small mammals. If *R. l. lacus* is confined to this type of vegetation, its distribution in the Atherton Tableland must be exceedingly restricted and patchy, and Lake Barrine, situated in the high rainfall region of the Atherton Tableland, appears to offer one of the few areas north of southeastern Queensland suitable for a member of the *R. lutreolus* group.

SYMPATRY: *Rattus lutreolus lacus* is sympatric with *Rattus fuscipes coracius* and *Rattus leucopus cooktownensis*. It is probably sympatric also with *Rattus sordidus sordidus* which has been taken at several localities on the Atherton Tableland.

TAXONOMIC HISTORY: When Tate (1951) described *R. lacus* as a new species, he apparently failed to recognize any affinity of this form with *R. lutreolus* largely because of his misevaluation of the latter (see Taylor and Horner, 1967). Troughton (1941–1967, Eighth edition) speculated that *R. lacus* might be either a subspecies of *R. lutreolus* or a member of a *sordidus-conatus-colletti* group, which by now he was aligning tentatively with *R. lutreolus*. Taylor and Horner (1967) presented evidence for the close affiliation of *R. l. lacus* with *R. lutreolus* and recommended that they be considered conspecific though subspecifically distinct. This recommendation is supported in our present paper.

Rattus sordidus (Gould)

DISTRIBUTION: Coastal Queensland from both east and west coasts of Cape York south to the vicinity of Brisbane; central eastern portion of Australia from the Gulf of Carpentaria and the Katherine district south to northeastern New South Wales and southwestern South Australia; northwestern Northern Territory (fig. 28).

GENERAL DESCRIPTION: These are all large-bodied rats in which the tail is usually shorter by 20–35 mm. than the combined head and body length. The pelage is coarse and often spinous, ranging from the buffy hue of the central Australian form to the somber color of the form in the Darwin area. The ears match the dorsal pelage in color. The tail is dark brown, and the hairs are more conspicuous than in most other subspecies. The ventral coloration is medium gray, often tinged with rust in the darker subspecies, and not sharply demarcated from the dorsum. The mammary formula is $3+3=12$.

The skull is more rugged in appearance than in any other native Australian *Rattus*. The lambdoidal crest reaches its maximum development in this species and provides an upward tilt to the posterodorsal profile of the skull. The supraorbital-temporal ridging is also more pronounced in this species, starting well forward in the supraorbital region and extending in most cases to the posterior limit of the parietals. This ridging fans out anteriorly on the premaxillaries. The incisive foramina extend posteriorly to a region in line with the anterior loph of m^1 and are relatively longer with reference to basal length than in other species. They tend to taper somewhat in younger animals, but in older adults the anterior and posterior widths of a foramen are about equal. The nasals overhang the anterior faces of the incisors only slightly or not at all. The bullae are inflated and larger in absolute size in this species than in any other native species except *R. tunneyi*. The bullae average 21.5 to 22.7 per cent of the basal skull length in the various subspecies and are usually larger than the length of the alveoli of m$^{1-3}$ (figs. 29–32). The only other species of *Rattus* in Australia that almost matches *R. sordidus* in relative bulla-to-basal length is *R. exulans*, which is a much smaller animal.

DIAGNOSTIC CHARACTERS: The most distinguishing skull character of this species is the combination of large bullae, long incisive

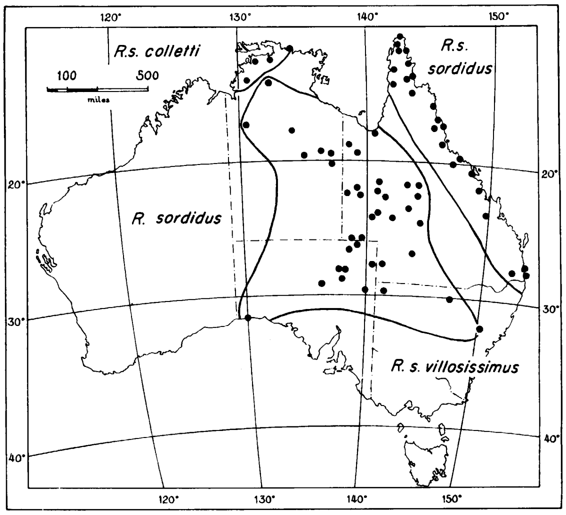
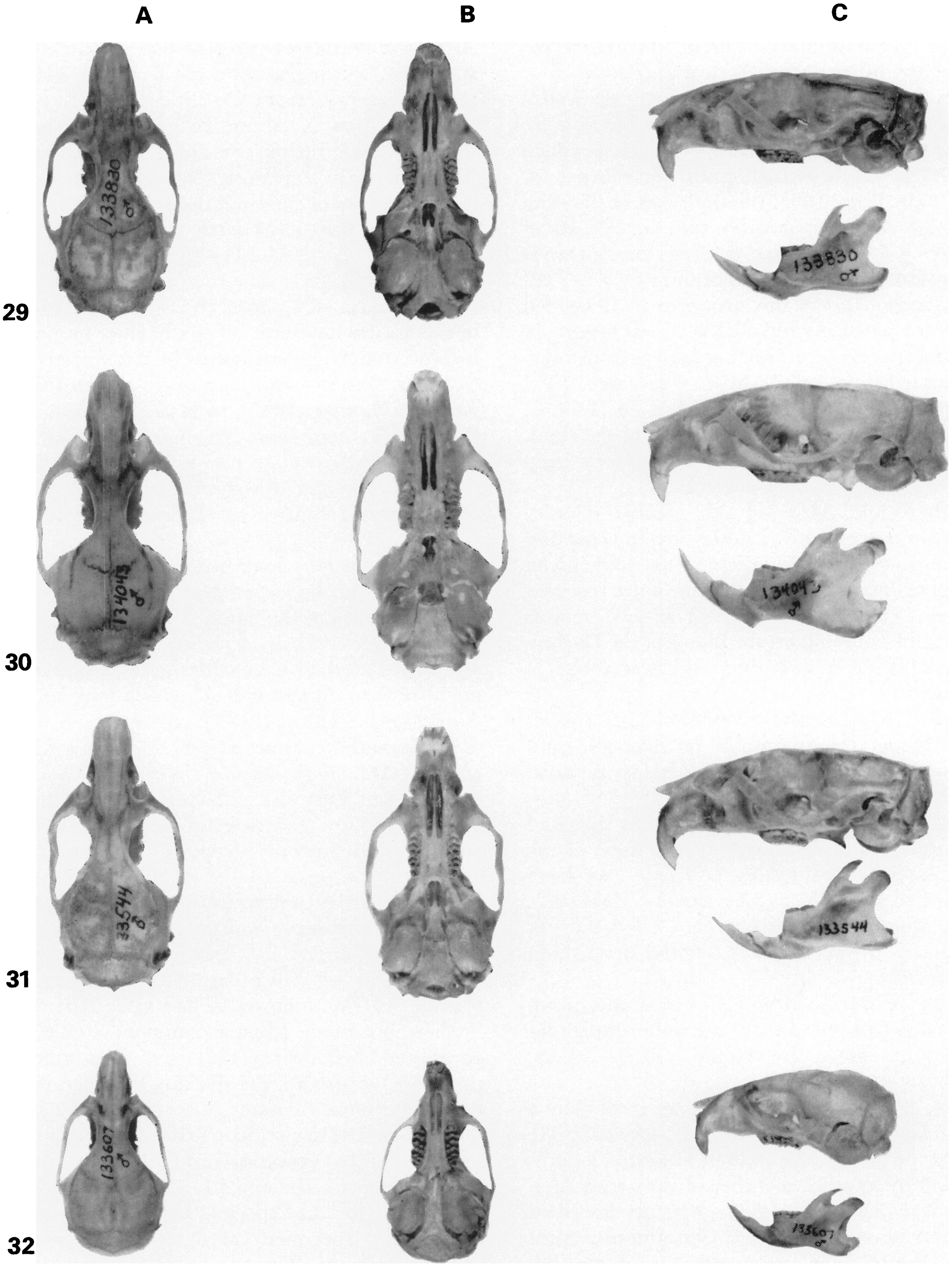


FIG. 28. Distribution map of *Rattus sordidus*. Locality records for each of the three subspecies are indicated by dots.



FIGS. 29–32. Dorsal (A), ventral (B), and lateral (C) views of skulls of *Rattus sordidus*. 29. Adult *R. s. sordidus*, MVZ 133830. Occipitonasal length 41.4 mm. 30. Adult *R. s. villosissimus*, MVZ 134043. Occipitonasal length 45.0 mm. 31. Adult *R. s. colletti*, MVZ 133544. Occipitonasal length 41.8 mm. 32. Juvenile *R. s. sordidus*, MVZ 133607. Occipitonasal length 30.4 mm.

foramina, and heavy supraorbital-temporal ridging. The mammary count of 12 teats exceeds that of any other native Australian *Rattus*.

TAXONOMIC HISTORY: The first rat of this group to be described was *Mus longipilis* (Gould, 1854), the description resting on one specimen only (AM 62) in which, until our request for removal in June, 1965, the skull was in the skin. The type locality is possibly the Victoria River (Barcoo River or Cooper's Creek of southwest Queensland) in a desert situation.

The second rat of this group to be described was *Mus sordidus* (Gould, 1858a), a rat originally known only from the Darling Downs and today represented by only three topotypes (BM 46.4.4.68, BM 58.11.24.5, and BM 58.11.24.6). Owing to the incomplete condition of the skull, *M. sordidus* has in its subsequent history been allied with other species of *Rattus*.

Later Gould discussed *M. sordidus* (Gould, 1858d) in more detail. In addition to repeating the morphological characters he had given earlier, he included a few habitat notes received from the collector, Gilbert. *Mus sordidus* was stated to be common on the plains of the Darling Downs and less frequently found near the edge of creeks.

Krefft (1871) mentioned both of these species in his list of the mammals of Australia and suggested that *M. longipilis* is probably identical with *M. vellerosus*.

In 1887 Collett described some rats that had been obtained at Coomooboolaroo and, of the specimens he identified as *Mus greyii*, we have reidentified one as *R. sordidus sordidus* (ZMO 99). At the time of his identification Collett did not have access to specimens or a good description of *M. sordidus*.

Ogilby (1892) listed both species of this group but his descriptions of them are only rewordings of accounts given by Gould (1854, 1858a, 1858d).

Waite (1898) was the first to recognize a nomenclatural problem with *M. longipilis*. He pointed out that the name *longipilis* is preoccupied by another member of the genus *Mus*, a form (now known as *Akodon longipilis*) described by Waterhouse (1837) from Coquimbo, central Chile. Waite then proposed the name *M. villosissimus* for the Australian rat and made an extended description of it based on two new specimens, one of each sex (AM M1305 and probably SAM M2410). The former is now without a skull and the latter is without a skin. Although Waite gave no locality data for either specimen, the registration card of AM M1305 states that it is from Wycliffe Creek, central Australia (now Northern Territory) and that it was collected during the Horn Expedition by Prof. Baldwin Spencer. By matching our measurements of the skull of SAM M2410 with those of Waite, it appears that this is his B female and that AM M1305 is his specimen A male.

Trouessart (1897) listed the two species of rats in the traditional sense, using the older name *M. longipilis* for *M. villosissimus*. He also referred to Collett's "*greyii*," which we now know to be *R. sordidus*. Thomas (1897), in his original description of *Mus gestri* from New Guinea, allied *M. gestri* to the Australian rats and particularly to *M. greyii*. He, too, was probably using the *M. sordidus* representative of Collett's "*greyii*" for comparison.

Thomas (1904a) described another member of this group that he called *Mus colletti*. This form had been taken at the South Alligator River. He likened *M. colletti* in many respects to *M. sordidus* and regarded their similarities to be of sufficient magnitude to suggest that *M. colletti* may be the tropical representative of *M. sordidus*.

Lucas and Le Souëf (1909) made no reference to *M. villosissimus* in their listing of the mammals of Australia and also neglected to list *M. colletti*. They gave a brief description of *M. sordidus*, this being only a copy of Ogilby's earlier account.

Thomas (1910) referred to the forms hitherto described, *sordidus*, *villosissimus*, and *colletti*, as full species under his listing of the generic arrangement of Australian *Epimys*. Longman (1916a, 1916b) followed Thomas (1910) and furthermore made passing comment about the occasional hordes of rats that occur from time to time in Queensland. He did not, however, refer to *E. villosissimus* by name.

Thomas (1921a), realizing that *R. sordidus* was represented by syntypes rather than a single type specimen, designated a lectotype (BM 58.11.24.6) for that species. Upon re-examination of two specimens of *R. villosissimus* from Liverpool Plains, Thomas (1921b) erected the subspecies *R. villosissimus profusus*, basing it largely on pelage differences.

Two years later Thomas (1923c) described *Rattus conatus*. He stated that it was allied to *R.*

colletti but was larger. Earlier, Thomas (1904a) had likened *M. colletti* to *M. sordidus* and had even suggested that *M. colletti* was a northern representative of the latter. By inference one might conclude that he also regarded *R. conatus* as being similar to *R. sordidus*, but he did not actually state this. His description (Thomas, 1923c) of *R. conatus*, which he compared with *R. colletti* in many features, was based on 10 specimens. In 1926 Thomas (1926b) described another form of this *R. sordidus* group, *Rattus youngi*, and allied it to *R. assimilis*.

Laurie and Hill (1954) regard *gestroi* of New Guinea as a subspecies of *R. sordidus*.

We recognize three subspecies of Australian *R. sordidus*: *R. s. sordidus*, *R. s. villosissimus*, and *R. s. colletti*.

Rattus sordidus sordidus (Gould)

Mus sordidus Gould, 1858a, p. 241.
Rattus conatus Thomas, 1923c, p. 159.
Rattus youngi Thomas, 1926b, p. 309.
Rattus gestri conatus Tate, 1951, p. 350.

Lectotype: Skin and incomplete skull with occipital and basal region to broken palate missing, adult, undetermined sex, BM 58.11.24.6, collected by Gilbert for Gould on open plains, Darling Downs, Queensland (Darling Downs was formerly a part of New South Wales). Selected as the lectotype by Thomas (1921a, p. 432).

Distribution: In the northern portion of Cape York *Rattus sordidus sordidus* is known from both east and west coastal areas. In the southern half of Cape York it occurs only on the eastern side in coastal and subcoastal areas southward to the vicinity of Brisbane. The locality records are scarce south of Mackay, where only four localities are backed up by specimens. McDougall (personal commun.), however, has found records of *R. s. sordidus* in Kenmore, a suburb of Brisbane and about 60 miles east of the type locality. In Darling Downs, in spite of intensive recent trapping by Kirkpatrick (1966) and others, *R. s. sordidus* has not been taken since the time of Gilbert a century ago. In addition to its mainland distribution, *R. s. sordidus* is known also from Albany Island at the tip of Cape York and from Moreton and Stradbroke Islands near Brisbane (fig. 28).

Mean Measurements (in Mm.): External: head and body 161; tail 126; hind foot (s.u.) 29.8; ear (from notch) 18. Skull: occipitonasal length 37.2; braincase width 15.8; bulla length 7.7; crowns m^{1-3} length 6.7. (See table 11 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 34.0 or less.

Description: This rat and *R. s. colletti* are both somewhat smaller than *R. s. villosissimus* and the tails and hind feet proportionally shorter. The rat is dark as the subspecific name implies but not so dark as *R. s. colletti*, becoming lighter and warmer in coloration in more southern areas. The pelage is coarse and usually spinous. Dorsally the body is a grizzled dark brown to olive brown. The main body hairs are about 9 mm. long, dark brown basally with the terminal 3.5 mm. a buff-yellow or rust. The fine gray underfur is lighter than that of *R. s. colletti*. The brown of the hairs is grayish, whereas in *R. s. colletti* it is blackish. Guard hairs measure about 30 to 45 mm. and are most conspicuous in the rump region. The basal portion is dark brown and the last 7 mm. or so are usually a light buff. The spines are about 12 to 16 mm. in length. Their basal portion is light and translucent and the last 4 mm. are black or dark brown. In the rats from the tip of Cape York the spines occur about one every 1 mm. as they emerge from the skin. In more southern areas around Cairns they are about one every 3 mm., and in the Brisbane area the spines are even less dense or may be lacking. The facial region is the same color as the dorsum. Muzzle vibrissae measure up to 40 mm. The more dorsal vibrissae are dark brown and the more ventral ones are light to almost white. The ears are sparsely covered with buff-colored hairs. The feet are clothed in silvery hairs often mixed with a few light brown hairs. The venter is a medium gray with a tinge of buff to yellowish. There is usually no buffy interzone between the dorsal coloration and that of the venter as there is in *R. s. colletti*. The predominant hair of the venter is a light buff-gray basally, tipped in white, and about 5 to 6 mm. long. The basal portion is darker in more southern forms. Spinous hairs about 7.5 mm. long also occur ventrally and are translucent white. The ventral facial region is similar in color to the ventral body. The tail is dark brown and the tail hairs are the same color and about 2 mm. long. The ventral portion of the tail is almost as dark as the dorsal region. There are about 9 scales per cm.

TABLE 11

MEASUREMENTS (IN MILLIMETERS) AND WEIGHTS (IN GRAMS) OF ADULT *Rattus sordidus sordidus*

Measurement	N	Mean±SE[a]	SD[a]	Range
Head and body length	99	160.80±1.46	14.48	123 -198
Tail length	99	126.22±1.23	12.28	100 -162
Hind foot (s.u.) length	99	29.83±0.16	1.60	25.5-32.4
Ear length (from notch)	105	17.92±0.18	1.84	13-22
Occipitonasal length of skull	126	37.24±0.18	2.02	34.1-43.5
Condylobasal length	132	36.34±0.18	2.06	32.6-42.2
Basal length	131	33.82±0.18	2.09	29.9-39.0
Zygomatic width	130	19.48±0.09	1.06	17.4-22.4
Interorbital width	146	4.85±0.03	0.36	4.1- 5.7
Interparietal length	139	4.26±0.04	0.45	3.0- 5.6
Interparietal width	136	9.61±0.06	0.76	7.1-11.3
Braincase width	137	15.75±0.05	0.58	13.8-17.7
Mastoid width	133	13.62±0.04	0.49	12.4-15.0
Nasal length	136	13.31±0.10	1.23	11.0-17.0
Nasal width	137	4.17±0.04	0.42	3.3- 5.6
Palatal length	143	20.16±0.10	1.24	16.5-23.3
Incisive foramen length	146	7.52±0.05	0.62	6.0- 9.1
Incisive foramina width	146	1.92±0.02	0.24	1.4- 2.6
Inside m^{1-1} width	145	2.73±0.04	0.44	1.8- 3.8
Outside m^{1-1} width	145	7.79±0.04	0.51	6.5- 9.0
Bulla length	141	7.68±0.04	0.49	6.4- 9.4
Crowns m^{1-3} length	147	6.68±0.03	0.40	5.8- 7.9
Alveoli m^{1-3} length	147	7.25±0.04	0.44	6.2- 8.4
Crowns m^{1-2} length	147	5.25±0.03	0.31	4.3- 5.9
M^{1-1} width × 2	145	5.06±0.02	0.28	4.4- 5.6
Body weight	55	117.62±5.53	41.04	50.4-248

[a] SE indicates standard error of the mean; SD, standard deviation from the mean.

The juvenile pelage is dark gray with only a slight amount of buff or rust in the tips of the dorsal hairs. The venter is gray, lighter than the dorsum, with white tips to some of the hairs. The guard hairs are inconspicuous and spines are absent. The feet are a mixture of dark gray and silvery hairs and the tail is dark brown. The appearance of the juvenile *R. s. sordidus* is very similar to that of the juvenile *R. s. colletti* but slightly lighter and grayer. Juveniles begin to acquire their adult pelage when they reach a total length of about 200 mm.

The mammary formula is 3+3=12.

The adult skull is heavy and elongate (fig. 29). The prominent supraorbital-temporal ridging approaches the midline between orbits less than in either *R. s. villosissimus* or *R. s. colletti*. The ridging is conspicuous from the anterior supraorbital region and usually to the posterior limit of the parietals. At the posterior portion of the supraorbital region the ridging is about 0.5 mm. wide and elevated about 0.5 mm. above the skull surface. The interorbital width is greater in *R. s. sordidus* than in the other two subspecies. The molar width is greater than in *R. s. colletti* and about the same as in *R. s. villosissimus*. The bullae are 22.7 per cent of the basal skull length and are relatively longer than in the other two subspecies. The palate terminates 0.5 mm. or less behind the end of the molar row.

The juvenile skull is usually lacking supraorbital-temporal ridging, the cranial region is inflated, and each incisive foramen usually tapers to a slit posteriorly (fig. 32).

PREVIOUS DESCRIPTIVE ACCOUNTS: Morphological accounts have been given by Gould (1858a, 1858d), Collett (1887 under the misnomer *M. greyii*), Ogilby (1892), Lucas and Le Souëf (1909), Thomas (1923c, 1926b), Le Souef and Burrell (1926), McDougall (1936, 1944–

1946), Troughton (1941 and later editions), and Tate (1951). Several of these are but rewordings of earlier descriptions.

The mammary formula was first given by Thomas (1923c). We have found only one exception to the formula of 3+3=12, on a rat from Iron Range (AMNH 153927) that has an extra pectoral teat.

Aspects of the reproductive biology of this form have been presented by McDougall (1944–1946, 1950) and Taylor and Horner (MS).

Colored plates are given in Gould (1858d, pl. 17) and Troughton (1941 and subsequent editions, pl. 19, fig. 6). Sawers (1938, p. 1091, fig. 1) and McDougall (1944 [1944–1946], p. 58, pl. 6) have photographs of the animal, and McDougall (1944 [1944–1946], p. 62, pl. 7) has skull photographs. Misonne (1969, fig. 128) has illustrated upper and lower molar rows.

REMARKS: Both *R. s. sordidus* from the type locality and the "*youngi*" from offshore islands near Brisbane belong to this group. Their bullae equal 20.4 (as estimated from the only measurements we were able to take on these damaged skulls) and 20.8 per cent of the basal length, respectively. The comparable average is 22.7 per cent for the entire *R. s. sordidus* group, 25.7 per cent for *Rattus tunneyi culmorum*, and 18.8 per cent for *Rattus fuscipes assimilis*, the last two being the other groups with which "*youngi*" has been allied. Although "*youngi*" has a glossy pelage similar to that of *R. t. culmorum* and strongly resembles it in many ways, the critical skull features do not fit. The type of "*youngi*" (BM 26.7.1.1) has spinous pelage both dorsally and ventrally. In interorbital width (5.0 mm.), palatal length (20.2 mm.), and length of incisive foramina (7.6 mm.) "*youngi*" is closer to *R. s. sordidus* than to the other subspecies. The extensive grassland areas on these islands are compatible with habitat requirements of either *R. s. sordidus* or *R. t. culmorum.*

Tate (1951) stated that the mammary formula is 2+3=10 for "*youngi*," which he treated as a full species. There is only one female recorded from the islands and we were unable to make out the formula. Our trapping on Stradbroke Island yielded no fresh material.

HABITS AND HABITAT: Although at the time of the original description of *M. sordidus* no mention was made of the habitat from which the specimens were taken except "open plains of Darling Downs" (Gould, 1858a, p. 242), Gould (1858d, text to pl. 17) stated that the collector, Gilbert, found it to be "common on the plains, and is occasionally found on the banks of creeks, and adds, that it mostly feeds on the roots of stunted shrubs." This was the only clue to the habitat of *R. s. sordidus* until Gard [1935 (under the misnomer *R. culmorum*)] published his account of the rat in canefields.

The biology of *R. s. sordidus* received little attention until the rat became an economic pest in Queensland canefields and careful studies of its habits became essential to control methods. Gard characterized *R. s. sordidus* as a burrower that nests underground and favors areas of thick grass. He described the burrows by dimension and form and suggested that the rats shift their burrowing efforts from low to higher ground during rainy periods. He also listed a number of plant species eaten by the rat and used for cover. He found that *R. s. sordidus* has omnivorous tendencies but is primarily a vegetarian.

The extensive study made by McDougall (1944–1946, 1950) of *R. s. sordidus* (=*R. conatus*) in canefields is the most thorough account of the general biology of any Australian rat as it occurs in a cultivated crop. McDougall stated that the rat is found most frequently in areas of friable soil that provide a close ground cover of vegetation. Neither he nor Harrison (1962a) took it in rain forest, but only in cane and grass. McDougall found *R. s. sordidus* to be a poor climber and could never locate a food cache in its burrows. Harrison (1962b) and Woods (1966) have contributed further information regarding the diet of the rat in canefields.

Although considerable work has been done on the biology of *R. s. sordidus* as it occurs in and adjacent to canefields, remarkably little is yet known of the rat in its native environment. Brass (1953) stated that it belongs to a *Rattus* species (*gestri*) that prevails in the drier interior regions of Australia and is rarely present in rain forests. He is no doubt referring to the *gestri* group established by Tate (1951), which includes *R. s. villosissimus* as well as *R. s. sordidus*, for *R. s. sordidus* itself is not an inland rat. It does, however, occur in rain forest situations of a very special nature, as discussed below, and has been trapped there by us and by other collectors.

Rattus sordidus sordidus is mainly a grassland inhabitant. This is clear from the extensive work done on this rat near and in canefields. Its primary vegetation requirement appears to be the close type of ground cover provided by the native grasses. A maturing cane crop offers a similar form of protection, as well as a food source, and *R. s. sordidus* moves easily into such crops, whereas *R. f. coracius* and *R. l. cooktownensis* are, by their ecological dependence on rain forest, barred from entry.

Rattus sordidus sordidus, is, however, not confined to open grassland. It occurs in drier rain forests where the nature of the canopy is sufficiently open that a ground cover of grass can grow, at least in patches, within the forest itself. This type of habitat is prevalent from Cooktown northward where tongues of rain forest follow watercourses down into the lowlands from the central highland ridge of Cape York. The rain forest abuts savanna woodland and *R. s. sordidus* seems to abound in the transitional zone (fig. 33). In fact, in the northern part of its range, at least, we found it to be largely confined to this zone. Some plants of this zone in the vicinity of the Jardine River are *Acacia leptocarpa* (Leguminoseae), *Melaleuca hakeoides* (Myrtaceae), *Banksia dentata* (Proteaceae), and *Schoenus sparteus* (Cyperaceae).

In areas of dense rain forest, such as that on the Atherton Tableland, *R. s. sordidus* occurs in grassy areas at the margins of the forests and along road cuts, but we never trapped it in the forest itself. On the Atherton Tableland it has been taken at an altitude of 3400 feet at Walsh Camp. It follows the wetter grasslands of the tropical and subtropical zones in Queensland.

SYMPATRY: Throughout most of its range *Rattus sordidus sordidus* is sympatric with *Rattus tunneyi culmorum*. In the north it is sympatric with *Rattus leucopus leucopus*, in the Atherton Tableland area with *Rattus leucopus cooktownensis*, *Rattus*

FIG. 33. Habitat of *Rattus sordidus sordidus* at creek near the Dulhunty River, Cape York, Queensland. Photographed July 21, 1964.

fuscipes coracius, and probably *Rattus lutreolus lacus*, and in the south with *Rattus fuscipes assimilis* and *Rattus lutreolus lutreolus*.

TAXONOMIC HISTORY: After the original description of *Mus sordidus* by Gould (1858a) and his subsequent account of its habitat preference (Gould, 1858d), little of an informative nature was published under the name *M. sordidus*. In the next century Thomas (1923c) described another species, *R. conatus*, and, although he allied it to *R. colletti*, he made no direct comment regarding its possible affinity to *R. sordidus*. Le Souef and Burrell (1926) referred to *R. sordidus* but never mentioned *R. conatus*. At this time Thomas (1926b) described another species, *Rattus youngi*, from Moreton Island and allied it to *R. assimilis*.

Iredale and Troughton (1934) listed *R. sordidus*, *R. conatus*, and *R. colletti* in their check list, calling *R. conatus* the Annam River rat, a misspelling of Annan River which Troughton carried through all editions of his book (1941–1967). In the checklist they treat *R. youngi* as a subspecies of *R. culmorum*.

Gard (1935) was the first to describe the damage that *R. s. sordidus* inflicts on canefields. He called this "field rat" *R. culmorum* as advised by Troughton. In the same year Raven (1935) listed all the above forms but ascribed the wrong date to the description Gould had made of *R. sordidus*.

McDougall (1936) who, like Gard, relied on Troughton's identification of the "field rat," made an extended description of *R. s. sordidus* under the name *R. culmorum*. Troughton (1939) corrected his error and in both this paper and an earlier one (1937b) made the point of distinguishing *R. sordidus* from *R. lutreolus*. In the latter paper he went on to suggest that "*conatus*" is a northern race of the "lost" *R. sordidus* of southern Queensland. However, for reasons of "simplifying field investigations and the tabulation of research" (1939, p. 279), he retained *R. conatus* as a full species. Later, Troughton (1941 and subsequent editions) suggested that both *R. conatus* and *R. colletti* may be geographical races of *R. sordidus*, but he still retained them as separate species.

Ellerman (1949) treated *R. sordidus* as a catch-all group for all Australian *Rattus* with large bullae. The forms he allied as subspecies of *R. sordidus* were not only *R. colletti* and *R. conatus* but also *R. tunneyi*, *R. woodwardi*, *R. culmorum*, *R. melvilleus*, *R. culmorum vallesius*, and questionably *R. culmorum austrinus* and he also included a New Guinea form, *R. gestri*. He excluded *R. villosissimus* from the species *R. sordidus* but placed it as a close ally. He was not satisfied with his placement of *R. woodwardi* under *R. sordidus* and suggested that it might be a distinct species. *Rattus youngi* he placed as a subspecies of *R. fuscipes*.

Tate (1951) went to the opposite extreme. He treated *R. sordidus* in a very restricted sense, placing no other subspecies within it but suggesting that it might be the southern counterpart to *R. lacus*. Under the species *R. gestri* Tate placed not only two New Guinea subspecies but also *R. conatus*, *R. colletti*, and *R. culmorum apex*. His judgment concerning *R. c. apex* must have been based largely on a misidentified series of specimens in the Archbold Collection rather than on the type specimen described by Troughton (1939). We have since examined the same material and find that all "*apex*" in the Archbold Collection is *R. s. sordidus* and not Troughton's *R. culmorum apex*. Tate regarded *R. youngi* as a full species and placed *R. c. vallesius* as a subspecies of it.

Brass (1953) recognized that *R. s. sordidus* (under the name *R. gestri*) was a close relative of the "plague-rat" (*R. s. villosissimus*).

As in 1941, Troughton (1941–1967, Ninth edition) continued to treat *R. colletti* and *R. conatus* as full species, suggesting a close relationship with *R. sordidus*. This time, however, he put forth a little more strongly the suggestion that *R. sordidus* may be linked with *R. lutreolus* and even italicized and unduly emphasized the collector's statement that *R. sordidus* frequented the banks of creeks. In actual fact, Gilbert had said, "it is common on the plains, and is occasionally found on the banks of creeks" (Gould, 1858d, text to pl. 17), a habitat note that is much more applicable to *R. sordidus* than to *R. lutreolus* when read in its original form. Troughton did not elucidate his views regarding the relationship of *R. conatus* and *R. lutreolus* to *R. sordidus*. The posterior cusps of m_1 and m_2 that Troughton (1920) indicated were absent on mainland *R. lutreolus* are present on the type specimen of *R. s. sordidus* and its topotypes, but Troughton has never made reference to them in this context. In his assessment of *R. lutreolus* Troughton (1941–1967, Ninth edition, p. 283) claimed that *R. sordidus* "may represent an intermediate race of *lutreolus*" and that *R. lacus* is "evidently the northern race of *lutreolus*." Again, he treated *R. youngi* as a subspecies of *R. culmorum*.

Kirkpatrick (personal commun.), who has done extensive mammal collecting in the Darling Downs within the last decade, has never trapped *R. s. sordidus*; nor did we take it in our very limited time there. He suggested that perhaps Gilbert collected *R. sordidus* near Westbrook in the Darling Downs (Kirkpatrick, 1966).

We treat *R. conatus* (type, BM 23.1.5.15♀, from Annan River) and *R. youngi* (type, BM 26.7.1.1♂, from Cowan Cowan) as synonyms of *R. s. sordidus*, and, as expressed previously (Taylor and Horner, 1967), view *R. lutreolus* as separable from *R. sordidus* at the species level.

Rattus sordidus villosissimus (Waite)

Mus longipilis GOULD, 1854, text to pl. 13.
Mus villosissimus WAITE, 1898, p. 125.
Rattus villosissimus profusus THOMAS, 1921b, p. 620.
Rattus villosissimus villosissimus TATE, 1951, pp. 351–352.

HOLOTYPE: Skin and incomplete skull with hind portion missing, sex unknown, AM 62, collected by Thomas Wall, ?Victoria River, southwestern Queensland, in 1847.

DISTRIBUTION: *Rattus sordidus villosissimus* occurs only west of the Great Dividing Range, its closest approach to the Range being the Liverpool Plains in the south and the Hughenden area in the north. The greatest numbers of records are from western Queensland. It is not known to occur on the west side of Cape York Peninsula but does occur at its west base in the Normanton area. It ranges throughout western Queensland and in the Northern Territory to as far north as Katherine and as far west as Humbert River Station. The southernmost locality is cave deposit material about 100 years old (Mahoney, personal commun.) from Weekes Cave on the Nullarbor Plain (in the private collection of Hans Micham of the South Australian Museum and registered as H. M. 10). There are no published records within the boundary of Western Australia. The known filtrations of *R. s. villosissimus* into New South Wales are poorly represented. The distribution of *R. s. villosissimus* (fig. 28) is based solely on data from museum specimens and does not account for unsubstantiated reports. In times of high population its distribution is undoubtedly less restricted than that presented here.

MEAN MEASUREMENTS (IN MM.): External: head and body 173; tail 147; hind foot (s.u.) 33.5; ear (from notch) 20. Skull: occipitonasal length 41.2; braincase width 16.3; bulla length 8.2; crowns m^{1-3} length 7.0. (See table 12 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 36.9 or less.

DESCRIPTION: This rat is the largest of the three subspecies, and the tail, hind feet, and ears are all relatively longer. The dorsal pelage is predominantly buffy gray with blackish penciling. The buff portion is less tinted with orange than in the two other subspecies and lacks warmth of color. The shorter hairs are gray at the base for about 9 to 12 mm., a lighter gray than in the other two subspecies, and the terminal 2 mm. is buff. Finlayson (1939a) measured these hairs to 20 mm. The guard hairs are black or dark brown and measure to 52 mm. long. Finlayson (1939a) measured them to 60 mm. They are conspicuous over the entire dorsum and especially prominent in the rump region. The spines are about 18 mm. long and occur at a density of about 1 per 2 mm., but this may vary considerably. The basal portion is translucent grayish white grading to dark brown or black distally for the last 7 mm. The dorsal pelage is softer and denser in the southern specimens taken from a less arid environment, such as Liverpool Plains, and is also darker in color. Spines are absent. The main body hairs measure more than 22 mm. long and the guard hairs more than 50 mm. (Thomas, 1921b) on the Liverpool Plains rats. The basal gray is also considerably darker. The upper facial portion is the same color as the dorsal body. The muzzle vibrissae are mostly dark, a few lighter ones below. There may be a small white spot on the light gray undersurface of the face. The ears have buff to rust-colored hairs and blend with the dorsum. The feet are light and covered with silvery white hairs. In specimens from less arid environments the feet are considerably darker. The ventral body is light gray. The predominant hairs are gray at the base (darker in the less arid environments) and are tipped with white. They are about 8 mm. long. A few spines may be present. If so, they are generally white and about 10 mm. long. There is a subtle blending in the ventrolateral region of the body between the

TABLE 12

MEASUREMENTS (IN MILLIMETERS) AND WEIGHTS (IN GRAMS) OF ADULT *Rattus sordidus villosissimus*

Measurement	N	Mean±SE[a]	SD[a]	Range
Head and body length	40	173.12± 3.19	20.16	138–223
Tail length	40	146.70± 2.12	13.42	122–190
Hind foot (s.u.) length	40	33.48± 0.37	2.35	29–39
Ear length (from notch)	48	20.40± 0.21	1.45	16–22
Occipitonasal length of skull	108	41.23± 0.21	2.16	37.0–45.0
Condylobasal length	121	40.17± 0.20	2.19	35.4–44.5
Basal length	121	37.49± 0.20	2.17	32.7–41.6
Zygomatic width	112	20.54± 0.10	1.01	18.2–22.8
Interorbital width	136	4.74± 0.02	0.28	3.8– 5.4
Interparietal length	128	4.37± 0.04	0.39	3.5– 5.6
Interparietal width	121	9.84± 0.05	0.54	8.3–11.8
Braincase width	123	16.28± 0.05	0.57	14.8–17.6
Mastoid width	113	14.16± 0.05	0.54	12.6–15.4
Nasal length	115	14.90± 0.10	1.04	12.5–17.1
Nasal width	117	4.15± 0.04	0.39	3.3– 5.2
Palatal length	130	22.00± 0.11	1.25	19.2–24.8
Incisive foramen length	134	8.31± 0.06	0.66	6.7–10.0
Incisive foramina width	130	2.06± 0.02	0.26	1.5– 2.7
Inside m^{1-1} width	131	2.88± 0.03	0.38	1.7– 4.0
Outside m^{1-1} width	131	8.04± 0.04	0.42	6.9– 9.2
Bulla length	126	8.20± 0.04	0.41	7.1– 9.2
Crowns m^{1-3} length	138	6.99± 0.03	0.39	6.0– 8.0
Alveoli m^{1-3} length	136	7.70± 0.04	0.45	6.5– 8.9
Crowns m^{1-2} length	139	5.48± 0.03	0.34	4.7– 6..3
M^{1-1} width×2	131	5.16± 0.02	0.28	4.3– 53
Body weight	19	167.26±11.52	50.22	105–288

[a]SE indicates standard error of the mean; SD, standard deviation from the mean.

darker coloration above and the lighter tones below. The tail is dark brown to blackish on all specimens we have seen and in lighter animals contrasts sharply with the dorsal body color. The tail hairs are usually more conspicuous than in other subspecies of *R. sordidus* and the dark hairs are about 2.5 mm. long.

The pelage of juveniles is approximately the same color as that of the adults. It lacks spines and the long guard hairs; the venter is slightly grayer than in the adult.

The mammary formula is $3+3=12$.

The skull averages longer than in the other two subspecies. The supraorbital-temporal ridging is very prominent and the two ridges approach each other closely at the interorbital region. They continue posteriorly through the length of each parietal. At the posterior portion of the supraorbital region each ridge measures about 0.5 mm. wide and as much as to 0.6 mm. above the skull surface. The palate is longest in this subspecies of *R. sordidus* and usually terminates behind the posterior limit of the molar row, but this is variable. The skull is elongate as in the *R. fuscipes* group, but much heavier in appearance (fig. 30). The incisive foramina are straight or slightly hourglass-shaped and average longer than in the other two subspecies. The bulla and the molar row are also longer in this form, although in relative length both features are greater in *R. s. sordidus*. The bullae of *R. s. villosissimus* are 21.9 per cent of the basal skull length, and they exceed the alveoli m^{1-3} length by about 0.5 mm.

The juvenile skull has an inflated cranial region, the supraorbital-temporal ridging is absent or barely discernible, and the incisive foramina taper posteriorly in a more conspicuous fashion (fig. 32).

PREVIOUS DESCRIPTIVE ACCOUNTS: The morphology of *R. s. villosissimus* has been described by Gould (1854), Ogilby (1892), Waite (1898), Thomas (1921b), Le Souef and Burrell (1926), Finlayson (1939a), Troughton (1941 and subsequent editions), and Tate (1951). Of these, the most extensive description is that made by Finlayson (1939a) of fresh specimens from the Lake Eyre Basin. He compared fresh pelage coloration with that from wet-preserved material and demonstrated that the latter turns to a warm brown suffusion of color. He erred in the mammary formula, and it is also surprising that he made no mention of the spines, unless they were absent in his material.

The mammary formula was erroneously given by Waite (1898) as $2+3=10$ and correctly stated by Tate (1951) as $3+3=12$.

Certain aspects of the reproductive biology of this subspecies are given by Taylor and Horner (MS).

Colored plates of *R. s. villosissimus* are given in Gould (1854, pl. 13) and Troughton (1941 and subsequent editions, pl. 19, fig. 8). Misonne (1969, fig. 127) has illustrated upper and lower molar rows. A photograph of the living animal appears in CSIRO Wildlife Research Report (1966–1968, p. 48).

REMARKS: White pectoral spotting occurs in a few rats (e.g. MVZ 133929) but is not common as it is on *R. f. coracius*. There are two cases of albinos among museum specimens [QM J6726 and QM J6725 (skull only but albinism indicated on tag)], both from Boulia.

HABITS AND HABITAT: Almost all the information on the habits and habitat of *R. s. villosissimus* comes from times when these rats are in vast numbers, the so-called plague condition (Cleland, 1918; Finlayson, 1939b; Crombie, 1944). Virtually nothing is known about where they occur in the more common nonplague situations between population outbreaks.

Rattus sordidus villosissimus is an inhabitant of the grasslands where the annual rainfall is generally below 30 inches (fig. 34). In times of high density its burrows are readily found in tussocks of Mitchell grass (*Astrebla*) and distinct runways are evident between tussocks (Dunnet, 1956). It is as much a burrower in the arid

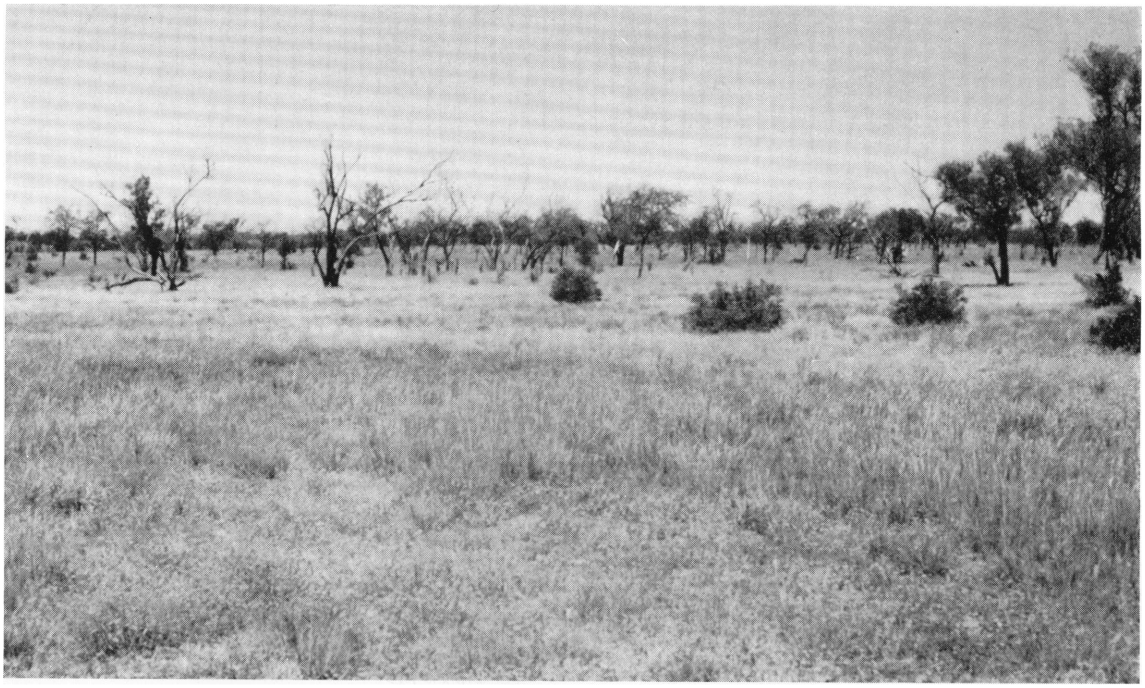


FIG. 34. Habitat of *Rattus sordidus villosissimus* on Brunette Downs Station, Barkly Tableland, Northern Territory. The dominant grass is Mitchell grass (*Astrebla pectinata*). This area is permanently occupied by the rat, and at the time the photograph was taken it was present in moderate numbers. Photographed by L. S. Hall March, 1968.

grassland environment as *R. s. sordidus* is in the moister grasslands of the east coast. *Rattus sordidus villosissimus* also forms burrows in open patches of soil and up to 300 burrows per acre have been recorded in times of plague (Dunnet, 1956). Finlayson (1939a) stated that the resident population of this rat in the Lake Eyre region forms long burrows near the base of sandhills that may invade the hill 10 feet or more at a depth of 3 to 4 feet below surface. In these recesses the microclimate is cool even though the burrow entrance is kept open throughout the day. He stated that they do not burrow on claypans or in gibber plains. In times of plague, *R. s. villosissimus* traverses habitats that are frequently incompatible both in scarcity of vegetation and soil friability. At plague times this rat, which is normally nocturnal, becomes the prey of diurnal predators (Dunnet, 1956; Hall, 1959) when presumably some of the rats are forced from their burrows because of overcrowding.

Rattus sordidus villosissimus is primarily a vegetarian. In an analysis of its fecal pellets Watts (1970) found seeds, insects, and green plant material, the proportion of water-rich food being greater than in the diet of the pseudomyine rodents inhabiting the same desert area. When population density is high, the rat has been known to attack root systems of grass and even bark of large trees (Troughton, 1941 and subsequent editions). It is also cannibalistic in times of plague (Gould, 1854) and is an effective predator of other murids and possibly ground birds as well (Finlayson, 1939a). Its invasion of cultivated crops together with its consumption of native pasture crops, has made this rat even more of an economic problem. In the past few decades sorghum has been planted more and more extensively to supplement the fodder yield of native pastures of inland Queensland, a situation that has ameliorated considerably the local conditions for *R. s. villosissimus*. Today, when *R. s. villosissimus* is in low density and not to be found in its native habitat by conventional trapping methods, the rat can often still be trapped in sorghum fields. This rat will also invade crops of oats.

The geographical distribution of *R. s. villosissimus* has never been clearly defined. How much its former range has been affected by extensive sheep and cattle grazing is unknown. It certainly seems to have contracted from the south and southeast. Liverpool Plains about the time *R. s. villosissimus* was collected there was a region of thick and luxuriant vegetation and the soil a "rich black mould" [Parry, 1963, p. 166 (description by Sir W. E. Parry in 1832)]. Our visit to the same area in 1964, took us through eroded, dry, undulating grasslands with the vegetation nipped down to within an inch or two of the ground by the close grazing of sheep. As late as 1929, however, a specimen was recorded less than 200 miles northwest of the Liverpool Plains, at Barwon Vale, Walgett (AM S2084). The Great Dividing Range appears to present an ecological impediment to its eastward migration.

SYMPATRY: *Rattus sordidus villosissimus* is sympatric with *Rattus tunneyi tunneyi* on the Sir Edward Pellew Group of islands and probably at numerous other localities not yet recorded. It is or was sympatric with *R. t. tunneyi* in the Alice Springs–Tennant's Creek region. *Rattus sordidus villosissimus* is probably sympatric with *Rattus tunneyi culmorum* in the western distribution of the latter, for they are known within 100 miles of each other in northeastern New South Wales.

TAXONOMIC HISTORY: Seventeen years after Gould described *Mus longipilis*, Krefft (1871) presented the view that it was probably the same as the earlier-described *Mus vellerosus*. No one has since supported Krefft's suggestion.

Palmer (1885) described a population outbreak of a rat of the western and northwestern plains of Queensland in the years 1869 and 1870. He suggested that it most closely resembled the brown rat, *Mus decumanus* (=*Rattus norvegicus*), but he did not appear to recognize this indigenous form as *M. longipilis*. This seems to be the first account of any aspect of the biology of *R. s. villosissimus* under plague conditions.

In 1887 Bennett gave an account of a rat that occurred in plague proportions in southwestern New South Wales between, and west of, Booligal to Wilcannia. He identified the rats as belonging to a species described by Ramsay (1882) as *Mus tompsoni*. *Mus tompsoni*, however, was later synonymized under *Rattus rattus* (McCulloch, 1907). At that time *R. s. villosissimus* was often mistaken for *R. rattus* or *R. norvegicus*. Unfortunately, Bennett (1887) gave virtually no description of the rats he witnessed in the plague, but his brief habitat notes suggest that the rat plague was indeed of *R. s. villosissimus* and not of *R. rattus*. He referred to their ground burrows and utilization of rabbit burrows, and he also stated that prior to their appearance in this region they had occurred in western Queensland. *Rattus sordidus villosissimus* is typically a ground dweller that burrows extensively, whereas *R. rattus* is a semiarboreal form. Great numbers of *R. s. villosissimus* have been recorded from western Queensland both before and since, but there is no authoritative account of *R. rattus* in plague proportions in this region. Another line of evidence that suggests that the rats Bennett witnessed were *R. s. villosissimus* is given in his account of rabbiters attempting to pass off the skins of these rats as young rabbit skins. The general coloration of *R. s. villosissimus* and the wild European rabbit, *Oryctolagus cuniculus*, is not dissimilar, whereas *R. rattus* is a more solid color than agouti, either black or grayish brown dorsally and often with a sharply contrasting white belly.

After Waite (1898) pointed out the preoccupation of the name *M. longipilis*, the rat has usually been known as *Rattus villosissimus*.

Thomas (1906b) added to the known range of *R. s. villosissimus* by recording a series of specimens taken at Alexandria in the southeastern portion of the Northern Territory. He was also responsible for adding a subspecies to *R. villosissimus*, *R. v. profusus* (Thomas, 1921b). Jones (1925) listed *R. villosissimus* as a *Rattus* that probably occurs in South Australia, but declared it a rare animal which may be threatened to extermination by the introduced fox.

Le Souef and Burrell (1926) listed *R. villosissimus* (including *R. v. profusus*) but their descriptions were only slight rewordings of the originals. Iredale and Troughton (1934), Raven (1935), and Troughton (1941 and subsequent editions) also listed these forms.

Finlayson (1939a), finding that *R. villosissimus* was still a poorly understood form and frequently misidentified as *R. rattus* or *R. norvegicus* in times of plague, made a thorough and highly informative description of the physical characters and habits of this animal based on a series of specimens he obtained from the Lake Eyre Basin. He was the first to question the type locality of *R. villosissimus*, which until 1939 had been generally stated to be the Victoria River. Ogilby (1892) had put a question mark after the locality but had given no explanation of its significance. Gould, in his original description of *Mus villosissimus*, gave no locality data but said only that it was taken by "Mr. Thomas Wall, during his expedition to the Victoria River, on a desert which abounded with these animals" (Gould, 1854, text to pl. 13). Krefft (1871) had been the first to state that the type locality was the Victoria River and this must have been only an assumption. Trouessart (1897) also stated this, as did Thomas (1906b). Furthermore, Thomas (1906b, p. 537) pinpointed the Victoria River as being about, "400 miles to the west of Alexandria," which would locate it in the northwestern section of the Northern Territory where there is a river by that name. Thomas (1921b) later corrected this error and stated that the Victoria River was the Barcoo that runs into Lake Eyre Basin. This places the type locality in southwestern Queensland. The entire route taken by Kennedy's Expedition into central Australia is mapped in his journal (Kennedy, 1852), and, although he mentioned a few specimens that Wall had preserved, he did not refer to the collection of rats. The type specimen (AM 62) bears the locality "Victoria River, Northern Territory," but as the expedition did not cross into the Northern Territory it seems likely that the label was marked according to the error in geographical designation made by Thomas (1906b). It should be noted, too, that although the Victoria (Barcoo) river system runs into the northeastern section of South Australia, the Kennedy Expedition turned back short of the border. Hence, if the type specimen was taken on the Victoria River, it would have come from some portion of the river system in southwestern Queensland.

Until the time that Finlayson cast doubt on the type locality, other workers followed Thomas (1921b) in assuming it was the Victoria River, known otherwise as the Barcoo River or Cooper's Creek. Finlayson (1939a), however, suggested that the *R. villosissimus* type locality might just as well have been in northwestern New South Wales en route to the Victoria River. In essence what Finlayson pointed out at the time, and to the present date has not been resolved, is that the type locality of *R. villosissimus* has really not been pinpointed. It must be along the portion of the Kennedy Expedition route between northwestern New South Wales and southwestern Queensland southeast of or at the site of the Victoria or Barcoo River. For lack of better evidence, we refer to the locality of these earlier specimens with query as did Ogilby: ?Victoria

River (=Barcoo or Cooper's Creek), southwestern Queensland.

Both Thomas (1921b) and Finlayson (1939a) commented about the great variability of the skull dimensions in *R. villosissimus*, a problem that Finlayson (1939a) believed was in part due to the difficulty of determining maturity in this rat. In his paper Finlayson noted the several differences between his series from the Lake Eyre Basin (exclusive of the northwest drainage area) and the material measured by Waite (1898) from west of the Basin. In 1941 Finlayson remeasured Waite's skulls and found the discrepancies still to exist, but to a lesser extent. Ellerman (1949) regarded *R. villosissimus* as a distinct species although he recognized its affinity to *R. sordidus*.

Tate (1951) included *R. profusus* under the species *R. villosissimus*, but he expressed some doubt as to whether *profusus* differs significantly from the nominate subspecies. He was the first to record accurately the mammary formula of *R. villosissimus*.

We treat *R. s. villosissimus* as a subspecies of *R. sordidus* and we find no grounds to retain *R. v. profusus* (type, BM 14.1262♂, from Liverpool Plains) as a distinct subspecies.

Rattus sordidus colletti (Thomas)

Mus colletti THOMAS, 1904a, p. 599.
Rattus gestri colletti TATE, 1951, pp. 350–351.

HOLOTYPE: Skin and incomplete skull with part of occipital region, right bulla, and part of right zygoma missing, adult female, BM 4.4.4.4, collected by J. T. Tunney, August 30, 1903, South Alligator River, Northern Territory.

DISTRIBUTION: *Rattus sordidus colletti* is known from only four localities, all of which are on the coastal flood plains of the Northern Territory, or river systems that empty into these plains. It appears to be one of the most geographically restricted subspecies of *Rattus* in Australia (fig. 28).

MEAN MEASUREMENTS (IN MM.): External: head and body 161; tail 125; hind foot (s.u.) 30.1; ear (from notch) 19. Skull: occipitonasal length 37.0; braincase width 15.2; bulla length 7.2; crowns m^{1-3} length 6.3. (See table 13 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 34.0 or less.

DESCRIPTION: *Rattus sordidus colletti* joins *R. s. sordidus* in having the tail and hind foot relatively shorter than in *R. s. villosissimus*. It is the darkest of the three subspecies. The pelage is harsh and spinous on the adults. There is a dull gray underfur of about 9 mm. long that is barely evident on the dorsum without parting the hairs. Three types of hair give the dorsum its color: the first type is coarse and relatively short, about 11–15 mm. long, dark brown or black basally, and tipped with yellowish buff for the last 2.5 mm. This hair gives the animal its grizzled appearance. The second type is guard hairs about 35 mm. long, all black and not so coarse as the first type. The third type is spines that are buffy gray basally for about 7 mm. and black distally for about 5.5 mm. They are closely spaced at about 1 mm. apart, or less, as they emerge from the dorsal skin. The hairs tend to be the same length in the rump region as on the middorsum, although the guard hairs are far more conspicuous on the rump. The grizzled effect of the yellow-buff and black is even in tone over the entire head and dorsum. Between the eyes and on the remainder of the head there is a mixture of coarse shorter hair (6 mm.) and fine fur (3 mm.). The middorsal region is somewhat darker and in some cases suggests a middorsal band about 15 mm. wide extending from the lower thoracic region to the rump. The ears are sparsely covered by yellow-buff hairs and are an over-all dark brown that blends with the dorsal coloration. The muzzle vibrissae are all black and are up to 42 mm. long. The ventral body fur is gray tinged with buff and there is usually a yellowish buff interzone between the dorsum and the venter. The ventral coloration lightens in the chin area. On some individuals the venter is conspicuously tinged with a reddish rust. A short, fine fur 3 to 6 mm. long that is medium gray tipped in white occurs on the ventral surface. Ventral spines are white, or buffy in more lateral positions, and are about 7.5 mm. long. Between the forelegs and in the throat area the fine fur may turn to rust to form a conspicuous reddish buff patch. The spines in this area, however, remain white. The feet are clothed in a mixture of silvery and dark brown hairs and they are slightly lighter in color than the dorsum. The outer parts of the legs are like the dorsum in color and the inner portions are the color of the venter. The tail is dark and is covered with dark brown or black hairs about 3 mm. long. The tail has a hairy appearance,

TABLE 13

Measurements (in Millimeters) and Weights (in Grams) of Adult *Rattus sordidus colletti*

Measurement	N	Mean ± SE[a]	SD[a]	Range
Head and body length	26	161.38 ± 2.39	12.19	144–195
Tail length	26	125.12 ± 2.10	10.73	104–145
Hind foot (s.u.) length	26	30.11 ± 0.30	1.55	26.7–33
Ear length (from notch)	29	18.87 ± 0.20	1.09	17–21
Occipitonasal length of skull	29	37.03 ± 0.36	1.97	34.3–42.0
Condylobasal length	28	35.88 ± 0.38	2.03	32.9–40.8
Basal length	27	33.42 ± 0.40	2.06	30.2–38.3
Zygomatic width	33	18.57 ± 0.15	0.85	16.9–20.7
Interorbital width	36	4.69 ± 0.04	0.25	4.2– 5.2
Interparietal length	32	4.05 ± 0.08	0.44	3.0– 4.8
Interparietal width	31	9.65 ± 0.09	0.49	8.4–10.6
Braincase width	32	15.15 ± 0.09	0.51	14.3–16.8
Mastoid width	29	13.17 ± 0.09	0.51	12.1–14.7
Nasal length	33	12.92 ± 0.18	1.05	11.3–16.0
Nasal width	34	3.83 ± 0.06	0.34	3.2– 4.9
Palatal length	35	19.66 ± 0.18	1.07	18.0–22.8
Incisive foramen length	35	7.46 ± 0.11	0.64	6.3– 9.2
Incisive foramina width	35	1.91 ± 0.04	0.22	1.6– 2.5
Inside m^{1-1} width	36	2.70 ± 0.06	0.35	1.9– 3.2
Outside m^{1-1} width	36	7.32 ± 0.06	0.38	6.6– 8.0
Bulla length	31	7.19 ± 0.07	0.40	6.5– 7.9
Crowns m^{1-3} length	36	6.32 ± 0.04	0.25	5.8– 6.7
Alveoli m^{1-3} length	36	6.96 ± 0.05	0.33	6.3– 7.5
Crowns m^{1-2} length	36	4.99 ± 0.04	0.26	4.4– 5.6
M^{1-1} width × 2	36	4.61 ± 0.04	0.27	4.0– 5.7
Body weight	15	123.71 ± 10.13	39.25	85.5–215.2

[a] SE indicates standard error of the mean; SD, standard deviation from the mean.

relative to most other Australian *Rattus*, as does that of *R. s. villosissimus* and, to a lesser extent, *R. s. sordidus*. There are nine scales to the cm. The tail is uniformly colored, and the hairs are mostly brown rather than a mixture of brown with black.

The juvenile pelage is also very dark dorsally, but there is only a faint suggestion of yellowish buff tips to the dorsal hairs. The pelage lacks spines and the guard hairs are inconspicuous except occasionally in the rump region. The fine gray fur of the dorsum is about 5 mm. long, and longer, also fine hairs are 7 mm. long, gray at the base, and tipped for 1 mm. with reddish or yellowish buff. The feet, covered with a mixture of blackish and some silvery buff hairs, are darker than those of the adult and the same color as the tail. The pinnae are finely covered with brown short hairs on the outside and reddish buff hairs on the inner surface. The ears are the same color as the dorsum. The venter is sooty to light gray. It has short gray fur and slightly longer all-white fur. Some of the short gray fur is tipped in white. The juvenile pelage begins to be replaced by adult pelage when the rat is about 200 mm. in total length.

The mammary formula is $3+3=12$.

The supraorbital-temporal ridges are very conspicuous, especially above the orbit and lessen to some degree as they expand on the parietals (fig. 31). They are still prominent, however, to the posterior limits of the parietals. At the posterior supraorbital region they measure 0.5–0.6 mm. wide and about 0.5 mm. high from the surface of the cranium. The almost straight-sided incisive foramina terminate in line with the first loph of m^1. Some animals have slightly tapering foramina and some have ones that are slightly hourglass in shape. The palate in most cases terminates in line with the posterior limit of the molar row. The bullae are elongated, but are relatively shorter than in either *R. s. sordidus* or *R. s. villosissimus*. They equal 21.5 per cent of the basal length of the skull. The molars are narrower and the molar row is shorter than in the other two subspecies.

In the juvenile skull the incisive foramina narrow posteriorly to a greater degree than seen in any adult skull, but not to the degree that occurs in *R. lutreolus*. The supraorbital-temporal ridging is lacking or barely discernible. The cranium is inflated (fig. 32).

PREVIOUS DESCRIPTIVE ACCOUNTS: Thomas (1904a), Le Souef and Burrell (1926), Troughton (1941 and subsequent editions), Tate (1951), and Johnson (1964) have given morphological accounts of *R. s. colletti*. They are all brief, except for the original description (Thomas, 1904a), and somewhat repetitive.

The mammary formula was given by Thomas (1904a) in the original description of the rat, and we have found only one deviation from his figure. MVZ 133579 has five right and four left pectoral teats along with three pairs of inguinal teats, or a total of 15 teats.

Aspects of the reproductive biology of *R. s. colletti* are given by Taylor and Horner (MS).

REMARKS: Johnson (1964) examined one topotype (USNM 141483) and commented that he was in agreement with the original description except that the pelage is soft and the color of the feet is darker. We have re-examined this specimen and it is a juvenile. The features mentioned by Johnson are characteristic of juveniles but are not carried into adulthood.

HABITS AND HABITAT: Prior to our interest in and subsequent collecting of *R. s. colletti*, the rat was known from 35 museum specimens, 10 of which were unweaned young. The notes of the habits and habitat of this species were negligible at the time we began to investigate this form in the field. To the collectors J. T. Tunney and G. H. Wilkins we owe what little is known about *R. s. colletti*. Tunney found the rat in holes in the ground in the vicinity of the head of tidal waters of the South Alligator River. He stated that the type specimen was "dug out of hole in open clay flats" (Thomas, 1904a, p. 599). Wilkins trapped a specimen "in grass in dry swamp" (BM 26.3.11.156 label data) at King River in the north coastal part of the Northern Territory.

Since there are two King rivers along the route that Wilkins took in 1924 (Wilkins, 1929) there has been some confusion as to which site is the proper locality of a number of mammals collected at King River. Thomas (1926a) claimed that the type specimen of the rock wallaby, *Petrogale venustula*, came from the more southern King River, a tributary of the upper Daly River. Johnson (1964) pointed out that Thomas had erred and that *P. venustula* actually came from the more northern river. As *P. venustula* was collected November 4 and *R. s. colletti* on October 30 and November 7, Wilkins must have collected *R. s. colletti* in the same vicinity as the rock wallaby (the southern King River is 200 miles distant). J. E. Hill (personal commun.) who has re-examined for us the original collector's numbers, found that Wilkins used consecutive numbering of the specimens he took on the north coast and that specimens 650 to 694 (except 661 to 667 and 690 that were mainly from Milingimbi, Crocodile Island) came from "near King River." All *R. s. colletti* field numbers fall within this span. Hence, the *R. s. colletti* collected by Wilkins are indeed from the northern King River, a coastal lowland habitat that is compatible with the ecology of this rat in other localities.

Our experience with *R. s. colletti* although very limited adds considerably to the information known about this rat. It is an inhabitant of the coastal plains. In 1953 the Northern Territory Administration began a pilot study of rice cultivation in one of these coastal plains. Since then *R. s. colletti* has on occasion become an economic pest when it invades the fields and eats the stems of growing rice (D. Tulloch, personal commun.). In certain years these rats are so numerous, particularly during February and March, that they are known to run ahead as one walks through the rice fields (D. Tulloch, personal commun.). When we trapped at the Coastal Plains Research Station at Humpty Doo the rats were not so plentiful, but we had no trouble in obtaining ample numbers. Although almost all the crop had been harvested, the rats were still occupying the embankments between rice fields (fig. 35), which were riddled with rat holes. One could locate five or six holes with each pace. These embankments were covered by dry grass about a foot tall at the time we trapped and the rats could move readily through it without being seen from above. The soil composing these embankments was extremely friable, made more so because the dikes were

FIG. 35. Habitat of *Rattus sordidus colletti* in the rice fields at Humpty Doo, Northern Territory. Photographed June 7, 1964.

man-made and continually reworked. The burrows were not dissected out to determine their extent and form, but because of the high-water table they could not have been more than 2 or 3 feet deep. These nocturnal animals are probably forced out into daylight only when disturbed by man or at peak times of population density. Stomach contents indicated a primarily vegetarian diet.

Adjacent to the rice fields at Humpty Doo are abandoned rice fields and native coastal plains. Although most of the rats we trapped came from the active rice fields, we did trap one *R. s. colletti* in the black-soil coastal plains itself. Runways here were not conspicuous, even though the vegetation was thick. Rat holes were relatively infrequent and other evidence of the presence of rats was also scarce. At present *R. s. colletti* is still considered only a minor pest of the rice fields, although in 1961 it was so numerous that some of the rice could not be harvested owing to the damage inflicted by the rat (G. Letts, personal commun.).

Like both *R. s. villosissimus* and *R. s. sordidus*, *R. s. colletti* is an excellent burrower, is found in a grassland environment, and has a pungent odor (adult males, particularly). Despite systematic trapping at both Humpty Doo and in numerous other localities in the northern coastal regions of the Northern Territory, we found *R. s. colletti* absent from both open forests and grasslands of the Koolpinyah and Marrakai land systems (Christian and Stewart, 1952). All evidence to date suggests that it is not only an inhabitant of the coastal plains but is largely confined to them.

The coastal plains habitat is to a large extent inaccessible to man. During the wet season of spring and summer, which lasts about six months, the coastal plains are flooded, at which time vehicular movement is impossible; and even in the dry season access to the coastal plains by road is very limited. No doubt this accounts in part for the poor collection and very limited knowledge of the geographical distribution of this rat. The few notes by Tunney suggest that it was in the coastal plains section of the tidal waters of the South Alligator River that he trapped *R. s. colletti.*

Rattus sordidus colletti appears to be confined to the coastal flood plains and we were very fortunate to fly over this area with H. J. Frith, an authority on the ecology of these plains. He explained that the coastal plains harboring dense grass 3 to 4 feet high occur from the Murgenella Creek (just south of the base of the Cobourg Peninsula) westward in a discontinuous expanse to the Daly River. North and east of Murgenella Creek the land becomes a saltpan with beaches lined by mangroves. To the west of Daly River the high-grass flood plains occur to a lesser extent all the way to the Ord River in the northeast corner of Western Australia. These coastal flood plains are unique in Australia. They are flooded each wet season for about six months. Inland to the coastal flood plains is the Koolpinyah land system (Christian and Stewart, 1952). Here stringybark eucalypts, *Pandanus*, and moderate grass cover exist, and the area is not subject to flooding. If *R. s. colletti* is indeed restricted to the coastal flood plains and to the rivers that flood them, it, along with the North Queensland *R. lutreolus lacus*, *R. fuscipes coracius*, *R. leucopus cooktownensis*, and *R. leucopus leucopus*, is one of the most geographically restricted subspecies of *Rattus* in Australia.

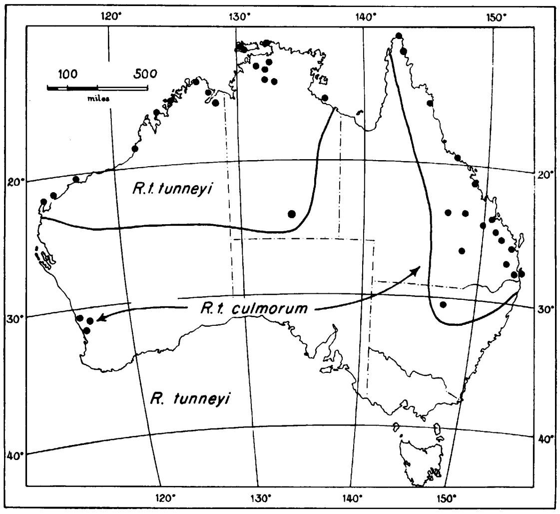


FIG. 36. Distribution map of *Rattus tunneyi*. Locality records for each of the two subspecies are indicated by dots.

SYMPATRY: *Rattus sordidus colletti* is probably sympatric with no other *Rattus* because it is so ecologically restricted, although it may possibly occur with *Rattus tunneyi tunneyi* in drier peripheries of the coastal plains habitat.

TAXONOMIC HISTORY: Following the original description of *Mus colletti* as a full species (Thomas, 1904a), most authors retained it at this rank (Longman, 1916a, 1916b; Le Souef and Burrell, 1926; Iredale and Troughton, 1934; Raven, 1935; Troughton, 1941 and subsequent editions). Ellerman (1949) was the first to treat it as a subspecies of *R. sordidus*, although several before him, including Thomas, had suggested an affinity of *M. colletti* either to *M. sordidus* or to *M. conatus*. Ride (1970) followed Ellerman's treatment of *R. s. colletti.* Tate (1951), who viewed *R. sordidus* differently from Ellerman, placed *colletti* as a subspecies of *R. gestri*, under which he also included two New Guinea forms.

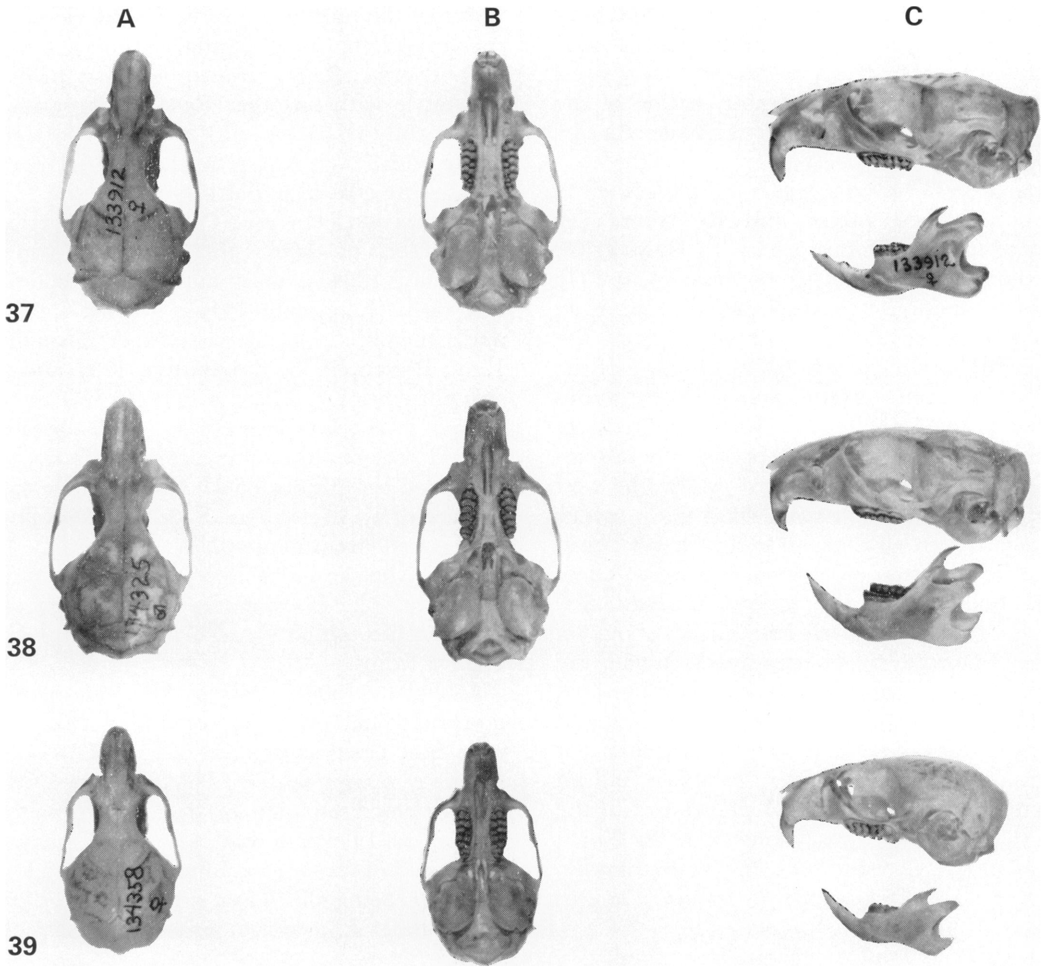
Johnson (1964), basing his judgment on morphological grounds, concluded that Ellerman had erred in making *R. s. colletti* a subspecies of *R. sordidus*. He objected particularly to the supposed alliance of *R. s. colletti* with *R. tunneyi*, as Ellerman had also made *tunneyi* a subspecies of *R. sordidus*. Johnson chose to follow Tate in placing *colletti* as a subspecies of *R. gestri*.

We treat *R. s. colletti* as a subspecies of *R. sordidus*.

Rattus tunneyi (Thomas)

DISTRIBUTION: Coastal and subcoastal areas and offshore islands of the Northern Territory westward through Western Australia as far southwest as North West Cape; Alice Springs and Tennant's Creek in inland Northern Territory; tip of Cape York, Queensland, south along the east coast to Brisbane and inland from Alpha south to Duck Creek, New South Wales; unknown localities in South Australia; southwestern Australia in vicinity of Perth (fig. 36).

GENERAL DESCRIPTION: These are among the smaller native *Rattus*. The tail is shorter than the head and body by about 20 mm. The pelage is light in color and dorsally is yellowish rust mixed with grayish brown. This color mixture tends to produce an over-all fulvous buff owing to the extent of yellow in the fur. Although the color is variable, with those from southeastern



FIGS. 37–39. Dorsal (A), ventral (B), and lateral (C) views of skulls of *Rattus tunneyi*. 37. Adult *R. t. tunneyi*, MVZ 133912. Occipitonasal length 34.4 mm. 38. Adult *R. t. culmorum*, MVZ 134325. Occipitonasal length 34.8 mm. 39. Juvenile *R. t. tunneyi*, MVZ 134358. Occipitonasal length 30.1 mm.

Queensland being the darkest, in general *R. tunneyi* has the lightest dorsal pelage of any species of native *Rattus*. The middorsal pelage tends to form a broad band along the body length that is perceptibly darker than the more dorsolateral portions. The dorsal facial pelage matches this middorsal color. The lateral body pelage lightens to yellowish gray and the venter is either grayish or creamy white. The pelage is spinous in more northern animals, but spines are usually absent in the south. The distinction between dorsal and ventral coloration is also less pronounced in more southern forms. Waite (1898), under the misnomer *Mus greyii*, gave the mammary formula as $2+3=10$.

The skull is not elongate. The nasals come just in line with the premaxillaries and incisors or overhang slightly when the skull is oriented to the horizontal plane. The supraorbital-temporal ridging is distinct and modestly developed. The incisive foramina taper inward along their posterolateral borders, but not to the degree seen in *R. lutreolus*. The medial walls of the highly inflated bullae tend to parallel one another and are closer together than are the medial faces of m^1. The bullae average 25.7 to

26.9 per cent of the basal skull length and are appreciably longer than the alveoli of m^{1-3} (figs. 37–39).

DIAGNOSTIC CHARACTERS: The most distinctive character of this species is the combination of a relatively small skull with strongly inflated tympanic bullae.

TAXONOMIC HISTORY: A specimen of *Rattus tunneyi* was known to science for more than 20 years before it was recognized as a new species. Collett (1887) collected two rats at Coomooboolaroo, one of which (specimen B) is a *Rattus tunneyi culmorum.* At that time, however, it was not recognized as such for Thomas identified it for Collett as *Mus greyii.* Collett gave an informative description of the skin and skull of this specimen and among other features commented on the strong inflation of the auditory bullae, a character typical of the whole *R. tunneyi* group but not diagnostic of *R. f. greyii.* At the time *M. greyii* itself was poorly understood, for two years after it was described (Gray, 1841) it was synonymized by Gray (1843) with another murid, *Mus gouldii* (now known generically as *Thetomys* or *Pseudomys*). For the ensuing 44 years there was no reference to *M. greyii* in the literature, and even that, Collett's published misidentification of 1877, was not refuted until years later. This error had considerable influence on the subsequent confusion of *Mus culmorum* with *Mus greyii.*

The next specimens of the *R. tunneyi* group to be mentioned in the literature, but again misidentified, were in a catalogue prepared by Jentink (1888). We have re-examined the specimens he listed as *a* and *e* under *Mus gouldii* and concur with Mahoney (1969) that they are *R. tunneyi.*

Ogilby (1892) referred to the *R. tunneyi* group (specifically *R. t. culmorum*) but did so unwittingly through his description of *Mus greyii.* He took some of the characters for *M. greyii* from Gray (1841) and some for "*greyii*" from Collett (1887) and combined them. He also cited two references to *Mus gouldii* (Waterhouse, 1837, p. 67; Gould, 1855, text to pl. 19), and his reason for doing so was probably that Gray (1843) had synonymized *M. greyii* under *M. gouldii.* Hence, Ogilby's description of *M. greyii* had little resemblance to the real *M. greyii* and was confused with both *M. gouldii* and what later came to be known as *Mus culmorum.*

It is not surprising then that Waite (1896) misidentified *R. tunneyi tunneyi* specimens from central Australia as *M. greyii.* He stated that his guide to their identification was the detailed description of skull morphology given by Collett (1887). Collett, however, was actually describing *R. tunneyi culmorum* and *R. sordidus sordidus.* Waite was not in agreement with Gray's synonymy of *M. greyii* and *M. gouldii,* so in his paper eliminated the confusion instigated by Ogilby a few years earlier. As Collett was his guide, Waite did not realize that he, too, was dealing with an undescribed species. In 1898 Waite described yet another *R. t. tunneyi* under the name *Mus greyii,* this one coming from Tennant's Creek rather than the Alice Springs area of his earlier material.

Trouessart (1897) cited the work of Collett and Ogilby, as well as the original description of *M. greyii,* under the name *M. greyii,* and by so doing included all previous errors.

Not until 1904 was the first member of the *Rattus tunneyi* group described as *tunneyi.* The description was made by Thomas (1904b) from three specimens taken in the Northern Territory by J. T. Tunney, in whose honor the species was named. Although Thomas said that *M. tunneyi* could be distinguished readily from other Australian rats, Thomas seemed unaware that this species had already been described several times under the misnomer *M. greyii,* including the one he himself had identified earlier for Collett.

Soon after the description of *M. tunneyi,* another member of the *R. tunneyi* group was described by Thomas and Dollman (1908) as a separate, but related, species, *Mus culmorum.* In their account they made evident that *M. culmorum* may have in the past been confused with other species such as *M. greyii, M. assimilis,* and *M. terrae-reginae.* The type locality of *M. culmorum,* Beach Mount, is only about 300 miles north of Coomooboolaroo, the locality of Collett's specimen B.

The next member of the *R. tunneyi* group, from La Grange Bay, was described under the name *Mus woodwardi* (Thomas, 1908). Thomas regarded *M. woodwardi* as closely related to *M. tunneyi* in most basic characters except certain size differences. Thomas continued to retain *M. tunneyi, M. culmorum,* and *M. woodwardi* as separate species under the genus *Epimys* in a later paper (1910). Longman (1916a, 1916b) followed Thomas in this respect, but not without error. He stated that Inkerman is in northwest Queensland rather than on the east coast, and he unwittingly grouped *E. tunneyi* under *E. greyii* by including central Australia in the range of *E. greyii.*

Thomas (1921a) described another new species, *Rattus melvilleus*, which also belongs in the *R. tunneyi* group. This is an insular form occurring on Melville Island. He said that this, like *R. culmorum* and *R. woodwardi*, is most closely related to *R. tunneyi.*

Brazenor (1936b) obtained further specimens of *R. tunneyi* that had been collected on the Horn Expedition, the source of Waite's "*greyii.*" On the strength of this material and comparison with *R. t. tunneyi*, Brazenor erected a new subspecies that he called *Rattus tunneyi dispar*. Waite's "*greyii*" is a synonym of Brazenor's *R. t. dispar.*

We recognize two subspecies of *R. tunneyi*, *Rattus tunneyi tunneyi* and *Rattus tunneyi culmorum.*

Rattus tunneyi tunneyi (Thomas)

Mus tunneyi Thomas, 1904b, p. 223.
Mus woodwardi Thomas, 1908, p. 374.
Rattus melvilleus Thomas, 1921a, p. 427.
Rattus tunneyi dispar Brazenor, 1936b, p. 5.

Holotype: Skin and complete skull, adult female, BM 4.1.3.30, collected September 13, 1902, by J. T. Tunney, at Mary River, Northern Territory.

Distribution: The present known distribution of *R. t. tunneyi* on the mainland is from the Chambers River, the easternmost record, to La Grange Bay on the west coast. The distribution is coastal, with few exceptions, those being a locality about 200 miles inland, in the river systems south and east of Darwin, and the two central Australian records, Alice Springs and Tennant's Creek. There are several insular records for *R. t. tunneyi* that extend it farther eastward and farther westward from its known mainland distribution. The Pellew Islands is the eastern island record and Middle Mangrove Island off Onslow is the westernmost locality. Within the last decade several range extensions have been reported for *R. t. tunneyi* and the extent of its geographic distribution is still unknown (fig. 36).

Mean Measurements (in Mm.): External: head and body 148; tail 123; hind foot (s.u.) 29.8; ear (from notch) 18. Skull: occipitonasal length 36.3; braincase width 15.6; bulla length 8.8; crowns m^{1-3} length 6.6. (See table 14 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 33.0 or less.

Description: The pelage, which is coarse and spinous, is a yellow-rust color mixed with a gray-brown on the dorsal surface. The middorsal pelage is about 11 mm. long. The basal 7–8 mm. is gray and terminates in a 3–4 mm. tip of rust. Dark brown guard hairs and spines, as well as the gray basal portion of the main pelage, give the coat a penciled effect. The guard hairs are about 16 mm. long in the middorsum, but become more conspicuous in the rump where they measure to 25 mm. The dorsal spines are about 12 mm. long, the basal two-thirds being translucent grayish white and the distal third, dark brown. They are at a density of one per mm. as they emerge from the dorsal skin. These spines are somewhat pliable. The texture, but not the color, of this dorsal pelage is reminiscent of that in northern *Rattus leucopus cooktownensis.* The upper facial region matches the dorsum in color. The hair length between the ears is 8 mm., and between the eyes 6 mm. There are short spines all over the facial region. The ears have a light brown pigment and are covered with short rust-colored hairs. This color blends in with the dorsum. Muzzle vibrissae measure up to 43 mm. and are lighter ventrally on the muzzle. The lateral body fades to yellowish gray ventrolaterally and to yellowish buff in the mouth region. The venter is creamy white in both regular hair color and in the color of the spines. The ventral hair is about 7.5 mm. long. The tail is dark brown and has 10 scales per cm. The scale row rings are dark and are marked by lighter regions between rows. The ventral tail is about the same shade. The tail hairs are brown and measure about 1.5 mm. long. The feet are clothed in white hairs.

The juvenile pelage is almost identical in color with that of the adult except that the venter is more pure white than creamy white. There are no spines except in large juveniles, and the guard hairs are poorly developed.

The mammary formula is $2+3=10$.

The adult skull is unelongated (fig. 37). The incisive foramina terminate in line with the first loph of m^1. The palate terminates in line with the posterior end of the molar row or within 0.5 mm. behind it. The supraorbital-temporal ridges are distinct but not strongly developed.

TABLE 14

MEASUREMENTS (IN MILLIMETERS) AND WEIGHTS (IN GRAMS) OF ADULT *Rattus tunneyi tunneyi*

Measurement	N	Mean ± SE[a]	SD[a]	Range
Head and body length	99	148.28 ± 1.52	15.14	118–194
Tail length	99	123.35 ± 1.22	12.16	78–151
Hind foot (s.u.) length	99	29.80 ± 0.19	1.89	25–35
Ear length (from notch)	101	18.48 ± 0.17	1.69	10–22.1
Occipitonasal length of skull	112	36.34 ± 0.20	2.14	33.1–42.2
Condylobasal length	112	35.12 ± 0.20	2.16	31.9–40.7
Basal length	111	32.62 ± 0.20	2.15	29.3–38.4
Zygomatic width	108	19.31 ± 0.09	0.93	17.7–22.0
Interorbital width	118	4.82 ± 0.03	0.31	4.2– 5.5
Interparietal length	115	4.76 ± 0.05	0.50	3.7– 6.0
Interparietal width	115	10.08 ± 0.06	0.69	8.5–11.6
Braincase width	116	15.59 ± 0.06	0.65	14.1–17.2
Mastoid width	116	13.65 ± 0.05	0.56	12.5–13.3
Nasal length	116	12.82 ± 0.11	1.17	10.5–16.4
Nasal width	116	4.06 ± 0.05	0.56	3.0– 5.4
Palatal length	117	19.35 ± 0.12	1.24	17.0–22.5
Incisive foramen length	117	7.14 ± 0.06	0.67	5.9– 9.3
Incisive foramina width	117	1.86 ± 0.02	0.24	1.4– 2.6
Inside m^{1-1} width	116	2.62 ± 0.03	0.36	1.8– 4.0
Outside m^{1-1} width	116	7.61 ± 0.04	0.46	6.7– 8.7
Bulla length	116	8.80 ± 0.06	0.62	7.5–10.3
Crowns m^{1-3} length	116	6.61 ± 0.04	0.39	5.7– 7.4
Alveoli m^{1-3} length	117	7.18 ± 0.04	0.44	6.3– 8.0
Crowns m^{1-2} length	116	5.23 ± 0.03	0.31	4.6– 6.0
M^{1-1} width × 2	116	4.99 ± 0.03	0.30	4.2– 5.7
Body weight	88	86.27 ± 2.86	26.83	46–165

[a] SE indicates standard error of the mean; SD, standard deviation from the mean.

They usually extend back to the posterior limit of the parietals. They measure about 0.3 mm. wide by about 0.2 mm. high in the posterior supraorbital region. The interorbital width is greater than in *R. t. culmorum*. The nasal bones are wide for their full length and terminate in line with the anterior faces of the incisors. The bullae are the most striking feature of the skull. They are relatively larger in *R. t. tunneyi* than in any other subspecies of native Australian *Rattus*, being about 27 per cent of the basal length of the skull. The interbullar distance is small, often being less than the molar width. The juvenile skull is similar except for cranial inflation and lack of supraorbital-temporal ridging (fig. 39).

PREVIOUS DESCRIPTIVE ACCOUNTS: Morphological descriptions have been given by Waite [1896 (under the misnomer *M. greyii*)], Thomas (1904b, 1908, 1921a), Le Souef and Burrell (1926), Brazenor (1936b), Troughton (1941 and subsequent editions), Tate (1951), and Johnson (1964). When Thomas (1921a) described *R. melvilleus* and based its distinction on size, so few mainland *R. t. tunneyi* had been collected that it was not then appreciated how large mainland forms can grow. They can equal the insular form in both size and in degree of spinous pelage. When Brazenor (1936b) described *R. tunneyi dispar* he stated that it was an old male with well-worn molars. Re-examination of this specimen (NMV R12642) both by Tate (1951) and by us has shown the teeth to be unworn. In fact, this specimen is a juvenile.

The supplementary cusps on m^2 and m^3 that Thomas (1904b) described for *R. tunneyi* occur on all native Australian *Rattus*.

The mammary formula of 2+3=10 was first recorded by Waite [1898 (under the misnomer *M. greyii*)]. When describing *R. melvilleus*, Thomas (1921a) found one extra pectoral teat in one of the specimens he examined. We have found five such cases, all of which represent an accessory teat in the pectoral region. One of these came from the South Alligator River, one from the Mary River, and three from the Cobourg Peninsula.

Certain aspects of the reproductive biology of this subspecies are given by Taylor and Horner (MS).

Waite (1896, fig. 3a–f) has presented drawings of the skull, molars, hind foot, and ear and Brazenor (1936b, pl. 1, figs. 1a, b) and Misonne (1969, fig. 130) have illustrated the molars. Two photographs of the living animal, taken by Messrs. E. Slater and K. Keith, have been published (Keith, 1968, p. 20; CSIRO Wildlife Research Report, 1966–1968, p. 48).

REMARKS: *Rattus tunneyi tunneyi* has been very poorly collected except on the Cobourg Peninsula where a good series was taken in 1965. It is largely on the basis of this series that we have chosen to reject *R. woodwardi*, *R. melvilleus*, and *R. t. dispar* as separate subspecies, for the morphological distinctions between them are no greater than are variants within the Cobourg series alone.

When Thomas (1908) proposed *M. woodwardi*, the "old female" (BM 5.1.9.1) from which he made his description was, in fact, a juvenile. The only other specimen was a subadult (BM 5.1.9.5). The distinguishing characters he used of smaller size compared to *M. tunneyi* and less developed supraorbital ridges are merely a function of its young status.

The case of *R. melvilleus* is a comparable type of circumstance and Thomas (1921a) described this as a new species mainly on its greater size when he compared it to *R. tunneyi*. The *R. tunneyi* he had previously described (Thomas, 1904b) were young adults and he apparently had no large mainland specimens for comparison. He distinguished *R. melvilleus* largely on the basis of size and greater development of supraorbital ridging, both features of older adults.

On the basis of a relatively wide interorbital width (4.93 mm.), bullae (8.87 mm.) that fall in relative size within the subspecies *R. t. tunneyi*, and short nasals (12.8 mm.) that barely come in line with the incisor face, we place *R. t. dispar* as a synonym of *R. t. tunneyi*. It is tempting on geographical grounds to place it with *R. t. culmorum*, but this alliance does not stand up as well morphologically. It is unfortunate that the type of *R. t. dispar* (NMV R12642) is also a juvenile.

HABITS AND HABITAT: The habits and habitat of *R. t. tunneyi* have never been discussed in the literature. The only previous remarks about the habitat of this rat are the notes of the collector, Hoy. He took *R. t. tunneyi* at Douglas River from the "bank of creek," from "dry creek bed," from "hole under tree," and, at Brocks Creek, from "bank of a dry creek" (Johnson, 1964, p. 489).

We have trapped *R. t. tunneyi* at the type locality and at several other localities in the Northern Territory. This rat is an inhabitant of the thicker grasslands of the north that grow near a watercourse, in a hollow, or near a beach. Unlike the coastal plains grasses that are subject to inundation for weeks or months at a time, the grasslands occupied by *R. t. tunneyi* are in this regard more upland grasses subject only to flooding from riverbanks and overflow from temporal streams. At the type locality, Mary River, *R. t. tunneyi* occurred in tall grass that bordered the steadily flowing river. The grass was 4 to 5 feet tall and was confined to a 100-foot band along either side. The grass, much of which was *Coelorhachis rottboellioides* (R. Br.) A. Camus, was somewhat patchy and thinned out in areas. *Rattus tunneyi tunneyi* was taken only in thick grasses where its runways were also conspicuous. The river was bordered by *Pandanus*, large eucalypts, and other large trees. The lower and less dense grass, including *Themeda australis* (R. Br.) Stapf., beyond the border band that yielded no *R. t. tunneyi*, grew on hard powdery soil that contrasted sharply with the more friable soil bordering the river.

Along the South Alligator River at the point where the vehicle track crosses en route to the Oenpelli Mission, the grass had been badly burned, camp sites had bared more ground, and cattle had grazed the vegetation extensively. Nonetheless, the thick grass patches occurring sporadically along the river bank yielded 14 *R. t. tunneyi* in a riverside strip about ¼ mile long (fig. 40). The situation was very similar to the Mary River location in that the thick grasses were full of runways. Tracks of *R. t. tunneyi* were among those on the sandy river banks, and for the first time we had ample evidence of their burrows. This rat also occurred among large piles of branches that, in times of flood, had been caught by the rising waters and piled against the trunks of large riverside trees. It also sought refuge in the dry dead bamboo by the river, but was not taken in sparse grass.

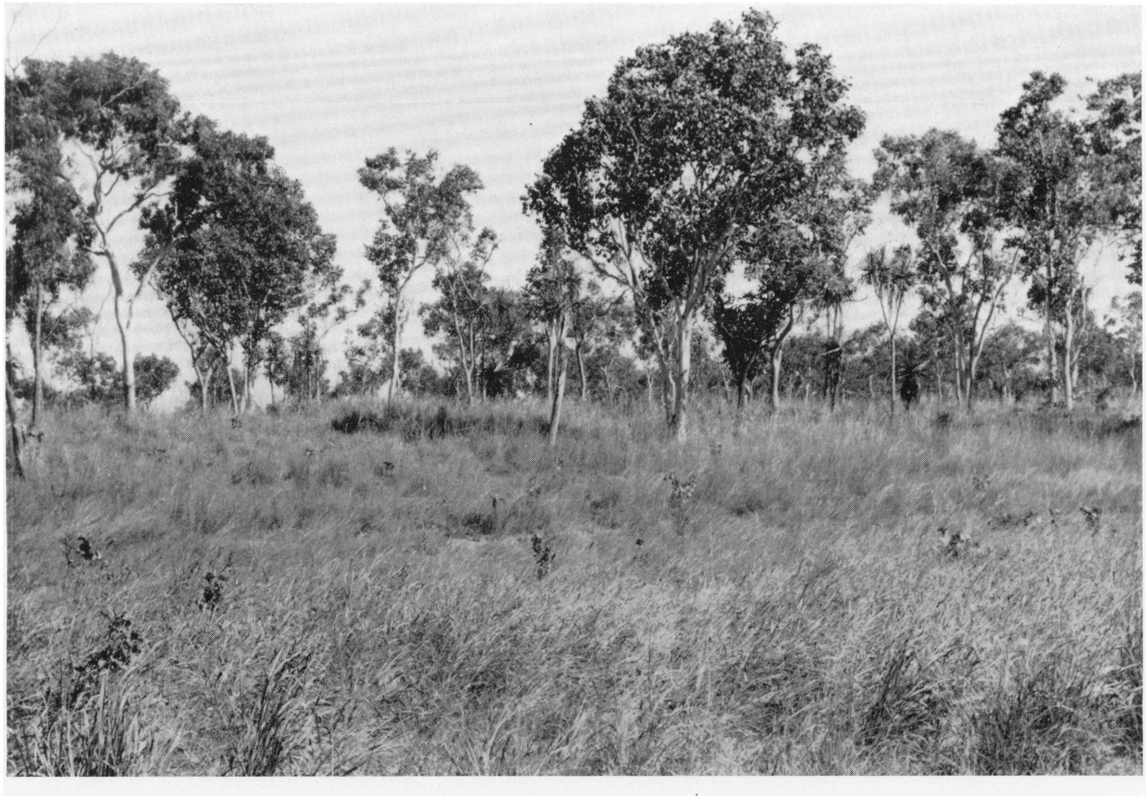


FIG. 40. Habitat of *Rattus tunneyi tunneyi* in tall grass near the bank of the South Alligator River, Northern Territory. Photographed June 15, 1964.

We did not excavate the burrow systems of *R. t. tunneyi*, but each burrow appears to go straight down from the entrance before becoming horizontal. The entrance to the burrow system is on level ground rather than on the slope of the riverbank. One *R. t. tunneyi* individual emerged from one of these burrows at 6:15 P.M. on June 16. This was at dusk while we were setting a trapline. This evidence and all our trapping results indicate that *R. t. tunneyi* is nocturnal. The contents of the stomachs are plant materials.

On the Cobourg Peninsula we trapped *R. t. tunneyi* near the shoreline in tall grass behind mangroves, in sand dunes, and also in more inland situations near watercourses and drainage hollows. The major forests of the Port Essington region of the Cobourg Peninsula are tropical eucalypt savanna woodland and monsoon forests of trees 15 to 40 feet high. In the monsoon forests trees are about 5 feet apart, there is ample leaf litter, and the substrate is stony clay loam. The woodland contains trees 40 to 50 feet high, about 10 to 20 feet apart, and they are mostly *Eucalyptus miniata* and *E. tetradonta*. Thin, short grass provides the only low cover. The introduced Banteng cattle (*Bos javanicus*), water buffalo (*Bubalus bubalis*), Indian sambar deer (*Cervus unicolor*), and Timor ponies (*Equus caballus*) graze this grass. *Rattus tunneyi tunneyi* is not common in the woodland, and we never trapped it in the monsoon forest. In the savanna woodland it occurs in areas where the undergrowth of grass is moderate and appears to avoid areas of sparse, shortly cropped grass.

Immediately inland to the mangrove, which marks the high-tide level, there is in many cases a relatively dense grass area (*Pseudopogonatherum* sp., *Eriachne triseta*, *Triraphis mollis*, *Panicum seminudum*, *Cymbopogon refractus*) growing in sandy soil. *Rattus tunneyi tunneyi* occurs here and its burrow systems can often be readily detected in the sandy, easily worked soil. Along river courses, such as the McArthur River 2 miles west of Victoria Settlement, where tall, dry grasses up to 2 feet high grow extensively (*Schizachyrium* sp., *Pseudopogonatherum* sp., *Eriachne* sp., *Setaria* sp.), and also in seasonally dry drainage areas harboring tall dense grasses, *R. t. tunneyi* may abound and its runways are conspicuous.

This rat seems to be most common in areas where the soil is both readily workable and supports good grass cover. The opportunity to burrow must be vitally important to this rat. The skin label of the type specimen (BM 4.1.3.30) bears the following statement of the collector, Tunney, "These rodents burrow in the ground and are difficult to get." Closer examination of the burrow systems of *R. t. tunneyi* on the Cobourg Peninsula was made by John H. Calaby, who kindly turned over his notes to us. He found the rat common on the sand dunes of beaches that were covered with a fairly dense cover of dry grass (*Pseudopogonatherum* sp., *Eragrostis* sp., *Aristida* sp.). Well-formed runways could be made out in the grass running both between burrows and also out into the grass itself. In the Smith Point region of the Cobourg Peninsula he found burrows of this rat about 200 yards from a monsoon forest and eucalypt woodland. Most of the warrens are in a flat, sandy area inland from the dunes and in long, fairly dense grass. One warren actually invaded the edge of the woodland where the grass was still thick. The runways are about 3 inches wide and can be 70 feet or more long. Some terminate in patches of turned-over soil which are 4 or 5 square feet in extent. Sand plains and sandy beaches occurring on the Dampier Archipelago also support the habitations of *R. t. tunneyi*.

Some of the burrows of *R. t. tunneyi* on the Cobourg Peninsula show evidence of being explored by goannas (*Varanus*), and no doubt some of the goanna warrens start out as *R. t. tunneyi* excavations. The rat burrows collapse easily in the sandy soil of the dunes and beach side of the forest edges. The large Banteng cattle graze the beach vegetation and their hoofs break through into the burrow systems. The present success of *R. t. tunneyi* settlement in the beach areas may be somewhat hampered by the presence of cattle.

SYMPATRY: *Rattus tunneyi tunneyi* is sympatric with *Rattus sordidus villosissimus* on the Sir Edward Pellew Group and probably elsewhere in that vicinity, and *R. t. tunneyi* is possibly sympatric with *Rattus sordidus colletti* in the northern portion of the Northern Territory. *Rattus exulans* is known from an offshore island only 50 miles from the adjacent mainland where *R. t. tunneyi* has been taken.

TAXONOMIC HISTORY: Since the time of the original description of *Mus tunneyi* (Thomas, 1904b), most workers regarded *R. woodwardi* and *R. melvilleus* as distinct from *R. t. tunneyi* at the species or subspecies level and *R. t. dispar* as a distinct subspecies. Le Souef and Burrell (1926) treated *R. melvilleus* and *R. tunneyi* as distinct species and their description is no more than a slight rewording of the original description. They did not mention *R. woodwardi*. Iredale and Troughton (1934) regarded all three forms as distinct species, as did Raven (1935). Unfortunately, Raven made some careless mistakes for he stated that *R. tunneyi* comes from Avera, Aroa, New Guinea, and under *R. woodwardi* he misspelled La Grange Bay.

Tate (1936) handled *R. tunneyi* in a most unusual fashion. He designated a *Rattus tunneyi* group that is apparently a superspecies category, for in this group he included four forms from New Guinea. His discussion in no way clarified the *R. tunneyi* complex.

Several years before Brazenor (1936b) proposed *R. t. dispar*, Jones (1925) questioned the identification made by Waite of the "*greyii*" from central Australia. He did not associate these specimens with *R. t. tunneyi* but seemed unwilling to accept fully their synonymy with *R. greyii*. He extended his doubt by presenting measurements of *R. greyii* obtained south of Adelaide at Cleland's Gully.

Troughton (1941 and subsequent editions) regarded *R. t. dispar* as a subspecies of *R. tunneyi* and also brought *R. woodwardi* into subspecific alliance with *R. tunneyi*. He suggested that *R. melvilleus* was possibly only an insular race of *R. tunneyi*, but still treated it as a full species.

Ellerman (1949) placed *R. tunneyi*, *R. t. woodwardi*, and *R. melvilleus*, as well as a number of other forms, under his catchall species, *Rattus sordidus*. In so doing, he was the first to place these three in conspecificity. Unfortunately he made no mention of *R. t. dispar*.

Tate (1951) did not accept Ellerman's grouping of these three forms under *R. sordidus*, but did follow him by placing the three as a subspecies of *R. tunneyi*, and treated *R. t. dispar* in this traditional sense.

Finlayson (1961), in spite of considerable trapping in the type locality of *R. t. dispar* and in other parts of central Australia, was unable to obtain further specimens of it. Hence, the only material available then and now are those specimens collected in the previous century by the Horn Expedition.

Johnson (1964), who retrieved a partially destroyed *R. t. tunneyi* from the claws of a Whistling Eagle at Oenpelli, was impressed by the large size of the rat and suggested that it might be *R. t. melvilleus*, although he provisionally assigned it to *R. t. tunneyi*. He was critical of Ellerman's decision to place both *R. t. tunneyi* and *R. s. colletti* in the species *R. sordidus* for the two are so distinct morphologically.

We place *R. t. dispar* (type, NMV R12642♂, from Central Australia), *R. t. melvilleus* (type, BM 13.6.28.33♂, from "Biro," Apsley Strait), and *R. t. woodwardi* (type, BM 5.1.9.1♀, from La Grange Bay) in synonymy with *R. t. tunneyi*.

Rattus tunneyi culmorum (Thomas and Dollman)

Mus culmorum Thomas and Dollman, 1908, p. 790.
Rattus culmorum vallesius Thomas, 1921a, p. 426.
Rattus culmorum austrinus Thomas, 1921a, p. 427.
Rattus culmorum apex Troughton, 1939, pp. 280–281.

Holotype: Skin and complete skull, adult female, BM 7.9.15.21, collected May 5, 1907, by W. Stalker, at Beach Mount, Inkerman, Queensland. Donated to the British Museum (Natural History) by Sir W. Ingram, Bt., and the Honorable John Forrest.

Distribution: *Rattus tunneyi culmorum* occurs from the tip of Cape York south to Brisbane along the coast. It extends inland about 250 miles, from Alpha south to Duck Creek, the only record in New South Wales. In this northern portion of its distribution, *R. t. culmorum* is known from only two records west of the Great Dividing Range, Roma and Duck Creek. Its occurrence on offshore islands has been recorded in the Burdekin River district and on Stradbroke Island. In South Australia it is known from only seven specimens, all collected in the mid-nineteenth century and of unknown locality (but including Eyre Peninsula or Kangaroo Island). The occurrence of *R. t. culmorum* in Western Australia is also known only from material collected in the mid-nineteenth century. This material consists of five specimens from Victoria Plains and two from the vicinity of Perth. There are additional specimens from cave deposits in this general area (fig. 36). The "*culmorum*" from Karumba, Queensland (W. Hosmer cited by Van Deusen, 1969), are in fact *Rattus sordidus villosissimus*.

Mean Measurements (in Mm.): External: head and body 145; tail 125; hind foot (s.u.) 29.2; ear (from notch) 18. Skull: occipitonasal length 35.9; braincase width 15.4; bulla length 8.2; crowns m^{1-3} length 6.5. (See table 15 for complete list of measurements and statistical presentation.) Juveniles: occipitonasal length 33.0 or less.

Description: The dorsal pelage of *R. t. culmorum* is similar to that of *R. t. tunneyi* in color in the more northern forms and is somewhat browner in specimens from around Inkerman and southward along the coast. It often has a glossy pelage, more so than any other Australian *Rattus*. The spinous quality of the pelage is conspicuous on specimens from the northern portion of Cape York, the degree of spinousness declining at Inkerman and southward along the coast until it disappears in southeastern Queensland. In drier inland localities, such as Belyando Creek, spines occur once again. The middorsal fur of *R. t. culmorum* in southeastern Queensland measures about 14 mm. The slate-gray of the basal portion is discernible in the over-all pelage coloration and is about 12 mm. long. The last 2 mm. is tipped with rust-brown. The gray basal portion is darker than that seen in *R. t. tunneyi*. Guard hairs are about 25 mm. long, the basal portion being gray and the distal half dark brown. They are conspicuous at the rump region. If spines are present, they are a grayish white translucent type about 12 mm. long and tipped with 1 mm. of dark gray-brown. The facial region is similar in color to that of the dorsum and lacks the yellowish buff cheek area that occurs on *R. t. tunneyi*. The sparse hairs on the ears are buff to whitish, and the ear color is mid-brown. The lateral body color is yellowish buff mixed with gray and blends into the venter. The ventral hairs are about 7 mm. long, the basal half being gray and the distal 3 mm. a buff white to yellowish. The hairs on the feet are white. The scales of the tail are buffy brown or medium brown, and the tail is lighter below than above. There are 10 scales per cm. The

TABLE 15

MEASUREMENTS (IN MILLIMETERS) AND WEIGHTS (IN GRAMS) OF ADULT *Rattus tunneyi culmorum*

Measurement	N	Mean±SE[a]	SD[a]	Range
Head and body length	86	144.87±1.24	11.52	121–174
Tail length	86	125.41±1.25	11.62	97–148
Hind foot (s.u.) length	86	29.18±0.20	1.82	26–36
Ear length (from notch)	95	17.87±0.15	1.45	14–20.5
Occipitonasal length of skull	134	35.88±0.14	1.57	33.1–40.3
Condylobasal length	138	34.41±0.14	1.59	30.4–39.0
Basal length	138	31.94±0.13	1.56	28.0–36.1
Zygomatic width	133	19.12±0.07	0.76	17.2–20.9
Interorbital width	169	4.56±0.02	0.26	3.9– 5.1
Interparietal length	144	4.41±0.03	0.33	3.4– 5.6
Interparietal width	144	9.81±0.06	0.68	6.8–11.3
Braincase width	147	15.42±0.04	0.44	14.3–16.4
Mastoid width	143	13.35±0.04	0.42	12.0–14.8
Nasal length	156	12.96±0.06	0.73	10.3–15.2
Nasal width	158	3.86±0.02	0.26	3.2– 4.6
Palatal length	162	18.94±0.07	0.93	16.7–21.4
Incisive foramen length	169	7.02±0.04	0.45	5.9– 8.0
Incisive foramina width	169	1.86±0.02	0.19	1.4– 2.5
Inside m^{1-1} width	168	2.69±0.03	0.37	2.0– 3.8
Outside m^{1-1} width	168	7.58±0.03	0.37	6.8– 8.9
Bulla length	150	8.22±0.04	0.44	7.3– 9.7
Crowns m^{1-3} length	170	6.49±0.02	0.33	5.5– 7.4
Alveoli m^{1-3} length	170	6.99±0.03	0.35	6.2– 7.8
Crowns m^{1-2} length	170	5.10±0.02	0.29	4.3– 5.8
M^{1-1} width × 2	168	4.89±0.02	0.25	4.3– 5.4
Body weight	23	66.33±2.76	13.26	42–85

[a] SE indicates standard error of the mean; SD, standard deviation from the mean.

tail is finely covered with medium to dark brown hairs about 1.5 mm. long.

The juvenile pelage is almost identical with that of the adult except for lack of guard hairs and spines.

The mammary formula is $2+3=10$.

The incisive foramina of the unelongated skull terminate in line with the anterior loph of m^1 (fig. 38). The nasal bones are longer than in *R. t. tunneyi* but are wide for their full length. They terminate in line with the anterior face of the incisors or overhang slightly. The palate terminates in line with the end of the molar row or within 0.5 mm. beyond. The supraorbital-temporal ridging is in general less well developed than in the other subspecies. It extends posteriorly to the midparietal on each side and is almost indistinguishable to the posterior limit of the parietal. It is about 0.2 mm. wide and about 0.1 mm. high. The interorbital width is less than in *R. t. tunneyi*. The bullae are greatly inflated, but smaller relative to occipitonasal length than in *R. t. tunneyi*. They are equal to 25.7 per cent of the basal length of the skull. The interbullar distance is wider than in *R. t. tunneyi*. Juvenile skulls lack supraorbital-temporal ridging and the cranium is more inflated (fig. 39).

PREVIOUS DESCRIPTIVE ACCOUNTS: Morphological descriptions of *R. t. culmorum* have been given by Collett [1887 (under the misnomer *Mus greyii*)], Thomas and Dollman (1908), Thomas (1921a), Jones (1925), Le Souef and Burrell (1926), Troughton (1939, 1941 and subsequent editions), Finlayson (1942), McDougall (1944–1946), and Tate (1951).

Finlayson (1942), in comparing *R. t. culmorum* with both *R. t. tunneyi* and *R. t. dispar*, suggested a close affinity of *R. t. dispar* with *R. t. culmorum*. His judgment was based in part on the absence in the last two forms of the supplementary cusps on m^2 and m^3 described by Thomas (1904b) for *R. tunneyi*. The figure Finlayson presented of the

R. t. culmorum (Finlayson, 1942, p. 247, pl. IX, B) lacks the extra cusps. However, these cusps are present initially on both *R. t. culmorum* and *R. t. dispar* (=*R. t. tunneyi*) (see figs. 37B and 38B, and Waite, 1896, fig. 3d), as well as on all other Australian *Rattus*, and disappear only with tooth wear. The specimen of *R. t. culmorum* described and illustrated by Finlayson has worn molars, and the supplementary cusps have disappeared with wear.

The mammary formula was first given by Thomas and Dollman (1908) as 2+3=10. We have found only one exception to this: a female from Emerald (MVZ 133654) had one extra pectoral teat.

Taylor and Horner (MS) have presented certain aspects of the reproductive biology of *R. t. culmorum*.

There is a colored plate of *R. t. culmorum* in Troughton (1941 and subsequent editions, pl. 19, fig. 7). Finlayson (1942, p. 247, pl. IX, A–E) illustrated the skull and feet of this subspecies and McDougall (1944, p. 62, pl. 7) has skull photographs.

REMARKS: The softer and longer quality of the pelage of *R. t. culmorum* in more southern areas of its distribution has been noted by Thomas (1921a) and Jones (1925). They also mention that the color is rather grayer in the South Australian *R. c. austrinus* material than in northern *R. culmorum*, but we found that the rats were similar in tone to those from southeastern Queensland, both being considerably rufous in dorsal coloration. The sheen on the coat is conspicuous on this southern material. Thomas (1921a) and Jones (1925) also commented on the smaller bullae on those from South Australia. Of the seven *R. c. austrinus* we examined from South Australia, only one had a bulla and none had a complete skull. By matching the measurable portions with complete skulls from more northern areas, we estimate that the bulla was probably about 25 per cent of the basal length, or less than 1 per cent below the average for *R. t. culmorum*. The *R. c. austrinus* skull characters that Thomas (1921a) used to separate it from *R. c. culmorum* are tooth-row length and bulla size. He stated that the tooth-row length is like that of *R. c. vallesius*. From our measurements "*austrinus*" averages 6.3 mm., or 0.1 mm. longer than the type specimen of "*vallesius*," and 0.2 mm. shorter than the average for *R. t. culmorum*. He also stated that the bullae are even shorter than those of *R. c. vallesius*. The one bulla available now is from one of the smaller skulls and measures 7.7. mm., which is well within the range of *R. t. culmorum* and only 0.4 mm. less than that of the type of *R. c. vallesius*.

The combined skull characters of large bullae, narrow incisive foramina (1.7 mm.), well-developed supraorbital-temporal ridges, broad molars (molar width ×2 equals 4.9 mm. for "*austrinus*," 4.9 mm. for the rest of *R. t. culmorum*, and 4.2 mm. for *R. f. greyii*), and short nasals (13.1 mm.) readily serve to exclude "*austrinus*" from *R. f. greyii*, an alliance proposed by Tate (1951) and followed by Troughton (1941–1967, Eighth and Ninth editions).

The two skull features that Thomas (1921a) used to distinguish "*vallesius*" from *R. t. culmorum* were smaller bullae and shorter tooth row. There are only two clearly traceable specimens of "*vallesius*" in existence, one of which (BM 47.8.14.4) is either a juvenile or a young adult (the skull is too badly damaged to determine). Even the type (BM 47.8.14.5) is a young adult. The left bulla of the type measures 8.1 mm. which is only 0.1 mm. less than the average for *R. t. culmorum*. The molar row at crown level is 6.2 mm. which is 0.3 mm. shorter than the average for *R. t. culmorum* and well within the range of variation.

Both "*austrinus*" and "*vallesius*" share the character of a relatively narrow interorbital width with the more northern *R. t. culmorum*.

We have found no features that serve to separate either "*austrinus*" or "*vallesius*" from *R. t. culmorum*, so we have elected to synonymize each of them with the subspecies *R. t. culmorum*.

Troughton (1939) stated in his description of *R. culmorum apex* that the bullae are longer than any recorded for the nominate *R. c. culmorum*. This statement does not hold, for an adult male (BM 7.9.15.17), taken at the type locality of *R. t. culmorum*, matches the bulla length of 9.2 mm. on his type of "*apex*." Furthermore, the specimen designated by Troughton (1939) as the type of *R. c. apex* (AM M3371) has a bulla length that is 26.6 per cent of the basal skull length. In the series of 20 specimens from the tip of Cape York we measured, including the type of "*apex*," the bulla is 24.5 per cent of the basal skull length. The average bulla length of *R. t. culmorum* is 25.6 per cent of the basal skull length. The one feature that is distinctive in the type of *R. c. apex* is the greater width of the incisive foramina, but the topotypes do not show this character. We find insufficient differences to justify separating "*apex*" from *R. t. culmorum* at the level of subspecies.

There is a small collection of rats taken in the nineteenth century from the vicinity of Perth [BM 44.2.15.29; 44.2.15.30; 44.2.15.31 (skin) and 44.3.12.2 (skull); 44.7.9.17 (skin) and 44.10.30.8 (skull missing?); 43.8.21.1 (skin) and 43.9.2.3 (skull); RNH *a* and *e* (under the misnomer *Mus gouldii*)], and cave material has since been found (Mahoney, 1969). These specimens had not received acknowledgment by identification until Mahoney (1969) determined them to be *R. tunneyi*. All noncave skulls are badly fragmented. The bullae are missing and an estimate of total length is impossible. We ally these forms to *R. t. culmorum* and, on the basis of such limited material, feel that separate subspecific designation is unwarranted, although such distinction is appealing on zoogeographic grounds. Most of the skin and skull material had been misidentified as *Rattus fuscipes fuscipes*. On the basis of the old and, at one time, wet-preserved skins they are difficult to distinguish from *R. f. fuscipes* skins of the same antiquity. Both rats have fuscous brown pelage dorsally and ventrally are buff with hairs gray at the base. However, the skull remnants consistently exclude *R. f. fuscipes* on the basis of molar width. These specimens average 5.0 mm. in molar width ×2, *R. t. culmorum* averages 4.9 mm., and *R. f. fuscipes* 4.6 mm. The skull remnants are more closely allied to *R. t. culmorum* than to *R. t. tunneyi* on two types of evidence. Firstly, in interorbital width (4.65 mm.) they approach *R. t. culmorum* (4.56 mm.) more closely than *R. t. tunneyi* (4.82 mm.); in molar row length at crown level (6.50 mm.) they are closer to *R. t. culmorum* (6.49 mm.) than to *R. t. tunneyi* (6.61 mm.); and in length of left incisive foramen (6.95 mm.) they approach *R. t. culmorum* (7.02 mm.) more closely than they do *R. t. tunneyi* (7.14 mm.). We could find no measurable characters of the skull that favored *R. t. tunneyi* over *R. t. culmorum*. The second type of evidence is speculative. These materials show sympatry (at least into the nineteenth century) with *R. f. fuscipes*, and hence a sharing to some degree of a type of environment now associated with a subspecies of *R. fuscipes*. Today *R. t. culmorum* is also sympatric with at least one other subspecies of *R. fuscipes*, *R. f. assimilis*, and possibly with *R. f. coracius*. Although subspecies of *R. fuscipes* are widespread throughout Australia, nowhere do they approach *R. t. tunneyi* in distribution or in similarity of habitat. Together these lines of evidence lead us to regard the Western Australian material as *R. t. culmorum* rather than *R. t. tunneyi*, even though today *R. t. tunneyi* occurs much closer to the Perth area than does *R. t. culmorum*.

Lundelius (1960) found in two subcoastal cave deposits, 100 and 130 miles north of Perth, skulls of both *R. fuscipes* and *Rattus* species. Lundelius's material allowed him to date by C^{14} only to 7850 ± 170 years B. P., although both species also occurred at much deeper levels. Mahoney (1969) found surface skulls of *R. tunneyi* at Hasting's Cave near the northernmost cave deposit, Drover's Cave, described by Lundelius (1960). Three good skulls between 50 and 150 years old (Mahoney, personal commun.) from Drover's Cave, and examined by one of us (Horner) through the courtesy of Mahoney, most closely resemble *R. tunneyi culmorum*. Lundelius (1964) has attempted the difficult task of making a key for these cave materials of *Rattus*.

HABITS AND HABITAT: At the time of its original description (Thomas and Dollman, 1908), *Mus culmorum* was claimed to be the most common species in central Queensland. The authors must have been referring to the central coastal part, for no *R. t. culmorum* have been reported in the heart of Queensland. Thomas (1921a) stated that *R. culmorum austrinus* was probably common in South Australia in the 1840s. There are no accounts of *R. t. culmorum* in abundance in its native habitat since these early reports. The paucity of museum specimens of *R. t. culmorum* from areas not under cultivation suggests that at least in the present century it has not been common in its native grasslands. However, in plantations of pine in southeastern Queensland it occurs from time to time in abundance and is there regarded an economic pest.

During the course of his extensive work on rat pests of the canefields of Queensland, McDougall (1938, 1944–1946) encountered *R. t. culmorum* in relatively small numbers in the canefields of the Mackay district, but he gave no numerical estimate. He found it to be primarily a vegetarian. Davis (MS) examined the rat-pest problem in the Benarkin and Gallangowan hoop pine (*Araucaria cunninghamii* Ait.) plantations of southeastern Queensland, where he found it along with *R. f. assimilis* and *R. l. lutreolus*. These three subspecies occurred in densities of 120 to 200 rats per acre. In one year 2700 rats were taken at Benarkin and 4000 at Gallangowan. Unfortunately, he does not break down the numbers according to the species of rat, but *R. t. culmorum* is by far the most abundant.

We took advantage of their abundance in hoop pine plantations in Benarkin and Googa state forests. With the valuable information relayed to us by the forestry officials and our own limited but informative trapping results, we were able to obtain some pictures of the habits of *R. t. culmorum* and the damage it inflicts on trees. The plantations are usually in areas that have formerly been mixed eucalypt forests, and they are still fringed by these forests. Within the plantations the soil is friable and, by using cattle as grazers, the grassy undercover is kept minimal. *Rattus tunneyi culmorum* focuses its attack on trees 5 to 10 feet tall and does no appreciable damage to very young or to mature trees. The rat burrows toward a tree from about 2 to 6 feet away from the main trunk and eats the lateral roots and eventually the tap root. All damage is done beneath the soil surface. The tree dies in a standing position and eventually topples. Runways and burrows were conspicuous at almost every tree planting in August, 1965, when we trapped and caught nothing but *R. t. culmorum*.

According to the forestry officials, the rats seem to move in waves and destroy up to 50 per cent of a plantation almost overnight. They appear to be most numerous from July through September when the juvenile population is probably high (Taylor and Horner, MS) and their natural foods may be the most scarce. The last major plague at Benarkin was in 1950. They are said to remain present the year-round in resident reservoir pockets. In some of the unplanted strips between plantation sectors there are occasional patches of bladey grass in gullies where the runways of *R. t. culmorum* may be conspicuous. This rat apparently likes the succulent roots of grasses, nettles, and other herbage. Runways are also conspicuous under fallen logs. In times of high density, runways are said to literally network the soil surface.

In spite of the familiarity gained by foresters in southern Queensland with the habits of *R. t. culmorum* and its damage to the hoop pine plantations, nothing has been published on any aspect of the biology of *R. t. culmorum* in its native haunts. We trapped *R. t. culmorum* in two natural areas.

Near Emerald the rat occurs close to the Nogoa River where within 100 yards of the bank the vegetation is tall tussock grass. The tussocks are separated from one another by deep water-worn or animal-worn depressions in the soil. The soil is black sandy to clayey and becomes slippery in the rain. Scattered throughout the grassy region are a few small eucalypts and spiny acacias from 4 to 6 feet tall, plus a few large eucalypts with a trunk diameter of up to 2 feet. Along the river bank, casuarinas and *Melaleuca* are common and stand up to 25 feet high. *Rattus tunneyi culmorum* occurs in the tallest region of the tussock grass (about 4 feet tall) and it shares this habitat with another native murid, *Pseudomys australis*.

Bordering a dry creek bed near Alpha we trapped *R. t. culmorum* again in tussock grass (fig. 41). Paperbark trees, *Casuarina*, and eucalypts up to $2\frac{1}{2}$ feet in diameter are scattered throughout the area. Spiny acacia and small gums occur along the creek bed. Again, *R. t. culmorum* occurs in the tallest section of the grass. This is the westernmost record of *R. t. culmorum* in Queensland and is in the western foothills of the Great Dividing Range. About 80 miles west of Alpha there is a marked vegetation change from tropical woodland and layered scrub to flat, semiarid tussock grassland. The latter type of vegetation seems far too thin and short to meet the habitat requirements of *R. t. culmorum*.

Our limited evidence suggests that *R. t. culmorum* today inhabits the dense grasslands of the tropical and subtropical portion of eastern Australia, and that such habitat is often in association with river channels and dry gullies. That it is primarily a grassland form is substantiated by the areas from which it has been collected in the past. The type locality, Beach Mount, is today a sandy beach area covered with grass, *Pandanus*, and a light cover of eucalypts and paperbarks. It seems to be seasonally swampy in parts and the soil is very friable. The type locality of the form described as "*vallesius*," Duck Creek, New South Wales, is today an intermittently flowing stream with scattered old *Eucalyptus* trees along its course, and reeds (*Typha* species) about 10 feet tall grow in most of the creek bed. Immediately above the reeds the

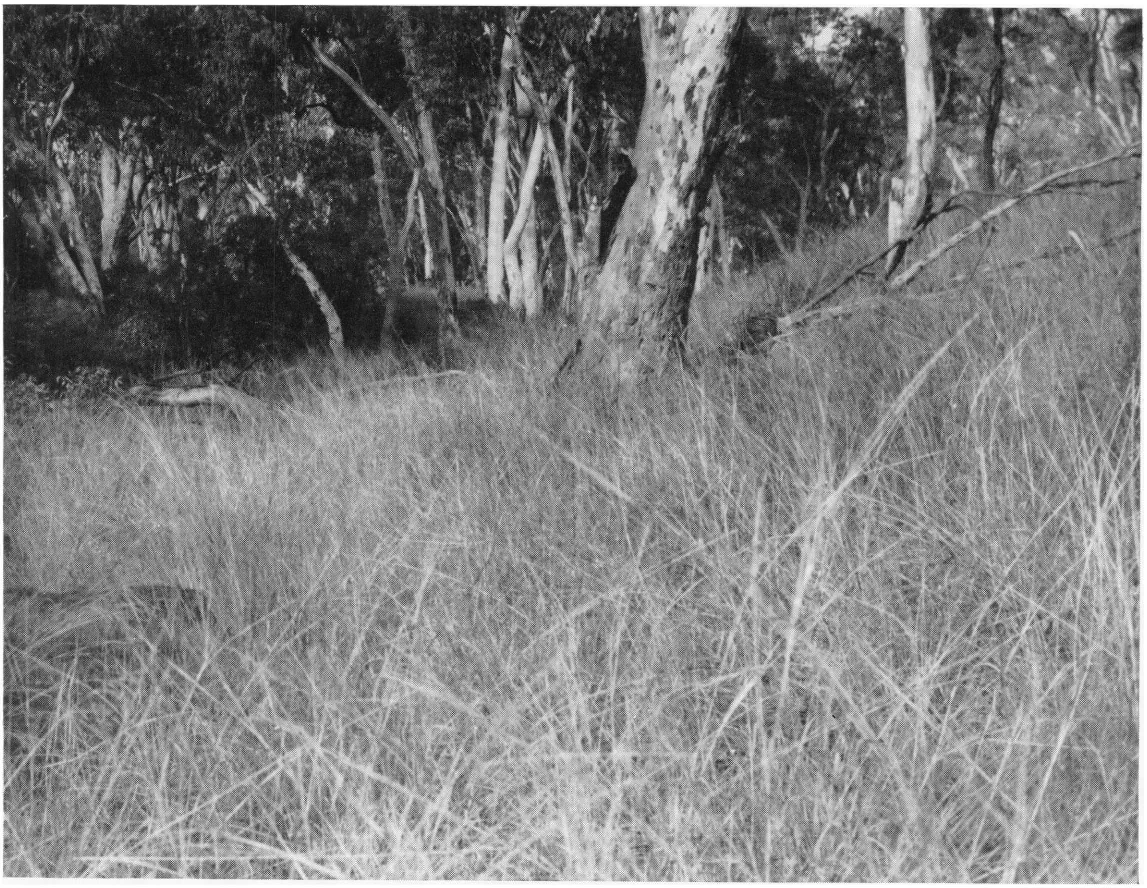


FIG. 41. Habitat of *Rattus tunneyi culmorum* in tall grass bordering creek bed at Alpha, Queensland. Photographed June 1, 1964.

vegetation consists of grasses, chiefly windmill grass (*Chloris* species), 2 to 3 feet high. As is typical of large areas in this region of New South Wales, there is a mosaic of fairly light sandy soils alternating with heavier clayey soils. Before it was settled and extensively grazed the area would have been a sparsely timbered plain with an abundance of long grass. The Beach Mount locality was also grassland prior to grazing and, with a nearby source of water, either permanent or seasonal, the grass must have been relatively thick and luxuriant. The occurrence of *R. t. culmorum* on offshore islands in the Burdekin River district and on Stradbroke Island is in coastal woodlands with extensive grass cover.

So little is known about the specific habitat requirements of *R. t. culmorum* that it is not possible to distinguish satisfactorily the characters of the habitat that separate it ecologically from *R. sordidus sordidus*. If anything, *R. t. culmorum* appears to occupy a somewhat drier environment except in areas of cultivation where the situation is otherwise ameliorative. McDougall (personal commun.) found that in the Mackay district *R. t. culmorum* inhabits areas of sandy soil and penetrates the canefields only where such soils are adjacent to the crops.

SYMPATRY: *Rattus tunneyi culmorum* is sympatric with *Rattus sordidus sordidus* in Queensland for the greater part of its extent in that state, including Stradbroke Island. It is sympatric with *Rattus fuscipes assimilis* and with *Rattus lutreolus lutreolus* in southeastern Queensland. It is sympatric with *Rattus leucopus leucopus* and *Rattus leucopus cooktownensis* on Cape York and possibly with *Rattus fuscipes coracius*, although in this instance the habitat separation may be too great. In historic times it may have been sympatric with *Rattus sordidus villosissimus* in north-central New South Wales, with *Rattus fuscipes greyii* and *Rattus lutreolus lutreolus* in South Australia, and with *Rattus fuscipes fuscipes* in Western Australia.

TAXONOMIC HISTORY: Within the group Thomas defined as the species *R. culmorum*, he described three forms that he considered were not only geographically but also morphologically distinct (1921a): *R. culmorum culmorum* from Queensland and two new forms, *R. culmorum vallesius* from Duck Creek in northern New South Wales and *R. culmorum austrinus* from South Australia. The type locality of *R. c. austrinus* was never ascertained, but of the two most probable choices, Kangaroo Island and Port Lincoln, Thomas favored the former.

The collector of the type of *R. c. austrinus*, J. B. Harvey, lived in Kingscote, Kangaroo Island, from late in 1838 to 1840, at which time he moved to Port Lincoln on Eyre Peninsula where he lived until he died in 1843. In April, 1840, he joined Governor Gawler on an expedition to Franklin Harbour on Spencer Gulf, about halfway up the Peninsula (Whittell, 1954). By 1841 Harvey had gathered 2000 to 3000 biological specimens from both the Port Lincoln area and Kangaroo Island, apparently without locality specifications in most cases. It is therefore difficult to establish whether the type specimen (BM 55.12.24.336), received December 3, 1841, is from Eyre Peninsula or the Island. Certainly, the mainland possibility is fully as likely in terms of Harvey's collecting itinerary and perhaps even more likely on ecological grounds. A second specimen of *R. c. austrinus* (BM 41.1265) is from the Gould Collection and the locality is given simply as South Australia. The remaining five *R. c. austrinus* that are known came from George Grey, Governor of South Australia from 1841 to 1845, who sent numerous natural history specimens to England from various parts of the state during his residency in Adelaide.

Thomas (1921a) discovered one of the specimens of *R. c. austrinus* among the lectoparatypes of *R. greyii*. Probably because of the similar external appearance of these specimens and the historical confusion of the two forms, he made a special effort to specify certain characters whereby *R. culmorum* could be distinguished from *R. greyii*.

When Jones (1925) was describing the mammals from South Australia he had no *R. c. austrinus* material available, so he relied on combining the original description of *Mus culmorum* (Thomas and Dollman, 1908) with that of *R. c. austrinus* (Thomas, 1921). Furthermore, he knew of no recent material in South Australia.

Le Souef and Burrell (1926) merely reworded the original description of *Mus culmorum* in their account and mistakenly cited northwest Queensland as part of its range. They did not refer by name to the two subspecies named by Thomas (1921a). In the same year Thomas (1926b) described a new species from Moreton Island, which he called *Rattus youngi*. At the time he allied it to *R. assimilis*, but subsequently it has most commonly been associated with *R. culmorum*. This was first done by Iredale and Troughton (1934) when, in their consideration of *R. culmorum* as a full species, they included *R. youngi* as one of the subspecies, along with *R. c. vallesius* and *R. c. austrinus*. In the case of *R. c. austrinus*, they favored Port Lincoln as the type locality.

Raven (1935) recognized *R. culmorum* as a full species and under it included the two subspecies proposed by Thomas (1921a). He followed the old error of including *R. culmorum* under *R. greyii* by citing Queensland as part of the range of the latter.

A new confusion evolved when Gard (1935) identified the "field rat" as *Rattus culmorum*, an identification that he had received from Troughton. It is obvious from his discussion that this rat is *R. sordidus sordidus*, not *R. t. culmorum*. One clue is the large litter size he recorded for this rat, one that is typical of *R. s. sordidus* but not of *R. t. culmorum*. This marked the beginning of considerable confusion between the two subspecies for they are sympatric over much of their range and both occur as pests in canefields. McDougall (1936) made the same mistake. In fact, between the years 1936 and 1939 the cane rat identified in literature concerning canefield damage, although called *R. culmorum*, was actually *R. s. sordidus* (known then as *R. conatus*) (McDougall, 1944–1946). This is the case, for instance, in the paper by Sawers (1938) wherein, in his discussion of leptospirosis among mammals in Queensland, he called the rat of the canefields *R. culmorum*.

In 1939 Troughton pointed out the error of identification that in actual fact he had originated, and clarified also that *R. conatus* (=*R. s.*

sordidus) is generally a much more plentiful form than *R. culmorum*. In the same review of *R. culmorum*, Troughton recognized a new form that he regarded so distinct from the rest that he erected a new subspecies for it. He called it *R. culmorum apex* and stated that it occurred at the tip of Cape York (Troughton, 1939). He also retained the view, first proposed by him and Iredale, that *R. youngi* be considered a subspecies of *R. culmorum*.

The work by Freeman et al. (1940) is one of the few ever to deal with the rat then known as *R. culmorum youngi*. The study involved the epidemiology of Q fever in native mammals of Moreton Island.

Troughton (1941–1967, First through Seventh editions) recognized five subspecies of *R. culmorum*: *R. c. culmorum*, *R. c. apex*, *R. c. youngi*, *R. c. vallesius*, and *R. c. austrinus*. The last-named subspecies he treated in an unusual way for he suggested that it may be linked with *R. fuscipes* from Western Australia. He specified, however, that *R. c. austrinus* could be distinguished from *R. greyii* by several skull characters which he listed.

Finlayson (1942) made a more extensive description of *R. c. culmorum* than had hitherto been presented. Furthermore, in the course of this work he became impressed by the close similarity of *R. c. culmorum* and Waite's "*greyii*" that had later been described as *R. tunneyi dispar* (Brazenor, 1936b). He concluded that *R. t. dispar* could just as reasonably be regarded *R. culmorum* as *R. tunneyi*. We have already discussed his viewpoint in another section.

The extensive work by McDougall (1944–1946; 1950) on the rodent pests of Queensland canefields includes considerable new information on the general biology of *R. t. culmorum*, which by now was distinguished from *R. s. sordidus* in the literature on cane plantations.

Ellerman (1949) was the first to propose conspecificity for *R. culmorum* and *R. tunneyi* and included both as subspecies of *R. sordidus*. He thought *R. c. austrinus* came from Port Lincoln and he placed it and *R. c. vallesius* as two more subspecies of *R. sordidus*. He excluded *R. c. youngi* from this grouping and allied it as a subspecies of *R. fuscipes*.

Tate (1951) handled those forms differently for, in the first place, he regarded *R. culmorum* as a monotypic species. He also treated *R. youngi* as a full species and incorporated *R. c. vallesius* as a subspecies of it. Although Troughton (1941 and subsequent editions) before him had specified characters whereby *R. c. austrinus* could be distinguished from *R. greyii*, Tate placed the former as a subspecies of *R. greyii*.

Finlayson (1960), in his long discussion of the systematic relationships of *R. greyii*, thought that the rats from Kangaroo Island did not represent *R. c. austrinus* as described by Thomas (1921a). Rather, he thought the island rats to be indistinguishable from *R. greyii* of the nearby Fleurieu Peninsula at the level of subspecies. Finlayson judged that, regardless of which locality was its real one, *R. c. austrinus* is a subspecies of *R. culmorum* and not of *R. greyii*.

Although Troughton (1941–1967, First through Seventh editions) placed *R. c. austrinus* as a subspecies of *R. culmorum*, suggested it may be linked with *R. fuscipes*, and made a case for its distinction from *R. greyii*, he reversed his stand in later editions of his book (Eighth and Ninth editions). There he treated *R. c. austrinus* as a subspecies of *R. greyii*, following Tate (1951). He still considered *R. culmorum* a full species, with *R. c. apex*, *R. c. youngi*, and *R. c. vallesius* as subspecies along with the nominate form.

Mahoney (1969) included *R. t. culmorum* and *R. t. woodwardi* under *R. tunneyi*, and Ride (1970) followed this arrangement.

We regard *R. t. culmorum* as a subspecies of *R. tunneyi*, with "*vallesius*" (type, BM 47.8.14.5♂, from Duck Creek), "*apex*" (type, AM M3371♀, from Skull Creek), and "*austrinus*" (type, BM 55.12.24.336♂, from Port Lincoln or Kingscote) as synonyms of *R. t. culmorum*. Under *R. t. culmorum* we also include the small collection of specimens taken in the Perth area and 75 miles to the north-northeast. We consider the insular *R. youngi* a synonym of *R. sordidus sordidus*. This insular rat is poorly represented in museum collections and the material available is inadequate for sound assessment. Although we are basing our judgment of "*youngi*" primarily on skull measurements, we are fully aware of the strong resemblances this form also has to *R. t. culmorum*.

COMPUTER ANALYSIS

Twenty measurements of adult skulls were the basic parameters used in a discriminant analysis program designed by Dana P. Snyder (personal commun.). This program requires inclusion of the full complement of dimensions selected.

Since many of the skulls of the 3351 specimens examined by us were either broken or immature, the numbers used in the various tests were considerably less than the total specimens examined (see table 16 for numbers used in each test).

All groups in each test have been compared by Mahalanobis's D^2. Of the total between-sample variation in the several tests, anywhere from 79 to 94 per cent of its sum was accounted for by the first two discriminant functions. The plotting of any group mean in terms of these two discriminants depicts, therefore, the general relationship of that group to others considered in the same test. Hotelling's T^2 has been used as the test statistic. Its graphic representation as a circle, with the plotted group mean as its center, indicates the confidence level of that mean at the 95 per cent level of significance (figs. 42, 43).

TABLE 16

NUMBER OF SPECIMENS OF EACH SUBSPECIES USED IN COMPUTER TESTS

Test Number	1	4	2	3	6	5	7	8
R. exulans subspecies	2	2	1♂ 1♀				2	
R. f. fuscipes	455	48	223♂ 213♀	330	40	48	9^a 9^b 40^c	9^a 9^b 40^c
R. f. greyii		56			42	56	56	56
R. f. assimilis		196			130	196	58^d 138^{ef}	58^d 82^e 56^f
R. f. coracius		155			118	155	155	155
R. l. leucopus	208	118	105♂ 100♀	182	105	75^g 43^h	118	75^g 43^h
R. l. cooktownensis		90			77	90	90	90
R. l. lutreolus	170	70	77♂ 79♀	129	42	70	70	70
R. l. velutinus		98			85	98	98	98
R. l. lacus		2			2	2	2	
R. s. sordidus	222	112	114♂ 75♀	113	76	112	112	112
R. s. villosissimus		85			17	85	85	85
R. s. colletti		25			20	25	25	25
R. t. tunneyi	217	99	108♂ 102♀	152	87	99	99	99
R. t. culmorum		118			65	118	118	118
Total	1274	1274	1198	906	906	1272	1284	1280

[a] "*R. f. glauerti.*" [b] "*R. f. mondraineus.*" [c] *R. f. fuscipes* of the mainland. [d] Northern *R. f. assimilis* (Coomooboolaroo to Clarence River). [e] Middle *R. f. assimilis* (Ebor to Milton). [f] Southern *R. f. assimilis* (Argalong to Hordern Vale). [g] *R. l. leucopus* [as defined by Tate (1951)]. [h] "*R. l. mcilwraithi*" [as defined by Tate (1951)].

When the data are combined for each of the six species, the computer results reveal a highly marked separation of each species from all others (Test 1). The 95 per cent confidence limits are tight for each species except *R. exulans* subspecies, which suffers statistically from being represented by only two specimens. Even so, *R. exulans* stands well apart at this confidence level. With the exception of *R. exulans*, the plot diagram of Discriminants 1 and 2 (covering about 93 per cent of the total variability) shows each species mean to be at least eight diameters (of the largest 95 per cent confidence limit) apart from all others (fig. 42). The diagram falls into a triangle with *R. lutreolus*, *R. tunneyi*, and *R. leucopus* forming the corners or the most morphologically divergent groups. *Rattus sordidus* is between *R. lutreolus* and *R. tunneyi* and shows more affinity to the latter; *R. fuscipes* lies between *R. lutreolus* and *R. leucopus* and closer to the latter; and *R. exulans* subspecies is between *R. leucopus* and *R. tunneyi* and shows a greater affinity to both *R. leucopus* and *R. fuscipes*.

When the same test is run again, but with the sexes treated separately, the results are virtually the same (Test 2). *Rattus exulans* subspecies forms a wider spread at the 95 per cent confidence level, but is still well separated from the other five species. In *R. fuscipes* alone there is a significant separation of the sexes at the 95 per cent confidence level, but not at the 99 per cent level, and it does not affect the marked separation between species.

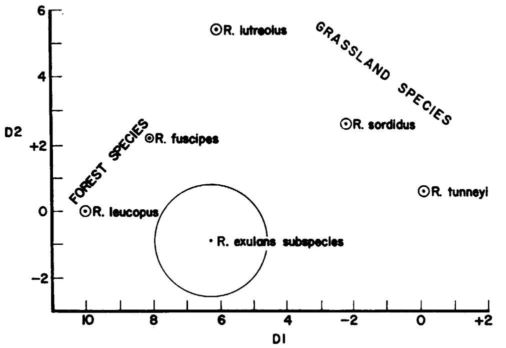


FIG. 42. Plot of group means of each species of Australian *Rattus* on the basis of the first two discriminant functions (D1 and D2) according to Mahalanobis's D^2. Hotelling's T^2 test statistic is represented in each case as a circle with the central point being the group mean. Confidence level of the circle is 95 per cent.

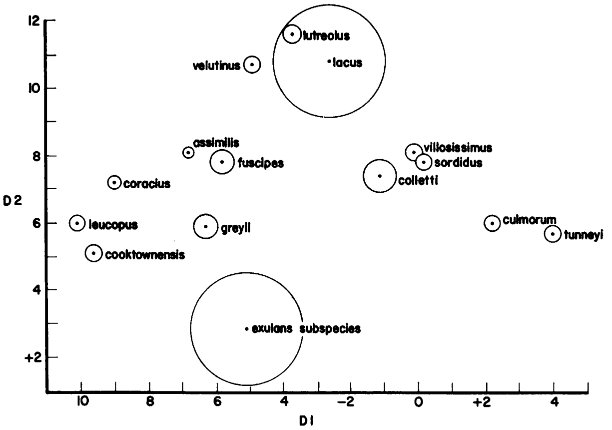


FIG. 43. Plot of group means of each subspecies of Australian *Rattus*. Statistical methods are the same as for figure 42.

When the data are again combined for each species without separate treatment of the sexes, this time substituting three external measurements [head and body length, tail length, and hind-foot length (s.u.)] for the three cranial measurements that appeared from correlation analysis to be least informative, the results (Test 3) are the same as in Test 1. *Rattus exulans* subspecies is excluded in this third test since fresh body measurements are not available.

A test of the 15 subspecies utilizes the 20 skull measurements (Test 4). The resulting plot diagram shows every subspecies, except for *R. lutreolus lutreolus* and *R. lutreolus lacus*, to be distinct at the 95 per cent confidence level (fig. 43). *Rattus lutreolus lacus*, like *R. exulans* subspecies, is represented by only two specimens and the confidence limits are very wide and include *R. lutreolus lutreolus* in a peripheral position. The same would, no doubt, occur for *R. exulans* subspecies if it, like *R. lutreolus lacus*, had a subspecific counterpart in the test. Once again the triangular pattern, although somewhat modified, is readily apparent, with each subspecies being closer to other members of its own species group than any is to another species, with the exception of *R. fuscipes coracius*. *Rattus fuscipes coracius* is actually closer to *R. leucopus leucopus* than it is to its nearest subspecies ally, *R. fuscipes assimilis*, and about equidistant from *R. f. assimilis* and *R. leucopus cooktownensis*. Within the *R. fuscipes* group, the nominate subspecies shows the most affinity to *R. f. assimilis* and the least to *R. f. coracius*. Another point of interest to emerge from this test is that *Rattus sordidus sordidus* and *R. sordidus villosissimus* are only just separable at the 95 per cent confidence level, showing more affinity to one another than either does to *R. sordidus colletti.* The large species triangle, referred to in Tests 1 through 3, has its corners held by *R. lutreolus lutreolus*, *R. tunneyi tunneyi* and *R. leucopus cooktownensis.*

If "*R. leucopus mcilwraithi*," the subspecies proposed by Tate (1951) and not recognized by us, is separated from the remaining *R. leucopus leucopus* and a test of the same nature as Test 4 is made (Test 5), "*mcilwraithi*" and *R. l. leucopus* overlap by about 50 per cent and fail the test at the 95 per cent confidence level. The test shows "*mcilwraithi*" to be slightly farther from *R. l. cooktownensis* than are the remaining *R. l. leucopus.*

When the three body measurements are substituted for three skull measurements (Test 6) as in Test 3, and the test otherwise run as in Test 4, the results are virtually the same as those of Test 4, except that *R. fuscipes coracius* is slightly closer to *R. fuscipes assimilis* than to *R. leucopus leucopus.*

In the last two tests *R. fuscipes* was subdivided by treating *R. f. assimilis* by geographical divisions and by separating the insular "*R. f. mondraineus*" of Western Australia, as well as "*R. f. glauerti*," from the rest of *R. f. fuscipes.* In the first of these tests (Test 7) both "*glauerti*" and "*mondraineus*" were utilized to more than the orthodox maximum by incorporating estimated missing values into the data in order to raise the small sample size for each to nine. *Rattus fuscipes assimilis* was divided into two groups, northern and southern. The plot diagram resulting from this test shows "*mondraineus*" and "*glauerti*" to overlap substantially with each other and with *R. f. greyii* and northern *R. f. assimilis.* The latter two do not overlap with each other, however. The southern sample of *R. f. assimilis* is closer to *R. f. fuscipes* than it is to any other member of the *R. fuscipes* group, including the northern *R. f. assimilis. Rattus fuscipes coracius* is slightly closer to *R. leucopus leucopus* than it is to any other member of the *R. fuscipes* group, as it was in Tests 4 and 5 but not Test 6. All other subspecies remain distinct (except *R. lutreolus lacus* which overlaps with *R. lutreolus lutreolus*) and maintain their basic relationship as seen in Tests 4 through 6.

In the last test (Test 8) the *R. fuscipes assimilis* are divided into three geographical groups, north, middle, and south. *Rattus lutreolus lacus* and *R. exulans* subspecies are omitted, and "*R. leucopus mcilwraithi*" is treated separately from *R. leucopus leucopus* (table 16). Otherwise it is like Test 7. There is no overlap between *R. f. assimilis* groups. Northern *R. f. assimilis* overlaps with "*R. f. mondraineus*" only. The middle *R. f. assimilis* are close to *R. f. fuscipes* but do not overlap, and southern *R. f. assimilis* are quite separate from any other group, but show equal alliance to middle *R. f. assimilis* and to *R. f. fuscipes.* Northern *R. f. assimilis* are as fully distinct from southern *R. f. assimilis* as *R. f. coracius* is from *R. f. greyii.* Both northern *R. f. assimilis* and *R. f. coracius* are closer to *R. leucopus* than either is to southern *R. f. assimilis.* Substantial overlap occurs between *R. sordidus sordidus* and *R. sordidus villosissimus. Rattus leucopus leucopus* and "*R. leucopus mcilwraithi*" are not separable. All other subspecies are as in Tests 4 through 7.

DISCUSSION

NATIVE MEMBERS of the genus *Rattus* are among the most recent prehistoric arrivals of terrestrial mammals to become established in Australia before the arrival of man. The first representatives of *Rattus* to reach Australia probably arrived no later than early Pleistocene (Simpson, 1961) and it is generally accepted that there has been further migration of *Rattus* between New Guinea and Australia in the later Pleistocene and possibly early Recent (Simpson, 1961).

THE SPECIES LEVEL

It is academic to treat *R. exulans* subspecies among the Australian *Rattus* fauna as it is allopatric with all native *Rattus* and has never become established on continental Australia. Furthermore, its gain of access to the islands falling within the political boundaries of Australia was probably by native canoe and Macassar prau and this undoubtedly occurred within the last few centuries. It is outside the province of the present paper to focus the geographical distribution of *R. exulans* in line with its widespread distribution in New Guinea and the many other insular situations of Australasia north of continental Australia. Until such a comprehensive study of the whole species *R. exulans* is made, it seems unwise to attempt subspecific designation of this species as it occurs within political Australia.

Rattus exulans is not included in our discussion of evolutionary relationships among *Rattus* in Australia as this species does not at present play a meaningful role. What is intriguing about *R. exulans* is that it has approached continental Australia to within 50 miles according to museum records and undoubtedly has come even closer at least by native craft; yet, to the present day, it has never become established on the mainland. Beach *Pandanus* habitats are plentiful along the north coast of Australia and presumably offer suitable requirements for this rat. It may be, however, that the seasonally dry conditions of most of northern Australia present a limiting factor. *Rattus exulans* holds its own in New Guinea among several other species of *Rattus*, some of which are close allies of two species inhabiting north Australia, so the problem is more subtle than can be settled by an interspecific competition explanation [see Watson (1961) for further discussion].

The truly native forms of *Rattus* fall into five species: *R. fuscipes*, *R. leucopus*, *R. lutreolus*, *R. sordidus*, and *R. tunneyi*. Two of these, *R. leucopus* and *R. sordidus*, have conspecific allies in New Guinea, *R. leucopus* and *R.* "*gestri*," and the other three are of sufficient morphological distinction as to be apparently separable from any New Guinea *Rattus* at the level of species. On this basis, the species are divisible into three groups: the closest representative to the oldest immigrant, *R. lutreolus*, and two diverging branches from the stem form. One branch consists of *R. fuscipes* and *R. leucopus*, both forest forms. Of these, *R. fuscipes*, through a northern representative, perhaps like *R. f. coracius*, may have given rise to *R. leucopus*. It is geologically feasible for a *coracius*-like population to have crossed the Torres Strait when, during a cool period, sea levels were lowered, to have been isolated in New Guinea during the subsequent interglacial, and to have re-entered northern Australia in a later glacial period as *R. leucopus*, a form which was by then reproductively isolated from *R. f. coracius*. This view, offered by Calaby (personal commun.) when he examined our Australian data, is substantiated on the New Guinea side by Tate (1951), who claimed that on that island *R. leucopus* is found chiefly in southern New Guinea where it inhabits the lower reaches of rain forest. The other branch consists of *R. sordidus* and *R. tunneyi*, both of which are grassland forms. It appears likely that they evolved in northern Australia and that *R. sordidus* alone spread to New Guinea during the last land connection across the present Torres Strait. In New Guinea *R. sordidus* appears to be confined to the southern lowland (Tate, 1951), an area that bears vegetation similar to that of Cape York (Calaby, personal commun.). The distribution of *R. sordidus* in New Guinea (Tate, 1951) is apparently much more circumscribed than is that of *R. leucopus* in this lowland country.

Rattus lutreolus is basically a grassland form which, at least in present association with other native *Rattus*, has come to occupy the grass, sedge, and heath of wetlands of Australia (including Tasmania). Presumably, *R. lutreolus* was never an occupant of arid grasslands, hence, is now barred from occupation of inland continental Australia. The very dark coloration is reflective of the humid environment the rat occupies (according to Gloger's Rule), and the extremely dense underfur is probably associated with its damp surroundings. The distribution in Australia is largely limited by wetland requirements, and this species now occurs only on the eastern seaboard and Tasmania.

Rattus tunneyi occurs in dry grasslands, either coastal or inland, having spread widely over the arid inland portions of continental Australia as well as over coastal Australia, except coastal New South Wales and Victoria where arid grasslands do not occur to any appreciable extent. *Rattus tunneyi* is generally a light-colored rat, darkening perceptibly only in southeastern Queensland where it is occupying a less arid grassland situation at an extremity of its range.

Rattus fuscipes is an inhabitant of the forests and associated brushlands of Australia. This rat has followed the distribution of forests virtually everywhere except into the drier forests of northern Australia and is essentially coastal in distribution, from Cape York to Victoria and west to southwestern Western Australia. The absence of this species from the forest lands of Tasmania is puzzling. It is sympatric with *R. lutreolus* in all other areas where the latter occurs. The broad Bassian Isthmus of the Upper Pleistocene, which housed a large centrally located depression (Jennings, 1971), was conceivably mainly wetlands. The islands of the Bass Strait have yielded only *R. lutreolus*, so *R. fuscipes* apparently never came close to the land mass of Tasmania as we know it today. Yet the present strength of occurrence in Victoria was probably extant in the Upper Pleistocene. Equally baffling is the fact that *R. fuscipes* reached southwestern Australia, whereas *R. lutreolus* did not. Inland Australia in parts of the Pleistocene was cold and wet, with abundant lakes and river systems, but apparently an ecological pathway was not available to *R. lutreolus* all the way to western Australia, even via the coastal plains south of the Nullarbor Plain that existed in the Upper Pleistocene (Jennings, 1971). The occurrence of *R. fuscipes* in the southwestern corner confirms that this species, however, was able to utilize the ecological corridor between southeastern and southwestern continental Australia, along with *R. tunneyi culmorum*. The end of the Pleistocene Epoch terminated this ecological bridge.

The *R. fuscipes* picture is complicated. Superimposed upon northern *R. f. assimilis* and *R. f. coracius* is the species *R. leucopus* to the extent that *R. f. coracius* shows strong affinity to *R. leucopus* and northern *R. f. assimilis* a moderate one (see Test 8). This complication suggests several factors, the most obvious of which is that *R. fuscipes* and *R. leucopus* probably share a common evolutionary line. Whether the evolutionary separation occurred on the Australian side or in the New Guinea area is speculative. What is important is the fact that migration of *R. leucopus*, or its prototype, to and from Australia may have occurred more than once and at times preceding full reproductive isolation from the *assimilis-coracius* part of the *R. fuscipes* line.

During its time of residence in Australia, *R. leucopus* has occupied the drier forests of the northern tip of continental Australia and the fringe of the Atherton rain forests. This species has never gained access to the seemingly suitable rain forests of the central coast of the Northern Territory, nor reached the drier rain forests of the Mackay area.

Rattus sordidus is a rat of the tropical and subtropical grasslands. It has spread widely over mainland Australia in the north, occupying the highly specialized black-soil flood plains of the Northern Territory, the entire central grassland region that has ephemeral water courses, and the northeast coastal grasslands. Both the flood plains and the coastal grasslands are largely humid habitats and this is reflected in the somber coat color of *R. sordidus colletti* and *R. sordidus sordidus*, respectively. The form occupying the inland savanna, *R. sordidus villosissimus*, inhabits, along with *R. tunneyi tunneyi*, the most arid environments utilized by *Rattus* in Australia. The pelage of this form is lighter than in any other subspecies and contains relatively less underfur. Of all Australian *Rattus*, *R. sordidus villosissimus* contrasts most markedly with *R. lutreolus* in this respect.

Among the Australian native *Rattus* there are then, two forest species and three grassland species. The forest forms, being restricted to the denser woods of the continent, are mainly coastal and subcoastal in distribution. Although their spread over the continent may be extensive, as it is in *R. fuscipes*, it is linear. The forest forms are also much more vulnerable to reproductively isolating factors such as geographically small ecological breaks between forest elements. The grassland form that occupies the more arid regions, *R. tunneyi*, has far more opportunity to spread widely since such grasslands cover a large portion of the continent, and *R. tunneyi* is the most geographically widespread of all the species. A close second is *R. sordidus* by virtue of the fact that the subspecies *R. s. villosissimus* also inhabits drier grasslands. The remaining *R. sordidus* are confined to the more humid grasslands and flood plains of the tropics and subtropics and are hence, like *R. fuscipes*, largely linear in distribution. *Rattus lutreolus* is also largely linear for it is restricted to the temperate (or tropical, in the case of *R. l. lacus*) wetlands, which are coastal and subcoastal in occurrence.

The pattern of relationships among the Australian species of *Rattus* forms an almost perfect V-shape on the basis of skull parameters and conventional body measurements (Tests 1 through 3 and fig. 42). *Rattus lutreolus* assumes the position of a "stem form" from which *R. fuscipes* and then *R. leucopus* rise to form one line and *R. sordidus* and then *R. tunneyi* rise to form the other. The close alliance between *R. fuscipes* and *R. leucopus* appears to be a real one as the north Queensland situation indicates. There is also an obvious close alliance between the nominate form of *R. sordidus* and the subspecies *R. t. culmorum* of *R. tunneyi*. *Rattus sordidus sordidus* and *R. t. culmorum* are so similar morphologically in many areas that they can be difficult to separate without extensive study (i.e., the "*youngi*" problem). Except for bulla size and the difference of the teloloph on m_1 and m_2 (on all but *R. l. velutinus*), the *R. lutreolus* line is often hard to separate from *R. sordidus sordidus* or *R. sordidus villossisimus*. Ample evidence of this comes forth in the historical controversy over the identification of "*vellerosus*" or of the original *R. sordidus* from the Darling Downs, both of which have been allied to both *R. lutreolus* and to *R. sordidus*.

We find the V-shaped pattern an acceptable one with a prototype of *R. lutreolus* serving as a stem form. *Rattus fuscipes* appears to be an old offshoot from this stem form on the one hand, and so does the *sordidus-tunneyi* line, on the other. Probably the most ancient offshoot from the ancestral stock of *R. lutreolus* is *R. fuscipes*. It is probable, too, that this original evolutionary step occurred in Australia, and not farther north, and that the separation of the *sordidus-tunneyi* line from *R. lutreolus* also took place here. Without fossil evidence one is forced to become increasingly speculative in trying to ascertain whether the evolution of the other lines took place here as well. A reassessment of the New Guinea *Rattus* is urgently needed for that type of evaluation. However, we postulate that *R. sordidus* and *R. tunneyi* speciated through an *R. t. culmorum–R. s. sordidus* ancestral type in what is now northeastern Australia and, as stated earlier, that *R. leucopus* evolved into a full species in southeastern New Guinea from an *R. fuscipes coracius*-like ancestor.

Late exchange with New Guinea *Rattus* has occurred in the *R. sordidus* line, with *R. "gestri"* being a conspecific ally of the latter. As we have not extended this study into a personal examination of New Guinea forms it is difficult to judge whether a "*gestri*"-like form may also be an ally of *R. tunneyi*. Certainly, *R. tunneyi* and *R. sordidus* are biologically separable in Australia at the species level for they maintain their integrity while being sympatric over much of their range.

Tate (1952, p. 572), in his study of the Cape York mammals, regarded *R. sordidus sordidus* and *R. lutreolus lacus* as Australian in origin, all *R. leucopus* as Papuan, and *R. fuscipes coracius* as both.

The recent interest in the karyotypes of murids in Australia has also given rise to suggestions as to the possible evolutionary origins of Australian *Rattus*. Unfortunately, at the time of this writing the karyotypes of only a few of the subspecies have been analyzed morphologically. The forms for which chromosome counts have been published are: *R. fuscipes fuscipes*, 38 (Kennedy, 1969); *R. fuscipes greyii*, 38 (Kennedy, 1969); *R. fuscipes assimilis*, 38 (Kennedy, 1969; Martin, 1969; Yosida et al., 1969); *R. lutreolus lutreolus*, 42 (Kennedy, 1969); *R. lutreolus velutinus*, 42 (Dartnall, 1970); *R. sordidus sordidus*, 32 (Martin, 1969; Yosida et al., 1969); and *R. sordidus villosissimus*, 50 (Kennedy, 1969). Kennedy (1969) postulated that *lutreolus* arose from an ancestral form closely related to *R. norvegicus*. Both Kennedy (1969), in her karyotypic analyses of *R. l. lutreolus*, *R. f. fuscipes*, *R. f. assimilis*, and *R. f. greyii* and Dartnall (1969) in her analysis of *R. l. velutinus*, have concluded that the *R. lutreolus* karyotype could represent a basic one. Kennedy (1969) suggested that *R. f. fuscipes*, *R. f. greyii*, and *R. f. assimilis* could be derived from *R. lutreolus*, and Dartnall (1969) suggested that *R. s. sordidus* (=*R. conatus*) could also be derived from *R. lutreolus* by a series of Robertsonian translocations. Kennedy (1969), however, illustrated that a direct derivation of *R. s. villosissimus* from a *R. lutreolus* type may be complicated in terms of chromosome rearrangements.

The recent study by Misonne (1969) describes a view of evolution of *Rattus* in Australia. His proposal is that *R. leucopus* and *R. greyii-R. assimilis* are of sufficient distinction from the remaining Australian *Rattus* to be placed in the subgenus *Stenomys*, in a grouping somewhat similar to that proposed by Tate (1951). The remaining *Rattus* he placed as an "Australian group" and suggested that "it is perhaps not so close to *Rattus* as it would seem; in this case, it would represent another subgenus on its own, distinct from both *Stenomys* and *Rattus*" (Misonne, 1969, p. 168). He regarded *R. s. villosissimus* as the oldest form and suggested that the entire Australian group is closely related, perhaps stemming from a few individuals (see Misonne, 1969, p. 134). He made no commitment as to the degree of relationship, however. This is a major departure from our own proposal, especially since our cross-breeding tests between *R. f. greyii* and *R. f. assimilis* (of his *Stenomys* subgenus) with *R. f. fuscipes* (of his Australian group) appear to give unequivocal evidence for not only consubgeneric but conspecific alliance (Horner and Taylor, 1965).

In addition to our ecological separation of species based on major habitat selections, there is a skull character which is very significant at the species level and is also reflective of habitat differences. This is the size of the auditory bullae. It has long been recognized that desert and tundra mammals throughout the world tend to have larger bullae and/or pinnae than those mammals inhabiting areas of dense vegetation. This correlation occurs within the Australian genus *Rattus*. The two species of the drier grasslands, *R. tunneyi* and *R. sordidus*, have large bullae, and range in ratio of bulla to basal length of skull from 26 to 27 per cent in *R. tunneyi* and from 22 to 23 per cent in *R. sordidus*. *Rattus tunneyi* is the more open-grassland form. The grassland form of the wetlands, *R. lutreolus*, inhabits much denser vegetation. The same ratio within this species is between 18 and 20 per cent. In the two forest forms, *R. fuscipes* and *R. leucopus*, the range is from 18 to 20 per cent in *R. fuscipes* and 18 per cent in *R. leucopus*.

Another morphological aspect significant at the species level is that of mammary formula. In three of the five species, *R. tunneyi*, *R. sordidus*, and *R. leucopus*, the mammary formula is consistent at the species level (except for minor individual variation). In *R. fuscipes* there is a distinct shift in the pectoral formula between two pairs and one pair. In *R. lutreolus* the nominate subspecies differs from *R. lutreolus velutinus* by one pair of inguinal teats, and the situation is unknown in *R. lutreolus lacus*. Among Australian *Rattus* there is a tendency for a constant mammary formula at the species level, varying at the subspecies level in *R. lutreolus* and within a subspecies, as well as between, in *R. fuscipes*. Hence, the mammary formula can be regarded as a moderately reliable character at the species level, and an exceedingly reliable one when the now-recognized pattern of subspecies or geographic variation is considered.

Sody (1941) took an extreme view when he emphasized the importance of the mammary formula in *Rattus*. Although he acknowledged that there is variability within *R. rattus* between $2+3=10$ and $3+3=12$, he dismissed this on the grounds that the difference correlates with two ecological races. This correlation, however, does not seem to hold, for we have found litter mates of wild *R. rattus* in Australia exhibiting the two formulas. He placed such reliability on differences in mammary formulas that he used this character as the basis for erecting a number of new genera of murids previously regarded as either *Rattus* or *Mus* in the Indo-Malayan and Indo-Australian regions (Sody, 1941, pp. 260–261). He thought that the eight different formulas found among *Rattus* in the Oriental species reflect heterogeneity at the generic level. Among the native Australian *Rattus* alone, a group that we regard as truly homogeneous at the generic level, there are five different formulas.

A third morphological variant, that of the presence or absence of spines in the pelage, knows no taxonomic boundaries. This appears to be a reflection of environmental aridity in the adult pelage. Spinous pelage occurs in *R. tunneyi*, *R. leucopus*, and in *R. sordidus*, among those geographical populations occupying a hot and, at least seasonally, dry climate. In all three groups, as they extend southward into a more temperate situation or into areas with more extended annual rainfall, the spines are reduced in number and size or lost completely. This, too, is a character that is often found in pelages of mammals occupying hot arid environments throughout the world. It is tempting to speculate that it may operate as part of a heat regulating device.

THE SUBSPECIES LEVEL

The division of *R. fuscipes* into four subspecies roughly coincides with the major groupings of denser sclerophyll and rain forests in continental Australia. Of these subspecies, *R. f. fuscipes* is the most isolated, being confined to the southwestern portion of the continent and at least 700 miles west of its nearest ally, *R. f. greyii*. It is separated from *R. f. greyii* by the Nullarbor Plain which is semi-arid mallee and shrub steppe country. *Rattus fuscipes greyii* occurs in the forests and tea-tree areas of coastal South Australia and into western Victoria. There are several areas of shrub steppe and mallee country that break up the distribution within *R. f. greyii* somewhat, but none is over 100 miles in span. Between *R. f. greyii* and *R. f. assimilis* is a major floral intervention of temperate tussock grassland and tree savanna, a span of only 60 miles, but one that produces a significant faunal break. *Rattus fuscipes assimilis* extends as a virtual continuum across eastern Victoria up the mountainous regions of the east and northeast coastline into New South Wales. The present small gap just south of the Victorian border is probably due only to lack of collecting in that area. It extends all the way up coastal New South Wales and into southern Queensland, the small gap in north-central New South Wales coast again probably reflecting only a lack of collecting in that vicinity. North of the Gympie area *R. f. assimilis* follows the patches of tropical rain forest and soon reaches its northern limit. A large intervening floral change composed of mixed coastal and tropical woodland forms a span of about 350 miles that separates *R. f. assimilis* from *R. f. coracius*. Although rain forests occur in patches along this span, they are all characterized by a stony forest floor and hard-packed soil. Our trapping efforts in lowland creeks just south of Townsville, the rain forests of Proserpine, Eungella National Park, the Mackay area, and Connor's Range yielded no *R. f. assimilis* or *R. f. coracius*. The latter subspecies is confined to the rain forests of the Townsville-to-Cooktown area that receive a high rainfall for no less than nine months of the year.

Although the species *R. fuscipes* is linear in distribution, there is very little in the way of obvious morphological trends between subspecies. The major trend is one of size; both *R. f. fuscipes* and *R. f. greyii* are distinctly smaller subspecies than are *R. f. assimilis* and *R. f. coracius*. The shift in mammary formula from $2+3=10$ in *R. f. fuscipes*, *R. f. greyii*, and the more southern *R. f. assimilis*, to $1+3=8$ in northern *R. f. assimilis* and in *R. f. coracius* is another trend. White pectoral spotting, present in some *R. f. assimilis* (but not significant in *R. f. fuscipes* or *R. f. greyii*), increases markedly in *R. f. coracius*. Kennedy (1969) suggested that *R. f. greyii* and *R. f. assimilis* were derived from an *R. lutreolus*-type rat later than was *R. f. fuscipes*.

An expression of the genetic compatibility of the species *R. fuscipes* has been shown by a series of cross-breeding experiments, using *R. f. fuscipes*, *R. f. greyii*, and *R. f. assimilis* that yielded hybrids through the F_2 generation in each cross (Horner and Taylor, 1965).

The two subspecies of *R. leucopus* are exceedingly restricted in their geographical distribution. The hiatus between them occurs where there is a break in rain forest, a region of about 150 miles between the Coen and Cooktown areas. The intervening area is coastal tussock grassland and tropical woodland. Although there are breaks in the occurrence of rain forest south of the Townsville area and a shift to a lower rainfall type of rain forest, it is somewhat surprising that *R. leucopus cooktownensis* has not spread farther south than has *R. f. coracius*, since it is more tolerant of open floor rain forests than is the latter form. The breaks between these rain forests are small, being usually less than 50 miles.

The most distinct morphological changes that *R. l. cooktownensis* demonstrates, when compared to its northern counterpart, *R. l. leucopus*, are a decrease in opisthodonty, a reduction in length of molar row, reduction or loss of spines, a shift to light gray basal fur ventrally, and a reduction or loss of mottling on the tail.

Rattus lutreolus is mainly a species of the southeastern portion of Australia, including Tasmania. *Rattus lutreolus velutinus* is the only native species of *Rattus* on Tasmania and is separated from its nearest ally, *R. l. lutreolus*, by the Bass Strait, a span of about 150 miles. *Rattus lutreolus lutreolus* occurs in an almost continuous span coastally from eastern South Australia up into southern Queensland. Between the Gympie area of Queensland and the Atherton Tableland where *R. lutreolus lacus* occurs suitable wetlands appear to be non-existent. This habitat break is about 800 miles. North of the Atherton Tableland where again *R. lutreolus* is absent suitable wetlands appear to be missing. Although *R. l. lutreolus* is geographically closer to *R. l. velutinus* and separated only by a strait that was a land bridge several times during the Pleistocene, it is morphologically closer to the isolated *R. l. lacus* of the Atherton Tableland. It is highly possible that wetlands were much more extensive up the eastern seaboard and that *R. l. lutreolus* and *R. l. lacus* were confluent more recently than the end of the last land connection to Tasmania between 10,000 to 12,500 years B.P. (Jennings, 1971).

Of the three subspecies of *R. sordidus*, the nominate form is restricted to the tropical and subtropical coastal grasslands of Queensland, and its southern termination at the New South Wales border coincides with the end of the monsoonal grasslands and the beginning of a southern coastal band of sclerophyll forest. It is separated from its ally, *R. sordidus villosissimus*, by the Great Dividing Range for most of its length and by the advent of dry inland savanna country to the west. *Rattus sordidus villosissimus* parallels *R. s. sordidus* in a north-south distribution with a hiatus of about 200 miles between them and extends over a vast area of the interior. The full extent of its range is still unknown. It is reputed to be a migrant at times of great population density and it appears to follow the drainage systems of the interior to a large extent. If indeed this is true (Finlayson, 1939b), *R. s. villosissimus* may be a more genetically homogeneous subspecies for its geographical extent than any other in Australia. To the northwest it comes very close to *R. sordidus colletti* but, although *R. s. villosissimus* is a rat of the dry tussock grasslands and arid scrub, *R. s. colletti* is sharply restricted to the coastal flood plains and humid tropical river systems that drain into the plains. The ecological separation appears so distinct that peripheral sympatry is highly unlikely.

Of the three subspecies, the middle one geographically, *R. s. villosissimus*, appears to be more closely allied morphologically with *R. s. sordidus* than with *R. s. colletti* (Tests 4 through 8). Whereas this morphological analysis indicates that *R. s. villosissimus* is close to both *R. s. sordidus* and *R. s. colletti*, *R. s. villosissimus* and *R. s. sordidus* being closer than is any other subspecies pair (fig. 43), the discrepancy in karyotypes is very large. *Rattus sordidus villosissimus* has 50 chromosomes and *R. s. sordidus* has only 32. The possibility exists that the difference in chromosome count would render these two allopatric forms reproductively incompatible when subjected to cross-breeding tests. If so, *R. s. villosissimus* would have to be regarded a full species. Until such tests are made, however, we regard *R. s. villosissimus* as a subspecies of *R. sordidus* on morphological grounds.

The two subspecies of *R. tunneyi* are today coastal and subcoastal in distribution along much of northern and eastern Australia. Only 100 years ago or so, however, they occurred not only well inland but also in the coastal and subcoastal southwestern portion of the continent and probably in subcoastal as well as coastal South Australia. The contraction of its distribution is no doubt due largely to human exploitation of the extensive grasslands for the grazing of domestic stock. Today *R. t. culmorum* and *R. t. tunneyi* appear widely separated by a distance of at least 600 miles, a hiatus through western Queensland. Both subspecies are rats of seasonally arid tussock grasslands. *Rattus tunneyi tunneyi* is confined to the tropical and subtropical regions, whereas *R. t. culmorum* can also tolerate the grasslands of the temperate regions in places of relatively low rainfall.

The ecological niche separation between *R. t. culmorum* and *R. s. sordidus* in their areas of sympatry is not clear. Both utilize the coastal and subcoastal grasslands, although, of the two, *R. t. culmorum* is more tolerant of greater aridity. *Rattus tunneyi culmorum* has not been trapped north of Mackay since 1923, and since then only rarely outside of plantations. The only material, except cave deposit skulls, ever taken outside of Queensland was collected between 1841 and 1846 in New South Wales, South Australia, and Western Australia. Although it is quite likely that these more southern members actually represent one or more separate subspecies, the present material is inadequate for such distinction. Since they align more closely with *R. t. culmorum* than with *R. t. tunneyi*, we have chosen to regard them as *R. t. culmorum* until such time as more and better material becomes available and their status can be reassessed.

The morphological trend in *R. t. culmorum* and *R. t. tunneyi* is toward an increase in bulla size and interorbital width and a decrease in nasal length in the latter form. The ventral body pelage is also white to the base in *R. t. tunneyi* and gray-based in *R. t. culmorum.*

Examination of the distribution of the various subspecies of *Rattus* in Australia (fig. 44) focuses attention on the eastern half of the continent where the greatest number of forms occur. Higher concentrations of subspecies exist on the eastern seaboard, particularly the northern two-thirds, than occur elsewhere in Australia. Although this coincides in part with the obligate pathway of *Rattus* between Australia and the north, the concentration is not attributable to this factor alone. The two regions of highest concentration, the Atherton Tableland and adjacent lowlands on the one hand, and the Brisbane area on the other, represent two major regions of extensive vegetational diversity. They are both coastal and have the potential of relatively high rainfall. Complicating the Atherton picture are great altitudinal differences creating the highest rainfall area on the continent and this abuts a dry interior situation. The diversity of the Brisbane area is due largely to its position as a transition zone between the northern monsoonal and the southern temperate climates. The subspecies of *Rattus* have utilized this diversity to the maximum, with representatives of all five species resident in the Atherton area and representatives of all four of the more southern species occurring in the southeastern Queensland region. Over most of the vast remaining portion of the continent inhabited by *Rattus* the subspecies occur as one or two representatives, or, in northern Cape York, as three. This general type of distribution is not confined to the *Rattus* segment of the Australian mammal fauna. Calaby (1966) found the area just south of Brisbane to be one of the richest on the continent in both marsupials and rodents. As most of the marsupial evolution was truly intra-Australian, the diversification of *Rattus* here must also be attributed largely to local exploitation of habitat differences rather than to the shadow of a pathway between Australian and Papuan faunas.

Opportunity for spread on the Australian continent is a factor which helps explain the impoverishment of *Rattus* in the far west. There are two likely routes for *Rattus* to take to the southwest. One is the coastal pathway south of the Nullarbor Plain which existed in the Upper Pleistocene (Jennings, 1971) and was a migration corridor for a number of mammals, including *R. f. fuscipes* and *R. t. culmorum* from the central south coast. *Rattus fuscipes fuscipes* left insular pockets along the way. Apparently, *R. lutreolus* was ecologically excluded from this route. The other route is from the northwest. Jennings (1971) stated that in the Upper Pleistocene the coastal area of the Great Sandy Desert remained arid despite continental climatic change and he considered it unlikely that this was ever a favorable migration route during that time. Among *Rattus*, only *R. t. tunneyi*, a natural inhabiter of arid environments, appears to have extended south along this route. The other arid form, *R. s. villosissimus*, has apparently been excluded.

Unlike the far west, the east has had a broad connection with land to the north and, except for the Bassian Isthmus, little in the way of restrictive routes. Jennings (1971) gave evidence for a broad connection between New Guinea and Australia involving what is now the Gulf of Carpentaria, the Arafura and Timor seas, and

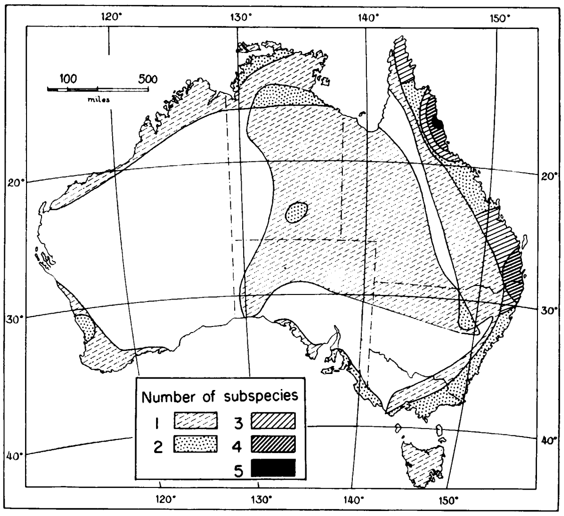


Fig. 44. Map of the geographical distribution of native Australian *Rattus* according to the number of subspecies. The eastern seaboard has the greatest overall representation, with the region of the Atherton Tableland reaching a maximum of five.

Torres Strait, a connection that terminated between 6500 and 8000 years B.P. In terms of exchange of *Rattus* between Australia and New Guinea, the Arnhem Land area would have as great a potential as the eastern seaboard of Australia. This potential is not realized, however, in the present faunal distribution of *Rattus*. The factor of habitat diversity, as discussed earlier, plays the major role and results in the greatest representation of *Rattus* along parts of the eastern seaboard.

CONCLUSIONS

The Australian members of the genus *Rattus* together represent the only group of terrestrial mammals native to the island continent that has congeneric relatives beyond the limits of the Australasian Region. In Australia, where genera and families of terrestrial mammals are almost exclusively autochthonous, native members of the genus *Rattus* rest in sharp contrast in terms of their evolutionary history. *Rattus* is thought to have gained access to Australia from southeast Asia as a late immigrant, possibly in the early Pleistocene, and, in the face of a substantial marsupial and pseudomyine fauna, it has radiated on this island land mass. Our study of the systematics of *Rattus* in Australia has sought to assess the extent of radiation which *Rattus* has been able to achieve since its arrival there, in terms of evolutionary relationships at the species and subspecies levels and in terms of utilization of habitats.

Rattus has diversified to the extent of five native species (excluding *R. exulans*) and 14 subspecies. In only one region of Australia do representatives of all five species occur, and over the majority of the continent only one or two representatives have become established. *Rattus* is a very conservative genus morphologically. Among Australian members the only characters which show much variation are pelage color and texture and relative size of the auditory bullae. It has remained terrestrial, nocturnal, and a moderate burrower.

The progenitor of the Australian *Rattus* appears to be an ancestral form of *R. lutreolus* which today is mainly an inhabitant of the temperate wetlands. Two main branches have evolved, both of which have had intermingling with Papuan *Rattus* during the course of their evolution. The two branches, represented by *R. fuscipes* and *R. leucopus* as one and *R. sordidus* and *R. tunneyi* as the other, have radiated ecologically into two major types of habitat. The first branch is a forest form and the second, a grassland form. The forest form is confined to the coastal and subcoastal regions of the eastern and southern portions of Australia, whereas the grassland branch has spread through much of the arid inland. The regions of greatest representation of species of *Rattus* coincide with the areas of greatest habitat diversity. As an essentially terrestrial form, *Rattus* appears to have made maximum utilization of the somewhat limited diversity of the Australian environment within the boundaries of a conservative evolutionary pathway.

KEY TO ADULT *Rattus* IN AUSTRALIA

1\. Posterior cusp lacking on m_1 and m_2 . . . 2
Posterior cusp present on m_1 and m_2 . . . 3
2(1). Nasal length over three times nasal width . . . . *R. lutreolus lutreolus*
Nasal length three times or less nasal width . . . . *R. lutreolus lacus*
3(1). Incisive foramina strongly bowed laterally . 4
Incisive foramina not strongly bowed laterally 8
4(3). Upper molar row less than 5 mm. . . . . *R. exulans* subspecies
Upper molar row longer than 5 mm . . . 5
5(4). Tail exceeds head and body length by 20 mm. or more; females with 10–12 teats . . . . *R. rattus*
Tail less than 20 mm. beyond head and body length; mammary formula 1+2=6 or 3+3=12 6
6(5). Strong supraorbital-temporal ridging; mammary formula 3+3=12 . . *R. norvegicus*
Weak supraorbital-temporal ridging; mammary formula 1+2=6 7
7(6). Tail tip white and/or body venter white or cream to base . . . . *R. leucopus leucopus*
Tail tip pigmented and/or body venter gray at base . . . . . *R. leucopus cooktownensis*
8(3). Skin of hind feet darkly pigmented; mammary formula 2+2=8 . . . . *R. lutreolus velutinus*
Skin of hind feet not darkly pigmented; mammary formula otherwise 9
9(8). Entire ventral pelage creamy white . . . 10
Entire ventral pelage not creamy white . . 11
10(9). Tail exceeds head and body length; uninflated bullae . . . . *R. rattus*
Tail equal to or less than head and body length; inflated bullae in which interbullar distance is less than half the width of one bulla . . . . *R. tunneyi tunneyi*

11(9). Bulla length one-third greater than interorbital width; supraorbital-temporal ridging moderate to strong 12
Bulla length less than one-third greater than interorbital width; supraorbital-temporal ridging weak. 15

12(11). Bulla exceeds incisive foramen length by 0.5 mm. or more; mammary formula 2+3=10 . . . . *R. tunneyi culmorum*
Bulla fails to exceed incisive foramen length by 0.5 mm.; mammary formula 3+3=12 13

13(12). Pelage light and grizzled dorsally . . . . *R. sordidus villosissimus*
Pelage dark brown to blackish and grizzled 14

14(13). Skull length more than five times that of bulla; buff zone between dorsal and ventral pelage . . . . *R. sordidus colletti*
Skull length five times or less that of bulla; buff interzone lacking . *R. sordidus sordidus*

15(11). Hind feet covered by mixture of brown and silvery white hairs 16
Hind feet covered by whitish hairs 17

16(15). Tail 85 per cent or less of head and body length . . . . *R. fuscipes fuscipes*
Tail longer than 85 per cent of head and body length . . . . . *R. fuscipes assimilis*

17(15). Hind foot in most cases 6 mm. broad or less; mammary formula 2+3=10 . . . . *R. fuscipes greyii*
Hind foot in most cases more than 6 mm. wide; mammary formula 2+3=10 or 1+3=8. 18

18(17). Hind foot hairs silvery white; mammary formula 2+3=10 or 1+3=8; usually no ventral white spotting . *R. fuscipes assimilis*
Hind foot hairs dull white; mammary formula 1+3=8; ventral white spotting common . . . . . . *R. fuscipes coracius*

LOCALITIES OF MUSEUM SPECIMENS EXAMINED

Rattus exulans subspecies

QUEENSLAND: Mer, Murray Islands, 110 mi. NE tip of Cape York in Torres Strait (BM 99.9.10.2).

WESTERN AUSTRALIA: Adele Island, 180 mi. N Broome (BM 91.10.9.1–91.10.9.3).

Rattus fuscipes fuscipes

WESTERN AUSTRALIA: Abrolhos Islands, 70 mi. WNW Geraldton, known also as Houtman's Abrolhos Islands (BM 26.7.12.2); Albany (RMNH a; WAM M3867); Augusta (BM 44.2.15.36); Bunbury (AM M6855); Byford, 22 mi. SSE Perth (WAM M5815); Cape Riche, 60 mi. ENE Albany (WAM M2533); Carey Brook, 18 mi. W Pemberton (AMNH 196678–196682); Cheyne Beach, 60 mi. ENE Albany (WAM M5268); Denmark (AM M4211; AMNH 196671–196677; MVZ 133691–133705, 133709–133751, 133906; WAM M3900, M4279, M4536, M4609, M5800, M5801, M5806, M5825); Drover's Cave, Hill River, 120 mi. NNW Perth (fragments without registration number collected by A. Douglas and H. Butler, May, 1958); East Wallabi Island, island of Houtman's Abrolhos group (WAM M3030, M5109, M5110, M6309); Gidley Brook, 6 mi. W Nannup (WAM 7302); Jalbarragup Walsall, 125 mi. S Perth on coast (WAM M2451); Jarrahdale, 30 mi. SSE Perth (CSIRO CM859); King Creek, 20 mi. ENE Albany (AMNH 196664–196670; WAM M7301, M7303, M7307); King George's Sound (AM 9–12, 14; BM 46.4.4.74, 46.4.4.75, 58.11.24.8, 58.11.24.11, 58.12.27.11; MM M279, M774; NMV C195); King River, mouth of river, 8 mi. NE Albany (BM 6.8.1.66–6.8.1.72; WAM 11363–11366); "Little Grove," Albany (WAM M6634); Manjimup (AM M4357); Maranup Farm, Greenbushes, 130 mi. S Perth (WAM M1354); Mondrain Island, island of Archipelago of the Recherche (BM 7.7.18.2, 7.7.18.3, 26.10.1.1, 26.10.1.2; QM J3349; USNM 218458, 218459; WAM 8501A, 8504, 8842–8847); Nannup (AMNH 196683); Nornalup (AM M4210); Oyster Harbour, 5 mi. NE Albany (BM 6.10.25.2); Pemberton (MCZ 27938–27942, 28059, 28060; WAM M6241); Perth (BM 44.2.15.37, 86.1.26.13); Tackalarup, Mt. Barker, 30 mi. NNW Albany (WAM M2054); Tea Umpy, Cape Riche (WAM M2031); Two People Bay, 20 mi. E Albany (WAM M3768, M4002, M4003, M4901–M4904); Waychinicup River, 26 mi. ENE Albany (AMNH 196651–196663; WAM M7283, M7291–M7300, M7304, M7306, M7311); West Wallabi Island, island of Houtman's Abrolhos group (AM M7842, M7843; WAM 4345, M4478, M5107, M5108, M5111–M5119); Wilson's Inlet, 35 mi. W Albany (WAM 9830); Woody Island, island of Archipelago of the Recherche (AM M3113, M3114); Yellanup, Narrikup, 22 mi. NNW Albany (WAM M2361, M2376); Yornup, 150 mi. S Perth and 40 mi. inland (WAM M2176).

LOCALITY IN AUSTRALIA UNKNOWN: (MM M775; NMV C141, C144; RMNH d, d (*Mus gouldii*), f, g; WAM M4298; ZM BZM1865).

Rattus fuscipes greyii

SOUTH AUSTRALIA: Big Swamp, 14 mi. NW Port Lincoln (MVZ 133786); Birchmore Lagoon, 12 mi. SW Kingscote, Kangaroo Island (AM M2826–M2829; USNM 236726–236728, 236740–236745); Blackwood, 7 mi. S Adelaide (SAM M5977, M5978); Cleland's Gully, 30 mi. S Adelaide (AM M3284; BM 21.7.3.1, 22.4.15.4, 22.4.15.5; SAM M2281, M2466); Coffin's Bay. 30 mi. NW Port Lincoln (WAM M828); Deep Creek, 20 mi. SW Kingscote, Kangaroo Island (AM M2835–M2838, M2846); Fleurieu Peninsula, peninsula S Adelaide (MCZ 34964, 34965); Goat Island, 15 mi. SW Ceduna (BM 25.10. 8.44; WAM M3311–M3315, M3329); Greenly Island, off W tip Eyre Peninsula (SAM M5738–M5749); Kangaroo Island (SAM M2283, M2284; USNM 236732–236734, 236736–236739, 236746–236749, 236790, 236791); Kelly Hill Cave, 48 mi. WSW Kingscote, Kangaroo Island (SAM M6075); Mt. Compass, 30 mi. S Adelaide (NMV R8381, C1364–C1366); Mt. Drummond, 50 mi. NW Port Lincoln (MVZ 133752, 133753); Pearson Island, 100 mi. NW Port Lincoln (BM 23.3.28.1–23.3.28.6; MCZ 29781, 29782; NMV C982, C983; SAM M2285, M2286, M2468; WAM M616, M617, M826); Penneshaw, 18 mi. ESE Kingscote, Kangaroo Island (SAM M6286, M6287); Point Sir Isaac, 30 mi. NW Port Lincoln (BM 25.3.2.1, 25.3.2.2); Port Lincoln (MVZ 133783–133785; USNM 236729–236731); Rocky River, 55 mi. WSW Kingscote, Kangaroo Island (BM 21.11.9.2; MVZ 133754–133781); Southwest River, 50 mi. WSW Kingscote, Kangaroo Island (MVZ 133782); Tapanappa, 56 mi. SSW Adelaide (SAM M5795B); Timber Creek, 18 mi. SW Kingscote, Kangaroo Island (AM S1875, M2830–M2833); Tulka, 8 mi. S Port Lincoln (AM M2848); locality in South Australia unknown (BM 41.1264, 41.1266, 43.8.12.51, 43.11.3.6, 45.11.3.5, 45.11.3.9, 45.11.3.10, 83.10.19.10; SAM M4229).

VICTORIA: Bridgewater Lakes, 12 mi. WSW Portland (FWD R2391, R2392, R2446); Cape Nelson (NMV C625); Devil's Den, on Glenelg River near coast and 3 mi. E border of South Australia (FWD R2216, R2217); Fitzroy River, 15 mi. N Portland (FWD R2194); Gorae, 10 mi. NW Portland (SAM M2355); Heathmere, 10 mi. N Portland (FWD R2037, R2038, R2040, R2450, R2451);

Heywood (MVZ 133787, 133788); Lake Bong Bong, on coast 14 mi. SE border of South Australia (FWD R2442); Mt. Clay, 10 mi. NNE Portland (FWD R2036, R2039); Nelson, near coast 3 mi. E border of South Australia (FWD R2206–R2209); Portland (AMNH 107405, 107406; AM M6563, M6567; BM 36.12.8.4, 36.12.8.5; FWD R2042, R2044, R2045; MVZ 133789–133824; NMV C387, C686–C688, C721, C723, C733, C735, C736, C745, C746, C752, C759, C760); The Pinnacles, 35 mi. NNE Portland (FWD R2212).

Locality in Australia Unknown: (SAM M2469–M2471).

Rattus fuscipes assimilis

Australian Capital Territory: Tidbinbilla, 20 mi. SW Canberra (MVZ 133377–133486, 134377).

New South Wales: Argalong, 37 mi. W Canberra (AM M3876, M3877, M4617, M4730–M4735; NMV C689); Bago Range, Victoria (mislabeling for Bago Forest, New South Wales), 70 mi. WSW Canberra (NMV C4286); Barrington Tops, 65 mi. NNW Newcastle (AM M7261–M7264); Bluegum Knob, 35 mi. N Newcastle (AM M3012, M3013); Bombah Point, 44 mi. NE Newcastle (MVZ 133487–133490); Booloombayt, 47 mi. NE Newcastle (AM M3187, M3188); Brush Creek, 12 mi. W Wyong (AM M7256); Carlos Gap, 33 mi. N Lithgow (AM M5033–M5037); Central Koreelah, 75 mi. WSW Coolangatta (CSIRO CM890); Clarence River, on old specimens this is believed to indicate the area near Grafton (BM 58.11.24.10); Colo Vale, 56 mi. SSW Sydney (CSIRO CM438, CM440); Coolong, 60 mi. WSW Sydney (AM M4052, M4054–M4063); Digger's Creek, 85 mi. SW Canberra in Kosciusko National Park (AM M3232); Duggan's Gully, 50 mi. N Newcastle (AM S1586, S1587, M3030–M3033); Ebor, 42 mi. E Armidale (AMNH 65850; USNM 237753–237756, 237759, 237760, 237765—237773, 237777); Glen Ferneigh, 42 mi. E Armidale (AMNH 65875–65878); Gloucester, 65 mi. N Newcastle (USNM 221258); Grady's Creek, The Risk, 40 mi. WSW Coolangatta (CSIRO CM376, CM377, CM384); Guy Fawkes, 41 mi. E Armidale (BM 25.8.1.14–25.8.1.18, 26.3.11.160, 26.3.11.161, 26.3.11.241, 26.3.11.242; QM J3806); Huonbrook, 28 mi. WSW Coolangatta (AM S1979, M6201–M6203); Jaran Creek, locality unknown but believed to be in Yarrangobilly area 42 mi. SW Canberra (SAM M2595, M2614); Jerriwangler Creek, 20 mi. SSW Sydney (AM M2795, M2796); Junction of Thredbo and Snowy rivers, 80 mi. SSW Canberra (AM M3536, M3537); Lindesay Creek, 5 mi. NE Woodenbong (CSIRO CM428); Lithgow (AM M202, M260); Megalong Valley, 55 mi. WNW Sydney (AM M2881; QM J3692, J3693); Milton, 33 mi. SSW Nowra (USNM 221262–221265, 236773, 236785, 236786); Minnamurra, 65 mi. S Sydney (AM M5202, M5203); Moseley's Ranch, 42 mi. E Armidale (AMNH 65852–65869, 65874); Mt. Irvine, 17 mi. NE Lithgow (AM M6894–M6896, M6949, M6950, M7612–M7614; USNM 277387–277392); Mt. Kosciusko (AM M329; MCZ 27968–27975, 28061, 28062); Mt. Victoria, 60 mi. W Sydney (FWD R2477, R2478); Mt. Wilson, 55 mi. NW Sydney (MCZ 29232, 29761); Nattai River, 58 mi. SSW Sydney (AM M4784); Nimbin Valley, 15 mi. N Lismore (CSIRO CM927, CM928); Pearl Beach, 22 mi. N Sydney (AMNH 160140–160184; MVZ 125099–125179); Pericoe, southeast corner of state (NMV C3954, C3955, C3957–C3959, C4290, C4294–C4297); Piper's Creek, 90 mi. SW Canberra in Kosciusko National Park (CSIRO CM418); Point Lookout, 45 mi. E Armidale (AMNH 65870–65873; AM M3243, M3245, M3246–M3248); Richmond River, NE corner of state and on old specimens this locality denotes lower reaches of river (AM 16; BM 58.11.24.9, 80.3.25.6); Salisbury, 48 mi. NNW Newcastle (MCZ 29231); Sassafras, 25 mi. SW Nowra (AM M6403; MVZ 133491–133494); Scout's Alley, 52 mi. NNW Newcastle (AM M8328); The Cabin, National Park, 19 mi. S Sydney (AM M5210, M5211); The Chalet, near Mt. Kosciusko (AM M5969, M7179); The Criel (spelled Creel on maps), 25 mi. NE Mt. Kosciusko and now flooded by Lake Jindabyne Snowy Mountains Authority Reservoir (AM M4519); Tom Groggin Hut, 100 mi. SSW Canberra on state border (AM M7175, M7176, M7178); Tooloom Scrub, 75 mi. WSW Coolangatta (CSIRO CM392, CM393); Upper Allyn River, 47 mi. NNW Newcastle (AMNH 160299; AM M7465, M7467); Upper Chichester River, 50 mi. N Newcastle (AM M3038, M3039); Upper Wallaby Creek, 75 mi. WSW Coolangatta (AM M8395); Vines Scrub, 25 mi. S Nowra, (CSIRO CM864–CM866); Wallaby Creek, 75 mi. WSW Coolangatta (AM M8396–M8401; CSIRO CM264, CM268, CM270, CM889); Wandandian, 19 mi. SSW Nowra (USNM 221244, 221253–221257, 221259–221261, 221266); White's River Hut, Kosciusko National Park, 90 mi. SW Canberra (AM M7171, M7172; CSIRO CM397–CM401); Wilson's Valley, Kosciusko National Park, 90 mi. SW Canberra (CSIRO CM623, CM922–CM926); Woodenbong, 57 mi. WSW Coolangatta (MVZ 133495, 133496); Wyong (AM M7253–M7255; MVZ 133497); Yarramalong Mt., 14 mi. WSW Wyong (AM M4794, M4795); Yerranderie, 60 mi. WSW Sydney (MCZ 25806).

Queensland: Beaudesert, 35 mi. S Brisbane (QM J12280); Bunya Mts., 100 mi. NW Brisbane (AM M2793); Coomooboolaroo, 75 mi. SW Rockhampton (ZMO 98); Cribb Island, 10 mi. NNE Brisbane (QM J7917); Dawes Range, 105 mi. S Rockhampton (MVZ 133498–133516); Eagle Heights, 33 mi. S Brisbane (QM J4812, J4814, J4815); Emu Vale, 70 mi. SW Brisbane (QM J12671, J12672, J12958);

Eurong Beach, Fraser Island (QM 11232); Forest Station, Fraser Island (QM J11223–J11231, J11233, J11234, J11252); Fraser Island (QM J11250, J11251, J11253–J11255); Imbil, 68 mi. NNW Brisbane (AM M6445, M6738); Lake McKenzie, Fraser Island (QM J11256); MacPherson Ranges, 65 mi. SSW Brisbane (MCZ 29813); Many Peak Range, 105 mi. SE Rockhampton (QM J11057–J11062); Mt. Glorious, 17 mi. WNW Brisbane (QM J10939, J10965, J10982); Mt. Stanley, Kingaroy (QM J4304); Mt. Tamborine, 36 mi. S Brisbane (QM J12291, J12292); National Park, 57 mi. SSW Brisbane (MCZ 29762); Pine Mts., 20 mi. WSW Brisbane (AM 17, 18); Upper Cedar Creek, 18 mi. NW Brisbane (QM J7509–J7512, J8060–J8062).

Victoria: Bago Range (see under New South Wales); Beech Forest, 55 mi. SW Geelong (MVZ 133526–133531; NMV C220, C851, C1375–C1379); Black Sands, 38 mi. E Melbourne (NMV C1398–C1400); Buchan (NMV C3956, C4291); Cape Horn, 6 mi. N Cape Otway (not on coast) (AMNH 193971–193974); Carter's Creek, 55 mi. E Melbourne (FWD R2754); Childer's Forest, 70 mi. ESE Melbourne [QM J9668 (or J9688?), J9685–J9687, J9689, J9690]; Cumberland, 55 mi. ENE Melbourne (NMV C3036, C3037); Don Road to Ben Cairn, 32 mi. ENE Melbourne (FWD R2817, R2818); Emerald, 26 mi. ESE Melbourne (BM 7.9.16.21–7.9.16.23; NMV R1839); Eskdale, 32 mi. SE Albury, New South Wales (BM 36.12.8.1–36.12.8.3; NMV R12970, R 13819); Evelyn (apparently Mt. Evelyn), 23 mi. E Melbourne (NMV C126); Forrest (FWD R2816; NMV C1380, C1384, C1385); Gippsland, southern portion of state E Melbourne (BM 88.6.30.1); Goulburn River, 55 mi. NNE Melbourne (NMV R11985–R11987); Hordern Vale, 65 mi. SW Geelong (NMV C421); Junction of Little River and Wombargo Creek, 65 mi. NE Bairnsdale (NMV C967); Junction of Snowy and Broadbent rivers, 50 mi. NE Bairnsdale (NMV C1361–C1363); Loch Valley, Noojee, 55 mi. E Melbourne (WAM M4227, M4228); Mt. Macedon, 35 mi. NW Melbourne (FWD R350, R357, R358, R366, R368, R373, R374); Mt. Monday, Woods Point Road, 15 mi. ESE Warragul (MM M282); Narracan, 75 mi. SE Melbourne (NMV C119); Northern Road Bridge, 55 mi. E Melbourne (FWD R2757); Olsen's Bridge, 80 mi. ESE Melbourne (FWD R2382, R2384, R2385); Parker River, 120 mi. SE Melbourne (NMV C1831–C1833, C1975, C2018–C2020); Pomborneit, 60 mi. WSW Geelong (FWD, R2389, R2390); Terang (MVZ 133532–133539); Tommy's Bend, 50 mi. NW Melbourne (FWD R2367–R2369, R2376, R2377, R2476); Tulloch Ard (not Tullochard), 75 mi. NE Bairnsdale (NMV C2147, C2148); Upper Ferntree Gully, 19 mi. ESE Melbourne (AM M8333; MSU 3016); Upper Ryan's Creek, 70 mi. ESE Albury, New South Wales (SAM M2366, M2367, M2370); Warburton (NMV C1397); Western Port, 45 mi. SSE Melbourne (NMV C120–C122, C125); Whittlesea, 23 mi. N Melbourne (NMV R39); Wilson's Promontory (AMNH 193975–193977); Wingan Inlet, on coast 30 mi. SW border of New South Wales (NMV C1389, C1392, C1396, C4292, C4293).

Locality in Australia Unknown: [BM 69.7.19.18; MNHN 215, 216, 1360, 1364, 1367; MVZ 134041; NMV C123; RMNH b (King George's Sound, Western Australia, subject to question)].

Rattus fuscipes coracius

Queensland: Abergowrie, 20 mi. NW Ingham (AM M6181, M6187); Atherton (QM J5911); Atherton Tableland, tableland inland from Cairns to Innisfail area (AMNH 65880–65884, 65886–65893, 65895–65898, 65900, 65902, 65904–65909, 65913–65915; AM M3206–M3209; QM J3677–J3684); Babinda Creek, at S edge of Babinda (AMNH 65946, 65947; AM M3210); Cedar Creek, 24 mi. WNW Cairns (NR 41); Charraba Creek, 10 mi. SE Ravenshoe (AM M8275, M8282, M8555); Danbulla, 18 mi. SW Cairns (MVZ 133517–133519; QM J9300, J9302, J9303); Dinner Creek, vicinity of Ravenshoe (AMNH 160062–160065, 194217; BM 22.12.18.22–22.12.18.39, 65.864–65.866; FMNH 35333, 35335; QM J3786, J3791; WAM M783–M784); Etty Bay Hills, 4 mi SE Innisfail (AMNH 194218, 194219); Euramoo Creek, 18 mi. SW Cairns (QM J9380–J9383); Herbert Vale, 30 mi. NW Ingham (BM 84.4.18.1); Hinchinbrook Island (AMNH 108956–108959; AM M4377); Junction Creek, tributary of Russell River and 30 mi. SSE Cairns (AMNH 153719–153721, 153728–153731, 153736–153767, 153771–153773, 154047); Koombooloomba Creek, vicinity of Ravenshoe to south (AMNH 183377; MSU 4414); Lake Barrine, Atherton Tableland and 25 mi. SSW Cairns (AMNH 107300–107302, 156703; MCZ 29227–29229, 29238); Main Camp, about 10 mi. S Cooktown (AMNH 194139–194141); Malanda, 33 mi. WSW Cairns (NR 18); Mena Creek, 10 mi. SW Innisfail (AMNH 194216); Millaa Millaa, 11 mi. NE Ravenshoe (MVZ 133520, 133521; NR 24); Mossman (QM J10141); Mossman Gorge, 2 mi. W Mossman (MVZ 133522); Mt. Bellenden Ker, 23 mi. S Cairns (AMNH 153768–153770); Mt. Finnegan, 30 mi. S Cooktown (AMNH 155029–155037; QM J9458–J9464); Mt. Kalorama, 18 mi. SW Cairns (QM J9385); Mt. Lewis, 40 mi. NW Cairns (AM M8332); Mt. Spec, 25 mi. S Ingham in Paluma Range (QM J10144–J10163, J10290, J10291, J10941, J10983); Mt. Spurgeon, in Great Dividing Range due W Mossman (AMNH 107281–107299, 107303; QM J6347); Palmerston National Park, 17 mi. WSW Innisfail (AMNH 194220–194223); Puzzle Creek, on Mt. Spec 25 mi. S Ingham (FMNH 60980–60987); Ravenshoe (AMNH 65885, 65910–65912, 65916–65935; AM M8161, M8270, M8272–M8274, M8276, M8283–M8288; FMNH 60972, 60992, 60993; MVZ 133523–133525;

QM J3614, J3615; USNM 238489–238498, 238530); Spewah, upper Clohesy River, 12 mi. W Cairns (AMNH 153703, 153708, 153718); Townsville (AMNH 162621, 162622, 162624, 162625); Walsh Camp, 7 mi. SW Atherton (QM J9384); Walter Hill Range, 15 mi. ESE Ravenshoe (AMNH 153670–153684); Wongabel, 4 mi. S Atherton (FMNH 60989–60991); locality in Queensland unknown (BM 85.7.4.5, 92.8.7.3; FMNH 60976–60978).

Locality in Australia Unknown: [BM 58.11.24.7 (locality of Port Essington subject to question)].

Rattus leucopus leucopus

Queensland: Brown's Creek, tributary of Pascoe River and 150 mi. SSE tip of Cape York (QM J9468); Camp Oven Pocket, upper Peach River, tributary of Archer River and 210 mi. SSE tip of Cape York (QM J8279); Cape Grenville, 100 mi. SSE tip of Cape York (BM 23.12.16.45–23.12.16.48; FMNH 35336; WAM 38, 41); Cape York Peninsula (AM 92; BM 67.5.6.2–67.5.6.4, 85.7.4.3, 92.8.7.5; ZM BZM3419, BZM3420); Claudie River, 150 mi. SSE tip of Cape York (QM J9465); Coen River (SAM M373); Iron Range (AMNH 153909–153924, 153929, 153933–153938, 153946, 153947; CSIRO CM777, CM781–CM783, CM785, CM792, CM796, CM802; MVZ 133825–133829; QM J9467); Lankelly Scrub, McIlwraith Range, 6 mi. NE Coen (MCZ 29234, 29236, 29237); Lockerbie, W coast of Cape York, 8 mi. S tip of Cape (AMNH 153774–153791, 153794–153816, 153819–153845, 153847–153854, 153856–153872, 153877–153880, 153883–153902, 154049, 155017–155020); Massy Creek, 17 mi. E Coen (MVZ 133609, 133610, 133612, 133831–133840, 133842–133845; NMV C3656, C3657); Naru Point, 3 mi. S tip of Cape York on E coast (AMNH 153881, 153882); Olive River, 110 mi. SSE tip of Cape York (BM 23.12.16.44); Peach River, 14 mi. NE Coen (QM J9472); Portland Roads (AMNH 153903–153908; QM J9466); Rocky River, 220 mi. SSE tip of Cape York on E coast (AM M8100–M8105, M8268, M8269, M8277); Rocky Scrub, 205 mi. SSE tip of Cape York and 10 mi. W of E coast (AMNH 108960, 108961; MCZ 29230, 29233, 29235; QM J8278); Shephard's Battery, Peach River, 210 mi. SSE tip of Cape York and 20 mi. W of E coast (AMNH 153949; QM J8280); Tozer Gap, 400-ft. elevation in Tozer Range, 150 mi. SSE tip of Cape York and 12 mi. W coast (QM J9469, J9470); Tozer Range, 150 mi. SSE tip of Cape York and 12 mi. W coast (AMNH 153943, 153944); upper Nesbit River, 205 mi. SSE tip of Cape York and 10 mi. W of E coast (AMNH 153951–153972); upper Peach River, tributary of Archer River, 210 mi. SSE tip of Cape York and 20 mi. W of E coast (AMNH 153976–153980); Utingu, 10 mi. SW tip of Cape York on W coast (BM 15.3.5.99); locality in Queensland unknown (BM 92.8.7.4).

Locality in Australia Unknown: (BM 83.10.19.8, 83.10.19.23).

Rattus leucopus cooktownensis

Queensland: Atherton (FMNH 60988; QM J5910); Babinda Creek, at S edge of Babinda (AMNH 65879, 65941–65945, 65948–65950, 65952–65954, 65956, 65958; AM M3211; QM J3685, J3686); Charraba Creek, 10 mi. SE Ravenshoe (AM M8142, M8289); China Camp, 48 mi. S Cooktown (AMNH 194146–194149); Clump Point, 80 mi. SSE Cairns (AM M8334; NMV C2632, C2633); Danbulla, 18 mi. SW Cairns (QM J9301); Fresh Water Creek, 5 mi. W Cairns (MVZ 133858–133860); Gap Creek, 40 mi. S Cooktown (QM J10821); Jackaroo, Shipton's Flat, 30 mi. S Cooktown (AMNH 155551–155557); Jullatten, 35 mi. NW Cairns (AMNH 153722–153727); Junction Creek, tributary of Russell River and 30 mi. SSE Cairns (AMNH 153732, 153733); Lake Barrine, Atherton Tableland and 25 mi. SSW Cairns (AM M5655, M5656); Main Camp, about 10 mi. S Cooktown (AMNH 194142–194145); Mossman (QM J10135–J10140, J10142, J10143, J10197); Mossman Gorge, 2 mi. W Mossman (AMNH 153686–153690, 153692–153699; MVZ 133852–133857, 134045); Mt. Finnegan, 30 mi. S Cooktown (AMNH 154008–154038; QM J8275, J9473, J9474); Mt. Lewis, 40 mi. NW Cairns (AMNH 160139); Mt. Poverty, Shipton's Flat, 30 mi. S Cooktown (AMNH 155525–155536, 155547–155550); Ravenshoe (AM M8141, M8162, M8271); Redlynch, 6 mi. NW Cairns (AM M6706); Rossville Creek, Shipton's Flat, 30 mi. S Cooktown (AMNH 155480–155489, 155205–155209, 155212); Shipton's Flat, 30 mi. S Cooktown (AMNH 153984–153990, 153993, 153994, 155210, 155211, 194123, 194124, 194127, 194130–194132, 194134–194138; MVZ 133846–133851; QM J8277, J10819, J10820); Spewah, upper Clohesy River, 12 mi. W Cairns (AMNH 153700, 153702, 153704–153707, 153709–153717; QM J8276); upper Parrott Creek Camp, Mt. Finnegan, 30 mi. S Cooktown (AMNH 153995–154006); Watermelon Creek, 34 mi. S Cooktown (AMNH 194150).

Rattus lutreolus lutreolus

New South Wales: Acacia Plateau, on Queensland border, 80 mi. W Coolangatta (CSIRO CM920); Bombah Point, 44 mi. NE Newcastle (AM M3190; MVZ 133861); Booloombayt, 47 mi. NE Newcastle (AM M3191–M3193); Clarence, 5 mi. NE Lithgow (MVZ 133862–133866); Ebor, 42 mi. E Armidale (USNM 237757, 237758, 237761–237764, 237775, 237776); Guy Fawkes, 41 mi. E Armidale (BM 65.867, 25.8.1.4–25.8.1.12, 26.3.11.229–26.3.11.236, 26.3.11.239; FMNH 35338; QM J3770, J3771; USNM 237774); Hazelbrook, 21 mi. SE Lithgow (AM M2808); Lawson, 20 mi. SE Lithgow (AM

S673, S674); Macdonald River, 55 mi. NNW Sydney (BM 41.1259); Maroubra, 6 mi. SSE Sydney (AM M1570); Moseley's Ranch, 42 mi. E Armidale (AMNH 65965–65968); Mosquito Island, Hunter River, 4 mi. N Newcastle (BM 41.1258); Mt. Irvine, 17 mi. NE Lithgow (AM M6901, M6902, 6948, 7219); National Park, 19 mi. S Sydney (AM M2746); North Avoca Beach, 6 mi. E Gosford (MVZ 133867–133873); Peteroy District, 50 mi. ESE Armidale (BM 65.868, 25.8.1.13, 26.3.11.237, 26.3.11.238, 26.3.11.240); Point Lookout, 45 mi. E Armidale (AM S1618, M3252–M3254); Port Macquarie (AM M2585, M2586); Port Stephens (BM 72.11.8.5, 72.11.8.6); Richmond River, NE corner of state and on old specimens this locality denotes lower reaches of river (AM M59–M61); Wallaby Creek, 75 mi. WSW Coolangatta (CSIRO CM560); Wallaby Knob, 75 mi. WSW Coolangatta (CSIRO CM229, CM234); locality in New South Wales unknown (AM 29; ZM BZM3925).

Queensland: Binna Burra, 53 mi. S Brisbane (QM J7415); Bribie Island (MVZ 133874, 133875); Bunyaville, suburb of Brisbane (QM J10945, J10984, J10987); Darling Downs, vicinity of Toowoomba (AM A9733); Eagle Heights, 33 mi. S Brisbane (QM J4813); Gallangowan, 33 mi. SW Gympie (QM J8922, J8923, J9021, J9022); Gympie (NMV C3067); Imbil, 68 mi. NNW Brisbane (AM M6228, M6736); Maleny, 50 mi. N Brisbane (QM J6282); Mt. Nebo, 20 mi. WNW Brisbane (AM M8402; CSIRO CM878, CM904, CM907); Nambour (AM 8261); National Park, 57 mi. SSW Brisbane (QM J3583); Palen Creek, 46 mi. W Coolangatta (CSIRO CM624); Upper Nerang, 42 mi. SSE Brisbane (QM J6169).

South Australia: Adelaide [BM 41.1254 (probably should be BM 41.1255)]; Fleurieu Peninsula (MCZ 34966, 34967); Hindmarsh Island, 35 mi. SW Murray Bridge (SAM M2688, M3045); Lake Alexandrina (SAM M4705, M4706); Mt. Compass, 30 mi. S Adelaide (SAM M4708); Mud Island, 37 mi. SSW Murray Bridge (MCZ 27987; SAM M2465); Narrung, Lake Albert, 28 mi. S Murray Bridge (SAM M3000); Rocky River, 55 mi. WSW Kingscote, Kangaroo Island (MVZ 133876); locality in South Australia unknown (BM 43.8.12.42 skin, 43.8.12.43 skull, 45.11.3.14, 86.8.26.7).

Victoria: Beech Forest, 55 mi. SW Geelong (NMV C852); Bridgewater Lakes, 14 mi. W Portland (FWD R2393, R2445, R2447, R2449; SAM M2445); Dunkeld, 70 mi. NE Portland (MVZ 133904); Evelyn (apparently Mt. Evelyn), 23 mi. E Melbourne (NMV R5095); Forrest (NMV C1381–C1383); French Island, 43 mi. SSE Melbourne (AM M4844; SAM M2445); Gippsland, southern portion of state E Melbourne (BM 86.5.15.10, 88.6.30.2; NMV C133); Glenelg to Murray rivers (BM 47.3.1.1, 47.3.1.2); Hordern Vale, 28 mi. S Colac (BM 36.12.8.6, 36.12.8.7; NMV C392, C393); Karlo Creek, Wingan, eastern corner of state 20 mi. S border of New South Wales (FWD R2240); Lake Bong Bong, 14 mi. E border of South Australia on coast (FWD R2441); Loch Valley, 55 mi. E Melbourne (FWD R2225); Parker River, 120 mi. SW Melbourne on coast (NMV C184); Port Danger, 4 mi. SE Portland (NMV C758); Portland (NMV C756, C757, R2781); Serra Road, Grampians Mts., 100 mi. NNE Portland (FWD R2321); Shoreham, at Western Port, 45 mi. SSE Melbourne (AMNH 193978–193985); Silver Band Falls, Grampians Mts., 100 mi. NNE Portland (FWD R2428, R2429, R2437); Sir Colin Mackenzie Sanctuary, Healesville, 32 mi. ENE Melbourne (FWD R2257); Western Port, 45 mi. SSE Melbourne (NMV C127–C130); locality in Victoria unknown (NMV R1770).

Locality in Australia Unknown: (AMNH 668; AM 23, B4362; BM 65.869, 45.11.3.16, 47.1.20.1; MNHN 217, 1366, 1370, 1711; RMNH e; SAM M5494; ZM BZM3741, BZM4128, BZM4130, BZM60109, BZM60110).

Rattus lutreolus velutinus

Tasmania: Arthur River, 15 mi. S Smithton (AMNH 65972–65988, 65990, 65992, 65994, 65995; AM M4870, M4871, M4879, M4880, M4882, M4883; MCZ 29741, 29743; SAM M2976, M2977; USNM 238510–238516); Arve River, 30 mi. SW Hobart (AMNH 65969–65971); Arve Valley, 30 mi. SW Hobart (TM 0213); Bass Strait (BM 41.1254); Binalong Bay, 60 mi. ENE Launceston (QVM 1963:1:224, 1963:1:226, 1963:1:240, 1963:1:241); Black River, 10 mi. E Smithton (MVZ 127745); Chudleigh Lakes, 3000 ft., presumably lakes S Chudleigh, 30 mi. S Devonport (TM 0214); Cox's Bight, 70 mi. SW Hobart (AM M6592); Cradle Mt., 35 mi. NNE Queenstown (QVM 1963:1:40–1963:1:42, 1963:1:64–1963:1:67, 1963:1:72, 1963:1:73, 1963:1:75, 1963:1:80, 1963:1:83–1963:1:86, 1963:1:91, 1963:1:92, 1963:1:94, 1963:1:257, 1963:1:258, 1963:1:266, 1963:1:303–1963:1:305); Florentine Valley, 50 mi. NW Hobart (CSIRO CM880); Flowery Gully, 25 mi. E Devonport (QVM 1963:1:23–1963:1:25, 1963:1:49, 1963:1:57, 1963:1:58); Green's Beach, 21 mi. ENE Devonport (MVZ 133878–133903; QVM 1962:1:41, 1963:1:101–1963:1:105, 1963:1:107, 1963:1:108, 1963:1:112, 1963:1:113, . 1963:1:146–1963:1:148, 1963:1:247–1963:1:250); Hellyer Gorge, 40 mi. SE Smithton (FWD R2255); QVM 1963:1:201–1963:1:208); Henty River, 10 mi. WNW Queenstown (AM M1730; BM 3.1.3.2, 3.1.3.3); Hobart (BM 100a); Hunting Ground, 35 mi. NNW Hobart (CSIRO CM681, CM682, CM685–CM688; TM 002); Kangaroo Point, on Tasman Peninsula, 35 mi. ESE Hobart (BM 41.1257); Kelso, 23 mi. ENE Devonport (QVM 1963:1:292; TM 003); Kindred, 8 mi. SW Devonport (QVM 20:11:52); King Island

(NMV R5447); Maria Island, 42 mi. ENE Hobart (TM 0218); Maydena (MVZ 133877); Mt. Magnet, 45 mi. N Queenstown (AM M1770, M1781, M2369, M2465; BM 3.1.3.1, 4.6.26.1, 4.6.26.2, 5.5.31.6, 5.5.31.7); Mt. Wellington, 4 mi. E Hobart (AM 21); Ouse River, 52 mi. NNW Hobart (AM 22); Perkins Island, 8 mi. NNW Smithton (AM M4884–M4887); Port Davey (MVZ 127747); Railton (AM S1395); Renison Bell, 20 mi. NNW Queenstown (QVM 1964:1:30, 1964:1:32–1964:1:40); Roger River, 11 mi. S Smithton (AM M4881); Sandfly, 10 mi. SSW Hobart (TM 0469); St. Patrick's River, 10 mi. NE Launceston (QVM 1959:1:5); St. Valentine's Peak, 50 mi. SE Smithton (TM 0189, 0333–0336, 0345, 0353–0355, 0358, 0359, 0361, 0362); Waratah (QVM 1963:1:118–1963:1:120, 1963:1:124, 1963:1:126, 1963:1:128, 1963:1:129, 1963:1:131, 1963:1:141, 1963:1:164–1963:1:172, 1963:1:174–1963:1:179, 1963:1:191–1963:1:196, 1963:1:215–1963:1:217, 1964:1:4, 1964:1:20–1964:1:27); Waratah Highway, 37 mi. W Devonport (FWD R2244); Wynyard (AM M5065, M5066); locality in Tasmania unknown (BM 45.5.2.3, 52.1.15.16, 52.1.15.17, 77.7.3.1, 77.7.3.2, 77.7.3.4, 77.7.3.6, 100b or 41.1268; MM M782–M784; NMV C1401, C1402; TM 001, 004).

Rattus lutreolus lacus

QUEENSLAND: Lake Barrine, Atherton Tableland and 25 mi. SSW Cairns (AMNH 107311–107315).

Rattus sordidus sordidus

QUEENSLAND: Albany Island, 1 mi. E tip of Cape York (AMNH 108962, 108988, 108989); Annan River, at mouth 3 mi. S Cooktown (BM 65.862, 23.1.5.7–23.1.5.16; QM J3835, J3836); Atherton (MSU 4682; KU 81939; QM J9631, J9632); Aurukun Mission, W coast of Cape York 180 mi. S tip of Cape (NMV C930, C932, C933); Babinda Creek, at S edge of Babinda (AMNH 65955); Boiling Springs, about 10 mi. S Cooktown (AMNH 194115–194119); Cape Grenville, 100 mi. SSE tip of Cape York (BM 23.12.16.53, 23.12.16.54); Coen (QM J8929); Cowan Cowan, west coast of Moreton Island (BM 26.7.1.1; QM J4074, J4076); Coomooboolaroo, 75 mi. SW Rockhampton (ZMO 99); Danbulla, 18 mi. SW Cairns (QM J9296, J9298); Darling Downs, 65 mi. W Brisbane (formerly part of New South Wales and still so indicated on labels of specimens) (BM 46.4.4.68, 58.11.24.5, 58.11.24.6; LM 407); Ebagoola, 22 mi. SSE Coen (AMNH 154207); Helenvale, 20 mi. S Cooktown (AMNH 154039–154041); Herbert River, Ingham to 100 mi. N Ingham (MM M754); Holyroyd River, junction with Kendall River (AM M4469–M4471); Ingham (AM M5747, M5934, M5935, M5939, M5947; MVZ 133590–133592); Iron Range (AMNH 153925–153928, 153930–153932, 153939; CSIRO CM786, CM795, CM801; MVZ 133593, 133594; QM J9471); Jardine River (MVZ 133595–133598, 133830); Junction Creek, tributary of Russell River and 30 mi. SSE Cairns (AMNH 153734, 153735); Lockerbie, 5 mi. S tip of Cape York (AMNH 153792, 153793, 153817, 153818, 153846, 153855, 153873–153876); Mackay (AM M6166, M6167, M6170, M6174, M6376, M6734; QM J6205, J9166–J9181, J9183–J9194, J9197, J9198); Macknade, 8 mi. NE Ingham (AM M5986, M6603; QM J9165, J9182); Magussen-Balnagowan, Mackay (MVZ 133599); Massy Creek, 17 mi. E Coen (MVZ 133601–133608, 133611, 133617, 133841, 134042); Milaroo, 40 mi. SW Ayr (QM J12741, J12742); Mt. Bolan, near Cooktown (AMNH 194120, 194121); Mt. Jukes, Mackay (MVZ 133600); Mulgrave River, 15 mi. SSE Cairns (MVZ 133618–133651); Musgrave Telegraph Station, 280 mi. SSE tip of Cape York (AMNH 153981, 153982); Olive River, at Temple Bay, 100 mi. SSE tip of Cape York (BM 23.12.16.50, 23.12.16.52); Pascoe River, 150 mi. SSE tip of Cape York (AMNH 153945); Proserpine (QM J10537, J10538, J10963, J10964, J10980); Redlynch, 6 mi. NW Cairns (AM M6699–M6702, M6704, M6705, M6709); Seagren's Farm, km. 10 of Cooktown-Laura railway (AMNH 154042–154046, 154495); Shipton's Flat, 30 mi. S Cooktown (AMNH 153991, 153992, 155204, 194122, 194125, 194126, 194128, 194129, 194133, 194151); Skardon River, 70 mi. S tip of Cape York (MVZ 133652); Stradbroke Island, presumably North Stradbroke Island (AM M6153, M6154, M6158); The Intake, 10 mi. NW Cairns (AM M6757–M6762); Tozer's Range, 150 mi. SSE tip of Cape York (AMNH 153940–153942); upper Peach River, tributary of Archer River, 210 mi. SSE tip of Cape York (AMNH 153974, 153975); Walsh Camp, 7 mi. SW Atherton (QM J9297, J9299, J9379); locality in Queensland unknown (QM J9195, J9196).

Rattus sordidus villosissimus

NEW SOUTH WALES: Barwon Vale, Walgett, 325 mi. NW Sydney (AM S2084); Liverpool Plains, 30 mi. S Tamworth (BM 14.1261, 14.1262); Sturt's Depot, Mt. Poole Creek, 20 mi. SW Tibooburra (NMV unnumbered specimen).

NORTHERN TERRITORY: Alexandria Downs (AM M5676–M5678; BM 6.3.9.19, 6.3.9.20, 6.3.9.23–6.3.9.28, 6.3.9.92–6.3.9.111, 6.3.9.113–6.3.9.118, 65.863); Alroy (BM 6.3.9.29–6.3.9.35); Avon Downs (AM M5663–M5665, M5670–M5672, M5674, M5675); Buchanan, Alexandria Downs (BM 6.3.9.21, 6.3.9.22); Humbert River Station, 280 mi. S Darwin (AMNH 193782–193789; CSIRO CM1356–CM 1358); Katherine Research Station, Katherine (CSIRO CM1388, CM1389, CM1392); Newcastle Waters Station (CSIRO CM1302–CM1305); Sir Edward Pellew Group, Underwara, Southwest Island (CSIRO CM2639); "Victoria River," see under Queensland; Wycliffe Creek, 200 mi. N Alice Springs (AM M1305).

Queensland: Adel's Grove, near Lawn Hill Station, 35 mi. E border of Northern Territory (AM M5679, M5681, M5682); Birdsville (AMNH 153419, 153427, 153428; QM J9681–J9684, J10940); Boulia (QM J6711, J6714, J6715, J6717–J6726); Brighton Downs (NMV R13759, R13760); "Currane," Dartmouth, 30 mi. E Longreach (QM J9157, J9158, J9162); Diamantina River, 200–350 mi. SE Mt. Isa (AM S1472); Dickaree Water Hole, Birdsville (AMNH 153417, 153418, 153422–153426, 153475–153477, 153495; NMV C1388); Dundee Station, 60 mi. S Richmond (CSIRO CM929–CM931); Forest Creek, near Norman River, 300 mi. WSW Cairns (MCZ 32432–32442); Gregory Downs, Bourke (probably error for Burketown) district, 140 mi. N Mt. Isa (NMV C914, C915); Hughenden (MCZ 29760); Ingella, 540 mi. W Brisbane (QM J6783); Karumba (AMNH 193928–193936; AM M8445); Kimberley, near Karumba (BM 85.7.4.1); Kynuna (AMNH 160185, 160186, 193986–193988); Marion Downs Station (AM M8446); Middleton (QM J6739); Murrahmurrah, Durham Downs (MVZ 133925–133934, 134043); Oban Station, 90 mi. SW Mt. Isa (AM M5660); Richmond (QM J7767); Roseberth, Birdsville area (AMNH 153420, 153421); Sedan Dip, 60 mi. NW Julia Creek (AM M8434–M8444); Templeton River, 17 mi. W (label says S.) Mt. Isa (AM M5658); Victoria River = Barcoo River or Cooper's Creek, SW region of state (AM 20, 62).

South Australia: Brady Water Hole, Innamincka (SAM M6130); Cooncherie, Diamantina River, NE corner of state (SAM M3168, M3169); Diamantina River, NE corner of state (MCZ 29742); Innamincka (SAM M6141, M6150, M6155); Lake Callabonna (MVZ 136360–136366); Lake Eyre (North and South) (SAM M5869); Mulka (NMV R13707, R13708; SAM M3371–M3384, M4574–M4576); Mungarannie (usually spelled Mungeranie) (QM J13324); Waddi Waddi Hills, 6 mi. SE Innamincka (SAM M6149); Weekes Cave, 50 mi. E western state border near coast (personal collection of Hans Mincham, South Australian Museum, collected Jan. 1961, and registered as H. M. 10).

Locality in Australia Unknown: (BM 66.197–66.212, 83.10.19.22; SAM M2410).

Rattus sordidus colletti

Northern Territory: Alligator River, probably South Alligator River (AM M3370; BM 65.870, 4.4.4.3, 4.4.4.5–4.4.4.7, 4.4.4.9–4.4.4.12; ZMO 143); Daly River, 80 mi. S Darwin [ZMO 674 (4 specimens), 716, 71/66, 72/66 (6 specimens)]; Humpty Doo, 30 mi. SE Darwin (MVZ 133540–133573, 133574A, 133574B, 133575–133589, 133655, 133656; WAM M4284–M4286); King River, 180 mi. ENE Darwin near coast (BM 26.3.11.156–26.3.11.159); South Alligator River [BM 4.4.4.4; USNM 141483; WAM BM6149; ZMO 149, no number (BM 1822)].

Rattus tunneyi tunneyi

Northern Territory: Alice Springs (AMNH 107404; AM M1068; NMV C514, C524); "Biro," Apsley Strait, probably same locality now known as "Paru," S entrance to Apsley Strait (BM 13.6.28.33–13.6.28.35); Black Point, Port Essington, Cobourg Peninsula (CSIRO CM1120–CM1125, CM1127); Chambers River, 230 mi. SE Darwin (BM 26.3.11.166); Katherine River (ZMO 1297); Lizard Bay, Port Bremer, Cobourg Peninsula (MVZ 134336); Mary River, 7 mi. NE Moline (MVZ 133907, 133909); Mary River, 120 mi. SE to 60 mi. E Darwin (BM 4.1.3.30, 4.1.3.31; WAM 469); Melville Island (SAM M387, M388, M4068); 100 mi. S Port Darwin, Douglas River and Brocks Creek (USNM 237780, 237781, 237788, 237790–237793); Point Priest, Port Bremer, Cobourg Peninsula (CSIRO CM1115, CM1118); Port MacArthur Island, Sir Edward Pellew Group (CSIRO CM1403); Sir Edward Pellew Group (CSIRO CM2501–CM2504, CM2510, CM2512–CM2520, CM2523, CM2528, CM2530–CM2532, CM2534, CM2547); Smith Point, Port Essington, Cobourg Peninsula (CSIRO CM 1084, CM1090–CM1096, CM1104–CM1108, CM 1131, CM1134, CM1193); South Alligator River, on Oenpelli Road, 50 mi. NE Pine Creek (MVZ 133911–133924); Underwara, Southwest Island, Sir Edward Pellew Group (CSIRO CM2640); Victoria Settlement, Port Essington, Cobourg Peninsula (MVZ 134337–134371).

Western Australia: Forrest River Mission, 25 mi. NW Wyndham (AM M7873, M7933); Kalumburu, 130 mi. NW Wyndham (WAM B1984); Kunmunya Mission, Port George IV, 240 mi. NE Broome on coast (WAM M1187, M1664, M2012); La Grange Bay (BM 5.1.9.1, 5.1.9.5; WAM 573, 620); Legendre Island, Dampier Archipelago (WAM M5047, M5049, M5050, M5052–M5054, M5099, M5100); Lewis Island, Dampier Archipelago (BM 26.7.12.1, 39.1934–39.1935; WAM 4518A); Middle Mangrove Island, off coast of Onslow (WAM H. Butler field nos. 786–789, 793); Parry's Creek, 20 mi. SE Wyndham (BM 9.2.16.1; WAM B1478, 9597); Port George IV, 240 mi. NE Broome (NMV C818, C819); West Lewis Island, Dampier Archipelago (WAM M5048, M5051, M5453); Wotjulum Mission, 150 mi. NE Broome on coast (WAM M3122–M3127).

Locality in Australia Unknown: [BM 42.5.26.12; NMV R12642 (Central Australia)].

Rattus tunneyi culmorum

New South Wales: Duck Creek, Macquarie River, 285 mi. NW Sydney (BM 47.8.14.4, 47.8.14.5).

Queensland: Beach Mount, 5 mi. NE Inkerman (BM 7.9.15.16–7.9.15.24); Belyando Creek, 4 mi. E Alpha (MVZ 133653); Benarkin, 65 mi. NW Brisbane (AM S2241, S2242, M7835, M7837; MVZ 134326, 134327; QM J8771–J8777); Biloela (QM

J9692); Cable Station, 6 mi. SW tip of Cape York (BM 15.3.5.37–15.3.5.46, 65.855, 65.859, 65.860, 66.194; WAM M782); Cooktown (AM M877); Coomooboolaroo, 75 mi. SW Rockhampton (ZMO 2121); Endeavour River, Cooktown (MM M756, M758, M759, M763); Gallangowan, 33 mi. SW Gympie (MVZ 133657–133680, 133682–133690, 134125–134130; QM J8925–J8928, J9023–J9026, J9199–J9206); Googa State Forest, 65 mi. NW Brisbane (MVZ 134314–134325, 134328–134335); Heath Island, 5 mi. NE Inkerman (BM 7.9.15.5–7.9.15.13, 7.9.15.15); Inkerman (BM 7.9.15.14, 8.8.8.34, 8.8.8.36–8.8.8.39, 8.8.8.150, 8.8.8.151, 65.861); Mackay (AM M6325, M6326, M6540, M6541, M6544–M6546; QM J6279); Monto (QM J9719–J9724, J9798–J9800); Mt. Abbot, 5 mi. NE Inkerman (BM 8.8.8.35); Mt. Nebo, 20 mi. WNW Brisbane (AM M8419); Nogoa River, Emerald (MVZ 133654); Olive River, 110 mi. SSE tip of Cape York (BM 23.12.16.49, 23.12.16.51); Pelican Island, in Burdekin River (BM 66.193); Piara NE tip of Cape York (BM 15.3.5.36, 65.856); Roma (AM M6834); Skull Creek, 15 mi. S tip of Cape York on west coast (BM 15.3.5.32–15.3.5.35, 65.858, 66.195; WAM M781); Stoney Range, Aramara, 135 mi. NNW Brisbane (QM J9950); Stradbroke Island, presumably North Stradbroke Island (BM 52.7.10.2); Upper Brookfield, 15 mi. W Brisbane (QM J13137); Walmul, 25 mi. SW Rockhampton (QM J9565–J9571); Yarraman (AM M7831; QM J8924, J9704–J9710, J9779–J9786).

WESTERN AUSTRALIA: "Bullang," Swan River district, vicinity of Perth [BM 43.8.21.1 skin (43.9.2.3 skull)]; Drover's Cave, Hill River, 120 mi. NNW Perth (skulls without registration numbers collected by A. Douglas and H. Butler, May, 1958); Perth Lakes, vicinity of Perth [RMNH e (*Mus gouldii*)]; Victoria Plains, near New Norcia [BM 44.2.15.29, 44.2.15.30, 44.2.15.31 skin (44.3.12.2 skull), 44.7.9.17 skin (44.10.30.8 skull missing); RMNH a (*Mus gouldii*)]; locality in Western Australia· unknown (BM 46.4.4.71).

LOCALITY IN SOUTH AUSTRALIA UNKNOWN: [BM 41.1265, 43.1.4.39 skin (43.8.10.3 skull), 45.11.3.7, 45.11.3.8, 45.11.3.11, 45.11.3.12, 55.12.24.336].

LOCALITY IN AUSTRALIA UNKNOWN: (BM 41.1263, 65.857).

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